

Contrasting resource allocation patterns in *Sedum lanceolatum* Torr.: Biomass versus energy estimates

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Summary. Biomass determinations and microbomb calorimetry were used to assess resource allocation in *Sedum lanceolatum* Torr. between 2,257 and 3,726 m above sea level in the Front Range of the Rocky Mountains, Colorado, USA. In general, energy values did not differ within a tissue among sites, but did differ among tissue types. Flowers and leaves had the greatest energy content per gram ash-free dry weight. Total kilojoules per plant were homogeneous along the elevational gradient.

Allocation patterns based on kilojoules of energy and grams of biomass were not highly correlated, with the exception of the percent investment in sexual tissues. Allocations to sexual tissues based on dry weight and energy were negatively correlated, revealing opposing trends of sexual investment with the increase in elevation. Due to the greater biomass investment in high energy leaves and flowers by populations of *Sedum lanceolatum* at higher elevations, allocation to sexual reproduction based on calorimetric analysis increased from 18.3 to 38.3% along the 1,469 m change in elevation. Although biomass can represent energy allocation in some taxa, for those species that change morphologically or physiologically along an environmental gradient, these two methods may not reveal similar trends.

Introduction

Theoretical and empirical studies suggest that resource allocation patterns may affect an organism's fitness (Cody 1966, Harper 1967, Harper and Ogden 1970, Ogden 1974, Gadgil and Solbrig 1972, Abrahamson 1975a, b, Hickman 1975, Soule and Werner 1981). Biomass, rather than time-consuming calorimetry, nutrients, or metabolic costs, typically is used as the currency in resource allocation studies. Hickman and Pitelka (1975) showed statistically similar allocation patterns based on grams and calories. It was concluded that calorimetry was unnecessary when comparing energy allocation of species with primarily carbohydrate seed reserves. The exclusive use of biomass alone often is justified by citing Hickman and Pitelka (1975), yet, caloric values differ among phyletic and ecological categories, among plant species, tissues of the same plant, and within a tissue among different seasons and microhabitats (Johnson and Robel 1968, Lieth 1968, Malone 1968, Harper and

Ogden 1970, Paine 1971, Gadgil and Solbrig 1972, Gaines et al. 1974, Ogden 1974, Hickman 1975, Hickman and Pitelka 1975, Hickman 1977).

Some alpine plants have higher caloric values, often paralleled by higher lipid contents, than plants at lower elevations (McNair 1945, Golley 1961, 1969, Bliss 1962, Hadley and Bliss 1964, Jordan 1971, Zachhuber and Larcher 1978). Hickman and Pitelka (1975) cautioned against equating gram and caloric investment patterns in taxa which store large proportions of lipids. Resource allocation patterns of a plant species that extends into alpine tundra from lower elevations will not be adequately described by biomass determinations alone.

Intraspecific differences in resource allocation patterns among populations at different elevations would be expected to occur based on differences in flower number, seed set, organ number, and size within a species along an elevational gradient (Clausen et al. 1940, 1948, Johnson and Cook 1968). These differences are most striking at the sub-alpine-alpine interface (Mooney 1963, Ward 1969, Rochow 1970, Jolls 1980a, b, Douglas 1981). The alpine has been characterized as an abiotically severe, unpredictable, heterogeneous environment, with high seedling and adult mortality, largely the result of physical factors (Osburn 1961, Marr 1967, Bonde 1968, Bliss 1971, Billings 1974). It has been hypothesized that the genetic diversity afforded by sexual reproduction will be selected in harsh, fluctuating environments (Giesel 1974). If abiotic factors affect the death rate more at high than low elevations, this higher density-independent mortality should produce a greater proportion of reproductive biomass in alpine populations of a species (Gadgil and Solbrig 1972). Yet Schaffer (1974) has shown that variation in the success of a sexual effort would lead to evolution for increasing vegetative growth and a decline in sexual allocation. Similarly, the empirical as well as theoretical literature presents conflicting views on the success of or investment in sexual reproduction above timberline (Osburn 1961, Bliss 1962, 1971, Marchand and Roach 1980, Jolls 1982, Jolls and Bock 1983).

Sedum lanceolatum Torr. is an herbaceous perennial, widely distributed in western North America (Clausen 1975). The biomass investment patterns reveal a decreased investment in sexual modes at higher elevations (Jolls 1980a). This study uses microbomb calorimetry to test hypotheses dealing with the greater energetic content of alpine plants and the similarity of biomass and energy for assessing resource allocation patterns.

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Materials and methods

Field sites were located at the University of Colorado's Institute of Arctic and Alpine Research Mountain Research Station, near Nederland, Colorado, USA. During the summer of 1977, a minimum of 20 flowering individuals of *Sedum lanceolatum* was harvested at each of the following four elevations: lower montane A site (2,257 m), upper montane B site (2,663 m), dry subalpine C site (3,033 m) and dry alpine D site (3,726 m). The two lowest elevation sites were located near Sugarloaf Mountain (40° 01' 12" N, 105° 24' 18" W) and the remaining pair were along Niwot Ridge (40° 02' N, 105° 32' W). Individual plants were harvested without bias from the perimeter of 5 × 10 m² study plots at each of the four elevations. Plants were washed free of soil and the plants dissected into roots, stems and rhizomes, leaves, flowers, peduncle, and peduncle leaves. These plant parts were oven-dried at 70° C to constant weight. After determining biomass of each plant's tissues, the tissues were combined by type for all individuals collected at each elevation. Each of the six types of tissue from each site was ground in a Wiley mill, pelleted, stored in a desiccator, and weighed a minimum of three times to the nearest 0.1 mg on a Mettler H35AR analytical balance for an accurate measure of dry weight. The energetic values of these pelleted samples were obtained by combustion in a Phillipson microbomb calorimeter (Gentry Instruments, Aiken, South Carolina). A minimum of three replicates of each tissue type from each site was combusted, with the exception of the peduncle leaves and the peduncle itself which were not present in large enough quantities for numerous replicates at each site.

A known amount of each of the five tissue types, pooled by elevation, was burned in a muffle furnace at 500° C for 4 h to determine ash content. Each of the pellet weights was reduced proportionately by this factor; each combustion was expressed as kilocalories per gram of ash-free biomass and converted to kJ/g. No acid corrections were made; other researchers have found that these corrections are less than 0.5% of the total energy content (Lieth 1968, Harper and Ogden 1970, Pitelka 1978).

The caloric values were subjected to a two-way analysis of variance among tissues and sites. The peduncle and peduncle leaves were deleted from this analysis. Due to the ANOVA's sensitivity to unequal cell sizes, a Student-Newman-Keuls multiple range test was performed on those main effect variables for which significant differences existed.

The total number of calories and proportional energy investment for each tissue type were computed for each elevation. The weight of each of the five tissues for each of the twenty harvested plants was multiplied by the tissue energy content (kJ/g ash-free dry weight). These products were summed to yield total calories per plant. Proportional energy investment was determined by expressing calories of each tissue as a percentage of total plant calories. These percentages were subjected to arcsine square root transformations to meet the assumptions of the analysis of variance and differences in mean values were compared among sites using the ANOVA and the Student-Newman-Keuls test (Sokal and Rohlf 1969, Nie et al. 1975). The investment percentages, based on biomass from Jolls 1980a and energy from this study, were compared using Kendall's coefficient of rank correlation (τ), a nonparametric test of association,

Table 1. Results of two-way and one-way analyses of variance comparing caloric values (kJ/ash-free gram dry weight) among sites and tissues, tissue caloric value among sites, and energetic investment within a tissue among sites (%)

Variable	df	F	P
Two-way anova			
main effects	6	13.966	0.001**
site	3	21.742	0.001**
tissue	3	4.365	0.008**
interaction	9	1.348	0.235 n.s.
One-way anovas			
site	3, 66	3.111	0.032*
tissue	5, 89	17.921	0**
leaves	3, 16	2.042	0.148 n.s.
stems and rhizomes	3, 9	1.225	0.356 n.s.
roots	3, 11	4.952	0.0205**
flowers ^a	3, 8	0.033	n.s.
total calories/plant	3, 59	0.118	0.949 n.s.
leaf energy % ^b	3, 59	4.481	0.007**
stem-rhizomes energy % ^b	3, 59	2.925	0.041*
root energy % ^b	3, 59	0.198	0.898 n.s.
sexual energy % ^b	3, 59	5.408	0.002**

n.s. = no significant difference among means

* $P < 0.05$ ** $P < 0.01$

^a Analysis was an approximate test of the equality of means assuming heterogeneous variances

^b Analysis was performed on transformed data

from the Michigan Interactive Data Analysis System (MIDAS), Statistical Research Laboratory, University of Michigan.

Results

The results of two-way analysis of variance comparing caloric value among sites and the four tissue types (excluding peduncles and peduncle leaves) are displayed in Table 1. Energy values were highly significantly different ($P < 0.001$) among sites and tissues; no significant interaction was present. A one-way ANOVA compared means within each of these two main effects (Table 1) and a SNK revealed the source of the differences (Table 2). The significant differences among sites found in the two-way ANOVA were due to the difference in average energy value computed from all tissue types between the upper montane and subalpine populations. By subjecting each tissue type to a one-way ANOVA among sites, it was shown that no variation existed within a tissue among elevations, with the exception of mean root kilojoules per ash-free dry weight. Root energy value from the upper montane was significantly greater than the values for the lower montane or subalpine. This same trend was reflected in the mean energy content of all tissues compared among sites.

A one-way ANOVA and SNK also were executed to compare energy values among tissues (Table 3). For the one-way analysis, all five tissue types, including peduncles and peduncle leaves, were analyzed; there were highly significant differences among the five organs ($P < 0.001$). The average kilojoules per ash-free gram dry biomass of leaves were significantly greater than those energy values of the stems and rhizomes, roots, peduncle leaves, and peduncles.

Table 2. Comparisons of average caloric value (kJ/ash-free gram dry weight) of tissues among sites

Site		All* $\bar{x} \pm \text{s.e.}$ (n)	Tissue caloric value (kJ)			
			Leaves $\bar{x} \pm \text{s.e.}$ (n)	Stems and rhizomes $\bar{x} \pm \text{s.e.}$ (n)	Roots* $\bar{x} \pm \text{s.e.}$ (n)	Flowers ^a $\bar{x} \pm \text{s.e.}$ (n)
A	Lower montane 2,257 m	16.66 ± 1.93 (22)	16.87 ± 0.67 (7)	14.99 ± 0.50 (3)	15.28 ± 0.29 (6)	18.63 ± 0.63 (6)
B	Upper montane 2,663 m	17.87 ± 1.51 (17)	17.87 ± 0.54 (5)	15.61 ± 0.25 (3)	18.38 ± 0.92 (3)	18.75 ± 0.38 (6)
C	Dry subalpine 3,033 m	16.16 ± 2.05 (16)	16.66 ± 0.38 (5)	14.73 ± 0.17 (4)	14.32 ± 0.59 (3)	18.33 ± 1.30 (4)
D	Dry alpine 3,726 m	17.58 ± 1.84 (15)	18.75 ± 0.38 (3)	15.20 ± 0.50 (3)	16.74 ± 1.42 (3)	18.63 ± 0.25 (6)

* $P < 0.05$ ^a Analysis was an approximate test of the equality of means assuming heterogeneous variances**Table 3.** Comparison of mean caloric value (kJ/ash-free gram dry weight) among tissue types. Vertical lines denote no significant difference among means

Tissue	Caloric value** (kJ/g) $(\bar{x} \pm \text{s.e.})$	(n)
Leaves	17.33 ± 0.33	(20)
Stems and rhizomes	15.11 ± 0.17	(13)
Roots	15.99 ± 0.50	(15)
Flowers	18.59 ± 0.29	(22)
Peduncle leaves	15.32 ± 0.25	(19)
Peduncle	15.61 ± 0.67	(6)

** $P < 0.01$

The flowers had the greatest energy content, 18.6 kJ/ash-free gm dry weight.

Total and proportional energy investments are presented in Table 4. The average total kilojoules per plant did not differ among sites. The proportion of total plant energy present in root tissue also was homogeneous among sites, averaging approximately 24.8%. The stem and rhizome proportion varied significantly ($P < 0.05$) among sites;

the SNK distinguished the greatest value, 29% in the upper montane, from the smallest value, 14.7% in the alpine. The differences among the percentage of total plant energy as leaf biomass were most pronounced between the lower montane (32.1%) versus the mid-elevation and alpine groups. The proportional energy investment in sexual tissues was reduced in the lower montane (18.3%). This value represents a 37.6% decrease compared to the average value (29.3%) at the higher elevations. There is a trend of greater allocation of energy to sexual tissues at higher elevation; however, the means of the three highest elevations were homogeneous. The differences were most pronounced at the subalpine-alpine interface.

Table 5 compares the elevational trends in energy investment from this study and corresponding trends in biomass allocation from Jolls 1980a. Sexual investment increased at higher elevation when energy was used as the currency for comparison. The greater investment in roots characteristic of the subalpine population is not seen when comparing energetic investment rather than biomass percentages. The upper montane rather than the alpine had greater investment in stem and rhizome proportions using calorimetry. Allocation patterns based on energy reversed the trends in leaf and sexual investment. The lower montane

Table 4. Comparisons of means of total plant energy (kJ/plant) and proportionate energetic investment in each tissue type among sites. Vertical lines denote no significant difference among means

Site	Total kilojoules $\bar{x} \pm \text{s.e.}$ (n)	Root proportion ^a $\bar{x} \pm \text{s.e.}$ (n)	Stem and rhizome* proportion ^a $\bar{x} \pm \text{s.e.}$ (n)	Leaf** proportion ^a $\bar{x} \pm \text{s.e.}$ (n)	Sexual** proportion ^a $\bar{x} \pm \text{s.e.}$ (n)	
A	Lower montane 2,257 m	8.89 ± 0.64 (20)	0.261 ± 0.032 (20)	0.236 ± 0.028 (20)	0.321 ± 0.035 (20)	0.183 ± 0.022 (20)
B	Upper montane 2,663 m	8.60 ± 0.64 (20)	0.252 ± 0.031 (20)	0.290 ± 0.020 (20)	0.189 ± 0.025 (20)	0.269 ± 0.028 (20)
C	Dry subalpine 3,033 m	8.74 ± 0.57 (17)	0.241 ± 0.033 (17)	0.269 ± 0.028 (17)	0.199 ± 0.026 (17)	0.290 ± 0.027 (17)
D	Dry alpine 3,726 m	9.28 ± 0.88 (6)	0.207 ± 0.038 (6)	0.147 ± 0.026 (6)	0.263 ± 0.035 (6)	0.383 ± 0.052 (6)

* $P < 0.05$ ** $P < 0.01$ ^a Analyses were performed on transformed data

Table 5. The allocation patterns among sites based on biomass and energy investment in *Sedum lanceolatum* and Kendall's coefficient of correlation (τ) comparing the two methods

Site	Allocation (%)							
	Leaves		Stems and rhizomes		Roots		Sexual	
	g	kJ	g	kJ	g	kJ	g	kJ
Lower montane	15.2	32.1	10.4	23.6	17.3	26.1	57.1	18.3
Upper montane	19.9	18.9	12.1	29.0	17.2	25.2	50.8	26.9
Subalpine	18.6	19.9	15.9	26.9	40.5	24.1	25.0	29.0
Alpine	39.0	26.3	26.7	14.7	10.0	20.7	24.3	38.3
Kendall's τ	-0.33 ^{n.s.}		-0.33 ^{n.s.}		+0.33 ^{n.s.}		-1.00**	

n.s. = not significant, df = 3

** $P < 0.01$

was characterized by a greater sexual and reduced leaf proportion using biomass assessment; caloric assessment distinguished reduced sexual and greater leaf proportions in this same population.

The two types of investment patterns were compared using Kendall's rank correlation coefficient. The average percentages of all the plants at a site were ranked and τ was computed for all tissues and each of the four tissue types individually (Table 5). Gram and energy allocations were not significantly correlated when all tissues were compared ($\tau = -0.2017$, $df = 14$, $P = 0.3049$) nor for comparisons of leaves, stems and rhizomes, or roots among elevations. The allocations of biomass and energy to sexual tissues were negatively correlated, revealing opposing trends ($\tau = -1.0000$, $P < 0.001$).

Discussion

Calorimetric analysis of elevational populations of *Sedum lanceolatum* revealed striking homogeneity within a tissue among sites as has been found for *Salix* (West and Meng 1966) and *Senecio vulgaris* in response to stress (Harper and Ogden 1970). This uniformity of energy content is corroborated by the lack of significant variation in total plant lipid content when corrections are made for differences in morphology among sites (Jolls 1980b). Although other researchers report variation in plant energy values in response to environmental differences (Golley 1961, 1969, Paine 1971, Hickman and Pitelka 1975), no clear trends were evident in their studies. Baruch (1982) found a suggestion of greater average energy content within vegetative tissues at higher elevations of Venezuela, however, this trend was not statistically significant.

The only difference among sites observed in this study was the reduced energy value of roots in the upper montane versus the subalpine population. These differences in root energy value of *Sedum lanceolatum* between the two sites may be an artifact due to differential ease of harvest among sites and a greater contamination of organic tissues by soil particles. However, Malone (1968) found greater energy values in *Ambrosia artemisiifolia* and *Lolium perenne* from an abandoned field in New Jersey in a drought year than in a wetter growing season. The upper montane sites in the Front Range experience a midsummer drought (Marr 1967) which may result in storage by *Sedum* as a response to water stress (Baruch 1982).

Differences did occur among tissues within individuals of *Sedum lanceolatum*, as found for other taxa (Golley 1961, Bliss 1962, Harper and Ogden 1970, Gaines et al. 1974, Hickman and Pitelka 1975, Zachhuber and Larcher 1978, Baruch 1982). The caloric values of stems and rhizomes, roots, peduncles, and peduncle leaves of *Sedum lanceolatum* were lower than other tissues of the plant. The low caloric values of these tissues appear to represent depleted reserves at the time of flowering and decreased investment in the support structure of the sexual organs. Reduced caloric values of roots and stems relative to other plant parts have been found for annual, herbaceous perennial, and shrubby species of *Lupinus* (Pitelka 1978) and for herbaceous perennials of the páramos (Baruch 1982). The results for *Sedum lanceolatum* suggest that stores in the roots, stems, rhizomes, and peduncle leaves are translocated for production of the inflorescence.

Leaves and flowers had the highest energy content per gram of all tissues in *Sedum lanceolatum*, as was found in *Senecio vulgaris* by Harper and Ogden (1970), *Helianthus* spp. (Gaines et al. 1974), *Polygonum cascadenense* (Hickman and Pitelka 1975), *Lupinus* spp. (Pitelka 1978), and 16 taxa of the Venezuelan páramos (Baruch 1982). The greater energy value of sexual tissues compared to vegetative organs has been used to stress the higher energy cost of sexual reproduction and may be accounted for by the presence of protein-rich pollen, plus amino acid and carbohydrate-enriched nectar (Pitelka 1978). The high leaf caloric values compared to other vegetative tissues are probably due to greater accumulations of proteins and fats in leaves from photosynthetic and storage activities than in woody stems or roots (Pitelka 1978).

A striking contrast in the resource patterns of *Sedum lanceolatum* was revealed by biomass and caloric value determinations. Although Abrahamson and Caswell (1982) found a strong correlation between allocation patterns based on biomass and those based on energy in *Solidago*, biomass allocation did not adequately reflect mineral allocation in *Solidago* or *Verbascum thapsus*. The correlation between biomass and energy may reflect the morphological and physiological stasis of *Solidago*, particularly within the limited geographic area sampled, and the insensitivity of calorimetry to the differences in nutrient content that Abrahamson and Caswell observed within the genus.

Caloric analysis reversed trends in the sexual allocation of *Sedum lanceolatum*, suggested by biomass patterns. Be-

cause the energetically-poor peduncle was shorter in alpine plants, a greater proportion of the inflorescence existed as energy-rich flowers, despite the decrease in flower production with elevation (Jolls 1980a). This same effect was seen in the total energy content per plant. Although alpine plants were somewhat smaller in their total dry weight (Jolls 1980a), a greater percentage of these grams was present in the highest caloric value tissues, the leaves and flowers. While biomass studies suggested a greater investment in asexual modes, energy allocation patterns indicated the reverse: almost 40% of the total calories of alpine plants were present as inflorescence tissues. This 40% reproductive effort suggests greater emphasis on sexual modes in the alpine. Greater allocation to reproduction in response to increases in elevation also has been observed in *Heloniopsis orientalis* (Kawano and Masuda 1980) and *Mimulus primuloides* (Douglas 1981).

These data warn against exclusive use of biomass when resource allocation is the basis for comparing populations of plants. Differential investment of plant biomass to various tissues among elevations can produce opposing patterns for resource allocation based on grams (biomass) and joules (energy). Plant resource allocation patterns, particularly of those species that change in morphology or physiology along an environmental gradient, can best be obtained by the combined use of methods based on biomass, calorimetry, metabolic costs (Jurik 1983), nutrients (Thompson and Stewart 1981), and number of structures (Antonovics 1980, Abrahamson and Caswell 1982).

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