

THE NATURALISATION HISTORY OF *ECHINOCHLOA MURICATA*
IN BELGIUM, WITH NOTES ON ITS IDENTITY AND
MORPHOLOGICAL VARIATION

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Received 5 February 2004 ; accepted 1 July 2004.

ABSTRACT. — In Western Europe and North America *Echinochloa muricata* (P. Beauv.) Fernald (native in North America) has long been confused with *Echinochloa crus-galli* (L.) P. Beauv. (native in Europe). After its introduction in Europe, it took a long time before it was recognised, and later confusion lingered on, in part because the variability of *E. muricata* was not sufficiently taken into account in keys and descriptions. In the present paper, the difference between *E. crus-galli* and *E. muricata* is discussed, and the variability of *E. muricata* is illustrated. Belgian herbarium specimens labelled *E. crus-galli* and *E. muricata* have been revised. Since 1887 (year of the first collection) *E. muricata* var. *microstachya* Wiegand has gradually spread and is now locally naturalised and abundant, whereas var. *muricata* is only known as a rare casual.

KEY WORDS. — *Echinochloa muricata*, Poaceae, aliens, Belgium.

INTRODUCTION

In 1492 Columbus made his first transatlantic crossing. It was the beginning of an unprecedented exchange of plants and animals between the Old and New Worlds. Named 'the Columbian exchange' by environmental historian Alfred CROSBY (1972), this exchange of important crops, garden plants and weeds has been going on uninterrupted for over five centuries. In the wake of an ever more globalised economy the process has even gained momentum in recent times.

Among conservationists the introduction of alien organisms is today seen as one of the most serious threats to biodiversity. More attention has therefore recently been paid to the processes of

introduction and naturalisation of potentially invasive plants and animals (see e.g. BASKIN 2002, SAKAI *et al.* 2001).

Once a suspected alien has been discovered several questions arise. First there is the topic of the identity of the plant and how it differs from other species (other aliens as well as native species). While still occupied with this first problem, more questions arise. Where did the plant come from, and how and when did it arrive in its introduction area? Have earlier collections perhaps been filed as unidentified specimens or under an erroneous name? The answers to these interrelated questions can result in a reconstruction of the plant's introduction and naturalisation history. Such a story may have a somewhat

hypothetical character, but it provides a good framework to generate new questions and new research.

In Belgium the recent discovery of *Echinochloa muricata* (P. Beauv.) Fernald is a case in point. In 1993 this North American species was added to the Belgian flora – as *E. microstachya* (Wiegand) Rydb. — by LAMBINON (1993), who stated that the published collection “pourrait être le prélude à une naturalisation”. Some years later VERLOOVE (2000) described *E. muricata* as probably no more than an ephemeral alien, at most locally naturalised along the Maas (Limburg), although by then it had also frequently been found in maize fields in the same province (C. Nagels and L. Andriessen, pers. comm.).

Echinochloa muricata was completely overlooked during field work in a large area between Bruges and Ghent between 1998 and 2000 (HOSTE & VERLOOVE 2001). Only one year later, after my attention had been drawn to it, I discovered plenty of large populations of *E. muricata* in the same area. Most plants were easy to identify, but some could not confidently be named either *E. muricata* or *E. crus-galli* (L.) P. Beauv. when using the keys and illustrations in Western European publications (JAUZEIN & MONTÉGUT 1983, JAUZEIN 1995, SCHOLZ 1995). Certain American publications (e.g. HITCHCOCK 1920, 1950) only added to the confusion.

The newly discovered populations, spread over a large area, and the problems encountered when trying to identify certain specimens generated two sets of questions: (1) How can *Echinochloa muricata* be distinguished from *E. crus-galli*, and how variable is the Belgian material of *E. muricata*? (2) When and how was *E. muricata* introduced in Belgium?

MATERIAL AND METHODS

The description of the differences between *Echinochloa crus-galli* and *E. muricata* is based on literature, collections in Belgian herbaria, and my own observations on fresh material from the area between Bruges and Ghent. The description of the variation within *E. muricata* is mainly based on material collected in Belgium. A restricted number of additional specimens from other countries in BR and LG have been

studied to check the validity of some of the described characters. With the exception of the most recent years (for which field observations have been included) the historical reconstruction is exclusively based on herbarium specimens. All the sheets of collections made in Belgium and labelled *Echinochloa crus-galli* or *E. muricata* from BR (including herbaria J.E. De Langhe, S. Depasse and J. Duvigneaud), LG and GENT were revised. Duplicates were also studied, but were not incorporated for calculations.

The distribution map is exclusively based on herbarium collections from BR, LG and GENT. The author's herbarium has not been used to compose the map, because this would have overemphasised the ‘importance’ of recent years and of the area between Bruges and Ghent. No attempt has been made to compose a distribution map of *E. muricata* based on field records, because this would only give an overview of prospected areas, hardly giving any information about the real distribution pattern of *E. muricata*.

NOTES ON TAXONOMY AND VARIATION

In 1915 *Echinochloa muricata*, described as *Panicum muricatum* Michx. (nom. illeg.) in 1803, was again brought under the attention of American botanists (FERNALD 1915). Fernald stated that in the indigenous *E. muricata* the spikelets had stiffer, coarser, strongly divergent trichomes with a conspicuous papillose base, whereas the introduced *E. crus-galli* (native in Europe) only had fine trichomes with at most a slightly thickened base. Unfortunately the proposed character did not allow a straightforward distinction between the two species. HITCHCOCK (1920), therefore, dismissed *E. muricata* as a good species and lumped it with *E. crus-galli*.

At about the same time WIEGAND (1921) published another revision of *Echinochloa* in North America. His approach was very different from Hitchcock's. He accepted *E. muricata* and *E. crus-galli* as clearly distinct species and introduced a new and better distinguishing feature: *E. muricata* has a subacuminate fertile lemma with a firmer tip, whereas in *E. crus-galli* the fertile lemma is subacute or obtuse, with a withering tip. The structure and position of the bristles on the spikelet were no longer used as the most important features. Another important difference,

TABLE 1

Differences between Echinochloa muricata var. microstachya and var. muricata, according to three American publications

| | var. <i>microstachya</i> | var. <i>muricata</i> |
|----------------------------|--|---|
| WIEGAND (1921) | spikelets (2.5-)2.8-3.4 mm (including var. <i>occidentalis</i> Wiegand and var. <i>multiflora</i> Wiegand) | spikelets 3.3-4.5 mm (including var. <i>ludoviciana</i> Wiegand) |
| GOULD <i>et al.</i> (1972) | spikelets < 3.5 mm ; lemma lower floret awnless or with an awn to 6, infrequently 10, mm long | spikelets 3.5 mm or more ; lemma lower floret with an awn usually 6 mm or more long, infrequently awnless |
| MICHAEL (2003) | spikelets 2.5-3.8 mm ; lower lemma unawned or awned, the awns to 10 mm long | spikelets 3.5-5 mm ; lower lemma usually awned, the awns 6-16 mm long |

i.e. the presence or absence of a ring of minute setae between body and tip of the lemma of the fertile flower, was added by FASSETT (1949).

For decades confusion lingered on (see e.g. HITCHCOCK 1950) and even today “this confusion is probably reflected in the mapping of both *E. crus-galli* and *E. muricata*” in North America (MICHAEL 2003). This certainly also applies to Western Europe, where *E. muricata* has long been completely overlooked and where confusion today persists because of the variability of the species. Great Britain provides us with a good illustration : whereas RYVES *et al.* (1996) listed *Echinochloa muricata* s.l. under two names [*E. muricata* (Michx.) Fernald and *E. pungens* (Poir.) Rydb., the latter as a wool alien], the up-to-date flora of STACE (1997) did not mention *E. muricata* at all.

MICHAEL (1983) recognised *E. muricata* and *E. microstachya* as separate species, but in a recent treatment MICHAEL (2003) described both taxa as varieties of *E. muricata* that, in his words, “tend to be distinct, but there is some overlap in both morphology and geography.” JAUZEIN (1993) and LAMBINON *et al.* (2004) described the two taxa as subspecies of *E. muricata*. WIEGAND (1921) also accepted only one species, but listed 5 varieties, linked by intergrades. In downplaying the importance of the variation in general appearance of the spikelet (bristles, awns, length of the spikelet) and emphasising the character of the acute lemma *E. muricata* was turned into what

Wiegand called “a well-defined unit”. As shown in Table 1, distinction between var. *muricata* and var. *microstachya* Wiegand is not always evident. Excluding the awn when measuring spikelets may lead to varying interpretations among botanists.

RESULTS AND DISCUSSION

THE DIFFERENCES BETWEEN *E. MURICATA* AND *E. CRUS-GALLI*

While studying Belgian material it soon became clear that *E. muricata* is more variable than usually reflected in keys and illustrations. In addition certain very useful characters are not fully exploited in most publications. In these circumstances, with the closely related *E. crus-galli* being a very variable species, ‘atypical’ specimens of *E. muricata* can easily be misidentified as *E. crus-galli*, even by people who have seen lots of ‘typical’ plants.

When mature material is available identification very rarely poses serious problems. I never found clear intermediates between *Echinochloa crus-galli* and *E. muricata* in the Belgian material I studied. This conforms to GOULD *et al.* (1972), who reported that putative hybrids involving the two taxa are not known, and to DESCHATRES *et al.* (1974), who never found intermediates among the large mixed stands of *Echinochloa* along the rivers Loire and Allier.

Field identification with the aid of a hand-lens is relatively easy in most cases. At home careful study of the spikelets, using a higher magnification, should eliminate any remaining doubt. Within both species the characters used for identification are (very) variable and some overlap between species does occur. Therefore, a balanced evaluation based on a combination of characters, as described in Table 2, is required for reliable identification.

In the field a good first indication is provided by the uppermost leaf, which in *E. muricata* shows a line in the form of an upside-down U between blade and sheath (leaf-blade decurrent). Especially in smaller plants this structure generally results in a stiff, upright position of the blade, whereas in *E. crus-galli* the upper blade is generally patent to reflexed.

Spikelets of both *E. crus-galli* and *E. muricata* are highly variable. Relying heavily on the shape and position of the bristles on the spikelets all too often raises confusion. Decisive for a correct identification is a careful study of the lemma and palea of the fertile flower (see Table 2). The line of minute hairs at the apex of the fertile lemma in *E. crus-galli* can be hard to see, but the distinction between the membranous tip and the coriaceous part of the lemma is usually clear-cut and visible with a hand-lens (Fig. 1A, B). When mature spikelets of *E. crus-galli* are rubbed between one's fingers some tips easily break off (G. Dirkse and F. Reijerse, pers. comm.).

The shape of the upper palea is rarely described in the literature (but see JAUZEIN 1995), although it is very useful. Seen in profile the combination of lemma and palea of the fertile flower in *E. muricata* resembles the fine beak of a passerine bird.

VARIATION WITHIN *E. MURICATA* IN BELGIUM

In the Belgian material distinction between var. *muricata* (so far only known as a rare casual) and var. *microstachya* (by far the most common variety) is not always straightforward. Two accessions with spikelets more than 4 mm long clearly belong to var. *muricata* (accessions 24 and 25 in the Appendix); a third accession is more or less

intermediate (accession 9 in the Appendix). All other accessions were named var. *microstachya*, with spikelets frequently well over 3 mm long.

In the Belgian material of var. *microstachya* two clearly distinct types, with some intermediate forms, can be recognised. One type has awnless spikelets with a short tip and strong, spreading bristles, which give the spikelet a rugged appearance (Fig. 2A, B). This type fits very well with the description and illustration in JAUZEIN (1993, 1995) and with var. *microstachya* as described by WIEGAND (1921). A second type has awned, slender spikelets with an acuminate upper lemma and palea, an acuminate or short-awned upper glume, and more appressed bristles (as in *E. crus-galli*; Fig. 3A, B). This type, which more or less fits the description of var. *occidentalis* WIEGAND (1921), is one that hardly harmonises with the descriptions of *E. muricata* in the European literature. It typically has slender inflorescences and is not rare in maize fields between Bruges and Ghent. FASSETT (1949) showed that "Wiegand's variety [var. *occidentalis*] is good, and all his cited specimens clearly belong with it, excepting only the type". *Echinochloa muricata* var. *occidentalis* thus became a synonym of *E. crus-galli*, and Fassett described a new taxon corresponding to the concept '*occidentalis*' as described by Wiegand: *E. pungens* (Poir.) Rydb. var. *wiegandii* Fassett [= *E. muricata* var. *occidentalis* auct. non Wiegand: Wiegand (1921) quoad descr., excl. typ.].

In the first type the 'passerine beak' of fertile lemma and palea may look somewhat less typical, but then the spreading bristles should tip the balance in favour of *E. muricata*; in the second type the 'beak' character is always very well developed.

ECHINOCHLOA MURICATA IN THE BELGIAN HERBARIA

Quite some specimens labelled *E. crus-galli* had to be renamed *E. muricata*. In all, 33 Belgian collections were identified as *E. muricata*, the first one going back as far as 1887. Until the 1990s all had originally been named *E. crus-galli*. On rare occasions the collector had expressed doubt about the identity in a remark written on the

TABLE 2

A selection of characters defining Echinochloa muricata and E. crus-galli

| | <i>E. muricata</i> | <i>E. crus-galli</i> |
|---|---|---|
| Panicle | Very variable ; usually erect, with a rather stiff general appearance ; the position of the primary branches varying from appressed (resulting in a dense cluster or a slender, elongated inflorescence) to spreading ; branches in large inflorescences sometimes reflexed Usually with at least a tinge of purple, sometimes purple-black | Very variable, erect or nodding, with primary branches usually spreading or reflexed ; general appearance often softer, less stiff than in <i>E. muricata</i> Very variable, from pure green to purple |
| Upper glume and lower lemma (sterile flower) | Hispid, with papillose-based hairs ; papillose basis of the bristles sometimes inconspicuous ; bristly hairs strongly spreading or not ; lower lemma without or with a short awn (Fig. 2A, 3A) ; awn in the Belgian specimens up to ca. 8(-10) mm (or longer in the rare var. <i>muricata</i>) ; variation of the length of the awns within a single inflorescence much less striking than in <i>E. crus-galli</i> | Hispid ; bristly hairs papillose-based or not, not conspicuously spreading ; lower lemma with or without an awn ; awns up to 50 mm, their length extremely variable within a single inflorescence ; a (large) majority of awnless spikelets often along with a limited number of long-awned spikelets ; sometimes the terminal inflorescence without awns, but some spikelets in the lateral inflorescences (long-) awned |
| Upper lemma (fertile flower) (best studied on mature spikelets) | Acute or acuminate, with a stiff tip ; membranous top portion not clearly differentiated from the coriaceous part of the lemma (Fig. 4) | Membranous tip less acute, clearly differentiated from the coriaceous part of the lemma, the boundary between both parts as a rule marked by a line of minute hairs (hairiness often very inconspicuous, showing strong variation within a single inflorescence) (Fig. 1A, B) |
| Upper palea (best studied on mature spikelets) | Coriaceous, acute or acuminate, with a stiff, (nearly) straight tip ; tip closely appressed against the lemma in mature florets or slightly reflexed (palea not appressed against the lemma when the floret is in bloom !) ; palea as long as or a little shorter than the lemma (Fig. 2B, 3B) | Coriaceous, but with a blunt, soft, frayed looking tip ; no sharp boundary between the tip and the coriaceous part of the palea ; tip slightly or, more often, strongly recurved, not closely appressed against the tip of the lemma ; tip not extending as far as the tip of the lemma (Fig. 5) |
| Leaves | Blade of the uppermost leave(s) strongly decurrent along the culm (demarcation between blade and sheath forming a clearly elongated upside-down U) | Blades of the leaves at most moderately decurrent along the culm (demarcation between blade and sheath forming a semicircular or slightly elongated U) |
| Caryopsis | Spheroid or a little elongated | Elongated |

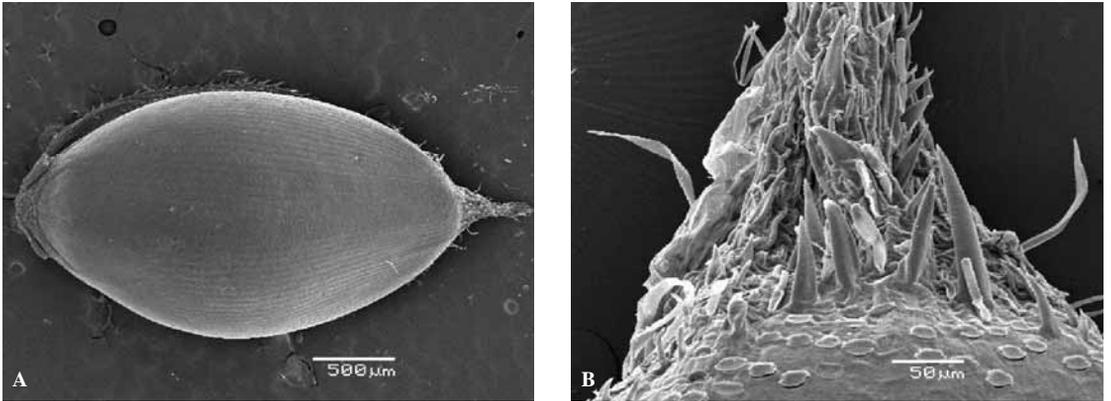


FIG. 1. — *Echinochloa crus-galli*. **A** : lemma of the fertile flower. **B** : tip of the lemma, with a line of minute hairs at the base. [Lotenhulle (Aalter), 2001. Coll. *I. Hoste*].

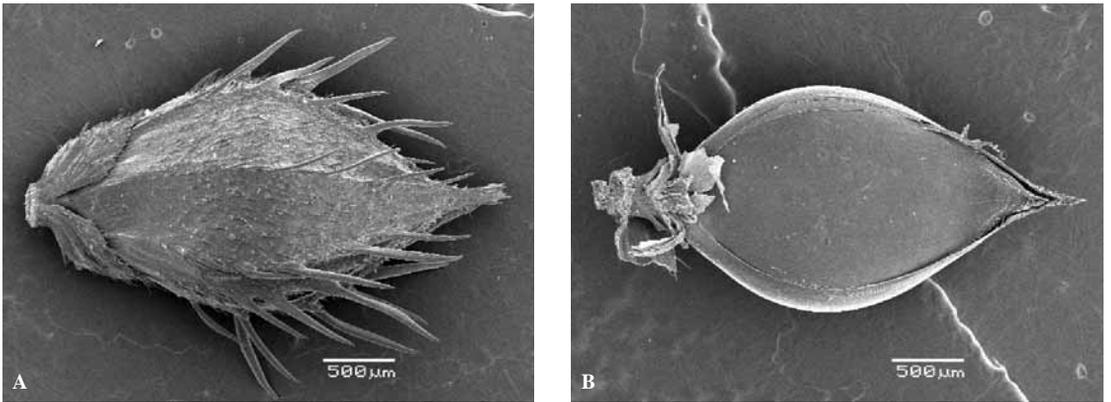


FIG. 2. — *Echinochloa muricata* var. *microstachya* : unawned, bristly spikelet. **A** : spikelet. **B** : palea of the fertile flower. [A : Tielt, 2001 ; B : Poeke (Aalter), 2001. Coll. *I. Hoste*].

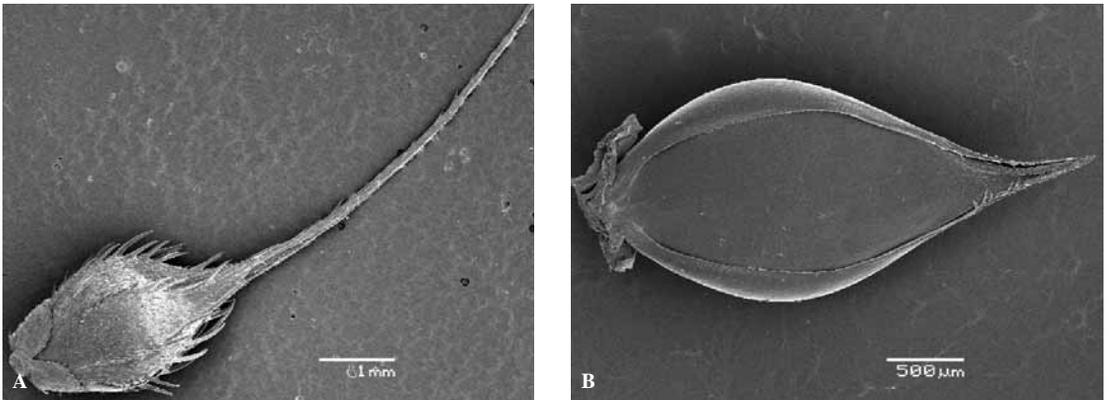


FIG. 3. — *Echinochloa muricata* var. *microstachya* : awned spikelet. **A** : spikelet. **B** : palea of the fertile flower. [Bellem (Aalter), 2003. Coll. *I. Hoste*].

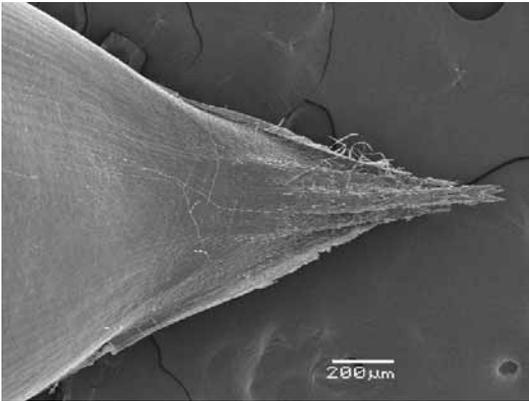


FIG. 4. — *Echinochloa muricata* var. *microstachya* : apex of the lemma of the fertile flower. [Bellem (Aalter), 2003. Coll. I. Hoste].

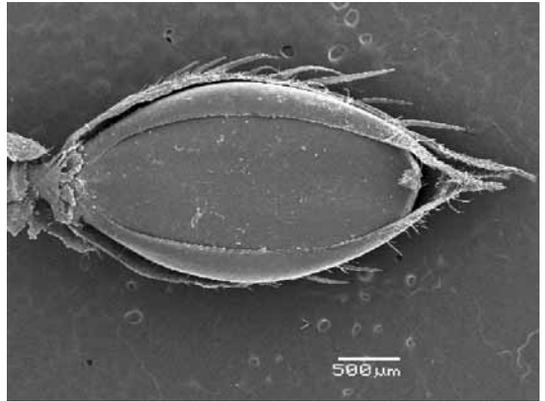


FIG. 5. — *Echinochloa crus-galli* : palea and lemma of the fertile flower (plus upper glume), with incurved top of the palea. [St.-Kruis (Brugge), 1942. BR, coll. P. Vande Vyvere].

TABLE 3

Belgian accessions of *Echinochloa crus-galli* and *E. muricata* (herbaria BR, LG and GENT), duplicates excluded

| Period | <i>E. crus-galli</i> | <i>E. muricata</i> | <i>E. crus-galli</i> + <i>E. muricata</i> | <i>E. muricata</i> /total (%) |
|-----------|----------------------|--------------------|--|----------------------------------|
| < 1910 | 110 | 2 | 112 | 1.8 |
| 1910-1939 | 40 | 3 | 43 | 7.0 |
| 1940-1969 | 63 | 4 | 67 | 6.0 |
| 1970-1989 | 40 | 11 | 51 | 21.6 |
| > 1989 | 38 | 13 | 51 | 25.5 |

Note : 13 undated specimens of *E. crus-galli* (almost all < 1940) could not be attributed to one of the four periods.

label, but in the end *E. crus-galli* was withheld as the name. *Echinochloa crus-galli* being variable, one can easily imagine that some collections of *E. muricata* were made by botanists who intended to document the variability of *E. crus-galli*. Careful selection in the field in those days of specimens of ‘*crus-galli*’ with a rather deviating look may help explain the presence of both *E. crus-galli* and *E. muricata* on three old herbarium sheets ; all three had been labelled *E. crus-galli* by the collectors.

Apart from a certain inclination to collect more or less aberrant, strange-looking specimens of presumed *E. crus-galli* (which would only much later turn out to be *E. muricata*), there is no reason to believe that until recently one species was collected relatively more often than the other one. In other words : the proportion of both species in the

total amount of collections gives us a good indication of their relative frequency in the past.

Table 3 gives an overview of all accessions found in BR, LG and GENT. The number of accessions is rather small, but still some conclusions are possible (see also the Appendix). Table 3 shows a steady increase of collections per time unit. In the 19th century *E. muricata* was collected in 1887 and 1890 only. From then on and until World War II accessions were often separated by large time gaps. More recently there has been a sharp rise in absolute and relative numbers of *E. muricata* accessions (Table 3). The cumulative frequency curve of the Belgian accessions since 1800, grouped per decade, shows a remarkably regular pattern (Fig. 6).

In the 19th century *E. muricata* accounted for only a very small percentage of the combined

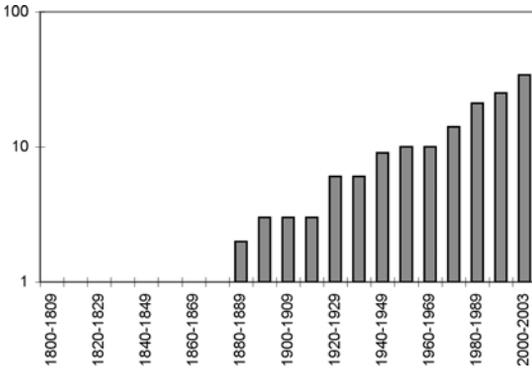


FIG. 6. — Cumulative frequency curve of accessions per decade of *E. muricata*, based on all 33 herbarium sheets in BR, LG and GENT. Y-axis logarithmic ; values given as $x + 1$.

crus-galli/muricata accessions. In the 20th century the ratio between *E. muricata* and *E. crus-galli* increasingly changed in favour of *E. muricata*. By the turn of the century *E. muricata* accounted for about a quarter of *crus-galli/muricata* accessions. Once it was known that *E. muricata* could be found in Belgium a few botanists actively searched for it during field trips, but this probably did not significantly increase the percentage of *E. muricata* accessions. Our revision of the ‘*crus-galli*’ accessions of the seventies and eighties has shown that already then, over 20% of them were *E. muricata*.

A HISTORICAL RECONSTRUCTION OF *ECHINOCHLOA MURICATA* IN BELGIUM

Compared with what is known from surrounding countries (e.g. SCHOLZ 1995, WISSKIRCHEN 1995, RYVES *et al.* 1996, LAMBINON 1997), but with France more or less an exception, the series of data for Belgium since the late 19th century and the present status of *E. muricata* as a well naturalised species, with numerous large populations in at least some parts of the country, comes as a surprise. Chances are that renewed study of the accessions labelled *E. crus-galli* in the herbaria of neighbouring countries will reveal that the situation in Belgium is less exceptional than appears at first sight.

An area where *E. muricata* was recognised long ago and where it was monitored in the

decades since its discovery, is along the river Loire and its tributary Allier (France). In this area *E. muricata* has been present on the river banks for half a century. According to DESCHATRES *et al.* (1974) the first collection was made in 1954. By the mid-seventies, when the distribution pattern already indicated “une immigration assez ancienne”, two clearly different types of *E. muricata* grew along Allier and Loire. For the same area KERGUÉLEN (1987) listed both subsp. *microstachya* (Allier and Loire) and subsp. *muricata* (Val de Loire).

The distribution map of collections of *E. muricata* since the 19th century (Fig. 7) is helpful for a tentative reconstruction of the species’ history in Belgium. A large proportion of the old accessions come from Verviers and environs, which during a good part of the 19th and 20th century was an important wool industry centre. Large quantities of wool, imported from several continents, were washed and worked in plants along the Vesdre river. This wool contained numerous seeds of alien plant species (VISÉ 1942).

Among botanists Verviers and the Vesdre were reputed for their flora of aliens. VISÉ (1942) indicated the two main habitats where aliens could be found : the gravel banks of the Vesdre and tips where waste from the wool plants was dumped. Fluctuating water levels (with the highest level in winter) prevented the development of permanent plant colonies on the riverbanks. Therefore, the possibilities for further dispersion of plants that germinated on the gravel banks were very limited : most plants collected there were mere ephemeral casuals. The same is probably true for the majority of plants found on tips.

Riverbanks and tips were easily located by ‘aliens hunters’ and yielded a rich and varied harvest of curiosities. But it appears there was a third manner of introducing alien seeds in the area around Verviers. CLEMENT & FOSTER (1994) indicated that in Great Britain the origin of certain wool aliens could be linked with the use of wool waste as a soil conditioner on market gardens and farms. VISÉ (1942) gives an example of gardens in the Verviers region that were manured with litter from imported wool ; the following summer this resulted in a long list of aliens. Such practices

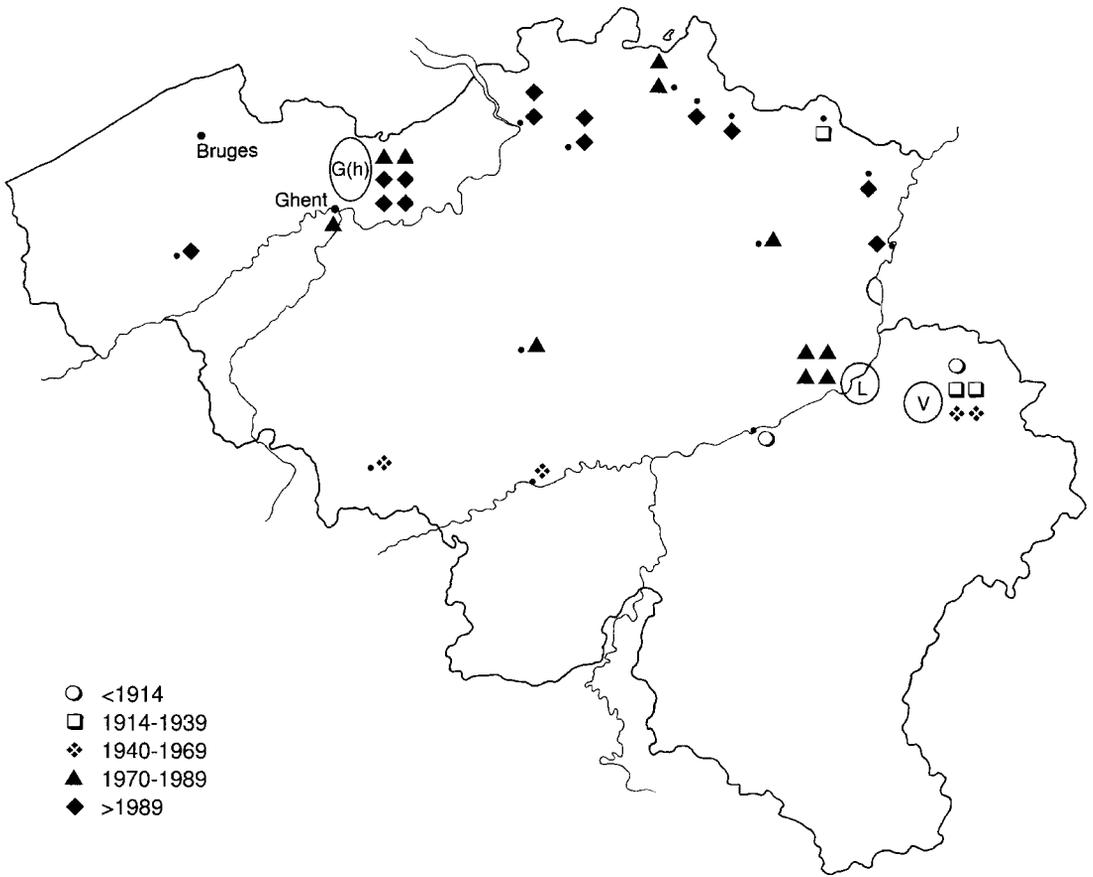


FIG. 7. — Distribution of Belgian accessions of *Echinochloa muricata* since the 19th century. Locations with 1 or 2 accessions are indicated with a black dot ; concentrations of accessions are indicated with an oval : **G(h)** : Ghent (harbour), 6 accessions ; **L** : Liège and environs, 4 accessions ; **V** : Verviers (Vesdre) and environs, 5 accessions.

may well have put *Echinochloa muricata* on the track towards naturalisation in a larger area. Could it be that the cluster of collections around Liège resulted from this process of colonisation of the agricultural landscape ?

VISÉ (1942) underlined that not all aliens found around Verviers had necessarily been introduced with wool. *Echinochloa muricata* (which was not in his list) is native to North America, a region that was not an important supplier for the Verviers wool industry (VISÉ 1942). This does not necessarily imply that *E. muricata* could not have been introduced in Belgium as a wool alien. Perhaps *E. muricata* arrived in Belgium only after it had been introduced in other parts of the world,

from where it later reached Verviers. Given the long-standing confusion between *E. muricata* and *E. crus-galli* (and possibly other *Echinochloa* species) the full, worldwide history of introduction and naturalisation of species of this complex genus (some of them reputed weeds) remains to be written.

Information is too scanty to explain the pattern of collections from scattered locations at the end of the 1970s. Since the mid-eighties all collections were made in the northern part of the country. Changing patterns of botanical activity in Flanders and Wallonia may have played a role, but this is not the whole story. The frequency of collections from harbours indicates the importance

of a continual transmarine import of seeds (contamination of fodder or raw materials for fodder production). We can assume that, through pathways that are still not completely understood, the bulk of today's naturalised populations in maize fields have originated from these imports (HOSTE 2003; today known from over 30 IFBL 4 × 4 km squares between Bruges and Ghent). The boom of maize cultivation in Flanders that started ca. three decades ago created optimal conditions for the establishment of permanent populations of *Echinochloa muricata*.

The variability of the plants found today in and along maize fields between Bruges and Ghent indicates that several successful introductions have taken place. Still they all belong to var. *microstachya*. No population of var. *muricata* has so far been found in this well prospected area.

ECOLOGY

In Belgium *Echinochloa crus-galli* and *E. muricata* often grow together in and along maize fields. Ecologically the two species resemble each other, with *E. muricata* performing slightly better on moister and heavier soils (e.g. in river valleys), although this point requires further study. Both species are also found on arable land and ruderal, recently disturbed sites, or sometimes in shallow ditches along fields that run dry in summer. In North America FERNALD (1915) reported *E. muricata* as typical of wet habitats (ditches, sloughs, pond-margins, etc.) whereas the introduced *E. crus-galli* was mainly restricted to cultivated fields and similar artificial habitats.

In Flanders the preference of *E. muricata* for maize fields is contradictory to the observations of WISSKIRCHEN (1995), who described *E. muricata* in France as growing foremost along riverbanks, with no tendency to spread in arable land. Along the Maas (see accession 21 in the Appendix) *E. muricata* has been found in a habitat comparable with the one known from the Loire and Allier (France). In Germany also *E. muricata* often grows on riverbanks (SCHOLZ 1995). In North America MICHAEL (2003) described a preference for moist, often disturbed sites, but not rice fields, whereas the same author (MICHAEL 1983)

cited *E. microstachya* as a vigorously growing weed in rice in Australia, where it is naturalised. For *E. crus-galli* MICHAEL (2003) mentioned moist sites, including rice fields.

The variety of descriptions of habitat preferences reflects reality as well as incomplete documentation. Aspects that should be considered when screening publications for ecological information include a lack of data for certain habitats or geographical regions, confusion because of opposite taxonomical opinions (accepting two or only one species), different pathways through which aliens have been introduced, a relatively short naturalisation history (temporarily preventing the introduction in all potential habitats in a recently colonised region), important changes in agricultural practices (e.g. the spread of maize cultivation in Flanders), and perhaps the existence of a number of ecotypes (as described for *E. crus-galli* and related taxa as rice mimics in rice fields; YABUNO 1966). Overall *E. muricata* is restricted to highly dynamic and strongly nitrophilous habitats that in general have only a limited conservation value.

CONCLUSION

The mutual exchange between North America and Western Europe of *Echinochloa muricata* and *E. crus-galli* is but a minor example of the Columbian exchange. Careful study of old and recent accessions of other taxa may reveal more histories of interactions between plants, animals and humans that in some cases cover longer time-spans than so far assumed. Such studies can help us improve our understanding of some aspects of the present biodiversity crisis and so-called biological pollution caused by the introduction of aliens in ecosystems. A good knowledge of the differences between closely related taxa is indispensable for anyone investigating naturalisation processes.

ACKNOWLEDGEMENTS

I thank the curators of the herbaria LG and GENT for permission to study their *Echinochloa* collections, J. Lambinon and an anonymous referee for their

constructive remarks, J. Lambinon and F. Verloove for assistance in my search for literature, Marcel Verhaegen (BR) for making the photographs, and Omer Van de Kerckhove (BR) for drawing the distribution map.

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APPENDIX

Collections of *Echinochloa muricata* made in Belgium and deposited in BR, LG, and GENT. Collections are placed in chronological order. Ecological data have been translated in English.

19.09.1887, Ensival, gravel beds of the Vesdre, in a grassy vegetation, *M. Halin* s.n. (BR) (on the same sheet also *E. crus-galli*) [1]; 10.10.1890, Huy, Etang Godin, tip, *A. Charlet* s.n. (LG) (on the same sheet also *E. crus-galli*) [2]; 1920, Verviers, gravel beds of the Vesdre, *A. Visé* (BR) [3]; 27.08.1920, Achel, sand, *J. Hamoir* s.n. (BR) [4]; 28.08.1920, Ensival, gravel beds of the Vesdre, *A. Isaäcson* s.n. (BR) (on the same sheet also *E. crus-galli*) [5]; 22.09.1946, Charleroi, tip, *J. Duvigneaud* s.n. (BR) [6]; 25.09.1947, sine loco, gravel beds of the Vesdre, *C. Pelgrims* s.n. (BR) [7]; 30.09.1948, Wasmuel, tip, *Frère Macédone* s.n. (BR) [8]; 19.09.1959, Verviers, banks of the Vesdre, *A. Lawalrée* 10.870 (BR) [9]; 25.09.1972, Turnhout, on dredged clay, *J. Aerts* s.n. (GENT) [10]; 19.08.1977, Turnhout, Watertappingstraat, tip in an abandoned clay pit, *J. Aerts* 77/50 (GENT) [11]; 23.08.1978, Angleur, ditch, *J. Hechtermans* s.n. (LG) [12]; 29.09.1979, Waterloo, maize field, *P. Sotiaux* s.n. (BR) [13]; 28.09.1980, Angleur, banks of the Ourthe, *J. Monfort & M. Delens* s.n. (LG) [14]; 22.08.1983, Beyne-Heusay, Ste Anne, field on sandy soil, *J. Beaujean* 83/58 (LG) [15]; 22.08.1983, Moulin-sous-Fléron, Queue-du-Bois, fallow land, *J. Beaujean* 83/63 (LG) [16]; 24.08.1983, Harbour of Ghent, Kennedylaan, IFBL C3.53.34, bed with shrubs in the central reserve, *E. Robbrecht* 2642 (BR, GENT) [17];

06.10.1983, Harbour of Ghent, road parallel with Sifferdok, IFBL C3.53.33, *E. Robbrecht* 2773 (BR, GENT) [18]; 10.10.1985, Ghent, St.-Hubertusstraat, waste ground, ruderal site, *P. Goetghebeur* 5487 (GENT, LG) [19]; 05.09.1987, Spalbeek, near 'Jans', IFBL D6.45.31, road verge, *H. Vannerom* 870905.3 (LG, BR) [20]; 10.09.1994, Kotem (Maasmechelen), IFBL D7.46.32, gravel banks of the Maas, *J. Lambinon* 94/B/664, *L. Andriessen & C. Nagels* (LG, BR) [21]; 25.09.1999, Harbour of Roeselare, IFBL D1.58.21, muddy disturbed road verge, *F. Verloove* 3908 (BR) [22]; 12.10.1999, Ghent, Wiedauwkaai, IFBL D3.12.41, at the border of the road, *W. Van Landuyt* 99-24 (GENT) [23]; 06.11.1999, Hooglede (ex Ghent), grown in the garden at Hooglede from soybean waste ex Ghent Grain Terminal, *F. Verloove* 4024 (BR, LG) (var. *muricata*) [24]; 03.09.2000, Harbour of Ghent, Rodenhuizedok, IFBL C3.43.42, heaps of soybean waste at Vamo Mills, *F. Verloove* 4640 (BR) (var. *muricata*) [25]; 23.09.2000, Harbour of Antwerp, Samga at Amerikadok, IFBL C4.16.34, discharging quay at the grain stores, *F. Verloove* 4642 (BR) [26]; 23.09.2000, Harbour of Antwerp, Samga at Amerikadok, IFBL C4.16.34, discharging quay at the grain stores, *F. Verloove* 4643 (BR) [27]; 09.2001, between Ranst and Broechem, IFBL C5.31.22, maize field, *E. Molenaar* s.n. (BR) [28]; 16.09.2001, Oud-Turnhout, Corsendonk, IFBL B6.51.34, border of a maize field, *F. Verloove* 4917 (BR, LG) [29]; 16.09.2001, Dessel, Pinken, IFBL C6.13.43, border of a maize field, *F. Verloove* 4913 (LG) [30]; 01.10.2001, Zoersel/Oelegem, IFBL C5.31.11, border of a maize field, *E. Molenaar* s.n. (BR) [31]; 07.09.2002, Opitter (Bree), border of a maize field, *J. Lambinon* 02/B/217, *L. Andriessen, C. Nagels & F. Verloove* (LG, BR) [32]; 27.07.2003, Zelzate, Kallemansputte, huge deposits of dredgings from the canal, *J. Lambinon* 03/B/506, *F. Verloove* et al. (LG) [33].