

Species diversity in wheat landrace populations from two regions of Ethiopia

Firdissa Eticha¹, Getachew Belay^{2,*} and Endashaw Bekele³

¹Bako Agricultural Research Center, P.O. Box 3, Bako, Ethiopia; ²Ethiopian Agricultural Research Organization, Debre Zeit Center, P.O. Box 32, Debre Zeit, Ethiopia; ³Addis Ababa University, Department of Biology, P.O. Box 1176, Addis Ababa, Ethiopia; *Author for correspondence (e-mail: tefres@telecom.net.et; phone: +251-1-331187; fax: +251-1-338061)

Received 17 April 2003; accepted in revised form 28 April 2004

Key words: Ethiopian wheats, Landrace, *Triticum* spp., Wheat taxonomy

Abstract

Wheat (*Triticum* spp.) landrace populations in Ethiopia are mostly species mixtures. However, no quantitative data is available with regard to their species components. We studied here 32 wheat landrace populations originating from two regions (Bale and Wello). A total of 2559 individual plants, 45–110 plants representing each population, were classified into their species components. Five tetraploid ($2n = 4x = 28$) and one hexaploid ($2n = 6x = 42$) wheat species were found in mixtures of varying proportions. These included the tetraploids *Triticum durum* Desf., *Triticum turgidum* L., *Triticum aethiopicum* Jakubcz., *Triticum polonicum* L., *Triticum dicoccon* Schrank and the hexaploid *Triticum aestivum* L. Also found, however in a rare frequency, in two populations from Wollo was *T. durum* Desf. convar. *durocompactoides* Flaksb. (*Triticum pyramidale* Percival), which is a very dense spiked durum. Discriminant analysis using seven qualitative traits revealed 91.5% correct classification of the wheat species, beak awn and awn length with the most significant importance. Single species were found in eight of the populations; six were for *T. durum* and two for *T. aethiopicum*. Two to three species-combinations were the most frequent; a maximum of four species was recorded in one population. The highest diversity index (H') observed was 0.44. *T. durum* was the most predominant species. The hexaploid *T. aestivum* was found in nine of the Wollo populations and, in one population, its frequency reached up to 35.5%. On altitudinal basis, no clear trend of clinal variation was observed both from the frequency distributions and H' estimates. The results confirmed that Ethiopian wheats, despite the morphological overlaps, could be classified into their species components with high degree of certainty. For the future, therefore, genetic diversity estimations should be dissolved into their species components for more expeditious utilization and conservation of this important genetic resource.

Introduction

Ethiopia is one of the world's secondary centers of diversity for tetraploid wheats (Vavilov 1951). The great majority of tetraploid ($2n = 4x = 28$) wheat cultivars grown in this country, even today, are landraces. Studies carried out on different aspects of this wheat genetic resources have tangibly contributed, among others, in providing genetic

materials for plant breeding purposes (Demissie and Habtemariam 1991), and for a better understanding of crop evolution (e.g., Kawahara and Taketa 2000; Belay and Furuta 2001).

The presence of continuous morphological variations in Ethiopian wheats has been considered as a hindering factor for unambiguous *sensu stricto* taxonomic treatment (Porceddu et al. 1973; Bekele 1984; Tesemma et al. 1991). In some reports, it has

even been mentioned that the ambiguity is so high that the observer cannot readily distinguish the ploidy (4x vs. 6x) level (e.g., Belay et al. 1994). In fact, this has been raised as one difficulty in the cataloguing of wheat accessions at the Institute of Biodiversity Conservation and Research, formerly known as Plant Genetic Resources Center of Ethiopia (Mesele 1989). One apparent reason is that Ethiopian wheats exhibit differences from other wheats of the world (Vavilov 1951), presumably as a result of isolation and differences in agricultural practices (Bekele 1984). Consequently, different terminologies, for instance, “intermediate types”, “morphotypes”, “botanical forms” and “agro-types”, have been used to designate those spike types that do not (according to the observer) readily fit into any one of the traditionally known taxonomic species. To our hindsight opinion, however, while morphological continuities have undoubtedly been exacerbated because of gene flows between the species – there is no reproduction barrier amongst the species – it is also possible that the knowledge and experiences of the observers had also contributed. For instance, Zeven and de Wet (1982) state, “Special spring wheats from Ethiopia are collectively classified in *Triticum aethiopicum*”.

Despite the difficulties, attempts have been made to classify Ethiopian wheats (Porceddu et al. 1973; Sylvia 1995). However, these and other relatively recent studies that mainly concentrated in estimating genetic diversities did not provide quantitative data on the species diversity of the landrace populations, other than mentioning their species admixture nature in qualitative terms (Bekele 1984; Tesemma et al. 1991; Tesemma and Belay 1991). We provide here such quantitative data by studying recent wheat collections from two regions of Ethiopia, and discuss the implications on both past and future diversity estimates of wheat landrace populations from that country.

Materials and methods

Thirty-two landrace populations of tetraploid wheats, 16 each collected from Wollo and Bale regions and consisting of 45–110 heads per population, were studied. The National Durum Wheat Improvement Project of the Debre Zeit Agricultural Research Center (DZARC), Ethiopian

Agricultural Research Organization, in collaboration with the Institute of Biodiversity Conservation and Research (IBCR), collected the populations from Bale and Wollo Regions in the years 1998 and 2000, respectively. They were made kindly available to us courtesy of Mr. Bemnet Gashawbeza, DZARC. A total of 2599 individual spikes were planted head-to-row in 1 m length and 30 cm between rows, at Akaki experimental station (38°45'E, 9°02'N) of DZARC, located at an elevation of 2200 m.a.s.l, in 2000/2001 growing season.

Each entry was assigned to its taxonomic species based on visual observation of the spike morphology (one of us, GB, was previously trained by Prof. Kozo Nishikawa of Gifu University, Japan). The proportions of each species were calculated on the basis of populations, regions and altitudinal gradients. Species diversity was estimated using the Shannon–Weaver diversity index (H'), using the formula below.

$$H = - \sum_{i=1}^n P_i \log_e P_i$$

where n is the number of species in a population and P_i is the proportion of the total number of entries in the i th class. Since the different populations contained different numbers of species, H was standardized by converting it to the relative index, H' .

$$H' = \frac{H}{H_{\max}}$$

where $H_{\max} = \log_e (n)$.

Discriminant analysis was used to estimate the accuracy of the species classifications based on spike morphology. Canonical discriminant analysis was also employed in order to identify the important traits to discriminating between the wheat species; the frequencies of seven morphological traits that have more than one character state's and adopted from IPGRI's (1994) wheat descriptor list (Table 1) were used. All computations were carried out using the MINITAB (1998) software package.

Results and discussion

The boundary between wheat species is hard to define. This is first, because of high genetic variability and the occurrence of crossability and hybrid viability within the groups of different

Table 1. Phenotypic traits used for the discriminant analysis and their character states.

Character	Phenotypic class
Glume hairiness	1. Hairy 2. Non-hairy
Awn color	1. Black 2. Non-black
Awn length	1. Short 2. Intermediate 3. Long
Beak awn	1. Acuminate 2. Pointed 3. Awnead
Glume and seed colors	1. White to yellow 2. Red to brown 3. Purple to black
Spike density	1. Lax 2. Intermediate 3. Dense 4. Very dense

ploidy levels, and second, due to the fact that the genus *Triticum* is a young unit (Mac Key 1966). This problem of unambiguous taxonomic treatment is exacerbated in Ethiopian tetraploid wheat landraces due to the presence of continuous variation (Porceddu et al. 1973; Bekele 1984; Tesemma et al. 1991). Nevertheless, with accumulated experience it is possible to classify Ethiopian wheats to their respective taxonomic species to a large degree of certainty (Belay and Furuta 2001). This was also seen from the discriminant analysis that showed 91.5% correct classification of the wheat species (data not shown). However, a considerable proportion (49.3%) of the hexaploid species, *Triticum aestivum*, was classified into *Triticum durum*. This may be attributed to the similarity between the species of the characters considered for the analysis, but it does not indicate the relative proximity of the genetic distance between these species as morphological similarity does not necessarily indicate genetic similarity.

Standardized canonical discriminant function (correlation) coefficients, Eigen-values, percent of total and cumulative variances of seven qualitative characters are given in Table 2. The first three canonical variables accounted for 99.4% of the total morphological variation, with 63.3% of the proportion of the variance explained by CAN-1 alone. This axis, which maximized the

Table 2. Standardized canonical discriminant function (correlation) coefficients, Eigen-value, and percent of total variance and cumulative variance of seven qualitative characters.

Characters	CAN1	CAN2	CAN3
Glume hairiness	0.080	-0.132	0.297
Awn color	0.208	-0.053	0.514*
Awn length	0.590*	0.519	-0.415
Beak awn	0.665**	-0.033	0.417
Glume color	0.366	-0.234	0.261
Seed color	0.347	-0.713*	-0.362
Spike density	0.041	0.470	-0.074
Eigenvalue	1.295	0.661	0.078
Percent total variance	63.30	32.30	3.80
Percent cumulative variance	63.30	95.60	99.40

* Largest absolute correlation between each variable and any discriminant function.

differentiation among the species, was closely related to beak awn (shape) and awn length, showing correlation coefficients of 0.665 and 0.590, respectively. The second function was responsible for 32.3% whereas the third was for 3.8% of the variation. Generally, the contribution of each character for classifying the wheat species in its own group varied. Beak awn and awn length had significant importance than the other traits in classifying the wheat spikes into the different species.

For the entire landrace collections studied herein, six wheat species from two ploidy levels, tetraploid and hexaploid, were found in mixtures of varying proportions (Table 3). These included *T. durum* Desf., *Triticum turgidum* L., *T. aethiopicum* Jakubz., *Triticum polonicum* L., *Triticum dicoccon* Schrank and *T. aestivum* L. Also found, however in a rare frequency, in two populations from Wollo was *Triticum durum* Desf. convar. *durocompactoides* Flaksb. (*Triticum pyramidale* Percival), which is a very dense spiked durum. The first attempt to classify Ethiopian wheats dates back more than a century (Körnicker 1885; cf. Porceddu and Perrino 1973). Since 1885, several explorers and scientists from different countries, mainly Russia, Italy, and Japan have launched collection missions followed by taxonomic work (Porceddu and Perrino 1973, and references therein). Although there were some differences between collections, almost all of them

Table 3. Frequency of the different wheat species in 32 landrace populations originating from Wollo and Bale regions of Ethiopia.

Population	TDU	TTR	TPO	TAE	TDI	TAS	TPY	SWDI
<i>Wollo</i>								
1	97.2	0.0	0.0	0.0	0.0	0.9	1.9	0.07
2	79.6	20.4	0.0	0.0	0.0	0.0	0.0	0.26
3	58.2	6.4	0.0	0.0	0.0	35.5	0.0	0.44
4	83.0	14.2	0.0	0.9	0.0	1.9	0.0	0.28
5	79.1	20.0	0.0	0.0	0.0	0.9	0.0	0.28
6	81.7	0.0	0.0	0.9	0.0	17.4	0.0	0.26
7	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
8	96.4	0.0	2.7	0.0	0.0	0.9	0.0	0.09
9	99.1	0.0	0.0	0.0	0.0	0.9	0.0	0.03
10	96.4	1.8	0.0	0.0	0.0	1.8	0.0	0.09
11	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
12	68.2	31.8	0.0	0.0	0.0	0.0	0.0	0.32
13	99.1	0.0	0.0	0.0	0.0	0.9	0.0	0.03
14	70.9	29.1	0.0	0.0	0.0	0.0	0.0	0.31
15	53.2	46.8	0.0	0.0	0.0	0.0	0.0	0.36
16	64.5	35.5	0.0	0.0	0.0	0.0	0.0	0.33
Mean	82.9	12.9	0.2	0.1	0.0	3.8	0.1	0.21
<i>Bale</i>								
17	1.6	0.0	0.0	96.7	1.6	0.0	0.0	0.08
18	74.6	0.0	1.7	23.7	0.0	0.0	0.0	0.33
19	88.4	0.0	0.0	11.6	0.0	0.0	0.0	0.18
20	20.8	0.0	0.0	75.0	4.2	0.0	0.0	0.35
21	20.0	0.0	0.0	80.0	0.0	0.0	0.0	0.26
22	83.3	1.7	0.0	15.0	0.0	0.0	0.0	0.26
23	91.7	0.0	0.0	8.3	0.0	0.0	0.0	0.11
24	20.0	1.7	0.0	78.3	0.0	0.0	0.0	0.30
25	21.7	0.0	0.0	78.3	0.0	0.0	0.0	0.27
26	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
27	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.00
28	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.00
29	62.2	0.0	0.0	37.8	0.0	0.0	0.0	0.34
30	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
31	66.7	0.0	0.0	33.3	0.0	0.0	0.0	0.33
32	76.7	0.0	0.0	23.3	0.0	0.0	0.0	0.28
Mean	51.7	0.2	0.1	47.6	0.4	0.0	0.0	0.38
Total	67.3	6.5	0.1	23.9	0.2	1.9	0.1	0.44

TDU, *T. durum*; TTR, *T. turgidum*; TPO, *T. polonicum*; TAE, *T. aethiopicum*; TDI, *T. dicoccon*; TAS, *T. aestivum*; TPY, *Triticum durum* Desf. convar. *durocompactoides* Flaksb. (*T. pyramidale* Percival).

identified the species found in the present study, except *T. aethiopicum*. Sylvia (1995) listed the wheats of Ethiopia as *T. polonicum*, *T. dicoccon*, *T. aethiopicum*, *T. turgidum*, *T. durum*, and *T. aestivum*. The presence of *Triticum carthlicum* Nevski, a tetraploid wheat species carrying the Q-factor (free-threshing property) and known to be found only in the Transcaucasus region (Feldman et al. 1995), was also reported by Porceddu and Perrino (1973). We believe that what Porceddu and Perrino (1973) classified as *T. carthlicum* were most likely *T. aethiopicum* types.

The later very much resemble *T. carthlicum*, except for their non-keeled glumes (therefore without the Q-factor), and in most cases, they have purple-seed color (Kozo Nishikawa, pers. comm.). The other spike types that raised great confusion in placing their ploidy-level, specially when accompanied by lax spikelet arrangements and short awns, were the ones which we classified here as *T. turgidum*. Based on the suggestion of Prof. James Mac Key (pers. comm.), Sweden, who had no prior knowledge of their existence, and after confirming their chromosome number ($2n = 4x = 28$), they were previously

designated as “hexaploid-like” and “carthlicum-like” (Belay et al. 1994). Such wheat forms were not included in the spike illustrations of Percival (1921) and Dorofeev et al. (1979), though it is possible that the later authors might have given written descriptions. The spike morphology of the *T. turgidum* we classified here is rather similar to the varietal forms of “*T. turgidum abyssinicum*”, as classified by Vavilov (1951, p. 340–341), and those spike types Watkins and Ellerton (1940) used to study the inheritance of awn length. Belay et al. (1997) reported that these wheats differentially show better resistance to stripe (yellow) rust (*Puccinia striiformis* West.) than the typical dense spiked Mediterranean-like durum types. Gross morphological features suggest that their origin could be through spontaneous tetraploid × hexaploid crosses, but requires further experimental evidence.

The frequencies of each species in the different populations from the two regions are given in Table 3. Single species (frequency >99%) were found in eight of the populations, out of which six were for *T. durum* (four from Wollo and two from Bale) and the rest two for *T. aethiopicum* from Bale. In addition, *T. durum* and *T. aethiopicum* were predominant (>50%) in 25 and 7 of the remaining populations, respectively. The most frequent number of species-combinations in the populations was 2–3. The maximum number of species recorded in the landrace populations was four, which was observed in one population from Wollo, and these species were *T. durum*, *T. turgidum*, *T. aethiopicum* and *T. aestivum*. The hexaploid *T. aestivum* was found in nine of the populations and, in one population, its frequency reached up to 35.5% while no population of Bale region contained hexaploid species.

The SWDI (H') values observed were generally low (Table 3). The highest value, $H' = 0.44$, was observed for one population from Wollo. This is mainly because, in most of the populations, single species predominated. It, however, should not obscure the evolutionary significance of species-mixtures, as opposed to within-species diversity. Recently, Belay and Furuta (2001) presented an isozyme evidence for gene flow between *T. dicoccon* (Szabó and Hammer 1996) and the free-threshing tetraploid wheat species. When considering the maximum 35.5% share of *T. aestivum*, therefore,

it is highly likely that introgression between the different ploidy levels would contribute to increased morphological variation, and to the reported chromosome structural rearrangements and C-band polymorphisms in Ethiopian tetraploid wheat landraces (Belay and Merker 1997, 1999).

Considering the proportional abundance in the entire collection, *T. durum* took the highest share (67.3%) followed by *T. aethiopicum* (23.9%) and *T. turgidum* (6.5%) (Table 3). The predominance of *T. durum* in most of the landrace populations may be attributed to its tolerance to stress environments (Tesemma et al. 1991). Artificial selection pressures are also responsible for the frequent appearance of one species over the other. Local farmers in Ethiopia deliberately, and unconsciously too, grow several varietal forms together to add variety to their diet, to reduce the risk of economic loss due to biotic or abiotic stresses (Bekele 1984). Human preferences for specialized traditional consumption might have played the major role for the persistence of *T. aethiopicum*, which is best preferred for “Areke” (locally prepared spirituous liquor) preparation (Belay et al. 1995). The frequency of the hexaploid species, *T. aestivum*, was small (1.9%). Interestingly, however, it was more abundant than the tetraploid species *T. polonicum* (0.1%), and *T. dicoccon* (0.2%). *T. polonicum* is distinct but has rarely, if any, been cultivated in pure fields. This is because, according to farmers, the peduncle falls after maturity and before harvest. On the other hand, *T. dicoccon* is rarely found in mixtures, but is grown to some extent as pure stand. Therefore the present results should not be misinterpreted, as *T. dicoccon* is a rare species in Ethiopia. Regardless of whether it is grown in pure stands or mixtures, it is highly likely that the abundance of *T. dicoccon* has been declining, due to the expansion of the free-threshing types, since Vavilov’s expedition to Ethiopia in the 1920s (Vavilov 1997). On regional basis, the frequency trend was similar except that *T. turgidum* was the second most abundant species in Wollo but rare in Bale, and *vice versa* for *T. aethiopicum*.

The frequency distribution of the wheat species on altitudinal basis is given in Table 4. *T. durum* was the most predominant species in all altitudinal classes; its lowest frequency (54.5%) was found between 2501 and 2700 m.a.s.l. Generally, no

Table 4. The frequency of the different species in tetraploid wheats across altitudinal gradients.

Altitude (m.a.s.l.)	TDU	TTR	TPO	TAE	TDI	TAS	TPY	SWDI
<2100	72.4	0.0	0.0	27.6	0.0	6.3	0.0	0.30
2101–2300	87.5	0.8	0.0	11.7	0.0	6.3	0.0	0.21
2301–2500	54.5	2.8	0.1	42.4	0.2	5.1	0.0	0.07
2501–2700	71.9	21.5	0.0	6.3	0.1	0.3	0.2	0.40
>2701	88.3	3.2	0.1	5.4	0.0	2.7	0.1	0.13

TDU, *T. durum*; TTR, *T. turgidum*; TPO, *T. polonicum*; TAE, *T. aestivum*; TDI, *T. dicoccon*; TAS, *T. aestivum*; TPY, *Triticum durum* Desf. convar. *durocompactoides* Flaksb. (*T. pyramidale* Percival).

clear trend of clinal variation was observed both from the frequency distributions and SWDI estimates. Worth mentioning may be, however, *T. turgidum* was accumulated in altitudes between 2501 and 2700 m.a.s.l, and *T. aestivum* and *T. aestivum* were abundant below 2500 m.a.s.l.

In conclusion, the results of the present study have confirmed that Ethiopian wheats, despite the morphological overlaps, can be classified into their species components with high degree of certainty (Belay and Furuta 2001). The implication is of wider significance. Lumping the different species together generated most previous diversity estimates and agronomic evaluations on Ethiopian wheat landraces. For the future, therefore, genetic diversity estimations should be dissolved in to their species components for unbiased estimate and more expeditious utilization and conservation of this important genetic resource.

Acknowledgements

We thank Yemane Tsehaye, IBCR, for his help in data analysis, and the technical staff of the National Durum Wheat Research Project at Debre Zeit for their help in data collection. The Agricultural Research and Training Project, through the Ethiopian Agricultural Research Organization, financed the study.

References

Bekele E. 1984. Analysis of regional patterns of phenotypic diversity in the Ethiopian tetraploid and hexaploid wheats. *Hereditas* 100: 131–154.
 Belay G. and Furuta Y. 2001. Zymogram patterns of α -amylase isozymes in Ethiopian tetraploid wheat landraces: insight into their evolutionary history and evidence for gene flow. *Genet. Resour. Crop Evol.* 48: 507–512.

Belay G. and Merker A. 1999. C-band polymorphism and chromosomal rearrangements in tetraploid wheat (*Triticum turgidum* L.) landraces from Ethiopia. *Wheat Info. Serv.* 88: 6–14.
 Belay G. and Merker A. 1997. Cytogenetic analysis of a spontaneous 5B/6B translocation in tetraploid wheat landraces from Ethiopia and implications for breeding. *Plant Breed.* 117: 537–542.
 Belay G., Tesemma T., Mitiku D., Badebo A. and Bechere E. 1997. Potential sources of stripe rust (*Puccinia striiformis*) resistance in durum wheat. *Rachis* 16: 70–74.
 Belay G., Tesemma T., Bechere E. and Mitiku D. 1995. Natural and human selection for purple-grain tetraploid wheats in the Ethiopian highlands. *Genet. Resour. Crop Evol.* 42: 387–391.
 Belay G., Merker A. and Tesemma T. 1994. Cytogenetic studies in Ethiopian landraces of tetraploid wheat (*Triticum turgidum* L.). I. Spike morphology vs. ploidy level and karyomorphology. *Hereditas* 121: 45–62.
 Demissie A. and Habtemariam G. 1991. Wheat genetic resources in Ethiopia. In: Gebremariam H. et al. (eds), *Wheat Research in Ethiopia: A Historical Perspective*, IAR/CIMMYT, Addis Ababa. pp. 33–46.
 Dorofeev V.F., Filatenko A.A., Migušova E.F., Udahin R.A. and Jakubziner M.M. 1979. *Flora of Cultivated Plants. I. Wheat*. Leningrad, 346 p. (Russian, English summary).
 Feldman M., Lupton F.G.H. and Miller T.E. 1995. *Wheats: Triticum spp.* (Gramineae–Triticinae). In: Smartt J. and Simmonds N.W. (eds), *Evolution of Crop Plants*, 2 edn. Longman Scientific and Technical, Singapore, pp. 184–192.
 IPGRI, 1994. *Descriptors of wheat (Triticum spp.)*. International Plant Genetic Resources Institute, Rome, Italy.
 Kawahara T. and Taketa S. 2000. Fixation of translocation 2A/4B infers the monophyletic origin of Ethiopian tetraploid wheat. *Theor. Appl. Genet.* 101: 705–710.
 Mac Key J. 1966. Species relationship in *Triticum*. *Hereditas* 2 (Suppl.): 237–276.
 Mesele T. 1989. Cytogenetic activities at PGRC/Ethiopia. PGRC/E-ILCA Germplasm Newsletter No. 20 April 1989. 24 pp.
 MINITAB, 1998. *MINITAB Users Guide*, released 12.22. MINITAB Inc.
 Percival J. 1921. *The Wheat Plant*. Duckworth, London.
 Porceddu E. and Perrino P. 1973. Wheat in Ethiopia: preliminary report of a collecting mission. *Plant Genet. Resour. Newslett.* 30: 33–36.
 Porceddu E., Perrino P. and Olita G. 1973. Preliminary information on an Ethiopian wheat germplasm collection mission.

- In: Scarascia-Mugnozza G.T. (ed.), Proceedings Symposium Genetics and Breeding of Durum Wheat, University of Bari, Italy, pp. 181–200.
- Sylvia P. 1995. Poaceae (Gramineae). In: Inga H. and Sue E. (eds), Flora of Ethiopia, Addis Ababa, Ethiopia/Uppsala, Sweden, pp. 68–63.
- Szabó A.T. and Hammer K. 1996. Notes on the taxonomy of farro: *Triticum monococcum*, *T. dicoccon* and *T. spelta*. In: Padulosi S. et al. (eds), Hulled Wheats, Proceedings of the International Symposium Castelvecchio Pascoli, Italy, pp. 2–40.
- Tesemma T. and Belay G. 1991. Aspects of tetraploid wheats with emphasis on durum wheat genetics and breeding. In: Gebremariam H., Hulluka M. and Tanner D.G. (eds), Wheat Research in Ethiopia: A Historical Perspective, IAR/CIMMYT, Addis Ababa, pp. 47–71.
- Tesemma T., Getachew B. and Worede M. 1991. Morphological diversity in wheat landrace populations from central highlands of Ethiopia. *Hereditas* 114: 172–176.
- Vavilov N.I. 1951. The origin, variation, immunity and breeding of cultivated plants. *Chronica Bot.* 13: 1–351.
- Vavilov N.I. 1997. Five Continents. IPGRI, Rome.
- Watkins A.E. and Ellerton S. 1940. Variation and genetics of the awn in *Triticum*. *J. Genet.* 40: 243–270.
- Zeven A.C. and de Wet J.M.J. 1982. Dictionary of Cultivated Plants and Their Regions of Diversity: Excluding Most Ornamentals, Forest Trees and Lower Plants. Center for Agricultural Publishing and Documentation, Wageningen.