Ecological, Ethnobotanical, and Nutritional Aspects of Yellow Glacier Lily, *Erythronium grandiflorum* Pursh (Liliaceae), in Western Canada

by

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ABSTRACT

This research examined a single bulb-bearing edible plant species, yellow glacier lily (*Erythronium grandiflorum*). Three main approaches to the research were taken:

1) an ecological study, to determine the general habitat requirements of the species in western Canada, and to investigate the nature of vegetative reproduction in the species;

2) an ethnobotanical study, consisting of an extensive literature search for all recorded First Nations' uses of the species (in Canada and elsewhere), in addition to interviews with contemporary Interior Salish elders;

3) a nutritional study, examining in detail the nutritional characteristics of the bulbs, and particularly changes in the carbohydrate content over the course of the growing season and with different types of treatments.

The ecological data indicate that *E. grandiflorum* is more abundant in meadow environments or sites with deciduous cover than in sites with coniferous forest cover. Flowering plants tended to be more abundant and robust at low elevation meadows, while seedlings and juveniles were disproportionately represented at high elevation meadows. Decreased juvenile success in the low-elevation meadows may be related to relatively high litter from shrubs and grasses. Experimental data indicate that appendages on the bulbs, which persist as remnants of previous years' bulbs, can act as vegetative propagules if mechanically separated. In addition, both bulbs and appendages were successfully transplanted over a two-year period from a subalpine meadow to a very different habitat type, 1500 m lower in elevation.

The ethnobotanical review confirms that the species was traditionally a highly significant root resource for northern plateau peoples, particularly the Secwepemc and Nlaka'pamux peoples, for probably thousands of years. These peoples collected, stored, and traded large quantities of the bulbs, and the traditional processing strategies generally included drying and pit-cooking. People developed a detailed ecological understanding of the species, and practiced active resource management strategies.

Nutritional results indicated a carbohydrate-rich food resource, with the main storage carbohydrate consisting of starch (not inulin or other fructan) through most of the growing season. There are significant quantities of sugars (including fructo-oligosaccharides) present at the beginning of the growing season, but starch increases rapidly and peaks (along with overall food value) in the early (green) fruit stage of growth. For bulbs at the fruiting stage, drying markedly increases sugars in the bulbs relative to starch, while pit-cooking the dried bulbs does not have significant effects on relative amounts of carbohydrates. However, pit-cooking has important qualitative effects on the appearance, taste, and possibly storage properties of the bulbs, as well as representing an efficient processing strategy.

I argue that traditional harvesting and management strategies practiced by First Nations people (including tilling, thinning, replanting of appendages, and landscape burning) mean that the ecology and ethnobotany of the species cannot be considered in isolation. Based on previous ecological and ethnoecological work on this and similar species, it seems likely that yellow glacier lily is adapted to a periodic, moderate disturbance regime, which traditional practices may have mimicked or enhanced.

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DEDICATION

This thesis is dedicated to past, present, and future generations of Secwepemc and other northern plateau peoples, whose relationships with the yellow glacier lily add a special dimension of meaning to its beauty.

1.0 Introduction

> It seems to be a general rule that sciences begin their development with the study of the unusual. They have to develop considerable sophistication before they interest themselves in the commonplace. (Linton 1944:369)

The yellow glacier lily, *Erythronium grandiflorum,* is not a rare or apparently unusual plant in western Canada. Yet, the very fact that it has an exceptionally large range makes *E. grandiflorum* unusual among western North American members of the genus, some of which are localized endemics (Shevock et al. 1990). However, no previous studies have examined the habitat requirements of this wide-ranging species within its Canadian range. Rather, studies of the species have focused on its pollination biology (Thomson and Stratton 1985, Fritz-Sheridan 1988, Thomson and Thomson 1989, Cruzan 1990a, b, Holsinger and Thomson 1994, Thomson et al. 1994, Rigney 1995, Cruzan and Thomson 1997), seed dispersal (Weiblen and Thomson 1995), seed dormancy (Baskin et al. 1995), photosynthetic physiology (Hamerlynck and Smith 1994), and phenology (Caldwell 1969). In addition, one study (Thomson et al. 1996) examined micro-distribution of glacier lilies in relation to pocket gopher activity in a meadow complex in Colorado.

The ecology of yellow glacier lily is of particular interest because the bulbs have been a highly significant food resource for First Peoples on the northern interior plateau for probably thousands of years. The ecology and ethnobotany of the species represent areas of inquiry that can be pursued fruitfully individually, but they are also interrelated. Ecological (and in this case, nutritional) characteristics determine whether a species will become culturally significant, but human use of a species can in turn influence its ecology. The more common and useful a species is for a group of people, the more significant the ethnobotanical/ecological interactions become.

My research on *E. grandiflorum* is interdisciplinary, as I have tried to address a wide range of apsects relating to this species. In Chapters 2 through 4, I consider ecological, ethnobotanical, and nutritional aspects of the species. Chapter 2 describes a preliminary examination of the autecology of yellow glacier lily in the Canadian portion

of its range, as well as new data concerning the capacity for vegetative reproduction in this species. Chapter 3 discusses the relationships of First Peoples with yellow glacier lily across its range, with the main focus on the extensive use of the edible bulbs by peoples of the northern interior plateau. Chapter 4 examines the nutritional, and particularly carbohydrate, characteristics of the bulbs in detail. Chapter 5 provides an integration of the ecological and ethnobotanical aspects of the species.

The remainder of this chapter reviews the taxonomy, distribution, and biology of *Erythronium grandiflorum*.

1.1 Background

> Sometimes, when one looks at a plant such as the erythronium, one realizes that here is a living lesson in aesthetics: the miraculous hoop of the arching peduncle, the intricate stamen and stigma structure, the winged stateliness of the reflexing petals, the silken texture, the blending of colour tones, the amazing exactitude of each part, each aspect of the total presentation. They are all minor miracles . . . (Watson and Woodward 1974:36)

1.1.1 Taxonomy of the Genus and Species

The genus *Erythronium* L. belongs to Tribe Tulipeae of the Family Liliaceae, and includes some 24-30 species distributed in the northern temperate regions of North America, Europe, and Asia (Mathew 1992). From one to four species occur in Europe and Asia, and six species occur in eastern North America (Mathew 1992). However, the greatest diversity of species in the genus (ca. 18) is found in North America west of the Rocky Mountains, particularly in California and Oregon (Mathew 1992). These western species have been divided into two sections by Applegate (1935). Section *Pardalinae* includes the species with mottled leaves, while Section *Concolorae* (in which *E. grandiflorum*, yellow glacier lily, is placed) includes those with unmottled leaves.

There are numerous English common names for *Erythronium grandiflorum* Pursh, in addition to yellow glacier lily: yellow avalanche lily, yellow fawn lily, snow lily, rock lily, yellow dogtooth violet, dogtooth lily, lamb's tongue, adder's tongue, kamara root,

yellow Easter lily, and Indian potato or Indian sweet potato (Indian potato is often used for *Claytonia lanceolata* Pursh, spring beauty, as well).

Scientific nomenclature has been even more prolific (see Mathew [1992] for details); however, most of the synonyms used historically are well out of date and rarely encountered today, and there is little taxonomic debate about what *Erythronium grandiflorum* does and does not include at the species level. However, there is some question as to whether anther colour variation is of subspecific taxonomic significance, as Applegate (1935) believed. The current consensus appears to be that this feature is of minor, if any, taxonomic importance (Hitchcock et al. 1969, Cronquist et al. 1977, Shevock et al. 1990). Therefore, such divisions as *E. grandiflorum* var. *pallidum* St. John, *E. grandiflorum* subsp. *chrysandrum* Applegate, and *E. grandiflorum* var. *parviflorum* S. Watson are not currently recognized. A recently included taxon is *Erythronium nudipetalum* Applegate, which is endemic to Bear Valley, Idaho. This taxon is now generally accepted as *E. grandiflorum* var. *nudipetalum* (Applegate) C.L. Hitchcock (Mancuso and Moseley 1991, Mathew 1992). Recent separations from the species include *E. pusaterii* (Munz & J.T. Howell) Shevock, Bartel & Allen, elevated from a subspecies of *E. grandiflorum* (Shevock et al. 1990), and *E. idahoense* St. John & Jones (Mathew 1992). Fritz-Sheridan (1988) presented evidence that the latter is in fact a separate biological species, and should no longer be designated *E. grandiflorum* var. *candidum* (Piper) Adams (or *E. grandiflorum* var. *albiflorum* Purdy, *E. grandiflorum* subsp. *candidum* Piper, *E. grandiflorum* var. *idahoense* [St. John & Jones] Davis). *E. grandiflorum* is not known to hybridize naturally with any congeners, including *E. idahoense* (Fritz-Sheridan 1988).

In summary, the most recent information suggests that *E. grandiflorum* represents a large and diverse taxon, with only two currently recognized varieties: *E. grandiflorum* var. *grandiflorum*, spanning the range of the species (see next section), and *E. grandiflorum* var. *nudipetalum*, endemic to a small area of Idaho. Since my research focuses on the species in its Canadian range, it can be assumed that *E. grandiflorum* var. *grandiflorum* is the taxon to which I refer throughout.

1.1.2 Distribution

The general distribution of *Erythronium grandiflorum* in western Canada is shown in Figure 1.1. The site shown in the far northwestern part of British Columbia (around Dease Lake) may be an erroneous report. Yellow glacier lily is common in the southern half of B.C. and southwestern Alberta, and is the only *Erythronium* east of the Coast Ranges in B.C. It follows the Coast/Cascade Mountains and the Rocky Mountains south as far as northern California and New Mexico, but it is apparently absent from the Sierra Nevada and the Great Basin (see Fritz-Sheridan [1988] for a distribution map covering the U.S. portion of the range).

Published sources from the Rocky Mountains indicate an elevational range for glacier lily in the U.S. of 700 to 3700 m (Spence and Shaw 1981, Fritz-Sheridan 1988, sources cited in Williams 1990), though populations in Washington around the Columbia Gorge occur as low as 200 to 300 m (Dr. Geraldine Allen, pers. comm. 1998). In Canada, herbarium specimen records indicate a range of 500 to 2300 m; most are closer to the high end of the range in British Columbia. Most sites in Alberta vary from the middle to upper end of the range.

A variety of habitat types have been described for *E. grandiflorum*: sagebrush slopes to montane forest (Hitchcock et al. 1969); semi-dry montane valleys to snowbank edges in alpine meadows (Fritz-Sheridan 1988); partial shade but also more open habitats (Kuijt 1982); open meadows and aspen woodlands in the Rocky Mountains (Rigney 1995); moist slopes and in shaded areas, in mountain brush, western hardwoods, lodgepole pine, spruce-fir, grand fir, Douglas-fir, Interior ponderosa pine, or wet meadow areas (Williams 1990). Various sources indicate that the species prefers fertile, fairly deep soils with high moisture-holding capacity (Kuijt 1982, Williams 1990); however, this is probably true for most plants, and there is no indication to what extent such substrates are required for this species to exist in an area. Even the more general statement that the species is "mesic" is called into question by Hitchcock et al.'s (1969) observation that it grows on sagebrush slopes, though to my knowledge glacier lilies have not been found in such habitats in British Columbia. Yellow glacier lily has been

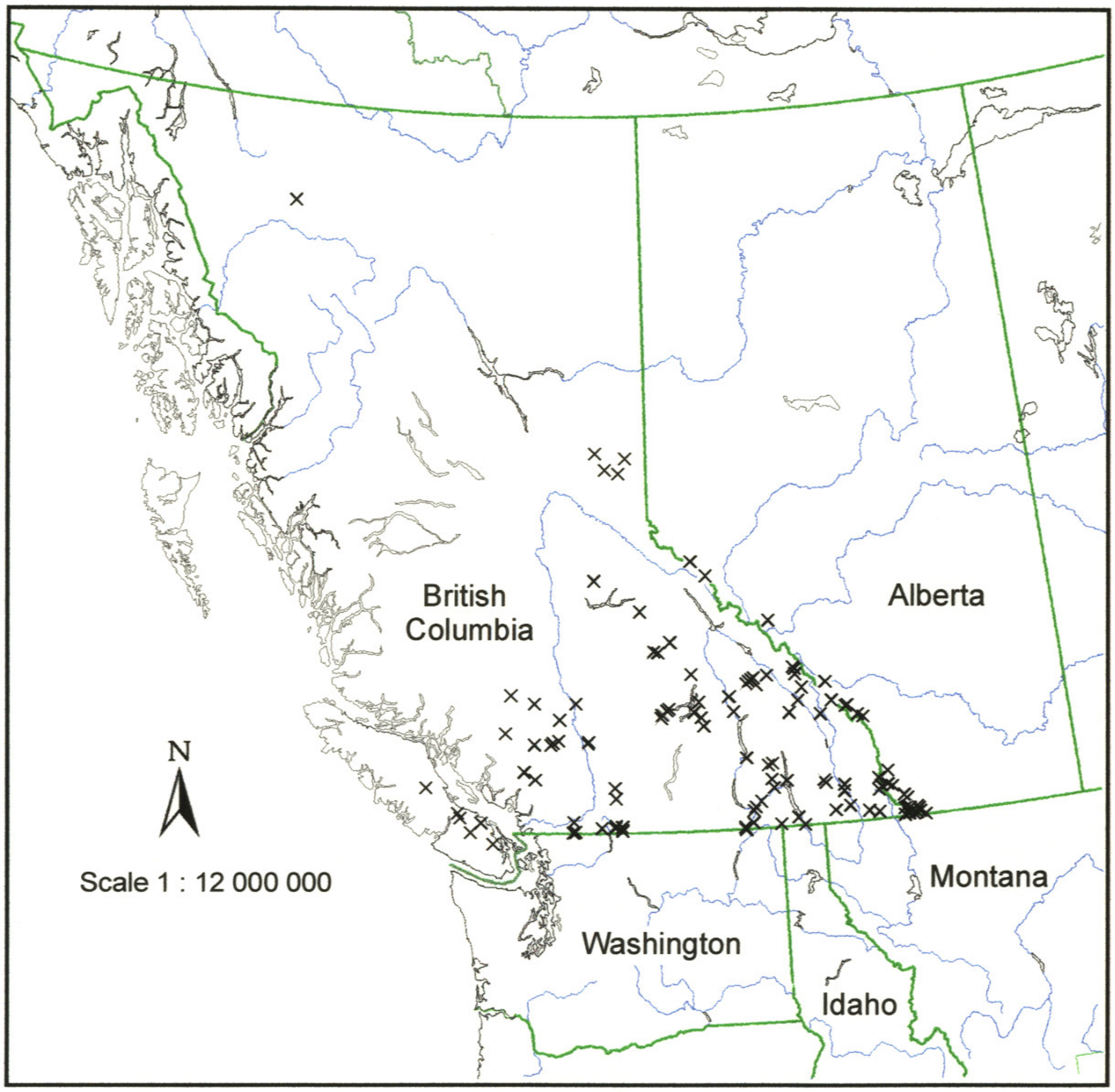

Figure 1.1 Range of *Erythronium grandiflorum* var. *grandiflorum* in western Canada. Marked locations indicate specimens at CMN, RBCM, UBC, and UVIC Herbaria (including specimens collected during this study).

reported from serpentine soils in the Serpentine Barrens area of Wenatchee National Forest, Washington by MaryAnn Spahr, owner of Native Origins Nursery, Auburn, WA (pers. comm. 1996), and the label for a herbarium specimen (UVIC; coll. Malcolm Martin, 1997) from mountains west of Tulameen, B.C., indicates that the substrate was likely serpentine.

According to Taylor and MacBryde (1977), *E. grandiflorum* is found in the following biogeoclimatic (BGC) zones of British Columbia: Alpine Tundra, Mountain Hemlock, Engelmann Spruce-Subalpine Fir, Interior Western Hemlock (now Interior Cedar-Hemlock [Meidinger and Pojar 1991]), and Coastal Western Hemlock. The Interior Douglas-fir zone should be added to this list (see Chapter 2).

In Alberta, the species is found in the Rocky Mountains and Front Ranges in subalpine meadows, as well as in lodgepole pine stands and extensive mid-elevation areas of stunted aspen in the southwestern part of the province. Therefore, it occurs in the following biogeoclimatic zones identified by Kojima (1980): Alpine Tundra, Engelmann Spruce-Subalpine Fir, and Aspen-Lodgepole Pine-White Spruce. In addition, site associations of the Montane Spruce BGC zone described for British Columbia (Hope et al. 1991) appear to describe some of my Alberta sites (see Chapter 2), so this zone may be added to the above list.

1.1.3 Physical Description

An adult *Erythronium grandiflorum* plant is shown in Figure 1.2. This geophytic herb grows from an elongate, "dogtooth"-shaped bulb 10 to 20 cm in depth (Figure 1.3); the bulb is of an unusual structure and is often mistakenly termed a corm. In *E. japonicum*, an Old World species with similar bulb morphology (Ogura 1952), the bulb consists of two to three fleshy leaf scales almost completely fused together, so that the typical layered bulb structure is not apparent. The bulb of *E. grandiflorum* (like that of many other *Erythronium* species) is covered by a thin brownish tunic that is easily removed; this probably represents the remains of the previous year's fused sheath, within which the new bulb develops. Remnants of previous years' bulbs commonly persist and

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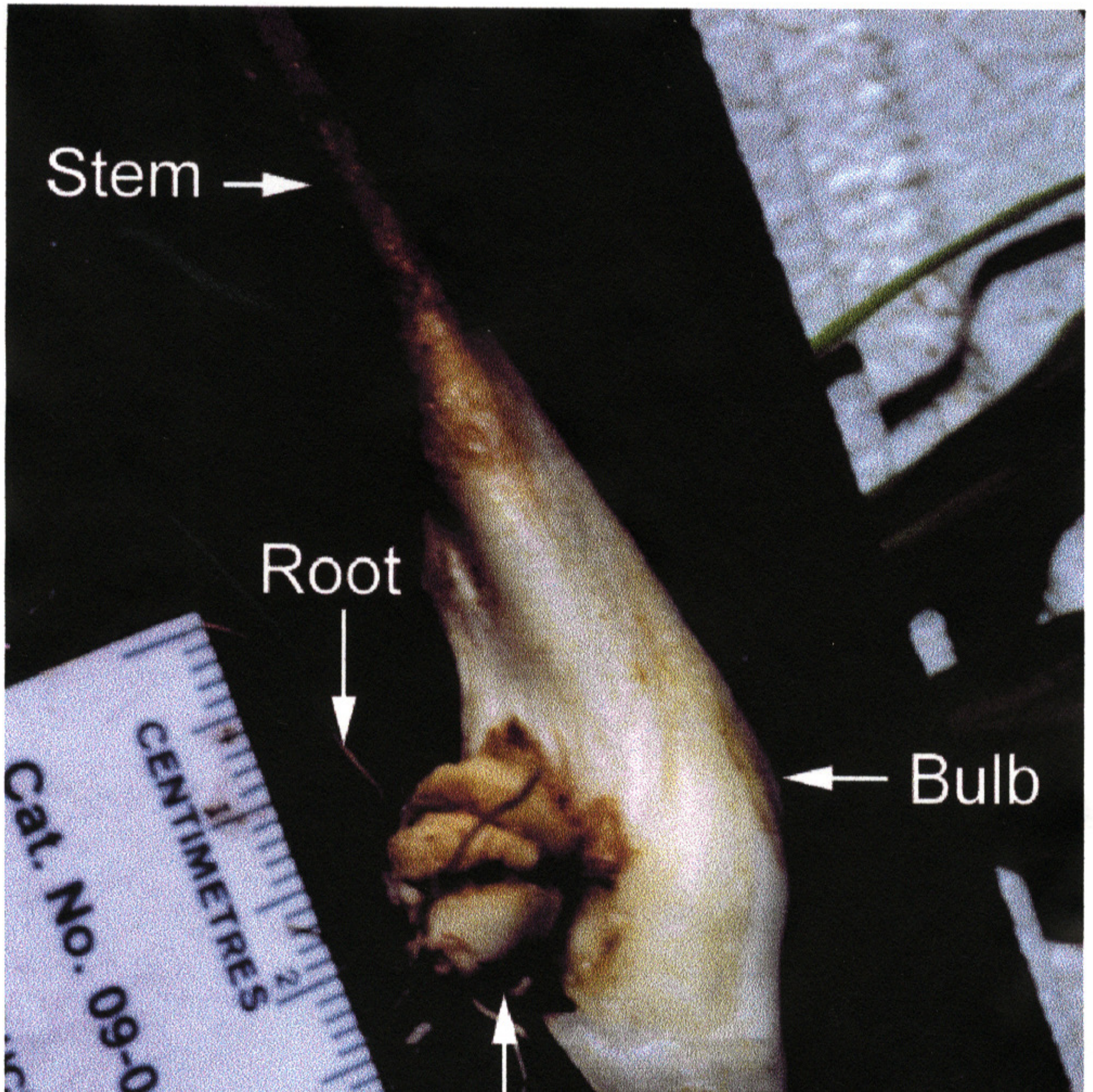
Stem
Root
Bulb
CENTIMETRES
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form a chain of small appendages. This chain has previously been called a "segmented corm" (Pojar and MacKinnon 1994). In this thesis the segments will be termed "bulb-appendages," following usage for *E. japonicum* (Ogura 1952, Kawano et al. 1982). In *E. japonicum*, bulb-appendages do not form until the seventh year; in the younger juvenile stages, the entire bulb reserves are consumed for growth (Kawano et al. 1982).

An adult plant, from 15 to 30 cm in height, normally bears two leaves, but may occasionally bear a reduced third leaf. The leaves are bright green, unmottled, glabrous, and broadly lanceolate. Sizes generally range from 10 to 20 cm in length, by two to six cm in width.

Above ground level, the stem is scapose and usually bears one to six flowers on ebracteolate pedicels, although plants with as many as 14 flowers have been (rarely) observed in Colorado (Rigney 1995). The nodding flowers have six bright yellow tepals two to four cm long, lighter-coloured in the throat, and reflexed at anthesis. Nectar is produced by sac-like appendages at the base of the inner three tepals. The six filaments are white and linear, 10 to 12 mm long, bearing anthers of one of a number of possible colours. In fact, the anthers and pollen may vary in colour independently, resulting in many interesting combinations, but by far the most common colours for both anthers and pollen are cream, yellow, and various shades of red. In my study sites I usually observed all three colours represented in each population, with either cream or yellow predominant (see Chapter 2). The slender style usually projects well beyond the dehiscent anthers, and bears a three-parted stigma with lobes at least one to two mm long.

After pollination, the scape becomes erect and the trilocular ovary develops into a cylindric-clavate capsule three to six cm in length. From 20-60 greenish to reddish-brown seeds are shed by three-way dehiscence of the capsule (Fritz-Sheridan 1988, Weiblen and Thomson 1995). Interestingly, for such a wide-ranging species, the seeds have no obvious dispersal mechanisms. Weighing approximately 5 mg, the seeds are too heavy for wind dispersal and do not bear elaiosomes for ant dispersal, unlike *E. americanum* and *E. japonicum* (Handel et al. 1981, Ohkawara et al. 1996). Rather, the seeds are gradually shaken free of the capsule by wind or other disturbances, and they

frequently grow near the capsule (even right out of the capsule) when the scape falls. Weiblen and Thomson (1995) found a mean seed dispersal distance of 0.33 m, and used a probability curve to suggest that more than 95% of seeds fall within 0.9 m of the parent plant. However, they were not able to measure the long tail of the seed dispersal curve, which they noted may be as important as the modal section of the curve. Fritz-Sheridan (1988) notes that animals and/or people may have influenced migration, while Pojar (1974) discusses the possibility that strong mountain winds could blow seeds from still-erect fruiting stalks for long distances along the first, encrusted snows of early winter. In addition, *E. grandiflorum* is a common species of avalanche tracks, and it is possible that the compressed air in front of an avalanche could move seeds very long distances.

1.1.4 Reproductive Biology

The pollination biology of *E. grandiflorum* has been studied extensively, yet a simple story has not emerged across its range, perhaps indicating variability in the species. Fritz-Sheridan (1988), whose study took place in Montana, calls it a weakly protogynous obligate outcrosser, with no seed set resulting from hand-applied self pollen or agamospermy. However, in Colorado populations the plant is described as weakly protandrous (Cruzan 1989) and as self-compatible (when pollen is transferred by insect or by hand), although self pollen is less successful than cross pollen (Rigney 1995). Pojar (1974), who studied the species in Manning Park in southern British Columbia, labels the species homogamous and self-compatible.

Most pollination in Colorado seems to be carried out by bumblebees (*Bombus* spp.) ; solitary bees and hummingbirds also visit the flowers, but the hummingbirds seldom actually carry out pollination (Thomson and Stratton 1985). Scientific names for the animals were not specified in the latter study but Inouye et al. (1991) observed Broad-tailed Hummingbirds (*Selasphorus platycercus*) visiting yellow glacier lilies in Colorado. Also, Dr. Geraldine Allen and I observed Rufous Hummingbirds (*Selasphorus rufus*) visiting *E. grandiflorum* flowers in Botanie Valley, near Lytton, B.C., in 1996. Pollinators identified by Fritz-Sheridan (1988) in Montana were *Bombus bisarius, Apis*

mellifera (introduced honeybee), and *Andrena nigrihirta* (short-tongued bee). According to Pojar (1974), the pollinating agents of *E. grandiflorum* in southern B.C. are, in order of importance: bumblebees; small, short-tongued bees (andrenid, halictid, megachilid); and Lepidoptera (especially butterflies and skippers). Selfing was the least common mode of pollination in Pojar's study. Pojar (1974) believes it is likely that insects are the limiting factor in sexual reproduction of many entomophilous species (such as *E. grandiflorum*) in subalpine meadows, and Holsinger and Thomson (1994) concur that insufficient pollination often limits fruit set in *E. grandiflorum*. However, Fritz-Sheridan (1988) found that manual crosses did not produce more seeds than did open pollination, and concluded that other factors (such as ovule abortion) limit seed set in *E. grandiflorum*. Additional information regarding mechanisms of ovule abortion can be found in the papers relating to pollination biology listed in the first paragraph of this chapter.

Vegetative reproduction is discussed in Chapters 2 and 5.

1.1.5 Phenology and Development

No data are available on the time from seed germination to reproductive maturity in *E. grandiflorum*, but in congeners it may take three to ten years (Watson and Woodward 1974, Kawano et al. 1982). During the time between the growth of the distinctive linear cotyledon of the first year and flowering are an unknown and probably variable number of juvenile stages (Figure 1.4). These non-flowering stages consist of one leaf of various sizes, with size likely correlated with age of the plant in a given site (cf. Kawano et al. 1982). After some critical bulb mass is attained, a flowering individual with two leaves can develop. However, plants may not flower every year upon reaching the critical size (cf. Kawano 1984). In almost all populations I visited, there were two-leaved, non-flowering individuals, which could represent an intermediate stage between the one-leaved and flowering condition, or plants of reproductive maturity reverting to the non-fertile condition. Large one-leaved plants may also fall into this post-juvenile sterile category, as in *E. japonicum* (that species, unlike *E. grandiflorum*, is either one-leaved and sterile, or two-leaved and fertile). This type of hiatus may be due to a

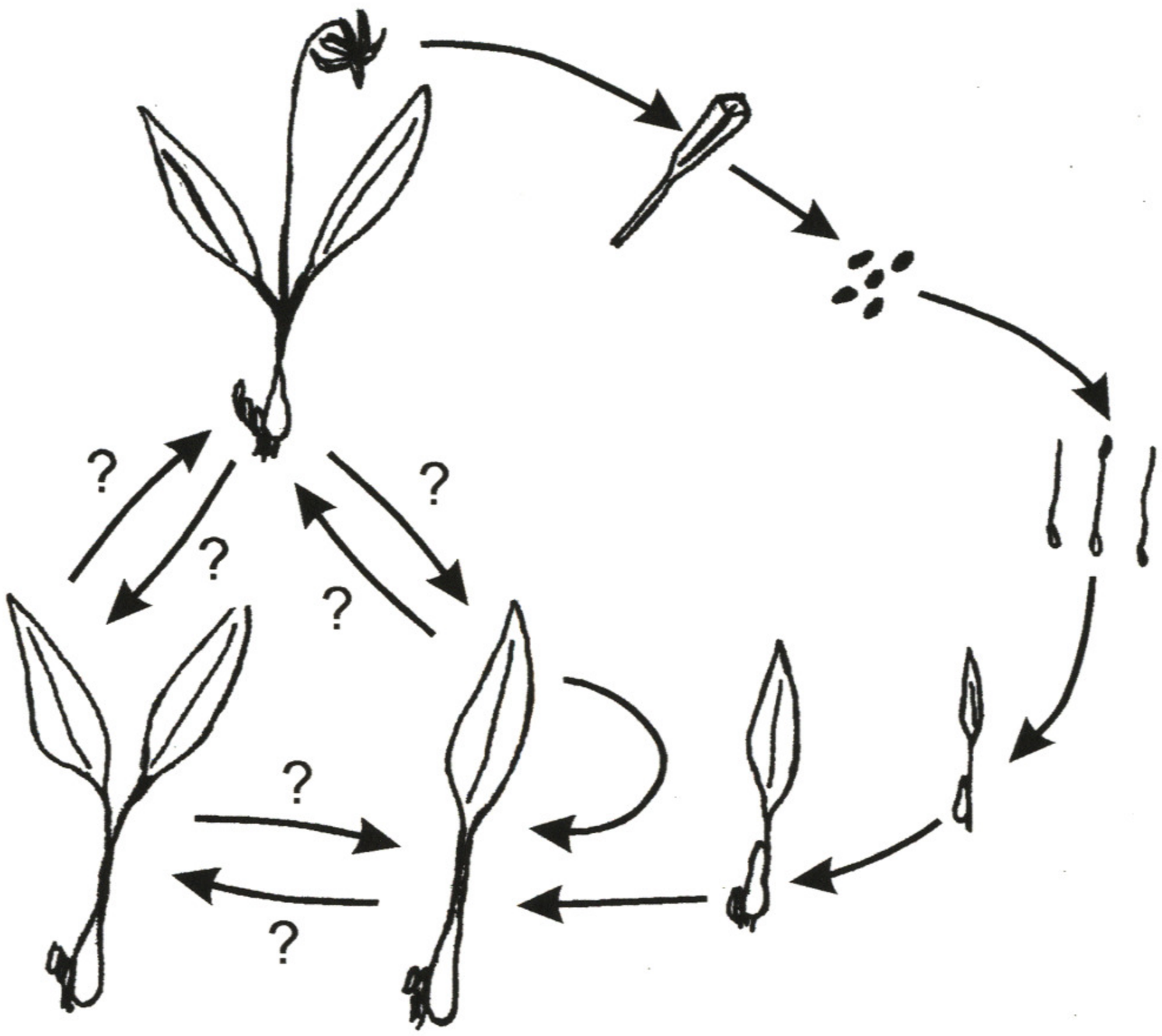


Figure 1.4 Life cycle of *Erythronium grandiflorum*, based on current information (see also Chapter 2).

draining previous season with high fecundity (Kawano et al. 1982), or to poor growing conditions in the previous or current year.

For flowering individuals, flowers may form and open between late March (in the Columbia Gorge [Jolley 1988]), to as late as September in very high elevation areas or beside late-lying snow patches. The species is a spring ephemeral, emerging soon after or even during snowmelt, and all events in the yearly cycle take place quickly. Anthers usually begin to dehisce within about two hours of tepal opening; pollen is completely dispersed in as few as 60 hours; and tepals wither within a week (all assuming warm weather) (Fritz-Sheridan 1988). Leaves have usually completely withered within about two months after emergence, after which the fruits mature and begin to release the ripe seeds (Fritz-Sheridan 1988, Rigney 1995; pers. observation).

1.1.6 Interactions with Fungi and Animals

In addition to the above-mentioned insect and bird species that pollinate and/or collect the nectar of glacier lily flowers, other species also directly interact with *E. grandiflorum*. One commonly overlooked type of interaction is the mycorrhizal association. Currah and Van Dyk (1986) confirmed that yellow glacier lilies from a montane site in southwestern Alberta have roots associated with mycorrhizae of both the V-A (vesicular-arbuscular) and DSF (dematiaceous surface fungi) types. Of the 13 montane species examined, yellow glacier lily was the only species to exhibit both types. Also, of the total 168 non-orchid species examined from a variety of habitats (prairie, parkland, boreal, montane, and alpine), yellow glacier lily was one of only 12 species that exhibited both types. Since these different types of mycorrhizae tend to be common in different types of habitats, the fact that *E. grandiflorum* is host to both types may be one indication of this species' wide ecological amplitude.

In addition, many animal species (aside from pollinators) use various parts of yellow glacier lily plants for food. For example, I collected larvae in glacier lily capsules from southwestern Alberta in 1996; these seed predators were later identified by Dr. Richard Ring (entomologist, University of Victoria) as sawfly larvae (Hymenoptera). I

also observed adult hymenoptera in glacier lily capsules at Chase meadows, B.C., in the same year.

Herbivores consuming the leaves of yellow glacier lilies include deer (scientific name/s unspecified), who also consume the immature seed pods (Clark 1973). In a study in Idaho, mule deer (*Odocoileus hemionus*) ate amounts of glacier lily leaves disproportionate to their availability, suggesting the possibility of some preference for the plant (Keay 1977). Domestic livestock such as sheep and cattle also graze the foliage (Williams 1990).

Herbivores consuming the bulbs of yellow glacier lily include a variety of small mammals. Hart (1976) stated that marmots, voles, and ground squirrels eat the bulbs. However, not all marmots consume the bulbs; according to researcher Andrew Bryant (pers. comm. 1996), Vancouver Island marmots (*Marmota vancouverensis*) eat the above-ground parts of the plant only. I observed hoary marmots (*Marmota caligata*) and porcupines (*Erethizon dorsatum*) foraging among lily leaves in the Rocky Mountains in 1996, but in neither case was I certain that the animals were actually consuming the leaves. Studies in Washington and Alberta showed that water voles (*Microtus richardsoni*) consume *E. grandiflorum* bulbs (Ludwig 1984). Martin et al. (1951) confirmed that Columbian ground squirrels (*Spermophilus columbianus*) feed on the bulbs, and stated that the bulbs of "*Erythronium*" (presumably *E. grandiflorum*) reportedly comprise 2-5% of the diet of the western pocket gopher (*Thomomys talpoides*) in Utah. Aldous (1951) found that a significant proportion of the items in pocket gopher caches in Utah consisted of glacier lily bulbs. Thomson et al.'s (1996) study suggested that pocket gopher predation exerts a significant impact on the spatial structure of *E. grandiflorum* populations in subalpine meadows of Colorado.

In many areas, the bulbs are an important food for grizzly bears (*Ursus arctos*) (Almack 1985, Martinka and Kendall 1985, Mace 1987, Hamer et al. 1991). In fact, glacier lily is considered an indicator of prime grizzly habitat in the mountain parks of Canada (Pat Dunn, naturalist, Mount Revelstoke and Glacier National Parks, pers. comm. 1996). Grizzly bears will stray from their normal course of travel to seek out yellow

glacier lily bulbs (Zager 1980). Similarly, in Glacier National Park (BC), grizzlies appear to exhibit a preference for the bulbs over other types of food at certain times of the season (Roger Ramcharita, M.Sc. student, UBC, pers. comm. 1998). It is commonly asserted that black bears (*Ursus americanus*) eat the bulbs as well (e.g. Clark 1973, Scotter and Flygare 1986); however, black bears rarely dig for their food (Herrero 1985). Grizzly bears' interactions with glacier lilies will be discussed further in Chapter 5.

Another important species that has used yellow glacier lily bulbs is, of course, *Homo sapiens sapiens*. Human uses of the bulbs and management of this food resource are described in detail in Chapters 3 and 5. The next chapter focuses on the ecological requirements and vegetative reproduction of the plant itself.

2.0 Autecology of *Erythronium grandiflorum* in Southern British Columbia and Southwestern Alberta

The review in Chapter 1 indicates that, while various aspects of the biology of *Erythronium grandiflorum* have been well studied, many of its ecological characteristics remain little understood. I therefore pursued an initial investigation of the habitat requirements of this species in western Canada.

There are various approaches one may take in investigating the autecology of a plant species. One approach is experimental, subjecting controlled populations to abiotic and biotic influences and attempting to isolate the factors of significance. Alternatively, one may study natural populations by forming hypotheses about important factors, finding populations with different levels of these factors, and comparing them. Both of these approaches assume some prior knowledge of the species in question. Lacking this, it is necessary to document the range of variation in habitats in which the species occurs, and then attempt to relate measures of the "success" of the species in these various habitats to environmental parameters. This type of research is *exploratory* - one is not testing hypotheses, but rather developing them. Statistical analyses may be used to help isolate factors of likely significance, but no statistical tests *per se* are being carried out. Rather, it is necessary that new data be collected to test hypotheses suggested by exploratory analysis (Kent and Coker 1992).

My research on the ecology of *E. grandiflorum* is of the exploratory type. My objectives were to document as much as possible the environmental amplitude of the species, and to try to determine what types of habitats were most conducive to growth and reproduction. I collected data on a variety of abiotic site parameters (e.g. slope, elevation, substrate), as well as characteristics of the glacier lilies (e.g. numbers in different age classes, size) in 38 sites of a variety of habitat types. I also collected information on cover of associated plant species. Plants respond to numerous interacting environmental factors, and can help in assessing the conditions present at a site (Mueller-Dombois and

Ellenberg 1974), even in the absence of any direct environmental data.

I also investigated the possibility that the species reproduces vegetatively by means of the bulb-appendages described in section 1.1.3. The extent of vegetative reproduction in *E. grandiflorum* is currently unknown. However, many eastern North American species (e.g. *E. americanum*) reproduce vegetatively by means of spreading rhizomes (Muller 1978); some western species (e.g. *E. tuolemnense*) reproduce by means of offsets (Watson and Woodward 1974); and still others (e.g. *E. japonicum*) have sessile offsets which do not act as propagules unless mechanically disturbed (Kawano et al. 1982). It has been suggested that *E. grandiflorum* has the latter type of system (Fritz-Sheridan 1988), but there has been no demonstration of this capacity until the present research. I carried out a small experiment to reveal whether the bulb-appendages can act as propagules if mechanically separated, and whether both the bulbs and appendages can be transplanted successfully from high to low elevations.

2.1 Habitat Analysis

2.1.1 Field Methods

Study Sites

A total of 38 sites were surveyed: 21 sites in 1996, and 17 sites in 1997. Figure 2.1 shows the locations of the sites, while Table 2.1 lists the site names, dates of sampling and revisiting, and other basic descriptive information. I located sites on the basis of herbarium specimen information, along with information obtained throughout each season from botanists and naturalists across B.C. and western Alberta. I performed the site surveys when *Erythronium* was flowering, both to ensure consistency of the cover and lily data, and to assess the characteristics of the community at the critical time for *Erythronium*.

I attempted to spread my sampling effort evenly over the geographic range and over the range of habitat types and elevations at which the species occurs in the study area. The Chase area (sites 22 to 31) is overrepresented, mainly due to the logistical ease of sampling in the area. Vancouver Island is completely unrepresented, because of the

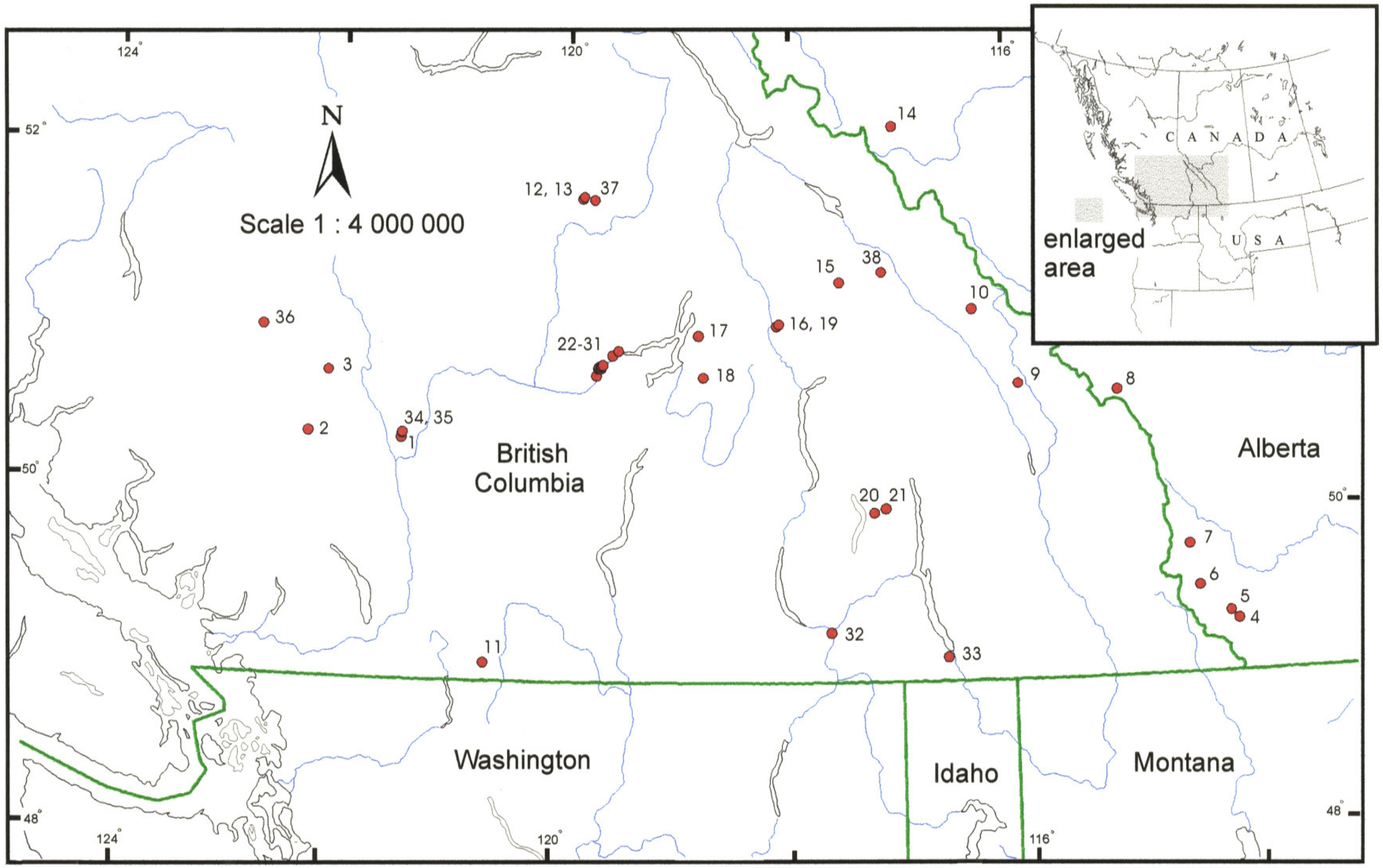


Figure 2.1 Sites surveyed for *Erythronium grandiflorum* and associated habitat parameters in 1996 and 1997. See Table 2.1 for site names associated with numerical codes.

Table 2.1 Study sites where *Erythronium grandiflorum* populations and habitats were surveyed, with dates of sampling and revisiting, site locality and brief description. All sites are in British Columbia, unless denoted (AB) for Alberta.

No.	Name	Sampling date (d/m/y)	Revisit date (d/m/y)	Site locality and description (Latitude, longitude; elevation; slope angle; slope aspect as bearing from true north; directions to site; habitat type and the 8 most common co-occurring species during *Erythronium* flowering, from most to least abundant [NB: individual grasses and sedges not distinguishable at this time and therefore not listed])
1	Botanie	16/05/96	26/06/96, 20/08/96	50°24'35" N, 121°32'20" W; 1191 m; 19°; 255°; On Bootahnie Indian Reserve (IR) 15, 4.3 km N up Botanie Lake road from dam at S end of lake; site ~ 250 m above road. Open *Populus tremuloides* stand with *Pseudotsuga menziesii* scattered in vicinity. With *Claytonia lanceolata, Symphoricarpos* sp., *Lomatium dissectum, Achillea millefolium, Fritillaria lanceolata, Balsamorhiza sagittata, Hydrophyllum capitatum, Senecio integerrimus.*
2	Duffey Lake	23/05/96	21/08/96	50°23'55" N, 122°23'25" W; 1280 m; 22°; 172°; Vicinity of Mt. Rohr, Cayoosh Range, 13.9 km SW from N end of Duffey Lake; site ~ 250 m above road (N side). Avalanche slope flanked by *Salix* sp. and *Alnus* sp. (those shrubs not in plot). With *Claytonia lanceolata, Thalictrum* sp., *Rubus parviflorus, Symphoricarpos* sp., *Hydrophyllum capitatum, Lilium columbianum, Heracleum lanatum, Sambucus racemosa.*
3	Mission Pass	25/05/96	21/08/96	50°45'10" N; 122°13'45" W; 1240 m; 13°; 241°; Mission Pass area (NW of Lillooet), 500 m E from Mission Mountain road on Mission Ridge Forest Service "road"; site ~ 30 m from latter road. *Pseudotsuga menziesii* stand with *Pachistima myrsinites, Arctostaphylos uva-ursi, Arnica cordifolia, Vaccinium membranaceum, Spiraea betulifolia, Antennaria racemosa, Pyrola secunda, Lupinus arcticus.*
4	Butcher Lake (AB)	27/05/96	13/06/96, 18/08/96	40°17'50" N; 114°04'07" W; 1656 m; 15°; 75°; W of sulfur plant S of Pincher Creek, AB; site ~ 1 km due SW of Butcher Lake. Dense *Populus tremuloides* (flagged by wind; max. height ~ 8 m) with *Angelica dawsonii, Claytonia lanceolata, Spiraea betulifolia, Osmorhiza occidentalis, Thalictrum occidentale, Senecio pseudaureus, S. integerrimus, Smilacina stellata.*
5	Whitney Creek (AB)	11-12/ 06/96	18/08/96	49°20'40" N; 114°08'12" W; 1572 m; 9°; 317°; SW of Pincher Creek, ~ 12 km NW of Butcher Lake between Whitney Creek and Prairie Bluff; site ~ 30 m from gas road. *Pinus contorta* stand with *Arnica cordifolia, Rubus parviflorus, Spiraea betulifolia, Symphoricarpos* sp., *Rosa* sp., *Chimaphila umbellata, Thalictrum* sp., *Osmorhiza occidentalis.*

Table 2.1, cont.

6	Hillcrest Mines (AB)	14/06/96	18/08/96	49°29'58" N; 114°24'00" W; 1712 m; 13°; 97°; E flank of Hastings Ridge, 8.3 km along road to Lynx Creek Rec. Area from turnoff S of Hillcrest Mines; site ~ 200 m upslope from road, through trees. Small meadow (~ 60 x 150 m) surrounded by *Picea engelmannii / Abies lasiocarpa / Pinus contorta* with *Claytonia lanceolata, Erigeron peregrinus, Achillea millefolium, Geranium richardsonii, G. viscosissimum, Hydrophyllum capitatum, Prunella vulgaris, Equisetum arvense.*
7	Forestry Trunk Road (AB)	16/06/96	17/08/96	49°44'15" N; 114°28'15" W; 1766 m; 7°; 104°; 14.8 km N of Coleman, AB, along Forestry Trunk Road; site ~ 30 m from road. *Pinus contorta* stand with *Picea engelmannii* and *Abies lasiocarpa* scattered in subcanopy; with *Angelica dawsonii, Shepherdia canadensis, Fragaria virginiana, Spiraea betulifolia, Thalictrum* sp., *Aster foliaceous, Zigadenus elegans, Dodecatheon conjugens.*
8	Valleyview Trail (AB)	18/06/96	17/08/96	50°38'30" N; 115°03'30" W; 2041 m; 17°; 216°; Valleyview Trail (gravel road), Kananaskis Country, 5.7 km from N entrance to Trail, site ~ 40 m upslope from Trail. Lower section of avalanche chute, in early stages of invasion by *Pinus contorta, Picea glauca, Abies lasiocarpa, Populus balsamifera*; with *Shepherdia canadensis, Fragaria virginiana, Allium cernuum, Epilobium angustifolium, Aster conspicuus, A. foliaceous, Vaccinium scoparium, Solidago multiradiata.*
9	Sinclair Creek	21-22/ 06/96	16/08/96	50°41'45" N; 115°57'25" W; 1846 m; 21°; 212°; Kootenay National Park, along Sinclair Cr. trail, ~ 2.5 km from upper trailhead; site ~ 50 m upslope from trail. Rocky avalanche chute thru *Picea engelmannii / Abies lasiocarpa* with *Thalictrum occidentale, Epilobium angustifolium, Aster engelmannii, Fragaria virginiana, Geranium richardsonii, Claytonia lanceolata, Valeriana sitchensis, Heracleum lanatum.*
10	Moose Creek	30/06/96, 01/07/96	15/08/96	51°07'37" N; 116°21'31" W; 1506 m; 22°; 90°; Between Yoho and Kootenay National Parks, lower E flank of Mt. Mollison, along Moose Creek Forest Service Recreation trail, ~ 1.5 km from trailhead; site ~ 100 m upslope from trail. *Alnus*- and *Salix*-edged avalanche chute thru *Picea engelmannii / Abies lasiocarpa* (those spp. not in plot) with *Claytonia lanceolata, Epilobium angustifolium, Erigeron peregrinus, Delphinium nuttallianum, Heracleum lanatum, Thalictrum* sp., *Geranium richardsonii, Pedicularis bracteosa.*
11	Blackwall Peak	07/07/96	20/08/96	49°06'15" N; 120°45'20" W; 1924 m; 9°; 176°; Manning Park, below Blackwall Peak, open area on E side of first parking area at Alpine Meadows; site ~ 20 m from road. Subalpine meadow with stunted plant growth; with *Vaccinium scoparium, Phlox diffusa, Luzula hitchcockii, Anenome occidentalis, Veronica cusickii, Antennaria lanata, Claytonia lanceolata, Arenaria capillaris.*

Table 2.1, cont.

12	Trophy I: Shepherd's Hut	16/07/96	09/08/96	51°46'48" N; 119°55'36" W; 2056 m; 7°; 265°; Wells Gray Provincial Park; Trophy Mountain meadows, above Shepherd's Hut; site close to rocky crest. Subalpine meadow with *Claytonia lanceolata, Valeriana sitchensis, Arnica latifolia, Antennaria umbrinella, Erigeron peregrinus, Anemone occidentalis, Mitella breweri, Artemisia norvegica.*
13	Trophy II: Forest	17/07/96	09/08/96	51°46'06" N; 119°56'00" W; 1900 m; 6°; 184°; Wells Gray Provincial Park, along Trophy Mtn. Interpretive Trail, between posts 4 and 5; site ~ 10 m from trail. Moderately open *Abies lasiocarpa / Picea engelmannii* forest with many young trees; with *Valeriana sitchensis, Arnica latifolia, Anemone occidentalis, Erigeron peregrinus, Lupinus arcticus, Claytonia lanceolata, Viola orbiculata, Trollius laxus.*
14	Nigel Creek (AB)	20/07/96	07/08/97	52°11'00" N; 117°03'40" W; 1829 m; 7°; 255°; Banff National Park, 8.5 km S of Sunwapta Pass, near Nigel Pass trailhead, ~ 50 m from Nigel Creek (on E side), and ~ 50 m S from trail. Uneven-aged *Picea engelmannii* with understory of *Abies lasiocarpa*; with *Vaccinium scoparium, Arnica cordifolia, Peltigera* sp., *Equisetum scirpoides, Cladonia* sp., *Thalictrum occidentale, Fragaria virginiana, Salix* spp.
15	Balu Pass	22/07/96	08/08/97	51°17'30" N; 117°34'15" W; 1891 m; 22°; 100°; Glacier National Park, just to E of Balu Pass, on N side of bowl, close to Connaught Creek (N side). Rocky subalpine meadow with *Valeriana sitchensis, Senecio triangularis, Claytonia lanceolata, Vaccinium membranaceum, Veratrum viride, Mitella breweri, Luetkea pectinata, Viola glabella.*
16	Mt. Revelstoke I: Balsam L.	23/07/96	15/08/96	51°02'40" N; 118°08'50" W; 1836 m; 14°; 185°; Mt. Revelstoke National Park, between Balsam Lake and summit, ~ 600 m up from parking lot and ~ 100 m W of road. Open, uneven-aged *Abies lasiocarpa* with *Valeriana sitchensis, Erigeron peregrinus, Arnica latifolia, Claytonia lanceolata, Castilleja parviflora, Luzula hitchcockii, Mitella breweri, Vaccinium membranaceum.*
17	Queest Mtn.	24/07/96	Not revisited (road closure)	50°59'25" N; 118°51'40" W; 1894 m; 14° 173°; Queest Mtn., N of Malakwa, in the Shuswap Range; site in the bowl below the summit on the E side. Subalpine meadow with *Claytonia lanceolata, Valeriana sitchensis, Erigeron peregrinus, Anemone occidentalis, Luzula* sp., *Mitella breweri, Epilobium angustifolium, Veratrum viride.*
18	Mt. Mara	25/07/96	14/08/96	50°44'55" N; 118°49'12" W; 1886 m; 7°; 180°; Mt. Mara, Hunters Range, NE of Enderby; site beside Mt. Mara lookout "road," 14.4 km from jn. with ThreeValley/Mara Forest Service road. Subalpine meadow with *Claytonia lanceolata, Arnica latifolia, Erigeron peregrinus, Anemone occidentalis, Lupinus arcticus, Valeriana sitchensis, Arnica mollis, Senecio triangularis.*

Table 2.1, cont.

19	Mt. Revelstoke II: Eva/Jade Lakes Trail	01/08/96	09/08/97	51°03'15" N; 118°07'35" W; 1837 m; 12°; 260°; Mt. Revelstoke National Park, ~ 800 m N along Eva/Jade Lakes Trail from trailhead at summit; site ~ 100 m upslope from trail. Opening in *Abies lasiocarpa* with *Valeriana sitchensis, Claytonia lanceolata, Luzula hitchcockii, Lupinus arcticus, Mitella breweri, Erigeron peregrinus, Arnica latifolia, Castilleja* sp.
20	Idaho Peak	03/08/96	10/08/97	49°58'05" N; 117°16'45" W; 2045 m; 28°; 329°; Idaho Peak (part of Silver Ridge in the Selkirk Mtns.), below summit in "Wild Goose Basin," 10.4 km up Idaho Peak Forest Service road from Sandon; site ~ 100 m upslope from road. Subalpine slope invaded by small *Abies lasiocarpa*; with *Valeriana sitchensis, Arnica latifolia, Luzula parviflora, Veratrum viride, Anemone occidentalis, Claytonia lanceolata, Erigeron peregrinus, Ranunculus eschscholtzii.*
21	Jackson Basin	05/08/96	11/08/97	49°59'30" N; 117°10'25" W; 2090 m; 21°; 109°; SE flank of Reco Mtn. (in the Selkirk Mtns.), E of Sandon, at head of Stenson Creek; site close to headwall at S end of basin, ~ 100 m upslope from old road. Avalanche slope flanked by stunted *Abies lasiocarpa*; with *Erigeron peregrinus, Vaccinium membranaceum, Luzula hitchcockii, Anemone occidentalis, Valeriana sitchensis, Fragaria virginiana, Castilleja parviflora, Viola orbiculata.*
22	Little Shuswap	16-17/ 04/97	26/06/97	50°52'23" N; 119°38'42" W; 412 m; 8°; 189°; Slopes on N side of Little Shuswap Lake, on Quaaout IR 1, ~ 700 m along dirt road leading to Banshee Lake; site ~50 m to E side of road. Open *Pinus ponderosa* stand with *Pseudotsuga menziesii* saplings and *Symphoricarpos* sp., *Taraxacum officinale, Amelanchier alnifolia, Claytonia lanceolata, Potentilla gracilis, Achillea millefolium, Vicia americana, Astragalus miser.*
23	Adams River	17-18/ 04/97	26/06/97	50°53'58" N; 119°35'26" W; 365 m; 3°; 39°; Adams River area, just inside Quaaout IR 1, ~ 350 m along Holding Road from jn. with Squilax-Anglemont Road; site ~ 50 m to E side of road. *Pseudotsuga menziesii* stand with *Arnica cordifolia, Mahonia aquifolium, Pachistima myrsinites, Spiraea betulifolia, Symphoricarpos* sp., *Zigadenus venenosus, Hieracium scouleri, Arctostaphylos uva-ursi.*
24	Rodeo	18-19/ 04/97	25/06/97	50°48'48" N; 119°44'56" W; 592 m; 15°; 208°; Neskonlith Meadows (Chase area), on Sahhaltkum IR 4; slopes to E side of Skmana Lake road, ~250 m N of turnoff to Niskonlith Lake Provincial Park; site ~200 m upslope from old rodeo grounds. Small *Populus tremuloides* stand surrounded by meadow; with *Claytonia lanceolata, Lomatium dissectum. Delphinium nuttallianum, Achillea millefolium, Lithophragma parviflorum, Taraxacum officinale, Rosa* sp., *Ranunculus glaberrimus.*

Table 2.1, cont.

25	Sahhaltkum	20/04/97	25/06/97	50°48'32" N; 119°44'31" W; 589 m; 15°; 257°; Neskonlith Meadows (Chase area), on Sahhaltkum IR 4, ~560 m from Niskonlith Lake road along trail to Aylmer Lake. Meadow (patches of *Pseudotsuga menziesii* and *Populus tremuloides* in the area but not in site); with *Rosa woodsii, Balsamorhiza sagittata, Achillea millefolium, Delphinium nuttallianum, Claytonia lanceolata, Lupinus sericeus, Ranunculus glaberrimus, Fritillaria pudica.*
26	South Thompson	21/04/97	25/06/97	50°49'05" N; 119°43'57" W; 680 m; 15°; 125°; Neskonlith Meadows (Chase area), on Sahhaltkum IR 4, ~1.8 km from Niskonlith Lake road along trail to Aylmer Lake; site ~ 100 m downslope from trail. Meadow (with patches of *Pseudotsuga menziesii* and *Crataegus douglasii* and scattered *Pinus ponderosa* and *Juniperus scopulorum* in the area but not site); with *Symphoricarpos* sp.,*Lomatium dissectum, Spiraea betulifolia, Zigadenus venenosus, Balsamorhiza sagittata, Rosa woodsii, Lithophragma parviflorum, Claytonia lanceolata.*
27	McGillivray Lake Road	22/04/97	23/06/97	50°45'25" N; 119°47'24" W; 531 m; 16°; 85°; S of Niskonlith Lake, knoll on N side of McGillivray Lake Forest Service Rd. close to 2 km marker. *Pseudotsuga menziesii* stand with *Symphoricarpos* sp., *Spiraea betulifolia, Mahonia aquifolium, Arnica cordifolia, Crataegus douglasii, Claytonia lanceolata, Delphinium nuttallianum, Achillea millefolium.*
28	Slough Hollow	26-27/ 04/97	23/06/97	50°45'28" N; 119°47'20" W; 510 m; 15°; 7°; Near road leading to S tip of Niskonlith Lake, ~ 100 m north of jn. with McGillivray Lake Forest Service Rd; site on plateau immed. above seasonally-inundated depression (which is between site and road). *Populus tremuloides* with scattered *Pseudotsuga menziesii* and *Pinus ponderosa* in the area; with *Symphoricarpos* sp., *Taraxacum officinale, Claytonia lanceolata, Fritillaria lanceolata, Amelanchier alnifolia, Zigadenus venenosus, Rosa* sp., *Achillea millefolium.*
29	Niskonlith Park I: Edge	29/04/97	24/06/97	50°48'24" N; 119°46'09" W; 572 m; 24°; 125°; Niskonlith Lake Provincial Park, 450 m from N entrance to park (along Louie Road); site ~ 50 m upslope from road. Lower edge of open upper slope, grading into *Pseudotsuga menziesii* forest, with thick shrub cover; with *Prunus virginiana, Rosa nutkana, Amelanchier alnifolia, Lomatium dissectum, Balsamorhiza sagittata, Crataegus douglasii, Pachistima myrsinites, Lithophragma parviflorum.*
30	Skunk Hollow	30/04/97	24/06/97	50°48'01" N; 119°44'55" W; 602 m; 4°; 244°; On Neskainlith IR 1, near top of hill between northeast tip of Niskonlith Lake and Niskonlith Lake Road. Open meadow (cattle pasture) with occasional *Pseudotsuga menziesii* in the area (not in site); with *Symphoricarpos albus, Crataegus douglasii, Balsamorhiza sagittata, Galium boreale, Zigadenus venenosus, Taraxacum officinale, Lupinus sericeus, Claytonia lanceolata.*

Table 2.1, cont.

31	Niskonlith Park II: Forest	01/05/97	24/06/97	50°48'00" N; 119°46'29" W; 529 m; 23°; 148°; Niskonlith Lake Provincial Park, 1.25 km from N entrance to park (along Louie Road), site ~ 30m upslope from road. Second-growth *Pseudotsuga menziesii* with scattered *Pinus ponderosa*; with *Symphoricarpos* sp., *Mahonia aquifolium, Spiraea betulifolia, Fritillaria lanceolata, Claytonia lanceolata, Lithophragma parviflorum, Vicia americana, Amelanchier alnifolia.*
32	Merry Creek	03/05/97	04/07/97	49°17'04" N; 117°40'32" W; 767 m; 25°; 64°; SW of Castlegar, 1.25 km along Merry Creek Forest Service Rd. from Hwy 3; site ~ 45 m upslope of road. Small opening (mossy seepage area) in mixed forest of *Thuja plicata, Pseudotsuga menziesii, Pinus contorta, Larix occidentalis*, *Betula papyrifera* (only *Pseudotsuga* in site); with *Holodiscus discolor, Symphoricarpos* sp., *Pachistima myrsinites, Rosa nutkana*, *Perideridia gairdneri*, *Fragaria virginiana, Cladonia* sp., *Montia parviflora*.
33	Fern Forest Trail	06-07/ 05/97	05/07/97	49°08'15" N; 116°38'48" W; 700 m; 20°; 22°; NE flank of Creston Mtn. (within Creston Valley Wildlife Management Area), along Fern Forest Interpretive Trail; site ~ 10 m from trail, between #8 and #9 markers. *Pseudotsuga menziesii / Pinus contorta* stand with *Holodiscus discolor, Peltigera* spp., *Spiraea betulifolia, Mahonia aquifolium, Fragaria virginiana, Heuchera cylindrica, Cladonia* sp., *Montia parviflora.*
34	Botanie Lake	12/05/97	16/07/97	50°22'55" N; 121°32'48" W; 1120 m; 24°; 142°; On Bootahnie IR 5 (just inside S border), slopes above south end of Botanie Lake; site ~ 200 m above road. *Populus tremuloides/Prunus* sp. stand adjacent to *Pseudotsuga menziesii* forest; with *Thalictrum* sp., *Hydrophyllum capitatum, Amelanchier alnifolia, Vicia americana, Symphoricarpos* sp., *Claytonia lanceolata, Triteleia grandiflora, Fritillaria lanceolata.*
35	Botanie View	13-14/ 05/97	16/07/97	50°24'42" N; 121°32'13" W; 1304 m; 10°; 228°; On Bootahnie IR 15, 4.3 km N up Botanie Lake road from dam at S end of lake; site ~500 m above road (~ 115 m elev. gain above site 1). Open meadow (pasture) adjacent to *Pseudotsuga menziesii* forest; with *Claytonia lanceolata, Lomatium dissectum, Fritillaria lanceolata, Achillea millefolium, Taraxacum officinale, Triteleia grandiflora, Delphinium nuttallianum, Hydrophyllum capitatum.*
36	Taylor Creek	21/06/97	17/07/97	50°59'50" N; 122°50'36" W; 1827 m; 24°; 166°; S flank of Eldorado Mountain, along Taylor Creek Forest Service Road/trail, ~ 8.5 km from junction with Tyaughton Lake road; site ~40 m upslope from trail. Avalanche slope thru *Abies lasiocarpa*; with *Thalictrum* sp., *Claytonia lanceolata, Valeriana sitchensis, Arnica parryi, Epilobium angustifolium, Erigeron peregrinus, Artemisia norvegica, Senecio integerrimus.*

Table 2.1, cont.

37	Raft View	30/06/97	05/08/97	51°45'50" N; 119°49'36" W; 2010 m; 30°; 198°; E flank of Trophy Mountain chain (across from Raft Mtn), near trail to Trophy Mountain Chalet owned by Wells Gray Backcountry Chalets; site ~ 500 m below chalet and ~ 100 m upslope from trail. Steep, rocky subalpine slope (mainly *Abies lasiocarpa* in area but some juvenile *Picea engelmannii*); with *Claytonia lanceolata, Valeriana sitchensis, Erigeron peregrinus, Thalictrum* sp., *Artemisia norvegica, Arnica latifolia, Trollius laxus, Lupinus arcticus.*
38	Gormon Lake	13/07/97	03/08/97	51°20'52" N; 117°10'55" W; 1998 m; 11°; 185°; E flank of Dogtooth Range of Purcell Mountains, just E of Glacier National Park and northwest of Golden; near end of Gormon Lake trail but below lake, across from large bare talus slope. Site in rocky, poorly drained area adjacent to continuous *Picea engelmannii / Abies lasiocarpa* forest (some stunted *Abies* in plot); with *Pedicularis bracteosa, Vaccinium scoparium, Veratrum viride, Valeriana sitchensis, Arnica latifolia, Viola orbiculata, Trollius laxus, Anemone occidentalis.*

difficulties in attempting to cover the whole provincial range with many locations flowering at the same time. Permission was obtained for sampling in national parks (sites 9, 14, 15, 16, 19), provincial parks (sites 8, 12, 13, 29, 31, 37), wildlife management areas (site 33), and on First Nations' lands (sites 1, 22, 24, 25, 26, 30, 34, 35). The remainder of the sites fell on public lands other than parks.

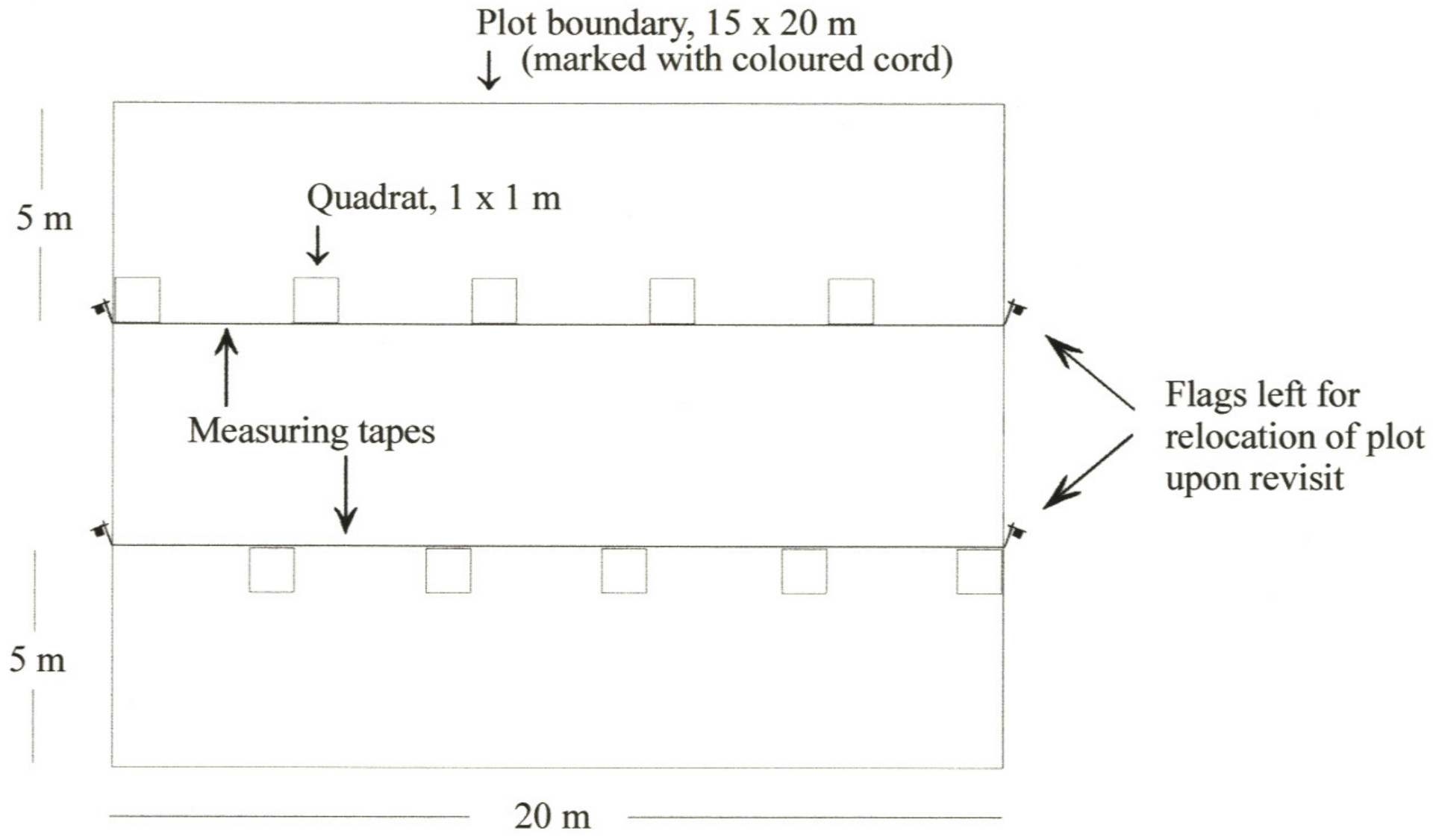
I established plots at each site within an area that was visually uniform in terms of physiognomy and *Erythronium* phenology. A plot 15 by 20 m (occasionally 10 by 30 m), was placed roughly in the center of such an area. Placement was therefore deliberately structured and not random, in an attempt to include a uniform and representative area of *Erythronium* growth. However, randomness was not critical since the data were not being used for hypothesis testing, as mentioned. Also, sampling was objective (not random *or* subjective) in that the two transects (or one transect for a 10 x 30 m plot) were established in a fixed location within the plot. The plot layout is shown in Figure 2.2.

The entire sampling protocol, with the help of two volunteer field assistants, took between six and eight hours to complete for each site. As indicated in Table 2.1, all sites (except for one, due to a road wash-out) were revisited later in the season (or late in the following season) to identify species that were too undeveloped to identify at the time of initial sampling. Revisits usually required one to two hours per site.

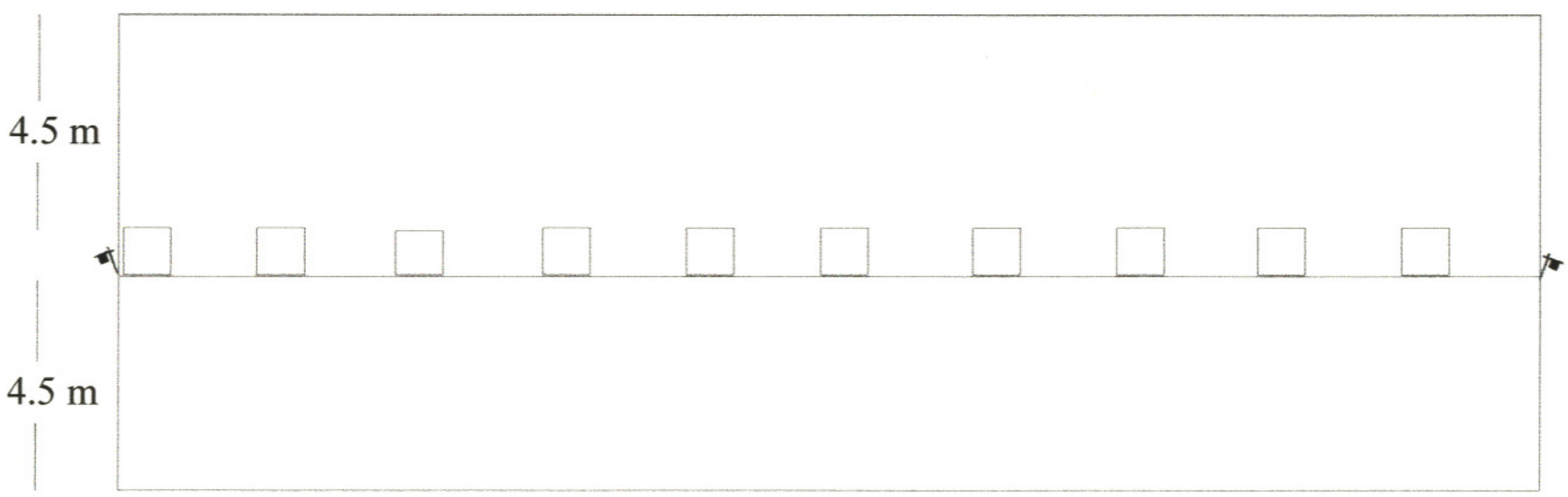
Plant Community Data

Along the transect/s at 10 fixed, evenly spaced intervals I laid down 1 x 1 m quadrats for vegetation sampling (Figure. 2.2). Within each quadrat, I estimated the percent cover of all herbaceous and shrub species. I defined trees as woody plants with one main bole over 1.5 m in height; therefore, young individuals of tree species were assessed within quadrats along with herb and shrub species. After doing the quadrat estimates, I walked through the entire plot and noted the approximate abundance of any additional species that had not been observed in the quadrats.

I identified, counted, and measured diameter at breast height for all trees (over 1.5 m tall) in the entire plot. I later calculated basal area using these data. In addition, at a



a)



b)

Figure 2.2 Sampling design for site surveys, a) usual design, b) design used for narrow sites. Drawn to scale (0.5 cm = 1 m).

specified corner of each quadrat, the presence or absence of overhead canopy was noted using a clinometer at 90°. These measurements in fact more appropriately represent environmental parameters (next section), as indices of shade.

Environmental Parameters

General site description: The following data were recorded for each plot: description of location (latitude, longitude, directions to site); elevation; and slope angle, aspect, and position. In addition, a number of characteristics of the site were subjectively described, including the general physiognomy; drainage conditions; microtopography; and disturbance (e.g. cattle, grizzly bear or small mammal activity; deer grazing, trails through plot, etc.).

Conditions of substrate: Within each quadrat, I estimated percent cover and depth of litter, and percent cover of coarse woody debris, bare soil, bare (or thinly lichen- or moss-covered) rock, and tree bases (I moved quadrats that were over half covered by tree bases, repositioning them just far enough to avoid the tree). In addition, at the four corners of each quadrat (40 measurements per plot), an assistant took a soil depth measurement by pushing and/or hammering in an aluminum pole until hitting a rock, or to a depth of 40 cm. The measurement was then taken from the ground level up to the 40 cm mark on the pole, so that high values indicate rocks near the surface. This method, following Thomson et al. (1996), provides an index of rockiness of the substrate.

Approximately 100 g of soil was taken from bulb depth (range: 4 to 32 cm; mean 13.9 cm) at each quadrat; we measured pH from these 10 samples later in the day using a pH meter (Oakton phTestr 2) calibrated with pH 4.0 and 7.0 buffering solutions. Afterwards, the samples were combined to form a composite sample, which was later air-dried and used for a laboratory analysis of particle size and organic matter content. The former was carried out with sieves of the following sizes (mm): 2, 1, 0.5, 0.25, 0.125, 0.075, 0.038. The smallest-mesh sieve separated coarse silts from finer silts and clays (using the texture classes of the Canada Soil Survey Committee [Day 1983]). A hydrometer is generally used to achieve separations of the fine fractions; however, given

that this fraction constituted less than about 25% of all samples, it was sufficient for my purposes to extrapolate the particle size curve from the sieve analysis and obtain a rough estimate of the clay/silt division.

I estimated organic matter content using the loss-on-ignition method of McKeague (1978). Two subsamples from the same bulk sample were ashed for each site, and the average taken of the resulting values. Where the two values had a relative percent difference (RPD) more than 10%, I ashed a third subsample and took the average of the two closest values of the three (which were always within 10% RPD).

Table 2.2 lists the environmental variables that I used in my analyses, and explains how derived variables were calculated. These represent a considerably abridged subset of all variables I initially analyzed; I eliminated those that were either redundant (e.g. canopy was tightly correlated with basal area; I chose the latter as being a more precise estimate of overall tree cover), or contained such limited data (i.e. only a few non-zero values) that they were not informative; e.g. cover of tree bases.

Characteristics of E. grandiflorum *populations*

Within each quadrat, I assessed cover of the glacier lilies, and, with the help of an assistant, counted all individuals in the following age/stage classes: seedling; one-leaved; two-leaved; and flowering, counting the numbers of plants with one, two, three, four, and more than four flowers separately. I also recorded the numbers of aborted flowers and the number of scapes that had experienced herbivory (probably by deer). In addition, length and width measurements were taken for the leaves of three plants in each quadrat (the longer leaf of each plant was measured, length measured from ground level to tip, and width measured at widest point). Two plants were measured in standard positions (the closest to the two outer corners of the quadrats), and the third plant was the one with the largest leaf length in the quadrat. Leaf area is strongly correlated with total plant biomass for *E. japonicum* (Kawano et al. 1982), so I assumed that these measurements are a good index of size for the plants sampled in each population. Further, size is one way to assess "vigour," since size is positively correlated with fecundity for *E. japonicum*

Table 2.2 Environmental variables used in habitat analysis; all are quantitative unless otherwise noted.

Variable name	Definition
tree-conif	Total basal area (m^2/ha) of coniferous trees over 1.5 m tall (calculated using dbh values of all trees in 300 m^2 plot)
tree-decid	Total basal area (m^2/ha) of all deciduous trees over 1.5 m tall (calculated using dbh values of all trees in 300 m^2 plot)
shrub	Sum of average percent cover values (means for 10 quadrats per site) for all woody non-tree species
herbcover	Sum of average percent cover values (means for 10 quadrats per site) for all associated herbaceous species
total-spp	Total number of vascular plant species present at site; used as an index of biodiversity
intro-spp	Number of introduced species present at site
native-spp	Number of native species present at site
rock	Rockiness index, values from 0 to 40 cm (high numbers=more rocky)
litdep	Average litter depth (cm)
litcover	Surface litter cover (%)
grass	Average percent cover of grass species (Poaceae) (mean for 10 quadrats)
CWD	Average surface cover of coarse woody debris (mean for 10 quadrats)
pH	Substrate pH at bulb depth
texture	Substrate texture index calculated as 1(proportion clay) + 5(proportion silt) + 10(proportion sand); i.e. 1=pure clay, 10=pure sand
organic	Percent organic matter estimated by loss on ignition
aspect	Slope aspect, transformed as $\cos(A_{max} - A) + 1$, where $A_{max} = 202.5$ (S-SW), and A is azimuth from true north; S-SW=2, N-NE=0
angle	Slope angle in degrees
elev	Elevation in metres above sea level
lat	Latitude (converted to decimal number)
long	Longitude (converted to decimal number)
phenology	Phenology index calculated as 1(proportion *E. grandiflorum* flowers in bud) + 5(proportion in full flower) + 10(proportion faded); i.e. 1=all bud, 10=all faded
cattle	Categorical variable, 2 levels: signs of cattle present or absent
fire	Categorical variable, 3 levels: charcoal obviously present in soil sample; trace amounts present (detected using dissecting scope); no charcoal found in sample

(Kawano and Nagai 1982) and *E. americanum* (Wolfe 1983). Finally, I made brief notes on the different anther colours present in each population, and their approximate proportions.

Table 2.3 lists the lily variables used in my analyses. Again, uninformative variables were dropped; e.g., number of aborted lily fruits and number of flowering lily plants suffering predation, both of which were too rare to show meaningful trends.

2.1.2 Plant Identification and Voucher Specimens

Unless otherwise noted, nomenclature follows Egan (1987) for lichens, Schofield (1992) for mosses, Cody and Britton (1989) for ferns and Hitchcock and Cronquist (1973) for all other vascular plants (exceptions follow Douglas et al. [1989, 1990, 1991, 1994] or Cronquist et al. [1977]) (see Appendix 1 for the complete names of all species found in my 38 sites). For those species that were not easily identified in the field, I collected samples for later examination in the herbarium. My identifications were checked by professional botanists.

Vouchers of *Erythronium grandiflorum* from all 38 sites, as well as specimens from the transplant experiment (see section 2.3), were mounted and deposited at the University of Victoria Herbarium. In addition, duplicate lily specimens from the 38 sites will be mounted and deposited at the Secwepemc Education Institute Herbarium in Kamloops. Suitable specimens of other species may be mounted and retained at the University of Victoria Herbarium at the discretion of the Assistant Curator.

2.1.3 Data Analysis

I first analyzed the species abundance data for my 38 sites using ordination, which aids in simplifying and interpreting multivariate data (Dale 1975). In community analysis, ordination methods arrange points along two or more orthogonal axes such that the points that are close together represent sites that are similar in species composition, and points far apart represent sites dissimilar in species composition (ter Braak 1995). This process often facilitates interpreting patterns of species occurrence in terms of

Table 2.3 *Erythronium* variables used in habitat analysis; all are quantitative unless otherwise noted.

Variable name	Definition
seedling	Average number of seedlings per m^2 (mean over 10 quadrats)
oneleaf	Average number of single-leaved plants, i.e. juveniles of all ages, per m^2 (mean over 10 quadrats)
twoleaf	Average number of two-leaved plants (non-flowering) per m^2 (mean over 10 quadrats)
flowplant	Average number of flowering plants per m^2 (mean over 10 quadrats)
multiflow	Proportion of plants with more than one flower (avg. number of plants with > 1 flower / flowplant)
propflow	Proportion of all non-seedling plants with flowers (flowplant / [oneleaf + twoleaf + flowplant])
prop2leaf	Proportion of all non-seedling plants that have two leaves (twoleaf / [oneleaf + twoleaf + flowplant])
ratioseed	Ratio of seedlings to flowering plants (seedling / flowplant)
ratio1leaf	Ratio of one-leaved plants to flowering plants (oneleaf / flowplant)
leaf-area	Average leaf area in cm^2 (20 plants per site, calculated from leaf length and width using the formula for area of an ellipse) as a general indication of plant size; highly correlated with largest leaf area so only this variable used
anther	Categorical variable, 3 levels: anthers mostly cream-coloured; anthers mostly yellow; anthers mostly red

environmental influences. I ordinated two matrices - one consisting of cover data for all species initially observed in sites, and one consisting of presence-absence data, which includes the former species as well as those only apparent upon revisit (or only reliably differentiated upon revisit; e.g. individual grass and sedge species). As Gauch (1982) and others recommend, I eliminated rare species from both matrices, defining as "rare" those species occurring in fewer than 5% of the samples (in my case, those in only 1 site).

A number of different algorithms are available to ordinate site-by-species data, and there is no one generally superior method; rather, the appropriate technique depends on the nature of the data and the purposes for doing the ordination. In addition, advanced computer technology has greatly increased the possibilities for multivariate analysis, and the relative advantages and disadvantages of different methods and new modifications are still being explored.

There do, however, seem to be some generally accepted guidelines. For example, principal components analysis (PCA) is appropriate for data sets with low species turnover among sites, in which species abundances vary more or less linearly with underlying environmental gradients (ter Braak 1995). ter Braak and Prentice (1988) give rules of thumb for determining when PCA may be appropriate, rather than a method assuming a unimodal species response model (i.e., a method in the correspondence analysis family). Using their rules of thumb, I determined that my gradient lengths were definitely too long for a linear approach.

Of the correspondence analysis (CA) group, canonical correspondence analysis (CCA) is becoming increasingly popular in ecology. While CCA has been widely lauded as escaping many of the problems that have plagued other types of CA (Palmer 1993), it too is not suited for every situation. Canonical methods link one set of variables to another set, combining aspects of ordination with aspects of regression (ter Braak 1995). In the case of CCA, the site scores are not freely chosen; rather, the axes are constrained to be linear combinations of measured environmental variables (ter Braak 1995). As McCune (1997) points out, CCA should not be used when the objective is to describe community structure, but may be appropriate when the objective is to examine species

responses to particular variables. As my analysis is exploratory in nature, I have no *a priori* reason to believe that any particular environmental variable is significant in interpreting the species data. Also, CCA requires that the number of environmental parameters be much lower than the number of sites (ter Braak 1995), which is not the case for my data. For these reasons, I decided that canonical techniques such as CCA were not suitable for my purposes.

Three viable options then remained: non-metric multidimensional scaling (NMDS), polar (Bray-Curtis) ordination (PO), and detrended correspondence analysis (DCA). I did try all three methods with my data (using PC-ORD for Windows, Version 3.09 [McCune and Mefford 1997]), but only the DCA results are presented in the next section.[1] I used the detailed guidelines for NMDS analysis given by Clarke (1993), and on that basis determined that my data required at least a 4-dimensional solution. However, PC-ORD can graph no more than 3 axes, and more than that are conceptually difficult in any case. PO gave similar results to DCA for the cover matrix, but very different (and for me, uninterpretable) results for the presence-absence matrix. Therefore, I decided that DCA was the best option. A number of problems have been identified with the mathematically inelegant detrending step of DCA, and the validity of this technique continues to be debated; e.g. see Jackson and Somers (1991). Yet, it is still popular with "practical field ecologists" (ter Braak 1995:108), and one relatively recent source still recommends it as the best overall choice among the non-canonical ordination techniques (Kent and Coker 1992).

However, deciding upon a technique is only one decision that must be made in an ordination analysis. Data transformations can have as much effect on the outcome of an analysis as the type of algorithm chosen. Beals smoothing (also known as the sociological favourability index) is a type of transformation highly recommended by

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[1] I used all the default options in PC-ORD for my detrended correspondence analyses, but did not choose the downweighting option, since I had already performed my own downweighting by omitting rare species.

McCune (1994) for heterogeneous community data (i.e. data in which the sites are quite different, so there are many zeros). The method converts cover estimates to presence-absence, and then replaces these values with continuous probabilities constructed from a matrix of joint occurrences between species. Since my data are decidedly heterogeneous, I tried this transformation, but found that there was hardly any difference between an ordination diagram based on my smoothed cover data, and one based on a presence-absence matrix. Therefore, it seemed that it was the act of converting to presence-absence data that had the main impact on the result. In addition, Beals smoothing changed the gradient lengths to an intermediate level not well suited to either linear or unimodal methods. I therefore decided to simply use my original cover and presence-absence matrices, without smoothing. Unless one sees an obvious benefit, caution is warranted, "because, like any smoothing function, this transformation can produce the appearance of reliable, consistent trends even from a series of random numbers" (McCune and Mefford 1997:41).

I did decide to use a logarithmic transformation on my species cover data. This transformation is often useful for highly variable data, e.g. when species abundances vary widely or there are many small values and a few large values (ter Braak 1995, McCune and Mefford 1997). This transformation allowed me to follow Gauch's (1982) suggestion that abundance data fall in the range of 0 to 10, so that there is both quantitative and qualitative information, but neither dominates. While the ordination diagram did not change dramatically as a result of the transformation, I did feel justified in using it, because it resulted in a much better fit between distances in the ordination space and distances in the original, unreduced space (PC-ORD calculates an R^2 statistic to assess this).

After ordinating the species, I then attempted to relate my environmental and lily data to the ordination axes. PC-ORD gives the option of doing graphical overlays of other data sets on the ordination diagram, such that the sizes of the points representing sites are proportional to the size of the overlay variable at each site. In addition, correlations are calculated between the overlay variable and each ordination axis; it

displays both the parametric Pearson's coefficient as well as the nonparametric Kendall's tau. I chose the latter, as most of my variables were highly non-normal (as assessed by the Wilk-Shapiro statistic available in Statistix for Windows Version 1.0 [Analytical Software 1996]), and many of them could not be transformed successfully.

Finally, while classification was not an objective of my analysis, I was interested in comparing the characteristics of two broad groups that became apparent on the ordination. I used the clustering algorithm TWINSPAN (available in PC-ORD), as an objective means of defining what particular sites would be included in the two groups. I chose TWINSPAN simply because it is currently widely used and accepted in community ecology for classification purposes (van Tongeren 1995). I felt this was adequate justification given the relatively minor role it plays in my analysis.

2.1.4 Results

Erythronium grandiflorum *Population Characteristics*

Table 2.4 presents the mean values of quantitative *Erythronium* variables for each site. Shown are not only the data for variables used in the analyses discussed in this chapter, but also some additional data to help characterize the populations. Seedling densities (per m^2) ranged from zero at Site 33, to 60.7 at Site 37 (mean for the 38 sites = 13.4). Seedling numbers were highly variable, both among sites and among quadrats at a given site, thus 10 quadrats per site may not have been sufficient to properly estimate this parameter. This variability was due to the fact that seedlings were often found in tight groups (see section 1.1.3). Densities of juvenile (one-leaved) plants per m^2 ranged from 15.1 at Site 6, to 388.4 at Site 21 (mean for the 38 sites = 130.3). More than half the sites had well over 100 juvenile plants/m^2. Densities of two-leaved (non-flowering) plants per m^2 were much lower, from 0.3 at site 33, to 106.3 at site 17 (mean for the 38 sites = 12.8). Thirty-two of 38 sites had fewer than 15 two-leaved plants/m^2. Flowering plant densities ranged from 0.8 at site 14, to 90.0 at site 30 (mean for the 38 sites = 28.6). The vast majority of flowering plants in all sites bore only one flower; the proportion of multiple-flowered plants among all flowering plants ranged from 0 at a number of sites to 0.41 at

Table 2.4 Mean values of quantitative *Erythronium grandiflorum* variables at the 38 sites surveyed in this study. The first 10 variables are those used in analyses and described in Table 2.3. Additional variables described below.

Site	seed-ling (#/m²)	one-leaf (#/m²)	two-leaf (#/m²)	flow-plant (#/m²)	multi-flow	prop-flow	prop-2leaf	ratio-seed	ratio-1leaf	leaf-area (cm²)	one-flow[1] (#/m²)	two-flow[2] (#/m²)	three-flow[3] (#/m²)	four-flow[4] (#/m²)	leaf length[5] (cm)	leaf width[6] (cm)	% cover[7]
1	7.2	120.8	11.8	39.7	0.04	0.23	0.07	0.18	3.05	57.5	38.1	1.5	0.1	0.0	17.7	4.1	33.8
2	10.9	26.6	3.8	21.3	0.41	0.41	0.07	0.51	1.25	68.2	12.5	5.9	2.5	0.4	21.0	4.1	14.6
3	1.4	64.8	10.7	5.3	0.02	0.07	0.13	0.26	12.23	58.9	5.2	0.1	0.0	0.0	20.5	3.7	17.3
4	44.2	140.3	6.8	21.2	0.05	0.13	0.04	2.08	6.62	41.5	20.1	1.1	0.0	0.0	14.6	3.3	20.7
5	1.6	20.8	6.4	6.7	0.03	0.20	0.19	0.24	3.10	99.8	6.5	0.2	0.0	0.0	24.8	5.1	13.8
6	2.0	15.1	0.6	6.1	0.20	0.28	0.03	0.33	2.48	63.4	4.9	0.8	0.3	0.0	19.6	4.1	7.4
7	0.5	35.6	8.4	3.7	0.00	0.08	0.18	0.14	9.62	70.1	3.7	0.0	0.0	0.0	19.3	4.6	13.5
8	13.3	62.3	9.2	14.0	0.14	0.16	0.11	0.95	4.45	64.1	12.1	1.8	0.1	0.0	19.8	4.1	15.0
9	12.0	64.5	8.4	19.3	0.01	0.21	0.09	0.62	3.34	56.5	19.1	0.2	0.0	0.0	16.6	4.2	17.5
10	24.4	18.9	8.7	11.2	0.21	0.29	0.22	2.18	1.69	83.4	8.8	2.4	0.0	0.0	22.3	4.7	11.3
11	14.3	43.1	10.2	9.2	0.00	0.15	0.16	1.55	4.68	13.4	9.2	0.0	0.0	0.0	9.0	1.9	5.3
12	19.8	86.4	22.2	42.3	0.03	0.28	0.15	0.47	2.04	41.2	41.2	1.0	0.1	0.0	16.1	3.2	27.2
13	1.0	33.9	8.1	3.6	0.03	0.08	0.18	0.28	9.42	67.9	3.5	0.1	0.0	0.0	20.1	4.4	9.7
14	0.2	31.7	8.1	0.8	0.00	0.02	0.20	0.25	39.63	73.0	0.8	0.0	0.0	0.0	22.2	4.0	16.1
15	34.9	228.0	11.9	24.0	0.05	0.09	0.05	1.45	9.50	57.3	22.8	1.1	0.1	0.0	17.4	4.0	23.9
16	5.2	156.4	6.1	5.7	0.00	0.03	0.04	0.91	27.44	30.4	5.7	0.0	0.0	0.0	14.9	2.6	13.4
17	35.5	285.7	106.3	51.6	0.00	0.12	0.24	0.69	5.54	50.5	51.5	0.1	0.0	0.0	17.8	3.6	64.1
18	23.1	122.9	22.9	34.5	0.02	0.19	0.13	0.67	3.56	33.6	33.8	0.6	0.1	0.0	14.3	3.0	27.9
19	0.1	34.5	2.4	3.6	0.11	0.09	0.06	0.03	9.58	37.0	3.2	0.4	0.0	0.0	16.1	2.9	6.8
20	22.9	124.8	17.9	23.2	0.00	0.14	0.11	0.99	5.38	45.6	23.2	0.0	0.0	0.0	16.9	3.4	20.3
21	13.6	388.4	53.8	29.4	0.00	0.06	0.11	0.46	13.21	32.2	29.4	0.0	0.0	0.0	14.7	2.8	36.6
22	28.3	182.0	3.8	23.9	0.01	0.11	0.02	1.18	7.62	43.0	23.6	0.3	0.0	0.0	16.0	3.4	26.8
23	11.1	286.6	1.8	10.9	0.01	0.04	0.01	1.02	26.29	32.1	10.8	0.0	0.1	0.0	14.8	2.7	24.1

Table 2.4, cont.

Site	seed-ling (#/m^2)	one-leaf (#/m^2)	two-leaf (#/m^2)	flow-plant (#/m^2)	multi-flow	prop-flow	prop-2leaf	ratio-seed	ratio-1leaf	leaf-area (cm^2)	one-flow[1] (#/m^2)	two-flow[2] (#/m^2)	three-flow[3] (#/m^2)	four-flow[4] (#/m^2)	leaf length[5] (cm)	leaf width[6] (cm)	% cover[7]
24	0.6	243.5	4.5	85.2	0.07	0.26	0.01	0.01	2.86	48.7	79.0	5.9	0.2	0.1	16.6	3.8	42.7
25	34.4	286.4	8.9	58.5	0.03	0.17	0.03	0.59	4.90	32.8	56.5	2.0	0.0	0.0	14.1	2.9	31.5
26	3.1	110.1	3.5	86.6	0.16	0.43	0.02	0.04	1.27	47.3	72.9	12.2	1.5	0.0	16.8	3.5	34.5
27	17.8	245.6	7.1	22.3	0.01	0.08	0.03	0.80	11.01	62.4	22.1	0.2	0.0	0.0	21.0	3.8	36.3
28	0.4	90.9	7.1	55.6	0.13	0.36	0.05	0.01	1.63	95.2	48.1	7.0	0.5	0.0	25.7	4.7	53.1
29	10.2	144.1	4.2	23.2	0.01	0.14	0.02	0.44	6.21	81.9	23.0	0.2	0.0	0.0	23.8	4.3	37.1
30	1.2	139.1	3.4	90.0	0.19	0.39	0.01	0.01	1.55	57.0	72.6	14.0	3.0	0.4	18.4	3.9	51.2
31	10.9	78.2	3.2	9.8	0.00	0.11	0.04	1.11	7.98	81.7	9.8	0.0	0.0	0.0	24.8	4.2	22.1
32	9.5	83.1	2.9	12.4	0.02	0.13	0.03	0.77	6.70	24.6	12.2	0.2	0.0	0.0	12.9	2.4	12.8
33	0.0	61.5	0.3	2.0	0.00	0.03	0.00	0.00	30.75	29.8	2.0	0.0	0.0	0.0	15.4	2.4	11.8
34	0.8	115.9	4.7	66.0	0.32	0.35	0.03	0.01	1.76	114.5	44.9	17.2	3.7	0.2	29.5	5.0	49.9
35	1.0	134.0	10.6	41.3	0.08	0.22	0.06	0.02	3.24	48.1	38.2	2.5	0.4	0.2	16.0	3.8	32.0
36	19.6	92.7	12.3	37.6	0.03	0.26	0.09	0.52	2.47	42.0	36.3	1.3	0.0	0.0	17.2	3.0	23.6
37	60.7	311.3	13.1	36.3	0.01	0.10	0.04	1.67	8.58	38.6	35.9	0.4	0.0	0.0	14.9	3.3	24.3
38	12.3	240.9	51.6	49.7	0.01	0.15	0.15	0.25	4.85	37.3	49.2	0.5	0.0	0.0	15.0	3.1	39.5

[1] Average number of plants with one flower per m^2 (mean over 10 quadrats)
[2] Average number of plants with two flowers per m^2 (mean over 10 quadrats)
[3] Average number of plants with three flowers per m^2 (mean over 10 quadrats)
[4] Average number of plants with four flowers per m^2 (mean over 10 quadrats)
[5] Average leaf length (mean of 20 leaves per site)
[6] Average leaf width (mean of 20 leaves per site)
[7] Average percent cover of *E. grandiflorum* per m^2 (mean over 10 quadrats)

site 2 (mean for the 38 sites = 0.06). In other words, on average for all sites, only about 6% of flowering plants bore more than one flower. Plants with increasing numbers of flowers were progressively more rare. The mean number of one-flowered plants per m^2 for all sites was 26.1, while for two-flowered plants it was 2.1, for three-flowered plants it was 0.33, and for four-flowered plants it was 0.034. Only one plant with more than four flowers was found in all quadrats sampled; this was a six-flowered plant at site 6. In addition to density, another way of looking at plant abundance is percent cover (I did not use this variable in my analyses as it was highly correlated with other variables). Cover values ranged from 5.3% at site 11, to 64.1% at site 17 (mean for the 38 sites = 25.5%). In terms of plant size, leaf length ranged from 9.0 cm at site 11 to 29.5 cm at site 34 (mean 18.1 cm), and leaf width ranged from 1.9 cm at site 11 to 5.1 cm at site 5 (mean 3.6 cm).

DCA Ordination and Environmental Gradients

Figure 2.3 shows the DCA ordinations for the log-transformed species cover data and for the presence-absence data from all 38 sites sampled. The presence-absence ordination appeared to form more distinct groups than the cover ordination, but was otherwise similar, and for further analyses I will present results only for the cover matrix. These figures provide an immediate impression of the relationships of these sites to one another. Two groups of similar sites occur at the left and right sides of the diagram, with other sites scattered between. In DCA, sites and species are ordinated simultaneously, and therefore one can also request that the species be shown on the diagram. I did the two diagrams separately to avoid clutter; the species ordination is shown in Figure 2.4. Using the two figures, it is apparent which sites are similar, and which groups of species characterize the different positions on the axes.

I interpreted the ordination axes[1] using the information on associated species and

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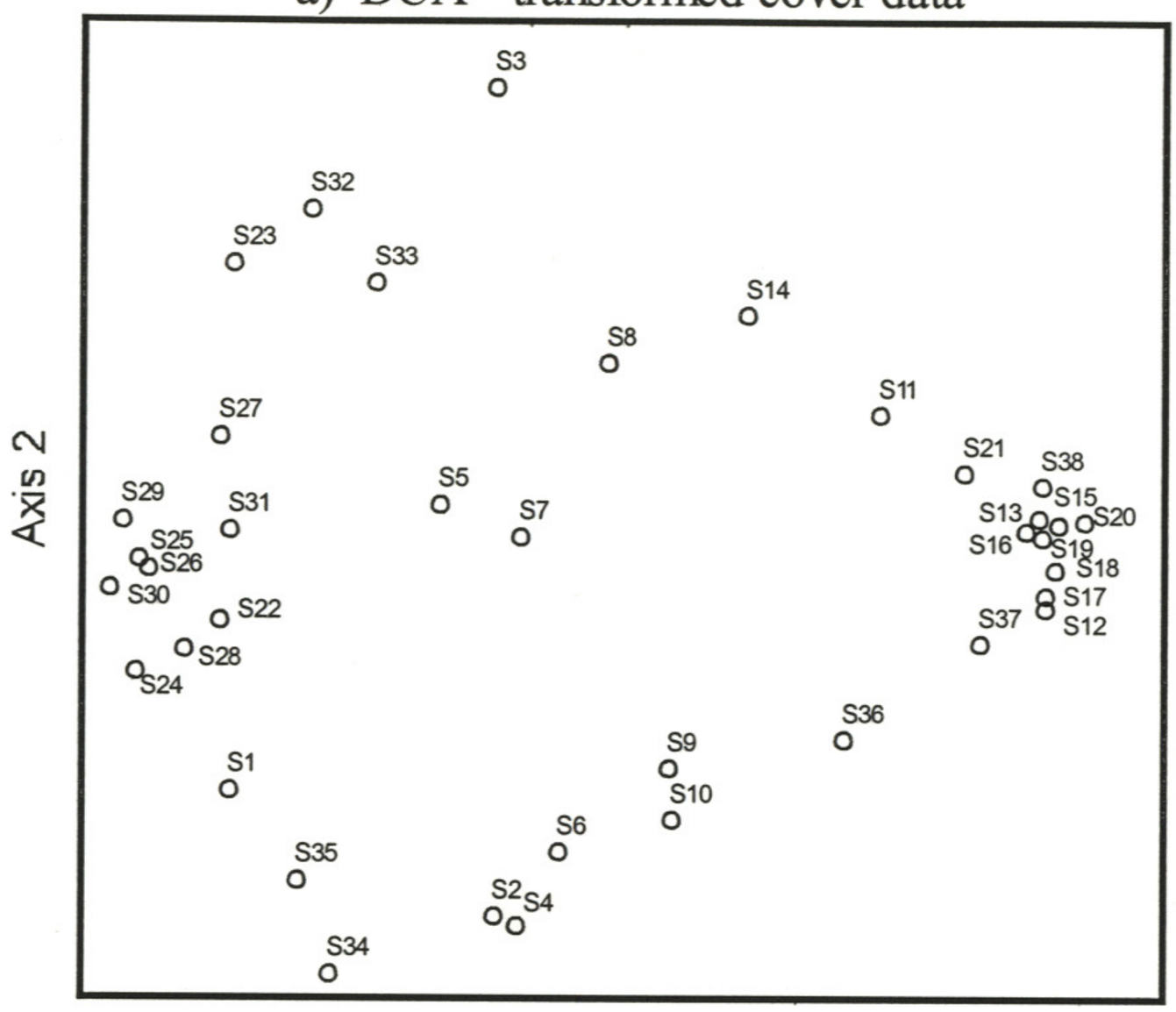
[1]The third axis is not shown or discussed; I was not able to interpret this axis in any meaningful way. It appeared that most of the variation in the species data was accounted for by the first two axes.

a) DCA - transformed cover data



b) DCA - presence-absence data

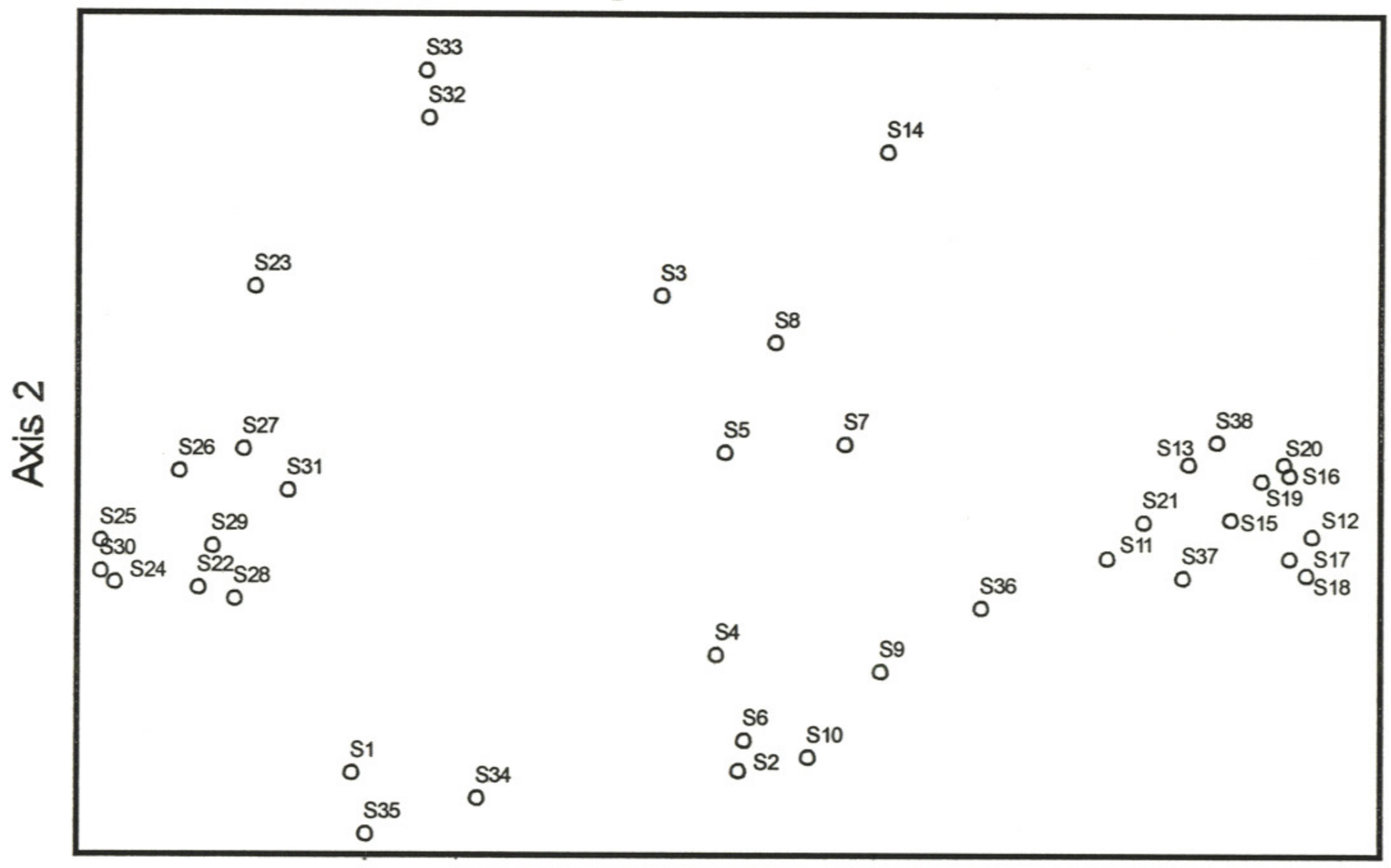


Figure 2.3 Site ordinations by DCA of a) cover data (157 taxa) and b) presence-absence data (210 taxa). Site numbers are those in Table 2.1.

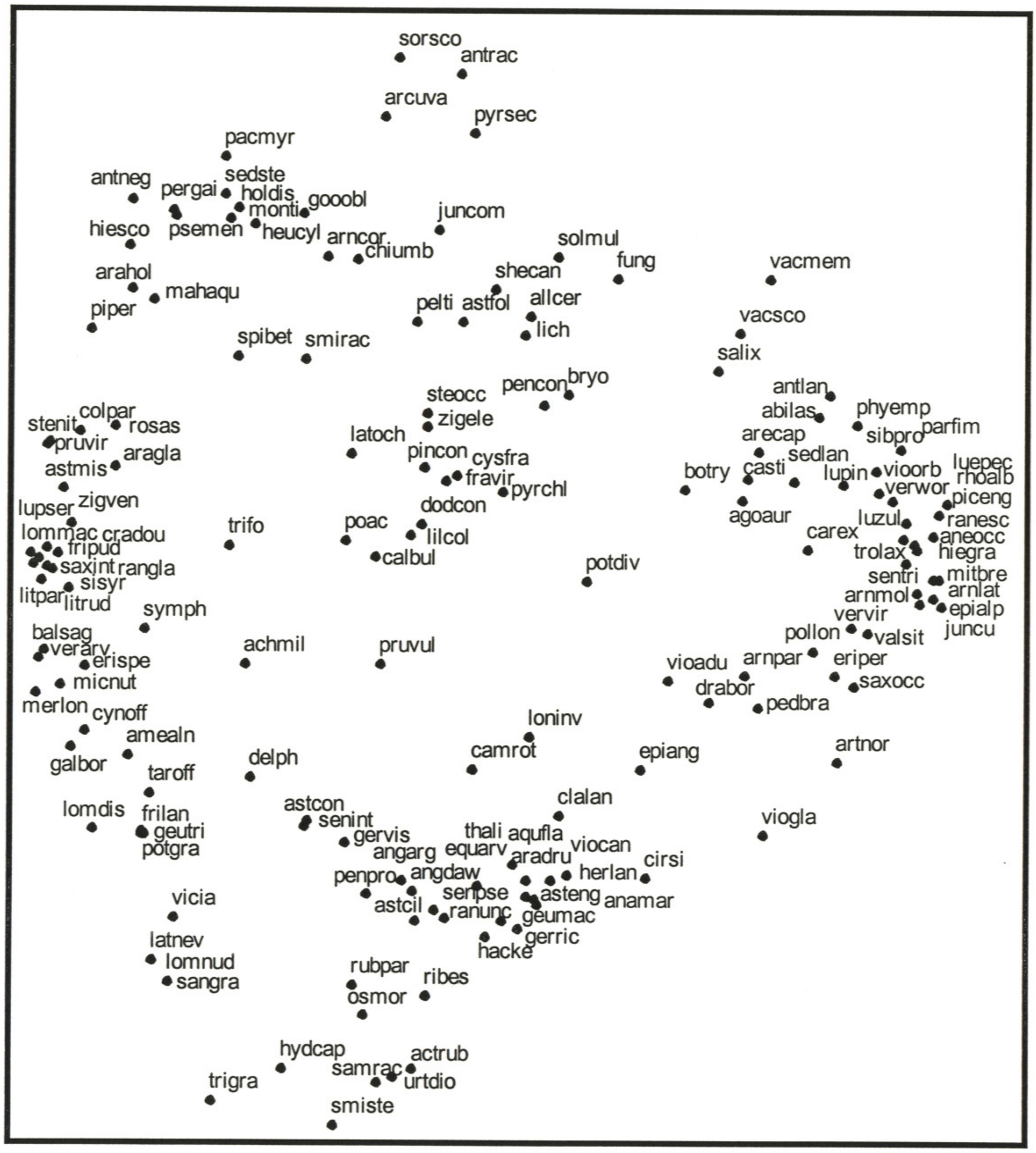


Figure 2.4 Species ordination from DCA of cover data for 38 sites. Labels have been jittered to ensure readability; positions are therefore only approximate. See Appendix 1 for translation of species codes.

the environmental data (Appendix 2). In both cases, I was most interested in the variables (species or environmental parameters) that exhibit significant and meaningful correlations with the ordination axes. The species correlations are given in Table 2.5, and the environmental correlations in Table 2.6. Overlay diagrams are also given for the major environmental variables in Figure 2.5, and a joint plot in Figure 2.6 summarizes the strength and direction of the relationships of these variables to the axes.

Elevation is the dominant factor associated with the first axis, with high-elevation sites at the right of the diagram and low-elevation sites at the left. Sites 12-13, 15-21, and 37-38 are all subalpine, and in spite of being widely dispersed geographically (Fig. 2.1) exhibit characteristic species including *Anemone occidentalis, Arnica latifolia, Carex* spp., *Epilobium alpinum*, *Erigeron peregrinus, Luzula* spp., *Mitella breweri, Senecio triangularis, Valeriana sitchensis,* and *Veratrum viride*. Sites 11 and 36 are also subalpine and similar to the high-elevation group in many respects, but may be more distinctive because they are far to the west of the others (and far from each other north to south). Sites at the left (22-31) represent the Chase/Adams River area, and are characterized by such species as *Achillea millefolium, Amelanchier alnifolia, Astragalus miser, Balsamorhiza sagittata, Collinsia parviflora, Lithophragma parviflora,* abundant grasses, *Rosa* spp., and *Zigadenus venenosus*, as well as a number of introduced species. There is some variation because some of the sites (23, 27, and 31) are under a *Pseudotsuga menziesii* canopy, and the others are under *Populus tremuloides* (24, 28), or in open meadow areas with patches of *Symphoricarpos* sp. and other shrubs.

Other environmental factors associated with the first axis include pH and rockiness. Higher elevation sites exhibit lower pH and slightly higher rockiness (the relationship with rockiness is weak, however, and would probably not be significant if adjusted for multiple comparisons). The higher organic matter at the subalpine sites reflects the fact that at these sites *E. grandiflorum* often grows in a substrate consisting largely of humus wedged between rocks. Shrub cover, soil texture, and species richness are associated with both the first and second axes, in the directions indicated on Figure 2.6. However, different species of shrubs are associated with the two axes; as shown by

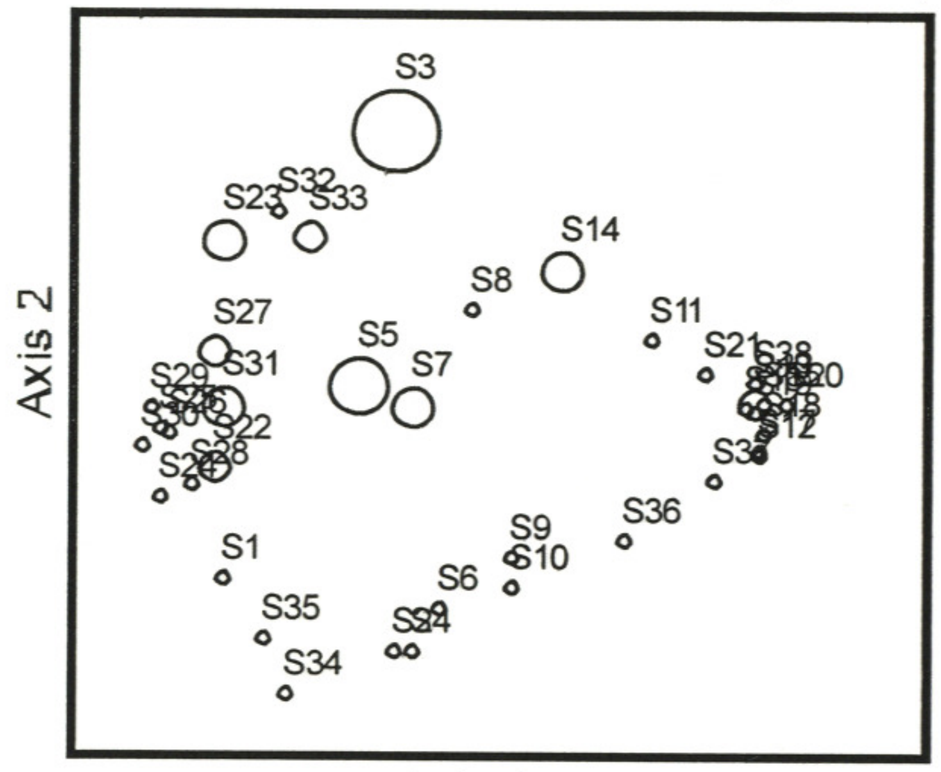
Table 2.5 Kendall's tau correlations of species abundance (cover) values with DCA ordination axes ($|tau_{(0.05)}| = 0.223$; $|tau_{(0.01)}| = 0.292$). Correlations significant at alpha <0.01 are shown in boldface. Only taxa found in more than 5 sites are shown.

SPECIES	AXIS		
	1	2	3
Abies lasiocarpa	**0.344**	0.282	0.195
Achillea millefolium	**-0.526**	-0.148	0.233
Amelanchier alnifolia	**-0.538**	0.061	-0.265
Anemone occidentalis	**0.554**	0.144	0.086
Arnica cordifolia	-0.158	**0.351**	-0.070
Arnica latifolia	**0.533**	0.065	0.015
Aster ciliolatus	-0.063	**-0.352**	-0.142
Aster conspicuus	-0.147	-0.166	0.051
Aster engelmannii	-0.005	**-0.381**	-0.044
Astragalus miser	**-0.464**	0.039	-0.003
Balsamorhiza sagittata	**-0.566**	-0.171	0.171
Bryophytes	0.222	**0.474**	-0.079
Carex sp. or spp.	**0.656**	0.059	-0.033
Castilleja sp. or spp.	**0.349**	0.215	0.215
Claytonia lanceolata	0.184	**-0.557**	0.048
Collinsia parviflora	**-0.653**	0.031	-0.002
Crataegus douglasii	**-0.523**	-0.073	0.152
Delphinium sp.	**-0.461**	-0.245	0.245
Epilobium alpinum complex	**0.536**	0.033	-0.037
Epilobium angustifolium	**0.302**	-0.166	0.076
Erigeron peregrinus	**0.596**	-0.032	0.117
Fragaria virginiana	-0.132	-0.050	0.160
Fritillaria lanceolata	**-0.404**	-0.203	-0.190
Galium boreale	**-0.452**	-0.189	0.198
Hackelia sp.	0.024	**-0.484**	0.034
Heracleum lanatum	0.115	**-0.378**	-0.018
Lichen (generally *Cladonia* sp.)	0.132	**0.475**	0.157
Lithophragma parviflorum	**-0.610**	-0.066	0.030
Lithospermum ruderale	**-0.586**	-0.086	0.155
Lomatium dissectum	**-0.590**	-0.284	0.168
Lupinus sp.	**0.382**	-0.032	-0.096
Lupinus sericeus	**-0.485**	-0.066	0.186
Luzula sp.	**0.574**	0.101	0.062
Mahonia aquifolium	**-0.307**	0.160	-0.244
Mitella breweri	**0.663**	0.076	-0.032
Pachistima myrsinites	-0.279	**0.450**	**-0.465**
Pedicularis bracteosa	**0.392**	-0.054	0.113
Peltigera sp. or spp.	-0.005	**0.357**	-0.011
Piperia sp.	**-0.326**	0.268	-0.326
Poaceae	**-0.673**	-0.034	0.120
Potentilla gracilis	**-0.407**	**-0.305**	0.277
Ranunculus eschscholtzii	**0.521**	0.138	0.083
Ranunculus glaberrimus	**-0.514**	-0.022	0.027
Rosa sp. or spp.	**-0.636**	0.080	-0.007
Senecio integerrimus	**-0.371**	**-0.330**	0.073
Senecio triangularis	**0.558**	0.055	0.015
Sibbaldia procumbens	**0.363**	0.131	0.116
Spiraea betulifolia	**-0.308**	0.203	-0.245
Stellaria nitens	**-0.525**	0.082	-0.040
Symphoricarpos sp.	**-0.591**	-0.077	-0.219
Taraxacum officinale	**-0.573**	-0.246	0.219
Thalictrum sp.	0.104	**-0.332**	0.012
Trifolium sp. or spp.	-0.274	0.082	0.130
Vaccinium membranaceum	**0.350**	**0.316**	-0.037
Valeriana sitchensis	**0.696**	-0.055	-0.002
Veratrum viride	**0.550**	-0.043	0.025
Vicia sp.	**-0.366**	-0.215	-0.082
Viola orbiculata	**0.328**	0.288	0.098
Zigadenus venenosus	**-0.657**	-0.062	0.086

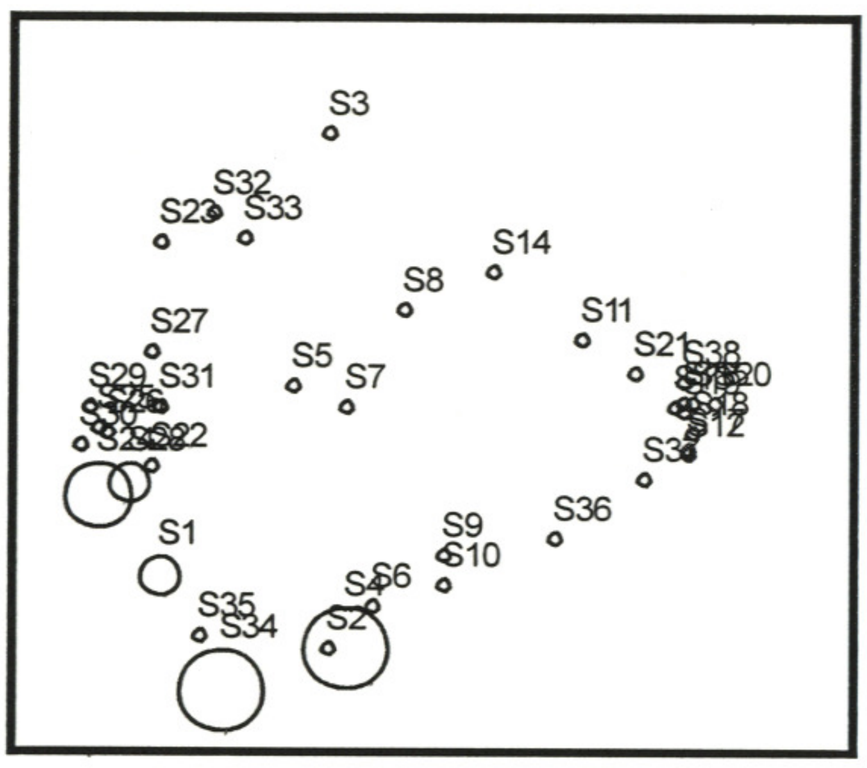
Table 2.6 Kendall's tau correlations of environmental variables with DCA ordination axes ($|tau_{(0.05)}| = 0.223$; $|tau_{(0.01)}| = 0.292$). Correlations significant at alpha < 0.01 are shown in boldface. Refer to Table 2.2 for descriptions of variables.

Environmental Variable	AXIS		
	1	2	3
Coniferous tree basal area	-0.002	**0.502**	-0.204
Deciduous tree basal area	-0.279	**-0.323**	0.152
Shrub cover	**-0.492**	0.259	-0.101
Herbaceous cover	0.144	-0.164	0.172
Total no. of species	**-0.330**	-0.172	0.253
No. of introduced species	**-0.640**	-0.244	0.071
No. of native species	-0.202	-0.141	0.254
Rockiness index	0.252	0.110	-0.021
Litter depth	**-0.486**	-0.161	-0.237
Litter cover	**-0.421**	0.034	-0.014
Grass cover	**-0.673**	-0.034	0.120
CWD cover	-0.294	0.052	-0.215
Soil pH	**-0.620**	-0.113	0.067
Soil texture	**0.523**	-0.224	0.060
Soil organic content	**0.474**	-0.061	0.149
Slope aspect	0.120	-0.157	0.208
Slope angle	-0.001	-0.132	-0.222
Elevation	**0.687**	0.084	0.158
Latitude	0.127	0.007	0.058
Longitude	-0.098	-0.189	-0.132
Phenology	0.083	-0.009	-0.028

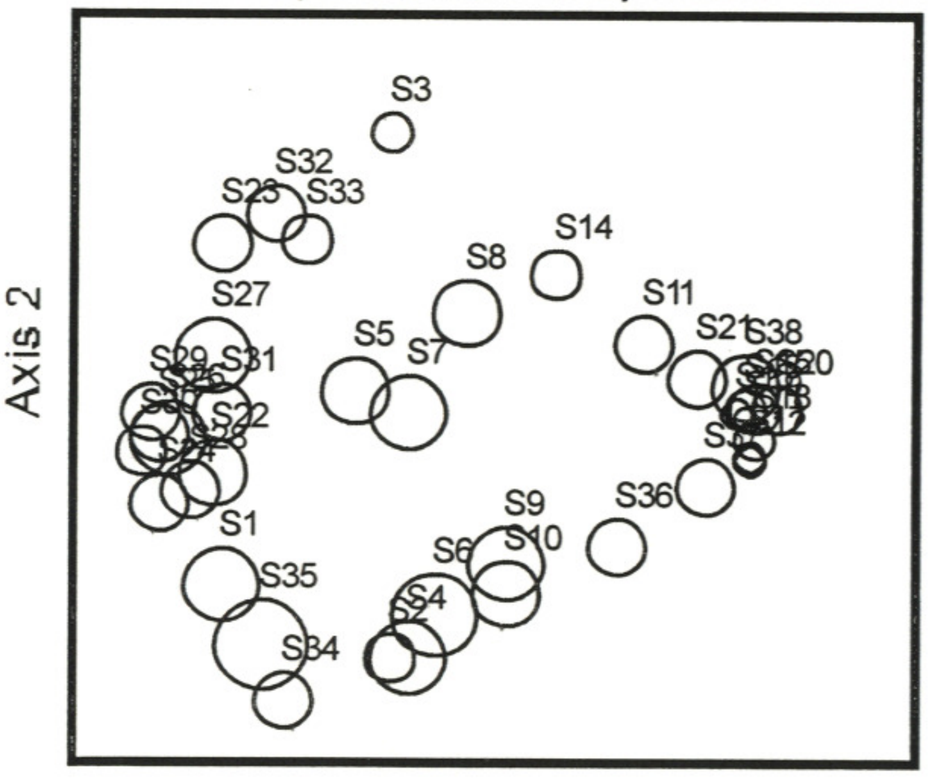
a) Coniferous tree basal area (m^2/ha)



b) Deciduous tree basal area (m^2/ha)



c) Total no. of species



d) No. of introduced species

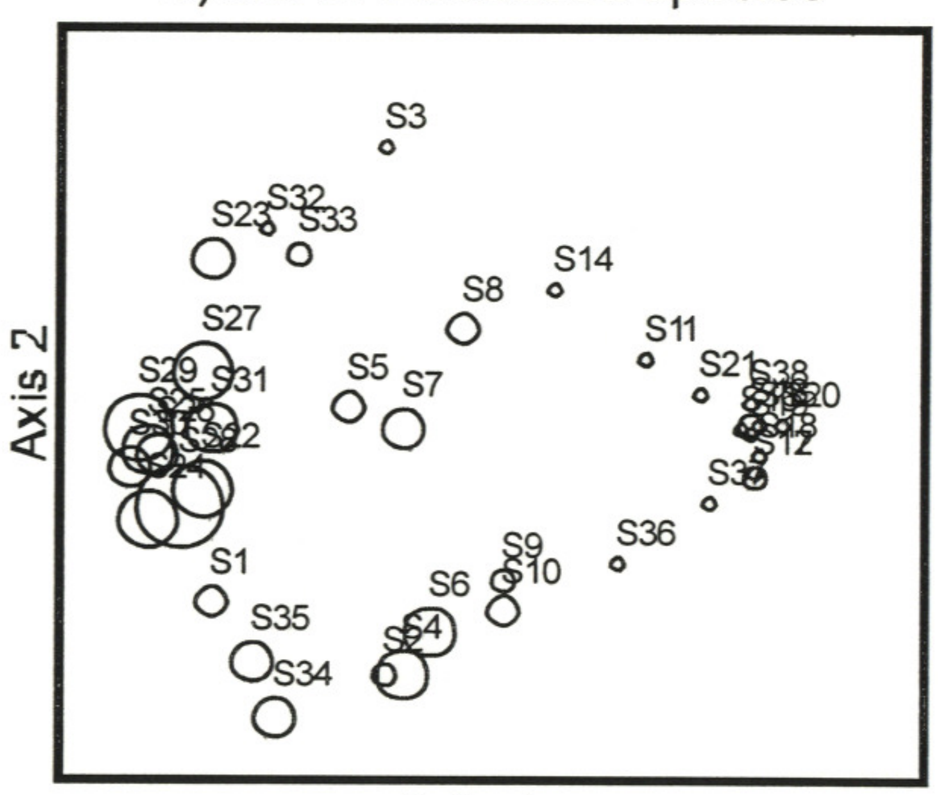
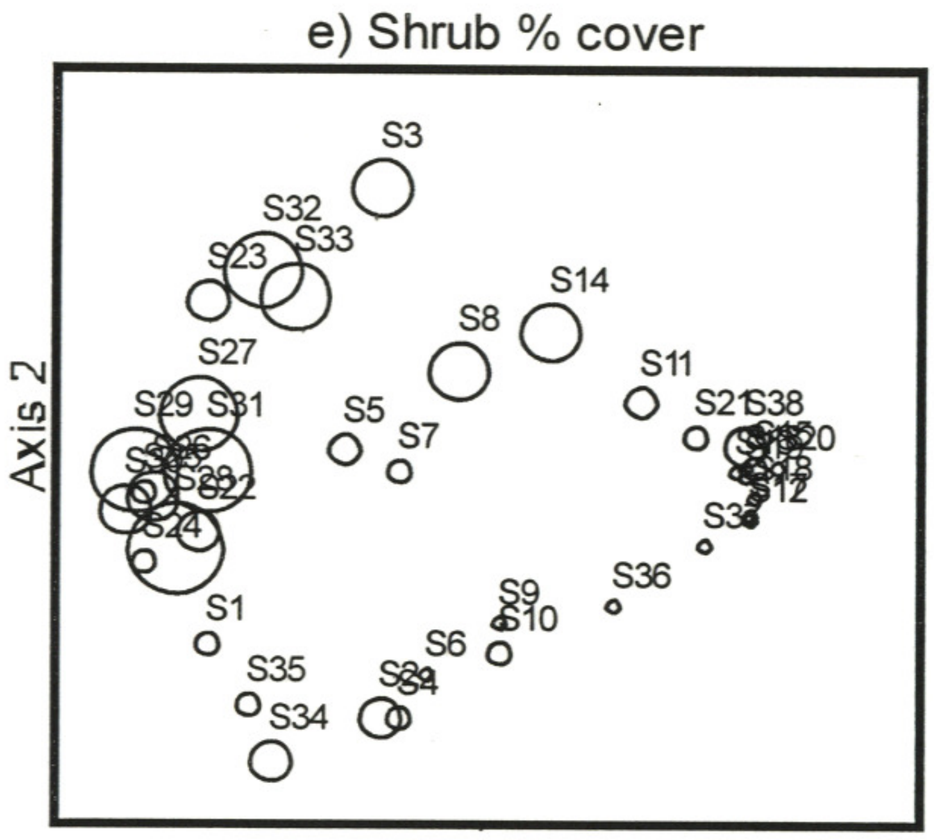
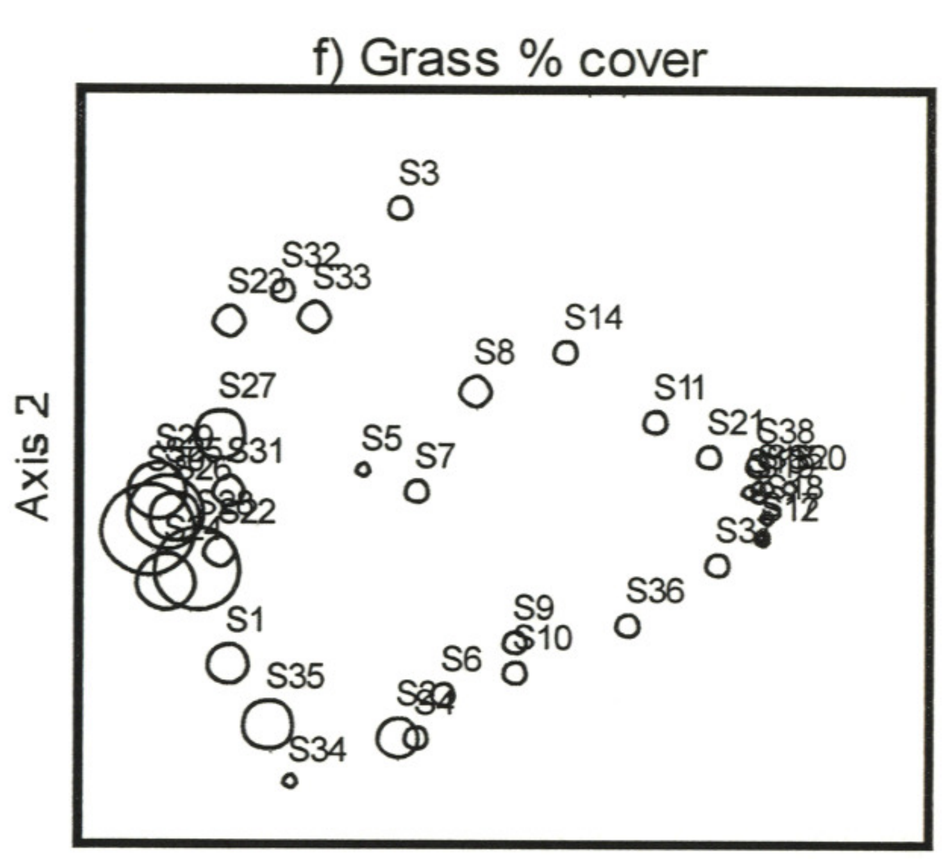
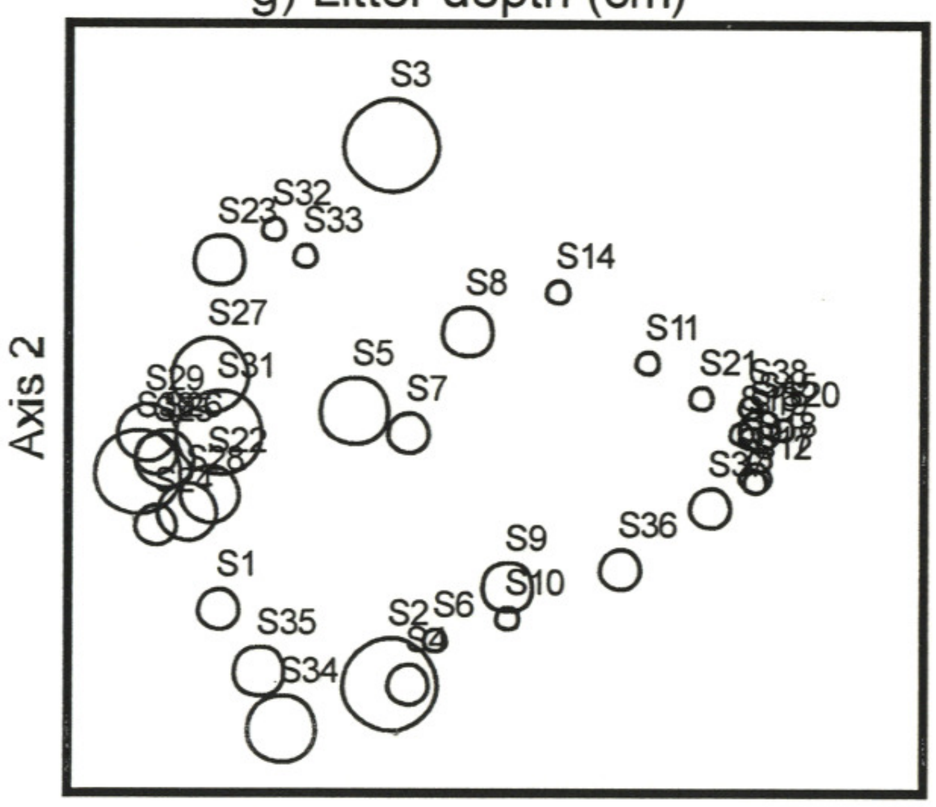


Figure 2.5 a) - l) Overlay diagrams showing relative values of environmental variables for the ordinated sites. The larger the circle, the larger the value of the variable. Shown are variables correlated with ordination axes at alpha < 0.01 (see Table 2.6). Refer to Table 2.2 for descriptions of variables.







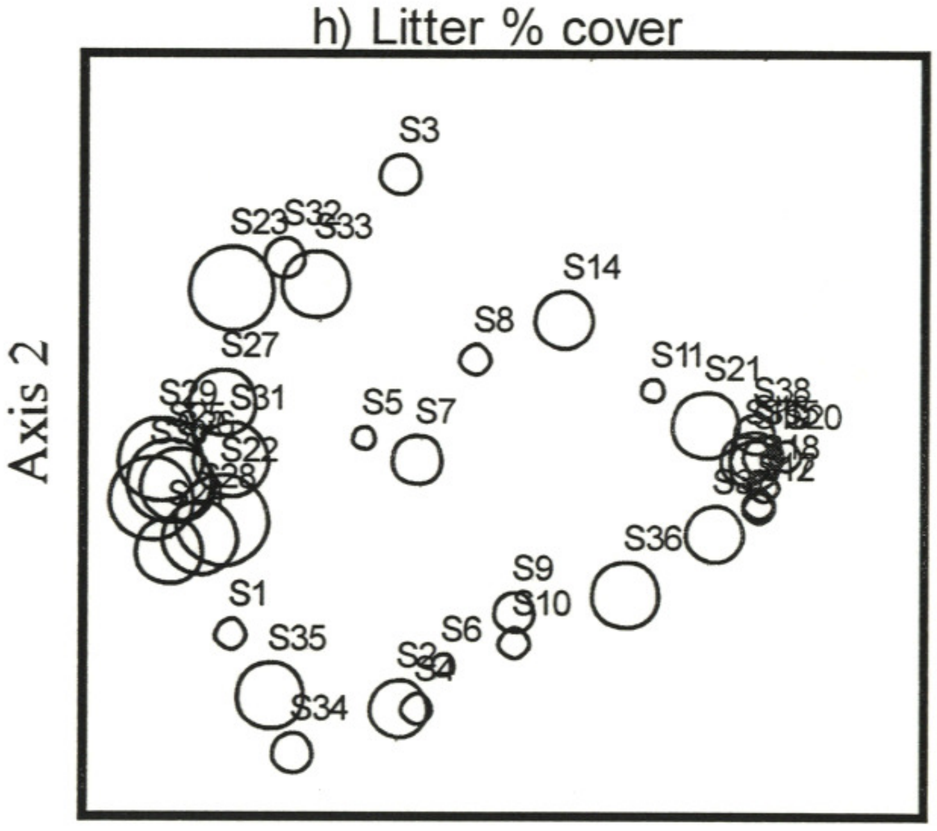
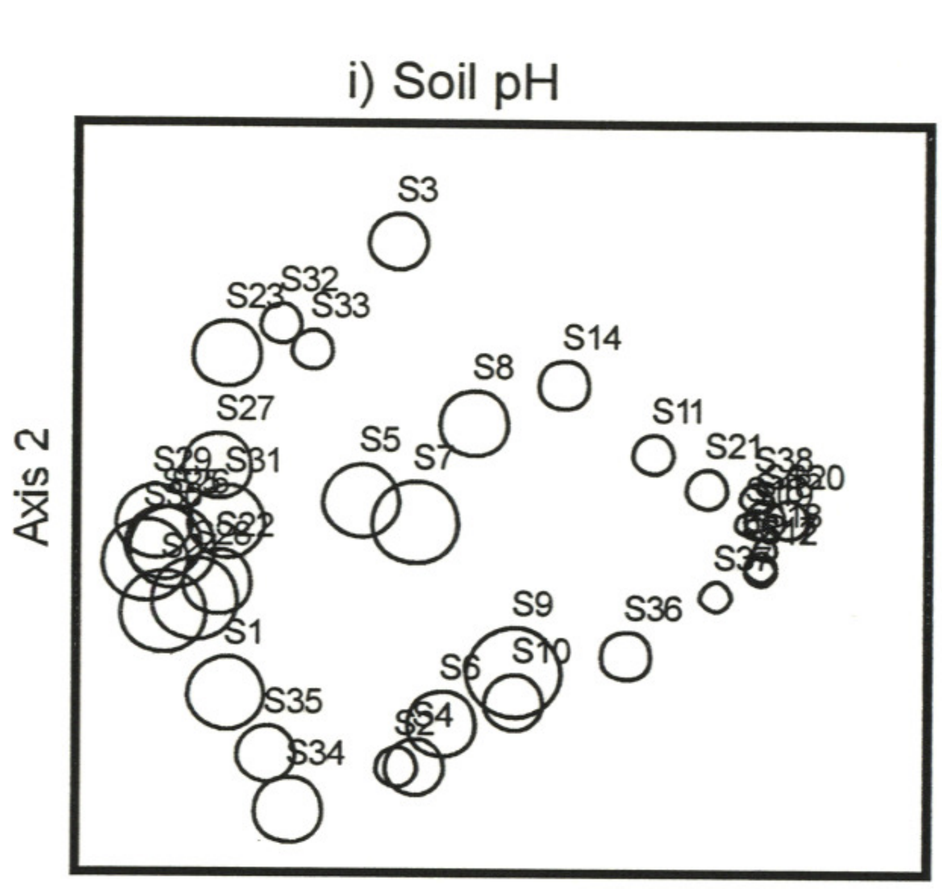
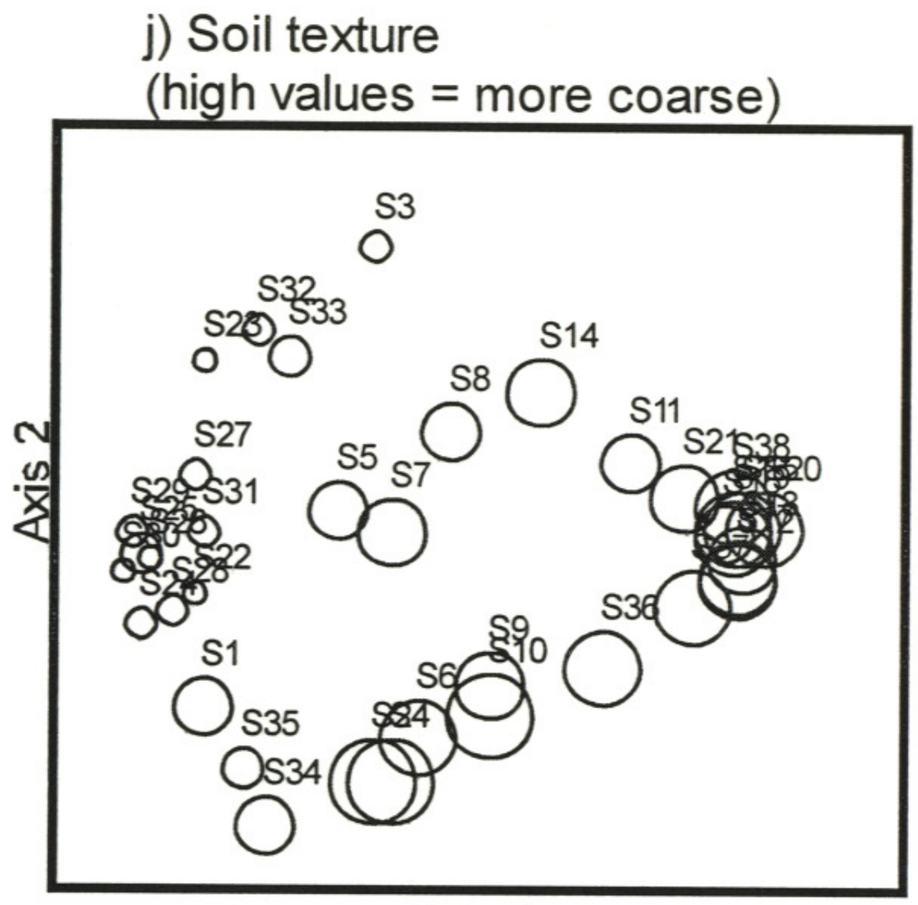
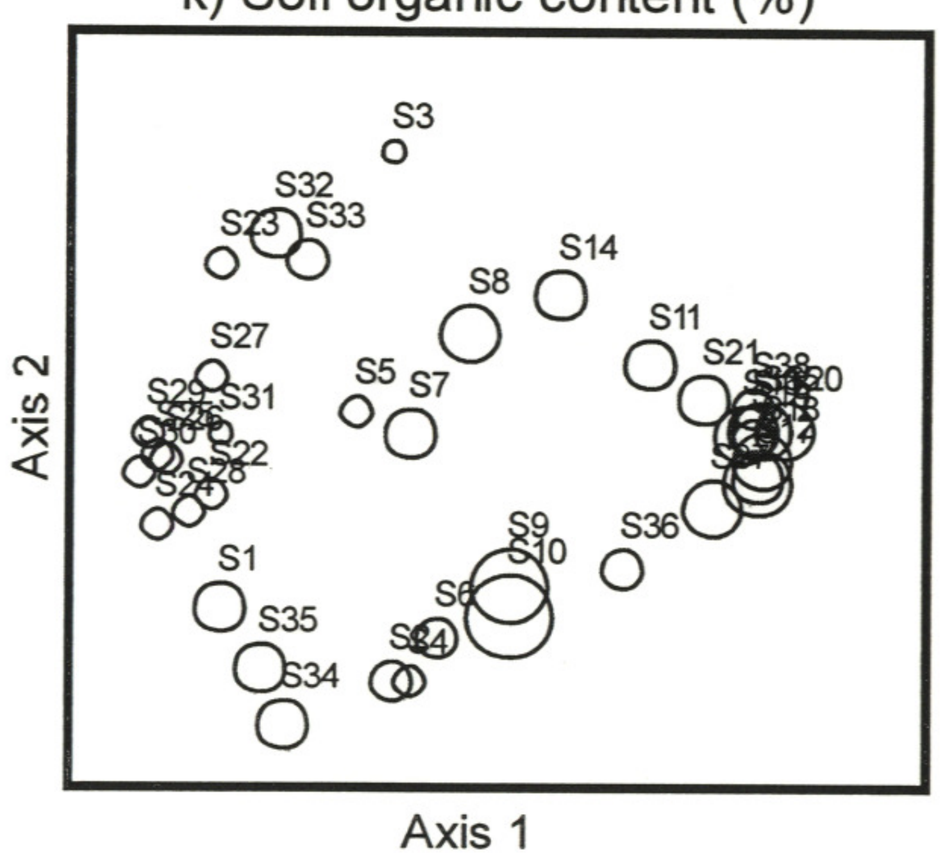


Figure 2.5, cont.







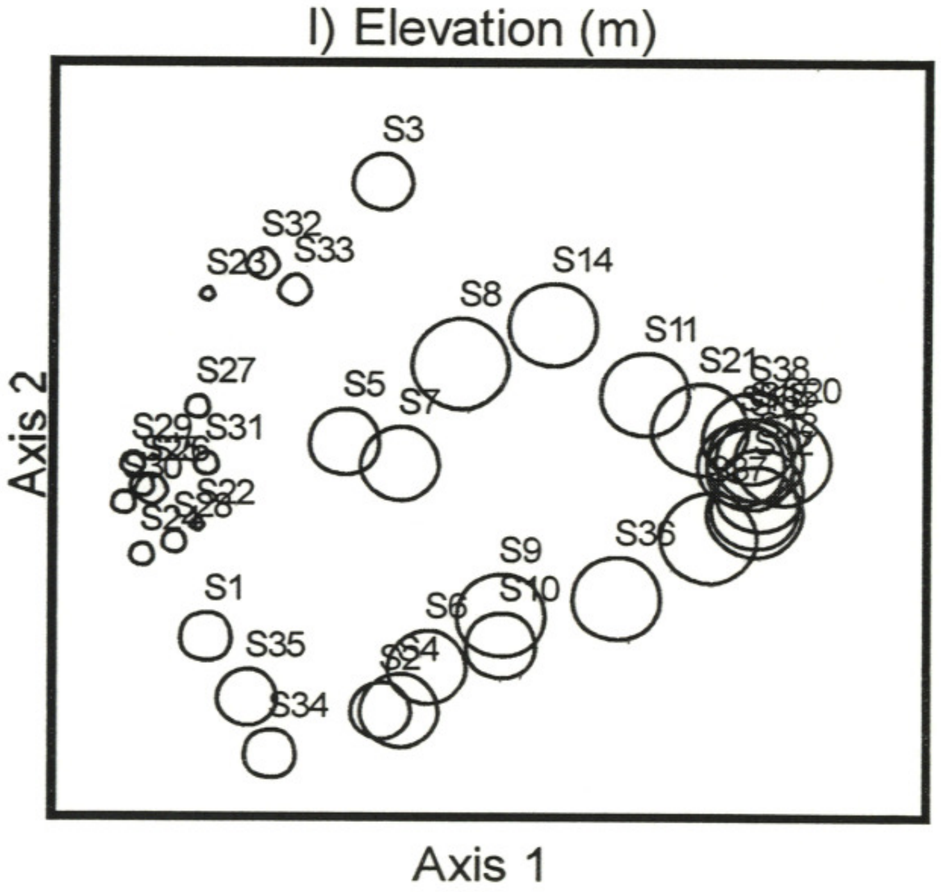


Figure 2.5, cont.

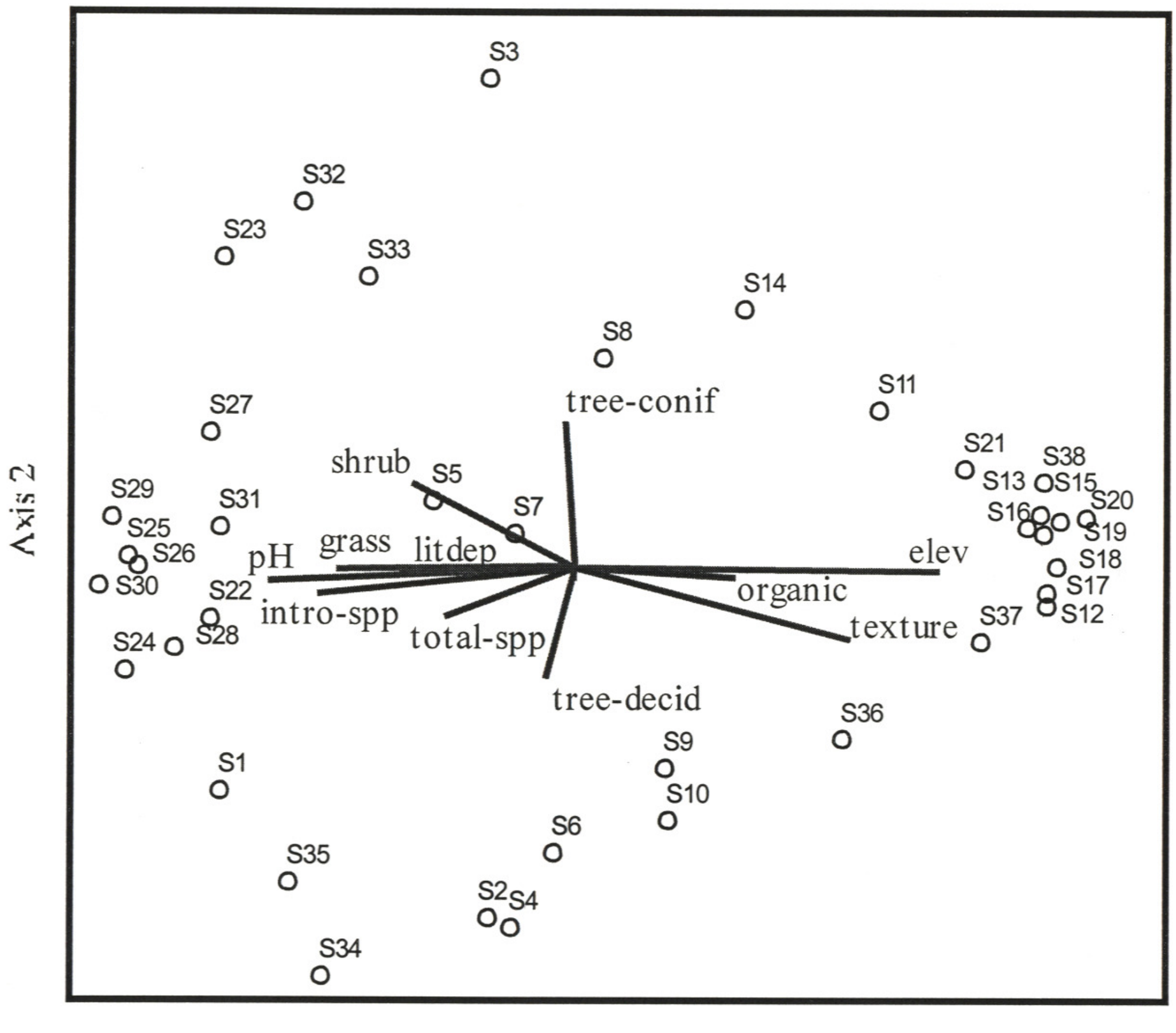


Figure 2.6 Joint plot showing environmental variables with statistically significant correlations (alpha < 0.01) to ordination axes. The angle and length of the line indicate the direction and strength of the relationship. Refer to Table 2.2 for descriptions of variables.

Figure 2.4, species including *Amelanchier alnifolia, Prunus virginiana,* and *Rosa* spp. are associated with Axis 1, while such species as *Holodiscus discolor, Mahonia aquifolium, Pachistima myrsinites, Shepherdia canadensis,* and *Spiraea betulifolia* are associated with Axis 2. The positive association of litter depth (and litter cover - not shown on joint plot for clarity) with lower elevations is probably due to the greater shrub and grass abundance in those areas (see below). The number of introduced species (often grasses) was higher at low elevations, not surprisingly.

The most significant factor contributing to the second axis appears to be tree cover; coniferous tree basal area is positively associated with this axis, while deciduous tree basal area is negatively associated with it. Deciduous basal area is also negatively associated with the first axis (Figure 2.6) since the deciduous-treed sites tend to be at lower elevations. No other variables are associated strongly with the second axis alone. Shrub cover is associated with the top and left of the diagram (low elevation and coniferous canopy), species richness is highest at the bottom and left (low elevation and deciduous canopy), and soil texture is coarsest at high elevations and in the sites at the lower right corner of the diagram.

While basal area explains the distribution of sites along the second axis to some extent, there are no groups as well-defined along this axis as at the two ends of the first axis. Many species are found only in a few sites; Table 2.5 displays only 59 species (out of 157) that are found in more than five sites. Because of the wide area in which I sampled, with very few sites in certain types of habitats, the points are widely scattered, and often (but not always) reflect the physical distance and resultant heterogeneity between sites rather than any ecological gradient. Therefore, I discuss these intermediate sites almost individually. Sites 1, 34 and 35 are located in Botanie Valley near Lytton (Table 2.1) (site 1 under *Populus tremuloides*, site 35 in open meadow, and site 34 under *Prunus* sp. - none far from *Pseudotsuga*); they are quite similar in species composition and general habitat characteristics to many of the Chase sites. Site 23, Adams River, shows similarity both to some of the Chase-area sites, and to sites 32 and 33 (near Castlegar and Creston, respectively); all three have coniferous tree cover (*Pseudotsuga*

menziesii and various tree species in the ICH zone) in or immediately surrounding the sites, and are distinguished by various combinations of the species shown in the upper left corner of Figure 2.4. Site 3, Mission Pass, is also in an open *Pseudotsuga* stand, but it has some species distinct from those of the last three sites, e.g. *Sorbus scopulina, Antennaria racemosa,* and *Pyrola secunda*. It may be distinctive partly because it is at a higher elevation than the *Pseudotsuga*-treed sites and partly because it has by the far the highest coniferous basal area value (Appendix 2). Sites 8 and 14 (in Kananaskis Country and Banff National Park, respectively) are within or adjacent to *Picea glauca,* with species such as *Shepherdia canadensis, Solidago multiradiata,* and *Vaccinium scoparium*), while sites 5 and 7 (southwestern Alberta) are under a *Pinus contorta* canopy. These last two sites, as might be expected from their central position on the ordination diagram (Fig. 2.3) share many species with a variety of other sites, but are the only two sites with, for example, *Calypso bulbosa*. Sites 9 and 10 (in and near Kootenay National Park) are steep avalanche chutes, and are similar in some respects to the subalpine sites, but have some species more characteristic of lower elevations (e.g. *Aster ciliolatus, Heracleum lanatum, Thalictrum* sp.). Finally, the juxtaposition of sites 2, 4, and 6 is interesting, as they seem quite distinctive geographically and in terms of general habitat characteristics. Site 2 (Duffey Lake) is located far to the west (Figure 2.1), and is a fairly steep avalanche chute flanked by *Salix* and *Alnus*. Sites 4 and 6 are in southwestern Alberta: site 4 is under wind-stunted *Populus tremuloides*, while site 6 is in a small meadow within *Picea engelmannii / Abies lasiocarpa / Pinus contorta* forest. Nonetheless, many species are shared among at least two of three of these mid-elevation sites (in varying combinations); e.g., *Angelica dawsonii, Aster ciliolatus, Hydrophyllum capitatum, Rubus parviflorus,* and *Urtica dioica*.

Two variables (cattle and fire) were categorical. I have presented overlays for these variables in Figure 2.7. Fire appears to be common in glacier lily habitats, as 30 of 38 sites showed at least traces of charcoal in the soil samples. Cattle are also fairly common (11 of 38 sites), particularly at the lower elevations, although cattle activity was noted at Mt. Mara at almost 1900 m. Note that all signs of cattle that I observed during

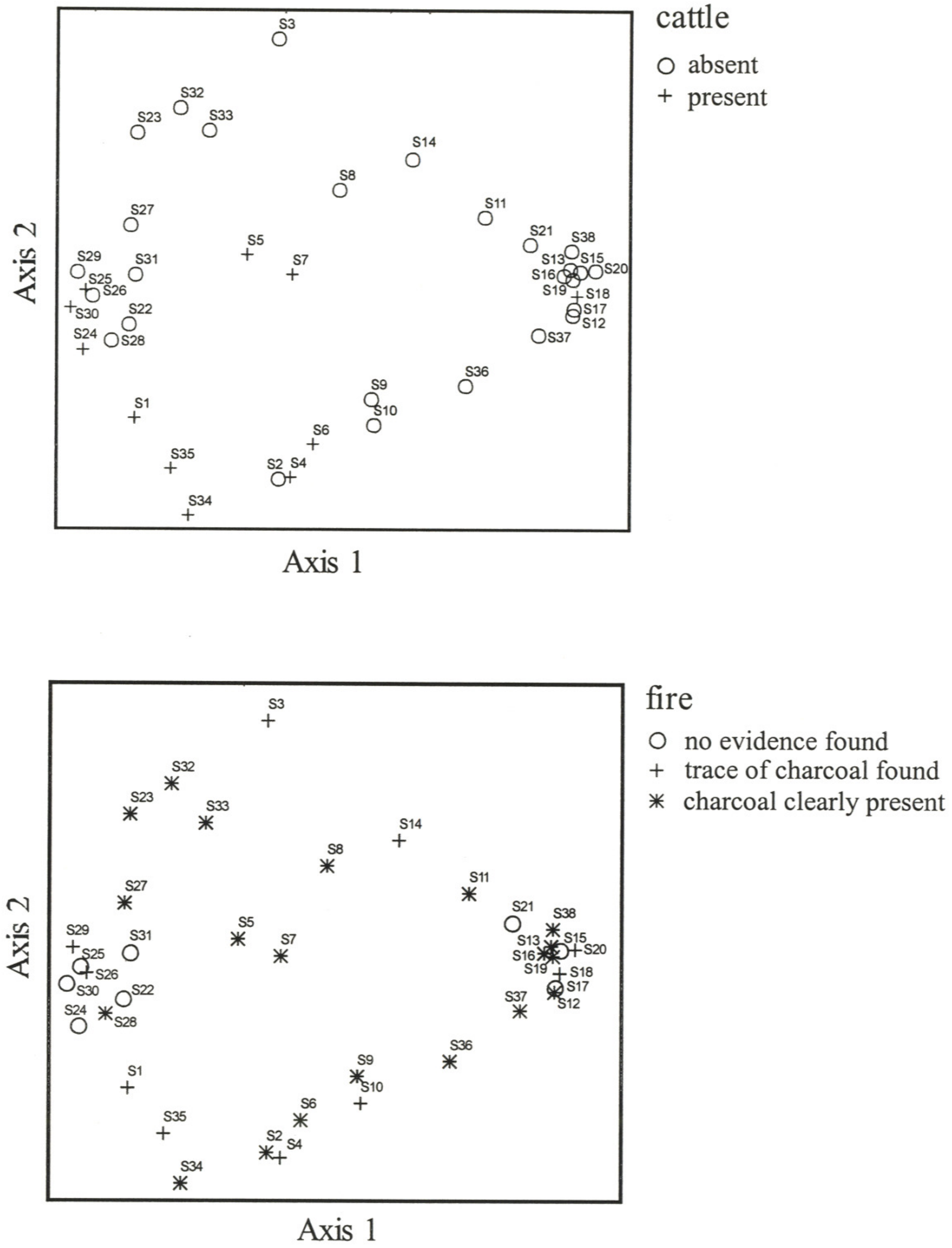


Figure 2.7. Overlays indicating values of the categorical variables cattle and fire for the 38 DCA-ordinated sites.

my initial sampling visits consisted of dung from a previous year. I did not observe any cattle or fresh dung during my initial visits, though I frequently did observe them in the vicinity of my sites during revisits, when the *Erythronium* was in fruit.

Relationships of Erythronium grandiflorum *Parameters with Ordination and Environmental Variables*

Table 2.7 shows the correlations of lily variables with the ordination axes (see Table 2.3 for definitions and derivations of the variables and Table 2.4 for values of the quantitative variables). I am not presenting a joint plot because some of the relationships of these variables with the axes were nonsignificant due to being nonlinear, or were otherwise complicated. Therefore, overlay diagrams are given in Figure 2.8. In addition, for the first four variables, scatterplots are shown underneath the overlays to help clarify the relationships between the variables and the first ordination axis. Number of seedlings showed some correlation with the first axis, but the overlay (Fig. 2.8a) shows that the relationship is not linear. In general, the sites at the sides and bottom right of the diagram have highest numbers of seedlings, while those at the top and bottom left (treed sites) have fewest. Number of one-leafed plants was not significantly correlated with axes 1 or 2, but Figure 2.8b shows that there is a bimodal distribution in which highest numbers of one-leafed plants occur at the low and high elevation areas, with fewer in the intermediate sites. The tau value for two-leafed plants on the first axis is highly significant, with higher-elevation sites generally having the largest number of these plants. The pattern for number of flowering plants is similar to that for one-leafed plants (non-significant correlation with the first axis but bimodal), but the scatterplot is not as evenly U-shaped; there appear to be more flowering plants at the low than high elevation sites. There is also a significant relationship of number (and proportion) of flowering plants with the second axis, which is apparently due to the low number of flowering plants under coniferous tree cover. The proportion of multiple-flowered plants similarly is highest at the left and bottom. The relationships with leaf area are not significant, but there does appear to be some pattern (smaller at high elevation sites); this will be explored further

Table 2.7 Kendall's tau correlations of *Erythronium grandiflorum* variables with DCA ordination axes ($|tau_{(0.05)}| = 0.223$; $|tau_{(0.01)}| = 0.292$). Correlations significant at alpha < 0.01 are shown in boldface. Refer to Table 2.3 for descriptions of variables.

Lily Variable	AXIS		
	1	2	3
Seedling (avg. no. per m^2)	0.229	-0.093	0.013
Oneleaf (avg. no. per m^2)	-0.098	0.021	0.067
Twoleaf (avg. no. per m^2)	**0.409**	0.013	0.204
Flowering plant (avg. no. per m^2)	-0.201	**-0.318**	0.144
Multiple-flowered plant (proportion of all flowering plants)	-0.161	**-0.428**	0.033
Proportion of flowering plants (among all non-seedling plants)	-0.186	**-0.465**	0.070
Proportion of twoleafs (among all non-seedling plants)	**0.451**	0.081	0.098
Ratio of seedlings to flowering plants	0.235	0.064	-0.073
Ratio of oneleaf to flowering plants	0.158	**0.454**	-0.075
Leaf area	-0.164	-0.209	-0.061

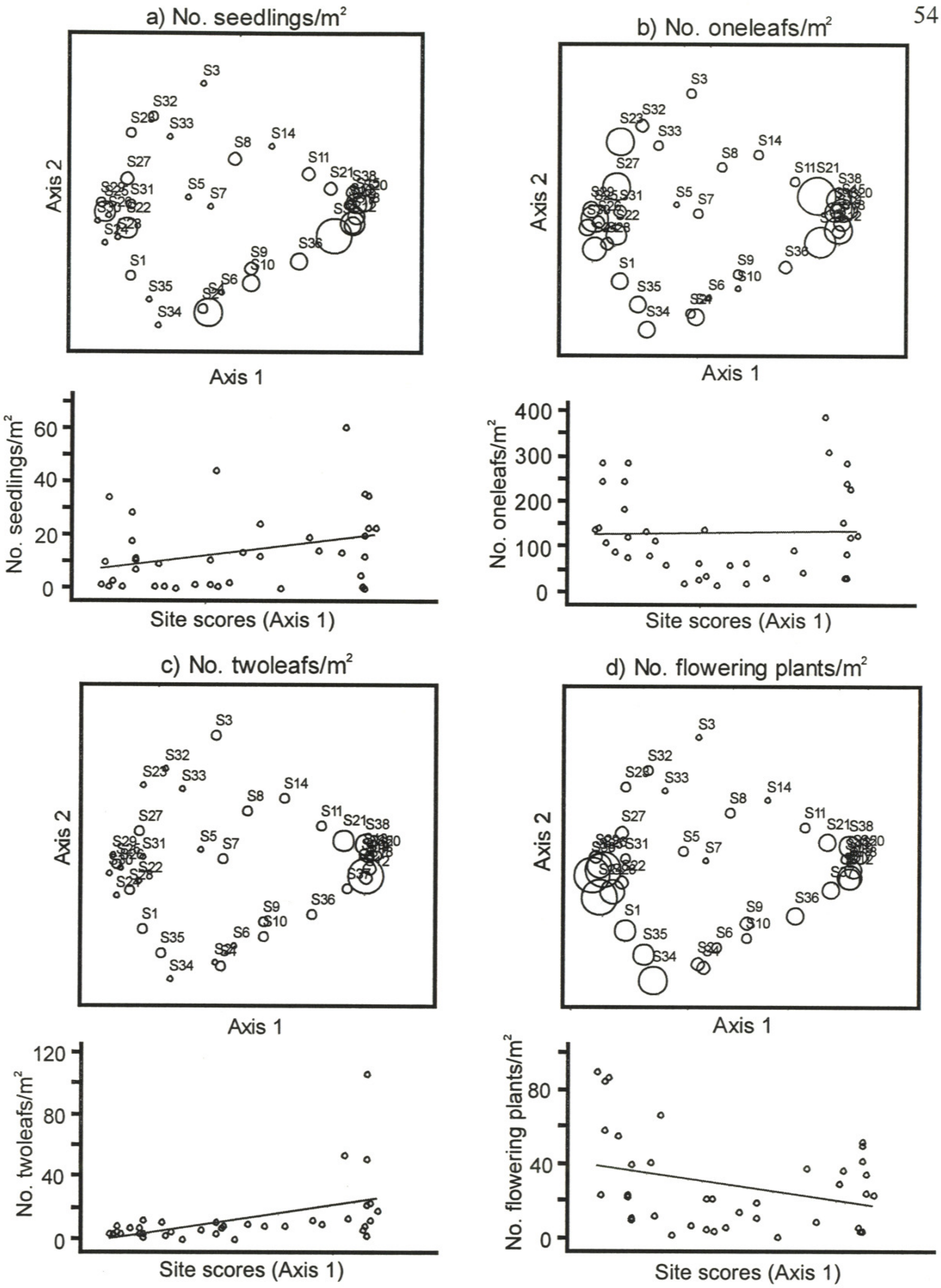
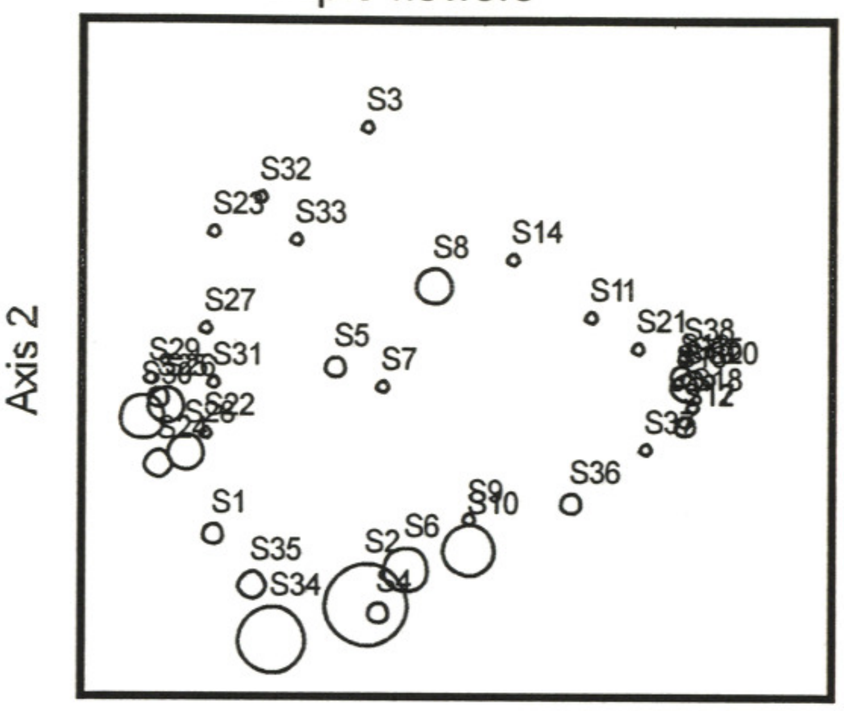
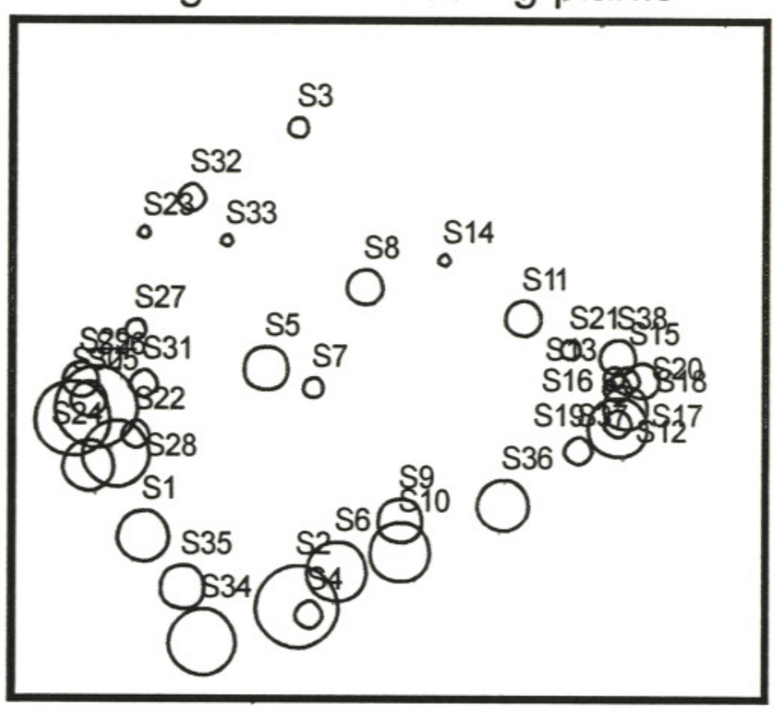


Figure 2.8 a) - j) Overlay diagrams showing relative values of *Erythronium grandiflorum* variables for the ordinated sites. The larger the circle, the larger the value of the variable. Also shown for the variables seedling, oneleaf, twoleaf, and flowplant are scatterplots for the relationships between these variables and the first ordination axis. Refer to Table 2.3 for descriptions of variables.

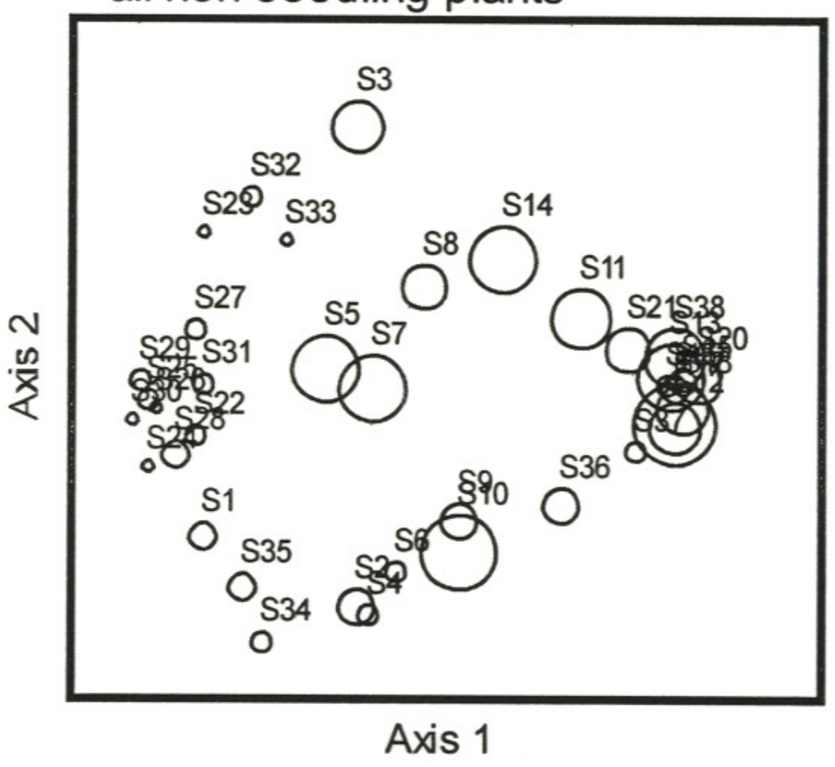
e) Proportion of flowering plants with multiple flowers



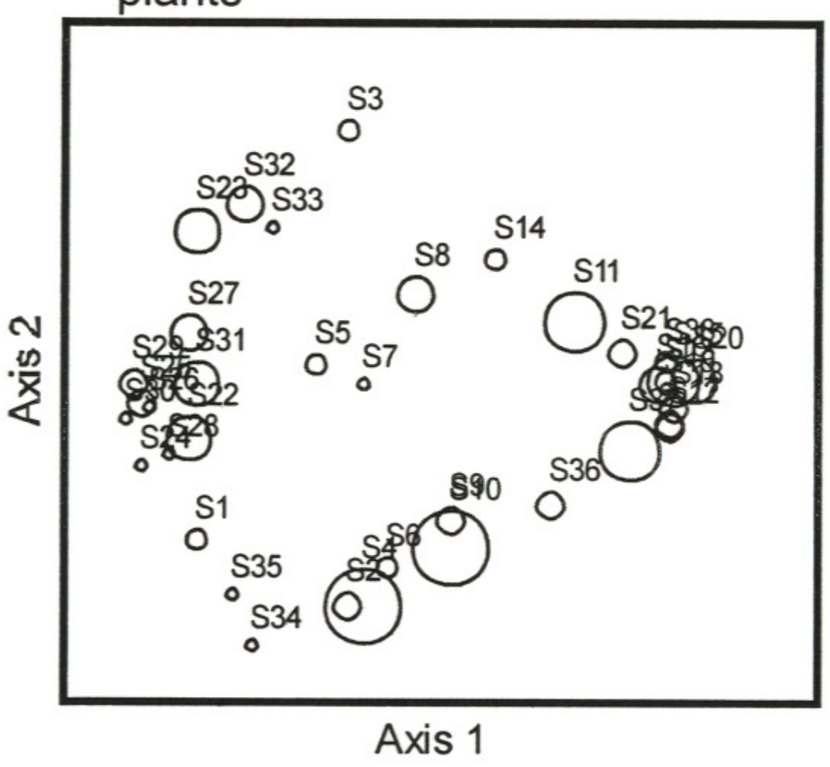
f) Proportion of flowering plants among all non-seedling plants



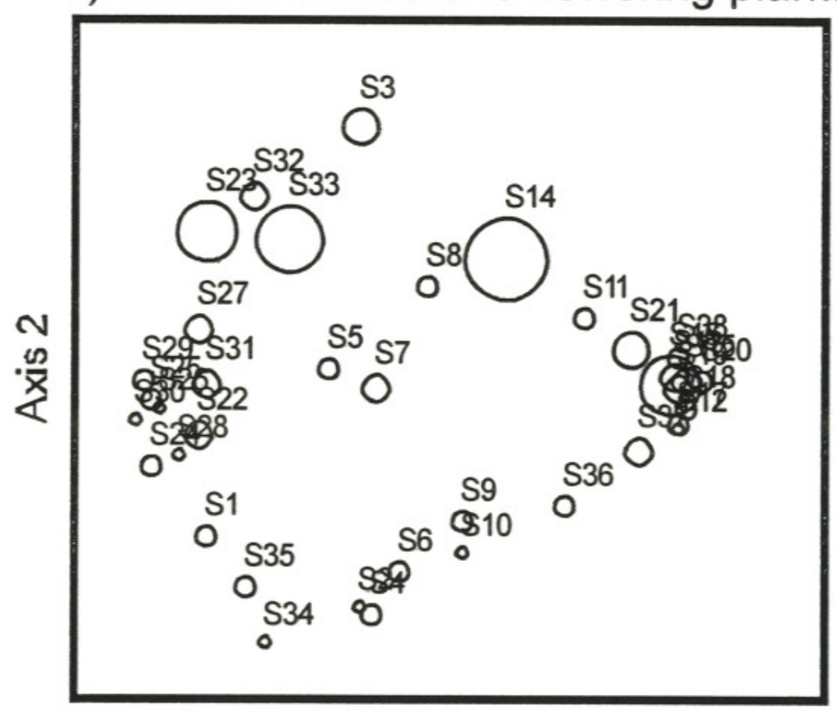
g) Proportion of twoleafs among all non-seedling plants



h) Ratio of seedlings to flowering plants



i) Ratio of oneleafs to flowering plants



j) Leaf area

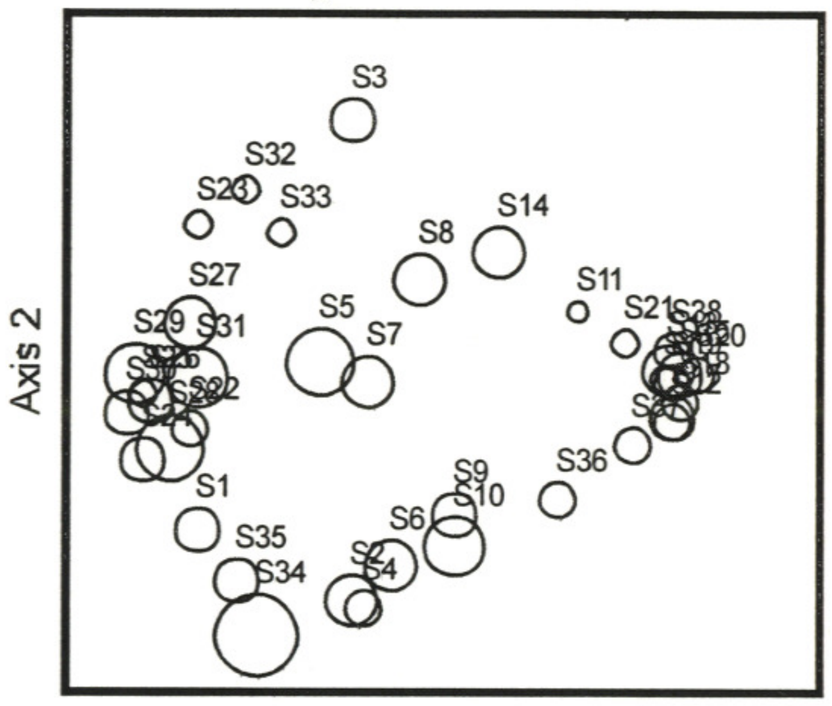


Figure 2.8, cont.

below.

The categorical variable anther colour exhibits an intriguing pattern (Figure 2.9), with most of the high-elevation and Chase-area sites dominated by yellow-coloured anthers, and almost all other sites dominated by cream-coloured anthers (only 2 were dominated by red).[1] It is not clear what ecological significance this might have, if any.

In addition to relating the lily variables to the ordination axes, I performed rank correlations of the lily variables against the environmental variables directly. The correlation matrix is shown in Table 2.8a (the coefficients are Spearman's, the nonparametric option available in Statistix). Intercorrelations are given among the environmental and lily variables, respectively, in Table 2.8b and 2.8c. Scatterplots are shown in Figure 2.10 for the lily variables vs. elevation correlations, in Figure 2.11 for the lily variables vs. coniferous tree cover relationships, and in Figure 2.12 for selected other correlations discussed in the text (in the order discussed).

Some of these correlations confirm the relationships suggested above. For example, numbers of flowering plants and multiple-flowered plants are negatively correlated with coniferous tree cover (Fig. 2.11d,e) and number of two-leafed plants is positively correlated with elevation (Fig. 2.10c). Also, the scatterplot in Figure 2.10b reveals that number of one-leafed plants has the same bimodal relationship with elevation as with the first ordination axis (cf. Fig. 2.8b). Yet, the first axis is not totally interchangeable with elevation, since the pattern for seedlings vs. elevation (Fig. 2.10a) becomes more bimodal than the ordination scatter (Fig. 2.8a), while the pattern for flowering plants (Fig. 2.10d) becomes less bimodal than the ordination scatter (Fig. 2.8d).

The intercorrelations of some of the variables are also evident; e.g. soil pH, organic content, and texture are all clearly related to elevation (Fig. 2.12a-c). However, these variables are not interchangeable. For example, number of native species is positively related to pH, but is not significantly related to elevation (Fig. 2.12d,e), so pH

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[1] There was almost invariably a mix of colours, from 50-90% cream (or yellow), with most of the remaining anthers yellow (or cream), and a small proportion red or some other colour. One colour was usually very obviously dominant.

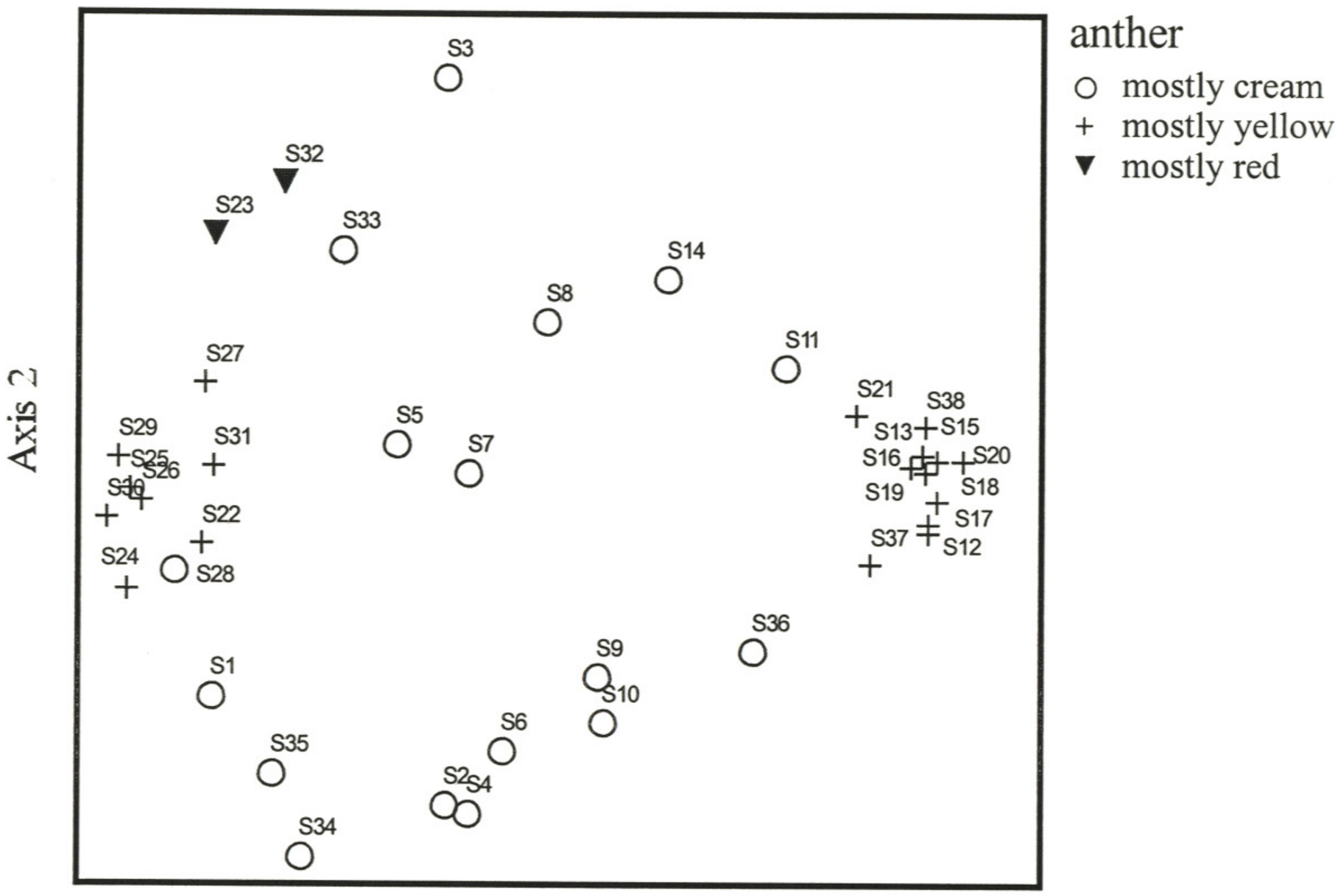


Figure 2.9 Overlay diagram indicating values of the categorical variable anther colour for the 38 DCA-ordinated sites.

Table 2.8 Spearman's rank correlations, corrected for ties, among a) environmental and *Erythronium grandiflorum* variables; b) environmental variables only; c) *E. grandiflorum* variables only ($|r_{s(0.05)}| = 0.322$; $|r_{s(0.01)}| = 0.423$). Correlations significant at alpha < 0.01 are shown in boldface. Refer to Tables 2.2 and 2.3 for variable descriptions.

a) Environment vs. *E. grandiflorum.*

	seed	oneleaf	twoleaf	flowplant	multiflow	propflow	prop2leaf	ratioseed	ratio1leaf	leaf-area
tree-conif	-0.276	-0.150	-0.252	**-0.610**	**-0.515**	**-0.673**	0.078	0.002	**0.646**	0.105
tree-decid	-0.079	0.124	-0.097	0.321	0.386	0.271	-0.246	-0.139	-0.269	0.235
shrub	-0.390	-0.102	**-0.483**	-0.078	-0.045	-0.039	-0.344	-0.219	0.060	0.329
herbcover	0.190	0.272	**0.468**	**0.507**	0.094	0.263	0.097	-0.115	-0.245	-0.181
total-spp	0.023	-0.001	-0.133	0.127	0.182	0.283	-0.179	-0.019	-0.255	0.176
intro-spp	-0.168	0.078	**-0.490**	0.244	0.314	0.319	**-0.540**	-0.195	-0.288	**0.424**
native-spp	0.068	-0.075	-0.034	0.045	0.147	0.232	-0.039	0.050	-0.212	0.102
rock	0.231	0.031	0.119	-0.101	-0.146	-0.137	0.016	0.335	0.162	-0.315
litdep	-0.109	0.062	-0.299	0.261	0.337	0.307	-0.367	-0.156	-0.294	**0.537**
litcover	-0.185	**0.423**	-0.343	0.252	-0.092	-0.119	**-0.613**	-0.213	0.155	-0.054
grass	-0.157	0.188	-0.305	0.337	0.195	0.298	**-0.535**	-0.231	-0.266	0.110
CWD	-0.140	-0.095	-0.292	-0.216	0.001	-0.122	-0.090	0.036	0.120	**0.423**
pH	-0.246	-0.008	-0.361	0.234	0.198	0.340	-0.395	-0.273	-0.309	**0.456**
texture	0.317	-0.256	**0.462**	-0.150	0.125	0.056	**0.606**	0.244	-0.097	0.060
organic	0.145	-0.172	**0.455**	-0.094	-0.046	-0.004	**0.484**	0.186	-0.015	-0.053
aspect	0.123	0.133	0.321	0.182	0.013	0.072	0.172	0.053	-0.099	-0.092
angle	0.264	0.117	0.052	0.162	0.047	0.135	-0.199	0.240	-0.105	0.097
elev	0.297	-0.095	**0.671**	-0.125	-0.187	-0.133	**0.678**	0.224	0.090	-0.227
lat	0.159	0.234	0.205	0.156	0.026	-0.116	0.109	0.105	0.102	0.025
long	-0.044	0.164	0.112	0.368	0.166	0.256	-0.144	-0.146	-0.252	0.048
phenology	-0.317	**-0.531**	0.078	-0.235	0.218	0.139	**0.467**	-0.250	-0.172	**0.667**

Table 2.8, cont.

b) Environment vs. Environment.

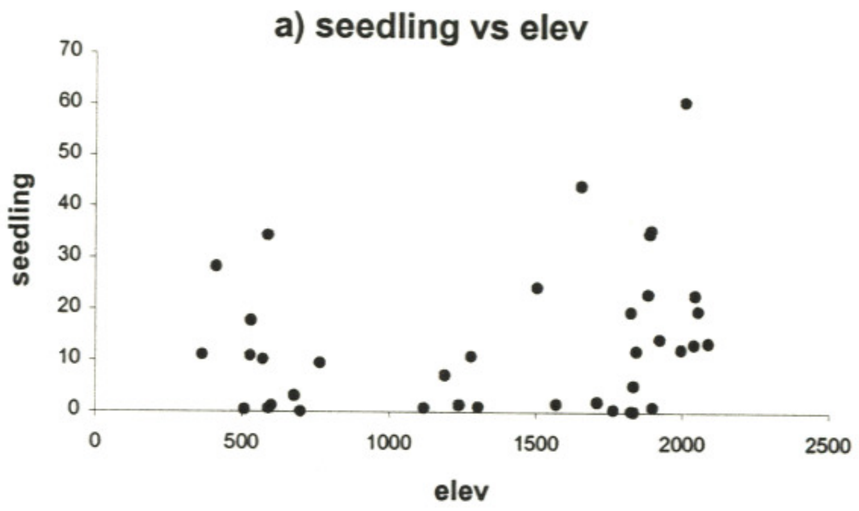
	tree-conif	tree-decid	shrub	herb cover	total-spp	intro-spp	native-spp	rock	litdep	litcover
tree-decid	-0.273									
shrub	0.321	0.225								
herb cover	**-0.452**	-0.102	-0.320							
total-spp	-0.162	0.234	0.238	-0.147						
intro-spp	-0.090	**0.458**	**0.433**	-0.275	**0.546**					
native-spp	-0.156	0.109	0.138	-0.089	**0.950**	0.306				
rock	-0.218	-0.132	-0.141	0.258	-0.191	**-0.434**	-0.071			
litdep	0.092	0.256	**0.536**	-0.356	0.331	**0.576**	0.223	-0.386		
litcover	0.175	-0.033	0.388	0.049	0.026	0.417	-0.083	-0.197	0.411	
grass	-0.124	0.221	**0.575**	-0.095	**0.457**	**0.666**	0.320	-0.343	**0.587**	**0.626**
CWD	0.363	**0.431**	**0.575**	-0.335	0.273	0.363	0.200	-0.104	**0.509**	0.025
pH	-0.043	0.315	**0.500**	-0.241	**0.634**	**0.761**	**0.484**	-0.327	**0.658**	0.379
texture	-0.264	-0.153	**-0.640**	0.288	-0.220	**-0.488**	-0.061	0.188	**-0.455**	**-0.545**
organic	-0.241	-0.202	**-0.519**	0.346	-0.208	**-0.537**	-0.051	**0.599**	**-0.539**	**-0.460**
aspect	-0.089	0.061	-0.311	0.259	-0.091	-0.225	-0.045	-0.002	-0.002	0.044
angle	-0.206	0.110	0.100	0.269	0.043	-0.067	0.077	0.396	0.127	0.010
elev	-0.155	-0.256	**-0.635**	0.278	-0.291	**-0.731**	-0.103	0.329	**-0.630**	**-0.602**
lat	0.141	-0.187	-0.271	0.313	-0.384	-0.159	-0.387	0.041	-0.146	0.257
long	-0.133	0.067	0.070	0.158	-0.208	0.049	-0.228	-0.191	0.324	0.331
pheno-logy	-0.002	-0.011	0.040	-0.032	-0.119	-0.063	-0.087	-0.053	0.016	-0.310

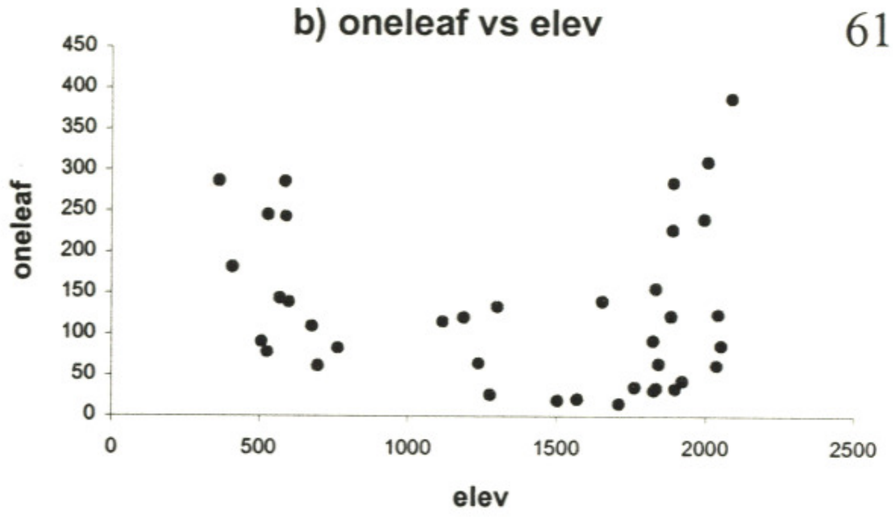
	grass	CWD	pH	texture	organic	aspect	angle	elev	lat	long
CWD	0.201									
pH	**0.676**	0.414								
texture	**-0.594**	-0.269	**-0.528**							
organic	**-0.605**	-0.408	**-0.424**	**0.523**						
aspect	-0.037	-0.110	-0.193	0.075	0.200					
angle	0.049	0.065	0.051	0.185	0.052	-0.140				
elev	**-0.661**	**-0.455**	**-0.658**	**0.707**	**0.702**	0.305	-0.008			
lat	-0.182	-0.115	-0.275	0.174	0.194	0.355	-0.183	0.121		
long	0.349	-0.105	-0.060	-0.190	-0.222	0.298	0.093	-0.235	0.196	
pheno-logy	-0.168	0.029	0.030	0.311	0.281	-0.034	0.001	0.243	0.005	-0.057

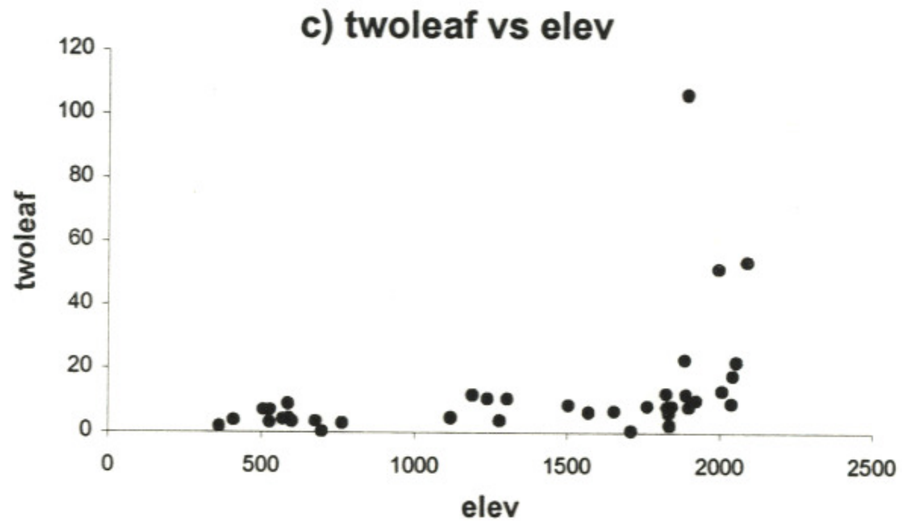
Table 2.8, cont.

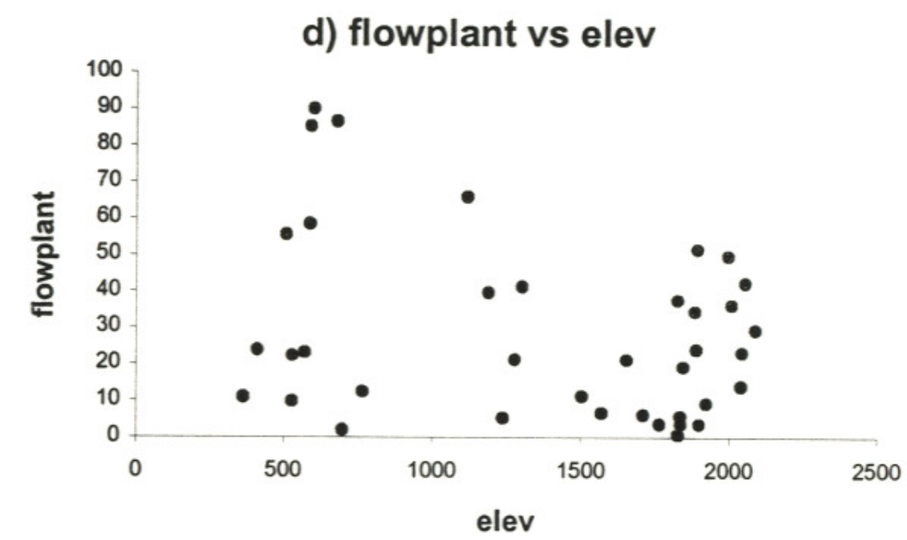
c) *E. grandiflorum* vs. *E. grandiflorum*.

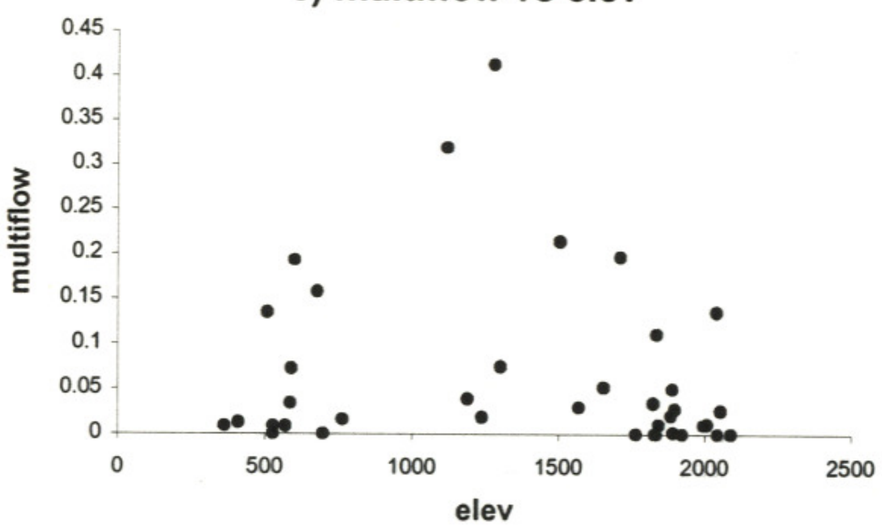
	seed	oneleaf	twoleaf	flowplant	multiflow	propflow	prop-2leaf	ratio seed	ratio 1leaf
one-leaf	**0.461**								
two-leaf	**0.518**	0.297							
flow-plant	0.284	**0.594**	0.312						
multi-flow	-0.109	-0.233	-0.204	0.375					
prop-flow	0.025	-0.189	-0.005	**0.622**	**0.734**				
prop-2leaf	0.136	-0.395	**0.651**	-0.269	-0.169	-0.068			
ratio-seed	**0.823**	0.196	0.225	-0.180	-0.249	-0.233	0.137		
ratio-1leaf	-0.026	0.218	-0.026	**-0.601**	**-0.722**	**-0.994**	0.000	0.229	
leaf-area	-0.288	-0.412	-0.108	-0.037	0.342	0.289	0.208	-0.225	-0.312

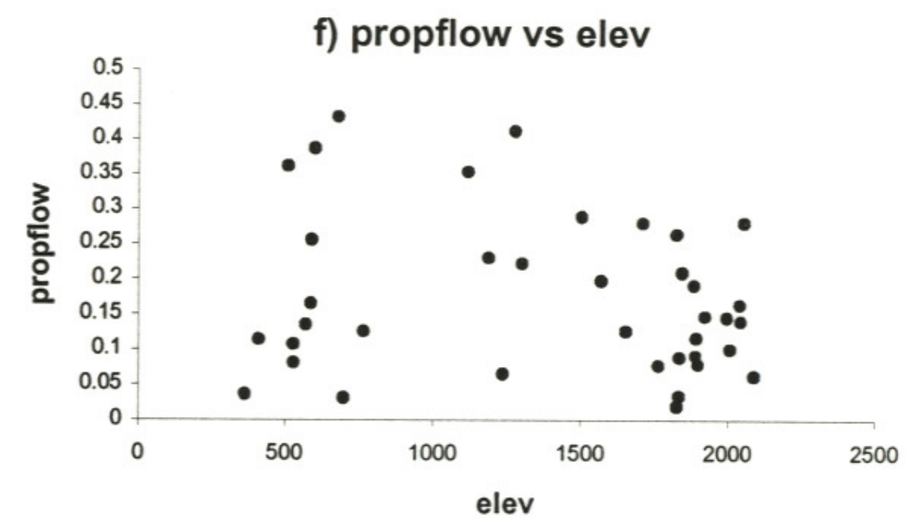


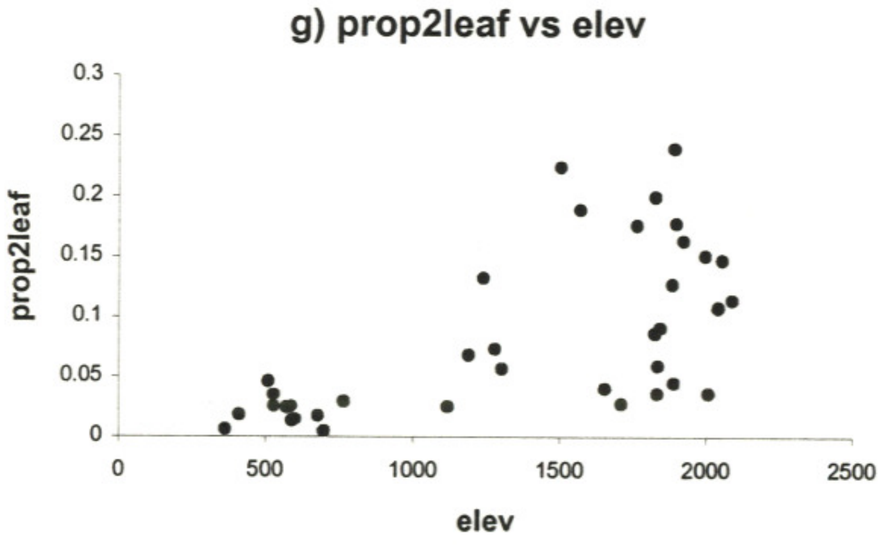












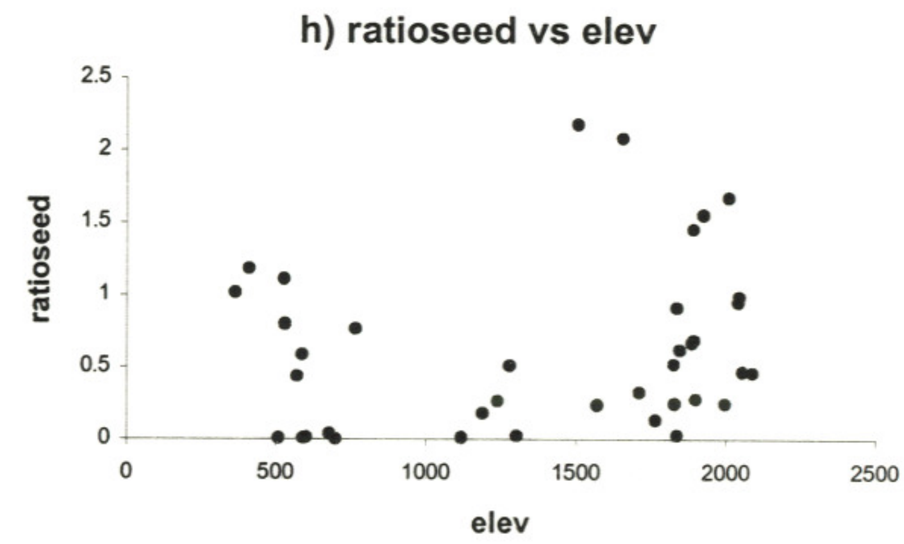
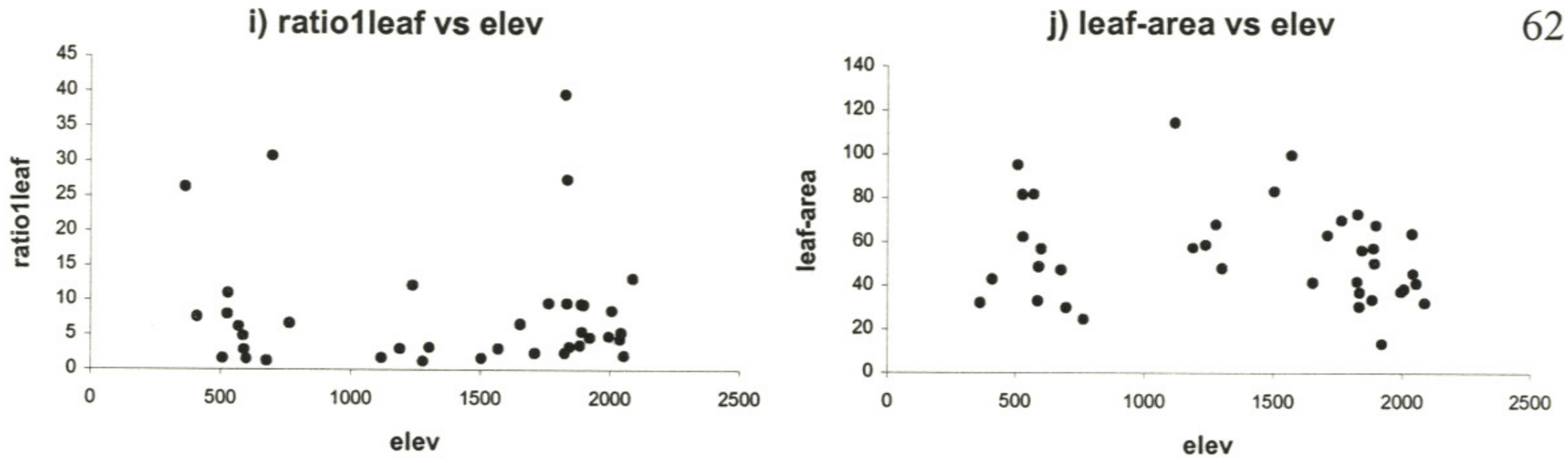


Figure 2.10 Scatterplots for *Erythronium grandiflorum* variables versus elevation. Refer to Table 2.2 and 2.3 for descriptions of variables.



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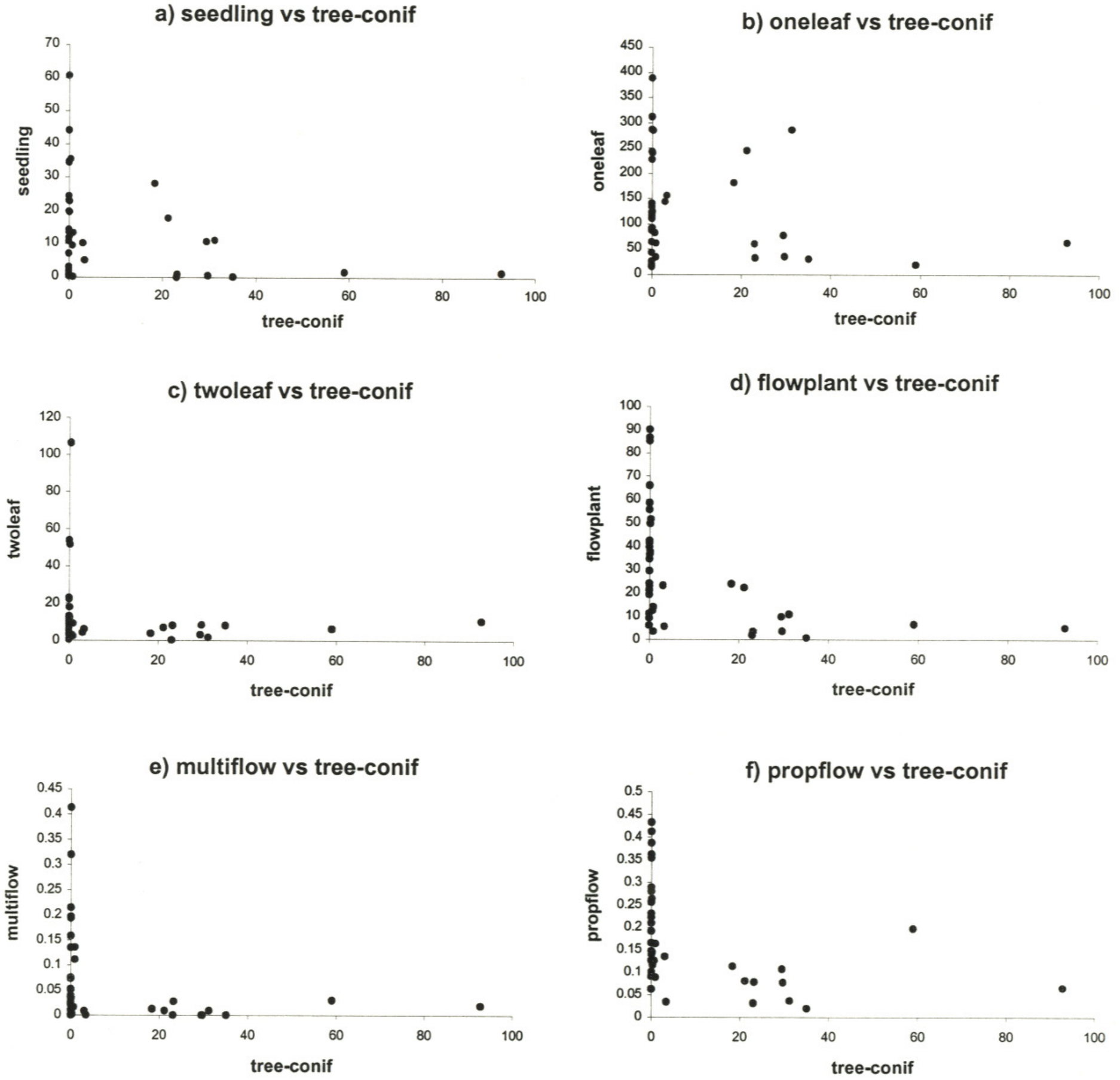
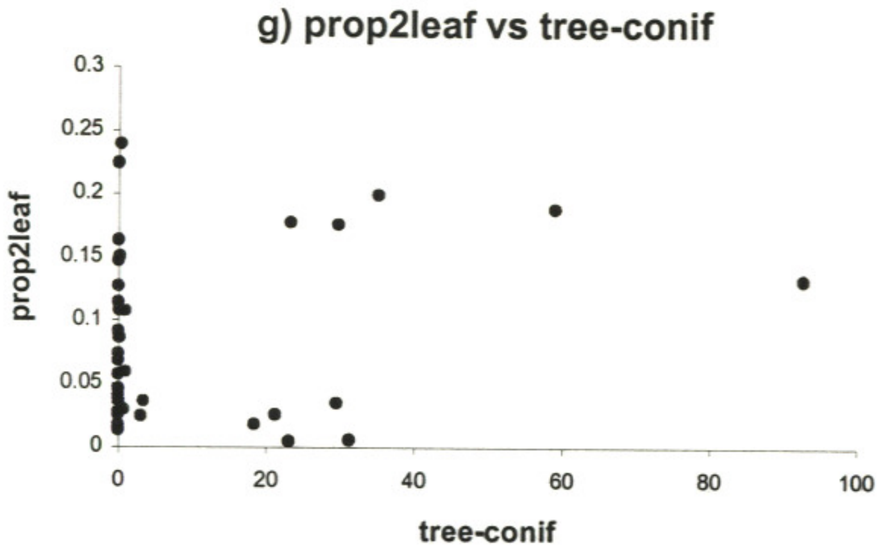
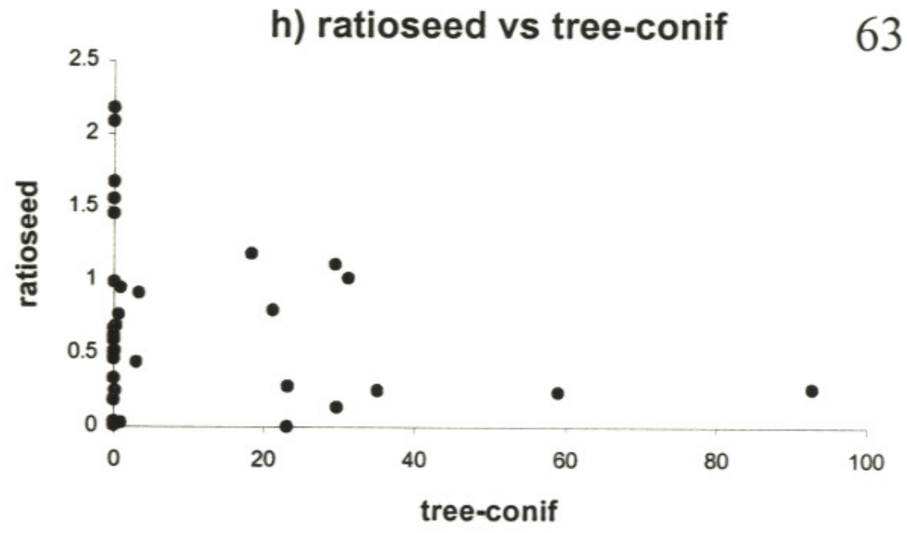
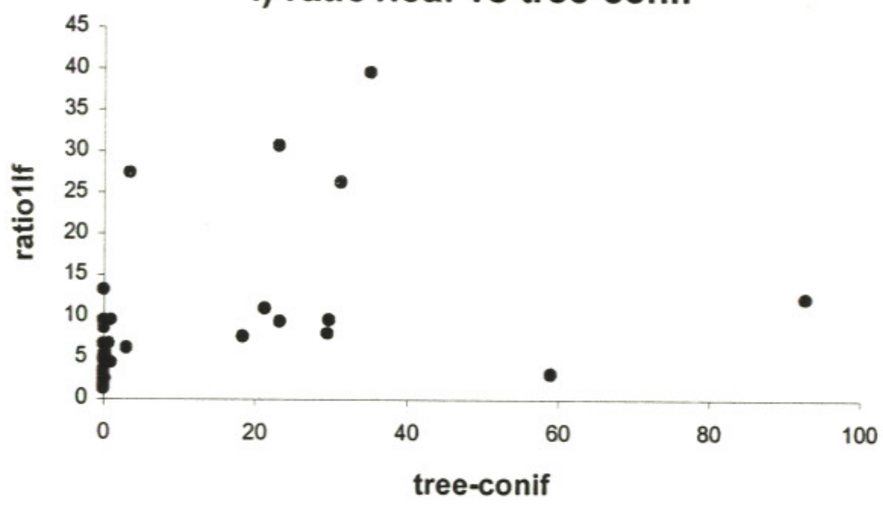
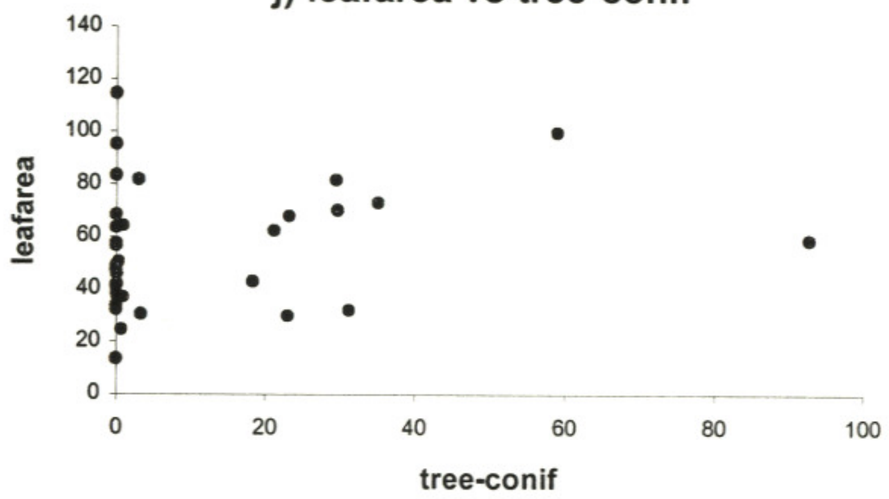


Figure 2.11 Scatterplots for *Erythronium grandiflorum* variables versus coniferous tree cover. Refer to Table 2.2 and 2.3 for descriptions of variables.









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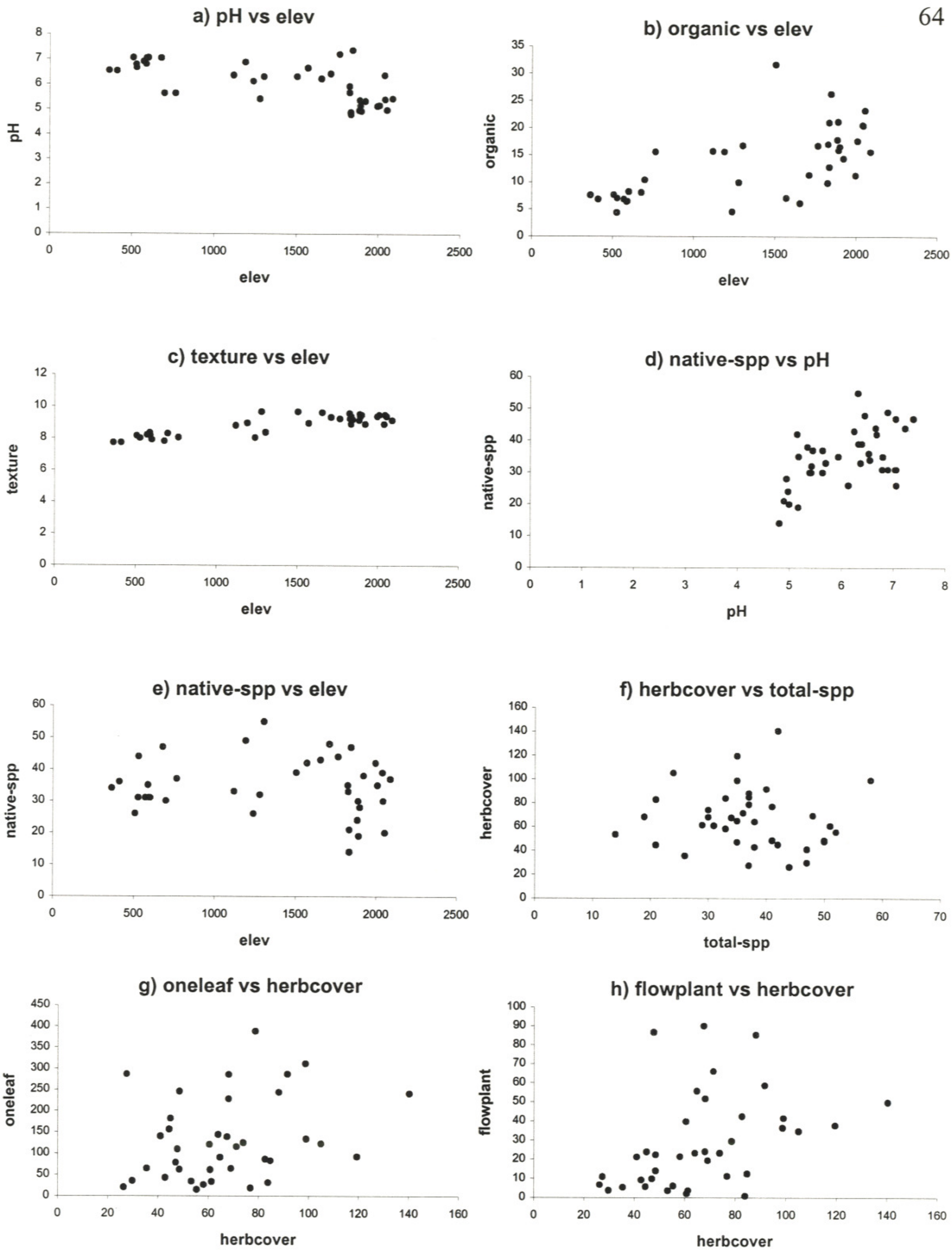
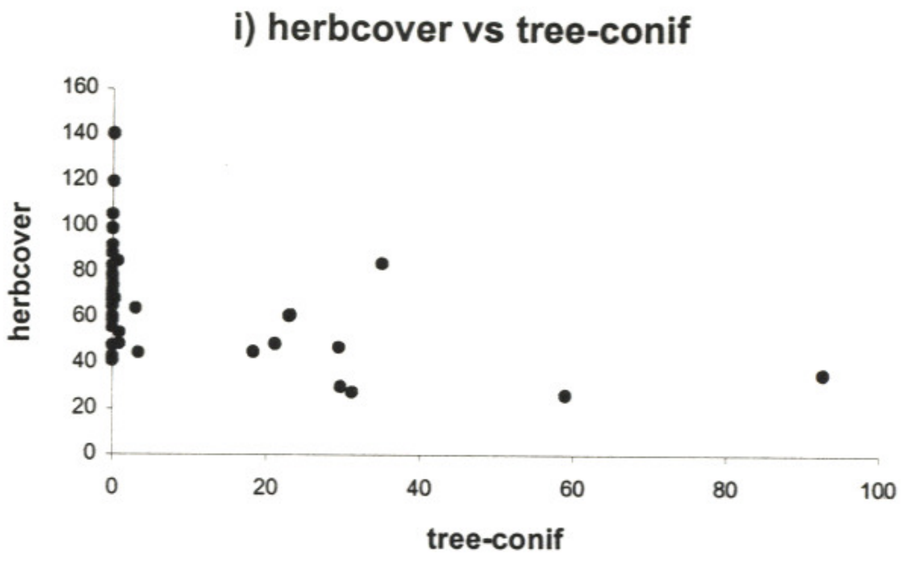
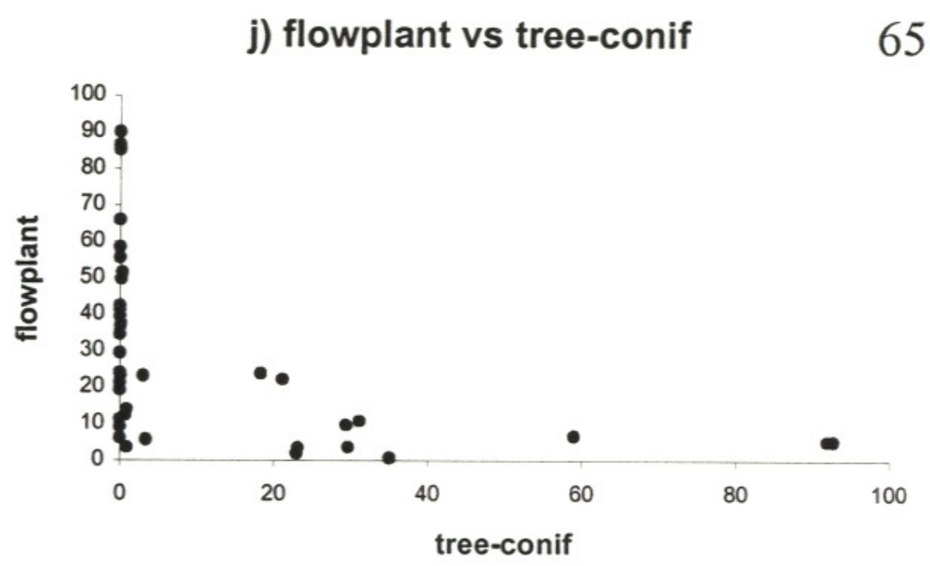
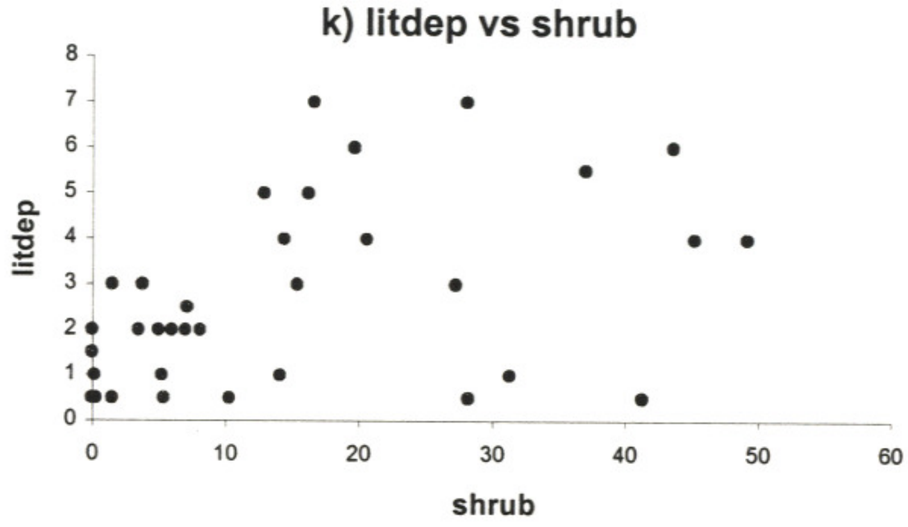
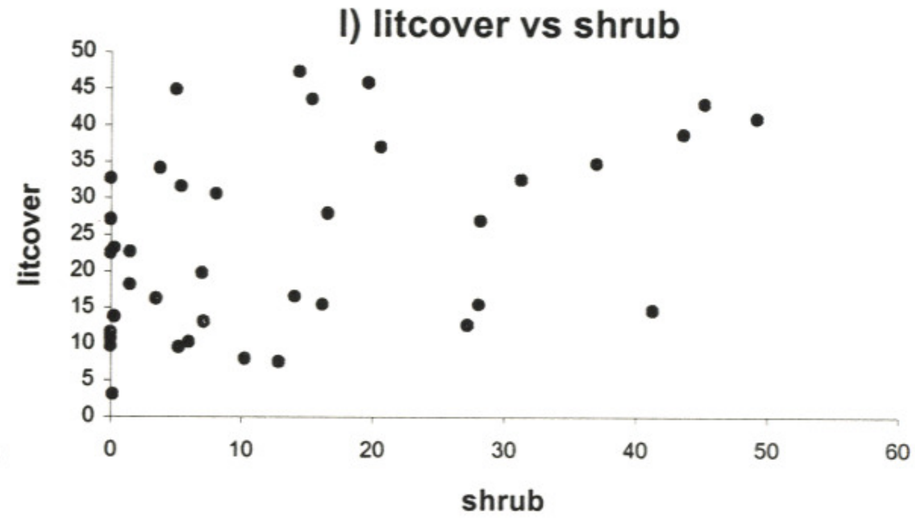


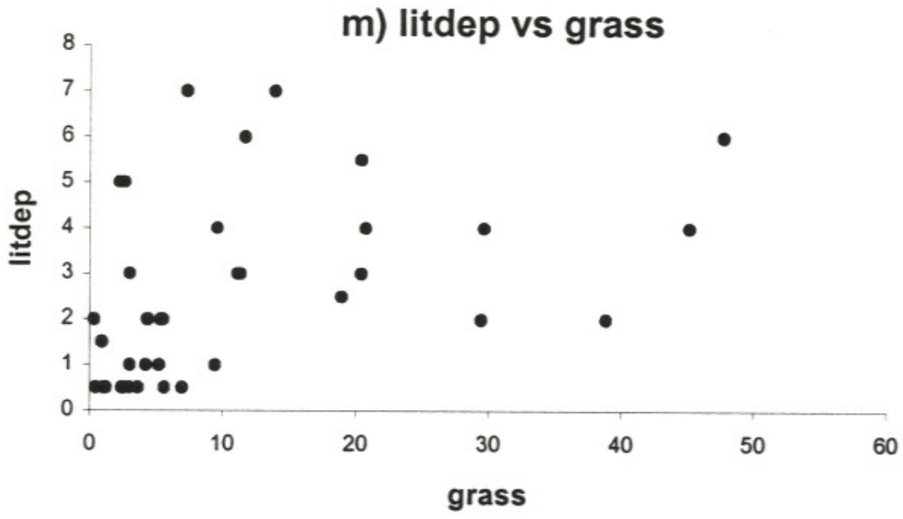
Figure 2.12 Scatterplots for correlations among selected *Erythronium grandiflorum* and environmental variables (as discussed in text). Refer to Tables 2.2 and 2.3 for descriptions of variables.

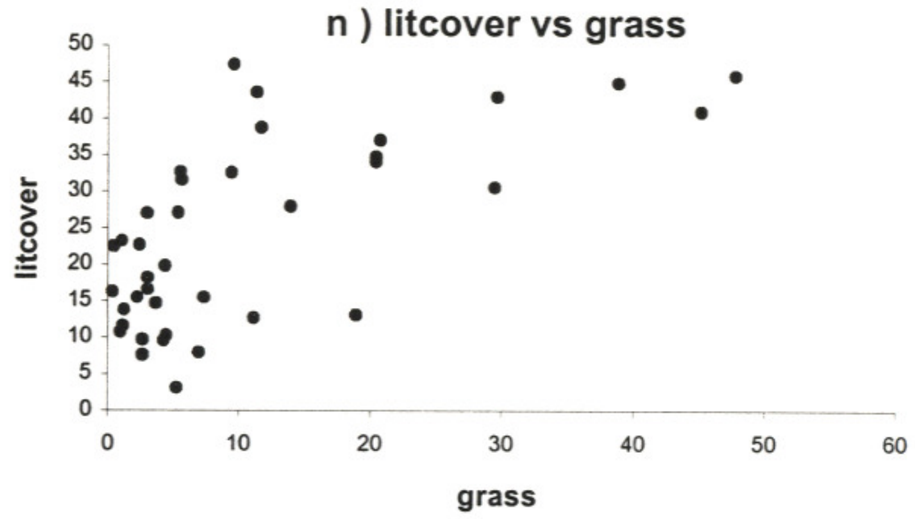


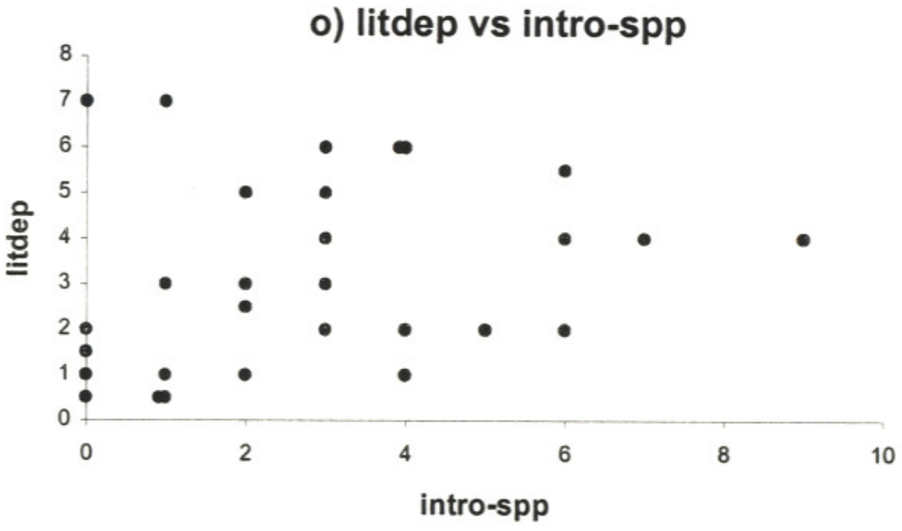


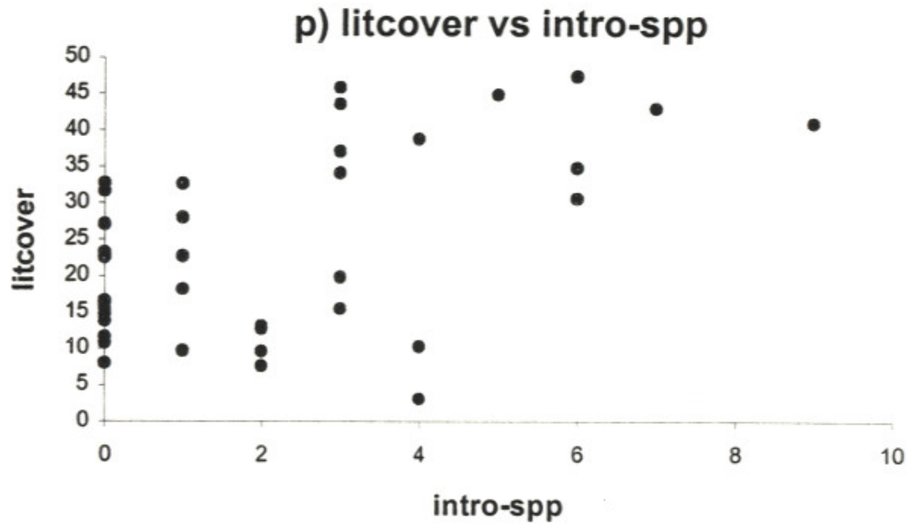












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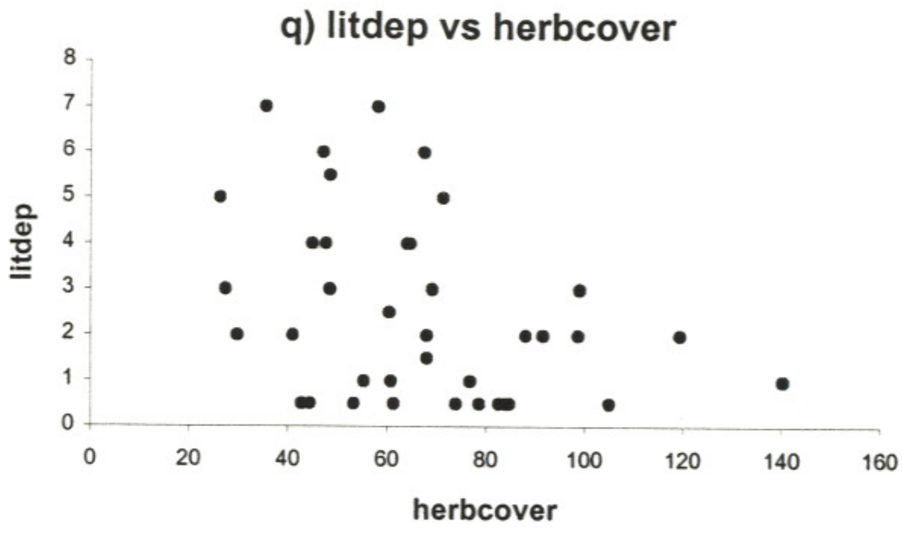

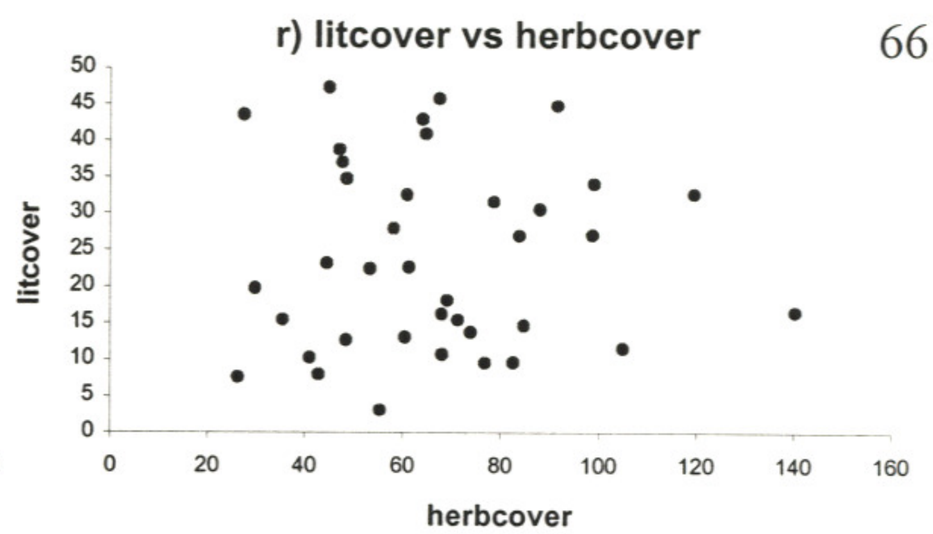

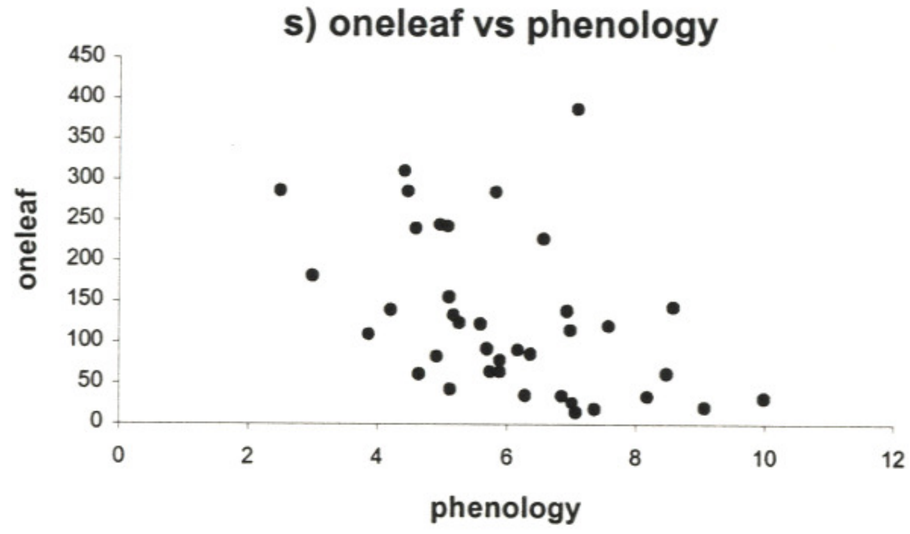

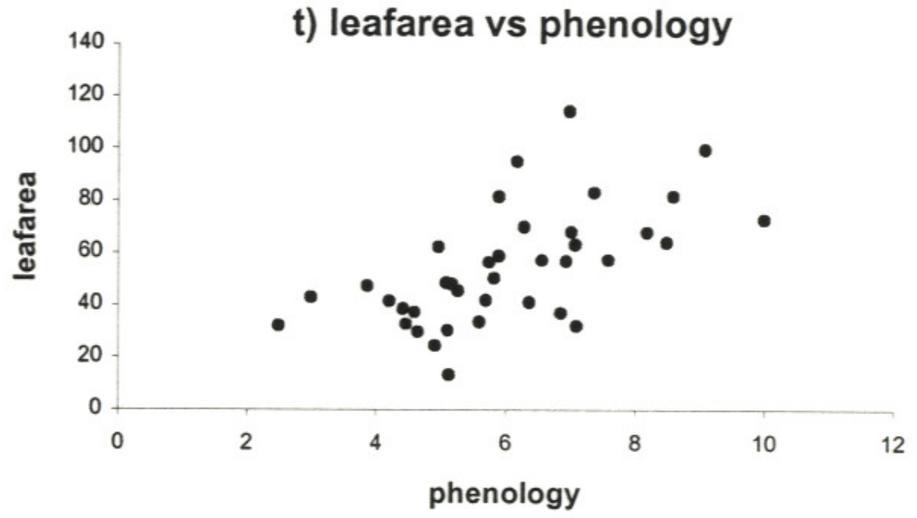

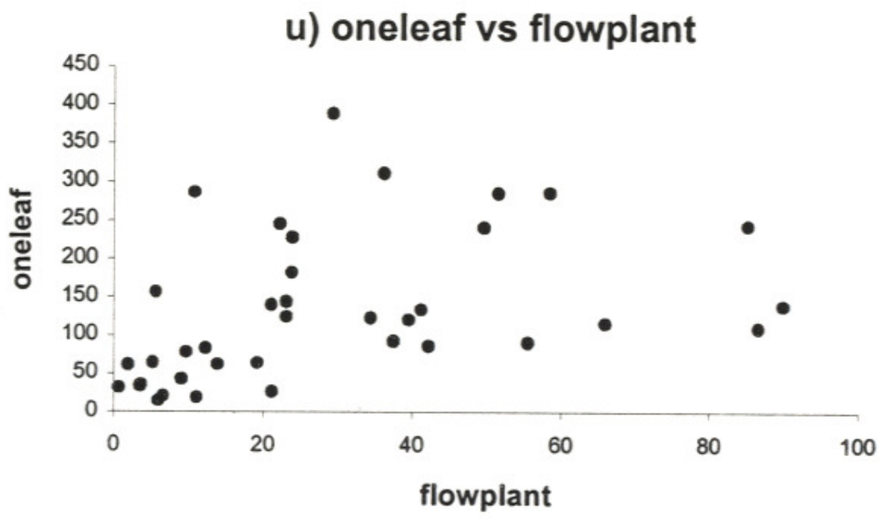

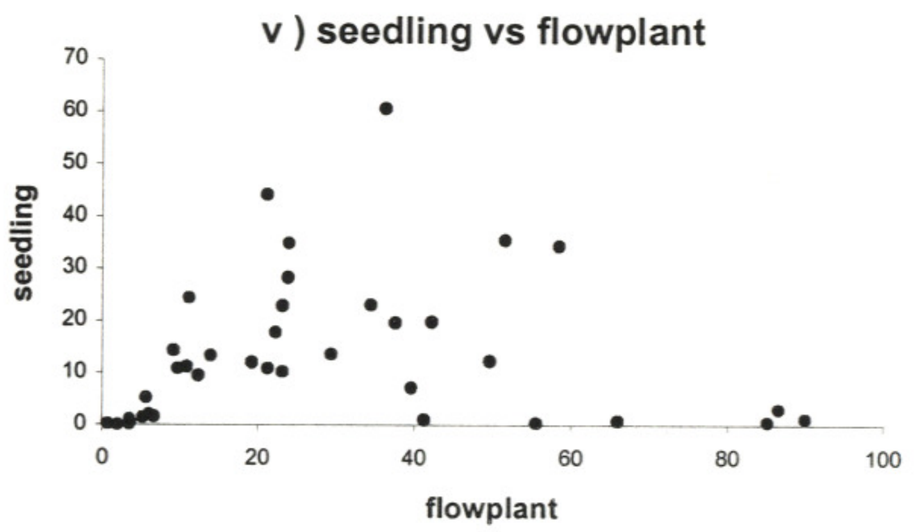

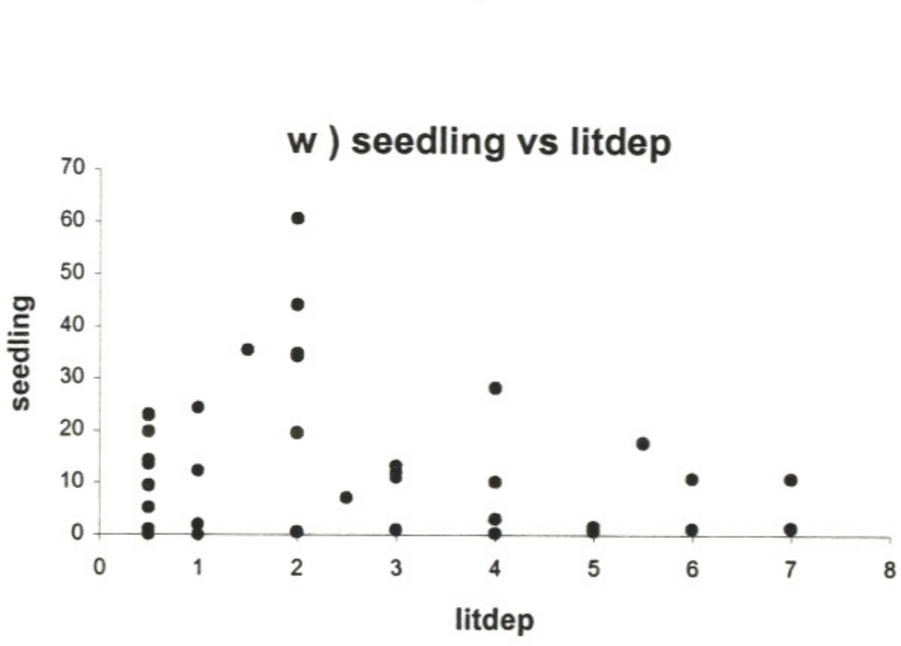

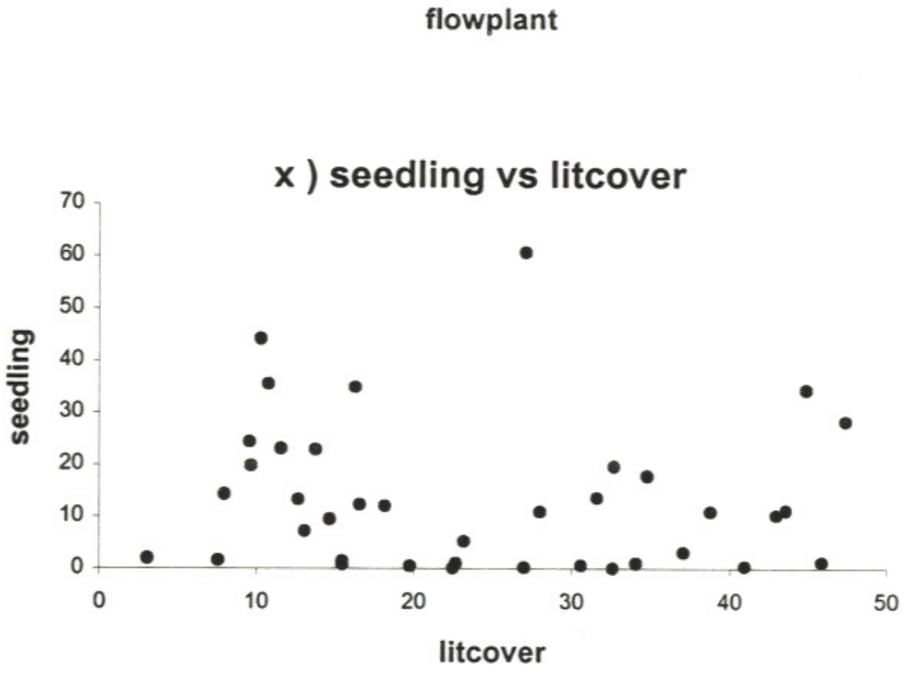

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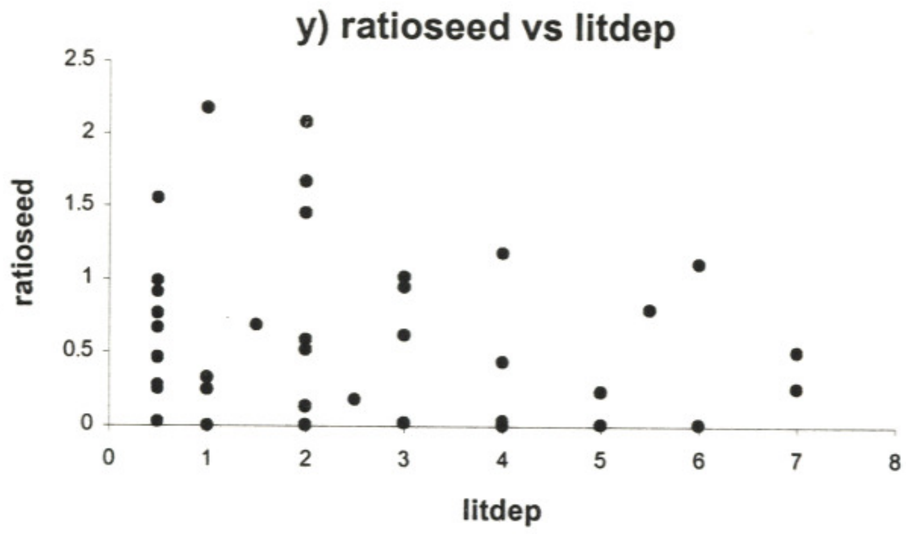

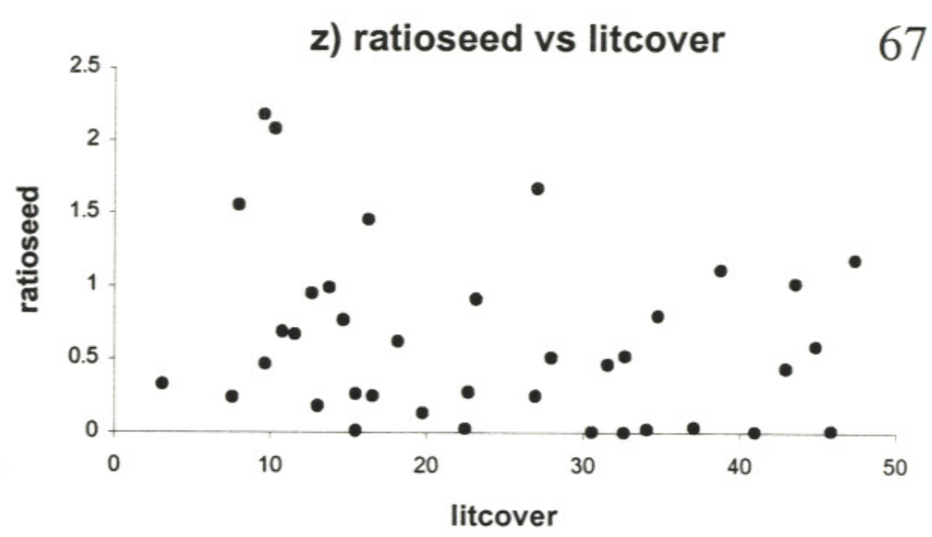

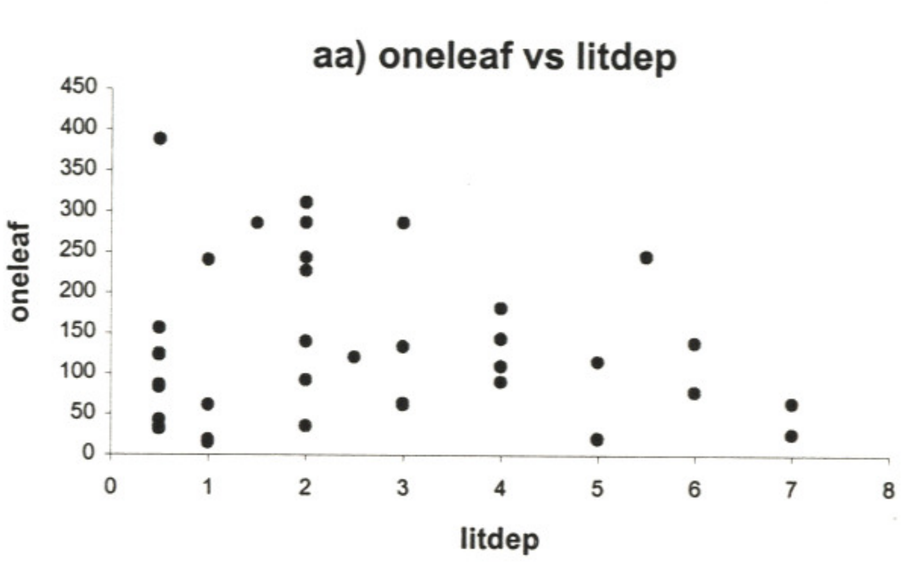

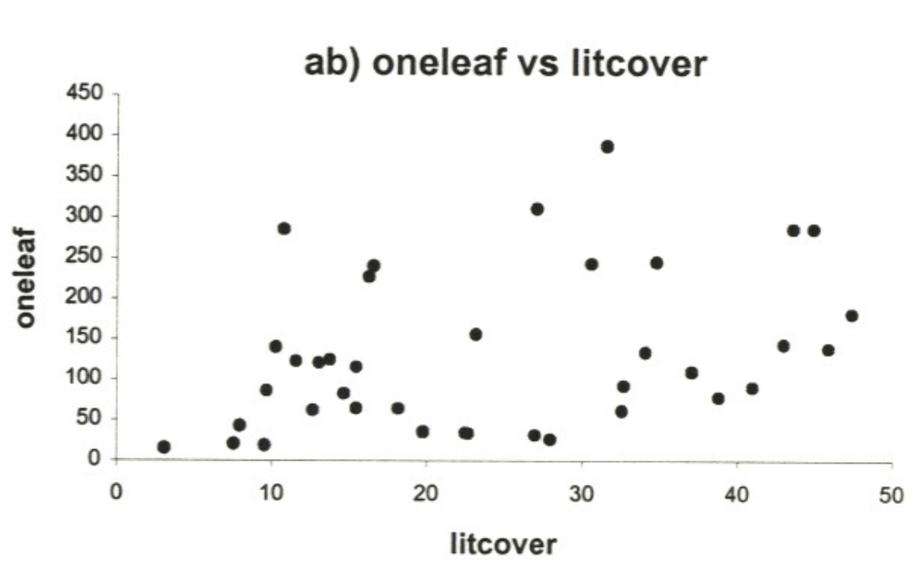

Figure 2.12, cont

may play some independent role in influencing the species present (or it may be a surrogate for another variable not measured).

There was no significant correlation between total herb cover and total number of species (Fig. 2.12f). I had expected that that more species would mean greater total cover, but this is not the case, probably because so many species are extremely small at the time *Erythronium* flowers. Total herb cover also does not seem to represent an index of competition as I expected; rather, *E. grandiflorum* parameters are generally positively correlated with herbcover (Fig. 2.12g,h). It seems that where the associated species are generally growing well or poorly, so are glacier lilies growing well or poorly (e.g. both herb cover and numbers of flowering plants are negatively correlated with coniferous basal area [Fig. 2.12i,j]). Also, while shrub cover, grass cover, and number of introduced species (often grasses) are positively related with litter depth and cover (Fig. 2.12k-p) as I expected based on my observations, total herb cover exhibits a negative or neutral relationship with litter (Fig. 2.12q,r). This may be because certain species that are abundant early in the growing season, such as *Claytonia lanceolata*, leave very little litter behind when they senesce.

Finally, I would like to point out the significant positive relationships of both number of one-leaved plants and *Erythronium* leaf area to the phenology of the site (Fig. 2.12s,t; see also Table 2.2 for derivation of the phenology variable). These relationships suggest that other correlations involving oneleaf and leaf-area should be interpreted cautiously, because they can be influenced by the particular stage of flowering. For oneleaf, this result may have been due to the greater ease of finding small plants when the adult *Erythronium* plants and other vegetation were less developed, although this hardly seems likely given the thoroughness with which the single leaves were counted. For leaf area, the result makes more sense, and underscores the extremely rapid development of glacier lilies, since the difference between the bud phase and fading flowers may only be a matter of days. By contrast, most other species with which *Erythronium* occurs do not change this rapidly. Associated herb cover is not related to phenology (Table 2.8b), though *Erythronium* habitats change substantially due to growth of other species after the

glacier lilies enter the fruiting stage.

Comparison of High and Low Elevation Meadow Habitats

The overlays and correlations presented above indicate that, in some cases, high and low elevation habitats exhibit similar lily characteristics as compared with intermediate sites. For example, numbers of one-leafed and flowering plants tended to have bimodal distributions, in which there were higher numbers of plants at high and low elevations than at intermediate sites (often treed). In other cases, variables such as number of two-leafed plants and leaf area did not exhibit a bimodal distribution but were distinctly different between the high and low elevation sites. I decided to pursue a finer level of comparison between the high and low elevation areas, using a more precise method of determining differences than simply examining overlays and scatterplots. In addition, I did not wish to simply compare "low" and "high," since the Chase-area sites include areas under coniferous tree cover.

I decided, then, to directly compare glacier lily and environmental variables for two relatively homogenous habitat types (high and low elevation meadows) using (nonparametric) Mann-Whitney U tests (Sokal and Rohlf 1995). TWINSPAN determined the particular sites included in the groups. It produced a hierarchical classification of sites with 6 levels; I have indicated the second-level groupings on the ordination diagram in Figure 2.13. I used the TWINSPAN groups 00 (low elevation sites 1, 22, 24-26, 28-30, 34-35) and 11 (high elevation sites 11-13, 15-21, 36-38) in my analysis; these seemed like reasonably distinct groups both in terms of the overlay diagrams and my own knowledge about the sites.

Results of comparisons for these two groups are given in Table 2.9. Characters relating to adult, reproductive *Erythronium* plants are all significantly higher in the low-elevation group: numbers of flowering plants, proportion of flowering plants, numbers of multiple-flowered plants, and leaf area. (Fortunately, there is no significant difference in phenology between these groups, and therefore all comparisons are valid.) There are a number of factors that could account for more vigourous plant growth in the low-

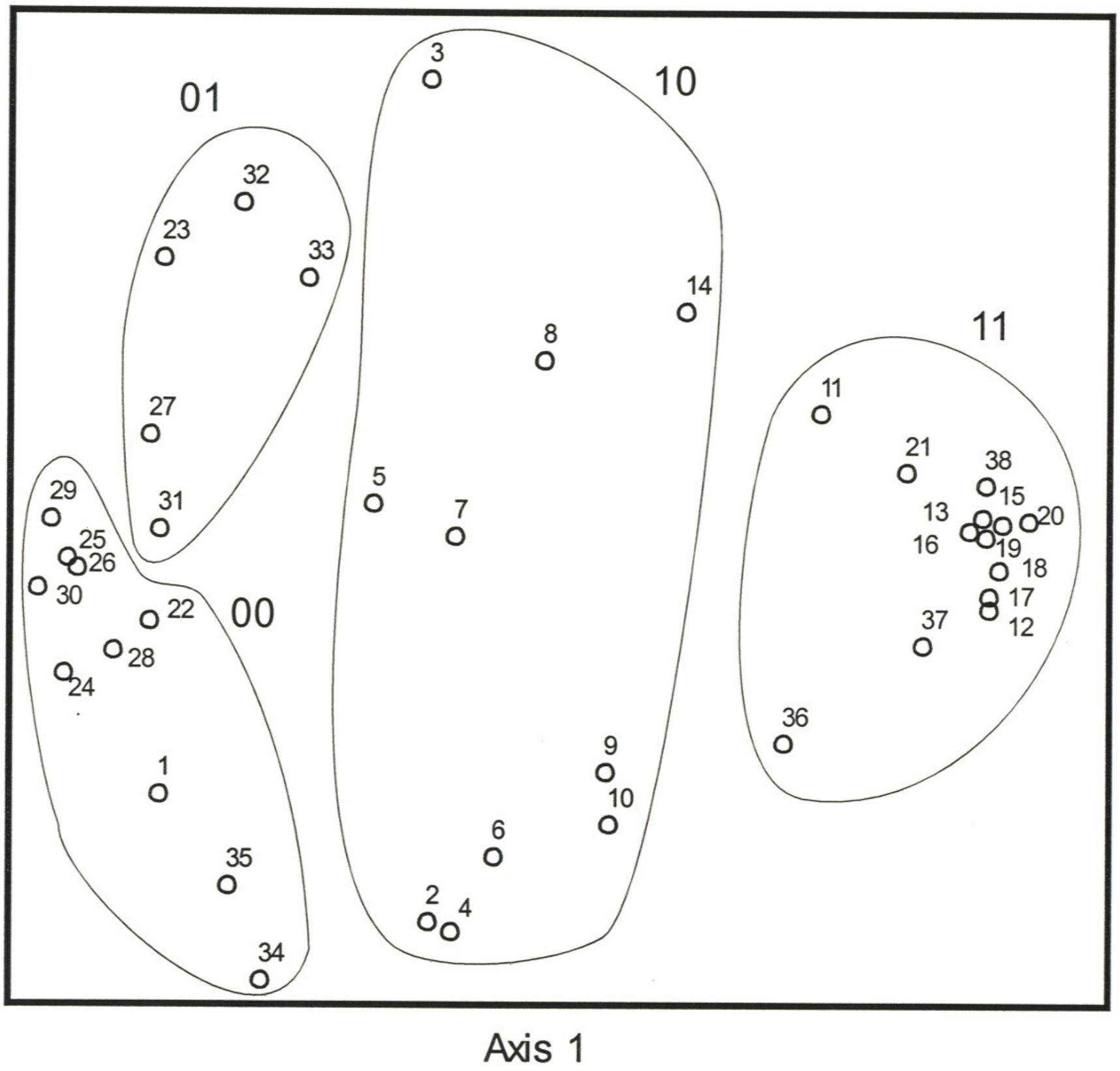

Figure 2.13 Second-order TWINSPAN groupings on DCA-ordinated sites.

Table 2.9 Comparisons of environmental and *Erythronium grandiflorum* characteristics for low- and high-elevation meadow groups (N=10 and N=13 respectively) as defined by TWINSPAN. Refer to Tables 2.2 and 2.3 for variable descriptions.

Variable	Low-elevation Meadow		High-elevation Meadow		p-value (2-tailed Mann-Whitney U test)
	Mean	Std. dev.	Mean	Std. dev.	
Seedlings/m^2	8.7	12.4	20.2	16.4	0.0628
Oneleafs/m^2	156.7	62.8	165.3	115.3	0.8282
Twoleafs/m^2	6.2	3.1	26.0	28.9	0.0048
Flowering plants/m^2	57.0	25.0	27.0	17.1	0.0092
Multiple-flowered plants (proportion of flowering plants)	0.10	0.09	0.02	0.03	0.0070
Proportion of flowering plants (among non-seedling plants)	0.27	0.11	0.13	0.07	0.0084
Proportion of twoleafs (among non-seedling plants)	0.03	0.02	0.11	0.06	0.0007
Ratio of seedlings to flowering plants	0.25	0.39	0.76	0.52	0.0070
Ratio of oneleafs to flowering plants	3.4	2.2	8.2	6.7	0.0143
Leaf area (cm^2)	62.6	26.0	40.5	13.4	0.0170
Shrub % cover	18.9	16.0	2.7	4.6	0.0007
Herbaceous % cover	70	18.0	79.9	29.2	0.4757
Total no. species	42.1	8.1	28.8	8.5	0.0036
No. introduced species	4.7	2.3	0.15	0.38	0.0001
No. native species	37.4	9.5	28.7	8.6	0.0673
Rockiness (cm)	13.9	4.5	20.0	9.1	0.0586
Litter depth (cm)	3.7	1.3	1.0	0.7	0.0001
Litter % cover	35.2	12.3	19.0	8.3	0.0048
Grass % cover	2.9	2.3	26.3	14.8	0.0004
Soil pH	6.8	0.3	5.2	0.3	0.0001
Soil texture	8.2	0.4	9.3	0.2	0.0001
Slope angle (degrees)	14.9	6.4	15.8	8.3	0.8768
Elevation (m)	757	320	1938	90	0.0001
Phenology index	5.8	1.8	5.9	1.1	0.8760

elevation meadows, such as more favourable climatic characteristics (e.g., less extreme temperature variations) and less rocky soils. Conversely, there are many more two-leafed plants (and a higher proportion of these plants) at the high meadows, which again indicates less favourable conditions for flowering (to the extent that these two-leafed plants represent early-aborted flowering attempts; see section 2.2.3).

There is no significant difference in the number of one-leafed plants and seedlings, though in both cases the trend is for higher numbers in the high-elevation meadows. This is a striking result, given that there are significantly higher densities of flowering plants at low elevations, and presumably many more seeds produced; Table 2.8c shows that the variables flowplant and oneleaf are significantly positively correlated (the correlation is positive but not quite significant for flowplant vs. seed) (see Fig. 2.12u,v for scatters). Further, when comparing numbers of seedlings and one-leafed plants as *ratios* of the number of flowering plants, these ratios are significantly *higher* in the high meadows. In other words, for a given number of flowering plants, there are many more seedlings and one-leafed plants in the high meadows. Therefore, while plants that survive to reproductive age seem to do better at low elevations, the juvenile stages (reflecting recruitment for the current growing season and ~ five or more previous years) seem to be more successful at high elevations.

Of the environmental parameters, shrub cover, grass cover, and introduced species are all higher at the lower meadows, and the relationships of these variables with litter depth cover have been noted previously (see Fig. 2.12k-p). The greater amount of litter may mean fewer safe sites for seedlings and may make it more difficult for young juvenile plants to survive. The across-site correlations give some support to this idea; Figures 2.12w and 2.11x show the negative relationships of seedling numbers to litter depth and litter cover respectively (Figures 2.12y and 2.12z show the same relationships for ratio of seedlings to flowering plants). The correlations are non-significant (Table 2.8a), but the scatters suggest a possible "factor-ceiling" relationship (Thomson et al.

1996).[1] Correlations for the one-leafed plants are also shown (Fig. 2.12aa and Fig. 2.12ab), though it must be kept in mind that phenology could be a confounding factor. In this case, there may be a negative "factor-ceiling" relationship with litter depth but none with litter cover. This makes some sense, since for an already-germinated juvenile, litter depth would be a more significant problem than litter cover in terms of blocking access to light. For seedlings, both cover and depth potentially block access to a favourable microsite for germination.

2.1.5 Discussion

Gauch (1982:31) said, "Essentially everything in the physical world is conceivably relevant to the life of community organisms. . . . Communities have countless complex interactions and causal connections, some of which defy observation and analysis." I certainly have not assessed all the factors potentially relevant to the ecology of *Erythronium grandiflorum* in western Canada. For example, soil nutrients, snow depth, and various biotic interactions may be important both on a macro- and micro-scale. In addition, historical factors (e.g. glacial history) and simple chance can help explain why species do or do not occur in an area.

In spite of these limitations, my observations suggest that the distribution and abundance of *E. grandiflorum* are mediated by a specific combination of light and moisture requirements. This species seems to require both abundant light and moisture, but only during its flowering period, early in the growing season, for optimal growth and reproduction. If "vigour" can be indexed by number and size of individuals, adult plants seem to thrive best in relatively low elevation, open meadow or parkland habitats. Yet, many botanists express surprise upon seeing the spectacular display of this species in areas like the Chase meadows, since glacier lilies seem more characteristic of subalpine

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[1]As Thomson et al. (1996) explain, these triangular distributions indicate a relationship between two variables such that one variable imposes on another not a particular value, but an upper bound. Such relationships may be common in ecology, but simple correlation analysis is seldom able to distinguish them from "shotgun blasts."

meadows. I believe that yellow glacier lilies are relatively uncommon at lower elevations in western Canada because not many of these areas have the particular light/moisture conditions they require (abundant light and moisture early in the growing season). Many areas of open grassland in the interior of British Columbia are probably too dry. While the Chase or Botanie meadows may seem quite dry in mid-summer, in early spring this is not the case. In fact, Klinka et al. (1989:109) state that *Collinsia parviflora* (a species common at my lower-elevation sites) is "characteristic of moisture-deficient sites" but also that it "often inhabits meadow-like communities on water shedding-sites where early spring moisture is followed by mid summer drought." The area around Chase (part of the Interior Douglas-fir zone) is transitional between the dry Bunchgrass and Ponderosa Pine zones around Kamloops, and the much moister ICH (Interior Cedar Hemlock) zone further east. In that zone, as the name implies, *Thuja plicata* and *Tsuga heterophylla* grow at low elevations and may preclude *Erythronium* growth, presumably due to insufficient light. Similarly, the meadows at Botanie Valley represent a transitional zone elevationally between the very dry Ponderosa Pine zone around Lytton, and the higher areas of continuous ESSF (Engelmann spruce-subalpine fir) canopy. In both Chase and Botanie Valley, there is often a gradient evident on a small scale from areas where *Erythronium* grows, to drier areas characterized by *Balsamorhiza sagittata*, for example (there is some overlap, hence the presence of *Balsamorhiza* in many of my low-elevation sites). There is often a patchy appearance to the glacier lily growth, with the *Erythronium* occupying moister microsites; e.g. it is often found in and around patches of *Symphoricarpos* and other shrubs in small swales. For the same reason, glacier lilies may be associated with wind-stunted *Populus tremuloides* in the rainshadow climate of southwestern Alberta. The lilies do not extend out from the aspen cover to open areas, and this may be due to more favourable moisture conditions associated with the trees. Apparently, light is sufficient under a deciduous canopy such as aspen (which bears no leaves at the time *Erythronium* flowers).

Erythronium grandiflorum is also relatively rare at intermediate elevations in western Canada, probably because these areas often bear a continuous coniferous canopy.

However, avalanches and fire open up sites in what would otherwise be closed forests. Avalanches may also transport yellow glacier lilies and their seeds from higher to lower elevations. At Nigel Creek in Banff National Park in 1996, I observed about 50 cm of debris-topped snow at the base of a once spruce-covered slope, and glacier lilies were growing in a thin layer of humus and soil on top of the snow.

As I have documented, glacier lilies can grow under certain types of coniferous canopies (*Pseudotsuga menziesii, Picea engelmannii*) but not as successfully as in the open. Also, these treed sites are usually not far from larger areas of open or parkland meadow. These coniferous-treed areas may represent "sink" habitats for the lilies. I frequently observed scattered glacier lilies in areas of more continuous coniferous cover, but usually along a roadside or occasionally in clearcuts (I did not lay out plots in such areas). Glacier lilies probably persist in such areas because fires or other disturbances periodically create openings. Thus, landscape burning once performed by First Nations may have been highly significant in maintaining glacier lily habitat in areas where coniferous trees would otherwise grow (see Chapters 3 and 5). Summer drought may also be significant for maintaining *E. grandiflorum* in many areas, as it would create conditions conducive to fire. I certainly had ample evidence for the existence of past fires in the sites I studied. David Blundon (plant ecologist, Camosun College, pers. comm. 1997) is currently doing an exclosure study in a high-elevation (2100 m) meadow in south-central B.C. (Mt. Scaia, Granby Provincial Park), and this meadow is very similar in species composition to many of my high-elevation sites. He believes that the area was closed forest in the 1930s, and has since become an open meadow maintained by fire, and more recently by grazing. It is possible that where fires are suppressed, cattle grazing helps maintain an open habitat and reduces litter loads from grasses (many of which are introduced). Therefore, if grazing is done in moderation and takes place after glacier lilies have gone to seed, it is possible that cattle may have a beneficial impact on the habitat (Rick Tucker, range agrologist, pers. comm. 1996). However, overgrazing is extremely common, and cattle may have negative impacts such as trampling (see next chapter). Exclosure experiments like Blundon's should help in assessing the net impacts.

Given the apparent limitations to *Erythronium* growth at low and intermediate elevations, the most extensive suitable habitat for *E. grandiflorum* in western Canada is currently the subalpine herb meadow. This habitat represents a transitional zone between continuous, low-light spruce-fir forest and the extremely harsh alpine tundra proper (cold and windy, with low growing season temperatures and a very short frost-free period) (Pojar and Stewart 1991). Such herb meadows have been considered both part of the ESSF zone (upper edge) and part of the AT (Alpine Tundra) zone (lower edge) (Coupé et al. 1991, Pojar and Stewart 1991). According to Pojar and Stewart (1991:266), herb meadows "develop on well-drained sites with deep soils, in seepage areas, or along alpine rivulets and streams." From my observations, many subalpine herb meadows with glacier lilies do not have particularly deep soils, but seepage conditions are very common during the brief period of active *Erythronium* growth early in the growing season. Many of the associated species found in my subalpine sites are indicators, at least on the coast, of water-shedding sites (and of medium to rich nitrogen conditions and moder and mull humus forms) (Klinka et al. 1989). The degree to which glacier lily can tolerate a saturated substrate (early in the season) is illustrated by site 32, an opening in mixed coniferous forest near Castlegar, where the plants were growing in a saturated moss layer on rock. One of the bryophytes present was *Aulacomnium palustre*. According to Schofield (1992), this species is "frequent in swampy, boggy, or seepage sites; on lake and pond margins and on cliff shelves." However, the habitats I observed were not saturated all through the growing season (after the glacier lilies have fruited).

My results suggest that *E. grandiflorum* is adapted to, or possibly even dependent upon, various types of disturbance. I have already noted the possible significance of fire and avalanche activity for creating suitable light conditions in otherwise unsuitable forested areas. In certain areas, natural fire cycles may also reduce litter loads from shrubs and grasses, which appear to be associated with reduced seed germination and juvenile survival. I will return to the topic of disturbance in Chapter 5.

Yellow glacier lily appears to be similar in certain respects to other *Erythronium* species that have been described. All are spring ephemerals, dependent on early-season

light and moisture, and are of probable significance in preventing leaching of nutrients from snowmelt (i.e. the "vernal dam hypothesis" put forth by Muller [1978] for *E. americanum*; see also Tardiff and Stanford [in press]). *Erythronium japonicum* is a spring geophyte found in deciduous broad-leaved forests of Japan. According to Kawano et al. (1982:129), "The presence of a bright light environment for at least one month in early spring (late March to late April) was found to be a necessary condition for the successful establishment of *Erythronium* populations." Kawano et al. also found that *E. japonicum* declined along a gradient from deciduous to evergreen canopy, with no seedlings or flowering individuals found under the latter.

It is not clear why *E. grandiflorum* has such a large range compared with the other western North American species; detailed ecological studies on those other species are needed. However, it may be that in the period immediately following deglaciation ca. 10,000 years ago, glacier lilies were widespread in the vast open areas, and that as the climate became warmer and drier and trees invaded from the south (Pielou 1991), glacier lily habitat became fragmented (see Allen et al. 1996). If the habitat were more suitable in immediate postglacial times for *E. grandiflorum* than the other western *Erythronium* species, this would help explain the current difference in the ranges. Also, certain aspects of the Sierra Nevadan geography (where many localized endemic *Erythronium* species are found) may have resulted in greater genetic diffferentiation there (Shevock et al. 1990). It is also possible that *E. grandiflorum* does comprise a group of genetically differentiated subtaxa, either at the specific or subspecific level. Some subtaxa have already been elevated to species level (see Chapter 1), such as *E. idahoense*, which exhibits reciprocal incompatibility with *E. grandiflorum* in sympatric populations (Fritz-Sheridan 1988). However, there is no evidence of other taxa as distinct as *E. idahoense* at the present time.

2.2 Bulb and Appendage Experiment

2.2.1 Methods

My experiment was carried out at the Trophy Mountain flower meadows on the

south edge of Wells Gray Provincial Park (near site 12 on Figure 2.1), and at Mrs. Nancy Millar's garden near Dunn Lake, 12 km south of Clearwater, British Columbia. Elevations were approximately 1950 m at the meadow (Engelmann Spruce-Subalpine Fir zone) and 450 m at Dunn Lake (Interior Douglas-fir zone).

On August 9, 1996, I collected bulbs from green-fruited and non-fruiting glacier lilies at the Trophy Mountain meadows. The bulbs were growing at depths ranging from 9 to 15 cm. Some appendages were taken from these bulbs, but additional bulbs had to be collected since not all the bulbs had appendages (due to decay, to separation in the process of excavation, or possibly to insufficient age [see section 1.1.3]). In total, five bulbs and five sets of detached appendages were replanted at Trophy meadows (approximately 500 m from point of collection), and 10 bulbs and 10 sets of appendages were transplanted to Dunn Lake. A "set" of appendages refers to a chain of appendages from a single bulb, generally consisting of from three to six easily separable segments.

I replanted the bulbs at Trophy meadows within an hour from time of collection. First, I cleared an area adjacent to a rotting log (i.e. easily relocatable landmark) so that it was free of all *Erythronium*. I then buried the bulbs along one side of the log, approximately 15 cm apart and 15 cm deep, and marked them with stakes. Along the other side of the log, I buried the sets of separated appendages similarly (thus there was more than one appendage in each hole). After refilling the holes with soil, I re-covered the area with a layer of litter.

I transported the bulbs and appendages for transplant at Dunn Lake in moist soil from the collection site. These transplants took place within three hours from time of collection. After clearing weeds from a small area in the garden, I established two rows: 10 bulbs and 10 sets of separated appendages. These were planted, covered, and marked in the same way as described for Trophy meadows.

2.2.2 Results

On April 28, 1997, I visited the transplant site at Dunn Lake, after Nancy Millar informed me that at least one lily plant had come up. One of the plants in the bulb-

transplant row had indeed come up, and bore a single flower. The plant was only 8.5 cm tall, which was certainly smaller than the average *Erythronium* plant at Trophy meadows. However, I had not been present at Trophy meadows during the flowering stage to measure the plants, and cannot be certain that the transplant had a negative impact on the plant's size. Five others in the bulb row were just starting to emerge from the ground as furled leaves extending up to 3.5 cm above the ground. In the appendage row, there was a single one-leaf *E. grandiflorum* individual (still furled) 2.3 cm tall beside one of the stakes.

I was unable to revisit the Clearwater area until much later in the season, when I returned to check on the experiment at Trophy meadows. However, Mrs. Millar continued to monitor the progress of the *Erythronium* in her garden. The final results are summarized in Table 2.10. By the the third week in May, *all* plants had come up in the bulb row: seven flowering (one with two flowers, five with one flower), and three with double leaves. All the flowers had faded by this time and the leaves were yellowing, but none was developing fruit, nor did any in the remainder of the season. As shown in Table 2.10, the status of the plant when the bulb was collected (flowering or sterile two-leaved) did not necessarily determine the status of the plant after transplanting. A one-leaved plant became two-leaved, fertile plants became sterile two-leaved plants, and two-leaved plants became fertile). In the appendage row, two additional one-leaved plants had come up since the end of April; i.e. a total of three.

Recently, Mrs. Millar has informed me of the results for the second year (1998); summarized in Table 2.11. In the bulb row, all 10 plants again emerged, six with single flowers and four non-flowering (she could not recall whether they had single or double leaves). Once again, none of the flowering plants developed capsules. In the appendage row, groups of from one to six leaves came up for *eight* of the ten sets of appendages planted; this in spite of heavy invasion by daisies. However, because of the daisies, it was difficult for Mrs. Miller to notice whether these leaves were from single-leaved plants or double-leaved.

I revisited the Trophy meadow site on June 29, 1997, and the results are

Table 2.10 Results of bulb and appendage transplant experiments at Dunn Lake, 1996 to 1997.

Experimental unit	No. of plants at collection in 1996	Result in 1997			
		Flower	2-leaf	1-leaf	Did not appear
Bulbs (N= 10)					
Flowering	4	2[1]	2	0	0
Two-leaf	5	5	0	0	0
One-leaf	1	0	1	0	0
	---	---	---	---	---
Total	10	7	3	0	0
Appendages (N=10 sets)					
Flowering	8	0	0	3	5
Two-leaf	2	0	0	0	2
	---	---	---	---	---
Total	10	0	0	3[2]	7

[1]One single-flowered and one double-flowered.
[2]A single leaf emerged from each of three sets of appendages.

Table 2.11 Results in 1998 for bulbs and appendages transplanted at Dunn Lake in 1996.

Experimental unit	No. of plants at collection in 1996	Result in 1998			
		Flower	2-leaf	1-leaf	Did not appear
Bulbs	10	6[1]	?	?	0
Appendages	10 (sets)	0	0[2]	8[2]	2

[1]All single-flowered.
[2]Within each set, from 1 to 6 leaves appeared, so that 27 leaves came up in total; some of these may have been two-leafed plants (see text).

Table 2.12 Results in 1997 for bulbs and appendages replanted at Trophy Meadows in 1996.

Experimental unit	No. of plants at collection in 1996	Result in 1997			
		Flower	2-leaf	1-leaf	Did not appear
Bulbs	5	5[1]	0	0	0
Appendages	5 (sets)	0	1	1[2]	3

[1]All single-flowered.
[2]Two single leaves emerged from this one set, thus a total of three separate plants originated from appendages.

summarized in Table 2.12. In this case, all the bulbs developed one-flowered plants, with the flowers just starting to open at the time of the visit (Figure 2.14). One plant in the bulb row had a third, small leaf. In the appendage row, three appendages from the five sets sprouted, with two single-leaved plants from a single set. The third was a two-leaved plant.

I decided to excavate all the plants at Trophy meadows as voucher specimens. It would have been interesting to leave them to see if any of the flowering plants would fruit, but I was not sure if I would be able to return to the area again (and, in fact, the road was later blocked by a massive mudslide). Upon excavating the plants, I noticed that the third small leaf on the above-mentioned flowering plant was growing from an appendage that was separating from the bulb. It is quite likely that this appendage was disturbed when I excavated and replanted the bulb. Figure 2.15 shows all of the one-leaved plants growing from appendages after being excavated. I also dug up the (unsprouted) appendages in the other holes to ensure they had not sprouted underground or rotted; neither was the case, and so I replanted them.

2.2.3 Discussion

On the basis of the information presented here, it is possible to modify the life cycle diagram given in Figure 1.4 to that shown in Figure 2.16. It is clear that bulb-appendages can act as vegetative propagules when mechanically separated from the parent plant. Two-leaved plants can apparently represent both an intermediate step between the one-leaf stage and flowering, as well as a reversion from a flowering stage. In these respects, as has been suspected, *Erythronium grandiflorum* closely resembles *E. japonicum* (Kawano 1982, 1984, Kawano and Nagai 1982, Kawano et al. 1982). *E. japonicum* has very similar bulb-appendages, which fluctuate in mass seasonally, apparently due to translocation from the main bulb. Also, while *E. japonicum* does not have a two-leaved non-flowering stage, it does flower intermittently, reverting occasionally to a large one-leaved individual.

Still, as noted in Figure 2.16, some questions remain regarding the life cycle. For

Figure 2.14 Flowering *Erythronium grandiflorum* plants one year after bulbs were transplanted within the Trophy Mountain meadow area. Note the small third leaf on the plant at the left.

Figure 2.15 One- and two-leaved *Erythronium grandiflorum* plants growing from bulb-appendages, one year after the appendages were removed from bulbs and transplanted within the Trophy Mountain meadow area.

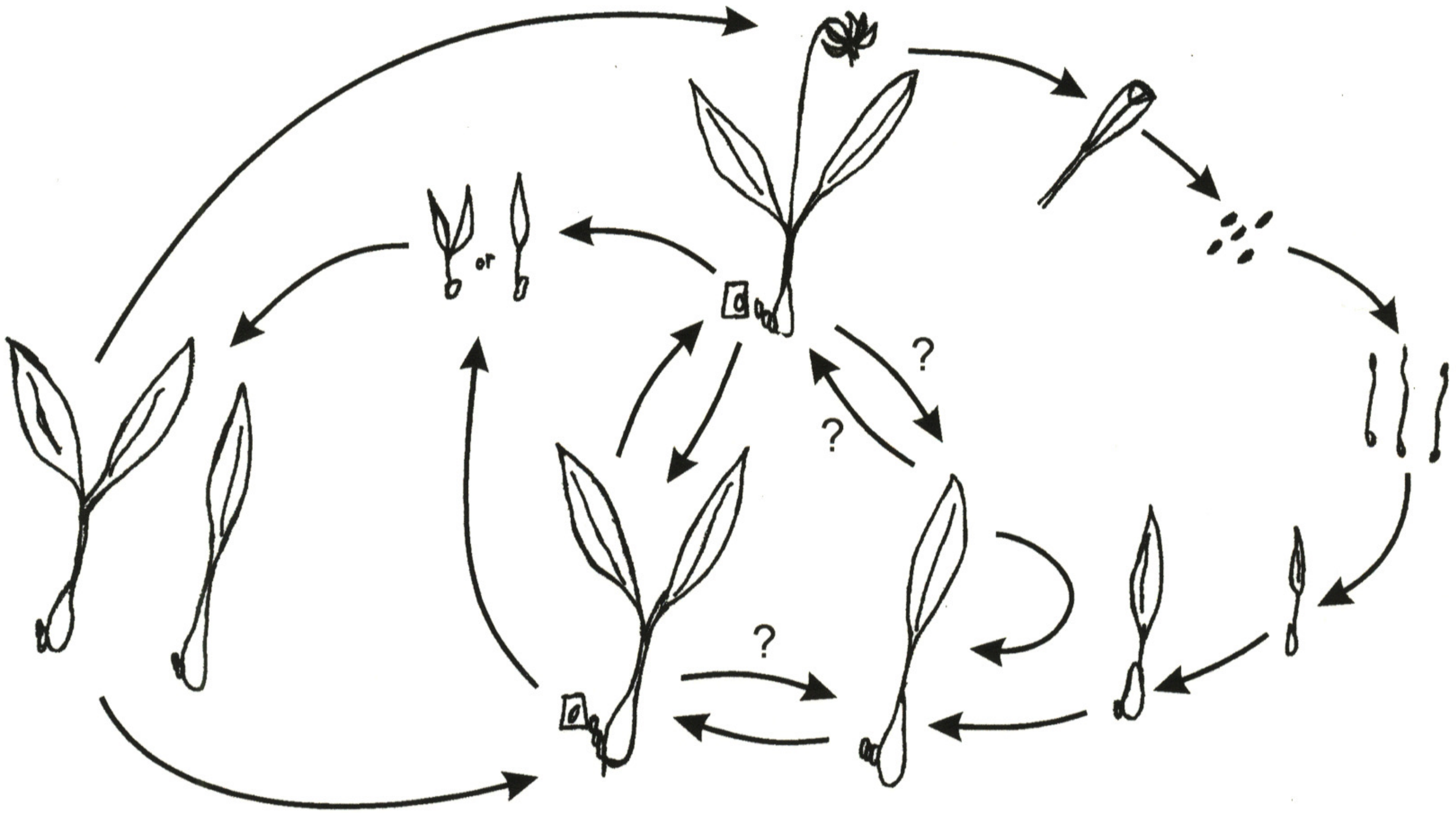

Figure 2.16 Revised life cycle diagram of *Erythronium grandiflorum*, based on new information presented in Chapter 2.

example, it is unknown whether a fertile or sterile double-leaved plant can revert to a single-leaved stage, or whether a one-leaved plant can progress directly to the flowering stage. While I have shown that one-leaved plants certainly *can* develop into two-leaved plants the following year, it is not clear whether this is always or often the case. The two-leaved stage could also indicate a plant that has aborted its attempt to produce a flower very early (before the scape emerges from the bud). In addition, I have shown that a two-leaved plant can develop from an appendage the first year after the appendage is separated. In this case, the two-leaved plant is unlikely to be the result of an aborted flowering attempt, since in many geophytes, including *E. japonicum*, a critical bulb mass (most likely larger than that of the appendage) must be attained over a number of years before flowering is initiated (Dafni et al. 1981, Kawano et al. 1982). It is possible that two-leaved plants can result from a number of different life history events.

Erythronium grandiflorum appears to be amenable to transplanting from high to low elevations, at least for the time frame and habitats involved in this experiment. This is true both for the bulbs and for the separated appendages. The plants were immediately able to adjust their time of emergence by two months, presumably using temperature cues (cf. Yoshie and Fukuda [1994]). This adaptability could have implications for dispersal. For example, grizzly bears could transport appendages from place to place in their claws, or it is even conceivable (though unlikely) that the appendages could survive intact through the short carnivore-type digestive tract. Additional implications related to human use of the bulbs are discussed in Chapter 5.

The plants involved in the high-low elevation bulb transplant did not set fruit in the first or second season. These plants will be monitored in the future to see if that situation changes. The lack of fruiting could well be due to pollinator limitation, since, aside from the few lily plants, there would have been little else in the small garden plot to attract insects at that early date.

2.3 Suggestions for Future Work

Since my analysis was exploratory, it will be necessary for future research to test

my tentative conclusions. Such research could be effective using an observational approach at a smaller scale, and/or by doing experiments. For example, using the observational approach, gradients could be examined from open meadow to coniferous forest, or from a moist hollow to a drier area. Ideally, such detailed observations would take place in a number of sites both at low and high elevations. Also, a variety of coniferous cover types should be examined since, for example, glacier lilies probably do not respond the same way to *Picea glauca* / *Abies lasiocarpa* forest as to a more open *Pseudotsuga mensiezii* or *Pinus contorta* forest. Thomson et al.'s (1996) study is an excellent example of small-scale observational work, which could be adapted to the conditions and phenomena of interest in the northern part of the range. Experimental work could include, for example, removing litter and creating more bare ground in an area to investigate the effect on *Erythronium* reproduction. Tardiff and Stanford's (in press) study is an example of a fruitful experimental approach. In Chapter 5, I will describe that study and return to the subject of investigating disturbance impacts.

A very important question to address is the extent to which there is genetic differentiation among different habitats (particularly low vs. high elevation), and among different areas of the species' large range. It is possible that the difference I noted in plant size, for example, from low to high elevation meadows, is due to ecotypic differentiation, rather than a phenotypic response to the environment. Reciprocal transplant experiments will be necessary to address this possibility. Even if ecotypic differentiation has not occurred, it will still be necessary to do exploratory ecological work in other parts of the species' range. Wide-ranging species often have different ecological responses in different areas; e.g. *Epilobium angustifolium* is confined to warm, sunny locations and south-facing slopes in the northern part of its range, and to cool, shaded locations and high elevations in the southern part, with a wide amplitude in the center of its range (Haeussler et al. 1990). The suggestion that *E. grandiflorum* occurs on "sagebrush slopes" in the U.S. (Hitchcock et al. 1969; see Chapter 1) is one indication that the autecology of the species may vary significantly.

Detailed genetic work (e.g. isozyme analysis) would be very useful in clarifying

relationships among *E. grandiflorum* populations, and relationships of the species to its congeners. Genetic work should be combined with detailed morphological analysis of *E. grandiflorum* throughout its range to aid in developing a more detailed taxonomy. The pattern I observed in anther colour may be explained in this way, or it may be found that I obtained the pattern in my 38 sites by chance.

There is a need for a long-term experiment to more adequately address how the plants develop in the years following a mechanical separation of the bulb-appendages. For example, it would be interesting to determine how long it takes for flowering to occur after a plant has sprouted from an appendage. Also, there is a need to systematically determine the extent to which vegetative reproduction happens without disturbance (or to determine how often a disturbance sufficient to dislodge an appendage occurs). From casual observation, I would suspect that vegetative reproduction occurs only rarely without mechanical intervention, as in *E. japonicum* (Kawano 1982). I did a fair amount of digging in my sites (for soil samples and vouchers), and never observed any one-leaved plants with the distinct appendage morphology shown in Figure 2.15. Rather, they all had miniature versions of the adult plants' bulbs, and thus were presumably derived from seed. My speculation is substantiated by the observations of horticulturalists (Watson and Woodward 1974), who have noted that *E. grandiflorum* offsets only rarely in the garden, unlike *E. tuolemnense*, for example. Of course, there may be variability among individuals in terms of readiness to vegetatively propagate, as occurs in *E. oregonum* (Dr. Geraldine Allen, pers. comm. 1996). There may also be variability in different areas of the species' large range.

Demographic studies are needed to work out the particulars of the life history for this species, e.g. in determining the precise nature of the two-leaf stage and of multiple flowers. A demographic study will also help clarify what stages in the life cycle are limiting for this species. Comparing demographic characteristics of *E. grandiflorum* with those of an *Erythronium* more restricted in range could yield interesting insights into the phenomenon of rarity.

Finally, more detailed and longer-term transplant experiments are necessary to

determine whether *Erythronium grandiflorum* from a given habitat can truly establish successfully in other habitats. Successful fruiting, with subsequent seedling recruitment and survival to reproductive maturity, must be demonstrated for this to be the case.

2.4 Summary

An initial investigation of the general habitat requirements of *Erythronium grandiflorum* was carried out at 38 sites in southern British Columbia and southwestern Alberta. Cover data for associated species were ordinated, resulting in an arrangement of sites largely related to elevation and the type of tree cover present. Sites varied from open meadows or pastures at 500 m ASL, to subalpine meadows over 2000 m ASL, with forested or semi-forested sites (*Pseudotsuga menziesii, Picea engelmannii, Pinus contorta, Populus tremuloides*) and other habitat types such as avalanche chutes at intermediate elevations. In general terms, all stages of *Erythronium* plants were more abundant in open areas or areas with deciduous tree cover than in coniferous-forested sites. A comparison of the meadow habitats at high and low elevations revealed that flowering plants appeared to be more abundant and robust at low elevations, while seedlings and juveniles were disproportionately represented at high elevations. I suggest that, while low-elevation meadows may represent favourable growing conditions for adult *Erythronium grandiflorum* plants, the relatively high amounts of shrub and grasses (many of the latter introduced) may inhibit seed germination and juvenile survival, at least in comparison with upper-elevation meadows. Yet, subalpine meadows represent the most common habitat for *E. grandiflorum* in western Canada. The particular combination of abundant early season light and moisture required by the species is relatively rare at low elevations, given current climates and plant associations.

An experiment was also carried out to determine whether the "bulb-appendages," which remain on bulbs as remnants of previous years' bulbs, can act as vegetative propagules. Bulbs and separated appendages were collected at a subalpine meadow, and one set of each was replanted within the same meadow area, while another set of each was transplanted 1500 metres lower in elevation to a garden setting. Regrowth was

observed the following year in all cases (and also the second year for the garden plants), confirming that the appendages can act as propagules if mechanically separated from the main bulb. The extent of this process in the absence of such disturbance remains unknown. The experiment also suggested that certain populations of the species are phenotypically plastic, i.e. adaptable to very different ecological conditions, at least over a period of two years.

3.0 Ethnobotany of *Erythronium grandiflorum*

> Annie York declared that it was the "boss" of all the roots, because it was so valuable. (Turner et al. 1990:122)

Ethnobotany has been defined in broad terms as "the study of the relationships between plants and people" (Balick and Cox 1996:3). An examination of the ethnobotany of the yellow glacier lily will therefore include many facets of the relationship between this species and humans. I will focus primarily on the most significant human interaction with the plant, namely the use of the bulbs as a root[1] vegetable by the northern interior plateau peoples highlighted in Figure 3.1. I will briefly describe these peoples and their food systems, followed by specific information relating to the indigenous use of glacier lily bulbs: nomenclature, harvesting, processing and storage, trade, resource management, role in ritual and mythology, and current uses. I will then consider other, less common, uses of this species, as well as uses of other *Erythronium* species. Further discussion of some of the ethnobotanical information compiled in this chapter is deferred to Chapters 4 and 5.

3.1 Data Collection

My project was part of a six-year Secwepemc Ethnobotany Project led by Dr. Nancy Turner at the University of Victoria and Dr. Marianne Boelscher Ignace of the Secwepemc Cultural Institute and Simon Fraser University. The Secwepemc Ethnobotany Project was approved by the Shuswap Nation Tribal Council to include extensive interviews with elders from the various Secwepemc Bands. Interviews were conducted by many individuals associated with the project, including the above-named researchers and others, Secwepemc students, and graduate students including myself.[2] Secwepemc elders who participated in the project and whose knowledge is respectfully represented here

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[1]"Root" is used in a generic sense to include a variety of types of underground structures (bulbs, corms, tubers, rhizomes, true roots, etc.).

[2]Approval for my interviewing was also granted by the University of Victoria Human Research Ethics Committee (May 1, 1996 to April 30, 1997).

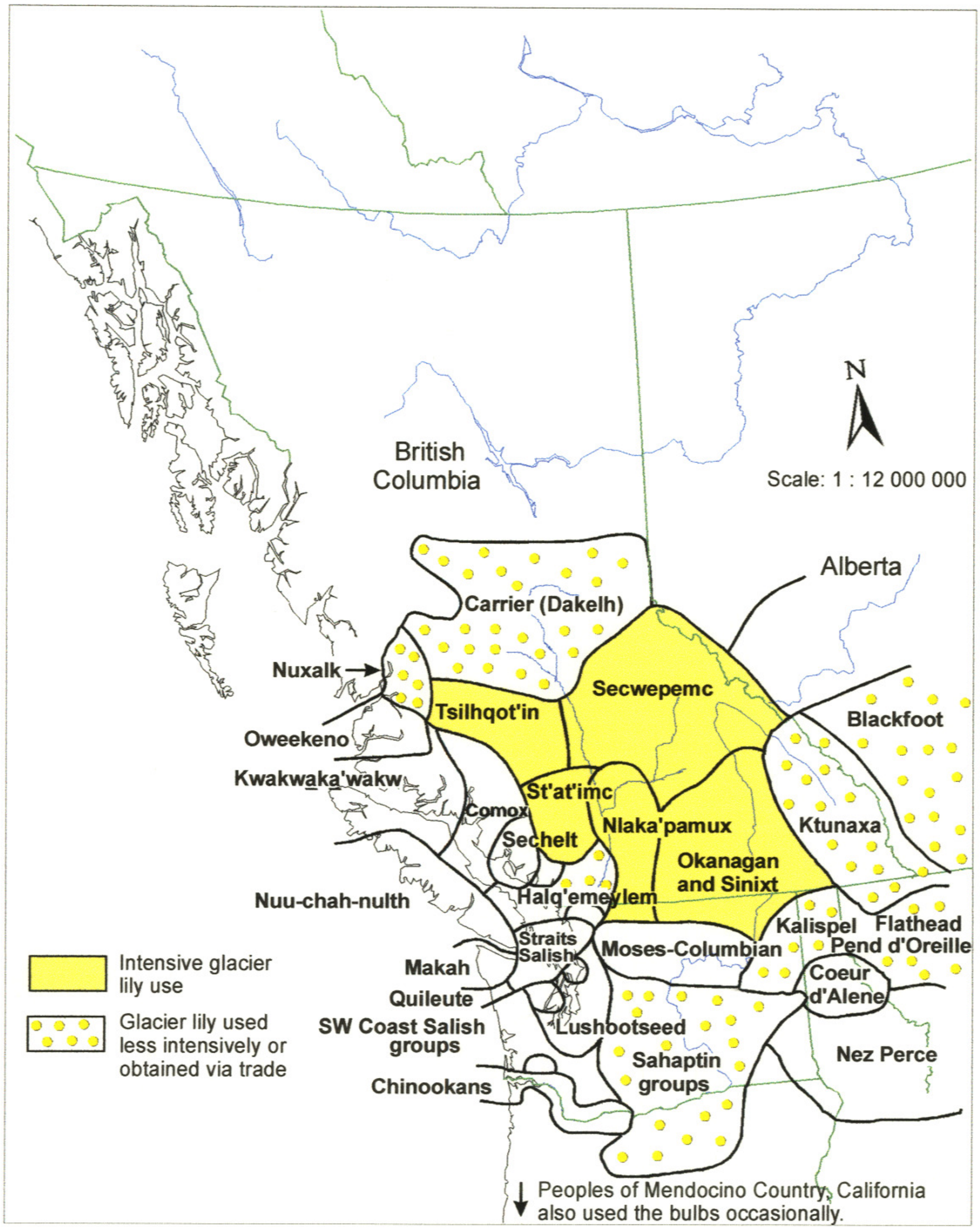

Figure 3.1 First Nations users of yellow glacier lily (shaded), and neighbouring groups. Boundaries are approximate and drawn without prejudice to any First Nations land claims in the area.

include: Mary Thomas (Figure 3.2), Aimee August, Ida William, Les Williams, and Bill and Mary Arnouse. Information from these (as yet unpublished) interviews is cited in this chapter as SEP (Secwepemc Ethnobotany Project) (1993-1997).[1]

Additional knowledge of Secwepemc people, and all knowledge from other peoples, is represented by means of previously written, published and unpublished documents. These include writings of such early ethnographers as Franz Boas (1890), George Dawson (1891), and James Teit (1898, 1900, 1906, 1909, 1912a, b). Also, more recent works are cited, including Palmer's (1975b) Shuswap ethnobotany (representing knowledge primarily of Isaac and Adeline Willard); Turner et al.'s (1990) Nlaka'pamux ethnobotany (representing knowledge of Annie York, Louie Phillips, Mary Anderson, Hilda Austin, Julia Kilroy, Bernadette Antoine, Mabel Joe, and Mamie Henry); Turner et al.'s (1980) Okanagan ethnobotany (representing knowledge of Selina Timoyakin, Larry Pierre, and Martin Louie); and Turner et al.'s (1987) St'at'imc (Lillooet) ethnobotany (representing knowledge of Sam Mitchell, Baptiste Ritchie, Martina LaRochelle, Edith O'Donaghey, Bill Edwards, Desmond Peters, Charlie Mack Seymour, Alec Peters, and Margaret Lester). Most information regarding the Tsilhqot'in use of *Erythronium* is derived from Alexander et al.'s (1985) report; indigenous consultants cited therein are identified by initials only.

It should be noted that, while every attempt has been made to include ethnobotanical information for all groups known to have used yellow glacier lily, most of the information is based on Secwepemc and Nlaka'pamux traditional uses. While it is likely that these groups did indeed use the species most intensively, it is also true that ethnobotanical research with these groups has been extensive. Therefore, the possibility of more widespread, but unrecorded, use cannot be ignored.

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[1]I am deliberately citing the information in this fashion to make it clear that, even though some of the information is appearing in print here for the first time, it is not subject to the restrictions of the copyright on my thesis. The information belongs entirely to the Secwepemc people.

Figure 3.2 Mary Thomas (in 1997, with yellow glacier lilies near Little Shuswap Lake): a Secwepemc elder whose extensive knowledge is frequently cited in this thesis.

3.2 The Northern Plateau Peoples and Food Systems

> This was when people around here didn't own any cattle or very many horses. They just moved around. Them days there was no moose at all and very few deers, just fishes is mostly what they lived on and also berries, wild potato [*Claytonia lanceolata*] and bearteeth plant [*Erythronium grandiflorum*]. Things like that. (Eugene William, Tsilhqot'in, quoted by Glavin et al. 1992:28)

The northern plateau peoples considered here include an Athapaskan group, the Tsilh'qotin (Chilcotin),[1] and four Interior Salish groups: the Secwepemc (Shuswap), Nlaka'pamux (Thompson), Okanagan, and St'at'imc[2] (Figure 3.1). Ancestors of these peoples inhabited south-central British Columbia 10,000 years ago (Rousseau 1993, Stryd and Rousseau 1996), with a basic subsistence-settlement pattern established for the Interior Salish at least 3000 years ago (references in Pokotylo and Froese [1983]). The food systems of these peoples have evolved continuously over time, and the details of this evolution are the subject of ongoing archaeological research and speculation. In particular, there has been debate about the relative contributions of animal and plant foods. The predominant view has been one of a highly meat- and fish-dominated diet, with ungulates and anadromous fish of overwhelming importance to the subsistence economy (e.g. Murdock's [1967] *Ethnographic Atlas*, Palmer 1975a). Because there was a strict gender division of labour, with men hunting and fishing and women gathering and preparing plant foods (Teit 1900, 1906, 1909, Alexander et al. 1985), this bias in the literature may be in part due to the fact that most researchers have been men, who

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[1]The Tsilhqot'in have cultural affinities both with the other Athapaskan groups of northwestern North America, and with the mainly Salishan Plateau groups (Pokotylo and Mitchell 1998). They have been variously classified as part of the Sub-Arctic Culture Area (e.g. Turner 1997a), or as part of the Northern Plateau Culture Area (e.g. Murdock 1967). It is therefore not improper for me to consider them as a northern plateau group, especially given the similarities in their food system to that of the Interior Salish (see Alexander et al. 1985).

[2]I recognize that the group known by the anglicized name "Lillooet" includes two distinct peoples speaking different dialects of the same language, the Fraser River St'at'imc (or Stl'atl'imx) and the Pemberton/Mt. Currie Lil'wet'ul. My use of only the first term to refer to the "Lillooet" peoples is done for convenience, and since it was evidently that group who used *E. grandiflorum* most intensively (Teit 1906).

therefore may have learned more about male activities. Also, the most enduring archaeological evidence is from stone and bone artifacts, such as those associated with hunting. More recently, however, there is increasing recognition of the importance of plant foods (and therefore women's contributions) both in the distant and more recent past (Norton 1981, Pokotylo and Froese 1983, Hunn et al. 1990, Gero and Conkey 1991, Lepofsky in press; see also Chapter 4).

In spite of the debate, and in spite of the variability among and within groups, some generalizations regarding the food system are reasonable. The plateau peoples followed a planned seasonal round.[1] They occupied pit-houses in valley bottoms and benchlands during the winter, and in the spring and summer, used temporary shelters as they acquired food, material, and medicinal resources spatiotemporally distributed by elevation and seasonality. There appears to have been a balance in the food system between specialization and diversification (Palmer 1975b); i.e., people used certain key foods (e.g. salmon and saskatoon berries [*Amelanchier alnifolia*]) heavily, but also exploited many other resources, providing variety and buffering intermittent scarcity. Many of these resources, including a variety of root vegetables, were obtained on seasonal migrations to high valleys and mountain slopes (Dawson 1891, Palmer 1975a, Teit 1900, 1906, 1909, Alexander et al. 1985). A Tsilhqot'in seasonal round is depicted in Figure 3.3; details vary for other groups but the general pattern is similar.

The diversity of plant foods used is particularly striking. For the Nlaka'pamux alone, plant foods included strips of cambium and phloem tissues from trees (7 species), green vegetables (16 species), nuts and seeds (3 species), berries and similar fruits (approx. 53 species), fungi (8 species), and root vegetables (at least 33 species) (Turner et al. 1990). These 120-odd food species were consumed on a regular basis, with many additional species used as casual or emergency foods (at least 10 species), beverages (18 species), chewing substances (at least 7 species), and flavourings (15 species) (Turner et

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[1]The common designation for such peoples is "hunter-gatherers"; however, the connotations associated with this label may not be entirely appropriate, as discussed later.

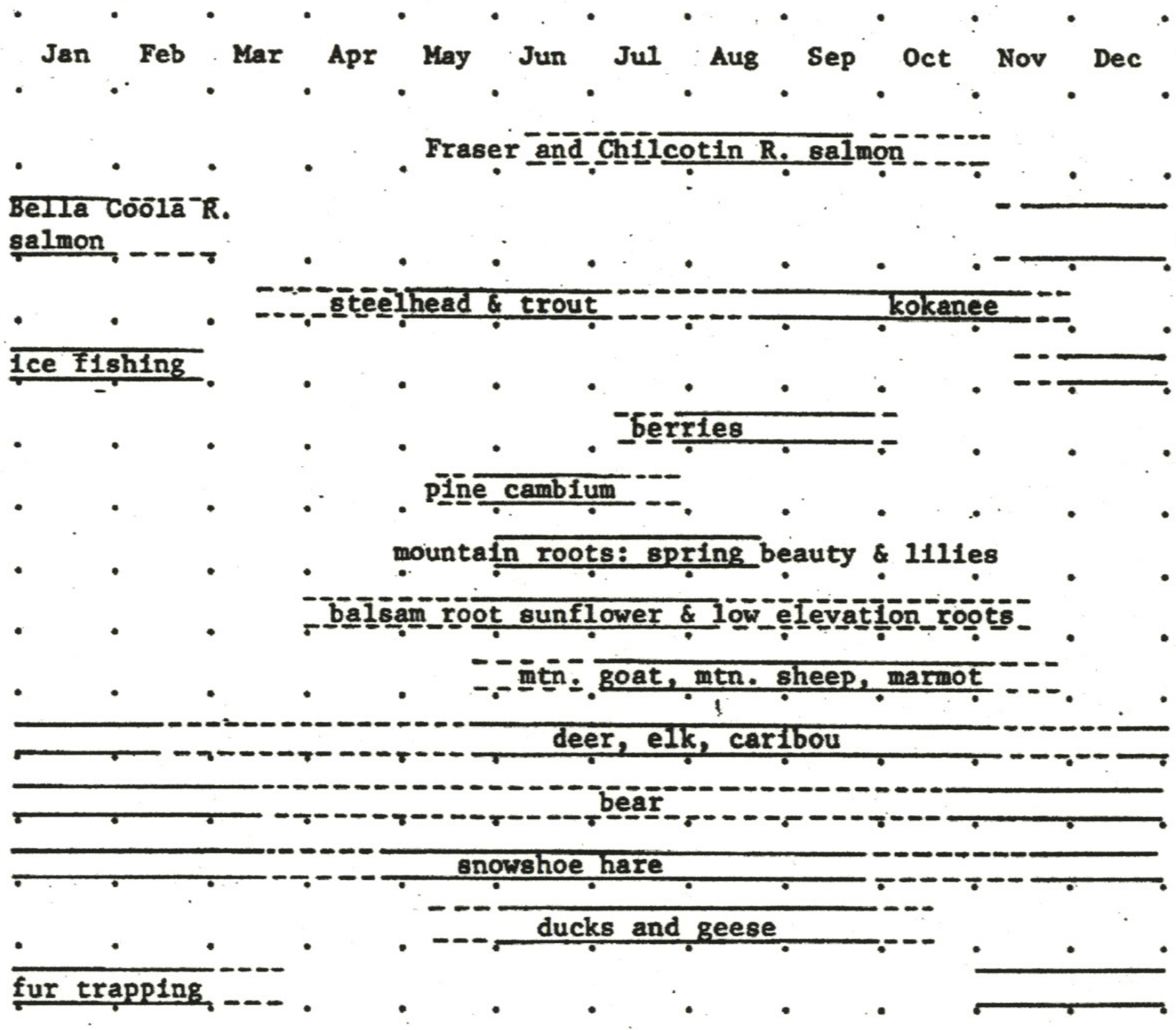

Figure 3.3 Tsilhqot'in traditional yearly subsistence cycle (Alexander et al. 1985:50).

al. 1990). By contrast, only about 200 plant food species, none native to northwestern North America, have been domesticated worldwide throughout history, and most of the world's people depend heavily on about 15 of these increasingly modified crops (Simpson and Conner-Ogorzaly 1986).

The diversity of species used was broadened by means of trade networks, which operated on a variety of spatial scales, from within families to among groups hundreds of kilometres apart (Turner and Loewen in press). In particular, the coastal-inland trade was significant in boosting the types of resources available to groups from each area. Social ties created by marriages between groups, and a minimal emphasis on individual or family ownership of resource areas, added to the security of the economic system in the face of fluctuating food supplies (Teit 1909, Palmer 1975a).

In addition to diversity in food, material, and medicinal resources used, a wide array of techniques was developed to prepare, preserve, and manage plant resources. Increasingly, these varied techniques are being recognized as an integral aspect of peoples' dependence on the resources (Stahl 1989). For example, cooking in earth ovens, or pit-cooking (described below), may have been one technique that allowed intensified use of certain root vegetable resources over time (Thoms 1989; Peacock 1998). I will discuss these techniques further as they pertain to root vegetables in general, and to *Erythronium* in particular, later in this chapter and in Chapters 4 and 5.

European contact brought fundamental changes to the traditional food system, all but eliminating many aspects of it (Turner 1992). People developed a more sedentary lifestyle, while, paradoxically, horses and modern forms of transportation greatly increased their range of travel. Many traditional plant foods, particularly root vegetables, were abandoned in favour of domesticated potatoes (*Solanum tuberosum*), grains, and flour-based foods. Traditional processing techniques such as pit-cooking were also largely abandoned, while new ones such as freezing, canning, and jamming were acquired (Turner 1992).

Yet, in spite of the changes wrought by enforced acculturation and the devastation of diseases, much has also endured. Accordingly, much can be and has been learned

from interviews with contemporary elders. When many of these elders were children, their languages were still widely spoken (Turner 1992), and language in itself reflects a good deal of knowledge about plant use. Beyond this, elders have often had direct experience with gathering, preparing, and consuming plant foods in the traditional manner with *their* elders. Many still value traditional foods and their cultural associations highly, and relish these foods when they can obtain them.

3.3 Yellow Glacier Lily Bulbs: A Staple Root Vegetable

3.3.1 Nomenclature and History of Use

Evidence presented in this chapter suggests that the Interior Salish Secwepemc, Nlaka'pamux, St'at'imc, and Okanagan peoples, as well as the Athapaskan Tsilhqoti'in, were the main groups using yellow glacier lily bulbs within the entire range of the species. All of these groups regularly harvested and consumed the bulbs, and stored them in quantity for the winter. In particular, the bulbs were highly significant to the Secwepemc and Nlaka'pamux peoples. As noted at the beginning of this chapter, yellow glacier lily was considered by at least one Nlaka'pamux elder to be "boss" of the roots, and Secwepemc elders held the plant in similar high regard. According to Aimee August (SEP 1993-1997), the bulbs were the "most important root," followed by wild carrot (*Lomatium macrocarpum*), and then "Indian potato" (spring beauty, *Claytonia lanceolata*). Similarly, Mary Thomas, Teresa Purdaby, and Christine Allen, paraphrased by Surtees (1974), noted that "Years ago, the Yellow Lily root was as much a part of our daily diet as potatoes are today. They were one of the very important winter foods." In contrast, while the Tsilhqot'in did apparently use glacier lily bulbs regularly, this food resource was clearly eclipsed by the more abundant spring beauty corms as a staple vegetable (Alexander et al. 1985).

There are brief references in the literature to the use of glacier lily as food by other groups. According to Hart (1976:24), the bulbs served "only as an occasional food source to the Indian tribes of our region," most likely the Montana Salish groups (Kalispel, Flathead, Pend d'Oreille), and Ktunaxa ("Kootenai" in the U.S.).

Contemporary Montana Salish elder Mike Durglo said it was “candy once a year” (Sarah G. Thomason, pers. comm. 1998). Blackfoot use of the bulbs ("eaten fresh or with soup") was confirmed by Hellson and Gadd (1974:103), as well as by Johnston ("eaten occasionally") (1987:25); see also section 3.4). Peoples of Mendocino County, California, also ate the bulbs, "but not in large quantity" (Chestnut 1974:326); see also section 3.4. Hunn et al. (1990:172) include *E. grandiflorum* in a list of root vegetable species that "the most knowledgeable" Sahaptin elders recall as "rarely used species that were once valued more highly." The Carrier, Stó:lo (Upriver Halq'emeylem) and possibly Nuxalk peoples acquired the bulbs through trade (section 3.3.4). Kay's (1995) thesis on the Ulkatcho Carrier reported a low index of cultural significance for *E. grandiflorum*; it was a species "used occasionally or in trading." It is unclear why the plant was not used more extensively and intensively by groups in other parts of the present-day U.S. range. Possibly, there are differences in the accessibility, nutritional value or even toxicity of the bulbs in different areas. Alternatively, the great availability of camas (*Camassia* spp.) and a variety of *Lomatium* species at relatively low elevations across Washington, Idaho and Montana made these more attractive as staple root vegetables.

No direct archaeological evidence currently exists for use of glacier lily, so it is only possible to speculate about the length of human assocation with it. Interior Salish cooking pits with charred remains of liliaceous species (possibly including *E. grandiflorum*) have been dated to more than 2000 years BP and the oldest known cooking pits in south-central B.C. have been dated to 2500 BP (Pokotylo and Froese 1983, Peacock 1998). Use of the species may predate the oldest cooking pits, since people may have consumed the bulbs in other ways (section 3.3.3). Pokotylo and Froese (1983) found that the oldest pits they surveyed were the largest, and they believe that this suggests people once relied even more heavily on root vegetables than they did in the

early historic period.[1] Therefore, it seems reasonable to assume that intensive use of *E. grandiflorum* bulbs, at least among the Interior Salish, is not just a recent phenomenon (see also Peacock and Turner [in press]).

Linguistic evidence can also shed light on past patterns of use of a species. All known names for *Erythronium grandiflorum* in indigenous languages are listed in Table 3.1. The Interior Salish names are from three distinct etymons, and appear to be unanalyzable in any of the five languages, indicating a probable long-term association with the species (Turner et al. submitted). It is not clear whether the Flathead name was borrowed from the Kootenai, or vice versa. The similarity of the Carrier and Stó:lo names to the Secwepemc and Nlaka'pamux names, respectively, almost certainly results from the former groups' acquiring the bulbs by trade. The lack of a known name for the species among other groups within its range lends support to the idea that yellow glacier lily has always been little used outside the northern interior plateau.

3.3.2 Harvesting

Where? Examples of harvesting sites used by northern interior plateau peoples are shown in Figure 3.4, with further information about the sites given in Table 3.2. A particularly important gathering area is Botanie Valley, located in Nlaka'pamux territory, and described in a number of ethnographic sources (e.g., Dawson 1891, Teit 1900). For example, Teit (1900:294) noted:

> Botani Valley, situated in the mountains, some ten miles from Spences Bridge, and about fifteen miles from Lytton, has been from time immemorial a gathering-place for the upper divisions of the tribe, chiefly for root-digging during the months of May and June. Sometimes over a thousand Indians, representing all the divisions of the [Nlaka'pamux] tribe, would gather there.

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[1] "Given the time and energy invested in the construction and maintenance of such large facilities, as well as the anticipated scale of root collecting necessary to fill the pits, we hypothesize that the period from ca. 300 B.C. to ca. A.D. 800 represents a time of more intensive root resource gathering, relative to the Kamloops Phase and the ethnohistoric period" (Pokotylo and Froese 1983:152).

Table 3.1 Names for yellow glacier lily (*Erythronium grandiflorum*) among aboriginal groups of northwestern North America (names refer to bulbs unless otherwise noted).

Group (language family)	Indigenous name(s)[1]	Reference(s)
Secwepemc (Interior Salish)	**scwicw** above-ground parts: **sxwexwúpiya?**	Palmer (1975b), Kuipers (1983), SEP (1993-1997)
Nlaka'pamux (Interior Salish)	**s/k'ém'ets** "small ends of corms" (may refer to bulb-appendages): **k'əm'·/k'em'ets-=ú[·c]pe?**	Turner et al. (1990)
St'at'imc (Interior Salish)	**(s-)k'ám'ts**	Turner et al. (1987)
Okanagan (Interior Salish)	**scwicw**	Turner et al. (1980)
Tsilhqot'in (Athapaskan)	**?əsɣ̲huynsh**	Linda and Helena Myers, pers. comm. to Nancy Turner (1988); R. Tyhurst (unpub. field notes 1975-1976)
Ulkatcho Carrier (Athapaskan)	**swih**	Kay (1995)
Stó:lo, or Upriver Halq'emeylem (Coast Salish)	**sk'ámeth**	Stó:lo Nation (1982)
Flathead, Pend d'Oreille, Kalispel (Interior Salish)	**/máx̲e?e/**	Hart (1974), Montana Salish elders (as reported by Sarah G. Thomason, pers. comm. 1998)
Kootenai (Montana Ktunaxa; linguistic isolate)	**/máx̲a/**	Hart (1974), Kootenai Culture Committee (via Dorothy A. Berney, pers. comm. 1998)
Sahaptin (Sahaptian)	**h^{w}ík'^{w}k**	Hunn et al. (1990)

[1]Orthography has been modified in some cases for consistency.

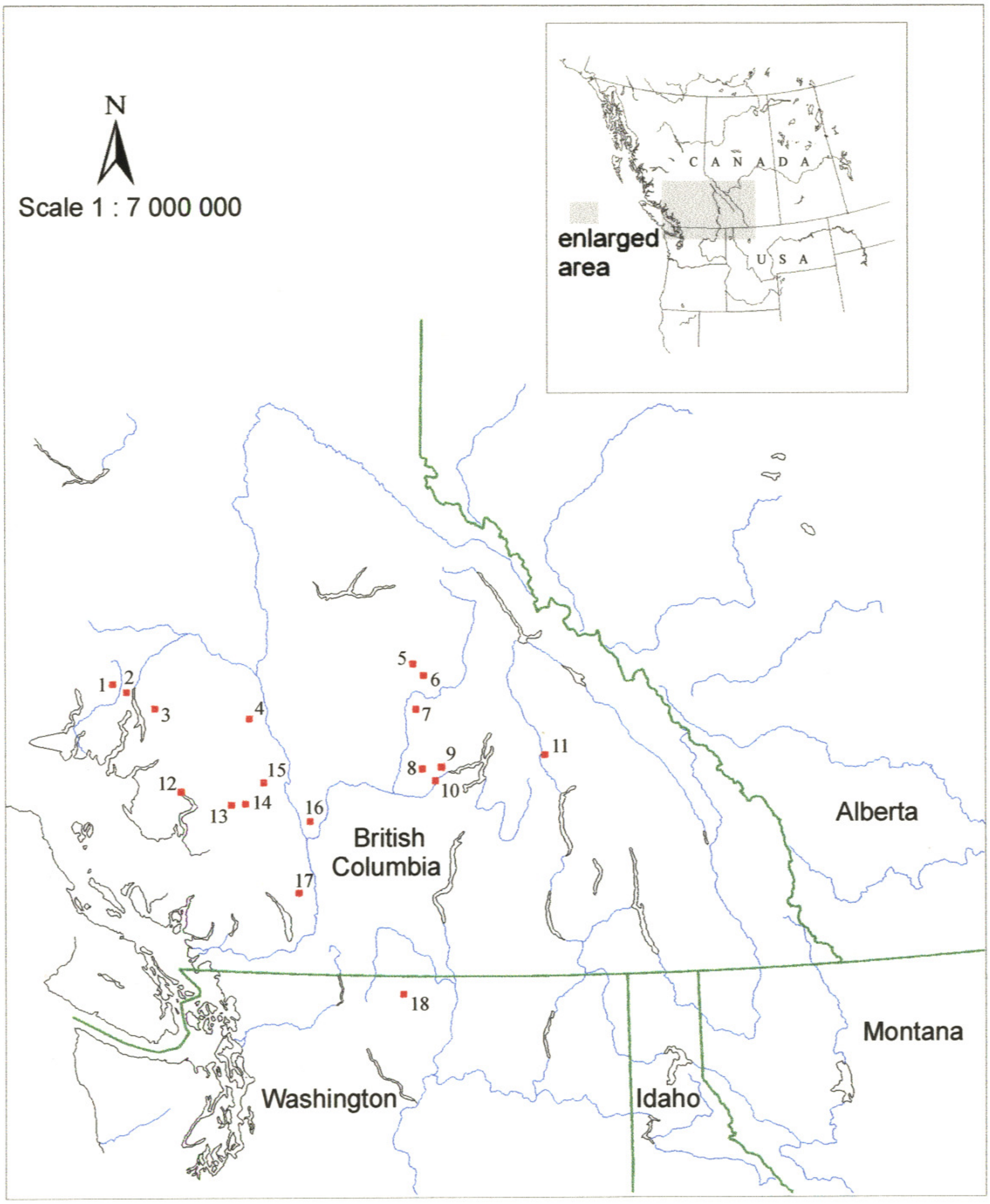

Figure 3.4 Some areas traditionally used by interior plateau peoples for harvesting bulbs of yellow glacier lily. See Table 3.2 for information corresponding to these numbered sites.

Table 3.2 Details regarding yellow glacier lily harvesting sites shown in Figure 3.4. Note that these sites are given as examples only; many additional areas for gathering the bulbs were and are known.

Site no.	Site description	Group/s using site	Reference
1	West side of Tatlayoko Lake	Tsilhqot'in	Alexander et al. (1985)
2	Cheshi Pass (in Potato Range)	Tsilhqot'in	Alexander et al. (1985)
3	Mt. Tatlow	Tsilhqot'in	Alexander et al. (1985); Glavin et al. (1992)
4	Black Dome Mountain	Secwepemc	SEP (1993-1997)
5	Green Mountain	Secwepemc	SEP (1993-1997)
6	Trophy Mountain	Secwepemc	SEP (1993-1997)
7	Baldy Mountain	Secwepemc	SEP (1993-1997)
8	Mt. Tod	Secwepemc	SEP (1993-1997)
9	Sidehills east of Adams Lake	Secwepemc	Palmer (1975b); Arcas Consulting (1990)
10	Neskonlith meadows	Secwepemc	SEP (1993-1997)
11	Mt. Revelstoke and area	Secwepemc	SEP (1993-1997)
12	Enderby/Mabel Lake area	Secwepemc	SEP (1993-1997)
13	56 km up Lillooet River from Pemberton	St'at'imc	Mack (1977)
14	West of Birkenhead Lake	St'at'imc	Mack (1977)
15	South side of the reserve at D'Arcy	St'at'imc	Mack (1977)
16	Mission Ridge	St'at'imc	Turner (1992)
17	Botanie Valley (north of Lytton)	Nlaka'pamux and others	Teit (1900); Turner et al. (1990); Hanna and Henry (1996)
18	Mountains behind Thompson Siding	Nlaka'pamux	Turner et al. (1990)
19	Headwaters of Spuzzum Cr.	Nlaka'pamux	Turner et al. (1990)
20	Methow Valley	Okanagan	Spier (1938)

Even in modern times, elders still vividly recall gatherings in Botanie Valley, as illustrated in the story "Trips to Petani," told by Mary Williams, and translated by Mamie Henry (Hanna and Henry 1996:149):

> In the month of August, the people gathered up in Petáni [Botanie Valley]. People gathered from all over - Spences Bridge, Nicola, and 30 Mile [30 miles north of Lytton on the Fraser River]. . . . Then the people dug roots such as **sk'ám'ats** [*Erythronium grandiflorum*], **tatúwen'** [*Claytonia lanceolata*], water leaf [*Hydrophyllum capitatum*], and tiger lily [*Lilium columbianum*], and gathered all the other kinds of food found there. They shot deer and roasted them over open fires. . . . My, we used to have nice times in those days!

Similarly, Louie Phillips (Turner et al. 1990) recalled good times in the valley, when people gathered to harvest, trade, socialize, and compete in activities such as horse races. Some women would dig **s/k'ém'ets** [*E. grandiflorum* bulbs] by the sackful on the valley sides, and bet their day's harvest on the horse races.

It is clear that harvesting of "roots" like glacier lily bulbs was not solely a subsistence activity, but rather was embedded in a cultural context of other economic and social relations.

When? There are two interrelated aspects to the seasonality of harvesting root foods like the glacier lily: the time of the season (later at higher elevations), and the phenology of the species. As shown in Figure 3.3, root harvesting could take place throughout the growing season, partly because of the different times when different species became available at a given elevation. Also, some individual species (including glacier lily) occur at a range of elevations, and people could follow these up into the mountains as they became available later in the season.

Some sources indicate only a time of the season when lily bulbs were harvested. For example, Teit (1900:238) stated that root foods (including glacier lily) were gathered by the Nlaka'pamux in the early summer and fall of the year. For the Okanagan-Colville, the bulbs were "one of the first foods to be collected in the spring," right after the snow,

from early April and May to the end of June, or even July (Turner et al. [1980:46], and sources cited therein). Similarly, the St'at'imc harvested glacier lily bulbs from June to August (Turner 1992).

Other sources indicate a stage of growth when the lilies were harvested. It appears that in some cases, people dug the bulbs when the plants were flowering. According to some contemporary Montana Salish elders, the bulbs are best in spring, "just when it starts to bloom"; they felt that the the bulb gets woody if one waits too long (Sarah G. Thomason, pers. comm. 1998). The Tsilhqot'in harvested glacier lily bulbs and spring beauty corms (*Claytonia lanceolata*) during the blooming season, "the only time of year when these plants are visible" (Alexander et al. 1985:46). The latter statement is in fact more accurate for spring beauty, as the fruiting capsules of glacier lilies remain upright and readily visible for at least two months after flowering. The reference to spring beauty is important, however, as these two species commonly occur and flower together, and were harvested together by all peoples known to have used glacier lily.[1] The fact that the two root foods could be harvested simultaneously enhanced the importance of each; a given amount of harvesting effort would result in essentially double the return. Therefore, in some cases, the desire to harvest both species may have led people to do so at a stage (full flower) when it was practical for spring beauty.

A number of other references indicate that the preferred stage for harvesting glacier lily bulbs was after flowering, when the leaves were fading and fruits were starting to form. Isaac and Adeline Willard (Secwepemc; Palmer [1975b:54]) stated that the bulbs were dug on the sidehills in the vicinity of Adams Lake in May and June, "when the leaves are all withered." According to Annie York (Nlaka'pamux[2]; Turner et al. 1990:123]), fall was the usual time for them to be dug, "...when they're picking those

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[1]Secwepemc elder Mary Thomas refers to glacier lily and spring beauty using the Secwepemc word for "sisters," indicating the close association between these species perceived by interior peoples.

[2]I do not mean to imply that Nlaka'pamux people in general harvested the plants after flowering. Hilda Austin, another Nlaka'pamux elder, noted that the bulbs could be collected when the plants were still in flower (Turner et al. 1990). Again, it is possible that the stage of harvest was to some degree influenced by external factors.

huckleberries up on the mountain." Since huckleberries (*Vaccinium membranaceum*) are just starting to leaf out when *Erythronium* flowers, the lilies certainly would have been in fruit by the time the berries were ready. Again, glacier lily harvesting was not done in isolation; the availability of other foods in the same area probably often played a role in determining at what stage glacier lily bulbs were harvested.

Yet, according to Mary Thomas, an extremely knowledgeable Secwepemc elder, there was a definite stage that was optimal for glacier lily harvesting (SEP 1993-1997). Mary has emphasized that when the leaves begin to dry up and wilt, the sugar content in the **scwicw** [*E. grandiflorum* bulbs] is highest. Earlier, when the plants are flowering, the sugar content is lower. However, Mary's mother had told her, and showed her, what the bulbs are like if one waits too long to harvest (i.e. late in the season, when the fruits are fully mature and the leaves have completely disappeared). At that point the bulb is preparing to grow for the next year, and the part of the bulb around the flower stem starts to get clear and mushy. The bulbs then develop a funny taste and do not have a good crisp texture.

Who? The different peoples known to have used the bulbs have been identified previously. However, not all members of each group shared equally in the work of harvesting root vegetables. Among all the peoples of the interior plateau, there was a strict division of labour, as put forth in the Nlaka'pamux story of a creator called "Old-One" (Teit 1912a:321):

> After this, the earth gave birth to people, who were very similar in form to ourselves, but they knew nothing, and required neither food nor drink. They had no appetites, desires, knowledge, or thoughts. Then Old-One travelled over the world and among the people, giving them appetities and desires . . . He taught the women how to make birch baskets, mats, and lodges and *how to dig roots*, gather berries, and cure them. He taught the men how to make fire, catch fish, shoot, snare, trap and spear game . . . [emphasis mine]

It was therefore largely women's work to gather and process root vegetables such

as glacier lily bulbs (Dawson 1891, Teit 1900, 1906, 1909, Alexander et al. 1985), although children would often help (Mary Thomas [SEP 1993-1997]). Also, for the Okanagan, at least, entire families would sometimes participate in large harvests (Turner et al. 1980).

How? The root-digging tool common to all peoples of the Pacific Northwest was the digging stick, or root-digger (descriptions may be found in most of the ethnographic and ethnobotanical sources to which I refer in this chapter). Various materials could be used to construct it, but in the interior, it was essentially a pointed stick of some hard wood (e.g. saskatoon, *Amelanchier alnifolia,* or hawthorn, *Crataegus douglasii*) or antler, with a cross-piece of wood or bone fitted at the other end to form the handle. The stick was sometimes curved, and the tip was often fire-hardened. After European contact, the shaft was often made from iron, for example the tine of a hay rake. Various sizes of digging sticks were used; Teit (1900, 1909) states that Nlaka'pamux digging sticks were about two to two and a half feet (60 to 76 cm) long, while Secwepemc sticks were about four feet (122 cm) long. However, other sources indicate that Secwepemc digging sticks varied. According to the Willards (Secwepemc; Palmer 1975b), different sizes of digging sticks were used for different types of roots. Yellow glacier lily bulbs were dug with the longer sticks, about 25 in. (64 cm) in length, while spring beauty corms, being shallower, were dug with shorter sticks.

Bulbs were located either by means of flowers, or by the fading leaves or fruit capsules, depending on the growth stage when gathered (Turner et al. 1990). They were harvested by prying with the digging stick, or by loosening a chunk of turf and breaking off the bulbs from the soil underneath (Turner et al. 1990, SEP 1993-1997). One Nlaka'pamux elder noted that the bulbs were much easier to dig when the ground is moist and soft (Turner et al. 1990). Some elders have stated that unwanted vegetation, such as grass, was deliberately "weeded out" during the harvesting process (SEP 1993-1997).

The bulbs were dug selectively; only the largest bulbs were harvested, and these were recognized as being associated with multiple-flowered or -fruited plants (Mary

Thomas [SEP 1993-1997], Turner et al. [1990]). Smaller bulbs were purposely left behind to regenerate. For example, both Mabel Joe and Annie York (Nlaka'pamux; Turner et al. 1990:28) said that it was considered important to "leave some for next year." Mary Thomas recalled that her grandmother would remove small bulbs from the children's harvesting baskets at the end of the day and replant them. She also replanted the "little whiskers" or **supupts'its'i** (bulb-appendages with roots attached) on plants like **scwicw** (*E. grandiflorum*), and the tiny bulblets of riceroot (*Fritillaria lanceolata*). Elders Sarah Denault and Les Williams have confirmed the practice of replanting bulb-appendages of **scwicw** (SEP 1993-1997). The existence of a Nlaka'pamux name for "small ends of corms" (Table 3.1) suggests that the appendages had some importance to that group of people as well. Mary Thomas and Les Williams (SEP 1993-1997) remembered that the harvests were rotated; a given gathering area would be left for four or five years before being used again. When people returned to that area, according to Les Williams, the glacier lilies would be "just thick."

How much? As previously noted, the amounts gathered may have changed significantly over the hundreds or thousands of years the species has likely been used, and decreased dramatically in the past 100 years. However, estimates provided by elders within the past 30 years give an idea of the likely minimum magnitude of the harvest. Mary Thomas (SEP 1993-1997) remembers going by horseback with her family to montane gathering grounds, and riding back on gunny sacks full of the bulbs. This perception is not likely to have been exaggerated. Independent reports from Nlaka'pamux (Louie Phillip in Turner et al. [1990]) and Secwepemc (Willards in Palmer [1975b]) sources indicate that four 50-pound potato sacks (90 kg) would be an average harvest by a single family group for their winter supply. This much could be harvested in perhaps 10 days to 2 weeks. Most of the harvest does appear to have been for winter use, but people consumed additional, unknown amounts during the growing season as well (Turner et al. 1990).

Such (minimum) quantities would apply to people with ready access to prolific

root grounds. In other areas, where the glacier lily resource was less abundant, acquired mainly by trade, or overshadowed by a more dominant root food, lesser quantities would have been harvested. Any of these scenarios may have applied to the St'at'imc, for whom it has been estimated that 5 to 20 kg of the bulbs were collected per family in historic times (Turner 1992).

3.3.3 Processing, Storage, and Preparation

Since most of the harvest was apparently for winter use, the bulbs had to be preserved in some way. This could be accomplished by drying alone, or by drying before or after steam-cooking the bulbs in an earth oven (pit-cooking; Figure 3.5). According to Teit (1909:516), nearly all roots were threaded on strings before cooking in earth ovens. Elders (SEP 1993-1997, Turner et al. 1987, 1990) have indicated that bulbs were left to wilt for a day at the harvesting grounds to soften them, so that they could be threaded (without breaking) on strings of maple bark (*Acer glabrum*), red-cedar bark (*Thuja plicata*), Indian-hemp (*Apocynum cannabinum*), willow bark (*Salix* sp.) or silverberry bark (*Elaeagnus commutata*), or on long thin sticks. After threading, it may have been most common for the bulbs to be pit-cooked before further drying. Archaeological evidence (Pokotylo and Froese 1983, Alexander et al. 1985) suggests that, at least 2000 years ago, root vegetables were processed by roasting in earth ovens close to the montane harvesting grounds. Dawson (1891:9) noted that "root-baking places are usually in the vicinity of root-gathering grounds." After baking, Dawson continued, the roots (including glacier lily bulbs) are taken out and "either at once eaten or dried for future use." Bulbs that were wilted, strung, pit-cooked, and dried would have been in a convenient form and light in weight for transport back to the winter dwellings for storage.

In this regime, pit-cooking would have acted not only as a preparation method but also as part of the preservation process (Laforet et al. 1993, Wandsnider 1997). Tsilhqot'in sources cited by Alexander et al. (1985) maintained that, in fact, pre-cooking was *necessary* for most root vegetables (including glacier lily bulbs) before drying; only

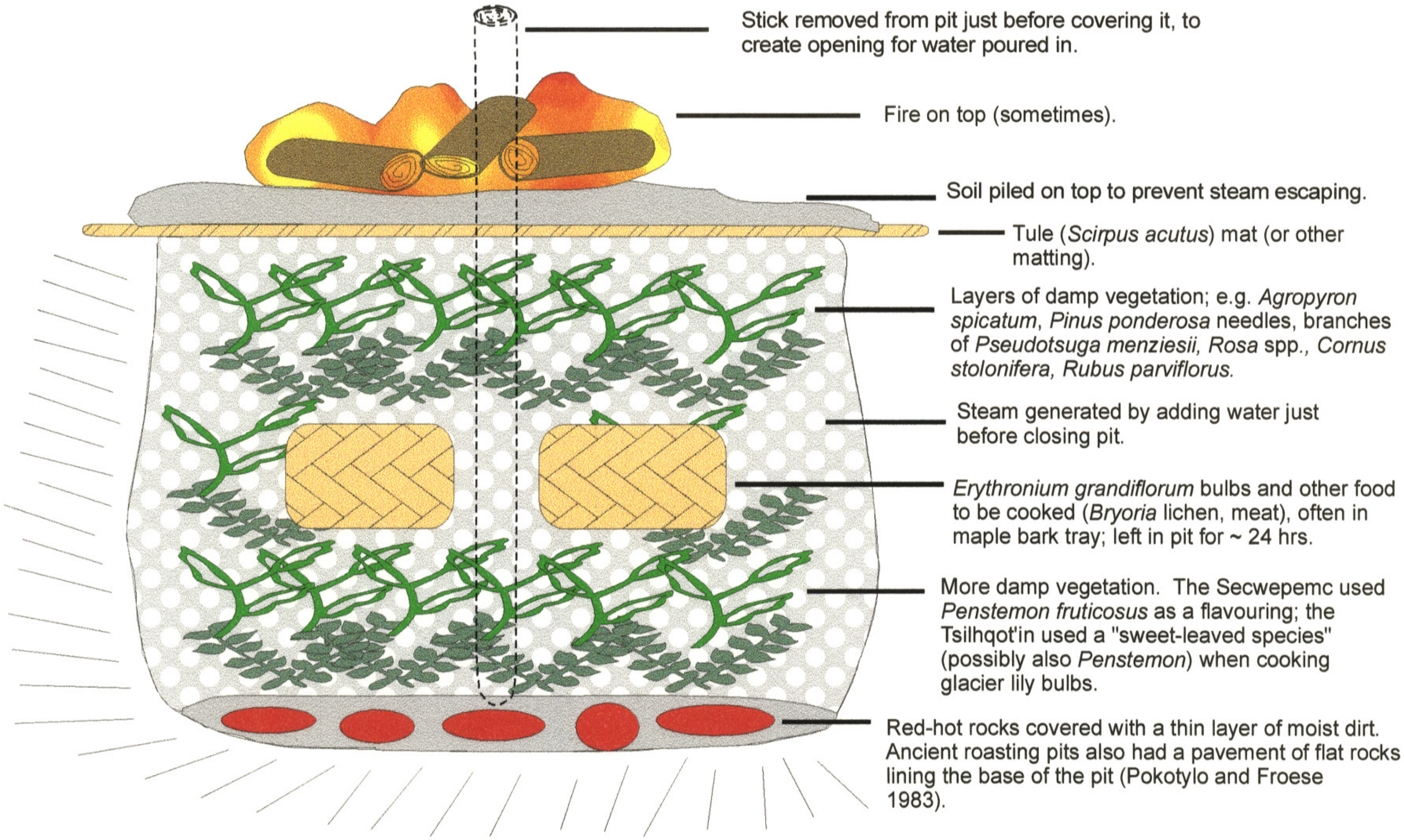

Figure 3.5 Schematic diagram of the type of roasting pit used by northern plateau peoples, based on descriptions by Mary Thomas, Aimee August (SEP 1993-1997), and others (Alexander et al. 1985, Turner et al. 1990).

for *Claytonia lanceolata* corms was this not the case. Annie York and Mary Anderson (Turner et al. 1990) have also indicated that their families pit-cooked the bulbs immediately, then dried them for storage.

Other preservation and processing strategies have also been reported. According to Okanagan and Secwepemc elders (Turner et al. 1980, SEP 1993-1997), the bulbs could be boiled or steamed (rather than pit-cooked) and then either eaten or dried for future use. Also, peoples from many groups partially dried the bulbs, without cooking them, at the harvesting grounds. The bulbs would be strung and hung up until the root gathering was completed, then transported back to the winter sites. There the strings of bulbs would be hung again to finish drying (often in the presence of smoke, to cure them and deter insects), and stored for later pit-cooking or other cooking. Drying took up to two weeks (Spier 1938). The bulbs could also be dried unstrung and stored in sacks made of silverberry fibre or tule stalks (*Scirpus acutus*). Annie York described another storage method, in which a number of cooked and dried foods, including salmon and glacier lily bulbs, were placed between layers of birch bark and stored on scaffolding (Turner et al. 1990).

Yellow glacier lily bulbs could also be stored fresh. Mary Thomas (SEP 1993-1997) described a type of "root cellar" used to store fresh roots:

> But some of the, most of the **scwicw** [*E. grandiflorum* bulbs] - if they're going to spend a week up there, the first ones they dug, yeah, they would have to dry them, and then the last day or two, when they were planning to come back, then they'd bring back the fresh ones. And if you don't break the **scwicw**, if it's not broken, you leave it with, you know, the dirt on it and the top, and if you put it away like that, they keep for a long time - you can keep them in pits. When they bring it back - I remember my grandma used to have a pit down by the river. If you dig a hole in the ground and you get - what do you call it - we call it **kéme** [dry pine needles]. My grandma used to gather all that and bring it back and put that on the bottom, and then put a little bit of dirt, and then put the **scwicw** and **sqwaqwina** [*Claytonia lanceolata* corms] in a pit and then bury it - put some more **kéme**, dry leaves, she'd put another bunch on top, and bury it - say about a good foot deep. As long as it's buried it will keep for a long time. I guess when you talk about the winter houses, the depression of a winter home, it was found that there were a lot of small

> ones [depressions] around the outside of the main winter home - those were used as their cache pits. I asked my mom about that one time, I said what were they used for and she said well you got cellars today - they had cellars then too. So that's the way they were put away.

Similarly, Hill Tout (1978b:109) noted that the St'at'imc stored roots in shallow cellars dug beneath the sleeping platforms of winter pit-houses. The use of these types of cellars or cache pits is certainly ancient, since (as Mary indicated) they have been uncovered archaeologically. However, it is not clear to what extent they were used for fresh, as opposed to processed, roots. It is possible that transporting and storing fresh roots became more common once the horse was introduced, since the weight of the roots would not have been as much a concern. For example, Nlaka'pamux elder Christine Bobb mentioned that when they went up in the mountains to collect different foods, they packed everything out with horses. Then, at home, they prepared and dried the food, and "when it was almost wintertime" they pit-cooked things like **s/k'ém'ets** (Hanna and Henry 1996:148).

A variety of methods were used to prepare the bulbs for eating. Dried bulbs were often partially reconstituted with water before pit-cooking (Palmer 1975b, Turner et al. 1990), although Mary Thomas feels that the steam from the pit is sufficient to do this as long as the rocks are very hot. In addition, dried bulbs (or pit-cooked, dried bulbs) were commonly boiled or steamed, or added to soups and stews. The reconstituted bulbs could also be eaten as a side dish with meat or fish, "like potatoes," according to Mary Anderson (Turner et al. 1990). Annie York stated that a family of four might eat a string of bulbs about 20 cm long as part of a meal (Turner et al. 1990); this probably would have been about 10-12 bulbs, or about three each. Fresh bulbs were also prepared and eaten in these ways, or could be roasted in hot coals, during the harvesting season (Surtees 1974). Eating raw bulbs was uncommon; Mary Thomas remembers casually nibbling on raw glacier lily bulbs as a child, but says that they tasted very different from the cooked ones. Annie York (Turner et al. 1990) felt that the bulbs were poisonous if eaten raw. However, she viewed *Erythronium oregonum* as being the same as *E.*

grandiflorum, only with white flowers that developed at low elevations, and section 3.5 describes the possible toxicity of the *E. oregonum.*[1] The Kootenai apparently ate the bulbs raw; but it was not an important food source for them (Kootenai Culture Committe, via Dorothy A. Berney, pers. comm. 1998).

Cooked bulbs were generally highly appreciated as a tasty food, and both drying and pit-cooking were perceived to be important in developing a sweet taste. Mary Thomas (SEP 1993-1997) said, referring to glacier lily bulbs, ". . . if you dry the natural foods and then steam it afterwards it has its own sugar content - you don't need to put any sweetener." Louie Phillips (Turner et al. 1990) stated that bulbs cooked and eaten immediately after harvesting were not as sweet and good as those that had been stored first. The sweetness of the dried bulbs is also indicated by Bernadette Antoine (Nlaka'pamux) in the following quote, though she may have been referring to bulbs that had been previously pit-cooked:

> . . . when they're dried, they're like candy . . . when I was a kid I used to get some from my uncle and eat it . . . it takes a while to soak it in your mouth when it's dry . . . then they taste sweet. . . . We used to call it candies when we were kids. (Turner et al. 1990:122)

Pit-cooking had a distinct effect on the bulbs, making them dark coloured and sweet, "like chocolates" (Louie Phillips in Turner et al. [1990:29]). Boiled bulbs, on the other hand, did not change colour and were not as sweet (Mary Thomas in SEP [1993-1997]). (See Chapter 4 for further discussion.)

Some particular dishes mentioned by Nlaka'pamux elders include bulbs marinated in saskatoon berry juice (*Amelanchier alnifolia*) (Laforet et al. 1993), and a special type of pudding called **n/kéxw** (Turner et al. 1990). It is made by boiling together some combination of the following ingredients: marrow of deer, bear, or mountain goat; deer fat; cured salmon eggs; processed black tree lichen (*Bryoria* sp.); dried saskatoon berries;

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[1]Hart (1976:24) states, "The [raw] bulbs and leaves [of *E. grandiflorum*] occasionally impart a burning sensation, however, and some have even found them to be emetic (causing vomiting) if taken in quantity." No further information or references are given. I have never noticed these effects in my own experiences eating the plant.

yellow glacier lily bulbs; spring beauty corms; tiger lily bulbs (*Lilium columbianum*); chocolate lily bulbs (*Fritillaria lanceolata*); and bitterroot roots (*Lewisia rediviva*). Glacier lily bulbs were also often cooked and eaten together with only black tree lichen. The Carrier people ate them, as they ate many other root vegetables, with eulachon fish oil, salmon oil, or bear grease (the first was imported from the coast) (Harlan Smith, unpublished notes on Carrier plant use ca. 1920-1922).

The bulbs were even used as the proverbial spoonful of sugar to help the medicine go down. According to the Willards (Palmer 1975b) and Aimee August (SEP 1993-1997), "bisquit root" (or chocolate-tips, *Lomatium dissectum*) was bitter, but was eaten occasionally for its tonic properties. A taste could be developed for the bitter roots, but glacier lily bulbs were often eaten along with them to make them more palatable.

The general perspective on the prepared bulbs is well summarized by Annie York:

> The man eats first. He eat a little piece of meat, and **tetuwn** (*Claytonia lanceolata* corms), and then when he's got through eating that, then they eat the **s/k'ém'ets** [*E. grandiflorum* bulbs]. And that's their dessert, the **s/k'ém'ets** is their dessert . . . (pers. comm. to Nancy Turner, 1980).

3.3.4 Trade

Strings of threaded, dried yellow glacier lily bulbs, of measured length from hand to elbow, were an important trading item on the northern interior plateau. They were widely traded within and among Interior Salish groups (Teit 1900, 1906, 1909). For example, they were a common item of trade at Botanie Valley (Turner et al. 1990), along with *Claytonia lanceolata* corms and *Frtillaria lanceolata* bulbs. Teit (1906:231-232) notes that the Upper Lillooet (St'at'imc) traded "*Erythronium grandiflorum* var. *minor* and other kinds of roots" along with Indian-hemp fibre, dried saskatoon berries, soapberries (*Shepherdia canadensis*), dried meat and fat, and other products, to the Lower Lillooet (Lil'wet'ul). In return, they received red-cedar bark, yew wood (*Taxus brevifolia*), black-tail deer skins, hazelnuts (*Corylus cornuta*), dried huckleberries (*Vaccinium* spp.), fish oil, and even slaves. According to the Willards (Palmer 1975b), a big string of *Erythronium* bulbs about one metre in diameter was worth $5 in the late 19th

century.

The bulbs were also traded farther coastward and northward. The Stó:lo (Upriver Halq'emeylem) acquired them from the Nlaka'pamux (Stó:lo Nation 1982), and the Carrier obtained them from the Tsilhqot'in (Harlan Smith, unpublished notes on Carrier plant use ca. 1920-1922). The Nuxalk may also have obtained them through trade. While there is no known Nuxalk name for yellow glacier lily, Felicity Walkus and Andy Schooner (Nuxalk; Turner 1973:211) recalled a type of "Indian potato" that was long and tapered. Felicity did not recall ever seeing the plants and suggested they might have been obtained via trade. On the basis of the elders' descriptions, Nancy Turner (pers. comm. 1998) believes that the plants in question were *E. grandiflorum*.

Much exchange in plant goods, including glacier lily bulbs, was also informal. Mary Thomas has described reciprocal "sharing" of plentiful items (including **scwicw**) that were valued by friends and relatives living in other areas, and has emphasized how important sharing has been as a general ethic of her people (see also Turner and Loewen in press). This type of exchange has persisted to the present day (see section 3.3.7).

Trade of the bulbs has a number of implications. First, it underscores the size of the harvests; people regularly gathered so much that they could afford to use some as "surplus," to obtain other desired items. Second, it means that the effective range of use of the species was much greater than it might otherwise have been. Third, the very fact that the bulbs were in demand as a trade item emphasizes the extent to which they were favoured as a food resource.

3.3.5 Traditional Resource Management and Other Traditional Ecological Knowledge

Indigenous peoples, having occupied a given area for generations, acquire a great deal of ecological knowledge. Northern plateau peoples' knowledge of glacier lily ecology serves as a good example and much traditional ecological knowledge (TEK) is apparent from the above discussion. People had to have an intimate knowledge of the growth characteristics of the species in order to know when, where, and how to harvest it so that it yielded maximal food value and remained prolific in future years (see also

Chapters 4 and 5). As well, people had knowledge of the plant's interactions with other species. For example, Lil'wet'ul elder Alec Peters remembered seeing grizzly bears dig the bulbs and then leave them to wilt before coming back to eat them (Turner 1997b:34):

> In a certain time of the years they pick it. . . . The oldtimers used to pick it and dry it for winter use. I know the grizzly bears they dig it out too. They use their big claws like that [raking motion], and they just leave it like that in the sun, you know. I guess they must taste good when they're dry. They don't eat it right away. I've watched them. A long time, I've watched the grizzly bear, digging it out. I've seen them **k'ám'ts** [*E. grandiflorum* bulbs] laying like that . . .

Isaac Willard (Secwepemc) also knew that grizzly bears ate yellow glacier lily bulbs; he remembered seeing the animals in May and June on the sidehills around Adam's Lake, where there are only cattle now (Palmer 1975b). Basil White (Kootenai) recalled being told as a child, "Don't you go near," as these plants were grizzly food (Kootenai Culture Committee, via Dorothy A. Berney, pers. comm. 1998). Close observation of animals such as grizzly bears may have led people to try the bulbs as a food resource in the first place (Turner 1997b).

An even broader level of knowledge is indicated by the management strategies indigenous peoples have applied to the habitats in which food resources occur. Burning was widely practiced by the peoples of the interior plateau (before governmental fire suppression) to maintain open habitats for growth of berry and root crops, and to facilitate travel and hunting (Turner 1991). Burned areas were rotated (any given site burned about every four to five years), and maximum productivity of certain root and berry species was said to occur after about three years. Contemporary elders recall that the edible portions of root plants were notably larger after burning (Baptiste Richie and Julia Kilroy, cited by Turner [1991]). Mary Thomas (SEP 1993-1997; pers. comm. 1998) believes that the ashes from fire add "food value" to resource plants like huckleberries and **scwicw**, and also that fire helps reduce populations of insect herbivores. Successful burning requires detailed knowledge of plant ecology, including concepts of ecological succession, geographic and climatic characteristics of the area to be burned, and responses of

individual plant and animal species to fire.

Like Mary Thomas (above), a number of other elders explicitly recognize yellow glacier lily as a resource species enhanced by landscape burning. Annie York (Nlaka'pamux) noted the importance of burning for maintaining habitats for root, berry, and nut plants, adding, "And the **s/k'ém'ets** [*E. grandiflorum*], that's when it grows, when you burn" (Turner 1991:63). Both Mary Thomas and Annie York mentioned that burning took place at a specific time of year, when people knew that the rains were coming. Baptiste Richie, a Lillooet elder, has given detailed information regarding burning, including the following (Turner 1991:62):

> When it gets too bushy, then the ripe berries disappear and the roots like **s/k'ém'ets** [*E. grandiflorum*], **swenkwina** [*Claytonia lanceolata*], **skimuta** [*Lilium columbianum*] disappear. . . . Then they burned. It was marked out, and there one did his own burning.

Early ethnographic sources confirm this practice. For example, Teit (1900:230) said of the Nlaka'pamux, "They sometimes set fire to the woods in order to secure a greater abundance of roots on the burnt hillside." Teit (1898:72-74) also recorded a story involving four brothers who "burned a piece of the mountain side so that the **s'ka'mitc** root [*E. grandiflorum*] should yield a better crop, and it was here that the little sister went to dig roots." Four grizzly bear sisters later "came to the spot which had been burned, and found the **s'ka'mitc** root very plentiful."

In modern times, TEK also includes observations regarding habitat degradation, and resulting impacts on traditional food species such as *Erythronium*. Such degradation, it is believed, has occurred partly due to cessation of traditional management practices. For example, Annie York (Nlaka'pamux) stated that edible roots are not as plentiful now because burning is not allowed (Turner et al. 1990). Similarly, Baptiste Richie noted, "Now they [root food species including *E. grandiflorum*] have disappeared because the hills grew weedy and no-one seems to tend them, no-one clears there as our forefathers did so thoroughly" (Turner 1991:62).

Modern disturbances, particularly cattle overgrazing and introduced weeds, have also been recognized as negative influences on resource species and their habitats. Mary Thomas (SEP 1993-1997) is concerned that glacier lilies are not producing nearly as much seed as formerly. She has also noted the effects of invading couch grass (*Agropyron repens*) and other weeds, as well as trampling by cattle, in creating a tough turf layer. It is no longer possible to use a digging stick in most traditional harvesting areas, and harvesting is even difficult with a sharp steel shovel or pick. Mary believes that this compacted turf layer has resulted in the bulbs' becoming smaller and more deeply buried. On a field excursion in 1996, I dug a bulb that I considered exceptionally large - 9.5 cm long by 2 cm wide at its widest point. Mary commented that the bulb was representative of the average size collected formerly, and smaller ones (i.e. currently of average size) would have been left to regenerate. Other elders have also noted a decrease in size of the bulbs since traditional management methods stopped and foreign disturbances were introduced. According to an Okanagan source, the bulbs were formerly the size of one's fist (reference cited by Turner et al. [1980]). While it will never be possible to know exactly how large the bulbs once were and how they have changed over time, the consensus of opinion from many different First Nations sources supports the idea that there has been some noticeable decrease in bulb size.

It is important to realize the significance of elders' recollections of the former status of individual species and habitats (and/or their statements regarding *their* elders' recollections). For example, it would be easy for a modern botanist to assume that the current size of the bulbs in a given area has always been the average size. As long as glacier lilies are still growing in an area, there might be no reason to believe that any serious habitat degradation has occurred. In effect, TEK can help provide "baseline data" in examining changes over time.

The information presented in this section supports recent suggestions (Anderson 1993a,b, Anderson 1996) that "hunter-gatherer" peoples were much more than passively adapted to their environment. Rather, these peoples actively managed the landscape, and the "pristine wilderness" the first Europeans perceived appears to have been a gross

misinterpretation. This subject will be revisited in Chapter 5.

3.3.6 Rituals, Mythology, and Other Cultural Aspects

Not surprisingly, the high significance of root vegetables for plateau peoples is reflected in many rituals, stories, traditions, and other aspects of culture. Some of the following discussion relates to root vegetables in general, but clearly yellow glacier lily was one important member of this group.

"First Fruits" ceremonies are much more widely known than "First Roots" ceremonies (Palmer 1975b), though both have been (and sometimes still are) practiced (Hunn et al. 1998). Even where the ceremony was labelled "First Fruits," it appears that the sentiments expressed extended to other types of foods, including root vegetables. As noted by Hill Tout (1978a:46) for the Nlaka'pamux:

> But no one under penalty of a severe punishment could take a fish, pick a berry, *or dig a root* until after the Feasts of First Fruits had been held. . . . Exactly to whom these prayers were addressed my informant could not tell me. All I could gather was that the 'old Indians' believed in some great and beneficent power who dwelt behind the clouds, and who gave them the salmon, fruits, roots, etc., who, if they showed themselves ungrateful or unthankful, could, and might, withdraw his gifts from them. [emphasis mine]

Hill Tout later (p. 47) refers to the "Feast of Berries and Roots," indicating the generality of the ritual (he gives a similar report for the Okanagan on p. 134). Teit (1906:282) noted that, on the day when the St'at'imc held their First Fruits ceremony, they could not gather more berries than could be eaten the same night: "If they gathered more than this, they would afterwards be unlucky in procuring *roots* or berries" [emphasis mine].

There is one record of a ceremony just for glacier lily (Arcas Consulting 1990). Mary Arnouse recalled that when she was about 10 years old, she went with her grandmother to a place called **skwnu7tús** near the headwaters of Nikwikwaia Creek (east of Adams Lake). Here she saw a first-root ceremony carried out for **scwicw**, but this was

the only time she observed such a ceremony.

Various other traditions also involved glacier lily specifically. According to Teit (1900), the Lower Nlaka'pamux were commonly named for plants, and one such name translated as "Yellow-lily" (presumably *E. grandiflorum*). Times of the year were also named for significant plants like the glacier lily. Mary Thomas (SEP 1993-1997) called the month of May **scwicw-xwu** (month for digging **scwicw**), while the Willards (Palmer 1975b:54) called the "third month" (approximately April) **plhsxwixwm**, "when the Kamara roots [*E. grandiflorum*] are showing growth."[1]

Many stories mention the digging of glacier lily bulbs in passing as part of the tale, showing the everyday importance of the plant.[2] In "Coyote and the Two Sisters" (Hanna and Henry 1996), Nlaka'pamux elder Mandy Brown tells of two sisters who were harassed by Coyote on a trip to Botanie Valley to gather **s/k'ém'ets**. In the Lillooet story "Origin of the Skîmqai'n People" (Teit 1912b), the hero's wives "dug roots in great abundance"; these were spring beauty corms and glacier lily bulbs. The hero caused the roots to assume the size and weight of two small bundles, and later at home caused them to return to their original proportions, "and they filled many scaffolds." Glacier lily bulbs were also recognized as a favourite food of grizzly bears and this relationship appears in a number of stories (e.g. Teit's [1898:72-74] story "The Grizzly Bears and the Hunters," already mentioned in section 3.3.5).

In some stories, glacier lily plays a more prominent role. For example, the St'at'imc "Myth of the Deserted Boy," reported by Hill Tout (1978b:150), lists "**skamitch** (long carrot-like roots)" (*E. grandiflorum*) along with dried saskatoon berries and cured salmon as the three foods for which the gluttonous boy begged. Also, Teit (1912b:334) recorded the St'at'imc story "The Loon and the Woman," in which a woman

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[1] In more general terms, Dawson (1891:40) said that for the Secwepemc, the month approximately corresponding to May was called **Pit-la-kāt'-lai-a-hin**, "root-digging month." Also, Teit (1900:238) said that the Nlaka'pamux knew the seventh moon (again, approximately May) as the time when "the people dig roots."

[2]Many more stories must involve glacier lily, but do not specify the type/s of "roots" involved.

gathered **skemtc**-root (*E. grandiflorum*) every day near two small lakes (on the Upper Lillooet River, above Pemberton Meadows). "She was fascinated by them, and began to have amorous desires." She became Loon's lover, and as a result of this distraction kept returning home with only a small harvest of bulbs, arousing her husband's suspicion and ultimately leading to her demise.

The association of plant foods with women is also strongly reflected in various aspects of culture. The Sinixt (Lakes Okanagan) people traditionally celebrated the "fruitful season" with a ceremony in which women danced all day, while the men cooked and served food. All the food had to be eaten or burned, in order to ensure that the herbs, roots, and berries would be fruitful in the coming season (Turner et al. 1980). Nlaka'pamux and St'at'imc girls, as part of their ritual isolation during puberty, dug trenches in preparation for root-digging (Teit 1900, 1906). "Each day at dusk and at daybreak she prayed, 'O Day Dawn! (or 'O Dusk!' as the case might be) may I be able to dig roots fast and easily, and may I always find plenty!'" (Teit 1906:265). During their menses, Secwepemc women were required to live "principally on roots" and were forbidden to eat fresh meat (Boas 1890:90). Conversely, pubescent Nlaka'pamux and St'at'imc boys did not eat berries or roots, as these were believed to make them heavy and slow-footed (Teit 1900, 1906). For the Secwepemc, mourning the dead involved a 12 month taboo on berry gathering and root-digging, and since these were female activities, the injunction applied mainly to women (Palmer 1975b).

Pit-cooking, too, had a broader cultural context than simply its practical use, and is mentioned in a number of stories. For example, Dawson (1891) reported that the Secwepemc name for the Pleiades means "people roasting," and comes from a story in which a group of women who were baking roots in the ground became transformed into that group of stars. Strict taboos also surrounded pit-cooking; Boas (1890:85) noted for the Secwepemc:

> The belief prevails that the roots must be cooked in this particular way by women only, and early in the morning, before they have taken any food, as else they could not be properly done. No man is allowed to come near the place when they are being steamed.

Similar practices were followed by other Interior Salish groups (e.g. see Hill Tout [1978a:59]). Okanagan women had to observe certain proscriptions regarding cleanliness and fasting while pit-cooking, and were not allowed in the area during their menses (Turner et al. 1980). Additional types of cultural influences on the Nlaka'pamux food system (including animal foods) are discussed by Laforet et al. (1993).

3.3.7 Current Use

The bulbs of yellow glacier lily are little used today compared with their former status as a staple food. As noted above, habitat degradation has meant that the bulbs are much more difficult and time-consuming to gather. Also, of course, there are the usual factors that have caused a decline in use of traditional foods: decreased time for traditional activities due to participation in the modern economy; interrupted transfer of knowledge to younger generations (e.g. due to residential schools); decreased access to traditional harvesting areas; changing cultural acceptability and tastes; and ready availability of modern foods (Kuhnlein 1989, Hopkinson et al. 1995). Even in the late 19th century, when Dawson observed the Secwepemc, European flour and potatoes were rapidly replacing native root vegetables (Dawson 1891).

However, glacier lily bulbs are still highly valued on the northern plateau, particularly by the oldest generations of First Nations. The bulbs are harvested for traditional feasts, or even by some for more regular use. They are also exchanged for other highly valued foods (e.g. bitterroot) from elders in other areas, and may be given as gifts. Mary Thomas has transplanted yellow glacier lily plants to her garden in Enderby, and she also buries fresh bulbs collected elsewhere in her garden (her "root cellar"). Freezing is probably now the most common means of preservation, although some people still dry the bulbs. In the early 1980s, Annie York still used her traditional storage method (see description in section 3.3.3), but with layers of heavy brown paper instead of birch bark (Turner et al. 1990). Even canning has apparently been used. Pit-cooking is rare (largely ceremonial or for cultural education); the bulbs are now generally boiled or

steamed, or sometimes deep-fried (Turner et al. 1990). The traditional pudding described earlier was still being prepared by Hilda Austin and Annie York in the early 1980s, with sugar added and flour often substituted for black tree lichen (Turner et al. 1990).

It is possible that use of glacier lily bulbs and other traditional root vegetables will increase, as First Nations reclaim their cultures and take renewed pride in the ways of their ancestors.

3.4 Medicinal Use of Yellow Glacier Lily

There are only a few accounts of medicinal use of *Erythronium grandiflorum*. The Wailaki, an Athapaskan group of northwest California, used the crushed bulb as a poultice for boils (Chestnut 1974).[1] Futhermore, they had "a peculiar superstition that if they wash themselves with a decoction of it they can stop a rattlesnake from having dreams, which, they say, make them more irritable and dangerous" (Chestnut 1974:326). Contemporary Montana Salish elders have also indicated that the bulbs were used medicinally by mashing and applying to swellings (Sarah G. Thomason, pers. comm. 1998).

Okanagan elder Selina Timoyakin stated that the bulbs were good medicine for a bad cold (Turner et al. 1980), but no further detail is given. Of the Secwepemc sources, Bill Arnouse remarked that the plant was good for a cold (part of the plant not specified), and Aimee August indicated that the plant was "a good medicine" (SEP 1993-1997).

Aimee August's statement requires further examination. While she might have meant that the plant was a good medicine in the sense of curing colds or other ills, one must be cautious in assuming a Western concept of medicine. In general, the Western view is that "food" and "medicine" represent independent, fairly well-defined entities. By contrast, in many First Nations cultures, this separation occurs to a lesser degree, and

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[1]The Chestnut reference (originally published in 1902) was cited by Blankinship (1905) in his "Native Economic Plants of Montana" as support for his statement that the bulbs were crushed and used as poultices for boils. Other reviews have since cited Blankinship for this use in Montana (e.g. Johnston 1987, Moerman 1986). It is not clear why Blankinship assumed that the Californian use applied to Montana peoples; however, as noted above, contemporary elders do support that assumption.

many plants are recognized as being useful both for their nutritive qualities and for maintaining good health. A variety of such "tonics" or health foods have been identified by Nlaka'pamux consultants; e.g., the fruits of hawthorn (*Crataegus douglasii*) or Oregon-grape (*Mahonia aquifolium*) (Turner et al. 1990). Hilda Austin, a Nlaka'pamux elder, explicitly stated, "Our food is all medicine. If you eat it often, that's a medicine." (Turner et al. 1990:43). Similarly, Aimee August (Secwepemc) has said that a variety of root vegetables (e.g. bisquit root [*Lomatium dissectum*], balsamroot, yellow glacier lily), "are all healing medicine, but food"; and of tiger lily, "it's good food and good medicine - to keep you healthy." Information presented in the next chapter suggests that modern science is beginning to develop this "functional food" perspective, which is relevant to the nutrients contained in glacier lily bulbs.

Nevertheless, given the above-mentioned suggestions of medicinal uses for glacier lily (as well as the medicinal uses of other *Erythronium* species - see section 3.5), researchers have pursued the possibility of more direct therapeutic qualities. Kelly Bannister, a doctoral candidate at the University of British Columbia and participant in the Secwepemc Ethnobotany Project, assayed many Secwepemc plant medicines for antimicrobial properties (Bannister 1998, pers. comm. 1998). Among these were *E. grandiflorum*, whose aerial parts and bulbs were assayed separately. The aerial parts showed antibacterial activity against all six bacterial species assayed, antifungal activity against two of five species assayed, and inconsistent antiviral activity (possibly due to deterioration during storage). The bulbs showed antibacterial activity against five species, antifungal activity against one species, and no antiviral activity.

While the active principles have not been fully elucidated, Diamond et al. (1985) found that *E. grandiflorum* (part of plant unspecified) contains alpha-methylene butyrolactone, which was shown to have slight antimutagenic activity. A previous study isolated this same lactone from all parts of *E. americanum*, and reported that it exhibited antibacterial activity (Cavallito and Haskell 1946). Other studies have found fungitoxic and allergenic activity associated with the compound (see Slob 1973). Stermitz et al. (1981) found that above-ground parts of *E. grandiflorum* contained relatively high

amounts of undetermined alkaloids, and that an extract had cytotoxic activity (but was not lethal for mice by intraperitoneal injection at the maximum dose of 400 mg/kg).

As Bannister (1998) stresses, it is not clear to what extent these results imply any therapeutic effectiveness *in vivo*; it can only be stated that the potential for such effectiveness exists.[1] In addition, the cultural context is always of the utmost importance. For glacier lily, it appears that, whatever the results of laboratory analyses, the significance of the plant for First Nations as an explicit "medicine" (in the Western sense) has been slight, while its importance as a "health food" has been widely recognized.

3.5 Ethnobotany of Other *Erythronium* Species

Information regarding uses of other *Erythronium* species is summarized in Table 3.3. The very fact that such a summary is possible indicates that the ethnobotanical importance of these species has been minor compared with that of *E. grandiflorum*, and/or that there has been little ethnobotanical documentation of these species. The first possibility is probably correct in most cases. As mentioned in Chapter 1, many of the other species are highly localized and simply would not represent a practical resource. However, for those species that are more widespread, the use may have been more extensive than the sparse information in the literature suggests.

Only one species (other than *E. grandiflorum*; see footnote in section 3.3.3) has been accused of ill effect, in the form of one instance of fatal poultry poisoning by bulbs of *E. oregonum* (Kingsbury 1964). It is possible that toxicity could account for the lack of use of *E. oregonum* by peoples of southern Vancouver Island; however, the dominance of camas (*Camassia* spp.) as a root food resource may also explain the apparent lack of interest. Also, as noted in Table 3.3, there is a vague reference (Brown 1868) to the use of the bulbs as food by some unspecified peoples of the Pacific Northwest (possibly the Songish). Brown actually uses the name *Erythronium grandiflorum* Pursh, but in a

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[1]The antibiotic properties may be extrapolated more reliably to "real-life" effects in the case of direct topical applications, such as those used by the Wailaki and Montana Salish peoples (Kelly Bannister, University of British Columbia, pers. comm. 1998).

Table 3.3 Other *Erythronium* species and documented uses.

Species (range)	Use	Reference(s)
E. albidum, E. mesochoreum (eastern and central U.S., respectively)	- Winnebago children "ate them [the bulbs, presumably] raw with avidity when freshly dug in the springtime."	Gilmore (1977:19)
E. americanum (and possibly other eastern North American species)	- Micmac of the Maritimes dug the bulbs in spring and ate them raw, boiled, or baked in hot ashes. - Abenakis of Saint John River ate the roots of a "yellow lily," probably this species. - Iroquois used with *Claytonia virginica* to prevent conception. "Young girls may eat these plants, but not the roots. They will never have children." Roots also smashed to make poultice for swellings. - Cherokee: "Root tea will break fever; crush warmed leaves and pour juice over wound that won't heal; ingredient in infusion for fainting; chew root and spit into river to make fish bite."	Stoddard (1962) Jack (1893) Herrick (1995:244) Hamel and Chiltoskey (1975:43)
E. dens-canis (Eurasia)	- 18th century Tartars (of Asia) collected and dried the bulbs and boiled them with milk or broth. - Medicinal "Vertues" for people of 17th century Europe: "A The Women that dwell about the place where these grew, and do grow, have with great profit put the dried meale or pouder of it in their children's pottage, against the wormes of the belly. B Being drunke with Wine it hath been proved marvellously to asswage the Collicke passion. C It strengthneth and nourisheth the body in great measure, and being drunke with water it cureth children of the falling sicknesse."	Sturtevant (1972) Gerard (1975:204)

Table 3.3, cont.

E. japonicum (Japan)	- Starch from bulbs of "Katakuri" once used as a thickener for soups and sauces, but has since been replaced by potato starch (which still retains the name "katakuri-ko", or Katakuri flour). Above-ground parts (including flowers) commercially available to eat as a vegetable; prepared by boiling, and said to taste sweet.	Yamaguchi (1997)
E. oregonum (south-coastal B.C. and west of Cascades in Washington and Oregon)	- Songish girls used the "roots" to "gain the affection of their sweethearts." Bulbs also eaten, though not clear which peoples involved.	Brown (1868:380,393)
E. revolutum (south-coastal B.C. and coastal U.S. from Washington to central California)	- Bulbs gathered and stored by Kwakwaka'wakw and possibly Nuu-chah-nulth. Dug "when the leaves first come out of the ground." Eaten raw on hot days (said to be cool and milky); otherwise boiled or baked in hot ashes. Eaten with oolichan grease to reduce the bitterness. Served boiled at feasts.	Boas (1921:197-198, 544-550); Turner (1995)

footnote refers to a specimen of his that was sent home and later pictured, flowering, in Curtis' Botanical Magazine in 1868. Brown says of this specimen that "Dr. Hooker thinks it is the *E. giganteum*, Dougl." (p. 380). Through nearly a century of taxonomic confusion, the synonym *E. giganteum* was applied variously to *E. oregonum* and *E. grandiflorum*, until Applegate (1935) resolved the situation and described *E. oregonum* as a separate species. Applegate refers to the same coloured plate noted by Brown and states that it clearly illustrates *E. oregonum*. Thus, there is limited evidence for toxicity and limited evidence for human food use of the bulbs of *E. oregonum*; a chemical analysis of the bulbs is clearly needed.

Not mentioned in the table is the modern use of *Erythronium* species in horticulture. Many species are available in nurseries, and some (e.g. *E. tuolemnense*) are much more amenable to gardening than others (e.g. *E. grandiflorum*). Further information on the gardening potential of North American erythroniums can be found in Watson and Woodward (1974) and Kruckeberg (1982).

3.6 Suggestions for Future Work

Very little archaeobotanical work has been done in British Columbia, and more work in this area will lead to a greater appreciation of the role of root vegetables in interior plateau cultures through time. More specifically, techniques have been developed to identify individual species, for example in ancient cooking pits, and it is likely that much more will be learned about yellow glacier lily in this way.

Also, as with all aspects of ethnobotanical work, time is of the essence in recording the knowledge of contemporary elders. While this is obviously significant in an academic sense, it is far more important for First Nations peoples themselves, in gaining as full an appreciation as possible of the past, present and potential role of different plants in their cultures. In addition, the traditional ecological knowledge accumulated by various cultures is of great importance to modern restoration efforts, if the goal is to return habitats to their pre-contact (often actively managed) state (Anderson 1996). See Chapter 5 for additional discussion of traditional resource management and

its ecological implications.

3.7 Summary

Yellow glacier lily bulbs have been a staple root vegetable for northern plateau peoples for hundreds or thousands of years. They appear to have been used most extensively by the Nlaka'pamux and Secwepemc peoples, and were collected in great abundance at such harvesting areas as Botanie Valley and the Neskonlith Meadows-Adams Lake region. The bulbs were collected throughout the spring and summer, depending on elevation, and were collected either when the plants were in flower or early fruit. Perhaps the most common preservation technique at one time was to pit-cook and then dry the bulbs at the harvesting area, before transporting them back to the winter villages for storage. However, a broad array of other processing and storage strategies have been reported. Bulbs were prepared for eating in an equally wide variety of ways, including pit-cooking, boiling, roasting in hot ashes, and adding to soups, stews or other dishes. Strings of dried bulbs were an important trade item on the northern plateau, and extended the range of use of the species coastward. Peoples who used this species had a detailed understanding of its ecology, and practiced resource management techniques such as selective harvesting and landscape burning to maintain and promote its growth over time. The importance of the species is also reflected in numerous aspects of culture, including rituals and stories. Modern indigenous elders still highly value this root vegetable species. Medicinal use of glacier lily was relatively insignificant, although it was recognized as being one of many foods that sustained health. Other *Erythronium* species apparently have been little used in comparison with *E. grandiflorum*, but some congeners have had food and medicinal uses for other peoples around the world.

4.0 Nutritional Aspects of *Erythronium grandiflorum* Bulbs

> They'd leave [the bulbs] to dry, or wilt, and then string [them] up on maple inner bark . . . to dry, and that was pit-cooked in winter or any other time. . . you bring out the sugar content after it was dried and then pit-cooked. (Mary Thomas, Secwepemc Elder, 1994)

Given the cultural importance of yellow glacier lily as a food plant, it is of interest to ascertain the nutritional significance of the bulbs for the peoples who consumed and still consume them. Of greatest nutritional interest is the carbohydrate content of the bulbs, since root vegetables in general are composed mainly of carbohydrates (FAO 1990). The constituent carbohydrates are of concern for *Erythronium grandiflorum* in particular, since there have been varied suggestions in the literature as to the nature of the carbohydrates in this species' bulbs (see below).

Although it is well recognized in anthropological work that the nutritional qualities of animal foods (e.g. lipid levels) vary significantly over the course of the year (Wandsnider 1997), there appears to have been less recognition of the fact that the same principle applies to plant foods. For certain types of foods, such as young spring greens or ripe fruits, there is an obvious stage of growth (and harvest) at which the optimal nutritional benefit is obtained. For root vegetables, however, this optimal harvest time may be less obvious. It is important to consider this variable in a nutritional analysis of such foods, given the clear evidence of carbohydrate cycles from botanists (e.g. Mooney and Billings 1960, Miller 1992) and food scientists (e.g. Limami and Fiala 1993).

Finally, the observations of elders regarding the effects of drying and pit-cooking on the sweetness of the bulbs invite a more detailed analysis of possible changes in carbohydrates due to different treatments. It is becoming increasingly recognized that processing has diverse and important effects on nutritional qualities of plant foods (Johns 1990, Wandsnider 1997). One such effect is the increased digestibility and palatability of a food. An example of this process involving a root vegetable consumed by indigenous northwestern North Americans is the case of camas (*Camassia* spp., Liliaceae). Camas bulbs were consumed in large quantities by the Coast Salish, Flathead, and peoples of

western Washington, and were also traded extensively (Kuhnlein and Turner 1991). Almost invariably, these bulbs were prepared by pit-cooking, after which they were described as being exceptionally sweet, with a characteristic dark colour (Malouf 1979). Analysis of the bulbs revealed that they contained almost no starch, but rather a fructose-based polysaccharide called inulin[1] (Yanovsky and Kingsbury 1931).

Inulin and other fructans are not digestible in the human small intestine, but rather are fermented in the colon and produce flatulence (a fact to which anyone who has eaten a quantity of raw Jerusalem artichoke tubers can uncomfortably attest) (see McGee 1990). However, under prolonged moist-heating conditions, the inulin will hydrolyze to its constituent fructose units and become both sweet and digestible. Konlande and Robson (1972) showed experimentally that pit-cooking breaks down the inulin in camas bulbs almost completely. It is likely that the same process occurs in pit-cooked bulbs of *Allium* species, which also contain fructan as a major storage carbohydrate (Van Loo et al. 1995).

On the basis of circumstantial evidence, it has been suggested that *Erythronium grandiflorum* bulbs also contain inulin (Turner et al. 1990, Kuhnlein and Turner 1991, Parish et al. 1996). As described in Chapter 3, these liliaceous bulbs were often pit-cooked traditionally and became sweet and brown-coloured following that treatment (like camas and onion bulbs). Contrary evidence comes from Yanovsky and Kingsbury (1938), who did not find inulin in the glacier lily bulbs they analyzed. However, they used an outdated and crude analytical method (optical rotation), and according to Incoll and Bonnett (1993), any analytical work on fructans that predates the advent of chromatography must be confirmed and refined with modern methods. Also, it is important to note that starch and fructans are not mutually exclusively stored carbohydrates, and Yanovsky and Kingsbury may not have detected low molecular weight fructans.

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[1]"Inulin" now has a more specific meaning, referring to fructans with predominantly (2-->1) fructosyl-fructose linkages. Other fructan types have (2-->6) linkages, or mixtures of linkage types (Waterhouse and Chatterton 1993). For the purposes of this discussion, inulin and fructan can be used interchangeably.

In the remainder of this chapter I will, first, outline the procedures used for bulb collection, preparation, and analysis in the present research. Second, I will present data addressing a number of separate but related issues: the general nutritional composition of yellow glacier lily bulbs; changes in the carbohydrate profile over the course of the season; and impacts of different preparation methods on the carbohydrate profile. Finally, I will discuss the nutritional and health implications of these results.

4.1 Methods

4.1.1 Field Collection and Treatments

Most of the bulbs for the seasonal and treatment analyses were collected at Neskonlith Meadows near Chase in south-central British Columbia, an area that has been traditionally significant to the Secwepemc for root gathering. In addition to yellow glacier lily, such root vegetable species as spring beauty (*Claytonia lanceolata*), balsamroot (*Balsamorhiza sagittata*), nodding onion (*Allium cernuum*), chocolate lily (*Fritillaria lanceolata*), and bisquit root or chocolate-tips (*Lomatium dissectum*) are abundant in this area. The relatively low elevation of the area (500 m), along with its proximity to the South Thompson River and Niskonlith[1] Lake were probably other reasons why this location was favoured.

For the seasonal comparison, bulbs of *E. grandiflorum* were collected at four stages of growth during the growing season of 1996 (Figure 4.1):

1) *Pre-flowering* - leaves expanding, unopened flower buds;

2) *Flowering* - leaves fully expanded, fully opened flowers;

3) *Early fruit* - leaves beginning to wither and turn yellow, tepals faded or shed and green fruits formed;

4) *Mature fruit* - leaves completely withered and brown, fruits straw-coloured and

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[1]The discrepancy in spelling (Neskonlith versus Niskonlith) is due to the different spelling of the word in the name of the Neskonlith Band and the name for Niskonlith Lake on government maps (there is also a third spelling used by government sources, for Neskainlith Indian Reserves 1 and 2). I choose the spelling currently used by the Neskonlith Band to refer to the traditional harvesting area known as Neskonlith Meadows.

Pre-flower

Photo: N.J. Turner

Flower

Early fruit
(note the erect green capsule)

Mature fruit

Figure 4.1 Stages of growth of *Erythronium grandiflorum* relevant to the carbohydrate analyses discussed in this chapter.

dehisced (or no longer evident if scapes detached and decayed).

Additional information regarding these samples is detailed in Table 4.1. As noted in the table, the pre-flowering and flowering specimens were collected at the same time, but on different slope aspects (less than 500 m apart), thus substituting space for time in the phenological sequence. The samples from early and mature fruiting plants were collected in the same location as the flowering samples. All samples were cleaned with tap water, then placed on ice or in a freezer until they could be freeze-dried at the University of Victoria (see section 4.1.2).

An additional set of samples collected from Neskonlith Meadows was subjected to all treatment types listed in the next paragraph. All of these bulbs were collected when the *Erythronium* plants were in the mature fruiting stage. While this was phenologically later than the "preferred" time described by Mary Thomas (see section 3.3.2), Mary Thomas was present during the digging and stated that the bulbs were not yet "watery" and therefore still quite suitable for consumption.

These bulbs were divided into five treatments, as follows (see also diagrammatic depiction of this protocol in Figure 4.2):

1) *Raw* - bulbs dug, cleaned, and immediately placed on ice;

2) *Wilted* - bulbs cleaned and left to dry at ambient temperature for ~ 24 hours;

3) *Boiled* - wilted bulbs cooked by boiling until tender, ~ five minutes;

4) *Dried* - wilted bulbs strung on cotton thread and hung to dry in well-ventilated location indoors for 14 or 21 days (see below and Table 4.2);

5) *Pit-cooked* - dried bulbs steam-cooked in earth oven for 20 or 21 hours (see below).

The samples are pictured in Figure 4.3, and additional pertinent information about the samples is listed in Table 4.2. As with the bulbs for the seasonal comparison, these samples were frozen immediately after the specified treatment and freeze-dried as soon as possible.

The "wilting" treatment was important since enzymatic activity can change rapidly and affect the carbohydrate profile once an underground structure is detached

Table 4.1. Sampling data for *Erythronium grandiflorum* bulbs collected at Neskonlith Meadows at different phenological stages, for carbohydrate analysis.

Sample description	Harvest date (dd/mm/yy)	Fresh mass (g)	Freeze-dried mass (g)
1: Pre-flowering	18/04/96	137.9	13.6
2: Flowering	18/04/96	70.9	9.6
3: Early fruit	31/05/96	232.9	78.8
4: Mature fruit	05/07/96	141.0	41.7

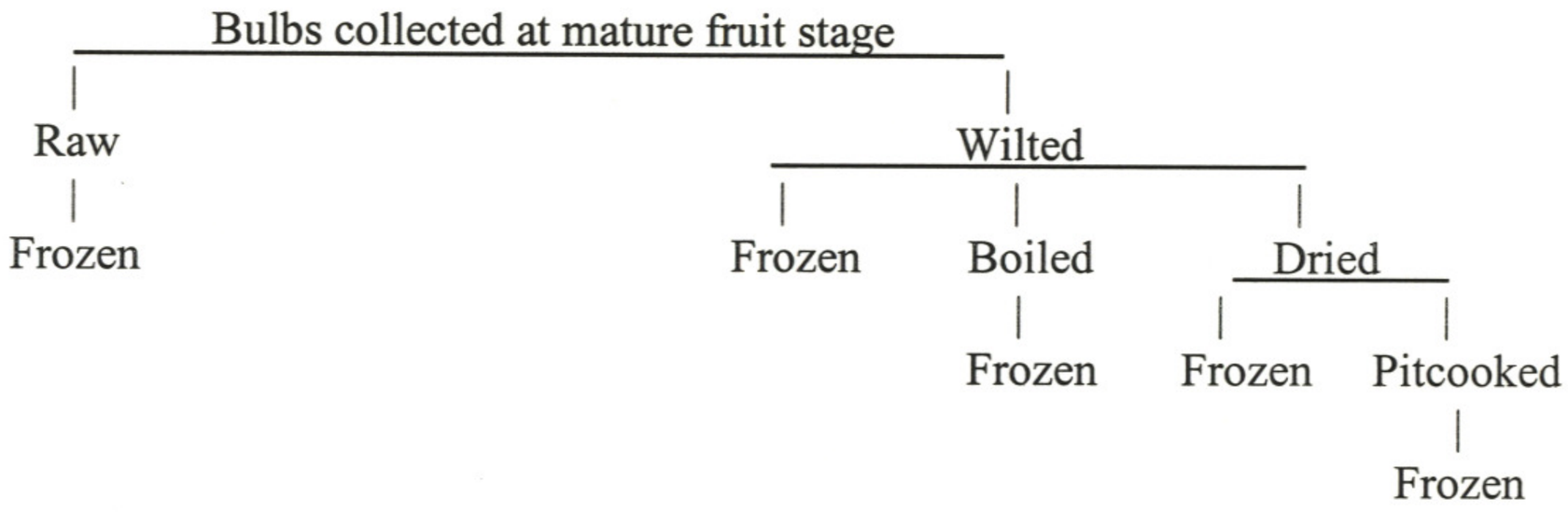
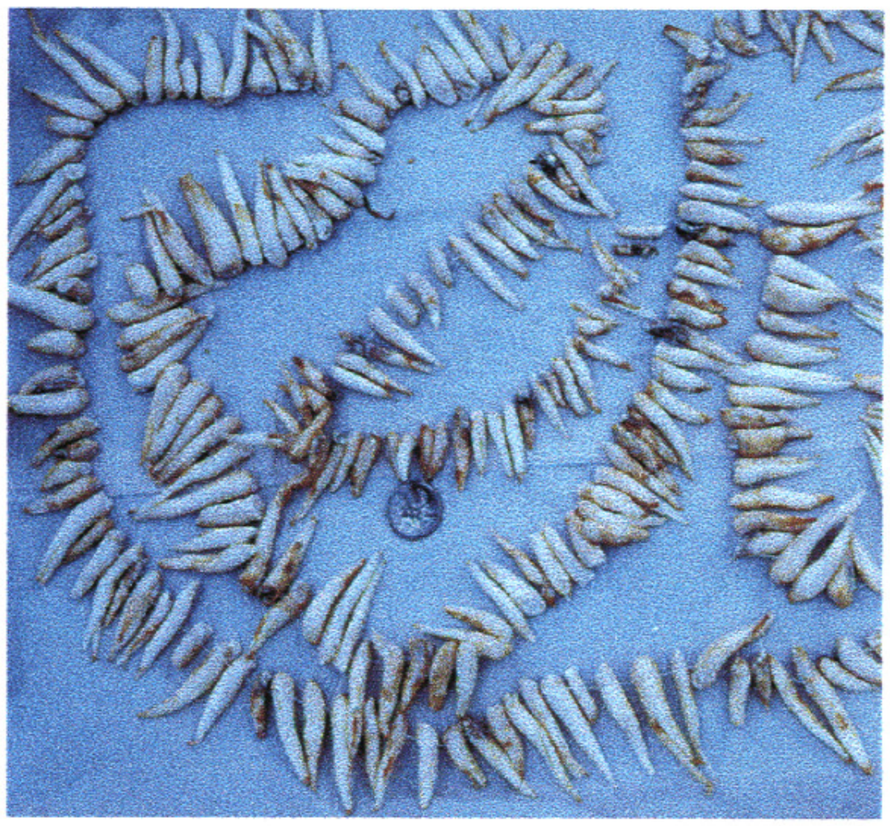
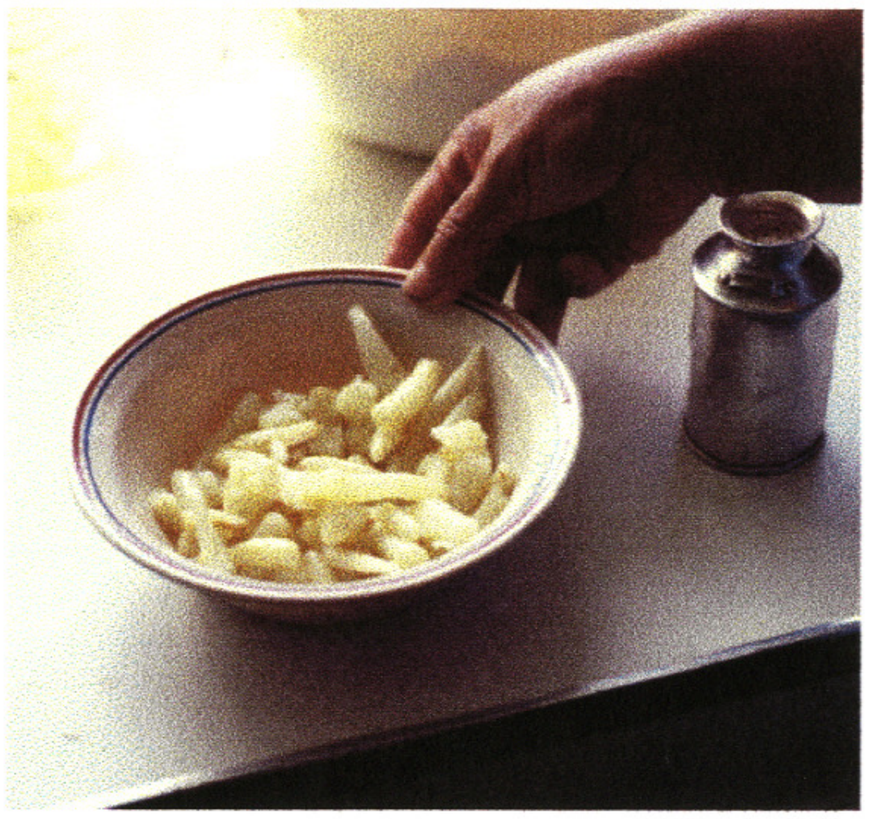


Figure 4.2. Diagrammatic scheme of processing procedures for *Erythronium grandiflorum* bulbs collected at Neskonlith Meadows for treatment comparison.



Wilted for 24 hrs



Wilted then **Boiled**

Wilted then air-**Dried** for 2-3 weeks

Dried then **Pit-Cooked**

Figure 4.3 Treatments applied to bulbs of *Erythronium grandiflorum*.

Table 4.2. Sampling data for *Erythronium grandiflorum* bulbs collected at Neskonlith Meadows and Ashton Creek and subjected to different treatments, for carbohydrate and general nutrient analysis.

Sample description	Harvest location	Harvest date (dd/mm/yy)	Phenological stage	Treating (=freezing) date (dd/mm/yy)	Treated mass (g)	Freeze-dried mass (g)
5: Raw	Neskonlith	05/07/96	Mature fruit	05/07/96	81.7	26.6
6: Wilted	Neskonlith	05/07/96	Mature fruit	06/07/96	75.1	29.5
7: Wilted/Boiled	Neskonlith	05/07/96	Mature fruit	06/07/96	92.9	29.6
8: Dried I	Neskonlith	05/07/96	Mature fruit	26/07/96	39.2	31
9: Dried/Pit-cooked I	Neskonlith	05/07/96	Mature fruit	26/07/96	57.8	32.4
10: Dried II	Ashton Creek	29/07/96	Early fruit	12/08/96	57.5	51.9
11a: Dried/Pit-cooked II	Ashton Creek	29/07/96	Early fruit	12/08/96	157.7	70.9
11b: Dried/Pit-cooked II (for general nutrient analysis)[1]	Ashton Creek	29/07/96	Early fruit	12/08/96	315.0	no data

[1] The final sample was the only one sent to CINE for standard food composition analysis; freeze-dried weight is not given as individual subsamples were freeze-dried at the CINE laboratory.

from the rest of the plant (Oparka et al. 1990, Geigenberger et al. 1994). Because the boiled bulbs could not be processed immediately after digging (and generally would not be by anyone out on a digging expedition), a wilted control was needed to separate the effects of temporary drying from those of boiling. In addition, it was of interest to see how much more the carbohydrates would change after drying the bulbs completely (for three weeks), beyond the changes induced by one-day drying.

Some of the dried bulbs were also pit-cooked. Cooking was performed at the Wells Gray Education and Research Centre in Wells Gray Provincial Park, 150 km north of Kamloops, B.C. We used a recipe that incorporated the essential elements of Interior Salish pit-cooking, as described in Chapter 3 (Figure 3.5). We dug a pit approximately 1 m in diameter and 1 m deep, and heated grapefruit-sized "lava rocks" (vesicular basalt) in a fire alongside the pit for approximately two hours. The pit was "glazed" (as Mary Thomas described) by using small, dry sticks as fuel to create a very hot fire in the pit, and this blackened its sides. Debris from this fire was removed, and red-hot rocks were placed on the bottom of the pit in a single layer of about 20 rocks. A thin layer of moistened dirt was spread on the rocks, and then water-soaked Douglas-fir (*Pseudotsuga menziesii*) boughs, rose (*Rosa* sp.) branches, and thimbleberry (*Rubus parviflorus*) branches (respectively) were layered on top. Next came the food: *Erythronium grandiflorum* bulbs, wrapped in cheesecloth, along with roots of balsamroot (*Balsamorhiza sagittata*),[1] wild nodding onion bulbs (*Allium cernuum*), whole salmon, moose meat, and garden potatoes, carrots, and onions. In this pit-cooking trial, the dried glacier lily bulbs were not pre-soaked.

On top of the food, more thimbleberry, rose and Douglas-fir branches were layered, followed by the addition of about four litres of clean stream water and temperature probes near the top and bottom of the pit. Finally, a large canvas was used to cover the pit, and dirt was shovelled on top until no steam could be seen escaping.

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[1]*Balsamorhiza sagittata* (Asteraceae), a known inulin-containing species, was also analyzed for its general nutritional and carbohydrate characteristics in the raw and pit-cooked states. Details of these analyses may be found in Sandra Peacock's (1998) dissertation and in Mullin et al. (in press).

The temperature of the pit was recorded periodically throughout the 21 hours of cooking time. An average of the values from the top and bottom of the pit probably gives a reasonable indication of the cooking temperature in the center of the pit where the food was located. As shown in Figure 4.4, the average temperature reached a maximum of ~ 78 °C, and declined gradually to ~ 36 °C after 21 hours, when the pit was opened.

In the first pit-cook trial, the bulbs did not appear to have been penetrated fully by the steam, as they were still somewhat dry in the center. For this reason, it was decided that another set of bulbs would be collected and dried, with some also to be pit-cooked (Table 4.2). These bulbs were collected along the Ashton Creek Forest Service road east of Enderby, at 1870 m elevation, and were from plants at the preferred green fruit / yellowing leaves stage of growth. This collection also included a larger sample for general nutrient analysis (proximate composition and some minerals). Bulbs in the latter collection were cleaned meticulously with distilled water to avoid traces of soil confounding the mineral analyses.

These bulbs were dried for 14 days, and then some were pit-cooked, again at the Wells Gray Education and Research Centre. In fact, the same pit was used; it had been filled in and was re-excavated to a depth of only 50 cm and a width of ~ 80 cm, since less food was being cooked in this trial. In general, the same procedure was followed, with the following exceptions. Fist-sized river cobbles (granite) were used instead of the "lava" rocks, as it was felt that they would perhaps retain heat better. Also, the fire used to heat the rocks was located in the pit instead of next to it (unburned wood was removed once the rocks were hot). Food items in the pit consisted of only glacier lily bulbs, balsamroot roots and prickly pear cactus (*Opuntia fragilis*) pads, and approximately three litres of stream water was used. And finally, in this trial the glacier lily bulbs were rehydrated by soaking for 5.5 hours in distilled water before being cooked.

Temperatures of this pit were higher, reaching a maximum of ~ 98 °C, and decreasing to ~ 58 °C after 20 hours (Figure 4.4). The lily bulbs were cooked through, and the bulbs looked much darker than after the first attempt. It was difficult to compare the taste, as in both cases other flavours from the pit (particularly those of the resinous

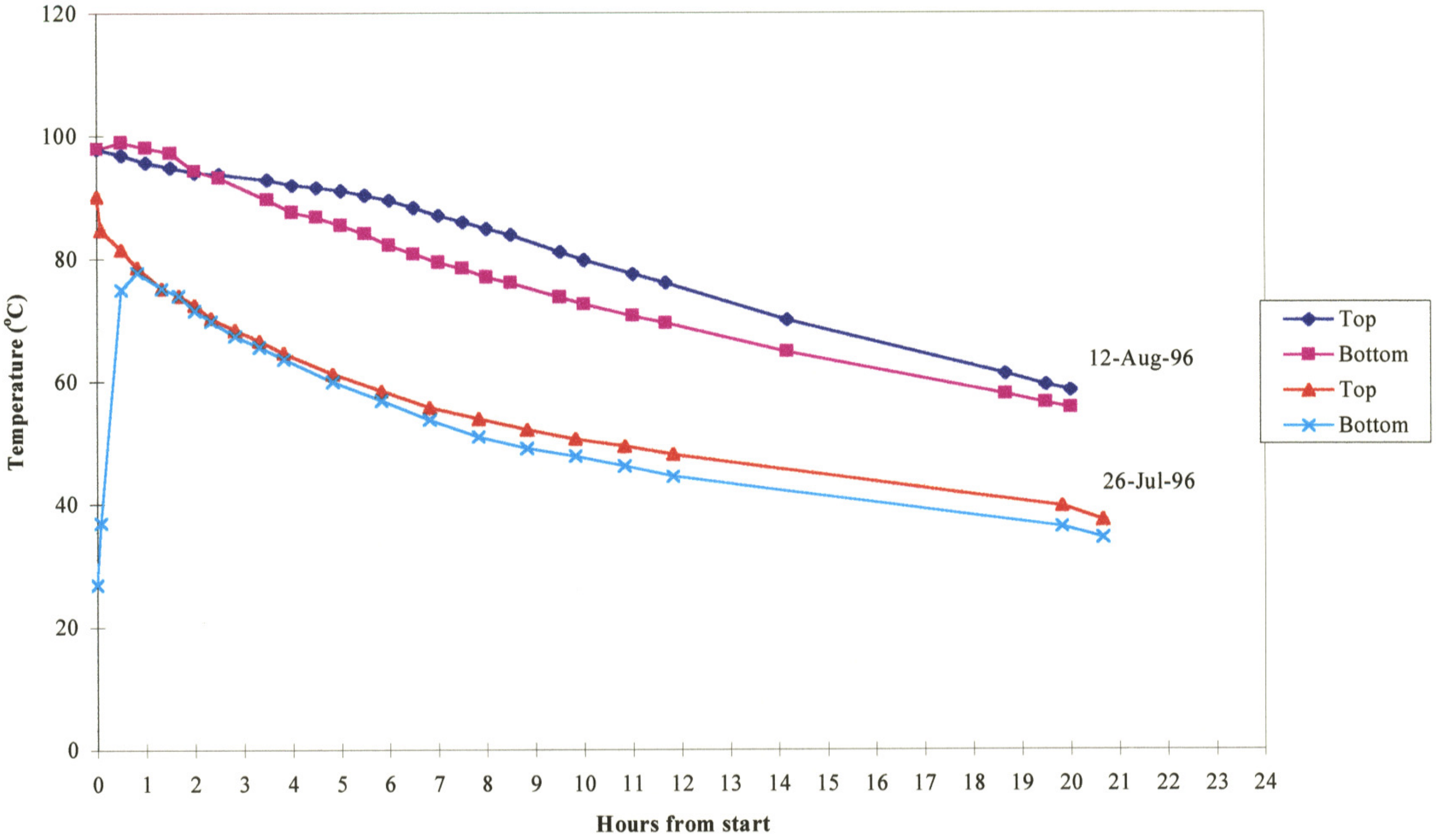

Figure 4.4 Temperature profiles in cooking pits used to cook two sets of *Erythronium grandiflorum* bulbs. Probes were placed at the top and bottom of the pit, thus there are two sets of measurements for each trial.

balsamroot) dominated.

4.1.2 Laboratory Methods

The dried/pit-cooked sample for general nutritional analysis (sample 11b in Table 4.2) was placed on ice upon removal from the pit, transported to Kamloops, then placed in a cooler with dry ice and shipped by air to CINE[1] for analysis. Subsamples were later freeze-dried at the CINE laboratory. Methods of analysis are described in detail in Kuhnlein et al. (in prep). Briefly, moisture, protein, ash, crude fat, and three nutritional minerals (calcium, iron and zinc) were determined with AOAC standardized techniques (AOAC 1984). Carbohydrate was determined by difference (100% - [%moisture + %protein + %ash + %fat]). Total dietary fibre was determined using the AOAC (1984) method with minor modifications. This fibre value was subtracted from the carbohydrate value to determine digestible carbohydrate, and energy was then determined using Atwater factors for protein, fat and digestible carbohydrate (4, 9, and 4 kcal/g respectively) (Watt and Merrill 1963). Duplicate subsamples were analyzed for minerals and total dietary fibre, and triplicate subsamples for the other components.

The rest of the samples, all for detailed carbohydrate analysis, were freeze-dried to constant weight at the University of Victoria, then shipped in sealed plastic bags to Agriculture Canada[2] (storage temperature after freeze-drying was 4 °C). Analytical details are given by Mullin et al. (in press). Briefly, starch was assayed by the enzymatic method of McCleary et al. (1994), in which samples were hydrolyzed with alpha-amylase and amyloglucosidase to free glucose; this was then reacted with colourimetric reagent and measured spectrophotometrically. Water-extractable sugars (glucose, fructose,

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[1]Centre for Indigenous Peoples' Nutrition and Environment, Macdonald Campus of McGill University, Ste-Anne-de-Bellevue, Québec. The current director of CINE is Dr. Harriet Kuhnlein; she is a participant in the Secwepemc Ethnobotany Project, of which my research is also a component. The general nutrient data cited here for *E. grandiflorum* will be part of a general publication on nutrients in Secwepemc plant foods (Kuhnlein et al. in prep.).

[2]Dr. W.J. (John) Mullin performed the analyses at the Centre for Food and Animal Research, Agriculture and Agri-Food Canada, Ottawa (his laboratory has since moved to Harrow, Ontario as part of the Greenhouse and Processing Crops Research Centre).

sucrose, and fructans) were separated by HPLC (HPAE type) on DIONEX PA-1 and PA-100 ion exchange columns, and detected with a pulsed amperometric detector (PAD). Soluble and insoluble fibre were determined separately, following the protocol of Mongeau and Brassard (1990).

It later became possible for additional analyses to be performed at Agriculture Canada (protein, ash and fat), which resulted in a partial duplication of, and useful comparison with, the analyses performed at CINE (for samples 11a and 11b). Ash and fat were determined using AOAC (1984) methods. Protein was determined from the nitrogen generated by the Kjeldahl digestion method, using a conversion factor of 6.25 (IDF 1993). Moisture, protein, ash, and dietary fibre analyses were done in duplicate at Agriculture Canada; subsampling for the other analyses varied and is indicated in the results accordingly.

4.2 Results

4.2.1 Proximate Analysis, Energy and Mineral Composition

Table 4.3 shows the analyses performed by CINE and AC (Agriculture Canada) on the dried/pit-cooked glacier lily bulb samples from Ashton Creek, in addition to an analysis performed on bulbs from Montana by Yanovsky and Kingsbury (Y&K) in 1938. In a comparison of these results, the most obvious discrepancy lies in the moisture contents. As will be evident in results from AC for the seasonal and treatment comparisons, the moisture value obtained by Y&K seems exceedingly low for raw bulbs, and in fact Y&K's paper does not indicate the state of the bulbs. Even the analysis of samples 11a and 11b (subsamples from the same treatment) by CINE and AC resulted in a 10% difference in the moisture values obtained. Therefore, it is more appropriate to compare the values on a dry basis. The bulbs then consist of 91-96% carbohydrate, with 6-10% in the form of dietary fibre and thus not considered digestible. Protein values are on the order of 3-5%, with ash low (~ 1%) for the CINE and AC samples and higher for the Y&K samples (3.6%). Protein was also slightly higher for the Y&K samples, at 5.3% compared with ~ 3% for CINE and AC. Only CINE detected an appreciable amount of

Table 4.3. Proximate composition and energy values for *Erythronium grandiflorum* bulbs, per 100 g fresh[1] and dry mass. The second line for each sample represents values calculated on a dry basis.

Source	Moisture (g)	Fat (g)	Protein (g)	Ash (g)	Soluble fibre (g)	Insoluble fibre (g)	Total fibre[2] (g)	Digestible CHO by diff.[3] (g)	Energy kcal	kJ
CINE (Sample 11a)	46.0	1.6	1.7	0.6	no data	no data	3.8	46.2	207	866
	-	3.0	3.1	1.1	no data	no data	7.0	85.6	383	1602
Agriculture Canada (Sample 11b)	56.0	trace	1.3	0.5	1.1	1.6	2.7	39.6	164	686
	-	trace	3.0	1.1	2.4	3.7	6.1	90.0	372	1556
Yanovsky & Kingsbury, 1938	20.8	--[4]	4.2	2.9	7.8	--	7.8	64.3	274	1146
	-	--	5.3	3.6	9.8	--	9.8	81.3	346	1448

[1]Bulbs analysed by CINE and Agriculture Canada were pit-cooked, while the bulbs analysed by Y&K were presumably raw; however, as supported by the data in Table 4.7, cooking should not change the gross nutrient profile significantly (aside from moisture). Y&K's bulbs were collected from Montana, but no information is given on time of year or phenology.

[2]Fibre was assayed differently by all sources; methods of CINE and Agriculture Canada are explained in the text. Y&K used the crude fibre assay, an outdated method providing a rough estimate of insoluble fibre, and calculated "hemicellulose" separately as the difference between the acid and diastase assays for starch (giving a rough estimate of soluble fibre).

[3]Digestible carbohydrate by difference = 100% - (%moisture + %protein + %ash + %fat + %total fibre).

[4]Y&K do not explain this symbol, but presumably it indicates that none of the substance was detected.

fat (3%). CINE was also the only source to assay some nutritional minerals; these results are given in Table 4.4. The bioavailability of these minerals is not known.

Table 4.4 also shows that the composition of pit-cooked yellow glacier lily bulbs is comparable to that of baked common potato (*Solanum tuberosum* L.) and baked sweet potato (*Ipomoea batatas* L.) (both flesh only, no peel). In fact, the lower moisture value of the dried/pit-cooked lily bulbs makes them a more nutrient-dense food source, in the same way that dried fruits are more nutrient-dense than the same fruits consumed raw. In other words, for a given amount of cooked product, more food energy is derived from lily bulbs than from baked potato or sweet potato. On a dry basis, lily bulbs are lower in protein but higher in fat than the other two sources; they are also higher in calcium and zinc than baked potatoes, and with about the same amount of iron as both potato and sweet potato. If the full spectrum of vitamins and minerals were analyzed, a more complete comparison could be made. However, it is clear that this root vegetable is certainly "potato-like" in fulfilling the role of a carbohydrate-rich food source in the traditional diet.

4.2.2 Seasonal Changes in Carbohydrates

General nutrient data for yellow glacier lily bulbs at the four seasonal stages are given in Table 4.5. Moisture levels are high during the early, most active period of plant growth, then decline to a low in the early fruit stage. Fibre and protein increase to a peak in the early fruit stage, but still represent a relatively small amount of the total mass. Carbohydrate (calculated by difference) represents a higher proportion of the fresh mass at the early fruit stage (almost 30%) than at any other stage measured, and therefore the bulbs are the most nutrient dense at early fruit.

The digestible carbohydrate fraction is examined in more detail in Table 4.6. Two main results are evident from an examination of these data:

1) *Starch, not sugars or fructan, is the dominant storage carbohydrate in yellow glacier lily bulbs over most of the growing season.* Kestose (a three-unit fructo-oligosaccharide) and traces of nystose (a four-unit fructo-oligosaccharide) were the only

Table 4.4. Proximate composition and mineral nutrients in cooked *Erythronium grandiflorum* bulbs, *Solanum tuberosum* (potato) tubers, and *Ipomoea batatas* (sweet potato) roots, per 100 g fresh and dry mass. The second line for each sample represents values calculated on a dry basis.

Food	Moisture (g)	Fat (g)	Protein (g)	Total fibre (g)	Digestible CHO by diff. (g)	Energy kcal	Energy kJ	Calcium (mg)	Copper (mg)	Iron (mg)	Zinc (mg)
Erythronium grandiflorum, dried/pit-cooked[1]	51.0	0.8	1.5	3.3	42.9	186	776	23.0	0.13	0.8	0.9
	-	1.6	3.1	6.7	87.6	380.	1584	42.6	0.24	1.5	1.7
Solanum tuberosum, baked, peeled[2]	75.0	trace	1.9	1.0	20.4	93	389	5.0	0.18	0.4	0.3
	-	trace	7.6	4.0	81.6	372	1556	20.0	0.62	1.6	1.0
Ipomoea batatas, baked, peeled[3]	73	trace	1.8	2.4	22.2	103	431	28.1	0.15	0.4	no
	-	trace	6.7	8.9	82.2	381	1596	104.1	0.53	1.5	data

[1]Average of values from CINE and AC from Table 4.3, except for minerals (analyzed by CINE only).
[2]Health and Welfare Canada (1988), except zinc and copper data from Paul and Southgate (1978).
[3]Health and Welfare Canada (1988), except copper data from Paul and Southgate (1978) for boiled sweet potato (zinc not available).

Table 4.5. Proximate composition and energy values for raw *Erythronium grandiflorum* bulbs at different seasonal stages, per 100 g fresh and dry mass[1]. The second line for each sample represents values calculated on a dry basis.

Stage	Moisture (g)	Fat (g)	Protein (g)	Ash[2] (g)	Soluble fibre (g)	Insoluble fibre (g)	Total fibre (g)	Digestible CHO by diff. (g)	Energy kcal	kJ
Pre-flowering	90.7	trace	0.4	0.5	0.2	0.3	0.5	7.9	33	139
	-	trace	4.2	5.1	2.6	3.2	5.8	84.9	356	1491
Flowering	87.3	trace	0.5	0.5	0.3	0.4	0.7	11.0	46	192
	-	trace	4.2	3.6	2.7	3.2	5.9	86.3	362	1515
Early fruit	66.9	trace	1.4	0.4	0.9	1.0	1.9	29.4	123	515
	-	trace	4.1	1.2	2.6	3.1	5.7	89.0	372	1558
Mature fruit	69.9	trace	1.2	0.8	0.8	0.9	1.7	26.4	110	462
	-	trace	4.1	2.6	2.6	3.1	5.7	87.6	367	1535

[1]All analyses performed at Agriculture Canada using methods as previously described.

[2]Variation in ash may be due to traces of soil clinging to the bulbs; these samples were not cleaned meticulously as they were not being assayed for nutritional minerals.

Table 4.6. Carbohydrate composition (except dietary fibre) of raw *Erythronium grandiflorum* bulbs at different seasonal stages, per 100 g dry mass.

Stage	Glucose[1] (g)	Fructose[1] (g)	Sucrose[1] (g)	Kestose[1] (g)	Starch[2] (g)	Total CHO[3] (g)	Discrepancy from CHO by diff. (g)[4]
Pre-flowering	11.2 (1.59)	12.9 (1.45)	16.3 (2.20)	4.4 (0.59)	19.4 (0.51)	64.1	20.8
Flowering	5.1 (0.79)	4.0 (0.64)	2.4 (0.16)	1.5 (0.58)	53.8 (0.44)	66.8	19.5
Early fruit	1.1 (0.10)	0.3 (0.06)	3.6 (0.34)	2.9 (0.36)	77.5 (0.30)	85.3	3.7
Mature fruit	1.2 (0.20)	0.5 (0.09)	4.7 (0.42)	3.5 (0.49)	74.0 (0.25)	83.8	3.8

[1]Standard deviation of mean given in parentheses; 6 subsamples.
[2]Standard deviation of mean given in parentheses; 3 subsamples
[3]Sum of the carbohydrate values listed here. Not included are traces of nystose (tetrasaccharide fructan consisting of three fructose units and one terminal glucose), which were also found in all samples.
[4]Carbohydrate by difference values given in Table 4.5.

fructans present in sufficient quantities to be detected and measured individually. These quantities were very low compared with the amount of starch present, at all stages. However, Table 4.6 shows that there are significant quantities of carbohydrates (as calculated by difference) that are not accounted for by the sum of all individual carbohydrates assayed. This type of discrepancy is a topic of current interest in food science now that detailed carbohydrate analysis is becoming more common, and is not an aberration unique to this study (Dr. W. J. Mullin, Agriculture Canada, pers. comm. 1997). One or more components are clearly not being accurately assessed. One such component may be resistant starch (see discussion below); if present, it will not have been included in the starch component. However, it should be included with dietary fibre. Alternatively, there could be water-soluble carbohydrates (higher molecular-weight fructans) that are present in quantities too small to detect individually, but may together add up to a more significant amount. The latter explanation is supported by the fact that the discrepancy becomes much smaller over the course of the season, suggesting that the "missing" carbohydrates act in a similar manner as the other water-soluble carbohydrates measured.

Another result supports the assertion that, in spite of the unaccounted fraction, fructans play a relatively minor role as a storage carbohydrate in glacier lily bulbs. The fructose/glucose ratio was determined for all glacier lily samples, using hydrolysis by 1% oxalic acid. Fructans, including sucrose, are hydrolyzed to fructose and glucose, while starch, cellulose, hemicellulose, and pectins are not affected. The resulting fructose/glucose ratio gives an indication of the mean fructan chain length. Ratios for all glacier lily samples ranged from 0.77 to 1.01 (with no obvious relationship to stage of growth or treatment). In contrast, values for *Balsamorhiza sagittata*, a known inulin-storer, ranged from 5.91 to 8.20 (smaller values associated with pit-cooked samples).

2) *The carbohydrate profile of the bulbs changes dramatically over the course of the season*. Figure 4.5 allows an easier comparison of the changes in carbohydrates in relation to one another. At the beginning of the growing season, the plant is using soluble sugars translocated from the bulb to support its early rapid growth; sucrose and reducing

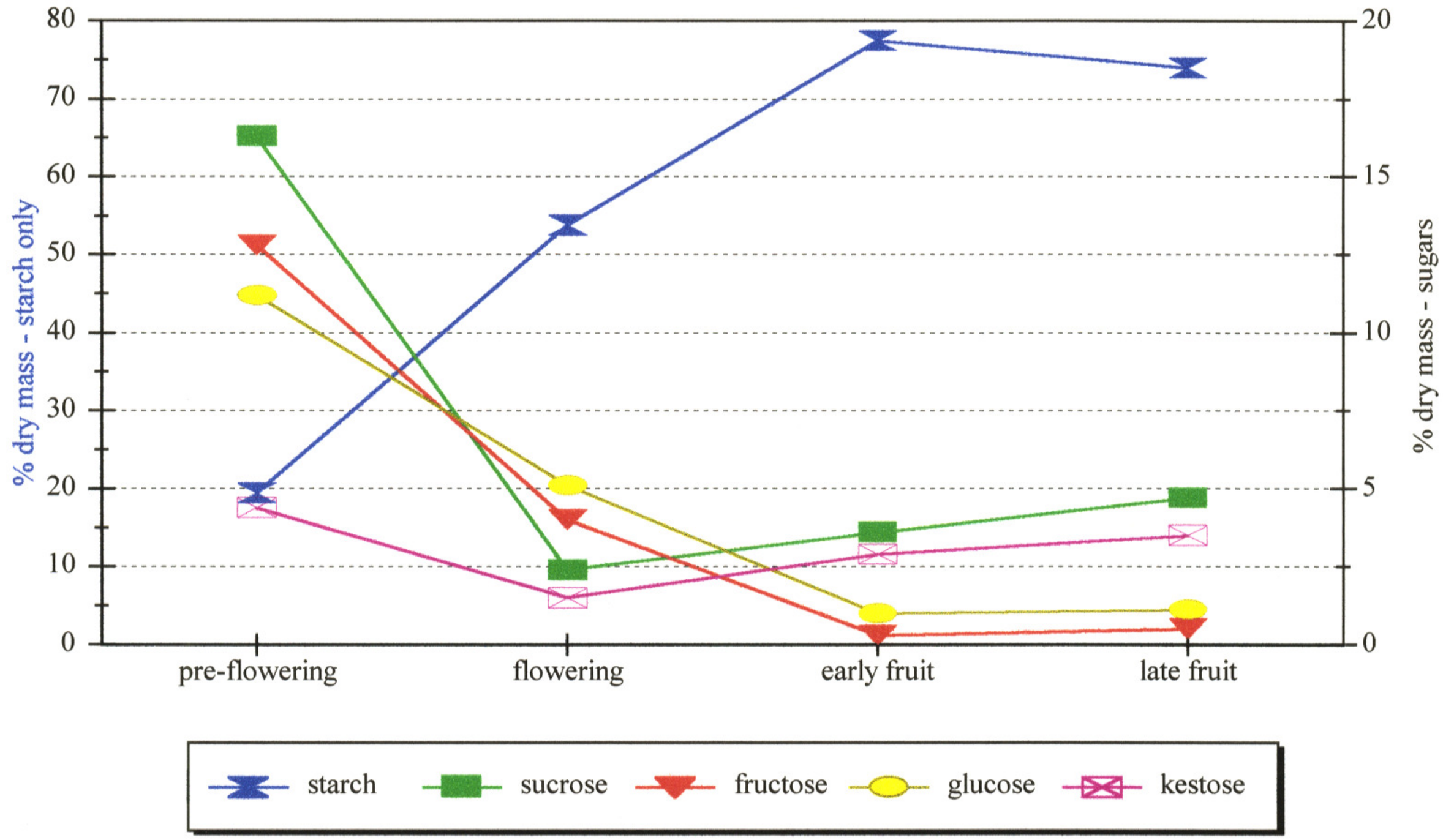

Figure 4.5 Changes in carbohydrates of *Erythronium grandiflorum* bulbs over the growing season. Note the exaggerated axis for sugars relative to starch.

sugars are the primary transport carbohydrates in geophytes (Miller 1992, Theron and Jacobs 1996). These sugars (glucose, fructose, kestose and particularly sucrose) are together present in an amount more than double that of starch. However, as a spring ephemeral, *Erythronium* begins to store energy in the new bulb in the form of starch almost as soon as the leaves unfold. The increase in starch and decrease in sugars from the pre-flowering to flowering stages is remarkable since these stages may be separated by only a matter of days (depending on weather). Starch is at a peak and sugars are at a minimum at the green fruit stage of growth. Later in the season, as the fruits mature, starch appears to begin to decline, while sugars increase; this likely reflects the fact that the active period of photosynthetic accumulation is at an end, and the plant will have to rely on stored carbohydrates until the following spring.

4.2.3 Anthropogenic Treatments

Proximate analysis data for lily bulbs subjected to different treatments are shown in Table 4.7. Again, few changes are evident in the gross nutrient profile, aside from the expected changes in moisture (decrease upon wilting or drying, full or partial rehydration upon boiling and pit-cooking). This relative constancy holds even though the first five samples consisted of bulbs from Neskonlith Meadows, and the last two of bulbs from Ashton Creek.

More interesting are the results from the detailed carbohydrate analysis (Table 4.8). Common to all samples is the high proportion of starch, which is not surprising given that all samples were collected when the plants were in fruit (see previous section). Effects of the first set of treatments (the first five listed in the table; bulbs from Neskonlith) are shown graphically in Figure 4.6. Kestose is omitted as it is generally found in trace quantities in these samples, and does not vary in any systematic way. It is evident that the wilting process does affect the sweetness of the bulbs to some degree, with an increase in all simple sugars and a corresponding decrease in starch. This increase in sugars at the expense of starch occurs much more noticeably after drying for three weeks. Therefore, it appears that enzymatic activity in the bulbs continues well into

Table 4.7. Proximate composition and energy values for *Erythronium grandiflorum* bulbs subjected to different treatments, per 100 g fresh and dry mass[1]. The second line for each sample represents values calculated on a dry basis.

Treatment	Moisture (g)	Fat (g)	Protein (g)	Ash (g)	Soluble fibre (g)	Insoluble fibre (g)	Total fibre (g)	Digestible CHO by diff. (g)	Energy kcal	kJ
Raw	68.1	trace	1.3	0.7	0.8	1.0	1.8	28.1	118	492
	-	trace	4.1	2.1	2.6	3.1	5.7	88.1	369	1543
Wilted	61.8	trace	1.6	0.8	0.7	1.0	1.7	34.1	143	597
	-	trace	4.1	2.2	1.9	2.7	4.6	89.1	373	1560
Wilted/ Boiled	69.1	trace	1.3	0.7	0.7	1.2	1.9	27.0	113	473
	-	trace	4.1	2.2	2.4	3.9	6.3	87.4	366	1531
Dried I	26.4	trace	4.2	1.7	2.2	2.6	4.8	62.9	268	1123
	-	trace	5.7	2.4	3.0	3.5	6.5	85.4	364	1525
Dried/ Pit-cooked I	46.7	trace	2.2	1.3	1.5	1.9	3.4	46.4	194	813
	-	trace	4.2	2.4	2.9	3.6	6.5	86.9	364	1525
Dried II	13.5	trace	3.6	1.1	1.9	2.3	4.2	77.6	325	1359
	-	trace	4.2	1.3	2.2	2.7	4.9	89.6	375	1569
Dried/ Pit-cooked II	56.0	trace	1.3	0.5	1.1	1.6	2.7	39.5	163	683
	-	trace	3.0	1.0	2.4	3.7	6.1	89.9	372	1555

[1]All analyses performed at Agriculture Canada using methods as previously described.

Table 4.8. Carbohydrate composition (except dietary fibre) of *Erythronium grandiflorum* bulbs subjected to different treatments, per 100 g dry mass.

Treatment	Glucose[1] (g)	Fructose[1] (g)	Sucrose[1] (g)	Kestose[1,3] (g)	Starch[2] (g)
Raw	1.0 (0.24)	0.5 (0.01)	3.9 (0.26)	3.2 (0.25)	76.9 (0.52)
Wilted	2.8 (0.38)	2.2 (0.20)	4.7 (0.58)	trace	71.7 (0.07)
Wilted/ Boiled	1.7 (0.33)	1.2 (0.22)	4.6 (0.49)	trace	72.4 (0.50)
Dried I	9.2 (1.97)	7.8 (1.50)	12.4 (2.39)	4.0 (0.63)	47.3 (0.45)
Dried/ Pit-cooked I	7.8 (0.48)	7.5 (1.42)	2.9 (0.15)	trace	62.0 (0.28)
Dried II	5.0 (0.46)	4.0 (0.22)	8.5 (0.52)	trace	64.6 (0.35)
Dried/ Pit-cooked II	3.8 (0.32)	3.6 (0.40)	5.9 (0.30)	trace	69.4 (0.21)

[1]Standard deviation of mean given in parentheses; 8 subsamples

[2]Standard deviation of mean given in parentheses; 3 subsamples.

[3]Traces of nystose were also found in all samples.

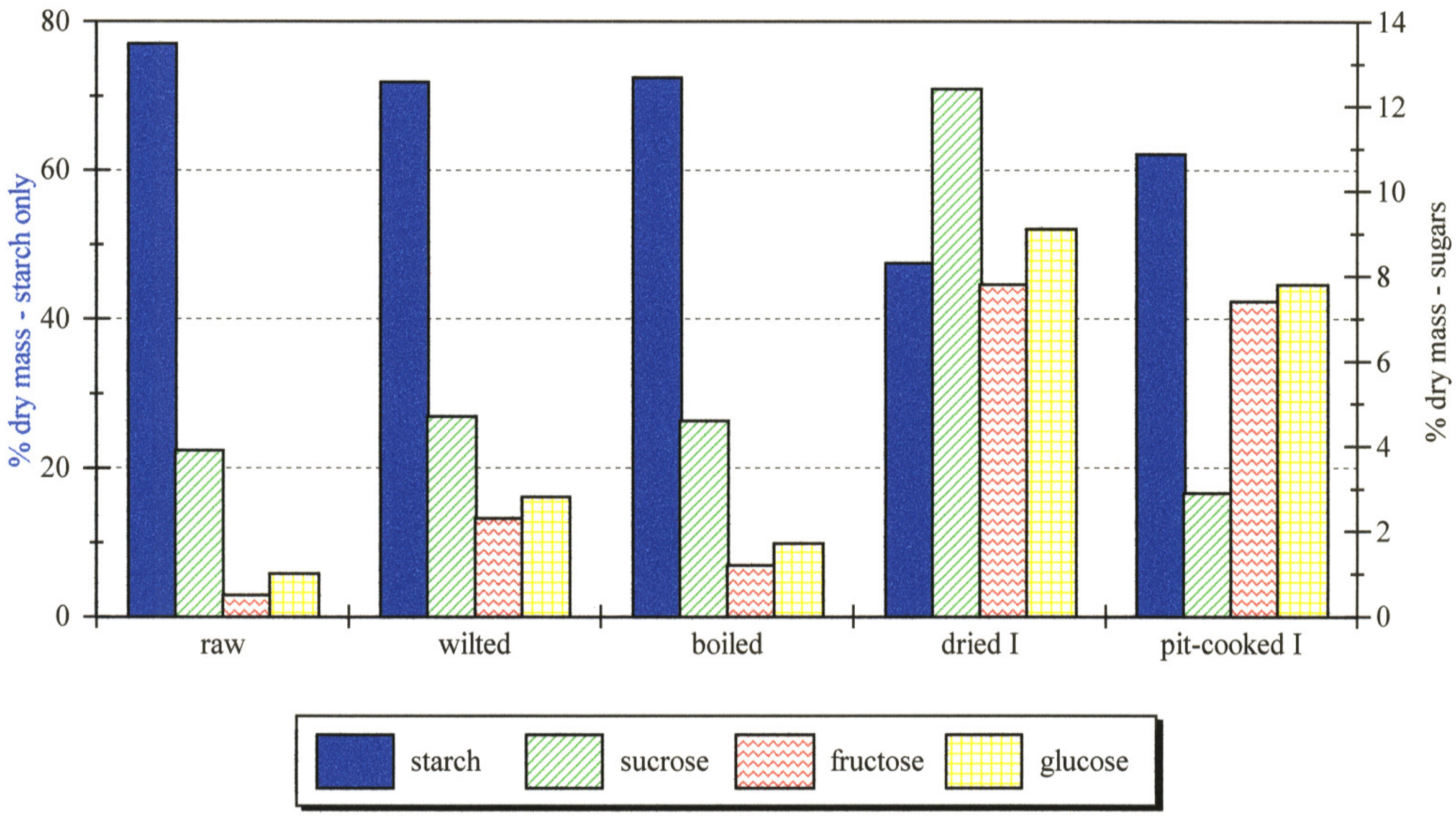

Figure 4.6 Carbohydrates in raw and anthropogenically altered *Erythronium grandiflorum* bulbs (all from plants at mature fruit stage). Note the exaggerated axis for sugars relative to starch.

the drying period. Boiling of the wilted bulbs has little impact, with the slight decrease in monosaccharides probably due to leaching. Finally, pit-cooking appears to actually *decrease* the level of sugars from the level in the dried bulbs, with a proportional increase in the dry mass that is starch. Sucrose is readily thermally degraded (Wursch 1989), and was likely hydrolyzed to its constituent monosaccharides by the hot steam in the pit. In turn, the decrease in monosaccharides may have been due to Maillard reactions (nonenzymatic browning), in which sugars react with free amino groups of amino acids. These reactions, which are encouraged by long exposure to heat (Wursch 1989), yield compounds which could account for the distinctive flavours and colour of pit-cooked bulbs.

As noted earlier, a second sample of bulbs was collected, with some dried and some dried-then-pit-cooked, because the bulbs did not appear to have been thoroughly cooked in the first pit-cooking trial. As shown in Table 4.8, the amounts of the various carbohydrates differ between the Dried I and Dried II samples, and between the Dried/Pit-cooked I and Dried/Pit-cooked II samples. This difference may be due to the fact that trial II bulbs were from early-fruiting plants, while trial I bulbs were from mature-fruiting plants (starch is higher and sugars lower in the former than the latter). However, in spite of this difference, the pattern of change remained the same when the second group of bulbs were pit-cooked, as shown in Figure 4.7. All sugars decrease, and there is a corresponding increase in the proportion of starch.

4.3 Discussion

4.3.1 Carbohydrate Composition and Seasonal Changes

This study is the most detailed to date of the carbohydrate composition of *Erythronium grandiflorum* bulbs. However, a limited comparison can be made with the results of three other studies on the same species. I have already presented some of the data of Yanovsky and Kingsbury (1938). I did not present their carbohydrate analysis; they found (on a dry basis) 44.8% starch, 12.2% "reducing sugar" (interpreted as glucose), and 9.2% "non-reducing sugar" (interpreted as sucrose or inulin, depending on

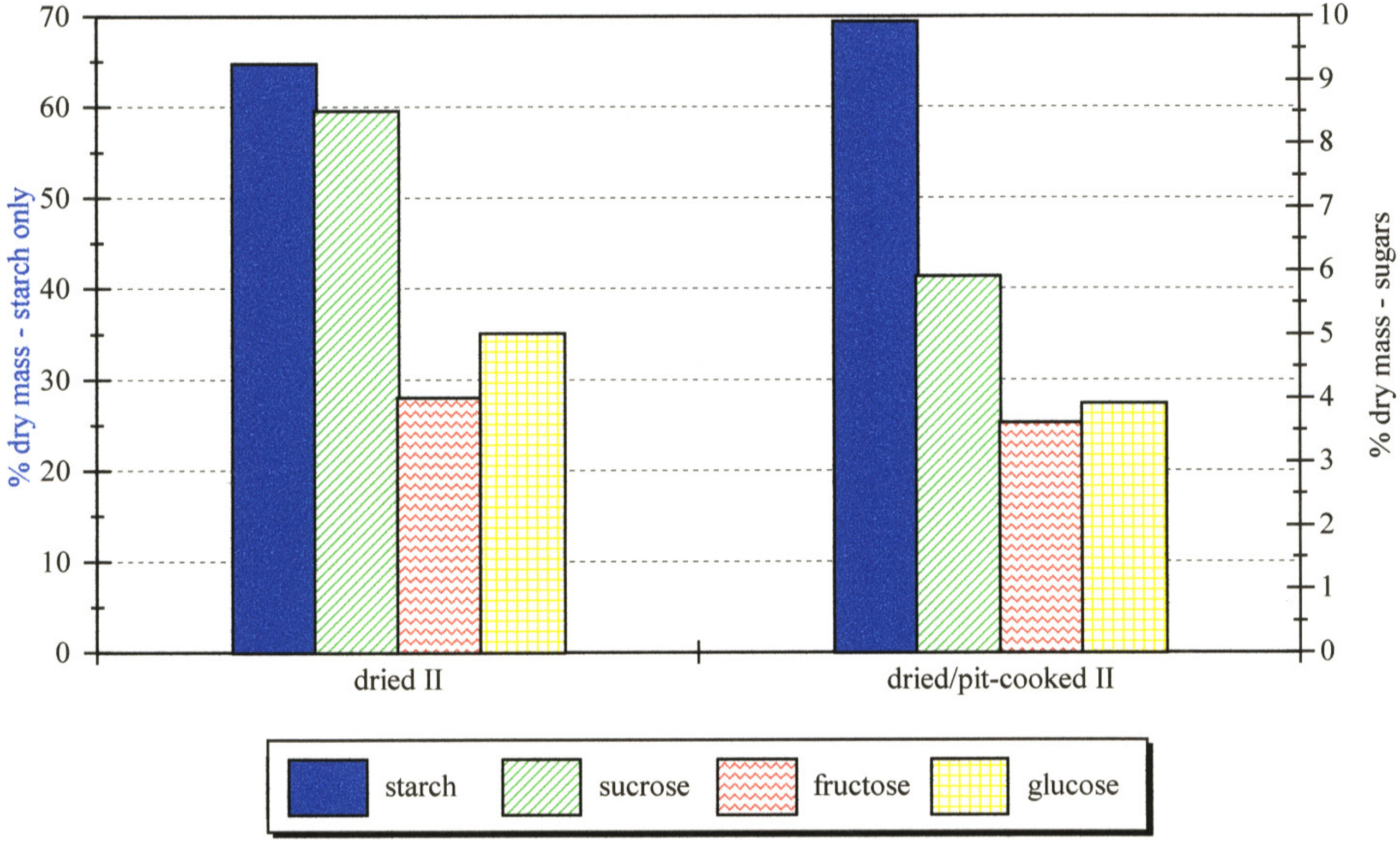

Figure 4.7 Carbohydrates in dried and pit-cooked *Erythronium grandiflorum* bulbs (from plants at early fruit stage), second trial. Note the exaggerated axis for sugars relative to starch.

the species).[1] Stage of growth was not specified but may have been early flowering, by deduction from my seasonal analysis (Table 4.6, Figure 4.5). Yanovsky and Kingsbury did not interpret the non-reducing sugar as inulin on the basis of optical rotation, unlike the non-reducing sugar in certain other species they analyzed (e.g. *Balsamorhiza sagittata, Camassia quamash*). My results support the idea that the bulb carbohydrates of *E. grandiflorum* are fundamentally different from these inulin-containing species, but still comprise a significant proportion of water-soluble carbohydrates (sugars and low molecular weight fructans) early in the growing season.

Two other studies, both very recent, have also contributed some information on the carbohydrates in glacier lily bulbs. Wittenberg (1998) found combined starch and glucose values for the bulbs ranging from 77.6% (dry weight) at full flower, rising to a maximum of 85.0% when the foliage started to brown, and falling again to 75.4% when the plant was completely desiccated. These values are quite similar to mine. On the other hand, Tardiff and Stanford (in press) found "water soluble carbohydrates" in the bulbs at a level of approximately 55% dry weight in full flower, and about 65% very late in fruit. These results are very different from mine, but the analysis method was also completely different. Tardiff and Stanford followed a method normally applied to forest litter, using a hot water extraction to assay the water soluble carbohydrates. According to Southgate (1991), such an extraction will also extract part of the starch fraction. Thus, it is not clear to what extent Tardiff and Stanford's "water soluble carbohydrates" represent sugars, fructans, or starch.

The seasonal changes in carbohydrates evident in *Erythronium grandiflorum* bulbs are very similar to those described by Risser and Cottam (1968) for two eastern congeners, *Erythronium albidum* and *E. americanum*. In those species, which have almost identical patterns to one another, starch content is low at the beginning of the growing season, and then increases rapidly (from 13 to 64% in 21 days in *E.*

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[1]The sum of these values differs by 15.1% from the digestible carbohydrate by difference value cited in Table 4.3, showing, again, that this discrepancy has been a common problem in carbohydrate analysis.

albidum). Following this burst of accumulation, starch decreases slowly over the summer and then drops off more rapidly in fall. Conversely, moisture and soluble sugars (especially sucrose),[1] are in high amounts at the beginning of the growing season, steadily decline until the end of the growing season, and then increase again in fall. This type of change in the form of storage carbohydrate, from sugars during the early, cold part of the season, to starch during the active part of the growing season (post-flower bud), has also been noted in certain alpine species such as *Polygonum bistortoides* (Mooney and Billings 1960). It has been suggested that soluble carbohydrates (including fructans) play a role in frost hardiness, but the evidence for this is equivocal (Pollock 1986).

Of course, the changes in relative amounts of carbohydrates in bulbs as described above do not necessarily correlate with changes in total bulb mass. Young (1998), however, recently determined that bulb biomass of *E. grandiflorum* increases over the growing season to a maximum at the last stage studied, which was when the leaves were beginning to senesce. No further stages were measured so it is not clear whether this stage represented peak biomass. However, Muller (1978) performed a detailed study of biomass accumulation in above- and below-ground parts of *E. americanum*. He identified phases in the growth cycle based on changes in plant weight. During the "lag phase" (immediately following snowmelt), bulb weight drops as material is translocated to the shoot. Following this, the "active phase" is characterized by a rapid, almost linear increase in plant (and bulb) weight, on the order of 190% in 18 days. The end of this phase, during which most of the bulb mass is added, occurs shortly after leaf senescence begins. A period of relative stasis and finally degradation in plant and bulb weight follows and continues through the fall and winter (the decrease in bulb weight is interrupted by a slight increase upon final shoot senescence, apparently due to resorption of shoot materials into the bulb).

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[1]Risser and Cottam (1968) state that they found raffinose and stachyose in variable amounts in the bulbs of both *Erythronium* species. It is quite possible that given the crude chromatographic techniques of the time they were not able to distinguish these compounds from the corresponding three- and four-unit fructans.

On the basis of these studies and my research, it seems reasonable to conclude that the cycles of starch and biomass accumulation coincide in *Erythronium grandiflorum*. Further evidence of this type of correlation in starchy geophytes comes from Theron and Jacobs (1996), who found that in *Nerine bowdenii* (Amaryllidaceae), changes in starch content closely followed dry weight changes in the bulb. Given then, that for *E. grandiflorum* bulbs:

a) bulb mass appears to be at a maximum when starch is at a maximum, and

b) carbohydrate content in the form of starch (relative to moisture) reaches a maximum in the early fruiting stage,

it appears that harvesting bulbs at the early fruiting stage would result in obtaining more mass per bulb, and more energy per unit mass, than at other stages of growth. Thus, as has been suggested by some indigenous elders, this stage is probably optimal in terms of maximum food value return on the harvesting effort. The bulbs would also remain a good food source well into the fruiting period.

4.3.2 Effect of Treatment on Bulb Carbohydrates

In inulin-containing root vegetables, long exposure to heat, moisture, and acidity in the form of pit-cooking is necessary to make the food digestible and sweet (Konlande and Robson 1972). In the starch-containing yellow glacier lily bulbs, digestibility is not an issue to the same degree, as any cooking process involving moisture and temperatures greater than approximately 65 ºC (Kearsley and Sicard 1989) will gelatinize the starch and make it available to digestive enzymes. In terms of sweetness, it appears that it is the *drying* process (or simple storage) that increases levels of sugars relative to starch. Certainly, some elders have noted the distinct sweetness of dried bulbs and the importance of drying bulbs before pit-cooking (see Chapter 3). The enzymatic process underlying the conversion of starch to sugars is unknown. In potatoes, it is common knowledge that low storage temperatures (below 10 ºC) induce an increase in hexose content, and the physiology of this process has been quite well studied (Oparka et al. 1990, Richardson et al. 1990, Geigenberger et al. 1994). However, in certain other

starchy root vegetables, storage at *warm* temperatures results in conversion of starch to sugars; e.g., when tubers of oca (*Oxalis tuberosa* Molina, an Andean root crop) are placed in the sun for a few days, the amount of glucose can nearly double (Flores and Flores 1997). As the latter authors point out, much work remains in understanding the biology and biochemistry of many underground storage organs.

Pit-cooking after drying actually reduces the sugars from their levels in dried bulbs, but these levels are still much higher than those in the raw state. Therefore, since indigenous people would have rarely eaten dried bulbs directly, it naturally would be noted that pit-cooked bulbs were distinctly sweet compared to the raw bulbs. However, I did not pit-cook any raw bulbs, and it is possible that pit-cooking may have different effects on raw as opposed to dried bulbs, in terms of changing the sweetness levels.

It should also be noted that, unlike fructan-containing plants such as balsamroot, lily bulbs were processed in other ways in addition to pit-cooking (see Chapter 3). This would support the suggestion that pit-cooking was not necessary in deriving maximal nutritional benefit from the bulbs.

However, the importance of pit-cooking in the ethnobotany of glacier lily bulbs should not be underestimated merely because it may not have had the same effects on digestibility as in fructan-containing plants. Pit-cooking represented an efficient means of processing the large quantities of bulbs that were gathered. Indeed, cooking such large quantities appears to be a general characteristic of pit-processing (Wandsnider 1997). Also, pit-cooking could have imparted distinctive flavours to the bulbs. Other foods and vegetation used to line the pit (e.g. rose branches) must have added flavours that were greatly appreciated traditionally, in the same way that balsamroot added its own special sinus-clearing touch in our experiment. Maillard reaction products produced in the bulbs may also have been significant; some of these compounds do in fact have sweet, caramel aroma notes (Rizzi 1994). It is interesting that Maillard products are known to reduce oxidative degradation in foods (Pischetsrieder and Severin 1994), a fact that may have been significant in winter storage of lily bulbs.

4.3.3 Nutritional Significance of Glacier Lily Bulbs

As is the case for root vegetables in general (FAO 1990), yellow glacier lily bulbs are rich in carbohydrates and food energy, and relatively low in protein, fat, and minerals.[1] Ascertaining the nutritional characteristics of a food source, however, is only one step in assessing its overall importance in the diet. It is also necessary to consider the total amounts of the food consumed, and how these compare to amounts of other plant and animal foods in the traditional diet (other cultural factors must be considered as well; some of these are discussed in Chapter 3).

It was noted in Chapter 3 that a northern Interior Salish family group might gather approximately 90 kg of bulbs as a winter supply.[2] Assuming a family group is approximately five people,[3] then for eight months (September to March), the average daily intake per person would be ~ 75 g. The bulbs would have been available either at low or high elevations for most of the remaining months. However, there may have been a few months when intakes were low, either due to the stores running out, or to people concentrating on gathering other foods. If it is conservatively assumed that the 90 kg represented the entire year's consumption by five people, the result is an average daily intake per person of just under 50 g. It may be that the estimate of 75 g/day is reasonable for peoples living in close proximity to abundant supplies of the lily (e.g. around Neskonlith), while the lower figure is more realistic for groups with less convenient supplies, or who acquired their supply through trade.

It is interesting to compare this crude estimate of 50-75 g/person/day with the modern consumption of potato, the root vegetable that has largely supplanted glacier lily

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[1]Some root vegetables do have exceptionally high contents of certain vitamins and minerals; e.g., sweet potatoes (Vitamin A), potatoes (Vitamin C), and yams (*Dioscorea* spp.) (manganese) (FAO 1990).

[2]This estimate, derived from post-contact interviews, is likely to be considerably less than the actual amounts harvested and consumed prior to any European influence.

[3]Eugene Hunn (in Hunn et al. 1990) assumes for his calculations of root staples' contributions to the Sahaptin food supply that one adult woman digs roots for herself and three other dependent family members. My assumption is therefore more conservative in terms of per capita intake.

bulbs and other traditional root foods in Interior Salish diets. The average per capita consumption of fresh potatoes in the United States in 1993 was about 65 g/day[1] (USDA 1995). The comparability of this value to the lily estimate suggests that lily bulbs did represent a starchy staple in the traditional diet, at least for those people who had ready access to the bulbs.

For most of the northern Interior Salish peoples, *E. grandiflorum* bulbs and spring beauty corms (*Claytonia lanceolata*) were probably the most significant root vegetables in terms of quantities eaten, based on comments by elders on the relative importance of different plant foods. Other root vegetables (e.g. balsamroot, wild carrot [*Lomatium macrocarpum*], chocolate lily, tiger lily [*Lilium columbianum*], bitterroot, wild nodding onion) and greens (e.g. cow parsnip, *Heracleum lanatum*) provided energy, fibre, and important vitamins and minerals. Fruits (e.g. saskatoon berries, chokecherries [*Prunus virginiana*], huckleberries (*Vaccinium* spp.)] may have been as significant as root vegetables in providing energy, as well as other nutrients.

In terms of animal foods, the dominant view of Plateau hunter-gatherer diets has been that they were dominated by fish and game (see section 3.2). Recent ethnobotanical research on the Plateau has led to a view favoring greater importance of plant material in the diet. Hunn et al. (1998) estimate that many Plateau groups, at least in the protohistoric period, derived more than 50% of their food energy from starchy roots, corms, and bulbs. Also, as Pokotylo and Froese (1983) point out, it is quite likely that prehistoric groups relied more heavily on native root foods than is apparent from ethnographic records, since new forms of carbohydrates (e.g., potatoes, flour, sugar) were rapidly adopted and quickly displaced the traditional carbohydrate sources (Dawson 1891).

Even if animal foods did dominate the Plateau diet, the consumption of even relatively small amounts of carbohydrate could have inordinately significant

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[1]Per capita utilization reflects the fresh market share of commodity production. It is thus an extremely crude measure of actual intake (an overestimate), but no more crude than the measure derived for glacier lily bulbs.

consequences for peoples' nutritional well-being. In human nutrition, carbohydrates play a major part in supplying the metabolic energy that enables the body to perform its different functions (Kearsley and Sicard 1989). The role of carbohydrates may have been especially critical for societies with pronounced seasonal fluctuations in food abundance, in which lean meat was often the only resource available in late winter/early spring (Speth and Spielmann 1983). Carbohydrate has been shown to have a greater protein sparing action than fat; i.e., consumption of carbohydrates, more so than fats, allows protein to be utilized for its normal structural functions instead of for energy. Therefore, even if protein and fat sources are readily available, it would benefit a hunter-gatherer society greatly to expend significant effort on gathering energy-rich, readily stored carbohydrate sources (Speth and Spielmann 1983).

From all accounts, it appears that glacier lily bulbs were indeed collected and stored in large quantities, and were highly valued (e.g. as a trade item). They truly appear to have been a staple root vegetable on the northern plateau, analogous to modern potatoes both in composition and consumption. The common nickname "Indian potatoes" used by many First Nations people is therefore quite appropriate.

4.3.4 Health Implications of Consuming Yellow Glacier Lily Bulbs

There are additional potential health impacts of consuming glacier lily bulbs and other root vegetables, beyond the basic nutritional contributions discussed above. Such considerations are particularly relevant given that diabetes and related disorders are severe problems in native North American populations today (Young 1993).

In particular, the starch component of the bulbs requires a closer examination. Although I have compared the bulbs to potatoes, they may have had very different properties in terms of the glycemic response induced. Increasingly, it is being recognized that not only the quantity but the quality of starch consumed may have major health implications (in the same way that not all dietary fat is considered equal) (Wolever 1991). Differences in starch digestibility, in fact, may have long-term implications with respect to risk factors for chronic diseases like diabetes (Wolever 1991). A variety of factors

influence starch digestibility, including its botanical origin, physical form of the food, interactions with other food components (such as dietary fibre, protein and anti-nutrients), amount of amylase and total starch in the gut, transit time, and processing (Englyst et al. 1993). In considering these factors, Englyst et al. (1993) classified starch as rapidly digested; slowly but completely digested; and resistant, i.e., passing through to the large intestine.

Thorburn et al. (1987) and Brand et al. (1990) demonstrated that traditional starchy Australian Aboriginal and Pima Indian foods were digested more slowly, and had correspondingly lower blood glucose and insulin responses, than modern starchy staples such as potato, bread and rice.[1] The authors impute an anti-diabetic role to the slow digestion and absorption of starch in traditional foods.

It will require further research to determine the degree to which the starch in cooked lily bulbs is slowly digested vs. "fast-release." However, it is almost certain that the bulbs do contain a measure of resistant (i.e. undigestible) starch under a typical traditional processing regime. Starch that is cooked (gelatinized) and then cooled regains some of its crystalline structure, in a process called retrogradation. Retrograded starch is highly resistant to digestion (Muir et al. 1993). Re-heating reverses the effect, but only partially, and successive cycles of heating and cooling (especially freezing) result in increasing amounts of resistant starch (Englyst and Cummings 1987). Traditionally, glacier lily bulbs were often cooked, cooled, cold-stored for winter, and reheated, processes that would result in some accumulation of resistant starch.

It has become appreciated in the past 15 years that as much as 10-20% of the starch we consume reaches the colon as resistant starch (Stephen 1991). This newly-recognized component of "dietary fibre" may be partly responsible for the positive health benefits previously attributed solely to various non-starch polysaccharides (Southgate

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[1]One factor that may contribute to this effect is a high amylose to amylopectin ratio in the starch of traditional foods (Thorburn et al. 1987). Amylose is a linear molecule and exhibits closer intermolecular association through hydrogen bonding than the branched amylopectin. Thus, amylose hydrates more slowly than amylopectin and is less available to amylolytic enzymes (Wolever 1991).

1989). These potential benefits include attenuated glucose and insulin responses, favourable influences on blood lipids and cholesterol, and improved colonic health (Muir et al. 1993).

Fructan, and particularly short-chain fructo-oligosaccharides (FOS), represent another category of newly recognized "dietary fibre" whose health benefits are only now being appreciated. FOS are present in relatively low amounts in glacier lily bulbs, but they cannot be ignored given the large quantities of the bulbs traditionally consumed. Also, Incoll and Bonnett (1993:319) point out that

> The greatest interest in occurrence of fructan in food plants has been in species containing high concentrations like Jerusalem artichoke and chicory [*Cichorium intybus* L.]. This is unfortunate in our opinion because beneficial effects of fructan in human diets may be apparent at much lower concentrations.

Many of the health benefits of FOS appear to stem from the fact that they selectively encourage the growth of bifidobacteria in the colon (Modler 1994), at the expense of such toxin-producing bacteria as clostridia. It is possible that once a bifidobacterial flora has developed in the colon through exposure to fructan, then small amounts of fructan may "keep the flora going" (Dr. L.D. Incoll, University of Leeds, pers. comm. 1998). In addition to increased health of the colon, other possible health benefits include lowered triglycerides and cholesterol, mediated by the absorbed fermentation products (Roberfroid 1993). In Japan and Europe, recognition of these benefits has advanced to the point where FOS are widely used as food additives (Modler 1994, Tomomatsu 1994).

Traditional forms of food processing culturally evolved to maximize the energy benefit from carbohydrate-rich foods, and to minimize contents of indigestible fructans and digestion-resistant raw starch (Wandsnider 1997). Yet, such efforts may not have been totally "successful," in the sense that nutritionally significant quantities of indigestible, or slowly digested, carbohydrates remained after processing. However, this "failure" appears to have its own positive health consequences, lending new meaning to the blurring of the food and medicine concepts in the Indigenous worldview (see Chapter

3). The modern concepts of "nutriceuticals" and "functional foods" show that science is increasingly recognizing the validity of this holistic viewpoint. Foods such as garlic (*Allium sativum*), for example, have taken on a new role as dietary supplements with scientifically recognized health benefits.

4.4 Suggestions for Future Work

According to Wandsnider (1997), much additional information is necessary in elucidating relationships among food composition, food chemistry and traditional processing treatments. Data are required from replicative experiments of traditional processing techniques, including temperatures attained; detailed information is needed on the carbohydrate fractions of traditional plant foods; and seasonal information is needed as well (Wandsnider referred to seasonal information in the context of animal foods, but it applies equally to plant foods).

This study of glacier lily bulbs provided information relevant to all of the above, but it must be considered a preliminary analysis only. While there was subsampling to ensure a level of precision in the lab results, there was no true replication in terms of collecting independent samples for each analysis. The only exception was the single replication of the drying and pit-cooking treatments, and the similarities to the other samples, both in general composition and in the change effected by pit-cooking, do lend some confidence in the results. Many additional collections are necessary for meaningful measures of variability.

It would be interesting to examine additional treatment types, such as pit-cooking raw bulbs, and boiling dried bulbs, and to compare the sweetness levels. Pit-cooking may have very different effects on raw bulbs than the effects on the dried bulbs shown here. Also, effects of treatments should be examined with bulbs collected at the flowering stage, because people apparently collected at that stage at least some of the time traditionally, and since the carbohydrate profile varies through the season. In addition, taste trials with elders and others, perhaps using a simple hedonic scale like that used by Kuhnlein et al. (1982), could help in understanding why certain treatments were

preferred.

Comparing bulbs from different areas within this species' large range may lend some insight into why the bulbs are used so intensively by the northern interior plateau peoples and not elsewhere, though it is likely other factors are more important (e.g., greater availability of camas or other root resources).

An analysis should be undertaken of the starch digestibility (e.g. amylose / amylopectin ratio) and resistant starch content of the bulbs under different treatment regimes. Wandsnider (1997) suggests that traditional foods with slowly digested starches were often pit-cooked (though with lower temperatures and less cooking time than fructan-containing roots), while foods with rapidly digested starches were not. It is possible that glacier lily bulbs were often pit-cooked while spring beauty (*Claytonia lanceolata*) corms were not, for this reason.

Ultimately, studies like those of Thorburn et al. (1987) and Brand et al. (1990), in which a variety of carbohydrate-rich traditional plant foods are examined for glycemic and insulin responses, are needed to investigate the potential preventative effects of Interior Salish diets against diabetes. This work should include a search for compounds that have a hypoglycemic effect via inhibition of alpha-glucosidases and alpha-amylases (see review by Johns and Chapman [1995]). This latter type of analysis is currently being performed on traditional food plants of North America (including yellow glacier lily bulbs), as part of a doctoral project by Letitia McCune at CINE.

4.5 Summary

Bulbs of *Erythronium grandiflorum* from south-central British Columbia were analyzed for their nutritional and carbohydrate composition. In particular the effects of growth stage (pre-flowering, flowering, early fruit, mature fruit) and traditional and modern treatment methods (wilting, boiling, drying, pit-cooking) on the carbohydrate profile were investigated. Results indicate that bulb carbohydrates change rapidly (both in amount and type) through the growing season, a phenomenon that is probably typical for spring ephemeral species. Starch content and probably bulb size reach a maximum,

and moisture content a minimum, at the early fruit stage of growth. Therefore, collecting at this stage of growth would result in the greatest nutrient return for effort invested, a fact that appears to have been appreciated by Indigenous harvesters. Drying / storage may be the traditional treatment with the greatest impact on sweetness of the bulbs. This differs from root vegetable species that store mainly fructan, for which pit-cooking is necessary to produce fructose and make the food sweet. However, the importance of pit-cooking should not be underestimated for *E. grandiflorum* bulbs. It would have allowed the flavours to be appreciated and enhanced, and was also of great advantage logistically in processing large amounts of this important food resource. It is also possible that pit-cooking influenced the starch digestibility and decay resistance of the bulbs. The bulbs were once consumed as a staple root vegetable and are a significant source of nutrients, particularly carbohydrates and food energy. They may also have promoted general good health in conjunction with other traditional root vegetables.

5.0 General Discussion and Conclusions

Many ecologists still tend to study plant ecology with the goal to understanding plant dynamics in "natural" or "pristine" environments, with human influence considered an "unnatural" disturbance factor. This view of human impacts may be appropriate in terms of modern effects such as urban sprawl, industrial logging, or pesticide spraying. However, many plant communities in western North America and elsewhere have been influenced for long periods of time by First Nations peoples (Blackburn and Anderson 1993), and therefore past human impacts legitimately may be considered a "natural" part of such ecosystems. An ecological examination of any plant species, and particularly one known to have been used intensively and managed by humans for centuries, is incomplete without a consideration of potential ethnobotanical influences. Conversely, ecological information can give insight into how and why a species came to be intensively used.

The commonness and abundance of *Erythronium grandiflorum* must have been key factors in allowing this species to become an important food resource for northern plateau peoples. Yet, the breadth of the species' range, and the fact that large populations of the plants still exist in traditional gathering areas, lead one to ask such questions as:

i) Could indigenous peoples have influenced the range of the species?

ii) How was the bulb resource harvested sustainably in large quantities over long periods of time, as appears to have been the case (Turner et al. 1990)?

iii) Is yellow glacier lily adapted to a disturbance regime such as that associated with First Nations' use and management?

These questions relate to distribution and abundance, the two major aspects of the ecology of species according to Krebs (1978). Of the two, distribution is more difficult to address. As noted in Chapter 2, many factors can influence why a species occurs in some areas and not others, including chance, and conditions may have been very different for dispersal in the distant past than today. For yellow glacier lily, there is no direct evidence or suggestion that northern plateau peoples deliberately started new populations with

seeds. In terms of transplanting the bulbs, opinions differ among contemporary Secwepemc elders. Although Mary Thomas has transplanted the bulbs into her garden, she feels that in the past people had no need to do this: "they just cultivated them where they were growing" (SEP 1993-1997). In contrast, George Keener (another Secwepemc elder), stated of transplanting **scwicw** or other roots that "our people were known to do that" (SEP 1993-1997). Based on ethnobotanical documentation, it seems unlikely that the practice of transplanting was common, at least in the ethnohistoric period. Still, it may have been more common long in the past, or it may have taken place accidentally. Certainly it is possible for the bulbs to be transplanted successfully, even to a very different elevation/climate zone, as both Mary Thomas (above) and I (Chapter 2) have shown (at least over the short term). The practice of storing bulbs fresh in cache pits may have led to this kind of accidental dispersal, if a pit were abandoned for some reason (Peacock and Turner in press) or if a few bulbs were left behind, though Mary Thomas (pers. comm. 1998) feels it is unlikely that any of these all-important stores would have been neglected. The pattern in anther colour I observed in the sites I studied (Chapter 2) gives an intriguing suggestion that the Chase populations may be related to those in certain subalpine areas. However, it is also possible that the pattern is simply due to chance.

Likely effects on abundance are easier to assess, and were probably more significant. A number of aspects of traditional use not only could have prevented decline of glacier lily populations due to overharvesting, but in fact may have positively affected them. These aspects may be grouped into three broad classes:

1. Tilling

Most gardeners are aware that tilling the soil can be beneficial for plant growth, and in fact "gardening" may be an apt description of the type of relationship plateau hunter-gatherers had with many plant resources (note title of Peacock and Turner [in press], derived from an indigenous elder's quote). The action of the digging stick aerated the soil, aiding the growth of microorganisms and thus nutrient cycling (Bidwell and

Hole 1965), as well as root growth. In addition, the churning of the soil and selective harvesting of the bulbs resulted in a "thinning" process, reducing competition both from other vegetation and from older *Erythronium* plants (cf. Gott 1982, Anderson 1993b, Gottesfeld 1994). Hughes (1992) showed experimentally that disturbance that results in removal of co-occurring vegetation dramatically increases the local distribution and abundance of *Erythronium americanum* in New Hampshire. That species normally spreads mainly by rhizomes, but the results indicated that sexual reproduction and seed dispersal also increased as a result of the decreased competition.

It is also likely that the disturbed substrate resulting from digging enhanced seed germination. In Chapter 2, I suggested that litter cover and depth may adversely influence seedling germination and juvenile survival. Digging would remove litter from small areas and promote direct contact of seeds with the soil. This idea is supported by Caldwell's (1969) observation that seedlings of *E. grandiflorum* established readily on exposed mineral soils disturbed by burrowing animals.

Furthermore, the fact that people often harvested glacier lilies during the fruiting stage may have been significant in helping to scatter the seeds, which would prevent the seeds from being eaten by seed predators in the capsules (see Chapter 1). Also, the act of digging would have promoted at least partial burial of the seeds, and in garden plots, broadcast seeds of this species seldom germinate, while seeds that are lightly buried by raking produce seedlings prolifically (Thomson et al. 1996). Digging with a digging stick may or may not exert a similar effect.

Indigenous peoples (and grizzly bears) once created such microdisturbances at lower elevations, but these effects are no longer present to a significant degree. At higher elevations, however, grizzly digging and small mammal activity probably help maintain these effects. Many microtines undergo periodic population irruptions (Smolen and Keller 1987), and in such peak years their digging activity may produce a substrate remarkably like cultivated soil. Bob Miller, a former Park Warden who has spent most of his life in the Wells Gray Park area, related to me (pers. comm. 1996) that about 20 years ago a population irruption of voles occurred at Table Mountain. The glacier lilies

appeared to be decimated, but the ones that were left behind were larger than normal and had more flowers. Fortuitously, Tay Briggs (proprietor, Wells Gray Backcountry Chalets, pers. comm. 1996) informed me of a similar phenomenon that was occurring that year on 52 Ridge in Wells Gray Park. I was able to observe the "rototiller"-like effect (Fig. 5.1), perhaps caused by *Microtus pennsylvanicus, M. richardsoni* or *M. longicaudus:* over an area of at least a square kilometre, vigorous subalpine plants were growing in a churned soil with absolutely no turf layer. Small mammal activity occurs at low elevations as well; for example, winter soil casts left by pocket gophers (*Thomomys talpoides*) were apparent in some of my sites in southwestern Alberta and possibly Mt. Mara. However, for unknown reasons I noticed very little small mammal activity in the Chase-area and Botanie sites. The current lack of human, grizzly bear, and apparently other mammal digging in these lower-elevation areas may now be compounded by the increased litter from introduced grasses, as well as by the absence of landscape burning (see next section) and perhaps presence of cattle, in terms of hindering glacier lily regeneration.

While experimental work investigating the impacts of indigenous digging and harvesting is still in its infancy (Anderson 1993b [see next section]), interesting comparisons can be made to studies of animal digging and burrowing. It is beyond the scope of my thesis to review this literature in detail,[1] but I will briefly discuss results for pocket gophers and grizzly bears, as these mammals are known to influence many areas where glacier lilies grow (see section 1.1.6).

Pocket gophers (*Thomomys* and *Geomys* spp.) are fossorial rodents that create extensive tunnel systems. They have broad vegetarian diets but consume below-ground storage organs preferentially (Huntly and Inouye 1988). Huntly and Inouye (1988) review the various effects of pocket gopher activity on ecosystem processes over a variety of spatial and temporal scales. They discuss in detail effects including altered species

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[1]See the series of articles in the journal BioScience (1988:750-800) on "How Animals Shape Their Ecosystems," as well as Huntly (1995) for an overview, and additional comments later in this chapter.

Figure 5.1 Churned soil in a subalpine meadow at 52 Ridge, Wells Gray Park, in 1996, presumably caused by vole activity.

composition and increased species diversity, changes in microtopography, soil structure and soil nutrients, and impacts on local and system-wide primary productivity. One study cited by Huntly and Inouye (1988) found that the area around pocket gopher mounds had significantly increased production that more than offset the local bare area of the mounds (soil nutrients were a likely cause). Of particular interest is the fact that plants preferred as food by the gophers (such as forbs) actually appear to *increase* in abundance as a direct result of gopher disturbance. As Huntly and Inouye (1988:791) remark: "These facts raise the interesting possibility that the overall effects of gophers, under at least some conditions, may result in gophers effectively farming their preferred resources." However, they also point out that this hypothesis has not been directly tested.

Recent studies on grizzly bear digging are even more relevant to this thesis, for two reasons. First, grizzly bear digging is probably much more similar to indigenous human digging than is pocket gopher tunnelling; compare the following description of grizzly digging (of yellow glacier lilies) with my description of human digging in section 3.3.2: "When digging for corms, the bears turn over chunks of sod at a fairly uniform depth of about 10 cm (the maximum depth of the majority of roots), exposing corms which are then nipped off. . . . many glacier lily corms and fragments remain to resprout in the following year" (Tardiff and Stanford in press). Young (1998:3) further notes that the bears "have been observed redigging old digs, as if they were 'farming' the glacier lilies."

Second, these recent studies have examined effects of digging in direct relation to aspects of glacier lily growth, reproduction, and physiology. Tardiff and Stanford (in press) and Young (1998) studied digs in a subalpine meadow in Glacier National Park, Montana, comparing soil and glacier lilies in dug areas with those in adjacent undisturbed meadow. Tardiff and Stanford (in press) obtained the following (statistically significant) results: higher levels of ammonium and nitrate in dug soil (even true for soil from a 10 year old dig); higher tissue nitrogen and water soluble carbohydrates in bulbs from digs; and twice as many seeds produced by glacier lilies in digs. They also created experimental digs and confirmed that digging results in higher ammonium and nitrate

levels (ruling out the possibility that the bears are choosing sites already high in nitrogen). Young (1998) further found that glacier lilies in digs had higher photosynthetic rates than plants in undisturbed areas, and she attributed this to the increased soil nitrogen in digs. (The release from competition due to the digging disturbance may also help explain the results of both studies). Young did not find significant differences in seed number, seed weight, bulb biomass, and bulb nitrogen and carbohydrates, though the trends were generally for higher values in digs (the issue of statistical power was not addressed). In both studies, the authors considered the broader ecosystem-level implications of the results; i.e., bears may increase the rate and amount of cycling of nitrogen, a limiting nutrient, and allow glacier lilies and other plants with a low C:N ratio (which in turn are more favourable for herbivores and microbial decomposers) to be maintained over time.

2. Vegetative Propagation

In the act of using their digging sticks and removing bulbs from the ground, indigenous women probably accidentally separated the bulb-appendages from the bulbs and thereby promoted vegetative reproduction, which is thought to occur infrequently in undisturbed conditions (see section 2.3).[1] This effect could be considered part of the incidental benefits of tillage discussed in the above section. However, this process was not always accidental. As discussed in Chapter 3, women often purposely separated and replanted these appendages, which will have made the process much more effective.

It is clear that indigenous hunter-gatherers had an understanding of the importance of selective harvesting and vegetative regeneration for root vegetables. At least 35 species were managed this way on the British Columbia interior plateau (Gottesfeld 1994, Peacock and Turner in press). For the Dena'ina of Alaska, "if a person digs the

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[1]Breaking of the bulbs themselves may also have contributed to this process (see section 2.3). I have observed when digging the bulbs that they often break off just above the base. However, this could be more common now due to soil compaction from cattle; elders state that the bulbs were once much easier to collect.

roots or other underground parts of a plant, he may bury a small piece to insure the growth of a new plant" (Kari 1991:19). Anderson's (1997) review cites numerous examples for various groups in the present-day United States. One example is the Cahuilla of southern California, who gathered the mature corms of blue dicks (*Dichelostemma capitatum*) in great quantity, but carefully replanted the cormlets. There are a number of examples of early European explorers and researchers observing these practices, and so it is unlikely that all of these cases could have resulted from indigenous peoples' learning horticulture from the Europeans.

The importance of purposeful replanting of small segments has been scientifically demonstrated by Anderson (1993b) in her traditional harvesting research using *Dichelostemma capitatum*. She used an experimental design with factorial combinations of two-level variables including harvest intensity (50% vs. 100%) and replanting of cormlets (yes or no). At the end of the four-year experiment, medium intensity harvests with replacement of cormlets resulted in the greatest number and weights of corms and cormlets. The fact that these values were higher than those in the control plots shows the importance of thinning (see previous section) for this highly vegetatively-productive species. Surprisingly, however, harvesting 100% of the corms produced no significant differences from the 50% rate, *when cormlets were replanted.* Therefore, even with very intensive harvesting, purposeful vegetative propagation could maintain a productive supply. While there are clearly differences in the capacity for vegetative propagation in *Dichelostemma* and *Erythronium grandiflorum*, Anderson's study still indicates that sustainable harvesting is possible for geophytic species and suggests an avenue for future research on *E. grandiflorum*.

3. Landscape Burning

As I discussed in section 3.3.5, landscape burning was widely practiced by plateau

First Nations[1] for a variety of purposes, including maintaining habitat for root vegetable species (Turner 1991). I further noted that *E. grandiflorum* has been specifically indicated in the ethnographical literature and by contemporary elders as being a root resource managed in this way.

It seems clear that glacier lilies are well equipped to survive fires, since they are safely ensconced underground well before conditions are warm and dry enough for an area to burn. In Chapter 2, I indicated that fire has been a common influence in the areas I studied (I found charcoal in 30 of my 38 soil samples). Even more direct proof that these plants survive fire is given by Christensen et al. (1989) in the form of a photo showing yellow glacier lilies coming up through blackened ground the year after the intense 1988 Yellowstone fires.

However, *E. grandiflorum* may not only be able to withstand fires, but may respond positively to them. In Chapter 2, I discussed the possibility that fire may be important in opening up areas of suitable habitat in otherwise unfavourable forested environments. First Nations' burning would actively maintain these habitats by preventing tree encroachment. Even in meadow areas where the woody cover consists of shrubs, fire may play a positive role. I did find apparently vigorous *Erythronium* growth under and around deciduous shrubs such as hawthorn (*Crataegus*), snowberry (*Symphoricarpos*), saskatoon (*Amelanchier*), and rose (*Rosa*). However, as I indicated in Chapter 2, shrubs are a major source of litter, which is negatively correlated with reproductive success. It may be that glacier lilies and shrubs often co-occur on the landscape in lower-elevation meadows due to microtopographic factors that influence moisture availability. If these areas were burned, it is possible that the lilies would be even *more* vigorous than they are now, in terms of increased juvenile survival and vegetative growth. Certainly many elders believe that when areas get too "bushy," they have to be burned to maintain optimal growth of root food species (see Baptiste Ritchie's

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[1]In fact, landscape burning has been utilized all over North America and the rest of the world by indigenous peoples for similar purposes; see, for example, Pyne (1982) and Gott (1983).

quote in Chapter 3). While many shrubs can resprout (the basis of First Nations' burning to enhance berry crops), burning would still remove litter and reduce competition from fire-intolerant species.

In addition to preventing tree encroachment, removing litter, and reducing competition, fire has other effects that would probably be beneficial for glacier lily growth. In general, soil pH increases after a fire, with the degree of change dependent on the type of cations released and the acidity of the soil before the fire (Barbour et al. 1987). This increase in pH, along with the released nutrients, in turn enhances growth of free-living, nitrogen-fixing bacteria (Barbour et al. 1987). The positive effects of nitrogen inputs on yellow glacier lily were discussed above; therefore, it seems that both digging and fire may be significant in promoting vigorous growth of this species. There is also scientific support for Mary Thomas' idea that controlled burning removes pathogenic organisms (Bidwell and Hole 1965), though research has not been done on yellow glacier lily habitats specifically.

While no studies have specifically examined the effects of fire on any *Erythronium* species, effects on other bulb-forming perennials have been documented. Californian species including *Zigadenus fremontii*, *Chlorogalum pomeridianum*, *Dichelostemma pulchella*, and several species of *Calochortus* all exhibit enhanced flowering following a fire (Muller et al. 1968, cited by Barbour et al. 1987). In addition, a recent prescribed burn experiment in the San Juan Islands revealed that, while many species decreased in abundance after the burn, *Camassia leichtlinii* increased dramatically, with cover values 3 to 4 times what they had been before the burn (Dunwiddie 1997). Nancy Turner (pers. comm. 1998) noted that *Calochortus macrocarpus* and *Allium cernuum* exhibited extremely vigorous growth in an area north of Lillooet that had been burned; the *Allium* were 65 cm tall. All of these species except *Zigadenus* were intensively used root food resources in the Pacific Northwest (Turner 1995, 1997a, Anderson 1997), and it is likely that *E. grandiflorum*, a similar geophytic, managed food resource, could exhibit a similar pattern.

It is unlikely that seeds of yellow glacier lily in the capsules or on the soil surface

could survive a fire. However, if, as noted earlier, post-flowering harvesting helped bury seeds in the ground, such harvesting would aid survival (since even just a few centimetres down is often enough to escape lethal temperatures) (Barbour et al. 1987). Even if the current seed crop were destroyed by a burn, the ca. five-year rotation of burning (see section 3.3.5) would have allowed ample time for seed reproduction between burns. Also, according to seed biologist Carol Baskin (pers. comm. 1998), *Erythronium* plants emerging the following year would probably be exceptionally vigorous and produce many seeds, so that the destruction of seeds in one year could be followed by a year of high seed production.

While I have discussed specific details of relevant literature above, I would like to examine on a broader, conceptual level, three fields of study related to human use and management of plant resources.

1. Anthropology

Alston Thoms' (1989) dissertation was an important advance in examining the potential past significance of root vegetables to hunter-gatherer diets in the Pacific Northwest. Using camas (*Camassia* spp.) as the main basis for his argument, he delineated the following five criteria for determining whether a root resource is "intensifiable" (i.e., a resource for which intensive and sustained exploitation is expected):

1) carbohydrate-rich bulbs, corms, or tubers, etc.;

2) reproductive systems well-adapted to regularly churned soils;

3) extensive abundance in accessible settings;

4) readily available (relative ease of digging);

5) resilience to environmental fluctuations.

In Chapter 4, I demonstrated clearly that bulbs of *E. grandiflorum* fit criterion 1, and I presented evidence and arguments for criterion 2 in Chapters 2 and 5. Criterion 3 is

also clearly met, with large tracts of the plant in such areas as Neskonlith Meadows and Botanie Valley, as well as in subalpine areas that people were known to frequent. Criterion 4 is more questionable today, with the tough turf layer in many areas, but elders indicate that at one time the bulbs were much easier to dig. Subalpine areas tend to be rocky and therefore bulbs may be less "available" in those areas than in the lower-elevation meadows. However, this is not always the case, and I found that certain subalpine meadows (e.g. Trophy Mountain, Taylor Creek) had rockiness values comparable to or even less than some lower elevation meadows. Finally, it seems clear that criterion 5 also applies to yellow glacier lily. The environmental amplitude is demonstrated in a basic way by the number of different habitat types that the species occupies. However, even if this is made possible by means of ecotypic differentiation, the transplant experiment discussed in Chapter 2 suggests that yellow glacier lilies from a given site can adjust successfully to an entirely different environment, at least over a two year period. The fact that two different types of mycorrhizae are associated with roots of *E. grandiflorum* may also be an indication of its environmental amplitude (section 1.1.6).

The fact that most or all of these criteria are met gives an added line of support for the likelihood that yellow glacier lily was (or could have been) intensively exploited in the past by plateau peoples. It would be interesting to examine whether these criteria are met in the southern (U.S.) part of the species' range, where the plant was little used for food. If they are met, it would suggest that Thoms' criteria may be necessary but not sufficient for intensive exploitation of a given root resource, and that other factors must be considered (e.g. the relative abundance of other root foods).

Another aspect of the anthropological literature worth considering is the relatively recent reexamination of the "hunter-gatherer" (commonly equated with simple "forager"), versus "agriculturalist" dichotomy. Previously, it was believed (and the attitude is still fairly prevalent), that hunter-gatherers in no way actively managed the food resource, as exemplified in the following quote:

> Previous to the advent of the Christian Missionaries, the Indians of British Columbia did no cultivation, as such. They depended for their vegetable food on certain kinds of roots, shoots, leaves and berries which grew in their immediate neighbourhood, or which they might come across in their wanderings. (Wilson 1916:17)

Ford (1985) was among the first to suggest that plant food production be viewed not as a dichotomy but as a continuum, from foraging, through cultivation (characterizing "incipient agriculture" and gardening), to domestication (an aspect of field agriculture, in which major genetic changes are produced through selection and hybridization). Cultivation strategies include, for example, tending, tilling, and transplanting. Deur (1997:1) has similarly defined cultivation as "a continuum of practices in which the repeated manipulation of both plants *and* their environments serves as a means toward the anticipated ends of quantitatively and qualitatively enhanced plants" [emphasis in original]. The traditional harvesting and management strategies used for *Erythronium grandiflorum* support these new perpectives, and suggest that the "hunter-gatherers" of the northern plateau be viewed not as simple foragers but as incipient agriculturalists.

2. Ecology

Increasingly, ecologists are recognizing that the roles of many organisms in a community are not limited to classic ecological interactions such as predation, parasitism, competition, and mutualism. The various interactions of many species may also have broader ecosystem-level implications. As noted by Huntly (1995:76):

> I also suggest that herbivores frequently are a cause of spatial and temporal structure in environmental conditions. Both trophic and nontrophic activities contribute to production of structure, which provides opportunities for different sorts of primary producers to persist in communities, often changing species composition, tending to increase diversity, and probably affecting spatial and temporal stability of ecosystem productivity and nutrient dynamics.

Lawton and Jones (1995) coined the term "ecosystem engineering" to refer to this

role of organisms in creating, modifiying and maintaining habitats. These authors do not recognize indigenous peoples as being significant in this regard; their only mention of humans is in terms of modern engineering "analogues" such as constructing dams, skyscrapers, and sea walls.[1] However, using their own definitions, hunter-gatherer peoples certainly qualify as natural "ecosystem engineers," with very similar effects to animals in terms of, for example, digging. (In other words, one might say that such effects of humans have not merely been *analogous*, but *homologous*). Lawton and Jones note that effects of ecosystem engineers may be incidental to an organism's lifestyle (e.g. alligator wallows) or may have positive benefits in terms of the organism's fitness. The effects on glacier lilies of digging, whether it be by the "engineering" of small mammals, grizzly bears, or humans, appear to be an example of the latter situation.

Of course, the purposeful and directed traditional management strategies used by First Nations mean that the effects of indigenous peoples are in many respects fundamentally different from those of other animals. These strategies include weeding of the harvesting grounds, selective harvesting of the largest bulbs, deliberate removal and replanting of bulb-appendages, landscape burning, and broader societal controls on harvesting (e.g. rotating harvests, prohibitions against waste and overuse, etc.). Yet, these differences in no way negate the fact that indigenous peoples in northwestern North America have had ecologically and potentially evolutionarily significant interactions with plants and their habitats.

3. Ethnoecology

It is evident from the above discussion that both anthropologists and ecologists are (or should be) rethinking two long-established, artificial dichotomies: that of foragers vs. agriculturalists, and that of "natural" ecosystems vs. those with indigenous human

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[1]The review papers and books on this topic represent a prime example of the consequences of academic specialization and lack of communication among disciplines. Often, effects are discussed which clearly apply to impacts of indigenous peoples on ecosystems, but most ecologists appear to be completely ignorant of this. Invariably, in the sources I consulted, if human impacts are mentioned, it is in the modern, industrial sense only.

impact. Clearly, these dichotomies are related. Both are addressed in the expanding field of ethnoecology, which examines the interrelationships of indigenous peoples with ecological patterns and processes. Kat Anderson, whom I have already frequently cited, is a leading researcher in this field. In particular, my work is relevant to and supports a recent paper by Anderson (1997), which deals specifically with indigenous cultivation of geophytes in California. The following commonalities between Anderson's and my conclusions are worth emphasizing, as they suggest that uses and characteristics of geophytes may be quite general among hunter-gatherers and their root resources:

1) Underground parts of many geophytes were once gathered and stored in great abundance.

2) Methods of tillage, selective harvesting, replanting of small parts, and general ethics of respect and conservation are common to Californian and northern plateau groups who used geophytes.

3) Disturbances of various types (e.g. mammalian digging, lightning-caused fires) are natural aspects of ecosystems in which many geophytes thrive, and may have been mimicked or increased by indigenous practices.

To summarize, and to address question (iii) put forth at the beginning of this chapter, it does appear that *E. grandiflorum* is adapted to a periodic, moderate disturbance regime such as that associated with First Nations' use and management. Bulb predation (whether by people, grizzly bears, or small mammals) occurs in patchy fashion across the landscape, and would allow populations in individual sites time to recover before being "farmed" again. Yet the relationship was not simply +/-, and is better described as mutualistic rather than predatory. Human use may have had far-reaching effects in terms of increasing vegetative and sexual reproduction, and even in terms of enhancing the nutritional characteristics of the resource. In addition, on a landscape level, human use of fire may have increased fire frequencies and initiated fires in areas that would otherwise be forested, opening suitable habitat and helping maintain favourable habitat characteristics over time. Thus, human use and management strategies may have led to a

coevolutionary situation in which disturbance led to positive feedback in both the quantity and quality of yellow glacier bulbs.

5.1 Suggestions for Future Research and Other Recommendations

Anderson (1997) believes that a full understanding of wild plant production systems will require three research approaches:

1) *Ethnobotanical studies* - "More ethnographic studies of native peoples that explore the multidimensionality of traditional ecological knowledge with respect to one focal plant species are needed." (p. 164);

2) *Observational studies* - "The natural history of most native plant species is not well known. . . . [and] information about . . . essential aspects of the species' biology and ecology are a very important complement to ethnobotanical research." (p. 164-165); and

3) *Greenhouse and field experiments* - "[The above] information would form a basis for the design of experiments which would empirically test the effects of various gathering and horticultural techniques . . . on the growth and reproduction of particular native plants . . . " (p. 165).

In my research, I have, at least in part, addressed the first and second requirements, and I have speculated on the likely ecological effects of traditional harvesting and management strategies. The obvious next step is to pursue experimental research that directly investigates the effects (on glacier lily growth, vegetative and sexual reproduction, and bulb nutrient characteristics) of tillage, appendage replanting, and landscape burning. These various components will likely have to be investigated separately, at least initially, in order to more clearly understand the various effects. Ultimately, however, they will have to be understood as being part of an integrated system of resource management.

Certain types of observational research may also be fruitful. One would expect human selection to favour bulbs with the greatest number of appendages (Anderson 1997), and thus there may be differences in the capacity for vegetative propagation between areas of intensive traditional use and areas where the species was not used.

Comparing underground morphology across the range was already suggested (section 2.3); the hypothesis that humans may have selected for greater vegetative reproduction could be explicitly tested. If replanting of the appendages was not a common practice, no differences are likely to be found between areas of human use and areas where (for example) only grizzly bears dug the bulbs and accidentally promoted this process.

Experimental research along the lines of Anderson's (1993b) could be combined with an initiative to allow local First Nations people access to resources in traditional harvesting areas currently located in protected areas. Large populations of glacier lilies are present in many provincial and national parks, and such a project could be initiated in an area of abundant growth without serious risk. Results of this research could ultimately inform management policies in protected areas, as well as restoration efforts elsewhere. As noted by Anderson (1996:155), ". . . restoration involves not only reintroducing plants and animals known to exist in the area historically, but also reproducing the forces that shaped the model community."

The cultural benefits of First Nations' involvement in such a project (either in or out of a park), and in general of reincorporating traditional foods into a modern diet, are likely to be significant. Next to language, food is probably the most fundamental defining element of any cultural group. (Witness any folk festival held in North America, and the central role of cultural foods.) A number of programs that have encouraged integrating traditional foods into the modern diet have been successful both in improving health and increasing cultural awareness and pride; e.g. the Nuxalk Food and Nutrition Program (Nuxalk Food and Nutrition Program 1984, Kuhnlein and Burgess 1997), and the Wai'anae Diet Program in Hawai'i (Shintani et al. 1991, Wai'anae Diet Program 1993). Yellow glacier lily bulbs can certainly be recommended as a traditional food that could be added to a modern diet. They are nutritious (see Chapter 4), tasty, and culturally significant. Gathering the bulbs will have benefits in terms of exercise, particularly given the very tough turf layer that has developed in many areas! The potential for overharvesting is always a concern when recommending use of a wild food, but in this case, if harvesting is done prudently (in keeping with traditional principles), it could

actually help maintain vigorous lily populations. In addition, the plants can be grown in a garden setting; as I have mentioned, Mary Thomas has successfully done this. Active encouragement of vegetative reproduction by means of removing and replanting the bulb-appendages, along with regular tilling and weeding, would probably result in a thriving garden crop.

In addition to studying and promoting traditional use, there is a need to examine the impacts of modern influences such as cattle and introduced plant species. In Chapter 2, I put forth the possibility that moderate levels of grazing may be beneficial in areas with many introduced grasses, and where natural fires have been suppressed. However, soil compaction due to trampling is a real concern, as noted by Mary Thomas and supported by the scientific literature (Bidwell and Hole 1965). Studying modern impacts will be complicated due to the difficulty of finding "control" areas, and because one negative "modern" impact on many habitats may be the *lack* of traditional harvesting and management strategies. Carefully designed experiments will be necessary to tease out these various possibilities. And, as noted in Chapter 3, traditional knowledge will be important in helping understand the nature of glacier lily populations and habitats before significant modern impacts were evident.

Finally, it is important to note that, in spite of its apparent adaptation to the digging disturbance, yellow glacier lily is almost certainly not immune to overharvesting. In fact, Kershaw et al. (1998) report that in some places, glacier lily populations have been greatly reduced by overharvesting (though I learned that this information came from a United States park flower guide, with no specific details). Gottesfeld (1994) states that, even with low human population densities, any level of human technology is likely to eliminate culturally significant species with unrestricted exploitation. As I have suggested, glacier lilies are probably adapted to *moderate* levels of disturbance (periodic digging and fires), and at some level of harvesting the balance may be tipped toward degrading the population. Future research will have to determine the nature of this balance for *E. grandiflorum,* and the particular degree of disturbance and removal that encourages vegetative growth and regeneration and sexual reproduction, but does not

overwhelm the population's ability to maintain itself. Such research may confirm that First Nations long ago empirically determined a level of disturbance that allowed or promoted sustainable use.

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Appendix 1. Codes and full botanical names for all taxa found in this study at 38 sites with *Erythronium grandiflorum*. Nomenclature follows Hitchcock and Cronquist (1973), except where indicated [D] for Douglas et al. (1989, 1990, 1991, 1994), or [C] for Cronquist et al. (1977). Non-native species are indicated with an asterisk.

abilas	*Abies lasiocarpa* (Hook.) Nutt.
acegla	*Acer glabrum* Torr.
achmil	*Achillea millefolium* L.
actrub	*Actaea rubra* (Ait.) Willd.
agoaur	*Agoseris aurantiaca* (Hook.) Greene
agogla	*Agoseris glauca* (Pursh) Raf.
agrsmi	*Agropyron smithii* Rydb.
agrtra	*Agropyron trachycaulum* (Link) Malte [C]
agrexa	*Agrostis exarata* Trin.
allcer	*Allium cernuum* Roth
alnsin	*Alnus sinuata* (Regel) Rydb.
amealn	*Amelanchier alnifolia* Nutt.
anamar	*Anaphalis margaritacea* (L.) B. & H.
aneocc	*Anemone occidentalis* Wats.
anepar	*Anemone parviflora* Michx.
angarg	*Angelica arguta* Nutt.
angdaw	*Angelica dawsonii* Wats.
antana	*Antennaria anaphaloides* Rydb.
antlan	*Antennaria lanata* (Hook.) Greene
antmic	*Antennaria microphylla* Rydb.
antneg	*Antennaria neglecta* Greene
antpar	*Antennaria parviflora* Nutt.
antrac	*Antennaria racemosa* Hook.
antumb	*Antennaria umbrinella* Rydb.
aqufla	*Aquilegia flavescens* Wats.
aradru	*Arabis drummondii* Gray
aragla	**Arabis glabra* (L.) Bernh.
arahol	*Arabis holboellii* Hornem.
arcuva	*Arctostaphylos uva-ursi* (L.) Spreng
arena	*Arenaria macrophylla* Hook. or *Arenaria laterifolia* L.
arecap	*Arenaria capillaris* Poir.
arncor	*Arnica cordifolia* Hook.
arnlat	*Arnica latifolia* Bong.
arnmol	*Arnica mollis* Hook.
arnpar	*Arnica parryi* Gray
arnryd	*Arnica rydbergii* Greene
artnor	*Artemisia norvegica* Fries
aspden	*Aspidotis densa* (Brack.) Lellinger
astcil	*Aster ciliolatus* Lindl.
astcon	*Aster conspicuus* Lindl.
asteng	*Aster engelmannii* (Eat.) Gray
astfol	*Aster foliaceous* Lindl.

astmod	*Aster modestus* Lindl.
astame	*Astragalus americanus* (Hook.) Jones
astmis	*Astragalus miser* Dougl.
astrob	*Astragalus robbinsii* (Oakes) Gray
balsag	*Balsamorhiza sagittata* (Pursh) Nutt.
betgla	*Betula glandulosa* Michx.
betpap	*Betula papyrifera* Marsh. var. *commutata* (Regel) Fern.
botry	*Botrychium* Sw. sp. (probably *B. lunaria* (L.) Sw.)
brocar	*Bromus carinatus* H. & A. var *carinatus*
broine	**Bromus inermis* Leys. ssp. *inermis*
brosit	*Bromus sitchensis* Trin.
brovul	*Bromus vulgaris* (Hook.) Shear var. *vulgaris*
bryo	bryophytes
calcan	*Calamagrostis canadensis* (Michx.) Beauv.
calpur	*Calamagrostis purpurascens* R. Br.
calrub	*Calamagrostis rubescens* Buckl.
calapi	*Calochortus apiculatus* Baker
calbul	*Calypso bulbosa* (L.)
camrot	*Campanula rotundifolia* L.
caroli	*Cardamine oligosperma* Nutt.
carex	*Carex sp.* or *spp.*
cararc	*Carex arcta* Boott
caratr	*Carex atrata* L.
carlen	*Carex lenticularis* Michx.
carhoo	*Carex hoodii* Boott
carmic	*Carex microptera* Mack.
carnig	*Carex nigricans* Retz.
carpet	*Carex petasata* Dewey
carpr1	*Carex praegracilis* W. Boott
carpr2	*Carex praticola* Rydb.
carray	*Carex raynoldsii* Dewey
carsci	*Carex scirpoidea* Michx.
carspe	*Carex spectabilis* Dewey
casmer	*Cassiope mertensiana* (Bong.) G. Don var. *mertensiana*
casti	*Castilleja* Mutis ex L. f. sp. or spp.
ceasan	*Ceanothus sanguineus* Pursh
cerarv	*Cerastium arvense* L.
chiumb	*Chimaphila umbellata* (L.) Bart.
cirsi	*?*Cirsium* Mill. sp. or spp.
clalan	*Claytonia lanceolata* Pursh
clecol	*Clematis columbiana* (Nutt.) T. & G.
colpar	*Collinsia parviflora* Lindl.
comumb	*Comandra umbellata* (L.) Nutt.
corcan	*Cornus canadensis* L.
cradou	*Crataegus douglasii* Lindl. var *douglasii*
creatr	*Crepis atrabarba* Heller
crycri	*Cryptogramma crispa* (L.) R.Br. var *acrostichoides* (R.Br.) C.B. Clarke
cynoff	**Cynoglossum officinale* L.

cysfra	*Cystopteris fragilis* (L.) Bernh. var. *fragilis*
dacglo	**Dactylis glomerata* L.
danspi	*Danthonia spicata* (L.) Beauv.
delph	*Delphinium* L. sp. (probably all *D. nuttallianum* Pritz. *var nuttallianum*)
distra	*Disporum trachycarpum* (Wats.) Benth. & Hook.
dodcon	*Dodecatheon conjugens* Greene
dodcus	*Dodecatheon cusickii* Greene
draaur	*Draba aurea* Vahl
drabor	*Draba borealis* DC. [D]
dracra	*Draba crassifolia* R. Grah.
elygla	*Elymus glaucus* Buckl.
elyinn	*Elymus innovatus* Beal
empnig	*Empetrum nigrum* L.
epialp	*Epilobium alpinum* L. complex
epiang	*Epilobium angustifolium* L.
epigla	*Epilobium glandulosum* Lehm.
equarv	*Equisetum arvense* L.
equpra	*Equisetum pratense* Ehrb.
equsci	*Equisetum scirpoides* Michx.
equvar	*Equisetum variegatum* Schleich.
erigla	*Erigeron glabellus* Nutt.
eriper	*Erigeron peregrinus* (Pursh) Greene
erispe	*Erigeron speciosus* (Lindl.) DC.
erisub	*Erigeron subtrinervis* Rydb.
eriher	*Eriogonum heracleoides* Nutt. var. *angustifolium* (Nutt.) T. & G.
fesida	*Festuca idahoensis* Elmer var. *idahoensis*
fesocc	*Festuca occidentalis* Hook.
fesrub	*Festuca rubra* L. var. *rubra*
fesvir	*Festuca viridula* Vasey
fravir	*Fragaria virginiana* Duchesne
frilan	*Fritillaria lanceolata* Pursh
fripud	*Fritillaria pudica* (Pursh) Spreng.
fung	unidentified fungi
galbor	*Galium boreale* L.
galtri	*Galium triflorum* Michx.
genama	*Gentiana amarella* L.
gerric	*Geranium richardsonii* Fisch. & Trautv.
gervis	*Geranium viscosissimum* F. & M.
geumac	*Geum macrophyllum* Willd.
geutri	*Geum triflorum* Pursh var. *triflorum*
gooobl	*Goodyera oblongifolia* Raf.
hacke	*Hackelia* Opiz sp. (*H. micrantha* [Eastw.] J.L. Gentry or *H. floribunda* [Lehm.] Johnst.)
hedsul	*Hedysarum sulphurescens* Rydb.
heluni	*Helianthella uniflora* (Nutt.) T. & G. var. *douglasii* (T. & G.) Weber
herlan	*Heracleum lanatum* Michx.
heucyl	*Heuchera cylindrica* Dougl. var. *cylindrica*
hiealb	*Hieracium albiflorum* Hook.
hiecyn	*Hieracium cynoglossoides* Arv.-Touv.

hiegra	*Hieracium gracile* Hook.
hiesco	*Hieracium scouleri* Hook.
hieodo	*Hierochloe odorata* (L.) Beauv.
holdis	*Holodiscus discolor* (Pursh) Maxim.
hydcap	*Hydrophyllum capitatum* Dougl. var. *capitatum*
juncu	*Juncus* L. sp. or spp. (mainly *J. drummondii* E. Meyer)
juncom	*Juniperus communis* L.
koenit	*Koeleria nitida* Nutt. [C]
latnev	*Lathyrus nevadensis* Wats.
latoch	*Lathyrus ochroleucus* Hook.
lich	unidentified lichen (mostly *Cladonia* Hill *ex.* Browne sp. or spp.)
lilcol	*Lilium columbianum* Hanson
linbor	*Linnaea borealis* L.
litpar	*Lithophragma parviflora* (Hook.) Nutt.
litrud	*Lithospermum ruderale* Dougl.
lomdis	*Lomatium dissectum* (Nutt.) Math. & Const.
lommac	*Lomatium macrocarpum* (Nutt.) Coult. & Rose
lomnud	*Lomatium nudicaule* (Pursh) Coult. & Rose
loncil	*Lonicera ciliosa* (Pursh) DC.
loninv	*Lonicera involucrata* (Rich.) Banks var. *involucrata*
lonuta	*Lonicera utahensis* Wats.
luepec	*Luetkea pectinata* (Pursh) Kuntze.
lupin	*Lupinus* L. sp. (probably always *L. arcticus* S. Wats. ssp. *subalpinus* [Piper & B.L. Robins.] Dunn) [D]
lupser	*Lupinus sericeus* Pursh
luzul	*Luzula* DC. sp. - either *L. hitchcockii* Hamet-Ahti or *L. parviflora* (Ehrh.) Desv.
luzcam	*Luzula campestris* (L.) DC.
mahaqu	*Mahonia aquifolium* (Pursh) Nutt. [D]
medlup	**Medicago lupulina* L.
melbul	*Melica bulbosa* Geyer var. *bulbosa*
melsub	*Melica subulata* (Griseb.) Scribn. var. *subulata*
merlon	*Mertensia longiflora* Greene
micnut	*Microseris nutans* Geyer (Schultz-Bip.)
micgra	*Microsteris gracilis* (Hook.) Greene
mitbre	*Mitella breweri* Gray
mitnud	*Mitella nuda* L.
mittri	*Mitella trifida* Grah.
monti	*Montia* L. sp.
orouni	*Orobanche uniflora* L.
osmor	*Osmorhiza* Raf. sp.
pacmyr	*Pachistima myrsinites* (Pursh) Raf.
parfim	*Parnassia fimbriata* Konig. var. *fimbriata*
pedbra	*Pedicularis bracteosa* Benth.
pedrac	*Pedicularis racemosa* Dougl. var. *alba* (Pennell) Cronq.
pelti	*Peltigera* Massal. sp. or spp.
pencon	*Penstemon confertus* Dougl.
penpro	*Penstemon procerus* Dougl. var *procerus*
pergai	*Perideridia gairdneri* (H. & A.) Math.

philew	*Philadelphus lewisii* Pursh
phlalp	*Phleum alpinum* L.
phlpra	**Phleum pratense* L.
phldif	*Phlox diffusa*
phyemp	*Phyllodoce empetriformis* (Sw.) D. Don
phymal	*Physocarpus malvaceus* (Greene) Kuntze
piceng	*Picea engelmannii* Parry / *P. glauca* (Moench) Voss
pincon	*Pinus contorta* Dougl. var. *latifolia* Engelm.
pinpon	*Pinus ponderosa* Dougl.
piper	*Piperia* Rydb. sp. (probably always *P. unalascensis* [Spreng.] Rydb.) [D]
plata	*Platanthera* L.C. Rich. sp. [D]
poac	Poaceae
poaalp	*Poa alpina* L.
poaepi	*Poa epilis* Scribn. [C]
poagla	*Poa glaucifolia* Scribn. & Will.
poagra	*Poa grayana* Vasey
poaint	*Poa interior* Rydb.
poalep	*Poa leptocoma* Trin.
poaner	*Poa nervosa* (Hook.) Vasey var. *wheeleri* (Vasey) Hitchc.
poapal	**Poa palustris* L.
poapra	**Poa pratensis* L.
poarup	*Poa rupicola* Nash
poasan	*Poa sandbergii* Vasey
poldou	*Polygonum douglasii* Greene
pollon	*Polystichum lonchitis* (L.) Roth
popbal	*Populus balsamifera* L.
potarg	*Potentilla arguta* Pursh
potdiv	*Potentilla diversifolia* Lehm.
potdru	*Potentilla drummondii* Lehm.
potfla	*Potentilla flabellifolia* Hook.
potfru	*Potentilla fruticosa* L.
potgla	*Potentilla glandulosa* Lindl.
potgra	*Potentilla gracilis* Dougl.
prunu	*Prunus* L. sp.
pruvir	*Prunus virginiana* L.
pruvul	*Prunella vulgaris* L.
psemen	*Pseudotsuga menziesii* (Mirbel) Franco var. *glauca* (Beissn.) Franco
pteaqu	*Pteridium aquilinum* (L.) Kuhn var. *pubescens* Underw.
pyrasa	*Pyrola asarifolia* Michx.
pyrchl	*Pyrola chlorantha* Sw.
pyrsec	*Pyrola secunda* L.
ranesc	*Ranunculus eschscholtzii* Schlecht.
rangla	*Ranunculus glaberrimus* Hook.
ranunc	*Ranunculus uncinatus* D. Don
rhicri	*Rhinanthus crista-galli* L.
rhoalb	*Rhododendron albiflorum* Hook.
ribes	*Ribes* L. sp.
rosas	*Rosa* L. sp.

rubpar	*Rubus parviflorus* Nutt.
rumac1	**Rumex acetosa* L.
rumac2	**Rumex acetosella* L.
salix	*Salix* L. sp. or spp.
samrac	*Sambucus racemosa* L.
sangra	*Sanicula graveolens* Poepp.
saxfer	*Saxifraga ferruginea* Grah.
saxint	*Saxifraga integrifolia* Hook.
saxocc	*Saxifraga occidentalis* Wats.
sedlan	*Sedum lanceolatum* Torr.
sedste	*Sedum stenopetalum* Pursh
senfoe	*Senecio foetidus* Howell var. *hydrophiloides* (Rydb.) T.M. Barkley
senint	*Senecio integerrimus* Nutt.
senpse	*Senecio pseudaureus* Rydb.
sentri	*Senecio triangularis* Hook. var *triangularis*
shecan	*Shepherdia canadensis* (L.) Nutt.
sibpro	*Sibbaldia procumbens* L.
silpar	*Silene parryi* (Wats.) Hitchc. & Mag.
sisloe	**Sisymbrium loeselii* L.
sisyr	*Sisyrinchium* L. sp.
smirac	*Smilacina racemosa* (L.) Desf.
smiste	*Smilacina stellata* (L.) Desf.
solmul	*Solidago multiradiata* Ait.
sorsco	*Sorbus scopulina* Greene
spibet	*Spiraea betulifolia* Pall.
spidou	*Spiraea douglasii* Hook.
stenit	*Stellaria nitens* Nutt.
steocc	*Stenanthium occidentale* Gray
stinel	*Stipa nelsonii* Scribn. var. *dorei* Barkw. & Maze [D]
stiocc	*Stipa occidentalis* Thurb. ex. S. Wats. var. *pubescens* Maze, Taylor & MacB. [D]
stramp	*Streptopus amplexifolius* (L.) DC.
strros	*Streptopus roseus* Michx.
sukvio	*Suksdorfia violacea* Gray
symph	*Symphoricarpos* Duhamel sp.
taroff	**Taraxacum officinale* Weber
thali	*Thalictrum* L. sp.
tiatri	*Tiarella trifoliata* L.
trago	**Tragopogon* L. sp.
trifo	**Trifolium* L. sp. or spp.
trican	*Trisetum canescens* Buckl.
trispi	*Trisetum spicatum* (L.) Richter
trigra	*Triteleia grandiflora* Lindl. [D]
trolax	*Trollius laxus* Salisb.
urtdio	*Urtica dioica* L.
vaccae	*Vaccinium caespitosum* Michx.
vacmem	*Vaccinium membranaceum* Dougl.
vacmyr	*Vaccinium myrtillus* L.
vacova	*Vaccinium ovalifolium* Smith

vacsco	*Vaccinium scoparium* Leiberg
vahatr	*Vahlodea atropurpurea* (Wahlenb.) Fries in Hartm. [D]
valdio	*Valeriana dioica* L.
valsit	*Valeriana sitchensis* Bong.
vervir	*Veratrum viride* Ait.
verarv	**Veronica arvensis* L.
vercus	*Veronica cusickii* Gray
verwor	*Veronica wormskjoldii* Roem. & Schult.
vicia	*Vicia* L. sp. (usually *V. americana* Muhl.)
vioadu	*Viola adunca* Sm.
viocan	*Viola canadensis* L.
viogla	*Viola glabella* Nutt.
vioorb	*Viola orbiculata* Geyer
vioval	*Viola vallicola* A. Nels. var. *major* (Hook.) Fabijan [D]
zigele	*Zigadenus elegans* Pursh
zigven	*Zigadenus venenosus* Wats.

Appendix 2. Values of quantitative environmental variables at the 38 sites surveyed in this study. Slope aspects, slope angles, elevations, latitudes and longitudes are in Table 2.1. Variable descriptions are in Table 2.2.

Site	tree-conif (m^2/ha)	tree-decid (m^2/ha)	shrub (% cover)	herbcover (% cover)	total-spp	intro-spp	native-spp	rock (cm)	litdep (cm)	litcover (% cover)	grass (% cover)	CWD (% cover)	pH	texture index	organic (%)	pheno-logy index
1	0.0	5.9	7.1	60.6	51	2	49	17.6	2.5	13.1	19	0.6	6.89	8.95	15.635	7.59
2	0.0	0.0	16.6	58.3	33	1	32	19.4	7.0	28	14	0.6	5.43	9.67	9.95	7.02
3	92.8	0.0	28.1	35.6	26	0	26	11.1	7.0	15.5	7.4	11.8	6.14	8.04	4.555	5.9
4	0.0	18.0	6.0	41.1	47	4	43	0.7	2.0	10.3	4.5	9.2	6.25	9.62	6.15	4.21
5	59.1	0.0	12.9	26.4	44	2	42	4.6	5.0	7.6	2.7	11.5	6.68	8.95	7.11	9.08
6	0.0	0.0	0.2	55.5	52	4	48	13.4	1.0	3.1	5.3	0	6.45	9.33	11.37	7.08
7	29.8	0.0	7.0	29.9	47	3	44	10.4	2.0	19.8	4.4	0.3	7.23	9.24	16.785	6.29
8	0.9	0.2	27.3	48.6	41	2	39	20.2	3.0	12.7	11.2	1.2	6.39	8.9	20.6	8.49
9	0.0	0.0	1.5	69.2	48	1	47	34.4	3.0	18.2	3.1	2.1	7.39	9.19	26.35	5.75
10	0.0	0.0	5.3	76.9	41	2	39	35.3	1.0	9.6	4.3	2.35	6.33	9.67	31.695	7.37
11	0.0	0.0	10.3	43.0	38	0	38	19.0	0.5	8	7	0	5.35	8.9	14.455	5.13
12	0.0	0.0	0.0	82.8	21	1	20	20.4	0.5	9.7	2.7	0	5.00	9.38	23.315	6.37
13	23.3	0.0	1.5	61.5	29	1	28	10.0	0.5	22.7	2.45	0	4.95	9.47	16.585	8.19
14	35.2	0.0	28.2	84.0	33	0	33	18.4	0.5	27	3.05	6.8	5.70	9.24	17.065	10
15	0.0	0.0	3.5	68.2	30	0	30	34.6	2.0	16.3	0.4	0	5.39	9.52	21.22	6.57
16	3.4	0.0	0.3	44.6	21	0	21	20.8	0.5	23.2	1.1	0	4.90	8.9	21.09	5.11
17	0.3	0.0	0.0	68.2	19	0	19	13.0	1.5	10.8	1	0	5.17	9.37	15.95	5.83
18	0.0	0.0	0.0	105.1	24	0	24	16.8	0.5	11.6	1.2	0	4.98	9.14	17.915	5.6
19	1.0	0.0	0.0	53.5	14	0	14	18.2	0.5	22.5	0.5	0	4.81	9.4	12.845	6.86
20	0.1	0.0	0.3	74.0	30	0	30	29.6	0.5	13.8	1.3	0	5.42	9.48	20.51	5.27
21	0.0	0.0	5.4	78.8	37	0	37	31.9	0.5	31.6	5.7	0	5.45	9.14	15.67	7.1
22	18.4	0.0	14.4	45.0	42	6	36	15.2	4.0	47.4	9.65	3.6	6.53	7.71	6.83	3
23	31.3	0.0	15.4	27.5	37	3	34	19.2	3.0	43.6	11.4	8.7	6.55	7.71	7.585	2.5

Site	tree-conif (m^2/ha)	tree-decid (m^2/ha)	shrub (% cover)	herbcover (% cover)	total-spp	intro-spp	native-spp	rock (cm)	litdep (cm)	litcover (% cover)	grass (% cover)	CWD (% cover)	pH	texture index	organic (%)	pheno-logy index
24	0.0	12.6	8.1	88.2	37	6	31	14.3	2.0	30.6	29.5	6.3	7.04	8.14	6.46	5.09
25	0.0	0.0	5.0	91.7	40	5	35	18.3	2.0	44.9	38.9	0	6.80	8.33	6.38	4.47
26	0.0	0.0	20.6	47.8	50	3	47	14.3	4.0	37.1	20.8	0	7.05	7.8	8.075	3.87
27	21.3	0.0	37.0	48.6	50	6	44	11.3	5.5	34.8	20.5	3.2	6.66	8	7.04	4.97
28	0.0	6.6	49.2	64.9	35	9	26	10.0	4.0	41	45.2	0.6	7.06	8.14	7.63	6.18
29	3.1	0.0	45.2	64.1	38	7	31	8.1	4.0	43	29.7	0.7	6.90	8.19	6.825	8.59
30	0.0	0.0	19.7	67.6	34	3	31	8.0	6.0	45.9	47.8	0	7.06	7.9	8.215	6.94
31	29.6	0.0	43.6	47.2	35	4	31	14.8	6.0	38.8	11.75	4.6	6.79	8	4.365	5.9
32	0.7	0.0	41.3	84.9	37	0	37	32.2	0.5	14.7	3.7	0.5	5.64	8.04	15.605	4.92
33	23.1	0.0	31.3	61.0	31	1	30	29.4	1.0	32.6	9.5	0.5	5.64	8.28	10.41	4.65
34	0.0	18.6	16.2	71.4	36	3	33	21.5	5.0	15.5	2.3	5.2	6.37	8.8	15.73	6.99
35	0.0	0.0	3.8	99.2	58	3	55	11.2	3.0	34.1	20.5	0	6.32	8.37	16.795	5.18
36	0.2	0.0	0.0	119.6	35	0	35	0.9	2.0	32.7	5.6	0	5.94	9.57	9.905	5.7
37	0.0	0.0	0.0	98.8	35	0	35	21.8	2.0	27.1	5.4	0.3	5.18	9.47	17.675	4.42
38	0.2	0.0	14.1	140.4	42	0	42	16.9	1.0	16.6	3.1	0.6	5.15	9.38	11.31	4.6

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Best Presentation Award, Biology Graduate Student Symposium	1996
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Natural Sciences and Engineering Research Council of Canada (NSERC):

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Undergraduate Summer Research Scholarships	1990-1992

University of Saskatchewan:

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J.M. Naylor Scholarship (Department of Biology)	1992
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Mullin, W. J., S. Peacock, D. C. Loewen, and N. J. Turner. in press. Macronutrients content of yellow glacier lily and balsamroot: root vegetables used by indigenous peoples of northwestern North America. Food Research International.

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Title of Thesis:

Ecological, Ethnobotanical, and Nutritional Aspects of Yellow Glacier Lily, *Erythronium grandiflorum* Pursh (Liliaceae), in Western Canada

Author [redacted]

Dawn Christy Loewen

August 4, 1998