

PROFESSIONAL PAPER
BIOMASS ALLOCATION RESPONSE OF SITANION HYSTRIX
TO SOIL WATER STRESS

Submitted by
M. Laurie McDonell
Department of Range Science

In partial fulfillment of the requirements
for the degree of Master of Science
Colorado State University
Fort Collins, Colorado
November, 1986

ACKNOWLEDGEMENTS

I would like to express my sincerest gratitude to Dr. Charles Bonham, for his continual faith in my efforts, and to my fiancè, Dr. Richard Aguilar, for his inspiration and encouragement. I also owe special thanks to my parents, Dr. and Mrs. William McDonell, for their guidance and support.

TABLE OF CONTENTS

	<u>Page</u>
I. Problem	1
II. Introduction	2
Development of Water Deficits	4
Effects of Water Deficits	7
Influence of Mineral Nutrition on Plant Response During Water Stress	10
III. Current Studies on Biomass	11
IV. Methods	14
V. Results and Discussion	16
Root Shoot Ratios	16
Optimum Biomass Production Pure Culture	19
Optimum Biomass Production Mixed Culture	21
Variance of Percentage Root Biomass	23
Variance of Differences Between Leaf and Stem	23
IX. Conclusions	25
X. Appendix	30

LIST OF TABLES

	<u>Page</u>
1. Percentages of Root, Stem, Leaf, and Seed Head Weights of Each Repitition of the Pure Cultures	31
2. Percentages of Root, Stem, Leaf, and Seed Head Weights of Each Repitition of the Mixed Cultures	32
3. Root Shoot Ratio Summary	17
4. Total Mean Leaf, Stem, and Root Percentages for the Pure Cultures	18
5. Total Mean Leaf, Stem, and Root Percentages for the Mixed Cultures	20
6. Means for Leaf, Stem, Root, and Total Plant Biomass for the Pure Cultures	20
7. Means for Leaf, Stem, Root, and Total Plant Biomass for the Mixed Cultures	22
8. Variance for percent Root Biomass for the Pure Cultures	24
9. Variance for Leaf and Stem Biomass Differences	24

LIST OF FIGURES

	<u>Page</u>
1. General Model Based on Diurnal Uptake of Soil Moisture and Transpiration of Plants	5
2. Carbon Flow in the Plant	26
3. Graphed Responses for the Dry Cycle Pure Culture	33
4. Graphed Responses for the Moist Cycle Pure Culture	35
5. Graphed Responses for the Wet Cycle Pure Culture	37
6. Graphed Responses for the Dry Cycle Mixed Culture	39
7. Graphed Responses for the Moist Cycle Mixed Culture	41
8. Graphed Responses for the Wet Cycle Mixed Culture	43

PROBLEM

I suspected the effects of association with snakeweed, Gutierrezia sarothrae and soil water application gradients would suppress biomass production of squirreltail, Sitanion hystrix, therefore, the following hypothesis was formulated:

Ho: There are no effects of snakeweed association on biomass production and allocation of squirreltail while undergoing different levels of soil water stress.

I proposed to test this hypothesis by observing biomass production of single plants of squirreltail each paired with single plants of snakeweed in isolated cultures. These species in combinations were subjected to three watering regimes and effects compared to those of interactions between pure pairs of squirreltail.

This experiment tested the effects of competition for soil water on plant biomass of squirreltail. Competition for soil oxygen may also be a significant factor due to the poor structure of the sifted heavy clay soil used in the cultures. The high soil clay content also caused a high soil matric potential which reduced soil water potential. This accentuated water stress effects. Success (or greatest biomass production) was determinant upon the vigor with which each species collected its resources from above and below ground and the effect this had on its neighbor.

Though very little previous information has been

generated for squirreltail on competition and water-stress, the following generalizations may be assumed: 1) Similar plants will compete the most vigorously for limited resources due to similar resource requirements, and subsequently, 2) plants with similar root systems will compete the most vigorously (as opposed to fibrous vs. taproot). Snakeweed possesses a taproot system unlike the fibrous roots of squirreltail. However, snakeweed should be an aggressive competitor due to an additional extensive lateral root system.

INTRODUCTION

Experiments in which two or more species are grown together in the same pot or plot are conducted to determine the effects associated plants have on each other. Such a study would contribute to the understanding of the development of rangelands, the use of one species to control another, or the effects of introduction of beneficial or harmful species. The present study will give somewhat limited results because it excluded factors possibly present in more diverse field situations. It will, however, lay a groundwork of knowledge and enable an observer to assess some of the effects which are likely to be important (Williams, 1962). Controlled-environment research identifies plant behavior simply and most rapidly without the complicating effects of environmental variability. This aids the researcher in identifying factors that may have importance in field environments (Boyer, 1982).

Competition arises when one individual is sufficiently close to another to modify its soil environment and, thereby, decrease or alter its rate of growth (Milthorpe, 1961). Competition is a mechanism which produces stress for water or nutrients in plants; barring allelopathy. Competition may then be a term defining or questioning merely the degree of stress induced on a given plant. The main issue of concern then is the stress which is induced from the lack of resources. Competition raises the question of "how much?". The physiological effects of water stress may be the primary factor influencing partitioning of biomass and is therefore presented in more detail from the literature.

Physiologically active plants are composed of approximately 85-90% water. Many physiological activities of many plant species are impaired if the water content falls much below this level (Turner and Kramer, 1980). Slayter (1967) stated "that water deficits interfere with plant growth, and if severe, cause death of plants, is undoubtedly one of the most common and self-evident observations which can be made". Yet over one-third of the earth's surface is classified as arid or semi-arid because it is subject to permanent drought (Kramer, 1983). Drought stress can be made possible or more severe also by plant competition in these dry areas and in other more mesic environments. Many studies have been conducted on the effects of competition and soil water stress on plants; however, little research has been done on biomass partitioning of the water-stressed plant.

Water deficits not only reduce the dry matter product of plants but also change the partitioning of carbohydrates among organs. Kramer (1983) stated "Perhaps the most important contribution that could be made toward increasing plant production would be sufficient understanding of the control of partitioning so more photosynthate could be channeled into economically important sinks such as seeds and fruits." The survival and economic value of plants is determined largely by the manner in which the products of photosynthesis are partitioned among the various plant organs.

Literature on physiological and morphological effects of water stress will be presented in this paper; followed by a number of recent studies conducted through competition induced situations. The studies place primary emphasis on plant biomass partitioning in response to competition induced stress. Biomass partitioning may be a survival mechanism and is a cumulative result of the physiological activities occurring under stress.

Development of Water Deficits

Water deficits occur at times when plant transpiration exceeds soil water absorption. This occurs daily to a slight degree and often has minimal effects on the plant (Figure 1). During morning hours there is an adequate volume of available water in the turgid parenchyma cells of the leaves and stems, and thus a major resistance to water flow from soil to root xylem. Water flows from non-evaporating parenchyma cells,

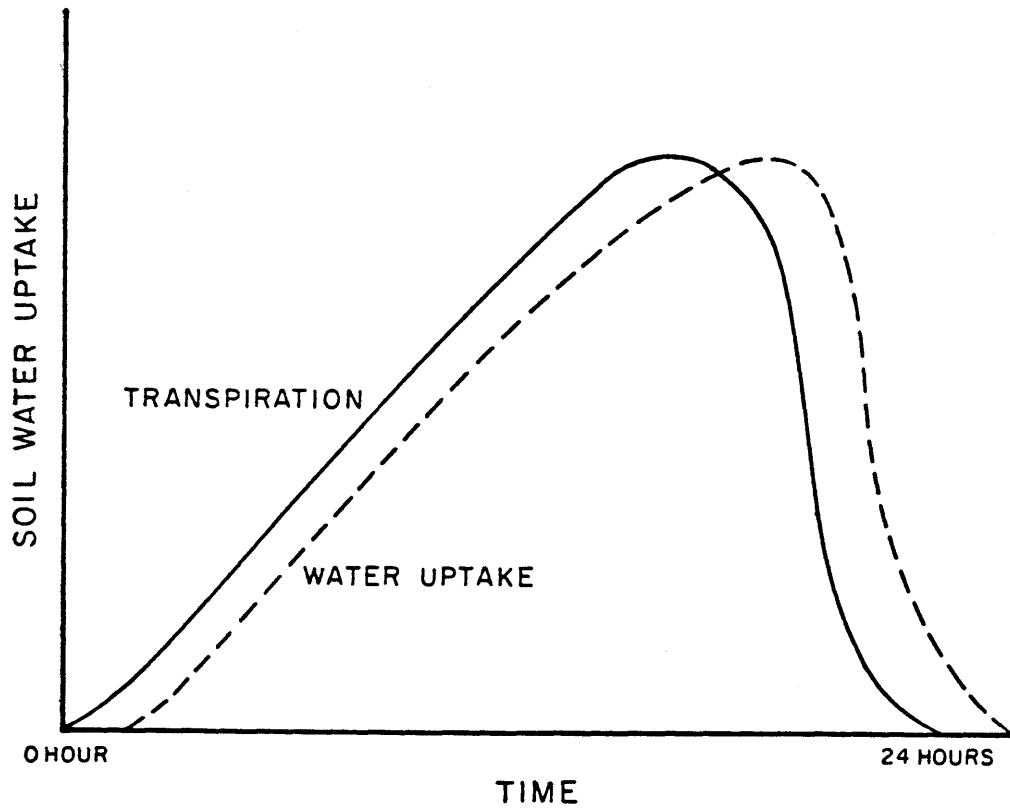


Figure 1. General Model Based on Diurnal Uptake of Soil Moisture and Transpiration of Plants.

The plant is not immediately recharged with soil water following commencement of transpiration, due to plant resistance. This creates a small daily water deficit in the plant which is recharged when absorption exceeds transpiration.

which have a low resistance to water loss, to the evaporating plant cells. By noon, leaves lose their turgor and bulk leaf water potential becomes so low that most water used by the plant is absorbed through the roots. Stomata begin to close by afternoon, decreasing transpiration, but absorption continues rapidly until parenchyma cells are saturated and water potential is too high to allow water movement (Kramer, 1983). Plant breeders in pursuit of higher yields have succeeded in altering midday water deficits, giving plants a more favorable water status (Boyer, 1982).

Competition and drought stress often cause development of long-term water deficits which begin with the daily cycle. As the soil continues to dry, less recovery is possible. Availability of soil water is decreased during drought stress until daytime water loss cannot be replaced, and causes the plant to wilt. Leaves do not recover turgor at night when the plant reaches wilting point. This occurs when soil water potential decreases to the level of wilting leaf water potential (Kramer, 1983).

Small values of soil water potential minus leaf water potential are adequate to sustain flow within plants with high root density and large root zones. Transpiration may be relatively unaffected almost to the plant's permanent wilting point under low evaporative conditions. Growth rate of the plant is, however, likely to be affected (Slayter, 1967).

Internal water deficits are dependent upon evaporative demand, root and soil water potentials, and gradients of

water potentials within the plant. Water potential gradients are a function of degree of stomatal closure within the plant. Root water potential is a factor dependent upon the amount of soil per unit length of root, bulk value of soil water potential and the hydraulic conductivity of the soil (Slayter, 1967).

Effects of Water Deficits

The amount of injury caused by water stress is largely dependent upon the stage of plant development at which the stress occurs (Kramer, 1983). An accelerated breakdown of RNA and possibly DNA occurs as water deficits become long-term for a plant. Leaf temperatures increase due to stomatal closure even during a low level of stress. Reduction in leaf turgor and exchange of CO₂, and an increase in respiration can result in a decrease of photosynthesis. Rate of cell enlargement is highly sensitive to a decrease in cell turgor, which reduces leaf area expansion. Cell division rate, also, becomes markedly reduced as water stress becomes more severe; though this has a less important impact on plant growth than cell enlargement. Stomata also remain closed for a substantial portion of the day as stress increases. Subsequently, leaf temperatures continue to rise. Overall plant growth rates approach zero, apparent photosynthesis almost completely comes to rest and respiration gradually diminishes (Slayter, 1967).

Disruption of normal cell metabolism causes carbohydrate and protein breakdown and brings about migration of soluble

leaf nitrogen and phosphorus compounds from older leaves to the stem. Cell division and elongation cease as dehydration continues. Subsequently, as respiration continues, there is an increased loss of dry weight. Overall growth rates become negative. As dessication continues, individual cells and tissues die. Often older, lower leaves die first, especially if stress occurs slowly (Slayter, 1967). Sufficient osmotic adjustment may occur when water stress increases slowly and may enable plant growth to continue at a lower water potential than would otherwise be possible (Kramer, 1983). Much of the solute derived to lower plant osmotic potential, however, is obtained from recent or stored photosynthate (Michelena and Boyer, 1981). Younger leaves with the lowest water potentials die first if stress is brought about suddenly. Whether the above ground portion or roots die first depends on the plant species and severity of drought (Slayter, 1967).

The response of the apical meristem to drought is often critical because of its role in development of the plant shoot. The apical meristem is able to survive severe levels of drought better than many other plant tissues possibly because the tissue is protected from evaporative losses due to its position within the mature leaf sheaths. This protection of the growing tissue from direct transpiration may be an adaptation to dry conditions that is unique to grasses (Michelena and Boyer, 1981). Water content of the apex changes little during stress because it is not connected to

the stem by functional xylem vessels. Subsequently, the meristem is able to continue accumulating solutes for osmotic adjustment. The apex is also a major nutrient sink and remains so throughout stress. Turner and Kramer (1980) stated that the characteristics mentioned above suggest that the position of the apex may be responsible for the plants tolerance to drought, rather than the unique qualities of meristematic cells.

Similarly, Watts ([1974] in Kramer, 1983) stated leaf elongation in grasses is controlled by the water status in the embryonic region at the base of leaves, which may be affected differently than the more exposed central and terminal regions. Michelena and Boyer (1981) reported elongation occurred in the basal region of maize (Zea mays L.) which was enclosed by other leaf sheaths. Leaf elongation decreased and finally ceased when water was withheld from the soil, even though solute potential had sufficiently decreased in the embryonic region to maintain turgor almost constant. The exposed leaf lost turgor, however, and wilt symptoms developed. Michelena and Boyer suggested that though the embryonic region is uniquely adapted to maintain turgor pressure under stress, some other unknown factor is perhaps also responsible for the low growth rates associated with the water stress.

Recovery of the plant following a soil water recharge is often delayed due to root damage which causes a reduction in water absorption rates. Normal metabolism including cell

division and photosynthesis takes time to re-establish after turgor recovery and leaf expansion because of the nutrient dislocation during stress. The increased rate of senescence of leaves is possibly associated with a partial permanent loss of stomatal function ([Slayter & Bierhuizen, 1964] in Slayter, 1967). Meristematic tissues and most active leaves will experience the most rapid growth rates of the overall plant because nitrogen and phosphorus migration is least pronounced in these tissues during stress (Slayter, 1967). Acevedo, et al (1971), however, reported completely compensated leaf length by a transitory rapid growth upon release of short and mild stress of maize seedlings. It is likely that the extent of growth re-establishment following stress is dependant upon stress severity and duration, and individual plant species.

Influence of Mineral Nutrition on Plant Response

During Water Stress

Conflicting evidence creates a difference of opinions over the effects of fertilizer application during water stress. Turner and Kramer (1980) stated that fertilizer applications will most likely be beneficial under sporadic drought conditions, though the benefits may not be as great as in well-irrigated crops. Fertilizer application is uncertain where soil water content is perpetually low. Factors influencing fertilizer effect are initial water status of the soil profile, root growth, and moisture use by plants where soil water content decreases steadily over the growing season.

CURRENT STUDIES ON BIOMASS

Eckert and Spencer (1982) reported an experiment on basal area growth of Thurber needlegrass (Stipa thurberiana (Nutt.) J.G. Smith) and squirreltail (Sitanion hystrix (Pursh) Britt. and Rusby) responses to weed control. Results showed that basal growth of squirreltail was more variable than that of Thurber needlegrass, particularly in low precipitation years. Reduction in basal cover of squirreltail occurred after two consecutive years of low precipitation during which time dead cover increased by 77%, as opposed to an increase in basal growth of Thurber needlegrass and a lower increase in dead cover by 16%. Basal growth resumed at a greater rate for squirreltail after the following moist year. In spite of this, by the end of the six year study, the Thurber needlegrass plants were significantly larger (140 cm) than the squirreltail plants (110 cm) due to the less exaggerated response to the dry years. Eckert and Spencer suggested that perhaps the squirreltail species is not as well adapted to dry habitats as climax-dominant Thurber needlegrass plants. This can be correlated to Kupper's (1985) statement that early successional species, such as squirreltail, have higher photosynthetic capacities than mid- or late-successional species. Thus, there is a need for more nitrogen, because photosynthetic capacity is closely linked to nitrogen content of leaves. Earlier successional species should, therefore, have a competitive disadvantage in drier environments because they require more nitrogen for carbon gain.

In a study on the effects of water stress on coastal bermudagrass (Cynodon dactylon (L.) Pers.) and Kleingrass "75" (Panicum coloratum L.), Bade, et al (1985) noted that cell enlargement, stem elongation, and yield were reduced as well as leaf area and shoot/root ratio. Leaf weight percentage relative to the entire plant for the stressed plants were, however, greater; even over a range of temperatures. The degree of reduction differed between the two species, though both showed reductions in total yield, tillers/pot, leaf area/pot, and plant height due to water stress. The reduced number of tillers per pot resulted in less dry matter yield and reduction of plant height indicated an overriding effect of water stress on stem elongation.

Interesting results were obtained through Kupper's (1985) study on carbon relations and competition between woody species. The proportion of carbohydrates partitioned into leaves was found to be similar in all species regardless of growth form or input of the actual plant. This result indicated that a certain percentage of photosynthesizing tissue is necessary to support respiring plant parts. A certain root/shoot ratio of biomass is essential to support above ground plant parts with water and nutrients and to keep transpiration and nutrient demand for growth balanced. This conclusion was indicated by the fraction of carbohydrates partitioned into roots which was about 30% for all species except for one. The stem/crown ratios were more independent of the physiological partitioning patterns and appeared to

have different adaptive responses to different environments.

The above results show an indication of how selected plants react to water stress and competition in order to increase their chances for survival. The responses are important when reseeding mined lands or in any situation where one is concerned with plant survival in stress situations. Species capable of different specializations obviously have the advantage of reducing detrimental competition effects.

Another area which calls for attention is how soil water stress affects the seed of a plant or in most cases it's "product". Drought stress can reduce the overall yield of some crop plants if it occurs at particular growth stages (Slayter, 1967). Data for seed head production of the present study is given in the results but is not discussed due to insignificant results.

The identification of the dynamics of carbon allocation to different plant components during water stress has economic and ecological relevance to agricultural production and conservation practices. This partitioning of carbon is a cumulative result of the physiological activities of an individual plant under stress. Many plants, understandably, react differently to competition and drought stress. Adaptation and responses under water stress are factors of resource requirements and accumulative abilities which differ considerably between individual plants and species.

Results of recent studies can be summarized to present a

projection of what results may be expected in the present study, if the plants studied responded in a similar manner. Squirreltail, perhaps, may be a stress-sensitive grass due to its early successional pattern. This was indicated through Eckert and Spencer's (1982) study. Responses to water stress may be more visible in a squirreltail-snakeweed association which receives the least water. The water-stressed squirreltail plants may show rather visibly, a larger leaf weight percent relative to the entire plant. Total yields will perhaps decrease with stress and stems may show a more elastic response by exhibiting a greater decrease in weight for the stressed plants.

METHODS

The study was conducted in a Colorado State University greenhouse with an environment corresponding to that of the Piceance Basin, in northwestern Colorado, during the months of July and August. The greenhouse had alternating temperatures of 28-32 C during the day, and 10-15 C at night. An artificially extended 15 hour day was created by the use of lamps.

The plants were germinated by seed and later transplanted into the pots containing a clay soil obtained from the Piceance Basin. Soil was sifted, mixed, and air-dried before being transferred into one gallon pots. Each pot contained 3920g of soil. The pots for this study were obtained with no drainage holes in order to insure even infiltration of water through the heavy clay soil. All pots were

watered daily for five weeks upon seedling transplantation to insure success of the seedlings. A two-factor randomized block design was used to determine the design lay-out of the study. Factor one represented the species Sitanion hystrix and Gutierrezia sarothrae. Two individuals of a species together comprised a pure culture while one individual of each species comprised a mixed culture. Factor two represented three watering regimes. The pots were subjected to an alternating water cycle treatment. Soil in the pots was brought to 80% field capacity water level each ten days (moist regime), and 15 days (dry regime). The wet regime was brought to 70% field capacity every five days. Each watering regime had five block repetitions. The plants were subjected to this regime for approximately 61 days. The wet regime received 11 water treatments, the moist received 6 and the dry received 4. Water treatments contained liquid fertilizer. This fertilizer was applied consistently with every treatment after the plants began showing nutrient deficiency. No signs of deficiency were evident after treatments were continued.

Plants were then harvested, after maturity, and separated into roots, leaves, stems, and seed heads. Total above and below ground biomass was recorded for each category after plants were oven-dried to a constant weight at 60 C. Analysis was based on biomass.

RESULTS AND DISCUSSION

Results are based on biomass weights of roots, stem, leaves, and total plant. Stem is defined as the culm and leaf sheaths of the plant. Means, variances, and general qualitative trends were used for this analysis and discussion.

Root to Shoot Ratios

Root to shoot ratios for the plants decreased as the moisture regime increased (Tables 1 and 2, Appendix). The dry regime water treatment plants had an average root shoot ratio of 62/38. In the moist regime of water, plants had a ratio of 41/59, and wet regime plants had a ratio of 25/75 for the pure cultures. Plants in the mixed cultures exhibited higher ratios of 70/30, 51/49 and 40/60 for the dry, moist, and wet cycles respectively. Root biomass decreased while stem and leaf biomass percentages increased as amounts of water increased. These ratios became more variable for the plants, however, with the moist and wet water levels (Table 3).

Leaf weight percentage averages for the pure cultures steadily increased with increasing amounts of water, from 20 to 31 to 46 percent (Table 4). Stem weight average percentages for the same cultures increased from dry (16) to moist (27) but remained similar between moist and wet (28). The leaf weight averages were lower for the mixed cultures but exhibited a similar pattern. Dry, moist and wet

Table 3.

Root Shoot Ratio Summary

	DRY	MOIST	WET
PURE			
	5/5	2/8	1/9
	5/5	3/7	1/9
	5/5	3/7	1/9
	6/4	3/7	2/8
	6/4	4/6	2/8
	6/4	4/6	2/8
	7/3	5/5	2/8
	7/3	6/4	4/6
	7/3	7/3	4/6
	7/3	7/3	5/5
MIXED			
	6/4	2/8	2/8
	6/4	4/6	3/7
	6/4	6/4	4/6
	8/2	6/4	5/5
	9/1	7/3	6/4

Table 4.

Total Mean Leaf, Stem and Root Percentages

for the Pure Culture

	DRY	MOIST	WET
LEAF	20	31	46
STEM	16	27	28
ROOT	62	41	25

percentages were 16, 25, and 34, respectively (Table 5). Stem weight percentage averages for the mixed cultures also followed a pattern similar to the pure culture. The dry regime produced 14 percent of the biomass allocated to stem while the moist and wet received 25 and 23 percent respectively. Calculated means also show the highest amount of root biomass was produced for both cultures in the dry cycle, and subsequently, the lowest means from the wet cycles.

Optimum Biomass Production

Pure Culture

A definite pattern is noted for percentages of biomass allocation, however, no discernable pattern can be noted for biomass production across treatments. Biomass production values are presented but no explanations are offered as to these results.

Average leaf biomass in grams was highest for the moist regime (.90g), and lowest for the dry regime (.41g). The wet regime produced a value of .58g (Table 6). Stem biomass averages decreased in the same manner; the moist regime produced the highest average of .81g with .41g and .36g respectively for the wet and dry regimes. The greatest root biomass average was evident for the moist regime (1.60g). The dry regime produced a very similar root biomass of 1.58g. Only an average of .41g was produced by the roots of plants in the wet regime.

Overall average biomasses for the plants were 2.38g,

Table 5.

**Total Mean Leaf, Stem and Root Percentages
for the Mixed Culture**

	DRY	MOIST	WET
LEAF	16	25	34
STEM	14	25	23
ROOT	70	51	40

Table 6.

**Means for Leaf, Stem, Root and Total Plant Biomass
for the Pure Culture**

	DRY	MOIST	WET
LEAF	.41g	.90g	.58g
STEM	.36g	.81g	.41g
ROOT	1.58g	1.60g	.41g
PLANT	2.38g	3.03g	1.42g

3.03g, and 1.42g for the dry, moist and wet regimes respectively. Optimum biomass production for the pure culture was produced in the moist regime, which contained the highest average values for leaves, stems, and roots. The second highest values for above ground biomass were present in the wet regime but the drastic decrease in average root production decreased the overall biomass production to the lowest value of the three moisture regimes.

Optimum Biomass Production

Mixed Culture

Biomass results of the mixed culture did not correlate strongly to that of the pure culture (Table 7). The greatest leaf weight average was evident in the wet regime (1.10g) followed by the moist (.62g) and dry (.51g). Stem biomass averages followed the same pattern with .73g, .62g, and .45g for the wet, moist, and dry, respectively. The highest average root biomass was produced by the dry regime (2.47) but the lowest was produced in the moist (1.40g). The wet regime produced the median value of 1.65g. Greatest biomass production values for overall plant averages were evident in the dry regime (3.58g) and the wet regime (3.53g). These values were very close but the allocation among compartments was quite different. The dry regime plants allocated a much greater proportion of biomass to roots. Wet regime plants had higher above ground weights than did the other plants.

Table 7.

Means for Leaf, Stem, Root and Total Plant Biomass
for the Mixed Culture

	DRY	MOIST	WET
LEAF	.51g	.62g	1.10g
STEM	.45g	.62g	.73g
ROOT	2.47g	1.40g	1.65g
PLANT	3.58g	2.64g	3.53g

Variance for Percentage Root Biomass

Variances were determined for the percentages of root biomass of each plant in a cycle. Data suggested the dry cycle water stress of the plants induced the most similar percentages of biomass to be partitioned to the roots of all the plants (Table 8). This plant response to the dry cycle possesses highest consistency of root biomass partitioning. As soil water increased, plant responses lost correlation to each other. Lowest variances were exhibited by plants in both the pure and mixed cultures of the dry cycles and lowest similarities in root weights within a cycle were observed by the high variances of the moist cycles for both cultures.

Variances of Differences between Leaf and Stem

Variances were determined for the differences between leaf and stem biomass for each plant in a regime (Table 9). Lowest variances were exhibited by the grasses in the dry cycle for both pure and mixed cultures. This indicated plants in the dry cycle shared the most similar leaf stem ratios over plants in other treatments. The proportion of biomass partitioned to the leaves and stems was very similar for the dry cycles but became less consistent for the moist and wet cycles. The largest leaf stem ratio variance was observed for the wet cycle for both pure and mixed cultures, which indicated less consistent ratios between the plants. This larger variance suggests the least consistent leaf stem ratios for the plants occurred when they received the most moisture. Figures 3-8 (Appendix) illustrate the differences

Table 8.

Variance for Percent Root Biomass

	DRY	MOIST	WET
PURE	75.80	289.65	232.50
MIXED	140.25	412.20	244.00

Table 9.

Variance for Leaf and Stem Biomass Differences

	DRY	MOIST	WET
PURE	29.88	54.60	471.32
MIXED	5.20	46.25	96.36

between both leaf and stem biomass through the degree of slope of the lines connecting the leaf and stem coordinate points. Graphs depicting the dry cycle illustrate similarities between leaf and stem weights for each plant. These similarities decreased for the moist and wet cycles, as the lines illustrate, by a decrease in correlation to each other.

The moist regime produced the most erratic results. The data would seem much more straight forward if the dry cycle had been compared only to the moist or dry. The Appendix graphs illustrate this lack of continuity of the moist regime as well as the data in the given tables. Irregularities of plant responses for this median regime are unexplainable. They may be due to the particular structure of the methods of this study, or perhaps due to a wide range of possible plant responses under this particular amount of available soil water.

CONCLUSIONS

Plant organs vary a great deal in their respective carbon requirements. Older, lower leaf strata often produce photosynthate which is translocated to roots and lower portions of the shoot (Figure 2). The terminal growing parts of the shoot are provided photosynthate from upper, younger leaves on the plant shoot. An obvious advantage of this procedure is evident in the minimized distances over which solutes are transported and likely expediencies of source and sink activities. Roots often require a higher amount of translocated carbon than do the growing plant shoots because

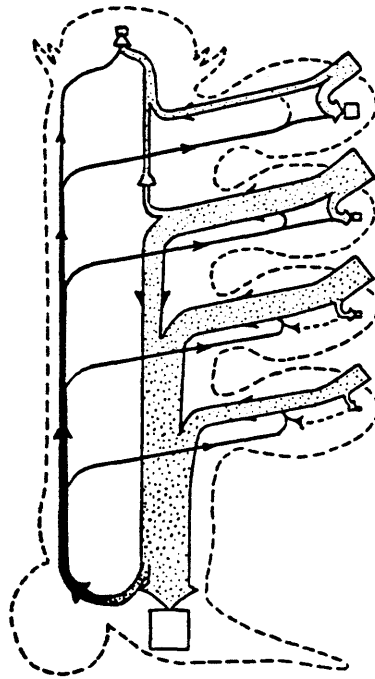


Figure 2. Carbon Flow in the Plant.

Model was built to conform to data obtained from a study including mass carbon flow in phloem of Lupinus albus (Pate and Layzell, 1981). Carbon inputs from leaves are shown as distributed in directions of carbon requirements in amounts which meet recorded consumption of carbon by plant parts.

roots suffer higher respiration losses of carbon. Subsequently, young shoot tissues receive a lower amount of carbon due to their ability to compensate for daytime respiration losses through photosynthesis (Pate and Layzell, 1981). It has been established that phloem transport of carbon can continue during chronic plant water deficit (Hanson and Hitz, 1982).

The dry cycle induced a situation in which the plant roots were compounded in order to increase water uptake efficiency from the soil. Root respiration relative to leaf respiration then functioned on a greater level than that of the wet cycle. Carbon expense of the roots in the dry cycle was high, in order for the roots to become able to take up adequate soil water needed by the plant. Biomass allocation to the roots was obviously a priority to plant survival, as indicated by the lower variances of root percentages and higher root means for the dry cycle. Stem and leaf material was less present in the dry cycle, indicating a lower than normal rate of carbon present.

Respiration often decreases more slowly than photosynthesis which leads to a further decrease of net photosynthesis under water stress, causing a depletion of food reserves and a change in proportion of various carbohydrates in a plant. Less carbon will remain for allocation of plant growth if photosynthetic carbon incomes are meeting greater maintenance demands (Hanson and Hitz, 1982). This translates to a lower photosynthetic rate of the plant, a lower amount

of carbon translocation to growing points, and higher carbon translocation from upper, photosynthesizing leaves to roots. Available carbohydrate reserves are only one factor in plant growth.

Another factor of primary importance is pressure potential. Pressure potential is the driving force from which photosynthate is utilized for growth. If turgor is reduced, existing plant cells fail to expand at the normal rate. Michelena and Boyer (1982) reported inhibition of elongation of maize leaves occurred even when solute accumulation was adequate to maintain turgor. They suggested that some factor other than photosynthate supply and turgor also affected growth, causing most of the growth losses in dry conditions.

This decrease in leaf weights for the dry cycle contradicts the finding of Bade's (1985) study which showed greater leaf weight percentages relative to the entire plant, for plants under stress. Different species were used for that study, however, and the degree of water stress subjected in Bade's (1985) study is not known.

The dry cycle is the cycle that may be compared to Kupper's (1985) results on carbon relations between woody plants, because of the competition factor present. Kupper's results indicated that a certain percentage of photosynthesizing tissue is necessary to support respiring plant parts. Data also showed that a certain root/shoot ratio of biomass was essential to support above ground plant parts with water

and nutrients, and to keep transpiration and nutrient demand for growth balanced. A fraction of approximately 30 percent of carbohydrates were partitioned into the roots of the woody species. The only major similarity to notice is the independence of Kupper's (1985) stem ratios to the partitioning patterns. The stems for the dry cycle generally show an elastic response to the water stress just as Kupper's woody stem ratios did. However, the major difference is, under competition, leaves and roots responded very obviously to the stress environment. Whereas Kupper's roots received a constant percentage, the roots of the dry cycle increased, to the expense of a decreased leaf and stem weight. Grass stems did not suffer a noticeable loss of photosynthate in favor of the leaves. The difference in the two studies is perhaps due to plant type selected. Grass stems photosynthesize whereas woody plant stems do not. Thus there would be no great advantage to the plant for the leaf percentages to remain more constant at the expense of the stems. This is a possible explanation for the greater similarities between stem and leaf biomass allocation under water stress.

The null hypothesis is accepted as true. Individual plant weights are too variable to state that snakeweed association had a negative impact on corresponding squirreltail plants. Regardless of plant size, however, percentages of biomass allocated to plant organs followed a general pattern. This pattern did not vary greatly between the pure and mixed treatments.

APPENDIX

Table 1.

 Percentages of Root, Stem, Leaf, and Seed Head Weights of
 Each Repetition of the Pure Cultures.

SQUIRRELTAIL 1				SQUIRRELTAIL 2			
root	leaf	stem	seed head	root	leaf	stem	seed head
DRY							
51	31	18		54	24	22	
62	18	20		62	22	17	
73	15	12		50	33	17	
62	17	16	05	74	15	11	
65	16	14	05	71	13	16	
MOIST							
47	24	28		65	18	18	
27	43	31		18	49	33	
32	30	39		27	40	32	
67	18	15		57	23	20	
36	31	23	10	35	35	30	
WET							
14	50	36		17	40	43	02
52	26	22		26	32	43	
03	78	18		14	63	23	
42	23	19	13	39	36	26	
22	53	16	09	16	54	30	

Table 2.

 Percentages of Root, Stem, Leaf, and Seed Head
 Weights of Each Repetition of the Mixed Cultures

SQUIRRELTAIL

	root	stem	leaf	seed head
DRY	78	13	09	
	86	09	06	
	64	19	17	
	64	19	17	
	57	19	21	03
MOIST	67	17	16	
	63	18	19	01
	63	18	19	
	42	27	32	
	19	43	40	
WET	24	43	33	
	54	25	21	
	26	47	20	07
	38	23	32	07
	58	32	10	

Figure 3. Graphed Responses for the Dry Cycle Pure Culture.

Coordinate points represent amounts in grams of biomass allocated to plant organs. Connecting lines provide a visual tool for comparison. Corresponding line types are provided so comparison may be made to plants which were grown together in one pot. This graph illustrates the high amounts of root material generated in response to a competitive environment of low soil water. There is a fairly high correlation between leaf and stem material for each plant.

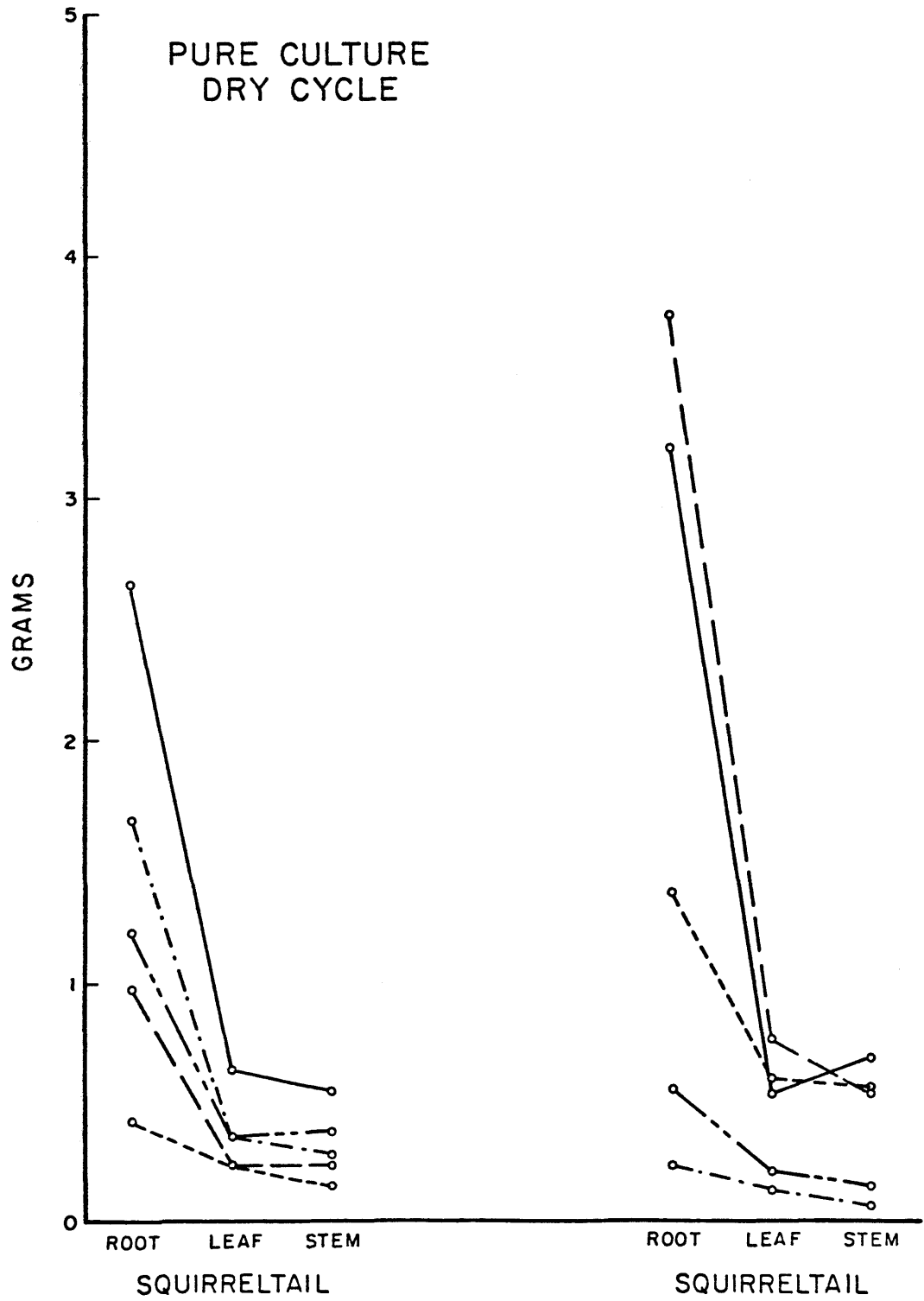


Figure 4. Graphed Responses for the Moist Cycle Pure Culture.

High and low amounts of root material are produced in this cycle. Correlation between leaf and stem material is more erratic than for the dry cycle. Inconsistent responses may be due to the fact that some pots were receiving more water than others. This is suggested because plants in corresponding pots are of somewhat similar size.

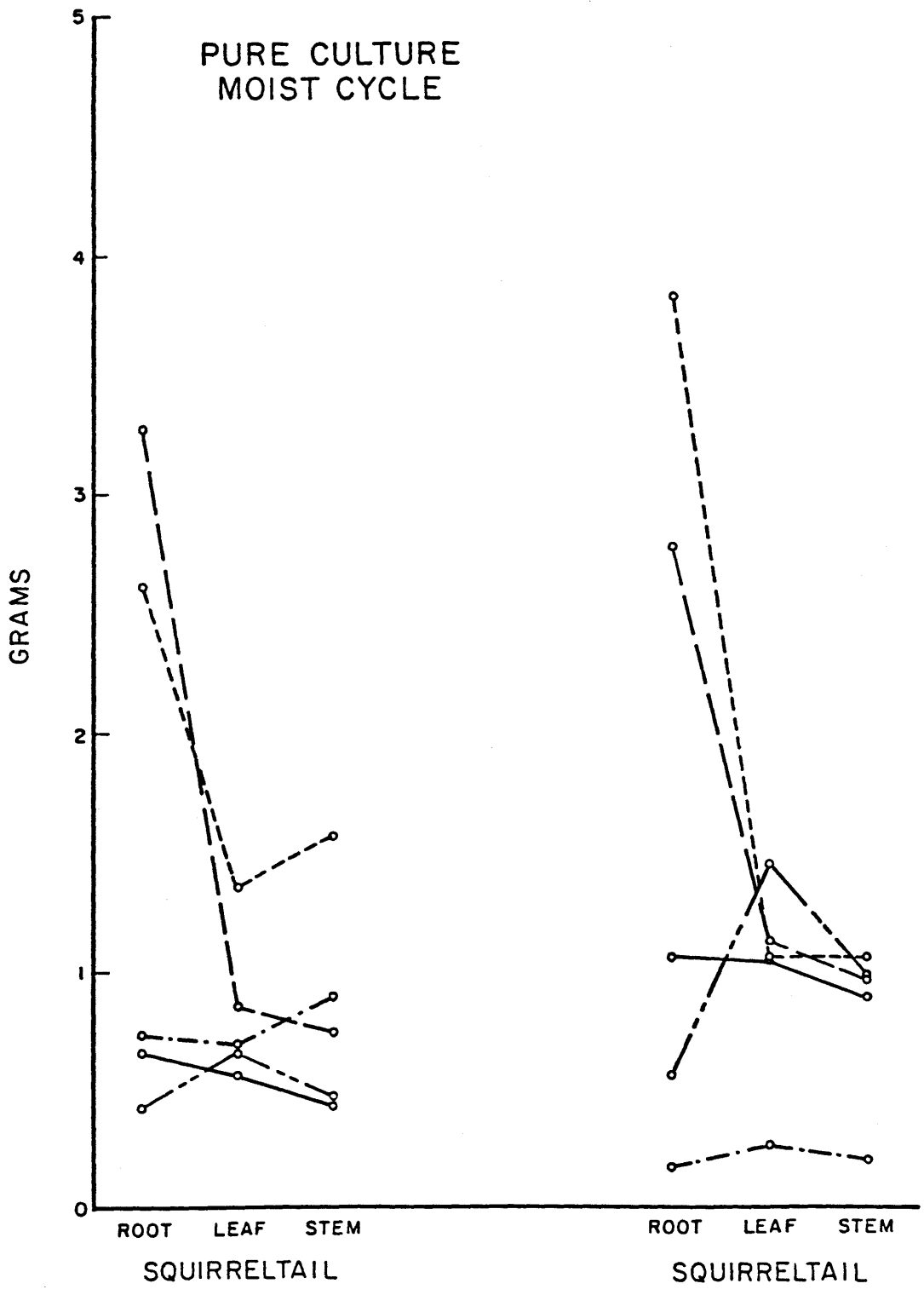


Figure 5. Graphed Responses for Wet Cycle Pure Culture.

Root material production is low. Overall plant production is also low. There is little correlation between production of leaf and stem material for each plant, in comparison to the dry cycle.

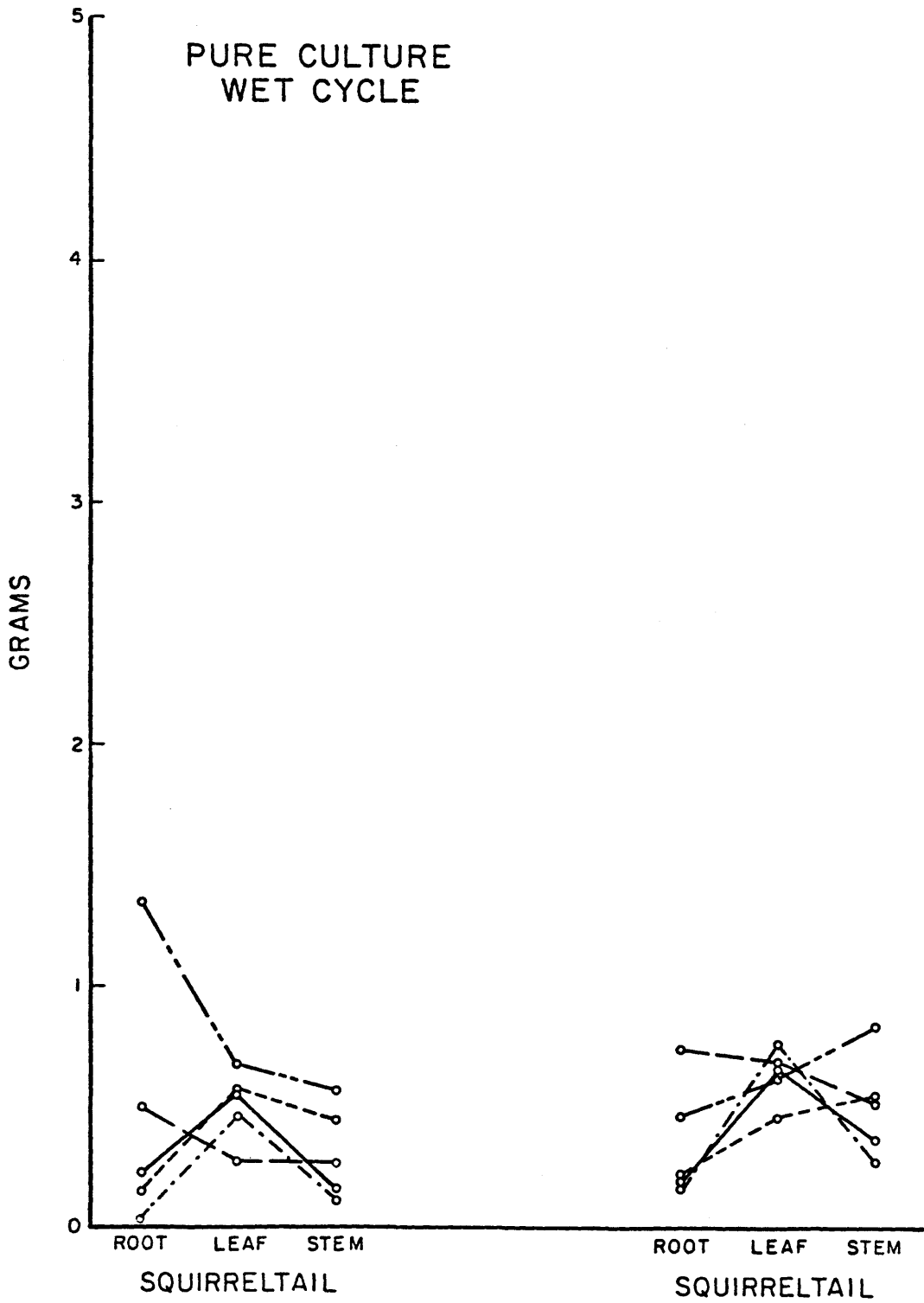


Figure 6. Graphed Responses for Dry Cycle Mixed Culture.

Snakeweed coordinates are shown only for size comparisons to corresponding squirreltail plants. Root production is very similar to the pure culture dry cycle production. High correlation of leaf to stem biomass is also representative of the pure culture.

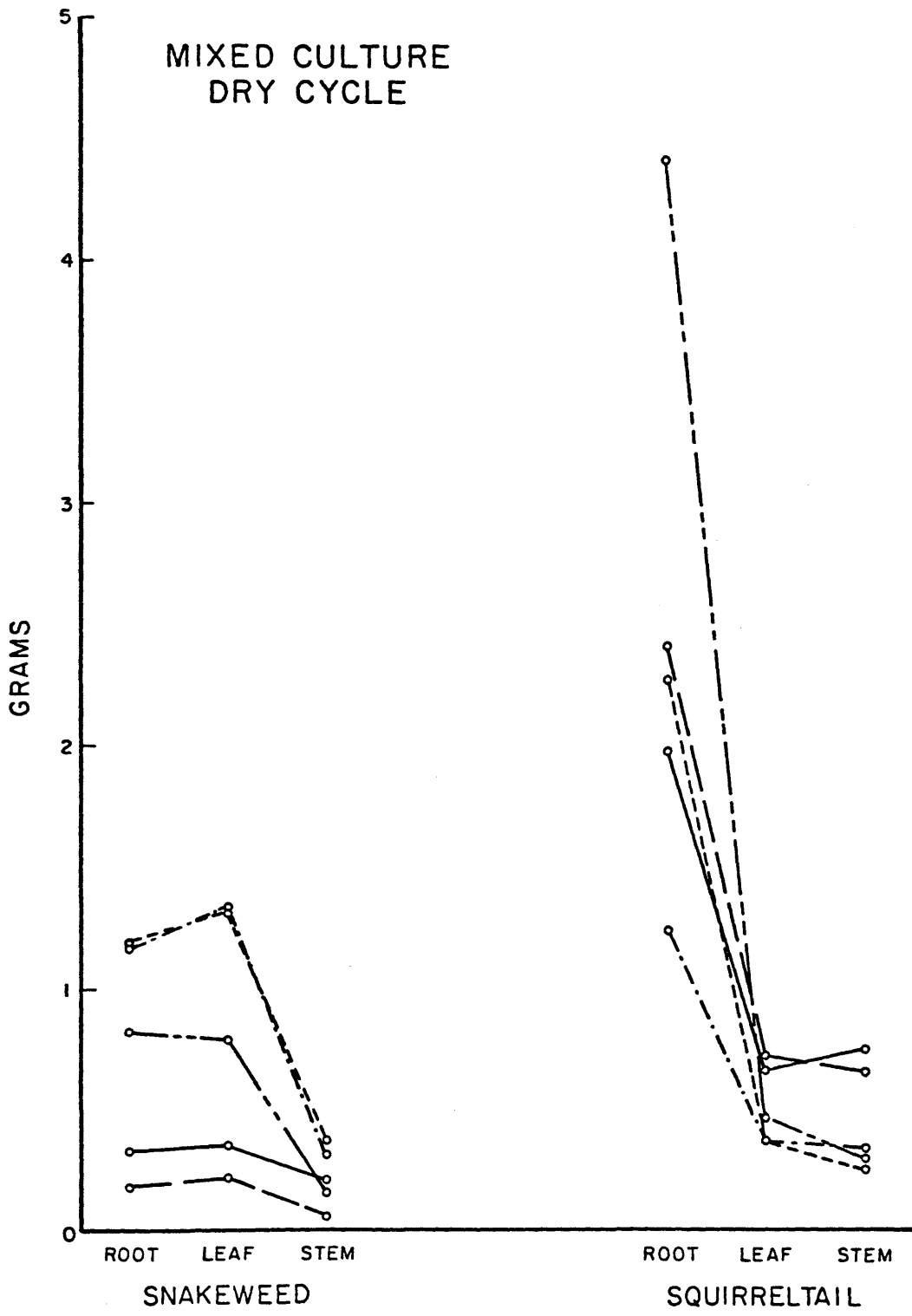
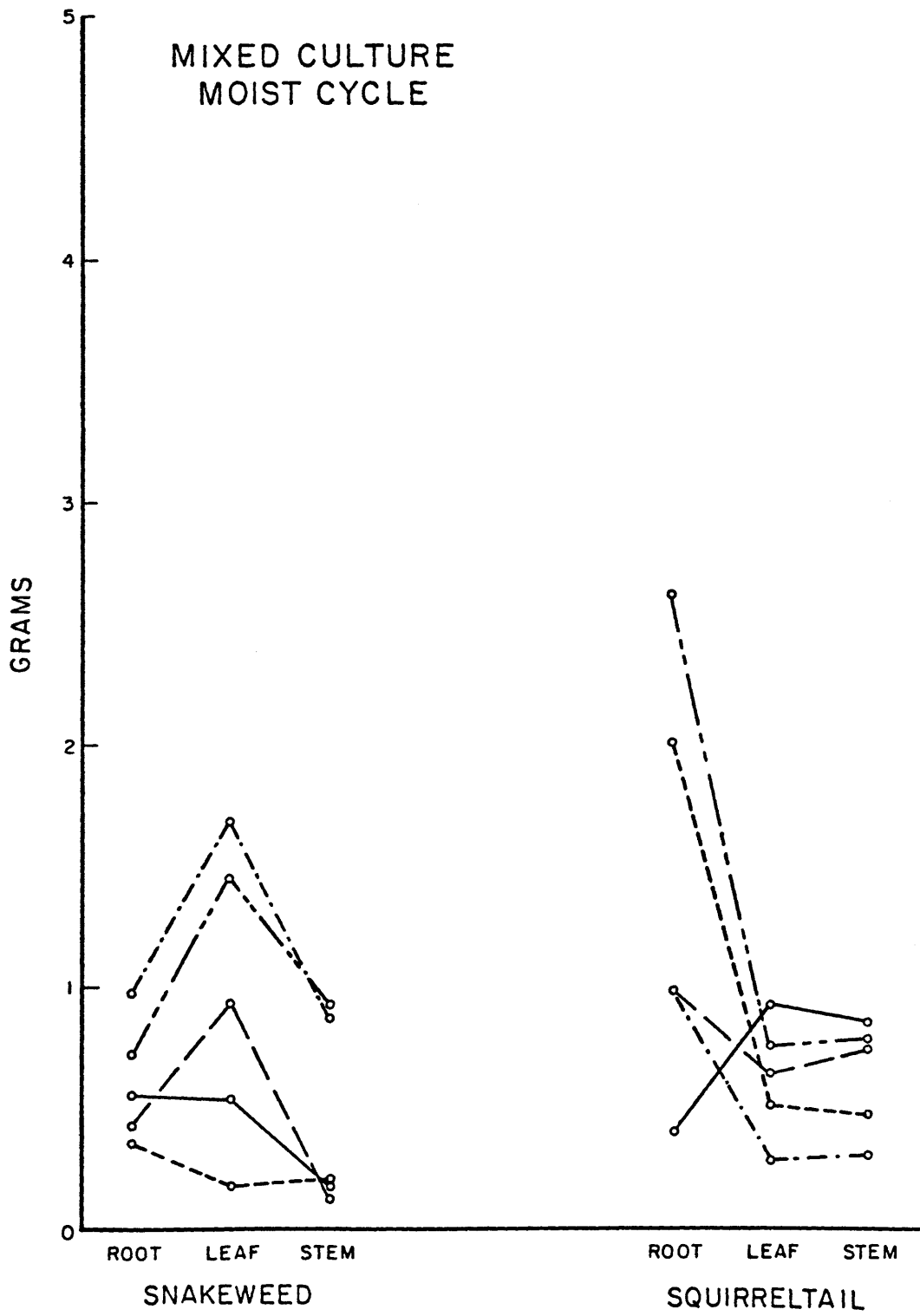
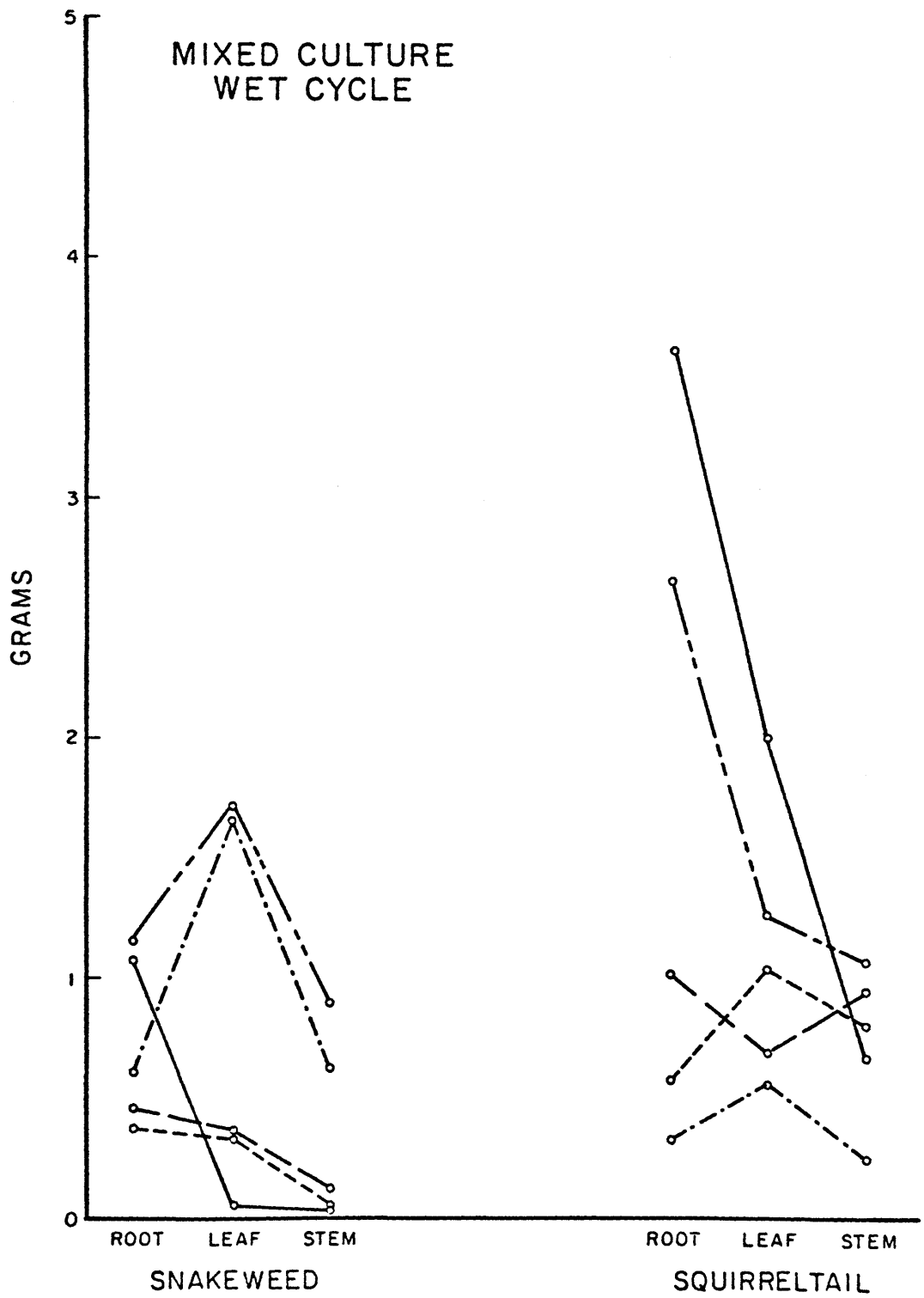


Figure 7. Graphed Responses for the Moist Cycle Mixed Culture.

Root production is erratic and decreased. Correlation between leaf and stem material is still fairly high, however.



**Figure 8. Graphed Responses for the Wet Cycle Mixed Culture.
Root, leaf and stem production is highly erratic.**



REFERENCES

- Acevedo, E., et al. 1971. Immediate and Subsequent Growth Responses of Maize Leaves to Changes in Water Status. *Plant Physiol.* 48:631-636.
- Bade, D.H., B.E. Conrad, and E.C. Holt. 1985. Temperature and Water Stress Effects on Growth of Tropical Grasses. *J. Range Manage.* 38:321-324.
- Boyer, J.S. 1982. Plant Productivity and Environment. *Science.* 218:443-448.
- Eckert Jr., R.E., and J.S. Spencer. 1982. Basal-Area Growth and Reproductive Responses of Thurber Needlegrass and Squirreltail to Weed Control and Nitrogen Fertilization. *J. Range Manage.* 35:610-613.
- Hanson, A.D., and W.D. Hitz. 1982. Metabolic Responses of Mesophytes to Plant Water Deficits. *Ann. Rev. Plant Physiol.* 33:163-203.
- Kramer, P.J. 1983. *Water Relationships of Plants.* Academic Press. New York.
- Kuppers, M. 1985. Carbon Relations and Competition Between Woody Species in a Central European Hedgerow. *Oecologia.* 66:343-352.
- Michelena, V.A., and J.S. Boyer. 1981. Complete Turgor Maintenance at Low Water Potentials in the Elongating Region of Maize Leaves. *Plant Physiol.* 69:1145-1149.
- Milthorpe, F.L. 1961. The Nature and Analysis of Competition Between Plants of Different Species. *Symp. Soc. Exptl. Bio.* 15:330-335.
- Newman, E.I. 1983. *Interactions Between Plants. Physiological Plant Ecology III.* Springer-Verlag. New York.

Pate, J.S., and D.B. Layzell. 1981. Carbon and Nitrogen Partitioning in the Whole Plant - A Thesis Based on Empirical Modeling. Nitrogen and Carbon Metabolism. Martinus Nijhoff/Dr. Junk Publishers. Boston.

Slayter, R.O. 1967. Plant Water Relationships. Academic Press. New York.

Turner, N.C. and P.J. Kramer. 1980. Adaptation of Plants to Water and High Temperature Stress. John Wiley & Sons. New York.

Williams, J.E. 1962. The Analysis of Competition Experiments. Aust. J. Bio. Sci. 15:509-525.