A Study of Stem Inflation in Wild Buckwheat, *Eriogonum inflatum*

Anne M. Stone[1] and Charles T. Mason, Jr.
Herbarium, University of Arizona

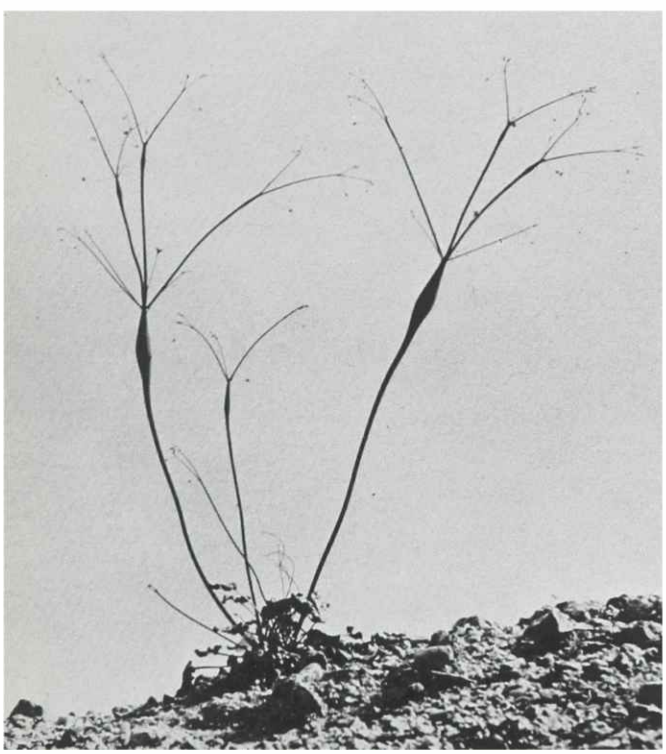

Figure 1. *Eriogonum inflatum* growing in the field.

1. Present address: 1170 Bonito Place, Casa Grande, AZ 85222.

Eriogonum inflatum, originally described by John Torrey, is a striking roadside plant in many parts of the arid Southwest because of the large swellings on the lowest internodes of the scapes. A perennial, it is characterized by a cluster of glaucous gray-green scapelike di-trichotomous stems from 15 cm to 1 m in height. These arise from a basal rosette of crisped, hairy leaves varying in shape from obcordate to oblong. The involucres are few flowered, five toothed and about 1 mm in diameter. The flowers are pale sulphur yellow. The plant is popularly known as "Inflated Wild Buckwheat" or "Desert Trumpet" because of the enlarged stems. These swellings are the chief identifying characteristics in taxonomic keys and also suggest the specific epithet of the scientific name (Fig. 1).

Johnston (1924) distinguished *E. inflatum* var *infltum* from another variety, *E. inflatum* var *deflatum*, only by its inflated stem. Stokes (1936) considered the two varieties to be synonymous and thought that the fistulae failed to develop under extremely dry conditions.

The purpose of this investigation was to determine the cause of the inflations in *E. inflatum* and to determine the validity of the variety *deflatum*. Anatomical and morphological aspects of the stem inflations were considered.

Field Studies

Eriogonum inflatum was studied in the field to determine the incidence of stem swellings. Plant populations were observed as far north as Walker Lake, Nevada, and in many areas of the state of Arizona. During three successive years, observations were made at all seasons on two of the populations.

The major flowering season is in the spring; however, in sheltered locations where moisture is available a few plants may bloom in the winter. All of the winter scapes that were seen were uninflated. The plant, a perennial, may flower in the first year, but such plants are sometimes extremely small and produce one delicate scape about 15 cm tall. In more favorable locations the plants achieve considerable size within the first year.

Specimens were potted in the field and transferred to the greenhouse. All of these plants had some inflated stems which had grown in the field, and several plants had both inflated and uninflated stems at the time of transplanting.

Sixty-seven young stems from the population of Tortilla Flat, Apache Trail, Maricopa County, were

Figure 2. Stem with pupal case attached near an opening filled with mucilaginous material. The dark object is the pupa.

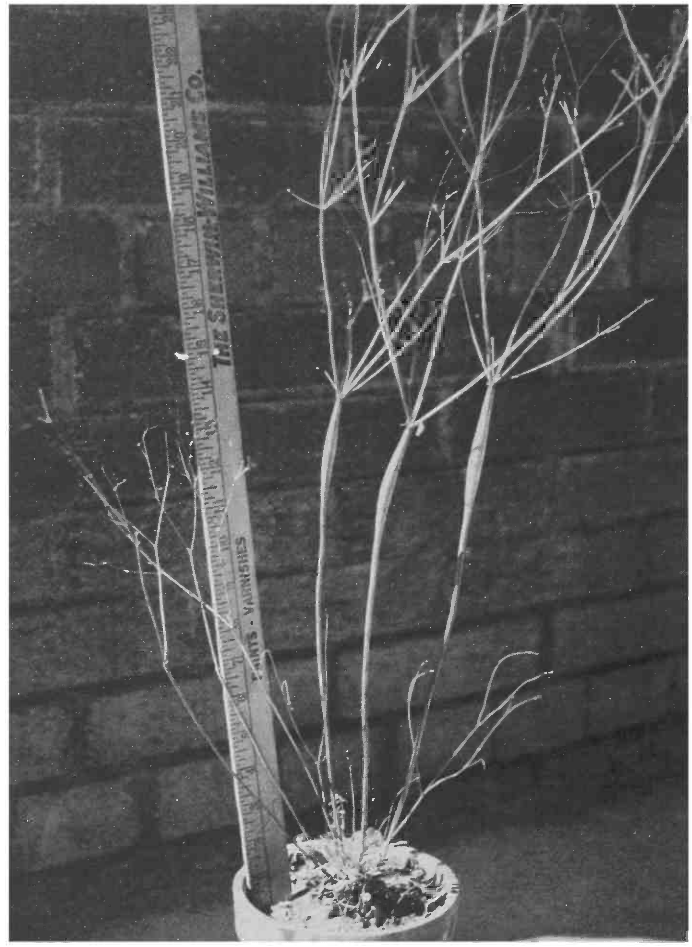

Figure 3. Plant transplanted from field to greenhouse showing a) inflated stems developed in the field, b) uninflated stems developed in the field, and c) uninflated stems developed in the greenhouse.

examined in early spring during the development of the swellings. Most of the stems were in active growth at that time; the youngest stems had just begun to enlarge, and were growing very rapidly. All of the stems with inflations also showed insect damage 2 to 10 cm above the base of the lowest internode of the scape, and 10 to 25 cm below the bottom of the inflation. Minute larvae, visible only with the aid of a hand lens, were found in the stems about 2 cm above the external lesion.

The population north of Wickenburg, Yavapai County, was examined in the winter and in the summer. In a random sample of this population, 93% of the stems examined had stem enlargements. Of the inflated stems, 97% showed insect damage, and many contained insect larvae feeding in the pith of the lowest internode.

Insect Damage

In each of the populations of plants examined, many of the old inflated stems had small round openings, about 11 mm in diameter, near the tip of the inflation. The cavities of these inflations were discolored and contained strands of webbing, pupal skins, hair and feces. The discolorations probably were made by the adult insects before they left the cavities, because only those cavities which had an open escape hole had discolorations of this type. A stem was found with a pupal case still attached to the inside of one of these unopened "portholes" (Fig. 2). The pupal case was attached to the walls of the cavity in several directions by single strands of webbing; there was no cocoon. The "portholes" from which the adult insects emerge are filled with a semi-translucent material, which is evidently an insect secretion. These plugs appear non-cellular and mucilaginous under the microscope.

In March, immature microlepidoptera larvae of the Pyralidae family were found feeding in the stem pith never far above the basal rosette. They were 1 to 2 mm in length at this time. Larger Pyralidae larvae were about the size of the pupa mentioned above.

Various attempts were made to rear the larvae to maturity without success. Consequently no adult insects have been recognized and identification is as yet impossible.

Another type of larva found in *E. inflatum* is a species of beetle. These larvae are of the Mordellidae family, and feed actively through the winter. In general, the swellings on stems which contained Mordellidae larvae were more slender than the swellings on dry stems which had been inhabited by Pyralidae during the previous summer. Specimens of plants which contained Mordellidae larvae were planted in the greenhouse in late January. By April these larvae had bored out of the stems, making fresh small holes of 1/2 mm to 1 mm in diameter. These minute larvae disappeared, possibly to pupate in the soil. Apparently pupation did not take place in the stem, because there were no pupal remains in the cavities of the stems.

Greenhouse Studies

Achenes were obtained for germination tests from plants with inflated stems. After various attempts it was determined that washing for 24 hours in running tap water was necessary to induce germination.

Seedling plants were grown in the greenhouse for about four months before an attempt to induce flowering was carried out. To do this, two plants were allowed to dry out while others were watered regularly. When watering of the dry plants was resumed, flower stalks were initiated in ten days to two weeks. All of the other seedlings reacted to a period of drought in the same way. It was found that the perennial transplants could be induced to form a few flower stalks at any season, if watered after a period of neglect. These stalks were smaller and fewer in number than those produced in the normal spring season of bloom.

Eriogonum inflatum is difficult to transplant, but once established, does very well in the greenhouse. Plants were transferred to pots in the field, watered at once, and covered with large plastic bags to retard wilting. Of the four groups of transplants the overall mortality was about 60%; slightly better results were obtained in the spring than in the fall.

All of the flower scapes which were grown in the greenhouse were uninflated, whether they grew on transplants which had produced inflated stems in the field, on seedlings from inflated plants, or on seedlings from uninflated plants. Seedlings produced uninflated scapes both the first and second year (Figs. 3 and 4).

In spring and early summer, during the growth of scapes on greenhouse plants, an attempt was made to induce inflations by artificial means. Some stems were mechanically wounded by pricking, others had growth substances applied, and some had a larval extract introduced. Of those which were mechanically wounded by pricking with a dissecting needle, none produced fistulae. On stems treated with 1.0% indole-acetic acid (IAA) in pure lanolin, abnormal elongation and deformity were obtained when the chemical was applied to the meristematic portions. When applied to basal areas of the scape, no abnormal growth occurred. Stems treated with 0.5% colchicine showed no deviation from the normal morphological pattern. No inflations were produced in either situation. When water extracts of the larvae were induced into the stems by micropipettes, one stem, the youngest of those treated, showed a slight swelling. The induction of larval extract was repeated when additional scapes were available, but no further swellings were produced. This line of experimentation needs to be carried further using very young scapes and repeated induction of larval extract.

Anatomical investigations were carried out using thin sections and cleared portions of stems. Mature fistulae were cleared in 5% sodium hydroxide (NaOH) for one week; tannins were then removed by two days of immersion in "Craf's A" (Johansen, 1940). Chloral hydrate was used to complete the clearing. The material was then washed in water and stained in safranin in 50% alcohol (Arnott, 1959), (Fig. 5). In the larger swellings where the distance between vascular bundles is greatly increased, new vascular tissue develops from the interfascicular cambium. These strands are faintly visible between the normal vascular bundles.

A series of thin sections across the end of the inflation in a very young stem disclosed pith cells which gradually increased in diameter as the cavity of the fistula was approached in successive sections. This stretching eventually ruptured a cell wall, and in successive sections several cells were found to be

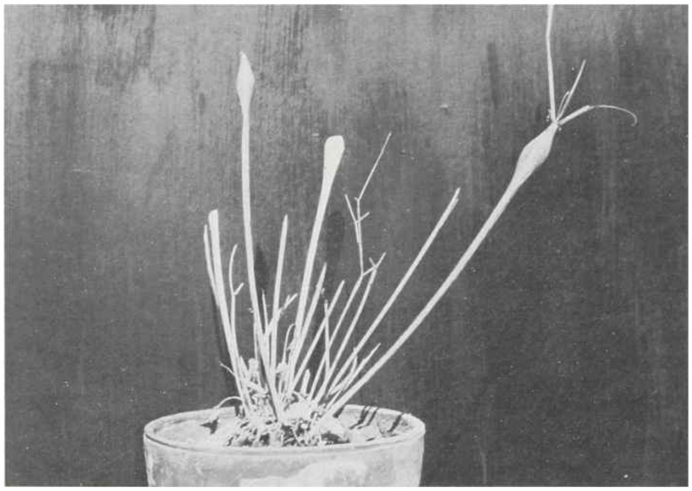

Figure 4a. Transplanted *Eriogonum inflatum* showing fistulae produced in the field.

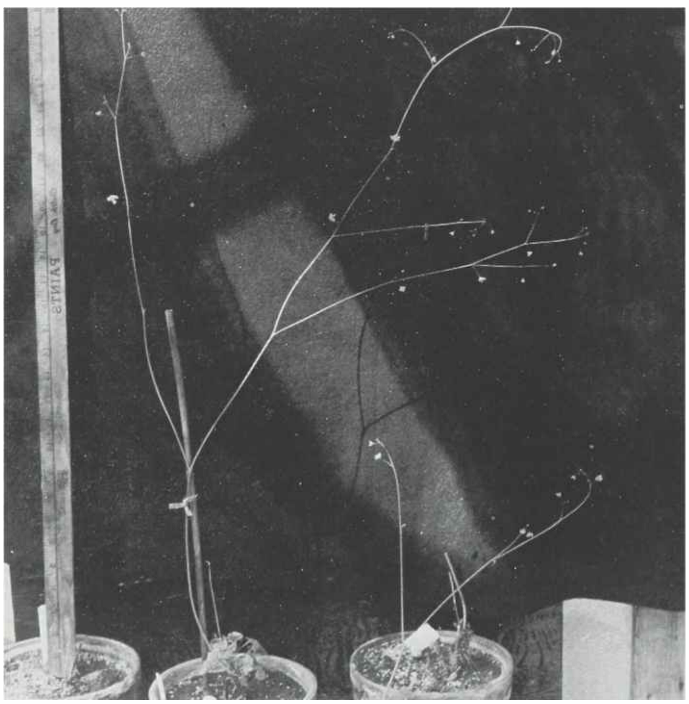

Figure 4b. Greenhouse grown seedlings grown from plant in Figure 4a. The stems are not inflated.

torn until the open cavity was reached. In older stems, the center of the stem is often hollow to the base, the cells having been eaten by insect larvae. Sometimes there is a hollow portion near the bottom occupied by the larva. Above this is a solid portion, and above this is the open fistula. If the larvae reach maturity in the stem, the entire internode will be hollow and there may be some evidence of feeding in the lower half of the fistula.

Discussion and Conclusions

Field observations indicate that the ultimate size of the fistula depends on several interacting conditions. If the plants are undergoing rapid stem growth, then the larger, more vigorous plants in the most favorable locations will have the largest swellings. In other plants or in different stems on the same plant, variance in fistula size appears also to be related to the time of initial insect damage and to the duration of larval inhabitation. Beck (1953) observed a similar situation in the galls on *Solidago*, which apparently ceased to develop when the insect larvae died, and concluded that the ultimate size of the gall depended on the duration of stimulation. Barber (1938), and Lieby (1922), working with other types of galls, came to the same conclusion. Beck (1953) also found that the proliferation of tissue in *Solidago* stems was induced not only by the mechanical feeding activity of the larvae, but also by a chemical stimulus received from silk deposit on the inner surface of the stem by the feeding larvae.

In plants with several scapes, two sizes of fistulae may be found on the lowest internodes of the stems. The stems with the larger swellings usually contain live larvae, while smaller fistulae on the same plant will occur on stems which exhibit evidence of insect damage, but which contain no live larvae. In a study of galls produced by sawflies (Hovanitz, 1959), it was shown that the abnormal growth began when the plant was wounded by the ovipositor of the adult fly. However, continued growth depended upon the stimulation by salivary secretions of the sawfly larvae. Microlepidoptera have no ovipositor, so this initial wound stimulus has to be discounted. The abnormality in *E. inflatum* stems must result entirely from larval feeding.

Eriogonum inflatum stems with injuries high on the first internode had very small swellings, if any, and rarely contained live larvae. Thus if the initial injury occurred when the first internode was nearing the end of the meristematic activity, the swelling was small. Occasionally the swelling did not develop at all, probably because the injury occurred when growth of the lower internode had ceased. The experiments in which *E. inflatum* was treated with IAA also indicated that the net hormonal effect depended on the degree of meristematic activity at the time of treatment.

Swellings on the second and third internodes occur on both large and small plants but rarely exhibit larvae or insect damage. It appears that the upper inflations occur as the result of stimulation

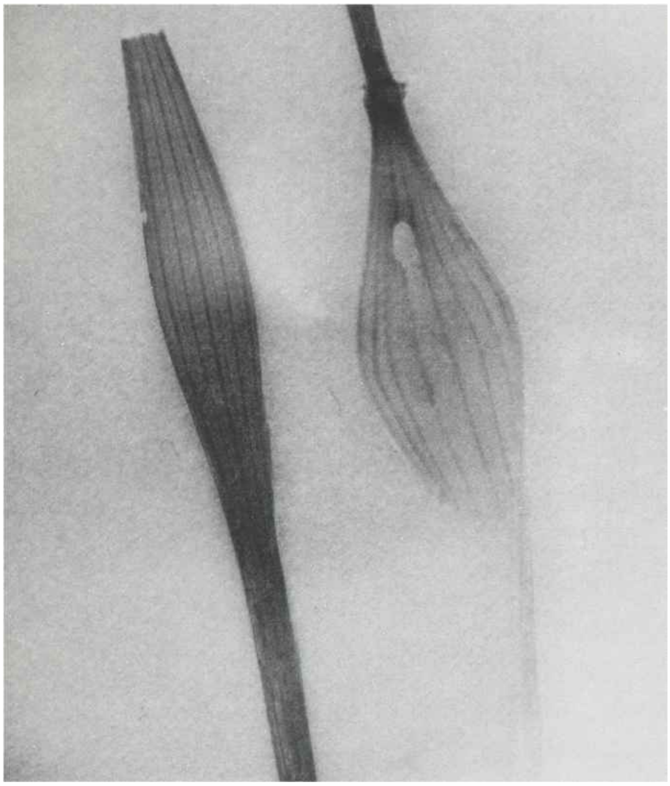

Figure 5. Cleared stem showing a) developing vascular bundles between mature vascular strands, and b) an opening made by a larva.

to the lower internode during meristematic activity of the second or third internode. Cessation of larval feeding before the development of the upper portions of the stem would probably allow normal development to take place, larval feeding being necessary to stimulate in the plant the production of growth substances which are responsible for gall development (Leonian and Lilly, 1937). Evidently this substance is transported in the stem. Parasitic depredation of the larvae may terminate the stimulus before the upper internodes develop.

In *Solidago* (Beck, 1953) it was found that the eggs of the gall-producing moth *Gnorimaschema* were deposited on the crown and on dead material near the crown of the plant. The eggs overwintered there, and in the spring the larvae hatched and burrowed into the soft meristematic tissues of the apical bud. Occasionally the larvae entered through other parts of the stem. Pyralidae larvae in *E. inflatum* pupate in the fistulae and emerge sometime in August. In March, recently hatched larvae are found in the stems, and as with *Gnorimaschema*, the eggs are evidently the overwintering stage of this Pyralidae.

The small "portholes" that are sometimes found in the fistulae of *E. inflatum* are thin enough to admit light. Barber (1938) described this type of plug in *Solidago* as a thin ring of epidermis; Beck (1953) says that the plug is an insect secretion which is dissolved by the digestive juices of the adult, thus allowing it to leave the cavity. From the stains inside the cavity it is evident that pupation takes place within the fistula, and since the moth has no chewing mouth parts, it must dissolve the plug with saliva.

In *Eriogonum inflatum*, the fistula develops through an increase in the number and size of the interfascicular cells, thus increasing the distance between vascular strands in the region of the swelling. The resulting increase in the circumference of the stem produces tensions on the large thin-walled cells of the pith, eventually causing them to rupture, forming an initially schizogenous cavity. Thin sections at the apex of the fistula showed the increased size of the central stem cells, then ruptured cells, and finally the main cavity.

The inflated stems of *E. inflatum* var. *inflatum* are not the normal morphogenetic condition of the plant, but are induced by cecidozoa including a Pyralidae and a Mordellidae. Therefore, the taxonomic recognition of the varieties *inflatum* and *deflatum* is not based on a genetic characteristic, but on a monstrosity, and has no validity.

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