WEED COLONIZATION OF EXPERIMENTAL GAPS IN THE CANOPY OF A WHEAT CROP[1]

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ABSTRACT - Gaps of different sizes were opened in the canopy of a wheat crop by removing all above ground vegetation in August and October. Half of the gaps opened in August were reopened in October. Composition of the weed community and abundance of individual species were measured in September and in November just before crop harvest. In September there were very little differences between treatments, and in November the most important differences were due to time of gap opening but not between gaps of different sizes. Most weed species are synchronous with the crop and are well adapted to coexist with it, so there is a marked negative effect of late opening of gaps on most of them. Gaps have a positive effect on weeds asynchronous with the crop and perhaps on rarities, i.e. species which are neither constant nor abundant.

Index terms: disturbance, gaps, weed colonization, weed community, wheat crop.

COLONIZAÇÃO DE ERVAS DANINHAS NAS CLAREIRAS EXPERIMENTAIS ABERTAS NA PARTE AÉREA DO TRIGAL

RESUMO - Foram abertas áreas de diversos tamanhos, na parte aérea do trigal, eliminando-se a vegetação do solo, em agosto e outubro. A metade das áreas abertas em agosto foram abertas novamente em outubro. A composição da comunidade de ervas daninhas e a grande quantidade de espécies individuais foram medidas em setembro e novembro antes da colheita. Em setembro não foram observadas diferenças entre tratamentos; em novembro, as diferenças mais importantes deveram-se à abertura das áreas, mas não entre áreas de tamanhos diferentes. A maioria das espécies de ervas daninhas coincidem com a cultura e são bem adaptadas para conviver com ela, existindo, assim, um efeito negativo de abertura tardia das áreas, na maioria delas. As áreas abertas têm um efeito positivo na sincronização das ervas daninhas com a cultura e talvez com espécies que não são constantes nem abundantes.

Termos para indexação: áreas abertas, comunidade de ervas daninhas.

INTRODUCTION

The development of a strong dominance often depresses floristic richness and diversity of plant communities (Perino & Risser 1972, Bazzaz 1975, Houssard et al. 1980, During & Willems 1984) through allelopathy, nutrient competition, shading or any other interference mechanism. Seedling establisment often fails in close vegetation, though seeds may germinate, but seedlings may not make a headway unless there is a definite gap in swards (Miles 1972, Fenner 1978, Gross 1980, Booth 1981) and this holds true in forests as well (Denslow 1980b, Whitmore 1982, 1983). Different species colonize gaps of different sizes and types or open at different times (Gross & Werner 1982, Denslow 1980a, Goldberg & Werner 1983, Verkaar et al. 1983, Hillier 1984) both in herbaceous and woody communities.

When gaps are open in the canopy, environmental conditions change within it as light impinges the soil, and the opened space is usually associated with changes in the availability of other resources (Denslow 1985); so they may become safe sites (Harper 1977) for seedling establishment. Therefore gaps may be an important part of the regeneration niche

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(Grubb 1977) of certain species. In the last few years a wide literature has cropped up about gap dynamics and floristic diversity of natural or spontaneous plant communities which can not be reviewed at large here, and lately Goldberg (1987) analysed seedling colonization of experimental gaps in old-field communities. However, as far as we know no attempt has been made to study the effect of gap opening in crops.

In crops a strong dominance is inforced by sowing the crop species, and gaps are opened spontaneously at an early stage by failures in sowing or germination of the seeds, and at later stages by localized herbivory, parasitism or disease. In this paper we report the spontaneous colonization of experimental gaps in a wheat crop and the behaviour of different species in relation to gap size and time of gap opening.

MATERIALS AND METHODS

Experimental lay out

A wheat crop cv. Marcos Juarez INTA was sown at the beginning of August 1986 at INTA Oliveros Research Station (Lat. 32°33'S). Previous to the wheat crop there was a soybean crop in the same field. Ten 7.5 x 3 m blocks were laid out in two rows of five blocks each from S to N; and each one was divided in ten 1.5 x 1.5 m quadrats for the ten treatments which were randomly distributed within each block. At the center of each quadrat gaps of different size were created at the beginning of August immediately after the emergence of the crop or at the beginning of October. Gaps were created by removing all wheat and weed plants with a hoe taking care of not disturbing the soil. Half the gaps opened in August were denudated again in October. Therefore the ten treatments were as follows:

1. Control. No vegetation removed (sample 30 x 60 cm).
2. 30 x 60 cm gap. Vegetation removed in August.
3. 45 x 75 cm gap.
4. 60 x 90 cm gap.
5. 30 x 60 cm gap. Vegetation removed in October.
6. 45 x 75 cm gap.
7. 60 x 90 cm gap.
8. 30 x 60 cm gap. Vegetation removed in August and in October.
9. 45 x 75 cm gap.
10. 60 x 90 cm gap.

Initial seed bank was estimated with the wet sieving technique (Leguizamón 1983) using two soil samples from each block. Recruitment percentage was estimated with average abundance in controls and early open gaps at the time when the species were more abundant.

The number of individuals of different species were counted in each gap and the controls in the middle of September and at the end of November, just before the crop harvest. Data were standarized to obtain the number of individuals per m^2.

Nomenclature follows Cabrera (1963, 1965a, 1965b, 1967, 1968, 1970).

Data analysis

Data were analysed considering first each treatment as a distinot weed community, and then the effect of treatments on the abundance of each relevant species was investigated.

In the first case the constancy of all species (i.e. the amount of quadrats where they were present) was calculated in each treatment and divided in five constancy classes (I, present in 1 or 2 quadrats, . . .V, present in 9 or all quadrats) and condensed constancy tables were constructed for booth countings (Mueller-Dombois & Ellenberg 1974). After the final counting quadrats were ordered by principal component analysis (PCA) with Orlóci & Kenkel (1985) programs using a covariance matrix.

In the second case, abundance differences among treatments of the relevant species were analysed with non-parametric ANOVA test (Friedman 1937) and rank sum multiple comparisons (McDonald & Thompson 1967, Hollander & Wolfe 1973). These methods were used to avoid the assumption of normality, as within treatments species abundance variability was very high, so data could not be normalized by any transformation. However, non parametric methods are not very powerful. Fiducial limits used were $p = 0.05$; $p = 0.10$ and $p = 0.20$.

RESULTS

Seed bank and recruitment

The average seed bank composition as well as recruitment % are given in Table 1. The variability of the seed bank is very high, and there are large differences on its composition at very short distances. But in any case there is an overwhelming abundance of *Stellaria* media and *Lamium amplexioaule* seeds. In general recruitment % from seed bank is within the normal range, however, those of *Silene gallica* and *Sorghum halepense* have no sense unless they were from immigrants during the crop season which is not the case. These two very high % may be correlated with the great variability of the seed bank.

Treatments' weed communities

Table 2 is the condensed constancy table for the first counting (September). Twenty five species (26 if *Sorghum halepense* from seeds and rhizomes sprouts are considered as two different populations) were recorded in all treatments, and there is a slight increase in the number of species when the gap size increases; however, the differences are due to the presence of rarities (i.e. species with very low constancy) and the number of species/area effect can not be ruled out either. According to their constancy, species can be divided in five groups:

1. highly constant throughout; 2. with only *Polygonum aviculare* which is less constant in the biggest gap; 3. less constant in controls than in gaps; 4. with an erratic behaviour, though *Sorghum halepense* sprouts from rhizomes is a rarity in all treatments but the biggest gap; and 5. rarities, i.e. species with very low constancy throughout. A constant species is not necessarily an abundant one. *Lamium amplexicaule* and *Stellaria media*

TABLE 1. Seed bank composition and recruitment.

Species	Seeds . m^{-2} X	Seeds . m^{-2} Gu-1	Recruitment %
1. *Stellaria media*	3893	3000	3.6
2. *Lamium amplexicaule*	1354	2290	16.1
3. *Anagallis arvensis*	448	270	25.4
4. *Capsella bursa-pastoris*	219	210	17.6
5. *Verbena* sp.	219	170	-
6. *Stachys arvensis*	169	30	3.9
7. *Veronica persica*	80	131	5.8
8. *Sisymbrium* sp.	75	84	-
9. *Polygonum aviculare*	64	96	10.0
10. *Amaranthus hybridus*	34	65	-
11. *Medicago lupulina*	30	61	25.6
12. *Coronopus didymus*	22	50	43.1
13. *Silene gallica*	22	90	133.2
14. *Nicotiana* sp.	20	90	-
15. *Chenopodium* sp.	10	36	-
16. *Triodanis biflora*	10	5	-
17. *Sorghum halepense*	4	19	396.7
18. *Bowlesa incana*	2	19	-

TABLE 2. Condensed constancy table - September.

Species	Treatment - Gap size: Control	30x60	45x60	60x90	
1. *Stellaria media*	V	V	V	V	1
2. *Lamium amplexicaule*	V	V	V	V	
3. *Polygonum aviculare*	IV	IV	IV	III	2
4. *Capsella bursa-pastoris*	IV	V	V	V	3
5. *Anthemis cotula*	IV	V	V	V	
6. *Avena fatua*	IV	V	V	V	
7. *Coronopus didymus*	III	IV	V	IV	
8. *Cyperus rotundus*	II	IV	V	V	
9. *Polygonum convolvulus*	II	III	III	III	
10. *Anagallis arvensis*	III	III	IV	IV	
11. *Glycine max*	II	II	III	III	
12. *Sorghum halepense* (Seed)	III	III	IV	V	
13. *Veronica persica*	I	IV	II	III	
14. *Tagetes minuta*	I	II	III	II	
15. *Gamochaeta* sp.	II	III	II	III	4
16. *Medicago lupulina*	IV	III	IV	V	
17. *Sorghum halepense* (Rhizome)	I	I	I	III	
18. *Ammi majus*	I			I	5
19. *Lolium multiflorum*		I		II	
20. *Galinsoga* sp.		I			
21. *Wedelia glauca*			I	I	
22. *Sonchus* sp.			I	I	
23. *Non identify*			I	I	
24. *Carduus acanthoides*			I		
25. *Digitaria sanguinalis*				I	
26. *Chenopodium album*				I	
Total number of species	18	19	21	24	

were the dominant species of the weed community, i.e. the more abundant ones throughout as well as constant. *Capsella bursa-pastoris, Cyperus rotundus* and *Anagallis arvensis* were the only other fairly abundant species. All other species, even constant ones were sparse species. The 17 populations in groups 1, 2, 3 and 4 build up the early weed community of the crop, and there is not substancial difference between treatments in their floristical composition.

Table 3 is the condensed constancy table for the second counting (November). Forty-two species (or populations) were recorded in all treatments, and slight differences in the number of species among treatments are produced by rarities. *Coronopus didymus* and *Tagetes minuta* present in September were absent altogether in November, and *Lamium amplexicaule* and even more *Stellaria media* were less constant in November than in September. According to their constancy species can be grouped in seven sets: 1. highly constant throughout, i.e. ubicuous species; 2. less constant than those in group 1, but evenly distributed among treatments; 3. more constant in controls and early opened gaps; 4. more constant in early opened gaps; 5. more constant in late opened gaps; 6. rarities evenly distributed among treatments; and 7. rarities restricted to one or at most two treatments. In October, *Anagallis arvensis* and *Cyperus rotundus* became the dominant and subdominant species. Most *Stellaria media* individuals had completed their cycle and died out, and *Lamium amplexicaule* though still abundant its density was far lower than in September. Differences among treatments are more evident at the end of the experiment than in September, but time of gap opening rather than gap size has more influence on the floristic composition of the weed community. The gap size has an effect only on the presence of rarities.

When the whole set of data collected in November was analysed with PCA, axes I, II and III accounted for 73.33%, 18.56% and 2.40% of the total variance respectively, therefore, the two first components are the only relevant ones. Fig. 1 is the quadrats scatter diagram in the plane of axes I and II. Controls, i.e. non-disturbed quadrats are pulled to the negative side of axis I, while most other qudrats, i.e. gap quadrats tend to be pulled to the positive side of this axis. Early open gaps quadrats are pulled to the positive side of axis II as well as controls, while those with gaps opened or reopened in October are at its negative side, but those disturbed twice tend to fall to the bottom of the diagram. Though it can not be shown in the diagram, quadrats on the same block tend to be clustered together, those in blocks 10, 5, 9 and 4, that were at one end of the field, are towards the positive side of axis I, and those in blocks 6, 7, and 1 that were at the other end of the field are towards the negative side of this axis. Therefore, again differences in the weed community of any treatment seem to be more related to the time and type of disturbance than to the size of gaps; and also there is a field position effect which may be the result of the seed bank variability.

Individual response of species

Though individual species abundance are different among treatments both in September and November; in the first counting Friedman's (1937)) ANOVA test shows that hardly any of them are significant.

First, those species which complete their cycle early, and become meaningless in November like *Stellaria media,* or disappear altogether at the end of the experiment like *Coronopus didynus* and *Tagetes minuta* will be considered. On Fig. 2 the average amount of individuals per m^2 in controls and gaps of different sizes in the first counting (September) of two of these species is shown. There are significantly less individuals per m^2 of *Stellaria media* in gaps of any size than in controls, but although it seems to be less abundant, the larger the gap size, differences between gaps of different sizes are not signifi-

TABLE 3. Condensed constancy table - November.

Species	Treatments										
	1	2	3	4	5	6	7	8	9	10	
1. *Anagallis arvensis*	V	V	V	V	V	V	V	V	V	V	1
2. *Cyperus rotundus*	V	V	V	IV	V	V	V	IV	V	V	
3. *Sorghum halepense* (Seed)	IV	IV	V	V	V	V	V	V	V	V	
4. *Lamium amplexicaule*	III	IV	IV	V	IV	IV	V	III	IV	IV	
5. *Bidens subalternans*	III	III	III	II	I	III	II	II	II	I	2
6. *Sorghum halepense* (Rhizome)	III	I	II	II	II	I	II	I	I	III	
7. *Veronica persica*	II	I	II	I	I	III	I	I	II	III	
8. *Stachys arvensis*	II	I	I	I	II	II	I	II	I	I	
9. *Wedelia glauca*	I		I	I	I	II	I	I	I	I	
10. *Sonchus* sp.	I	I	II	III	I	I	I	I	I		
11. *Anthemis cotula*	IV	IV	V	V	II	II	II	II	III	IV	3
12. *Silene gallica*	V	IV	V	V	II	III	III	III	IV	IV	
13. *Glycine max*	II	II	IV	III		I	I		I		
14. *Polygonum aviculare*	III	II	IV	IV	I	II	III	I	II	I	
15. *Polygonum convolvulus*	II	II	I	III	I	I	I	I		I	
16. *Gamochaeta* sp.	III	V	IV	III	III	IV	III	II	IV	IV	4
17. *Avena fatua*	II	IV	V	IV	I	I	I	I	II	II	
18. *Medicago lupulina*	II	III	IV	V	I	I	III	I	II	II	
19. *Linaria texana*		I	II	I							
20. *Capsella bursa-pastoris*	I	II	II	II	IV	IV	IV	I	III	III	5
21. *Portulaca oleracea*			I	I	III	IV	IV	II	II	III	
22. *Amaranthus hybridus*					II	II	I				
23. *Digitaria sanguinalis*		I	II	I	I	I	I		I	II	6
24. *Cynodon dactylon*	I	I	I				I		I	I	
25. *Ammi majus*	I			I	I						
26. *Euphorbia* sp.		I				I		I			
27. *Stellaria media*	I				III		I		I		
28. *Chenopodium almum*	I						I				7
29. *Echinochloa colonum*	I										
30. *Carduus acanthoides*		I									
31. *Non identify* I		II		I							
32. *Spergularia* sp.			I	I							
33. *Triodanis biflora*				I							
34. *Oxalis* sp.				I							
35. *Anthirrimum corontium*				I							
36. *Unknown labiate*				I							
37. *Panicum bergii*				I							
38. *Non identify* II				I							
39. *Euphorbia serpens*				I	I						
40. *Non identify* III						I					
41. *Non identify* IV							I				
42. *Non identify* V										I	
Total number of species	24	25	24	32	24	24	26	21	23	23	

cant. On the other hand, differences in the abundance of *Coronopus didymus* between treatments are not significant; and though *Tagetes minuta* is less constant in the control than in gaps, the differences in the amount of individuals between treatments are even less significant than in the case of *Coronopus didymus*.

Then, the species that accompany the crop through the whole cycle will be studied. These species can be divided in four groups: 1. species more abundant in controls than in gaps; 2. more abundant in gaps of any type and size; 3. more abundant in early open gaps; and 4. more abundant in late open gaps.

The species of the first group are *Anagallis*

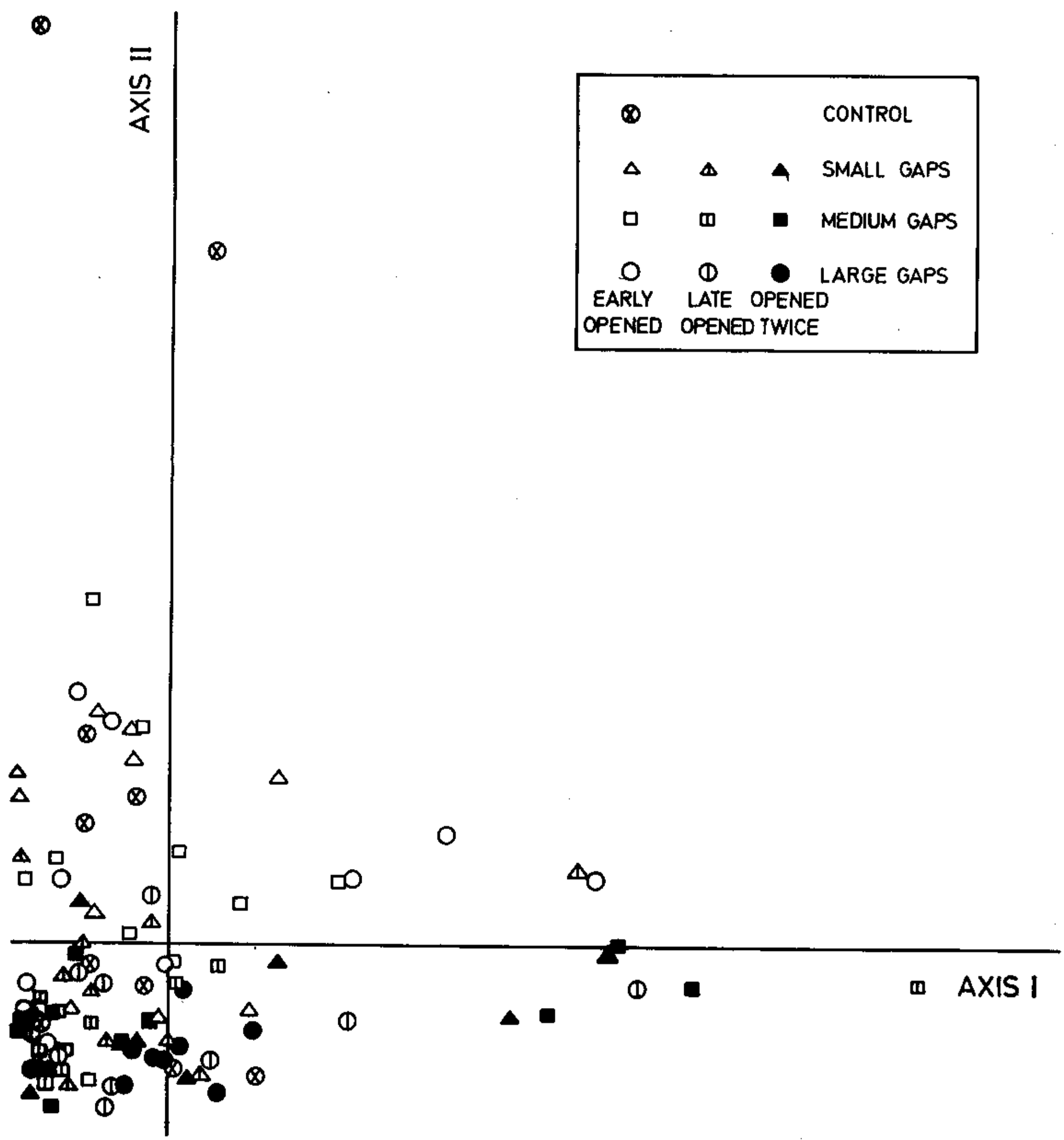

FIG. 1. PAC quadrats soatter diagram for axes I and II.

arvensis, *Avena fatua*, *Lamium amplexicaule* and *Polygonum aviculare* (Fig. 3). *Anagallis arvensis* and *Lamium amplexicaule* are constant in all treatments, but while the former's constancy and abundance increase from September to November, the latter's constancy and abundance decrease towards the end of the experiment. The constancy of *Avena fatua* and *Polygonum aviculare* also decrease from September to November, and at the end of the experiment the first one is far more constant in

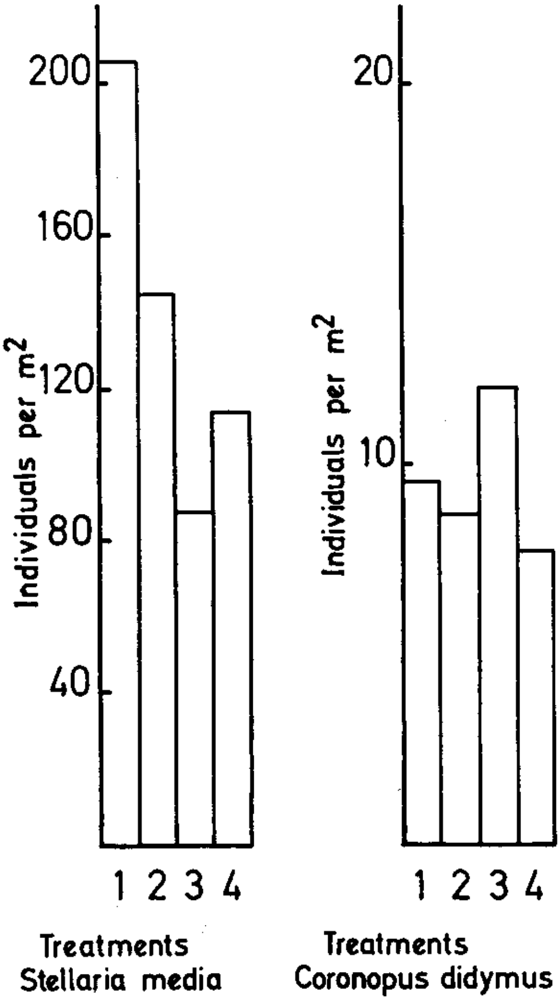

FIG. 2. Average number of individuals/m² in different treatments in September of the early cycle species. (Treatment 2=2+8; 3=3+9 and 4=4+10).

early open gaps than elsewhere and the second one appears to be more constant in early open gaps as well as in controls than in late open or reopen gaps. In September there are no significant differences between treatments in the abundance of any of these four species, as well as in November between controls and early open gaps. But in November all these species are more abundant in controls and early open gaps than in late open ones. However, differences are significant in the case of *Anagallis arvensis*, especially between the smallest early open gap (tr. 2 and 3) and the largest late open or reopen gaps (tr. 6, 7, 9 and 10) where most differences are highly significant (more than $p = 0.05$); and in *Avena fatua* between early open gaps (especially tr. 3) and late open or reopen ones. In the other two species the most important differences between treatments have a significance lower than $p = 0.20$).

The only species that seems to be more abundant in gaps of any type and size in *Cyperus rotundus* (Fig. 4), a species always constant, and its constancy as well as its abundance increase towards the end of the experiment. However, differences between treatments are not significant at all, but there is not a depresive effect of late opening or reopening of gaps on the abundance of the species as in the previous four species.

Anthemis cotula and *Medicago lupulina* are the species that are more abundant in early open gaps than elsewhere (Fig. 5). The first species is highly constant in controls and early opened gaps of any size, and remains so by the end of the experiment, but is not constant and even less abundant in late open or reopen gaps, while *Medicago lupulina* that is fairly constant throughout in September, by the end of the experiment remains fairly constant only in early open gaps. *Anthemis cotula* abundance is not significanttly different between controls and early open gaps both in September and November, but at the end of the experiment it is significantly more abundant in early open gaps especially in the largest one (tr. 4), where differences in abundance with late open

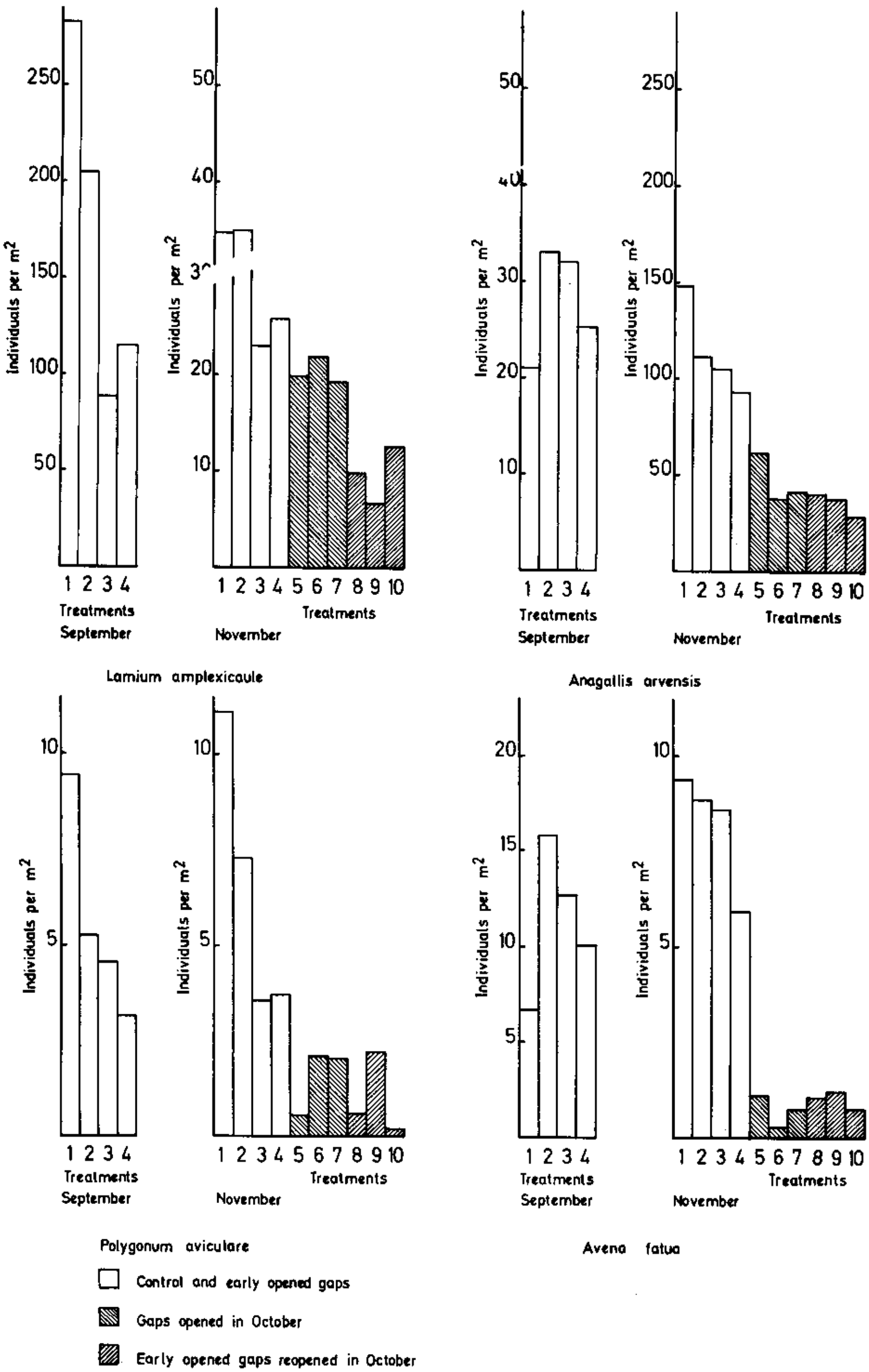

FIG. 3. Average number of individuals/m² in different treatments in September (Treatment 2=2+8; 3=3+9 and 4=4+1) and November of species that tend to be more abundant in control than in gaps.

gaps (save with tr. 10) are always highly significant (p = 0.05). Differences between treatments are less important in *Medicago lupulina* that is significantly more abundant only in the largest early opened gap (tr. 4) than in controls or late open gaps.

Capsella bursa-pastoris and *Sorghum halepense* sprout from seeds are more abundant in late open gaps than elsewhere (Fig. 6). However, differences between treatments are not very important, as in the first species only in the largest late open gap (tr. 7) is significantly more abundant than in some other treatments and the most important difference between treatments in *Sorghum halepense* abundance are always less significant than p = 0.20.

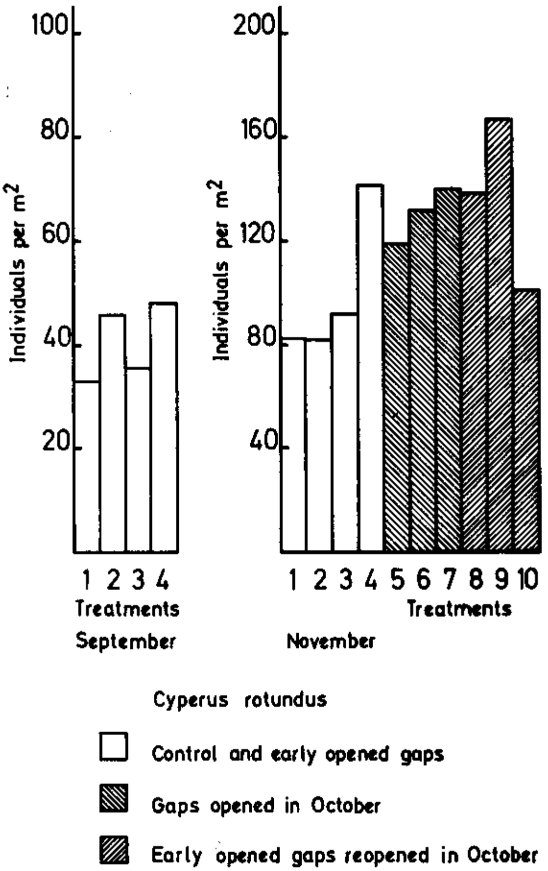

FIG. 4. Average number of individuals/m² in different treatments in September (Treatment 2=2+8; 3=3+9 and 4=4+10) and November of species that tend to be more abundant in gaps of any type and size than in controls.

Finally, the most relevant species that do not appear in September will be considered (Fig. 7). *Bidens subalternans* is fairly constant throughout, though it is slightly more constant in controls and some early open gaps, but abundance differences between treatments are not significant at all. *Silene gallica* is more constant as well as significantly more abundant in controls and early open gaps than in late open gaps, but the differences between controls or early open gaps and gaps reopened in October are far less significant or not significant at all. *Portulaca oleracea* is almost absent from early open gaps and absent altogether from controls, therefore it is significantly more abundant in late open gaps, especially the largest one; nevertheless there seems to be a slightly depressive effect of twice disturbing the site.

DISCUSSION

Principal component analysis is widely used in community ecology research but so far it has not been used in experimental approaches. It is not useful for testing hypothesis, but it shows quite clearly the structure of data sets involving too many species with rather variable populations, which otherwise can not be visualized. In this experiment, in spite of its limitations, it has proved to be a quite promising method for experimental approaches in weed research. Weed populations commonly have a very high internal variability, so statistical methods based on an assumption of normality become useless, therefore non-parametric methods should be used, and usually they are not very powerful and fail to detect differences which are really significant, therefore fiducial limits must be lower than those used when less variable populations are analysed with parametric statistical methods.

Variability of the seed bank is very high, which is usually the case of weed seed banks of crops, therefore any statistical test of these data has very little valididty (Chauvel et al. 1989) and the only solid conclusion that can be drawn from them is that abundant weeds in any treatment have large seed banks.

The results presented in this paper show very little differences between treatments in September, and most differences appear later on the crop cycle. This is not surprising, as at this time crop has not yet developed a full canopy, therefore treatments and controls are not very different environments.

The weed community analysis, PCA and the individual behaviour of the most relevant species show that gap size has little, if any, effect on the floristic composition and relative abundance of the species, but time of gap creation or amount of disturbance is far more important. Also the position in the field has an effect on the weed composition of quadrats, and this should be accounted for the variability of the seed bank. Gap size may have an effect on the presence of certain rarities and almost nothing else, but this can be a species number/area effect, or at least this can not be ruled out. All this comes as a result of that weed colonization of a spring crop is dependent on propagules bank composition and not

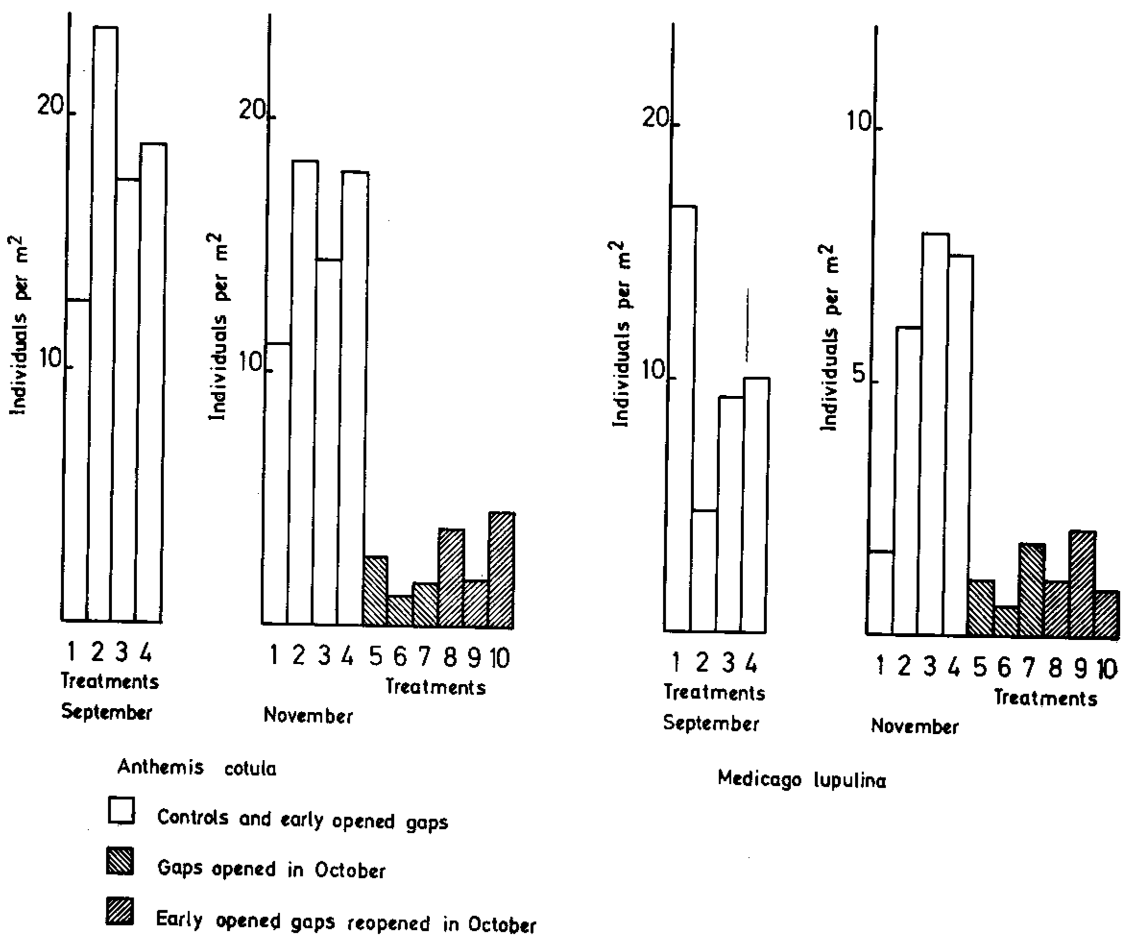

FIG. 5. Average number of individuals/m² in different treatments in September (Treatment 2=2+8; 3=3+9 and 4=4+10) and November of species more abundant in early opened gaps.

on immigration during its cycle and most processes leading to the invasion of the crop are already triggered at its onset.

The most important species of the weed community, i.e. frequent and abundant ones, *Stellaria media, Lamium amplexicaule, Anagallis arvenis* and *Cyperus rotundus* have a large propagules reservoir in the seed bank or as tubers like the last one. These species are well adapted to the crop conditions so they are indifferent to gap creation in the crop canopy or they are in better conditions inside the crop. Their regeneration niche is the plantless seed bed. The same applies to most other species but few ones, especially the most rare ones.

The weed community cycle is synchronous with the crop cycle, though some species like *Stellaria media* and *Coronopus didymus* complete their cycle earlier than others like *Anagallis arvensis;* and this explains the negative effect on most species of late open gaps and even more of late reopen ones. When a gap was created or reopened late all vegetation was removed, and colonization was prevented by the possible exhaustion or impoverishment of the recruitable segment of the seed bank, or due to the fact that several species germinate simultaneously with the crop and not later on. Late gap creation may have a positive effect on species that germinate late, and this seems

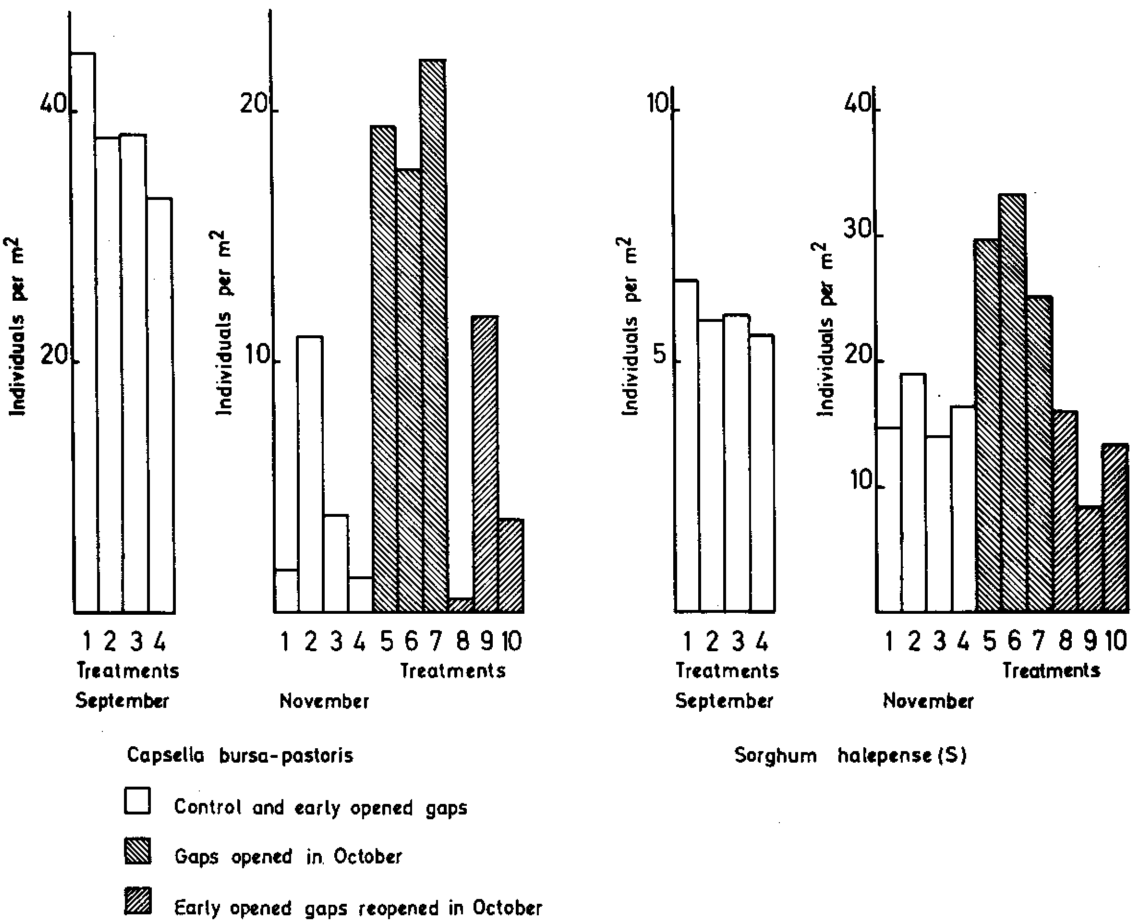

FIG. 6. Average number of individuals/m² in different treatments in September (Treatment 2=2+8; 3=3+9 and 4=4+10) and November of species more abundant in late opened gaps.

to be the case of *Portulaca oleracea* that is a Summer crop weed; however this is not the case of *Silene gallica* and *Bidens subalternans* that are late germination weeds. These last two species appear to be members of the weed community, and although germinate later than other species may have done so and impoverished their seed banks before late gaps were created. *Portulaca oleracea* seems to need and open seed bed of Summer crops to germinate and fail to colonize early open gaps which although deprived of a wheat canopy, have a close canopy of *Anagallis arvensis* and other weeds. *Capsella bursa-pastoris* may escape the negative effect of late open gaps with a second germination wave, and certaintly this is the case of *Sorghum halepense*, which is a preferential weed of Summer crops and has late germination waves (Leguizamón 1983). *Cyperus rotundus* sprouts from tubers, and when above ground vegetation is removed, the tubers remain in the soil and are able to resprout again, therefore late gap creation has not a negative effect on this weed.

These results do not contrast with what happens in natural communities. A steady-state natural community has a matrix of long lived important species (Grubb et al. 1982)

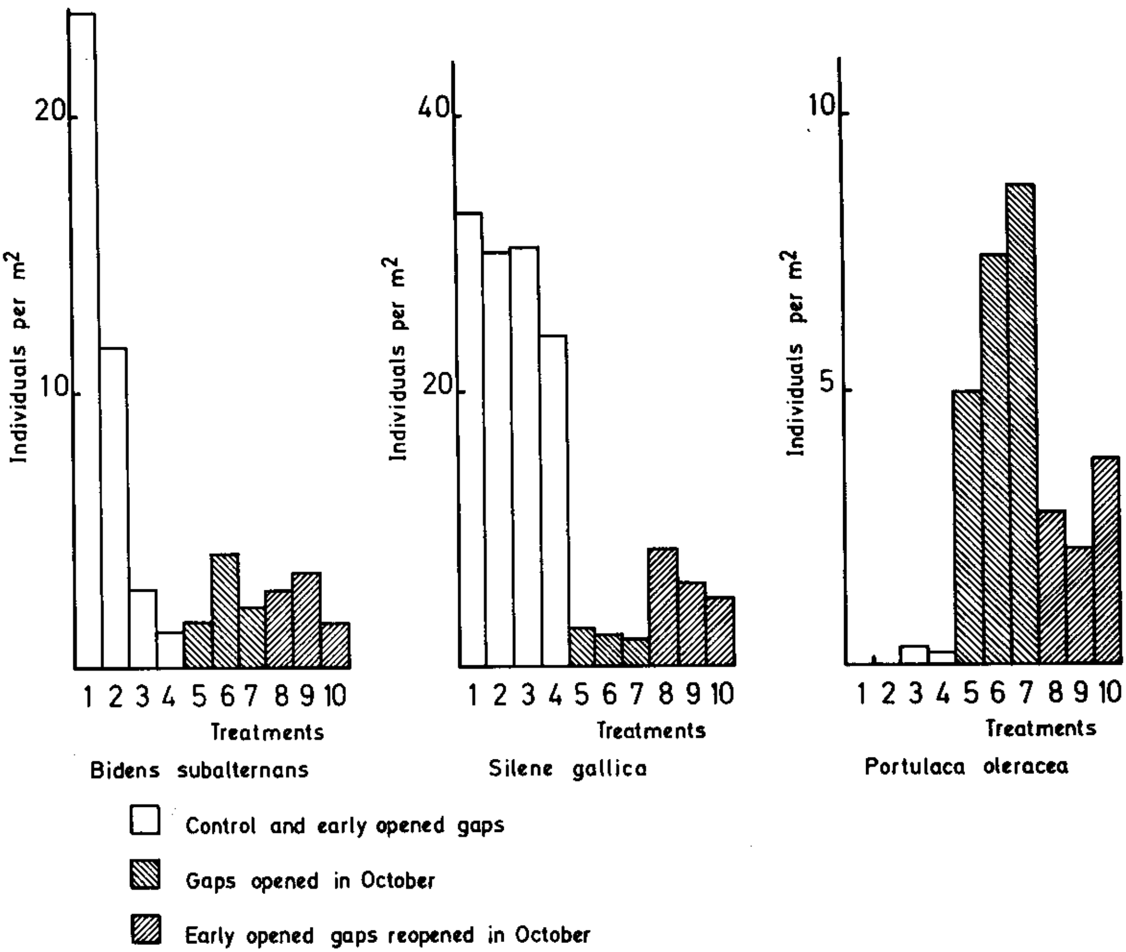

FIG. 7. Average number of individuals/m^2 in different treatments in November of species that do not appear in September.

and a fairly large amount of short lived rare species which thrive in microsites within the matrix (Grubb 1986). Gaps in the canopy of the matrix provide microsites for certain species. In a crop ecosystem another steady-state develops, where the plant community is formed by seasonal guilds with a matrix of short lived therophytes, the crop and synchroncus weeds, and a few geophytes, all well adapted to live together and selected by the disturbance (cultivation) regime.

Gaps open in the canopy of this crop-weed community could have only an effect on the regeneration of crop asynchronous species or on rarities, which are also short lived. Rarities of natural steady-state communities need microsites of different characteristics for emergence, survival and growth to maturity, and there are threshold gap sizes which are species-specific (Goldberg & Werner 1983, McConnaughay & Bazzaz 1987) but quite often far smaller gaps than the experimental ones were per forzza already created by row separation. Therefore sparse species of the weed community may have had their threshold size gaps and escape the experimental analysis.

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