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Temporal differentiation in maximum biomass and nutrient accumulation rates in two coexisting annual plant species

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Abstract

The temporal patterns of growth and nutrient accumulation into above-ground biomass of two annual coexisting plant species were studied in a semi-arid unfertile grassland. The hypothesis that temporal differences in growth and in nutrient accumulation into above-ground biomass facilitate species coexistence was also tested. Of the annual species identified, only the growth data of *Vulpia myuros* (L.) C.C. Gmel. and *Trifolium campestre* Schreb., for two growing seasons, 1991 (wet) and 1993 (dry) were used. The timing of maximum rates were estimated for above-ground biomass growth and accumulation of N, P, and K in above-ground biomass, as well as for the respective rates from the best fitted curves to data of the seven harvests for 1991 and six for 1993 made. The mean timing of maximum rates for the species, averaged over all growth parameters (absolute growth rates, and rates of nutrient accumulation) and years were significantly earlier for the *Vulpia*. Mean maximum rates of growth parameters, averaged over all species and years followed this order: significantly earlier $K < P = N <$ biomass. Absolute growth rates, averaged over all species were significantly earlier in the dry than in the wet year. On the contrary, the K accumulation rates were earlier in the wet than in the dry year. In the wet year 1991 in comparison to dry 1993, higher moisture levels affected the growing period, and the temporal separation of species maxima

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was more pronounced, which may have resulted in moderate interspecific competition between *Vulpia* and *Trifolium*.

Keywords: Growth analysis; Growth curves; Nutrient uptake; *Trifolium campestre* Schreb.; *Vulpia myuros* (L.) C.C. Gmel

1. Introduction

Plant scientists investigating plant growth often have to estimate growth parameters from experimental data. Parameters of growth analysis such as absolute growth rate, net assimilation rate, and rate of nutrient accumulation are influenced by competition and are important in understanding the structure and dynamics of vegetation (Grime, 1979; Tilman, 1982).

The competitive exclusion principle predicts that species occupying the same niche cannot coexist, or that the number of species cannot exceed the number of limiting resources (Armstrong and McGehee, 1980). All plants need similar resources (e.g. light, carbon, water, and the same mineral nutrients) for growth (Harper, 1977), which are found in the form of ions and not in the form of packages like the food items of animals. Field experiments also indicate that at most, three or four resources are limiting in any plant community (Tilman, 1982). The importance of niche in structuring plant communities has been difficult to resolve (Silvertown et al., 1999), mainly because of difficulties in studying how plants compete for below-ground resources (Casper and Jackson, 1997).

Annual plants invest most nutrients directly into growth with minimal reserve storage. At the initiation of reproduction, roots and leaves begin to senesce. Mobile nutrients are allocated from vegetative to reproductive tissues. Typically 50–90% of N and P but less than 5% of carbon is allocated from vegetative to reproductive tissues (Chapin and Wardlaw, 1988). Annuals also show relatively modest short-term nutrient accumulation in response to pulses of nutrient supply, because their rapid growth enables pulses of growth to follow pulses of supply (Chapin et al., 1990).

In plant species, the basic demographic parameters, birth and death, are very closely linked with the process of growth (Bruna, 2003). In semi-natural lowland communities in northern Greece most plant growth occurs from mid-March to mid-June (Papanastasis, 1981). Such communities include many annual species. Annuals may partition nutrients preferentially to reproductive structures slowing root elongation and subsequent nutrient uptake (Doodson et al., 1964; Rawson and Hofstra, 1969). Nutrient supply varies spatially as well as temporally (Campell and Grime, 1992). Spatial and temporal differences among such species seem to reduce the intensity of competition (Veresoglou and Fitter, 1984; Mamolos et al., 1995a; Vasilikos, 2001; Jumpponen et al., 2002). Different species may also utilize different nutrient sources, for example, plants with symbiotic nitrogen-fixing bacteria, plants able to utilize organic nitrogen (McKane et al., 2002), and plants with mycorrhizal