

## Preface

Wild oats are no new problem. As old as history itself, they have accompanied and hindered man's efforts to grow cereal crops for food. Yet it is only during the past two decades that they have become a serious menace on a world-wide scale. Intensification of cereal production, facilitated by the advent of the combine harvester and herbicides, has favoured the spread of wild oats in temperate agriculture to an extent undreamed of a few years ago.

As their importance has increased, so has the attention paid to them. Farmers, advisers, those connected with the seed trade, manufacturers and distributors of agrochemicals, weed scientists and others concerned with the well-being of agriculture have found it necessary to learn about wild oats. But how? It has proved no easy task. The information is scattered throughout numerous publications and in a variety of languages. It has been appearing in the world literature since the end of the last century and recently it has become a spate. Some is based on practical investigations which may be of great local importance but may not apply to other agricultural systems or climates. Some is concerned with basic principles which are universally relevant regardless of the country of origin. Topics range from scientific research to surveys, from seeds to legislation, from genetics to machines.

Wild oats have become a very serious problem in Britain and there are no longer any major cereal-growing areas free from them. When in 1970 my colleagues and I at the Weed Research Organization decided that the time had come to make an all out research effort on a national scale, we quickly reached the conclusion that the tremendous amount of information on wild oats already available could not—or at least should not—be ignored. It needed to be collected, sifted and appraised if the new programme was to build on what was already known rather than run the risk of being unproductively repetitive. Encouraged by G. D. H. Bell, then Director of the Plant Breeding Institute, Cambridge and Chairman of the ARC Technical Committee on Cereals Research, and by the late F. R. Horne, who had recently retired as Director of the National Institute of Agricultural Botany and who had become an enthusiastic member of the Home Grown Cereals Authority, I decided with the full backing of my WRO colleagues that we had no alternative but to undertake ourselves the formidable task of reviewing the world's wild oat literature. Our objectives were thus twofold: first to assemble this literature in a form which could be of permanent value to research workers and others at WRO; second, as part of the institute's information function, to make available for the benefit of those interested in wild oats everywhere a comprehensive digest of this literature.

The two Annotated Bibliographies, which provided the data base for much of this Review, were themselves derived from material pertaining to the biology and control of wild oats (in the broad sense) abstracted in, or known



to the compilers of, the journal *Weed Abstracts* from 1952-1972. The coverage of *Weed Abstracts* is worldwide but, by its terms of reference, is restricted to scientific literature in which various species of wild oat are treated as weeds. A total of 1,057 references were finally included in the Bibliographies of which 990 had appeared in *Weed Abstracts*. Approximately 260 additional references were added by various contributors from literature sources more relevant to their own field of study, eg taxonomy, plant pathology, entomology, or from papers published after 1972. Nevertheless, 87% of the relevant references reviewed were retrieved from *Weed Abstracts*.

Reviewers were asked to contribute a comprehensive and critical review of the world literature relevant to their topic and to draw attention to work of lasting relevance to the wild oat problem in the UK where it existed. They were expected to use their discretion concerning the selection of the most relevant material and discard or summarise that which was more ephemeral or of purely local significance. Some idea of the magnitude of the task involved is indicated by the fact that the Bibliography of this Review contains only 754 of the original 1,057 references. In presenting their conclusions reviewers were required to draw attention to discrepancies between their own and those of the authors of previous major reviews. The last comprehensive review of both the biology and control of wild oats was that of Thurston (1962), made soon after the introduction of the herbicides barban and di-allate. Latterly, the volume of literature on the chemical control of wild oats has expanded enormously and, though some aspects of the biology and the control of wild oats have been reviewed by individual authors, the scope of a really, comprehensive review has obviously passed beyond the abilities or time of any single author. The sheer volume of the literature reviewed here indicates the urgent necessity for identifying the important deficiencies in our knowledge and thereby the areas for further research. To this end, contributors were invited to indicate those areas of wild oat research which, in their opinion, were most in need of initiation or reinforcement.

The result of our efforts is this book. Needless to say the job was too large to be undertaken by WRO staff alone, although they have done the major share with the expenditure of much voluntary effort in private time. I hope they know how much this has been appreciated. I am also extremely grateful to the following who willingly responded to my request for assistance—sometimes at very short notice: J. M. Thurston, Rothamsted Experimental Station, Harpenden; H. Thomas and I. T. Jones, Welsh Plant Breeding Station, Aberystwyth; D. B. MacKay, National Institute of Agricultural Botany.

With so many contributors and such a diversity of styles, also the need for standardisation of terms and units, the services of an experienced editor to hammer the texts into a unified shape were vital for the success of the project. It was fortunate that an old friend and former colleague, D. Price Jones, who had recently retired, responded to my plea for assistance. Without his skilled and painstaking editing and unbounded patience, this book would certainly be of much lesser stature and its publication long delayed. I wish also to pay tribute to John Hardcastle who not only organised the



preparation of the original Annotated Bibliographies containing some 1200 references, on which this Review is based, but acted as project co-ordinator and manager from the start.

Finally, I should like to say how pleased I was when I heard that the Agricultural Research Council was prepared—and indeed wished—to act as publisher for this Review. I am also most grateful to the Home Grown Cereals Authority for a grant of £500 towards the cost of production.

Above all I hope that the book will prove of use to all who want to find out what is known about wild oats—those fascinating plants which somehow or other have managed to thrive and grow in the face of the formidable armoury of herbicides and technology available to the modern farmer.

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## CHAPTER 1

# Origins and Identification of Weed Species of *Avena*

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This review of the origins and identification of the different species of *Avena* is directed primarily at the common weed forms. However, the status of these species can be appreciated only by placing them in the context of the genus as a whole. The numerous species of *Avena*—not all of which are discussed herein—fall into three categories according to their agronomic status:

- (1) Cultivated oats include *A. sativa* L. and some varieties of *A. strigosa* Schreb.; also, *A. byzantina* C. Koch and *A. nuda* L.
- (2) Weeds (the 'wild oats' of agriculture) include *A. fatua* L. and certain varieties or sub-species of *A. sterilis* L., of which the best known is commonly referred to as *A. ludoviciana* Dur. These are characteristically weeds of cereals and certain other arable crops.
- (3) Truly wild plants, ie normal constituents of local vegetation in areas where they are native, include *A. hirtula* (Lag.) Malzew, *A. wiestii* Steud., *A. canariensis* Baum, Rajhathy and Sampson, *A. murphyi* Ladizinsky. At best these may provide some grazing.

The most comprehensive works on the taxonomy and classification were published by Malzew (1930), Mordvinkina (1936), Sampson (1954) and Stanton (1955). A number of species described recently have not appeared in any classification scheme to date. Although this review of the taxonomy of the genus must inevitably have many weaknesses, an attempt is nevertheless made to present the means of identifying the most common wild species of *Avena* occurring as weeds. The morphological features used to identify species are described and more detailed descriptions of the most common weed species presented.

Emphasis has been placed on the identification of species, with the result that systems of classification in relation to phylogeny are not discussed in detail. We do not believe that there is a single classification which readily indicates phylogenetic relationships. The classification of Malzew (1930) based on morphological characters is not completely valid when the cytogenetic evidence of recent years (Rajhathy and Thomas 1974) is considered. On the other hand, the delimitation of species on cytogenetic parameters, as proposed by Ladizinsky and Zohary (1971), also has severe limitations.

In addition to a description of the classification and identification of species, a short review of the genetic relationships between the wild weed



species and the cultivated forms is also presented, since the cultivated and wild hexaploids have a similar genetic structure. They form an inter-fertile group, although natural gene flow from the weed to the cultivated species is very restricted, as the breeding system only allows a minimal amount of cross-pollination. The cultivated species evolved from the wild species by conscious or unconscious exploitation of characters adaptable to domestication. Plant breeders have further exploited this close relationship by introducing desirable variation from wild species into cultivated varieties. Although the areas of domestication do not coincide with the primary areas of distribution, or the centres of origin of the weed progenitors, the genetic relationships between the wild and cultivated species clearly indicate the derivation of the latter from the wild hexaploid species.

#### *Acknowledgements*

We wish to thank Miss Joan Thurston, of Rothamsted Experimental Station, Harpenden, Herts, for reading the manuscript and for making many useful and constructive suggestions during its preparation; also Dr J. D. Hayes, of the Welsh Plant Breeding Station, Aberystwyth, for his comments and suggestions on the original draft. We would also like to thank Mr H. M. Thomas for the line drawings and Mr H. Richards for photographic work.

## CLASSIFICATION AND IDENTIFICATION OF SPECIES

### DIAGNOSTIC FEATURES

Variations in growth habit and gross morphology between species of *Avena* have been described by Malzew (1930) and Stanton (1955), but their importance as diagnostic features in the identification and classification of *Avena* species is limited. The most useful characters relate mainly to the morphology of the spikelet.

The spikelet of the oat species is made up of the glumes and florets, the latter forming the seeds at maturity. In naked oats (a cultivated form) the caryopsis is loosely enclosed by the lemma and pale, but in all the other species of *Avena* they tightly enclose the kernel and form the husk of the mature grain.

#### *Separation of spikelet at maturity*

The manner in which the spikelet separates from the plant at maturity is the most important diagnostic character in identifying the species. In the cultivated species, the spikelet is retained on the plant at maturity and separates by fracture at the base of the first floret during threshing. In the wild species the spikelet disarticulates by means of an oblique abscission layer, apparently located in the cleavage plane between the basal rachilla segment and the callus of the lower floret (Coffman, Parker and Quisenberry 1925). Separation leaves a well-defined oval cavity commonly known as the



sucker-mouth, the shape and size of which differs from species to species. In *A. sterilis* L. the second and succeeding floret do not separate by disarticulation, but in *A. fatua* L. all the florets disarticulate, leaving a distinct sucker-mouth (Plate 1a-d). In those species where the second floret does not form a sucker-mouth, the location of the fracture on the second rachilla is a useful diagnostic character. In *A. byzantina* C. Koch (cultivated) and *A. sterilis* the fracture occurs at the lower end of the rachilla which remains attached to the second floret (basifracture according to Stanton 1955) while in *A. sativa* (cultivated oats) L. the fracture occurs at the base of the second floret and the rachilla remains attached to the primary floret.

#### *Structure of the lemma*

Lemma colour is useful for the identification of cultivars of the cultivated oat, but is of no use in differentiating between taxonomic species. The shape of the lemma tip is a more specific character in delimiting taxonomic species (Fig. 1.1). It is the main character used by Malzew (1930) for separating the sub-sections *Aristulatae* and *Denticulatae*. Within the *Aristulatae*, the lemma tips end in fine bristle-points, whilst in the *Denticulatae* they end in two small teeth. Until the recent descriptions of *A. canariensis* (Baum *et al* 1973) and the tetraploids *A. magna* (Murphy *et al* 1968) and *A. murphyi* (Ladizinsky 1971a) the bidentate lemma tip was confined to the hexaploid species.

In most wild species of *Avena*, the lemma is usually pubescent and the degree of pubescence distinguishes some taxonomic species. Glabrous forms of *A. fatua* and *A. sterilis* ssp. *ludoviciana* Malzew (= *A. ludoviciana* Durier) do exist but are not frequent in occurrence. In general the cultivated forms are glabrous, but some cultivars have small tufts of hair at the base of the lemma.

The awns, which appear to be extensions of the midrib of the lemma arising a little above the middle of the dorsal surface, are useful characters in the identification of species. Awns occur on only the first floret in cultivated oats and are usually weak, but in wild species the awns are prominent and are usually bent and twisted. Most wild species have awns on all the florets, but *A. sterilis* (including ssp. *ludoviciana* Malzew = *A. ludoviciana* Durieu) has only two awns per spikelet. The awns have an adaptive role in the wild species in that they are responsible in part for burying the seed after dispersal.

#### *Chromosome number*

It is extremely difficult to differentiate between some species of *Avena* without counting the chromosomes. The diploid species *A. hirtula* and its desert form *A. wiestii* are morphologically similar to the tetraploid species *A. barbata*, which is more widely distributed (Ladizinsky and Zohary 1971). The diploid species *A. canariensis*, the tetraploid *A. magna* and the hexaploid *A. sterilis* have all the characteristic morphological features of *A. sterilis* and it is difficult to distinguish between these species without chromosome counts. These examples clearly indicate that chromosome number can in some cases be important as a diagnostic feature in the classification of the wild species of *Avena*.



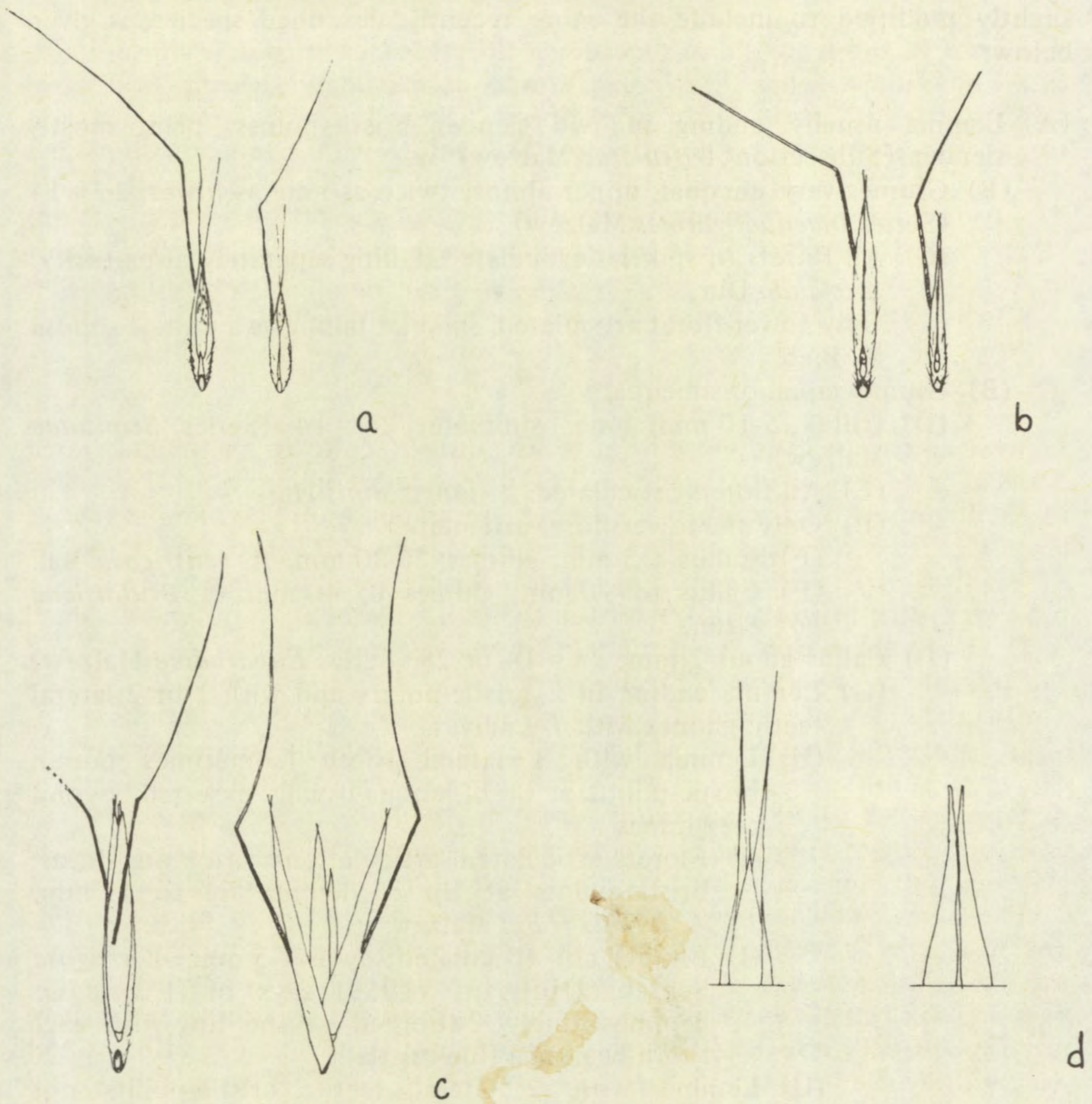


Fig. 1.1. (a) Primary and secondary florets of *A. barbata*; (b) primary and secondary florets of *A. fatua*; (c) spikelet of *A. sterilis*; (d) lemma tips showing the two slender bristle-points of *A. barbata* and the typical bidentate lemma tips of *A. sterilis* and *A. fatua*.

#### KEY TO CLASSIFICATION AND IDENTIFICATION OF SPECIES

Based on the distinct morphological characters that have been briefly described, a number of keys for distinguishing *Avena* species have been proposed (Malzew 1930, Sampson 1954, Stanton 1955). Unfortunately no key incorporating the more recently described species is available. The key provided by Sampson (1954), which is based largely on that of Mordvinkina (1936), seems to be the most satisfactory available at present. This key,



slightly modified to include the more recently described species, is given below:

- (A) Lemma usually ending in two slender bristle-points: plant mostly slender. (Subsection *Aristulatae* Malzew)
- (B) Glumes very unequal, upper almost twice as long as lower;  $2n = 14$  (Series *Inaequaliglumes* Malzew)
  - (C) All florets of spikelet articulated, falling separately at maturity. *A. clauda* Dur.
  - (C) Only lower floret articulated, spikelet falling as a unit. *A. pilosa* M. Bieb.
- (B) Glumes equal or subequal
  - (D) Callus 5-10 mm long, subulate;  $2n = 14$  (Series *Stipitatae* Malzew)
    - (E) All florets articulated. *A. longiglumis* Dur.
    - (E) Only the lower floret articulated.
      - (F) Callus  $\pm 5$  mm; glumes 25-30 mm. *A. ventricosa* Bal.
      - (F) Callus to 10 mm; glumes to 40 mm; *A. Bruhnsiana* Grun.
  - (D) Callus about 2 mm;  $2n = 14$  or 28 (Series *Eubarbatae* Malzew)
    - (G) Lemma ending in 2 bristle-points and with 1 or 2 lateral teeth, glumes with 7-9 nerves.
      - (H) Lemma with 1 lateral tooth (sometimes none); bristle-points at tip of lemma usually exerted beyond the glumes
        - (I) Florets articulated, articulation-scar oblong-linear; bristle-points at tip of lemma up to 12 mm. *A. hirtula* (Lag) Malzew
        - (I) Florets not articulated; awns 1-5 mm. *A. strigosa* Schreb. (Hubbard (1959) says of *A. strigosa*: 'lemmas finely 2-toothed at the tip, with each tooth bearing a fine bristle.')
      - (H) Lemma with 2 lateral teeth; bristle-points not exerted beyond the glumes.
        - (J) Florets articulated, scar oval or round.
          - (K) Bristle-points at tip of lemma, 3-6 mm. *A. wiestii* Steud.
          - (K) Bristle-points  $\pm 1$  mm. *A. vaviloviana* (Malzew) Mordv.
        - (J) Florets not articulated; bristle-points 1-4 mm *A. abyssinica* Hochst.
  - (G) Lemma ending in 2 bristle-points up to 5 mm long, lateral teeth wanting; glumes with 9 or 10 nerves, articulation-scar oblong. *A. barbata* Pott.
- (A) Lemma usually ending in two small teeth, never produced into two bristle-points, plants mostly robust (subsection *Denticulatae* Malzew)
  - (L) Lower floret articulated with the rachilla.



- (M) Upper florets not articulated, spikelet falling as a unit of dispersal.
- (N) Chromosome number  $2n = 42$ , spikelet 23-32 mm. *A. sterilis* L.
- (N) Chromosome number  $2n = 28$ .
  - (O) Awn attached on lower third of lemma; lemma glabrous, spikelets 25-30 mm. *A. murphyi* Ladizinsky.
  - (O) Awn attached near middle of lemma; lemma densely pubescent, lower part of awn covered with fine hairs, spikelet 25-30 mm. *A. magna* Murphy & Terrell.
- (N) Chromosome number  $2n = 14$ , spikelet smaller, 10-14 mm, lemma densely pubescent, lower part of awn glabrous. *A. canariensis* Baum, Rajhathy and Sampson.
- (M) All florets articulated. *A. fatua* L.
- (L) None of the florets articulated, separated by fracture of rachilla.
  - (P) Most of rachilla segment remains attached to upper floret on threshing; fracture surface at base of lower floret slanting. *A. byzantina* C. Koch
  - (P) Rachilla segment remains attached to lower floret; fracture surface not slanting. *A. sativa* L.

Malzew's classification adopted in the key does not always reflect phylogeny, eg in series *Stipitatae*, *A. longiglumis* and *A. ventricosa* are included, although *A. longiglumis* is more closely related to series *Eubarbatae* and *A. ventricosa* to the *clauda-pilosa* complex (Rajhathy and Thomas 1974). However, as a means of identifying species, this classification is effective.

Taxonomic classifications in the genus *Avena* are based on typical morphological characters which facilitate easy identification, but do not necessarily reflect the cytogenetic and phylogenetic relationships of the taxonomic entities. Groups of such species within a polyploid level, although normally self-pollinated, are often interfertile, thus allowing some gene flow between populations. They represent the variation within a biological species (Rajhathy and Thomas 1974). However, a classification based on the criteria associated with biological species as proposed by Ladizinsky and Zohary (1971) could lead to considerable confusion, especially in wild oats. All the hexaploid species of *Avena* are interfertile and form a biological species. If the whole group, including the wild and cultivated species, was reclassified in terms of a biological species, it would appear as one species. The splitting down of species into a whole range of sub-species which reflect variation within taxonomic species can also be misleading. The taxonomy and classification of the genus *Avena* require revision, but a lengthy discussion on this topic is beyond the scope of this review. Only the most important characters for identifying species of wild oats have been described.

#### DESCRIPTION OF THE MAIN WEED SPECIES

Detailed descriptions are given only for those species of wild oats that are important weeds of cereal and arable crops. These include *A fatua* L. and



*A. sterilis* ssp. *ludoviciana* Malzew occurring as weeds in the United Kingdom (Thurston 1954, MAFF 1972). *Avena barbata* Pott. is also described, although there is some doubt about its status as a weed of cereals in the Mediterranean and Middle East countries.

Morphological characters of the vegetative plant, together with head and grain distinguishing features for the three species, are compared in Table 1.1. The information in the table is based on data from MAFF (1956, 1972), Stanton (1955), Thurston (1957) and Hubbard (1959). Marked variation from the general type occurs in each species, hence a short review is given to supplement the table.

#### *Avena fatua* L. (common or spring wild oat)

The main distinguishing morphological features of this species are the disarticulation of each floret or ripe grain in the spikelet at maturity, and the lemma tips ending in small teeth and not in two slender bristles as in *A. barbata* (Fig. 1.1d). The awn on the third seed separates it from *A. ludoviciana* but not necessarily from all forms of *A. sterilis*. Other useful identification characteristics given in Table 1.1 show considerable variation, and taxonomists have accordingly divided the species into sub-species and varieties.

In the classification given by Malzew (1930) there were eight sub-species of *A. fatua* L., each of which had several varieties. Sampson (1954) described four sub-species which had also been described by Malzew, namely ssp. *meridionalis* Malzew, ssp. *septentrionalis* Malzew, ssp. *fatua* Malzew and ssp. *cultiformis* Malzew. Differentiation was based mainly on glume and lemma length, and hairiness of culm nodes.

The variation occurring in plants of *Avena fatua* found in Britain has been investigated very fully by Thurston (1957) (see p. 000 *et seq*). Based on material collected in the 1951 wild oat survey (Thurston 1954), at least 12 different types of *Avena fatua* were distinguished (Thurston 1957). Lemma colour, hairiness of lemma, length and colour of hairs at callus were the main characters used. Other features, such as tillering capacity, presence of hairs on culm nodes, dormancy and size of grains, were also used in identifying five separate varieties, four of which belonged to the sub-species *fatua*. This is characterised by glumes up to 25 mm long, the lanceolate lemma up to 20 mm, glabrous culm nodes and the spindle shaped caryopses in their husks are 2 mm wide and 1.5 mm thick (Malzew 1930).

#### *Avena sterilis* L. (wild red oat or animated oat)

The common names quoted reflect American usage: red is not a description applicable to all forms of *A. sterilis*. The main distinguishing feature is the lack of separation (articulation) between the florets of the spikelet, the second floret separating from the first by basifracture of the rachilla segment. The lowermost floret, however, separates from its pedicel by abscission, leaving an obvious basal scar or sucker-mouth, the whole spikelet at maturity falling as a single unit of dispersal from the plant (Fig. 1.1c, Plate 1a).

The lemma is generally covered with dense hairs and the first two florets have long, twisted and bent (geniculate) awns. Considerable variation occurs



Table 1.1 Diagnostic features of the three main wild oat weeds

CHARACTER	<i>Avena fatua</i> L. (common or spring wild oat)	<i>A. sterilis</i> ssp. <i>ludoviciana</i> Malzew (winter wild oat)	<i>Avena barbata</i> Pott.
*Habit and chromosome number	Annual, hexaploid (2n = 42)	Annual, hexaploid (2n = 42)	Annual, tetraploid (2n = 28)
*Season of germination	A few in autumn usually September-October. Most in spring usually March-April.	Winter, usually late October early March	
Habit at maximum tillering stage (not shown when crowded).	Generally shoots few and erect as in a spring cereal.	Shoots many, forming flat rosette (as in a winter cereal) at low density.	Juvenile growth prostrate to semi-prostrate.
Hairs on leaf sheath.	Individual plants vary from none to very hairy.	Nearly always very hairy.	Hairy.
Ligules.	Blunt, membranous, up to 6 mm long.	Blunt, membranous, up to 8 mm long.	Long, membranous, separated, up to 10 mm long.
Culms.	Tufted or solitary, erect or bent at the base, stout, 3-5 noded, smooth.	Tufted or solitary, erect or bent at the base, stout, 2-4 noded, smooth.	Tall, narrow, weak, with a decumbent habit of growth, glabrous or slightly hairy at the nodes.
<b>HEAD CHARACTERISTICS</b>			
Panicles.	Narrowly to broadly pyramidal. Open 10-40 cm long up to 20 cm wide. Branches widely spreading, mostly clustered.	Pyramidal, very loose and open 15-45 cm long 8-25 cm wide. Branches clustered and spreading.	Open, equilateral, rather large and drooping. Branches short to long.



Spikelets.	Loosely scattered, pendulous, 18-25 (rarely 30) mm long, 2-3 flowered.	Scattered, pendulous, lanceolate 23-32 mm long, 2-3 flowered.	Numerous, lanceolate small, 2-3 flowered.
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*GRAIN CHARACTERISTICS*

Number of seeds/spikelet.	2 or 3	2 or 3	Generally, 2 seeds per spikelet.
*Lemmas	Narrowly oblong-lanceolate, shortly 2-4 toothed at the apex, 14-20 mm long, becoming tough and rigid. Usually stiffly hairy in the lower half, rough above, sometimes glabrous, 7-9 nerved. Commonly brown, may be grey or yellow.	Narrowly lanceolate, 2-toothed membranous tip, 15-22 mm long becoming tough and rigid. Mostly stiffly hairy except for the rough upper third, 7 nerved. Commonly brown, less often grey or yellow.	Very narrowly lanceolate, greyish brown. The lemma tip ends in 2 slender bristle-like points 4-7 mm long.
6 Awns.	Awned from the middle of the back of the lemma, with strong awn 2.5-4.0 cm long, bent, lower half twisted, dark brown.	Awned from middle of back of lemma, with stout awn 3-5.5 cm long, bent, lower half twisted, dark brown and minutely hairy.	Awned from middle of back of lemma with a strong twisted and bent awn 3-4 cm long. Dark coloured on lower parts.
*Awn on third seed.	Present.	Absent.	
*Abscission scar, or suckermouth or callus.	Present at base of every seed.	At base of first seed only (second and third seeds end in stalk).	At base of every seed, scar narrow.
*Hairs around callus at base of seed.	Always present, long or short silver or gold, 1.5-4 mm long.	Always present, almost always long up to 5 mm long. Dark colour on brown and on most grey husks, otherwise silver or gold.	Always present, but not very distinct from hairs on grain. Dark colour or brown.



Table 1.1—(cont.)

CHARACTER	<i>Avena fatua</i> L. (common or spring wild oat).	<i>A. sterilis</i> ssp. <i>ludoviciana</i> Malzew (winter wild oat).	<i>Avena barbata</i> Pott.
Colour and hairiness of husk.	Medium or very dark brown, light or dark grey, cream yellow. Hairy, moderately hairy, hairless. Any combination of colour and hairiness. Hairs silver or gold. Husk of second seed less hairy than first. Third seed hairless.	As for <i>A. fatua</i> .	As for <i>A. fatua</i> .
*Shedding of ripe seed.	All seeds of spikelet fall separately.	Seeds of spikelet fall together as a unit. Force necessary to separate the grains within a spikelet.	All seeds of spikelet fall separately.
Dormancy.	90% of viable seeds at harvest are dormant.	First seeds not dormant at harvest; 2nd and 3rd seeds dormant.	Dormancy variable from 0-50% of seeds.

\* Most important diagnostic characters.



in the size, colour and hairiness of the lemma, and in the presence or absence of awns on 3rd and subsequent florets and size of basal scars. These characteristics have been used by Stanton (1955, 1961) in recognizing three subspecies or varieties, namely *ludoviciana*, *maxima* and *macrocarpa*. His descriptions, with slight modifications, are reproduced below:

- (2a) First lemma very long to extremely long (22-30 mm), usually hairy, sometimes glabrous; first florets with very long awns (30-40 mm); second lemma also awned, third awnless. *ludoviciana* Dur.
- (2b) First lemma extremely long (24-40 mm), very hairy; awn extremely long (40-80 mm); second lemma also awned, third and subsequent usually awnless.
- (3a) Awns glabrous or very hairy. *maxima* Perez Lara.
- (3b) Awns often densely covered with short, fine hairs on the lower parts. 1st lemmas much shorter. *macrocarpa* Moench

A detailed description of these is given by Stanton (1955). Marquand (1922) considered *macrocarpa* to be synonymous with *A. sterilis* var *maxima*. *Avena sterilis* has been divided by Sampson (1954) into three subspecies, namely *ludoviciana* (Dur.), *trichophylla* (C. Koch) Malz. and *sterilis*, the latter sub-species being equivalent to *macrocarpa*. The size of the grain and spikelet varies from the slender *ludoviciana* to the large *macrocarpa*.

Malzew (1929), quoted by Sampson (1954), regarded ssp. *macrocarpa* with the larger grain as strictly Mediterranean, while ssp. *trichophylla* with grain of medium size, was considered more Eastern in distribution, growing together with ssp. *macrocarpa* in Palestine, Syria and western Asia Minor, but extending eastward through Asia Minor to Transcaucasia, western Iran and Iraq.

The smaller-grained ssp. *ludoviciana*, on the other hand, ranges from the British Isles through to the Mediterranean regions to Afghanistan and Turkistan (Malzew 1929). It is described in greater detail below.

*Avena sterilis* ssp. *ludoviciana* Malzew (winter wild oat).

This oat may be distinguished morphologically from both *A. fatua* and *A. barbata* by the mode of attachment of the second and third grains. These are firmly held to the first and second grains respectively, pressure being required to separate them. The first or basal grain in the spikelet, however, separates easily from the pedicel, leaving a round to oval sucker-mouth base to the primary grain; in the other two species all the florets within the spikelet have a sucker-mouth and fall separately. The lemma apex in *ludoviciana* ends in two small teeth similar to *A. fatua*, but unlike *A. barbata*, which has two slender bristles at the tip of the lemma (Fig. 1.1d). The second floret is always awned and the third almost always awnless. Four-seeded spikelets of *A. ludoviciana* are very rare indeed.

Considerable variation occurs again within ssp. *ludoviciana*. Malzew (1930) subdivided *A. sterilis* ssp. *ludoviciana* into four varieties. Characters such as hairiness of lemma, awns and leaf sheaths have been used to differentiate the types.





Plate I. (a) Spikelet of *A. sterilis*—only the first floret separates by abscission; (b) Detail of sucker-mouth of *A. sterilis*; (c, d) primary and secondary grain respectively, of *A. fatua*—both grains separate by abscission; (e, f) primary and secondary grain, respectively of *A. barbata*. The sucker-mouth is longer and narrower than *A. sterilis* and *A. fatua*. The lemma ends in two bristle-points; (g) spikelet of heterozygote fatuoid—only the primary floret is awned; (h) spikelet of homozygote fatuoid (Type B)—both florets awned. Secondary floret also separates by abscission; (i) primary floret of homozygote fatuoid—distinct sucker-mouth.



The variation occurring in *A. ludoviciana* in Britain has been examined by Thurston (1957). At least 10 different types were recognised using lemma characteristics, and 5 varieties or sub-varieties were identified based on Malzew's classification.

Thurston (1957) has discussed difficulties that arise in classifying and attaching varietal and subvarietal names to living specimens because most classifications have been based only on those lemma characters that survive well under herbarium conditions. Others, such as lemma colour, juvenile habit of growth or coleoptile colour, generally do not enter into classifications.

The most common type of *ludoviciana* observed in the wild oat survey of England and Wales has brown, very hairy lemmas; long brown hairs at the callus, and the awn rough, hairless or moderately hairy. This type was identified as *A. sterilis* ssp. *ludoviciana* var *typica* Malz. (Thurston 1957) (see also p. 47).

#### *Avena barbata* Pott. (slender oat)

One characteristic distinguishes this oat from both weed oats already described: it has the two slender bristle-points at the tip of the lemma which are absent in *fatua* and *ludoviciana*. Another feature distinguishes it from *ludoviciana*, but not from *fatua*: the separation of each grain of a spikelet by abscission leaving an oval sucker-mouth at the base of every grain (Fig. 1.1a and Plate 1e,f).

This tetraploid species does not occur in Britain, but is a common weed in the Mediterranean countries where it is mainly in waste places, on roadsides and in cultivated fields. It is morphologically very similar to the *wiestii-hirtula* groups of diploids (Rajhathy and Thomas 1974). It is difficult to distinguish *A. barbata* morphologically from *A. hirtula-wiestii* as both groups have the two slender bristles at the apex of the lemma, and all grains fall off individually from the plant at maturity leaving a sucker-mouth base in each grain.

*A. barbata* is a slender oat with tall, narrow and very weak culms; the grains are also slender, hence the name 'slender oat'. The panicles are large, equilateral and drooping. Generally, the spikelets have two florets, and the grains have long, twisted and bent awns. The lemma is hairy, and ends in two slender bristles being similar in this latter character to *Avena strigosa* although the bristles are not so long and distinct. Other characters which distinguish it from *strigosa* include the hairy lemma, and the mode of separation of the spikelet and florets, which in *strigosa* are very firm and require pressure to separate them from each other and from the plant (Stanton 1955, 1961).

Malzew (1930) regarded *barbata* as a sub-species of *A. strigosa* while other botanists, such as Körnicke and Werner (1885), Schulz (1913), Zade (1918), Stanton (1955), Rajhathy and Thomas (1974), have given this oat specific status.

Malzew (1930), using mainly the extent of hairiness on the lemma as a criterion, divided *A. strigosa* Schreb. ssp. *barbata* Pott. into two varieties, namely, *typica*, the most frequent type with hairy lemmas, and *subtypica*, a rarer form, with the back of the lemma hairless.



## RELATIONSHIPS BETWEEN WILD AND CULTIVATED SPECIES

The species of the genus *Avena* form a polyploid series with the basic chromosome number of  $n = 7$ . The polyploid species have evolved by the combination of diploid genomes through hybridization and chromosome doubling (Rajhathy and Thomas 1974). In the course of the evolution of these species, the meiotic behaviour of the polyploids has been stabilized by genetic control of diploid-like chromosome pairing, which ensures regular disjunction of the chromosomes and disomic inheritance.

Diploid species of *Avena* have specific habitat requirements and their distribution is localized (Baum *et al* 1972, Holden 1969). These are often found in rough grazing although they are extremely sensitive to grazing; they rarely compete with cereals. In general the diploid species occupy undisturbed habitats, and if grazing is controlled large populations become established. This is particularly clear in the distribution of *A. pilosa* and *A. clauda* in Iran, where they were well established in enclosed areas when cultivation and grazing were minimal (Baum *et al* 1972). The abundance of diploid species of *Avena* in Israel is the direct result of reduction in grazing intensity. In contrast, the aggressive weed species of *Avena* are polyploids. *A. sterilis* is a common weed in its primary region of distribution in the Mediterranean and Middle East, occupying a diversity of habitats from hilly outcrops to urban waste areas and along railway tracks (Baum *et al* 1973). It also forms an aggressive weed of cultivated crops in these regions, in which *A. fatua* is also found, but less frequently. The hexaploid species are widely distributed from the Mediterranean and Middle East region to the more temperate climatic regions of northern and western Europe.

Polyploid species of *Avena*, probably on account of their genetic architecture, can compete successfully as weeds in cultivated crops over a wider climatic range than their diploid progenitors. It is doubtful whether polyploidy *per se* is responsible for the aggressiveness of the wild weed species, but the integration of three diploid genomes into a reproductively effective hexaploid species, with its inbuilt genetic variation in a true breeding form, probably accounts for the versatility of the wild hexaploid species as colonizers and competitors.

The wild hexaploid species and the cultivated oat, *A. sativa*, form fertile hybrids when crossed and the chromosome complements of the wild species are basically similar to *A. sativa* (Joshi and Howard 1955; Ladizinsky 1970). The main morphological features that differentiate the wild species *A. fatua* and *A. sterilis* from the cultivated forms are (a) the articulation of the spikelet or floret at maturity, (b) pubescence and (c) awn development.

Jensen (1961) reviewed the literature on the inheritance of spikelet disjunction and it was clear that in crosses between wild species with free-threshing grains and the cultivated forms in which the grains were retained at maturity the latter was dominant. The  $F_1$  hybrids were of the cultivated form and selfed progenies of the hybrids could be readily classified into wild and cultivated forms of grain disjunction in a simple Mendelian ratio of 3 cultivated to one wild type. Jones (1940), on the other hand, found that in



inter- and intra-specific hybrids between free-threshing and the cultivated type of grain involving diploid and tetraploid species, the wild base type was dominant. However, in all interspecific hybrids in which *A. sativa* was one of the parents the grain type of the cultivated species was always dominant. He concluded that 'the monohybrid segregation is not a segregation of wild and normal type genes acting as allelomorphic units but segregation of the linked genes which inhibit the development of the awn and wild base—which genes are specific to the cultivated base'.

In a population of cultivated oats it would be difficult to identify  $F_1$  hybrids between wild and cultivated oats in view of their close resemblance to the cultivated forms, but in the subsequent generation a third of the progeny would have the characters of the wild species. The importance of this form of contamination depends on the extent of cross-pollination between wild and cultivated forms. The *Avena* species are self-pollinating and this is mainly responsible for the isolation of discrete taxonomic entities without any marked sterility barriers. Natural crossing between the wild species and *A. sativa* is extremely low. Derick (1933) planted *A. sativa* var Alaska around a 1 yd (0.914 m) square block of *A. fatua* and reported approximately 0.1% natural crossing.

Natural crossing between the wild weed species and the cultivated forms is not a serious source of contamination, although the appearance of fatuoids in populations of cultivated oats was originally thought to be the products of natural crossing (Huskins 1946). Fatuoids are off-types that appear occasionally in crops of *A. sativa* (Huskins 1927, Jones 1930) and they have some of the characteristics of *A. fatua* in spikelet morphology. Jones (1930) gave the following description of fatuoids: 'All grains of the spikelet, primary, secondary and tertiary have horseshoe-shaped articulation at the base in the form of a sucker-mouth, the development of which causes the grain to shed readily when ripe. The callus forming the horseshoe prominence is fringed laterally and dorsally with dense tufted pubescence, the rachilla is densely pubescent and a strong twisted and geniculate awn is invariably present in all the grains of the spikelets. In other morphological characters fatuoids are identical with the varieties in which they arise. The three main distinguishing features of the fatuoid grain have been found to behave in inheritance as a completely linked group' (Plate 1g-i).

Huskins (1927) distinguished three types of fatuoids:

Type A. Except for the fatuoid characters, specimens are equal in vigour and fertility to the *sativa* variety in which they appear. Segregation occurs in the approximate ratio of 1:2:1, the heterozygote being intermediate to the normal and fatuoid types with weak awns, partial abscission-scars, a tuft of hairs at each side of the basal floret only, and usually at least some hairs on the lemmas. They have the normal chromosome complement of 42.

Type B. The segregates appear in ratios varying from 1:5 to 1:10 normals and heterozygotes, respectively, plus a few sterile dwarf fatuoids. The normals, heterozygotes and fatuoids have 42, 41 and 40 chromosomes respectively.

Type C. Fatuoids of this type give ratios of 1 normal to 1 heterozygote plus a few dwarf and sterile fatuoids, and occasionally ratios approximating 1:2:1



are obtained. The fatuoids have 44 chromosomes, heterozygotes 43 and the normal 42.

The appearance of fatuoid Types B and C are clearly the result of aberrant chromosome behaviour. Jones (1930) maintained that the Type A fatuoids were under genic control, whilst Huskins (1927, 1946), claimed that chromosome deletion or rearrangement, probably involving corresponding chromosomes from different genomes was responsible for the expression of fatuoid characters. Disturbance involving whole chromosomes resulted in reduced vigour and sterility, whilst minor deletions could be tolerated on account of the genetic duplication inherent in the polyploid structure. In Type A fatuoids, aberrant types were identical to the cultivar in which they appeared except for the fatuoid characteristics of the inflorescence. Fatuoids occur only rarely in seed crops of *A. sativa* and are not an important source of potential weed off-types of the cultivated oat. Seeds of the fertile fatuoids may have the same germinating capacity as the cultivar in which they originated, but many show some degree of dormancy.

#### WILD SPECIES AS PROGENITORS OF CULTIVATED SPECIES

The expression of the fatuoid characters when a pair of chromosomes is lost (Huskins 1946, Nishiyama 1929, Singh and Wallace 1967, Hacker and Riley 1966, Thomas and Mytton 1970) gives some indication of the possible evolution of *A. sativa* from the wild hexaploid plant species. The loss of this particular pair of chromosomes results in a plant which morphologically resembles *A. fatua*. A gene or genes are located on this chromosome which inhibit the expression of these characters in the cultivated oat. Most of the wild species related to cultivated cereal crops are free-threshing and the capacity to retain the grain at maturity was the most significant step in the evolution of the cultivated species (Harlan *et al* 1973). The expression of *fatua*-like characters in the absence of this chromosome indicates that the hexaploid progenitor of the cultivated *A. sativa* was of the *fatua* type.

Baum (1972a) claimed that *A. septentrionalis* (*A. fatua* L. ssp. *septentrionalis* Malzew, see p. 000) is the closest taxon to the cultivated oat. This species is closely related to *A. fatua* but differs in a number of micro-morphological attributes in respect of the shape of the sucker-mouth at the base of the grain and the structure of the lodicules and epiblasts. The shape of the scar at the base of the florets and the lodicule type, bear greater resemblance to *A. sativa* than any other wild species. As a result of a study of the variation in 21 traits in cultivars of cultivated oats, Baum (1972b) made a compound description of the primitive ancestor of the pre-domesticated cultivated oats, and concluded that *A. septentrionalis* fits this description better than any other wild species of *Avena*. The distribution from Mongolia to the Ural mountains also supports this hypothesis. The distribution links the European centre with the Chinese centres of diversity of cultivated oats. The naked types were confined to Northern China and Mongolia (Vavilov 1926, Nakào 1950) until their introduction into Europe. *A. septentrionalis* is



morphologically close to *A. fatua* and is possibly a variant of this species. *A. fatua* is probably derived from *A. sterilis* since the latter seems the most likely primitive form when the diploid and tetraploid progenitors of the hexaploids are considered (Rajhathy and Thomas 1974). Griffiths and Johnston (1956) were able to isolate *fatua*-like mutants after irradiating seeds of *A. sterilis*, and, since this is the main diagnostic feature separating these two species, the mutants also indicate the phylogenetic relationship between *A. fatua* and *A. sterilis*. The cultivated species *A. byzantina* is assumed by Coffman (1946) to have been derived from *A. sterilis* and to be of Mediterranean origin.

According to Vavilov (1926), the domestication of oats is tied up with the cultivation of Emmer wheat. Oats probably spread northwards as a weed of Emmer and, supplanting it in the more temperate climate of northern regions, became established as a crop plant. Vavilov (1926) reported that crops of Emmer grown in Armenian settlements near Hamadan in Persia had admixtures of *A. sativa*. This is in an area where oats are not cultivated. Other populations of Emmer in which oats occurred as weeds were found in the region of the river Kama. The oats often showed variation in articulation and in the ease with which spikelets separated at maturity. The earliest archaeological evidence for oats in primitive agriculture is from the lake dwellings of Switzerland. Evidence on the domestication of oats is sparse, but it is reasonable to conclude that cultivation of oats developed in areas remote from the centres of origin of the wild progenitors. It is not grown as a crop in the area of origin and primary distribution.

### WILD SPECIES IN OAT IMPROVEMENT

The wild hexaploid species of *Avena* and the cultivated forms constitute a biological species in that they form fertile hybrids. This means that any desirable genes in the wild hexaploid species can be readily transferred into the gene pool of the cultivated species by a backcrossing programme.

Natural populations of wild oat species are continually subjected to pests and diseases which devastate cultivated crops. Resistant genotypes are often found in such natural populations. Wild species exist in equilibrium with the indigenous pathogens and the development of resistance is an adaptive factor in the survival of such natural populations. Extensive collections of wild *Avena* species in their primary habitats have been made (Rajhathy *et al* 1966, Baum *et al* 1972) and genotypes resistant to powdery mildew, stem and crown rust, cereal root nematode and tolerance to barley yellow dwarf virus (BYDV) have been isolated from these collections (Zillinsky and Murphy 1967). A collection of wild, weed species of *Avena* is maintained by the Canada Department of Agriculture.

The cultivar Mostyn bred at the Welsh Plant Breeding Station incorporates mildew resistance from a genotype of *A. sterilis* and demonstrates the value of screening these weed populations for desirable genes for incorporation into the gene pool of the cultivated species (Hayes and Jones 1966, WPBS 1968).



Another example of the use of a wild oat in a breeding programme is in development of dormoats (Burrows 1964). Dormoats have been derived from crosses between *A. sativa* and *A. fatua*, in which a degree of the seed dormancy of the wild oat has been introduced into the cultivated oat. The advantage of this delayed germination is that dormoats sown in the autumn remain dormant until the spring, when they germinate and emerge. This new growth pattern provides for very early germination and a better utilization of moisture with its consequent improvement in yield under Canadian conditions.