Taxonomy and Phylogeny in Triticeae: A Historical Review and Current Status

Abstract

The Triticeae is an economically important tribe within the Poaceae. Because a number of cereal crops and forage grasses belong to the tribe it has attracted much scientific attention covering many species: taxonomy, phylogeny, genetics, cytogenetic, genome analyses (crossing ability and chromosome pairing), isoenzymes, molecular biology (RFLP, RAPD, PCR sequencing) and breeding. This paper contains a brief historical outline of the taxonomy of the tribe. Phylogenetic hypotheses regarding this tribe inferred from different methods, techniques and approaches, are reviewed. The different phylogenies are discussed and compared and conflicts are elucidated.

Keywords: Triticeae; Phylogeny; Taxonomy; Poaceae; Perennial species; Durum wheat; Phylogenies; Genetic diversity; Cytogenetics; molecular biology; Chromosomes; Perennial; Caespitose; Thizomatous species

Introduction

The tribe Triticeae Dum is economically the most important tribe in the grass family (Poaceae). It encompasses between 350 and 500 annual or perennial species [1-3] including the important cereal crops wheat (Triticum aestivium L.), durum wheat (T. turgidum sup. durum (Desf. MacKay) barley (Hordeum vulgare L.), rye (Secale cereal L.) and triticale (Triticosecale Wittm). In addition, this diverse group of grasses also includes some often overlooked, but agronomically important perennial forage grasses, mainly species of Agropyron Gaertn., Thinopyron A. Löve, Elymus L., Psedoragneria (Nevski) A. Löve, Pascopyron A. Löve, Leymus Hochst. and Psathyrostachs Nevski [4]. Naturally, this tribe has received much attention because of the economical importance of some members, but it is also an excellent model group for research in genetics, genetic diversity, cytogenetics, molecular biology, taxonomy, phylogeny and speciation.

The Triticeae have been placed together with Brachypodioideae (Hack.) Hayek and Bromoeae Dum, in the monophyletic subgroup Triticeae Macfarlane and Watson of the Pooideae A. Brown [5,6] characterized by having endosperm with simple and rounded starch grains (type 1 of Tateoka [7]). In addition the lodicules are nearly always hairy and the hilum is linear and as long as the grain. By using the rest of the Pooideae as an out group, the three tribe’s can each is characterized by the following autopomorphies: distinct apical appendages on the ovary (the Bromeeae), small chromosomes and racemose inflorescences (the Brachypodioideae) and spicate inflorescences (the Triticeae). This grouping based on morphology is party in accordance with classification based on molecular techniques [8,9], Clayton & Renvoize [10] included Brachypodium P. Beauv. in the Triticeae as an aberrant member. Some studies, morphological [11] and molecular [12] have Brachypodium as sister group to a clade including the Triticeae and Bromus L. However, new molecular studies [9] and new morphological studies [13] indicate that Brachypodium is not closely related to the Triticeae at all, but that Bromus is the sister group to the monophyletic Triticeae. Chloroplast DNA restriction site studies by Soreng et al. [14] did not contradict the monophyletic nature of Triticeae. It was also revealed that Bromus is more closely related to the Triticeae than to Brachypodium, thus contradicting Clayton & Renvoize [10] as cited above. We can therefore conclude that the most appropriate outgroup for the tribe will be Bromus.

Definition

The Triticeae encompasses annual and perennial, caespitose or thizomatous species. The culms are slender to robust and most often erect. The leaves have linear leaf blades, are usually articulate at the orifice and have open or rarely more or less closed sheaths; the ligules are membranaceous and usually truncate. The inflorescences are usually spicate with, at maturity, a tough or fragile rachis and are erect or nodding. The spikelets are alternate in two opposite rows, single or in groups 9-23 (rarely more). The spikelets are sessile or sub sessile, all alike (very rarely lacking), with the broad side to the rachis and with 1-12 perfect florets; incomplete or sterile spikelets may occur together with female fertile ones. The rachises are prolonged and usually articulate beneath each flower. The glumes are persistent (or rarely lacking), awned, muticous or awnless, conicaceous to membranaceous and conspicuously 1-9 veined. The lemmas are herbaceous to coriaceous, with 3-100 veins and, when present, with terminal straight or recurved awns.

The paleas are well developed and 2-keeled. The two lodicules are hairy and membranaceous. The ovaries are hairy, without any appendages and the Caryopses are hairy at the apex, free or adherent to the lemma and palea and have a longitudinal groove and linear hilum. The embryos are rather small and the endosperm has simple starch grains. The chromosomes are large, the basic number is 7 and diploids (2n=2x=14) to dodecaploids (2n=12x=94) occur. The polyploids are predominantly of allopolyploid origin, but autoploidy occurs. Photosynthesis is C3. The type genus is Triticum L.
Classification Concepts

The classificatory methods and concepts have changed with time. Artificial classifications prevailing in the pre-Darwinian period grouped organisms on the basis of a few, easily identifiable character such as we see today in modern wildflower books. This system has very little to do with phylogeny. Evolution is composed of dadogenesis, the process which splits one existing species into two and anagenesis, where a species differentiates through character changes. Today most scientists agree that classification should reflect the evolutionary history. However, classificatory methodology does not take both processes into account and this has always divided the taxonomists, especially the ones dealing with difficult groups such as the Triticeae. Since the turning point of neodarwinism in the 1940s, controversies between three schools have existed, viz. the eclectic, the strict phonetic and the phylogenetic (cladistics), respectively. A phonetic classification, which here also includes artificial classification, reflects observable similarities and differences and the higher taxa emerge as Operational Taxonomic Units with greatest possible overall similarity. A phylogenetic classification should reflect the evolutionary history and accepts only monophyletic groups and the clades are identified by synapomorphies. It assumes that evolution is divergent.

However, more than 46% of the species in the Triticeae are polyploids [15] and most of them are of hybrid origin (hybridization followed by polyploidy). This implies difficulties for a direct cladistics analysis of the tribe and complicates the phylogenetic reconstruction. The conflict between strict monophyletic classification and the Linnaean hierarchical model leaves the question open whether mono- and paraphyletic groups should be accepted. It has been documented [16-18] that a cladistics analysis is only appropriate for mono genomic groups, i.e. taxa which have only one genome. Only mono genomic groups are accepted as terminal taxa, but the hetero genomic groups, i.e. taxa that have a combination of two or more genomes, can be superimposed and added to the phylogeny shown as reticulations [19]. The implication of genome analyses in evolutionary hypotheses has been criticized as these have been demonstrated to be inconsistent with phylogenetic reconstruction [20,21]. The eclectic (evolutionary, traditional) classification defines and classifies on the basis of phenotype, but also includes that are not defined phylogenetic aspects.

Taxonomic Classification of the Tribe – A Historical Review

Within the Triticeae classification, especially at the generic level, is complicated by the large variability, the frequent lack of synapomorphies and the numerous supposed alloploids and thus be reticulate evolution. Different concepts, strict phonetic to genomic classification, have been applied and have lately caused considerable debate and conflicting treatments. The extreme points are Krause [22] Stebbins [23] and Stebbins and Stebbins and Snyder [24] on the one hand who proposed that all species should be united in a single genus and Löve [2,25] who on the other advocated genomically defined genera and thus split the tribe up into 37 genera. Recently most treatments recognize a number of genera between 1 and 37, but still genera are predominantly defined genomically, i.e. mono genomic taxa having one genome and hetero genomic taxa having combinations of two or more genomes [19,25].

The history of the tribe Triticeae started with Linnaeus [26] who included 5 genera that still remain the tribe plus Lolium L. and Nardus L.; one species (Agropyron cristatum (L.) Gaertner was placed in Bromus. The artificial classifications by Beauvois [27]) were also solely based on a few inflorescence characters. Bentham [28] recognized the tribe as Hordeae Spen. Defined by simple spikes and included 12 genera. Six of these have later been excluded from the tribe. Bentham’s classification was similar to that of Hackel Hochst [29]. Both were based on a broad generic concept and both used a wide range of morphological characters. During the Phenetic period from 1933 and up to now, 24 new generic names have been proposed. However, many of these names have proved to be superfluous and have been reduced to synonyms.

Nevski [30,31] was the first who adopted a phylogenetetic approach and his taxonomy differed from Bentham’s more traditional phonetic concept. Nevski’s generic circumscriptions were rather narrow and he recognized 25 genera of which 5 were new. The tribe (called Hordeae Benth.) was subdivided into seven sub tribes (including the Brachypodioideae Holmb). Nevski came up with some evolutionary theories for the tribe in which a change from grouped to solitary spikelets and tough to brittle rachis, respectively, entered parallelly several times in the different evolutionary groups. Three major evolutionary groups were observed among the sub tribes. The first included the subtribes Elyminae Nevski and Agropyrine Nevski, with Leymus and Aneurolepidium Nevski derived from a common ancestor and the former genus was regarded as an evolutionary line leading to Elytrigia Desv. and Agropyron. The evolution of this group should have taken place in the eastern Mediterranean region. The second group included the sub tribes Clylinelyminae Nevski and Roegneria Nevski, with Terellia Lunn, as the most primitive one leading to Elymus, Hystrix and Roegneria C. Koch. He suggested that this group evolved in the Pacific Floristic center with connections to Asia and South America. The third group, the sub tribes Hordeinae Nevski and Aegilopinae Nevski had Hordeum as the primitive member and included Heterantherium, Hordeum (Jessen) Hartz and Psathyrostachys. The evolution of this diverse group should have occurred in central and western parts of the Mediterranean. Nevski [30,31] based his taxonomy not only on morphology, but also on anatomical, geographical and cytological data. In the beginning of the thirties the latter was in its initial phase of development. Presently, few taxonomists accept his phylogenetic theories, mainly because he was not aware of the role of polyploidy in the evolution of the tribe. Some general of his system have been rejected, but Nevski’s influence on later classifications [32,33] cannot be underestimated.

Bentham’s [28] morphological approach had an influence on [34] treatment of North American Triticeae and also partly on Melderis [35] in his work with European species. Compared to Bentham, Hitchcock [34] only included two additional genera, viz. Aegilops and Stenian Raf. in the tribe. Melderis [32] recognized 21 general, mainly based on morphology, but he included anatomical and cytological information and thus, some of Nevski’s [30,31]
The biosystem work of Stebbins [24] resulted in a classification where all species were lumped into one large genus. The large variability and very often the lack of crossing barriers make this a defendable suggestion, but because of the importance of some of the genera, not practical. His school argued that Bentham’s artificial classification just as well could be used, because the weak crossing barriers between many species will make it impossible to construct a generally recognized phylogenetic classification of the Triticeae. Runemark & Heneen [36] advocated a broad concept and combined data from morphology, mainly based on spikelet characters (number of spikelets per node, number of florets), anatomy and cytology, basically the same criteria as the ones later used by Sakamoto [37]. The recognition of genera was nearly identical between authors. Runemark & Heneen [36] classified the tribe into 6 morphologically distinct groups viz. the Hordeum, Henrardia, Elymus, Triticum, Secale and Heteranthelium groups, but within and among the groups no phylogenetic hypothesis was proposed.

Baum [38] proposed a classification based on various phenetic techniques. This classification suffers from several flaws. Some of Baum’s taxa were allowed to overlap and some species were allowed to belong to more than one genus “depending on the purpose of the user”. The phenetic, numerical approach was retained by Macfarlane & Watson [5] in the classification of the subfamily Pooidae, which they divide into five and three tribes, respectively. This study was based on 90 morphological characters. The numerical analysis of the Poaceae by Watson et al. [39] included 298 mainly morphological, anatomical, physiological and cytological characters. The eclectic study by Clayton & Renvoize [10] was based on a very broad concept. It mainly included morphological and anatomical features. These were also used by Watson & Dallwitz [6], who expanded the number of characters to cover all aspects of variation. They regarded cladistics computer techniques as inappropriate to be used at the super species level and advocated prior recognition of phenetic groups before cladistics inferences. Macfarlane and Watson [5, Watson et al. [39] and Watson & Dallwitz [6] all used overall similarity as an indication of phylogenetic relationship; however, by this procedure both mono- and paraphyletic groups may appear.

During the last few decades the classification of the Triticeae has been based primarily on genome analyses. This method was founded Kihara [40]. After accumulation of cytogenetic information Löve [25] and Dewey [1] proposed a classification of the whole tribe and the North American perennial species, respectively, solely based on genomic relationship. The basic concept is that species with the same genome, or the same combination of genomes, are united in a single genus. This naturally creates monophyletic and/or non-monophyletic groups.

Genome analysis is founded on the assumption that like (homologous) chromosomes pair completely; similar, but not identical (homologous) chromosomes pair to a certain degree and unlike (non-homologous) chromosomes do not pair at all during meiosis. The chromosome-pairing level (chiasma frequency) in an inter specific or intergeneric hybrid meiotic metaphase I (MI) indicates the degree of relationship between the species. The genomic system of classification immediately gained worldwide attention and considerable research in this discipline has been carried out in the Triticeae resulting in a number of phylogenetic hypotheses [41-43]. However, apart from the practical difficulties, criticism of the implication of genome analysis for elucidating evolutionary relationship (phylogenetic reconstruction) has appeared recently mainly from advocates of the cladistic school. The theoretical, methodological and biological criticism can be summarized as follows:

a. A phylogenetic analysis is only appropriate for mono genomic groups;
b. Pairing is a plesiomorphic character state;
c. The definition of homology I morphology and molecular biology is clear, but in genome analyses homology becomes purely operational;
d. Chromosome pairing is distance data, not discrete character data (except when full or no pairing occur) and thus not transformable to character data;
e. A division to arbitrary categories based on the degree of pairing (chiasma frequency level) is subjective;
f. The questions of auto-/allysynede and pairing suppressing/promoting genes are often not considered or are used at random, respectively;
g. The biological basis of using an average chiasma value for inferring relationships is dubious;
h. Genomic genera may be a mixture of monophyletic and non-monophyletic groups;
i. The nature of the genomes is ambiguous; and
j. The genomic genera are not practical units.

The arguments against the use of genome analyses for phylogenetic reconstruction seem reasonable. So the observed correspondence between the genomically defined genera and traditional classifications may be coincidental. The only data from genome analyses, which can be used for phylogenetic inference, are those when no pairing occurs between species (non-homology). However, genome analysis should not be neglected, as it is important and usable for plant breeding because it indicates the difficulty of transferring genetic material between species.

The first phylogenetic (cladistics) investigation of the Triticeae was made by Baum [44]. However, this analysis suffers from several inconsistencies. The main criticisms are that some characters are overlapping and their polarities are determined by Ad hoc criteria, the algorithms will not find the most parsimonious trees and that Psathyrostachys is used as an outgroup. The same criticisms, plus the large number of unknown character states, can be raised when Baum [44] evaluates Löve’s [2,25] genomic system of classification cladistically. However, in both of Baum’s studies [44] it was documented that parallelism prevails in the tribe.

A phylogenetic analysis of the mono genomic genera based on morphology was made by Kellogg [19]. The mono genomic genera were used as terminal taxa, but the hetero genomic general of Löve [25] was then added afterwards to the final tree as reticulations. However, when the data were reexamined.
with newer algorithms a completely unresolved consensus tree appeared [19]. Morphological data are often unstable and due to homoplasy (parallelism and convergence), inadequate for phylogenetic reconstruction in the Triticeae [19]. Frederiksen & Seberg [16] followed the same principles as Kellogg [19] but included additional characters and further taxa. Their consensus tree is well resolved although weakly supported. Frederiksen & Seberg [16] also reexamined their data and a nearly completely resolved tree appears.

Lately, modern techniques have been applied to the phylogenetic classification of the Triticeae, but often with deviating results and often with a limited number of taxa. Cladistic analyses have been made by McIntyre [45] based on the electrophoretic variation of isozymes and by Monte et al. [46] and Mason-Gamer & Kellogg [47] based on plastid restriction fragment length polymorphism (RFLP) variation. Sequence data of nuclear, ribosomal and/or chloroplast DNA based on PCR (polymerase chain reaction) are also accumulating. It has resulted in hypotheses of phylogenetic relationships [45] and phylogenetic relationships [17,18,47]. Petersen & Seberg [48] and Mason-Gamer, Kellogg et al. [47] reanalyzed the data sets of Kellogg & Apples [17], Hsiao et al. [18] and Mason-Gamer & Kellogg [47] and combined the data sets. Limited congruence was found but also the bootstrap support in many of the trees was rather low. RAPD (random amplified polymorphic DNA) techniques have been applied in phylogenetic studies of the Triticeae [49,50]. However, the reproducibility and reliability of this technique have been questioned.

Unfortunately, a cladistic analysis of the whole tribe does not exist. A phylogenetic hypothesis based on morphology exists for the mono genomic genera and from an eclectic point of view the latest taxonomic treatment of the tribe by Watson & Dallwitz [6] seems at present appropriate. Several phylogenetic hypotheses based on molecular studies exist, but the gene trees are often in conflict with the morphology - based hypotheses and/or with each other [19]. The incongruence among gene trees is often attributed to poor support, intra specific polymorphism and methodological causes. Some of the conflicts may be solved through the total evidence approach [51]. However, the hybridogenous origin of many Triticeae species implies that taxonomic congruence may provide useful information. The evolutionary trees derived from different sequence studies all show more or less congruence with many recurring cladates. When congruence between several hypotheses are found they deserve credence and it is likely that they represent the phylogeny quite accurately. The discrepancies of phylogenetic studies based on morphology might be faults in the outgroup comparison scoring non-homologous characters. Having the discrepancies with the hetero genomic genera and the cladistics hypothesis in mind, main efforts should be continued on the phylogeny of the mono genomic genera as suggested by Kellogg et al. [19]. Hopefully, the results of morphological and molecular studies an in the future be incorporated in a comprehensive cladistics analysis.

Conclusion

The perspective of future Triticeae research can be found under the following headlines and future success will depend on the establishment of networks and collaboration between research groups:

a. Systematics, phytogeography and ecology;

b. Phylogeny and evolution;

c. Cytogenetics and wide hybridization;

d. Genetic diversity and genetic resources; and

e. Breeding.

References

1. Dewey DR (1984) The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. Gene manipulation in plant improvement pp. 209-279.

2. Love A (1982) Generic evolution of the wheat grasses. New Zealand J Bot 20: 169-186.

3. West JG, McIntyre GL, Apples R (1988) Evolution and systematic relationships in the Triticeae (Poaceae). PI Syst Evol 160(1): 1-28.

4. Miller DA (1984) Forage Crops. McGraw-Hill Book Company, New York.

5. MacFarlane TD, Watson L (1982) The classification of Poaceae subfamily Pooidaeae. Taxon 31(2): 178-203.

6. Watson L, Dallwitz MJ (1992) The grasses genera of the world. CAB.

7. Tateoka T (1962) Starch grains of endosperm in grass systemsatics. Bot Mag (Tokyo) 75: 377-383.

8. Hiiu KW, Johnson JM (1991) Chloroplast DNA reassociation and grass phylogeny. PI Syst Evol 176(1): 21-31.

9. Kellogg EA, Apples R, Mason-Gamer RJ (1996) When genes tell different stories: The diploid genera of Triticeae Graminaeae. Syst Bot 21(3): 321-347.

10. Clayton WD, Renvoise SA (1986) General Grammium. Grasses of the world. The University of Chicago Press Books, USA.

11. Petersen G, Sebert O (1992) Phylogenetic analysis of the Triticeae (Poaceae). Hereditas 116: 15-19.

12. Vershinin A, Svitasev S, Guzmesson PO, Salomon B, Bothmer R et al. (1994) Characterization of a family of tandemly repeated DNA sequences in Triticeae. Theor Appl Genet 89(2-3): 217-225.

13. Kellogg EA, Watson L (1993) Phylogenetic studies of a large data set I. Bambusoideae, Andropogonoideae and Pooidaeae (Gramineae). Bot Rev 59: 273-343.

14. Soreng RJ, Davis JL, Doyle JJ (1990) A phylogenetic analysis of chloroplast DNA restriction site variation in Poaceae subfamily Pooidaeae. PISyst Evol 172(1/4): 83-97.

15. Dvorak J, Zhang, HB (1992) Application of molecular tools for study of the phylogeny of diploid and polyploid taxa in Triticeae. Hereditas 116(1-2): 37-42.

16. Frederiksen S, Bothmer R (1986) Relationships in Taenioatherum (Poaceae). Canadian journal of botany 64(10): 2343-2347.

17. Kellogg EA, Apples R (1995) Intra specific and inter specific variation in SS RNA genes are decoupled in diploid wheat relatives. Genetics 140(1): 325-343.

18. Hsiao C, Chatterton NJ, Asay KH, Jensen KB (1995) Phylogenetic relationships of the mono genomic species of the wheat tribe Triticeae (Poaceae), inferred from nuclear rDNA (internal transcribed spacer) sequences. Genome 38(2): 211-223.

19. Kellogg EA (1989) Comments on genomic genera in the Triticeae (Poaceae). Amer J Bot 76(6): 796-805.
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20. Petersen G, Seberg O (1996) Chromosomes, genomes and the concept homology. In: RRC Wang, et al. (Eds.), Proc. Second International Triticeae Symposium. Logan, Utah, USA, p. 13-18.

21. Petersen G, Seberg O (1998) Phylogeny of the genus Hordeum (Poaceae). In: A Karp, et al. (Eds.), Molecular tools for screening biodiversity: plants and animals. Chapman and Hall.

22. Krause EHL (1903) Eitage zum naturliche System de Graser. VerhandL. Naturhist. Verein. Preussische Rheinland 59: 135-172.

23. Stebbins GL (1956) Taxonomy and the evolution of genera, with special reference to the family Gramineae. Evolution 10(3): 235-245.

24. Stebbins GL, Synder LA (1956) Artificial and natural hybrids in the Gramineae, tribe Hordeae. IX Hybrids between western and eastern North American species. American Journal of Botany 43(4): 305-312.

25. Löve A (1984) Conspectus of the Triticeae. Feddes Repertorium 95: 425-521.

26. Linnaeus C (1753) Species Plantarum. Facsimile edition.

27. Beauvois PDe (1812) Essaie d'une nouvelle agrostoprapjie. Fain, Paris.

28. Bentham G (1882) Notes on Gramineae. Bot J Linn Soc 18: 14-134.

29. Hackel E (1887) Gramineae. In: Engler A, et al. (Eds.), Die Naturlichen Pflanzenfamilien 2, Engelmann, Leipzig, Germany, pp. 1-197.

30. Nevski SA (1933) Agrostological studies. IV. On the tribe Hordeae. Akad Nauk SSSR Botan Inst Trudy 1: 262-270.

31. Nevski SA (1934) Hordeae. In: Komarov VL, et al. (Eds.), Flora URSS 2. Leningrad, Germany, pp. 590-728.

32. Melderis A (1953) Generic problems within the tribe Hordeae. Proc VII Intern, Bot Congr, Stockholm 1950: 853-854.

33. Tzvelev NN (1976) Poaceae URSS. Nauka, Leningrad, Germany.

34. Hitchcock AS (1951) Manual of the Grasses of the United States. Washington, USA.

35. Melderis A (1980) The Triticeae. In: Tutin TG, et al. (Eds.), Flora Europaea 5, Cambridge University Press, pp. 192-200.

36. Runemark H, Heneen WK (1968) Elymus and Agropyron, a problem of generic delimitation. Bot Nottiser 112: 51-79.

37. Sakamoto S (1973) Patterns of phylogenetic differentiation in the tribe Triticeae. Seiken Ziho 24: 11-31.

38. Baum BR (1978) Taxonomy of the tribe Triticeae (Poaceae) using various numerical techniques. III. Synopsis key to general and synopsis. Can J Bot 56: 374-385.

39. Watson L, Clifford HT, Dallwitz MJ (1985) The classification of Poaceae: subfamilies and sub tribes. Aust J Bot 33: 433-484.

40. Kihara H (1930) Genome analyses bei Triticum and Aegilops. Cytologia 1: 262-270.

41. Bothmer R (1979) Revision of the Asiatic taxa of Hordeum sect. Stenotachya. Bot Tidsskr 74: 117-147.

42. Bothmer R, Flink J, Jacobsen N, Kotimaki M, Landstrom T (1983) Interspecific hybridization with cultivated barley (Hordeum vulgare L.). Hereditas 99(2): 219-244.

43. Bothmer R, Flink J, Landstrom T (1987) Meosis in interspecific Hordeum hybrids. III. Tetraploid combinations. Evol Trends in Plants 1: 41-50.

44. Baum BR (1983) A phylogenetic analysis of the tribe Triticeae based on morphological characters of the genera. Can J Bot 61(2): 519-535.

45. McIntyre CL (1988) Variation in isozyme loci in Triticeae. Plant Syst Evol 160(1/2): 123-142.

46. Monte JV, McIntyre CL, Gustafson JP (1993) Analysis of phylogenetic relationships in the Triticeae using RFLPs. Theor Appl Genet 86(5): 649-655.

47. Mason-Gamer RJ, Kellogg EA (1996) Chloroplast DNA analysis of the mono genomic Triticeae: phylogenetic implications and genome specific markers. In: PO Jauhar (Ed.), Methods of genome analysis in plants. CRC Press, Boca Raton, USA, pp. 301-325.

48. Petersen G, Seberg O (1997) Phylogenetic analysis of the Triticeae (Poaceae) based on rpoA sequence data. Mol Phylogenet Evol 7(2): 217-230.

49. Marillia EF, Scoles GI (1996) The use of RAPD markers in Hordeum phylogeny. Genome 39(4): 646-654.

50. Svitashev S, Brygelsson T, Vershinin A, Pedersen C, Sall T, et al. (1994) Phylogenetic analysis of the genus Hordeum using repetitive DNA sequences. Theor Appl Genet 89(7-8): 801-810.

51. Eräsaar DJ, Kluge AG (1993) Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. Mol Bio Evol 10(6): 1170-1095.