RESEARCH ARTICLE

Disturbance-enabled Invasion of *Tussilago farfara* (L.) in Gros Morne National Park, Newfoundland: Management Implications

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ABSTRACT: The recent invasion of the exotic weed *Tussilago farfara* L. (coltsfoot) in Gros Morne National Park (GMNP) Newfoundland, Canada, was examined to determine which resource changes accompanying disturbance enabled population expansion. Resource levels reflecting environmental variables are defined here as the abiotic components of the environment used by plants. The environmental variables of pH, soil moisture, soil type, duff cover and photosynthetically active radiation were measured in 17 disturbance types of natural and anthropogenic origin – notably hiking trails, roads, gravel quarries, shorelines, slopes, hydro corridors, and forests killed by spruce budworm – and across a gradient from disturbed to undisturbed in 12 vegetation types. Balsam fir forest comprises 36% of the park and has the highest number of disturbance types.

Disturbances favoring *Tussilago* 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 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.

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

Not all disturbance types present resource levels favorable for *Tussilago* establishment. However, resource levels associated with some disturbance types of anthropogenic origin indicate that aggregate quarry management practices have unintentionally enabled the invasion of *Tussilago* in GMNP. Control of invasive vegetation can be addressed by identifying disturbance-related plant resource shifts that may have been caused by policies and procedures under local control.

Index terms: aggregate, disturbance, invasive species, national parks, Newfoundland, *Tussilago farfara*

INTRODUCTION

The exotic ruderal weed *Tussilago farfara* L. (coltsfoot) invaded Gros Morne National Park (GMNP), Canada, (Figure 1) when a high-density population moved into an area of previously low density. This invasion began in 1973 when the park opened to the public (Bouchard et al. 1978) and it occurs nowhere else in Newfoundland in such densities except between the park and Channel-Port aux Basques, where the ferry arrives from mainland Canada (Figure 1). The profile of *Tussilago* has been raised in recent years as the jurisdictions in which it has been declared an invasive species or noxious weed grows, including Tennessee (Tennessee Exotic Pest Plant Council 2001), Ontario, Canada (Ontario 1990, Havinga et al. 2000), Connecticut, Maine, North Carolina, and New Jersey, as well as in three American national parks: Acadia, Blue Ridge Parkway and Great Smokey Mountains National Park (Plant Conservation Alliance website).

The maintenance of ecological integrity is the paramount principle guiding all National Parks in Canada (Parks Canada 1996, Woodley 1996), and is defined as "a condition where the structure and function of an ecosystem are unimpaired by stresses induced by human activity and are likely to persist" (Parks Canada 1996). This study was undertaken to assess whether or not *Tussilago* would replace native species and compromise the integrity of the vegetation communities in GMNP.

The approach taken here follows Bazzaz (1983) who maintained that botanical invasion is a function of the biology of the species, the receiving environment, and the nature of disturbance. Bazzaz 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." Similarly, Fox and Fox (1986) described disturbance as a resource amplification or resource shift (concluding that there is no invasion without disturbance) with a trend to greater invasion with more prolonged, repeated, or more intense disturbance. More recently, Davis et al. (2000) have also proposed a general theory of invasibility based on fluctuating resources. They have embraced Lonsdale's (1999) concept that invasibility results from a combination of propagule pressure (the availability of seeds or other

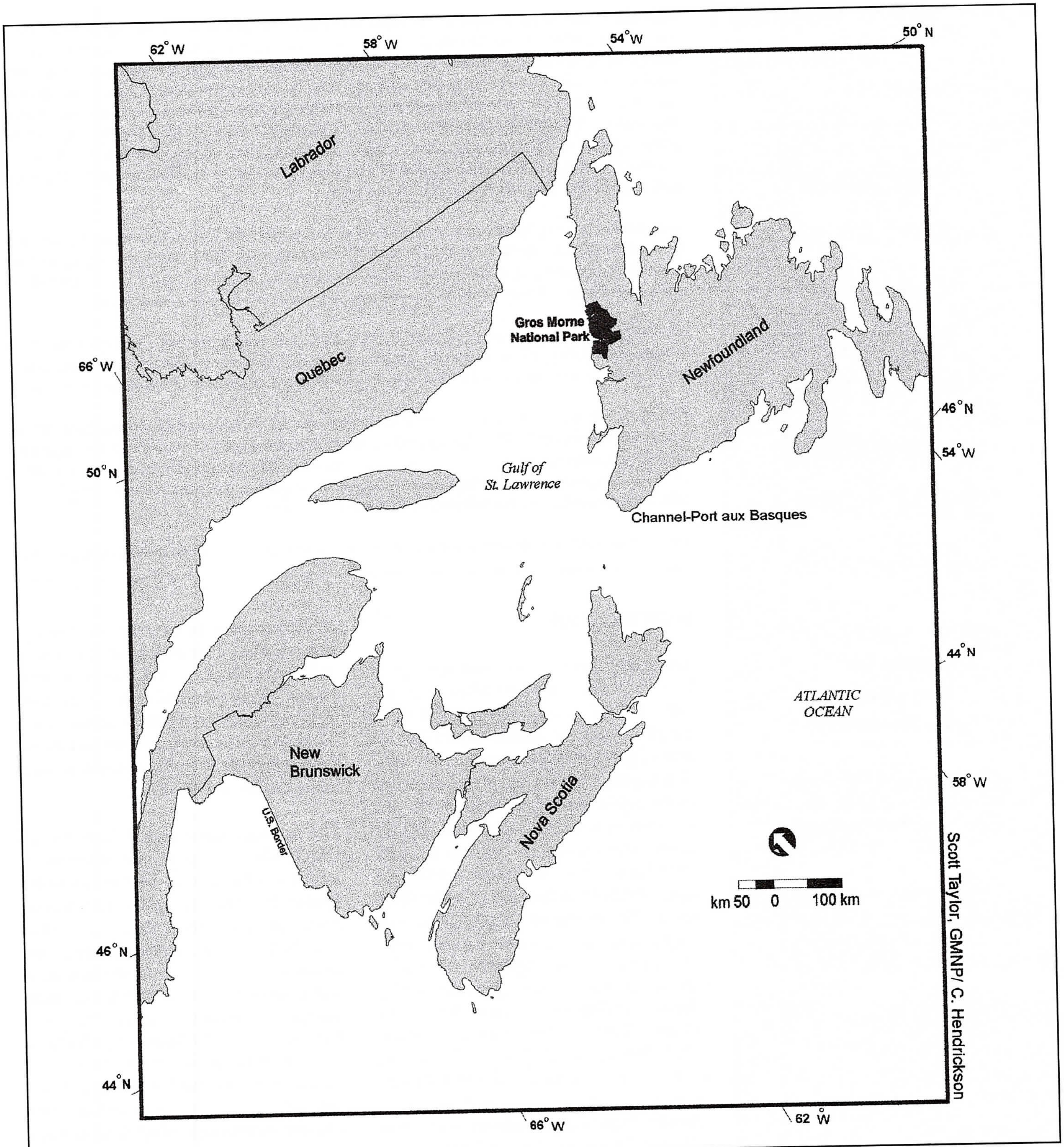

Figure 1. Gros Morne National Park in the Atlantic Region of Canada.

reproductive structures), the characteristics of the new species (Bazzaz's "biology of the species"), and an area's inherent invasibility, defined as a combination of factors including climate, disturbance regime, and competitive abilities of resident species (Bazzaz's "receiving environment").

In ecosystems that are explicitly driven by disturbance, recruitment of native species has been explored using a similar approach to that used in this study and as set out by Davis et al. (2000). For example, Rowe (1978) examined the frequency, intensity, and extent of forest fires in combination with the biological strategies of native boreal species to predict the direction of succession after fires and to reconstruct fire history. Similarly, for wetland ecosystems subject to fluctuating water levels, Van der Valk (1981) has constructed the environmental sieve model to explain wetland succession. He proposed that when species are classified according to potential life span, propagule longevity, and establishment requirements, wetland environmental factors compose the sieve that selects some species and excludes others for recruitment.

Disturbance is defined here as a sudden change in resources, where resources are the abiotic components of the environment used by plants. The hypothesis to be tested is that a resource shift has occurred to enable the invasion of *Tussilago* in GMNP. Selected resources across disturbance types were quantified and correlated with the presence of *Tussilago* and were compared to those found in undisturbed vegetation communities as an indicator of their invasibility. Resource levels among different natural and anthropogenic disturbance types were compared to determine if some types were more favorable to *Tussilago* than others and, if so, whether they were associated with park activities, given the coincidence of its invasion with park development.

DESCRIPTION OF STUDY AREA

Gros Morne National Park covers 1805 km^2, divided topographically into the settled Coastal Plain below 150 m above sea level (asl) and the more remote Alpine Plateau between 450 and 800 m asl (Figure 2).

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 (Figure 2) 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 favorable sites on the outer coast (Banfield 1988). Annual average precipitation on the Coastal Plain is approximately 1200 mm increasing approximately 207 mm for each 100 m rise in elevation (Banfield 1988).

Bedrock geology consists 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). The most unusual constituent of the geology is the exposure of peridotite, characterized by naturally occurring phytotoxic heavy metals on the Tablelands (Figure 2). Other soils in the park are imperfectly drained acidic, humo-ferric Podzols, formed by the influence of the parent material, humid to perhumid climate, and coniferous vegetation (Clayton et al. 1977).

Pleistocene glacial landscapes 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, riverbanks, deltas, and flood plains (Bouchard et al. 1991).

The vascular flora of GMNP contains 727 species of which 96 are considered provincially rare, while 10 are rare in Canada (Anions 1994). The park lies entirely within the Boreal Forest Region of Canada with 70% of the vascular flora of the park characteristic of this boreal region (Anions 1994). Twelve vegetation types (grassy dunes, intertidal salt marsh, sedge fen and bog, sphagnum bog, riverain thicket and meadow, larch scrub, black spruce forest and scrub, tuckamore (krummholz), heath dwarf-scrub, balsam fir forest, heath-lichen tundra, and serpentine barrens) have been identified and mapped in the park (Bouchard and Hay 1992), each described and identified by a minimum of three indicator species.

Gros Morne gained national park status in 1973 and the development of park infrastructure, including the upgrading of the main highways, occurred from the late 1970s through to the early 1980s. Settlement areas as well as recreational facilities are concentrated on the Coastal Plain, along with the main highways, which connect north and south ends of the park. It became a UNESCO World Heritage Site in 1987, based on the park's geological wealth, dramatic glacier-carved landscapes, biological diversity, and its 4500-year history of human habitation.

BIOLOGY OF *TUSSILAGO FARFARA*

The production of rhizomes and the ability to withstand erosion or deposition of substrates are key biological features contributing to the success of *Tussilago* in GMNP. *Tussilago* is a species whose short-lived diaspores (<5 months, Namura-Ochalska 1987) 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. *Tussilago* faces less competition on low nutrient sites where the production of rhizomes is favored over flowers (Ogden 1974). Once established, *Tussilago* can quickly dominate a site through radial extension of rhizomes, which can reach up to 2.5 m in the second year (Bakker 1960, Ogden 1974). Vegetative rather than sexual reproduction enables a successful genotype to saturate a favorable site (Korshikov et al. 1994, Brown and Burdon 1987).

Tussilago is well adapted to withstand unstable substrate levels caused by ongoing physical disturbance. Morphological adaptations include: (1) rhizome buds at various depths, (2) the emergence of vegetative shoots less than a few millimeters above the soil to avoid breakage (Myerscough and Whitehead 1967), and (3) variability in the location of the flower bud above or below the soil surface (Waltz 1962).

Tussilago reproduces successfully through the fracturing of brittle rhizomes that occurs during soil disturbance (Bostock and Benton 1979; Namura-Ochalska 1993b, 1993c; Leuchs 1961). Ogden (1974) has observed a mean number of 102 nodes per plant after two years, and Leuchs (1961) reported that a rhizome buried in compost

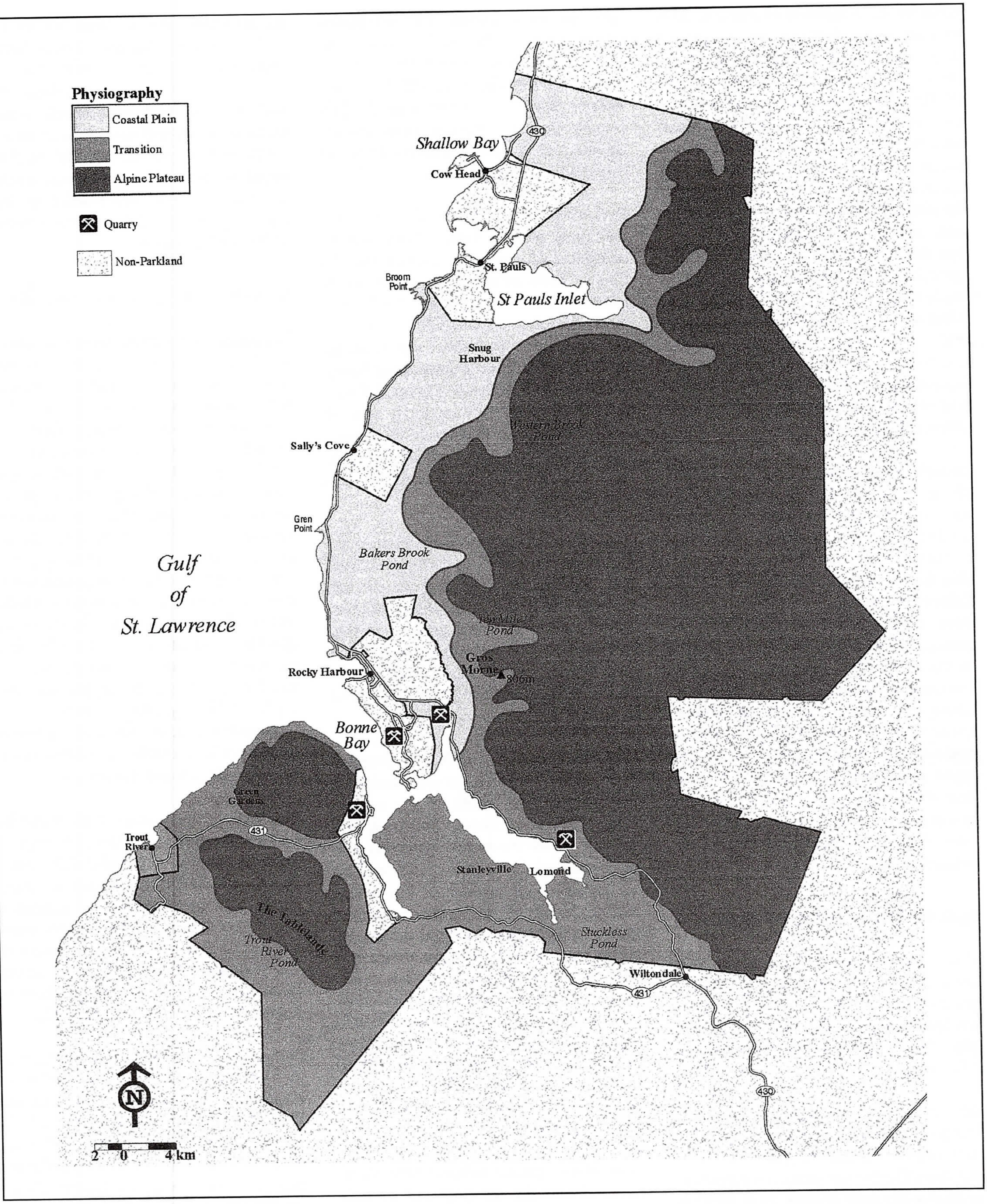

Figure 2. Physiography, Settlements and Major Roads in Gros Morne National Park, Newfoundland, Canada.

soil 75 cm below ground level in September emerged by the following March. Disturbance that mitigates competition and promotes clonal reproduction is necessary for the persistence of *Tussilago* (Namura-Ochalska 1993a).

Tussilago thrives in conditions of physical disturbance, and the literature indicates that it is a poor competitor as succession progresses (Bakker 1960; Namura-Ochalska 1988, 1989). Given this, and assuming that shifting resources enable invasion, this study focused on measuring the resources in certain disturbances in which *Tussilago* was found and comparing them to nearby undisturbed vegetation. In order to determine whether or not *Tussilago* invasion had been enabled by "stress induced by human activity" (Parks Canada 1996), disturbances were grouped according to natural or anthropogenic origin.

METHODS

We categorized disturbance in terms of "type," "origin," and "level." Disturbance types are distinctive patterns of physical alterations to the landscape, such as roads and active slopes. Seventeen different disturbance types were recognized and these are grouped by origin. Anthropogenic disturbance types are those that are directly associated with intentional human activity, such as gravel pits and roads. Natural disturbance types occur as the result of predominantly physical or biological (other than human) processes, such as insect kills (forests killed by spruce budworm) and unstable dunes. Some disturbances clearly had multiple origins, such as combined moose and hiking trails, and they are grouped separately as multiple disturbances.

A non-random sampling strategy was chosen in order to measure resources associated with the presence of *Tussilago*. Disturbance types and locations were identified from park reports and personnel, and they were plotted on vegetation maps at a scale of 1:50,000 (Bouchard and Hay 1992). These vegetation types represent the "receiving environment" according to Bazzaz's framework. All vegetation types in GMNP were sampled or observed except heath dwarf scrub which was not sampled due to time constraints, inaccessibility of backcountry locations, and its minor occurrence (0.5% of GMNP). *Tussilago* was rarely encountered in grassy dunes, sphagnum bog, and tuckamore; and this is reflected in the small number of quadrats sampled in these vegetation types. Disturbance locations were the starting point for study transects.

"Disturbance level" refers to one of three $1 m^2$ sampling quadrats along a transect representing a gradient of disturbance from chronic, to maturing, to undisturbed vegetation. The first quadrat represented chronic disturbances such as roadsides, trails, and slopes, which are subject to changing resources (particularly those accompanying soil disturbances) once or more annually. Here the vegetation type was not forested.

The third quadrat – the undisturbed control plot which terminated the transect – was determined by the presence of trees, moss layer, or species indicators. Eight of the 12 vegetation cover types are described by woody vegetation and one by mosses, indicating an absence of recent soil disturbance. Grassy dunes, intertidal salt marsh, and sedge fen and bog have as their indicators several herbaceous grasses and sedges previously identified and described by botanists (Bouchard and Hay 1992); and the indication of two or more of these species was also deemed to indicate the absence of recent soil disturbance.

Maturing disturbances in named vegetation types associated with each disturbance type had neither an ongoing physical disturbance nor the presence of trees, moss layer, or species indicators of the vegetation type. Quadrats were placed on *Tussilago* if it was present midway between quadrats one and three, or, if absent, simply at midpoint in order to sample the environmental variables associated with this intermediate zone.

Ideally, each transect had a quadrat with a representative disturbance level (chronic, undisturbed, maturing); however, once in the field, transects did not always fit this ideal. As a result, some disturbance types were characterized by only two of the three disturbance types. For example, the disturbance type labeled "rehabilitation site" was drawn from a document listing sites that were regraded after road access changes. On site, these disturbances clearly had no ongoing chronic disturbance, but they were excellent examples of datable, maturing disturbances. As a result, rehabilitation sites were characterized by the maturing and undisturbed pair only. In other disturbance types, such as moose/animal trail, there was no gradient between chronic and undisturbed quadrat (e.g., where a well-used trail was immediately surrounded by mature, boreal vegetation). Therefore, these transects were characterized by these two gradients only.

Resource levels measured in each quadrat were: photosynthetically active radiation (PAR), soil particle size, soil pH, soil moisture, percent bare ground, and duff cover. PAR was measured at the upper leaf surface with a LiCor photometer in units of $\mu E\ m^{-2}\ s^{-1}$. Absolute values of PAR were recorded for each quadrat at each disturbance level. To eliminate the effect of variable cloud cover during data collection, PAR readings for quadrats in chronic and maturing disturbance levels were converted to a relative measure of the undisturbed quadrat in each transect, and are referred to as relative PAR.

Some resources, such as pH, are more accurately a proxy or measurement for actual resources that become available or limiting as are a function of soil pH. However, to be consistent with previous studies in invasion biology (Bazzaz 1983, Fox and Fox 1986, Lonsdale 2000), the environmental variables measured and described above will be referred to as "resources."

Tussilago was frequently found growing on various types of inorganic substrates. For this analysis, substrates were grouped into three descriptive categories: (1) gravel/aggregate (coarse aggregate larger than 5 cm in diameter; and gravel composed of granite, shale and peridotite between 0.05 and 5 cm in diameter); (2) organic (greater than 2 cm thickness of organic material (including moss), the seeding depth of *Tussilago* (Namura-Ochalska 1987)); and

(3) mineral soils. Gravel/aggregate size represents sorting for specific purposes by the Park and was grouped together to examine the relationship between the introduction of gravel and the presence of *Tussilago*.

Soil pH was measured using a Kelway soil acidity meter (which measures a range of 3.5-8.0) inserted into the substrate to a depth of approximately 6 cm. From 5-10 cm below the surface, approximately 10 ml of soil was retrieved and described as saturated if water could be squeezed from the sample, moist if it contained water but not to the point of saturation, or dry if moisture could not be seen or felt. For gravel substrates, visible moisture was judged as moist, while non-visible moisture was considered dry. Because sampling of soil moisture took place over the month of August, results are presented in the context of the precipitation record for this period.

Percent bare ground and percent cover of duff and *Tussilago* were estimated using the Braun-Blanquet scale (Kent and Coker 1992). This method is commonly used for percent cover of vegetation, but when used to estimate bare ground in a quadrat, high values indicate little vegetation cover. Duff consists of deciduous or coniferous leaf litter.

Spearman's rank correlation coefficients were generated for *Tussilago* abundance and individual resource variables (α=0.01). Variation in resource levels among the three levels of disturbance (chronic, maturing, and undisturbed) and between natural and anthropogenic disturbances were tested using Kruskal Wallis nonparametric ANOVA.

Nominal data for the three substrate types (organic, gravel, mineral) were analyzed separately to show whether certain disturbances were characterized by distinctive substrates. The percent occurrence of each substrate type was calculated for each of the three levels of disturbance – between anthropogenic, natural and multiple disturbances and between disturbance types. Box and whisker plots show median, interquartile range, and extreme values of pH associated with different substrates. The relationship between substrate, 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.

RESULTS

The data set consists of 153 transects, comprising 253 quadrats, 84 of which were chronic disturbances, 100 maturing disturbances, and 69 undisturbed (Table 1). 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 represented the highest number of quadrats in the natural disturbance category (n=24, total natural n=47), followed by slopes (n=6) and sand dunes, animal trails, beaver dams, beaver cut, and insect kills (n<4 each). Multiple disturbances made up 39 quadrats.

Tussilago abundance is significantly correlated with increasing pH (r_s = 0.371) and light level (r_s = 0.546), but negatively correlated with duff cover (r_s = 0.378; Table 2). The strongest correlation shown here is related to light levels as a direct result of disturbance. While there are also correlations with pH, the weaker correlation indicates wider amplitude of tolerance. *Tussilago* is abundant in disturbances where overstory vegetation has been cleared leaving an open site, and where soil disturbance has removed 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. 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 (Table 2). Undisturbed sites where *Tussilago* was absent are characterized by greater shade, more duff cover, more acidic substrates, and less bare ground – all of which are a function of a well developed vegetation layer.

Soil moisture was determined over a 23-day period, 14 of which experienced rain (total precipitation 71.6 mm), and moist soil was the dominant category in all disturbance levels. Moist soil was present in 83.3% of all quadrats sampled, while 10.3% were saturated, and 6.4% were dry. Given the high percentage of quadrats containing moist and saturated substrates (total = 93.6%) and the regular occurrence of precipitation in August, inadequate moisture for *Tussilago* germination does not appear to be a limiting factor in GMNP.

There is a significant difference among disturbance levels for both pH (x^2=38.824, p<0.001) and percent cover of *Tussilago* (x^2=113.354, p<0.001; Table 3). As a calciphile, soil pH may be the most important limiting factor for *Tussilago* (Myerscough and Whitehead 1965, 1967).

pH is closely associated with gravel substrates (mean=7, Figure 3). Organic substrates typically have the lowest range of pH (mean=6.2), while mineral substrates are slightly acidic to neutral (mean=6.6). Gravel substrates dominate almost 50% of chronic disturbances (Figure 4), but were absent in undisturbed quadrats. Mineral soils were present in almost 50% of maturing disturbances, whereas organic substrates dominate almost 80% of undisturbed quadrats (Figure 4).

When natural and anthropogenic disturbance types are compared, there is no significant difference in physical (pH and relative PAR) and biotic (percent cover of *Tussilago*, percent cover of duff, and percent bare ground) variables (Table 4). Although aggregate substrate is present in most disturbances, it dominates anthropogenic disturbances (Figure 5). Bedrock aggregate (artificially crushed stone) dominates roads and ski and hiking trails, where it is used for construction and maintenance, as well as gravel pits, where maintenance stockpiles originate (Figure 6). Granular aggregate (material crushed by ice or water) dominates streams, slopes, shorelines, and other disturbances of natural origin (Figure 6).

Organic substrates dominate undisturbed sites, and occur exclusively in hydro rights-of-way and forest insect kills (Figure 6). In these disturbances, the canopy is removed,

Table 1. Disturbance types categorized according to natural, anthropogenic, or multiple origin, disturbance level, and disturbance age. Numbered vegetation types 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, 10. balsam fir forest, 11. heath lichen tundra, 12. serpentine barrens, 13. calcareous cliffs. Vegetation cover names and numbers after Bouchard and Hay (1992).

			Number of quadrats			
Origin and type	**level**	**vegetation type**	**chronic**	**maturing**	**undist.**	**total**
Anthropogenic						
road	chronic	1, 3, 5-8, 10, 12	13	9	7	**29**
hiking trail	chronic	1, 3, 5-8, 10-12	20	7	14	**41**
snow vehicle trails	chronic	10	0	0	0	**0**
gravel pit	maturing	10, 12	0	18	4	**22**
cross-country ski trail	maturing	10	0	2	2	**4**
forest cut blocks	chronic	10	0	2	0	**2**
rehabilitated sites	maturing	3, 5, 6, 10, 12	5	39	14	**58**
abandoned garden	maturing	8	0	1	0	**1**
hydro right of way	maturing	7, 10	0	4	1	**5**
Natural						
shoreline	chronic	2, 10	2	1	1	**4**
slope	chronic	8, 10, 13	4	1	1	**6**
stream	chronic	5	10	8	6	**24**
sand dune	chronic	1	1	0	0	**1**
moose/animal trail	chronic	3, 8, 10	3	0	1	**4**
beaver dam	chronic	3, 7	3	0	0	**3**
beaver cut	maturing	10	1	0	0	**1**
insect kill	chronic	10	2	0	2	**4**
Multiple	chronic	1-4, 7, 8, 10	17	11	11	**39**
Undisturbed (pH only):		3, 11, 12	0	0	5	**5**
Total			**84**	**100**	**69**	**253**

but the native soils are left intact. Unlike other anthropogenic disturbances, bedrock aggregate is not added.

DISCUSSION

Resource levels are significantly different in disturbed environments where *Tussilago* occurs vs. an undisturbed environment in which *Tussilago* is absent. Based on our results, undisturbed vegetation will not be invaded. 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 cover increases, light levels lower and, in the case of conifer development, soils acidify with the increasing duff layer. These resource levels are unsuitable for *Tussilago* (yet suitable for competing species), and should cause *Tussilago* to decline over time.

Both anthropogenic and natural disturbances provide suitable conditions for *Tussilago* colonization. In the case of natural disturbance environments such as slopes, streams, and shorelines where *Tussilago* is present, resource levels reflect chronic disturbances that inhibit the establishment of other competing vegetation as well as the accumulation of organic soils or duff. Riverain thicket and meadow, or any vegetation type where streams traverse or interface with shorelines, are likely to be colonized given the frequency of hydrological disturbance.

Roads, ski and hiking trails, and gravel pits where *Tussilago* is abundant are all disturbances associated with the building and maintenance of Parks Canada infrastructure. While similar resource levels are found on the natural disturbances of shorelines and slopes, they existed be-

Table 2. Spearman's coefficient correlation matrix r_s among physical and biotic variables and percent cover of *Tussilago*. Sample numbers (quadrats) are in brackets. All correlations significant at $p \leq 0.01$ except as noted *.

	pH	relative PAR	% cover duff	% bare ground
% cover *Tussilago*	0.371 (212)	0.546 (162)	-0.378 (200)	0.148* (203)
pH		0.365 (164)	-0.36 (198)	0.505 (201)
relative PAR			-0.409 (153)	0.207 (156)
% cover duff				-0.453 (200)

Table 3. Differences among disturbance levels (chronic n = 57, maturing n = 90, undisturbed n = 64) in resource levels tested using Kruskal-Wallis ANOVA.

	% cover *Tussilago*	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

Table 4. Differences between anthropogenic (n = 78) and natural (n = 17) disturbances tested using Kruskal-Wallis ANOVA.

	% cover coltsfoot	pH	relative PAR	% duff	% bare ground
Chi-Square	0.778	1.595	2.114	0	0.072
df	1	1	1	1	1
p value	0.378	0.207	0.146	1	0.789

fore park establishment, when *Tussilago* plants were "relatively few" (Bouchard et al. 1978). This suggests that the invasion of *Tussilago* is associated with park activities – specifically the development and use of aggregate stockpiles, the common link in the development of the park infrastructure.

The noticeable presence of *Tussilago* along roadsides in the mid 1980s coincides with three development events: (1) road reconstruction during the late 1970s to mid 1980s, (2) a local housing boom (Anions 1993), and (3) changes in trail maintenance and construction from using materials borrowed from trailsides to importing bedrock aggregate from centralized quarries (B. Jenniex, Gros Morne National Park, pers. comm.). The residency time of bedrock aggregate stockpiles of up to eight years allowed for the above and belowground establishment of *Tussilago*, which favors belowground production of rhizomes in such low nutrient sites. The establishment of populations from rhizome fragments distributed in the bedrock aggregate was likely followed by the dissemination of diaspores over 115 km of suitable habitat at roadside. 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.

Disturbances that included the importation of bedrock aggregate that neutralizes or buries acidic soils and the concomitant transport of rhizomes enabled the colonization and spread of *Tussilago*. In tuckamore (krummholz), serpentine barrens, and sphagnum bog, *Tussilago* occurred only in the presence of aggregate, and in the case of serpentine barrens, seemed to mediate the phytotoxic effects of the naturally occurring heavy metals. *Tussilago* was not found on the acidic organic substrates of over snow vehicle 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 rights-of-way, and selective logging, are not hospitable environments for the colonization or proliferation of *Tussilago*.

The balsam fir forest is the most susceptible to *Tussilago* 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 17 disturbance types are found in the balsam fir forest due to recreational activities, wood harvesting, and browse, as well as its proximity to shores and brooks and the populated coastal plain. *Tussilago* may now be a permanent component of the balsam fir forest given the disturbance types in place, particularly those that involve the importation of bedrock aggregate that carries propagules and raises pH.

With their general theory of invasibility, Davis et al. (2000) concluded that the study of invasions could be transformed into a quantifiable and predictive science. This study has characterized disturbance types and undisturbed vegetation communities in terms of quantifiable resources suitable for *Tussilago*. This, along with the individual biological characteristics of *Tussilago*, which allowed it to capitalize on those resources, has provided the tools to both predict the invasibility of vegetation communities and to reconstruct the invasion scenario.

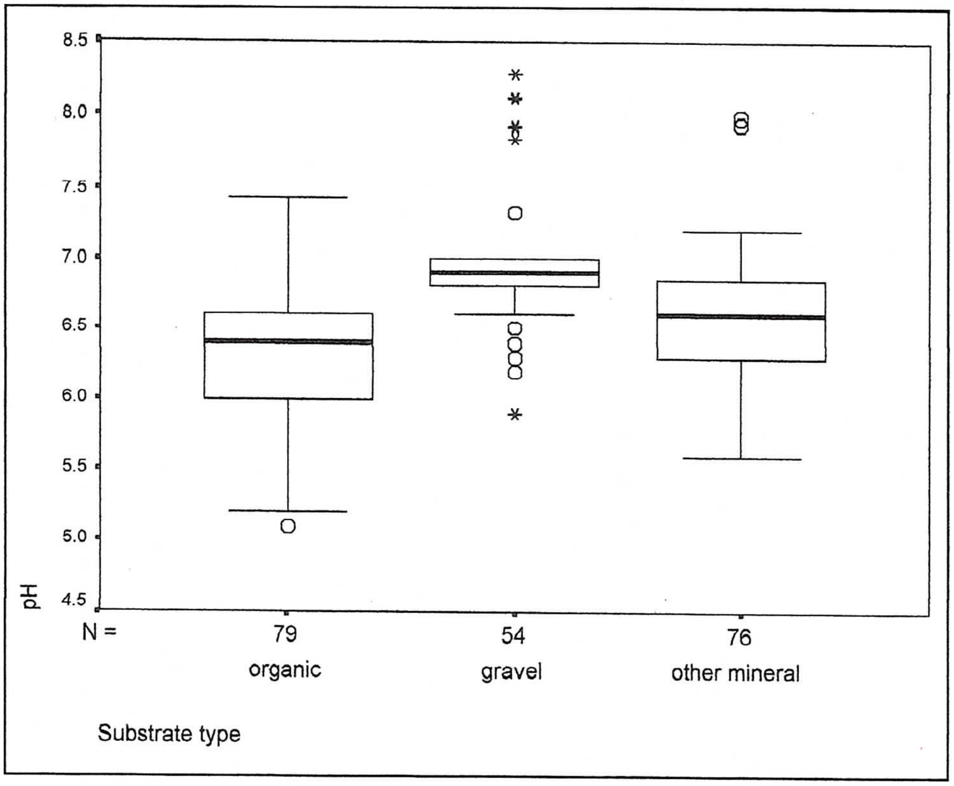

Figure 3. Box and whiskers plots of pH of substrate types. Horizontal bar = median; box = interquartile range; whiskers = highest and lowest extremes; circles = outliers (1.5-3 box lengths from either end); stars = extreme values (>3 box lengths from either end). Sample size equals number of quadrats.

The theories of invasibility previously cited share the common element of a fluctuation (Davis et al. 2000), change (Bazzaz 1983), shift, or amplification (Fox and Fox 1986) in resources that provides a window of opportunity for the invasion of exotic species. Other theoretical elements such as the biology of the species, receiving environment, and propagule pressure are integral but not shared by all theorists. However, these ideas are complimentary to those already in place to explain native species recruitment in explicitly disturbance driven ecosystems (Rowe 1978, Van der Valk 1981). Disturbances of all kinds (regardless of cultural or natural origin) and receiving environments can be defined in terms of a suite of resources that, over time and space, are enabling or limiting to various species (regardless of origin) based on their biological characteristics.

The invasion of exotic species, rather than being a phenomenon solely of plants with superior reproductive and competitive abilities, should be seen as an indication

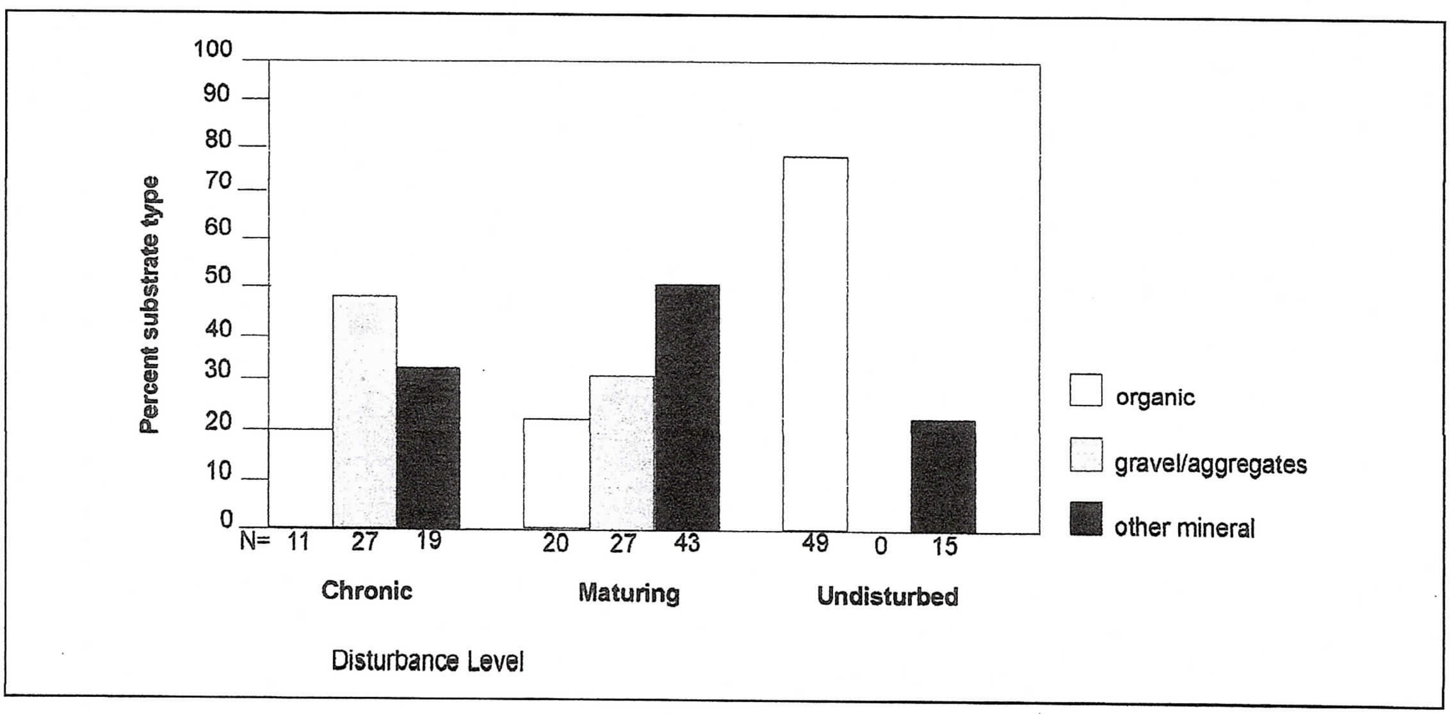

Figure 4. Percentage of substrate types in three levels of disturbance. Sample size equals number of quadrats.

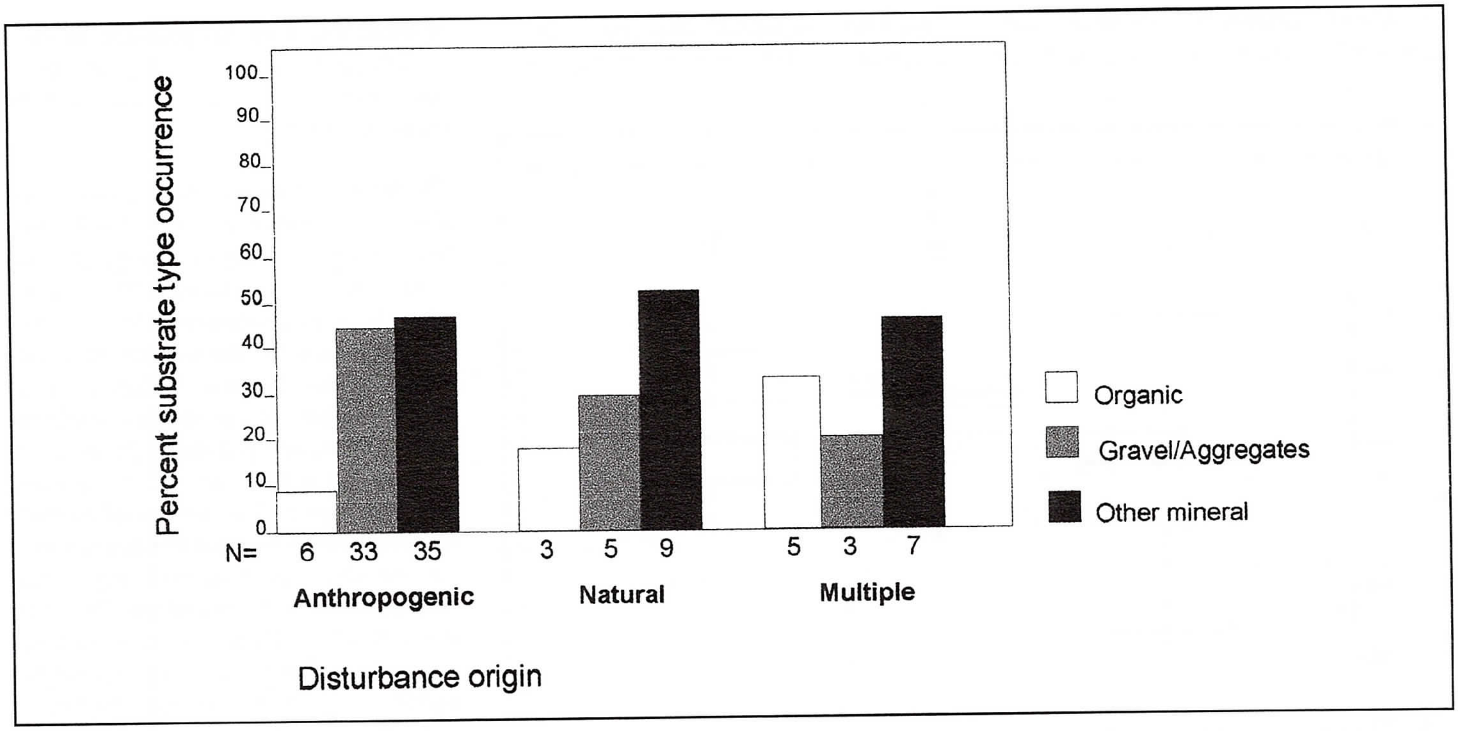

Figure 5. Percentage of substrate types among disturbance origins. Sample size equals number of quadrats.

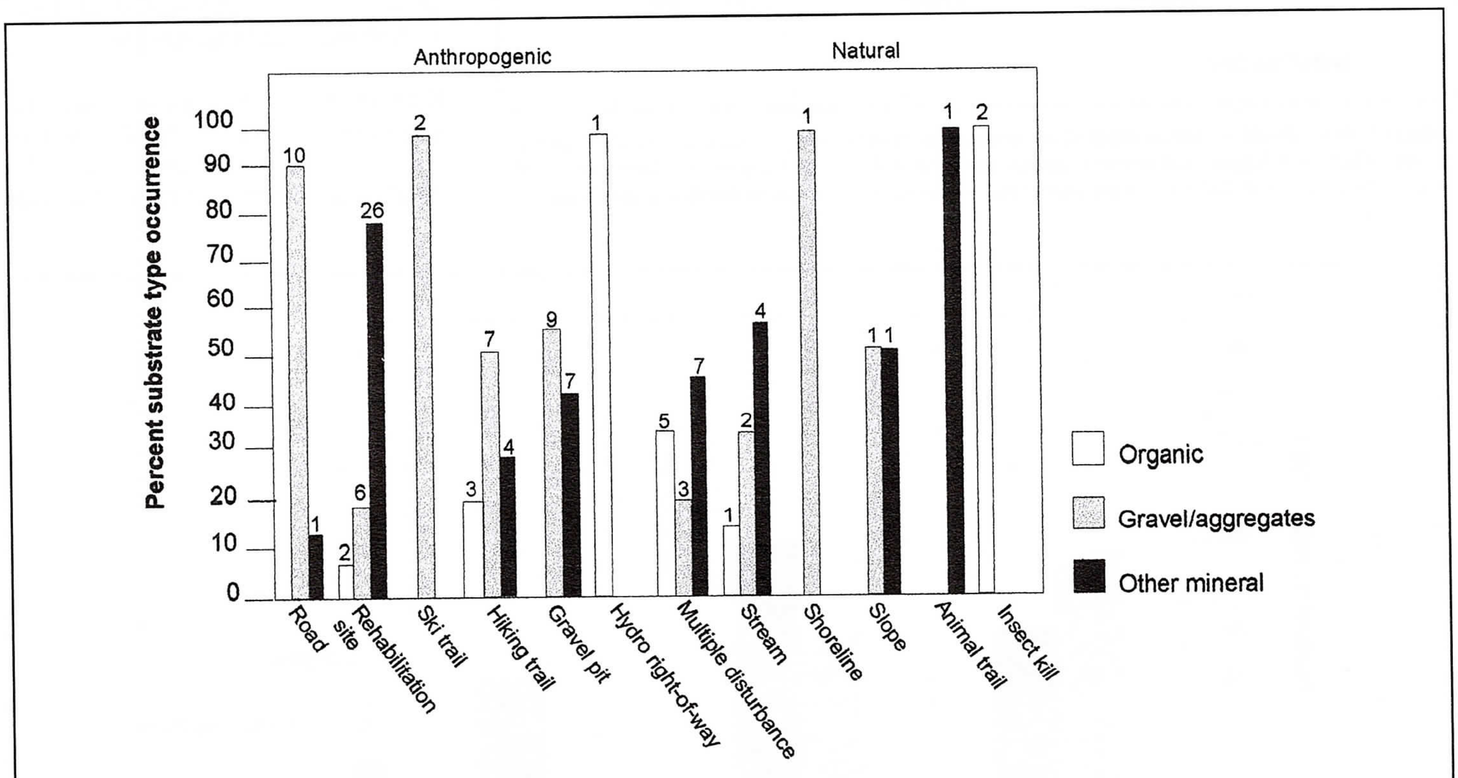

Figure 6. Percentage of substrate types among disturbance types. Number of quadrats sampled at the top of bars.

of disturbance-related resource changes. An alternative or additional approach to biological, mechanical, or chemical control would be, therefore, to identify the change in resources that has occurred in the impacted area relative to the undisturbed vegetation type and to determine whether or not the agent of disturbance is subject to local policy or procedure which could be addressed to control or decrease the spread of invasive species.

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