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NATURAL PENTAPLOIDS IN THE OPUNTIA LINDHEIMERI-PHAEACANTHA GROUP IN TEXAS

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The hexaploid and tetraploid semispecies, *Opuntia lindheimeri*, *O. phaeacantha* var. *major*, and *O. edwardsii* ($x = 11$), are known to hybridize in all combinations in central Texas; therefore, pentaploids are expected to occur. A search in four populations at two localities turned up at least one pentaploid individual ($2n = 55$) in each population and a total of 13 pentaploid plants in the four populations. The pentaploids are mainly hybrids of *O. lindheimeri* ($6x$) × *O. edwardsii* ($4x$), and *O. phaeacantha* var. *major* ($6x$) × *O. edwardsii* ($4x$). These examples of pentaploidy in *Opuntia* can be added to the relatively few recorded cases of naturally occurring pentaploids in nonagamospermous angiosperms.

Introduction

The *Opuntia lindheimeri* group is represented in central Texas by three hybridizing semispecies: *O. lindheimeri*, *O. phaeacantha* var. *major*, and *O. edwardsii* (GRANT and GRANT 1979*a*). Two ploidy levels, $4x$ and $6x$, are found in these semispecies in this central Texas area (GRANT and GRANT 1979*a*). Since the three semispecies hybridize in the three possible combinations (GRANT and GRANT 1979*b*), pentaploid products of hybridization could be expected to occur.

In our original cytotaxonomic study of the *O. lindheimeri* group (GRANT and GRANT 1979*a*), the objective was to obtain chromosome counts from populations in as many geographical areas as possible. This approach revealed the main cytotaxonomic outlines of the group. For the purpose of the present study, which was to look for pentaploid hybrids, we changed from an extensive to a more intensive type of survey, obtaining counts for series of individuals in selected local populations. The expected pentaploids were actually found in two localities.

Naturally occurring pentaploids in nonagamospermous plant groups have been recorded only rarely. Therefore, it seems worthwhile to report the finding of pentaploids in the *O. lindheimeri* group.

Material and methods

The three semispecies were known at the beginning of this study to exhibit the following ploidy levels in central Texas ($x = 11$): *Opuntia lindheimeri*, $4x$ and $6x$; *O. phaeacantha* var. *major*, $6x$; and *O. edwardsii*, mainly $4x$, rarely $6x$ (see list in GRANT and GRANT [1979*a*]). We also knew certain localities in which semispecies of different ploidy levels coexisted sympatrically. Two widely separated localities containing both tetraploid and hexaploid forms were selected for more detailed study.

The first locality is Seguin, Guadalupe County, Texas, in the black-earth prairie belt. One mixed population occurs in a mesquite-grassland formation east of Seguin. The second locality is Pedernales Falls State Park, Blanco County, in the hill country or Edwards Plateau. Three mixed populations growing in live oak-juniper savannah were examined at this locality and are designated the Pedernales River, Pedernales Falls, and Wolf Mountain populations.

As the populations themselves are large, subpopulations of manageable size, containing contrasting semispecies, were blocked out for study and were mapped. Chromosome counts were obtained for as many plants as possible in the subpopulations. We tried to avoid collecting cytological material from members of the same clone. The diagnostic morphological characters were recorded for each individual plant in the cytological samples.

Chromosome counts were made primarily from root tips of adventive roots on stem joints, supplemented wherever possible by counts of PMCs. Stem joints growing on moist sphagnum in the laboratory yield root tips almost all year, whereas PMCs may be collected only during a very short blooming season. Root tips were pretreated in 0.05%–0.1% colchicine for 2–3 h, put in fixation solution, squashed with acetic orcein, and examined by a Leitz phase microscope.

Voucher specimens of the plants studied cytologically are deposited in the University of Texas Herbarium.

Results

SEGUIN POPULATION.—A moderately large population here consists almost entirely of plants belonging to the prairie race of *Opuntia lindheimeri*. The subpopulation blocked out for study contains 17

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individuals of *O. lindheimeri* and several individuals of *O. edwardsii*.

Twelve *O. lindheimeri* plants were found to be $6x$ with $2n = 66$ or ca. 66, as expected. One individual of *O. edwardsii* was counted and found to be $4x$ with $2n = 44$. Two individuals were pentaploids with $2n = 55$. Both plants were intermediate between *O. lindheimeri* and *O. edwardsii* in their spine characters.

PEDERNALES POPULATIONS.—All three semispecies are present in the three mixed populations studied in Pedernales Falls State Park. The number of hybrid combinations is thus greater, and the results of hybridization more complex, than in the Seguin population. Pentaploids were found in each of the three populations.

The Wolf Mountain population exhibits three-way hybridization (GRANT and GRANT 1979*b*). The bulk of the mixed population consists of *O. phaeacantha* var. *major*, *O. edwardsii*, and their hybrids. One individual of *O. lindheimeri* is present and has contributed a few hybrid plants.

For this study we concentrated on the *O. phaeacantha* and *O. edwardsii* types and their intermediates in the Wolf Mountain population. Six individuals of *O. phaeacantha* var. *major* were hexaploid. *Opuntia edwardsii* was represented in our small sample by both hexaploids (two plants) and tetraploids (one plant). One pentaploid ($2n = 55$) was found and is interpreted provisionally as a product of *O. phaeacantha* var. *major* ($6x$) $\times$ *O. edwardsii* ($4x$).

The Pedernales Falls population consists mostly of *O. edwardsii* plants intermixed with scattered plants of the other two semispecies and their hybrids. *Opuntia edwardsii* is represented by both tetraploid and hexaploid forms here, as on Wolf Mountain. We found three pentaploid individuals ($2n = 55$). Judging by their morphological characters, two of these pentaploids may be hybrids of *O. phaeacantha* var. *major* ($6x$) $\times$ *O. edwardsii* ($4x$).

In the Pedernales River population, *O. edwardsii* and *O. lindheimeri* are both common, and *O. phaeacantha* var. *major* is represented by a few scattered individuals. *Opuntia lindheimeri* is hexaploid here, and *O. phaeacantha* var. *major* is probably hexaploid here as it is elsewhere in the area. We found hexaploid individuals in our subpopulation of *O. edwardsii;* tetraploid *O. edwardsii* is almost certainly present here too, since we found it in the same general population a mile from this subpopulation.

Seven pentaploid individuals were found in our subpopulation of the Pedernales River population ($2n = 55$ in six individuals and ca. 55 or 55 ± 3 in one other). These individuals differ among themselves in the stem-joint and spine characters that differentiate the semispecies. This variation was puzzling to us at first since we could not see how a hybrid population could be segregating and still stay on the pentaploid level. Further inspection of the morphological characters suggests that the pentaploids in our sample have had three independent origins: *O. lindheimeri* ($6x$) $\times$ *O. edwardsii* ($4x$), *O. phaeacantha* var. *major* ($6x$) $\times$ *O. edwardsii* ($4x$), and *O. edwardsii* ($6x$) $\times$ *O. edwardsii* ($4x$).

FERTILITY.—The parental semispecies are highly to fully fertile as to pollen and seeds. The pollen stainability of *O. lindheimeri* ranges from 66% to 99% in different individuals at Seguin and from 87% to 94% at Pedernales River; that of *O. edwardsii* at Pedernales River, from 81% to 93%; and that of *O. phaeacantha* var. *major* on Wolf Mountain, from 71% to 99%. Seed fertility is high in all three semispecies.

The pollen stainability and seed set of the pentaploids are unknown. In general, it is difficult to correlate cytological data with fertility in plants growing in open public land. This difficulty was overcome in the Seguin population but not in the Pedernales populations.

The two pentaploids at Seguin were effectively completely sterile during 3 yr (1979–1981) of observation. They produced flower buds which either aborted or developed into sterile immature ovaries in each of the three flowering seasons. Their unfruitfulness could be a result of genic sterility. In any case, their pollen and seed fertility could not be determined. The course of hybridization does not get beyond the sterile F_1's in the Seguin population. There is no sign of backcrossing or introgression.

This complete sterility is not necessarily expected in other pentaploids in other areas. We know that hybrid intermediates (cytologically undetermined) in the Edwards Plateau often have medium to high pollen stainabilities (60%–90%) and set abundant seed.

Hybrid swarms and introgressive types in the Pedernales populations (GRANT and GRANT 1979*b*) indicate that some pentaploid hybrids are at least partially fertile in this area. The progeny of the pentaploid hybrids would be expected to show aneuploid variation around a mode of $2n = 55$. The one individual in the Pedernales River subpopulation with $2n =$ ca. 55 may represent such an aneuploid. Aneuploid variation in these *Opuntias* requires further study.

JONES (1958) reported much individual variation in pollen stainability in pentaploid plants of *Holcus mollis*, from nearly 0% and 5% to 80% stainable pollen. HIESEY and NOBS (1970) also found variation in seed fertility in a series of pentaploid hybrids derived from different $6x \times 4x$ crosses in the *Achillea millefolium* group. Four families of pentaploid hybrids were only moderately less seed fertile than the parental tetraploid and hexaploid species, but one other pentaploid hybrid family was highly, though not completely, seed sterile.

Discussion

Spontaneous triploids are known in a fairly large number of sexually reproducing plant groups (GRANT [1981], chap. 34, for review). Most of the recorded cases of spontaneous triploids involve cultivated plants, but natural nonagamospermous triploids, while uncommon, are now well known. Familiar examples include *Populus tremula* (MÜNTZING 1936), *Lilium tigrinum* (NODA 1974), *Leucopogon juniperinus* (SMITH-WHITE 1948, 1955), and *Cardamine insueta* (URBANSKA-WORYTKIEWICZ 1977).

Odd euploids at higher ploidy levels in sexual plants are, as would be expected, known in far fewer instances. At the pentaploid level the best-known examples are the *Rosa canina* group ($2n = 35$) (TÄCKHOLM 1922) and *Solanum curtilobum* (*S. tuberosum* group) ($2n = 60$) (SWAMINATHAN and HOWARD 1953; DODDS 1962); the first of these has a special genetic system and the second is cultivated. Other natural pentaploids occur in *Agrostis stolonifera* ($2n = 35$) (BJÖRKMAN 1954), *Holcus mollis* ($2n = 35$) (JONES 1958; WALTER 1977), the *Achillea millefolium* group ($2n = 45$ and ca. 45) (EHRENDORFER 1959, 1973; HIESEY and NOBS 1970), the *Fragaria chiloensis* group ($2n = 35$) (BRINGHURST and KHAN 1963), *Lemna minor* and *L. gibba* ($2n = 50$) (URBANSKA-WORYTKIEWICZ 1975), and in two species of *Opuntia* to be mentioned below (HIROSHI et al. 1973).

Natural nonagamospermous heptaploids are even less common than pentaploids. The examples known to us are *H. mollis* ($2n = 49$) (JONES 1958), *L. gibba* ($2n = 70$) (URBANSKA-WORYTKIEWICZ 1975), and an *Opuntia ficus-indica* hybrid ($2n = 77$) (MCLEOD 1975).

The previously reported odd euploids in the cacti all occur in *Opuntia*. Triploids ($2n = 33$) are known in two otherwise diploid species of subgenus *Opuntia* (= *Platyopuntia*), namely, *O. vulgaris* (KATAGIRI 1953; HIROSHI et al. 1973) and *O. basilaris* var. *treleasei* (PINKAVA et al. 1977); and in one species of subgenus *Cylindropuntia*, *O. prolifera* (HIROSHI et al. 1973). The triploid in *O. basilaris* var. *treleasei* is a plant from Kern County, California, which is morphologically like the diploid population and usually exhibits 11 trivalents at meiosis. It is probably a product of one-sided doubling (PINKAVA et al. 1977).

Pentaploid opuntias ($2n = 55$) have been recorded by HIROSHI et al. (1973) in two South American subgenera: in *O. salmiana* (subgen. *Australocylindropuntia*) and an unnamed species in the *O. boliviana* group (subgen. *Tephrocactus*).

A heptaploid ($2n = 77$) in *Opuntia* is a hybrid between *O. ficus-indica* ($8x$) and *O. phaeacantha* var. *major* ($6x$) in San Luis Obispo County, California (MCLEOD 1975). MCLEOD reports irregularities of meiosis in this hybrid. It parallels the pentaploid hybrids in the same species group reported here.

High odd euploids are reported by HIROSHI et al. (1973) in three South American species belonging to the subgenera *Australocylindropuntia* (*O. exaltata*) and *Tephrocactus* (*O.* aff. *zehenderi* and *O. dimorpha*). The chromosome counts and ploidy levels are: *O. exaltata* ($2n = 121 = 11x$), *O.* aff. *zehenderi* ($2n = 143 = 13x$), and *O. dimorpha* ($2n =$ ca. $209 = 19x$).

The odd euploids in nonagamospermous groups all have means of vegetative propagation, and some reproduce mainly vegetatively. Most, but not all, odd euploids are hybrids. Vegetative propagation permits the adaptive hybrid types to persist in nature (e.g., *O. lindheimeri-phaeacantha* group), and in some cases to spread widely (*H. mollis*), despite their unbalanced chromosomal constitution.

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