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A Facultative Gymnosperm from an Interspecific Cotton Hybrid

Abstract. *A plant population from an interspecific cotton hybrid produces flowers with exposed ovules on petal margins. The variability of these abnormal flowers suggests the possibility that angiosperms may have evolved by accumulating regulator genes which narrow the range of response to fluctuations in the environment. Progressive canalization of development within a population like the "carpelloid petal" plants could have resulted in both angiospermy and speciation.*

Cotton plants with the "carpelloid petal" (c.p.) flower abnormality produce organs strikingly similar to fossil megasporophylls described by Mamay (*1*). The degree of abnormality varies from plant to plant and from day to day. This complicates genetic studies, but this same variability suggests some mechanisms for canalization of development (*2*) which may have been involved in the evolution of angiosperms and their speciation. Whether we consider the carpelloid petals to be an entirely new property or a reversion to a more primitive form, their very existence in a living plant population demonstrates the possibility that something similar could have happened before.

The carpelloid petal abnormality first appeared in 1966 in an F_2 progeny row from a male-sterile plant with *Gossypium anomalum* cytoplasm, crossed with the *G. barbadense* L. variety "Coastland 401." The male-sterile strain was a highly male-sterile pure line produced by self-pollinating a fifth backcross to Upland cotton (*G. hirsutum* L.) of [(*G. anomalum* Wawra & Peyr. × *G. thurberi* Tod.) × G. *hirsutum* L.]. Since 1966 the abnormal strain has been maintained by self-pollinating c.p. plants whenever suitable flowers appeared either in the field or in the greenhouse. The c.p. strain has been crossed with Upland cotton and also with advanced-generation backcrosses to Upland cotton with cytoplasms from four other species. From these hybrids F_1 and F_2 progeny rows have been grown with cytoplasms from *G. anomalum, G. arboreum* L., *G. barbadense, G. hirsutum*, and *G. tomentosum* Nutt.

Figure 1 shows a c.p. flower with exposed ovules on a petal margin. A typical flower has yellow or white petals with a green margin bearing ovules, an androecium consisting either of a tube bearing many anthers or of five stalked "bouquets" of anthers, and a central compound ovary with one style. The most abnormal flowers have the androecium replaced by a ring of (usually five) separate or fused carpels, each with a style, surrounding the central ovary, which may be either compound with one style or formed of separate carpels, each with its own style. Whenever the androecium is represented by stalked clusters of anthers or by carpels, the anthers or styles are rolled up inside the petal margins when the flowers open, but they become free later in the day. Any combination of organs may occur between the ring of petals and the central ovary, including petaloid open carpels enclosing exposed ovules, bearing a stamen or two at the margin and a style at the tip. The exposed ovules have a micropyle which can be seen with a hand lens, and frequently they have a fuzzy coat of seed hairs (on the ovules inside the central ovary the seed hairs develop into cotton fiber). The only obvious difference between the exposed and enclosed ovules is that sometimes the external ones are larger and the seed hairs are longer at anthesis. Normal cotton flowers usually shed their petals and androecium the day after the flowers open. Few of the abnormal flowers produce seed, and no exposed ovules have ever developed into seeds.

Selfed progeny rows from carpelloid petal plants were grown in 1967, 1968, and 1969 as field plots at Stoneville, Mississippi. The total of 58 plants represents all of the viable seed available up to 1969 from self-pollinated flowers. Exposed ovules were observed on petal margins of all but one of these plants. Since expression of the abnormality is extremely variable, and since rainy weather prevented checking some of the flowers produced by these plants, the original c.p. plant is assumed to have been homozygous for whatever gene or genes may be responsible for producing ovules on the petal margins. Since none of the F_1 populations produced any carpelloid petals, the gene or genes may be assumed to be recessive. No exposed ovules were produced by the F_2 populations with cytoplasms from *G. arboreum, G. barbadense, G. hirsutum*, or *G. tomentosum*, but both the F_2 and the first backcross to c.p. with *G. anomalum* cytoplasm produced some plants with carpelloid petals. In the backcross eight of the 18 plants which flowered had ovules on the petal margins. The F_2 also had 18 plants which flowered; three of these had carpelloid petals. The data now available are insufficient for determining whether only *G. anomalum* cytoplasm permitted expression of the c.p. abnormality, or whether only the *G. anomalum* strain carried associated genes necessary for its expression. The reciprocal crosses necessary to test these alternatives have not yet been successful because of the low fertility of the c.p. plants.

Variability in expression is characteristic of the carpelloid petal abnormality. Shifts toward normal or c.p. flower development are synchronized for the plants within a progeny row. In the summer of 1969 all of the flowers produced by the c.p. row were checked daily for number of external ovules, percentage of c.p. flowers, anther number, and percentage of flowers with no anthers. These data cover the period from 31 July to 12 September, except for the week of 18 August, when Hurricane Camille made it impossible to get into the field to collect the flowers. Solar radiation, evaporation, and relative humidity were all significantly correlated with measurable aspects of development of the c.p. abnormality (*3*). Table 1 presents correlations significant at the .05 or .01 probability level, together with positive and negative nonsignificant correlations. The environmental factors which seem to alter the development of c.p. flowers are interrelated. On the basis of the 1969 data, it looks as if conditions which favor water loss shift the petal primordia toward female development and suppress anther development. At 25 to 26 days before anthesis, with high evaporation, the percentage of c.p. flowers increases, the mean number of ovules on petal margins goes up, the percentage of flowers without anthers increases, and the mean number of anthers per flower goes down. A few days later (21 days before anthesis), after flowers are committed to petal development, the same conditions have an opposite but weaker effect. Sixteen days before anthesis the anther primordia are extremely sensitive to some condition associated with very low solar radiation. The percentage of flowers without anthers increases enormously whenever solar radiation drops below 400 cal/cm^2 per day (Fig. 2).

Some other aspects of cotton flower development are correlated with environmental factors which seem to be

Table 1. Correlation coefficients (r) between development of carpelloid petal flowers and environmental conditions before anthesis. The figures are based on all flowers produced in 38 days of the 1969 flowering season. Plus and minus signs denote positive and negative correlations not significant at the $P = .05$ level.

Environmental variable	Days before anthesis	Correlations with: Percentage of c.p. flowers	Mean number of exposed ovules per flower	Percentage of flowers without anthers	Mean anther number
Solar radiation	26	+.37*	+	+	−
Relative humidity	26	−.39*	−.37*	−	+
Evaporation	25	+.49†	+.37*	+.35*	−.44*
Relative humidity	21	+	+.46†	+.33*	−
Solar radiation	17	−	−	−.50†	+
Evaporation	16	−	−	−.47†	+

* Significant at the .05 probability level. † Significant at the .01 probability level.

Fig. 1. "Carpelloid petal" flower showing ovules on petal margin.

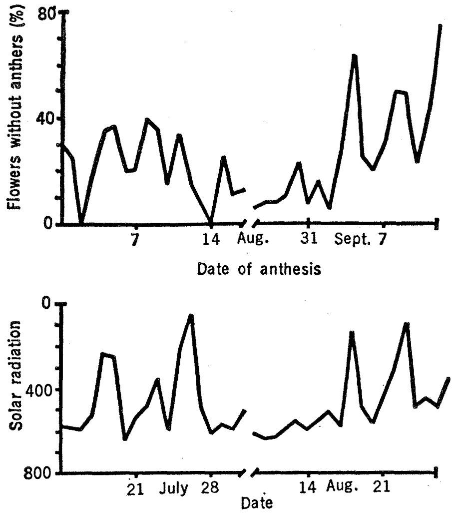

Fig. 2. Relation between percentage of flowers without anthers and solar radiation 17 days before anthesis. Solar radiation was measured as calories per square centimeter per day. The coefficient of correlation $r = .50$, significant at the .01 level of probability.

of only minor importance in the development of c.p. flowers. The highly significant correlations with temperature which were observed with male-sterile flowers and with the External Ovule abnormality (*4*) were not obtained for c.p. flowers. Both the c.p. studies and the earlier research on cotton flower development show clearly that changes in the weather can bring about changes in flower structure.

The carpelloid petal flowers develop gymnosperm structure in response to hot, dry weather. Under cool, moist conditions they are likely to produce normal angiosperm flowers. Perhaps a sudden shift in climate caused many different kinds of gymnosperms to develop abnormal flowers. A gymnosperm which had evolved a "flower" structure adapted to vector pollination might well have a central ring or cone of megasporophylls. A change in growth rate could delay separation of the ring of tissue into separate carpel primordia and cause the fusion of some or all of the carpels. Climatic change after some gymnosperms had already begun genetic evolution to accommodate different pollen vectors, and different ecological niches could produce a similar developmental change in many separated groups from a common origin without requiring any simultaneous genetic mutations. The result would be a sudden development of angiosperms over a wide area from groups already morphologically distinct.

The carpelloid petal flowers suggest that gene repression may be a very important aspect of flower development. The same c.p. abnormality has occurred in other stocks derived from crosses with *Gossypium anomalum* cytoplasm; this would indicate that the abnormality is not due to a new gene mutation, but comes from expression of genes which are present at least in *G. anomalum*, but not usually expressed. All of the wild and cultivated cotton species have evolved control systems for flower development which result in a ring of bracts, a ring of calyx tissue, a ring of petals, and a tubular androecium surrounding a single style at the tip of a compound ovary. Interspecific hybrids make drastic changes in the controls. They introduce new combinations of genes into cytoplasms which evolved to fit other species growing in other places. Repressor genes get left out of new combinations. A cytoplasmic organelle may produce a 2-carbon side-chain where a 3-carbon one "ought" to be. The enzyme or hormone that is supposed to fit needs twice as long to get around to turning on the next set of genes.

The great variety of patterns of differentiation of c.p. flowers fits very well into Heslop-Harrison's concept (*5*) of a relay system of genes activated in an irreversible order, accompanied by inhibition (repression) of other genes. His requirement that competence for differentiation of sex organs be accompanied by loss of capacity for growth would apply to most of the flower organ abnormalities. In carpelloid petal plants part of each petal primordium would remain meristematic; the bud could switch to carpel production at any stage from outgrowth of petal primordia to the normal period for producing carpels and ovules. The fate of the primordia which normally develop into anthers would depend on both the rate of development and the timing of the switch from petal to anther to carpel programming within any one flower bud. Probably androecial tissue which was not already committed to anther production when the bud's chemistry changed to "carpel mix" would simply produce carpels. Tissue started on the program for anther production would produce anthers or cease development according to how far it had gone in the program, or perhaps according to how strongly the new signals countermanded the old ones.

The genetic mechanisms responsible for flower abnormalities could fit either the structural-operator-regulator complexes required by the Jacob-Monod theory of gene activity (*6*) or the more complicated Britten-Davidson hypothesis derived from it (*7*). In either case, a small population of living plants may offer some suggestions about possible courses for evolving control of the gene action which results in the usual rigidly specified flower structure of angiosperms.

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"Sex Ratio" in Drosophila pseudoobscura: Spermiogenic Failure

Abstract. *Contrary to earlier reports, testes of "sex ratio"* Drosophila pseudoobscura *males have only half as many sperm per bundle as testes of normal males do. This fact, determined from electron micrographs, indicates that the functional pole hypothesis is not applicable to the action of "sex ratio."*

"Sex ratio" is a widespread genetic condition of the X chromosome in *Drosophila*. It was first described in detail for *D. obscura*, a European species (*1*), and has since been studied in other members of the genus (*2–4*). During these studies it was observed that males carrying the "sex ratio" X