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CHANGES IN LEAF CHARACTERISTICS OF SPECIES ALONG ELEVATIONAL GRADIENTS IN THE WASATCH FRONT, UTAH[1]

JAMES R. EHLERINGER

Department of Biology, University of Utah, Salt Lake City, Utah 84112

ABSTRACT

Leaf absorptances and leaf angles were measured on 159 of the most common vascular plant species along a precipitation/elevation transect in the Wasatch Mountains. At the community level, leaf angles were steepest in the driest saltbush community sites, became progressively more horizontal in wetter communities, and reached a minimum in the midelevation mountain brush communities. At higher elevation plant communities, where growth is delayed until summer months because of heavy snowfall, leaf angles were again steeper. Leaf absorptances among all life forms were uniformly high along the entire transect until the driest saltbush communities where a number of species exhibited reduced leaf absorptances. The results are discussed within the context of mechanisms for reducing solar radiation absorption along an aridity transect.

THERE HAS LONG BEEN an interest in understanding the means by which plants are adapted to different environmental conditions. Haberlandt (1884), Schimper (1903) and Warming (1909) were among the first to document changes in leaf morphological properties along diverse environment gradients and to infer that these changes in leaf characteristics played a role in enhancing plant performance or survival. However, at that time little was known of the mechanisms by which changes in leaf morphological parameters could play a role in plant adaptation.

A major advancement came several decades ago when Raschke (1960) and Gates (1962) introduced the leaf energy balance equations. Leaves interact with their surrounding physical environment through processes of energy exchange. These processes include radiation absorption and reradiation, convection and transpiration. A primary consequence of leaf energy exchange is its effect on leaf energy balance, which is physiologically manifested as changes in both leaf temperature and transpirational water loss rates (Ehleringer and Mooney, 1978; Smith, 1978; Field, Chiariello, and Williams, 1982; Ehleringer and Werk, 1986; Ehleringer and Comstock, 1987). The structural characteristics of leaves will greatly influence the extent of the coupling between the leaf and its physical environment. Of particular importance in this respect are the leaf absorptance (leaf color), leaf angle and leaf size. Decreasing leaf absorptance and/or increasing leaf angle both have the effect of decreasing overall light interception, although the patterning will differ (Ehleringer and Werk, 1986). Increasing leaf angles affect the diurnal pattern of radiation absorbed, but not necessarily the peak amount, whereas decreasing leaf absorptance may not affect the diurnal patterning, but will greatly influence the peak amount absorbed.

For single species and for intrageneric comparisons, there has been substantial progress in understanding the significance of certain morphological features to the leaf energy balance and its role in adaptation (Taylor and Sexton, 1972; Thomas and Barber, 1974; Mooney, Ehleringer, and Björkman, 1977; Ehleringer and Mooney, 1978; Smith, 1978; Ehleringer et al., 1981). On a larger scale, there has been less progress in determining the patterns used by different species at the community level since the study of Billings and Morris (1951). They investigated changes in leaf spectral properties of 20 species along a precipitation cline in Nevada and showed that leaf absorptance was lower at drier sites. The inference from the Billings and Morris (1951) study and from single-species studies is that decreased leaf absorptance translates into reduced energy loads and thus a lowering of both leaf temperature and water loss rates. No other studies have examined the general changes in leaf energy exchange parameters of members of a plant community along an environmental gradient.

In northern Utah, there is a steep precipitation/elevation gradient associated with Wasatch Mountains. Along this cline, there are extensive changes in plant community com-

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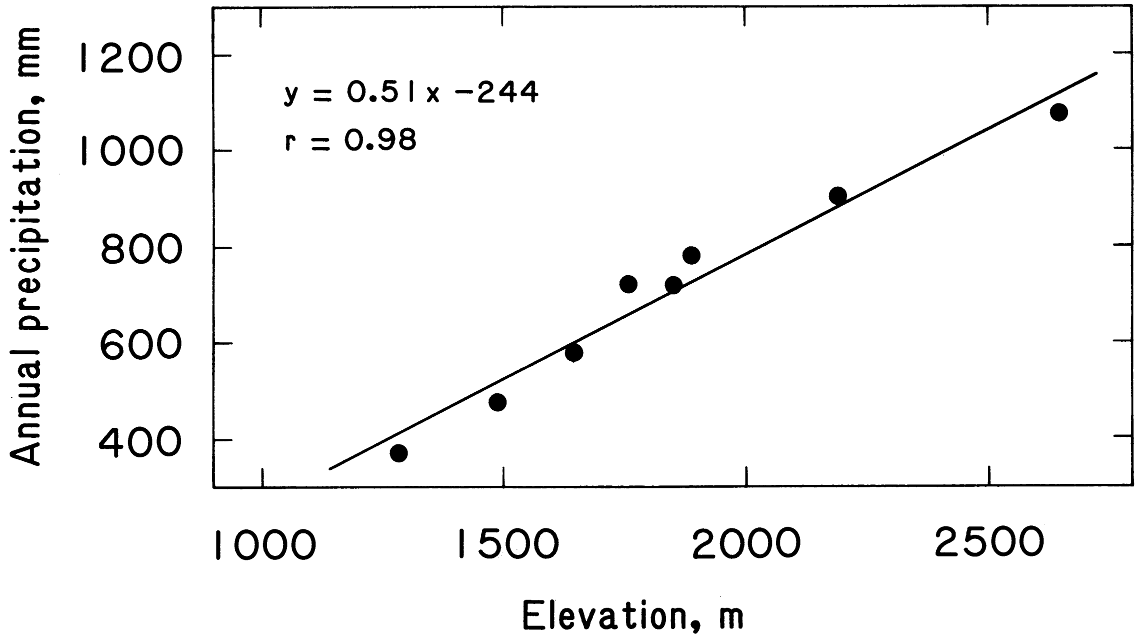

Fig. 1. Regression of mean annual precipitation against elevation for six different stations located in the northern part of Salt Lake Valley along the Wasatch Front, Utah.

position extending from cold desert scrub at the lowest elevations to alpine meadow at the highest (Foster, 1968). The purpose of this study was to determine the leaf energy exchange parameters of each of the dominant species within each community along this environmental cline and to see what if any general patterns emerged at the community and life form levels.

MATERIALS AND METHODS—Samples were collected from mature plants during the peak of the growing season at several sites along the Wasatch Front in the immediate vicinity of Salt Lake City, Utah. Nine specific plant communities were identified and the dominant plant species within each community were sampled in Red Butte Canyon, Mill Creek Canyon, Little Cottonwood Canyon and the areas surrounding the Great Salt Lake. These canyons are essentially parallel to each other within the Salt Lake Valley. The plant communities sampled in order of increasing elevation are cold desert scrub (1,250 m), foothills grassland (1,450 m), juniper woodland (1,650 m), oak-maple scrub (1,800 m), mountain brush (2,000 m), aspen-coniferous forest (2,400 m), and alpine meadow (2,700 m). Additionally, plants in two distinct riparian communities, differing in elevation (1,800 and 2,400 m), were sampled. Plant identification follows Arnow, Albee, and Wyckoff (1980).

Four sets of measurements were collected on each species. These were the leaf absorptance, leaf angle, leaf width and leaf area. Leaf absorptances to solar radiation in the 400–700 nm waveband were measured using an Ulbricht integrating sphere as described previously by Ehleringer (1981). Three leaves per species were measured at each site. Leaf angles from the horizontal were measured with an inclinometer, mean leaf width with a ruler, and leaf area with a leaf area meter (model 3100, LICOR, Lincoln, Nebraska). For angles, widths and areas, 25 leaves per species were measured at each site. All data presented are the means plus or minus one standard error.

The precipitation at each site was determined through regression analysis since individual site data were not available. Long-term U.S. Weather Bureau precipitation records for several adjacent locations along the Wasatch Front within Salt Lake Valley were regressed against elevation. These sites were Salt Lake City, Red Butte No. 1, Red Butte No. 2, Red Butte No. 3, Red Butte No. 4, Red Butte No. 5, Red Butte No. 6, and Brighton.

The long-term weather record between 1942–1971 indicated that mean annual precipitation was very significantly related to elevation (Fig. 1). The regression of precipitation in mm (y) against elevation in m (x) was $y = 0.51x - 244$ with a regression coefficient of 0.98. Since precipitation was not measured at each of the sites where plants were sampled, the average expected precipitation for each community was calculated based on this regression equation.

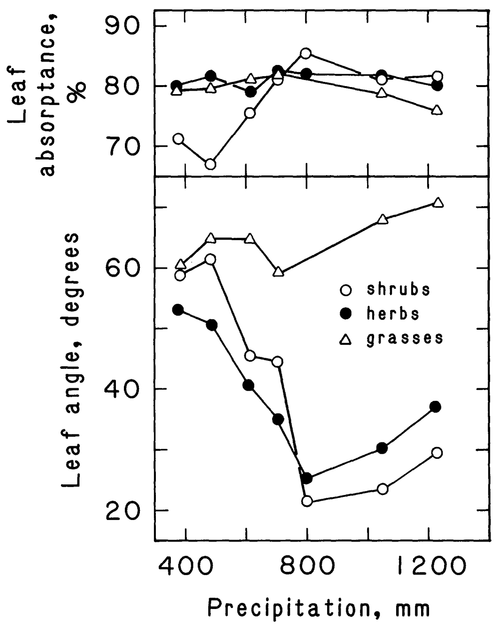

Fig. 2. The relationships between mean leaf absorptance and mean leaf angle for different life forms along the precipitation gradient in the Wasatch Front, Utah.

RESULTS AND DISCUSSION—One hundred fifty-nine of the most common species were sampled in the seven communities along this transect. The number of observations made was larger than this (N = 196), since 37 species occurred in more than one vegetation type. Although only 14% of the total number of species known to occur along the Wasatch Front (Arnow et al., 1980) were sampled, the species in our survey represented approximately 80–90% of the total biomass at any given sample site and included the dominant species as described by Foster (1968) and Arnow et al. (1980). Means and standard errors for each of the individual species observations are presented in the Appendix.

When grouped by life form, several distinct patterns appeared with respect to leaf absorptance and leaf angle values as a function of habitat aridity. First, the average leaf absorptances within a life form were more or less constant in the grasses and herbs, but decreased in shrubs with decreased precipitation (Fig. 2). The decrease in average leaf absorptance of shrub species amounts to 15% between the saltbush and mountain brush communities. A two-way analysis of variance revealed a significant effect of habitat on leaf absorptance, but no effects associated with life form (Table 1).

Second, there were large changes in the leaf angles along this precipitation transect (Fig. 2). The average leaf angle increased from 25–53° in herbs and from 21–61° in shrubs in going from the mountain brush to the driest saltbush community sites. At the two wetter nonriparian communities, leaf angles of herbaceous and shrub species tended to increase again. Leaf angles of the grass species were already steep (above 60°) and tended to decrease with decreasing precipitation. A two-way analysis of variance revealed both significant effects due to life form and to habitat, although the interaction of these two factors was not significant (Table 2).

TABLE 1. *Two-way ANOVA testing for significant effects of life form (grass, herb, shrub and tree) and habitat on leaf absorptance*

Source	df	*F* ratio	*P*<
Life form	3	0.74	0.529
Habitat	6	4.07	0.001
Interaction	12	1.40	0.173

The integrated effects of the leaf absorptance and leaf angle differences among vegetation types were determined by simulations of the expected absorbed photon flux (400–700 nm) on a daily basis (Fig. 3). These simulations indicated that at the driest plant community (cold desert shrub), the total daily photon flux ranged from 15.2–21.9 mol m^{-2} day^{-1}. For perspective, the calculated incident daily total on a horizontal surface would be 63.6 mol m^{-2} day^{-1}. As precipitation increased at higher elevation plant communities, the calculated daily photon flux for grass and sedge leaves decreased from 16.0–7.4 mol m^{-2} day^{-1}. In contrast, for both herb and shrub life forms, the calculated daily photon flux increased to above 40 mol m^{-2} day^{-1} in wetter plant communities, reaching a maximum at the mountain brush sites and then decreasing only slightly at wetter sites.

Leaf absorptances and leaf angles of riparian plants exhibited consistent differences between the two sites. At the warmer, low elevation riparian sites, leaf absorptances of shrub and tree species tended to be lower by 6–7% than in riparian species from the higher elevation. There were no detectable patterns among the

TABLE 2. *Two-way ANOVA testing for significant effects of life form (grass, herb, shrub and tree) and habitat on leaf angle*

Source	df	*F* ratio	*P*<
Life form	3	12.41	0.001
Habitat	6	10.30	0.001
Interaction	12	1.74	0.070

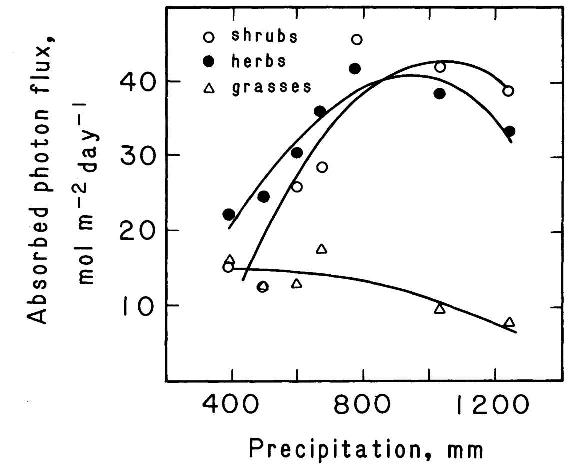

Fig. 3. Calculated absorbed photon flux on a daily basis (mol m^{-2} day^{-1}) for leaves of grass, herb and shrub life forms using the measured mean values for each life form at different Wasatch Front sites. Simulations are for a solar declination of +20°, an atmospheric transmission coefficient of 0.78, and assuming a 10% solar diffuse component. No qualitative changes were noted in the shapes of these simulation response curves at higher solar elevations; thus these curves represent the expected absorbed solar radiation patterns between approximately 14 May and 1 August. Curves represent third-order polynomial regressions through data points.

herbaceous species at either of these two vegetation types. There was a similar and perhaps expected pattern with respect to leaf angles. In this case, for trees, shrubs and herbaceous life forms, leaf angles were steepest at the low elevation riparian site. The difference in mean leaf angle was approximately 11° between vegetation types. The combination of lower leaf absorptances and steeper leaf angles at the low elevation riparian site, which will tend to reduce the amount of solar radiation absorbed by the leaf, are consistent with the notion that the low elevation site is more stressful (higher temperatures and lowered humidities creating a greater evaporational demand).

While leaf area was strongly correlated with leaf width ($r = 0.89$, $P < 0.01$), there were no consistent patterns at the community level in leaf area with life form or leaf area with aridity (Table 3, 4). To some extent this was due to the wide variation in leaf areas and widths among species at a site (see Appendix for individual values), so that life form-averaged observations provided little insight.

It is perhaps unexpected that the minimum leaf angles (most near horizontal) should be observed in species from the mountain brush community as it implies that this is perhaps the most mesic of the nonriparian plant communities. However, upon closer examination this pattern might be expected. Most of the plant growth in all vegetation communities depends on the extent of winter–spring precipitation. In plant communities above the mountain brush zone, this precipitation comes almost exclusively as snowfall, whereas below it comes as a combination of rain and snow. In particular, during the spring when much of the growth is occurring in the lower elevation communities, the precipitation comes as rain. Because of the warmer temperatures, plants at lower elevations are able to utilize this spring precipitation. That is less likely to be the case with the higher elevation communities which do not commence growth until late spring or early summer after snowmelt has occurred. In effect then, growth in these higher elevation communities occurs with an initially charged soil moisture profile, but one in which there is less likely to be more moisture recharge during the latter phases of the growing season. This could tend to produce a pattern where the highest amounts of effectively available soil moisture are at the mountain brush sites.

Most, if not all, of the ecosystems of western North America experience water stress arising from soil moisture depletion. In terms of phys-

TABLE 3. *Summary of average leaf areas (cm^2) for different life forms in different plant communities along the Wasatch Front, Utah*

	Trees	Shrubs	Herbs	Grasses
Cold desert scrub	—	2.6	2.7	3.5
Foothill grassland	—	1.4	24.9	2.8
Juniper woodland	—	1.8	8.6	2.2
Oak-maple scrub	—	19.6	14.2	6.7
Mountain brush	—	31.4	28.2	—
Aspen-coniferous forest	6.1	5.0	9.0	4.0
Alpine meadow	—	22.7	32.8	7.1
Upper riparian	23.9	44.4	5.9	—
Lower riparian	8.4	0.9	40.2	8.9

TABLE 4. *Summary of average leaf widths (mm) for different life forms in different plant communities along the Wasatch Front, Utah*

	Trees	Shrubs	Herbs	Grasses
Cold desert scrub	—	4.6	13.0	0.9
Foothill grassland	—	3.9	29.2	4.2
Juniper woodland	1.5	7.6	15.2	3.6
Oak-maple scrub	—	45.1	21.7	6.2
Mountain brush	—	55.0	40.3	—
Aspen-coniferous forest	15.1	18.5	30.9	2.2
Alpine meadow	—	33.9	37.1	4.0
Upper riparian	46.9	66.2	8.5	—
Lower riparian	18.3	7.6	34.2	6.4

iological activity, the water stress results in a decreased leaf conductance, and since the carbon dioxide supply rate decreases with leaf conductance, a decreased need for photons to operate the photosynthetic light reactions. Photon flux levels beyond that required to saturate photosynthesis serve only to increase the energy load and heat the leaf; they may also be detrimental to the photosynthetic apparatus resulting in photoinhibitory damage to the leaf (Björkman and Powles, 1984; Ludlow and Björkman, 1984). The increased leaf temperatures associated with high light absorption and low leaf conductances would only increase the leaf to air water vapor concentration gradient and thus aggravate the water stress experienced by the plant. Under natural conditions where the water stress periods may be short or where there is still sufficient moisture to allow low rates of gas exchange, leaf retention and adjustment of water stress may result in low but positive rates of carbon gain. It is reasonable that as an adjustment to water stress, natural selection may have favored the evolution of features which result in a reduction of the amount of solar radiation absorbed by the leaf without going to the extreme of leaf abscission. Two possible responses would include decreased leaf absorptance and increased leaf angle.

Leaf angle changes have two potential advantages over leaf absorptance changes as a means of reducing the amount of solar radiation on the leaf surface. First, leaf angle changes are likely to be more economical in cost, since little carbon/energy investment is required, and second, leaf angle changes can be reversible during a leaf's lifetime (Comstock and Mahall, 1985). The disadvantage of leaf angle changes are that while they may reduce the total daily radiation incident on the leaf, leaf angle changes do not necessarily reduce the peak incident solar radiation levels. Only leaf absorptance changes will necessarily reduce the peak radiation levels on a leaf. Thus, from a carbon and/or water economic standpoint, we might expect leaf angle changes to occur as the initial means of reducing the incident solar radiation levels under water stress conditions. The Wasatch Front transect data support this expectation because reduced leaf absorptances are observed only after the average leaf angles have already become steep. In other western North American habitats (such as coastal sage and warm desert communities) where the drought periods are longer than those experienced by plants along the Wasatch Front, we might expect that a reduced leaf absorptance would be a more common mechanism for reducing solar radiation absorption over extended periods and this is in fact what has been observed (Harrison, Small, and Mooney, 1971; Shaver, 1978; Rundel et al., 1980; Ehleringer, 1981).

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APPENDIX. *Leaf absorptance (%), leaf angle (°), leaf area (cm²) and leaf width (mm) of species along the Wasatch Front, Utah*

Species	Absorptance	Angle	Leaf area	Leaf width
Cold desert scrub (Saltbush) community				
Shrubs				
Allenrolfea occidentalis (Wats.) Kuntze	79.6 ± 1.5	—	—	3.6 ± 0.1
Atriplex confertifolia (Torr. & Frem.) Wats.	56.3 ± 1.8	72.0 ± 2.4	3.9 ± 0.1	8.9 ± 0.2
Atriplex gardneri (Moq.) Dietr.	69.6 ± 0.7	34.0 ± 3.7	4.3 ± 0.1	5.9 ± 0.1
Chrysothamnus nauseosus (Pall.) Britt.	75.3 ± 1.7	64.2 ± 2.4	2.1 ± 0.1	2.5 ± 0.1
Sarcobatus vermiculatus (Hook.) Torr.	75.2 ± 1.7	66.4 ± 3.1	0.2 ± 0.0	2.0 ± 0.1
Grasses and sedges				
Agropyron elongatum (Host) Beauv.	79.7 ± 1.1	61.4 ± 3.5	4.4 ± 0.3	3.4 ± 0.2
Distichlis spicata (L.) Greene	79.1 ± 0.7	59.4 ± 3.2	2.6 ± 0.1	4.0 ± 0.1
Herbs				
Ambrosia artemisiifolia L.	77.1 ± 1.2	32.8 ± 3.2	1.9 ± 0.1	14.6 ± 0.5
Cardaria draba (L.) Desv.	80.9 ± 1.2	65.8 ± 2.6	4.4 ± 0.5	13.7 ± 0.8
Lactuca serriola L.	77.0 ± 2.0	73.6 ± 3.2	11.5 ± 0.9	19.7 ± 0.7
Machaeranthera canescens Pursh	83.0 ± 0.5	39.4 ± 4.6	1.1 ± 0.5	3.8 ± 0.1
Polygonum ramosissimum Michx.	82.0 ± 0.6	—	—	—
Foothill grassland community				
Shrubs				
Artemisia tridentata Nutt.	54.0 ± 1.2	66.6 ± 2.8	0.7 ± 0.0	5.4 ± 2.3
Chrysothamnus nauseosus (Pall.) Britt.	63.0 ± 1.0	57.0 ± 2.9	2.1 ± 0.1	2.5 ± 0.1
Rhus trilobata Nutt.	83.0 ± 0.0	—	7.8 ± 0.6	30.9 ± 1.3
Herbs				
Ambrosia psilostachya DC.	81.6 ± 0.9	40.8 ± 2.7	7.8 ± 0.6	30.9 ± 1.3
Artemisia ludoviciana Nutt.	62.3 ± 2.6	59.0 ± 2.7	1.5 ± 0.1	11.7 ± 0.4
Aster chilensis Nees	84.3 ± 0.8	63.2 ± 4.4	4.3 ± 0.3	10.5 ± 0.5
Astragalus cibarius Sheld.	87.1 ± 0.5	35.8 ± 3.9	0.5 ± 0.0	6.7 ± 0.3
Astragalus utahensis (Torr.) T. & G.	70.6 ± 0.0	53.8 ± 0.6	0.4 ± 0.0	5.7 ± 0.1
Balsamorhiza macrophylla Nutt.	86.2 ± 1.7	49.6 ± 8.6	131.1 ± 8.5	96.7 ± 3.5
Balsamorhiza sagittata (Pursh) Nutt.	68.0 ± 2.0	47.0 ± 2.4	41.7 ± 2.2	64.4 ± 2.3
Cirsium undulatum (Nutt.) Spreng.	77.6 ± 0.5	43.6 ± 3.2	27.3 ± 3.0	45.7 ± 3.4
Crepis occidentalis Nutt.	84.3 ± 0.8	56.0 ± 6.4	15.2 ± 2.7	37.9 ± 3.3
Erodium cicutarium (L.) L'Her.	85.0 ± 1.3	56.0 ± 3.3	0.4 ± 0.0	5.6 ± 0.3
Grindelia squarrosa (Pursh) Dunal	80.6 ± 0.6	45.0 ± 4.4	4.4 ± 0.3	12.6 ± 0.4
Helianthus annuus L.	82.3 ± 0.7	tracker	231.6 ± 9.2	203.1 ± 8.8
Heterotheca villosa (Pursh) Shinners	84.6 ± 0.0	42.0 ± 0.8	2.8 ± 0.1	11.6 ± 0.3
Lactuca serriola L.	83.9 ± 0.9	68.6 ± 2.6	22.1 ± 1.1	28.2 ± 0.8
Linaria genistifolia (L.) Mill.	84.3 ± 0.0	43.6 ± 1.0	6.3 ± 0.4	24.5 ± 1.0
Lithospermum arvensis (L.) Johnst.	83.5 ± 0.6	49.0 ± 4.8	0.7 ± 0.1	4.4 ± 0.2
Lupinus argenteus Pursh	86.3 ± 0.0	tracker	2.2 ± 0.1	8.0 ± 0.3
Lupinus sericeus Pursh	79.8 ± 0.6	tracker	0.8 ± 0.1	6.2 ± 0.2
Melilotus alba Medic.	85.0 ± 0.5	tracker	1.8 ± 0.1	11.2 ± 0.6
Microseris nutans (Geyer) Schultz-Bip.	87.6 ± 0.8	61.4 ± 6.7	6.9 ± 0.5	11.0 ± 0.6
Phlox longifolia Nutt.	85.0 ± 0.0	36.4 ± 1.0	1.1 ± 0.1	3.4 ± 0.2
Tragopogon dubius Scop.	86.9 ± 1.5	64.6 ± 3.6	8.2 ± 0.5	13.4 ± 0.4
Trifolium repens L.	80.9 ± 3.1	tracker	0.3 ± 0.0	6.7 ± 0.2
Vicia americana Muhl.	84.3 ± 0.6	39.0 ± 7.2	0.6 ± 0.0	6.3 ± 0.1
Wyethia amplexicaulis Nutt.	86.6 ± 0.3	56.8 ± 6.5	103.0 ± 7.2	62.6 ± 2.7
Grasses and sedges				
Agropyron smithii Rydb.	81.3 ± 0.0	68.6 ± 0.4	1.8 ± 0.1	3.3 ± 0.1
Agropyron spicatum (Pursh) Scribn. & Sm.	80.6 ± 0.7	69.8 ± 3.2	3.9 ± 0.2	4.8 ± 0.1
Bromus brizaeformis Fisch. & Mey.	79.3 ± 1.2	70.8 ± 6.4	1.1 ± 0.1	2.2 ± 0.1
Bromus inermis Leyss.	80.9 ± 0.9	59.4 ± 4.3	5.4 ± 0.4	7.2 ± 0.4
Poa bulbosa L.	77.2 ± 0.7	55.8 ± 4.0	1.7 ± 0.1	3.7 ± 0.1
Juniper woodland community				
Trees				
Juniperus osteosperma (Torr.) Little	85.3 ± 0.5	36.2 ± 4.5	—	1.5 ± 0.0
Shrubs				
Artemisia tridentata Nutt.	68.0 ± 0.8	46.6 ± 1.1	1.1 ± 0.1	7.5 ± 0.3
Berberis repens Lindl.	80.3 ± 1.5	33.2 ± 4.0	8.5 ± 0.6	29.0 ± 1.2

APPENDIX. *Continued*

Species	Absorptance	Angle	Leaf area	Leaf width
Chrysothamnus nauseosus (Pall.) Britt.	51.7 ± 0.9	44.8 ± 3.5	1.5 ± 0.1	3.3 ± 0.1
Chrysothamnus viscidiflorus (Hook.) Nutt.	83.0 ± 0.6	60.4 ± 2.0	0.2 ± 0.0	1.6 ± 0.1
Cowania mexicana D. Don.	88.7 ± 0.7	29.0 ± 3.0	0.9 ± 0.0	0.5 ± 0.4
Purshia tridentata (Pursh) DC.	86.0 ± 0.2	36.0 ± 0.5	0.5 ± 0.0	7.4 ± 0.2
Symphoricarpos oreophilus Gray	76.0 ± 0.6	42.5 ± 2.4	2.0 ± 0.1	12.6 ± 0.2
Tetradymia canescens DC.	63.0 ± 1.5	59.6 ± 2.6	0.4 ± 0.0	2.4 ± 0.1
Xanthocephalum sarothrae (Pursh) Shinners	83.2 ± 0.2	54.4 ± 3.2	0.7 ± 0.0	3.8 ± 0.1
Herbs				
Argemone munita Dur. & Hilg.	81.3 ± 0.7	27.2 ± 2.8	41.3 ± 2.3	54.4 ± 1.8
Chaenactis douglasii (Hook.) H. & A.	82.0 ± 1.5	27.4 ± 4.1	1.9 ± 0.1	17.1 ± 0.7
Commandra umbellata (L.) Nutt.	80.0 ± 0.6	35.2 ± 3.6	1.8 ± 0.1	6.8 ± 0.1
Eriogonum kearneyi Tidestr.	70.3 ± 2.3	63.4 ± 3.2	2.0 ± 0.7	10.5 ± 0.2
Eriogonum ovalifolium Nutt.	67.7 ± 2.0	tracker	0.9 ± 0.1	8.7 ± 0.2
Galium aparine L.	75.4 ± 2.2	29.4 ± 2.7	0.4 ± 0.0	2.6 ± 0.1
Grindelia squarrosa (Pursh) Dunal	78.7 ± 0.7	46.4 ± 3.7	10.7 ± 0.5	21.4 ± 0.6
Hackelia patens (Nutt.) Johnst.	82.3 ± 1.3	43.2 ± 4.4	9.4 ± 0.8	14.4 ± 0.8
Hedysarum boreale Nutt.	83.3 ± 2.9	40.6 ± 3.0	1.4 ± 0.1	8.7 ± 0.5
Lygodesmia dianthopsis (D. C. Eat.) Tomb	75.3 ± 1.5	27.6 ± 3.0	0.7 ± 0.0	2.3 ± 0.1
Oenothera pallida Lindl.	80.3 ± 1.2	30.6 ± 3.6	0.7 ± 0.0	3.0 ± 0.1
Petradoria pumila (Nutt.) Greene	79.7 ± 2.1	55.4 ± 2.9	2.5 ± 0.1	5.6 ± 0.2
Psoralea lanceolata Pursh	83.7 ± 0.9	67.6 ± 2.6	1.0 ± 0.1	6.2 ± 0.4
Verbascum thapsus L.	78.8 ± 0.4	42.4 ± 2.5	38.8 ± 1.8	45.6 ± 1.3
Viola purpurea Kell.	83.5 ± 0.7	23.8 ± 2.2	5.7 ± 0.2	24.4 ± 0.8
Zigadenus paniculatus (Nutt.) Wats.	82.0 ± 0.2	50.0 ± 5.1	18.8 ± 1.0	11.6 ± 0.5
Grasses and sedges				
Agropyron trachycaulum (Link) Malte	83.5 ± 0.3	67.4 ± 3.2	3.1 ± 0.2	2.9 ± 0.1
Bromus tectorum L.	78.8 ± 0.5	62.2 ± 3.1	1.3 ± 0.1	4.2 ± 0.1
Oak–maple scrub community				
Shrubs				
Acer grandidentatum Nutt.	87.3 ± 0.3	41.6 ± 3.9	44.6 ± 2.3	99.5 ± 2.9
Artemisia tridentata Nutt.	66.0 ± 0.5	60.0 ± 3.9	1.0 ± 0.1	7.4 ± 0.3
Berberis repens Lindl.	86.0 ± 0.7	28.8 ± 4.4	10.1 ± 0.8	27.2 ± 1.3
Prunus virginiana L.	85.7 ± 0.5	43.2 ± 3.4	9.3 ± 0.6	26.1 ± 0.8
Quercus gambelii Nutt.	87.6 ± 2.4	52.7 ± 8.0	33.2 ± 2.5	65.2 ± 2.4
Symphoricarpos oreophilus Gray	78.3 ± 1.3	42.6 ± 3.7	—	—
Herbs				
Aster chilensis Nees	82.0 ± 0.4	—	9.7 ± 0.3	14.2 ± 0.4
Galium aparine L.	84.6 ± 1.3	41.4 ± 2.7	0.3 ± 0.0	2.2 ± 0.1
Iva axillaris Pursh	80.0 ± 0.3	—	—	—
Lupinus sericeus Pursh	86.7 ± 0.3	tracker	—	—
Melilotus alba Medic.	84.4 ± 0.6	tracker	1.7 ± 0.1	15.1 ± 0.4
Thalictrum fendleri Engelm.	82.4 ± 0.9	35.2 ± 3.1	1.6 ± 0.1	15.4 ± 0.5
Verbascum thapsus L.	75.8 ± 0.6	28.4 ± 5.2	57.7 ± 8.3	61.4 ± 4.8
Viguiera multiflora (Nutt.) Blake	85.7 ± 0.7	—	—	—
Grasses and sedges				
Agropyron trachycaulum (Link) Malte	82.5 ± 0.5	49.2 ± 6.3	6.6 ± 0.4	5.5 ± 0.2
Poa bulbosa L.	81.5 ± 1.0	52.6 ± 4.8	0.6 ± 0.1	2.6 ± 0.1
Dactylis glomerata L.	80.9 ± 0.9	75.2 ± 3.1	12.8 ± 0.9	10.6 ± 0.2
Mountain brush community				
Shrubs				
Acer grandidentatum Nutt.	88.7 ± 0.3	14.6 ± 1.8	45.8 ± 2.0	101.0 ± 2.2
Amelanchier alnifolia Nutt.	84.7 ± 0.5	—	—	—
Berberis repens Lindl.	86.5 ± 0.3	15.2 ± 1.7	5.0 ± 1.3	19.4 ± 1.2
Cercocarpus ledifolius Nutt.	87.7 ± 0.7	36.0 ± 3.9	1.4 ± 0.1	7.3 ± 0.2
Pachistima myrsinites (Pursh) Raf.	85.0 ± 0.5	—	—	—
Physocarpus malvaceus (Greene) Kuntze	81.3 ± 0.5	—	—	—
Prunus virginiana L.	84.3 ± 0.7	30.0 ± 2.5	70.2 ± 13.0	101.3 ± 4.2
Sambucus racemosa L.	87.7 ± 0.3	12.8 ± 1.8	34.5 ± 2.0	45.9 ± 1.2
Herbs				
Apocynum androsaemifolium L.	84.7 ± 0.5	—	—	—
Cirsium eatonii (Gray) Rob.	81.7 ± 0.5	—	—	—

APPENDIX. *Continued*

Species	Absorptance	Angle	Leaf area	Leaf width
Nepeta cataria L.	83.7 ± 0.3	—	—	—
Osmorhiza occidentalis (Nutt.) Torr.	—	17.2 ± 2.2	11.6 ± 0.7	26.5 ± 0.8
Rudbeckia occidentalis Nutt.	84.3 ± 0.3	29.0 ± 2.5	34.9 ± 1.3	55.4 ± 1.2
Smilacina stellata (L.) Desf.	76.0 ± 0.7	29.8 ± 2.7	38.2 ± 3.7	39.1 ± 2.4
Solidago sparsiflora Gray	85.7 ± 0.3	—	—	—
Viguiera multiflora (Nutt.) Blake	79.5 ± 1.8	—	—	—
Aspen–coniferous forest community				
Trees				
Abies lasiocarpa (Hook.) Nutt.	87.3 ± 0.7	39.0 ± 4.1	0.4 ± 0.0	1.5 ± 0.1
Abies concolor (Gord. & Glend.) Lindl.	81.7 ± 0.9	58.6 ± 3.1	0.6 ± 0.0	2.0 ± 0.0
Picea engelmannii Parry	82.0 ± 0.8	34.8 ± 3.8	0.2 ± 0.0	1.0 ± 0.0
Picea pungens Engelm.	85.0 ± 1.4	—	—	—
Populus tremuloides Michx.	85.7 ± 0.5	46.4 ± 3.8	12.3 ± 0.4	41.7 ± 0.8
Prunus virginiana L.	87.0 ± 0.0	29.2 ± 3.4	22.8 ± 1.3	42.8 ± 1.3
Pseudotsuga menziesii (Mirb.) Franco	80.3 ± 0.7	42.2 ± 5.3	0.3 ± 0.0	1.8 ± 0.1
Shrubs				
Acer glabrum Torr.	—	26.2 ± 3.1	8.6 ± 2.9	25.8 ± 0.8
Lonicera involucrata (Rich.) Banks	78.7 ± 1.5	20.6 ± 2.5	10.3 ± 0.4	31.7 ± 0.8
Pachistima myrsinites (Pursh) Raf.	84.3 ± 0.5	24.4 ± 3.0	0.9 ± 0.1	7.3 ± 0.2
Rosa nutkana Presl.	75.0 ± 0.8	24.4 ± 3.6	4.0 ± 0.2	18.5 ± 0.5
Rubus parviflorus Nutt.	80.0 ± 0.9	—	—	—
Sambucus racemosa L.	81.0 ± 0.0	—	—	—
Symphoricarpos oreophilus Gray	82.7 ± 1.0	—	—	—
Vaccinium scoparium Leib.	85.3 ± 0.9	22.8 ± 2.5	1.2 ± 0.0	9.3 ± 0.2
Herbs				
Artemisia ludoviciana Nutt.	—	27.4 ± 2.9	9.1 ± 0.4	48.0 ± 2.5
Aster engelmannii (Eat.) Gray	82.3 ± 1.1	16.0 ± 2.2	10.0 ± 0.4	21.0 ± 0.5
Cirsium eatonii (Gray) Rob.	78.0 ± 0.5	—	—	—
Epilobium angustifolium L.	79.3 ± 1.0	—	—	—
Fragaria vesca L.	85.0 ± 2.0	24.8 ± 2.7	6.1 ± 0.2	23.7 ± 0.6
Geranium viscosissimum F. & M.	82.0 ± 0.9	31.2 ± 3.0	27.0 ± 2.3	75.0 ± 3.2
Hackelia micrantha (Eastw.) J. L. Gentry	81.7 ± 0.3	—	—	—
Mitella pentandra Hook.	81.3 ± 0.5	—	—	—
Penstemon cyananthus Hook.	—	42.8 ± 4.7	12.0 ± 0.6	30.2 ± 0.9
Potentilla gracilis Dougl.	—	24.8 ± 2.8	1.3 ± 0.1	3.4 ± 0.1
Pyrola secunda L.	84.7 ± 0.3	—	—	—
Rudbeckia occidentalis Nutt.	83.7 ± 1.0	—	—	—
Senecio multilobatus T. & G.	—	44.2 ± 4.1	2.7 ± 0.1	15.0 ± 0.6
Senecio strepanthifolius Greene	84.0 ± 0.5	—	—	—
Thalictrum fendleri Engelm.	73.0 ± 3.3	—	—	—
Grasses and sedges				
Agropyron trachycaulum (Link) Malte	78.0 ± 0.8	—	—	—
Carex backii Boott	79.7 ± 1.9	—	—	—
Carex microptera Mkze.	—	68.6 ± 2.5	4.0 ± 0.3	2.2 ± 0.1
Alpine meadow community				
Shrubs				
Ribes montigenum McClatchie	81.7 ± 0.9	21.4 ± 2.0	6.5 ± 0.3	34.0 ± 0.8
Salix drummondiana Barr.	84.3 ± 0.9	34.8 ± 3.9	7.3 ± 0.4	15.5 ± 0.4
Sambucus racemosa L.	81.0 ± 0.0	32.6 ± 3.3	54.3 ± 2.0	52.1 ± 1.1
Symphoricarpos oreophilus Gray	79.0 ± 1.2	—	—	—
Herbs				
Angelica pinnata Wats.	81.3 ± 0.7	—	—	—
Artemisia ludoviciana Nutt.	75.7 ± 1.2	36.6 ± 3.4	6.4 ± 0.3	27.8 ± 1.1
Aster engelmannii (Eat.) Gray	82.0 ± 0.5	17.8 ± 2.4	10.2 ± 0.4	21.6 ± 0.5
Aster foliaceus Lindl.	81.0 ± 0.5	—	—	—
Castilleja rhexifolia Rydb.	76.0 ± 0.5	42.4 ± 2.3	6.7 ± 0.3	16.1 ± 0.5
Geranium viscosissimum F. & M.	83.0 ± 1.0	20.4 ± 2.2	36.5 ± 3.1	84.5 ± 4.4
Hackelia micrantha (Eastw.) J. L. Gentry	—	40.6 ± 3.8	15.3 ± 0.8	19.6 ± 1.0
Lupinus argenteus Pursh	86.7 ± 0.7	tracker	17.3 ± 0.8	34.5 ± 1.9
Mertensia ciliata (James) G. Don	80.0 ± 1.2	59.6 ± 2.9	14.5 ± 0.6	28.6 ± 0.6
Orthocarpus tolmiei H. & A.	77.7 ± 1.0	—	—	—

APPENDIX. *Continued*

Species	Absorptance	Angle	Leaf area	Leaf width
Polemonium foliossimum Gray	—	39.2 ± 2.5	1.4 ± 0.0	7.4 ± 0.2
Potentilla glandulosa Lindl.	80.7 ± 0.5	—	7.2 ± 0.3	24.4 ± 0.7
Potentilla gracilis Dougl.	82.7 ± 0.7	31.8 ± 3.3	—	—
Rudbeckia occidentalis Nutt.	80.0 ± 1.7	30.8 ± 3.2	51.0 ± 1.8	67.5 ± 1.7
Veratrum californicum Durand	72.0 ± 2.5	52.6 ± 3.6	246.2 ± 14.9	141.9 ± 7.4
Grasses and sedges				
Bromus carinatus H. & A.	67.0 ± 1.2	—	—	—
Bromus inermis Leyss.	78.0 ± 0.6	—	—	—
Carex hoodii Boott	83.7 ± 1.2	66.8 ± 2.2	3.4 ± 0.2	2.6 ± 0.2
Poa alpina L.	—	75.0 ± 1.9	10.8 ± 0.6	5.3 ± 0.3
Stipa lettermanii Vasey	74.3 ± 1.3	—	—	—
Upper riparian community				
Trees				
Acer negundo L.	77.3 ± 0.9	50.6 ± 8.3	27.6 ± 1.8	56.0 ± 2.6
Betula occidentalis Hook.	79.7 ± 1.7	43.0 ± 3.9	10.8 ± 0.5	36.6 ± 0.8
Prunus virginiana L.	87.0 ± 0.0	29.4 ± 2.8	33.4 ± 0.9	48.1 ± 0.8
Shrubs				
Cornus stolonifera Michx.	—	26.4 ± 3.0	44.4 ± 2.3	66.2 ± 2.3
Salix scouleriana Barr.	84.0 ± 0.5	—	—	—
Herbs				
Aster eatonii (Gray) Howell	86.7 ± 0.5	14.4 ± 2.5	10.6 ± 0.4	16.0 ± 0.4
Equisetum arvense L.	—	52.6 ± 3.7	1.2 ± 0.1	1.0 ± 0.0
Galium mexicanum Kunth	85.0 ± 0.5	—	—	—
Heracleum sphondylium L.	78.0 ± 1.2	—	—	—
Lathyrus lanszwertii Kell.	86.0 ± 0.8	—	—	—
Lower riparian community				
Trees				
Cornus stolonifera Michx.	84.0 ± 1.2	—	—	—
Populus angustifolia James	69.0 ± 1.5	39.0 ± 4.8	12.8 ± 0.2	24.0 ± 0.6
Salix exigua Nutt.	72.8 ± 2.9	68.6 ± 4.7	4.3 ± 0.3	4.4 ± 0.1
Salix lasiandra Benth.	77.9 ± 0.5	48.4 ± 3.8	8.1 ± 0.4	26.4 ± 0.7
Shrubs				
Artemisia tridentata Nutt.	70.9 ± 1.1	46.5 ± 4.0	0.6 ± 0.0	5.1 ± 0.2
Rosa woodsii Lindl.	82.7 ± 1.6	28.6 ± 4.0	1.2 ± 0.1	10.1 ± 0.2
Herbs				
Arctium minus (Hill) Bernh.	85.5 ± 0.2	33.6 ± 3.3	103.0 ± 7.8	100.5 ± 4.4
Apocynum androsaemifolium L.	87.3 ± 0.5	—	—	—
Artemisia ludoviciana Nutt.	74.8 ± 1.4	30.6 ± 3.3	3.8 ± 0.3	17.8 ± 1.0
Aster eatonii (Gray) Howell	84.9 ± 0.7	52.6 ± 3.9	7.5 ± 0.5	14.3 ± 0.4
Aster engelmannii (Eat.) Gray	86.0 ± 1.7	—	86.0 ± 1.7	—
Equisetum hyemale L.	91.8 ± 0.6	77.4 ± 2.2	—	6.0 ± 0.2
Lomatium dissectum (Nutt.) Math. & Const.	88.1 ± 0.0	27.4 ± 3.0	1.9 ± 0.2	14.3 ± 0.7
Marrubium vulgare L.	84.1 ± 1.2	23.2 ± 3.7	7.4 ± 0.7	27.5 ± 1.5
Melilotus alba Medic.	85.7 ± 0.3	tracker	—	—
Nepeta cataria L.	79.3 ± 2.3	—	—	—
Osmorhiza chilensis H. & A.	76.7 ± 0.3	—	—	—
Smilacina stellata (L.) Desf.	87.0 ± 0.5	—	—	—
Taraxacum officinale Weber	80.2 ± 1.3	56.6 ± 3.7	8.1 ± 0.4	16.2 ± 0.5
Urtica dioica L.	82.0 ± 0.5	—	—	—
Verbena bracteata Lag. & Rodr.	82.0 ± 0.5	—	—	—
Wyethia amplexicaulis Nutt.	87.7 ± 0.7	53.6 ± 4.4	103.6 ± 9.1	77.0 ± 3.6
Grasses and sedges				
Dactylis glomerata L.	86.7 ± 0.8	64.4 ± 3.3	8.9 ± 0.6	6.4 ± 0.2