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Western Ironweed: Research on Anatomy, Physiology, Life History and Control

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INTRODUCTION

Western ironweed (*Vernonia baldwini* Torr.) is a member of a widespread and diverse genus. According to Gleason (9), there are over 500 species of *Vernonia* ranging from Argentina to Manitoba. He found that only a few species are comparatively isolated from all others, and those are so similar in form and structure that they must be of nearly the same genetic constitution.

Gleason (10) showed that the genus was well developed in southern Brazil, Paraguay, and Uruguay, where it is an important component of the flora. He places western ironweed in his group "Interiores" formed from *V. interior* Small (9). Western ironweed is found in central and northern Texas, and extends north to Nebraska and then east to the Mississippi River. According to Gleason (9) *Vernonia baldwini* is of recent phylogenetic origin and an Ozarkian derivative. The genus is characterized by perennial herbs and shrubs.

Weaver and Darland (33) listed the increase of western ironweed, at one time sparsely distributed, as an indication of degeneration of the true prairie. They described the invasion, spread, and ultimate dominance of western ironweed in many pastures after the drought years. Weaver (34) measured ironweed roots to a depth of 11 or 12 ft., and remarked that it was one of "the most abundant and worst weeds in native pastures derived from the true prairie."

Research has been conducted for the past 20 years on various phases of the biology of western ironweed near Lincoln, Nebraska. It is the objective of this study to summarize the present status of research efforts on western ironweed. Unpublished studies will be

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described and related in tabular or pictorial form. Many of the principles developed during the course of research on this plant may relate directly to many other perennial plants.

DESCRIPTION OF WESTERN IRONWEED

Western ironweed usually varies from .6 to 1.2 m. in height at maturity (Figure 1). It grows in clumps of 8 to 12 stems but solitary stems or clumps with one hundred or more stems are not uncommon. Leaves are borne alternately on the stem. They are lanceolate, serrate and lightly pubescent beneath. The leathery feel and coarseness of leaves is characteristic. The reddish to purple, perfect flowers are borne in a corymbose cyme. The involucral bracts are recurved at the ends with prominent midribs. The fruit is a light brown to tan achene about 3 mm. long and is attached to a short, stiff pappus (Figure 2).

Western ironweed reproduces vegetatively from a short, long-lived rhizome system. The horizontal underground stems grow 3 to 4 inches below the soil surface and bear vegetative buds. The rhizome does not branch profusely and is incremented annually by sprouting of buds.

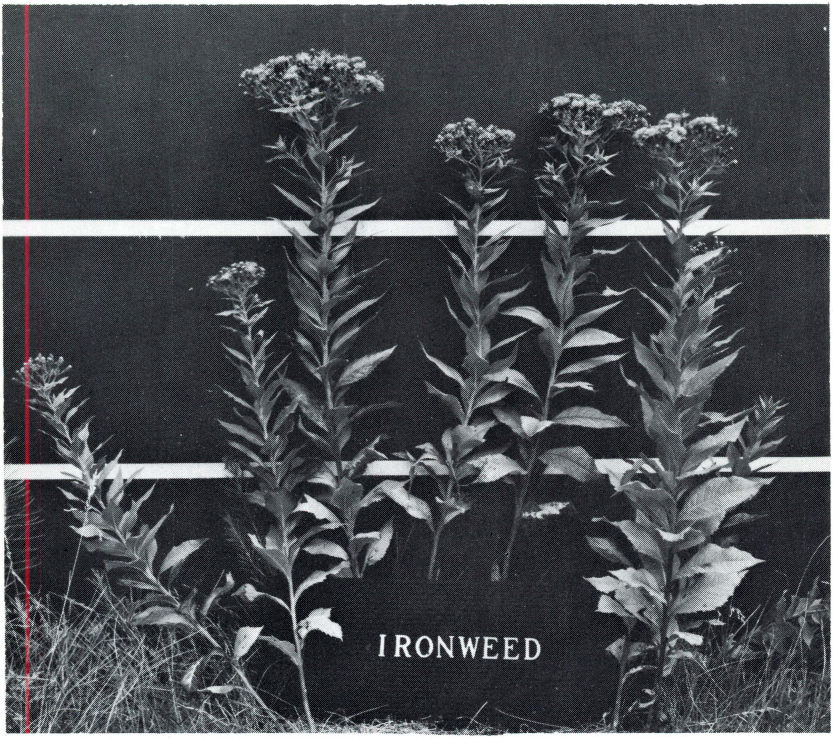

Figure 1. Mature western ironweed plants photographed August 4, 1966, near Lincoln, Nebraska.

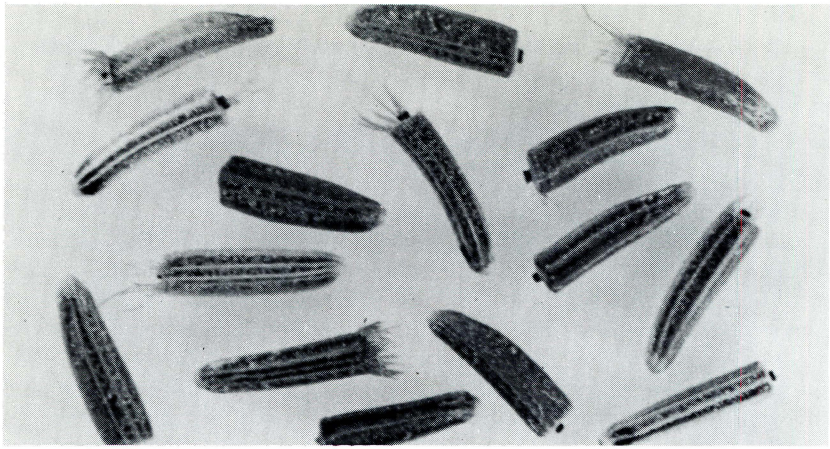

Figure 2. Western ironweed achenes with pappus partially removed.

From 5 to 19 buds have been recorded per year of rhizome growth, but about 8 is average. Numerous fleshy roots are borne at right angles to the rhizomes.

OCCURRENCE OF VERNONIA IN NEBRASKA

Western ironweed is the most common species of *Vernonia* in Nebraska. There is some variation in *V. baldwini*, and Rydberg (26) indicated var. *interior* (Small) Schub. as a distinct species. The difference lies in a minor variation in the involucral bract. In western ironweed the phyllary (involucral bract) is squarrose, e.g., spreading or recurved at the end whereas those of var. *interior* lie flat against the floral cup (appressed).

Winter (36) lists *V. fasciculata* Michx. and *V. marginata* (Torr.) Raf. as occurring in Nebraska, but the latter has never been positively identified. Fernald (6) indicates that *V. baldwini* hybridizes with *V. crinata* Raf. as does var. *interior* which also hybridizes with *V. fasciculata* and *V. missourica*.

Western ironweed is widespread in Nebraska, but tends to occur on the more fertile soils of lowland areas. It seems to be best adapted to southeastern Nebraska and becomes sparse in stand and low in vigor in the northwestern part of the state. It was previously referred to as "Baldwin's ironweed" and *V. fasciculata* was called "western ironweed."

The Weed Science Society of America's latest terminology report lists western ironweed for *V. baldwini*.[3] *V. fasciculata* inhabits poorly

[3] Standardized names of weeds. Report by the subcommittee on standardization of common and botanical names of weeds, Weed Society of America, 1966. Weeds 14:347-386.

drained areas of fairly heavy soils. It is common along roadside ditches in eastern and central Nebraska. Tall ironweed (*Vernonia altissima* Nutt.) is found occasionally in Nebraska which is considered as the northwestern portion of its range.

MATERIALS AND METHODS

Phenology

Observations on the growth and development of western ironweed have been recorded from 1958 to 1967, near Lincoln, Nebraska. These data were collected as frequently as needed to describe the rate of growth and development of western ironweed.

Seed Studies

Twenty-five western ironweed plants were collected in October, 1967 near Lincoln, Nebraska. They were brought to the laboratory, and the number of fruiting branches, heads per branch, and fruits per head were recorded.

Achenes collected in 1956, 1961, and 1966 were placed in 100-unit lots on germination towels. Ten such towels were placed in a germinator under an alternating temperature and light regime that provided an 8-hr. period with fluorescent light at 30 C. and 16 hrs. in the dark at 20 C. The towels were removed after 15 days and germination of ironweed achenes recorded.

Studies on Apical Dominance

An experiment was conducted in 1966 to evaluate the effect of top removal on activity of the vegetative buds of western ironweed plants at various heights on four dates. The experiment was designed as a randomized complete block arranged in a split plot. Clipping dates of July 11, July 16, July 23, and August 1 constituted the main plots. Subplot clipping heights were: 24, 12, 6, and 1 inch above ground, ground level, and 1 inch below ground level. Two to 10 plants in each 5 x 10-ft. sub-plot were clipped. Five replications were used in each clipping date.

Enough plants of similar development for the whole experiment were selected and tagged at the July 11 clipping. The ten plants marked for no treatment were measured immediately before each clipping to serve as the standard. These measurements served to determine the height and growth stage of western ironweed to be used for each clipping treatment. This insured homogeneity of the two variables in the treated population.

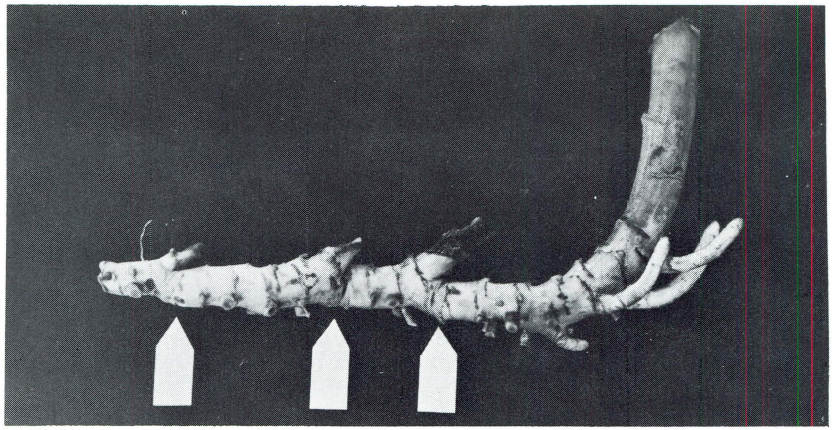

Figure 3. Western ironweed rhizome with current season aerial stem cut off at ground line. Three large buds are shown. The three preceding years stem locations are indicated by the white markers.

Data were taken 15 to 21 days after treatment. The rhizomes of the clipped plants were dug, washed free of soil and percent sprouting, number of buds, and bud length by years of rhizome development determined. The 1966 section was divided into aerial stem and rhizome sections by separating them at the ground line (Figure 3).

The effect of bud age on activity was studied in the greenhouse in 1965 and 1966. On August 15, 1966, 175 ironweed plants ranging from 38 to 42 inches tall and in full bloom were harvested near Lincoln, Nebraska. Tops were removed and the rhizomes washed free of soil in the field. Rhizomes were then taken to the greenhouse for treatment and planting.

Treatments of groups of 30 plants were: (a) clipped so that an inch of the stem would remain, (b) stem removed to scar denoting beginning of the 1966 section, (c) 1966 section removed, (d) 1965 section removed, and (e) 1964 section removed. The method of dating is shown in Figure 4.

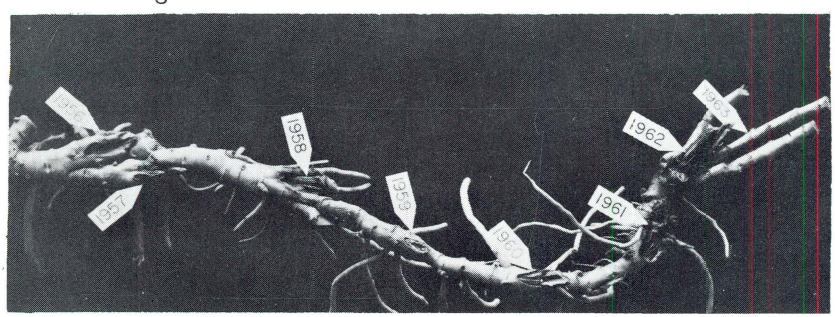

Figure 4. A typical rhizome segment of western ironweed showing areas of development by dating stem scars.

Sections were planted about 1 inch deep in sand media in rows of five sections each and watered to wet to 6 inches deep. Each row served as a replication. The experimental design was a randomized complete block with the six blocks arranged in rows in the sand bench. The sand was watered as needed to maintain a moist condition. We recorded emergence of shoots until it appeared that no more sprouting would occur. Then we determined the percent sprouting, bud length and bud number.

Gibberellic acid and indoleacetic acid were applied as sprays to the foliage and in lanolin directly to the buds of rhizome sections. The sections were dug in the field April 28 and transplanted to sand benches in rows of five sections each as described earlier.

On May 2 treatments applied were: (a) check—no treatment, (b) 250 μg gibberellic acid, or (c) 250 μg indoleacetic acid in 10 ml. water + .1% surfactant (X-77) applied to foliage, (d) 250 μg gibberellic acid, or (e) 250 μg indoleacetic acid in 1 g. lanolin paste applied to previous year's rhizome section, (f) apex removed, or (g) entire stem removed. On May 18, sections from the sand bench were removed and the number of sprouts recorded.

Anatomical Studies

The anatomy of western ironweed was studied both qualitatively and quantitatively. To obtain comparative data, plants of uniform height and comparable age were collected from the field at given dates. Thus, plants were not necessarily taken at random from the population. In a descriptive study the mean value of any particular measurement is most important. Therefore, the mean value, a confidence interval for the mean, and the number of plants are shown.

Procedures for tissue preparation are given in detail by Scifres (27). The tissue was fixed in ethanol-glacial acetic acid-formaldehyde solution, dehydrated stepwise in increasing concentrations of *n*-butanol, embedded in paraffin with melting point of 58 to 60 C., and sections cut on a rotary microtome.

Stem and rhizome sections were softened by soaking in a solution of glycerine-hydroflouric acid-ethanol before embedding. Sections were stained in a rapid safranin-fast green series. Observations and measurements were made with a light microscope.

RESULTS AND DISCUSSION

Phenology of Western Ironweed

Shoots rose from buds on rhizomes from 1958 to 1967 near Lincoln, Nebraska. Seedlings occurred at irregular intervals depending upon spring and early summer moisture conditions. The shoots borne on rhizomes usually emerged the first week in May (Figure 5). Rapid

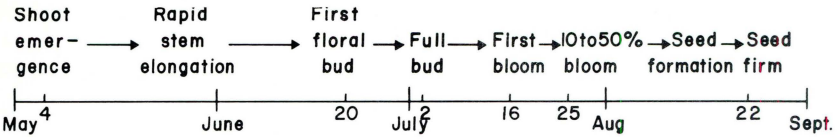

Figure 5. Summary of growth activities of established western ironweed plants from 1958 through 1967 near Lincoln, Nebraska.

elongation of the new stem occurred until about the third week in June, (21) when the first floral buds appeared. All floral buds were fully developed by the first of July and the first bloom appeared about mid-July. By the last week in July, 10 to 50% of the flowers were opened. The achenes were usually firm and ready for dissemination by the last of August or first week in September.

Intensive studies of seedling development in the field have not been conducted. However, a few observations have been recorded. In 1963, a group of ironweed seedlings emerged about mid-June in an area that was being kept weed-free as part of another study. These plants made fairly rapid growth and averaged about 35 cm. tall by early October, ranging in height from 18 to 55 cm.

All of these seedlings reached a bud stage of development with a few showing bloom before frost about mid-November. Ten seedlings that emerged in March, 1967 in the greenhouse and were transplanted to the thistle nursery in June, flowered in October. Under full competition conditions in the pasture it often takes three growing seasons for ironweed plants to attain enough size and vigor to reach the flowering stage.

Seed Production and Germination

Twenty-five western ironweed stems were collected in October, 1967 so that an estimate of seed production per stem could be obtained. There was an average of 11 main fruiting branches per stem. These branches supported 103 heads. However, there was an average of 24 heads per stem that did not set seed. The 79 heads that formed fruit bore an average of 18 achenes per head. This gave an average of 1,422 achenes formed per stem. The range was from 330 to 3,400 achenes per stem.

Western ironweed seed viability is very low according to laboratory tests. The exalbuminous achene houses a small, often rudimentary embryo (30). This could, in part, account for low viability of achenes. Western ironweed achenes usually germinated about 12% the year of harvest (Figure 6). Viability decreases with dry storage at room temperature.

Highest seedling populations have been noted during 1957 and 1965 in pastures near Lincoln. Above normal rainfall occurred in

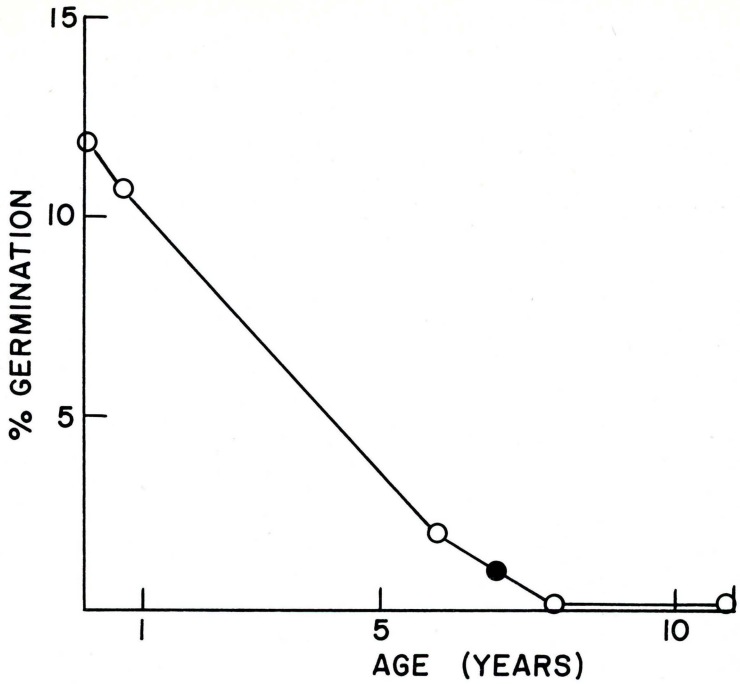

Figure 6. Effect of age of achene on germination in western ironweed.

these years. Variable populations of seedlings were noted in 1967 after heavy rains in late May and early June. In most seasons the population of western ironweed is primarily from vegetative propagation.

Seedling Growth and Bud Development

Western ironweed seedlings emerged with two photosynthetic cotyledons. They were attached to the transition area between the hypocotyl and plumule by short, broad petioles.

The main vascular bundle bifurcated just above the hypocotyl (about 200 μ in these seedlings) and gave rise to the median bundle of each cotyledon (Figure 7). Each of these bundles branched once again forming one median trace and two lateral traces to each cotyledon. Each trace branches somewhat into minor veins above the main junction. Vascular differentiation begins in the lower part of the cotyledons and moves acropetally from the hypocotyl.

The vascular arrangement (Figure 7) was verified using serial sections through the hypocotyl, cotyledonary nodes and cotyledons of several 6-day-old seedlings and of embryos just before germination, where germination was considered as extrusion of the primary radicle to at least 2 mm. The first leaf primordia became visible between 6 and 10 days after emergence. In the axil of each cotyledon, there was

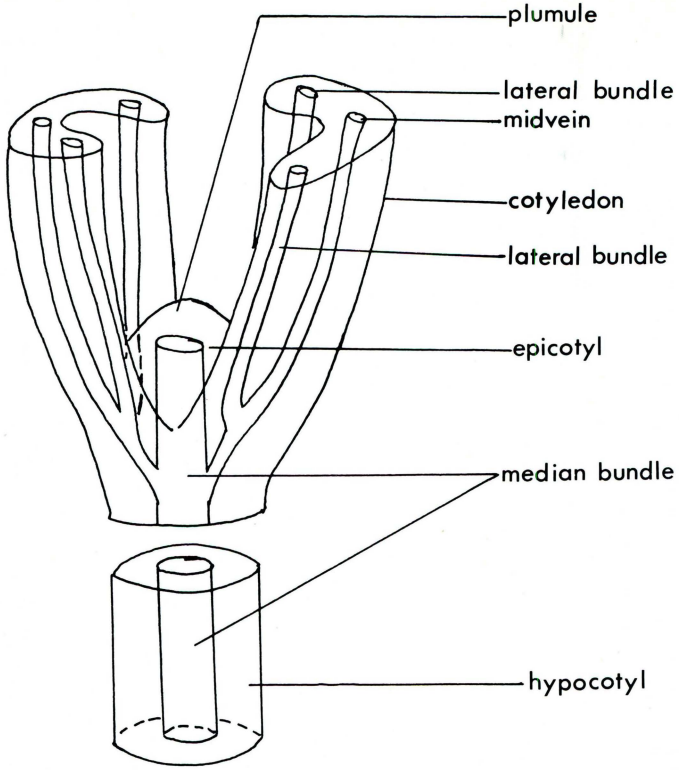

Figure 7. Vasculature of cotyledons at six days after germination and general morphological relationship of the growing point to cotyledons in western ironweed. Taken from Scifres, C. J. 1969. Ph.D. thesis (27).

a single row of deeply staining cells which divide into a double row of 5 at the axil base. These cells presumably serve the same function as axillary meristems in true leaves. They are about 9 μ wide and appear meristematic. In case of damage to the terminal meristems, and each new leaf, the meristem in the cotyledonary axils could become stimulated to form new branches.

New leaves were visible and were forming rapidly at 19 days after germination in greenhouse (29). The new leaves each had a discernible axillary bud, or in the younger primordia, definite formation of axillary initials. The meristematic areas in the axils of the cotyledons formed axillary buds characteristic of those formed by true leaves. The cotyledons were still attached when the plants were about 48 to 56 days old. The leaves arose from both tunica layers and corpus in the apical meristem.

The hypocotyl is the first "stem" of dicotyledonous plants. It is delineated by the cotyledons at its apical end and the *hypocotyl-root* transition zone at its lower end. According to Esau (5) the hypocotyl

is not an internode since it is located beneath the cotyledonary node but not between two nodes. This was true in western ironweed seedlings for only a short period of time. The buds of western ironweed seedlings arose from the hypocotyl-root transition zone (30). At the point in time of lateral bud origin, there was another node formed and the hypocotyl became an internode.

The hypocotyl was comprised of thin-walled parenchymatous cells surrounding the vascular bundle. The epidermis was one cell layer thick. There was great variation of cell size in the body of the hypocotyl. Since the hypocotyl was the area of change form exarch protoxylem in the root to the endarch protoxylem in the seedling stem, the vascularization was not arranged in exactly the same manner at any two points.

The hypocotyl is not set off sharply from the root and stem of most species. However, in some taxa there is an external line of limitation between the hypocotyl and root which is called the "collet" (5). The term collet was applied to this transition zone in leafy spurge seedlings by Meyers *et al.* (17).

However, the term collet implies definite structural limitations which are not so pronounced in western ironweed seedlings. Although the cortical collar between the root and hypocotyl was larger in diameter than either of the latter organs, no differences were apparent with the exception of vascularization. However, the vascular differences were transitory and not confined to the cortical collar only. Therefore, the term hypocotyl-root axis is used here.

The hypocotyl-root axis was located approximately at ground line on the seedlings and was not visible unless seedlings were removed from the soil. Its presence was significant from two standpoints (30). First, it was approximately the beginning of the change from exarch to endarch protoxylem. At about 100 μ below the hypocotyl-root axis of the 6-day-old seedlings examined in this study, the protoxylem began to invert. Therefore, without serial sections from the root through the hypocotyl-root axis, the vascularization of the structure would be difficult to interpret. Pith development was pronounced in the transition zone but the vascular strands were scattered around it without orderly arrangement.

According to Esau (5), "Depending on the closeness of connection between the root and epicotyl, the transitional characteristics of the vascular system are extended more or less far into the epicotylary shoot, sometimes through more than one internode." The transition zone of western ironweed extended almost completely through the entire hypocotyl, with the change to tetrarch protoxylem from diarch in the root. At the distal-most part of the hypocotyl, the strands became endarch and the traces diverged to serve the cotyledons and epicotyl.

The second major point of importance of the hypocotyl-root axis was that it was the point of origin of the first buds on the western

ironweed seedlings (30). From the time the primary radicle extruded from the seed coat of western ironweed, it was destined to become the central root of the juvenile plant. It functioned as a taproot for the first season of growth or until for some reason, the first buds were activated. When one of the seedling buds sprout, the first rhizome is formed at a right angle to the seedling stem. The seedling root system is retained after bud activation and denotes the origin of the rhizome system for any particular plant.

The central root of 6-day-old western ironweed had a diarch protoxylem with exarch strands. Lateral roots arising from the pericyle were numerous. This phenomenon demonstrates endogenous ontogenetic origin of plant organs since all lateral roots originated from within the plant body rather than from superficial tissue such as the epidermis or cortex. This should be kept in mind since the bud shoot of western ironweed arose superficially. In some species, the vegetative buds arise from the roots in the same fashion as do secondary roots. The xylem remained diarch in the hypocotyl-root axis but bifurcated to give four strands into the hypocotyl.

Two types of roots were produced in the seedling year (27). The first type to appear was a highly branched taproot. It formed by elongation from the embryonic radicular tissues. At about 21 days after emergence, a large unbranched lateral root appeared at the uppermost end of the taproot. A second one, immediately adjacent to the first, was noticeable at 28 to 30 days. Neither of these roots branched to form secondary roots until about 47 days after emergence when both branched in the upper 10 cm. of soil and gave lateral roots exactly like the parent organs. The roots, from a gross morphological viewpoint, were much like the adventitious roots of the mature plant. They arose after formation of the seedling bud.

The function of the adventitious-like seedling roots of western ironweed can only be hypothesized, but they may serve as storage organs. Thus, they would give the seedling a source of energy when it renewed vegetative growth the following season.

There are two general areas of bud origin in plants as previously mentioned. Buds usually arise from the main axis of a root as in leafy spurge (17), or from one to several cortical layers of stem or stem-like organs (30).

Ontogeny of the bud shoot of western ironweed can be thought of in terms of two sites, both of which are located in the dermal system. They are the hypocotyl-root axis of the seedling or the cortex of bud shoots, stems, or rhizomes (29). In general, these sites are alike.

Cross sections through 19-day-old seedling hypocotyl-root axes of western ironweed showed well-developed cataphylls (30). At this time it could be established that the buds were not opposite, but alternate. The cataphylls had arisen phyllotactically like foliage leaves, and definitely preceded the bud in formation. Thus, the first buds of

western ironweed followed the botanical rule that all branches and branch-like structures arise in the axil of a leaf or leaf-like organ.

The first buds developed at the cortical collar separating the hypocotyl and root of western ironweed. This collar always occurred at, or just below, the ground line.

Annual Cycles of Bud Dormancy

Western ironweed has strong internal dormancy. Monson and Davis (23) sampled western ironweed near Lincoln at weekly intervals from 1954 through 1956 and in 1961 to measure internal dormancy. They found lowest sprouting activity of field grown plants, when brought into the greenhouse, to occur in late summer and early fall. There was no indication of dormancy after soil temperatures were near freezing at a 5-inch depth for 2 weeks. This trend is shown by many plants, including other weeds such as tanweed (*Polygonum coccineum* Muhl.) (15) and quackgrass (*Agropyron repens* (L.) Beauv.) (11).

Davis and McCarty (4) studied several factors affecting dormancy of the vegetative bud in more detail. They found internal dormancy to be cyclic in nature with recurring annual periods of high and low activity with transitional periods between. In no case did they recover samples from the field in which all were dormant or all were active. From this they concluded that internal dormancy in western ironweed is a population phenomenon. There was less difference in the state of activity among buds as internal dormancy deepened. However, there was a difference in the growth rate of plants from active buds sampled in winter or late fall.

The temperature of the sprouting media has a definite effect on the bud activity; in quackgrass for instance, 20 to 27 C. was optimum (18). Western ironweed buds were apparently capable of re-entering their rest state with the onset of unfavorable environmental conditions. Consequently, the inability of western ironweed buds to sprout the second season after initiation was due to an apical dominance phenomenon.

Davis and McCarty (3) found respiration rate, as expected, differed in active and dormant buds and was detectable after buds had spent 28 hours in the sprouting medium. The respiratory quotients for dormant buds was slightly lower than those obtained from active meristems, but both centered around 1.2 and there was not a significant difference between means for the two activity levels. There was no significant difference in polyphenoloxidase activity between dormant and active buds but there was a trend towards higher specific activity in active meristems.

Lipke *et al.* (5) found the reverse to be true in tanweed; thus, it appears that the use of polyphenoloxidase activity as a correlative factor with bud activity has little value. Peroxidase activity was slightly

higher in dormant ironweed buds (3) which was in agreement with data on tanweed (15). Specific maleic dehydrogenase activities of active ironweed buds were significantly higher than those of dormant buds.

Influence of Apical Dominance on Bud Activity

The classical explanation of apical dominance uses the inhibitory effect of the terminal meristem on the elongation of lateral buds borne in the axils of leaves. This can be demonstrated in most herbaceous plants by removing or damaging the terminal meristem and releasing the lateral buds for elongation. However, this inhibitory effect of a terminal bud upon lateral bud development is much more pronounced in some species than others. Apical dominance is a feature of growth correlation attributed to auxins. Paleg (25) demonstrated that auxin appears to be the only hormone stimulus capable of imposing apical dominance, but it is a characteristic which is strongly enhanced by gibberellic acid treatment.

The classical explanation of apical dominance usually deals with aerial plant parts and not the effect of aerial meristems on underground apices. Western ironweed rhizomes may be divided into zones by years of development (Figure 4). The rhizome does not die due to seasonal mortality of the above ground stems, but remains alive and contains vegetative buds which give rise to next year's aerial stems.

As the buds undergo elongation in the production of a new aerial stem, new rhizome material is produced beyond the scar of the preceding season. Therefore, the ironweed plant may be divided into sections of stem, current years rhizome growth (1966), rhizome growth from the previous year (1965), two years previous (1964) and so forth. The division between above ground stem and current years rhizome growth is almost an arbitrary one, since there is no distinct physical division. In these studies, the above ground stem section included that portion growing at a 90-degree angle to the rhizome or all the aerial portion to about 1 inch below the soil surface. Growth from preceding years was readily discernible because of the presence of old stem scars on the rhizome.

The only sure way to evaluate growth activity was to allow the buds to sprout. However, under field conditions the buds may become activated but not emerge because of ambient factors. Moisture and temperature were assumed to be the most important limiting factors on activity of unsprouted buds in the field. A series of observations were made as follows: (1) Elongation—As a general rule, the buds had to be greater than 2 mm. in length to be considered active, (2) Color—Inactive buds are very near the same color as the rhizome, i.e., light brown or tan. Under field conditions activation was marked by white to pink color. Presence or lack of significant differences in bud length when comparing treated versus nontreated plants did not alone denote

Table 1. Percent sprouting of buds from aerial stems and rhizomes after various amounts of top removal in western ironweed.[1]

Clipping height	Date of top removal							
	July 11		July 18		July 25		August 1	
	Stem	Rhizome	Stem	Rhizome	Stem	Rhizome	Stem	Rhizome
24 inches	18 b	0 a	27 b	0 a	23 d	0 a	5 b	0
12 inches	20 b	0 a	17 ab	0 a	14 c	0 a	0 a	0
6 inches	16 b	0 a	16 ab	0 a	11 bc	1 a	0 a	0
1 inch	16 b	0 a	10 ab	3 a	12 c	1 a	0 a	0
Ground level	15 b	0 a	31 b	0 a	7 b	1 a	0 a	0
–1 inch	...	16 b	...	23 b	...	6 b	...	0
Check[2]	0 a	0 a	0 a	0 a	0 a	0 a	0 a	0
Standard[3]	0 a	0 a	0 a	0 a	0 a	0 a	0 a	0

[1] Means in columns followed by the same letter are not significantly different at the 5% level.
[2] Refers to unclipped plants measured at respective harvest date.
[3] Refers to plants dug at clipping time to check percent sprouting on treatment date.

activity. However, buds significantly longer than unclipped plants which were greater than 2 mm. in length and of white or pink color were considered activated. The above mentioned conditions had to be met before activation was established.

Table 1 gives the percent sprouting from stem sections after top removal at various heights on four dates. Percent sprouting was based on the total number of visible meristems and calculated as:

$$\frac{\text{number of sprouts}}{\text{number of meristems not activated} + \text{number of sprouts}} \times 100.$$

Sprouting reported in plants clipped at 24, 12, or 6 inches actually represents branching from leaf axils (each leaf was counted as having a potential bud) (Table 1). Those clipped at 1 inch above ground and at ground level sprouted from vegetative buds borne under cataphyllic scales. All clippings made at ground level or above followed the general "rules" of apical dominance. Two or 3 sprouts or branches were found per stem with the ones nearest the excised terminal apex invariably the longest and the one farthest below the cut stem tip the shortest.

There were no significant differences among clipping heights in sprouting from the first two dates of clipping except that sprouting on stems clipped exceeded that of stems not clipped (Table 1). The July 25 clipping showed the same high bud sprouting percentage in those plants clipped at 24 inches as observed with the two previous dates. However, a notable decrease occurred in percentage sprouting in those clipped at shorter heights. At the August 1 date, only the plants clipped at 24 inches sprouted.

Clipping the stem 1 inch below the ground surface had the same effect on the 1966 section of the rhizome as did the other clipping on the aerial stem section (Table 1). Note the percent sprouting in the 1966 section of rhizome from clipping heights other than –1 inch.

Table 2. Bud lengths (mm.) after top removal in western ironweed on July 11, 1966.

Clipping height	Rhizome section by year[1]				
	Stem	1966	1965	1964	1963
24 inches	1.7 bc	1.8	1.8	1.4	1.2 bc
12 inches	1.9 b	1.8	1.6	1.4	1.4 bc
6 inches	1.5 bc	1.6	1.7	1.3	2.0 a
1 inch	2.5 a[4]	1.5	2.3	1.3	1.6 ab
Ground level	2.6 a[4]	2.0[4]	1.6	1.7	1.4 bc
−1 inch	. . .	2.2[4]	1.7	1.7	1.2 bc
Check[2]	1.2 c	1.7	1.7	1.3	1.1 c
Standard[3]	1.2 c	1.6	1.7	1.6	1.2 bc
C.V.	25	25	33	23	24

[1] Means within a column followed by the same letter are not significantly different at the 5% level. Columns without letters have no significant differences.

[2] Refers to unclipped plants dug August 1 when the study was harvested.

[3] Refers to plants dug July 11 to check status of buds on treatment date.

[4] White to pinkish in color and apparently elongating.

No sprouting occurred from the rhizome portion from the July 11 clipping. Slight sprouting occurred from the 1-inch clipping in addition to that from the −1 clipping on July 18. On the July 25 clipping, slight sprouting from the rhizome occurred from the lower heights above ground clipping attended by a sharp drop from the −1 inch depth. There was no rhizome sprouting from any depth of clipping on August 1.

Buds on the stem section were activated by clippings at 1 inch or at the ground level on July 11 (Table 2). Buds on the 1966 rhizome section were activated only by the clippings made at the ground level or 1-inch-below ground level. Buds on other sections were not activated

Table 3. Bud lengths (mm.) after top removal in western ironweed on July 18, 1966.

Clipping height	Rhizome section by year[1]				
	Stem	1966	1965	1964	1963
24 inches	1.4 bc	2.4 abc[4]	2.3	1.8 ab	1.4 ab
12 inches	2.2 ab[4]	2.3 abc[4]	1.8	1.5 b	1.4 ab
6 inches	1.9 abc	1.8 ab	2.1	1.4 b	1.4 ab
1 inch	2.3 ab[4]	1.6 bc	1.9	1.4 b	1.4 ab
Ground level	2.4 a[4]	1.6 bc	1.8	2.2 a	1.8 a
−1 inch	. . .	2.7 ab[4]	1.7	1.4 b	1.3 ab
Check[2]	1.5 bc	1.7 bc	1.7	1.3 b	1.1 b
Standard[3]	1.2 c	2.8 a[4]	2.3	2.2 a	1.6 ab
C.V.	37	35	29	27	31

[1] Means within a column followed by the same letter are not significantly different at the 5% level. Columns without letters have no significant differences.

[2] Refers to unclipped plants dug August 2 when the study was harvested.

[3] Refers to plants dug July 18 to check status of buds on treatment date.

[4] White to pinkish in color and apparently elongating.

Table 4. Bud lengths (mm.) after top removal in western ironweed on July 25, 1966.

Clipping height	Rhizome section by year[1]				
	Stem	1966	1965	1964	1963
24 inches	1.6 c	3.0 a[4]	1.7	1.2	1.1
12 inches	1.6 c	2.8 ab[4]	1.6	1.3	1.1
6 inches	1.8 b	2.4 cd[4]	1.7	1.5	1.2
1 inch	1.9 a	2.1 de[4]	1.9	1.4	1.2
Ground level	1.8 b	2.0 e[4]	1.7	1.4	1.1
−1 inch	...	2.6 bc[4]	1.9	1.4	1.3
Check[2]	1.1 e	1.7 f	1.7	1.3	1.1
Standard[3]	1.3 d	1.7 f	1.8	1.5	1.1
C.V.	23	20	9	19	15

[1] Means within a column followed by the same letter are not significantly different at the 5% level. Columns without letters have no significant differences.

[2] Refers to unclipped plants dug August 11 when the study was harvested.

[3] Refers to plants dug July 25 to check status of buds on treatment date.

[4] White to pinkish in color and apparently elongating.

although there were some statistically significant differences apparent on the 1963 sections. The same general trend was evident at the July 18 clipping date (Table 3). Activation was noted in the 1966 section from plants clipped at 24 and 12 inches. This was attributed to the growth stage of western ironweed since the standard plants also appeared activated. By July 25, all buds on the 1966 section were activated (Table 4). There was no activation of buds from August 1 clippings.

Two-year-old buds had highest total emergence in the greenhouse (Table 5). There was a decrease in activity with age, but buds four years old were about as active as those formed the year of evaluation. Unsprouted buds were always longest on the youngest sections, and length decreased with age of the rhizome segment (Table 6). Removal of anterior rhizome segments always stimulated elongation of buds on the adjacent segment although some did not sprout.

Buds three years old did not appear capable of sprouting. However, when rhizome segments anterior to them were removed, 86% of the rhizomes developed sprouts which accounted for 26% of the

Table 5. Sprouting activity of western ironweed buds of different ages.[1]

Bud age (years)	Emergence by rhizome sections		Avg. bud no/section	% buds active
	b-value[2]	%		
1 (current season)	4.7	73 b	9 a	16 b
2	6.7	92 a	6 b	27 a
3	5.9	86 ab	4 b	26 a
4	4.4	66 bc	6 b	27 a

[1] Means followed by the same letter are not significantly different at the 5% level.

[2] "b-value" estimates the percent of the sections that emerged each day after planting. Percent emergence refers to average emergence by sections after 22 days.

Table 6. Lengths of unsprouted buds of various ages after removal of anterior rhizome sections in western ironweed.

Treatment	Position of buds on rhizome by year of development[1]			
	1966	1965	1964	1963
	Bud Lengths (mm.)			
Stem left to 1 inch	52 a	22 a	15 a	10 a
Stem removed	59 a	17 a	12 a	11 a
1966 section removed	...	31 b	15 a	11 a
1965 section removed	...	...	24 b	15 b
1964 section removed	...	...	...	20 c

[1] All bud lengths expressed in millimeters. Means followed by the same letter are not significantly different at the 5% level.

total buds available (Table 5). The remaining buds doubled in length (Table 6) but did not sprout. These data indicate the strong influence of apical dominance in western ironweed and the operation of cyclic dormant-active periods.

Treatments with gibberellic acid (GA) by Shafer and Monson (31) had no effect on western ironweed. However, in our studies conducted in the greenhouse in 1967, GA was found to stimulate activity in dormant ironweed buds (Table 7). After the active buds from the sections collected in November and planted in sand had sprouted, and when the new plants were 6 to 8 inches tall, we sprayed 250 p.p.m.w. GA or indoleacetic acid (IAA) on the foliage. All sections that did not sprout received the same chemicals in lanolin paste applied directly to the buds. There was a noted response to GA but little or none to IAA (Table 7).

The application of 250 p.p.m.w. GA to foliage released the buds from the apical effect of the stem. Sprouting was equal to those sections from which the entire stem had been removed. GA applied in lanolin paste to dormant buds caused 25% of them to sprout but IAA was ineffective in stimulating sprouting. It could have been that the 100 p.p.m.w. GA rate applied by Shafer and Monson was not adequate

Table 7. Percent increased sprouting of buds of western ironweed as affected by gibberellic acid and indoleacetic acid.

Treatment	Area of treatment	Increase in sprouting (%)
Untreated	...	0
250 p.p.m.w. GA[1]	foliage	92
250 p.p.m.w. IAA[1]	foliage	24
250 p.p.m.w. GA[2]	buds	25
250 p.p.m.w. IAA[2]	buds	0
Removal of apex	...	16
Removal of entire stem	...	92

[1] 0.5% surfactant (x–77) v/v was used for spray treatments.

[2] Applied in lanolin paste.

for growth stimulation. McCarty and Linscott (21) have shown that rhizome sections planted in the greenhouse should be at least two inches long with portions of the fleshy root attached in order to obtain good growth response.

Buds on rhizome sections were less responsive to GA treatment than where foliage treatment had been made, probably due to their low state of activity and thus lack of active uptake of the chemical. Meyer and Buchholtz (19) showed that IAA had no effect on quackgrass buds and that 1-napthalenacetic acid (NAA) reduced bud activity. They also found that IAA acted antagonistically with GA.

Frank (8) reported that soaking the buds of American pondweed (*Potamogeton nodosus* Poir.) with 1000 p.p.m. of IAA for 18 hours broke dormancy of all buds. They concluded that low levels of this substance may be the primary cause of dormancy. Mudd *et al.* (24) isolated an IAA-oxidase system in quackgrass buds. Correlative work of this nature has not been completed on ironweed buds and is needed for clarification of the role of IAA and other chemicals in promoting or breaking bud dormancy.

Anatomy of the Bud and Bud Ontogeny

The vegetative bud of western ironweed was a compressed shoot (29). It had nodes and internodes, lateral organs, and an apical meristem. Each main bud had 15 or 20 axillary buds which formed rhizome buds after emergence of the main bud shoot. The outer tissue of western ironweed was oriented as described by the tunica-corpus theory.

There were two distinct layers of tunica in a mature bud. These cells were the outer two layers of the apex. Their walls were anticlinal to the main axis and they gave rise to cataphylls, axillary buds, and lateral branches.

The corpus, a tissue region beneath the tunica with no pattern to wall formation, was responsible for volume growth of the bud shoot. The tunica and corpus jointly formed the promeristem which was an ellipsoidal tissue region about 125 to 150 microns in diameter. The promeristem rested on a bud stalk which was composed of large parenchymatous cells separated by large air spaces.

The factor responsible for bud dormancy was probably located in the promeristem. When dormancy was broken in the spring, the promeristem elongated to form the aerial stem and its lateral appendages. The bud stalk, however, remained underground (29). The zone of elongation, which was just beneath and arose from the promeristem, was responsible for increasing length of the rhizome. The zone of elongation soon became the zone of maturation which is responsible for increase in girth of the rhizome. The rhizome then undergoes secondary growth and becomes a stable part of the system for years to come.

Destiny of the Cataphyll and Its Relation to the Bud

Foster (7) showed that placing the rhizomes of a number of species in light for about a month would transform some of the cataphylls into a form and structure almost identical to foliage leaves. In an experiment to study the effect of exposure to light on the bud of western ironweed, the following occurred.

All buds exposed, or portions of the buds exposed to light, turned green after two days. However, buds completely exposed began to dehydrate and wilting was apparent by the fourth day. After one week, only one completely exposed bud was alive (Table 8). It was light green and sprouted from the apex. The cataphylls did not expand, but instead became closely appressed to the new stem and bud stalk. New leaves from the apical promeristem and the bud stalk assumed the outward characteristics of an aerial stem. No buds below this newly formed shoot were able to sprout. However, in pots where the exposed bud had died, one or two buried bud shoots sprouted. This once again points up the strong apical dominance effect exhibited by this plant.

All leaves that expanded on new bud shoots came from the promeristems. Thus, there was no doubt, even though they apparently may become photosynthetic upon exposure to light, that the destiny of the cataphylls was to become stem or rhizome scales or the outer covering for aerial axillary buds. They arose from the same tissues as did the bud shoots in western ironweed.

This may be clarified by a comparison of the tissues making up the cataphylls. The tissue making up the cataphyll was either epidermal, vascular, or parenchymatous exactly like the ground tissue of the bud stalk. It did not have differentiated chlorenchyma as the mesophyll of leaves. Stomata were not observed on the surface of the cataphylls. The epidermis was unicellular as in the leaves, but was less cutinized and was free of trichomes and other extrusions.

The primordia of cataphylls and leaves were indistinguishable in very early stages. The cataphyll of western ironweed developed from

Table 8. Percentage sprouting of bud shoots of western ironweed after 35 days exposure to 600-ft. candle fluorescent light.

Approximate amount of bud shoot exposed	Percent rhizomes sprouted[1]	Area of sprouting
100	5 a	Promeristem of exposed buds.
75	95 b	
50	85 b	
25	95 b	
10	80 b	Promeristem of exposed buds or covered buds near anterior end of rhizome.
0	90 b	Buds near anterior end of rhizome including the promeristem.

[1] Means followed by the same letter are not significantly different at the 5% level.

the tunica layers, the foliage leaves from tunica and an indefinite amount of corpus. Thus, ontogeny of cataphylls of western ironweed paralleled that of buds, not of foliage leaves.

The tendency to interpret cataphylls on the bud shoot of western ironweed as leaf-like probably arose from two factors. First, from a gross morphological view they appeared laminate in shape and possessed a similar venation pattern. Second, the phyllotactic arrangement of the cataphylls around the bud shoot was alternate just as the arrangement of foliar organs around the aerial stems.

It may be that the cataphylls covering the apices of western ironweed shoots in some way regulate level of sprouting activity. Frank (8) found that activity could be restored in dormant winter buds of American pondweed by removing the bud scales. This type of regulation could be through an effect on gas exchange or by monitoring hormone levels moving to the promeristem.

Another function of the cataphyll could be in food storage. Histologically, it was similar to the cortical regions of the aerial stems, rhizomes, and roots. Structurally, it was continuous with the cortex and may share its role as an area for storage of food reserves.

There was no doubt that the cataphyll served as a protective covering for the promeristems. The apical end of the bud shoot was covered by several layers of this structure. It is the only mechanical protection separating the promeristem from the surrounding environment.

Anatomy of the Aerial Stem

The character of "woodiness" relates to the amount of secondary xylem development. Wood development may be quite pronounced in plants considered to be strictly herbaceous. Carlquist (1) has shown wood formation to be extensive in some species of *Vernonia*. Extensive formation of secondary xylem tissue caused the stems of western ironweed to be quite woody in nature (Figure 8).

The walls of all cells in the xylem were thick and rigid which caused much difficulty in sectioning ironweed stems. The medullary rays were 8 to 10 cells wide and emerged from a central core of pith. They terminated in a cambial region that separated the phloem and wood tissue.

Two types of initials are present in the cambium of plants such as western ironweed. The fusiform initials give rise to tracheids, fibers, vessels, sieve tubes, etc., and the ray initials give rise to horizontal sheets of radially disposed parenchyma. Rays may be eliminated from the secondary xylem of dicots. This is a specialized condition associated with a reduction of cambial activity and thus the woody habit.

Alternate bordered pits were noted on the long slender tracheids and vessels of western ironweed. The vessels ranged from 6.5 to 49.4 μ in width, and 32.3 to 226.1 μ in length (Table 9). The vessel end

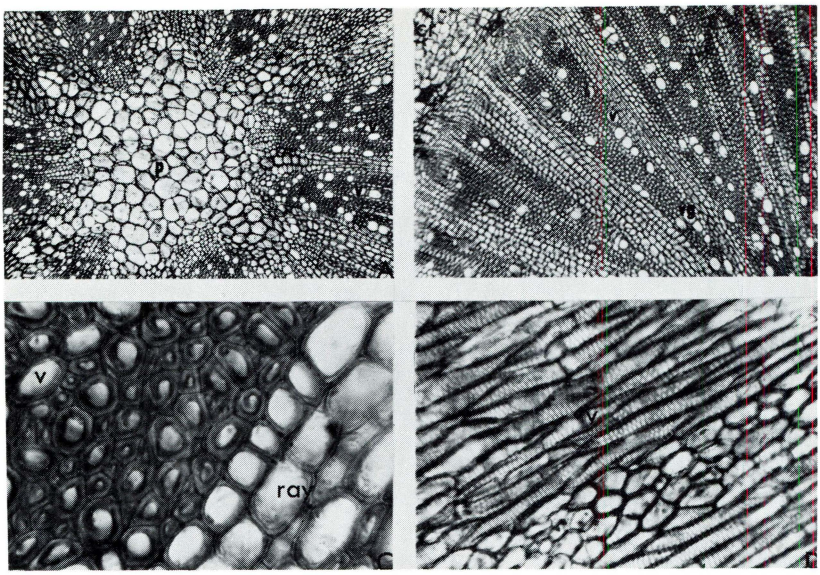

Figure 8. Anatomy of the aerial stem of vegetative western ironweed plants collected in June of 1965 and 1966. The secondary xylem surrounding the pith causes the stems to be quite woody (A). Rays extend from the pith to the cambial region (B). The vessels (v) and other xylem elements are quite thick walled (C). The vessels are highly tapered to nearly flat on the end walls and have alternate simple pits (D). Cr indicates cortex, vg indicates vessel group.

walls ranged from extremely tapered to flat. The longer, more narrow vessels characteristically had tapered end walls. The shorter vessels were usually the widest and were flat on the ends. The vessels of western ironweed were smaller in all dimensions than those of any species of *Vernonia* studied by Carlquist. Shortening of vessels, change in tapered to flat end walls and small pits indicate phylogenetic specialization (5).

In his study of *Vernonia,* Carlquist (1) found that secondary walls ranged from those with pits absent, to those with fine bands on the secondary walls or with grooves connecting the pits. Western ironweed was not included in his study, but on occasion elements with helical secondary wall thickenings have been noted in the stems. A cross section of the stems of western ironweed showed that fibers were numerous in secondary xylem (Figure 8). The phloem was also capped with large bundles of fibers.

Simple perforation plates characterize the Compositae (2) while those in western ironweed occasionally appeared scalariform. Carlquist notes that many times these plates may only appear scalariform since the cross bars often run tangentially. The number of simple perforation plates would indicate this to be the primary type. The

Table 9. Characteristics of wood tissue in the aerial and underground stems of western ironweed plants collected near Lincoln, Nebraska on June 1965 and 1966.

Characteristic	Range		Avg.	Confidence Limits = 0.95
	Max.	Min.		
	Aerial stem[1]			
Vessel length (μ)	226.1	32.3	167.0	±42.0
Vessel diameter (μ)	48.4	6.5	20.4	±19.1
Vessels/group	5	1	1.7	± 0.1
Pith diameter (μ)	226.1	48.4	157.9	±29.5
	Rhizome[2]			
Vessel length (μ)	226.1	32.3	129.2	±66.3
Vessel diameter (μ)	51.6	6.5	16.9	± 8.3
Vessels/group	5	1	1.8	± 0.2
Pith diameter (μ)	258.4	38.8	141.2	±58.6

[1] Represents average of 25 observations on each of 12 stems.
[2] Represents average of 50 observations on each of 5 rhizomes.

rhizome vessels were definitely characterized by simple perforation plates.

Some species of Compositae incorporate interxylary cork to form growth rings (2). However, no such formation exists in western ironweed. According to Carlquist, it was rare in the species of *Vernonia* in his study.

The vessels of western ironweed were scattered rather uniformly throughout the xylem with no tendency to form large groups of cells. They often occurred singly or in pairs (Table 9) or seldom in groups of three or four. The maximum number of vessels found in any one group was five. All cells in the rays were procumbent.

The vascular cambium, per se, was not investigated in this study. It accounts for radial growth of the stem and may consist of only one to a few cells and thus is difficult to study.

Anatomy of the Rhizome

Rhizomes are underground stems and thus are distinguishable from roots from a gross morphological standpoint by the presence of nodes and internodes. Bud shoots are produced at these nodes so that the aerial stem is actually a branch from the rhizome of western ironweed. Rhizomes are a common component of many perennial species, but the rhizomes of western ironweed are shallow in relation to depths attained by those of some plants.

As the bud shoot elongated with the inception of activity in the spring, the lower portion of it was retained in the form of the rhizome. Structurally, the rhizome wood of western ironweed was very similar to that of the aerial stem (Table 9). The amount of pith in aerial and

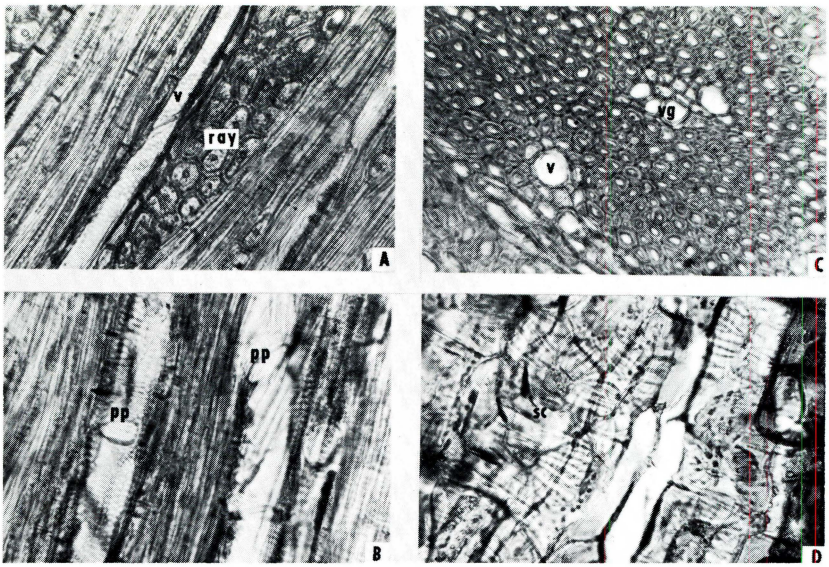

Figure 9. Anatomy of underground stem of western ironweed plants collected in June 1966. Sections are from a 5-year-old segment. Longitudinal sections (A, B) show vessels (v), ray, and simple perforation plates (pp) on vessels. The vessels are thick walled, and in small groups (vg) (C). Large groups of sclerids (sc) are present in cortex (D).

underground stems appeared to be more than was formed during ontogenetic development of the bud shoot (Figure 9). The pith was undoubtedly retained after increased activities of the interfascicular and fascicular cambia of the bud shoot initiated secondary growth and thus wood production with the breaking of dormancy.

The rhizome wood contained more fibers and fiber tracheids than were found in the aerial stems. However, the vessels were grouped as in the aerial stems, but there was a tendency toward greater variation in size. Although the extremes of vessel lengths in stems and rhizomes were the same, there was a tendency for a greater expected range of lengths at the 95% confidence level (Table 9). This tendency was toward shorter, wider vessels.

There was no difference in the size of vessel groups. All species of *Vernonia* sampled by Carlquist (1) centered around groups of two for vessels in the stem section. Due to the perennating nature of the rhizome, we expected its growth to be incremented annually by cambial activity during the growing season. However, there was no evidence of growth rings in the wood of the rhizome and the sections studied were sampled from segments known to be 2 to 5 years of age. This type of growth was difficult to interpret.

Vessel pitting was alternate and exactly like that of the above ground stems. Vessels with helical secondary walls, similar to those

found in aerial stems or roots, were not observed in the rhizomes, however. Several sections verified that simple perforation plates were predominate in the vessels of the rhizome. Multiseriate rays appeared to be more prevalent in the rhizome than in the aerial stem, but no direct comparison was made. The ratio of ray to axial tissue was governed by activity of the fusiform and ray initials of the cambium.

The phloem was very inconspicuous in the aerial stem and few intact sieve elements were found in the rhizome. However, those noted were accompanied by two or three companion cells. Slime bodies and plugs were well developed. The high rate and amount of wood production undoubtedly resulted in some reduction of intact phloem. There appeared to be two to three times more cortical parenchyma present in the rhizomes than in the aerial stems. The cortex, in view of the small amount of pith produced (Table 9) served as the major area of storage. The rhizome cortex was interlain with high amounts of sclerenchyma and groups of from 2 to as many as 25 sclerids. These undoubtedly served in some support role.

The adventitious root also served as a lateral appendage on the rhizomes. It arose from the tissue region between phloem and cortex, but whether this area was endodermic, pericyclic, or neither could not be determined.

Homology of Bud Shoot, Stem and Rhizome

The stems, rhizomes, and vegetative bud shoots of western ironweed are morphologically homologous structures. This entire portion of the plant may be interpreted as a highly branched stem. The bud stalk is destined to form the rhizome through secondary growth and elongation. The promeristem forms the stem and its lateral appendages. All buds, in terms of ontogeny, are axillary.

There are no discernible structural differences between the primary bud shoot and axillary meristems subtending it. The first bud formed on the hypocotyl-root axis is borne in the axil of a cataphyll. It gives rise to the first perennating organ, the rhizome; the axillary bud shoots borne on it give rise to rhizomes and stems of future years. Therefore, the main axis of the western ironweed plant is actually areas of the same structure, part aerial, part underground. The final position of the organ, then, undoubtedly decides type and rate of secondary growth.

The axillary buds on the bud shoot are homologous to the buds in the axils of leaves. All these structures arise superficially. All portions of the primary axis are exogenous in origin which separates them from roots arising from the pericycle of the main axis, that is, endogenously. Leaves and cataphylls arose from the same general histological region as the stem and stem-like structures, but were destined to function in a completely different capacity. The cataphyllic scales

were destined to become a part of the lower stem and rhizome, and became so closely appressed to these structures to appear only as small scars.

Anatomy of the Adventitious Root

The roots of mature western ironweed were adventitious in nature. They arose from the underground portion of the stem. The bulk of western ironweed roots consisted of parenchymatous tissue surrounding a conduit of vascular tissue (Figure 10). The differences in tensile strength and rigidity of tissues in the vascular bundle and surrounding parenchyma caused them to separate readily. This characteristic caused difficulty in obtaining intact sections for study.

The xylem elements ranged in characteristics from those found in the stem and rhizome, to extremely long, slender vessels with spiral secondary walls (Figure 11). The pericycle was well defined, and in

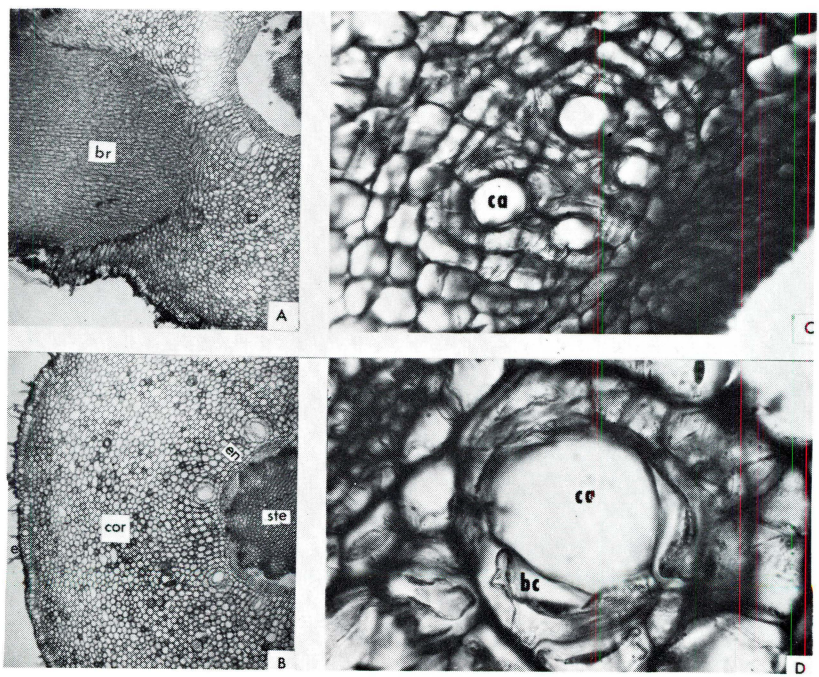

Figure 10. Anatomy of adventitious roots taken from rhizome segments three to five years old near Lincoln, Nebraska in June of 1965 and 1966. The occurrence of branch root (br) formation (A) from the adventitious root which is composed of a central stele (ste) and large amounts of cortex (cor) surrounded by an epidermis (e) two cell layers thick (B). Note canals (ca) occurring exterior to the endodermis in (B). These are large openings bordered by large cells (bc) in C and D. The canals occasionally occur in groups of as many as 4 (C). En indicates endodermis.

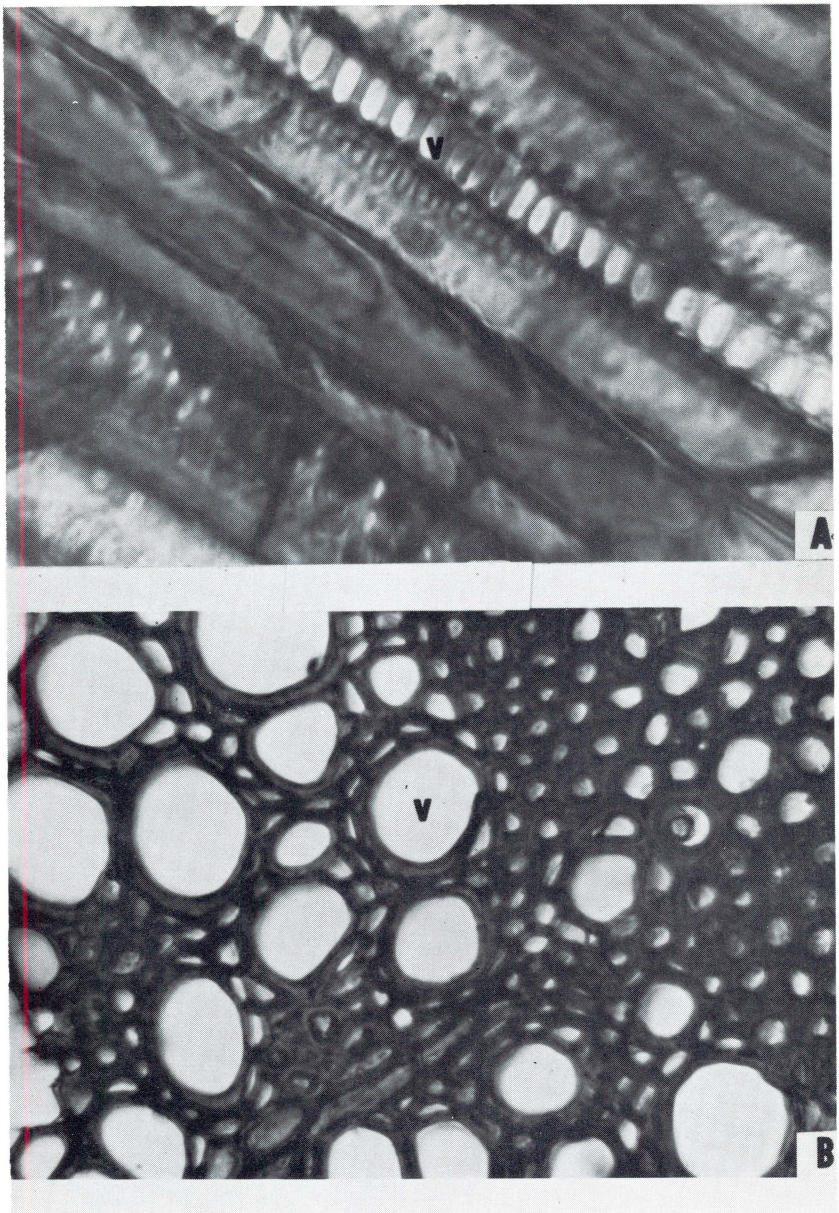

Figure 11. Xylem of adventitious roots of western ironweed from rhizome segments three to five years old collected near Lincoln, Nebraska in June, 1965 and 1966. Longitudinal section of adventitious roots (A) showing types of vessels (v) and cross section (B) showing size and distribution of vessels within the central core of xylem.

the seedling root gave rise to numerous lateral roots. However, the formation of lateral roots from adventitious roots was relatively rare. The few lateral roots produced arose from the pericycle (Figure 10). The adventitious roots grew at right angles from the rhizome, and had only a few root hairs. The cortex was highly developed, undoubtedly serving in the role as a storage area. This abundance of cortex has caused these roots to be called "fleshy roots" or "storage roots."

Many genera of Compositae are known to possess canals in the cortex of the roots, especially at their apical end (16). Western ironweed had canals spread throughout the cortical region of the adventitious roots. The canals were developed in the proximity of the central vascular cylinder and usually occurred singly although they were present in pairs or groups of four (Figure 10). The function of these canals is not well understood. They may correspond to oil ducts which arise schizogenously between the double endodermis. These canals in Compositae are morphologically associated with the area that includes primary phloem, although they are exterior to the endodermis (35).

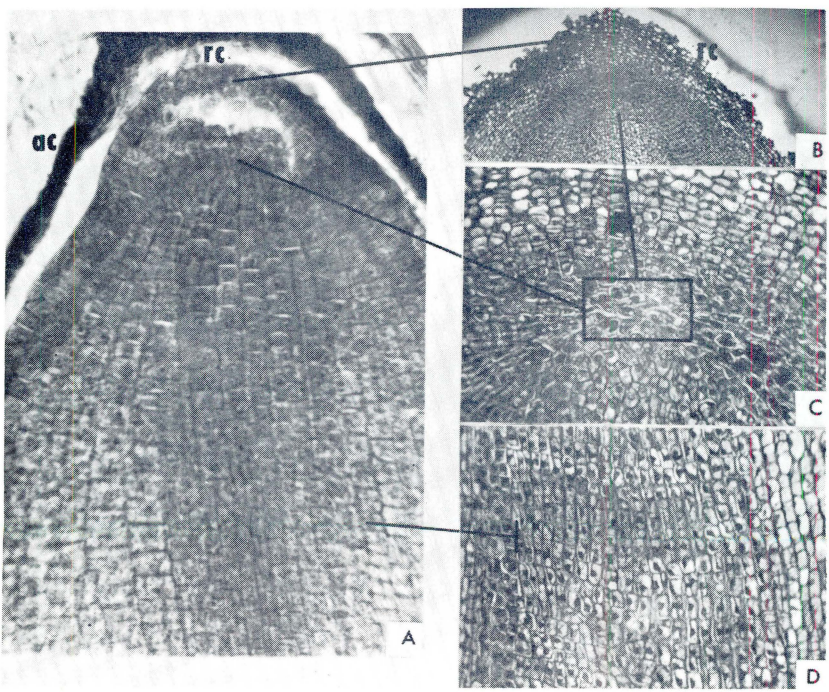

Figure 12. Meristematic areas of root apex of western ironweed. Embryonic root tip (A) and corresponding portions of mature root tip (B, C, D). The root cap (rc) is formed from the outermost initial shown in square in C, the lower initial forms the stele and the central ones the dermal and cortical systems (D). Ac indicates achene coat.

They have been called resin canals, and heretofore have been associated only with herbaceous Composites.

The apical initials and meristem of western ironweed roots were well delimited prior to emergence of the radicle during germination. The root meristem cannot be described in the same terms as the shoot apex. The promeristem is shaped like an inverted cup with initiating cells well behind the end of the root (Figure 12). This was due to the root cap of which there was no similar tissue in the shoot apex. Location of the meristematic cells was the primary difference between root and shoot apices.

There were three layers of initials in the root meristem. The set (calyptrogen) nearest the tip gave rise to the root cap. The central set of initials gave rise to the cortex and dermal system. Increasing diameter of the cortex was responsible for broadening of the apex. The innermost set of initials gave rise to the central cylinder, the stele, of the root. The tissues below the root cap were in radial files, and delineation between tissue regions was fairly simple even in the youngest roots.

Anatomy of the Leaf

The leaves of western ironweed arose from the tunica and several layers of corpus. The outer layer of tunica probably gave rise to the epidermis and the inner layer of mesophyll and conductive tissue. Its provascular system developed in the same sequence as that of the bud. Leaf buttresses were usually noticeable on the terminal apex of the bud shoot between the apex proper and the first cataphyll. The initiation of leaf primordia was responsible for the characteristic shape of the apex since initiation of leaf primordia is responsible for decreasing diameter of apices (32). The three main tissue regions of western ironweed leaves were the epidermis, the vascular system, and the mesophyll. The epidermis was composed of epidermal cells, stomata, stomatal guard cells, and 2 to 3-celled trichomes (Figure 13).

The stomata were anomocytic, i.e., subsidiary cells were absent. They were present on both the upper and lower epidermis, but were about seven times more abundant on the lower surface. They ranged from about 10 by 12 to 29 by 36 μ in size. They were over cavities in the spongy parenchyma that ranged from 32 to 226 sq. μ.

Histologically, the bulk of western ironweed's dorsiventral lamina was comprised of mesophyll tissue. The mesophyll had a well-defined layer of palisade cells averaging about 11 by 41 μ in length (Table 10) over the layer of spongy parenchyma. A small portion of the mature leaf volume of western ironweed was occupied by air space among the spongy tissue. Venation was shown by the coarse vascular network.

The leaf midrib was composed of an epidermal layer surrounding the central vascular bundle and trace bundles embedded in parenchyma. The central bundle branched into several lateral bundles

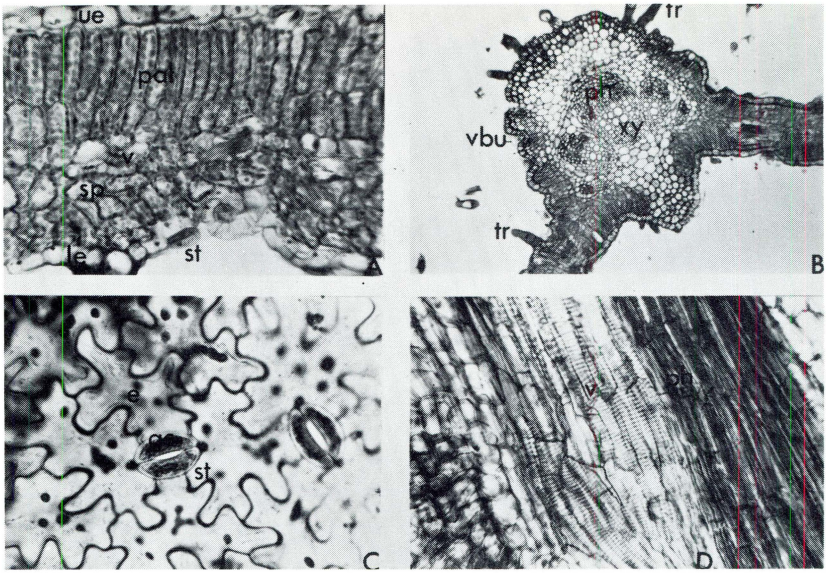

Figure 13. Various views of western ironweed leaves collected at twentieth node from the apex. Cross section of laminate portion of leaf (A) shows upper (ue) and lower epidermis (le), mesophyll made up of palisade (pal) and spongy parenchyma (sp). Cross section of midrib (B) shows relation of phloem (ph) and xylem (xy) in vascular bundles (vbu.). Note several multicellular trichomes (tr) on epidermis. A close-up of lower epidermis (C) shows peridermal section illustrating shape of epidermal cells (e), stomata slightly opened, and nature of guard cells (gc). A longitudinal view of vascular bundle (D) illustrates characteristic vessels (v) and their relation to phloem (ph).

which served the lamina. The vascular bundle was capped with a fibrous bundle sheath. Wyler (37) believed that the bundle sheath extensions share in extravascular translocation of the blade. They probably also serve in a mechanical support role. The vascular bundles are collateral.

Vessels in the leaf were very similar in shape to those in other portions of the plant. They ranged from extremely tapered to flat on the end walls (Figure 13). The vessel walls had alternately arranged simple pits and simple perforation plates. They were considerably smaller, however, than those occurring in wood tissue and averaged about 18 μ in diameter and 36μ in length (Table 10).

Seasonal Trends in Root Reserves

Annual mowing treatments applied to pasture plots at two dates, early June and early July, for five years gave roughly 35% reduction in stem number of western ironweed at the early date and no reduc-

Table 10. Structural characteristics of the twentieth leaf of western ironweed plants collected on June 20, 1965 near Lincoln, Nebraska.[1]

Character	Range		Avg.	Confidence Limit = 0.95
	Max.	Min.		
Stomata/(1000 sq μ)[2]	5.6	1.2	1.4	± 0.5
Distance between stomata (μ)	103.4	22.6	45.1	± 9.4
Stomatal width (μ)	29.1	9.7	13.9	± 6.0
Stomatal length (μ)	33.5	11.6	23.3	± 4.1
Stomatal index				
Upper epidermis (%)	7.4	1.9	3.6	± 1.1
Lower epidermis (%)	32.3	12.5	21.3	± 7.2
Stomatal cavity (sq μ)	226.1	32.0	85.8	±23.0
Palisade length (μ)	64.6	19.4	41.4	±17.2
Palisade width (μ)	19.4	6.4	10.5	± 1.9
Spongy parenchyma, diameter (μ)	19.4	6.4	12.2	± 0.8
Epidermal thickness (μ)	16.2	6.5	13.0	± 0.8
Cuticle thickness (μ)[3]	6.5	3.2	4.2	± 0.3
Vessel diameter (μ)	38.8	6.5	18.4	± 8.3
Vessel length (μ)	51.7	22.6	35.9	± 3.2

[1] Data represents mean of 25 plants which were 1 to 1.5 ft. tall at harvest.
[2] Stomata closed, lower epidermis only.
[3] Upper cuticle only.

tion at the later date (12). The optimum dates of spraying with 2,4-D and the optimum dates of mowing tended to coincide.

Studies were conducted by Linscott and McCarty (14) in 1958 and 1959 to determine the effect of mowing and 2,4-D on the carbohydrate status of western ironweed roots. Data from analyses of untreated western ironweed roots showed that the classical pattern of carbohydrate reduction prior to bloom stage did not occur under Nebraska conditions. Total carbohydrate concentrations reached an initial low point during late May and early June following a period of very rapid vegetative growth. A second low level occurred during the latter part of June and early July during the development of flowering buds. There was considerable fluctuation in carbohydrate content in the roots during the growing season. This variation was thought to be due to a number of variables including stage of growth and climatic effects.

Control of Western Ironweed

Eight or nine successive annual mowing treatments reduced western ironweed vigor but did not decrease its numbers (20). Mowed western ironweed plants were approximately ⅔ as tall as untreated plants. This reduction in vigor was attributed to an approximate reduction of 50% in total root production. However, percent carbohydrates was not affected.

Investigators found early that 2,4-dichlorophenoxyacetic acid (2,4-D) treatments arrested terminal growth in western ironweed, but the plants did not die for a fairly long time after treatment (12). These

observations stimulated research on translocation of 2,4-D in western ironweed.

The 2,4-D-C^{14} was rapidly translocated to western ironweed underground structures with a high percentage metabolized to compounds not extractable with alcohol (13). Vegetative ironweed plants accumulated 2,4-D in sinks such as newly expanding leaves and petioles. However, at that time, there was no 2,4-D-C^{14} detected in underground vegetative buds and little in roots and rhizomes. However, when the plants became fully developed vegetatively, the translocation pattern changed. When the flowering and underground buds became active, C^{14} was detected in rhizomes, roots and vegetative underground buds.

Maximum 2,4-D-C^{14} movement correlated with an increase in percent carbohydrates in the western ironweed roots. Treatment with 2,4-D did not permanently affect carbohydrate levels in ironweed roots (14) but several successive annual applications of 1 lb/A in mid- to late June killed most plants.

The isopropyl and butoxyethanol esters and amine salts of 2,4-D were compared for control of western ironweed (12, 22). All formulations gave good control if at least 1 lb/A of 2,4-D was applied for two successive seasons. The amine salt tended to be less effective than either ester, but differences were not statistically significant.

In a comparison of the effectiveness of 2,4-D with 2-methoxy-3,6-dichlorobenzoic acid (dicamba) and 4-amino-3,5,6-trichloropicolinic acid (picloram), dicamba was the least effective. It rarely gave adequate control of western ironweed. Picloram was the most effective herbicide tested. Picloram at 0.5 lb/A killed top growth and subsequently destroyed roots and rhizomes. One or 2 lb/A of picloram killed top growth more quickly than 0.5 lb/A. The ability of picloram at 2 lb/A to destroy subterranean parts of western ironweed maintained ironweed free plots through four seasons.

Part of the rapid herbicidal action of picloram on western ironweed was through its induction of rapid vascular cambium activity in the leaves (27). The vascular cambium in leaves treated with 0.5 lb/A picloram was almost twice as wide as that of check plants five days after treatment. It increased number of periclinal divisions in the cambium of treated leaves. This was followed by destruction of phloem parenchyma, sieve elements and companion cells. The mesophyll was destroyed shortly after changes were evident in the cambial region.

SUMMARY AND CONCLUSIONS

Initial invasion of western ironweed into any pasture or rangeland site is by achenes, probably wind blown or animal transported (Figure 14). Although little is known about germination and establishment of this species, seedlings are present in the field only in seasons of high spring rainfall.

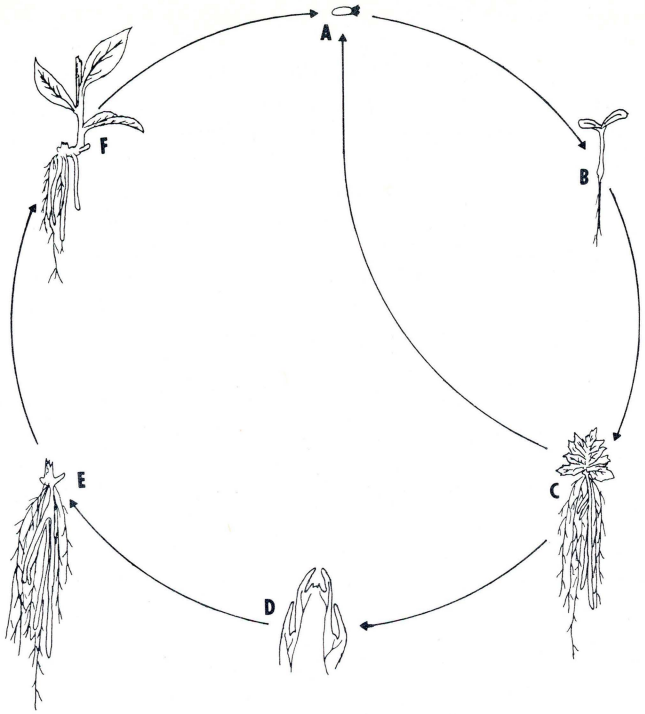

Figure 14. Summary of life cycle of western ironweed from invasion by achenes to development of the vegetative reproduction system.

The exalbuminous achene houses a small embryo within its three-layered seed coat. The seedling emerges from the achene fully differentiated into radicle, hypocotyl, plumule and cotyledons.

About six days after germination, which probably occurs in late May under field conditions, the seedling develops a noticeable swelling in the cortical region separating the hypocotyl and root. The hypocotyl-root transition zone occurs at or just below the soil line and enlarges through differentiation of the cortical parenchyma until the primordia for the first cataphylls are formed. These arise from the two outer cortical layers. The two cataphylls are borne at right angles to each other, and bud initials form in their axils.

In greenhouse studies, a few of the plants had buds capable of regeneration by 15 days after germination and 90% were capable of activating at least one of the pair of buds by 56 days. However, under field conditions, these buds are probably only rarely activated the season of their development. The apical meristem and buds in leaf and cotyledonary axils must be removed before the seedling buds are released for sprouting.

By June 1, seedlings under conditions of limited competition ini-

tiated stem elongation and new leaves appeared rapidly. By the last week in September or the first week in October, the seedlings may produce floral structures and set fruit. The two seedling buds were fully formed by the time of floral initiation. These buds served as the overwintering organs and propagated the plant vegetatively the following spring.

The terminal (apical) end of the bud shoot is composed of two layers of tunica and a body of corpus, 125 to 150 μ deep. Dormancy mechanisms probably exert their strongest influence in this histological area. The bud is merely a compressed shoot complete with nodes, internodes, axillary meristems and foliar-like organs or cataphylls that probably serve in food storage and protection. The apical promeristem is the plumule of the seedling or apex of the aerial stem.

As dormancy recedes with spring, the promeristem is activated. The bud shoots emerge from the soil the first week in May to form the aerial stem and its lateral appendages. The zone of elongation, that part of the bud shoot below the promeristem, increases the rhizome in length as the tip of the bud shoot approaches emergence from the soil.

The first vegetatively produced shoot elongated rapidly until mid-June. As the tissues mature, the fascicular and interfascicular cambia were activated, primary growth ceased and secondary xylem, or wood, developed. The only difference between the aerial and underground portion of the bud shoots is relative abundance of tissues, not tissue types. Both are portions of the same central axis which is a stem. The rhizomes are higher in both wood and storage tissues. Large, adventitious roots arise from the rhizome to serve as storage as well as conductive organs. The lateral appendages of the aerial stem are dorsiventral leaves possessing a thick cuticle and stomata on both the upper and lower epidermis.

As the promeristem was activated in the spring, buds in the axils of cataphylls two and three nodes down from the apical meristem were stimulated. These meristems elongate forming new bud shoots which are destined to repeat the cycle of growth followed by the meristems anterior to them.

All vascular elements are apparently capable of transport, even those extending to the distal-most part of the bud. Thus, structural immaturity can be disregarded as a contributing factor to herbicide ineffectiveness. In the bud shoots studied there were no collenchymatous crowns, as found in many gymnosperms and some angiosperms, or any other structural barrier that might impede movement of water and assimilates from rhizome to bud shoot. Also, the vascular connection was continuous from the bud shoot into the rhizome. There were no apparent structural factors that could account for the sublethal effect of commonly used herbicides on buds on the rhizomes of this species.

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