IMPACT OF PRE-DISPERSAL PREDATION BY RED SQUIRRELS (*Tamiasciurus hudsonicus*) AND CONE INSECTS ON BALSAM FIR (*Abies balsamea*) SEED PRODUCTION IN EASTERN NEWFOUNDLAND

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by

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Abstract

Predispersal seed predation is a critical factor limiting population recruitment among a number of coniferous species in natural systems. Introduced species, a major threat to biodiversity, can cause high levels of predispersal seed predation. Balsam fir (*Abies balsamea*) regeneration and establishment has been an ongoing challenge for land managers on the island of Newfoundland due to paucity of adult trees producing female cones, and the fact that fir recruitment requires annual seed production as there is no seed bank. This study focused on the combined impact of a mammal and a suite of insects on pre-dispersal cone and seed mortality of balsam fir through investigation of ecological impacts of non-native red squirrels (*Tamiasciurus hudsonicus*) and a variety of pre-dispersal cone/seed insects on this dominant tree species. Specifically, the impact of red squirrels and cone/seed insects were compared between balsam fir stands with different disturbance types and stem densities: Intact sites with no recent history of insect-infestation; and Insect Kill sites with recent history of insect infestation, around a range of stem densities (286-3100 trees/ha). The study was conducted within Terra Nova National Park and the surrounding forest management area in the southern Bonavista Bay region of the island of Newfoundland, Canada.

The percentage of pollen cones lost to red squirrels (3.5 ± 7.3% to 84.6 ± 9.3%), with an average loss of 47.6 ± 3.9%, was significantly higher in study sites with low balsam fir stem densities (229 ± 76 trees/ha) than in sites with high balsam fir stem densities (826 ± 189 trees/ha). Pollen cone loss to red squirrels showed no significant variation between disturbance types and among sites with respect to tree height and diameter at breast height (DBH). The percentage of seed cone loss to red squirrels (33.0 ±

15.7% to 93.5 ± 3.3%), with an average loss of 58.9 ± 15.5%, was not significantly between high and low stem density sites, nor between disturbance types. The number of female cones taken by red squirrels also did not vary among trees with respect to DBH, height and cone crop size of trees. All cones sampled in the study showed some signs of insect damage with 21.4 ± 5.9% of sampled seeds in balsam fir stands showing signs of insect infestation. However, stem densities of study sites did not significantly influence seed loss to insects among trees. Furthermore, seed loss to insects did not appear to be influenced by age class, DBH, height, and average cone size of trees. However, the proportion of viable seeds prior to seed release was stem density-dependent, and increased with increasing balsam fir stem density.

The results of the study suggest that red squirrel and insect populations were high, and hence were ubiquitous across the landscape. The combined effect of red squirrel and cone/seed insect predation resulted in over 2/3 reduction in potential seed production in all study sites combined. This may pose challenges to natural recruitment of balsam fir in the area, and a combination of Assisted Natural Regeneration, and seedling planting should be investigated as remedial options by managers of this area.

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Chapter 1: Introduction

1.1 Description of vegetation in Newfoundland and Labrador

The province of Newfoundland and Labrador falls within the Canadian Boreal Shield ecozone and is part of the southern-most range of the boreal forest biome. This region's canopy (overstory) is characterized by coniferous trees including black spruce (*Picea mariana*), white spruce, balsam fir, larch (*Larix laricina*) and the pines (*Pinus* spp.) which dominate the vegetation (Scott, 1994). These coniferous forests are interspersed with stands of broad-leaf deciduous trees, including trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and white birch (*Betula papyrifera*) (Ryan, 1995). The understory is represented by shrubs and herbs in families including willows (*Salix* spp.), Ericaceae, Liliaceae, Orchidaceae, Rosaceae, Asteraceae, Cyperaceae, a variety of ferns, club-mosses, and horsetails, as well as members of the bryophytes which dominate the mosaic of wetlands including bogs and fens that are typical of boreal ecosystems (Charest *et al.*, 1999). Insular Newfoundland itself is demarcated into 9 ecoregions reflecting subtle differences in vegetation structure across the island influenced by varying microclimatic and soil conditions, and disturbance regimes (Meades and Moores, 1989). The region's boreal forests, as in similar biomes on the mainland, are continuously shaped by naturally recurrent disturbances including fire, wind, and insects (Diotte and Bergeron, 1989; Johnson *et al.*, 1998; Payette and Delwaide, 2003; Schulte and Maddenoff, 2005). The Province of Newfoundland and Labrador has established national parks with representative vegetation structure of typical boreal forests in several locations within its boundaries; these include Gros Morne and Terra Nova national parks (Charest *et al.*, 2000).

1.2 Terra Nova National Park: Challenges to the Ecological Integrity Mandate

With the 1988 and 2001 amendments to the National Parks Act, the prime mandate of national parks has focused on the maintenance of ecological integrity using ecosystem management, so that natural areas are protected unimpaired into the future (Keith, 1996). The 2002 Report of the Panel on the Ecological Integrity of Canada's National Parks highlighted the need to examine Parks Canada's approach to maintaining ecological integrity and provide recommendations for improvement (Parks Canada, 2002). Hence, present challenges to ecological integrity in national parks on the island of Newfoundland have focused attention on the impacts of non-native and invasive herbivore species, including moose, snowshoe hare, red squirrel and other small mammals on vegetation; seedling predation by slugs, and impacts of non-native/native cone and seed insects on conifer species in these parks (Bergerud and Manuel, 1968; West, 1989; Connor *et al.*, 2000; Gosse *et al.*, 2002; McLaren *et al.*, 2004; Noel, 2004; Tulk, 2004; Kasimos, 2007; Holloway, 2008).

1.3 An introduction to invasive species

Non-native species are one of the most serious threats to biodiversity, second only to habitat degradation (Clout and Lowe, 1996; Crooks and Soule, 1996; Illueca, 1996; Everett, 2000). There is wide agreement among ecologists and conservation biologists that invasions by non-native species are a major cause of species extinctions in recent times

(Rhymer and Simberloff, 1996; Wilcove, 1998), although Gurevitch *et al.* (2004) have challenged this assertion. Increased level of predation, competition, introduction and transmission of diseases, disruption of food webs, physical alteration of natural habitats and ecosystem dynamics are some of the issues associated with species introductions (Lever, 1994; Elton, 2000), and collectively impact on native plant and animal populations. Insular ecosystems, especially islands and protected areas, are particularly vulnerable to introduced species because of the potential to deplete unique local flora and fauna populations (Lóvel, 1997).

Non-native species introductions have been responsible for significant economic losses in agriculture, forestry, and several other sectors of the global economy (Pimentel *et al.*, 2005). Over 400 of 958 species listed as threatened or endangered under the Endangered Species Act of the United States of America are considered to be at risk mainly because of competition with or predation by non-native species (Wilcove *et al.*, 1998). A preliminary report on economic cost resulting from invasive alien species in Canada conservatively estimates cumulative costs for 16 species at between $13.3 and $34.5 billion (Environment Canada, 2004).

Around the world, as many as 80% of endangered species are threatened and at risk due to the impact of non-native species (Armstrong, 1995). Invasive species have been implicated in various reviews of particular taxa by expert groups as the leading cause of extinction of birds and the second cause of extinction of North American and world fish species as well as mammals (Clavero and García-Berthou, 2005). Numerous cases of local extinctions of plant species have also been attributable to invasive species (Drake, 1990; Huxel, 1999). Climate change may result in the expansion of the latitudinal and elevational range of some invasive insects as formerly inhospitable parts of the forest become more attractive (Caroll, 2003). Invasive small mammals are also known to negatively impact on natural ecosystems (Bobrov *et al.* 2008). Squirrels, for example, often prey on other animals as well as plants (O'Donoghue, 1994). In particular, nesting birds and their offspring are especially vulnerable to squirrel predation (Sullivan, 1991; Willson and Comet 1996, Darveau *et al.*, 1997; Lewis, 2004). It is predicted that introduced gray squirrels (*Sciurus carolinensis*) on Vancouver Island will not only result in displacement of native rodents which share similar niches, but will also negatively impact the threatened Garry oak (*Quercus garryana*) ecosystem in the region through prevention of natural regeneration, bark stripping damage, predation, and food competition with other native seed-eaters (Lurz *et al*, 1999).

1.4 Squirrel biology and impact on forest regeneration

The North American red squirrel (*Tamiasciurus hudsonicus*) is a forest generalist found in a wide variety of forest types, but is particularly abundant in conifer-dominated forests (Rusch and Reeder, 1978; Burt and Grossenheider, 1980). Red squirrels exhibit territoriality, with males and females typically occupying non-overlapping territories with densities of 1-2 individuals per hectare (Larsen and Boutin, 1995; Corkum *et al.*, 1999). One or two litters with three or four offspring are common (Kemp and Keith, 1970; Miller, 1970), depending on food resource availability (West, 1989). Life expectancy of 90% of individuals in the wild is less than three years although ages of over eight years have been documented (Davis and Sealander, 1971). Territorial behaviour by red squirrels enables them to secure limited food resources in the form of conifer cone caches, which are critical to survival during winter (Kemp and Keith, 1970; Smith, 1968). Previous studies have documented reduced mobility of red squirrels and other sciurids in fragmented habitat, as they are reluctant to cross open fields or clear-cuts between forest patches (Henderson *et al.*, 1985; Delin and Andrén , 1999; Wauters *et al.*, 1994; Sheperd and Swihart, 1995).

Red squirrels feed on a variety of foods (Smith, 1968), with harvested conifer seeds providing half of the annual energy requirements (Finley, 1969), and buds eaten during winter and early spring (Rusch and Reeder, 1978). Their higher growth rates and larger litter sizes relative to other North American squirrel species allow their populations to react to environmental variability more quickly than other species (Swihart and Nupp, 1998; Réale *et al.* 2003).

Squirrels are generally regarded as important seed predators and may potentially influence the recruitment of trees, which in turn, may alter habitat structure for other animals (McCarthy, 1994; Hutchins *et al.*, 1996). The North American red squirrel, for example, is the major vertebrate predator of white spruce (*Picea glauca*) and other conifer seeds because of its efficiency in harvesting cones (Halvorson, 1986). Cones cached by squirrels do not contribute significantly to natural regeneration, because most cached seeds lose their viability, and therefore are not suitable for germination (Brink and Dean, 1966; Nienstaedt and Zasada, 1990; DeLong *et al.*, 1997; Tulk, 2004). Red squirrels may not only retard natural regeneration from cone harvesting activities (Finley, 1969), but may also affect growth of conifers by debarking and girdling (Sullivan and Sullivan, 1982; Brockley and Elmes, 1987), as well as through bud and shoot removal (Viidik, 1973; Prevost *et al.*, 1988).

Seed source strength, the number of seeds per unit area, and seedbed conditions are important to natural recruitment of many conifers including white spruce and balsam fir, which both lack seed banks (Coates *et al.*, 1994; Purdy *et al.*, 2002; Messaoud *et al.*, 2007). Hence spatial and temporal factors may have significant impact on regeneration such as density of cone-producing trees, annual cone crop size, and seed predation (Peters *et al.*, 2003). Foraging behaviour of red squirrels is influenced by tree height and stem density, with a preference for tall trees in high stem density sites (Summers and Proctor, 1999). There is also documented evidence of preference of squirrels for cones of some conifer species over others, which could impact on natural regeneration potential of targeted tree species by forming a natural sieve which could affect future forest dynamics (Brink and Dean, 1966). Studies have documented squirrels selecting between trees for cone harvest on the basis of level of secondary chemical production or protective tissue of host plants (Smith, 1970; Elliott, 1973). Studies suggest evolutionary responses of trees to heavy seed predation by squirrels. For example, lodgepole pine (*Pinus contorta*) has increasing amounts of protective tissue particularly cone scales, with a reduction in number of seeds per cone suggesting a trade-off for the energy expenditure in enhancing defence structures (Elliott, 1973). The predator satiation hypothesis of Janzen (1971) suggests that plant species subjected to heavy seed predation may evolve ways to escape total seed loss by producing a large cone crop in mast years, thereby overwhelming the potential seed predators, and hence leaving enough seeds for recruitment (Peters *et al.*, 2003). Conifers such as white spruce and balsam fir (*Abies balsamea*) rely on annual seed production for regeneration, due to lack of a persistent seed bank. Hence, cone (seed) predation (Nienstaedt and Zasada, 1990), as well as male (pollen) cone predation, may be impediments to the regeneration process. The production of an abundant cone crop of filled seeds requires that large quantities of conspecific pollen are in the air during the short period of strobili (female flower) receptivity (Greene *et al.*, 1999), as self-pollination among many coniferous species generally results in high rates of ovule abortion (Dogra, 1967). Therefore, herbivory of pollen cones could potentially reduce pollen density and impact pollination success rate, and has been cited as one of the major sources of non-viable seeds in some conifer species (Owen and Molders, 1980; Singh and Owens, 1981).

1.5 Impact of cone insects on forest regeneration and seed productivity

Nearly 2000 insect species have invaded North America over the past 500 years (Sailer, 1983; Kim and McPheron, 1993; Stuckey and Barkley, 1993), and some are important predators of seed cones prior to seed dispersal. More than 100 genera of insects infest conifer cones (Rouault, 2004); however, the number of non-native cone insects in North America is not known.

Predation by insects is an important factor limiting coniferous seed production, and responsible for close to 100% seed loss in coniferous trees, with 25% being a rough average (Knight, 1952; Tripp and Hedlin, 1956; Mattson, 1978; Cameron, 1981; Miller, 1986). Entomologists first documented insect predation on cones and seeds of North American conifers over 100 years ago (West, 1989). The leaffooted pine seed bug (*Leptoglossus corculus*) was first described in 1831, but only became a pest in North America during the early 1900s (Debarr, 1967). Problems of poor natural regeneration of forest trees were first linked to cone and seed insects; for example, Harrington (1902) reported that "*the ground beneath the trees was strewn with aborted and undeveloped* *cones…*" killed by the white pine cone beetle (*Conophthorus coniperda*). Whiles some cone insects known to cause significant seed mortality, including the Jack pine budworm (*Choristoneura pinus*) and Douglas-fir seed chalcid (*Megastigmus spermotrophus*), are native to North America (Volney, 1994; Roques *et al.*, 2006), significant numbers of cone insect species have wide distribution from Europe to North America, and may have crossed continents with commercial activity (Turgeon *et al.*, 1994).

Alternating good and poor cone crop sizes in natural forest stands is a major factor regulating populations of cone and seed insects (Mattson, 1971, 1980; Hedlin, 1964; Shea, 1989). Periodic synchronized large cone crop production (masting) among many conifer species may be an adaptation to cone and seed insect predation, and affords the possibility of avoiding total seed loss by overwhelming predators (Janzen, 1971). Frequently, a lagged, density-dependent relationship exists between annual cone crop size and insect population size, with a trend of insect populations increasing when good cone crops occur for 2 or more consecutive years, and crashing in years when few cones are produced (West, 1989). In white spruce, for instance, insect damage is high in poor cone crop years due to the upsurge of insect numbers in preceding mast years, whereas the reverse is often the case in good crop years (Werner, 1964). Similar relationships have been documented in other conifer trees (Mattson, 1971; Shea *et al.*, 1984).

Many insects adapt strategies over time to improve their chances to survive years of low cone production or low pollination success. The seed chalcids (*Megastigmus* spp.), for instance, have evolved prolonged diapause and parthenogenesis in their life cycles to adapt to host plants (Hussey, 1955; Roques, 1981; 1989; Annila, 1982). Also very few insects adapt to just one plant species: even the more specialized monophagous feeders can feed on congeneric species (Niemelä and Mattson, 1996). Insects, in general, may show a preference for larger fruits which have higher seed densities (Kirkland and Goeden, 1978; Marshall *et al.*, 1986). Monterey pines (*Pinus radiata*) in natural stands had higher level of infestation of spider mites (*Oligonychus* spp.) on younger trees, suggesting an age-dependent relationship (Landwehr, 1979, Landwehr and Allen, 1982).

Insect feeding affects strobili production both directly, by the destruction of cones and cone buds, and indirectly, through other types of damage that reduce bud production or bud burst (Crawley, 1990). Female cone loss in conifers attributable to insects commonly averages about 20% (Hedlin, 1964; Dewey, 1986; Miller, 1986; Mattson, 1986; Frank and Jenkins, 1987). This is, however, substantially lower than female cone losses in conifers attributable to mammals, especially red squirrels, which is between 40% to over 80% (Benkman *et al.*, 1984; Halvorson, 1986; West, 1989; Peters *et al.* 2003). Insect predation of ripening fruits and seeds prior to dispersal is responsible for substantial losses in reproductive ability in many plant species (Crawley, 1989). A recent study on impact of invasive pests of eastern hemlock (*Tsuga canadensis*) dominated forest in New England suggest that the decline associated with chronic hemlock woolly adelgid (*Adelges tsugae*) infestation is causing significant changes in structure, composition, and ecosystem function in these forests through the gradual thinning of canopies, replacement of eastern hemlock by black birch (*Betula lenta*) with associated changes in the composition of forest understory (Kizlinski *et al.*, 2002). Such shifts in forest species composition impact on the ecosystem in many ways because tree species vary in their properties of nutrient and water uptake, growth rate, litter quality, soil organic matter production, and habitat and food quality for animals (Lovett *et al.*, 2006).

1.6 Introduced Terrestrial Fauna of Newfoundland

Insular ecosystems, especially islands and protected areas, are particularly vulnerable to introduced species because of the potential to deplete unique local flora and fauna populations (Lóvel, 1997). Over the past century there has been a steady introduction of terrestrial animals to the island. Although a number of such introductions have been unsuccessful, such as bison (*Bison bison*) in 1964, several others have resulted in the establishment of viable populations, including a number of rodent species such as the eastern chipmunks (*Tamias straitus*) introduced in the 1960's (Northcott *et al*., 1974), and snowshoe hare (*Lepus americanus*) (Environment and Conservation, Newfoundland and Labrador, 2008). However, moose (*Alces alces*) introduced in 1904 and red squirrels have had the most impact on terrestrial vegetation and native fauna on the island (Bateman, 1977; Reynolds, 1997; West, 1989; Connor *et al*., 2000; Tulk, 2004; Lewis, 2004).

1.7 Red Squirrel Introduction to Newfoundland

Red squirrels have a wide distribution throughout North America (Wilson and Ruff, 1999) and are the only known squirrels in Newfoundland, with a recent history of introduction. There were likely three successful introductions to the island of Newfoundland in 1963, 1964 and 1974, and have entirely populated insular Newfoundland since then (Northcott *et al*., 1974; Payne, 1976; Goudie, 1978; Reynold, 1997). Red squirrel population densities on the island are presently believed to be twice that on the mainland (Benkman, 1989; Pimm, 1990), although it has been suggested that a tenfold difference in population densities is closer to reality (Benkman, 1992). However, two recent studies estimated red squirrel population density in black spruce habitat in Terra Nova National Park at between 0.5-2.3/ha (Lewis, 2004) and 0.4-3.7/ha (Reynolds, 1997).

Red squirrels are a major vertebrate cone predator (Halvorson, 1986) and are known to feed on large numbers of the cone crops of numerous North American conifers (Hurley *et al.*, 1987). They were first documented as mass consumers of black spruce cones in Newfoundland in the mid 1980s (West, 1986), and it has been suggested that red squirrels are capable of consuming anywhere between 60% and 100% of cone crop, especially in moderate or poor seed years (West, 1989; Tulk, 2004).

1.8 Cone insect infestation in Newfoundland

Insects of at least five orders (Coleoptera, Homoptera, Hymenoptera, Diptera and Lepidoptera) feed on conifers, including spruce, fir and hemlock on the Canadian mainland (Hedlin *et al.*, 1980; Rose and Lindquist, 1994) and on the island of Newfoundland. Some cone insects that are pests of spruce and fir in eastern Canada, including Newfoundland, are the spruce seed moth (*Cydia youngana*), fir coneworm (*Dioryctria abietivorella*), balsam fir seed chalcid (*Megastigmus specularis*), larvae of the midges (*Dasineura* spp. and *Mayetiola* spp.), and spruce cone maggot (*Hylemya anthracina*) (Rose and Lindquist, 1994). Cone and seed insects may be the most important impediment to seed availability in genus *Abies* (Owens and Morris, 1998).

1.9 Project Goals

Cone and seed herbivory by insects together with activities by the other aforementioned biological agents are collectively influencing plant species composition and forest successional patterns: selective browsing of moose on balsam fir and some deciduous species resulting in asymmetrical regeneration; selective browsing by non-native snowshoe hare and slugs; cone caching by non-native red squirrel; and reproduction suppression by non-native/native cone and seed insects by their influence on seed rain and recruitment (Hermanutz *et al.* unpublished data). The cumulative effect of these impacts is the suppression of balsam fir advanced regeneration, resulting in the inability of boreal forest in these parks to regenerate new, dense stands, and possibly eliminating a broad range of indigenous plant and animal species from the landscape (West, 1989).

My research focused on cone mortality of an indigenous coniferous species, balsam fir, in Terra Nova National Park and surrounding forests, including investigation of the ecological impacts of non-native/native cone and seed insects, level of impact of red squirrel populations on seed availability, and how they collectively affect seed availability for recruitment and hence advanced regeneration of balsam fir. The combined impact of these pests may result in the inability of fir to maintain healthy advanced regeneration, resulting in challenges to naturally produce healthy forests. The objectives of this study were therefore: (1) to quantify the impact of red squirrels on male and female cones of balsam fir in the study area; (2) to determine whether male and female cone losses to red squirrels are: (i) density dependent, (ii) influenced by height, diameter at breast height (DBH), and cone crop size, (iii) influenced by recent history of insect disturbance among balsam fir stands; (3) to quantify cone/seed loss to insects in the study sites; (4) to assess whether proportion of cones/seeds infested with insects: (i) is dependent on stem densities of study sites, (ii) varies significantly among sites depending on recent history of insect disturbance, (iii) is influenced by tree size (height and DBH), (iv) is influenced by cone size and weight, (v) varies significantly among trees depending on age-group; (5) to determine whether proportions of viable seeds among trees are influenced by the stem densities of study sites; and (6) to explore the cumulative impacts of these sources of cone loss on balsam fir forest stands in the region, which will contribute to management of forests, particularly with respect to forest renewal, in Terra Nova and Gros Morne national parks, and provincially managed forests.

Chapter 2: Materials and Methods

2.1 Study Area

Terra Nova National Park (TNNP) is located on the east coast of Newfoundland (ca. 48° 30'N, 54°00'W) (Charest *et al.*, 2000). It lies within the southern Bonavista Bay and preserves a representative sample of Eastern Newfoundland Island Atlantic Region, which is characterized by real maritime forest (Keith, 1996). The park has a maritime climate with precipitation of 900-1200 mm/year, mild winters, cool and late spring, with ice and snow persisting until mid-May, with generally warm and fairly sunny summers. July is the driest and warmest month (16.4°C) and November the wettest. Geologically, the Park belongs to the Avalon Zone, in the Appalachian Mountain System, with elevations ranging from sea level to 278m (Colman-Sadd *et al.*, 1990). The forests in TNNP vary from dense in the western part to open with numerous rock outcrops in the east. Approximately 70% of the land area is covered by forest, with barrens occupying the remainder (Charest *et al.*, 2000). The major forest types are black spruce – moss, kalmia – black spruce, and balsam fir. Deciduous forests, usually of white birch, or trembling aspen, are successional (Charest, *et al.* 2000). Major bog-fen complexes are distributed throughout the park but are more prevalent in the western zone, and are often ombrotrophic (rain-fed). Heathlands are dominated by ericaceous shrubs and may appear after disturbances such as fire or logging (Meades, 1983). Natural disturbances including fire, wind, and insects play a major role in shaping forest structure within the park. Documented history of insect infestation of balsam fir stands within the park and surrounding forests in central Newfoundland include infestations by Spruce budworm (*Choristoneura fumiferana*), Hemlock looper (*Lambdina fiscellaria fiscellaria*), and Balsam fir sawfly (*Neodiprion abietis*) (Dept. of Natural Resources, Newfoundland and Labrador).

Natural stands of balsam fir, one of the dominant phanerophytes in the coastal areas in and bordering TNNP were selected for study, beginning in late May 2007 (Fig 2.1 and Fig 2.2). Sites of varying levels of insect disturbance and stem densities were selected to be representative of balsam fir forests types within the study area. The study consisted of three components: quantifying male and female cone herbivory by red squirrels among study sites; and the level of insect predation of female cones. Study sites used to assess level of insect predation of female cones had to be located outside TNNP, as female cone sample collection involved felling of selected trees, which is prohibited within the park boundaries. Balsam fir and other tree species densities in each of the study sites were estimated using the point-centered quarter analysis method (PCQ); (Mitchell, 2001). For this method, data collection points were randomly generated along two 50 m transects placed 50 m apart. Each point along the transect, at least 5 m apart, was divided into 4 quarters, and the distance to the nearest tree with a minimum diameter at breast height (DBH) of 4 cm within each quarter was measured. The minimum distance of 5 m between data collection points was selected to avoid measuring the same trees repeatedly. Also, the data points were divided into quarters by running an imaginary line perpendicular to the transect. This line and the transect divide the area into four quarters at each point. The sum of the distances of trees from the collection points was divided by the total number of quarters to generate $\bar{A}$ meters, which represents the mean distance between trees for the site. Total density in hectares is then equal to: $(10{,}000\ m^2 / ha) / \{(\bar{A}\ m)^2 / tree\}$; and balsam fir stem density is equal to the product of total density and the fraction of quarters in which balsam fir trees were measured. The heights, DBHs, and GPS coordinates of all trees involved in all three studies were also recorded.

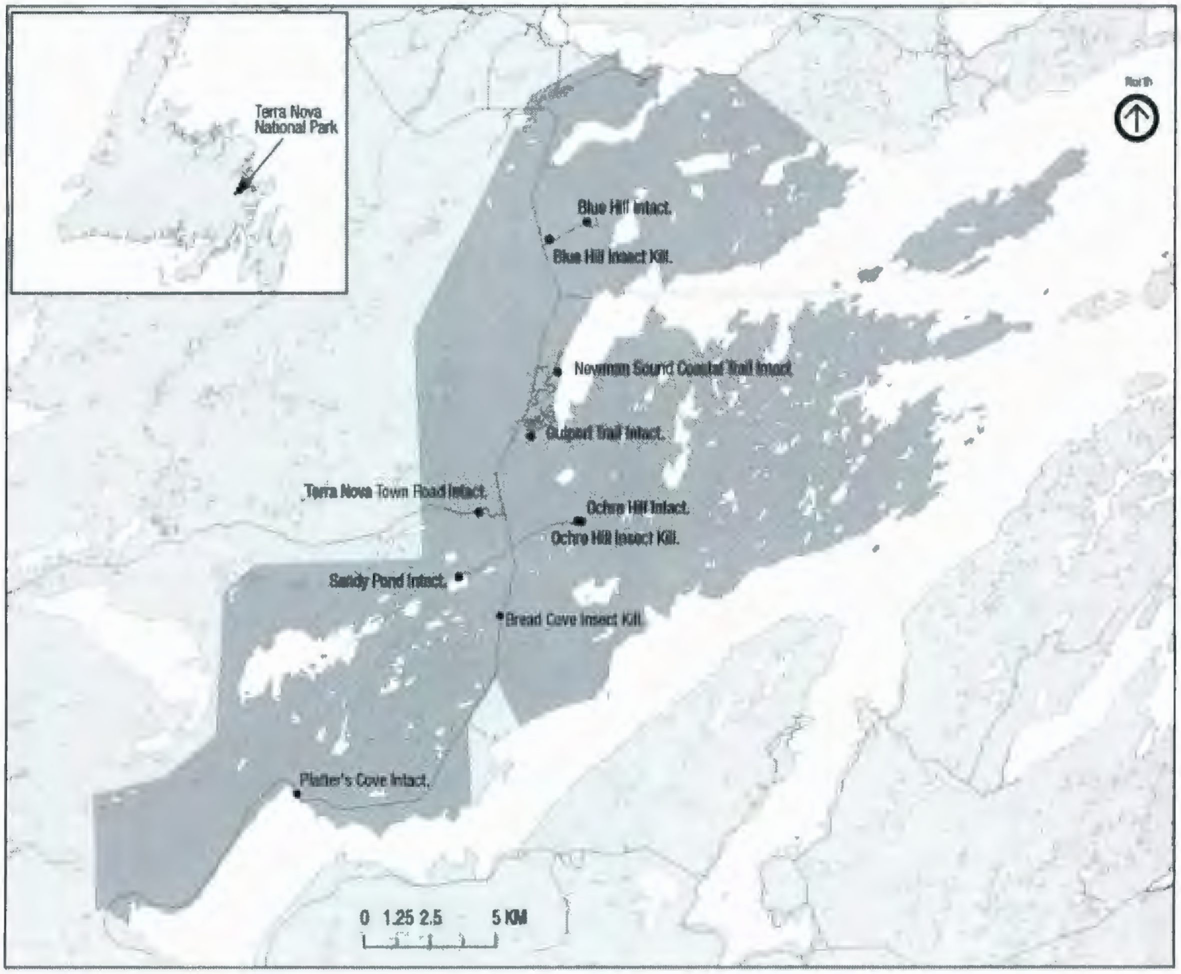


Figure 2.1. Location of study sites for red squirrel male and female cone predation study in TNNP, Newfoundland.

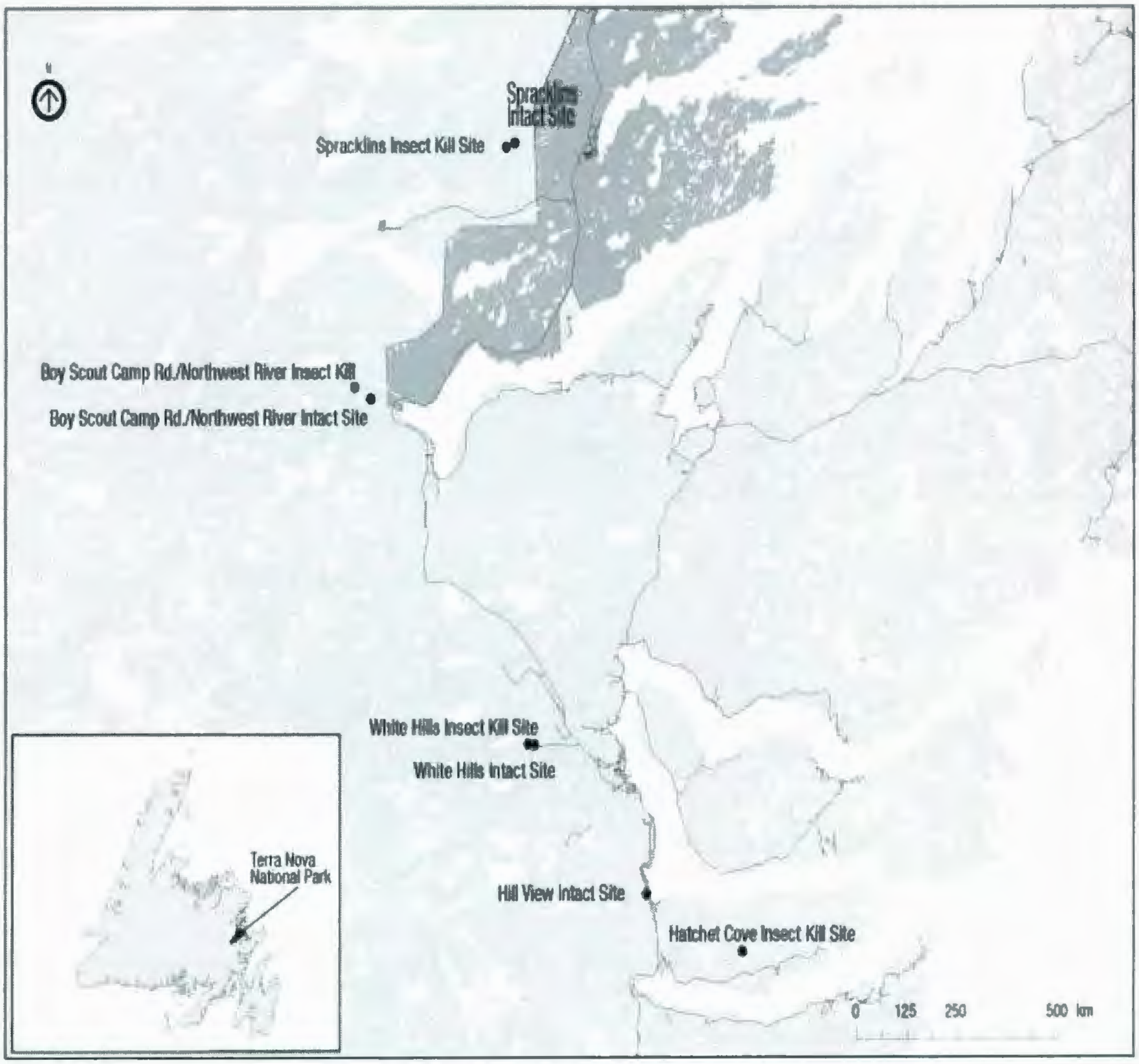


Figure 2.2. Location of study sites for insect female cone herbivory study outside TNNP.

2.2 Balsam Fir Male Cone Predation by Red Squirrel Study

The male/pollen cone study commenced in late May 2007, when cones were large enough to be counted with a spotting scope, and involved random selection of focal trees from ten sites of varying balsam fir tree densities (Table 3.1), and different histories of insect infestation from across the breadth of the park. One group of sites (n=5) had a history of insect infestation in the last 20 years, and the other group (n=5) had no such history in the same time period (J. Gosse, 2007. pers. comm.). For site delineation two parallel 50 m transects were established, at least 50 m apart, to cover each study site. Four balsam fir trees were selected from each study site for pollen cone counts, with consideration given to the visibility of the tree crown for pollen cone observations and counts. Focal branches in the selected trees were photographed (refer to attached Compact Disc) and their locations identified relative to other branches in each tree crown by markings on the photographs, which afforded easy location during subsequent counts. All counts were performed with a Bushnell spotting scope with maximum magnification of 60X from marked points where initial pictures were taken for each tree. The positioning of the spotting scope and height of the supporting tripod from the ground were also recorded to reduce variation in counts. Five sets of counts were performed for each of four trees in the ten sites, from late May to mid June just before pollen dispersal, for a total of 200 counts.

2.3 Balsam Fir Female Cone Predation by Red Squirrel Study

The female cone removal study commenced in mid June 2007 when cones were large enough to be counted with binoculars, and involved study sites of varying balsam fir densities and history of insect infestations: Intact (n = 6) and Insect Kill (n = 4) sites (Table 3.1); (J. Gosse, 2007. pers. comm.). The sites were demarcated using same method as in the male cone study, and four focal seed trees were selected, based on visibility of female cones in crowns of trees, from ten sites of varying balsam fir stem densities. The year of the study was a good crop year with high cone crop production (J. Gosse, 2007. unpublished data). Hence in some cases, the same trees used in the pollen cone study were used as focal trees in the female cone counts. The study ended in mid-October when seeds began to disperse. The crowns of focal trees involved in the counts were initially photographed (refer to attached Compact Disc) from one aspect before commencement of counts. The counts were performed with Bushnell binoculars with maximum magnification of 42X rather than the spotting scope used in the male cone counts because of the comparatively larger female cones. The counts were conducted from marked spots used for taking photographs. Each count was the average of two separate counts except when there was greater than a ten percent variation between counts, that then necessitated a third count before taking the average. Seventeen sets of counts for all focal trees in the ten sites were undertaken over the period of the study. Blind tests were performed to determine repeatability of counting procedure, and involved two persons conducting counts on same set of 10 focal trees at different study sites. Individual counts showed less than 5% variation between counts over 90% of the time.

A supplementary observation of female cone loss to red squirrels, albeit on a much smaller scale, was conducted in 2008 (a low crop year; J. Gosse, 2008, pers. comm.) on 36 of the 40 trees involved in the 2007 study, as 4 trees could not be located. This study involved all ten sites with 5 sets of cone counts conducted from June to September 2008.

As in the 2007 study, cone loss was quantified for all ten sites to compare level of cone loss between high and low cone crop years.

2.4 Balsam Fir Female Cone Predation by Insect Study

The insect predation study, which commenced in mid June and ended in late August 2007, involved the harvesting of female cones from randomly selected trees in eight different sites of varying balsam fir stem densities (Table 3.2), and history of insect infestations (Intact sites, n = 4; Insect-Kill sites, n = 4) (S. Avery, 2007. pers. comm.), in the Bonavista Peninsula adjacent to the park in Forest Management District 2. Cones from four trees, two old and two young, from each of the eight sites for each of four harvesting periods were harvested from mid-June to late August. A sample of between 10 and 40 female cones was collected, depending on tree crop size and cone availability, from all aspects of the tree crowns of each tree. The two age groups were used in the study to assess whether the level of cone insect infestation was age-dependent. The age categories of trees were determined by texture of tree bark: "young" trees have smooth barks dotted with resin blisters; and "older" trees have rough, indented barks. The samples of the collected cones were then dissected from base to tip and examined using microscope and magnifying glass for signs of insect infestation. This process was repeated monthly for each harvest from mid June to late August, thereby tracking insect infestation through the various developmental stages: pre-pollination stage; pollination stage; and stage just prior to seed dispersal. The proportion of viable seeds was estimated from cone samples in final harvest in late August, just before seed dispersal, via tetrazolium tests, which is a biochemical test used to differentiate live from dead tissues of seed embryos on the basis of dehydrogenase enzyme activity (AOSA., 2000). Voucher specimens of insects collected from cones and seeds were identified using two identification manuals: *Cone and Seed Insects of North American Conifers* (Hedlin *et al.*, 1980); and *Insects of Eastern Spruces, Fir and Hemlock* (Rose and Lindquist, 1994).

2.5 Statistical Analyses

Multiple linear regression analysis (α = 0.05) was used to test relationship between (1) percent pollen cone loss per tree, balsam fir stem density per site, and height and DBH of focal trees; (2) percent female cone loss per tree, balsam fir stem density per site, heights of focal trees, DBH of trees, and cone crop per tree for both study years; (3) percent of seeds per cone infested with insects per tree, balsam fir stem densities per site and heights of focal trees; and (4) percent of seeds infested with insects per cone per tree, average cone length, average cone width, and average cone weight of focal trees in study sites. Nested-analysis of variance (ANOVA, α = 0.05) was used to test whether there were differences between disturbance types (Insect kill; Intact forests) and among sites, nested within disturbance types in the following dependent variables: (1) percent male cone loss per tree in 2007; (2) percent female cone loss per tree in both 2007 and 2008; and (3) percent seeds infested by insects per tree in 2007. Nested ANOVA was further used to test whether there were differences in percent seeds infested by insects among tree age groups. Tests were performed on data gathered from subsample of female cones from fourth (final) tree harvest in 2007. Nested ANOVA was used in these analyses to account for variation in seed and cone loss, to insects and red squirrels respectively, among individual trees at study sites.

Examination of residual plots of nested ANOVA analyses showed that residuals did not depart from normality; however, residuals did not appear to be independent based on divergent plots. This necessitated arcsine-transforming cone and seed loss data for analysis. Residual plots and residual versus fit plots for all regression analyses showed that residuals were independent and homogeneous, and did not depart from normality (Sokal and Rohlf, 1995).

Binary logistic regression ($\alpha = 0.05$) was used to test the relationship between proportion of viable seeds, a binomial response variable, and balsam fir stem densities of each study site, as well as weight of seed lots (5 seeds per lot) for subsample of cones from the fourth (final) cone harvest. No assumptions about the independence and normality of residuals were made for binary logistic regression analysis (Sokal and Rohlf, 1995). Minitab 15 Statistical Software® was used for all statistical analyses.

Chapter 3: Results

3.1 Pollen cone predation by red squirrel study

Height and DBH of focal trees ranged from 7.6-15.6 m and 8.5-31.5 cm, respectively (Appendix: Table A.1). The absolute stem densities of study sites ranged from 285-1528 trees/ha at Ochre Hill Insect Kill and Blue Hill Intact sites, respectively. The balsam fir densities ranged from 29 trees/ha and 1528 trees/ha at Blue Hill Insect Kill and Blue Hill Intact sites, respectively (Table 3.1).

Percent change in final pollen cone counts in mid June from initial counts in late May on focal branches ranged from 100% decrease to 12.5% increase (Appendix: Table A.1). The average decrease in cone numbers was 54.2 ± 7.0% (n = 5) and 43.1 ± 5.0% (n = 5) across Insect Kill and Intact sites respectively (Table 3.2). With the exception of Blue Hill Intact site, all sites showed net loss of pollen cones, with a decrease in final pollen cone numbers in mid July just before pollen release from initial counts in late May (Figure 3.1a; b).

There is a very strong positive correlation between absolute stem density per site and balsam fir density per site ($r = 0.948 \;\; n = 10 \;\; p < 0.001$), therefore only balsam fir stem density was used in the regression analysis so as to assess the direct relationship between pollen cone loss and balsam fir stem density of study sites. There was a significant difference in pollen cone losses among trees with respect to balsam fir stem density per site ($F_{[1,36]} = 6.51$, $p = 0.015$), with low density sites suffering a higher loss than higher density sites (Figure 3.2; Appendix: Table A.2). There also is a positive correlation between heights and DBHs of focal trees ($r = 0.600 \;\; n = 40 \;\; p < 0.001$); however, tree size (height and DBH) did not affect number of cones lost to squirrels ($F_{[1,36]} = 0.001$, $p = 0.969$) and

$F_{[1,36]} = 0.86$, $p = 0.36$ respectively, see Appendix: Table A.2). Disturbance types (Intact; Insect Kill sites) did not differ in the percent cone loss per tree ($F_{[1,8]} = 0.25$, $p = 0.632$) as there was significant site to site variation ($F_{[8,30]} = 3.27$, $p = 0.008$, see Appendix: Table A.3).

Table 3.1. Total and balsam fir stem densities of study sites for male (n = 10) and female (n = 10) cone predation study*. Total and balsam fir stem densities were computed using Point-Centered Quarter method with 50 m transects (Mitchell, 2001). Total density refers to number of stems of all tree species with minimum DBH of 4 cm in a hectare; and balsam fir stem density refers to number of balsam fir trees with minimum DBH of 4 cm in a hectare.

Study Sites	Total stem density(trees/ha)	Balsam fir stem density(trees/ha)
Louil Hill Insect Kill	473	378
Blue Hill Insect Kill	290	29
Blue Hill Intact	1528	1528
Newman Sound Coastal Trail Intact	633	395
Terra Nova Town Road Intact	577	317
Ochre Hill Insect Kill	286	200
Ochre Hill Intact	1238	1052
Sandy Pond Intact	1425	1033
Platter's Cove Insect Kill	1151	633
Bread Cove Insect Kill	441	308
Outport Trail Intact	296	81

*Same study sites for both male and female cone study with the exception of Louil Hill (used in male cone study only), and Outport Trail (used in female cone study only).

Table 3.2. Percent male cone loss* to red squirrels averaged for each site (n = 10), with significant site variation in cone loss but not disturbance types (Insect Kill vs Intact).

Study Sites	No. of trees	% cone loss	Std Error
Louil Hill Insect Kill	4	42.7	11.8
Blue Hill Insect Kill	4	57.5	20.4
Blue Hill Intact	4	-3.5	7.3
Coastal Trail Intact	4	84.6	9.3
Terra Nova Intact	4	64.9	10.4
Ochre Hill Insect Kill	4	43.9	10.2
Ochre Hill Intact	4	33.5	15.8
Sandy Pond Intact	4	46.5	14.2
Platter's Cove Intact	4	32.8	6.2
Bread Cove I.K	4	72.7	8.8

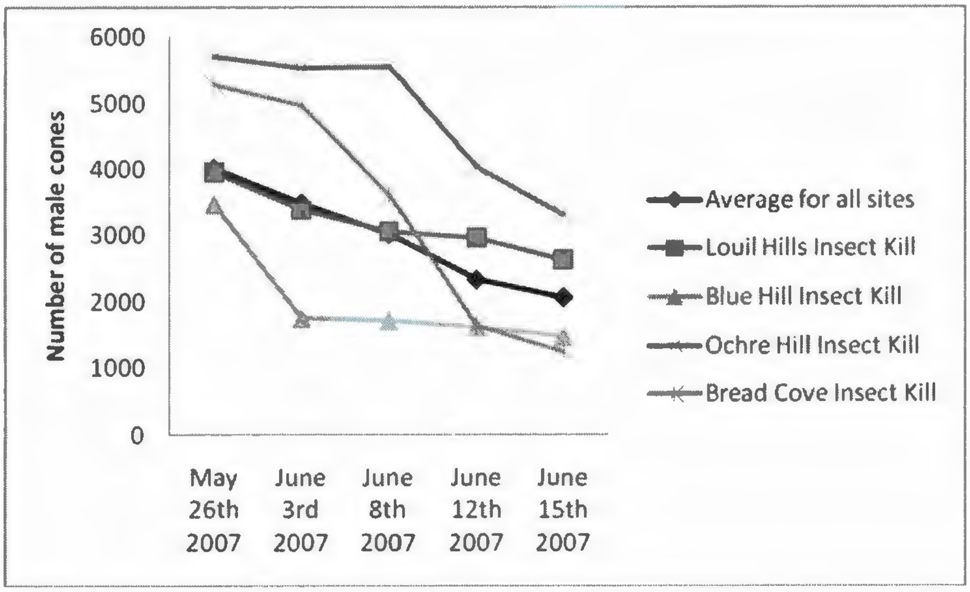
* % cone loss = $\{(X - Y)/ X\} \times 100$

Where, X represents initial male cone count, and Y represents final cone count.

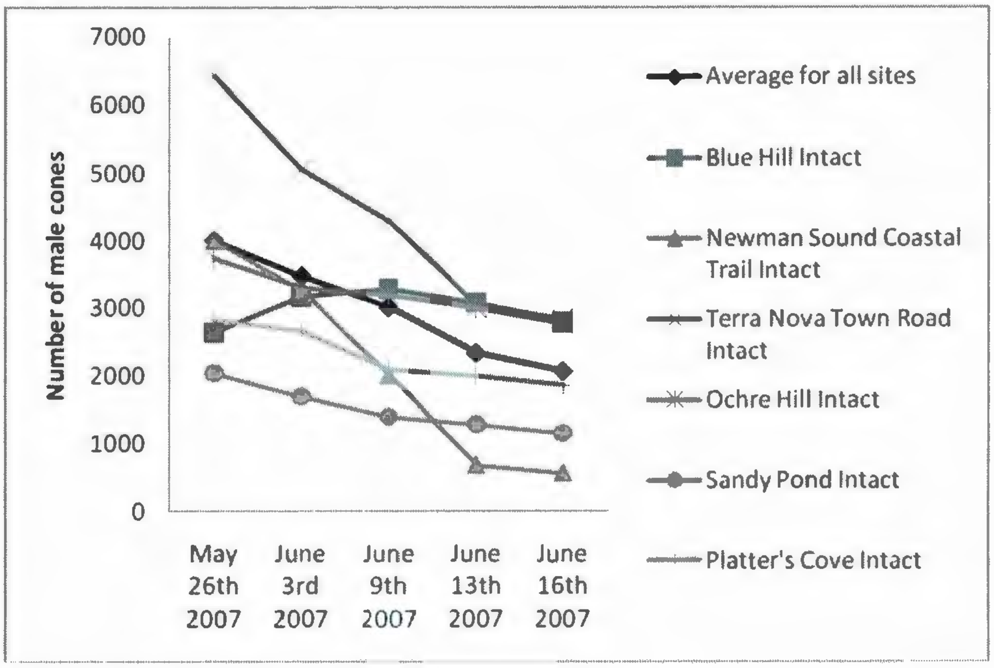
Example: X = 100 male cones

Y = 20 male cones.

Therefore, % cone loss = $[(100 - 20)/100] \times 100 = 80\%$ male cone loss.



(a) Insect Kill sites



(b) Intact sites

Fig 3.1. Balsam fir male cone removal curves for individual study sites with: (a) Insect Kill sites; (b) Intact sites. Note difference in axes between the two panels. Refer to Table 3.2 for sample sizes.

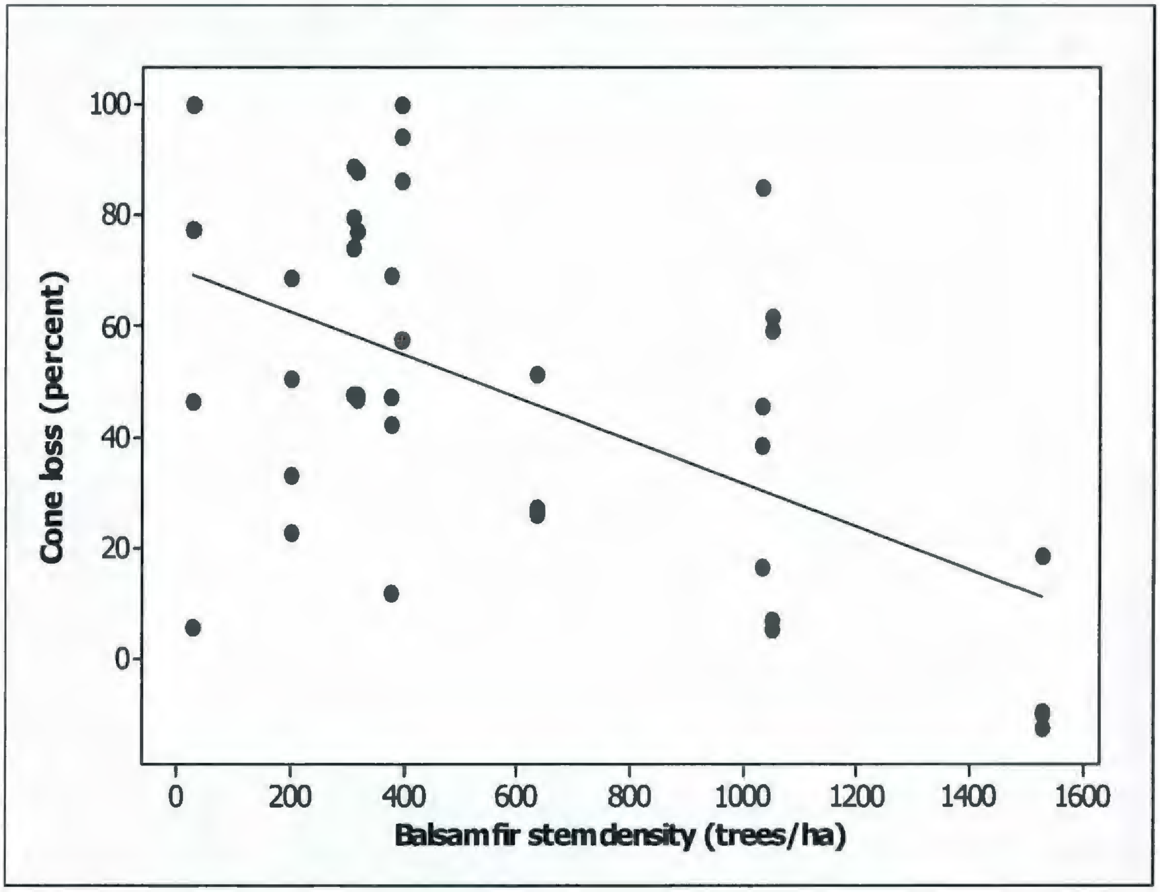


Figure 3.2. Regression of percent pollen cone loss (%cone loss) per tree and balsam fir stem density per site. The level of cone loss per tree was inversely related to density of balsam fir stands. Regression equation: %cone loss = 70.40 – 0.03891 stem density; $P = 0.015$.

3.2 Female cone predation by red squirrel study

The height and DBH of focal trees ranged from 6.6-18.1 m and 12.1-41.3 cm respectively (Appendix: Table A.4). The stem densities were, however, the same as in the male cone study as the same sites were used, with the exception of Outport Trail site which replaced Louil Hill site in this study.

Over 70% of focal trees from 2007 (good cone crop year) did not produce cones in 2008 (poor cone crop year). The percentage change in final female cone counts in early October 2007 from initial cone counts for individual trees in late June 2007 ranged from 0% to 100% decrease, and 25% to 100% decrease for a similar period in 2008 (Appendix: Tables A.4 and A.5). The average female cone loss for the 2007 study was 47.2 ± 9.9% ($n = 4$) and 63.9 ± 5.3% ($n = 6$) across Insect Kill and Intact sites (Table 3.3; Figure 3.3a; b). For the 2008 study, the average cone loss was 81.9 ± 18.1% ($n = 3$) and 82.2 ± 13.4% ($n = 5$) across Insect Kill and Intact sites respectively (Table 3.4; Figure 3.4 a; b). Disturbance types (Intact; Insect Kill sites) did not differ in percent cone loss per tree ($F[1,8] = 3.50$, $p = 0.098$, see Appendix: Table A.8).

The 2007 study data showed a positive correlation between height and DBH of focal trees ($r = 0.593$, $n = 40$, $p < 0.001$), and a very strong positive correlation between balsam fir stem density and absolute stem density per site ($r = 0.956$, $n = 10$, $p < 0.001$), that permitted using one of the variables, balsam fir stem density, in the regression analysis to assess the direct relationship between female cone loss and balsam fir stem density of study sites. There was no significant differences in female cone loss among individual trees with respect to balsam fir stem density per site ($F_{[1,35]} = 0.22$, $p = 0.642$); and tree size did not affect female cone loss ($F_{[1,35]} = 0.18$, $p = 0.675$ and $F_{[1,35]} = 0.44$, $p = 0.512$) for height and DBH respectively. Cone loss to red squirrels was not affected by cone crop size of trees ($F_{[1,35]} = 0.25$, $p = 0.621$, see Appendix: Table A.6). Disturbance types (Intact; Insect Kill sites) did not differ in percent cone loss per tree ($F_{[1,8]} = 3.50$, $p = 0.098$, see Appendix: Table A.8).

Multiple regression analysis of data from 2008 showed no significant differences in female cone loss among individual trees in relation to heights of focal trees ($F_{[1,6]} = 4.75$ $n = 11$ $p = 0.072$), balsam fir stem densities per site ($F_{[1,6]} = 0.95$ $n = 11$ $p = 0.367$), DBH of focal trees ($F_{[1,6]} = 1.94$ $n = 11$ $p = 0.213$), and cone crop size of trees ($F_{[1,6]} = 2.78$ $n = 11$ $p = 0.342$, see Appendix: Table A.7). There also was no significant variation in percent cone loss per tree between disturbance types ($F_{[1,3]} = 0.00$, $p = 0.992$, see Appendix: Table A.9). There was no correlation between percent cone loss of focal trees in 2007 study, and percent cone loss among same set of trees in 2008 study ($r = 0.100$ $n = 11$ $p = 0.100$).

Table 3.3. Percent female cone loss* to red squirrels averaged for each site (n = 10) for 2007 study.

Study Sites	No. of trees	% cone loss	Std. Error
Outport Trail Intact.	4	93.5	3.3
Blue Hill Insect Kill.	4	42.5	6.0
Blue Hill Intact.	4	65.6	14.7
Newman Sound Coastal Trail Intact.	4	56.0	18.7
Terra Nova Town Road Intact.	4	64.1	19.0
Ochre Hill Insect Kill.	4	33.0	15.7
Ochre Hill Intact.	4	58.6	16.2
Sandy Pond Intact.	4	49.8	15.2
Platter's Cove Intact.	4	59.8	9.6
Bread Cove Insect Kill.	4	66.3	22.6

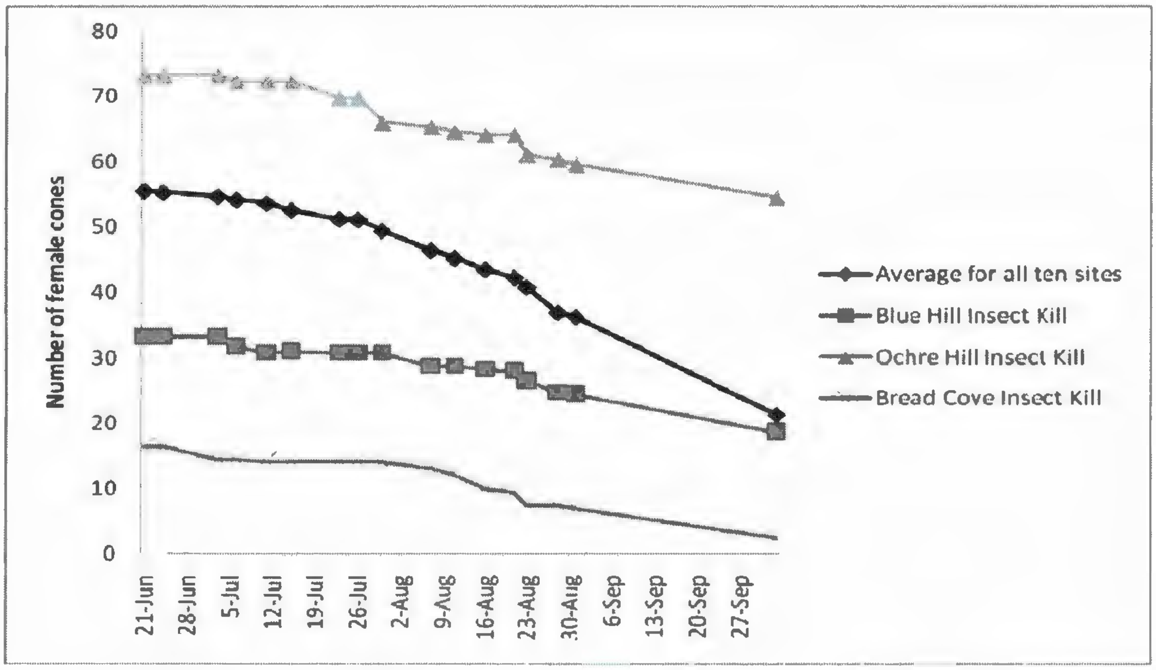
* % cone loss = $\{(X - Y)/ X\} \times 100$
Where, X represents initial female cone count, and Y represents final cone count.

Example: X = 100 female cones
Y = 20 female cones.
Therefore, % cone loss = $[(100 - 20)/100] \times 100 = 80\%$ female cone loss.

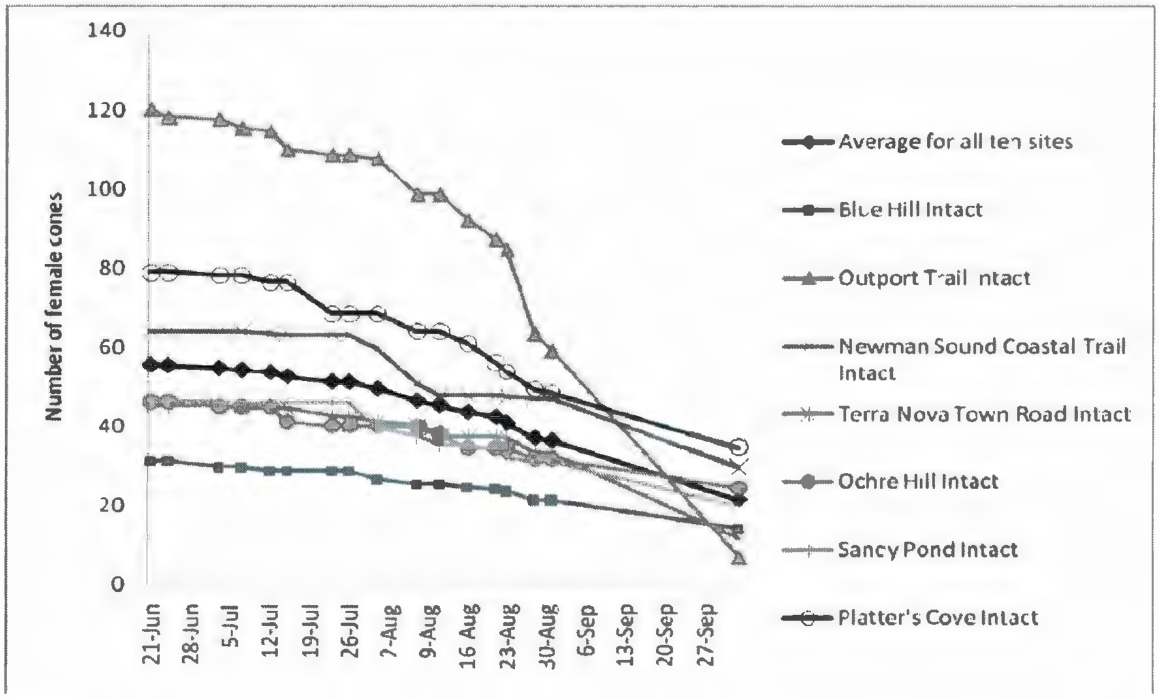
Table 3.4. Percent female cone loss to red squirrels averaged for each site* (n = 8) for 2008 study.

Study Sites	No. of Trees	% cone loss	Std. Error
Outport Trail Intact.	1	100	-
Blue Hill Insect Kill.	2	45.8	20.8
Blue Hill Intact.	2	80.0	20.0
Newman Sound Coastal Trail Intact.	1	30.9	-
Terra Nova Town Road Intact.	1	100	-
Ochre Hill Insect Kill.	1	100	-
Platter's Cove Intact.	2	100	0.0
Bread Cove Insect Kill.	1	100	-

*Focal trees in Sandy Pond and Ochre Hill Intact sites had no female cones.

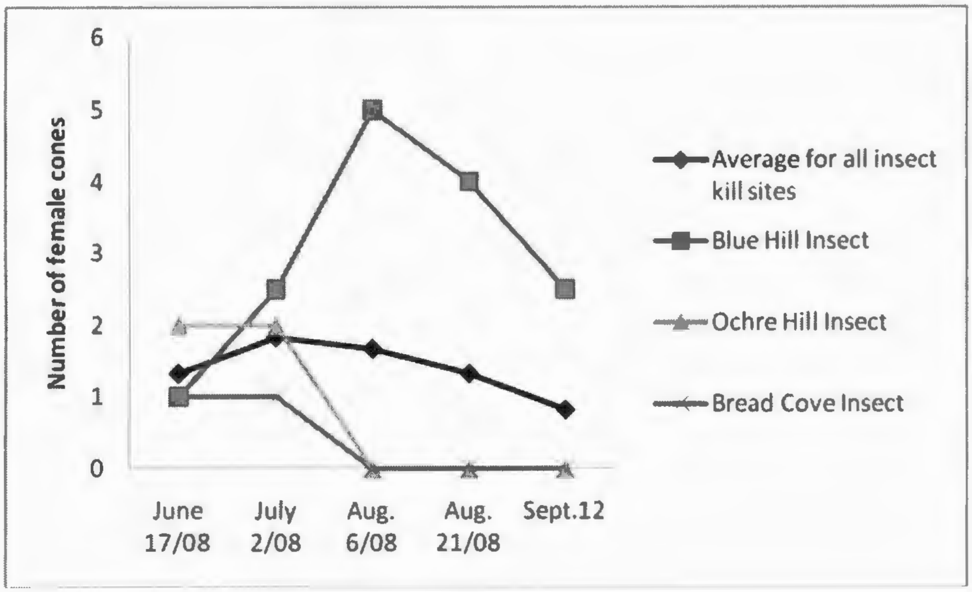


(a) Insect Kill sites

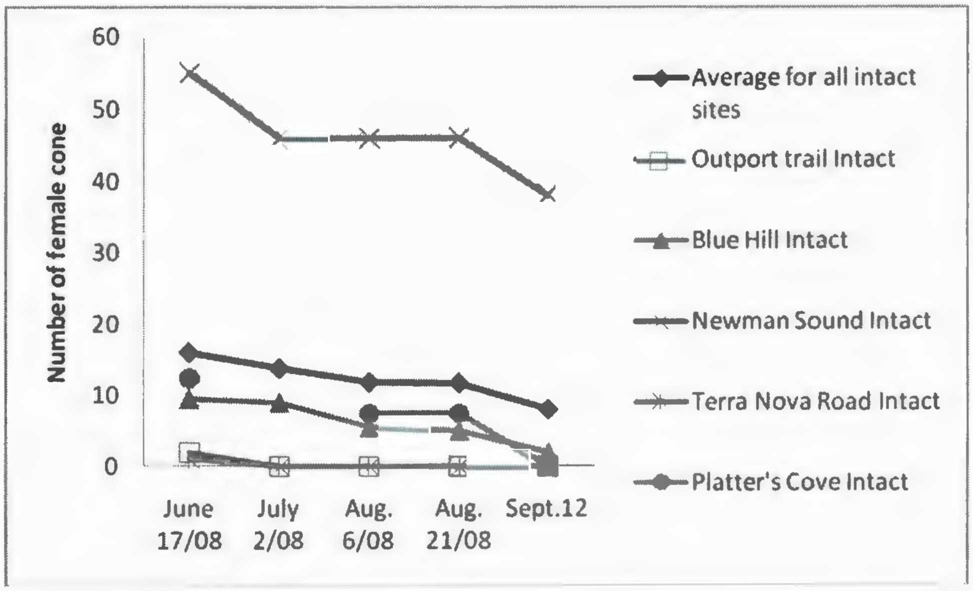


(b) Intact sites

Figure 3.3 a; b. Balsam fir female cone removal curve for individual study sites in 2007: (a) Insect Kill; (b) Intact sites. Note: Y-axis scale changes between panels. Refer to Table 3.3 for sample sizes.



(a) Insect Kill sites



(b) Intact sites

Figure 3.4. Balsam fir female cone removal curve for individual study sites (2008): (a) Insect Kill sites; (b) Intact sites. Note: Y-axis scale changes between panels. Refer to Table 3.4 for sample sizes.

3.3 Insect Predation of Female Cones Study

Total stem density of study sites ranged from 454 - 3104 trees/ha at White Hills Insect Kill and White Hills Intact sites respectively. Balsam fir stem density was lowest at White Hills Insect Kill site, 431 trees/ha, and highest at White Hills Intact site, 2949 trees/ha (Table 3.5). Out of 29 balsam fir trees sampled across the eight sites in late August 2007 just before seed release, 100% of sub-sampled cones (n = 444) showed signs of insect infestations such as entry/exit holes, insect larval activity in cones including tunnelling, and presence of larvae in seeds. The percentage of sub-sampled balsam fir seeds eaten or with insect larvae present per cone in the 2007 study ranged between 6.7 ± 1.52% (n = 12,311) at Spracklins Intact site, and 63.37 ± 8.87% (n = 13,200) at Boy Scout Insect Kill site with an overall average of 21.35 ± 5.91% (n = 96,932) (Figure 3.5).

There was a strong positive correlation between balsam fir stem density and absolute stem density per site ($r = 0.904$ $n = 8$ $p < 0.001$) which permitted using one of the variables, balsam fir stem density, in the regression analysis so as to assess the direct relationship between percent cone/seed infestation by insects and balsam fir stem density of study sites. Percentage of seeds infested per cone per tree did not depend on balsam fir stem density per site ($F_{[1,26]} = 3.15$, $p = 0.087$, see Appendix: Table A.12). Cone/seed infestation did not differ between disturbance types ($F_{[1,21]} = 0.96$, $p = 0.365$) or between age groups ($F_{[1,21]} = 0.01$, $p = 0.926$, see Appendix: Tables A.14 and A.15). There was a strong correlation between height and DBH of trees ($r = 0.746$ $n = 8$ $p < 0.001$), which allowed the use of the height variable to represent tree size. Percentage of seeds infested by insects per tree was not affected by tree size ($F_{[1,26]} = 0.39$, $p = 0.540$, see Appendix: Table A.12). Percent of seeds infested per cone per tree also showed no significant differences with respect to cone length ($F_{[1,25]} = 1.20$, $p = 0.283$), cone width ($F_{[1,25]} = 0.01$, $p = 0.937$), and cone weight ($F_{[1,25]} = 1.26$, $p = 0.272$, see Appendix: Table A.13). Proportion of viable seeds was low (0-20%), but varied significantly between sites with respect to balsam fir stem densities ($G_1 = 3.940$, $p = 0.047$, Figure 3.6; Appendix: Tables A.16 and A.18), illustrating a density-dependent relationship, with the proportion of viable seeds among trees increasing with increasing balsam fir stem density of study sites. No significant difference, however, was detected in proportion of viable seeds and average weights of seed lots ($G_1 = 0.049$, $p = 0.825$, see Appendix: Tables A.16 and A.19).

Table 3.5. Total and balsam fir stem densities of study sites for female cone insect predation study (n = 10). Total and Balsam fir stem densities were computed using Point-Centered Quarter method with 50 m transects (Mitchell, 2001). Total density refers to number of stems of all trees species with minimum DBH of 4 cm in a hectare; and balsam fir stem density refers to number of balsam fir trees with minimum DBH of 4 cm in a hectare.

Study Sites	Total stem density trees/ha	Balsam fir stem density trees/ha
Boy Scout Camp Insect Kill	801	481
Boy Scout Camp Intact	1342	839
White Hills Insect Kill	454	431
White Hills Intact	3105	2949
Spracklins Intact	2153	2153
Spracklins Insect Kill	1180	929
Hatchet Cove Insect Kill	1060	822
Hill View Intact	2989	1569

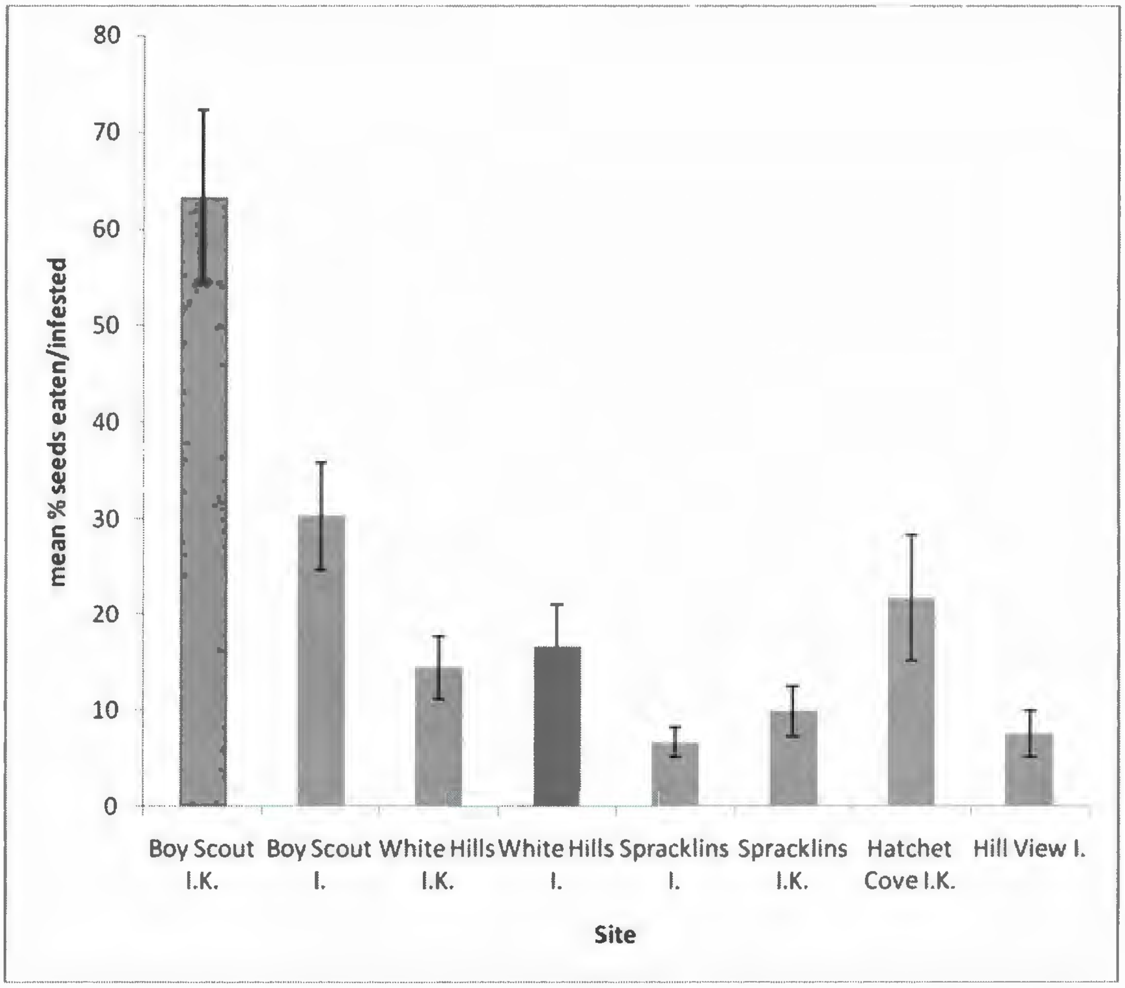


Figure 3.5. Mean percentage (± S.E) of seeds eaten or infested with insect larvae per cone for each study site (I = Intact site; I.K. = Insect kill site) illustrating some level of insect infestation in all study sites and across disturbance types.

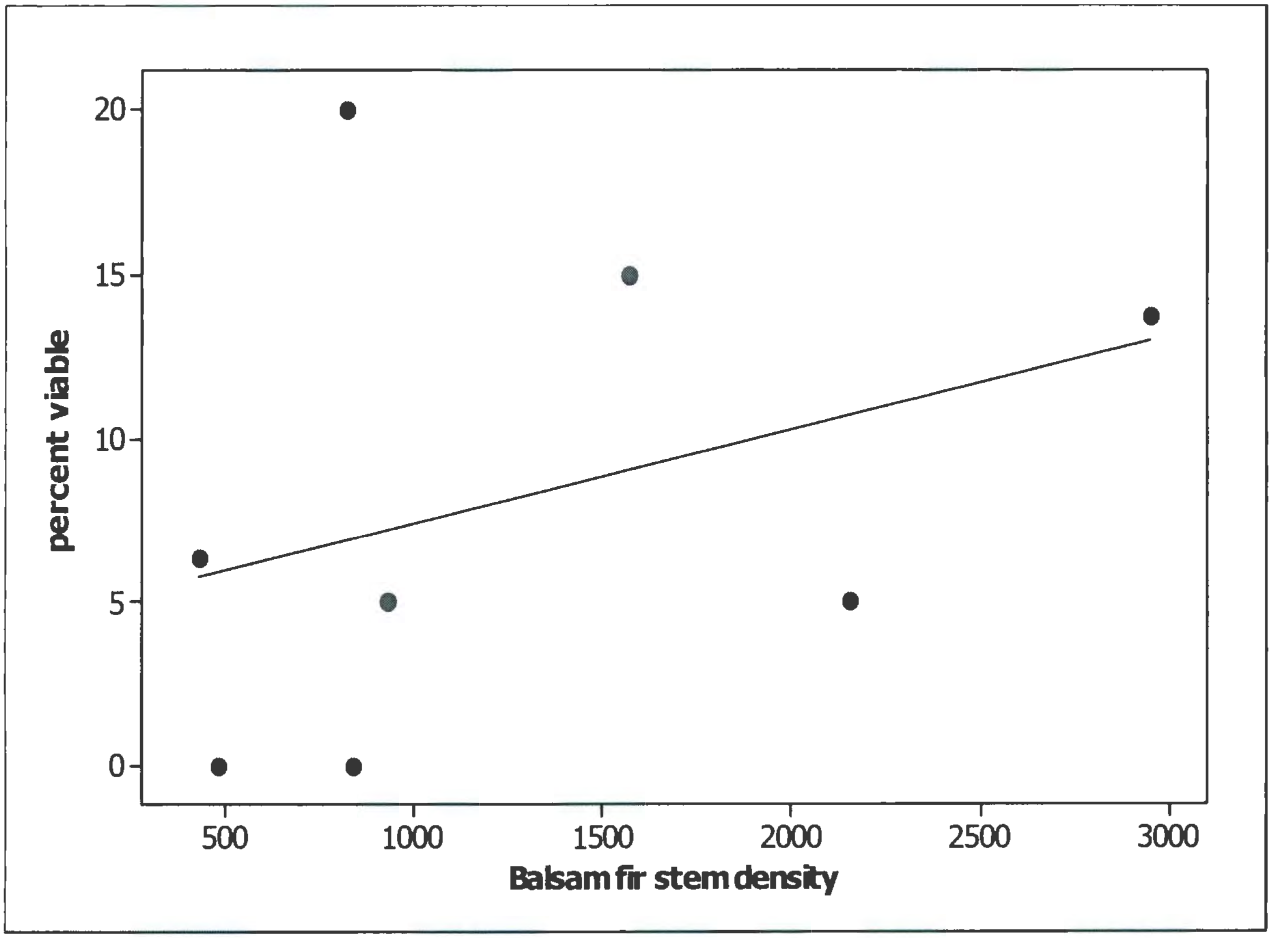


Figure 3.6. Regression of percentage of viable seeds per cone per tree (%viable) and balsam fir stem density of sites (BDen) with significant slope. The proportion of viable seeds per cone was directly related to the balsam fir stem density of stands. Regression equation: %viable = 4.481 + 0.002877 BDen; P = 0.047.

3.3.1 Summary of Cone/Seed Insect Activity in Study Sites

All study sites showed signs of external and internal insect damage to balsam fir female cones, with 21.35% ± 5.91% of balsam fir seeds sampled (n = 96,932) in late August just before seed release either eaten or showing presence of insect larvae. However, these estimations of insect damage did not include the many seed cones totally destroyed during development.

Signs of early insect damage in the form of entry holes, premature browning of cone bracts and internal tissue damage were observed in cones sampled in some sites in first cone harvest from late May to early June 2007 (Figure 3.7).

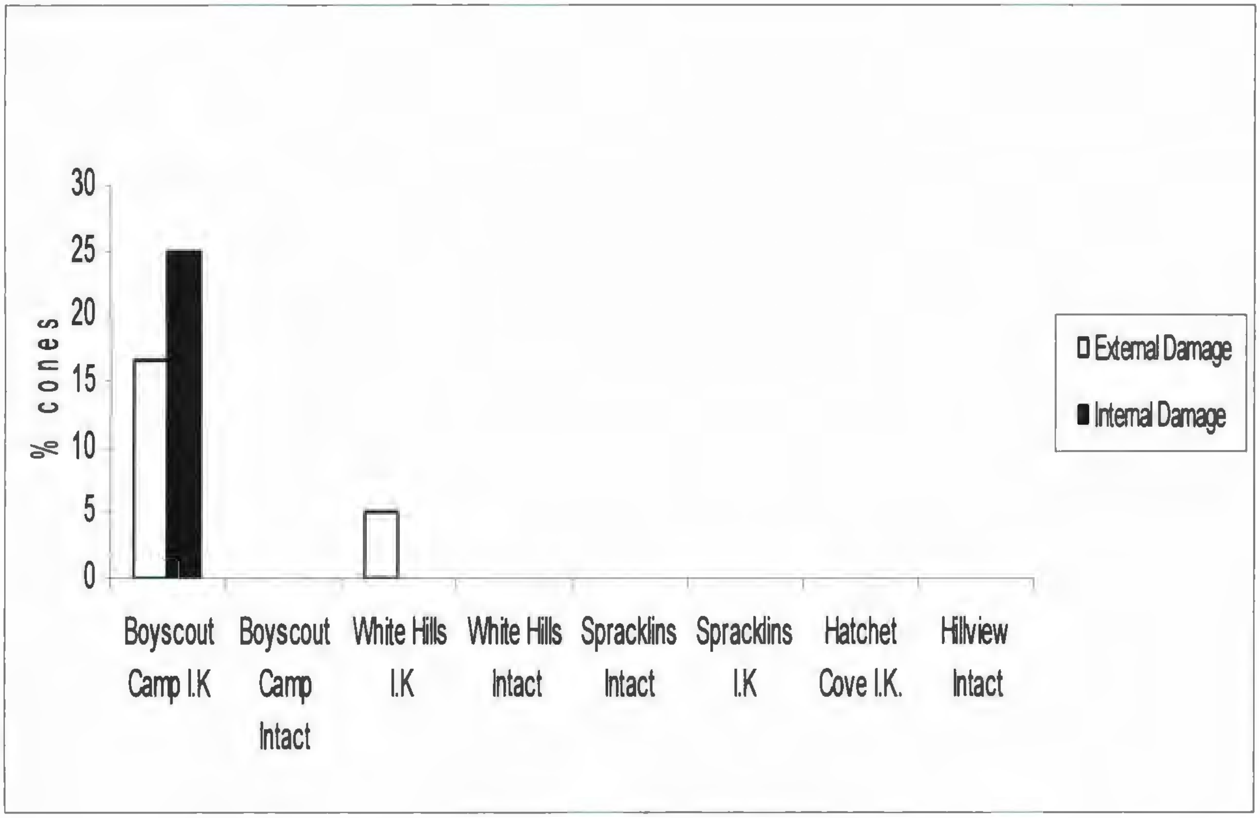


Figure 3.7. Percentage of female cones showing signs of external and internal damage among study sites (Intact and Insect Kill) in first cone harvest between late May and early June 2007.

The second harvest in late June 2007 had a variety of insects and signs of insect activity among cones sampled. Coneworms (Lepidoptera) were found between cone bracts in all eight sites involved in the study. The average percentage of cones with signs of external damage ranged from 8.8 ± 3.4% for intact sites and 9.6 ± 4.5% for insect kill sites. One site, Hatchet Cove, had significant presence of common thrips (Thysanoptera); (Figure 3.8). Coneworms responsible for most external insect damage to the balsam fir cones peaked in activity during this stage of cone development with numbers dropping drastically in subsequent weeks, and virtually non-existent in the latter stages of cone maturation in late August just prior to seed dispersal (Figure 3.9). Although the trend was of increasing percentage of female cones showing signs of external damage in the third and fourth harvests (Figure 3.10), this was most likely due to sampling of remnant insect-damaged cones from earlier stages of cone development.

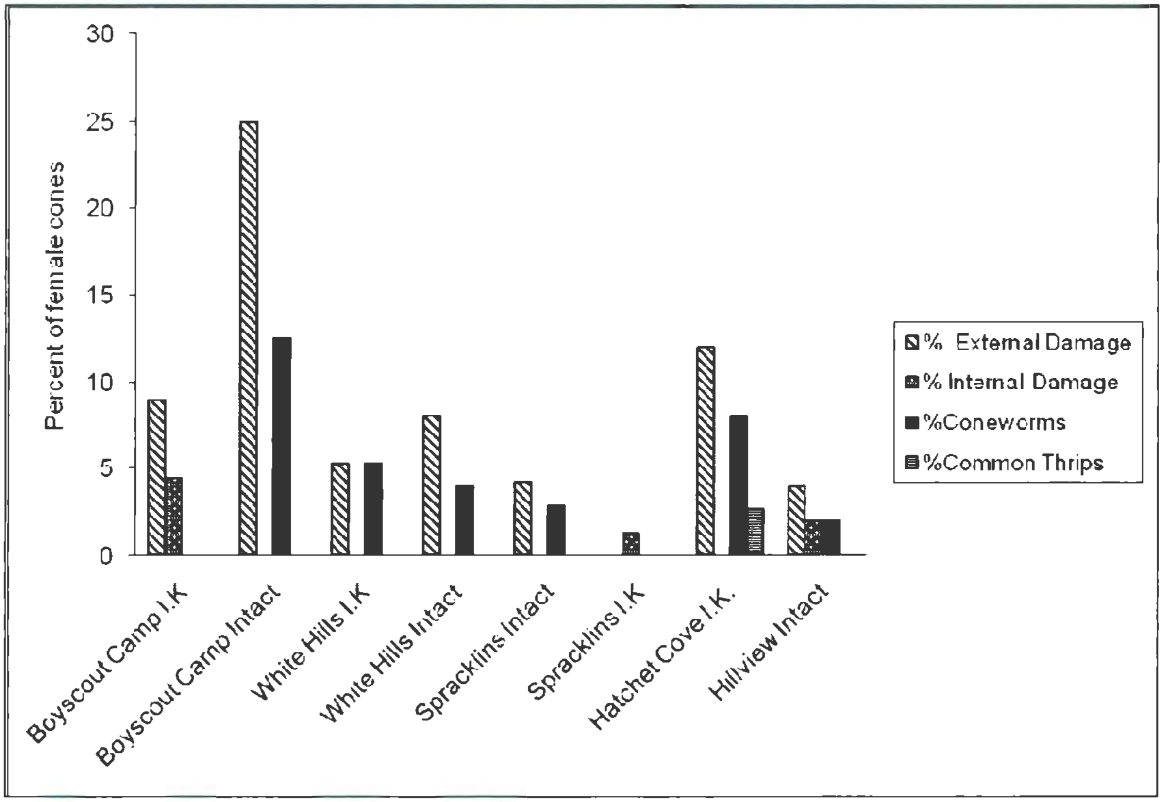


Figure 3.8. Percentage of female cones showing signs of external and internal damage, and coneworm and common thrip infestation among study sites (Intact and Insect Kill) in second cone harvest in late June 2007. Lack of a bar indicates no infestation by that insect.

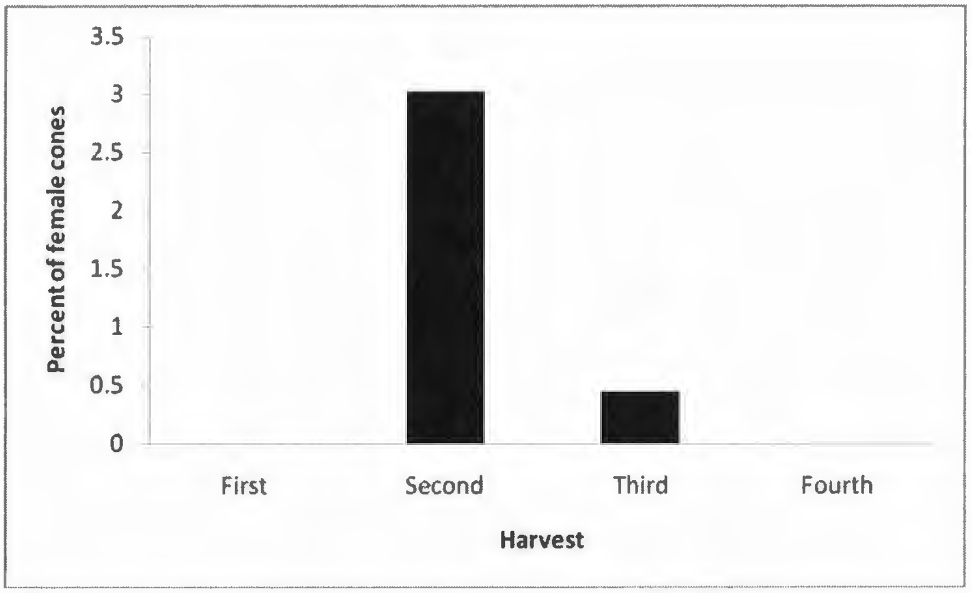


Figure 3.9. Percentage of cones with recovered Lepidopteran larvae (coneworms) for each harvest period. First and fourth harvests had no Lepidopteran larvae recovered.

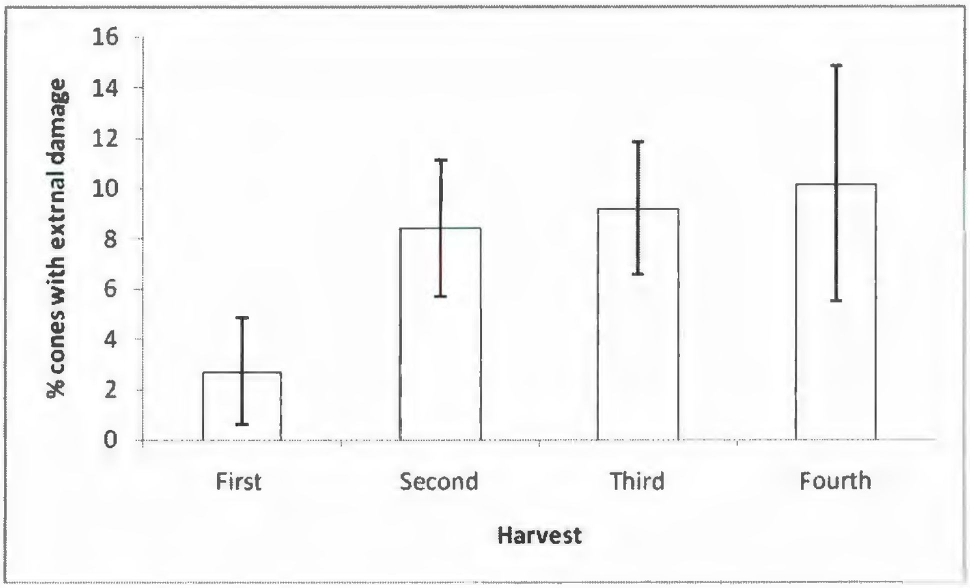


Figure 3.10. Mean percentage (±SE) of female cones showing signs of external damage in each harvest period.

Heavy infestation of cones with insect larvae was observed in the cone samples collected from all sites in the third harvest in early August 2007. The main insects were Diptera: cone maggots, *Hylemya* spp., found tunnelling in mid-rib of some cones sampled; and cone midge, *Dasineura* spp., located within seeds in cone samples from most sites (Figure 3.11). Cone seed insect damage, however, was most pronounced in the fourth harvest in late August with all sites showing significant presence of cone midge larvae in seeds. Many sites also showed signs of seed chalcid infestation (Hymenoptera, *Megastigmus* spp.) with characteristic white coma-shaped larvae present in about half of the sites studied. The cone resin midge (Diptera, *Asynapta* spp.) was present between seed wings in most sites (Figure 3.12), and looper moth larvae (Lepidoptera, Geometridae) were recovered from the mid-rib of cone samples collected from the two Boyscout Camp sites.

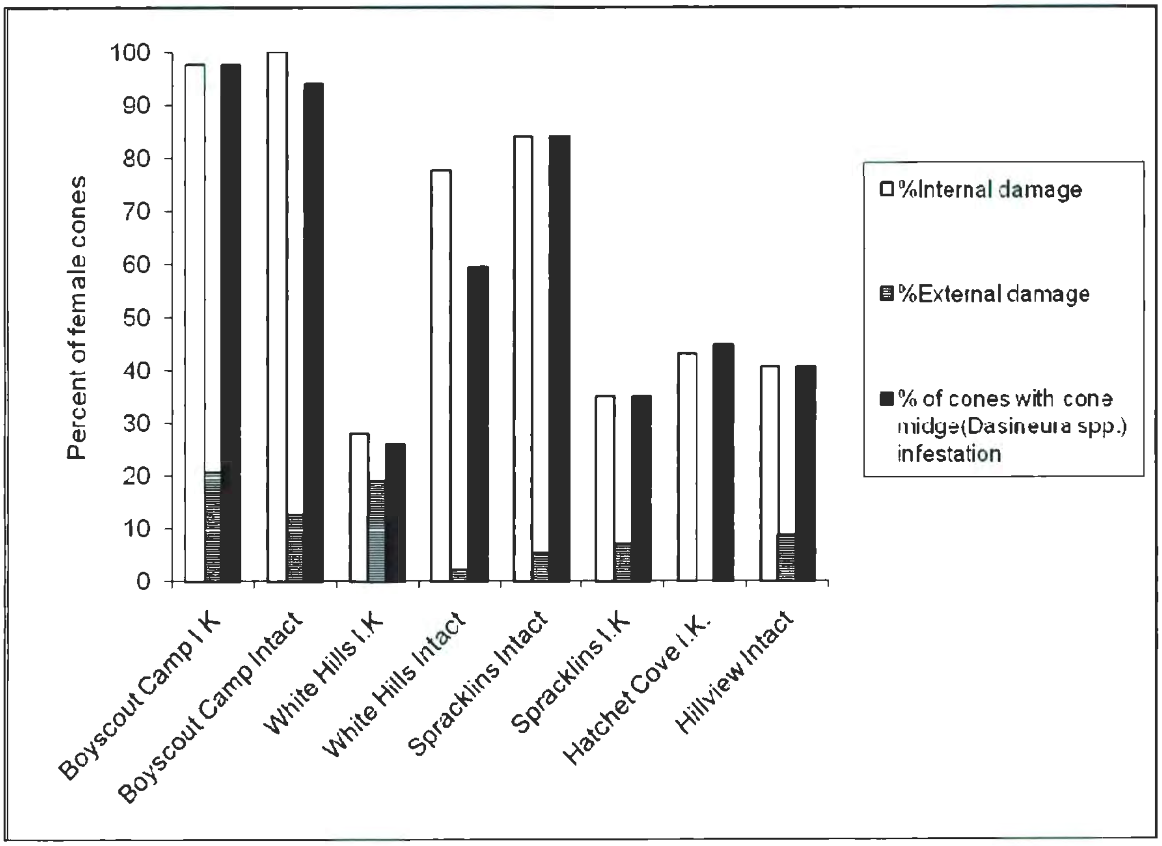


Figure 3.11. Percentage of cones with signs of external and internal (presence of larvae in seed) damage, and percentage of cones with cone midge damage for individual sites in third harvest in early August 2007.

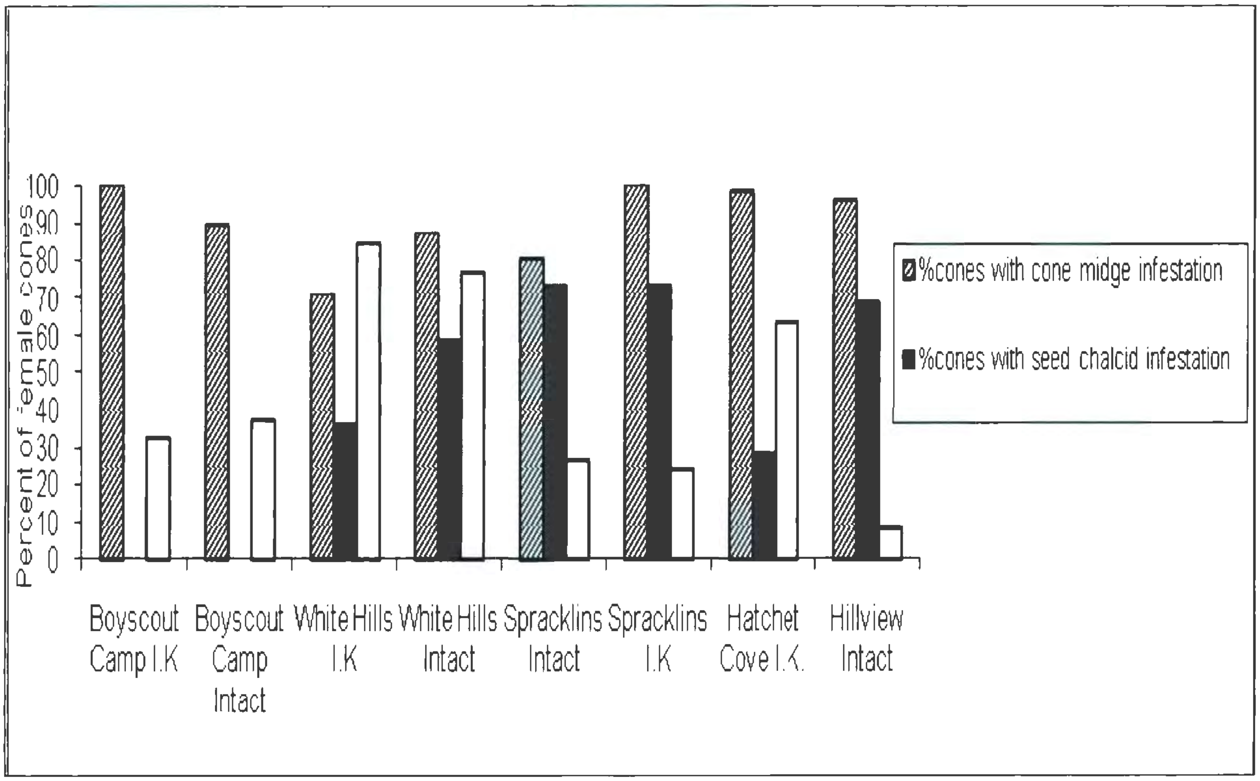


Figure 3.12. Percentage of cones with cone midge; seed chalcid; and cone resin midge infestations for individual sites (Intact site and Insect Kill) in fourth harvest.

3.4 Cumulative Assessment of cone/seed losses to Red Squirrels and Insects

The percent female cone loss to red squirrels ranged from 50.4 ± 7.5% in Insect Kill sites to 64.6 ± 6.3% in Intact sites, and the percentage of seeds lost to insect infestations ranged from 16 ± 3.1% in Intact sites to 25.0 ± 7.3% in Insect Kill sites. The cumulative seed loss ranged from 60-85% and 73.4-89.4% in Insect Kill and Intact sites respectively. The maximum and minimum cumulative seed loss computations are based on whether or not red squirrels discriminate between cones with no external damage but with internal seed infestation, and cones with no external and internal damage. I observed that red squirrels avoided cones with disfigurement, holes, and other external signs of insect infestation.

Chapter 4: Discussion

Neither male nor female cone predation by red squirrels was affected by tree size or disturbance type. Foraging on female cones did not appear to be influenced by cone crop size of trees. However, foraging on male cones was density-dependent. Levels of seeds infested or eaten by insects were not affected by stem density or disturbance type. Size and age group of trees also did not affect seed infestation levels, nor did the size of cones. Proportion of viable seeds per cone in trees was, however, significantly higher in study sites with higher balsam fir stem densities. The combined effect of red squirrel and cone/seed insect predation resulted in over 2/3 reduction in potential seed production in all study sites combined.

4.1 Squirrel predation of male cones

Blue Hill intact site was the only site that showed a net increase in final pollen cone counts in mid-June from counts in late May. This site had the highest balsam fir stem densities among study sites, with site-unique characteristics of a large pollen cone crop, which may have afforded some branches with pollen cones to escape red squirrels herbivory.

Red squirrel predation accounted for average pollen losses ranging from 32.8 ± 6.2% to 84.5 ± 9.3% among the study sites, with an average decrease of 47.6 ± 3.9% across sites. Although evidence exists of red squirrels and other squirrel species feeding on pollen (Price and Boutin, 1993; Maser, 1998), little information is available on the magnitude of pollen cone losses to scuirids in natural systems and their resultant impact on pollination success. This limitation, notwithstanding, such high pollen losses to red squirrels may influence pollination success, especially if pollen grain densities are low (Owens and Molders, 1980; Singh and Owens, 1981; Greene *et al.*, 1999). Although pollination does not appear to limit seed production within TNNP due to long distance-dispersal (Noel, 2004), it is predicted that as pollen bearing trees decrease pollen may become limited; therefore pollination success should be monitored in future years.

The study results suggest that selection of pollen cone-bearing trees for foraging by red squirrels is not influenced by tree heights. In contrast, Eurasian red squirrels (*Sciurus vulgaris*) prefer tall trees in natural stands of Scots pine (*Pinus sylvestris*); (Summers and Proctor, 1999). In this study, pollen cone predation by red squirrels was higher in low balsam fir stem density stands than in high balsam fir stem density stands, implying that pollen cone removal is negatively density-dependent. The sites with high stem densities had higher number of pollen cone bearing trees per hectare than low stem density sites. This afforded the possibility of some cones escaping predation by overwhelming the predator with their large numbers (Janzen, 1971). The high pollen cone losses recorded across the study sites suggests that red squirrels in this study area are not reluctant to forage in disturbed, low density stands, as has been previously reported for red squirrels and other sciurids in earlier studies (Henderson *et al.* 1985; Fisher and Holler, 1991; Andrén and Delin, 1994; Wauters *et al.*, 1994; Sheperd and Swihart, 1995). Bayne and Hobson (2000), suggest that red squirrels have fairly general habitat requirements in terms of forest structure and have no problem moving in open areas. There was no significant difference in pollen cone predation intensity among trees in sites with or without recent history of insect infestation, suggesting that balsam fir stem density of forest patches is more critical to predictions of levels of pollen cone predation by red squirrels than is a forest's recent history of insect infestation.

4.2 Squirrel predation of female cones

The average cone loss to red squirrels for study sites ranged from 32.9 ± 15.7% to 93.5 ± 3.3% and 39.1% to 100% for 2007 and 2008 studies respectively. Cone loss to red squirrels in other forest systems varied from 19% to 82% of ponderosa pine (*Pinus ponderosa*) cone crop (Halvorson, 1986), 47% to 58.3% of white spruce cone crop (Peters *et al*., 2003), 80% of limber pine (*Pinus flexilis*) and southwestern white pine (*Pinus strobiformis*) cone crops (Benkman *et al*., 1984), and 54% of sugar pine (*Pinus lambertiana*) cone crop (Tevis, 1953). Hence, although red squirrels are not native to Newfoundland their level of impact on conifer cone crop was similar to their impact in the aforementioned forest systems where they are considered native. Although no significant variation in red squirrel predation of female cones among seed trees in the study sites was observed, red squirrels, on the whole, consumed a large percentage of female cones that were monitored, with an average decrease of 58.9 ± 5.1% and 74.8 ± 8.9% across sites in 2007 and 2008 respectively. The results, suggests that although cone crop declined in the second year, there was no significant increase in percentage of cones harvested by red squirrels, as was also found by Peters *et al*. (2003).

Red squirrels, in my study, did not seem to select seed trees for foraging based on tree heights as was suggested by Summers and Proctor (1999). Unlike in the male cone study, female cone predation levels did not vary significantly among sites, and site stem densities did not influence red squirrel foraging intensity. This result contradicts those of

Peters *et al.* (2003), who observed lower cone losses to red squirrel in industrial forests than in intact white spruce forests due to the reluctance of squirrels to move in open areas with heightened exposure to potential predators. Summers and Proctor (1999) also observed a foraging preference of red squirrels for dense stands where they could move among trees without exposing themselves to predation on the ground. The northern goshawk (*Accipiter gentilis*) and the American marten (*Martes americana*) are predators of red squirrels in Newfoundland and on the mainland (Price *et al.*, 1990; Whitaker *et al.* 1996; Sturtevant *et al.* 1996), however, results of this study may imply that in TNNP, predator avoidance may not be as important in influencing red squirrel foraging behaviour as in other boreal regions especially considering the low populations of American marten on the island (Bergurud, 1969; Snyder, 1984; Thompson, 1991; Forsey *et al.* 1995; McGowan *et al.* 1999). Also, the hypothesis that red squirrels will select trees with large cone crop sizes for foraging so as to conserve energy in locating cones was unsupported, as their foraging intensity varied little between trees with large and small crop sizes.

Red squirrels in this study commenced intensive harvesting of female cones, based on level of cone loss, in mid August, when energy content and nutrient value was highest, and continued well into the seed dispersal stage in early September through October. The average female cone loss to red squirrel for all sites in 2007 was high, especially considering that the study was undertaken in a large cone-crop year. Similar results were recorded in other conifer species in the region albeit in low and moderate cone crop years (West, 1989; Tulk, 2004). Ultimately, the loss of cones to red squirrels is one of a number of factors that may act as a bottleneck in the natural regeneration of some conifers (Peters *et al.*, 2003).

4.3 Insect herbivory of female cones and seeds

The average percent of seed loss to insects across study sites ranged from 6.7 ± 1.5% to 63.4 ± 8.9%. Previous studies on seed loss to insect among conifers range from 12.5% to 47% of seeds of white fir (*Abies concolor*), 32% to 39% of seeds of Pacific silver fir (*Abies amabilis*) (Owens and Morris, 1998), 40% of seeds of Douglas-fir (*Pseudotsuga menziessi*) (Dewey, 1986), and Mattson (1978) reporting a range of 10-100% with an average of 25% cone loss from a number of earlier studies.

The suite of insects implicated in cone and seed loss in this study included members of at least four (Lepidoptera; Diptera; Hymenoptera; and Thysanoptera) of the seven orders with phytophagous insects known to feed on seed cones of conifers (Turgeon *et al.* 1994). The genera identified in this study could be divided into three feeding guilds: the seed-mining guild, seed chalcid, *Megastigmus* spp. (Hymenoptera: Torymidae), cone midge, *Dasineura* spp. (Diptera: Cecidomyiidae); the cone-and seed-mining guild, fir coneworm, *Dioryctria* spp. (Lepidoptera: Pyralidae); the scale-and bract-feeding guild, common thrips, *Frankliniella* spp. (Thysanoptera: Phlaeothripidae), cone maggot, *Hylemya* spp. (Diptera: Anthomyiidae). This diversity was reflected in a similar study of cone insects of white fir (Shea, 1989). Other studies on boreal forest systems have implicated one or more of these insects in cone mortality and seed damage (Mattson, 1978; Mosseler *et al.*, 1992; Owens and Morris, 1998; Rouault *et al.*, 2004)

It has been suggested from earlier studies that cone and fruit losses to insects portray an inverse density-dependent relationship, that is, larger fruit crops suffer lower loss rates than small ones (Solomon, 1981; Miller *et al.*, 1984; Borowicz and Juliano, 1986; Randall, 1986). However, I found no significant variation in insect infestation rates among trees in the study sites despite the sites having a potentially wide range of cone crop sizes based on balsam fir stem densities. Insect infestation did not differ between sites with respect to their recent history of insect disturbance, nor did insects show a bias for larger sized cones as has been documented in earlier studies (Kirkland and Goeden, 1978; Marshall *et al*., 1986). There are three possible explanations for these results: 1. the cone/seed insect populations were large enough to mask possible influences of the tree and site characteristics, 2. the sites chosen for the study were not of a spatial scale large enough to detect the relationship between insect predation levels and the site characteristics used in the models and, 3. the presence of cone bearing trees of other species at some study sites, especially black spruce, may have attracted a higher population of cone insects to the study sites than attributable to balsam fir stands alone. The intensity of insect infestation did not differ between young and old trees, which supports Karban's study in 1987, but contrasts with the age-dependent relationship reported by Landwehr and Allen (1982).

All study sites showed signs of external and internal insect damage to balsam fir female cones, with 21.4% ± 5.9% of sampled seeds either eaten or showing presence of insect larvae. It must be stressed, however, that this represents a minimal estimate of loss, as it did not include the many seed cones totally destroyed by insects in early development or abscised by the time counts were done.

4.4 Cumulative impacts of red squirrel and cone insects on balsam fir seed production

Feeding on ripening fruits/cones and on seeds, prior to dispersal, can account for massive losses in reproductive potential in many plant species (Crawley, 1989). Balsam fir cone and seed losses in the 2007, a large cone crop year, were moderately high. Cone and seed losses, especially to red squirrels, were even higher in 2008, a lean crop year, and are comparable to previous studies (Janzen, 1971; Sivertown, 1980; Kelly, 1994; Houle, 1999; Koenig and Ashley, 2003). A similar study in the same region that assessed squirrel predation predicted that balsam fir releases sufficient seedfall for regeneration in a mast year (Tulk, 2004). However, in spite of 2007 being a mast year, the combined effect of both red squirrel predation of female cones and insect predation of cones and seeds resulted in over 2/3 reduction in potential cone and seed production for all sites combined. It appears that red squirrels and cone insects have similar impact on balsam fir seeds in all study sites, with none of the distinct site characteristics associated with less predation. This is likely because the red squirrels and cone insects are so pervasive in this study area and impact all available seeds. That is, the populations "blanket" the area, and will hunt until they find all available food resources. Another possible explanation for the results is that both red squirrels and insects respond to multiple factors at multiple scales across the landscape which makes developing predictive models challenging.

I observed during that red squirrels avoided cones with external signs of insect infestation. It is however, unknown whether they discriminate among cones with no external or internal insect damage, and cones with no external damage but with internal insect infestation.

The results of the cumulative seed loss to red squirrels and insects did not take into account the actual proportion of seeds that escape predation that are viable: 4.8% and 8.9% in Insect Kill and Intact sites respectively. Hence based on these results, for every 100,000 seeds produced in an Insect Kill site, the actual number of seeds that escape predation and potentially add to the seedling recruitment pool range from 713-1,900; and for the Intact sites, from 963-2,328 (see Appendix B for details). This estimation, however, does not include the number of seeds that actually germinate and survive seedling stage, which is known to be low for balsam fir (Hedlin, 1974; Hedlin *et al.*, 1980; Calogeropoulos *et al.* 2004; Parent *et al.*, 2006). For instance, a study in the general area by Noel (2004) elaborated on the negative impact of slug herbivory on seeds after release, and attributed greater than 90% of balsam fir seedling mortality to small rodents including meadow voles (*Microtus pennsylvanicus*). A recent study by Holloway (2008), also reported post-dispersal seed predation by ants in the study area.

The cumulative assessment is based on results from 2007 study, which was a good cone crop year. Considering that good crop seasons in balsam fir occur in 2-5 year intervals (Johnston, 1986), the impact of red squirrels and insects on cone/seed numbers may be even higher when studied over a number of sequential seasons. Also this assessment does not take into account cones destroyed by insect and red squirrels at the bud and pre-pollination and fertilization stages of development which were not available for assessment. Hence impact of red squirrels and insects on seed potential may be even greater than these results suggest.

It has been documented from earlier studies that red squirrel densities as low as 2 squirrels/ha have significant impact on availability of mature cones in a year with a small cone crop (West, 1989). Although a significant proportion of mature balsam fir cones harvested by red squirrels are cached, these do not contribute significantly to seed dispersal of balsam fir (Tulk, 2004). Red squirrel population in TNNP and surrounding areas are estimated at between 0.5 and 2.3 squirrels/ha (Lewis, 2004), well within densities of concern. Hence, the combined effect of both red squirrel cone predation and insect herbivory of cones and seed predation was high enough to pose serious challenges to natural recruitment even in the mast year. Unlike pollen cones, most seeds of wind dispersed trees are not expected to move great distances because of their considerably greater mass (Latta *et al.* 1998). Therefore local seed production may be an important limiting factor affecting the regeneration of balsam fir (Noel, 2004) especially considering that balsam fir does not have a persistent seed bank.

Following this trend, coupled with the fact that such mast events, which offer potential for some seeds to escape predation (Janzen, 1971), are infrequent at best (Fowells, 1965), it is likely that balsam fir natural recruitment in the study area will continue to be insufficient to meet requirements to maintain healthy balsam fir stands as was supported by Noel (2004). This has potential ramifications in the ecosystem at large and may lead to further reductions in populations of listed endangered species heavily reliant on balsam fir forests. For example, lower density of balsam fir stands may result in lower seed production and amplify the present intense competition of the endangered red crossbills (*Loxia curvirostra*) and red squirrels which both use balsam fir seeds as a prime food source (Parchman and Benkman, 2002). Reduction in mature balsam fir forest also puts endangered Newfoundland subpopulation of American marten and boreal felt lichen (*Erioderma pedicellatum*), as well as other organisms that rely on healthy balsam fir forests in the region at even greater risk of local extinction (Sturtevant *et al.*, 1999; Environment Canada, 2007).

4.5 Management Implications

Based on the results of this study, percent cone loss to both red squirrels and insects in balsam fir stands appear to vary little over the landscape at the spatial scale examined in this study.

The combined impact of red squirrels and insects together with previously documented herbivory by non-native moose on different stages of balsam fir development (Bergerund and Manuel, 1968; Thompson *et al.*, 1989; McLaren *et al.*, 2000; 2004) may pose significant challenge to natural recruitment of balsam fir in the study area. The results of the study suggest that balsam fir recruitment may be seed limited. Therefore, barring red squirrel population reduction measures, which may be difficult to implement, a combination of Assisted Natural Regeneration (which involves removing barriers to seedling growth such as soil degradation, competition, and recurring disturbances); (Leinonen *et al.*, 2007; Chazdon, 2008), and seedling planting should be investigated by management of TNNP and Newfoundland Forest Service as a potential strategy to reverse the current trajectory. The availability of suitable microsites for seed germination (Place, 1950; McLaren *et al.* 1996; Duchesneau and Morin, 1999; Noel, 2004) should, however, be investigated as should the proportion of post-dispersal seed and seedling predation prior to any large scale direct seeding or planting exercise.

Long-term studies on suite of cone/seed insects and their annual impact on seed production, in high, moderate and low cone crops seasons, are also necessary to better understand effects of the insects on the population dynamics of balsam fir.

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Appendix A: Data and Statistical Analyses for Focal Trees

Table A.1. Balsam fir male cone study: individual tree (n = 40) heights in meters (Height), DBH in centimeters, balsam fir stem densities in (BDen, trees/ha), absolute stem densities in (AbsDen, trees/ha), percentage cone loss per tree (%cone loss), and disturbance type, DT, (1 = Insect Kill (n = 5); 2 = Intact (n = 5)) are given for study sites (n = 10).

Study Sites	DBH	Height	AbsDen	Bden	%cone loss	Regime
Louil Hill Insect Kill	14.9	9	473	378.4	69.2	1
Louil Hill Insect Kill	25.9	10.8	473	378.4	11.8	1
Louil Hill Insect Kill	26.9	12.3	473	378.4	47.4	1
Louil Hill Insect Kill	15.4	10.2	473	378.4	42.4	1
Blue Hill Insect Kill	29.4	8.4	290	29	46.4	1
Blue Hill Insect Kill	25.3	10.6	290	29	77.8	1
Blue Hill Insect Kill	18.3	7.8	290	29	5.9	1
Blue Hill Insect Kill	28	9	290	29	100	1
Blue Hill Intact	23	8.6	1528	1528	-10	2
Blue Hill Intact	16.3	10.7	1528	1528	-9.7	2
Blue Hill Intact	16	7.6	1528	1528	18.4	2
Blue Hill Intact	22	9.3	1528	1528	-12.5	2
Newman Sound Intact	27.3	12.6	632.5	395.3	86.2	2
Newman Sound Intact	22	10.6	632.5	395.3	100	2
Newman Sound Intact	18	9.3	632.5	395.3	57.6	2
Newman Sound Intact	19	10.2	632.5	395.3	94.1	2
Terra Nova Rd. Intact	25	11.4	577	317.35	47.7	2
Terra Nova Rd. Intact	31.5	15.4	577	317.35	46.8	2
Terra Nova Rd. Intact	22.2	11.2	577	317.35	87.9	2
Terra Nova Rd. Intact	26	13.6	577	317.35	77.1	2
Ochre Hill Insect Kill	20	10	285.5	199.5	50.8	1
Ochre Hill Insect Kill	28	12.6	285.5	199.5	22.6	1
Ochre Hill Insect Kill	19	10.6	285.5	199.5	33.3	1
Ochre Hill Insect Kill	26	11.6	285.5	199.5	68.9	1
Ochre Hill Intact	15.8	6	1237.5	1052	62	2
Ochre Hill Intact	13	7.6	1237.5	1052	7.1	2
Ochre Hill Intact	8.5	5.2	1237.5	1052	5.3	2
Ochre Hill Intact	13.5	8.3	1237.5	1052	59.4	2
Sandy Pond Intact	17.5	15.6	1425	1033.13	16.7	2
Sandy Pond Intact	23	10.5	1425	1033.13	38.6	2
Sandy Pond Intact	21	12	1425	1033.13	85	2
Sandy Pond Intact	30.8	16	1425	1033.13	45.5	2

Table A.1 continued.

Study Sites	**DBH**	**Height**	**AbsDen**	**Bden**	**%cone loss**	**Regime**
Platter's Cove Insect Kill	23	10.8	1151	633.05	26.1	2
Platter's Cove Insect Kill	21	10.8	1151	633.05	51.4	2
Platter's Cove Insect Kill	24	11.3	1151	633.05	27.3	2
Platter's Cove Insect Kill	16.5	9.75	1151	633.05	26.4	2
Bread Cove Insect Kill	25.5	11.1	440.5	308.35	79.8	1
Bread Cove Insect Kill	23.5	9.75	440.5	308.35	74.3	1
Bread Cove Insect Kill	32	10.5	440.5	308.35	88.9	1
Bread Cove Insect Kill	21	11.3	440.5	308.35	47.8	1

Table A.2. Balsam fir male cone study: Summary of regression analysis (α = 0.05) used to test relationship between percent pollen cone loss per tree and balsam fir stem density per site(BDen), focal tree height (height), and DBH of trees. Residual plots showed residuals to be independent, homogeneous and have normal distribution (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
height	1	1061.6	1	1	0.001	0.969
DBH	1	3161.9	587.6	587.6	0.86	0.36
Bden	1	4454.1	4454.1	4454.1	6.51	**0.015**
error	36	24629.5	24629.5	684.2		

Table A.3. Balsam fir male cone study: Summary of Nested-ANOVA, (α = 0.05) used to test relationship between percent male cone loss per tree per site and the disturbance type (Intact; Insect-kill) per site (DT), based recent history of insect infestation for each site (J. Gosse, pers. comm. 2007). Residual plots showed residuals are normally distributed but not independent, and were arcsine-transformed before for analysis (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
DT	1	0.0902	0.0902	0.0902	0.25	0.632
site(DT)	8	2.9096	2.9096	0.3637	3.27	**0.008**
Error	30	3.3334	3.3334	0.1111		
Total	39	6.3332				

Table A.4. Balsam fir female cone study in 2007: individual tree (n = 40) heights in meters (Height), DBH of trees in centimeters, cone crop size per tree (Ccrop), balsam fir stem densities in (BDen, trees/ha), absolute stem densities in (AbsDen, trees/ha), and disturbance type, DT, (1 = Insect Kill (n = 4); 2 = Intact (n = 6)) as given for study sites (n = 10).

Study Sites	**Height**	**DBH**	**Crop size**	**%cone loss**	**BDen**	**AbsDen**	**regim**
Outport Trail Intact	10	22	168	97.02	81.6	295.5	2
Outport Trail Intact	13.8	41.3	36	97.2	81.6	295.5	2
Outport Trail Intact	16	38.5	91	83.52	81.6	295.5	2
Outport Trail Intact	13.4	32.5	186	96.24	81.6	295.5	2
Blue Hill Insect Kill	10.6	25.3	20	30	29	290	1
Blue Hill Insect Kill	8	17.7	75	45.33	29	290	1
Blue Hill Insect Kill	9.6	20.5	19	36.84	29	290	1
Blue Hill Insect Kill	7.2	22.2	19	57.89	29	290	1
Blue Hill Intact	10.4	15.2	20	100	1528	1528	2
Blue Hill Intact	11.6	21	10	80	1528	1528	2
Blue Hill Intact	13.2	24	32	37.5	1528	1528	2
Blue Hill Intact	11.6	17	62	45.16	1528	1528	2
Newman Sound Intact	12.6	26.7	95	9.47	395.3	632	2
Newman Sound Intact	12.6	27.3	91	98.9	395.3	632	2
Newman Sound Intact	10.2	19	28	67.86	395.3	632	2
Newman Sound Intact	9.3	18	42	47.62	395.3	632	2
Terra Nova Rd. Intact	11.4	25	8	50	317.35	577	2
Terra Nova Rd. Intact	9	23.2	35	17.14	317.35	577	2
Terra Nova Rd. Intact	9.3	18	5	100	317.25	577	2
Terra Nova Rd. Intact	15.4	31.5	132	89.39	317.35	577	2
Ochre Hill Insect Kill	10.6	17.3	64	3.13	199.5	285.5	1
Ochre Hill Insect Kill	12.6	28	85	24.71	199.5	285.5	1
Ochre Hill Insect Kill	10.6	19	22	77.27	199.5	285.5	1
Ochre Hill Insect Kill	10	20	122	26.69	199.5	285.5	1
Ochre Hill Intact	13	17.5	28	100	1052	1237.5	2
Ochre Hill Intact	11.4	28	30	66.67	1052	1237.5	2
Ochre Hill Intact	14.8	35	47	42.55	1052	1237.5	2
Ochre Hill Intact	13	27	80	25	1052	1237.5	2
Sandy Pond Intact	12.5	18	6	32.61	1033.13	1425	2
Sandy Pond Intact	13.4	20.5	78	48.72	1033.13	1425	2
Sandy Pond Intact	7.4	12.5	4	25	1033.13	1425	2
Sandy Pond Intact	12.9	12.1	57	92.98	1033.13	1425	2

Table A.4 continued

Study Sites	Height	DBH	Crop size	%cone loss	BDen	AbsDen	regime
Platter's Cove Insect Kill	11.3	20	7	42.86	633.05	1151	2
Platter's Cove Insect Kill	18.1	28	237	55.27	633.05	1151	2
Platter's Cove Insect Kill	11.3	24	56	53.57	633.05	1151	2
Platter's Cove Insect Kill	9.8	16.5	16	87.5	633.05	1151	2
Bread Cove Insect Kill	10.2	23.5	21	76.19	308.35	440.5	1
Bread Cove Insect Kill	10.2	21	4	0	308.35	440.5	1
Bread Cove Insect Kill	6.8	22.5	32	100	308.35	440.5	1
Bread Cove Insect Kill	6.6	19	9	88.89	308.35	440.5	1

Table A.5. Balsam fir female cone study in 2008 of individual trees (n = 11): Percentage cone loss per tree (%closs 2nd), tree heights in meters (Height), DBH of trees in centimeters, cone crop size per tree (crop size), balsam fir stem densities in trees/ha (BDen), and disturbance type (1 = Insect Kill (n = 4); 2 = Intact (n = 4)) of study sites (n = 8).

Study Sites	%closs 2nd	Height	crop size	Bden	DT
Outport Trail Intact	100	16	2	81.26	2
Blue Hill Insect Kill	66.66	9.6	6	29	1
Blue Hill Insect Kill	25	7.2	4	29	1
Blue Hill Intact	100	13.2	9	1528	2
Blue Hill Intact	60	11.6	10	1528	2
Newman Sound Intact	30.91	9.3	55	395.3	2
Terra Nova Rd. Intact	100	11.4	1	317.35	2
Ochre Hill Insect Kill	100	10.6	2	199.5	1
Platter's Cove Insect Kill	100	11.3	24	633.05	2
Platter's Cove Insect Kill	100	9.8	1	633.05	2
Bread Cove Insect Kill	100	10.2	1	308.35	1

Table A.6. Balsam fir female cone study in 2007: Results of regression analysis ($\alpha = 0.05$) to test relationship between percent female cone loss per tree, and balsam fir stem density per site (BDen), focal tree height (Height), DBH of trees, and cone crop size per tree (crop size). Residual plots showed residuals to be independent, homogeneous and have normal distribution. (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
Bden	1	2	230	230	0.22	0.642
Height	1	126	187	187	0.18	0.675
DBH	1	362	459	459	0.44	0.512
crop size	1	260	260	260	0.25	0.621
Error	35	36551	36551	1044		

Table A.7. Balsam fir female cone study in 2008: Results of regression analysis ($\alpha = 0.05$) to test relationship between percent female cone loss per tree, and balsam fir stem density per site (BDen), focal tree height (Height), DBH of trees, and cone crop size per tree (crop size). Residual plots showed residuals to be independent, homogeneous and have normal distribution. (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
Bden	1	146.4	502	502	0.95	0.367
Height	1	3098	2504.2	2504.2	4.75	0.072
DBH	1	942.1	1021.6	1021.6	1.94	0.213
crop size	1	1463.6	1463.6	1463.6	2.78	0.147
Error	6	3162	3162	527		

Table A.8. Balsam fir female cone study in 2007: Results of nested-ANOVA, ($\alpha = 0.05$) to test relationship between percent female cone loss per tree and the disturbance type (Insect kill = 1; Intact = 2) per site (DT) (J. Gosse, pers. comm. 2007). Residuals were normaly distributed but not independent, and were arcsine-transformed for analysis (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
DT	1	0.446	0.446	0.446	3.5	0.098
site(DT)	8	1.0191	1.0191	0.1274	0.77	0.633
Error	30	4.9736	4.9736	0.1658		
Total	39	6.4387				

Table A.9. Balsam fir female cone study in 2008: Results of nested-ANOVA, ($\alpha = 0.05$) to test relationship between percent female cone loss per tree and the disturbance regime (Insect kill = 1; Intact = 2) per site (DT) (J. Gosse, pers. comm. 2007). Residuals were normally distributed, but were not independent, and were arcsine-transformed for analysis (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
DT	1	0.03367	0.00001	0.00001	0	0.992
site(DT)	6	0.68077	0.68077	0.11346	2.04	0.298
Error	3	0.16678	0.16678	0.05559		
Total	10	0.88122				

Table A.10. Balsam fir female cone insect study of individual trees (n = 29) in study sites (n = 8): Percentage seeds per cone infested with insects per tree (%seeds tree), tree heights (Height), diameter at breast height of focal trees (DBH),balsam fir stem densities (BDen, trees/ha), absolute stem densities (AbsDen, trees/ha).

Study Sites	%seeds tree	BDen	AbsDen	Height	DBH
Boy Scout Insect Kill	65.26	480.45	800.75	9.6	15.3
Boy Scout Insect Kill	78.98	480.45	800.75	10.1	16
Boy Scout Insect Kill	48.32	480.45	800.75	11.8	22.4
Boy Scout Intact	27.76	838.75	1342	12.8	25.7
Boy Scout Intact	42.04	838.75	1342	12.6	24.8
Boy Scout Intact	15.17	838.75	1342	9.5	18.9
Boy Scout Intact	26.27	838.75	1342	9.2	17.6
White Hills Insect Kill	22.01	430.83	453.5	9.4	11.2
White Hills Insect Kill	6.26	430.83	453.5	9.8	14
White Hills Insect Kill	12.2	430.83	453.5	10.4	16.3
White Hills Insect Kill	13.1	430.83	453.5	10.9	9.2
White Hills Intact	19.67	2949.28	3104.5	10.2	15.7
White Hills Intact	28.63	2949.28	3104.5	10.2	15.5
White Hills Intact	7.17	2949.28	3104.5	8.8	12.1
White Hills Intact	15.4	2949.28	3104.5	10.4	14.4
Spracklins Intact	8.71	2153	2153	8.78	14.5
Spracklins Intact	7.94	2153	2153	10.3	18.1
Spracklins Intact	3.81	2153	2153	7.5	15.9
Spracklins Insect Kill	17.94	928.85	1179.5	10.2	16
Spracklins Insect Kill	8.5	928.85	1179.5	13.6	21.9
Spracklins Insect Kill	8.91	928.85	1179.5	8.23	13.7
Spracklins Insect Kill	5.94	928.85	1179.5	9.72	14.2
Hatchet Cove Insect Kill	39.03	821.5	1060	7.4	13.6
Hatchet Cove Insect Kill	12.31	821.5	1060	9.3	17
Hatchet Cove Insect Kill	8.05	821.5	1060	4.1	5.3
Hatchet Cove Insect Kill	28.11	921.5	1060	7.4	13.7
Hill View Intact	5.76	1568.96	2988.5	11.7	16.4
Hill View Intact	4.13	1568.96	2988.5	9.8	13.7
Hill View Intact	11.86	1568.96	2988.5	12.2	18

Table A.11. Balsam fir female cone insect study of individual trees (n = 29): Average cone length per tree (clength tree), average cone width per tree (cwidth tree), average cone weight per tree (cweight tree), age class of trees (Young = 1; Old = 2), and disturbance type (1 = Insect Kill (n = 4); 2 = Intact (n = 4)) of study sites (n = 8).

Study Sites	clength tree	cwidth tree	cweight tree	DT	age class
Boy Scout Insect Kill	53	20.33	13.33	1	1
Boy Scout Insect Kill	71.9	20.95	18.4	1	1
Boy Scout Insect Kill	76.7	24.1	23.5	1	2
Boy Scout Intact	67.7	23.7	20	2	2
Boy Scout Intact	77.2	20	20.35	2	2
Boy Scout Intact	77.8	23.6	24.8	2	1
Boy Scout Intact	96.6	25.3	36.25	2	1
White Hills Insect Kill	64.2	23.08	21.85	1	1
White Hills Insect Kill	62.6	24.8	20.4	1	2
White Hills Insect Kill	59.9	22	17.55	1	2
White Hills Insect Kill	57.55	20.75	14.45	1	1
White Hills Intact	52	22.6	14.5	2	1
White Hills Intact	62.83	22.33	18.67	2	2
White Hills Intact	68.14	23.29	22.71	2	1
White Hills Intact	77.4	21.55	21.9	2	1
Spracklins Intact	67.15	20.85	19.6	2	1
Spracklins Intact	73.7	23.35	22.9	2	2
Spracklins Intact	80.4	21.4	24.3	2	1
Spracklins Insect Kill	55.9	21.1	14.4	1	2
Spracklins Insect Kill	65.35	22.15	16.95	1	2
Spracklins Insect Kill	64.9	23.8	23.45	1	1
Spracklins Insect Kill	68.7	23.75	24.65	1	1
Hatchet Cove Insect Kill	68.9	24.82	26.27	1	1
Hatchet Cove Insect Kill	67.75	21.5	21.08	1	2
Hatchet Cove Insect Kill	83.56	25.89	34.89	1	1
Hatchet Cove Insect Kill	65.41	21.18	18.47	1	1
Hill View Intact	76.45	28	33.1	2	1
Hill View Intact	98.88	26	38	2	1
Hill View Intact	80.4	23.55	29.75	2	2

Table A.12. Balsam fir female cone insect study: Summary of regression analysis ($\alpha = 0.05$) to test the relationship between percent seed loss per cone per tree and balsam fir stem density per site (BDen), and height of focal trees. Residual plots showed residuals to be independent, homogeneous and have normal distribution. (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
Bden	1	1051.2	1025.4	1025.4	3.15	0.087
Height	1	125.2	125.2	125.2	0.39	0.54
Error	26	8453.1	8453.1	325.1		

Table A.13. Balsam fir female cone insect study: Summary of regression ($\alpha = 0.05$) to test the relationship between percent seed loss per cone per tree and average cone width per tree (cwidth tree), average cone weight per tree (cweight tree) and average cone length per tree (clength tree). Residual plots showed residuals to be independent, homogeneous and have normal distribution. (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P
clength tree	1	220.1	387.4	387.4	1.2	0.283
cwidth tree	1	959	2.1	2.1	0.01	0.937
cweight tree	1	406.6	406.6	406.6	1.26	0.272
Error	25	8043.8	8043.8	321.8		

Table A.14. Balsam fir female cone insect study: Summary of nested-ANOVA, ($\alpha = 0.05$) to test relationship between percent seed loss per cone per tree and the disturbance type (Intact; Insect kill) per site (DT), based on recent history of insect infestation for each site (J. Gosse, 2007 pers. comm.; S. Avery, 2007 pers. comm.). Residuals were normally distributed, but not independent, and were arcsine-transformed before analysis (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
DT	1	582.9	1119.1	1119.1	0.96	0.365
site(DT)	6	7098.7	7098.7	1183.1	12.75	0
Error	21	1948.0	1948.0	92.8		
Total	28	9629.6				

Table A.15. Balsam fir female cone insect study: Summary of nested-ANOVA, of percentage seed loss per cone among trees based on the two age categories, Age, ('Young'; and 'Old') ($\alpha = 0.05$). Residuals were normally distributed, but not independent, and were arcsine-transformed before analysis (Sokal and Rohlf, 1995; MINITAB 15®).

Source	DF	Seq SS	Adj SS	Adj MS	F	P-value
Age	1	0.0018	0.00068	0.00068	0.01	0.926
site(Age)	14	1.19657	1.19657	0.08547	6.93	0.001
Error	13	0.16041	0.16041	0.01234		
Total	28	1.35716				

Table A.16. Balsam fir female cone insect study: Seed viability test data summary for study sites (n =8).

Site	No. of seeds	No. of seeds viable	% of seeds viable	Average weight of lots of 5 seeds (mg)
Boy Scout Camp Rd.Insect Kill Site	40	0	0	0.0508 ± 0.0053
Boy Scout Camp Rd. Intact Site	65	0	0	0.0583 ± 0.004
White Hills Insect Kill Site	110	7	6.36	0.0436 ± 0.0029
White Hills Intact Site	80	11	13.75	0.0429 ± 0.0036
Spracklins Intact	120	6	5	0.0535 ± 0.0035
Spracklins Insect Kill	80	4	5	0.0718 ± 0.0065
Hatchet Cove Insect Kill	40	8	20	0.0538 ± 0.0017
Hill View Intact	120	18	15	0.0627 ± 0.003

Table A.17. Balsam fir female cone insect study: Summary of binary logistic regression analysis to test relationship between proportion of viable seeds per cone per tree and disturbance regime (Intact; Insect kill) of individual sites (DT). No assumptions about the independence and normality of residuals distribution were made (Sokal and Rohlf, 1995; MINITAB 15®).

Predictor	Coef	SE Coef	Z	P	Odds Ratio	95% Lower	CI Upper
Constant	-2.85944	0.50783	-5.63	0			
DT	0.278429	0.296722	0.94	0.348	1.32	0.74	2.36

Table A.18. Balsam fir female cone insect study: Summary of binary logistic regression analysis to test relationship between proportion of viable seeds per cone per tree and balsam fir stem densities per site (BDen). No assumptions about the independence and normality of residuals distribution were made (Sokal and Rohlf, 1995; MINITAB 15$^{®}$).

Predictor	Coef	SE Coef	Z	P	odds ratio	95% lower	CI Upper
Constant	-2.89977	0.297347	-9.75	0			
Bden	0.000329	0.000164	2	0.045	1	1	1

Table A.19. Balsam fir female cone insect study: Summary of binary logistic regression analysis to test relationship between proportion of viable seeds per cone per tree and weights of lots of five seeds per cone (weight). No assumptions about the independence and normality of residuals distribution were made (Sokal and Rohlf, 1995; MINITAB 15$^{®}$).

Predictor	Coef	SE Coef	Z	P	odds ratio	95% lower	CI Upper
Constant	-2.22596	0.843282	-2.64	0.008			
weight	-3.35917	15.2385	-0.22	0.826	0.03	0	3.25E+11

Appendix B: Study Site Characteristics and Cumulative Assessment of Cone/Seed Losses

Table B.1 Height and diameter at breast height (DBH) averaged for sites (insect kill = 5; intact = 5) in male cone predation study. Individual focal tree heights and DBHs were estimated using a clinometer and DBH tape respectively.

Study Sites	average height(m)	Std.Error	average DBH(cm)	Std. Error
Louil Hill Insect Kill	10.58	0.69	20.78	3.25
Blue Hill Insect Kill.	8.95	0.6	25.25	2.46
Blue Hill Intact.	9.05	0.65	19.33	1.84
Newman Sound Coastal Trail Intact.	10.68	0.7	21.56	2.1
Terra Nova Town Road Intact.	12.9	0.99	26.17	1.9
Ochre Hill Insect Kill.	11.2	0.57	23.25	2.21
Ochre Hill Intact.	6.78	0.71	12.7	1.53
Sandy Pond Intact.	13.53	1.35	23.1	2.81
Platter's Cove Insect kill.	10.66	0.33	21.13	1.66
Bread Cove Insect Kill.	10.66	0.35	25.5	2.35

Table B.2. Study sites for male cone predation study (n = 10).

Study Sites	GPS Coordinates
Louil Hill Insect Kill	N48° 38.750' W053° 57.141'
Blue Hill Insect Kill.	N48° 35.946' W053° 58.068'
Blue Hill Intact.	N48° 36.227' W053° 56.871'
Newman Sound Coastal Trail Intact.	N48° 33.412' W053° 57.927'
Terra Nova Town Road Intact.	N48° 30.813' W054° 00.561'
Ochre Hill Insect Kill.	N48° 30.544' W053° 57.377'
Ochre Hill Intact.	N48° 30.555' W053° 57.481'
Sandy Pond Intact.	N48° 29.590' W054° 01.234'
Platter's Cove Insect kill.	N48° 25.553' W054° 06.464'
Bread Cove Insect Kill.	N48° 28.813' W054° 00.010'

Table B.3. Height and diameter at breast height (DBH) averaged for sites (insect kill = 5; intact = 5) in female cone predation study. Individual focal tree heights and DBHs were estimated using a clinometer and DBH tape respectively.

Study Sites	average height(m)	Std. Error	average DBH	Std. Error
Outport Trail Intact.	13.3	1.23	33.58	4.27
Blue Hill Insect Kill.	8.85	0.76	21.43	1.59
Blue Hill Intact.	11.7	0.57	19.3	1.98
Newman Sound Coastal Trail Intact.	11.18	0.84	22.75	2.46
Terra Nova Town Road Intact.	11.28	1.47	24.43	2.77
Ochre Hill Insect Kill.	10.95	0.57	21.08	2.37
Ochre Hill Intact.	13.05	0.69	26.88	3.6
Sandy Pond Intact.	11.55	1.4	15.78	2.07
Platter's Cove Insect Kill.	12.63	1.86	22.13	2.46
Bread Cove Insect Kill.	8.45	1.01	21.5	0.98

Table B.4. Study sites for female cone predation study (n = 10).

Study Sites	GPS Coordinates
Outport Trail Intact.	N48° 32.205' W053° 58.860'
Blue Hill Insect Kill.	N48° 35.946' W053° 58.068'
Blue Hill Intact.	N48° 36.227' W053° 56.871'
Newman Sound Coastal Trail Intact.	N48° 33.412' W053° 57.927'
Terra Nova Town Road Intact.	N48° 30.813' W054° 00.561'
Ochre Hill Insect Kill.	N48° 30.544' W053 °57.377'
Ochre Hill Intact.	N48° 30.555' W053° 57.481'
Sandy Pond Intact.	N48° 29.590' W054° 01.234'
Platter's Cove Intact.	N48° 25.553' W054° 06.464'
Bread Cove Insect Kill.	N48° 28.813' W054° 00.010'

Table B.5. Height and diameter at breast height (DBH) averaged for sites (insect kill = 4; intact = 4) in female cone insect predation study. Individual focal tree heights and DBHs were estimated using a clinometer and DBH tape respectively.

Study Sites	Ave. tree height (m)	Std. Error	Average. DBH (cm)	Std.Error
Boy Scout Camp Insect Kill	10.5	0.66	17.9	2.26
Boy Scout Camp Intact	11	0.97	21.75	2.05
White Hills Insect Kill	10.1	0.33	12.68	1.56
White Hills Intact	9.9	0.37	14.3	0.83
Spracklins Intact	8.86	0.81	16.17	1.05
Spracklins Insect Kill	10.48	1.13	16.55	1.87
Hatchet Cove Insect Kill	7.1	1.08	12.4	2.5
Hill View Intact	11.2	0.73	16	1.25

Table B.6. Study sites for cone insect study (n = 8).

Study Sites	GPS Coordinates
Boy Scout Camp Insect Kill	N48 24.219' W054 14.900'
Boy Scout Camp Intact	N48 23.770' W054 13.872'
White Hills Insect Kill	N48 10.632 W054 3.644
White Hills Intact	N48 10.658' W054 3.662
Spracklins Intact	N48 32.970' W054 3.787'
Spracklins Insect Kill	N48 32.900' W054 3.966'
Hatchet Cove Insect Kill	N48 2.593' W053 50.243'
Hill View Intact	N48 4.893' W053 56.517'

Table B.7. Percentage of seeds eaten or infested with insect larvae averaged for each study site (n = 8).

Study Sites	% seeds eaten per site	Std. Error
Boy Scout Camp Insect Kill	63.37	8.87
Boy Scout Camp Intact	30.27	5.51
White Hills Insect Kill	14.52	3.25
White Hills Intact	16.64	4.47
Spracklins Intact	6.7	1.52
Spracklins Insect Kill	9.96	2.62
Hatchet Cove Insect Kill	21.75	6.53
Hill View Intact	7.62	2.35

Cumulative Assessment of cone/seed losses to red squirrels and insects

(1) Percentage female cone loss per tree to red squirrels in insect kill sites = 50.4 ± 7.5%

(2) Percentage female cone loss per tree to red squirrels in intact sites = 64.6 ± 6.3%

(3) Percentage seeds lost to insects in Insect Kill sites = 25.0 ± 7.3%

(4) Percentage seeds lost to insects in Intact sites = 16.0 ± 3.1%

(5) Percentage cones from 2nd harvest with external cone damage in Insect Kill sites = 9.6 ± 4.5%

(6) Percentage cones from 2nd harvest with external cone damage in Intact sites = 8.8 ± 3.4%

Maximum cumulative seed loss to red squirrels and insects in Insect Kill sites (assuming: red squirrels avoid cones with no signs of external damage but with internal insect infestation of seeds; and do not feed on cones with external signs of insect infestation):

(1) + (3) + (5) = 85%

Where (1) = 50.4%; (3) = 25%; and (5) = 9.6%.

Maximum cumulative seed loss to red squirrels and insects in Intact sites (assuming: red squirrels avoid cones with no signs of external damage but with internal insect infestation of seeds; and do not feed on cones with external signs of insect infestation):

(2) + (4) + (6) = 89.4%

Where (2) = 64.6%; (4) = 16.0%; and (6) = 8.8%.

Minimum cumulative seed loss to red squirrels and insects in insect kill sites (assuming: red squirrels do not discriminate between cones with no external and internal insect infestation and cones with no external but with internal insect infestation; and do not feed on cones with external signs of insect infestation):

(1) + (5) = 60%

Where (1) = 50.4%; and (5) = 9.6%.

Minimum cumulative seed loss to red squirrels and insects in insect kill sites (assuming: red squirrels do not discriminate between cones with no external and internal insect infestation and cones with no external but with internal insect infestation; and do not feed on cones with external signs of insect infestation):

(2) + (6) = 73.4%

Where (2) = 64.6%; and (6) = 8.8%.

Percentage of viable seeds per cone in insect kill sites = 4.75%

Percentage of viable seeds per cone in intact sites = 8.75%

Maximum proportion of viable seeds in Insect Kill sites

100,000 seeds

60% loss to red squirrels and insects

40,000 seeds

4.75% of seeds viable

Hence, approximately 1,900 seeds viable.

Minimum proportion of viable seeds in Insect Kill sites

100,000 seeds

85% loss to red squirrels and insects

15,000 seeds

4.75% of seeds viable

Hence, approximately 713 seeds viable.

Maximum proportion of viable seeds in intact site

100,000 seeds

73.4% loss to red squirrels and insects

26,600 seeds

8.75% of seeds viable

Hence, approximately 2,328 seeds viable.

Minimum proportion of viable seeds in Intact site

100,000 seeds

89.4% loss to red squirrels and insects

11,000 seeds

8.75% of seeds viable

Hence, approximately 963 seeds viable.

Appendix C: Images and Identity of Cone/Seed Insects Recovered from Study Sites

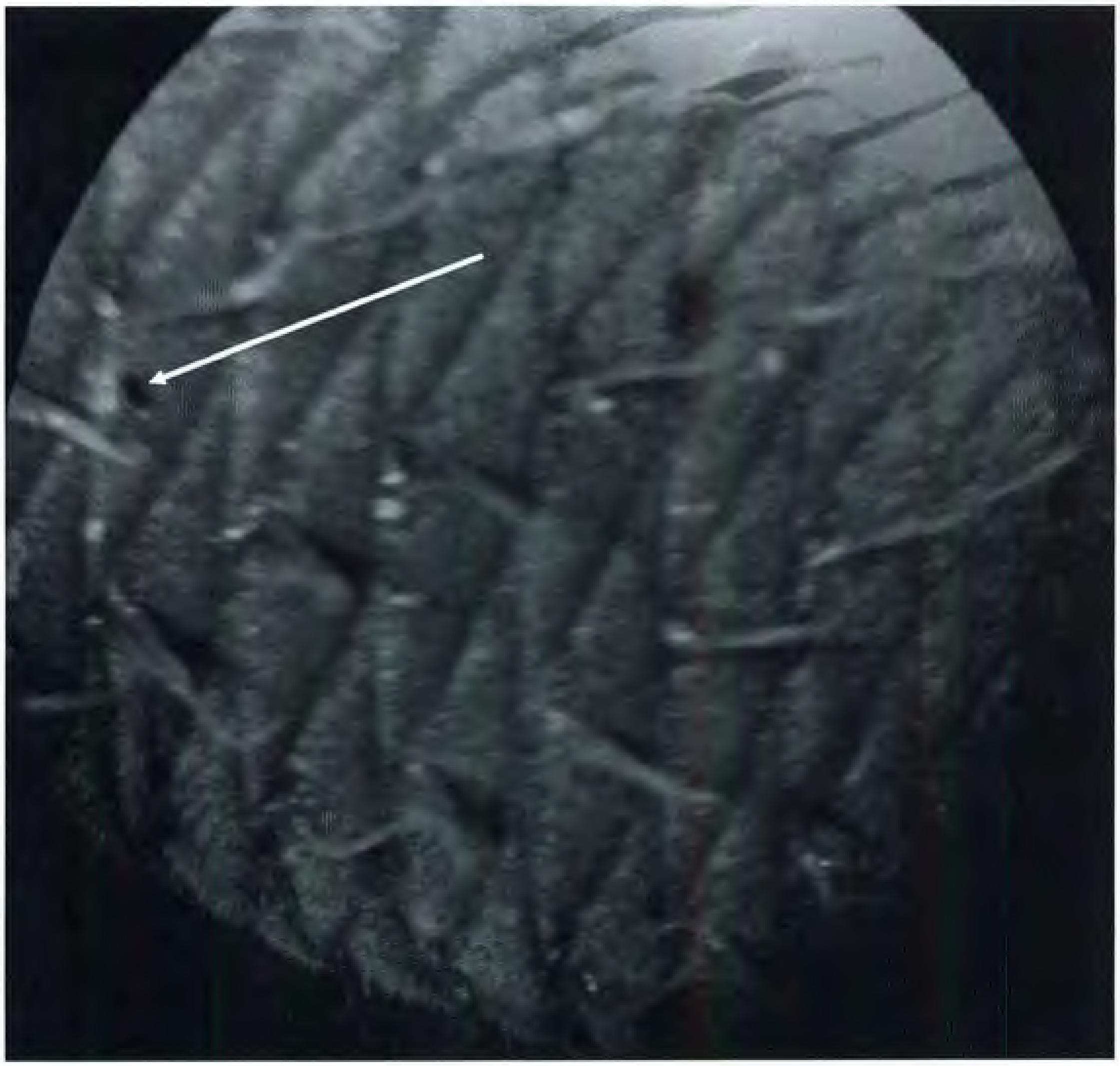

Figure C-1. Arrow indicates insect entry hole in cone scales (recovered from Hillview Intact site during first harvest). Scale: 14X.

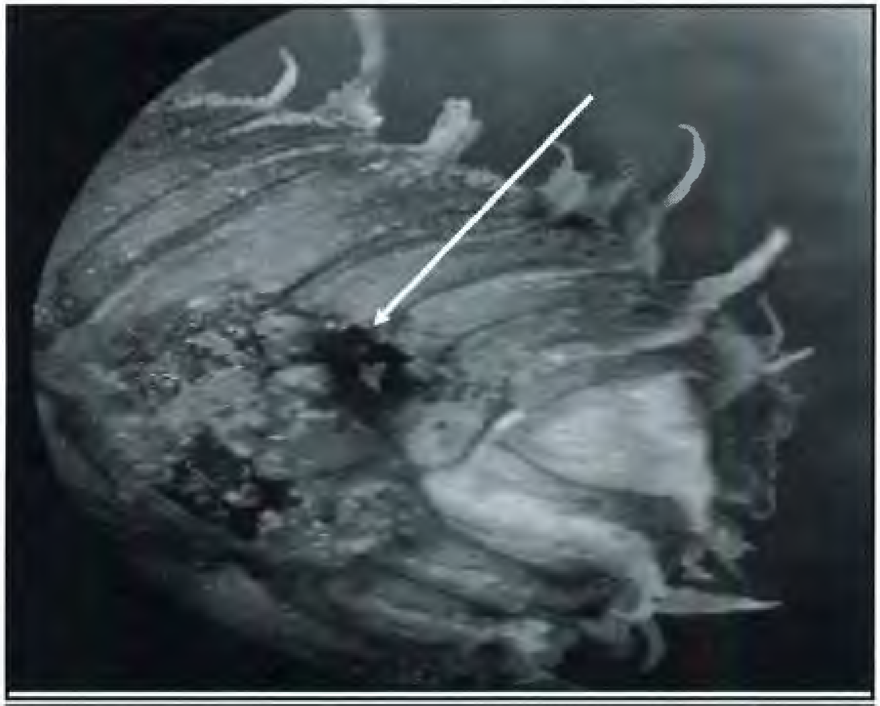

Fig C-2. Arrow indicates signs of internal cone damage (recovered from Boyscout Camp Insect Kill site during second harvest). Scale: 8X.

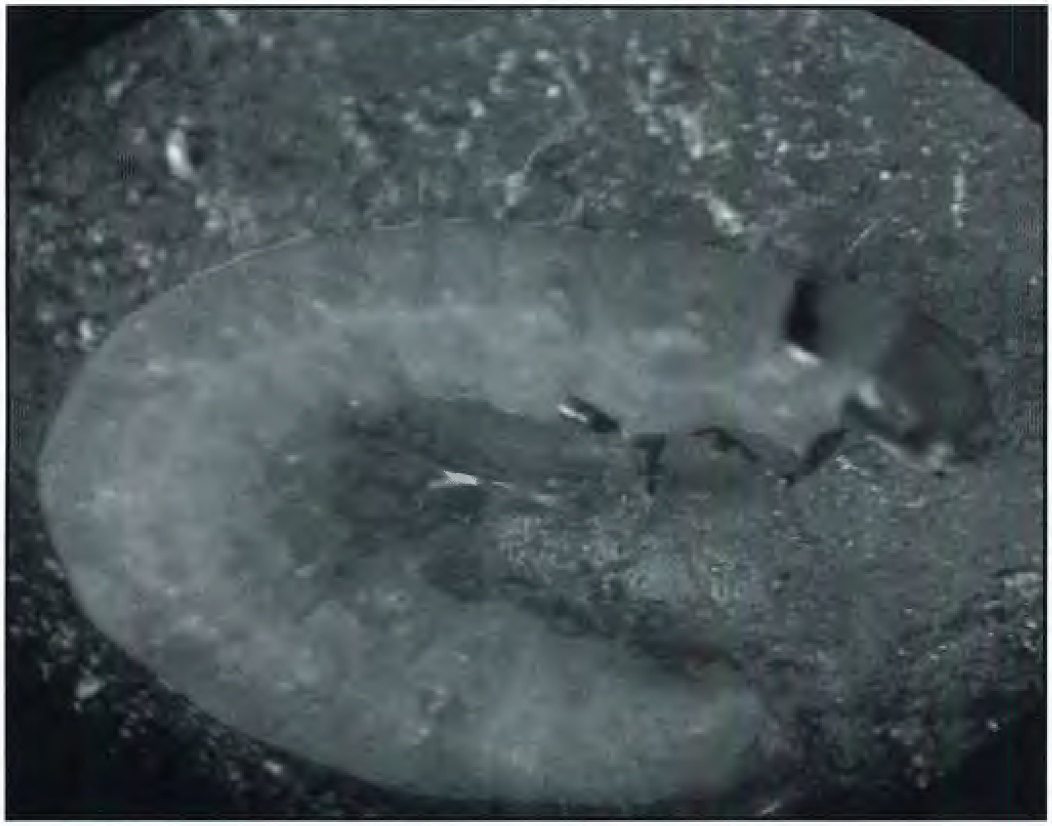

Fig C-3. Green larva outside cone with distinct head and dark thickening on dorsal side of first segment of thoracic region. Three pair of legs in thoracic region, and four or five pairs in abdominal segment. Lepidoptera, possibly one of the coneworms (recovered from Boyscout Camp Intact site during second harvest). Scale 30X.

Fig C-4. Lepidoptera, one of the coneworms. Fits description for fir coneworm, *Dioryctria abietivorella* with arrows showing characteristic row of dark spots on body (recovered from Boyscout Camp Intact site). Scale: 30X.

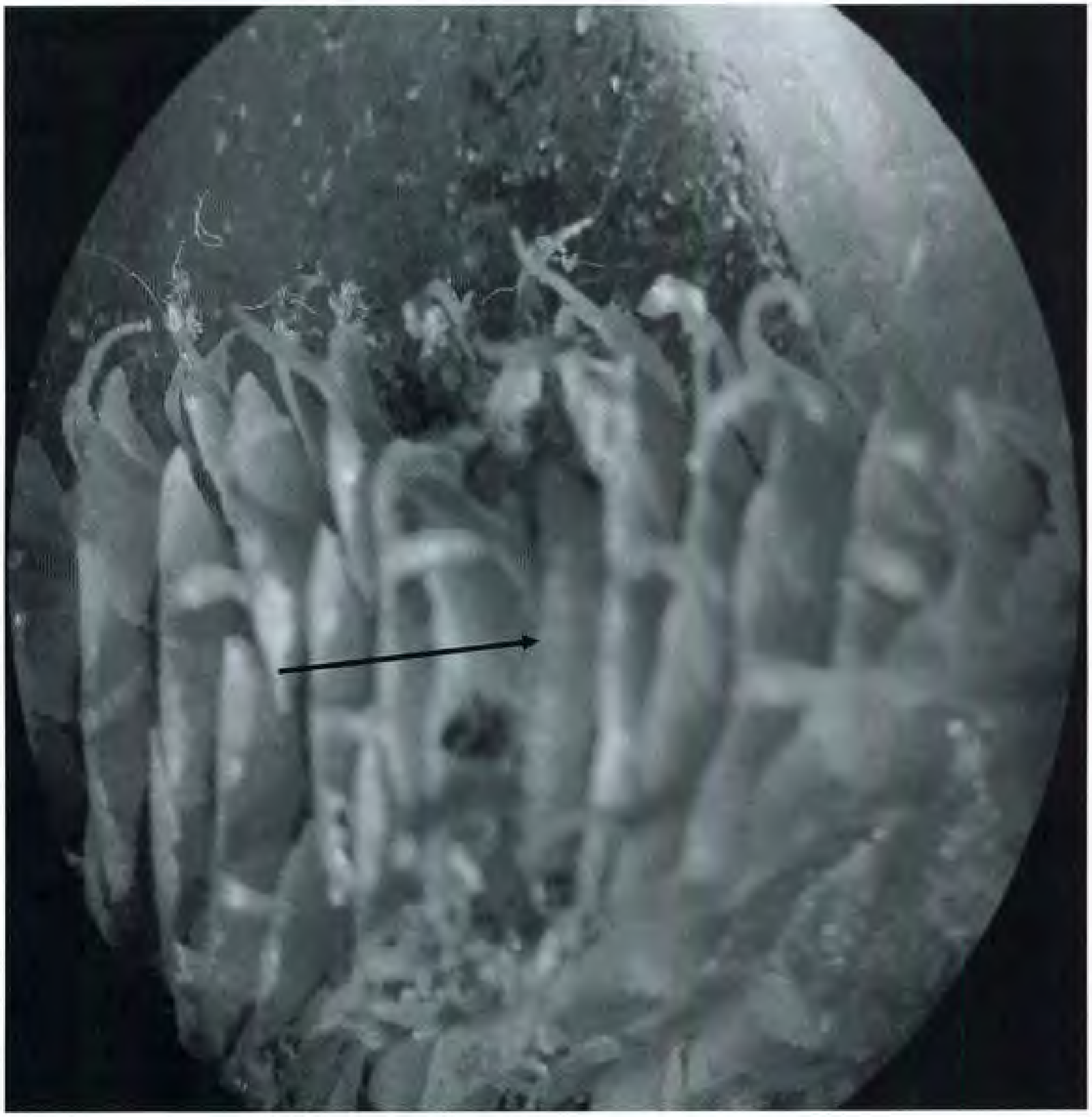

Fig C-5. Arrow shows Lepidoptera, coneworm between bracts; signs of webbing and frass (recovered from White Hills Insect Kill site). Scale 6X

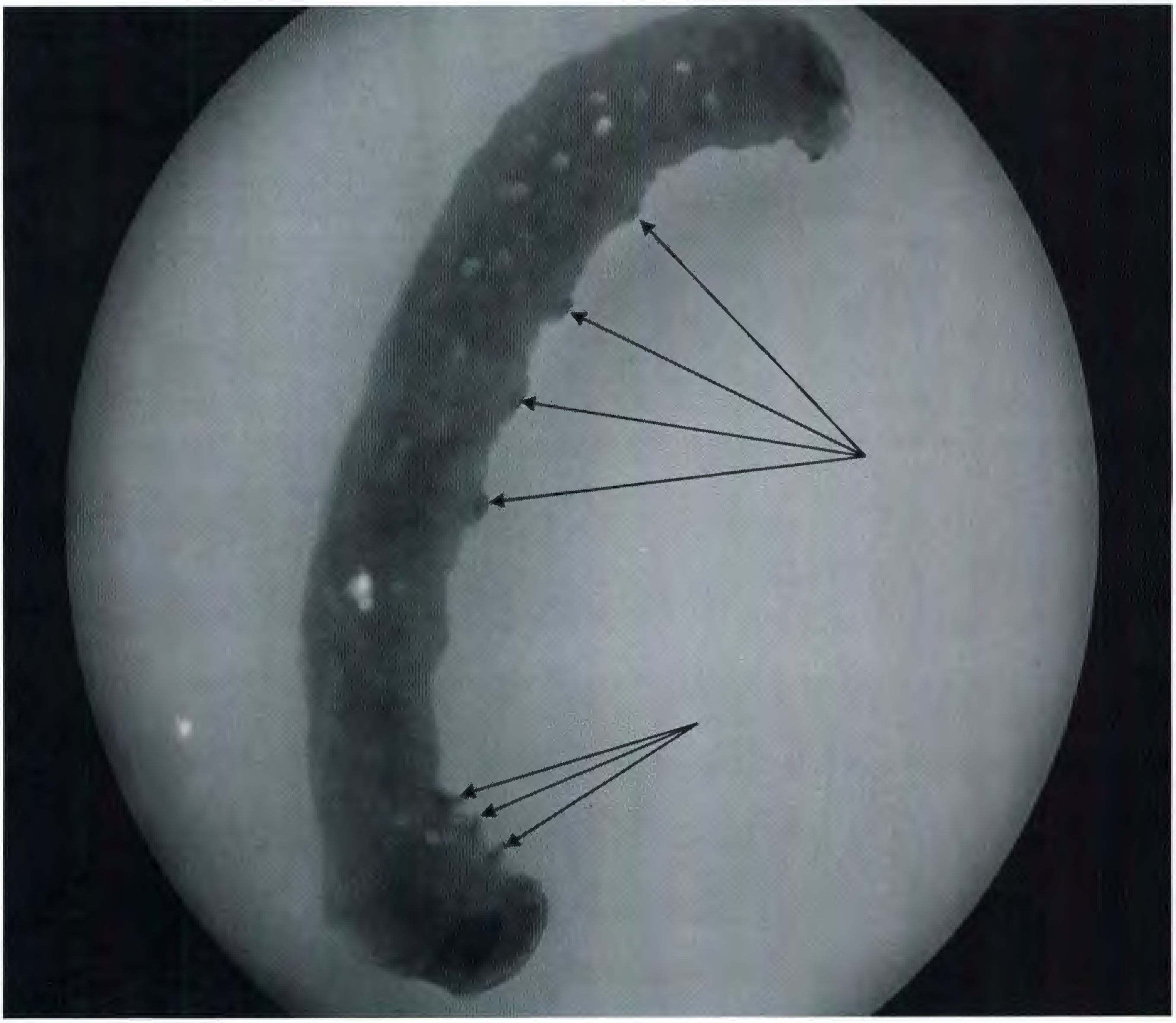

Fig C-6. Lepidoptera, coneworm, with arrows showing 3 pair of legs on thoracic segments and 4 pairs on abdominal segments (recovered from White Hill Insect Kill site). Scale: 16X.

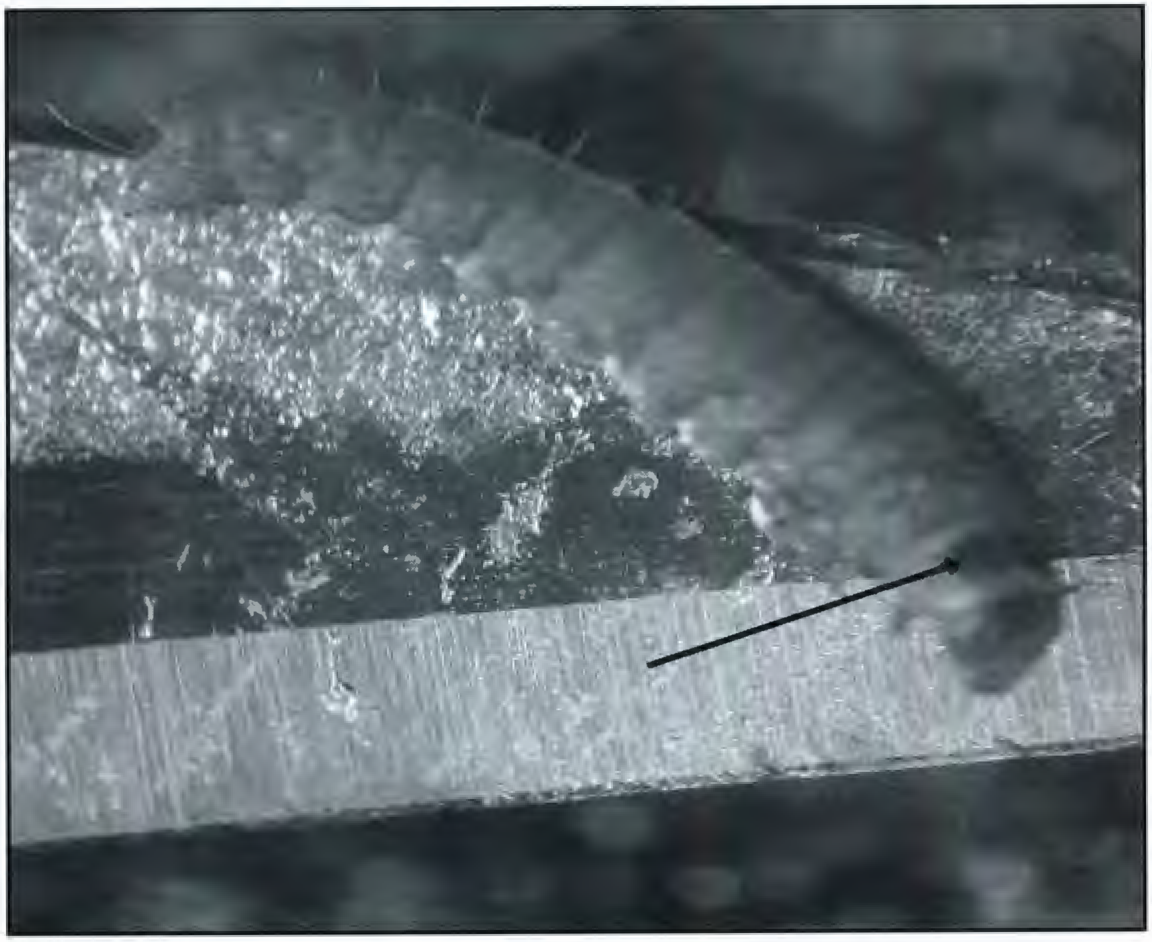

Fig. C-7. Lepidoptera, coneworm. Arrow showing distinct head with characteristic dark thickening on dorsal side of first thoracic segment (recovered from Spracklins Intact site). Scale 14X.

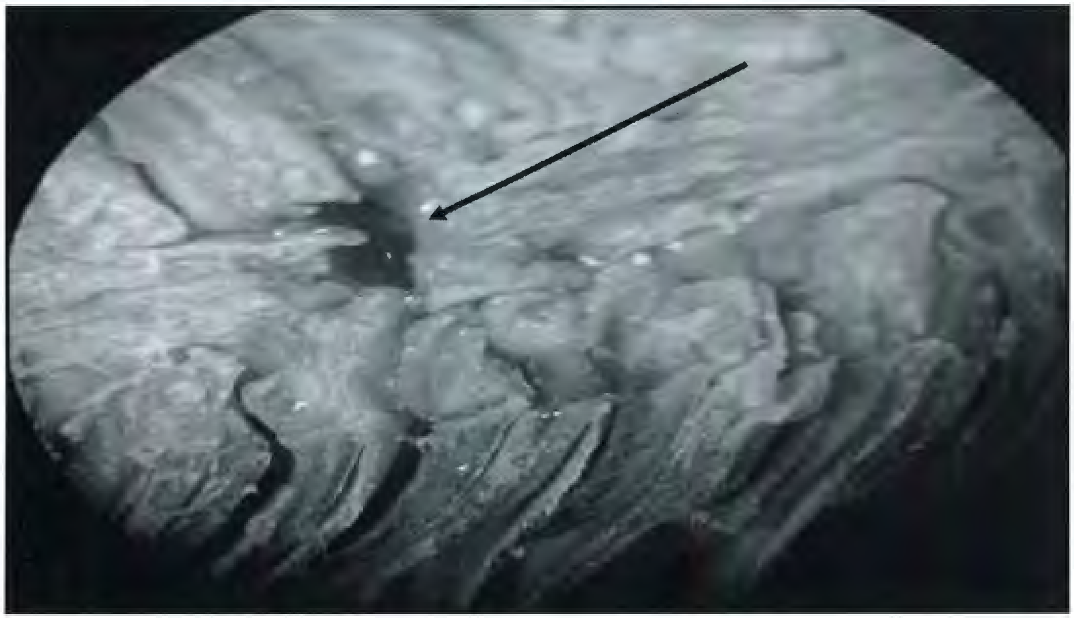

Fig. C-8. Arrow showing tissue damage in L.S. of female cone (recovered from Spracklins Insect Kill site). Scale: 15X.

Fig C-9. Thysanoptera, common thrips located between cone bracts with arrows showing 3 pair of relatively long legs and 2 folded antennae in the head region (recovered from Hatchet Cove Insect Kill site). Scale: 15X.

Fig C-10. Arrow shows exit hole in seed recovered from third harvest in Boyscout Insect Kill site. Scale: 45X.

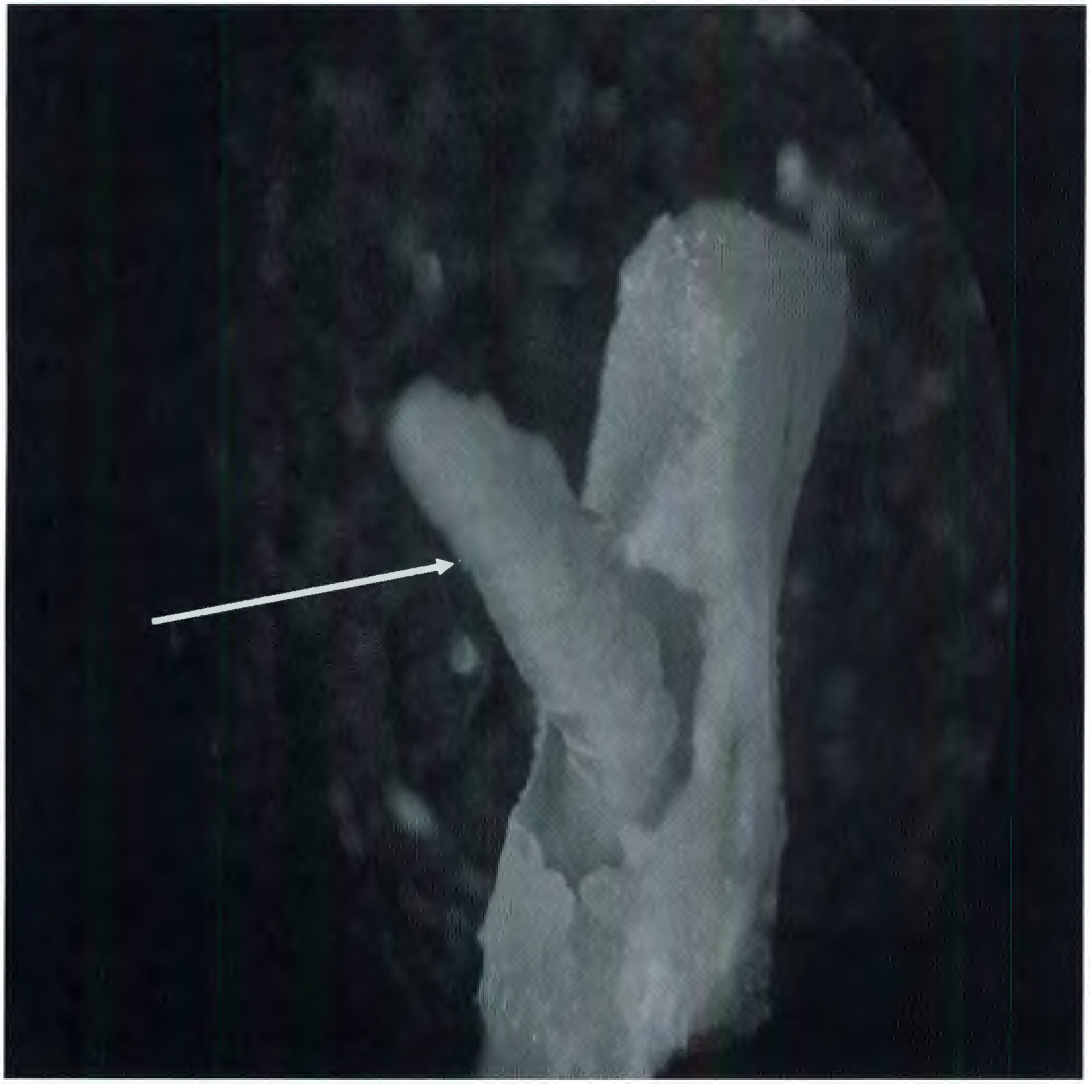

Fig C-11. Arrow showing legless reddish larva (cone midge) exiting single seed. Diptera, *Dasineura* spp. Scale: 42X.

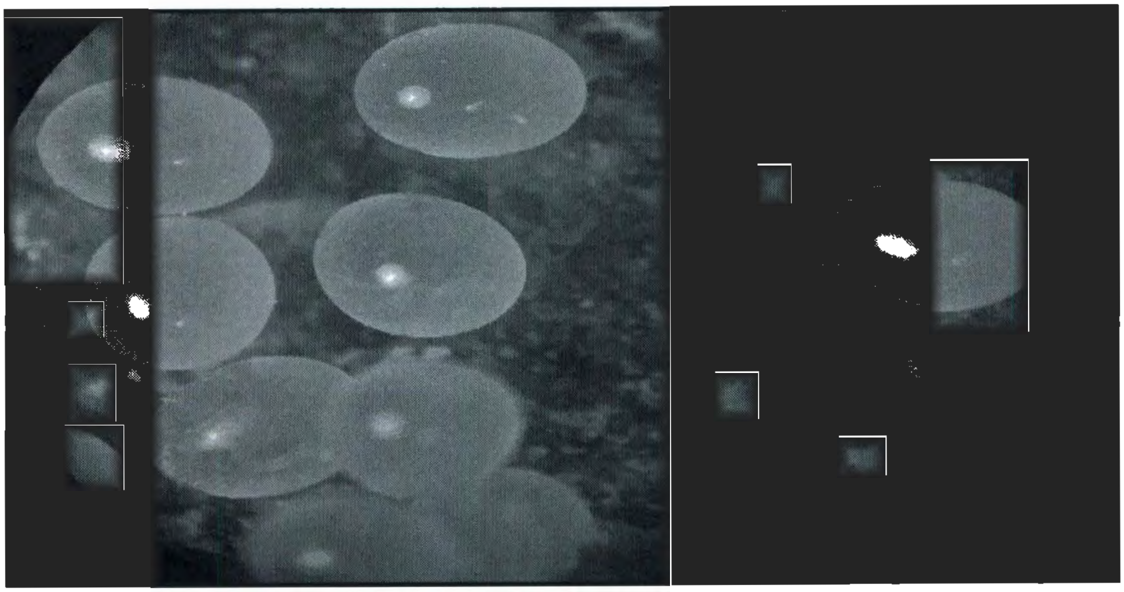

Fig. C-12. Egg cluster collected from surface of cone (recovered from Boyscout Camp Intact site). Scale: 40X.

Fig C-13. Legless larvae with indistinct head recovered tunneling in mid rib of cone. Diptera, cone maggot. Possibly, *Hylemya* spp (Spracklins Intact site). Scale: 25X.

Fig C-14: Reddish larva, legless with indistinct head recovered from seed. Possibly Diptera, cone midge, *Dasineura* spp (Spracklins Intact site). Scale: 80X.

Fig C-15. Reddish larvae with indistinct head and no legs recovered from seed. Possibly Diptera, cone midge, *Dasineura* spp. (Third harvest at Hillview Intact site). Scale: 50X.

Fig C-16. Coma-shaped larva with no distinct head or legs recovered from seed. Hymenoptera, seed chalcid, *Megastigmus* spp. (Fourth harvest at Spracklins Insect Kill site). Scale: 70X.

Fig C-17. Larva with indistinct head and no legs recovered between scales. Possibly Diptera, cone resin midge, *Asynapta* spp. (recovered from Spracklins Insect Kill site). Scale: 30X.

Fig C-18. Movement involves arcing of body characteristic of Looper moth larvae. Arrows show 3 pair of legs on thoracic segments and 2 pairs on the posterior abdominal segments (recovered from Boyscout Camp Intact site). Scale: 15X.