Intermedium mutants in barley (*Hordeum vulgare* L.) – diversity, interactions and plant breeding value

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Abstract. Mutation research has given an insight into the rather complex genetics of kernel rows in barley. At least 12 gene loci can act to promote the spike development, fertility, and kernel development. Mutants with such effects as six-row and intermedium phenotypes show clear morphological distinctions among different loci, but also among different allelic mutants. These genes, without exception, are capable of unexpected synergistic reinforcing or disturbing intraction, the extremes being typically six-rowed or deformed spikes, respectively. The investigations have centered on 69 intermedium mutants, representing 9 loci, in double mutant combinations, in double combinations with the six-row gene *hex-v*, in triple combinations with *hex-v*, and in triple and quadruple mutant combinations. The effects of the interaction may differ among the three characters of lateral floret development, among *intermedium* loci, and among alleles of the particular locus. Particular types of gene interaction are indicated, particular loci being more competent than others, and the particular alleles being more competent in relation to the constellation of loci. Accumulation of *intermedium* genes in more complex gene systems leads to progressive promotion of lateral floret development, but there are indications that such systems may be more sensitive to environmental stress, leading to irregular or even deformed spike formation. Probably, representatives of the *hex-v* locus should form the fundamental constituent in the synthesis of gene systems with the most efficient promotion of lateral floret development in the breeding of six-row barley.

Key words: gene interaction, *Hordeum vulgare*, intermedium genes, lateral floret development.

Introduction

Mutation research has given an insight into the rather complex genetics of kernel rows in barley (*Hordeum vulgare* L.). At least 12 gene loci in barley

can act to promote the spike development of lateral florets, their size, awn development, fertility and kernel development (LUNDQVIST, LUNDQVIST 1987a).

Normal two-row barley, with its additional four rows of reduced, sterile, and awnless lateral florets, can, in a single mutational step, produce six-rowed mutants with well-developed lateral florets that are fully fertile and with long awns. So far, 41 cases have been isolated in the Svalöv collection and are localized to one and the same locus, *hex-v* (GUSTAFSSON et al. 1969, LUNDQVIST, LUNDQVIST 1988a), located in the long arm of chromosome 2 (NILAN 1964, PERSSON 1969). Locus *hex-v* is semidominant with the heterozygote being no longer six-rowed, although clearly distinguishable from normal two-row barley by the pointed lemma of its awnless, sterile lateral florets, in contrast to the rounded tip of the normal homozygote. It is an interesting fact that, among mutants at the *hex-v* locus, the development of lateral florets is variable and that, compared with commercial six-row varieties, their lateral kernels are considerably smaller, with clearly shorter awns.

Two-row barley may also produce mutants with spike development intermediate between the two-row and six-row states. The enlarged lateral florets of these mutants vary in characteristic ways with regard to awn development, fertility and kernel development, not only among mutants, but also depending on environmental conditions. The 103 *intermedium* mutants so far localized in our studies have been assigned to 11 loci, 10 of which are recessive *int* loci, and 1 semidominant to dominant *Int* locus.

Tendencies toward cooperation among these genes have been established, leading to enhanced promotion of lateral floret development. Thus, *intermedium* genes combined in double homozygous state have frequently resulted in typical six-row spikes (GUSTAFSSON, LUNDQVIST 1980, LUNDQVIST, LUNDQVIST 1988b). Such double mutants combined with the *hex-v* gene in triple mutants may give rise to extremely beautiful six-row types (LUNDQVIST, LUNDQVIST 1987a). This cooperation between the semidominant *hex-v* gene and recessive *intermedium* genes has been distinguishable even at the heterozygous state of these genes (LUNDQVIST, LUNDQVIST 1987a). In the control of the six-row/two-row difference, an enhancing interaction between an *intermedium* allellic series and alleles at the *hex-v* locus has long been recognized (e.g., ROBERTSSON 1933, LEONARD 1942, ROBERTSSON et al. 1955, GYMER 1978, LUNDQVIST, LUNDQVIST 1987b). The competence to cooperate efficiently depends on particular kinds of gene interaction, particular *intermedium* loci being more competent than others, and the competence of the individual *intermedium* allele depending on the specific constellation of loci, also with regard to the *hex-v* locus.

Diversity of *intermedium* genes

Of the 103 *intermedium* mutants sufficiently studied to specifically assign them to a locus, 88 were produced in series of different treatments equally attributed to ionizing radiations and chemical mutagens. No less than 67 (76.1%) of these mutants have arisen after treatments with chemical mutagens, mainly ethylene imine, ethyl methanesulfonate, and sodium azide; the main part of the rest was produced by various kinds of sparsely and densely ionizing radiations. The mutants are distributed to 11 loci as follows: *int-a*: 31; *int-b*: 3; *int-c*: 23; *Int-d*: 21; *int-e*: 14; *int-f*: 1; *int-h*: 6; *int-i*: 1; *int-k*: 1; *int-l*: 1; and *int-m*: 1. It is obvious that the different *intermedium* loci have different mutabilities irrespective of treatment with one or another mutagen.

There are clear morphological distinctions among *intermedium* mutants belonging to different loci, but also among allelic mutants (LUNDQVIST, LUNDQVIST 1988a). The characteristics of the lateral florets, for the 69 more closely investigated mutants (the values 0, 0, 0 and 5, 5, 5 for awn development, fertility, and kernel development being assigned to normal two- and six-row barleys, respectively) can be summarized as follows in Table 1.

Table 1. Diversities among intermedium mutants in lateral floret development, when the values 0, 0, 0 and 5, 5, 5 for awn development (I), fertility (II), and kernel development (III), are assigned to normal two-row and six-row barleys, respectively

Locus	Alleles	Ranges among values for			Extremes among alleles for					
		I	II	III	I	II	III	I	II	III
int-a	23	0.3-3.9	0.4-2.5	0.6-3.7	0.5	0.4	0.6	3.5	2	3.7
int-b	2	0.5-0.7	1-1.8	1.4-2.6	0.5	1	1.4	0.7	1.8	2.6
int-c	18	0-2.1	0-3.2	0-3.4	0	0	0	2.1	2.8	2.9
								0	3.2	3.4
Int-d	13	0.7-4.0	0-3.7	0-4.0	0.7	0	0	4.0	3.5	4.0
int-e	7	1-4	1-2	2-4	1	2	2	4	2	4
int-f	1	2.8	1.5	2.4						
int-h	3	0	0	0						
int-i	1	2	0	0						
int-k	1	0.5	0	0						

Cases of synteny should be inevitable when only 7 pairs of chromosomes are at hand for 9 *intermedium* loci. Nevertheless, no case of undisputable linkage has been established among these loci in their normal positions (LUNDQVIST, LUNDQVIST 1988a).

Interaction of *intermedium* genes

Double mutant combinations

Combinations of these *intermedium* genes in double homozygous state have, without exception, shown an apparent, strong degree of synergistic interaction between genes that by themselves cause rather modest changes of the normal two-row spike. These double mutants rank in three groups in their spike development: six-rowed, irregular, and deformed (GUSTAFSSON, LUNDQVIST 1980). There is a continuous transition between irregular and deformed types of spike, and even six-rowed types may now and then have a somewhat irregular fertility of their lateral florets. Anyhow, typically six-rowed spikes and irregular spikes always belong to different progenies, as unequivocal indications of different kinds of interaction among different gene loci.

A study of the four most frequently mutated *intermedium* loci (*int-a, int-c, Int-d,* and *int-e*) (LUNDQVIST, LUNDQVIST 1988b) has revealed apparent differences, not only among loci, but also among the alleles, in the ability to cooperate for six-rowed spikes in double mutants. Whereas, *int*-a and *int-e* both cooperate successfully with *int-c* and *Int-d,* they are poor partners to one another. As for individual alleles there are no clear signs of outstanding performance: success seems to depend on the particular constellation of loci and alleles. The combinations between *int-a* and *int-e* excepted, the majority of double mutants have a more or less regular six-rowed phenotype, but a very wide range of phenotypes is covered among the remaining double mutant combinations of alleles. In fact, a bimodal distribution of types of spike development is revealed for each of the six combinations among alleles of these four *intermedium* loci. Besides being a sign of clear differences among alleles, this bimodality may point to thresholds on the way to the six-rowed state for the double mutant. The development of lateral florets being sensitive to environmental influences may also be due to the presence of such thresholds.

To be sure, recessive *int* genes alone and in double and triple heterozygous combinations are unable to promote lateral floret development (ABEBE 1990a). However, recessive *int* alleles have turned out to act as enhancers, if a promotion of lateral floret development has been initiated in a recessive *int* homozygote (LUNDQVIST et al. 1988b, ABEBE 1990a). The degree of enhancement may differ among the three characters of lateral floret development, among *int* loci, and among alleles of an *int* locus. The addition of a second potential enhancer to the initial effector leads to progressive enhancement.

When the initial effect is formed by allelic representatives of the semi-dominant/dominant locus *Int-d,* there are, again, enhancements resulting from

heterozygous recessive *int* genes, and progressive enhancement of lateral floret development when a second potential enhancer is added. And again, the degree of enhancement differs among lateral floret characters, among *int* loci, and among the effector *Int-d* alleles (ABEBE 1990b). Among the recessive *int* loci, *int-c* has turned out to be the most efficient one, not only as enhancer in double heterozygous constellations with *Int-d*, but also in the *Dd cc* constellation (LUNDQVIST et al. 1989a). Concerning the basic effect produced by the heterozygous *Int-d*, the three alleles ranking in the top of enhancement are those showing the most pronounced degrees of dominance, which could indicate that the stronger the effector, the more efficiently will an enhancer work (LUNDQVIST et al. 1989a).

Among the recessive loci, *int-c* proved to be particularly efficient as an enhancer in interactions with other genes with a promoting influence on lateral floret development. Outstandingly most efficient combiners are *Int-d* and *int-c*.

It is remarkable that, whereas *int-a* and *int-e* both cooperate successfully with *int-c* and *Int-d*, they are quite poor partners to one another. One can speculate that the alleles of *int-c* and *Int-d* are more flexible, more prone to adapt themselves, which would facilitate the development of a regular six-rowed double mutant. The alleles of *int-a* and *int-e*, one the other hand, may be visualized as more rigid, which would hamper this development. As a matter of fact, *int-a* as partner to form double mutants has served to reveal differences within series of alleles at the other three main loci (LUNDQVIST, LUNDQVIST 1988b). A rigid state within *int-a* would force the alleles of the other locus to "show their hands".

Interaction with the six-row gene *hex-v*

For none of the recessive *int* loci studied are there any clear indications of failure to cooperate with a selected member, *hex-v*^{3}, of the six-row locus to form regular six-rowed spikes in double mutants *intint/vv* (LUNDQVIST et al. 1988a, ABEBE et al. 1990). There are some indications from a limited material that *int* genes (*-a*, *-c*, *-e*) are more efficient enhancers of lateral floret fertility in the double mutant *int/int* state than in double mutant combinations with the *hex-v*^{3} gene (LUNDQVIST et al. 1989b). On the other hand, a practically import ant enhancing interaction between the *int-c* locus and the *hex-v* locus has long been recognized in six-row barley varieties (e.g., ROBERTSON 1933, GYMER 1978). These conditions have been studied in considerable detail with the Svalöf commercial variety Agneta (LUNDQVIST, LUNDQVIST 1987b).

In crosses between representatives of *int-c* and Agneta, F_2 plants classed as six-row occur in very strong excess relative to the ordinary 1/4 ratio expected for -- *vv* plants. Obviously, plants *cc Vv* are, to a considerable extent, classed as six-row. Among the 18 *int-c* alleles studied in these crosses, there was a variable competence to confer a six-row phenotype to *cc Vv*, with a single *v* allele from Agneta. The six *int-c* alleles giving a significant excess of six-row plants show an interesting agreement with the hypothesis of 6/16 six-row F_2 plants. The *int-c* allele originally carried by Agneta is not among these "strong" alleles. The enhancing *int-c* alleles seem to exert their influence only in the homozygous state, the heterozygotes with the "Agneta *c* allele" apparently being inefficient (LUNDQVIST, LUNDQVIST 1987b).

A closer investigation of the Agneta *int-c* allele and its interactive competence together with three other alleles of the *int-c* locus (LUNDQVIST, LUNDQVIST 1989), neither of which were singled out as eminently competent enhancers, led to the following main conclusions. The degrees of phenotypic enhancement may differ among characters of lateral floret and among mutant genes. There are no indications that the *int-c* allele present in Agneta is the superior enhancer of the *hex-v* gene in this variety. Nor, are there indications that this *hex-v* gene is a superior one. It is, however, of interest that whereas the *int-c* allele of Agneta has a poor phenotypic expression on the awn length character, it has a stronger influence on fertility and seed size of lateral florets.

Other investigations (LUNDQVIST et al. 1989a) of F_2 dihybrid classification patterns for *hex-v*[3] and recessive *int* loci, indicate that homozygotes for *int-a*, *int-b*, and, especially, *int-c* are able to interact with a single *hex-v* gene in a way that makes *Vv* plants form six-rowed plants.

Recessive *int* genes are able, in single doses already, to add an effect if a promotion of lateral floret development has been initiated by the semidominant *hex-v* gene (LUNDQVIST et al. 1988a, ABEBE et al. 1990). This effect is reinforced when several such recessive genes are brought together in single doses. The degrees of phenotypic enhancement may differ among characters of lateral floret development (awn length, fertility, seed size), among *int* loci, and among allelic states of the latter, whereas differences between the two allelic representatives of *hex-v* were not discernible.

Triple combinations with *hex-v*

Cross combinations of double mutants *int/int* and the *hex-v* gene have produced beautiful six-row types with conspicuously large spikes and thick culms, to the degree that we denoted them King-size (LUNDQVIST, LUNDQVIST 1987a). Such six-rowed segregants had not been observed before in crosses

leading to double mutants with *int* genes and the *hex-v* gene in various two-gene combinations. No strict genetical verification of their triple mutant state could be done at that time, but there were interesting indications of a connection between the competence of the *int* genes to produce the surmised triple mutant type in combinations with *hex-v*, and their efficiency to produce double mutants *int/int* with regular six-rowed spikes. The King-size phenotype apparently depended on particular types of gene interaction, particular *int* loci being more competent than others, and the particular *int* allele being competent in relation to the constellation of loci.

LUNDQVIST et al. (1989b) have further studied the effects of the accumulating of genes promoting lateral floret development in barley. This material consists of a sample of 19 genotypically verified triple combinations *int/int/hex-v* (6 with *hex-v³*, and 13 with *hex-v$_A$* from the commercial six-row variety Sv Agneta). A total of four among the 10 recessive *int* loci, and 24 among the 50 alleles of these four loci were involved. The triple combinations were based on 15 different *int/int* double mutant combinations, where *int-c* and *int-a* were the main contributors, with 11 and 9 alleles, respectively. The crosses to produce these triple combinations had, for technical reasons, utilized regular six-rowed double mutants *int/int*.

In systematical comparisons of different constellations of *int* genes and *hex-v* genes (LUNDQVIST et al. 1989b) the subtraction of one *hex-v³* gene from the *int/int/hex-v³* combinations caused a slightly significant reduction in awn length and seed size of lateral florets, whereas the subtraction of one *hex-v$_A$* gene from the triple *int/int/hex-v$_A$* combinations conferred clearly significant reductions for all three lateral floret characters. No positive effects could be demonstrated, in either case, for the addition of the *hex-v* gene to the *int/int* combinations.

The addition of the *hex-v* gene to *int/int* double mutants, in the *int/int/hex-v* constellation promoted lateral floret development. Probably, *hex-v* should form the fundamental constituent in gene systems with the most efficient promotion of lateral floret development in barley.

More complex gene systems

Investigations have been initiated in more complex systems of *intermedium* genes (LUNDQVIST, LUNDQVIST 1990, 1991). These studies are based on four independently inherited loci, the three recessive *int-a, int-c,* and *int-e,* an the semidominant *Int-d,* represented by a total of 7 alleles. These seven single mutant genes were deliberately selected, being reliably efficient to produce double mutants of regular six-rowed phenotype. We consider this an ade-

quate platform for the study of lateral floret development, to look for evidence of progressive promotion or for indications of an optimum in the number of *intermedium* genes involved in lateral floret development.

Sets of standards consisting of two-rowed mother variety, single mutants, and double mutants, were compared with the range of phenotypes expected to be due to a segregation with up to triple or quadruple mutants obtained in the F_2, when double mutants with one or none of their *intermedium* genes in common had been combined in crosses (LUNDQVIST, LUNDQVIST 1991). Applying to these data the standards in the proportions expected on a Mendelian segregation of independently inherited genes, any statistically significant incremental difference between data expected from the standards and F_2 data observed, should indicate the presence of enhancing genes. The three lateral floret characters showed enhancement effects over the whole range of character grades. The enhancement effects differed among the 20 combinations in the three-gene segregations, different *intermedium* genes offering differing bases for enhancement effects. An apparent further progressive enhancement for lateral floret characters was indicated when a fourth *intermedium* gene was introduced into the segregation, in the four-gene cross, particularly for fertility and seed size.

The potential progressive enhancing effects indicated for these higher ranges of *intermedium* gene constellations were investigated further in F_3 offspring derived from segregants selected as prominent in the previous F_2 materials (LUNDQVIST, LUNDQVIST 1990). The superiority of the three-gene segregant state, relative to the double mutant state, was more pronounced for the fertility and seed size character than for the awn length. The sometimes rather wide range of variation in the F_3 data may indicate that the prominence of selected three-gene segregants in the F_2 generation was not necessarily bound to triple homozygosity for the *intermedium* genes involved. When a fourth *intermedium* gene was introduced into the segregation, the progressive promotion continued at an increased rate. Again, the progressive promotion of lateral floret development was particularly apparent for the fertility and seed size characters.

The progressive promotion of lateral floret development being particularly apparent for the fertility and seed size characters may have practically important implications for plant breeding in six-rowed barley, when specifically efficient constellations of alleles belonging to different *intermedium* loci have been attempted. It should, however, be observed that our investigations have not yet been able to definitely pinpoint individual plants homozygous at three or four *intermedium* loci.

Additional aspects

The use of clearly defined mutants evaluated against one another in allelic tests has demonstrated that there are many degrees in the development of lateral florets in cultivated barley, both among loci and among alleles, and that genes promoting lateral floret development may interact in unexpected reinforcing or disturbing manners. Such a complex genetic situation gives a key to the somewhat confused literature with conflicting publications on the genetics of kernel rows in barley, and may explain the deviating and deformed offspring often arising in crosses between primitive or advanced six-rowed and two-rowed barley strains.

By themselves the *intermedium* genes may cause rather modest changes in the normal two-row spike. Nevertheless, they are, without exception, capable of a surprisingly strong degree of synergistic interaction when they are brought together in double mutant plants. Attention to this cooperative ability was first drawn by GUSTAFSSON and LUNDQVIST (1980), observing that *intermedium* genes in double mutant homozygous state are frequently producing typical six-row spikes. Even in heterozygous state, recessive *int* alleles have turned out to act as enhancers if a promotion of lateral floret development has been initiated in a recessive *int* homozygote (LUNDQVIST et al. 1988b, ABEBE 1990a) or by the semidominant *Int-d* locus (LUNDQVIST et al. 1989a, ABEBE 1990b). There may, however, be a fundamental difference between the enhancement caused by an additional *int* gene in the heterozygous state and, on the other hand, the complementary interaction when the two *intermedium* loci are, by themselves, both capable of a promotion of lateral floret development.

The same kinds of enhancing interaction can be established between heterozygous recessive *int* genes and the weakly semidominant *hex-v* gene (LUNDQVIST et al. 1988a, ABEBE et al. 1990). The interaction between locus *int-c* and the *hex-v* gene is a matter of specific interest, since *int-c* has proved to be particularly efficient as an enhancer in interactions promoting lateral floret development, in double mutants *int/int*, together with *Int-d*, and with locus *hex-v*. It is, therefore, not unexpected that the enhancing interaction between *int-c* genes and the *hex-v* locus has long been recognized, and that alleles of *int-c* have been suggested to be important in the control of the six-row character and to occur frequently among cultivated six-rowed barleys (ROBERTSON 1933, GYMER 1978).

Plant breeding aspects

An unintentional selection for enhancing *int* genes occurring as spontaneous mutations seems likely in commercial six-row varieties. The question arises

whether optimal levels of gene cooperations have been attained. Data fro the Agneta six-row variety gave no indications that $int-c_A$ is the superior enhancer of the $v_A v_A$ genotypic state (LUNDQVIST, LUNDQVIST 1989). Nor do the data indicate that $hex-v_A$ is a superior six-row gene (LUNDQVIST et al. 1989b). Most probably, it would pay the efforts in a plant breeding program to try various constellations of $hex-v$ and $int-c$ mutants, in a deliberate use of the possibilities inherent in the cooperation between int genes and alleles at the $hex-v$ locus.

In our studies of 1, 2, or 3 heterozygous $intermedium$ loci added to a single $hex-v$ allele, the semidominant to dominant $Int-d$ alleles have shown the strongest efficiency to make lateral floret development in the six-row direction (LUNDQVIST et al. 1988a). Because of the tight linkage between these two loci, we have not yet been able to single out $Int-d/hex-v$ segregants. We have started some genotypic screening among potential triple constellations with $Int-d$ by means of crosses to normal two-row barley, since more or less pronounced six-rowed status of the F1 should reveal the presence of both $hex-v$ and $Int-d$ as contributed in the coupling state. Such $Int-d/hex-v$ recombinants are likely to form immensely valuable complex building-stones in the trial for still more successful complex gene systems to promote lateral floret development in barley.

The King-size six-rowed types segregating in some progenies after cross combinations of double mutants int/int and the $hex-v$ gene are still enigmatic, no strict genetical verification of their surmised triple mutant state $int/int/hex-v$ being available yet. Both for $hex-v^3$ and for the Agneta allele of $hex-v$, there appear very strong tendencies to heterogeneity among alleles of the individual $intermedium$ locus in their ability to produce King-size type in combinations with a second $intermedium$ locus (LUNDQVIST, LUNDQVIST 1987a). Locus $int-c$, $Int-d$, and $int-e$ show the highest competence to produce the King-size phenotype. The attractive combination of conspicuously big spikes and thick culms in a plant breeding program, is likely to make a deepening investigation into the origin of this kind of segregating gene combination highly desirable.

The comparison between double mutant combinations of $intermedium$ genes and segregants from corresponding three-gene and four-gene crosses, indicates apparent progressive enhancements when a third and, still more, when a fourth $intermedium$ gene is introduced into the segregation (LUNDQVIST, LUNDQVIST 1990, 1991). This observation may have important implications for plant breeding, when specifically efficient constellations of alleles belonging to different $intermedium$ loci have been tried out.

The efforts to specifically pinpoint individual plants as $intermedium$ homozygous at three or four loci should be carried on. Such segregants should

form invaluable building-stones to further investigate how far an accumulation of genes promoting lateral floret development can be practically utilized. There are suggestive indications that spike development, in complex combinations of *intermedium* genes, may be sensitive to environmental stress, in the field or under greenhouse conditions with artificial light. Thus, offspring derived from selected regular six-rowed plants may show tendencies to form spikes that are irregular (in the field) or even clearly deformed (in the greenhouse) (LUNDQVIST, LUNDQVIST, unpubl.). Whether such tendencies are due to gene interactions that make deformed spikes appear already at the double mutant state, is a matter of great interest, both theoretically and for practical purpose.

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