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GROWTH FORM AND ECOPHYSIOLOGY OF WESTERN NORTH AMERICAN ALPINE PLANTS

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ABSTRACT

Alpine plants of Western North America possess very different growth forms, yet they may occupy the same habitat. Snowbec species may be dwarf evergreen shrubs that conserve carbon and nutrients through retention of leaves or they may be deciduous or wintergreen forbs and graminoids that conserve carbon and nutrients with large root and rhizome systems. Only the wintergreen forb, *Eriogonum* allocates large amounts of carbon to reproduction.

The wintergreen forb and graminoid species grow in more exposed (higher winds, less snow) habitats, yet these species allocate less carbon belowground and their ability to adjust osmotically is less than in the shrub species. The shrub growth forms (evergreen and deciduous) have the greatest drought tolerance (low leaf water potentials, greatest osmotic regulation, lowest minimum stomatal conductance). The forb species have the least drought resistance while the graminoid species are intermediate. A mixture of plant growth forms occurs in each major alpine habitat (snowbed, meadow, exposed ridges and slopes). This indicates that there is no single growth form best adapted to a given habitat and that species with different growth forms can successfully co-exist in the same habitat.

INTRODUCTION

Alpine environments of Western North America impose a wide variety of stresses upon plants. Their environments have moderate to deep winter snow, moist to dry summer climates, and a 3—4 month growing season. The more coastal climates of the Cascade Range and the volcanic peaks have deep snows (1—5 m) that do not melt until late June or mid July. Plants become dormant in mid to late September. Alpine plants of the Alberta Rocky Mountains grow in more continental climates where winter snows are less deep (0.1—1 m). Snow melts in early to mid-June and plants become dormant in late August to early September.

The alpine floras of the areas reported here are relatively small. In the Signal Mountain area of Jasper National Park, Alberta there are 157 species (Hrapko and La Roi 1978). There are about 200 alpine species in the North Cascade Range (Douglas and Bliss 1977) but only about 60 species on the isolated volcanoes within that same region. Alpine vegetation is limited near the coast because of deep snow and steep mountain slopes with little soil.

Plants with very different growth forms inhabit these alpine environments. There are deciduous and evergreen shrub species, deciduous and wintergreen forbs, and deciduous and wintergreen graminoids. The objective of this paper is to briefly describe how species with a different life form allocate carbon, nitrogen, and phosphorus and how they control their summer water balance. More detailed information on the physiological ecology of alpine plants is contained in the reviews of Billings (1974), Bliss (1971, 1985), and Tieszen and Wieland (1975).

GROWTH FORMS AND PHYSIOLOGICAL RESPONSES

Shrubs

Both deciduous and evergreen shrubs are present in these alpine regions, although they form a small percentage of the total plant cover and biomass. *Salix arctica* is representative of the deciduous shrub form and has been studied near Jasper National Park, Alberta. *Salix arctica* has large woody belowground stems with many small adventitious roots (aboveground: belowground ratio 1:3—4). Leaves represent 3—8% and reproductive structures <3% of total plant biomass (Table 1). Nitrogen levels are high in dormant buds and are translocated to developing leaves and catkins which retain high levels throughout the most active part of the growing season. Phosphorus follows much the same pattern, although an order of magnitude lower and shows little seasonal translocation.

Salix arctica grows in warmer microsites and where the soils are moist (>1.0 MPa) much of the summer. Water loss is controlled primarily in two ways; osmotic regulation (daily and seasonally) and by stomatal control, reducing transpiration (stomatal conductance). Water loss is well correlated with atmospheric moisture vapor pressure deficit (VPD) and by soil-root temperature.

Cassiope tetragona is representative of the evergreen shrub growth form. These plants have large root systems (4—6 times aboveground) and long-lived (2—4 yr), fleshy leaves. Their allocation of carbon to reproduction is very small (<1%). The carbon data are from the Arctic (Bliss et al. 1977). We lack data on nutrient allocation in this species but hypothesize that this is a nutrient conservative species that maintains relatively low levels of N and P tissue content and that only low levels of nutrient translocation occur each year.

Cassiope tetragona regulates water loss osmotically and is able to maintain a favorable leaf water balance −3.5 to −5.0 MPa (Table 1). This species is quite tolerant of high VPD and very low soil moisture. This shrub grows in snowbed habitats but it also grows where winter snow depth is minimal and in such sites plants are exposed to winter desiccation and temperature below −35°C. Under these conditions the plants show little injury (Harter 1981).

Forbs

Both deciduous and wintergreen forbs are common to these alpine environments and they account for a high percentage of total plant cover and biomass in many plant communities. We have chosen *Polygonum newberryi* to represent the deciduous growth form. This species is common in late snowmelt habitats on well-drained soils, often of volcanic origin (pumice material) in the Cascade Range. These plants has a very large, deep-penetrating root system with aboveground: belowground ratios of 1:8—10. The shoot systems are produced annually and consist of about equal amounts of stem and leaf tissue, reproductive tissues account for <0.5%. *Polygonum* often grows in sites that do not melt until August, yet it can produce its shoot system, flower and fruit before dormancy is forced in late September to early October.

Table 1. Morphological and physiological characteristics of alpine plants.

Growth form	Peak Season Allocation								Seasonal Water Relations				Mid-day Stomatal Conductance (m mol · m⁻². sec⁻¹)	
	Biomass(%)				Nitrogen(%)				Leaf water potential (M Pa)		Turgor loss point (M Pa)			
	R	S	L	F*	R	S	L	F	max	min	max	min	min	max
Shrubs														
Deciduous (*Salix*)	80	12	5	3	18	11	38	33	−0.2	−1.6	−0.8	−2.5	12—30	50—700
Evergreen (*Cassiope*)	81	18	18	1+	—	—	—	—	−0.5	−5.0	−2.7	−5.7	7—15	200—400
Forbs														
Deciduous (*Polygonum*)	87	6	7	<1	69	7	23	1	−0.1	−1.3	−0.86	−1.1	45	360
Wintergreen (*Eriogonum*)	24	35	26	15	18	34	29	17	−0.1	−1.7	−1.2	−1.5	55	485
(*Lupinus*)	20	22	51	7	15	17	62	6		−1.4	−0.8	−1.2	42	
Graminoids														
Deciduous (*Carex spectabilis*)	92	8		<1	81	19		—	−0.05	−1.7	−1.6	−2.4	10—20	110—160
Wintergreen (*Carex nardina*)	40	60		<1	93	7		—	−0.2	−1.9	—	—	8—12	75—105

* R = roots, rhizomes, underground stems; S = stems; L = leaves; F = fruits
+ Biomass data for *Cassiope* are from the Arctic
– No data

Polygonum is able to avoid summer drought because of its large tap root that can obtain water at depth (50—80 cm). This species does not appear to be sensitive to high VPD or to low leaf water potentials. Turgor loss point (TLP) is relatively high compared with species of the other growth forms: osmoregulation is quite limited (Table 1). With its more elevated leaf mass, leaves are typically only 1 to 2°C above ambient air temperature.

We have chosen *Eriogonum pyrolifolium* and *Lupinus lepidus* to represent the wintergreen forb growth form. These species, although having the same growth form, solve their water stress problems and their allocation of carbon in different ways. *Eriogonum* and *Lupinus* allocate relatively little carbon belowground (1:0.3 and 1.0.2 shoot-root ratio, respectively) although the rooting patterns are quite different. *Eriogonum* has a shallow root system (25—30 cm) while *Lupinus* has a deeper tapoott system (30—45 cm). *Lupinus* allocates about 50% of its carbon to leaves, but *Eriogonum* only about 25%. Reproductive effort is much greater in *Eriogonum* (Table 1).

With its deep root system, *Lupinus* like *Polygonum* can avoid summer drought. Leaves of *Lupinus* are small and highly pubescent, characteristics which help reduce heat load for these leaves track the sun on clear days. Leaf temperatures are maintained close to ambient air temperature (0.5 to 1.0°C higher) although the plants are prostrate and therefore within the zone of higher near-surface temperatures. *Eriogonum* with its prostate rosette form maintains leaf temperatures 2 to 5°C above ambient air on sunny days with moderate wind. *Eriogonum* maintains moderately low leaf water potentials and turgor loss points, thus enabling its root system to take up water from the sandy, gravelly soils. The data on turgor loss point indicate only limited osmoregulation in both species (Table 1). Water loss from these wintergreen leaves is relatively high compared with deciduous species.

Graminoids

To illustrate the graminoid growth form we have chosen the deciduous *Carex spectabilis* which grows in meadows that receive considerable winter snow cover and *Carex nardina,* a wintergreen species that grows in exposed sites with little winter snow cover.

Carex spectabilis allocates over 90% of its carbon to roots and rhizomes; reproductive tissues are quite minor (Table 1). The large belowground system permits rapid shoot growth with summer snowmelt. Nitrogen levels are relatively high for this herbaceous species.

This species is able to maintain quite high leaf water potentials throughout most of the summer and has rather high predawn leaf potentials of -0.05 m Pa, yet minimum daytime values of -1.0 to -1.7 m Pa. The turgor loss points are also variable and quite low, indicating that the plants probably osmoregulate. Leaf conductances are relatively high, again indicating that this species can maintain a positive water balance with its large root system. Soil water potentials were always greater than —0.1 mPa.

Carex nardina, the wintergreen graminoid species allocates more carbon aboveground, but also has a very small reproductive mass. Nitrogen levels are lower in this species, a rather common response of species that do not need to replace their entire leaf surface each year.

The somewhat more exposed habitats of this species result in lower leaf water potentials both at predown (-0.2 to -0.05 mPa) and lower minimum daily values. Although not determined, we predict that turgor loss point would also be lower. Correlated with more drought stressed habitats, this species maintains lower leaf conductances. Leaves of this species are thin, wiry compared with the flat leaves of *C. spectabilis.*

SUMMARY

These morphological and physiological measurements help explain how the different species are adapted to their various mesohabitats. The evergreen shrub *Cassiope* is well adapted to snowbed habitats with a limited growing season and thus a minimal requirement for expending carbon on new leaves each year. The deciduous forb *Polygonum,* also adapted to late snowbed sites solves its carbon allocation problems of a short growing season by maintaining a large root system for both carbon and nutrient storage as well as for providing an adequate water supply during droughty summers. The deciduous species *(Salix, Polygonum, Carex spectabilis)* regardless of growth form all have large root systems which function to maintain carbon and nutrient reserves as well as maintain adequate supply of soil water. *Salix* and other deciduous shrubs grow in more sheltered sites, where site water balance is favorable for growth and reproduction during the short growing season.

Drought tolerance is greater in the shrub than in the forb species and the graminoid species are intermediate. Osmotic adjustnent is much greater in the shrubs than in the herbaceous species; only the evergreen shrub develops low leaf water potentials. Stomatal conductance is relatively low in only the graminoid species. Based upon the literature, we find it rather surprising that species from the Cascades in each growth form appear less drought resistant than from the more continental climate of the Rocky Mountains. The length of the dry season is often longer in these west coast mountains where a mone Mediterranean climate dominates in summer.

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美国西北部高山植物的生长型和生态生理学

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摘　要

美国西北部的高山植物在相同的生境条件下，具有非常不同的生长型．在雪地，小常绿灌木通过保存叶片来贮存碳和养分，而落叶或者冬绿的杂类草与禾草以大量的根和根茎系统来贮存碳和养分．冬绿杂类草（*Eriogonum*）所提供的大量碳素用于繁殖．

冬绿杂类草和禾草多在裸露的(风大、雪少)生境下生长，然而这些种类提供很少的地下碳素，它们的渗透调节能力比灌丛种类还小．灌木的生长型(常绿和落叶)具有极大的耐旱性(低叶水势、最大的渗透调节、最小的气孔传导)；杂类草具有最小的抗旱性；而禾草居于中间．在每一个主要的高山生境(雪地、草甸、裸地边缘和坡地)共存着多种植物生活型．这些表明了没有最好适应一定生境的单独的生长型，而不同生长型的种类可以很好地共存于相同的生境．