

HORDEUM VULGARE L. – CYTOTAXONOMICAL ASPECTS

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Systematic approach of *Hordeum* genus

Hordeum L. genus (considered as being a monophyletic one), belongs to *Triticeae* tribe, *Poaceae* family, together with *Triticum*, *Secale* genera and with *Triticosecale* – artificial amphyploid. *Triticeae* tribe includes entirely almost 350 of species. Its delimitation is not entirely solved being many different opinions between botanists and cytogeneticians (Bothmer et al., 1995).

All wild species have been considered from the very first time as being related to cultivated barley and as being also a significant resource for improving methods (in spite of some strong interspecific barriers). It was assessed that *Hordeum* genus also comprises species which are less related to, having at its basis some recent researches especially those implying genomic interrelations. Therefore, this genus has been divided into two units:

- *Hordeum sensu stricto*, which comprises only two species: *H. vulgare* and *H. bulbosum*;
- *Crisetion* Raf, which comprises all the remaining *Hordeum* taxa).

This opinion is not entirely agreed with. One can assent with the idea of existing four or even five genera taking into consideration genomic difference. *Hordeum* genus is assigned 32 species and a total number of 45 taxa in biology literature.

Linné (1753) in his study “Species Plantarum” found 8 species, 5 of which belonging to cultivated barley, *Hordeum vulgare* L. (as with in accordance with present taxonomical criteria). Koch, in 1837 (quoted by Drăghici et al., 1975) divided *Hordeum* genus into two units: *Sativa* (comprising cultivated barley) and *Murina* (wild barley). Döll (quoted by Drăghici et al., 1975) use *Chrite* unit for cultivated barley species and for *Hordeastrum*, for wild species of barley and Anderson (1852) assigned the name of *Cerealina* to the unit that comprised cultivated forms and the name of *Campestris* to the one with wild species.

Nevski, in 1934 (Drăghici et al., 1975) divided *Hordeum* genus in four sections (*Stenostachys*, *Bulbohordeum*, *Campestra* and *Cerealina*), which were later described by Åberg and it was realized the first modern monography in 1941 and which comprised all the known species at that moment.

Trofimovskaya – 1972 (Bothmer et al., 1995) divided most of the species and Bothmer and Jacobsen (1985) checked again all the species. Canadian botanist Bowden (1962), Baum and Bailey (1989 a, b) analysed many species of the genus in a large number of studies.

Cultivated barley and its wild forms (*spontaneum* and *agriochriton* considered as being *Hordeum vulgare*) have been initially placed in only one section (*Chrite* Döll section and *Cerealina* Ands one), and all the other annual forms in another section (*Hordeastrum* Döll one). The American perennial species with long-awned were included in *Crisetion* (Raf.) Nevski section those with short ones from South America in Nevski *Anisolepis* section, the European Asiatic and North American perennial species in Nevski *Stenostachys* section and *H. bulbosum* in Nevski *Bulbohordeum* section. Based on morphology date Bothmer and Jacobsen (1985) recognized four sections, namely *Hordeum* section, *Stenostachys* section, *Chrisetion* section. These units have been maintained even if cytogenetic and biochemical data show that the relationships inside the genus are not completely emphasized in morphology.

The most related to *Hordeum* genus are probably *Taeniaterum* Nevski (Frederikson, 1986) which is present in Mediterranean area, Nevski *Psathyrostachys* perennial genus with eight species from Central and Southwest Asia (Baden, 1991) and *Hordelymus* (Jenssen) Jenssen (Bothmer and Jacobsen, 1986b) all these one belong to *Triticum* tribe. These genera together with *Hordeum* genus complete *Hordeinae* subtribe.

***Hordeum* species – delimitation and description**

Most species of *Hordeum* represent separate entities from a biological or only a morphological point of view. Reproduction barriers have been some insurmountable ones in natural environment even when two taxa have a sympatric distribution. There are although numerous accounts about sterile natural hybrid (*H. jubatum* x *H. brachyantherum*, in North America; *H. lechleri* x *H. parodii*, *H. tetraploidum* x *H. fuegianum* in South America; *H. jubatum* x *H. secalinum*, in Europe).

It is important to be used s combination of cytogenetical, biochemical and morphological characters in order to assure a correct delimitation of one species. Some characters are common to most of the species, for example fragile rachis to maturity while the others have characteristics just for one or for some species.

Some taxa are considered as being some “critical” ones because the patterns of variability assurance are still insufficiently clarified yet. This is the reason for which it has sometimes reached to sub-divide species in two or more subspecies. Subspecies occupy different areas in accordance with traditional concept (having a partial overlapping) and “typical” representatives of each species are morphologically different from one another. There are sometimes forms of transition between subspecies, in areas where their distributions overlap because of incomplete sterility barriers.

Hybridization and genes transfer from one species to another are possible because of that fact that is the case of *H. patagonicum* diploid from South America to which were found five subspecies (Bothmer et al., 1986a, 1988c) and also that of *H. brevisubulatum sensu lato* an Asiatic complex polyploid which also had five subspecies (Landström et al., 1984).

There is another situation to the species of *H. bulbosum* where are known only diploid and tetraploid cytotypes (cytotype is a group of members within the species and having definite cytotaxonomical and cytological features). Both cytotypes may help to taxonomic recognition (Baum and Bailey 1985a).

They are not recognized as distinct taxa because there is no morphological characteristic (or a characters combination) to make a clear distinction between the two cytological forms (Jørgensen, 1982). The situation has been similar somehow to *H. brachyantherum* from North America as to that from East Asia. Diploid form has been described as a separate species – *H. californicum* – having a limited distribution in California. Characters used to divide diploid from of tetraploid one (appearance of the lateral spikelets) allowed to maintain both forms as distinct.

Morphological data

The main character of diagnosis within *Hordeum* genus is represented by the presence of mono-flowered spikelets at each node of rachis. There are pedicles only to lateral spikelet, excepting some forms of *H. vulgare*. The most wilde species of the genus resemble among them by size and general aspect. Only *H. vulgare* has a big variability of the size and very variable spikes. *H. bulbosum* are wide/spread but they are placed inside wild species group.

The specie of *Hordeum* genus was divided in annual and perennial forms. *H. brevisubulatum* and *H. guatemalense* are the only ones which presents short rhizomes (these two species have sterile shoot, especially in cultivation). Basic leaves sheaths are generally hairy but the superior ones are glabrous. An exception is represented by *H. intercedens* who has hairy upper leaf sheaths.

The nodes are glabrous to hairy and the culms are mostly erect but in a few cases they are de- or procumbent.

Leaves are flat or more or less involute and hairy on the abaxial part as well as in adaxial one, especially above the nerves.

The spikelets are identically formed, varying in form, size and color. The rachis is flat with shorter or longer hairs or with bristles on the edges, being generally longer at the upper part, close to spikelets. There are three mono-flowered spikelets of each node, making the so-called triplet.

Central spikelets usually have a very well developed rachilla, while in most species the rachilla is lacking in the lateral spikelets. Each group of three spikelets is inserted alternately and distichously on either side of the rachis. The central spikelet is sessile in most species. The glabrous to hair lemma extends into an awn the palea can be glabrous to hairy one, more or less bifid in the apex. The central spikelet is subtended by two glumes that are setaceous to more or less flat at their basal part.

The lateral spikelets are pedicellate and sustained by two glumes which are different in shape and size to some species. The pedicel of lateral spikelets can be curved or straight.

Lateral flowers are staminate or completely sterile, being sometime both fertile females and males. Lemma is so much reduced in some cases that it can be described as a rudiment (the palea lacking). According to species, the lemma extends into a shorter or longer awn.

Anthers vary a lot in size the longest being found to species in outcrossing species, the smaller ones in self-pollination species, usually fixed at their basis, yellow or with spotted pigmentation.

The ovary is hairy having two long or short pinnate stigmas.

Mature caryopses are usually tightly enclosed in the lemma and palea. At maturity the rachis becomes fragile and it shatters dehisced the three spikelets just above each node as a unit. *H. bogdani* has (in most cases) a tough rachis at maturity and its spikelets shatter independently. Most cultivated forms of *H. vulgare* have a tough rachis at maturity.

Specific spreading area of *Hordeum* genus

Hordeum is occurs in temperate areas both in northern and hemisphere and in the southern on, just as many other genera of *Triticeae* tribe, reaching in subtropical areas from central South America, arctic part of North America and Central Asia, from the sea level to over 4500m height in Andes and Himalayas.

Centres of diversity for *Hordeum* are placed in four areas of the globe:

- a) Southwest Asia where barley has been cultivated since Antiquity
- b) Central Asia
- c) Western North America
- d) Southern South America where there is recorded the greatest number of native species (seventeen).

Some species (*H. brevisubulatum*, *H. bulbosum* and *H. brachyantherum*) are largely wide spread. Some of them (*H. erectifolium* from Central Argentina, *H. guatemalense* from north of Guatemala and *H. arizonicum* from South of USA and northern Mexico) are known just in one or few location. Some species (*H. murinum*, *H. marinum* and *H. jubatum*) became weeds in many areas of the world.

Ecology

The majority of the *Hordeum* species are confined to grassland habitats being some annual or perennial ones. Some perennial species may become annual because of limiting climatic factors.

Annual taxa are met where the summer rainfall does not permit a permanent vegetation cover. The Mediterranean area, for instance, contain annual species (*H. vulgare* subsp. *spontaneum*, *H. murinum* and *H. marinum* are natives. All three species have summer and winter types, the latter one occurring in arid areas where it flowers and ripens in the early spring before the dryness summer. Other annual species are found in central and western part of North America which also has a Mediterranean climate. Thus, *H. pusillum*, *H. intercedens* and *H. depressum* are found in spring climate areas which have saline soils. *H. arizonicum* is a perennial species with a short period of vegetation in most of the cases and adapted to drained riverbeds and to saline areas which manifest a severe drying in summer time when it is cultivated it also has a short life, being unable to produce bushes (the true annual species can produce strong leafy tufts).

H. euclaston, an annual species having its origins in South America grows in habitats similar to *H. pusillum* species but also in grazed fields (not necessarily saline), the perennial *H. flexuosum* and *H. stenostachys* occupying more humid sites in the same field.

Annual species are met mostly to low heights but they can reach to almost 1000m and even more in prairies, pampas and steppe areas. The perennial *Hordeum* species can be found frequently nearby perennial grassland. *H. secalinum* grows along the seashore as well as in inland meadows in Europe and North Africa. *H. brevisubulatum sensu lato*, *H. bogdanii* and *H. roshevitzii* are found on grasslands and on those parts around rivers, with salty soils, to heights between 1000 to more 4000m in the whole Asia.

H. bulbosum can be found in Mediterranean area and Southwest of Asia, its perennial in these dry areas being determined by its bulbous, basal stem internodes.

H. jubatum and *H. brachyantherum*, perennial species having their origins in North America can be found on seacoasts and on low meadows and *H. brachyantherum* being also found to heights even on Alpine meadows to 4000m. *H. jubatum* is found most of the times in more saline and drier areas. These two species are rarely met together and when this thing happens they can spontaneously hybridize and form hybrids. The diploid cytotype of *H. brachyantherum* subsp. *californicus* is often found in alkaline soils. Tetraploid form of *H. bulbosum* grows in riverside areas and around field cultivated with *H. vulgare*, in Greece.

South American perennial species are found on the seaside and until to 4000m height. Some species are found to low heights especially in the southern part of South America but in Andes many of them may be found also at higher elevation.

On Tierra del Fuego *H. lechleri*, *H. fuegianum* and *H. pubiflorum* occur in seashore meadow and grassland in river estuaries, both fresh and salty. Further north these species go up into the mountains. *H. pubiflorum* is sometimes encountered in open *Nothofagus* forest meadow.

Characteristic *Hordeum* habitats in South America are depressions, hilly areas and river coasts. The subsp. *H. patagonicum* and also *H. lechleri* and *H. halophilum* are common to areas with still waters during wintertime and salty riverbeds in summer time. The last two species are also found together with *H. parodii* and *H. tetraploidum* in richer meadows.

A peripheral biotope for *Hordeum* genus belongs to *H. patagonicum* subsp. *magellanicum* which is found on sandy beaches of the coast of Atlantic (South Argentina). *H. halophilum* and *H. lechleri* are found to high altitudes from central and north of Argentina. *H. comosum* can be found in dry and stony hilly areas with sparse vegetation having sometimes different associations met to over 4000m height. This species has a well-developed root system.

H. halophilum and *H. muticum* can be found to over 4000m altitude in the puna steppes in Andes (North Argentina and Bolivia) or in marshy meadow and regularly submerged alpine grassland. The latter two habitats are also common to *H. guatemalense* in Central America.

There are hybrids forms in southern part of South America. There had been sometimes recorded hybrids presence in other parts of the world because of the fact that there are no different species in the same place (the case is met in South America).

Reproduction and infraspecific variability

Many of the species of *Hordeum* genus are either annual or perennial ones; the first ones including both winter and summer annual forms.

The endogamy prevails to annual species even if some of them may show a crossed pollination. For example, *H. vulgare* subsp. *spontaneum* and sometime subsp. *vulgare* show rather open flowering which promote out-breeding. However there are variations about the degree of external pollination even in the middle of populations. It is not really necessary that pollination may be “auto” type, this fact being mostly represented by biochemical and morphological variation within populations.

Most of perennial taxa have a variable system of reproduction having no specialization. Some species as it is *H. patagonicum* are mainly inbreeders, having short anthers and stigmas and flowers which mostly do not open.

Two species (*H. bulbosum* and *H. brevisubulatum*) are almost obligate outbreeders. Both of them present a self-incompatibility system which prevent self-fertilization (Lundqvist 1962, Bothmer, 1979), even if this process has a frequency of 2-3%. Usually some of the species, *H. secalinum* and *H. tetrapolidum* are mainly outbreeders, even if they do not have a typical morphology for external pollination: long and pollen-rich anthers (which out freely) large stigmas, open flowers and a certain protandry in some case.

There are two obvious situation regarding seed dispersal:

a) One evolutionary line is towards wind dispersal. These species have small and light seeds, with very long, light and slender awn, and glumes which bend outwards to around 90° and thus serve as an elegant flying and tumbling apparatus. *H. jubatum*, *H. lechleri*, *H. procerum* and *h. comosum* belong to this category.

b).The other evolutionary trend is towards zoochory, dispersal by animals. This is found in *H. vulgare* (including both subspecies), *H. murinum* and *H. bulbosum*. This species have big, heavy seeds. The awns and rachis are densely covered with stiff, straight hairs which attach to the fur animals or the clothes of humans.

Relationships between genome and filiation in *Hordeum* genus

Homologous chromosomes pairing completely realized in meiosis; non-homologous chromosomes do not form pairs while the homoeologous ones do but it is an incomplete process. The pairing behavior of the genome of two species is normally analyzed in meiotic mataphase I of hybrid and it is expressed by medium number of chiasmata per cell. There is the possibility of some errors in meiotic pairing assessment but valid conclusions can be shown by the analysis of corresponding cells number and hybrid combination. There are known the attempts of realizing an affiliation based only on genomes studies, but this criterion has not been entirely agreed with until present time.

Genomic interrelations are complicated within *Hordeum* genus because of the presence of many genomes. There are four fundamental genomes to diploid level. *H. vulgare* x *H. bulbosum* hybrid is usually characterized by a very high meiotic pairing (up to seven ring bivalents). Each of the two species share the genome named **I**, which is not present in any other species of *Hordeum* (Figure 1). The tetraploid cytotype of *H. bulbosum* forms a high frequency of tri- and quadrivalents, indicating it is a true autotetraploid with genomic designation **II** (Jørgensen, 1982).

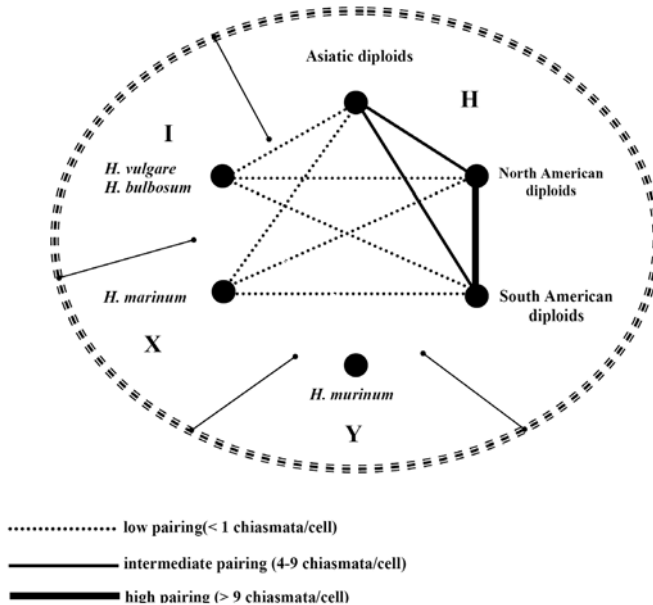


Figure 1. Average meiotic pairing between different diploid species in *Hordeum*.

I, X, Y and H represent the genomic designation.

No diploid hybrids with *H. murinum* were available for meiotic analysis (cf. Bothmer et al., 1986a - modified).

H. murinum annual species does not show any chromosomal homologies with other species in spite its morphological similarities to some of the other *Hordeum* species, having a special genome which has initially been **X** noticed (Figure 1). This genome is common to *marinum* and *gussoneanum* subspecies (Bothmer et al., 1989c). The cytogenetic behavior of

H. marinum subsp. *gussoneanum* tetraploid has been a disputed one. This forms almost exclusive bivalent ones in meiosis, these indicating an allopolyploid nature. The pattern of some isoenzymes and the presence of only one satellited chromosome pair in the karyotype gives reason for the hypothesis according to which there are present to unrelated genomes within this tetraploid (Jørgensen, 1982, 1986; Jaaska and Jaaska, 1986; Jaaska, 1992).

The hybrid resulted presents a complete meiotic pairing between di- and tetraploid forms of *H. marinum* has full meiotic pairing. This one forms (trivalent ones) almost exclusively trivalent ones, a fact that indicates a high degree of homology among the chromosomes (Bothmer et al., 1989c). This fact shows autopolyploid nature of *H. marinum*, 4x, combined with a very strong genetic regulation for bivalent pairing. A supplementary reason for autopolyploid origin is emphasized by a pair of chromosomes with a similar morphology to the satellited chromosomes pair having an inactive nucleolus organizer region (Linde-Laursen et al., 1992b). One chromosome of each of the two pairs contributes to a bivalent formation in *H. marinum* subsp. *gussoneanum* (4x) x *Secale cereale* – hybrids with up to seven *Hordeum* ring bivalents. Thus, the tetraploid *H. marinum* has most probably originated as a hybrid between two biotype of diploid *H. marinum*.

As it results from the study of interspecific hybrids, the diploid form of *H. marinum* (subsp. *glaucum*) has already had another genome, initially called “Y”. There is no chromosomal homology among the polyploid of the *H. marinum* complex (subsp. *murinum*, 4x, and subsp. *leporinum*, 4x and 6x), and other *Hordeum* species (Bothmer et al., 1988b).

The hybrids show an intermediate to high meiotic pairing in hybrids of all the other diploid species of *Hordeum* genus (3-7 bivalents and 5-14 chiasmata/cell) indicating the fact that they have a common genome, named **H** (Bothmer et al., 1986a). There are certain differences between the diploids of Europe and those of America (Figure 1). All the eleven South American diploids species show a much or less complete pairing in their hybrids indicating little genomic differentiation in spite of some important morphological differences. *H. intercedens* and *H. pusillum* the North American annual diploids are closely related to diploid species of South America, and they have no genomic difference than the other ones (Bothmer et al., 1985b, 1986a). The perennial diploid *H. brachyantherum* subsp. *californicum*, native to western North America, is more closely related to the Asiatic diploids, *H. bogdanii*, *H. roshevitzii*, and *H. brevisubulatum* subsp. *brevisubulatum* than to the South America taxa.

The genome pattern is much more complicated at the polyploid levels (4x and 6x). The polyploids (4x and 6x) which belong to the complex with Asian *H. brevisubulatum* outbreeding, with all the five subspecies, are autopolyploids, based on the **H** genome (Dewey, 1979; Landström et al., 1984). Most of the other polyploid taxa belonging to *Hordeum* genus are of the segmental allopolyploid type with an intricate pattern of relationship based on the **H** genome. The American tetraploids (*H. jubatum*, *H. brachiantherum*, *H. guatemalense*, *H. tetraploidum*, and *H. fuegianum*) are genomically very similar (Bothmer et al., 1988b). They behave as real allopolyploids with two unrelated genomes. However, a relatively high pairing indicate an important degree of homology between the *Hordeum* chromosomes and intergeneric hybrids, especially to *Secale cereale*. It has been decided that both genomes are closely related. The lack of pairing between homocologous chromosomes has been shown in *H. jubatum* species (Wagennar, 1960; Gupta and Fedak, 1985).

H. depressum, the annual tetraploid, from North America, has been considered a typical allopolyploid with the **H** genome in combination with an unrelated genome (Bothmer et al., 1988b). It can be a segmental allopolyploid or even an autopolyploid, but with a very strong diploidizing mechanism, similar to that formed to *H. marinum* and *H. murinum*. This fact is assessed by results from *Secale* sp. x *H. depressum* hybrids that show a very high pairing between the two genome of *H. depressum* (Petersen, 1991a, b). The nature of *H. secalinum*, perennial tetraploid (Europe) and *H. capense* (South Africa) is still not clear. They behave as allopolyploids having one **H** genome together with a second unidentified genome (Bothmer et al., 1988b). The American hexaploids *H. procerum*, *H. lechleri*, *H. parodii* (all in South America) and *H. ariyonicum* (North America), are all segmental allopolyploids with different variants of the **H** genome.

Interspecific relations grafted onto enzymatic differences

Jørgensen, in 1986, suggested the formation of some relations between different species taking into account the study of some isoenzyme systems in *Hordeum* genus.

These relations have been inferred by the process of electrophoresis of six enzymes: glutamate oxaloacetate transaminase (Got), phosphogluconate dehydrogenase (6-Pgd), malate dehydrogenase (Mdh), isocitric acid dehydrogenase (Idh), and alfa and beta-amylase. These systems have been chosen among 21 different enzymes, because they display a high level of interspecific variation and a minimum of intraspecific variation which allow its use as markers in the study of taxonomic relations among species. Eleven loci were scored for in the selected systems revealing altogether 153 different alleles.

Diploids

The *Hordeum* species can be grouped in three ones taking into account electrophoretic data (Jørgensen, 1986):

1. *H. vulgare* group which comprises three species: *H. vulgare sensu lato*, *H. bulbosum*, and *H. murinum sensu lato*. *H. murinum* is more connected to *H. pubiflorum* group than to *H. vulgare*. *H. vulgare* subsp. *vulgare* and subsp. *Spontaneum* could not be differentiated by enzymatic characters used in the experiment. Both tetraploid cytotypes *H. murinum* subsp. *murinum* and subsp. *leporinum* could not be separated either. A detailed analysis of seed proteins of *H. murinum* aggregate was carried out by Booth and Richards (1978).

2. This group comprises *H. marinum sensu lato* monotypic. The subspecies *marinum* and *gusoneanum* present very distinct isoenzymes.

3. *H. pubiflorum* group comprises all the other species of *Hordeum* genus. *H. pubiflorum* and *H. stenostakys* has a central position as most of evolutive directions which seem to be connected to these species. The diploids of this group can be divided into four subgroups:

- a. The first subgroup contains only one species – *H. muticum*. This species only differs enzymatically spreading but its area of distribution is also different from that of other species of genus.
- b. *H. chilense* from Chile and *H. roshevitzii* from Central Asia form the second subgroup. This unexpected relation is also represented by high frequency of bivalents in meiosis to the hybrids of the two species.
- c. The third subgroup comprises diploid species from South America (with the exception of *H. muticum* and *H. chilense*) and *H. pusillum* and *H. intercedens* from North America. These relations have been in accordance with interspecific crosses realized by Bothmer et al. (1985b, 1986a).
- d. The Asian species of *H. bogdanii* and *h. brevisubulatum* and also the North American species of *H. brachyantherum* are included in the fourth subgroup. This subgroup may show a certain phytogeographical relation between the continents still evident from the presence of the tetraploids *H. jubatum* and *H. brachyantherum*, both in Asia and North America.

Polyploids

The polyploidy has the greatest significance for speciation within *Hordeum* genus. A comparison between enzymes of intraspecific cytotypes may demonstrate the fact that diploid phenotype can be distinguished among polyploids. Allopolyploid nature of some polyploids is also displayed by the frequency of heterozygotic phenotypes connection. For instance, Got allele has been found to most polyploids of *H. pubiflorum* group and it only appeared in *H. marinum* among diploid *Hordeum* taxa. This allele has been expressed as part of three electrophoretic bands in polyploidy and which fixed heterozygotic pattern. Another allele that emphasized fixed heterozygosity in this pattern plays an important role in diploid species of *H. pubiflorum* group. Got allele determines the synthesis of some dimmer enzyme and the third band of electrophoresis in a hybride one. The intensity of the third band in phenotypisation of the Got allele within *H. lechlerii* and *H. procerum* hexaploids suggest the fact that this gene has been identified in only one dose of *H. marinum*; the other one is found in two doses. The two alleles have the same intensity within the tetraploids having the same pattern.

The variability of chromosomes number and the karyotype

The 45 taxa of *Hordeum* genus are essentially some diploids ($2n=2x=14$), tetraploids ($2n=4x=28$) or hexaploids ($2n=6x=42$) ones having $x=7$ as a basic number. There have noticed aneuploid plants in some cases which originated by elimination or duplication of some chromosomes (Linde-Laursen et al., 1980, 1986b, 1990a).

The karyotypes are symmetrical with centromeres located at median and submedian positions. The length of mitotic chromosomes varies enough from 5 to 12 μm . This variability can be due somehow to differences induced by applied cytological techniques. Some chromosomes, especially those that have satellites have such a characteristic morphology that they can be used as markers for species identification (Rajhathy and Symko, 1966).

Many diploid species of *Hordeum* have karyotypes comprising four pairs of metacentrics one pair of submetacentrics and two pairs with satellite chromosomes, but some taxa (*H. marinum* and *H. muticum*) have only one pair with satellite. In contrast, *H. brevisubulatum* subsp. *Brevisubulatum* and some population of the cytotype of subsp. *violaceum* have three chromosome pairs with satellite.

There are cytotypes having one two, three or four pairs of chromosomes with satellites among tetraploid and the number of chromosomes pairs with satellites can be either two, four, five or six to hexaploids.

Population with an obvious chromosomal rearrangement have been identified only to *H. vulgare* (translocations, inversions), *H. procerum* (translocation) *H. brevisubulatum* subsp. *violaceum*, 2x (translocation), and *H. brachyantherum*, 4x (translocation) (Linde-Laursen et al. 1980, 1986a, 1990a; Konishi and Linde-Laursen, 1988).

There have been accumulated knowledge about the karyotypes of the species that belonged to *Hordeum* genus by use of banding techniques (C- or N-banding) thus making possible the acknowledgement of chromosome complements of all the 53 cytotypes within the genus, in the last 15-20 years. All inbreeders have a polymorphism of banding which make them different from one another, while there have been emphasized no such polymorphism within the populations and in cultivated species (excepted in single cultivated barley and *H. bogdanii*). Except for a population of *H. secalinum* from southern Spain and the two South American species, *H. tetraploidum* and *H. parodii*, that are considered more or less allogamous (Bothmer et al., 1986c), all outbreeding material has shown intrapopulational and intraplant banding pattern polymorphism. The banding pattern allows homologous identification among populations in some diploids and in a certain extent in some polyploids inbreeders.

The number of visible bands per chromosome varies from zero to fifteen but the variation within the species has been more reduced. Most of the bands are thin, but they can vary in size from very small to large (representing more than 10% of arm length). The chromosomes with most obvious bands have been found to a population of *H. murinum* subsp. *Leporinum*, 6x (Linde-Laursen et al., 1989b). In the majority of the species, the bands tend to be randomly disposed. However, in *H. bulbosum* nearly all bands are paracentromeric (Linde-Laursen et al., 1990b), and the karyotype of *H.*

vulgare is distinguished by having mostly pericentromeric and paracentromeric bands. Most taxa of *H. brevisubulatum* have telomeric bands which are some obvious as well as a reduced number of intercalary and centromeric bands (Linde-Laursen et al., 1980). The bands are normally present on one or both sides of the nucleolar constriction of chromosomes with satellites.

The analysis of C-banding and chromosomes morphology shows that all diploid species of *Hordeum* from America have similar karyotypes, excepting *H. muticum* and *H. cordobense*. These aspects are relevant for their framing into three different sections. American tetraploid species of *Hordeum* (with the exception of *H. depressum*) have karyotype (obtained by C-banding techniques) similar enough, a fact that suggest a common origin. The marker chromosomes of the constituent genomes show the greatest similitude with *H. roshevitzii* (Asia) and with *H. brachyantherum* subsp. *californicum* (North America) suggesting an allopolyploid origin of these two diploid taxa. American hexaploids are allopolyploids. All the other combine genomes in a similar way those found to most of American tetraploids with the exception of *H. brachyantherum* (6x) and to which it is added a genome of one American diploid species. *H. brachyantherum* (6x) may combine genomes similar to *H. depressum* and *H. brachyantherum* subsp. *californicum* (Rajhathy and Symko, 1966; Linde-Laursen et al., 1986a, 1990a, 1992a; Baum and Bailey, 1989a).

H. secalinum and *H. capense* have similar karyotypes (which have been recorded with C-banding help) indicate their close relation (Linde-Laursen et al., 1986b).

Even if *H. vulgare* and *H. bulbosum* contain the same genome, named **I** (Bothmer et al., 1986a) the differences between C-banded karyotype will emphasize the fact that these species are not very close related (Xu and Snape, 1988; Linde-Laursen et al., 1990a).

The karyotype of *H. bulbosum* (4x) represents an argument for the fact that it is a derived autopolyploid of a diploid cytotype. Such a close connection has not been noticed to karyotypes of *H. brevisubulatum* autopolyploid complex (Linde-Laursen et al., 1980). *H. marinum* subsp. *gussoneanum* (4x) karyotype obtained from C-banding techniques and as well as *in situ* hybridization (Linde-Laursen et al., 1992b) has agreed with the idea that this one is an autopolyploid derived from *H. marinum*. *H. marinum* tetraploids and hexaploids contain the genome of *H. marinum* (2x). The sources of the other genomes have not been identified yet. The C-banded karyotypes of the remaining taxa give no clear indication of the closer relationship.

Gene resources in *Hordeum* genus

The utilisation of wild *Hordeum* species in the barley breeding for the transfer of some useful genes has not had a great success on it was the case of cultivated wheat. This situation has two causes:

- Barley is a diploid one and it is much more sensitive to minor genetic imbalances comparing to wheat which is a polyploidy one and it displays a buffering effect;
- Most of the wild species of the *Hordeum* genus are much more distantly to cultivated barley than are *Aegilops* and *Triticum* species to bread wheat (which have given the genes to it).

The species of *Hordeum* can be divided in three categories based on their relation to cultivated barley and how accessible they are as gene donors to the crop species.

Primary gene pool

This species are closely related to cultivated species (there are no biologic barriers or if they are these are unimportant ones) for gene transfer. The primary gene pool is represented by local races to barley, races that are still cultivated or they have been used recently. However, landraces disappear very quickly and they cannot be used for long in large regions as there are those of Central and North Europe. They are still used as food in Central and Southwest Asia as well as in North Africa (including Ethiopia). The progenitor of cultivated barley – *H. vulgare* subsp. *spontaneum* also belongs to the primary gene pool.

A major problem for the use of subsp. *spontaneum* in barley breeding is the presence of the several non-desirable characters as: rachis frailty, uneven germination, stiff awns, shrunken seeds as well as the necessity of a variable period of vernalization. There are necessary some generation of pre-breeding to transfer the genetic material in a genotype and afterwards this will be used in conventional breeding programmes. The resistance to different diseases and the one determined by specific genes become part of the features that are important for the transfer.

Secondary gene pool

All wild species are included in here and which have a good capacity of pairing with cultivated ones but a series of sterility factors have been determined to them.

Perennial *H. bulbosum* (di- and tetraploid species) originating in Mediterranean region has been the closest related to cultivated barley and separated from subsp. *spontaneum* and which has **I** genome type. *H. bulbosum* has been widely used in cereal breeding because its chromosomes are normally eliminated in the young *H. vulgare* x *H. bulbosum* hybrid embryos during the first days of development, leaving one set (7) of barley chromosomes. The embryo develops into a haploid barley plant which can be chromosome-doubled through application of colchicine. It gives rise to a completely homozygous line of barley, which may be used directly in a breeding programme. Sometimes chromosome elimination does not take place and the embryo develops into a true stable hybrid. The chromosomal pairing during meiosis is often very high in the hybrids, but the fertility is extremely low (Bothmer et al., 1983; Xu and Snape, 1988). Sometimes during

latter meiotic phases or during the pollen development the normal process fails, leading to formation of sterile gametes but this process has not been entirely known. *H. bulbosum* presents some interesting characters for transfer to cultivated barley as it is: resistance to powdery mildew (Jones and Peikering, 1978; Gustafsson and Claesson, 1988; Xu and Snape, 1989).

Tertiary gene pool

All the other *Hordeum* species belong to the tertiary gene pool of cultivated barley. This fact shows that interspecific hybrids can be established through embryo rescue techniques. These species have a different genome of that cultivated barley, and the hybrids with it are high sterile. So far, the germoplasm of these wild species has not contributed to the progress of barley breeding. The development of new techniques as are: somatic hybridization and gene transformation may make the genetic content of these taxa available for transfer in the future. Several of the wild species have been shown to contain interesting resistance genes (Bothmer et al., 1995)

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