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Multiple Genotypes in Individuals of *Claytonia virginica*

Abstract. *Supernumerary chromosomes are common among plants of Claytonia virginica found in a weedy population near the southwestern edge of its distribution. Roots, stems, and microsporocytes vary in chromosome number within the same plant in 68 percent of the population studied.*

Constancy of chromosome number within all individuals is merely a convenient fiction (1), for there is considerable evidence indicating that polyploidy and aneuploidy occur in various parts of many plants and animals (2). This largely ignored intra-individual variation in relation to cell, tissue, and organ differentiation needs critical exploration (3).

In November 1969, underground stems (corms) of *Claytonia virginica* L. were obtained from Carthage, Texas, and grown in the greenhouses of the Missouri Botanical Garden.

Twenty-two polyploid plants were studied from one population for both root mitosis from corms and microsporocyte meiosis, in addition to 12 plants previously examined (4). Once counts of chromosomes were made in these organs, floral stems were cut from each just below the paired floral leaves and planted in perlite under mist. A few developed adventitious roots from callus and these were studied for chromosome number when roots were about 1 cm long. Successful cuttings were potted and several plantlets with corms formed. Chromosome counts were made in cells from elongated roots as well as in the microsporocytes from the new floral stems.

Meiosis was largely regular with supernumerary chromosomes pairing normally [table 2 in (3)]. In mitotic plates supernumerary chromosomes appeared similar and indistinguishable from the characteristic complement of chromosomes which numbered 28.

Of the 23 plants from a total of 34 found to have multiple genotypes (68 percent), roots from corms averaged $2n = 28.3 \pm 0.4$ chromosomes per cell, roots from floral stems averaged $2n = 29.8 \pm 4.5$ chromosomes, and micro-

sporocytes averaged $2n = 29.5 \pm 0.8$ chromosomes (Tables 1 and 2).

Few supernumerary chromosomes were found in those roots originating annually from the corm—the basic genome of $2n = 28$ was found in 80 percent of all cells studied, and only 15 and 5 percent of cells had one or two extra chromosomes, respectively. This conservatism in multiple genotypic organisms appears more common for roots than for other organs in most species (5) although not universally so (6).

In contrast, supernumerary chromosomes are most frequent in meiotic cells of the anther. A total of 74 percent of cells had from one to five extra chromosomes. This high frequency is reflected by an average of 1.2 chromosomes more per cell than found in corm-originating root cells. Yet the average chromosome number of cells from adventitious roots arising from callus on floral stems is similar to the average found for microsporocytes, and not that seen in roots formed from corms, as might be expected. In fact, they averaged 1.5 chromosomes per cell higher with a wide range of $2n = 28-52$ and a large standard deviation. These adventitious roots, however, presumably arose from multiple tissues of an organ known or suspected to have great chromosomal variability (7), which is confirmed by the polyploidy found in this study. Even though a correlation exists between greatest cellular differentiation and greatest chromosomal variation, the number of cells having supernumerary chromosomes was only 47 percent, much less than that of the microsporocytes.

Two plantlets grew to sufficient maturity to be examined chromosomally. Results for one are given in Table 2. The second plantlet, propagated from a plant with $2n = 28$ (roots), 30, and 31 (microsporocytes), proved more complex. Its mature adventitious roots arising from a floral stem had $2n = 28, 29$, and 30 chromosomes (one root with each number), $2n = 31$ for microsporocytes from three different floral stems, and $2n = 25, 29, 33$, and 35 for microsporocytes from a single bud of a fourth floral stem. Vegetative reproduction has apparently been an inciting factor in genotypic variability for this individual.

Other correlations have been observed for those organisms with multiple genotypes. For example, a high number of supernumerary chromosomes in *Centaurea* is associated with dry climates (8), whereas individuals

Table 1. Multiple genotypes in roots from corms and microsporocytes of *Claytonia virginica*. Numbers in parentheses indicate number of roots and floral stem apices studied.

Chromosome number in		Plants (No.)
Roots from corms ($2n$)	Microsporocytes (as $2n$)	
28 (11)	29 (10)	5
28 (11)	30 (4)	3
28 (6)	31 (7)	3
28 (1)	30 (1), 31 (2)	1*
28 (3)	31 (1), 33 (1)	1
28 (3), 29 (1)	28 (4)	1
29 (1)	28 (2)	1

* Plus plantlet number 2 (see text).

Table 2. Multiple genotypes in roots from corms and floral stems and from microsporocytes of individual plants of *Claytonia virginica*. Numbers in parentheses indicate number of roots and floral stem apices studied. Each line is for one plant.

Diploid chromosome number		
Roots from corms	Roots from floral stems	Microsporocytes*
28 (2)	28 (1)	29 (2)
28 (4)	30 (2)	30 (5)
28 (2), 29 (2)	28 (1)	28 (5)
28 (3), 29 (1)	28 (2), 28 and 29 (1) †	28 (2), 29 (1)
28 (2), 29 (2)	28 (1), 32 (1)	28 (2)
28 (1), 29 (3)	28 (2)	29 (3), 31 (1), 33 (1)
28 (4), 29 (1)	31 (1)	29 (8), 31 (3)
28 (3), 30 (4)	28 (1), 30 (1), 31 (1)	30 (1)
	30 and 52 (1) † ‡	

* Chromosome number expressed as $2n$. † Two numbers in a single adventitious root (aneuploidy). ‡ Plus plantlet number 1 having $2n = 28$ in floral stem roots.

of *Festuca* growing in clay soils were found with higher frequencies of extra chromosomes than were those in light, sandy soils (9). Further examples associating habitat and presence of supernumeraries are known, but none as unusual as that reported for *Allium* (10). When diploid plants with two to ten supernumeraries from the mountains of Darjeeling were moved to the hot climate of Calcutta they soon evolved into tetraploids with or without (rare) extra chromosomes. In still another kind of relationship, Jackson and Newmark (11) found an increase in pigment production in fruits of *Haplopappus* in plants with from one to four excess chromosomes.

However, no ready explanation is apparent in *C. virginica* either for the presence of supernumerary chromosomes or of their variation in different organs and tissues of an individual plant. Noteworthy perhaps is that the population studied is weedy and occurs near the extreme southwestern edge of distribution for the species. In other localities, particularly in the eastern United States where the more primitive cytotypes occur (12), the species is not weedy.

Yet the ability to sustain intra-individual variability even of the germ line suggests a selective advantage. This is sufficiently locked genetically, for multiple genotypes are just as common among plants grown in the greenhouse as they are for those collected in the field. Their presence cannot be attributed to signs of breakdown of control in cells at the end of their reproductive phase when selection is not so stern (1), because more cells in the male germ line possess excess chromosomes than do cells examined from elsewhere. Factors initiating the phenomenon of multiple genotypes remain highly speculative even as to their intrinsic or extrinsic origin.

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Unique Type of Angiosperm Pollen from the Family Annonaceae

Abstract. *The primitive angiosperm family Annonaceae possesses a remarkable type of pollen that appears unique in its size (diameter up to 350 micrometers), lack of exine over nearly 50 percent of the grain surface at maturity, and proximalipolar aperture. This unique pollen is further distinguished by being in polyads which are compartmentalized individually within septate stamens.*

During a palynological survey of the primitive angiosperm family Annonaceae (1), a natural group of genera was found with a remarkable type of pollen grain that appears to be unique among angiospermous pollen with regard to grain size, nature of the pollen exine, and type of aperture. In addition, the pollen units (2) of these genera (polyads) and their infrastaminal arrangement (in septate stamens) are highly distinctive. The unusual pollen characters of this group, which I informally propose to call the *Cymbopetalum* tribe at this time, will be outlined in this report. Since the characters under discussion are well developed in *Cymbopetalum* Benth., which typifies the salient trends of the genera in the tribe, and since this particular genus is represented by abundant, fresh material in my collections, the greater part of the following discussion is concerned with this genus.

Angiosperm pollen exhibits a tremendous size range, from about 2 to 5 μm in *Myosotis* L. (Boraginaceae) to over 200 μm in some species of flowering plants. Erdtman (3) considers medium-sized pollen to be between 25 and 50 μm , whereas grains in the range of from 100 to 200 μm are termed very large and anything over 200 μm is called gigantic. There are approximately a dozen angiosperm families that have species of some genera with pollen grains close to or greater than 200 μm (3, 4), including the Nyctaginaceae (*Acleisanthes* A. Gray), Malvaceae (*Kokia* Lewton),

Cucurbitaceae (*Cucurbita* L.), Onagraceae [*Oenothera* L. (= *Megapterium* Spach)], Convolvulaceae (*Ipomoea* L.), Polemoniaceae (*Cobaea* Cav.), Dipsacaceae (*Morina* L.), Xyridaceae (*Orectanthe* Maguire & Wurdack), Musaceae (*Musa* L.), Zingiberaceae, and Marantaceae. Up to now the largest recorded pollen grains include those of *Acleisanthes obtusa* (Choisy) Standley (= *A. berlandieri* Gray), with some grains about 230 μm (3) and *Cucurbita* species, with pollen up to 250 μm (5). Mention must also be made of the so-called nonfixiform, threadlike pollen of some marine angiosperms, which may be over 2000 μm (3), for example, *Zostera* L. (Zosteraceae) and *Cymodocea* Koen. (Zannichelliaceae). The family Annonaceae must be added to the list of angiosperm families with pollen grains larger than 200 μm . Grains averaging 280 μm occur in species of two genera in this family—*Annona* L. (*A. rigida* R. E. Fries) and *Cymbopetalum*. *Cymbopetalum odoratissimum* Barb. Rodr., with some individual grains as large as 350 μm , probably represents the largest, fixiform pollen grain in the flowering plants (Fig. 1, A and B). The exine of this species may be 20 μm thick, with columellae that are 15 μm long. The tectal perforations in the exine may be as large as 15 μm .

The pollen wall (sporoderm) consists of two fundamentally different layers: an inner, more or less cellulosic layer (6) which is destroyed during pollen preparation by acetolysis—the