Compatibility Studies in *Hydrangea*[1]

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Abstract

Improvement in cold-hardiness is needed in bigleaf hydrangea (*Hydrangea macrophylla*). Potential sources of cold-hardiness for enhancing the usefulness of this popular shrub include panicle hydrangea (*H. paniculata*), smooth hydrangea (*H. arborescens*), and oakleaf hydrangea (*H. quercifolia*). The objective of this study was to investigate the possibility of creating hybrids between these three species and *H. macrophylla*. In addition, self-compatibility of each of the species was evaluated to determine the need for emasculation when making controlled pollinations. Numerous cultivars of the species were utilized in both the self-pollination and interspecific hybridization studies. Number of flowers self-pollinated ranged from 1000 in *H. arborescens* to 3000 in *H. quercifolia*. Viable seeds were obtained from all species except *H. arborescens*. All five of *H. quercifolia*, 9 of the 18 *H. paniculata*, and 1 of the 8 *H. macrophylla* self progeny obtained survived. Emasculation of *Hydrangea* flowers to be used in controlled pollinations is therefore recommended. Seedlings were obtained from all interspecific crosses in which *H. macrophylla* was used as the maternal parent. All putative hybrid seedlings died either at the cotyledonary stage or while the first set of true leaves was expanding.

Index words: interspecific hybridization, self-compatibility, incompatibility, breeding, hydrangea.

Species used in this study: bigleaf hydrangea (*H. macrophylla* (Thunb. Ex J.A. Murr.) Ser.); panicle hydrangea (*H. paniculata* Sieb.); smooth hydrangea (*H. arborescens* L.); oakleaf hydrangea (*H. quercifolia* Bartr.).

Significance to the Nursery Industry

Hydrangea macrophylla, or bigleaf hydrangea, is a popular summer-flowering shrub that is valued for its large inflorescences of bright blue or pink flowers. Unfortunately, its use in areas colder than USDA hardiness zone 6 is limited by the lack of cold-hardiness in flower buds, which are formed on previous year's growth. The development of a cold-hardy *H. macrophylla* would greatly expand the market in which this plant could be grown and marketed, and would provide landscapers and home gardeners in the North with a plant that provides tremendous visual impact in the summer garden. In an effort to increase the cold-hardiness of *H. macrophylla*, an interspecific hybridization project was initiated. Crosses were made between *H. macrophylla* and three cold-hardy *Hydrangea* species, *H. paniculata*, *H. arborescens*, and *H. quercifolia*. A few viable seeds of each hybrid were obtained when *H. macrophylla* was used as the maternal parent, but all of these seedlings died at a very young stage. Work is continuing on identifying causes of this hybridization failure and ways of overcoming it.

Introduction

The genus *Hydrangea* is comprised of approximately 80 species (8), several of which are cultivated in gardens throughout the world. *H. macrophylla* (Thunb. Ex J.A. Murr.) Ser., or bigleaf hydrangea, is the most popular species. A native of Asia, it is grown as both a garden and greenhouse plant. It is valued for its large corymbs that, depending on soil pH and cultivar, range in color from pink to blue and in intensity from pale to deeply colored. The major limitation to outdoor use of *H. macrophylla* is its cold-hardiness (2). Flower buds are set on previous year's growth and are damaged by low temperatures. It cannot be reliably grown in climates colder than USDA hardiness zone 6. Even in zones 6 and 7, late spring freezes may damage floral buds, resulting in greatly reduced flowering.

Three other *Hydrangea* species are widely cultivated in the United States (2). Panicle hydrangea (*H. paniculata* Sieb.) is the most cold-hardy *Hydrangea* species, and can be grown as far north as zone 3. Native to Asia, it has large white to pale pink panicles that bloom in mid summer. Smooth hydrangea (*H. arborescens* L.), which is native to the eastern United States, is cold hardy to zone 4. It produces delicate corymbs of pure white flowers in early summer. Although less cold hardy than these two species, oakleaf hydrangea (*H. quercifolia* Bartr.) is more tolerant of cold winters and late spring freezes than is *H. macrophylla*. Native to the southeastern United States, it has large white panicles that turn a dull, deep pink color as they age. Its mahogany autumn foliage and exfoliating bark provide autumn and winter interest in the landscape.

The development of interspecific hybrids between the various *Hydrangea* species may lead to unique combinations of desirable traits. A hybridization between *H. macrophylla* and one of the more cold-hardy species could result in a *Hydrangea* with brightly colored inflorescences that could be grown in colder parts of the country. *H. paniculata* and *H. arborescens* appear to be the best sources of cold-hardiness, but *H. quercifolia* may also be a useable source.

A hybrid between *H. macrophylla* and *H. paniculata* was reportedly made in 1910, but was lost during World War I (4). Results of an effort to hybridize *H. macrophylla* and *H. arborescens* have recently been reported (5). Viable seeds were obtained when *H. macrophylla* was used as the maternal parent, but seedlings died at the cotyledonary stage. Plants were obtained from tissue cultures initiated from the cotyledons of the seedlings, but the hybridity of these was not verified by either molecular or cytological analysis.

While many cultivars of *Hydrangea* species, particularly *H. macrophylla*, have been developed through extensive

[1]Received for publication December 3, 1999; in revised form January 12, 2000. This research was funded in part by a grant from **The Horticultural Research Institute, Inc., 1250 I Street, NW, Suite 500, Washington, DC 20005.**

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breeding efforts in Europe and Japan (6, 7), little has been published concerning the genetics and breeding behavior of *Hydrangea*. Information on self-compatibility and pollination techniques is generally lacking.

The primary objective of this study was to investigate the interspecific compatibility of *H. macrophylla* with *H. paniculata*, H. *arborescens*, and *H. quercifolia*. Particular effort was made to reproduce the *H. macrophylla* x *H. paniculata* hybrid, because of the desirability of combining the flower color of *H. macrophylla* with the extreme cold-hardiness of *H. paniculata*, but hybrids involving *H. quercifolia* and H. *arborescens* were also pursued. In addition, the self-compatibility of these four species was assessed to determine the need for emasculation in making controlled pollinations.

Materials and Methods

Self-pollination. Self-pollinations were made using container-grown plants of *H. macrophylla*, *H. paniculata*, *H. quercifolia*, and *H. arborescens*. Plants were grown outside in #7 or #15 containers under 60% shade. The following cultivars were used in this study: *H. arborescens* 'Annabelle'; *H. macrophylla* f. *macrophylla* 'All Summer Beauty', 'Alpengluhen', 'General Vicomtesse de Vibraye', 'Horben', 'Marechal Foch', 'Masja', 'Pia'; *H. macrophylla* f. *normalis* 'Blaumeise', 'Blue Billow', 'Kardinal'; *H. macrophylla* subsp. *serrata* 'Bluebird', 'Coerulea'; *H. paniculata* 'Brussels Lace', 'Burgundy Lace', 'Unique'; and, *H. quercifolia* 'Back Porch', 'John Wayne', 'Luverne Pink', 'Patio Pink', 'Pee Wee', 'Sikes Dwarf', 'Snow Queen'. Self-pollinations were also made on a *H. arborescens* plant collected from the wild.

Inflorescences used for self-pollinations were covered with breathable plastic bags prior to opening of any flowers. During flowering, the inflorescences were gently shaken at least three times a week to distribute pollen onto stigmas of open flowers. Bags were removed two weeks after the final flower had opened. Seed were collected when all capsules in an inflorescence had turned brown, which was approximately 4 months after the inflorescences were bagged. Seed capsules were cut open with a scalpel and examined under a stereomicroscope. Seeds that remained attached to the inside wall of the capsule were removed with a pair of fine-tipped forceps. Numbers of seed capsules and seed were recorded.

Seed were stored in a 5C (41F) refrigerator for 4 to 6 weeks prior to being sown on a soilless media and placed in a 25C (77F), 80% humidity lighted growth chamber. Seeds from intraspecific crosses of *H. macrophylla*, *H. paniculata*, and *H. quercifolia* were collected and planted at the same time and under the same conditions as the seed from the self-pollinations to monitor for disease or other germination problems.

Interspecific hybridization. Plants of *H. arborescens* 'Annabelle', *H. macrophylla* f. *macrophylla* 'All Summer Beauty', 'Alpengluhen', 'General Vicomtesse de Vibraye', 'Horben', 'Madame Emile Mouillere', 'Marechal Foch', 'Masja', 'Mousseline', 'Pia'; *H. macrophylla* f. *normalis* 'Blaumeise', 'Blue Billow', 'Blue Wave' 'Fasan', 'Kardinal', 'Mariesii', 'Pink Lacecap', 'Taube'; *H. macrophylla* subsp. *serrata* 'Bluebird', 'Grayswood', 'Tokyo Delight'; *H. paniculata* 'Boskoop', 'Brussels Lace', 'Burgundy Lace', 'Grandiflora' ('Pee Gee'), 'Kyushu', 'Pink Diamond', 'Tardiva', 'Unique', 'Webb'; and, *H. quercifolia* 'Gloster 5-Sepal', 'Patio Pink', 'Pee Wee' were grown in #7 or #15 containers outside under 60% shade. Just prior to making crosses, plants were brought into a greenhouse covered with 65% shadecloth. Plants remained in the greenhouse until seed were collected.

Reciprocal crosses of *H. macrophylla* with *H. arborescens*, *H. paniculata*, and *H. quercifolia* were made during the summers of 1997 and 1998. For each interspecific cross, 3 to 33 different combinations of parental cultivars were tested. Sterile flowers were removed from inflorescences that were to be used as females prior to opening of the fertile flowers. These inflorescences were observed for the opening of the first fertile flowers. The open flowers, along with all extremely immature fertile flowers, were removed. The remaining flowers were emasculated by removing petals and anthers using a pair of fine-tipped forceps. The inflorescence was securely covered with a breathable plastic bag.

Inflorescences that were to be used as males in crosses were also bagged prior to flower opening. Pollinations were made 1 to 4 days after emasculation. For pollinations, flowers with newly dehisced pollen were removed and used immediately. The bag was removed from the inflorescence of the maternal parent, and the dehiscing anthers were touched directly to the exposed stigmas of the emasculated flowers. The bag was placed back over the female inflorescence, where it remained for two to three weeks after pollination. Seeds were collected as described for the self-pollinations.

Seeds were sown on a soilless media. In 1997, seeds were germinated under mist in a greenhouse. A 25C (77F), 80% relative humidity lighted growth chamber was used for seed germination in 1998. As with the self-pollinations, seed from intraspecific crosses of *H. macrophylla*, *H. paniculata*, and *H. quercifolia* were collected and sown at the same time and under the same conditions as the seed from the interspecific crosses.

Results and Discussion

Self-pollinations. Approximately one-half of the flowers of the wild collected *H. arborescens* plant produced fruit (Table 1). The remaining flowers of this plant and all of the 'Annabelle' flowers abscised before the bags were removed from the inflorescences. None of the fruit that was collected contained any seed. This is in contrast to a recent report (5) that indicates that abundant self-seed are produced in *H. arborescens*.

All self-pollinated flowers of *H. macrophylla* subsp. *serrata* and 80% of the self-pollinated *H. macrophylla* f. *macrophylla* and *H. macrophylla* f. *normalis* flowers abscised from the plants within two weeks following the completion of flowering (Table 1). Seedless fruit were obtained in one *H. macrophylla* f. *normalis* and three *H. macrophylla* f. *macrophylla* cultivars. Only one cultivar, 'Alpengluhen', produced seed. The 105 seeds that were obtained were collected from 13 seed capsules, none of which contained more than 20 seeds. Although 8 seed germinated, seven died before any true leaves were formed. The one surviving plant appears healthy, but is slow growing and consists of many short, slender stems arising from the crown.

Fruit were formed from 90% of the *H. paniculata* self pollinations, but most of these were void of seeds (Table 1). Seeds were obtained from all three cultivars, with number of seed per successful cross ranging from one to ten. Only the

Table 1. Fruit set, seed set and seedling germination following self-pollination of four *Hydrangea* species.

Genotype	No. of selfed flowers	No. of seedless fruit	No. of fruit with seeds	No. of seed obtained	No. of seed germinated
H. arborescens					
'Annabelle'	~500	0	0	—	—
wild collected plant	~500	256	0	—	—
H. macrophylla f. *macrophylla*					
'All Summer Beauty'	123	0	0	—	—
'Alpengluhen'	30	7	13	105	8
'General Vicomtesse de Vibraye'	23	0	0	—	—
'Horben'	65	0	0	—	—
'Marechal Foch'	100	0	0	—	—
'Masja'	68	45	0	—	—
'Pia'	218	57	0	—	
H. macrophylla f. *normalis*	—				
'Blaumeise'	258	136	0	—	—
'Blue Billow'	207	0	0	—	—
'Kardinal'	273	0	0	—	—
H. macrophylla subsp. *serrata*					
'Bluebird'	208	0	0	—	—
'Coerulea'	187	0	0	—	—
H. paniculata					
'Brussels Lace'	~550	494	1	1	0
'Burgundy Lace'	~350	329	3	4	0
'Unique'	~600	457	55	161	18
H. quercifolia					
'Back Porch'	~500	0	0	—	—
'John Wayne'	~500	0	0	—	—
'Luverne Pink;	~500	0	0	—	—
'Patio Pink'	~250	0	0	—	—
'Pee Wee'	~600	145	5	9	5
'Sikes Dwarf'	~250	0	0	—	—
'Snow Queen'	~500	57	0	—	—

seed from 'Unique' germinated. Half of the seedlings died at a very small stage, but the nine plants that survived are healthy and have foliage that is similar in appearance to that of 'Unique'. One plant has flowered; its sole inflorescence is approximately one-half the length and width of those of 'Unique'.

Approximately 93% of the *H. quercifolia* self-pollinated flowers abscised shortly after flowering (Table 1). Seedless fruit was formed on two cultivars, 'Pee Wee' and 'Snow Queen'. The only *H. quercifolia* cultivar that produced seed was 'Pee Wee'. Five of the nine seed obtained germinated, and all survived. The plants appear healthy and are similar in appearance to 'Pee Wee'. None has flowered.

Low fruit set in *H. arborescens*, *H. macrophylla* and *H. quercifolia* self-pollinated flowers, along with low seed set in all species tested, may have been due to the technique that was used for making the self-pollinations. Shaking the inflorescence on a regular basis may not have been sufficient to transfer fresh pollen onto receptive stigmas. However, self-pollinations of all four species were repeated in 1999 using a brush to transfer pollen among open flowers within an inflorescence. Results of fruit and seed set are similar to those observed when pollen was distributed by shaking the plants. Seed obtained from these self-pollinations has not yet been germinated. Examination of pollen germination and growth on stigmas and styles of self-pollinated flowers is needed to determine if a self-incompatibility barrier is preventing pollen germination or pollen tube growth.

Seedless fruit was formed following self-pollination in all four species, although only in some cultivars. This fruit contained numerous very small seed-like structures. While these may have represented seed in which the embryos aborted very early in development, it is also possible that they were remnants of unfertilized ovules. Similar structures have been observed in fruit that developed from emasculated, bagged flowers of *H. macrophylla* 'Masja' and Pia' and *H. paniculata* 'Tardiva' that were left unpollinated.

Most of the seeds obtained from the self-pollinations did not germinate, and many of those that did died at a very early stage. Since seed of *H. arborescens*, *H. macrophylla*, *H. paniculata* and *H. quercifolia* do not have a cold requirement for germination (3), the lack of germination that was encountered does not appear to be caused by dormancy. Seeds of intraspecific crosses that were sown at the same time and under the same conditions germinated freely, and did not experience damping-off or nutritional problems. The seedlings obtained from the selfed crosses, however, may have been more susceptible to these germination problems due to inbreeding depression. The weakness and eventual death of these seedlings may also have been caused by a late-acting self-incompatibility system or the action of recessive lethals that were uncovered by selfing (1). While the vigor of the surviving *H. macrophylla*, *H. paniculata*, and *H. quercifolia* plants argues against strong inbreeding depression, it is possible that these plants may have been of parthogenetic rather than selfed origin. Histological studies of seed development following self-pollination in *Hydrangea* are needed to identify the origin of the plants obtained from these pollinations. Until such work is completed, however, emasculation of *Hydrangea* flowers is recommended when making controlled

Table 2. **Seed set and seed germination in three reciprocal sets of *Hydrangea* interspecific crosses.**

Hybrid	No. of crosses	No. of parental cultivar combinations	Mean no. (range) of crosses per cultivar combination	No. of seedless fruit	No. of fruit with seed	No. of seeds collected	No. of seeds germinated
H. arborescens x *H. macrophylla*	210	3	70 (32–135)	70	130	178	0
H. macrophylla x *H. arborescens*	192	3	64 (51– 76)	36	22	37	2
H. paniculata x *H. macrophylla*	1008	13	78 (23–166)	820	0	—	—
H. macrophylla x *H. paniculata*	2212	33	67 (9–225)	523	490	2112	50
H. quercifolia x *H. macrophylla*	108	3	36 (20– 55)	45	0	—	—
H. macrophylla x *H. quercifolia*	193	4	48 (23– 76)	122	34	65	10

pollinations for genetic and breeding projects to avoid possible contamination with self pollen.

Interspecific hybridization. Fruit was formed in all hybrid combinations, but all of the *H. paniculata* x *H. macrophylla* and *H. quercifolia* x *H. macrophylla* fruits were void of seeds (Table 2). Seed were obtained from only one *H. arborescens* x *H. macrophylla* cultivar combination, 'Annabelle' x 'Blue Billow'. None of this seed germinated.

Fruit were produced in all three *H. macrophylla* x *H. arborescens* cultivar combinations. Thirty seed were obtained from 18 'Bluebird' x 'Annabelle' fruits; two of these germinated. Four 'Taube' x 'Annabelle' fruit yielded a total of seven seed, but none germinated. No seed were produced from 'Kardinal' x 'Annabelle' crosses.

All flowers abscised within 2 weeks of pollination, producing neither seed nor fruit, in 16 *H. macrophylla* x *H. paniculata* cultivar combinations (Table 3). Two cultivar combinations produced fruit but no seed. Seed were obtained from 15 *H. macrophylla* x *H. paniculata* cultivar combinations. Seeds were fairly evenly distributed among the fruit that contained seed. Many of the fruit contained only 1 or 2 seeds, although a few fruit with up to 17 seeds were observed. Seeds germinated in eight *H. macrophylla* x *H. paniculata* parental cultivar combinations.

All *H. macrophylla* x *H. quercifolia* cultivar combination produced fruit, but the 'Horben' x 'Patio Pink' fruits did not contain seeds. 'Fasan' x 'Patio Pink' yielded 59 seeds from 29 fruits, 10 of which germinated. Five seeds were obtained from 'Blaumeise' x 'Gloster 5-sepal', and 'Majsa' x 'Gloster 5-sepal' produced a single seed; none of these germinated.

The procedure that was used for making the interspecific pollinations has been used in making intraspecific pollinations of *H. macrophylla*, *H. paniculata*, and *H. quercifolia.* Approximately two-thirds of the intraspecific crosses that have been made over a 3-year period have set seed. Over 80% of the intraspecific fruit have contained 75 or more seeds each. Intraspecific crosses have not been made with *H. arborescens*, but open-pollinated seed capsules of this species contain similar numbers of seeds. The low fruit and seed set that were observed in the three *Hydrangea* interspecific hybridizations attempted in this study do not appear to be due to inadequate pollination technique. However, identification of periods of stigma receptivity in *Hydrangea* cultivars to be used as maternal parents in either intra- and interspecific pollinations would likely improve the efficiency of the pollination procedure.

Seedlings of the *H. macrophylla* x *H. arborescens*, *H. macrophylla* x *H. paniculata*, and *H. macrophylla* x *H. quercifolia* hybrids behaved similarly. Approximately 75% of the seedlings died at the cotyledonary stage. The remaining seedlings died after the first set of true leaves had begun to emerge, but before they had fully expanded. In all cases, the seedlings were much smaller than intraspecific seedlings that germinated at the same time and under the same conditions. No obvious disease or nutritional deficiency problem was noted in the intraspecific crosses that would explain the death of the interspecific seedlings.

A range in size was observed among the seeds that were collected from the *Hydrangea* interspecific crosses. All obviously shrunken seed were eliminated from the seed count; however, it is possible that some of the seed that were included in the counts in Tables 2 and 3 contained immature embryos. A few fruit from each of the crosses that utilized *H. macrophylla* as the maternal parent, along with intraspecific crosses made at the same time, were opened 2 to 3 months after pollination, and ovules excised and examined under a stereomicroscope. Embryos were observed in a few ovules of each hybrid, but they appeared to be smaller than those excised from intraspecific crosses.

In vitro embryo rescue procedures have been successful in raising hybrids from a number of incompatible crosses that fail due to embryo abortion or the presence of immature embryos in hybrid seed (9). The production of seed, the presence of embryos in 2- to 3-month old ovules, and the germination and death of seedlings from *H. macrophylla* x *H. arborescens, H. macrophylla* x *H. paniculata*, *H. macrophylla* x *H. quercifolia* crosses are indications of embryo abortion and/or the presence of immature embryos in ripe seeds. However, it is not known whether the embryos observed and the seedlings produced were of hybrid origin. Haploids have occasionally been obtained in other genera following interspecific hybridization, as have parthenogenetic diploids. Histological studies that compare pollination, fertilization, and seed development in intra- and interspecific *Hydrangea* hybrids are needed to identify the cause of seed failure in these three interspecific hybrids.

Chromosome counts should also be made on cultivars to be used in future crosses. While the basic chromosome number in *Hydrangea* is 2n = 36, some tetraploid *H. paniculata* (4) and *H. macrophylla* (R. J. Griesbach, personal communication) cultivars have been identified. Crosses involving a diploid and a tetraploid cultivar may fail due to an endosperm imbalance. While it seems unlikely that all 33 *H. macrophylla* x *H. paniculata* and 13 *H. paniculata* x *H. macrophylla* cultivar combination involved parents of different ploidy levels, this could have been a problem with the interspecific crosses in which fewer parental combinations were tested.

Table 3. Fruit set, seed set, and seed germination in *H. macrophylla* x *H. paniculata* hybrids.

H. macrophylla maternal cultivar	*H. paniculata* paternal cultivar	No. of crosses made	No. of seedless fruit	No. of fruit with seed	No. of seed obtained	No. of seed germinated
All Summer Beauty	Unique	10	0	0	—	—
Alpengluhen	Burgundy Lace	25	13	3	6	2
Alpengluhen	Kyushu	42	0	0	—	—
Alpengluhen	Unique	39	0	0	—	—
Bluebird	Unique	157	58	89	290	11
General Vicomtesse de Vibraye	Unique	29	0	0	—	—
Grayswood	Pink Diamond	225	171	54	256	2
Grayswood	Tardiva	174	82	88	345	18
Grayswood	Unique	218	0	35	55	2
Horben	Webb	85	35	45	314	2
Madame Emile Mouillere	Kyushu	89	35	44	126	0
Madame Emile Mouillere	Pee Gee	10	0	0	—	—
Madame Emile Mouillere	Unique	22	12	8	42	0
Marechal Foch	Boskoop	20	16	0	—	—
Marechal Foch	Tardiva	42	0	0	—	—
Marechal Foch	Unique	9	2	6	15	0
Mariesii	Boskoop	90	0	0	—	—
Mousseline	Tardiva	11	0	0	—	—
Pia	Boskoop	32	32	0	—	—
Pia	Burgundy Lace	46	3	43	200	1
Pia	Kyushu	25	12	13	48	0
Pia	Pee Gee	38	0	0	—	—
Pia	Pink Diamond	19	14	5	35	0
Pia	Tardiva	28	0	10	120	10
Pia	Unique	88	37	33	173	2
Pia	Webb	16	1	14	87	0
Pink Lace Cap	Pee Gee	82	0	0	—	—
Pink Lace Cap	Pink Diamond	50	0	0	—	—
Pink Lace Cap	Tardiva	90	0	0	—	—
Tokyo Delight	Brussels Lace	48	0	0	—	—
Tokyo Delight	Pink Diamond	98	0	0	—	—
Tokyo Delight	Tardiva	67	0	0	—	—
Tokyo Delight	Unique	188	0	0	—	—

However, none of the cultivars used in this study have been identified as tetraploid. The potential value of a cold-hardy hydrangea with brightly colored flowers to nursery and landscape professionals and home gardeners warrants the additional studies necessary for recovering interspecific hybrids between *H. macrophylla* and cold-hardy *Hydrangea* species.

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