

# What determines emergence and net recruitment in an early succession plant community? Disentangling biotic and abiotic effects

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## Abstract

**Question:** How do different regeneration scenarios shape species composition at two stages of plant community establishment (emergence and net recruitment) in an early succession?

**Location:** Northern Spain.

**Methods:** In a recently ploughed field, we created eight regeneration scenarios with light, water and nitrogen availability (five replicates each). Seedlings of all species were monitored from emergence to death during one year. Abiotic and biotic variables were measured per quadrat, i.e. soil texture, nutrient contents, seed bank densities and composition, neighbour plant species density and cover. We used partial ordination methods in order to separate the effect of each environmental variable on species composition during emergence and adult net recruitment.

**Results:** Light treatment determined annual plant density at time of emergence and recruitment, while water addition controlled the recruitment of perennials. Resource levels explained the emerged species composition; this effect was not translated into the recruited species composition. N-addition and N + water addition were strongly associated to species abundances at the time of emergence. Seedling composition in summer was correlated with seed abundance of *Cerastium* spp. Neighbour species density and cover (mainly *Arrhenatherum bulbosum*, *Agropyron repens* and *Picris echioides*) explained significant fractions of species composition in the emergence and recruitment of the different cohorts. Interactions between species seem to vary in intensity among cohorts and in the key plant species that determined species abundance along succession.

**Conclusions:** Our scenarios exerted contrasting and multilevel effects on the development of our early succession community. Resource availability differently affected plant density and species composition at different life stages. It is relevant to consider different life stages in plant community studies. However, regeneration conditions and other abiotic factors are not enough to explain how community composition varies.

**Keywords:** Community establishment; Experimental approach; Neighbour effect; Nutrient availability; Seed bank; Soil physico-chemical characteristics.

**Nomenclature:** Aizpuru et al. (1999).

**Abbreviations:** CCA = Canonical Correspondence Analysis; DCA = Detrended Correspondence Analysis; RDA = Redundancy Analysis; TVE = Total Variation Explained.

## Introduction

Plant community recovery after total destruction of above-ground vegetation is usually followed by single species domination in the first year of succession (Abul-Fatih & Bazzaz 1979; Pickett 1982; Miller & Werner 1987). Scarce microhabitat differentiation in recently disturbed systems avoids microhabitat segregation among species and it is argued that this explains such dominance. However, it is known that small differences in resource levels play a major role in the occurrence of different microhabitats, and consequently in early species composition and dominance (Carson & Pickett 1990). This links with the ‘regeneration niche’ concept (Grubb 1977) which stresses the importance of plant establishment requirements to the control of the whole community dynamics.

Resource levels modulate floristic diversity in newly established communities through influence on above-ground productivity (Bakelaar & Odum 1978; Tilman 1982, 1984, 1987; Carson & Barrett 1988; Wilson & Tilman 1991; Pyšek & Lepš 1991; Mitchley et al. 1996; Baer et al. 2003), or through differences in plant soil preferences (Andreasen et al. 1991). In this sense, nitrogen availability is considered the most limiting nutrient in the development of terrestrial plant communities (Tilman 1984; Chapin & Shaver 1985). Water has the potential to not only enhance growth but also seedling germination (Regehr & Bazzaz 1979) and establishment (Inouye et al. 1980; Weller 1985), especially in early succession plant communities (Bazzaz 1996). Simultaneously, increased soil moisture tends to enhance nitrogen mineralization rates (Chapin et al. 2002). Nutrients and water may also interact in their effects on individuals, for instance mineral nutrient addition may increase individual above-ground biomass, leading to increased water requirements and, ultimately, increasing mortality (Goldberg & Novoplansky 1997). Finally, light usually determines species competition hierarchies and consequently plant community composition (Miller & Werner 1987; Keddy & Shipley 1989; Foster 1999).

Few studies have considered the simultaneous effects and probable interactions among nutrients, water and light on early plant community composition and structure (see Glauning & Holzner 1982; Carson & Pickett 1990; Luzuriaga et al. 2002; Stevens et al. 2006)

Once a community begins its recovery, different plant-plant interactions occur which iteratively modify the structure and composition of the emerging community. We are aware that species composition in herbaceous plant communities not only depends on abiotic conditions but also on biotic environmental factors (Grace 1999). Among them, the effect of the seed bank species composition and structure on above-ground vegetation has been highlighted (Lavorel & Lebreton 1992; Luzuriaga et al. 2005; Olano et al. 2005), not only as the main source of species for the community but also because some kind of regulation of the germination may occur. Some studies also stressed the effect of coetaneous neighbours in terms of competition (Gurevitch et al. 1992; Goldberg et al. 1999) or facilitation (Maestre et al. 2001; Sans et al. 2002) in plant community composition. In addition, the emergence time – i.e. the cohort – may be decisive in the response of individuals (Escudero et al. 1999).

Although initial establishment is thought to be of great importance in determining the temporal and spatial distribution of plants (Grubb 1977; Gross & Werner 1982; Foster & Gross 1997), few studies have examined how the performance of different species at earlier life-history stages controls the composition of the emerging community. The magnitude, or even the direction, of interactions change over the life history of a single species (Gurevitch 1986; De Steven 1991a, b) and such changes are reflected in the composition of the plant community (Howard & Goldberg 2001). In this study, we tried to disentangle the effect of abiotic and biotic variables on two early community stages: the emergence time and the adult plants that survived to the first unfavourable season. We experimentally created different regeneration niches in a recently disturbed and homogenized old-field by manipulating resource levels. Our main aim was to determine to what extent these new environmental scenarios are reflected in the species composition of the first year old-field community. We hypothesized that creation of new regeneration niches would result in different plant species composition. However, differences due to this initial community filtering was exacerbated or mitigated by a complex response of other biotic and abiotic variables at the emergence and at the adult recruitment time. We specifically wanted to establish the relative importance of a complex set of predictors such as soil physico-chemical variables, seed bank composition and density, neighbour performance and the experimental environmental scenarios on the species composition of our early plant community. We also

wanted to know how the composition of the emerging assembly was translated into other community stages and which factors affected this change. Finally, we wanted to evaluate to what extent different cohorts responded similarly to the abiotic and biotic variables.

## Methods

### *The study area*

The study site was located 3 km east of Vitoria-Gasteiz (Basque country) in northern Spain (42°51' N; 2°37' W and 510 m a.s.l.), very close to the boundary between the Eurosiberian and Mediterranean regions (Rivas-Martínez 1987). Climatic conditions in this territory show annual mean rainfall of 843 mm and mean temperatures around 11.7°C, ranging between 1.3°C in the coldest and 26.1°C in the warmest months. Rainfall is highly unpredictable in time and quantity, and pronounced summer droughts are common. The study was carried out in a perennial grassland that had been cultivated five years ago, following which it developed under moderate sheep grazing conditions. The early old-field vegetation that developed after disturbance was mainly composed of annuals (ca. 60% cover) such as *Sinapis arvensis*, *Picris echioides*, *Anagallis arvensis*, *Kickxia spuria* etc. (see App. 1). The remaining 40% were perennial plants mainly consisting of grasses (82.7%), especially *Agropyron repens* and *Arrhenatherum bulbosum*. These grasses mainly developed from the propagule bank, thus they were the first species to dominate the site, being able to achieve nearly 30 cm height at the end of the first summer. Soil physico-chemical analyses showed that the study area was on a clayish soil with values of nutrients ranging as follows: total N (0.13%-2%), total P (2.5-14.3 mg.kg<sup>-1</sup>), Ca (30.8-39.2 meq.100g<sup>-1</sup>), Mg (0.30-0.51 meq.100g<sup>-1</sup>), the C:N ratio (6.3-8.5) and cation exchange capacity (11.2-19.7 meq.100g<sup>-1</sup>). This clayish soil developed a hard soil physical crust under the high evapotranspiration conditions in the summer.

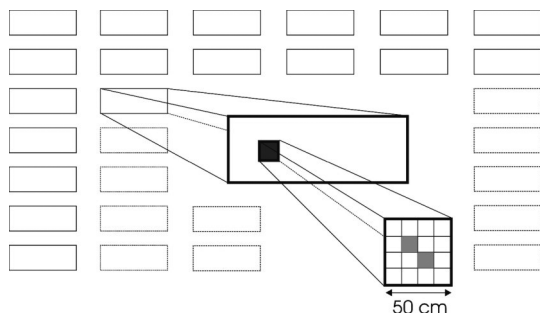
### *Experimental design*

In early spring soil was ploughed to a depth of 30 cm and hand-raked to smooth the surface, and to remove all vegetation. Then, 40 plots (4.75 m × 1.75 m) were regularly distributed with a 1.75 m wide buffer between them. Levels of nitrogen availability (nitrogen addition: N<sup>+</sup>; no nitrogen addition: N<sup>-</sup>), water (watered: W<sup>+</sup>; not watered: W<sup>-</sup>) and light availability (natural light availability: L<sup>+</sup>; light availability experimentally reduced: L<sup>-</sup>) were manipulated in a factorial way, resulting in eight treatments. We used a randomized design, with

five replicates per treatment.

On N<sup>+</sup> plots, 6 g.m<sup>-2</sup> of nitrogen was added (similar to Baer et al. 2003) by manually scattering urea in granular form from the walkways in the last week of March. On W<sup>+</sup> plots we added 8.65 l.m<sup>-2</sup> fortnightly during June and July (five irrigations) when summer drought usually begins. The intent was to ameliorate water stress, not to apply an arbitrary total amount. Mean precipitation in the previous five years during summer drought (June and July) was 101 mm.m<sup>-2</sup>, ranging from 53 mm.m<sup>-2</sup> to 188 mm.m<sup>-2</sup>. Thus, total increase of water experimental supply above mean rainfall during these two months was 42.76%. On L<sup>-</sup> plots a wooden frame was installed, covered with a neutral shading cloth 1.5 m above the soil. This device filtered 20% of daylight photosynthetically active radiation (PAR). In the centre of each of these 40 plots, a quadrat of 50 cm × 50 cm (0.25 m<sup>2</sup>) was established in order to estimate species densities and cover, tillers of all species were counted and percentage cover for those species with at least 1.5% of total above-ground vegetation cover was estimated in each plot. Simultaneously, all seedlings in two areas (156.25 cm<sup>2</sup>) in each 50 cm × 50 cm quadrat were marked and monitored from April to October (Fig. 1). They were inspected fortnightly during the first two months and monthly afterwards (total: nine sampling dates). Thus, we monitored all individuals in an area of 312.5 cm<sup>2</sup> in each of the 40 plots.

Species identification followed Aizpuru et al. (1999). For each monitored plant we recorded species identity, emergence time, reproduction time and death time during one year. We considered that these plants were definitively recruited when they produced seeds in the case of annuals and when they surpass their first summer drought in the case of perennials. Individuals were classified into three cohorts depending on emergence time. The spring cohort consisted of the individuals that



**Fig. 1.** The experimental design consisted of eight resource availability scenarios replicated five times resulting in 40 plots (4.75 m × 1.75 m). Each plot contained a sampling quadrat (50 cm × 50 cm) where species individuals and cover values were measured and in two smaller areas randomly chosen (12.5 cm × 12.5 cm) where each single individual emerged was monitored during nine months (nine sampling dates).

emerged from early April to mid May, the summer cohort included the individuals emerging from June to August and the autumn cohort were those seedlings emerging from August to October.

We considered emergence of the three cohorts (spring, summer and autumn) and recruitment of the spring and summer cohorts, because recruitment of the autumn cohort was ruined due to colonization of moles of the experimental field. In each cohort emergence of annuals and perennials were considered independently.

#### *Soil and seed bank sampling*

In March, immediately after the ploughing treatment, we collected three soil cores (11 cm diameter and 3 cm deep) per plot ( $n = 40$ ). Soil samples were thoroughly mixed and then separated into two fractions. The soil analysis fraction was air-dried at room temperature for a month, sieved in the laboratory and analysed for clay (< 2  $\mu$ m), silt (20  $\mu$ m - 2  $\mu$ m), fine sand (200  $\mu$ m - 20  $\mu$ m) and coarse sand (2 mm - 0.2 mm) percentages, pH in H<sub>2</sub>O (1:2.5), organic matter content, total N, P, Ca, Mg, the C:N ratio and cation exchange capacity (12 variables). The other soil fraction, 140.45 cm<sup>3</sup>, was spread in 10 cm × 10 cm × 1 cm pots mixed with vermiculite (1:1) and placed in a glasshouse. Pots were regularly watered and the seedlings identified, counted and removed throughout a year to estimate seed bank size and composition.

#### *Statistical analysis*

When variables did not fulfil normality assumptions they were transformed in order to undertake three way ANOVAs (nitrogen, shade and water). In case normality was not achieved, Mann-Whitney non-parametric analyses were performed. Models were built with the statistical programme SPSS (v. 9.0).

Species emergence and recruitment data had a multidimensional nature, thus multiple ordination methods were also used. The emergence and recruitment matrices were subjected to constrained ordination for hypothesis testing (ter Braak & Prentice 1988; Legendre & Anderson 1999; Luzuriaga et al. 2002). The major advantages of this technique over classical multivariate ANOVA are that it is distribution free and has no restrictive upper limit to the number of species included (Verdonschot & ter Braak 1994). Our null hypothesis ( $H_0$ ) is that the resource addition treatments did not exert any significant effect on plant emergence or species recruitment. Five main matrices were built. Three corresponded to the emergence data (spring, summer and autumn) and two to the recruitment cohorts (spring and summer) (Table 1). Each matrix was built with the 40 plots (rows) and with the species that appeared in more than the 10% of

the plots. Those species appearing in four plots or less were eliminated from the matrices. Then, a detrended correspondence analysis (DCA) was performed with each of them (Hill & Gauch 1980), detrending by segments and non-linear rescaling of the axes, which has the property that the extracted axes are scaled in units of mean standard deviation (SD) (Gauch 1982). Following the recommendations of ter Braak (1986) and of Legendre & Anderson (1999), when axis length was above 3 SD units, a canonical constrained analysis (CCA) was performed to relate the main data matrices with other environmental variables, when it was below this value a redundancy analysis (RDA) was undertaken (see Table 1).

Twelve constraining matrices for the three emergence data sets and ten for the two species net recruitment data sets were built:

1. The treatment matrix consisted of the seven resource availability treatments previously transformed to *dummy* variables: the control treatment (N<sup>-</sup>W<sup>-</sup>L<sup>+</sup>) and all the combinations of resource availabilities: N<sup>+</sup>W<sup>+</sup>L<sup>+</sup>, N<sup>+</sup>W<sup>-</sup>L<sup>-</sup>, N<sup>+</sup>W<sup>-</sup>L<sup>+</sup>, N<sup>-</sup>W<sup>-</sup>L<sup>-</sup>, N<sup>-</sup>W<sup>+</sup>L<sup>+</sup>, N<sup>-</sup>W<sup>+</sup>L<sup>-</sup>. To avoid variable multidimensionality problems the triple interaction was eliminated from the analyses (N<sup>+</sup>W<sup>+</sup>L<sup>-</sup>).

2. The seed bank density matrix consisted of a single vector with the total seed density per plot.

3. The seed species composition matrix was the number of seeds of each species detected after germination in the greenhouse (22 species).

4. The soil matrix consisted of 12 vectors: soil texture measured as mean particle size (clay, silt, fine sand and coarse sand), organic matter content, pH, total N, P, Ca and Mg content, the C:N ratio and cation exchange capacity. 5-8) Four matrices were built with the most abundant species densities in four succession moments: early May matrix, early June matrix, mid July matrix and October matrix. 9-12) Another four matrices were built with species that showed cover values above 1.5% in the same succession moments. The density and cover matrices of October were only used to constraint the emergence matrix because October recruitment was lost.

Total variation explained (TVE) by each constraining matrix was calculated as the sum of all canonical

extracted axes (Borcard et al. 1992). A Monte Carlo permutation test was performed to determine the accuracy of the relationship (1000 randomizations) between the two data sets. The sum of all canonical eigenvalues was used to build the *F*-ratio statistic (ter Braak 1990; Legendre & Anderson 1999). Only when  $p < 0.05$  (adjusted for multiple comparisons by Holm's method; Legendre & Legendre 1998) was the relationship between the two data sets considered significant. If the model was significant, a forward stepwise procedure was carried out to select a reduced model including only significant variables. We incorporated explanatory variables one at a time and step by step in the order of their decreasing eigenvalues after partialling out the variation accounted for the already included variables. The process stopped when the new variable was not significant ( $p > 0.05$ ). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 1000 randomizations. In the analyses with species densities and cover values as the explaining matrices those species included as explanatory variables were removed from the main matrix to avoid correlation among the explaining variables and their presence in the main matrix. These species were *Arrhenatherum bulbosum* and *Agropyron repens* in the analyses of the effect of plant species cover on plant emergences and both species together with *Picris echioides* in the case of plant recruitment. All these analyses were performed with the programme CANOCO for Windows v 4.0 (ter Braak & Šmilauer 1997).

## Results

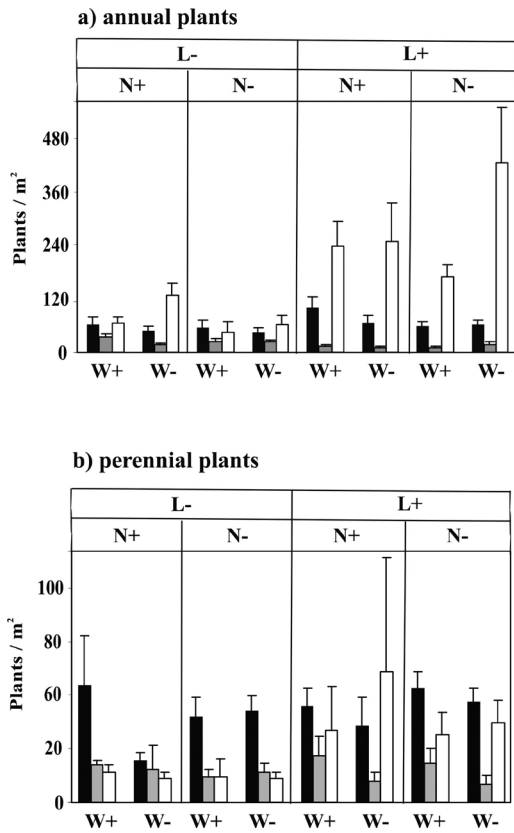
### *Effect of resource availability on total emergence and recruitment*

The light restriction treatment was the only resource factor that affected total density of annual plants both in the emergence and in the net recruitment stages (Tables 2 and 3; Figs. 2 and 3). Although emergence of annuals of the spring cohort did not suffer any resource availability restriction, adult recruitment was negatively affected by shade. Conversely, reduced light conditions positively affected annual seedling emergence in summer and negatively in autumn (Fig. 2). Annual recruitment in summer closely reflected the positive effect of shading on emergences (Fig. 3). Perennial plants showed a completely different pattern. Emergence of perennials was not affected by any of the resource availability scenarios (Table 2), but adult recruitment of the summer cohort was positively affected by irrigation (Table 3 and Fig. 3).

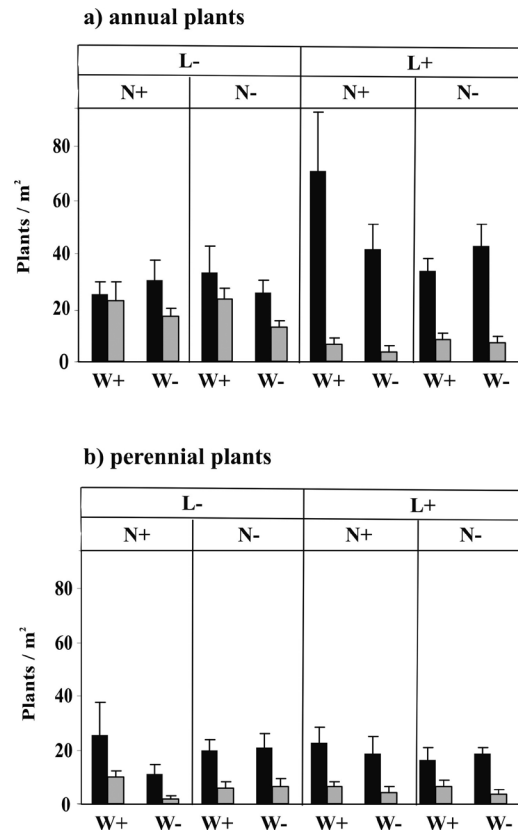
**Table 1.** Length of the principal axis of the DCA analysis in SD units and type of the constrained analysis undertaken for each of the main matrices analysed.

Main matrix	DCA gradient	Analysis type
Seedling emergence		
spring cohort	2.47	RDA
summer cohort	3.87	CCA
autumn cohort	1.71	RDA
Net recruitment		
spring cohort	3.17	CCA
summer cohort	3.7	CCA





**Fig. 2.** Mean number of individuals emerged in spring (black bars), summer (grey bars) and autumn (white bars), (a) annual seedlings (b) perennial seedlings. Water addition treatment started in June so it did not affect spring emergence. Vertical bars indicate SE. L<sup>+</sup> = no light restriction, L<sup>-</sup> = light restriction treatments, N<sup>+</sup> = nitrogen addition, N<sup>-</sup> = no nitrogen addition, W<sup>+</sup> = water addition, W<sup>-</sup> = no water addition.



**Fig. 3.** Adult net recruitment of the spring (black bars) and summer cohorts (grey bars) (a) annual plant recruitment (b) perennial plant recruitment. Vertical bars indicate SE. L<sup>+</sup> = no light restriction, L<sup>-</sup> = light restriction treatments, N<sup>+</sup> = nitrogen addition, N<sup>-</sup> = no nitrogen addition, W<sup>+</sup> = water addition, W<sup>-</sup> = no water addition.

*Effect of resource availability on species composition*

Resource levels only exerted a significant effect on species composition in the emergence time, but this effect was not translated into the adult recruitment event (Table 4). Treatments that affected species composition shifted depending on the cohort. Emergence of the spring cohort

did not suffer from any restriction of the experimental resource availability conditions, species emergence in the summer cohort was significantly explained by nitrogen and water addition without light restriction (N<sup>+</sup>W<sup>+</sup>L<sup>+</sup> treatment) and species emergence in the autumn cohort was modulated by nitrogen addition without light restriction (N<sup>+</sup>W<sup>-</sup>L<sup>+</sup>) together with the control treatment

**Table 2.** Mann-Whitney and three-way ANOVA analyses for nitrogen (N), light (L) and water addition (W) treatments on the annual and perennial seedling numbers emerged in spring, summer and autumn. Water addition treatment started in June. *F* = *F* statistic. *U* = Mann-Whitney *U* statistic. LOG = logarithmic transformation. Significant *p*-values in bold.

	Spring				Summer				Autumn			
	Annuals (LOG)		Perennials (LOG)		Annuals		Perennials		Annuals (LOG)		Perennials	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>U</i>	<i>p</i>	<i>U</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>U</i>	<i>p</i>
N	0.36	N.S.	3.01	N.S.	190.5	N.S.	193	N.S.	1.42	N.S.	141.5	N.S.
L	2.75	N.S.	1.56	N.S.	96.5	<b>0.005</b>	196.5	N.S.	26.57	<b>0.000</b>	112.5	N.S.
W					186.5	N.S.	136	N.S.	2.56	N.S.	168.5	N.S.
N×L	0.15	N.S.	<b>0.005</b>	N.S.					3.42	N.S.		
N×W									0.46	N.S.		
L×W									0.47	N.S.		
N×L×W									1.03	N.S.		

**Table 3.** Three-way ANOVA and Mann-Whitney analysis for nitrogen addition treatment (N), light (L) and water addition (W) on annual and perennial plant net recruitment in spring and summer. *F* = *F* statistic. *U* = Mann-Whitney *U* statistic. LOG = logarithmic transformation. SQRT = square root transformation. Significant *p*-values in bold.

	Spring				Summer			
	Annuals (LOG)		Perennials (SQRT)		Annuals (SQRT)		Perennials	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>U</i>	<i>p</i>
N	0.34	N.S.	0.18	N.S.	0.91	N.S.	179	N.S.
L	5.85	<b>0.02</b>	0.08	N.S.	18.06	<b>0.000</b>	165.5	N.S.
W	0.74	N.S.	0.34	N.S.	1.5	N.S.	109	<b>0.03</b>
N×L	0.45	N.S.	0.85	N.S.	0.83	N.S.		
N×W	0.24	N.S.	0.97	N.S.	0.004	N.S.		
L×W	0.1	N.S.	0.4	N.S.	0.016	N.S.		
N×L×W	1.4	N.S.	0.03	N.S.	1.51	N.S.		

(N-W-L<sup>+</sup>) (Table 4; Fig. 4).

Soil physico-chemical initial heterogeneity was not reflected in the seedling or adult species composition (Table 4).

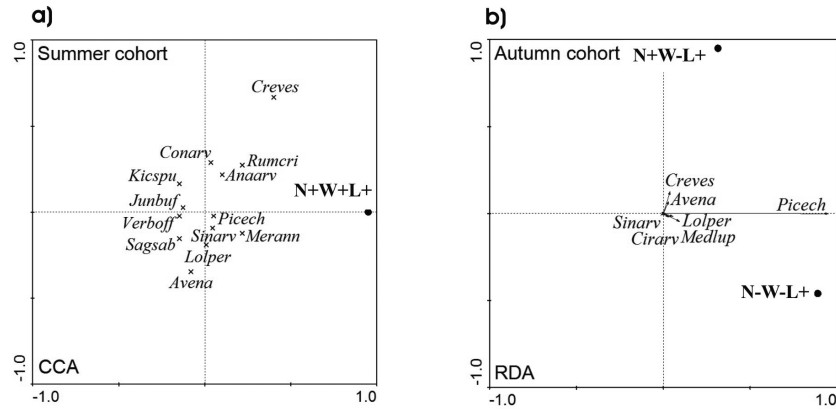
#### Effect of seed bank on emergence and net recruitment

Seed abundance and seed species richness were relatively low (29.6 to 45.7 seeds dm<sup>-3</sup> and 3 to 4.2 species 0.25m<sup>-2</sup> respectively), probably due to the strong soil ploughing imposed (see details in Luzuriaga et al.

2005). It was not surprising that seed bank density did not exert any significant effect on seedling emergence and adult recruitment (Table 4). However, composition of the emerged seedlings in summer was highly correlated to the seed abundance of *Cerastium* spp. (26% of the variability explained). Specifically, the abundance of *Cerastium* spp. seeds was mainly associated in the corresponding CCA biplot to the emergence of *Crepis vesicaria* and *Anagallis arvensis*. Nevertheless, no effect of the seed bank composition was reflected in adult net recruitment (Table 4).

**Table 4.** Percentage of variability explained by the reduced models built with the emergence matrices (spring, summer and autumn) and the recruitment matrices (spring and summer). As constraining matrices we used those with the variables selected in the forward stepwise procedure. The variables that following Monte Carlo explained significant fractions of variability (*p* < 0.03) are expressed in italics. These variables are arranged in the order of decreasing variation explained. Analysis type is expressed in brackets below the main matrix (see also Table 1). \* In the analyses with species densities and cover values as the explaining matrices, those species included as explanatory variables were removed from the main matrix in order to avoid correlation among the explaining variables and their presence in the main matrix (see Methods). N.S. = not significant. -: analysis not done; 1v = one constraining variable, 2v = two constraining variables. N<sup>+</sup>W<sup>-</sup>L<sup>+</sup> = nitrogen addition treatment, N<sup>+</sup>W<sup>+</sup>L<sup>+</sup> = nitrogen and water simultaneous addition treatment, N<sup>-</sup>W<sup>-</sup>L<sup>+</sup> = control treatment. See species abbreviations in App. 1.

Constraining matrices	Main matrix: Emergences			Main matrix: Recruitment	
	Spring cohort (RDA)	Summer cohort (CCA)	Autumn cohort (RDA)	Spring cohort (CCA)	Summer cohort (CCA)
<b>Treatments</b> (7v)	N.S.	1v: N <sup>+</sup> W <sup>+</sup> L <sup>+</sup> 16.2%	2v: N <sup>+</sup> W <sup>-</sup> L <sup>+</sup> , N <sup>-</sup> W <sup>-</sup> L <sup>+</sup> 34.9%	N.S.	N.S.
<b>Soil features</b> (12v)	N.S.	N.S.	N.S.	N.S.	N.S.
<b>Seed bank</b>					
Seed density (1v)	N.S.	N.S.	N.S.	N.S.	N.S.
Sp. Composition (22v)	N.S.	1v: <i>Cerssp</i> 26%	N.S.	N.S.	N.S.
<b>Plant density</b> *					
Early May (12v)	N.S.	-	-	N.S.	-
Early June (15v)	-	N.S.	-	N.S.	1v: <i>Arrh+Agrop</i> 21.6%
Mid July (17v)	-	N.S.	-	N.S.	2v: <i>Arrh+Agrop</i> , <i>Junbuf</i> 33.2%
October (24v)	-	-	N.S.	-	-
<b>Plant cover</b> *					
Early May (4v)	N.S.	-	-	N.S.	-
Early June (8v)	-	1v: <i>Arrh+Agrop</i> 15.9%	-	N.S.	2v: <i>Arrh+Agrop</i> , <i>Picech</i> 26.6%
Mid July (4v)	-	1v: <i>Arrh+Agrop</i> 15.5%	-	N.S.	2v: <i>Arrh+Agrop</i> , <i>Picech</i> 35.6%
October (6v)	-	-	N.S.	-	-

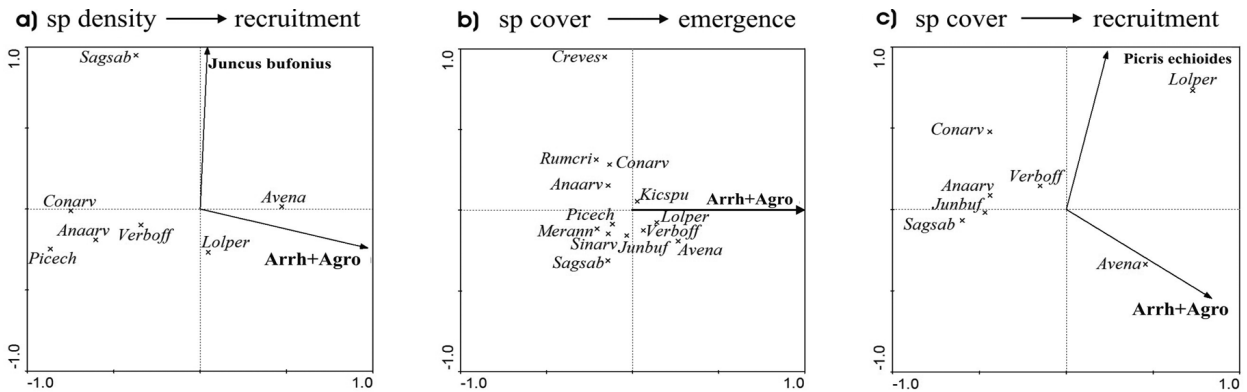


**Fig. 4.** Biplot of the principal axes of the reduced models for (a) CCA and (b) RDA using as main matrices seedling emergence in (a) summer and (b) in autumn and using as constraining matrices the variables selected for the experimental treatments. N<sup>+</sup> = nitrogen addition, N<sup>-</sup> = no nitrogen addition, W<sup>+</sup> = water addition, W<sup>-</sup> = no water addition, L<sup>+</sup> = no light restriction, L<sup>-</sup> = light restriction treatments. Species codes are the first three letters of the genus and specific epithet (See App. 1).

*Neighbour effect on emergence and recruitment*

The effect of neighbouring plants was disentangled in terms of neighbour species densities and cover values. Neighbour densities did not affect species composition in the emergence time but it significantly explained composition of summer net recruitment (Table 4). Total density of *Arrhenatherum* and *Agropyron* explained a high fraction of the variability in adult composition and, specifically, it was associated to other grasses (Fig. 5a). Conversely, neighbour composition in terms of species cover values, explained a significant fraction of variation in species composition of the summer cohort both in the emergence and in the adult recruitment stages (Table 4).

Specifically, cover of *Arrhenatherum* and *Agropyron* was positively associated to the emergence and recruitment of species such as *Avena* and *Lolium perenne* and negatively to the emergence of *Rumex*, *Picris* and *Sinapis* (Fig. 5b, c), while cover of *Picris* was positively associated to the recruitment of *Lolium perenne* and *Convolvulus arvensis*, and negatively to *Sagina sabuletorum* and *Avena* spp. (Fig. 5c).



**Fig. 5.** Biplot of the principal axes of the reduced models for the CCAs performed with the summer cohort. The constraining matrices consist in the species selected by means of the forward stepwise procedure. (a) Main matrix: species recruitment. Constraining matrix: species densities in July. (b) Main matrix: species emergences. Constraining matrix: species cover values in July. (c) Main matrix: species recruitment. Constraining matrix: species cover in July. When only one explaining variable was considered (b), the second axis was free and the explaining environmental vector necessarily appeared on the axis 1 (Hybrid RDA). Species codes are the first three letters of the genus and specific epithet (App. 1).

## Discussion

### *How did abiotic regeneration scenarios shape species composition?*

Total plant density and species composition were affected by our experimental regeneration scenarios. At emergence time, light determined annual plant density but seedling composition was mainly determined by the addition of N and water in summer and N only in autumn. This result suggests that light was probably the main factor that triggered germination but initial composition is filtered by other resources. Water is considered an important germination cue for some species in early successional habitats (Regehr & Bazzaz 1979; Bazzaz 1996), especially in summer, which may differently affect emergence and growth. The simultaneous effect of nitrogen and water on species emergences of the summer cohort may be explained due to the fact that when nitrogen is added, seedlings may become more sensitive to drought stress because the quicker growth of seedlings may increase water requirements (Goldberg & Novoplansky 1997). Thus, those species that were able to take advantage of the higher nutrient and water availability conditions at the seedling stage became the most abundant at emergence time. Our study also confirms the importance of water, not only for dry Mediterranean systems but also in mesic habitats (see also Carson & Pickett 1990; Stevens et al. 2006), at least with respect to emergence time.

At recruitment time, the initial effect of light restriction still persisted on annual plant density. In addition, water availability determined the density of perennial plants. However, composition of recruited adults was not affected by any of our regeneration scenarios, but by some biotic variables. It could be argued that this lack of effect may be due to the fact that our experimental resource levels are not limiting. However, we discard this explanation because in previous work we detected a significant effect of light and N manipulation on species biomass (Luzuriaga et al. 2002), which is usually considered a good indicator of ecosystem function (Tilman 1982). Furthermore, the main forces structuring this early succession community were not due to microhabitat segregation caused by differences in resource availability (i.e. Chapin & Shaver 1985; Tilman 1987; Carson & Pickett 1990), but most probably depend on complex biotic interactions among emerging and neighbour plants (see below).

Soil physico-chemical characteristics did not affect emergence or net recruitment. We had found that some of these soil variables (such as magnesium level) could explain differences in the primary productivity between plots (Luzuriaga et al. 2002). However, this is not strong enough to set differences in species composition that would be probably obscured by other environmental factors.

### *How do biotic features shape species composition?*

Seed bank species density may affect seedling emergence positively (Linhart & Pickett 1973; Gutterman 1993), negatively (Speer & Tupper 1975; Froud-Williams & Ferris 1987) or even may not exert a major influence at all (Baskin & Baskin 1998; Fenner 2000; Rebollo et al. 2001). Our findings concur within the latter studies, i.e. total seed density did not affect seedling emergence. This result needs to be taken with caution because of the steep decay in seed density following our soil ploughing treatment (Luzuriaga et al. 2005). Nevertheless, the presence of *Cerastium* seeds in the soil had a significant effect on the seedling community composition in summer although the mechanism is not clear. Interference among germinating seeds due to physiological processes (Knap 1954; Mack & Harper 1977) or to allelochemical products (Wurzburger & Leshem 1969; Dyer et al. 2000) have been suggested. However, we think a physical explanation could be a better solution. Germination of *Cerastium* spp. might favour emergence of other species by breaking the hard soil crust formed under summer drought conditions (pers. obs.), but we cannot rule out spurious effects due to other correlated factors not measured in this study.

Several studies detected a negative effect of neighbours on germination and seedling survival (Silvertown 1980; Goldberg et al. 1999; Rebollo et al. 2001). Contrarily others found a facilitative effect of neighbour plants, mainly in stressful conditions (Bertness & Callaway 1994; Holmgren et al. 1997). However, few studies have explored if such effects are consistent among life history stages (Howard & Goldberg 2001; Goldberg et al. 2001). Our results suggest that interactions at emergence and net recruitment stages in natural conditions vary between cohorts in intensity and also in the key plant species that determined species abundance in each stage. We must highlight that in our study – unlike the above mentioned studies – seedling emergence and recruitment did not depend on the reproductive performance of these neighbours because they belong to previous cohorts.

Neighbour effects on composition were more intense for adult recruitment than for seedling emergence. Composition in the emergence time was exclusively affected by grass cover (almost 16% of the variance explained). In contrast, composition of adult recruitment was affected not only by grasses but also by cover of *Picris echioides* (up to 35.6% of the variability explained). Early effect of grasses on emergence may be because these plants quickly occupied the available space thanks to the vegetative propagule bank they originated from. Later in the succession, *Picris echioides* also became a key species in the community and its canopy dominant.

These results suggest that plant canopy – through



light amount and quality – determined seedling species emerged and that these initial differences were also exacerbated and finally reflected in the species composition of recruited plants. Conversely, experimental light restriction did not exert any significant effect on adult species composition. This suggests that the differential effect of light on species abundance was probably based on quality rather than on quantity. Together with the effect of species cover, we also detected an effect of species densities. Neighbour density did not affect plant emergence but explained a large proportion of the variability in the composition at the recruitment time. This suggests that along plant community development, competition was becoming more important in determining plant community composition.

*Are effects of abiotic and biotic factors on emergence reflected into the adult recruitment stage?*

Many studies have detected that effects on plant emergence were finally translated to the adult recruitment stage (Suding & Goldberg 1999; Rebollo et al. 2001), while others have reported that effects of environmental factors can vary among demographic stages (Battaglia et al. 2000). In our study we detected contrasting results. For instance, the beneficial effect of light restriction on annual seedling density at emergence was also passed on to the recruitment stage. Nevertheless, the effect of our regeneration scenarios on species composition at emergence was undetectable in the recruitment time. This suggests that the effect of factors that controlled seedling density extended along community dynamics whereas the species hierarchies established at the emergence time based on resource availability disappeared along plant community development or at least they were masked by other stronger forces. These results contrast with other studies that detected an early establishment of competitive hierarchies (Keddy & Shipley 1989; Howard & Goldberg 2001).

We have also observed the opposite effect, i.e. no effect of a key resource at emergence but a significant effect on adult recruitment. Although it was spring, shade did not affect annual seedling emergence or survival (Luzuriaga & Escudero unpubl.), it reduced net recruitment of annuals. Similarly, irrigation did not affect perennial emergence or survival (unpubl. results) but it enhanced adult recruitment in terms of density. In addition, the effect of neighbours on species composition became stronger later in succession. This may be due to the fact that net recruitment was the result of joint effects of several processes along succession and thus, slight undetectable differences along succession may have resulted in significant differences in net recruitment in terms of density.

*How does each cohort respond to the abiotic and biotic environmental conditions measured?*

Emergence of the spring cohort did not suffer any effects of the biotic and abiotic variables, either in terms of density or species composition. This result was probably related to the benign conditions for plant establishment of this season, i.e. following ploughing neither water nor light availability were limiting factors and, in addition, at this first stage of succession, competition was probably negligible due to the low plant density. Nevertheless, annual adult recruitment of the spring cohort suffered a significant decrease under shaded conditions. Thus, although the requirements for seedling emergence were fulfilled in the first stage of succession even in experimentally light restricted conditions, ultimately adult recruitment was highly controlled by light availability conditions.

Shade positively affected total emergence in summer and negatively in autumn. The positive effect of shade in summer was probably due to improvement of soil water conditions under meshes. These results suggest that the limiting factor for emergence shifted from water in summer to light in autumn. As mentioned above, in the summer cohort we also detected a significant effect of neighbour species on community species composition. This may be related to a facilitative effect of canopies on seedling performance through water amelioration (Bertness & Hacker 1994; Callaway 1995; Greenlee & Callaway 1996; Callaway & Walker 1997).

*Conclusions*

Regeneration scenarios exerted contrasting and multilevel effects on the development of our early succession community. The effects of these conditions varied along community development on some community level attributes (density, richness and species composition) but also on different community stages (emergence time and recruitment). Although at the early recruitment stage no effect of resource availability on species composition was detected, our results emphasize the importance of differences in regeneration conditions in plant community development and the relevance of considering different life-stages. In the course of succession, biotic variables acquired more importance in determining species-specific recruitments than experimental abiotic variables. Furthermore, our results suggest the importance of neighbours during community development as the main determinants of community species composition. In conclusion, there is still a long way to go to improve our understanding of plant community response to environmental conditions in order to apply integral management strategies at the community level.

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*For App. 1, see below (online version)*  
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**App. 1.** Main species present in the early succession community. Mean plant cover values (%) after disturbance (July). Mean seed densities (number/dm<sup>3</sup>) previous (SB\_pre) and after (SB\_post) disturbance. \* = cover value < 1%. + = seed number < 0.5 seeds dm<sup>-3</sup>.

Species	Abbr.	Family	Life form	Veg cover	SB_pre	SB_post
<i>Agropyron repens</i>	<i>Agro</i>	<i>Gramineae</i>	Geophyte	30.8	0	0
<i>Arrhenatherum elatius</i> var. <i>bulbosum</i>	<i>Arrh</i>	<i>Gramineae</i>	Geophyte	0	0	
<i>Anagallis arvensis</i>	<i>Anaarv</i>	<i>Primulaceae</i>	Annual	*	1.4	1.8
<i>Avena</i> spp.	<i>Avena</i>	<i>Gramineae</i>	Annual	*	0	0
<i>Cerastium</i> spp.	<i>Cerspp</i>	<i>Caryophyllaceae</i>	Annual	*	7.8	+
<i>Cirsium arvense</i>	<i>Cirarv</i>	<i>Compositae</i>	Geophyte	6.7	+	+
<i>Convolvulus arvensis</i>	<i>Conarv</i>	<i>Convolvulaceae</i>	Geophyte	*	+	+
<i>Crepis vesicaria</i>	<i>Creves</i>	<i>Compositae</i>	Biennial	3.1	3.3	+
<i>Juncus bufonius</i>	<i>Junbuf</i>	<i>Juncaceae</i>	Annual	*	7.1	7.3
<i>Kickxia spuria</i>	<i>Kicspu</i>	<i>Scrophulariaceae</i>	Annual	*	+	+
<i>Lolium perenne</i>	<i>Lolper</i>	<i>Gramineae</i>	Geophyte	*	38.7	5.9
<i>Medicago lupulina</i>	<i>Medlup</i>	<i>Leguminosae</i>	Annual	9.4	4.9	+
<i>Mercurialis annua</i>	<i>Merann</i>	<i>Euphorbiaceae</i>	Annual	*	+	1.9
<i>Picris echioides</i>	<i>Picech</i>	<i>Compositae</i>	Biennial	13.5	39.4	+
<i>Rumex crispus</i>	<i>Rumcri</i>	<i>Polygonaceae</i>	Geophyte	*	7.6	+
<i>Sagina sabuletorum</i>	<i>Sagsab</i>	<i>Caryophyllaceae</i>	Annual	*	0.7	2.1
<i>Sinapis arvensis</i>	<i>Sinarv</i>	<i>Cruciferae</i>	Annual	8.3	4.7	+
<i>Verbena officinalis</i>	<i>Verboff</i>	<i>Verbenaceae</i>	Annual	*	4.7	4.6