ALLOCATION OF RESOURCES, POPULATION BIOLOGY, AND ANATOMY OF THE PHREATOPHYTE, *CNIDOSCOLUS TEXANUS*

By

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ALLOCATION OF RESOURCES, POPULATION BIOLOGY,

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CHAPTER I

INTRODUCTION

Phreatophytes are deep-rooted plants which use deep soil moisture as their primary water source during periods of limited superficial soil moisture. The xeric, often well drained soils inhabited by them have led ecologists to postulate that establishment of these plants occurs during exceptionally wet periods. During these times soil moisture is favorable for seed germination and rapid growth, especially of the root system. This idea, however, is only intuitive and has been little tested.

A significant question in phreatophyte biology needing clarification is what is the nature of juvenile stages before groundwater-tapping root systems are established. The objectives of this study were to elucidate parts of this question using a local phreatophyte, *Cnidoscolus texanus*, examining juvenile root growth characteristics, and allocaation of resources. Aspects of *C. texanus* population biology were also studied to try to determine if exceptionally wet years produced a pulsed population age structure. Field studies of seedling establishment through one year were carried out. Adult plants were also monitored for winter survival. Seedling vigor was studied to discern

condition-specific mortality. The unusual anatomy of the subterranean parts of Cnidoscolus texanus was examined. It has a contractile root and a fleshy, thick root in both adults and seedlings.

Cnidoscolus texanus (Muell. Arg.)Small is an herbaceous perennial found in deep, sandy, well-drained soils throughout Oklahoma, Texas, Louisiana, and Tamaulipas, Mexico (McVaugh 1944). Such soils are located on stabilized dunes and terrace deposits on the north side of the Cimarron River in Payne County, the study site. Its unusually high root-shoot ratio, habitat preference, and ability to photosynthesize in superficially dry soils makes C. texanus a good candidate for the study of phreatophyte biology. It also possesses a contractile root which appears to be an adaptation for living in xeric, occasionally unstable environments.

CHAPTER II

LITERATURE REVIEW

Phreatophytes

The most extensive studies of phreatophyte biology have been conducted on species of Prosopis (Fabaceae) which is a genus of small, sometimes weedy trees distributed throughout southwestern North America. Turner (1972) reported that, under experimental conditions, seed germination and seedling establishment of Prosopis spp. did not require water in addition to rainfall. In contrast, Tamarix required extra moisture for six weeks in order for seedlings to become established. Scifres and Brock (1969, 1972) found that establishment of P. glandulosa was not necessarily correlated with seasons of high precipitation and germination can occur with minimal ambient moisture. Prosopis glandulosa can also become established quickly, strongly influencing its successful establishment (Scifres and Hahn 1971). Seeds of P. glandulosa germinated most rapidly and successfully at 27 C and a planting depth of 0.5 to 1.5 cm. Root growth rate of P. glandulosa seedlings during the first 30 days was 24.3 mm/day. After the first 30 days, top growth increased at the expense of root growth (Brock 1986). Brock (1986) proposed that it was adaptive for seedlings to

have an initial accentuation of root growth to increase the probability of contacting soil moisture.

Anatomical Studies

Contractile roots have been most extensively studied in the monocot families (Wilson and Honey 1966), although the number of dicot families possessing them is estimated to be four times greater (Rimbach 1929).

The precise mechanism of root contraction is not known. It is generally accepted that the contraction involves a change in the direction of growth from longitudinal to radial (Wilson and Honey 1966). Zamski et al. (1983) report that directional growth changes necessitate the secretion of hydrolytic enzymes into the cell wall to permit plasticity. Wavy cell walls were present after root contraction in *Gymnarrhena micrantha* (Asteraceae). Secondary cell wall material was then deposited over the existing cell wall, thus fixing the wavy structure. Bottum (1941) likewise noted in *Medicago* that the central xylem became undulate after root contraction. He also noted that a sinuous xylem core was observed in connection with root shortening. In *Panax* and *Taraxacum*, contraction was observed in the same root for several years (Rimbach 1898; Grishvitskii 1952).

Population Biology

Recruitment studies of herbaceous perennials have been difficult. Because some perennials are long-lived and have

transient or fleshy underground structures, exact plant age generally cannot be determined. This precludes the calculation of age-specific population characteristics.

In a very few instances, herbaceous perennials develop annual growth rings and the plants' ages can be determined accurately. Kerster (1968) determined the age structure of Liatris aspera by examining corm growth rings. For Liatris, the younger aged categories were under-represented suggesting the population was declining. However, one quadrat showed an abundance of young plants on a soil profile buried by wind-blown sand. Possibly Liatris is a long-lived, colonizing perennial which is doomed to local extinction and migrates to disturbed patches in the climax prairie.

Uranov and Smirnova (1969) postulated that age is a limited, misleading predictor of individual plant characteristics. They suggested that plant demography should be based on a series of ontogenetic life states related directly to plant size. Among a group of herbaceous plants of different sizes, almost certainly the largest will be the oldest (Harper 1977).

Some herbaceous perennials accumulate non-photosynthetic tissues and this dependent tissue acts as an increasing respiratory burden as the plant ages. This burden lowers the net assimilation rate and produces senescence (Kershaw 1964). The population biology of perennials differs from that of annuals in that generations overlap unless a disaster produces a pulsed, even-aged

population (Harper 1977). Also, generation overlap may be reduced if seedlings are recruited only occasionally.

Allocation of Resources

Mooney (1972) postulated that an understanding of how plants gain and allocate their resources will allow prediction of their success in any given physical environment in combination with any competitor or predator. A method of analyzing resource allocation is to obtain dry-weight root-shoot ratios.

Perennials generally have increased root-shoot ratios when growing under unfavorable conditions (Mooney 1972). Examples of these unfavorable conditions include water (Struik and Bray 1970) or mineral (Biddscome et al. 1969) limiting environments, periodic fire (Whittaker and Woodwell 1968) or grazing (Mooney 1972). Root-shoot ratios for plants growing in several environments are presented in Table 1. Root-shoot ratios increase when an element required for root growth is limiting while shoot growth is favored when an element for shoot growth is limiting. Developmental changes shift the root-shoot ratio several times before maturity (Brouwer 1983). After maturity the carbon allocation shifts mainly in response to seasonal changes instead of ontogenetic seedling states.

TABLE I

ROOT-SHOOT RATIOS OF PLANTS CHARACTERISTIC OF VARIOUS COMMUNITIES1

Plant	root-shoot ratio
Evergreen trees of tropical and subtropical forests	0.18
Deciduous trees of temperate forests	0.25
Evergreen trees of boreal forests	0.25
Graminoids of grasslands	1.52
Plants of Desert and Alpine communities	5.56
C. texanus	
seedling2	2.54
adult3	13.33

(1 After Larcher, 1980 and Schulze, 1982)
(2 Present Work)
(3 After Stewart, et al. 1936)

Studies of *Cnidoscolus texanus*

Although several studies have been conducted on species of *Cnidoscolus*, only three papers have directly dealt with *C. texanus*. Perkins and coworkers (1975) studied its pollination, Pollard (1986) studied it in relation to herbivory, and Stewart et al. (1936) briefly described some characteristics of its unusually large root.

Stewart and his colleagues reported that a "medium-to-large" plant had an underground portion weighing approximately 20.0 kg while the aboveground portion weighed only about 1.5 kg. The top of the root was found 67.5 cm below the surface and the first root branching occurred at 110 cm. No annual growth rings could be found in the root. They excavated plants of various sizes and, presumably, ages. In seedlings, the top of the root was 15 cm below the surface. Depth of root-shoot junctions steadily increased with plant size and they concluded that *C. texanus* possessed a contractile root which pulled the root-shoot junction downward.

CHAPTER III

PROCEDURE

Anatomy

Seedlings collected in the field were used for the study of the underground organ. Whole seedlings were fixed in a FPA (formalin: propionic acid:95% ethanol:water, 2:1:10:7, v:v:v:v) solution (Sass 1958 p15). Tissues were prepared for infiltration via a series of tertiary butyl alcohol (TBA) solutions (Johansen 1940 p130). Tissues were soaked in each solution for 45 to 60 min. Three changes of TBA solution #6 were used and the last change left overnight on a warming tray. Paraffin was added progressively over three days with warming, the last 3-4 hr in a 60 C oven. The solution was decanted and replaced hourly with melted paraffin until the smell of TBA had disappeared. The tissues were imbedded in plastic molds containing melted paraffin and allowed to cool. Tissues were sectioned at 12 um using a Spencer rotary microtome. Sections were mounted on microscope slides using Haupt's solution and 4% formalin, carried through a staining schedule (Sass 1958 p70), and preserved under a cover slip mounted with Histoclad.

A mature plant was excavated from the field and refrigerated several days before sectioning. Due to the large,

fleshy nature of the tissue, whole preservation was not practical. Fresh tissue was sectioned at 20 and 40 um using a Spencer sliding microtome. These sections were stained before mounting using the schedule described above.

Anatomical study was accomplished with a compound light microscope and a binocular dissecting microscope. Fresh sections were stained with Lygol's iodine solution to determine if starch was present.

Population Biology

Five study sites with naturally occurring seedlings were selected in spring 1988. These were "Perkins" (R2E, T17N, S12 and 13), "washout" (R1E, T17N, S9), "windmill" (R1E, T17N, S9 and 16), "bridge" (R1E, T17N, S16), and "dairy" (R1E, T17N, S15). All sites were located in Payne County, Oklahoma.

The soil at the Perkins site was a deep Hawley fine sandy loam characterized by little or no slope. The soil type at the other sites was a Derby fine sandy loam with 5 to 15 percent slope characterized by hummocks to rolling hills on broad convex uplands (USDA 1987). Derby fine sandy loam was deep and somewhat excessively drained.

While *C. texanus* grew in other soil types, these soils were also sandy, deep, and well drained. Associated species included *Ambrosia psilostachya*, *Aphanostephus skirrhobasis*, *Helianthus petiolaris*, *Prunus mexicana*, and *Solanum carolinense.*

It was important to distinguish seedlings from yearings in order to study recruitment for one year. Potential seedlings were tentatively identified (small, single stem, non-flowering, small leaves with little lobing) then confirmed by carefully digging beside the plant until a seed attached to the stem was found. This could be done without harm to the plants. Older plants which could be confused with seedlings were also checked. No seed was found attached to any of these older plants.

Seedlings were marked with a flag. At intervals during the growing season seedlings were recorded as present or absent. After 17 September, seedling vigor was estimated by noting leaf number, amount of defoliation, and presence/absence. Seedlings were ranked from 0 (dead) to 5 (excellent) (fig. 1). Seedlings were again rated on two occasions the following spring.

Determining whether seedlings were dormant or dead when they were recorded as being absent was not possible. September 8 was arbitrarily chosen as a cut-off point; and seedlings absent before this date were considered to have died. Seedlings absent after 8 September were judged as being "absent" and not necessarily dead because end-of-season dormancy was possible. Hereafter, seedling "presence" means evidently alive, and "absence" means dead (before 8 September) or dead or dormant (after 8 September).

One hundred forty-four adult plants at the five sites were monitored to determine winter mortality. Every adult

plant in the sites was observed. Adults were ranked by the number of stems arising from the ground on 14 September. These plants were also monitored twice the following spring.

0	1	2	3	4	5
dead	dieback	naked stem no leaves	1-2 leaves	3-4 leaves	5+ leaves

Figure 1. Criteria used for estimating seedling vigor.

Allocation of Resources

In order to study the nature of seedling growth, deep pots were constructed from schedule 20 PVC (polyvinyl chloride) plastic pipe. Pipes 122 x 10 cm (length x dia) were split along one side, and the split taped closed. Splitting the pipes facilitated subsequent extraction of plants and soil. The bottom of the deep pots was closed and drain holes provided.

Washed sand from the floodplain of the Cimarron River was used for the growing medium to simulate natural growing conditions. The sand was oven dried for not less than 6 hr at 120 C, in order to kill most pathogens and weed seeds.

Seeds were germinated in Grace Metro-Mix in the lab at 30 C and were transplanted when they had at least one true leaf. Seedlings were planted in deep pots with the entire soil column moist and were rewatered as needed.

The pots were supported outdoors by a wooden frame. A 1.2 x 2.1m clear acrylic plastic top was fitted approximately 60 cm above the top of the pots. The design allowed normal light intensities, normal temperatures, and good air circulation while excluding rainfall and damaging weather.

Eleven-plant lots were harvested at 10-day intervals on 8 occasions. Plant and soil were removed from the pot and carefully separated. The experiment was conducted from 20 June to 18 September, 1989. Harvested plants were cut into root and shoot portions. Tissues were oven dried at 105 C for 48 hr, then allowed to equilibrate in laboratory

conditions for 24 hr. Dry weights were measured using a Mettler analytical balance.

CHAPTER IV

RESULTS

Anatomy

All seedlings exhibited a thickened underground tissue, the top of which was 3-8 cm below the soil surface. The surface of the thickened tissue was brown and slightly corky. No visible buds or internodes were present. Many seedlings had horizontal wrinkles near the top of the thickened tissue. Internally, this thick, underground tissue exhibited a xylem core, centripetal xylem maturation, and lacked a pith. Secondary growth was occurring in all seedling tissue. Crystals were present in all thickened, underground tissue. Lygol's iodine solution turned the crystals blue-black, indicating the presence of starch. In the center, some xylem elements lay in many planes relative to the organ axis. Longitudinal sections revealed xylem elements which were wavy throughout their length.

Arising from the top of the thickened tissue was an apparent stem to which the seed was often attached, and which extended above the soil surface. Dormant buds were present along this apparent stem. It exhibited centrifugal xylem maturation, a pith, and a tetrarch stele in primary growth. No crystalline granules were present.

Older plants also possessed a thick, underground tissue with a similar brown surface. Above the root, a perennial stem extended to 10-15 cm below the soil surface. At the top of this perennial stem were buds from which arise next years' growth. Buds and internodes were lacking. The internal features of older plants were similar to those of seedlings except that the innermost xylem was entirely twisted. The twisted xylem occupied a greater cross-sectional area in the upper part of the tissue than in the lower part. Longitudinal sections revealed some long xylary elements which undulated strongly throughout their length, while others were only slightly wavy. A branch from the thick underground portion exhibited the same anatomical features except that a twisted xylem core was lacking.

Population Biology

Two-hundred four seedlings were monitored in five sites. Newly emerged seedlings were first observed on 24 May. Newly emerged seedlings were also observed on 11 June, 25 June, and 11 July. However, only 15 and 2 seedlings were seen on 25 June and 11 July, respectively.

Numbers of seedlings in the 1988 cohort declined as the growing season progressed (fig 2). Seedling presence decreased to 65% on 8 September, then declined more rapidly until no seedlings were present after 3 November. Eighteen seedlings from the Bridge population were destroyed after the growing season but before emergence the following

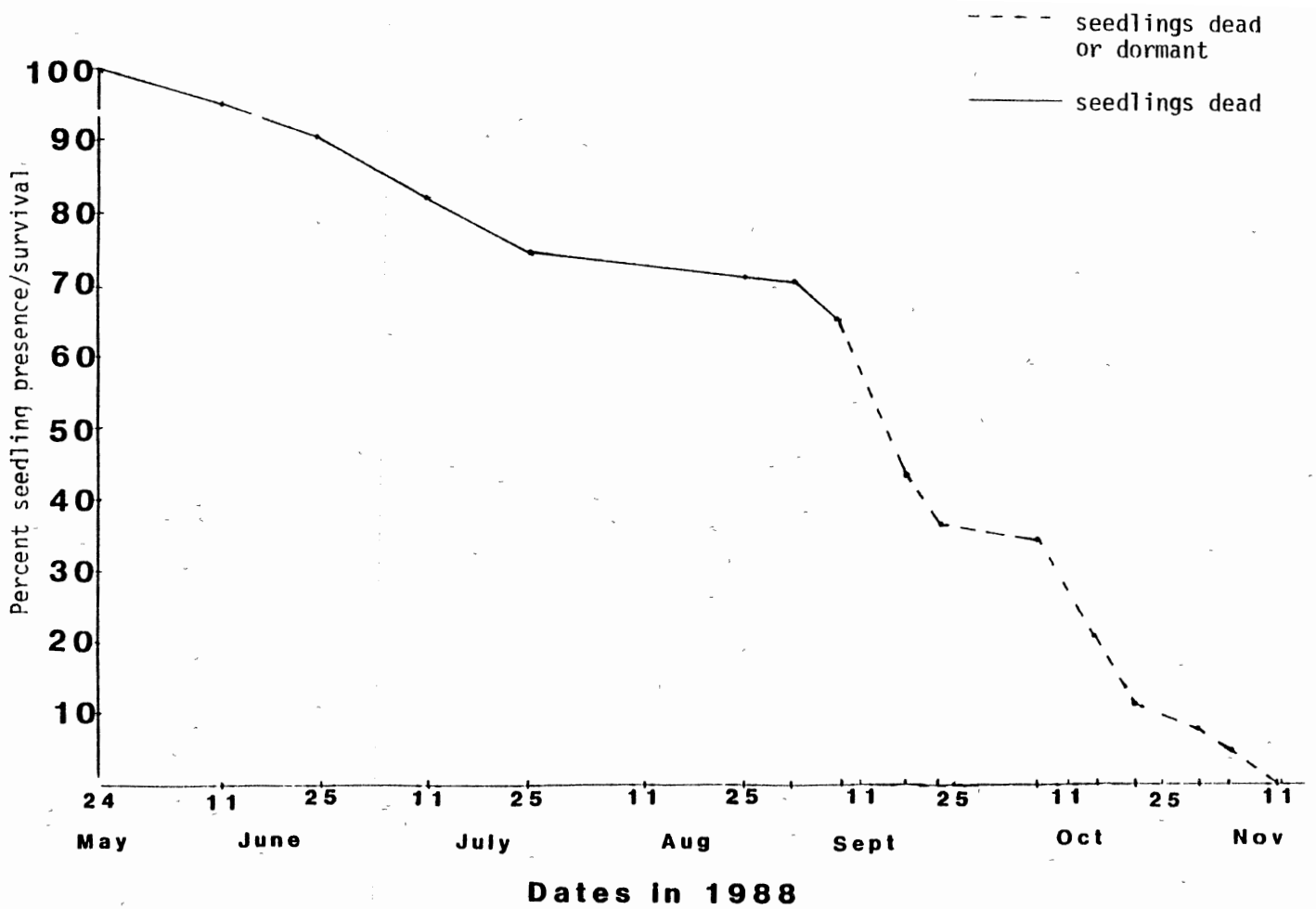

Figure 2. Percent seedling presence/survival for C. texanus. New seedlings marked and rechecked at 2-3 week intervals; N=186. Seedlings absent before 8 September were assumed to have died. Seedlings absent after 8 September were assumed to have died or gone dormant.

spring. Twenty-five of 186 seedlings emerged the following spring, a 13.4% survivorship for one year.

Washout, Windmill, and Perkins sites were not significantly different for fall 1988 average seedling rank (tables II and III). The Dairy and Bridge populations were different statistically at the $p < 0.05$ level. After the destruction of the bridge population, seedlings from all other sites were combined for statistical purposes.

In 1988, May and June each received about 56 mm less than average precipitation (table IV). The two dates, however, when most seedlings were observed to have emerged, 24 May and 11 June, were both preceded by a substantial rain 8 days earlier.

Rate of seedling overwintering showed a positive relationship to the previous fall's average vigor rank (table V), with the most vigorous seedlings surviving best.

Of the 144 adult plants monitored, only one died over winter, a mortality rate of 0.69%. Adult plant size based on stem number in adult plants is presented in figure 3.

TABLE II

ANOVA COMPARING FIELD SITES USING SEEDLING RANK AS A MEASURE OF SITE DIFFERENCE

Source	df	ss	ms	F
among	3	9.968	3.323	4.134**
within 74	59.478	0.804		

** significant at the $p < 0.01$ level

TABLE III

AVERAGE SEEDLING RANK FROM 8 SEPTEMBER TO END OF GROWING SEASON FOR FIELD STUDY SITES

Site	x	N
Perkins	2.48	55
washout	3.18	10
windmill	2.16	8
dairy	3.53	5

TABLE IV

1988 MONTHLY RAINFALL RECORD AND
LONG TERM AVERAGE FOR
PERKINS, OKLAHOMA

	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT
Total	141.0	123.5	70.8	30.7	66.5	21.6	196.1	34.0
Long term average	5.1	68.1	129.1	87.1	93.0	48.5	102.1	77.5
Deviation	90.4	61.5	58.2	25.4	27.4	27.0	85.6	29.7

Rainfall amounts are recorded in mm.

TABLE V

RELATIONSHIP OF AVERAGE SEEDLING VIGOR RANK IN FALL 1988 AND PERCENT SEEDLING EMERGENCE IN SPRING 1989

Avg Fall 1988 vigor rank	N	% seedling emergence spring 1989
1.00 - 1.99	16	12.5
2.00 - 2.99	31	29.0
3.00 - 3.99	26	38.5
4.00 - 4.99	8	50.0

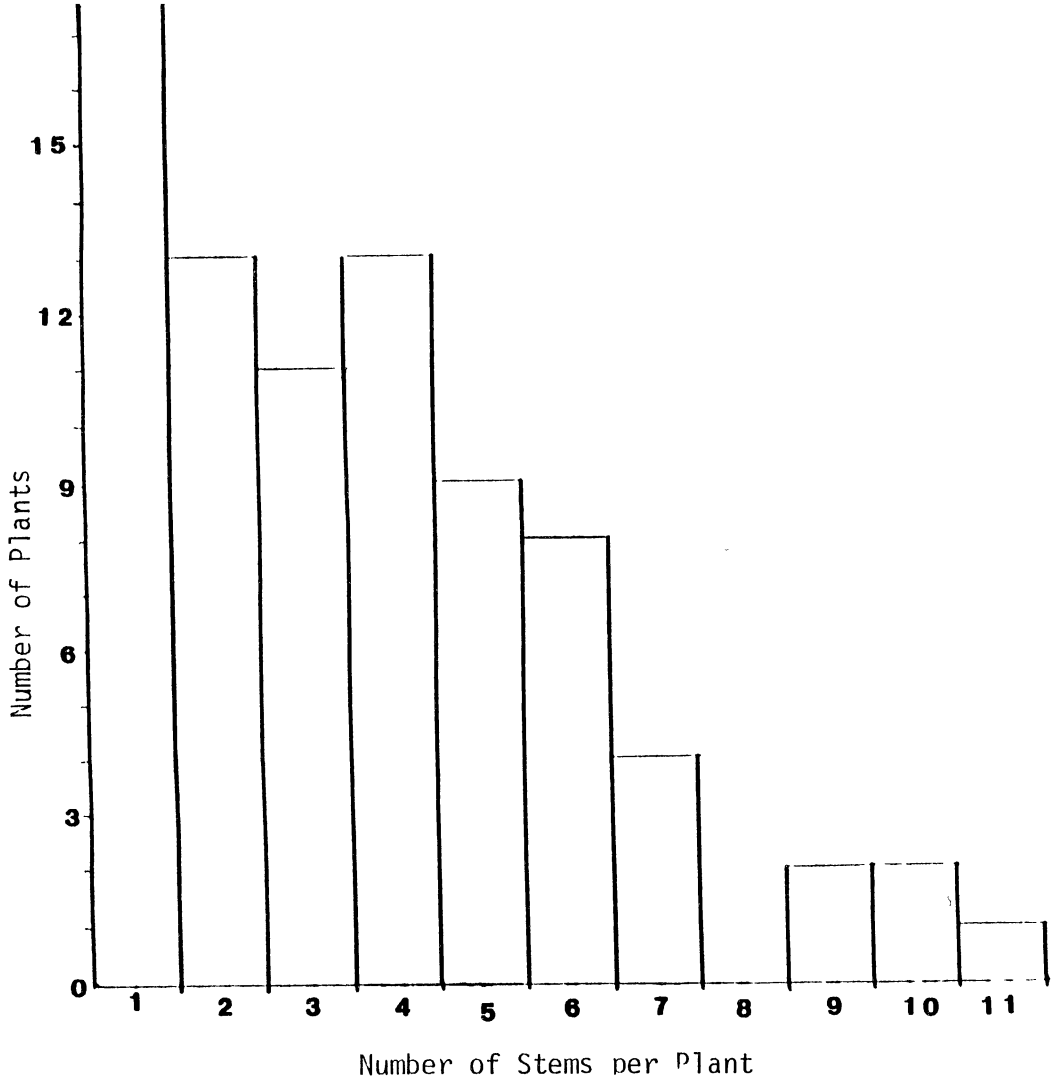

Figure 3. Distribution of stem number in adult C. texanus; N=144. First-year seedlings not included.

ALLOCATION OF RESOURCES

Shoots (figure 4) showed increasing mean weights through the 60-day interval, then a decline for the 70 and 80-day old plants. The least significant difference (LSD) at the $p < 0.05$ level was 55.18 mg. The 10 and 20-day old plants were not significantly different from each other however, they were different from the 30, 40, and 50-day old plants. Sixty day old plants were significantly different from the 70 and 80-day old plants.

Root weights (figure 5) also showed increasing mean weights to the 60 day interval, then a decline for the 70 and 80-day old plants. The LSD at the $p < 0.05$ level was 136.9 mg. The 10 and 20-day old plants were significantly different from the 30-day old plants. Forty and 50-day old plants were different from the highest average root weight at 60 days. Seventy and 80-day old plants were significantly lower than the 60 day old plants.

Correlated with stem dry weight was stem length (figure 6). Ten day old plants were different ($p < 0.05$) from 20-day old plants. Thirty and 40-day old plants differed from the 50, 60, 70, and 80-day old plants. However, the 50, 60, 70, and 80-day old plants were not significantly different from each other. Stem length increased through 60 days and then declined. The LSD for stem length was 2.18 cm.

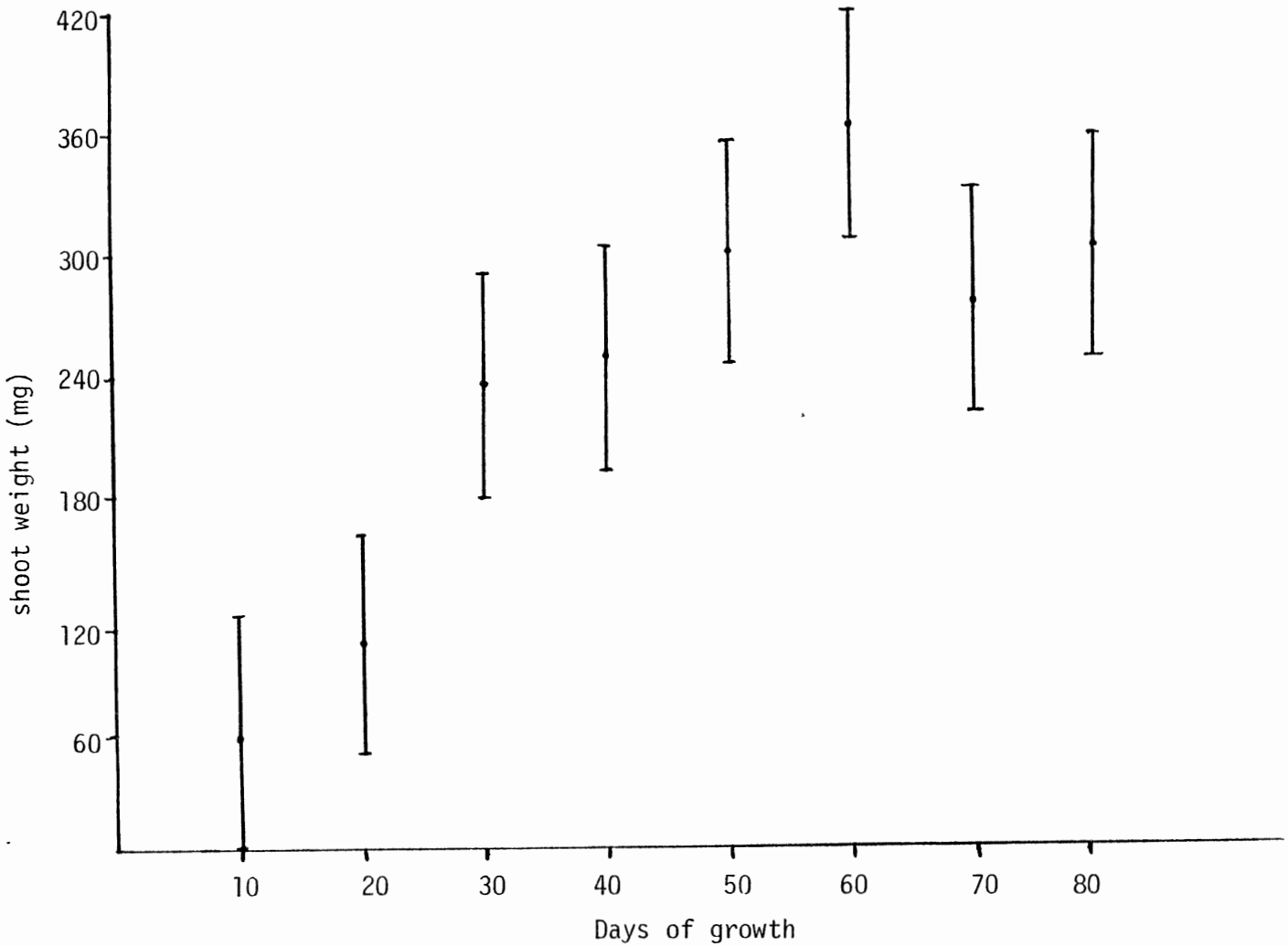

Figure 4. Oven dry shoot weight of experimental, container-grown *C. texanus* seedlings. Confidence bars represent $LSD_{0.05}$

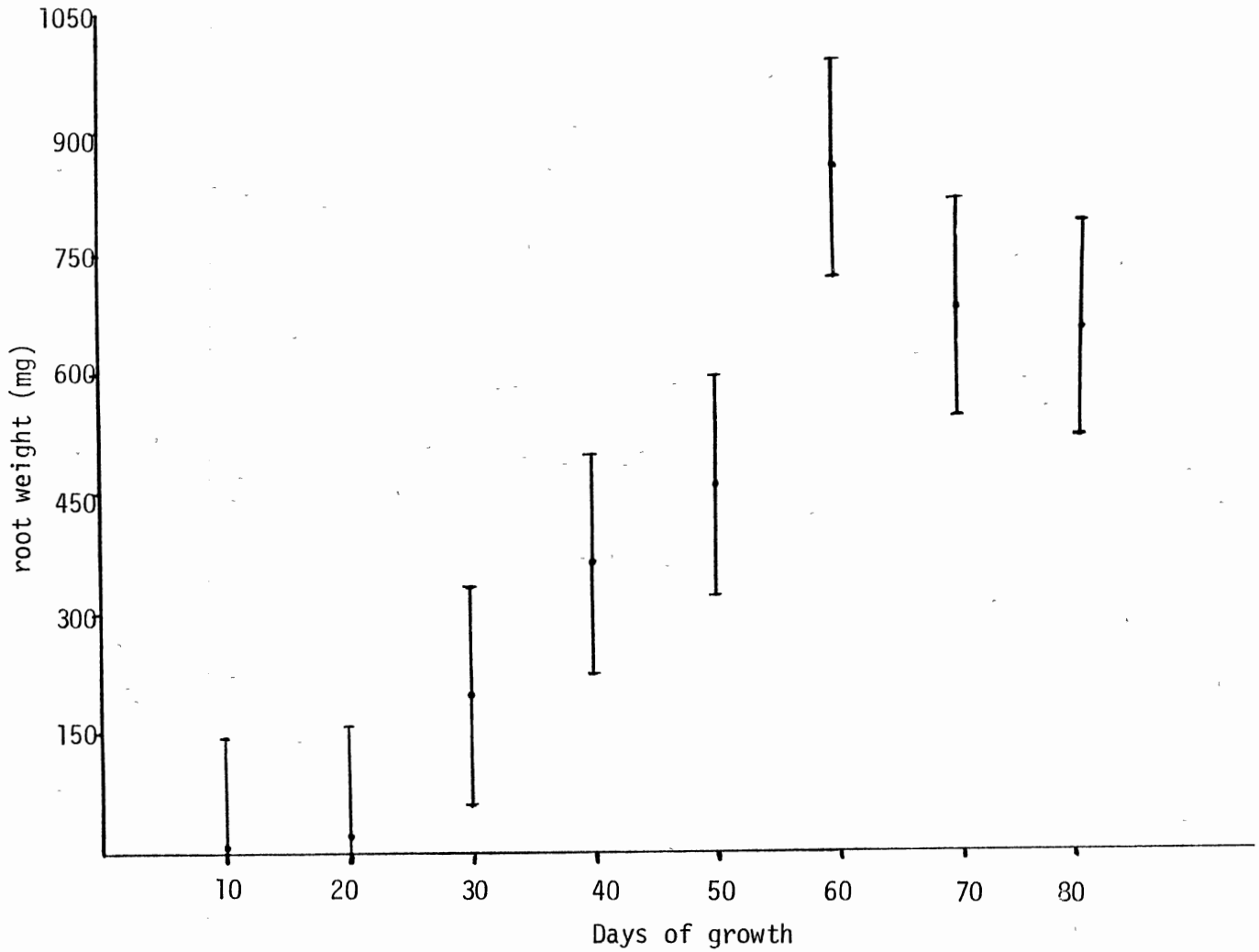

Figure 5. Oven dry root weight of experimental, container-grown C. texanus seedlings. Confidence bars represent $LSD_{0.05}$

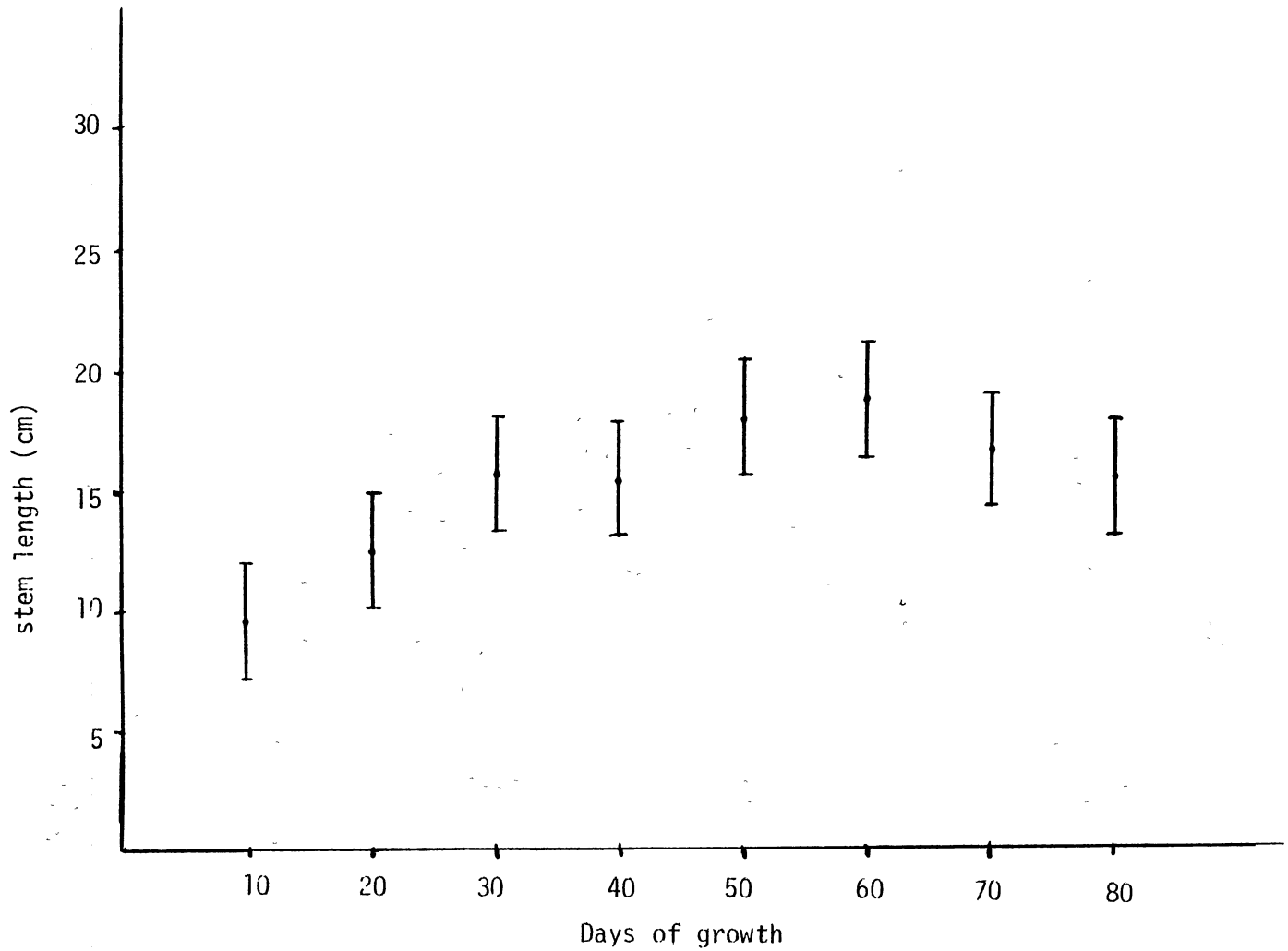

Figure 6. Stem length of experimental, container-grown C. texanus seedlings Confidence bars represent $LSD_{0.05}$

Related to stem length and shoot weight was leaf number. Ten-day old plants differed from 20-day old plants ($p < 0.05$; LSD = 0.61). Thirty, 40, and 50-day old plants were not significantly different from each other but were higher than 60 and 70-day old plants. The 60 and 70-day old plants were higher than the 80-day old plants (figure 7).

Root-shoot ratios were less than 1.0 during the 10, 20, and 30-day intervals. Root-shoot ratios surpassed 1.0 between the 30 and 40-day intervals and peaked at the 70-day interval (table VI).

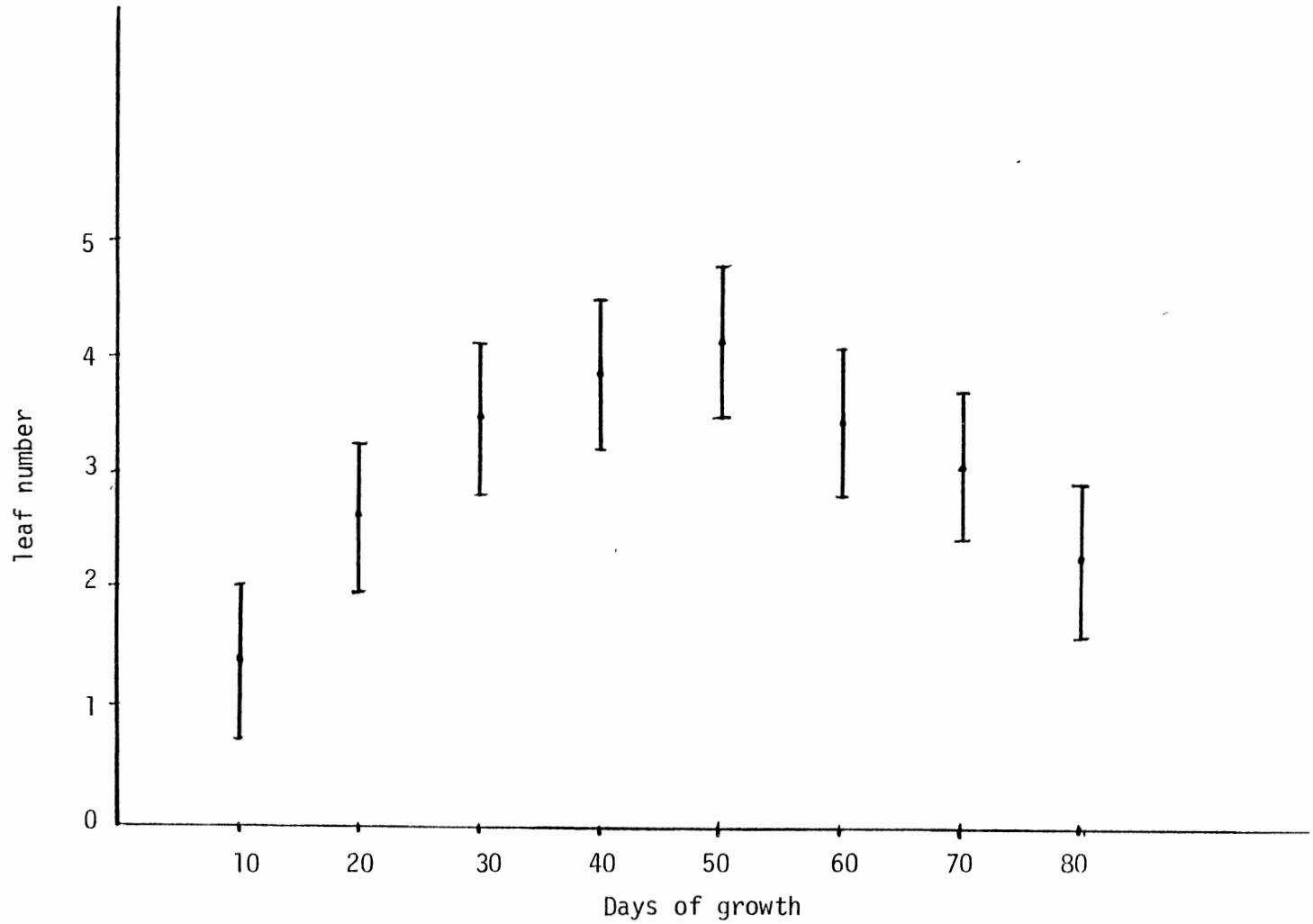

Figure 7. Leaf number of experimental, container-grown C. texanus seedlings. Confidence bars represent $LSD_{0.05}$

TABLE VI

SEEDLING ROOT-SHOOT RATIOS OF CONTAINER GROWN PLANTS FOR 10-80 DAYS

days of growth	N	root-shoot ratio
10	9	0.20
20	10	0.32
30	11	0.87
40	9	1.47
50	9	1.52
60	11	2.28
70	10	2.54
80	11	2.28

CHAPTER V

DISCUSSION

Anatomy

Externally, the absence of nodes or internodes and internally, the xylem core, centripetal xylem maturation, and lack of pith confirms that the large underground organ is root tissue. Wrinkled periderm near the top of the root indicates that contraction occurs. The root grows thicker during contraction, and also serves as a storage organ as indicated by the starch granules present in large quantities. Thickening of roots during contraction (Esau 1965) and the development of contractile roots into a storage organ has been reported for other plants such as Melilotus and Asparagus (Bottum 1941, Rimbach 1899). Arising from the top of the large root perennial stem tissue persists from year to year which extends upward to 10-15 cm below the soil surface. Above this tissue, the tissue dies back at the end of the growing season. Stewart et al. (1936) correctly identified the annual portion as stem tissue on the basis of its external features. I confirmed their findings via anatomical studies.

Older plants also possessed a much-thickened root, the top of which occurs progressively deeper with increasing age. Thus the plant contraction appears to continue at least for several years. The twisted xylem core, more prominent near the top of the root and lack of contraction in smaller, thickened branch roots arising from the base of the large root suggests that contraction has occurred for a substantial time in the same root. This phenomenon has also been reported in Panax and Taraxacum (Grishvitskii 1952; Rimbach 1899).

The depth of perennation in C. texanus remains constant throughout its life. Perennial stem tissue above the root in adults maintains a constant depth (10-15 cm) for overwintering buds. The contractile root pulls the upper part of the root system deeper into the ground by a small amount every year. To maintain a constant depth, the perennial stem grows a compensatory amount towards the soil surface each year.

The adaptive significance of a contractile root in C. texanus is unclear. Esau (1965) postulated that contractile roots in general draw the shoot apex near or belowground placing it in an optimal environment for growth and development of adventitious roots. While this may be true in other species, the depth of the root-shoot junction in C. texanus (10-67 cm) seems excessive for this purpose. Further, no adventitious or lateral roots are present. Drawing the shoot apex a few centimeters belowground would seem

sufficient. I suggest, as an alternative hypothesis, that the contractile root, by withdrawing progressively further below the surface, lessens the chances of the root-shoot junction being uncovered by wind erosion. C. texanus commonly occurs in marginally stabilized dune habitats which are subject to such erosion, and a mechanism for minimizing these effects seems adaptive.

Population Biology

Seedling presence declined steadily through the growing season. A steady decline in the field indicated that seedling mortality was age-independent. The causes of seedling mortality were unclear.

Seedlings with the highest vigor at the end of the growing season had the highest survival for one year. Therefore, selection favored larger seedlings during the period of establishment. However, it has been shown in some perennial populations that recruitment varies dramatically from year to year (Tamm 1972). Each cohort presumably, would be established under different conditions.

I assumed that a positive relationship existed between adult plant size and age. Harper (1977) stated that if exact plant age cannot be determined, the largest plants are certainly the oldest. The populations monitored were typical of invasive populations, with a high proportion of young age classes and few older individuals. The survivorship overwinter for adults was very high. High survival

suggests few senescent plants which is also typical of invasive populations. Some caution is needed with this interpretation, however, because nothing is known about the normal longevity of the plants.

Seedlings were twice observed to have emerged 8 days after a significant rainfall event. This suggests that rainfall could trigger germination. However, germination could have occurred steadily with no relationship to the rain. Seedlings were observed only on these dates and not between.

Assuming May and June 1988 were "normal" rainfall months, no seedlings should have survived if the hypothesis that an exceptionally favorable season is required is correct. Despite May and June 1988 being below normal for rainfall, seedlings did survive. Therefore, recruitment appears to be an ongoing process. This is contrary to the pulsed recruitment typical for many phreatophytes (Turner 1972).

Allocation of Resources

Increasing root-shoot ratios of C. texanus during the growing period supported the hypothesis that phreatophytes establish a deep root system before extensive growth occurs (Brock 1986; Williams 1972). Root-shoot ratios less than 1.0 are normal for very young plants which are establishing a root and shoot system (Brouwer 1983). The energy in the endosperm presumably drives early growth. Later, the plants

possess root-shoot ratios which are characteristic for plants growing in specific communities (Table I) (Mooney, 1972).

While the young plants of C. texanus do not possess an extremely high root-shoot ratio, older plants almost certainly do. A mature plant weighed by Stewart, et al. (1936) had a wet root-shoot ratio of 13.33. Compared to other plants of various communities (table I), the root-shoot ratio of C. texanus is extremely high.

Both root and shoot dry weights peaked at 60 days then declined significantly. The most probable explanation for this drop in weight was the partial leaf senescence of the 70 and 80-day old plants. The 70 and 80-day old plants were somewhat chlorotic and less robust than the younger plants. Analysis of leaf showed the highest values occurred on the 30, 40, and 50-day old plants then significantly declined with increasing age. I hypothesize that the older plants were in the process of producing their second crop of leaves for the season when dry weights were taken and were temporarily using reserves of carbohydrates before a second surge of growth. Bazzaz and Harper (1977) and Abul-Faith and Bazzaz (1980) have shown that plants produce leaf cohorts through the growing season. These leaf cohorts have a specific life span and senesce through the growing season. Analysis of stem length showed a steady increase with increasing plant age. The greatest stem lengths occurred on the oldest plants even though shoot weight declined during

this same period. The most likely explanation for decreasing shoot weight was leaf loss.

Seedlings were observed to either go dormant or die in the field after 8 September. The dormancy mechanism was unclear and but unrelated to seedling rank. The growing period for older container-grown seedlings extended 10 days past 8 September so dormancy must not be excluded as a possible explanation for leaf drop and chlorosis.

In summary, C. texanus possesses a fleshy contractile root which also functions as a storage organ. The root pulls the root-shoot junction very deep into the ground. This seems adaptive to living in marginally stabilized habitats where being uncovered is a possibility. Seedlings several weeks old develop a deep groundwater-tapping root system before putting on much top growth. This is typical of the phreatophyte habit and maximizes the seedlings' chances for survival. Data from one year suggests that, contrary to other phreatophytes, C. texanus recruitment is ongoing rather than pulsed. Adult plant mortality was extremely low indicating that C. texanus is a fairly long-lived herbaceous perennial.

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VITA

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