9-1-1992

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## Publication Info

Published in *American Journal of Botany*, ed. Judy Jernstedt, Volume 79, Issue 9, 1992, pages 1081-1086.

American Journal of Botany 79(9): 1081–1086. 1992.

# NUCLEAR DNA CONTENT VARIATION WITHIN THE ROSACEAE[1]

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Nuclear DNA content has been estimated using flow cytometry for 17 species and eight cultivars of *Malus* and for 44 species of 29 other genera within the Rosaceae. Compared to other angiosperms, diploid genome sizes vary little within the family Rosaceae and within the genus *Malus*. C-values of genera within the subfamilies Spiraeoideae and Rosoideae are among the smallest of flowering plants thus far reported. In general, the Maloideae have the largest diploid genomes of the family, consistent with their higher chromosome numbers and presumed polyploid origin.

The Rosaceae, including such economically important plants as almond, apple, strawberry, and rose, is considered a natural group held together by similarities in floral structures. The four subfamilies are defined by fruit type (Robertson, 1974), and each includes polyploid series with fairly consistent chromosome base numbers: Spiraeoideae ($x = 9$); Amygdaloideae ($x = 8$); Rosoideae ($x = 7$, 8, and 9); and Maloideae ($x = 17$) (Sax, 1931, 1932). The subfamily Maloideae, with its relatively high base chromosome number, has been hypothesized to be either of autopolyploid (Darlington and Moffett, 1930) or allopolyploid origin (Sax, 1931, 1932; Stebbins, 1950).

Although numerous chromosome numbers have been reported for Rosaceae, the amount of DNA per nucleus (C-value) has been reported for only 14 species of the family (Bennett and Smith, 1976, 1991; Bennett, Smith, and Heslop-Harrison, 1982; Arumuganathan and Earle, 1991b). Apart from the utility of genome size data in ongoing molecular studies in this important plant family, the amount and distribution of nuclear DNA content variation among related taxa may give insights into genomic evolution that underlies or parallels speciation (Raina and Narayan, 1984; Ohri and Khoshoo, 1986; Price, 1988).

In this study, flow cytometry was used to estimate nuclear DNA contents of 28 genera from each of the four Rosaceae subfamilies. Compared to Feulgen densitometry or reassociation kinetics, flow cytometry is a rapid and reliable method for estimating C-values in plants (Galbraith et al., 1983; De Laat, Gohde, and Vogelzang, 1987; Rayburn et al., 1989; Rayburn, 1990; Michaelson et al., 1991a). We here report low levels of nuclear DNA variation within the Rosaceae and find that Spiraeoideae C-values are among the smallest of angiosperms. Relatively large C-values of Maloideae support the polyploid origin of the subfamily.

## MATERIALS AND METHODS

Leaf material of rosaceous taxa was collected from several sources (Table 1). Voucher specimens are deposited at the L. H. Bailey Hortorium (BH). Chromosome counts, where available, were gathered from the literature (Table 2).

For the determination of nuclear DNA content, suspensions of intact nuclei were prepared from young leaves by chopping (Galbraith et al., 1983) according to the procedure of Arumuganathan and Earle (1991a) and stained with propidium iodide. The isolation procedure was further modified for some members of the subfamily Rosoideae by the addition of 1% polyvinyl pyrrolidone (PVP-40) to the initial isolation solution, without the addition of propidium iodide. The modified procedure increased the number of intact nuclei isolated. The mean fluorescence intensity, frequency, standard deviation, and coefficient of variation of the propidium iodide-stained nuclei at 488 nm were recorded with an EPICS PROFILE flow cytometer (Coulter Electronics, Hialeah, FL). Chicken erythrocytes (2.33 pg DNA/2C; Galbraith et al., 1983) were included with our samples as internal standards (Fig. 1).

The mean 2C-value of each sample was determined by multiplying the ratio of the fluorescence means of the sample nuclei and chicken erythrocytes by the amount of DNA per chicken erythrocyte (2.33 pg). The standard deviation for the mean 2C-value of each sample was calculated by taking into account the variances of the fluorescence from both the sample and the internal standard (W. Lamboy, personal communication):

$$\sigma^2(\text{samp/crbc}) = \sigma^2(\text{samp})/\text{M}(\text{crbc})^2 + [\sigma^2(\text{crbc}) \times \text{M}(\text{samp})^2]/\text{M}(\text{crbc})^4$$

$$\text{Sample C-value standard deviation} = \sigma(\text{samp/crbc}) \times 2.33$$

where

$\sigma^2$ = fluorescence variance
M = fluorescence mean
samp = sample nuclei
crbc = chicken erythrocytes

Our standard deviations are up to twice as large as for

[1] Received for publication 25 November 1991; revision accepted 27 April 1992.

The authors thank Steven Spongberg of the Arnold Arboretum for helping in the collection of leaf samples; Martha Rangel-Lugo for providing chicken blood; and Kathy Anderson and Jim Slattery for assisting in the operation of the flow cytometer.

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those in which we assumed no variance for the standard. Previous reports of C-value standard deviations: 1) assume the standard is constant without variance (Rothfels et al., 1966; Narayan, 1982; Price et al., 1983; Goldblatt, Walbot, and Zimmer, 1984; Laurie and Bennett, 1985; Sims and Price, 1985); 2) use a standard assuming a constant mean and a constant standard deviation (Galbraith et al., 1983); or 3) give standard deviations around the mean fluorescence or mean density of the sample in arbitrary units (Chooi, 1971; Price and Bachmann, 1975; Rayburn et al., 1989; Rayburn, 1990; McMurphy and Rayburn, 1991).

## RESULTS AND DISCUSSION

The genomic DNA contents of 44 rosaceous plants (29 genera), estimated from the mean fluorescence values of 500–2,000 nuclei per sample, are listed in Table 2. The coefficients of variation were less than 5% for all reported samples. Previously obtained 2C-values of Rosaceae are included in Table 2: six estimated by Feulgen microdensitometry (Bennett and Smith, 1976, 1991; Bennett, Smith, and Heslop-Harrison, 1982) and eight others obtained by flow cytometry recently reported by one of us (Arugumanathan and Earle, 1991b). The values obtained by Feulgen densitometry agree closely with the flow cytometry values of other species within the same subfamily.

***Polyploid series***—The 2C-values of *Malus* × *domestica* and *Prunus* species correlate with their chromosome counts. *Malus* × *domestica* accessions with chromosome numbers of 2*x*, 3*x*, and 4*x* have 2C-values (standard deviation) of 1.55 (0.21), 2.51 (0.20), and 2.86 (0.43) pg, respectively, deviations from a perfect numerical series well within the variation found within apple (Table 3). The 2C value of the diploid sweet cherry *Prunus avium* (0.67 pg) is approximately half that of the tetraploid hybrid cherry *Prunus* × sp. '4X' (1.36 pg).

In contrast, the nuclear DNA contents of *Spiraea pubescens* and *S. nipponica*, reportedly diploids, are two and four times larger than the diploid genome of *S. chinensis* (Table 2). Because polyploidy is reported in this genus, it is reasonable to conclude that our accessions of *S. pubescens* and *S. nipponica* are polyploids. Chromosome counts are necessary, however, to confirm polyploidy for these *Spiraea* accessions. If their chromosome numbers are diploid, the 2C-value variation among diploid *Spiraea* species would be remarkably large, with nearly as much variation as found within the Rosaceae as a whole.

***Diploid Rosaceae C-values are low among angiosperms***—*Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) is widely known for its very small nuclear genome, with estimates of its 2C-value varying from 0.15 pg (Leutwiler, Hough-Evans, and Meyerowitz, 1984), 0.30 pg (Arumuganathan and Earle, 1991a), to 0.4 pg (Bennett and Smith, 1991) determined by reassociation kinetics, flow cytometry, and Feulgen microdensitometry, respectively (discussed by Arumuganathan and Earle, 1991a). The discrepancy among these reported 2C-values may be due to the multiple ploidy levels in *Arabidopsis thaliana* (Fig. 1) (Arumuganathan and Earle, 1991a; Galbraith, Harkins, and Knapp, 1991). Recently, an even smaller nuclear genome was reported for *Cardamine amara* L. (0.11 pg/2C) (Bennett and Smith, 1991), another member of the Brassicaceae.

Other small C-values occur within the Rosaceae. *Rosa wichuraiana* Crepin (Rosoideae) has a genome size of 0.2 pg/2C (Bennett and Smith, 1991). Within the Spiraeoideae, several woody species of *Spiraea* and *Physocarpus* gave fluorescence peaks between 0.42 and 0.46 pg/2C (Table 2) (Figs. 2, 3). Outside the Brassicaceae and Rosaceae, a genome smaller than these Spiraeoideae has only been reported for *Aesculus hippocastanum* L. (0.3 pg/2C, Feulgen microdensitometry) (Bennett, Smith, and Heslop-Harrison, 1982). However, we were unable to substantiate this value using leaf tissue sampled from an *A. hippocastanum* on the Cornell campus (1.04 pg/2C; SD 0.05; flow cytometry).

The subfamily Amygdaloideae also has relatively small 2C-values (Table 2); however, *Prunus* diploid genomes, with 2C values between 0.54 and 0.66 pg, are comparable with the genomes of other diploid angiosperms with small 2C-values, e.g., *Urtica urens* L. (Urticaceae) (0.6 pg/2C) and *Lablab niger* Medik. (Fabaceae) (0.7 pg/2C) (Bennett and Smith, 1976).

***Rosaceae diploid 2C-value variation***—A range in DNA content among diploid species of nearly eightfold was detected among 28 genera of the four Rosaceae subfamilies (Fig. 4). The range of C-values reported for a family is meaningful only if sampling of taxa is extensive. Al-

TABLE 1. *Original sources and vouchers of plants used in this study. AA = Arnold Arboretum; CU = Cornell University; NYSAES = New York State Agricultural Experiment Station, Geneva, New York*

Spiraeoideae:

*Exochorda giraldii*, AA 1503-52A, EED 872. *Neillia simensis*, AA 144-81, EED 875. *Physocarpus bracteatus*, AA 1235-85, EED 856; *P. opulifolius*, AA 1279-82-A, EED 857. *Spiraea chinensis*, AA 223-83, EED 855; *S. crenata*, AA 1230-85, EED 859; *S. pubescens*, AA 541-83, EED 853; *S. nipponica*, CU, EED 900; *S. sargentiana*, AA 1233-85, EED 854; *S. wilsonii*, AA 953-85-A, EED 852. *Stephanandra incisa*, CU, EED 902.

Amygdaloideae:

*Osmaronia cerasiformis*, AA 274-85, EED 879. *Prinsepia uniflora*, AA 7188-A, EED 848. *Prunus persica* "Red Haven," NYSAES, no voucher; *P. serotina*, NYSAES, EED 879; *P. subhirtella*, CU, EED 903.

Rosoideae:

*Dryas octopetala*, CU, EED 892. *Duchesnea indica*, Geneva, NY, EED 898. *Neviusia alabamensis*, AA 1809-71, EED 873. *Potentilla fructicosa*, CU, EED 899. *Rhodotypus scandens*, AA 680-79, EED 851. *Rosa multiflora*, Geneva, NY, EED 897. *Rubus odoratus*, CU, EED 896.

Maloideae:

*Amelanchier* sp., NYSAES, EED 876. *Aronia arbutifolia*, AA 1905-81, EED 870. *Chaenomeles speciosa*, NYSAES, EED 881. *Cotoneaster melanocarpa*, Geneva, NY, EED 882. *Crataegus crus-galli*, Geneva, NY, EED 883. *Cydonia oblonga*, NYSAES, EED 877. *Eriobotrya japonica*, CU, no voucher. *Malus* spp., NYSAES. *Mespilus germanica*, NYSAES, EED 878. *Photinea parvifolia*, AA 577-76, EED 867. *Pyracantha coccinea*, CU, EED 901; *P.* sp. "Royal," AA 194-49-A, EED 869. *Pyrus calleryana*, CU, EED 895. *Sorbus alnifolia*, CU, EED 880; *S. americana*, NYSAES, EED 894.

TABLE 2. *Mean 2C-values, standard deviations (SD), and ploidy levels of Rosaceae species with citations of source and ploidy reference*

| | 2C (pg) | SD | Source[a] | Ploidy | Ploidy ref[b] |
|---|---|---|---|---|---|
| Spiraeoideae $x = 9$ | | | | | |
| *Physocarpus opulifolius* (L.) Maxim. | 0.42 | 0.09 | 1 | 2*x* | 6 |
| *Spiraea chinensis* Maxim. | 0.42 | 0.11 | 1 | | |
| *Physocarpus bracteatus* (Rydb.) Rehd. | 0.43 | 0.07 | 1 | | |
| *Spiraea crenata* L. | 0.46 | 0.10 | 1 | | |
| *Stephanandra incisa* (Thunb.) Zabel | 0.53 | 0.06 | 1 | | |
| *Neillia simensis* D. Oliver | 0.54 | 0.08 | 1 | 2*x* | 3 |
| *Spiraea pubescens* Turcz. | 0.94 | 0.11 | 1 | 2*x* | 7 |
| *Exochorda giraldii* Hesse. $x = 8$ | 1.11 | 0.19 | 1 | 2*x* | 7 |
| *Spiraea wilsonii* Duthie | 1.59 | 0.15 | 1 | | |
| *Spiraea nipponica* Maxim. | 1.75 | 0.13 | 1 | 2*x* | 7 |
| *Spiraea sargentiana* Rehd. | 1.84 | 0.11 | 1 | | |
| Amygdaloideae $x = 8$ | | | | | |
| *Prunus persica* (L.) Batch. "Madison" | 0.54 | 0.05 | 3 | 2*x* | 7 |
| *Prunus persica* (L.) Batch. "Red Haven" | 0.55 | 0.06 | 1 | 2*x* | 7 |
| *Prunus armenaica* L. "Sundrop" | 0.60 | 0.06 | 3 | 2*x* | 7 |
| *Prunus subhirtella* Miq. | 0.60 | 0.09 | 1 | 2*x* | 7 |
| *Prunus avium* (L.) L. "Van" | 0.67 | 0.06 | 3 | 2*x* | 5 |
| *Osmaronia cerasiformis x* = 6 | 0.98 | 0.11 | 1 | 2*x* | 6 |
| (Torr. & Gray ex Hook. & Arn.) Greene | | | | | |
| *Prunus serotina* J.F. Ehrh. | 1.00 | 0.13 | 1 | 4*x*; 5*x*; 6*x* | 3 |
| *Prunus* × spp. "4X" | 1.36 | 0.12 | 3 | 4*x* | |
| *Prunus cerasus* L. "Montmorency" | 1.42 | 0.08 | 3 | 4*x* | 2 |
| *Prunus* × spp. "Standley" | 1.83 | 0.07 | 3 | 6*x* | |
| *Prinsepia uniflora* Batal. | 3.09 | 0.28 | 1 | 4*x* | 7 |
| Rosoideae | | | | | |
| *Rosa wichuraiana* Crepin $x = 7$ | 0.2 | | 2 | 2*x* | |
| *Rubus idaeus* L. $x = 7$ | 0.58 | 0.10 | 3 | 2*x*; 4*x* | 1 |
| *Rosa blanda* Aiton $x = 7$ | 0.6 | | 2 | 3*x* | |
| *Acaena magellanica* (Lam.) Vahl. $x = 7$ | 0.6 | | 4 | 6*x* | 2 |
| *Potentilla fructicosa* L. | 0.80 | 0.70 | 1 | 2*x*; 4*x*; 6*x* | 8 |
| *Rhodotypus scandens* (Thunb.) Mak. $x = 9$ | 0.74 | 0.10 | 1 | 2*x* | 7 |
| *Rubus odoratus* L. $x = 7$ | 0.76 | 0.22 | 1 | 2*x* | 8 |
| *Neviusia alabamensis* A. Gray $x = 9$ | 1.02 | 0.11 | 1 | 2*x* | 6 |
| *Sanguisorba minor* Scop. $x = 7$ | 1.1 | | 2 | 4*x* | |
| *Aphanes arvensis* L. $x = 8$ | 1.1 | | 5 | 6*x* | 7 |
| *Dryas octopetala* L. $x = 9$ | 1.16 | 0.25 | 1 | 2*x* | 1 |
| *Rosa acicularis* Lindley $x = 7$ | 1.3 | | 2 | 6*x* | |
| *Rosa multiflora* Thunb. ex J. Murr. $x = 7$ | 1.65 | 0.11 | 1 | 2*x*; 4*x* | 1 |
| *Duchesnea indica* (Andr.) Focke $x = 7$ | 3.00 | 0.14 | 1 | 6*x*; 12*x* | 8 |
| Maloideae $x = 17$ | | | | | |
| *Pyracantha* "Royal" | 0.99 | 0.16 | 1 | | |
| *Pyrus communis* L. "Bartlett" | 1.11 | 0.06 | 3 | 2*x* | 7 |
| *Chaenomeles speciosa* (Sweet) Nakai | 1.20 | 0.16 | 1 | 2*x* | 7 |
| *Pyrus calleryana* Decne. | 1.26 | 0.29 | 1 | 2*x* | 7 |
| *Amelanchier* sp. | 1.31 | 0.25 | 1 | | |
| *Sorbus alnifolia* (Siebold & Zucc.) Koch | 1.36 | 0.32 | 1 | 2*x* | 7 |
| *Sorbus americana* Marsh | 1.30 | 0.37 | 1 | 2*x* | 7 |
| *Pyracantha coccinea* E. J. Roem. | 1.41 | 0.31 | 1 | 2*x* | 7 |
| *Cydonia oblonga* Mill. | 1.45 | 0.14 | 1 | 2*x* | 1 |
| *Mespilus germanica* L. | 1.48 | 0.15 | 1 | 2*x* | 3 |
| *Eriobotrya japonica* (Thunb.) Lindl. | 1.54 | 0.17 | 1 | 2*x* | 1 |
| *Cotoneaster melanocarpa* Lodd. | 2.24 | 0.20 | 1 | 4*x* | 4 |
| *Photinea parvifolia* (E. Pritz.) Schneid. | 2.29 | 0.26 | 1 | | |
| *Aronia arbutifolia* (L.) Pers. | 2.57 | 0.20 | 1 | 2*x*; 4*x* | 7 |
| *Crataegus crus-galli* L. | 2.71 | 0.24 | 1 | 3*x*; 4*x* | 7 |

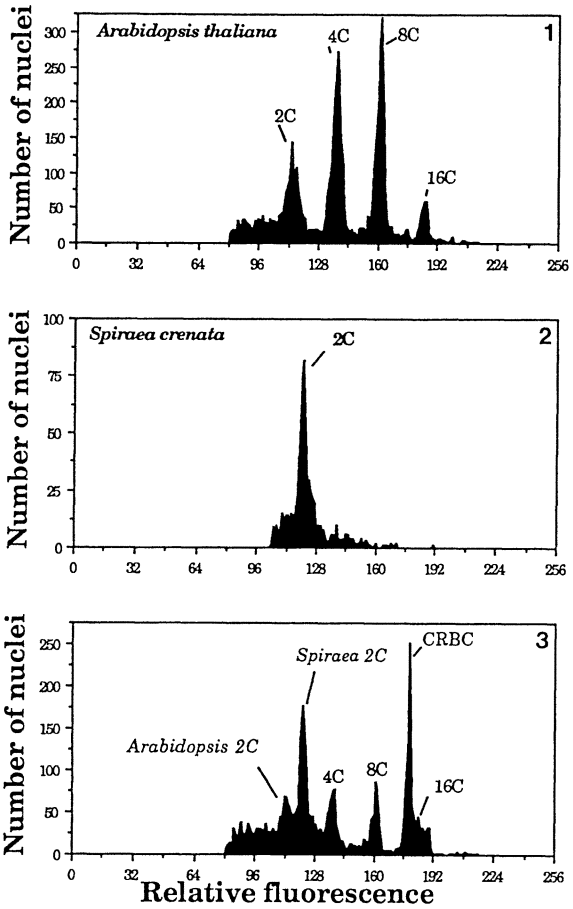
[a] Source: 1 = this paper; 2 = Bennett and Smith, 1991; 3 = Arumuganathan and Earle, 1991b; 4 = Bennett, Smith, and Heslop-Harrison, 1982; 5 = Bennett and Smith, 1976.

[b] Ploidy reference: 1 = Index to plant chromosome numbers 1984–1985. (Peter Goldblatt, ed. 1988. *Monographs in Systematic Botany from the Missouri Botanical Garden* 23.) 2 = Index to plant chromosome numbers 1982–1983. (Peter Goldblatt, ed. 1985. *Monographs in Systematic Botany from the Missouri Botanical Garden* 13.) 3 = Index to plant chromosome numbers 1972. (R. J. Moore, ed. 1974. *Regnum Vegetabile* 91.) 4 = Index to plant chromosome numbers 1967–1971. (R. J. Moore, ed. 1973. *Regnum Vegetabile* 90.) 5 = Index to plant chromosome numbers 1966. (R. Ornduff, ed. 1968. *Regnum Vegetabile* 55.) 6 = Index to plant chromosome numbers 1958–1960. (1–4 and Supplement.) (M. S. Cave, ed. University of North Carolina Press, Chapel Hill, NC.) 7 = Chromosome atlas of flowering plants. (C. D. Darlington and A. P. Wylie, 1955. George Allen and Unwin, London.) 8 = Chromosome numbers of flowering plants. (Z. Bolkovskikh, V. Grif, T. Matejeva, and O. Zakharyeva, eds. 1969. Izdatel'stvo Nauka, Leningrad.)

TABLE 3. *Mean C-values and standard deviations of* Malus *species and cultivars. Samples of* Malus *species were collected from trees grown at the USDA-ARS Plant Genetic Resources Unit, Geneva, New York*

| | pg/2C | SD |
|---|---|---|
| *M. angustifolia* (Aiton) Michaux GMAL[a]-2347 | 1.46 | 0.08 |
| *M. baccata* (L.) Borkh. GMAL-0434 | 1.61 | 0.30 |
| *M. coronaria* (L.) Mill. GMAL-2906 (3*x*) | 2.23 | 0.07 |
| *M. coronaria* (L.) Mill. GMAL-3064 (4*x*) | 3.11 | 0.13 |
| *M. florentina* (Zuccagni) Schneid. GMAL-1546 | 1.63 | 0.23 |
| *M. formosana* Kaw. & Koidz. GMAL-2726 | 1.23 | 0.30 |
| *M. fusca* (Raf.) Schneid. GMAL-1234 | 1.54 | 0.26 |
| *M. honanensis* Rehd. GMAL-2721 | 1.33 | 0.23 |
| *M. hupehensis* (Pamp.) Rehd. GMAL-1022 (3*x*) | 2.30 | 0.24 |
| *M. ioensis* (A. Wood) Britt. GMAL-2941 | 1.55 | 0.10 |
| *M. kansuensis* (Batal.) Schneid. GMAL-1840 | 1.33 | 0.25 |
| *M. prunifolia* (Willd.) Borkh. GMAL-1069 | 1.63 | 0.27 |
| *M. pumila* Mill. GMAL-1061 | 1.67 | 0.21 |
| *M. sargentii* Rehd. GMAL-0539 (3*x*, 4*x*) | 1.97 | 0.23 |
| *M. trilobata* (Labill.) Schneid. GMAL-1836 | 1.63 | 0.25 |
| *M. tschonskii* (Maxim.) Schneid. GMAL-1834 | 1.21 | 0.24 |
| *M. transitoria* (Batal.) Schneid. GMAL-1822 | 1.51 | 0.30 |
| *M. yunnanensis* (Franch.) Schneid. GMAL-1819 | 1.39 | 0.16 |
| *M.* × *domestica* Borkh. | | |
| "0523" GMAL-0523 | 1.50 | 0.29 |
| "Liberty" GMAL-0824 | 1.55 | 0.21 |
| "Bedford" | 1.56 | 0.25 |
| "Prima" GMAL-1064 | 1.59 | 0.29 |
| "Prince George" | 1.64 | 0.24 |
| "Spartan" GMAL-1247 | 1.73 | 0.33 |
| "Jonagold" GMAL-0619 (3*x*) | 2.51 | 0.20 |
| "E8" (4*x*) | 2.86 | 0.43 |

[a] GMAL refers to the catalog number for *Malus* at the National Germplasm Repository for Apple and Grape, Geneva, NY.




Figs. 1–3. Numbers of nuclei as a function of fluorescence intensity (log scale). **1.** *Arabidopsis thaliana.* The multiple peaks correspond to multiple ploidy levels of nuclei within a single plant's leaves. **2.** *Spiraea crenata.* **3.** *Arabidopsis thaliana, Spiraea crenata,* and chicken red blood cells (CRBC) combined.

though little is known about C-value variation in many angiosperm families, five- to tenfold differences among diploids are found within other flowering plant families with up to 30-fold ranges in 19 genera (30 species) of Iridaceae (Goldblatt, Walbot, and Zimmer, 1984), 40-fold in two genera (seven species) of Droseraceae (Rothfels and Heimburger, 1968), and 80-fold in six genera (22 species) of Ranunculaceae (Rothfels et al., 1966). With the very recent publication of the extremely small C-value of *Rosa wichuraiana* (Bennett and Smith, 1991) (Table 2), the range of known Rosaceae C-values has been doubled. Nevertheless, compared to that of other angiosperm families, Rosaceae C-value variation is low, even including the Maloideae which is thought to be of polyploid origin.

Because 2C-value variation within the family is relatively low, we did not expect to find much variation within genera or species. 2C values of 17 diploid *Malus* species, including representatives from the five sections of Huckins (1972) (Table 3), ranged only from 1.21 to 1.67 pg. In contrast to this rather small range of variation, Laurie and Bennett (1985) found about twofold differences in nuclear DNA contents among diploid *Zea* species, while threefold differences in DNA content have been reported among diploid *Microseris* species (Price and Bachmann, 1975), fourfold in *Helianthus* and *Anemone* (Sims and Price, 1985; Rothfels et al., 1966), fivefold in *Vicia* (Raina and Narayan, 1984), and ninefold in *Crepis* (Jones and Brown, 1976).

C-values of diploid *M.* × *domestica* cultivars ranged from 1.50 to 1.73 pg/2C (Table 3). Similarly, within several species of *Malus* (three species of *Malus* section *Chloromeles*; Dickson, unpublished data), the 2C variation (less than 2%) is lower than that between species of *Malus*. In comparison, C-values of inbred lines of *Helianthus annuus* have as much as 32% variation (Michaelson, et al., 1991b).

***Evolution of the Maloideae***—The relatively high chromosome number of the Maloideae ($x = 17$) suggested to early workers that the subfamily had a polyploid origin. Controversies arose, however, concerning whether 7, 8, or 9 was the progenitor chromosome base number of an autopolyploid Maloideae, and later, whether the subfamily was allopolyploid (Nebel, 1929; Tishler, 1929; Darlington and Moffett, 1930; Sax, 1931). Isozyme studies of *Malus* show duplicated gene systems indicative of polyploidy, and allele segregations and fixed heterozygosities suggestive of allopolyploidy (Chevreau, Lespinasse, and Gallet, 1985; Chevreau and Laurens, 1987; Weeden and Lamb, 1987; Dickson, Kresovich, and Weeden, 1991). The meiotic behavior of triploid apple convinced Sax (1932) that the Maloideae arose following hybridization between ancestors within the Rosaceae having $x = 8$ and $x = 9$. Stebbins (1950) argued on morphological grounds

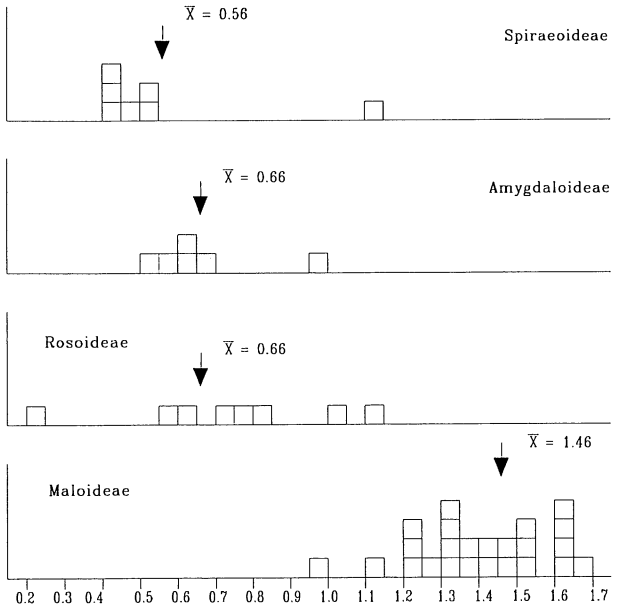



Fig. 4. Distribution and mean (arrows) 2C-values of diploid plants of Rosaceae subfamilies (from Table 1).

that a primitive amygdaloid ($x = 8$) and a primitive spiraeoid ($x = 9$) were the likely parents. More recent morphological (Phipps et al., 1991) and chemical (Challice, 1974, 1981) data support this view.

Diploid nuclear DNA contents of the four Rosaceae subfamilies overlap in value, and subfamily C-value means are not correlated with chromosome numbers. However, the DNA contents within the Maloideae are broadly consistent with a polyploid origin of the subfamily (Table 1; Fig. 4). Diploid Maloideae values correspond to the sum of two diploid genomes from any of the other subfamilies that could be the result of either an autopolyploid or allopolyploid doubling of genomes. Assuming allopolyploidy, C-value data cannot resolve whether an originating hybridization occurred between genera or species within the same or from different subfamilies. Therefore, none of the other subfamilies can be excluded as possible ancestors of the Maloideae based on nuclear DNA content alone.

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## ERRATUM

The cover photograph on the June 1992 *American Journal of Botany* was printed upside down. The species listed for top and bottom rows should be reversed in the caption for the cover illustration at the top of the Contents page in that issue.