A STUDY OF CULTIVATED BARLEYS FROM NEPAL HIMALAYA AND NORTH INDIA WITH SPECIAL REFERENCE TO THEIR PHYLOGENETIC DIFFERENTIATION

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I. INTRODUCTION

Since Nepal had been isolated from outside by a high mountain barrier and also by her national policy, actual situation of agriculture and the crops in Nepal Himalaya had only been known fragmentarily until recent time. Nakao (1956) is the first who has made an extensive collection of barley samples in this region and studied their morphological characteristics in detail. According to him, as many as thirty five varieties representing different combinations of several endemic morphological characteristics were found within this narrow region, which could be grouped into Indian, Himalayan and Tibetan types. The Indian type barley occurred mostly in the southern foot of Himalayan mountain ranges below 1,000 m, the Himalayan type in the central region at altitude of 1,000 to 2,500 m and the Tibetan type at localities above 2,500 m in the northeastern part of Nepal. Stimulated by Vavilov's classical work (1926) which has demonstrated that East Asia is one of the centers of diversity of cultivated barley forms, research workers began to take especial interest in the barley forms distributed in the high mountainous regions of eastern Asia, including Tibet and Nepal. Åberg (1940) made a close study of the barley materials collected in 1934-35 by H. Smith in the region around Tachenlu of eastern Tibet (now included in Szechwan Province, China). Subsequently Freisleben (1943) and Brücher and Åberg (1950) disclosed characteristics of the barley forms endemic to southern Tibet and Sikkim, materials of which were collected by Dr. E. Schäfer-Expedition in 1938-39. These efforts were rewarded not only with detailed information about the nature and variation of Tibetan cultivated barleys, but also with the discovery of *Hordeum agriocrithon* E. Åberg, a six-rowed, brittle, covered barley distributing in Taofu (Szechwan), Lhasa, and Sikkim (Åberg 1938, Freisleben 1943, Brücher and Åberg 1950 and Schiemann 1951).

In an expatiation of Vavilov's work, the present writers have been working on barley extensively and in 1955 attained to a tentative conclusion that there are two types of cultivated barley, Oriental and Occidental, each of which is characterized by a number of characters or genes endemic to the respective regions and further that there might be the border of the geographical distribution of these two types in the region near Nepal and India. In 1956 we received from Dr. Nakao 229 head samples of the Nepalese barley from his collection. In addition, a number of seed or head samples of Nepalese and Indian barleys were given to us by Mr. Yaichi Hotta and Mr. Guru Dayal Pershad. These materials have since been grown in our experimental field for more than ten years and subjected to morphological, physiological and genetical studies. The results so far obtained will be presented in this paper.

II. MATERIALS AND METHOD

A total of 290 strains of Nepalese and Indian barleys were used in this investigation. They are as follows:

Nakao's collection: 229 head samples from Nepal Himalaya with one exception which was obtained in Muzaffarpur, Bihar State, India. Received in 1956.

Hotta's collection: 17 head samples from Sipche and Philem located in the upper basin of the river Buri Gandaki, central Nepal. Received in 1954.

Pershad's collection: 14 seed samples from foothill of Nepal Himalaya and 30 seed samples from five northern States of India. Received in 1953 and 1954.

All of these materials had been grown every year in the experimental field of the Ohara Institute at Kurashiki, south-western Japan before 1957, but thereafter they were subdivided into three groups and grown in a three-year cycle. The seeds were generally sown in mid-November and cultured by the conventional method. Records were repeatedly taken at the field for the following characters: growth type of seedling, presence or absence of hairs on lower leaf-sheaths and also pig-

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ment and its shade of various plant parts, head type and time of heading and harvest. Stem length was measured in 1957 at their maturity. Detailed observation and/or measurements were made after harvest regarding the several head characters, such as lengths of rachis internode (spike density), spike length, awn lengths of the central spikelet on middle and lateral rows, hairs on and length of empty glumes, hair types of rachilla, color of caryopsis, etc. Some of the physiological and genetical characters were investigated using specially prepared materials, mostly under the controlled growing conditions, the details of which will be stated in the respective paragraphs.

III. CLASSIFICATION OF VARIETIES AND THEIR GEOGRAPHICAL DISTRIBUTION

As Nakao (1956) classified his Nepalese materials after the morphological system by Mansfeld, the same system was adopted for the classification of our materials in order to compare ours with Nakao's result. This system proposed to embrace all the cultivated barley forms in a single species, *Hordeum vulgare* L. s. l. and then subdivide them into the following five convars: (1) *hexastichon*(L.) Alef. s. l. (2) *intermedium* (Körn.) Mansf. (3) *distichon* Alef. s. l. (4) *deficiens* Alef. s. l. and (5) *labile* (Schiemann) Mansf. The development and fertility of the lateral spikelets, which are known to be determined by multiple alleles on *V*-locus, with the exception of *labile* type, are the main characteristics that differentiate these convars. Under each of these convars, varieties are further classified according to the differences in combinations of the following characteristics of spike and kernels: covered and naked kernel, spike density, awn length or development and site of trifurcate appendages on lemma, awn dentation, length of empty glumes, color of lemma, awn and kernels, etc.

Table 1 gives the varieties identified and number of samples of each variety, found among our Nepalese and Indian samples, together with the places of collection and their altitude. The diagnostic characteristics of these varieties are shown in Appendix 1 and a map showing the places of collection in Fig. 1.

As the matter of course, the results presented in Table 1 accord well with Nakao's results published in 1956. Namely, Nepalese and Indian barleys are wholly consisted of the varieties belonging to either convar. *hexastichon* (L.) Alef. s. l. or convar. *intermedium* (Körn.) Mansf., and no varieties of three other convars were found in these regions. Moreover, 28 out of the 35 varieties listed in Nakao's paper were found among our Nepalese materials. The remaining seven varieties were, we suppose, rare in his collection and hence not sent to us.

It must be mentioned, however, that our Nepalese materials included the following six varieties which were not listed in Nakao's paper.

1) Convar. *hexastichon* (L.) Alef. s. l. var. *violaceum* Körn.: This is almost the same as var. *coelesta* as to head and awn structure, but has deeply purple colored chaff and kernels. Places of collection of this type are Chame, Thonje, Gho and Ngyak in Nepal.

	State					Com	Co	six-	rowe ker	ed be nel	arley								
Country or Region NORTH	(India) or locality (Nepal)	(India) or locality	(India) or locality	(India) or locality	(India) or locality	(India) or locality	Altitude (m)	hybernum	breviaristatum	coerulescens	nigrum	parallelum	collinum	hypatherum	nepalense	nigrihypatherum	ullerense	subhy patherum	horsfordianum
NORTH INDIA NEPAL	Bombay Rajasthan Punjab Uttar Pradesh Bihar Unknown		1 	11111	372433	111111			11111		111111								
Lowland	Terai Trisuli Bazar Birkna Camp Macha Khola Kakani Katmandu	600 720 800 1000 2075 1338		11111	1 4 2 5	111111			1 1 1			3 2	1 2 1 2						
Upper Kali Gandaki basin	Phalatey Ulleri Yangebashi Sikha Lumley Ghara Dhumpu Tukucha Jomosom Kagbeni	2302 2019 1138 2031 1586 1821 2422 2554 2707 2798	2 2 2 1 1	111111111111	 1 3 1 1 -		2				2	5 1							
Mid-mountain and Upper Marsyandi basin	Annapurna B. C. Pisang Tilman Camp Chame Thangia Zaganim Thonje Gho Bimtakothi	3500 3084 2800 2641 2615 2600 2023 2512 3539	2 1 1 2 2 3	1 1 1 1	2 2 1					 2 				1 1					
Upper Buri Gandaki basin	Sama Lih Dhanra Prok Tsumje Thomje Sipche Philem Ngyak Keronja Unknown	3396 2907 2300 3132 2550 2600 2600 2200 2000 2029 —			2				s			2							
	Total		31	7	46	2	5	2	7	3	2	13	8	1					

Geographical distribution of thirty four barley

varieties in North India and Nepal Himalaya

1

		Com	mon Na	six- aked	rowe	ad ba	urley			Ir	Cov	ered	um ker	barle	ey	In	term Na	ediu ked	im b keri	arle	у
coelesta	violaceum	asiaticum	tibetanum	revelatum	hangaicum	nudipyramidatum	ankoberense	trifurcatum	pisangense	montanum	harlani	japonicum	nana-prasadii	tonsum	ni grichinense	nudimontanum	nudini pponicum	nudicapitatum	cornutum	philemense	boteanum
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2 1 1 2 2	1111	1111	111		111			111	111	1111	111			111		111			111		111
2	11	_			2			1		-	22			11	=		_	11			-
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5	1						111	3		111	3		111	111		3	1 2 2	1 1	1 1		
1	11	11	2 1	-	-	_	-		_	-	-	-		-	_	-	2		11		5
2																	2	1			52
1	1			1111	1111	1111	1111		1			1 1	1111			$\frac{1}{4}$	4	1111	1111	1	2
37	4	11	4	3	2	2	1	8	1	5	18	6	1	4	2	13	15	4	1	1	20

2) Convar. *hexastichon* (L.) Alef. s. l. var. *hangaicum* (Vav. et Orl.) Mansf. : This is almost similar to var. *violaceum* Körn. as to the structure of head and awn, and also color of lemma and kernels, but the rachis internode length is somewhat shorter (2.7 mm) than the above listed var. *violaceum* (3.4 mm). Two samples of this type were found among the collection at Pisang in mid-mountain region of Nepal.

3) Convar. *hexastichon* (L.) Alef. s. l. var. *asiaticum* (Vav.) Mansf.: This is a lax-eared, short-awned, naked form or may be called as naked type of var. *breviaristatum* (Vav.) Mansf. This is not found among Nakao's collection, but is a major component of the samples collected by Hotta at Sipche in the upper basin of the river Buri Gandaki.

4) Convar. *hexastichon* (L.) Alef. s. l. var. *collinum* R. Takahashi var. nova.: Rachis tough, ear dense, rachis internode about 2.5 mm in length, glume narrow and linear lanceolate, awn long with dentation, color of ear bluish grey, kernel covered, aleurone green. This was found among the samples from Ulleri.

5) Convar. *hexastichon* (L.) Alef. s. l. var. *nigrihypatherum* R. Takahashi var. nova.: Rachis tough, ear dense, rachis internode about 2.6 mm in length, glume narrow, awn short with dentation, kernel covered, color of ear and awn black, kernel black. Two samples were found among the materials from Ulleri.

6) Convar. *intermedium* (Körn.) Mansf. var. *philemense* R. Takahashi var. nova.: This is a lax-eared form of var. *boteanum* Nakao, namely, spikelets in triplets, all the flowers fertile, ear lax, rachis internode 3.0 mm in length, trifurcate appendages (hoods) attached to lemma awns longer than 1 cm in the central row and almost awnless in the lateral rows, glume narrow, kernel naked, color of ear and awn yellow. This was found among the collection at Philem in the upper basin of Buri Gandaki (Hotta's collection).

Geographical distribution of these varieties in Nepal and India is not haphazard. As is already pointed out by Nakao (1956) and recognizable also in Table 1 which is prepared from our result, the following four regions of central Nepal and North India are each occupied by different groups of varieties.

North India: Varietal composition of North Indian barley is rather simple; the principal forms are var. *coerulescens* and var. *hybernum*, which may be called true Indian type.

Lowland Nepal: In the southern foot area of Himalayan ranges in central Nepal, mostly less than 1,000 m high, are found the common six-rowed, covered forms only. About one half of them look like the Indian type and the remaining are the dense eared forms with long or short awns, such as *parallelum*, *hypatherum*, *ullerense* or *subhypatherum*. Thus, the varieties in this region are somewhat different from those found in North India, although Nakao (1956) has maintained that this region is solely occupied by the Indian type barley.

Kali Gandaki basin : Going upstream Kali Gandaki, we enter the region of a diversity of covered barley forms, wherein a number of varieties belonging to convar. *intermedium* appear besides those of convar. *hexastichon*. Naked varieties are

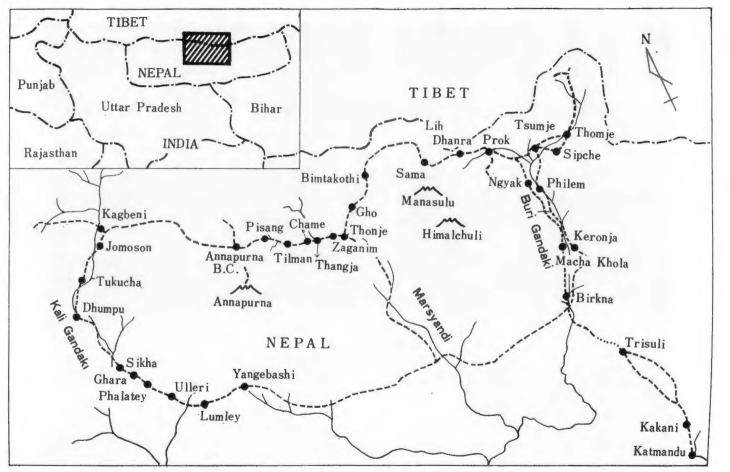


Fig. 1. A map showing the places of collection of barley samples in central Nepal and the northern States of India



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still not so many in this region, however.

Buri Gandaki basin: Covered varieties are rarely met with in this region, and instead, there appear multifarious naked varieties of both convar. *hexastichon* and convar. *intermedium*. These naked varieties were named by Nakao as Tibetan type.

Marsyandi basin: As is seen in Fig. 1, upper basin of Marsyandi river is the region lying between upper basins of Kali Gandaki and Buri Gandaki so that a large number of varieties, both covered and naked, occur altogether. Most of the varieties distributing in central Nepal, excepting Indian type varieties, are accessible in this narrow region.

IV. INVESTIGATION OF THE INDIVIDUAL MORPHOLOGICAL CHARACTERS

Nepalese barleys include a number of peculiar characters of practical as well as genetical interest, of which Nakao (1956) has already made brief comments In order to supplement Nakao's remarks and to elucidate the feature of Nepalese barleys, variation, genetics and geographical distribution of some of these characters have been studied in some more details. The results will be given below.

1. Intermedium or Laterally Awnless Character

The *intermedium* barley of both covered and naked types occurs abundantly in Nepal. All of them are of six-rowed type whose lateral spikelets are entirely lacking their awns, but nevertheless are completely fertile. As to the length of awns on central florets they are considerably variable and can be classified into three types, long-awned $(150 \sim 80 \text{ mm})$, short-awned $(65 \sim 20 \text{ mm})$ and almost awnless (less than 20 mm) (Figs. 3 and 4). It is interesting to note that the naked *intermedium* barleys are markedly different from the covered ones in the length of central awns or lemma appendages : all the naked barleys we received from Nakao are of long-awned type, though Nakao (1956) found a few short-awned forms such as var. *nudicapitatum* and *nudinipponicum*. Besides these, hooded *intermedium* barleys with naked kernels, such as *cornutum*, *boteanum* and *philemense* are also not rare. On the contrary, the majority of the covered *intermedium* barleys are short-awned or awnless in central row of spikelets, and long-awned forms occur infrequently.

Genetics of the fertile *intermedium* character was studied by many authors. According to Syakudo (1947), there are five alleles on a single locus designated I by him where i is the allele for normal awn development and four others, I_1 to I_4 , all incompletely dominant over i, are those having different diminishing effect upon the awn lengths of central as well as lateral florets as shown in the following. We have not yet tried to identify the genes involved in the Nepalese *intermedium* barleys, but it seems as possible to infer that the long-awned *intermedium* forms might have I_3I_3 gene in common and the short-awned and awnless forms have the genes I_3I_8 and I_4I_4 , respectively, if no other gene or genes to diminish the awn

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Alleles	Reduction of awn length (mm) in						
(homozygous)	Central row	Lateral rows					
 I_1I_1	0.164	2.514					
I_2I_2	1.912	12.892					
$I_{3}I_{3}$	4.536	11.630					
I4I4	13.230	12.077					

length are included togeher in their genotypes.

2. Hooded Character

A glance at Table 1 reveals that the hooded barleys occur frequently in Nepal. The same table also shows that, with one exception of var. *horsfordianum*, all the hooded barleys are of naked type distributing upper basin of the rivers Marsyandi and Buri Gandaki. As the hooded barley is known to occur very rarely in the other parts of the world except Tibet and central China, above-stated facts naturally lead us to a supposition that this character might have arisen in the naked barley in the high altitudinal region of Nepal or its neighboring region, Tibet. And, this view may be supported, though in part, by the evidence provided by Suneson and Stevens (1957) that the hooded type is favorable only in the high mountainous places, but definitely inferior in productivity to the normal, awned type in the lower places.

Nepalese hooded barleys are seemingly multifarious. Nakao (1956) classified them into four types: the normal, elevated, subjacent and knot-like hooded ones, according to the development and site of the lemma appendages (see Fig. 5). Among them the normal or sessile hooded type is the commonest, and the three others are not so frequent.

It is interesting and useful for the varietal classification to know what kinds of genes are responsible for these different hooded types. As is well-known, the normal or sessile hood is governed by a gene, K, which is completely dominant over k for long awn. There are, it seems, some genes that modify the effect of K, resulting in elevated or subjacent-like hood in the presence of K, inasmuch as such modified forms have often appeared in the segregating generations of the crosses between the normal hooded and long-awned varieties. Takahashi *et al.* (1953) have shown that K^e and sk are responsible for the elevated and subjacent hoods, respectively, and that K^e is allelic to K and semidominant over k for long awn, while sk is independent of K-series and completely recessive to Sk for long awned condition. Further, it has been demonstrated that there are a number of modifiers for K^e , which markedly arrest the development of hood-like appendage and, when accumulated, reduce the appendage to a tiny knot or projection attached near the top of long awn (Takahashi and Hayashi 1956).

Two series of genetic experiments were carried out. One was to determine whether the subjacent-like forms have the gene sk or not. Five crosses were made



Fig. 3. Three awned types of intermedium barley: almost awnless(left), short awned (middle) and long awned (right).

- Fig. 4. Spikes of intermedium barley differing in density.
 Left: very dense (var. dundar-beyi from Japan)
 middle: dense (var. nana-prasadii)
 right: lax (var. tonsum)



Fig. 5. Hooded spikes.

Left: intermedium barley with elevated hoods (var. *philemense*) Three others: normal hooded spikes differing in the site of hoods (var. *trifurcatum*).



Fig. 6. Variable expression of lemma appendages with years in var. *boteanum*, an elevated hooded, intermedium barley. between the subjacent-hood-like strains, 1498, 1511, 1604, 1606 and 1620, and a long awned form, Natsudaikon-mugi. The F_1 plants resulted from these crosses were found to develop, without exception, normal hood. This suggested that all these forms tested had no sk gene, but a dominant normal hood gene, K, in common, together with some modifiers having effects of lowering the site of hood. The second experiment aimed to identify the hooded gene involved in a group of strains of var. *boteanum*. Judging from their appearance of heads, it is almost certain that they belong to convar. *intermedium* and have some certain kind of gene for hood. But the expression of hooded character in the central row is considerably irregular and moreover it varies from head to head and from year to year (Fig. 6). Four crosses were made between the representative strains of var. *boteanum*, 1391, 1645, 1647 and 1650, and a long-awned, six-rowed variety, Natsudaikon-mugi, and the segregation in F_2 generation of the hooded and awned characters was investigated. The result, shown in Table 2, indicates that the

			TABLE			
Segregation of between four				awn characte a long awned		
Vatsudaikon-mugi crossed by	Elevated hood (A)	Long awn(B)	A/B	Total	χ^2	Р
1391	141	59	2.39	200	2.1600	.21
1645	161	75	2.15	236	5.7853	<.02
1647	89	37	2.41	126	1.2804	.32
1650	210	78	2.69	288	0.6667	.53
Total	601	249	2.41	850	9.8924	•••••
		d. f.	χ^2	Р		
Sum of the 4 x	(2's	4	9.8924	.0502		
Pooled χ^2		1	8.3592	<. 01		
Heterogeneity		3	1.5332	.75		

elevated and long-awned characters are governed by a single gene pair, the elevated hood being dominant over the long awn. A close analysis of the data discloses however a general tendency of segregating elevated hooded plants slightly less than expectation, which suggests incomplete expressivity of the gene for hooded character presumably in heterozygous condition. It must be mentioned also that among the "elevated hooded" segregants there were observed a series of markedly different expression of hooded character, ranging from typical elevated to tiny knoted-awn types. These situations are just the same as was observed in the F_2 and later generations of a number of crosses with Chengchou-5 which has been demonstrated to have a gene, K^e , for the elevated hood (Takahashi *et al.* 1953 and 1956). It seems appropriate to conceive that these Nepalese strains of var. *boteanum* may also have the same gene, K^e , in common.

3. Short Awn

Vavilov (1926) is the first to point out that the short-awned forms of barley are concentrated in the South-East Asian gene center of barley, including China and Japan. Freisleben (1940) was in success to demarcate the region of the shortawned barley, indicating that the short-awned naked barleys are distributed in the regions of upper basin of Yangtse river, Nepal and North India (Almora and Dehri districts), and the short-awned covered barleys are found in the regions of southern foothills of Himalayas and Hindukush, but neither of them can be found in the west thereof.

As seen in Table 3, which represents the result in Table 1 in a simpler form,

TABLE 3

Frequencies of strains with different lemma appendages in different parts of Nepal and North India. Numerals in parenthesis are cited from Nakao (1956)

		C	onvar. h	exastic	hon			Convar	. inter	rmediu	m
Region		Covere	ed		Nake	d	Cov	ered	Naked		
	Long awn	Short awn	Hooded	Long awn	Short awn	Hooded	Long awn	Short awn	Long awn	Short awn	Hooded
North India	29		-	1		-			1		
Nepal lowland	16 (192)	14 (24)	-	-	-	-	-	-	-	-	-
Kali Gandaki basin	12 (142)	13 (222)		13 (200)	_	0 (8)	2 (5)	14 (245)	0 (2)	0 (64)	6 (10)
Marsyandi basin	18 (292)	6 (53)	(¹ ₂)	26 (975)		7 (233)	2 (1)	12 (136)	15 (76)	_	2 (1)
Buri Gandaki basin	5 (15)	4 (8)	_	10 (603)	11 (0)		(9)	3 (0)	10 (76)	=	15 (66)
Others	5	4	-	3	-	1	1	1	6	-	-
Total	85 (641)	41 (307)	1 (2)	53 (1778)	11 (0)	8 (291)	6 (15)	30 (381)	32 (154)	0 (64)	23 (77)

the short-awned barleys are widely distributed over the central Nepal, just as Freisleben has pointed out. It is worthy to note that this character is principally carried by the covered barley only (var. *breviaristatum*, *hypatherum*, *ullerense* and others), but very rarely by the naked forms, with one exception of var. *asiaticum* found only in Sipche. This is a situation quite similar to that found among the *intermedium* barleys. Should we consider these as a mere coincidence, or as the consequence of adaptive differentiation? The solution is certainly an interesting future problem.

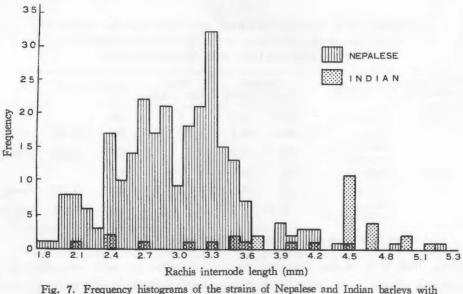
Inheritance of the short-awn character of the Nepalese barleys was not studied so closely. The only information hitherto obtained is that the short-awn

98

character of two strains, 1481 and 1672, was inherited as simple recessive to the long awned condition.

4. Ear Density

Ear density has long received serious consideration and discussion from barley taxonomists. Some authors separate the varieties into two classes, lax and dense, while some others into three classes, lax, dense and very dense. In the classification of ear density types, visual inspection of the overlapping of the lateral kernels or measurement of the average rachis-internode length are carried out, and in the latter case the following criterion is generally applied : lax = longer than 2.8 mm; dense = $2.8 \sim 2.2$ mm and very dense = shorter than 2.2 mm (see Fig. 4). In this study, both methods were applied for the classification of the strains. Fig. 7 shows variation histogram of the Nepalese and Indian barleys regarding the rachis-internode length.



rig. 7. Frequency histograms of the strains of Nepalese and Indian barleys corresponding rachis internode lengths.

Aberg and Wiebe (1945) are of opinion that this character has only a limited taxonomic value, because density measurements vary from spike to spike, year to year and place to place. Another weak point as a taxonomic character is, as was pointed out by some authors, the continuous nature of varietal variation of rachis internode lengths. This may probably due in part to the fact that rachis internode length is governed by a number of major and minor genes with different effects upon this character. For these reasons, we sometimes encountered difficulties in sorting the strains into three definite classes, which is required for Mansfeld's classification system.

In spite of these difficulties in density determination, it is possible to say

without hesitation from Fig. 7 that Nepalese and Indian barleys are exceedingly variable as to the spike density, ranging from 1.9 to 5.2 mm in rachis-internode length, and further that India is rich in forms with very lax spikes, while Nepal is abundant in varieties with dense or very dense spikes. It seems that the extreme laxness of spikes, accompanied by slender kernels, in Indian barleys results in the complete exposure of the considerably long empty glumes from the kernels of the lateral rows, and this gives us such an impression that Indian barleys are characterized by the markedly protruded empty glumes from the lateral kernel rows, and thereby easily distinguished from the barleys of similar ear types from Nepal and the other parts of the world.

Inheritance of the lax vs. dense spike character pair and its relation to the covered vs. naked character pair was studied using two crosses of naked, dense strains, 1645 and 1647, both belonging to var. *boteanum*, with a covered, lax variety, Natsudaikon-mugi. The F₂ segregation data, presented in Table 4, clearly

TABLE 4

	ionships be d kernel cl							75.
		1645 and				-		
tsudaikon-mugi	Items	Cov	reed		ked	Total	χ^2	D
crossed with	Items	Lax	Dense	Lax	Dense	Total	, X*	r

Natsudaikon-n		Cov	ered	Na	ked	Total	χ^2	P
crossed with	h	Lax	Dense	Lax	Dense	Total	, X-	r
1645	Observed no.	168	8	6	50	232		
	Calc. on 9:3:3:1	130.5	43.5	43.5	14.5	232	158.988	small
	Calc. on 6.38% recombination	166.7	7.3	7.3	50.7	232	0.318	. 98 95
1647	Observed no.	87	10	7	24	128		
	Calc. on 9:3:3:1	72	24	24	8	128	55.333	small
	Calc. on 14.01% recombination	87.7	8.3	8.3	23.7	128	0.561	. 95 9

A weighted, average recombination value=9.16±6.0909 (%)

indicate that both of the character pairs in question are each controlled by a single pair of gene, and they are not independently inherited. Excessive parental types suggest a close linkage between them. The recombination values, calculated from these data by Immer's product method, were 14.01 and 6.38 per cent, respectively. Although the discrepancy between these two values was somewhat large, a weighted, average values was claculated, which was 9.2 per cent. It is interesting to note that the linkage value found here is very close to 9.38 per cent that was obtained in the experiment with a number of Japanese dense spike varieties (Takahashi *et al.* 1953), which fact leads to a speculation that the same gene for dense spike might be distributed in Nepal and Japan.

5. Color of Caryopsis

As to the color of caryopsis, Indian and Nepalese strains can be classified into

four types, blue, black, purple and white colored. Blue or green kernel, due to anthocyanin in aleurone layer, is most common among our materials. This character is known to be governed by a dominant gene, Bl, in general, but color expression is not so simple. It varies with variety and environment, from dark blue to light green. If weathered severely, light green one is hardly distinguished from the white one, especially in covered forms. For these reasons, this character is not regarded as a good taxonomic character. Repeated observations before and after maturity have revealed that majority parts of Indian barley strains and about two fifths of the Nepalese covered barleys have blue aleurone kernel, while the naked barleys are all white with only a few exceptions.

Anthocyanin in pericarp and hull appears as red color. Depth and shade of red color in barley caryopsis differ considerably with varieties. Red color in lemma nerves is more or less conspicuous for sometimes after heading, but fades out at maturity. Only the deepest purple color of lemma and kernel is generally used as a taxonomic character. Several samples of the naked forms with violet kernels could be found among the Nepalese materials (var. *violaceum* and var. *hangaicum*), which were almost similar to those found in Tibetan materials received from Åberg.

As pointed out by Åberg and Wiebe (1946), black color of caryopsis, due to a melanin-like substance, is most conspicuous and unfading among others, and useful for classification. Several varieties with black caryopsis have been collected by Nakao in Nepal. According to him, a naked variety, *tibetanum*, was met with most frequently in the upper basin of Buri Gandaki river. Several covered varieties with black caryopsis occurred also, though not so frequently as *tibetanum*, in Nepal. They are *nigrum*, *nepalense*, *nigrihypatherum*, of convar. *hexastichon*, and *nana-prasadii* and *nigrichinense* of convar. *intermedium*.

6. Hairs on Rachilla Surface

It is well-known that there are two types of hairs, long and short, on the rachilla surface among the cultivated barley varieties, which are conditioned by a single pair of gene, Ss, the long haired one being dominant over the short-haired condition. One of the writers, Takahashi (1955), has confirmed that the short-haired rachilla is found only in the "Occidental region", while the long-haired rachilla is distributed world-wide. In this investigation, it was found that almost all of the Nepalese and Indian barley strains are characterized by the long-haired rachilla, and only eight strains have the short-haired rachilla. Among the latter type strains six are from Bimtakothi, Thonje, Pisang and Annapurna Base Camp in upper basin of Marsyandi river in Nepal and two are from India.

7. Uzu or Semi-brachytic Growth

Nakao (1956) has maintained in his paper that all the strains of var. boteanum and the majority parts of the strains of var. nudicongestum can be regarded as uzu or semi-brachytic type on the basis of the similarity to uzu in a few characteristics of their adult plant. With some reasons, however, we could hardly agree with his opinion and hence thought as necessary to ascertain the truth.

As was shown before (Takahashi 1942), one of the most conspicuous characters distinguishing the uzu from the normal is a markedly short coleoptile afforded with a peculiar notch and/or a tiny projection near its top. The first leaf is also markedly shorter and darker green colored in general. Firstly, therefore, the coleoptile lengths and seedling heights were compared between sixteen strains of var. *boteanum* and some typical normal and uzu type varieties, chiefly from Japan. The seedlings were grown at 25°C in an incubator made of glass and the measurements were made 10 days after sowing. The results were that these Nepalese strains are almost the same in both the mean lengths of coleoptile and plant height as the normal varieties, but were about 11 mm for coleoptile length and 35 mm for seedling height longer than the means of the uzu varieties. Moreover, no seedling characteristics peculiar to the uzu form was exhibited by these Nepalese strains.

Another information about the nature of these Nepalese strains was obtained by a genetic experiment made with the use of the F_2 hybrids of these Nepalese strains crossed to both the normal type varieties (Hayakiso No. 2 and Natsudaikonmugi) and the uzu type variety (Sakigake). Namely, segregation of the normal

Crosses	$\overline{\mathbf{P}}$ (Nepal barley)	P (Japan var.)	\overline{F}_2	Normal & uzu
Nepalese ba	urleys $ imes$ normal var.			
1391×H*	32.9±2.0788	39.3±3.8364	36.4±4.0731	
1645×H	32.6±2.5418	"	36.0±3.6038	No segregation
1387×N*	34.2±2.3947	36.5±1.6053	33.9±3.3706	of
1627×N	38.6±2.6479	"	33.0 ± 2.5495	uzu type plant
1646×N	32.5±2.1699	"	31.3±3.7188	
Nepalese ba	rleys × uzu var. (Se	akigake)		
1646×S*	32.5±2.1699	22.7±2.1718	31.1±11.4316	{Norm. 34.0±3.1950 {Uzu 18.7±2.0544
1626×S	39.4±3.1479	"	30.1± 8.1327	$\begin{cases} Norm. 34.6 \pm 3.6483 \\ Uzu & 18.5 \pm 3.5523 \end{cases}$
1647×S	35.6±2.0445	"	32.6± 7.5048	{Norm. 36.2±3.7768 {Uzu 20.8±2.8323
1650×S	35.4±2.8719	"	32.2± 7.8112	$\begin{cases} Norm. 36.9 \pm 3.4696 \\ Uzu & 20.6 \pm 2.3546 \end{cases}$
1648×S	34.5±2.5525	"	30.8±10.5280	

TABLE 5

Coleoptile lengths of the F₂ plants from the crosses of Nepalese barleys (*boteanum*) with two normal or uzu varieties, together

with those of their parents

*H=Hayakiso No.2; N=Natsudaikon-mugi; S=Sakigake

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and uzu type plants in a 3:1 ratio was confirmed only in those crosses with the Japanese uzu variety, while the crosses with the normal varieties gave the normal type seedlings only. The cross combinations and the coleoptile lengths of the F₂ plants and their parents are given in Table 5, in which special attention is called to the fact that the standard deviation of the coleoptile length is much larger in the crosses with the uzu variety than in the crosses with the normal varieties, because of the segregation of the uzu type plants with much shorter coleoptile in the former crosses only. Thus, all evidence obtained here points to the fact that presumably all the strains of var. *boteanum* in Nepal are not of the uzu type, but are of the normal type.

8. Some Other Morphological Characters

Empty glume length: As to the size and shape of the empty glume, all the strains in India and Nepal are not so much different and hence can be said to be normal. Not a single strain with so-called wide glumes could be found. As pointed out before, Indian barleys are for the most part characterized by somewhat longer glumes conspicuously protruding out from the lateral kernels rows.

Distribution of hairs on the glumes: Åberg and Wiebe (1946) classified barley varieties into four types as to the distribution of hairs on the glumes, namely, covered, band, midline and no hairs. Observation of the character in question of Indian and Nepalese barleys revealed that the majority of these strains have glume hairs running in narrow to wide band. Barley strains with glumes covered by hairs or those with glume hairs in line were not so frequent. There was no appreciable difference as to this character between the covered and naked barleys in these regions.

Waxy endosperm: Glutinous or waxy barleys are known to exist, though rarely, in East Asiatic region, including Korea, Japan and probably China Proper. In order to know whether this character is extending to Nepal and India, an iodine test was made with the kernels of all the strains in these regions. The effort was in vain; not a single strain with waxy endosperm was found among the samples tested.

Hairs on lower leaf-sheaths: Nakao (1956) has already reported that all the barleys of his Nepalese collection were, without exception, hairless on their lower leaf-sheaths, and this was reconfirmed with our materials from Nepal and India.

Lemma teeth: Distribution of lemma teeth, especially on the lateral nerves, varies with variety, and they can be roughly classed into four: very rough (numerous), rough (several), semi-smooth (a few) and smooth (none). Visual inspection of this character of Nepalese and Indian barleys has revealed that very rough one is rich among the naked forms and those with several lemma teeth are frequent among the covered barleys. There is no strain without teeth or with long hairs on lemma nerves.

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V. PHYSIOLOGICAL CHARACTERISTICS

1. Genotype Analysis of the Nonbrittle Rachis Character

It has already been demonstrated by Takahashi (1955 and later publications) that the cultivated barley has differentiated as to the genetic constitution for the nonbrittle rachis character into two types, type W or $btbtBt_3Bt_3$ and type E or $BtBtbt_2bt_2$, and further that the barleys in the Oriental region consist, with rare exceptions, of type E varieties, while those in the Occidental region include 60~80 per cent type W and 20~40 per cent type E. Because of the close linkage between bt and bt_2 , there is no doubly recessive genotype, $btbtbt_2bt_3$, among the existing cultivated varieties.

More than half of the Nepalese strains and all the Indian barleys were subjected to genotype analysis of this character. The method adopted was as follows: each of the strains was crossed to two kinds of the genotype analysers, known to be of type W and type E, respectively, and the brittleness or toughness of the rachises of the resulting two kinds of F_1 hybrids was tested at their maturity. This test enabled us to determine the genotype of each strain, because if F_1 (W) was tough and F_1 (E) brittle, the strain should be type W, and if the relation was the reverse, it should be type E.

A summarized result is given in Table 6, which indicates that about one half of the strains tested were of type W, and the remaining were of type E. The most conspicuous and interesting feature found in the result is that the covered barleys and the naked barleys are quite different in their genetic constitution for nonbrittle rachis: The naked barleys, mostly concentrated in upper basin of the river Buri Gandaki and mid-mountain region in Nepal, are wholly of type E or Oriental type, while more than 80 per cent of the covered forms in Nepal and India are of type W or Occidental type.

		$=btbtBt_2Bt_2;$	type $E = Bt$.	Btbt ₂ bt ₂	
	Covered	barley	Naked	barley	Total
	type W	type E	type W	type E	Totat
India	27	2	1	1	31
Nepal	61	15	0	73	149
Total	88	17	1	74	180

TABLE 6

The covered and naked barleys in Nepal and India as classified according to their genotypic constitution for nonbrittle rachis, type $W = btbtBt_2Bt_2$: type $E = BtBtbt_2bt_2$

2. Heading Time under Natural Growing Conditions

The Nepalese and Indian barley strains have been sown in the field in Kurashiki, southern Japan, on around 15th of November, every year, since we received them, and their heading dates have been recorded in spring when about eighty

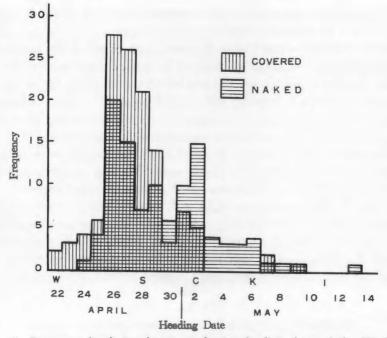


Fig. 8. Frequency distribution histogram showing heading dates of the Nepalese covered and naked barley strains. Five Japanese varieties are shown as the control. W (Wase Hadaka), S (Sekitori), C (Shiro Chinko), K (Kobinkatagi) and I (Iwate Ohmugi). Data obtained in the spring of 1957.

per cent of the heads of each row of the strains had appeared. In Fig. 8 are shown the data obtained in the spring of the year 1957 for the Nepalese covered and naked strains by frequency distribution histograms. For comparison the heading date of the five Japanese commercial varieties, Wase Hadaka (very early), Sekitori (early), Shiro Chinko (medium early), Kobinkatagi (mid-season to late) and Iwate Ohmugi No. 3 (latest) are given in the same figure.

As seen in Fig. 8, variation range of the heading times of the Nepalese strains is roughly in accordance with that of the Japanese cultivars, but it may be said that the Nepalese barley involves comparatively earlier forms more than the Japanese barley. The same figure also indicates clearly that the covered forms chiefly consist of very early to medium early types, and hence are somewhat earlier in an average than the naked ones, which seems to reflect the difference in their distribution areas. The strains from India are still earlier than the Nepalese covered barleys in general.

3. The Grade of Spring (Winter) Habit of Growth and its Regional Difference

The spring and winter habit of growth, and earliness as well, are the characters of ecological importance for winter cereals. A number of studies, made especially by Japanese workers, have revealed that the spring and winter habit of growth are not two discrete, contrasting characters, but there are a continuous

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series of intergrades between the two extremes (Takahashi 1943, Takahashi and Yasuda 1956). By definition, the physiological nature which is generally called the grade of spring (or winter) habit of growth is expressed by the length of period of cold pretreatment (vernalization) required for ready ear formation under long day condition. Practically, however, this can be determined either by sowing seeds of each variety to be tested, together with several standard varieties of known grade of spring habit, in early spring to summer at weekly or ten day intervals or by growing them under the continuous illumination in a greenhouse at moderately high temperature. The criterion in the first test is lateness or earliness of the critical time of sowing to allow the plants normal heading, and that in the second test is earliness of heading time as compared with the standard varieties.

A total of 178 strains from India and Nepal Himalaya were tested for the character by these two methods above-mentioned. The results of these tests were mostly consistent, although a number of strains, mostly of covered forms, which were graded as II by the first test, proved to be intermediate between II and III by the second test. A summarized result is given in Table 7, which indicates that

D. 1	11)	II		II	Ι	IV		V	
Region	Covered	Naked								
Îndia	27		1	1				—		
Nepal lowland	-	-	1*	-	15	-		-		
Kali Gandaki basin	-	2	4+11*	7	6	-	-	-		-
Marsyandi basin	1	6	1+8*	6+2*	10	12				
Buri Gandaki basin	-	13	1*	8+1*	5	5	1	4	-	1
Others(Nepal)	2	2	3	3	6	2			-	-
Total	30	23	9+21*	25+3*	42	19	1	4	0	1

TABLE 7	ABLE	7
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Geographical distribution of the covered and naked strains differing in grade of spring habit

1) I stands for the highest, V for the lowest, and II, III, IV for intergrades of spring habit, respectively.

* The numeral with an asterisk is number of strains which behaved as the intermediate between grade II and III under continuous illumination in a greenhouse, though graded II by the outdoor test in spring.

the strains from India are of highly spring habit (grade I), while the Nepalese strains, both covered and naked, are considerably variable as to this character, with moderately spring habit type (II-III) predominant. There seems to be a slight tendency of becoming lower in the grade of spring habit with the rise of altitude from India to highland Nepal, but in the high altitudinal places highly spring habit type again becomes somewhat numerous. This may be of some interest as an

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example of vertical distribution of barley varieties differing in the grade of spring habit in a low latitudinal region. It may be noted in this connection that in the Northwest India barley is sown in October and harvested in March or April (Watt 1890). According to Kawakita's study (1956) on crop zone in Nepal, Nepalese barley is generally sown in autumn (September to December) and harvested in May to June, but in the places higher than 3200 m it is sown in spring and harvested in autumn.

4. Genetic Analyses of the Spring Barleys

Takahashi and Yasuda (1956 and later publications) from their extensive studies on the genetics of spring and winter habit with more than 200 varieties of different origin have drawn the following conclusion: At least three independent pairs of genes, Shsh, Sh_2sh_2 and Sh_3sh_3 , are responsible for spring vs. winter habit. The genes, sh, Sh_2 and Sh_3 , are for the spring habit and their allelic genes for the winter habit. Since both of the dominant spring genes, Sh_2 and Sh_3 , are epistatic to the dominant winter gene Sh and the recessive spring gene sh is epistatic to both sh_2 and sh_3 for winter habit, only a single genotype $ShShsh_2sh_2sh_3sh_3$ is capable of exhibiting winter habit, while the seven other possible genotypes are expected to be of spring habit. Among the existing spring barley varieties we have so far been successful to find the following five genotypes: 1. $(Sh)Sh_2(sh_3)$, 2. $(Sh)Sh_2Sh_3$, 3. $sh(sh_2sh_3)$, 4. $shSh_2(sh_3)$, 5. $shSh_2Sh_3$, where the gene symbols in parenthesis are for the winter habit. It is also known that differences in the grades of the spring habit are attributable to the different multiple alleles of the dominant spring gene Sh_2 of which the respective varieties possessed.

Among a large number of spring barleys from Nepal and India, eighteen strains have been subjected to genetic analysis. The accession number, place of collection, grade of spring habit, and the genetic constitution as determined by this test, are shown in Table 8. They were all crossed each to any one of the winter barleys listed in the same table. In addition, the majority of them were "three-way" crossed to some certain genotypes for identifying the spring gene involved in them. The hybrid plants, together with their parents, were then grown under continuous illumination in a green house. For all crosses, daily records were taken on a single plant basis for the time of flag-leaf emergence. Presence or absence of hairs on lower leaf-sheaths, if differentiated among the hybrid plants, was investigated also, as the character pair is known to be closely associated with the first spring gene sh.

Table 9 shows interrelationships between spring vs. winter habit and hairy vs. nonhairy sheath character pairs in the F_2 generations of the fifteen crosses. It is evident in the table that the observed counts for spring and winter types fit well to a 3:1 ratio in 13 out of the 15 crosses, and in most cases the spring vs. winter habit has inherited independently of hairy vs. nonhairy sheath character (*Hshs*). The three-way test crosses made for Sipche Nos. 1 and 12 afforded evidence that these two had no recessive spring gene *sh*. The crosses with 1528 and 1604

Strains	Origin	Covered or Naked	Grade of spring habit	Spring gene (si identified
(1) Spring barleys test	ted			
1368	Thonje	naked	II	Sh211
1381	Bimtakothi	"	I	sh(Shs11)*
1393	Gho	"	II	(Sh211)
1409	Thonje	"	I	(Sh_2^{I})
1526	Ngyak	"	II	Shall
1528	Ngyak	"	II	Sh211
1604	Chame	"	II	(Sh211)
1628	Sikha	"	I	(Sh_2^{I})
1632	Sikha	"	II	Sh211
1650	Thomje	"	II	Sh211
1697	Nepal	11	II	(Sh211)
N-5	Nepal	covered	II	Sh211
N-11	Nepal	"	II	Shall
Sipche 11	Sipche	naked	I	Sh21
Sipche 12	Sipche	"	II	Shall
Naked 304	Nepal	"	I	Sh:(Sha)
J. B. S. 21	India	covered	I	sh Sh2 ^I
Pb. T. 4	India	"	I	Sh21
(2) Testers (Spring ty	pe)			
Mensury C (M.C.)	Japan	covered	I	sh
Natsudaikon-mugi	Korea	"	I	sh Sh21
(3) Testers (Winter ty	rpe)			
Sakigake (S)	Japan	covered	IV	Shsh2sh3
Hayakiso No. 2 (H)	Japan	"	IV	"
Taisho-mugi (T)	Japan	"	IV	11

Materials used for the genetic analyses

* The spring gene in parenthesis is not yet genetically identified.

gave a puzzling result, however. The segregation of spring and winter types fitted well to a 13:3 ratio, but not to a 3:1 ratio, suggesting that two spring genes, one dominant and one recessive, were involved. Despite this, the results of the F₃ progeny tests and also χ_1^2 tests of the F₂ data have indicated no recessive spring gene *sh* involved. It may therefore be safe to consider that these 15 spring type strains have each a single dominant gene, presumably either Sh_2 or Sh_3 .

In Table 10 are shown the results of the crosses with Naked 304 from Nepal. The segregation in F_2 of the spring and winter types occurred in a ratio of 15:1, but not in a ratio of 61:3. Furthermore, when the F_1 plants were crossed to Mensury C with $shsh_2sh_8$ genotype, the observed counts fitted to a 3:1 segregation ratio, suggesting no recessive spring gene sh involved. Therefore, it seems reasonable to consider that Naked 304 is possessed of two dominant spring genes, presumably Sh_2 and Sh_3 .

Segregation in F_2 or F_1 generation of the spring and winter type plants in the simple or three-way crosses with 15 strains having single dominant spring gene, and its relation to the hairy-sheath character pair (*Hshs*)

Cross	Sprin	g type	Wint	er type	Total	χ^2 for	
	Hairy	Hairless	Hairy	Hairless	TOLAL	3:1 or 1:1	* X ² _L
1368×S ⁽⁾	:	214	8	4	298	1.615	
1393 × H	163	59	55	16	293	0.092	0.465
1409 ×S	1	196	8	4	280	3.733	
1526 × H	169	57	49	22	297	0.190	0.898
1528×H	152	59	36	8	255	8.158	1.621
1604 × H	168	62	36	17	283	5.938	0.286
1628×H	73	21	29	11	134	1.682	0.401
1632×H	165	50	54	20	289	0.057	0.419
1650 ×S	1	226	6	9	295	0.408	
1697 ×S		148	4	5	193	0.292	
N-5 \times H	135	72	43	16	266	3.133	1.820
N-11×H	163	53	56	25	297	0.818	1.392
Sipche 1×T	:	329	11	.2	441	0.037	
$(Sip. 1 \times T) \times M.C.$		56	5	8	114	0.035*	
Sipche 12×T	3	349	9	4	443	3.378	
$(Sip. 12 \times T) \times M. C.$		59	6	50	119	0.009*	
Pb. T. 4×H	184	53	58	16	311	0.241	0.009

1) S, H, T, and M. C. stand for Sakigake, Hayakiso No. 2, Taisho-mugi and Mensury C, respectively.

TABLE 10

Segregation in F_2 or F_1 generation of the spring and winter type plants in the simple or three-way cross with Naked 304 having two dominant spring genes

Item	Spring type	Winter type	Total	χ^2	Р
Naked 304 × Taisho-mugi		in a start and another			
Observed number	331	26	357		
Calculated on 15:1	334.69	22.31	357.00	0.650	.53
Calculated on 61:3	340.27	16.73	357.00	5.387	small
(Naked 304 × Taisho-mugi)	\times Mensury C				
Observed number	65	28	93		
Calculated on 3:1	69.75	23.25	93.00	1.294	.32
Calculated on 1:1	46.5	46.5	93.0	14.720	small

The crosses with 1381 from Bimtakothi and J. B. S. 21 from Rajasthan State, India, behaved differently from the above-mentioned crosses. Table 11 shows that the observed counts in F₂ of the crosses with 1381 and J B. S. 21 did not fit to a 3:1 calculated ratio, but gave a good fit to a 13:3 ratio, which suggested two spring genes, one dominant and one recessive, being involved in these two strains.

Item	Spring type Winter type		Total	χ^2	Р
1381 × Sakigake					
Observed number	246	42	288		
Calculated on 3:1	216	72	288	large	small
Calculated on 13:3	234	54	288	3.282	. 1 05
J. B. S. 21 $ imes$ Sakigake					
Observed number	349	68	417		
Calculated on 3:1	312.75	104.25	417.00	large	small
Calculated on 13:3	338.81	78.19	417.00	1.635	.32

Segregation in F_2 of the spring and winter type plants in the crosses with two strains having one recessive and one dominant spring genes

An F_s test made with the seeds of 19 winter type plants randomly taken from the F_2 population of the cross with 1381 gave a result to justify the above-mentioned assumption, namely, 9 lines were heterozygous for winter and spring habit. while the remainings bred true to winter habit.

Finally, two series of test crosses were performed in order to know which of the dominant spring genes, Sh_2 or Sh_3 , was involved in the ten strains indicated below. The first series of the crosses were all in the form of $F_1(A \times Sh_2) \times W$ inter variety, and the second ones $F_1(A \times Sh_3) \times W$ inter variety, where A stands for the strains to be tested and Sh_2 and Sh_3 for the genotype analysers having the respective spring genes indicated.

1st series: 1368, 1526, 1528, 1632, 1650, Sipche 1, Sipche 12, N-11, J. B. S. 21, -2nd series: - - - 1960, Sipche 1, Sipche 12, N-11, J. B. S. 21, N-5

In the first series of the three-way crosses involving the Sh_2 , all the hybrid plants of each cross headed almost simultaneously within about one month after sowing under long day. On the other hand, in the second series of crosses involving the Sh_3 , segregation of winter type plants, and the spring type plants as well, was observed. These doubtlessly indicate that all the strains tested are each possessed of a dominant spring gene Sh_2 or its allelic genes, but not Sh_3 .

It is simple to determine what kinds of alleles on Sh_2 locus is involved in the strains tested. If the mean heading date of the spring type F_2 plants just corresponds to that of the standard spring type variety of, say grade II, the gene involved must be Sh_2^{II} . If they headed somewhat earlier, corresponding to the standard variety of grade I, the gene involved must be either sh or Sh_2^{I} or Sh_3 .

5. Reaction to Barley Mildew Races Prevalent in Japan

Disease resistance is the subject of practical as well as scientific interest. Geographical regularities of distribution of different reaction types or of resistant genes are also useful for the insight into the problem of phylogeny of crop plants. In order to contribute to knowledge about these problems, Hiura has investigated the reactions of all the Indian and Nepalese barley strains to the eleven physiologic races of powdery mildew, *Erysiphe graminis hordei*, now prevalent in Japan. Seedlings to be tested were grown in a wooden box, $58 \text{ cm} \times 35 \text{ cm} \times 12 \text{ cm}$, on a greenhouse bench at a temperature of 10° to 25° C. A box contained 15 rows, and each row consisted of 5 plants of each of 3 varieties, making a total of 15 plants in a row. The seedlings were inoculated at their first-leaf stage with conidia of the race to be tested by shaking the heavily-mildewed plants over the seedlings in an inoculation chamber held at a temperature of approximately 17° C. Three days after inoculation, the seedlings were moved to the greenhouse. Notes were taken 7 to 10 days after inoculation. The following criteria were employed for distinguishing reaction types produced on the first leaf of the inoculated seedling.

- R (resistant): No visible signs of infection, or no visible development mycelium even if necrotic spots present.
- M (moderately resistant): Necrotic or chlorotic spots may present, with a slight to moderate development of mycelium.
- S (susceptible): Abundant mycelium and conidia formation. No necrotic spots.

As the results, these strains of barley could be classified into eleven groups that differed each from others in their reactions to the mildew races. Six out of these eleven reaction groups were the same as identified in the previous test made with our world barley collections (Hiura 1960), but the remaining five were those newly found in this test. Table 12 shows reactions of these eleven groups of the barley strains to each of the eleven mildew races, together with the name of type variety representing the respective group or the name of locality or region wherein the strain or group of strains exhibiting the particular reactions are chiefly distributed. In Table 13 are given the frequencies of barley strains of these reaction groups in different parts of India and Nepal.

It is noted in the first place in these two tables that the greater part of the naked forms are highly susceptible to all the races (reaction group 11) with only 10 exceptional strains which belong to reaction group of either A. 222 or Pisang, while about two thirds of the covered forms are resistant to one or more physiologic races. Thus, the covered and naked forms in Nepal and India were known to be distinctly different in the reaction to the Japanese mildew races, just as in the genotypic constitutions for nonbrittle rachis.

Geographical distribution of the barley strains of different reaction groups is a matter of another interest. As seen in Table 13, Indian barleys involve a number of strains exhibiting reaction of "India resistant", Kwan or H. E. S. 4 types, among them the first mentioned type being most frequent. The Nepalese resistant barleys are quite different from those of India : They do not involve any strain of the above-mentioned groups, but are composed of those of the seven other groups. The most frequent among them is the "Himalayan resistant" type which is highly resistant to all the races with the exception of race IX. Its principal distribution area is the upper basins of Kali Gandaki and Marsyandi. The *H. spontaneum nigrum* type strains, which is resistant to all the races, seem to occur, though less

Reactions of the varietal groups of Indian and Nepalese barleys to the eleven Japanese physiologic races of mildew.

-	Varietal group	Reactions to the races indicated									No. of strains			
	Type variety	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Cov.	Naked
1.	H. spont. nigrum	R	R	R	R	R	R	R	R	R	R	R	9	0
2.	Himalayan Res. group (=Russian 74)	R	R	R	R	R	R	R	R	S	R	R	60	0
3.	A. 222	М	Μ	M	М	М	М	М	М	S	Μ	М	8	3
4.	Kwan, C. I. 1016	М	М	М	м	М	М	М	м	М	М	М	1	0
5.	Hanna, C. I. 906	S	S	S	S	S	S	S	S	R	S	S	5	0
6.	H.E.S. 4	R	S	R	S	R	R	S	S	S	R	R	2	0
7.	Keronja group	S	S	М	S	S	M	S	М	S	Μ	м	6	0
8.	Pisang group	S	S	S	S	S	S	S	R	S	S	S	3	7
9.	Kakani	Μ	М	S	Μ	М	М	S	Μ	M	Μ	S	1	0
10.	Indian Res. group	М	М	М	S	М	S	М	R	S	М	M	9	0
11.	Susceptible	S	S	S	S	S	S	S	S	S	S	S	59	117

TABLE 13

Geographical distribution in India and Nepal of the barley strains of eleven reaction groups

Reaction type Region	10 Indian	4 Kwan	6 HES.4	5 Hanna	1 Spont.	2 Himal.	3 A.222	7 Keronja	8 Pisang	9 Kakani	11 Suscept.
India	5			-		-	(1)		-		16(1)
India (others)	4	1	2	-			-	-	-	_	1
Nepal Lowland		·······			_	1	6	—		1	22
Kali Gandaki			-		2	27	-		2		10(19)
Marsyandi	_		-	_	7	29	1(2) —	(3)	-	2(45)
Buri Gandaki	-	_	-		_	3	1	6	(2)		3(44)
Nepal (others)			-	5			-	-	1(2)	-	5(8)

* Numeral in parenthesis is the number of naked forms.

frequently, in the same regions. In contrast, the A. 222 type that differs from the "Himalayan resistant" type only in degree of resistance to all races except IX, is found mainly in the lower part of Nepal. Three other reaction types, Keronja, Pisang and Kakani types, are confined to the particular localities as their names indicate, but the places of occurrence of the Hanna type are unknown.

In order to identify the resistant genes involved in the strains belonging to some of the reaction groups, a further investigation was carried out by Hiura *et al.* (1961). The method used involves production of 100 single spore cultures resulted from a cross between two Japanese physiologic races of barley mildew, IX and XI, and the inoculation with these different pathogen cultures onto the seedlings of various strains to be tested, together with those of several type varieties having each a single known resistant gene. The principle, on which the method is based, has also been stated by Moseman (1963).

As shown in Table 12, the reactions of all the Himalayan resistant type strains to the eleven Japanese mildew races were found to be in complete agreement with those of the type variety Russian 74, suggesting that they might have the same resistant gene JMlr:4 in common. Contrary to this expectation, 28 Himalayan resistant strains tested on the one hand and Russian 74 on the other showed different reactions to these 100 pathogen cultures: to the 40 cultures their reactions were quite reverse, though to the remaining 60 cultures their reactions were in accord. Thus, it was suggested that these Himalayan resistant strains possessed each of a resistant gene different from JMI_{r74} On the other hand, it was observed that the behaviors of these Himalayan resistant strains entirely accorded with that of the type variety A. 222: All of them showed susceptible reactions to 49 out of these 100 pathogen cultures, and to the remaining 51 cultures they behaved as resistant, though the degree of resistance was always higher (R) in Himalayan type stains than in A. 222 which showed moderate resistance (M). So, if the difference in degree of resistance is neglected and only the resistance and susceptibility to these 100 pathogen cultures is referred to, the "Himalayan resistant" type may well be included in the A. 222 type. For the reason, these Himalayan group was tentatively classified as A. 222 in the previous report (Hiura et al. 1961). Nevertheless, it is doubtlessly more reasonable to conclude that the resistant gene involved in the Himalayan resistant type strains is different from either *JML*^{an} in A. 222 or JML, in Russian 74.

Similar inoculation tests, made with the strains of Hanna group from Nepal and those of H. E. S. 4 group from India, gave results as expected. Their reactions to the 100 pathogen cultures were in exact accordance with the reactions of the type varieties, Hanna and H. E. S. 4, respectively, suggesting the identities of the resistant genes involved in these two groups of the strains with those of the respective type varieties.

6. Post-Harvest Dormancy

Post-harvest dormancy is characteristic of the wild species, and its adaptive significance has long been well-accepted. The situation is somewhat different in the cultivated forms. Although this character has also been inherited by them, their degree of dormancy is usually much less than their wild progenitor(s) and its ecological significance has not been thoroughly understood. In order to find a clue to the last problem, a series of germination tests were performed in 1966 with the seeds of 93 barley strains originated from Nepal Himalaya and India. A number of heads of each strain were harvested 35 days after anthesis, exposed to dried air at 35°C for two days, and then stored in a paper bag at room temperature. Fifty seeds were sown on a filter paper moistened with distilled water in a Petri dish of 9 cm in diameter. Two of these consist a set. Germination temperature was kept at 25°C throughout. The final counts of the germinated seeds were made 10 days after sowing. Such a test was repeated four times using the seeds of 10, 25, 40 and 60 days after harvest. The inherent germinability of each sample used in this experiment was tested further by sowing the seeds of about 100 days old at 17°C after one day's prechilling. The results obtained are summarized and presented in Table 14.

One of the most remarkable facts in the results is that the naked barleys are capable of germinating by far earlier after harvest than the covered barleys, and so they are irrespective of their origins. On the other hand, the covered barleys differ markedly in degree of post-harvest dormancy according to their origins : namely, Indian barleys is most dormant, which is followed by the strains of Nepal lowland, Kali Gandaki basin, Buri Gandaki basin and finally by the strains of Marsyandi basin which is the least of all. It is interesting to note that among these coverd barley groups there is a close inverse correlation between degree of dormancy and the mean altitude of their native places.

Such a geographical differentiation of barleys as to the post-harvest dormancy

Deine	Mean	No. of	N	lumber of da	ys after ha	rvest	
Regions	altitude (m)	strains tested	10	25	40	60	- Average
		CO	VERED BAR	LEY			
India		9	15.00	12.89	17.56	40.00	21.36
Nepal lowland	1230	9	15.00	20.44	38.11	66.89	35.11
Kali Gandaki	2087	13	22.46	33.77	48.31	59.23	40.94
Marsyandi	2947	9	50.89	66.22	74.89	79.00	67.75
Buri Gandaki	2244	8	29.13	54.88	67.50	75.13	56.66
Others (Nepal)		4	29.25	44.75	65.75	68.25	52.00
		N	AKED BARL	EY			
Kali Gandaki	2106	6	65.50	92.83	95.83	96.83	87.75
Marsyandi	2935	20	68.10	79.85	91.90	97.95	84.40
Buri Gandaki	2515	13	61.00	85.08	93.77	97.23	84.27
Others (Nepal)	-	2	47.00	94.00	99.50	99.50	85.00

TABLE 14 Average germination percentages on 10, 25, 40 and 60 days after harvest of the covered and naked barleys from different areas in India and Nepal.

is an interesting, but unexplainable, phenomenon. There might be a number of agents responsible for it, but only two are now conceivable. One is the meteological condition which prevails during the maturity and harvest season. If it is usually rainy in the harvest season as in southern parts of Japan and Korea and Central China, the barley varieties with less viviparous nature will certainly be favored by natural as well as artificial selection. The length of period from the harvest to sowing for the next crop is possibly another causative agent for the regional difference in the degree of seed dormancy. If the period is short, the non-dormant varieties are doubtlessly preferable because uniform and prompt emergence will be expected.

VI. CONSIDERATION ABOUT THE PHYLOGENETIC AND REGIONAL DIFFEREN-TIATION OF NEPALESE AND INDIAN CULTIVATED BARLEYS

In order to contribute to the knowledge of origin and phylogeny of the cultivated barleys, one of the present writers has made extensive studies on the geographical distribution of various morphological and physiological characters in the Old World (Takahashi 1955 and 1963). As the results, he has found that there is a geographical regularity in their distribution as follows: Several characters which occur in the barleys of Tibet, China Proper and southern parts of Korea and Japan (Oriental region) are quite different from those found only in the barleys of the remaining parts of the world or Occidental region. The characters peculiar to Oriental barleys are reduced lateral awn (Ir or I-series), short awn (lk_2) , trifurcate awn (K, K'), semi-brachytic growth (uz) and waxy kernel (wx). Those found only in the Occidental barleys are two-rowed head (V, Va), shorthaired rachilla (s), smooth awn (r), wide glume (e), a gene for spring habit (sh), a gene for nonbrittle rachis (bt) and various genes for resistance to Japanese powdery mildew races. It was also shown that such genes as bt_2 for nonbrittle rachis-2, v for six-row, those of which occur in almost all of the Oriental barleys, are found also among the Occidental barleys in lower frequencies. Thus, it was suggested that cultivated barleys could be classified into two distinct geographical types, Oriental and Occidental.

It seems appropriate to deduce phylogenies and regional differentiation of the barleys grown in Nepal Himalaya and North India in the light of the facts and hypothesis above-mentioned. And, the present materials are well suited for the purpose since they are morphologically and physiologically diversified. Nakao (1956) and we could distinguish a total of 41 varieties among them, which are different in the combination of the following characters: covered and naked kernel, lax, dense and very dense spike; long and short awn; normal and elevated hoods; black, purple, blue and yellow caryopsis. It is mentioned here that these strains involve either those characters peculiar to Oriental barleys or those common to both regional types, but no characters peculiar to Occidental barleys such as tworow head, smooth awn, wide glume, etc. The short-haired rachilla is the only one morphological character of Occidental type that occur sporadically in Mid mountain region and India.

Genetic and physiological studies have provided evidence suggesting that the covered and naked barleys in Nepal and India are phylogenetically different. Namely, it was known that 82 per cent of the covered barleys were of type W, involving a gene bt native to Occidental region, while almost all of the naked barleys were of type E. Similarly, 60 per cent of the covered barleys were shown to be possessed of one or more genes for resistance to Japanese mildew reces, while

91 per cent of the naked barleys have no resistant gene at all.

Let us first consider the problem of origin of the naked barleys in Nepal. As stated before, Nakao has proposed to classify the Nepalese barleys into three types, Indian, Himalayan and Tibetan, based on the geographical distribution of various major morphological characters. As to the last mentioned Tibetan group of barleys which is mainly composed of naked barleys, he has suggested that they might be of Tibetan origin. One of the reasons adduced is that the naked barley is still now chiefly grown by Tibetans living in the northern slopes of the great Himalayan mountain ranges (Fig. 1). It may be said in this connection that Tibetans are known to live on "tsampa" which is made from purched naked barley grains. The second reason is the mode of geographical distribution of naked barleys in relation to traffic: Upper basin of the river Buri Gandaki has three passes open to Tibet and a route leading to the upper basin of Marsyandi, but is hard to access from the south, while Marsyandi basin is closed from Tibet. This may adequately explain, with the above-mentioned proposition, the fact that the naked barleys are concentrated in Buri Gandaki basin, and tends to decrease its area going westwards, amounting to one half and one fourth in the upper basins of Marsyandi and Kali Gendaki, respectively.

Botanical evidence other than these will be required in order to furnish a sufficient basis for aforementioned assumption as to the origin of Nepalese naked barleys. For this purpose, various characters of Nepalese and Tibetan naked

Comparison of the morphological and physiological characteristics of the five barley groups, Indian, Lowland Nepal, Himalayan covered, Himalayan naked and Tibetan naked

TABLE 15

	India		NEPAL		- Tibet
Characters (genes)	covered %	Lowland covered %	Himalayan covered %	Himalayan naked %	naked %
Intermedium (lr or I)	0	0	37	42	261)
Short awn (1k2 ?)	0	47	24	8	102)
Dense spike (1)	7	33	16	37	422)
Hooded awn (K, Ke)	0	0	1	25	52)
Blue aleurone (Bl)	79	80	30	2	72)
Purple kernel (Re2)	0	0	0	5	62)
Black kernel (B)	0	0	0	3	142)
Short hair rachilla (s)	3	0	9	0	0
Nonbrittle rachis (bt) W type	93	93	72	0	6
Mildew resistance (JMI's)	41	27	84	9	6
Fresh seed germination %	21.4	35.1	53.2	84.9	94.5
Grade of spring habit	I	III	II~III	I~III	I~III

1) Cited from Åberg (1940)

2) Cited from Brücher and Åberg (1950)

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barleys were compared. The results are presented in a summarized form in Table 15, where the data of Tibetan barleys are cited from Åberg (1940), Brücher and Åberg (1950) and ours (unpublished). This clearly indicates that the naked barleys from these two regions are almost similar in every respects. The most noteworthy among others are the facts that the barleys of both regions are commonly characterized by the same nonbrittle rachis genotype, E or $BtBtbt_2bt_3$, high susceptibility to all the Japanese mildew races and also by very low degree of post-harvest dormancy. In conclusion, there seems little doubt that the naked barleys distributing in the northern Nepal have their origin in Tibet, and that they are of Oriental type.

The problems of phylogeny and geographic differentiation of the covered barleys in Nepal and India are more complicated. Nakao is of opinion that the Nepalese covered barleys can further be classified into two groups, and one of them, which is found in lowland Nepal, may well be called as Indian group because of the similarity in appearance of heads. In fact, lowland Nepalese barleys are, as seen in Table 15, quite similar to the true Indian barleys in that they are very high in frequencies of bt (type W) and Bl (blue aleurone). Moreover, one half of the lowland Nepalese barleys are consisted of var. coerulescens or var. hybernum, which are the principal types of India. But several other varieties are lacking in the true Indian barleys. Further, Indian barleys are distinctly higher in the grade of spring habit, being mostly grade I, and also to some extent higher in post-harvest dormancy than the lowland Nepal barleys, which might be attributable to the ecological differnces between these two areas. It seems more appropriate, therefore, to distinguish the lowland Nepal barleys as a separate regional group from the true Indian barleys. Both the Indian and lowland Nepalese barleys deem to belong to the Occidental barley type on the basis that they are mostly of type W as regard the nonbrittle rachis genotype. It is hard to assume where these barleys have originated from. As for the lowland Nepal barleys, there are a slight sign of introgression of a few characters from the Nepalese highland barleys.

The covered barleys distributing in the upper basins of Kali Gandaki and those in the upper basins of Marsyandi and Buri Gandaki are all quite similar in every respects to each other, but differ markedly in some important characters from the barleys in lowland Nepal and the Tibetan type barleys. So, these covered barleys may constitute a distinct barley group that may be called Himalayan covered barley group. Generally speaking, the Himalayan covered barleys are, as seen in Table 15, akin to the Tibetan naked barleys as to the morphological features, but are very similar to those of Nepal lowland and India as to the physiological and genetical features investigated. Exceptions to this rule may be low frequencies of trifurcate appendages (K), blue aleurone (Bl) and high frequency of short awn character. It appears therefore as reasonable to assume that the Himalayan covered barleys might have arisen by the hybridization between the Tibetan naked forms and some covered barleys of Occidental type. Of course, this is a tentative conclusion, and further studies are needed in order to clarify how these hybrid barleys have been established in these areas. Origin of a few new genes for resistance to Japanese mildew races is another problem to be solved in the future.

We have thus been in success to demonstrate that Nepalese and Indian barleys can be classified into four groups, Indian, Lowland Nepal, Himalayan covered and Himalayan naked or Tibetan group, which differ with each other not only in morphological and physiological features, but also in geographical distributions. It is worth mentioning in the result that, while Indian and Tibetan barley groups are typical of the Occidental and Oriental barleys, respectively, two other groups, Himalayan covered and Lowland Nepal, which cover the area intervening between India and northern slopes of the Himalayan mountain ranges, are possessed of the characters of both the Oriental and Occidental barleys, suggesting the hybrid origin. These facts clearly indicate that Nepal is on the border of the distribution of the Oriental and Occidental barleys. It is not difficult to suppose further that hybridization of different barley types have fostered diversification of barley forms in Nepal. Of course, diversities of climatic, edaphic and ethnic conditions prevailing in Nepal and India might be the other causal agents of diversification of barley forms.

SUMMARY

Present study aimed to elucidate the morphological, physiological and genetical features of the cultivated barleys distributing in Nepal Himalaya and North India, and thereby to get some insight into the phylogenetic and geographic differentiation of these barleys. A total of 290 strains of barleys collected by Nakao and others were used as the materials. Observation, measurements and physiological and genetical studies have been made during past ten years. The results hitherto obtained may be summarized as follows :

- 1. All the materials are of six-rowed type, belonging to either convar. *hexastichon* or convar. *intermedium*. According to Mansfeld's morphological system they were classified into 34 varieties.
- 2. The *intermedium* barleys, of both covered and naked types, are very popular in Nepal highland area. The naked forms of this kind are mostly long-awned in the central row, while the covered forms are variable as to the length of central awns.
- 3. Hooded character is confined to the naked barleys in Nepal highland area. Though site and shape of the hoods of these barleys are considerably variable, only two genes, K and K° were found to be responsible for them.
- 4. Short awn character is frequent among the Nepalese covered barleys, but is rather rare among the naked ones.
- 5. India is rich in forms with very lax spikes, while Nepal is abundant in varieties with dense or very dense spikes. Some of the Nepalese dense spike forms seem to involve the same gene on chromosome 1 as is possessed by some of the Japanese dense spike varieties.

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- 6. Blue aleurone character is very frequently met with among the Indian and Nepal lowland barleys, but is rare among the naked barleys. On the contrary, black or purple caryopses are found only among the naked barleys.
- 7. The short-haired rachilla is found sporadically among the Indian and Himalayan covered barleys.
- 8. There is no strain which is characterized by semi-brachytic growth, hairy leafsheath, colorless plant parts and waxy endosperm.
- 9. Genotype analysis for the nonbrittle rachis character has shown that the naked barleys are wholly of type E (*btbtBt*₂*Bt*₂), while more than 80 per cent of the covered forms in Nepal and India are of type W (*BtBtbt*₂*bt*₂).
- 10. A test for reaction to eleven Japanese mildew races has disclosed that almost all of the Nepalese naked barleys are susceptible to all these races, while the Indian and Nepalese covered barleys include a large number of resistant strains. Based on the differential behaviors to these races, Indian and Nepalese barleys could be classified into eleven reaction groups.
- 11. Barley is sown in autumn in general in India and Nepal excepting the places higher than 3200 m wherein it is sown in spring. They are however variable as to the grade of spring (winter) habit : Indian barleys are of highly spring habit, while the majority of the Nepalese barleys are of semi-spring to semi-winter habit (grade II-III). It seems that most of the spring barleys in Nepal have each a single dominant spring gene, Sh_2 .
- 12. All the naked barleys from Nepal are readily germinable after harvest, while the covered barleys differ markedly in degree of post-harvest dormancy according to their origins. There is a definite tendency that the degree of dormancy becomes lower with the rise of altitude of their native places.
- 13. Based on the morphological and physiological features and also on their geographical distribution, Nepalese and Indian barleys could be classified into four groups; Indian, Lowland Nepal, Himalayan covered and Himalayan naked or Tibetan types. Indian and Tibetan barley groups are typical of the Occidental and Oriental barleys, respectively, while Himalayan covered and Lowland Nepal groups of barley seem to have been originated by hybridization between abovementioned two groups of barley.

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Characteristics and Phylogeny of Nepalese and Indian Barleys

LATIN DIAGNOSES OF NEW VARIETIES

- 1. Convar. hexastichon (L.) Alef. s. l. var. collinum R. Takahashi, var. nov. Var. parallelo affinis sed fructibus viridibus.
- 2. Convar. hexastichon (L.) Alef. s. l. var. nigrihypatherum R. Takahashi, var. nov.

Var. hypathero affinis sed spiculis, glumis et fructibus nigris.

3. Concar. intermedium (Körn.) Mansf. var. philemense R. Takahashi, var. nov. Var. boteano affinis sed spica laxa.

Appendix 1

An abstract from Mansfeld's morphological system of cultivated barley, Hordeum vulgare L. s. l., for identification of the varieties found in Nepal and India

	Ear lax	Ear dense	Ear very dense
I. convar. hexastichon (L.) Alef. s.l. 1a. Kernel covered			
 2a, awn rough, long, glume narrow 3a. ear yellow 3b. ear bluish green 3c. ear black to black grey 2b. awn rough, short as long as head 	hybernum coerulescens nigrum	parallelum collinum	
lengh 3a. ear yellow 3b. ear blue-green 3c. ear black 2c. all spikelets with normal hood 3a. ear yellow	breviaristatum ullerense nepalense horsfordianum	hypatherum subhypatherum nigrihypathe- rum	
1b. kernel naked			
2a. awn rough long, glume narrow3a. ear yellow3b. kernel green	coelesta	revelatum ankoberense	nudi pyramidatun (uljastaicum)*
3c. ear and kernel violet 3d. ear black to black brown	violaceum tibetanum	hangaicum	
2b. awn rough, as long as ear length 3a. ear yellow	asiaticum		
 2c. all spikelets with normal hood 3a. ear yellow 2d. all spikelets with elevated hood (attached to 1 cm awn) 	tri furcatum	pisangense	
3a. ear yellow	(dananum)		
 convar. intermedium (Körn.) Mansfeld kernel covered awn rough, long (central row only) a. ear yellow 3b. ear black 	montanum (mortoni)	(ni pponicum)	
 2b. awn rough short, laterally awnless 3a. ear yellow 3b. ear black 	harlani	japponicum nana-prasadii	
2c. all spikelets without awn or hood 3a. ear yellow 3b. ear black	tonsum	nigrichinense	
1b. kernel naked			
 2a. awns of central row rough, long, laterally awnless 3a. ear yellow 2b. central awn short, laterally awnless 	nudimontanum	nudinipponicum	nudicapitatum
3a. ear yellow	-	(nudijaponicum)	(nudicongestum)
 2c. central row with normal hoods laterals without awn or hood 3a. ear yellow 2d. central row with elevated hood laterals reduced hood-like appen- 	cornutum	(gymnanomalum)	
dage 3a. ear yellow	philemense	boteanum	

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* The varieties in parenthesis were identified only by Nakao (1956).