GROWTH, WATER RELATIONS AND NUTRITION OF THREE GRASSLAND ANNUALS AS AFFECTED BY DROUGHT

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INTRODUCTION

Although the Mediterranean type of climate is typified by cool-wet winters and hot-dry summers, drought may be frequent in the cool season, influencing the botanical composition of annual-type vegetation (Bentley & Talbot 1951; Heady 1958; Williams & Elliott 1960; McKell, Whalley & Williams 1971). In California, U.S.A., variations in the amount and pattern of precipitation, especially the date of germinating rains, have been associated with the phenomena referred to as 'good clover', 'good filaree', and 'good grass' years (Talbot, Biswell & Hormay 1939). In Australia, early opening rains result in 'clover years', whereas a 'false break' (early rains followed by a long period of dry weather) favours drought-tolerant species and leads to the death of clover seedlings (Rossiter 1966). Of great significance is earliness of flowering and seed production, which are partly a function of the soil moisture reserve. Seed production can have a profound effect on subsequent fall germination (Wagnon & Biswell 1943; Rossiter 1959; Donald 1960). Rossiter (1966), in an excellent review of annual-type ecology, also discussed a probable temperature × moisture × species interaction and seed dormancy as factors influencing botanical composition. McKell, Major & Perrier (1959) have demonstrated that fertilization of annual-type range increases the depletion of soil moisture. Among the other factors that can also influence botanical composition, Biswell (1956) implicated grazing, fire, and mulch removal.

Since variability in precipitation is associated with extreme fluctuations in species abundance, it is suggested that the common annual species respond differently to moisture stress. One advantage that *Erodium* has over *Trifolium* and *Bromus* under conditions of drought and poor fertility is its superior rooting habit (Cameron & McGowan 1964; Ozanne, Asher & Kirton 1965; Rossiter 1966; Cayley 1968; McCown & Williams 1968). Information is lacking on the effect of moisture stress *per se* on the growth of winter annual species.

Winter annuals are admittedly mesophytic, but the importance of drought tolerance as a factor in determining the relative success of annual species should not be minimized. The ability to tolerate dry spells is of great economic importance, as Meadly (1945) indicated in investigations of the virtual elimination of clover and subsequent dominance by *Erodium* in some pastures in western Australia. He attributed the change to an early 'break' followed by a dry spell. Costly range improvement programs can be made more costly by the additional reseeding necessitated when such a pattern reduces reserves of seed.

This investigation was conducted to develop information on the effects of moisture stress and population density on the early growth of three winter annuals that are

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important components of our range forage. Of secondary interest were the effects of these factors on the tissue concentration of major nutrients. The main aim was to relate this information to principles of plant-water relations and contribute to a better understanding of the physiological ecology and management of these species.

MATERIALS AND METHODS

The study was conducted using a $3 \times 3 \times 3$ factorial experimental design with four replications in a randomized complete block. The factors were three species of winter annuals, three soil moisture regimes and three plant densities. Seeds of *Erodium botrys* (Cav.) Bertol. (broad-leaf filaree) and *Bromus mollis* L. (soft chess) were collected from a typical annual range site. The seed of *Trifolium subterraneum* L. (cv. Woogenellup) was obtained commercially. Sufficient seeds were sown (17 September 1972), in plastic pots (14·6 cm diameter) lined with polyethylene bags, to achieve population densities of 25, 50 and 100 plants per pot, corresponding to 1500, 3000 and 6000 plants/m^2. The seeds were then covered with 1 cm of washed sand.

The relation of soil water potentials of −0·3, −1, −3 and −15 bars to soil moisture percentage was established using the pressure membrane method. Each pot contained 1289 g of Yolo loam soil (oven-dry basis) rich in Mg and K. A total of 120 ml of 0·5 Hoagland solution was put in each pot in three aliquots. The pots were kept in a clear glass, greenhouse with the diurnal temperature and relative humidity maintained at 18–25° C and 50–90% respectively. External radiation during the treatment period averaged 325 ly/day.

For three weeks after emergence all pots were kept close to field capacity; thereafter, the pots were weighed daily or twice daily and if the pots were at the predetermined weights corresponding to −1, −3 and −15 bars they were watered and brought up to −0·3 bars. The amount of water added was recorded and considered as a measure of transpiration. Evaporation from the soil surface was included as transpiration loss since all pots after three weeks has attained a closed canopy and had a LAI (leaf area index) of at least 2–3. According to Ritchie & Burnett (1971) soil evaporation under these conditions is negligible.

To relate soil moisture to the internal plant water, the relative water content (RWC) of the plants (Weatherly 1950) was determined by weighing leaf laminae of *Erodium* and *Trifolium* and leaf segments of *Bromus* and immediately floating them in covered Petri-dishes filled with de-ionized water. The dishes were placed in a chamber kept at 20° C and 450 lux for four hours (determined by prior tests as sufficient to achieve full turgidity. The leaf parts were then weighed, oven-dried (70° C, twenty-four hours) and reweighed). We computed RWC using the expression:

$$\mathrm{RWC} = \frac{\text{Fresh wt} - \text{oven dry wt}}{\text{Turgid wt} - \text{oven dry wt}} \times 100$$

The data were obtained just prior to harvest by selecting pots which were at the desired soil water potential then clipping the leaves early in the morning before sunrise.

Harvesting was done after three weeks of growth (7 November 1972) in the aforementioned moisture regimes by clipping plants at soil surface. The soil was carefully washed from the roots by placing the soil mass on a screen and using a jet of water. The plant material was oven-dried at 70° C for twenty-four hours. Due to insufficient plant material, tissue analysis was done after combining replications. Macro-Kjeldahl was used for total N. Total P was determined by the vanadate-molybdate-yellow method of Kitson & Mellon as outlined by Chapman & Pratt (1961). Calcium, Mg and K were determined using a Perkin-Elmer 303 atomic absorption spectrophotometer (Isaac & Kerber 1971).

RESULTS

Growth

Moisture stress reduced the total dry matter (biomass) of all three species in a similar

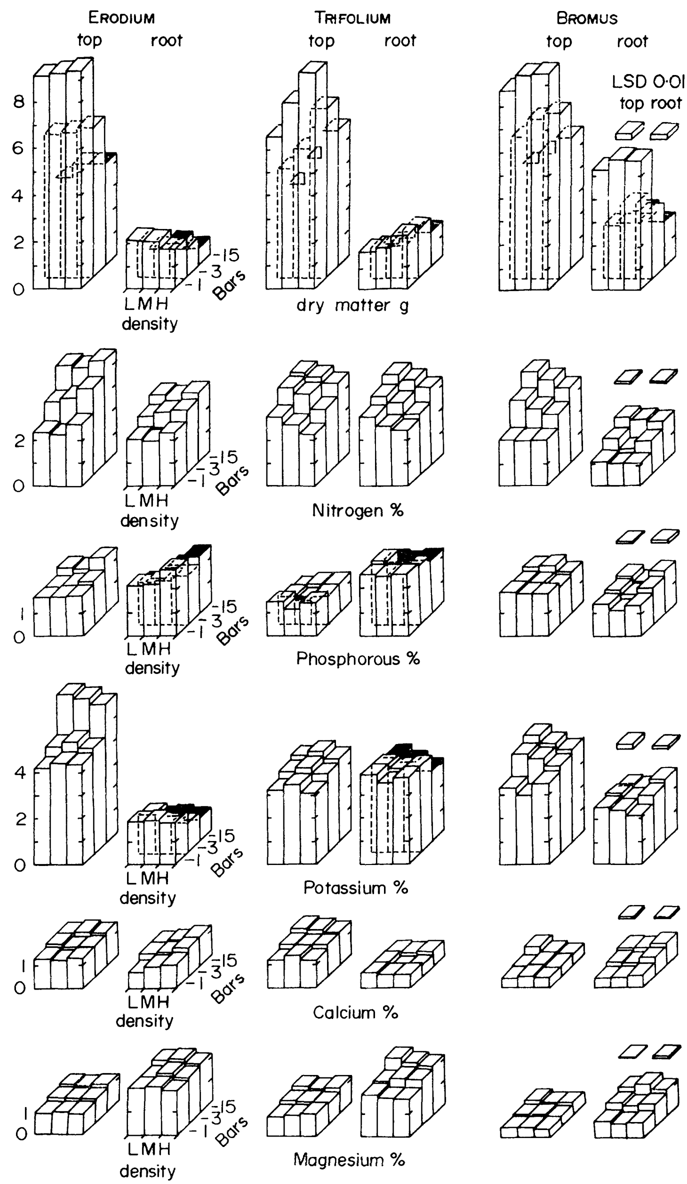

FIG. 1. Dry matter production (biomass) and nutrient element concentration (tops and roots) of *Erodium*, *Trifolium* and *Bromus* as affected by moisture stress and plant population density (LSDs apply to each species over all moisture or over all density levels).

stepwise fashion (Fig. 1). *Bromus* with a massive root system had the highest total biomass. Comparing top weights only, all three species had comparable yields with high population density and low soil moisture stress conditions.

The decrease in total biomass as a function of moisture stress was greater for *Erodium* and *Bromus* than for *Trifolium* (Table 1), with the decrease being less for the tops and greater for the roots in *Erodium* and *Bromus* and vice-versa for *Trifolium*. This is also reflected in the root:top ratios shown in Table 2. *Bromus* had a high root:top ratio of 0·60 as compared to 0·21 and 0·23 for *Erodium* and *Trifolium*, respectively, under low

Table 1. *Relative dry matter production (biomass) of* Erodium, Trifolium *and* Bromus *as affected by soil moisture stress and plant population density*

Treatments	Total *Erodium*	Total *Trifolium*	Total *Bromus*	Tops *Erodium*	Tops *Trifolium*	Tops *Bromus*	Roots *Erodium*	Roots *Trifolium*	Roots *Bromus*
Moisture (bars)									
−1	100	100	100	100	100	100	100	100	100
−3	67	75	65	67	73	73	68	84	50
−15	44	59	48	45	58	55	42	74	38
Density									
Low	100	100	100	100	100	100	100	100	100
Medium	103	122	113	104	125	110	96	111	120
High	102	159	114	106	153	114	85	150	112

Table 2. *Root: top ratios* for dry matter of* Erodium, Trifolium *and* Bromus *as affected by soil moisture stress and plant population density*

	Erodium	*Trifolium*	*Bromus*
Moisture (bars)			
—1	0·21 a	0·23 a	0·60 a
—3	0·22 a	0·28 b	0·41 b
−15	0·21 a	0·27 b	0·42 b
Density			
Low	0·23 a	0·28 a	0·46 a
Medium	0·22 ab	0·25 a	0·52 b
High	0·19 b	0·27 a	0·45 a

* Values followed by the same letter do not differ significantly (0·05).

moisture stress. McCown (1965) also showed similar root:top ratios for *Erodium* and *Bromus* after six weeks of growth. The mean ratio for *Bromus* in his study was 0·76. He also showed a decrease in the root:top ratio of *Erodium* with increasing population density as occurred in this study.

However, the root:top ratio for *Trifolium* remained unchanged with increasing population density. Increasing density also resulted in a highly significant increase in total growth for *Trifolium*, a smaller increase for *Bromus*, and no increase for *Erodium* (Table 1). There was no significant interaction between moisture and density on the growth of any species.

Water relations

Moisture stress caused a significant decrease of total water used by all species (Fig. 2). Increasing population density resulted in increased water use by *Trifolium* at all moisture levels and at the lower moisture level for *Bromus*, but results were variable for *Erodium*. *Bromus* used the most water and *Erodium* the least at all levels of moisture and density.

Increasing moisture stress decreased the transpiration ratio of all species and so did increasing density, although only slightly for *Bromus* (Fig. 2). The transpiration ratio was significantly lower for *Erodium* than for the other species, which had similar ratios.

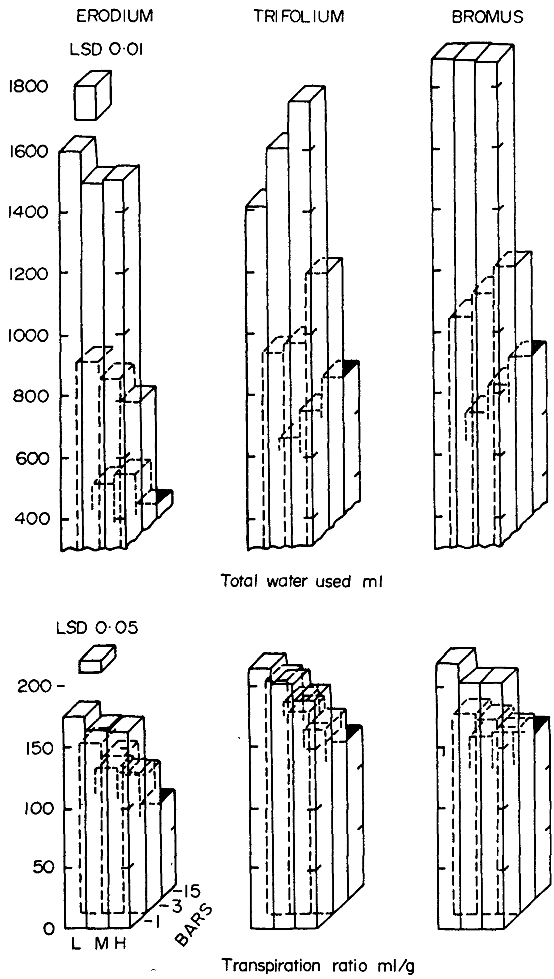

FIG. 2. The transpiration ratio and total water use of *Erodium*, *Trifolium* and *Bromus* as affected by moisture stress and plant population density (LSDs apply to each species over all moisture or over all density levels).

Although there were no significant moisture × density interactions for either total water use or transpiration ratio, it is interesting that total water use for *Trifolium* increased at all moisture levels with increasing density and that the transpiration ratio decreased at all moisture levels with increasing density.

The relative water content is shown on Fig. 3. Moisture stress resulted in a decreased RWC, but increasing population density had very little effect on the RWC. At −3 bars the RWC dropped considerably for *Erodium* and only slightly for *Trifolium* and *Bromus*.

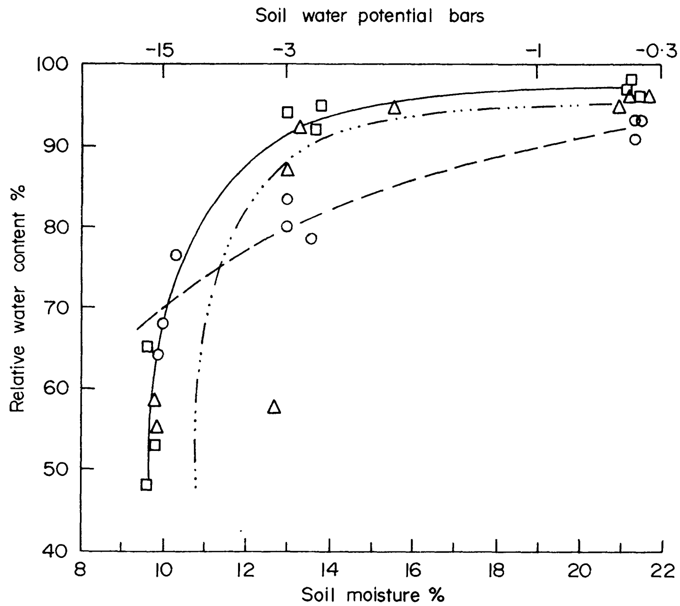

FIG. 3. The relative water content of *Erodium*, *Trifolium* and *Bromus* as a function of soil moisture. ○—— ——○ *Erodium*, □————□ *Trifolium*, △ . . . —△ *Bromus*.

Table 3. *Dry matter production and nutrient element content expressed as concentrations (% dry matter) and total uptake (mg/pot) of* Erodium, Trifolium *and* Bromus *as a function of increasing soil moisture stress (relative values are shown in parentheses*)*

	Erodium		*Trifolium*		*Bromus*	
Total dry matter*	g/pot		g/pot		g/pot	
—1 (bar)	11·25 (100)		9·91 (100)		14·62 (100)	
—3	7·58 (67)		7·46 (75)		9·45 (65)	
—15	4·98 (44)		5·89 (59)		7·05 (48)	
Nitrogen	%	mg/pot	%	mg/pot	%	mg/pot
—1	2·36 (100)	266 (100)	2·62 (100)	260 (100)	1·66 (100)	243 (100)
—3	3·30 (140)	250 (94)	3·26 (124)	243 (93)	2·50 (151)	236 (97)
—15	4·04 (171)	201 (76)	3·67 (140)	216 (83)	3·16 (190)	223 (92)
Phosphorus						
−1	1·83 (100)	206 (100)	1·62 (100)	161 (100)	1·63 (100)	238 (100)
−3	1·77 (97)	134 (65)	1·49 (92)	111 (69)	1·70 (104)	161 (68)
−15	2·11 (115)	105 (51)	1·48 (91)	87 (54)	1·83 (112)	129 (54)
Potassium						
−1	3·90 (100)	439 (100)	3·39 (100)	336 (100)	2·93 (100)	429 (100)
−3	4·13 (113)	313 (71)	3·61 (106)	269 (80)	3·59 (123)	339 (79)
−15	5·32 (136)	265 (60)	3·74 (110)	220 (65)	3·76 (128)	265 (62)
Calcium						
−1	1·23 (100)	139 (100)	1·16 (100)	115 (100)	0·73 (100)	106 (100)
−3	1·35 (110)	102 (73)	1·19 (103)	89 (77)	0·55 (75)	52 (49)
−15	1·43 (116)	71 (51)	1·38 (119)	81 (70)	0·65 (89)	46 (43)
Magnesium						
−1	1·13 (100)	127 (100)	1·09 (100)	108 (100)	0·53 (100)	78 (100)
−3	1·27 (112)	96 (76)	1·23 (113)	92 (85)	0·63 (119)	60 (77)
−15	1·37 (121)	68 (54)	1·39 (128)	82 (76)	0·78 (147)	55 (71)

* The dry matter values are the average of four replications and the nutrient element values the average of two replications.

From −3 to −15 bars the latter two species decreased in RWC much more than *Erodium*. The horizontal variation in the location of the points reflects the variability in soil moisture percentage at the time leaves were harvested for RWC determination.

Nutrient element availability

Nutrient concentrations were generally higher in the tops than in the roots except for P and Mg in *Erodium* and *Trifolium*, for K in *Trifolium* and for Ca in *Bromus* where the reverse occurred (Fig. 1). The concentrations generally increased with increasing moisture stress, whereas the effects of density were highly variable. Although nutrient concentration increased with increasing moisture stress, the decrease in total biomass was so great that absolute nutrient content (mg/pot) decreased. Therefore the nutrient element composition is presented both in terms of dry matter percentage and absolute nutrient content (Table 3). All nutrients expressed in a concentration mode increased with increasing moisture stress except for P in *Trifolium* and Ca in *Bromus*. *Erodium* had the highest concentration for all nutrients at all moisture levels. Potassium reached a very high concentration in *Erodium* of 5·32% at −15 bars. *Bromus* had relatively low concentrations of Ca and Mg.

When nutrient element content is expressed on an absolute basis the opposite occurs, i.e., with increasing moisture stress there is a decrease in total uptake. *Erodium* shows a decrease for all nutrients with increasing moisture stress and, except for P in *Trifolium* and P and Ca in *Bromus*, this is also the case for other species. Nutrient uptake was less affected by water stress than was dry matter production.

DISCUSSION

Growth

Moisture stress generally increases the root:top ratios of plants (reviews by Peters & Runkles 1967; Black 1968). It has been suggested that moisture stress slows leaf expansion before photosynthesis is affected, while roots being close to the source of limited water are able to become the dominant sink for assimilates (Brouwer & de Wit 1969). At any rate moisture stress slows shoot growth more and sooner than it does root growth (Loomis, Williams & Hall 1971). In the present study this hypothesis is supported by the data for *Trifolium*, but *Bromus*' response was the opposite and *Erodium* did not respond (Table 2). Root growth rate of all species was slowed by increasing moisture stress. However, the concomitant decrease in top yields were of differing magnitude, and an increase in root:top ratio occurred for *Trifolium*. Williams & Shapter (1955) also showed a decrease in root:top ratio in Graminaceous species with increasing moisture stress. The extremely high root:top ratio of *Bromus* (0·60) and its large biomass indicate that the root system permeated the soil volume; therefore, with fluctuating moisture levels it would display a greater relative reduction if the suggestion by Loomis, Williams & Hall (1971) is correct. They suggest that a sudden enhancement of moisture (periodic irrigation) after a period of impoverishment would result in rapid shoot growth for a while with very little root growth.

The increased yield with increasing density as shown by *Trifolium* indicates that the carrying capacity afforded by the soil volume had not been utilized at the lower densities. Previous yield-density studies (unpublished) revealed that *Erodium* is a much larger plant than this cultivar of subclover at these densities. Also Spedding & Diekmahns (1972) point out that legumes generally have a slower post-emergence development than grasses.

Trifolium withstood soil moisture stress much better than the other species, as indicated by the relative decreases in biomass with increasing moisture stress (Table 1). One might attribute this to the fact that *Trifolium* was not limited in moisture supply because of its relatively smaller plant size, however statistical analysis did not indicate that there was a moisture × density interaction, hence, the relative decreases (over all densities) in biomass were valid. *Trifolium* also showed an increase in root: top ratio enabling it to better cope with increasing moisture stress. The ability of *Trifolium* to withstand moisture stress has been recorded by McGowan & Williams (1973) under field conditions. They noted that *Trifolium* growth and seed production was only slightly restricted by competition with associated barley (*Hordeum vulgare*) in spite of low soil water potential.

Erodium and *Bromus* were about equally intolerant to increasing moisture stress as evidenced by their relative decrease in total biomass. However, the greatest reduction occurred in the root yield of *Bromus* whereas the reduction in top yield was similar to that of *Trifolium*. Two important characteristics of roots which were not examined in this experiment are the rate of root elongation and depth of penetration. These would be very important under field conditions where root penetration is not limited by a hard pan layer or bedrock. The rate of root elongation and depth of penetration for *Erodium* is substantially greater than for either *Trifolium* or *Bromus* (Ozanne *et al.* 1965; McCown & Williams 1968).

Water relations

The increase in dry weight with increasing density as exhibited by *Trifolium* parallels the increase in total water used. This increase resulted in an observed increase in leaf area as well as in root mass leading to greater transpiration. This is also true for *Bromus* at −3 and −15 bars. However, *Erodium* used less water with increasing density and this is associated with a decrease in root mass (Table 1).

The relative reduction in total biomass with increasing moisture stress was least for *Trifolium* which was associated with the highest transpiration ratio. This indicates that conditions for growth as a function of higher leaf water potential were nearer to the optimum than for *Erodium* and *Bromus*. Storage of moisture in parenchymatous tissue following irrigation or replenishment at night could have been the moisture source for greater water loss.

The high transpiration ratio of *Bromus* may be related to its fibrous root system. Although the hydraulic conductivity of soil decreases with decrease in soil water potential the permeation of the soil volume by a fine network of roots could reduce the distance water need travel to be absorbed.

If low transpiration ratios are an index to water use efficiency, then *Erodium* must be considered the most efficient. It had the lowest transpiration ratios at all three moisture regimes, and also total water used was the lowest. During the sunny afternoons in the greenhouse *Erodium* wilted even at −1 bar when soil moisture should have been adequate.

In the light of these results we may concur with the conclusion of Wilson, McKell & Williams (1968) that transpiration ratios are not a good indicator of drought resistance. As Vaadia, Raney & Hagan (1961) concluded soil moisture content and transpiration rates are not sufficient to predict plant water deficits. Therefore RWC data was obtained. The higher RWC of *Erodium* at −15 bars does relate to the lower water loss and at −3 bars *Trifolium* did show the highest RWC and the least reduction in yield. However, the relationship overall was rather tenuous. Hsiao (1973) suggests that when water deficit is not severe that RWC is a rather insensitive indicator of water status.

Nutrient element availability

Investigations of the effect of moisture stress on nutrient accumulation in plant tissues are often conflicting. Richards & Wadleigh (1952) concluded that moisture stress increases N and decreases K while it has variable effects on Ca, Mg and P concentrations. Hawthorne (1956) stated that twelve out of twenty-one papers reviewed reported decreases in P concentration resulting from moisture stress, and the remainder reported no effect. Vaadia *et al.* (1961) have identified the existence of contradictory evidence but have tried to generalize by stating that the literature indicates a definite decrease in P and K. Viets (1967) has also concluded that the evidence supports more nutrient uptake under nonstress conditions but emphasized the complexities in interpreting data obtained from situations where soil moisture was widely fluctuating.

The results presented here show increased concentrations with increasing soil moisture stress, however there was a general decrease in total nutrient uptake with increasing moisture stress. The relatively high concentrations of K and Mg can be attributed to the high soil concentrations of these elements which is characteristic of Yolo loam soil.

The fact that yield reductions decreased faster than total nutrient uptake with increasing moisture stress indicates that growth was more susceptible to moisture stress than was nutrient uptake. The difference in total nutrient content between the dicots and *Bromus* is not very great in spite of the differences in total dry weight and the fact that *Bromus* had a larger root system and a supposedly larger reservoir and mechanism by which to obtain more nutrients. Our tissue analysis also shows a higher proportion of Ca and Mg in the dicots, and if ratios of divalent to monovalent ions were compared the dicots would show a higher ratio than the monocot. Although some workers show a correlation between high cation exchange capacity of roots and differential rates of uptake for divalent and monovalent ions, Epstein (1972) cautions against acceptance of this hypothesis.

The relative decrease in N accumulation as a function of increasing moisture stress was considerably less than growth and the accumulation of the other nutrients. This agrees well with the data presented by Jensen (1962) who concluded that 3/4 of nitrate uptake is passive therefore one would expect that N uptake to be less affected. Also Viets (1972) states that the concentration of nitrate should double as the volume of soil water declines by half.

The accumulation of greater quantities of nutrients by *Erodium* might impart some competitive advantage over the other species in a less favorable nutrient environment. These stored nutrients can serve as a source for subsequent growth which is considerable in the spring when the constraint of temperature is lifted. One other possible advantage suggested by Hsiao (1973) is osmotic regulation as a result of solute accumulation. Since *Erodium* had the highest RWC at -15 bars soil water potential it is possible that due to its high solute concentration (Table 3) especially K, a high osmotic potential could result in continued water uptake.

The effects of density on total nutrient uptake were not very marked in this experiment, probably because the population densities were high. Nutrient uptake by *Trifolium* increased as density increased, due to its small plant size add slow initial growth rate.

CONCLUSIONS

Trifolium had the highest drought tolerance on the basis of the greatest relative increase in biomass under the influence of moisture stress. Although *Erodium* had the highest RWC, transpired the least, and had the lowest transpiration ratio under severe moisture stress it appeared to be similar to *Bromus* in sensitivity to drought. However, the pronounced wilting of *Erodium*, which would account for high RWC, minimal transpiration and low transpiration ratio, could be advantageous as a survival mechanism in tolerating drought. *Bromus*, a fibrous-rooted species, had the largest root biomass.

The conditions of this experiment did not permit a complete evaluation of their ability to withstand drought. For example with a brief period of precipitation and subsequent moisture percolation to a shallow depth a fibrous-rooted species like *Bromus* would be at an advantage; whereas, tap-rooted species like *Erodium* and *Trifolium* would be able to obtain moisture from greater depths, if it were available. Moreover, information on the effects of moisture and temperature on germination are necessary as well as an understanding of the contribution of phenotypic plasticity and ecotypic differentiation as they affect growth parameters and earliness in flowering.

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SUMMARY

Three winter annuals were grown under greenhouse conditions to evaluate their behaviour under varying soil moisture stress and population density. The reduction in total biomass was significant when soil water potential was decreased from field capacity to −3 bars. *Trifolium subterraneum* appeared to be the least sensitive to soil moisture stress. *Erodium botrys* had the lowest transpiration rate and the lowest total water use. *Bromus mollis* used the greatest amount of water and also had the highest total biomass. Increases in plant population density did not affect *Erodium* and *Bromus* but the total biomass of *Trifolium* increased significantly. Total nutrient uptake was reduced by increasing soil moisture stress.

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