ADAPTATION OF GRASSES TO WATER STRESS—LEAF ROLLING AND STOMATE DISTRIBUTION[1]

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ABSTRACT

Leaf dimension, degree of leaf rolling or folding, and stomatal densities on adaxial and abaxial leaf surfaces were measured on herbarium specimens of 39 grass species from a range of dry to wet habitats in western Canada. Stomata were counted on vinyl leaf impressions taken from the herbarium specimens. Representative surfaces also were examined using scanning electron microscopy. All species from dry habitats had narrow rolled or folded leaves (4 mm or less). The proportion of stomata on the abaxial surface of species from dry habitats ranged from 0 to 65%, but 56% of the species were strongly amphistomatous. The results were compatible with a conceptual model predicting that rolling, amphistomatous leaves would be selected for habitats in which water supply and demand fluctuate widely on seasonal or diurnal time scales.

The evolutionary adaptation of grasses involves a syndrome of physiological, anatomical, and morphological characteristics. Grass leaf structure is closely coupled with major physiological processes such as photosynthesis, water relations, and energy balance. For example, vascular bundle and mesophyll cell arrangement are related to the type of photosynthetic pathway (Black et al., 1973; Hattersley & Watson, 1975), which, in turn, can influence niche separation in grasses (Monson et al., 1983). Specialized leaf tissue structure in some grasses results in leaf rolling, which strongly influences water and energy balances by changing the characteristic leaf dimension and the conductance of heat, water vapor, and carbon dioxide (Ripley & Redmann, 1976). This paper concentrates on the relationship between leaf rolling and stomatal distribution and conductance.

The anatomy and mechanism of leaf rolling in grasses have been studied for over a century (Tschirch, 1882; Shields, 1951). Loss of turgor in the bulliform cells on the adaxial (upper) surface generally is considered to induce rolling. Shrinkage of the adaxial subepidermal sclerenchyma and mesophyll, due to water loss, also contributes to involution; rolling can occur in leaves that lack bulliform cells (Shields, 1951). Some grasses have permanently rolled or folded leaves.

Leaves of native grasses from semi-arid grassland roll in response to increased plant water stress during dry periods (Ripley & Redmann, 1976). More mesic grasses such as cereal crops also exhibit leaf rolling when exposed to water stress (Hurd, 1976; O'Toole et al., 1979). Leaves of *Sorghum bicolor* roll and unroll in response to diurnal changes in plant water status, provided stress is not too severe (Begg, 1980).

The early textbooks on plant ecology generally explained rolling as a xeromorphic adaptation for reducing transpiration by "protecting" the stomata, which were considered to be concentrated on the upper surface (Warming, 1909; Weaver & Clements, 1929; McDougall, 1949). Unfortunately, references to data supporting this explanation were not given, but the idea probably originated with early work on ecological plant anatomy. Tschirch (1882) classified grasses as meadow type, with flat leaves, or steppe type, with rolling leaves. Lewton-Brain (1904) grouped British grasses into four categories representing progressively more drought resistant types: (1) leaves with flat upper surfaces, amphistomatous, (2) leaves with ribbed upper surfaces, amphistomatous, (3) leaves with ridged upper surfaces, rolled with drying, epistomatous, and (4) leaves permanently rolled or folded, epistomatous.

I was unable to find published comparative data on relative stomatal distributions on grass leaves in relation to rolling or drought resistance that would verify the generalizations described above. Parkhurst (1978) pointed out that the limited data in the literature show no clear trends

TABLE 1. Leaf characteristics of grasses from a range of habitats. All collections from Saskatchewan unless noted otherwise.

Species	Leaf Shape[a]	Stomata ad/ab %	Leaf Type[c]	Measured Leaf Width (mm)[b]	Drought Resistance Index	Habitat
Festuceae						
Bromus ciliatus L.	fl	95/5	Fe	10	7	Boreal forest
B. pumpellianus Scribn.	fl	40/60	Fa	5	6	Boreal forest opening
Festuca saximontana Rydb.	fo	100/0	PRe	1.5 (0.5)	1	Sandy grassland
F. scabrella Torr.	fo	100/0	PRe	3 (1)	4	Mesic grassland
Poa arida Vasey	fl-fo	70/30	Ra	2.5	1	Sandy grassland
P. palustris L.	fl	60/40	Fa	6.5	8	Floodplain forest
P. secunda Presl.	fl-fo	70/30	Ra	1.5	1	Xeric grassland
Scholochloa festucacea (Willd.) Link	fl-i	60/40	Ra	7	10	Prairie wetland
Aveneae						
Alopecurus aequalis Sobol.	fl	50/50	Fa	5	9	Boreal wetland
Beckmannia syzigachne (Stued.) Fernald	fl	50/50	Fa	8	9	Prairie wetland
Calamagrostis canadensis (Michx.) Beauv.	fl	100/0	Fe	5	8	Boreal forest
C. montanensis Scribn.	fl-i	60/40	Ra	3	1	Xeric grassland (Alberta)
Cinna latifolia (Trevir.) Griseb.	fl	50/50	Fa	9	7	Boreal forest
Helictotrichon hookeri (Scribn.) Henr.	fl-fo	85/15	Re	4	4	Mesic grassland
Hierochloe odorata (L.) Beauv.	fl-i	70/30	Ra	5	8	Boreal wetland
Koeleria cristata (L.) Pers.	fl-i	60/40	Ra	2	2	Clayey grassland
Phalaris arundinacea L.	fl	55/45	Fa	14	10	Prairie wetland
Triticeae						
Agropyron dasystachyum (Hook.) Scribn.	fl-i	65/35	Ra	3	3	Clayey grassland
A. smithii Rydb.	fl-i	50/50	Ra	4	2	Clayey grassland
A. spicatum (Pursh) Scribn. & Smith	fl-i	65/35	Ra	3	2	Sagebrush (Wyoming)

TABLE 1. Continued.

Species	Leaf Shape[a]	Stomata ad/ab %	Leaf Type[c]	Measured Leaf Width (mm)[b]	Drought Resistance Index	Habitat
A. subsecundum (Link) Hitchc.	fl	60/40	Fa	7	6	Boreal forest opening
A. trachycaulum (Link) Malte.	fl	75/25	Fa	7	6	Boreal forest
Elymus canadensis L.	fl-i	70/30	Ra	8	6	Sandy river bank
E. cinereus Scribn. & Merr.	fl-i	55/45	Ra	15	6	Cultivated plots
E. innovatus Beal.	fl	80/20	Fe	6	6	Boreal forest
E. virginicus L.	fl	90/10	Fe	7	7	Deciduous forest
Meliceae						
Catabrosa aquatica (L.) Beauv.	fl	40/60	Fa	8	9	Streamside
Glyceria grandis S. Wats.	fl	60/40	Fa	7.5	9	Streamside
G. striata (Lam.) Hitchc.	fl	70/30	Fa	5.5	9	Streamside
Schizachne purpurascens (Torr.) Swallen	fl-fo	95/5	Re	4	5	Boreal forest opening (Alberta)
Stipeae						
Oryzopsis asperifolia Michx.	fl-i	90/10	Re	7	7	Boreal forest
O. hymenoides (Roem. & Shult.) Ricker	i-fl	35/65	PRa	3 (1)	3	Sandy grassland
O. pungens (Torr.) Hitchc.	fl-i	100/0	Re	2	3	Boreal forest opening
Stipa comata Trin. & Rupr.	fl-i	85/15	Re	3.5	1	Xeric grassland
S. curtiseta (A. S. Hitchc.) Barkworth	fl-i	95/5	Re	2.5	3	Boreal forest opening
S. richardsonii Link	i	100/0	PRe	2 (1)	5	Boreal forest opening
S. spartea Trin.	fl-i	60/40	Ra	2.5	5	Mesic grassland
S. viridula Trin.	fl-i	75/25	Ra	3	4	Mesic grassland
Arundineae						
Phragmites communis Trin.	fl	45/55	Fa	25	10	Boreal wetland

[a] fl = flat, fo = folded, i = involute or convolute.
[b] Folded or involuted width is given parenthetically only for permanently rolled or folded leaves.
[c] Fa = flat, amphistomatous; Fe = flat, epistomatous; Ra = rolling or folding amphistomatous; Re = rolling or folding, epistomatous; PRa = permanently rolled or folded, amphistomatous; PRe = permanently rolled or folded, epistomatous.

regarding the relationship of drought resistance to adaxial-abaxial stomatal distributions. Parkhurst concluded from a survey of four families that amphistomatous leaves occur most often in xeric and hydric habitats; however, he did not include grasses in his analysis.

Absolute stomatal density varies widely among species and with environmental preconditioning (Muenscher, 1915; Salisbury, 1927). The relative numbers of stomata on upper and lower surfaces are not as strongly influenced by preconditioning. Salisbury (1927) found that stomatal density on upper and lower surfaces tends to "augment or diminish in a parallel manner" depending on growth conditions. Tan and Dunn (1975) showed highly significant positive correlations between adaxial and abaxial surfaces of *Bromus inermis* for both stomatal frequency and length.

Pospisilova and Solarova (1980) concluded that the ratio of adaxial and abaxial conductances was only "crudely" related to the ratio of stomatal densities on the two surfaces. However, the proportion of carbon dioxide exchange through the adaxial and abaxial surfaces of *Zea mays* is related to the relative number of stomata on each surface (Bertsch & Domes, 1969). For purposes of the conductance model described later in this paper it is sufficient that the ratio of stomata on each leaf surface indicates at least the trend in the proportion of total conductance contributed by each surface.

The first objective of the work reported here was to determine the relationships between degree of leaf rolling, leaf dimension, and stomatal distribution for grass species collected from native habitats with different water stress regimes. The second objective was to develop a conceptual model to help explain the advantages of different stomatal distribution patterns and leaf rolling in wet or dry habitats.

METHODS

The grass flora of the Prairie Provinces of western Canada was surveyed in order to select species from a range of habitat types along a gradient of water availability. The species were assigned a drought resistance index (DRI) value based on information from descriptions in Best et al. (1971) and Hitchcock (1950), in addition to discussions with V. L. Harms, a taxonomist with extensive experience collecting in western Canada. The DRI ranged from 1 (species present in the driest habitat) to 10 (species present in the wettest habitat).

Specimens from the W. P. Fraser Herbarium, University of Saskatchewan, were selected for measurements of leaf width, degree of rolling or folding, and stomatal density on adaxial and abaxial surfaces. In a few cases the DRI was modified slightly depending on annotation data for the particular specimen selected.

Stomatal density was determined on fully-developed leaves from mid-culm position, or on basal leaves, where culm-leaves were small or absent. In all cases impressions were made at the mid-blade position of the adaxial and abaxial surfaces in order to standardize the sampling. Impressions were made using 0.3 mm thick transparent polyvinyl chloride film. Details of the method are described in Redmann (1985). This technique was successful even with leaves having trichomes and corrugated adaxial surfaces.

The number of stomata in a minimum of ten fields randomly located on the impression was determined at $500 \times$ magnification. In a few cases where stomatal density was small, counts were made at $125 \times$. The mean stomatal density per mm^2 for each surface was used to calculate percentages of total number of stomata on adaxial and abaxial surfaces. Variation in percentages of the total number of stomata on the two surfaces of leaves from five plants in a population of *Phalaris arundinacea* was smaller than variation in absolute stomatal density. This was because densities on the surfaces increased or decreased together, as was found by Salisbury (1927) and Tan and Dunn (1975). Only percentage ratios are presented here in order to avoid some of the difficulty in comparing species with widely-differing absolute stomatal densities. Because only one or two populations of each species were sampled, variability among different populations of each species was not assessed. Even relatively large variation in percentage ratios (e.g., 15–20%) probably would have little effect on the conclusions reached.

Maximum flattened leaf width was determined on each herbarium specimen. The degree of rolling or folding on the dried specimens was noted and used to supplement information on folding, involution, or convolution reported in Best et al. (1971) and Hitchcock (1950). Leaf surfaces of eight species with widely different DRI values were examined using a Philips 505 scanning electron microscope. Micrographs for three species with distinctive surface features were selected for inclusion here.
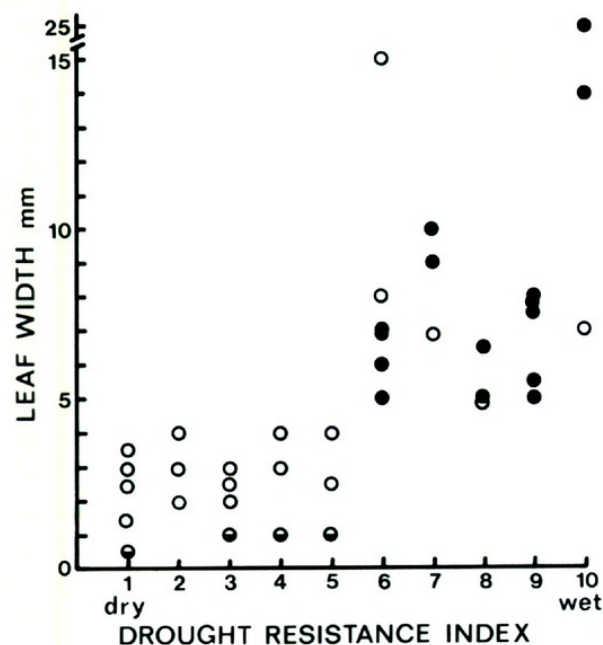
FIGURE 1. Relationship between measured leaf width and drought resistance index for 39 grass species from Saskatchewan and adjacent areas. Closed circles represent flat leaves, open circles are rolling or folding leaves, and half-closed circles are permanently rolled or folded leaves.
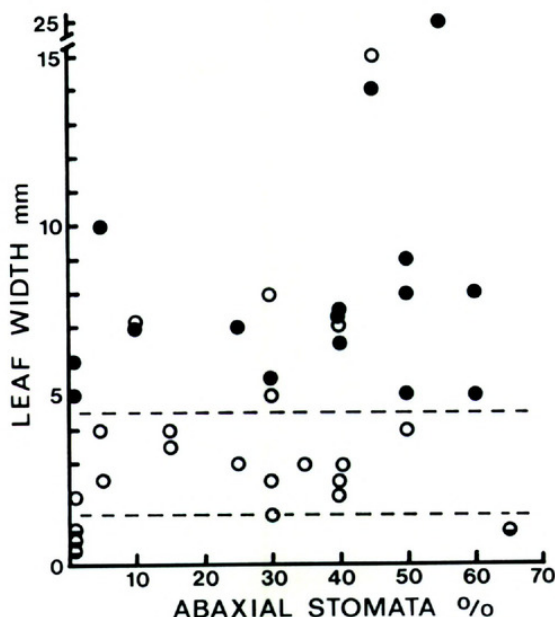
FIGURE 2. Relationship between leaf width and percentage of stomata on the abaxial surface for 39 grass species from Saskatchewan and adjacent areas. Closed circles represent flat leaves, open circles are rolling or folding leaves, and half-closed circles are permanently rolled or folded leaves. Upper dashed line at 4.5 mm is the approximate border between dry-site species and wet-site species. Lower dashed line is the approximate-border between permanently rolled or folded leaves and other types.

RESULTS

The 39 grass species included in Table 1 occur in a range of habitats in western Canada and adjacent geographic regions. The four major tribes (Gould, 1968), Festuceae, Aveneae, Triticeae, and Stipeae each have representatives from several habitat types. The minor tribes, Meliceae and Arundineae, include mainly wetland types. Tribes with the C4 photosynthetic pathway (Waller & Lewis, 1979) were excluded because their special physiology and higher water use efficiency might have complicated the analysis.

In the populations sampled, 19 species have flat leaves that either roll or fold on drying. *Festuca saximontana, F. scabrella, Oryzopsis hymenoides*, and *Stipa richardsonii* have leaves that are more or less permanently folded or rolled. The remaining 16 species have flat, non-rolling leaves.

Leaf widths ranged from 1.5 mm in *F. saximontana* and *Poa secunda* to 25 mm in *Phragmites communis*. There was a clear relationship between drought resistance index (DRI) and leaf width (Fig. 1). No species with a DRI of 5 or lower had a maximum leaf width greater than 4 mm. All four species with more or less permanently rolled or folded leaves had diameters or

widths of 1 mm or less. None of the species with a DRI of 6–10 had a leaf width less than 5 mm.

Neither leaf width nor stomatal distribution showed a clear relationship to tribe (Table 1). In the Stipeae, five of the eight species had stomata mainly on the adaxial surface; the exceptions were *O. hymenoides, Stipa spartea*, and *S. viridula*. The average adaxial/abaxial stomatal ratio for each tribe was: Stipeae 80/20, Festuceae 74/26, Triticeae 68/32, and Aveneae 64/36.

There was no correlation of stomatal density on leaf surfaces with either DRI or leaf width (Fig. 2). The results do show that all species with leaves less than about 4.5 mm wide either had flat leaves that rolled or folded, or had permanently rolled or folded leaves. However, the proportion of stomata on the abaxial surfaces of these leaves varied from 0 to 65%. Ten of 18 species (56%) classified as DRI 1–5 had at least 25% of their stomates on the abaxial leaf surface. Six of 21 species with a DRI of 6–10 had 25% or fewer stomata on the abaxial surface. The mean percentage of abaxial stomata (and coefficient of variation, c.v.) for the 18 species with DRI 1–5 was 23.9% (c.v. = 83%), and for the 21 species with DRI 6–10 was 35% (c.v. = 51%). These
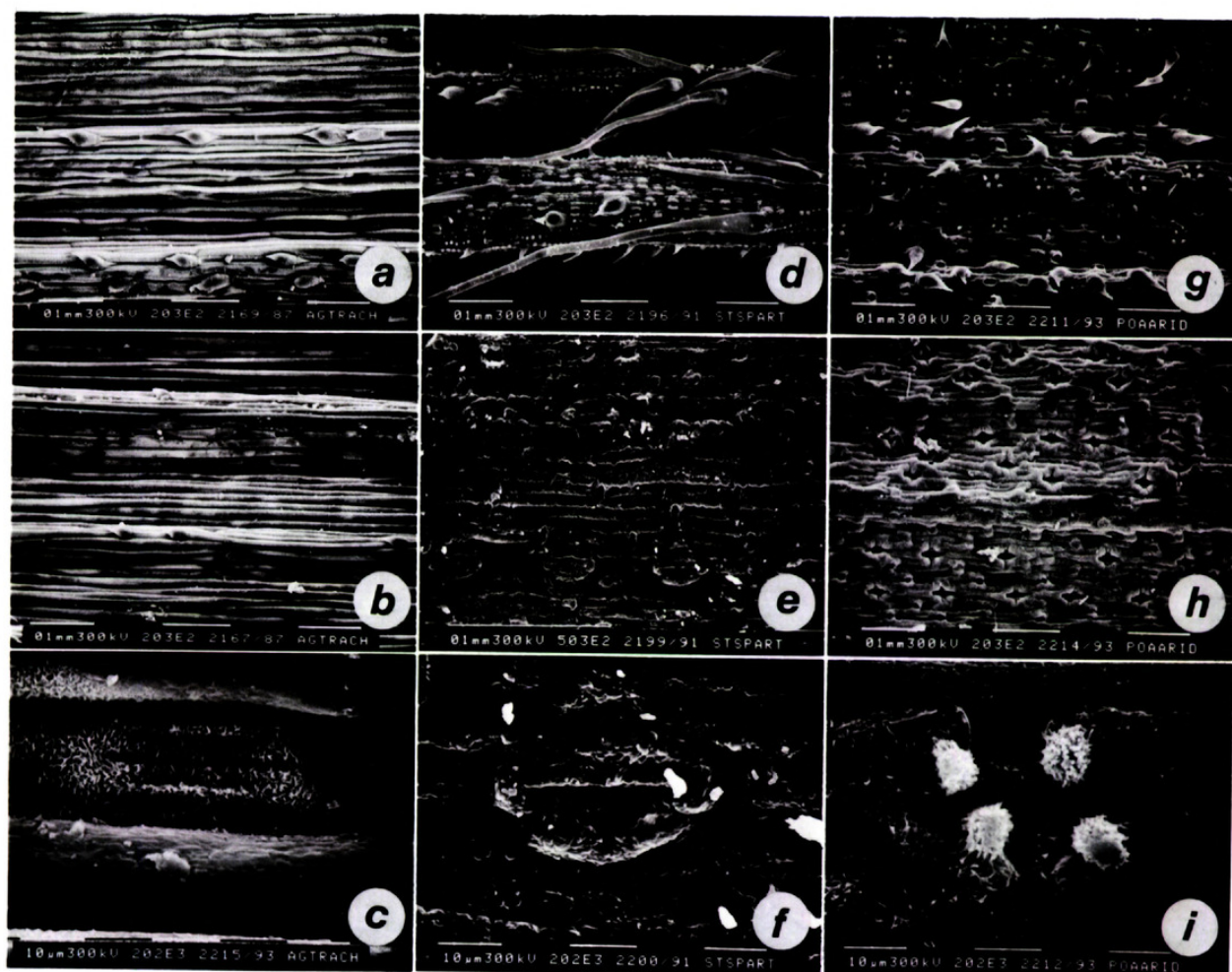
FIGURE 3.   Scanning electron micrographs of adaxial (ad) and abaxial (ab) leaf surfaces.—a. *Agropyron trachycaulum*, ad.—b. *A. trachycaulum*, ab.—c. *A. trachycaulum*, ab, stomate.—d. *Stipa spartea*, ad.—e. *S. spartea*, ab.—f. *S. spartea*, ab, stomate.—g. *Poa arida*, ad.—h. *P. arida*, ab.—i. *P. arida*, ad, stomate. Alternating black and white bars indicate the scale (0.1 mm in a, b, d, e, g, h, and 10 μm in c, f, i).

means were not significantly different (*t*-test, Steel & Torrie, 1960). Variation among species in numbers of abaxial stomata was greater in the more drought resistant group (DRI 1–5).

The adaxial surfaces of species exhibiting leaf rolling were strongly ridged or corrugated. An extreme example of this is *Stipa spartea* (Fig. 3d). Stomata were in rows at the bottoms of the furrows between ridges. *Stipa spartea* had 40% of the total stomata located on the abaxial surface, which was relatively smooth and encrusted with cuticular wax (Fig. 3e). *Poa arida* had a less strongly corrugated adaxial surface; however, the stomata on both surfaces were sunken into distinctive pits, which, in the case of the adaxial surface, were surrounded by peculiar wax "balls" and protruding outgrowths of epidermal cells (Fig. 3i). Flat-leaved species, as represented by *Agropyron trachycaulum*, had non-corrugated adaxial surfaces similar to abaxial surfaces (Fig. 3a, b).

Only one species with non-rolling epistomatous leaves, *Calamagrostis canadensis*, appeared among the 39 grasses studied (Table 1). This grass is common in moist to wet sites, sometimes shaded, in the boreal forest. Two other flat-leaved forest grasses, *Bromus ciliatus* and *Elymus virginicus*, and one leaf-roller, *Oryzopsis asperifolia*, also tended strongly toward the epistomatous condition and could be grouped with *C. canadensis*. All other strongly epistomatous species, including *Festuca saximontana*, *F. scabrella*, *Oryzopsis pungens*, *Stipa curiseta*, and *S. richardsonii* have rolling or folding leaves and are found on relatively dry sites in western Canada (DRI 1–5).

Flat-leaved amphistomatous species were mesic forest- or wetland-grasses (DRI 6–10): *Bromus pumpellianus*, *Cinna latifolia*, *Catabrosa aquatica*, and ten other species. All other amphistomatous species had rolling or folding leaves.
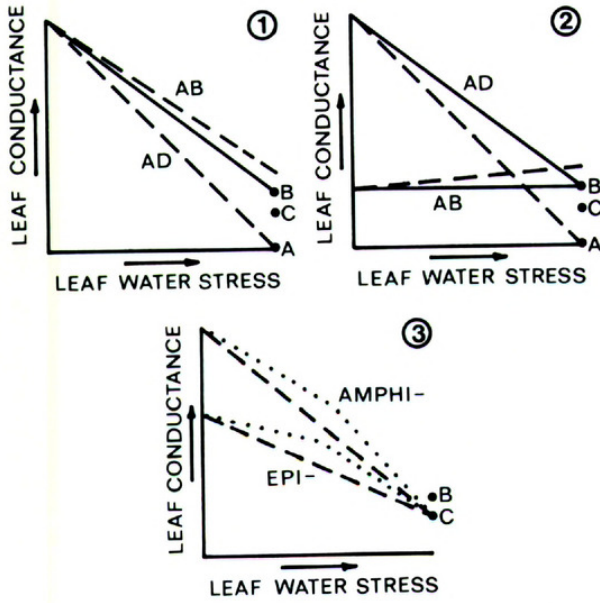
FIGURE 4. Generalized graphs showing relative conductances of amphistomatous and epistomatous leaves in relation to leaf water stress. Solid lines are for flat leaves, dashed lines are for leaves that roll in response to water stress.—1. Amphistomatous leaf, AB = abaxial surface, AD = adaxial surface.—2. Epistomatous leaf.—3. Mean conductances of adaxial and abaxial surfaces in amphistomatous (AMPHI-) and epistomatous (EPI-) leaves. Dotted line shows possible enhanced conductance at a particular stress level due to leaf rolling. See text for further explanation.

FIGURE 5. Rolled leaf of *Elymus cinereus* photographed several minutes after excision from shoot. Diameter is 3.5 mm.

All those that occurred in habitats with DRI of 1–5 had rolling or folding leaves. A few species from relatively wetter habitats (DRI 6–10) also had leaves that tended to roll: *Scolochloa festucacea* and *Hierochloe odorata* are found in wetlands that can dry out in late season; *Elymus canadensis* and *E. cinereus* occur on sites with wide variation in water availability.

The relationship of leaf type to habitat may be summarized as follows:

(1) Flat amphistomatous leaves—all 12 species with this leaf type occurred only in relatively moist sites.

(2) Flat, epistomatous leaves—four species with this type were from moist, often shaded, forest edge habitats.

(3) Rolling or folding amphistomatous leaves—nine of 13 species in this category were from relatively dry sites.

(4) Rolling or folding epistomatous leaves—five of six species came from relatively dry habitats.

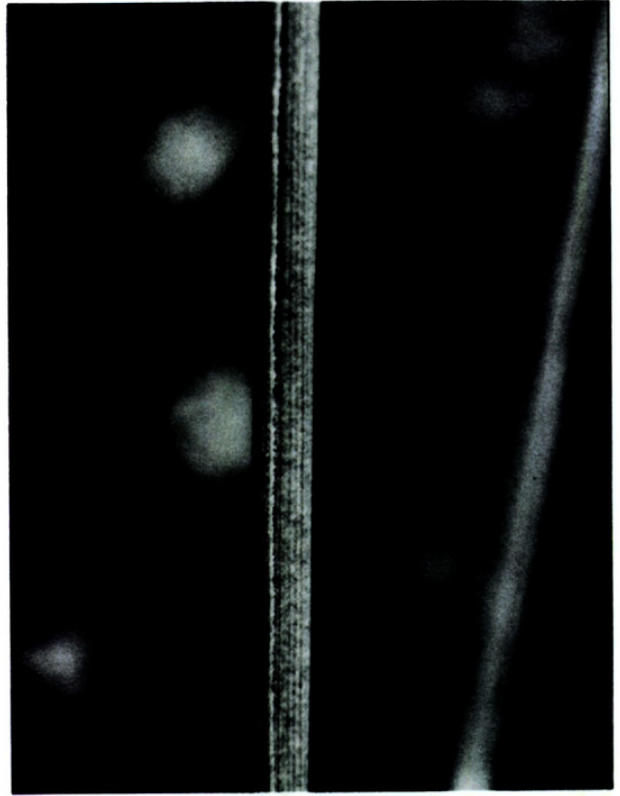(5) Permanently rolled amphistomatous leaves—the only species in this category, *Oryzopsis*

hymenoides, was collected in its typical sand-dune habitat.

(6) Permanently rolled epistomatous leaves—all three species were from dry habitats.

DISCUSSION

The strong trend toward reduction in leaf dimension in grass species from dry habitats (Fig. 1) confirms a well-known trend toward leaf reduction in plants from dry habitats (Daubenmire, 1974). Narrow leaves are more efficient heat exchangers and are less likely to overheat when exposed to drought and high irradiance (Parkhurst & Loucks, 1972; Gates, 1980). Leaf rolling reduces leaf dimension even further, reducing radiation intercepted *per leaf,* and enhancing sensible heat transfer, especially under conditions of free convection (Ripley & Redmann, 1976). Rolling influences latent heat transfer through its effects on (1) leaf temperature, and therefore on water vapor density in the leaf, and (2) boundary layer conductance.

Stomatal distribution is an important factor in determining the degree to which rolling reduces leaf water vapor conductance. A simple, concep-

tual model was devised to help explain how leaf conductance is related to stomatal distribution, leaf rolling, and water stress regime (Fig. 4). The model presented here is meant to aid in interpretation of the observations of leaf characteristics. Hypotheses derived from this analysis should be examined using a quantitative simulation model, and verified by field measurements of leaf conductance.

The model assumes that at low water stress, conductances of the adaxial and abaxial surfaces of the amphistomatous flat and rolling leaves are the same. With greater water stress, rolling increases until complete closure is reached and adaxial conductance drops to zero (Fig. 4-1, point A). Whether rolling completely closes off the adaxial surface is uncertain; however, this seems to be the case for species that I have observed (Fig. 5). The conductance of the abaxial surface of the rolled leaf is considered to be somewhat higher than for the flat leaf, owing to the smaller dimension and thinner boundary layer of the former. At point B, stomatal conductance is zero, and only cuticular water loss occurs from the two surfaces of the flat leaf. Point C represents the average cuticular conductance of the adaxial and abaxial surfaces of the rolled leaf. A complete average curve for the rolling amphistomatous leaf is given in Figure 4-3.

The adaxial surfaces of the flat and rolled epistomatous leaves are assumed to respond in the same way as the amphistomatous types (Fig. 4-2). The abaxial surface has only cuticular conductance, which increases slightly with rolling.

The average whole leaf conductance of the epistomatous leaf is lower than the amphistomatous type, except at high water stress, where they are equal (Fig. 4-3). The average conductance for the upper and lower surfaces (point C) is the same for both the epistomatous and amphistomatous rolled leaves and is lower than the average of the surfaces of flat leaves (point B).

The major reason for decreasing conductance with water stress is stomatal closure. Boundary layer resistance is a relatively small component of total leaf resistance to water vapor transfer, at least in the open canopies typical of dry grassland. Only at maximum water stresses, assuming there is a complete "seal" of the rolled leaf edges, does boundary layer resistance become large (and conductance very small).

Natural selection of leaf form and function must optimize all of the following for any environmental regime: (1) maximum carbon dioxide conductance, (2) minimum water vapor conductance (when water supply is limiting), and (3) leaf temperature (Parkhurst & Loucks, 1972). Cost of constructing a particular leaf form also is a factor in the Parkhurst and Loucks analysis. A rolling-type leaf, with its extensive support tissue and other non-photosynthetic cells, thick cuticle and wax layers, trichomes, etc., must be more "costly" to produce than a simple, flat leaf.

The model (Fig. 4) suggests a hypothesis that rolled epistomatous leaves with their lower total conductance are disadvantageous except in habitats with sustained water stress, where minimization of water vapor conductance and avoidance of leaf overheating are important factors. Some recent data (Cohen et al., 1982) support this idea: The lowest-yielding of several slections of *Festuca arundinacea* had 44% lower abaxial stomatal frequency, and 10% higher adaxial stomatal frequency compared with other selections in field plot studies. Flat amphistomatous leaves would be favored in habitats with lower water stress, where high carbon dioxide conductance is a benefit and water loss is less a problem. Amphistomatous rolling leaves are a "compromise" design selected for in habitats where water availability fluctuates widely on a seasonal or diurnal basis. In this way the contradictory goals of maximizing carbon dioxide conductance and minimizing water conductance can be resolved.

A number of studies suggest that partial rolling might actually be a mechanism to sustain rather than reduce transpiration when evaporative demands are high. For example, Stocker (1972) described *Aristida pungens* as a dune grass with rolled leaves "of highest perfection," which maintains positive photosynthesis and low transpiration even during extreme dry periods. This implies that leaf conductance might be *higher* than for an equivalent unrolled leaf. From data in Willis and Jefferies (1963) it appears that with water stress the transpiration of *Ammophila arenaria* is sustained, even though "inrolling" of the leaves occurs. More recently, O'Toole and Cruz (1980) speculated that leaf rolling shelters the upper surface in such a way that adaxial conductance is higher than abaxial in rolled leaves. Johns (1978) found that conductance of forcibly unrolled leaves of *Festuca arundinacea* was similar to the normally flat leaves of other species. Bennett-Clark (1935, cited in Grieve, 1955) argued that xeromorphic modifications, such as leaf rolling, maintain a moister atmosphere around stomata, thus inhibiting closure and

maintaining conductance. Recently much attention has been paid to the direct response of stomata to humidity (e.g., Losch & Tenhunen, 1981). Rolling might be a mechanism to reduce this sensitivity, permitting higher stomatal conductance under conditions of high evaporative demand. This could result in lowering of tissue water content in rolled leaves, as reported by Rychnovska and Kvet (1963). Higher stress would still result in complete stomatal closure and low conductance. This modified type of response is included in the conceptual model (Fig. 4-3, dotted lines).

Of the 18 species from dry habitats that I examined, only seven (39%) had predominantly epistomatous, rolled or folded leaves. The relative number of species with epistomatous leaves may become larger in consistently drier habitats. When low total leaf conductance is a strong selective advantage, then species with epistomatous leaves may be selected for. This could be tested by measuring stomatal distribution in grass species from more arid habitats than those examined here.

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