Variation in Reproductive Characteristics and Seed Production in the USDA Garlic Germplasm Collection

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Abstract. Diverse garlic germplasm has proven to be essential for production of true seed. Yet, fertile accessions in garlic germplasm collections have not been characterized for breeders and researchers, and information on morphological characteristics associated with seed producing plants is very limited. The objective of this study was to evaluate reproductive characteristics and true seed production capacity in the USDA garlic germplasm collection. Most stable traits, such as flower stem appearance, opening ability of spathe, level of difficulty to remove bulbils, tepal color, umbel shape, and the number of flowers per umbel, were similar across populations evaluated. Other characteristics including position of stigma, tepal closure, pollen viability, time of flowering, scape senescence rate, and number of seeds produced by individual plants varied within accession evaluated. Of 47 accessions, 19 produced true seeds (from 48.5 to 1.5 seeds per plant) in the Central Valley of California. Seed production in the germplasm evaluated is adequate to initiate garlic breeding projects.

True seed development in garlic (*Allium sativum* L. and *A. longicuspis* Regel) has been reported in literature for almost 50 years (Kononkow, 1953). In the past 18 years, several reports on the production of large numbers of seed were published (Etoh, 1986; Etoh et al., 1988; Inaba et al., 1995; Jenderek, 1998; Jenderek and Hannan, 2000; Konvicka, 1984; Pooler and Simon, 1994). In spite of this, seed-producing germplasm is not readily available for garlic breeders and seed producers. Fertile germplasm is of great interest not only to breeders, but also to small farm garlic producers interested in developing novel products for niche markets. Garlic florogenesis was described by Hua et al. (1994) and Kamenetsky and Rabinowitch (2001), but comprehensive description of flower traits and seed production ability is very limited.

The USDA National Plant Germplasm System garlic collection is maintained at the Western Regional Plant Introduction Station (WRIPS), Pullman, Wash. Currently, 195 accessions of *A. sativum* and 10 accessions of *A. longicuspis* from 27 countries are available for research. A preliminary evaluation of seed production ability of selected accessions in this collection was reported by Jenderek and Hannan (2000), but the variation in flowering and fertility was not described. The objective of this study was to evaluate garlic clones selected from the NPGS collection for seed producing ability, and to identify characteristics that were associated with reproductive capacity.

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Material and Methods

Forty-seven garlic accessions, which formed flower stalks at the WRIPS in Pullman were selected for evaluation in 1999, and ten of the accessions were evaluated again during 2000–01. The evaluated material originated from 18 countries (Table 1). In October preceding the evaluation years, 12 cloves per accession were planted in the field, at ≈ 3.5 cm apart and 5 cm deep, at the National Arid Land Plant Genetic Resource Unit (NALPGRU), Parlier, Calif. Fertilizer application, water management and pest control were similar to common production procedures (Mann, 1957; Mann et al., 1961). From the time spathe on umbels opened to the time of complete stalk senescence, plants were sprayed with a 0.2% to 0.4% fertilizer solution. Pollination and seed production were performed as described by Simon and Jenderek (2003). As bulbils present in inflorescences developed, they were removed manually using forceps. Following the first removal, bulbils were removed 1 to 2 times additionally from each plant that developed an inflorescence. Before anthesis, plants were covered with screen cages for insect exclusion, and blue bottle flies (*Protophormia tarraenovae* Robineau-Deavoidy, purchased from Forked Tree Ranch, Porthill, Idaho) were used as pollen vectors. During anthesis, ≈ 100 flies per a 3×3 -m cage were applied twice a week. Ten to twelve plants of each accession were evaluated for scape development, opening of spathe, scape height, ease of bulbil removal, number of flowers per umbel, umbel shape, time of flowering, tepal

and bulbil appearance, anther color (at full anthesis), pollen viability, scape senescence rate, and the number of seeds.

Pollen germination tests were conducted in vitro, on 1% water agar containing 15% sucrose. After ≈ 20 h of incubation at room temperature, slides were stained with Iacmoid/martius yellow dye (pH 8.0). The number of stainable pollen grains (stained green-purple), and the number of germinated grains (with tubes) were counted under a compound microscope (100 $\times$). For each accession, pollen grains from two anthers of five flowers were evaluated. Data on stainable and germinated pollen were analyzed by one way ANOVA, using Duncan's new multiple range for mean separation at 1% level (SPSS, 2001).

Results and Discussion

Of 47 garlic clones evaluated, plants of 17 accessions developed a strong scape (round in shape, 5 to 7 mm in diameter), 10 clones had a weak scape (with an oval or flattened cross section, 1 to 3 mm), 18 accessions senesced and were harvested before flower stalk extended over the youngest leaf, and 2 accessions (PI 250662 and W6 2560) did not bolt at all (Table 2). In the 10 accessions with a weak scape, the stalk grew slightly over the youngest leaves and senesced shortly after, similar to the incomplete bolting clones described by Takagi (1990). In bolting garlic types, the presence of plants without a fully developed flower stalk (scape) or any stalk is not uncommon (Kazakova, 1971; Pooler and Simon, 1993). In addition to genetic factors, the initiation of a flower stalk in garlic is influenced by environmental factors (Mann, 1952, 1958; Pooler and Simon, 1993; Takagi, 1990), and the size of planting material. In this study, only plants derived from bulbs with a strong scape produced seeds. The height of flower stalks, measured from the soil level to the top of the inflorescence, varied from 45 to 121 cm and was not related to seed producing ability of the accessions evaluated (Tables 2 and 3). However, large differences in the flower stalk height may present difficulties in potential crosses of specific breeding lines. Flower stalks longer than 70 cm had a tendency to bend, and in some instances, required a physical support to prevent lodging.

Among seed producing accessions, the spathe on plants of four accessions did not open in early stages of flower bud development (PI 493099, PI 515972, PI 540316, and PI 540327) so the spathe was mechanically opened to enable flower development and bulbil removal. In plants of the four accessions grown in a separate plot, the spathe opened 2 to 3 weeks after stalks were fully extended, but the flower buds were already overgrown by bulbils. A spathe opening naturally early in umbel development eliminated the need for spathe removal, and therefore, such clones were more suitable for seed production.

All plants evaluated developed bulbils in inflorescences. The bulbils were removed mechanically to enable flower development. Three accessions were ranked into an easy bulbil removal group (PI 491116, PI 540319,

BREEDING, CULTIVARS, ROOTSTOCKS, AND GERMPLASM RESOURCES

and PI 540337), and five accessions were classified as intermediate. All others were rated as difficult bulbil removal. Plants of PI 540319 and W6 1861 developed typical flowers without bulbil removal, but they did not develop seeds in separate plots. Bulbils on the plants of PI 540319 shed easily when flower stalks were shaken by hand. The shedding characteristic substantially lowered the time needed for bulbil removal. The color, size and number of bulbils varied across the accessions evaluated, but were uniform within each accession. Small bulbils (5.0 to 5.8 mm long and 2.0 to 2.6 mm wide) were usually white or purple white. With maturity, upper tips of the white bulbils turned slight purple or brown. Medium size (6.6 to 9.5 mm long and 4.5 to 7.8 mm wide) and large size (11.1 to 15.8 mm long and 7.1 to 16 mm wide) bulbils were either brown or shades of purple (Table 3). Different color intensities among bulbils within an umbel and between umbels of the same accession were observed. The color of the bulbils was often

similar to the color of the clove and outer bulb skin, with some difference in color intensity. In preliminary observations of selected plants, the number of bulbils that developed before first bulbil removal was similar to the number of flowers present in the umbel. At each subsequent bulbil removal, the number of bulbils was lower than previously, but proportional to the flower number in the umbel.

In 1999, plants began to bloom on June 10 (PI 493099 and PI 540319), and the last accessions flowered on July 30 (PI 540316 and PI 540327, Table 3). The time of garlic flowering varied from year to year. For the 10 accessions evaluated over 3 years, the earliest observed bloom occurred in the last week of May (25 May 2000, PI 540319) and the latest bloom was observed at the beginning of August (3 Aug. 2000, PI 540356). For a given clone, plants usually bloomed over 25 to 50 d. The number of flowers/umbel was evaluated using the following scale: 1 = ≤ 10 , 2 = 11 to 50, 3 = 51 to 100, 4 = 101 to 200, and 5 = >200 .

The largest number of flowers observed was slightly over 300 (309 flowers, PI 540319, in all 3 years). The top seed producers in 1999 (PI 540314, PI 493116, and PI 493099, Table 2) had over 100 flowers per umbel, but none of them produced seed in all flowers. Since each flower has a potential of producing 6 seeds, in an ideal situation each inflorescence of those accessions could produce at least 600 seeds. However, such a high level of seed production was never observed. Based on appearance, the umbel shape was classified as either round umbel or flat umbel (Harris and Woolf Harris, 1994). The shape of the umbel was associated with the number of flowers developed. In flat umbels (PI 515972, PI 540349, W6 1890, W6 2558, and W6 12825, Table 3) the number of flowers was usually below 100 (up to 60 flowers), with stiffer pedicels than in round umbels which usually had >100 flowers.

The most common tepal color was purple or light purple, with or without darker veins, and with or without darker tips. In most flowers, tepal attitude was open, however in two accessions (PI 540319 and W6 1861) beside open tepal flowers, flowers with 'closed' tepals were observed (Table 3). In open flowers, the tepals were positioned at less than a 45° angle to the style. Whereas, in closed flowers the tepal was adjacent to the style. The height of the stigma in plants with closed flowers was either above, or slightly below the tepal tips. This study suggested that garlic flowers exhibited heterostyly within the two clones ($\approx 20\%$ to 30% of plants). However, more observations are needed to determine if this characteristic is stable across the species.

Most anthers with fertile pollen were purple, except in PI 540340, which had yellow anthers. Within 5 accessions (PI 493116, PI 540314, PI 540337, W6 1861, and W6 1890) with predominantly purple anthers, 20% to 30% of plants had yellow anthers (Table 3). Male fertility was usually associated with purple colored anthers (Etoh, 1983; Konvicka, 1984). However, yellow anthers with viable pollen, were also observed previously (Jenderek and Hannan, 2000; Pooler and Simon, 1994). Yellow anthers without viable pollen grains usually shriveled shortly after anthesis, before their pollen grains were released. The highest percentage of viable (stainable) pollen was observed in plants of W6 1885 (97.8%), however the pollen viability of 5 other accessions (PI 540319, PI 540335, PI 540337, PI 540356, and W6 1861) was statistically similar to W6 1885 (Table 3). Pollen tube development was highest in pollen from PI 540340 (27.3%); statistically similar level of pollen tubes was observed in PI 540335. Filament length varied between plants not only among the accessions, but also within plants of the same accession. In closed flowers with short filaments only tips of anthers protruded and no pollen was visible outside the flowers. This may influence the pollen availability to pollination vectors.

Leaves in garlic senesce rapidly, following full bloom. At this point, some flower stalks began to senesce too. Chlorosis started at the base of the flower stalk and progressed upwards to the umbel. Konvicka (1984) described this

Table 1. Garlic accessions from 18 countries evaluated for flowering and seed production in the Central Valley of California.

Accession	Species	Origin	Year introduced to the USDA collection
PI 250662	<i>Allium sativum</i>	USSR	1958
PI 470923	<i>Allium sativum</i>	Philippines	1982
PI 493105	<i>Allium sativum</i>	Turkey	1984
PI 493116	<i>Allium sativum</i>	Czechoslovakia	1984
PI 497951	<i>Allium sativum</i>	Syria	1985
PI 515972	<i>Allium sativum</i>	U.S., Washington	1988
PI 540316	<i>Allium sativum</i>	USSR	1985
PI 540318	<i>Allium sativum</i>	Pakistan	1988
PI 540319	<i>Allium sativum</i>	USSR	1988
PI 540321	<i>Allium sativum</i>	Syria	1988
PI 540327	<i>Allium sativum</i>	Brazil	1986
PI 540328	<i>Allium sativum</i>	Brazil	1986
PI 540335	<i>Allium sativum</i>	Czechoslovakia	1986
PI 540337	<i>Allium sativum</i>	Czechoslovakia	1986
PI 540340	<i>Allium sativum</i>	Czechoslovakia	1986
PI 540346	<i>Allium sativum</i>	Germany	1986
PI 540349	<i>Allium sativum</i>	Germany	1986
PI 540356	<i>Allium sativum</i>	Georgia	1985
PI 540360	<i>Allium sativum</i>	U.S., Washington	1985
PI 540362	<i>Allium sativum</i>	U.S., Iowa	1985
PI 540371	<i>Allium sativum</i>	U.S., Illinois	1985
PI 543049	<i>Allium sativum</i>	Pakistan	1988
W6 670	<i>Allium sativum</i>	Turkey	1989
W6 1860	<i>Allium sativum</i>	Turkmenistan	1989
W6 1861	<i>Allium sativum</i>	Uzbekistan	1989
W6 1862	<i>Allium sativum</i>	Uzbekistan	1989
W6 1883	<i>Allium sativum</i>	Uzbekistan	1989
W6 1885	<i>Allium sativum</i>	Uzbekistan	1989
W6 1890	<i>Allium sativum</i>	Uzbekistan	1989
W6 2558	<i>Allium sativum</i>	USSR	1989
W6 2560	<i>Allium sativum</i>	Greece	1989
W6 4462	<i>Allium sativum</i>	China	1990
W6 4464	<i>Allium sativum</i>	China	1990
W6 10472	<i>Allium sativum</i>	Syria	1992
W6 10473	<i>Allium sativum</i>	Egypt	1992
W6 10734	<i>Allium sativum</i>	Bulgaria	1992
W6 10738	<i>Allium sativum</i>	Bulgaria	1992
W6 10739	<i>Allium sativum</i>	Bulgaria	1992
W6 12825	<i>Allium sativum</i>	Germany	1990
W6 12911	<i>Allium sativum</i>	Korea	1993
W6 17260	<i>Allium sativum</i>	China	1995
W6 17281	<i>Allium sativum</i>	Turkmenistan	1995
PI 493099	<i>Allium longicuspis</i>	USSR, Moldavia	1984
PI 540314	<i>Allium longicuspis</i>	USSR	1985
PI 540315	<i>Allium longicuspis</i>	USSR	1985
PI 540357	<i>Allium longicuspis</i>	USSR	1985
W6 12820	<i>Allium longicuspis</i>	U.S., Illinois	1990

process as a typical phenomenon occurring in the genus *Allium*. The onset of chlorosis due to senescence varied across and within the accessions and was described as slow, intermediate and rapid (Table 3). Stalks with slow chlorophyll degradation remained green or light green until bloom of all flowers in the umbel was completed, where stalks with rapid senescence lost their green color before anthesis of first flowers in the umbel. Eventually all stalks senesce, and plants with the most rapid chlorophyll degradation did not produce seeds. One possible reason for lack of true seed development on those plants may be due to a shortage of nutrients provided by the scape.

Umbels exhibited a wide variation of flower anomalies. Presence of numerous leaf bracts on the peripheries of an umbel or in the whole inflorescence was frequently noted. In several

accessions the development of bulbils in the place of ovaries and styles (epigynous flowers), the growth of a second whorl of flowers growing from the primary flowers, or the presence of bulbils without flowers was observed. Splitting of mature flower receptacles was observed among umbels with >200 flowers. In split umbels, typical garlic flowers shed pollen, but the whole inflorescence wilted very quickly. The number of plants with flowering anomalies varied between clones, and was highest in PI 540349 and W6 12825. As expected, the number of seeds harvested from plants with umbel anomalies was very low (1.8 and 1.5 seeds/stalk, respectively for PI 540349 and W6 12825).

Of 36 accessions with a strong stem base in bulbs used as the planting material, 19 developed true seeds (Table 2). PI 540314 (48.5

seeds/umbel), PI 493116 (15.4 seed/umbel), and PI 493099 (12.5 seeds/umbel) produced the most seeds (Table 2). The ability to bear true seed among the garlic clones evaluated was 40.4% out of 47 bolting accessions, including a male sterile clone, PI 540357. The number of seeds developed on plants of the accessions evaluated in this study may differ under growing conditions other than the Central Valley of California. The seed fertility described in this study might be viewed as an indication of the fertility characteristic present in the NPGS germplasm. However, during three years of observations of 10 clones, the number of seeds per plant of the same accession varied up to 15-fold (W6 12825, Table 2).

Some phenotypic variation was present among the 10 to 12 plants evaluated within each accession. Table 3 describes the predominant phenotypic trait observed within each accession. The most stable traits, such as flower stem appearance, opening ability of spathe in early stages of flower development, the level of difficulty to remove bulbils, tepal color, umbel shape and the number of flowers per umbel, were similar across the populations evaluated. The position of stigma, the closure of tepals, pollen shed, pollen viability, time of flowering, length of filaments, scape senescence rate, and number of seeds produced by individual plants (data not shown) varied more between plants within an accession. The WRPIS garlic collection is a valuable source of selection material for developing true seed fertile garlic.

To date, the most significant technique applied to improve garlic production has been in vitro virus free plant production. To a limited extent, some garlic improvement has been realized by selection of clonal material or the selection of somaclonal variants. In the future, however, seed fertile clones and sexual reproduction can provide a base for development of new phenotypes by syngamy and recombination. After breeding and selection, new phenotypes may be either propagated vegetatively or from true seed. Important benefits from true seed in garlic may include their novelty, reduction of virus titer (Walkey et al., 1987), and nematodes, the two most serious pests in garlic clove seed at the present time. The development of true seeded garlic cultivars may enable garlic cultivation using practices common for onion and leek, but production from true seed may not be widely used commercially until high bulb yielding seed cultivars are developed.

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Table 2. Number of seeds and scape appearance in bulbs of garlic accessions.

Accession	Appearance of scape in bulbs ²		Seeds /plant (no.)		
	Before planting (as received from	After harvest			
	Pullman, Wash.)	(Parlier, Calif.)	1999	2000	2001
PI 540314	sg	sg	48.5	8.0	5.5
PI 493116	sg	sg	15.4	3.4	1.6
PI 493099	sg	sg	12.5		
PI 540337	sg	sg	11.7		
PI 540356	sg	sg	9.7	0.7	5.2
PI 540319	sg	sg	9.5	14.3	7.0
PI 540357	sg	sg	9.1	1.0	10.0
PI 540340	sg	sg	8.3		
PI 540316	sg	sg	7.8		
PI 540335	sg	sg	7.8		
PI 540327	sg	wk	5.0		
W6 1885	sg	sg	5.0	0.6	0.7
W6 2558	sg	sg	4.5		
W6 1890	sg	wk	4.4		
PI 540362	sg	wk	3.9	1.3	2.7
PI 515972	sg	wk	3.5		
W6 1861	sg	sg	2.9	0.8	nf
PI 540349	sg	wk	1.8	1.0	nf
W6 12825	sg	sg	1.5	0.1	nf
PI 540346	sg	wk	0.0		
PI 540360	sg	sg	0.0		
W6 1862	sg	wk	0.0		
W6 1883	sg	wk	0.0		
W6 4462	wk	wk	0.0		
W6 10738	sg	sg	0.0		
W6 12820	sg	sg	0.0		
W6 17260	wk and ns	wk	0.0		
PI 250662	sg	ns			
PI 470923	sg	harv			
PI 493105	sg	harv			
PI 497951	sg	harv			
PI 540315	wk and ns	harv			
PI 540318	sg	harv			
PI 540321	wk and ns	harv			
PI 540328	wk and ns	harv			
PI 540371	wk and ns	harv			
PI 543049	sg	harv			
W6 670	wk and ns	harv			
W6 1860	wk and ns	harv			
W6 2560	wk and ns	ns			
W6 4464	wk and ns	harv			
W610472	sg	harv			
W6 10473	sg	harv			
W6 10734	wk and ns	harv			
W6 10739	wk and ns	harv			
W6 12911	sg	harv			
W6 17281	wk and ns	harv			

²sg = Strong, wk = weak , ns = nonstalking (no scape), harv = harvested before flower stalk (scape) development was completed, nf = no flowers developed.

BREEDING, CULTIVARS, ROOTSTOCKS, AND GERMPLASM RESOURCES

Table 3. Scape, umbel and flowering characteristics of seed producing garlic accessions.

Accession	Scape ht (cm)		Bulbil removal ^o	Flowers/ umbel ^p (no.)	Flowering date ^q	Tepal color ^r	Tepal angle ^s	Anther color ^t	Pollen viability (%) ^u			Umbel shape ^v	Bulbil size ^w	Bulbil color ^x	Scape senescence rate ^y	
									Stain- able	w/Pollen tubes						
PI 493099	112	c	d	4	6/10/99	lp	o	p	17.5	G ^z	0.0	C	r	s	wp	s, i, r
PI 493116	92	o	e	4	7/5/99	lp	o	p, y	67.6	BCDE	0.0	C	r	s	w, wp	s, i
PI 515972	77	c	d	2	7/15/99	p	o	p	nt				f	s	pw	i
PI 540314	95	o	d	5	6/30/99	lp	o	p, y	12.7	FG	0.5	C	r	s	pw	s
PI 540316	92	c	d	5	7/30/99	p	o	p	25.0	FG	8.0	BC	r	s	wp	s
PI 540319	121	o	e	5	6/10/99	lp	o, c	p	82.3	ABC	2.2	C	r	s	w, p	s
PI 540327	55	c	i	4	7/30/99	p	o	p	nt				r	m	pb	s
PI 540335	72	o	d	4	6/25/99	p	o	p	76.5	ABCD	20.0	AB	r	m	pw	s
PI 540337	45	o	e	3	6/30/99	lp	o	p, y	75.6	ABCD	10.9	BC	r	m	w, wp	s, i, r
PI 540340	105	o	d	4	6/30/99	p	o	y	46.1	EF	27.3	A	r	s	w	s
PI 540349	80	o	i	3	7/5/99	p	o	p	9.8	G	8.2	BC	f	m, l	wb	s
PI 540356	97	o	d	4	7/20/99	p	o	p	92.3	AB	1.5	C	r	s	w p	s
PI 540357	92	o	i	5	7/15/99	p	o	p	0.0	G	0.0	C	r	s	pw	s
PI 540362	55	o	i	4	6/30/99	p	o	p	49.5	DEF	4.5	C	r	s, m	w, p	i, r
W6 1861	68	o	d	4	6/30/99	p	o, c	p, y	78.5	ABC	3.2	C	r	s	pw	i, r
W6 1885	91	o	d	4	7/5/99	p	o	p	97.8	A	2.2	C	r	s	p	s
W6 1890	110	o	d	3	6/10/99	p	o	p, y	61.9	CDE	2.9	C	f	s	w, p	s
W6 2558	60	o	d	2	6/30/99	p	o	p	nt				f	m	p	i
W6 12825	66	o	i	2	7/5/99	p	o	p	nt				f	m	wp	s, i, r

^aSpathe: c = closed, o = open naturally.
^oBulbil removal: d = difficult, e = easy, i = intermediate.
^pFlower number/umbel ranking: 1 = ≤10, 2 = 11 to 50, 3 = 51 to 100, 4 = 101 to 200, 5 = >200
^qFlowering date: beginning of flowering when 10 flowers were opened on 1/3 of umbels..
^rTepal color: lp = light purple, p = purple.
^sTepal angle: o = open , c = closed.
^tAnther color: p = purple, y = yellow.
^uPollen germination rate: nt = not tested.
^vUmbel shape: f = flat, r = round.
^wBulbil size: s = small, m = medium, l = large.
^xBulbil color: p = purple, pb = purple brown, pw = purple white, w = white.
^yScape senescence rate: s = slow, i = intermediate, r = rapid.
^zMean separation, LSD, *P* ≤ 0.01.

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