THE BIOGEOGRAPHY OF COLTSFOOT (TUSSILAGO FARFARA L.) INVASION IN GROS MORNE NATIONAL PARK, NEWFOUNDLAND

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by

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For my son Amos,

who says that the next book I write should be

about Tasmanian devils or dinosaurs.

Abstract

The invasion of the Eurasian weed coltsfoot (*Tussilago farfara* L.) in Gros Morne National Park (GMNP), Newfoundland, was examined to determine which resource changes accompanying disturbance enabled population expansion. Resource levels were measured in 17 disturbance types of natural and anthropogenic origin – notably hiking trails, roads, gravel quarries, shorelines, slopes, hydro corridors and insect kills – and across a gradient from disturbed to undisturbed in 12 vegetation types. Balsam fir forest comprises 36 percent of the park and has the highest number of disturbance types.

Disturbances favouring coltsfoot were characterized by a pH of 6.8-8.3, high light intensity, increased bare ground, absence of duff cover and moist, gravelly substrates. These resource levels were typical of both natural and anthropogenic disturbances in which the canopy and duff cover were absent, and the pH of acidic native soils had been raised by the addition of quarried limestone or granitic gravel. These represent resource shifts or amplifications relative to undisturbed vegetation types in which coltsfoot was absent.

The difference in resource levels across the disturbance gradient indicates that coltsfoot is unable to colonize undisturbed native vegetation. Likewise, a change in resource levels over time, which favours other species and is unsuitable for coltsfoot, appears to be the mechanism of coltsfoot's recession.

Coltsfoot is subject to grazing by other species, indicating its success in GMNP is not entirely a function of its escape from Old World predators, as is often thought to be the case for other invasives.

Elevation was not a limiting factor for coltsfoot in GMNP as it was found to be on

the Gaspé Peninsula where it does not occur in elevations greater than 150 m asl. Where coltsfoot occurs at high altitudes it is found on all exposures, so that aspect is not a factor in overcoming the climatic changes that accompany increasing elevation.

Not all disturbance types present resource levels favourable for coltsfoot establishment. However, resource levels associated with some disturbance types of anthropogenic origin indicate that park activities have played an important role in the invasion of coltsfoot in GMNP. Gravel of neutral to basic pH provided a medium for rhizome dispersal during the road and trail construction phase of the park from the late 1970s to mid 1980s. Redistribution of gravel allowed coltsfoot, a calciphile limited by low pH, to obtain exponential population growth over a relatively short period of time.

Invasion represents a change in resources from historic levels that accompanies certain disturbance types. In chronic (sustained) disturbances associated with roadsides and streams, coltsfoot may persist indefinitely. However, if native vegetation communities are not subjected to disturbances that produce favourable resource levels for coltsfoot, the biodiversity of native vegetation and the fauna that depend upon it, are not threatened.

Acknowledgements

My inspiration to pursue graduate studies in Newfoundland was born in the fall of 1995 with my first visit to Gros Morne National Park, where I was determined to undertake field research. I thank Paul MacNab for his part in encouraging this vision. Committee member Karyn Butler deserves the credit for identifying the invasion of coltsfoot in GMNP as a topic worthy of research.

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1. Introduction

The conspicuous proliferation of the exotic weed coltsfoot (*Tussilago farfara* L.) along roadsides in Gros Morne National Park on the west coast of insular Newfoundland (Fig. 1.1; Fig.1.2, Appendix I), has occurred only since 1973 when the park opened to the public (Bouchard *et al.* 1978). It occurs nowhere else in Newfoundland in such densities except from south of the park to Channel-Port aux Basques (personal observation), the location of the ferry terminal from Nova Scotia (Fig. 1.2). Coltsfoot has not been reported elsewhere as a prolific weed in a natural area.

The invasion of alien weeds into natural areas often threatens native biological diversity by outcompeting native plants and dominating natural habitats (White *et al.* 1993). Invasion affects native species at the population level, and at the community level, so that changes occur in the numbers of individuals, and in the composition of all species in the vegetation type. Invasion may also cause trophic cascades affecting the fauna that depend on particular vegetation assemblages for food and shelter (MacDonald *et al.* 1989).

Addressing the threat to the floral and faunal composition of shrinking natural areas has fueled research on the biology and management of invasive species (White *et al.* 1993). The maintenance of ecological integrity is the paramount principle guiding all national parks in Canada (Parks Canada 1996; Woodley 1996). The definition of ecological integrity has been extensively discussed by other authors (Woodley *et al.* 1993; Woodley 1996; Department of Canadian Heritage 1996). Parks Canada has defined ecological integrity as "a condition where the structure and function of an ecosystem are unimpaired by stresses induced by human activity and are likely to persist." (Department of Canadian Heritage 1996, p. 21).

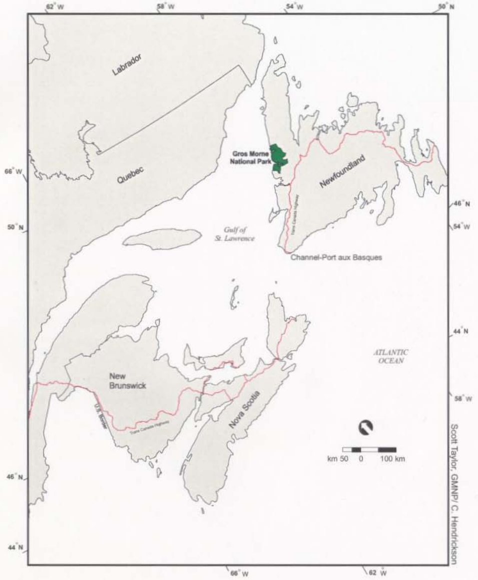


Figure 1.1. Gros Morne National Park in the Atlantic Region of Canada.

Figure 1.2. Distribution of coltsfoot along 134 km of roadsides on Highways 430 and 431 in Gros Morne National Park. Based on Roadside Survey (Appendix I), undertaken August 25, 1997.

Gros Morne National Park (GMNP) has developed an Ecosystem Conservation Plan to address issues of ecological integrity in the park (Parks Canada 1996). The preservation of native diversity and the assessment of the ecological impact of non-native species in the park are two of the ten objectives stated in the plan. Research into the invasion of coltsfoot clearly falls into these management objectives.

The primary objective of this thesis is to identify the resource changes caused by disturbance that enable the establishment of coltsfoot, and by doing so evaluate coltsfoot's impact on native vegetation communities in GMNP. Other research objectives, as well as definitions of important terms used in this study, are presented in Chapter 2, "Background and Literature Review".

Chapter 3 provides the reader with a biophysical description of the study area and previous surveys of park flora. Specifically, the scarcity of coltsfoot in the park area before it was opened to the public is documented. The spread of coltsfoot was found to be associated with the reconstruction and establishment of the park infrastructure, and so the history of this and methods of constructing and maintaining roads, quarries and hiking trails are also set out in Chapter 3.

Fieldwork for this study was undertaken from August 7-29, 1997. Field methods for gathering data, along with the statistical tests used to analyze the data, are presented in Chapter 4. The results of data analysis are found in Chapter 5.

Chapter 6 revisits the objectives in light of the statistical analysis, and discusses the degree to which coltsfoot poses a threat to ecological integrity in GMNP. Finally, the contributions of this study to the body of literature on coltsfoot in particular, and invasion in general, are presented, along with suggestions for further work.

2. Background and Literature Review

2.1 Introduction

This chapter sets out and defines many of the key terms used in this study and situates this research within the literature. The specific research objectives of this study are presented first in this chapter.

The conditions of coltsfoot's distribution beyond GMNP are presented to anticipate what might be expected from park populations based on its occurrence elsewhere. The biology of coltsfoot, its tolerances and preferences for certain physical parameters, and its interaction with other biota are reviewed. This background material suggests the opportunities and constraints within which invasion has occurred in GMNP.

Next, this study is situated within the body of literature on biological invasions and weed research in general. The terms "weed", "invasion", and "invasive" will be discussed and defined. One of the differences between invasive plants and weeds is the degree to which invasion is viewed as a consequence of disturbance. How disturbance is defined by other researchers, and the definition of disturbance around which this study pivots, are presented.

2.2 Objectives

The primary objective of this study is to determine which resource levels are correlated with coltsfoot abundance in GMNP. Broadly defined, a resource is an environmental component used by a living organism (Smith 1992). The specific resources measured are photosynthetically active radiation (PAR), soil moisture, pH, substrate type, percent bare ground and duff cover.

The results are then used to address more specific research objectives. Does coltsfoot threaten native diversity in GMNP by invading undisturbed vegetation types? If there is no significant difference in resource levels between disturbed and undisturbed sites, then undisturbed native vegetation may present conditions that are favourable to coltsfoot colonization. Whether or not vegetation types at higher elevations are immune to coltsfoot colonization is also addressed.

Coltsfoot is a weak competitor and populations recede as succession progresses from an initial disturbance. However, the mechanism for species replacement is undetermined, and has not been analyzed entirely as a function of resource changes over time. A significant difference in resource levels between disturbed and undisturbed sites indicates whether resource shifts occur over time that are unsuitable for coltsfoot. Whether or not interspecific competition contributes to the recession of coltsfoot populations is also examined.

Is invasion related to park activities, given the accelerated expansion of coltsfoot since the establishment of the park? The resource levels of individual disturbance types of anthropogenic and natural origin will be compared to those found to be correlated with coltsfoot invasion. This will help to identify which, if any, activities associated with the park infrastructure have contributed to the invasion of coltsfoot.

2.3 The conditions of coltsfoot distribution beyond GMNP

Coltsfoot is native to northern Europe and Asia (Gleason 1968, Myerscough and Whitehead 1965), extending eastwards from the British Isles to Siberia, northwards from the Himalayas to within the Arctic Circle (Myerscough and Whitehead 1965) and as far south as Italy in Europe and Iran in Asia (Holm *et al.* 1979).

Coltsfoot is listed as either common or present, but not as a serious or principal agricultural weed, in the countries in which it is found (Holm *et al.* 1979). It has been listed in the floras of Nova Scotia, Quebec, New Jersey, Pennsylvania, West Virginia, Ontario, Minnesota (Gleason 1968) and Newfoundland (Rouleau and Lamoureaux 1992)(Fig. 2.1), but populations in Canada and the United States have not been extensive or harmful enough to have drawn research interest, with the exception of Waltz's (1962) study of coltsfoot on the Gaspé Peninsula.

In Eurasia, where coltsfoot is native, it has been noted as a colonizing species of natural areas. Coltsfoot, in association with *Equisetum arvense*, has been noted on post-glacial shorelines (Englund 1942) and part of the early successional community in birch-fir and beech forests in Germany (Meusel 1943). It was also found in Germany in the muddy sand of protected shorelines (Steubing 1948) and as a colonizer of cliffs in northern Sweden (Karlsson 1969). Coltsfoot is therefore likely to be found in GMNP as a colonizing species of forests, shorelines and active slopes.

In its native range, coltsfoot is equally able to colonize anthropogenic and natural disturbances. Its ecological value is in its ability to colonize severely contaminated areas, such as mine tailings from ores and ametallic raw materials (Pysek 1988), mercury dumps (Korshikov *et al.* 1994), and red mud created as a byproduct of aluminum processing (Terpo and Balint 1985). Some researchers have explored the potential of using coltsfoot to rehabilitate degraded sites (Ploeg 1950; Salesbury 1943; Seraya and Komov 1972; Namura-Ochalska 1987, 1988, 1989, 1993a, 1993b, 1993c). Melhuish *et al.* (1987), for example, preferred coltsfoot to grass as a companion species in the reforestation of strip mines because it has been proven to be less competitive, and is able to take advantage of low nutrient sites with poor soil aeration.

On the Gaspé Peninsula in Canada, Waltz (1962) correlated the location of coltsfoot with topography, climate, edaphic conditions and disturbance origins. Its distribution along coastal areas and at the mouths of rivers is similar to the distribution

○ 1948-1969; 1981	Avalon Peninsula	Rouleau[1]; Cooper[2]
● 1948-1969	near Corner Brook	Rouleau[1]
■ 1972-74; 1994	near Channel-Port aux Basques	Bouchard-Hay-Brouillet[1]; White[4]
□ 1972-74	Lomond	Bouchard-Hay-Brouillet[1]
▲ 1986	Miquelon	Etcheberry and Abraham[1]
✕ 1998	Terra Nova National Park	Rose[4]

Figure 2.1. Locations of coltsfoot (*Tussilago farfara* L.) based on herbarium specimens and literature citations. ([1]Rouleau and Lamoureux 1992, [2]Cooper 1981, [3]White 1994, [4]Rose 1998)

of coltsfoot in Nova Scotia. While his study included sites of obvious anthropogenic disturbance, such as roadsides and waste areas, it also included areas considered to be naturally disturbed, such as erosional and depositional banks and gravel bars of streams, and talus slopes. He also noted that road building created microhabitats and soil structure favourable to coltsfoot establishment in this region. These anthropogenic and natural disturbance types are similar to the habitats in which coltsfoot is found in GMNP, particularly its presence on roadsides.

Coltsfoot has been described as a common element in snowpatch vegetation in Europe (Ogden 1974) and has been studied at elevations of 2180 m asl in the Alps (Gerola 1940) and 1050 m asl in Perthshire, Scotland (Myerscough and Whitehead 1967). In the Gaspé region of Canada, however, with a climate similar to Newfoundland, coltsfoot was not found above ca. 150 m (Waltz 1962). Coltsfoot may, therefore, be limited in GMNP as it appears to be on the Gaspé by the climatic gradients associated with elevation.

2.4 Biology of coltsfoot

Coltsfoot reproduces both sexually through diaspore dissemination, and clonally through the extension or fracturing of rhizomes. Research has mostly focused on specific upper and lower limits of suitable conditions for the germination of diaspores, such as light levels, pH, diaspore longevity, dispersal distances, and suitable substrates. Less is known about the absolute limits of these factors on clonal reproduction (references listed in Table 2.1). Temperature requirements for germination are apparently high - 30°C, and "strongly intermittent 10 - 28°C" (Bakker 1960). The precise definition of "strongly intermittent" was not presented by the author, but is assumed to mean daily minimum and maximum temperatures. Diaspore viability is short: reduced viability after 2 months, totally inviable at 5 months (Namura-

Table 2.1. Comparison of limiting conditions for sexual and vegetative reproduction of coltsfoot.

Condition	Diaspores	Rhizomes
light	seedlings die if light intensity below 20%; development delayed at 60-70% (Bakker 1960); stunted below 10μE m^{-2} s^{-1}, at 80 μE m^{-2} s^{-1} development of rhizomes in 8 weeks	development of rhizomes in 8 weeks (Bakker 1960) produces shade leaves with decreased light intensities; decrease in leaf size at very low intensities (Namura-Ochalska 1988, Myerscough and Whitehead 1967). No absolute measurements.
pH	4.0-10, "neutral to alkaline" (Myerscough and Whitehead 1965); Optimum pH 6.0-7.0 (Myerscough and Whitehead 1967).	unknown
soils	humus, potting soil, sand-loam, loamy soil, sand, sand and gravel and clay loam. Prefers humus and loam (Namura-Ochalska 1987, 1993c)	mature plants found on medium to rough soil structure on stone and pebbles mixed with clay and lime soils (Waltz 1962); heavy loam, medium to coarse sand (Namura-Ochalska 1987); muddy sand (Steubing 1948); sandy sludge dumps (Ploeg 1950) mine tailings from ores and ametallic raw materials (Pysek 1988); mercury dumps (Korshikov *et al.* 1994); red mud created as a byproduct of aluminum processing (Terpo and Balint 1985); milled over peat bogs (Curran and Macnaeidhe 1986); moist ash (Seraya 1972); moist clay banks (Meunscher 1980); and limestone quarry rubble, chalk talus, and calcareous seepage fens (Myerscough and Whitehead 1965).
soil moisture	needs surface moisture to germinate, intolerant of dry conditions (Bakker 1960); intolerant of dry soil (Namura-Ochalska 1987)	good to intermittent drainage (Waltz 1962); moist, heavy soils (Montgomery 1964)
propagule viability	reduced viability after 2 months, inviable at 5 months (Namura-Ochalska 1987)	will continue to grow in frost free temperatures to 2-3° C (Leuchs 1961)
propagule production	1000-8000 seeds, as high as 20,000 (Bakker 1960)	mean node number on rhizomes of 2 year old plants - 102 (Ogden 1974)
depth of "seeding"	not > 2 cm (Namura-Ochalska 1987)	12 cm with fragments 4-5 cm (Namura-Ochalska (1993c); approximately proportional to the length of the fragment (Leuchs 1961)
dispersal distance	average 100 m; as far as 4 km (Bakker 1960)	unknown
competitive ability	pioneer of disturbed ground (Bakker 1960; Namura-Ochalska 1987, 1993c; Myerscough and Whitehead 1965)	outcompeted by dense sod formed by grasses (Namura-Ochalska 1988, 1989); disagreement over tolerance for shading (Myerscough and Whitehead 1967; Bakker 1960; Namura-Ochalska 1988, Leuchs 1961)

Ochalska 1987). However, even given the short viability time and temperature requirements, germination is rapid and highly successful under optimum conditions: one hundred percent within 48 hours when sown on the moist surface of humus, potting soil and sand-loam (Namura-Ochalska 1987). Because vegetative reproduction is less sensitive to light and temperature (Leuchs 1961) it may overcome some of the factors limiting successful reproduction encountered by diaspores.

2.4.1 Vegetative reproduction of coltsfoot

Coltsfoot is superbly adapted to clonal reproduction through the fracturing of brittle rhizomes that can occur during soil disturbance (Bostock and Benton 1979; Namura-Ochalska 1993b, 1993c; Leuchs 1961), although Ogden (1974) also reported the spontaneous fragmentation of rhizomes following flowering. Namur-Ochalska (1993c) and Leuchs (1961) have simulated the fragmentation and burial of rhizomes in agricultural situations. In Namura-Ochalska's experiment 4-5 cm rhizome fragments of different ages (young white fragments, old brown woody fragments) with one node were buried at different densities and depths. The emergence from rhizomes was intense in the first year of growth, with each single node giving rise to shoots and underground organs, followed by an increase in cover (Namura-Ochalska 1993b). Rhizomes can continue to grow during frost-free weather at temperatures of 2 to 3° C (Leuchs 1961). In Ontario, flowering shoots were observed in April from unrooted rhizome fragments on topsoil stockpiled the previous fall (personal observation).

Radial expansion of rhizomes from a seedling can extend up to 2.5 m to 3.5 m in the second year (Bakker 1960; Ogden 1974). Ogden (1974) has observed a mean number of 102 nodes per plant after 2 years, so the potential for an abundance of new clones following rhizome fragmentation is high. The emergence of new shoots, however, is limited by the depth of burial. Leuchs (1961) reported the vigour of shoot growth from a rhizome fragment approximately proportional to the length of the fragment, and in Namura-Ochalska's (1993c) experiments, buried 4-5 cm segments did not emerge from depths greater than 12 cm. Mature, woody rhizomes produced three times more emergent shoots than young rhizomes (Namura-Ochalska 1993c), and at all densities and depths, the below-ground biomass was equal to or greater than that above ground. In Leuchs' (1961) work rhizomes of an unspecified length buried at 75 cm below compost soil in September had grown to the surface by the following March. Rhizomes penetrated the soil to a depth of 16 cm or less the first year, but to much greater depths in the second.

2.4.2 Morphological adaptations to physical disturbance

Coltsfoot is not only well adapted to clonal and sexual reproduction following disturbance, but researchers have also observed morphological adaptations that enable mature plants to withstand changing soil levels. These include rhizome buds at various depths; the emergence of vegetative shoots less than a few millimeters above the soil to avoid breakage (Myerscough and Whitehead 1967); and variablity in the location of the flower bud above or below the soil surface (Waltz 1962). Namura-Ochalska (1993b) has observed the elongation of flower stems after burial if they are not broken. Coltsfoot takes advantage of the changing resources brought about by disturbance, and its ability to withstand changing substrate levels accompanying frequent disturbance gives it a competitive advantage over other species. Disturbance that mitigates competition and promotes clonal reproduction is necessary for the persistence of coltsfoot (Namura-Ochalska 1993a).

Coltsfoot's reproductive shoots, vegetative shoots, and perennating structures - the rhizomes - are spatially and temporally separated (Ogden 1974). A ramet of the parent plant exists in the first year as a rhizome, in the second as a vegetative shoot, and in the third as a reproductive shoot which dies and vacates the location of the previous two year's growth (Ogden 1974). Coltsfoot is not stationary in the usual sense of perennials and the vigour of an individual ramet cannot be measured from year to year. Abundance of coltsfoot is therefore largely a function of rhizome expansion and the vigour of the vegetative shoots in one particular year in a precise location.

2.4.3 The recession of coltsfoot populations

Coltsfoot is a weak competitor as succession progresses on a disturbed site. While the mechanism for its replacement by other species has not been proven decisively, the following review shows that it has been seen as a function either of interspecies competition for unspecified below-ground resources, or for light.

Coltsfoot was eliminated from fallow agricultural fields in four years by competition from two stoloniferous grasses, *Agropyron repens* and *Dactylis glomerata* (Namura-Ochalska 1988, 1989). Namura-Ochalska (1988) interprets the competition as occurring below ground due to the dense sod produced by the two grasses through which coltsfoot rhizomes are unable to penetrate. In densely sodded plots, rhizomes grow deeper and vegetative shoots emerge; however Namura-Ochalska (1993a) regards this as an expensive strategy where more energy is allocated to rhizome rather than leaf or flower production, resulting in the eventual recession of the population.

Other research does not agree on the effect of low light levels on the persistence of coltsfoot. Bakker (1960) successfully eliminated coltsfoot from polders in the Netherlands by planting another aggressive stoloniferous grass, *Phragmites communis*. But he attributes the elimination of coltsfoot by the 2-3 m-tall *Phragmites* to competition for light. Myerscough and Whitehead (1967) observed that coltsfoot rarely grows under forest canopy, but Leuchs (1961) noted that coltsfoot succeeds in the shade of densely seeded crops under measured light levels similar to those found under closed canopy. Likewise, Namura-Ochalska (1988) reports that while shading by meter-high grass may affect its development unfavourably, it does not significantly reduce its density.

Bakker (1960) also attributed mortality of coltsfoot to gastropod and insect attack, and fungal infection. Likewise, Namura-Ochalska (1993a) observed that densely growing coltsfoot was attacked by the fungus, *Coleosporium tussilaginis*, and Lepidoptera larvae attacked the inside of shoots.

2.4.4 Summary of biological characteristics

Coltsfoot can be characterized as a plant whose diaspores disperse to newly disturbed, open sites where the seeds germinate quickly on the moist surface of a wide variety of substrates of low to high nutrients and pH. Once established, coltsfoot can quickly dominate a site through radial extension of rhizomes, the production of which is favoured over flower production in low nutrient sites (Ogden 1974). Low nutrient sites are also less favourable to competition from other species (Namura-Ochalska 1988). The wandering perennating structures are an advantage in these sites, however they are a disadvantage in shaded disturbances where vegetative shoots may emerge in a canopied location with more competition for light (Ogden 1974; Myerscough and Whitehead 1967). Vegetative rather than sexual reproduction enables a successful genotype to saturate a favourable site (Korshikov *et al.* 1994; Brown and Burdon 1987). Continued physical disturbance, to which coltsfoot is adapted, mitigates against competition and also serves to fracture brittle rhizomes which produce new clones (Bostock and Benton 1979; Namura-Ochalska 1993a).

As densities increase on the site, energy is allocated to the production of flowers rather than clones and migration to new sites occurs (Melhuish *et al.* 1987; Ogden 1974). In this last point, however, Namura-Ochalska (1987) has not observed higher flower production in the receding coltsfoot population in her study of Polish grassland populations. Coltsfoot populations recede in the absence of continuous, or chronic disturbance, (Bakker 1960; Namura-Ochalska 1988, 1989) however the precise reason for this has not been determined.

2.5 Weeds, Invaders and Invasives

The study of invasive species of natural areas has been approached from two separate but related fields: weed research and the study of biological invasions. This section situates the occurrence of coltsfoot in GMNP within the context of these two fields, and defines the terms "weed", "invader" and "invasive species".

Weeds have many ecological and historical characteristics in common, but they are culturally, not taxonomically or biologically, defined (Holzner 1982; Van der Zweep 1982; Bunting 1960; Radosovich and Holt 1984; Randall 1997). The simplest definition of a weed is a plant pest (Williamson, 1996), which can be either a native or an introduced species.

Weeds usually interfere with human economic activities and in doing so incur a cost either by their existence or in their removal. Agrestal and grassland weeds reduce crop yields or poison livestock. Lawn weeds and ruderals in waste areas are thought to be unsightly, but ruderals along roadsides may affect road maintenance procedures, safe visibility, and the stability of road surfaces (Gangstad 1982). Forestry weeds interfere with the efficient production of lumber and pulpwood.

Biological invasions are said to occur when a plant or an animal enters a region where it was previously absent, or as a high density population wave into areas of previously low density (Hengeveld 1989). Unlike weeds, invaders by definition are non-native species. Some, but not all invading plants, will become pests, or weeds (Williamson, 1996). The sphere of research on biological invasions centers around identifying the characteristics that make certain species successful in their new environment; whether or not certain habitats are more invasible than others; and patterns and rates of spread of invading organisms (Williamson 1996; Kornberg and Williamson1987; Drake *et al.* 1988; Bright 1998; Groves and Burdon 1986; Shigesada and Kawasaki 1997; Hengeveld 1989). The study of biological invasions does not usually include controlling pest species, which is the domain of weed research.

Plant invaders are considered to be "invasive" when their numbers increase to the extent that they replace the original components of a vegetation community in a natural area (White *et al.* 1993; Hengeveld 1989). Invasive species that become established in natural areas may then alter ecosystem function and structure from established patterns. Examples of these include changing rates and patterns of sediment accumulation, such as sand dunes and tidal flats; altering biogeochemical cycling, such as nitrogen fixing or salt accretion; changing hydrological cycles in wetlands and riparian areas through the uptake and transpiration of water; increasing or decreasing fire cycles; and preventing the recruitment of native species. At the biotic level, invasive plants can cause the extinction of other species in the food web, and can hybridize with native species thereby threatening their genetic integrity (MacDonald *et al.* 1989).

Invasive plants in natural areas are of ecological concern because of the factors just mentioned. When means are sought to control invasive plants, or "environmental weeds" (Holzner 1982), they also become an economic liability. This is the juncture where weed science and the study of biological invasions meet.

Invasive plants of natural areas are also referred to as non-native, exotic, introduced, or alien species (White *et al.* 1993).

2.6 Disturbance in ecosystems

The ecological idea of climax in vegetation communities is becoming surpassed by the idea that ecosystems, particularly boreal ecosystems, are driven by disturbance events that renew vegetation assemblages (Kay and Schneider 1994). A very simple definition of disturbance is the partial or total destruction of biomass (Grime 1979). Bazzaz (1983, p. 272) described disturbance as "a sudden change in the resource base of a unit of the landscape that is expressed as a readily detectable change in populations response". Bazzaz specifically described disturbance in terms of time, frequency, size, and intensity - a similar approach taken by researchers studying the nature of revegetation after forest fires (Rowe 1978).

Similarly, Fox and Fox (1986) described disturbance as resource amplification or resource shift. In the first case, disturbance amplifies an existing resource, such as the increase in sunlight caused by a fallen tree. In the second case, there is a loss of an existing resource and the biota that depend upon it, and the creation of a new resource that may be exploited by a new species. For example, the building of roads removes existing vegetation and soils and provides a different substrate and surface layer in the form of roadbed gravel.

Disturbance has also been categorized according to whether it is anthropogenic or natural in origin. Natural disturbances occur at a scale as small as frost wedging or the death of an individual plant, to intermediate scale slope failures and erosion of and deposition onto riverbanks, to large-scale hurricanes and volcanic eruptions. Both anthropogenic and natural disturbances can be described in terms of resource changes (Bazzaz 1983). Natural disturbances at all scales are considered acceptable within nature reserves, while "significant human stress" on ecosystems is not (Parks Canada 1996; Woodley 1996).

For the purposes of this study, disturbance is defined as a sudden change in resources, where resources are the abiotic components of the environment used by plants.

2.6.1 Disturbance and Invasion

Disturbance is an obvious component of the establishment of most weeds; the annual sowing, tilling and harvesting of crops provide the best example of this. Invasives differ from other categories of weeds because the role of disturbance in their establishment is often overlooked. There are two reasons for this. First, disturbance in natural areas may occur in less obvious and more systemic forms, such as a change in atmospheric deposition of nutrients (Aber 1993) or the fluctuation or stabilization of water levels (White *et al.* 1993). Consequently, native vegetation communities are assumed to be undisturbed at the larger scale. Second, disturbance agents may be acknowledged but impossible or too expensive to control (White *et al.* 1993). The approach to managing invasives therefore tends to focus on understanding the biology of the species so that methods can be found to control its productivity in natural areas.

Analyses that examine the relationship between disturbance and invasion are less common than those that detail the biology of invading species and their ecological repercussions. Approaches to exploring the relationship between invasion and disturbance are summarized below.

Bazzaz (1983) described invasion as the function not only of the biology of the species, but also the nature of the disturbance and the receiving environment (Fig. 2.2). Fox and Fox (1986) also concluded that there is no invasion without

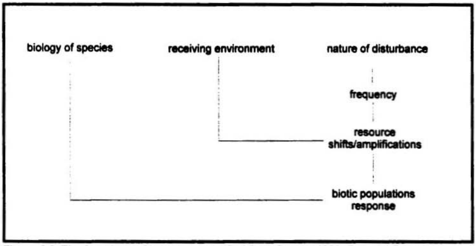


Figure 2.2. The functions of invasion (modified from Bazzaz 1983; Fox and Fox 1986).

disturbance, and that there is a trend to greater invasion with more prolonged, repeated or more intense disturbance.

White *et al.* (1993) postulated that a decline in native species may be due to the same disturbance factors that favour invasives. Orians (1986) examined components of disturbance that enable invasion through resource enhancement. Hobbes (1989) concluded in his field experiments that certain types of disturbance, such as the shallow upheaval of soils, need not significantly increase resource availability that would favour the persistence of invasive plants over the long term.

Alternatively, Fox and Fox (1986) demonstrated that rich communities - those with high diversity - are less susceptible to invasion. However, Rejmanek (1989) concluded that the amount of biomass or vegetation cover may be the most efficient indices of community resistance to invasion in some situations. Crawley (1989) examined the flora of the British Isles and also concluded that high rates of exotic flora are associated with communities with both low average plant cover levels and frequent disturbance.

2.7 Summary

From the definitions provided, coltsfoot has invaded GMNP as a ruderal weed, having moved as a high-density population wave, especially along roadsides, into areas of previously low density. However, it is not yet known whether or not coltsfoot will become invasive, that is, replace the original components of the vegetation community of the park.

The research approach is that invasion is a function of the biology of the species (detailed earlier in this chapter), the receiving environment (to be described in Chapter 3), and the nature of disturbance. Disturbance has been defined in this thesis as a sudden change in resources, where resources are the abiotic components of the environment used by plants. That certain resource levels enable the invasion of coltsfoot is a given, and determining the level of the chosen resources is therefore the primary objective of this study. Whether or not those resources also describe undisturbed vegetation types, and can be associated specifically with activities related to the establishment and maintenance of park infrastructure, is the matter of the remaining objectives. Definitions of anthropogenic and natural disturbances and disturbance types will be discussed in Chapter 4.

3. Study Area

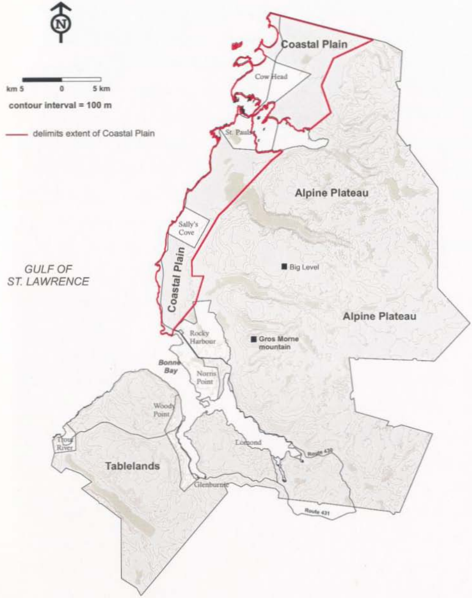
3.1 Introduction

This chapter provides an overview of the physiography and climate of Gros Morne National Park that have influenced the development and distribution of the present vegetation communities. The flora in GMNP includes both rare species and unusual phytogeographic distributions not characterized by the dominant boreal vegetation found in the park and typical of northern Canadian latitudes (Anions 1994; Bouchard and Hay 1976; Bouchard *et al.* 1978; Bouchard *et al.* 1991). The identification and mapping of distinct vegetation communities (Bouchard 1974; Bouchard *et al.* 1978, 1988, 1991; Bouchard and Hay 1992) are based on dominant indicator species that reflect climatic, geologic, and physiographic factors. These vegetation communities comprise the different receiving environments of coltsfoot invasion.

The historic scarcity and increasing abundance of coltsfoot in GMNP is also documented. Finally, the history of park construction and maintenance procedures for trails, roads, and gravel pits, is presented. This will be shown later to have been a critical factor in the present distribution of coltsfoot in GMNP. Information on park procedures, unless otherwise noted, is from interviews with Bruce Jenniex, Senior Maintenance Supervisor for GMNP since 1973.

3.2 Climate and physiography

The Gulf of St. Lawrence directly to the west of GMNP (Fig. 3.1) exerts a significant influence on the climate of the park in the form of high annual precipitation and relatively few temperature extremes (Banfield 1988). The abrupt transition from the Coastal Plain, corresponding to altitudes below 150 above sea level (asl), to the Alpine Plateau at altitudes from 450-800 m asl (Fig. 3.1), produces two measurably



Scott Taylor, GMNP/C. Hendrickson

Figure 3.1. Gros Morne National Park showing Coastal Plain, Alpine Plateau, and enclaves (settlement areas).

distinct climatic zones within the predominant maritime climate (Bouchard *et al.* 1978, 1991; Banfield 1988).

GMNP has a cool, short growing season and adequate (Clayton *et al.* 1977) to excessive (Bouchard and Hay 1976) moisture. The average summer temperature at Rocky Harbour (Fig. 3.1) is 15° C in July and August and the frost-free period ranges from 100 days in low-lying areas to 150 days in more favourable sites on the outer coast (Banfield 1988). Temperatures at Big Level on the Alpine Plateau are 6.3°C lower than Rocky Harbour on the Coastal Plain between June 18 and August 6, based on daily maximum temperatures (Banfield, pers. comm. 1997). The mean daily average temperature for January is between -9.4° C and -6.7° C (Bouchard and Hay 1976).

The annual average precipitation on the Coastal Plain is approximately 1200 mm (Banfield 1988). Increase in precipitation with increasing altitudes is calculated to be approximately 207 mm for each 100 m rise in elevation. The period of June through September is characterized as "moderately wet" and intervening dry spells rarely last for more than two or three days (Banfield 1988). The heaviest and most frequent precipitation occurs from October through January, after which precipitation decreases until May, the driest month of the year (Banfield 1988).

An unnamed biophysiographic region of intermediate status exists between the Alpine Plateau and the Coastal Plain (Fig. 3.1) on slopes between 150 to 450 m asl. These abrupt slopes that run from north to south in the park are subject to changing altitudinal temperature gradients. Latitudinal gradients, as well as slope and aspect differences also produce variable micro-climates (Banfield 1988).

The diverse native flora in GMNP is an expression of the varied geology, geomorphology, and climate of the park (Bouchard 1974; Bouchard *et al.* 1978, 1988, 1991; Bouchard and Hay 1992). The bedrock geology is composed of 18 different rock types with the Alpine Plateau largely composed of gneiss and granite, and the Coastal Plain of limestone, shale, sandstone and dolomite (Stevens 1992). In the Bonne Bay (Fig. 3.1) region the most unusual constituent of the bedrock geology is the exposure of ophiolites, notably peridotite, in the Tablelands (Fig. 3.1). Vegetation here is sparse and growth meager due to heavy metals occurring naturally in the soils. Other bedrock in this area is composed predominantly of limestone, sandstone and granite (Stevens 1992).

Soils in the park are primarily humo-ferric Podzols, which are characterized by imperfectly drained acidic, mineral soils, formed by the influence of the parent material, humid to perhumid climate, and coniferous vegetation (Clayton *et al.* 1977) The other soil orders in the park include Brunisols, Regosols, Gleysols and Organic soils (Canadian Parks Service, 1990).

Both past and present geomorphic processes present a variety of physiographic features with characteristic plant communities. Pleistocene glacial landforms include the ice-scoured uplands, glacier-carved valleys, lowland moraines and coastal rock terraces (Bouchard *et al.* 1991). Marine, fluvial and aeolian processes are expressed in Holocene landforms that include tidal flats, beaches, sand dunes, sea cliffs, river banks, deltas and flood plains (Bouchard *et al.* 1991).

3.3 Phytogeography in GMNP

The park flora is of particular interest due to the unusual phytogeographic distributions and number of rare species. While the native flora has been studied comprehensively (*e.g.* Fernald 1911, 1926, 1933; Bouchard 1974; Bouchard and Hay 1976; Bouchard *et al.* 1978; Bouchard *et al.* 1988; Bouchard *et al.* 1991; Anions 1994), research interest in the introduced flora is recent. Parks Canada produced a four page internal report on purple loosestrife (*Lythrum salicaria*; Deichmann 1991), and a comprehensive study of introduced flora began in 1998 (Rose, in progress).

The vascular flora of GMNP contains 727 species of which 96 are considered rare in Newfoundland, while 10 are rare in Canada (Anions 1994). The park lies entirely within the Boreal Forest Region of Canada with 70 percent of the vascular flora of the park characteristic of this boreal region (Anions 1994). However, many unusual phytogeographic elements exist within the park that are not characteristic of the boreal forest (Bouchard *et al.* 1978). These elements have been categorized as: cosmopolitan; circumpolar - Northern hemisphere; Amphiatlantic; North American - transcontinental at Canadian latitudes; North American - discontinuous in continental interior; endemic in Northeastern North America; eastern deciduous forest; Atlantic coastal plain; endemic; and naturalized (Bouchard *et al.* 1978). Coltsfoot is a naturalized non-native element of the vegetation, along with 6 percent of the park's flora.

3.3.1 Vegetation zones

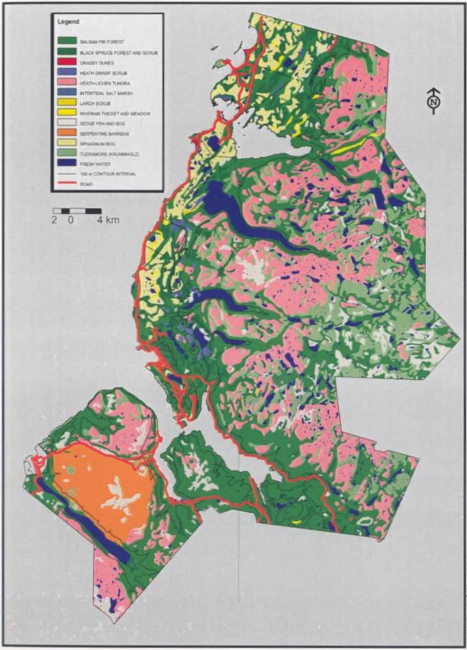
Bouchard (1974) produced biophysiographic maps of GMNP's vascular vegetation from fieldwork undertaken between 1972 and1974. The vegetation of the Coastal Plain was categorized and mapped into 18 units (Bouchard 1974). The vegetation of both the Coastal Plain and Alpine Plateau was characterized into 11 biophysiographic units and 21 habitats in 1978 (Bouchard *et al.* 1978). A 1988 version revised the categories into four land regions (Coastal Plain, Alpine Plateau, Limestone Escarpments and Serpentine Tableland), 13 biophysiographic units and 37 habitats (Bouchard *et al.* 1988). In 1991, Bouchard reverted to the original two land regions containing 35 habitats (Bouchard *et al.* 1991). None of the above biophysiographic categories were mapped except for the 1974 work that only included the Coastal Plain. However, in 1992 the entire park area was categorized and mapped into 14 vegetation units without reference to land region (Fig. 3.2; Bouchard and Hay 1992). All map versions from 1974 to 1992 include indicator species of habitat types, and the 1992 version represents an accurate generalization of earlier versions of the vegetation mapping (Table 3.1). These vegetation types will be used in this study to represent differences in receiving environments.

3.3.2 Coltsfoot in GMNP

The introduced vegetation of GMNP was described by Bouchard (1974) from his 1972-74 field seasons. Introduced plants were the primary constituent of the mapping units called "cleared areas" and "mosaic of herbaceous communities". These areas were located in a narrow band along the coast where settlers lived, gardened and raised livestock to augment fishing. Coltsfoot is not mentioned as either common or conspicuous, and was not listed for these areas until 1978 when it was referred to, along with other weeds, as relatively few in disturbed areas on the Coastal Plain (Bouchard *et al.* 1978). The categorization of the flora into 35 habitat types placed coltsfoot in the category of "ruderal areas" only (Bouchard *et al.* 1991).

Two reports on actions undertaken to mitigate damage to natural plant communities do not mention coltsfoot in their floristic site inventories: coltsfoot is not mentioned in Bridgland and Brassard's (1984) study of vegetation damage on the James Callaghan Trail on Gros Morne mountain (Fig. 3.1), nor in Burzynski's (1989) report on mitigation of damage to showy lady's slipper populations before the reconstruction of the Lomond Road off Highway 431 (Fig. 3.1). Coltsfoot is now abundant on the roadside and in the orchid fen mapped by Burzynski (1989).

Based on the roadside survey (Appendix I) coltsfoot is now present and easily observed by car for 100 of the 115 kilometers of roadside on Highways 430 and 431 (Fig. 3.1) that serve the park. Coltsfoot appears to have become unusually abundant



Scott Taylor GMNP

Figure 3.2. Vegetation cover types of Gros Morne National Park, Newfoundland (Bouchard and Hay 1992).

Table 3.1. Vegetation types and indicator species in Gros Morne National Park, Newfoundland (Bouchard and Hay 1992).

Grassy dunes	Grassy sand dunes with Marram grass[40] and lyme grass[41] on active unstable surfaces, with scrub balsam fir[15] on stable surfaces
Intertidal saltmarsh	Salt-tolerant herbaceous plants in the intertidal zone; samphire[37] typifies the lower mud flats; salt-marsh sedges (chaffy sedge[38], salt sedge[39]) dominate the higher marshes
Sedge fen and bog	Meadow-like fens and slope bogs, mainly of sedges (meagre sedge[34], woolly sedge[35], lead sedge[36] and sphagnum mosses[23].
Sphagnum bog	Domed bog of sphagnum mosses[23], lichens (reindeer moss[30]), and tussock rush[31] with a dense dwarf-scrub border of black spruce[22], sheep laurel[18], leatherleaf[32], and bog rosemary[33].
Riverain thicket and meadow	Thickets of speckled alder[27], sweet gale[24], and meadow-sweet[28], wet meadows of meadow-rue[25], bottlebrush[26], and reed grass[29].
Larch scrub	Semi-open larch[2] scrub with sweet gale[24], dwarf birch[3], and a herb layer of meadow-rue[25] and bottlebrush[26].
Black spruce forest and scrub	Black spruce[22] and balsam fir[15], mainly on boggy ground of sphagnum mosses[23], and with a shrub layer of sheep laurel[18].
Tuckamore (Krummholz)	Dense wind-shaped thickets of balsam fir[15] with white spruce[16] on the coast and black spruce[22] on exposed upland slopes
Heath dwarf-scrub	Dense, low shrubs, mainly sheep laurel[18], lowbush blueberry[19], Labrador tea[20], rhododendron[21].
Balsam fir forest	Balsam fir[15], with white spruce[16] and white birch[17] as mature stands and successional scrub after logging
Heath-lichen tundra	Wind-exposed mat of black crowberry[8], tundra bilberry[9], alpine bearberry[10], and diapensia[11], interspersed with rock and rubble covered with lichen (rock tripe[12]) and moss[4]. Several arctic alpine plants (alpine clubmoss[13], sibbaldia[14]) occur in late-lying snow sites
Serpentine barrens	Rock barrens with sparse dwarf-scrub (juniper[1], larch, dwarf birch), cushion mosses[4], and unusual arctic-alpine plants (sea thrift[5], alpine campion[6], Lapland rosebay[7].)
calcareous cliffs spot locations	Sparsely vegetated cliffs and talus of carbonate rock with several rare calcium-loving plants (cut-leaved anenome[42], green spleenwort[43], bulblet fern[44]).
Cleared, settled areas	

1. Juniperus communis
2. Larix laricina
3. Betula pumila
4. Rhacomitrium spp.
5. Armeria maritima
6. Lychnis alpina
7. Rhododendron lapponicum
8. Empetrum nigrum
9. Vaccinium uliginosum
10. Arctostaphylos alpina
11. Diapensia lapponica
12. Umbilicaria spp.
13. Lycopodium alpinum
14 Sibbaldia procumbens
15. Abies balsamea
16. Picea glauca
17. Betula papyrifera
18. Kalmia angustifolia
19. Vaccinium angustifolium
20. Ledum groenlandicum
21 Rhododendron canadense
22. Picea mariana
23. Sphagnum spp.
24. Myrica gale
25. Thalictrum polygamum
26. Sanguisorba canadensis
27. Alnus rugosa
28. Spiraea latifolia
29. Calamagrostis canadensis
30. Cladina spp.
31 Scirpus cespitosus
32. Chamaedaphne calyculata
33. Andromeda glaucophylla
34. Carex exilis
35. Carex lanuginosa
36. Carex livida
37. Salicornia europaea
38. Carex paleacea
39. Carex salina
40. Ammophila breviligulata
41. Elymus mollis
42. Anemone multifida
43. Asplenium viride
44. Cystopteris bulbifera

relatively recently along roadsides, parking areas, trails and in the enclaves (villages)(Plates. 3.1-3.4). The recollection of observers places its dominance on roadsides within the last 13 years (Butler, Hermanutz, pers. comm. 1997). Another indication of its recent spread comes from local residents, who in general are knowledgeable of local names of common plants, but do not have a local name for coltsfoot, nor do they know its common published name.

3.4 The establishment of park infrastructures

Road construction, and the significant disturbance which accompanies it, was undertaken in the relatively short time span of about 6 years (between 1979 and 1984), providing a corridor for colonizing species for over 115 km of road edge within the park. Four of the seven road segments (Fig. 3.3) were realigned and upgraded subsequent to the establishment of the park from 1981 to 1984, during which time $70-80 million were spent on road construction.

Three major sources of gravel in GMNP are the Rocky Barachois glaciofluvial deposits, the shale bedrock of Cod Knox, and the privately owned shale quarries near Norris Point (Fig. 3.3). The glaciofluvial deposits at Rocky Barachois, predominantly composed of granitic gravel, were developed to meet the needs of road construction in the late 1970s to mid 1980s. Typically, material is extracted, sorted and stockpiled. These stores are expected to last the duration of the particular construction project, minimally five years for the early road construction phase. Current stockpiles in Rocky Barachois were extracted in 1995 and are expected to last another 3-5 years. The age of the stockpiles will be 6-8 years by the time they are exhausted.

Material at Rocky Barachois quarry is used for shoulder maintenance, road repairs, trail and general maintenance. The Department of Works, Services and

Cheryl Hendrickson

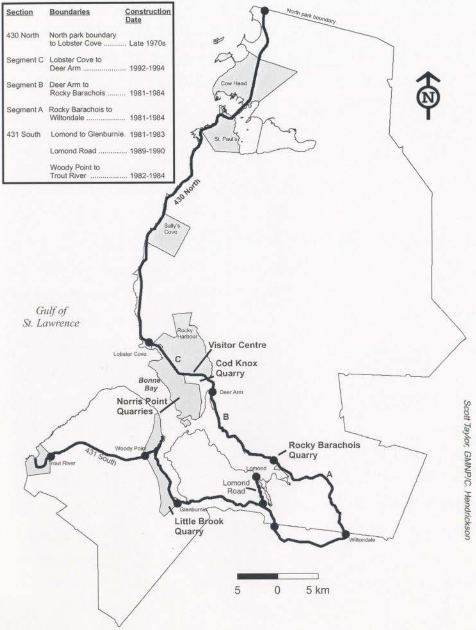
Plate 3.1 Coltsfoot with *Cirsium arvense* and *Ammophila breviligulata* on basalt cliffs on Green Gardens trail, August 1997.

Michael Rose

Plate 3.2. Coltsfoot at roadside leading to the GMNP Administration building, August 1998.

Plate 3.3. Coltsfoot on embankment near Glenburnie, Highway 431. Dissemination stage, mid-June, 1998.

Plate 3.4. Coltsfoot on embankment near Glenburnie, Highway 431. Vegetative stage, mid-August, 1998.



Section	Boundaries	Construction Date
430 North	North park boundary to Lobster Cove	Late 1970s
Segment C	Lobster Cove to Deer Arm	1992-1994
Segment B	Deer Arm to Rocky Barachois	1981-1984
Segment A	Rocky Barachois to Wiltondale	1981-1984
431 South	Lomond to Glenburnie.	1981-1983
	Lomond Road	1989-1990
	Woody Point to Trout River	1982-1984

Figure 3.3. Road maintenance sections and construction dates in Gros Morne National Park.

Transportation screens sand for winter maintenance, although it is stockpiled elsewhere. Domestic extraction for house building is also permitted.

The shale deposits in Cod Knox quarry were used in the early to mid 1980s, after which time the quarry was left dormant for approximately 10 years. It was reopened to upgrade segment C (Fig. 3.3) during the period 1992-94. Cod Knox shale is also used to fill low lying or wet areas to make them more convenient for public use.

Seven of the eight shale extraction sites at Norris Point are privately owned, the other is owned by the Department of Works, Services and Transportation. All of the private contractors supplied material for the construction of the ski trails near the Visitor Centre (Fig. 3.3). The use of these extraction sites is sporadic over the years, and varies by volume from contractor to contractor.

Trails were originally constructed of materials adjacent to the trail. Twelve to fifteen years ago, maintenance and construction procedures were changed so that materials were brought from off site, particularly aggregates from Rocky Barachois. Upgrading of original trails has been ongoing for the last 10 years. The park currently maintains about 75 km of hiking trails, and the area of disturbance associated with them is typically a meter or less to each side.

It has been shown that coltsfoot was relatively inconspicuous previous to the park's opening in 1973, and that the subsequent development of park infrastructures is coincidental to the noticeable appearance of coltsfoot at roadsides. This relationship will be explored more fully in later chapters.

4. Methods

4.1 Introduction

The invasion of coltsfoot in Gros Morne National Park is examined as a function of resource changes that accompany disturbance. The definitions of "disturbance level", "disturbance type", and "disturbance origin" are discussed. Field methods are described which sample the levels of specific resources that accompany different disturbance levels, types and origins. The method of vegetation sampling and the occurrence of fungal infection and herbivory are also described. Statistical methods are described which will be used to address the research objectives of this study.

4.2 Disturbance levels, types and origins

Disturbance was categorized in terms of "level", "type" and "origin". Disturbance level refers to a gradient of disturbance frequency from chronic, through maturing, to undisturbed. It was assumed that most disturbances originally occurred in an area of mature, relatively undisturbed, native vegetation. Most disturbances measured continued to have active or chronic disturbance, such as the use of roads and trails. An area of maturing or recovering vegetation dating from the time of the original disturbance event (*e.g.* road construction) was usually found adjacent to the active disturbance. The maturing disturbance represents successional physical conditions that are intermediate between and distinct from the surrounding chronic and undisturbed areas.

Disturbance types are culturally defined, distinctive patterns of physical alterations to the landscape such as roads and active slopes. It is assumed that individual disturbance types share common, measurable resource levels. Seventeen different disturbance types were sampled. For the analysis, disturbance types were classified as either anthropogenic or natural in origin.

Anthropogenic disturbance types were those that are directly associated with intentional human activity, such as gravel pits and roads. Natural disturbance types occurred as the result of predominantly physical or biological (other than human) processes. While natural disturbances may be distantly related to human activities, such as the deliberate introduction of moose to insular Newfoundland, it is the direct effect of the organism or process that was identified. Anthropogenic disturbances differ from natural disturbances because their product is more directly under human control. It is easier not to build a hiking trail, or construct it of different materials, than it is to remove all the moose from Newfoundland.

Some disturbances were clearly the result of combined anthropogenic and natural processes, and were not characteristic of a single disturbance type. They are referred to as "multiple disturbances". They include combinations of rehabilitation sites, animal trails, over snow vehicle (OSV) trails, streams, hiking trails, shorelines, slopes, roads, insect kills, and sand dunes (Plate 4.1). These sites indicate a tendency for disturbed sites, particularly where a break in the canopy occurs, to remain disturbed or in use for other purposes. For example, moose trails are often found on hiking trails or beside streams.

The location of the transects for each disturbance type that follow are identified on Figure 4.1 (folded colour map in jacket pocket).

4.2.1 Anthropogenic

Disturbance types that were categorized as anthropogenic are further described below.

Roads: Disturbances measured were typically gravel shoulders of Highways 430 and 431.

Plate 4.1. Multiple disturbances of trail, rehabilitation site (former highway) and active dunes. Grassy dunes are dominated by marram grass, *Ammophila breviligulata.*

Hiking trails: Hiking trails were usually composed of gravel, and less frequently, only compacted soil. Coltsfoot was usually found next to the trodden surface, especially where gravel was mixed with native soils. Native vegetation was typically within 1 m of the trail edge.

OSV (over snow vehicle) trails: Sites sampled occurred only in conjunction with other disturbances such as streams and moose trails.

Gravel pits: Aggregate stockpiles were sampled at Rocky Barachois, Cod Knox, Norris Point, Trout River, and the privately owned shale quarry near Cow Head on Highway 430. No chronically disturbed plots were sampled as the disturbance at the active edge of the pile is characterized by extraction and removal of material, rather than a resource shift. Maturing disturbances were sampled at the top or back of the stockpile.

Ski trail: The Chickadee ski trail near the Visitor Centre was constructed of crushed shale over native soils in 1994-95. Clearing of trees also occurred. It differs from hiking trails by its width, age, and homogeneity of material. At approximately 5 m wide, it is minimally twice as wide as most hiking, animal, or OSV trails. Its surface is without mineral or organic soil interspersed in the stone matrix, and weathering, compaction, and colonization were minimal due to the relative youth of the trail compared to others that have existed since at least 1973. The disturbance measured was that of trail construction rather than the ongoing disturbance of ski trail use.

Domestic cutting blocks/clearcut: The cutting block sampled was another multiple disturbance, occurring originally as an insect kill after which salvage logging was permitted. Coltsfoot was also noted to be absent on a clearcut on the Chickadee ski trail and land cleared for pasture on the former highway near St. Paul's.

Rehabilitation sites: Sixteen sites were located through a document produced by Resource Conservation (1985) whose mandate was to rehabilitate former farmsteads, access roads, and road allowances. The work, carried out between 1985 and 1987, involved various treatments of scarification, topsoiling and seeding of sites. A seed mixture of creeping red fescue (*Festuca rubra*), Canada bluegrass (*Poa pratensis*) and annual rye grass (*Lolium* sp.) was used. Other rehabilitation sites include restoration of the Rocky Barachois and Cod Knox quarries, and former roads abandoned up to 20 years ago and allowed to naturally regenerate. In all locations but one (transect 76) the work proposed in the document (Resource Conservation (1985) was observed to have been completed. All rehabilitation sites represent maturing disturbances.

Abandoned gardens: Raised beds abandoned approximately 20 years ago at the gently sloping area behind the cliff edge of the Green Gardens trail contained predominantly Canada thistle (*Cirsium arvense*) and no coltsfoot.

Hydro right-of-ways: Right-of-ways, approximately 50 m wide, were cleared in the early 1970s and disturbance consists mostly of brush clearing. More recent brush clearing occurred two to three years ago in some sections.

4.2.2 Natural

The specific conditions of sampled disturbance types that were categorized as natural are described below.

Slopes: Slopes included the calcareous cliffs at Tucker's Head where coltsfoot was absent, and where coltsfoot was found on unstable slopes on the Berry Hill trail, and near the shore on the Green Gardens trail.

Streams: While approximately half these sites were natural channels, others were anthropogenic in origin (*e.g.* moving water in the ditches of former roads). Species such as *Alnus rugosa*, which indicate riverain habitat according to Bouchard and Hay (1992) were present in the ditches.

Sand dunes: Coltsfoot was absent at Shallow Bay beach and the day use area there. The beach area is comprised of a sandy shoreline interfaced by active and stable dunes. The only observed occurrence of coltsfoot in the dunes was at a steeply-sloped dune bank at the bridge over Stanford Brook.

Shorelines: Shorelines sampled were the lake shoreline of Western Brook Pond and the sea shoreline adjacent to the Green Gardens trail. They consisted of cobble beaches (Plate 4.2).

Animal trails: All sampled moose trails but one exist in conjunction with other disturbances, such as rehabilitation sites, streams, and OSV trails. Moose tend to take advantage of previous disturbances for grazing and travel. The one moose trail appeared to have no other associated disturbance, and was specifically assigned to the disturbance type "moose trail". All other moose trails that occured in conjunction with other disturbances were assigned the category of "multiple disturbance". Two sites in which coltsfoot was absent represent caribou trails on Big Level (Plate 4.3).

Beaver dams: Coltsfoot was not found in any of the beaver dams observed.

Beaver cut: One site, in which coltsfoot was absent, included the selective felling of *Populus* species by beaver on a slope.

Insect kills: The most obvious resource shift in areas of insect kills is increased solar radiation over a several-year period as the trees are defoliated, and later as limbs decay and fall. The original infestation at this site at St. Paul's inlet (transects 93 and 94) occurred 2-3 years earlier.

4.3 Sampling strategy

A non-random sampling strategy was selected in order to measure resources associated with the presence of coltsfoot in certain disturbance types. This allowed the comparison of similarities or differences in resources among disturbance types

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Plate 4.2. Coltsfoot in natural, chronic disturbance of the sea shoreline near Green Gardens trail.

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Plate 4.3. Caribou trails in heath lichen tundra on Big Level, Alpine Plateau.

and between disturbance origins, and from disturbed to undisturbed (control) vegetation. Transects were chosen as the survey method in order to sample across a disturbance gradient within a vegetation type in the shortest distance possible. Transects are also by design a non-random sampling method (Kent and Coker 1992). A random sampling strategy would have yielded a great deal of data on resource levels where coltsfoot did not occur, and unrelated to the disturbance types under investigation. The process of site selection is outlined below.

4.3.1 Selecting transect sites

Bouchard and Hay's (1992) map of vegetation cover types of GMNP (Fig. 3.2) was reproduced at a scale of 1:50,000 (from the original scale of 1:150,000) and vegetation type boundaries of these maps were transferred to the more culturally and topographically detailed NTS maps (Canada 1990a, 1990b, 1990c, 1990d, 1992) of the same scale.

From information on the NTS maps, and from other park literature and personnel, the locations of different disturbance types were determined and marked on the maps. This ensured that as many disturbance types within vegetation types as possible were sampled. These sites became the starting point for locating individual transects, which were situated at the first occurrence of coltsfoot found on the transect site.

4.3.2 Laying transects across a disturbance gradient

Transects contained three separate 1 m^2 quadrats. Placement of quadrats one, two and three in each transect was designed to sample the vegetation and resources representing a gradient of disturbance frequency from chronic through maturing to undisturbed, respectively.

Quadrat one represented chronic disturbances such as roadsides, trails, and slopes, which are subject to changing resources, particularly those accompanying soil disturbances, once or more annually. Ideally, quadrat one was placed linearly across a gradient of disturbance. The longest transect was 44 meters long. Exceptions to this rule are outlined below.

Quadrat three - the undisturbed control plot which terminated the transect - was determined by the presence of trees, moss layer, or characteristic species of the vegetation type as indicated by Bouchard and Hay (1992). The absence of coltsfoot also determined the placement of quadrat three, so that its absence was the rule, indicating a hostile receiving environment. Sampling was done within the forest where possible to reduce the edge effects of light and air movement.

Quadrat two, or maturing disturbances, was located in the transitional zone between the chronic disturbance (quadrat one) and the associated undisturbed vegetation (quadrat three). Maturing disturbances had neither an ongoing physical disturbance, nor the presence of trees, moss layer or characteristic species of the vegetation type. Quadrats were placed on coltsfoot if it was present midway between quadrats one and three, or simply at midpoint if absent.

The ideal transect was linear. Some undisturbed quadrats were laid at right angles relative to maturing quadrats in sites where the disturbance was linear and the distance to the undisturbed quadrat was considerable (Fig. 4.2).

Transects did not include a maturing disturbance where there was little or no gradient from chronically disturbed to undisturbed; that is, if the distance between quadrat one and quadrat three was less than 3 m. Also, if the undisturbed vegetation type was inaccessible, such as at a cliff edge, or if there was no related chronic disturbance, such as in hydro right-of-ways, these quadrats were excluded from the transect.

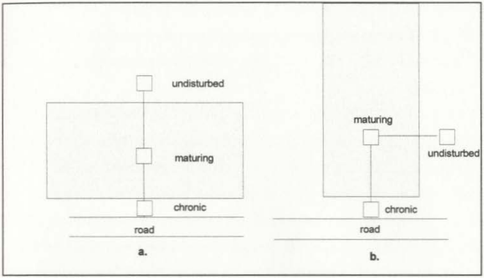


Figure 4.2. Ideal transect across disturbance gradient (a); and right angled transect (b) where undisturbed vegetation was closest at right angles to original bearing.

Only disturbance types which included coltsfoot were sampled. However, notes were kept of casual observations or in predetermined disturbance types (described in section 4.3.1) where coltsfoot appeared to be absent (n=35). These data reflect vegetation types that appeared to be unsuitable for coltsfoot regardless of the disturbance, or of certain disturbance types that seemed to be unsuitable for coltsfoot establishment.

Transect numbers were mapped and correlated to disturbance type, origin and vegetation type on Fig. 4.1 (folded colour map in jacket pocket, UTM co-ordinates Appendix II). Numbers 1-116 and 152 represent transects in which plots were sampled, while 117-151 represent observations only of disturbances in which coltsfoot was absent.

4.4 Resource levels

Measurements of soil pH, photosynthetically active radiation (PAR), soil particle size, soil moisture, duff cover and percent bare ground were sampled across the gradient of disturbance represented by chronic, maturing and undisturbed quadrats. Measurement procedures are outlined below.

4.4.1 Light intensity

Photosynthetically active radiation (PAR) was measured at the upper leaf surface with a LiCor photometer in units of $\mu E\ m^{-2}\ s^{-1}$. During August 1997, absolute values of PAR were recorded for each quadrat at each disturbance level. To eliminate the effect of variable cloud cover over time, PAR readings for chronic and maturing disturbances were converted to a relative measure of the undisturbed quadrat, and are referred to as relative PAR or light intensity. The formula used to convert absolute PAR to relative PAR is:

a = absolute PAR reading for undisturbed quadrat

b = absolute PAR reading for maturing quadrat

c = absolute PAR reading for disturbed quadrat

$$\text{Relative PAR} = \frac{a}{a}, \frac{b}{a}, \frac{c}{a}$$

Relative PAR therefore measures only the difference in light intensity between levels of disturbance. The tolerance of coltsfoot to low light intensity can only be shown at one location over one or more growing seasons.

4.4.2 Substrate

The term "substrate" is used rather than "soil" because much of the growing medium where coltsfoot was found was partially or wholly gravel, aggregate, or rock. The designation of "rock" indicates exposed parent material or coarse aggregate larger than 5 cm in diameter. "Gravel" was rock of any material, such as granite, shale and peridotite, between 0.05 and 5 cm in diameter. These diameters for gravel were chosen because they represent the specific coarseness sorted for different purposes by the park.

"Substrates" with greater than 2 cm thickness of organic material (the seeding depth of coltsfoot, Namura-Ochalska 1987) were designated as organic. Thick moss was therefore considered to be an organic substrate.

Predominant soil particle size (sand, silt or clay) of mineral soils was determined by the soil texture field tests developed by the Ontario Institute of Pedology (1982). In the moist cast test, moist soil is compressed in the fist, and the strength of the cast tested by tossing from hand to hand. The results are calibrated against a table which matches the cast characteristics with soil texture classes.

For this analysis soils were grouped into three descriptive categories: wholly or partially gravel/aggregate, wholly or partially organic, and other mineral soils. These categories were chosen to examine the connection between the introduction of gravel and the presence of coltsfoot.

4.4.3 Soil pH

For most transects a Kelway soil acidity meter was inserted into the soil to a depth of approximately 6 cm to obtain a reading for pH. Because the soil meter broke towards the end of the field season, for 23 of the 253 quadrats pH was determined by collecting soil for analysis in the lab. These were done on September 24, 1997, from soil samples collected 27 and 28 days previously. Soil and distilled water were mixed in equal parts and tested with a pH meter. Both instruments measure pH in tenths of units. Calibration between the Kelway soil acidity meter and the pH meter was not possible because damage to the Kelway meter was not repairable.

Five undisturbed control plots represent pH measurements for three sites in the Tablelands, a sedge fen near Woody Point, and an undisturbed site in heath-lichen tundra on Big Level where no coltsfoot occurred. In these sites pH was randomly tested and recorded, and so are included separately in the data set. These measurements were taken out of curiousity, because the sampling strategy did not allow for the establishment of quadrats in large undisturbed areas in which there was little or no adjacent disturbance.

4.4.4 Soil moisture

Soil moisture was described as saturated, moist or dry from soil retrieved from the hole created by the pH meter. Soil was saturated if water could be squeezed from the same size sample used in the feel test (about 10 ml of soil). Moist soil contained water but not to the point of saturation, while in dry soil, moisture could not be seen or felt.

Because sampling of soil moisture took place over the duration of the field season (August 7-29), results are presented in conjunction with precipitation data recorded in the park for the same time period.

4.4.5 Percent bare ground and duff cover

Percent bare ground and percentage cover of duff was estimated using the Braun-Blanquet scale (Kent and Coker 1992) as follows:

Value	%
+	< 1
1	1-5
2	6-25
3	26-50
4	51-75
5	76-100

The Braun-Blanquet scale is commonly used for percent cover of vegetation, but when used to estimate bare ground in a quadrat high values indicate little vegetation cover. Percentage cover of duff consists of deciduous or coniferous leaf litter.

4.5 Coltsfoot and other vegetation

For chronic and maturing disturbances percentage cover was estimated for all species of herbs, shrubs and trees within the 1 m^2 quadrat. Percent cover of moss was noted but recorded only as "moss" and not identified to species. The difference in coltsfoot cover and the composition of other plant species in chronic and maturing disturbances should indicate if a species shift has occurred as a disturbance matures.

For undisturbed plots, only tree species cover was noted as well as duff. At the beginning of the field season the decision was made, given time constraints, not to identify the native vegetation in undisturbed plots in favour of sampling more disturbances over all.

Vegetation cover was estimated using the Braun-Blanquet scale (Kent and Coker 1992) as used for percent bare ground (see section 4.3.5). The authority used for species identification was Gleason (1968), although nomenclature was updated according to Kartesz (1994). Determination of native status of species was assigned according to Rouleau and Lamoureux (1992). The status of "unknown" was assigned to genera not identified to species level where both native and introduced species are known. A species list for chronic and maturing disturbances is included in Appendix III. Vouchers of collected specimens are deposited in the Newfoundland Museum, St. John's, Newfoundland.

4.6 Herbivory and infection

Presence or absence of evidence of herbivory and infection (fungal, bacterial or viral) was noted on coltsfoot in chronic and maturing plots. No distinction was made between types of infection, but evidence was recorded as black, brown or red spots on leaves. Insect herbivory was noted as "chew holes" on leaves.

4.7 Receiving environments

The receiving environment is a component of the "functions of invasion" (Bazzaz 1983) that acknowledges that there are physical and biotic differences among undisturbed vegetation communities. The receiving environment was characterized according to the 14 vegetation types of GMNP described by Bouchard and Hay (1992), and by elevation.

4.7.1 Elevation and aspect

Sampling was further stratified by elevation following Waltz's (1962) observation that coltsfoot was not found above ca. 150 m on the Gaspé Peninsula. Elevations of sampled and observed sites were interpolated from NTS maps (contour interval = 10 m). Aspect of sampled and observed sites was determined with a compass.

4.8 Data analysis

4.8.1 Correlation between coltsfoot abundance and physical variables

Spearman's rank correlation coefficients were generated between coltsfoot abundance and the variables of pH, relative PAR, percent cover of coltsfoot, duff, and bare mineral soil (α=0.01). This analysis identified the significant determinants of coltsfoot abundance and resource levels.

4.8.1.1 Substrate types, pH, and soil moisture associated with coltsfoot

Data for the three substrate types (organic, gravel, mineral) were analyzed separately from other resources because of their nominal nature. The percentage of each substrate type was calculated for each of the three levels of disturbance, between anthropogenic, natural and multiple disturbances, and between disturbance types, and indicated whether certain disturbances were characterized by distinctive substrates. Box and whisker plots show median, interquartile range, and extreme values of pH associated with different substrate types. The relationship between substrate type, disturbance, and pH, indicates whether pH is associated with specific disturbance types, levels, and origins. Ordinal data for soil moisture levels were compared as percentages among disturbance levels in each transect.

4.8.2 Disturbance and resource changes

Differences in biotic and physical variables were tested among the three levels of disturbance (chronic, maturing, and undisturbed) using Kruskal Wallis nonparametric ANOVA. Variables tested included percent bare mineral soil, percent cover of coltsfoot and duff, relative PAR, and pH. This nonparametric test was used because the assumptions of normality of the data were not met.

4.8.3 Interspecies competition

The various plant species' response (other than coltsfoot) to disturbance between chronic and maturing disturbances was characterized by species similarity index (SSI) (Krebs 1985):

$$SSI = \frac{2c}{a+b}$$

a= number of species in chronic disturbances

b= number of species in maturing disturbances

c= number of species occurring in both

The seven vegetation communities for which species data were collected are grassy dunes, sedge fen and bog, riverain thicket and meadow, black spruce forest and scrub, tuckamore, balsam fir forest, and serpentine barrens. A species similarity index between disturbance levels for each vegetation type was calculated. This analysis indicates the degree of overlap between the two levels of disturbance, and whether a species shift occurs between chronic and maturing disturbances which displaces coltsfoot.

4.8.4 Herbivory and Infection

Percent occurrence of infection and herbivory was compared between chronic and maturing disturbances using a T-test for proportions. This indicates whether coltsfoot is subject to predation or infection from other biota, and whether this occurs significantly more often in one disturbance level or another.

4.8.5 The invasibility of vegetation types at high elevations

Presence or absence of coltsfoot at elevations greater than 150 m was noted, and if present, correlated to aspect on a scatterplot. This determined if coltsfoot was limited to elevations below 150 m asl as was found on the Gaspé Peninsula (Waltz 1962). The absolute altitudinal limits of coltsfoot in GMNP were not determined because a complete survey of areas in the park above 150 m was impossible given the time constraints. For the purposes of this study, it was sufficient to identify the presence or absence of coltsfoot at locations above 150 m. If coltsfoot was found above 150 m, the correlation between elevation and aspect indicated whether climatic limitations were overcome by a favourable (southerly) aspect.

4.8.6 The anthropogenic and natural origins of coltsfoot invasion in GMNP

Differences in resources between anthropogenic and natural disturbances were tested using the Kruskal Wallis nonparametric ANOVA, described in section 4.7.2. Statistical significance between disturbance origins shows whether resource levels favourable to coltsfoot are characteristic of either anthropogenic or natural disturbances. Analyses of substrates described in section 4.7.1.1. were undertaken for both disturbance origin and disturbance type.

Analysis of variance was not undertaken among disturbance types (*e.g.* ski trails, slopes, etc.) because many of the sample sizes were too small. Instead, resource levels of individual disturbance types were compared to resource levels shown to be correlated to coltsfoot abundance. The mean and standard error for the measurements of pH, relative PAR, percent cover of coltsfoot, duff, and bare mineral soil, are given as bar graphs among 12 disturbance types. If the mean of the resource level for a disturbance type was shown to be higher than average for the group, it was considered to be favourable to coltsfoot abundance. A separate table following the bar graphs collated the results for all disturbance types and all resources. This analysis shows if the resource levels characteristic of certain disturbance types are more favourable for coltsfoot than others. Specifically, this will address the question of whether disturbance types related to park development (e.g. roads, hiking trails, gravel pits) have assisted in the spread of coltsfoot.

5. Results

5.1 Introduction

The purpose of this chapter is to present the results of the analysis of field data as they address the study objectives.

5.2 Description of data

The data set consists of 153 transects, comprising 253 quadrats of which 84 were chronic, 100 maturing and 69 undisturbed (Appendix IV). Roads (n=29), hiking trails (n= 41), gravel pits (n=22), and rehabilitation sites (n=58) make up most of the anthropogenic disturbances sampled (n=162). Streams were the highest number of quadrats in the natural disturbance category (n=24, total natural n=86), and 39 plots sampled were multiple disturbances (Table 5.1).

All vegetation types in GMNP were sampled or observed except heath dwarf scrub, which was not sampled because of time constraints, inaccessibility and the small area (0.5 percent) it comprises in the park. Table 5.2 indicates the number of quadrats completed in each vegetation type, the percent they represent of the total quadrats, and the percent of the park covered by those vegetation types. Coltsfoot was rarely encountered in grassy dunes, sphagnum bog, and tuckamore, and this is reflected in the small number of quadrats compared to the total park area covered by these vegetation types. Quadrats in the balsam fir forest were almost double that of the area the forest comprises in the park, and this reflects the high number of disturbance types associated with this vegetation type: fourteen of the seventeen disturbance types were found in the balsam fir forest. All fourteen vegetation types were found below 150 m, however only eight of these occurred at higher elevations as well.

Table 5.1. Description of data.
Disturbance types have been categorized according to natural or anthropogenic origin, frequency of disturbance, and age of disturbance. Age of mature disturbances were determined by archival documents such as photos and reports, or by interviews with park personnel. Numbered vegetation types in which disturbances are found are: 1. grassy dunes; 2. intertidal saltmarsh; 3. sedge fen and bog; 4. sphagnum bog; 5. riverain thicket and meadow; 6. larch scrub; 7. black spruce forest and scrub; 8. tuckamore; 9. heath dwarf scrub; 10. balsam fir forest; 11. heath lichen tundra; 12. serpentine barrens; 13. calcareous cliffs. (OSV = over snow vehicle; r.o.w. = right-of-way)

Disturbance type	frequency of dist.	age of dist. (years)	veg. types in which dist. found		no. of plots		total plots for dist. type
				chronic dist.	maturing dist.	Undist.	
Anthropogenic							
road	chronic	<1	1,3,5,6,7,8, 10, 12	13	9	7	29
hiking trail	chronic	<1	1,3,5,6,7,8, 10,11,12	20	7	14	41
OSV trails	chronic	<1	10	0	0	0	0
gravel pit	maturing	2	10,12	0	18	4	22
x-country ski trail	maturing	2	10	0	2	2	4
cutting blocks	chronic	?	10	0	2	0	2
rehabilitation sites	maturing	3-13	3,5,6, 10,12	5	39	14	58
abandoned garden	maturing	15	8	0	1	0	1
hydro r.o.w.	maturing	2-3	7,10	0	4	1	5
Natural							
shoreline	chronic	<1	2,10	2	1	1	4
slope	chronic	<1	8,10,13	4	1	1	6
stream	chronic	<1	5	10	8	6	24
sand dunes	chronic	<1	1	1	0	0	1
moose/animal trail	chronic	<1	3,8,10	3	0	1	4
beaver dam	chronic	<1	3,7	3	0	0	3
beaver cut	maturing	<1	10	1	0	0	1
insect kill	chronic	<1	10	2	0	2	4
Multiple	chronic		1,2,3,4,7,8, 10	17	11	11	39
Undisturbed: pH only			3,11,12	0	0	5	5
Total				84	100	69	253

Table 5.2. Percentage of total quadrats by vegetation type compared to percentage of Park area covered by individual vegetation types.

vegetation type	number of quadrats	% of total quadrats	% of vegetation type in GMNP (Parks Canada 1996)
grassy dunes	5	2	0.1
intertidal salt marsh	1	0.4	0.1
sedge fen and bog	15	5.9	5.1
sphagnum bog	2	0.8	4.4
riverain thicket and meadow	7	2.8	0.4
larch scrub	2	0.8	0.05
black spruce forest and scrub	19	7.5	6.2
tuckamore	19	7.5	12.9
heath dwarf scrub	0	0	0.5
balsam fir forest	158	62.6	36
heath lichen tundra	2	0.8	21.6
serpentine barrens	22	8.7	4.9
calcareous cliffs	1	0.4	no figure
cleared, settled areas	observed	0	0.3
total	**253**	**100**	**92.55***

*6.8% of the park area is covered by water

Two subsets of the data were used for analysis. Of the total of 253 quadrats and observations, 227 of these were used to test for correlation between the abundance of coltsfoot and certain resource levels and for the analysis of variance among disturbance levels only. The 26 samples omitted were observations only of disturbance types in which coltsfoot was absent: beaver cut, beaver dams, abandoned garden and sand dunes. Over snow vehicle (OSV) trails were sampled, but occurred only in conjunction with other disturbances, and are therefore included under the category "multiple disturbances".

A smaller subset of 115 samples was used to analyze individual disturbance types and origins. These were selected from the larger data set to measure the resource levels that were specific to these disturbance types. These are the chronic disturbances of road, stream, shore, slope, animal trail, hiking trail, insect kill and multiple disturbances, and the maturing disturbances of rehabilitation sites, ski trail, gravel pit and hydro right-of-way.

Generalizations about resources levels among disturbance types are described by the statistical tests that follow.

5.3 Resource levels correlated to coltsfoot abundance

The abundance of coltsfoot (measured by cover categories) increases with pH (r_s = 0.371) and light level (r_s = 0.546), but decreases as duff cover increases (r_s = 0.378)(Table 5.3). As bare ground increases, duff cover (r_s = -0.453) decreases, but pH (r_s = 0.505) and relative PAR (r_s =0.207) increase. All coefficients are significant at $p < 0.05$, and all but one to $p = 0.01$ (Table 5.3).

Coltsfoot is abundant in disturbances where overstory vegetation has been cleared leaving an open, sunny site, and the soil has been disturbed, removing the existing ground cover and duff. The absence of acidic coniferous duff and/or other organic material contributes to the higher pH of these disturbed sites. Conversely, undisturbed sites where coltsfoot is absent are characterized by greater shade, more duff cover, more acidic soils, and less bare ground, all of which are a function of a well developed vegetation layer.

5.3.1 Soil moisture

Although soil moisture was determined over a 23-day period, moist soil was the dominant category in all disturbance levels (Fig. 5.1). Soil was moist for 83.3% of all plots sampled, while 10.3% were saturated and 6.4% were dry. Rain was recorded for 14 of the 23 field days, and a total of 71.6 mm of precipitation was recorded for the north end of the park. Given the high percentage of moist and saturated plots (total = 93.6%), the regular occurrence of precipitation in August, the low mean

Table 5.3. Correlation matrix using Spearman's rank correlation coefficients (r_s) among physical and biotic variables. Sample sizes are in brackets. All correlations significant at p= 0.01 except as noted (*).

	pH	relative PAR	% cover duff	% bare ground
% cover coltsfoot	0.371 (212)	0.546 (162)	-0.378 (200)	0.148* (203)
pH		0.365 (164)	-0.360 (198)	0.505 (201)
relative PAR			-0.409 (153)	0.207 (156)
% cover duff				-0.453 (200)

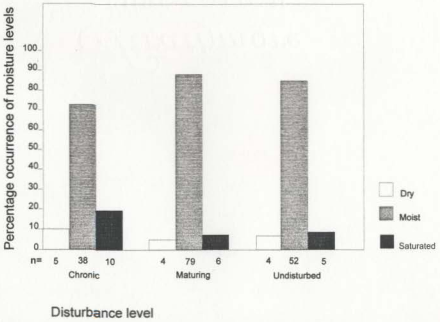


Figure 5.1. Soil moisture among disturbance levels. n=number of plots.

daily temperature during this period (13.9° C , Appendix V), and the documentation by other authors (Clayton *et al.* 1977; Bouchard and Hay 1976; Banfield 1988)of adequate to excessive moisture in the park, it can be generalized that adequate moisture for coltsfoot germination is not a limiting factor in GMNP.

5.3.2 Substrate types associated with pH levels

Table 5.3 shows that coltsfoot abundance is correlated with increasing pH. Figure 5.2 shows that pH is also associated with substrate type, specifically that the higher pH substrates preferred by coltsfoot are associated with gravel. Organic substrates

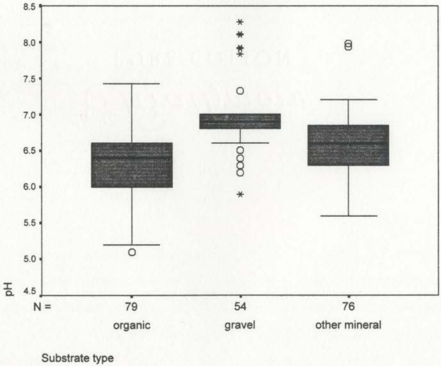


Figure. 5.2. Box and whiskers plots of pH of substrate types. (Horizontal bar = median; box = interquartile range; whiskers = highest and lowest extremes; circles = outliers – 1.5-3 box lengths from either end; stars = extreme values - >3 box lengths from either end.)

are associated with the lowest range of pH, substrates containing gravel the highest, while other mineral substrates are intermediate between these, from slightly acidic to neutral. The mean pH for organic, gravel, and mineral substrates is 6.2, 7.0 and 6.6, respectively.

5.4 The invasibility of undisturbed vegetation and the recession of coltsfoot

There were significant differences among the disturbance levels for all variables (Table 5.4), demonstrating that resource shifts or amplifications that favour coltsfoot do occur with disturbance. Undisturbed vegetation types should therefore not be invasible based on resource suitability, but would need to be verified by transplant experiments.

Table 5.4 Kruskal-Wallis ANOVA among three disturbance levels (chronic: n=57; maturing: n=90; undisturbed: n=64).

	% cover coltsfoot	pH	relative PAR	% duff cover	% bare ground
Chi-Square	113.354	38.824	82.116	67.744	23.677
df	2	2	2	2	2
p value	<0.001	<0.001	<0.001	<0.001	<0.001

Analysis of substrate type between disturbance levels (Fig. 5.3) shows that substrate types characterize disturbance levels. Neutral gravel substrates account for almost 50 percent of chronic disturbances; other neutral to mildly acidic mineral soils account for almost 50 percent of maturing disturbances; and acidic organic substrates account for almost 80 percent of undisturbed plots (Fig. 5.3). Soils containing neutral gravel were absent in undisturbed plots.

Percent cover of coltsfoot is positively correlated to pH (Table 5.3) and there is

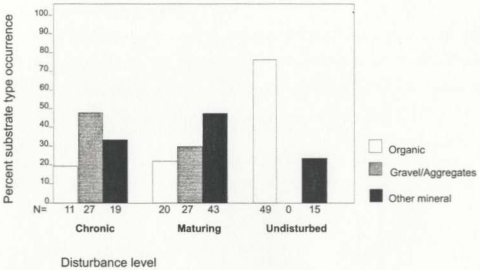


Figure 5.3. Percentage of substrate types in three levels of disturbance.

a significant difference among disturbance levels for both pH (x^2=38.824, p<0.001) and percent cover of coltsfoot (x^2=113.354, p<0.001)(Table 5.2). Soil pH appears to be the most important limiting factor for coltsfoot, which is a calciphile (Myerscough and Whitehead 1965, 1967). The acidic native soils of GMNP may therefore be unsuitable for colonization by coltsfoot regardless of whether or not there is disturbance, so long as pH is sufficiently low.

The difference in resources among disturbance levels suggests that as a disturbance matures (increase in duff cover, decrease in bare ground, pH, PAR), resources will return to the unsuitable levels found in undisturbed vegetation, causing the recession of coltsfoot populations. However, these results were not split out by substrate type for maturing disturbances. The fate of gravel in native soils and its effect on pH over the long term is not known.

5.4.1 Interspecific competition

Less than 50 percent of species were similar between the chronic and maturing disturbance levels in the seven vegetation types for which data was available (Table 5.5). The low SSI (.20) for the balsam fir forest is particularly notable because of the

Table 5.5 Species similarity indices (SSI) for chronic and maturing disturbances in seven vegetation types.

chronic n=	maturing n=	vegetation type	SSI
2	1	grassy dunes	0.44
4	5	sedge fen and bog	0.4
2	2	riverain thicket and meadow	0.05
6	4	black spruce forest and scrub	0.45
5	5	tuckamore	0.46
42	62	balsam fir forest	0.2
3	7	serpentine barrens	0.15

large sample size (n= 42, chronic; n= 62 maturing) and because it comprises the single largest vegetation type in the park, with the largest number of disturbances.

Introduced plant species are a component of succession in GMNP. When data for different vegetation types are aggregated, there is a similar percentage of native and introduced species in both chronic and maturing disturbances, with native species comprising averages of 50.3 and 59.4 percent, and introduced species comprising 37.4 and 34.1 percent of chronic and maturing disturbances respectively (Table 5.6).

There is an inverse relationship between frequency of occurrence and number of species with the greatest number of species appearing only once, and a few species appearing frequently (Fig. 5.4). Native species make up the highest proportion of species appearing infrequently, while a small number of introduced species occur most frequently. *Taraxacum officinale* is the most frequently occurring species for both chronic and maturing disturbances.

Table 5.6. Percentage of native, introduced, and unknown (not identified to species level) species in chronic and maturing disturbances in seven vegetation communities in Gros Morne National Park.

vegetation type	native		introduced		unknown	
	chronic	*maturing*	*chronic*	*maturing*	*chronic*	*maturing*
grassy dunes	14.3	50.0	85.7	50.0	0.0	0.0
sedge fen and bog	59.1	70.0	18.2	25.0	22.7	5.0
riverain thicket and meadow	66.7	62.5	11.1	37.5	22.2	0.0
black spruce forest and scrub	63.0	57.7	25.9	42.3	11.1	0.0
tuckamore	47.1	73.1	41.2	26.9	11.8	0.0
balsam fir forest	60.7	52.5	29.5	35.6	9.8	11.9
serpentine barrens	41.7	50.0	50.0	21.4	8.3	28.6
mean	**50.3**	**59.4**	**37.4**	**34.1**	**12.3**	**6.5**

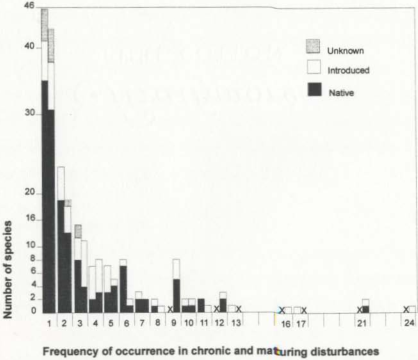


Figure 5.4. Comparison of frequency of species origin and occurrence between two disturbance levels (left bar in pair = chronic; right bar in pair = maturing; x = no species

5.4.2 Herbivory and Infection

Herbivory of coltsfoot leaves by snails occurred in 38 percent of chronically disturbed sites and 28 percent of maturing disturbances. There was no significant difference in herbivory between disturbance levels ($t=1.14$, $p=0.2569$).

Infection occurred in 52 percent of chronic disturbances and 36 percent of maturing disturbances. There was no significant difference between disturbance levels ($t=1.85$, $p=0.0672$).

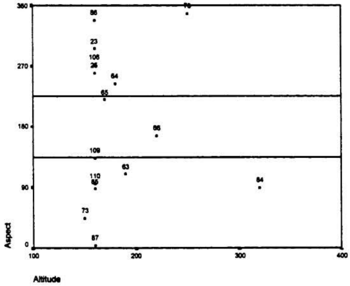
Coltsfoot in GMNP is eaten by other species, including moose that graze the flowers in the spring (Burzynski, personal communication, 1997). Both snail herbivory and fungal infection are higher in chronic disturbances than in maturing disturbances. In other studies snails were also found to prefer grazing on coltsfoot infected with rust fungus (Ramsell and Paul 1990, Namura-Ochalska 1193a, Bakker 1960). The higher incidence of fungal infection on coltsfoot populations in chronically disturbed plots may be indicative of their clonal origin since ramets would be more susceptible to fungal attack, while populations with greater genetic diversity would be less so. Fungal infections may also be influenced by environmental conditions such as airflow and humidity, or the poor physiological condition of the plant.

5.4.3 Elevational limitations

The small sample size ($n=15$) of coltsfoot locations at elevations above 150 m asl is due to the smaller number of disturbance types and their limited accessibility at high elevations. However, these 15 locations show that coltsfoot can establish well above the altitudinal limits found in the Gaspé Peninsula (Waltz 1962). Coltsfoot was found at a maximum elevation of 550 m asl in Ferry Gulch at a site where gravel was air-lifted into a construction camp (Fig. 4.1 transect 11; B. Jenniex, personal communication, 1997). The other 14 locations above 150 m elevation were at the

Tablelands Trail and nearby rehabilitation sites (Fig. 4.1 transect 63-66, 73); Cod Knox quarry (Fig. 4.1 transects 85-87, 108-110); a rehabilitated section of the old highway 431 outside of Glenburnie (Fig. 4.1 transect 78, 79); and near the cabin at Angle Pond (Fig. 4.1 transect 84). Climatic limitations at high elevations are not overcome by aspect, with only 1 of the 5 sites where coltsfoot was found above 150 m facing south (Fig. 5.5).

Figure 5.5 Aspect (magnetic north) of plots with coltsfoot at elevations greater than 150 m asl.



5.5 Origins of coltsfoot invasion

When natural and anthropogenic disturbance types are compared, there is no significant difference in physical (pH and relative PAR) and biotic (percent cover of coltsfoot, percent cover of duff, and percent bare ground) variables (Table 5.7).

Table 5.7 Kruskal-Wallis ANOVA between disturbances of anthropogenic (n=78) and natural (n=17) origins.

	% colts-foot	pH	relative PAR	% duff	% bare ground
Chi-Square	0.778	1.595	2.114	0.000	0.072
df	1	1	1	1	1
p value	0.378	0.207	0.146	1.000	0.789

However, while gravel substrates occur in natural, anthropogenic, and multiple disturbances, anthropogenic disturbances have the highest percentage of gravel substrates (Fig. 5.6). Gravel occurs notably in the anthropogenic disturbances of roads, ski and hiking trails, where it is used for construction and maintenance, and in gravel pits, where maintenance stockpiles originate (Fig. 5.7). Naturally occurring aggregate such as in streams, slopes and shorelines, accounts for its presence in disturbances of natural origin (Fig. 5.7).

Acidic organic substrates dominate undisturbed sites, and occur exclusively in hydro right-of-ways and insect kills (Fig. 5.7). In these disturbances, the canopy is removed, but the native soils are left intact. Unlike other anthropogenic disturbances, gravel is not added. The neutral to basic soils preferred by coltsfoot are caused not only by the removal of existing vegetation and duff layer, but also by the addition of gravel to acidic native soils in chronic disturbances.

Comparisons of other resource levels among disturbance types are difficult because of small sample sizes; of the twelve disturbance types, six have sample sizes of less than three. In order to draw some conclusions given the limitations of the data, the means of variables for each disturbance type are compared for percent cover of coltsfoot (Fig. 5.8); percent bare ground (Figure 5.9); pH (Figure 5.10); relative PAR (Fig. 5.11); and percent cover of duff (no figure is presented for percent cover of duff because it is absent - 0 percent - in all disturbance types). The total mean for each variable among disturbance types is shown as a horizontal bar across

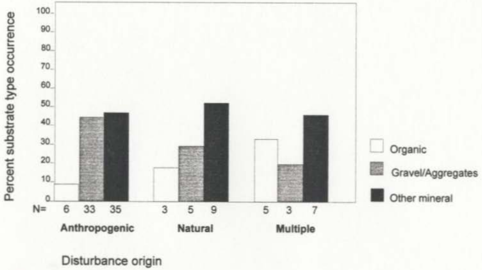


Figure 5.6. Percentage of substrate types among disturbance origins.

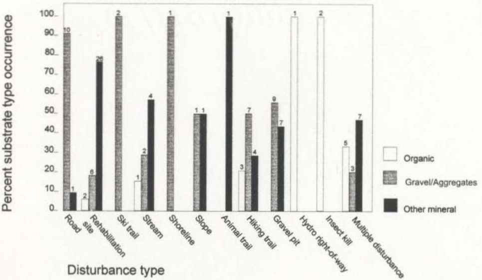


Figure 5.7. Percentage of substrate types among disturbance types. (sample size at top of bars)

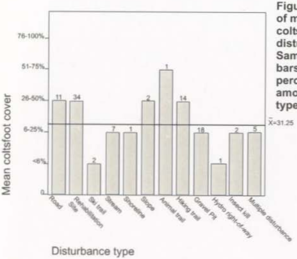


Figure 5.8. Comparison of mean percent cover of coltsfoot among disturbance types. Sample size at top of bars. $\bar{X}$ = total mean for percent cover of coltsfoot among disturbance types.

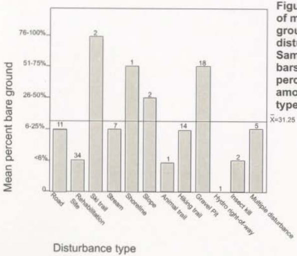


Figure 5.9. Comparison of mean percent bare ground among disturbance types. Sample size at top of bars. $\bar{X}$ = total mean for percent bare ground among disturbance types.

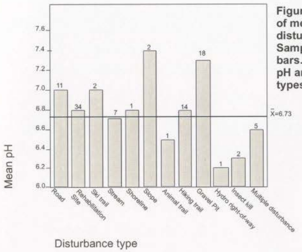


Figure 5.10. Comparison of mean pH among disturbance types. Sample size at top of bars. $\bar{X}$ = total mean for pH among disturbance types.

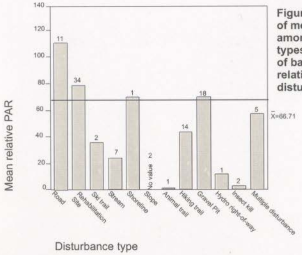


Figure 5.11. Comparison of mean relative PAR among disturbance types. Sample size at top of bars. $\bar{X}$ = total mean for relative PAR among disturbance types.

each graph, and disturbance types with higher than average values are considered to be more favourable to coltsfoot colonization based on the correlation between coltsfoot abundance and physical variables found in Table 5.3. Standard errors of the means are included in Appendix VI.

Table 5.8 summarizes and scores the disturbance types that have higher than average values for all variables except duff cover. In all disturbance types duff is absent, which is correlated to the presence of coltsfoot and scored in the table as a favourable condition. Gravel and mineral substrates and their associated pH are suitable for coltsfoot, and are also scored as a favourable condition.

Disturbance types with a high score out of a possible total of six are more favourable to coltsfoot colonization: roads, rehabilitation sites, ski trails, shorelines, slopes and gravel pits. Hydro right-of ways and insect kills have the lowest scores and are considered to be disturbances with resource levels less favourable for coltsfoot.

Table 5.8. Summary of disturbance types *vs.* resources conducive to coltsfoot colonization. (x= value higher than mean for all disturbance types for variable, except for duff which is absent in all disturbance types; g=gravel; m=mineral; o=organic).

variable	road	rehab	ski trail	stream	shore	slope	animal trail	hiking trail	gravel pit	hydro r.o.w.	insect kill
absence of duff	x	x	x	x	x	x	x	x	x	x	x
% coltsfoot	x	x				x	x	x			
% bare ground			x		x	x			x		
pH	x	x	x		x	x			x		
relative PAR	x	x			x				x		
dominant substrate	g	m	g	m	g	g/m	m	g	g	o	o
total score	5	5	4	2	5	5	3	3	5	1	1

6. Discussion

6.1 Introduction

This chapter discusses the results of the statistical analyses in the context of the objectives of this study. The contributions of this study to the literature on coltsfoot specifically, and biological invasion in general, are presented. Finally, directions for further work are suggested.

6.2 Coltsfoot's impact on native diversity

Based on the analysis of resource levels, the data show that coltsfoot will not invade undisturbed native vegetation communities in GMNP. Resource levels in undisturbed vegetation communities occur over time as an interaction between successional vegetation changes and its effect on soil development. Some, but not all, disturbance types shift resources from these historic levels to those that enable coltsfoot invasion.

The comparison of resource levels favourable to coltsfoot with resource levels found in specific disturbances and vegetation types identifies those that are most vulnerable. Because the type of disturbance is often determined by the vegetation type (for example, large-scale defoliation by insects is specific to conifer forests in GMNP), the threat to native diversity is discussed as a function of both the receiving environments and their associated disturbance types.

The negative correlations between coltsfoot abundance and duff, relative PAR and pH describe densely forested vegetation types where light levels are limited and pH is low due to the acidity of coniferous litter and the absence of gravel. These resource levels apply specifically to undisturbed balsam fir forest, heath dwarf scrub, tuckamore, and black spruce forest and scrub, and therefore represent receiving environments with resource levels unsuitable for coltsfoot. Coltsfoot also was not observed in the intertidal saltmarsh, heath lichen tundra, and larch scrub, and was rare in sandy dunes, serpentine barrens and sphagnum bog. Heath dwarf scrub was not observed or sampled.

In the case of natural disturbance environments such as slopes, streams, and shorelines where coltsfoot is present, these resource levels reflect chronic disturbances that inhibit the establishment of most vegetation and the accumulation of organic soils or duff. Riverain thicket and meadow, or any vegetation type through which streams traverse or interface with shorelines, are prone to colonization given the frequency of hydrological disturbance. Only one calcareous cliff site was sampled at Tucker's Head (Fig. 4.1, transect 91), and while in theory this should be an ideal site for coltsfoot because of the chronically disturbed, high pH (7.98) substrate, it was rare and in lower frequency than other introduced species observed. This may be due to an absence of diaspores at the site.

Receiving environments that have acidic native soils should not be subject to coltsfoot invasion, even when disturbed, unless gravel is brought in. Disturbance types (such as hiking trails and roads) that include the importation of gravel that neutralizes or buries acidic soils, and the concomitant transport of rhizomes, will encourage coltsfoot to colonize. In tuckamore, serpentine barrens and sphagnum bog, coltsfoot occurred only in the presence of gravel, and in the case of serpentine barrens, gravel seemed to mediate the toxic effects of the naturally occurring heavy metals. Coltsfoot was not found on the acidic organic substrates of OSV trails on bogs or on caribou trails in the heath lichen tundra. Disturbances that leave native soils and some vegetation intact, such as grazing, hydro right-of-ways, and selective logging, are not hospitable environments for the colonization or proliferation of coltsfoot.

The balsam fir forest is the most susceptible to coltsfoot colonization because it comprises the largest single vegetation type in the park, and because of the high number of disturbances to which it is subjected. Thirteen of the seventeen disturbance types are found in the balsam fir forest because of its aesthetic appeal to visitors, the usefulness of its wood and browse to humans and animals respectively, and its proximity to shores and brooks and the populated coastal plain. Coltsfoot may now be a permanent component of the balsam fir forest given the disturbance regimes in place, particularly those that involve the importation of gravel.

Coltsfoot can also colonize suitable natural disturbances in the back country through wind dissemination of diaspores, carried in mud on hooves, or by the transfer of rhizomes with aggregate for trail maintenance and construction. Coltsfoot was found in relatively isolated sites, presumably as a result of wind dispersal, on a gravel bar in a brook on St. Paul's Inlet, and near the Angle Pond cabin (Fig. 4.1, transects 15, 84).

6.3 The recession of coltsfoot in maturing disturbances

Maturing disturbances were characterized by significantly different resource levels, a lower abundance of coltsfoot, and a different suite of other vegetative species (< 50 percent similar between chronic and maturing disturbances). Both changing resources and interspecific competition may, therefore, play a role in the recession of coltsfoot over time. However, it is not known whether or not coltsfoot was an original colonizer of these disturbances. Long-term plot studies that measure the change in resources and track the concomitant species shift over time may be able to isolate the mechanisms of competition that replace coltsfoot.

While Namura-Ochalska (1988, 1989) and Bakker (1960) reported the exclusion of coltsfoot by other species in their studies, it was under more homogeneous physical conditions with competition provided by only two other species in Namura-Ochalska's

(1988, 1989) study, and one other species in Bakker's (1960) study. Namura-Ochalska (1988) predicted that the process of species replacement might take longer in low nutrient sites, and this may be the case in GMNP. Compared to the Polish studies, which were conducted in fallow agricultural fields, (Namura-Ochalska 1987, 1988, 1989, 1993a,b,c), conditions in GMNP show a greater heterogeneity of receiving environments and a greater diversity of competition. The process of species replacement observed in Poland is unlikely to be replicated in GMNP.

With the exception of soil moisture, significant shifts in, or amplification of, resources occur with disturbance. Adequate moisture for coltsfoot, particularly for germination, is not a limitation in GMNP where there is little or no moisture deficit during the growing season (Clayton *et al.* 1977).

The intermediate level of resources found in maturing disturbances indicates a tendency for resources to return towards the levels found in undisturbed vegetation types as canopy increases, lowering light levels and acidifying soils due to the increase in duff layer. These resource levels are unsuitable for coltsfoot, and should cause it to decline over time. However in chronic disturbances that maintain favourable conditions such as along roads, hiking trails, shorelines, streams and slopes, coltsfoot may persist indefinitely.

6.4 Origins of coltsfoot invasion in GMNP

Coltsfoot invasion in GMNP is not a result of either anthropogenic or natural disturbance alone. When disturbance origin is analyzed according to resource levels, both anthropogenic and natural disturbances provide suitable conditions for its colonization. However, the establishment of roads, ski and hiking trails, and gravel pits are all activities associated with the building and maintenance of parks infrastructure. The suitable conditions found on shorelines and slopes are unrelated to park activities and existed before the opening of the park when coltsfoot plants were "relatively few" (Bouchard *et al.* 1978).

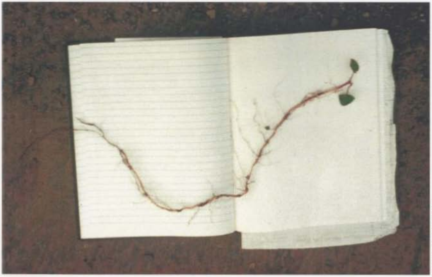
The association between coltsfoot and the presence of gravel indicates that the recent abundance of coltsfoot is connected to park activities. The development and use of aggregate stockpiles is the common link in the development of the park infrastructure, specifically road and trail construction and maintenance. Gravel is not only associated with increased soil pH, but carries rhizomes which are dispersed when and where gravel is used. The reconstruction of roads and the establishment of trails over a relatively short time provided an ideal habitat for the establishment of both diaspores and vegetative propagules.

The process of coltsfoot invasion in GMNP can be reconstructed by observations of contemporary quarry conditions, discussions with local residents, combined with the biological characteristics of coltsfoot. Following initial gravel exploitation, quarry rims were colonized by coltsfoot, where it was also found abundantly during fieldwork for this study (Plate 6.1). Stockpiles provided adequate habitat for the establishment of colonizing species, particularly coltsfoot, which supplied ample diaspores from the nearby rims. The residency time of stockpiles allowed for the above and below ground establishment of coltsfoot, which favours below ground production of rhizomes in low nutrient sites such as gravel stockpiles (Plate 6.2). Road and trailside colonization occurred initially through the distribution of viable rhizomes in the aggregate.

During fieldwork for this research, rhizome-laden fill was observed to be excavated at Little Brook gravel pit, Glenburnie (Fig. 3.3). The operator of the power shovel was requested to deposit a shovelful of excavate (approximately 2m^3) on to an unvegetated surface. The largest coltsfoot plants were extracted from the fill and photographed (Plates 6.3, 6.4). Further material from this extraction was observed

Cheryl Hendrickson

Plate 6.1 Coltsfoot on Cod Knox Quarry rim, August, 1997. (white bar in foreground = one meter)



Cheryl Hendrickson

Plate 6.2. Coltsfoot favours below-ground production of rhizomes in low-nutrient sites such as gravel pits. Little Brook Quarry, Glenburnie, August 1997.

Cheryl Hendrickson

Plate 6.3. Freshly extracted aggregate from slope vegetated with coltsfoot. Little Brook Quarry, Glenburnie, August 1997.

Cheryl Hendrickson

Plate 6.4. Coltsfoot extracted from power shovel bucket-load (approximately $2m^3$) of aggregate. Little Brook Quarry, Glenburnie, August 1997.

to be spread immediately after excavation, and coltsfoot's successful establishment under this condition is likely.

The timing of road construction from the late 1970s to mid 1980s, a local housing boom (Anions 1993), along with changes in trail maintenance and construction procedures 13-18 years ago, coincide with the noticeable presence of coltsfoot at the roadsides approximately 13 years ago (Butler, Hermanutz, personal communication, 1997). The establishment of populations from rhizome fragments distributed in the construction gravel was likely followed by the dissemination of diaspores over large areas of suitable habitat that was provided in a relatively short time. Suitable habitat includes an abundance of neutral soils on the road shoulder frequently disturbed by grading, sand and gravel deposition, and slope instability on steeper grades. Vegetation clearing for roads and trails also provided appropriate light levels.

Based on other studies (Rouleau and Lamoureux 1992; White 1994) coltsfoot was present in locations south of the park and in the park previous to its opening in 1973 (Fig. 2.1). At this time, coltsfoot was not found elsewhere on insular Newfoundland other than the Avalon Peninsula (Fig. 2.1). Channel-Port aux Basques (Fig. 2.1) may have been the entry point from North Sydney, Nova Scotia, for propagules for western Newfoundland. One observer has noted that during the period of dissemination in mid-June in GMNP, airborne diaspores adhere to the mud on vehicles using the park's highways (Hooper, personal communication, 1997). It is likely that Nova Scotia populations crossed to Newfoundland as diaspores attached to mud on vehicular ferry traffic, as well. Populations moved as a northward front and were available to colonize the suitable habitat provided by road construction in GMNP.

6.5 Coltsfoot as an Invasive

In GMNP rhizome fragmentation and dispersal in gravel appear to have been the mode of invasion. But the spread of rhizomes from the parent plant is another form of clonal reproduction that may be of concern for the park. The spreading of attached rhizomes may take place at different levels in the substrate, so that the emerging shoots may not be subject to surface soil conditions such as particle size, moisture and pH, or to interspecific competition from shallow-rooted plant species. For example, adventitious roots that supply water in dry periods reach depths of 1-1.5 m (Bakker 1960), and on loosely sodded plots from 1-5.6 m (Namura-Ochalska 1993a) and may overcome moisture limitations encountered by diaspores. However, the absolute lower limit of light which is tolerated by emerging coltsfoot shoots has not been established, nor whether populations are sustainable under low light conditions.

In two instances coltsfoot was found to have spread from a disturbed area into adjacent undisturbed vegetation. In the St. Paul's Inlet site (Fig. 4.1, transects 13, 14, 92, 93), coltsfoot was found beneath defoliated conifers sparsely distributed among the native herbaceous ground cover and moss of the balsam fir forest 4 m from plants growing on an erosional back of a stream. The insect kill represents an amplification of radiation, but there was no obvious soil disturbance.

Similarly, coltsfoot invaded a sloping fen from the shoulder of the Lomond road (Fig. 4.1, transects 90, 11, 112). While the upgrading of the road in 1989 represents a disturbance that may have changed water quality or quantity, there was no obvious soil disturbance in the fen. Coltsfoot was sparsely distributed about 50 m perpendicular to the road edge following the downhill grade, emerging among dense native vegetation.

If vegetatively-reproducing coltsfoot is more tolerant of low pH, light levels and interspecific competition than are sexually-reproducing individuals, it may have invasive capabilities in sites with no obvious soil disturbance. Coltsfoot found in these conditions is, however, rare, with only two such sites observed during the course of fieldwork.

6.6 Contributions of this study

Most of the published literature on coltsfoot originates in Europe and Great Britain where coltsfoot is native, and research was undertaken in reference to its status as an agricultural and ruderal weed, and not as potentially invasive component of natural ecosystems. This study contributes to an understanding of the factors affecting its distribution in a native, North American ecosystem.

Soil pH has not been explored or identified as a limiting factor for coltsfoot, and this is likely a consequence of the context of the studies. Coltsfoot as a ruderal and agricultural weed abroad occurs where adjacent soils are likely of neutral to basic pH. In GMNP, soils adjacent to coltsfoot populations are predominantly the acidic native soils found as a consequence of peat accumulation in bogs and coniferous litter, both of which occur as a component of the boreal ecosystem.

Coltsfoot does not have the same tolerance for acidic soils in GMNP as has been reported in the literature: in England, Myerscough and Whitehead (1965) successfully germinated coltsfoot at a pH of 4.0, although survival rates were not reported. Coltsfoot's preference for neutral to basic soils does agree with other findings, although the highest pH of 8.3 in the present study falls short of its upper limit of 10.0 in the lime waste dumps reported by Myerscough and Whitehead (1965). It is likely that substrates with a pH of 10 do not occur in GMNP.

Previous research has identified light intensity as a limiting factor in coltsfoot distribution. In GMNP, coltsfoot was found growing at the lowest reading of 2.31μE

$m^{-2} s^{-1}$, and it was found occasionally growing beneath alder (*Alnus* spp.) where the leaves and petioles exhibited the morphology of shade leaves. Bakker (1960) reported stunted growth below 10μE $m^{-2} s^{-1}$, the lowest light reading published for coltsfoot. It is possible that mature coltsfoot is more tolerant of low light levels, at least in the short term, than anticipated. This would allow it to colonize soil disturbances where the canopy is still intact and pH levels are high, although the vigour and survival of subsequent generations may not be guaranteed.

Coltsfoot does not face similar altitudinal limitations in GMNP such as those found by Waltz (1962) on the Gaspé Peninsula. Where it is found at elevations above 150 m in GMNP, it is not enabled by aspect. Waltz's study did not include vegetation types or soil pH above 150 m, the limitations may not be necessarily those of climate changes accompanying increasing elevation. However, coltsfoot was not observed on Big Level at approximately 650 m asl at streams or on animal trails, but soil pH in these disturbances ranged from 3.99-5.2 (Fig. 4.1, transects 145-147).

Rock, sand and gravel have were identified previously as suitable substrates for coltsfoot (Steubing 1948, Ploeg 1950, Waltz 1962, Myerscough and Whitehead 1965, Namura-Ochalska 1987, 1993c). However, the effect of gravel on acidic native soils, and the anthropogenic use of gravel as a factor contributing to the spread of coltsfoot, has only been discovered as a result of this research into the phenomenon of the invasion of coltsfoot in GMNP.

Although coltsfoot rhizome transport assisted by human activities occurs elsewhere, such as the topsoil piles observed in Waterloo, Ontario, (personal observation) it has not been reported in the literature. Dispersal distances under these conditions are limited by the viability time of the rhizome (which is not known) and the depth of burial. Dispersal by dumptruck and other construction equipment is also limited by the economic viability of long distance aggregate or topsoil transport.

In the larger context, this study has contributed to the study of invasive species by analyzing invasion as a function of a change in resources that accompanies disturbance. The approach of using resource shifts and amplifications as described by Fox and Fox (1986), in combination with Bazzaz's (1983) functions of invasion, has proven to be useful and accurate in describing the invasion of coltsfoot in Gros Morne National Park. This demonstrates that invasion is not solely a consequence of the biology of the species, the approach which is often taken in the literature.

The invasion of alien species indicates a resource change in a unit of landscape - particularly parks and nature reserves - different from historic levels. Invasive monocultures may cause trophic cascades and systemic physical feedbacks, but their establishment is only an indication of a change in resources, whose cause may be local or distant, and whose effects may be subtle or obvious, upon which invasive species depend. The nature, type, and origin of the disturbance that is represented by invasion should be investigated and identified if more dramatic changes to native ecosystems are to be effectively addressed.

Knowledge of disturbance types associated with resource changes favourable to coltsfoot will allow GMNP to address their maintenance and construction procedures so as not to further contribute to its expansion (see Appendix VII for management considerations). For example, rhizome-laden gravel should not be transported to sensitive areas adjacent to populations of rare plants. The revegetation of bare quarry rims before they become colonized by coltsfoot will also be useful in limiting propagules available to stockpiles. This may prove to be more effective in controlling coltsfoot compared to implementing biological controls alone.

6.7 Further research

Long-term plot studies of disturbances in GMNP among different vegetation types will determine the role of species replacement as a component of coltsfoot recession, and should track the specific resource changes from undisturbed, to those immediately following the initial disturbance, through early succession. In particular, tracking the fate of rhizome-laden fill would confirm the invasion scenario presented in this study.

An excellent opportunity for long term monitoring of coltsfoot and its effect on rare species is the orchid site where the showy lady's slipper populations (*Cypripedium reginae*) were investigated by Burzynski (1989) and where coltsfoot was absent previous to the upgrading of the Lomond Road (Fig. 4.1, transects 90, 111, 112). *Cypripedium reginae* is a rare plant in Newfoundland and in Canada. Baseline species data exist in Burzynski's (1989) report in addition to data collected for this study. Future data collection should include species, light levels at different times of year, coltsfoot cover and range, soil type and pH. Water quality and quantity should also be investigated as a component of changing resources given the lack of obvious soil disturbance.

Light level measurements in the Lomond orchid site and other field plots would allow for the prediction of coltsfoot's longevity under the reduced light levels of canopies. Comprehensive greenhouse experiments of limiting light levels would also fill this gap in the literature.

The exponential increase of coltsfoot populations is likely to occur in other landscapes undergoing rapid transformation through development by the stockpiling and redistribution of both gravel and topsoil. Where this occurs in jurisdictions where the spread of non-native species is a concern, methods should be investigated to prevent it.

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Appendix I

Survey for the presence of coltsfoot along Highways 430 and 431 in GMNP

map ref.	total kms. surveyed	no. of kms. where coltsfoot absent	UTM ref/ kms. from north boundary	no. of walking checks	kms. from north boundary
St. Paul's Inlet 12 H/13 (Hwy 430)	30	0		6	15,16,17,18,21, 24
Gros Morne 12 H/12 (Hwy 430)	41	1	34 km 283912 Sally's Cove	2	49
Lomond 12 H/5 Robinson's Cpve (north map edge) to south park entrance (Hwy 430)	18	0		2	73, 74
					kms from Hwy 431 entrance
Lomond 12 H/5 (Hwy 431 to Trout River turnoff)	23	0		1	22
Trout River 12 G/8 (NAD 1983) (Hwy 431 Trout River turnoff to s.w. exit)	21	2	184799 39 km Trout River 187792 40 km Trout River	3	27

The extent of roadside colonization by coltsfoot on Highways 430 and 431 was assessed from a car traveling at 80 km/hr. Starting at the flagpole at the north boundary marker of the park and driving south, the presence or absence of coltsfoot was noted in the first 100 m of each measured kilometer. If coltsfoot was not observed from the car in the first 100 m, a walking check of both road sides of that length was undertaken. Location of sections where coltsfoot was absent were noted with a GPS. Walking checks were noted as a kilometer distances from the flagpole at the north park boundary for Highway 430, and from the park entrance on Highway 431.

Of 134 measured kilometers of survey on Highways 430 and 431 (Fig. 1.2) coltsfoot was absent in only three one-km sections. These occurred in the enclaves of Sally's Cove, Trout River, and one km south of Trout River. Although coltsfoot was continuously present along the highway in the north of the park, more walking checks were carried out there than for the central or southern part of the park. Coltsfoot was observed from the roadside survey and other fieldwork to be less abundant in the north of the park than elsewhere.

Appendix II

UTM co-ordinates for transect sites to accompany Figure 4.1

First two digits in series are the transect number, followed by the six digit easting-northing UTM co-ordinate. Easting-northing references are unique within Gros Morne National Park.

01 334 968	29 328 970	56 385 197
02 334 968	30 328 970	57 382 148
03 334 968	31 328 970	58 385 146
04 334 968	32 328 970	59 422 136
05 334 968	33 328 970	60 418 138
06 334 968	34 328 970	61 415 149
07 328 970	35 470 813	62 397 152
08 328 970	36 470 813	63 299 806
09 328 970	37 470 813	64 298 806
10 333 959	38 470 813	65 295 807
11 443 936	39 470 813	66 219 824
12 400 908	40 470 813	67 329 809
13 464 181	41 448 258	68 236 854
14 464 181	42 459 338	69 234 857
15 455 181	42 458 335	70 222 859
16 368 912	43 458 334	71 222 859
17 368 912	44 438 268	72 215 853
18 368 912	45 438 268	73 275 817
19 427 832	46 436 243	74 185 789
20 446 308	47 435 240	75 198 818
21 376 912	48 432 235	76 382 760
22 376 912	49 376 206	77 382 760
23 358 888	50 376 206	78 398 765
24 358 888	51 458 322	79 398 765
25 358 888	52 458 322	80 468 807
26 467 810	53 376 206	81 471 808
27 328 970	54 349 131	82 472 809
28 328 970	55 373 160	83 514 789

84 385 042	118 425 283	152 435 240
85 379 908	119 425 283	
86 379 908	120 299 806	
87 379 908	121 299 806	
88 465 746	122 299 806	
89 465 746	123 327 810	
90 455 765	124 414 915	
91 444 796	125 440 943	
92 333 959	126 333 959	
93 464 181	127 319 948	
94 464 181	128 428 834	
95 427 832	129 368 912	
96 427 832	130 358 888	
97 446 308	131 308 036	
98 467 810	132 467 813	
99 467 810	133 445 311	
100 467 810	134 432 248	
101 467 810	135 377 201	
102 467 810	136 437 269	
103 467 810	137 436 263	
104 467 810	138 382 148	
105 467 810	139 247 832	
106 467 810	140 247 833	
107 379 908	141 216 839	
108 379 908	142 211 849	
109 379 908	143 424 924	
110 379 908	144 402 908	
111 455 765	145 452 058	
112 455 765	146 453 067	
113 198 818	147 452 058	
114 458 322	148 452 058	
115 349 131	149 453 320	
116 397 152	150 459 329	
117 376 206	151 457 329	

Appendix III

Species found in chronic and maturing disturbances

Species are listed for chronic (c) and maturing (m) disturbances. Origin is native (n), introduced (i) or unknown (u). Unknown refers to genera not identified to species where both native and introduced species of the genera are known. Gleason (1968) was the authority used for nomenclature, but updated according to Kartesz (1994).

Disturbance level	Origin	Species	Synonyms (Kartesz 1994)
cm	n	*Abies balsamea*	
cm	n	*Acer spicatum*	
cm	i	*Achillea millefolium*	
cm	n	*Agrostis perennans*	
cm	n	*Agrostis scabra*	
cm	i	*Agrostis stolonifera*	
cm	i	*Agrostis tenuis*	*Agrostis capillaris*
m	i	*Agropyron repens*	*Elytrigia repens* var. *repens*
cm	n	*Alnus crispa*	*Alnus vividis* spp. *crispa*
cm	n	*Alnus rugosa*	*Alnus incana* spp. *rugosa*
m	n	*Alnus* sp.	
cm	n	*Ammophila breviligulata*	
cm	n	*Anaphalis margaritacea*	
m	n	*Angelica atropurpurea*	
c	i	*Anthoxanthum odoratum*	
c	u	*Arenaria stricta*	*Minuartia michauxii* var. *michauxii*
c	n	*Aster nemoralis*	*Oclemena nemoralis*
cm	n	*Aster novi-belgii*	
cm	n	*Aster puniceus*	
c	u	*Aster* sp.	
cm	n	*Betula papyrifera*	
m	i	*Bromus inermis*	
cm	n	*Calamagrostis canadensis*	
cm	n	*Caltha palustris*	
m	n	*Campanula rotundifolia*	
c	n	*Carex disperma*	
c	n	*Carex eburnea*	
cm	n	*Carex flava*	
c	n	*Carex interior*	
cm	n	*Carex nigra*	
cm	u	*Carex* spp.	
cm	n	*Carex stipata*	
c	n	*Carex trisperma*	
cm	i	*Centaurea nigra*	
cm	i	*Cerastium vulgatum*	*Cerastium fontanum* spp. *vulgare*
cm	i	*Chysanthemum leucanthemum*	*Leucanthemum vulgare*

cm	n	*Circaea alpina*	
cm	i	*Cirsium arvense*	
cm	n	*Clintonia borealis*	
cm	n	*Cornus canadensis*	
cm	n	*Cornus stolonifera*	*Cornus sericea* ssp. *sericea*
m	n	*Cypripedium reginae*	
cm	i	*Dactylis glomerata*	
cm	n	*Danthonia spicata*	
m	n	*Drosera rotundifolia*	
m	u	*Dryopteris expansa*	*Dryopteris carthusiana*
m	u	*Dryopteris* sp.	
c	n	*Dryopteris expansa*	
cm	n	*Epilobium angustifolium*	
c	n	*Epilobium ciliatum*	*Epilobium ciliatum* ssp. *ciliatum*
cm	u	*Epilobium* sp.	
cm	n	*Equisetum arvense*	
c	n	*Equisetum palustre*	
cm	n	*Equisetum sylvaticum*	
cm	n	*Euphrasia americana*	*Euphrasia nemorosa*
cm	i	*Festuca rubra*	
cm	n	*Fragaria virginiana*	
cm	n	*Galium triflorum*	
cm	n	*Gaultheria hispidula*	
cm	n	*Geum maculatum*	
c	u	*Glyceria obtusa*	
c	n	*Glyceria striata*	
cm	u	Grass spp.	
cm	n	*Heracleum lanatum*	*Heracleum maximum*
m	i	*Hieracium pilosella*	
cm	i	*Hieracium pratense*	*Hieracium caespitosum*
cm	u	*Hieracium* sp.	
cm	n	*Impatiens capensis*	
m	n	*Iris* sp.	
m	n	*Juncus articulatus*	
cm	n	*Juncus brevicaudatus*	
cm	i	*Juncus effusus*	
cm	n	*Kalmia angustifolia*	
c	n	*Larix laricina*	
cm	n	*Ledum groenlandicum*	
cm	i	*Leontodon autumnalis*	
cm	n	*Linnaea borealis*	
cm	n	*Lonicera villosa*	
cm	i	*Lotus corniculatus*	
c	n	*Luzula campestris*	
cm	n	*Lycopus uniflorus*	
cm	n	*Maianthemum canadense*	
cm	n	*Mitella nuda*	
m	n	*Mentha arvensis*	
c	n	*Moneses uniflora*	
c	i	*Myosotis laxa*	
c	n	*Myrica gale*	

m	i	*Nasturtium officinale*	*Rorippa nasturtium-aquaticum*
c	n	*Nemopanthus mucronatus*	
c	i	*Oenothera biennis*	
c	n	*Osmunda cinnamomea*	
c	n	*Phegopteris connectilis*	
cm	i	*Phleum pratense*	
cm	n	*Picea glauca*	
cm	n	*Pinguicula vulgaris*	
c	n	*Plantago juncoides*	
c	i	*Plantago lanceolata*	
c	i	*Plantago major*	
c	i	*Plantago maritima*	
cm	i	*Poa compressa*	
cm	i	*Poa pratensis*	
c	n	*Populus balsamifera*	
m	i	*Potentilla anserina*	*Argentina anserina*
cm	n	*Potentilla fruticosa*	*Pentaphylloides floribunda*
c	n	*Primula mistassinica*	
cm	i	*Prunella vulgaris*	
c	n	*Pyrola* sp.	
c	n	*Ranunculus abortivus*	
cm	i	*Ranunculus acris*	
cm	i	*Ranunculus repens*	
m	u	*Ranunculus septentrionalis*	
cm	u	*Ranunculus* sp.	
m	n	*Rhamnus alnifolia*	
c	i	*Rhinanthus crista-galli*	*Rhinanthes minor*
m	n	*Ribes lacustre*	
cm	n	*Ribes* sp.	
cm	n	*Rubus idaeus*	
cm	n	*Rubus pubescens*	
m	i	*Rumex acetosella*	
cm	i	*Rumex crispus*	
c	u	*Rumex* sp.	
cm	n	*Sagina procumbens*	
m	n	*Salix discolor*	
cm	n	*Sambucus pubens*	*Sambucus racemosa*
cm	n	*Sanguisorba canadensis*	
m	n	*Senecio aureus*	
m	n	*Senecio pauperculus*	
m	u	*Senecio* sp.	
c	n	*Sisyrinchium montanum*	
c	n	*Sisyrinchium* sp.	
c	u	*Solidago gigantea*	
cm	n	*Solidago hispida*	
cm	n	*Solidago rugosa*	
m	n	*Solidago* sp.	
c	n	*Sorbus americana*	
m	n	*Spiraea latifolia*	*Spiraea alba*
m	n	*Spiranthes romanzoffiana.*	
m	u	*Stellaria* sp.	

cm	i	*Taraxacum officinale*	
cm	n	*Taxus canadensis*	
cm	n	*Thalictrum polygamum*	*Thalictrum pubescens*
m	n	*Thalictrum* sp.	
cm	n	*Trientalis borealis*	
m	i	*Trifolium agrarium*	
m	i	*Trifolium hybridum*	
cm	i	*Trifolium pratense*	
cm	i	*Trifolium repens*	
cm	i	*Trifolium* sp.	
m	u	*Veronica filiformis*	
c	u	*Veronica* sp.	
cm	n	*Viburnum edule*	
cm	i	*Vicia cracca*	
cm	u	*Viola* sp.	

Appendix IV

Variable codes and raw data

SITE (transect number)

PLOT (disturbance level)

1 chronic
2 maturing
3 undisturbed

VEGTYPE: (vegetation type)

1 grassy dunes
2 intertidal saltmarsh
3 sedge fen and bog
4 sphagnum bog
5 riverain thicket and meadow
6 larch scrub
7 black spruce forest and scrub
8 tuckamore
9 heath dwarf scrub
10 balsam fir forest
11 heath lichen tundra
12 serpentine barrens
13 calcareous cliffs
14 settled areas

ALT (elevation)

ASPECT (aspect)

99 flat

DISTYPE (disturbance type)

1 road
2 rehabilitation site
3 ski trail
4 over snow vehicle (osv) trail
5 stream
6 shore
7 slope
8 moose trail
9 hiking trail
10 gravel pit
11 sand dunes
12 cutting blocks
13 hydro right of way
14 insect kill
15 beaver dam
16 beaver cut
17 old garden
28 rehab/moosetrail
45 osv/stream
48 OSV trail/moose trail
49 osv/hiking trail
69 shore/hiking trail
79 slope/trail
89 hiking trail/moosetrail
99 undisturbed
689 shore/moose trail/hiking trail
914 trail/bugkill
1214 bugkill/cutover
5814 stream/moose trail/bugkill
5911 stream, trail, dune
5914 stream/hiking trail/bugkill

DISTAGE (disturbance age)

1 chronic disturbance
99 n/a

COLTCOV (percentage cover of coltsfoot)

0 0
1 >0-5%
2 6-25%
3 26-50
4 51-75%
5 76-100%

PAR photosynthetically active radiation level (microeinsteins)

DELTPAR (relative PAR)

SOILCOMP (soil composition)

1 clay
2 silt
3 sand
4 gravel
5 rock
6 organic
12 clay silt
13 clay sand

14 clay gravel
15 clay rock
16 clay organic
23 silt sand
24 silt gravel
25 silt rock
34 sand gravel
35 sand rock
36 sand organic
45 gravel rock
46 gravel organic
134 clay sand gravel
145 clay gravel rock
345 sand gravel rock

SOILMOIS (soil moisture)
1 dry
2 moist
3 saturated

PH

BAREGRD (percentage bare mineral soil)
0 absent
1 >0-5%
2 6-25%
3 26-50%
4 51-75%
5 76-100%

DUFFCOV (percentage cover of duff)
0 absent
1 >0-5%
2 6-25%
3 26-50%
4 51-75%
5 76-100%

HERBIV (herbivory)
0 no
1 yes
9 missing

FUNGUS (fungus)
0 no
1 yes

SOILGRP (soil group)
1 wholly or partially organic soils
2 wholly or partially gravel
3 other mineral soils

DGRP (disturbance type)

1 road
2 rehabilitation site
3 ski trail
4 OSV trail
5 stream
6 shore
7 slope
8 animal trail
9 hiking trail
10 gravel pit
11 sand dunes
12 clear cut
13 hydro right of way
14 bug kill
15 beaver dam
16 beaver cut
17 old garden
18 multiple disturbances
99 undisturbed

ORIG (disturbance origin)

1 anthropogenic
2 natural
3 multiple

null = no data

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
44	1	1	2	61	5911	1	3	138.00	.00	3	2	7.0	2	0	0	0	3	18	3
149	1	1	null	null	9	1	0	null	null	3	null	null	null	null	null	1	3	9	1
150	1	1	null	null	1	1	0	null	null	3	null	null	null	null	null	1	3	1	1
151	1	1	null	null	11	1	0	null	null	3	null	null	null	null	null	1	3	11	2
134	1	2	null	null	6	1	0	null	null	null	null	null	null	null	null	1	null	6	2
11	1	3	550	99	689	1	1	90.00	.96	34	2	6.6	3	0	0	0	2	18	3
55	1	3	12	104	1	1	2	1470.00	2.07	23	2	7.0	3	0	0	1	3	1	1
90	1	3	60	78	1	1	5	183.00	7.26	134	2	7.3	1	0	1	1	2	1	1
140	1	3	null	null	9	1	0	null	null	null	null	null	null	null	null	1	null	9	1
143	1	3	null	null	15	1	0	null	null	null	null	null	null	null	null	1	null	15	2
146	1	3	null	null	5	1	0	null	null	null	null	5.2	null	null	null	1	null	5	2
147	1	3	null	null	8	1	0	null	null	null	null	5.2	null	null	null	1	null	8	1
118	1	4	null	null	49	1	0	null	null	6	null	4.8	null	null	null	1	1	18	3
119	1	4	null	null	49	1	0	null	null	6	null	6.2	null	null	null	1	1	18	3
3	1	5	110	99	9	1	2	1020.00	34.00	3	2	6.3	2	0	9	0	3	18	3
48	1	5	10	null	5	5	0	10.50	1.00	13	2	6.5	3	0	0	0	3	5	2
149	1	5	10	99	5	5	0	17.10	1.00	3	2	6.9	3	0	0	0	3	5	2
45	1	6	18	99	2	15	3	165.00	.00	3	2	6.5	3	0	0	1	3	2	1
141	1	6	null	null	9	1	0	null	null	null	null	null	null	null	null	1	null	9	1
10	1	7	105	32	1	1	5	1440.00	40.00	4	1	7.0	1	0	1	1	2	1	1
12	1	7	30	198	79	1	2	52.00	36.10	13	3	6.5	0	2	0	0	3	18	3
13	1	7	2	99	5814	1	4	290.00	3.11	6	3	6.5	3	0	1	0	1	18	3
47	1	7	10	99	5	1	4	940.00	54.97	13	2	6.7	0	0	0	1	3	5	2
57	1	7	30	99	9	1	2	54.00	2.68	6	2	6.5	1	0	0	1	1	9	1
92	1	7	105	99	5	1	2	207.00	5.30	12	3	6.4	1	0	0	1	3	5	2
138	1	7	null	null	15	1	0	null	null	null	null	null	null	null	null	1	null	15	2
144	1	7	null	null	15	1	0	null	null	null	null	null	null	null	null	1	null	15	2
49	1	8	8	35	1	1	2	400.00	40.40	34	2	7.0	3	0	0	0	2	1	1
50	1	8	8	99	1	1	1	900.00	576.92	4	2	6.2	0	0	1	0	2	1	1
53	1	8	8	99	9	1	5	1350.00	355.26	34	2	6.9	0	0	1	1	2	9	1
70	1	8	15	342	7	1	5	240.00	.00	4	1	6.8	1	0	1	1	2	7	2
71	1	8	0	330	69	1	2	17.10	.00	45	2	7.0	5	0	0	1	2	18	3
72	1	8	10	356	9	1	5	141.00	.00	34	2	6.8	1	0	1	1	2	9	1
135	1	8	null	null	9	1	0	null	null	null	null	null	null	null	null	1	null	9	1
145	1	8	null	null	8	1	0	null	null	null	null	4.0	null	null	null	1	null	8	1
1	1	10	110	140	9	1	1	47.00	15.16	3	2	7.0	1	0	1	0	3	9	1

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
2	1	10	110	10	3	1	1	870.00	1.24	6	3	6.5	3	0	9	0	1	5	2
4	1	10	110	99	9	1	2	1530.00	14.57	4	1	7.0	2	0	9	0	2	9	1
5	1	10	110	99	9	1	1	7.50	.16	4	2	6.8	2	0	0	0	2	9	1
6	1	10	110	54	9	1	2	13.50	3.33	6	null	5.4	1	0	9	0	1	9	1
7	1	10	80	70	9	1	3	255.00	13.70	46	2	6.8	2	0	9	0	2	9	1
8	1	10	80	270	7	1	null	87.00	5.37	2	2	6.6	2	0	9	0	3	7	2
9	1	10	80	212	914	1	2	null	null	46	2	7.0	1	0	9	0	2	18	3
14	1	10	2	0	45	1	2	450.00	15.50	36	3	6.5	2	0	0	0	1	18	3
15	1	10	1	99	5	1	3	126.00	8.40	34	2	6.8	3	0	0	1	2	5	2
20	1	10	20	99	1	1	3	540.00	94.70	34	2	7.0	3	0	0	1	2	1	1
21	1	10	80	99	8	1	4	2.50	1.08	1	2	6.3	1	0	0	0	3	8	1
42	1	10	10	null	2	12	1	1050.00	276.31	34	2	6.9	5	0	1	1	2	2	1
43	1	10	10	99	9	1	4	1500.00	68.66	23	2	6.2	1	0	0	1	3	9	1
46	1	10	10	99	2	15	3	270.00	15.25	34	null	6.9	0	0	0	1	2	2	1
51	1	10	7	99	28	12	2	600.00	122.44	13	2	6.3	0	0	1	0	3	18	3
56	1	10	12	138	1	1	3	1140.00	271.42	34	2	7.0	2	0	1	1	2	1	1
58	1	10	30	99	9	1	5	1650.00	68.75	6	3	6.8	1	0	0	1	1	9	1
59	1	10	10	6	914	1	4	6.10	.33	6	2	6.5	2	0	1	1	1	18	3
60	1	10	1	0	5914	1	4	1020.00	275.67	3	2	6.6	1	0	0	0	3	18	3
61	1	10	1	332	6	1	2	1230.00	71.92	45	3	6.8	4	0	0	0	2	6	2
67	1	10	50	30	5	1	4	12.90	1.65	1	2	6.2	2	0	0	0	3	5	2
68	1	10	50	348	89	1	1	37.00	1.23	6	3	6.8	3	0	0	0	1	18	3
69	1	10	60	248	9	1	3	38.00	3.95	1	2	5.9	2	0	0	1	3	9	1
74	1	10	50	99	2	11	0	430.00	107.50	13	2	6.2	3	0	0	0	3	2	1
77	1	10	100	175	1	1	2	300.00	18.51	34	2	7.0	5	0	0	0	2	1	1
78	1	10	250	348	1	1	3	192.00	41.70	34	2	6.6	2	0	1	1	2	1	1
80	1	10	10	99	48	1	4	25.20	.00	1	2	6.2	1	0	1	0	3	18	3
82	1	10	60	228	1214	10	1	231.00	57.75	6	3	6.6	3	0	1	1	1	18	3
83	1	10	100	99	9	1	5	126.00	1.27	13	2	6.7	1	0	1	1	3	9	1
84	1	10	320	90	48	1	3	null	null	12	2	null	1	0	0	1	3	18	3
88	1	10	40	55	1	1	5	830.00	15.60	34	2	7.9	1	0	1	1	2	1	1
89	1	10	40	204	5	1	2	285.00	19.38	13	3	7.2	2	0	1	1	3	5	2
93	1	10	2	null	14	2	2	126.00	4.34	6	2	6.5	1	0	1	1	1	14	2
94	1	10	2	99	14	2	1	98.00	2.34	6	2	6.0	0	0	0	0	1	14	2
95	1	10	20	null	16	1	0	42.00	28.57	null	null	6.8	0	3	0	0	null	16	2

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
96	1	10	20	240	4	1	0	15.60	10.61	5	null	7.0	null	null	0	0	3	7	2
125	1	11	null	null	9	1	0	null	null	null	null	null	null	null	null	1	null	9	1
63	1	12	190	110	9	1	2	1410.00	50.00	24	null	6.9	5	0	0	1	2	9	1
64	1	12	180	244	9	1	2	1740.00	1.11	24	null	6.5	4	0	0	0	2	9	1
65	1	12	170	220	1	1	3	2190.00	100.00	4	1	7.0	4	0	0	0	2	1	1
66	1	12	220	167	5	1	1	1560.00	70.27	4	1	6.8	5	0	0	0	2	5	2
73	1	12	150	44	2	1	3	420.00	1.44	34	2	6.9	4	0	0	1	2	2	1
139	1	12	null	null	9	1	0	null	null	null	null	null	null	null	null	1	null	9	1
91	1	13	10	22	7	1	1	255.00	.00	15	2	8.0	5	0	0	1	3	7	2
44	2	1	2	61	99	99	0	87.00	.00	3	2	6.9	2	0	0	0	3	18	3
11	2	3	550	99	99	99	0	168.00	1.80	6	2	5.1	3	0	0	0	1	18	3
55	2	3	12	99	2	11	1	1560.00	2.19	36	2	6.6	1	0	0	0	1	1	1
90	2	3	60	94	99	7	null	228.00	9.04	6	3	7.4	null	null	0	1	1	1	1
111	2	3	60	66	99	7	null	165.00	6.54	6	3	7.0	null	null	0	0	1	1	1
112	2	3	60	79	99	7	1	204.00	8.09	6	3	6.7	1	null	1	0	1	1	1
3	2	5	110	99	99	99	0	1590.00	53.00	6	2	6.4	1	null	9	0	1	18	3
43	2	5	10	null	99	99	0	27.00	1.20	1	2	6.3	3	0	0	0	3	9	1
136	2	5	null	null	2	15	0	null	null	null	null	null	null	null	null	1	null	2	1
10	2	7	105	348	99	99	2	900.00	25.00	4	2	7.0	2	0	0	0	2	1	1
47	2	7	10	99	99	99	0	310.00	18.10	3	2	7.0	4	0	0	0	3	5	2
92	2	7	105	null	99	99	1	600.00	15.38	6	3	6.6	2	0	0	0	1	5	2
124	2	7	null	null	13	19	0	null	null	null	null	null	null	null	null	1	null	13	1
126	2	7	null	null	13	19	0	null	null	null	null	null	null	null	null	1	null	13	1
137	2	7	null	null	12	null	0	null	null	null	null	null	null	null	null	1	null	12	1
49	2	8	8	99	99	99	0	49.00	4.94	13	2	6.3	0	0	0	0	3	1	1
50	2	8	8	99	99	99	0	132.00	84.61	4	2	5.9	0	0	0	0	2	1	1
53	2	8	8	142	99	99	0	14.40	3.78	34	2	6.2	0	0	0	0	2	9	1
70	2	8	15	342	99	99	0	25.80	.00	4	1	6.3	4	0	0	0	2	7	2
71	2	8	0	330	99	99	0	138.00	.00	5	1	7.0	5	0	0	0	3	18	3
72	2	8	10	0	99	99	null	52.00	.00	24	null	6.8	null	null	0	0	2	9	1
142	2	8	null	null	17	15	0	null	null	null	null	null	null	null	null	1	null	17	1
2	2	10	110	99	5	99	0	700.00	47.61	6	2	6.0	0	0	9	0	1	5	2
9	2	10	80	212	99	99	0	156.00	3.18	6	2	6.0	null	null	9	0	1	18	3
13	2	10	2	54	99	99	5	51.00	.56	6	2	6.0	2	0	0	0	1	18	3
16	2	10	75	70	3	2	1	276.00	24.21	134	2	7.0	5	0	1	0	2	3	1

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
17	2	10	75	0	3	2	1	52.00	41.26	14	2	6.9	5	0	0	0	2	3	1
19	2	10	20	99	2	11	0	63.00	42.80	5	2	7.0	3	0	0	0	3	2	1
20	2	10	20	99	2	11	3	14.10	2.47	14	2	6.8	1	0	0	0	2	2	1
22	2	10	80	99	2	11	2	44.00	47.30	13	2	6.5	2	0	0	0	3	2	1
23	2	10	160	296	10	99	3	770.00	106.90	5	2	7.0	4	0	0	1	3	10	1
24	2	10	160	null	10	99	1	430.00	153.57	15	2	6.9	5	0	0	0	3	10	1
25	2	10	160	260	10	99	1	273.00	97.50	25	1	7.0	5	0	0	0	3	10	1
26	2	10	15	280	2	12	2	273.00	.00	3	2	6.8	0	0	0	0	3	2	1
27	2	10	15	88	2	12	2	204.00	.00	3	2	6.5	2	0	0	0	3	2	1
28	2	10	15	28	2	12	2	267.00	.00	3	2	6.5	0	0	0	0	3	2	1
29	2	10	15	108	2	13	4	360.00	.00	3	2	6.5	0	0	0	0	3	2	1
30	2	10	15	278	2	13	3	320.00	.00	3	2	6.6	0	0	0	1	3	2	1
31	2	10	15	187	2	13	3	430.00	.00	3	2	6.4	0	0	0	1	3	2	1
32	2	10	15	365	2	3	5	1.80	.00	3	2	6.9	0	0	0	1	3	2	1
33	2	10	15	258	2	3	1	590.00	.00	3	2	6.9	5	0	0	1	3	2	1
34	2	10	15	207	2	3	5	880.00	.00	134	2	6.4	1	0	1	0	2	2	1
35	2	10	60	325	10	2	0	1050.00	.00	35	null	6.9	5	0	0	0	3	10	1
36	2	10	60	8	10	2	2	1020.00	.00	34	2	7.0	5	0	0	0	2	10	1
37	2	10	60	332	10	2	2	1140.00	.00	34	2	7.0	5	0	1	1	2	10	1
38	2	10	60	156	10	2	2	490.00	.00	34	2	7.0	5	0	0	1	2	10	1
39	2	10	60	85	10	2	1	540.00	.00	34	2	7.0	5	0	0	0	2	10	1
41	2	10	30	121	10	99	3	1710.00	.00	1	2	6.9	3	0	0	1	3	10	1
46	2	10	10	212	null	99	3	370.00	35.23	34	2	6.9	3	0	0	1	2	5	2
48	2	10	10	99	99	99	0	135.00	12.85	34	2	7.0	2	0	0	0	2	5	2
51	2	10	7	99	99	99	0	2.40	.48	13	2	6.2	null	null	0	0	3	18	3
52	2	10	7	138	2	11	0	1440.00	320.00	6	2	6.1	0	0	0	0	1	2	1
54	2	10	20	99	2	11	0	17.10	3.97	1	2	6.4	0	0	0	0	3	2	1
56	2	10	12	99	2	11	0	1320.00	314.28	1	2	6.2	0	0	0	0	3	1	1
58	2	10	30	null	99	99	3	105.00	4.37	6	2	6.7	0	2	1	1	1	9	1
59	2	10	10	99	99	99	0	15.30	.85	6	2	6.2	0	0	0	0	1	18	3
60	2	10	1	null	99	99	0	8.60	2.32	6	3	6.2	0	0	0	0	1	18	3
61	2	10	1	274	99	99	0	1500.00	87.71	6	2	5.9	1	0	0	0	1	6	2
62	2	10	5	99	9	99	1	13.80	.00	6	2	6.9	0	0	0	0	1	9	1
67	2	10	50	96	99	99	1	8.60	1.10	1	2	6.6	4	0	0	0	3	5	2
68	2	10	50	348	99	99	0	32.00	1.06	6	3	6.7	2	0	0	0	1	18	3

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
74	2	10	50	129	99	99	4	330.00	82.50	13	2	6.4	0	0	0	0	3	2	1
76	2	10	100	300	2	11	5	280.00	15.30	1	2	6.1	2	0	1	1	3	2	1
77	2	10	100	99	2	11	1	650.00	40.12	14	2	6.2	2	0	1	1	2	2	1
78	2	10	250	288	2	11	0	120.00	28.08	1	2	6.5	0	0	0	0	3	2	1
79	2	10	250	99	2	11	5	201.00	52.89	13	2	6.6	0	0	1	1	3	2	1
80	2	10	10	99	99	99	4	5.50	.00	1	2	6.2	1	0	1	0	3	18	3
81	2	10	45	99	13	19	3	201.00	14.25	6	2	6.2	0	0	1	1	1	13	1
85	2	10	160	88	10	3	5	102.00	.00	15	2	7.9	1	0	1	1	3	10	1
86	2	10	160	338	10	12	1	141.00	.00	14	2	7.9	5	0	0	1	2	10	1
87	2	10	160	4	10	12	5	207.00	.00	34	2	8.1	1	0	0	1	2	10	1
88	2	10	40	null	2	11	0	960.00	18.11	34	2	7.8	3	0	0	0	2	2	1
89	2	10	40	99	2	11	0	750.00	51.02	34	2	7.0	5	0	0	0	2	5	2
98	2	10	15	280	2	12	0	370.00	.00	35	2	6.8	1	0	0	0	3	2	1
99	2	10	15	88	2	12	1	98.00	.00	3	2	6.5	1	0	0	0	3	2	1
100	2	10	15	28	2	12	2	147.00	.00	34	2	7.0	null	null	0	0	2	2	1
101	2	10	15	108	2	13	2	540.00	.00	3	2	6.7	0	0	0	0	3	2	1
102	2	10	15	278	2	13	0	219.00	.00	3	2	6.6	0	0	0	0	3	2	1
103	2	10	15	187	2	13	1	450.00	.00	3	2	6.6	0	0	1	0	3	2	1
104	2	10	15	365	2	3	0	450.00	.00	3	2	6.8	0	0	0	0	3	2	1
105	2	10	15	null	2	3	0	650.00	.00	3	2	6.8	5	0	0	0	3	2	1
106	2	10	15	207	2	3	4	400.00	.00	13	2	6.4	1	0	1	0	3	2	1
107	2	10	160	214	2	3	0	156.00	.00	6	2	6.0	0	0	0	0	1	2	1
108	2	10	160	272	10	12	2	168.00	.00	145	2	8.1	5	0	0	0	2	10	1
109	2	10	160	134	10	12	3	159.00	.00	23	2	7.9	4	0	0	0	3	10	1
110	2	10	160	96	10	12	4	246.00	.00	14	2	8.3	1	0	0	1	2	10	1
114	2	10	7	null	2	11	3	270.00	60.00	13	2	6.2	0	0	1	0	3	2	1
115	2	10	20	null	2	11	5	1650.00	383.72	12	2	6.6	0	0	1	1	3	2	1
116	2	10	5	99	2	99	3	55.00	.00	3	2	6.5	3	0	0	0	3	2	1
127	2	10	null	null	2	11	0	null	null	null	null	null	null	null	null	1	null	2	1
128	2	10	null	null	2	11	0	null	null	null	null	null	null	null	null	1	null	2	1
129	2	10	null	null	12	2	0	null	null	null	null	null	null	null	null	1	null	12	1
130	2	10	null	null	10	2	0	null	null	null	null	null	null	null	null	1	null	10	1
131	2	10	null	null	2	11	0	null	null	null	null	null	null	null	null	1	null	2	1
132	2	10	null	null	13	19	0	null	null	null	null	null	null	null	null	1	null	13	1
133	2	10	null	null	2	11	0	null	null	null	null	null	null	null	null	1	null	2	1

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
63	2	12	190	null	99	99	0	10.50	.37	36	2	6.5	4	0	0	0	1	9	1
64	2	12	180	50	99	99	0	61.00	.04	4	1	6.9	3	0	0	0	2	9	1
65	2	12	170	0	99	99	0	1740.00	79.40	2	2	6.8	5	0	0	0	3	1	1
66	2	12	220	99	99	99	0	1440.00	64.86	4	2	7.0	5	0	0	0	2	5	2
73	2	12	150	99	99	11	2	360.00	.80	345	2	6.8	5	0	1	0	2	2	1
75	2	12	80	160	10	15	2	69.00	1.76	145	2	6.8	null	null	0	0	2	10	1
113	2	12	80	246	10	15	4	54.00	1.38	123	2	6.8	1	0	0	0	null	10	1
11	3	3	550	99	99	99	0	93.00	1.00	6	3	5.5	0	0	0	1	1	18	3
55	3	3	12	99	99	99	0	710.00	1.00	6	3	6.5	0	0	0	0	1	1	1
123	3	3	null	null	99	99	0	null	null	null	null	null	null	null	null	1	null	99	null
3	3	5	110	99	5	99	0	30.00	1.00	6	3	6.2	1	0	9	0	1	18	3
10	3	7	105	99	99	99	0	36.00	1.00	6	3	6.8	3	0	0	0	1	1	1
12	3	7	30	null	99	99	0	1.44	1.00	6	1	6.4	0	4	0	0	1	18	3
57	3	7	30	99	99	99	0	20.10	1.00	6	3	6.7	2	0	0	0	1	9	1
90	3	7	60	316	99	99	0	25.20	1.00	6	2	5.3	0	4	0	0	1	1	1
92	3	7	105	99	99	99	0	39.00	1.00	6	2	6.0	2	0	0	0	1	5	2
49	3	8	8	99	99	99	0	9.90	1.00	6	2	5.7	0	3	0	0	1	1	1
50	3	8	8	99	99	99	0	1.56	1.00	36	2	6.0	0	5	0	0	1	1	1
53	3	8	8	142	99	99	0	3.80	1.00	13	2	6.5	0	5	0	0	3	9	1
117	3	8	null	null	99	1	0	7.30	null	null	null	null	null	null	null	1	null	9	1
1	3	10	110	140	99	99	0	3.10	1.00	6	2	7.0	1	null	9	0	1	9	1
2	3	10	110	99	5	99	0	14.70	1.00	6	2	5.5	0	0	9	0	1	5	2
4	3	10	110	null	99	99	0	105.00	1.00	6	2	5.4	2	0	9	0	1	9	1
5	3	10	110	99	99	99	0	45.00	1.00	6	2	5.4	1	0	9	0	1	9	1
6	3	10	110	null	99	99	0	6.00	1.00	6	2	5.8	2	0	9	0	1	9	1
7	3	10	80	null	99	99	0	18.60	1.00	6	null	6.8	null	null	9	0	1	9	1
8	3	10	80	270	99	99	0	16.20	1.00	6	2	6.8	0	0	9	0	1	7	2
9	3	10	80	null	99	99	0	49.00	1.00	6	2	6.2	null	null	9	0	1	18	3
13	3	10	2	null	99	99	0	93.00	1.00	6	2	6.7	0	0	0	0	1	18	3
15	3	10	1	null	99	99	0	15.00	1.00	12	2	6.6	2	0	0	0	3	5	2
16	3	10	75	null	99	99	0	11.40	1.00	1	2	6.2	0	5	0	0	3	3	1
17	3	10	75	null	99	99	0	1.26	1.00	6	null	5.5	0	5	0	0	1	3	1
19	3	10	20	240	99	99	0	1.47	1.00	6	null	6.8	null	null	0	0	1	2	1
20	3	10	20	99	99	99	0	5.70	1.00	2	1	6.6	2	0	0	0	3	2	1
21	3	10	80	99	99	99	0	2.31	1.00	6	2	5.8	0	5	0	0	1	8	1

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
22	3	10	80	99	99	99	0	.93	1.00	6	2	6.5	0	5	0	0	1	2	1
23	3	10	160	99	99	99	0	7.20	1.00	6	2	6.2	0	5	0	0	1	10	1
24	3	10	160	null	99	99	0	2.80	1.00	6	2	6.0	0	4	0	0	1	10	1
25	3	10	160	99	99	99	0	2.31	1.00	6	2	6.2	0	5	0	0	1	10	1
42	3	10	10	0	99	99	0	3.80	1.00	13	2	6.5	0	5	0	0	3	2	1
43	3	10	10	99	99	99	0	22.50	1.00	6	2	6.5	0	5	0	0	1	9	1
46	3	10	10	348	99	99	0	17.70	1.00	1	2	5.7	5	0	0	0	3	2	1
51	3	10	7	null	99	99	0	4.90	1.00	6	2	6.2	0	2	0	0	1	18	3
52	3	10	7	99	99	99	0	4.50	1.00	23	1	6.6	0	5	0	0	3	2	1
54	3	10	20	110	99	99	0	4.30	1.00	6	2	6.4	0	5	0	0	1	2	1
56	3	10	12	0	99	99	0	4.20	1.00	6	2	6.5	0	5	0	0	1	1	1
58	3	10	30	99	99	99	0	24.00	1.00	6	2	6.6	1	0	0	0	1	9	1
59	3	10	10	20	99	99	0	18.00	1.00	6	2	6.4	0	2	0	0	1	18	3
60	3	10	1	null	99	99	0	3.70	1.00	6	2	6.5	1	0	0	0	1	18	3
61	3	10	1	262	99	99	0	17.10	1.00	6	1	6.8	0	0	0	0	1	6	2
67	3	10	50	20	99	99	0	7.80	1.00	1	2	5.8	0	2	0	0	3	5	2
68	3	10	50	null	99	99	0	30.00	1.00	6	2	6.4	3	0	0	0	1	18	3
69	3	10	60	99	99	99	0	9.60	1.00	6	2	6.2	0	0	0	1	1	9	1
74	3	10	50	116	99	99	0	4.00	1.00	36	2	6.5	5	0	0	0	1	2	1
76	3	10	100	200	99	99	0	18.30	1.00	1	2	6.6	0	4	0	0	3	2	1
77	3	10	100	175	99	99	0	16.20	1.00	6	2	6.0	0	5	0	0	1	2	1
78	3	10	250	194	99	99	0	4.60	1.00	16	2	6.2	0	3	0	0	1	2	1
79	3	10	250	180	99	99	0	3.80	1.00	6	2	6.3	0	5	0	0	1	2	1
81	3	10	45	99	99	99	0	14.10	1.00	6	2	5.5	2	0	0	0	1	13	1
82	3	10	60	99	99	99	0	4.00	1.00	6	2	5.2	0	3	0	0	1	18	3
83	3	10	100	0	99	99	0	99.00	1.00	6	2	6.8	0	0	0	0	1	9	1
84	3	10	320	90	99	99	0	null	null	6	2	null	1	0	0	0	1	18	3
88	3	10	40	99	99	99	0	53.00	1.00	6	2	5.5	0	3	0	0	1	2	1
89	3	10	40	99	99	99	0	14.70	1.00	6	2	5.5	0	1	0	0	1	5	2
93	3	10	2	99	99	99	0	29.00	1.00	23	2	6.2	1	0	0	0	3	14	2
94	3	10	2	99	99	99	0	41.00	1.00	6	2	5.2	2	0	0	0	1	14	2
97	3	10	20	null	99	99	0	2.76	1.00	1	2	6.3	0	4	0	0	3	4	1
148	3	11	null	null	99	99	0	null	null	null	null	4.8	null	null	null	1	null	99	null
63	3	12	190	164	99	99	0	28.20	1.00	23	2	6.7	4	0	0	0	3	9	1
64	3	12	180	50	99	99	0	1560.00	1.00	5	2	7.0	5	0	0	0	3	9	1

SITE	PLOT	VEGTYPE	ALT	ASPECT	DISTYPE	DISTAGE	COLTCOV	PAR	DELTPAR	SOILCOMP	SOILMOIS	PH	BRGRD	DUFFCOV	HERBIV	FUNG	SOILGRP	DGRP	ORIG
65	3	12	170	25	99	99	0	21.90	1.00	6	2	6.2	0	0	0	0	1	1	1
66	3	12	220	99	99	99	0	22.20	1.00	6	2	6.9	3	0	0	0	1	5	2
73	3	12	150	99	99	99	0	290.00	.00	1	2	6.6	3	0	0	0	3	2	1
75	3	12	80	180	99	99	0	39.00	1.00	1	2	5.6	0	0	0	0	3	10	1
120	3	12	null	null	99	99	0	null	null	null	null	6.8	null	null	null	1	null	99	null
121	3	12	null	null	99	99	0	null	null	null	null	6.2	null	null	null	1	null	99	null
122	3	12	null	null	99	99	0	null	null	null	null	5.8	null	null	null	1	null	99	null

Appendix V

Mean daily temperatures and rainfall at Cow Head, Gros Morne National Park, Newfoundland, August 7-29,1997

AES Station ID# 8401335

day of month (August 1997)	max. temp. (C)	min. temp. (C)	mean temp. (C)	rainfall (mm)
7	18.5	6.0	12.3	4.6
8	16.0	12.0	14.0	0.0
9	20.0	10.5	15.3	2.6
10	19.0	10.0	14.5	2.0
11	21.0	14.5	17.8	0.0
12	20.0	14.5	17.3	5.0
13	13.0	9.0	11.0	0.8
14	16.5	9.0	12.8	1.4
15	18.0	11.5	14.8	0.0
16	20.0	10.0	15.0	4.0
17	16.5	12.0	14.3	17.8
18	17.0	11.0	14.0	0.8
19	13.0	7.0	10.0	0.0
20	16.5	3.0	9.8	0.0
21	18.0	6.5	12.3	0.0
22	18.5	5.5	12.0	0.0
23	17.0	8.5	12.8	15.8
24	17.5	10.0	13.8	11.8
25	18.5	11.5	15.0	0.8
26	17.0	13.0	15.0	0.0
27	17.0	10.5	13.8	0.0
28	19.0	11.0	15.0	3.2
29	20.0	13.0	16.5	1.0
		monthly total		71.60
		daily mean	13.85	3.11

Appendix VI
Standard error tables for Figures 5.8-5.11

Disturbance type	Fig. 5.7 % coltsfoot		Fig. 5.8 % bare ground		Fig. 5.9 pH		Fig 5.10 relative PAR	
	mean	*SE*	*mean*	*SE*	*mean*	*SE*	*mean*	*SE*
road	3	0	2	0	7.0	0.1	109.87	52.08
rehabilitation site	2	0	1	0	6.6	0.1	78.29	31.79
ski trail	1	0	5	0	7.0	0.0	32.74	8.52
stream	2	0	2	1	6.7	0.1	23.03	10.61
shoreline	2	n.v.	4	n.v.	6.8	n.v.	71.92	n.v.
slope	3	2	3	2	7.4	0.6	n.v	n.v.
animal trail	4	n.v.	1	n.v.	6.3	n.v.	1.08	n.v.
hiking trail	3	0	2	0	6.6	0.1	45.89	26.69
gravel pit	2	0	4	0	7.3	0.1	72.22	30.37
hydro r.o.w.	1	1	0	n.v.	6.2	n.v.	14.25	n.v.
insect kill	2	1	1	1	6.3	0.3	3.34	1.00
multiple	2	0	2	0	6.6	0.1	54.71	27.31

n.v. = no value

Appendix VII

Considerations for active management of coltsfoot in GMNP

The distribution of gravel is associated with anthropogenic disturbance and enables much of the colonization of coltsfoot. Management decisions that enabled the spread of coltsfoot could also limit or discourage it. Similarly, the sites in which coltsfoot is abundant - at roadsides, quarries and in enclaves - are not habitats of concern for the maintenance of biodiversity, but these dense populations serve as seed sources for the wind borne colonization of more remote natural disturbances. Quarry stockpiles, in particular, promote the spread of coltsfoot through rhizome dispersal that may be a more successful reproductive strategy. Control of coltsfoot through restoration of quarries in particular may be effective in restricting the spread of coltsfoot into remote areas.

Anions (1993) lists 28 aggregate extraction sites in and around GMNP, 18 of which are unsuitable for further development, while 5 are suitable for limited production and 5 for full development. Rocky Barachois, Cod Knox (Fig. 3.3), and deposits in Glenburnie, the Lomond Valley and Trout River (Fig. 3.1) are designated for full development for parks purposes, although no new sites will be developed within the park. Future aggregate material will be obtained outside park boundaries (Parks Canada 1996).

Demand for aggregate within the park over the next 50 years is estimated to be a million cubic meters (Anions 1993). Park policy requires the rehabilitation of quarries, and that an Environmental Assessment and Review Process (EARP) be applied to all plans, projects and developments, including aggregate development

(Anions 1993). However, insufficient funds have been available for adequate restoration efforts, contrary to management directives that "no extractive activity shall proceed unless financial resources for rehabilitation have been identified" (Parks Canada 1996, p. 40).

Control of coltsfoot should be included in the EARPs of aggregate removal and quarry rehabilitation. In all the quarries sampled or observed in the park, coltsfoot was abundant on the mineral slopes on the periphery of the excavations. Possible remediation could include the immediate topsoiling and seeding of quarry rims with competitive native species which would exclude coltsfoot. For example, a visible east-facing rim of the Cod Knox Quarry was topsoiled and seeded around 1994 with non-native *Trifolium* sp. and grass. The forbs have taken successfully and provide slope stability as well as aesthetic improvement over the former bare rim. Coltsfoot is absent from this rehabilitation site. Until measures have been taken to eliminate coltsfoot from quarries, gravel for trail maintenance and construction should not be brought into sensitive areas.

While the proliferation of exotic species is not seen as desirable in National Parks, coltsfoot does perform the function of stabilizing slopes, (including erosion caused by trail use such as at Green Gardens, Fig. 4.1 transect 70), and colonizing disturbances inhospitable to many other species. However, while coltsfoot may be replaced by native species over time, the natural rate of replacement may be too slow for management objectives. Ecological restoration of quarries would not only control the spread of propagules, but encourage vegetation types more desirable for a national park. Native diversity will be increased through the creation of habitat, and protected by the containment of coltsfoot.