

Interspecific and Intergeneric Hybridization in *Baptisia* and *Thermopsis*

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Additional index words. *Baptisia*, *Thermopsis*, interspecific hybrid, intergeneric hybrid, Fabaceae

Abstract. Interspecific and intergeneric crosses were performed between species in the genera *Baptisia* and *Thermopsis* with the goal of creating hybrids with the best qualities of both parents. *Baptisia australis* (L.) R. Br. was used as both the male and female parent in intergeneric crosses. *Thermopsis chinensis* Benth. ex S. Moore, *T. lupinoides* (L.) Link, and *T. villosa* Fernald & B.G. Schub. were used as male and female parents in both interspecific and intergeneric crosses. Pollen was collected from *B. alba* (L.) Vent., *B. bracteata* Muhl. ex Elliott, and *B. lanceolata* (Walt.) Ell. and used to make interspecific and intergeneric crosses. Putative hybrids were obtained from both interspecific and intergeneric crosses. Interspecific crosses produced a higher percentage of pollinations resulting in seed set and the number of seeds per pollination than intergeneric crosses. Morphological differences between parent species and progeny were evident in putative hybrids resulting from intergeneric crosses between *T. villosa* and *B. australis* and *T. villosa* and *B. alba*. Most putative hybrids bloomed during the second year after germination. Because seedlings could be obtained from both interspecific and intergeneric crosses, hybrids within and between the genera *Baptisia* and *Thermopsis* are feasible. The Fabaceae family contains 670–750 genera and 18,000–19,000 species. *Baptisia* (commonly called false or wild indigo) and *Thermopsis* (commonly named false lupine) of the Fabaceae belong to the tribe Thermopsidae, which comprises 46 species in six genera. All species in *Thermopsis* and *Baptisia* are herbaceous; they are the only two genera in Thermopsidae that do not have woody species. *Thermopsis* contains 23 species and has a wide-spread distribution with species endemic to Asia and much of temperate North America. Although *Thermopsis* is considered to have originated in central Asia, *T. chinensis* Benth. ex S. Moore and *T. fabacea* (Pallas) Candolle are thought to have originated in North America and migrated over the Bering Land Strait to Asia. Three *Thermopsis* species, *T. fraxinifolia* Nutt. ex M.A. Curtis, *T. mollis* (Michx.) M.A. Curtis ex A. Gray, and *T. villosa* Fernald & B.G. Schub., are native to the southeastern United States. *Baptisia* contains 15–17 species that are endemic to the southeastern and midwestern United States.

Except for *Thermopsis barbata* Benth. ex Royle, which produces reddish-purple flowers, all species in *Thermopsis* have yellow flowers (Chen et al., 1994; Wu and Raven, 1994). Flower color in *Baptisia* ranges from white to yellow to blue (Larisey, 1940). In both *Baptisia* and *Thermopsis*,

perfect flowers with superior ovaries are borne on terminal racemes, though some *Baptisia* species produce flowers that occur individually in leaf axils (Chen et al., 1994; Larisey, 1940). Seed pods of *Baptisia* are inflated while those of *Thermopsis* are compressed (Chen et al., 1994). Although polyploidy is wide-spread in the Fabaceae, no polyploids have been found in *Baptisia* and only two polyploids have been found in *Thermopsis*, *T. gracillis* Howell and *T. divicarpa* A. Nelson (Chen et al., 1994). The chromosome numbers of both *Baptisia* and *Thermopsis* are based on $x = 9$, with $2n = 18$ for all species, except for *T. gracillis* and *T. divicarpa*, which are $2n = 36$ (Chen et al., 1994; Cooper, 1936).

Biochemical evidence suggests that *Baptisia* evolved from *Thermopsis* in the southeastern United States (Dement and Mabry, 1975). Two phylogenies of Thermopsidae places *T. chinensis* and *T. villosa* in the same clade as several species of *Baptisia*, including *B. australis*, based on internal transcribed spacer sequences (Wang et al., 2006; Zhang et al., 2015). *Thermopsis* interspecific hybrids have not been observed by taxonomists (Dement and Mabry, 1975). However, hybridization readily occurs between species of *Baptisia* (Alston and Turner, 1963; Baetcke and Alston, 1968; Dement and Mabry, 1975; Larisey, 1940; Leebens-Mack and Milligan, 1998).

In the genus *Baptisia*, interspecific crosses have been used to create many novel cultivars (Ault, 2003; Avent, 2002; Cullina, 2000), some of which are widely available commercially. *Thermopsis* has not been used to create hybrids to our knowledge and is also not much known or used in the ornamental plant industry. Many species of *Thermopsis*, particularly *T. villosa*, are very tolerant of both drought and heat, making *Thermopsis* a good substitute for lupines in the southeastern United States (Armitage, 1989). Some species of *Thermopsis*, such as *T. lupinoides*, originated in coastal areas and are salt tolerant (Hotes et al., 2001; Probatova and Seledets, 2012). *Baptisia* has proven difficult to propagate vegetatively through cuttings (Ault, 2003; Cullina, 2000). *Thermopsis* is easier to root than *Baptisia* (Hawkins et al., 2013) and will bloom 2 years after germination, whereas *Baptisia* requires 3 years to bloom from seed (personal communication, Heather Alley, State Botanical Garden of Georgia, 2013).

The overall goal of this project was to investigate the feasibility of hybridization within and between species of *Baptisia* and *Thermopsis*. Hybrids could potentially have improved drought tolerance, earlier flowering, and higher rates of rooting compared with the parent species. Ideally, the hybrids would combine desirable ornamental qualities with these improved traits. Hybrids could also serve as bridge parents in future breeding to obtain intergeneric cultivars.

Materials and Methods

B. australis, *T. chinensis*, and *T. villosa* plants were obtained from Northcreek Nurseries, Inc., Landenberg, PA, as seed-grown liners. An additional genotype of *T. villosa* was obtained from the State Botanical Garden of Georgia, Athens, GA. *T. lupinoides* (L.) Link plants were vegetatively produced from a stock plant obtained from Plant Delights Nursery, Raleigh, NC. Plants were potted into 7.6 L trade containers with Fafard 3B Potting Mix (Sun Grow Horticulture, Agawam, MA) consisting of Canadian sphagnum peat (45%), processed pine bark, perlite, and vermiculite, and placed in an enclosed shade house (50% shade) at the University of Georgia (UGA) Horticulture Farm, Watkinsville, GA. All crosses were carried out in the shade house. To increase

Received for publication 20 Apr. 2017. Accepted for publication 15 July 2017.

We thank Vickie Waters for technical assistance and help with data collection.

This article is part of a thesis submitted by Susan M. Hawkins as part of the fulfillment of a Master's Degree.

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Table 1. Detailed data for Fabaceae crosses. The number of pollinations for each cross, the percentage of pollinations resulting in seed, the number of seed obtained from all pollinations, the percentage of germination of the seed, and the number of seedlings per pollination.

Seed parent	Pollen parent	No. pollinations	Pollinations with seed (%)	No. seed obtained	Germination (%)	No. seedlings per pollination
<i>B. australis</i>	<i>B. bracteata</i>	5	20.0	3	33.3	0.6
<i>B. australis</i>	<i>B. lanceolata</i>	10	40.0	12	58.3	1.2
<i>B. australis</i>	<i>T. chinensis</i>	5	0.0	0	0.0	0.0
<i>B. australis</i>	<i>T. villosa</i> (NC)	340	12.1	42	85.7	0.1
<i>T. chinensis</i>	<i>B. alba</i>	25	12.0	22	86.4	0.9
<i>T. chinensis</i>	<i>T. lupinoides</i>	635	21.1	1,617	89.4	2.5
<i>T. chinensis</i>	<i>T. villosa</i> (NC)	130	19.2	248	63.7	1.9
<i>T. lupinoides</i>	<i>B. alba</i>	25	0.0	0	0.0	0.0
<i>T. lupinoides</i>	<i>B. australis</i>	10	0.0	0	0.0	0.0
<i>T. lupinoides</i>	<i>T. chinensis</i>	600	44.0	2,228	81.1	3.7
<i>T. lupinoides</i>	<i>T. villosa</i> (NC)	160	13.1	221	77.4	1.4
<i>T. villosa</i> (NC) ^z	<i>B. alba</i>	15	26.7	26	88.5	1.7
<i>T. villosa</i> (NC)	<i>B. australis</i>	459	10.0	63	81.0	0.1
<i>T. villosa</i> (NC)	<i>B. lanceolata</i>	15	20.0	17	76.5	1.1
<i>T. villosa</i> (NC)	<i>T. lupinoides</i>	10	40.0	46	93.5	4.6
<i>T. villosa</i> (BG) ^y	<i>B. australis</i>	100	9.0	20	40.0	0.2

^z*T. villosa* (NC) was obtained from Northcreek Nurseries.

^y*T. villosa* (BG) was obtained from State Botanical Garden of Georgia, Athens, GA.

the diversity of male *Baptisia* parents, pollen was collected from *B. alba* (L.) Vent., *B. bracteata* Muhl. ex Elliott, and *B. lanceolata* (Walt.) Ell. in Apr. 2013 and used to make crosses (Table 1). The *B. alba* plant from which the pollen was collected was in the Trial Gardens at the UGA. The *B. lanceolata* plants were located in Dodge and Laurens County, GA. The *B. bracteata* plants were from Hancock County, GA.

Interspecific and intergeneric crosses were made from March to May 2013. A total of 2544 crosses were made; of the crosses, 1550 were interspecific and 994 were intergeneric. Details of all crosses are shown in Table 1.

Flowers of the female parents were emasculated immediately before pollination. Pollen was collected from the male parent onto a small paintbrush and used to pollinate the female parent. Reciprocal crosses were made where possible. Because some species bloomed at different times or had brief periods of overlapped blooming, reciprocal crosses could not always be performed. Seed pods were collected once ripe from May to Aug. 2013. Seeds were extracted from the pods and counted. Seeds were scarified in 0.1 M sulfuric acid for 20 min, rinsed, and soaked for several hours in water to imbibe before being sown in a potting media containing bark, peatmoss, and perlite. Germination data were taken at 4 weeks after sowing. A maximum of 25 seedlings of each interspecific and intergeneric cross were potted up into 2.8-L trade containers with a pine bark-based medium containing added micronutrients and moved into an enclosed shade house at the UGA Horticulture Farm. In Oct. 2013, the seedlings were transplanted to the field at the UGA Horticulture Farm for overwintering and further evaluation. The seeds from the crosses between the genotype of *T. villosa* obtained from the State Botanical Garden and *B. australis* were sown and germinated later than that of the other crosses. The seedlings resulting from those crosses were overwintered in a shade

Table 2. Interspecific crosses by seed parent and by pollen parent. For seed parent—the number of pollen parent species crossed with seed parent species and total number of pollinations made per seed parent species. For pollen parent—the number of seed parent species crossed with pollen parent species and the total number of pollinations made per pollen parent species. For both seed and pollen parents—the percentage of pollinations resulting in seed set, the total number of seeds resulting from all pollinations, and the percentage of germination of the seed.

	No. species mating	No. cross-pollinated flowers	Flowers setting seed (%)	No. seeds obtained	Seed germination (%)
Seed parent					
<i>B. australis</i>	2	15	33.3	8	53.3
<i>T. chinensis</i>	2	765	20.8	1,865	86.0
<i>T. lupinoides</i>	2	760	37.5	2,449	80.8
<i>T. villosa</i> (NC) ^z	1	10	40.0	46	93.5
Pollen parent					
<i>B. bracteata</i>	1	5	20.0	3	33.3
<i>B. lanceolata</i>	1	10	40.0	12	58.3
<i>T. chinensis</i>	1	600	44.0	2,228	81.1
<i>T. lupinoides</i>	2	645	21.4	1,663	89.5
<i>T. villosa</i> (NC) ^z	2	290	15.9	469	70.1

^z*T. villosa* (NC) was obtained from Northcreek Nurseries.

Table 3. Intergeneric crosses by seed parent and by pollen parent. For seed parent—the number of pollen parent species crossed with seed parent species and the total number of pollinations made per seed parent species. For pollen parent—the number of seed parent species crossed with pollen parent species and the total number of pollinations made per pollen parent species. For both seed and pollen parents—the percentage of pollinations resulting in seed set, the total number of seeds resulting from all pollinations, and the percentage germination of the seed.

	No. species mating	No. cross-pollinated flowers	Flowers setting seed (%)	No. seeds obtained	Seed germination (%)
Seed parent					
<i>B. australis</i>	2	345	11.9	42	85.7
<i>T. chinensis</i>	1	25	12.0	22	86.4
<i>T. lupinoides</i>	2	35	0.0	0	0.0
<i>T. villosa</i> (NC) ^z	3	489	10.8	106	82.1
<i>T. villosa</i> (BG) ^y	1	100	9.0	20	40.0
Pollen parent					
<i>B. alba</i>	3	65	10.8	48	87.5
<i>B. australis</i>	3	569	9.7	83	71.1
<i>B. lanceolata</i>	1	15	20.0	17	76.5
<i>T. chinensis</i>	1	5	0.0	0	0.0
<i>T. villosa</i> (NC) ^z	1	340	12.1	42	85.7

^z*T. villosa* (NC) was obtained from Northcreek Nurseries.

^y*T. villosa* (BG) was obtained from State Botanical Garden of Georgia, Athens, GA.

house as they were too young to be overwintered in the field.

During 2014 and 2015, morphological traits of the putative hybrids were assessed. The shapes of leaflets and stipules were

evaluated and compared with the characteristics of the parent species.

In 2015, 25 of the F₁ plants were selected to continue in the breeding program. Cuttings were taken of the 25 plants in May, rooted,

Table 4. Mortality and bloom rates for 2014 and 2015. Initial seedlings from each cross, seedling mortality in 2014 and 2015, seedlings remaining by second year after planting, percent seedling mortality by second year after planting, seedlings blooming in 2014 and 2015, and percent of seedlings blooming by second year after planting.

Cross	Total seedlings (Initial)	2014 seedling mortality (no.)	2015 seedling mortality (no.)	Number remaining seedlings by second year after planting	Seedling mortality by second year after planting (%)	Number seedlings blooming in 2014	Number seedlings blooming in 2015	Seedlings blooming by second year after planting (%)
<i>B. australis</i> x <i>B. bracteata</i>	1	1	0	0	100.0	0	0	0.0
<i>B. australis</i> x <i>B. lanceolata</i>	4	3	0	1	75.0	0	0	0.0
<i>B. australis</i> x <i>T. villosa</i> (NC) ²	25	2	2	21	16.0	0	19	90.5
<i>T. chinensis</i> x <i>B. alba</i>	19	6	2	11	42.1	1	11	100.0
<i>T. chinensis</i> x <i>T. lupinoides</i>	25	4	0	21	16.0	3	18	85.7
<i>T. chinensis</i> x <i>T. villosa</i> (NC)	25	1	0	24	4.0	10	24	100.0
<i>T. lupinoides</i> x <i>T. chinensis</i>	25	0	0	25	0.0	13	25	100.0
<i>T. lupinoides</i> x <i>T. villosa</i> (NC)	25	0	5	20	20.0	4	20	100.0
<i>T. villosa</i> (NC) x <i>B. alba</i>	23	0	7	16	30.4	3	16	100.0
<i>T. villosa</i> (NC) x <i>B. australis</i>	25	2	7	16	36.0	6	14	87.5
<i>T. villosa</i> (NC) x <i>B. lanceolata</i>	15	1	5	9	40.0	0	2	22.2
<i>T. villosa</i> (NC) x <i>T. lupinoides</i>	25	1	1	23	8.0	6	22	95.7
Total	237	21	29	187		46	171	

²*T. villosa* (NC) was obtained from Northcreek Nurseries.

Table 5. Leaflet morphology of parent species and putative hybrids.

Cross	Leaflet shape of hybrid	Leaflet shape of female parent	Leaflet shape of male parent
<i>B. australis</i> x <i>B. lanceolata</i>	Obovate to ovate	Obovate	Lanceolate
<i>B. australis</i> x <i>T. villosa</i> (NC) ²	Obovate	Obovate	Ovate
<i>T. chinensis</i> x <i>B. alba</i>	Ovate	Obovate or narrowly obovate	Elliptic
<i>T. chinensis</i> x <i>T. lupinoides</i>	Ovate	Obovate or narrowly obovate	Elliptic
<i>T. chinensis</i> x <i>T. villosa</i> (NC)	Ovate	Obovate or narrowly obovate	Ovate
<i>T. lupinoides</i> x <i>T. chinensis</i>	Ovate	Elliptic	Obovate or narrowly obovate
<i>T. lupinoides</i> x <i>T. villosa</i> (NC)	Ovate	Elliptic	Ovate
<i>T. villosa</i> (NC) x <i>B. alba</i>	Ovate	Ovate	Elliptic
<i>T. villosa</i> (NC) x <i>B. australis</i>	Ovate	Ovate	Obovate
<i>T. villosa</i> (NC) x <i>B. lanceolata</i>	Ovate	Ovate	Lanceolate
<i>T. villosa</i> (NC) x <i>T. lupinoides</i>	Ovate	Ovate	Elliptic

²*T. villosa* (NC) was obtained from Northcreek Nurseries.

Table 6. Stipule morphology of parent species and putative hybrids.

Cross	Stipule shape of hybrid	Stipule shape of female parent	Stipule shape of male parent
<i>B. australis</i> x <i>B. lanceolata</i>	Lanceolate	Lanceolate	Deciduous, not present
<i>B. australis</i> x <i>T. villosa</i> (NC) ²	Lanceolate	Lanceolate	Ovate, clasping
<i>T. chinensis</i> x <i>B. alba</i>	Lanceolate or linear to lanceolate	Linear-ovate or lanceolate	Lanceolate to ovate
<i>T. chinensis</i> x <i>T. lupinoides</i>	Lanceolate or linear to lanceolate	Linear-ovate or lanceolate	Elliptic or ovate
<i>T. chinensis</i> x <i>T. villosa</i> (NC)	Lanceolate	Linear-ovate or lanceolate	Ovate, clasping
<i>T. lupinoides</i> x <i>T. chinensis</i>	Lanceolate	Elliptic or ovate	Linear-ovate or lanceolate
<i>T. lupinoides</i> x <i>T. villosa</i> (NC)	Lanceolate or linear to lanceolate	Elliptic or ovate	Ovate, clasping
<i>T. villosa</i> (NC) x <i>B. alba</i>	Lanceolate	Ovate, clasping	Lanceolate to ovate
<i>T. villosa</i> (NC) x <i>B. australis</i>	Lanceolate (21 plants) ovate, clasping (2 plants)	Ovate, clasping	Lanceolate
<i>T. villosa</i> (NC) x <i>B. lanceolata</i>	Lanceolate	Ovate, clasping	Deciduous, not present
<i>T. villosa</i> (NC) x <i>T. lupinoides</i>	Lanceolate	Ovate, clasping	Elliptic or ovate

²*T. villosa* (NC) was obtained from Northcreek Nurseries.

planted in 2.8-L trade containers with a pine bark-based media, and placed upon the nursery pad at the UGA Horticulture Farm for evaluation of growth and form in containers.

Results

Success rate of individual crosses varied widely (Table 1). All interspecific combinations of parents set seed and had seed germination (Table 2). Rates of seed set among seed parents in interspecific crosses ranged from 20.8% to 40.0% (Table 2). Seed germination percentages among interspecific crosses grouped by seed parent ranged from 53.3% to 93.5% (Table 2). Rates of seed set among pollen parents in interspecific crosses

ranged from 15.9% to 44.0% (Table 2). The percentage of seed germination among interspecific crosses grouped by pollen parents ranged from 33.3% to 89.5% (Table 2).

Most but not all intergeneric combinations of parents had seed set and germination (Tables 1 and 3). When used as a seed parent, *T. lupinoides* set no seed when crossed with either *B. alba* or *B. australis*. The cross of *B. australis* as a seed parent to *T. chinensis* as a pollen parent also yielded no seed (Table 1). However, all other intergeneric cross combinations resulted in seed set and germination.

Among seed parents in intergeneric crosses that set seed, the rate of seed set ranged from 9.0% to 12.0% (Table 3). The

seed germination percentage among seed parents in intergeneric crosses that set seed ranged from 40.0% to 86.4% (Table 3). Among pollen parents in intergeneric crosses that set seed, the rate of seed set ranged from 9.7% to 20.0% (Table 3). The percentage of seed germination among pollen parents in intergeneric crosses that set seed ranged from 71.1% to 87.5% (Table 3).

Seedlings began to break winter dormancy in Mar. 2014. During the spring of 2014, 46 of the initial 237 seedlings bloomed (Table 4). Survival during the first year was high, with all but 21 seedlings surviving (Table 4). In 2015, 171 of the surviving seedlings bloomed (Table 4). During 2015, 29 additional seedlings died (Table 4).

Morphological differences in leaflet shape varied widely among crosses (Table 5). The leaflet shape of the putative hybrids of the *T. lupinoides* x *T. villosa* (NC) cross was ovate, as is typical of *T. villosa*, instead of the elliptic shape characteristic of *T. lupinoides* (Table 5). Putative hybrids of the *T. chinensis* x *T. villosa* (NC) also had ovate leaflets instead of the obovate leaflets typical of *T. chinensis* (Table 5).

Morphological differences in stipule shape also varied widely among crosses (Table 6). For example, of the 23 surviving putative hybrids of the *T. villosa* (NC) x *B. australis* cross in May 2014, 21 plants had stipules that were lanceolate in shape instead of being ovate and clasping as is characteristic of the seed parent (Table 6). However, all putative hybrids of the *B. australis* x *T. villosa* (NC) cross had stipules resembling those of the seed parent. In addition, putative hybrids of this cross looked just like the female parent in growth habit and flowering morphology. All 23 of the putative hybrids from the *T. villosa* (NC) x *B. alba* cross had lanceolate stipules, as did the 13 putative hybrids from the *T. villosa* (NC) x *B. lanceolata* cross and the 24 surviving putative hybrids of the *T. villosa* (NC) x *T. lupinoides* cross (Table 6). By contrast, all the putative hybrids between the *T. villosa* (BG) obtained from the State Botanical Garden of Georgia and *B. australis* looked exactly like *T. villosa* (BG) (data not shown).

Remarkably, putative hybrids of the *T. lupinoides* x *T. villosa* (NC) cross all had lanceolate or linear to lanceolate stipules, which did not resemble those of either parent. However, the stipules of the putative hybrids from the *T. chinensis* x *T. villosa* (NC) cross were all similar to those of the female parent.

Growth habit of some putative hybrids where *T. villosa* (NC) was the female parent also showed differences from that of the seed parent. Growth habit of the 21–23 surviving putative *T. villosa* (NC) x *B. australis* hybrids looked more compact than *T. villosa* in the first year in the field and had a branching structure similar to *B. australis* instead of being largely single-stemmed as is typical of *T. villosa* (Fig. 1A–C). All putative hybrids from the *T. villosa* (NC) x *B. alba* cross, the *T. villosa* (NC) x *B. lanceolata* cross, and the *T. villosa* (NC) x *T. lupinoides* cross also had a multistem branching habit. Height data taken in the third year in the field of putative hybrids with *T. villosa* female parentage that had undergone selection showed a marked decrease in height from the average height of *T. villosa* (Table 7).

Cuttings taken of the selected F₁ plants rooted at the rate of 84.0% to 100.0%, with the exception of the putative hybrids of the *T. chinensis* x *B. alba* cross which rooted at 36.7% (Table 8). Cuttings rooted within 4 weeks. Most of the plants produced by cuttings and potted into containers in 2015 bloomed in Spring 2016 (data not shown).

Discussion

Crossing between species in *Baptisia* and *Thermopsis* appears feasible as putative



Fig. 1. (A) Seedling of *T. villosa* x *B. australis* cross with examples of parent species. Note multibranching habit of hybrid, unlike female parent. Inflorescence morphology of hybrid is also different from female parent, with flowers more widely spaced along inflorescence. (B) *T. villosa* (NC) was obtained from Northcreek Nurseries. (C) *B. australis*.

hybrids of several of the intergeneric crosses made in this study had morphological differences as compared with the female parent or had a combination of traits of both parents. Further evaluation is needed to determine whether the intergeneric crosses where *B. australis* is the female parent produced true hybrids, because the F₁ progenies of the *B. australis* x *T. villosa* cross all resembled the female parent. Other factors can help indicate hybridity. Ninety percent of the progenies of the *B. australis* x *T. villosa* crosses bloomed during the second year from seed, even though *B. australis* normally blooms during the third year from seed. Earlier blooming might indicate hybridity of these plants, as changes in flowering time are sometimes seen in hybrid plants. In a project to create ornamental *Allium* hybrids from fall-blooming and summer-blooming species, hybrids of *Allium chinense* x *A. schubertii* and of *A. thunbergii* x *A. caeruleum* bloomed at a time intermediate to both parents (Nomura et al.,

Table 7. Height in cm of putative interspecific and intergeneric F₁ hybrids having *T. villosa* female parents compared with mean height of female parent species. Putative hybrids were selected from the original F₁ population. Mean height of female parent species was 92.0 cm in the field.

Cross	Ht (cm)
<i>T. villosa</i> (NC) ^z x <i>B. alba</i>	66.0
<i>T. villosa</i> (NC) x <i>B. alba</i>	43.2
<i>T. villosa</i> (NC) x <i>B. alba</i>	66.0
<i>T. villosa</i> (NC) x <i>B. australis</i>	50.8
<i>T. villosa</i> (NC) x <i>B. australis</i>	50.8
<i>T. villosa</i> (NC) x <i>B. australis</i>	55.9
<i>T. villosa</i> (NC) x <i>T. lupinoides</i>	78.7
<i>T. villosa</i> (NC) x <i>T. lupinoides</i>	78.7

^z*T. villosa* (NC) was obtained from Northcreek Nurseries.

2002). Moreover, the ornamental *Allium* hybrids created from these crosses bloomed by 2 years after pollination, more quickly than other ornamental *Alliums* (Nomura et al., 2002). Furthermore, rooting data

Table 8. Rooting data for putative hybrids.

Cross	No. hybrids	Date cuttings stuck	No. of cuttings stuck	Date potted up	No. cuttings rooted	Cuttings rooted (%)
<i>B. australis</i> x <i>T. villosa</i> (NC) ²	1	7 May 2015	10	2 June 2015	10	100.0
<i>T. chinensis</i> x <i>B. alba</i>	3	7 May 2015	30	2 June 2015	11	36.7
<i>T. chinensis</i> x <i>T. villosa</i> (NC)	5	7 May 2015	50	2 June 2015	42	84.0
<i>T. lupinoides</i> x <i>T. chinensis</i>	3	7 May 2015	30	2 June 2015	28	93.3
<i>T. lupinoides</i> x <i>T. villosa</i> (NC)	5	7 May 2015	50	2 June 2015	48	96.0
<i>T. villosa</i> (NC) x <i>B. alba</i>	3	7 May 2015	30	2 June 2015	29	96.7
<i>T. villosa</i> (NC) x <i>B. australis</i>	2	7 May 2015	20	2 June 2015	20	100.0
<i>T. villosa</i> (NC) x <i>T. lupinoides</i>	3	7 May 2015	30	2 June 2015	30	100.0

²*T. villosa* (NC) was obtained from Northcreek Nurseries.

may support hybridity in the *T. chinensis* x *B. alba* progenies, as *T. chinensis* roots well but putative hybrids with *B. alba* had a decreased rooting percentage. Intergeneric hybrids of chrysanthemum [*Chrysanthemum grandiflorum* (Ramat.) Kitamura] and mugwort (*Artemisia vulgaris* L.) had a rooting ability that was less than that of the easily-rooted mugwort parent but greater than that of the chrysanthemum parent (Deng et al., 2012).

Pre- or post-zygotic barriers between parents in interspecific and intergeneric crosses will often preclude fertilization of the ovule after pollination, resulting in low seed set. Because the percentage of crosses with seed was higher in interspecific crosses than in intergeneric crosses, barriers to fertilization seem to be much lower in the interspecific crosses. Although such a result is typical in many species, it is not always the case. Intergeneric crosses in brooms (genera *Genista* and *Cystisus*, family Fabaceae) showed greater fertility than interspecific crosses (Bellenot-Kapusta et al., 2006). However, the number of seedlings recovered from intergeneric crosses could be increased using embryo rescue or ovule culture. Ovule culture was necessary to produce an intergeneric hybrid from a cross between *Dendranthema nankingense* and *Tanacetum vulgare* because of the post-zygotic barriers to fertilization (Tang et al., 2011).

Pollen collection and storage may be tools to increase the variety of crosses that may be made, as well as the number of pollinations for each type of cross. Stored pollen was used successfully to create interspecific hybrids of *Acacia auriculiformis* and *A. mangium* (Kato et al., 2012). Pollen storage was also used to create interspecific hybrids between summer- and autumn-flowering ornamental *Allium* species (Nomura et al., 2002). The blooming period for *T. lupinoides* and *T. chinensis* did not overlap substantially with the blooming period for *B. australis*, whereas that of *T. villosa* did. Storage of pollen from all three species could allow more intergeneric crosses to be made between *B. australis* and the Asian species of *Thermopsis*.

Other *Baptisia* and *Thermopsis* species should be added to the breeding program to increase genetic diversity. *B. alba* would be

a good addition, because using the species as a male parent in intergeneric crosses with *T. villosa* and *T. chinensis* yielded progeny. Additional genotypes of *B. australis* could be added to increase the genetic diversity. Because *B. cinera* (Raf.) Fernald & B.G. Schub. and *B. sphaerocarpa* Nutt. were found to be in the same phylogenetic clade as *T. chinensis* and *T. villosa* (Wang et al., 2006; Zhang et al., 2015), these species would also be good additions to the breeding program. Additional *Thermopsis* species to consider adding to the program, based on phylogenetic studies, would be *T. montana* Nutt. and *T. rhombifolia* (Nutt. ex Pursh) Nutt. ex Richardson (Wang et al., 2006; Zhang et al., 2015).

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