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# Interallelic relations among endosperm variants in sorghum

*Abstract:* The inheritance of four endosperm variants of sorghum that exhibit xenia effects was studied in the $F_1$, $F_2$, and backcross seed of crosses among variants and with the normal type. It was concluded that the endosperm variants vani, sugary (*su*), and high lysine (*h1*) are controlled by three independent single recessive alleles and that dimpled endosperm is controlled by a single recessive allele (*dp*) allelic to that controlling the *vani* endosperm trait.

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Several natural endosperm variants exhibiting shrivelled or deformed grains are known in sorghum (*Sorghum bicolor* L. Moench). Dimpled seed exhibit a depression on the grain and are controlled by a single recessive allele designated as *dp*[1]. Sugary grains are characterized by a hard and crystalline endosperm and large depressions or pitting near the stylar as well as hilar ends, thus giving the grain a wrinkled appearance. Karper and Quinby[4] found that sugary grains were controlled by a single recessive allele (*su*). Vani sorghums, popularly used in the Maharashtra state of India to make a sweet snack called hurda, are characterized by grains with a soft endosperm exhibiting a dimple on the side opposite to the hilum. Karper and Quinby[4] discussed the inheritance of vani grains reported from India and concluded that the alleles governing vani and sugary grains were synonymous. Schertz and Stephens[7] recommended the gene symbol *su* for the characters sugary and dimpled. It was found that the endosperm variants sugary, dent, and defective were controlled independently by single recessive alleles[3]. Murty et al.[5] reported the inheritance of dimpled grains exhibiting the basmati (scented) character in the sorghum cultivar, KEP-472 (IS 19907), and found that dimpled and scented characters were controlled by two independent recessive alleles. During the course of these investigations the authors observed that crosses of the dimpled basmati (hereafter called dimpled) with vani and sugary variants resulted in contrasting behavior. We therefore undertook a detailed study of the interrelationships among the alleles controlling the sugary, vani, and dimpled endosperm variants. Another important endosperm variant exhibiting shrivelled seed, namely, high lysine (*h1*)[8] also was included in these studies. This paper presents the results obtained from intercrosses of these four endosperm variants with a normal parent and among themselves.

## Materials and Methods

Seed of sugary grain sorghum IS 5614 and the dimpled variant KEP 472 (IS 19907)[5] were obtained from the Genetic Resources Unit (GRU) of ICRISAT. Seed of two vani cultivars, namely, Rambhapur vani (R vani) and Malkapur vani (M vani), which were reported to be superior hurda types, were obtained from D. R. Bapat, Mahatma Phule Krishi Vidyapeeth, Rahuri, Maharashtra, India[2]. The high lysine sorghum of Ethiopia, namely, IS 11758 is photoperiod-sensitive. In order to avoid floral nonsynchronization problems, seed of a photoperiod-insensitive derivative (L2) of IS 11758 possessing the shrivelled endosperm and the *h1* gene were obtained from V. J. M. Rao of the All India Coordinated Sorghum Improvement Project, Hyderabad, India. Seed of a plump grain cultivar, SPV 350, were chosen to represent the normal parent.

Seed of all the endosperm variants and the normal parent were planted at the ICRISAT Center farm during November 1981 and all possible crosses (including reciprocals) of the five variants were made. The nature of the

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endosperms of the $F_1$ seed resulting from pollinations among the various parents was noted. All the $F_1$ hybrids were grown during November 1982–March 1983 and the segregation for endosperm characteristics on panicles of $F_1$ plants ($F_2$ seed) was noted. In some of the crosses, the $F_1$ panicles were emasculated and pollinated in separate backcrosses with either of the parents. Segregation for endosperm characteristics among the resulting seed (backcross) was noted. Although $F_1$ seed were examined in all the hybrids including reciprocals, segregation in the $F_2$ and backcross generations of reciprocal crosses was studied only in some cases.

## Results and Discussion

When, the sugary, vani, dimpled, and high lysine parents were emasculated and pollinated with normal parent SPV 350, the resulting $F_1$ seed were always plump and confirmed the dominance and xenia effects of the allele governing plump grains. Crosses of dimpled, M vani, R vani, and sugary parents with the high lysine parent resulted in normal plump $F_1$ seed. Similarly, crosses of dimpled, M vani, R vani parents with the sugary parent resulted in normal plump $F_1$ endosperm. However, crosses among dimpled, R vani and M vani parents resulted in grains with dimpled endosperm in the $F_1$ generation. Morphologically the dimpled seed of the cultivar KEP 472 and the grains of the vani parents appeared very similar.

In all the five crosses of mutant parents with the normal parent, the $F_2$ segregation conformed to a ratio of 3 normal: 1 mutant (Table I). In crosses of dimpled with R vani and M vani, the endosperm nature of all grains in their $F_2$ generation was similar and there was no segregation. In the $F_2$ generation of crosses of dimpled, M vani and R vani with the sugary parent, a segregation ratio of 9:3:3:1 of grains with normal endosperm, those akin to the two parents and another

**Table I. Segregation for endosperm characteristics on the $F_1$ panicles ($F_2$ seed) of crosses between six endosperm variants of sorghum**

| Cross | Panicle no. | Endosperm class frequency: normal plump | sugary | dimpled | R vani | M vani | high lysine | double recessive | Total | $\chi^2$ P |
|---|---|---|---|---|---|---|---|---|---|---|
| Normal × mutant | | | | Expected segregation ratio—3:1 | | | | | | |
| Normal × sugary | 1 | 1860 | 631 | — | — | — | — | — | 2491 | 0.50 |
| | 2 | 1355 | 425 | — | — | — | — | — | 1780 | 0.25 |
| Normal × dimpled | 1 | 1131 | — | 383 | — | — | — | — | 1514 | 0.75 |
| | 2 | 1399 | — | 460 | — | — | — | — | 1859 | 0.75 |
| | 3 | 1052 | — | 369 | — | — | — | — | 1421 | 0.25 |
| Normal × R vani | 1 | 710 | — | — | 243 | — | — | — | 953 | 0.50 |
| | 2 | 87 | — | — | 297 | — | — | — | 1173 | 0.75 |
| | 3 | 508 | — | — | 162 | — | — | — | 670 | 0.50 |
| Normal × M vani | 1 | 1035 | — | — | — | 348 | — | — | 1383 | 0.97 |
| | 2 | 879 | — | — | — | 282 | — | — | 1161 | 0.50 |
| Normal × high lysine* | 1 | 1560 | — | — | — | — | 497 | — | 2057 | 0.25 |
| | 2 | 705 | — | — | — | — | 239 | — | 944 | 0.75 |
| | 3 | 1335 | — | — | — | — | 421 | — | 1756 | 0.25 |
| | 4 | 902 | — | — | — | — | 291 | — | 1193 | 0.50 |
| Mutant × mutant | | | | Expected segregation ratio—9:3:3:1 | | | | | | |
| Dimpled × R vani* | 1 | — | — | 1661 | — | — | — | — | 1661 | 0.00 |
| | 2 | — | — | 1641 | — | — | — | — | 1641 | 0.00 |
| | 3 | — | — | 1409 | — | — | — | — | 1409 | 0.00 |
| | 4 | — | — | 2273 | — | — | — | — | 2273 | 0.00 |
| | 5 | — | — | 1453 | — | — | — | — | 1453 | 0.00 |
| Dimpled × M vani* | 1 | — | — | 1418 | — | — | — | — | 1418 | 0.00 |
| | 2 | — | — | 1907 | — | — | — | — | 1907 | 0.00 |
| | 3 | — | — | 1237 | — | — | — | — | 1237 | 0.00 |
| | 4 | — | — | 2230 | — | — | — | — | 2230 | 0.00 |
| | 5 | — | — | 1922 | — | — | — | — | 1922 | 0.00 |
| Sugary × dimpled* | 1 | 620 | 218 | 194 | — | — | — | 65 | 1097 | 0.50 |
| | 2 | 546 | 173 | 169 | — | — | — | 54 | 942 | 0.50 |
| | 3 | 843 | 265 | 248 | — | — | — | 83 | 1439 | 0.25 |
| Sugary × R vani* | 1 | 937 | 319 | — | 314 | — | — | 102 | 1672 | 0.97 |
| | 2 | 1306 | 400 | — | 427 | — | — | 153 | 2286 | 0.25 |
| | 3 | 929 | 298 | — | 293 | — | — | 91 | 1611 | 0.75 |
| Sugary × M vani | 1 | 829 | 257 | — | — | 285 | — | 98 | 1469 | 0.50 |
| | 2 | 1095 | 372 | — | — | 374 | — | 110 | 1951 | 0.50 |
| Sugary × high lysine* | 1 | 1263 | 419 | — | — | — | 427 | 139 | 2248 | 0.97 |
| | 2 | 1256 | 404 | — | — | — | 412 | 135 | 2207 | 0.90 |
| | 3 | 1063 | 341 | — | — | — | 346 | 108 | 1858 | 0.75 |
| Dimpled × high lysine | 1 | 982 | — | 318 | — | — | 327 | 107 | 1734 | 0.95 |
| | 2 | 974 | — | 322 | — | — | 332 | 112 | 1740 | 0.95 |
| | 3 | 1055 | — | 360 | — | — | 359 | 119 | 1893 | 0.95 |

* Data on panicles of the reciprocal cross were combined

class of defective endosperm types not conforming to any of the parents was observed (Figure 1). Apparently, the new class of defective grains represent homozygous double recessive recombinants of the respective parents. Similar results were obtained in crosses of sugary × high lysine and dimpled × high lysine. Crosses of vani × high lysine type were not studied in their $F_2$ generation.

The results obtained from the backcrosses of the mutant × mutant hybrids are presented in Table II. Backcrosses involving the high lysine parent were not attempted. In all the backcrosses of sugary × dimpled, sugary × R vani and sugary × M vani hybrids, a segregation ratio of 1 normal: 1 mutant parent type was obtained. However, in the backcrosses of dimpled × R vani and dimpled × M vani, no

**Table II. Segregation for endosperm characteristics among backcross derived seed (BCO) $F_1$ panicles of crosses between five endosperm variants of sorghum**

| Cross | Panicle no. | Endosperm class frequency: normal plump | sugary | dimpled | R vani | M vani | Total | $\chi^2$ P (1:1 ratio) |
|---|---|---|---|---|---|---|---|---|
| (Dimpled × R vani) dimpled* | 1 | — | — | 181 | — | — | 181 | 0.00 |
| | 2 | — | — | 450 | — | — | 450 | 0.00 |
| | 3 | — | — | 429 | — | — | 429 | 0.00 |
| | 4 | — | — | 232 | — | — | 232 | 0.00 |
| | 5 | — | — | 161 | — | — | 161 | 0.00 |
| (Dimpled × R vani) R vani* | 1 | — | — | 341 | — | — | 341 | 0.00 |
| | 2 | — | — | 186 | — | — | 186 | 0.00 |
| | 3 | — | — | 715 | — | — | 715 | 0.00 |
| | 4 | — | — | 429 | — | — | 429 | 0.00 |
| (Dimpled × M vani) M vani* | 1 | — | — | 740 | — | — | 740 | 0.00 |
| | 2 | — | — | 620 | — | — | 620 | 0.00 |
| | 3 | — | — | 480 | — | — | 480 | 0.00 |
| | 4 | — | — | 390 | — | — | 390 | 0.00 |
| (Dimpled × M vani) dimpled | 1 | — | — | 767 | — | — | 767 | 0.00 |
| | 2 | — | — | 886 | — | — | 886 | 0.00 |
| | 3 | — | — | 269 | — | — | 269 | 0.00 |
| (Sugary × dimpled) sugary* | 1 | 220 | 210 | — | — | — | 430 | 0.50 |
| | 2 | 121 | 115 | — | — | — | 236 | 0.50 |
| | 3 | 205 | 200 | — | — | — | 405 | 0.75 |
| | 4 | 222 | 232 | — | — | — | 454 | 0.50 |
| | 5 | 221 | 223 | — | — | — | 444 | 0.90 |
| | 6 | 247 | 255 | — | — | — | 502 | 0.50 |
| (Sugary × dimpled) dimpled* | 1 | 70 | — | 60 | — | — | 130 | 0.25 |
| | 2 | 175 | — | 173 | — | — | 348 | 0.90 |
| | 3 | 208 | — | 209 | — | — | 417 | 0.90 |
| | 4 | 169 | — | 161 | — | — | 330 | 0.50 |
| | 5 | 258 | — | 250 | — | — | 508 | 0.50 |
| (Sugary × R vani) sugary* | 1 | 247 | 235 | — | — | — | 482 | 0.50 |
| | 2 | 311 | 325 | — | — | — | 636 | 0.50 |
| | 3 | 449 | 436 | — | — | — | 885 | 0.50 |
| | 4 | 41 | 39 | — | — | — | 80 | 0.75 |
| | 5 | 277 | 280 | — | — | — | 557 | 0.90 |
| | 6 | 56 | 66 | — | — | — | 122 | 0.25 |
| (Sugary × R vani) R vani* | 1 | 138 | — | — | 134 | — | 272 | 0.75 |
| | 2 | 324 | — | — | 318 | — | 642 | 0.75 |
| | 3 | 244 | — | — | 237 | — | 481 | 0.75 |
| | 4 | 276 | — | — | 288 | — | 564 | 0.50 |
| | 5 | 91 | — | — | 81 | — | 172 | 0.25 |
| | 6 | 86 | — | — | 77 | — | 163 | 0.25 |
| (Sugary × M vani) sugary | 1 | 63 | — | — | — | 71 | 134 | 0.25 |
| | 2 | 239 | — | — | — | 219 | 458 | 0.25 |
| | 3 | 425 | — | — | — | 421 | 846 | 0.90 |
| | 4 | 134 | — | — | — | 132 | 266 | 0.90 |
| | 5 | 235 | — | — | — | 236 | 471 | 0.90 |
| | 6 | 213 | — | — | — | 226 | 439 | 0.50 |
| (Sugary × M vani) M vani | 1 | 436 | — | — | — | 442 | 878 | 0.75 |
| | 2 | 108 | — | — | — | 110 | 218 | 0.90 |
| | 3 | 32 | — | — | — | 30 | 62 | 0.75 |
| | 4 | 101 | — | — | — | 93 | 194 | 0.50 |

* Data on panicles of backcrosses from the reciprocal $F_1$ hybrid were combined

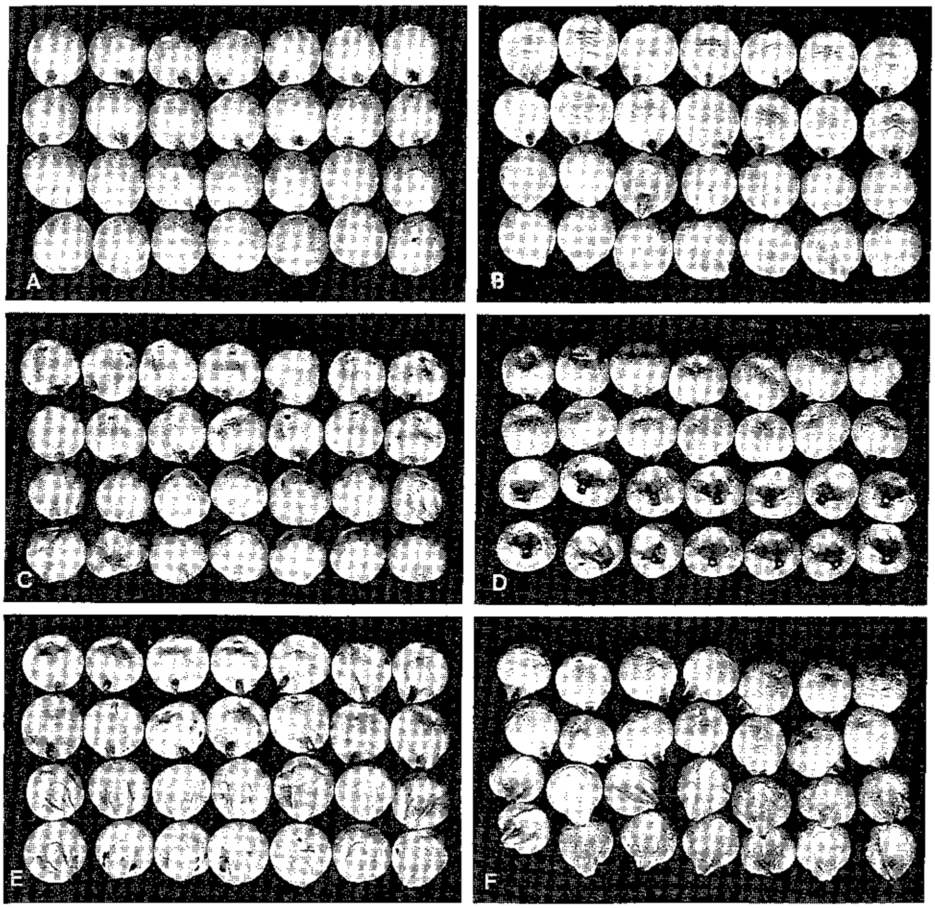

**FIGURE 1** Endosperm variants in sorghum. *A*—normal (SPV 350); *B*—dimpled (KEP 472); *C*—vani (Malkapur vani); *D*—sugary (IS 5614); *E*—high lysine (L2); *F*—sugary/vani (segregant from the cross IS 5614 × M vani).

segregation was observed and all the grains exhibited the same endosperm nature.

Murty et al.[6] reported contrasting differences in the soluble sugar composition of the mutant grains included in the present study. The sugary and high lysine grains were characterized by a relatively higher proportion of glucose + fructose fraction while the vani and dimpled types possessed a higher proportion of sucrose. The $F_2$ ($F_1$ panicle) and backcross (BCO) segregation ratios presented here indicate that sugary, high lysine and vani endosperm mutants are controlled by three independent recessive ~~alleles~~. Observation of grains with normal plump endosperm in the $F_1$ generation of crosses involving these mutants, which was the result of complementation of dominant alleles from both the parents, corroborated this conclusion. However, absence of such a complementation in the $F_1$ generation of the crosses dimpled × M vani and dimpled × R vani and no further segregation in their $F_2$ and backcross generations indicated that the genes controlling these mutants are allelic. It is therefore suggested that the gene symbol *dp* assigned to dimpled seed by Ayyangar et al.[1] should be retained to designate the allele controlling the vani and dimpled endosperm variants.

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