

LEAF AREA RATIOS FOR SELECTED RANGELAND PLANT SPECIES

Mark A. Weltz¹, Wilbert H. Blackburn², and J. Roger Simanton¹

ABSTRACT.—Leaf area estimates are required by hydrologic, erosion, and growth/yield simulation models and are important to the understanding of transpiration, interception, CO₂ fixation, and the energy balance for native plant communities. Leaf biomass (g) to leaf area (mm²) linear regression relationships were evaluated for 15 perennial grasses, 12 shrubs, and 1 tree. The slope coefficient (β_0) of the linear regression equation is a ratio of leaf area to leaf biomass and is defined as the leaf area ratio [LAR = one-sided leaf area (mm²)/oven-dry leaf weight (g)]. LAR represents β_0 in each regression equation, where $Y = \beta_0(X)$. Linear regression relationships for leaf area were computed ($r^2 = .84-.98$) for all 28 native range species after full leaf extension. Within-plant estimates of leaf area for mesquite (*Prosopis glandulosa* Torr. var. *glandulosa* [Torr.] Cockll.) or lime prickly ash (*Zanthoxylum fagara* [L.] Sarg.) were not significantly different ($P \leq .05$). LARs for three of the shrubs and the tree were established at four different phenological stages. There were no significant differences ($P \leq .05$) in LARs for lime prickly ash, mesquite, and Texas persimmon (*Diospyros texana* Scheele) after full leaf extension during the growing season. The LAR relationship for Texas persimmon changed significantly after full leaf extension. LAR relationships for Texas colubrina (*Colubrina texensis* [T. & G.] Gray) changed in response to water stress.

Key words: leaf area index, drought response, leaf biomass.

Eighty percent of the world's rangeland is classified as arid or semiarid (Branson et al. 1981), i.e., precipitation is less than evapotranspiration. Under these conditions water availability is the most important environmental factor controlling plant production and survival (Brown 1977). Evapotranspiration (ET) is the major component of the water balance and is estimated to account for 96% of annual precipitation for rangeland ecosystems (Branson et al. 1981, Carlson et al. 1990), with surface runoff accounting for most of the remaining 4% (Gifford 1975, Lauenroth and Sims 1976, Carlson et al. 1990).

Evapotranspiration has been measured for selected rangeland plant communities with lysimeters and the Bowen ratio method (Wight 1971, Hanson 1976, Gay and Fritschen 1979, Carlson et al. 1990). Estimates of ET for unmeasured rangeland plant communities are usually simulated from hydrologic models (Lane et al. 1984, Wight 1986). For hydrologic simulation models to be biologically meaningful, improved methods of simulating evapotranspiration from rangeland plant communities are needed. Two different approaches are currently being used. One approach is to use a crop coefficient (Kc)

(Wight 1986). Kc is defined as the ratio of actual evapotranspiration to evapotranspiration when water is nonlimiting. This empirical method is extremely difficult to parameterize for rangelands because water is often limiting and estimates of transpiration are confounded by soil water evaporation (Wight and Hansen 1990). Thus, Wight and Hansen (1990) reported that Kc values were not transferable across range sites. The second method is based on leaf area index (LAI) (Ritchie 1972). LAI is defined as the foliage area per unit land area (Watson 1947). The LAI method is more process-based than the Kc approach and has been successfully used in several rangeland hydrologic, erosion, and growth/yield simulation models (Wight and Skiles 1987, Lane and Nearing 1989, Arnold et al. 1990).

A limitation in using natural resource models, like the Water Erosion Prediction Project (WEPP) (Lane and Nearing 1989), is in developing LAI coefficients for rangeland plants. LAI is difficult to measure because of the drought-deciduous nature of certain shrubs, in which several cycles of leaf initiation and defoliation occur within a single growing season (Ganskopp and Miller 1986) and seasonal

¹USDA, Agricultural Research Service, Southwest Watershed Research Center, 2000 East Allen Road, Tucson, Arizona 85719-1596.

²Northern Plains Area Administrative Office, 2625 Redwing Road, Suite 350, Fort Collins, Colorado 80526.

TABLE 1. Description of study sites, range sites, and soil series of species evaluated for leaf area to leaf biomass relationships.

Location	Range site	Mean PPT (mm)	Frost-free period (days)	Soil series	Soil family
Tombstone, AZ	Limey upland	356	239	Stronghold	Coarse-loamy, mixed thermic, Ustollic Calciorthid
Meeker, CO	Clayey slopes	200	180	Degater	Clay, montmorillonitic, mesic, Typic Camborthid
Sidney, MT	Silty	300	130	Vida	Fine-loamy, mixed, Typic Argboroll
Chickasha, OK	Loamy prairie	927	200	Grant	Fine-silty, mixed, Udic Argjustoll
Chickasha, OK	Eroded prairie	927	200	Eroded Grant	Fine-silty, mixed, Udic Argjustoll
Ft. Supply, OK	Dune	597	200	Pratt	Sandy, mixed, thermic, Psammentic Haplustalf
Woodward, OK	Shallow prairie	584	200	Quinlan	Loamy, mixed, thermic, shallow Typic Ustochrept
Alice, TX	Fine sandy loam	710	280	Miguel	Fine, mixed, hyperthermic, Udic Paleustalf
Sonora, TX	Shallow	609	240	Purves	Fine-loamy, mixed, thermic, Typic Calcjustoll

changes in leaf size, shape, and/or thickness result from water, nutrient, and chemical stresses (Cutler et al. 1977, Curtis and Luchli 1987). Foliar surface area of irregular-shaped tree leaves has been estimated by coating the leaves with a monolayer of glass beads and measuring displacement (Thompson and Leyton 1971) and by estimating from photographs (Miller and Schultz 1987). Miller et al. (1987) estimated total surface area of juniper foliage from projected leaf area determined from a leaf area meter. Miller et al. suggested this method underestimated leaf area by 10% due to leaf overlap. Cregg (1992) reported that leaf area could be satisfactorily estimated from leaf weight or volume for *Juniperus virginiana* and *J. scopulorum*. However, leaf area relationships differed by crown position and seed source. Sapwood area, stem diameter, tree height, canopy area, and canopy volume have been correlated to total shrub biomass and leaf biomass (Ludwig et al. 1975, Brown 1976, Rittenhouse and Sneva 1977, Whisenant and Burzlaff 1978, Ganskopp and Miller 1986, Hughes et al. 1987). In contrast, only a few studies have estimated leaf area and LAI for rangeland plant communities (Goff 1985, Ganskopp and Miller 1986, and Ansley et al. 1992).

An effective method is needed to improve LAI estimates for natural resource models. One potential approach for improving LAI estimates

is with the leaf area ratio (LAR) method (Radford 1967). LAR is defined as the ratio of leaf area per unit weight of plant material. The slope coefficient (β_0) of the linear regression equation is a ratio of leaf area to leaf biomass and is defined as the leaf area ratio [LAR = one-sided leaf area (mm^2)/oven-dry leaf weight (g)]. LAR represents β_0 in each regression equation, where $Y = \beta_0(X)$. LAI can be calculated as the product of LAR and live biomass per unit area. The objective of this study was to determine LARs for selected rangeland species.

MATERIALS AND METHODS

The study area included nine range sites in five states and was part of the USDA Water Erosion Prediction Project (WEPP) (Table 1). The dominant plants on each range site were evaluated. LARs for 15 grasses, 12 shrubs, and 1 tree were developed (Table 2). Selected rangeland species were sampled once during the summer of 1987 near Tombstone, Arizona; and in 1987 near Meeker, Colorado; Sidney, Montana; Chickasha, Ft. Supply, and Woodward, Oklahoma; and Sonora, Texas, sites. Seasonal fluctuations in LAR for three shrubs and one tree were evaluated near Alice, Texas, in 1985 and 1986.

For leaf area determination grass leaf biomass from 10 randomly located 0.25-m² quadrats was

TABLE 2. Location of study sites, sample dates, height class, number of samples, and species evaluated for leaf area to leaf biomass relationships.

Location	Sample date	Height class (m)					Species	
		0-1	1-2	2-3	3-4	>4	Common name	Scientific name
Tombstone, AZ	Aug. 1983	6	6				Little leaf sumac	<i>Rhus microphylla</i> Engelm.
	Aug. 1983	7	8				Tarbrush	<i>Flourensia cernua</i> DC.
	Aug. 1983	8					Broom snakeweed	<i>Cutierrezia sarothrae</i> (Pursh) Britt. & Rusby.
	Aug. 1983	10	10				Creosotebush	<i>Larrea tridentata</i> (DC.) Coville
	Aug. 1983	15					Desert zinnia	<i>Zinnia pumila</i> Gray
Meeker, CO	Aug. 1983	15					Mariola	<i>Parthenium incanum</i> H.B.K.
	June 1987	10					Shadscale saltbush	<i>Atriplex confertifolia</i> (Torr. & Frem.) Wats.
	June 1987	10					Wyoming big sagebrush	<i>Artemisia tridentata</i> subsp. <i>wyomingensis</i> Beetle & Young
Sidney, MT	July 1987	10					Needle-and-thread	<i>Stipa comata</i> Trin. & Rupr.
	July 1987	10					Western wheatgrass	<i>Agropyron smithii</i> Rydb.
Chickasha, OK	June 1987	10					Indiangrass	<i>Sorghastrum nutans</i> (L.) Nash
	June 1987	10					Big bluestem	<i>Andropogon gerardii</i> Vitman
	June 1987	10					Little bluestem	<i>Schizachyrium scoparium</i> (Michx.) Nash
Chickasha, OK	June 1987	10					Buffalograss	<i>Buchloe dactyloides</i> (Nutt.) Engelm.
	June 1987	10					Scribners dichanthelium	<i>Dichanthelium oligoanthos</i> (Schult.) Guild var. <i>scribnerianum</i> (Nash) Gould
Ft. Supply, OK	June 1987	10					Sand paspalum	<i>Paspalum setaceum</i> Michx. var. <i>stramineum</i> (Nash) D. Banks
	June 1987	10					Sand sagebrush	<i>Artemisia filifolia</i> Torr.
	June 1987	10					Tall dropseed	<i>Sporobolus asper</i> (Michx.) Kunth
Woodward, OK	June 1987	10					Sand lovegrass	<i>Erogrostis trichodes</i> (Nutt.) Wood
	June 1987	10					Hairy grama	<i>Bouteloua hirsuta</i> Lag.
Alice, TX	June 1987	10					Sideoats grama	<i>Bouteloua curtipendula</i> (Michx.) Torr.
	May 1985	4	4	4	4	4	Honey mesquite	<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i> (Torr.) Cockll.
	Aug. 1985	2	2	2	2	2		
	Nov. 1985	2	2	2	2	2		
	Jan. 1986	NA ^a						
	Apr. 1986	2	2	2	2	2		
	May 1985	5	5	5	5	5	Lime prickly ash	<i>Zanthoxylum fagara</i> (L.) Sarg.
	Aug. 1985	3	3	3	3			
	Nov. 1985	3	3	3	3			
	Jan. 1986	3	3	3	3			
	Apr. 1986	3	3	3	3			
	May 1985	5	5				Texas colubrina	<i>Colubrina texensis</i> (T. & G.) Gray
	Aug. 1985	5	5					
	Nov. 1985	5	5					
	Jan. 1986	5	5					
	Apr. 1986	5	5					
May 1985	5	5				Texas persimmon	<i>Diospyros texana</i> Scheele	
Aug. 1985	5	5						
Nov. 1985	5	5						
Jan. 1986	NA							
Apr. 1986	5	5						
Sonora, TX	June 1987	10					White tridens	<i>Tridens albescens</i> (Vasey) Woot. & Standl.
	June 1987	10					Curly mesquite	<i>Hilaria belangeria</i> (Steud.) Nash
	June 1987	10					Texas wintergrass	<i>Stipa leucotricha</i> Trin. & Rupr.

^aNo sample collected for deciduous shrubs and trees.

TABLE 3. Mean and standard error of leaf biomass and leaf area, and linear regression^a model slope coefficients (LAR^b) relating leaf area to leaf biomass for selected rangeland grasses and shrubs sampled after full leaf extension.

Species	Leaf biomass (g)	SE	Leaf area (mm ²)	SE	LAR (mm ² g ⁻¹)	r ²
GRASSES						
Needle-and-thread	3.6	0.80	3,580	900	1,040	.98
Western wheatgrass	2.0	0.33	5,760	902	2,910	.98
Indiangrass	8.5	1.56	82,670	1,350	9,440	.96
Little bluestem	2.7	0.38	28,030	4,710	10,780	.98
Big bluestem	1.3	0.45	11,290	2,213	12,970	.86
Buffalo grass	1.5	0.22	6,820	1,091	5,680	.97
Scribners dichanthelium	1.3	0.21	15,300	2,601	16,110	.96
Sand paspalum	1.5	0.23	7,580	1,136	6,890	.95
Tall dropseed	0.9	0.15	8,500	1,334	9,390	.99
Sand lovegrass	0.8	0.12	8,650	1,383	11,380	.98
Hairy grama	0.7	0.13	4,360	769	5,890	.99
Sideoats grama	0.6	0.22	5,240	2,836	10,210	.98
White tridens	0.7	0.16	3,980	1,007	5,830	.98
Texas wintergrass	1.2	0.24	8,320	1,361	6,720	.95
Curly mesquite	0.8	0.15	5,270	925	6,620	.99
SHRUBS						
Desert zinnia	1.6	0.10	9,440	580	5,700	.89
Mariola	3.5	0.40	19,410	1,280	5,690	.84
Broom snakeweed	3.7	0.51	11,160	920	2,700	.96
Little leaf sumac	3.9	0.71	22,050	331	4,700	.91
Tarbrush	3.7	1.00	23,360	203	6,100	.97
Creosotebush	3.0	0.19	16,790	910	3,660	.86
Sand sagebrush	3.2	0.58	5,950	1,257	2,010	.98
Shadscale saltbush	3.9	0.81	10,530	2,047	2,640	.98
Wyoming big sagebrush	5.3	0.83	18,220	2,715	3,340	.97

^aAll area:weight regressions were significant at $P < .05$.

^bLeaf area ratio (LAR) represents β_0 in each regression, where $Y = \beta_0(X)$.

used. Grass biomass in each quadrat was clipped to a 20-mm stubble height and separated by species into live or dead leaves. Live leaves were placed in plastic bags on ice for later determination of leaf area. The leaves were flattened and placed between clear plastic sheets and then processed through a leaf area meter. Leaf area was determined with a Li-Cor 3000³ leaf area meter to the nearest 1 mm². The samples were then oven-dried at 60 C for three days and dry mass determined.

To ensure that samples of shrubs and trees represented the full range of size of plants present, a stratified random sampling procedure was used. Height classes of 1 m were arbitrarily chosen, and plants were selected randomly from each class. As a result, total number of plants sampled varied among species depending upon the range of plant heights (Table 2).

An open-ended cube (250 mm on a side) was used to sample shrub and tree leaf biomass. The

sample cube was placed in an area considered representative of the entire canopy, and the leaves within the area were removed by hand. LARs were determined in the same manner as for grasses.

Within-plant variability of LARs was evaluated for four mesquite trees and four lime prickly ash shrubs in May 1985 near Alice, Texas. Fifteen sample cubes were randomly located and sampled from each of the four mesquite trees. For the lime prickly ash shrubs 12 sample cubes were harvested from each of the four shrubs. LAR was determined in the same manner as previously described. A one-way analysis of variance was used to test for differences ($P \leq .05$) among the slopes of the regression equations within plant canopy by species (Steel and Torrie 1980). Within-plant LARs were not significantly different for lime prickly ash and mesquite in May 1985. Based on these relationships, one sample per plant was utilized during the remainder of the study.

Three shrubs, lime prickly ash, Texas persimmon, and Texas colubrina, and one tree,

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TABLE 4. Mean and standard error of leaf biomass and leaf area, and linear regression^a model slope coefficients (LAR^b) relating leaf area to leaf biomass for selected rangeland shrubs and tree on a fine sandy loam range site near Alice, Texas.

Species	Date	Leaf biomass (g)	SE	Leaf area (mm ²)	SE	LAR (mm ² g ⁻¹)	r ²
Lime prickly ash	May 1985	4.7	0.73	45,180	1,450	8,760 a ^c	.99
	Aug. 1985	4.2	0.63	40,330	1,530	8,730 a	.98
	Nov. 1985	5.6	0.89	43,360	1,460	8,670 a	.98
	Jan. 1985	4.9	0.76	44,310	1,450	8,870 a	.98
	Apr. 1986	5.3	0.65	52,730	1,580	8,690 a	.98
Mesquite	May 1985	6.5	0.87	57,830	1,610	8,990 a	.98
	Aug. 1985	5.7	0.64	56,040	1,470	8,780 a	.98
	Nov. 1985	5.5	0.70	48,460	1,410	8,630 a	.98
	Jan. 1985	NA ^d					
	Apr. 1986	6.4	0.81	59,100	1,470	9,290 a	.98
Texas persimmon	May 1985	4.6	0.64	49,960	1,940	10,590 b	.96
	Aug. 1985	4.1	0.65	41,670	1,780	10,360 b	.98
	Nov. 1985	4.8	0.59	51,060	1,790	10,130 b	.98
	Jan. 1986	4.6	0.68	44,720	1,900	10,020 b	.98
	Apr. 1986	4.7	0.69	64,150	2,070	12,660 a	.97
Texas colubrina	May 1985	4.9	0.78	55,070	2,020	10,310 b	.98
	Aug. 1985	5.2	0.89	57,010	1,720	10,110 b	.98
	Nov. 1985	3.8	0.65	55,380	2,090	13,360 a	.98
	Jan. 1986	NA					
	Apr. 1986	4.1	0.71	41,760	1,880	10,230 b	.98

^aAll area: weight regressions were significant at $P < .05$.

^bLeaf area ratio (LAR) represents β_0 in each regression, where $Y = \beta_0(X)$.

^cParameters in the columns by species sharing a common letter are not significantly different ($P \leq .05$) based on homogeneity of slope test.

^dNo sample was collected for deciduous shrubs.

honey mesquite, were selected for evaluation of seasonal fluctuation in LAR. Honey mesquite, Texas persimmon, and Texas colubrina are drought-deciduous while lime prickly ash is an evergreen. Sample dates were selected to correspond to the phenological stages of (1) maximum leaf area, (2) peak drought defoliation, (3) autumn, just prior to winter leaf fall and dormancy, and (4) after winter leaf fall for the deciduous shrub.

The Statistical Analysis System (SAS 1982) was utilized to evaluate linear regression relationships, $Y = \beta_0 + \beta_1(X)$, between leaf biomass and leaf area. Where Y is estimated leaf area (mm²), β_0 is the intercept, β_1 is the slope (LAR coefficient as defined by Radford 1967 in mm²g⁻¹), and X is leaf biomass (g). The intercept was tested to determine if it was significantly different ($P \leq .05$) from zero. The intercept was not significantly different from zero for all species. Therefore, the data were reanalyzed and presented using a linear regression model, $Y = \beta_0(X)$, similar to that reported by Coombs et al. (1987) and Ansley et al. (1992) for estimating LAR. All statistical tests were judged significant at $P \leq .05$ unless otherwise stated. A homogeneity of slope test was used to test for differences

among the slopes of the regression equations (LAR) between sample periods within species (Steel and Torrie 1980).

RESULTS AND DISCUSSION

Leaf area of graminoids was highly correlated with leaf biomass for all species within sample dates (Table 3). The LAR for perennial grass leaf area ranged from 2910 to 16,110 mm²g⁻¹. The LAR for shrubs and trees ranged from 2010 to 13,360 mm²g⁻¹. Goff (1985) also reported significant linear regression relationships ($r^2 = .83-.97$) for LAR for 11 native grass species in southern Arizona. Goff reported that the linear regression coefficients for stem area to stem biomass (SAR) ranged from 32 to 73% of the LAR and the mean SAR was 44% of the mean LAR.

There was no significant seasonal variation in LAR for lime prickly ash and mesquite (Table 4). Although there was no significant seasonal difference between mesquite LAR relationships, a gradual decrease in the LAR from May through November was apparent in 1985. Furthermore, the LAR was larger in April 1986, though it was not significantly different from 1985 sampling dates. Mooney et al. (1977) found that the specific

leaf density (mg mm^{-2}) of mesquite leaves increased over the growing season. The density ranged from $0.0004 \text{ mg mm}^{-2}$ in the spring to 0.017 mg mm^{-2} in the fall. This corresponds with a leaf area change of 5880 to $25,000 \text{ mm}^2 \text{ g}^{-1}$.

Ansley et al. (1992), working in north central Texas, reported that LAR of mesquite ranged from 9916 to $5944 \text{ mm}^2 \text{ g}^{-1}$. Mesquite LAR declined from May through August 1987, but stabilized from August through September following substantial precipitation. In 1988 precipitation was substantially less than in 1987, and the mean LAR was significantly lower than in 1987. LAR followed the same pattern in 1988, declining from a high of 6877 in the spring to a low of $4996 \text{ mm}^2 \text{ g}^{-1}$ in October. Ansley et al. (1992) speculated that the decline in LAR was caused by cell-wall thickening in response to drying conditions, based on the work of Kramer and Kozlowski (1979).

The similarity in LAR across sampling dates from this study may be partially explained in that sampling was not initiated until all leaves were fully expanded for approximately four weeks. In addition, April, May, June, and September precipitation was significantly above the long-term average precipitation and no noticeable water stress was apparent in the trees sampled. Nilsen et al. (1986) indicated that relative leaf area of phreatophytic mesquite (*P. glandulosa* var. *torreyana*) in the Sonoran desert of southern California remained nearly constant from May through November. Maximum leaf area was maintained throughout the hottest and driest months of the year via access of deep stored soil water by taproots. When water availability to the normally phreatophytic mesquite was reduced, total leaf area was reduced (Nilsen, Virginia, and Jarrell 1986). We hypothesized that mesquite leaves reach a stable weight at maturity and the lack of water stress during the growing season prevents the changes in leaf weight to leaf area reported by Ansley et al. (1992). Changes in leaf weight as a result of translocation of sugars, starches, other compounds, and insect damage could not be detected or separated from cell-wall thickening from water stress within the precision of sampling in our study.

Texas persimmon LAR in April 1986 was significantly greater than for sampling dates in 1985. Meyer (1974) reported that Texas persimmon produces two types of leaves: a large leaf in the center of the canopy and a smaller leaf around the perimeter of the plant. The leaves

are initially light green in color and become glabrous after elongation ceases. As the leaf matures, the xylem and bundle fibers become increasingly lignified and the leaf turns dark green, with the underside becoming densely covered with trichomes. Leaf modification is complete by early July. The lower LAR of Texas persimmon leaves in 1986 was attributed to the leaves not being fully elongated, with incomplete development of trichomes and lignification.

LAR relationships for Texas colubrina varied seasonally. LAR was similar during the early growing seasons in May 1985 and April 1986, and in August 1985. In November the LAR was 33% greater than during other sample dates (Table 4). Basal leaves of Texas colubrina are approximately 10 times larger than the outer canopy leaves. In response to an extended dry period in July and August, Texas colubrina dropped 95% of its leaves. The only leaves retained during this dry period were the large basal leaves in the center of the shrub. The significant difference in LAR between the sample dates was attributed to the different proportion of leaf types and not the change in specific weight of the leaves.

Ganskopp and Miller (1986) reported similar significant seasonal changes in LAR for Wyoming big sagebrush. They speculated that the greatest proportion of seasonal variation was due not to the development or alterations in starch and sugar accumulations but rather to changes in the proportion of larger persistent leaves to smaller ephemeral leaves.

Shrub leaf biomass to leaf area was highly correlated for the nine other shrubs sampled (Table 3). The LAR for shrub leaf area ranged from 2010 to $6100 \text{ mm}^2 \text{ g}^{-1}$. Other researchers have also reported satisfactory results in relating leaf biomass to leaf area (Schilesinger and Chabot 1977, Kaufmann et al. 1982, Ganskopp and Miller 1986) within sample date. Based on the seasonal variability in LAR for Texas persimmon and Texas colubrina in this study and the findings of Ganskopp and Miller (1986) in eastern Oregon for Wyoming big sagebrush, we can state that seasonal variability in these and other drought-deciduous shrubs is an important source of variation that needs to be accounted for when simulating LAI over the entire growing season.

CONCLUSION

For the species sampled, leaf biomass is a reliable estimator of leaf area. However, for some shrub species, seasonal differences in development and shedding of different types of leaves and leaf morphological development can produce significant temporal fluctuations in LAR. Caldwell et al. (1981) reported that for semiarid bunchgrasses, leaf blades of regrowing tillers had greater photosynthetic capacity than blades on unclipped plants. This resulted in greater carbon gain for clipped plants and an increased photosynthesis/transpiration ratio. Nowak and Caldwell (1984) reported that the photosynthetic rate for both clipped and unclipped plants decreased with age of the leaves. Current rangeland hydrologic simulation models do not account for changes in LAR or evapotranspiration rates as a function of age of the leaf, proportion of leaf type, or compensatory photosynthesis rate increases following defoliation due to grazing. Models currently utilize a fixed coefficient for calculating LAI. If significant advances in modeling evapotranspiration on rangelands are to be made, improvements in the relationships used to simulate evapotranspiration that incorporate these processes will be needed. The LAR method of calculating LAI evaluated in this study provides a fast, reliable method of estimating LAI necessary to parameterize these hydrologic simulation models. To account for the seasonal differences in LAR for Texas persimmon and Texas colubrina, a weighted average based on season of year is recommended for parameterizing the WEPP model. For plants like mesquite and lime prickly ash, one LAR value can be used in non-drought years. For years with significant dry periods, a decrease in LAR of 10–40% may need to be accounted for with non-phreatophytic mesquite, as indicated by this work and that of Ansley et al. (1992).

LITERATURE CITED

- ANSLEY, R. J., D. L. PRICE, S. L. DOWHOWER, and D. H. CARLSON. 1992. Seasonal trends in leaf area of honey mesquite trees: determination using image analysis. *Journal of Range Management* 45: 339–344.
- ARNOLD, J. G., J. R. WILLIAMS, A. D. NICKS, and N. B. SAMMONS. 1990. SWRRB—a basin scale simulation model for soil and water resource management. Texas A&M University Press, College Station.
- BRANSON, F. A., G. F. GIFFORD, K. G. RENARD, and R. F. HADLEY. 1981. Rangeland hydrology. Range Science Series No. 1. 2nd ed. Society of Range Management, Denver, Colorado. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- BROWN, J. K. 1976. Estimating shrub biomass from basal stem diameters. *Canada Journal of Forest Research* 6: 153–158.
- BROWN, R. W. 1977. Water relations of range plants. Pages 98–140 in R. E. Sosebee, ed., *Rangeland plant physiology*. Range Science Series No. 4. Society of Range Management, Denver, Colorado.
- CALDWELL, M. M., J. H. RICHARDS, D. A. JOHNSON, R. S. NOWAK, and R. S. DZUREC. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid agropyron bunchgrasses. *Oecologia* 50: 14–24.
- CARLSON, D. H., T. L. THURLOW, R. W. KNIGHT, and R. K. HEITSCHMIDT. 1990. Effect of honey mesquite on the water balance of Texas rolling plains. *Journal of Range Management* 43: 486–490.
- COOMBS, J., D. O. HALL, S. P. LONG, and J. M. O. SCURLOCK. 1987. *Techniques in bioproductivity and photosynthesis*. 2nd edition. Pergamon Press, New York.
- CREGG, B. M. 1992. Leaf area estimation of foliage of *Juniperus*. *Forest Science* 38: 61–67.
- CURTIS, P. S., and A. LUCHLI. 1987. The effect of moderate salt stress on leaf anatomy in *Hibiscus cannabinus* (kenaf) and its relation to leaf area. *American Journal of Botany* 74: 538–542.
- CUTLER, J. R., D. W. RAINS, and R. S. LOOMIS. 1977. The importance of cell size in water relations of plants. *Physiology of Plants* 40: 255–260.
- GANSKOPP, D., and R. MILLER. 1986. Estimating leaf area of big sagebrush from measurement of sapwood. *Journal of Range Management* 39: 338–340.
- GAY, L. W., and L. J. FRITSCHEN. 1979. An energy budget analysis of water use by salt cedar. *Water Resource Bulletin* 26: 1589–1597.
- GIFFORD, G. F. 1975. Approximate annual water budget of two chained pinyon-juniper sites. *Journal of Range Management* 38: 73–74.
- GOFF, B. F. 1985. Dynamics of canopy structure and soil surface cover in a semiarid grassland. Unpublished master's thesis, University of Arizona, Tucson.
- HANSON, C. L. 1976. Model for predicting evapotranspiration from native rangelands in the Northern Great Plains. *Transactions of the American Society of Agricultural Engineering* 19: 471–477.
- HUGHES, H. G., L. W. VARNER, and L. H. BLANKENSHIP. 1987. Estimating shrub production from plant dimensions. *Journal of Range Management* 40: 367–369.
- KAUFMANN, M. R., C. B. EDMISTER, and C. A. TROENDLE. 1982. Leaf area determinations for subalpine tree species in the Central Rocky Mountains. USDA Forest Service, Research Paper RM-228.
- KRAMER, P. J., and T. T. KOZLOWSKI. 1979. *Physiology of woody plants*. Academic Press, New York.
- LANE, L. J., and M. A. NEARING. 1989. USDA—Water Erosion Prediction Project: hillslope profile model documentation. USDA-ARS National Soil Erosion Research Laboratory, Purdue University, Report 2. West Lafayette, Indiana.
- LANE, L. J., E. M. ROMNEY, and T. E. HAKONSON. 1984. Water balance calculations and net production of perennial vegetation in the northern Mojave desert. *Journal of Range Management* 37: 12–18.
- LAUFENROTH, W. K., and P. L. SIMS. 1976. Evapotranspiration from a shortgrass prairie subjected to water and

- nitrogen treatments. *Water Resource Research* 12: 437-442.
- LUDWIG, J. A., J. F. REYNOLDS, and P. D. WHITSON. 1975. Size-biomass relationships of several Chihuahuan desert shrubs. *American Midland Naturalist* 94: 451-461.
- MEYER, R. E. 1974. Morphology and anatomy of Texas persimmon (*Diospyros texana* Scheele). Texas Agricultural Experiment Station Bulletin 1147. Texas A&M University, College Station.
- MILLER, R. F., L. E. EDDLEMAN, and R. F. ANGEL. 1987. Relationship of western juniper stem conducting tissue and basal circumference to leaf area and biomass. *Great Basin Naturalist* 47: 349-354.
- MILLER, R. F., and L. M. SCHULTZ. 1987. Water relations and leaf morphology of *Juniperus occidentalis* in the northern Great Basin. *Forest Science* 33: 690-706.
- MOONEY, H. A., B. B. SIMPSON, and O. T. SOLBRIG. 1977. Pages 26-44 in B. B. Simpson, ed., *Mesquite: its biology in two ecosystems*. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania.
- NILSEN, E. T., M. R. SHARIFI, P. W. RUNDEL, and R. A. VIRGINIA. 1986. Influences of microclimatic conditions and water relations on seasonal dimorphism of *Prosopis glandulosa* var. *torreyana* in the Sonoran Desert, California. *Oecologia* 69: 95-100.
- NILSEN, E. T., R. A. VIRGINIA, and W. M. JARRELL. 1986. Water relations and growth characteristics of *Prosopis glandulosa* var. *torreyana* in a simulated phreatophytic environment. *American Journal of Botany* 73: 427-433.
- NOWAK, R. S., and M. M. CALDWELL. 1984. A test of compensatory photosynthesis in the field: implications for herbivory tolerance. *Oecologia* 61: 311-318.
- RADFORD, P. J. 1967. Growth analysis formulae—their use and abuse. *Crop Science* 7: 171-175.
- RITCHIE, J. T. 1972. A model for predicting evaporation from a row crop with incomplete cover. *Water Resource Research* 8: 1204-1213.
- RITTENHOUSE, L. R., and F. A. SNEVA. 1977. A technique for estimating big sagebrush production. *Journal of Range Management* 30: 68-70.
- SAS. 1982. SAS user's guide: basics. SAS Institute, Inc. Cary, North Carolina.
- SCHLESINGER, W. H., and B. F. CHABOT. 1977. The use of water and minerals by evergreen and deciduous shrubs in the Okefenokee swamp. *Botanical Gazette* 138: 490-497.
- STEELE, R. G. D., and J. H. TORRIE. 1980. Principles and procedures of statistics—a biometric approach. McGraw-Hill Book Company, New York.
- THOMPSON, F. B., and L. LEYTON. 1971. Method for measuring the leaf surface area of complex shoots. *Nature* 229: 572.
- WATSON, D. J. 1947. Comparative physiological studies on the growth of field crops: 1. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Annals of Botany* 11: 41-76.
- WHISENANT, S. G., and D. F. BURZLAFF. 1978. Predicting green weight of mesquite (*Prosopis glandulosa* Torr.). *Journal of Range Management* 31: 395-397.
- WIGHT, J. R. 1971. Comparison of lysimeter and neutron scatter techniques for measuring evapotranspiration from semiarid rangelands. *Journal of Range Management* 24: 390-393.
- _____. 1986. ERHYM-II: model description and user guide for the basic version. USDA, Agricultural Research Service, ARS 59. National Technical Information Service, Springfield, Virginia.
- WIGHT, J. R., and C. L. HANSON. 1990. Crop coefficients for rangeland. *Journal of Range Management* 43: 482-485.
- WIGHT, J. R., C. L. HANSON, and K. R. COOLEY. 1986. Modeling evapotranspiration from sagebrush-grass rangelands. *Journal of Range Management* 31: 81-85.
- WIGHT, J. R., and J. W. SKILES, EDs. 1987. SPUR: Simulation of production and utilization of rangelands. Documentation and User Guide. U.S. Department of Agriculture, Agricultural Research Service, ARS-63, Boise, Idaho.

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