AN INVESTIGATION OF ENVIRONMENTAL PARAMETERS INFLUENCING THE DISTRIBUTION OF Platanthera blephariglottis (WILLDENOW) LINDLEY AND P. clavellata (MICHAUX) LUER (ORCHIDACEAE) IN PEATLANDS, AND SOME ASPECTS OF THEIR POPULATION DYNAMICS

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An Investigation of Environmental Parameters Influencing the Distribution of *Platanthera blephariglottis* (Willdenow) Lindley and *P. clavellata* (Michaux) Luer (Orchidaceae) in Peatlands, and Some Aspects of Their Population Dynamics

by

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A Thesis Submitted to the School of Graduate Studies in

Partial Fulfilment of the Requirements for the Degree

of Master of Science

Department of Biology

Memorial University of Newfoundland

September 1995

St.John's Newfoundland Canada

ISBN 0-612-13880-1

ABSTRACT

Populations of two terrestrial species of orchids, *P. blephariglottis* and *P. clavellata*, were investigated for two field seasons (1991-1992) to observe population dynamics and to explore what environmental factors (peat constituents, water pH and water level, endophytic fungi) may influence their distribution within a peatland. The dynamics of the populations were similar to each other and to that observed for other North American and European orchid species. Both populations increased in plant numbers, while showing a marked decline in flowering percentages in 1992. The populations, while having a net gain of individuals, also lost individuals, but it was not determined if these plants had died or returned to a subterranean stage. *P. blephariglottis* did not set any capsules, and capsule set was very low for *P. clavellata* due to a late frost at the time of flowering in both years.

Peat constituent values associated with *P. blephariglottis* and *P. clavellata* were, for the most part, not significantly different, although the values associated with *P. clavellata* tended to be higher and to have a greater range than those associated with *P. blephariglottis*. Water level values were significantly different between species, suggesting that it is on this basis that these species partition the habitat. This is similar to the results of Boland and Scott (1992) for other peatland orchids. The relationship of water level and crown depth implies that *P. clavellata* can spend a significant period of time, when actively growing and flowering, with the crown submerged.

Two mycorrhizal fungi were isolated and found to be associated with both species, suggesting that the fungi do not play a role in the distribution of these species.

ACKNOWLEDGEMENTS

I would like to acknowledge the encouragement and advice given by my supervisor and friend, Dr. Peter J. Scott, without whom this project would never have been undertaken. Drs. M. Colbo and A. Bal of my supervisory committee have also contributed much in the way of useful criticisms and suggestions.

I would like to thank Dr. Doyle Wells, Canadian Forestry Service, for his assistance in classifying the peatlands, advice on peat sampling, and allowing the use of photographs and a previously published figure.

I wish to acknowledge the advice on peat sampling and preparation given by Mr. Bruce Roberts, Canadian Forestry Service, and the assistance with peat sample preparation given by Mrs. Sandra Morgan, Canadian Forest Service. Many thanks to the Chemical and Physical Analysis Laboratory staff who carried out the peat sample analysis.

I wish to thank Dr. Keith Egger for his assistance and advice on isolating endophytic fungi, Mrs. Cathy Antle, Mrs. Marilyn Collins and Ms Debbie Bruce for help with media preparation and Dr. R. Currah at the University of Alberta for identifying the isolates.

I would like to thank Dr. Dave Schneider for his endless patience and advice on statistical analyses. In addition, I wish to thank Drs. Luise Hermanutz and Dave Innis for their useful criticisms and advice on statistical analyses.

I would like to thank my husband Derek Brown, whose willingness to undertake everything required to make a household function allowed me time to undertake this project.

Many thanks to my children, Audrey and Alison, for asking Dad when Mom was busy with her" homework".

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1. INTRODUCTION

1.1 The Orchidaceae

The Orchidaceae is considered to be one of the largest and most diverse groups of plants, comprising 7-10% of all angiosperms, about 20,000-25,000 species. There are both terrestrial and epiphytic species. The greatest diversity of species occurs in the tropical and subtropical regions of the world where hundreds of genera and thousands of species are found, most of them epiphytic. The estimate of terrestrial species is between 4,000 and 6,000 and these are most common in subtropical and temperate regions. North America has approximately 26 genera and 153 species (Dressler, 1981). Newfoundland has 13 genera and 35 species, 2 are saprophytic (Scott, 1985).

Members of the Orchidaceae are best known for their flowers, which range from exquisitely beautiful to extremely bizarre, and for this reason they have long been sought by collectors and horticulturalists. The flowers have inspired many studies on pollination and related areas (Darwin, 1877; van der Pijl and Dodson, 1966; Thien, 1969), while the desire to propagate the plants has stimulated much research on the germination of seedlings (Arditti, 1967, 1968; Blowers and Arditti, 1970; Harvais, 1972, 1973; Warcup, 1973; Arditti *et al.*, 1981; Rassmussen *et al.*, 1990).

The terrestrial orchids of north temperate regions generally possess smaller, less conspicuous flowers and therefore have not been the focus of as much study as tropical and subtropical orchids, until recently. The majority of these studies has focused on reproductive ecology (Ackerman, 1981; Catling, 1983b; Cole and Firmage, 1984; Gregg, 1991), seed germination requirements and embryological development (Harvais, 1973; Warcup, 1973; Wilkinson *et al.*, 1989; Fredrikson, 1991), and mycorrhizae isolation and identification (Filipello *et al.*, 1985; Currah, 1987; Currah *et al.* 1987,1989; Ramsey *et al.*, 1989; Peterson and Currah, 1990). There have been very few long-term population studies (Curtis and Greene, 1953; Wells, 1967; Tamm, 1972a; Calvo, 1990a; Primack and Hall, 1990) and very little is known about the ecology of northern terrestrial orchids (Correll, 1950; Luer, 1975; Boland and Scott, 1992).

After seed germination, terrestrial orchids form a subterranean protocorm (mycorrhizome), which will be replaced by a perennating organ, either a tuber or rhizome , depending on the growth habit of the species. The perennating organ will give rise to the first leaf and eventually an inflorescence (Wells, 1967; Light and MacConaill, 1991). The time spent from germination through these stages of development varies considerably from species to species. The time elapsed between germination and emergence of the first leaf can be as short as 2 years or as long as 10 or more years. More time elapses before an inflorescence is produced, and again considerable variation exists between species. Various species may spend from 3 to 13 years in an aboveground vegetative state before flowering (Wells, 1981).

Little is known of the subterranean stages of development for North American terrestrial orchids, since many of the procedures for making these observations are destructive. Most studies have been limited to common or alien species (Light and MacConaill, 1991; Whigham and O'Neill, 1991). The difficult nature of making these observations has limited the information available even for species that have been studied extensively (Wells, 1967; Tamm, 1972a).

Orchids, like most vascular and nonvascular plants, form mutualistic associations with fungi. In orchids, this association is formed with the embryo during seed germination and, as the name mycorrhiza (from the Greek for "fungus" and "root") implies, with the absorptive structures of mature and developing plants (Blowers and Arditti, 1970). This mycorrhizal association is required for the successful development of both epiphytic and terrestrial orchid species (Hadley, 1982; Currah *et al.*, 1989).

Fungi that form mycorrhizal associations with absorptive structures are, for the most part, designated as ectomycorrhizae or endomycorrhizae. Ectomycorrhizae form a sheath around the absorptive structure with hyphae penetrating between cortical cells but not within them. Endomycorrhizae do not form a sheath and the hyphae penetrate the cells of the absorptive structure. Both associations are considered to be mutualistic; with the host providing carbon compounds to the fungus and the fungus enhancing phosphorus and nitrogen uptake by the host (Smith, 1967,1974; Purves and Hadley, 1975).

The endomycorrhizae can be subdivided into several groups: the vesicular-arbuscular mycorrhizae, ericoid mycorrhizae and orchidaceous mycorrhizae. The fungi forming orchidaceous mycorrhizae come from widely different taxonomic groups and the way in which they function is considered to be quite different in that, unlike other mycorrhizae, the carbon flow is from the fungus to the plant (Smith, 1967, 1974). The fungal hyphae enter the cortical cells of orchid roots where they begin to coil and produce lateral branches, and eventually form a complex network called a peloton. The orchid cells react to the presence of the fungus by producing enzymes.The digestion of the peloton by these enzymes is thought to provide the orchid with nutrients (Cooke, 1977; Arditti, 1979). Other studies have indicated that the living fungus is capable of providing the orchid with vitamins and may in fact be of greater importance than nutrients derived from digestion (Harvais and Pekkala, 1975).

It is this mycorrhizal association that allows terrestrial orchids to obtain nutrients during the protocorm stage and at times when mature plants revert to a subterranean stage. Mature plants have been known to be 'absent' in a particular growing season and to re-emerge in a subsequent year (Wells, 1967; Tamm, 1972a; Calvo, 1990a; Light and MacConaill, 1991; Whigham and O'Neill, 1991). The number of years a plant can be 'absent' and still have the ability to re-emerge is unknown for most species. Wells (1967) suggests that for *Spiranthes spiralis* an absence of 2 or more years may indicate the death of the individual, while Light and MacConaill observed the emergence of an individual of *Epipactis helleborine* after a 3 year absence. It is suggested by Light and MacConaill (1991) and Calvo (1990a) that the

mycorrhizae are capable of providing the 'absent' plants with enough nutrients to allow flowering immediately following re-emergence.

Terrestrial orchids tend to be fairly long-lived and populations consist of many age classes of individuals (Wells, 1967,1981; Tamm, 1972a; Wells and Cox, 1991). The ability to age an individual varies with the type of perennating organ. The species that form a persistant rhizome can provide some information as to the age of the individual after excavation and observation of the yearly growth (Kull and Kull, 1991). The species that form tubers may replace the vegetative growth every year. In such instances excavation of the tubers would not provide any information concerning the age of individuals. Long term observations of the population would be the only means of obtaining accurate information pertaining to the age of individuals. Since some species replace all the vegetative structures each year, age of the individuals may not be of any relevance to the population as a whole (Wells, 1981; Willems and Bik, 1991).

Species that have tubers, produce a perennating bud and a shoot primordia below soil level at the crown. The crown being the point at which the shoot, tubers and roots originate. New tubers and roots grow alongside the old roots and tubers until a change in conditions causes the plant to die back below ground. The following growing season, the old tubers and roots have degenerated leaving only the new tubers and roots. The leaf shoot and inflorescence is produced from the primordia formed the previous season.

1.2 The Genus *Platanthera*

Platanthera is distinguished by an unusually wide anther. All members of the genus are terrestrial and are distributed in north and south temperate regions. Luer (1975) estimates that there are about two hundred species. There are twelve species on the Island of Newfoundland (Scott, 1985). The plants of this genus have an erect stem with basal or cauline leaves, elongate fusiform or somewhat palmate tuberoids, slender roots, and a raceme of small to medium flowers. The flowers are usually resupinate (the ovary twists 180° during development to invert the flower). The tepals are free and the dorsal sepal, along with the petals, forms a hood over a central structure, known as the column, formed by the fusion of stamens, style and other tissue. The lip or labellum can be entire, divided, or fringed with a spur at the base while the lateral petals are spreading or recurved. The anther is found on the column and is composed of two anther cells or locules. Within each anther cell is found the pollinium (sometimes two pollinia), a more or less compact and coherent aggregation of pollen grains. Attached to each pollinium is a stalk-like structure, the caudicle, which has a sticky pad, the viscidium. All the pollinia and associated parts of an anther are known as the pollinarium (Dressler, 1981). The anther cells are separated by connective tissue or the stigma. In most species of *Platanthera* the pollinia are removed when the viscidium becomes attached to a visiting insect. It is then carried away and deposited as a discreet package on the stigma of another flower (Luer, 1975). In some self-pollinating species, the pollinia are

incoherent and the pollen grains fall in loosely attached groups onto the stigmatic surface (Catling, 1983a).

1.3 *Platanthera blephariglottis*

1.3.1 Morphology

Platanthera blephariglottis (Willdenow) Lindley var. *blephariglottis*, the white fringed orchid, is one of the larger white-flowered species of this genus found on the island of Newfoundland. It is recognized by the deeply-fringed lip, hence the name *blephariglottis*, from the Greek, meaning "eyebrow-tongued" (Correll, 1950) (Figure 1). This species has basal and cauline leaves. The plants are erect, stout and glabrous, with green, lanceolate, keeled leaves that sheath the stem below, and are much reduced above. All flowering plants examined in this study had two basal leaves while non-flowering specimens, for the most part, had one. The below ground structures consist of 3-4 slender roots extending horizontally from the crown and one fusiform tuber growing more or less vertically. Developing roots and tuber for following seasons growth may also be present (Figure 2).

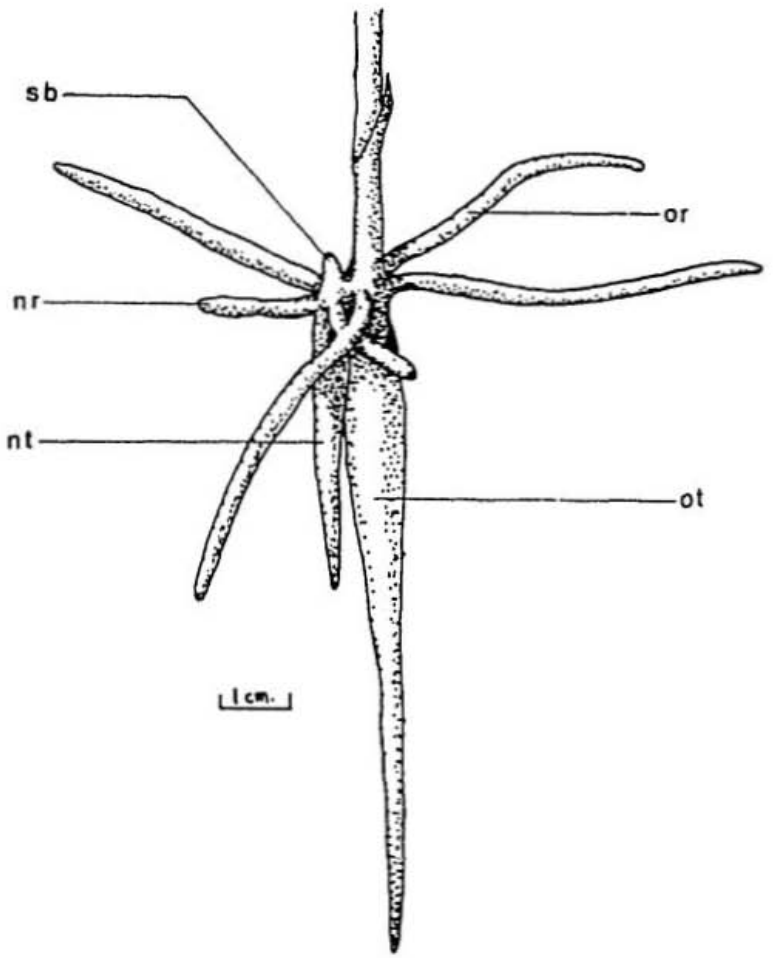
Cole and Firmage (1984) describe the flower colour as ranging from white to cream, Correll (1950) as white often tinged with cream and Luer (1975) as pure soft white. Although no pollinators were observed, the white colour, presence of fragrance and nectar, and lack of nectar guides and ultraviolet reflective patterns suggest a moth pollinated flower (Faegri and van der Pijl, 1971). Smith and Snow (1976) concluded from pollinator observations in

Figure 1. Photograph of an infloresence of *P. blephariglottis* by Doyle Wells.

Figure 2. Diagram of the below ground structures of *P. blephariglottis** and *P. clavellata**

ot - old tuber
or - old root
nt - new tuber
nr - new root
sb - shoot bud

*note: scale given for *P. blephariglottis*, scale for *P. clavellata* would be approximately ⅔ of scale shown


sb
or
nr
nt
ot
1 cm.

Michigan that these are primarily moth-pollinated flowers. with butterflies playing a minor role in pollination. They made their observations on a population of *P. blephariglottis* that coexisted with a population of *P. ciliaris*. Cole and Firmage (1984) observed a population in Maine that was not mixed with *P. ciliaris* and came to the conclusion that butterflies were the major pollinators and moths the minor pollinators. Catling (1984) also states that butterflies appear to be the main pollinators with dayflying sphinx moths playing a lesser role in the pollination of this species. In this study no pollinators were observed during 1991 or 1992, but it should be noted that very little field work coincided with peak flowering period and that early frost damage occurred during flowering in 1991 and before flowering in 1992.

1.3.2 Distribution and Habitat

P. blephariglottis is found along the Atlantic seaboard from Newfoundland to Florida. This species, which ranges over an area that has a great deal of geographical and ecological variation, has been segregated into two varieties. Variety *conspicua* is the larger southern form with larger flowers, a more open raceme, and a longer spur. The range of this variety is from Florida north to the southern half of New Jersey and west from Florida to the southeastern corner of Texas (Luer, 1975).

Variety *blephariglottis* is the typical northern form with smaller flowers, a less open raceme, and a shorter spur (Correll, 1950; Luer, 1975). The range of variety *blephariglottis* extends from Newfoundland south to the northern half of Pennsylvania and New Jersey and

west to Michigan, with an isolated population in Illinois (Luer, 1975). While Luer (1975) and Petrie (1981) include the Illinois population, Sheviack (1974) suggests that this population may be extinct.

This species has been reported throughout the island of Newfoundland with the exception of the Great Northern Peninsula (Scott, 1985). The typical habitat of *P. blephariglottis* is a *Sphagnum* or sedge bog (Luer, 1975). The blooming period is from mid-July to early August on the Avalon Peninsula. The summers of 1991 and 1992 were cold with frost in early August 1991 and late July 1992. In both years the first blooms did not open until early August. In the year previous to this study, the first blooms were open during the third week of July. The inflorescence is indeterminate and the flowers continue to open over a two week period.

1.4 *Platanthera clavellata*

1.4.1 Morphology

Platanthera clavellata (Michaux) Luer, the little club-spur orchid or the small green wood orchid, is one of the least conspicuous orchids found on the island of Newfoundland. It is recognized by the swollen tip of the spur, which gives it a club-like appearance. The name *clavellata* is from the Latin meaning "small club" (Figure 3). These plants are usually small, erect, glabrous, with one or sometimes two green, oblanceolate, keeled leaves sheathing the stem approximately midway up. This characteristic positioning of the leaf was

Figure 3. Photograph of an inflorescence of *P. clavellata* by Doyle Wells.

not evident at the study sites, since the junction of the leaf and stem was often below the surface of the *Sphagnum*. The leaves form bracts on the upper portion of the stem. All plants in this study had only one leaf. The below ground structures consist of 3-4 slender roots and a fusiform tuber as well as buds or partially developed roots and tuber that will give rise to the next season's leaves and inflorescence (Figure 2).

The flower colour ranges from pale green or pale yellow to yellow-green to greenish white or cream (Correll, 1950; Luer, 1975; Petrie, 1981). Plants growing in open, sunny areas produce whiter flowers while those growing in more shaded areas tend to be greener. While the flowers are considered to be resupinate, they are not rotated a full 180° and this gives the raceme a dishevelled appearance. Unlike *P. blephariglottis, P. clavellata* does not require a pollinator, although insects have been observed removing pollinia (Luer, 1975). The pollinia are incoherent, allowing clumps of pollen grains to fall onto the stigma, resulting in self-pollination (Catling, 1984).

1.4.2 Distribution and Habitat

The range of *P. clavellata* in North America extends from Newfoundland to northern Florida. The range of this species extends farther west than *P. blephariglottis*, to Ontario and Minnesota in the north and to Texas in the south. As is typical of most species with an extensive north-south distribution, plant size is considerably larger to the south (Correll, 1950). Some authors (Catling, 1983a) recognize a southern variety, *clavellata*, and a northern

variety, *ophioglossoides*, with the latter being the form commonly found north of Virginia. Other authors (Correll, 1950; Luer, 1975) do not make this distinction.

This species is found throughout the island of Newfoundland with the exception of the Great Northern Peninsula (Luer, 1975). The habitat of this species is more varied than that of *P. blephariglottis*. *P. clavellata* can be found in swampy forest, in water, or at the edge of water along rivers and streams, wet meadows, or open *Sphagnum* bogs (Correll, 1950; Luer, 1975; Scott, 1985). Plants in this study were growing in an open *Sphagnum* bog, or a fen that was inundated with flowing water at certain times of the year.

The blooming period of this species, on the Avalon Peninsula, is from mid-July to early August. The summers of 1991 and 1992 were cold with frost in early August 1991 and late July 1992. In both years the first blooms did not open until the first week in August, while in the year previous to this study the first blooms opened during the third week in July. The inflorescence is indeterminate and the flowers continued to open over a two week period in all of the study sites.

1.5 Peatlands Types of the Avalon Peninsula

Both *P. blephariglottis* and *P. clavellata* are peatland species. While in this study these species are observed on slope bogs and a slope fen, they have been observed on various types of peatlands. *P. blephariglottis* has been observed on sphagnum and sedge bogs

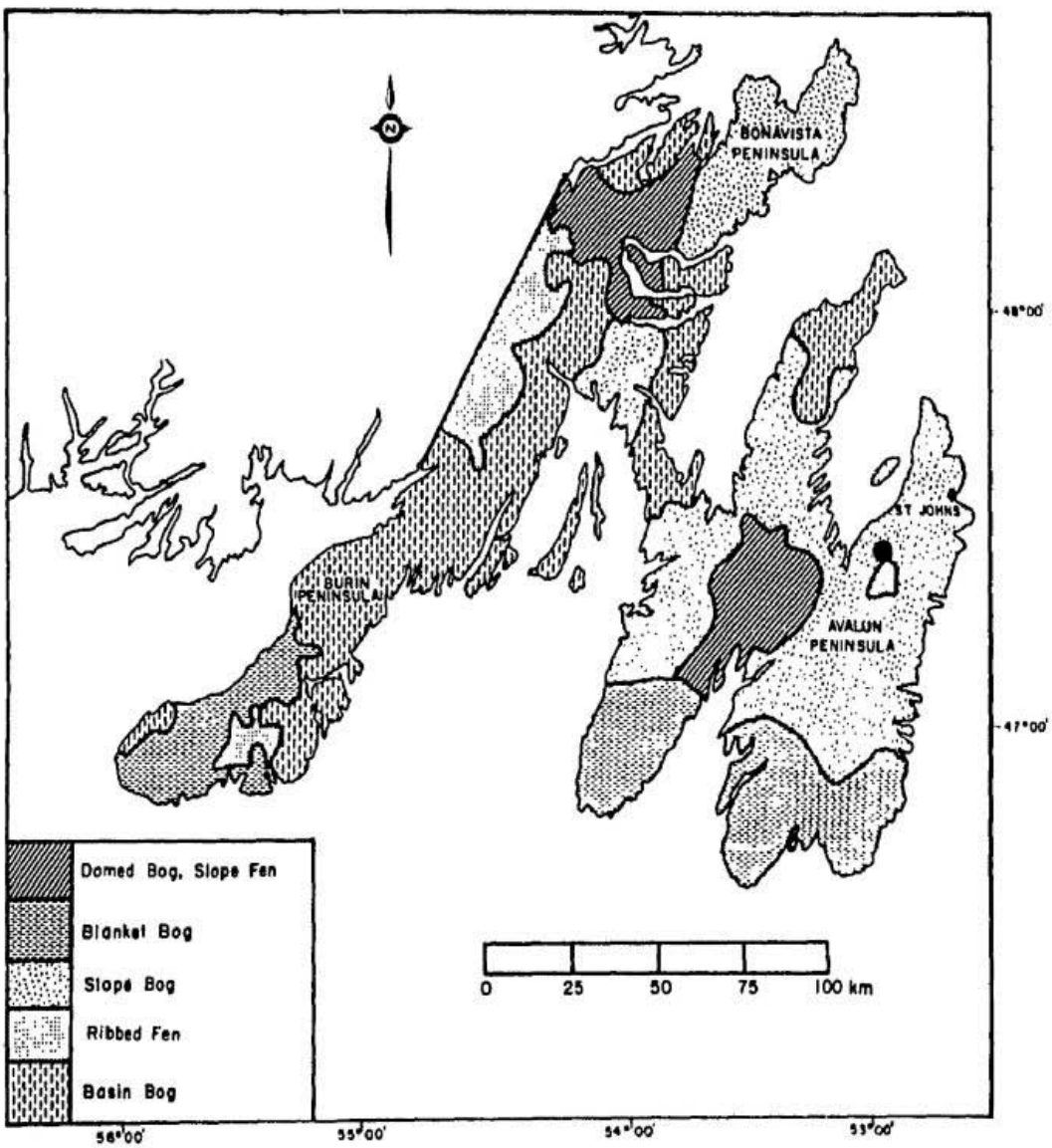
(Correll, 1950), quaking bogs (Luer, 1975), slope bogs (Wells, 1980), plateau bogs (Damman and Dowhan, 1981) and raised bogs and fens (Glaser, 1992), while the peatland types where *P. clavellata* has been observed range from sphagnum bog (Correll, 1950) to swampy forest (Luer, 1975) to fen (Wells,1980; Damman and Dowhan, 1981).

Six morphological types of peatland have been described by Wells (1980) for the Avalon Peninsula: domed bog, blanket bog, slope bog, basin bog, slope fen, and ribbed fen (Figure 4). While all six peatland types have distinctive characteristics, they all have wetter and drier areas and more nutrient-rich and less nutrient-rich areas contained within their boundaries (Wells, 1980; Glaser, 1992). It is in the wetter and more nutrient rich areas that *P. blephariglottis*, *P. clavellata* and other *Platanthera* species are usually found (Glaser, 1992).

The stratigraphy of all four types of bogs shows a fen-to-bog successional pattern. The bottom peat layers consist of sedge remains and the amount of sedge material present decreases towards the upper strata while the amount of *Sphagnum* peat increases. This transition from sedge peat to *Sphagnum* peat indicates a change in the availability of nutrients. *Sphagnum* peat replaces sedge peat as nutrient abundance decreases (Wells, 1980).

The nutrient content of peatlands is affected by water movement, geology, and the composition of the peat. Although all peatlands are considered to be nutrient-poor, fens are

Figure 4. Distribution of six morphological peatland types on the Avalon Peninsula (modified from Wells, 1980) (● - study sites).


N
BONAVISTA PENINSULA
BURIN PENINSULA
AVALON PENINSULA
ST JOHN'S
48°00'
47°00'
Domed Bog, Slope Fen
Blanket Bog
Slope Bog
Ribbed Fen
Basin Bog
0 25 50 75 100 km
56°00'
55°00'
54°00'
53°00'

considered to be more nutrient-rich than bogs, with the difference between the two being small (Wells, 1980; Damman and Dowhan, 1981). Subsurface water and seepage waters from surrounding areas carry nutrients to the fen, increasing the pH and the abundance of nutrients such as nitrogen, phosphorus, potassium, calcium, magnesium and iron, and causing a faster rate of decomposition of plant material. Bogs tend to be stagnant, with the influence of seepage water restricted to the outer edges. The greater part of the water entering a bog is due to precipitation. Little water movement results in low nutrient content, low pH, and a slow rate of decomposition (Wells, 1980).

The only peatland types present in the study area were slope bogs and slope fens (Figure 4). During this study both *P. blephariglottis* and *P. clavellata* were observed on slope bogs. These bogs are treeless and shallow, rarely exceeding 2 m in depth. They are usually found in forested regions on poorly-drained slopes with a gradient between 5% and 15% or in areas of high precipitation and frequent fog. Pools are uncommon on this type of bog.

Platanthera clavellata was also observed on a slope fen, which was inundated with water at particular times of the year. These fens, which are common in forested areas, are treeless and rarely exceed 1.5 m in depth. The slope is between 5% and 15%. Shallow pools and small streams are often present. An increase in *Sphagnum* in the upper strata suggests that these fens may be in transition from fen to bog. A slope fen can be distinguished from a ribbed fen by the absence of the pools oriented at right angles to the slope which are

characteristic of ribbed fens. While pools are present in slope fens they are not arranged in a 'ribbed' pattern and they do not occupy as much area of the fen as they do in ribbed fens. Pools can cover as much as 40% of the surface of a ribbed fen (Wells, 1980).

1.6 Research Objectives

As seen from the previous review, *P. blephariglottis* and *P. clavellata* are both known to be peatland orchids and their geographical distribution is well documented. On the other hand, little is known about their specific habitat requirements or population dynamics. Observation of their microdistribution within a peatland and their population dynamics would provide information allowing comparisons with published data on other terrestrial orchid species.

Closely-related species partition their habitat along various environmental gradients: nutrient content of the substrate, moisture content of the substrate or depth of substrate (Werner and Platt, 1976; Cody, 1978; Silvertown, 1983; Russell *et al.*, 1985; Tilman and Wedin, 1991). A species will be present where the habitat fullfills the nutritional and physical needs of the indvidual (Russell *et al.*, 1985).

Within a peatland, *P. blephariglottis* and *P. clavellata* may be observed growing side by side, yet clumped in what appeared to be distinct areas with little overlap. They may also be found in separate areas some distance apart on the same or different peatlands. Casual

observations of the habitat in which these species are found would suggest a common microhabitat. This could be the result of the species being equally adapted to the same microhabitat. Another possibility could be that slight variations in some factors of the environment are producing a continuum of a number of different micohabitats that are not easily distinguishable (Sanford, 1974). Information pertaining to niche requirements and how they differ may provide some insight into the variability of habitat parameters for these locally-abundant species as well as what parameters may have the greatest influence on less common species of orchids.

The specific objectives of this study were:

1) to observe populations of these two species over two field seasons to elucidate short term changes within and between habitats;
2) to measure a number of environmental parameters (peat constituents, peat pH, water pH and water level) within habitats supporting populations of *P. blephariglottis* and *P. clavellata* to elucidate some of the parameters for both species that may define their niche.

2. MATERIALS AND METHODS

2.1 Site Selection and Description

Four sites were originally selected; site 1 with *P. blephariglottis* only , site 2 with *P. clavellata* only, and sites 4 and 5 with both. An additional site, site 3 with *P. clavellata* only, was known to be a fen (Wells, 1980), and therefore a more nutrient-rich site, and was included to sample a broader range of peat nutrients. All sites are located along a 3km length of the Trans-Canada Highway, between 1.9 km and 5 km west of the junction of Route 61 and the Trans-Canada Highway, near St. John's, Newfoundland (Figures 5 & 6).

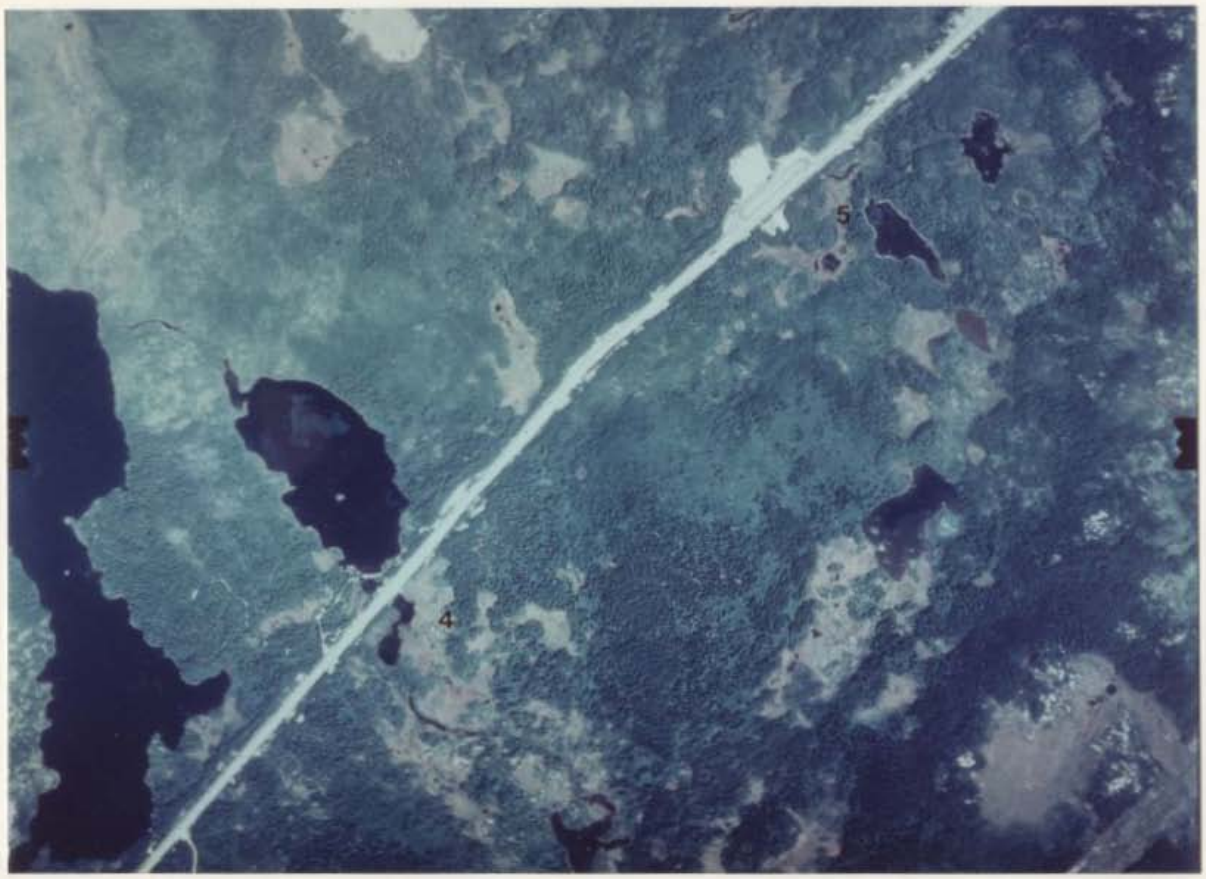
Site 1 (47°25'19.6"N, 53°00'12.1"W) contains only *P. blephariglottis*, covers an area of approximately 225 square metres and is located along the northwest edge of a slope bog. The site is located at the base of an incline (37.5%) in a slightly minerotropic zone (Wells, 1980). The area is dominated by sedges and *Sphagnum* spp. with low shrubs interspersed (Appendix A). A treed zone, dominated by black spruce (*Picea mariana*), bounds site 1 to the northwest and the southeast. A slight incline, dominated by *Cladonia* spp. and low shrubs, lies to the southwest, and an open bog lies to the northeast.

Site 2 (47°25'16.3"N, 53°00'20.6"W) contains only *P. clavellata*, covers an area of

Figure 5. Aerial photograph of sites 1,2 and 3 (Department of Mines and Energy) (road is the Trans-Canada Highway)


82020-149
3
1
2

Figure 6. Aerial photograph of sites 4 and 5 (Department of Mines and Energy) (road is the Trans-Canada Highway)


5
4

approximately 10 square metres and is located within a slightly minerotropic area (Wells, 1980) of a slope bog. The slope of the bog is from southwest to northeast. A treed area dominated by birch (*Betula papyrifera*) bounds site 2 to the southeast and there are large boulders to the northwest. Open bog lies to the northeast and the southwest. The site is dominated by sedge (Appendix A) and *Sphagnum* spp.

Site 3 (47°25'22.8"N, 53°00'14.5"W) contains only *P. clavellata*, covers an area of approximately 200 square metres and is located within a ribbed fen (Wells, 1980) that lies on the northwest edge of a slope bog. A treed area dominated by black spruce (*Picea mariana*) bounds site 3 to the northwest. A river, within the black spruce forest, runs parallel to the fen and after heavy rain overflows into the fen itself. Open fen lies to the northeast and the southwest and open bog to the southeast. The site is dominated by sedges, with low shrubs and larch (*Larix laricina*) interspersed (Appendix A).

Site 4 (47°25'48.9"N, 52°59'24.9"W) contains both *P. blephariglottis* and *P. clavellata*, covers an area of approximately 126 square metres and is located within a slightly minerotropic zone (Wells, 1980) of a slope bog. The slope of the bog runs from east to west. A treed area dominated by black spruce (*Picea mariana*) bounds site 4 to the north, east and south. Open bog lies to the southwest. The site is dominated by sedges (Appendix A) and *Sphagnum* spp. with low shrubs interspersed.

Site 5 (47°26'20.7"N, 52°58'20.8"W) contains both *P. blepharigiottis* and *P. clavellata*, covers an area of approximately 24 square metres and is located within a slightly minerotropic zone (Wells, 1980) of a slope bog. The slope of the bog runs from south to north. A treed zone dominated by black spruce (*P. mariana*) bounds site 5 to the east and the west. Open bog lies to the north and south. The site is dominated by sedges (Appendix A) and *Sphagnum* spp.

2.2 Plant and Flower Sampling

To establish the density and distribution of each species alone and in the presence of the other species, transects were established in each site using pieces of 12 mm deformed steel reinforcing bars (rebar). The individuals of both species tended to occupy small areas of the peatlands and therefore the transects were not placed randomly but established to sample the largest number of individuals. The length of the transect was dependent on plant density and distribution. In sites 3 and 4 the transects were discontinued when the distance to the next individual became too great (2 m or more) or when continuing the transect would only include one or two more individuals. In sites 1, 2 and 5 the transects ended at physical barriers such as rocks or trees.

One transect was laid in each of the study sites, with the exception of site 1 where two transects were laid. In this site, transect 1a was laid through the area with the greatest density of individuals of *P. blepharigiottis* and transect 1b was placed at right angles to pass through

transect 1a and out into the open bog where no individuals were present. Transect 1a intersects transect 1b at 5.5m and transect 1b intersects transect 1a at 9m. Transect 1a ran approximately south to north for 15m. (Orientation of all transects was in relationship to true north.) Transect 1b ran approximately west to east for 15m. The purpose of transect 1b was to compare environmental parameters in the presence and absence of individuals. This was not possible in the other sites due to the small area, physical obstructions or lack of a distinct area where the species were not present. Only one transect was established in each of sites 2 to 5.

Transect 2 was established in site 2, where it ran approximately south to north for 5m, with meter 0 to the south. Transect 3 was established in site 3 where it ran approximately north to south for 10m, with meter 0 to the north. Transect 4 ran approximately east to west for 21m, with meter 0 to the east, and was established in site 4. Transect 5 was established in site 5, where it ran approximately south to north for 12m, with meter 0 to the south.

In order to record the contours of each transect, elevation measurements were taken by running a string along the length of the transect. A line level was used to determine if the string was level and measurements from the string to the surface of the peat were taken at each meter.

A metre wide strip was established and divided into metre squares along the side of the transect with the greatest number of individuals. In each square metre all plants were

counted and recorded as flowering or non-flowering. The nearest flowering individual and non-flowering individual to the metre marks were permanently tagged with a galvanized steel stake placed on the side away from the transect line. Each stake was numbered using Dymo tape.

In order to determine if the individuals sampled fell within the North American size range and to determine intraspecific size differences, the following measurements were recorded for individuals permanently tagged: height, stem diameter, leaf length and width, number of flowers and number of capsules. Measurements were recorded to the nearest 0.1cm, with the exception of stem diameter (to the nearest 0.1mm, with calipers) when the majority of individuals in all sites had the first flower open in 1991 and 1992. The size range of each vegetative and floral characteristic for each species was determined as the mean plus or minus one standard deviation. Measurements to the nearest individual (nearest neighbour) of the same species and the other species were also taken to the nearest 0.5 cm at this time. The measurements of distances between individual plants were taken to determine how the species were distributed in relation to one another when both species were present.

In order to increase sample size of the permanently tagged individuals, a permanent metre square quadrat for each species was placed within each study site, with the exception of site 2, where all individuals were measured along the transect. Each quadrat was established to include only one species. All plants were permanently tagged and numbered

following the same procedure as for tagged individuals along the transects. Each plant was recorded as flowering or non-flowering and the same measurements as were taken for individuals along the transect were recorded during 1991 and 1992. Individuals not present in 1991, were noted in 1992.

To determine intraspecific site differences in flower size, the lowermost flower of the inflorescence was collected from each of twenty-five individuals of each species present in the site in 1991. Flowers were one day post-anthesis. For *P. blephariglottis*, sepals, petals and lip were measured to the nearest 0.1mm using an eyepiece micrometer, while ovary and spur length (Figure 7) were measured to the nearest 1.0mm using a ruler and dissecting microscope. Because of the small size of the flowers of *P. clavellata* measurements of natural flower spread and flower depth (Figure 8) were taken in place of measurements of sepals and petals. For *P. clavellata*, natural flower spread and flower depth were measured to the nearest 0.1mm with an eyepiece micrometer. Ovary and spur length were measured to the nearest 1.0mm with a ruler and dissecting microscope. Flowers were not sampled from permanently-tagged individuals.

In order to determine the relationship between water level and depth of crown, the depth of crown was measured to the nearest 0.5cm for twelve individuals of each species from site 4 in 1992. Site 4 was chosen since both species were present and the measurements could be taken with minimal disturbance of the plants. Although both species were present in site 5, the peat was much more densely packed than in site 4, and measurements of crown depth would have entailed total excavation of the plants.

Figure 7. Flower stucture of *P. blephariglottis*

ds - dorsal sepal
ls - lateral sepal
l - lip
lp - lateral petal
s - spur

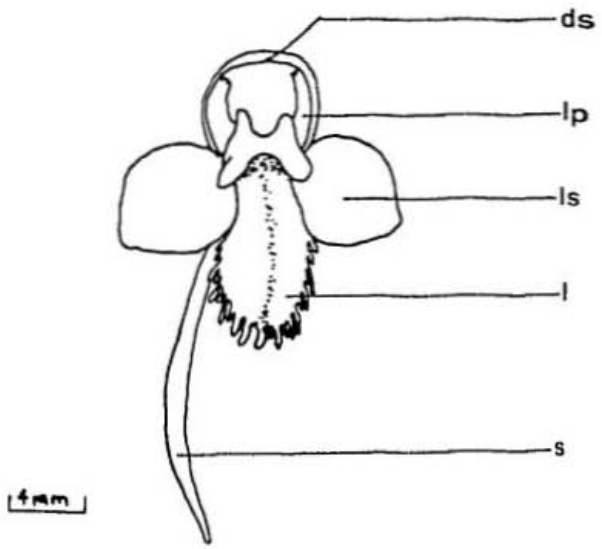
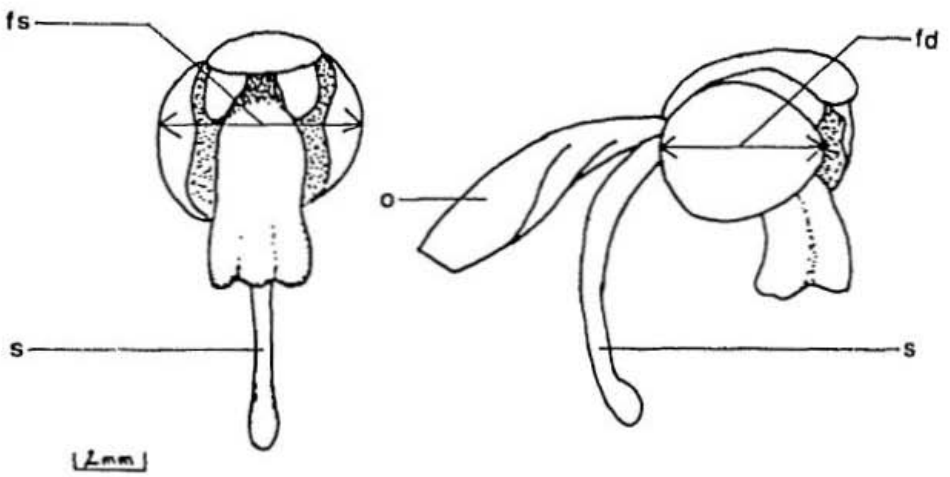

ds
lp
ls
l
s
4mm

Figure 8. Flower structure of *P. clavellata*

fs - flower spread
fd - flower depth
s - spur
o - ovary


fs
fd
o
s
s
1mm

2.3 pH and Water Level Sampling

To observe variation in water level and pH associated with each species, permanent sampling stations were established, either adjacent to the transect or within the transect, without disturbing the plants. Two sampling stations were established in sites 1, 3-5. The size of site 2 only allowed the establishment of one station. Holes were dug until water could be seen seeping into the hole. A 15 cm piece of PVC pipe was placed at the top of each hole so that the pipe extended 3 cm above the surface of the peat. Each pipe had a peat plug placed over the top. The holes were left undisturbed for a week before the first water level reading was taken. If the hole had to be relocated due to disturbance (eg., moose trampling), an adjustment period of a few days was allowed.

PH readings were taken from the standing water in the holes, using a portable pH meter. Water level readings were measured from the top of the pipe to the top of the standing water and adjusted to reflect the distance to the surface of peat. Two readings were taken during each of September and November of 1991 and then approximately monthly from May to September of 1992.

2.4 Peat Sampling and Analyses

In August 1992, peat cores were collected at all sites from areas adjacent to the transects to prevent disturbance of the sampling area. In site 1 six cores were collected along

transect 2. In site 2 three cores were collected along transect 3. The small area of site 2 and the presence of rocks limited the number of peat samples that could be taken. Due to the presence of pools of standing water only three cores were collected in site 3 along transect 3. In site 4 six cores were collected along transect 4, three adjacent to an area with *P. blephariglottis* only and three adjacent to an area with *P. clavellata* only. In site 5 six cores were collected along transect 5 in the same manner as for site 4.

Peat cores approximately 10 cm square were cut using a double-edged serrated knife. The actively growing portion was measured and discarded since nutrients present in the living material was not available for use by the plants being observed. The lower 15 cm was divided into 5 cm samples. Peat below 15 cm was measured and discarded since it was below tuber depth and nutrients present were not considered to be available for use by plants under observation. Samples were collected in plastic bags and labelled. In the laboratory, samples were weighed, placed in cardboard boxes and placed in a drying oven at 40°C. Dried samples were weighed, ground and placed in sealed cardboard containers until nutrient analyses could be completed.

All nutrient analyses of peat samples were carried out by the Chemical and Physical Analysis Laboratory, Forestry Resources Centre, Pleasantville, St. John's following procedures specified in the Methods Manual (Zakrevsky, 1984).

Samples (0.5 g) for total nitrogen and phosphorus determination were digested in concentrated sulphuric acid at 390°C in the presence of potassium sulphate (K_2SO_4) and mercuric oxide (HgO). Levels of nitrogen and phosphorus were measured using a Technicon Auto-analyzer II.

Samples (2.0 g) for total potassium, calcium, magnesium and iron determination were dry-ashed and treated with hydrochloric (HCl) and hydrofluoric (HF) acids. Levels of these metals were measured using an atomic absorption spectrophotometer, Perkin-Elmer Model 403.

Moisture content was determined after drying at 105°C for 16 hours. Organic matter and ash content were determined after ashing at 450°C for 16 hours.

Sample pH was measured using an Orion model 901 digital pH meter after saturating sample (1:1) with calcium chloride solution.

2.5 Isolation of Endophytic Fungi

One plant of each species was collected from site 4 in July, 1991 in order to determine the endophytic fungi associated with *P. blephariglottis* and *P. clavellata.* The procedure follows that used by Currah *et al.* (1989) to isolate endophytic fungi from other North American species of terrestrial orchids (*P. hyperborea, P. obtusata, P. orbiculata* and *Coeloglossum viride*).

The specimens were placed in plastic bags and refrigerated over night. The specimens were then washed free of peat. The roots and tubers of each specimen were cut into 5-6 mm sections using a sterile scalpel and designated as either root or tuber. Each root and tuber was also designated as old (present year) or new. The specimens were then placed in a 20% solution of household bleach for 1 min., followed by 2 rinses of sterile distilled water. The sections were cut into slices (approximately 2 mm thick) and plated on modified Melin-Norkan's agar (MMN), cooled to room temperature (Marx, 1969). Plates were incubated in the dark at 25°C and checked for fungal growth approximately every 48 hrs. Sections of agar with fungal growth were transferred to potato dextrose agar and incubated at 25°C in the dark.

2.6 Statistical Analyses

All data were tested for normality using the Kolmogorov-Smirnov goodness of fit test for a normal distribution (Sokal and Rolf, 1995). Homogeneity of variance was determined using the Levene Median test (Kuo *et al*, 1992). Residuals were observed for data that did not pass the normality test but passed the equal variance test. If the residuals were considered to be normally distributed then a one-way ANOVA or t test were performed (Neter *et al.*, 1983). Data that were not normally distributed were log transformed (Zar, 1984) and again tested for normality. If data passed the normality test after transformation, a one-way ANOVA or t test were performed. If data did not show a normal distribution after

transformation or if data did not show homogeneity of variance, then nonparametric tests were performed, either a Kruskal-Wallis one-way ANOVA on ranks or a Mann-Whitney rank sum test (Zar, 1984). The significance level was determined by dividing 0.05 by the number of variables (Sokal and Rolf, 1995). A Student-Newman-Keuls Test was performed if a significant difference was found (Zar, 1984).

In order to determine any inter-site differences, height, stem diameter, first and second leaf area, bract length, number of flowers, dorsal sepal area, lip area and spur length of *P. blephariglottis* and stem diameter, flower spread, flower depth and bract length of *P.clavellata* were analyzed using one way ANOVA. Lateral sepal area, lateral petal area and ovary length of *P. blephariglottis* and height, leaf area, number of flowers, number of capsules, spur length and ovary length of *P. clavellata* were analyzed using Kruskal-Wallis one way ANOVA on ranks.

Magnesium and phosphorus were analyzed using one way ANOVA to determine if there was any significant difference between sites. Data for nitrogen, potassium, iron, calcium, pH, moisture, organic matter, ash, water level and water pH from all sites were analyzed using a Kruskal-Wallis one way ANOVA on ranks.

Species differences in levels of magnesium, phosphorus, calcium, moisture in peat and water level were analyzed using t test to determine any significant difference. Data for iron, potassium, nitrogen, pH, organic matter, ash, water level and crown depth were analyzed

using the Mann-Whitney rank sum test to determine any significant difference between species.

Data for phosphorus, iron, potassium, nitrogen, peat pH, moisture, organic matter, ash and water pH were analyzed using the t-test to determine any significant difference between sites 4 and 5. Levels of magnesium, calcium in peat and water level from sites 4 and 5 were analyzed using the Mann-Whitney rank sum test to determine any significant difference.

3. RESULTS

3.1 Comparison of the Morphology of *P. blephariglottis* and *P. clavellata* at Study Sites and Representitives of North American Populations

The measurements of morphological characteristics taken from individuals of both species within the study sites and Luer (1975) and Correll (1950) are given for *P. blephariglottis* in Table 1 and for *P. clavellata* Table 2. The measurements given by Correll for *P. blephariglottis* exhibit a far greater range than those given by Luer, as Correll includes the larger variety *conspicua*. Floral number, bract length and dorsal sepal measurements for *P. blephariglottis* and ovary length, leaf length and leaf width measurements for *P. clavellata* taken in this study have ranges falling outside the measurements given by Correll and Luer. The measurments outside the range fall below those given for North American populations.

3.2 Population Dynamics of *P. blephariglottis* and *P. clavellata*

In 1991 and 1992 two populations, one consisting of tagged and untagged individuals of *P. blephariglottis* and the other consisting of tagged and untagged individuals of *P. clavellata*, were observed at five sites (Figures 9-14; Table 3; Appendix B). Site 1 had the

Table 1. Size ranges of morphological characteristics of *P. blephariglottis* at present study sites and those representing continental North America.

Plant Characteristics	Luer (1975)	Correll (1950)	This Study 1991-1992
Plant Height	up to 60cm	60-90cm*	11-21cm*
Leaf Length	up to 20cm	5 to 35cm	5 to 10cm
Leaf Width	up to 3cm	1 to 5cm	1 to 2cm
Stem Diameter	--------	--------	2.6-3.6mm
Flower Number	20 to 30	--------	6 to 16
Floral Bract	15mm	15-25mm	10-18mm
Ovary Length	10-20mm	20mm	15-18.5mm
Lateral Sepal	5-11 x 4-9mm	5-11 x 4-9mm	6.5-7.5 x 5-6mm
Dorsal Sepal	5-8 x 4-6mm	5-10 x 4-8mm	6-7 x 3.7-4.5mm
Petal	3-8 x 1.5-3mm	3-8 x 1-3mm	4.6-5.8 x 1.3-1.7mm
Lip	10 x 6mm	4-13 x 2-4mm	7-9 x 4.2-5.6mm
Spur	15-20mm	15-50mm	16.5-20.5mm

* height measurement to base of inflorescence

Table 2. Size ranges of morphological characteristics of *P. clavellata* at present study sites and those representing continental North America.

Plant Characteristics	Luer (1975)	Correll (1950)	This Study 1991-1992
Plant Height	15-35cm	6-36cm*	6.7-14cm*
Leaf Length	5-15cm	5-18cm	4.4-8.4cm
Leaf Width	1-3cm	1-3.5cm	0.6-1.6cm
Stem Diameter	--------	--------	1.1-1.7mm
Flower Number	3-15	--------	4-10
Floral Bract	6mm	3-10mm	5.4-8.8mm
Ovary Length	10mm	10mm	7.0-8.9mm
Sepal	4 x 2.5mm	4-5 x 2.5mm	4-4.5mm
Petal	5 x 2mm	3-5 x 2mm	--------
Lip	6 x 3mm	3-7 x 3-4mm	--------
Spur	10mm	8-12mm	8.3-10.7mm

* Height measurement to base of inflorescence

Figure 9. Population dynamics and distribution of *P. blephariglottis* and elevations (indicated by ——) along transect 1a, site 1, 1991 and 1992 (1991 flowering n=26, non-flowering n=92; 1992 flowering n=6, non-flowering n=141).

Site 1

Transect 1a

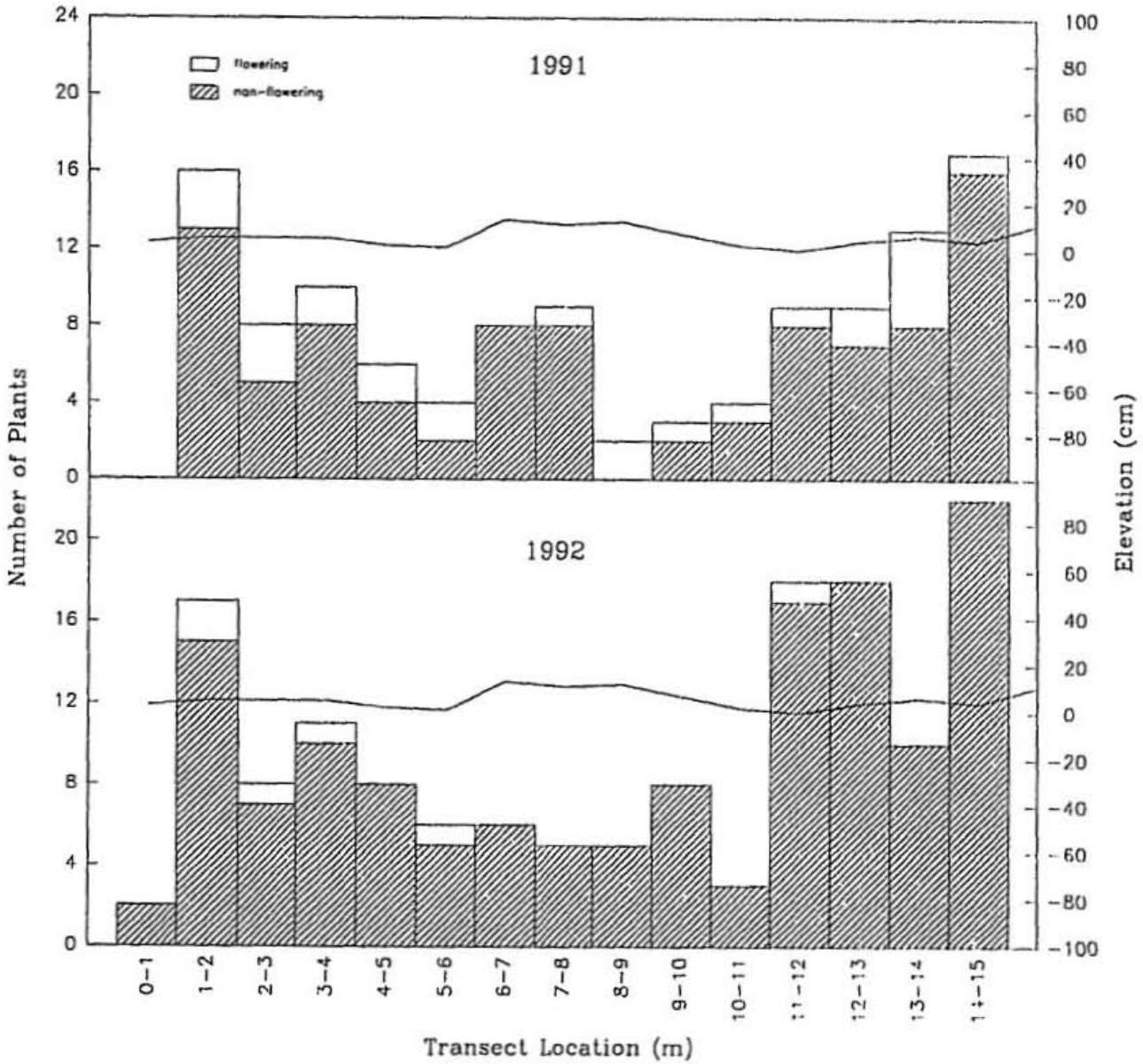


Figure 10. Population dynamics and distribution of *P. blephariglottis* and elevations (indicated by ——) along transect 1b, site 1, 1991 and 1992 (1991 flowering n=10, non-flowering n=48; 1992 flowering n=2, non-flowering n=62).

Site 1

Transect 1b

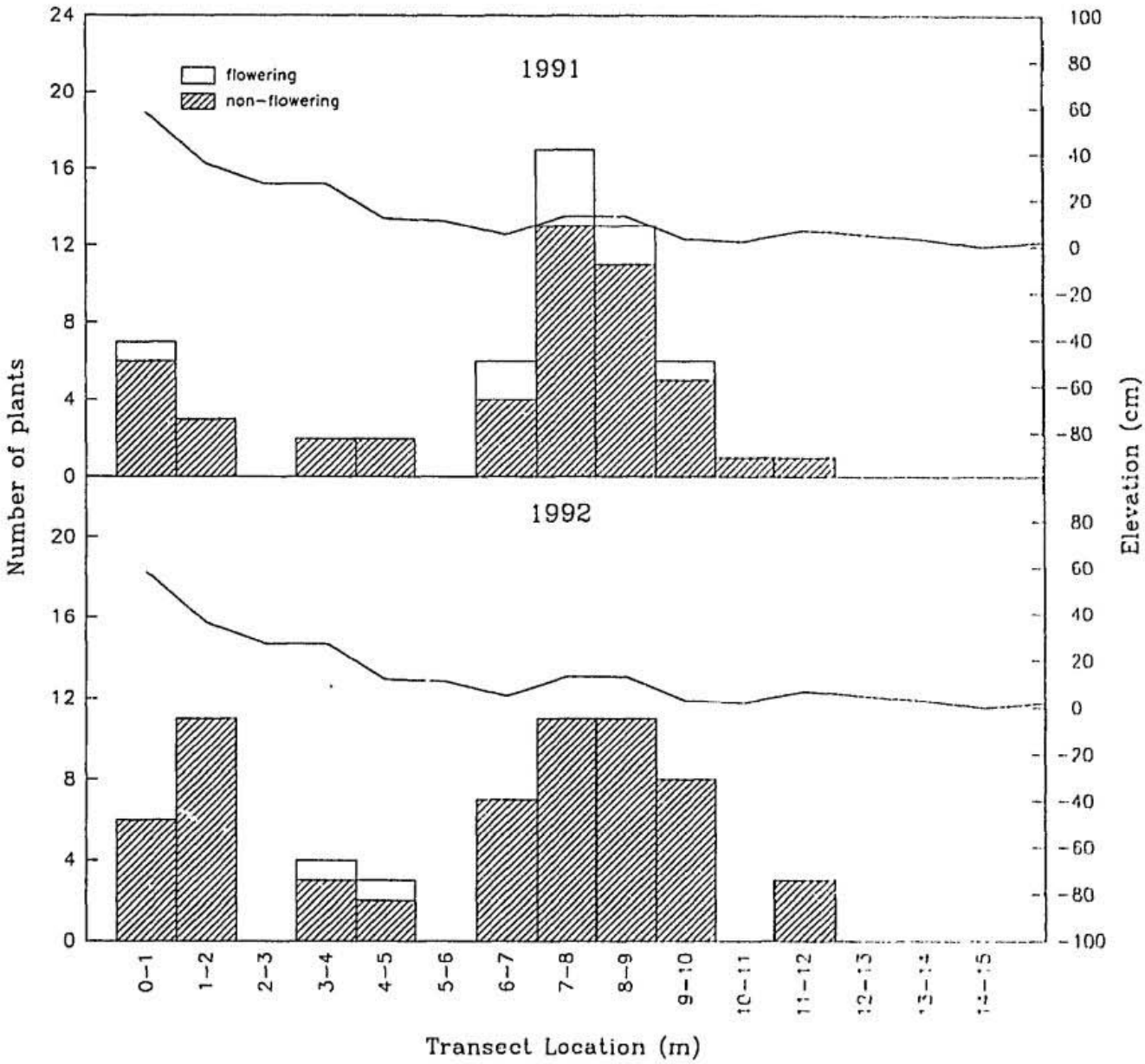


Figure 11. Population dynamics and distribution of *P. clavellata* and elevations (indicated by ——) along transect 2, site 2, 1991 and 1992 (1991 flowering n=13, non-flowering n=13; 1992 flowering n=11, non-flowering n=33).

Site 2

Transect 2

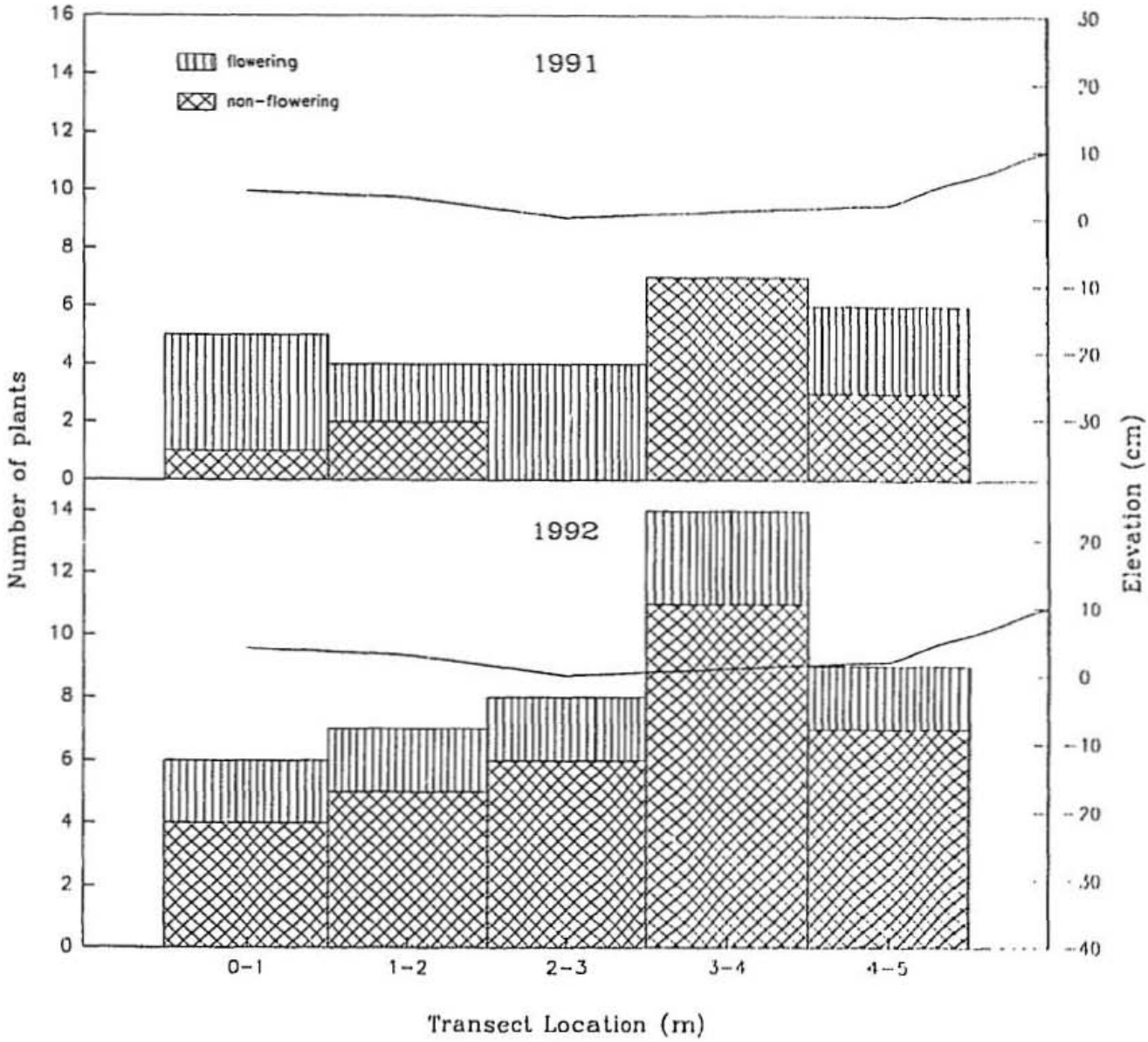


Figure 12. Population dynamics and distribution of *P. clavellata* and elevations (indicated by ——) along transect 3, site 3, 1991 and 1992 (1991 flowering n=29, non-flowering n=14; 1992 flowering n=26, non-flowering n=27).

Site 3

Transect 3

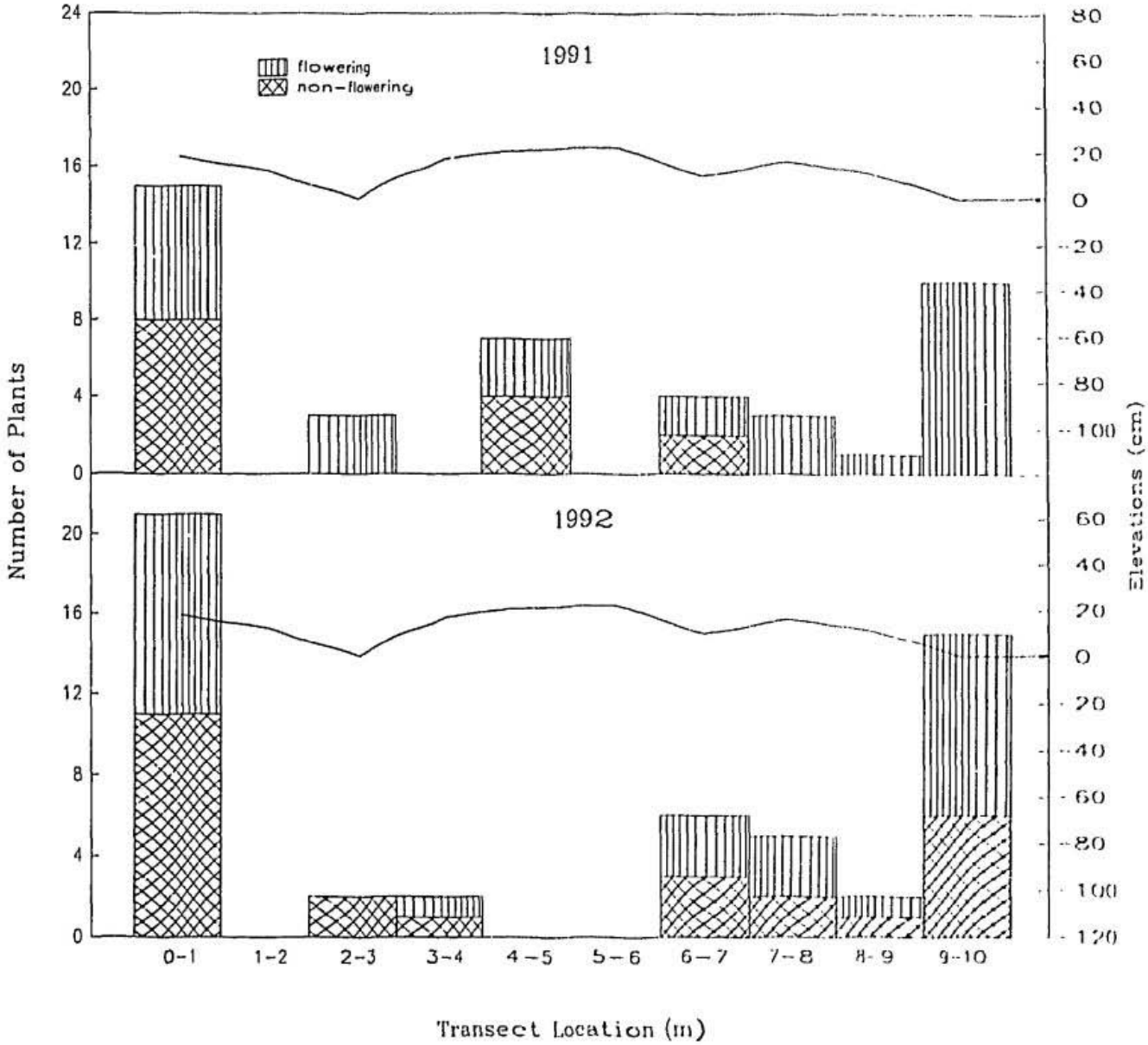


Figure 13. Population dynamics and distribution of *P. blephariglottis* and *P. clavellata* and elevations (indicated by ——) along transect 4, site 4, 1991 and 1992. (b - *P. blephariglottis*. 1991 flowering n=21, non-flowering n=71; 1992 flowering n=17, non-flowering n=67 ; c - *P. clavellata*. 1991 flowering n=55, non-flowering n=145; 1992 flowering n=29, non-flowering n=219).

Site 4

Transect 4

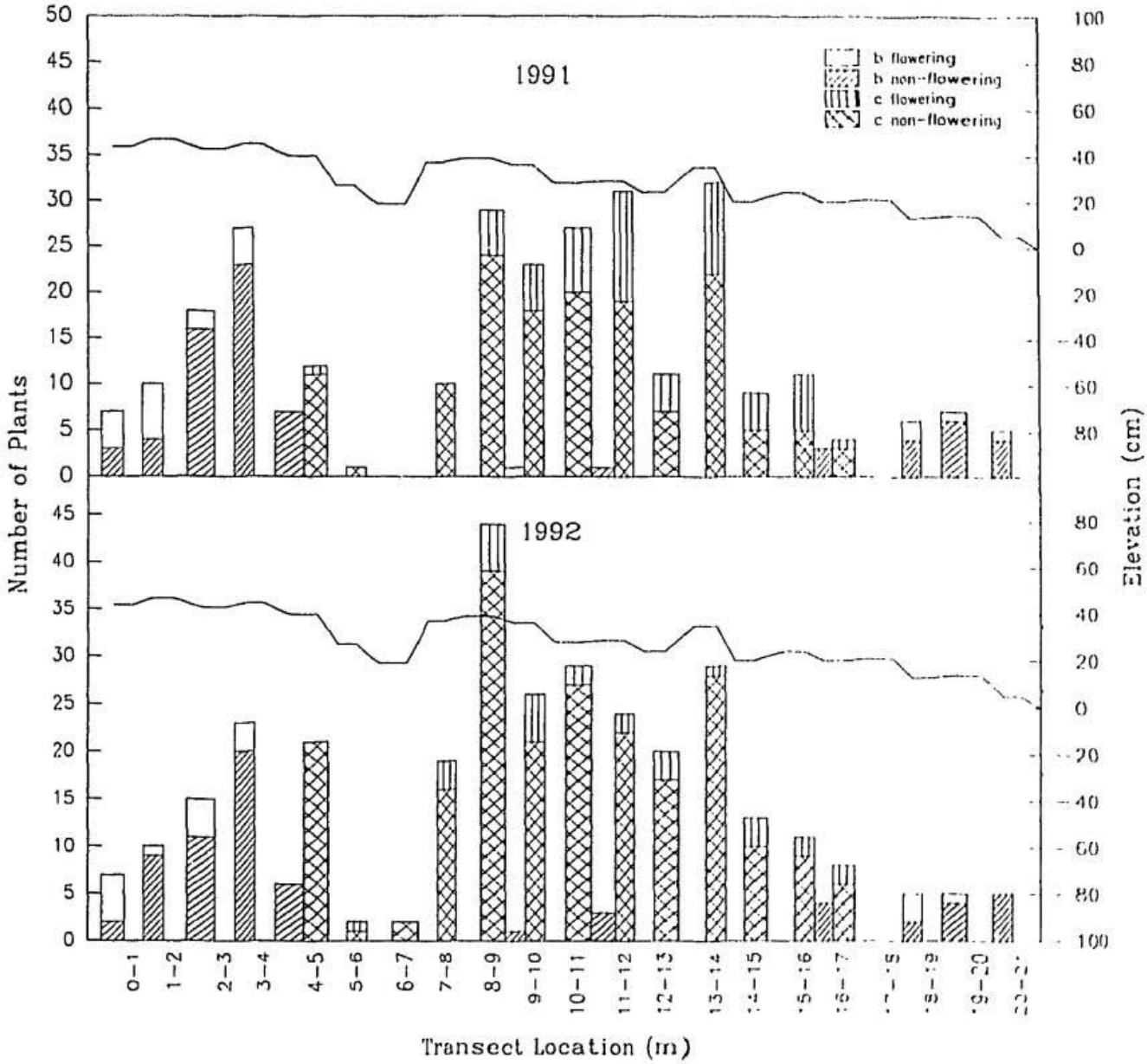


Figure 14. Population dynamics and distribution of *P. blepharigiottis* and *P. clavellata* and elevations (indicated by ——) along transect 5, site 5, 1991 and 1992 (b - *P. blepharigiottis*. 1991 flowering n=34, non-flowering n=33; 1992 flowering n=9, non-flowerig n=63; c - *P. clavellata*. 1991 flowering n=41, non-flowering n=206; 1992 flowering n=19, non-flowering n=246).

Site 5

Transect 5

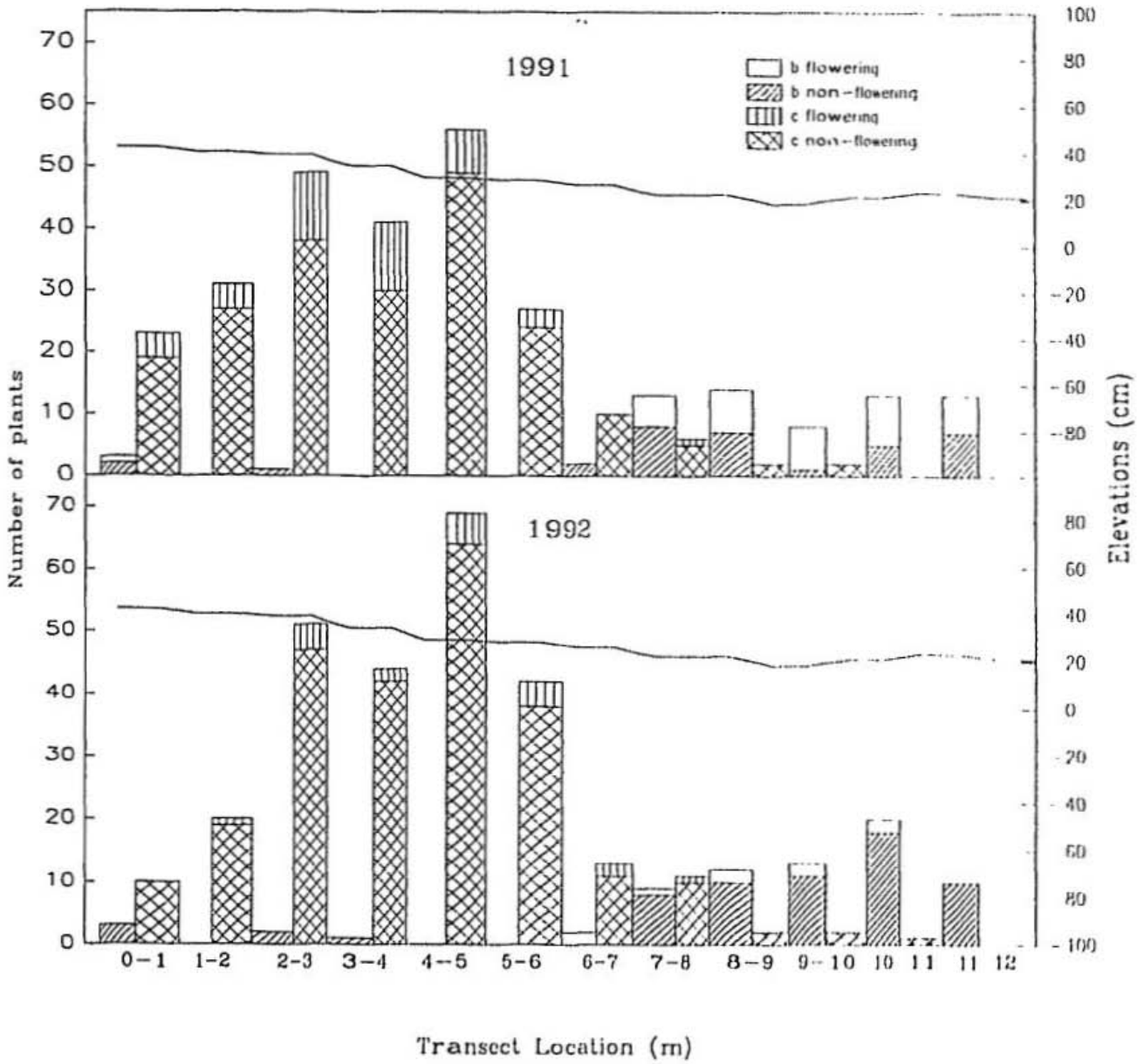


Table 3. A summary of the total population dynamics of *P. blephariglottis* and *P. clavellata* along the transect at each site and the percent of those populations flowering in 1991 and 1992.

Species	Sites	1991 Total Numbers of Individuals and Density (#/m²)	1992 Total Numbers of Individuals and Density (#/m²)	1991 Individuals in Flower (%)	1992 Individuals in Flower (%)	1992 Changes in Number of Individuals (%)
b	1	176, 6.1	211, 7.3	20.5	3.8	19.9↑
b	4	92, 4.3	84, 4.0	22.8	20.2	8.7↓
b	5	67, 5.6	72, 6.0	50.7	12.5	7.5↑
b	all	335, 5.4	367, 5.9	27.2	9.3	9.6↑
c	2	26, 5.2	44, 8.8	50.0	25.0	69.2↑
c	3	43, 4.3	53, 5.3	67.4	49.1	23.3↑
c	4	200, 9.5	248, 11.8	27.5	11.7	24.0↑
c	5	247, 20.6	265, 22.1	16.6	7.2	7.3↑
c	all	516, 7.7	610, 9.1	26.7	16.4	18.2↑

greatest and site 4 the lowest abundance of individuals of *P. blephariglottis* in both years, while *P. clavellata* had the greatest abundance of individuals at site 5 and the lowest abundance of individuals at site 2 in both years. The total population of both species increased in number in 1992 and all sites showed an increase, with the exception of *P. blephariglottis* at site 4 which decreased in number. Site 1 for *P. blephariglottis* and site 2 for *P. clavellata* showed the greatest increase in number of individuals present in 1992. Both populations and all sites exhibited a marked decline in number of individuals in flower in 1992. Flowering percentages for all sites ranged from 20.4% to 50.7% in 1991 and 3.8% to 20.2% in 1992 for *P. blephariglottis* and from 16.6% to 67.4% in 1991 and 7.2% to 49.1% in 1992 for *P. clavellata*. Site 5 in 1991 and site 4 in 1992 had the highest percentage of individuals of *P. blephariglottis* in flower, while site 1 in both years had the lowest percentage of individuals of *P. blephariglottis* in flower. Site 3 had the highest percentages and site 5 had the lowest percentages of individuals of *P. clavellata* in flower in both years.

The total of the subsamples of tagged plants for both species exhibited the same trend as the total population with regard to the percentage of individuals in flower, in that both subsamples showed a decrease (Table 4; Appendix C). All sites, with the exception of site 3 which remained the same, also showed a decrease in the percentage of individuals flowering in 1992. While the total population in the study of *P.blephariglottis* and *P. clavellata* increased in 1992, the subsamples of tagged plants showed a decrease in 1992. The loss of tagged individuals was a trend for both species at all sites.

Table 4. A summary of the population subsample dynamics for tagged individuals of *P. blephariglottis* and *P. clavellata* and the percentage flowering in 1991 and 1992.

Species	Sites	1991 Total Numbers of Individuals	1992 Numbers of Tags Remaining	1992 Total Numbers of Individuals	1991 Individuals in Flower (%)	1992 Individuals in Flower (%)	1992 Individuals Lost (%)
b	1	91	63	53	65.9	7.5	15.9
b	4	50	49	43	24	9.3	12.2
b	5	36	33	30	38.9	6.7	9.1
b	all	177	145	126	48.6	7.9	13.1
c	2	26	26	21	50	23.8	19.2
c	3	18	14	12	66.7	66.7	14.3
c	4	76	59	50	34.2	20	15.3
c	5	74	69	64	18.9	3.1	7.2
c	all	194	168	147	33.3	17	12.5

An individual was considered absent if the tag was present but the plant could not be found. The decrease in the number of tags in 1992 was due to vandalism of site 1 and 4. The loss of tagsat other sites was possibly due to vandalism or trampling by people or moose.

The distribution of individuals along the transects, where only one species occurred, was not uniform and did not appear to be related to the presence or absence of trees nearby. Where the two species occurred along a transect, each species occupied a more or less distinct area. The distribution of the individuals in these areas was not uniform and did not seem to be related to any observable features of the site.

3.3 Inter-site Studies at Sites 1-5

3.3.1 Variability of Morphological Characteristics of *P. blephariglottis*

Observations of height, stem diameter, leaf area, bract length, number of flowers, dorsal sepal area, lip area, spur length and ovary length showed no significant differences between sites. Floral characteristics, lateral sepal area and lateral petal area were significantly different (Figures 15 & 16, Tables 5 & 6). A multiple comparison test showed all pairs of sites to be significantly different from each other. In an attempt to distinguish between sites the actual means were ranked from largest to smallest but ranking did not show any site to have consistently larger or smaller means for morphological characteristics (Table 7).

Figure 15. Inter-site variability of the mean height (a), stem diameter (b), first leaf area (c), second leaf area (d), bract length (e) and number of flowers (f) of *P. blephariglottis* (bars are one standard error)

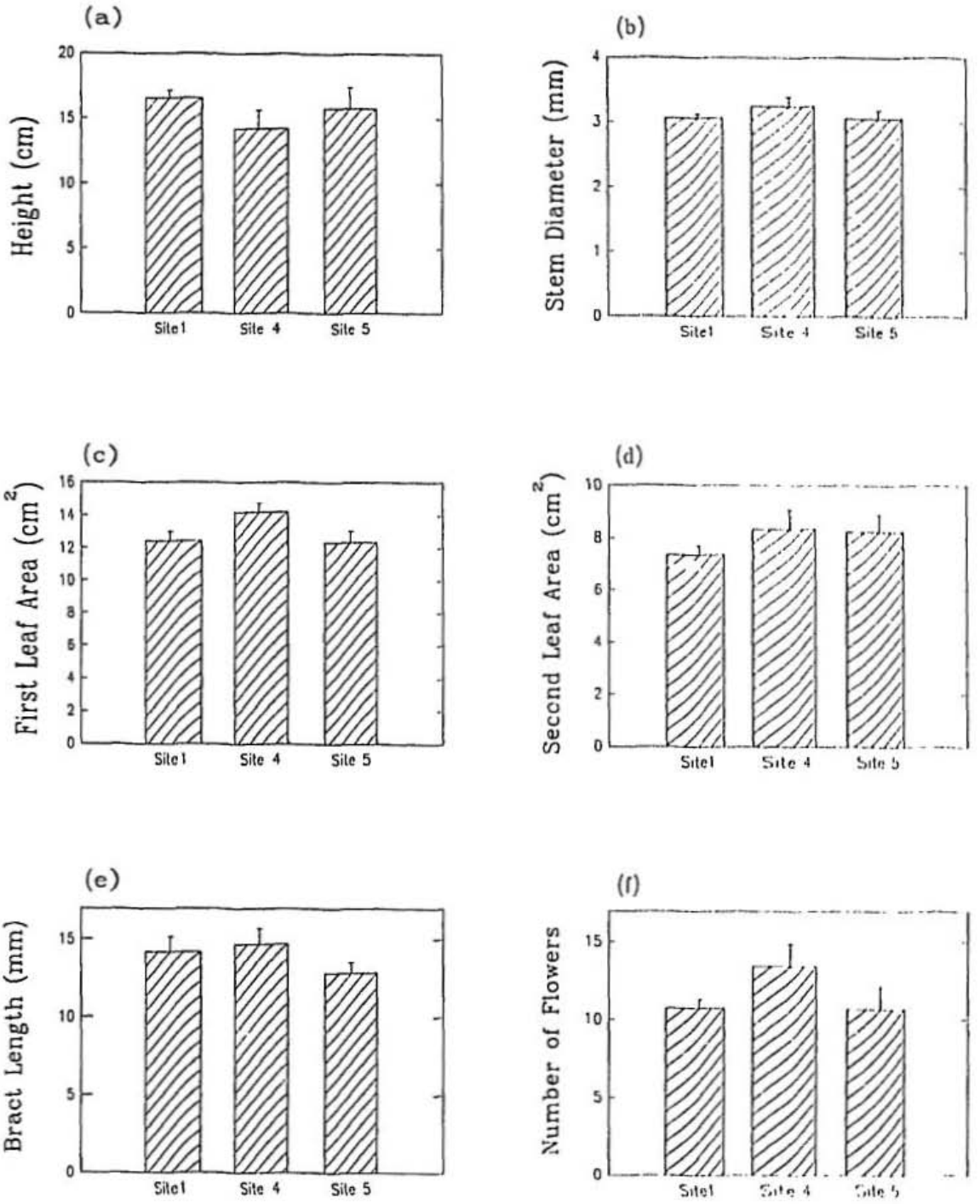

(a)
Height (cm)
20
15
10
5
0
Site1
Site 4
Site 5
(b)
Stem Diameter (mm)
4
3
2
1
0
Site1
Site 4
Site 5
(c)
First Leaf Area (cm²)
16
14
12
10
8
6
4
2
0
Site1
Site 4
Site 5
(d)
Second Leaf Area (cm²)
10
8
6
4
2
0
Site1
Site 4
Site 5
(e)
Bract Length (mm)
15
10
5
0
Site1
Site 4
Site 5
(f)
Number of Flowers
15
10
5
0
Site1
Site 4
Site 5

Figure 16. Inter-site variability of the mean spur length (a), ovary length (b), lateral sepal area (c), dorsal sepal area (d), lateral petal area (e) and lip area (f) of *P. blephariglottis* (bars are one standard error)

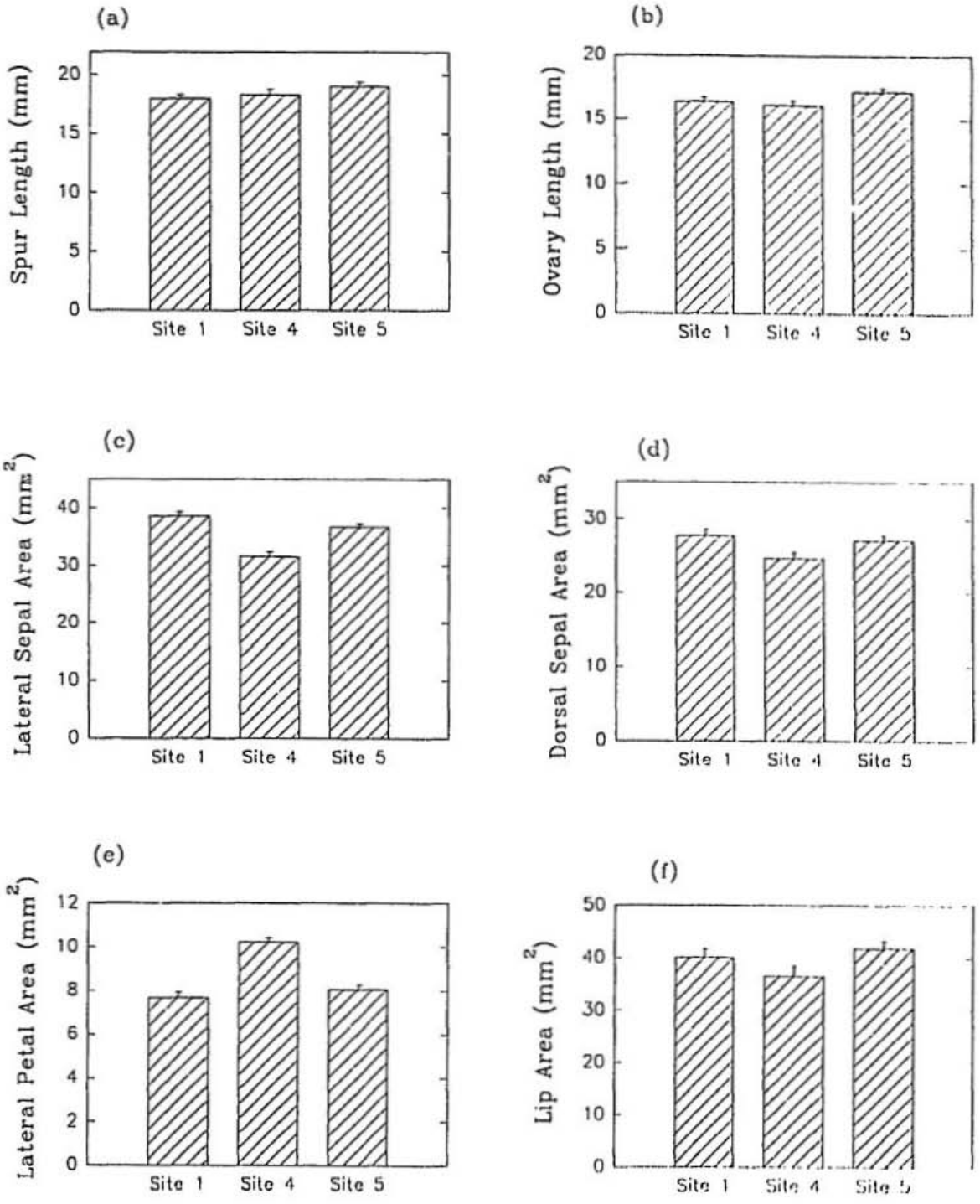

(a)
Spur Length (mm)
0
5
10
15
20
Site 1
Site 4
Site 5
(b)
Ovary Length (mm)
0
5
10
15
20
Site 1
Site 4
Site 5
(c)
Lateral Sepal Area (mm2)
0
10
20
30
40
Site 1
Site 4
Site 5
(d)
Dorsal Sepal Area (mm2)
0
10
20
30
Site 1
Site 4
Site 5
(e)
Lateral Petal Area (mm2)
0
2
4
6
8
10
12
Site 1
Site 4
Site 5
(f)
Lip Area (mm2)
0
10
20
30
40
50
Site 1
Site 4
Site 5

Table 5. One way ANOVA on measurements of morphological characteristics of *P. blephariglottis* from all sites. (P<0.004 significant)

Characteristics	SS	MS	F	P
Height	71.8840	35.9420	1.4100	0.249
Stem Diameter	0.4170	0.2080	0.7550	0.473
First Leaf Length	183.7784	91.8892	2.6540	0.072
Second Leaf Length	15.7546	7.8773	1.1320	0.328
Bract Length	0.0290	0.0140	0.8610	0.428
Number of Flowers	76.0440	38.0220	1.6430	0.200
Dorsal Sepal Area	130.3480	65.1740	3.7250	0.029
Lip Area	356.5357	178.2679	2.5320	0.087
Spur Length	14.4800	7.2400	1.8100	0.171

Table 6. Kruskal-Wallis one way ANOVA on Ranks on measurements of morphological characteristics of *P. blephariglottis* from all sites. (P<0.004 significant)

Characteristics	df	H	P
Lateral Sepal Area	2	39.348	<0.001*
Lateral Petal Area	2	49.69	<0.001*
Ovary Length	2	4.927	0.085

Table 7. Ranking of actual means of morphological characteristics of each site for *P. blephariglottis* from largest to smallest.

Characteristics	Mean s(Ranks)		
	Site 1	Site 4	Site 5
Height (cm)	16.57(1)	14.22(3)	15.81(2)
Stem Diameter (mm)	3.07(2)	3.25(1)	3.06(3)
First Leaf Area (cm^2)	12.42(2)	14.19(1)	12.37(3)
Second Leaf Area (cm^2)	7.34(3)	8.35(1)	8.26(2)
Bract Length (mm)	14.18(2)	14.68(1)	12.82(3)
Number of Flowers	10.72(2)	13.42(1)	10.64(3)
Dorsal Sepal Area (mm^2)	27.70(1)	24.67(3)	27.15(2)
Lip Area (mm^2)	40.60(2)	36.58(3)	41.82(1)
Spur Length (mm)	18.00(3)	18.28(2)	19.04(1)
Lateral Sepal Area (mm^2)	38.61(1)	31.63(3)	36.69(2)
Lateral Petal Area (mm^2)	7.69(3)	10.22(1)	8.08(2)
Ovary Length (mm)	16.40(2)	16.12(3)	17.60(1)

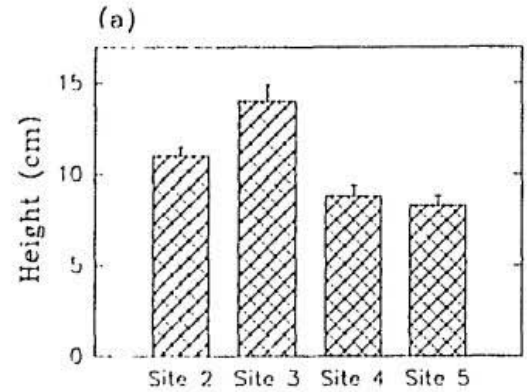
3.3.2 Variability of Morphological Characteristics of *P. clavellata*

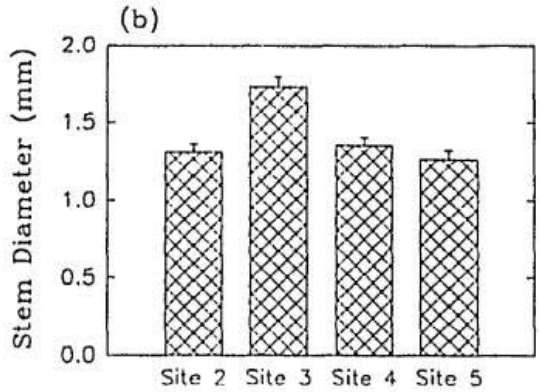
Observations of height, stem diameter, leaf area, bract length, number of flowers, flower spread, flower depth, spur length and ovary length showed significant differences between sites. The number of capsules showed no significant difference between sites (Figures 17&18; Tables 8&9). A multiple comparison test showed no pair of sites to be significantly different for all characteristics or to consistently show no difference for all characteristics. Ranking of the actual means from largest to smallest showed site 3 to consistently have the largest means and site 5 to consistently have the smallest means for all morphological characteristics with the exception of spur length (Table 10).

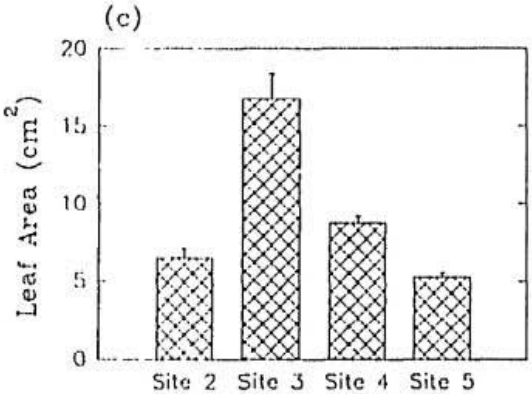
3.3.3 Variability of Peat Constituents, Water Level and Water pH

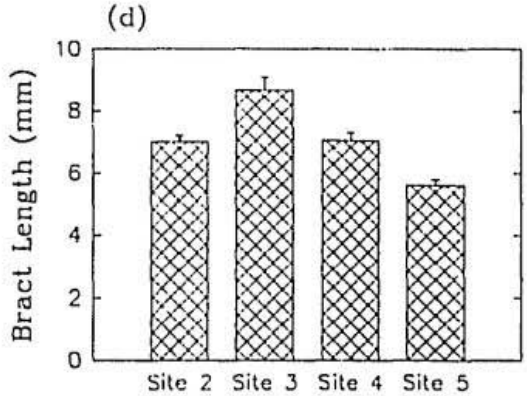
Observations of magnesium, phosphorus, nitrogen, potassium, calcium, organic matter and ash content of peat showed no significant differences between sites. Iron, pH, and moisture content of peat, water level and water pH showed significant differences between sites (Tables 11&12). A multiple comparison test showed neither site to be consistently significantly different from all of the others. Ranking of the actual means of peat nutrient content from largest to smallest means showed sites 2 and 3 (*P. clavellata* only) to most often have the largest mean and site 1 (*P. blephariglottis* only) to most often have the smallest mean (Table 13). Sites 2 and 3 show the smallest means for organic matter and the largest means for ash. The means for site 5 are the largest for organic matter and the smallest for ash.

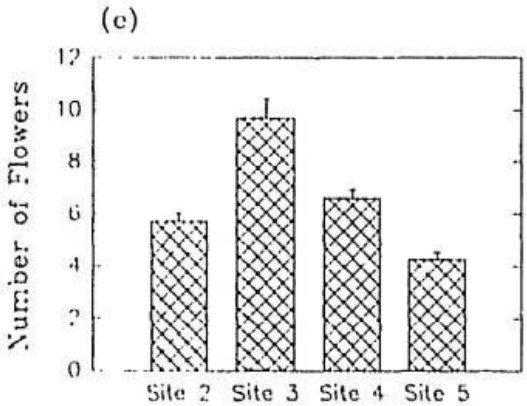
Figure 17. Inter-site variability of the mean height (a), stem diameter (b), leaf area (c), bract length (d), number of flowers (e) and number of capsules (f) of *P. clavellata*. (bars are one standard error).


(a)
Height (cm)
0
5
10
15
Site 2
Site 3
Site 4
Site 5


(b)
Stem Diameter (mm)
0.0
0.5
1.0
1.5
2.0
Site 2
Site 3
Site 4
Site 5


(c)
Leaf Area (cm2)
0
5
10
15
20
Site 2
Site 3
Site 4
Site 5


(d)
Bract Length (mm)
0
2
4
6
8
10
Site 2
Site 3
Site 4
Site 5


(e)
Number of Flowers
0
2
4
6
8
10
12
Site 2
Site 3
Site 4
Site 5

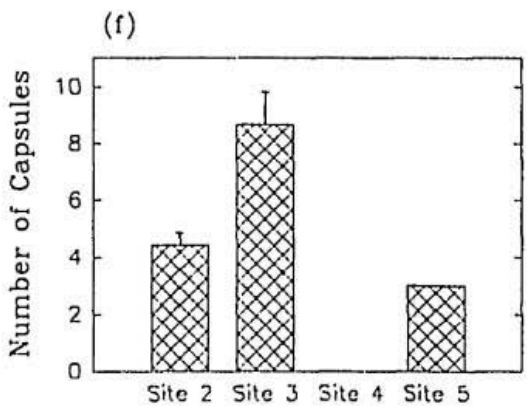

(f)
Number of Capsules
0
2
4
6
8
10
Site 2
Site 3
Site 4
Site 5

Figure 18. Inter-site variability of the mean spur length (a), ovary length (b), flower spread (c) and flower depth (d) of *P. clavellata.* (bars are one standard error)

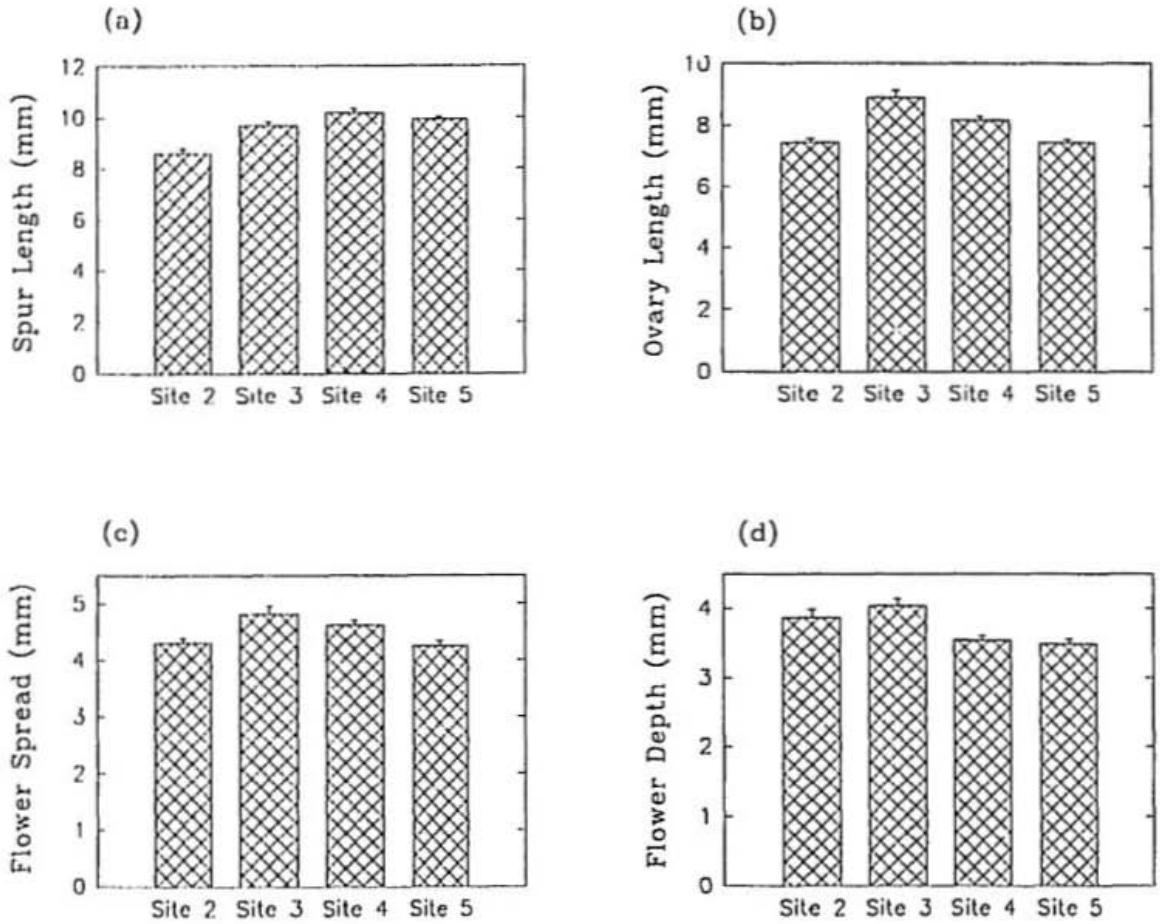

(a)
Spur Length (mm)
12
10
8
6
4
2
0
Site 2
Site 3
Site 4
Site 5
(b)
Ovary Length (mm)
10
8
6
4
2
0
Site 2
Site 3
Site 4
Site 5
(c)
Flower Spread (mm)
5
4
3
2
1
0
Site 2
Site 3
Site 4
Site 5
(d)
Flower Depth (mm)
4
3
2
1
0
Site 2
Site 3
Site 4
Site 5

Table 8. One-way ANOVA on measurements of morphological characteristics of *P. clavellata* from all sites. (P<0.005 significant)

Characteristics	SS	MS	F	P
Stem Diameter	0.222	0.074	12.032	<0.001*
Flower Depth	5.1300	1.7100	8.0170	<0.001*
Flower Spread	5.4923	1.8308	6.8770	<0.001*
Bract Length	0.404	0.135	25.037	<0.001*

Table 9. Kruskal-Wallis one-way ANOVA on Ranks on measurments of morphological characteristics of *P. clavellata* from all sites.(P<0.005 significant)

Characteristics	df	H	P
Height	3	27.100	<0.001*
Leaf Area	3	84.640	<0.001*
Number of Flowers	3	35.735	<0.001*
Number of Capsules	3	8.706	0.013
Spur Length	3	40.320	<0.001*
Ovary Length	3	40.682	<0.001*

Table 10. Ranking of actual means of morphological characteristics of each site for *P. clavellata* from largest to smallest.

Characteristics	Means (Ranks)			
	Site2	Site 3	Site 4	Site 5
Stem Diameter (mm)	1.31(3)	1.73(1)	1.36(2)	1.26(4)
Flower Depth (mm)	3.86(2)	4.03(1)	3.54(3)	3.48(4)
Flower Spread (mm)	4.30(3)	4.82(1)	4.62(2)	4.24(4)
Bract Length (mm)	7.03(3)	8.69(1)	7.06(2)	5.61(4)
Height (cm)	11.04(2)	14.00(1)	8.81(3)	8.28(4)
Leaf Area (cm^2)	6.49(3)	16.78(1)	8.73(2)	5.25(4)
Number of Flowers	5.72(3)	9.70(1)	6.61(2)	4.27(4)
Number of Capsules*	4.00(2)	9.00(1)	0.00(4)	3.00(3)
Spur Length (mm)	8.60(4)	9.68(3)	10.20(1)	9.94(2)
Ovary Length (mm)	7.40(3)	8.90(1)	8.20(2)	7.40(3)

* no capsules were found in site 4

Table 11. One-way ANOVA on peat constituents from all sites. (P<0.004 significant)

Constituents	SS	MS	F	P
Magnesium (ppm)	617342.209	154335.552	2.304	0.098
Phosphorus (ppm)	16736.014	4184.004	0.594	0.672

Table 12. Kruskal-Wallis one-way ANOVA on Ranks on peat constituents, water level and water pH from all sites. (P<0.004 significant)

Constituents	df	H	P
Nitrogen (ppm)	4	7.3970	0.116
Potassium (ppm)	4	13.4400	0.009
Iron (ppm)	4	16.6010	0.002*
Calcium (ppm)	4	14.2810	0.006
pH	4	9.0941	<0.001*
Moisture (%)	4	19.0860	<0.001*
Organic Matter (%)	4	14.4060	0.006
Ash (%)	4	14.3770	0.006
Water Level	4	28.8760	<0.001*
Water pH	4	47.8710	<0.001*

Table 13. Ranking of actual means of peat constituents, water level and water pH for each site from largest to smallest.

Constituents	Means (Ranks)				
	Site 1	Site 2	Site 3	Site 4	Site 5
Magnesium (ppm)	447.77(5)	797.05(4)	800.37(3)	908.75(1)	893.07(2)
Phosphorus (ppm)	338.54(5)	403.42(2)	429.49(1)	372.98(4)	377.48(3)
Nitrogen (ppm)	14500.00(1)	13100.00(2)	8635.47(4)	7657.53(5)	9171.42(3)
Potassium (ppm)	456.10(5)	13500.00(1)	850.55(4)	1070.92(2)	916.30(3)
Iron (ppm)	766.32(5)	3525.88(2)	68600.00(1)	2083.53(4)	3229.45(3)
Calcium (ppm)	542.70(5)	1560.73(4)	4150.93(1)	1895.72(2)	1700.87(3)
Peat pH	3.82(5)	4.25(2)	5.14(1)	4.21(3)	3.94(4)
Moisture (%)	8.88(4)	6.41(5)	10.37(1)	10.34(2)	9.39(3)
Organic Matter (%)	85.51(2)	55.15(5)	65.40(4)	84.72(3)	85.74(1)
Ash (%)	5.62(3)	38.44(1)	24.19(2)	4.94(4)	4.86(5)
Water Level (cm)	-11.16(5)	-2.06(2)	0.96(1)	-5.58(3)	-9.16(5)
Water pH	4.45(5)	5.32(2)	6.06(1)	4.52(3)	4.46(4)

Peat pH, water pH and water level means are also largest for site 3 and smallest for site 1 (Table 13). Seasonal fluctuations in water pH and water level were also observed. For the most part, observations of water pH and water level showed an increase in water pH as water level increased (Figures 19a-c).

3.4 Studies on Co-occurring Populations at Sites 4 and 5

3.4.1 Variability of Morphological Characteristics of *P. blephariglottis*

Observations of morphological characteristics of *P. blephariglottis* from sites 4 and 5, where both species were present, showed no significant difference in height, stem diameter, leaf area, number of flowers, spur length, lip area, dorsal sepal area,bract length and ovary length. Lateral sepal area and lateral petal area showed significant differences between sites (Tables 14-15). Ranking of the actual means from the largest to the smallest did not show either site to have a consistantly larger or smaller mean for morphological characteristics (Table 7).

Figure 19a. Fluctuation in the mean water level (i.e. the distance from the surface of the peat to standing water) and the water pH in sites 1-3, 1991-1992.

(—— *P. blephariglottis*, ---- *P. clavellata*)

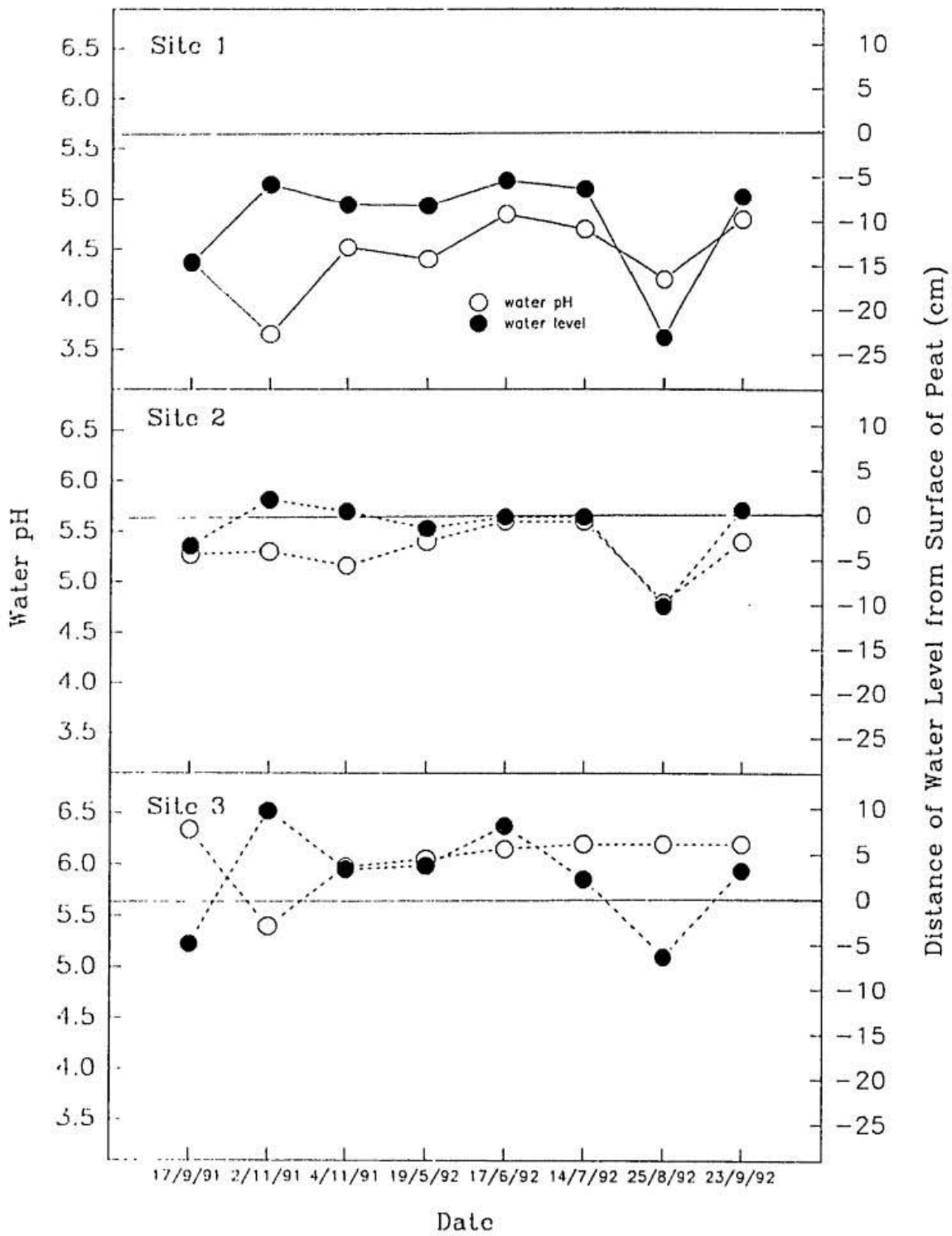

Site 1
Site 2
Site 3
water pH
water level
Water pH
Distance of Water Level from Surface of Peat (cm)
6.5
6.0
5.5
5.0
4.5
4.0
3.5
10
5
0
−5
−10
−15
−20
−25
17/9/91
2/11/91
4/11/91
19/5/92
17/6/92
14/7/92
25/8/92
23/9/92
Date

Figure 19b. Fluctuation in the mean water level (i.e. the distance from the surface of the peat to standing water) and the water pH in site 4, 1991-1992.

(— *P. blephariglottis*, --- *P. clavellata*)

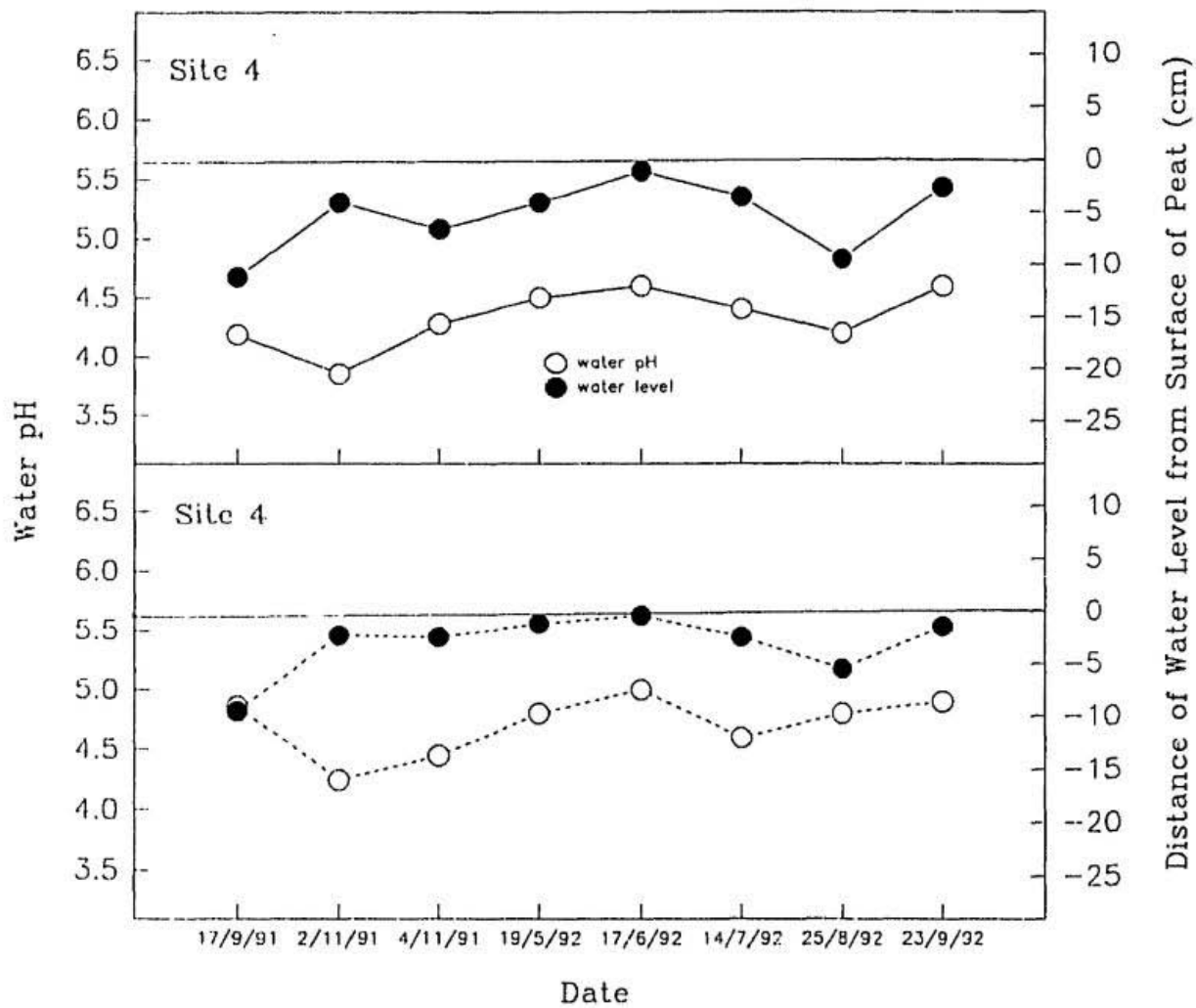

Site 4
Site 4
water pH
water level
Water pH
Distance of Water Level from Surface of Peat (cm)
6.5
6.0
5.5
5.0
4.5
4.0
3.5
10
5
0
-5
-10
-15
-20
-25
17/9/91
2/11/91
4/11/91
19/5/92
17/6/92
14/7/92
25/8/92
23/9/92
Date

Figure 19c. Fluctuation in the mean water level (i.e. the distance from the surface of the peat to standing water) and the water pH in site 5, 1991-1992.

(—— *P. blephariglottis*, --- *P. clavellata*)

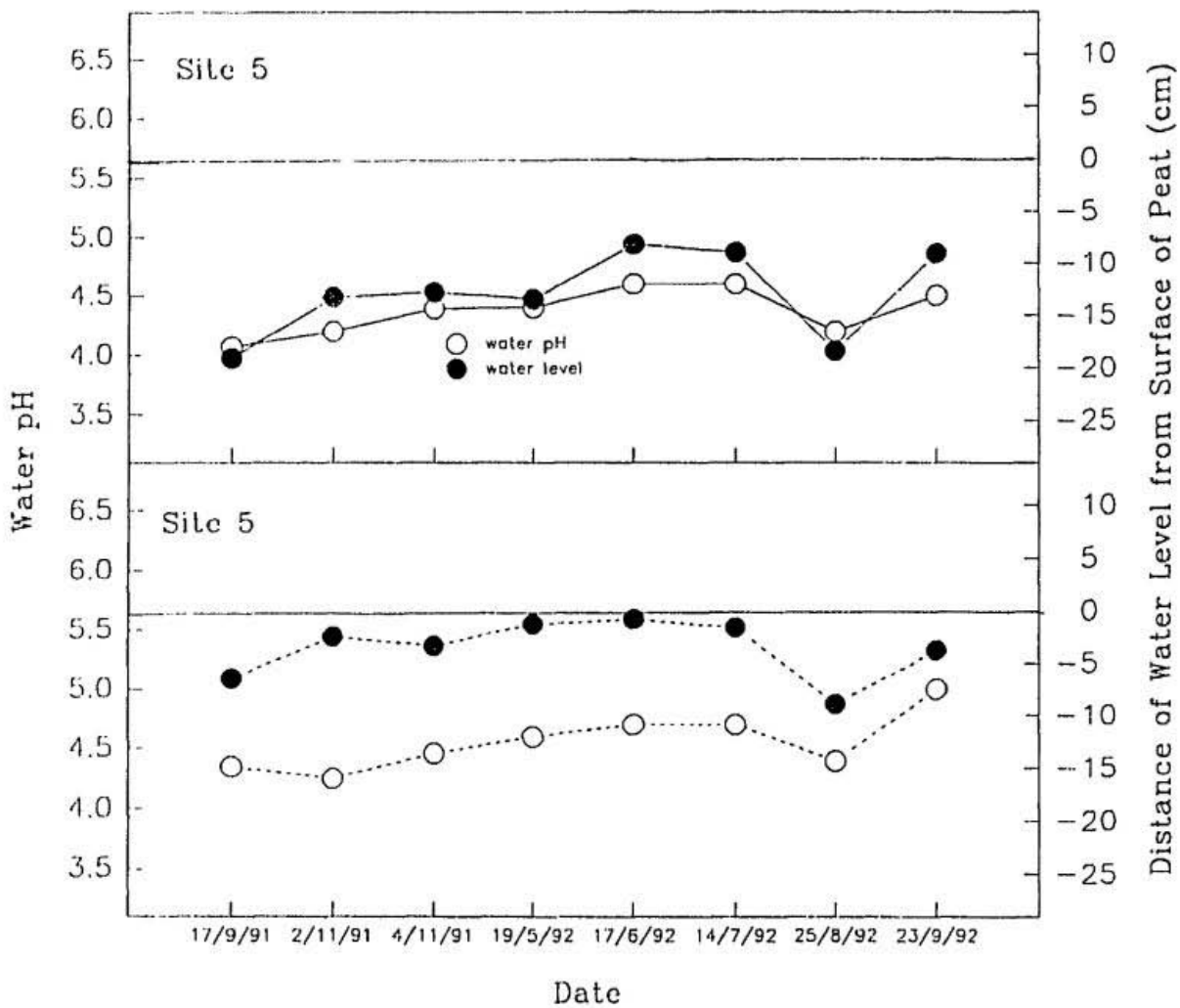

Site 5
Site 5
water pH
water level
Water pH
Distance of Water Level from Surface of Peat (cm)
6.5
6.0
5.5
5.0
4.5
4.0
3.5
10
5
0
−5
−10
−15
−20
−25
17/9/91
2/11/91
4/11/91
19/5/92
17/6/92
14/7/92
25/8/92
23/9/92
Date

Table 14. t test on morphological characteristics of *P. blephariglottis* from sites 4 and 5. (P<0.004 significant)

Characteristics	t	df	P
Height	-0.74	30	0.465
Stem Diameter	0.975	30	0.337
First Leaf Area	1.993	138	0.048
Second Leaf Area	0.095	23	0.925
Number of Flowers	1.34	24	0.193
Spur Length	-1.228	48	0.226
Lip Area	-2.142	48	0.037
Dorsal Sepal Area	-2.232	48	0.030

Table 15. Mann Whitney rank sum test on morphological characteristics of *P. blephariglottis* from sites 4 and 5. (P<0.004 significant)

Characteristics	T	P
Bract Length	393	0.072
Lateral Sepal Area	1805	<0.001*
Lateral Petal Area	1640	<0.001*
Ovary Length	532	0.038

3.4.2 Variability of Morphological Characteristics of *P. clavellata*

Observations of morphological characteristics of *P. claveliata* from sites 4 and 5, where both species were present, showed no significant differences in height, stem diameter, flower spread and spur length. Number of flowers, bract length, flower depth, ovary length and leaf area showed significant differences between sites (Tables 16-17). Ranking of the actual means from largest to smallest means showed site 4 to consistently have the largest mean for morphological characteristics (Table 10).

3.4.3 Variability of Peat Constituents, Water Level and Water pH

Observations of peat constituents, water level and water pH from sites 4 and 5, where both species were present, showed no significant differences between phosphorus, iron, potassium, nitrogen, peat pH, organic matter, ash, magnesium, calcium, water pH or water level. Peat moisture levels were significantly different between sites (Tables 18-19). Neither site showed consistently higher means for peat constituents, water level and water pH (Table 13).

Table 16. t test on morphological characteristics of *P. clavellata* from sites 4 and 5. (P<0.005 significant)

Characteristics	t	df	P
Number of Flowers	4.79	41	<0.001*
Bract Length	4.59	41	<0.001*
Flower Depth	3.04	48	0.004*
Ovary Length	4.553	48	<0.001*

Table 17. Mann Whitney rank sum test on morphological characteristics of *P. clavellata* from sites 4 and 5. (P<0.005 significant)

Characteristics	T	P
Height	357	0.292
Stem Diameter	339	0.154
Leaf Area	13449	<0.001*
Flower Spread	581	0.710
Spur Length	489	0.467

Table 18. t test on peat constituents and water pH for sites 4 and 5. (P<0.004 significant)

Constituents	t	df	P
Phosphorus (ppm)	-0.101	10	0.921
Iron (ppm)	-2.139	10	0.058
Potassium (ppm)	0.739	10	0.477
Nitrogen (ppm)	-1.618	10	0.137
Peat pH	3.340	10	0.007
Moisture (%)	5.394	10	<0.001*
Organic Matter (%)	-1.284	10	0.228
Ash (%)	0.102	10	0.921
Water pH	0.549	30	0.587

Table 19. Mann Whitney rank sum test on peat constituents and water level for sites 4 and 5. (P<0.004 significant)

Constituents	T	P
Magnesium (ppm)	39	>0.100
Calcium (ppm)	39	>0.100
Water level	286	0.141

3.5 Inter-specific Comparisons

3.5.1 Variability of Peat Constituents, Water Level, Water pH and Crown Depth

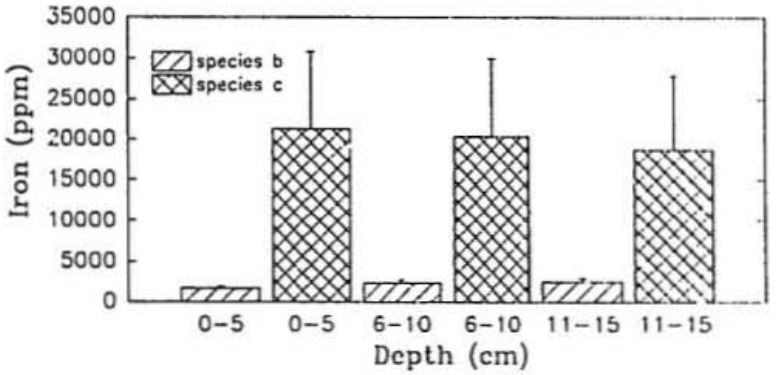
Observations of magnesium, potassium, nitrogen, moisture and organic matter content of peat and crown depth associated with each species showed no significant differences between species, while phosphorus, calcium, iron, peat pH, ash, water level and water pH showed significant differences (Figures 20-25; Tables 20&21). All the variables that were significantly different had the highest means associated with *P. clavellata* (Table 22). Only nitrogen, organic matter and crown depth, when all variables were considered, had the highest means associated with *P. blephariglottis*. The greatest ranges of means were also associated with *P. clavellata*, with the exception of magnesium, nitrogen, crown depth and water level.

Water levels in the vicinity of *P. clavellata*, where it occurred alone in a site or with *P. blephariglottis*, were higher than water levels in proximity to *P. blephariglottis* (Figure 26). Water pH also showed the same association. The sites where *P. clavellata* occurred alone had the highest pH readings and when *P. clavellata* occurred with *P. blephariglottis* the pH readings that were associated with *P. clavellata* were always higher than those associated with *P. blepariglottis* (Figure 27).

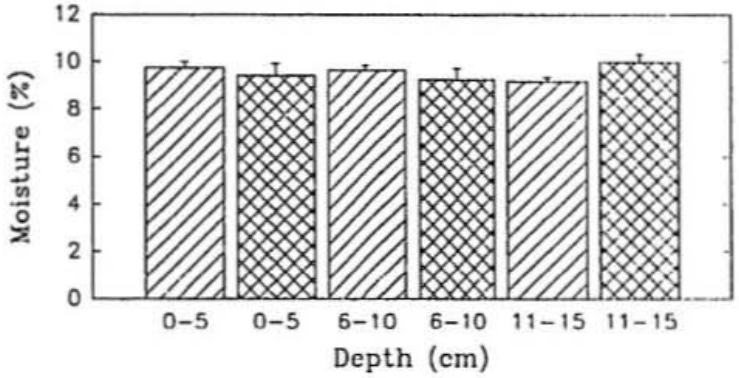
Mean distance measurements between individuals of the same species were much smaller than means for the distance between the different species. They were as follows for sites 4 and 5 respectively: *P. blephariglottis* to *P. blephariglottis* - 1.76cm, 1.98cm; *P.*

Figure 20. Mean iron (a), moisture (b) and organic matter (c) content of peat subsamples associated with *P. blephariglottis* and *P. clavellata* at all sites (bars are one standard error).

(a)


35000
30000
25000
20000
15000
10000
5000
0
Iron (ppm)
species b
species c
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)

(b)


12
10
8
6
4
2
0
Moisture (%)
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)

(c)

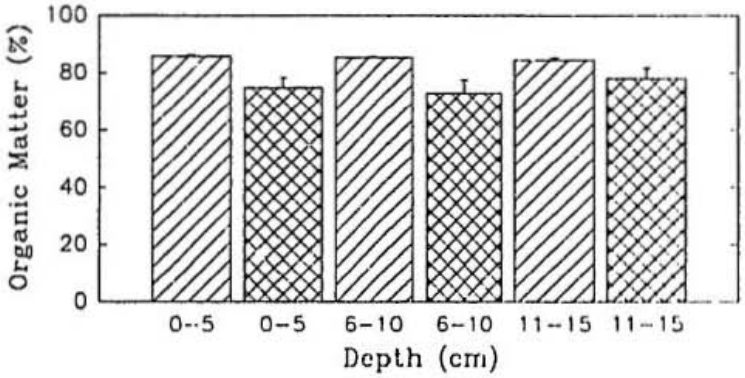
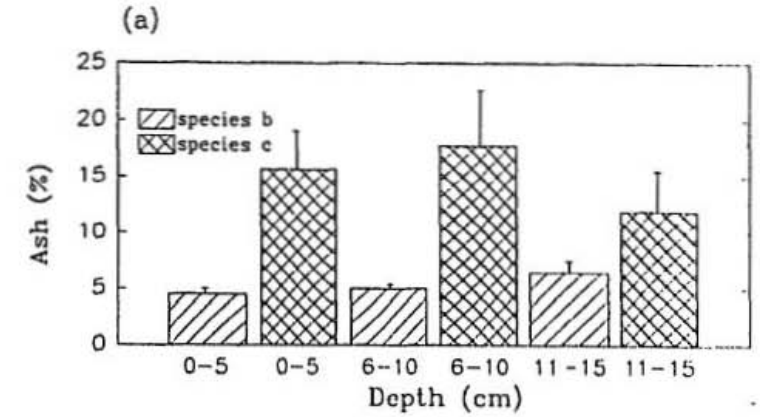
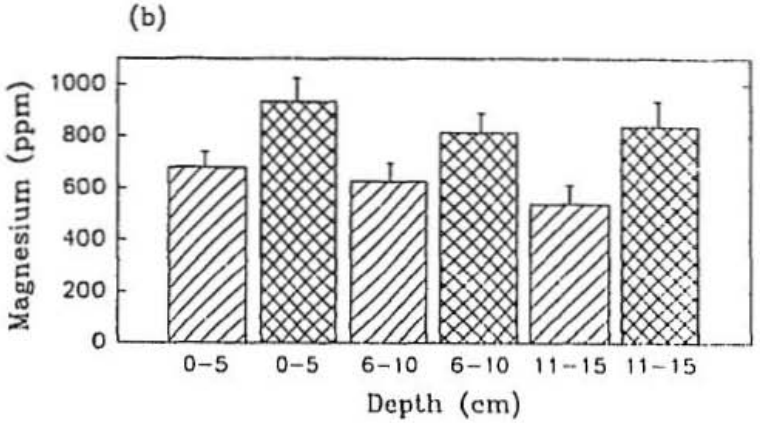

100
80
60
40
20
0
Organic Matter (%)
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)

Figure 21. Mean ash (a), magnesium (b) and calcium (c) content of peat subsamples associated with *P. blephariglottis* and *P. clavellata* at all sites (bars are one standard error).


(a)
25
20
15
10
5
0
Ash (%)
species b
species c
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)


(b)
1000
800
600
400
200
0
Magnesium (ppm)
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)

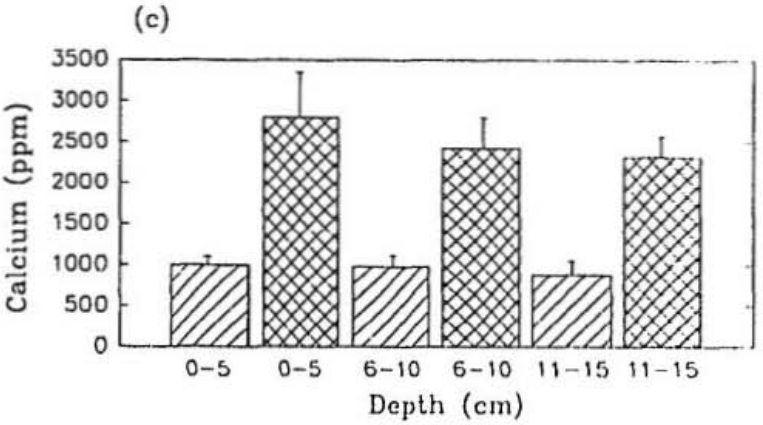
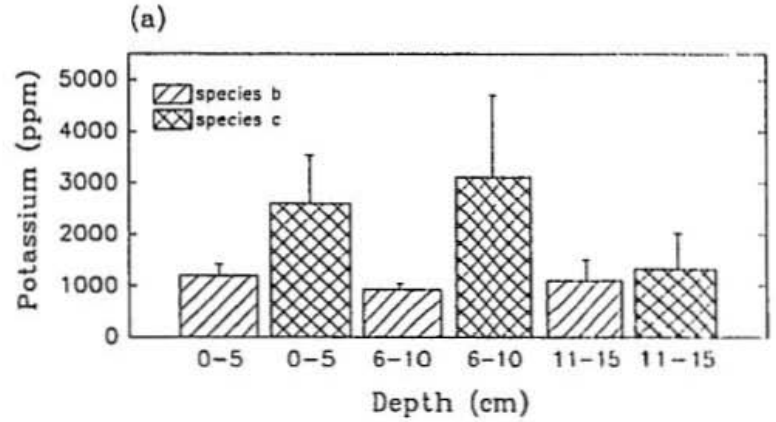
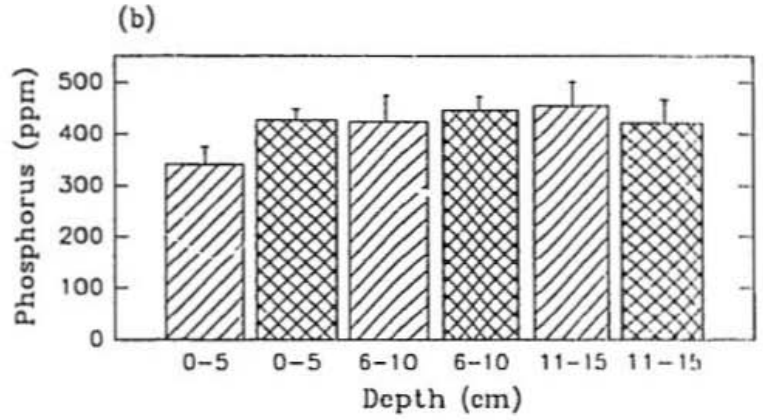

(c)
3500
3000
2500
2000
1500
1000
500
0
Calcium (ppm)
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)

Figure 22. Mean potassium (a), phosphorus (b) and nitrogen (c) content of peat subsamples associated with *P. blephariglottis* and *P. clavellata* at all sites (bars are one standard error).


(a)
Potassium (ppm)
5000
4000
3000
2000
1000
0
species b
species c
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)


(b)
Phosphorus (ppm)
500
400
300
200
100
0
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)

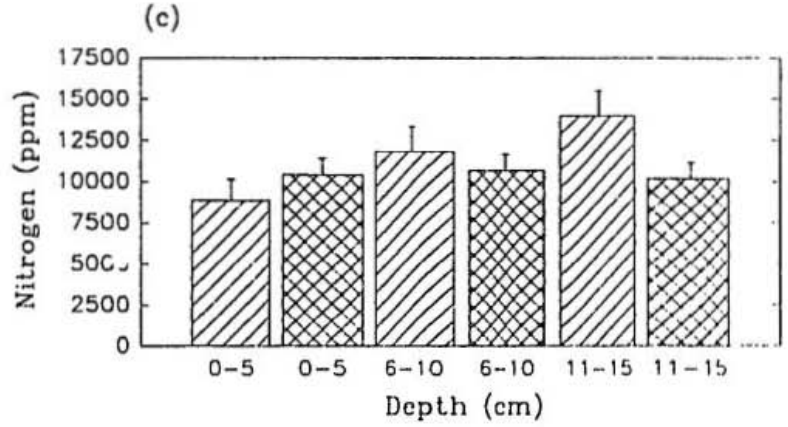

(c)
Nitrogen (ppm)
17500
15000
12500
10000
7500
2500
0
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)

Figure 23. Mean pH of peat subsamples associated with *P. blephariglottis* and *P. clavellata* at all sites (bars are one standard error).

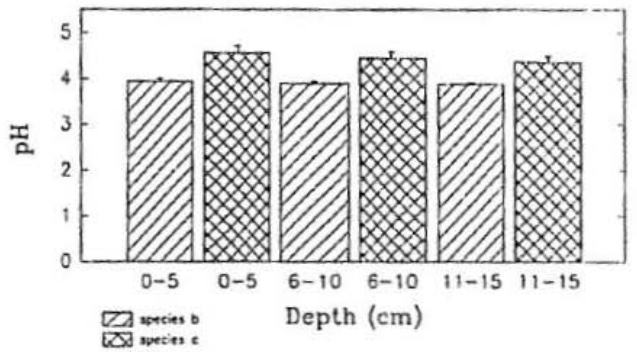
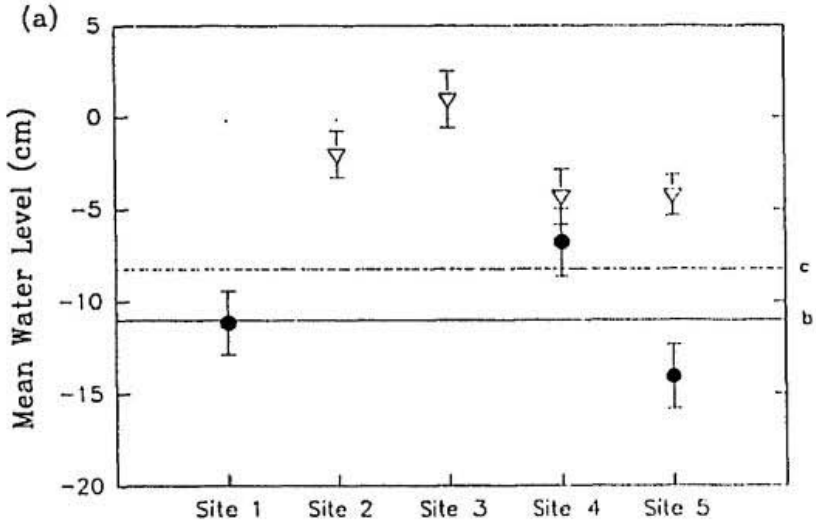

pH
5
4
3
2
1
0
0-5
0-5
6-10
6-10
11-15
11-15
Depth (cm)
species b
species c

Figure 24a. The relationship of mean water level and mean crown depth for *P. blephariglottis* and *P. clavellata* in sites 1-5 (Bars are one standard error).

Figure 24b The relationship of mean range (mean minimum to mean maximum) of water level and crown depth for *P. blephariglottis* and *P. clavellata* at all sites.

water level : ● - *P. blepariglottis*, ∇ - *P. clavellata*
crown depth : —— *P. blephariglottis* (b), --- *P. clavellata* (c)


(a)
Mean Water Level (cm)
5
0
-5
-10
-15
-20
c
b
Site 1
Site 2
Site 3
Site 4
Site 5

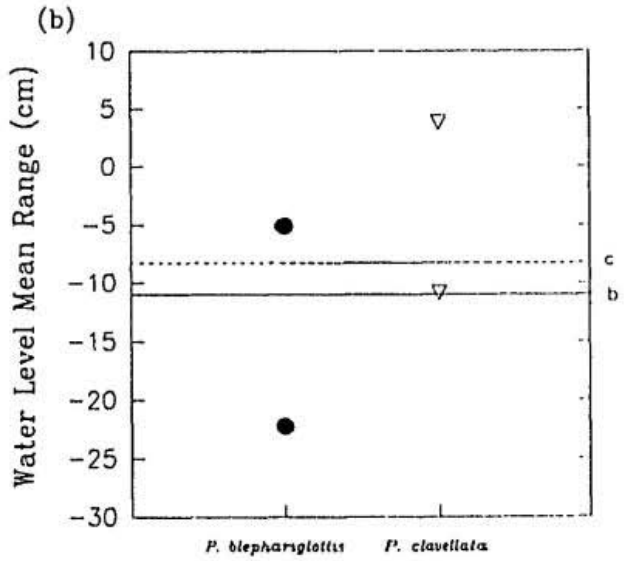
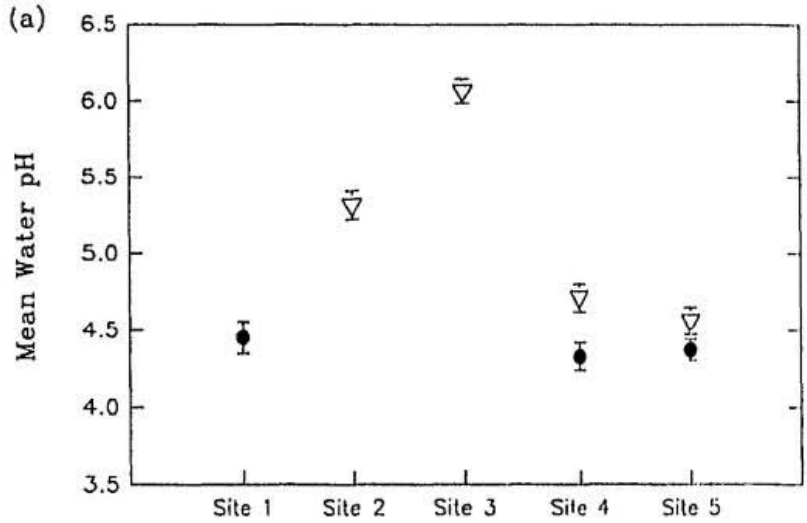

(b)
Water Level Mean Range (cm)
10
5
0
-5
-10
-15
-20
-25
-30
c
b
P. blepharigiottis
P. clavellata

Figure 25a. Mean water pH associated with *P. blephariglottis* and *P. clavellata* in sites 1-5 (Bars are one standard error).

Figure 25b. Mean water pH range (mean minimum to mean maximum) associated with *P. blephariglottis* and *P. clavellata* at all sites.

● - *P. blephariglottis*, ∇ - *P. clavellata*


(a)
Mean Water pH
6.5
6.0
5.5
5.0
4.5
4.0
3.5
Site 1
Site 2
Site 3
Site 4
Site 5

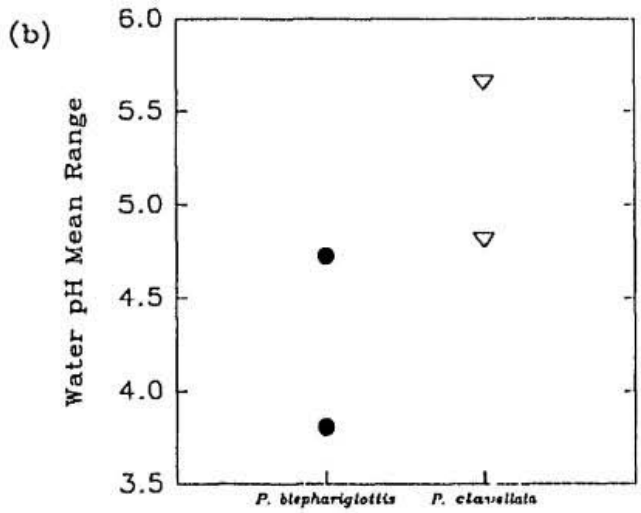

(b)
Water pH Mean Range
6.0
5.5
5.0
4.5
4.0
3.5
P. blepharigiottis
P. clavellata

Table 20. t test on peat constituents and water level associated with *P. blephariglottis* and *P. clavellata* at all sites. (P<0.004 significant)

Constituents	t	df	P
Magnesium (ppm)	-2.254	21	0.035
Phosphorus (ppm)	-3.568	21	0.002*
Calcium (ppm)	-3.588	21	0.002*
Moisture (ppm)	0.622	21	0.540
Water Level	-6.661	79	<0.001*

Table 21. Mann Whitney rank sum test on peat constituents, water pH and crown depth associated with *P. blephariglottis* and *P. clavellata* at all sites. (P<0.004 significant)

Constituents	T	P
Iron (ppm)	66	0.001*
Potassium (ppm)	104	0.336
Nitrogen (ppm)	107	0.438
Peat pH	67	0.001*
Organic Matter (%)	96	>1.00
Ash (%)	67	0.001*
Water pH	718	<0.001*
Crown Depth	102	0.006

Table 22. Range of means for peat constituents, water level and pH associated with *P. blephariglottis* and *P. clavellata* at all sites and range of crown depth measurements at site 4.

Constituents	Range of means for *P. blephariglottis*	Range of means for *P. clavellata*
Iron (ppm)	766.32 - 2,041.50	2,356.90 - 68,566.33
Potassium (ppm)	456.09 - 1,292.00	800.93 - 13,477.52
Calcium (ppm)	542.70 - 1,064.40	1,506.72 - 4,150.93
Magnesium (ppm)	447.76 - 881.93	797.05 -1,132.40
Nitrogen (ppm)	6,678.83 - 14,510.30	8,635.46 - 13,131.20
Phosphorus (ppm)	304.38 - 338.53	403.42 - 450.57
Peat pH	3.81 - 4.07	3.96 - 5.14
Moisture (%)	8.87 - 10.32	6.41 - 10.37
Organic Matter (%)	85.51 - 86.49	55.15 - 84.99
Ash (%)	3.65 - 5.61	5.42 - 38.44
Crown Depth (cm)	8.0 - 14.0	6.0 - 11.0
Water Level (cm)	-14.06 - -6.82	-4.33 - +0.96
Water pH	4.32 - 4.45	4.55 - 6.06

Figure 26. Water level in proximity of *P. blephariglottis* and *P. clavellata* in sites 1-5, 1991-1992 (— *P. blephariglottis*, --- *P. clavellata*).

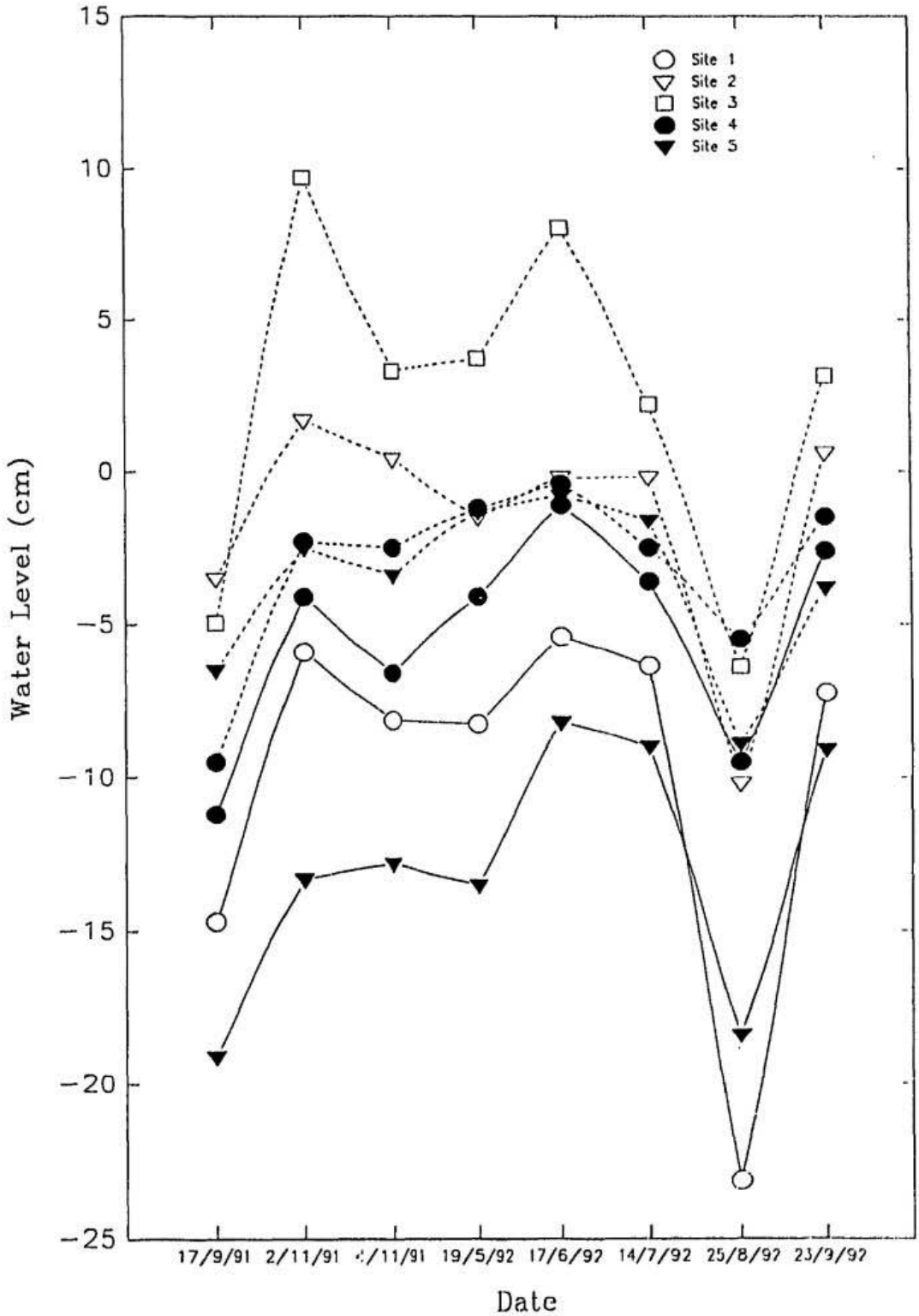
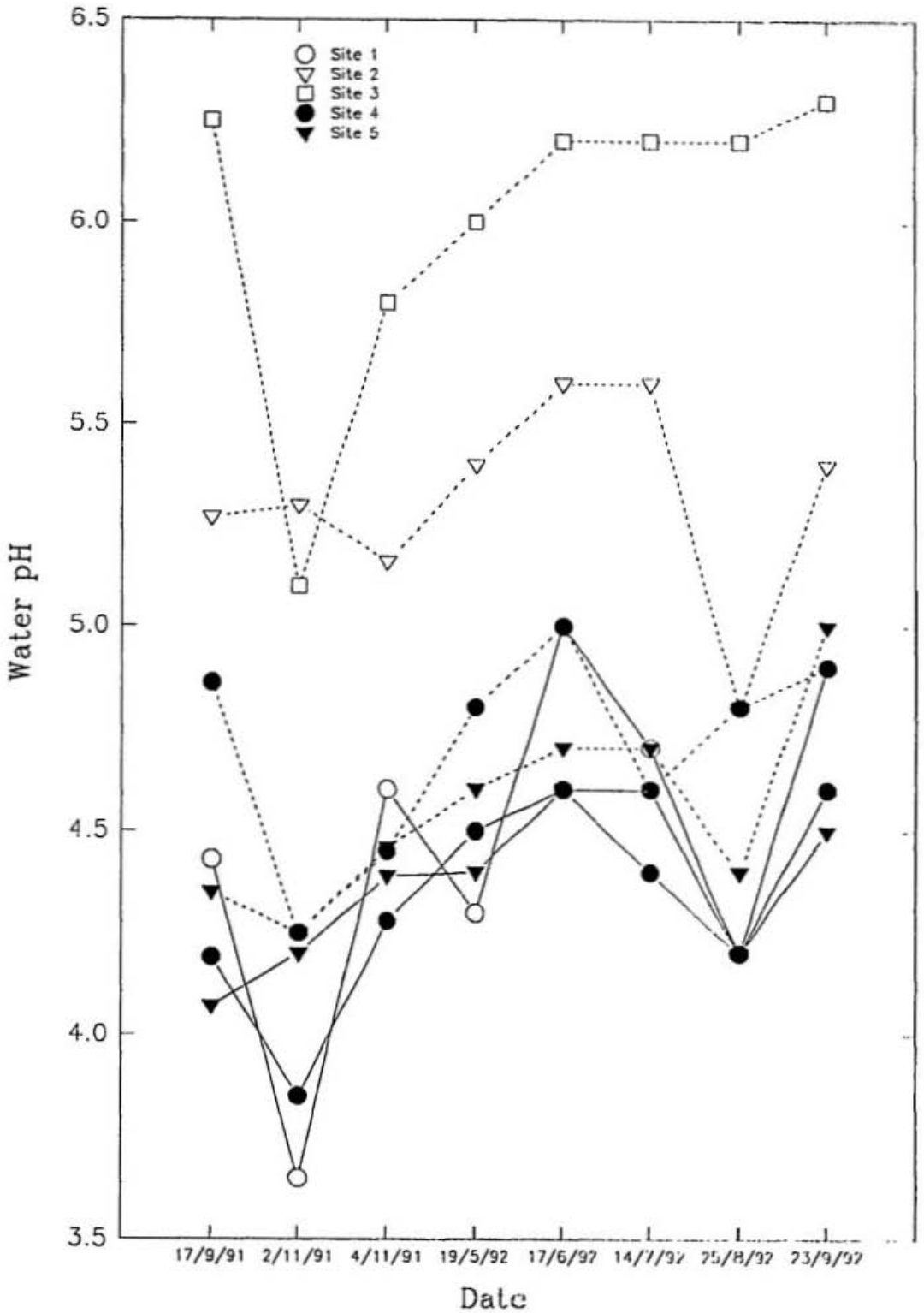

Site 1
Site 2
Site 3
Site 4
Site 5
15
10
5
0
−5
−10
−15
−20
−25
Water Level (cm)
17/9/91
2/11/91
19/5/92
17/6/92
14/7/92
25/8/92
Date

Figure 27. Water pH in the vicinity of *P. blephariglottis* and *P. clavellata* in sites 1-5, 1991-1992 (— *P. blephariglottis*, --- *P. clavellata*).


Site 1
Site 2
Site 3
Site 4
Site 5
6.5
6.0
5.5
5.0
4.5
4.0
3.5
Water pH
17/9/91
2/11/91
4/11/91
19/5/92
17/6/92
14/7/92
25/8/92
23/9/92
Date

blephariglottis to *P. clavellata* - 17.35cm, 15.4cm; *P. clavellata* to *P. clavellata* - 1.21cm, 1.16cm; *P. clavellata* to *P. blephariglottis* - 12.15cm, 12.38cm.

3.5.2 Isolation of Endophytic Fungi

Observations of isolates showed two saprophytic fungi, *Cylindrocarpon* and *Trichoderma sporulosum*,and two endophytic fungi, *Ceratorhiza* and *Phialocephala fortinii*, to be present. All isolates were identified by R. Currah, University of Alberta.*Ceratorhiza* and *P. fortinii* were found associated with both *P. blephariglottis* and *P. clavellata*, while *T. sporulosum* was found associated with *P. clavellata* only and *Cylindrocarpon* was found associated with *P. blephariglottis* only (Table 23).

Table 23. Fungal isolates from the roots and tubers of *P. blephariglottis* and *P. clavellata*.

Sources of isolates	Identifications of isolates
P. clavellata new tuber	*Ceratorhiza* *Trichoderma sporulosum* *Phialocephala fortinii*
P. clavellata new root	*Trichoderma sporulosum* *Ceratorhiza*
P. blephariglottis old tuber	*Phialocephala fortinii*
P. blephariglottis old root	*Cylindrocarpon*
P. blephariglottis new tuber	*Ceratorhiza*
P. blephariglottis new root	*Ceratorhiza*
P. blephariglottis new tuber and root	*Ceratorhiza*

4. DISCUSSION

4.1 Comparison of the Morphology of *P. blephariglottis* and *P. clavellata* at Study Sites and Representatives of North American Populations

All measurements of morphological characterstics made during this study were for the most part, either below or at the lower end of the range give for these species by Correll (1950) or Luer (1975). These species exhibit extreme variabilty in size over their north-south distributions (Correll, 1950; Hardin, 1961; Luer, 1975). Given that Newfoundland is at the northern end of these distributions, the small size of the individuals observed during this study would seem to agree with the observations of Correll (1950), Hardin (1961) and Luer (1975) of declining size with a more northern latitude. Flower number for *P. blephariglottis* and ovary length for *P. clavellata* being below the ranges given by Correll (1950) and Luer (1975) is most likely a result of the individuals in this study being at or near the limit of their northern distributions. The flower numbers for *P. blephariglottis* in this study more closely resemble those given by Cole and Firmage (1984) from a population in Kennebec County, Maine.

Hardin (1961) observed that, although the overall size of individuals of *P. blephariglottis* decreased with increased latitude, the decrease in size of morphological characteristics of the flowers of *P. blephariglottis* did not necessarily decrease in proportion to one another. This could explain the ovary length of *P. clavellata* being below the range

given for North America while all other flower characteristics had at least some measurements within the range. Bateman and Farrington (1989) also observed that the description given for *Orchis simia* in *Flora Europaea* tended to exclude individuals at or near the limit of the northern distribution. This could imply that the descriptions given by Correll (1950) and Luer (1975) are not sufficient to include the more northern individuals.

4.2 Population Dynamics of *P. blephariglottis* and *P. clavellata*

All sites showed an increase in number of individuals from 1991 to 1992 with the exception of *P. blephariglottis* in site 4. Although the populations increased in 1992, observations of marked plants showed a loss of individuals in both populations and in all sites. The increase in numbers of individuals could be a result of 'old' plants re-emerging after a subterranean dormant stage or the initial emergence of 'new' plants from the protocorm. The loss of indivduals could be due to the death of the plant or due to the plant returning to a subterranean stage (Wells, 1967; Tamm, 1972a). Since the time frame for this study was only 2 years and the individuals would have to be observed for a number of years to ascertain their approximate age or stage of development, this determination could not be made.

The sites that showed the greatest increase in the number of individuals were those where the species occurred alone: site 1 for *P. blephariglottis* and sites 2 & 3 for *P. clavellata*. The time elapsed between seed germination and emergence above ground is unkown for these species, but it would be reasonable to assume that the time period falls

somewhere in the ranges given for other terrestrial species, 2 to 10 or more years (Wells, 1981). If this is the case then factors influencing the sites, 2 or more years previous to this study, would be responsible for the increase in numbers of individuals. Since peatlands tend to change very slowly (Gore, 1983), it is unlikely that the habitat of these sites has changed drastically in 2 or 3 years. If the time frame for initial emergence from seed is longer, then the sites may be different at the present time from when the seed was released. Because of this it is difficult to assess if the present condition of the sites is suitable for successful seed germination.

If the assumption is made that the sites have not changed considerably since the seed was released (Gore, 1983) then the present conditions can be observed in terms of suitability for seed germination and growth, and survival of the protocorm. Site 1 had the lowest mean nutrient levels, with the exception of nitrogen. The presence of droppings along a moose path through the site may be the explanation for this site having the highest mean for nitrogen. The lowest means for peat and water pH, and water level were also observed in site 1.

Site 2 or 3 had the highest means for nutrient content of peat, with the exception of magnesium and nitrogen, as well as the highest means for peat and water pH, and water level. If these results can be related to success of seed germination and protocorm survival, then low pH, water level and nutrient content are the conditions best suited for *P. blephariglottis* recruitment, while a higher pH, water level and nutrient content are best suited for recruitment of *P. clavellata*. Another factor relavent to recruitment of orchids is the presence

of a fungus capable of forming a mycorrhizal association with the protocorm (Hadley, 1982; Currah *et al.*, 1989; Dixon, 1991). It may well be that an abundance of the symbionts is responsible for these sites having the greatest increase in the number of individuals.

While the populations of *P. blephariglottis* and *P. clavellata* increased, the number of individuals of both species in flower in 1992 decreased considerably from what was observed in 1991. This observation is similar to what has been observed for other species of terrestrial orchids (Robertson and Wyatt, 1990b; Kull and Kull, 1991; Wells and Cox, 1991). Wells (1967) states that a population of *Spiranthes spiralis* increased steadily while the number of flowering plants decreased. Tamm (1972a,b) describes the irregularity of flowering of 4 species of orchids, *Dactylorchis incarnata, D. sambucina, Orchis mascula,* and *Listera ovata,* as striking and noted that the frequency of flowering was more variable than that of *Primula veris* in the same meadow. The cause of fluctuations in numbers of flowering individuals of an orchid population is unknown, but it is thought to be due to a combination of factors that can vary with species and habitat.

An increase in precipitation the previous year may effect the flowering of a species positively in some sites and negatively in other sites. The effect will be determined by the moisture level the species normally tolerate and the condition of the site. Increased precipitation may make a 'dry' site more favourable and a 'wet' site less favourable for flowering (Tamm, 1991). Drought has been observed to reduce or prevent flowering (Willems and Bik, 1991). Low temperatures that delay emergence are thought to reduce the resources

translocated to the tuber and thus the possibility of flowering the following year. The present year's flowering can also be prevented if not enough carbohydrate reserves are present to allow the plant to respond to flowering stimulus (Willems and Bik, 1991). The summer of 1991 was cold (Appendix D) and a late frost occurred shortly after the flowers in the study sites began to open. The 1992 flower buds of *P. blephariglottis* and *P. clavellata* would have been formed during the late summer of 1991. The cold temperatures could have affected the development of bud primordia, tubers and roots by reducing nutrient uptake during 1991 and thereby limiting the nutrients available for plant growth in 1992.

Other studies suggest that weather is not the prime factor affecting flowering, but that the activity of the fungal symbiont may be of as great a significance in determining an individual's ability to flower (Light and MacConaill, 1991). Wells (1981) noted that plants exposed to similar conditions (temperature, moisture, microhabitat) did not flower with any predictability and suggested that fluctuation in mycorrhizal activity over a large area may be the cause of variations in flowering behaviour.

In order to be capable of flowering, an individual has to reach a certain size. Since individuals in this study had attained a size sufficient for flowering in 1991, this would not seem to be a factor influencing flowering percentages in 1992, unless the cost of flowering is very high. The reproductive effort of orchids varies considerably among species (Tamm, 1991) and the cost of reproduction for *P. blephariglottis* and *P.clavellata* is unknown.

Both populations were subjected to a late frost in 1991 when most of the flowers were open and again in 1992 when only a few of the flowers had opened. A consequence of this was that *P. blephariglottis* did not form any capsules in either year and *P. clavellata* produced a few capsules in three sites in 1991 and none in 1992. The difference in capsule set is probably due to the methods of pollination employed by the two species. *P. blephariglottis* requires a pollen vector, and capsule set has been shown to be pollinator-limited (Smith and Snow, 1976; Cole and Firmage, 1984), while *P. clavellata* is autogamous and is able to shed pollen onto the stigma as soon as the flower is open (Catling, 1983a). Calvo (1990b) also noted higher capsule set in autogamous species than in non-autogamous species. Since *P. blephariglottis* did not set fruit in 1991, it would seem that the cost of fruit production is not the reason for the decrease in flowering percentages in 1992. The *P. clavellata* population, which did form some capsules in 1991, had a 1992 flowering percentage of 14.1%. This percentage was higher than that of *P. blephariglottis* in 1992 (7.7%). If the cost of fruit production is similar in these two species then it would be expected that *P. clavellata* would have a lower flowering percentage in 1992 than *P. blephariglottis*. Since this was not the case, it seems unlikely that fruit production was the cause of the decrease in flowering percentages for *P. clavellata* in 1992. This is further supported by the fact that site 3 (*P. clavellata* only) had the greatest capsule set in 1991 and the largest percentage of individuals in flower in 1992. The results of a study on *Cyclopogon cranichoides* by Calvo (1990a) showed that fruit set had no effect on reproduction the following year.

4.3 Inter-site Studies

The morphological characteristics of *P. blephariglottis* showed no significant differences between the sites, with the exception of lateral sepal and lateral petal area. The ranking of the actual means of morphological characteristics showed neither site to be consistently larger or smaller, including the characteristics that showed significant differences. A study conducted by Robertson and Wyatt (1990a) on two populations of *P. ciliaris* suggests that variation in the size of floral structures could be the result of selection pressure by primary pollinators. The lip area needs to be the correct size to support the pollinator on landing and the spur length needs to be such that the pollinator comes in contact with the viscidia when probing for nectar. If the primary pollinators are different in different areas, then the size of floral structures could reflect that. There is nothing to suggest that the pollinators are different for the sites in this study, since all the sites are within a 6 km^2 area. It is unclear how differences in the size of lateral petals and sepals could affect pollinator success since the function of these structures would be to attract pollintors, and they constitute a very small part of the flower as a whole. The difference in the size of these strucutures between sites is unlikely to change the size of the flower to such a degree that pollinator activity would be affected. The lack of consistency in size of the morphological characteristics in relationship to site suggests that the differences observed are probably due to variation within the population itself (Hardin, 1961) and not due to environmental factors related to the site. The differences between environmental factors of the sites are not great enough to produce

individuals of *P. blephariglottis* that could be determined to belong to a particular site by observation of flower measurements.

All morphological characteristics of *P. clavellata* were significantly different between sites with the exception of the number of capsules. The ranking of the actual means for morphological characteristics showed site 3 to have the largest means and site 5 to have the smallest means for all characteristics with the exception of spur length. This would suggest that the environmental aspects of these sites are different enough to affect the size of individuals present in the sites.

Levels of total magnesium, phosphorus, nitrogen, potassium and calcium were not significantly different between sites. The only nutrient that showed any significant difference between sites was iron, with the fen (site 3) having the largest mean. A possible explanation for there being no significant difference between sites in the levels of other nutrients could be that sites 1,2 4 and 5 were located in areas of bogs that were slightly minerotropic. The slope of the bog, in sites 4 and 5, would allow for run-off from the surrounding wooded area to increase the nutrient content of the peat in the location of the orchids. Site 2 was down-slope from a gravel trail and the nutrient content of the peat was probably influenced by substances leached from the gravel by rain water flowing down through the site. Site 1 was also located next to a small incline that would have directed run-off into the area occupied by *P. blephariglottis* (Damman and Dowhan, 1981). It is interesting to note that Damman and

Dowhan (1981), in their study of a plateau bog in Nova Scotia, did not find any significant difference in the nutrient content of the bog and in that of the surrounding fen.

It should be noted that while the means for nitrogen and pH obtained during this study were comparable to those given by Wells (1981) for peatlands of the Avalon Peninsula, the means for calcium and iron were much higher than those reported by Wells.

The overlap in the species present in the fen and the bogs given in the species lists for the sites (Appendix A) would also support the notion of sites 1,2,4 and 5 being slightly minerotropic areas. Two species, *Myrica gale* and *Scirpus cespitosus*, that are listed by Damman and Dowhan (1981) as being present in particular types of extremely nutrient-poor fens were present in all 5 sites. Other species (*Aster nemoralis, Solidago uliginosa, Carex rostrata*) that are known to occupy minerotropic areas of slope bogs (Wells, 1981) were also present in all or some of the bog sites.

Although the nutrient content of peat was, for the most part, not significantly different between sites, the actual means for phosporus, iron and calcium were highest for site 3. High iron content in the fen is likely the result of run-off from mineral soil (Damman and Dowhan, 1981). There were periods in both 1991 and 1992 that site 3 was inundated by water flowing from a forested area. The large amounts of water moving into site 3 would also increase the presence of other nutrients, such as phosphorus and calcium (Damman, 1978). Magnesium, nitrogen and potassium levels were not highest in site 3, but this may be a reflection of a

higher productivity level (Damman and Dowhan, 1981) and the presence of larger plants of *P. clavellata* in this site would seem to support this. Although nitrogen was most abundant in site 1 (bog), the availibility of nitrogen is related to pH. The solubility of nitrogen, as well as other nutrients, decreases with pH and the amount available for uptake by plants is reduced (Bidwell, 1979). The presence of bacteria responsible for converting nitrogen into a form that can be utilized by the bog flora also decreases with pH (Moore and Bellamy, 1974).

Peat pH, water pH and water level were highest in sites 2 and 3 (*P. clavellata* only), followed by sites 4 and 5 (both species) and then site 1 (*P. blepharigiottis* only). The rate of water flow through a peatland has a direct effect on pH. As the rate of water flow increases so does the pH, since acidic by-products will be flushed away (Moore and Bellamy, 1974; Wells, 1981). This same phenomenon was observed in the study sites. When rain increased the water level, the water pH also increased. The pH also has an effect on the presence of bacteria that break down the peat and, thus, has an effect on the amount of organic matter and ash present in the peat samples. Peat samples from sites 2 and 3 had the lowest organic matter content and the highest ash content as an indirect result of increased water flow and pH.

The general trend exhibited by the sites seems to suggest that if the sites were ranked on the basis of nutrient content, site 3 would rank highest and site 1 lowest. Although the sites do not consistently have higher or lower means, they can be ranked on the basis of most often having means that are higher or lower than all other sites. Site 2 appears to rank next after site 3 and site 5 tends to fall below site 2 and above site 1. Site 4 means tend to be lower

than site 3 means and higher than site 1 means with no distinct position in between. This same trend is shown by the means of peat pH, water pH and water level. Based on these trends, site 3 can be described as a nutrient-rich, very wet peatland with a fairly high pH and site 1 can be described as a nutrient-poor, fairly dry peatland with a more acidic pH.

Based on the observations of the largest plants in site 3, one can make the assumption that this is an optimum site for *P. clavellata.* If this is true then it would naturally follow that *P. clavellata* should be most abundant in this site. In actual fact site 3 had one of the lowest numbers of individuals present and sites 4 and 5 had the greatest numbers of *P. clavellata.* The most likely explanation for this is probably the number of 'safe sites' available for seed germination (Harper, 1977). Site 3 was hummocky with pools of standing water. During periods of heavy rainfall, water flowed through the site leaving only some of the hummocks above water. Any seed deposited in areas other than the hummocks that remained above water would be washed away. Sites 4 and 5, which may not have optimal conditions for plant size and flowering, had more 'safe sites' to receive seed once it was released for dispersal.

The sites where *P. blephariglottis* and *P. clavellata* occurred alone (sites 1,2,3) showed a more or less even distribution of individuals along the transects and the sites where both species were present (sites 4,5) had *P. blephariglottis* and *P. clavellata* clumped in fairly distinct areas. Dixon (1991) suggests that the presence of an orchid can increase the presence of mycorrhizal fungi in the soil and thus the potential for seed germination. Both of the fungi isolated, that are mycorrhizal with orchids, were found associated with both species. If it is

assumed that the presence of these fungi can have an equal affect on the success of seed germination in both species, it would appear that some other factor is influencing their distribution in sites 4 and 5.

A comparison of morphological characteristics of *P. blephariglottis* from sites 4 and 5 showed significant differences in lateral sepal and lateral petal area and, as discussed previously, it is assumed that this is a reflection of the variability within the population, since neither site had the largest mean for both characteristics. Unlike *P. blephariglottis*, *P. clavellata* from site 5 had consistently smaller means for those characteristics that were significantly different when the two sites were compared. Although a comparison of the peat constituents from sites 4 and 5 did not show any significant differences, with the exception of moisture, site 5 had the smallest mean for 8 of the 12 constituents considered. This would seem to suggest that *P. clavellata* is affected to a greater degree by slight variations in peat constituents and that the effect is reflected in plant size. Although nutrient content of the peat was somewhat variable when comparing the two sites, the peat pH, water pH and water level were consistently lower in site 5 than in site 4. Site 5 had the lowest peat pH, water pH and water level of all the sites where *P. clavellata* was present. The small size of the plants in site 5 may be due to the plants being in a site that is at or near the lower limit of their tolerance for water level and pH rather than a reflection of the nutrient content.

4.5 Interspecific Studies

The results of the measurements between individual plants, as well as the graphs for transects 4 and 5 suggest something other than a random arrangement of these species within a peatland. The fact that the two species appear to be clumped in distinct areas implies that they are partitioning the habitat on the basis of some environmental parameter.

Of the peat constituents that were significantly different between species (iron, calcium, phosphorus, ash, peat pH), the means for *P. clavellata* were higher than those of *P. blephariglottis*. Of the variables that were not significantly different between species, only crown depth, nitrogen and magnesium had higher means associated with *P. blephariglottis*. When the range of means was considered, the largest ranges, with the exception of magnesium, nitrogen, crown depth and water level, were also associated with *P. clavellata*.

The *P. clavellata* population observed during this study would appear to be found in peatlands with a much wider range of nutrient content as well as a much wider range of peat pH and water pH , while the range of nutrient content of peat and peat pH and water pH in areas of peatland occupied by *P. blephariglottis* would seem to be narrower.

The means for water level associated with *P. clavellata* were higher, with a narrower range, while the mean water levels and range of means for water levels associated with *P. blephariglottis* were lower with a greater range. This suggests that *P. blephariglottis*

occupies sites that are drier than those occupied by *P. clavellata*. This was also evident when *P. blephariglottis* and *P. clavellata* were found in the same site. The actual water level measurements for *P. clavellata* were always higher than those for *P. blephariglottis*. The crown depths of the two species were not significantly different, but the mean crown depth for *P. blephariglottis* was greater than that of *P. clavellata* and is most likely a reflection of the size of the individuals of the species. The crown of the two species is also placed in different positions in relation to the water level, with *P. clavellata* having its crown for the most part below the water level and *P. blephariglottis* being more variable with the crown below, above or at the water level.

As discussed previously, water pH and peat pH are affected by water flow into a peatland and the higher pH levels were found in the areas with the highest water levels and thus are also associated with *P. clavellata.* The fluctuation in water pH corresponded with the fluctuation in water level and an increase in precipitation caused an increase in water levels and an increase in water pH.

It would appear that although *P. clavellata* occupies areas with a higher nutrient content (site 3) than *P. blephariglottis* (site 1), *P. clavellata* can also occupy sites with a lower nutrient content (sites 4&5). Since *P. blephariglottis* was also found in sites 4 and 5 and for the most part nutrient content of all the sites was not significantly different, it would seem that *P. blephariglottis* and *P. clavellata* do not partition the habitat on the basis of nutrient content of peat.

The environmental factor that appears to determine the distribution of these two species within a peatland is water level. *P. clavellata* was consistently found in areas with higher water levels, while *P. blephariglottis* occupied the areas with lower water levels. This was true when the species occurred alone or together. Higher pH values are also associated with *P. clavellata*, but that may only be a consequence of the higher water levels and not relevant to how *P. blephariglottis* and *P. clavellata* partition the habitat. The actual water level reading for the species show virtually no overlap, while the pH values tend not to be so distinctly separated on the basis of association with species. A study of a number of species of *Phlox* states that the sensitivity of a population to an environmental parameter can be independent of the sensitivity to other environmental variables. A correlation of responses to a pair of variables may not mean that the population is sensitive to both but that one variable may have an influence on another; for example moisture in soil can affect nutrient content and close proximity of plants can be viewed in terms of competition or as an effect on light availability (Schwaegerle and Bazzaz, 1987). The results of a study of co-occurring species of *Solidago* found that the species have distinct positions along the soil moisture gradient (Werner and Platt, 1976). If soil moisture can influence plant distribution in other areas, it would not seem unreasonable that water level could be the determining factor for the distribution of *P. blephariglottis* and *P. clavellata* within peatlands. This would also be similar to the results of a study by Boland and Scott (1992) where water level had an effect on the distribution of the peatland orchids, *Arethusa bulbosa, Calopogon tuberosus* and *Pogonia ophioglossoides*.

The presence of fungi that can form mycorrhizae is another factor that can determine if an orchid species can become established in a particular area. Two fungi that are mycorrhizal with orchids, *Ceratorhiza* sp.and *Phialocephala fortinii* (Currah and Zelmer, 1992), were isolated and found to be associated with both *P. clavellata* and *P. blephariglottis*. Both fungi are common in isolates of orchid mycorrhizas and *Phialocephala fortinii* has also been isolated from *Pinus resinosa* and *P. sylvestris* (Currah *et al.*, 1987). Since the two endophytes were found associated with both species, it would seem that these fungi would not be a factor in how the two species partition the habitat. The fact that both endophytic fungi were associated with both species would be consistent with the belief that endophytic fungi exhibit more specificity with habitat than with particular orchid species (Smith, 1974; Ramsay *et al.*, 1987).

The saprophytic fungi, *Cylindrocarpon* and *Trichoderma sporulosum*, were not found associated with both species, but it would be unlikely that their presence would have any effect on the success of the individual plants in a particular area, as they are commonly encountered as isolates from both terrestrial and epiphytic orchid mycorrhizae and there is no evidence that they have any detrimental effect on plant growth (Currah and Zelmer, 1992).

5. CONCLUSIONS

The morphological characteristics of *P. blephariglottis* and *P. clavellata* in the sites observed tended to be towards the lower end or below the size ranges given for North American populations. This is most likely the result of these species being at or near the northern limit of their distributons. Differences in size of morphological characteristics for *P. blephariglottis* appear to be due to variation within the population itself, and for *P. clavellata* the variability would seem to be due to a combination of variability within the population and differences between the environmental parameters in the sites.

Both populations exhibited fluctuations in flowering percentages, similar to those observed in populations of other species of terrestrial orchids. The cause of substantial decreases in flowering percentages is unknown but is thought to be due to one or all of: weather, cost of production of flower structures, activity of endophytic fungi. Any or all of the factors could have played a role during this study. An increase in size of population was seen for both *P. blephariglottis* and *P. clavellata*. This would indicate that conditions are such that successful reproduction can occur in these sites, if not every growing season.

Nutrient content of the sites was variable and for the most part showed no significant differences between sites. Ranking of the means for peat constituents, water pH and water level place the sites within a gradient from more nutrient-rich with a higher water and peat pH and water level to less nutrient-rich with a lower water and peat pH and lower water level.

P. clavellata was present in all sites with the exception of the site with the combination of lower nutrient content and lower water pH and water level. *P. blepharigIottis* was present in the sites with the lower nutrient content and lower water pH and water level. The tendency for *P. clavellata* to be associated with the areas with higher water and peat pH and higher water levels and *P. blepharigIottis* to be associated with areas of lower water and peat pH and lower water levels was also evident when both species occurred in the same site. Some overlap in water and peat pH was evident, while water level associated with the species shows a greater separation. This would suggest that water level is the parameter that these species utilize to partition their habitat.

If indeed water level is the parameter that determines the distribution of these species, then any factor that changes the hydology of a peatland would also have an effect on the success of these species. Draining of peatlands has a drastic effect on these and many more peatland species, but the use of all-terrain vehicles also can change peatland hydrology. Some areas, where the same trails have been used for years by people with all-terrain vehicles, have had the growing portion of the peat completely destroyed, resulting in erosion of peat down to bedrock. The channels formed by peat erosion change the water flow considerably by causing water that would have been held by the peat to seep into the ruts from the sides of the channels. Even areas where the growing portion of the peat is still intact after all-terrain vehicle use have depressions that direct water flow through the peatland in a much different manner.

The endophytic fungi that were isolated were found associated with both species and this would seem to agree with the suggestion that the fungi are more closely associated with habitat than with a particular species. This would also imply that the distribution of each species is not depend upon a particular fungus. Since both species were associated with both endophytic fungi then both species can make use of a site where either fungus is present. It would be unlikely then that *P. blephariglottis* and *P. clavellata* partition the habitat on the basis of the presence of endophytic fungi.

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APPENDIX A

Vascular plant list for all sites

Vascular Plant	Site				
	1	2	3	4	5
Lycopodium obscurum	+				
Osmunda regalis		+			p
O. cinnamomea					p
Pteridium aquilinum	+				
Picea mariana	1				p
Larix laricina			+	+	+
Juniperus communis	2				
Calamagrostis pickeringii	1	1	3	1	2
Scirpus cespitosus	2	4	1	2	1
Eriophorum angustifolium					+
Carex exilis	+	+	4	2	1
C. interior					p
C. livida					p
C. flava				+	p
C. pauciflora	2		+	+	
C. rostrata					1
Smilacina trifolia			1	r	
Maianthemum canadense	r				
Iris versicolor					p
Platanthera clavellata		+	+	1	1
P. dilatata			p		p
P. blephariglottis	+			1	1
P. lacera		p			
Arethusa bulbosa	+				
Myrica gale	1	+	1	1	1
Betula papyrifera		+			
B. michauxii	+	1		+	+
Geocaulon lividum	+			r	
Thalictrum polygamum					+
Coptis trifolia	1	+	+	+	
Sarracenia purpurea	1	+	1	1	+
Drosera rotundifolia	+	+	+	+	+
Aronia prunifolia	+	+		+	p
Amelanchier bartramiana		+	r		
Rosa nitida				+	p
Empetrum nigrum					p

Nemopanthus mucronata	1		+	+	
Viola cucullata					+
V. pallens					+
Cornus canadensis	+	+		1	
Ledum groenlandicum	+	+	r	+	
Rhododendron canadense	+		r	+	
Kalmia angustifolia	1	+	+	+	
K. polifolia	+		+	+	
Andromeda glaucophylla	+	+	2		
A. polifolia				1	
Chamaedaphne calyculata	+		+	+	p
Gaylussacia dumosa	1	+		1	
Vaccinium angustifolium	+	+			p
V. oxycoccos	1	+	2	1	+
V. macrocarpon				r	
Trientalis borealis			r	r	
Lonicera villosa					p
Linnaea borealis		+			p
Viburnum cassinoides	+			+	
Solidago uliginosa	+	+	+	1	+
Aster nemoralis	+	+		+	+
A. blakei		+	r	r	

APPENDIX B

Population dynamics of total populations of *P. blepharigiottis* (b) and *P. clavellata* (c) for 1991 and 1992

Year	Site	Species	Total Flowering	Total Non-flowering	Total Number of Individuals	Total Recruits *
1991	1	b	36	140	176	35
1992	1	b	8	203	211	
1991	2	c	13	13	26	18
1992	2	c	11	33	44	
1991	3	c	29	14	43	10
1992	3	c	26	27	53	
1991	4	b	21	71	92	-8**
1992	4	b	17	67	84	
1991	4	c	55	145	200	48
1992	4	c	29	219	248	
1991	5	b	34	33	67	5
1992	5	b	9	63	72	
1991	5	c	41	206	247	18
1992	5	c	19	246	265	
1991	all	b	91	244	335	32
1992	all	b	34	333	367	
1991	all	c	138	378	516	94
1992	all	c	85	525	610	

* individuals not marked in 1991 ** loss of individuals

APPENDIX C

Number of permanently tagged individuals in 1991 and 1992 (b = *P. blephariglottis* and c = *P. clavellata.*)

	Site 1 b	Site 2 c	Site 3 c	Site 4 b	Site 4 c	Site 5 b	Site 5 c	Total b	Total c	Total b & c
Number of plants 1991	91	26	18	50	76	36	74	177	194	371
Number of plants 1992	53	21	12	43	50	30	64	126	147	273
Number flowering 1991	60	13	12	12	26	14	14	86	65	151
Number flowering 1992	4	5	8	4	10	2	2	10	25	35
Number nonflowering 1991	31	13	6	38	50	22	60	91	129	220
Number nonflowering 1992	49	16	4	39	40	28	62	116	122	238
Number flowering 1991 & 1992	2	1	6	1	2	0	0	3	9	12
Number nonflowering 1991 & 1992	18	9	1	30	21	16	50	64	81	145
Number flowering 1991 & nonflowering 1992	31	7	3	9	19	12	12	52	41	94
Number nonflowering 1991 & flowering 1992	2	4	2	3	8	2	2	7	16	23
Number of missing tags 1992	28	0	4	1	17	3	5	32	26	58
Number of missing plants 1992	10	5	2	6	9	3	5	19	21	40

APPENDIX D

Mean monthly temperatures for the St.John's area for June to September in the years 1989 to 1994 from the Monthly Meterological Summary at St.John's, Environment Canada, Atmospheric Environmental Service.

Year	June	July	August	September
1989	11.8	15.5	17.3	13.1
1990	12.1	14.2	17.7	12.6
1991	9.0	13.8	14.3	11.9
1992	10.6	12.5	15.1	12.9
1993	9.2	12.4	14.1	12.2
1994	11.4	16.8	17.6	11.8