Breeding systems in some representatives of the genus Lycium (Solanaceae)

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ABSTRACT

The development of the ovule and the embryo sac of five of the 17 species of Lycium and of one hybrid, recorded for southern Africa, was investigated. All specimens of four of the species and the hybrid (between a hermaphroditic and a functionally dioecious species) were found to be functionally dioecious: they express only one sex, although both male and female organs are present in the same flower. One species was hermaphroditic. The embryo sacs of all species, and of the hybrid, were of the normal eight-nucleate Polygonum type. The structure of the ovary and the development of the embryo sac are similar to those of L. europaeum L. The absence of unreduced embryo sacs indicates that apomixis does not occur at any ploidy level in the species studied.

UITTEKSEL

Die ontwikkeling van die saadknop en die embriosak van vyf van die 17 Lycium-spesies en van een baster wat in sydelike Afrika aangeteken is, is ondersoek. Daar is bevind dat alle eksemplare van vier van die spesies en die baster (tussen 'n hermafroditiese en 'n funksioneel tweehuissige spesie) funksioneel tweehuissig is: hulle gee uitdrukking aan slees 'n geslag, hoewel manlike en vroulike organe albei in dieselfde blom teenwoordig is. Een spesie was hermafrodities. Die embriosakke van al die spesies, en van die baster, was van die normale agt-kemige Polygonum-tipe. Die bou van die vrugbevattende en die ontwikkeling van die embriosak is soortgelyk aan dié van L. europaeum L. Die afwesigheid van ongereduseerde embriosakke daarmee dat apomiksie nie by enige ploidievlak by die spesies wat ondersoek is, voorkom nie.

INTRODUCTION

The genus Lycium (Solanaceae) consists of small to large shrubs with a wide distribution in arid to subarid, temperate to subtropical regions of the world (Joubert 1981; Bernardello 1982). The only exceptions, which are more treelike, are L. afrum L. and L. horridum Thunb. (= L. austrinum Miers) (Palmer & Pitman 1973). Seventeen Lycium species are known in southern Africa, whereas 50–60 species are found in the western hemisphere (Joubert 1981).

Polyploidy occurs in the genus Lycium (Minne 1992; Spies et al. 1993). As polyploidy and apomixis are often associated (Stebbins 1971), the aim of this research was to determine whether apomixis occurs in the polyploid specimens. The mode of development of the ovule and the type of embryo sac present in L. afrum, L. arenicolum, L. horridum and L. tetrandrum was therefore studied.

MATERIALS AND METHODS

The material used during this study was collected and fixed in the field. Voucher specimens are housed in the Geo Potts Herbarium, Bloemfontein (BLFU).

Specimens examined [haploid chromosome numbers from Minne (1992) and/or Spies et al. (1993)]

L. afrum n = 12

CAPE.—3318 (Cape Town): Bokbaai, (-CB), A. Venter 346, 348; Melkbostrand, R27 road, (-CD), A. Venter 353; Melkbostrand, Otto du Plessis Ave., 50 m north of Dutch Reformed Church on road shoulder, (-CD), A. Venter 371, 373.

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L. afrum × L. ferocissimum n = 12

CAPE.—3318 (Cape Town): Melkbostrand, R27 road, (-CD), A. Venter 352, 355; Melkbostrand, Otto du Plessis Ave., 50 m north of Dutch Reformed Church on road shoulder, (-CD), A. Venter 372.

L. arenicolum n = 36

CAPE.—2824 (Kimberley): on Barkly West road, 6 km from the Windsorton turnoff to Riverton, (-DA), A. Venter 361, Kimberley Dist., Middelburg, on Nooitgedagt road, (-DB), Joubert 339, 345.

ORANGE FREE STATE.—2925 (Boshof): Modder River Bridge on Petrusburg-Kimberley road, (-CD), Joubert 324, 325; Flammink Pan, 5.5 km west of Modder River Bridge on Petrusburg-Kimberley road, (-CD), Joubert 329, 330, 2926 (Bloemfontein): Bloemfontein, University of the Orange Free State Campus, (-AA), Spies 5173.

L. horridum n = 24

CAPE.—2824 (Kimberley): Middelburg, Kimberley Dist. on Nooitgedagt road, (-DB), Joubert 338; A. Venter 384, 3119 (Calvina): 17 km outside Calvinia on the way to Williston (R27) at the R554 turnoff to Middelpos and Sutherland, (-BD), A. Venter 384, 3123 (Victoria West): 7.2 km from Richmond on N1 to Beaufort West, (-BD), A. Venter 366, 13.7 km from Richmond on N1 to Beaufort West, (-BD), A. Venter 368, 3220 (Sutherland): 25 km north of Sutherland, (-BC), Joubert 333, 334, 3224 (Graaff-Reinet): 102 km from Uitenhage to Graaff-Reinet, (-DC), Spies 5234.

ORANGE FREE STATE.—2925 (Boshof): 1 km east of Modder River Bridge on Petrusburg-Kimberley road, (-CD), H. Venter 9222, 2925 (Jagersfontein): 36 km from Petrusburg to Kimberley, (-AB), H. Venter 9230, 9231.

L. tetrandrum n = 36

CAPE.—3218 (Cape Town): Bokbaai, (-CB), A. Venter 346, 348; Melkbostrand, R27 road, (-CD), A. Venter 353; Melkbostrand, Otto du Plessis Ave., 50 m north of Dutch Reformed Church on road shoulder, (-CD), A. Venter 371, 373.

L. villosum n = 24

CAPE.—2824 (Kimberley): 24.7 km to Barkly West from the Kimberley-Gniewaskad turnoff, (-DA), Joubert 312, 313; at the Nooitgedagt turnoff on the Kimberley-Riverton road, (-DA), A. Venter 388, 389, 6.5.
km past the Nooitgedacht turnoff on the Kimberley-Barkly West road, (—DA), A. Venter 357; 7 km past the Nooitgedacht turnoff on the Kimberley-Barkly West road, (—DA), A. Venter 358; 8 km from the turnoff to Riverton on the Kimberley-Windsorton road, (—DA), A. Venter 362, 363.

The ovules and anthers of flowers of varying ages were fixed in Carnoy’s fixative in the field. The fixative was replaced after 24–48 hours by 70% ethanol. Dehydration was done in ethanol and tertiary butanol after which the flowers were embedded in pastulated synthetic paraffin wax, sectioned at 5–7 mm and stained with Safranin and Fast Green as described by Spies & Du Plessis (1986). At least twenty embryo sacs were studied per specimen.

For the scanning electron microscope (SEM) study, flowers were dissected in order to expose the stamens, ovaries and pistils of the specimens. The dissected flowers were mounted on aluminium stubs with the aid of a fast setting glue. The mounted material was then covered with carbon gold (Spurr 1969) for 135 seconds in the Bio Rad SEM coating system. The structure of the pistil, stamen, and pollen of both sexes of the dioecious species were studied with a Jeol Winsem JSM-6400 scanning electron microscope.

RESULTS AND DISCUSSION

A study of a large number of specimens of Lycium in southern African herbaria, Kew (K), British Museum (BM), Paris (P) and a few other herbaria revealed that all specimens of L. arenicolum, L. horridum, L. tetrandrum and L. villosum are functionally dioecious*. Such plants express only one sex, although both male and female organs are present in the same flower. In Lycium the term functionally dioecious means the following:

1, functionally male plants have fully developed anthers with seemingly fertile pollen (Figures 1A, B; 2B). Usually two of the stamens of the functionally male plants are included in the corolla tube, whereas two or three are a little exserted. These plants also carry female reproductive organs, but the pistil is underdeveloped and not functional (Figure 2A). The ovule will experience difficulties in receiving pollen, since only a rudimentary style without a stigma may occur on the ovary, or the style and stigma are totally absent (Figure 2A). Occasionally fruit can be found on functionally male plants, but this condition is rare.

2, in functionally female plants the ovary, style and stigma are normal in structure and slightly exserted from the corolla tube (Figure 2C), whereas the anthers of these flowers are underdeveloped and produce no pollen (Figures 1C, D; 2D). Fruit formation is normal. In the hermaphroditic Lycium species every flower bears normal male and female organs.

The ovaries of the Lycium specimens are subsessile, glabrous and have two fused carpels with axile placentation. The base of the ovary is enclosed by a greenish, red, orange or yellow-brown nectar gland. The ovules of both functionally male and functionally female plants are unitegmic, tenuinucellate (Figure 3A, B) and anatropous to hemi-campylotropous. These findings correspond to the
results obtained by Chiang-Cabrera (1981) on L. europaeum L.

During early stages of development, one cell, lying directly below the nucellar epidermis, differentiates into a primary archesporial cell that is conspicuous by its larger size (Figure 3B), denser cytoplasmic contents and more prominent nucleus. This archesporial cell gives rise to the primary sporogenous cell, which divides meiotically. Usually, a linear tetrad of macrospores is formed in Lycium. The chalazal macrospore develops into a Polygonum type embryo sac that contains an egg cell (Figure 3F), two synergids (Figure 3C, G), two polar nuclei (Figure 3C, D) and three antipodal cells (Figure 3H, I). These findings correspond to the results obtained by Chiang-Cabrera (1981) on L. europaeum.

In Lycium the ovules of both the functionally male and functionally female plants have a monosporic eight-nucleate Polygonum type embryo sac. In the functionally male plants the embryo sac is fully developed, although no fertilization takes place because there is no stigma, only an ovary with, at most, a rudimentary style.

Lycium horridum is functionally dioecious, whereas L. ferocissimum is hermaphroditic. All the L. horridum × L. ferocissimum hybrid specimens examined were functionally dioecious. Therefore, the gene(s) causing functional dioecy is/are dominant over the gene(s) for hermaphroditism.

The embryo sacs of L. afrum and the L. afrum × L. ferocissimum hybrid are of the normal eight-nucleate Polygonum type. All the nuclei in the embryo sacs of the studied species and hybrid, are of similar size. In the dioecious L. horridum the nuclei of the embryo sac differ in size. In the functionally male plant, all the nuclei are of the same size, but in the functionally female plants, the polar nuclei are much larger than any of the other nuclei. Both the functionally male and functionally female plants of L. arenicolum and L. tetrandrum have larger polar nuclei than the functionally female plants of L. horridum, although these larger nuclei only occurred in one of the two functionally male specimens of L. arenicolum examined.

Cytogenetic studies showed that L. arenicolum and L. tetrandrum display more meiotic abnormalities, such as univalents and bivalents during metaphase, as well as an anaphase bridge in L. tetrandrum, than L. afrum and L. horridum (Minne 1992; Spies et al. 1993). Although poly-ploidy and meiotic abnormalities occur during microsporogenesis in the anthers of the functionally male plants,
all the functionally female plants have normal embryo sacs (Minne 1992). The pollen of the functionally male plants was fully developed, whereas the pollen in the functionally female plants degenerated.

CONCLUSIONS

Functionally dioecious species are present in *Lycium*. All species studied, the hermaphroditic as well as the dioecious ones, have an eight-nucleate *Polygonum* type of embryo sac. The nuclei of the synergids, egg cell, central cell and antipodal cells were the same size in the hermaphroditic *L. afrum* and the functionally male plants of *L. horridum*. In the functionally female plants of *L. horridum*, the nuclei of the central cell, i.e. the polar nuclei, were larger than the other nuclei of the embryo sac. However, in *L. arenicolum* and *L. tetrandrum*, the polar nuclei of both sexes were larger than the other nuclei of the embryo sac. At all polyploid levels *Polygonum* type embryo sacs were formed, irrespective of the nature and number of meiotic abnormalities in the anthers. The absence of unreduced embryo sacs indicates that apomixis does not occur at any ploidy level in the species studied. A conspicuous difference in pollen development was also evident. Seemingly viable pollen was found in the functionally male plants, but none in the functionally female plants.

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