

**PATTERNS OF DIVERSIFICATION IN
MEDITERRANEAN OAT GRASSES (POACEAE:
AVENEAE)**

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Abstract

Several genera of the *Aveneae* have a centre of species diversity in the Mediterranean Region and its vicinity. Based originally on the life form of a perennial herb, numerous edaphically, climatically and altitudinally differently adapted species complexes have evolved in the area. Most of these complexes show west-east disjunctions and contain geographically, sometimes even edaphically vicarious taxa with complementary distribution. A transition from mesomorphic to xeromorphic habit occurred independently in different genera and species groups. The correlations of this process with polyploidization, geographical distribution and wide or narrow ecological amplitudes are critically examined. The transition to an annual life form is regarded as a further way of adaptation to Mediterranean type climate which permitted to expand specifically in unstable, ephemeral habitats.

Tribe Aveneae

The tribe *Aveneae* is part of the grass subfamily Pooideae, a subfamily with worldwide distribution, but with clear centres of diversity in the temperate regions of both hemispheres. Most genera occur in Eurasia which suggests that the subfamily originated on the northern land mass. The physiological adaptation to non-tropical, strongly seasonal and partly cool climates was supposedly one of the most significant processes in the early evolution of the subfamily. Another important trait, characteristic of the *Pooideae* and in particular of the *Aveneae*, was the evolution of numerous annual genera adapted to the Mediterranean winter rainfall regime (cf. CLAYTON & RENVOIZE, 1986). Uncommon characters of the subfamily *Pooideae* are the frequent occurrence of large chromosomes, and modifications of the storage material of the endosperm found especially in the tribes *Aveneae* (see below) and *Bromeae/Triticeae* (starch grains simple, rounded).

Although the detailed taxonomic delimitation of the trib. *Aveneae* and its taxonomic subdivision into subtribes are still in dispute (cf. STEBBINS & CRAMPTON, 1961; MACFARLANE & WATSON, 1982; TSVELEV, 1983, 1989; CONERT, 1983-1992), there is no doubt that the genera *Avena*, *Helictotrichon* (incl. *Avenula*), *Trisetum*, *Arrhenatherum*, *Pseudarrhenatherum*, *Koeleria*, and some others form the core of this tribe. Morphologically and anatomically, the *Aveneae* are characterised by usually many-flowered, laterally compressed spikelets, a rudimentary uppermost floret or rachilla extension, two large glumes, lemmas with an elaborate and geniculate dorsal awn which is seldom found elsewhere in grasses. The awn has a twisted column except for some genera (*Deschampsia*, *Koeleria*, etc.). However, there are many exceptions, and these

characters do not always occur together. The architecture of lodicules, seeds and leaf blades is festucoid. The occurrence of frequently soft or liquid endosperm is a peculiarity of the tribe *Aveneae* since it is else found only in a few genera of *Poeae* and *Hainardieae*, but never outside of the subfamily *Pooideae*. It was argued that this type of storage material might have adaptive significance (CLAYTON & RENVOIZE, 1986: 118) since, weight for weight, lipids contain about twice the energy of carbohydrates.

The *Aveneae* comprise roughly 60 genera and more than 1000 species. Geographically they are virtually limited to the temperate zones of both hemispheres, but bridge the tropics mainly on the tops of high mountains, in Africa for example, *Helictotrichon*, *Koeleria*, *Deschampsia*, *Agrostis*, *Aira* (cf. MEUSEL & al., 1965; LANGE, 1995a).

Subtribes of *Aveneae*: *Duthieinae*, *Aveninae*, *Phalaridinae*, *Alopecurinae*

The mentioned genera of *Aveneae* were included by CLAYTON & RENVOIZE (1986) together with 17 other genera (*Gaudinia*, *Ventenata*, *Deschampsia*, *Holcus*, *Corynephorus*, *Aira*, etc.) in the subtribe *Aveninae* which was defined thus in a comparatively broad sense if compared, for example, with the much narrower subtribe concept of CONERT (1983-1992).

The subtribe *Duthieinae* comprises a few genera which are characterised by the occurrence of frequently more original floral structures than found in the *Aveninae*: three lodicules are present in the Mexican genus *Metcalfia* and the Balcanic-Caucasian *Danthoniastrum* instead of two in the *Aveninae*, three stigmas in the mainly Himalayan genus *Pseudodanthonia* instead of two in the *Aveninae*. Based on such grounds, the *Duthieinae* are regarded as being the most primitive subtribe of *Aveneae*. An interesting observation refers to the occurrence of two-celled microhairs in *Danthoniastrum* (SAVILE, 1987), which are otherwise absent in the whole subfamily *Pooideae* except for the tribes *Lygeae* and *Nardeae* which were tentatively included in the *Pooideae* by PILGER (1954) and CLAYTON & RENVOIZE (1986). The presence of such microhairs in these taxa might be interpreted as the retention of a primitive character state, or else would cast further doubt on the view (cf. WATSON & al. 1985) that these taxa belong to the *Aveneae*.

The remaining subtribes of *Aveneae* are the *Phalaridinae* with *Hierochloe*, *Phalaris*, and *Anthoxanthum* and the *Alopecurinae* with approximately 27 genera. The subtribe *Alopecurinae* comprises apart from *Alopecurus* some other well known genera such as *Agrostis*, *Calamagrostis*, *Ammophila*, *Triplachne*, *Lagurus*, *Apera*, *Mibora*, *Beckmannia*, *Phleum* and a number of small genera with restricted geographical distribution in the Southern Hemisphere, frequently Australia and New Zealand. However, the *Phalaridinae* are not always included in the *Aveneae* (TSVELEV, 1983; CONERT, 1983-1992), whereas there is general consensus that a considerable part of the mentioned genera of *Alopecurinae* really belong to the *Aveneae*, especially when following the narrower circumscription of the latter subtribe by CONERT (1983-1992). This circumscription excludes, for example, the genera *Phleum* and *Alopecurus* from the

Aveneae and consequently names the largest part of the *Alopecurinae* sensu CLAYTON & RENVOIZE (1986) as subtribe *Agrostidinae*.

Despite of these minor uncertainties in the taxonomic delimitation of the tribe *Aveneae* and its subtribes, it is evident that reductional series have occurred here in the arrangement of floral organs. It leads from a more basic monocotyledonous 3 + 3 groundplan such as partly still present in the subtribe *Duthieinae* to an invariable 2 + 2 scheme of lodicules and stigmas in the much larger subtribe *Aveninae*.

Life cycles of Mediterranean *Aveneae*

Most genera of *Aveneae* present in the Mediterranean Region belong to the subtribe *Aveninae*. This subtribe shows a rich generic splitting in the Mediterranean (Table 1), but comprises additionally a few genera in the Southern Hemisphere (*Amphibromus*, *Relchela*, *Tovarochloa*, *Dielsiochloa*) and North to Central America (*Graphephorum*, *Sphenopholis*, *Peyritschia*). Several genera of *Aveninae* are widely distributed and centred in the more humid regions of Eurasia and reach the Mediterranean only peripherically, and are frequently restricted here to damp places, woodland vegetation, mountain slopes or alpine zones, e.g. *Trisetum*, *Koeleria*, *Deschampsia*, *Holcus* (Table 1).

The typically Mediterranean distributed *Aveneae*: *Aveninae* show a considerable proliferation of biennial to annual genera which are adapted to the Mediterranean type seasonal climate (Table 1): Flowering and fruiting starts near the end of the wet season. The plants decay in the dry season after having dispersed the drought-resistant diaspores. This adaptation to an expressedly strong seasonal climate with a severe drought period is usually connected with the occurrence at open sites in which woody plants are hardly able to compete and dense arboreal vegetation is absent.

Annual life form and this preference for open sites undoubtedly were the prerequisite that some of the annual *Aveneae* could become widely distributed as weeds on arable land outside of their original range. Especially *Avena fatua* ranks among the world's worst weeds. On the other hand, the cultivated oat species including *Avena sativa* were selected by man from such annual weed communities. Noticably, this pattern of being prominent either as weed or as crop plant occurs also in some other pooid grasses with a Mediterranean centre of diversity and appears to have significance also, e.g., in *Secale* or *Hordeum* with their relatives and in the *Triticum/Aegilops* alliance (SIMMONDS, 1976; BAUM, 1977; SIMON, 1980).

The genus *Avena* comprises the largest number of annual species of all Mediterranean *Aveneae*, but contains also the enigmatic perennial *A. macrostachya* (Table 1). This relic species, endemic to the alpine zone of a few high mountains of northern Algeria, fits morphologically the annual species of *Avena* (BAUM, 1968, 1977). However, it deviates from them not only by perennial life form, but also by outbreeding behaviour and its karyotype structure (BAUM & RAJHATHY, 1976). Karyotypes such as found in *A. macrostachya* do not occur elsewhere in the genus *Avena* (RAJHATHY & THOMAS, 1974) but are rather characteristic of the species of the strictly perennial genus *Helictotrichon* (RÖSER, 1989; GREBENSTEIN, 1992). Crossing and DNA *in situ*

| Genus | Life form | Number of species (worldwide) | Habitats | Ploidy levels |
|-------------------------------------|-----------|-------------------------------|--|---------------|
| <i>Helictotrichon</i> ¹ | 2l | ± 100 | dry grasslands, margins of thermophilic woods, open rocky mountain vegetation, rarely damp places | 2x - 20x |
| <i>Pseudarrhenatherum</i> | 2l | 2 | dry grasslands and heaths | 2x |
| <i>Arrhenatherum</i> | 2l | 4 | dry to moderately moist grassland, rocky mountain vegetation | 2x - 4x |
| <i>Avena</i> | (2l)⊙ | ± 25 | dry rocky and weedy places (⊙ only) rocky mountain vegetation (2l only) | 2x - 6x |
| <i>Gaudinia</i> | ⊙ ⊙ | 4 | weedy places | 2x |
| [<i>Trisetum</i>] | 2l ⊙ | ± 70 | meadows, mountain slopes, alpine grassland, sometimes wet meadows (2l only) dry, open places (⊙ only) | 2x - 8x |
| <i>Trisetaria</i> ² | ⊙ | ± 15 | dry open, sandy places | 2x |
| <i>Ventenata</i> ³ | ⊙ | 5 | dry open places | 2x |
| [<i>Koeleria</i>] | 2l | ± 35 | dry grassland, open rocky places | 2x - 18x |
| <i>Rostraria</i> ⁴ | ⊙ | ± 10 | dry sandy, weedy places | 2x - 4x |
| [<i>Deschampsia</i>] ⁵ | 2l | ± 40 | grassland, woodland, moorland | 2x - 10x |
| [<i>Holcus</i>] | 2l | 6 | woodland, open mountain slopes, wetland | 2x - 6x |
| <i>Corynephorus</i> | 2l ⊙ | 5 | sandy places, littoral dunes | 2x - 4x |
| <i>Periballia</i> ⁶ | ⊙ | 3 | sandy places | 2x |
| <i>Aira</i> | ⊙ | 8 | open sandy places | 2x - 4x |
| <i>Aiopsis</i> | ⊙ | 1 | open sandy places | 2x |
| <i>Antinoria</i> | (2l)⊙ | 2 | damp places | 2x |

1, acknowledged here as including *Avenula*, but not the Australian-New Zealand-South American genus *Amphibromus* (cf. Lange 1995b). 2, with *Avellinia* and *Parvotrisetum*. 3, with *Pilgerochloa* and *Gaudiniopsis*. 4, with *Lophochloa*. 5, with *Avenella*, *Vahlodea*, and *Aristavena*. 6, with *Molineriella*.

Table 1. Genera of Mediterranean *Aveneae: Aveninae*. Square brackets indicate genera with a centre of diversity in more humid areas of Eurasia and which reach the Mediterranean Region only peripherally or are restricted here to special sites.

hybridization experiments show that *A. macrostachya* has little cytological relationship with any other species of *Avena* (LEGGETT, 1990; POHLER & HOPPE, 1991, LEGGETT & MARKHAND, 1995), and it is not clear which role *A. macrostachya* might have played in the evolution of annual *Avenas*.

The other biennial to annual genera of Mediterranean *Aveneae* are frequently monotypic (*Aiopsis*, *Antinoria*) or contain only a few species (*Aira*, *Periballia*, *Ventenata*, *Gaudinia*, *Corynephorus*). They have uncommon and probably highly derived morphological characters in floral and inflorescence morphology. Examples

would be the odd structure of awns in *Corynephorus* or the disarticulating axis of the spike in *Gaudinia*. Other floral peculiarities clearly result from reductive processes leading from many- to few- or single-flowered spikelets, from elaborate to minute or absent awns, from hairy to glabrous ovaries, etc. Some genera are ecologically specialised to nutrient-poor sands or \pm salinic soils (Table 1).

The strictly annual to biennial Mediterranean genera of *Aveneae*: *Aveninae* are opposed to an approximately equal number of perennial genera which contain a much higher number of species not only in the Mediterranean Region, but also worldwide (Table 1). With respect to species diversity the perennial genus *Helictotrichon* with its satellite genera *Pseudarrhenatherum* and *Arrhenatherum* shows a much richer evolutionary splitting in the Mediterranean than any other group of the *Aveneae*. These perennials are characterised by

- 1, the establishment of many different and partly large species complexes,
- 2, repeated internal west-east disjunctions,
- 3, edaphic specializations,
- 4, altitudinally differently adapted species groups (primary/secondary) on the base of 3,
- 5, different patterns of parapatric or sympatric distribution,
- 6, extensive polyploid series,
- 7, transitions from mesomorphic to xeromorphic habit,
- 8, floral specializations (dispersal units),
- 9, extended variation of growth forms.

Most of these features are absent in the annual genera of the *Aveneae*, especially 6, 7 and 9. This is partly due to their breeding system (self-fertilizing) and accords to their life form (7, 9) which requires efforts to produce a minimum of elaboration of the vegetative organs. The absence (6) of extensive polyploidy in the annuals (2x-4x, rarely 6x) contrasted with 2x-20x in the perennial genus *Helictotrichon* indicates that the annual *Aveneae* tend to have comparatively small genomes. Important nucleotypic effects of small genomes are, among others, a short duration of DNA replication and cell cycle, which enables annual plants to establish mature, flowering and fruiting individuals within a given time. This correlation between annual life form and comparative small genomes is generally significant in angiosperms (BENNETT, 1972, 1987).

The transition from perennial to annual life form, an important general trait of Mediterranean *Aveneae*, is represented within extant genera only by *Avena* and *Trisetum* (Table 1). The sibling genera *Koeleria* (perennial) and *Rostraria* (annual) can be regarded as a further example, because they are separated from each other only by life form while conspicuous floral differences apparently are absent.

Species complexes

The perennial genera have established the largest species complexes of all *Aveneae* in the Mediterranean Region. While weed communities are dominated by the annuals, the perennial *Aveneae* are very significant in the natural or semi-natural vegetation and may even become physiognomically prominent in some grassland communities. In such types of vegetation, *Helictotrichon* with its allied genera *Pseudarrhenatherum* and *Arrhenatherum* is represented by approximately 40 species in the Mediterranean Region (cf. RÖSER, 1989, 1996; LANGE, 1995a). The occurrence of other perennial genera of *Aveneae* in the Mediterranean, namely *Trisetum*, *Koeleria*, *Deschampsia*, and *Holcus* (Table 1), has to be interpreted rather as an extension from a more northern, Eurasian and North American (holarctic) centre of diversity, where they show an almost closed geographical distribution. However, also in some of these genera a few typical "Mediterranean" species have evolved which usually are orophytic and have a narrow geographical distribution such as several Balkanic or Iberian mountain endemics of *Trisetum* (cf. JONSELL, 1980) or *Holcus caespitosus*, endemic to the Sierra Nevada.

The species of *Helictotrichon* are grouped in four subgenera and a number of species complexes which are informally ranked (cf. Fig. 1). While subgenus *Pubavenastrum* is monotypic (*H. pubescens*) and subgenus *Tricholemma* contains 1-2 species, the subgenera *Helictotrichon* and *Pratavenastrum* comprise a considerable number of species groups, some of which are characteristic of the Mediterranean. These are the *H. marginatum* group (no. 8 in Fig. 1) with 6 species, the *H. bromoides* group with 7 species (no. 9) and the *H. sarracenorum* group with 4 species (no. 12). Other large species groups have a centre of distribution and diversity north of the Mediterranean Sea in the more humid areas of western Eurasia, but reach the Mediterranean by particular, geographically frequently isolated and endemic taxa. Examples are *H. pratense* subsp. *lusitanicum* in northern Portugal (ROMERO ZARCO, 1984; RÖSER, 1996), and the disjunctively distributed Illyrian-Caucasian *H. blaui* (LANGE, 1995a). These are members of the large and except for the Mediterranean widespread Eurasian *H. pratense* group (no. 6 in Fig. 1). This type of representation in the Mediterranean resembles the situation in *Trisetum* and *Holcus*.

Two further species groups of *Helictotrichon* are characteristic of the larger mountain systems of the Mediterranean or its closest vicinity. The *H. sedenense* group (no. 10 in Fig. 1) is represented in the highest mountains of the western Mediterranean by *H. sedenense* which shows a scattered distribution between the western Alps and the Grand Atlas (Fig. 2; RÖSER, 1989). This species is related to *H. decorum*, an endemic of the Carpathians (Fig. 2). The *H. parlatoarei* group (no. 13 in Fig. 1) is endemic to the Alps (Fig. 3). This group of species has a certain centre of diversity at the southwestern edge of this mountain range (Alpes Maritimes, Dauphine, Alpes Graies), where the thermally favourable climate of the Mediterranean still has some influence. The altogether comparatively wide range of the *H. parlatoarei* group in the Alps is largely due to the distribution of a single species, namely *H. parlatoarei* (cf. Gervais 1973).

The closely allied genus *Pseudarrhenatherum* comprises two species (Table 1). *Pseudarrhenatherum longifolium* is distributed between the Normandie and

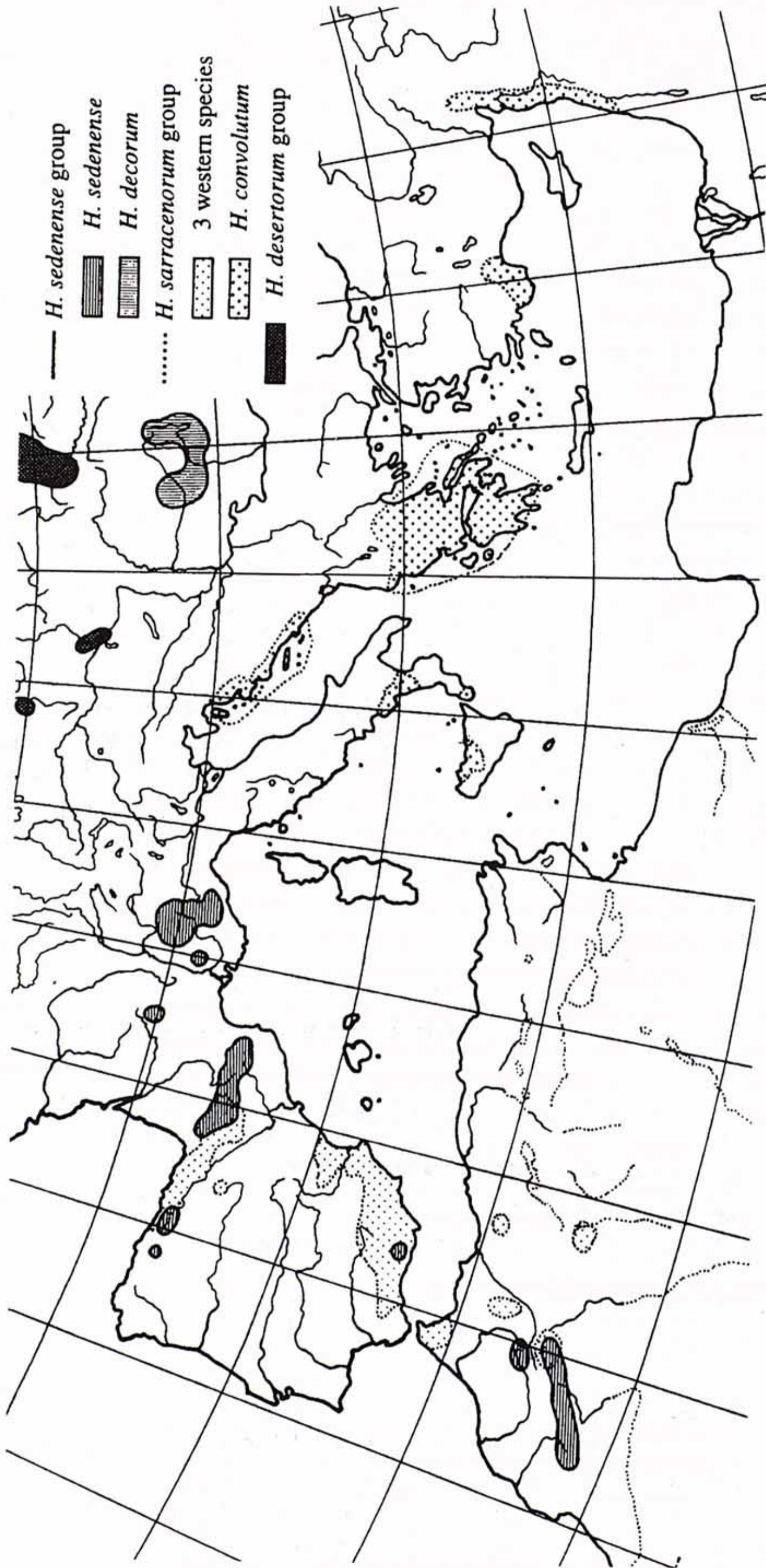


Fig. 2. Species complexes of *Helictotrichon* with disjunctive distribution in the Mediterranean area and its vicinity. The Euro-Siberian *H. desertorum* group is represented in the map by its westernmost outposts.

northwestern Africa in regions close to the Atlantic Ocean (MAIRE, 1953; GUINOCHET & VILMORIN, 1978; KERGUÉLEN, 1975, 1979). On the Iberian Peninsula the distribution is almost closed in the North and West, but isolated stands are also present in the Cordillera Central and southernmost Andalucía (ROMERO ZARCO, 1985a). This type of distribution comes close to that of the *H. marginatum* group in the western Mediterranean (Fig. 3), especially with regard to *H. marginatum* itself (RÖSER, 1989). The second species of this genus, *P. pallens*, is endemic to the coastal mountains of central Portugal (ROMERO ZARCO, 1985a).

The genus *Arrhenatherum* contains 4 species which are partly very polymorphic (HOLUB, 1980, ROMERO ZARCO, 1985b). Especially in the Mediterranean some of them comprise a number of \pm well-defined infraspecific taxa. *Arrhenatherum kotschyi* is the most unmistakable species of the genus and is geographically restricted to southern Transcaucasia, eastern Turkey and northern to central Iran (TSVELEV, 1983). The range of *A. palaestinum* extends from the Near East to the southern and eastern Balkan Peninsula, but the species appears to be hardly different from *A. album* incl. *A. erianthum* (ROMERO ZARCO, 1985b) with Ibero-Mauritanian distribution. *Arrhenatherum elatius* is the most widespread species of the genus. It is very common in the more humid regions of Europe and western Asia. In the drier regions of the Iberian and Balkan Peninsula, Northern Africa and Caucasia it becomes restricted to mountainous zones. As noted by MEUSEL & al. (1965) the distribution of *A. elatius* resembles that of *Helictotrichon pubescens* since both mesophilic species extend from submediterranean/montane exclaves through humid Central Europe to the climatically more continental regions of Middle Asia and Central Siberia (MEUSEL & al., 1965: map 44c; CONERT, 1983-1992: 244). These species evidently possess a considerable ecological variability.

West-east disjunctions

Several genera of perennial *Aveneae* have a disjunctive type of distribution in the Mediterranean Region. Usually these disjunctions are west-east-directed, and the partial areas may be separated by distances of up to c. 1500 km (cf. Figs. 2, 3). Disjunctions are repeatedly found in the genus *Helictotrichon* with the most striking examples in the *H. sedenense* group, the *H. sarracenorum* group and the *H. marginatum* group (Figs. 2, 3). Less wide disjunctions are apparent in the endemic North African subgenus *Tricholemma* and the *H. bromoides* group, where *H. agropyroides* forms a well-defined outpost of this large species group in the eastern Mediterranean (Fig. 3). Similar disjunctive distributions also occur outside of the Mediterranean within the Alpine *H. parlatoei* group (cf. Fig. 3) and the largely Asian *H. desertorum* group (cf. RÖSER, 1996). Given that their close relationship can be confirmed in further taxonomic studies, *Arrhenatherum album* and *A. palaestinum* would be another example for west-east disjunctions resembling that of the *H. sarracenorum* group.

A peculiarity of these disjunctive distributions is that they concern species groups with quite different edaphic and altitudinal specializations. The particular taxa of each species group, though geographically separated, have usually retained their original ecological adaptations in different geographical background.

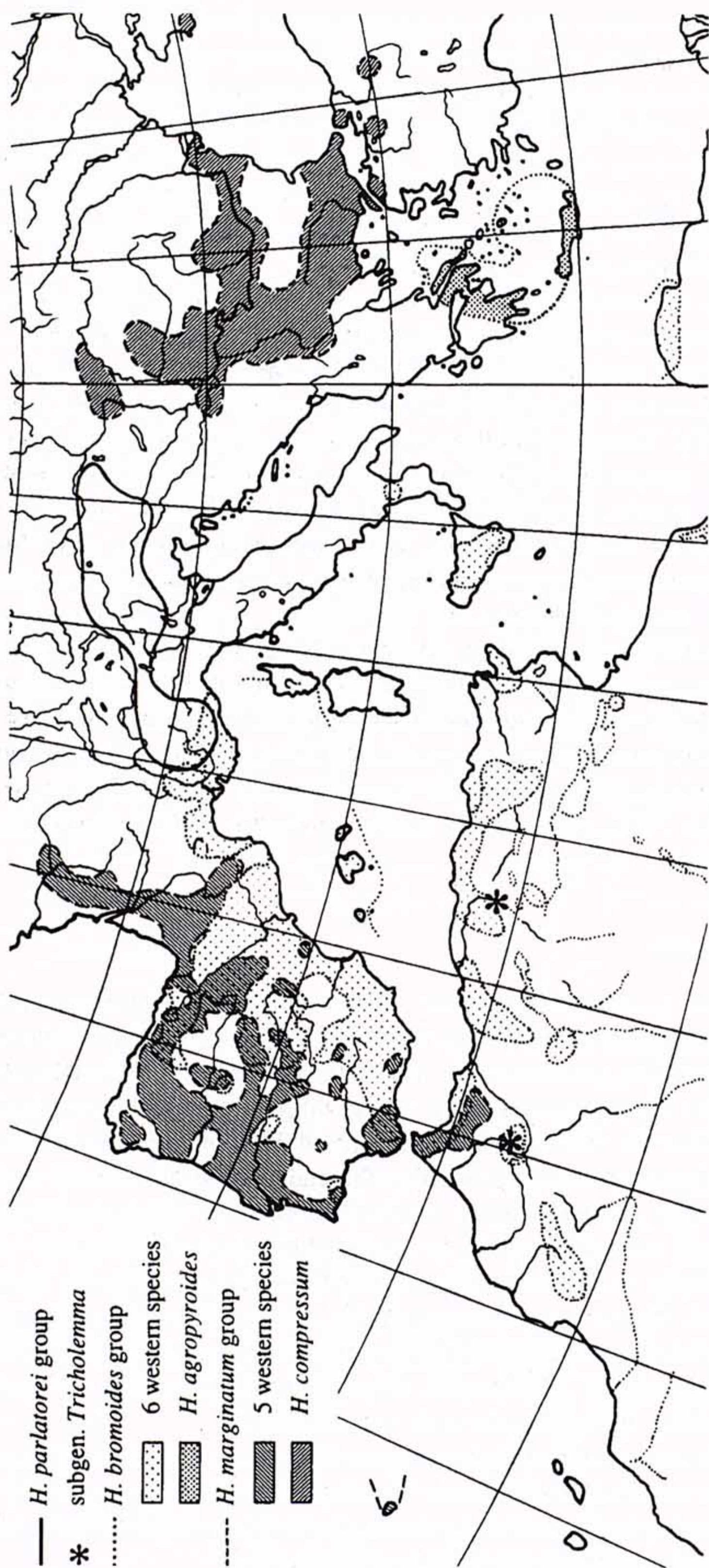


Fig. 3. Species complexes of *Helictotrichon* with disjunctive distribution in the Mediterranean area and its vicinity. The range of the *H. bromoides* groups adjacent to the Mediterranean Sea, while the *H. marginatum* group is distributed mainly in the climatically \pm oceanic European-Macaronesian and the subcontinental Pontic-Pannonian region. *Helictotrichon* subgen. *Tricholemma* shows a relic distribution in North Africa. The distribution of the endemic Alpine *H. parlatoarei* group (subgenus *Helictotrichon*) is indicated by an outline.

Edaphic specialization

Several genera and species complexes show a clear adaptation to either base-rich or base-poor soils. Within the genus *Helictotrichon* the *H. parlatorei*-, the *H. sarracenorum*- and the *H. bromoides* group are strongly basiphilic whereas the *H. marginatum* group is acidophilic. Also the species of the genus *Pseudarrhenatherum* differ in this respect from each other since *P. longifolium* is acidophilic and *P. pallens* basiphilic (ROMERO ZARCO, 1985a). All species of *Arrhenatherum* and also the perennial *Avena macrostachya* are basiphilic. Some of the annual genera (*Aira*, *Corynephorus*, the annuals of *Trisetum*, etc.) are specialised to sandy places with poor or completely absent soil development (cf. Table 1). Sands are usually poor in nutrients and bases (leaching out of nutrients), only in littoral zones and dry climates sands may be sometimes comparatively base-rich. It seems that the annual *Avenaeae* are much less selective than the perennials with respect to the chemical properties of the substrate. Seemingly they only take advantage from either mechanically unstable or shallow grounds with irregular or hazardous availability of water, which are important factors that eliminate perennial competitors including phanerophytic plants.

The specialization to either base-rich or base-poor soils of the perennial *Avenaeae* has an enormous impact on distribution and the representation of the particular taxa in various types of Mediterranean vegetation. In several species or species groups the ranges are thus defined rather by edaphic than climatical reasons. The most impressive example is the differential distribution of the *H. marginatum*- and the *H. bromoides* group on the Iberian Peninsula which largely accords to the distribution of base-poor and base-rich soils produced over the different bedrocks of this region (Fig. 4).

Altitudinal zonation

Most annual *Avenaeae* are colonisers of the Mediterranean lowlands. Lowlands fulfill their ecological requirements (open places) and enable them to complete their life cycle within a given time (available water in the essential periods of germination and vegetative growth coupled with suitably high temperatures and insolation).

In perennial *Avenaeae* the altitudinal patterns of distribution are much more varied. A number of genera or species groups of perennial *Avenaeae* concentrates on low altitudes. In the *Helictotrichon sarracenorum*-, *H. bromoides*- and *H. marginatum* group, in *Arrhenatherum*, *Pseudarrhenatherum*, parts of *Koeleria* and in the *H. pratense*- and *H. desertorum* group, the latter ones being situated largely outside of the Mediterranean Region (nos. 6, 11 in Fig. 1), most species occur in lowlands to lower montane zones.

Others are strictly orophytic (Fig. 1), e.g., *Avena macrostachya*, *Helictotrichon* subgen. *Tricholemma*, the *H. sedenense*-, *H. parlatorei*-, *H. versicolor*- group and most perennial species of the genus *Trisetum*.

Further orophytic taxa with partly narrow geographical distribution belong to otherwise clearly lowland-centred species complexes. Examples would be *Helictotrichon leve* (central Sierra Nevada, endemic) in the *H. marginatum* group, *H.*

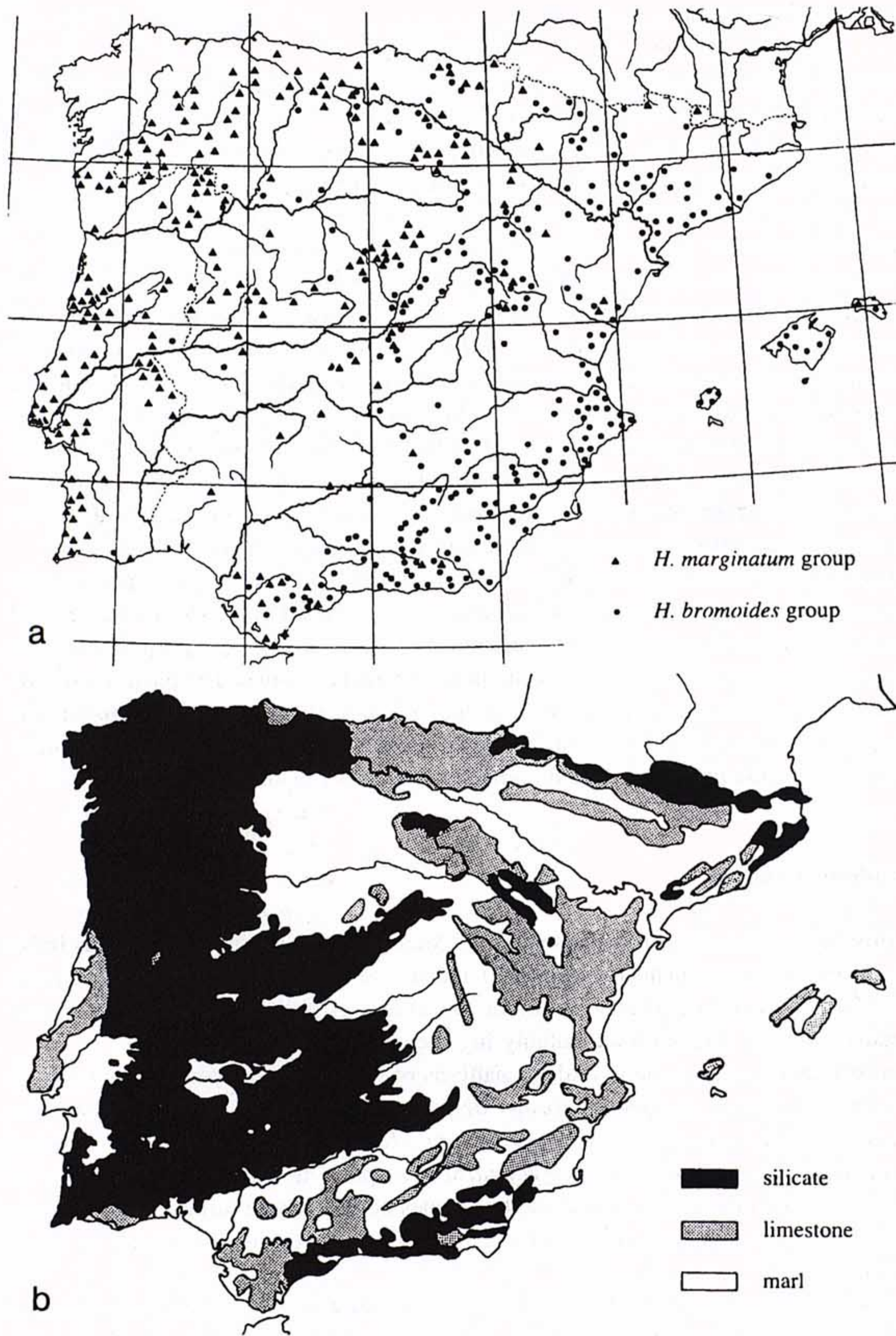


Fig. 4. Dot-map distribution of the taxa of the *Helictotrichon bromoides*- and *H. marginatum* groups (a) in comparison with the dominating bedrocks (b) on the Iberian Peninsula.

bromoides subsp. *pauneroi* (highest Betic/Atlasic Mountains) in the *H. bromoides* group and *H. praeustum* (endemic Alpine) in the *H. pratense* group (nos. 8, 9, 6 in Fig. 1). Since these orophytic species or subspecies show particular, partly unique habitual and anatomical features (SAUER & CHMELITSCHK, 1976; RÖSER, 1989, 1996) they can be regarded as secondary derivatives of their respective species groups. In extant genera the outlined differences between altitudinal ranges of perennials (potentially variable) and annuals (narrow) can be traced in *Avena* and *Trisetum* (Table 1).

Parapatric or sympatric distribution

Parapatric distribution is the rule in the perennial species, sympatric distribution can frequently be observed in the annuals and is especially well-known in the genus *Avena* (cf. BAUM, 1977). Closely related perennial species with similar ecological behaviour are usually geographically separated, e.g., in the *Helictotrichon marginatum* group the western species *H. marginatum* and the eastern *H. compressum*. If closely related species occur within the same geographical area, they usually colonise sites which are altitudinally or micro-climatically separated. The richly evolved *H. bromoides* group on the Iberian Peninsula shows this phenomenon most clearly (fig. 4). In horizontal overlap areas of their ranges the different taxa, sometimes even the different chromosome races of this species group are restricted to particular sites and never were found to occur actually side by side in the same type of vegetation (RÖSER, 1989). In the centre of diversity of the *H. bromoides*- and *H. sarracenorum* group, i.e. the geomorphologically highly varied southern Iberian Peninsula, the inventory of species/subspecies/chromosome races changes dramatically within comparatively short absolute distances at different altitudinal zones (from sea level to the oromediterranean region) and exposition (northern slopes with rather mesic, southern with xeric conditions). The different species/subspecies/chromosome races of each species group behave largely complementary in having different climatical/micro-climatical adaptations (RÖSER, 1996).

In the eastern Mediterranean, the *H. bromoides*- and *H. sarracenorum* groups are represented by only one respective species, namely *H. agropyroides* and *H. convolutum* (Figs. 2, 3). *Helictotrichon agropyroides* is a xerophilic species with rather narrow ecological amplitude and scattered distribution, whose ecologically comparable counterparts would be *H. crassifolium* or *H. gervaisii* subsp. *gervaisii* in the western Mediterranean (coastal cliffs, lowland to montane habitats). *Helictotrichon convolutum*, instead, is distributed in the eastern Mediterranean between near sea level up to the alpine zone, occurs in mesic and even very xeric types of vegetation. This morphologically and chromosomally rather uniform species (cf. LANGE, 1995a) fully seems to cover the entire spectrum of sites that is shared in the western Mediterranean by a large number of species, subspecies, or chromosomally different races of the same species group (*H. sarracenorum* group).

However, a conspicuous example for sympatric distribution is known also in perennial *Aveneae*. It refers to the narrow ranges of *H. cintranum* and especially *H. hackelii* in the outmost southwestern Iberian Peninsula. These species are highly

xeromorphic members of the *H. marginatum* group and have few, apparently relic stands with only 3 populations, e.g., known for *H. hackelii*. *Helictotrichon hackelii* and *H. cintranum* are frequently accompanied by the mesomorphic species *H. marginatum* and *H. albinerve* at the same site. There are some indications that due to climatic reasons the most xeromorphic species of the *H. marginatum* group do not dispose of many habitats at present, where the mesomorphic taxa of the same species group would be unable to compete (RÖSER, 1996).

Species from different species complexes of the perennials may freely occur within the same plant communities such as *H. tenuifolium* und *H. filifolium* subsp. *filifolium* in the semi-arid regions of southeastern Spain or *H. gervaisii* subsp. *arundanum* and *H. filifolium* subsp. *arundanum* in some of the Betic mountains, etc. As far as is known from observations in the field and crossing experiments, such species are separated from each other by strong reproductive barriers (cf. GERVAIS, 1981, 1983).

6. Extensive polyploid series

Polyploidy is much more significant in the perennial than in the annual *Aveneae* (Table 1). The most comprehensive ploidy spectra are found in *Koeleria* (2x - 18x) and *Helictotrichon* (2x - 20x). In the genus *Helictotrichon* polyploidy arose independently several times in the different subgenera or species complexes (Fig. 1).

Polyploidy is frequently connected with speciation processes and may be involved in the colonization of new habitats (STEBBINS, 1985), but it is by no means constrained that polyploids always are "efficient and aggressive" colonisers. As shown by EHRENDORFER (1980) no generally valid correlation between polyploidization and chorological patterns can be established. This applies also to the Mediterranean *Aveneae*.

In most polyploid species complexes of the genus *Helictotrichon* extant diploid taxa are still present (Fig. 1). In some of the Mediterranean species groups these diploids have a much wider distribution than the polyploids, e.g., *H. marginatum* (2x, rarely 4x) and *H. compressum* (2x) in the *H. marginatum*- and *H. bromoides* (2x) in the *H. bromoides* group (cf. nos. 8, 9 in Fig. 1). The polyploids of these groups are usually restricted to quite small, sometimes minute ranges in some of the driest areas of the Mediterranean, e.g., *H. tenuifolium* (4x) in semi-arid southeastern Spain or *H. crassifolium* (12x) growing on few coastal cliffs of Ibiza. Polyploidy seemingly is connected here with the evolution of physiologically and eco-morphologically extremely well drought-adapted species.

However, there are no causal interdependences of both processes (polyploidy and conquest of very dry habitats) as demonstrated by examples of the same species groups: (1) The widespread *H. marginatum* itself comprises a number of locally distributed polyploid populations in mountainous regions of the Iberian Peninsula. These polyploids are colonisers not of dry, but of very humid areas. (2) In *H. albinerve* diploid populations are known to date only for a very small region of southern Andalucía while tetraploids are widespread in the total range of the species. In this case the polyploids have a much wider distribution than the diploids and polyploidy might be seen here in context with a geographical expansion of the polyploids as assumed before in *H.*

sedense and the distribution of its Pyrenean cytotypes (GERVAIS, 1973, KÜPFER, 1974).

In the largely non-Mediterranean *H. pratense* group (no. 6 in Fig. 1) a further pattern of eco-geographical differences between taxa with different levels of ploidy can be observed: The taxa with the lowest chromosome numbers are situated at the northern margin of the Mediterranean area and have quite narrow geographical distribution, namely the disjunctive Illyrian-Caucasian *H. blaii* (4x in the Balkanic partial range) and some infraspecific taxa of *H. pratense* with 12x or 14x in Cantabria and the Pyrenees (GERVAIS, 1973, SAUER, 1984, ROMERO ZARCO, 1984, LANGE, 1995a). Their closest relative, *H. pratense* s.str., is widespread under suboceanic climate in Central and northern Europe (map: CONERT, 1983-1992: 252) and has at least 18x, in some Alpine and Pyrenean populations even 20x. Although the earlier hypothesis that the *H. pratense* group would represent a direct derivative of the Mediterranean *H. bromoides* group (GERVAIS, 1973) was questioned in the meantime (cf. RÖSER, 1989) and no clear evidence could be found so far on how and when *H. pratense* s.str. separated from its Iberian-Illyrian-Caucasian relatives, the *H. pratense* group has to be regarded as the only species complex of *Helictotrichon* that links the Mediterranean with the Central European flora (cf. EHRENDORFER, 1970). Clearly, *H. pratense* s.str. cannot be ranked among the examples for Central European-west Asian taxa that appear to be derived from "more ancient" Mediterranean ancestors, but it can be stated that this widespread taxon has close extant relatives in the Mediterranean (cf. *Carlina*; MEUSEL & KÄSTNER, 1990, 1994), especially at its northern borders.

The four examples presented (out of many more; see RÖSER, 1996) show that in the perennial *Aveneae* polyploidy is usually connected with chorological differentiation. The observed distribution patterns in diploids versus polyploids are not uniform which undoubtedly is due to the variety of different adaptive ecological processes active in these species.

Transition from mesomorphic to xeromorphic habit

Mesomorphic habit is most probably a primitive character in the *Aveneae*, according to all available arguments (RÖSER, 1989; LANGE, 1995a). As far as is known, the annuals have retained mesomorphic structures of leaves and roots without exception, corresponding well to their life cycle which makes long-lived and drought-resistant vegetative organs dispensable (see above; cf. the mesomorphic annuals of *Avena* in Fig. 1). Many perennials especially of the humid tropics/subtropics and the temperate regions of both hemispheres show the same mesomorphic habit. Examples of the latter would be the genera *Arrhenatherum*, *Trisetum*, *Holcus* and the perennial *Avena macrostachya* (cf. Table 1, Fig. 1). Other perennials have acquired meso-xeromorphic to xeromorphic habit which is reflected by a large number of striking anatomical and morphological features of roots and leaves (cf. GERVAIS, 1968; RÖSER, 1989, 1996; LANGE, 1995a). The eco-physiological significance as reducing transpiration is evident in many characters of the leaves (indumentum, stomata arranged in deep furrows, etc.).

Within the Mediterranean genera the mesomorphic genus *Arrhenatherum* is opposed to the closely related, more xeromorphic genus *Pseudarrhenatherum* (Fig. 1) whereas *Helictotrichon* comprises both types of habits. The distribution of mesomorphic and xeromorphic species in the different infrageneric taxa of *Helictotrichon* is conspicuous (cf. Fig. 1): The subgenus *Helictotrichon* is throughout xeromorphic. The subgenus *Pubavenastrum* comprises only the mesomorphic *H. pubescens*. In the large subgenus *Pratavenastrum* some species complexes are constantly mesomorphic, e.g. the largely non-Mediterranean distributed *H. versicolor*-, *H. pratense*- and *H. adsurgens*-group (nos. 5, 6, 7 in Fig. 1). The *H. marginatum*- and the *H. bromoides* group (nos. 8, 9) comprise mesomorphic as well as xeromorphic taxa. The diploids are always mesomorphic (1 species in the *H. bromoides*-, 4 in the *H. marginatum* group), whereas most polyploids are xeromorphic. At the ploidy level of 4x both types are represented and the transition between them still can be traced in the Ibero-Mauritanian species *H. gervaisii* (RÖSER, 1989, 1996). Xeromorphic habit and the colonization of very dry Mediterranean habitats is a secondary development in the subgenus *Pratavenastrum* and perhaps also in the relic North African subgenus *Tricholemma*. The xeromorphic polyploids are able to colonise as arid sites as the species of the subgenus *Helictotrichon*, and partly even seem to supersede them. Some of them are present in large dry areas where, for several reasons, the subgenus *Helictotrichon* is absent (southwestern Iberian Peninsula, Algeria, Libya, Aegean Islands). In terms of species diversity and geographical extension the production of xeromorphic polyploids was enormously successful in the subgenus *Pratavenastrum*.

Floral specialization, dispersal units

In the *Aveneae* reductive processes are frequently leading from paniculate to spicate inflorescences, from multi- to few- or single-flowered spikelets, from spikelets with constantly bisexual florets to spikelets with sexually dimorphic florets in different arrangements (e.g. *Arrhenatherum* with the lower floret male and the upper bisexual, or *Holcus* with the lower floret bisexual and the upper male). Some floral specializations are directly connected with the production of dispersal units as seen in the way of spikelet disarticulation at maturity of seeds.

Spikelets frequently disarticulate above the glumes and between the florets. The diaspores consequently consist of single florets as found in most species of *Helictotrichon*, in *Trisetum*, *Trisetaria*, *Koeleria*, *Rostraria*, etc. Spikelets disarticulating only above the glumes, and florets consequently falling together are characteristic of the genera *Arrhenatherum* and *Pseudarrhenatherum*, but also of particular taxa of the genera *Helictotrichon* (subgenus *Tricholemma*, *H. parlatorei* group in the subgenus *Helictotrichon*) and *Avena* (Fig. 1). Obviously, this type of disarticulation arose within the *Aveneae* several times in parallel. This is frequently connected with other changes in the floral morphology, e.g., the absence of fully developed awns in the upper florets (RÖSER, 1989). Further types of dispersal units are found among the wild *Aveneae*: *Aveninae* in the genus *Holcus*, where the spikelets disarticulate below the glumes and in *Gaudinia*, where the axis of the inflorescence disintegrates at maturity (see above).

A complete loss of disarticulation of spikelets and inflorescences is found in cultivated species of *Avena* where the seeds are harvested and dispersed by man (*A. sativa*, *A. brevis*, *A. nuda*, etc.).

In wild *Aveneae*, the type of producing dispersal units is evidently not correlated with the sizes of spikelets or florets. Species or genera with large heavy florets may have the same type of dispersal units as taxa with small florets (e.g., most species of *Helictotrichon* versus *Trisetum*). Genera with few- or single flowered spikelets have dispersal units which are usually produced by a single disarticulation above the glumes (*Arrhenatherum*, *Pseudarrhenatherum*, other subtribes of *Aveneae*), but the same type of disarticulation occurs in taxa with many-flowered spikelets as well, e.g., in the perennial *Helictotrichon* or in some annual species of *Avena*. The adaptive significance of this character is unknown. Dispersal units such as found in *Gaudinia* or *Holcus* (see above) and many *Agrostidinae* (cf. CLAYTON & RENVOIZE, 1986) appear to be highly derived. They are correlated with the complete loss of any disarticulation within the spikelet and have to be regarded as the strongest deviation from the supposedly basic type of dispersal unit in the *Aveneae*, i.e. the floret with a firm, elaborately awned lemma which encloses the papery inner floral organs and the karyopsis at maturity.

Variation of growth forms

The growth forms of the annual *Aveneae* are largely uniform. The plants produce usually small, dense or loose tufts with \pm numerous fertile and sometimes also sterile shoots. As seen in greenhouse experiments under constant climatic conditions, many species can survive for several years. These are not obligatory annual, only their life time becomes delimited in the wild by climatic factors (drought, cold).

Perennials show huge variation of growth forms, comparable to their elaboration of anatomically and mechanically highly differentiated leaves (see above 7), corresponding well to their ability to colonise extremely different habitats (cf. Table 1). The growth forms are frequently constant within the same species and show a clear correspondence to the demands of the particular sites. Densely tufted, tussocky grasses are characteristic of mechanically largely stable grounds. The sheaths of the basal leaves are persistent in these tussocky grasses and probably have a protective function against desiccation and strong day-night fluctuations of temperature such as demonstrated by HEDBERG (1973) in African alpine grasses.

Less densely tufted, stoloniferous species occur on mechanically labile grounds, frequently in mountainous regions (tali), or on soils with loose, frequently humose layers (alpine grassland, woodlands, moorland). Extensive production of stolons coupled with the dissolvment of the tufted growth form is known in some species of the perennial genus *Helictotrichon* (cf. SAUER & CHMELITSCHK, 1976; RÖSER, 1989), but occurs also in various species of *Koeleria*, *Trisetum* and *Holcus*.

Conclusions

The Mediterranean *Aveneae* show a considerable variation of ecological, habitual and ecomorphological adaptations (soil, climate, altitudinal spectrum, growth form, anatomy and morphology of the vegetative organs). These adaptations may be accompanied by floral specializations (dispersal units) and the establishment of large polyploid complexes. This variation is most elaborate in the perennials which are with respect to species diversity clearly the most richly differentiated *Aveneae* of the Mediterranean Region. Perennials are widespread in the natural or semi-natural vegetation. The colonization of ephemeral, in many cases anthropogenic habitats is characteristic of the annual *Aveneae*.

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