

Annual *versus* perennial growth cycle in *Ruppia maritima* L.: temporal variation in population characteristics in Mediterranean lagoons (Monolimni and Drana Lagoons, Northern Aegean Sea)

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Abstract

A perennial population of *Ruppia maritima* in a permanent lagoon in the Evros Delta grew from April to October and reproduced during summer. Numbers of rhizome and stem internodes increased in spring–summer and in late summer–autumn, revealing two successive periods of both horizontal and vertical expansion; leaf density increased continuously until October (78,210 leaves m⁻²). An annual population in a temporary lagoon grew and reproduced from May to August, and died afterwards leaving seeds as the habitat temporarily dried. Numbers of rhizome internodes sharply increased only in August, while numbers of stem internodes increased in June, indicating that a slow horizontal expansion was followed by a fast and brief vertical expansion; subsequently a second intense horizontal expansion occurred; leaf density peaked in August (58,080 leaves m⁻²). Several characteristics increased after mid-spring, attaining similar maximum values in annual and perennial populations. However, the perennial population had larger leaves and higher root biomass, but lower reproductive organ biomass. Rhizome, stem and leaf biomass increased sharply in August (113.2 g dw m⁻²) in the annual population and progressively up to October (167.8 g dw m⁻²) in the perennial population. Using principal component analysis, growth and reproduction were found to be mainly affected by temperature.

Keywords: abundance; morphological characteristics; permanent lagoon; *Ruppia maritima*; temporary lagoon.

Introduction

Ruppia is a cosmopolitan genus of aquatic angiosperms. Species of *Ruppia* occur in both permanent and temporary water bodies; ephemeral habitats are inhabited by annual *Ruppia* species, while perennial species are restricted to the permanent habitats (Brock 1982, Husband and Hickman 1985). The perennial *Ruppia* species

maintain their vegetative plant structure throughout a quiescent period over winter and then grow during the warm period of the year; most propagation occurs by the lateral spread of rhizomes (Verhoeven 1979, Brock 1982). Annual species synchronize their life cycle stages to the wet and dry phases of their habitats; these species die off as the habitats dry, leaving seeds and some asexual turions, which generally germinate after the dry period (Verhoeven 1979, Brock 1982). *Ruppia maritima* L. has the widest salinity tolerance known for any submerged angiosperm (Kantrud 1991) and occurs world-wide in a variety of permanent and ephemeral habitats, probably because it has both annual and perennial reproductive strategies (Pulich 1985, Flores-Verdugo et al. 1988, Koch and Seeliger 1988, Dunton 1990). Some aspects of the autoecology of American and western European stands have been studied. However, our knowledge of fine scale differences between the annual and perennial *R. maritima* growth cycles, particularly the variations in abundance and morphological characteristics, is restricted.

The Evros Delta (Northern Aegean, Mediterranean Sea) is of notable natural historical interest, and, according to the Ramsar convention, it is protected as a wetland of international value. Within the delta, Monolimni Lagoon is permanently flooded, while unfortunately, Drana Lagoon has been isolated from the sea due to the obstruction of its narrow opening since 1987. From that year on, Drana Lagoon has often experienced episodes of complete dryness during the warm period; the duration of the dry period depends on the highly variable winter and spring rain. The macrophytobenthos of Drana Lagoon and of the innermost part of Monolimni Lagoon is composed mainly of *R. maritima*.

The main goal of this study is to present fine scale differences between the annual and perennial growth cycles of *R. maritima* by: (1) describing the monthly variation in several characteristics of two populations from the Evros Delta, one from the permanently flooded Monolimni Lagoon and the other from its neighboring, temporarily dry Drana Lagoon; (2) comparing several morphometric characteristics and abundance measured as leaf density, number of internodes and biomass, of these populations; (3) identifying the key environmental factors affecting the variation in biomass of various plant parts.

Materials and methods

Study area

The Evros Delta is located in the north-eastern corner of

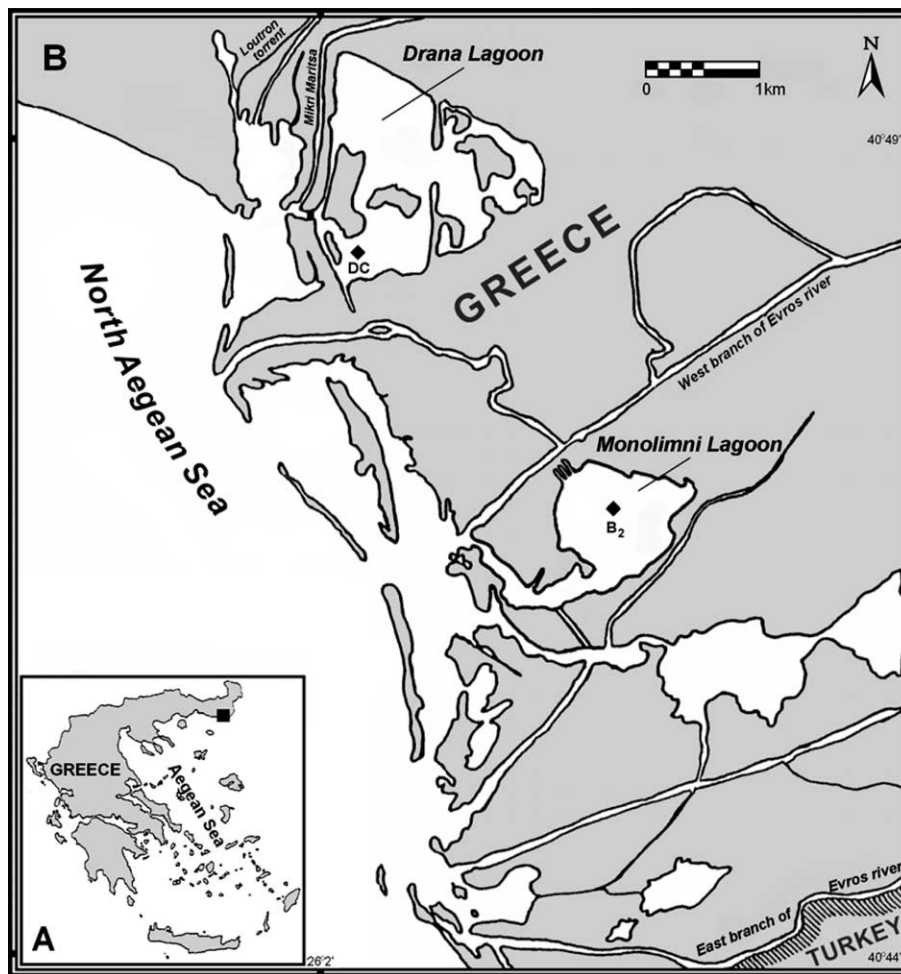


Figure 1 *Ruppia maritima*: (A) geographical location of the study site; (B) map of Evros Delta indicating the sampling stations.

the Aegean Sea (Figure 1). Fresh water reaches the delta area primarily through the eastern branch of the Evros River, and occasionally from the western branch of the same river and the streams Mikri Maritsa and Loutron (late autumn-early summer) (Figure 1). Three islets and some lagoons have formed in the delta area. Monolimni (or Paloukia) Lagoon, occupying an area of about 1.12 km², communicates with the sea mainly through a 15 m wide opening and is permanently flooded (Figure 1). In July 1997, the vegetation composition at the innermost part of that lagoon was rather homogeneous, consisting mainly of *Ruppia maritima*, while at the outer part only macroalgae occurred. Drana Lagoon occupies about 2.2 km² of the delta area. Fresh water occasionally enters Drana Lagoon mainly from drainage channels (Figure 1). In the past, Drana Lagoon connected to the sea through a narrow opening 4 m wide. Possibly, in order for the lagoon to be drained, its opening was obstructed in 1987 and, since then, there has been no direct communication with the sea. Thereafter, Drana Lagoon has dried out during the warm period of the year. In July 1997, vegetation composition in this lagoon was rather homogeneous, consisting mainly of *R. maritima*, less of the angiosperm *Zannichellia palustris* L., and sporadically by charophyte macroalgae.

Drana Lagoon was flooded from March 1998 to August 1998. In September 1998, the major part of the lagoon was temporarily drained for 3 weeks; the lagoon was

flooded again in October 1998. The monthly variation in some water parameters at site B₂ in Monolimni and at site DC in Drana Lagoon (Figure 1) from March 1998 to February 1999, and in May 1999, is given in Table 1 (taken from Kevrekidis 2004). Salinity varied between 0.3 and 5.7 psu in Monolimni Lagoon, and between 0.9 and 8.7 psu in Drana Lagoon during these periods, with lowest values in spring. Water temperature showed a larger fluctuation during the annual cycle in the isolated Drana than in Monolimni Lagoon. Day length (time from sunrise to sunset) in the middle of each month in Alexandroupolis, Evros Prefecture, Greece is also given in Table 1.

Sampling and laboratory techniques

Monthly samples of *Ruppia maritima* were collected from March 1998 to February 1999 at sampling stations B₂ and DC (Figure 1). Three random replicate units were taken at each station with a 20 cm diameter acrylic plastic corer, which penetrated to a depth of 20 cm. Macrophytes were kept in a 5% formalin solution. Sampling was not conducted in September 1998 at station DC, since the lagoon was largely dried out. Additional sampling was carried out in May 1999.

Visually dead plant parts were discarded in the laboratory. The number of rhizome internodes, of stem internodes, of nodes where leaves emerge and of leaves per node were counted in each sampling unit. The total num-

Table 1 *Ruppia maritima*: variables of water at station B₂ in Monolimni Lagoon and at station DC in Drana Lagoon, and day length (time from sunrise to sunset) in Alexandroupolis, Evros Prefecture, Greece at the sampling dates (from Kevrekidis 2004, A. Mogias unpublished data and National Observatory of Athens, respectively).

	Mar '98	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan '99	Feb	May
Station B ₂													
Depth (cm)	30	40	50	45	35	30	40	35	50	30	35	55	
Transparency (cm)	20	20	45	45	35	30	15	35	50	30	35	15	
Temperature (°C)	8.2	17.4	16.7	26.6	28.5	26.5	23.1	17.8	10.2	4.2	8.6	5.0	
Salinity (psu)	0.3	0.3	1.2	1.3	2.8	5.6	5.7	4.6	3.0	1.7	0.7	0.5	
Day length (h)	11.52	13.13	14.31	15.04	14.50	13.56	12.35	11.07	9.55	9.17	9.52	10.40	
Station DC													
Depth (cm)	60	50	50	45	45	20	–*	25	25	55	65	85	30
Transparency (cm)	50	35	35	45	45	20	–	25	5	45	55	60	20
Temperature (°C)	7.7	19.7	18.6	27.1	34.0	26.8	–	15.4	9.2	2.0	8.2	6.1	19.6
Salinity (psu)	0.9	1.1	1.5	2.0	3.5	8.7	–	7.6	3.2	1.9	1.8	1.5	2.3
Day length (h)	11.54	13.15	14.40	15.05	14.48	13.52	–	11.01	9.57	9.15	9.35	10.45	14.21

* Sampling was not conducted at station DC in September 1998, since its broader area was temporarily dried.

ber of leaves was calculated by multiplying the average number of leaves per node by the number of nodes. The length of a number (approximately 20) of rhizome internodes, of stem internodes and of roots, as well as the lengths and widths of about 30 leaves were measured with a vernier caliper to the nearest 0.02 mm. Plant material was subsequently partitioned into rhizomes plus stems, leaves, roots and reproductive organs (flowers and fruits); each plant fraction was dried separately for five days at 70°C and weighed to the nearest 0.1 mg.

Data analyses

A principal component analysis (PCA) was conducted in each station separately using the figures for environmental variables (water depth, transparency, temperature, salinity and day length). The figures throughout the sampling period at station B₂ and from March to August 1998 at station DC (Table 1) were used. In the cases of inter-correlated variables, only one of the highly correlated variables was used. Variables were first normalized, then PCA was performed. Spearman's rank correlation coefficient (ρ) was applied to identify correlations (a) between environmental variables and (b) between the first or second component produced by PCA and the biomass of the various plant parts. The significance of the temporal variation in the biomass of the various plant parts was tested by Kruskal-Wallis one-way analysis of variance. The significance of the differences between the populations of *Ruppia maritima* at stations B₂ and DC for the characteristics examined was tested by the Mann-Whitney U-test. Non parametric statistical tests were performed since the sample size was usually small, leading to statistics based on ranks rather than on raw values (Zar 1984).

Results

Variation in characteristics of *Ruppia maritima* populations

Population at station B₂ Vegetative growth of the population of *Ruppia maritima* in Monolimni Lagoon began in mid spring. The number of rhizome internodes increased from April to June and sharply from July to September–October, attaining a maximum mean value of 60,060 internodes m⁻²; it decreased in July and sharply from October onwards (Figure 2). Vertical stems were first observed in May. The number of stem internodes peaked in July and September (mean value about 20,300 internodes m⁻²); it temporarily decreased in August and sharply after September–October (Figure 2). These variations indicate that (a) only a few rhizomes occurred during winter–early spring, (b) an initial horizontal expansion in spring–early summer was followed by a vertical expansion in early–mid summer, (c) a decay of rhizomes and stems in mid or late summer was followed by a second intense horizontal expansion and a second brief vertical growth period, and (d) a decay of rhizomes and the stems from early or mid autumn onwards was followed by winter quiescence.

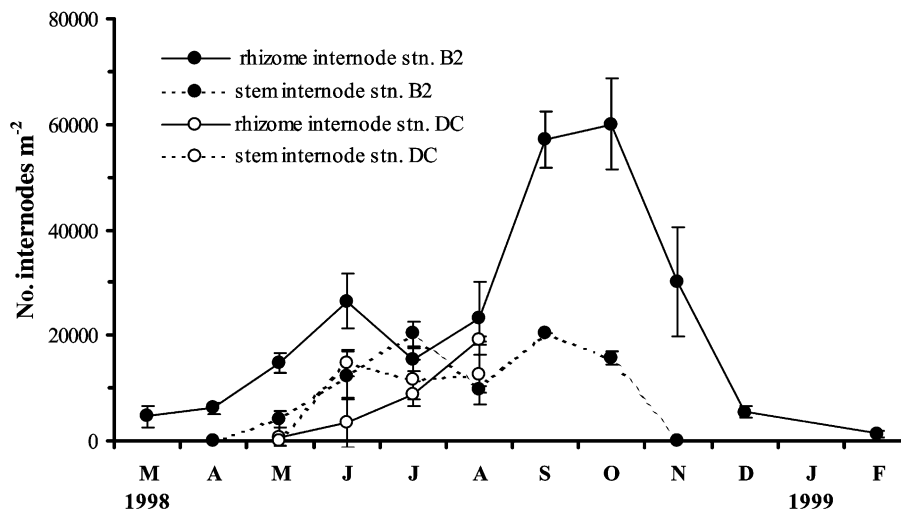


Figure 2 *Ruppia maritima*: monthly variation in number of rhizome internodes and stem internodes at stations B₂ and DC. Dots=mean; bar lines=standard error.

Rhizome internode length increased during the periods of horizontal expansion; its mean value varied between 0.3 and 0.9 cm throughout the year (Figure 3). Stem internode length increased during the initial vertical growth and peaked in August (mean value 3.4 cm); its sharp decline from late summer onwards indicated a continuous decay of long stems (Figure 3). Root length showed a variation similar to that of rhizome internode length; it attained its highest mean value in May (5.8 cm) (Figure 4).

Leaf density continuously increased from April to October (mean value 78,210 leaves m⁻²) (Figure 5), indicating a continuous production of new leaves during the growth season. Leaves were small and narrow during late autumn–winter and relatively long and wide in early summer; both the highest mean leaf length and width (8.0 cm and 1.22 mm, respectively) were observed in June (Figure 6).

Rhizome plus stem biomass and leaf biomass of the population at station B₂ displayed a significant monthly variation (Kruskal-Wallis one-way ANOVA: $H=22.943$ and 23.210 , respectively; $p<0.01$, $DF=9$); biomass of both

plant parts increased progressively most of the time from April to October attaining maximum mean values of 52.9 and 114.9 g dw m⁻², respectively. The increase in biomass of leaves was temporarily interrupted in July (Figure 7), when mean leaf length and width decreased. Root biomass also showed a statistically significant seasonal variation ($H=18.662$, $p<0.05$, $DF=9$) following that of root length; its highest mean values were observed in June (9.4 g dw m⁻²) and October (9.2 g dw m⁻²) (Figure 7). The ratio of the leaf biomass to that of roots, rhizomes and stems displayed an average value of 1.32 throughout the annual cycle; that ratio was higher than 1.0 from April to November with a highest value in September (2.21), while it varied between 0.37 and 0.89 throughout winter and early spring.

Reproductive organs were observed in summer; their biomass varied between 0.4 to 7.7 g dw m⁻² (Figure 7), while their percentage in the total plant biomass varied between 0.3 and 7.0%.

Total plant biomass displayed its highest value (176.9 g dw m⁻²) in October.

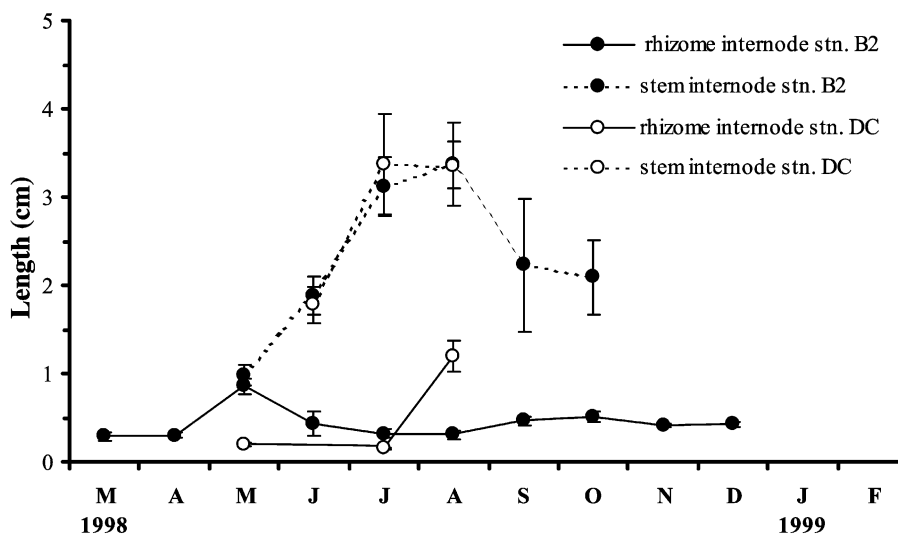


Figure 3 *Ruppia maritima*: monthly variation in length of rhizome internodes and stem internodes at stations B₂ and DC. Dots=mean; bar lines=standard error.

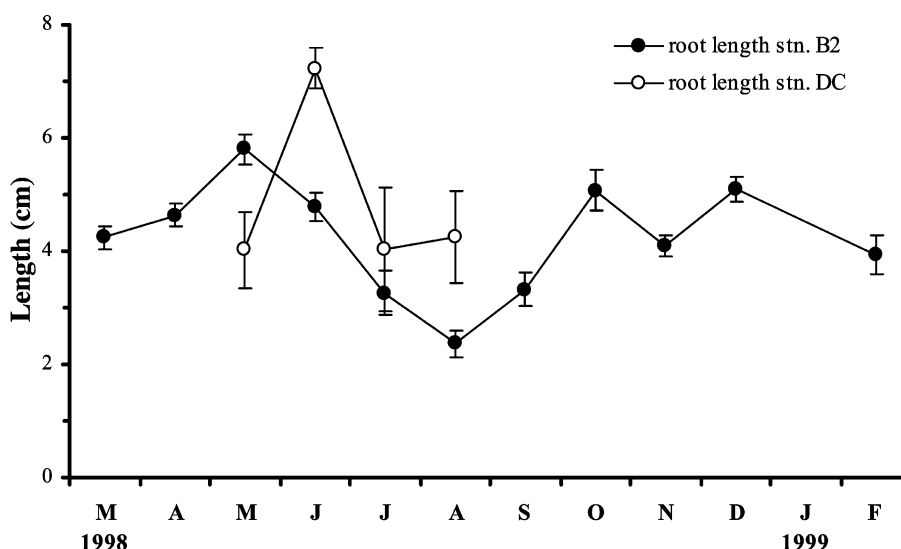


Figure 4 *Ruppia maritima*: monthly variation in length of roots at stations B₂ and DC. Dots=mean; bar lines=standard error.

Population at station DC In Drana Lagoon *Ruppia maritima* was observed continuously from March 1998 to the partial reclaiming of the lagoon in early autumn 1998. Seedlings were observed in March and April.

Rhizome growth was initiated in mid May. The number of rhizome internodes slowly increased in early summer and rapidly in late summer attaining a mean value of 19,270 internodes m⁻² (Figure 2). A few stems were found in May. The number of stem internodes sharply increased in June (mean value 14,830 internodes m⁻²), showing a small decline afterwards (Figure 2). The variation in both rhizome and stem internode numbers indicates that: (a) an initial slow horizontal expansion was followed by a fast and brief vertical expansion in early summer, (b) a decay of some vertical stems in mid summer was followed by an intense horizontal branching especially in late summer. The highest mean values of both internode numbers in the population at station DC were only slightly lower than the highest at station B₂ through August.

Rhizome internode length increased only during the period of the fast horizontal branching in late summer (mean value 1.2 cm) (Figure 3). Stem internode length

sharply increased in July attaining a mean value of 3.4 cm (Figure 3). Root length increased during the period of the initial horizontal expansion (mean value 7.2 cm) (Figure 4). The highest mean values of the above characteristics did not differ significantly from those of the population at Monolimni Lagoon (Mann-Whitney U-test, $p > 0.05$).

Leaf density increased from May to August reaching a mean value of 58,080 leaves m⁻² (Figure 5); it temporarily decreased in July reflecting the possible decay of stems. Its highest mean value was only slightly lower than the highest in the population at station B₂ through August. Leaf length increased in early summer (mean value 6.1 cm), while leaf width increased in mid and late summer (mean value 1.04 mm) (Figure 6). The highest values of mean leaf length and width of the population at station DC were significantly lower than those of the population at station B₂ (Mann-Whitney U-test, $p < 0.001$ and $p < 0.05$, respectively).

The standing crop of rhizomes plus stems and of leaves of *R. maritima* in Drana Lagoon showed a significant monthly variation from March to August (Kruskal-

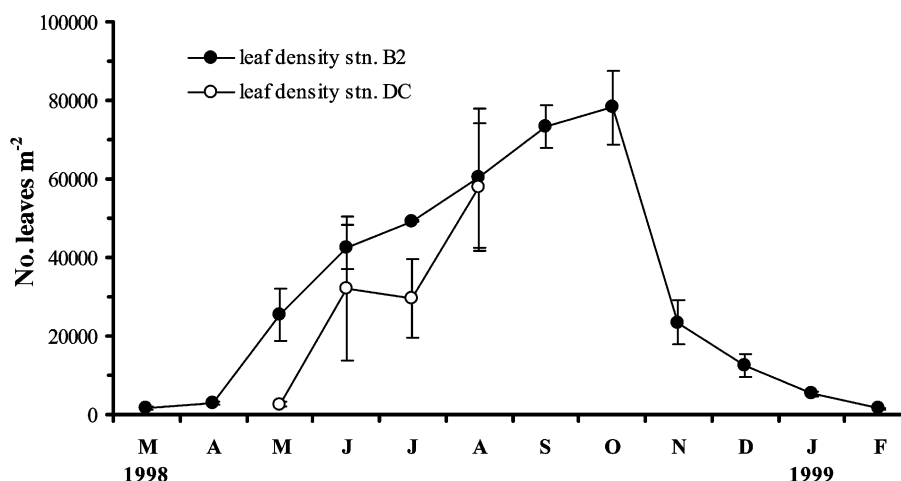


Figure 5 *Ruppia maritima*: monthly variation in leaf density at stations B₂ and DC. Dots=mean; bar lines=standard error.

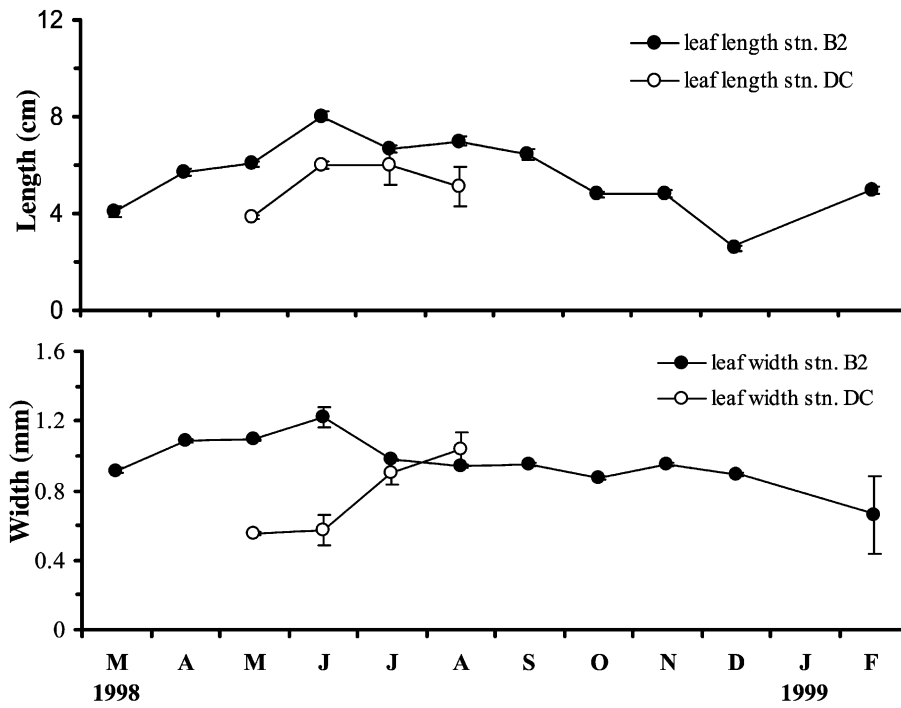


Figure 6 *Ruppia maritima*: monthly variation in leaf length and width at stations B₂ and DC. Dots=mean; bar lines=standard error.

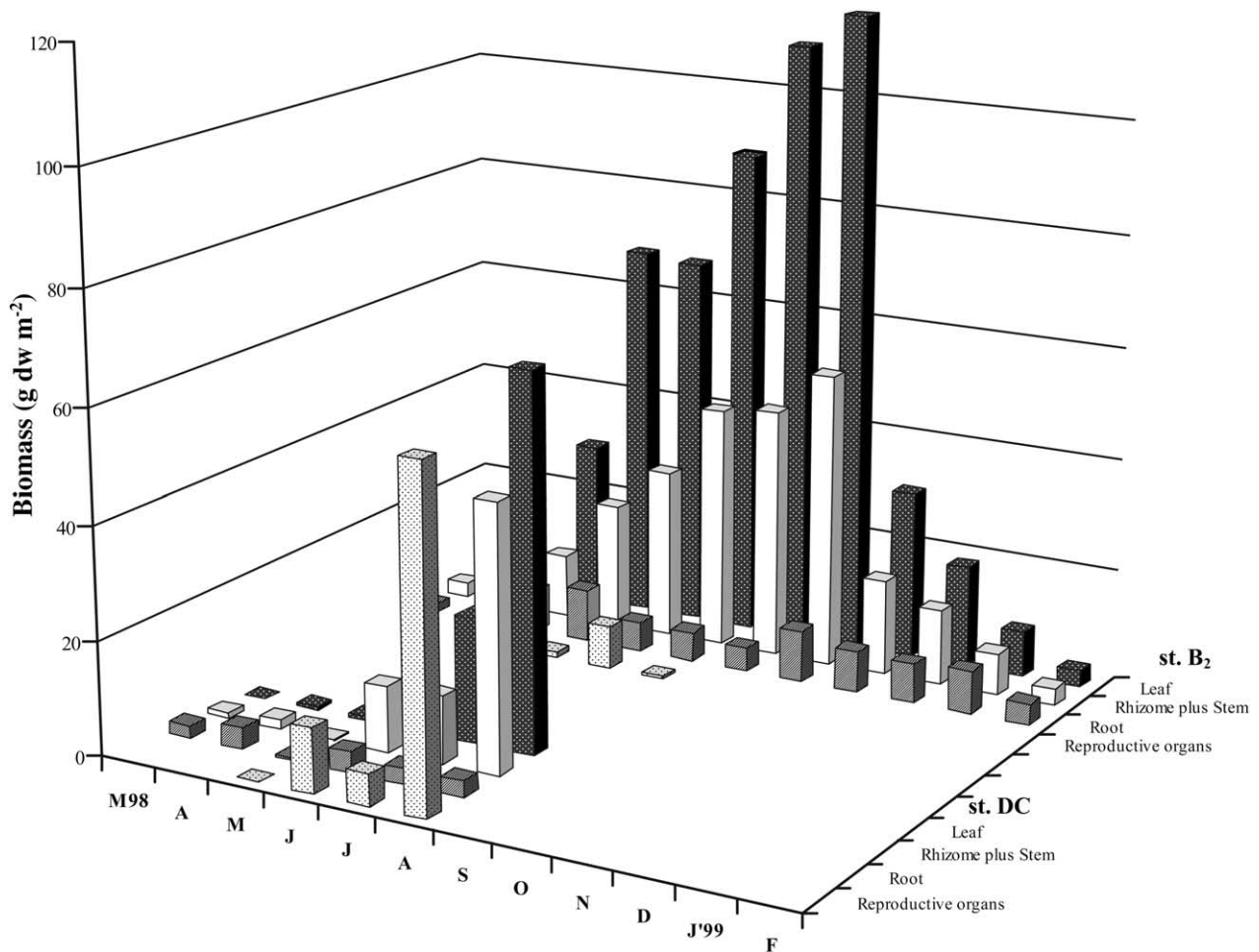


Figure 7 *Ruppia maritima*: monthly variation in mean biomass of leaves, rhizomes plus stems, roots and reproductive organs at stations B₂ and DC.

Table 2 *Ruppia maritima*: component weights in principal component analysis.

Variables	Station B ₂		Station DC	
	Component		Component	
	1	2 (68.8%)	1	2 (90.0%)
Depth	0.111	-0.696		
Transparency	-0.169	-0.536	-0.458	0.543
Temperature	-0.677	-0.014	0.561	0.389
Salinity	-0.416	0.405	0.531	-0.440
Day length	-0.573	-0.253	0.440	0.600

Wallis one-way ANOVA: $H=15.362$, $p<0.01$ and $H=15.074$, $p<0.05$, respectively; $DF=5$). Biomass of these plant parts increased in June; this increase was interrupted temporarily in July reflecting the possible decay of some stems and the decline in leaf density. It later increased sharply until August (mean values 46.9 and 66.3 g dw m⁻², respectively) (Figure 7). The highest mean values of rhizomes plus stem and of leaf biomass in the population at station DC were similar to the highest in the population at station B₂ through August (Mann-Whitney's U-test).

Root biomass of the population at station DC did not vary significantly from March to August (0.4–3.8 g dw m⁻²) (Kruskal-Wallis one-way ANOVA, $p>0.05$) (Figure 7); the highest mean value was significantly lower than that of the population at station B₂ (Mann-Whitney U-test, $p<0.05$). The ratio of leaf biomass to that of roots, rhizomes and stems varied between 1.3 to 1.5 from May to August, while it was lower than 1.0 in March and April (0.03 and 0.11, respectively).

Reproductive organs were first observed in May and then continuously until August; their biomass increased in June, temporarily decreased in July and sharply peaked in August attaining a mean value of 59.5 g dw m⁻² (Figure 7). The percentage of the biomass of the reproductive organs in the total plant biomass of the population at station DC, which varied between 13.2 and 33.9% throughout September, was significantly higher than the respective percentage in the population at station B₂ (Mann-Whitney U-test, $p<0.05$). Total plant biomass attained its highest value (175.5 g dw m⁻²) in August.

Station DC dried out temporarily in September 1998 and *R. maritima* died off. The lagoon was flooded again in October. Some germinating seeds were found in October, December 1998 and February 1999. However, a successful germination and establishment of *R. maritima* was observed only during spring 1999. In May 1999, leaf density showed a mean value of 335 leaves m⁻², dry weight biomass of leaves a mean value of 0.0140 g m⁻², that of rhizomes 0.0020 g m⁻² and of roots 0.0016 g m⁻².

Associated environmental variables

The PCA detected two components, which jointly accounted for 68.8% of the variability in the original data for Monolimni Lagoon and for 90.0% for Drana Lagoon. According to the eigenvectors, water temperature was the most important variable in the first component and

depth and salinity in the second component for Monolimni Lagoon, while water temperature and water transparency were the most important variables in the first component and day length and salinity in the second component for Drana Lagoon (Table 2).

Rhizome plus stem biomass, leaf and reproductive organs biomass of *Ruppia maritima* at station B₂ displayed a significant negative correlation only with the first component of the PCA ($\rho=-0.636$, $p<0.05$; $\rho=-0.685$, $p<0.05$; $\rho=-0.734$, $p<0.01$, respectively; $n=12$) thus indicating that the onset and development of vegetative growth and of reproduction were potentially affected by water temperature. Root biomass did not show a significant correlation with the components. Late spring to mid autumn months were distributed in the left half of the two dimensional PCA plot, April was located in the middle, while the late autumn to early spring months were located in the right half of the plot (Figure 8). In particular, the summer months were placed towards the left end of the plot. Vegetative growth of *R. maritima* at station B₂ occurred throughout the April to October period, and reproduction occurred in summer. Water temperature was lower than 10°C throughout the rest of the year (Table 1).

Biomass of rhizomes plus stems, of leaves and of reproductive organs at station DC showed a significant positive correlation with only the first component of the PCA ($\rho=0.829$, $p<0.05$; $\rho=0.943$, $p<0.01$; $\rho=0.928$, $p<0.01$, respectively; $n=6$) thus indicating that water temperature and transparency had the most important effects on vegetative growth and reproduction in the population at station DC. Root biomass did not show a significant correlation with the PCA components. The PCA defined a close relationship between April and May, as well as June and July, while March was placed towards the left end of the first axis and August to the right end (Figure 8).

Discussion

The population of *Ruppia maritima* in the permanently flooded Monolimni Lagoon displayed a perennial life cycle; it maintained its vegetative structure throughout the period of quiescence. However, the population of *R. maritima* in Drana Lagoon demonstrated an annual life cycle; it dried out with the habitat. During the dry phase, seeds were the only live parts present and they played an important role regenerating the population. Seed germination was observed right after the brief dry period, in

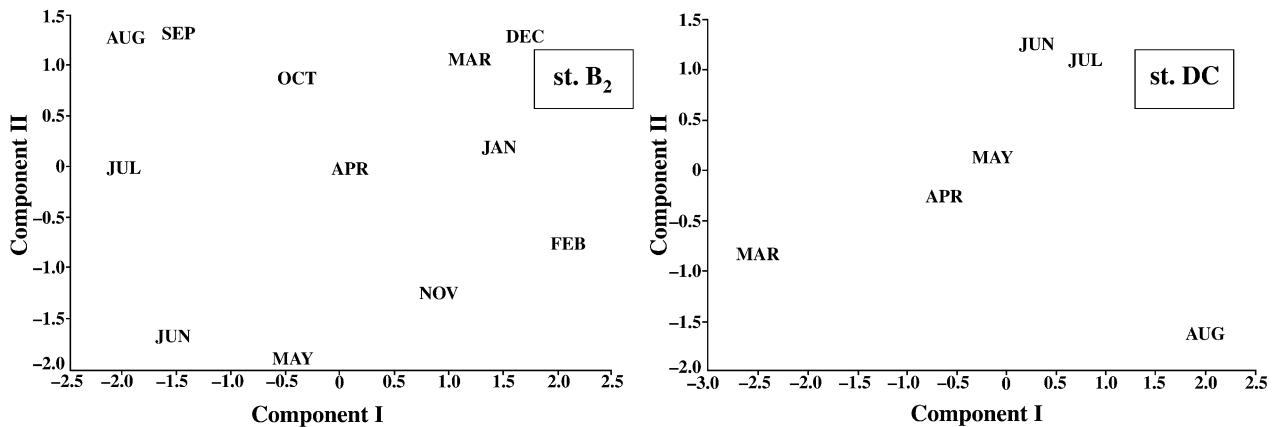


Figure 8 *Ruppia maritima*: principal component analysis conducted at stations B₂ and DC using the figures for environmental variables.

October 1998, but also in December 1998 and February 1999; however, successful germination and establishment were observed only during spring with increasing temperatures and low salinities. The synergistic effect of these environmental variables on seed germination of *Ruppia* has been noted by Verhoeven (1979) and Koch and Seeliger (1988).

Vegetative growth and reproduction of *R. maritima* in Monolimni Lagoon were found to be affected mainly by water temperature. Growth occurred when water temperature was higher than 16.5°C. Similarly, Verhoeven (1979) has reported that the vegetative growth in western European populations of *R. maritima* and *R. cirrhosa* (Petagna) Grande is related to temperature: growth occurs when minimum water temperatures are above 10°C and maxima above 15°C.

The perennial population of *R. maritima* in Monolimni lagoon showed two successive periods of both horizontal and vertical expansion. The relatively high water temperatures during late summer and autumn probably allowed *R. maritima* to display a second branching after the summer decay of plant material and, thereby, a prolonged growth season. A similar development pattern has been described for perennial *R. maritima* populations in western Mediterranean permanent brackish habitats, while in northern European populations the summer decay was followed by quiescence (Verhoeven 1979). Decomposition of material in perennial *Ruppia* forms occurred from mid summer onwards (Husband and Hickman 1985, Menéndez 2002). According to Verhoeven (1979) the decay of *Ruppia* vegetation is mainly caused by a complex of factors, such as the tendency of the vertical stems to decompose at their bases, severe water turbulence, salinity increase, etc.

Reproduction of *R. maritima* in Monolimni Lagoon occurred when water temperatures were higher than 25°C. Temperature plays a major role in the induction of flowering in *R.* species, although photoperiod and irradiance also influence the production of flowers and seeds (see Verhoeven 1979, Santamaría and Hootsmans 1998). Resource allocation of the perennial *R. maritima* in Monolimni Lagoon into reproductive structures was low, confirming previous findings on perennial *Ruppia* populations (Brock 1983).

Vegetative growth and reproduction of the annual population of *R. maritima* in Drana Lagoon were found to be mainly affected by water temperature and transparency. An increased turbidity during spring was possibly responsible for the delay in the induction of growth; growth had hardly begun in mid May, that is one month later than that of the perennial population, in spite of the higher water temperatures during mid and late spring in Drana Lagoon in comparison with those in Monolimni; attenuation of light has been observed to limit growth, flowering and fruiting in *Ruppia* populations (Verhoeven 1979, Schutten et al. 1994).

The data from the annual population in Drana Lagoon indicated that an initial slow horizontal branching was followed immediately by a brief but fast vertical expansion, a rapid leaf production and the appearance of reproductive parts, which afterwards constituted a high part of the total plant biomass; a decay of some vertical stems in mid summer was followed by a second but intense horizontal branching especially in late summer. Thereby, the annual population displayed a development pattern characterized mainly by early and abrupt vertical expansion, early maturity and a high resource allocation into reproduction, differing from that shown by the perennial population in Monolimni Lagoon. These traits, which typify annual *Ruppia* forms (Brock 1982, 1983), enable the annual population to recolonize the fluctuating ephemeral habitat each year. In addition, it attained relatively high numbers of internodes and leaf density, indicating that *R. maritima* is capable of completing its growth cycle in few months in temporary environments (see also Harrison 1982, Flores-Verdugo et al. 1988, Dunton 1990), and it can also establish dense populations.

The populations of *R. maritima* in the Evros Delta lagoons displayed similar maximum mean values in most of the morphometric characteristics examined (rhizome and stem internode length, root length), and also a similar variation until August in some of these (stem internode and root length). The range of the mean values of the rhizome internode length of the population in Monolimni Lagoon throughout the annual cycle (0.3–0.9 cm) was expected, since internodes shorter than 0.3 cm in winter and longer than 1 cm during the growth season have been observed in western European perennial *Ruppia*

populations (Verhoeven 1979, Kiørboe 1980). The maximum mean root length of *R. maritima* in Monolimni Lagoon (about 6 cm) was similar to that of the perennial *R. cirrhosa* in a western Mediterranean coastal lagoon (Menéndez 2002), but lower than that of the annual population in Drana Lagoon (7.2 cm).

Leaf density of both *R. maritima* populations in the Evros Delta lagoons increased almost continuously during the growth season, suggesting an intense production of new leaves throughout that period, since a considerable loss of leaves takes place during the growth season in *Ruppia* species (Kiørboe 1980). Leaf length increased during the beginning of the growth period in both *R. maritima* populations, but the continuous loss of long leaves possibly contributed to the decrease in the mean leaf length after early or mid summer. The perennial population in Monolimni Lagoon displayed maximum mean leaf length and width higher than those of the annual population in Drana Lagoon, but the maximum mean leaf lengths of both Evros Delta populations (about 8 cm in Monolimni Lagoon and about 6.5 cm in Drana Lagoon) were much shorter than the mean lengths of the longest leaves (13–16 cm) of northern American intertidal populations of *R. maritima* (Bigley and Harrison 1986).

Biomass of most parts of *R. maritima* in Monolimni Lagoon increased almost progressively from April to October. A similar variation pattern was displayed by the above-ground biomass of the perennial *R. cirrhosa* in a western Mediterranean coastal lagoon (Menéndez 2002), while, in general, *R. maritima* attains its highest biomass during summer (Milchakova 1989, 1999, Dawes et al. 1995). The maximum total biomass of *R. maritima* in Monolimni Lagoon (177 g dw m⁻²) is in the range reported for perennial populations of the species (about 60–235 g dw m⁻²) and for the perennial *R. cirrhosa* (about 5–895 g dw m⁻²) in northern and southern western European brackish habitats (see Grøntved 1958, Muus 1967, Jerling and Lindhe 1977, Verhoeven 1980, Calado and Duarte 2000, Menéndez 2002). Moderate water temperatures occurred in Monolimni Lagoon over a long period of the year, and, also, the favorable summer water temperatures may have contributed to the moderate biomass values attained by *R. maritima* (see Verhoeven 1979, Santamaría and Hootsmans 1998). In addition, low salinities (<6 psu) and the long day length (>11 h) during the growth season could have been favorable for *R. maritima* growth in Monolimni Lagoon (see Verhoeven 1979, Koch and Dawes 1991, Bird et al. 1993). Our finding that root biomass in Monolimni Lagoon displayed a higher maximal value than that in Drana is in accordance with the observations of Brock (1982) that root biomass constituted a higher part of the total plant dry weight in a perennial *Ruppia* species than in annual populations.

High summer temperatures (>30°C) most probably contributed to the limited vegetation decay, and negatively affected growth rates and reproduction in Drana Lagoon (see Verhoeven 1979, Santamaría and Hootsmans 1998). Such extreme temperatures may explain the absence of biomass increase in Drana Lagoon in mid summer. Biomass of most plant parts of the annual population in Drana Lagoon sharply increased in late summer with maximum values similar to those of the perennial

population in Monolimni Lagoon through August. The increasing biomass of most plant parts in Drana Lagoon during late summer was interrupted by the drying of the lagoon. However, the late drying out of the habitat enabled the annual population to attain a relatively high maximum total biomass (175.5 g dw m⁻²), to which the contribution of reproductive organs was high (34%), similar to that attained by the perennial population in Monolimni Lagoon (177 g dw m⁻²) throughout its growing season. The maximum total biomass values reported for annual *R. maritima* populations in western Mediterranean temporary brackish habitats vary between 25 and 290 g afdw m⁻² depending on the time of drying out of the habitat (Verhoeven 1980).

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