EFFECTS OF THE GENES FOR COVERED AND NAKED KERNELS ON SOME AGRONOMIC CHARACTERS IN BARLEY[1)]

I. Comparison of Two Covered Barleys and Their Naked Mutants

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INTRODUCTION

Demand for barley as the staple human food has steadily been decreasing on account of an abrupt change in dietary life in Japan, and this aroused a serious problem especially for farmers in western Japan wherein the naked barley for food has customarily been grown as one of the principal winter crops. To cope with this situation, a plan of replacing the naked barley with the covered one for feed or malt is now under a serious consideration. Before putting this plan into action, we should investigate from all angles as to the reason why naked barley growing has long been concentrated in this region, but did not extend further to central and northern parts of Japan. One of the reason may be such a historical one that naked barley happened to have first been introduced from some region with warm climate in the Asiatic Continent. And, so far as the existing varieties are concerned, the naked forms are superior in many respects to the covered ones in western Japan. Because, the former have long survived artificial as well as natural selection in this region. Nevertheless, most of the Japanese breeders harbor an entirely contradicting thought that the naked barley may inherently be inferior in productivity, stem strength and also winter hardiness to the covered one. Since we have no decisive evidence to support this inference, it is of necessity to disclose the intrinsical difference between the covered and naked barleys.

It is well-known to us that the covered and naked barley can only be discriminated according to whether or not the lemma adheres to kernel at maturity, and the character pair is governed by the gene, *Nn*, in chromosome 1 of barley. But, it is hard to suppose that nakedness of kernel is the unique phenotypic effect of a mutation from *N* to *n*. Perhaps a number of physiological and morphological characters will be altered, if not markedly, by the same gene change, just as has already been observed in many other organisms. If so, the total range of the phenotypic differences resulting from the gene change under consideration can also be regarded as the intrinsical differences of the covered and naked barleys.

We have been performing these several years some experiments in order to contribute from the standpoint of barley geneticists and breeders to above-mentioned problem that confronts us. This paper presents the results obtained in a

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comparative study on the pleiotropic effects of the gene *Nn* for covered and naked kernel of barley on some agronomic characters by the use of two covered barleys of German origin and their naked mutants induced by X-ray irradiation.

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MATERIALS AND METHODS

The materials used in this experiment are two-rowed covered barleys, Haisa and Ackermann's Donaria, and two naked mutant lines, Mut. 4129 and Mut. 3041/6a, each induced by irradiating the former varieties with X-ray. Both of the naked lines had been approved by Scholz (1955) to be a simple recessive mutant at *N* locus in chromosome 1 by a series of experiments using a number of crosses with the covered barleys, Haisa and A. Donaria, and several existing naked barleys of different origin. Behaviors of these two line pairs under German growing conditions have already been studied closely by Bandlow (1951) and Scholz (1955 and later publications). But, the writers planned to repeat similar experiments under Japanese conditions utilizing these rare materials provided by the courtesy of Dr. Scholz. Locations, experimental design, and planting scheme are outlined in Table 1. Quantity and time of application of manure, sowing time and cultivating practice were determined at each location following the respective conventional method. It may be noted that Kurashiki and Kitami are located in the center of fall-sown and spring-sown naked barley regions, respectively, and Konosu in the fall-sown covered barley region, and moreover, climate and soil conditions in these three locations are markedly different from one another.

Table 1. Experimental methods

Year	Location	Sowing time	Design	Method of planting
1959	Kurashiki	Nov. 15, '58	Randomized block 4 replications	100 plants/plot, 8×8 cm in a zigzag line
1960	Kurashiki (A)	Nov. 18, '59	Randomized block 3 replications	30 plants/plot, 8×8 cm in a zigzag line
1960	Kurashiki (B)	Nov. 18, '59	Randomized block 6 replications	320 plants in row/3. 3m² plot
1960	Konosu	Oct. 31, '59		
1960	Kitami	May. 9, '60		

EXPERIMENTAL RESULTS

Grain Yield

Since yield of the covered barley could not be compared directly with that of the naked one, the latter was represented in term of the covered barley for this comparison. As compared with the ordinary method in which covered kernels were dehulled one by one and compared with the naked kernels, this measure was found to be expedient and to give accurate data, inasmuch as in both of the naked lines the kernels with hulls on were liable to be detached from the rachis. The hull contents thus determined varied with the year, line and location, the rough estimates being 8% in 1959 and 11% in 1960 at Kurashiki, and 13 % at Kitami. Table 2 indicates average yields per plant or plot in different locations and the difference between the covered and naked line pairs. The relative yield of the covered and naked forms in percent as determined by three years' experiments at Gatersleben, Germany, is also shown for reference.

Table 2. Comparison of covered barleys and their naked mutants, I. Yield

Items	Gatersleben	Kurashiki			Konosu	Kitami
	1952–4	1959 (A) g/plant	1960 (A) g/plant	1960 (B) kg/a	1960 (B) kg/a	1960 (B) kg/a
Haisa (Covered)	100.0	9.48	13.6	45.50	42.2	17.43
Mut. 4129 (Naked)	100.5	11.32	12.0	44.27	39.5	18.27
Difference	*−0.5*	*−1.84**	*1.6*	*1.23*	*2.7*	*−0.84*
A. Donaria (Covered)	100.0	10.19	13.4	44.68	42.9	16.38
Mut. 3041/6a (Naked)	96.2	8.55	9.6	40.01	37.8	15.78
Difference	*3.8*	*1.64**	*3.8**	*4.66**	*5.1***	*0.60*
L. S. D. 1% (**)	—	1.99	4.79	4.96	4.95	2.19
L. S. D. 5% (*)	—	1.37	3.16	3.58	3.58	1.59

According to Table 2, yields of these four lines varied markedly with locations: Kurashiki always topranked in yields of all lines, which was followed by Konosu and at last by Kitami. The yield at Kitami was only about one third of that of Kurashiki. However, it is notable that the difference in yield between Haisa and its naked mutant line, Mut. 4129, was not statistically significant in all but one cases. On the contrary, Mut. 3041/6a always yielded less than the contrasting variety, A. Donaria, the difference being significant excepting the case for Kitami.

In this investigation it was aimed also to know whether there is a significant interaction between location and genotype. A statistical analysis for it was tried using the data which were obtained from the experiments performed under the almost same design at three locations in 1960. First, uniformity of error variances was tested by Bartlett's method (Inamura *et al.* 1955), which indicated to be significant at 5% level but not at 1% level. The estimate of error variance obtained at Kitami was too small as compared with those found at two other locations. This has thrown some doubt whether it is adequate to regard these three data as random samples taken from a population, but analysis of variance was made using all the data obtained at three locations.

The result in Table 3 indicates obviously that the interaction between variety and location was very small and statistically insignificant, although difference in yield was marked between varieties as well as between locations. It may therefore be concluded that, as far as the materials used in this experiment are concerned, different locations exhibit no decided preference between the covered and naked types, in spite of the fact that Konosu is located in the covered barley region and two other places in the naked barley region.

Table 3. Analysis of variance of yield data obtained at three locations in 1960

Source of variation	D. F.	S. S.	M. S.	F
Replication	15	229, 446. 04	15, 296. 40	2. 41*
Variety	3	167, 941. 64	55, 980. 55	8. 82**
Location	2	10, 242, 395. 57	5, 121, 197. 79	80. 71**
Var. × Loc.	6	45, 923. 51	7, 653. 92	1. 21
Error	45	285, 533. 12	6, 345. 18	
Total	71	10, 971, 239. 88		

** and * significant at 1% & 5% levels, respectively.

Number of Heads and 1000 Kernel Weight

In Table 4 are shown average number of heads and 1000 kernel weight of each of the four varieties or strains at Kurashiki and Kitami and also magnitude and significance of the differences between each pair of the covered and naked forms. The head number of the space-planted plot was determined on a single plant basis, counting the heads of all plants within each plot, and that of the drilled plot was represented by the average of the head numbers of four (Kurashiki) or two (Kitami) 50cm-rows randomly cut within each row. For the determination of 1000 kernel weight, 3 or 4 samples were taken from the bulked seeds of each plot.

Table 4. Comparison of covered barleys and their naked mutants, II. Number of heads and 1000 kernel weight

Items	Number of Heads				1000 Kernel Weight		
	Kurashiki			Kitami	Kurashiki		Kitami
	1959	1960 A	1960 B	1960	1959	1960 B	1960
Haisa (Covered)	13. 1	16. 2	245. 0	90. 5	34. 28	32. 58	34. 04
Mut. 4129 (Naked)	15. 9	16. 4	283. 2	98. 8	35. 48	29. 70	34. 99
Difference	*−2. 8***	*−0. 2*	*−38. 2***	*−8. 3*	*−1. 20*	*2. 88***	*−0. 95*
A. Donaria (Covered)	14. 4	15. 7	240. 2	88. 7	34. 46	32. 32	35. 51
Mut. 3041/6a (Naked)	13. 5	15. 3	252. 5	92. 5	29. 74	29. 52	35. 48
Difference	*0. 9*	*0. 4*	*−12. 3*	*−3. 8*	*4. 72***	*2. 80***	*0. 03*
L. S. D. 1% (**)	2. 1	3. 0	25. 2	—	2. 80	1. 96	—
L. S. D. 5% (*)	1. 4	2. 0	18. 2	—	2. 02	1. 42	—

The result of the head number shown in Table 4 reveals that the naked mutant of Haisa, Mut. 4129, produced more heads per plant or per 50 cm-row than the covered form, the difference being significant statistically in two experiments. However, little difference in head number was found in the other paired varieties.

With regard to 1000 kernel weight, on the other hand, there was a general lighter tendency that the naked mutants were somewhat lighter than the covered forms, and the difference seemed to be marked in A. Donaria and Mut. 3041/6a pair. A similar result was reported by Scholz (1955).

Ear Density and Stem Length

In this comparison ear density was expressed by average length of a single rachis-internode, measuring the whole length of about 20 of them in the middle portion of each ear. The samples used were taken from the space-planted plot, grown at Kurashiki in 1959 and 1960. The results are given in Table 5, which reveal that both of the naked mutants have somewhat longer internodes than their contrasting covered varieties. However, partly contradicting results were obtained in other locations, suggesting interaction of genotype and location or year. According to Scholz, the naked mutant, Mut. 4129, had denser head than the covered variety, Haisa, and the result obtained at Kitami, Hokkaido, was that Mut. 3041/6a and A. Donaria were almost the same in head length.

Table 5. Comparison of covered barleys and their naked mutants, III. Ear density and stem length

Items	Ear density (mm)			Stem length (cm)			
	Gatersleben	Kurashiki		Kurashiki			Kitami
	1952–4	1959	1960 A	1959	1960 A	1960 B	1960
Haisa (Covered)	3.21	2.86	2.89	112.4	118.3	114.3	94
Mut. 4129 (Naked)	3.11	3.15	3.06	109.4	116.9	108.6	91
Difference	*0.10*	*−0.29***	*−0.17***	*3.0*	*1.4*	*5.7***	*3*
A. Donaria (Covered)	3.12	2.96	2.86	112.0	120.0	113.1	93
Mut. 3041/6a (Naked)	3.30	3.13	2.98	107.3	112.5	109.9	89
Difference	*−0.18*	*−0.17**	*−0.12**	*4.7**	*7.5***	*3.2**	*4*
L. S. D. 1% (**)	—	—	0.135	—	4.41	3.37	
L. S. D. 5% (*)	—	—	0.089	—	2.91	2.43	—

Effects of *Nn* alleles on stem length seem to be well-definable, on the contrary. All the results shown in Table 5 unanimously indicate the stem length of the naked mutants being shorter to some extent than the covered forms, irrespective of line pair, year and location. It may also be noted here that quite the same relations were found in some other comparisons of this kind.

Elasticity and Breaking Strength of Culm

As the criteria of lodging resistance elasticity and breaking strength of the culms of the covered and naked forms were studied. Upper two internodes taken from each of the several clums of a plant were used as the materials. Each line consisted of 10 plants, which had been digged up at maturity and thoroughly air-dried. The modulus of elasticity was determined by the same method as employed by Wettstein (1954) for the comparison of an erectoides mutant and its mother line. The formula used was: $E=\frac{1^3W}{3\pi a^3 e v}$, where 1 = length of straw, mostly 10 or 15 cm; W = weight loaded on the point 1 cm apart from the free end of the straw; a = radius of the straw; v = thickness of stem wall; and e = linear measure of the free end of the straw lowered by the weight loaded. The breaking strength of the straw was expressed by the minimum weight that broke the straw (Takahashi and Akaki 1954). The results obtained in 1959 and 1961 at Kurashiki are given in Table 6.

Table 6. Comparison of covered barleys and its naked mutant, IV.
Stem strength

Variety	Young's modulus (E)		Breaking strength (g/mm²)	
	1. Internode	2. Internode	1. Internode	2. Internode
Haisa (Covered)	356000	322000	3.28	3.08
Mut. 4129 (Naked)	385000	394000	3.91	3.61
A. Donaria (Covered)	273000	259000	2.91	2.72
Mut. 3041/6a (Naked)	274000	223000	2.48	2.32

It is apparent from the table that the straw of the naked mutant, Mut. 4129, is obviously more flexible and unbreakable than that of the mother line, Haisa, while there is no marked difference in these characters of the straw between A. Donaria and Mut. 3041/6a. In any way, the result disagrees with the general view that naked barley has weaker straw than the covered barley.

DISCUSSION AND CONCLUSION

Since both of the naked lines used in this experiment have been approved by Scholz (1955) to be arisen from the covered barleys, Haisa and A. Donaria, by a simple recessive mutation at the same *N* locus in chromosome 1, it seems plausible to consider each pair of the covered and naked lines being isogenic excepting the gene *Nn*. So, these are useful for investigating how and to what extent changes occur in various agronomic characters when a covered barley has been converted into the naked type without altering residual genetic constitution. The results obtained with these materials are again shown in Table 7 in a summarized form. This indicates that a change from *N* to *n* was always accompanied by diminution of stem length and elongation of rachis-internode in both line pairs, regardless of location and year. It may be defined therefore that the genes, *N* and *n*, have different pleiotropic effects as such on these characters. However, with respect to those characters other than the above two,

Table 7. A summary of the comparison regarding several agonomic characters

Character & Variety		Kurashiki 1959	Kurashiki 1960 A	Kurashiki 1960 B	Konosu 1960	Kitami 1960	Average
Yield	Haisa	19.4*	−11.8	− 2.7	− 6.4	4.8	0.7
	Donaria	−16.1*	−28.4*	−10.5*	−11.9**	− 3.7	−14.1
Number of Heads	Haisa	21.4**	1.2	15.6**		9.2	11.9
	Donaria	− 6.2	− 2.5	5.1		4.3	0.2
1000 K. W.	Haisa	3.5		− 8.8**		2.8	− 0.8
	Donaria	−13.7**		− 8.7**		− 0.1	− 7.5
Rachis-internode	Haisa	10.1**	6.6**				8.4
	Donaria	5.7*	4.2*				5.0
Stem Length	Haisa	− 2.7	− 1.2	− 5.0**		− 3.2	− 3.0
	Donaria	− 4.2*	− 6.2**	− 2.8*		− 4.3	− 4.4

Increase or dicrease in naked mutants as expressed in percentage of the values of the original covered forms.

magnitude of the covered-naked differences, and even their direction in some cases, varied with the isogenic line pair: Mut. 3041/6a was 14% less productive than A. Donaria, whereas the yield of Mut. 4129 was comparable to that of Haisa. Similarly, the differences in other characters studied were larger in one paired lines, but little in the other pair. It is apparently difficult to explain these inconsistent results simply on the basis of differential pleiotropic effects of the gene, *N* and *n*. Some other cause or causes must have been involved in the phenomenon. In this connection, it is pointed out from the results in Table 7 that we are dealing with differences in quantitative characters so small as to be modified and often to become indiscernible by environmental as well as genetical effects. A thought that environment has favored either covered or naked type may, however, be ruled out, because our experiment has shown that interaction between location and genotype was insignificantly small. Another possible cause that may account for the differences in various characters between two isogenic pairs will then be the differential interactions of the alleles, *N* and *n*, with different genetic backgrounds: that is to say, the phenotypic effects of *nn* plus a certain gene complex, say A, are almost the same as that of *NN* plus the same gene complex A, whereas another genotype with *nn* plus gene complex B is less favorable than that with *NN* plus B. Such a phenomenon seems to be not rare. In fact, one of the writers has exemplified this in barley using a number of *Uzuz* isogenic line pairs (Takahashi *et al.* 1961).

It may be concluded from the results that, as far as these materials are concerned, naked barley is inferior to the covered one in yield, kernel weight and stem length, but it produces more heads with longer rachis-internodes, and its straw is more flexible and unbreakable than the covered barley. However, the differences between the covered and naked types in respect to these characters are mostly small, and sometimes become indiscernible on account of the interaction of the genetic background and the gene, *Nn*. A converse statement of the above words will constitute an answer, though of course tentative, for the question raised in the beginning of this paper. It may be represented as such that the covered form is intrinsically no less better in productivity and some other agronomic characters than the naked barley even in western Japan wherein naked barley has customarily been grown exclusively. It must be admitted that the materials used are only two pairs of isogenic lines, and moreover, they are of foreign origin. Naturally, final conclusion requires further studies of this kind with more materials that are adaptive to our growing conditions.

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