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Genetic control of fruit polymorphism in the Genus *Fedia* (*Valerianaceae*) in the light of dimorphic and trimorphic populations of *F. pallescens*

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Abstract: The genus *Fedia* consists of three species (*F. cornucopiae*, *F. graciliflora* and *F. pallescens*) of winter annual herbs, endemic to the western Mediterranean Basin. The deciduous terminal fruits of these taxa are polymorphic in the development of their pericarp and/or calyx, and each population is dimorphic or more rarely trimorphic. The three main fruit types are dispersed in several manners, and are specialized for either epizoochory or myrmecochory. On the basis of our experimental study of dimorphic and trimorphic populations of *F. pallescens* subsp. *pallescens*, a genetic model is presented in order to explain the control of this intrapopulational polymorphism. It is postulated that two diallelic loci are tightly linked on the same chromosome in a functional supergene. One allele of each locus displays a dominance effect in the heterozygous state. Within the four possible homologous allelic segments, only two are present in the dimorphic populations, three in the trimorphic ones, and are otherwise associated in diverse combinations in the remaining taxa of the genus. Similar examples of fruit polymorphism are already documented in the tribe *Valerianeae*, subtribe *Fediinae*. The hypothesis is put forward that this fruit polymorphism is a synapomorphy for the subtribe.

In the tribe *Valerianeae* HÖCK (*Valerianaceae*), several cases of genetic intrapopulational fruit polymorphism have been described, i.e. in various species of *Valerianella* MILLER (EGGERS-WARE 1969, 1983; ERNET 1978; MARTIN & MATHEZ 1990), *Plectritis* DC. (DEMPSTER 1958; GANDERS & al. 1977a, b; CAREY & GANDERS 1980), and *Fedia* GAERTNER (MATHEZ 1984; MATHEZ & XENA DE ENRECH 1985a, b; XENA DE ENRECH 1987; XENA DE ENRECH & MATHEZ 1990). *Valerianaceae* fruits are always achenes developing from an inferior ovary (cypselas). The ovary is made of two sterile locules and a fertile uniovular one. In the tribe *Valerianeae*, the documented cases of intrapopulational fruit polymorphism relate to the degree of development of the pericarp surrounding the sterile locules, and of the calyx, or of structures derived from tissues of these two organs.

The genus *Fedia* consists of three species of winter annual herbs endemic to the western Mediterranean Basin, especially North Africa, where one species is highly polytypic. As in other *Valerianaceae*, inflorescences of *Fedia* are cymoid in the sense of TROLL (1964). These monotelic truncate synflorescences are characterized by the constant lack of the terminal flower. In *Fedia*, the upper end of the main axis is thus always represented by a fork formed from the two uppermost, dichasially branched paraclades (WEBERLING 1961, 1989). Flowers may lack on the branches of lower order of these cymose partial inflorescences, repeatedly branched in a dichasial and finally scorpioid fashion (ERNET 1977). Flowers are zygomorphic with a long nectariferous tube, brightly colored, strongly protandrous and entomogamous. The basal fruits are persistent and the distal ones deciduous.

Many types of fruits have been described in the genus, the shape of which depends both on the genotype of the individual and on their basal or distal location in the infructescence. Moreover, in any *Fedia* population, two or more types of individuals differing by the shape of their terminal deciduous fruits may coexist. So two different mechanisms, i.e. heterocarpy and genetic polymorphism, work towards determining the shape of one fruit. The existence of fruit genetic polymorphism was first suspected in *Fedia* by ERNET (1978), and later demonstrated by MATHEZ (1984) for one species. Other instances of genetically controlled fruit polymorphism in the genus have been demonstrated by MATHEZ & XENA DE ENRECH (1985a, b). It should be noted that the proximal persistent fruits are not polymorphic. The polymorphism of distal deciduous fruits results from the differential development of the pericarp of the sterile locules and of the persistent calyx. The well-developed calyx takes the shape of two horns. There are three main types of deciduous fruits recorded for the genus (Fig. 1): Fruits with reduced, narrow sterile locules, either (i) with horns (C fruits, from french 'cornu', horny) or (ii) without (E fruits, from 'étroit', narrow), and (iii) fruits with developed, inflated sterile locules, never bearing horns (G fruits, from 'gonflé', inflated). We include here under type G all fruit shapes that share inflated sterile locules. In a previous publication (XENA DE ENRECH & MATHEZ 1990: 17), we have distinguished within this type five subtypes named G, H, Q, B and S.

We have undertaken biosystematic studies of the genus (MATHEZ 1984, XENA DE ENRECH 1987), and currently recognize three species and seven subspecies: *Fedia cornucopiae* (L.) GAERTN., *F. pallescens* (MAIRE) MATHEZ with the two subspp. *pallescens* and *hirsuta* (EMBERGER & MAIRE) MATHEZ & XENA, and *F. graciliflora* FISCH. & MEYER with the five subspp. *graciliflora*, *snassenorum* MATHEZ & XENA, *sulcata* (POMEL) MATHEZ & XENA, *calycina* (MAIRE) MATHEZ & XENA and *diana* MATHEZ & XENA (XENA DE ENRECH & MATHEZ 1990). All chromosomes numbers counted were $2n = 32$, except in a few individuals from a single population of *F. graciliflora* subsp. *snassenorum* collected near Oran (Algeria), where $2n = 48$ was recorded (XENA de ENRECH & al. 1991). All taxa show different patterns of intrapopulational fruit polymorphism, *F. cornucopiae* being the only exclusively dimorphic one (G and E fruits). *Fedia graciliflora* populations are basically dimorphic, with combinations of the main fruit types E, C or subtypes of G depending on the different subspecies. Where these different subspecies overlap or come into contact (for instance in central and central-eastern Algeria), the situation becomes more complex: some populations display up to six different fruit types or subtypes (Xena de Enrech 1987, Xena de Enrech & Mathez 1990).

In the dimorphic populations of *F. cornucopiae* as well as in those of *F. graciliflora*, the simplest explanation of the genetical control of the shape of sterile locules is a mendelian one whereby one dominant allele controls the development of the pericarp (Mathez & Xena de Enrech 1985a). However, in several subspecies of *F. graciliflora*, the fruit polymorphism affects not only the pericarp, but also the calyx. Each of these organs can present two different states, i.e. reduced or developed.

For the most part, populations of the endemic moroccan species *F. pallescens* are dimorphic and present G and C type fruits, similar to those of *F. graciliflora*. Very rarely, a third morph appears among them. The individuals making up the third type bear distal fruits with inflated sterile locules like G fruits and a horny calyx like C ones. We named this third fruit morph "M" because of its "mixed" character (Fig. 1). Such M fruits are also found in populations of *F. graciliflora* subsp. *calycina* (Xena de Enrech & Mathez 1990).

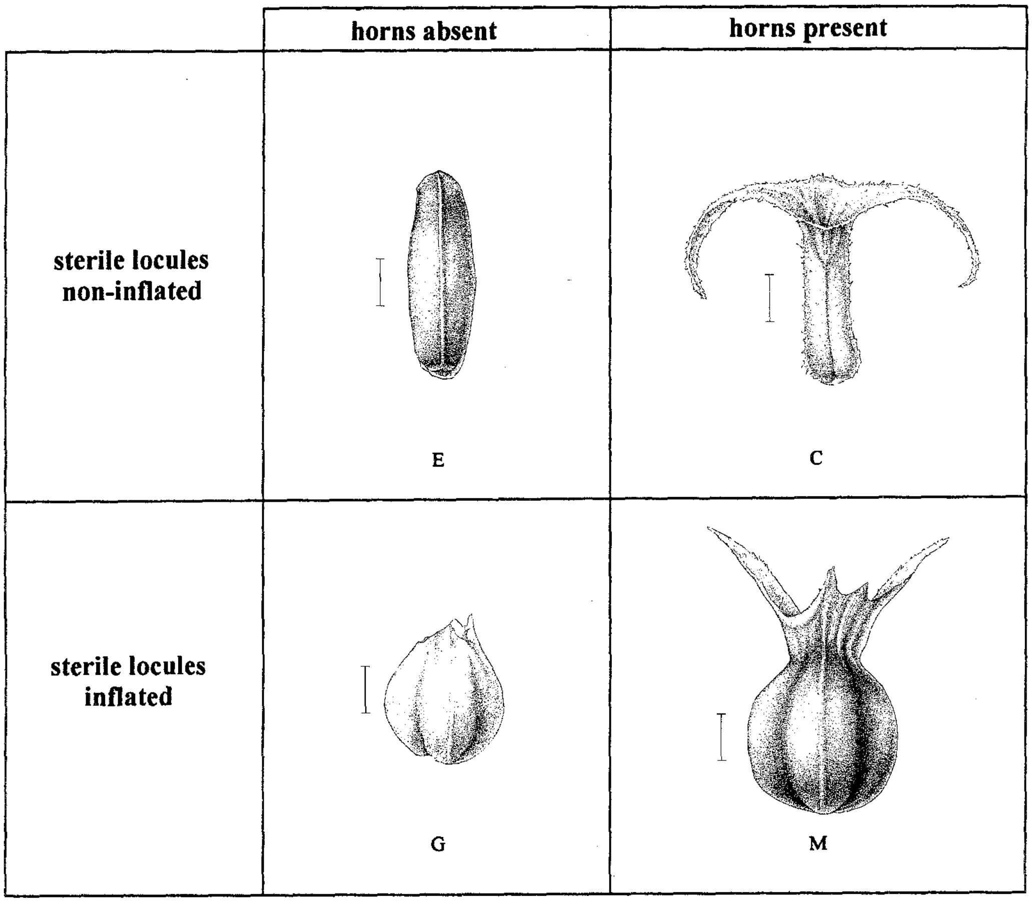

Fig. 1. Main fruit types of *Fedia*. *E F. cornucopiae*, E. fruit, with narrow sterile locules and abortive calyx. *C, G, M F. pallescens* subsp. *pallescens*, population 44; C fruit, with narrow sterile locules and calyx developed in horns; G fruit, with inflated sterile locules; M fruit, with inflated sterile locules and calyx developed in horns. – Bars: 1 mm

The major goals of our research are to understand the genetic mechanism which gives rise to the rare trimorphism observed in *F. pallescens* and to provide a general theory for the evolution and diversification of this genetic system within *Fedia*.

Materials and methods

Experimental crosses between cultivated plants collected from the following natural dimorphic and trimorphic populations of *F. pallescens* subsp. *pallescens* form the basis of our study of inherited fruit characters:

(1) Population 143 (dimorphic) = MATHEZ 7759; Morocco, Natural Reserve of Mehdiya, E side of the lake, 3.5.1980. Morphs: [G], [C].

(2) Population 44 (trimorphic) = XENA 769; Morocco, Natural Reserve of Mehdiya, W side of the lake. 17.4.1983. Morphs: [G], [M], [C].

The numbers designating these populations conform to those previously published (MATHEZ & XENA DE ENRECH 1985a; XENA DE ENRECH 1987; XENA DE ENRECH & MATHEZ 1990); the corresponding voucher specimens are deposited in MPU and RAB herbaria.

When placed between brackets [ ], fruit type abbreviations designate their corresponding individual phenotypes and morphs in the fruit polymorphism hypothesis.

The plants were cultivated in a greenhouse at the Botanical Institute, Montpellier (France), under controlled conditions of temperature (15 °C) and additional lighting (10 h of total day length) during autumn and winter; seeds were sown in autumn. Upon commencement of anthesis, the inflorescences were isolated in textile bags. Two methods of artificial pollination were used: autopollination by geitonogamy and cross pollination (after emasculation). Each plant was submitted to only one proof. Plants were maintained for two or three generations.

Artificial pollinations can be conducted only during anthesis. Before flowers wither, no terminal fruit is sufficiently developed to allow identification of the fruit type of the crossed plant. So, only the type of each sown fruit is known at this time. Moreover this fruit type is determined by the female parental genotype, not by the genotype of the embryo it contains. Hence, crosses were blind, and the fruit types of crossed individuals became apparent only at fruit set.

Results

Determination of the mechanism of genetic control in population 143 (dimorphic: [G], [C]) of *F. pallescens* subsp. *pallescens*. In the wild, two types of individuals, or morphs, are observed in this population: terminal fruits exhibit a developed pericarp and a reduced calyx (fruits G, morph [G]), or the pericarp is reduced and the calyx developed in horns (fruits C, morph [C]). Table 1 displays

Table 1. *Fedia pallescens* subsp. *pallescens* (dimorphic population 143); results of sowing of seeds issued from wild plants

Fruit type	Number of sown fruits	Number of seedlings (%)	Number of adult plants (%)	Progeny morph [G] (%)	[C] (%)
G	110	93 (85)	74 (80)	54 (73)	20 (27)
C	98	58 (59)	54 (55)	7 (13)	47 (87)

Table 2. Crosses performed between different morphs of *Fedia pallescens* subsp. *pallescens* (population 143); comparisons of observed results with expected Mendelian ratios (for the G × G crosses, the ratios 2:1 and 3:1 correspond to the lethal and viable *GGCC* genotype respectively). ** non-significant upon chi-square test, $P > 0.05$

Parental phenotypes (putative genotypes)	Number of crosses	Number of progeny [G]	Number of progeny [C]	Observed/expected G:C progeny ratios	χ^2
C × C					
(*ggcc* × *ggcc*)	9	0	68	0:1/0:1	0
G × C					
GgCc × *ggcc*)	2	7	9	1:1.29/1:1	0.25**
G × G					
(*GgCc* × *GgCc*)	5	34	12	2.83:1/2:1	6.09**
				3:1	5.96**

the results of sowing of 110 G fruits and 98 C fruits collected from this population. Each fruit type is able to produce both morphs of the population in its progeny (Gn_1), proving the presence of a genetically determined intrapopulational polymorphism.

It is postulated that the fruit polymorphism is the product of two diallelic loci, *Gg* and *Cc*, one allele of a locus tightly linked to that of the other one on the same chromosome in a "supergene". One allele of each locus displays a dominance effect in the heterozygous state.

Table 2 presents a summary of the results of the experimental crosses and self-fertilizations of generation Gn_1 individuals, leading to a new generation Gn_2 and in some cases a third one Gn_3. Results from these crosses allow us to establish the dominant or recessive character of the alleles in each locus: the presence of the dominant allele *C* inhibits calyx development (horns fail), that of *G* increases the pericarp development of the sterile locules (fruit inflated).

Given the fact that only two morphs occur in this population, our results suggest the existence of only two gametic combinations of linked genes, *GC* and *gc*. Moreover, all crosses [G] × [G] produce the two different morphs, indicating that the linkage combination of both dominant genes *GC* only exists in the heterozygous state (*GgCc*), when accompanied with the two linked genes *gc*. The corollary of this is that the double dominant homozygote (*GGCC*) is probably lethal or very rare in the population.

The model we here propose is that the genetic control of the polymorphism in this population results from (i) two linked genes, each one with two possible alleles (*G*, *g*; *C*,*c*), (ii) two gametic combinations of linked genes, *GC* and *gc*, and (iii) only two genotypes: (*GgCc*) for [G] morph and (*ggcc*) for [C] morph individuals. However, from our study, the existence of the (*GGCC*) genotype cannot be formally excluded.

Determination of the mechanism of genetical control in population 44 (trimorphic: [G], [M], [C]) of *F. pallescens* subsp. *pallescens*. We observed another natural population of the same taxon, also located in the Natural Reserve of Mehdiya, north of Rabat, which presents, in addition to the two previously

Table 3. *Fedia pallescens* subsp. *pallescens* (trimorphic population 44); results of sowing of seeds issued from wild plants

Fruit type	Number of sown fruits	Number of seedlings (%)	Number of adult plants (%)	Progeny morph		
				[G] (%)	[M] (%)	[C] (%)
G	360	243 (68)	221 (61)	119 (54)	18 (8)	84 (38)
M	425	323 (76)	222 (52)	3 (1)	127 (57)	92 (42)
C	450	310 (56)	259 (47)	1 (-)	20 (8)	238 (92)

described morphs [G] and [C], a third morph we have designated as [M]. The minor variations observed in the population in the G fruits (i.e. degree of extension of the membranous ventral zone) and in the C fruits (i.e. size of the horns or number of calyx teeth) also occur in the M fruits. The frequency of each morph was estimated in the field to be 12% [G], 29% [M] and 59% [C].

The results of the sowing of 360 G fruits, 425 M fruits and 550 C fruits are presented in Table 3. Analysis of the progenies of the three fruit types shows that they are always heterogeneous: each of them seems to be able to produce progeny of any of the three morphs. In each case, however, one of the morphs is less frequent, principally the [G] morph in the progenies issued from M and C fruits. This result is not surprising in view of the frequency of the observed morphs in the natural population: the lower frequency of the [G] morph lessens its probability of crossing with other morphs. Conversely, each type of fruit is produced in greater abundance from its own progeny, this percentage being particularly noteworthy in the C fruits (92%).

The heterogeneous morphology of the fruits of the F_1 generation indicates that the three morphs of this population are the products of a genetic polymorphism. Information culled from studies of the dimorphic population leads us to the interpretation that the new morph results from a new combination of alleles in the linkage group.

Table 4 presents the results of the experimental crosses using the Gn_1 generation to obtain a Gn_2 generation of controlled origin. These crosses are aimed at determining the patterns of genetic control of this trimorphism. Analysis of subsequent progenies of the different crosses provides the following information:

(i) The [C] morph behaves as a double recessive homozygote (*ggcc*) as evidenced by the fact that in all crosses between [C] morphs, the same [C] morph is recovered.

(ii) Only crosses between [G] and [M] morphs give rise to the three morphs of the population. This result is only possible if these two morphs possess all the alleles existing in the population and the gametic combinations of linked genes required to produce the three morphs, i.e. the already known *GC* and *gc*, and the new one *Gc*.

(iii) The crosses between [M] and [C] morphs produce one or the other of the same two morphs, and never the [G] morph. From this it may be deduced that the two genotypes must carry the double recessive *cc* responsible for the formation of horns on the calyx.

Table 4. Crosses between different morphs of *Fedia pallescens* subsp. *pallescens* (population 44); comparisons of observed results with expected Mendelian ratios. ** non-significant upon chi-square test, P > 0.05; * non-significant upon chi-square test, P > 0.01

Parental phenotypes (putative genotypes)	Number of crosses	Number of progeny [G]	Number of progeny [M]	Number of progeny [C]	Observed/expected G:M:C progeny ratios	χ^2
C × C						
(*ggcc* × *ggcc*)	2	0	0	10	0:0:1/0:0:1	0
C × G or G × C						
(*ggcc* × *GgCc*)	6	28	0	22	1.27:0:1/1:0:1	5.63**
(*ggcc* × *GGCc*)	1	20	11	0	1.82:1:0/1:1:0	2.61**
C × M or M × C						
(*ggcc* × *GGcc*)	4	0	12	0	0:1:0/0:1:0	0
(*ggcc* × *Ggcc*)	4	0	20	8	0:2.5:1/0:1:1	5.6**
G × M						
(*GgCc* × *Ggcc*)	3	34	17	5	6.8:3.4:1/2:1:1	11.85*

(iv) The [G] morph appears in the progeny only if it is present in the parental morphs. Such crosses reveal the dominant alleles: *G* responsible for the presence of developed pericarp, and *C* of reduced calyx.

(v) The crosses between [G] and [C] morphs give two types of results: either they produce the same morphs, or the [M] morph is found together with the [G] one in the progeny. If we accept, as suggested by the aforementioned results, that the [C] morph corresponds to the double recessive homozygote (*ggcc*), then there exist at least two genotypes for the [G] morph: one including the *g* allele (the double heterozygote *GgCc*) and the other one without it (*GGCc*). In the first case the cross produces the two parental morphs, and in the second one, the [M] morph appears.

(vi) In spite of the fact that no self-fertilization tests were made on the [G] and [M] morphs, our results support the interpretation that the same relations of dominance in the heterozygote loci exist as in the dimorphic population. The *G* and *C* alleles are responsible for the swollen pericarp and the reduced calyx, and dominate, in the heterozygous state, the expression of the *g* and *c* alleles (themselves responsible for the reduced pericarp and the calyx developed into horns, respectively).

Based on our results and interpreted in light of our model, the genetic control of terminal fruit polymorphism in this trimorphic population involves at least five genotypes for the three observed phenotypes: (*GGCc*) and (*GgCc*) → [G], (*Ggcc*) and (*GGcc*) → [M], and (*ggcc*) → [C].

These five genotypes are combinations of three gametic groups of linked alleles: *GC*, *Gc* and *gc*. A sixth genotypic diploid combination is then possible, the double dominant homozygote (*GGCC*), which would produce the [G] morph. Our results neither confirm nor deny its existence in the population: if existing, it would be rare, as not one of our crosses gave rise to it. It may also be lethal, as we earlier hypothesized for the dimorphic population. If so, only two combinations of linked genes would be viable in the homozygote condition: the (*GcGc*) genotype, restricted to the trimorphic population and responsible for the production of M fruits; and the double recessive (*gcgc*), responsible for the formation of the C fruits in the dimorphic as well as in the trimorphic populations.

Discussion

The significance of fruit polymorphism. Several cases of phenotypes with discontinuous intrapopulational expressions, controlled by one or two genes, are mentioned in the literature. In a recent review of genetic coevolution in plants (Gottlieb 1984), only a few documented cases of polymorphic fruits were noted. Gottlieb (1984) cites the previously mentioned examples in *Valerianella* and *Plectritis* (*Valerianaceae*) as well as that of *Coreopsis* (*Compositae*) which exhibits winged and non-winged fruits (Smith & Parker 1971, Smith 1973). Curiously, polymorphic achenes found in both families originate from inferior uniovular ovaries (cypselas).

Although a somewhat neglected aspect of reproductive/dispersal systems, several studies have attempted to relate the maintainance of fruit polymorphism to the notion of "heterozygote advantage" (Ganders & al. 1977a, b; Carey & Ganders 1980; Mathez & Xena de Enrech 1985a). In these cases and in the present one, a more likely explanation appears to relate to the selective advantage conferred by spatially and temporally differentiated dissemination patterns (Gouyon & al. 1979). In effect, in *Fedia*, each deciduous terminal fruit type corresponds to a more or less specific dissemination mode: epizoochory for the C fruits, myrmecochory for the G and E fruits (Mathez & Xena de Enrech 1985b, 1991).

The genetic system of *F. pallescens*. The genetic system we propose here accounts for the observations of fruits encountered in dimorphic as well as trimorphic populations. There are many other well-known examples of supergenes linking tightly many loci. The best studied and more frequently mentioned in the literature is the supergene responsible for heterostyly in several genera, e.g. *Primula*, *Linum*, and *Armeria*. The interpretation of this phenomenon is well understood: if the linked genes confer an adaptive advantage, then selection will favour every system reducing recombination frequency within the linked group (Demarly 1977). It is for this reason that such coadapted linked groups arise and become particularly stable. Reciprocally, the fact that such a system determines the fruit form in *F. pallescens* seems an indirect proof of the functional importance of this form. This is consistent with our hypothesis (Mathez & Xena de Enrech 1985b) that the diversified dissemination system related to fruit polymorphism of *Fedia* allows it a selective advantage.

The genetic system of fruit polymorphism in *Fedia* and its origin. Within *F. pallescens*, the great majority of populations are dimorphic. The presence of G and C fruit types in the same population appears to be the normal, ancestral state in this species. The appearance of M type fruits in rare trimorphic populations may be easily interpreted in light of the genetic system we propose, i.e. they result from a crossing-over between *GC* and *gc*, leading to *Gc*. The production of recombinant gametes can be non-existent or very low, but a crossing-over is always possible

(Webster & Grant 1990). In plants, such linkage groups have been recently documented for *Secale cereale* (Wehling & Schmidt-Stohn 1984), *Phaseolus vulgaris* (Osborn & al. 1986) and *Pisum sativum* (Folkeson 1990).

Dimorphic and trimorphic populations of *F. pallescens* coexist in the same geographical and ecological area. This observation strongly suggests that the determination of the fruit shape is exclusively genetical, not ecological or physiological. Given the reproductive strategy of this predominantly autogamous taxon (Xena de Enrech 1987), the interchange of genes between the di- and trimorphic populations is likely to be very restricted. The genesis of new morphs and even new taxa as a result of cross-overs between linked genes has long been accepted in relation to heterostyly (Dowrick 1956).

The combination of G and C fruit types found in *F. pallescens* is also the most common combination in *F. graciliflora*. In addition, the M type also appears in some trimorphic populations of this species (subsp. *calycina*). On the basis of this similarity, we propose that the fruit polymorphism in these two species results from the same underlying genetic system involving the linked alleles *GC* and *gc* and the rare recombinant *Gc*.

Notwithstanding, any recombination between *GC* and *gc* should produce not only *Gc* but also *gC*. The last, when associated with *gc* or *gC* in a diploid individual, would produce fruits without horns and with non-inflated sterile locules. Such fruits are found within *Fedia* and we have designated them the E type (Fig. 1).

Thus our interpretation of the genetic system responsible for trimorphic populations in *Fedia pallescens* is also capable of explaining the four principal fruit types found in the genus. It is important to state that we have yet to encounter a tetramorphic population in which all four principal fruit types (G, C, E and M) occur. However, we have found a trimorphic population of *F. graciliflora* subsp. *sulcata* in Algeria (near Collo, Little Kabyly; Xena de Enrech & Mathez no. 870) associating rare C fruits with G and E ones (Xena de Enrech & Mathez 1989). The combination of these three fruit types is unlike any we have hitherto described. The fact that all possible combinations do not occur in all taxa can be explained by postulating the presence of a gene associated with a linkage group, which could control recombination within the chromosome segment (Klekowski 1988). This gene would be active exclusively in dimorphic populations and inactive in all others having more than two morphs. Furthermore, activation factors related to linked genes may also be implicated as suggested for *Primula vulgaris* (Webster & Grant 1990).

We can suppose that the combination of fruit types present in the different taxa of *Fedia* correspond with the following linked allele pairs:
Fedia cornucopiae: fruit types E and G, alleles *GC* and *gC*.
Fedia pallescens: fruit types C and G (and M); alleles *GC* and *gc* (and *Gc*).
Fedia graciliflora subspp. *graciliflora*, *snassenorum*, and *diana*: fruit types C and G; alleles *GC* and *gc*; *F. graciliflora* subsp. *calycina*: fruit types C and G (and M); alleles *GC* and *gc* (and *Gc*); *F. graciliflora* subsp. *sulcata*: fruit types G and E (and C); alleles *GC* and *gC* (and *gc*).

It is interesting to speculate on the possible origin of the genetic system which has given rise to fruit polymorphism in *Fedia*. Two likely scenarios are:

(i) The system which produces the E and G fruit types results from an association of the linked allele pairs *GC* and *gC*. This system could have arisen from the monomorphic system *GC/GC* by a single mutation $G \rightarrow g$. Another mutation $C \rightarrow c$ and a crossing-over event would then produce all the observed fruit types. However, as earlier mentioned, our crossing experiments suggest that the diploid genotype *GGCC* is lethal. If this is true, then it is unlikely that this genotype is the ancestral one.

(ii) The system which produces the G and C fruit types results from an association of the linked allele pairs *Gc* and *gc*. A single crossing-over event between these linked pairs would lead to the E and M fruit types. The E and M fruit types have as yet to be found in the same natural population. So that a simple unique crossing-over event is not sufficient to explain the independent appearance of the linked groups *gC* and *Gc* from an ancestral *GC/gc* system. Notwithstanding, within *Fedia*, the *GC/gc* system is the most common condition and those taxa which carry it have a wide geographical distribution. For these reasons, we favour the notion that it is the ancestral type within *Fedia*.

Phylogenetic perspectives: fruit polymorphism in the *Valerianaceae*. Recently, a fruit polymorphism was described in a European species of *Valerianella* [*V. coronata* (L.) DC.], a genus closely related to *Fedia* (Martin & Mathez 1991). One fruit type is characterized by non-inflated sterile locules and well-developed calyx having six teeth; this type is comparable to the type C fruit in *Fedia*. The other fruit type has inflated sterile locules and a reduced calyx and appears similar to *Fedia* G type fruits. *Valerianella coronata* was previously treated as two distinct species because it was not recognized as having polymorphic fruits. Unlike *Fedia* which is mostly allogamous, *Valerianella coronata* is strongly autogamous and its fruit polymorphism genetic system exhibits no dominance. Notwithstanding these differences in their genetic systems, one can still draw parallels between them. In particular, they share two similar fruit types, again suggesting that these represent the ancestral state of the *Fedia* dimorphism. As mentioned earlier, other documented examples of fruit polymorphism in *Valerianaceae* are those of several American species of *Valerianella* and all *Plectritis* species, in which only the pericarp is involved. As far as is known, fruit polymorphism within the family *Valerianaceae* is restricted to aforementioned three genera. It is interesting that Weberling (1970) emended the subtribe *Fediinae* Graebn. to accommodate these three genera: all their species are annual and lack pappus on their fruits, and we do not know any case of development of the sterile locules pericarp in other genera of the family. Within the subtribe, not all species exhibit fruit polymorphism, however, when it is present, it seems likely to be the product of a single ancestral genetic system, i.e. the fruit polymorphism represents a synapomorphy for the subtribe.

The best known example of plant polymorphisms both in terms of genetics and evolution is that of heterostyly. In the case of heterostyly there is a whole suite of morphological and biological characters that converge to favour outbreeding. The benefits derived from allogamy are many-fold and may explain why several comparable genetic systems have evolved a similar type of '*S*' supergene in unrelated angiosperm families (Vuilleumier 1965, Heitz 1973, Vekemans & al. 1990). Although rarely encountered, fruit polymorphisms are similarly implicated in important biological functions, i.e. dissemination of diaspores, and therefore have been a target for natural selection. The fruit polymorphisms here discussed are poorly known in comparison to the heterostyly genetic system and merit more profound study.

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