

## Biomass accumulation and resource utilization in co-occurring grassland annuals

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**Abstract.** Mediterranean-climate annuals growing on serpentine soils in central California differ greatly in their life spans and reproductive periods dependent on their access to soil moisture. The longer-lived annuals accumulate a greater lifetime biomass, have a higher total, but lower proportional, reproductive output, and produce leaves with a higher C/N ratios at the time of reproduction.

**Key words:** Serpentine – Annuals – Water-use – Nitrogen-use – Reproduction

In coastal California many areas underlain by serpentine rock develop grassland communities which are rich in native annual species. These communities have been described by MacNaughton (1968) and others. These annual plants germinate more or less synchronously with the initial fall rains, with most completing their life cycle as the annual drought is initiated around May. A few however persist into the summer drought period.

Gulmon (et al. 1983) studied three annual species which represent the total range of life spans found in one of these communities. They noted that the longer-lived annuals were able to extend their growth period and attain considerably greater biomass by tapping deeper soil water reserves than could the shorter-lived annuals.

In this study we extend these observations to a broader base to determine if the relationships among life span, biomass accumulation, and resource availability are general.

### Materials and methods

**Study site.** All observations were made at the Jasper Ridge Biological Preserve of Stanford University which is located in the interior foothills of the Santa Cruz Mountains in San Mateo County, California.

**Phenological and Water Potential Observations.** 10–1 m<sup>2</sup> plots were established at regular intervals along a 50 m long transect within the serpentine grassland community. At approximately weekly intervals during 1983–85 the number of plots containing annuals at given reproductive states were noted. Species encountered in the quadrants are listed in Table 1. Xylem water potential was also measured on several individuals of selected species during 1983 utilizing a Scholander pressure bomb.

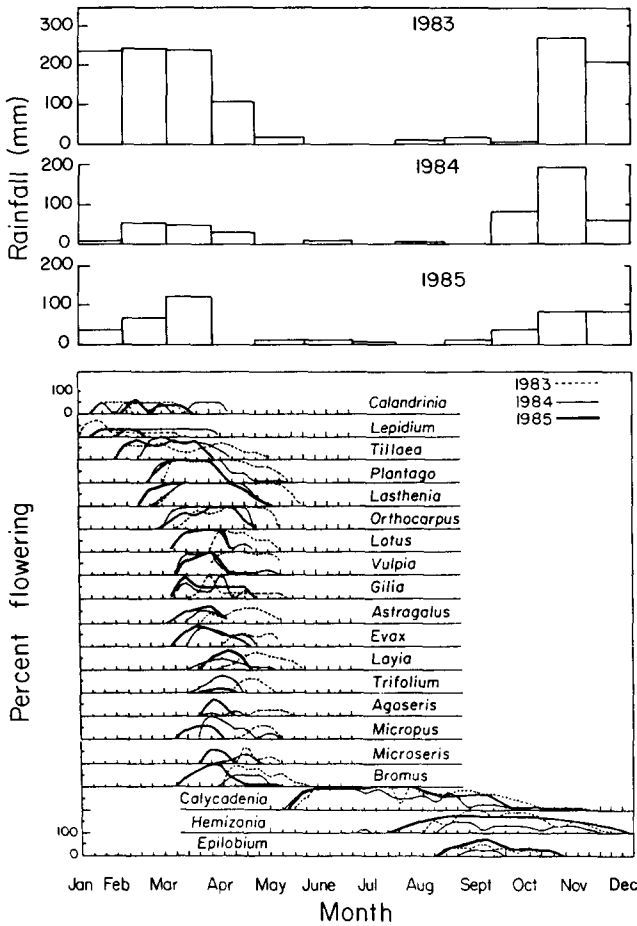
**Biomass.** During 1985, at the time of apparent maximum biomass, generally during the fruiting stage before leaf loss, the above-ground portions of 10 individuals of each species were harvested and dried at 70 C for weight analysis. Samples were partitioned into reproductive (buds, flowers, seeds) and vegetative portions. Leaves of a number of species were additionally collected just at the initiation of reproduction and dried and ground for carbon and nitrogen content analyses utilizing a Perkin-Elmer Elemental Analyzer.

### Results

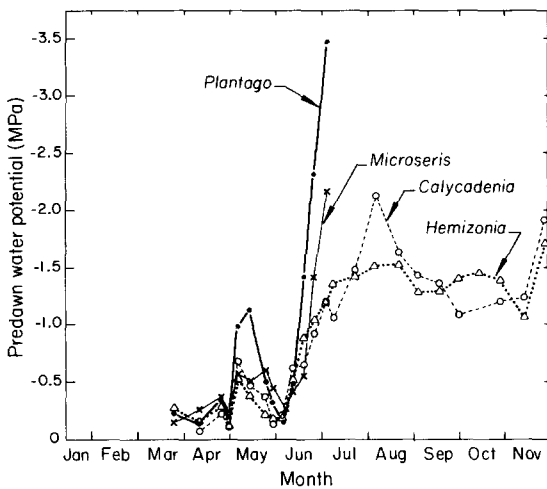
**Phenology.** Over 20 annual species were encountered in the study plots. There was a large spread in the flowering dates of the various species of annuals which were studied, some flowering as early as January and others not starting until August (Fig. 1). This spread occurred even though there was little difference among species in their initial germination date which commenced with the first significant fall rains (Hobbs and Mooney 1985). Differences in the flowering dates were noted between years for the various species with most, but not all, flowering several weeks earlier in the dry years of 1984 and 1985. Some species varied greatly between years in time of onset of flowering (e.g. *Evax*, *Micropus*, *Bromus*), while others varied little (e.g. *Plantago*, *Lasthenia*, *Calycadenia*). The later-blooming species generally had a more protracted flowering period than the earlier ones.

**Water availability.** Measurements of dawn water potential of two early and two late blooming species indicated dissimilar water availabilities (Fig. 2). The late blooming species did not experience the same degree of water stress as the early blooming ones. These dissimilarities relate to differences in their rooting depths (Gulmon et al. 1983).

**Biomass allocation.** There was a large range in the size of the annuals studied (*Gilia* and *Trifolium* biomass data not available) with later blooming species attaining nearly an order of magnitude greater biomass than the earlier ones (Fig. 3). The absolute reproductive output per individual generally followed these trends (Fig. 4A) although the proportional effort significantly declined with plant size (Fig. 4B). The variance in the biomass attained at flowering was much greater for the later blooming species than the earlier ones (Fig. 3). This can be attributed to the attain-



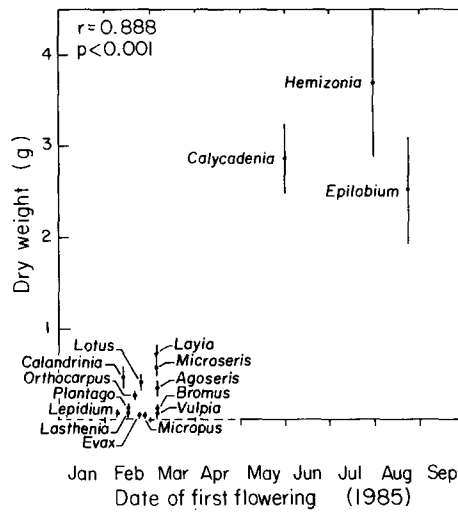
**Fig. 1.** Flowering period for a set of Jasper Ridge annuals during three different years



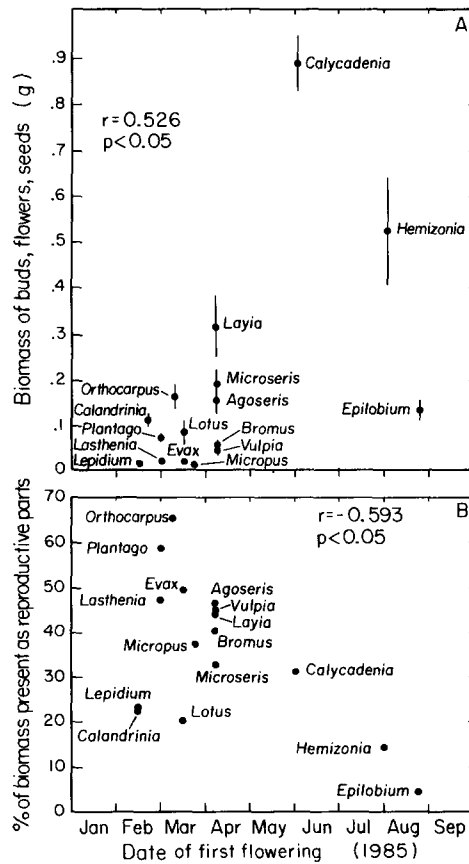
**Fig. 2.** Dawn xylem water potential for two early (*Plantago* and *Microseris*) and two late (*Calycadenia* and *Hemizonia*) blooming species during 1983

ment of water at depth by some individuals but not others (Gulmon et al. 1983).

**Carbon/nitrogen contents.** The carbon/nitrogen ratio of leaf tissue was significantly higher in the late blooming species (Fig. 5). The increasing C/N ratio with blooming time was due to a lower leaf nitrogen content of the longer lived



**Fig. 3.** Mean biomass attained at time of first flowering for a series of annual species



**Fig. 4.** A Mean dry weight of reproductive tissue of annuals blooming at different times. B Proportion of reproductive tissue on annuals of differing longevity

species since the carbon content was fairly constant across species (40–45%).

**Discussion**

These results confirm and extend those found earlier by Gulmon et al. (1983). Biomass attained by annuals is pro-

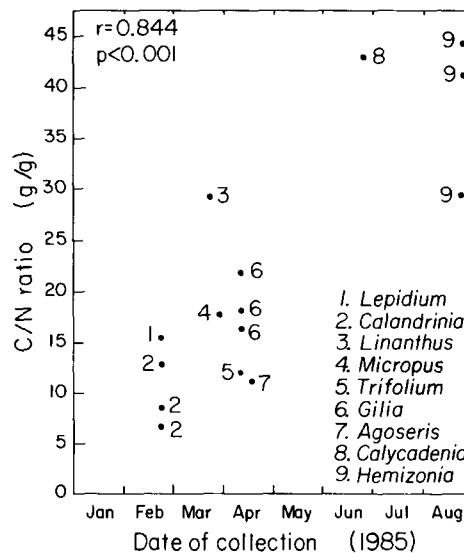
**Table 1.** Species analyzed or encountered in phenology plots

Agoseris heterophylla (Nutt.) Greene
Astragalus gambellianus Sheldon
Bromus mollis L.
Calandrinia ciliata (R. & P.) DC. var menziesii (Hook) Macbr
Calycadenia multiglandulosa DC.
Epilobium paniculatum (Nutt.)
Evax sparsiflora (Gray) Jeps.
Gilia clivorum (Jeps.) V. Grant
Hemizonia luzulaefolia DC.
Lasthenia californica DC. ex Lindley
Layia platyglossa (F. & M.) Gray
Lepidium nitidum (Nutt.)
Linanthus androsaceus (Benth) Greene
Lotus subpinnatus (Lag.)
Micropus californicus (F. & M.)
Microseris douglasii DC. Sch.-Bip.
Orthocarpus densiflorus Benth.
Plantago erecta Morris
Tillea erecta (H. & A.)
Trifolium albopurpureum (T. & G.)
Vulpia microstachys (Nutt.) Benth. var pauciflora (Beak) Lonard & Gould.

portionate to the length of their respective growing seasons which is apparently controlled by the differential amounts of water resource available to them. These results are a temporal analogy of the spatial linear relationship described for grassland productivity versus rainfall amount received in Africa (Walter 1939).

There are a number of consequences of the extended productive activities of the longer lived annuals. One consequence is on the nature of the plant tissue formed. Growth during the rainless summer for the long-lived annuals is at the expense of soil moisture at depth (Gulmon et al. 1983). Nitrogen availability is likely limited at this time although carbon through photosynthesis is not. Thus the carbon to nitrogen ratio of the leaf tissue is lower than that found in those species growing only during the wet season. This difference has implications in herbivore susceptibility and in decomposition patterns of these plants. Two of the late blooming species, *Hemizonia luzulaefolia* and *Calycadenia multiglandulosa*, form dimorphic leaves. In *Hemizonia* the winter leaves have high nitrogen contents and do not produce resins, whereas those produced during the summer, during the nitrogen poor carbon rich periods, are low in nitrogen and high in resin content (Mooney and Chu, Unpublished).

Another important consequence of the different longevities of these plants is in their reproductive potential. The longer lived the plant, the greater biomass it accumulates and the higher its seed output. Reproductive trends within and among species in relation to environmental gradients have generally been studied on perennials and then principally along successional gradients (see Abrahamson 1980). There has been less work on the reproductive effort of annuals in relation to habitat diversity. Hickman (1975) found that annual plants of *Polygonum cascadenense* produced a greater proportion of seeds in water stressed over non-stressed habitats. Over a decreasing available-moisture gradient he found a 16-fold decrease in dry matter production and an increase in reproductive effort from 0.38 to 0.58. These differences were plastic since seeds of plants from these habitat types produced similar seed allocation pat-



**Fig. 5.** Carbon/nitrogen ratios of leaves of plants flowering at different times. Each individual number represents a different individual plant

terns when grown in a common environment. Similarly Jaksic and Montenegro (1979) found that a number of Chilean annual plants increased their biomass in wet years but decreased their proportional reproductive effort. The results from the Jasper Ridge annuals confirm these general trends. The results indicate a large variation in reproductive effort within one life history type (i.e. annuals) at one site (from 65% for *Orthocarpus* to 5% for *Epilobium*).

We did not follow possible differences in productivity of the annuals among the three years of study. However we did find that the phenological patterns varied considerably from year to year with the commencement of flowering varying by two to four weeks depending on species. A variance of this magnitude can be found during a given year between slopes for a given species (Schmitt 1983; Dobkin et al. unpublished work). Chiariello (1986) has discussed the general relationship between water potential and onset of flowering and has illustrated that summer-active species begin to flower at a water potential lower than those of early flowering species.

If the trigger to commence reproductive activity is related to the onset of drought one would expect that those longer-lived species which utilize deep water reserves and hence have a resource supply which does not disappear so rapidly in time might bloom more regularly from year to year. This does seem to be the case for *Calycadenia*. However, as noted above not all plants of late blooming species reach a deep water supply and thus there is great variability in the sizes they attain and in the water stress they experience.

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