DEVELOPMENT AND LONGEVITY OF EPHEMERAL AND PERENNIAL LEAVES ON *ARTEMISIA TRIDENTATA* NUTT. SSP. *WYOMINGENSIS*[1]

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ABSTRACT.—Big sagebrush (*Artemisia tridentata* Nutt.) is one of the most successful plants in the Great Basin based on its abundance and wide distribution. The development of dimorphic leaves may be an important mechanism attributing to its adaptive and competitive abilities. Development, persistence, and proportions of ephemeral and perennial leaves on Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) were studied for two years. The large ephemeral leaves are the first to develop in early spring. As early developing ephemerals mature and stems elongate, new ephemeral and perennial leaves develop in the axes of these large ephemerals. Perennial leaves expanded in the summer of their first growing season, persisting on the shrub until their abscission during summer drought of the second growing season. Plants maintained 33% of their leaf weight through the winters of 1985 and 1986. Active leaf and stem growth occurred at soil water potentials above −0.2 MPa.

During the past 100 years, big sagebrush (*Artemisia tridentata* Nutt.) has increased in abundance and distribution in many areas of the Great Basin. Success of this shrub throughout its range may be attributed in large part to the dimorphic development of ephemeral and perennial leaves. Caldwell (1979) suggests that the ability of the plant to maintain part of its leaf crop through the winter enables it to begin growth and utilization of water in early spring. Development and maintenance of large ephemeral leaves during optimum growing conditions may also increase photosynthetic potential by reducing mesophyll resistance (DePuit and Caldwell 1973).

Development and persistence of ephemeral and perennial leaves on big sagebrush growing in the Great Basin are poorly understood. Little work is available on timing and position of ephemeral leaf development in relation to perennial leaves. Confusion exists regarding the longevity of ephemeral and perennial leaves. On big sagebrush growing east of the Rocky Mountains, mature leaves remaining on the plant over winter are discarded soon after spring growth resumes (Diettert 1938, Branson et al. 1976). On three subspecies of big sagebrush growing in the Great Basin, Miller et al. (1986) reported overwintering leaves remained green on the plant through the subsequent growing season. These leaves senesced during initiation of summer drought, concurrent with abscission of the large ephemeral leaves. A clear picture of big sagebrush leaf development will enhance our understanding of why this plant is the most abundant and widespread shrub throughout the Great Basin. Objectives of this study were: (1) define the sequence and development of ephemeral and perennial leaves, (2) measure retention of the different leaf types, (3) define the proportion of both leaf types occurring on the plant, and (4) relate the developmental sequence to soil moisture.

MATERIALS AND METHODS

Research was conducted at the Squaw Butte Experimental Range in southeastern Oregon on the northern fringe of the Great Basin. The study site was located in a Wyoming big sagebrush–Thurber's needlegrass (*Artemisia tridentata* ssp. *wyomingensis* Nutt.–*Stipa thurberiana* Piper) habitat type. The 40-year mean annual precipitation is 300 mm. The study was conducted from September 1984 through August 1986.

In November of 1984 and 1985 three branches from each of five Wyoming big sagebrush plants were marked with metal tags. At the terminus of each branch all leaves were marked with a dot of black indelible ink, counted, and leaf length measured. On 1

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April 1984 and 1985, prior to leaf elongation, all marked leaves were counted and leaf length measured. Measurements on marked leaves were continued at two-week intervals throughout both growing seasons. Detailed notes and drawings were also made on current year's leaf and stem development.

Ten Wyoming big sagebrush plants were randomly selected for measurement of proportion of leaf types in 1985. These plants were harvested just past peak leaf development, when leaf growth and vegetative stem elongation had terminated and early signs of senescence were visible. Each plant was placed in a large plastic bag, brought into the lab, and leaves separated into four categories. The four leaf categories were 1984 perennial, 1985 perennial, lobed ephemeral, and nonlobed ephemeral occurring on reproductive stems. The 1984 and 1985 perennial leaves were easily differentiated by color, the current year's crop being lighter. Leaves were then dried for 48 hours at 60 C and weighed.

Soil water and soil temperature measurements were recorded concurrently with phenology. Soil water was measured gravimetrically at two depths, 2–20 cm and 20 cm to the hardpan, which varied from 40 to 50 cm. Soil moisture release curves for each of the two layers sampled were developed to convert percent soil water to soil water potential. Soil temperatures were measured with a soil thermometer at 15-cm and 30-cm depths.

RESULTS

Big sagebrush is a semi-evergreen shrub, maintaining a portion of its leaves through the winter. All perennial leaves marked in the fall of 1984 and 1985 persisted through the winter, spring, and early summer, senescing at the onset of summer drought in late July of 1985 and 1986, respectively. Leaf longevity totaled 12 to 13 months, with no leaves persisting through two winters. Winter-persistent leaves, which only partially elongated during the previous growing season, did not reinitiate elongation the subsequent spring.

The large ephemeral leaves are the first to develop early in the spring from small leaf buds, less than 1 mm in length, at the stem apex. Leaf elongation begins in early spring forming tight clusters or fascicles at stem apices prior to stem elongation. When stems begin to elongate, ephemeral leaves are alternately positioned along the stem (Fig. 1). These early ephemeral leaves are the largest leaves on the plant. As spring progresses and the early ephemeral leaves near maturity (full leaf extension), a small cluster of leaves begins to develop in the axes of ephemeral leaves. These leaf fascicles contain both ephemeral and perennial leaves.

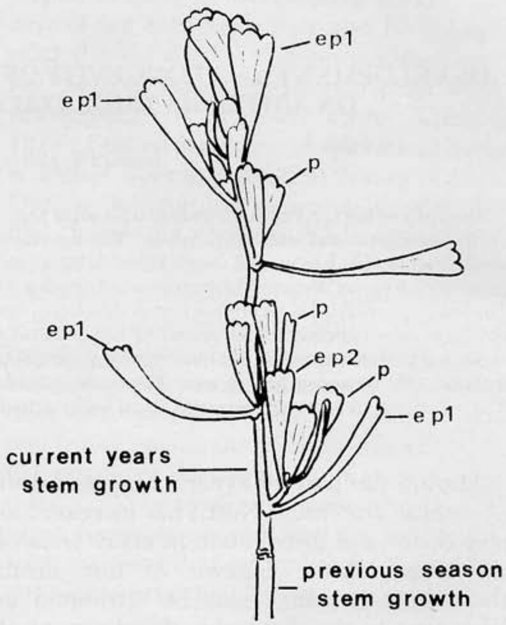

Fig. 1. Current year's growth near peak development with large early ephemeral leaves (ep1), later-developing ephemerals (ep2), and winter-persistent leaves (p). If stems do not elongate, separation of individual leaf clusters is more difficult to distinguish. Last year's winter-persistent leaves are not included.

Lateral leaf fascicles are properly termed "short shoots." Each short shoot fascicle is subtended by a long shoot and large eral leaf (Fig. 1). Later-developing ephemeral leaves are smaller than the early ephemerals but larger than the fully expanded perennial leaves. Not all fascicles contain this smaller ephemeral leaf, while some contain two. Ephemeral leaves on the reproductive stems are nonlobed and have no short shoot fascicles in their axes. At the onset of drought, both the previous season perennial and large, early-developing ephemeral leaves begin to senesce. Later-developing ephemerals, including nonlobed leaves, persist during the initial phase of leaf fall, senescing in late sum-

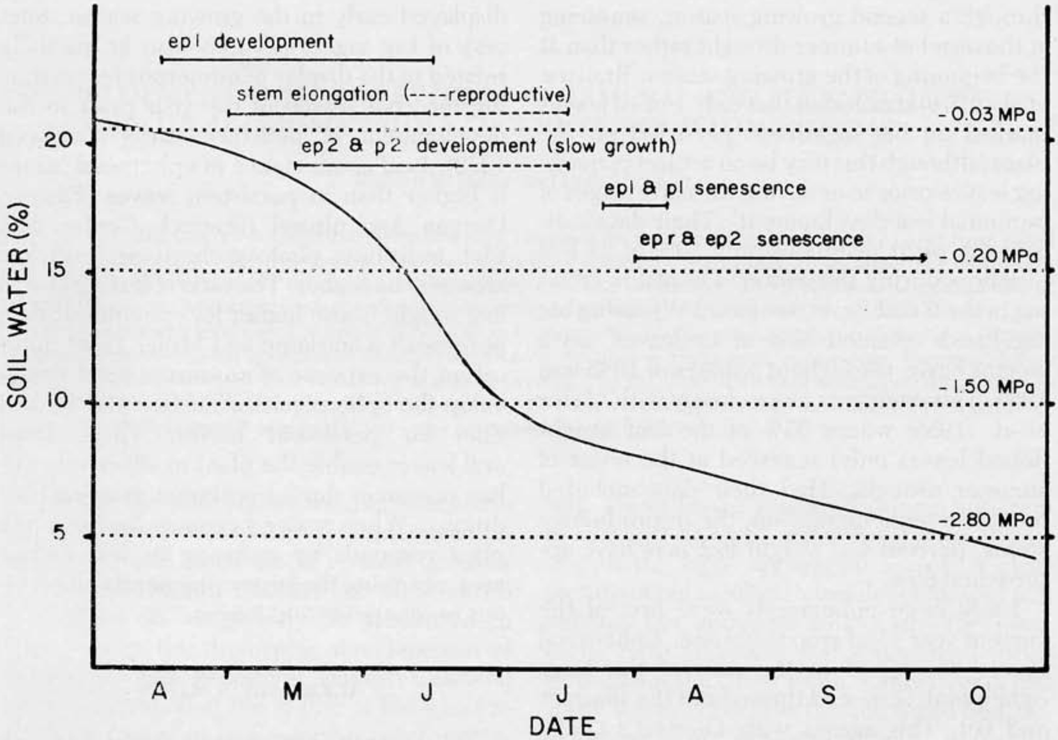

Fig. 2. Relationship of various stages of leaf development and senescence with soil water at 20 to 40+ cm; early ephemerals (ep1), ephemerals in axes of ep1 (ep2), previous year's perennials (p1), current year's perennials (p2), nonlobed ephemerals on reproductive stems (epr). Plant growth and soil water data derived from 1981, 1982, 1985, and 1986.

mer and fall. By November only the current crop of perennial leaves persists.

At initiation of plant growth, soil temperatures were 9 and 5 C at both 15- and 30-cm depths in 1985 and 1986, respectively. The majority of leaf and stem development occurred when soil water potentials were above −0.2 MPa in the wettest soil layer (Fig. 2). All the large ephemeral leaves were developed at this time. Once soil water potential in the wettest soil layer dropped below −0.2 MPa, elongation of primary vegetative stems terminated and leaf growth declined at a rapid rate. At soil water potentials between −0.2 MPa and −1.5 MPa, reproductive stems continued to elongate and short shoots elongated to a small degree. Limited growth of current year's perennial leaves continued, while previous season's winter-persistent leaves and the early large ephemerals began to senesce. All stem elongation and leaf growth terminated when soil water potentials dropped below −1.5 MPa. The majority of winter-persistent leaves of the previous growing season and early ephemerals senesced within a two-week period.

The relative proportion of perennial leaves remained nearly constant during the two growing seasons. At peak leaf development, leaf biomass on vegetative stems was $38 \pm 4\%$ previous season's perennial leaves (1984), $24 \pm 3\%$ ephemeral leaves, and $37 \pm 3\%$ current season's perennial leaves (1985) (at $P = 0.90$). Total leaf biomass consisted of $87 \pm 6\%$ lobed leaves and $13 \pm 6\%$ nonlobed leaves on the reproductive stems. Reproductive stem numbers were highly variable across the 10 shrubs, with nonlobed leaf biomass ranging from 2.5 to 28.5%.

DISCUSSION

Our observations of leaf development and longevity of Great Basin big sagebrush do not fully agree with those reported by Diettert (1938) and Branson et al. (1976). We conclude that the life span of winter-persistent leaves is approximately one year and that they persist through a second growing season, senescing at the onset of summer drought rather than at the beginning of the growing season. Branson et al. (1976) concluded that only 1 of 10 leaves marked on big sagebrush persisted on the plant (although this may be an artifact of marking leaves prior to or during the early stages of perennial leaf development). Their data indicate the plant maintains only 10% of its leaf numbers during the winter. On plants growing in the Great Basin, we found Wyoming big sagebrush retained 33% of its leaves, on a weight basis, throughout winters of 1985 and 1986. This compares more closely with Miller et al. (1986) where 53% of the leaf weight (lobed leaves only) senesced at the onset of summer drought. Had their data included nonlobed ephemerals on the reproductive stems, percent leaf weight lost may have approached 66%.

Early large ephemerals were first of the current year's leaf crop to abscise. Ephemeral leaves developed in the axes of the large ephemerals senesced throughout the summer and fall. This agrees with Diettert's (1938) observation that those leaves produced early in the year may be shed before the hot, dry periods of summer, although there is continuous but less conspicuous fall throughout the year.

The majority of plant growth, with the exclusion of reproductive stems, occurred at soil water potentials above −0.2MPa. This is consistent with plant growth and soil water data collected in 1981 and 1982 for three subspecies of big sagebrush (Miller et al. 1986). DePuit and Caldwell (1973) reported photosynthesis in big sagebrush is inhibited by moderate plant water stress.

Persistence of winter leaves allows evergreen plants an earlier start in utilizing nutrients and soil water than herbaceous or deciduous shrub species which have little or no leaf area displayed at the beginning of the growing season. Soil water is depleted more rapidly early in the growing season around isolated Wyoming big sagebrush plants than around isolated plants of green rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus*), as well as in plots containing only perennial grasses (Eastern Oregon Agricultural Research Center data file). This is primarily due to a larger transpiration surface displayed early in the growing season. Success of big sagebrush may also be partially related to the display of numerous leaves during the cool season of the year prior to the development of moisture stress (Caldwell 1979). Leaf conductance of ephemeral leaves is higher than in persistent leaves (Eastern Oregon Agricultural Research Center data file), indicating photosynthesis per unit leaf area may be higher. The ratio of leaf surface to leaf weight is also higher for ephemerals than perennials (Ganskopp and Miller 1986), indicating the expense of resources used to develop the ephemeral leaf surface may be less than for persistent leaves. These large eral leaves enable the plant to effectively utilize resources during optimum growing conditions. When water becomes limiting, the plant responds by reducing its leaf surface area, abscising the large ephemeral and previous season persistent leaves.

Acknowledgments

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