



Dry Weight Production and Partitioning in *Medicago minima* and *Erodium cicutarium* Under Water Stress

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Medicago minima and *Erodium cicutarium* are two naturalized annual species in extensive semi-arid, temperate rangelands of central Argentina. A field study was conducted during 1989 and 1990 to evaluate the effects of different levels of soil water availability on above- and below-ground dry weight production and partitioning in these species. Dry weight production by *M. minima* was more sensitive to water stress than that by *E. cicutarium*. Although the response was more marked in *M. minima*, both species allocated a larger proportion of total plant dry weight to fruits under water stress than under irrigated conditions during early spring. Percentage allocation of total plant dry weight into reproductive organs in both species, and stems and peduncles in *E. cicutarium*, was correlated with total dry weight of these organs; this might indicate a correlation between sink size and strength. Persistence of both species in the local flora appears to be associated with their capacity to colonize open, degraded areas and grow in association with native perennial grasses, as well as to tolerate severe drought periods. © 1998 Annals of Botany Company

Key words: *Medicago minima* (L.) Grufb. var. *minima*, *Erodium cicutarium* (L.) L'Herit, water stress, dry matter production and partitioning.

INTRODUCTION

Medicago minima (L.) Grufb. var. *minima* (Leguminosae) and *Erodium cicutarium* (L.) L'Herit (Geraniaceae) are important, high quality forage species during spring in both overgrazed and properly managed areas in the Calden District, a phytogeographic region of approx. 10 million hectares in Central Argentina (Cairnie and Monesiglio, 1967; Fresnillo Fedorenko, Fernández and Busso, 1991). Overgrazing and inadequate rangeland management have led to incipient or increased soil erosion, and the creation of desert environments in this temperate, semi-arid region where cattle raising on natural vegetation is the main economic activity (Busso, 1997). Periods of soil water deficit of varying length and severity commonly occur during the growing season of *M. minima* and *E. cicutarium* (e.g. Distel and Fernández, 1987; Peláez and Bóo, 1987). Since water stress can reduce plant growth (e.g. Schulze, 1986), soil water availability may thus be an important production determinant of both species. This was demonstrated for *M. minima* in a growth chamber study (Fresnillo Fedorenko, Fernández and Busso, 1995). Several demographic and growth parameters, however, have been shown to be much less sensitive in *E. cicutarium* than in *M. minima* (Peláez *et al.*, 1995).

Plant productivity is determined in part by the distribution of photosynthates among various organs (Monsi and Murata, 1970). Water stress, however, can affect the growth of each plant organ differently (Sobrado and Turner, 1986;

Carvalho and Schank, 1989), and the pattern of dry mass accumulation within the plant may thus be altered (e.g. French and Turner, 1991; Singh, 1991; Cox and Conran, 1996). Studies on partitioning of dry weight between different plant organs are scarce (Marcelis, 1996), and lacking in *M. minima* and *E. cicutarium*. Such studies are important because they may give information about the way plants modify their dry weight distribution under conditions of water stress. This study determined the effects of water stress on above- and below-ground dry mass production and partitioning in *M. minima* and *E. cicutarium*. It was conducted over an extended period in a minimally-modified natural environment using adjacent experimental field plots. The fact that responses can differ substantially between field and controlled environments, especially with regard to water stress (Ludlow and Ng, 1976; Bunce, 1977; Turner and Begg, 1978), emphasizes the importance of evaluating long-term plant performance under field conditions.

MATERIALS AND METHODS

Site and cultural details

This study was conducted in 1989 and 1990 at the research field area of the Department of Agronomy, Univ. Nacional del Sur, Bahía Blanca, Argentina (38° 41' S, 62° 15' W, 40 m above sea level). Seedlings of *Medicago minima* and *Erodium cicutarium* were obtained from soil blocks at the study site in the Calden District, Province of La Pampa (38° 45' S, 63° 45' W). At the time of transplanting in both years, *M. minima* and *E. cicutarium* were in early and

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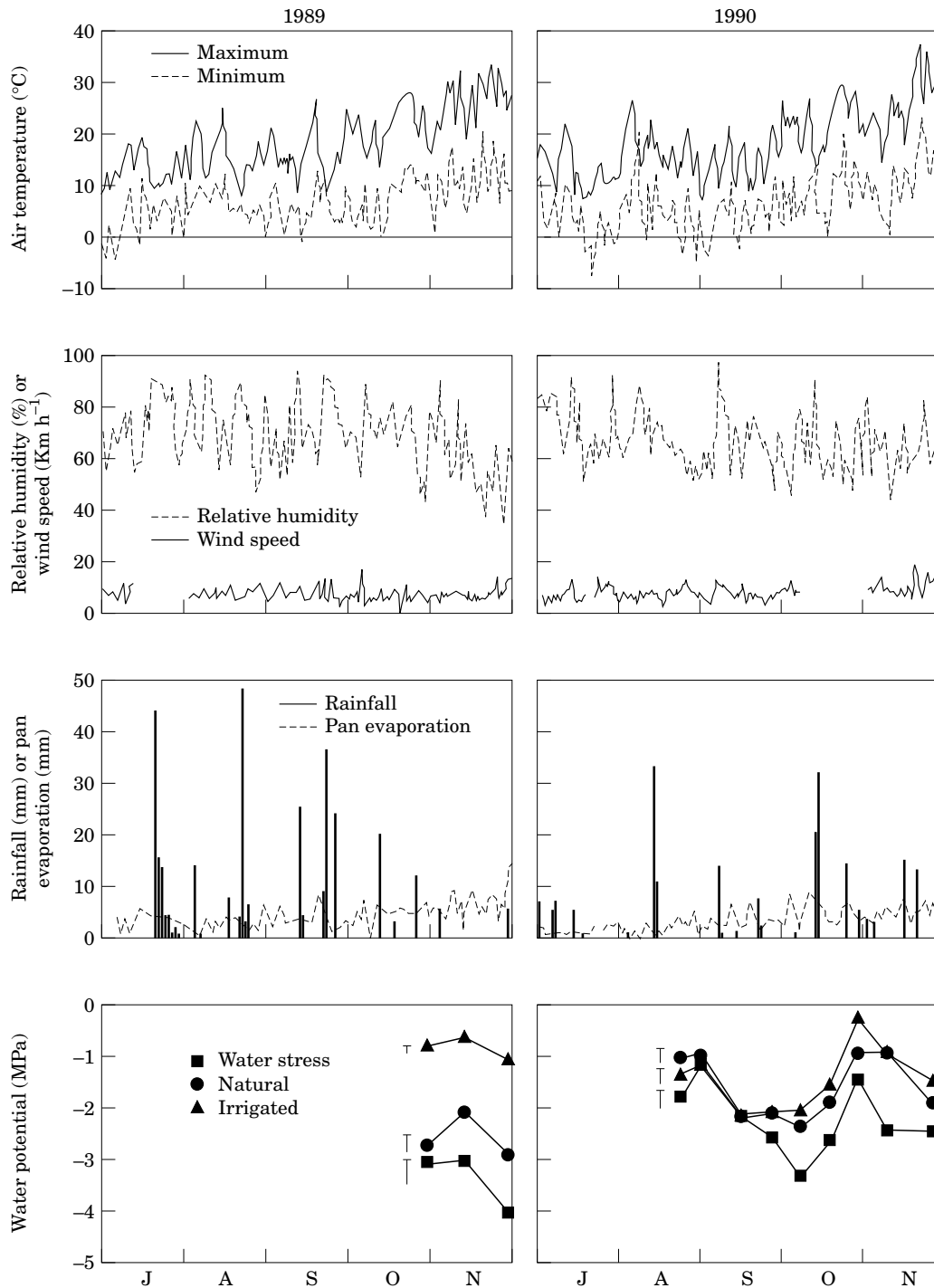


FIG. 1. Air temperature, relative humidity, wind speed, rainfall, pan evaporation and soil water potential at various times after transplanting of *M. minima* and *E. cicutarium* under water stress, natural or irrigated conditions in 1989 and 1990. Values of soil water potential are means ($n = 9$ in 1989 and $n = 5$ in 1990) and vertical bars indicate one s.e.m.

intermediate vegetative growth phases, respectively (Fresnillo Fedorenko *et al.*, 1996). Seedlings of both species were transplanted to PVC soil containers (0.15 m diameter, 0.50 m deep; one plant per container) which were buried in the soil. PVC containers have been demonstrated to be an effective system in which to study rooting of several plant

species (Thomas, 1985). Container depth was similar to the depth of the soil profile (0.40–0.60 m: Distel and Fernández, 1987) at the study area in the Calden District. Soil within the containers was obtained from this research area; it is a Typic Paleorthid, well-drained and of medium to thick texture that has been classified as thermic and arid (Van

Wambeke and Scoppa, 1976). Before treatment application, the soil within the containers was watered until its water-holding capacity was reached. Plants of both species were then exposed to water stress, natural, or irrigated conditions.

There were three plots for each water regime in 1989 and five plots in 1990. We decided to increase the number of plots and decrease the intensity of sampling on each plot in 1990 due to the small within-plot variability obtained for samples in 1989. Distance between plots was 2 m in both years. Each plot contained 28 plants in 1989 and 18 plants in 1990 (50% *M. minima*, 50% *E. cicutarium*). Plants were randomly assigned to soil containers. Containers were spaced at 0.50 m intervals and were wrapped in plastic at one end to prevent roots growing out (the plastic had some small diameter holes to allow water to percolate).

The water-stressed plots were covered with plastic sheets (0.2 mm thick) whenever rain fell during the course of the study. These plastic sheets were mounted on a specially designed wooden structure that provided an open-sided rain shelter. The plots used as an experimental control (natural) received only natural precipitation (247.4 and 192.7 mm in 1989 and 1990, respectively, Fig. 1). A third plot received supplemental water (1300 mm applied manually each year) during the study periods (22 Jul.–27 Nov. 1989, 4 Jul.–22 Nov. 1990).

Measurements

A micrometeorological station at the study site allowed measurements of relative humidity and air temperature at a height of 2 m using a thermohygrograph from the firm Sociedad Industrial de Aparatos de Precisión (SIAP), wind speed at 2 m using an anemometer (SIAP), pan evaporation with a type A tank and rainfall using a type B pluviometer (Fig. 1).

Soil water potential. Midday soil water potential was measured periodically in 1989 ($n = 9$) and 1990 ($n = 5$) using ceramic-cup thermocouple psychrometers (WESCOR Inc.) placed 15 cm deep within the containers. Psychrometers were calibrated individually following Brown and Bartos (1982). Microvolt outputs were measured with a WESCOR HR 33-T microvoltmeter.

Production and dry weight partitioning. Whole plants of both species were harvested on 27 October, 12 November and 27 November in 1989. Sampling dates in 1990 were 4 July, 30 August, 17 October and 22 November for *M. minima* and these dates plus 24 September and 5 November for *E. cicutarium*. In 1990, plant death in *M. minima* shortly after initiation of the experiment led to fewer plants being available for sampling, and thus a smaller number of destructive harvests. Also, the use of shoot samples of both species harvested on 22 Nov. 1990 for a concurrent study ruined these samples. On each sampling date, three plants per plot in 1989 and one plant per plot in 1990 were harvested for each species and water treatment. The individual plant samples were divided into stems, leaves, flowers, fruits and roots in *M. minima* and stems, leaves, peduncles, flowers, fruits and roots in *E. cicutarium*. Roots were collected in a 1 mm screen after washing them free of

soil. Root material was then cleaned from organic debris. Oven dry weights of all plant parts were recorded after drying at 60 °C for 72 h; organs which dropped from the plant were gathered from the soil surface and their dry weight added to the corresponding standing biomass. Hereafter, above-ground weight refers to weight summed over all aerial organs, and plant weight will refer to above-ground plus below-ground weights. Dry weight partitioning will refer to the distribution of dry weight between the organs of a plant, expressed as a percentage of the dry weight of the whole plant (Marcelis, 1996). Ratios of root-to-shoot weights were also calculated. Mean relative growth rates (R , d^{-1}) were calculated following Radford (1967) as

$$R = (\ln W_2 - \ln W_1) / (t_2 - t_1)$$

where W_1 and W_2 are organ dry weights at the beginning (t_1) and end (t_2) of the time interval $t_2 - t_1$.

Statistical analysis

Dry weights for each water level treatment and date were compared within each species and plant organ using a factorial design of three factors: water level treatment and date were used as main factors (fixed effects), and plots were nested within water level treatment (random effect). The percentage allocation of total plant dry weight among organs in each water level treatment was analysed using one-way ANOVA within each date and species. Root/shoot ratios were analysed using two-way ANOVA to compare water level treatments and dates within each species. Means were separated where appropriate using Fisher's Least Significant Difference ($P < 0.05$). The relationship between dry weight of an organ and the percentage of total plant dry weight allocated to this organ was studied using simple linear regression analysis. Within each species, regression lines were compared among water level treatments, and data were pooled if they were not significantly different ($P > 0.05$). Equality of regression lines was tested following the procedure of Neter, Wasserman and Kutner (1985).

RESULTS

Soil water potentials

During 1989 and beyond mid-October 1990, soil water potentials were lower ($P < 0.05$) under water stress than under irrigated conditions, and values ranged from -0.6 (irrigated) to -4.1 (water stress) MPa in 1989 and -0.3 (irrigated) to -3.4 (water stress) MPa in 1990 (Fig. 1).

Dry weight production

Between 97 and 113 d after transplanting in 1989, relative growth rates (d^{-1}) under water stress were positive for roots in both species ($\bar{x} \pm 1$ s.e.: 0.039 ± 0.013 in *M. minima*, 0.014 ± 0.001 in *E. cicutarium*) and fruits (0.039 ± 0.019) in *M. minima*; and negative for stems (-0.042 ± 0.014), leaves (-0.028 ± 0.011) and flowers (-0.065 ± 0.019) in *M. minima*, and for stems (-0.023 ± 0.005), leaves (-0.026 ± 0.001),

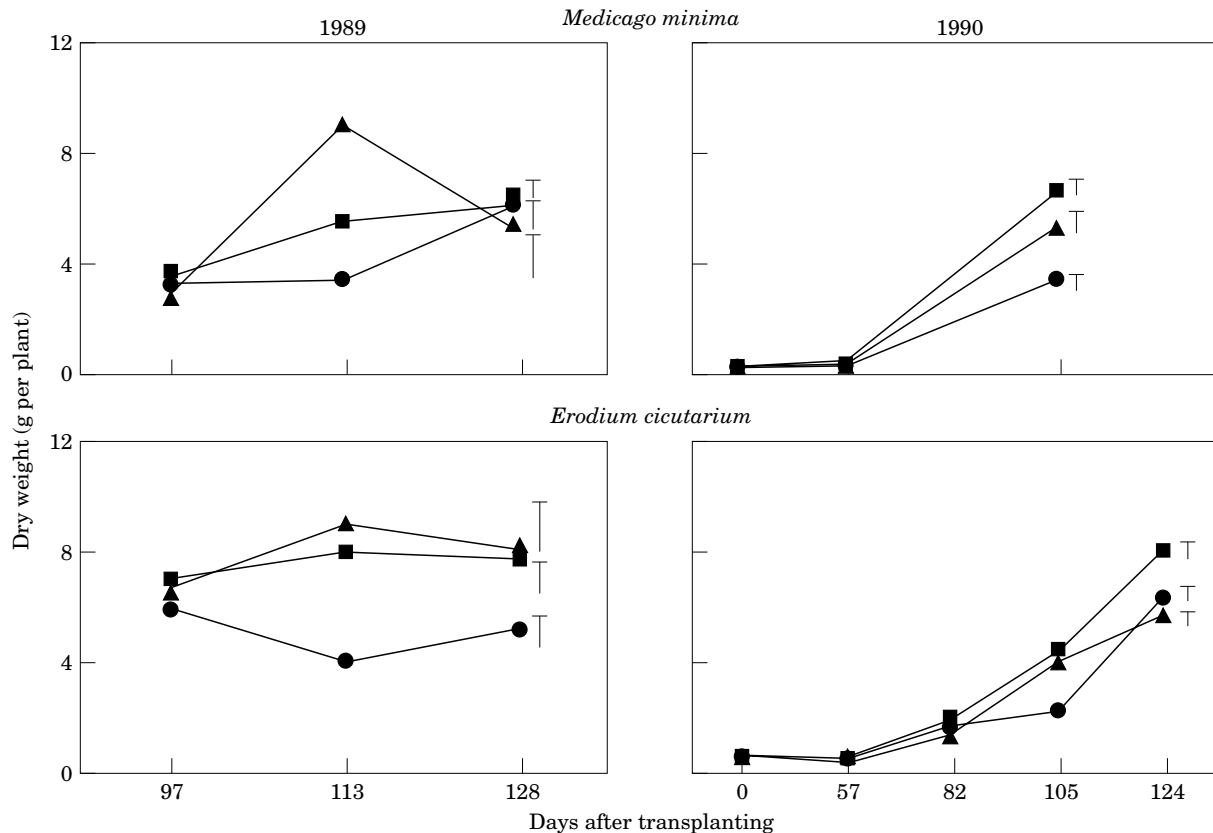


FIG. 2. Changes in plant dry weight of *M. minima* or *E. cicutarium* exposed to water stress (●), natural (■) or irrigated (▲) conditions after transplanting to field conditions in 1989 and 1990. Each value is the mean of $n = 3$ in 1989 and $n = 5$ in 1990. An average s.e.m. is shown as a vertical bar for each water level treatment.

peduncles (-0.021 ± 0.003), flowers (-0.034 ± 0.008) and fruits (-0.051 ± 0.007) in *E. cicutarium*. At the same time, relative growth rates in *M. minima* were positive for flowers (0.021 ± 0.022), leaves (0.034 ± 0.015), roots (0.051 ± 0.016), shoots (0.063 ± 0.013) and fruits (0.182 ± 0.011) under irrigated conditions. This contributed to the fact that above-ground and plant dry weights, and the dry weight of stems, leaves and flowers in *M. minima* were greater ($P < 0.05$) under irrigated than under natural or water stress conditions 16 weeks after transplanting in 1989 (Figs 2 and 3). Thereafter, however, relative growth rates for roots, stems, leaves and fruits in *M. minima* were negative under irrigated conditions (-0.021 ± 0.018 , -0.048 ± 0.012 , -0.077 ± 0.004 and -0.017 ± 0.013 , respectively) and positive in the water stress treatment (0.022 ± 0.038 , 0.039 ± 0.023 , 0.004 ± 0.025 and 0.055 ± 0.025 , respectively). This led to similar ($P > 0.05$) plant, above-ground and organ dry weights in this species under all water levels at the last sampling date in 1989 (Figs 2 and 3). From 113 to 128 d after transplanting in 1989, decreases in dry weight in *M. minima* under irrigated conditions were only significant ($P < 0.05$) for stems, leaves and flowers (Fig. 3). Although above-ground and plant dry weights in *M. minima* were similar ($P > 0.05$) among water level treatments in 1990 (Fig. 2), plants of this species showed lower ($P < 0.1$) stem, leaf and root dry weights under water stress than under more favourable soil moisture levels (Fig. 3). Above-ground and plant dry

weights, and dry weights of organs were similar ($P > 0.05$) in each water level treatment in *E. cicutarium* during 1989 and 1990 (Figs 2, 3 and 4), the only exception being the dry weight of flowers and roots which were 12–68% (1989, Fig. 3) and 10–37% (1990, Fig. 4) lower ($P < 0.05$), respectively, under water stress than under more favourable moisture levels.

Dry weight of roots in both species, and fruits in *M. minima*, increased ($P < 0.05$), and that of fruits in *E. cicutarium* decreased, after the end of October 1989 (Fig. 3). During 1990, the dry weight of all organs increased ($P < 0.05$) from August to November in both species (Fig. 4).

Dry weight partitioning

Partitioning of total plant dry weight to fruits was greater ($P < 0.05$) under water stress than under irrigated conditions during October in both years for *M. minima*, and towards the end of September in 1990 for *E. cicutarium* (Figs 5 and 6). By mid-October 1990, percentage allocation of total plant dry weight to stems and leaves in *M. minima* was lower ($P < 0.05$) under water stress than under irrigated conditions (Fig. 6).

The relationships between dry weight of an organ and the percentage of dry matter partitioned to this organ in 1989 were significant ($P < 0.05$) for flowers and fruits in *M.*

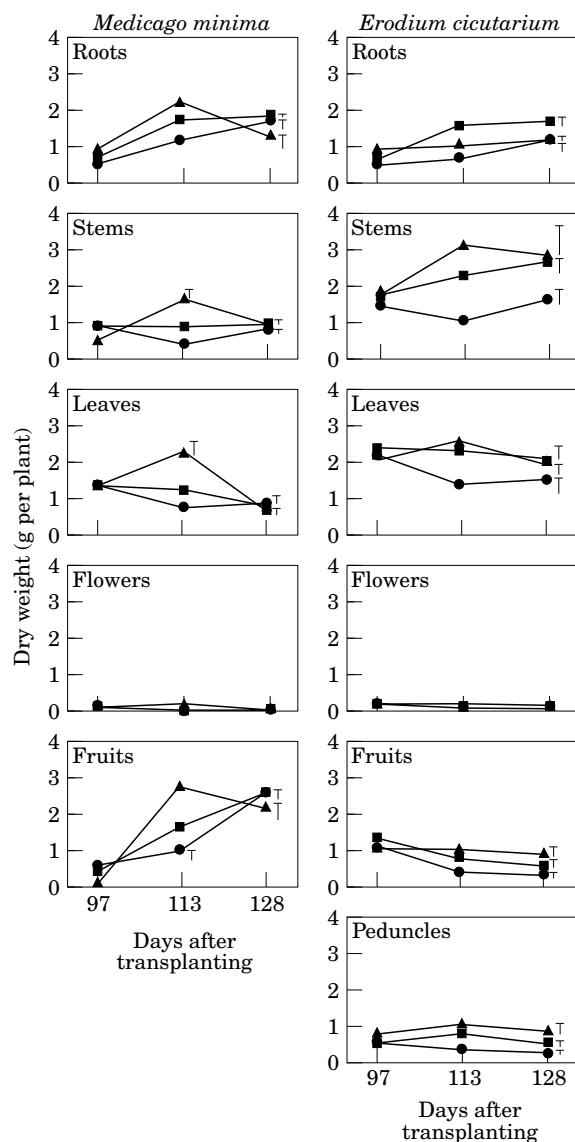


FIG. 3. Changes in root, stem, leaf, flower, fruit or peduncle dry weight of *M. minima* or *E. cicutarium* exposed to water stress (●), natural (■) or irrigated (▲) conditions after transplanting to field conditions in 1989. Each value is the mean of $n = 3$. An average s.e.m. is shown as a vertical bar for each water level treatment.

minima and for flowers, fruits, stems and peduncles in *E. cicutarium* (Fig. 7); they were not significant ($P > 0.05$) for all other organs in either species. In 1990, there were not sufficient data points to perform regression analysis for *M. minima*. During this year, however, *E. cicutarium* again showed significant ($P < 0.05$) relationships for fruits, stem and peduncles, but not for flowers, leaves or roots (Fig. 7).

Root/shoot dry weight ratios were similar ($P > 0.05$) for all water level treatments and dates in both species and both years, and mean values ranged from 0.19 ± 0.01 to 0.72 ± 0.13 in *M. minima* and 0.05 ± 0.01 to 0.47 ± 0.09 in *E. cicutarium*. The only exception was in *E. cicutarium* where root/shoot dry weight ratios decreased ($P < 0.05$) steadily from 0.43 ± 0.06 (30 August) to 0.07 ± 0.02 (5 November) as the growing season progressed in 1990.

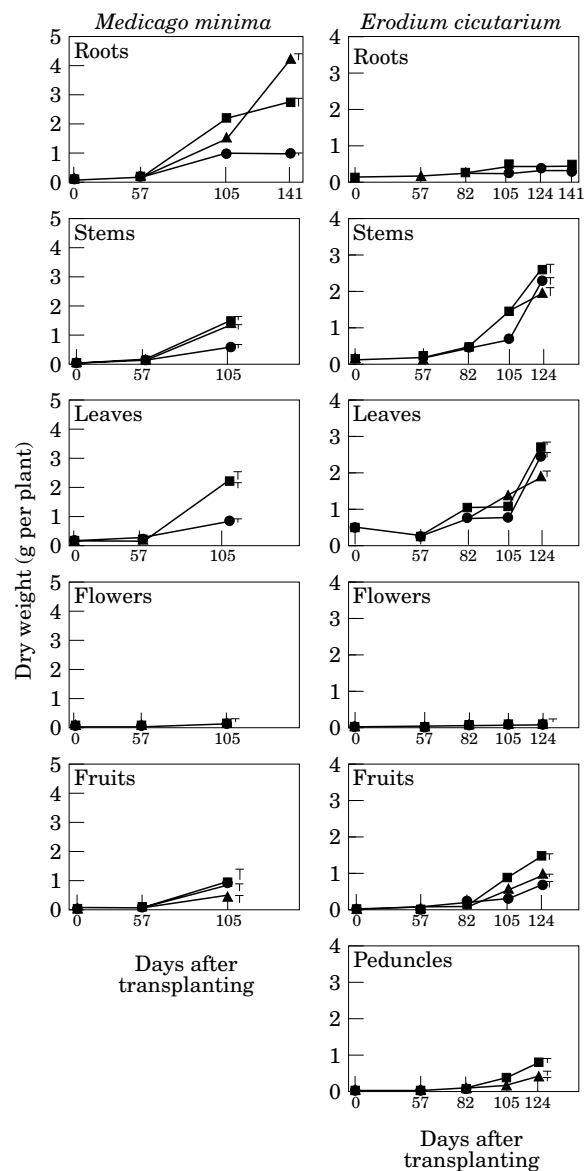


FIG. 4. Changes in root, stem, leaf, flower, fruit or peduncle dry weight of *M. minima* or *E. cicutarium* exposed to water stress (●), natural (■) or irrigated (▲) conditions after transplanting to field conditions in 1990. Each value is the mean of $n = 5$. An average s.e.m. is shown as a vertical bar for each water level treatment.

DISCUSSION

Water stress appears to affect shoots more than roots, and may even stimulate deep root production at the expense of shoots in herbaceous rangeland and crop species (Carvalho and Schank, 1989; Brown, 1995). Thus, water stress had a greater effect on the stems, leaves and peduncles compared to roots in both species 113 d after transplanting in 1989 (Fig. 3). Any potential differences in sensitivity of shoots and roots of *M. minima* and *E. cicutarium* to water stress, however, were not strong enough to affect root/shoot dry weight ratios which remained similar in all water level treatments in both species and both years. This result is in agreement with the findings of Grzesiak, Filek and

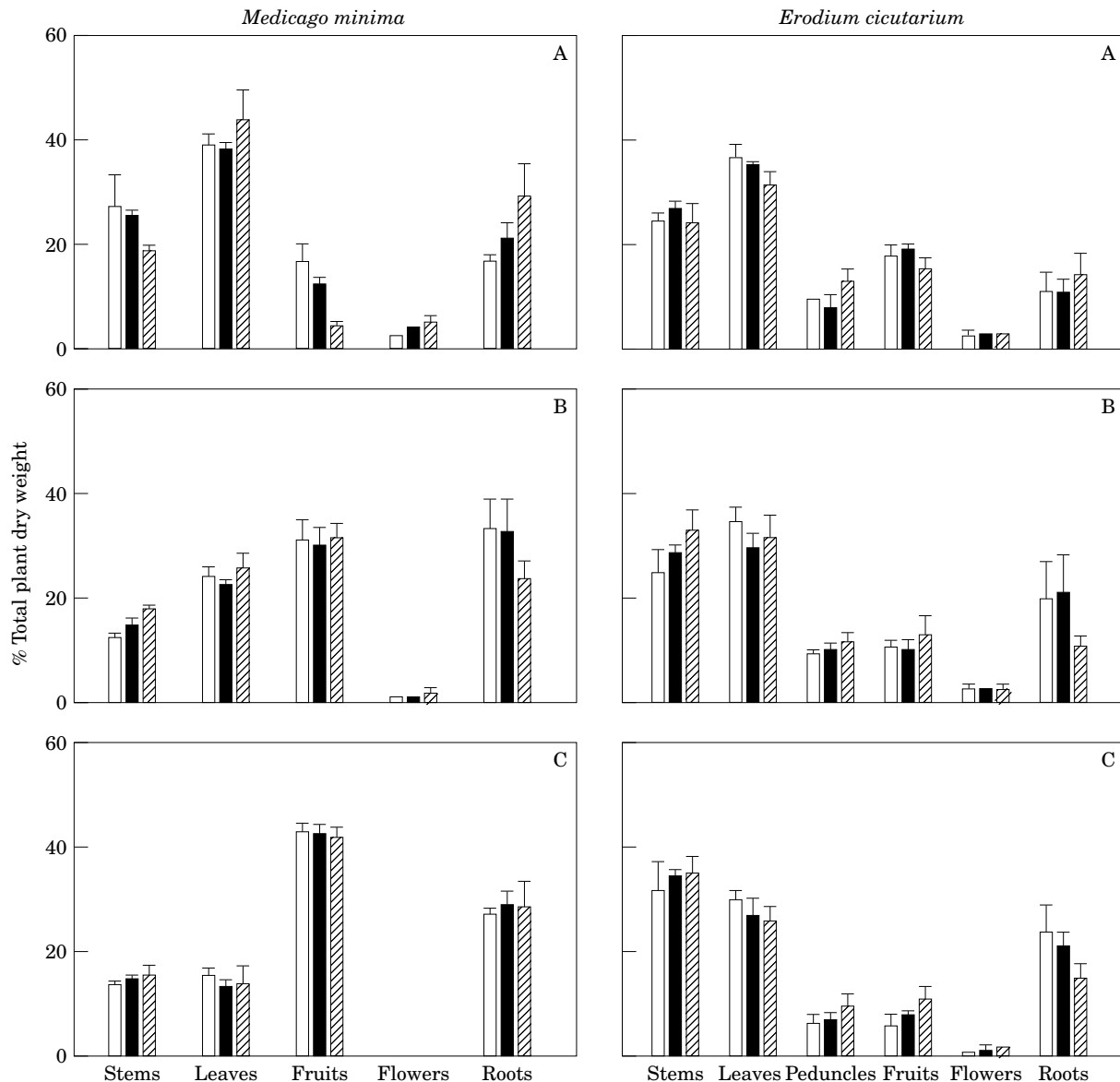


FIG. 5. Dry weight partitioning into various organ categories expressed as a percentage of total plant dry weight in *M. minima* and *E. cicutarium* exposed to water stress (□), natural (■) or irrigated (▨) conditions during 1989 (A, 27 October; B, 12 November; C, 27 November). Columns are means of $n = 3$. Vertical bars represent one s.e.m.

Koscielniak (1989) for *Vicia faba* L. var. *minor*, Sobrado and Turner (1986) for *Helianthus petiolaris* Nutt. and *H. annuus* L., and Fernández, Cothren and McInnes (1991) for *Gossypium hirsutum* L. Sobrado and Turner (1986) suggested that a similar degree of osmotic adjustment in root and leaf cells would help explain the similar root/shoot ratios which they found in water-stressed and unstressed *Helianthus* species. This result contrasts, however, with reports of increases in root/shoot ratios with increased water stress in several crop, cultivated pasture, desert and Mediterranean annual species (Dwyer and Stewart, 1987; Hall, Sheaffer and Heichel, 1988; Blaikie and Mason, 1990; Hamblin, Tennant and Perry, 1990; Aronson *et al.*, 1992; Chartzoulakis, Noitsakis and Therios, 1993). Chartzoulakis *et al.* (1993) suggested that a higher osmotic adjustment in

root than in leaf cells caused greater root/shoot ratios in water-stressed plants of *Actinidia sinensis*.

Dry weights of some aerial organs and roots were greater in irrigated than in water stressed *M. minima* during 1989 and 1990 (Figs 3 and 4). This must have been associated with the lower soil water potentials under water stress than under natural or irrigated conditions in both years (Fig. 1). Reductions in plant and organ dry weights under water stress have also been reported for other annual or perennial legumes (Hall *et al.*, 1988; Ong, Simmonds and Matthews, 1987; French and Turner, 1991). Dry weights of these plant parts, however, appeared to be much less affected by water stress in *E. cicutarium* (Figs 3 and 4). These results agree with those found by Peláez *et al.* (1995) in a concurrent study in 1990 using the same plants. These authors reported

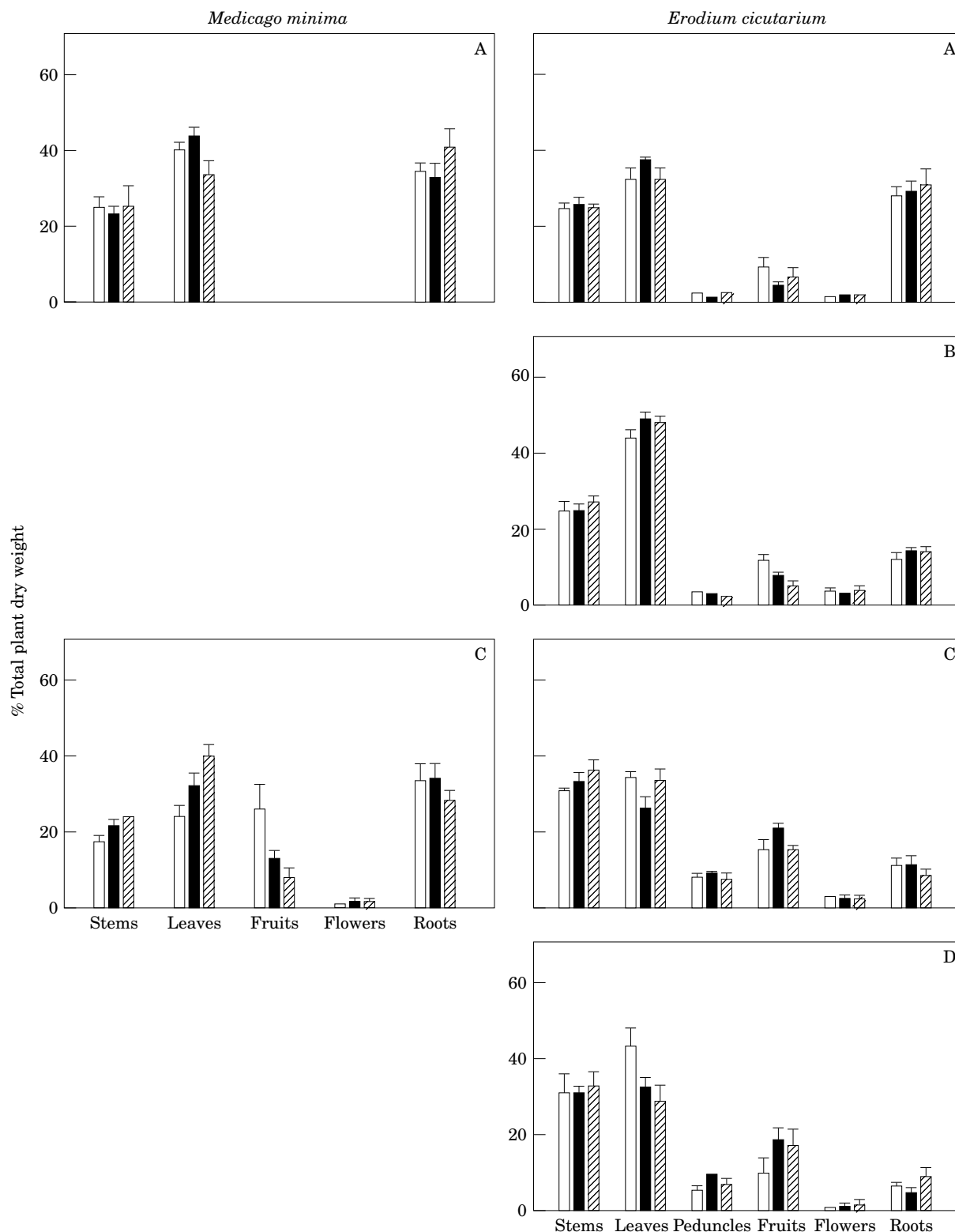


FIG. 6. Dry weight partitioning into various organ categories expressed as a percentage of total plant dry weight in *M. minima* and *E. cicutarium* exposed to water stress (□), natural (■) or irrigated (▨) conditions during 1990 (A, 30 August; B, 24 September; C, 17 October; D, 5 November). Each column is the mean of $n = 5$. Vertical bars represent one s.e.m.

that while the total number of leaves, number of green leaves, height, total green leaf and petiole lengths, length of secondary ramifications, and number of flowers and fruits

were lower in water stressed *M. minima*, these parameters were similar under all levels of soil water availability in *E. cicutarium*. These findings complement the growth chamber

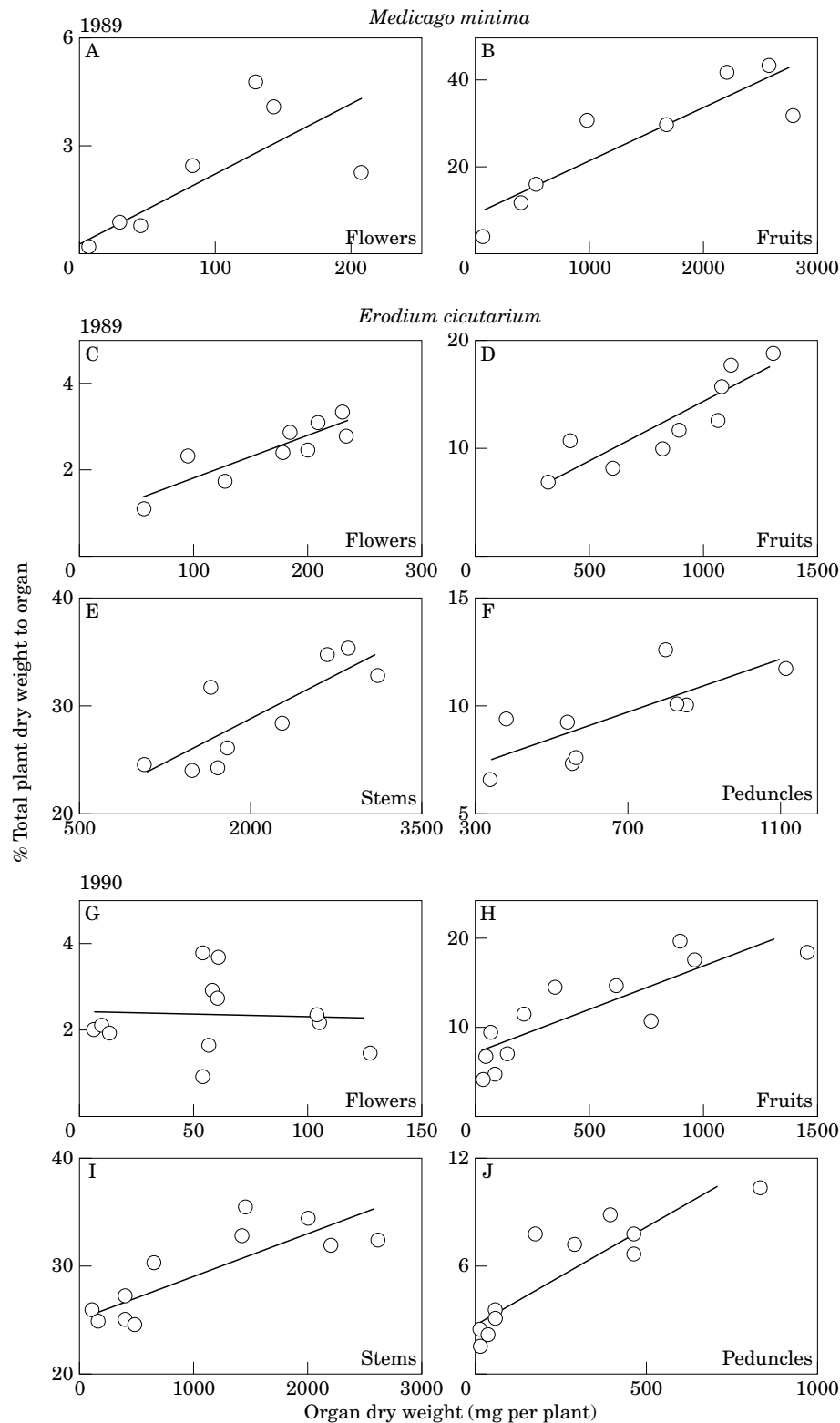


FIG. 7. Percentage of total plant dry weight partitioned into flowers, fruits, stems or peduncles (y) as a function of total dry weight of these organs (x) of *M. minima* and *E. cicutarium* in 1989 or 1990. Each value is the mean of $n = 3$ in 1989 and $n = 5$ in 1990. Data were pooled for all water level treatments since their individual regression lines were not significantly different ($P > 0.05$). Regression statistics: A, $y = 0.335 + 18.7x$, $r^2 = 0.60$, $P = 0.014$; B, $y = 8.90 + 12.1x$, $r^2 = 0.81$, $P < 0.001$; C, $y = 0.841 + 9.50x$, $r^2 = 0.75$, $P < 0.001$; D, $y = 3.01 + 10.7x$, $r^2 = 0.78$, $P < 0.001$; E, $y = 17.7 + 5.39x$, $r^2 = 0.67$, $P = 0.007$; F, $y = 5.49 + 5.85x$, $r^2 = 0.55$, $P = 0.021$; G, $y = 2.41 - 1.64x$, $r^2 = 0.005$, $P = 0.825$; H, $y = 7.30 + 9.86x$, $r^2 = 0.71$, $P < 0.001$; I, $y = 25.2 + 3.72x$, $r^2 = 0.68$, $P < 0.001$; J, $y = 2.62 + 10.8x$, $r^2 = 0.79$, $P < 0.001$.

work of Fresnillo Fedorenko *et al.* (1995) using *M. minima*, in which the above mentioned demographic and growth parameters were reduced under water stress. Cox and Conran (1996) also found that the total mass of *E. cicutarium* was unaffected after exposing this species to artificial drought conditions.

The lack of sensitivity of *E. cicutarium* to water level treatments could help to explain why this species is found in a wide variety of habitats, ranging from very dry and hot semi-deserts to moist and cool, high-altitude mountain slopes (Venter and Verhoeven, 1990). As suggested by Peláez *et al.* (1995), future research should aim to elucidate the mechanisms which allow *E. cicutarium* to maintain its growth unabated by water stress. Despite the legume appearing to be more susceptible than *E. cicutarium* to water stress, *M. minima* has survived repeated exposure to soil water potentials of -6 MPa (Fresnillo Fedorenko *et al.*, 1995), and both species survived until the end of study in the water stress treatment in 1990 when soil water potentials were lower than -2 MPa (Fig. 1). This response could help to explain the persistence of both species in the Southern Caldenal, occupying degraded areas or associated with native grasses. The high phenotypic plasticity shown by *M. minima* under different levels of water availability also indicates that this species can exploit abundant environmental resources when they are available (Kemp, 1989; Fresnillo Fedorenko *et al.*, 1995).

From 113 d to the end of the study in 1989, plants of *M. minima* underwent senescence. A concurrent field study in a temperate semi-arid region in central Argentina reported plant death of *M. minima* by 22 November (Fresnillo Fedorenko *et al.*, 1996). Enhanced rates of respiration concomitant with declining photosynthetic rates have been reported in several species during leaf senescence (Rhodes, 1980). These changes may be correlated with the oxidation of carbon skeletons of the amino acids that accumulate in the senescing leaves as a result of proteolysis (Rhodes, 1980). Rises in respiration rate associated with leaf senescence can be up to 2.5-times greater than the previous basal, sustained level (Rhodes, 1980). Increases in the respiration rate have also been reported for flowers and fruits as they undergo senescence (Rhodes, 1980). It is these periods of enhanced respiration that are of particular interest in attempting to understand the underlying processes occurring in senescence. Our results suggest that respiration during senescence of *M. minima* under irrigated conditions may have been highly enhanced, and could partly explain the decrease in dry weight in all organs observed in this species between 113 and 128 d after transplanting in 1989 (Fig. 3). Decreases in various organ or plant dry weights towards the end of the growing cycle have been observed in other studies of carbon partitioning in herbaceous species (Szarek, Smith and Ryan, 1982; Grashoff, 1990; French and Turner, 1991; Hardy, Huyghe and Papineau, 1997). Organ dry weight decreases under irrigated conditions were not observed towards the end of the study in 1990, when experimental sampling finished 1 week earlier than in 1989. Phenological changes in *M. minima* can occur very quickly during the later stages of development: plants can have open flowers, green and mature fruits by mid November,

and die a week later (Fresnillo Fedorenko *et al.*, 1996).

The decrease in fruit weight in *E. cicutarium* under natural and water stress conditions after the end of October 1989 (Fig. 3) could be due, in part, to fruit loss from the plant to the soil in this species. Fresnillo Fedorenko *et al.* (1996) reported fruits of *E. cicutarium* were mature by the end of this month in a parallel study conducted in the south of the Calden District during 1989. Mature fruits of *E. cicutarium* are rarely found on the plant towards the end of the growing cycle because this species explosively discharges its awned, mature fruits, which can bury themselves into the soil by hygroscopic movements (Stamp, 1984; Fresnillo Fedorenko *et al.*, 1996). Thus, we were unable to gather all fruits produced by each plant since some of them were probably buried in the soil.

Because *M. minima* and *E. cicutarium* have indeterminate growth (Fresnillo Fedorenko *et al.*, 1996), dry weight allocation to vegetative parts continues during the reproductive phase, thus competing with reproductive organs for assimilates. When considering the priority rank order between alternative sinks, however, seeds would obtain a greater resource share than shoot apices, leaves and roots (Wright, 1989; Wardlaw, 1990). However, although the response was more marked in *M. minima* than in *E. cicutarium*, plants of both species exposed to water stress allocated a higher proportion of the total plant dry weight to fruits than those grown under the irrigated treatment during early spring (Figs 5 and 6). This plastic response observed in both species is a beneficial feature under drought conditions because it enables plants to complete their life cycle and ensure seed production. Changes in assimilate partitioning in favour of reproductive growth under water stress have also been reported in *Erodium crinitum* Carolin and other ephemeral species adapted to arid or semi-arid conditions, as well as in several annual crops (Sobrado and Turner, 1986; French and Turner, 1991; Singh, 1991; Cox and Conran, 1996). However, Cox and Conran (1996) reported a significant decrease in the proportion of fruiting *vs.* vegetative organs in droughted *E. cicutarium*. Differences in dry matter partitioning between vegetative and reproductive growth were not reported for some water-stressed and unstressed annual crops or perennial grasses (e.g. Egli, Guffy and Leggett, 1985; Alcocer-Ruthling, Robberecht and Thill, 1989).

Percentage allocation of total plant dry weight into flowers and fruits in both species, and stems and peduncles in *E. cicutarium*, correlated with total dry weight (sink size) of these organs (Fig. 7) which might indicate a correlation between sink size and strength. However, sink strength of an organ is probably not causally related to its size, and it may also depend on its age, potential growth rate, carbohydrate supply, other sinks and resistance to flow of the transport pathway (Marcelis, 1996; Minchin and Thorpe, 1993; Minchin, Thorpe and Farrar, 1993; Minchin and Thorpe, 1996).

One important limitation to animal production on rangelands is the scarcity of leguminous species to complement the animals' diets. In areas such as the southwestern United States, much effort has been invested in evaluating

the potential for establishing *Medicago* species in rangelands or dryland pastures that receive between 100 and 200 mm winter precipitation (Brahim and Smith, 1993). The natural presence of *Medicago minima* in extensive areas of the Southern Caldenal complements animal diets in this semi-arid region during part of the year. This is in contrast to most rangelands which suffer a scarcity of natural leguminous species (Fresnillo Fedorenko *et al.*, 1991).

Medicago minima showed a high phenotypic plasticity under different levels of soil water availability which may enhance its capacity to survive and reproduce under varying conditions. Kemp (1989) emphasized the extreme developmental plasticity found in annual legumes after germination which increased their chance of seed production under conditions of erratic and low precipitation. *E. cicutarium*, however, appeared to be less sensitive to water stress than the legume. Both species can survive under severe drought conditions and exploit abundant environmental resources when they are available. Their persistence in the local flora appears to be ensured by their capacity to colonize open, degraded areas as well as to grow in association with perennial grasses. Further research should seek the inclusion of *M. minima* in conventional plant breeding programmes or more advanced biotechnological manipulations in an attempt to obtain a domesticated legume for semi-arid territories.

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