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Breeding systems and cytology in Greek populations of five *Limonium* species (*Plumbaginaceae*)*

Abstract

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Information is provided about the reproductive mechanisms and the chromosome numbers of *Limonium palmare*, *L. roridum*, *L. graecum*, *L. virgatum* and *L. narbonense*, notes on their taxonomy are given and the correlation between their breeding systems and cytology is discussed. *L. palmare* and *L. roridum* are facultatively apomictic with $2n = 4x = 34$ and $2n = 5x = 43$, respectively. *L. graecum* is apomictic and its chromosome number of $2n = 6x = 52$ is reported for the first time, *L. virgatum* is also apomictic with $2n = 3x = 27$ and *L. narbonense* is sexual with $2n = 6x = 54$ and $2n = 8x = 72$. The latter number is a new record and the highest number reported so far for the genus *Limonium*.

Key words: angiosperms, sea lavender, Greece, chromosome number, sexual reproduction, apomictic reproduction.

Introduction

The genus *Limonium* comprises about 350 (Kubitzki 1993) or even 400 species (Palacios & Gonzales-Candelas 1997), most of them concentrated in the Mediterranean region, which constitutes the centre of its diversity. Due to its reproductive behaviour, i.e. both sexual and apomictic reproduction, as well as the frequent occurrence of polyploidy, *Limonium* is one of the most interesting and taxonomically difficult plant groups.

Limonium is characterized by an incompatibility system linked with pollen and stigma dimorphism. According to Baker (1948, 1953b-c) and Erben (1978, 1979) the following four pollen and stigma combinations occur: (A) cob-like stigmata and coarsely reticulate pollen grain surface; (B) papillate stigmata and finely reticulate pollen grain surface; (C) cob-like stigmata and finely reticulate pollen grain surface, (D) papillate stigmata and coarsely reticulate pollen grains. Combinations A and B are self-incompatible (plants self-sterile), while C and D are

* The present paper is dedicated to Prof. Werner Greuter on the occasion of his 68th birthday.

self-compatible (plants self-fertile). Species presenting both combinations A and B in each population are sexually reproduced (cross-fertilized), while those with only A or B are apomictic. Species with the combinations C or D are self-fertilized.

In Greece, *Limonium* is represented by c. 40 species, some of which need taxonomic clarification. According to our cytological and breeding system data, in western Greece sexual diploid taxa with $2n = 18$ dominate, having their easternmost limit of distribution in the Messenian Mani (Kardamili) of S Peloponnisos (Artelari 1984, Artelari & Kamari 1986, 1995, 2000). In contrast, in the Aegean area most taxa are polyploid and apomictic (Artelari 1989a-c, 1992, Artelari & Georgiou 1999, 2000, 2002).

In this work reproductive mechanism and cytology of Greek populations of *Limonium palmare* (Sm.) Rech. f., which is endemic to the Aegean area, *L. roridum* (Sibth. & Sm.) Brullo & Guarino and *L. graecum* (Poir.) Rech. f., which are endemic to the E Mediterranean, and of *L. virgatum* (Willd.) Fourr. and *L. narbonense* Mill. aggr., which have a wider Mediterranean distribution, are studied, notes on their taxonomy are given and the correlation between their reproductive mechanisms and cytology is discussed.

Material and methods

This study is based on plants collected by the authors as well as on herbarium specimens used for comparison. Voucher specimens of our collections are kept in UPA.

41 populations of *Limonium palmare* from Kiklades (Tinos, Siros, Paros, Antiparos and Naxos), 25 of *L. roridum* from Kiklades (Tinos, Siros, Dilos, Serifos, Paros and Naxos), Elafonisos island (SW of Peloponnisos) and N Kriti, one of *L. graecum* from Naxos, 14 of *L. virgatum* and 11 of *L. narbonense* from the area of Magnisia were studied to assess the reproductive mechanism. Pollen and stigma type combinations of the flowers were determined according to Erben (1978, 1979). The pollen stainability was estimated by using cotton blue, as is described in Artelari & Kamari (1986).

For the cytological study five populations of *Limonium palmare*, four of *L. roridum*, one of *L. graecum*, three of *L. virgatum* and four of *L. narbonense* have been used (Table 1). Seeds were germinated in Petri dishes on moistened filter paper and root tips were pretreated according to the method described in previous papers (Artelari 1984, Artelari & Kamari 1986).

Results and discussion

Notes on the taxonomy of the material studied

Limonium palmare, *L. roridum* and *L. graecum* are very closely related taxa and subject of considerable taxonomic and nomenclatural confusion. *L. roridum* has been treated by many authors as a synonym of *L. graecum* (Halácsy 1904, Hayek 1928, Rechinger 1943, Pignatti 1972, Bokhari & Edmondson 1982, Mayer 1995, Raus 1996, Artelari & Georgiou 2002, Chilton & Turland 2004), while *L. palmare* was included either in *L. graecum* (Halácsy 1904, Rechinger 1943) or *L. roridum* (Boissier 1879), or was considered synonymous with *L. graecum* (Hayek 1928). Greuter & al. (1989) include all three taxa in the *L. palmare* group, considering *L. roridum* as synonym of *L. graecum*, and *L. palmare* as a distinct species. Brullo & Guarino (2000) distinguish *L. roridum* as a separate species, while Artelari & Georgiou (2002) follow the majority of the authors and place it under *L. graecum*.

The populations from Kiklades, Elafonisos and N Kriti used in the present paper belong to the *Limonium palmare* group and present differentiation in a number of morphological characters correlated with different chromosome numbers. After consultation with Dr Erben (pers. comm.), we adopt the recognition of three separate species, *L. palmare*, *L. roridum* and *L. graecum*.

Thus, we place under *Limonium palmare* plants with branches \pm straight, tuberculate-scarious, leaves abruptly tapering into a petiole longer than the rotundate to obcordate lamina, inner bract glabrous, middle bract oblong, calyx sparsely hairy to subglabrous with limb about equal to

the tube and lobes acute up to 0.8 mm long; they have a chromosome number of $2n = 34$.

Plants having the same habitus with the iconotype of *Statice rorida*, characterized by strongly and densely tuberculate, zig-zag articulate segments forming mostly wide angles, leaves gradually tapering into petiole about equal to the lamina which is usually oblong, inner bract hairy at the upper part, middle bract rotundate, calyx usually densely hairy with limb shorter than the tube and lobes obtuse up to 0.3 mm long, are placed under *L. roridum*; they have a chromosome number of $2n = 43$.

Finally, plants with stems forming acute angles, finely tuberculate, with less sterile branches, leaves gradually tapering into petiole longer than the lamina which is oblong, longer spikes, inner bract glabrous and middle bract oblong, are placed under *L. graecum*; they have a chromosome number of $2n = 52$ (Table 1).

Based on the above data, material treated in previous papers as *Limonium graecum* (Artelari 1989a, Artelari & Georgiou 2002) is considered now either as *L. palmare* or *L. roridum* (see further comments under “Reproductive mechanism” and “Cytology”).

Given that *Limonium palmare* and *L. roridum* coexist on some of the Kiklades islands (Tinos, Siros, Paros and Naxos), intermediates with unstable characters are found. On Siros, *L. palmare* is limited to the west coast, *L. roridum* occurs on the south and southeast coast and intermediate populations are found between these areas, while on the other islands the intermediates are scattered. On Naxos, besides the above two taxa, *L. graecum* was also found only in a locality on the northeast coast (Lionas bay) opposite to the Donoussa island, which is the “locus classicus” of this taxon.

Limonium virgatum is a common taxon in Greece, often growing together with other *Limonium* taxa and forming intermediates with them (Pignatti 1972, Artelari 1984, Erben 1993). The populations studied here are stable and present the typical morphological characters of the species given in detail by Artelari & Georgiou (2002).

For *Limonium narbonense* we use here the term “aggregate”, because the Greek plants are very polymorphic and not well distinguished from the closely related *L. brevipetiolatum* Artelari & Erben. *L. brevipetiolatum* has been described from the Ionian islands and W Greece by Artelari & Erben (1986) and according to them, it mainly differs from *L. narbonense* Mill. [= *L. angustifolium* (Tausch) Turrit] in having shorter petioles and bracts, calyces and petals, and a different chromosome number ($2n = 54$ for *L. brevipetiolatum* and $2n = 36$ for *L. narbonense*). Having studied in the past years numerous populations and herbarium specimens from many Greek localities and found $2n = 36$ also in plants with the characters of *L. brevipetalum*, it became obvious that the morphological and cytological distinctions of these two taxa cannot be held up and that this group needs a detailed revision.

Reproductive mechanism

The populations of *Limonium palmare* were found to be dimorphic or monomorphic in respect to their pollen and stigma combination. In each dimorphic population both self-incompatible combinations A and B occur, while in each monomorphic population only one combination A or B is present. All populations have extremely ranging pollen stainability (0-99 %) and good seed production. The above data reveal that *L. palmare* is facultatively apomictic. Monomorphic populations with the combinations A (Naxos, *Phitos 16380*) and B (Milos, *Artelari 435*) treated in Artelari (1989a) as *L. graecum* has been revised as *L. palmare* according to the morphological and cytological differentiation given above of these closely related taxa.

The populations of *Limonium roridum* were also found to be monomorphic (A or B) or dimorphic. All populations have extremely ranging pollen stainability (0-86 %) and good seed production. The above data indicate that *L. roridum* is facultatively apomictic, too. Additionally, the fact that populations from Serifos (*Tiniakou 76, 90, 283*), Milos (*Artelari 429, 431, 438, 446*), Amorgos

(Tzanoudakis 7423, 7445, 7448, 7463) and Kithira (Artelari & Georgiou 1505, 1526), cited in Artelari (1989a) and Artelari & Georgiou (2002) as *L. graecum* and considered now as *L. roridum*, were either monomorphic or dimorphic, supports the facultatively apomictic behaviour of this taxon. Of great interest is the finding of a monomorphic population of *L. roridum* with the self-compatible combination D on the island of Dilos. According to Baker (1953b), combination D occurs in the majority of the “secondarily monomorphic species, which are not apomictic, but self-compatible”. However, the evidence from the above population suggests that it is probably apomictic and not self-fertilized. The pollen grains present the picture that characterizes apomictic taxa. They are variable in size, conspicuously large or conspicuously small, many of them have a bowl-like shape and the pollen stainability is low, 1-18(-28) %. The stained grains are always some of the larger ones, well-shaped and 4-5-colpate, but none of them has been observed germinating on the stigmata. These pollen grains according to Erben (1979) can be considered containing unreduced gametes. The probable apomictic behaviour of the above population is also supported by its pentaploid chromosome number of $2n = 43$. In an analogous case the Italian *L. avei* (De Not.) Brullo & Erben (= *L. longispicatum* Erben), which has the self-compatible combination C (‘B’ pollen and ‘Cob’ stigma), low pollen fertility (7-18 %) and the chromosome number $2n = 27$ (Erben 1978), is considered by Ingrouille (1984) “probably agamospermic” because it is triploid. A breeding system of similar complexity has been found in the heteromorphous triploid ($2n = 27$) Spanish *L. viciosoi* (Pau) Erben, in which dimorphic populations with the combinations A and B, monomorphic populations with the combination A or B, as well as monomorphic populations with the combination D have been observed (Erben 1979).

The population of *Limonium graecum* was found to be monomorphic with the self-incompatible combination B, low pollen stainability (0-4 %) and good seed production. The above data show that *L. graecum* is apomictic. Previous reports of *L. graecum* as facultatively apomictic (Artelari 1989a, Artelari & Georgiou 2002) actually refer to *L. roridum* (see above).

The populations of *Limonium virgatum* were found to be monomorphic with the self-incompatible combination B, low pollen stainability (0-35 %) and good seed production. These data confirm the apomictic behaviour of the species already reported by D’Amato (1949), Dulberger (1975), Erben (1979), Artelari (1984, 1989a) and Artelari & Georgiou (2002). Noticeable is that all the typical Greek populations of *L. virgatum* studied so far have the combination B (Artelari 1984, 1989a, Artelari & Georgiou 2002), while some intermediate populations of this taxon with other *Limonium* species present the combination A (Artelari 1984). Combination B is also reported for *L. virgatum* from Israel (Dulberger 1975), Mallorca (Llorens 1985) and Spain (Soler & Rosselo 1997). On the contrary, Baker (1953b) mentions *L. virgatum* as a dimorphic and sexual taxon, but states that “some varieties of it may not be dimorphic”.

All the populations of *Limonium narbonense* studied here were found to be dimorphic with both self-incompatible combinations A and B and high pollen stainability (50-96 %). Also the populations found in many other Greek localities were dimorphic with the same combinations A and B, e.g., in Evvia, the East Aegean islands, Peloponnisos, etc. (Artelari & Georgiou, unpublished data). The above data suggest that *L. narbonense* is sexually reproduced.

Cytology

Limonium palmare was found to be tetraploid with $2n = 4x = 34$ (Table 1, Fig. 1A). The karyotype possesses two long metacentric (m) ‘marker’ chromosomes, which, according to Erben (1978, 1979), are characteristic for the karyotypes of the taxa of *L.* subg. *Limonium* with the basic number $x = 8$ and are missing in the taxa with $x = 9$. Thus, $2n = 34$ has derived from the combination of $2 \times 8 + 2 \times 9$ genomes and indicates the hybrid origin of *L. palmare*. The above number has already been reported for material from Naxos (*Phitos 16380*) and Milos (*Artelari 435*), which, as mentioned above, was referred to as “*L. graecum*” Artelari (1989a) but is placed now

Table 1. Chromosome numbers and ploidy levels of *Limonium palmare*, *L. roridum*, *L. graecum*, *L. virgatum* and *L. narbonense* from the Aegean area (collectors: AC = Artelari & Chondropoulos, AG = Artelari & Georgiou, GM = Georgakopoulou & Manousou).

Taxon	Locality	Chromosome number	Ploidy level
<i>L. palmare</i>	Paros, Kolibithres (AC 1643)	$2n = 34$	4x
	Paros, Pounta (AC 1628)	$2n = 34$	4x
	Paros, Ag. Fokas (AC 1649)	$2n = 34$	4x
	Antiparos, Sifneikos Gialos (AC 1664)	$2n = 34$	4x
	Naxos, Moni Chrisostomou bay (AC 1677)	$2n = 34$	4x
<i>L. roridum</i>	Dilos (AC 1609)	$2n = 43$	5x
	Siros, Fabrika (AC 1765)	$2n = 43$	5x
	Siros, Lazareto (AC 1794)	$2n = 43$	5x
	Elafonnisos, Panagitsa bay (AG 1741)	$2n = 43$	5x
<i>L. graecum</i>	Naxos, Lionas (AC 1698)	$2n = 52$	6x
<i>L. virgatum</i>	Pref. Magnisia, Mamidakis bay (GM 215)	$2n = 27$	3x
	Pref. Magnisia, Afissos bay (GM 205)	$2n = 27$	3x
	Pref. Magnisia, Kalamos (GM 208)	$2n = 27$	3x
<i>L. narbonense</i>	Pref. Magnisia, Mamidakis bay (GM 216)	$2n = 54$	6x
	Pref. Magnisia, Chrisi Akti Panagias (GM 214 α)	$2n = 54$	6x
	Pref. Magnisia, Chrisi Akti Panagias (GM 214)	$2n = 72$	8x
	Pref. Magnisia, Alikes bay (GM 219)	$2n = 72$	8x

under *L. palmare*.

Limonium roridum was found to be pentaploid with $2n = 5x = 43$ (Table 1, Fig. 1B). In its karyotype also one pair of long metacentric (m) ‘marker’ chromosomes is present, showing that the above number has been derived from the combination of $2 \times 8 + 3 \times 9$ genomes and that *L. roridum* also originates from hybridization. The number $2n = 43$ is known from material from Andros (Artelari & al. 451, 454), Milos (Artelari 429, 431), Serifos (Tiniakou 76, 283) and Kithira (Artelari & Georgiou 1505, 1526) referred to by Artelari (1989a) and Artelari & Georgiou (2002) as *L. graecum* and placed now under *L. roridum*.

Limonium graecum was found to be hexaploid with $2n = 6x = 52$ (Table 1, Fig. 1C). The number of $2n = 52$ is counted for the first time for this taxon. The karyotype possesses two long metacentric ‘marker’ chromosomes, indicating that it has been derived from the combination of $2 \times 8 + 4 \times 9$ genomes and that it has a hybrid origin, too. Previous reports of $2n = 34$ and 43 for *L. graecum* (Artelari 1989a, Artelari & Georgiou 2002) actually refer to *L. palmare* and *L. roridum*, respectively (see above).

Limonium virgatum was found to be triploid with $2n = 3x = 27$ (Table 1, Fig. 1D). As is shown in Fig. 1D and has also been reported previously (Erben 1978, Artelari 1984, 1989a, 1992, Artelari & Georgiou 2002) the karyotype lacks the characteristic ‘marker’ chromosomes. The above chromosome number is also known from other Greek localities (Artelari 1984, 1989a, 1992, Artelari & Georgiou 2002) as well as from the Mediterranean region in general (D’Amato 1949, Erben 1978, 1979, 1993, Chichiricco & Tammara 1980, Brullo & Pavone 1981, Arrigoni & Diana 1993). Dolcher & Pignatti (1971) state this taxon to be both triploid with the number range $2n = 24-27$ and tetraploid with the number “c. 32”.

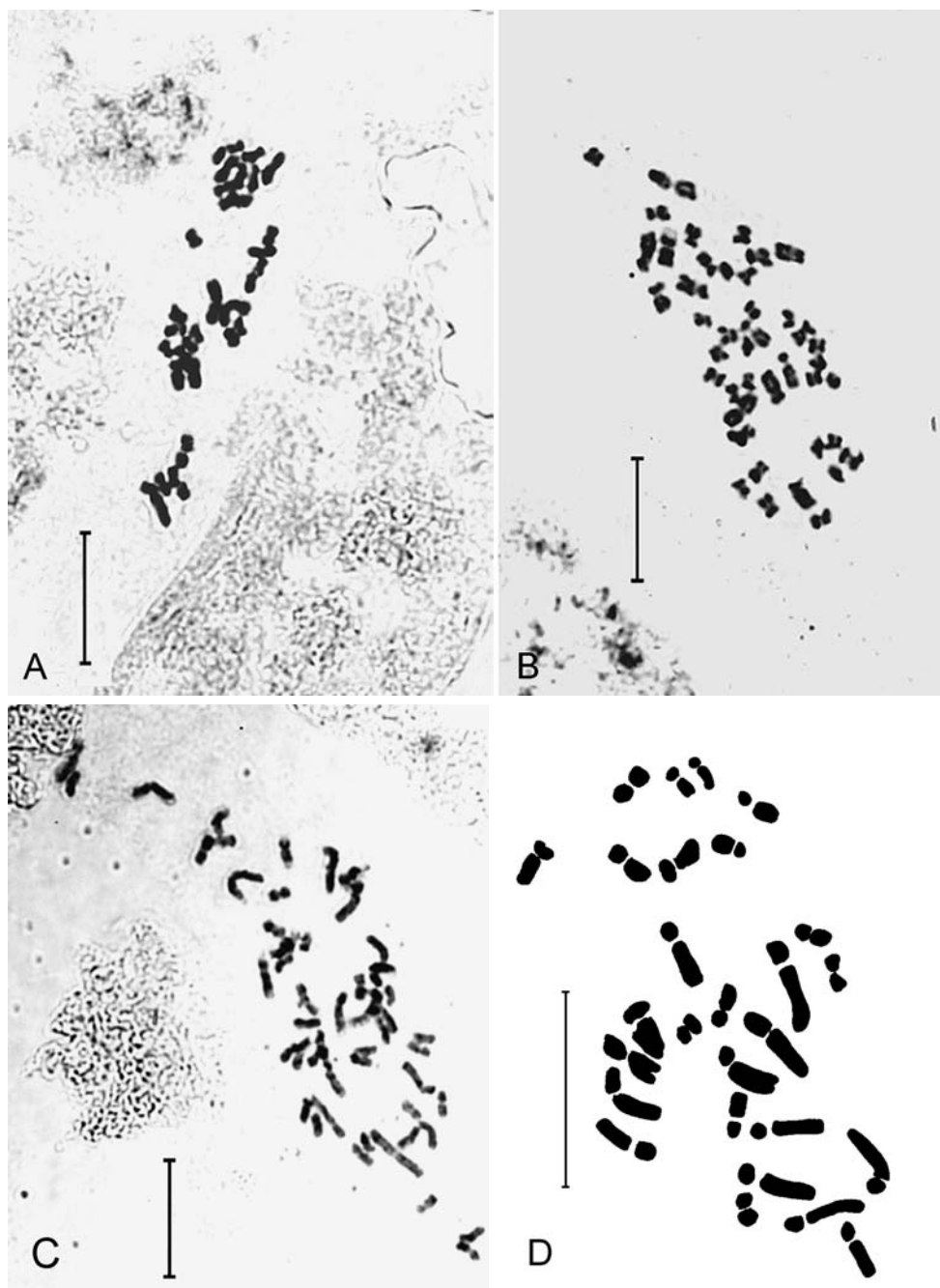


Fig. 1. Microphotographs of mitotic metaphase plates – A: *Limonium palmare* with $2n = 4x = 34$, material from Paros, Kolibithres (Artelari & Chondropoulos 1643); B: *L. roridum* with $2n = 5x = 43$, material from Dilos (Artelari & Chondropoulos 1609); C: *L. graecum* with $2n = 6x = 52$; material from Naxos, Lionas (Artelari & Chondropoulos 1698); D: *L. virgatum* with $2n = 3x = 27$; material from Magnisia, Kalamos (Georgakopoulou & Manousou 2008). – Scale bars = 10 μ m.

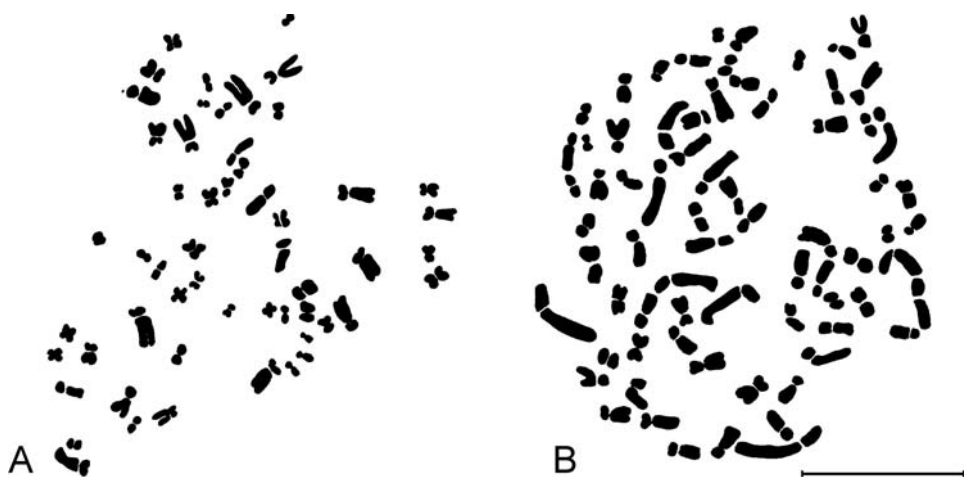


Fig. 2. Mitotic metaphase plates of *Limonium narbonense* – A: $2n = 6x = 54$, material from Magnisia, Chrisi Akti Panagias (Georgakopoulou & Manousou 214a); B: $2n = 8x = 72$ (Georgakopoulos & Manousou 214). – Scale bar = 10 μm .

The populations of *Limonium narbonense* were found to be hexaploid with $2n = 6x = 54$ and octoploid with $2n = 8x = 72$ (Table 1, Fig. 2). The chromosome number $2n = 6x = 54$ has also been counted for the closely related Greek endemic *L. brevipetiolatum* (Artelari & Erben 1986) as well as for the European relative *L. humile* Mill. (Erben 1979). *L. narbonense* was known so far as tetraploid with $2n = 36$ from Greece (Artelari 1992) and as diploid with $2n = 18$ and as tetraploid from the wider Mediterranean region (Baker 1953c, Erben 1978, 1979, 1993, Brullo & Pavone 1981, Palacios & al. 2000). Both hexaploid and octaploid karyotypes lack the ‘marker’ chromosomes (Fig. 2) and this is also the case in the karyotype with $2n = 36$ (Erben 1978, Artelari 1992). As is shown in Table 1, at the locality “Chrisi Akti Panagias” both chromosome numbers $2n = 54$ and 72 were counted. In this place, individuals with $2n = 72$ were found in the exterior side of the bay, exposed to wind and waves and it seems that their high ploidy level is a response to the extreme ecological conditions. These plants are more robust and advanced in flowering than those with $2n = 54$, but the detailed study of their morphological characters did not show any other significant difference. The octaploid number $2n = 72$ is the highest reported so far for the genus *Limonium*.

The pentaploid chromosome number of *Limonium roridum*, the hexaploid number of *L. graecum*, as well as the hexaploid and octaploid numbers of *L. narbonense* give support to the view expressed by Artelari & Georgiou (2002), that the Aegean region has a concentration of *Limonium* taxa with higher ploidy levels compared to the western and central Mediterranean.

Correlations between breeding system and cytology

Baker (1953a) first suggested that in *Limonium* apomixis arose through hybridization. Erben (1978, 1979) revealed the importance of cytological studies for the taxonomy of the genus and demonstrated the correlation between chromosome numbers and reproductive mechanisms. Thus, according to Erben’s hypothesis, the taxa of *L.* subg. *Limonium* with $2n = 25, 26, 34, 35, 42, 43$ (derived from different combinations of the basic numbers $x = 8$ and $x = 9$), as well as the triploid taxa with $2n = 27$ are apomictic hybrids. On the contrary, diploid and polyploid taxa with chromosome numbers derived from the basic number $x = 9$ are sexual.

Our results are in agreement with Erben's hypothesis (1978, 1979). The facultatively apomictic behaviour of *Limonium palmare* and *L. roridum* is correlated with the presence of both dimorphic and monomorphic populations and the chromosome numbers $2n = 34$ ($2 \times 8 + 2 \times 9$), $2n = 43$ ($2 \times 8 + 3 \times 9$) respectively. The apomictic behaviour of *L. graecum* is correlated with the chromosome number $2n = 52$ ($2 \times 8 + 4 \times 9$), the apomictic behaviour of *L. virgatum* with the triploid number $2n = 27$. The sexual reproduction of *L. narbonense* is correlated with the chromosome numbers $2n = 18, 36, 54$ and 72 .

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