IMPACT OF SEED AND SEEDLING PREDATORS ON RECRUITMENT OF NEWFOUNDLAND RED MAPLE

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Impact of seed and seedling predators on recruitment of Newfoundland red maple

by

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Abstract

Island ecosystems evolve in geographic isolation, making them particularly vulnerable to synergistic, sometimes irreversible, effects of non-native invasive species. The recent introduction of the southern red-backed vole (*Clethrionomys gapperi*) to Newfoundland adds another species to the growing list of understudied introduced herbivores. This study focused on the effects of red-backed voles on the early life history stages of red maple (*Acer rubrum*). The recruitment capacity of red maple on the east coast of Newfoundland, where red-backed voles have not yet invaded, and the maples on the west coast, where red-backed voles are abundant were compared. Seeds were marked and monitored to determine the effects of post-dispersal seed predation on seed survival. Predator activities were monitored using tracking stations baited with dormant and fresh red maple seeds. Semi-permeable cages were used to determine the effect of the various herbivores on seedling survival. Insects caused the greatest seed loss, followed by non-native slugs and lastly small mammals. Seedling mortality was highest in dry microsites, probably do to desiccation. The cumulative effects of pre- and post-dispersal insect seed predation, as well as shrew, slug, and red-backed vole seed predation are resulting in 100% red maple seed loss in western Newfoundland. Because red maple regeneration in disturbed areas is dependent on recruitment from seed, as opposed to vegetative growth, the presence of red backed voles increases the potential for recruitment failure in red maple, especially in combination with the effects of other non-native seed herbivores.

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"A man ceases to be a beginner in any given science and becomes a master in that science when he has learned that he is going to be a beginner all his life."
- Robin G. Collingwood

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Co-authorship Statement

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

Chapter 1: Introduction

1.1 Background

Due to their evolutionary isolation, island ecosystems are particularly vulnerable to the effects of non-native species (Vitousek *et al.*, 1997; Pimentel *et al.*, 2000; Courchamp *et al.*, 2003). The direct and indirect effects of non-native species can disrupt the natural ecology of species that coevolved in geographic isolation (Parchman and Benkman, 2002). The synergistic effects of multiple non-native species can lead to "invasional meltdowns" of ecosystems (Simberloff and Von Holle, 1999), resulting in cascading effects on an island's ecosystems, including massive extirpations (Fritts and Rodda, 1998). Non-native species can cause irreversible damage, even after their removal or control (Coomes *et al.*, 2003).

The island of Newfoundland's isolated ecosystems are under increasing pressures from a suite of non-native herbivores, including moose (*Alces alces americana* (Clinton)), red squirrels (*Tamiasciurus hudsonicus ungavensis* Anderson), snowshoe hare (*Lepus americanus struthopus* Bangs), and slugs (*Arion* spp., *Limax* spp. and *Deroceras* spp.). Red squirrels, the "omnipresent omnivore," are known seed predators (Layne, 1954) and, in Newfoundland, may reduce the ability of black spruce to regenerate (Tulk, 2004). Slugs are a known conifer seedling herbivore (Noel, 2004; Côté *et al.*, 2005) and can affect plant biodiversity (Buschmann *et al.*, 2005). The impact of these non-native herbivores on Newfoundland's floral biodiversity and community structure has received little attention, as have their possible interactions (McLaren *et al.*, 2004).

The recently introduced herbivorous southern red-backed vole (*Clethrionomys gapperi* (Vigors)) to the island of Newfoundland potentially adds to the pressures on

Newfoundland's ecosystems, with potential for impacts on the island's floral biodiversity and community structure. Red-backed voles were first documented near Little Grand Lake in 1999, after which an expanding population was documented near Red Indian Lake in 2001 (B. Hearn, pers. comm., 2004). They are spreading eastward across the island from western Newfoundland, and are expected to invade the east coast of the island (J. Gosse, pers. comm., 2004).

Predation by small mammals, such as red-backed voles, on tree seeds and seedlings can have significant effects on the distribution and abundance of tree species (Bergeron and Tardif, 1988; Bergeron and Jodoin, 1993; Bowers and Dooley, 1993; Ostfeld *et al.*, 1997; Puettmann and Saunders, 2001; Pusenius and Ostfeld, 2002; Schnurr *et al.*, 2002). In the boreal forest of eastern Canada, during years of high rodent abundance, red-backed voles, deer mice (*Peromyscus maniculatus* (Wagner)), and heather voles (*Phenacomys intermedius* Merriam), negatively affect the establishment of black spruce (Côté *et al.*, 2003) through seed and seedling predation. Gill and Marks (1991) found that seed predation in abandoned agricultural fields in New York by *Peromyscus* spp. caused the highest rates of post-dispersal seed mortality, and seedling predation by meadow voles (*Microtus pennsylvanicus* (Ord)) caused the highest rates of tree seedling mortality. In old fields undergoing succession meadow voles can act as a keystone species by affecting seedling abundances and distributions (Ostfeld and Canham, 1993; Manson *et al.* 2001).

Plant species that have naturally low population densities, such as maples (Oterdoom, 1994), are particularly vulnerable to negative effects from introduced herbivores (Primack, 2002) as they may represent a novel food source. Schnurr *et al.*

(2002) found that in north-eastern temperate deciduous forests, red maple (*Acer rubrum* L.) seed removal was correlated with the relative abundance of red-backed voles, such that for every additional red-backed vole captured per hectare, seed removal increased by 2%. Red-backed vole populations also increased in response to red maple seed masting, and were consistently higher in stands with higher red maple basal area. Moreover, because voles generally clip seedlings close to the ground, leaving only a small portion of the stem, the chance for recovery following vole herbivory is low (Cadenasso and Pickett, 2000).

As red maple seeds and seedlings are known food items of red-backed voles (Plucinski and Hunter, 2001; Schnurr *et al.*, 2002), and maple recruitment has been reduced on the east coast of Newfoundland due to herbivory by hyperabundant, introduced moose (McLaren *et al.*, 2004), a comparison between seed and seedling predation in areas with (western Newfoundland) and areas, as of yet, without (eastern Newfoundland) red-backed voles will help elucidate the effects of voles on this tree species.

1.2 Study Species

1.2.1 The maples of Newfoundland

In Newfoundland, there are two native maple species, mountain maple (*Acer spicatum* Lam.) and red maple. Mountain maple is found throughout Newfoundland and southern Labrador, and is most abundant on the southwestern portion of the island. Red maple reaches its northern limit in Newfoundland and is found everywhere on the island except the Great Northern Peninsula; it is not found in Labrador (Ryan, 1978). Both species are found on medium to very fertile and moist to wet soils (Meades and Moores, 1989). When mature, red maple and mountain maple are physically distinct (Table 1.1). Red maple can grow up to 40 m tall (Van Gelderen, 1994a), though usually grow less than 12 m in Newfoundland, whereas mountain maple can occur as a many branched shrub to a small tree (Ryan, 1978). Due to the restricted distribution of mountain maple, this study focused on red maple.

Although red maples are "super-generalists" (Abrams, 1998), like most maple species, they are sparsely distributed throughout their entire range (Tift and Fajvan, 1999). While red maple is a sub-dominant tree species on the island, it adds structural complexity and variety to the landscape, which in turn increases biodiversity. For example, in Terra Nova National Park, red maples support distinct epiphytic lichen communities, including species of lichen found on no other trees (Yetman, 1999).

Climatic conditions are usually cited as the most important factor determining the northern limit of trees (Hosie, 1979). Tremblay *et al.* (2002) found that the potential for red maples to maintain northern populations through sexual reproduction alone progressively decreased with increasing latitude because of reduced seed production. Red maples have wind-pollinated flowers borne on lateral, umbel inflorescences (Oterdoom and De Jong, 1994). They bloom in late winter to early spring (Farrar, 1995) before leaf bud burst, allowing for less obstructed movement of pollen (Judd *et al.* 1999). The timing of anthesis makes their flowers susceptible to spring frosts that reduce seed production. Because red maples are at their northern limits in Newfoundland, the potential for seed crop failure exists.

Table 1.1: A comparison of physical and reproductive characteristics of mountain maple and red maple in Newfoundland.

Characteristic	**Mountain Maple**	**Red Maple**	**Source**
Max height (m)	7.5	12	Ryan (1978)
Leaves	- 3-5 lobed - 6-12cm long - Rugose, puberulous above; glabrous below - Coarsely double serrate - Summer: light green - Fall: yellowish to reddish brown	- 3-5 lobed - 6- 10 cm long - Fully glabrous - Crenate-serrate - Summer: dark green above, silvery gray below - Fall: distinctive scarlet to orange	Van Gelderen (1994a)
Flowers	- Terminal - Compound inflorescences - Yellowish green - Calyces and corollas distinct - 5 sepals, 5 petals, 8 stamens	- Lateral - Umbel inflorescences - Red - 5 sepals, 0-5 petals, 4-6 stamens	Oterdoom and De Jong (1994)
Sexual expression	Duodichogany	Protogyny	Oterdoom and De Jong (1994)
Mode of pollination	Entomophily	Anemophily/ Entomophily	De Jong (1994)
Anthesis	One month after leaf bud burst; mid-summer	Before leaf bud burst; late winter to late spring	Oterdoom and De Jong (1994)
Timing of seed dispersal	Fall; after leaves dropped	Mid to late summer	Oterdoom and De Jong (1994)
Germination	Growing season following dispersal	Immediately following dispersal or growing season following dispersal	Oterdoom and De Jong (1994); Tremblay *et al.* (1996)

Most red maple populations disperse their seeds in early summer and seeds do not usually require stratification prior to germination, usually germinating following dispersal (Oterdoom and De Jong, 1994). Along its northern limit, red maple seed production and dispersal is delayed to mid to late summer, coinciding with the hottest and driest time of the year. Tremblay *et al.* (2002) found that red maple populations display a heterogeneous germination response, with the proportion of red maple seeds that require stratification prior to germination increasing with increasing latitude. As red maple seeds are dispersed when soil conditions are not optimal for seedling establishment, the ability to enter dormancy prior to spring germination is hypothesised to increase seedling survival (Tremblay *et al.*, 2002). Another advantage for entering dormancy is that more time is available to become established and induce cold hardiness before winter. In Newfoundland, both mountain and red maple seeds enter dormancy after dispersal and germinate the following spring (personal observation).

1.2.2 The granivorous small mammals of Newfoundland

The following mammals may act as red maple seed and seedling predators on the island: meadow voles, snowshoe hares, masked shrew (*Sorex cinereus acadicus* Gilpin), red squirrels, chipmunks (*Tamias striatus lysteri* (Richardson)) and deer mice (*Peromyscus maniculatus* (Wagner)). Of these six species, meadow voles (the only indigenous species), snowshoe hares, shrews, and red squirrels are present in any great abundance, while chipmunks and deer mice have very restricted ranges and are found mainly on the west coast (Gould and Pruitt, 1969; Criddle, 1973; Northcott, 1974; Northcott *et al.*, 1974; Payne, 1974; Dodds, 1983; Tucker *et al.*, 1988; B. Hearn, pers.

comm., 2004; J. Gosse, pers. comm., 2004). In a seed predation study in Maine, rodents were the main seed predators of red maple, white pine (*Pinus strobus* L.), and red oak (*Quercus rubra* L.) seeds (Plucinski and Hunter, 2001). Meiners and LoGiudice (2003) also noted that rodents were the major woody plant seed predators in New Jersey, and that avian seed predators consumed mainly seeds from herbaceous species. In Newfoundland, Tulk (2004) found that red squirrels have the potential to reduce black spruce regeneration through cone depredation and selection. It is important to estimate the effects of other red maple seed and seedling predators present on the island to determine the level of impact on maple recruitment by red-backed voles.

1.3 Project goals

This study compared the reproductive capacity of red maple in Newfoundland and potential limitations of seedling and sapling recruitment in two locations with different red-backed vole presence. The effects that small mammals are having on the regeneration of red maple on the east coast of Newfoundland where red-backed voles were not present, to the west coast of Newfoundland, where red-backed voles were recently introduced was compared. To be able to differentiate the effects of seed and seedling predation by red-backed voles, it was first necessary to quantify the reproductive output of red maple trees. Seeds were collected from red maple trees prior to seed dispersal to compare the reproductive output of red maple trees in both populations. The rate of pre-dispersal seed predation on red maple was quantified. Healthy seeds were cold stratified and germinated, and the rates of seed viability and germination in the two study areas were compared.

To investigated the extent to which the newly introduced red-backed voles are maple seed and seedling predators on the west coast of insular Newfoundland, and what implications this introduced species may have on the persistence of red maples on the island of Newfoundland, seed plots were used to monitor the survival rates and causes of mortality of newly dispersed seeds on both coasts. Tracking stations baited with fresh and dormant red maple seeds were used to monitor predator activity. On the west coast, seeds were also placed in experimental plots with selectively permeable exclosures and monitored to determine which predators cause the greatest mortality. To determine if seedling survival differs between the two populations, and whether red-backed voles are causing an increase in seedling mortality, selectively permeable cages were used to monitor newly germinated seedlings. Age surveys of red maple seedlings and saplings were also conducted to compare past recruitment rates, prior to the introduction of red-backed voles, to determine if recruitment has been hindered in recent years.

Three hypotheses were explored in this study: 1) Red maple from the west coast of Newfoundland have the same recruitment potential as red maple from the east coast of Newfoundland; 2) red maple seeds on the west coast, where red-backed voles are present, experience higher rates of small mammal predation than seeds on the east coast, where red-backed voles are absent; 3) red maple seedlings on the west coast experience higher rates of small mammal predation than seedlings on the east coast.

Chapter 2: Materials and Methods

2.1 Study areas and selection of study sites

This study was conducted on the east coast of Newfoundland where sites were selected in 2004 and red-backed voles had not yet invaded, and the west coast of Newfoundland where sites were selected in 2005, and red-backed voles were present (Fig. 2.1). Seven east coast study sites and four west coast study sites were selected. At each site, one reproductive red maple tree was selected and monitoring was established around the focal tree at each site. A 15 m x 15 m area (0.0225 ha) around each tree was marked, and the diameter at breast height (DBH) of every tree greater than 5 cm and over 2 m tall within the sampling area was measured. The basal area of red maples per hectare at each site was calculated (Table 2.1). The DBH of each tree was converted to basal area by multiplying the square of half the DBH by л. The sum of the basal area of all the maple trees was then divided by 0.0225 ha, which is equivalent to the area sampled.

East coast study sites were located and selected in Terra Nova National Park (404 km^2; 54° 00' W, 48° 30' N). The North Shore and Central Ecoregions are represented within the Park (Meades and Moores, 1989). Red and mountain maples are sub-dominant tree species in these ecoregions, which contain forests composed mainly of black spruce, balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and white pine. Black spruce-feathermoss stands are the dominant forest type, which also includes balsam fir-feathermoss stands and intermixed hardwood stands. This region

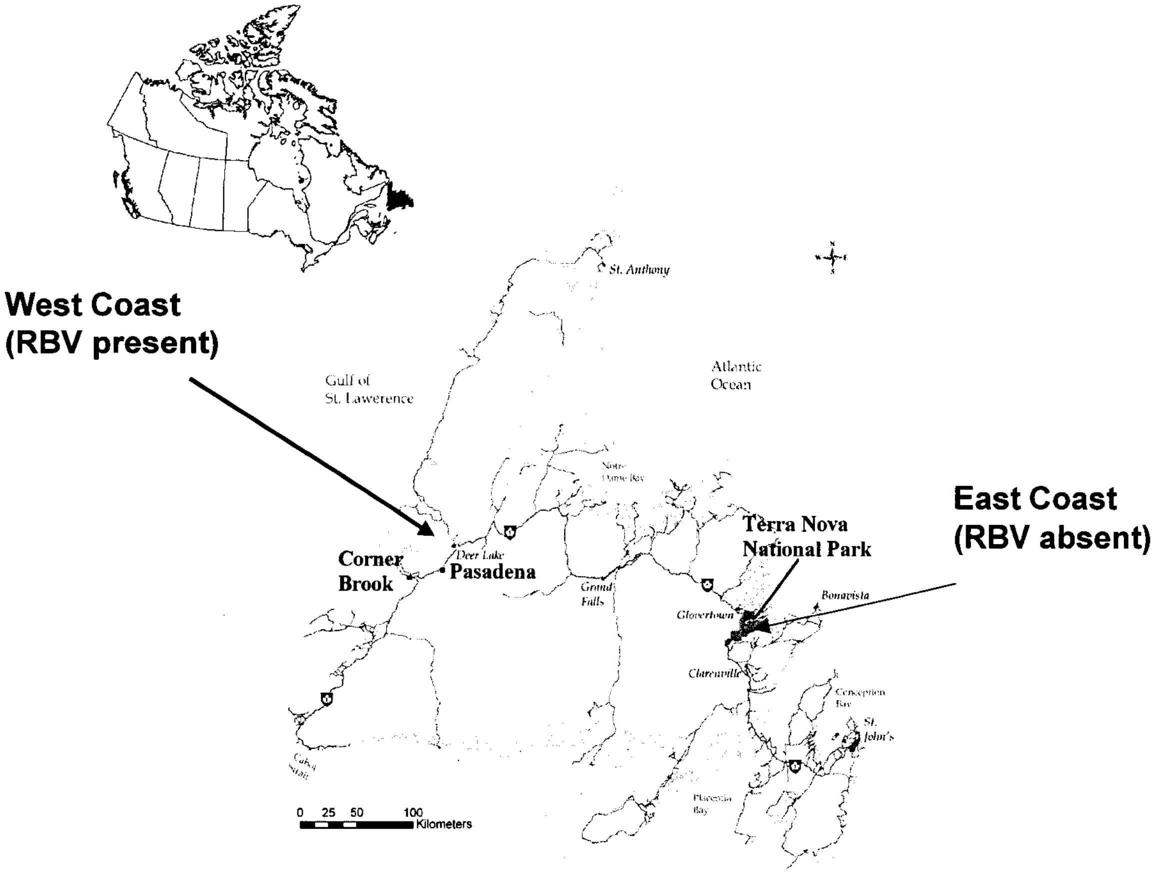

Figure 2.1: Map of Newfoundland showing locations of study areas, with inset of map of Canada with Newfoundland in black. (RBV = red-backed voles). Two west coast study sites were located near Corner Brook and the other two were near Pasadena. Study sites on the east coast were dispersed through out Terra Nova National Park (shaded area). Appendix A lists coordinates for study sites.

Table 2.1: Basal area of red maple on study sites. Within 15 x 15 m plots at each site, the number of stems of red maple trees with a diameter at breast height (DBH) greater than 5 cm and over 2 m tall were counted and DBH was measured. The DBH of the red maples were then converted to area covered by each stem, summed, and then converted to m^2/ha.

Study Area	Study Site	Number of main stems	Basal Area (m^2) / ha
East Coast	Blue Hill East Site 1	3	3.27
East Coast	Blue Hill East Site 2	3	5.99
East Coast	Blue Hill	5	10.52
East Coast	Terra Nova Grade Site 1	8	9.72
East Coast	Terra Nova Grade Site 2	5	8.59
East Coast	Dunphy's Pond	3	2.64
East Coast	Louil's Hill	13	9.62
West Coast	Pasadena Site 1	8	10.66
West Coast	Pasadena Site 2	21	15.49
West Coast	Hughe's Brook Site 3	6	2.53
West Coast	Hughe's Brook 4	25	1.55

experiences warm, dry summers, occasionally creating summer soil moisture deficiencies (Damman, 1983).

West coast study sites were located near Corner Brook and Pasadena (NL), where red-backed voles have become common in recent years. West coast sites were selected during the spring of 2005. This area is part of the Western Newfoundland Ecoregion (Meades and Moores, 1989), which has the most favourable climatic conditions for plant growth in Newfoundland. Soils tend to be more fertile than anywhere else on the island. Mountain maple thickets are abundant on certain sites but red maple is at its northern limit in this ecoregion. Balsam fir is the predominant forest tree, with black spruce occurring on poorly drained sites and bedrock outcrops. Western Newfoundland is characterized by a longer frost-free season with warmer summers, as compared to the Central Ecoregion. It has a wet climate with measurable precipitation occurring >180 days/year (Damman, 1983).

Vegetation maps were used to locate east coast study sites that had deciduous trees. Sites were also found by scouting and visual inspections. A wide range of habitat types were surveyed for the presence of reproductive red maple trees, including alder swamps, birch stands, black spruce sites, balsam fir sites, graminoid fields, ericaceous fields, and mixed coniferous-deciduous sites (Meades and Moores, 1989). In all, 30 sites were examined; 24 of which contained red maple trees. Of these 24, only seven sites had red maple trees in fruit. Reproductive red maple trees in 2004 also had seeds in 2005. The presence of seedlings and saplings was confirmed through visual inspection under the canopies of red maple trees. Generally, east coast sites with reproductive maples were balsam fir forest types intermixed with a strong hardwood component (Meades and

Moores, 1989). Seven sites with reproductive red maples were selected for this study. They ranged from insect disturbed patches of 1000 m^2 to large, continuous forests with smaller canopy gaps.

In 2005, four west coast sites were selected to compare to east coast sites. Vegetation maps and scouting were used to find potential sites. Sites included balsam fir forest types with a high hardwood component and a canopy cover ranging from 50% to 75%. The sites were chosen to match established east coast sites in terms of ground cover, tree species, and percent canopy cover within the known variability of forest types. Each site had mature red maples with developing seeds. Although many places had reproductive red maple trees with abundant developing seeds, sites with seedlings and saplings could not be found. An area, about 10 m from the study tree, was extensively searched for red maple seedlings for approximately 20 minutes. Unlike the east coast where care had to be taken not to step on the numerous seedlings and saplings growing around reproductive red maple trees, there was an obvious lack of seedlings and saplings on the west coast. It was decided to plant seedlings at these sites to be able to determine whether seedlings were absent due to herbivory or seed crop failure.

2.2 Pre-dispersal seed predation and viability

To compare germination rates and levels of pre-dispersal seed predation on red maple seeds of trees growing on east coast and west coast sites, red maple seeds were collected from tree tops growing adjacent to west coast sites ($n = 4$) and two east coast sites ($n = 2$). The pre-dispersal status (viable (filled), non-viable (hollow), or damaged) of the seeds was determined. Seeds were considered healthy if they were round, filled and firm. Undeveloped or aborted seeds were flat, while small, pin-sized holes in the seeds indicated insect damage. Over 360 seeds from each site were screened, for a total of 2160 seeds.

Germination rates of healthy seeds from each west coast site and two east coast sites were examined to determine if the lack of seedlings on west coast sites was due to low germination and viability rates. Forty-five seeds were used from each site, as this was the lowest number of healthy seeds collected from one of the sites after seeds were screened for damage. Seeds were placed on moistened Promix^{TM} and germination checked for 14 days following Van Gelderen (1994b) and Tremblay *et al.*, (1996). Non-germinated seeds were then cold stratified for 12 weeks, and allowed to germinate for 31 days. During the germination periods, seeds were kept moist and stored at room temperature under glass. Following seven days without germination, the viability of non-germinated seeds was determined by examining the embryos using the crush method (Sawma and Mohler, 2002). Green embryos and endosperm were an indication of viable seeds (Tremblay *et al.*, 1996) that did not germinate, possibly because pre-germination requirements were not met, although they had been stratified.

2.3 Post-dispersal seed predation

Monitoring of naturally occurring seeds for seed predation

To determine if the presence of red-backed voles was associated with an increase in red maple seed removal, seed removal rates of red maple seeds from the natural seed rain of sites with and without red-backed voles were monitored following seed dispersal.

Dispersal on west coast sites began between June 28 and 29, 2005, while on east coast sites dispersal began between July 4 and 5, 2005.

Between July 28 and 29 of 2004, immediately following seed dispersal, 1 m x 1 m plots were established under the canopy of study trees on east coast sites. All maple seeds within the plots were marked using round coloured toothpicks. The 1 m^2 plots were established over an area with the highest density of seeds relative to the rest of the area under the canopy. Seeds were checked after four weeks and any new seeds were marked, and the number of missing seeds was noted. Seeds were rechecked the following spring.

In 2005, to compare the fate of seeds on the east and the west coast study areas, twelve 30 x 30 cm seed plots were established at each of the seven east coast sites and the four west coast sites. Plots were located 1 m and 3 m north, east, south, and west, and 5 m northeast, southeast, southwest, and northwest from the focal tree within each site. Seed dispersal began in late June and seed plots were monitored regularly for new seeds, damage to seeds, or removal of seeds until the end of August. If it was necessary to move seeds, twigs were used to manipulate seeds to avoid handling effects. Only healthy seeds were marked and monitored, using the same method as in 2004. If seeds were partially damaged, the source of damage was noted and then the remnants were discarded from the plots. Since on the east coast meadow voles are the only small mammals known to eat maple seeds, any rodent-like teeth marks were attributed to them.

Monitoring of seed addition experiments

East coast sites had lower levels of pre- and post-dispersal seed predation as compared to the west coast, allowing for a natural set of seeds to be monitored throughout the summer. Due to high rates of pre-dispersal and post-dispersal seed predation on the west coast, seeds from red maple trees adjacent to the study sites were placed around the study trees on control plots and in selectively permeable cages to ensure that there were sufficient numbers of healthy seeds available to monitor.

It was necessary to selectively exclude predators to be able to accurately measure the amount of mortality caused by each suite of predators without interference from other predators, since the high rate of pre-dispersal seed predation resulted in most seeds being damaged before they could be counted. Selectively permeable cages were used to compare the amount of seed mortality caused by introduced snowshoe hare, small mammals, and invertebrates. Cages were constructed using 1.27 cm^2 hard wire mesh and measured approximately 9 x 9 x 10 cm and prevented potential small mammal predators from eating seeds, but allowed access by slugs and other invertebrates. Ten cages were staked to the ground using two 10 cm nails. Plots were located 2 m north, east, south and west, and 4 m north, north east, south east, south, southwest, and northwest from the focal tree. To allow access to the seeds by shrews, voles, slugs and other invertebrates, but not hare and red squirrel, open cages were constructed by cutting openings in the cages measuring approximately 2.5 x 2.5 cm on two sides of the cages (Plucinski and Hunter, 2001). Control plots were placed next to the set of cages and marked using numbered aluminium tags pegged to the ground with a nail approximately 5 cm away from the seeds. Seeds were monitored through out the summer and causes of death or damage were noted.

2.4 Seedling monitoring

Surveys were conducted at east coast sites in 2004 to determine if red maple seedlings are preferred by snowshoe hare. Vegetation was surveyed along 1 to 3, 20 m x 1 m transects for hare herbivory. The number of transects was determined by the size and variability of the vegetation at the site. Surveys were conducted throughout the summer, after red maple seedling emergence.

Cages similar to those used to monitor placed seeds were used to compare the various causes of seedling death. Exclosure cages were not accessible to potential small mammal predators, but allowed access by slugs and other invertebrates, while open cages were accessible by both small mammals and invertebrates, but not larger mammals. Control plots were marked using numbered aluminium tags pegged to the ground with a nail approximately 5 cm to the right of the seedling in relation to the focal tree of the study site. Seedlings were monitored through out the summer and causes of death or damage were noted.

On the east coast, control plots, exclosure cages and open cages were established at each site. The survival of 411 newly emerged, naturally occurring red maple seedlings on the east coast at all seven sites was monitored throughout the summers of 2004 and 2005. The presence of cotyledons, absence of bud scars, and the absence of a woody stem were used as indicators of newly germinated seedlings. During the summer of 2004, 180 seedlings were randomly selected and monitored, with 90 in control plots and 90 in exclosure cages. No seedlings were monitored on the west coast is 2004. During the summer of 2005, 231 new seedlings that emerged within a 10 m radius of study trees at each site were monitored along with seedlings that survived from 2004. Ten open cages were established at each site and control plots and exclosure cages were randomly established around the remaining seedlings. There was one seedling per treatment.

Due to the lack of seedlings on west coast study sites, seedlings were grown in nursery flats and then transplanted to the field. Seedlings were grown from seeds collected from the east coast shortly after dispersal in late July to early August 2004. Seeds were stored at 4°C and planted 23 May 2005 in Promix$^{\text{TM}}$ in a plastic tray. Seedlings were transplanted to west coast sites on 14 June 2005.

At each west coast site, a total of 900 seedlings were planted in 10 plots, each plot containing an exclosure cage, an open cage, and a control plot. Three seedlings were planted per treatment to account for the possibility of high mortality, with 3 seedlings per open cage and exclosure cage and a control plot marked by an aluminium tag pegged to the ground. Seedling plots were located adjacent to seed plots.

2.5 Rates of recruitment and growth patterns

To determine whether recruitment is episodic or annual, seedlings and saplings <200 cm in height were collected and aged. In October of 2004 and early spring 2005, seedlings and saplings were collected from six sites adjacent to east coast study sites, and from three areas adjacent to the four west coast sites (<50 m away). On east coast sites, line transects 15 m long starting at a parent tree were followed in the four cardinal directions and at every metre the closest seedling or sapling <200 cm tall was collected. Since the same procedure as was carried out on the east coast only yielded 12 seedlings or saplings on the west coast, only one of which appeared to be a newly germinated seedling, areas adjacent to the sites were scouted and 15 saplings from each site were randomly selected. No seedlings were found. Specimens were aged in the laboratory by counting the number of terminal bud scars or by counting the number of annual growth rings (Lorimer *et al.*, 1999). To compare the growth of maples on the west coast and the east coast, the height and the basal diameter of the specimens collected were measured.

2.6 Monitoring predator activity

To determine the identity of the rodents that consume maple seeds, sooted track stations were used. Such stations are often used to monitor mammalian activity (Zielinski, 1995; Loukmas, 2002).

Track stations were constructed using 15 x 10 cm pieces of aluminium sheet metal covered with kerosene soot placed inside 30 cm long PVC tubes (7.68 cm diameter). White tacky paper (usually used as cupboard lining) cut into 12 x 10 cm sheets were attached to the underside of the metal, at both ends, sticky side up so that approximately 10 cm of the sheets extended beyond the metal. Bait was placed in the middle of the metal sheet, which was then inserted into the centre of the PVC tube, which provided protection from precipitation. The metal sheets were slightly curved to fit the shape of the tube. Tracks were identified using Gibbons (2003) and Chase and Chase (1969).

Three dormant red maple seeds, collected from the east coast from various sources in 2004, and 3 local fresh red maple seeds, collected in 2005 were used as bait in each tracking station. Track stations baited with dormant seeds were deployed on the east coast 28 June 2005 and checked 8 July 2005 (70 trapping nights), and deployed on the west coast 29 June 2005 and checked 5 July 2005 (42 trapping nights). Track stations baited with fresh red maple seeds were deployed on the east coast 19 July 2005 and checked 29 July 2005 (70 trapping nights), and deployed on the west coast 23 July and checked 23 August 2005 (217 trapping nights).

Seven track stations were used per site. Stations were strategically placed approximately 3 m apart in a straight line. If possible, stations were placed on small mammal runways, or lined up parallel with logs or boulders. Small twigs were stuck into the ground on either side of the tubes to prevent them from rolling. This arrangement blocked the areas adjacent to the tubes, creating a tunnelling effect that directed the animals into the tubes.

Because the distribution of red-backed voles in Newfoundland is unknown, and only anecdotal evidence of their presence in the Pasadena and Corner Brook area exists, west coast sites were trapped to unambiguously establish their presence. Since meadow voles and red-backed voles have similar tracks, and in Newfoundland it has been documented that they have similar sized feet (Moss, 2002), sooted tracking stations did not suffice to establish the presence or absence of either of the species on west coast sites. Provincial Wildlife Division (Department of Environment and Conservation) personnel trapped all four west coast sites using small mammal snap traps. Twenty-five traps were laid out in a 5 X 5 grid, 3 m apart, covering an area of 144 m^2, with the study red maple tree at the centre of the grid. Peanut butter mixed with rolled oats was used as bait. Trapping occurred between 22 August 2005 and 24 August 2005, totalling 50 trap nights per site. Traps were checked and re-set 23 August 2005. Trapping occurred at the end of the field season to ensure that the experiments were not negatively impacted. Trapping at east coast sites was not necessary since other ongoing mammal studies within the

National Park would have established the presence of red-backed voles in that area (J. Gosse, unpublished data).

Slug species presence and abundance were monitored through the use of cardboard slug traps. Four pieces of 45 x 45 cm corrugated cardboard were placed around red maple trees at each site in the four cardinal directions. They were pegged to a flat area of ground, approximately 3 to 5 meters away from the tree. The slug traps were checked during each visit to the site. The number of slugs under the cardboard was recorded. To compare the abundance of slugs across sites, the total number of slugs counted at each site was divided by the total number of traps checked at each site. For example, if all four traps at a site were checked on four separate visits, then the total number of slugs counted at that site throughout the summer of 2005 was be divided by 16.

2.7 Data analysis

A generalized linear model, with a log link was used to analyse seed and seedling data. Statistical analysis was carried out using SAS® statistical software, version 9.1 (SAS Institute, 1996). Data were assumed to conform to a Poisson distribution. To correct for over dispersion in the variance, a p-scale was used, which reports results as an F-statistic (Littell *et al.*, 2002). The level of significance was set after applying Bonferroni correction for the number of comparisons carried out on each data set (Sokal and Rohlf, 1995).

The proportion of viable seeds, seeds with insect damage, and hollow samaras collected from both study areas, and the proportion of viable seeds collected that germinated, remained dormant, and died following stratification were compared using a logistic regression model analogous to ANOVA, with a Bonferroni corrected α of 0.05/3 = 0.017 (Lewis, 2004). Proportions of post-dispersed seeds lost to slug, small mammal, and insect predation and the proportion that survived to the end of the monitoring period in 2005 were compared by study area, with a Bonferroni corrected α of 0.05/4 = 0.0125. Proportions of experimentally placed seeds on the west coast lost to slug, small mammal, or insect predation, disappeared, or survived were compared by site and treatment, with a Bonferroni corrected α of 0.05/5 = 0.0100. Proportions of seedlings that survived, died due to dry conditions, rodents, slugs, or disappeared were also compared using logistic regression with a Bonferroni corrected α of 0.05/5 = 0.0100.

The growth patterns of red maple were analyzed by multiple regressions, with height, basal diameter, and year of recruitment as regressors. Analysis was carried out using Minitab® statistical software, version 13 (Minitab Inc., 2003).

Chapter 3: Results

3.1 Pre-dispersal seed predation

On average, the proportion of viable seeds harvested from trees was greater from east coast sites (90 ± 3%) than from west coast sites (47 ± 33%) but because of high site variation on the west coast the difference was not significant ($F_{1,4} = 5.76$; $p = 0.07$; Fig. 3.1a). Seeds from west coast sites were released at a very early stage in development, while seeds from east coast sites were dispersed when fully mature and beginning to dry. More seeds from west coast sites were not viable as a result of incomplete development (seed did not develop in samara) (west coast = 17 ± 15%, east coast = 6 ± 1%), and seeds had higher rates of damage by unidentified insects than seeds from east coast sites (west coast = 38 ± 35%, east coast = 4 ± 2%).

Of the viable, undamaged seeds collected, there was no significant difference between the proportion of seeds from west and east coast sites that germinated (west coast = 33 ± 12%, east coast = 27 ± 13%; $F_{1,4} = 0.72$; $p = 0.44$; (Fig. 3.1b)). Over 70% of germinations occurred within the first 8 days of the second germination period. Germination rates of healthy seeds did not vary between study areas. There was no significant difference between the proportions of seeds that died during the germination period (west coast = 21 ± 7%, east coast = 17 ± 6%; $F_{1,4} = 1.69$; $p = 0.26$).

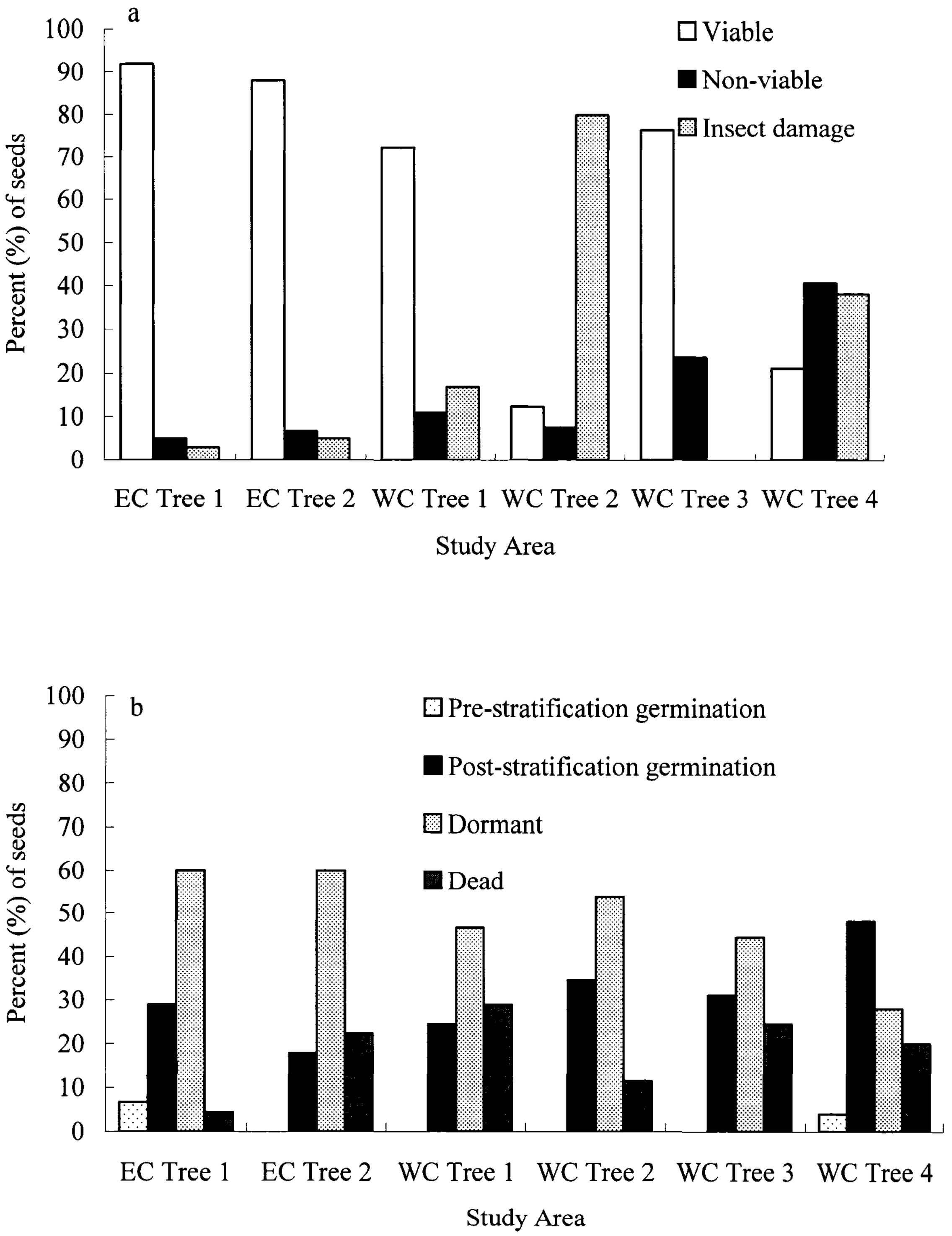

Figure 3.1: Status of predispersed seeds collected from individual trees from east coast (EC; red-backed voles absent) and west coast (WC; red-backed voles present) study sites (a). While the number of viable seeds is not greater on EC sites as compared to WC sites ($F_{1,4} = 5.76$; $p = 0.07$), more seeds from WC sites were damaged by insects. Of the healthy viable seeds, the germination percentages were similar between study areas ($F_{1,4} = 0.72$; $p = 0.44$) (b).

3.2 Post-dispersal seed predation

The natural seed rain was monitored to determine the fate of seeds. Of the 887 seeds monitored on the east coast in 2004, 194 (21.9%) survived to May 2005, and 107 (12.1%) germinated, which were included in the caged seedling experiment of 2005. Of the seeds that did not survive, meadow voles (the only small mammal on the east coast which consumes maple seeds) consumed 2.4%, insects damaged 16.9%, slugs damaged 17.0%, and 41.8% disappeared and were presumed to be dead.

In 2005, seeds on the west coast began dispersing on June 27 while on the east coast seeds began dispersing July 5. A total of 274 seeds fell into the forty-eight 30 x 30 cm seed monitoring plots on the west coast, for an average of 65 seeds/m^2. A total of 448 seeds fell into the eighty-four 30 x 30 cm seed monitoring plots on the west coast, for an average of 59.3 seeds/m^2. No seeds from west coast sites survived past October 27 whereas almost half of the seeds from east coast sites were still alive (Fig 3.2).

In 2005, predation by invertebrates and small mammals on naturally deposited viable seeds at west coast sites occurred relatively soon after seed dispersal (Fig 3.3). In 2005, predation by insects caused the greatest amount of seed mortality in both study areas, and was significantly greater on the west coast. Over 74 ± 15% of seeds from west coast sites had pre- and post-dispersal insect damage, compared to only 26 ± 14% from east coast sites ($F_{1,9} = 54.93$; $p = 0.0001$). Slug predation, which did not differ between sites ($F_{1,9} = 0.00$; $p = 0.96$), caused the next greatest amount of seed damage (west coast = 13 ± 10%; east coast = 12 ± 8%). Small mammal predation was higher on the west coast ($F_{1,9} = 11.24$; $p = 0.008$) reducing the number of available seeds by 8 ± 3% on west coast sites as compared to 4 ± 2% on east sites.

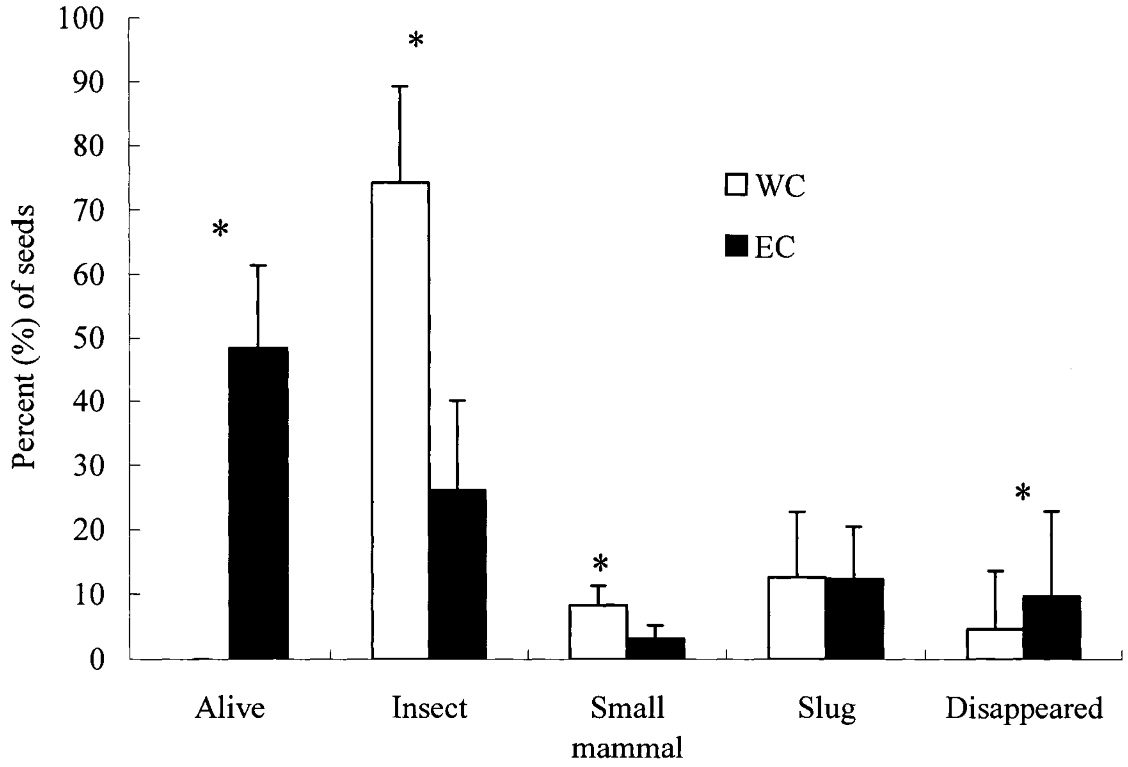

Figure 3.2: Fate of all red maple seeds that fell into seed monitoring plots in 2005 on east coast (EC) and west coast (WC) study sites. A total of 274 seeds on 4 WC sites and 448 seeds on 7 EC sites were monitored. By the end of the monitoring period, no seeds were alive on the WC. Insects were the highest cause of mortality in both areas.

* = significant difference

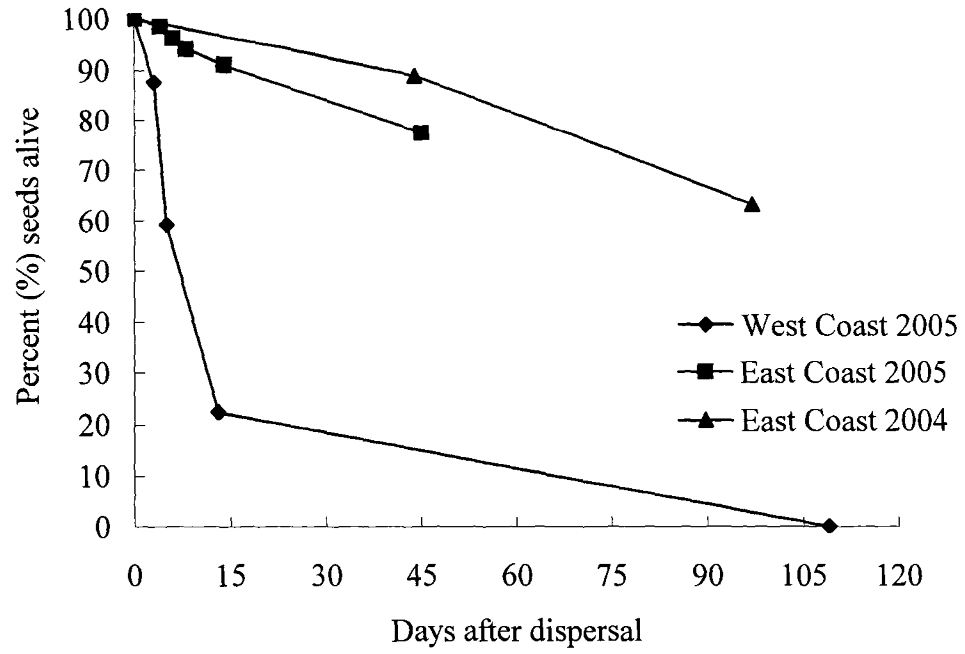

Figure 3.3: Survivorship curve of undamaged, healthy red maple seeds that fell into seed monitoring plots. Data were not collected after the 45th day from east coast sites in 2005. Damaged or undeveloped seeds were discarded from seed plots so that only healthy seeds were monitored. Dispersal on the east coast in 2004 began July 13. In 2005, on the east coast dispersal began July 5 while on the west coast it began June 27. In 2005, seed predation was high the first two weeks following dispersal. However, on the west coast, predation was much higher and continued until all seeds were damaged, while on the east coast, predation occurred at a lower rate.

Small mammals did not significantly increase seed mortality in either site. Trapping established the presence of red-backed voles at each site on the west coast (Table 3.1). No meadow voles were caught on any of the west coast sites. Of the 360 seeds used in the seed addition experiment on the west coast, insects caused the greatest amount of mortality (37%), followed by slugs (10.5%), and then small mammals (2.5%), while 20% disappeared or could not be accounted for. Only 30% of seeds survived. The survival of fresh red maple seeds placed in cages on west coast sites varied significantly across sites ($F_{3,6} = 42.72$; $p = 0.0002$; Fig. 3.4). The proportion of seeds taken by small mammals from each site did not vary significantly, after applying the Bonferroni correction ($F_{3,6} = 5.48$; $p = 0.04$). Cages were effective in preventing seed predation by small mammals since small mammals took no seeds from closed cages, but the difference between control plots, and both types of cages was not significant after applying the Bonferroni correction ($F_{2,6} = 7.50$; $p = 0.02$).

Abundance of seed predators across west coast sites was not indicative of seed survival and seed loss was highly variable among sites. Hughe's Brook (Site 4) had the highest survival rate (81%), with no small mammal seed predation, despite the presence of red-backed voles (Table 3.1). There was a moderate amount of slug predation (8%) despite the fact that this site contained the highest density of slugs (Table 3.2). Insect seed predation was low (8%) despite the fact seeds collected from a tree approximately 100 m away had the second highest amount of pre-dispersal insect predation. In contrast, Pasadena (Site 2) had the highest rate of pre- and post-dispersal insect seed predation of natural seeds (80% and 75%, respectively), and the highest rates of experimental seed insect predation (61%).

Table 3.1: Number of small mammals trapped on 50 trap nights on a 144m^2 grid at each west coast (WC) site. Red-backed voles (RBV) were trapped on every site. No meadow voles were trapped.

WC Site	RBV	Masked Shrew	Deer Mouse
1	4	0	0
2	3	0	1
3	3	3	0
4	2	1	0

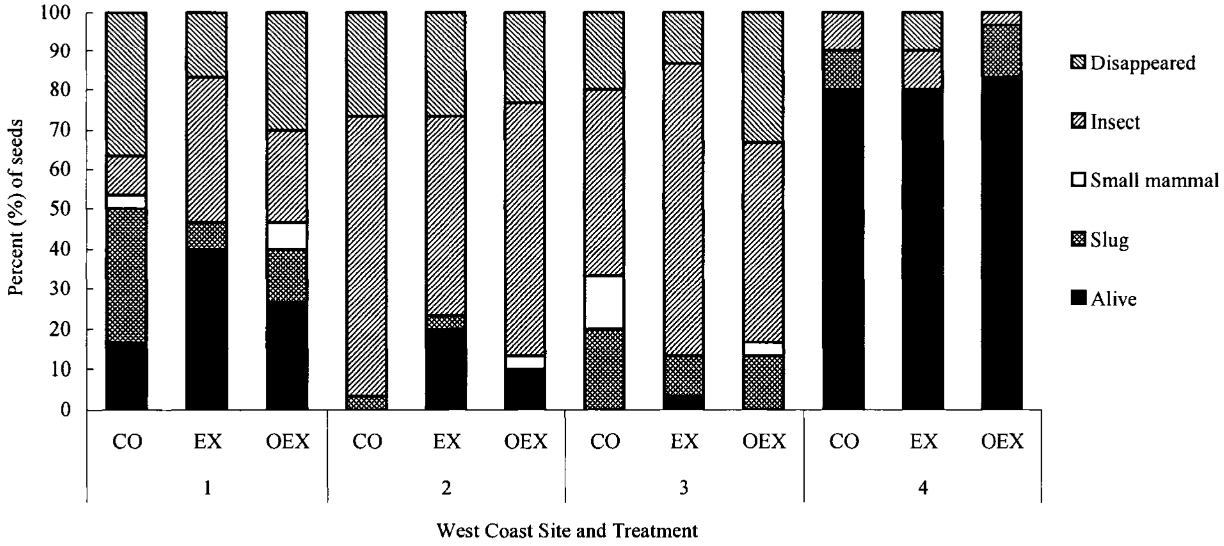

Figure 3.4: The fate of red maple seeds (30 seeds/ treatment/site) placed in cages accessible to only invertebrates (EX), in open cages accessible to invertebrates and mammals smaller than red squirrels (OEX), and in control plots accessible to all seed predators (CO). Seeds disappeared, suffered insect damage, were eaten by small mammals, were grazed by slugs, or were alive by the end of the monitoring period. Survival varied across sites ($F_{3,6} = 42.72$; $p = 0.0002$). Small mammals were not able to penetrate EX cages and caused the least amount of mortality.

Table 3.2: Comparison of slug presence among sites (Slug index per site = number of slugs trapped per cardboard trap at each site (4 traps per site) divided by the number of times a site was visited). (EC = east coast; WC = west coast).

Study Area	Study Site	Slug Index
East Coast	Dunphy's Pond	0.00
East Coast	Blue Hill East 1	0.67
East Coast	Blue Hill East 2	0.54
East Coast	Terra Nova Grade Site 1	0.55
East Coast	Terra Nova Grade Site 2	1.10
East Coast	Blue Hill	0.17
East Coast	Louil's Hill	0.54
West Coast	Pasadena Site 1	0.19
West Coast	Pasadena Site 2	0.75
West Coast	Hughe's Brook Site 3	0.50
West Coast	Hughe's Brook Site 4	0.88

3.3 Seedling monitoring

Out of the 180 east coast seedlings monitored in 2004, 13.3% died (Fig. 3.5a) and there was a significant treatment effect on the survival of seedlings ($F = 5.25_{1,25}$; $p = 0.03$). Only 3.3% of the caged seedlings died or went missing as compared to 23.3% of seedlings in control plots. All missing seedlings were from control plots except for one, suggesting that seedlings in cages were protected from vertebrate herbivores. The one missing caged seedling could not be located due to an animal displacing the cage. Slugs consumed the same number of seedlings in control plots as in cages (2.2% per treatment). Meadow voles consumed only 4 seedlings (4.4%) in control plots, at 2 different sites. Intensive surveys for hare herbivory in 2004 indicated that this was not a source of seedling mortality (Appendix B), probably due to the naturally occurring population low in the hare cycle (Reynolds, *et al.*, 2004).

Of the 360 seedlings monitored on the west coast in 2005 none survived, as compared to 64% survival (209 of 325) on the east coast (Fig. 3.6). Desiccation, the most common cause of death in both study areas, was significantly greater on the west coast (west coast: $n = 291$; east coast: $n = 61$; $F_{1, 27} = 158.40$; $p < 0.0001$). A significantly greater proportion of seedlings on the east coast as compared to the west coast died of slug damage (east coast = 15; west coast = 0; $F_{1, 27} = 14.85$; $p < 0.0001$), while a greater proportion of seedlings on the west coast as compared to the east coast were eaten by voles (east coast = 0; west coast = 5; $F_{1, 27} = 33.17$; $p < 0.0001$; Fig. 3.5b).

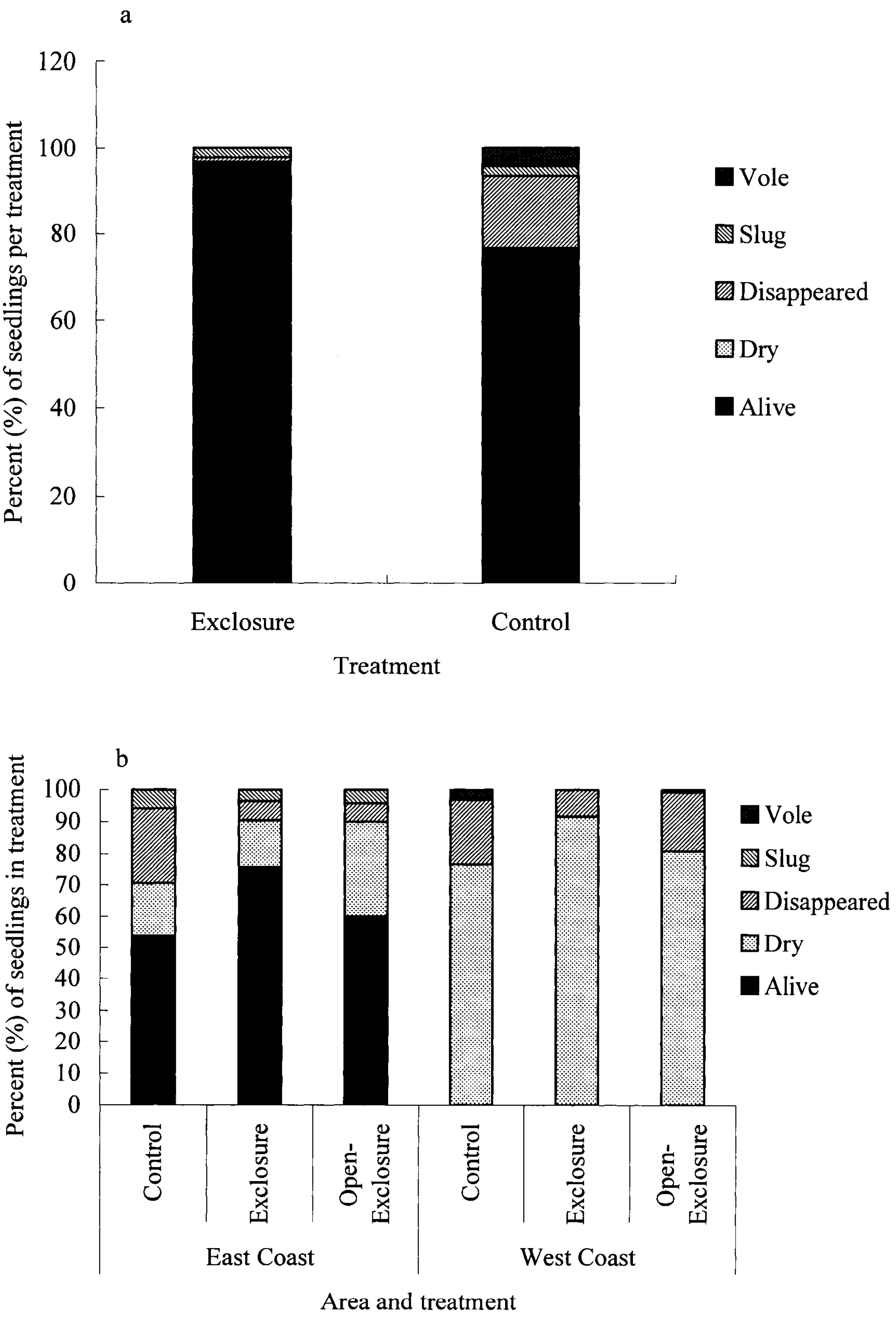

Figure 3.5: Percent survival of 180 naturally occurring red maple seedlings on east coast (EC) study sites in 2004 (a). Meadow voles consumed 4 seedlings in control plots. Slugs consumed the same number of seedlings in control plots as in cages. Meadow voles did not consume any seedlings on the east coast in 2005 (b), but red-backed voles did consume seedlings on the west coast.

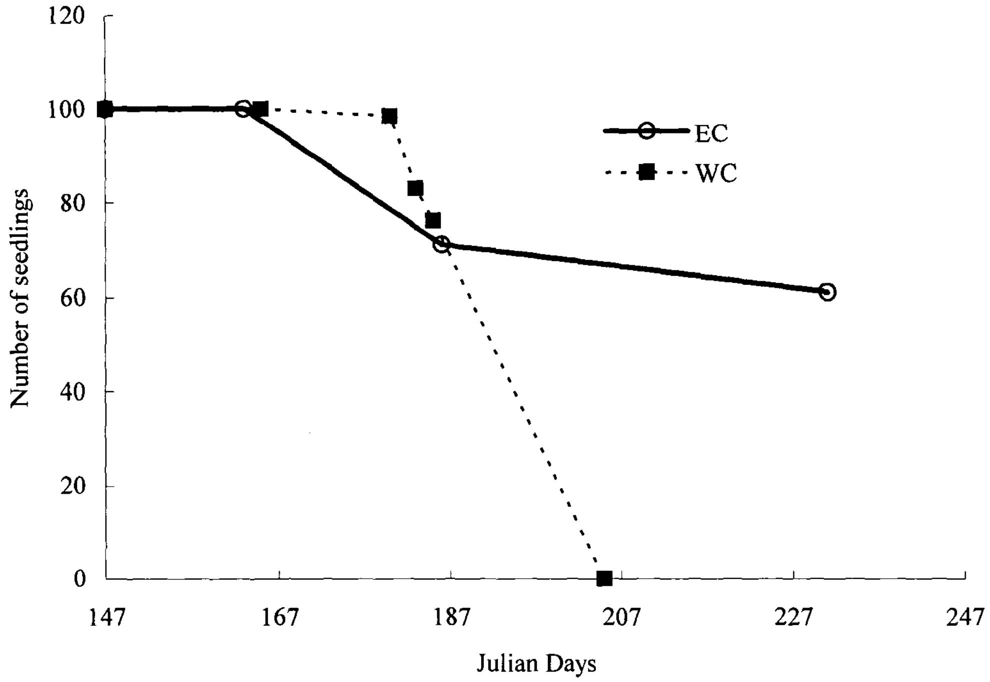

Figure 3.6: Survivorship of naturally occurring red maple seedlings on east coast (EC) and of planted seedlings on west coast (WC) study sites. A lack of naturally occurring seedlings on the WC necessitated planting. No seedlings survived on the WC.

Cages were effective in preventing small mammal seedling predation. On the west coast, small mammals did not consume any seedlings in cages, while four seedlings in control plots and one in an open cage were eaten by small mammals. Small mammals did not consume any seedlings on the east coast in 2005. There was no significant difference in the proportion of seedlings that disappeared ($F_{1,27} = 6.90$; $p = 0.0140$; $\alpha = 0.01$) between the west coast and the east coast. It is assumed that seedlings were removed by seedling predators, most likely slugs.

Since the proportion of seedlings that went missing from the three different types of treatments did not differ significantly when the two study areas are compared ($F_{2,27} = 2.59$; $p = 0.0939$), and there was no significant difference in the proportion of seedlings that disappeared, a *post hoc* analysis of the effects of study area on each type of treatment, and of the treatments in each study area could not be carried out.

None of the seedlings on the west coast survived. In both study areas, most seedling mortalities were due to dry conditions, and these deaths occurred over a short period of time (Fig. 3.6). In 2004, meadow voles were a source of mortality on the east coast, while in 2005 meadow voles did not consume any seedlings. Slug predation occurred on the east coast but not the west coast. Small mammal seedling predation was higher on the west coast than the east coast.

3.4 Comparison of recruitment and growth between east and west coast populations

At east coast sites, the reconstructed recruitment curve is episodic, with peaks occurring in 1993, 1997, 2000 and 2003 (Fig 3.7). Red maple seedlings and saplings appear to follow a reverse-J curve, explained by higher mortality in the younger age classes.

Although west coast sites were chosen in areas with high densities of reproductively active maples, there were few surviving seedlings and saplings. Along four 15 m transects at each site, the number of seedlings ranged from 1 to 8 on west coast sites, compared to 16 to 45 on east coast sites. Due to the scarcity of seedlings and saplings on west coast sites, and to reduce the effect of sampling on the study sites, 45 seedlings and saplings were collected from adjacent areas. Sites 1 and 2 were in close proximity to each other (~1km apart); therefore, an area in between both sites was chosen.

It is difficult to draw any conclusions on recruitment patterns on the west coast because of small number of seedlings available for aging. The low number of seedling collected and aged (n = 43; two could not be aged) on the west coast spanned a considerable age range (≤26 years of age) and it is possible that some age classes are not fully represented. However, the lack of recurring peaks in seedlings entering the west coast population suggests that recruitment was not episodic. To accurately reconstruct recruitment patterns on the west coast, a larger sample would be required, but such a large sample may damage the future populations.

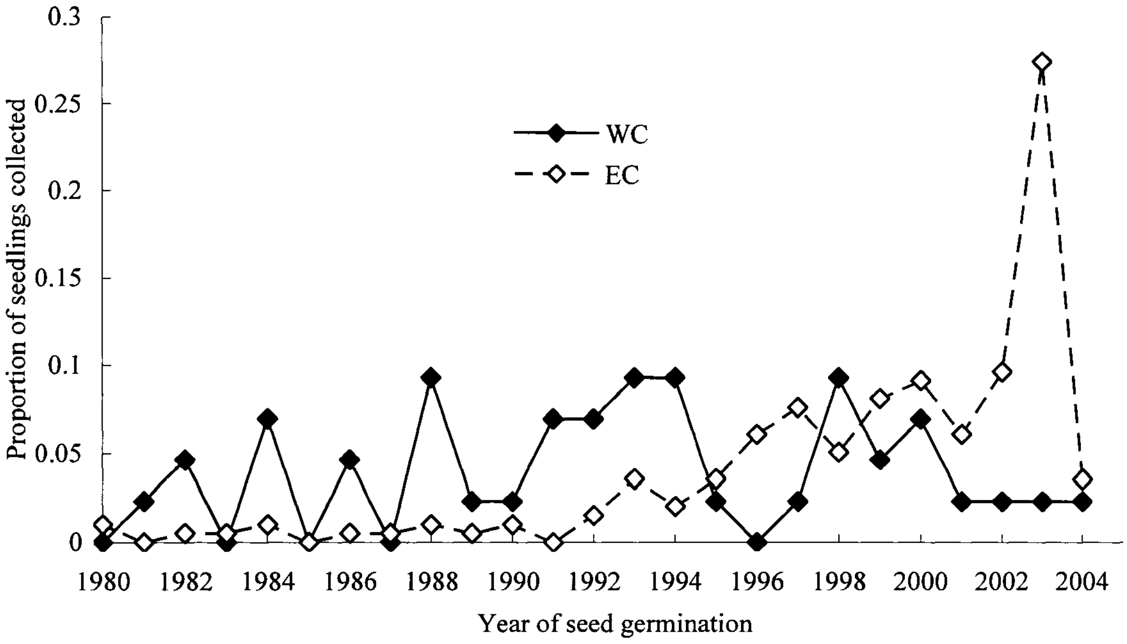

Figure 3.7: Year of seedling recruitment from counting annual growth rings and terminal bud scars of seedlings collected from west coast (WC; n = 43) and east coast (EC; n = 197) sites.

Moose are affecting the growth patterns of seedlings over 15 cm tall. Height and basal diameter of the red maple specimens collected from both areas are positively associated (east coast: $R^2adj = 70.6\%$, $F_{1, 194} = 468.49$, $p < 0.001$; west coast: $R^2adj = 65.1\%$, $F_{1, 40} = 77.43$, $p < 0.001$). On the east coast, the growth of saplings >15 cm tall were affected by moose herbivory, and when seedlings <15 cm, which were not browsed by moose, were removed from the analysis, the variation between the relationship of height and basal diameter increased on the east coast, (east coast: $R^2adj = 44.8\%$; west coast: $R^2adj = 63.5\%$), but the overall relationship still remained significant (east coast: $F_{1, 38} = 32.61$, $p < 0.001$; west coast: $F_{1, 36} = 65.35$, $p < 0.001$; Fig. 3.8a).

Due to moose herbivory, year of recruitment is not a good predictor of the height of saplings >15 cm tall (east coast: $R^2adj = 46.8\%$; west coast: $R^2adj = 11.9\%$), but the relationship remains significant (east coast: $F_{1, 38} = 35.28$, $p < 0.001$; west coast: $F_{1, 36} = 6.01$, $p = 0.019$; Fig 3.8b). Due to herbivory by moose and hares, year of recruitment is not a good predictor of the growth of seedlings and saplings. All collected red maple >15 cm tall (west coast = 90.7% of samples; east coast = 20.8% of samples) were browsed by moose or hare or the leader was damaged. Moose did not browse plants that were less than 15 cm tall.

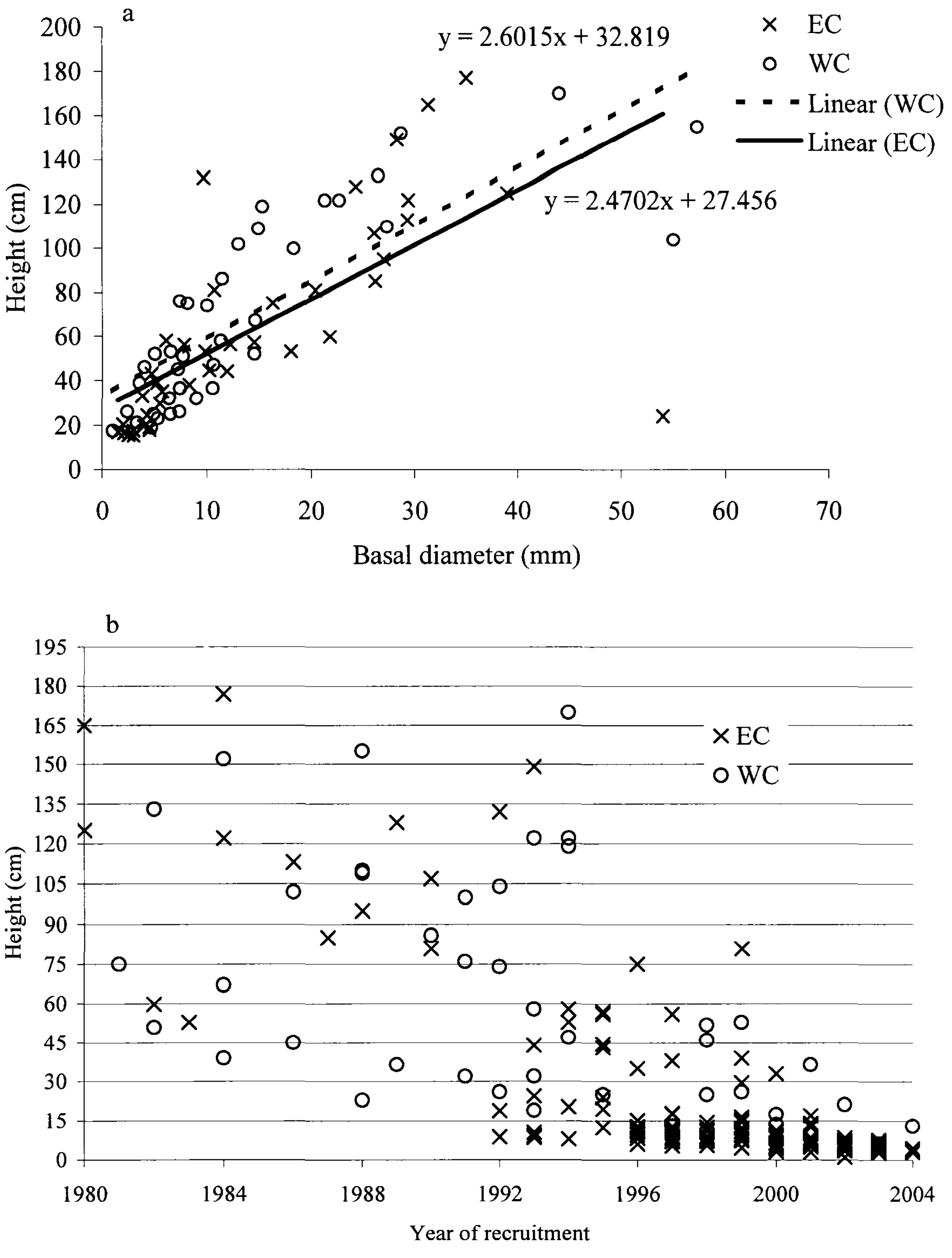

Fig 3.8: Pattern of red maple growth and recruitment. Height is associated with basal diameter (EC: R^2adj = 70.6%, $F_{1,194} = 468.49$, $p < 0.001$; WC: R^2adj = 65.1%, $F_{1,40} = 77.43$, $p < 0.001$) (a), and the year of recruitment (EC: R^2adj = 58.7%, $F_{1,194} = 278.64$, $p < 0.001$; WC: R^2adj = 21.4%, $F_{1,40} = 12.19$, $p = 0.001$) (b), but the variation increases when seedlings <15 cm are removed from the analysis (EC: R^2adj = 46.8%, $F_{1,38} = 35.28$, $p < 0.001$; WC: R^2adj = 11.9%, $F_{1,36} = 6.01$, $p = 0.019$). EC = east coast; WC = west coast.

3.5 Tracking stations

Small mammals that visited tracking stations included meadow voles on east coast sites, red-backed voles on west coast sites, and masked shrews in both study areas. Along with small mammal tracks, slug trails were visible through the soot.

Small mammals and slugs do not appear to be active predators of dormant red maple seeds. Slugs, red-backed voles, and masked shrews on the west coast, but not meadow voles and masked shrews on the east coast, were active predators of fresh red maple seeds. Although dormant red maple seeds disappeared, none used as bait had slug or small mammal damage. It is possible that missing seeds may have been completely consumed or washed away by rain. If seeds were consumed, it was expected that remnants from some seeds would have been found since the remnants of fresh red maple seeds were found with signs of small mammal and slug predation. Some stations did show evidence to suggest that seeds may have been washed out by rain.

3.5.1 Tracking stations and voles

Red-backed voles in Newfoundland may be larger than their mainland counterparts (Moss, 2002) making the tracks of these two species indistinguishable. Since no meadow voles were trapped on the west coast, it is assumed that red-backed voles and not meadow voles visited stations that experienced vole tracks on the west coast. Red-backed voles did not consume dormant red maple seeds on the west coast. When dormant red maple seeds were used as bait, 10.7% of stations experienced red-backed vole tracks. None of the seeds in these tracking stations went missing or showed signs of small mammal damage.

Red-backed voles may be a fresh red maple seed predator on the west coast. While there were no tracking stations with only red-backed vole tracks, 35.7% of stations on the west coast experienced both red-backed vole and shrew tracks. In these stations, 36.7% of available seeds were damaged by small mammals and 46.7% disappeared. The increase in small mammal damage and missing seeds compared to stations that experienced only shrew tracks (20.8% and 27.1%, respectively) suggests that fresh red maple seed predation increases in the presence of red-backed voles.

Meadow voles did not consume red maple seeds on the east coast of Newfoundland in 2005. On the east coast, when dormant red maple seeds were used as bait, meadow vole tracks occurred in 5.7% of tracking stations. When fresh red maple seeds were used as bait, meadow vole tracks occurred in 8.6% of tracking stations. In stations visited by meadow voles, all seeds were present and none showed signs of small mammal damage.

3.5.2 Tracking stations and slugs

Slugs did not consume or damage dormant red maple seeds, even though they were abundant in baited tracking stations (east coast = 40% of stations; west coast = 57% of stations). On the west and east coasts, 11.9% and 10.4% of seeds went missing, yet none of the seeds recovered showed any signs of slug damage. Since slug damage was only observed on green seeds, where only the photosynthetic part of the samaras but not the actual seeds were consumed, it is doubtful that dormant seeds that went missing were consumed by slugs.

Slugs graze immature red maple seeds and are an indirect factor in seed mortality. All tracking stations on east coast sites and 96.4% of tracking stations on west coast sites had slug trails when fresh seeds were used as bait. Tracking stations with fresh seeds were deployed later during periods of higher slug activity than those with dormant seeds. Of the stations with slug trails, slugs damaged 17.1% and 25.9% of fresh red maple seeds on east and west coast sites, respectively. When fresh red maple seeds were used as bait, damage by slugs was evident, especially on seeds used as bait from the west coast, which were greener and less dry than seeds from the east coast. While slugs did not consume the actual seeds, they did graze the samara and seed casing often resulting in death through fungal and/or bacterial infections.

3.5.3 Tracking stations and shrews

There was no direct evidence that masked shrews consumed dormant red maple seeds in 2005. When dormant red maple seeds were used as bait, shrew tracks were present in 11.4% and 53.6% of tracking stations on east coast sites and west coast sites, respectively. However, no seeds and 10.4% of seeds went missing on east coast sites and west coast sites, respectively. None of the recovered seeds showed any signs of small mammal damage and no remnants of seeds were found; therefore it is doubtful that shrews consumed the seeds that disappeared.

Shrews are active fresh maple seed predators on the west coast but not the east coast of Newfoundland. When fresh red maple seeds were used as bait, shrew tracks were present in 48.6% and 96.4% of stations on east and west coast sites, respectively. If the only tracks present were shrew tracks, seeds in stations on east coast sites did not incur any damage, while 20.8% of seeds in stations on west coast sites had damage and 27.1% disappeared.

In general, while some dormant red maple seeds disappeared, there is no evidence to suggest that small mammals or slugs consumed them. In the presence of red-backed voles, seed mortality increases. There are more active seed predators on the west coast as compared to the east coast. On the west coast, fresh red maple seeds are consumed by shrews, red-backed voles, and slugs, while on the east coast, only slugs damaged seeds.

Chapter 4: Discussion

The impacts of the newly introduced red-backed vole on the early life history stages of red maple in Newfoundland, a known red maple seed and seedling predator, are relatively minor when compared to other sources of mortality. An age survey of seedlings and saplings on the east and west coasts of the island showed that recruitment on the east coast, where red-backed voles are absent, is cyclical but high in recent years, while on the west coast recruitment has been extremely low, especially since 2001, which coincides with the arrival of red-backed voles to the area. This study revealed that rather than a simple reduction of seeds and seedlings by the non-native red-backed vole, it is the cumulative effects of high pre- and post-dispersal seed predation by unidentified insects, and high post-dispersal seed predation by introduced shrews, introduced red-backed voles, and slugs, and high seedling mortality due to desiccation that result in high mortality of the early life history stages of red maple on the west coast (Fig. 4.1).

The cumulative effects of numerous non-native species are exacerbating the effects on the regeneration abilities of a tree species at its northern range (Tremblay *et al.*, 1996) which evolved in an isolated ecosystem. Not only do red maples face competition from trees adapted to cooler conditions (Loehle, 1998), but early blooms may be damaged by late frosts, reducing seed productivity. Seedling and sapling growth is also constrained by the cooler climate and they face competition from other trees adapted to northern climates. Adding to these limitations, red maple is now vulnerable to the cumulative effects of introduced seed and seedling predators, which may lead to "invasional meltdowns" (Simberloff and Von Holle, 1999) of Newfoundland's ecosystems and increase their vulnerability to disturbances (Courchamp, 2000).

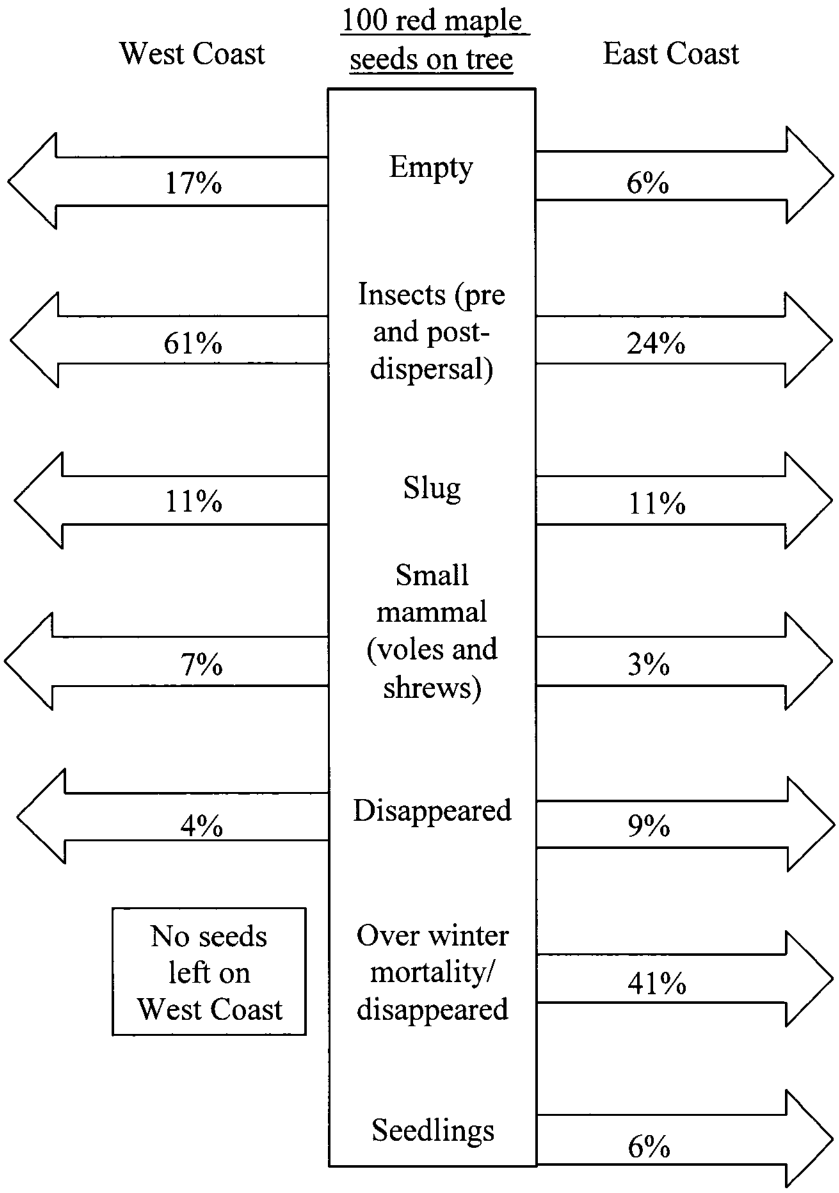

Figure 4.1: Comparison of the fate of 100 red maple seeds, showing causes of seed loss and resultant seedlings. On the west coast, no seeds survived to overwinter, while 6% of seeds on the east coast are recruited to the seedling stage. Results are based on pooled data from 2004 and 2005. Percent of empty seeds is based on pre-dispersal seed surveys of 2005. Percent of seeds lost to insects is based on pre- and post-dispersal seed surveys in 2005. Percent of seeds lost to slugs, small mammals or disappearances are based on post-dispersal seed surveys in 2005. Over winter mortality and percent germination are based on 2004 seed surveys.

Observations from the summer of 2005 suggest that the lack of red maple seedlings on the west coast can mainly be explained by high pre-dispersal seed predation by insects that results in early fruit dispersal. This not only reduced the seed crop, but also left the viable, although immature, seeds vulnerable to post-dispersal seed predation by a larger suite of seed predators than on the east coast. The cumulative effects of pre- and post- dispersal seed predation by insects, slugs, and small mammals on the west coast resulted in 100% seed loss at the four west coast study sites. In comparison, on the east coast 63.2% of viable seeds that were dispersed during the 2004 seed rain survived through to October, 21.9% survived to spring 2005, and 12.1% of dispersed seeds germinating in 2005.

Currently red maple sapling recruitment is greater on east coast than on west coast study sites. On the west coast, an extensive search for seedlings revealed that seedling recruitment has been hindered in recent years, while an age survey of saplings revealed that recruitment after 2001 was low. In contrast, seedling recruitment on the east coast is cyclical with peaks every 3 to 4 years, with a major peak in 2003. Red maple seedling banks are important for recruitment of red maple into the canopy when a gap becomes available (Tift and Fajvan, 1999). The lack of seedling populations on the west coast suggests that red maple will not be maintained as a canopy species, as opposed to the east coast which has an abundant seedling population.

4.1 Pre- and post-dispersal insect seed predation

Both on the east and west coasts, insects, their presence indicated by holes used to burrow into red maple seeds, were the most active seed predators. The identity of the insects requires further investigation. Insect seed predation is often cited as a major force in controlling plant population dynamics (Crawley, 1989). Graber and Leak (1992) found that unidentified burrowing Lepidoptera larvae were responsible for pre-dispersal seed predation for sugar maple (*Acer saccharum* Marsh.) seeds. On the west coast, insects reduced the number of pre-dispersed seeds by half, therefore did not cause total loss of the year's seed crop. Due to high rates of insect predation, dispersing seeds on the west coast were green and appeared to be aborted, whereas seeds on the east coast were mature and beginning to dry. About half of the seeds on the west coast were healthy and undamaged when dispersed and germination rates of undamaged seeds were similar to germination rates of healthy seeds from the east coast. Most plants respond to insect infestations by reducing seed size and mass, or by increasing seed and fruit abortion rates, but germination rates are usually not affected (Harper, 1977; Stephenson, 1981). This survival mechanism allows plants to reduce nutrient and energy losses and increases predator mortality (Fernandes and Whitham, 1989). The high rate of pre-dispersal insect predation does not completely explain the lack of seedling recruitment on the west coast. Pre-dispersal seed predation greatly reduced the number of healthy seeds but did not cause total loss of the year's seed output.

High seed predation immediately following dispersal on the west coast compared to the constant rate of seed predation on the east coast could indicate that seeds on the west coast were dispersed at a more palatable stage of development. Plucinski and Hunter (2001) found that most of the red maple seeds removed by rodents occurred within the first two weeks of seed placement. Some possible explanations included changing food preferences as finding seeds became more difficult, changing seed palatability with age, or increased availability of alternate food sources. Red maple seeds are known to have alkaloids that deter insect predators (Barbosa and Krischik, 1987), and seeds dispersed early may have reduced chemical defences, increasing vulnerability to post-dispersal seed predators. It is also possible that anti-predatory adaptations vary between the two study areas, although this would be unlikely due to the relatively close proximity and similar history. Testing the alkaloid levels of red maple seeds from east and west coast sites can determine whether seeds completely lacked chemical anti-predatory mechanisms or whether the high predation rates were due to immaturity.

4.2 Slugs and red maple seeds and seedlings

Slugs reduced seed survival both on east and west coast sites. There are ten species of slugs established on the island (Maunder, 1985) and in balsam fir forests, higher densities of slugs are associated with higher amounts of deciduous litter (Goudie, 1997). Research sites in this study were predominantly balsam fir forest types intermixed with a high hardwood component, therefore deciduous leaf litter was abundant allowing for high slug activity. While slugs did not consume the entire seed, but rather grazed the photosynthetic parts of the samara, this activity increased seed mortality through increased exposure to pathogens. Damage caused by slugs to plants and other sources of abrasions can lead to increased rates of infections because damaged areas provide entry points for pathogens (Beute and Benson, 1979; Bateman, 1997).

In our study, slugs were an important source of seedling mortality on the east coast, but were not on the west coast. It is possible that slugs did not consume seedlings on the west coast as more palatable food was available, such as the immature red maple seeds, or that the seedlings died due to desiccation before the slugs had a chance to eat them. In contrast to the west coast, slug herbivory was a source of red maple seedling mortality on the east coast. Slugs consumed just as many seedlings in 2004 as meadow voles and 4.6% of seedlings in 2005. Red maple seeds were also a food source for slugs, suggesting that slug herbivory on red maple seed and seedlings since they were dropped at a more mature and drier state with no photosynthetic material available for consumption.

Other studies have demonstrated that slugs and snails can be an important source of maple seedling mortality. For example, in New York forests, Gardescu (2003) found that slug herbivory was an important cause of mortality for first year sugar maple seedlings. Hotopp (2002) found that in hardwood forests, snails and slugs were positively associated with the basal area of sugar maples, but were negatively associated with the basal area of red maple, which ranged from 1.70 to 6.22 m^2/ha. The difference in gastropod activity with this study could be due to differences in forest types between west coast sites and Hotopp's study sites. Also, Hotopp did not distinguish between slugs and snails, therefore it may be possible that the correlation is strongly influenced by snails which have higher calcium requirements than slugs. Red maples are negatively correlated with the calcium in the forest duff soil horizon (Hotopp, 2002). On the east coast, Noel (2004) found that slugs were a source of balsam fir seedling mortality through herbivory. A more in depth investigation into the effects of slugs on the biodiversity and structure of Newfoundland forests is required.

4.3 Shrews and red maple seeds

Introduced in 1958 (Dodds, 1983), masked shrews have become one of the most abundant mammals in Newfoundland (Tucker *et al.*, 1988). They are known to act as seed predators (Criddle, 1973), and are known to be predators of black spruce and white pine seed (Hermanutz and Kasimos, unpublished). A stomach content analysis of shrews caught in prairie fields revealed that while they tend to be insectivorous, their diets are dependent on the availability of food and are able to switch to a granivorous diet when insects are not available in the winter (Criddle, 1973).

While shrews did not consume red maple seedlings or dormant red maple seeds, they did consume fresh red maple seeds from the west coast. Wings of immature red maple seeds with teeth marks were found in tracking stations, even if the only tracks present were shrew tracks, unambiguously indicating that shrews consume fresh red maple seeds. The difference in shrew diets between the east coast and the west coast may be a reflection of food availability or food quality. Since a larger suite of seed predators is present on the west coast, including red-backed vole population which may be at its peak, there may be more competition for food forcing shrews to switch to a less preferred food. Alternatively, the incidence of shrew predation could be an indication of the difference in seed palatability between the east and the west coast, as was already discussed.

It is also possible that the higher incidence of apparent shrew seed predation was a result of shrews attempting to retrieve insects within seeds. If this were the case, seeds would have shown evidence of, and been classified as shrew damaged as opposed to insect damaged as shrew damage would mask any damage caused by insects. To account for this possibility, seeds used as bait in tracking stations were screened for insect damage before and after each trial.

4.4 Meadow voles and red maple seeds and seedlings

Indigenous meadow voles were not trapped on the west coast and low populations were recorded for 2005 on the east coast (J. Gosse, pers. comm., 2005). The lack of meadow voles on the west coast is probably due to a naturally occurring low in their population cycle as was observed on the east coast (J. Sharpe, pers. com., 2005) or due to competitive exclusion by other rodent species (Eadie, 1953; Cameron, 1964; Birney *et al.*, 1976; Martell, 1981; Manson and Stiles, 1998; Manson *et al.*, 1998; Manson *et al.*, 1999; Nickel *et al.*, 2003). However, Payne (1974) observed how an experimental population of introduced red-backed voles on Camel Island, Newfoundland co-habited with meadow voles in 4 of the 5 types of areas studied, including forests, partial tuckamore, bogs, and heath-shrub barrens. Meadow voles were not found on the fifth type of site, burn sites, and red-backed voles were rarely trapped on this type of site. Meadow voles occupy more habitats in Newfoundland than on mainland North America, which may offer foods which are preferred over red maple seeds. In western Labrador (Simon *et al.*, 1998) and in New York (Manson *et al.*, 1999), meadow voles are positively associated with grasses and sedges that provide both food and cover, whereas in Newfoundland, meadow voles likewise also prefer grassy and herbaceous fields, but are also found throughout the forested habitats (Cameron, 1964; Riewe, 1971; Riewe, 1973; Payne, 1974). The diet of meadow voles on islands in Notre Dame Bay, Newfoundland, consists of non-vascular plants commonly found in densely forested areas. In subnivian food caches, fall dandelion and various clover species are commonly found (Riewe, 1971; 1973).

There is no direct evidence to suggest that meadow voles are important red maple seed or seedlings predators on insular Newfoundland. Unlike studies in New York, where red maple seedling colonization in old fields is negatively correlated with meadow vole density and vole seed predation was more important than seed predation by deer mice (Manson *et al.,* 2001), small mammal seed predation does not appear to be an important source of red maple seed mortality on the east coast. In central New York State, seedling predation by meadow voles is the largest source of seedling mortality, especially under the herb canopy where competition from taller forbs is usually assumed to be more significant (Gill and Marks, 1999). Ostfeld and Canham (1993) suggested that by predation of seeds and seedlings, meadow voles act as a keystone species by affecting seedling abundances and distributions.

4.5 Red-backed voles and red maple seeds and seedlings

Red-backed voles, unlike meadow voles, did appear to be significant red maple seed predators but were not a major source of mortality. The food habits of red-backed voles in Newfoundland have not been investigated because their presence has only been recently documented (B. Hearn, pers. comm., 2004), with the exception of Payne's (1974) experiments. In northern Ontario, red-backed voles exhibit a seasonal pattern of dietary preference, probably based on availability (Martell, 1981). Lichens, such as *Cladina* spp. and *Cladonia* spp., dominate the diets from early May and throughout the summer. Lichens and fungi make up 80-89% of their diets. Herbaceous plant matter is consumed as it becomes available from mid-May to mid-July. Seeds are important from June to July and berries are important in late July. Despite the importance of lichens in the diets of populations in northern Ontario, in western Labrador the presence of red-backed voles is negatively associated with the presence of lichens (Simon *et al.*, 1998).

It is only recently that the significant effects of small mammals on their habitats have been recognized (Gill and Marks, 1991; Bergeron and Jodoin, 1993; Ostefeld *et al.*, 1997; Manson *et al.*, 2001; Puettmann and Saunders, 2001; Pusenius and Ostfeld, 2002; Schnurr *et al.*, 2002; Côté *et al.*, 2003). While small mammals on the west coast had a significant impact on naturally occurring and experimental seeds, it is not possible to unequivocally attribute this solely to red-backed voles due to high shrew activity on these sites. However, fresh red maple seed predation was greater in tracking stations having red-backed vole tracks, suggesting that red-backed voles are significant predators of red maple seeds.

On the west coast, it appears that red-backed voles ate only 1.4% of seedlings, and at only 2 sites, despite their high densities around the immediate area of the study trees. It is possible, such as with slugs, that seedlings died due to desiccation before red-backed voles even had a chance to consume them. The high density of red-backed voles can be explained by the fact that only a small area was intensively trapped over a two-day period. It is possible the high number of red-backed voles may be due to an attraction to the area by the presence of red maple seeds. It is also possible that the high density of red-backed voles is due to an exponential increase that is typical of new species, or the lack of a full suite of competitors.

In the absence of other seed predators, or in years of low pre-dispersal insect seed predation resulting in an increase in the amount of available seeds, it is predicted that re-backed voles, and possibly shrews, will be important red maple seed predators. It is also predicted that seed predation by red-backed voles will have the greatest effect in newly disturbed sites or sites where the forest canopy is opening, because recruitment of red maples in these habitats is mostly through seeds as opposed to sprouting from stumps or roots (Abrams, 1998; Tift and Fajvan, 1999). Red maples tend to follow a Type III survivorship curve, where seeds, seedlings and saplings experience high mortality, but survival of larger size classes is high (Volk and Fahey, 1994). Therefore, red-backed voles may contribute to the failure of red maple recruitment to the canopy layer through seed predation in areas where the level of seed predation by other animals, such as introduced slugs and shrews is already high. Red-backed voles do have the potential to increase seed mortality through seed predation, thereby reducing recruitment of red maples from seeds in areas where other sources of seed predation are low. However, further investigation into the interactions between red-backed voles and other seed predators is required to determine whether red-backed voles will act as seed predators in the absence of other seed predators.

4.6 Hare and red maple seedlings

Extensive surveys quantifying snowshoe hare herbivory showed no evidence that hare, which were at a low in their population cycle during this study (Reynolds, *et al.*, 2004) are red maple seedling predators. Wolff (1978) concluded that the frequency of occurrence and density of a plant species is an important factor determining the food preferences of hares, and this preference is best examined during low population densities. While they may not have preferred red maple seedlings, during peak population years hare, like other small mammals with cyclical populations, may play an important role in maple seedling survival. Dodds (1960) investigated habitat usage by hares in Newfoundland. Moose have a significant effect on suitable cover for hare, especially in regenerating balsam fir stands. Sites used in this investigation were disturbed balsam fir dominated stands, with high moose activity. This limited suitable cover for hare, which may explain the lack of hare activity at these sites.

4.7 Seedling survival and leaf litter

Most naturally occurring seedlings on the east coast and planted seedlings on the west coast died due to dry soil and this mortality may explain the relative unimportance of both slugs and red-backed voles on the west coast as seedling predators. On the east coast, the leaf litter in which most seeds germinated was unsuitable for their survival because the radicles were unable to physically penetrate the leaf litter and into the moist soil below. While the germination requirements of seeds were met in the leaf litter, seedlings were unable to survive. The moist microenvironment created by the leaf litter may be important for the germination of seedlings in the spring, but if the seedlings cannot penetrate the undecomposed leaf litter, it is a hindrance to survival (Koroleff, 1954; Sydes and Grime, 1981). While red maple seeds were dispersed before leaves abscised in the fall, there was a considerable amount of undecomposed leaf litter on the forest floor from previous years that prevented roots from reaching the soil.

The removal of the leaf litter when seedlings were planted on the west coast may have removed the moist microenvironment and the protection from desiccation. On the west coast, the leaf litter was partially removed to expose the soil before seedlings were planted. This meant that the soil where the seedlings were planted dried whereas the soil under the leaf litter was moist. While a small amount of leaf litter is favourable to keep the soil moist, too much can actually hinder the establishment of seedlings.

Chapter 5: Conclusion

The three hypothesis tested can all be accepted: red maple from the west coast of Newfoundland have the same recruitment potential as red maple from the east coast of Newfoundland; red maple seeds on the west coast, where red-backed voles are present, experience higher rates of small mammal predation than seeds on the east coast, where red-backed voles are absent; and red maple seedlings on the west coast experience higher rates of small mammal predation than seedlings on the east coast.

The cumulative effects of introduced slugs, masked shrews, and red-backed voles on seeds, coupled with high pre-dispersal seed predation by insects, are preventing the regeneration of red maple in western Newfoundland in sites dominated by balsam fir; while on the east coast despite seed predation by insects, slugs and meadow voles, 12.1% of monitored seeds from the 2004 seed rain germinated in 2005, and there is a significantly greater percentage of seedling survival. This study has shown that masked shrews are a major red maple seed predator in Newfoundland on the west coast. Due to the early release of red maple seeds, possibly due to high levels of insect infestation, slugs were able to exploit the immature seeds, making them a significant seed predator on the west coast. Seed predation also increased in the presence of the newly introduced red-backed voles. Due to the cumulative effects of all of these seed predators, none of the naturally occurring red maple seeds on the west coast survived to the end of the monitoring period in 2005, threatening the persistence of red maple in disturbed habitats. With the invasion of red-backed voles to the east coast, it is possible that the cumulative effects of another red maple predator will cause a decline in the recruitment of red maple.

Their presence may cause these and other predators to seek food sources previously under utilized, such as red maple seeds.

Further investigation is required into the identity of the insects causing the high pre-dispersal mortality of red maple seeds, the importance of slugs as red maple seed predators on the west coast and as red maple seedling predators, and the importance of shrews as red maple seed predators. Future studies need to investigate the effects of these predators on forest structure. Research is needed to determine if population dynamics of seed and seedling predators pose a long term threat to red maple and possible interspecific interactions with other seed predators should be investigated. Management of these seed and seedling predators may be necessary to prevent a decline of red maple populations.

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Appendix A

Table A.1: UTM (Zone 21, North latitude) of study sites on the west coast and east coast of Newfoundland.

West Coast	**Northing**	**Easting**
Pasadena Site 1	5421903	455454
Pasadena Site 2	5420786	455557
Hughe's Brook Site 3	5432101	437499
Hughe's Brook Site 4	5429798	442618
East Coast		
Terra Nova Grade Site 1	5379462	721029
Terra Nova Grade Site 2	5379468	720890
Blue Hill	5387168	723694
Blue Hill East Site 1	5387498	723077
Blue Hill East Site 2	5387539	723146
Louil's Hill	5392699	724822
Dunphy's Pond	5367606	712153

Appendix B

Table B.1: Descriptions of sites where transects were used to survey hare browsing. Site richness and site descriptions from Meades and Moores (1989). Potential browse points are the number of plant tips available to hare, below the highest tip browsed. No seedlings were browsed. (vp = very poor; p = poor; m = medium; r = rich; vr = very rich).

Site	Site Richness	Area Surveyed (m^2)	Potential Browse Points	Total Points Browsed	Number of *Acer rubrum* seedlings
Arnold's Pond Site 1	m - r	60	122	34	
Arnold's Pond Site 2	p	20	6859	62	
Blue Hill Site 1	m - r	40	5331	161	7
Blue Hill Site 2	m - r	30	367	5	3
Blue Hill Site 3	m - r	20	340	0	3
Bread Cove Brook Site 1	m - r	30	182	12	
Bread Cove Brook Site 2	m - r	30	545	0	
Davey Anne Pond Site 1	p - m	30	629	0	
Davey Anne's Pond Site 2	m - r	20	497	0	
Davey Anne's Pond Site 3	m - r	30	79	0	
Dunphy's Pond Site 1	m - r	40	641	41	167
Dunphy's Pond Site 2	m - r	20	1908	0	
Dunphy's Pond Site 3	m - r	20	298	0	
Dunphy's Pond Site 4	m - r	20	166	3	6
Dunphy's Pond Site 5	r - vr	30	1943	60	
Louil's Hill Site 1	r - vr	20	236	6	3
Louil's Hill Site 2	r - vr	30	408	27	9
Malady Head	r - vr	30	256	72	
Pine Hill Pond	m - r	60	388	186	
Rocky Pond Site 1	vp - p	50	71	7	
Rocky Pond Site 2	r - vr	30	669	3	
Rocky Pond Site 3	p - m	40	4699	87	
Swale Island	r - vr	40	2678	194	
Terra Nova Grade Site 1	m - r	22	314	1	15
Terra Nova Grade Site 2	m - r	14	132	67	1
Terra Nova Grade Site 3	m - r	20	84	19	
Terra Nova Road Site 1	m - r	30	147	2	
Terra Nova Road Site 2	m - r	80	203	90	
Terra Nova Road Site 3	m - r	30	231	0	
Terra Nova Road Site 4	m - r	30	2347	15	

Table B.2: Total number of potential browse points, number of points browsed, percent availability, percent use by hare, and palatability factors for each site. Percent availability is the number of potential browse points of the plant, divided by total number of potential browse points for all plants within the transect, multiplied by 100. Percent use is the total number of points browsed, divided by the number of potential browse points for that plant, multiplied by 100. Palatability factor is a ratio of percent use to percent available.

Arnold's Pond Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Populus tremuloides	10	0.12	4	40.00	333.48
Sorbus sp.	12	0.14	1	8.33	57.90
Abies balsamea	18	0.22	2	11.11	51.46
Alnus crispa	1532	18.38	40	2.61	0.14
Picea mariana	6540	78.45	5	0.08	0.00
Acer rubrum	4	0.05	0	0.00	0.00
Amelanchier sp.	1	0.01	0	0.00	0.00
Nemopanthus mucronata	113	1.36	0	0.00	0.00
Viburnum cassinoides	2	0.02	0	0.00	0.00
Acer spicatum	0	0.00			
Betula papyrifera	0	0.00			

Arnold's Pond Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Viburnum cassinoides	10	0.14	2	20.00	147.80
Alnus crispa	628	8.50	7	1.11	0.13
Picea mariana	6640	89.85	60	0.90	0.01
Nemopanthus mucronata	55	0.74	0	0.00	0.00
Sorbus sp.	13	0.18	0	0.00	0.00
Abies balsamea	0	0.00			
Acer rubrum	0	0.00			
Acer spicatum	0	0.00			
Amelanchier sp.	0	0.00			
Betula papyrifera	0	0.00			
Populus tremuloides	0	0.00			

Blue Hill Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Sorbus sp.	13	0.24	2	15.38	63.09
Betula papyrifera	22	0.41	5	22.73	55.07
Viburnum cassinoides	31	0.58	5	16.13	27.74
Acer rubrum	107	2.01	44	41.12	20.49
Amelanchier sp.	109	2.04	11	10.09	4.94
Nemopanthus mucronata	65	1.22	1	1.54	1.26
Alnus crispa	801	15.03	4	0.50	0.03
Picea mariana	3760	70.53	73	1.94	0.03
Abies balsamea	261	4.90	0	0.00	0.00
Acer spicatum	0	0.00			
Populus tremuloides	0	0.00			

Blue Hill Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Populus tremuloides	12	3.27	1	8.33	2.55
Amelanchier sp.	16	4.36	1	6.25	1.43
Acer rubrum	91	24.80	3	3.30	0.13
Acer spicatum	11	3.00	0	0.00	0.00
Betula papyrifera	39	10.63	0	0.00	0.00
Nemopanthus mucronata	23	6.27	0	0.00	0.00
Picea mariana	122	33.24	0	0.00	0.00
Sorbus sp.	30	8.17	0	0.00	0.00
Abies balsamea	0	0.00			
Alnus crispa	0	0.00			
Viburnum cassinoides	0	0.00			

Blue Hill Site 3

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Abies balsamea	18	5.29	0	0.00	0.00
Acer rubrum	150	44.12	0	0.00	0.00
Amelanchier sp.	61	17.94	0	0.00	0.00
Nemopanthus mucronata	13	3.82	0	0.00	0.00
Sorbus sp.	5	1.47	0	0.00	0.00
Viburnum cassinoides	55	16.18	0	0.00	0.00
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Betula papyrifera	0	0.00			
Picea mariana	0	0.00			
Populus tremuloides	0	0.00			

Bread Cove Brook Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Betula papyrifera	19	4.09	2	10.53	2.58
Acer spicatum	71	15.27	10	14.08	0.92
Abies balsamea	254	54.62	0	0.00	0.00
Nemopanthus mucronata	7	1.51	0	0.00	0.00
Picea mariana	29	6.24	0	0.00	0.00
Populus tremuloides	5	1.08	0	0.00	0.00
Sorbus sp.	3	0.65	0	0.00	0.00
Acer rubrum	0	0.00			
Alnus crispa	0	0.00			
Amelanchier sp.	0	0.00			
Viburnum cassinoides	0	0.00			

Bread Cove Brook Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Abies balsamea	113	20.73	0	0.00	0.00
Acer rubrum	10	1.83	0	0.00	0.00
Amelanchier sp.	14	2.57	0	0.00	0.00
Betula papyrifera	407	74.68	0	0.00	0.00
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Nemopanthus mucronata	0	0.00			
Picea mariana	0	0.00			
Populus tremuloides	0	0.00			
Sorbus sp.	0	0.00			
Viburnum cassinoides	0	0.00			

Davey Anne's Pond Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	189	30.05	0	0.00	0.00
Amelanchier sp.	42	6.68	0	0.00	0.00
Betula papyrifera	91	14.47	0	0.00	0.00
Nemopanthus mucronata	62	9.86	0	0.00	0.00
Sorbus sp.	175	27.82	0	0.00	0.00
Viburnum cassinoides	39	6.20	0	0.00	0.00
Abies balsamea	0	0.00			
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Picea mariana	0	0.00			
Populus tremuloides	0	0.00			

Davey Anne's Pond Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	19	3.82	0	0.00	0.00
Alnus crispa	175	35.21	0	0.00	0.00
Amelanchier sp.	87	17.51	0	0.00	0.00
Nemopanthus mucronata	74	14.89	0	0.00	0.00
Sorbus sp.	25	5.03	0	0.00	0.00
Viburnum cassinoides	58	11.67	0	0.00	0.00
Abies balsamea	0	0.00			
Acer spicatum	0	0.00			
Betula papyrifera	0	0.00			
Picea mariana	0	0.00			
Populus tremuloides	0	0.00			

Davey Anne's Pond Site 3

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Amelanchier sp.	16	20.25	0	0.00	0.00
Nemopanthus mucronata	33	41.77	0	0.00	0.00
Sorbus sp.	21	26.58	0	0.00	0.00
Abies balsamea	0	0.00			
Acer rubrum	0	0.00			
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Betula papyrifera	0	0.00			
Picea mariana	0	0.00			
Populus tremuloides	0	0.00			
Viburnum cassinoides	0	0.00			

Dunphy's Pond Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Betula papyrifera	6	0.94	5	83.33	89.03
Sorbus sp.	3	0.47	1	33.33	71.22
Acer rubrum	292	45.55	30	10.27	0.23
Alnus crispa	136	21.22	3	2.21	0.10
Abies balsamea	189	29.49	2	1.06	0.04
Amelanchier sp.	12	1.87	0	0.00	0.00
Picea mariana	18	2.81	0	0.00	0.00
Viburnum cassinoides	3	0.47	0	0.00	0.00
Acer spicatum	0	0.00			
Nemopanthus mucronata	0	0.00			
Populus tremuloides	0	0.00			

Dunphy's Pond Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Betula papyrifera	20	1.05	7	35.00	33.39
Abies balsamea	38	1.99	0	0.00	0.00
Acer rubrum	57	2.99	0	0.00	0.00
Alnus crispa	35	1.83	0	0.00	0.00
Amelanchier sp.	7	0.37	0	0.00	0.00
Nemopanthus mucronata	5	0.26	0	0.00	0.00
Picea mariana	1741	91.25	0	0.00	0.00
Sorbus sp.	4	0.21	0	0.00	0.00
Viburnum cassinoides	14	0.73	0	0.00	0.00
Acer spicatum	0	0.00			
Populus tremuloides	0	0.00			

Dunphy's Pond Site 3

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Abies balsamea	79	26.51	0	0.00	0.00
Acer rubrum	79	26.51	0	0.00	0.00
Amelanchier sp.	46	15.44	0	0.00	0.00
Nemopanthus mucronata	10	3.36	0	0.00	0.00
Populus tremuloides	54	18.12	0	0.00	0.00
Sorbus sp.	3	1.01	0	0.00	0.00
Viburnum cassinoides	27	9.06	0	0.00	0.00
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Betula papyrifera	0	0.00			
Picea mariana	0	0.00			

Dunphy's Pond Site 4

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	66	39.76	3	4.55	0.11
Abies balsamea	50	30.12	0	0.00	0.00
Amelanchier sp.	24	14.46	0	0.00	0.00
Populus tremuloides	3	1.81	0	0.00	0.00
Sorbus sp.	12	7.23	0	0.00	0.00
Viburnum cassinoides	2	1.20	0	0.00	0.00
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Betula papyrifera	0	0.00			
Nemopanthus mucronata	0	0.00			
Picea mariana	0	0.00			

Dunphy's Pond Site 5

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Betula papyrifera	8	0.41	3	37.50	91.08
Acer rubrum	23	1.18	23	100.00	84.48
Alnus crispa	144	7.41	10	6.94	0.94
Abies balsamea	137	7.05	3	2.19	0.31
Picea mariana	1485	76.43	14	0.94	0.01
Acer spicatum	3	0.15	0	0.00	0.00
Sorbus sp.	2	0.10	0	0.00	0.00
Amelanchier sp.	0	0.00			
Nemopanthus mucronata	0	0.00			
Populus tremuloides	0	0.00			
Viburnum cassinoides	0	0.00			

Louil's Hill Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Populus tremuloides	21	8.90	1	4.76	0.54
Acer rubrum	27	11.44	1	3.70	0.32
Acer spicatum	63	26.69	1	1.59	0.06
Abies balsamea	80	33.90	0	0.00	0.00
Amelanchier sp.	14	5.93	0	0.00	0.00
Sorbus sp.	2	0.85	0	0.00	0.00
Viburnum cassinoides	4	1.69	0	0.00	0.00
Alnus crispa	0	0.00			
Betula papyrifera	0	0.00			
Nemopanthus mucronata	0	0.00			
Picea mariana	0	0.00			

Louil's Hill Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Alnus crispa	30	7.35	10	33.33	4.53
Acer rubrum	52	12.75	25	48.08	3.77
Acer spicatum	14	3.43	1	7.14	2.08
Viburnum cassinoides	14	3.43	1	7.14	2.08
Abies balsamea	273	66.91	0	0.00	0.00
Amelanchier sp.	2	0.49	0	0.00	0.00
Betula papyrifera	8	1.96	0	0.00	0.00
Nemopanthus mucronata	10	2.45	0	0.00	0.00
Picea mariana	0	0.00			
Populus tremuloides	0	0.00			
Sorbus sp.	0	0.00			

Malady Head

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Populus tremuloides	22	8.59	5	22.73	2.64
Sorbus sp.	63	24.61	25	39.68	1.61
Acer spicatum	105	41.02	43	40.95	1.00
Viburnum cassinoides	44	17.19	2	4.55	0.26
Abies balsamea	15	5.86	0	0.00	0.00
Acer rubrum	5	1.95	0	0.00	0.00
Nemopanthus mucronata	18	7.03	0	0.00	0.00
Alnus crispa	0	0.00			
Amelanchier sp.	0	0.00			
Betula papyrifera	0	0.00			
Picea mariana	0	0.00			

Pine Hill Pond

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Betula papyrifera	71	2.01	67	94.37	46.89
Acer rubrum	115	3.26	87	75.65	23.21
Sorbus sp.	39	1.11	10	25.64	23.20
Viburnum cassinoides	33	0.94	1	3.03	3.24
Alnus crispa	393	11.14	64	16.28	1.46
Amelanchier sp.	195	5.53	7	3.59	0.65
Abies balsamea	789	22.36	5	0.63	0.03
Nemopanthus mucronata	73	2.07	0.00	0.00	0.00
Picea mariana	1746	49.49	0.00	0.00	0.00
Acer spicatum	0	0.00			
Populus tremuloides	0	0.00			

Rocky Pond Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Populus tremuloides	152	99.35	24	15.79	0.16
Abies balsamea	0	0.00			
Acer rubrum	0	0.00			
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Amelanchier sp.	0	0.00			
Betula papyrifera	0	0.00			
Nemopanthus mucronata	0	0.00			
Picea mariana	0	0.00			
Sorbus sp.	0	0.00			
Viburnum cassinoides	0	0.00			

Rocky Pond Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	16	2.39	2	12.50	5.23
Populus tremuloides	34	5.08	1	2.94	0.58
Amelanchier sp.	7	1.05	0	0.00	0.00
Picea mariana	606	90.58	0	0.00	0.00
Sorbus sp.	3	0.45	0	0.00	0.00
Viburnum cassinoides	3	0.45	0	0.00	0.00
Abies balsamea	0	0.00			
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Betula papyrifera	0	0.00			
Nemopanthus mucronata	0	0.00			

Rocky Pond Site 3

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Alnus crispa	781	16.62	86	11.01	0.66
Betula papyrifera	27	0.57	0	0.00	0.00
Picea mariana	3867	82.29	0	0.00	0.00
Abies balsamea	0	0.00			
Acer rubrum	0	0.00			
Acer spicatum	0	0.00			
Amelanchier sp.	0	0.00			
Nemopanthus mucronata	0	0.00			
Populus tremuloides	0	0.00			
Sorbus sp.	0	0.00			
Viburnum cassinoides	0	0.00			

Swale Island

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Sorbus sp.	64	2.39	9	14.06	5.88
Acer spicatum	233	8.70	112	48.07	5.52
Populus tremuloides	140	5.23	23	16.43	3.14
Abies balsamea	125	4.67	9	7.20	1.54
Alnus crispa	911	34.02	14	1.54	0.05
Betula papyrifera	4	0.15	0	0.00	0.00
Nemopanthus mucronata	56	2.09	0	0.00	0.00
Acer rubrum	0	0.00			
Amelanchier sp.	0	0.00			
Picea mariana	0	0.00			
Viburnum cassinoides	0	0.00			

Terra Nova Grade Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	114	36.31	1	0.88	0.02
Abies balsamea	43	13.69	0	0.00	0.00
Amelanchier sp.	20	6.37	0	0.00	0.00
Betula papyrifera	17	5.41	0	0.00	0.00
Picea mariana	63	20.06	0	0.00	0.00
Sorbus sp.	35	11.15	0	0.00	0.00
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Nemopanthus mucronata	0	0.00			
Populus tremuloides	0	0.00			
Viburnum cassinoides	0	0.00			

Terra Nova Grade Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Betula papyrifera	23	3.85	8	34.78	9.03
Populus tremuloides	27	4.52	11	40.74	9.01
Acer rubrum	68	11.39	46	67.65	5.94
Abies balsamea	54	9.05	3	5.56	0.61
Alnus crispa	389	65.16	9	2.31	0.04
Nemopanthus mucronata	22	3.69	0	0.00	0.00
Picea mariana	24	4.02	0	0.00	0.00
Sorbus sp.	4	0.67	0	0.00	0.00
Viburnum cassinoides	4	0.67	0	0.00	0.00
Acer spicatum	0	0.00			
Amelanchier sp.	0	0.00			

Terra Nova Grade Site 3

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Betula papyrifera	20	23.81	17	85.00	3.57
Sorbus sp.	10	11.90	2	20.00	1.68
Abies balsamea	48	57.14	0	0.00	0.00
Acer rubrum	3	3.57	0	0.00	0.00
Picea mariana	3	3.57	0	0.00	0.00
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			
Amelanchier sp.	0	0.00			
Nemopanthus mucronata	0	0.00			
Populus tremuloides	0	0.00			
Viburnum cassinoides	0	0.00			

Terra Nova Road Site 1

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	14	3.10	0	0.00	0.00
Alnus crispa	304	67.41	0	0.00	0.00
Amelanchier sp.	29	6.43	0	0.00	0.00
Betula papyrifera	30	6.65	0	0.00	0.00
Populus tremuloides	11	2.44		0.00	0.00
Abies balsamea	0	0.00			
Acer spicatum	0	0.00			
Nemopanthus mucronata	0	0.00			
Picea mariana	0	0.00			
Sorbus sp.	0	0.00			
Viburnum cassinoides	0	0.00			

Terra Nova Road Site 2

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Populus tremuloides	58	1.84	49	84.48	46.03
Acer rubrum	47	1.49	21	44.68	30.04
Viburnum cassinoides	29	0.92	7	24.14	26.30
Sorbus sp.	55	1.74	10	18.18	10.45
Amelanchier sp.	115	3.64	13	11.30	3.11
Alnus crispa	236	7.47	40	16.95	2.27
Nemopanthus mucronata	90	2.85	4	4.44	1.56
Picea mariana	2552	80.76	118	4.62	0.06
Acer spicatum	25	0.79	0	0.00	0.00
Abies balsamea	0	0.00			
Betula papyrifera	0	0.00			

Terra Nova Road Site 3

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	52	8.00	0	0.00	0.00
Alnus crispa	347	53.38	0	0.00	0.00
Amelanchier sp.	72	11.08	0	0.00	0.00
Picea mariana	31	4.77	0	0.00	0.00
Populus tremuloides	59	9.08	0	0.00	0.00
Viburnum cassinoides	84	12.92	0	0.00	0.00
Abies balsamea	0	0.00			
Acer spicatum	0	0.00			
Betula papyrifera	0	0.00			
Nemopanthus mucronata	0	0.00			
Sorbus sp.	0	0.00			

Terra Nova Road Site 4

Species	Potential Browse Points	Percent Available (%)	Number Browsed	Percent Use (%)	Palatability Factor
Acer rubrum	99	4.22	8	8.08	1.92
Picea mariana	2028	86.41	7	0.35	0.00
Amelanchier sp.	97	4.13	0	0.00	0.00
Betula papyrifera	80	3.41	0	0.00	0.00
Nemopanthus mucronata	3	0.13	0	0.00	0.00
Populus tremuloides	13	0.55	0	0.00	0.00
Sorbus sp.	14	0.60	0	0.00	0.00
Viburnum cassinoides	8	0.34	0	0.00	0.00
Abies balsamea	0	0.00			
Acer spicatum	0	0.00			
Alnus crispa	0	0.00			