Genetics, phenotypes, agronomic and malting performance of glossy sheath mutants in barley, Hordeum vulgare L.
by Wayne Lucas McProud

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Genetics
Montana State University

Abstract:
Twenty four different glossy sheath mutational events, including both spontaneous and induced mutants were found to comprise six different loci. The seventeen spontaneous glossy sheath mutants occurred at random over these six loci. The tentative location of gsl is on chromosome 4. It has been reported that gsl and cer-q are allelic. The gene gs2 is located on either chromosome 2 or, more probably, chromosome 3.

The location of gs3 is on chromosome I with the probable gene order of wx-gs3-br. The gene gs4 is located on chromosome 6. Chromosome 2 is the location of gs5, having the probable gene order V-gs5-Ms2. The gene gs6 is located on chromosome 2.

The microscopic wax morphology of the glossy sheath mutants can be classified into four groups. Group 1, "short rods", corresponds to the locus gsl. Group 2, "peaks and ridges", corresponds to the loci gs2 and gs5. The loci gs3 and gs6 comprise group 3, "flakes". Group 4, "knolls", corresponds to the locus gs4.

Nine barley varieties and their glossy sheath mutants were compared for yield, and for various agronomic and malting traits. Two effects may be ascribed to the glossy sheath mutants': . The glossy sheath mutant, as compared to the normal genotype, heads earlier and may have superior yielding capacity when grown under stress conditions at lower elevations.

GENETICS, PHENOTYPES, AGRONOMIC AND MALTING PERFORMANCE OF GLOSSY SHEATH MUTANTS IN BARLEY, *HORDEUM VULGARE* L.

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WAYNE LUCAS MCPROUD

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

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in

Genetics

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ABSTRACT

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Nine barley varieties and their glossy sheath mutants were compared for yield, and for various agronomic and malting traits. Two effects may be ascribed to the glossy sheath mutants. The glossy sheath mutant, as compared to the normal genotype, heads earlier and may have superior yielding capacity when grown under stress conditions at lower elevations.

INTRODUCTION

Mutants with altered wax coatings are a common mutational event in barley. Lundqvist and von Wettstein (1962) report that mutants with reduced or absent wax coating on various organs are almost as readily induced as erectoides, the most frequent viable mutants in barley. The name eceriferum (from Latin: cer=wax and ferre=bear) was suggested by Lundqvist and von Wettstein (1962) to describe barley mutants having little or no wax coating on the spike, stem, leaf sheath or blades, on several organs or involving the whole plant. The Swedish source of eceriferum mutants is primarily from artificially induced mutations.

The eceriferum family of mutants contains many specific glossy mutant types. Of concern in this thesis are the combined glossy sheath, stem and spike mutants, and glossy sheath mutants with normal wax covering on the stem and spike. The sources of the glossy mutants herein reported are largely spontaneous.

The purposes of this study were to determine allelism of the combined glossy sheath, stem and spike mutants plus the two glossy sheath mutants with normal wax covering on the stem and spike, to establish linkage relationships of the various glossy sheath loci, to determine if morphological differences existed between the different glossy sheath loci on a microscopic level, and to compare agronomic and malting characteristics of normal and glossy sheath mutants.

LITERATURE REVIEW

Early "waxless" mutants

Gustafsson (1947) reported on an unpublished collection by H. Tedin of a spontaneous "waxless" mutant in the barley variety 'Primus'. Tedin found the mutant line equalled the mother line in yield. Gustafsson noted that Tedin's mutant did not have the same peculiar bright green color of the later induced waxless mutants.

The occurrence of another spontaneous eceriferum mutant was reported by A. V. Tokhluyev in 1935 (Gustafsson, 1947, and Smith, 1951). This mutant, described by Smith (1951) as lacking wax on the leaves, was given the gene symbol Wlwl. Smith reported on the finding of two additional waxless mutants by K. V. Ivanova. One mutant, designated Whwh, lacked waxy bloom on the spike while the second, designated Wh2wh2, lacked waxy bloom on the spike and stem. Other waxless or bloomless mutants reported on by Smith were Gege, normal vs. non-glaucous ear, and Gsgs, normal vs. non-glaucous sheath. All were reported as monofactorial recessive mutants.

Stadler (1930) reported inducing two "non-glaucous" recessive barley mutants. Gustafsson (1947) reported inducing several mutants involving wax variation. Some appeared to be extremely waxy. Other mutants induced in the varieties Maja, Ymer, and Bonus were characterized by a "bright" green color and were found to be entirely or partially waxless.

Glossy sheath mutants

The first report of a glossy sheath mutant, designated by the symbol gsgs, was made by Immer and Henderson (1943). The symbol was later changed to (cer-)gs (Robertson, et.al., 1965). The glossy sheath mutant Immer and Henderson studied, C.I. 5818, was originally obtained from Vavilov's collection at Valkie, U.S.S.R. (J. C. Craddock, Personal communication).

The identification of a second gene for the glossy sheath characteristic, (cer-)gs2, was made by R. F. Eslick (unpublished) in the barley variety Vantage. This mutant was selected from a foundation seed field at Bozeman, Montana.

Researchers at the University of Alberta, Canada (Wälker, et.al., 1963) identified two additional glossy sheath genes. The first gene, induced in the variety Mars by x-radiation was designated (cer-)gs3. A second glossy sheath gene designated (cer-)gs4, was induced in the variety Gateway by treating seed with the mutagen aldrin.

Rasmusson and Lambert (1965) reported that the two glossy sheath genes in Mars and Gateway were allelic. In addition, Rasmusson and Lambert reported on two glossy sheath mutants obtained from K. Mikaelson of Norway. The mutant in Jotun was designated (cer-)gs5 while the mutant in Domen was designated (cer-)gs6.

Takahashi and Hayashi (1966) found a spontaneous glossy sheath mutant in the Japanese barley variety Sekitori. The gene symbol (cer-)gs7 was assigned to this mutant, Kogane-mugi.

A second spontaneous glossy sheath mutant reported by Takahashi et.al. (1965) (corrected by Takahashi and Hayashi, 1968) was named Okaiku No. 3. This mutant, assigned the symbol (cer-)gs8, was selected at the Okayama Agricultural Experiment Station, Japan.

Lundqvust, von Wettstein-Knowles, and von Wettstein (1968) reported on 380 induced and 4 spontaneous eceriferum mutants. They found seven different loci producing mutants with phenotypes similar to five of the six glossy sheath mutants discussed in this thesis. The glossy sheath phenotype is an apparent absence of wax on the spike, leaf sheath, and stem. The leaf blades appear normal. The eceriferum loci associated with the glossy sheath, stem and spike phenotype are cer-a, cer-c, cer-q, cer-x, cer-z, cer-z1.

Lundqvist et.al. (1968) found three other genes, cer-n, cer-r, and cer-zm, causing an absence of wax on the spike, reduced wax on the leaf sheath and stem, and normal appearing leaf blades. One gene, cer-s, caused a reduction of wax on the spike, an absence of wax on the leaf sheath and stem, with normal appearing leaf blades.

Linkages

Five of the presently identified genes for the glossy sheath characteristic in barley have been assigned to a chromosome. Albrechtsen (1957) reported a recombination value of 23.9 between gs1 and Colorado zoned leaf z_c; on chromosome 4. Anderson (1958) reported gs1 and the break point of the translocation T3-4a to be 15.0 map units apart. These

data indicate that gs1 is located on chromosome 4.

Walker, et.al. (1963), reported gs3 to be 24.1±6.1 map units from brachytic, br, on chromosome 1. Using F_2 data, McProud and Eslick (1968) reported (cer-)gs3 and br to be linked, being 0.3±9.0 map units apart. Rasmusson and Lambert (1965) found (cer-)gs3 linked with chlorina, fc, and waxy, wx, both on chromosome 1. The recombination values between (cer-)gs3 and fc, and between (cer-)gs3 and wx, were 2.0±1.05 and 20.7± 5.3, respectively.

Walker et.al. (1963) located gs4 on chromosome 6 and found it linked with orange lemma, o, and glossy leaf-4, gl4. The o gene had no recombination with gs4 while gl4 had a recombination value with gs4 of 29.4±2.6.

Rasmusson and Lambert (1965) located (cer-)gs5 on chromosome 2. They found (cer-)gs5 to be linked with long glume awn, e, and with six row, v, with the respective recombination values of 2.5±0.79 and 32.0± 2.55. They report a probable gene order of (cer-)gs5, e, v.

Rasmusson and Lambert (1965) reported (cer-)gs6 to segregate independently from the following marker genes on chromosome 1; brachytic, br, naked carypsis, n and chlorina, fc. In addition, they found (cer-) gs6 independent of six row, v, on chromosome 2; white seedling, a_c, and xantha seedling, x_c, on chromosome 3; hooded, K, glossy seedling, gl, and blue alcurone, Bl, on chromosome 4; black lemma and pericarp, B, albino seedling, a_t, on chromosome 5; and orange lemma, o, on chromosome

6. No marker genes on chromosome 7 were tested with (cer-)gs6 by Rasmusson and Lambert.

Takahashi and Hayashi (1966) located (cer-)gs7 on chromosome 2 through the use of trisomic analysis.

Takhashi, et.al. (1965) (corrected by Takahashi and Hayashi, 1968) located (cer-)gs8 on chromosome 2 by the use of trisomics. They found (cer-)gs8 to be linked with purple stem, Pr, and with six row, v, with a recombination value of 36.6 and 25.1, respectively. The probable gene order is Pr, v, (cer-)gs8.

Physical and Chemical Properties

Lundqvist and von Wettstein (1962) and Eglinton and Hamilton (1967) have reported on DeBary's observations regarding wax structures. Using a light microscope, DeBary identified four structural configurations of surface waxes. Two of these structural types he identified as being present on barley surfaces were heaped wax layer and single granulated layer. Lundqvist and von Wettstein (1962) found that in barley "the spike, and the central and lateral florets are covered with a heaped layer of needles, whereas the awns are covered with relatively few isolated granules. The stem nodes and internodes as well as the leaf sheaths are coated with a thick heaped layer of needles. The leaf blades have only a granular coating either in the form of isolated wax granules or of a continuous granules layer". It was determined by von Wettstein-Knowles (1971) that the average length of the rods or needles on the

barley sheath is five microns. She points out that the rods may be single or branched, and that their entire length may lay flat along the cuticle or may stand erect.

Lundqvist and von Wettstein (1962) stated no wax could be detected microscopically on the concerned organs of eceriferum mutants. It was found by von Wettstein-Knowles (1971) that there were changes in structure density and/or distribution of the epidermal waxes on four eceriferum mutants. A glossy sheath mutant, cer-c, was found to have a 34% reduction in the amount of wax present on the internodes. The internodes of Bonus barley had 51 mg/cm^2 of wax while the mutant cer-c had 17 mg/cm^2 of wax.

Chemical analyses of the normal and the glossy sheath, an eceriferum mutant, have been conducted by Jackson (1971) and von Wettstein-Knowles (1971). Jackson (1971) investigated the chemical composition of surface lipid extracts from the internode region of both normal and glossy sheath barley plants. In both normal and glossy sheath mutant plants hydrocarbons made up 5-7% of the surface lipids while alcohols (as acetates) accounted for 15-20% of the surface lipid extract. From normal barley 25-30% of the surface lipids were made up of the B-diketones hentriacontane-14-16-dione, plus 0-1% hydroxy-B-diketones. The glossy sheath mutants lack these compounds in their epidermal waxes.

It has been noted by von Wettstein-Knowles that the internode waxes from normal Bonus contain paraffins, esters, primary alcohols,

aldehydes, lactones, B-diketones and hydroxy-B-diketones (1971). Wax bodies which contain B-diketones and hydroxy-B-diketones are long thin rods. When these two B-diketones classes are missing, as in the waxes on wild type leaves, no such rods are formed.

Agronomic properties of normal and of eceriferum mutants.

X-ray induced eceriferum mutants have been tested by the Swedish Seed Association for yield and other agronomic characteristics (Fröier, 1954). Fröier characterized bright green 2 by "less waxiness and lighter green-leaf colour". Nine years data show that bright green 2 yielded 98.1% of its mother line, Maja. Date ripe, hectoliter weight, 1000-kernel weight, sifting percentages (percent plump barley) and percent crude protein were about the same as Maja. Eight years data show that the glossy mutant bright green 3 yielded 96.5% of its mother line, Bonus. The mutant was similar to Bonus for hectoliter weight and 1000-kernel weight, but somewhat superior in kernel shape and development and ripened at least one day earlier (Fröier, 1954).

Lundqvist et.al. (1968) reported "rather unspecific pleiotropic effects caused by the eceriferum loci on viability, plant height, or fertility. In some cases these effects could signify deletions, including pieces of adjacent genes".

Function of surface waxes.

Eglington and Hamilton (1967) suggested various functions for the surface waxes. Such functions may be to protect the plant from

mechanical damage, from insect, fungal and bacterial attack, and possibly protect the plant from frost damage. Epidermal waxes may help preserve the plants water balance or alter the ability of substances to penetrate through the leaf. Surface waxes may scatter light or other radiations striking the plants surface. Jackson (1971) noted that "the B-diketones, nucleic acids and amino acids absorb ultraviolet light in about the same region of the spectrum and the B-diketone may serve a dual role in preventing ultraviolet damage and desecration in the plant".

Lundqvist, et.al. (1968) and Jackson (1971) pointed out that the glossy appearance of plant organs is due to the wax's chemical and physical properties and not to the actual absence of wax.

MATERIALS AND METHODS

Allelism

A collection of 24 different glossy sheath mutants was assembled at Bozeman, Montana. The glossy sheath mutants of Ymer, Mars, Jotun, Domen, and C.I. 9132 are believed to have originated by radiation treatments while the glossy sheath mutant of Gateway arose from a seed treatment with the mutagen aldrin. The glossy sheath mutants of the varieties Piroline, Velvon, Vantage, Atlas 1, Atlas 2, Compana 1, Compana 2, Compana3, Compana 4, Betzes, and Heines Hanna were found as spontaneous mutants in the Rocky Mountain region of the northern United States and probably represent separate mutational events. The remaining spontaneous glossy sheath mutants are from various parts of the world. A complete resume of the various sources of the glossy sheath mutants, as far as they are known to the author, is included as Table 1. Letters following the locus symbol represent, presumably, separate mutational events. The letters were assigned arbitrarily to the stocks available.

Tests for allelisms were made by inter-crossing the glossy sheath mutants. Most crosses were made using male sterile glossy sheath plants as females; otherwise, crosses were made utilizing hand emasculated plants. The resulting F_1's were grown in the greenhouse and selected F_2 populations were grown.

Linkage and Inheritance Studies

Crosses were made between the glossy sheath, genes and lines carrying known marker genes. A translocation tester set was crossed

Table 1. Source and origin of the glossy sheath mutants.

Variety	Suggested gene symbol locus and event	C.I. No. of parental variety	Origin	History and/or source
Piroline	gs1b	9558 11330*	Spontaneous	Selected from a head row at Tetonia, Idaho
Glossy Tester	gs1a	5818*	Vavilov's collection	Supplied by D. W. Robertson Fort Collins, Colorado
Velvon	gs1c	6109	Spontaneous	Supplied by R. W. Woodward Logan, Utah
Vantage	gs2d	7324	Spontaneous	Selected from a foundation seed field at Bozeman, Montana, in 1958
Atlas 1 Atlas 2	gs2f gs2g	4118 4118	Spontaneous Spontaneous	Selected as 2 sources from a commercial field at Dayton, Washington, in 1964 and 1966
Ymer	gs2e	7275	Irradiation	Mutation from Ymer (P.I.184886) received from the Institute of Genetics at Lund, Sweden via USDA, Beltsville, Maryland
Klargrin	gs2h		Believed irradiation induced	Supplied by D. C. Rasmusson, St. Paul, Minnesota (originally from A. Gustaffson Lund, Sweden).

Table 1. Continued

Variety	Suggested gene symbol locus and event	C.I. No. of parental variety	Origin	History and/or source
Mars	gs3i	7015	Irradiation	Supplied by J. W. Lambert, St. Paul, Minnesota. Additional sources G. W. Walker, Edmonton, Alberta, Canada, and D. C. Rasmusson, St. Paul, Minnesota
Chevron	gs3j	1111	Spontaneous	Selected as a single plant in the 1953 Beltsville Greenhouse. Supplied by G. A. Weibe, USDA
Atlas[4] x Algerian x Atlas 57[2]	gs3k		Spontaneous	Supplied by C. O. Qualset, Davis, California
Gateway	gs4l	10072	Chemical mutagen aldrin	Supplied by G. W. Walker, Edmonton, Alberta, Canada
Jotun	gs5m		Irradiation	Supplied by D. C. Rasmusson, St. Paul, Minnesota (supplied to Minnesota by K. Mikaelsen, Norway).
Okaiku No. 3	gs5n		Spontaneous	Supplied by R. Takahashi, Ohara Institute, Japan
Domen	gs6o	9562	Irradiation	Supplied by D. C. Rasmusson, St. Paul, Minnesota (supplied to Minnesota by K. Mikaelsen, Norway)

Table 1. Continued.

Variety	Suggested gene symbol locus and event	C.I. No. of parental variety	Origin	History and/or source
Sekitori	gs6q		Spontaneous	Spontaneous mutant Kogane-mugi. Supplied by R. Takahashi, Ohara Institute, Japan
Barbless	gs6r	5105	Spontaneous	Selected from a head row at Madison, Wisconsin
Compana 1	gs6u	5438	Spontaneous	Selected from four separate commercial sources in Montana
Compana 2	gs6v	5438	Spontaneous	
Compana 3	gs6w	5438	Spontaneous	
Compana 4	gs6x	5438	Spontaneous	
Betzes	gs6s	6398 10863*	Spontaneous	Selected from a commercial field in Pondera County, Montana
Heines Hanna	gs6t	8060 10862*	Spontaneous	Selected from a malting barley nursery plot at Manhattan, Montana. This seed source was imported as a commercial lot from Idaho
C.I. 9132	gs6p	9132*	Irradiation	Supplied from the USDA world collections

(* = C.I. number of the glossy sheath mutant).

to gs1 and gs2. F_1 plants were grown in the greenhouse while F_2 rows and F_3 head hills were field grown. Allard's tables (1956) were used to facilitate linkage calculations.

Morphological determination of the wax particles

Field-grown plants representing the six identified glossy sheath genes were used in producing micrographs utilizing the penetrating and scanning electron microscopes. Those plants used for the light microscopic study were grown in the greenhouse. For the penetrating electron microscope, epidermal surfaces were prepared according to the techniques of Juniper and Bradley (1958). Plant parts were mounted on a glass slide and placed in a shadow cast unit under high vacuum. Palladium was deposited onto the leaf surface at an angle of 45° and carbon was evaporated on the specimen at an angle of 60°. The 100-200 A° thick carbon film thus produced was backed with Formvar from a 2% solution in chloroform, then with Bedacryl from a 5% solution in acetone, and finally with "sellotape". The replica was stripped from the specimen, fastened to a glass slide and immersed in acetone. After the Bedacryl had dissolved, EM-specimen grids were inserted between the tape and the Formvar film. The Formvar was removed with chloroform, preparing the grid for examination.

Scanning electron micrographs of normal and glossy sheath barleys were prepared by R. Bronson of S. C. Johnson and Son, Inc., Racine, Wisconsin. Samples of the six glossy sheath genes plus normal Betzes

were prepared for mailing by suspending six inch segments of the upper most leaf sheath by nylon line through the holes of a peg board partition into moistened cotton. These samples were shipped to Racine by parcel post.

Samples for examination by light microscopy were prepared by stripping away the lower sections of sheath tissue leaving the upper cuticle. The upper cuticle was stained with a saturated solution Sudan III in 70% ethyl alcohol-water for one to two minutes. The sample was then washed with 0.2% phenol in 50% glycerol after which the specimen was mounted for examination.

Agronomic and Malting Characteristics

Nine pairs of normal and glossy sheath mutant barleys were tested for yield. Comparative yield trials were conducted between the normal and the glossy sheath mutants of the varieties Mars and Barbless at Bozeman, Montana, for four and three years, respectively. Three years of trials comparing two glossy sheath mutants and the normal genotype of the variety Compana were conducted at Bozeman. In addition, two years of yield trials at Bozeman compared the normal and one glossy sheath mutant of the variety Compana. Further yield trials comparing the normal and glossy sheath mutants of the varieties Mars, Barbless and Compana were conducted for two years at Moccasin, Montana, and for one year at Havre, Montana.

Comparative yield trials were conducted between the normal and

glossy sheath mutants of the varieties Chevron (3 years), Velvon (3 years), Vantage (1 year), Heines Hanna (3 years), Betzes (2 years), and Piroline (1 year) at Bozeman. In 1959, yield trials compared the normal and glossy sheath mutants of the varieties Betzes, Compana, Piroline, Heines Hanna, and Vantage under irrigated and dryland conditions at Sidney, Huntley, and Creston, Montana; dryland conditions at Moccasin and Havre; and irrigated conditions at Bozeman.

Montana yield trials were grown in 3 or 4 row plots with three meters of the center row (s) harvested. Plots were grown in randomized block or split plot designs with four replications. Agronomic data were obtained from six Montana Agricultural Research Centers. Percent protein data were obtained from Kjeldahl analysis by the Montana Cereal Quality Laboratory.

Data from the 1960 Western 2-Row Barley Nursery, grown in the northwestern portion of the United States, includes a comparison of the normal and glossy sheath mutants of the varieties Betzes and Heines Hanna for yield and agronomic characteristics. Yield and agronomic data for the normal and glossy sheath mutant of the variety Piroline were obtained from the 1961 Western 2-Row Barley Nursery. These data are presented with the permission of the many agronomists who cooperated in growing the Western 2-Row Barley Nurseries.

Malting quality data were summarized from the "Malting Quality of Barley Varieties and Selections Grown in Rocky Mountain and West-

tern Stations in 1960" and "in 1961" for Betzes, Heines Hanna and Piroline and their respective glossy sheath mutants. The data were obtained by the United States Department of Agriculture Barley and Malt Laboratory, Madison, Wisconsin and is presented with their permission.

The range of elevations used in calculating correlations between elevation of the trial site and yields of the glossy sheath mutants expressed as a percent of their normal genotype were from 61.0 to 2337.1 meters.

Differences between normal and mutant types for agronomic and malting characteristics were evaluated by the paired t-test. Approximate significance of a difference for clarity of wort was determined by an interaction chi-square test.

RESULTS AND DISCUSSION

Allelism

From crosses between the different glossy sheath mutants, F_1 plants were classified as being either normal or glossy. If the F_1 plants were glossy, the two parental sources were considered allelic, if normal, they were considered non-allelic. All F_2 populations from glossy sheath F_1 plants were glossy sheathed while F_2 populations from F_1 normal plants segregated in the ratio of 9 normal plants to 7 glossy sheathed plants. The homozygous double recessive was indistinguishable from those plants carrying only one of the recessive glossy sheath genes in a homozygous condition.

The F_1 plant phenotypes from crosses made between different glossy sheath mutants are recorded as Table 2. The 24 different glossy sheath mutational events were assigned to six different loci, gs1 through gs6. It was found that the reported glossy sheath genes (cer-)gs5 (Rasmusson and Lambert, 1965) and (cer-)gs8 (Takahashi, et.al., 1965; corrected by Takahashi and Hayashi, 1968) were allelic. The glossy sheath mutant Okaiku No. 3 (cer-)gs8, has been reassigned to the locus gs5. The reported glossy sheath genes (cer-)gs6 (Rasmusson and Lambert, 1965) and (cer-)gs7 (Takahashi and Hayashi, 1966) were found to be allelic. The glossy sheath mutant Kogane-mugi, (cer-)gs7, has been reassigned to the locus gs6.

The suggested gene symbolization is to use gs to identify the mutants phenotype, (glossy sheathed), to use numbers one through six

Table 2. F_1 Phenotypic classification of crosses between glossy sheath (gsgs) x glossy sheath (gsgs) lines.

Parent A	Genotype and suggested gene symbol[1/]	Genotype of Parent B					
		gs1 gs1	gs2 gs2	gs3 gs3	gs4 gs4	gs5 gs5	gs6 gs6
		Number of F_1 plants and phenotype*					
Piroline	gs1 gs1	25 gs	32 Gs	41 Gs	20 Gs	20 Gs	36 Gs
C.I. 5818	gs1 gs1	24 gs	14 Gs	18 Gs	-----	-----	4 Gs
Velvon	gs1 gs1	21 gs	17 Gs	8 Gs	-----	-----	9 Gs
Vantage	gs2 gs2	32 Gs	48 gs	45 Gs	20 Gs	20 Gs	46 Gs
Atlas 1	gs2 gs2	5 Gs	7 gs	17 Gs	-----	-----	11 Gs
Atlas 2	gs2 gs2	10 Gs	10 gs	10 Gs	-----	-----	15 Gs
Ymer	gs2 gs2	6 Gs	29 gs	8 Gs	-----	-----	10 Gs**
Klargrin	gs2 gs2	10 Gs	10 gs	10 Gs	-----	-----	10 Gs
Mars	gs3 gs3	43 Gs	69 Gs	16 gs	20 Gs	20 Gs	71 Gs
Chevron	gs3 gs3	11 Gs	11 Gs	6 gs	-----	-----	8 Gs
Atlas[4] x Algerian Atlas 57[2]	gs3 gs3	13 Gs	10 Gs	10 gs	-----	-----	10 Gs
Gateway	gs4 gs4	20 Gs	20 Gs	20 Gs	-----	9 Gs	24 Gs
Jotun	gs5 gs5	10 Gs	10 Gs	10 Gs	5 Gs	10 gs	17 Gs
Okaiku No. 3	gs5 gs5	10 Gs	10 Gs	10 Gs	4 Gs	10 gs	15 Gs**
Domen	gs6 gs6	10 Gs	10 Gs	10 Gs	-----	-----	10 gs
Kogane-mugi	gs6 gs6	2 Gs	3 Gs	5 Gs	-----	10 Gs	2 gs
Barbless	gs6 gs6	10 Gs	46 Gs	39 Gs	20 Gs	20 Gs	35 gs
Heines Hanna	gs6 gs6	3 Gs	8 Gs	12 Gs	-----	-----	16 gs
C.I. 9132	gs6 gs6	7 Gs	5 Gs	5 Gs	-----	-----	10 gs
Betzes	gs6 gs6	7 Gs	8 Gs**	6 Gs	-----	-----	22 gs
Compana 1	gs6 gs6	9 Gs	7 Gs	24 Gs	-----	-----	16 gs
Compana 2	gs6 gs6	-----	-----	7 Gs	-----	-----	18 gs
Compana 3	gs6 gs6	-----	-----	-----	-----	-----	6 gs
Compana 4	gs6 gs6	1 Gs	5 Gs	-----	4 Gs	2 Gs**	2 gs

* Gs = normal, gs = glossy

** 5 glossy plants noted

1/ See Table 3 for gene symbol changes from gene designations by previous authors