

## COMPOSITION OF RHIZOMES OF FOREST HERBACEOUS PLANTS IN RELATION TO MORPHOLOGY, ECOLOGY, AND BURIAL BY TEPHRA

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Nine herbaceous species of variable but known belowground morphology were sampled in subalpine forests of the Cascade Range, Oregon and Washington. We measured variation of belowground concentrations of energy, ash, carbohydrates (starch plus sugar), nutrients, and water among morphological types and between areas with and without recent volcanic tephra. Chemical composition of belowground parts varied among species and, to a lesser extent, among morphological groups, with season, and following burial by tephra. Some aspects of rhizome chemistry were related to rhizome length and degree of shoot perenniality: (1) short rhizomes contain more resources because of their greater mass per unit length, although chemical concentrations do not differ with rhizome length, and (2) species with ephemeral shoots contain higher proportions of mobile macronutrients, compared with other elements, than those with perennial shoots. Even so, many chemical differences among rhizomes cannot be predicted from morphology. Plants recently buried by volcanic tephra contained more ash, water, K, S, Fe, and Cu than those elsewhere. Water and often carbohydrate content declined during the growing season. Tissue near shoots in long-rhizomatous species had higher concentrations of water, N, and P and, in tephra, of carbohydrates. Composition of belowground organs varied among species to a degree and with a pattern that indicates adaptive significance. Explanations of behavior of forest understory plants that ignore belowground differences are likely to be inadequate because of chemical as well as morphological differences among species.

### Introduction

The deposition of tephra (volcanic aerial ejecta) during the 1980 eruption of Mount St. Helens, Washington, produced a spectrum of responses by forest understory herbs (ANTOS and ZOBEL 1985a, 1985b). The nature and function of rhizomes were critical to vegetation recovery after tephra deposition. The species varied in the plasticity of the responses of their rhizomes when covered by tephra. Of the species studied, only *Tiarella trifoliata* effectively reproduced by seed after the 1980 eruption (ANTOS and ZOBEL 1986); most other species depended on vegetative spread.

All species studied are common perennial herbs in the understory of subalpine forests of the Cascade Range. These species differ in the longevity of genets and shoots, in size and complexity of belowground parts, and in the usual rate of rhizome growth (ANTOS and ZOBEL 1984). Chemical differences among taxa may accompany such variable phenology and morphology; one might expect, e.g., to find more variable and higher maximal belowground resource concentrations in species that must completely renew their shoots each year. Burial may induce belowground differences in plant chemistry and produce lower resource levels in those parts of long rhizomes away from shoots, where rhizomes appear to be dying in some species (AN-

TOS and ZOBEL 1985b). Chemistry within an individual may vary seasonally with episodes of resource uptake, storage, and expenditure. Belowground chemistry of understory plants has seldom been measured; we examined how it varies within and among species for which we have described morphology and response to burial. Thus, we hoped to assess our supposition that belowground chemical differences might have adaptive value.

Our objective was to determine patterns of variation in chemical characteristics of belowground parts of species that differ in morphology but occupy the same habitat. Concentrations of moisture, ash, calories, storage carbohydrate, and nutrient elements, and location of starch in the major belowground organs, were measured for eight or nine species. Where possible, comparisons were made among different seasons, between tissues of different positions on long rhizomes, and between areas with and without recent volcanic tephra.

### Material and methods

#### STUDY SITES AND TISSUE SAMPLING

Plants were collected from two sites (ANTOS and ZOBEL 1984, 1985b) in the *Abies amabilis* vegetation zone (FRANKLIN and DYRNESS 1973): (1) old-growth forests at 800–1,250 m elevation, 22–30 km NE of Mount St. Helens, Washington, where plants were buried in 1980 by 8–18 cm of tephra; and (2) forests at 1,150–1,400 m elevation in the Western Cascade Range, 79–86 km ENE of Eugene, Oregon. Site 1 is the “tephra” location; site 2, the “control.”

Plants were sampled by choosing a single healthy

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Manuscript received November 1986; revised manuscript received May 1987.

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shoot, one that had emerged from tephra of typical depth at the tephra site, and carefully excavating all belowground organs and shoots connected to it, using hand tools (ANTOS and ZOBEL 1984, 1985b). Extraction of the deeper fine roots of some specimens was incomplete, however. Belowground tissue was divided into two portions: "proximal" tissue was the half of the rhizome and roots closer to an aerial shoot; the half farther away was "distal." For some rhizomes, distal tissue was the oldest part; in multishooted plants with long rhizomes, it was interspersed with proximal tissue. Root tissue was collected from four species in which roots appeared to function as storage organs, based on their large diameter and the presence of starch as indicated by staining with I-KI. Roots and rhizomes were combined before analysis of each sample, but results of chemical analyses will refer only to "rhizomes."

Two major sets of sample plants were collected: (1) in late summer 1981 or 1982 for morphological study (ANTOS and ZOBEL 1984, 1985b), and (2) throughout the summers 1982 and 1983. Plants in collection 2 were excavated at different seasons: "early" = before flowering; "middle" = during flowering or fruit development; and "late" = when ephemeral shoots were senescing. Measurements of caloric content were made only on samples from collection 1. Nutrient and ash analyses were carried out on late-summer samples (collected

August 31–October 1) combined from both collections. Water and carbohydrate concentrations and rhizome and root dimensions were determined for all samples in collection 2. Location of starch was measured on plants not used for chemical analysis. Nine species were examined (table 1); *Chimaphila umbellata* was used only for calorimetry and I-KI staining, and *Smilacina racemosa* was not analyzed for caloric content.

All samples were washed in tap or creek water to remove soil. Samples for calorimetric, moisture-content, and nutrient analyses were dried at 70 C within a few hours of collection or frozen until drying. Samples for carbohydrate determination were placed in 80% ethanol. Samples for carbohydrate analysis and those for nutrient and moisture-content analyses were derived by splitting each field sample into homogeneous halves and determining fresh weights of both. Dry weight (DW) of each sample placed into ethanol was estimated using the moisture content of its paired sample. Staining with I-KI was done within 1 day of collection on fresh tissue collected at the tephra location June 28, 1982, and refrigerated until use.

#### CHEMICAL ANALYSIS

Caloric content was determined in duplicate, using a microbomb calorimeter, at the Department of Biology, Utah State University. Results are presented as megajoules (MJ)/kg total DW.

TABLE 1

SPECIES STUDIED, GROUPED BY GENERAL MORPHOLOGY AND PHENOLOGY, WITH CHARACTERISTICS USED TO GROUP THEM

Morphological group <sup>a</sup> and species	Shoot phenology	Rhizome length	Rhizome <sup>b</sup> plasticity after burial	Normal rhizome growth rate	Apparent longevity of genets
LE:					
<i>Achlys triphylla</i> . . . . .	Ephemeral	Long	Moderate	Fast	Long
<i>Clintonia uniflora</i> . . . . .	Ephemeral	Long	Moderate	Fast	Long
<i>Smilacina stellata</i> . . . . .	Ephemeral	Long	Moderate	Fast	Long
LP:					
<i>Arnica latifolia</i> . . . . .	Perennial	Long	High	Fast	Uncertain
<i>Chimaphila umbellata</i> . . . . .	Perennial	Long	Moderate	Fast	Long
SP:					
<i>Tiarella trifoliata</i> . . . . . var. <i>unifoliata</i>	Perennial	Short	High	Slow	Short
<i>Valeriana sitchensis</i> . . . . .	Perennial	Short	High	Slow	Short
CE:					
<i>Erythronium montanum</i> . . . . .	Ephemeral	Short <sup>c</sup>	Nil	Very slow <sup>c</sup>	Short
SE:					
<i>Smilacina racemosa</i> . . . . .	Ephemeral	Short	Low	Slow	Short

NOTE.—Characteristics are based on data in ANTOS and ZOBEL (1984, 1985a, 1985b), except for *S. racemosa*, which is classified using observations during this study. Nomenclature follows HITCHCOCK and CRONQUIST (1973).

<sup>a</sup> L = long rhizome, S = short rhizome, C = cormlike perennating organ; E = ephemeral shoots, P = perennial shoots.

<sup>b</sup> High plasticity occurred when a horizontal rhizome became vertical and growth rate increased greatly. Moderate plasticity included a less extreme reorientation with no change in growth rate. Low plasticity involved delayed partial reorientation of rhizome growth with little increase in rate of elongation.

<sup>c</sup> Perennating organ is cormlike.

Nutrient and ash analyses (CHAPLIN and DIXON 1974) were performed by the Plant Analysis Laboratory, Department of Horticulture, Oregon State University, for all macronutrients; the micronutrients Mn, Fe, Cu, B, Zn, and Mo; and Na, Se, As, Ba, Cd, Co, Li, Ni, Si, Sr, and Pb. Nutrient data are expressed as concentrations per unit total DW and as nutrient ratios; the ratios among all macronutrients and of N to all micronutrients were calculated. Nutrient ratios were calculated with concentrations of important elements mobile within plant tissues (e.g., N, P, K) as the numerator and less mobile or micronutrient elements as the denominator of the ratio.

Reducing sugar concentrations in the tissue were determined by a Somogyi-Nelson analysis of an extract after tissue grinding and acid hydrolysis; then, after amyloglucosidase treatment to hydrolyze starch, the content of reducing sugars was determined again. The precise method was developed for analysis of mint rhizomes by DE ANGELIS (1982). Total sugar concentration, the sum of both analyses, was reported as mol fructose/kg tissue total DW; hereafter, this value will be called carbohydrate concentration.

Chemical contents per unit length of rhizome are also presented; such values allow estimation of chemistry from field observations of plant size.

Starch was located by staining with 1% I-KI; vascular tissue, by phloroglucinol. Freehand cross sections of rhizomes of various ages and positions were observed at  $\times 45$ , and dimensions of concentric zones of differential staining were measured using an ocular micrometer. The intensity of I-KI staining of each zone in each cross section was subjectively rated as a percentage of a stained thin section of fresh potato. A weighted mean "percentage of potato staining" was calculated for each rhizome cross section, using the cross-sectional area and rating of each differently stained zone.

#### MORPHOLOGY

Five characteristics were calculated to supplement the data of ANTOS and ZOBEL (1984): mean rhizome diameter, mean diameter of large roots, length:diameter ratio of rhizome, aboveground:belowground biomass ratio, and shoot biomass per unit of rhizome length. The mean diameters of larger roots and rhizomes were determined by dividing each sample of each tissue into three to six groups of pieces with similar diameter; representative sections were measured with a hand-held micrometer to determine a mean diameter; and the lengths of all sections in each group were recorded. The mean diameter of each group was weighted by total length of all sections in that group to calculate a mean diameter for each tissue in each sample.

#### STATISTICAL ANALYSIS

Differences among species, morphologically based species groups, seasons, and collection locations were analyzed using one-way ANOVA. Differences within groups of samples containing significant variability were determined using Duncan's new multiple-range test (STEEL and TORRIE 1960). Differences between proximal and distal tissue were determined for paired data from the same samples, using a paired *t*-test. Unless stated otherwise,  $P < .05$  was used for tests of significance.

Linear regression and rank correlation analyses were used to relate species means of various chemical and morphological characteristics. We considered 14 morphological variables, 10 defined in ANTOS and ZOBEL (1984) and four from our data; chemical traits used were concentrations of water, carbohydrates, and calories, concentrations of nine required elements, and five ratios of elements.

#### Results

##### MORPHOLOGY OF SAMPLE PLANTS

Four morphological indices derived from our samples differed significantly among species (table 2). Long-rhizomatous species had smaller diameter rhizomes, a larger rhizome length:diameter ratio, and less mid-to-late-season shoot biomass per unit rhizome length. Species with ephemeral shoots (except *Erythronium montanum*) had a smaller shoot:belowground biomass ratio than species with perennial shoots. Large roots had similar mean diameters for the four species measured (table 2).

Rhizomes in tephra were thicker for *Clintonia uniflora* than at the control site but were thinner in *Smilacina stellata* and *Tiarella trifoliata*. Roots of *C. uniflora* were significantly thicker at the tephra (0.98 mm) than at the control site (0.64 mm). Species with short rhizomes had a higher length:diameter ratio at the tephra than at the control site.

##### ENERGY AND ASH CONTENT

Caloric content of major belowground parts differed among species but not among morphological groups (table 3). Proximal and distal tissue differed in one of two long-rhizomatous species for which both tissues were measured; distal tissue of *S. stellata* had higher caloric content than proximal (18.6 vs. 17.9 MJ/kg), while *C. uniflora* did not vary by location (17.7 vs. 17.6).

Ash content varied significantly only between sites. For all species, tissue from the tephra site had higher values (table 3).

##### WATER CONTENT

The water content of rhizomes varied with species, usually varied with morphological group,

TABLE 2  
MORPHOLOGICAL CHARACTERISTICS OF SAMPLE PLANTS AND NUMBER OF SAMPLES

MORPHOLOGICAL GROUP AND SPECIES	SAMPLE NO.		MEAN DIAMETER (mm)		RHIZOME LENGTH: DIAMETER	SHOOT: RHIZOME (g/m) <sup>a</sup>	ABOVE-: BELOW-GROUND BIOMASS RATIO <sup>a</sup>
	N <sub>s</sub>	N <sub>p</sub>	Rhizome	Root			
LE:							
<i>Achlys triphylla</i> .....	11	29	1.85d	NA	1,114ab	.47b	.31b
<i>Clintonia uniflora</i> .....	10	27	1.26e	.84	1,069ab	.31b	.50b
<i>Smilacina stellata</i> .....	10	19	2.54c	NA	1,278a	.51b	.32b
LP:							
<i>Arnica latifolia</i> .....	7	17	1.91d	NA	464bc	.56b	.77ab
SP:							
<i>Tiarella trifoliata</i> .....	10	54	2.65c	.76	82c	3.76a	1.27a
<i>Valeriana sitchensis</i> .....	10	29	3.57b	.84	90c	2.95a	.63b
CE:							
<i>Erythronium montanum</i> .....	8	24	NA <sup>b</sup>	NA	NA <sup>b</sup>	4.48a	.80ab
SE:							
<i>Smilacina racemosa</i> .....	9	13	6.02a	.87	35c	3.11a	.32b

NOTE.—Root diameter is for large roots only. N<sub>s</sub> = no. samples analyzed; N<sub>p</sub> = total no. of plants in N<sub>s</sub> samples. Species means sharing the same letter in a column are not significantly different. Abbreviations for morphological groups are defined in table 1. NA = data not collected.

<sup>a</sup> Mid- and late-season samples.

<sup>b</sup> ANTOS (unpublished data) reported 5.1 mm diameter and 7.7 cm length for the corm, a ratio of 15.

season, and tissue location, and occasionally differed between sites.

*Achlys triphylla* usually had the lowest water content (table 4). Late-season values for *E. montanum* at the tephra site were also low. Significant variation among morphological groups was associated only with the low value for *E. montanum* and the high value for *Smilacina racemosa*. Plants from the control site usually had significantly less moisture at a given season than those from the tephra site (table 4). In three species, proximal

tissue had higher moisture content than distal parts (table 4).

Moisture content declined significantly in late season for all species except *C. uniflora*, *S. racemosa*, and *T. trifoliata* (table 4). No species varied significantly between early and mid-season.

#### LOCATION OF STARCH IN RHIZOMES

Species varied substantially in the degree and location of starch staining (fig. 1). In general, the pith and the cortex stained. Sometimes, however,

TABLE 3  
CALORIC CONTENT AND ASH CONTENT OF PROXIMAL TISSUE OF MAJOR BELOWGROUND PARTS

MORPHOLOGICAL GROUP AND SPECIES	ASH <sup>a</sup> (%)		ENERGY (MJ/kg total DW)		
	Tephra	Control	Tephra	Control	Mean
LE:					
<i>Achlys triphylla</i> .....	3.7	3.7	17.0	17.4	17.2abc
<i>Clintonia uniflora</i> .....	7.4	4.5	18.0	* 17.1	17.6ab
<i>Smilacina stellata</i> .....	4.7	2.7	17.8	18.0	17.9a
LP:					
<i>Arnica latifolia</i> .....	6.4	6.1	16.6	16.2	16.4c
<i>Chimaphila umbellata</i> .....	NA	NA	17.2	17.6	17.4ab
SP:					
<i>Tiarella trifoliata</i> .....	7.4	2.7	16.7	16.7 <sup>b</sup>	16.7bc
<i>Valeriana sitchensis</i> .....	3.4	3.3	17.4	* 18.3	17.9a
CE:					
<i>Erythronium montanum</i> .....	2.1	1.8	16.8 <sup>b</sup>	NA	16.8abc

NOTE.—Most values are the mean of two determinations. Means with the same letter do not differ significantly from each other. \* = Significant differences ( $P < .05$ ) between tephra and control sites. NA = data not available. Morphological group abbreviations are defined in table 1.

<sup>a</sup> Ash content of *Smilacina racemosa* is 3.9% (tephra) and 3.5% (control).

<sup>b</sup> Represented by a single measurement.



TABLE 4  
WATER CONTENT AS PROPORTION OF FRESH WEIGHT IN ALL TISSUES OF MAJOR UNDERGROUND  
PARTS BY SPECIES, SITE, AND SEASON

MORPHOLOGICAL GROUP AND SPECIES	SITE AND SEASON					PROXIMAL TISSUE HIGHER
	Tephra			Control		
	Early	Mid	Late	Early	Late	
LE:						
<i>Achlys triphylla</i> .....	.76a	.78a	.70bCD	.70b	.64cB	**
<i>Clintonia uniflora</i> .....	.85a	.81ab	.80abA	.75b	.77abA	***
<i>Smilacina stellata</i> .....	NA	.83a	.78bA	.77b	.74cA	NS
LP:						
<i>Arnica latifolia</i> .....	.80a	.81a	.72bBC	NA	NA	NS
SP:						
<i>Tiarella trifoliata</i> .....	NA	NA	.76aAB	.67b	.65bB	***
<i>Valeriana sitchensis</i> .....	.85a	.83a	.78bA	.79b	.75cA	NS
CE:						
<i>Erythronium montanum</i> .....	.84a	.85a	.65bD	NA	NA	NA
SE:						
<i>Smilacina racemosa</i> .....	NA	.80a	.79aA	NA	.78aA	NS

NOTE.—For each species, values followed by the same lowercase letter do not differ significantly among seasons or sites. Within each site, late-season values followed by the same capital letter do not differ significantly among species. NA = no data available; NS = nonsignificant. \*\* =  $P < .01$ ; \*\*\* =  $P < .001$ . Morphological group abbreviations are defined in table 1.

there were nonstaining bands (*Tiarella*, *Arnica*, *Chimaphila*); cortex was absent (*Achlys*, old *Clintonia*); or pith was hollow or nonstaining (highly variable in *Valeriana*). With age, the outer cortex collapsed in *Clintonia* (fig. 1) and *Chimaphila*, and an outer layer of dark, dead tissue thickened in *Clintonia* and *Tiarella*.

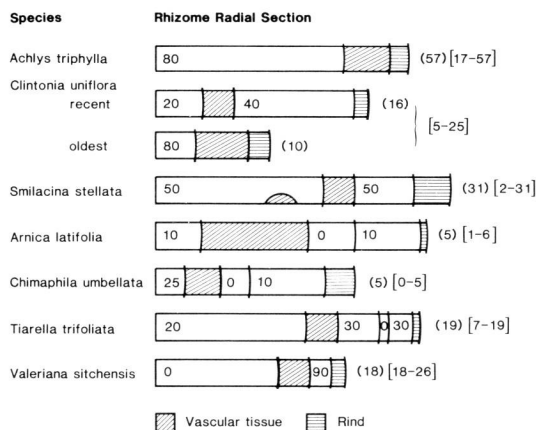


FIG. 1.—Diagrams representing the anatomy and degree of staining with I-KI of representative radial cross sections of rhizomes. The center of the rhizome is the left end of the bar; the right-hand margin represents the outer surface of the rhizome. Thickness and location of xylem (▨) and an outer rind (▨) are shown. Values in other compartments indicate the relative degrees of staining in percentages (potato = 100%). Values in parentheses are weighted average staining values for the whole cross section of the rhizome, with staining estimates for each compartment weighted by the cross-sectional area of the compartment. Figures in square brackets indicate the range of weighted average staining values for the several portions and ages of rhizomes sampled.

In most rhizomes, starch was stored both inside and outside the potentially protective vascular tissues; in others, however, it was all outside or, in older rhizomes without a cortex, all inside the vascular tissue. Large roots of *Clintonia* and *Valeriana* stained more heavily than any part of their rhizomes.

Much of the cormlike perennating structure of *E. montanum* stained similarly to fresh potato, including the fleshy leaf primordium, most of the preformed flower, and the connected series of small segments remaining from past years. A major exception, the fleshy short rhizome of *S. racemosa*, stained slightly only in the bud containing next year's shoot and near the sites of root emergence from the most recent segment.

#### CARBOHYDRATE CONCENTRATION

Carbohydrate concentration varied significantly among species and with season, but not between sites; therefore, the means include both sites (table 5). Species with ephemeral shoots and a short rhizome or corm had the highest values (table 5); monocots (except *Clintonia*) had more carbohydrate than dicots. An exception occurred in late season when *Erythronium* had the least carbohydrate. Morphological groups with long rhizomes or perennial shoots differed little.

Seasonal variability was significant for all species with ephemeral shoots except *S. stellata* ( $P$  just above .05) but for no species with perennial shoots (table 5). *Achlys*, *Clintonia*, and *Erythronium* had their highest concentrations early, whereas *Smilacina* spp. were high in late season.

TABLE 5  
CONCENTRATIONS OF CARBOHYDRATE—STARCH PLUS SUGAR AS mol FRUCTOSE/kg  
TOTAL DW—IN MAJOR BELOWGROUND ORGANS

MORPHOLOGICAL GROUP AND SPECIES	SEASON			SIGNIFICANCE OF SEASONAL DIFFERENCES
	Early	Middle <sup>a</sup>	Late	
LE:				
<i>Achlys triphylla</i> .....	.450c	.311cde	.255d	**
<i>Clintonia uniflora</i> .....	.389c	.194e	.294cd	**
<i>Smilacina stellata</i> .....	.805b	.688b	1.066b	NS
LP:				
<i>Arnica latifolia</i> <sup>a</sup> .....	.416c	.405cd	.344cd	NS
SP:				
<i>Tiarella trifoliata</i> .....	.233c	.222de	.250d	NS
<i>Valeriana sitchensis</i> .....	.511c	.450c	.633c	NS
CE:				
<i>Erythronium montanum</i> <sup>a</sup> .....	1.105a	.699b	.222d	**
SE:				
<i>Smilacina racemosa</i> .....	1.227a <sup>a</sup>	.894a	1.693a	*

NOTE.—Values are means of 2–10 measurements (usually 4–8); measurements from both study areas are included. Species means followed by the same letter within one season do not differ significantly. NS = nonsignificant, \* =  $P < .05$ ; \*\* =  $P < .01$ . Morphological group abbreviations are defined in table 1.

<sup>a</sup> No data available from the control location.

Proximal tissue had significantly more carbohydrate than distal tissue at the tephra site (when all species were combined in one paired  $t$ -test), but the difference was nonsignificant (and in the opposite direction) at the control site.

#### NUTRIENT CONCENTRATIONS

Variation between sites was significant for two macronutrients (K, S) and for several micronutrient and nonrequired elements (table 6); elements that differed, except Ba and Sr, were higher in plants from the tephra site.

Concentrations varied significantly among species for all macronutrients except S and for several other elements (tables 6, 7). Average concentrations of required elements that did not differ significantly among species were S (0.29%), Cu (25 mg/kg), and B (23 mg/kg).

*Erythronium montanum* had relatively low values of all required elements, the lowest for all except N and P; *S. stellata* often had low concentrations (table 7). *Tiarella trifoliata* most consistently

had high concentrations of required elements except N and K.

Within two long-rhizomatous species, *C. uniflora* and *S. stellata*, element concentration varied significantly between proximal and distal tissue only for N (proximal = 0.70% vs. distal = 0.46%), P (proximal = 0.31% vs. distal = 0.21%), and Mo (proximal = 0.13 vs. distal = 0.17 mg/kg).

Concentrations of only N, Mg, and Mo varied significantly among morphological species groups (table 8). The two species groups that included more than one species (LE, SP) differed significantly in N and Mg.

#### NUTRIENT RATIOS

All ratios of macronutrients to each other and ratios of N to micronutrients, except N/P, Ca/Mg, and Ca/S, varied significantly among morphological species groups. This contrasted with the few differences among groups in their nutrient concentrations. Ratios of N/Ca, P/Ca, N/Mn, and N/Fe were most variable. Ratios of mobile to nonmobile

TABLE 6  
SIGNIFICANCE OF DIFFERENCES AMONG SPECIES AND BETWEEN SITES FOR ELEMENT CONCENTRATIONS OF MAJOR BELOWGROUND PARTS

SITE DIFFERENCE (significance)	SIGNIFICANCE OF SPECIES DIFFERENCES			
	$P < .001$	$P < .01$	$P < .05$	NS
Tephra > control ( $P < .05$ ) .....	...	Fe	K	S, Cd, Cu, Co, Na
Control > tephra ( $P < .05$ ) .....	...	...	...	Ba, Sr
NS .....	Ca, Se, Mg, Pb	Zn, Mo	N, Al, P, As, Mn, Si	B, Li, Ni

NOTE.—NS = nonsignificant.

TABLE 7  
CONCENTRATIONS OF NUTRIENT ELEMENTS, BASED ON TOTAL DW, IN MAJOR BELOWGROUND ORGANS SAMPLED IN LATE SUMMER

MORPHOLOGICAL GROUP AND SPECIES	ELEMENT								
	%					(mg/kg)			
	N	P	K	Ca	Mg	Mn	Fe	Zn	Mo
LE:									
<i>Achlys triphylla</i> .....	.62bc	.32b	.86cd	.67b	.14c	153a	190cd	54cd	.17ab
<i>Clintonia uniflora</i> .....	.80ab	.31b	2.14ab	.24c	.15bc	97bc	375a	97b	.22a
<i>Smilacina stellata</i> .....	.61bc	.31b	1.51bc	.19c	.08d	46cd	102de	32d	.05cd
LP:									
<i>Arnica latifolia</i> .....	.26d	.15d	2.27a	.57b	.16bc	121ab	339ab	68bc	.24a
SP:									
<i>Tiarella trifoliata</i> .....	.54c	.33b	1.36cd	1.17a	.27a	111ab	285abc	129a	.22a
<i>Valeriana sitchensis</i> .....	.41cd	.17d	1.08cd	.29c	.17b	93bc	227bc	51d	.13bc
CE:									
<i>Eythronium montanum</i> .....	.39cd	.22c	.68d	.04d	.06d	10d	34e	25d	.01d
SE:									
<i>Smilacina racemosa</i> .....	.99a	.45a	.92cd	.65b	.14c	109ab	56e	36d	.12bc

NOTE.—Values are for required elements that varied significantly among species; they are averages for all locations and types of tissue samples. Values with the same letter for a given element are not significantly different. Morphological group abbreviations are defined in table 1.

elements were highest in species with ephemeral shoots and slow-growing rhizomes and lowest in those with perennial shoots (patterns 1–3, table 8). The high ratios in *E. montanum* resulted from very low concentrations of most elements and only moderately low N (table 7); high ratios in *S. racemosa* related more to its very high N concentration (table 7). All monocots had higher ratios of N/Ca, P/Ca, N/Mg, and N/Mn than did all dicots.

#### CORRELATION AMONG CHARACTERISTICS

Substantial variability occurred among species in most characteristics (tables 2–7). The pattern of interspecific variability, however, shows few consistencies among traits (fig. 2); this is reflected by correlation analyses.

MORPHOLOGY:MORPHOLOGY.—There were few

strong correlations among species means of morphological characteristics. Species with a low ratio of shoot to belowground biomass in mid- and late season tended to be larger (with longer rhizomes, more DW and leaf area, and more roots) and to have less shoot biomass per unit of rhizome length. Larger-diameter rhizomes contained more biomass and bore more roots per unit length.

MORPHOLOGY:CHEMICAL COMPOSITION.—Larger plants (with a lower shoot:belowground biomass ratio) had higher caloric and N concentrations. Deeper-rooted plants had higher concentrations of energy, water, and N. Species with longer roots contained more Mg and Fe, and those with heavier rhizomes (g/m) had less Fe and Mo. Large-diameter rhizomes, with high biomass per unit length, had high N/Fe ratios.

CHEMICAL:CHEMICAL.—Energy, water, and car-

TABLE 8  
SIGNIFICANCE OF DIFFERENCES AMONG MORPHOLOGICAL GROUPS FOR SEVERAL CHARACTERISTICS

MORPHOLOGICAL GROUPS	CHARACTERISTIC										
	Rhizome diameter	Moisture content	Maximum carbohydrate	Nutrient Concentration			Pattern of nutrient ratios <sup>a</sup>				
				N	Mg	Mo	1	2	3	4	5
LE .....	c	ab	c	b	bc	a	b	bc	c	a	b
LP .....	c	b	c	c	ab	a	b	c	c	b	c
SP .....	b	ab	c	c	a	a	b	c	c	b	bc
CE .....		c	b	c	c	b	a	a	b	a	b
SE .....	a	a	a	a	b	ab	b	b	a	a	a

NOTE.—Groups with the same letter do not differ significantly for a given characteristic. Groups designated "a" have the highest mean.

<sup>a</sup> Ratios with each pattern: pattern 1: N/Ca, N/Mn, P/Ca, K/Ca; pattern 2: N/S, P/S; pattern 3: N/Fe, N/Mo; pattern 4: N/Mg, N/B, P/Mg; pattern 5: N/K, N/Cu, N/Zn, P/K.



*Arnica latifolia*. Among species with short rhizomes, the two monocots had higher belowground investment per unit length than dicots.

Belowground chemical content per shoot (calculated from table 9) varied inconsistently between species with long and short rhizomes and between monocots and dicots; *S. racemosa*, however, had much higher values per shoot than other species.

### Discussion

Composition of belowground parts of subalpine understory plants differed among species. Mean concentrations varied by a factor of 1.1-fold for energy; 2–3-fold for ash, water, P, and K; 4–8-fold for carbohydrates, N, Mg, and Zn; and greater than 10-fold for Fe, Mn, Mo, and Ca. The resource investment per unit length of rhizome was more variable than concentration values for the same substance.

Some chemical variability was associated with belowground morphology. Short rhizomes contained more resources per unit length because of their greater diameter and greater mass per unit length, although values per unit DW did not vary consistently with rhizome length. Low nutrient concentrations of *Erythronium montanum* may have been related to its shallow, sparse root system (ANTOS and ZOBEL 1984).

Chemical composition was also associated with the degree of shoot perenniality; species with perennial shoots had rhizomes with more Mg and lower ratios of N and P to other nutrients than species with annual shoots. Within short-rhizomatous species, the two monocots with annual shoots had higher carbohydrate concentrations than did dicots with perennial shoots. In general, evergreen species have lower nutrient requirements and retain mobile nutrients in the shoot (CHAPIN 1980); both of these factors may contribute to low relative belowground concentrations of N and P in species with perennial shoots.

Chemical differences may also be related to phylogenetic lineage. Monocots, e.g., accumulate less Ca than dicots from soils with similar Ca concentrations (RORISON and ROBINSON 1984). In our study, monocot species had the highest three belowground concentrations of water and carbohydrates and the lowest three of Ca, Zn, and Mo. In each case, however, the fourth monocot species (not always the same one) was a distinct exception, preventing generalizations about monocot-dicot concentration differences. Some nutrient ratios were consistently higher for monocots, however.

Other species differences were unrelated to morphology, phenology, or phylogeny. Correlations of species means of most chemical attributes to mean values of morphological attributes were not significant. Species-specific variability was important

among the species we studied (fig. 2); e.g., the fleshy, carbohydrate-rich rhizome of *S. racemosa* stored no starch. Although both *Smilacina* spp. store fructose-based carbohydrates (POLLARD 1982), only *S. stellata* stained with I-KI.

Some chemical variability within species was related to site, season, and location and age of the tissue. Plants in tephra generally had higher nutrient (K, S, Fe, Cu), ash, and water concentrations. Large amounts of K, S, and Cu were present in the tephra (FRUCHTER et al. 1980; RADWAN and CAMPBELL 1981; ANTOS 1984); their availability may explain high tissue concentrations of these elements. However, much Ca was present in the tephra but not obvious in the tissue, and Fe was lower in tephra than in soil. Higher moisture may reflect a greater proportion of new tissue on plants that had grown into the tephra. Tissue water content declined during the season in most species, and carbohydrate generally declined in three of the four species that changed significantly. Tissue closer to shoots had higher water content (three species), higher N and P concentrations (in both species tested), and higher carbohydrate concentrations (generally in tephra, but not control). This probably reflects its younger average age and, in some species, greater proportion of parenchyma tissue; it may indicate a lesser chance of rhizome senescence near a shoot. For *S. stellata*, however, caloric content was higher in distal tissue.

Differences in belowground characteristics appear to have adaptive value. There are striking belowground differences in morphology among species with very similar shoots (ANTOS and ZOBEL 1984). Species with long rhizomes usually have more shoots, more rooting nodes, a longer life span, vegetative mobility, less dependence on sexual reproduction for our species, and a larger area from which to extract resources (ASHMUN et al. 1982; ANTOS and ZOBEL 1984; ANGEVINE and HANDEL 1986). Interconnected shoots have the opportunity for physiological integration, sharing resources and risks, although the ecological significance of interconnections is still uncertain (HUTCHINGS and BRADBURY 1986). Belowground chemistry also appears to be adaptive. Rhizomes of *S. racemosa* and *S. stellata* and of *E. montanum* and *Clintonia uniflora*, two species pairs with similar shoots, differed chemically as well as in morphology. Long and short rhizomes consistently differed in concentrations of some constituents. Among long-rhizomatous species, minimal resource investment per unit rhizome length was made by *C. uniflora*, an extreme shade tolerator, and by *Arnica latifolia*, a morphologically plastic species producing the least persistent rhizome (ANTOS and ZOBEL 1984). A more wide-ranging, morphologically flexible species, *S. stellata*, produced the most resource-rich long rhizome. Short-rhizomatous species with perennial



shoots differed chemically from those with ephemeral shoots.

Growth and yield are sometimes more closely related to nutrient ratios than to concentrations (INGESTAD 1979; BEVERLY et al. 1984). The ratios of N and P to other nutrients, especially Ca and Fe, that are less mobile within the plant were highest in our species with ephemeral shoots and slow-growing perennating organs and increased as did carbohydrate concentration. Organs with high ratios serve primarily as storage for the annual shoot and thus contain more translocatable substances and less structural tissue, producing high ratios of N to Ca.

This study demonstrates only chemical variation, revealing the potential for adaptive value. Adding belowground chemistry to adaptive "strategies" (GRIME 1979; CHAPIN 1980; HICKS and CHABOT 1985) must remain hypothetical for our species.

Our study area differs substantially from the deciduous forests where adaptation of understory herbs has usually been described (e.g., HICKS and CHABOT 1985; PITELKA et al. 1985). Critical adaptive features for our plants probably differ also. A short snow-free season and evergreen canopy eliminate the advantages gained from the phenological diversification found among deciduous forest herbs (HICKS and CHABOT 1985). In old-growth Cascade forests, substantial microhabitat diversity occurs, associated with canopy thickness (STEWART 1986), large woody debris (HARMON et al. 1986), patterns of snow accumulation and snow melt, and seepage. A mechanism for persistence in long-lasting, isolated, favorable microsites may be especially

important in our study area.

Few data are available for chemical composition of belowground parts of subalpine herbs. Mean energy content of belowground parts of subalpine herbs from Utah meadows is 17.8–18.5 MJ/kg of ash-free DW (ANDERSEN and MACMAHON 1981; STEUBE and ANDERSEN 1985). Our values (table 3, converted to an ash-free basis) ranged from 17.2 to 18.5, less than or similar to rhizomes from Utah. Variation among Utah species is also low (15%). Ash-free N content of six Utah species is 0.33%–1.76% (mean 0.94), somewhat higher and more variable than our range of 0.28%–1.03% (converted from table 7). The only closely related taxa in the two studies are *E. montanum* and *E. grandiflorum*; both had relatively low caloric content, but they differed drastically in N concentration: *E. grandiflorum* had the highest N in the Utah collection, whereas *E. montanum* had our second lowest N concentration (table 7). Ash contents in our study were substantially lower than most values reported for Utah perennials (ANDERSEN 1980; STEUBE and ANDERSEN 1985).

#### Acknowledgments

Financial support was provided by grants to DONALD ZOBEL from the National Science Foundation (DEB-8109906) and the U.S. Department of Agriculture Science and Education Administration (59-2411-1-2-009-0). Caloric content was measured at Utah State University, courtesy JAMES MACMAHON and MARK MESCH. We thank TOM HILL, SUSAN SEYER, and SHIRLEY ATWOOD for field and laboratory assistance.

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