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A Morphological and Anatomical Comparison of Winter Rosette Leaves and Summer Leaves of Some Prairie Forbs

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A MORPHOLOGICAL AND ANATOMICAL COMPARISON

OF

WINTER ROSETTE LEAVES AND SUMMER LEAVES

OF

SOME PRAIRIE FORBS

being

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THESIS ABSTRACT

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Morphological characteristics including leaf size, shape, color, type of margins, type and degree of pubescence, and stomatal density, and anatomical characteristics including arrangement of tissues, relative size and shape of cells, and types of cells or tissues, of winter rosette leaves and summer leaves of some native forbs were compared.

Morphological results were obtained by observing whole leaves. Later the leaves were pressed and then photographed. Comparison of stomatal densities were made by observing miscroscopic slides of epidermal peels. Photomicrographs of the epidermal sections were taken. Anatomical results were obtained by observing microscopic slides containing leaf cross-sections. Photomicrographs of the cross-sections were taken.

Morphologically, the winter rosette leaves differed from summer leaves in that rosette leaves: (1) usually had fewer lobes when leaves were divided, (2) were relatively smaller, (3) often contained purple coloration, and (4) usually had a slightly higher density of trichomes. Two species showed variations in leaf margins. Variations of stomatal densities were also observed.

Anatomically, winter rosette leaves differed from summer leaves

in that most rosette leaves had: (1) a lower length to width ratio of palisade parenchyma cells, (2) a cross-section of reduced length and width, (3) a reduced amount of spongy or water storage parenchyma cells, and (4) a reduced amount of palisade parenchyma per volume of leaf.

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INTRODUCTION

Three types of prairie forbs are classified according to the plants' life cycle: annuals, biennials, and perennials. Annuals produce total vegetative growth and flower in one growing season. In biennials, only vegetative growth occurs during the first growing season followed by formation of crown buds or winter rosettes. After vegetative growth and flower and seed formation during the second growing season, the life of biennials is terminated. Perennials are characterized by annual formation of flowers and renewed vegetative growth at the beginning of each growing season. Renewed growth starts from either crown buds, rhizomes, or rosettes which have formed during late fall or early winter months. Since most taxonomic keys describe only summer leaves, and since no literature is available on the anatomical differences of winter rosette leaves and summer leaves, pursuance of this problem seemed desirable.

Rosette plants are characterized by the proximity of leaves, caused by shortened internodes, which is the natural form of many plants, such as, dandelion (<u>Taraxacum officinale</u>). In the present study winter rosette plants will refer only to rosette plants having elongated internodes during the normal growing season. Leaves produced during the normal growing season will be referred to as summer leaves.

No substantial evidence is available indicating whether or not winter rosette leaves are beneficial to the plant. Reduced leaf size, relatively lower temperature, shorter period of daylight, and shading of lower leaves would tend to reduce photosynthesis occurring in a winter rosette. Relatively lower temperatures would also reduce respiration rate (Meyers, et al., 1960). The ratio of photosynthetic to nonphotosynthetic tissue is greater in winter rosettes than in summer plants. Perhaps factors favoring apparent photosynthesis outweigh factors opposing apparent photosynthesis, thereby causing a photosynthetic rate above compensation point.

In most cases, the limiting factor for photosynthesis of winter rosettes is temperature. Basal winter rosettes (Singh, 1962), in particular, inhabit a microenvironment. Situated close to the soil, basal winter rosettes are usually subjected to warmer day temperatures compared to air temperature a few feet above because of heat radiated by the soil. Winter rosettes are partially protected from extremely cold night temperatures by heat radiated from the soil, since soil cools slower than the surrounding air.

The morphological portion of this study pertains to differences in winter rosette and summer leaves as to: (1) leaf size, (2) leaf shape, (3) type and degree of pubescence, (4) leaf color, (5) type of leaf margin, and (6) stomatal density. The anatomical portion deals with differences in: (1) arrangement of tissue, (2) relative size and shape of cells, and (3) types of cells or tissues.

RELATED LITERATURE

By applying gibberellic acid to rosette plants, Sachs et al. (1959) discovered an increase in cell division occurring mostly in the subapical region of the stem, contrary to popular belief that cell division occurs only in the apical region. Cell elongation began 72 hours after application.

Gray (1957) investigated the effects of gibberellins on leaf size and shape. When subjected to gibberellic acid, tomato leaves developed entire margins instead of indented margins; tobacco leaves were more elongated and pointed at the apex; and bean leaves increased up to 32 per cent in size.

Austin (1941) exposed several rosette plants of one species to different lengths of photoperiod. At an 8-hour photoperiod all plants remained in the rosette stage. An increasing photoperiod caused an increased number of plants to elongate. The number of internodes did not change.

When orchard grass seedlings were grown under 8- and 16-hour photoperiods, Struckey (1942) discovered that epidermal cell size varied directly with total organ size, indicating leaf length differences were mainly due to cell size and not cell number. Increases in intercellular spaces in the mesophyll probably accounted for some differences in leaf size.

Wylie (1951) found that leaves collected from the south periphery of several deciduous dicotyledonous trees were relatively xeromorphic; leaves from the interior crown were relatively mesomorphic; and leaves from the north periphery were intermediate between the two extremes. Some factors studied were: (1) blade thickness, (2) epidermal thickness, (3) palisade development, and (4) spongy mesophyll development.

According to Ryder (1954), relationship of stomatal number to epidermal cell number is independent of age, position, and habitat of leaves. Frequency of stomates increases from leaf base toward apex and from midrib toward margin. Final leaf shape is determined by: shape of leaf primordium; number, distribution, and orientation of cell divisions; and, amount and distribution of cell enlargement. Each determinant is affected by environment and heredity.

The only study available pertaining entirely to winter rosettes was conducted by Singh (1962). His study consisted of the behavior of prairie forbs during winter months. Winter rosettes were classified as basal, stem, and terminal rosettes. A brief description of the plants and plant habits were included.

CLIMATE AND HABITAT

Most of the winter rosettes studied inhabited hillsides with a slope of 10 to 30 per cent. The soil is relatively shallow, 6 to 12 inches in depth, contains numerous rock fragments, and supports a sparse stand of grasses and a wide variety of forbs. Apparently, on these rocky hillsides forbs compete more successfully with native grasses. Vegetation is dominated by four grasses: (1) big bluestem (*Andropogon gerardi*), (2) little bluestem (*Andropogon scoparius*), (3) side oats grama (*Bouteloua curtipendula*), and (4) hairy grama (*Bouteloua hirsuta*).

Winter months were characterized by an average temperature for December, 1962; below average for January, 1963; and above average for February, 1962 (Table I). Few winter rosettes were evident during the extreme cold temperatures of January. There were only 6 days with sufficient snow depth to provide any protection for winter rosettes. Total precipitation for the 3 winter months was 0.52 of an inch which was 1.12 of an inch below normal for the period.

TABLE I. Summary of some climatic conditions for Hays, Kansas, during winter 1962-63.[1]

	Dec. 1962	Jan. 1963	Feb. 1963
Average max. temp. (deg. F.)	46.0	32.7	52.6
Average min. temp. (deg. F.)	19.9	4.2	18.8
No. days min. temp. 10° F. or lower	7	21	4
Total precipitation (in.)	0.26	0.15	0.11
No. days with 2 in. or more snow on ground. .	0	6	0

[1]Compiled from: U. S. Department of Commerce. 1886- Climatological data, Kansas. Asheville, N. C. 77v.

METHODS

Rosette leaves of 17 forbs were collected from the college pasture, $2\frac{1}{2}$ miles west of Hays, Ellis County, Kansas, during the first 2 weeks in February. Leaves of each species were preserved in a separate bottle containing FAA solution (Johansen, 1940). Two plants of each species studied were placed in pots and transferred to the greenhouse. Stems began elongating in about 2 weeks and were the source of summer leaves used in the anatomical portion of the present study. Efforts were made in the greenhouse to simulate the winter rosettes's natural environment during April, which was accomplished by lengthening the photoperiod 2 hours with artifical lighting and by maintaining a relatively high soil water content similar to soil moisture conditions in the field during April. Greenhouse temperature ranged from 70° F. to 90° F. After summer leaves developed on field plants, a few from each species were collected and used as a check on leaves from plants grown in the greenhouse.

According to Johansen (1940), because of variance in photosynthetic activity, each leaf may require a slightly different technique in obtaining cross-sections. Except for slight alterations when required, Johansen's technique was employed. A rotary microtome was used to cut the tissue about 25 microns thick. The sections were stained in safranin and fast green and mounted in Kleermount.[1] Data were obtained

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[1]Trade name of mounting medium processed by Carolina Biological Supply Company, Elon College, N. C.

by observing several microscopic slides of young and mature leaves of each species. Photomicrographs were taken of slides containing the cross-section best representing the general characteristics of each species.

Collodion peel method was used in making a stomatal count. The leaf was first washed in 80 per cent ethyl alcohol. After removing from the bath and allowing excess alcohol to dry, a thin film of flexible collodion was spread on with a small brush. After drying for 30 minutes, the collodion was peeled off and placed on a slide. Small amounts of Kleermount were applied to the corners of the cover slip. A microscope containing an ocular micrometer was used in making several random counts of each epidermis, and after observing several leaves, an average number of stomates was obtained. Photomicrographs were taken of the slide containing an average number of stomates for that species.

Observations concerning morphological leaf characteristics were recorded from winter rosette leaves and summer leaves of plants grown in the greenhouse and later was checked by observing winter rosette leaves and summer leaves in their natural habitat. The leaf best representing the characteristics of each species was photographed.

A 35 mm. Exakta camera with Tri-X film was used in the photography. A close-up lens attachment was used to photograph entire leaves.

RESULTS AND DISCUSSION

Morphological Comparison

External leaf features and stomatal densities of winter rosette and summer leaves were the morphological characteristics studied.

External leaf features. Differences in characteristics of winter rosette leaves and summer leaves were recorded. Dimension of leaf size will indicate average maximum size. Common names were taken from Anderson (1961). Additional information on leaf description may be obtained from Rydberg (1932), Stevens (1948), or Gates (1934).

Ratibida columnifera Woot. & Standl. (Fig. 1)
(upright prairieconeflower)

Winter rosette leaves generally have two lateral and a terminal lobe; but may have only one lateral and a terminal lobe or just a terminal lobe. Lateral lobes 1 cm. long and 4 mm. wide; terminal lobes 2 cm. long and 5 mm. wide.

Summer leaves have five to seven pairs of lobes; some lobes may be subdivided. Lobes 3 cm. long and 5 mm. wide, smaller at apical and basal stem regions; entire leaf 7 cm. long.

Verbena bipinnatifida Nutt. (Fig. 2)
(Dakota verbena)

Winter rosette leaves 2 cm. long and 1.5 cm. wide; summer leaves 4.5 cm. long and 3.5 cm. wide. Winter rosette leaves contain relatively fewer lateral lobes. No difference in margin was visible.

Figure 1. Winter rosette leaf (left) and summer leaf (right) of upright prairiecone-flower (Ratibida columnifera). Note difference in number of lateral lobes. Each square is a sq. cm.

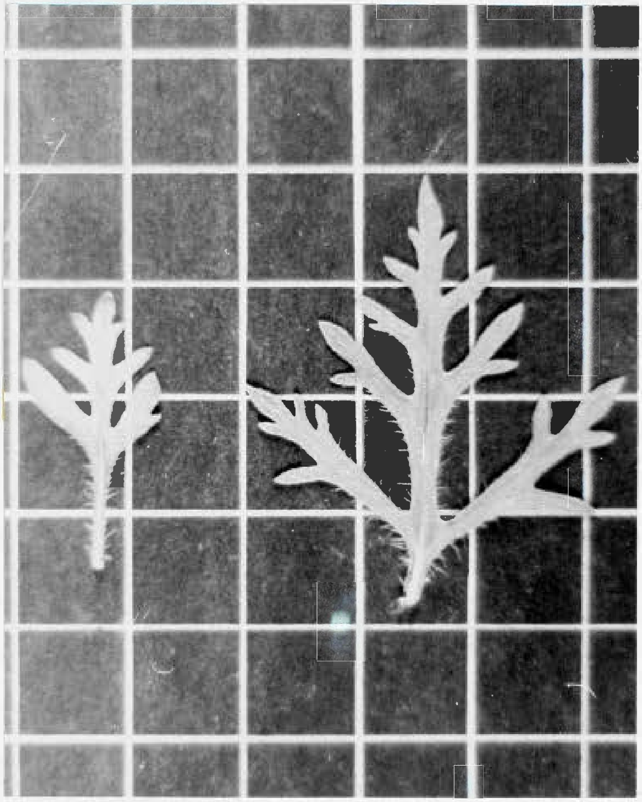

Figure 2. Winter rosette leaf (left) and summer leaf (right) of Dakota verbena (Verbena bipinnatifida). Each square is a sq. cm.

Senecio plattensis Nutt. (Fig. 3)
(Prairie groundsel)

Shape, size, color, and margins of winter rosette leaves vary. Margins may be dentate or entire; sizes range from 1.5 to 6 cm. long and 1 to 2 cm. wide; abaxial sides usually deep purple; leaf shape may be orbicular, elliptic, or lyrate pinnatifid.

Summer leaves 2 to 10 cm. long and 6 to 30 mm. wide; upper leaves lanceolate in outline and pinnately divided; lower ones lyrate pinnatifid; margins dentate; no purple visible.

Oenothera serrulata Nutt. (Fig. 4)
(serrateleaf eveningprimrose)

Winter rosette leaves oval to elliptic, 4 mm. long and 2 mm. wide; splotches of reddish-purple may be visible; margins entire or minutely serrate.

Summer leaves linear-oblanceolate, 3.5 cm. long and 5 mm. wide, dentate margins, with no reddish-purple visible.

Stenosiphon linifolius (Nutt.) Britt. (Fig. 5)
(Stenosiphon)

Winter rosette leaves linear-oblanceolate to oblanceolate, 1.5 to 3 cm. long and 3 to 8 mm. wide; margins and midribs may be purple.

Summer leaves linear to linear-oblanceolate, 3 cm. long and 2 mm. wide; no evidence of purple. Margins were similar on each type of leaf.

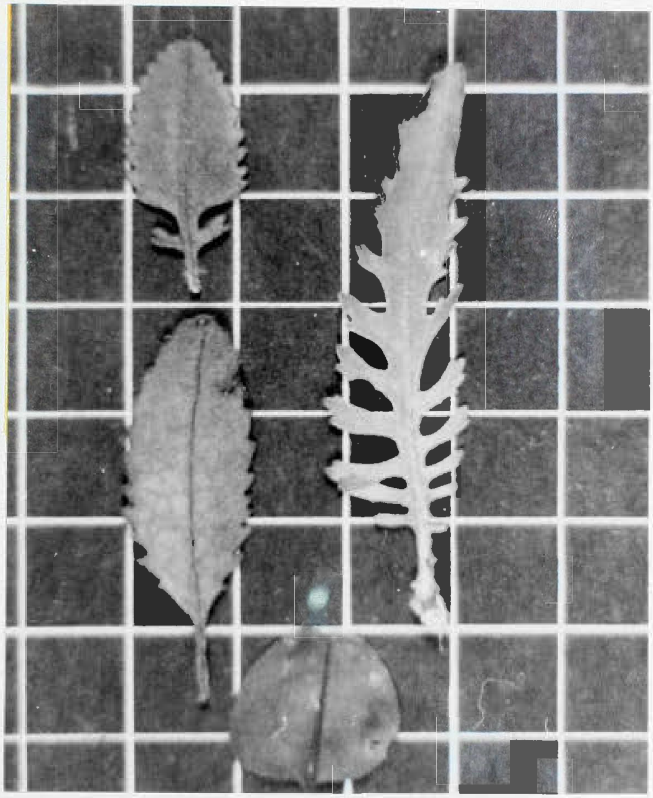

Figure 3. Winter rosette leaves (three on left) and summer leaf (right) of prairie groundsel (Senecio plattensis). Note variations of winter rosette leaves. Each square is a sq. cm.

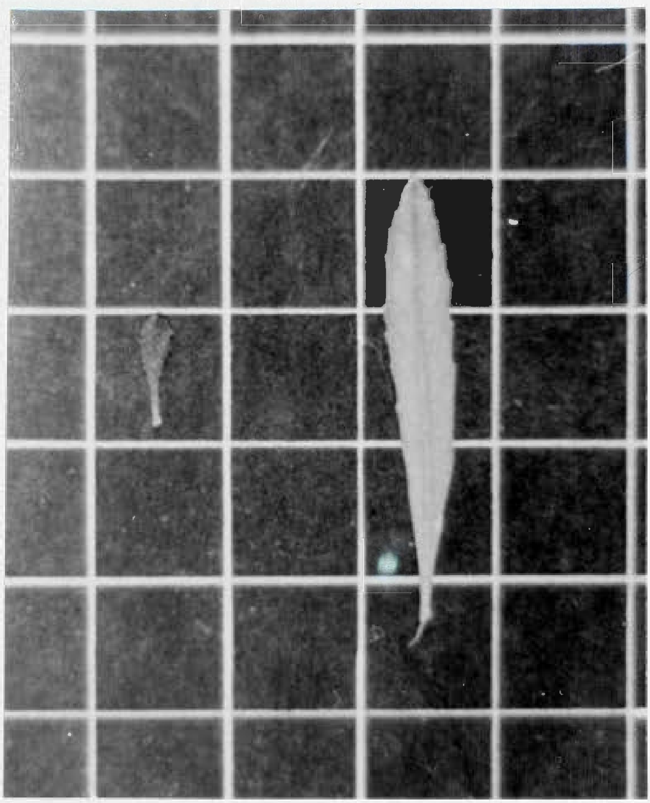

Figure 4. Winter rosette leaf (left) and summer leaf (right) of serrateleaf eveningprimrose (*Oenothera serrulata*). Note darkness of rosette leaf caused by purple coloration. Each square is a sq. cm.

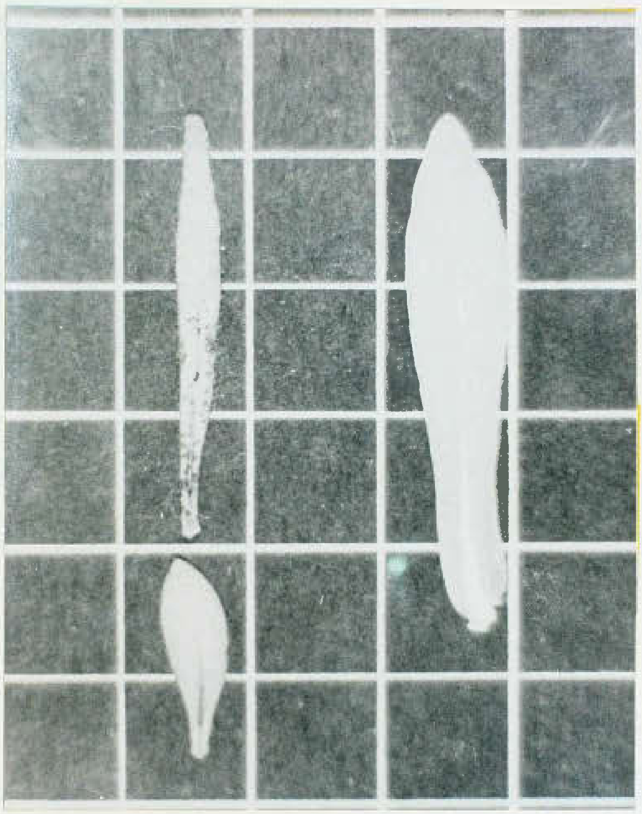

Figure 5. Winter rosette leaves (left) and summer leaf (right) of stensiphon (Stenosiphon linifolius). Note differences in winter rosette leaves. Each square is a sq. cm.

Oenothera lavandulaefolia T. & G. (Fig. 6)
(lavenderleaf eveningprimrose)

Winter rosette leaves linear-oblanceolate, 6 to 9 mm. long and 2 mm. wide, with purple tips.

Summer leaves linear, 3 cm. long and 2 mm. wide; no evidence of purple. Margins did not differ.

Cirsium undulatum (Nutt.) Spreng. (Fig. 7)
(wavyleaf thistle)

Winter rosette leaves 4 cm. long and 2 cm. wide; summer leaves 15 cm. long and 5 cm. wide. No difference in shape or margin was visible.

Paronychia jamesii T. & G.
(james nailwort)

Winter rosette leaves 1 cm. long and 0.5 mm. wide; summer leaves 4 cm. long and 1 mm. wide. Shape and margin are similar for the two types of leaves.

Tetraneuris stenophylla Rydb. (Fig. 9)
(stemless tetraneuris)

Winter rosette leaves linear-elliptical, 1 cm. long and 2 mm. wide, sometimes having a purple-tinged tip.

Summer leaves narrowly linear, 5 cm. long and 1.5 mm. wide; no purple visible. No difference in margin was visible.

Aster fendleri A. Gray (Fig. 10)
(fendler aster)

Winter rosette leaves 1.5 cm. long and 1.5 mm. wide; summer leaves 5 cm. long and 2 mm. wide. No difference in shape or margin was visible.

Figure 6. Winter rosette leaf (right) and summer leaf (left) of lavenderleaf eveningprimrose (Oenothera lavandulaefolia). Each square is a sq. cm.

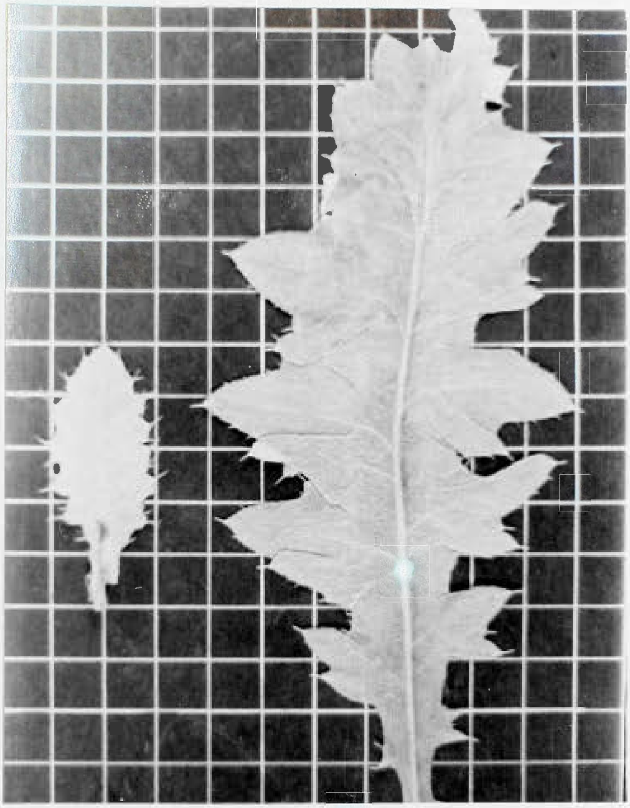

Figure 7. Winter rosette leaf (left) and summer leaf (right) of wavyleaf thistle (*Cirsium undulatum*). Each square is a sq. cm.

Figure 8. Winter rosette leaf (left) and summer leaf (right) of james nailwort (<u>Paronychia jamesii</u>). Each square is a sq. cm.

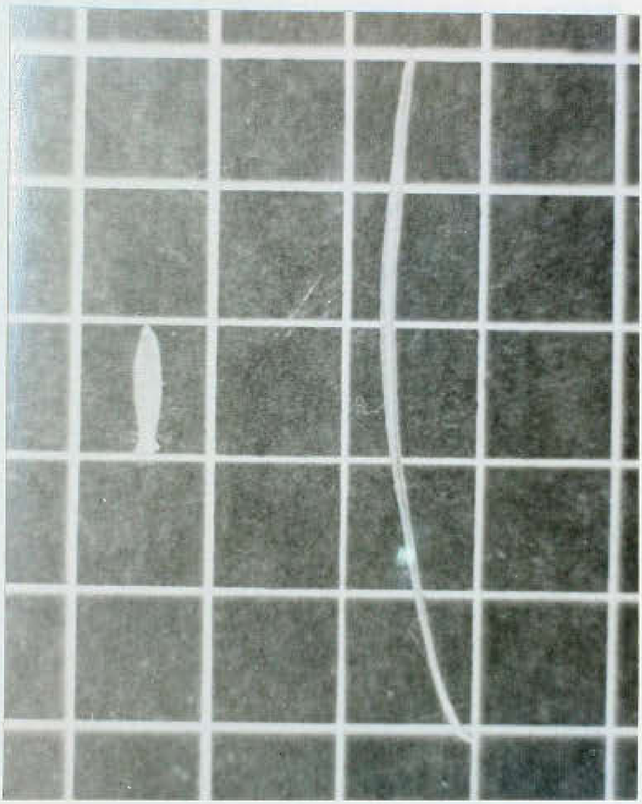

Figure 9. Winter rosette leaf (left) and summer leaf (right) of stemless tetraneuris (Tetraneuris stenophylla). Each square is a sq. cm.

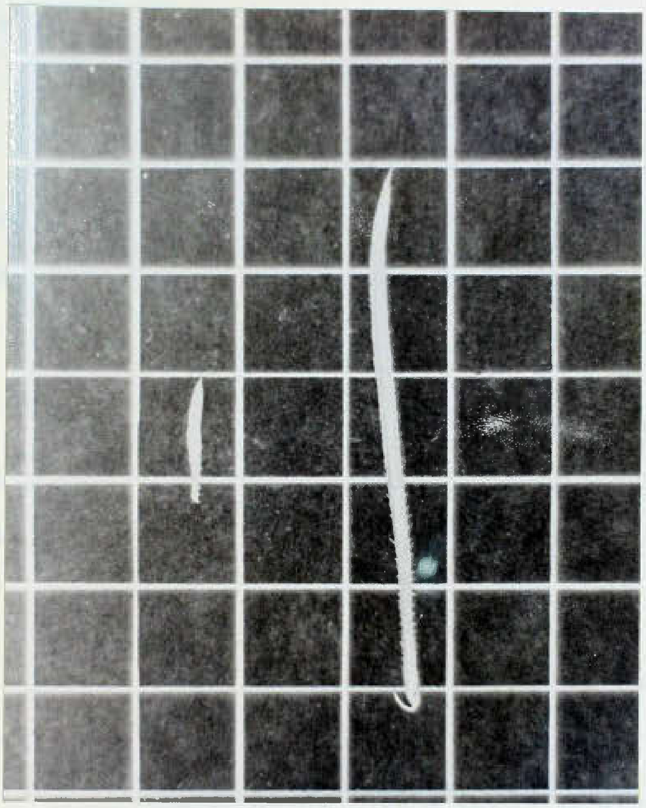

Figure 10. Winter rosette leaf (left) and summer leaf (right) of fendler aster (Aster fendleri). Each square is a sq. cm.

Hymenopappus corymbosus T. & G. (Fig. 11)
(hymenopappus)

Winter rosette leaves 2.5 cm. long and 1.5 cm. wide; summer leaves 6 cm. long and 4.5 cm. wide. No difference in shape or margin was visible.

Linum rigidum Pursh (Fig. 12)
(stiffstem flax)

Winter rosette leaves 1 cm. long and 1 mm. wide; summer leaves 2.5 cm. long and 2 mm. wide. No difference in shape or margin was visible.

Gutierrezia sarothrae (Pursh) Britt. & Rusby
(broom snakeweed)

Winter rosette leaves 3 mm. long and 1 mm. wide; summer leaves 2.5 cm. long and 2 mm. wide. No difference in shape or margin was visible.

Scutellaria resinosa Torr.
(resinous skullcap)

Winter rosette leaves 5 mm. long, 3 mm. wide, and usually purple tinged.

Summer leaves 1.5 cm. long, 1 cm. wide, and no purple coloring visible. No difference in shape or margin was visible.

Lesquerella ovalifolia Rydg.
(ovalleaf bladderpod)

Winter rosette leaves 1 cm. long and 8 mm. wide; summer leaves 1.8 cm. long and 1 cm. wide. No difference in shape or margin was visible.

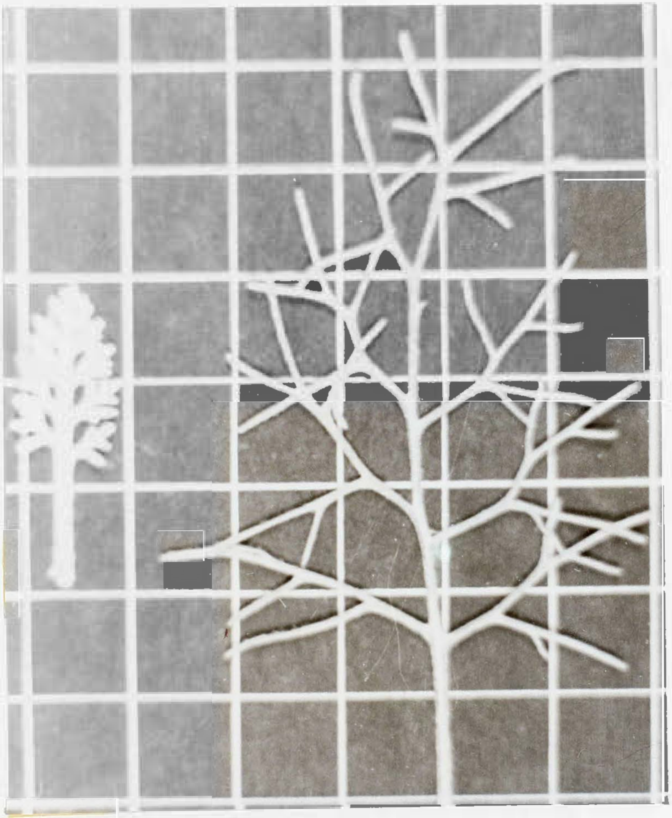

Figure 11. Winter rosette leaf (left) and summer leaf (right) of hymenopappus (Hymenopappus corymbosus). Note rosette leaf has as many lateral divisions as summer leaf, but reduced in length and width. Each square is a sq. cm.

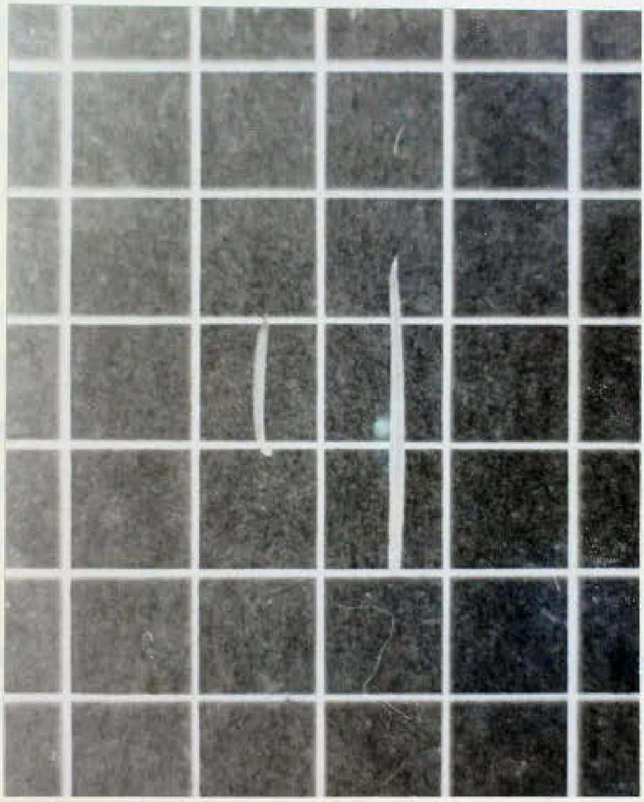

Figure 12. Winter rosette leaf (left) and summer leaf (right) of stiffstem flax (Linum rigidum). Each square is a sq. cm.

<u>Arenaria</u> <u>texana</u> Britt.
(Texas sandwort)

Winter rosette leaves 5 mm. long; summer leaves 1 cm. long. No difference in shape or margin was visible.

<u>Callirrhoe</u> <u>involucrata</u> (T. & G.) A. Gray
(purple poppymallow)

Winter rosette leaves have a rounded leaf outline, 2 cm. in diameter, compared to summer leaves 5 cm. in diameter. No difference in shape or margin was visible.

Discussion of external leaf features

Leaves originate as protrusions near the apical meristem. A protrusion, resulting from rapid divisions of the outer four of five layers of cells, is called a leaf buttress. The leaf buttress lengthens by apical and intercalary growth, forming the leaf axis. Marginal meristems, two rows of meristematic cells located along the margins of the leaf axis, form the lamina. A petiole, if present, does not contain marginal meristems (Esau, 1953). Lateral lobes develop from primodia arising from the main leaf axis (Eames and MacDaniels, 1947).

Final leaf form is regulated by: (1) shape of leaf primordia, (2) differential distribution of growth in different areas, including differential cell division and differential cell enlargement, and (3) greater growth in one dimension than in another (Avery, 1933). Growth characteristics are regulated by heredity and are influenced by environmental conditions, such as, water, minerals, intensity of light, photoperiod, and temperature (Esau, 1953). Environmental conditions fluctuate widely from summer to winter; hence, different growth characteristics result in different leaf sizes and shapes.

Differences in external leaf form of winter rosette and summer leaves are quite obvious. The first three species, upright prairie-coneflower, Dakota verbena, and Prairie groundsel, show differences in both size and shape. Variations in the number of lateral lobes is the main difference in leaf shape. Apparently, the number of lateral primordia originating on the main leaf axis is reduced in winter rosette leaves, perhaps resulting from a short primary axis laid down by the apical leaf meristem or because few lateral primordia develop.

The remainder of the species contain winter rosette leaves differing from summer leaves in size, but shape is relatively constant. Two possible components causing variation in sizes are reduction of cell division and reduction of cell elongation. Of the five environmental conditions mentioned above (water, minerals, intensity of light, photoperiod, and temperature) all directly or indirectly influence cell division and elongation. Photoperiod and temperature are the main factors controlling synthesis of auxin and other growth affecting substances which influence rate of cell division and elongation (Meyer, _et al._, 1960). Although further investigations are necessary before conclusions can be formed, photoperiod seems to be a major factor in regulating leaf size.

A marked variation in the color of winter rosette and summer leaves, and even among winter rosette leaves of the same species, was observed. The purple coloration, due to a build-up of anthocyanin pigment, visible in many winter rosette leaves, was not evident in most summer leaves. Interactions of many factors determine if anthocyanins are visible. Generally, any environmental factor, such as low temperature or drought, favoring accumulation of sugars in leaves also accommodates anthocyanin synthesis (Meyer, et al., 1960).

Some winter rosette leaves studied appear to possess a slightly higher density of trichomes. If size of epidermal cells of winter rosette leaves is reduced compared to summer leaves, density of trichomes would be higher on winter rosette leaves.

Variations in leaf margins were observed only for prairie groundsel and serrateleaf eveningprimrose. Since plant hormones affect development of leaf margins (Gray, 1957), environmental conditions are probably indirectly responsible for variation of leaf margins.

Stomatal comparison. Comparisons were made between stomatal density of winter rosette leaves and stomatal density of summer leaves. About 0.4 sq. mm. of surface area is represented in each photomicrograph.

Winter rosette leaves of stenosiphon and fendler aster differed from their summer leaves mainly in size (Figs. 5 and 10). Results of the stomatal count (Table II) corresponded to Struckey's (1942) results. She concluded the final leaf size is dependent on size of epidermal

TABLE II. Number of stomates per sq. cm. occurring on adaxial and abaxial epidermis of winter rosette and summer leaves of three prairie forbs.

	EPIDERMIS			
	Adaxial		Abaxial	
	Rosette leaf	Summer leaf	Rosette leaf	Summer leaf
Stenosiphon (Stenosiphon linifolius)	25,000	17,000	40,000	26,000
Prairie groundsel (Sencio plattensis)	8,000	13,000	10,000	17,000
Fendler aster (Aster fendleri)	20,000	15,000	15,000	9,000

cells. If winter rosette leaves contain relatively smaller epidermal cells, more stomates per unit area will be present compared to summer leaves (Figs. 13, 14, 15, and 16).

Prairie groundsel winter rosette leaves differed from summer leaves in size and shape (Fig. 3). Results of stomatal count indicated a relatively higher density on summer leaves, contradicting the stomatal comparison of stenosiphon and fendler aster. Prairie groundsel forms basal winter rosette leaves; summer leaves are formed 4 to 10 inches above ground. Increases in stomatal density with increased height above ground (Ryder, 1954) may be a possible explanation for relatively higher stomatal density on summer leaves.

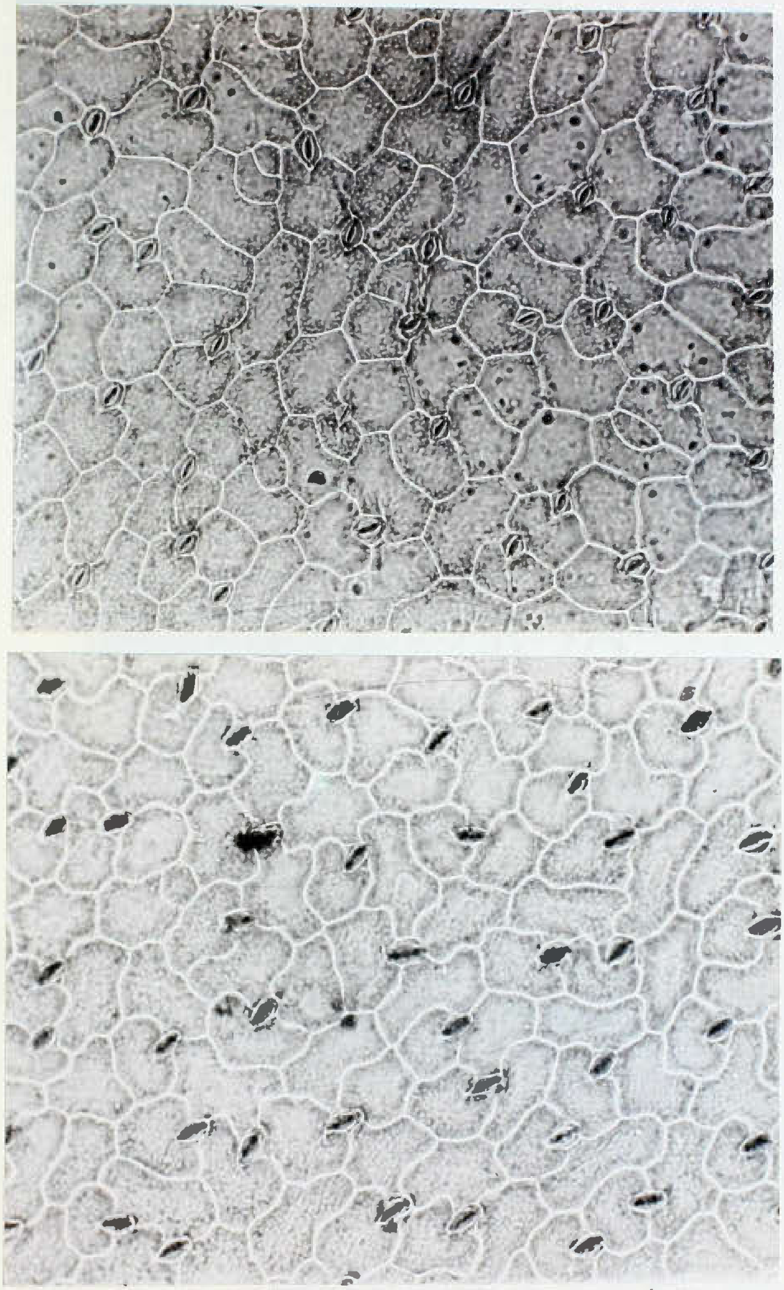

Figure 13. Adaxial epidermis of stenosiphon (Stenosiphon linifolius) winter rosette leaf (above) and adaxial epidermis of stenosiphon summer leaf (below). Note slightly smaller epidermal cells and higher density of stomates on rosette leaf. (X250)

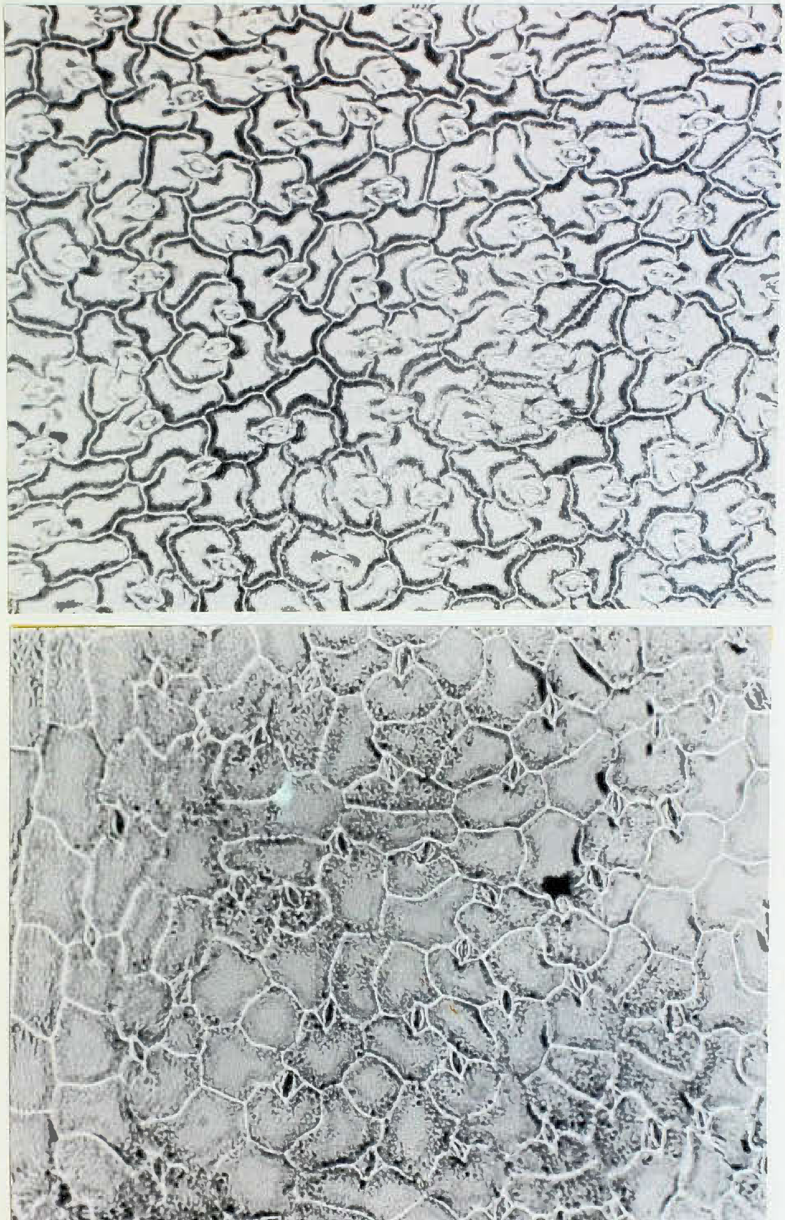

Figure 14. Abaxial epidermis of stenosiphon (Stenosiphon linifolius) winter rosette leave (above) and abaxial epidermis of stenosiphon summer leaf (below). Epidermal cells on the left of bottom photograph are directly below midvein. Note smaller epidermal cells and higher stomatal density on rosette leaf. (X250)

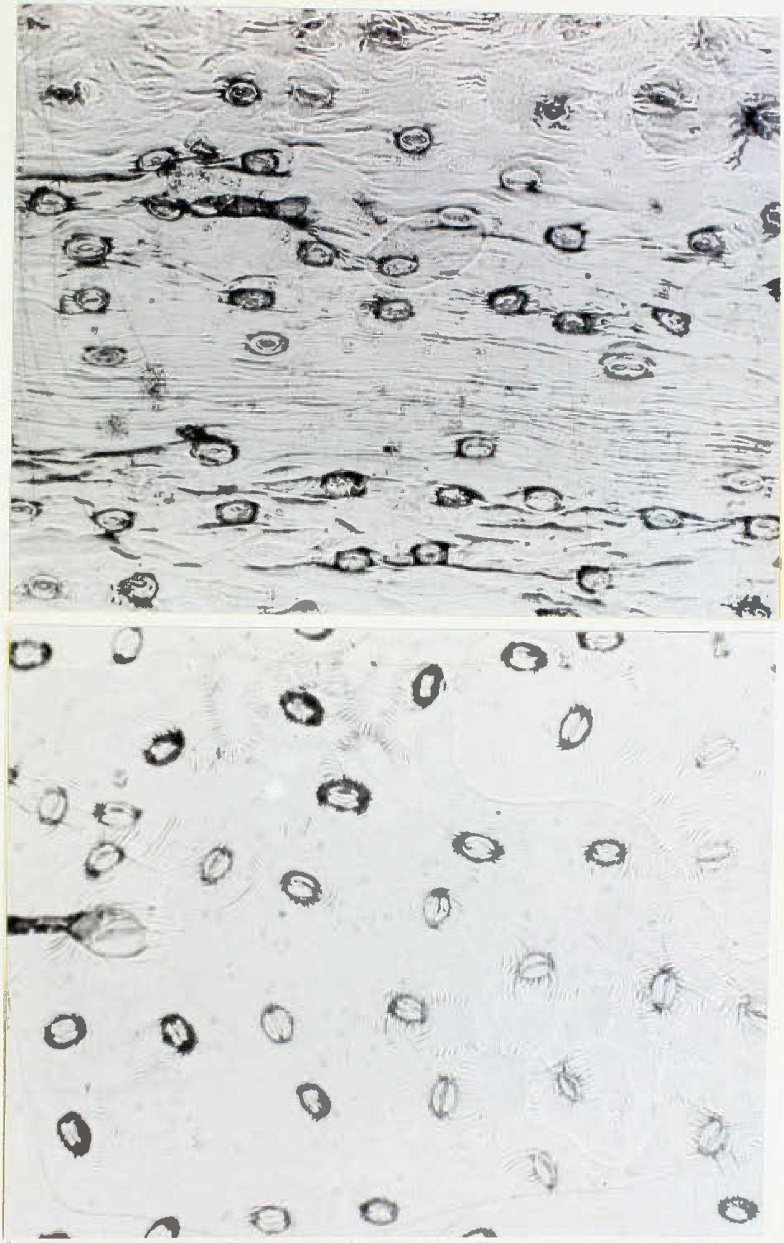

Figure 15. Adaxial epidermis of fendler aster (*Aster fendleri*) winter rosette leaf (above) and adaxial epidermis of fendler aster summer leaf (below). Note higher stomatal density on rosette leaf. (X250)

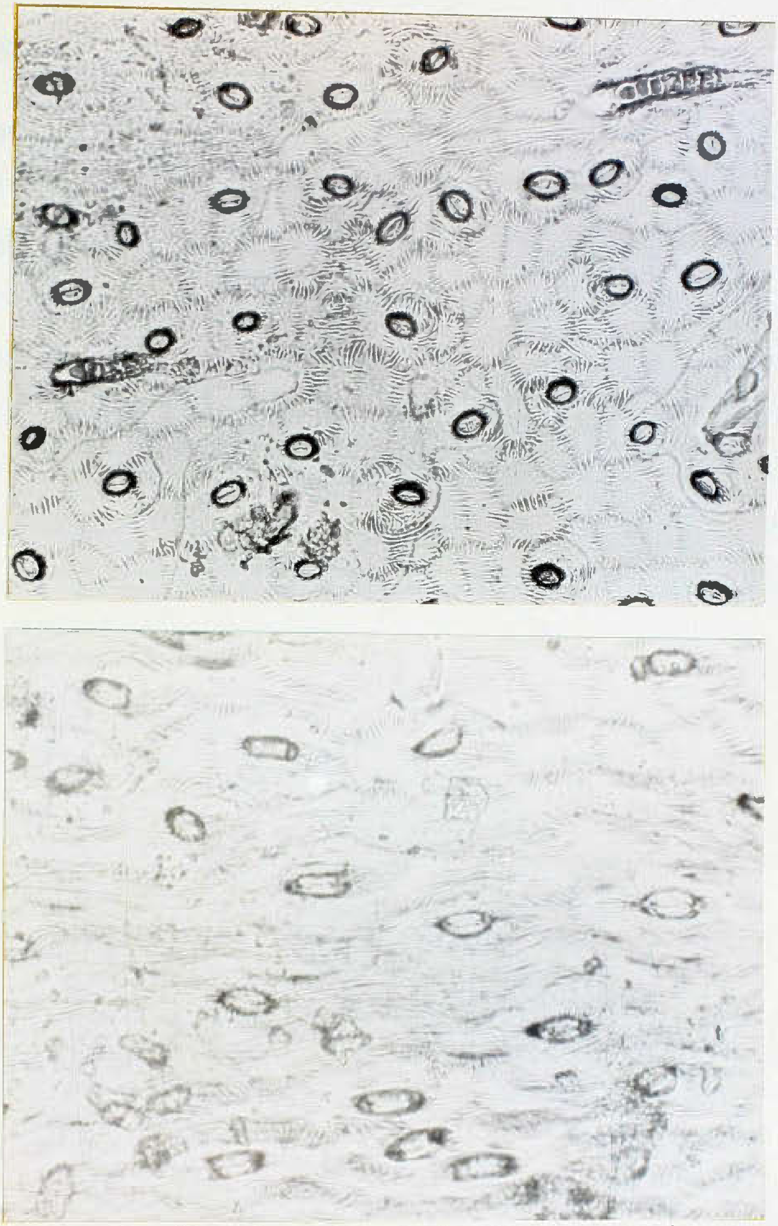

Figure 16. Abaxial epidermis of fendler aster (*Aster fendleri*) winter rosette leaf (above) and abaxial epidermis of fendler aster summer leaf (below). Note higher stomatal density on rosette leaf and relatively elongated stomates on summer leaf. (X250)

Anatomical Comparison

Differentiation of mesophyll arises from unequal growth in various leaf layers. Division of adaxial palisade cells, occurring at right angles to the surface, continues relatively longer than divisions of adaxial epidermal cells. Enlargement of adaxial epidermal cells continues after palisade cell division and enlargement ceases, resulting in palisade intercellular spaces. Spongy mesophyll is formed by tangential enlargement of spongy parenchyma accompanied by enlargement of the abaxial epidermis, thereby, forming large intercellular spaces. Epidermal hairs, stomates, and large veins differentiate ahead of the mesophyll (Esau, 1953).

Four mesophytic and six xerophytic species were studied. Xeromorphic leaves were characterized by containing some of the following: (1) inrolled margins, (2) abaxial and adaxial palisade parenchyma, (4) thickened leaves with dorsiventral development of water storage tissue, (5) relatively smaller surface-volume ratio, (6) relatively thicker epidermis, and (7) reduced amount of spongy mesophyll (Shields, 1950 and 1951).

Since the amount of literature pertaining to anatomy of prairie forbs is limited, some major anatomical characteristics of summer leaves and deviations of winter rosette leaves from summer leaves are included. Young leaves, as well as mature leaves, were used in the comparison. Little discriminatory differences were observed between young winter rosette leaves and young summer leaves; therefore, results will refer to mature leaves.

The sketch above each photomicrograph refers to relationship of photomicrograph to total cross-section.

Stenosiphon. Midvein surrounded by a bundle-sheath and a bundle-sheath extension, composed of chlorophyll-lacking parenchyma cells, extending to each epidermis; adaxial and abaxial epidermis directly above and below midvein is multiseriated (Fig. 17). By observing young leaves, the second epidermal layer appears to originate from the protoderm, distinguishing it from a hypodermis (Esau, 1953). Upper and lower mesophyll equally differentiated into palisade parenchyma, length to width ratio of 5:1. Between the two layers of palisade parenchyma are one to three layers of compactly arranged spongy parenchyma. Druses, probably composed of united calcium oxalate crystals (Esau, 1953), present around the midvein.

Winter rosette leaves contain relatively shorter palisade parenchyma, having a 2:1 length to width ratio (Fig. 18). Spongy parenchyma, located in the median portion of the leaf, is not clearly distinguishable.

Ovalleaf bladderpod. Two layers of adaxial palisade parenchyma, length to width ratio of 3:1, are clearly distinguishable from the spongy parenchyma (Fig. 19).

Winter rosette leaves usually contain only one layer of adaxial palisade parenchyma, 2:1 length to width ratio; spongy parenchyma relatively more compactly arranged (Fig. 20).

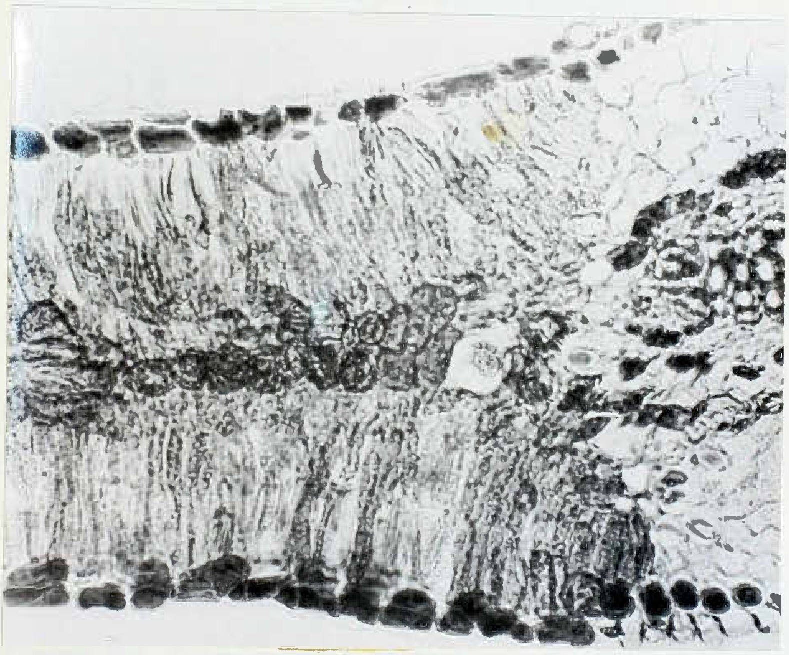

Figure 17. Cross-section of stenosiphon (Stenosiphon linifolius) summer leaf. Note elongated palisade parenchyma and multiseriate epidermis protecting vascular tissue. (X250)

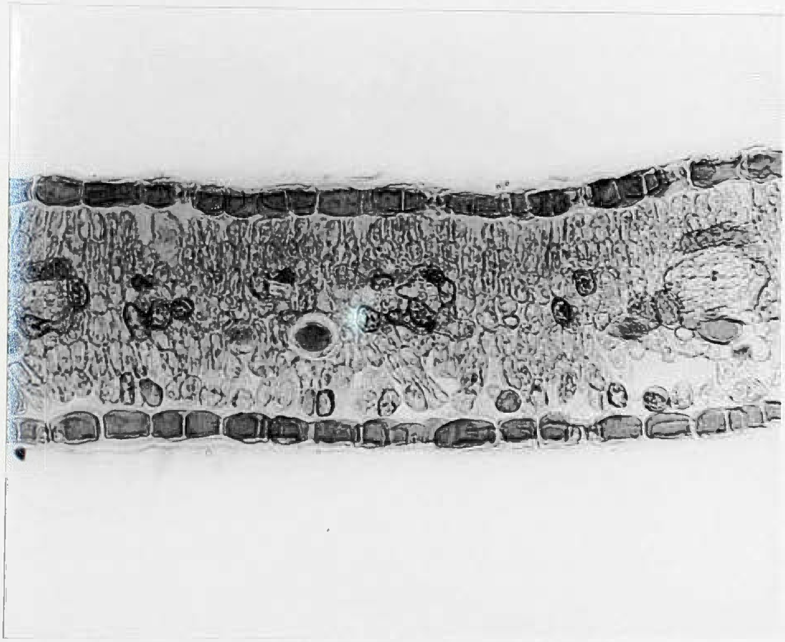

Figure 18. Cross-section of stenosiphon (Stenosiphon linifolius) winter rosette leaf. Note short palisade parenchyma. (X250)

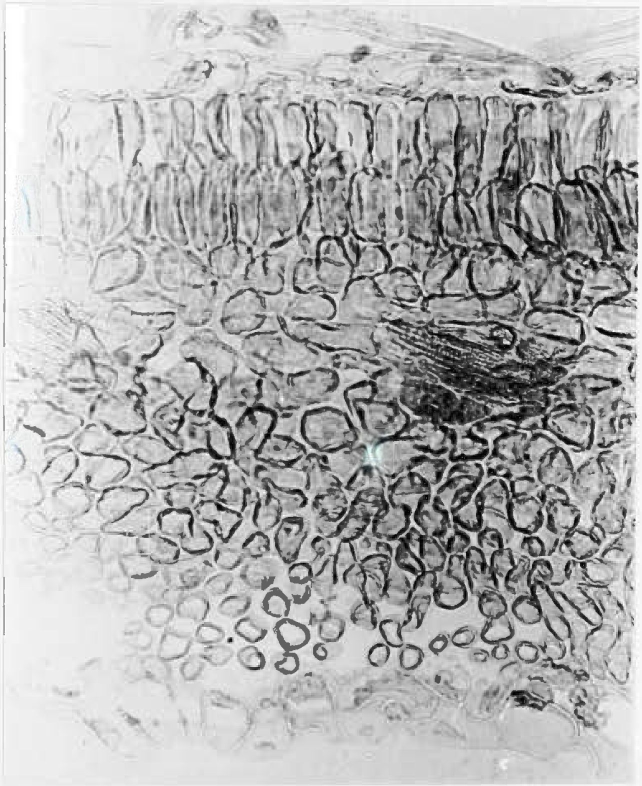

Figure 19. Cross-section of ovalleaf bladderpod (Lesquerella ovalifolia) summer leaf. Note two distinct layers of adaxial palisade parenchyma. (X250)

Figure 20. Cross-section of ovalleaf bladderpod (Lesquerella ovalifolia) winter rosette leaf. Note relatively undifferentiated mesophyll and stellate trichome. (X250)

Prairie groundsel. Adaxial palisade parenchyma layer has a length to width ratio of 4:1; sometimes two adaxial palisade parenchyma layers are present with second layer having 2:1 length to width ratio; remainder of mesophyll differentiated into spongy parenchyma (Fig. 21).

Only the adaxial layer of cells is differentiated into palisade parenchyma, 3:1 length to width ratio, in winter rosette leaves (Fig. 22).

Dakota verbena. Two adaxial layers of palisade parenchyma have 4:1 length to width ratio; remainder of mesophyll differentiated into spongy parenchyma (Fig. 23).

Winter rosette leaves comprised of only one layer of palisade parenchyma, 2:1 length to width ratio; remainder of mesophyll differentiated into spongy parenchyma (Fig. 24).

Broom snakeweed. Inner periphery of leaf lined with two to five layers of small, compactly arranged, palisade parenchyma (Fig. 25), which is interrupted above and below the midvein by a bundle-sheath extension. Large parenchyma cells, acting as water storage, supporting, and conducting tissue (Esau, 1953), run laterally between the two layers of palisade tissue and contain four lateral veins and two to four resin ducts; sometimes a resin duct is located above the midvein.

Cross-section length of winter rosette leaves is about one-half of the cross-section length of summer leaves (Fig. 26). Only three

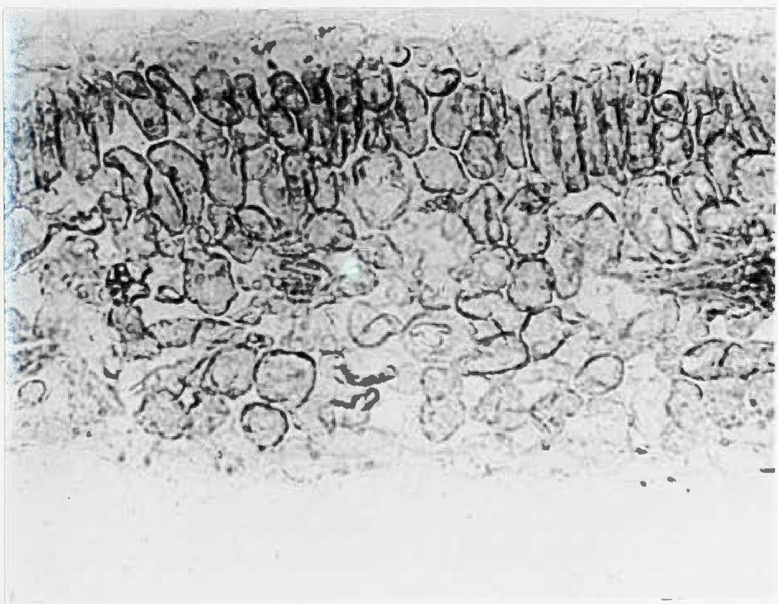

Figure 21. Cross-section of prairie groundsel (Senecio plattensis) summer leaf. Note large amount of spongy parenchyma which is characteristic of mesomorphic leaves. (X250)

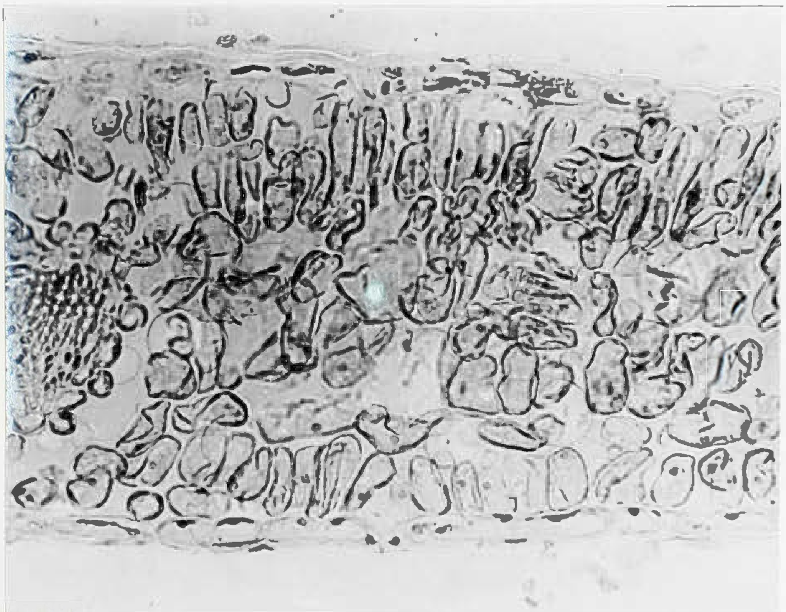

Figure 22. Cross-section of prairie groundsel (Senecio plattensis) winter rosette leaf. Note large amount of spongy parenchyma which is characteristic of mesomorphic leaves. (X250)

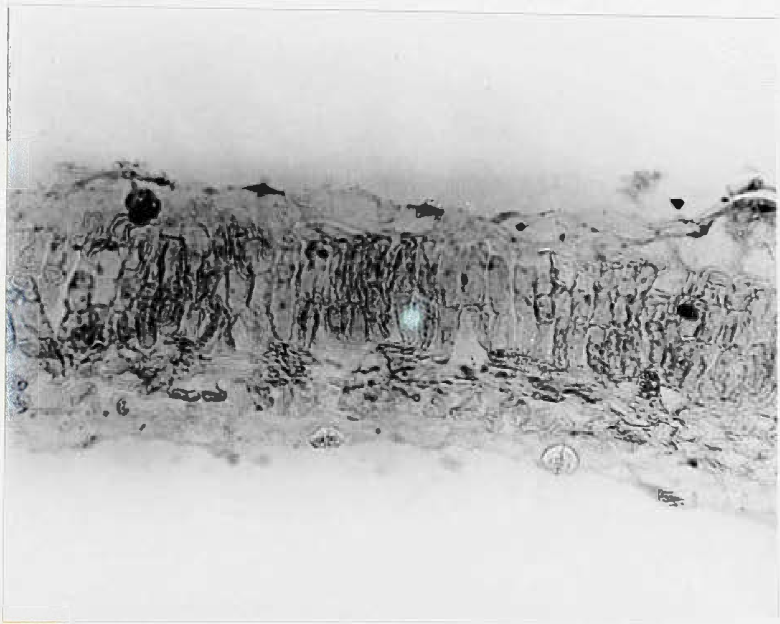

Figure 23. Cross-section of Dakota verbena (Verbena bipinnatifida) summer leaf. Note two stomates on abaxial epidermis and well developed palisade tissue. (X250)

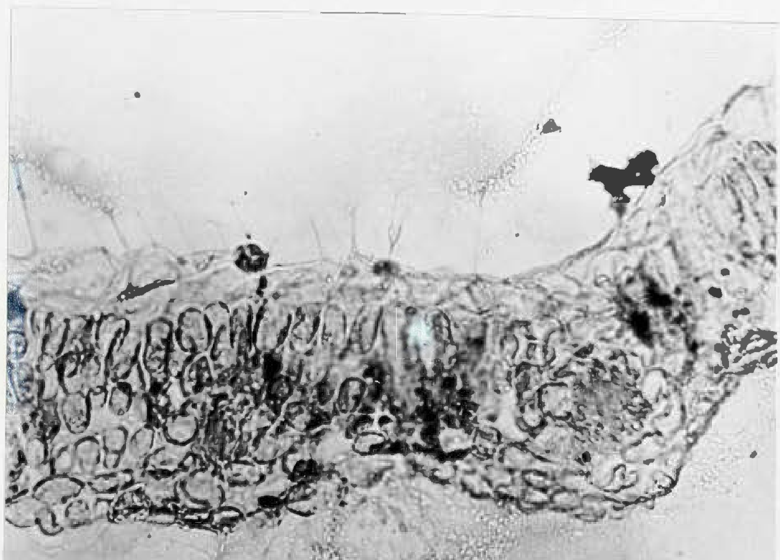

Figure 24. Cross-section of Dakota verbena (Verbena bipinnatifida) winter rosette leaf. Note relatively undifferentiated tissue. (X250)

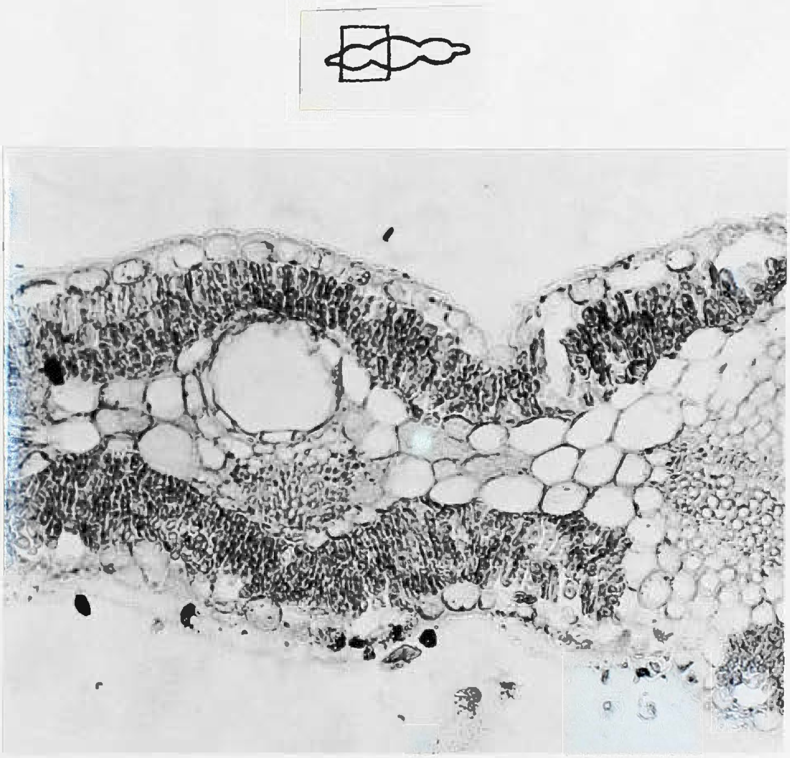

Figure 25. Cross-section of broom snakeweed (Gutierrezia sarothrae) summer **leaf.** Note resin duct and relatively large amount of water-storing parenchyma cells. (X250)

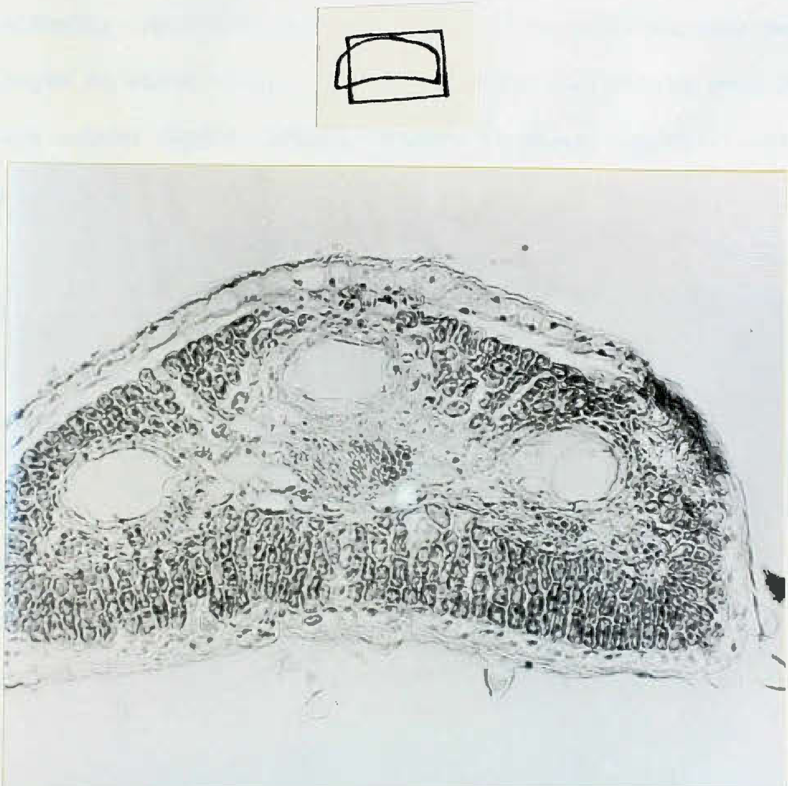

Figure 26. Cross-section of broom snakeweed (Gutierrezia sarothrae) winter rosette leaf. Note small amount of water-storing parenchyma cells and nearly isodiametric palisade parenchyma. (X250)

resin ducts present; palisade parenchyma, forming a continuous circle, is composed of small, nearly isodiametric cells; no bundle-sheath extension present.

Fendler aster. A wide bundle-sheath connects each epidermis with midvein; mesophyll differentiated into small palisade parenchyma; 2:1 length to width ratio. Epidermal cells constitute over 20 per cent of blade volume (Wylie, 1943). Figure 27 shows the close association of epidermis with midvein.

Winter rosette leaves contain nearly isodiametric, compactly arranged, palisade parenchyma (Fig. 28). Cross-sections of winter rosette leaves are wider than cross-section of summer leaves.

Hymenopappus. Two to three layers of palisade parenchyma on adaxial side, length to width ratio 4:1; spongy parenchyma located on abaxial side; large parenchyma cells form a rib on abaxial side of midvein (Fig. 29). Usually three indentations present in adaxial epidermis which allows blade to roll and unroll without damaging internal tissue.

In winter rosette leaves one layer of palisade parenchyma, 3:1 length to width ratio, and sometimes a second layer, 2:1 length to width ratio, differentiates on adaxial side (Fig. 30).

James nailwort. Two to three layers of adaxial and abaxial palisade parenchyma present, 5:1 and 3:1 length to width ratio, respectively (Fig. 31). Large parenchyma cells link two lateral

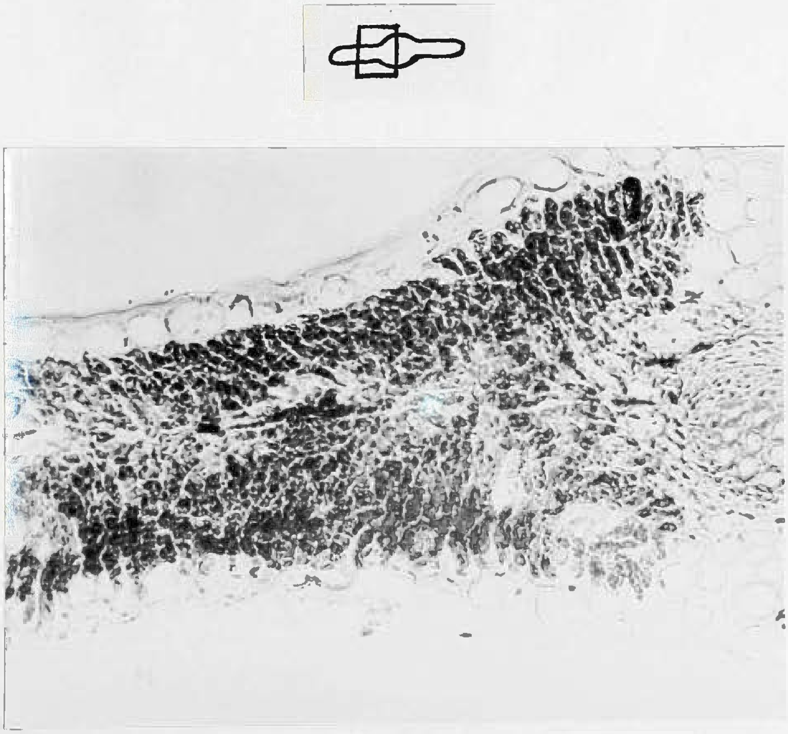

Figure 27. Cross-section of fendler aster (<u>Aster fendleri</u>) summer leaf. Note possible pathway for water: from vein, through bundle-sheath extension, into epidermis, and out to the photosynthetic palisade tissue. (X250)

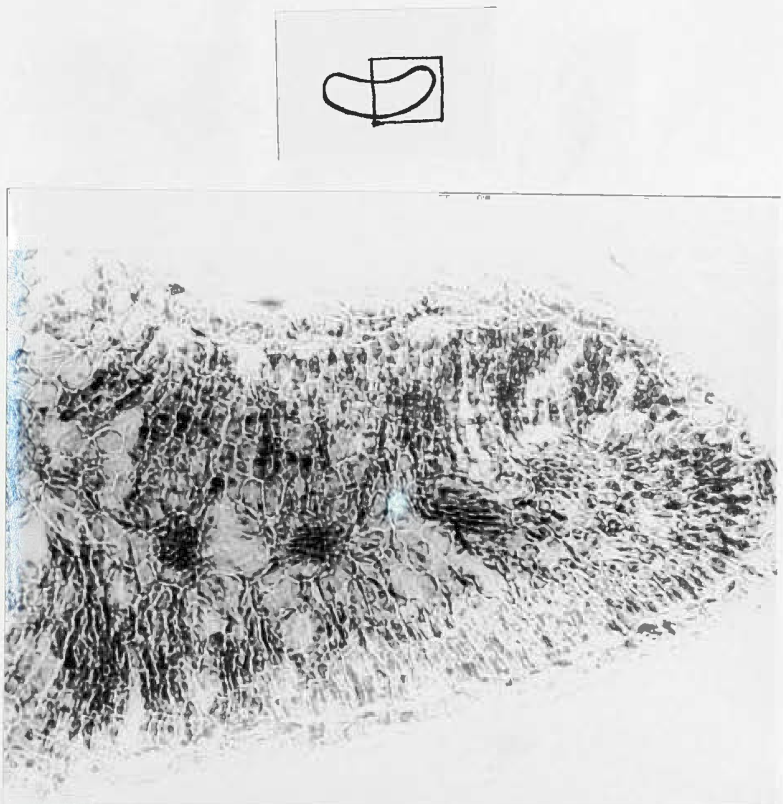

Figure 28. Cross-section of fendler aster (*Aster fendleri*) winter rosette leaf. Note compactly arranged mesophyll. (X250)

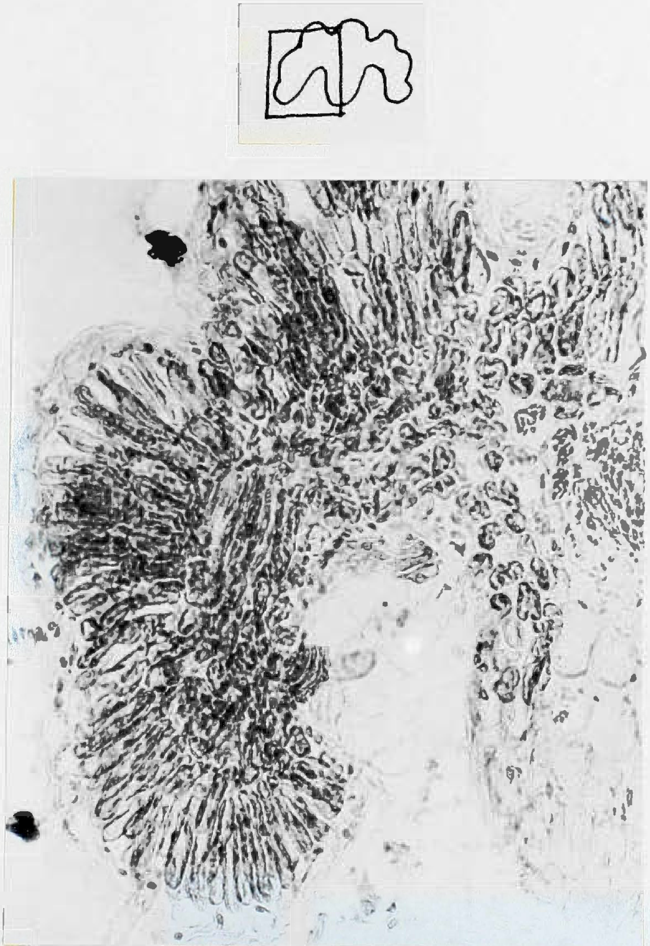

Figure 29. Cross-section of hymenopappus (Hymenopappus corymbosus) summer leaf. Note three indentations adaxial epidermis. (X250)

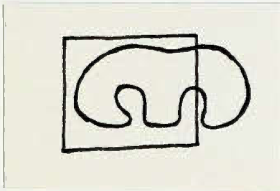

Figure 30. Cross-section of hymenopappus (Hymenopappus corymbosus) winter rosette leaf. Note inrolled margins of leaf. (X250)

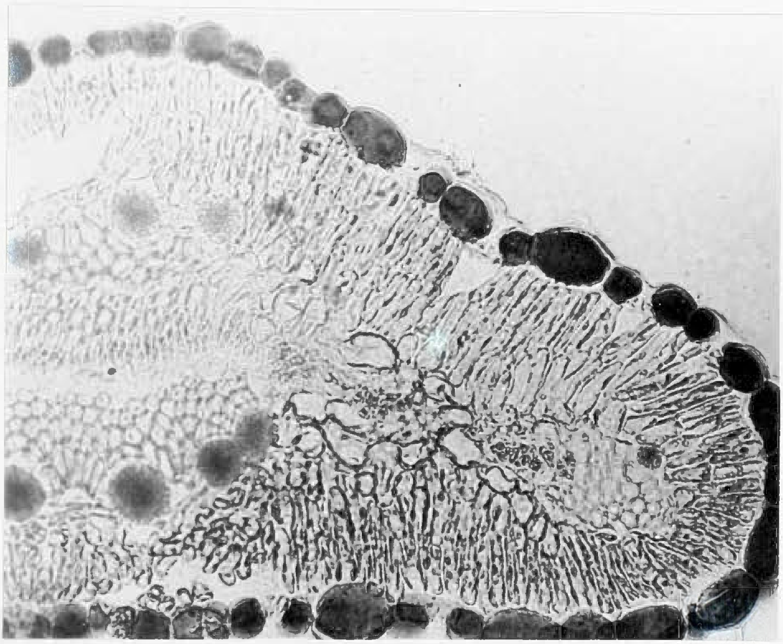

Figure 31. Cross-section of james nailwort (Paronychia jamesii) summer leaf. Note druses surrounding midvein. (X250)

veins with midvein. Epidermal cells relatively thick; many druses located around periphery of midvein and lateral veins.

In winter rosette leaves palisade parenchyma 2:1 length to width ratio; veins and druses relatively smaller (Fig. 32).

Texas sandwort. Midvein and two lateral veins comprise over two-thirds of total leaf volume; many druses located around periphery of midvein (Fig. 33). Mesophyll differentiated into small palisade parenchyma, 2:1 length to width ratio.

Palisade parenchyma of winter rosette leaves differentiated slightly less than 2:1 length to width ratio; veins relatively smaller (Fig. 34).

Resinous skullcap. Mesophyll comprised of relatively small, compactly arranged, palisade parenchyma with a 2:1 length to width ratio; abaxial cells have slightly smaller ratio; midvein and two minor veins contain ribs, composed of chlorophyll-lacking parenchyma and maybe come collenchyma cells on its abaxial side (Fig. 35).

Winter rosette leaves have relatively shorter palisade parenchyma cells and smaller ribs (Fig. 36).

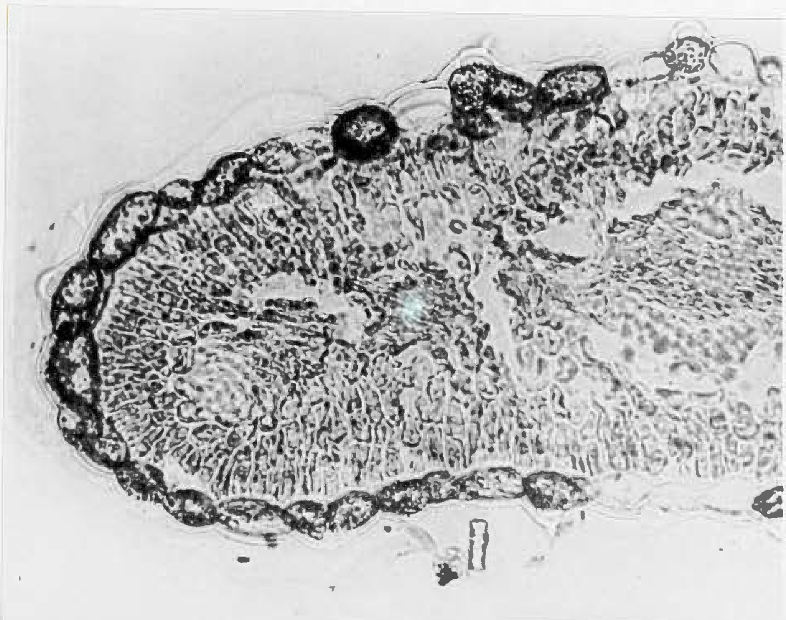

Figure 32. Cross-section of james nailwort (*Paronychia jamesii*) winter rosette leaf. (X250)

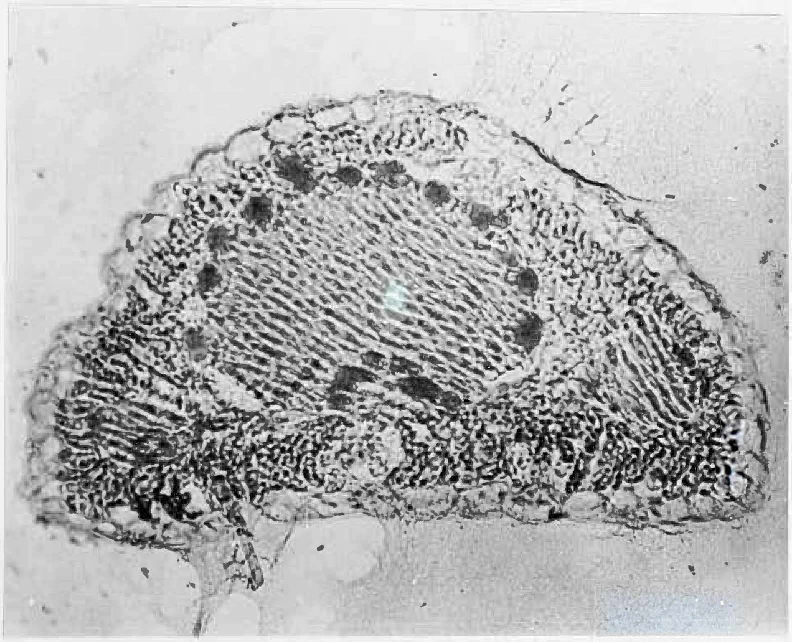

Figure 33. Cross-section of Texas sandwort (Arenaria texana) summer leaf. Note druses surrounding midvein and relatively large volume of vascular tissue. (X250)

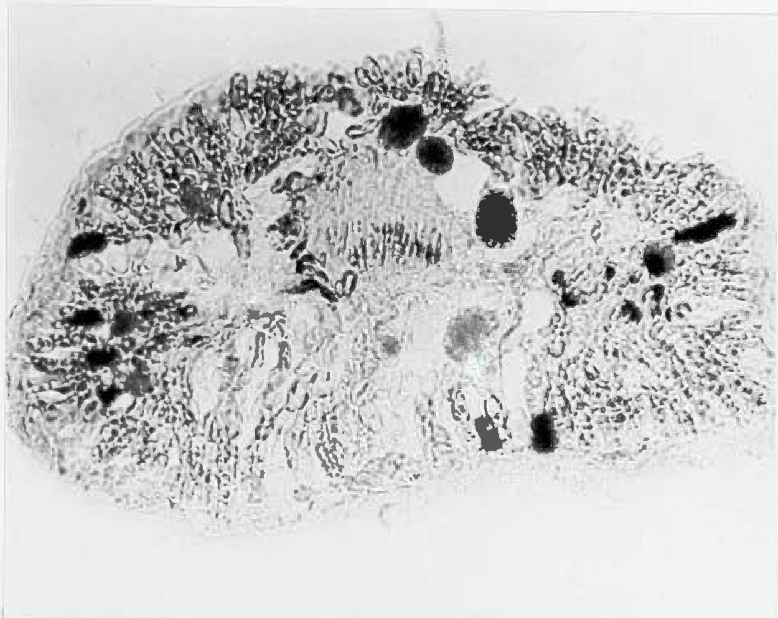

Figure 34. Cross-section of Texas sandwort (Arenaria texana) winter rosette leaf. (X250)

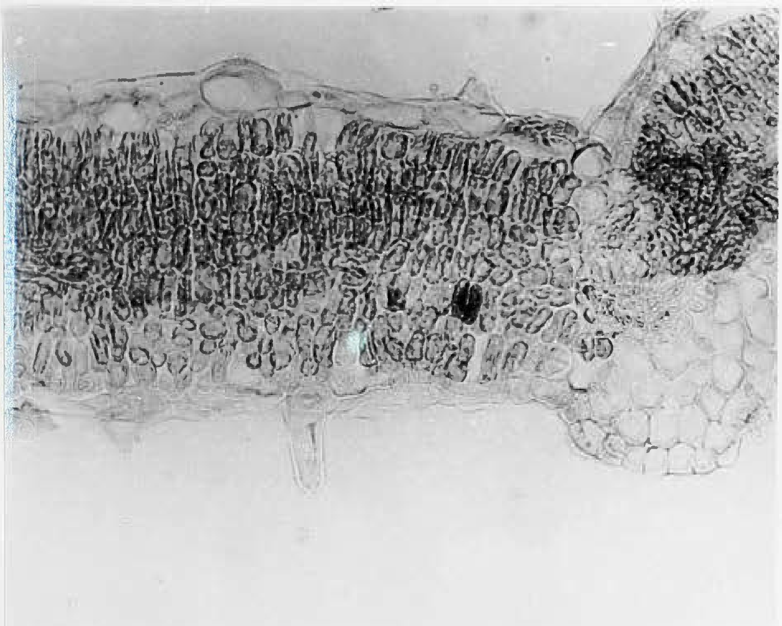

Figure 35. Cross-section of resinous skullcap (Scutellaria resinosa) summer leaf. Note supporting cells forming a rib beneath a major vein. (X250)

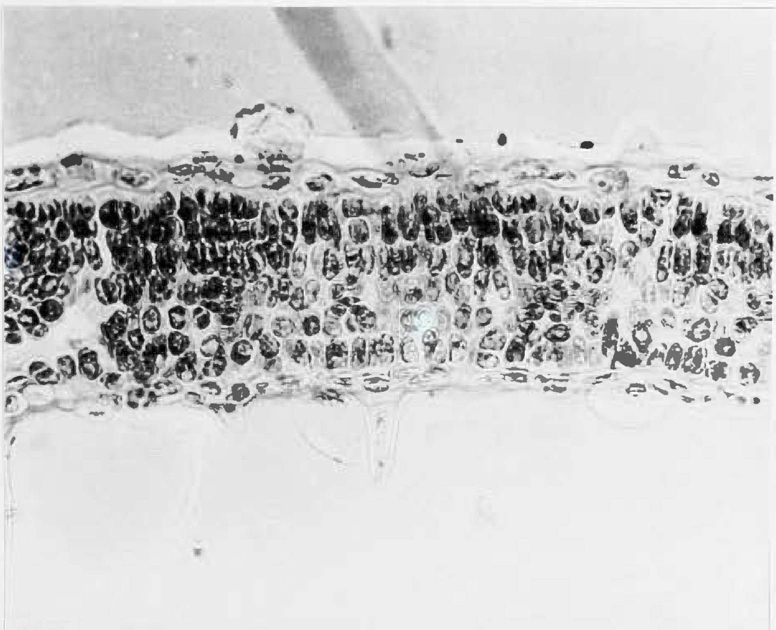

Figure 36. Cross-section of resinous skullcap (<u>Scutellaria resinosa</u>) winter rosette leaf. Note relatively undifferentiated mesophyll. (X250)

SUMMARY

Some biennial and perennial plants form rosettes during the winter months. Studies were made to compare some morphological and anatomical characteristics of winter rosette leaves and summer leaves of some prairie forbs.

Three species, upright prairieconeflower, Dakota verbena, and prairie groundsel, produced winter rosette leaves differing from summer leaves in size and shape. Variation in shape was primarily due to a reduction in number of lateral lobes on winter rosette leaves.

The remainder of the plants studied produced winter rosette leaves differing from summer leaves only in size; rosette leaves being much smaller than summer leaves. Reduction in size is due to a decreased rate of cell division and/or a decreased rate of cell elongation. Each metabolic process is influenced directly or indirectly by availability of water and minerals, intensity of light, photoperiod, and temperature. Probably the most common factor directly affecting cell division and elongation is auxin, a growth substance synthesized in leaf and stem apices.

Many winter rosette leaves showed purple coloration, due to an increased rate of anthocyanin synthesis.

Some winter rosette leaves contained a slightly higher density of trichomes, apparently resulting from a reduction in epidermal cell size.

Variations in leaf margins of winter rosette and summer leaves were observed for two species.

Two species, stenosiphon and fendler aster, produced terminal winter rosette leaves with a relatively higher density of stomates, due to reduced epidermal cell size. Prairie groundsel, which produced a basal winter rosette, contained a relatively higher density of stomates on summer leaves, possibly because of differences in location of the leaves.

An anatomical leaf comparison of winter rosette and summer leaves of each species was made for ten different species. Some of the main differences were as follows: (1) length to width ratio of palisade parenchyma was lower for all winter rosette leaves, (2) length of cross-section was reduced for nine winter rosette leaves, (3) amount of parenchyma cells (spongy or water storage type) was reduced for seven winter rosette leaves, (4) amount of palisade tissue per volume of leaf was reduced for six winter rosette leaves, (5) width of cross-sections was reduced for six winter rosette leaves, (6) mesophyll was more compactly arranged for four winter rosette leaves, and (7) a definite decrease in the vascular system of one winter rosette leaf.

The above differences in winter rosette leaves were due to reduced cell elongation and reduced cell division.

Although more work is necessary on where and when reduced cell division and reduced cell elongation occur, some hypothetical conclusions will be presented and those included in the discussion will be reviewed. They are:

I. Differences in external features of winter rosette leaves from summer leaves are due to: (1) a reduction in cell division and/or elongation during formation and elongation of the leaf primordium, and (2) a reduction in the elongation of cells produced by the marginal meristem and a reduction of marginal meristem cell division.

II. Differences in stomatal density of winter rosette leaves from summer leaves are due to: (1) a reduction in epidermal cell size due to a difference in environment, and (2) a difference in distance from base of stem to leaf.

III. Differences in anatomical characteristics of winter rosette leaves from summer leaves are due to: (1) a reduction of marginal meristem cell division, (2) a reduction of cell growth in the mesophyll, including reduction of polarized growth, and (3) a reduction of epidermal cell growth.

Further problems relating to winter rosettes which could be investigated are: (1) a physiological comparison of winter rosette and summer plants, (2) an anatomical comparison of winter rosette stems and stems from summer plants, and (3) a study to determine the dominant environmental factor or factors responsible for formation of winter rosettes on certain species.

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