

POPULATION DYNAMICS OF THE SPECIES *PLANTAGO MAJOR* L. AND *POA ANNUA* L. IN A REPLACEMENT SERIES EXPERIMENT

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Abstract — Population dynamics of the species *Plantago major* L. and *Poa annua* L., typical representatives of ruderal vegetation, was analyzed in a replacement series experiment. The analyzed species were sown in an area with meadow vegetation, where the vegetation present had been previously removed by a total herbicide and additionally by hoeing. The objective of the experiment was to monitor growth dynamics and the effect of intra- and inter-specific interaction of the species *Plantago major* and *Poa annua* in conditions of different sowing densities and proportions. The effects of intra- and inter-specific interference and the density-dependent responses were assessed on the basis of several parameters (natality, mortality, age structure, and measures of ontogenetic changes). Based on the study results, it can be concluded that the responses of the species in the experiment were different, which is explained by different adaptive mechanisms, i.e., strategies, in the specific environmental conditions. An effect of the density dependent response was present in both species in the replacement series experiment. The response was amplified by water deficit caused by intensive evaporation of the bare soil. No effect of inter-specific interference was observed at the given densities of the study species on the sample plots. An effect of intra-specific interference of the species *Plantago major* and *Poa annua* was observed in the guise of a density-negative response of the rate of ontogenetic changes and fecundity.

Key words: Density-dependent response, *Plantago major*, *Poa annua*, replacement series experiment, ruderal vegetation

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INTRODUCTION

The species *Plantago major* and *Poa annua* are typical colonizers of unoccupied spaces created by destruction within ruderal habitats. As these highly reproductive species do not have special seed dispersion mechanisms, seed invasion of the unoccupied spaces is never massive, nor therefore is the initial density of their populations. Still, even in such conditions, there is interaction within and between the species, which can be reflected on growth and development of the populations.

Many demographic studies are based on the idea that plant behavior in populations is decided by age (Leverich and Levin, 1979; Law, 1981), but some authors (Weiner and Caswell, 1977; Hara, 1984; Kirkpatrick, 1984) claim that plant size is

much more significant. The explicit emphasis of any of the above conceptions does not contribute to a better understanding of the effects of size and age. The effect of a given parameter depends on inherent traits of the species in the concrete environmental conditions.

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According to Rabotnov (1950), the plant life cycle can be divided into the following growth categories or age states: latent period (seed), virginile period (juvenile, immature and adult virginile), generative period, and postgenerative period (subsenile and senescent). Harper and White (1974) define the plant life cycle in a similar way.

In practice, in most plants it is very difficult to

determine all the above life-cycle stages, especially if specificities of the plant species are considered. Classification of individuals into age states makes it possible to classify populations themselves. Based on the presence or absence of individual age states, Rabotnov (1950) distinguishes three types of populations: invasive, normal, and regressive populations.

The aim of the experiment was to investigate the mechanisms of invasion of unoccupied spaces, as well as the intra- and inter-specific relations established in conditions of permanent disturbance of the spaces by permanent removal of all other species.

MATERIALS AND METHODS

Experimental plots were established at a meadow site on the grounds of the Siniša Stanković Institute for Biological Research in Belgrade. The meadow did not contain the species *Plantago major* L. and *Poa annua* L., consisting instead of a high percentage of the grass species *Sorghum halepense* (L.) Pers., *Arrhenatherum elatius* (L.) P. Beauv., *Apera spica-venti* L., and *Echinochloa crus-galli* L.

A plot measuring 12 x 8 m was treated with a rapidly degradable total herbicide (glyphosate) with the aim of removing the vegetation present. Seven days after the treatment, additional removal of underground vegetative structures was carried out by hoeing to a depth of 20 cm. After that, the species *Plantago major* L. and *Poa annua* L. were sown. Their seeds had been collected from a number of ruderal habitats on the territory of Belgrade.

The experiment was performed by the principle of replacement series (de Wit, 1960) in a substitutive type of experiment in which total densities of the species are kept constant, and their proportions vary. During the experiment, other species were mechanically removed. The open vegetation canopy caused intensive evaporation on the plot, so in keeping with C-S-R theory, the population dynamics of the study species in this habitat was monitored in stress conditions (water deficit), i.e., in conditions of stress and competition.

In contrast to numerous experiments with high

sowing densities, this research was focused on interactions in conditions of low initial densities.

Total seed densities of the species *Plantago major* and *Poa annua* were $\Sigma I+J=600$ with the following sowing proportions:

$I:J=[(100\%:0\%); (80\%:20\%); (50\%:50\%); (20\%:80\%); (0\%:100\%)]$

The experimental plot was divided into gridded squares measuring 50 x 50 cm. Each sown square was surrounded by eight unsown squares of the same size.

Samples of the complete plant material were taken from squares (20 x 20 cm) twice a year (in August and October). The samples were at least 10 cm distant from the edges, in order to eliminate fringe effects (Hawthorn and Cavers, 1982; Tilman and Wedin, 1991). The results obtained from sample plots measuring 20 x 20 cm were calculated and presented by values for the squares of 50 x 50 cm.

The number of repetitions (minimum two, maximum 10) varied depending on the need and quantity of the available material, as well as on the time of sampling and the ontogenetic stage of the species in the experiment. Goldberg and Scheiner (1993) recommend a minimum of two repetitions, claiming that it is better to take a greater number of density series with few or no repetitions than a small number of density series with many repetitions. There are experiments with only one sampling per treatment (Wedin and Tilman, 1993).

The life cycle of the study species is divided into age states. To calculate the age state spectrum index of the species on the plot (Uranov, 1975), each age state was assigned a numerical value.

$$\text{Age spectrum index} = \Sigma k_i m_i / \Sigma k_i$$

where:

k_i is the number of individuals in the i^{th} age state, or life state; and

m_i is the value of the i^{th} age state or life state.

The classification of growth categories used in

this study is a modification of the age state spectrum of perennial plants employed by Russian botanists (Uranov, 1975; Vorontzova and Zaugolnova, 1985). A similar principle was applied in study of the age state spectrum of annual plants in psammophyte vegetation (Mijović, 1993).

The numerical categorization of growth categories-age states of the species *Plantago major* was as follows: seedling-juvenile (Sd-Juv) **0.5**; immature-vegetative stage (Im-V) **1.0**; reproductive adult (RA) **2.0**; and subsenile and senile stage (subS-Ss) **3.0**.

Due to its short life cycle, the ontogenetic development of the species *Poa annua* was presented in a different way: pre-reproductive individual (PRI) **1.0**; reproductive adult (RA) **2.0**; and subsenile and senile stage (subS-Ss) **3.0**.

The measure of ontogenetic change (Vorontzova and Zaugolnova, 1985) defines the rate of ontogenetic change of the species in the period between two observations, based on the defined age states or age groups: $M.O.C. = q \cdot 100 / N_1$, where q is the number of individuals in the area which changed the age s during the period between two observations and N_1 is the number of plants in the first of the two observations.

RESULTS AND DISCUSSION

Summer census

The study species had a relatively low germination percentage in the first year of the experiment (Table 1). There are data indicating much higher germination percentages of these species. Wells (1974) found that *P. annua* seeds in natural conditions reached a germination of 75-84% in a period of three months. At similar sowing density, *P. major* reached a germination percentage of about 93% (Palmlblad, 1968). Also, in a glasshouse experiment at sowing density of 500 seeds/0.25m², *P. major* reached a germination percentage of 98% 11 days after sowing (Hawthorn and Cavers, 1982). Still, there are also different results. Harper et al. (1965) reported that, at sowing density of 416 seeds/0.25 m², the germination percentage was only 28%.

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Table 1. Ratio of number of individuals of the study species in August and number of seeds in experiment.

Sowing densities <i>Plantago-Poa</i>	% realization <i>Plantago</i>	% realization <i>Poa</i>
600:0	11.1	
480:120	22.1	26.1
300:300	15.1	28.5
120:480	13.9	22.5
0:600		31.4

Plantago major

The highest number of *Plantago major* individuals in the summer census (Fig. 1) was found on

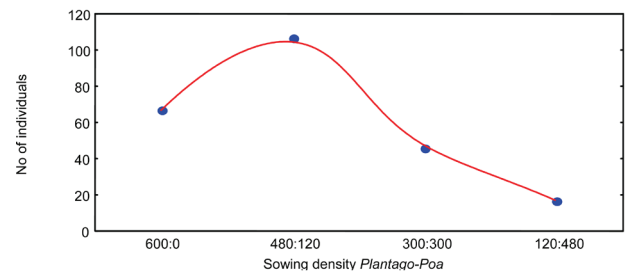


Fig. 1. Average number of *P. major* individuals on sample plots.

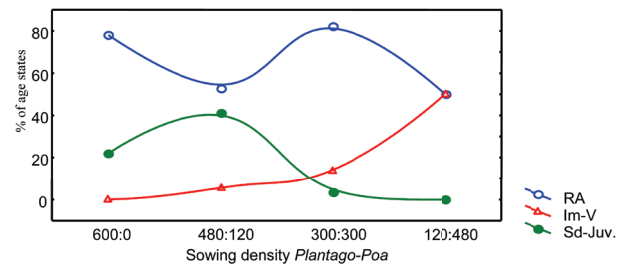


Fig. 2. Percentage of *P. major* age states.

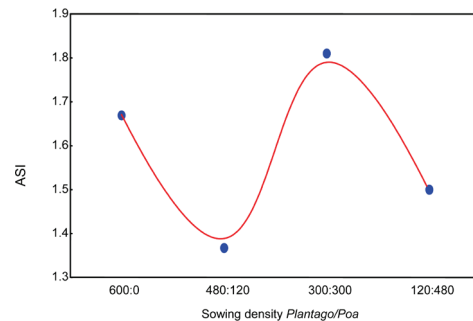


Fig. 3. *Plantago major* age spectrum index.

plot P480:120. There was a rather clear dependence of the relative percentage of age states on the density of *Plantago* individuals (Fig. 2). On plots with lower densities (P300:300 and P120:480), there was a decrease in the percentage of individuals in the youngest age state (seedling-juvenile) and an increase in the number of individuals in the immature-virginile age state (Im-V). The plot with the highest density of *P. major* individuals (P480:120) had the highest percentage of individuals of the youngest age states, i.e., a clear stagnation in ontogenetic development. An experiment with this species in controlled glasshouse conditions (Hawthorn and Cavers, 1982) showed that increase in density caused retardation of the ontogenetic process. However, the conditions and range of densities in this experiment were substantially different. The results of our experiment indicate that at lower densities, the combined effect of stress (water deficit) and competition caused retardation of the ontogenetic process.

The age spectrum index (Fig. 3) had similar values on the plots with highest and lowest densities

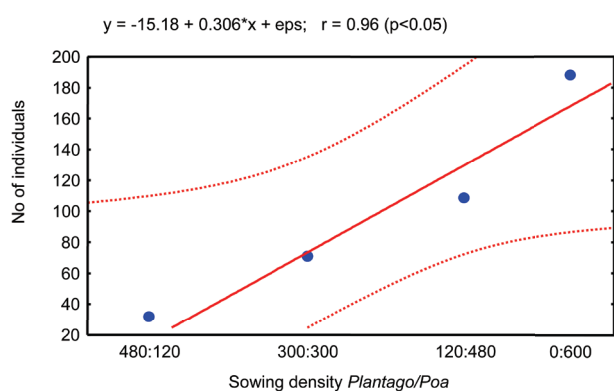


Fig. 4. Average number of *P. annua* individuals on sample plots.

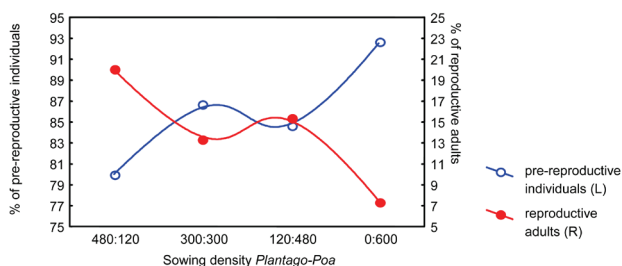


Fig. 5. Percentage of *P. annua* age states.

(P480:120 and P120:480), but between these plots there were evident differences in the percentage of ontogenetic categories (Fig. 2). This is good proof that assessment and comparison of ontogenetic development based exclusively on the age spectrum index can, in some cases, result in deceptive information about the similarity of samples being compared.

Poa annua

In contrast to *P. major*, density of the species *P. annua* on the sample plots was directly dependent on sowing density (Fig. 4).

The effect of density stress influenced dynamics of the ontogenetic process, with the result that the proportionally highest number of reproductive adults was found on the plot with lowest density of the species *P. annua* (P480:120) (Fig. 5). Similarly, Law (1975) concluded that length of the pre-reproductive period increased with increase of *P. annua* density.

The age spectrum index, in contrast to the relative percentage of age spectra, did not show any high differences in age spectrum of the given species on the sample plots (Table 2).

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Table 2. Age spectrum index of the species *P. annua* on sample plots in the summer census.

Sample plot	Age spectrum index
P 480:120	1.2
P 300:300	1.1
P 120:480	1.2
P 0:600	1.1

The autumn census

Plantago major

Table 3 shows that, compared to the summer census, in the autumn census the density of *P. major* decreased on all plots except in monoculture. Plot P480:120 retained the highest abundance of individuals, but there was a rather clear trend of increasing density along the sowing gradient of this species (Fig. 6).

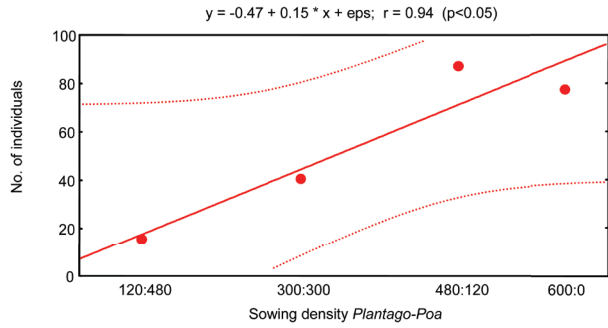


Fig. 6. Average number of *P. major* individuals on sample plots.

Table 3. Changes in *P. major* density and ontogenetic structure in October compared to the summer census. (*The individuals in the V-Im category were not recorded on P600:0 in the August census, and on plot P120:480 the seedling-juvenile category was not observed in the summer and autumn censuses).

Plot	No. of individuals	Number of RA	Number of V-Im	Number of Sd-Juv	M.O.C.
P600:0	+17%	-4%	*	-57%	48.5%
P480:120	-18%	+6%	+13%	-73%	29.4%
P300:300	-10%	0%	-50%	-100%	10.6%
P120:480	-6%	+50%	-62%	*	56.6%

The most intensive ontogenetic changes compared to the summer census occurred on the plots with minimal (P120:480) and maximal (P600:0) densities. During the period between the two censuses, the most reduced percentage of individuals was in the seedling-juvenile age state (Fig. 7, Table 3). The distribution of age states points to dominance of reproductive individuals (Fig. 7). The proportionally highest percentage of RA was on the plots with lower densities of *P. major* (P300:300 and P120:480). Density dependence of the rate of ontogenetic changes can also be seen in values of the age spectrum index (Fig. 8).

Poa annua

Thanks to its short life cycle, the number of individuals of the species *Poa annua* in the autumn census was low. As a typically opportune species, *Poa annua* in experimental conditions had a relatively short life cycle, with the result that most of its surviving individuals in October were in the post-reproductive subsenile stage. Because of the low number of individuals on the sample plots, it was impossible

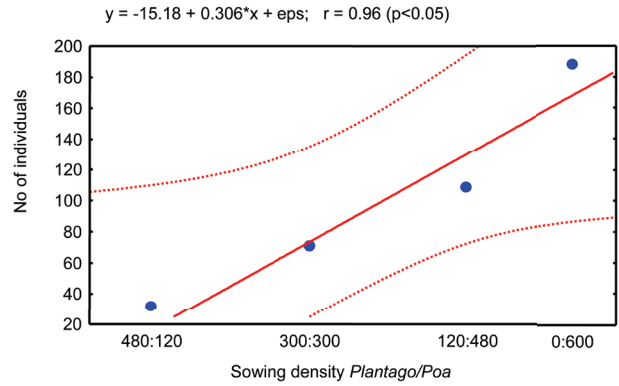


Fig. 7. Percentage of *Plantago major* age states.

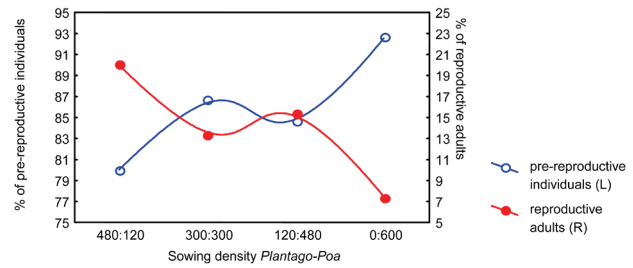


Fig. 8. *Plantago major* age spectrum index.

to explain the obtained results. The highest number of individuals (15.7) was recorded on plot P120:480, while in monocultures there were only individual samples of this species. Except for plot P300:300, on which reproductive adults were found, on all other plots all individuals of this species were in the post-reproductive subsenile stages.

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CONCLUSION

An effect of negative density-dependent processes was observed through intra-specific interference in a replacement series experiment. The effect of intra-specific interference increased in stress conditions owing to intensive evaporation of moisture from the denuded soil.

In the species *Plantago major*, density stress and water deficit caused retardation of ontogenetic development. Higher density caused the increase in the percentage of individuals in the youngest age groups (seedling + juvenile) and decrease in the

percentage of individuals in the group of reproductive adults and the virginile + immature group. Similarity in the effects of density stress and water deficit on ontogenetic development was evident primarily in the summer census, with the result that the plots with highest and the lowest densities had the lowest number of reproductive adults in the experiment and almost an identical age spectrum index. The rate of ontogenetic transformation from the seedling-juvenile stage to the immature-virginile stage also indicated the presence of density stress.

The stress effect caused by water deficit led to shortening of the life cycle of the species *Poa annua*. Increase of density caused retardation of the ontogenetic process, with the result that the distribution of age states was characterized by a negative density-dependent response. Aimed at detecting a density-dependent response of ontogenetic development, the age spectrum index in this case did not indicate any significant differences in the age spectrum of this species at the given densities.

Application of the age spectrum index in the study showed that the interpretation of values of this parameter is complex: because it can indicate essentially different processes, in some cases it points not only to density response, but also to the presence of abiotic factors (stress).

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ПОПУЛАЦИОНА ДИНАМИКА ВРСТА *PLANTAGO MAJOR* L. И *POA ANNUA* L. У ЕКСПЕРИМЕНТУ ЗАМЕНСКИХ СЕРИЈАА. МИЈОВИЋ¹, Н. СТАВРЕТОВИЋ² и ЗОРИЦА ПОПОВИЋ³¹Завод за заштиту природе Србије, 11070 Београд, Србија²Шумарски факултет, Универзитет у Београду, 11000 Београд, Србија³Институт за биолошка истраживања "Синиша Станковић", 11000 Београд, Србија

Истраживања популационе динамике типичних представника рудералне вегетације (*Plantago major* L. и *Poa annua* L.) у експерименту заменских серија извршена су у циљу праћења динамике раста типичних колонизатора у условима обрастања "празног простора", насталог уклањањем вегетације са експерименталне површине, као и односи унутар и између анализираних

врста који се успостављају у условима сталне нарушености таквих површина перманентним уклањањем осталих врста. На основу различитих популационих параметара установљене су разлике у динамици и стратегији раста ових врста, као и ефекат интра- и интерспецифичних интеракција у дефинисаним условима иницијалних густина и пропорција сејања.