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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 $K < P = N < \text{biomass}$. 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*.

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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 (Campbell 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

mutualisms that allow greater access to organically bound phosphorus (Fitter, 1990). The complementary resource use by plants in combination with niche separation along environmental axes (Silvertown, 2004) and the differential use of soil resources (Tilman, 1982) could reduce interspecific competition and thus promote coexistence of plant species.

The relatively short growing period and the shallow soil in grasslands prevent the temporal differentiation of coexisting annual plant species in growth and soil resources acquisition. The shallow soil also does not allow high differentiation of annual plant species in root distribution with soil depth. Thus, competition for soil resources is expected to be especially intense in dry years and therefore shape the structure of plant communities.

The aim of this work was to examine the temporal pattern of growth and nutrient acquisition of two annual coexisting plant species *Trifolium campestre* Schreb. and *Vulpia myuros* (L.) C.C. Gmel. in a dry and a wet year in a lowland grassland of northern Greece with unfertile shallow soil. It was hypothesized that temporal separation in growth and nutrient acquisition will be more evident in the wet year, and the intensity of competition will be greater in the dry year.

2. Materials and methods

2.1. Study site

The study was carried out in 1991, 1992, and 1993 in a moderately acid lowland grassland 70 km north of Thessaloniki Greece (40°56'N, 22°53'E). The soil was classified as Typic Xeralf (Soil Survey Staff, 1975). In the study area during the experimental period there are large variations of mean monthly rainfall and mean monthly high and low temperatures within and between years (Fig. 1). The plant community is quite diverse (Mamolos et al., 1995b).

In a 30 × 20-m fenced area, eight plots (6 × 1.9-m) used as replicates were arranged perpendicular to the site slope (3–5%). Seven harvests in 1991 and six in 1993 were made during the growing season (mid-March to late-June). In 1991, samples were harvested on March 27, April 11 and 24, May 8 and 29, and June 5 and 19; in 1993, harvest dates were April 10 and 24, May 8 and 22, and June 3 and 18. Vegetation harvests were also made in 1992. However, the extremely cold and dry winter that year hindered the growth of the winter germinating annual species. Therefore, data from 1992 harvests were excluded from this work. On each harvest date, two samples (25 × 25-cm) of the above-ground vegetation were randomly selected from each plot, cut, sorted into the component species, dried at 72 °C for 48 h and weighed. The means of these two samples for each plot and species was taken into account in statistical analysis. Soil cores to a depth of 10 cm from the center of each 25 × 25-cm quadrat at the time of each harvest were taken. Of the species identified, only the data (mean relative abundance ± 1 SE; $n = 8$, %) from the most abundant annual species, *T. campestre* Schreb. (24.5 ± 3.3) and *V. myuros* (L.) C.C. Gmel. (4.9 ± 0.6) are presented because the root systems of these species are not storage organs. Also,

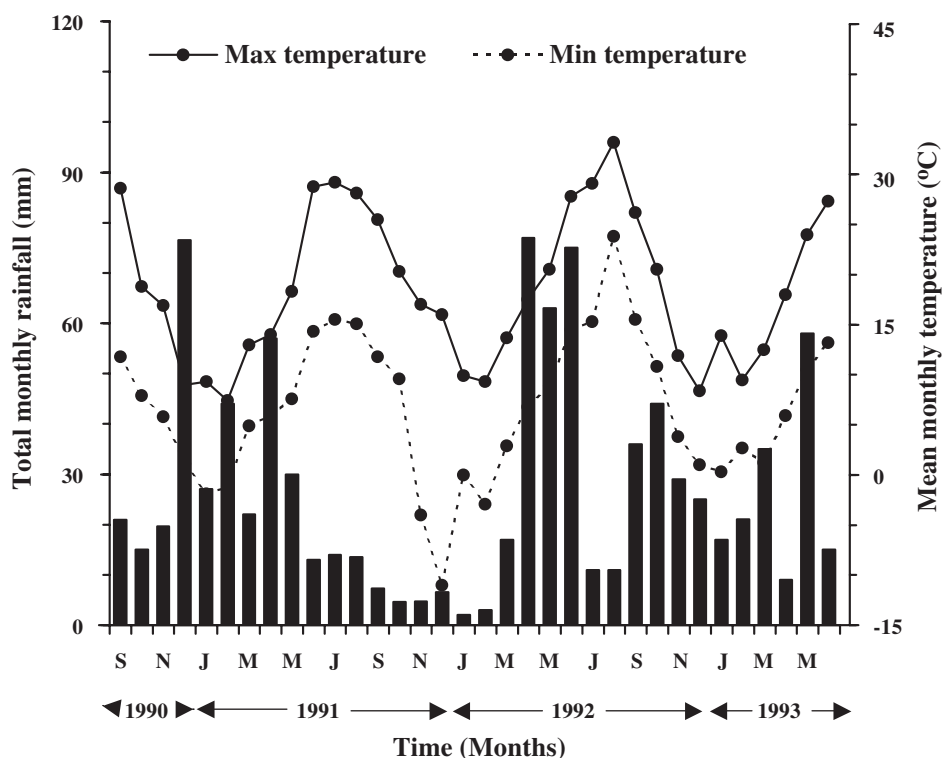


Fig. 1. Total monthly rainfall and mean monthly high and low temperatures from September 1990 to June 1993.

both species increased intermingling; had about the same size (height), density, and germination time, which started at the end of November and then slow growth rates were observed until the end of February because of low temperatures. Perennial herbs in temperate regions on the other hands send most photosynthetic material in the root and below-ground storage organs. Consequently, below-ground biomass in the early stages of growth is greater than above-ground biomass, but progressively the root-to-shoot ratio of biomass is reduced during the period before seed production (Mamolos et al., 1995b). The same trend has been observed for total N, P, and K content. For this reason, data from perennial species were not used.

2.2. Vegetation and soil analysis

All plant materials were dried at 72 °C for 48 h, weighed, ground, and stored in airtight containers at room temperature (20 °C). Nitrogen was determined by the Kjeldahl method. For P and K concentration determination, the ground material was digested with triple acid reagent $\text{HNO}_3 : \text{H}_2\text{SO}_4 : \text{HClO}_4$; 10:1:1 (Allen, 1989). Total P was determined colorimetrically with a Perkin-Elmer 403 at 882-nm using

Murphy and Riley's (1962) reagent, and K by flame photometry (Jenway Pep 7, Dunmow, Essex, UK).

Soil moisture was determined by the soil weight differences before and after drying at 105 °C for 48 h.

2.3. Growth analysis

Data of above-ground biomass and N, P, and K accumulation were ln-transformed to render their variability more homogeneous over time. The order of polynomial fitted to the parameters (above-ground biomass, N, P and K accumulation) are best represented by general formula (Evans, 1972; Hunt and Parsons, 1974; Hunt, 1978, 1982):

$$f(T) = \ln(W) = \sum_{i=0}^n a_i T^i,$$

where W is the biomass or N, P, and K content, n is the order of polynomial ($0 \leq n \leq 3$), a_i is the coefficient, and T the time in days.

The shoot of plants was used to calculate the timing of maximum rates of above-ground biomass growth and of N, P, and K accumulation with the assumption that the annual species use the root systems to transfer nutrients and water especially the month before anthesis.

As Elias and Causton (1976) suggested, regression lines were fitted by using harvest mean values and polynomials of varying degrees. When the F -test was not significant, then the sum of squares corresponding to that degree of fit was pooled with the residual sum of squares and a new residual mean square was calculated (Hunt and Parsons, 1974). The degree of polynomial was calculated with mean values and this order of polynomial was simulated for the data of each plot. The first derivative of $W = \exp f(T)$ gives the absolute growth rates or the rates of N, P, and K accumulation with time. When the second derivative d^2W/dT^2 was 0, the absolute growth rate or the rates of N, P, and K accumulation were maximum at time (T).

2.4. Statistical analysis

Soil moisture data for each year were subjected to two-way ANOVA, using depths and sampling dates as main factors (Steel et al., 1997). Also, data of the timing of maximum rates were subjected to three-way ANOVA, using species, growth parameters (growth rates and rates of nutrient accumulation) and years as main factors (Steel et al., 1997).

3. Results

The surface soil layer (0–5 cm) generally showed the highest values for soil moisture (Fig. 2). Water moisture declined sharply in the first few days of May

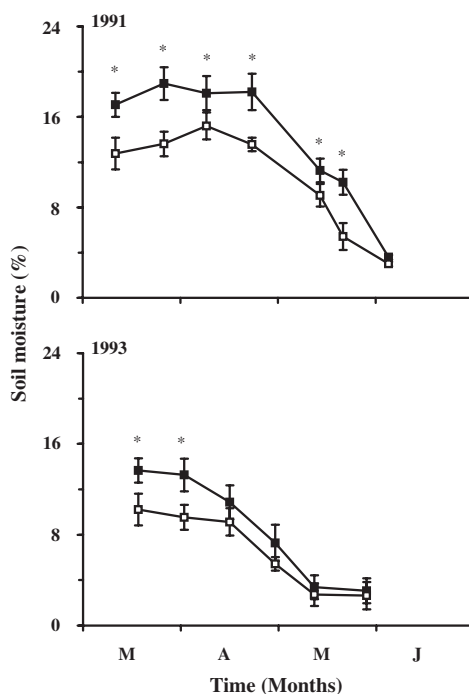


Fig. 2. Seasonal changes of soil moisture at the depths, 0–5 cm (■) and 5–10 cm (□) during the growing season of 1991 and 1993. Bars show the standard errors of the means ($n = 8$). *Show the significant differences for different soil depths on the same date.

because of the low rainfall and high evapotranspiration. Generally, the soil moisture in 1991 was significantly higher than in 1992 and 1993.

All parameters of *Vulpia* and *Trifolium* were found to be significant for cubic polynomial in 1991 and 1993, except for the total K accumulation of *Vulpia* in 1991 (Table 1). Coefficients of the polynomials for all parameters in 1991 and 1993 are shown in Table 1. Changes in the above-ground parameters in time and the absolute growth rates of *Vulpia* and *Trifolium* are shown in Figs. 3 and 4, for 1991 and for 1993, respectively. Analysis of variance (F values) for data of the timing of the maximum rates of species are shown in Table 2.

The mean timing of the maximum rates for the species, averaged over all growth parameters (absolute growth rates and rates of nutrient accumulation) and years, was significantly earlier for *Vulpia* compared to *Trifolium* (Table 2; Fig. 4). Mean maximum rates of growth parameters, averaged over all species and years followed this order: significantly earlier $K < P = N < \text{biomass}$ (Table 2; Fig. 4).

Absolute growth rates, averaged over all species were significantly earlier in 1993 than in 1991 (Fig. 4; Table 2). On the contrary, K accumulation rates, averaged over all species, were earlier in 1991 than in 1993 (Fig. 4; Table 2). Finally, there were no significant inter-annual differences in maximum N and P accumulation rates, averaged over all species (Fig. 4).

Table 1

Coefficients (a_0 , a_1 , a_2 , a_3) of the fitted curve for above-ground biomass, total N, P, and K accumulation of the annual species *Vulpia* and *Trifolium*

	1991					1993				
	a_0	$a_1 \times 10^{-3}$	$a_2 \times 10^{-4}$	$a_3 \times 10^{-5}$	R^2	a_0	$a_1 \times 10^{-3}$	$a_2 \times 10^{-4}$	$a_3 \times 10^{-5}$	R^2
<i>Vulpia myuros</i>										
Biomass	2.64	−1.13	10.45	−0.99	0.99**	2.14	11.81	11.10	−1.80	0.99**
Total N	5.73	−6.57	6.46	−0.69	0.96*	5.08	−3.07	15.72	−2.46	0.99***
Total P	3.49	6.78	4.82	−0.56	0.98*	2.47	32.00	7.81	−2.03	1.00***
Total K	5.13	58.06	−7.04	—	0.84*	5.35	−24.87	20.19	2.87	1.00***
<i>Trifolium campestre</i>										
Biomass	0.64	−7.24	14.70	−1.43	0.98*	1.39	−13.69	11.29	−1.46	0.97*
Total N	3.29	−47.60	30.34	−3.30	0.94*	4.47	−13.74	13.06	−1.56	0.99***
Total P	1.16	−8.56	13.85	−1.36	0.97*	1.52	−5.96	11.32	−1.59	0.98*
Total K	3.00	16.56	12.98	−1.76	0.98*	4.17	−65.50	34.81	−4.20	0.99**

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

4. Discussion

In the semi-arid lowland grassland of the Mediterranean region, the prolonged summer dry period, in combination with high temperatures, favors seeds as perennating parts of plants during the summer. Many cold tolerant but drought intolerant perennial species cannot survive the inter-storm dry summer periods. The cold tolerant annual species start growing without competition during winter and produce relatively high biomass when rainfall in early spring is adequate. Germination and growth of cold tolerant annual species was therefore further favored in the wet year 1991 by the accelerated decomposition of plant material produced in the previous years. On the other hand, the drier conditions of the dry year and the lower N and P availabilities, and the greater undecomposed litter probably inhibited the germination of seeds.

The growth and total N, P, and K content of plants over the study period were sigmoid growth curves, except for 1992 (data not shown). The phenological pattern in the field indicates differentiation in the time of the nutrient accumulation of coexisting annual species. *Vulpia* and *Trifolium* displayed maximum N, P, and K uptake in April and the first few days of May for both years under different soil moisture, nutrient availability, and climatic conditions. It has been reported that nutrient and water supply vary spatially as well as temporally (Gupta and Rorison, 1975; Veresoglou and Fitter, 1984; Campell and Grime, 1992; Mamolos et al., 1995b). In semi-arid grassland, low P concentrations and moisture at the end of spring support low N_2 fixation rates for the *Trifolium* because of the important role of P and soil moisture (Leung and Bottomley, 1994) in the energetics of N_2 fixation. *Trifolium* probably relied on its symbiotic N_2 fixation, thus avoiding competition for available soil N with *Vulpia* (Jumpponen et al., 2002). Although the growing period

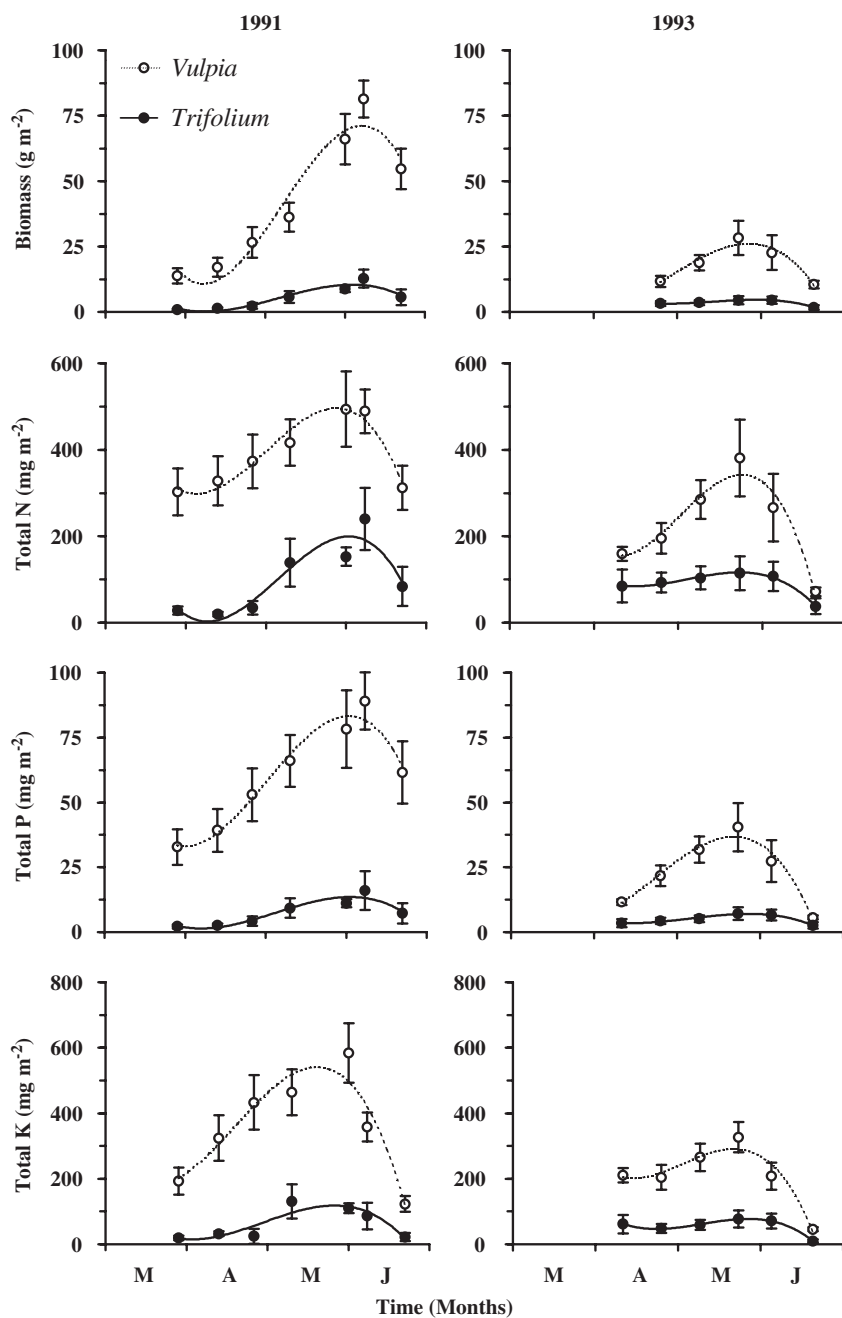


Fig. 3. Fitted curves for the changes of above-ground biomass, total N, P, and K of *Vulpia* and *Trifolium* during the growing season of 1991 and 1993. Bars show the standard errors of the means ($n = 8$).

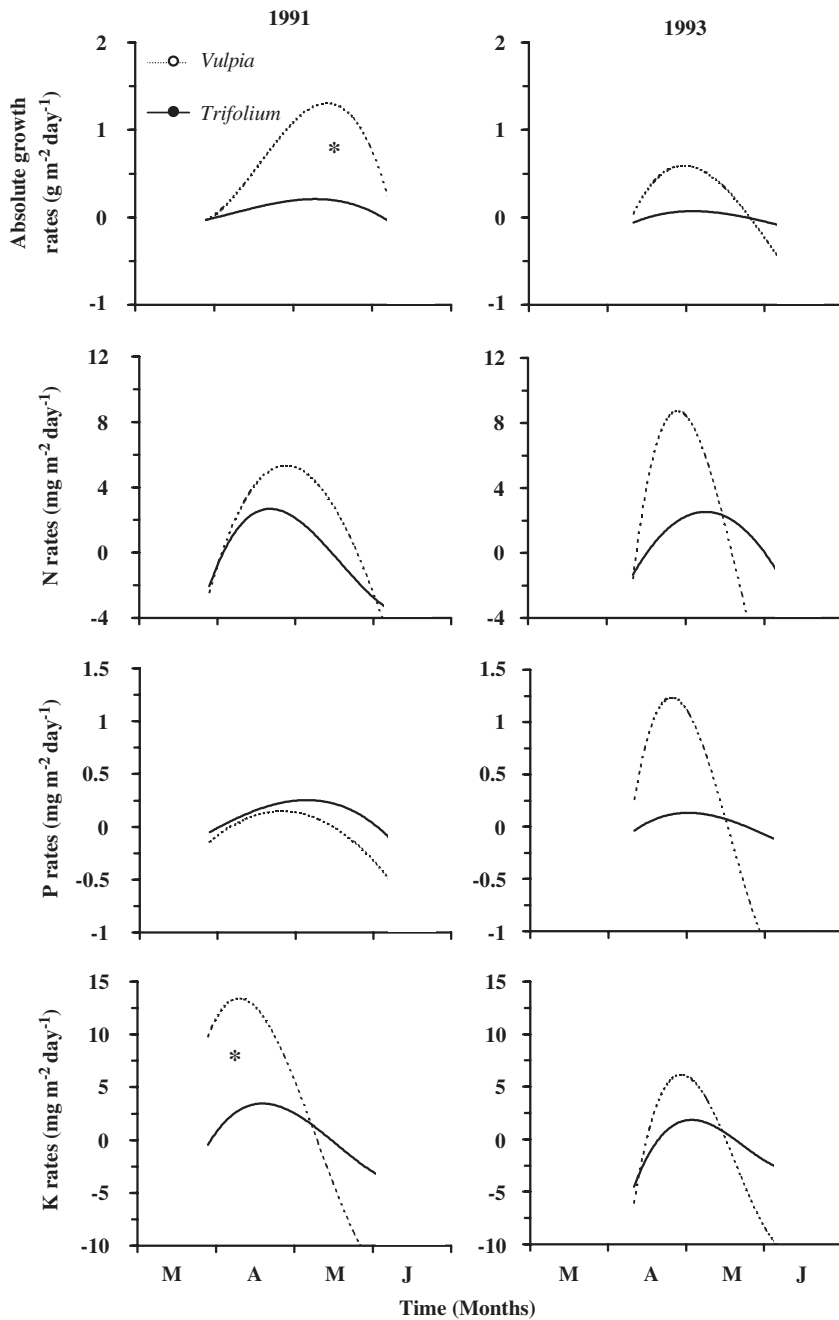


Fig. 4. Fitted curves for the changes of absolute growth rates and the rates of total N, P and K of *Vulpia* and *Trifolium* during the growing season of 1991 and 1993. *Show that there are significant differences between years for the mean timing of the maximum rates, averaged over all species.

Table 2

F values from three-way ANOVA for the timing of the maximum rates in the four characteristics (productivity and rates of N, P, and K accumulation in above-ground biomass) of the two species in the two years. Error d.f. are 105

Source of variation	d.f.	Timing of maximum rates
Blocks	7	1.7
Species	1	4.1*
Maxima	3	7.4***
Species × Maxima	3	1.2
Years	1	29.8***
Species × Years	1	1.3
Maxima × Years	3	4.7**
Species × Maxima × Years	3	1.8

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

in this grassland is short, the coexisting species showed a marked temporal difference in growth and in accumulation of nutrients into above-ground biomass. Even in the dry year, where the growing period is even shorter compared to wet year, the species were distinguished to share temporally the growing period. In the wet year, the greater availability of soil moisture resulted in the expansion of the growing period, tended to delay the exhibition of species' maxima, and allowed the species to share the temporal axis of niche. Exhibition of species' maxima in growth and root activity are determined by the environmental conditions, but they must be also influenced by interspecific competition (Silvertown et al., 1999; Silvertown, 2004).

These differences are not always reflected in similar phenological differences in dry matter production. The seasonal order in growth (*Vulpia*, *Trifolium*) can possibly be explained by differences in response to seasonal variables in soil (soil moisture and nutrient availability) and climate (temperature and irradiation). In early spring, when water availability is relatively high, low temperatures constrain the performance of plant species in the natural habitat. As temperatures become more optimal in late spring, high light and low water availability limit growth and reproduction (Dillon and Forcella, 1984; Leung and Bottomley, 1994). The species phenology is thus the result of a compromise in a season when resource availability is optimal, but when climatic conditions are limiting. The sensitivity of legumes and symbiotic N₂ fixation to drought, for example, have been reported by Serraj et al. (1999). There are several reasons why the absolute growth rates of plants decrease over time, including reduction in resource per unit tissue with increasing size, and allocation increase to structural and reproductive rather than photosynthetic tissues (Weiner, 1990).

Evidence that differences in time of vegetation activity can contribute to the coexistence of species has been reported in several studies (Wells, 1971; Rogers and Westman, 1979; Veresoglou and Fitter, 1984; Fitter, 1986; Vasilikos, 2001). These differences do not arise directly from inherent differences in nutrient uptake; it is rather the response of plants to environmental factors (soil moisture, nutrient

availability, rainfall, temperature, light intensity), which permit them to partition these resources (Hunt and Lloyd, 1987). Plant requirements for nutrients increased with increasing light and temperature during the spring, but decreased at the end of spring as a result of a drought stress in Mediterranean areas. Oscillations in plant production have also been related to long-term impacts of severe weather events (Figueora and Davy, 1991; Tilman and El Haddi, 1992; Steenekamp and Bosch, 1995; Polis et al., 1997). Differentiation in resource use may help to maintain species diversity and minimize competition for resources in some plant communities (Tilman, 1982).

Temporal separation is evident in lowland herbaceous grasslands of northern Greece. A group of species consisting of C_3 annuals and perennials start growing slowly during autumn and winter, if the weather is mild, and then rapidly in the spring and set seed by the end of the spring (Papanastasis, 1981). Late-season species, including C_4 species, start growing in late winter or early spring and start to seed during the summer.

With the techniques used, the timing of the maxima in the rates of growth and nutrient accumulation in above-ground biomass in two contrasting years, with respect to soil water content were estimated. This procedure allowed the quantitative determination of significant differences between species and years in the timing of maximum rates in growth and nutrient accumulation. I postulate that times of nutrient accumulation maxima in above-ground biomass coincide with times of respective maxima in nutrient uptake, suggest that temporal differentiation in maximum root activity does exist between species though species start to grow simultaneously in the spring when temperatures become favorable. This differentiation seems to depend on environmental conditions and must be influenced by interspecific competition.

In conclusion, temporal separation in the growth and the root activity of species, which was induced by the greater soil moisture in the wet year, reduced the intensity of interspecific competition and thus promoted coexistence. In the dry year, the shorter growing period, and thereby the lower temporal separation of species in root activity may have intensified interspecific competition for soil resources.

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