Theor Appl Genet (1985) 69:293–295

Heterosis in the hybridisation between the monoecious and dioecious subspecies of *Ecballium elaterium* (L.) Richard

J. Gonzalez-Julian and F. Galan-Estella
Laboratory of Biology, Faculty of Science, University of Salamanca, Salamanca, Spain

Received May 1, 1984; Accepted May 25, 1984
Communicated by H. F. Linskens

Summary. By means of a statistical analysis carried out on a number of samples grown in balanced incomplete blocks, respectively corresponding to filial generations which (pure, hybrid or backcross) can be discerned in the hybridisation between the monoecious and dioecious subspecies of the Mediterranean wild cucurbitaceae *Ecballium elaterium* (L.) Richard, the possible presence of a group of polygenes which modify or regulate the durability of the life of the plants has been investigated, studying especially the most frequent and the most characteristic observable effect of polygenes, the heterosis or hybrid vigour. Experimental results indicates that there is heterosis with respect to the survival of the individual plant. The occurrence of the phenomenon of heterosis is experimental evidence of the presence of a system of polygenes which has influence upon this particular quality of the plant (survival). Every one of these polygenes in the genotype of a subspecies has alleles somehow different from those of another (of *E. elaterium*).

Key words: Heterosis – Polygenes – Survival – *Ecballium*

Introduction

The aim of this work was to carry out a study on the frequency of the occurrence of heterosis, related to the durability of life of the plant, in the hybridisation between the monoecious and dioecious subspecies of *Ecballium elaterium* (L.) Richard. These two subspecies, the one monoecious [*E. elaterium* (L.) Richard subsp. *elaterium*] and the other dioecious [*E. elaterium* (L.) Richard subsp. *dioicum* Battandier], are allopatric, Galán (1971), because they occupy mutually exclusive areas of geographical distribution in the Iberian Peninsula. The sex of the plant – which is the only genetic difference between the two subspecies – is determined by a multiple series of three alleles for which Galán (1946, 1951, 1954, 1964) proposed the symbols a^D, a^+, a^d. The enumeration of the sexes of the plants, or sexual phenotypes, is as follows:

Subspecies	Genotype	Sexual phenotype
monoecia	a^+a^+	androgyne plant
dioecia	a^Da^d	male plant
	a^da^d	female plant

The occurrence of heterosis, related to the durability of the life of the plant as a result of the activity of the polygenes, shows an essential and complex genetic diversity. Phenotypic effects are not very apparent at first sight but are important and probably exist between these two forementioned subspecies of *E. elaterium*.

Material and methods

During the same flowering and fructification season 2,840 artifial pollinations[1] were performed in the Laboratory of Biology, Faculty of Science, Salamanca, which produced germinating seeds. The plantulas obtained in this way were transferred to individual clay pots. During the interval between September and December of the fourth year of life of these plants, these were taken to an experimental field methodically arranged in a system of balanced incomplete blocks

[1] Corresponding to the experiments in hybridisation between the monoecious and dioecious subspecies of *Ecballium elaterium* which are being carried out in the forementioned Laboratory of Biology

(Fisher and Yates 1963). In this experimental field, each plant (from an initial total of 2,700) was given an area of 4 m^2.

These plants, which sum up the samples corresponding to filial generations which (pure, hybrid or backcross) can be discerned in the hybridisation between the monoecious and dioecious subspecies of *E. elaterium,* were classified according to their parental affinities:

1. Sample "Pm" – with a total of 399 plants, defined as the genuine plants of the monoecious subspecies;
2. Sample "Pd" – with a total of 207 plants, defined as the genuine plants of the dioecious subspecies;
3. Sample "F_1" – with a total of 215 plants, defined as the intersubspecific hybrids (between the monoecious and dioecious subspecies);
4. Sample "F_2" – with a total of 781 plants, defined by having as parents only individuals from the "F_1" sample;
5. Sample "R_2m" – with a total of 530 plants, defined by having as parents one individual from the "F_1" sample and the other individual from the "Pm" sample;
6. Sample "R_2d" – with a total of 516 plants, defined by having as parents one individual from the "F_1" sample and another from the "Pd" sample.

With the individual phenotypic values being obtained directly from these samples and by calculating the number of individual-plants dead during every one of the 7 consecutive years of our experiments (1975–1981), "relative frequencies of survivors" are obtained; and with these we performed a strict comparison between the 6 samples.

Heterosis was estimated as the difference between the statistical mean corresponding to "F_1" and the arithmetic mean of the statistical means, respectively, corresponding to the sample of genuine generations to which the parents of this "F_1" belong (Falconer 1970).

Table 1. Frequencies of survivors from the different samples in successive years

Sample	1975	1976	1977	1978	1979	1980	1981
Pm	0.977	0.865	0.789	0.251	0.055	0.023	0.013
Pd	0.990	0.971	0.928	0.758	0.589	0.440	0.280
F_1	0.981	0.893	0.860	0.707	0.567	0.447	0.298
F_2	0.969	0.882	0.802	0.429	0.222	0.131	0.082
R_2m	0.987	0.902	0.838	0.479	0.253	0.155	0.077
R_2d	0.994	0.971	0.928	0.736	0.531	0.370	0.234

Results

Frequency of individual plant survivors is represented in Table 1 for all of the 6 sample groups during the seven years of experimental observation.

The statistical comparisons between relative frequencies of surviving individual plants during each year of observation (conducted to discover whether differences between two relative frequencies of surviving individual plants belonging to two different samples is due to different internal conditions derived from within the plants themselves or to external factors affecting plants of both samples) show the values of normal deviates (Table 2).

The formal expression of the general result ensued from this Table 2 is that the differences between two relative frequencies of surviving individual-plants is:

1 Significant,

i) between the "Pm" sample and every one of the other 5 samples;
ii) between the "Pd" sample and every one of the "F_2" or "R_2m" samples;
iii) between the "F_1" sample and every one of the above-mentioned samples ("F_2" or "R_2m");
iv) between the "R_2d" sample and every one of the "F_2" or "R_2m" samples.

Table 2. Normal deviates corresponding to the differences of the relative frequencies of survivors between two samples during the consecutive years of observation

Sample	1975	1976	1977	1978	1979	1980	1981
Pm vs Pd	1.18	3.92**	4.41**	11.52**	14.05**	12.63**	9.88**
Pm vs F_1	0.33	0.99	2.02*	10.36**	13.47**	12.47**	10.17**
Pm vs F_2	0.88	0.81	0.52	5.93**	7.26**	6.00**	4.60**
Pm vs R_2m	1.11	1.68	1.82	6.70**	7.61**	6.28**	4.26**
Pm vs R_2d	2.12*	5.27**	5.79**	13.85**	14.42**	11.96**	9.25**
Pd vs F_1	0.75	3.12**	2.01*	1.15	0.44	0.14	0.40
Pd vs F_2	1.75	3.87**	4.34**	8.43**	10.48**	9.96**	7.92**
Pd vs R_2m	0.33	3.00**	3.10**	6.64**	8.40**	8.14**	7.00**
Pd vs R_2d	0.57	0.00	0.00	0.59	1.38	1.70	1.25
F_1 vs F_2	0.92	0.44	1.93	7.31**	9.85**	10.19**	8.30**
F_1 vs R_2m	0.60	0.36	0.73	5.42**	7.85**	8.11**	7.62**
F_1 vs R_2d	1.62	4.10**	2.83**	0.78	0.85	1.87	1.75
F_2 vs R_2m	2.25*	1.18	1.71	1.85	1.35	1.26	0.33
F_2 vs R_2d	3.12**	5.93**	6.63**	11.37**	11.88**	10.39**	8.05**
R_2m vs R_2d	1.16	4.60**	4.50**	8.29**	8.96**	7.67**	6.87**

* Significant at 5% level; ** Significant at 1% level

2 Non-significant,

in every one of the other possible pairs of samples ("Pd" and "F_1", "Pd" and "R_2d", "F_1" and "R_2d", "F_2" and "R_2m").

By calculating concretely the value of heterosis for every one of the 7 years of our samples of filial generations, the following values of heterosis are:

1975	−0.002
1976	−0.025
1977	0.001
1978	0.202
1979	0.245
1980	0.215
1981	0.151

The absolute values of heterosis are small for the first three years (1975, 1976, 1977) and negative for the first two (1975, 1976). For the other 4 years (1978, 1979, 1980, 1981) they are positive with a considerable absolute value.

The interpretation of these results about the quantity of heterosis is that at the beginning there are no dead plants (all are survivors); afterwards, only a few dead plants and by the end there are a lot of dead plants (and very few surviving plants).

Together with the presence of heterosis, there is an inbreeding depression in the "F_2" sample showing an important reduction in the relative frequency of survivors in the "F_2" sample.

Conclusion

There is heterosis in the hybridisation between the monoecious and dioecious subspecies of the Mediterranean wild *Ecballium elaterium* (L.) Richard with respect to the survival of individual plants observed experimentally from germination for a certain number of years. This relative frequency was estimated each year, from the 6th to the 12th year of their lives (1975–1981) on samples from suitable filial generations.

The occurrence of heterosis concerning the life durability of the individual plant is experimental evidence of a system of polygenes which has influence upon this particular quality of the plant (life durability, longevity, survival). With respect to every one of these polygenes, the genotype of a subspecies has alleles somehow different from the ones of another (of *E. elaterium*).

References

Falconer DS (1970) Introducción a la Genética cuantitativa. C.E.S.A, México

Fisher RA, Yates F (1968) Statistical tables for biological, agricultural and medical research. Oliver and Boyd, Edinburgh

Galán F (1946) Sur la génétique de la monoecie et de la dioecie zygotique chez *Ecballium elaterium* Rich. CR Acad Sci Paris 222:1130–1131

Galán F (1951) Analyse génétique de la monoecie et de la dioecie zygotiques et de leur différence dans *Ecballium elaterium.* Acta Salmant, Cienc: Sec Biol, Universidad de Salamanca, Spain

Galán F (1954) Genética y fenogenética del sexo en *Ecballium elaterium.* In: Atti 9. Congr Int Genét, Bellagio, Como 1953. Caryologia (suppl 1954), pp 942–944

Galán F (1964) Teoría genética del sexo zigótico en el caso de *Ecballium elaterium.* Rev Bras Portug Biol Geral 4:187–220

Galán F (1971) Oral communication