AUTECOLOGY OF EMPETRUM NIGRUM AND EMPETRUM EAMESII ON THE AVALON PENINSULA, NEWFOUNDLAND

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Autecology of *Empetrum nigrum* and *Empetrum eamesii* on the Avalon Peninsula, Newfoundland

by

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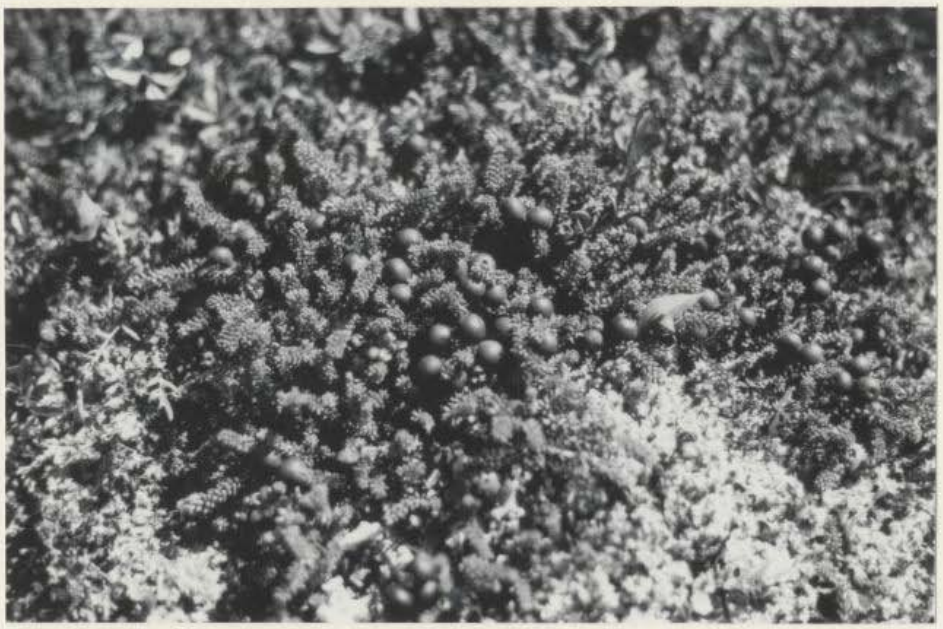
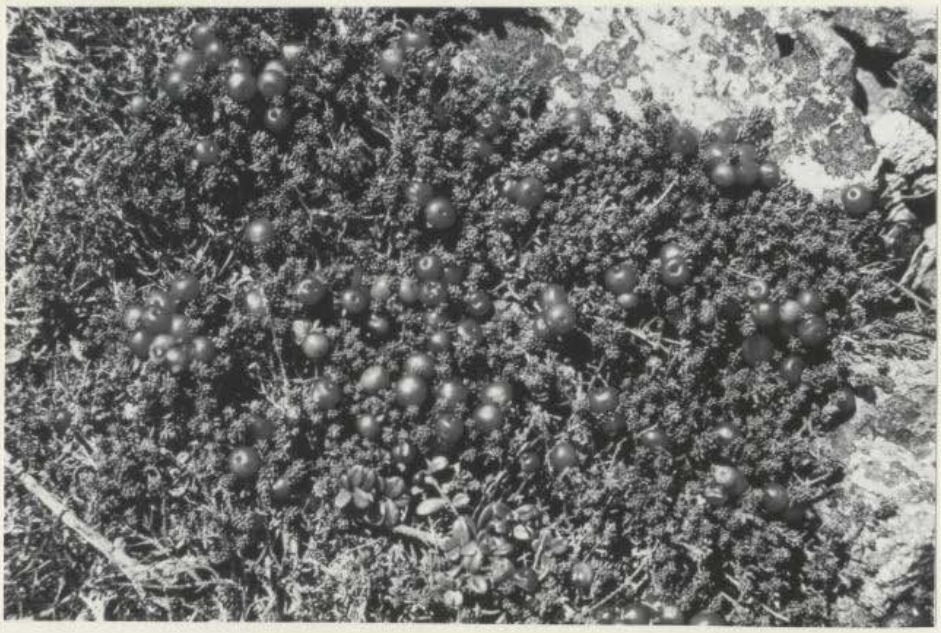


Empetrum nigrum L.



Empetrum eamesii Fern. & Wieg.

Abstract

Empetrum nigrum L. is a common evergreen shrub in Newfoundland where it forms extensive coastal heathland communities. *Empetrum eamesii* Fern. & Wieg. is an endemic to the Gulf of St. Lawrence and is most abundant in Newfoundland; this dwarf shrub species forms subarctic-heath communities on the most elevated and windswept areas in Newfoundland.

A comparative autecological study was undertaken for these two *Empetrum* species on the eastern Avalon Peninsula. Although *E. nigrum* has been studied extensively, little is known ecologically of *E. eamesii*. I investigated phenology, shoot growth, germination success and microhabitat of both *Empetrum* species. Attempts were made to relate these variables to the distribution patterns of *E. nigrum* and *E. eamesii* on the Avalon Peninsula.

Phenological development of the two species coincided. The blooming period occurred from mid- to late April and was followed by fruit formation from the beginning to late May. Fruit maturation was initiated at the beginning of July and all development ceased in mid-late August.

Shoot growth was significantly greater for *E. nigrum* in both the field and greenhouse monitoring programs. The mean annual growth of *E. nigrum* in the field was 15.0 mm and in the greenhouse 77.5 mm. *E. eamesii* grew less than *E. nigrum*, and measurements were carried out only in the field for *E. eamesii* since propagation of this species in the greenhouse was unsuccessful. The mean annual shoot growth of *E. eamesii* was 8.5 mm. The differences were related to microhabitat conditions such as windspeed and soil nutrient availability at the sites.

Germination experiments conducted in the laboratory showed that *E. eamesii* had an overall significantly greater germination success than *E. nigrum* at 10° and 5°C. This may be related to the variation in sites and microhabitats. Both *E. nigrum* and *E. eamesii* had optimal germination at 25°C.

A Discriminant Function Analysis was performed on the microhabitat variables. The microhabitat differences were found to be generated from an exposure gradient, that is windspeed and elevation contributed the most to interspecific variation. The remaining microhabitat variables, air and soil temperature, available soil nutrients, soil pH, and organic matter concentration of the soil contributed little to the interspecific difference between *E. nigrum* and *E. eamesii*.

A stepwise Multiple Regression was performed to explain the distributions of *E. nigrum* and *E. eamesii* based on their abundance and microhabitat variables. A regression for *E. eamesii* showed windspeed to be negatively related to abundance. These results indicate that windspeed is a major factor influencing to *Empetrum* distribution on the Avalon Peninsula. *Empetrum nigrum* grows in relatively more protected areas, whereas *E. eamesii* occurs in more exposed and windswept sites.

Résumé

Empetrum nigrum L. est un arbuste commun à Terre-Neuve, où il forme de vastes communautés au voisinage des côtes. *Empetrum eamesii* Fern. & Wieg. est endémique du golfe du St-Laurent et pousse aussi en abondance à Terre-Neuve, mais cette espèce forme une communauté de lande subarctique, dans les régions les plus élevées et venteuses de l'île. Une étude comparative a été menée sur l'auto-écologie des deux espèces sur la péninsule d'Avalon. Quoique *E. nigrum* ait été bien étudié, *E. eamesii* demeure mal connu du point de vue écologique. La phénologie, la croissance des tiges, la germination et le microhabitat des deux espéces sont examinées et mises en relation avec la répartition de chaque espèce sur la péninsule d'Avalon.

Les deux espéces avaient un développement phénologique identique. La floraison s'est produite de la mi-avril à la fin d'avril, suivie par la formation des fruits du début à la fin de mai. La maturation des fruits débutait au début de juillet et se terminait entre la mi-août et la fin d'août.

La croissance des tiges de *E. nigrum* était significativement plus élévée, tant sur le terrain qu'en serre. La croissance moyenne annuelle de *E. nigrum* était de 15.0 mm sur le terrain, et de 77.5 mm en serre. Les tiges de *E. eamesii* ont été mesurées seulement sur terrain vu que sa propagation en serre n'a pas été réussie; l'espèce a moins allongé que *E. nigrum*. La croissance moyenne de *E. eamesii* était de 8.5 mm. Les différences des sites étaient reliées aux conditions de microhabitat telles que la vitesse du vent et la disponibilité des nutriments du sol.

Empetrum eamesii a eu une germination plus élevée que *E. nigrum* à 10° et à 5°C. Ceci est peu être relié à la variation des sites et des microhabitats. La

germination maximale de *E. nigrum* et de *E. eamesii* a été atteinte à 25°C.

Une analyse discriminante a été menée sur les variables de microhabitat. La vitesse du vent et l'élévation contribuait le plus à la variation interspécifique; les différences de microhabitat sont générées par un gradient d'exposition. Les autres variables de microhabitat contribuaient très peu aux différences interspécifiques de *E. nigrum* et de *E. eamesii*; température atmosphérique et du sol, nutriments disponibles du sol, pH du sol et contenu de matière organique du sol.

Une régression multiple a été menée sur *E. nigrum* et *E. eamesii*, à partir de leur abondance et des variables de microhabitat, pour expliquer leur répartition. La régression de *E. eamesii*, montre une relation négative entre la vitesse du vent et l'abondance de l'espèce. Ces résultats indiquent que la vitesse du vent est un facteur majeur qui influence la répartition de *Empetrum* sur la péninsule d'Avalon. *E. nigrum* pousse dans des régions relativement plus abritées que *E. eamesii*; celle-ci pousse dans des aires très exposées et venteuses.

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Chapter 1

Introduction

1.1. Research Objectives

Empetrum nigrum L. has been the subject of detailed ecological, phytosociological and taxonomic studies (Ahti 1950, Barclay-Estrup and Nuttall 1974, Barendregt 1982, Bell 1969, Bell and Tallis 1973, 1974, Blackburn 1939, Dalby 1961, De Smidt 1977, Fernald and Wiegand 1913, Flower-Ellis 1973, Good 1927, Grantner 1977, Hansen 1976, Lindholm 1980, Löve and Löve 1959, Meades 1983, Soper and Voss 1964). Most studies of *E. eamesii* Fern. & Wieg. have dealt with its taxonomic position in the *Empetrum nigrum* complex (Fernald 1902, Fernald and Wiegand 1913, Good 1927, and Löve and Löve 1959). Little is known about the habitat requirements of *E. eamesii*, probably because of its more restricted distribution as an endemic to the Gulf of St. Lawrence region.

Damman (1965, 1976) included *E. eamesii* in the arctic-alpine element in Newfoundland. He speculated that it was absent from the NE coast of Newfoundland due to relatively higher summer temperatures. Meades (1983) provided a general habitat classification for Newfoundland heaths, in which *E. eamesii* is a differential species for the Alpine Heath type. These studies suggest that although the morphological features of *E. nigrum* and *E. eamesii* are very similar, their habitat requirements are distinct. Although the distinctness of the

habitats has been noted, no research has been undertaken to study the microhabitat differences of *E. nigrum* and *E. eamesii*. The hypothesis tested here is that the microhabitats of the two species are sufficiently different to require specific adaptations with respect to physiology, phenology and germination. Therefore the objectives of the study are:

1. To investigate interspecific differences in terms of phenological development, shoot elongation and seed germination that may be explained by microhabitat differences.
2. To investigate and compare the distribution patterns of both species on the Avalon Peninsula, in relation to microhabitat.

This is a comparative study of the autecology of both *E. nigrum* and *E. eamesii* on the Avalon Peninsula of Newfoundland. Autecology is defined by Mueller-Dombois and Ellenberg (1974) as the ecological study at or below the level of a species. Phenological observations can be part of such studies, which may be helpful in detecting environmental controls on the seasonal patterns of plant development (Dierschke 1972, Nams and Freedman 1987a). This requires consideration of micro-environmental factors that directly or indirectly affect the growth and establishment of a plant in a particular region. Such an approach has been widely applied in autecological studies of various tundra plant species (McGraw 1985, Nams and Freedman 1987b, Nietfeld-Nams 1980, 1981, Teeri 1974, Wijk 1986a, 1986b).

In Newfoundland few autecological studies have been undertaken. The arctic-alpine species *Diapensia lapponica* L. was studied intensively by Day (1978) and Day and Scott (1981, 1984), and a few boreal species have also been investigated, *Pinus resinosa* Ait. (Roberts 1985) and *Rubus chamaemorus* L. (Savory 1981).

1.2. Empetrum in Newfoundland

The distribution of *E. nigrum* is circumpolar (Bell and Tallis 1973), and the species is found throughout Newfoundland (Fig. 1-1) (Porsild 1957, Rouleau 1978, Scoggan 1978, Soper and Maycock 1963).

In contrast, *E. eamesii* is endemic to the Gulf of St. Lawrence (Fernald 1950, Scoggan 1978). It is reported from Nova Scotia (Cape Breton Island), St. Pierre and Miquelon, the North Shore of Quebec, south-east Labrador, and Newfoundland (Fernald 1950, Rouleau 1978, Scoggan 1978). In Newfoundland, *E. eamesii* is especially abundant on the west coast in the Long Range Mountains and it is also found in three areas on the Avalon Peninsula, in the Avalon Wilderness Area, on the isthmus, and on the Hawke Hills (Fig. 1-1).

For the purpose of this study, the taxonomy of *Empetrum* follows Fernald (1950). There is, however, no general consensus on the taxonomy of the *Empetrum nigrum* group, although *E. nigrum* and *E. eamesii* have distinct morphological characteristics. Their general habit has been described as creeping, mat-forming, microphyllous, evergreen dwarf shrubs (Barclay-Estrup and Nuttall 1974, Fernald 1950). The distinguishing features of the species are: *E. nigrum* is procumbent and spreading, with creeping branches, has glandular non-tomentose leaves, and black fruit, while *E. eamesii* is prostrate with non-glandular leaves, white-tomentose branchlets and pink to light red fruits (Fernald 1950).

Two other *Empetrum* species are recorded for Newfoundland: *Empetrum atropurpureum* Fern. & Wieg. and *E. hermaphroditum* (Lge) Hagerup. *Empetrum atropurpureum* has a distribution that coincides with that of *E. eamesii* in the Gulf of St. Lawrence and has also been recorded in Prince Edward

Figure 1-1: Distribution of *Empetrum nigrum* and *E. eamesii* in Newfoundland (after Meades 1983).

E. nigrum

E. eamesii

Island (Fernald 1950). In Newfoundland, it is found mainly along the northeastern coast (Damman 1976, 1983). The distinctive morphological characters of *E. atropurpureum* are: 1) tomentose leaves and branchlets when young; 2) purplish-black, oval fruits (Fernald and Wiegand 1913).

Empetrum hermaphroditum, has a circumpolar distribution; it has been recorded from the Avalon Peninsula of Newfoundland. This shrub has polygamous and monoecious flowers, its young shoots are green and not trailing, and the leaves are relatively broader than for *E. nigrum* (Hagerup 1927, Löve and Löve 1959). It produces the same shape and colour fruits as *E. nigrum*.

1.3. Research Approach

The selection of the study sites was largely based on the general description of the habitats of *E. nigrum* and *E. eamesii* by Meades (1983). *Empetrum nigrum* sites (1-5) (Fig. 1-2) were found along the coast where few trees occur and where *Vaccinium angustifolium* Ait. and *V. vitis-idaea* L. grow abundantly. *Empetrum eamesii* sites (6-10) were found in an alpine area on the Avalon Peninsula. These sites were more exposed, consisting mainly of rocks with little vegetation cover. *Empetrum nigrum* sites did not have *E. eamesii* and *vice-versa* with the exception of the mixed site (11) where sympatric populations were studied for the germination experiments.

The study focuses on the microhabitat aspects of *E. nigrum* and *E. eamesii* in relation to their distribution on the Avalon Peninsula. The microhabitat will be analysed in terms of its effects on the phenological development, shoot growth and germination performance of both *Empetrum* species. This will demonstrate to what extent microhabitat differences are important to the establishment and

growth of *E. nigrum* and *E. eamesii*.

Figure 1-2: Locations of the study sites on the Avalon Peninsula, Newfoundland.

Empetrum nigrum Locations

Site 1 = Cape St. Francis

Site 2 = Red Head

Site 3 = Torbay Head

Site 4 = Blackhead

Site 5 = Gallows Cove

Empetrum eamesii Locations

Site 6 = Bay Bulls Junction

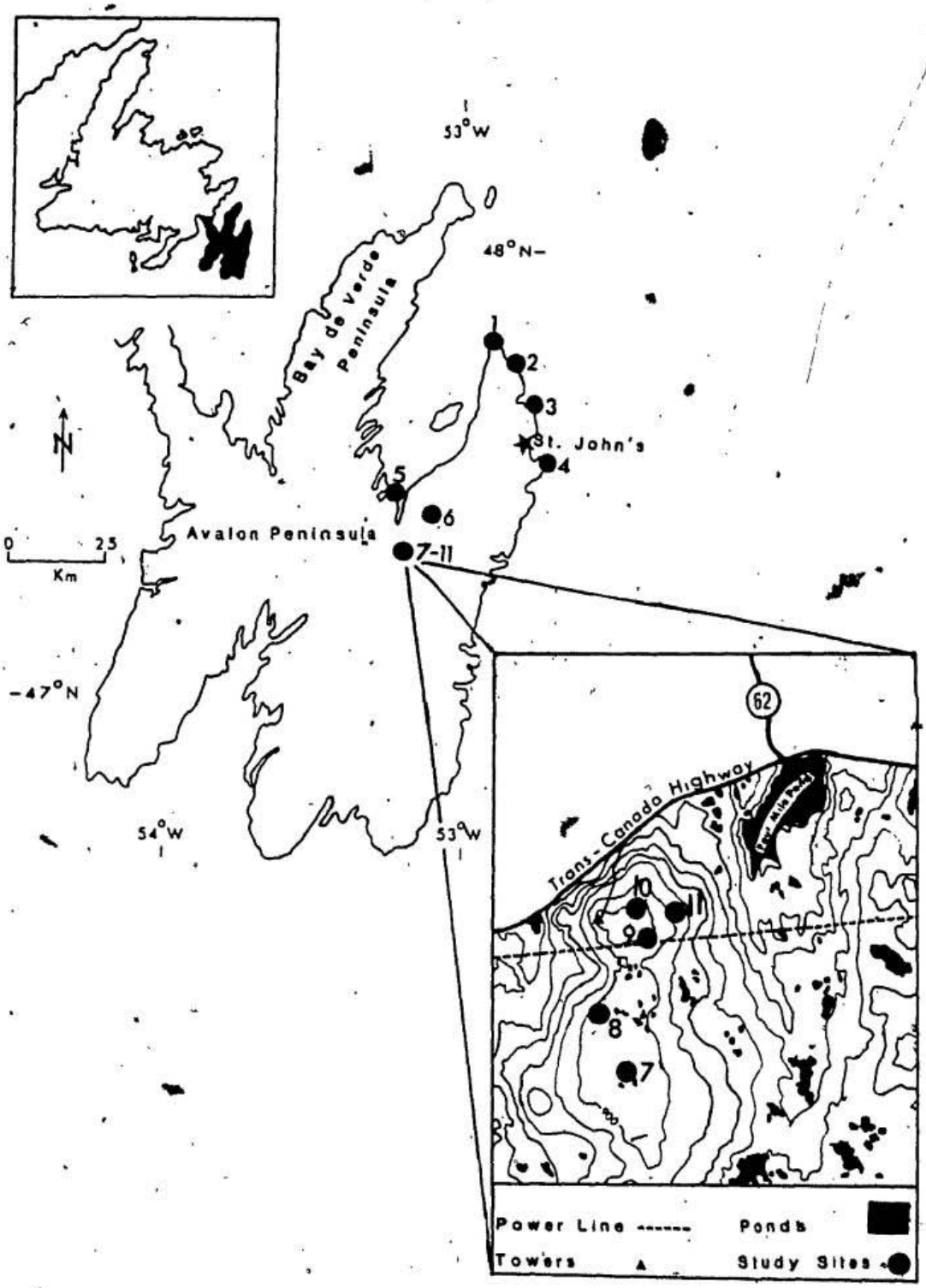
Site 7 = Hawke Hills, on top of the second ridge

Site 8 = Hawke Hills, on the lower section of the second ridge

Site 9 = Hawke Hills, at the back of the first ridge

Site 10 = Hawke Hills, on the front of the first ridge

Mixed Site (11) = Hawke Hills


53°W
48°N
Bay de Verde Peninsula
St. John's
1
2
3
4
5
6
7-11
N
0 25
Km
Avalon Peninsula
47°N
54°W
53°W
62
Trans-Canada Highway
Power Line
Towers
Ponds
Study Sites

Chapter 2

Description of the Avalon Peninsula and the Study Sites

2.1. General Description of the Avalon Peninsula

2.1.1. Geology and Physiography

The physiography of the Avalon Peninsula is discussed by MacClintock and Twenhofel (1940) and Roberts (1983), classified as the Eastern Upland. The landscape of this region is a hummocky, rolling plateau. Podzols are the most common soil group of the Avalon Peninsula, covering 77% of the area. These are well- to moderately-drained, acidic soils derived from a parent material of very stony glacial till (Heringa 1981, Rogerson and Tucker 1972).

Cryoturbation greatly affects the stability of the soil, which in turn restricts the establishment of plant communities. The types of patterned ground found on the Avalon Peninsula are described by Henderson (1968). Sorted stripes and polygons (Washburn 1956) were found at the *E. eamesii* study sites at the Hawke Hills, whereas the *E. nigrum* dominated heaths were found on the coast, mostly on solifluçted slopes and hummocky terrain (Fig. 1-2).

2.1.2. Climate

The climate of Newfoundland is oceanic and is influenced by the cold Labrador current. The climate throughout the island is extremely variable and localized and influenced by Newfoundland's rugged topography. Climatic factors such as temperature, precipitation and wind, are important in determining the distribution of arctic-alpine plants (Dahl 1951).

A phenomenon that affects the Island's temperature is the presence of pack-ice in late winter (March - April) along coastal Newfoundland. This delays the spring season by keeping sea temperatures close to the freezing point until late May (Hare 1952), lowering air temperature and delaying the beginning of the growing season.

The northern part of the Avalon Peninsula (St. John's area and Bay de Verde Peninsula) is considered to have the strongest maritime influence, with no extremes in winter and summer temperatures (Banfield 1981, 1983). The Avalon Peninsula is one of the regions of Newfoundland that has the earliest rise of mean daily air temperature to 0°C and the latest (*ca* second week of December) decrease in mean daily air temperature to 0°C. Temperatures recorded for the coldest and warmest months are presented in Table 2-1. Frequent cloud cover and fog is responsible for keeping temperatures low.

The Avalon Peninsula receives the highest rainfall in Newfoundland, with a mean annual total of about 150 cm . Approximately half of this precipitation falls between November and March, averaging 200 cm of snow for the whole of the Avalon Peninsula and 350 cm for the St. John's area. The snow cover is intermittent in the region, especially at high altitudes, such as the Hawke Hills

Table 2-1: Daily mean air temperature (°C) at the St. John's Airport, from Banfield (1981).

Month	Maximum	Minimum
January	-0.8	-7.0
July	20.1	10.4

where snow cover was practically non-existent on wind-blown tops of knolls and ridges during the field season 1985-1986.

Wind greatly affects temperature and snow cover. In areas with low temperatures and little snow cover, plants are subject to severe desiccation (Tiffney 1972). On the Avalon Peninsula, would blow mainly from a SW-W direction.

2.1.3. Vegetation

The vegetation of the Avalon Peninsula is mainly represented by Maritime Barrens. However, a small section, the southern part of the Avalon Peninsula and the northern tip of Bay de Verde Peninsula, consists of Hyper-Oceanic Barrens (Damman 1983). The study sites are all included in the Maritime Barrens, specifically in dwarf shrub heaths. The Maritime Barrens ecoregion is characterized by dwarf shrub heath, bogs and fens. Only a small portion of the Avalon Peninsula is covered by forest, mainly in valleys and on slopes.

The flora of these barrens changes along a gradient of severity of exposure, mostly indicative of snow accumulation. The dominant species of the dwarf shrub heath in the less exposed regions is *Kalmia angustifolia* L., followed by *Rhododendron canadense* (L.) Torr., *Vaccinium angustifolium* and the moss *Pleurozium schreberi* (Brid.) Mitt. However, in the more exposed areas *K. angustifolia* is replaced by *Empetrum nigrum* and *Vaccinium vitis-idaea*.

The *Empetrum* heath of Newfoundland, classified by Meades (1983), is dominated by *E. nigrum* and *E. eamesii*. However, Meades (1983) distinguishes the Alpine Heath type as dominated by *E. eamesii* and representative of alpine barrens. *Empetrum nigrum* dominated heaths are found mainly on the south

coast of Newfoundland, as described for the Maritime Barrens. In the southern extremities of the Avalon Peninsula, the *Empetrum* heath is located on windswept inland ridges. It is also found on severely exposed coastal headlands along the eastern coast of the Avalon Peninsula, including the Bay de Verde Peninsula.

The *Empetrum* heath community is further replaced on the most severely exposed ridges by the Alpine heath community in which *E. eamesii* is the dominant species, along with the arctic-alpine species *Diapensia lapponica* and *Loiseleuria procumbens* (L.) Desv. (Meades 1983). The Alpine heath has its most extensive range in the Long Range Mountains in western Newfoundland and is restricted to a few areas on the Avalon Peninsula. These are located at the southern end of Conception Bay on the Hawke Hills, in the Avalon Wilderness Area and on the isthmus of the Peninsula.

The Hyper-Oceanic Barrens ecoregion is represented by coastal barrens without forest cover but have krummholz. This ecoregion also includes moss-lichen carpets and blanket bogs (Damman 1983). The Hyper-Oceanic Barrens are the most oceanic part of Newfoundland, with mild winters and cool summers where the fog is most persistent. Arctic-alpine species are common in this ecoregion due to low summer temperatures (Damman 1965, 1983).

2.2. Description of Study Sites

The study sites were located in the eastern Avalon Peninsula, Newfoundland (Fig. 1-2). Selection of the study sites was based on the dominance of *Empetrum* and the homogeneity of the vegetation of the sites at the chosen locations. Five sites were chosen for each species (total n = 10 sites) in which five (1 x 1 m) plots per site were established and monitored.

2.2.1. *Empetrum nigrum* Sites

Figure 2-1 shows typical *E. nigrum* sites on the Avalon Peninsula. These sites (1-5) consisted of exposed coastal headlands with *E. nigrum* as the dominant species. The sites measured between 300 to 2900 m^2. The vegetation cover ranged between 60 to 98%, with the remaining cover made up of rocks and mineral soil. The plant communities of these *E. nigrum* dominated sites consisted of *Juniperus communis* L., *Vaccinium angustifolium*, *V. vitis-idaea*, *Deschampsia flexuosa* (L.) Trin., and *Cladonia* spp. along with scattered clumps of *Abies balsamea* (L.) Mill. The microtopography is hummocky, formed by solifluction, and underlain by well-drained soils. The elevation of the study sites ranged from 30 to 140 m, and they had a N and NE aspect.

2.2.2. *Empetrum eamesii* Sites

Because of the rarity of the Alpine heath community on the Avalon Peninsula, all of the *E. eamesii* dominated sites were selected from the relatively accessible Hawke Hills.

Figure 2-2 shows the two ridges of the Hawke Hills with a typical plant community dominated by *E. eamesii* along with *Loiseleuria procumbens*. These sites were selected on top of ridges and knolls, and measured between 510 and 840 m^2. The vegetation cover at these sites (6-10) was low, 10 to 15%, with the remainder of the sites covered by rocks and gravel. Plant species associated with these alpine communities include *Arctostaphylos alpina* (L.) Spreng., *L. procumbens*, *D. lapponica*, *Potentilla tridentata* Ait., the moss *Rhacomitrium lanuginosum* (Hedw.) Brid. and a lichen *Cladonia* sp.

Empetrum nigrum occurred in the vicinity of the sites at the Hawke Hills in

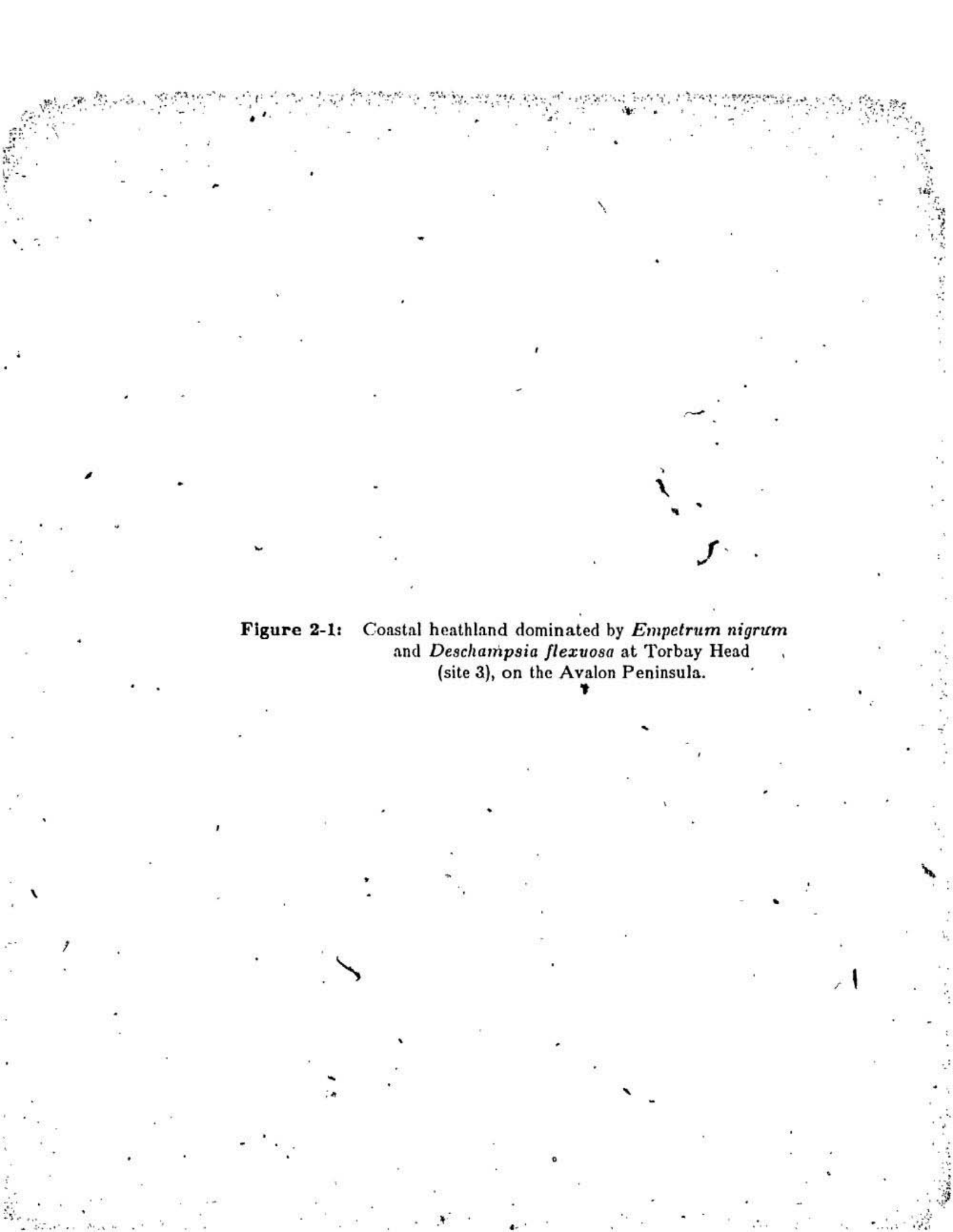


Figure 2-1: Coastal heathland dominated by *Empetrum nigrum* and *Deschampsia flexuosa* at Torbay Head (site 3), on the Avalon Peninsula.

more sheltered microhabitats but not directly in the *E. eamesii* study sites. *Empetrum eamesii* did not occur in the coastal sites of *E. nigrum* (1-5).

High wind velocities occur at high elevation and across exposed barrens such as the Hawke Hills area. Windspeeds recorded by Newfoundland and Labrador Hydro (Anonymous 1981) at the top of the Hawke Hills, show a mean monthly windspeed of *ca* 33 km h^{-1} (June 1979 - March 1982, and June 1983 - April 1984). The St. John's Airport (Monthly Reports) recorded mean windspeeds, for the same time period of 23 km h^{-1}.

Cryoturbation features are prominent at these sites, and the soils are well-drained. The elevation of these sites ranged from 280 to 370 m, and the sites had a N and NE aspect.

2.2.3. Mixed Site

This site (site 11) had a mixture of both species *E. nigrum* and *E. eamesii*. The site was located on exposed barrens at the Hawke Hills and measured 380 m^2. The plant community consisted of *Kalmia angustifolia* L., *Vaccinium angustifolium*, *V. vitis-idaea*, *Lariz laricina* (DuRoi) K. Koch, the moss *R. lanuginosum* and the lichen *Cladonia* spp. The vegetation cover was *ca* 70% with the remaining cover made up of rocks and mineral soil. The microtopography is hummocky at an elevation of 290 m on a NE facing slope.

Figure 2-2: Alpine heath habitat dominated by *Empetrum eamesii* and *Diapensia lapponica* at the Hawke Hills, on the Avalon Peninsula.

Chapter 3

Methods and Materials

Sampling was carried out during the fall (mid-November) of 1985 to the end of August 1986 and from April to August 1987.

3.1. Abundance of Empetrum

The abundance of *E. nigrum* and *E. eamesii* was estimated by percent cover, for each 1 m^2 plot for all sites.

3.2. Phenological Observations

Phenological observations of both species of *Empetrum* were initiated at the onset of flowering, in late April (27 April 1986 and 21 April 1987) and terminated once the fruit had ripened, at the end of August. The dates of the following observations were recorded for each species at all sites throughout the growing season: blooming period, fruit and seed formation, colour changes of fruits and foliage.

The blooming period in this instance is defined as the beginning of floral expansion to the falling off of petals. Following this stage, once pollination occurred, fruit formation, defined as the expansion of the ovary, started. The maturation of seeds was verified by breaking open fruits at all sites and checking for the formation of a hard testa.

Colour changes of fruit and foliage is a gradual process, so dates were recorded once the fruit changed from a green to a mature colour, black for *E. nigrum* and pink for *E. eamesii.* The colour change of the foliage were noted once it started to change from a green to a brown colour.

3.3. Shoot Elongation

3.3.1. Field Shoot Measurement

Shoot growth was recorded for all sampling sites to assess seasonal growth of the two species. Four shoots per plot (five shoots per plot in 1986) for all sites were randomly selected, numbered and the stems marked. Measurement of shoot elongation, was from the top of the mark to the top of the uppermost leaves of the stem. Shoot lengths were measured using a vernier caliper (accurate to 0.005 cm).

Shoot measurements were first carried out on a weekly basis in 1986 starting at flowering time (*i.e.* at the end of April 1986), and from July to the end of August, shoots were measured every other week or when weather permitted. If shoots were found to be damaged during the first month of measurement, new shoots were tagged. Shoots damaged after the first month were discarded from the analysis.

During the 1987 field season, shoots were first measured in mid-April (21-23 April 1987) and at the end of flowering (May 1987), giving a total shoot growth for the spring season. A final measurement was done at the end of August 1987, resulting in a total shoot elongation for the summer season.

Mean growth rate (GR) for the growing season of tagged shoots was calculated using:

$$GR = \frac{\sum \frac{L_2 - L_1}{\Delta T}}{N}$$

where L_1 was the first day of shoot measurement of the year (4 May 1986 and 23 April 1987); L_2 was the last day of shoot measurement of the year (9 September 1986 and 21 August 1987); ΔT was the number of days between measurements; and N the total number of shoots measured (Nams and Freedman 1987a).

3.3.2. Greenhouse Shoot Measurement

Shoots of both species were collected and grown in a 5:2:1 (peat:leaf mold:sand) soil mixture in a greenhouse at the Memorial University Botanical Garden at Oxen Pond, during the fall of 1985. The shoots were kept under a mist until initiation of the root system and then watered on a regular basis. Shoot elongation was measured as above.

3.4. Seed Germination

3.4.1. Growth Chamber Seed Germination

Germination experiments were carried out in growth chambers at 25°, 10° and 5°C, in the dark. Fruit of *E. nigrum* and *E. eamesii* were collected in September 1986 from sites 3, 9, and from a site where both species grew together (mixed, site 11) at the Hawke Hills. The seeds were removed from the pulp of the

fruit and allowed to air dry. Two hundred seeds from 200 fruits, for each species from all sites, were randomly selected. These were then separated in groups of 40 seeds each, totalling 5 replicates for each species at each site. The seeds were placed on moist filter paper (Whatman #1) inside plastic Petri dishes (10 cm diameter). The filter paper was kept moist using a solution of 10^{-3} M gibberellic acid in distilled water to break dormancy (Bell 1969, Bell and Tallis 1973, 1974). The number of germinated seeds was recorded daily by species, site and temperature treatment. The experiment was terminated 65 days following its initiation. Ungerminated seeds were further tested for viability using a 1% tetrazolium chloride assay to detect the presence of respiration (Bell 1969, Rice 1985). This assay was applied to 50% of the ungerminated seeds of all replicates and these were verified under a dissecting microscope.

3.4.2. Greenhouse Seed Germination

Germination experiments were also set up in a greenhouse at Oxen Pond. Fruit of both *Empetrum* species were collected from the same sites as above, in October 1985. One hundred and fifty seeds from 200 fruits, were randomly selected for each species from all sites. Seed beds (25 x 40 cm) were prepared for the transfer of seeds with a soil mixture consisting of 5:2:1 (peat:leaf mold:sand). In March, the seed beds were transferred to a cold house to initiate seed germination. In August 1987 the total number of germinated seeds for the 2 year period (October 1985 to August 1987) was recorded.

3.5. Microhabitat Measurements

Physical measurements that were noted or investigated, included elevation, temperature (air and soil), snow depth (in 1986), windspeed, available soil nutrients, and soil pH. Windspeed was divided into seasonal periods from the annual data.

3.5.1. Elevation

Elevation was measured using a Thommen pocket altimeter, standardized at sea level (0 m) before proceeding to the sites.

3.5.2. Temperature

Temperature, during the 1986 field season, was recorded at 7 cm above the soil and 15 cm below the soil surface. Thermocouple sensors in stainless steel were used for temperature measurements. Two thermocouples were attached to each stake which were driven into the ground to the appropriate depth. A Bailey digital recorder (Thermazip 4, accurate to 0.1°C). was used to read the temperatures. Each site (sites 3 and 9) had 3 plots containing temperature stations. Temperatures were only recorded once a week (18 November 1985 to 19 August 1986) at *ca* the same time of day, that is between 1330 and 1500 h.

Temperature measurements in 1987 were carried out using the sucrose inversion method (Jones 1972, Jones and Court 1980). This method was adopted because temperature readings were recorded simultaneously at all sites, increasing the accuracy of sampling temperatures at several sites (Walton 1982). Two sucrose solutions were prepared, the first solution was for spring temperatures (17 April to 17 May 1987) and the second one for summer temperature (16 May to 26

August 1987), the summer solution was unsuccessful. The spring period, in this case, is the blooming period, therefore temperatures were recorded for the flowering time.

The spring sucrose solution was specifically prepared for temperatures ranging between -20° to 20°C for 30 days. This sucrose solution was made up by mixing 120g sucrose per litre of distilled water. The buffer solution consisted of dissolving 42g analytical grade citric acid hydrate crystals in 200 ml 2M CO_2-free NaOH which was diluted up to 1 litre with distilled water. A few drops of 2% formaldehyde were added to the buffer solution to prevent the growth of microorganisms. 404 ml of this buffer solution was mixed with 596 ml 1M HCl. A 1% solution of NaCl was added to the solution to prevent freezing by temperatures below -2°C (Lee 1969). Temperatures as low as -20°C could be recorded, as temperatures in alpine areas in April can get below -2°C. The pH of the buffer solution was adjusted to 2.06 by adding HCl. Equal volumes of the sucrose and buffer solutions were mixed and the pH was again adjusted to 2.06 using HCl. Immediately after the sucrose solution was prepared; it was transferred to 15 ml vials and frozen at -20°C.

Two vials were set out in each plot on the 17 and 18 April 1987. One vial was placed at ground level under the *Empetrum* mat to record air temperatures, but protected from direct solar radiation. A second vial was placed 5 cm below ground surface for soil temperatures. As a control, 5 vials were transported to and from the field; these were then read to verify that no inversion of the solution had occurred during transportation. Vials for spring temperature measurements were collected after 28 days in the field. After collection, vials were again frozen

at -20°C. Readings of the sucrose solutions were made using a Bellingam & Stanley Polarimeter with a Na-d lamp ($\lambda = 589$ nm). Temperature values (T_e) were calculated using the equations of Jones and Court (1980).

3.5.3. Snow Depth

Snow depth (cm) was measured on a weekly basis (17 November 1985 to 6 April 1986) using graduated stakes (Walton 1982) installed in each plot in sites 3 and 9. When measuring snow depth, a measuring tape was placed from the meter mark on the stake down to the snow surface. A trace amount of snow and ice was given a "+" value. Rain was not measured during the winter months.

3.5.4. Windspeed

Wind velocity was measured on a monthly basis (1 December 1985 to 1 August 1986) using a three-cup, hand held, anemometer (Anemo Wind Indicator) in all plots. Readings were recorded 20 sec. after the instrument was placed at the appropriate height, just above the shrub mat (7 cm).

Windspeed recording during the 1987 field season was carried out on a monthly basis by recording ten readings, 10 sec. apart, above the shrub mat (7 cm).

3.5.5. Edaphic Factors

Soil pits were dug in mid-August 1986 at sites 3 and 9 for the soil taxonomy and textural features from these representative sites of both *Empetrum* species (Appendix A). The description and naming of soils follows the Canadian System of Soil Classification (McKeague 1978). One pit per site was dug measuring 1 x 1 m and down to the bedrock. Depths of the horizons were measured and each was

sampled. The samples were brought back to the laboratory and refrigerated until analysis. These were divided into three replicates and physical analysis was carried out (refer below to Physical Analysis). The samples were dried for three weeks at 70°C, prior to processing for chemical analysis (refer below for Chemical Analysis).

In 1987 (8-9 September) soil sampling was carried out to investigate soil fertility for all plots at all sites. A small hole (20 cm x 15 cm) was dug up underneath the *Empetrum* mat and samples were taken from the ground surface down to 15 cm, the depth to which the root system of *Empetrum* extends. The samples were processed for chemical analysis.

Physical Analysis

Texture. Procedures for soil texture follows Day (1983).

Colour. Identification of soil colours was carried out in the laboratory under uniform light condition. Moist soil samples were used and compared with the Munsell Soil Color Charts (Anonymous 1971).

Soil samples were sieved using a 2 mm mesh sieve. Subsequent treatments of the samples were 1) weighed 2) crushed in a grinding dish, 3) sieved (steps 2 and 3 were repeated twice), 4) samples less than 2 mm in size were then stored; the remaining particles (> 2 mm in the sieve) were re-weighed to take the percent particles greater than 2 mm and were then discarded.

Chemical Analysis

Chemical analysis was carried out for organic matter and ash concentration, along with available soil nutrients for nitrogen, phosphorus, potassium, sodium, calcium and magnesium.

pH. Sample preparation for pH readings follows the "Sticky-Paste Method" (McKeague 1978). A small amount of each soil sample was mixed with distilled water for extraction of the hydrogen ions. The samples were then analyzed using a pH meter (Fischer Accumet^R, model 805 MP).

Percent Organic Matter. 1.0g of each sample was weighed and dried overnight at 105°C. They were cooled in a desiccator prior to weighing. Finally, the sample was ashed for 12 hours at 475°C, and weighed (ash weight). The final results are a percentage of organic matter and ash in the soil samples.

Available Nutrients. Each soil sample was analyzed for the following available nutrients: N, P, K, Na. The methods for available soil nutrients follow Black (1965). The available nitrogen was extracted using a solution of 2N KCl, by steam-distillation and titration. Concentrations of K, Na, Ca, and Mg were analyzed by atomic absorption spectrophotometry. Phosphorus was measured colorimetrically by the molybdenum blue method.

3.6. Statistical Analysis

All statistical analysis was conducted utilizing SPSS-X (Anonymous 1986) implemented on a DEC-VAX 8800 computer. All data are presented as means $\pm$ SE.

3.6.1. Shoot Elongation and Germination Study

The shoot elongation and seed germination data were analyzed using analysis of variance (ONEWAY with Duncan's Multiple Range Test, and ANOVA) with the null hypothesis that no significant differences existed between species and among the sites. Data recorded as percentages, such as the seed

germination results, were arcsine transformed to approach linearity prior to analysis of variance (Sokal and Rohlf 1981).

3.6.2. Microhabitat Variables

Two multivariate statistical methods were used to analyze the environmental variables, Multiple Discriminant Function Analysis (DFA) and Multiple Regression Analysis (MRA).

Multiple Discriminant Function Analysis

A species-by-environmental variables matrix was generated for the Discriminant Analysis. The objectives of the DFA are to assess the separation of the two species in a twelve-dimensional microhabitat space (Green 1974, Green and Vascotto 1978, Williams 1983). This statistical technique assumes linear relationships of the variables and, therefore, data transformation is appropriate. Data transformation was carried out using the logarithmic transformation for all environmental variables, except for the soil pH which is a logarithmic measurement (Green and Vascotto 1978, Sokal and Rohlf 1981). Rotation of the axes (VARIMAX) was used to interpret the functions.

Multiple Regression Analysis

A stepwise Multiple Regression was used to determine the variation of species abundance (percent cover) with the microhabitat variables, where some of these variables may control the species distribution. Regressions were performed using average percent cover and average microhabitat variables for each site, rather than individual plot data (Inouye *et al.* 1987). The abundance data was arcsine transformed to meet the assumptions of linearity (Sokal and Rohlf 1981).

Chapter 4

Results

4.1. Phenology

Figure 4-1 shows phenological stages of both *Empetrum* species. Flowers of *E. nigrum* and *E. eamesii* are unisexual and small (*ca* 1.6 mm), consisting of three green sepals and three purple petals, with three long purple filaments (*ca* 3.5 mm) (Fig. 4-1A, B).

During 1986, fruit could be distinguished by the 16-20 May for both species (Fig. 4-1C). However, in 1987 fruit formation was eleven days earlier (5-6 May). The immature fruits of both species are green. In *E. nigrum* they become progressively redder by mid-June (Fig. 4-1D), in *E. eamesii* the fruit turns pale pink during the same period (Fig. 4-1E). The seeds remain immature during this stage. Fruits of the two species change to their mature colours, at the beginning of July (7-9 1986 and 1987), black for *E. nigrum* (Fig. 4-1F) and pink-red for *E. eamesii* (Fig. 4-1G).

Once the fruit have taken on their mature colour, the seeds mature, forming a hard testa (beginning of August). There are 8-9 seeds per berry for each species. During maturation of the fruits, flowering buds are forming for the following year. These will open as soon as the weather permits in early spring of the next year. The berries mature at the end of August to September and the foliage changes to

Figure 4-1: Phenological observations of *Empetrum nigrum* and *E. eamesii* for 1986-1987 on the Avalon Peninsula.

A. Female flower of *E. eamesii*.

B. Male flower of *E. eamesii*.

C. Immature fruit of *E. nigrum*.

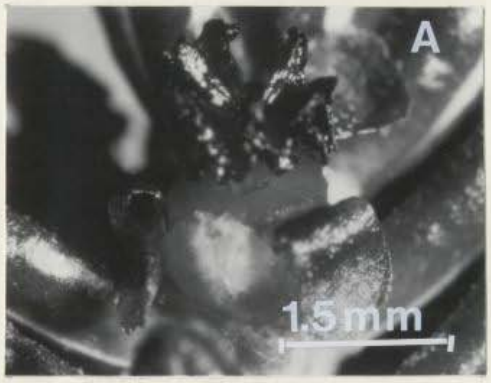
D. Fruit colour change of *E. nigrum*.

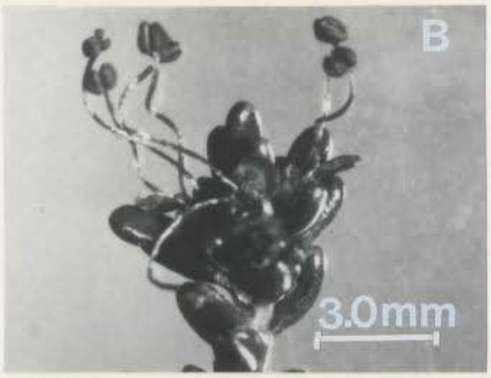
E. Fruit colour change of *E. eamesii*.

F. Mature fruit colour of *E. nigrum*.

G. Mature fruit colour of *E. eamesii*.

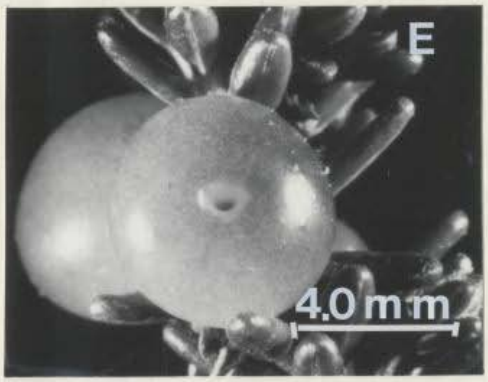
H. Foliage colour change of *E. eamesii*.


A
1.5 mm


B
3.0 mm

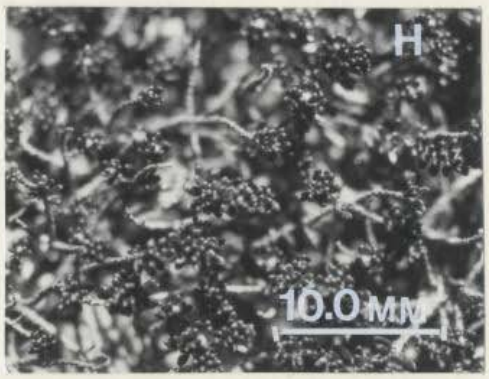

C
8.0 mm


D
4.0 mm


E
4.0 mm


F


G
10.0 mm


H
10.0 MM

a dark brown during the autumn (Fig. 4-1H).

Table 4-1 presents phenological observations recorded from the study sites during 1986 and 1987. *Empetrum nigrum* and *E. eamesii* were found to flower, bud and fruit at the same time. Anthesis occurred one week earlier for both species in 1987.

4.2. Shoot Elongation

4.2.1. Daily Growth Rates

The data for this section are presented in Table B-1 (Appendix B). The daily growth rate (GR) of tagged shoots was very small for both species. Figure 4-2 shows that *E. nigrum* had a higher daily GR compared to *E. eamesii* for both year, 1986 and 1987. However, these differences are not statistically significant. The greenhouse grown *E. nigrum* had the highest GR.

4.2.2. Annual Growth

The annual and seasonal growth data are presented in Table B-3 (Appendix B). Figure 4-3 shows that there is little vegetative growth (*i.e.* 5 - 20 mm) throughout the growing season for both species. In 1986 and 1987 *E. nigrum* had a higher shoot growth than *E. eamesii*, and in 1987 this was significant at $P < 0.01$. The growth rates seen in sites 3 and 9 in 1987 were comparable in magnitude to the growth observed in 1986 at these sites.

The 1987 data show differences among and between species. The *E. nigrum* sites (1, 3, and 5) have significantly higher shoot elongation ($P < 0.05$) than the *E. eamesii* sites 7 and 10; *E. nigrum* in sites 1 and 5 show significantly higher ($P < 0.05$) shoot growth than for site 4, the latter having the lowest shoot elongation

Table 4-1: Phenological observations of *Empetrum nigrum* and *E. eamesii* for the field seasons 1986-1987 on the Avalon Peninsula.

Species	Blooming Period	Fruit Formation	Fruit Maturation	Brown Foliage
E. nigrum				
1986	27 April - 12 May	16-20 May	7-8 July	mid-August
1987	21 April - 5 May	5-6 May	8 July	end-August
E. eamesii				
1986	28 April - 12 May	16-20 May	7-8 July	mid-August
1987	21 April - 6 May	5-6 May	9 July	end-August

Figure 4-2: Daily growth rate (± SE) of *Empetrum nigrum* (sites 1-5) and *E. eamesii* (sites 6-10) for 1986 and 1987; for the number of samples see Table B-1 and B-2 in Appendix B.

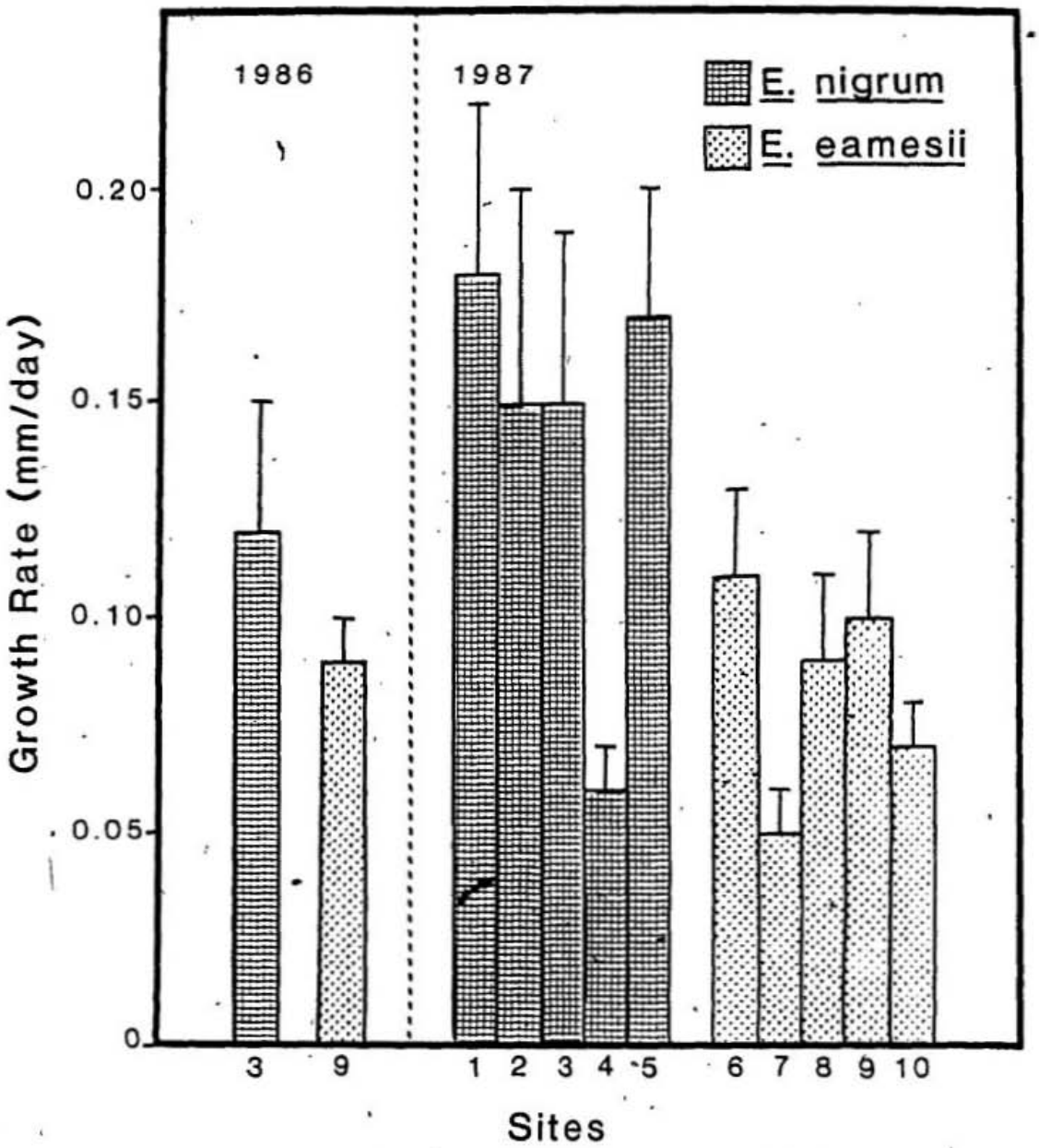
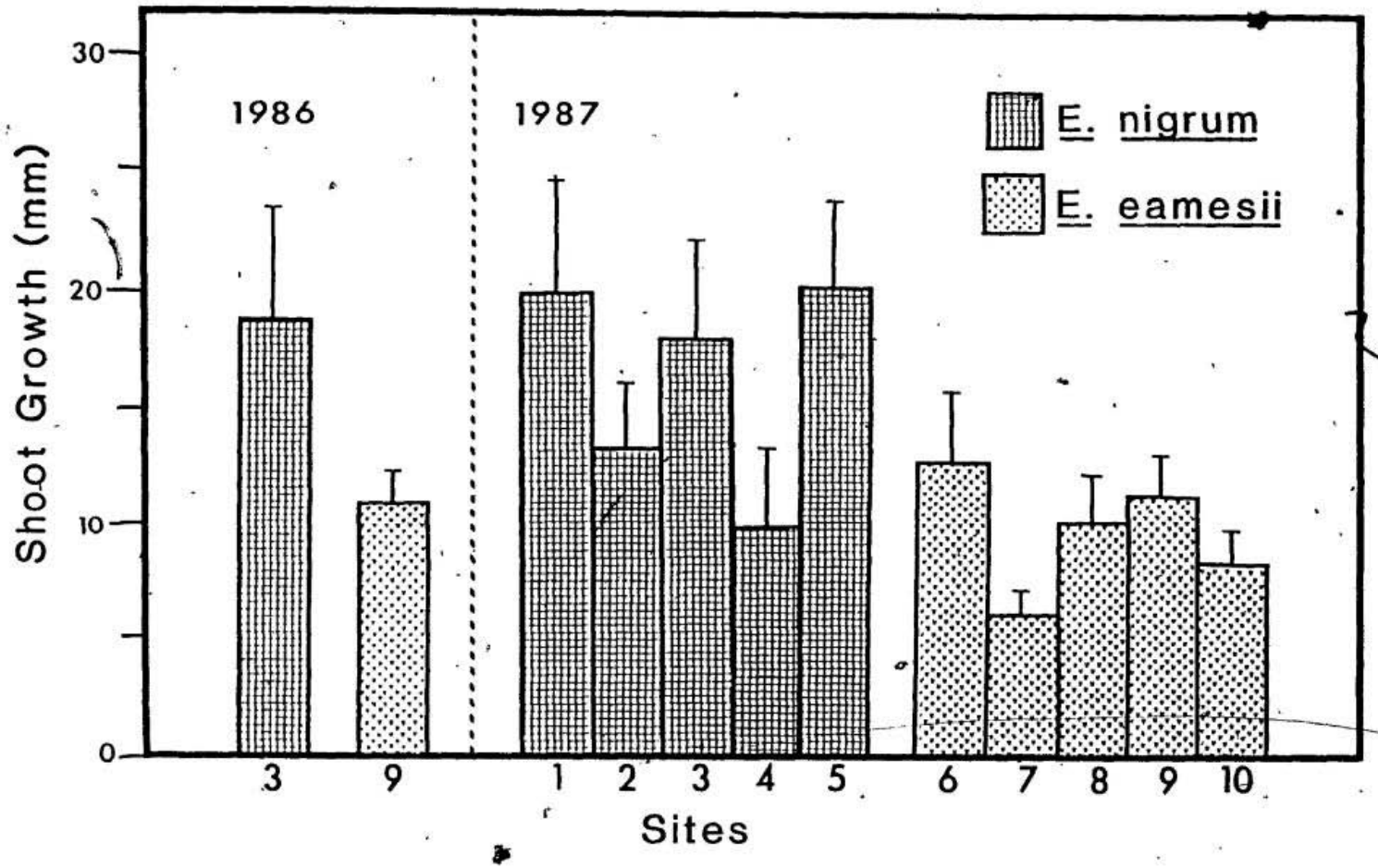

1986
1987
E. nigrum
E. eamesii
0.20
0.15
0.10
0.05
0
Growth Rate (mm/day)
3
9
1
2
3
4
5
6
7
8
9
10
Sites

Figure 4-3: Mean annual shoot elongation (± SE) of *Empetrum nigrum* (sites 1-5) and *E. eamesii* (sites 6-10) for 1986 and 1987.


1986
1987
E. nigrum
E. eamesii
Shoot Growth (mm)
30
20
10
0
3
9
1
2
3
4
5
6
7
8
9
10
Sites

of the *E. nigrum* sites (Fig. 4-3).

However, when *E. nigrum* grows under favourable conditions, such as in a greenhouse, its mean shoot growth increases dramatically from 15.0 to 77.5 mm. *Empetrum eamesii*, on the other hand, was not grown successfully in the greenhouse.

4.2.3. Seasonal Growth

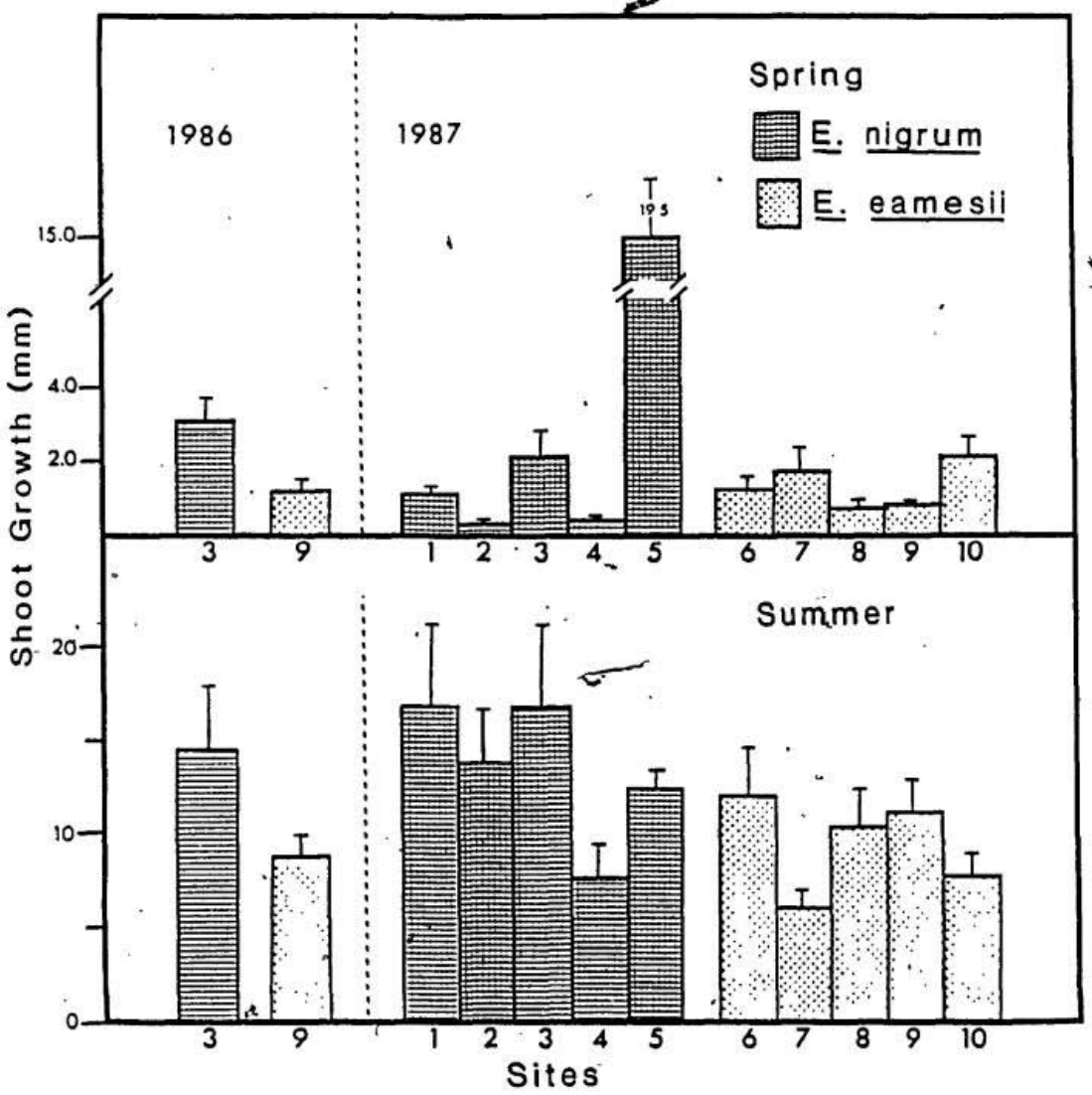
Spring Growth

Figure 4-4 shows the shoot elongation data divided into seasonal periods; spring which represents the period of the blooming period and the onset of fruit formation (30 days), and summer from the end of the spring period to the end of August to September (91 days). In general, little shoot extension occurred in the spring of 1987, and therefore no differences were found between *E. nigrum* and *E. eamesii*. However, when considering sites, site 5 has the highest shoot elongation compared to all the other sites ($P < 0.05$).

Summer Growth

The summer period had the highest shoot elongation compared to the spring data (Fig. 4-4). Overall for the 1987 data, *E. nigrum* had a significantly higher shoot elongation than *E. eamesii* ($P < 0.025$). *Empetrum nigrum* in sites 1 and 3 were significantly higher than the *E. eamesii* sites, 7 and 10 ($P < 0.05$).

Figure 4-4: Mean seasonal (spring and summer) shoot elongation (± SE) of *Empetrum nigrum* (sites 1-5) and *E. eamesii* (sites 6-10) for 1986 and 1987.


Spring
1986
1987
E. nigrum
E. eamesii
19.5
15.0
4.0
2.0
Shoot Growth (mm)
3 9 1 2 3 4 5 6 7 8 9 10
Summer
20
10
0
3 9 1 2 3 4 5 6 7 8 9 10
Sites

4.2.4. Monthly Growth

Table B-5 (Appendix B) shows the monthly growth data. Table 4-2 shows shoot elongation on a monthly basis for the 1986 data. *Empetrum nigrum* grew more than *E. eamesii* throughout the summer, with a maximum mean difference of 4.4 mm in June, the month of maximum growth.

4.3. Germination Experiments

The germination data are presented in Table C-1 (Appendix C).

4.3.1. Variation with Temperature

Table 4-3 shows the germination success of both *E. nigrum* and *E. eamesii*. The 25°C treatment was found to be the optimal temperature for both species. At the lower temperatures, 10° and 5°C, *E. eamesii* showed a higher germination percentage compared to *E. nigrum*. The mixed site consistently had better germination for all temperature treatments than did the alpine (*E. eamesii*) and coastal (*E. nigrum*) sites (Fig. 4-5).

4.3.2. Variation with Sites

Sites were also found to contribute to the variation within and between *Empetrum* populations (Fig. 4-5). At 25°C no significant differences were found between and within sites. The 10°C treatment, however, showed (Fig. 4-5) that *E. nigrum*, site 3, had the lowest mean ($P < 0.05$) compared to all other sites. *Empetrum nigrum* at 10°C had a fungal infection which might have contributed to these results. At the same temperature treatment, site 11 showed significant differences between *E. eamesii*, which had the highest mean germination success,

Table 4-2: Mean monthly shoot elongation (mm) of *Empetrum nigrum* and *E. eamesii* from sites 3 and 9, on the Avalon Peninsula for the 1986 field season. Standard errors are shown in parenthesis with the number of measured shoots indicated below.

Species	May	June	July	August
E. nigrum	2.3 (0.5) (n = 16)	7.6** (1.6) (n = 16)	3.2 (0.7) (n = 21)	2.6 (1.6) (n = 10)
E. eamesii	1.2 (0.3) (n = 18)	3.2** (0.4) (n = 22)	2.3 (0.2) (n = 22)	0.9 (0.2) (n = 15)

** values are significantly different at $P < 0.01$

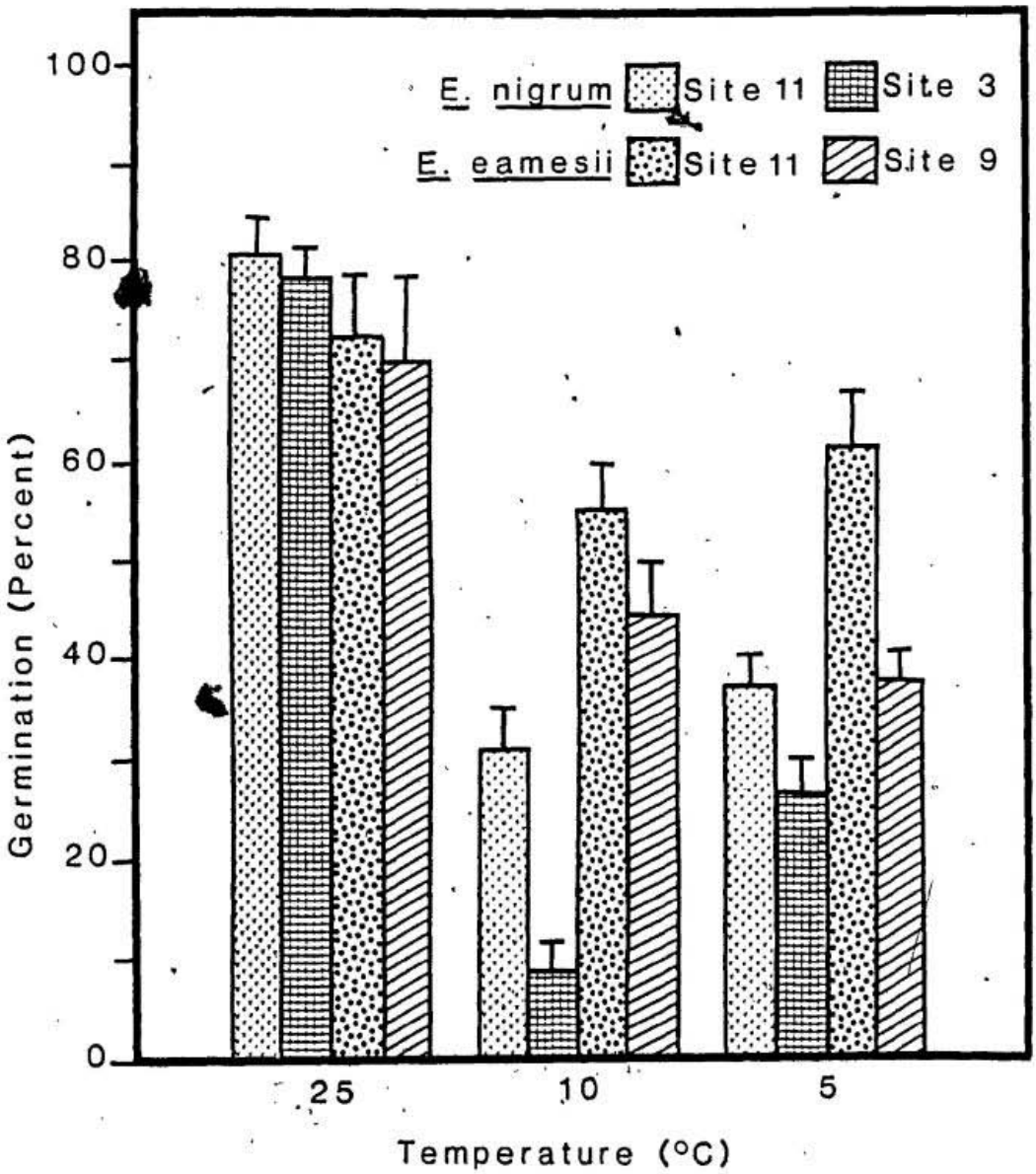
Table 4-3: Percent seed germination (± SE) of *Empetrum nigrum* and *E. eamesii* from the Avalon Peninsula, in relation to different temperature treatments. A total of 200 seeds was used for all treatments.

Temperature (°C)	Species	Total % Germination
25°	E. nigrum	79.8 ± 3.7
	E. eamesii	71.3 ± 7.6
10°	E. nigrum	19.8 ± 3.7*
	E. eamesii	49.8 ± 5.1*
5°	E. nigrum	32.3 ± 3.5**
	E. eamesii	49.8 ± 4.2**

* values are significantly different at $P < 0.05$

** values are significantly different at $P < 0.01$

Figure 4-5: Mean germination (± SE) of *Empetrum nigrum* and *E. eamesii* for 25°, 10°, and 5°C treatments; n = 5 replicates.


E. nigrum Site 11 Site 3
E. eamesii Site 11 Site 9
100
80
60
40
20
0
Germination (Percent)
25
10
5
Temperature (°C)

and *E. nigrum*. However, the germination success of *E. eamesii* from site 11 at 5°C, was found to be significantly higher ($P < 0.05$) than all other sites, including the *E. nigrum* population at the mixed site.

The species were tested for differences between temperature treatments. *Empetrum eamesii* and *E. nigrum* at the mixed site, did not show statistical differences between temperature treatments (Fig. 4-6). However, *E. eamesii* at the alpine site was significantly higher ($P < 0.05$) at 25° than at 5°C. The germination success of *E. nigrum*, on the other hand, differed significantly between all temperature treatments. That is, the mean germination percentage of *E. nigrum* at 25°C was significantly higher than at 10°C ($P < 0.01$); but the 10°C treatment was lower than the 5°C.

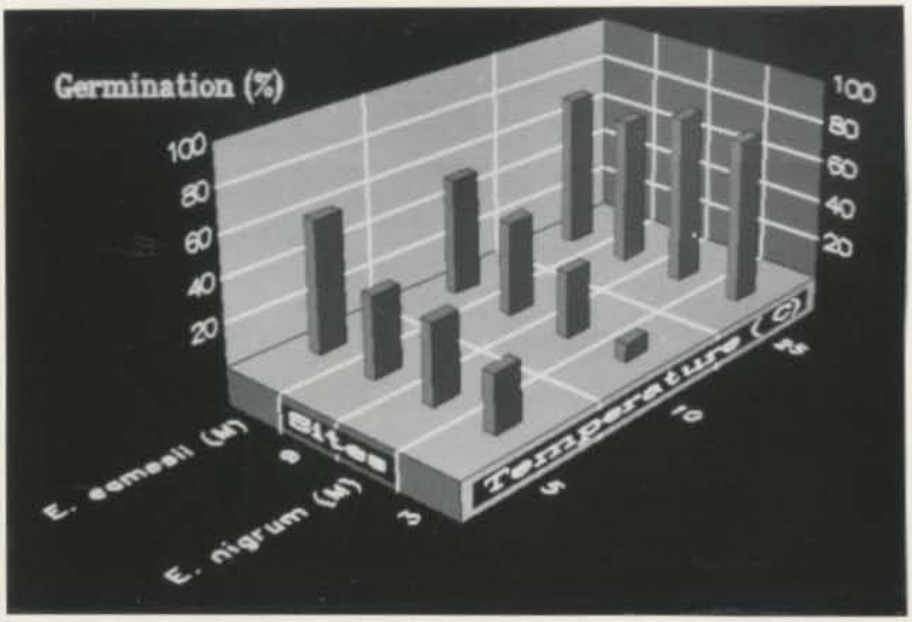
Germination was also tried in a greenhouse using a soil mixture, but was unsuccessful. *Empetrum nigrum* had an average of 17.5 seedlings and *E. eamesii* 24 ($n = 300$ seeds/species).

4.3.3. Viability of Ungerminated Seeds

Data from this section is presented in Table C-2 (Appendix C). Table 4-4 shows the seed viability data resulting from the tetrazolium chloride testing of seeds failing to germinate in above trials. At 25°C, *E. eamesii* had the highest seed viability compared to *E. nigrum*. However, the remaining temperature treatments had an inverse relationship from the 25°C results, and *E. nigrum* showed higher seed viability than *E. eamesii*.

At 25°C, *E. eamesii* (site 9) had the highest seed viability (40%), and differed significantly ($P < 0.05$) from *E. nigrum* (site 3), which had the lowest viability (3.3%). Also, the two populations of *E. nigrum* showed differences

Figure 4-6: Variation of the percent germination and temperature treatments with sites.


Germination (%)
100
80
60
40
20
E. aemasii (M)
E. nigrum (M)
Temperature (C)
5
10
15
20
100
80
60
40
20

between each other, with the population in site 11 showing a higher viability than site 3.

At 10°C, *E. nigrum* had higher seed viability (82.2%) than *E. eamesii* (65.4%). Viability of *E. nigrum* for site 11 was higher (82.3%) than *E. eamesii* (61%) from the same site ($P < 0.05$).

The 5°C treatment, shows the same pattern as for 10°C, that is *E. nigrum* had higher viability success (83.4%) than *E. eamesii* (49.3%) (Table 4-4). Both populations of *E. eamesii* (sites 9 and 11) had a lower viability than *E. nigrum* ($P < 0.05$). In addition, *E. eamesii* (site 9) at 5°C, was found to have the lowest seed viability (42%). Furthermore, *E. eamesii* at site 11 was also lower (56.5%) in viability than *E. nigrum* at site 3 (81%).

4.3.4. Daily Germination Rate

Figure 4-7 shows daily germination rates for all three temperatures, in relation to sites. With the exception of the 25°C treatment, the germination rate for *E. eamesii* was higher than that of *E. nigrum* (Table 4-5). The general pattern depicted in Table 4-5, is that as the temperature decreased the germination rate also decreased, except in the case of both populations of *E. nigrum* at 10° and 5°C, where the rates remained stable.

For the majority of seeds of both *Empetrum* species at 25°C, germination took place within 15 to 25 days from the onset of the experiment (Fig. 4-7). *Empetrum nigrum* showing a higher germination success than *E. eamesii*, once *E. eamesii* reached a plateau.

At 10°C, however, most seeds germinated between 25 and 35 days, with *E. eamesii* starting to germinate at day 14 and *E. nigrum* at day 18 and 21 for site

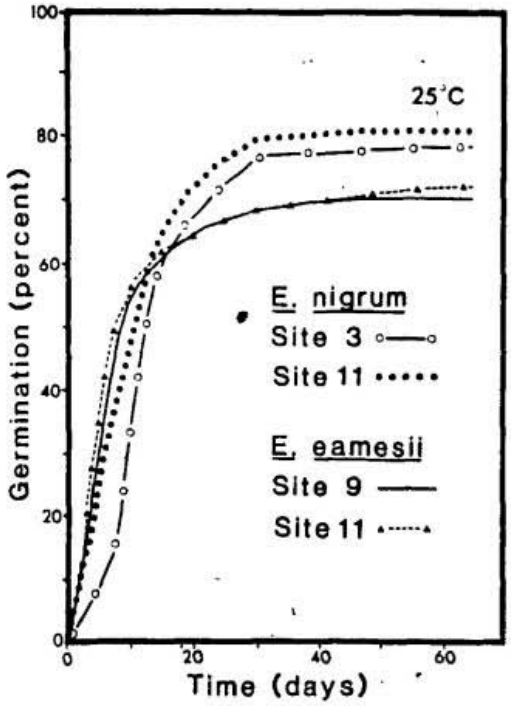
Table 4.4: Mean percent seed viability (± SE) of *Empetrum nigrum* and *E. eamesii* remaining from the germination experiment. The total number of seeds is indicated in parenthesis; a total of 10 plots each species was measured.

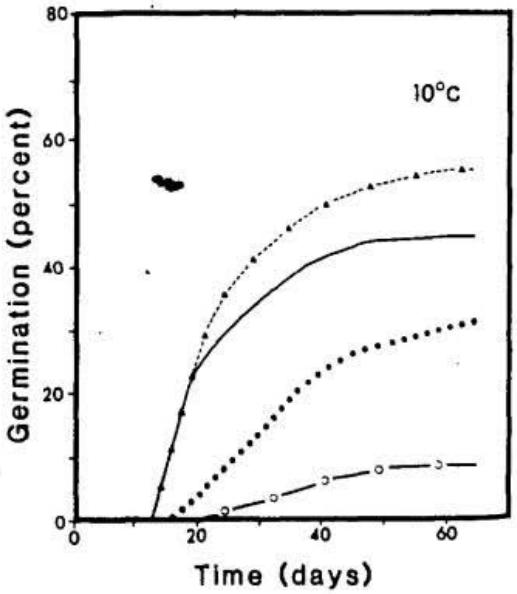
Species	Temperature (°C) 25°	10°	5°
E. nigrum	25.8 ± 11.5 (n = 276)	82.2 ± 3.2* (n = 154)	83.4 ± 4.5** (n = 145)
E. eamesii	39.9 ± 8.2 (n = 142)	65.4 ± 5.6* (n = 199)	49.3 ± 4.1** (n = 90)

* values are significantly different at $P < 0.05$

** values are significantly different at $P < 0.01$

Figure 4-7: Cumulative germination of *Empetrum nigrum* and *E. eamesii* at 25°, 10°, and 5°C with respect to sites.


25°C
Germination (percent)
Time (days)
E. nigrum
Site 3
Site 11
E. eamesii
Site 9
Site 11


10°C
Germination (percent)
Time (days)

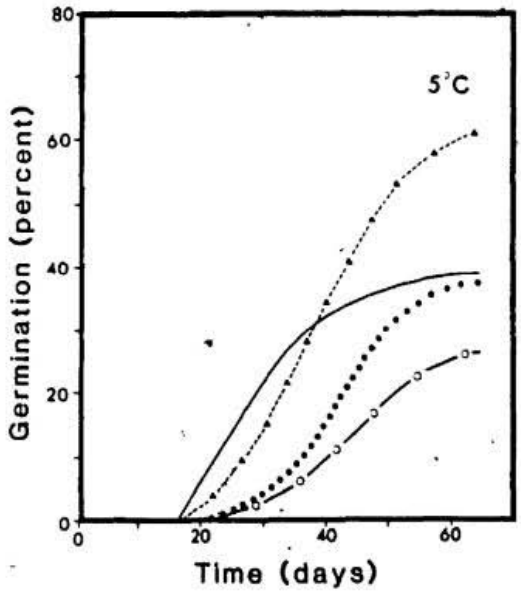

5°C
Germination (percent)
Time (days)

Table 4-5: Germination rates (seeds day^{-1}) from the germination curves of Fig. 4-7.

Species	Temperature (°C) 25°	10°	5°
E. nigrum	3.2	0.4	0.5
E. eamesii	2.8	1.5	1.0

11 and site 3, respectively (Fig. 4-7).

Seeds in the 5°C treatment, germinated mainly between 25 and 35 days from the beginning of the experiment (Fig. 4-7). Both populations of *E. eamesii* along with the coastal population of *E. nigrum*, began germination on day 20 of the experiment, whereas, *E. nigrum* from site 11, began on day 21. The germination rate in Fig. 4-7 shows that *E. eamesii* from site 11, had the highest germination success compared to the remaining populations of *Empetrum*; *E. nigrum* from the coastal site having the lowest germination success. The two remaining sites show an intermediate germination, with *E. eamesii* from site 9 having a higher seed germination than *E. nigrum* from the mixed site (site 11).

4.4. Microhabitat Analysis

A summary of the microhabitat variables (means $\pm$ SE) monitored during 1986 is presented in Table 4-6 and the data for 1987 are shown in Table 4-7. The data set for 1986 are presented in Table D-1 and for 1987 in Table D-3 (Appendix D). Data for both field seasons show that the mean annual air temperatures at *E. nigrum* sites are warmer (an average of 1.1°C) than at the *E. eamesii* sites. In contrast, soil temperature are warmer at the *E. eamesii* sites (an average of 1.4°C) than at the *E. nigrum* sites.

Windspeed was higher at the exposed sites of *E. eamesii* compared to the *E. nigrum* sites (an average of 2.6 m s^{-1}). Snow depth was recorded for only the 1986 season, and little snow accumulation was recorded for *E. eamesii* compared to *E. nigrum*.

Table 4-7 shows significant altitudinal differences between the species and the same is observed for available nutrients. *Empetrum nigrum* was found to

have greater nutrient concentrations than *E. eamesii*. The 1987 data was the data set used in the statistical analyses that follow.

4.4.1. Discriminant Function Analysis

One discriminant function was extracted from the data in Table 4-7, accounting for 100% of the variation between *E. eamesii* and *E. nigrum*. The discriminant function is a function of windspeed (Table 4-8). This function is, therefore, interpreted as an exposure gradient. *Empetrum eamesii* grows in more exposed areas where higher windspeeds occur compared to the *E. nigrum* sites (Table 4-6 and 4-7). Little snow accumulation was recorded for *E. eamesii* in 1986, which is also an indication of high wind. Greater snow depths were measured for the *E. nigrum* sites (Table 4-6).

The classification results of the Discriminant Function Analysis shows 100% classification for each species (Table 4-9). Therefore, complete separation of the species was found, based on the selected microhabitat variables.

4.4.2. Multiple Regression Analysis

The stepwise regression results are summarized in Table 4-10. A significant regression equation for *E. eamesii* was calculated, accounting for 77% of the variation in abundance. Windspeed was the variable responsible for this linear relationship. *Empetrum eamesii* was found to be present in low abundance ($\bar{x}$ = 37%, n = 5 sites) in the sampled sites, indicative of high windspeeds. *Empetrum nigrum*, on the other hand, shows no relationship and it is present in greater abundance ($\bar{x}$ = 60%, n = 5 sites) than *E. eamesii*.

Table 4-6: Means (± SE) of microhabitat variables for the 1986 field season. These are based on annual and seasonal periods; n = number of measurements.

Species	Air Temp. (°C)	Soil Temp. (°C)	Wind ($m\ s^{-1}$)	Snow (cm)
E. nigrum				
annual	7.4 ± .4 (n = 38)	3.0 ± .2 (n = 38)	1.0 ± .2 (n = 8)	5.3 ± 1.4 (n = 18)
winter	-0.4 ± .3 (n = 21)	-0.6 ± .3 (n = 22)	0.3 ± .1 (n = 4)	
spring	10.1 ± .8 (n = 4)	1.3 ± .4 (n = 4)	----	
summer	19.0 ± .5 (n = 13)	9.3 ± .6 (n = 13)	1.8 ± .3 (n = 4)	
E. eamesii				
annual	6.4 ± .2 (n = 39)	4.6 ± .3 (n = 39)	4.1 ± .2 (n = 9)	1.4 ± .7 (n = 19)
winter	-0.8 ± .1 (n = 22)	-1.3 ± .2 (n = 22)	4.0 ± .3 (n = 5)	
spring	9.7 ± .6 (n = 4)	6.5 ± .6 (n = 4)	----	
summer	21.3 ± 3.6 (n = 13)	13.8 ± .5 (n = 13)	4.3 ± .2 (n = 4)	

Table 4-7: Means (± SE) of microhabitat variables for the 1987 field season. Windspeed is divided into annual and seasonal periods. The total number of plots is indicated below each species.

Microhabitat Variables	Species	
	E. eamesii (n = 25)	*E. nigrum* (n = 25)
Elevation (m)	324.0 ± 5.4	98.0 ± 7.6
Air Temperature (T_e)	6.7 ± 0.3	7.9 ± 0.3
Soil Temperature (T_e)	5.0 ± 0.2	3.8 ± 0.6
Annual Windspeed (m s^{-1})	3.2 ± 0.1	1.1 ± 0.1
Spring Windspeed (m s^{-1})	3.3 ± 0.1	1.5 ± 0.1
Summer Windspeed (m s^{-1})	3.0 ± 0.1	0.6 ± 0.1
pH	4.2 ± 0.1	3.9 ± 0.1
Organic Matter (%)	11.3 ± 3.3	57.9 ± 5.7
Nitrogen (ppm)	6.5 ± 1.1	29.5 ± 3.4
Phosphorus (ppm)	2.7 ± 1.2	24.5 ± 3.2
Potassium (ppm)	57.4 ± 21.3	605.7 ± 158.0
Sodium (ppm)	8.3 ± 3.6	378.0 ± 88.1

Table 4-8: Discriminant Function in a twelve microhabitat space.

Microhabitat Variables	Function 1
Summer Windspeed	0.615
Annual Windspeed	0.402
Sodium	-0.332
Elevation	0.314
Nitrogen	-0.255
Phosphorus	-0.254
Potassium	-0.250
Organic Matter	-0.243
Spring Windspeed	-0.229
pH	0.072
Soil Temperature	0.069
Air Temperature	-0.068
Percent Among-Species Variation	100%
Cumulative Percent of Variance	100%

Table 4-9: Classification results of the Discriminant Function Analysis for both species.

Species		N	Predicted Group Membership	
			1	2
E. nigrum	1	25	25 (100%)	0
E. eamesii	2	25	0	25 (100%)
Overall Classification Success = 100%				

Table 4-10: Summary of the stepwise regression on abundance of *Empetrum nigrum* and *E. eamesii*, and the selected microhabitat variables.

Species	N	Step	R^2	Equation*	P
E. nigrum	5	1	----	none	-----
E. eamesii	5	1	0.77	y = 1.62 - 0.326WS	< 0.05

* $y = \text{arcsine}(\text{proportion cover})^{0.5}$
WS = summer windspeed ($m\ s^{-1}$)

Chapter 5

Discussion

5.1. Empetrum Microhabitat

Windspeed was found to contribute most to the difference in the microhabitat of *E. nigrum* and *E. eamesii*. The *Empetrum* genus can be considered stress-tolerant, growing in inorganically and physically-stressed sites (Grime 1979), however, at the species level stress tolerance may vary in intensity. Wind is an ever-present climatic factor on exposed alpine ridges and slopes. Because of the treeless alpine environment wind can reach high speeds influencing the growth of arctic-alpine plants (Nobel 1981, Warren-Wilson 1959). This is seen in the different growth forms of *E. nigrum* which is procumbent and trailing; *E. eamesii* is prostrate with short branches. Windspeeds, however, decrease closer to the ground, reducing air flow within the vegetation canopy, resulting in reduced plant dehydration. Temperatures rise a few degrees higher in the vegetation canopy than the ambient air temperature (Grabherr and Cernusca 1977, Mølgaard 1982, Sohlberg and Bliss 1984).

Furthermore, wind is primary factor that can affect the distribution of plant communities; only the well adapted species will colonize and survive in wind-swept areas. In this instance, *E. eamesii* was the colonizer of the alpine communities. The abundance of *E. eamesii* was negatively associated with mean

windspeed, that is, as windspeed increased such as in the alpine areas, vegetation cover decreased. This observation is consistent with the finding of the multivariate analysis that windspeed is a primary factor determining *E. eamesii* microhabitat and subsequently *Empetrum* distribution. However, other variables that were not considered but may correlate with windspeed (*e.g.*, increase evaporation of plants) may influence wind and so windspeed is not the only variable responsible for such a relationship. This indicates that *E. eamesii* is adapted to exposed areas, in contrast to *E. nigrum* which grows in more protected areas.

The microtopography of alpine areas contributes to the suitability of microsites for plants and therefore, to their distribution. Small depressions in these sites are associated with higher soil temperature, snow drifting, and less severe wind effects; soil erosion is also minimized (Billings and Mooney 1968, Bliss 1962, Nobel 1981, Warren-Wilson 1959). Since windspeeds are low at these microsites, less abrasion and desiccation of plant tissue occurs, and vegetation is better protected (Nams and Freedman 1987b, Tiffney 1972). Abrasion and dehydration of the leaves over a period of time causes death (Hadley and Smith 1983, 1986). Observations of *E. eamesii* showed that the middle branches of a clump died-off first, and then this open space became colonized by lichens and grasses; the surrounding branches of *E. eamesii* clumps survived. Arctic-alpine plants living in a treeless environment colonize microsites where the effects of wind are reduced. This was observed for *E. eamesii*, which grows scattered around rocks and in small depressions where wind-blown matter (*e.g.*, soil, plant material) was able to accumulate.

Heath soils are characteristically acidic and impoverished in available nutrients (Gimingham 1972, Good 1927, Karlsson 1987, Meades 1983). The pH of the study sites were acidic, ranging between 3.3-4.6 for *E. nigrum*, and 3.8-5.1, for *E. eamesii*. Hansen (1976) reported *E. nigrum* sites to range in pH between 3.9-4.2, whereas, Bell and Tallis (1973) gave a wider range of pH 2.5-7.7, which included different types of *Empetrum* habitats. The soil samples from the study sites were found to be deficient in nitrogen, phosphorus, and potassium, compared to deciduous shrub habitat (Jonasson 1983). *Empetrum eamesii* sites had the lowest nutrient concentrations. The average nutrient levels for both species sites were K > Na > N > P. The nutrient deficiency of heathland soils has been well documented (Gimingham 1972, Hansen 1976, Karlsson 1987, Malmer and Wallén 1986, Marrs 1978).

Available nutrients contributed to the interspecific variation in the multivariate analysis. Sodium was the first nutrient to show a high variation between the two species. Sodium had higher soil concentrations on the coastal sites of *E. nigrum* and was virtually absent at the *E. eamesii* sites. It might be suggested that *E. nigrum* is more tolerant to high sodium concentrations than *E. eamesii*, especially considering how common *E. nigrum* is along the coasts.

Marrs (1978) conducted a study on the distribution of certain ericaceous species and concluded that species with high sodium concentrations had an oceanic distribution, whereas species with low sodium concentrations had a continental distribution. Based on these observations *E. nigrum* is an oceanic species compared to *E. eamesii*, which grows farther away from the coasts. Although sodium is not a particular requirement for *E. nigrum* to grow (Hansen

1976), it can substitute for some plant needs otherwise satisfied by potassium (Janick *et al.* 1981).

Potassium is an essential plant nutrient for the formation of carbohydrates (Janick *et al.* 1981). Lipids and carbohydrate levels are high in evergreen shrubs and consequently contribute to cold hardiness (Bliss 1962, Fonda and Bliss 1966). This is important for arctic-alpine plants since it minimizes winter damage. Interestingly, potassium was found to have the highest concentration among all other nutrients for both species. *Empetrum nigrum* sites had higher potassium concentrations than *E. eamesii* sites. These results confirm observations reported by Fernald (1907), who found *E. nigrum* growing in areas rich in potassium.

Nutrient cycling is restricted by cold soil temperatures (Van Cleve and Alexander 1981), which was also observed at the study sites. Soil temperatures, in 1986, of the alpine sites were higher than at the coastal sites; these were probably low enough to restrict nitrification and other nutrient diffusion. Nitrogen is the primary limiting nutrient for plant communities in cold soils, followed by phosphorus (Haag 1974, Henry *et al.* 1986). Organic matter decomposes slowly in cold soils and nitrogen and phosphorus may stay bound to organic material in an unavailable state (Babb and Whitfield 1977). Heathland soils are not very active in nitrification (Gimingham 1972), and the low nitrogen levels of the study sites is indicative of the lack of nitrification occurring in these soils. Phosphorus was also in very low quantities; *E. nigrum* had higher concentrations than *E. eamesii* sites. The latter sites had only trace amounts of phosphorus (range = 0.7 to 30.5 ppm, $\bar{x}$ = 2.7 ppm), whereas, *E. nigrum* had concentrations ranging from 2.2 to 42.9 ppm ($\bar{x}$ = 24.5 ppm). To increase the efficiency of nutrient diffusion and

uptake by the root system of *Empetrum*, a symbiotic relationship exists with an ericoid mycorrhiza (Read 1983).

Empetrum has been found to react to high levels of nutrients (N, P, K) by actually decreasing in abundance when heavily fertilized (Chapin and Shaver 1985, Karlsson 1987), but in some cases slight increases in net production in evergreens and graminoids were observed (Henry *et al.* 1986, Shaver and Lechowicz 1985). Thus, evergreen shrubs are specifically adapted to low nutrient concentrations. The present study found overall nutrient levels to be low for all sites, similar to observations from other studies on alpine plant communities (Henry *et al.* 1986, Karlsson 1987), although high biomass is maintained under such conditions. This is particularly visible for *E. nigrum* which forms extensive communities covering large areas along the coasts.

Elevation was another variable that contributed to the exposure gradient. *Empetrum eamesii* dominated sites are always found at high elevations on the Avalon Peninsula and on the West coast of the island of Newfoundland. In contrast, *E. nigrum* dominated sites are mainly found along the coasts, where humidity is high, and summer temperature maxima are low (Dahl 1951, Damman 1976). Elevation of the sites was correlated with cooler temperatures and higher windspeeds, this in turn, causes an increase in carbohydrate levels in plants, which increases the respiration rate (Mooney and Billings 1965). Alpine plants are adapted to these conditions and cannot survive in areas with high average summer temperatures (Dahl 1951, Damman 1976). This is true of *E. eamesii* which grows in wind-swept areas and due to wind, temperatures remain cool.

Air and soil temperature did not contribute significantly in the

discrimination of the species. *Empetrum nigrum* sites have a higher air temperature than *E. eamesii*, however, the inverse is true for soil temperature. The difference in soil temperature between species was 1.2°C. One reason which may account for this is that the *E. eamesii* sites have a much sparser vegetation cover, thus allowing more solar radiation to reach the ground, heating the soil more quickly following snowmelt. *Empetrum nigrum* sites have a denser vegetation cover which insulates the soil, delaying soil thaw. The lack of a significant air and soil temperature difference may be due to the restricted study region. However if sampling had been extended to the populations of the West coast temperature may have been a discriminating factor in the multivariate analysis because of the greater spatial range. Damman (1976) found the temperature difference between the coastal sites of *E. nigrum* and of *E. eamesii* at the Hawke Hills to be 1.9°C. In this study the average summer temperature, (3.5 cm below the ground surface) of the coastal and Hawke Hills sites was *ca* 15°C.

5.2. Phenology

Although there has been some work done on the phenology of *E. nigrum* no such work has been undertaken on *E. eamesii*. This aspect of the study attempted to detect minute differences between the species, which may have indicated differences between microhabitats. However, the phenological development of *E. nigrum* and *E. eamesii* was not found to differ. Early blooming is common for arctic-alpine plants (Bannister 1978). The blooming period recorded in this study, which was immediately after snowmelt, is corroborated by the long term observations undertaken by Roger Etcheberry

(pers. comm.) of both species on the islands of St. Pierre and Miquelon. It also follows the general phenological descriptions given by Dalby (1961), Good (1927) and Mentz (1912).

Primary factors influencing plant phenology in alpine areas are snow cover and soil temperature (Bliss 1985, Sørensen 1941, Wielgolaski and Kärenlampi 1975, Woodley 1980, 1981). Snow depth and the time of melting are important for habitat selection of species and plant communities in alpine areas.

The snow cover, particularly at the alpine site (site 9), was found to be intermittent with an average snow accumulation of only 1.4 cm during the winter 1986. The coastal site (site 3), however, had a more permanent snow cover throughout the winter, with an average accumulation of 5.3 cm. Although a significant difference in snow cover was recorded (in 1986) between the sites this was not accompanied by an observed difference in phenology and snow cover may not be critical for determining the flowering period of both species.

Mean surface soil temperatures during the spring of 1986 and 1987 were higher for *E. camesii* sites than for *E. nigrum* sites. Even with this difference in soil temperatures between the two species, phenological development was not delayed even though the temperature factor was found to be critical in other studies (Wielgolaski and Kärenlampi 1975, Woodley 1980, 1981). As with the differences in snow cover, the differences in temperature recorded for this study may not have been large enough to result in any variation in phenological development between the species.

Snowmelt is one of the triggering factors for plants to start flowering. At all sites snowmelt occurred at the end of March for 1986 and 1 week earlier in 1987.

This slightly earlier spring of 1987 was accompanied by the earlier blooming period of *Empetrum* compared to 1986 (Table 4-1). Snowmelt, therefore, can be considered important in controlling flowering in *Empetrum* species, as in other alpine plants. The arctic-alpine shrubs *Cassiope tetragona* (L.) D. Don and *Salix arctica* Pall. have been observed to flower following snowmelt in response to the sudden release of nutrients, an increase in soil moisture and soil temperature (Bliss 1985, Nietfeld-Nams 1981, Woodley 1980). The results indicate that the measured microhabitat variables, although significant, did not show large enough differences among species to correlate with phenology.

5.3. Shoot Elongation

Although shoot elongation was measured at only two sites (sites 3 and 9) in 1986, measurements taken at ten sites in 1987 showed the same trend. In 1987 *E. nigrum* had a significantly higher shoot growth and growth rate than *E. eamesii*. Both species were found to grow between 0.4-77.1 mm in a growing season (Tables B-3, B-4, Appendix B), with *E. nigrum* having greater length increment than *E. eamesii*. The present study confirms previous shoot growth studies undertaken on *E. nigrum* (Kirchner *et al.* 1925, Lindholm 1980, Mentz 1912). Other heath shrubs (*Erica cinerea* L., *E. tetralix* L., and *Calluna vulgaris* (L.) Hull) that have been studied for growth development showed a greater shoot elongation than *Empetrum*, (94, 68 and 155 mm, respectively) (Bannister 1978). Thus, *Empetrum* is a slow growing plant, which may be indicative of the harshness of its microhabitats.

Empetrum nigrum grows *ca* 48 mm per year in the Lake Superior region in contrast to more northern populations, where growth is 10-20 mm per year

(Barclay-Estrup and Nuttall 1974, Mentz 1912). A greater annual shoot growth was measured in the protected site (5) for *E. nigrum* where the windspeed was the lowest (0.6 m s^{-1}). During this period, *E. nigrum* shoots grown in the greenhouse elongated 128 mm providing another example of the importance of microhabitat in affecting plant growth. Similar growth rates to *E. eamesii* have been reported for *Cassiope tetragona* from a tundra habitat (Nams and Freedman 1987a).

The present study confirms that *Empetrum* has a higher shoot elongation in less exposed sites (sites 1-5). An exposure factor and possibly the nutrient aspect of the sites, are responsible for low shoot growth of both species. These environmental factors are clearly more extreme for *E. eamesii*, contributing to a certain extent to its lower shoot growth compared to *E. nigrum*.

The age of the plants was not considered in this study, but as Wijk (1986a, 1986b) demonstrated, the age of the plant will affect growth rate. For example, a decrease in shoot elongation was observed in *Salix herbacea* L. (Wijk 1986a, 1986b) as shoot age increased; this was related to the slowing down of physiological processes (*e.g.* decreasing transport capacity). Therefore, part of the variation seen in the growth of *Empetrum* may be due to age and also to the types of shoots measured.

Vegetative growth of *Empetrum* occurs in two stages. The early spring growth takes place after flowering in the main axis or primary shoots; summer shoots, which are secondary branches, are much shorter and begin to grow in June (Good 1927, Kirchner *et al.* 1925, Mentz 1912). Shoots in this study were selected at random, which may have produced greater variation in the data than

if one type of shoot had been selected.

Shoot elongation of *Empetrum* does not indicate how the species succeeds in colonizing and establishing itself in an area. This be better assessed by seed germination experiments.

5.4. Germination Experiments

Successful seed germination is important in determining the composition and relative abundance of species in plant communities (Gartner 1983). The germination experiments undertaken here, showed an optimum germination at 25°C for both *E. nigrum* and *E. eamesii*. This is common for arctic-alpine plants germinating under ideal conditions (Bell 1969, Bell and Tallis 1973, Billings and Mooney 1968, Gartner 1983, Karlin and Bliss 1983, Wein and MacLean 1973). Optimum germination at such high temperature is probably a selective mechanism that evolved in alpine and arctic plant species to avoid germination when frost is prominent, which would select against seedling establishment (Bliss 1985).

Ideal conditions can occur briefly in the field during the warmest month of the summer; however, competition with other plants under such conditions has an important role in determining germination of these seeds. Marchand and Roach (1980) did a comparative germination study for different arctic-alpine species (*Arenaria groenlandica* (Retz.) Spreng., *Juncus trifidus* L., and *Potentilla tridentata* Ait.) under laboratory and field conditions. Although their laboratory experiments were successful (88%, 88%, and 52%, respectively), their field trials showed a decrease in germination (38%, 17%, and 0%, respectively). This suggests that low seedling survival occurs in the natural environment and that

seed germination in the field is infrequent. Although field germination was not considered in this study, I did not observe seedling establishment at the study sites during the study period.

The germination success for *E. nigrum* at the 25° and 10°C treatments (79.8% and 19.8%, respectively) was higher compared to the results of Bell (1969) (67% and 6%, respectively). This latter study did not test seed germination of *E. nigrum* at 5°C. However, Gartner (1983) reported that *E. nigrum* germinated readily at 5°C.

Another interesting feature emerges when the germination experiments are considered in relation to sites. Although *E. eamesii* showed higher germination at the mixed site than *E. nigrum*, the mixed site consistently had higher germination for both species than the sites in which either *E. nigrum* and *E. eamesii* was the dominant species. This may demonstrate the abilities of both species to compete with other plant species present at the mixed site (*e.g. Kalmia angustifolia, Vaccinium vitis-idaea, V. angustifolium*, and others). *Empetrum* species may increase their competition abilities by having seeds that germinate more readily in the mixed site. The alpine and coastal sites (3 and 9) are nutrient-poor and have fewer species for *Empetrum* to compete with. *Empetrum* dominates these sites and seed germination becomes less important than at the mixed site where a greater number of plant species grow.

The results with respect to the differences in the germination of seeds from the *E. eamesii* alpine sites and *E. nigrum* coastal sites, may be explained by the heterogeneity of the sites (Harper 1977, Sohlberg and Bliss 1984). A large portion of the alpine sites consist of exposed rocks, clearly unsuitable microsites for

germination to occur; the remaining area consists of small patches of vegetation (microsite here is defined as a small area, *i.e.* centimetres in scale, within the study sites). More effort is required for *E. eamesii* to survive in these sites and this is expressed in increased seed germination.

Soil temperature has also been found to be an important germination cue (Rice 1985). As found here, winter soil temperature was *ca* -1.0°C (Table 4-6) and the spring soil temperature went up to 1-6°C, suitable for the germination of *Empetrum* seeds, as demonstrated by the germination experiments carried out at 5°C.

The present study found that *E. eamesii* had a reduced germination at 25°C compared to *E. nigrum* but at 10° and 5°C *E. eamesii* had greater germination success than *E. nigrum*. This indicates that it is adapted to a severe environment and that microhabitat is important in determining germination in *Empetrum*. A comparable study, on the closely related taxa *Ledum groenlandicum* Oeder and *L. palustre* ssp. *decumbens* (Ait.) Hult., showed similar trends (Karlin and Bliss 1983). *L. palustre*, a more northern species adapted to severe environments, had higher germination (66%) than *L. groenlandicum* (53%), the more southern species.

5.5. Summary

Interspecific differences, between *E. nigrum* and *E. eamesii* have micro-environmental, as well as, physiological implications. *Empetrum nigrum* microhabitat had low windspeed, high sodium concentrations and low elevation compared to *E. eamesii*. The remaining micro-environmental variables that were considered did not contribute to the discrimination of the two species in the

multivariate analysis. These microhabitat differences were then related to the interspecific differences of shoot growth and germination of both species.

Favourable microsites for germination were taken into consideration for the germination experiment. There were few favourable microsites at the alpine sites due to their heterogeneous state. A large portion of *E. eamesii* sites consists of rocks, clearly unfavourable for germination.

The microhabitat data showed that wind and elevation contributed the most to interspecific differences. This was interpreted from the mutivariate analysis as an exposure gradient, with *E. eamesii* growing in wind-swept areas and higher elevations than *E. nigrum*. *Empetrum eamesii* sites were also found to have lower air temperature, higher soil temperature and low nutrient levels compared to *E. nigrum*. However, temperatures and nutrients did not contribute much in the separation of the two species, due to the lower variation they showed compared to wind and elevation. High windspeed was correlated with low abundance of *E. eamesii*.

Phenological development of both species was found to occur at the same time. The primary microhabitat variable that influences the early phenological stages, such as flowering and fruit formation, was time of snowmelt.

Shoot growth showed significant interspecific variation that may be related to microhabitat differences. The mirohabitat variables that have an effect on shoot growth are wind and available nutrients in the soils. An exposure gradient was developed with the multivariate analysis, with wind being the variable that contributed most of the variation between the species. *Empetrum eamesii*, growing in wind-swept alpine areas, was found to have the lowest shoot growth.

Empetrum nigrum forms coastal plant communities where wind is not as strong as alpine areas, and this species grew at a greater rate than *E. eamesii*.

Another factor that may be involved in shoot growth is the concentration of available soil nutrients for the plants. *Empetrum eamesii* sites were found to have the lowest nutrient concentrations compared to *E. nigrum* sites. These nutrient levels are consistent with the findings for shoot growth for both species. That is, *E. eamesii* sites were low in soil nutrients and the species had the lowest shoot growth; *E. nigrum* sites had richer soils and the species had a higher shoot growth. Finally, age of the shoots may also affect growth, as the shoots become older, shoot incrementation decreases, but this was not taken into consideration in this study.

The seed germination experiments indicated that *E. eamesii* is physiologically better adapted to exposed habitats than *E. nigrum*. Optimal germination temperature was 25°C, which is common for arctic-alpine plants. *Empetrum eamesii* had higher germination at 10° and 5°C, compared to *E. nigrum*. The 5°C temperature treatment is closer to the natural conditions under which these plants germinated, such temperatures occur after snowmelt.

Another finding for the germination study was that the mixed site (site 11) had higher germination success for both species, than the other sites (3 and 9). This may be related to competition strategies and microsite conditions. Competition would increase in a habitat with a larger number of plant species, as in site 11, than found in the alpine and coastal sites. The increased competition would necessitate having seeds that germinate more readily.

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Appendix A

Representative Soil Types of Empetrum

Table A-1: Soil profile description of a representative *Empetrum nigrum* site (site 3).

Habitat: Hummocky coastal heath.

Soil Type: Typic Folisol over shattered rock and soliflucted material.

Horizon	Depth (cm)	Description
FH1	1-0	Black (5YR 2.5/1) litter layer; 67% of particles > 2 mm; pH 6; numerous fine to coarse horizontal roots.
HF	1-9	Dark brown (7.5YR 2.5/0) humus; 20% of particles > 2 mm; pH 5.3; few lateral roots; lower boundary wavy.
C1u	9-21	Light grey (10YR 4/2) loamy sand; soliflucted material; 36% of particles > 2 mm; pH 5.6; few lateral roots.
C2u	21-31	Dark grey (10YR 3/2) loamy sand; soliflucted material; 27% of particles > 2 mm; pH 5.3; very few lateral roots.
R	31 +	Bedrock, sandstone (pink).

Table A-2: Soil profile description of a representative *Empetrum eamesii* site (site 0).

Habitat: Cryoturbated alpine area.

Soil Type: Orthic Humo-Ferric Podzol, cryoturbated phase.

Horizon	Depth (cm)	Description
Gravel	0-3	Light brown (7.5YR 6/4) gravel, silicate rock and granite; 79% of particles > 2 mm; pH 5.4.
Bf1y	3-15	Dark brown (7.5YR 4/4) loam; 33% of particles > 2 mm; pH 5.4; fine to coarse horizontal roots; wavy boundary.
Bf2y	15-24	Dark reddish brown (7.5YR 4/4) loam; 36% of particles > 2 mm; pH 5.3.
Bf3y	24-35	Grey (10YR 4/4) loam; 39% of particles > 2 mm; pH 5.1.
C	35 +	Grey (10YR 5/3) sandy clay loam; 37% of particles > 2 mm; pH 5.3.

Appendix B

Shoot Elongation Data

Table B-1: Daily shoot growth rate (mm day^{-1}) for 1986; n = number of shoots.

E. nigrum (site 3, n = 23)	E. eamesii (site 9, n = 21)	E. nigrum (greenhouse, n = 10)
0.050	0.001	0.456
0.006	0.048	0.546
0.026	0.164	0.548
0.017	0.183	0.519
0.015	0.107	0.528
0.224	0.021	1.158
0.082	0.027	0.150
0.071	0.097	0.534
0.172	0.003	0.731
0.060	0.073	0.564
0.041	0.115	
0.065	0.050	
0.095	0.114	
0.602	0.056	
0.386	0.099	
0.266	0.159	
0.042	0.096	
0.104	0.131	
0.227	0.176	
0.041	0.019	
0.119	0.106	
0.032		
0.057		

Table B-2: Daily shoot growth rate (GR) (mm day^{-1}) for 1987; n = number of shoots.

Site No.	GR	Site No.	GR	Site No.	GR
1 (n = 14)	0.106	3	0.448	5	0.157
	0.077		0.079		0.400
	0.317		0.108		0.429
	0.597		0.031		0.209
	0.161		0.155		0.059
	0.093		0.246		0.075
	0.063		0.119		
	0.066		0.063	6 (n = 16)	0.060
	0.025				0.411
	0.067	4 (n = 16)	0.118		0.126
	0.100		0.036		0.131
	0.211		0.099		0.025
	0.185		0.016		0.147
	0.396		0.068		0.025
			0.166		0.158
2 (n = 14)	0.088		0.054		0.099
	0.248		0.033		0.113
	0.070		0.024		0.135
	0.056		0.106		0.032
	0.075		0.066		0.114
	0.158		0.048		0.066
	0.045		0.124		0.034
	0.086		0.036		0.057
	0.141		0.004		
	0.337		0.031	7 (n = 17)	0.032
	0.689				0.062
	0.026	5 (n = 14)	0.222		0.005
	0.026		0.236		0.047
	0.076		0.083		0.021
			0.058		0.101
3 (n = 11)	0.140		0.139		0.062
	0.205		0.105		0.012
	0.069		0.097		0.063
			0.106		

(continued next page)

Site No.	GR	Site No.	GR
7	0.082	9	0.008
	0.156		0.114
	0.031		0.152
	0.035		0.095
	0.020		0.213
	0.053		0.054
	0.044		0.103
	0.067		0.026
			0.174
8 (n = 19)	0.100		
	0.072	10 (n = 19)	0.112
	0.141		0.101
	0.031		0.050
	0.058		0.076
	0.054		0.024
	0.060		0.161
	0.116		0.126
	0.028		0.136
	0.043		0.133
	0.021		0.005
	0.039		0.082
	0.061		0.091
	0.115		0.093
	0.244		0.040
	0.029		0.034
	0.268		0.031
	0.024		0.007
	0.246		0.041
			0.017
9 (n = 15)	0.083		
	0.063		
	0.132		
	0.187		
	0.095		
	0.031		

Table B-3: Total mean annual and seasonal shoot growth (mm) for 1986; n = number of shoots.

Site No.	Annual Growth	Spring Growth	Summer Growth	Site No.	Annual Growth	Spring Growth	Summer Growth
E. nigrum	(n = 18)	(n = 19)	(n = 21)	E. eamesii	(n = 20)	(n = 19)	(n = 23)
3	2.20	----	2.00	9	20.95	1.10	15.20
	2.80	1.30	8.95		15.40	0.50	9.10
	----	0.05	22.10		13.65	0.60	8.40
	----	2.15	----		6.15	3.15	0.15
	6.40	9.05	11.90		10.40	----	4.95
	----	----	5.35		3.45	0.25	13.35
	22.05	1.80	17.65		----	----	18.85
	10.45	2.25	8.50		12.45	0.80	4.30
	9.10	4.10	12.25		----	0.80	11.95
	2.870	1.45	4.90		2.70	1.58	16.20
	----	2.50	----		14.75	1.95	15.45
	12.15	----	5.30		6.35	4.95	5.20
	5.25	1.20	----		14.60	0.65	13.65
	6.60	6.65	43.70		----	2.00	9.65
	2.00	0.90	5.10		----	0.30	2.20
	3.50	----	----		0.70	0.30	4.65
	13.35	----	9.95		----	1.65	----
	49.35	2.70	6.60		13.60	0.10	6.10
	----	8.95	7.80		9.05	----	9.05
	77.10	2.90	15.75		7.15	0.35	5.50
	----	----	8.35		11.70	----	8.05
	30.85	3.60	15.80		22.55	----	4.90
	5.25	7.05	2.00		1.70	1.05	----
	----	0.45	69.95		12.35	----	3.30
	49.40	0.05	20.70		20.35	0.50	12.60

* Annual = first day of spring to the last day of summer
Spring = 14 April - 20 May
Summer = 21 May - 10 Sept.

Table B-4: Total mean annual and seasonal shoot growth (mm) for 1987; n = number of shoots.

Site No.	Annual Growth	Spring Growth	Summer Growth	Site No.	Annual Growth	Spring Growth	Summer Growth
E. nigrum							
1 (n = 19)	----	----	1.10	2	3.05	----	3.15
	12.60	0.75	11.85		3.10	----	3.10
	9.20	----	11.00		9.00	0.30	8.70
	37.75	1.30	36.45				
	71.10	1.50	69.60	3 (n = 17)	----	6.45	----
	----	----	0.65		24.40	4.75	19.65
	19.10	0.95	18.15		16.70	5.55	11.15
	11.10	0.35	10.75		8.25	0.80	7.45
	----	1.35	----		18.50	0.20	17.40
	7.50	1.00	6.50		29.25	0.25	29.00
	7.90	----	8.40		14.20	1.35	12.85
	3.00	0.15	2.85		7.55	----	7.70
	8.00	----	8.75		3.70	0.30	3.40
	11.85	0.45	11.40		----	1.05	----
	25.10	1.50	23.60		53.30	1.15	52.15
	4.55	----	0		----	1.35	----
	----	0.20	----		9.45	----	9.60
	22.05	1.05	21.00		12.80	----	13.40
	47.10	3.90	43.20				
				4 (n = 19)	59.00	1.25	18.55
2(n = 17)	10.50	0.25	10.25		2.80	0.05	2.75
	29.55	----	30.20		----	0.15	----
	8.35	----	9.30		14.70	----	15.50
	6.65	0.10	6.55		4.30	0.20	4.10
	8.95	----	9.40		0.40	0.10	0.30
	18.80	0.30	18.50		3.65	0.05	3.60
	----	1.00	----		14.10	0.50	13.60
	5.40	0.15	0.525		----	0.10	----
	10.20	----	10.20		1.50	----	4.45
	16.75	0.15	16.60		11.75	0.25	11.50
	40.05	0.05	40.00		1.95	----	2.35
	15.25	----	21.40		8.15	----	8.80
	----	1.05	----				
	----	0.10	----				

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Site No.	Annual Growth	Spring Growth	Summer Growth	Site No.	Annual Growth	Spring Growth	Summer Growth
4	6.45	0.75	5.70	6	11.80	----	12.40
	3.90	1.20	2.70		13.45	----	14.25
	----	0.10	----		16.05	1.00	15.05
	12.60	----	13.90		3.80	3.20	0.60
	7.80	----	9.20		13.55	0.55	13.00
	5.70	----	6.50		7.90	0.50	7.40
					4.05	2.95	1.10
5 (n = 18)	16.60	9.85	6.75		6.80	----	7.05
	12.50	7.80	4.70				
	----	----	13.55	7 (n = 18)	3.85	0.50	3.35
	11.60	----	12.75		7.95	----	8.70
	24.90	12.55	12.35		7.35	3.05	4.30
	7.05	0.20	6.85		0.55	----	1.95
	----	----	8.10		5.60	4.30	1.30
	8.95	----	12.10		2.45	1.05	1.40
	18.65	3.10	15.55		----	----	2.20
	47.65	36.30	11.35		12.00	----	12.75
	51.05	36.15	14.90		7.35	----	7.95
	----	----	16.60		1.40	----	2.00
	26.40	9.90	16.50		7.50	----	9.00
	----	----	5.45		9.75	----	10.40
	12.60	----	21.15		18.55	----	19.35
	28.05	19.20	8.85		3.70	1.10	2.60
	9.85	----	10.00		4.15	0.40	3.75
	8.90	----	22.20		2.35	----	4.25
					6.20	----	5.65
					5.20	----	5.55
E. eamesii							
6 (n = 19)	7.15	----	7.15	8 (n = 20)	29.05	1.65	27.40
	----	0.45	----		13.70	0.10	13.60
	48.90	2.10	46.80		----	----	0.25
	15.00	1.75	13.25		3.45	0.90	2.55
	----	0.50	----		31.95	----	32.35
	15.60	0.10	15.50		2.90	1.95	0.95
	----	0.55	----		29.30	----	29.85
	2.95	0.15	2.80		12.00	----	12.45
	17.45	2.75	14.70		8.60	0.45	8.15
	3.00	----	3.05		16.80	0.90	15.90
	18.85	0.90	17.95				

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Site No.	Annual Growth	Spring Growth	Summer Growth	Site No.	Annual Growth	Spring Growth	Summer Growth
8	3.70	0.30	3.40	10 (n = 19)	13.30	7.00	12.60
	6.95	----	7.05		12.00	1.10	10.90
	7.15	----	7.75		6.00	1.15	4.85
	6.40	0.05	6.35		9.10	0.90	8.20
	13.75	----	14.35		2.85	----	5.00
	3.35	0.10	3.25		19.15	1.85	17.30
	5.10	----	5.15		15.00	2.15	12.85
	2.50	0.35	2.15		16.20	0.55	15.65
	4.60	----	4.95		4.90	4.80	0.10
	7.30	----	7.45		2.00	1.75	0.25
					10.85	3.35	7.50
9 (n = 17)	11.35	----	11.80		11.05	1.05	10.00
	25.35	----	25.70		4.80	0.25	4.55
	18.05	0.10	12.15		4.00	----	4.45
	6.40	0.60	5.80		3.65	----	4.65
	12.20	----	12.20		0.80	----	1.50
	----	0.50	----		15.80	----	15.90
	3.10	1.10	2.00		0.55	----	1.30
	20.75	1.55	19.20		9.70	1.55	8.15
	9.90	1.20	8.70				
	7.50	0.20	7.30				
	15.70	0.60	15.10				
	22.20	1.35	20.85				
	----	0.10	----				
	11.25	0.45	10.80				
	3.70	1.10	2.60				
	1.00	----	1.10				
	8.95	----	11.20				

* Annual = first day of spring to the last day of summer
Spring = 23 April - 21 May
Summer = 22 May - 21 August

Table B-5: Total monthly shoot growth (mm) for 1986; n = number of shoots.

Species	Site No.	May	June	July	August
E. nigrum	3	(n = 16)	(n = 16)	(n = 21)	(n = 10)
		2.50	6.40	2.65	0.50
		0.90	0.40	1.35	3.50
		3.60	15.55	0.80	0.20
		1.45	5.65	4.80	0.30
		0.50	4.10	4.95	1.00
		1.75	6.20	1.80	1.90
		0.85	5.10	1.55	0.30
		2.00	10.70	3.10	16.50
		2.75	0.50	7.05	0.30
		2.35	2.05	0.25	1.25
		3.55	19.75	3.35	
		2.75	17.70	1.10	
		9.50	6.40	1.15	
		1.05	1.80	0.70	
		0.85	14.65	4.85	
		0.15	4.95	13.45	
				0.70	
				0.95	
				1.30	
				7.55	
				4.20	
E. eamesii	9	(n = 18)	(n = 22)	(n = 22)	(n = 15)
		1.10	4.15	3.45	0.30
		1.95	4.15	4.75	1.30
		0.30	4.45	3.45	1.15
		0.50	2.15	0.75	0.35
		4.95	2.95	2.30	0.35
		1.65	0.80	2.40	0.10
		0.60	4.70	3.40	0.60
		0.80	0.90	1.50	0.95
		0.65	1.80	1.30	3.90
		0.10	2.60	1.60	0.50
		1.05	4.95	1.20	0.55
		3.15	6.25	0.85	1.20
		0.80	0.10	0.25	0.25

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Species	Site No.	May	June	July	August
E. eamesii	9	2.00	2.45	3.30	0.65
		1.55	3.95	1.90	1.95
		0.30	1.55	2.70	
		0.35	1.95	3.00	
		0.50	0.50	2.40	
			5.20	2.50	
			6.85	3.85	
			5.80	1.55	
			3.00	2.05	

Appendix C

Seed Germination Data

Table C-1: Total mean germination (percent) data, (n = 200 seeds per site).

Species	Site No.	Replicate	Temperature (°C) 25	10	5
E. nigrum	3	1	82.5	10.0	20.0
		2	75.0	20.0	37.5
		3	67.5	5.0	30.0
		4	80.0	7.5	30.0
		5	87.5	0	17.5
	11	1	77.5	20.0	35.0
		2	85.0	30.0	45.0
		3	67.5	37.5	32.5
		4	90.0	42.5	45.0
		5	85.0	25.0	30.0
E. eamesii	9	1	82.5	42.5	30.0
		2	85.0	42.5	45.0
		3	47.5	60.0	45.0
		4	85.0	50.0	35.0
		5	50.0	27.5	35.0
	11	1	57.5	72.5	50.0
		2	70.0	57.5	50.0
		3	60.0	47.5	72.5
		4	90.0	52.5	60.0
		5	85.0	45.0	75.0

Table C-2: Percent seed viability of germination experiments. The total number of seeds tested is shown in parenthesis.

Species	Site No.	Replicate	Temperature (°C) 25	10	5
E. nigrum	3	1	0 (n = 4)	88.9 (n = 18)	100.0 (n = 16)
		2	0 (n = 5)	75.0 (n = 16)	52.9 (n = 17)
		3	16.7 (n = 6)	78.9 (n = 19)	88.2 (n = 17)
		4	0 (n = 4)	77.8 (n = 18)	76.5 (n = 17)
		5	0 (n = 2)	90.0 (n = 20)	87.5 (n = 16)
	11	1	50.0 (n = 4)	93.8 (n = 16)	92.3 (n = 13)
		2	100.0 (n = 3)	78.6 (n = 14)	81.8 (n = 11)
		3	16.7 (n = 6)	88.2 (n = 17)	69.2 (n = 13)
		4	75.0 (n = 4)	90.9 (n = 11)	100.0 (n = 11)
		5	0 ----	60.0 (n = 5)	85.7 (n = 14)

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Species	Site No.	Replicate	Temperature (°C) 25	10	5
E. eamesii	9	1	25.0 (n = 4)	72.7 (n = 11)	50.0 (n = 14)
		2	66.7 (n = 3)	72.7 (n = 11)	54.5 (n = 11)
		3	50.0 (n = 10)	62.5 (n = 8)	36.4 (n = 11)
		4	33.3 (n = 3)	70.0 (n = 10)	23.1 (n = 13)
		5	70.0 (n = 10)	71.4 (n = 14)	46.2 (n = 13)
	11	1	0 (n = 7)	20.0 (n = 5)	40.0 (n = 5)
		2	50.0 (n = 6)	62.5 (n = 8)	60.0 (n = 5)
		3	37.5 (n = 8)	70.0 (n = 10)	60.0 (n = 5)
		4	0 (n = 2)	88.9 (n = 9)	62.5 (n = 8)
		5	66.4 (n = 3)	63.6 (n = 11)	60.0 (n = 5)

Appendix D

Microhabitat Measurements

Table D-1: Total mean annual microhabitat data for 1986.

Species	Site No.	Replicate	Temperature (°C) Air	Soil	Windspeed (m s^{-1})	Snow (cm)
E. nigrum	3	1	6.69	2.70	0.75	4.46
		2	----	----	1.56	4.40
		3	7.93	3.10	1.06	3.18
		4	----	----	0.56	3.79
		5	7.50	3.19	0.88	10.66
E. eamesii	9	1	6.06	4.00	4.44	1.42
		2	----	----	4.56	0.26
		3	6.49	5.16	3.50	4.28
		4	----	----	3.83	0.33
		5	6.53	4.55	4.39	0.72

Table D-2: Total mean seasonal microhabitat data for 1986.

*	Winter			Spring		Summer		
Replicate	Air	Soil	Wind	Air	Soil	Air	Soil	Wind
E. nigrum								
1	-0.90	-0.30	0	8.63	0.6	18.35	8.18	1.5
2	----	----	0.75	----	----	----	----	2.88
3	-0.02	-1.11	0.38	10.15	1.93	20.02	10.26	1.75
4	----	----	0.13	----	----	----	----	1.00
5	-0.13	-0.33	0	11.45	1.48	18.62	9.42	2.00
E. eamesii								
1	-1.07	-1.76	4.20	9.20	5.88	28.50	13.18	4.75
2	----	----	4.60	----	----	----	----	4.50
3	-0.73	-1.04	3.00	8.95	7.65	17.95	14.88	4.13
4	----	----	4.10	----	----	----	----	3.50
5	-0.69	-0.99	4.10	10.85	6.03	17.42	13.45	4.75

* Winter = 18 Nov. 1985 - 14 April 1986
Spring = 14 April - 20 May
Summer = 21 May - 25 August

Air = air temperature (°C)
Soil = soil temperature (°C)
Wind = windspeed ($m\ s^{-1}$)

Table D-3: Total means of the microhabitat data for 1987.

Site No.	Rep.	% Cover	Elev. (m)	Air (°C)	Soil (°C)	Windspeed ($m\ s^{-1}$) Annual	Spring	Summer	pH	N (ppm)	P (ppm)	K (ppm)	Na (ppm)	% Organic Matter
E. nigrum														
1	1	50	120	7.00	4.05	0.9	1.2	0.6	3.67	48.9	26.4	341	387.4	80.41
	2	35	120	6.65	3.25	1.7	2.0	1.4	3.61	64.8	35.7	296	312.1	89.04
	3	25	120	10.10	6.75	1.3	1.6	1.0	3.59	36.0	24.0	254	210.6	71.21
	4	60	120	7.40	5.25	0.8	1.2	0.3	3.82	75.3	27.4	323	416.8	80.04
	5	90	120	8.70	4.00	0.4	0.4	0.4	3.49	28.6	26.9	416	563.2	88.72
2	1	80	100	7.00	6.90	0.8	1.2	0.3	3.29	48.7	13.3	255	70.5	34.61
	2	60	100	8.05	0.90	1.1	1.4	0.7	4.11	28.0	11.6	190	58.5	28.28
	3	75	100	8.00	3.60	1.1	1.5	0.6	4.07	26.3	21.3	704	269.3	70.85
	4	20	100	8.50	4.60	0.6	0.7	0.5	4.14	11.3	4.6	187	57.6	20.09
	5	40	100	7.80	2.60	1.0	1.5	0.5	4.42	20.5	2.2	131	75.8	27.87
3	1	75	100	7.00	0.90	1.4	2.1	0.6	4.36	32.7	44.2	651	1236.5	82.02
	2	70	100	6.90	-0.50	1.6	2.3	0.9	4.59	28.9	40.2	445	1125.8	53.92
	3	85	100	7.00	-0.20	1.4	2.4	0.4	4.47	20.5	29.7	2536	711.1	39.01
	4	15	100	7.75	3.60	1.2	1.8	0.6	4.38	17.3	11.0	1577	220.3	13.99
	5	98	100	6.55	-0.20	1.3	1.8	0.7	4.67	34.8	65.5	3484	1831.9	75.57
4	1	10	140	6.50	4.50	1.6	2.3	0.8	3.67	34.4	34.3	360	134.7	84.77
	2	55	140	4.45	0.90	1.4	2.3	0.5	3.53	25.5	37.5	476	386.2	89.94
	3	65	140	7.90	0.20	1.9	2.9	0.8	3.48	41.7	43.1	465	374.3	90.67
	4	80	140	6.65	2.00	1.2	1.8	0.5	3.59	34.3	27.8	403	366.8	89.68
	5	60	140	6.50	4.80	1.6	2.3	0.8	3.53	28.6	42.9	592	449.8	88.26

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Site No	Rep	% Cover	Elev. (m)	Air (°C)	Soil (°C)	Windspeed ($m\ s^{-1}$) Annual	Spring	Summer	pH	N (ppm)	P (ppm)	K (ppm)	Na (ppm)	% Organic Matter
5	1	95	30	9.00	6.45	0.5	0.3	0.6	3.69	8.2	2.4	80.9	22.6	17.17
	2	85	30	12.15	8.45	0.6	0.7	0.5	3.66	12.5	10.3	205	39.4	34.75
	3	15	30	11.10	8.20	0.6	0.7	0.4	3.72	7.1	2.7	163	21.6	13.98
	4	70	30	8.90	6.90	0.8	1.2	0.3	3.76	13.0	8.6	206	58.6	42.25
	5	60	30	9.45	7.90	0.5	0.5	0.4	3.47	10.1	17.9	402	49.0	39.67
E. camesii														
6	1	60	290	2.35	5.90	3.4	2.9	3.8	3.97	3.8	1.1	40.4	4.6	7.23
	2	35	290	5.90	4.95	2.5	2.8	2.2	3.68	5.1	2.8	32.5	7.1	8.03
	3	10	290	6.35	3.75	2.7	2.5	2.8	3.91	3.8	1.2	33.1	4.7	4.38
	4	70	290	5.90	4.60	2.7	2.8	2.5	3.75	4.0	1.1	19.2	3.5	3.09
	5	45	290	7.10	7.25	2.6	2.7	2.5	3.75	5.2	1.9	28.4	4.7	6.43
7	1	40	370	5.40	1.80	3.2	3.6	2.8	3.86	21.9	30.5	525	82.1	73.36
	2	10	370	8.45	4.55	3.1	3.5	2.7	5.12	7.6	0.27	5.2	1.5	3.92
	3	50	370	7.25	5.50	3.4	3.4	3.3	5.11	5.6	0.81	18.4	2.8	6.70
	4	30	370	7.30	4.45	3.3	2.7	3.8	4.28	9.3	2.4	110	11.3	26.63
	5	60	370	5.90	5.50	2.1	2.2	2.0	4.63	4.8	1.6	6.6	1.6	5.91
8	1	5	330	7.10	4.80	3.2	3.2	3.2	4.85	5.0	0.7	43.7	1.9	3.13
	2	90	330	7.40	5.25	2.9	3.7	2.0	4.33	4.0	1.8	43.8	4.7	8.55
	3	45	330	6.00	5.00	3.4	3.8	3.0	4.44	5.9	2.2	86.2	5.9	18.20
	4	10	330	8.50	4.55	3.1	3.9	2.3	4.68	4.1	0.81	40.4	3.5	8.47
	5	75	330	6.25	3.10	2.9	2.9	2.9	4.26	26.1	7.9	204	47.3	49.61

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Site No.	Rep.	% Cover	Elev. (m)	Air (°C)	Soil (°C)	Windspeed ($m\ s^{-1}$) Annual	Spring	Summer	pH	N (ppm)	P (ppm)	K (ppm)	Na (ppm)	% Organic Matter
9	1	55	320	6.35	5.75	3.4	3.2	3.5	3.76	5.5	0.9	22.6	2.8	5.78
	2	10	320	6.25	6.25	3.2	3.0	3.4	3.96	4.1	1.1	7.5	2.0	2.60
	3	15	320	6.25	5.25	4.0	4.3	3.6	3.81	3.8	1.3	44.6	3.5	9.57
	4	10	320	6.65	5.45	3.4	3.7	3.1	3.95	3.3	1.2	4.9	1.6	2.90
	5	5	320	5.45	5.00	3.5	3.5	3.4	3.95	3.8	0.9	5.0	1.5	1.84
10	1	30	310	7.00	5.70	3.4	3.3	3.5	4.22	3.2	1.2	8.0	1.2	2.21
	2	45	310	8.35	3.20	2.8	2.9	2.7	4.25	3.3	0.7	25.9	1.6	4.90
	3	25	310	8.20	5.30	3.3	3.1	3.5	3.90	5.1	0.9	43.1	2.7	8.31
	4	5	310	8.35	7.25	3.9	4.3	3.4	3.90	9.2	0.7	28.6	2.8	8.29
	5	80	310	8.30	5.70	4.1	5.0	3.1	4.14	3.8	0.8	8.2	1.4	3.49

* Windspeed: Annual = the first day of spring and last day of summer
Spring = 23 April - 21 May
Summer = 22 May - 9 Sept.