REGENERATIVE STRATEGY OF RUMEX OBTUSIFOLIUS L. IN MEDITERRANEAN FORAGE CROPS: THE ROLE OF SEED BANK AND ANNUAL SEED PRODUCTION

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Abstract

The regenerative strategy of *Rumex obtusifolius* L. in alfalfa (*Medicago sativa* L.) crops was studied by analysing the role of annual seed production and seed bank on young plant establishment. Shallow soil seed bank, seed production, seed rain and seedling emergence were monitored in plots with and without removal of fruiting shoots before crop harvest. Data were summarized in a population flux diagram in order to show the relative importance of the different seed sources for seedling emergence. Results show that shallow seed bank, the only which is functional in environments with scarce soil disturbance, is temporal and its maintenance depends mainly on periodic seed inputs from annual seed production, which consequently has the strongest influence on the regeneration of *Rumex* populations. Biological and ecological implications of this regenerative strategy are discussed.

Introduction

Herbaceous perennial communities such as mesic grasslands or irrigated forage crops are subjected to a regular and noticeable disturbance regime at canopy level, as a result of grazing or periodic harvesting, and a low level of soil disturbance. Dominant species in these environments are perennials whose regenerative strategy is commonly characterized by the lack of a persistent soil seed bank. Seeds of grasses such as *Arrhenatherum elatius*, *Bromus* sp.pl., *Festuca* sp. pl. and *Lolium* sp. pl. are able to germinate soon after release and form short-lived seed banks type I or II according to THOMPSON & GRIME (1979). In common dicotyledon species such as *Plantago lanceolata*, *Ranunculus acris* and *R. bulbosus* only a small proportion of seeds remains ungerminated one year after release and the resulting seed bank is type III, long-term persistent but small (SARUKHAN, 1974; GRIME & al. 1989).

The lack of large persistent seed banks in grassland species can be related to low frequency of soil disturbance (THOMPSON, 1992). The regenerative strategy of dominant grassland species essentially exploits gaps appearing, for example, after periodic harvestings of following grazing (GRIME, 1979), which are the only sites where establishment is possible (FENNER, 1978; PANETTA & WARDLE, 1992).

In contrast, a group of subordinate grassland species shows the opposite regenerative strategy, characterized by the presence of dormant seeds which constitute large long-term persistent seed banks (type IV). This strategy, common in arable weeds, is also found in some grassland dicotyledons such as *Rumex acetosella* and *Ranunculus repens* (SARUKHAN, 1974; GRIME & al. 1989). In grasslands, these species are commonly

restricted to disturbed areas, e. g. molehills or trampled areas (JALLOQ, 1974), where seeding establishment is enhanced by the lack of competitors (FENNER, 1978).

The regenerative strategy of *Rumex obtusifolius*, a common species in herbaceous perennial communities, is not well known. Sexual reproduction is considered the main regenerative mechanism (CAVERS & HARPER, 1964; HONGO, 1989). According to some authors, seedling emergence in closed communities is restricted to vegetation gaps (CAVERS & HARPER, 1967) and occurs mainly after ploughing, because of a long-term persistent seed bank (CAVERS & HARPER, 1964; HONGO, 1989).

However, the appearance of a persistent seed bank is prevented near or at the soil surface by the rapid loss of seed viability and by the lack of innate dormancy, which promotes the immediate germination of seeds exposed to light or alternating temperatures (WEAVER & CAVERS, 1979; ROBERTS & TOTTERDELL, 1981). Deeply buried seeds are quiescent or undergo a seasonal secondary dormancy cycle, and maintain their viability for several years (CAVERS & HARPER, 1964; ROBERTS & NEILSON, 1980; ROBERTS & TOTTERDELL, 1981; VAN ASSCHE & VANLERBERGHE, 1989). In spite of this, the effectiveness of a deep, persistent seed bank in *Rumex* regeneration is greatly reduced by the low frequency of soil disturbance.

The aim of our study was to analyze seedling emergence of *Rumex obtusifolius* in alfalfa crops and its relationships to annual seed production and the soil seed bank. The results obtained may elucidate the regenerative strategy of the species in herbaceous perennial communities.

Material and methods

Study site and experimental design

The study was carried out in an irrigated alfalfa crop in the Segre valley (Catalonia, NE Spain). The area has a continental mediterranean climate. Alfalfa is usually left to grow for 5-6 years before ploughing. From April to October the crop is watered fortnigthly or monthly, depending on season, and harvested every 30-40 days at a height of 4-5 cm. The harvested crop is left to dry for a few days in rows in the field before balling.

In January 1992, two adjacent 20x20 m plots were marked out in a commercial alfalfa field with a resident population of about 25 mature individuals m^{-2}. In one plot, shoots fruited normally until the harvest (Seed rain treatment, SR), after which they were left to dry and were removed with the crop. In the other plot, flowering shoots of *Rumex obtusifolius* were cut before each harvest, thus preventing seed rain (No seed rain treatment, NSR) in order to study the dynamics of seeds in soil and the role of seed bank on seedling emergence.

Sampling

Seed bank was estimated by collecting soil samples in late March 1992 and 1993, before and after *Rumex* fruiting. Sampling was limited to the top 4 cm of soil, since

Rumex germination has not been found below this depth (VAN ASSCHE & VANLENBERGHE, 1989). In SR treatment, four 1.5 x 0.9 m sub-plots were marked out in two parallel lines, and each of them was divided into 15 areas using a 30 cm mesh grid. In NSR treatment, two 1.25 x 1.25 m sub-plots were marked out and divided into 25 areas using a 25 cm mesh grid. A soil core (22.9 cm²) was taken from each area and seeds were separated by washing in a 0.5 mm mesh sieve, and counted. In order to test their viability seeds were exposed in a growth chamber to optimal conditions for germination, which are a daily 14-h-photoperiod with temperatures of 25°C in light and 10°C in darkness (ROBERTS & TOTTERDELL, 1981).

From March to November 1992 seed production was estimated in the SR treatment just before each harvest, by recording stem basal diameters of all fruiting shoots in eight 1.5 m² sub-plots. At each sampling, a variable number of fruiting shoots, ranging from 46 to 90, were collected in adjacent areas in the same field, the basal diameter of their stems was measured and their fecundity (number of fruits) was evaluated. A significant allometric relationship was found between both parameters and was used to estimate seed production in the field.

In order to estimate the seed rain, 20 seed traps (14 cm diameter and 5 cm height pots) were buried at ground level in SR plot and 16 in NSR plot. Seed trap contents were collected after each crop removal following balling, and seeds were counted. Their viability was tested in a growth chamber with the same procedure as for the seed bank estimation.

From April 1992 to March 1993 seedling emergence was monitored in SR treatment in two 50x25 cm permanent quadrats within each 1.5x1 m sub-plot. Samplings were taken following harvests, every 4-6 weeks, since recording was only feasible when the crop had recently been cut. Two different phenological stages were distinguished: seedlings (individuals with cotyledons) and immatures (non-fertile individuals without cotyledons). In NSR treatment, sixteen 25x25 cm permanent quadrats were marked out and arranged in four rows. Immatures were recorded after each harvest and removed after counting.

Total seedling emergence was estimated because a great number of seedlings emerged and died between two samplings or were directly recorded as immatures. At each sampling date, seedling establishment probability was calculated as the proportion of seedlings of the previous sampling that had passed to the immature stage. The number of new immatures recorded at each sampling was then divided by the establishment probability in order to obtain the number of seedlings germinating in the previous sampling. This procedure was used to estimate seedling emergence in both SR and NSR plot.

Results

No significant differences in seed bank size were found between SR and NSR plots in March 1992, at the beginning of the experiment (Table 1). In November 1992 values had decreased significantly in both treatments, especially in the NSR plot, where the seed bank was almost completely depleted.

Rumex obtusifolius fruiting began in the second harvest, in June. There was a high seed production in several fruiting waves throughout the year, with a maximum at the first fruiting (23,000 seeds/ m²), and a gradual decrease thereafter (Fig. 1). Seed rain followed a similar pattern to seed production in SR plot, but 73% of viable seeds produced in the year were probably removed from the field in the crop balling process. Despite this reduction, seed rain was much higher than initial soil seed bank (Table 1). Some seeds were also found in NSR traps, but they were probably the outcome of surface movements of seeds into the same plot due to irrigation; results obtained in 1993 (data not shown), after a significant decrease of the shallow soil seed bank in NSR plot, showed extremely low seed rain and corroborate the hypothesis that seed dispersal from outside the plot was negligible.

Estimated seedling emergence in SR plot increased gradually until July and decreased afterwards (Fig. 2). Seedling emergence in NSR plot showed a gradual decrease over the year.

The relative importance of the different seed sources for *Rumex obtusifolius* seedling emergence was analyzed by means of a population dynamics diagram (Fig. 3). Seed bank remaining and seed bank germination probabilities were calculated using NSR data. NSR seed rain values were not taken into consideration. The probabilities of shed,
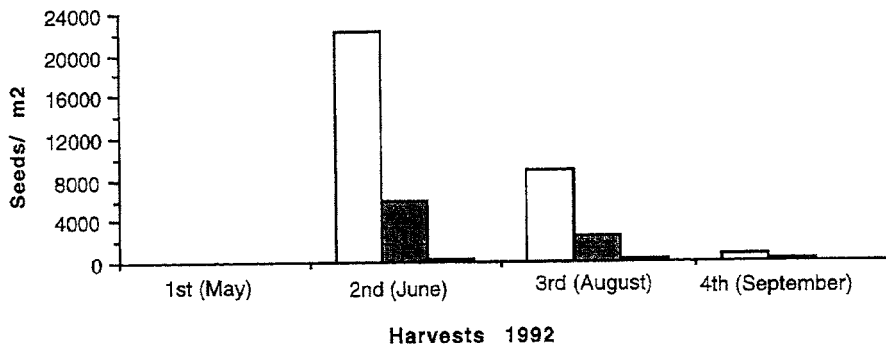

Fig. 1. Seed production and seed rain of *Rumex obtusifolius* over the different harvestings. White bars: seed production in SR plot. White bars: seed rain in SR plot. Grey bars: seed rain in NSR plot.

	SR plot	NSR plot
March 1992	2471.37 (40.17) a	2357.80 (57.11) a
March 1993	1004.26 (22.94) b	244.51 (7.92) c

Table 1. Viable seeds/ m² in the top 4 cm of soil in March 1992 and 1993. Means and standart error (in brackets) are included. Means are compared using A.N.O.V.A. (F=29.20; df=3; P<0.001). Figures followed by the same letter are not significantly different for P<0.05 with L.S.D. test after log transformation.
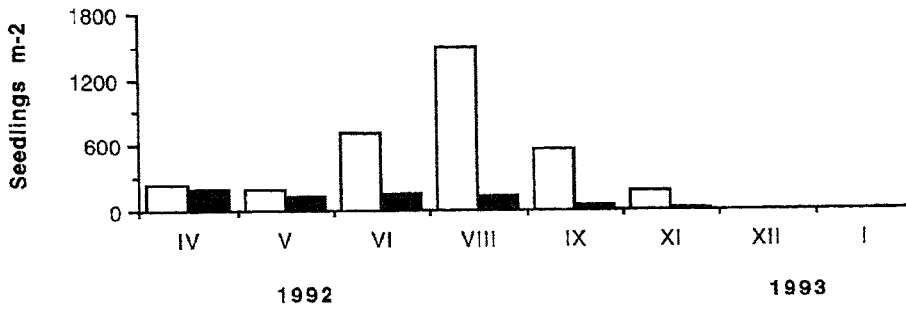
Fig. 2. Estimated seedling emergence of *Rumex obtusifolius* from March to December 1992. White bars: SR plot. Black bars: NSR plot.

germination and seed bank incorporation were calculated for the annual seed input, using data obtained in SR plot. Previously, initial seed bank remaining and seed bank germination calculated from NSR data were substracted, respectively, from SR seed bank incorporation and SR seedling emergence.

The diagram of seed and seedling population dynamics shows that only 27% of the annual seed production falls to the ground, and the rest is probably removed from the field in the crop balling process (Fig. 3). Most of the seed shed germinates or dies in the release year, while 9% becomes incorporated into the shallow seed bank. This pool is markedly temporal and, in most of the cases, seeds germinate or die in a year and only 10% remain viable in soil. Consequently, the probability that a seed remains viable in the shallow seed bank for more than two years, considering this probability constant between years, is 0.01.

Discussion

The constitution of a permanent seed bank depends on the existence of mechanisms that prevent germination and ensure long-term seed viability (MURDOCH & ELLIS, 1992). *Rumex obtusifolius* seeds do not have innate dormancy mechanisms and they are particularly sensitive to light and temperature changes (ROBERTS & TOTTERDELL, 1981). The phytochrome system provides a light-sensing device which contributes to promoting germination of seeds situated at or near the soil surface. Buried seeds, in darkness and in less fluctuating temperatures, are maintained in quiescence or in secondary dormancy induced by temperatures higher than 15°C. In spite of this, secondary dormancy may be lost by a cold stratification (chilling) followed by an increase in temperature (ROBERTS & TOTTERDELL, 1981). Therefore, shallowly buried seeds, in the top 4 cm of soil where germination is possible, undergo a seasonal dormancy cycle, with a summer increase in dormancy and a decrease in spring, after the winter chilling effect and the spring temperature shift (VAN ASSCHE & VANLENBERGHE, 1989). In established alfalfa crops, seed burial is largely prevented by the lack of soil disturbances like ploughing, and most seeds remain on the surface.
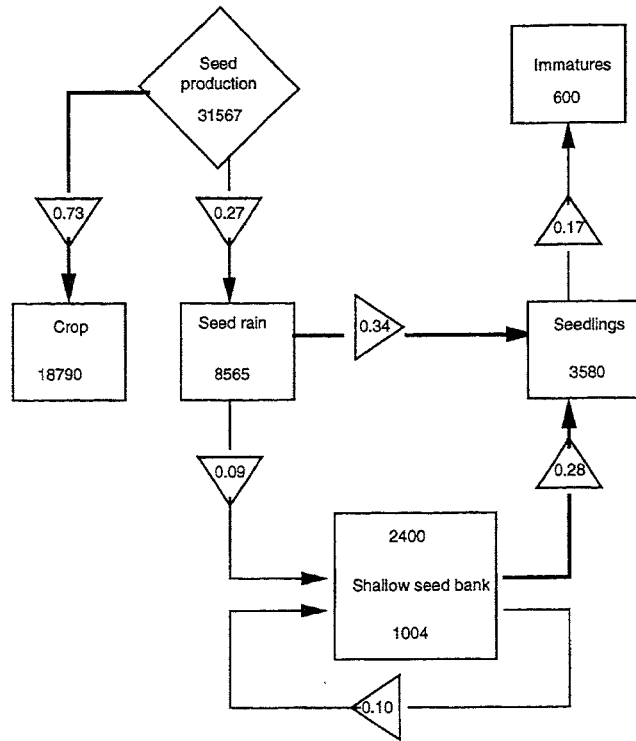
Fig. 3. Seed and seedling population dynamics of *Rumex obtusifolius* in alfalfa crops. By convention, rectangles represent stages, triangles represent transition probabilities between stages and the diamond represents seed production. Values/ m² are shown. In the case of the shallow seed bank, initial value, the mean of both SR and NSR values, is presented above and final value, corresponding to SR plot, is shown below.

These seeds, exposed to light and daily-fluctuating temperatures, germinate rapidly and make up the majority of late summer and autumn recruitment in crop drying rows. A small proportion of seeds that are shallowly buried by crop harvest management acquire secondary dormancy until the following spring, when they form an early germination peak that decreases gradually.

In consequence, two main seed sources can be recognized in alfalfa crops: the annual seed rain and the shallow seed bank. This seed bank is temporal and clearly dependent on the annual seed rain, since it becomes severely depleted after a year without new seed inputs. A third seed source, the deep permanent seed bank, could also be important in *Rumex* regeneration. However, little is known about it; some authors claimed that *Rumex* seeds are able to survive for several years when they are buried deep (CAVERS & HARPER, 1964). The first results of studies carried out recently in alfalfa crops have shown that the *Rumex* deep seed bank is negligible (<10 viable seeds/ m² from 5 to 20 cm deep). The incorporation of seeds to the deep soil layers is probably prevented by the scarce soil disturbance, which is only important every 6 or 7 years

when alfalfa is ploughed and usually replaced by another crop, and the lack of innate seed dormancy, which enhances the rapid germination of seeds. Further studies are needed in order to elucidate the longevity of seeds buried deep in soil.

The seed bank of *Rumex obtusifolius* in alfalfa crops is, consequently, type III, like other grassland dicotyledon species such as *Plantago lanceolata, Ranunculus acris* and *R. bulbosus* (SARUKHAN, 1974; GRIME & al. 1989). Annual seed production plays, thus, the main role in *Rumex* recruitment in alfalfa crops as a consequence of the low soil-disturbance frequency. Regenerative strategy is, in some, a simple mechanism of gap exploitation, common in species from environments subject to predictable damage such as grazing (GRIME, 1979). Seedling establishment is also affected by the lack of soil disturbance, which promotes closed vegetation and restricts establishment to small gaps. However, establishment probability is increased by the iteroparous strategy of the species, which has a great longevity and an increasing fecundity with age and ensures a great number of offsprings during its life. This strategy, also exhibited by other grassland species, is commonly found in stable environments, such as herbaceous perennial communities, where mortality is density-dependent and concentrated to the early life-stages as a consequence of the high competition level (BELL, 1976).

Acknowledgements

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