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MALE STERILITY AND ECOLOGY OF DUTCH ORIGANUM VULGARE POPULATIONS

J. H. IETSWAART, R. A. BAREL and M. E. IKELAAR

Vakgroep Biosystematiek, Biologisch Laboratorium, Vrije Universiteit, De Boelelaan 1087, 1081 HV Amsterdam

SUMMARY

Male sterility was investigated in 19 Dutch *Origanum vulgare* populations by counting stamens and relating the numbers to several environmental factors. A mean of 11.5% male sterility was found for all populations, while 12 populations had a low value of 0–4.5% and the other 7 a higher one of 8.9–64.2%. Of the 53 plants counted 43% showed no staminal reduction and 57% a reduction of 0.2–100%. Only 2 plants were found with a 100% reduction, which is c. 4%. Considerable variation in male sterility was established for individual plants within one population and also, rather frequently, for different stems on one plant. Of 4384 flowers counted 9.5% had no stamens, while 1.3% had 1, 1.5% had 2 and 1.0% had 3 well developed stamens. The remaining 86.7% had all 4 stamens well developed. It was found that populations growing in relatively undisturbed *Mesobromion/Trifolion* vegetation possessed low male sterility values, and that populations in disturbed *Arrhenatherion/Lolio-Potentillion* vegetation often had much higher male sterility percentages. Further it was ascertained that small, isolated populations usually had a much higher male sterility than compact populations. No correlations could be found between male sterility and the following environmental factors: acidity, calcium, phosphorus, organic matter, sand, clay, gradient and aspect.

1. INTRODUCTION

Reduction of stamens is found in several plant groups. The extent of this reduction shows much variation. Generally speaking this phenomenon can be best indicated as male sterility, however, when completely female plants occur the term gynodioecy can be used (see e.g. KÜGLER 1970). An up to date literature survey on the subject is given by VAN DAMME (1983), who worked on *Plantago lanceolata*.

In the Labiatae male sterility and gynodioecy occur rather frequently (HEYWOOD & RICHARDSON 1972), and in the genus *Origanum* c. 35% of all (38) species show male sterility (IETSWAART 1980). Female flowers, as in all other genera of the Labiatae, are smaller than the bisexual ones. The only *Origanum* taxon for which male sterility was comprehensively investigated is *O. vulgare*. LEWIS & CROWE (1956) state that in European *O. vulgare* populations 30–50% male sterility occurs while KHEYR-POUR (1980) gives 1–62% for West-Europe; both percentages are based on counting whole plants and not individual flowers. Several theories have been developed on the heredity of male sterility in *O. vulgare*, some supported by computer simulated models (JAIN 1968; LEWIS 1941; LEWIS

& Crowe 1956; Valdeyron et al. 1973). For the moment the most likely theory is that drafted by Kheyr-Pour (1975, 1980): several cytoplasmatic factors in combination with nuclear genes on several loci determine the rate of male sterility. The related *Thymus vulgaris* has also been studied in this respect (Dommée 1976; Dommée et al. 1978; Valdeyron et al. 1977). The results from both the *Origanum* and the *Thymus* investigations are basically the same.

Much has been written on the advantages of the production of female flowers. In general it can be said that they are "cheaper" to produce and that they promote cross-fertilization (Lewis & Crowe 1956). For the Labiatae investigated it was found that female flowers produce more vigorous (Kheyr-Pour 1975) and more numerous progeny (Assouad et al. 1978).

The aim of the present study is to examine male sterility in a number of Dutch populations of *O. vulgare* ssp. *vulgare* in relation to some environmental parameters.

2. METHODS

The present study was carried out in the field in 1980. In all 19 *O. vulgare* populations were selected. Of these 8 were found in Zuid-Limburg, 6 in the southwestern part of The Netherlands, mainly in Zeeland, and the remaining 5 in the eastern part of Gelderland, in the area of Rivers Rhine and Waal.

The vegetation from these populations was analysed, and at the same time gradient and aspect of the sites etc. were measured. Per population 1–4 relevés were made according to the methods described by Den Held & Den Held (1980), using the decimal scale for estimation of the quantitative occurrence as given by Londo (1975). Ten square meters were established as the minimum area value. A synthesis of the relevés data was made with the aid of the computer program TABORD (Van der Maarel et al. 1978).

In connection with each relevé, a soil sample was taken from the upper 10 cm layer, which was analysed for its content of phosphate, calcium and organic matter, as well as for its particle size and pH, with methods mainly from Faniran & Areola (1978).

For each population the percentage male sterility was determined by counting the stamens in all the flowers from 1–8 selected plants. These plants had from 1–10 stems, and the number of stamens was counted only once in the season. The plants were always chosen by taking first a rough impression of the degree of variation of male sterility in the populations. Because *O. vulgare* produces stolons, specimens were considered only to be two different plants, when they were more than 1 m apart.

3. RESULTS

3.1. Description of populations

In *table 1* some data are given regarding size, geographical position and similar

Table 1. Size, position etc. of the *O. vulgare* populations investigated.

Zuid-Limburg		
1. Dolsberg	some 100 plants on c. 750 m²	1–6 in the same area of Zuid-Limburg; neighbouring populations always within 1–2 km
2. Reijmerstok	some 20 plants on c. 10 m²	
3. Wijlre	several thousands of plants on several hectares	
4. Gulpen	c. 20 plants on c. 30 m²	
5. Schin op Geul 1	several hundreds of plants on a few hectares	
6. Schin op Geul 2		
7. Maastricht	c. 7 plants on 2 m²	7 and 8 isolated from the other Zuid-Limburg populations and probably also from the Belgian ones consequent on distance and position with respect to river Maas, canals and the city of Maastricht; 8 intensively grazed
8. Neercanne	c. 75 plants on c. 100 m²	
Zeeland region		
9. 's-Gravenpolder	c. 50 plants on c. 100 m²	at c. 3 km from the other populations in the Zak van Zuid-Beveland
10. Yerseke	c. 7 plants on c. 500 m²	10–12 at the moment more or less isolated from the other Zeeland populations, consequent on dike-strengthening, but until very recently connected with these, and also themselves part of large populations
11. Koekoek	c. 15 plants on c. 20 m²	11 and 13 in the Zak van Zuid-Beveland; neighbouring populations within c. 1.5 km
12. Wemeldinge	c. 50 plants on c. 750 m²	see 10
13. Driewegen	c. 5 plants on c. 10 m²	see 11; heavily manured
14. Welberg	c. 500 plants on c. 1000 m²	isolated in western Brabant
Rhine-Waal region		
15. Winssen	c. 150 plants on c. 10.000 m²	size of this and neighbouring populations (now at c. 3 km) much reduced, consequent on recent dike-strengthening
16. Babberich 1	5 plants on c. 4 m²	isolated from the other Rhine-Waal populations (7 km), except Babberich 2
17. Rhenen	c. 200 plants on c. 3000 m²	isolated from the other Rhine-Waal populations (11 km)
18. Babberich 2	c. 40 plants on c. 200 m²	see 16; heavily manured
19. Doornenburg	several hundreds of plants on c. 10.000 m²	isolated from the other Rhine-Waal populations (7 km)

factors of the populations. The number of specimens per population varies from 5 to several thousands, and the area from 2 m² to several hectares. In Zuid-Limburg most populations merge into each other. In the Zeeland and the Rhine-Waal region, however, populations are more or less separate and have been for a long time, or they have been recently separated through dyke-strengthening. This strengthening of outer dykes also has caused a sharp decrease in the number of plants in some populations, e.g. those in the area of Yerseke and Winssen. Further it has been observed that intensive grazing, including manuring, also caused a decrease in the number of plants, e.g. the populations of Neercanne, Driewegen and Babberich 2. Populations are not only separated from each other by distance, but also in a number of cases by the presence of rivers and/or canals, e.g. the populations of Maastricht, Neercanne, Rhenen and Doornenburg.

3.2. Male sterility

In *table 2* are brought together the data of the stamen counts in the 19 *O. vulgare* populations, resulting in male sterility percentages for stems, individual plants and populations. Because these data are largely self evident, only a few additional remarks are made. For the populations investigated male sterility varies from 0–64.2%, while the mean value is 11.5%. For the Zuid-Limburg, Zeeland and Rhine-Waal populations the averages are 9.9%, 9.4% and 13.4%, respectively.

Between individual plants within one population often much variation in male sterility exists, e.g. Doornenburg, but also different stems of the same plant rather frequently show considerable variation, e.g. the last plant of the Rhenen population. Of the 53 plants counted 43% show no reduction of stamens, while the other 57% show a reduction of 0.2–100%. Only 2 plants were found with a 100% reduction, which is c. 4%. Of all 4384 flowers counted 9.5% have no stamens, 1.3% 1 stamen, 1.5% 2 stamens and 1.0% 3 stamens developed. the remaining 86.7% have all 4 stamens well developed. Finally it should be concluded that the maximum male sterility found, 64.2%, agrees with the maxima given by KHEYR-POUR (1980).

3.3. Vegetation

One of the issues of the vegetation analyses with TABORD was the division of the relevés in two clusters, which will be discussed below. The nomenclature used here for the syntaxa, which are mainly treated on the alliance level, is chiefly according to WESTHOFF & DEN HELD (1969). The first cluster consists of the relevés of the population 1, 2, 3, 5 and 6 from the Zuid-Limburg group and 12 from the Zeeland group. The vegetation in this cluster belongs to the *Mesobromion* and *Trifolion medii*, but several character taxa from the *Arrhenatherion elatioris* are present and some of the order *Festuco-Sedetalia*. The second cluster, comprising mainly relevés of the Zeeland and Rhine-Waal populations, principally consists of *Arrhenatherion elatioris* vegetation, but fairly strong influences are present from the *Lolio-Potentillion* and the *Trifolion medii*, and some weaker from the order *Artemisietalia vulgaris*. According to SÝKORA (1980, 1982) *Lolio-Potentillion* is now the correct name for *Agropyro-Rumicion crispi*.

To summarize it can be stated that *O. vulgare* in The Netherlands is found in vegetations with character species chiefly from the *Arrhenatherion elatioris* and the *Lolio-Potentillion*, and to a lesser degree from the *Trifolion medii* and

Table 2. Male sterility values at various levels for the *O. vulgare* populations, all in % and based on stamen counts. A; separates the values for the individual plants.

	mean value for popula-tion	value(s) for plant(s)	values for stems	flowers with resp. 0, 1, 2 and 3 stamens	
1. Dolsberg	0	0	0, 0	0, 0, 0, 0	(n= 85)
2. Reijmerstok	0	0; 0; 0; 0	0; 0; 0; 0;	0, 0, 0, 0,	(n=309)
3. Wijlre	0.5	0; 1.0	0, 0; 0, 1.6	0, 0, 0, 2.2	(n= 46)
4. Gulpen	0.9	0; 1.6	0, 0; 0, 4.8	0, 0.9, 0.5, 0	(n=212)
5. Schin op Geul 1	3.1	0; 7.1	0, 0; 0, 20.0	0, 0, 6.3, 0	(n= 32)
6. Schin op Geul 2	4.5	0; 0.9; 22.9	0; 0, 1.3; 22.9	2.0, 0, 4.0,2.0	(n= 50)
7. Maastricht	17.7	0.5; 26.4	0, 0.8; 33.1, 43.2, 92.4	16.8, 0.9, 0.3, 0.6	(n=334)
8. Neercanne	21.5	1.2; 27.2	0, 1.8; 21.7, 42.9, 44.3, 54.0	13.6, 5.3, 6.4, 2.9	(n=376)
9. 's-Gravenpolder	0	0	0, 0	0, 0, 0, 0	(n= 8)
10. Yerseke	0	0; 0	0; 0	0, 0, 0, 0	(n=247)
11. Koekoek	1.5	0; 2.8	0, 0; 0, 4.2	1.6, 0, 0, 0	(n= 65)
12. Wemeldinge	2.2	0.9; 5.6	0, 0, 6.5; 0, 0, 12.5	1.1, 0.7, 0.7, 0.4	(n=281)
13. Driewegen	17.4	13.6; 23.8	9.3, 17.9; 14.3, 42.9	12.5, 2.7, 4.5, 2.7	(n=112)
14. Welberg	27.4	27.4	3.5, 16.2, 22.7, 93.1	22.0, 3.5, 4.0, 3.1	(n=227)
15. Winssen	0	0; 0; 0; 0	0, 0; 0; 0, 0; 0, 0	0, 0, 0, 0,	(n=231)
16. Babberich 1	1.0	0.2; 1.7; 25.0	0, 0, 0, 0, 0, 0, 16.7; 0, 0, 0, 0, 0, 0, 5.9, 1.7; 25.0	0.8, 0, 0, 0.8	(n=369)
17. Rhenen	8.9	0; 0.9; 1.2; 9.9; 24.7	0; 0.9; 1.2; 9.9; 0, 0, 0, 0, 0, 2.7, 4.2, 12.8, 29.3, 91.1	7.1, 2.1, 1.4, 1.4	(n=863)
18. Babberich 2	10.5	0; 0; 1.0; 2.7; 51.5	0, 0; 0; 0.4, 7.1; 0, 4.3; 18.3; 30.4	7.9, 2.1, 1.4, 1.4	(n=292)
19. Doornenburg	64.2	0; 0; 0; 12.2; 39.3; 82.1; 100; 100	0; 0; 0, 0; 3.4, 6.3, 12.5, 25.0; 33.3, 44.4, 50.0; 82.1; 100, 100, 100, 100	62.9, 0.4, 1.6, 0.8	(n=245)

the *Mesobromion*. This means that *O. vulgare* here mainly grows in relatively moist vegetation which is more or less rich in nutrients. This vegetation chiefly comprises high growing grasses and other herbs, and is considerably affected by man through manure, cutting and grazing. It seems likely that *O. vulgare* tolerates these conditions rather than prefers them, considering the situation

Table 3. pH and percentage dry weights of $CaCO_3$, phosphate (in K_2HPO_4 equivalents) and organic matter for the *O. vulgare* populations investigated.

population	pH	Ca	P	organic matter
1. Dolsberg	7.1	25	3.5	5.7
2. Reijmerstok	–	–	–	–
3. Wijlre	7.1	15	2.8	3.5
4. Gulpen	7.0	22	0.6	4.9
5. Schin op Geul 1	7.1	2	1.9	4.8
6. Schin op Geul 2	7.2	7	3.7	2.9
7. Maastricht	6.9	3	1.8	3.7
8. Neercanne	6.8	14	1.7	5.5
9. 's-Gravenpolder	6.8	3	1.4	5.1
10. Yerseke	6.5	2	2.4	3.0
11. Koekoek	7.2	5	3.0	3.5
12. Wemeldinge	6.7	4	1.5	2.5
13. Driewegen	7.1	5	3.3	5.9
14. Welberg	7.2	3	3.6	3.6
15. Winssen	7.8	6	0.7	4.8
16. Babberich 1	6.7	0	0.9	3.7
17. Rhenen	4.5	1	0	5.1
18. Babberich 2	6.9	0	1.3	0.9
19. Doornenburg	6.7	8	1.7	1.9

elsewhere in West-Europe (GARCKE 1972; GRIME & LLOYD 1973; GUINOCHET & DE VILMORIN 1975; HEGI 1927).

3.4. Abiotic environment

In *table 3* the following soil factors are given for the populations: pH, and percentages calcium-carbonate, phosphate and organic matter. From this table the following conclusions can be drawn. The spread in the pH values (4.5–7.8) is nearly the same as GRIME & LLOYD (1973) give for *O. vulgare* in Central-England. Some of the values for calcium are high, but not unusual for the marly soils of Zuid-Limburg. None of the values for phosphate and organic matter are at all extreme (DE BAKKER 1979).

In *fig. 1* the sand-clay ratio is plotted for the populations. From this it becomes clear that all soils contain a large amount of sand, besides some clay and silt.

For all populations the aspect was established in degrees with north as zero, west = 90°, south = 180° etc. Further, the angle of inclination was measured. In this way it was ascertained that sixteen populations were found on a slope, and that the mean value for all populations is 28° ± 17°. In Zuid-Limburg these slopes are formed by natural hills, in the other areas by dykes. Fourteen populations grew on a slope with a southern aspect. The mean value for the populations here is 161° ± 60° (see also *fig. 2*).

Summarizing, it can be said that *O. vulgare* in The Netherlands is found on more or less neutral sandy loam with a normal percentage of phosphate and

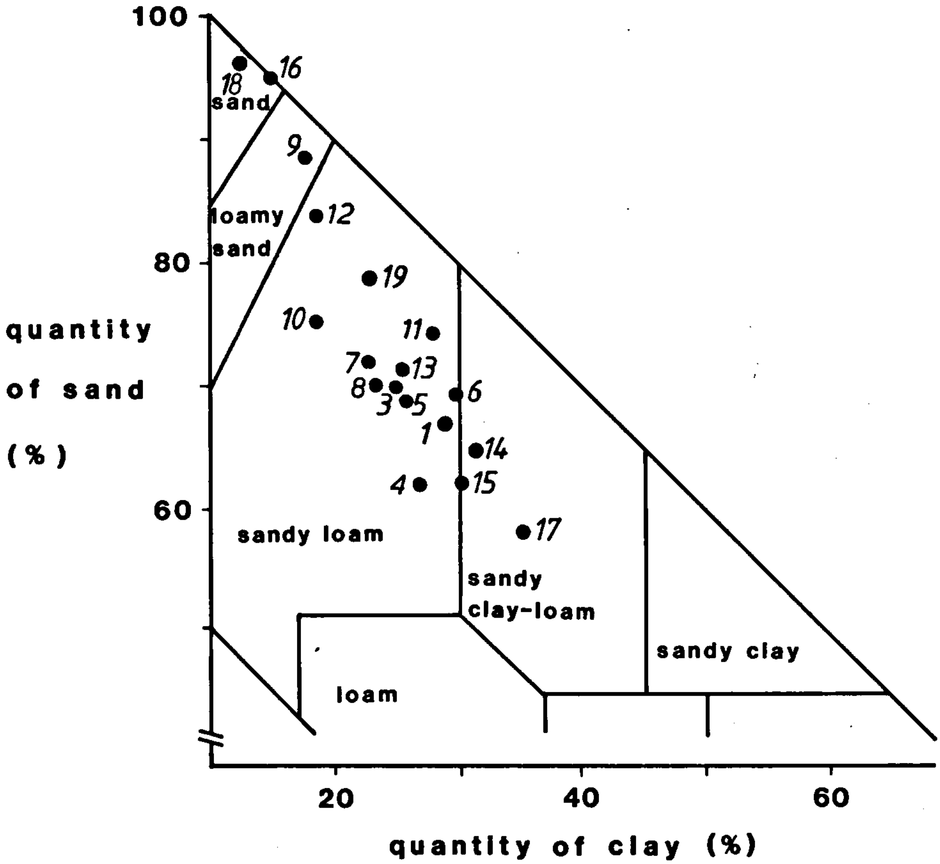

Fig. 1. Scatter diagram of the sand-clay ratio for the *O. vulgare* populations investigated. The silt fraction is not considered, and the value for this has to be added to the sand and clay values to obtain 100% for each population.

organic matter, and a varying, sometimes, high, percentage lime. Some of these data are confirmed by KRUYNE et al. (1967). Further it can be concluded that *O. vulgare* in The Netherlands grows on slopes, and principally on those with a southern aspect.

4. CORRELATIONS

In order to correlate the male sterility data with the values measured for the environmental circumstances and similar factors, the *O. vulgare* populations are divided in two groups, one with a male sterility of 0–5% (group 1), and another with a male sterility of more than 5% (group 2). So group 1 comprises 12 popula-

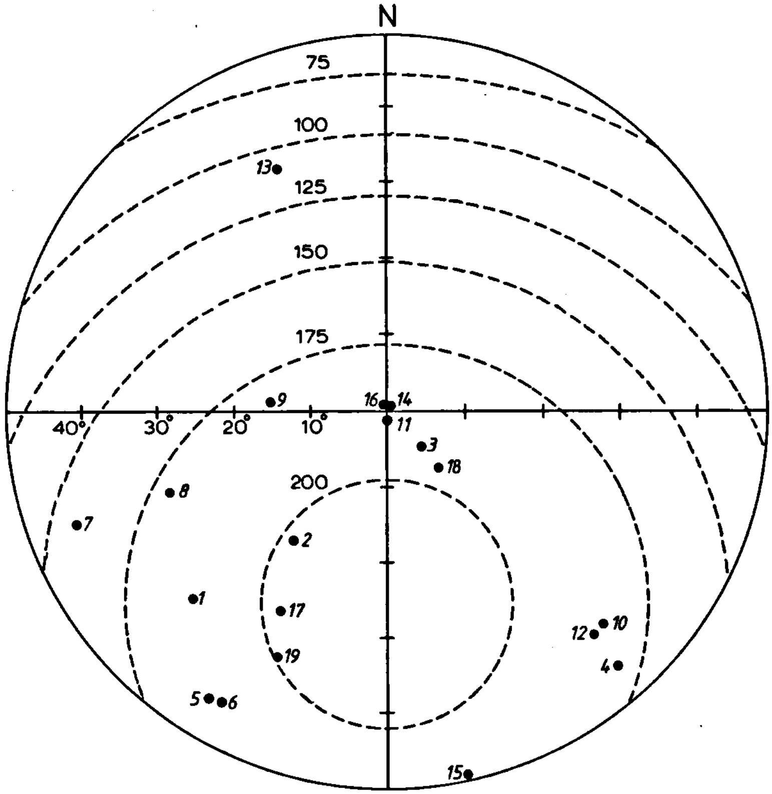

Fig. 2. Projection on the top of a globe of the combined values of gradient and aspect for the *O. vulgare* populations investigated, according to GRIME & LLOYD (1973). The broken lines give the total minutes of direct sushine per day in July.

tions: Dolsberg (1), Reijmerstok (2), Wijlre (3), Gulpen (4), Schin op Geul 1 (5), Schin op Geul 2 (6), 's-Gravenpolder (9), Yerseke (10), Koekoek (11), Wemeldinge (12), Winssen (15) and Babberich 1 (18); while group 2 includes the other 7 populations: Maastricht (7), Neercanne (8), Driewegen (13), Welberg (14), Rhenen (17), Babberich 2 (18) and Doornenburg (19). From *table 4* it is evident that there is almost no difference in the values for acidity, phosphate, organic matter, sand, clay and gradient between the two groups. More or less different values are found for calcium and aspect, but these differences are not significant. In contrast with the just established non-correlations with the occurrence of male sterility, vegetation and position of the population show a positive correlation, which will be dealt with below. The *Mesobromion* vegetation cluster (see 3.3) comprises the populations 1, 2, 3, 5, 6 and 12, which are all constituents of population group 1. The mean male sterility in this cluster is 1.7% ± 1.9%. The other vegetation cluster, *Arrhenatherion*, comprises the populations 4, 7–11 and 13–19, of which 6 populations belong to group 1 (4, 9, 10, 11, 15 and 16)

Table 4. Mean values for a number of environmental factors for *O. vulgare* populations with a low male sterility (group 1; n = 12), and for populations with a high male sterility (group 2; n = 7).

	pH	Ca (%)	P (%)	organic matter (%)	sand (%)	clay (%)	inclination (degrees)	aspect (degrees)
group 1 (male sterility < 5%)	6.5–7.8	8.3±8.5	2.0±1.1	4.0±1.1	74±12	14±5	28±16	188±65
group 2 (male sterility > 5%)	4.5–7.2	4.9±4.8	1.9±1.2	3.8±1.9	72±11	16±7	29±17	134±51

and the other 7 to population group 2 (7, 8, 13, 14, 17, 18, 19). The mean male sterility value for this cluster is 13.1% ± 18.0%. This correlation can be translated as follows: in *Origanum* populations strongly influenced (= disturbed) by man a higher percentage male sterility occurs than in populations with a relatively low disturbance.

A combination of the data in *tables 1* and *2* shows that population group 1 comprises all populations which are found in a situation of non-isolation. There is one exception in the population of Babberich 1. On the other hand group 2 covers populations which are all, except the one at Driewegen, more or less isolated from each other. These isolated populations are usually also small. So in small and isolated populations a higher percentage male sterility is found than in non-isolated (or large) populations.

5. DISCUSSION

A relatively high percentage male sterility in *O. vulgare* populations growing in disturbed vegetations in The Netherlands agrees with data for southern France given by ELENA-ROSSELLO et al. (1976) for *O. vulgare* and by DOMMÉE et al. (1978) for *Thymus vulgaris*. Remarkably, however, we found a very low percentage of 100% male sterile plants and a comparatively high percentage of so-called (KHEYR-POUR 1980) intermediates. The following explanation for this phenomenon can be given. Female (= 100% male sterile) plants have the advantage of producing more vigorous and numerous progeny (see introduction), but have the handicap of obligatory outcrossing (DOMMÉE et al. 1978). The intermediate forms combine the advantage of the female flowers with those of the bisexual ones, i.e. being not completely dependent upon pollinating insects. For small and isolated populations visiting honey bees are an uncertain factor in reproduction. A number of the investigated *Origanum* populations are small and isolated, in addition to which they are often associated with relatively high and dense vegetation. None of these factors promote pollination, so it seems functional that in these populations a comparatively large number of intermediated occurs, and seldom completely female plants.

The main influence of the environment on male sterility is most probably by selection (see amongst others VALDEYRON et al. 1973). However, from the presence of differences in percentage male sterile flowers between the stems of one specimen and the branches of one stem, which also has been observed, it can be supposed that the environmental conditions also influence, to some degree, the expression of the male sterility controlling factors. The same may be concluded from the presence of flowers with 1–3 stamens reduced. This assumption agrees with data of VERESCHAGINA & MALANINA (1974) and WILLSON (1979).

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