Giant Hill Selection for Control of *Verticillium dahliae* in Potato

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ABSTRACT

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Verticillium wilt resistance and productivity of Russet Burbank giant hill clones were evaluated over a 3-yr period. Most clones remained healthy until harvest even though infected with *Verticillium dahliae.* When grown in competition with each other, most clones had a lower yield and fewer U.S. No. 1 tubers than standard Russet Burbank non-giant hill clones; however, seven of 112 giant hill selections had yields and tuber quality equal to or exceeding that of standard Russet Burbank. Currently, the only control of *V. dahliae* is through costly soil fumigation. Development of these and similar selections offers the promise of more economical control and reduced dependence on pesticides.

Giant hill (GH) was first reported as a potato plant abnormality in 1924 (12). Plants with this abnormality have been called bolters (1,10,22), males (6), bull plants, and wild types. It is thought to be a mutation or alteration involving photoperiodism (1,3,10,11,16,17,20, 22,25). GH plants grow normally under short days but develop exaggerated growth characteristics under long days (10). There is apparently a mutation of an unstable gene controlling response to day length that causes a reversion to the short-day tuberization types found in South America (11). Different GH strains or clones have been reported (27).

GH plants usually develop a large canopy from a single stem 2–3 cm in diameter (14) with large cracks in the epidermis (12). They have more than normal numbers of leaves (18), leaves that are smaller and thinner (12), and profuse flowering (1,13). Most of the tubers produced are knobby, pointed, or spindle-shaped and occasionally have "stitched," fasciated, or dimpled areas at the bud end of the tubers (2,5) and deep eyes (26). Tuber buds have a longer than normal period of dormancy (26). Occasionally, GH plants have been reported with relatively smooth tubers (26).

In general, GH plants are reported to produce more and larger tubers than the standard cultivar from which they arise, but the tubers are of inferior quality (14,16,26) and immature (1). The tubers of GH plants have generally processed into usable products. It has been reported that the specific gravity of GH tubers increases with length of season and can surpass normal Russet Burbank (26). GH plants have been reported resistant to several potato disease organisms, including *Verticillium dahliae* Kleb. (1,13,16,26).

Selection of GH tubers to increase yields is not new (26). In 1917, Gilbert (8) suggested that growers go through commercial fields and select tubers that show unusual vigor and desirable habit; however, grower-selected GH plants were often discarded later because of undesirable tuber shape.

Occasional GH plants in the cultivar Russet Burbank have been observed for years in Washington fields. Since 1975, many fields have been observed to contain up to 5% GH. GH was present in 3.8% of 77 lots in 1979 and in 44.4% of 54

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Table 1. *Verticillium dahliae* content, yield, and grade of giant hill (GH) and non-GH (NG) clones selected from commercial fields of Russet Burbank in 1981 and 1982 and grown in a *V. dahliae*-infested field in 1982 and 1983

Seed supplier (SS) and plant type[y] (PT)	*V. dahliae* stem propagules ($\times 10^3$) on Oct. 1982	Yield (q/ha)	U.S. No. 1 tubers (%)
1981 Selections grown in 1982			
1-GH	56 ab[z]	703 cd	38 f
1-NG	101 a	881 a	51 abc
2-GH	63 ab	689 cd	45 cde
2-NG	66 ab	832 ab	46 bcde
5-GH	54 ab	829 ab	42 def
5-NG	72 ab	841 ab	49 abc
9-GH	48 b	679 cd	41 ef
9-NG	81 ab	817 ab	53 a
10-GH	57 ab	645 d	37 f
10-NG	72 ab	766 abc	45 cde
CSC	80 ab	824 ab	48 abcd
Mean GH	56 b	709 b	41 b
Mean NG	78 a	827 a	49 a
Interactions			
SS × PT	ns	ns	sig
1982 Selections grown in 1983			
1-GH	37 d	780 def	26 de
1-NG	64 abcd	754 ef	41 bc
2-GH	56 bd	788 def	24 de
2-NG	79 ab	860 abcd	43 bc
3-GH	47 cd	744 ef	22 e
3-NG	68 abc	872 abc	50 a
4-GH	65 abcd	700 f	30 d
4-NG	74 abc	810 bcde	43 bc
5-GH	45 cd	794 cde	27 de
5-NG	94 a	936 a	39 c
6-GH	47 cd	742 ef	24 de
6-NG	83 ab	864 abcd	45 abc
7-GH	69 abc	810 bcde	24 de
7-NG	66 abcd	942 a	41 bc
CSC	85 ab	896 a	47 ab
Mean GH	52 b	765 b	25 b
Mean NG	75 a	862 a	43 a
Interaction			
SS × PT	ns	sig	sig

[y] Plant types: GH = tubers selected from healthy giant hill plants resistant to *V. dahliae*; NG = tubers selected from dead non-giant hill plants, and CSC = tubers from a certified seed control.
[z] Means with the same letter within a column are not significantly different at $P = 0.05$ according to Duncan's multiple range test.

lots in 1980 in the Northwest Voluntary Foundation Seed trials (23,24). One lot had 9% GH in 1980. GH was present in some lots of seed from certified seed programs of Idaho, Montana, Oregon, Washington, and Alberta, Canada (23,24).

In Washington State, frequency of GH has apparently increased in Russet Burbank cultivar, probably because of emphasis on selection of vigorous plants in stem-cutting programs intended for control of black leg (9). Before the use of heat treatment and meristem culturing to rid Russet Burbank and other cultivars of latent mosaic viruses, mutations to GH occurred at a low frequency (15,19,21). Probably, the frequency of this mutation has been accentuated by heat treatment and meristem culturing, but no data have been published to support this speculation.

In 1981, we started collecting GH clones that appeared to have good yields of smooth tubers from commercial fields of Russet Burbank. Yield, tuber quality, and resistance to Verticillium wilt of GH clones were compared with those of clones from normal plants collected in the same commercial fields. Both were compared with crops grown from standard certified seed potatoes.

MATERIALS AND METHODS

Comparison of bulk samples of GH vs. non-GH tubers. In September of 1981 and 1982 in south central Washington, 11 fields (51 ha each) of commercial Russet Burbank potatoes with at least 1% GH, irrigated by center-pivot irrigation, were located. Three of 11 seed sources grown in these commercial fields were from the same supplier. A bulk sample (about 45 kg) of large (0.4–0.6 kg) smooth tubers was hand-harvested from green, healthy GH plants (a few tubers per hill) in a portion (8–16 ha) of each field. A similar sample of tubers was collected from non-GH hills killed by *V. dahliae*. The tubers were stored over winter at 4 C. In April, the tubers were warmed to 10–14 C for 3 wk to promote sprouting. Tubers from both GH and non-GH sources were cut into seed pieces (60–90 g) and hand-planted 30.5 cm apart in three 3-m open-furrow rows (10 seed pieces per row). Tubers of similar size selected at random from Elite III Foundation seed from Montana were cut similarly and hand-planted. Discs covered the open furrows after planting.

Treatments were arranged in a randomized complete block design with six replicates. The middle row of each plot was machine-harvested in October to obtain yield and grade data (Table 1).

Fields selected for these experiments had produced potatoes the previous year and, according to soil and potato stem assays, were heavily infested with *V. dahliae*. Ten stems 25 cm long, cut 3 cm from ground level, were collected from each plot in October to assay for *V. dahliae*. These were air-dried, stored at about 21 C for 3 mo, then ground and screened through a 0.074-mm (200-mesh) sieve. The screened stem tissue (0.5 g) from each plot was diluted 1:50 in sterile tap water and spread on five plates of ethanol-streptomycin-Penicillin G medium, incubated for 7 days at 24 C, and the propagule numbers were estimated (7).

Evaluation of performance of individual GH clones to a standard. In another experiment, conducted concurrently, an effort was made to select GH clones with superior disease resistance, yield, and grade characteristics.

In September 1981 and 1982, in the same areas (8–16 ha) of the 11 fields sampled, tubers from GH plants producing at least six smooth tubers were bagged individually, stored over winter, and warmed for cutting as previously described. Tubers from 10 hills from each of the 11 seed sources were cut in half longitudinally. One-half of each tuber was saved for seed increase. The other half was cut horizontally into three seed pieces (60–90 g) and bagged for planting. For comparison, tubers of similar-sized Elite III Foundation seed were also cut into seed pieces and bagged. The three seed pieces from each half tuber were hand-planted as a unit into an open furrow in the field. A seed piece of a red potato was planted between the seed pieces so hills could be separated at harvest. All seed pieces were planted about 30 cm apart. Tractor-mounted

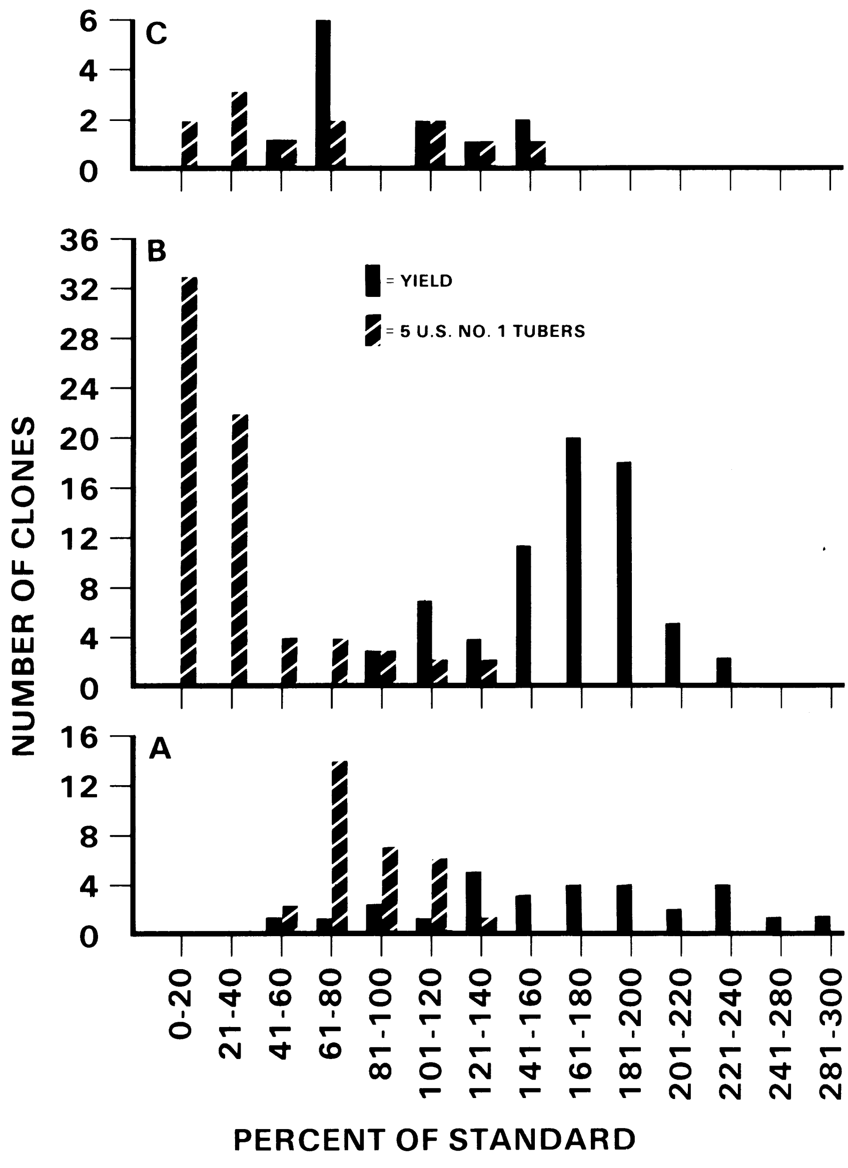

Fig. 1. Population distribution of giant hill potato clones on percentage of standard for yield and U.S. No. 1 grade tubers. **(A)** Thirty clones from three commercial fields selected in 1981 and grown in 1982 (standard yielded 338 q/ha = 100% and 74% U.S. No. 1 tubers = 100%); **(B)** 70 clones from seven commercial fields selected in 1982 and grown in 1983 (standard yielded 580 q/ha = 100% and 54% U.S. No. 1 tubers = 100%); and **(C)** 12 clones selected from commercial fields, propagated, and grown in 1983 (standard yielded same as B). Note: The bar graphs for yield and grade of tubers are separate population curves and not necessarily related.

discs covered the open furrows after planting. The six half tubers from each GH clone were randomly arranged in a complete block design to provide six replicates. Two guard rows of Elite III Foundation Russet Burbank were machine-planted on each side of the plot row to separate plots and provide plant competition. In November, readings were taken for resistance to Verticillium wilt and tubers from individual hills were hand-dug, graded, and weighed in the field. Yield data from the three seed pieces of each half tuber were combined and compared as a population distribution (Fig. 1A,B).

In 1983 and 1984, the promising GH selections originally collected from commercial fields in 1981 and 1982 and subsequently increased in a dryland area under sprinkler irrigation were further evaluated for *Verticillium* disease and production. In 1983, three seed pieces per half tuber for 11 selected clones and a standard were planted and replicated as previously described (Fig. 1C). In 1984, each plot was hand-planted with 10 seed pieces (85–113 g) of each GH selected clone (Table 2). Verticillium wilt scores were recorded on 11 October 1984 as the percentage of plants dead (0 = healthy and 100 = all plants dead). The plots were machine-harvested in October.

Split-split-plot (Table 1), factorial (Table 3), and randomized complete block (Table 2) statistical analyses were used to determine treatment differences.

RESULTS

Comparison of bulk sample of GH vs. non-GH tubers. In 1982 and 1983, Verticillium wilt resistance of GH clones was very obvious when plants grown from a bulk tuber seed sample from GH plants were compared with those grown from bulk samples from non-GH plants or certified seed (Table 1). By mid-September, plants grown from non-GH and certified seed were dead; those grown from GH seed were healthy until harvest in late October. There were small but significant differences in number of *V. dahliae* propagules in stems of GH and non-GH groups. Overall, plants grown from GH seed yielded significantly less and had fewer U.S. No. 1 tubers than non-GH seed. There was no difference in specific gravity in 1982, but in 1983, tubers produced from non-GH seed had significantly higher specific gravity than those from GH seed. The GH characteristic negatively influenced the percentage of U.S. No. 1 tubers in both years and yield in 1983.

Evaluation of performance of individual GH clones to a standard. In 1982, plants of the standard cultivar died by September. Foliage from all 30 GH clones of the three seed suppliers appeared healthy and resistant to Verticillium wilt at harvest. Many of the clones outyielded the standard (more than 100%), but only a few had more U.S. No. 1 tubers than the standard (Fig. 1A). Six clones (5-1, 5-2, 9-2, 9-4, 9-7, and 9-9) had the same or greater yield and percentage of U.S. No. 1 tubers than the standard (Table 3). Clone 9-10 had about three-fourths the percentage of U.S. No. 1 tubers as the standard but 2.45 times the yield.

Resistance to Verticillium wilt varied within the 10 single-hill selections of the 10 sources collected from commercial fields in 1982. In 1983, 49 clones were resistant and 21 were susceptible to Verticillium wilt; all resistant clones and 18 susceptible clones outyielded the standard. Most of the clones outyielded the standard; however, only four clones produced more U.S. No. 1 tubers (Fig. 1B). None of the 70 clones appeared better than the standard.

Of 12 selected GH clones from 1981 collections and replanted in 1983, only four clones were resistant to Verticillium wilt. These resistant clones and one susceptible clone had yields equal to or greater than the standard, but all had fewer U.S. No. 1 tubers. None of the clones appeared better than the standard (Fig. 1C).

In 1984, in a replant of 11 selected GH clones from 1981 and 1982 collections, six (3-4, 4-10, 5-5, 6-3, 6-4, and 9-1) had significantly less Verticillium wilt than the standard (Table 2). Seven (1-2, 4-10, 5-1, 5-5, 6-4, 6-10, and 7-7) had percentage of U.S. No. 1 tubers about equal to the standard, but most yielded less than the standard and three (1-4, 5-1, and 6-10) yielded significantly less than the standard.

Only seven GH clones (5-1, 5-2, 9-2, 9-4, 9-7, 9-9, and 9-10) from two (no. 5 and no. 9) of the 11 seed suppliers appeared equal to or better than the standard (Table 3).

DISCUSSION

Selection of superior Russet Burbank clones from a bulk sample of smooth tubers from GH plants was ineffective (Table 1). These selections were resistant to Verticillium wilt and had fewer propagules of *V. dahliae* than standard Russet Burbank but, when grown in competition, yielded less than the standard and had poorer tuber quality. Selection of GH single hills in commercial fields, however, resulted in seven of 112

Table 2. Verticillium wilt index, yield, and grade of clones derived from single giant hills collected from commercial fields in 1981 and 1982 and grown in a *Verticillium dahliae*-infested field in 1984

Seed supplier and hill numbers	Verticillium wilt index[x] (11 Oct.)	Yield (q/ha)	U.S. No. 1 (%)
Standard[y]	88 abc[z]	647 ab	77 a
1-2	63 bcde	435 abcde	62 abc
1-4	93 ab	414 bcdef	56 c
3-4	30 f	607 abcd	59 c
4-10	53 def	446 abcde	69 abc
5-1	86 abc	357 bcdef	63 abc
5-5	29 f	601 abcd	65 abc
6-3	31 f	628 abc	61 bc
6-4	39 ef	720 a	68 abc
6-10	79 abcd	336 cdef	66 abc
7-7	58 cdef	460 abcde	72 abc
9-1	50 def	565 abcd	56 c

[x] Index 0–100, where 0 = no wilt and 100 = all plants dead.
[y] Grown from Elite III certified Russet Burbank seed potatoes obtained from Montana.
[z] Means with the same letter within a column are not significantly different at $P = 0.05$ according to Duncan's multiple range test.

Table 3. Verticillium wilt response, yield, and grade of single hill giant hill clones selected from three commercial fields in 1981 and grown in a *Verticillium dahliae* infested field in 1982

Seed supplier and hill numbers	Verticillium wilt response[w] (12 Oct.)	Percentage of standard[x] Yield (q/ha)	U.S. No. 1 (%)
Standard[y]	S	338 = 100	74 = 100
5-1	R	164 bcdefghi[z]	100 abcd
5-2	R	126 defghij	116 ab
9-2	R	178 bcdefgh	111 abcd
9-4	R	126 defghij	113 abc
9-7	R	135 cdefghij	122 a
9-9	R	123 efghij	101 abcd
9-10	R	245 abc	74 abcdef

[w] Resistant (R) or susceptible (S).
[x] Standard = grown from Elite III certified Russet Burbank seed potatoes obtained from Montana.
[y] Actual yield (q/ha) and percentage of U.S. No. 1 tubers of standard.
[z] Means with the same letter within a column are not significantly different at $P = 0.05$ according to Duncan's multiple range test.

such selections, which appear equal or better than the standard (Table 3). These lines were resistant to Verticillium wilt and, when grown in competition, had tuber quality and yield equal to or better than standard Russet Burbank. If these or similar lines were developed, chemical control of *V. dahliae* at a cost of about $250/acre would be unnecessary in the production of these lines.

After several years of testing, especially after seed increase in a commercial area, some plants of GH selections showed mosaic and leafroll symptoms. These were verified by enzyme-linked immunosorbent assay (4) as caused by virus X, S, Y, or leafroll. Presence of viruses in some selections tested in Table 2 may be the reason for their poor yields; however, we now have methods to obtain virus-free seed that were not available in the 1940s, when GH lines were previously considered for propagation (18,27). Development of Verticillium wilt-resistant cultivars by single-hill selections of GH mutants should be explored as a means of cultivar improvement.

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