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Clarifying Taxonomy and Nomenclature of *Fothergilla* (Hamamelidaceae) Cultivars and Hybrids

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***Abstract. Fothergilla* L. spp. are valuable nursery and garden plants. However, clear differentiation among *F. gardenii* Murray, *F. major* Lodd., and potential hybrids can be difficult based solely on morphological characteristics. The objectives of this work were to verify and describe the existence of interspecific hybrids and to clarify the proper nomenclature for cultivars of *Fothergilla* that are commonly grown in the nursery industry. A comparison of morphological characteristics was made among diverse clones representing both species and potential hybrids. A combination of chromosome counts and DNA contents was used to clearly differentiate among *F. gardenii* (*2n* = 4*x* = 48), *F. major* (*2n* = 6*x* = 72), and hybrids (*2n* = 5*x* = 60). It was determined that the majority of cultivars represented in commerce were hybrids. *Fothergilla* ×*intermedia* Ranney and Fantz (hybrid fothergilla) is proposed as the name for these hybrids and is validated with a Latin diagnosis. Although certain morphological characteristics can be used to differentiate between *F. gardenii* and *F. major*, the hybrids tend to be intermediate and are particularly difficult to separate from *F. major* on the basis of appearance. The correct classification and nomenclature for 17 different taxa are presented.**

Fothergilla L. spp. (fothergilla or witch-alder; Hamamelidaceae R. Brown) are exceptional garden plants (Clark, 1987; Dirr, 1998; Flint, 1984; Weaver, 1971) that display showy, white, fragrant flowers in a terminal spike that resembles a bottlebrush. Summer foliage color can be dark green to blue-green with fall foliage ranging from and including multicolored combinations of yellow, orange, maroon, and scarlet. *Fothergilla* have few pest problems, and they tolerate a broad range of climates (USDA hardiness zones 4–9), soil types, and shade. As a result, *Fothergilla* have become valuable nursery and garden plants.

There are two species of *Fothergilla*: *F. gardenii* Murray and *F. major* Lodd. Both are native to the Southeastern United States. *Fothergilla gardenii* is found in wet savannas and pocosins in the coastal plains of North Carolina, South Carolina, Georgia, Florida, and Alabama (Flora of North America Editorial Committee, 1993+; Weakley, 2006; Weaver, Jr., 1969). This species generally is smaller in stature (3–10 dm) than *F. major* and is distinguished sometimes by smaller leaves ranging from 1.9 to 6 cm long and from 1.3 to 5.2 cm wide that are generally toothed only on the upper half and symmetric at the base. Stipules are 1.5–4 (6.1) mm long. Stamens generally number from 12 to 24. The hypanthium at anthesis ranges from 1.5 to 2.6 mm wide and from 0.9 to 1.5 mm deep. Cytology determined a chromosome number of *2n* = 4*x* = 48 (Weaver, Jr., 1969). In contrast, *F. major* is found on upland sites in the piedmont and mountains of North Carolina, South Carolina, Georgia, Alabama, Tennessee, and Arkansas (Flora of North America Editorial Committee, 1993+; Weakley, 2006; Weaver, Jr., 1969). This species generally is larger in stature (7–65 dm) than *F. gardenii* and is distinguished by larger leaves ranging from 2.5 to 13 cm long and 4.2 to 12.5 cm wide that generally are toothed from below the middle and conspicuously asymmetric at the base. Stipules are 2.8–7 (10.2) mm long. Stamens generally number (18) 22–32. The hypanthium at anthesis ranges from 2.4 to 3.9 mm wide and from 1.5 to 3 mm deep. Cytology determined a chromosome number of *2n* = 6*x* = 72 (Weaver, Jr., 1969). Although there is no known diploid species of fothergilla, *Parrotiopsis* (Niedenzu) C. Schneid. is a closely allied genus with *2n* = 2*x* = 24 (Goldblatt and Endress, 1977; Li and Bogle, 2001; Weaver, Jr., 1969) and may represent a parallel lineage from an ancestral diploid.

Often, the two species of *Fothergilla* are confused, but they can be separated by comparing key characteristics (Clark, 1988). Also, there has been speculation that the two species of *Fothergilla* hybridize (Dirr, 1998). Hybrids between these species should have a chromosome number of *2n* = 5*x* = 60. Microscopic determination of chromosome numbers is not a practical approach for separating species and hybrids among large numbers of cultivars. However, flow cytometry can provide a fast and accurate determination of nuclear DNA content that is related directly to ploidy level (among closely related taxa) and can be used as a taxonomic tool (de Laat et al., 1987; Doležel, 1991; Doležel et al., 1998; Galbraith et al., 1983).

The objectives of this research were to verify the existence of hybrids between *F. gardenii* and *F. major* and to clarify the proper taxa designations for clones of *Fothergilla* commonly grown in the nursery industry.

Materials and Methods

Plant material and morphology. Collections of *Fothergilla* at the North Carolina State University, Mountain Horticultural Crops Research and Extension Center, Fletcher, N.C. (NCSU) and Yew Dell Gardens, Crestwood, Ky. (YDG), were used for this project (Table 1). Morphological measurements were taken on lamina length, lamina width, leaf margin dentation location (strictly above the middle, to the middle, or extending to below the middle), symmetry of leaf base (symmetrical, variable, or asymmetrical), stipule length, stamen number, and hypanthium depth and width at anthesis. Twelve measurements were taken for each leaf morphology character, and six measurements were taken for each flower morphology character for each clone.

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Table 1. Comparison of selected characteristics among taxa of *Fothergilla* species and hybrids.

Taxa	Accession no.	Genome size (pg)	Lamina length (cm)	Lamina width (cm)	Leaf dentation	Leaf base	Stamen no.	Hypanthium Depth (mm)	Hypanthium width (mm)	Stipule length (mm)
F. gardenii										
'Appalachia'	NCSU 2004–069	4.32 ± 0.03[z]	3.9–5.4	2.3–3.2	Above middle	Symmetrical	16–28	1.8–2.3	2.0–2.2	3.9–8.6
'Bill's True Dwarf'	YDG 2005–317-A	4.20 ± 0.04	4.0–5.0	3.0–3.5	Above Middle	Variable	Not available	1.2–1.7	1.7–2.1	4.0–5.0
'Blue Mist'	YDG-2005–1-A	4.46 ± 0.04	6.5–8.0	3.5–4.0	Above middle	Symmetrical	14–22	1.5–2.1	1.9–3.1	4.0–5.0
	YDG-2005–320-A									
'Harold Epstein'	NCSU 2001–047	4.44 ± 0.04	3.4–4.4	2.1–2.7	Above middle	Symmetrical	12–17	0.8–1.2	1.0–1.8	2.5–3.9
'Jane Platt'	NCSU 2005–136	4.36 ± 0.04	4.2–5.1	2.1–3.4	Above middle	Symmetrical	14–18	0.7–1.7	1.1–1.7	3.9–8.8
F. ×intermedia										
'Blue Shadow'	NCSU 2005–051	5.52 ± 0.02	5.6–8.9	4.3–6.8	Middle	Variable	18–23	1.5–2.2	1.7–2.6	3.8–8.6
'Eastern Form'	YDG 2005–322-A	5.28 ± 0.02	7.0–8.5	6.0–6.5	Above middle	Variable	19–24	1.5–2.4	1.6–2.5	6
'KLMtwo' Beaver Creek®	NCSU 2002–128	5.30 ± 0.06	5.6–8.0	4.8–6.6	Middle	Asymmetrical	17–23	1.6–2.3	1.8–2.4	5.0–9.7
'KLMfifteen' Red Monarch™	YDG 2004–602-A	5.30 ± 0.02	7.6–9.4	5.4–7.7	Middle to above	Variable	24–30	1.1–2.2	1.8–2.5	NM[y]
'KLMsixteen' May Bouquet™	YDG 2004–535-A	5.24 ± 0.01	8.0–11.1	5.1–9.5	Below middle	Asymmetrical	27–33	1.5–2.0	2.5–3.4	6.2–10.9
F. sp.	YDG 2005–323-A	5.22 ± 0.02	8.0–10.0	6.5–7.5	Above middle	Asymmetrical	14–21	2.0–2.6	1.7–2.7	5.0–7.0
'Mt. Airy'	NCSU 2005–137	5.25 ± 0.12	7.0–9.5	5.5–7.8	Below middle	Variable	18–26	1.5–2.3	1.7–2.5	3.8–6.9
'Red Licorice'	NCSU 2001–234	5.21 ± 0.08	5.3–8.1	4.5–6.3	Below middle	Asymmetrical	18–23	1.5–2.2	1.7–2.4	4.6–8.6
'Sea Spray'	NCSU 2001–235	5.32 ± 0.04	5.3–7.2	4.6–6.1	Middle	Asymmetrical	22–26	1.9–2.4	1.7–2.0	4.8–6.9
'Windy City'	YDG 2005–310-A	5.36 ± 0.10	7.0–9.0	5.5–6.0	Above middle	Variable	16–19	0.9–1.4	1.0–1.6	5.0
F. major										
'Arkansas Beauty'	YDG 2005–318-A	6.35 ± 0.06	6.0–8.5	6.0–8.0	Below middle	Variable	18–27	1.7–2.7	2.0–3.0	10
'KLMG' Mystic Harbor™	YDG 2005–312-A	6.18 ± 0.01	9.0–11.5	8.0–11.0	Below middle	Variable	16–23	1.0–1.6	1.4–2.2	6.0–7.0

[z]Values for genome size are means, $n = 2$ to 6, ±1 SEM.
[y]NM, stipules not measured.

Flow cytometry. Holoploid, 2C DNA contents (i.e., DNA content of the entire non-replicated, chromosome complement irrespective of ploidy level) were determined via flow cytometry (de Laat et al., 1987; Doležel, 1991; Galbraith et al., 1983; Greilhuber et al., 2005). Nuclei isolation and staining followed protocols provided by Partec GmbH (Münster, Germany). About 12 stamen filaments were chopped with a razor blade in a petri dish containing 400 µL of extraction buffer (CyStain ultraviolet Precise P, Partec). The suspension was filtered through 50-µm nylon mesh, and nuclei were stained using 1.6 mL of staining buffer containing 4′,6-diamidino-2-phenylindole (DAPI) (CyStain ultraviolet Precise P, Partec). The suspension was analyzed using a flow cytometer with fluorescence excitation provided by a mercury arc lamp (PA-I Ploidy Analyzer, Partec). The mean fluorescence of each sample was compared with an internal standard of known genome size (*Pisum sativum* L. 'Ctirad', 2C = 9.09 pg; Doležel et al., 1998). A minimum of 4,500 nuclei were analyzed to calculate the ratio of sample peak to the internal standard for determining genome size [2C pg = (mean fluorescence of sample peak/mean fluorescence of internal standard peak) × 9.09 pg]. Two to six subsamples were analyzed for each taxa.

Chromosome counts. Root tips were collected in the morning from newly rooted stem cuttings of *Fothergilla* 'Mt. Airy' and placed in 2 mM 8-hydroxyquioline for 3–5 h at 12 °C. Roots were then rinsed with cold (4 °C) distilled water and placed in 3:1 solution of 95% ethanol/propionic acid fixative for ≈24 h at room temperature. Samples were rinsed with cold distilled water, transferred to a 70% ethanol storage solution, and placed in a refrigerator at 4 °C. The following week, samples were removed from storage and transferred to 30% aqueous ethanol for 12 min, followed by two 15-min rinses in distilled water. Roots were then hydrolyzed for 30 min at room temperature in 1 N HCl and then for 15 min at 60 °C, followed by a quick rinse in distilled H_2O. Small samples of root tips were excised and placed on a glass microscope slide with a drop of 1% acetocarmine stain, squashed with a coverslip, and viewed at 1500×.

Results and Discussion

Cytological examination of 14 mitotic cells revealed that *Fothergilla* 'Mt. Airy' was a pentaploid with $2n = 5x = 60$ (Fig. 1), thereby confirming that it is a hybrid between tetraploid *F. gardenii* and hexaploid *F. major*. Flow cytometry was an effective method for determining genome size and ploidy levels of the species and their hybrids (Fig. 2). *Fothergilla* 'Mt. Airy', a confirmed pentaploid, was used as a reference to compare the approximate genome sizes (DNA content) for the different ploidy levels. Mean 2C holoploid genome sizes for *F. gardenii* ranged from 4.2 to 4.5 pg, hybrids ranged from 5.2 to 5.5 pg, and *F. major* ranged from 6.2 to 6.4 pg

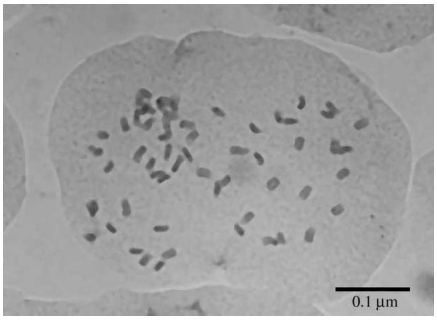

Fig. 1. Photomicrograph of root tip cell of *Fothergilla ×intermedia* 'Mt. Airy' in prophase with 60 somatic chromosomes.

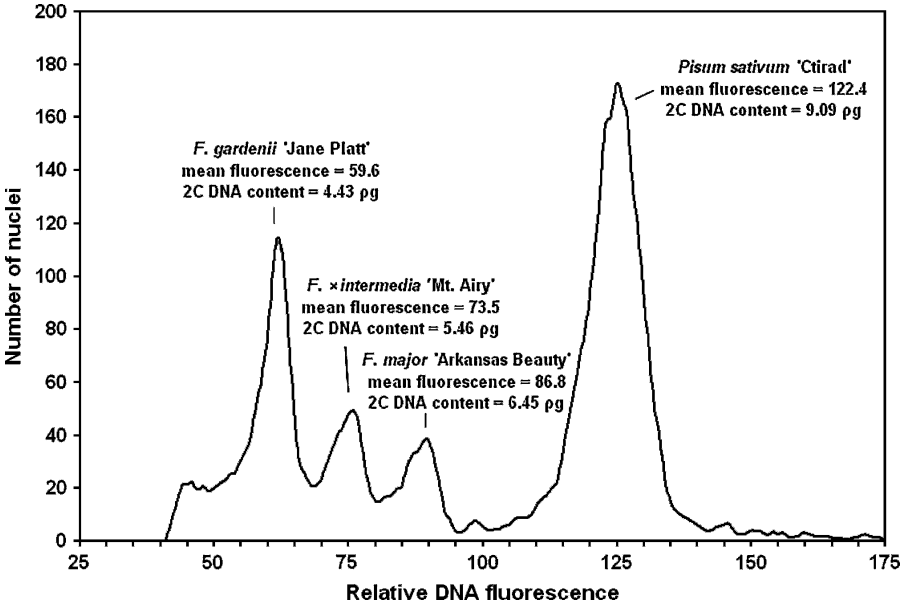

Fig. 2. Flow cytometry histogram of a combined sample containing nuclei from *F. gardenii* 'Jane Platt' ($2n = 4x = 48$), *F. ×intermedia* 'Mt. Airy' ($2n = 5x = 60$), *F. major* 'Arkansas Beauty' ($2n = 6x = 72$), and an internal standard, *Pisum sativum* 'Ctirad', with a known 2C holoploid DNA content of 9.09 pg. The DNA contents of *Fothergilla* samples were calculated based on mean sample fluorescence relative to the internal standard.

(Tables 1 and 2). Genome sizes within species and hybrids had a narrow range, providing clear distinction between the three taxonomic groups consistent with variations in ploidy levels. Mean 1C*x* monoploid genome size (i.e., DNA content of one nonreplicated base set of chromosomes with $x = 12$) was similar at 1.09 pg DNA for *F. gardenii,* 1.06 pg DNA for the hybrids, and 1.04 pg DNA for *F. major,* indicating that monoploid genome size is highly conserved among species and ploidy level in *Fothergilla*.

Differentiation between species was often ambiguous based on foliar and floral characteristics (Tables 1 and 2). Ranges for lamina length, stipule length, and hypanthium depth and width tended to overlap between these two species. Due to considerable variation within species and overlap in ranges between species in our sample set, leaf margin dentation, symmetry of the leaf base, and stamen number provided little value for separating these two species. Lamina width was the only characteristic, with distinct ranges from 2.1 to 4.0 cm for *F. gardenii* and from 6.0 to 11.0 cm for *F. major*. Although we did not compare plant height and emergence of flowers relative to foliage, it was reported generally that *F. gardenii* had a smaller mature height and bloomed before leaf emergence, while *F. major* had a larger mature height and bloomed with the emergence of new foliage (Clark, 1988; Weaver, Jr., 1969).

Separating hybrids from parental species was particularly challenging when based strictly on morphology. Most ranges for morphological measurements of hybrids overlapped with one or the other parent (Table 2). One exception was that the lamina width of *F. gardenii* was consistently narrower than either *F. major* or the hybrids. In general, hybrids tended to resemble *F. major* more closely, likely resulting from higher ploidy level and gene dose that was contributed from *F. major.*

To help clarify the taxonomy and nomenclature of *Fothergilla* spp., nothospecies *F. ×intermedia* Ranney and Fantz is proposed for the hybrid species name in accordance with Article H.3–5 (Greuter et al., 2000). The new hybrid species is described as follows: *Nothospecies Fothergilla ×intermedia* Ranney and Fantz *hybrida nova a F. gardenii* Murray *et F. major* Lodd. *cum characteribus morphologica intermedius, tamen distinguibili cytologia ambospecies pentaploidis cum chromosomatum 2n = 60, et genomibus amplitude 5.2–5.5 pg DNA, et distinguibili latofolius ad F. gardenia et folius dentibus ad super vs. infra medium ad F. major.* Pentaploid hybrid shrub, $2n = 60$ with genome size of 5.2–5.5 pg DNA. Leaf blade, 5.3–11.1 cm long, 4.3–7.8 (9.5) cm wide, base asymmetrical or variable, margins toothed from above the middle to below the middle; stipules, 3.8–10.9 cm long. Fruit and seed typically lacking. Flowers with hypanthium, 0.9–2.6 mm wide and 1.0–3.4 mm deep; stamens, 14–30 in number. Holotype: *Fothergilla* 'Mt. Airy', plant, 1.5 m tall, NCSU 2006–137, Mountain Horticultural Crops Research Station, Fletcher N.C., 25 Sept. 2006, *Fantz and Ranney 8911* (NCSC). Isotype: NA.

Table 2. Comparison of characteristics of *Fothergilla gardenii, F. ×intermedia*, and *F. major*.

Characteristic	*F. gardenii*	*F. ×intermedia*	*F. major*
Chromosomes			
Chromosome no.[z]	$2n = 4x = 48$	$2n = 5x = 60$	$2n = 6x = 72$
Genome size (2C)[y]	4.2–4.5 pg DNA	5.2–5.5 pg DNA	6.2–6.4 pg DNA
Leaves			
Lamina length (cm)	3.4–5.4 (8)[x]	5.3–11.1	6.0–11.5
Lamina width (cm)	2.1–4.0	4.3–7.8 (9.5)	6.0–11.0
Leaf dentation location	Mostly toothed above the middle	Toothed above, interm., or below the middle	Toothed from below the middle
Leaf base	Symmetrical or variable	Asymmetrical or variable	Variable
Stipule length	3.9–8.8	3.8–10.9	6.0–10.0
Flowers			
Stamen no.	12–28	14–30	16–27
Hypanthium depth (mm)	0.7–2.3	0.9–2.6	1.0–2.7
Hypanthium width (mm)	1.0–2.2	1.0–3.4	1.4–3.0

[z]Chromosome numbers for *F. gardenii* and *F. major* were determined by Weaver, Jr. (1969).
[y]Ranges for cytometry and morphological traits are a compilation of data from Table 1.
[x]Numbers in parentheses indicate extreme ranges, but uncommon occurrences.

On the basis of this study, we further identified the cultivars 'Appalachia', 'Bill's True Dwarf', 'Blue Mist', 'Harold Epstein', and 'Jane Platt' as *F. gardenii*. Cultivars 'Arkansas Beauty' and 'KLMG' Mystic Harbor were found to be *F. major*. The remaining cultivars, representing the majority of named selections in commerce, including 'Blue Shadow', 'Eastern Form', 'KLMtwo' Beaver Creek, one unnamed clone (YDG 2005–323-A), 'KLMfifteen' Red Monarch, 'KLMsixteen' May Bouquet, 'Mt. Airy', 'Red Licorice', 'Sea Spray', and 'Windy City' were hybrids, *F.* ×*intermedia.*

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