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A comparison of the growth patterns and the competitive ability of four annual weeds

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Abstract – The competitive effects and responses of four annual weeds (*Avena sterilis*, *Bromus diandrus*, *Galium tricornutum* and *Veronica hederifolia*) were compared under greenhouse and field conditions. The two grasses had similar competitive effects that were much greater than the effects of the two dicotyledonous weeds. In all the experiments, *A. fatua* was the most competitive species and *V. hederifolia* was the least competitive. In terms of response, *A. sterilis* demonstrated the highest tolerance to competition, followed by *B. diandrus*, *V. hederifolia* and *G. tricornutum*. The correlations between the rankings of competitive effect and response were generally poor: the species that cause larger reductions in growth of their neighbours are not always the least affected by the presence of competitors. The observed competitive hierarchies were not consistently associated with early season weed parameters. The only plant trait that presents a certain correlation with competitive effect is seed weight. However, the response to competition seems to be well correlated with biomass and leaf area in the early stages of growth.

Competitive ability / *Avena sterilis* / *Bromus diandrus* / *Galium tricornutum* / *Veronica hederifolia*

Résumé – Comparaison du développement et de la capacité de concurrence de quatre adventices annuelles. Quatre adventices annuelles (*Avena sterilis*, *Bromus diandrus*, *Galium tricornutum* et *Veronica hederifolia*) ont été comparées du point de vue des effets de et des réponses à la concurrence entre elles, en conditions de serre et en plein air. Les deux graminées ont eu les mêmes effets de concurrence, toujours supérieurs à ceux dus aux deux dicotylédones. Dans toutes les expériences, *A. fatua* a été l'espèce la plus compétitive et *V. hederifolia* la moins compétitive. En termes de réaction, *A. sterilis* a montré la tolérance la plus grande à la concurrence, suivie de *B. diandrus*, *V. hederifolia* et *G. tricornutum*. Les corrélations entre le rang selon l'effet de la concurrence et le rang selon la réponse à la concurrence

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ont été faibles. Les espèces qui réduisent le plus la croissance chez leurs voisines n'ont pas toujours été les moins affectées par la présence des plantes concurrentes. Les hiérarchies de concurrence observées ne sont pas très bien corrélées avec les paramètres des adventices en début de saison. Le seul trait qui présente une certaine corrélation avec les effets de la concurrence est le poids de la graine. Cependant, la réaction à la concurrence semble être bien corrélée avec la biomasse et la surface foliaire mesurées en début de croissance des plantes.

Capacité de concurrence / *Avena sterilis* / *Bromus diandrus* / *Galium tricornutum* / *Veronica hederifolia* / adventice

1. Introduction

In order to establish weed control strategies it is important to recognize the natural strategies of the major weeds infesting the crop. According to Grime [8], annual plants may be considered under three major strategic types: competitors, ruderals and stress-tolerators. Although most of our troublesome weeds can be classified as “competitive-ruderals”, considerable differences exist in the behaviour of individual species. These differences can be associated with different growth patterns or with other traits that determine plant competitiveness.

The competitive ability of a weed involves two distinct aspects: competitive effect, which is the ability of a plant to reduce the performance of other plants, and competitive response (or tolerance), which is the ability of a plant to continue to perform relatively well in the presence of competitors [6, 7]. These two aspects of competitive ability are not necessarily correlated: for example, the traits that determine the extent to which one plant may shade another may not be the same traits that confer tolerance of low light levels. Comparisons of both aspects of competitive ability among species are critical for connecting various plant traits to ability to compete successfully in a given environment.

Neighbourhood experiments are specifically designed to analyze the interactions among various species, separating competitive effects and responses [6, 7, 10]. In these experiments, one single “target” plant is subjected to competition from one or various densities of “neighbour” species. This type of design allow us to address three major questions: 1) Are the rankings of competitive effect among neighbour species consistent for all target species? Are the rankings of response among target

species consistent for all neighbours?; 2) Are the rankings of competitive effect and response correlated?; 3) Are the rankings of competitive effect or response related to morphological or physiological traits?

Within the weed communities commonly present in winter cereals in central Spain, some species seem to be more important than others. *Avena sterilis* L. ssp. *ludoviciana* (Durieu) Nyman and *Bromus diandrus* Roth. are two troublesome grasses in these crops due to their high competitiveness and their good adaptation to the growth cycle of the crop [4, 12]. On the other hand, *Veronica hederifolia* L. and *Galium tricornutum* Dandy are also important weeds in winter cereal crops in Spain. Although these two broadleaf weeds have proved to prosper successfully when growing in these crops, their morphological and physiological characteristics are quite different from those of the two grasses, suggesting that they may have different adaptations to persist in such competitive environments.

The major objectives of this work were: a) to identify differences in the growth patterns of these four annual weeds, b) to study the rankings of competitive effects/responses of the four species, and c) to define which plant traits may determine their competitive ability.

2. Materials and methods

2.1. Greenhouse studies

Growth analysis

The growth of the four weeds was investigated in pure stands in two identical experiments separated by one week. Seeds of all species were planted

in pots (13 cm diameter and 12 cm depth) filled with organic soil amended with sand. Due to the high natural fertility of the soil, no fertilizer was added. Sufficient seeds were planted so that 10 or more seedlings would emerge per pot. The pots (ten for each individual species) were arranged randomly in a thermoregulated greenhouse, rotating their positions weekly. Maximum temperatures were 17 ± 3 °C during the early stages of growth, and 24 ± 1 °C during the final stages. Minimum temperatures ranged from 3 to 14 °C. All pots were watered daily. Fifteen days after planting, a 20-cm high cylinder made of green plastic mesh was placed on each pot to prevent lodging and to avoid light competition from neighbouring pots. Aerial biomass was harvested 20, 30, 40 and 50 days after planting, extracting two plants from each pot (20 per experiment). Dry matter was determined by pressing the plants and drying at 65 °C for 48 h. Plant dry weights were transformed using $\ln(x + 1)$ and these values were linearly regressed against accumulated degree days ($^{\circ}\text{C days} = \sum (t_i - 1) ^{\circ}\text{C}$), using a base temperature of 1 °C. In order to compare the growth rates of the four weed species a test of homogeneity of regression coefficients was performed.

Competition study

A “neighbourhood experiment” was established under greenhouse conditions. The four weed species were grown in pots in a diallelic design, in all possible combinations as both targets and neighbours (16 combinations in total). For each species combination there were three pots, each with one individual of the target species in the centre of the pot surrounded by four individuals of the neighbouring species (each plant was at a 5 cm distance of its closest neighbours). In addition, there were six pots for each species with a single target individual and no neighbours. These pots were used in the analysis of the effects of all neighbour species on that target.

Seeds of all species were germinated in a growth chamber on filter paper and cotton, being transplanted to the pots as soon as the coleoptiles/radicles emerged. All the plants of the same species were transplanted on the same day and there was a

maximum of two days between the transplants of the different species. Pot size and experimental conditions were the same as in the previous study.

Each pot was harvested fifty days after planting. Target individuals were separated from neighbours and both types of plants were placed in a plant press, dried for 48 hours at 65 °C and weighed. In order to compare competitive responses among target species of different sizes, the data for target weight were expressed as a percentage of the mean weight of isolated plants. Statistical analysis were performed on these percentages after square root transformation. Comparisons between means were made by the Tukey-test.

In order to test whether competitive effects/responses are correlated with simple measurable plant traits, various parameters were measured throughout the growing period. Seed weight was determined individually on a sample of 30 seeds of each species. Twenty and fifty days after planting, plant height and biomass were determined for 12 plants of each species grown as single plants in pots located randomly within the competition experiment. The logarithms of these values and the Relative Growth Rate (RGR) during that period were correlated with the mean effect and mean response values obtained previously.

2.2. Field studies

All the field studies were performed at El Encin Research Station, Alcala de Henares, Madrid. The experimental site has a north-mediterranean climate with an average annual rainfall of 470 mm. The experiments were located on a fine loam soil (32% sand, 42% silt, 26% clay), with 1.1% organic matter and a pH of 8.1. Prior to planting, soil was fertilized with 32 kg/ha of N, 96 kg/ha of P and 36 kg/ha of K.

Growth study

This experiment was conducted in two consecutive years (1994/95 and 1995/96) in a randomized block design with six replications. Each block contained four individual plots with monocultures of the four weed species. In 1994/95, these

monocultures consisted in 12 plants transplanted from nearby plots at an early seedling stage (in mid January). Each individual plant was separated from its neighbours by 50 cm in order to avoid interference among them. In 1995/96, seeds (4 per site) were sown in mid November with the same spatial arrangement, leaving only one plant per site after emergence was completed. From seedling stage until plant maturity, various destructive samplings (4 in 1994/95 and 10 in 1995/96) were conducted, determining the aerial biomass of each plant. A logistic model ($y = b_0 / (1 + \exp(-b_1 * (x - b_2)))$) was used to describe the relationship between thermal time and plant biomass accumulation.

Competition study

In November 1994, each of the four neighbour species were seeded in field plots (1 × 4 m) using a seeding density calculated to produce final populations of 70 plants/m². Within each plot, sixteen 0.25 m² quadrats were randomly assigned to each target species. With this design, approximately five neighbour plants were within a 10 cm radius round each target plant. Each neighbour treatment was replicated five times.

In January 1995, when most of the grasses were at the two leaf stage and the dicotyledonous species had already developed the first whorl of true leaves, a single plant of each target species was transplanted into the centre of each of the quadrats. These transplants were taken with an 8-cm diameter bulb planter from nearby plots which had been seeded with the four species at the same time as the test plots. In early March, when all the plants were well established, individuals of the neighbour species were removed by hand until the target density (50 plants/m²) was attained. All undesired species from each quadrat were also removed. The quadrats were weeded periodically to prevent reinvasion of unwanted species.

V. hederifolia targets were harvested in early May, when plants had already completed their life cycle and most of the seeds had been shed. In order to determine total biomass produced, vegetative and reproductive biomasses were considered independently. Each individual plant was clipped at ground level and all the seeds still present on the

plant were removed. Seed production was estimated by counting the number of seed marks within the empty capsules under the dissecting microscope. The remaining structures were dried for 48 h at 80 °C and weighed to determine aboveground vegetative biomass. The relationship between vegetative biomass and seed production was determined from a random sample of 47 neighbour plants. This ratio was used to calculate total biomass (vegetative + reproductive) of target plants.

Targets of *A. sterilis*, *B. diandrus* and *G. tricornutum* were harvested in early June, when plants had already finished seed production, but before they started seed shedding. Plants were clipped at ground level, dried and weighed.

3. Results

3.1. Greenhouse studies

Growth analysis

Seedling emergence was faster in the two grass species than in the two dicotyledonous weeds. The thermal times required to obtain 50% emergence ranged from 95 °C days for *B. diandrus* to 165 °C days for *V. hederifolia* (Tab. I). The initial differences in seed size and time for emergence were responsible for most of the differences observed later in dry weight accumulation. No significant differences were observed between the RGR of the four species. At the end of the 50 day period, the ranking of plant growth, measured both for biomass and height, was: *A. sterilis*, *B. diandrus*, *G. tricornutum* and *V. hederifolia* (Tab. I).

Competition

At the end of the 50 day growing period, clear differences were observed among the mean competitive effects of the four neighbour species. *A. sterilis* and *B. diandrus* reduced target weight similarly, 59% and 55%, whereas *G. tricornutum* and *V. hederifolia* caused mean weight reductions of 36% and 23% respectively (Tab. II). The rankings of effects of the first three species were consistent over all targets. However, in the case of

Table I. Seed weight (n = 30) and major morphological and physiological parameters of plants grown in pots (greenhouse study) in monoculture (n = 12). Values are means + SE.

	Seed weight (mg)	Time 50% emergence (° Day)	20 days		50 days		20-50 days RGR (mg/° Day)
			Biomass (mg)	Height (cm)	Biomass (mg)	Height (cm)	
<i>A. sterilis</i>	44.3 ± 1.1	114	46.7 ± 4.4	16.1 ± 0.5	2967 ± 265	55.2	0.00332
<i>B. diandrus</i>	12.7 ± 0.5	95	21.0 ± 1.1	10.2 ± 0.3	1747 ± 216	32.5	0.00362
<i>G. tricornutum</i>	10.9 ± 0.4	160	9.7 ± 0.6	4.2 ± 0.2	877 ± 108	23.8	0.00366
<i>V. hederifolia</i>	5.3 ± 0.2	165	11.3 ± 0.4	3.6 ± 0.1	458 ± 80	7.8	0.00306

Table II. Comparison of competitive effects among neighbour species and competitive responses among target species. Plants grown in the greenhouse for fifty days. Target weight is expressed as percentage of the mean value for isolated plants for each target species. Values with the same letter are not significantly different by a Tukey test ($P > 0.05$): a, b for within row comparisons (among neighbours); w, x for within column comparisons (among targets).

Target species	Neighbour species				Mean response
	<i>A. sterilis</i>	<i>B. diandrus</i>	<i>G. tricornutum</i>	<i>V. hederifolia</i>	
<i>A. sterilis</i>	50.0 a	60.7 a	91.3 b	86.3 b	73.6 z
<i>B. diandrus</i>	38.7 a	40.7 a	73.7 b	112.0 c	66.3 y
<i>G. tricornutum</i>	31.7 a	30.3 a	41.3 b	63.0 c	41.6 w
<i>V. hederifolia</i>	36.0 a	49.7 a	49.0 a	45.0 a	44.9 x
Mean effect	40.6 a	45.3 a	63.8 b	76.6 c	

V. hederifolia, this species was similarly affected when grown with any neighbour.

The ranking of response of the target species was, on the whole, the inverse of the ranking of effect: *G. tricornutum* showed the greatest mean reduction in growth (58%), followed by *V. hederifolia* (55%), *B. diandrus* (34%) and *A. sterilis* (26%) (Tab. II).

The correlation between the rankings of competitive effect and response was rather poor ($r = -0.85$, $p = 0.14$), indicating that the species that cause larger reductions in growth on their neighbours are not always the least affected by the presence of competitors. This lack of correlation was primarily due to the relative performance of *G. tricornutum* and *V. hederifolia*: *G. tricornutum* had a greater effect on the other species whereas *V. hederifolia* had a greater tolerance to competition.

In order to identify the plant traits that are associated with high competitive effect or response,

we attempted to correlate these two parameters with various morphological and physiological parameters of the four species. The competitive effect at the end of the 50-day experimental period was correlated ($P > 0.05$) with plant height of 20-day old plants and with height and biomass of 50-day old plants (Tab. III). In regard to competitive responses, good correlations were obtained with the plant traits (biomass and height) considered at the 20-day period. In contrast, poor correlations were obtained with the values measured after 50 days of growth. The Relative Growth Rates (RGR) during the 20 to 50 day period did not present any correlation for either effect or response.

3.2. Field studies

Growth analysis

Although there were absolute differences in the rates of growth observed in the two experimental

Table III. Correlation coefficients and significance levels (between brackets) between various traits of the four test species grown in pots (greenhouse study) with no neighbours and their competitive effects and responses at the end of the 50-day period.

Marked correlations (*) are significant at $P < 0.05$.

	Seed weight	20 days Biomass	Height	50 days Biomass	Height	20-50 days RGR
Competitive effect	-0.87 (0.13)	-0.86 (0.14)	-0.96* (0.04)*	-0.99* (0.01)*	-0.95* (0.05)*	-0.44 (0.56)
Competitive response	0.81 (0.19)	0.96* (0.04)	0.98* (0.02)*	0.91 (0.09)	0.78 (0.22)	0.06 (0.94)

Table IV. Parameter estimates (with standard errors in parentheses) obtained for the logistic model ($y = b_0 / (1 + \exp(-b_1 * (x - b_2)))$) fitting biomass accumulation of the four weed species growing in the field in two consecutive seasons.

Species	b_0	b_1	b_2	r
<i>A. sterilis</i>				
1994/95	145.7 (0.01)	0.011(0.00)	1289 (0.02)	0.999
1995/96	87.0 (3.18)	0.013 (0.003)	1404 (14.49)	0.997
<i>B. diandrus</i>				
1994/95	59.3 (0.10)	0.012 (0.0001)	1295 (0.53)	0.999
1995/96	52.5 (1.90)	0.010 (0.002)	1399 (14.23)	0.988
<i>G. tricornutum</i>				
1994/95	64.6 (0.15)	0.012 (0.0001)	1359 (0.31)	0.999
1995/96	38.5 (0.80)	0.012(0.001)	1383 (8.18)	0.998
<i>V. hederifolia</i>				
1994/95				
1995/96	12.28 (1.57)	0.009 (0.004)	1141 (95.45)	0.909

years (with a faster growth in 1994/95) the relative performance of the four species was similar in both years. *A. sterilis* grew fastest, *B. diandrus* and *G. tricornutum* were intermediate and *V. hederifolia* grew the slowest (Fig. 1). Various logistic equations fitted well the relationship between thermal time and biomass accumulation in practically all cases (Tab. IV).

Competition

The results obtained in the field experiment, with plants competing under natural conditions and throughout their life cycle differ slightly from the results obtained in the pot experiment.

The ranking of effects of the four neighbour species is headed by *A. sterilis*, causing an average weight reduction of 81% of all neighbours. *B. diandrus* and *G. tricornutum* caused similar, but non-significantly different reductions in target dry weight (73% to 75%) and these effects were greater than the reductions in growth due to *V. hederifolia* (61%) (Tab. V). The rankings of competitive effects on the two grass targets were consistent with the general trend. However, when the target plants were *G. tricornutum*, growth was equally suppressed by intra-specific competition or by competition with the two grass neighbours. In the case of *V. hederifolia*, the differences in the

Figure 1. Mean and fitted logistic equation for plant biomass accumulation and thermal time of the four weed species growing in the field in two consecutive seasons (—●— *A. sterilis*; -○- *B. diandrus*; -△- *G. tricornutum*; ----*--- *V. hederifolia*).

Table V. Comparison of competitive effects among neighbour species and competitive responses among target species. Plants grown in the field during the entire life cycle with the same initial neighbour density. Target weight is expressed as percentage of the mean value for isolated plants for each target species. Values with the same letter are not significantly different by a Tukey test ($P > 0.05$): a, b for within row comparisons (among neighbours); w, x for within column comparisons (among targets).

Targets species	Neighbour species				Mean response
	<i>A. sterilis</i>	<i>B. diandrus</i>	<i>G. tricornutum</i>	<i>V. hederifolia</i>	
<i>A. sterilis</i>	21.4 a	29.9 ab	33.8 b	71.6 c	39.2 y
<i>B. diandrus</i>	18.2 a	26.4 b	23.5 ab	35.1 c	25.8 x
<i>G. tricornutum</i>	10.1 a	13.0 a	11.8 a	29.0 b	16.0 w
<i>V. hederifolia</i>	25.7 ab	30.3 b	21.9 a	21.5 a	24.9 x
Mean effect	18.9 a	24.9 b	22.8 b	39.3 c	

competitive effects caused by the four neighbours were only slight.

In relation to the responses of the targets, *A. sterilis* was, once more, the least responsive to competition (61% reduction in dry weight). *B. diandrus* and *V. hederifolia* showed larger responses, with approximately 75% reductions in dry weight. *G. tricornutum* was strongly suppressed by all the neighbours, suffering 84% reduction in growth. Although this trend was generally consistent over all the neighbour species, there were a few exceptions. In those cases where the neighbour was *A. sterilis*, all targets suffered similar reductions in growth. In contrast, where the neighbour was *V. hederifolia*, marked differences were observed among the four species: *A. sterilis* was the least responsive species and *V. hederifolia* was the most responsive (intra-specific competition).

The correlations between the rankings of competitive effect and competitive response in the field ($r = -0.44$, $p = 0.56$) were still lower than the values obtained in the greenhouse experiment. This poor relationship can be attributed primarily to the performance of *G. tricornutum*: this species was the second in the ranking of effects, but the last in the ranking of responses.

In order to identify factors associated with competitive effect or response, we tried to correlate these two parameters for the four weeds with their respective biomasses at an early stage of development (80° Days after planting) and their Relative Growth Rates. No significant correlation was found in any case (Tab. VI).

4. Discussion

As expected, *A. sterilis* was the most competitive species, both in terms of competitive effect and response. This weed has been shown to compete strongly with winter wheat in southern Spain, with densities as low as 5 plants/m² reducing grain yield by 10% [13, 14]. On the other hand, *A. sterilis* was clearly affected by competition from the other weeds. The largest effect (78.6% reduction in

Table VI. Correlation coefficients and significance levels (between brackets) between various traits of the four species grown in the field with no neighbours and their competitive effects and responses.

		Early Biomass	Relative Growth Rate
Competitive effect	1994/95	0.67 (0.48)	-0.98 (0.48)
	1995/96	-0.37 (0.48)	-0.74 (0.48)
Competitive response	1994/95	0.51 (0.48)	0.12 (0.48)
	1995/96	0.76 (0.48)	-0.05 (0.48)

growth) occurred when the neighbour plants were of the same species (intra-specific competition). Previous studies have shown that *A. sterilis* responds markedly to increased competition from cereal crops [11, 14]. *Avena fatua*, a closely related species, has been considered as one of the most competitive weeds in cereal crops [2, 15].

B. diandrus was also a strong competitor, reducing growth of its neighbours drastically. This weed presented growth patterns similar to those of *A. sterilis*. Previous results in Australia have shown that this weed is extremely aggressive in wheat, with densities of 25-30 plants/m² reducing grain yield by about 10% [5]. According to the ranking of competitive effects established by Black and Dyson [2], the competitiveness of this weed is 12% lower than that of *A. fatua*. The mean competitive response of *B. diandrus* (74.2% reduction in growth) was slightly lower than in the case of *A. sterilis* (60.8% reduction). The differences between these two species were more pronounced when the neighbour species had a low canopy (such as *V. hederifolia*) than when it had a high canopy (such as *A. sterilis*). This may indicate that *B. diandrus* responds better to light competition than to competition for nutrients. Mahall et al. [9] found that the RGR of *A. fatua* and *B. Diandrus* were not significantly different at high light intensities, but under low light the RGR of *Avena* was only about half that of *Bromus*. On the other hand, it is known that *V. hederifolia* competes primarily for nitrogen with cereals [1].

The competitive effect of *G. tricornutum* was much lower than those of *A. sterilis* and *B. diandrus* in the greenhouse study, with plants growing for only 50 days. However, when the experiment was conducted in the field, over the whole life cycle of the species, the effects of *Bromus* and *Galium* were very similar. This may be explained by the climbing habit of *G. tricornutum*. This trait allows this weed to compete strongly for light in late stages of growth. According to the ranking of competitive effects established by Black and Dyson [2], the competitiveness of this weed is 19% lower than that of *A. fatua* and 7% lower than that of *B. diandrus*. The comparisons made by Wilson and Wright [15] with the relative biomasses of two closely related species, *G. aparine* and *A. fatua*, show that *Galium* is 60% less competitive than *Avena*. Regarding the competitive responses, *G. tricornutum* was the species that showed least tolerance to weed competition, both in greenhouse (50 days period) and in field (whole life cycle) experiments. The average response in the field (84% reduction in growth) was substantially lower than the values obtained for the other three weeds. The strong suppression caused by all the neighbours to this species is remarkable considering its climbing habit (that allows it to avoid light competition) and its high competitive effect. This behaviour may be explained by the relatively high requirements of nitrogen and soil moisture of *G. tricornutum* and the strong limitation of these two factors under the experimental conditions.

V. hederifolia was the least effective of the four weeds in terms of competitive effect. The average growth reduction observed when this weed acted as neighbour species was 25% lower than when the neighbour was *A. sterilis*. Previous studies indicate a low competitiveness of this weed and suggest that this species could be given a reduced priority for control in weed management systems [2, 15]. However, high densities of this weed and inadequate nitrogen fertilization practices may result in clear effects on crop yields [1, 3]. The low competitive effect of *V. hederifolia* may be explained by its low canopy structure and its short life cycle. According to our results, this species starts its cycle with a reduced vigour due to a small seed

size and a long emergence period. These initial differences, together with its low height, were responsible for most of the differences observed in growth later. Although in one of the field experiments (1994/95) the RGR of this weed species was clearly lower than those of the other three weeds, in all the other studies no significant differences were observed. The tolerance of *V. hederifolia* to competition from its neighbours was relatively good and similar to that of *B. diandrus*.

It is remarkable that the ranking of competitive effects of these four weeds is very similar to the estimates of relative competitive ability obtained for South and Western Australia [2]. This supports the validity of these conclusions under mediterranean type conditions and indicates a good agreement between results obtained in neighbourhood experiments and subjective opinions of weed research officers.

The results obtained in these studies do not allow us to establish any general relationship between specific plant traits and competitive ability. On the contrary, they illustrate the difficulties involved in reaching such a general conclusion. Competitive effect seems to be mostly associated with initial plant size. This, in turn, is determined by seed weight and rate of emergence. Since the RGR of the four species were very similar, initial differences in sizes were maintained during the whole life cycle. The differences in competitive responses were more difficult to explain. With some species (*A. sterilis*, *B. diandrus*), their large initial size makes them very tolerant to competition exerted by their neighbours. However, other species may have more elaborate mechanisms to avoid competition. Apparently, the ability of *V. hederifolia* to tolerate the presence of competitors may be associated with its short developmental period and with its ability to tolerate shading and capture soil nutrients. In contrast, the strong suppression observed in the case of *G. tricornutum* may be associated with its lack of ability to compete for scarce water and nutrients.

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