

Remarks to the Breeding Systems of the *Triticeae* with Special Reference to the Pollen to Ovule Ratios

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Abstract: The pollen to ovule ratio (P/O ratio) is a conservative indicator of the breeding system. Low P/O ratios are characteristic for self-pollinated plants whereas high P/O ratios indicate cross pollination. Data on p/o ratios have been compiled for the tribus *Triticeae* (10 genera of the subtribus *Triticinae*, genera of the subtribus *Hordeinae*), including important genera as *Triticum*, *Aegilops*, *Secale* and *Hordeum*.

Keywords: pollen to ovules ratios; *Triticinae*; breeding system

The data on the P/O ratios in the *Triticeae* are still limited. There have been studies at the beginning of the scientific breeding period to investigate the breeding system of the important cereals, including those from the *Triticeae*. Later on, the breeding system seemed to be of minor importance, e.g. breeding barley for closed flowering (pseudo-resistance against loose smut) or isolation requirements for cross pollinators (rye).

In the 1960ies started the era of hybrid breeding and the question arose if a strong self-pollinator, like wheat or barley has maintained sufficient capacity for allowing a hybrid seed production. In the 1970ies started a new period with increased inclusion of wild relatives of crop plants. This resulted in building up large collections of wild relatives (e.g. *Aegilops*) in genebanks. And, again, the breeding system turned out to be of high importance for ensuring the genetic integrity of the accessions. This period is still going on and the number of wild *Triticeae* is further increasing in the collections.

In the last years in connection with GMO, pollination ecology is, again, highlighted.

In this paper data concerning breeding system and pollen to ovule ratios are summarized for 10 genera of the subtribus *Triticinae* and 7 genera of the subtribus *Hordeinae*. The P/O ratios also allow phylogenetic conclusions and indicate the pollination requirements for material in genebanks.

Some examples from *Aegilops*, *Triticum*, *Secale* and *Hordeum* are discussed.

Brief historical account

Wilhelm Rimpau (1842–1903) has to be recognized as one of the founders of scientifically based plant breeding (MEINEL 2003). He published an early account on the pollination ecology of cereals (RIMPAU 1882) which stressed the importance of this discipline for the emerging plant breeding. Cross and self-pollinators have been characterized and both could be found within the tribus *Triticeae*. Also in the following decades, plant breeders played an important role in developing our discipline. With the further development of plant breeding data could be obtained, concerning e.g. the outcrossing rates of self-pollinators like barley (Table 1). The participation of the female and male sides for the occasional success in outcrossings was studied and especially the specific adaptation of the male side to wind pollination (anemophily) like anther length (Table 2), pollen diameter (Table 3) and flying characteristics of the pollen (Table 4).

As an interesting indicator of the breeding system the number of pollen grains per anther was characterized (Table 5).

Intensive studies of the breeding systems in the *Triticeae* started with the beginning of hybrid

Table 1. Outcrossing rate of barley (data from literature, after HAMMER 1974)

| Outcrossing rate | Authors |
|------------------|-----------------------------|
| 2 | VESTERGAARD (1915) |
| 0.04–0.15 | STEVENSON (1928) |
| 3.285–20.708 | ROBERTSON and DEMING (1931) |
| 0.07–0.16 | HARRINGTON (1932) |
| 0.081 | UEKI (1952) |
| 1.2 | TOCHTUEV (1955) |
| 1–2 | JAIN and ALLARD (1960) |
| 0.1 | FAVRET (1961) |
| 0.02 | JAIN and SUNESON (1963) |
| 0.23–0.67 | DAY <i>et al.</i> (1971) |
| 5 | KRAUSSE (1972) |

breeding. The central question was if strong self-pollinators like barley and wheat have sufficient capacity for cross-pollination in the fields for hybrid production (see HAMMER 1974 for barley).

The plant genetic resources movement (PISTORIUS 1997) lead to an intensified collection of wild *Triticeae*, too. Genebanks had to respond to large collections of this material which had to be properly maintained. Breeders have been encouraged to use this material (HARLAN & DE WET 1971; HAWKES 1977) and the genebank-specific aspects have been accumulated in monographic treatments (HAMMER 1980, 1985; HAMMER *et al.* 1987).

New interest in pollination ecology arrived from the emerging molecular work and the release of GMOs.

The crop-to-wild geneflow is a common phenomenon and part of plant evolution. Many cultivated plants hybridize spontaneously with wild or weedy relatives (SMALL 1984; ELLSTRAND 2003). This is also characteristic for the *Triticeae* (e.g. barley, HAMMER *et al.* 1985). With transgenic plants, the problem of gene flow, which may ultimately cause possible ecological risks, has acquired special significance (SNOW 2002) and resulted in many new investigations concerning the breeding system.

Pollen to ovule ratios

Within the biological sciences, the ecological approach lead to the formation of a special discipline, namely “pollination ecology” (FAEGRI & VAN DER PIJL 1971). A particular development started with CRUDEN’s (1977) concept considering the pollen to ovule ratio (P/O ratio) as an important evolutionary indicator. The P/O ratios in the genus *Hordeum* range from about 9000 for the predominantly self-pollinated cultivated races to about 23 000 in the allogamous wild *Hordeum bulbosum* (see Table 6).

An intensive programme was started within important genera of *Triticeae* (*Aegilops* – HAMMER 1978b; HAMMER & KNÜPFER 1979; HAMMER 1980, *Hordeum* – HAMMER 1974, 1975, 1976b, 1984a, b) and also anemophilous species of *Plantago* (HAMMER 1978a) to investigate the correlations between the different characters determining the efficiency of foreign pollination.

The length of anther was always highly correlated to the number of pollen grains per anther.

Tabelle 2. Anther lengths in barley and some related cereals

| Species | Anther length | Authors |
|-------------------------------------|---------------|-----------------------------|
| <i>Hordeum vulgare</i> | 3 (2–4.5) | ÅBERG and WIEBE (1946) |
| <i>Hordeum vulgare</i> | 2.20–2.79 | ROATH and HOCKETT (1971) |
| <i>Hordeum vulgare</i> diploid | 3–4 | LANGE (1969) |
| tetraploid | 4–5 | |
| <i>Hordeum bulbosum</i> diploid | 6–7 | LANGE (1969) |
| tetraploid | 7–8 | |
| <i>Triticum aestivum</i> open field | 2.83–3.86 | CAHN (1925) |
| greenhouse | 1.84–3.41 | |
| <i>Triticum aestivum</i> | 3.19–4.41 | KHERDE <i>et al.</i> (1967) |
| <i>Triticum aestivum</i> | 3.45 | ATHWAL and KIMBER (1970) |
| <i>Secale cereale</i> | 8.25 | ATHWAL and KIMBER (1970) |
| <i>Secale silvestre</i> | 3.5 | KHUSH (1962) |
| <i>Secale vavilovii</i> | 4.8 | KHUSH (1963) |

Table 3. Pollen size in barley and some other cereals

| Species | Pollen diameter (μm) | Authors |
|---------------------------------|-----------------------------------|-----------------------|
| <i>Hordeum distichon</i> | 43.4 | GRIFEE (1927) |
| <i>Hordeum vulgare</i> | 43.5–45 | ERDTMANN (1944) |
| <i>Hordeum vulgare</i> | 35.2–53.7 | BEUG (1961) |
| <i>Hordeum distichon</i> | 37.8–58.4 | BEUG (1961) |
| <i>Hordeum vulgare</i> diploid | 43.7–48.5 | LANGE (1969) |
| tetraploid | 55.1–64.8 | |
| <i>Hordeum bulbosum</i> diploid | 48.5–50.5 | LANGE (1969) |
| tetraploid | 51.9–59.5 | |
| <i>Triticum aestivum</i> | (42.6–61.0) 51.6 | HYDE and ADAMS (1958) |
| <i>Triticum aestivum</i> | 39.8–69.0 | BEUG (1961) |
| <i>Avena sativa</i> | 56–59 | WODEHOUSE (1935) |
| <i>Secale cereale</i> | 31.9–65.0 | BEUG (1961) |
| <i>Zea mays</i> | 90–100 | WODEHOUSE (1935) |

As there are only few results concerning the P/O ratio of *Triticeae* available (Table 7) showing the large differences between cross pollinators (60,000–80,000) and self-pollinators (only data on *Triticum* available

about 5,000–ca. 7,300) according to the recent compilation of ERBAR and LANGLOTZ (2005), P/O ratios were calculated for important *Triticeae*, including both *Triticinae* and *Hordeinae* (Table 8).

Table 4. Data on falling time and sinking speed of *Gramineae* pollen

| Species | Falling time (s/m) | Sinking speed (cm/sec) ¹ | Authors |
|---------------------------|----------------------------|-------------------------------------|----------------|
| <i>Zea mays</i> | (3.33–4.54) ¹ | 22.0–30.0 | POHL (1937 b) |
| <i>Secale cereale</i> | (11.36–16.66) ¹ | 6.0–8.8 | POHL (1937 b) |
| <i>Triticum aestivum</i> | (1.66–1.82) ¹ | 55–60 | LELLEY (1966) |
| <i>Triticum aestivum</i> | 5.27 | 18.97 | D'SOUZA (1970) |
| <i>Secale cereale</i> | 7.28 | 12.79 | D'SOUZA (1970) |
| <i>Dactylis glomerata</i> | (32.25) ¹ | 3.1 | KNOLL (1932) |

¹calculated according to basic data

Table 5. Number of pollen grains per anther in cultivated *Triticeae*

| Species | Pollen grains per anther | Authors |
|-------------------------------------|--------------------------|-----------------------------|
| <i>Hordeum vulgare</i> | (3,300) ¹ | PRICE (1966) |
| <i>Hordeum vulgare</i> diploid | 2,630–3,460 | ESLICK <i>et al.</i> (1967) |
| tetraploid | 1,710–3,370 | |
| <i>Triticum aestivum</i> open field | 855–1380 | CAHN (1925) |
| greenhouse | 416–1,360 | |
| <i>Triticum aestivum</i> | 2,697–3,867 | JOPPA <i>et al.</i> (1968) |
| | 2,236–3,022 | D'SOUZA (1970) |
| | 19103 | POHL (1937a) |
| <i>Secale cereale</i> | 36,000–50,000 | DIMITRIEVA (1968) |
| | 21,434 | D'SOUZA (1970) |

¹calculated from data of PRICE (1966)

Table 6. Pollen to Ovule ratios (P/O ratios) in different barley varieties (after HAMMER 1974, 1976a) and *Hordeum bulbosum* (GRA 24)

| Accession number | P/O ratios |
|------------------|------------|
| HOR 2872 | 11,379 |
| HOR 3989 | 10,528 |
| HOR 3021 | 12,434 |
| HOR 2611 | 9,020 |
| C 1170 | 8,030 |
| H-HOR 973 | 7,125 |
| GRA 24 | 23,187 |

In the *Triticinae* the P/O ratios reach from 2,000 to about 50,000. A large variation is present in the genera *Aegilops*, *Secale* and *Agropyron*.

In the *Hordeinae* the P/O ratios are generally somewhat lower reaching from 2,000 to about 28,000. There is also a large variation within some genera.

Table 7. Pollen to ovule ratios for different *Triticeae* as reported by ERBAR and LANGLOTZ (2005)

| Species/race | Pollen to ovule ratios |
|--------------------------|------------------------|
| <i>Leymus chinensis</i> | 79,333 |
| <i>Secale cereale</i> | 57,310 |
| <i>Triticum aestivum</i> | |
| Gaby | 5,240 |
| July | 7,297 |
| Opal | 6,248 |
| Orca | 7,210 |

The usefulness of P/O ratios

P/O ratios have been proved as conservative indicators of breeding systems in the sense of CRUDEN (1977). When we compare the data found by CRUDEN (1977) with our own results (Table 8),

Table 8. Anther length and pollen/ovule ratios in the tribus *Triticeae*

| | Anther length (mm) (after CVELEV 1976) | Anther length (mm) (own data) | Pollen/ovule ratios (calculated) |
|-----------------------------|---|----------------------------------|-------------------------------------|
| Subtribus <i>Triticinae</i> | | | |
| <i>Elymus</i> | 0.7–4.7 | | 2,807–18,850 |
| <i>Elytrigia</i> | 2(3)–5(7) | | 8,020(12,030)–20,050 (28,070) |
| <i>Agropyron</i> | 2.5–6 | | 10,020–24,060 |
| <i>Eremopyrum</i> | 0.5–1.3 | | 2,000–5,260 |
| <i>Heterantherium</i> | 0.8–1.2 | | 3,240–4,860 |
| <i>Amblyopyrum</i> | 6.3–8 | | 25,500–32,080 |
| <i>Aegilops</i> | (1.5–4.5) | 1.6–7.5 ¹ | 6,400–30,080 |
| <i>Triticum</i> | 2–4.5 | | 8,020–18,200 |
| <i>Dasypyrum</i> | 5–7 | | 20,050–28,070 |
| <i>Secale</i> | 2.3–12 | | 9,200–48,100 |
| Subtribus <i>Hordeinae</i> | | | |
| <i>Hystrix</i> | 2–7 | | 8,020–28,070 |
| <i>Leymus</i> | 2.5–5(7) | | 10,020–20,050 (28,070) |
| <i>Psathyrostachys</i> | 2.5–6 | | 10,020–24,060 |
| <i>Hordeum</i> | 0.2–5 | 0.8–7.0 ² | 3,240–28,070 |
| <i>Hordelymus</i> | 3–4 | | 12,030–16,040 |
| <i>Taeniatherum</i> | 0.7–1.4 | | 2,800–5,600 |
| <i>Henrardia</i> | 0.5–2.2 | | 2,000–,8820 |

¹HAMMER (1980); ²HAMMER and MATZK (1993)

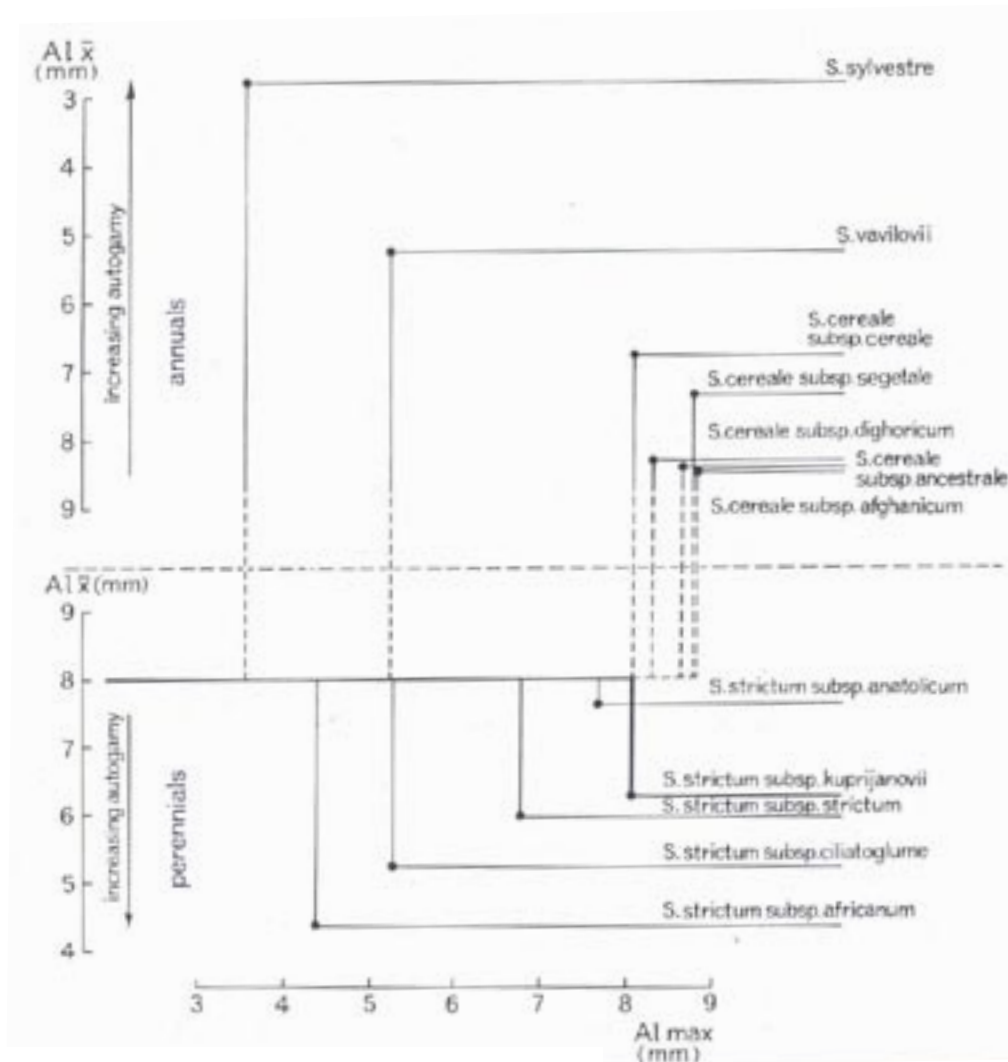


Figure 1. Relationships in *Secale* constructed on the basis of anther characters (after HAMMER 1990) (Al = anther length)

most taxa clearly show xenogamy ($5,859.5 \pm 936.5$). Only a few races are facultatively xenogamous (796.6 ± 936.5). Therefore, we can conclude that the evolution of the *Triticaceae* went clearly in the direction of anemophily. The shift from outbreeding to inbreeding systems lead to the reduction of the P/O ratio, but the original situation is still expressed.

On the basis of these findings the P/O ratio in related plant groups can also serve as a powerful indicator for conclusions concerning evolution.

Specific investigations in amphidiploid plants, several of them in the *Triticinae*, showed that anther length and consequently P/O ratio and other characters of pollination ecology, is intermediate in reticulate evolution (see D'SOUZA 1970 for *Triticum*, *Secale* and *Triticosecale*).

Consequently evolutionary schemes can be constructed. This has been done for *Secale* (HAMMER *et al.* 1987; HAMMER 1990 see Figure 1). The results of these studies have been largely considered in recent taxonomic treatment. Similar results are available for *Aegilops* (HAMMER 1980, 1987, Figures 2 and 3) which have been also considered in recent taxonomic treatment (VAN SLAGEREN 1994). The data from *Aegilops* are of great interest for the evolution of *Triticum* (HAMMER 1980). In *Hordeum* evolutionary tendencies could be followed, too, by using characters of pollination ecology including also infraspecific ones (HAMMER 1984a, b).

CONCLUSIONS

P/O ratios have attracted much attention since the early studies of POHL (1937a) and particularly

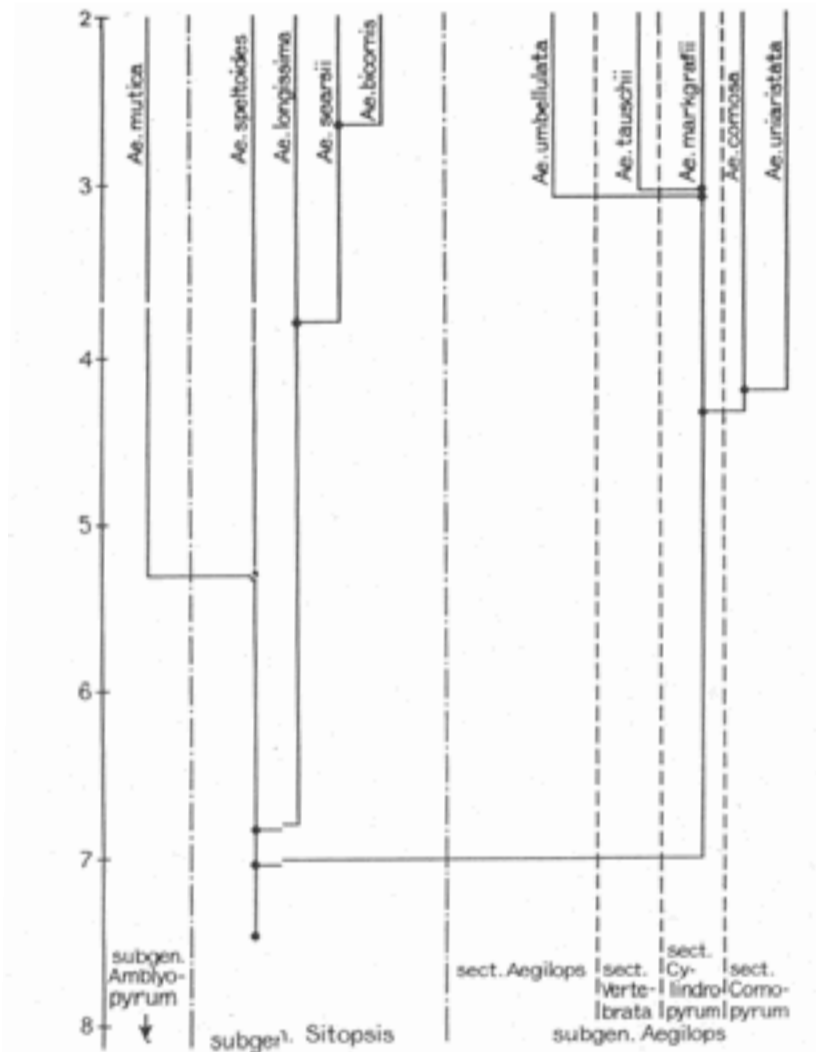


Fig. 2. Relationships in diploid *Aegilops* species constructed on the basis of anther characters (after HAMMER 1980) (Scale = anther length (mm))

since CRUDEN (1977). Generally the principle is confirmed but there are also important deviations (ERBAR & LANGLOTZ 2005).

In the *Triticeae* evolutionary patterns can be followed up to the infraspecific races. But in this tribus, as in many other taxonomic groups, the breeding systems are extremely variable so that only some indications can be obtained from the P/O ratios.

In the following a short characterization of the breeding systems (general characterization according to BROWN 1990) in the *Triticeae* is presented (see HAMMER & MATZK 1993).

Predominantly outcrossing

This condition, often in connection with perennial life form, is not so common in the *Triticeae*

– possible reasons are anemophily (BARRETT & ECKERT 1990) and the general tendency to colonizing behaviour (ZOHARY 1965; ARROYO & SQUEO 1990). P/O ratio = 20 000

Mixed outcrossing and selfing

This mixed system provides high flexibility for most of the *Triticeae*. P/O ratio = 2,000–< 20,000

Intragametophytic or haploid selfing

In nature, this system can be observed only in homosporous ferns (BROWN 1990). Such processes are used artificially in breeding. In the *hap*-mutant of barley (HAGBERG & HAGBERG 1980) and in alloplasmic wheat lines (TSUNEWAKI *et al.* 1968) haploid embryos arise without fertilization.

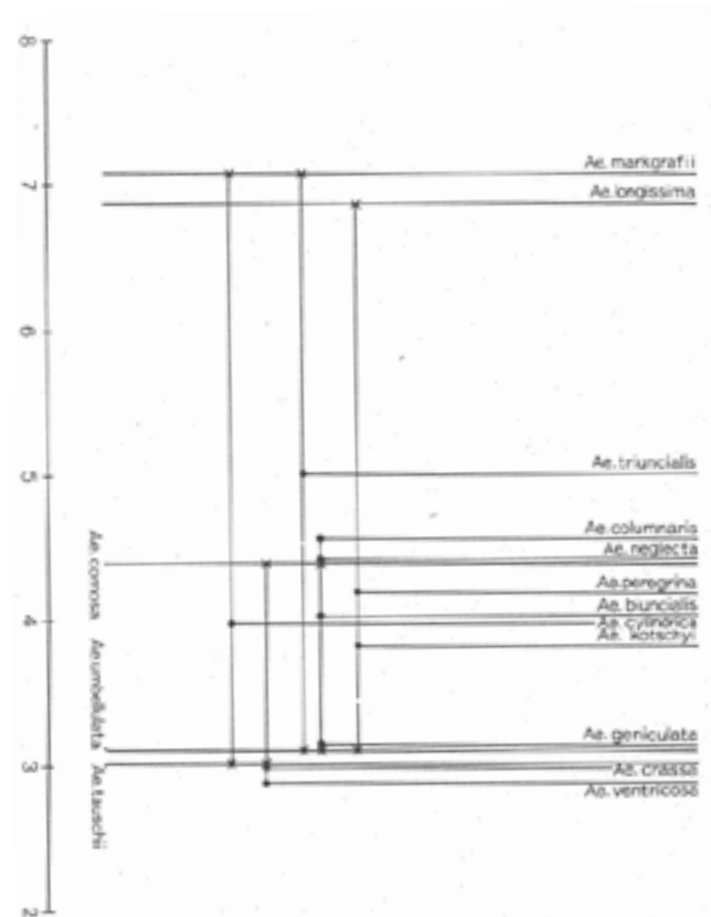


Fig. 3. Relationships in diploid and tetraploid *Aegilops* species constructed on the basis of anther characters (after HAMMER 1980)

(Scale = anther length (mm))

Facultative or obligate apomixis

Apomixis is only known from *Elymus rectisetus* (*Agropyron scabrum*), a species from Eastern Australia and New Zealand (CRANE & CARMAN 1987). Hybrids between *Triticum aestivum* and *Elymus rectisetus* have been produced (CARMAN & WANG 1991) with the aim to transfer apomixis into wheat.

Vegetative reproduction

Vegetative reproduction is always connected with seed propagation and mostly with perennial life form in the *Triticeae*. Vegetative reproduction is common in the *Triticinae* and occurs occasionally in the *Hordeinae*.

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