Theor Appl Genet (1990) 80:687–692

Inheritance of some Mendelian factors in intra- and interspecific crosses between *Setaria italica* and *Setaria viridis*

I. Till-Bottraud [1,*] **and P. Brabant** [2]

[1] Laboratoire d' Evolution et de Systematique des Végétaux, Université Paris-Sud, Bat. 362, F-91405 Orsay, France
[2] CNRS-INRA-UPS, Ferme du Moulon, F-91190 Gif sur Yvette, France

Received May 1, 1990; Accepted May 15, 1990
Communicated by J. Mac Key

Summary. The inheritance of seed coat color, pericarp color, polyphenoloxidase activity and bristle, glume, collar, and leaf-base anthocyanic colorations was investigated using intra- and interspecific crosses between *Setaria italica* and *S. viridis*. The results were compared to inheritance results obtained by previous authors. In most cases, the inheritance is simple (one or two loci) and data from different crosses (intra- and interspecific) and from different authors can be compared. Two sets of two characters were found to share common loci: the polyphenoloxidase locus is one of the loci responsible for seed coat color, and bristle and glume color are determined by the same two loci. The evolutionary significance of these results is discussed.

Key words: Inheritance – Intra- and interspecific crosses – Evolution of *Setaria*

Introduction

Setaria italica (L.) P. Beauv., the foxtail millet, has been widely cultivated across the temperate zone in Asia and Europe. It is still a major crop in China and Japan but is only occasionally cultivated in Europe. Its wild relative, *Setaria viridis* (L.) P. Beauv., the green foxtail (Harlan and de Wet 1971; de Wet et al. 1979), is abundant throughout the temperate zone and is often found as a weed in the millet fields. Interspecific crosses between wild and cultivated species were reported to be only partly sterile (Li et al. 1945; Darmency and Pernès 1985). *S. viridis* is usually divided into two morphological types: *S. viridis* minor, the wild type, and *S. viridis* major, a weedy type probably originating from hybridization and backcrossing between *S. italica* and *S. viridis* minor, and therefore probably genetically closer to the cultivated species (de Wet et al. 1979; Darmency and Pernès 1985). Both species are selfing annuals.

The aim of this paper is to present the inheritance of some simple characters [seed coat color, pericarp color, polyphenoloxidase (PPO) activity and bristle, glume, collar, and leaf-base anthocyanic coloration] determined through intra- and interspecific crosses. These results will then be compared to existing data in the literature. The taxonomical consequences of these results will be discussed.

Materials and methods

Four crosses between varieties of *S. italica* and a cross between *S. viridis* minor and a variety of *S. italica* (Table 1) were performed. As the plants are highly selfed (Takashi and Hoshino 1934; Li et al. 1935 and personal observations), the varieties and the *S. viridis* plant used can be considered homozygous for most loci, and therefore one progeny from each cross was observed. The F_1 were assured with electrophoretic and morphological markers and the spikes were bagged to ensure self-fertilization. From the interspecific cross, five F_2 plants (named 213-87 to 217-87), chosen for their morphology, were self-fertilized giving the F_3 generation. For the F_2 and F_3 plants studied, seeds were sown in peat in the greenhouse and seedlings were planted in the field at the four-leaf stage. The characters were observed on the seeds collected when the panicles were fully ripe. The seed coat is composed of the lemma and the palea, which stay attached to the seen when threshed (Li et al. 1940). The pericarp color, which is determined by maternal genotype (all the seeds from one plant have the same pericarp color) (Darmency and Pernès 1987), was observed on 10–20 seeds per plant. The polyphenoloxidase (PPO) activity was tested by soaking ten seeds (from the same spike) in a 1% phenol solution for 24 h or more. When PPO is active, the solution turns pink (Takahashi and Hamza 1983). Anthocyanic pigmentations (red), if present, were noted during development on the following parts of plants: bristle, glume, collar, and leaf base.

* Tho whom reprint requests should be addressed

Table 1. Description of the parents and F_1 hybrids from the different crosses studied. For each character, the F_1 phenotype is listed below the female/male phenotype

♀ Parent F_1 hybrid	♂ Parent	Seed coat color	Pericarp color	PPO activity	Bristle color	Glume color	Collar color	Leaf-base color
26–80	22–80							
B.T.	B.T.	yellow yellow		PPO+ PPO−	–	–	–	–
121–80		black	–	PPO+				
26–80	24–80							
B.T.	B.T.	yellow black						
123–80		black	–	–	–	–	–	–
26–80	59–79							
B.T.	Ch.		grey yellow	PPO+ PPO−	green red	green green	green red	green green
125–80		–	yellow	PPO+	red	red	red	red
26–80	72–79							
B.T.	Ch.		grey yellow	PPO+ PPO−	green red	green green		
127–80		–	yellow	PPO+	red	red	–	–
107–84	66–81							
SVm F.	*SI* F.	black yellow	grey yellow	PPO+ PPO−				
612–84		black	yellow	PPO+	–	–	–	–

B.T.: origin Botel-Tabago; Ch.: origin China; F.: origin France; *SVm*: *S. viridis* minor; *SI*: *S. italica*. All other parents are *S. italica*; −: no difference between the parents and no segregation in the F_2 generation

Results

All the results are shown in Tables 2 and 3. We will present here genetic interpretations that are in accordance with these data. Several interpretations were tested and only the ones that fitted with the data (nonsignificant Chi-square test) are presented. We will discuss the significance and compare the results with the literature data in the "Discussion."

Seed coat color

The difference in seed coat color (Table 2) between the parents of the 121-80 F_2 and between *S. viridis* minor and *S. italica* (F_2 612-84) can be explained by two epistatic factors, giving a 7:9 (yellow:black) segregation in the F_2 generation. To explain the 123-80 F_2 segregation, only one factor is necessary, black being dominant over yellow. Following this interpretation, since the yellow F_2 plants are homozygous for the recessive allele at at least one locus, their selfed progeny (F_3 generation) should not segregate. An F_3 from a black F_2 plant can either not segregate (in one case out of nine) or segregate in a 1:3 ratio (in four cases out of nine) or a 7:9 ratio (in four cases out of nine). Our F_3 results are in agreement with these predictions (Table 2): the four F_3 derived from a yellow F_2 plant do not segregate, and the only F_3 from a black F_2 plant segregates in a 1:3 ratio.

Pericarp color

In both crosses, two factors can explain the differences between the parents (Table 2). For the intraspecific crosses, the simplest explanation is that one factor codes for pigmentation and a second dominant factor at an independent locus inhibits the former, giving a 13:3 (yellow:grey) segregation. The interspecific cross (F_2 612-84) fits a 3:1 segregation but, in this case, an F_3 family from an F_2 plant with a grey pericarp should not segregate (it is homozygous for the recessive allele). In the only F_3 from a grey F_2 plant (215-87), we observed a 1:3 segregation for this character. Therefore, at least two factors are involved and the simplest explanation is allelic dosage effect: to obtain a yellow pericarp, at least two dominant alleles are necessary, but they can be at the same locus or at different loci (11:5 segregation). An F_2 plant from 612-84 with a grey pericarp can thus either not segregate (one-fifth) or segregate with a 1:3 (Y:G) ratio (four-fifths), and an F_2 plant with a yellow pericarp segregates in a 11:5 ratio (4/11) or does not segregate (7/11). Accordingly, the F_3 family from a grey F_2 segregates with a 1:3 ratio and one of the four F_3 families from a yellow F_2 segregates with an 11:5 ratio (Table 2).

Polyphenoloxidase activity

Our data (Table 2) suggest the presence of one locus with two alleles, active PPO (PPO+) being dominant over inactive (PPO−). In the F_3 generation, only progenies from PPO+ plants can segregate. In our results, none of the F_3 families segregate but in another experiment, F_3 from the same cross and from PPO+ F_2 have both PPO+ and PPO− plants (data not shown).

Anthocyanic colorations

Bristle color (Table 2) segregates in a different way in the two F_2 studied. Two factors are necessary to explain the

Table 2. Proposed segregations for single characters in the F_2 and F_3 generations (all F_3 families are from the F_2 612–84). The segregations given here are the ones that best fit the results (other segregations were tested but discarded, as the Chi-square tests showed a significant difference between expected and observed segregation)

Family	Parent phenotype[a]	Observed		Proposed segregation	χ^2*
Seed coat color		yellow	black		
F_2 121–80	black	32	40	7:9	0.02
123–80	black	13	48	1:3	0.44
612–84	black	50	74	7:9	0.59
F_3 213–87	yellow	12	0	1:0	
214–87	yellow	22	0	1:0	
215–87	black	2	22	1:3	3.55
216–87	yellow	23	0	1:0	
217–87	yellow	15	0	1:0	
Pericarp color		yellow	grey		
F_2 125–80	yellow	137	29	13:3	0.19
127–80	yellow	39	6	13:3	0.84
612–84	yellow	87	37	11:5	0.12
F_3 213–87	yellow	12	0	1:0	
214–87	yellow	22	0	1:0	
215–87	grey	5	19	1:3	0.22
216–87	yellow	17	6	11:5	0.29
217–87	yellow	15	0	1:0	
Polyphenoloxidase		PPO+	PPO−		
F_2 121–80	PPO+	53	19	3:1	0.07
125–80	PPO+	34	12	3:1	0.03
127–80	PPO+	129	37	3:1	1.32
612–84	PPO+	87	37	3:1	1.55
F_3 213–87	PPO−	0	12	0:1	
214–87	PPO−	0	22	0:1	
215–87	PPO+	24	0	1:0	
216–87	PPO−	0	23	0:1	
217–87	PPO−	0	15	0:1	
Bristle color		red	green		
F_2 125–80	red	178	38	13:3	0.19
127–80	red	63	30	11:5	0.68
Glume color		red	green		
F_2 125–80	red	130	86	9:7	1.36
127–80	red	54	39	9:7	0.13
Collar color		red	green		
F_2 125–80	red	186	140	9:7	0.08
Leaf-base color		red	green		
F_2 125–80	red	140	186		
in red collar plants		140	46	3:1	0.01

[a] Phenotype of the hybrid plant for the F_2 generation and phenotype of the F_2 mother plant of the F_3 family

* Value of the Chi-square test. All the values are nonsignificant ($\chi_1^2 = 3.84$; $p = 0.05$)

segregations, however, the F_2 125-80 fits a 13:3 segregation, whereas the F_2 127-80 fits an 11:5 segregation. To explain these two segregations, we can invoke allelic dosage effect with different alleles at one locus in the two crosses, the dominant allele being less efficient in the 125-80 family.

The segregation for glume color (Table 2) can be explained for the two F_2 by two epistatic factors (9:7 segregation).

The anthocyanic colorations of the collar and the leaf base were studied on the F_2 125-80. One parent of the cross had a red collar and green leaf bases and the other had both green collar and green leaf bases (Table 1). The collar color can be explained by the presence of two epistatic (and independent) factors (Table 2). In this progeny, none of the plants with a green collar had red leaf bases, and the segregation for leaf-base color within the red collar plants fits a 3:1 ratio (red:green) (Table 2). This suggests the action of a third independent locus responsible for the accumulation of the pigments (when they are produced) at the base of the leaves.

Joint segregations

Table 3 shows that seed coat color and pericarp color, pericarp color and PPO, and anthocyanic colorations of collar and bristles segregate independently. The joint segregation of seed coat color and PPO suggests that the PPO locus is one of the loci that determines seed coat color. In this case, all the black seed coats are PPO+ (they have at least one dominant allele at each locus), which is what we found. For the anthocyanic colorations we have already noted that leaf-base and collar color are not genetically independent. Glumes and bristles are each determined by two factors with different segregation, but the joint segregations suggests that only one set of two factors is necessary to explain the segregations, one locus giving different segregations for glumes or bristles.

Discussion

All these characters seem to have a simple inheritance (one or two loci). However, for two characters out of the five for which more than one cross was studied, different inheritances had to be proposed to explain the different segregations. Some of these characters have already been studied by different authors and in this section, we will attempt to determine whether "consensus segregation", simultaneously consistent with everyone's data, can be proposed.

The first investigation of the inheritance of seed coat color in *S. italica* was done by Raganswami-Ayyangar (1934, in Li et al. 1940). He determined the presence of three epistatic factors responsible for the difference between six color types (Black, Korra Buff, Tawny Buff, Red, Sepia, and Tawny Red). The first factor (K) is present in the first three color types and absent in the last three (reddish colors). This confirms our result that there are one or two (epistatic) factors differentiating "yellow" from "black" seed coat [as we called "yellow" anything from light brown (tawny buff) to white (korra buff)]. Li et al. (1940) found the same results, also on *S. italica*,

Table 3. Joint segregations in the F_2 and F_3 generations. The independent Chi-square (1) tests for the independence of the joint segregations. When this test is significant, another segregation is proposed (2) and tested (3)

Family	Parent phenotype[a]	Observed				Indep. χ^2 (1)	Segregation (2)	χ^2 (3)
Collar color/leaf-base color		R/R	R/G	G/R	G/G			
F_2 125–80	R/R	140	46	0	140	184.3	27:9:0:28	0.09
Seed coat color/pericarp color		B/G	B/Y	Y/G	Y/Y			
F_2 612–84	B/Y	22	52	15	35	0.002		
F_3 213–87	Y/Y	0	0	0	12		0:0:0:1	
214–87	Y/Y	0	0	0	22		0:0:0:1	
215–87	B/G	17	5	2	0		9:3:3:1	
216–87	Y/Y	0	0	6	17		0:0:5:11	0.29
217–87	Y/Y	0	0	0	15		0:0:0:1	
Pericarp color/PPO		G/+	G/−	Y/+	Y/−			
F_2 612–84	Y/+	24	13	63	24	0.74		
F_3 213–87	Y/−	0	0	0	12		0:0:0:1	
214–87	Y/−	0	0	0	22		0:0:0:1	
215–87	G/+	19	0	5	0		3:0:1:0	0.22
216–87	Y/−	0	0	0	23		0:0:0:1	
217–87	Y/−	0	0	0	15		0:0:0:1	
Collar color /bristle color		R/R	R/G	G/R	G/G			
F_2 125–80	R/R	105	21	73	17	0.19		
Seed coat color/PPO		B/+	B/−	Y/+	Y/−			
F_2 121–80	B/+	40	0	13	19	32.6	9:0:3:4	0.08
612–84	B/+	73	0	14	37	75.6	9:0:3:4	4.99
F_3 213–87	Y/−	0	0	0	12		0:0:0:1	
214–87	Y/−	0	0	0	22		0:0:0:1	
215–87	B/+	22	0	2	0		3:0:1:0	3.56
216–87	Y/−	0	0	0	23		0:0:0:1	
217–87	Y/−	0	0	0	15		0:0:0:1	
Bristle color/glume color		R/R	R/G	G/R	G/G			
F_2 125–80	R/R	130	48	0	38	70.7	9:4:0:3	1.42
127–80	R/R	54	9	0	30	62.0	9:2:0:5	0.67

[a] Phenotype of the hybrid plant for the F_2 generation and phenotype of the F_2 mother plant of the F_3 family.
(1) and (3): $\chi_1^2=3.84$, $p=0.05$; $\chi_2^2=5.99$, $p=0.05$; $\chi_3^2=7.81$, $p=0.05$

Table 4. Segregations in literature data

Author	Cross[a]			Segregations	
				Author	Alternative
Seedcoat color		yellow	black		
Li et al. 1945	I × V	705	542	37:27	9:7
Pericarp color		yellow	grey		
Li et al. 1945	I × V	1,020	230	3:1 (+linkage)	13:3
Darmency & Pernès 1987	VM × I	(B) 103	189	?	
		(B) 47	43	7:9	
		(Y) 42	3	13:3	
Polyphenol oxidase		+	−		
Kawase & Sakamoto 1982	I × I	297	91	3:1	
Darmency & Pernès 1987	VM × I	206	86	3:1	
Bristle color		red	green		
Li. et al. 1945	I × V	1,201	49	3 factors 2 (linked)	
Collar color		red	green		
Li et al. 1945	I × V	700	550	9:7	
Darmency & Pernès 1987	VM × I	222	74	3:1	

[a] I = *Setaria italica*. V = *S. viridis* (V = *S. viridis*, VM = *S. viridis* major). The first parent listed is the female parent

whereas Li et al. (1945) found that three factors were needed to explain their segregation (Table 4). The segregation obtained by other authors (Table 4) is explained by the presence of either one or two factors segregating as described by Raganswami-Ayyangar (1934).

Pericarp pigmentation seems to be determined in our experiment by two loci with different alleles in the segregations. The authors who studied pericarp pigmentation (Table 4) demonstrated the presence of either one factor with a distortion (Li et al. 1945) or two epistatic factors. All the segregations cited are significantly different from the 11:5 ratio we found in the interspecific cross (612-84). The latter does not fit a 13:3 ratio ($p<0.001$). Therefore, either the segregation is distorted in one of the crosses, or different alleles or even loci are involved in the different crosses studied. Another possibility is that, as the color notation is still somewhat subjective, we did not look at the same character.

One locus seems to determine the segregation for the polyphenoloxidase activity. Likewise, data from the literature (Table 4) suggest the action of only one locus with PPO+ dominant (the F_1 is PPO+). The role of polyphenoloxidase has been much discussed in plants; it is not only used as a Mendlian marker, but is also widely said to be responsible for dormancy (Lenoir et al. 1983) by fixing oxygen and therefore limiting O_2 access to the embryo, as it is present in high quantities in the grain coat in wheat (Kruger 1976) and other grasses (Kawase and Sakamoto 1982; Lenoir et al. 1986 in barley). In *S. italica*, varieties that show PPO activity in the seed coat originate from latitudes of 32°N or more southerly (Kawase and Sakamoto 1982 and personal observations). In northern latitudes, foxtail millet is harvested in dry weather, whereas in southern latitudes, it is often harvested in warm and moist weather. Only the seeds that do not germinate on the spike (and that are therefore somewhat dormant) are harvested and take part in the next generation. PPO activity could therefore have been selected as a means of providing dormancy at harvest. However, Codignola et al. (1988) could not find any relationship between phenolic metabolism and dormancy in buds of *Fagus sylvatica*, and Lenoir et al. (1986) found "no close correlation between PPO activity and the germinability of the seeds" in in vitro assays on barley. Moreover, Vaughn and Duke (1984) report that in *Sida spinosa* there is no relationship between PPO and the dark pigments of the seed coat, but that there is one with peroxydase which, like PPO, catalyzes the formation of quinones from phenolic compounds.

The anthocyanic coloration of the bristles is determined by two loci with different segregations in the two crosses. Li et al. (1945) found that three factors (two linked and one independent) are responsible for the differences they observed (Table 4). The color of the bristles changes during maturation of the spike (a Chinese variety is even called "changes with aging") so that the differences in the proportions in different studies are very difficult to compare. Our results on collar color agree with some data in the literature (Table 4), i.e., the presence of two epistatic factors. The other authors (Table 4 and de Cherisey et al. 1985) found an even simpler inheritance (one locus). Li et al. (1945) actually observed the coloration of the whole plants and did not report any offspring with red collar and green leaf base. We found that an additional locus was needed to explain the accumulation of pigments at the base of the leaves.

Data on the joint segregations (Li et al. 1945; Darmency and Pernès 1987) confirm that seed coat and pericarp colors, on the one hand, and pericarp color and PPO, on the other hand, are not linked, whereas PPO and seed coat color are somewhat linked. We found that the PPO locus is one of the loci that determines seed coat color. Similarly, in rice, Kuriyama and Kudo (1967) showed that one of the loci responsible for seed coat color is the phenol reaction gene, while the other "seems to be a gene producing some phenol substance". This result is not surprising as it is known that there is polyphenoloxidase in the seed coat. Moreover, phenoloxidases catalyze the aerobic oxidation of phenolic substrates to quinones, which are then autoxidized to dark-brown pigments (Palmer 1963). To follow Kuriyama and Kudo's reasoning, the "PPO locus" could be the R factor described in Li et al. (1940) for seed coat color, and the B factor could encode for the phenolic substrate. It is interesting to note that Kawase and Sakamoto (1982) tested the polyphenoloxidase activity by looking at the color of the seed coat after the seeds had been soaked in the phenol solution. The plants were PPO+ if the seed coat turned black. They noted that for some varieties, PPO activity was impossible to determine because of the black seed coat.

We found no linkage between collar and bristle color, whereas Li et al. (1945) found that one of the collar color loci was linked to the two linked, bristle color loci. We found a discrepancy between our results on bristle color and theirs, which could be explained by a difference in maturity of the spikes at the time the observations were made. Another explanation could be that, for these characters, they worked on an interspecific cross, whereas we used only intraspecific crosses. The number of factors that differ between the parents could easily be greater.

We found no report on linkage between bristle and glume anthocyanic coloration, and therefore could not confirm our interpretation that the same two loci determine both colorations.

Conclusion

Most of the characters studied have a simple inheritance (one or two loci) in the crosses observed, and data from

different crosses and different authors can be compared. However, the fact that consensus segregations can be found does not necessarily mean that the loci involved are the same for all crosses. Moreover, additional crosses could very well involve different loci. Indeed, for the pericarp and bristle color, differences occur among the authors and no general inheritance can be proposed. A diallel cross involving all types of plants as female and male parents would be necessary to clarify this situation.

For seed coat color and PPO, all the segregations obtained by the different authors on the different crosses (within or between the wild and cultivated species) can be interpreted in the same manner, and we have shown that PPO is probably one of the loci responsible for seed coat color. Moreover, bristle and glume color seem to be determined by the same two loci.

The fact that some characters show the same inheritance in intra- as well as in interspecific crosses confirms that *S. italica* and *S. viridis* are genetically very close. Indeed, as they can be easily crossed, Harlan and de Wet (1971) proposed that they be classified as subspecies. These results also lead us to believe that up to now no intense and divergent selection has taken place to improve the cultivated varieties. Moreover, as interspecific hybrids are easily obtained by artificial crosses, gene flow probably still occurs under natural conditions between these two species impeding strong differentiation.

Acknowledgements. We wish to thank Prof. J. Bronstein for help with the manuscript.

References

Cherisey H de, Barreneche MT, Jusuf M, Ouin C, Pernes J (1985) Inheritance of some marker genes in *Setaria italica* (L.) P.Beauv. Theor Appl Genet 71:57–60

Codignola A, Maffei M, Fieschi M (1988) Phenols and bud dormancy. II. Qualitative variations in endogenous phenols in dormant buds of *Fagus sylvatica* L. New Phytol 110:473–477

Darmency H, Pernès J (1985) Use of wild *Setaria viridis* (L.) Beauv. to improve triazine resistance in cultivated *S. italica* by hybridization. Weed Res 25:175–179

Darmency H, Pernès J (1987) An inheritance study of domestication in foxtail millet using an interspecific cross. Plant Breed 99:30–33

Harlan JR, Wet JMJ de (1971) Towards a rational taxonomy of cultivated plants. Taxon 20:509–517

Kawase M, Sakamoto S (1982) Geographical distribution and genetic analysis of phenol color reaction in foxtail millet, *Setaria italica* (L.) P. Beauv. Theor Appl Genet 63:117–119

Kruger JE (1976) Changes in the polyphenol oxidase of wheat during kernel growth and maturation. Cereal Chem 53: 201–213

Kuriyama H, Kudo M (1967) Complementary genes *Ph* and *Bh* controlling ripening-black coloration of rice hulls and their geographical distribution. Jpn J Breed 17:13–19

Lenoir C, Corbineau F, Come D (1983) Principales caractéristiques de la dormance de l'orge de brasserie et de son élimination. Bios Nancy 14:24–29

Lenoir C, Corbineau F, Come D (1986) Barley (*Hordeum vulgare*) seed dormancy as related to glumella characteristics. Physiol Plant 68:301–307

Li HW, Meng CJ, Liu TN (1935) Problems in the breeding of millet [*Setaria italica* (L.) Beauv.] J Am Soc Agron 27: 963–970

Li HW, Meng CJ, Liu TN (1940) Genetic studies with foxtail millet, *Setaria italica* (L.) Beauv. J Am Soc Agron 32:426–438

Li HW, Li CH, Pao WK (1945) Cytological and genetical studies of the interspecific cross of the cultivated foxtail millet *Setaria italica* (L.) Beauv., and the green foxtail millet *S. viridis* L. J Am Soc Agron 37:32–54

Palmer JK (1963) Banana polyphenoloxidase. Preparation and properties. Plant Physiol 38:508–513

Takahashi N, Hamza A (1983) Differentiation of ecotypes in *Oryza sativa* L. I. Re-examination for color reaction with phenol. Jpn J Breed 33:243–250

Takahashi N, Hoshino T (1934) Natural crossing in *Setaria italica* (Beauv.). Proc Crop Sci Soc Jpn 6:3–19

Vaughn KC, Duke SO (1984) Function of polyphenol oxidase in higher plants. Physiol Plant 60:106–112

Wet JMJ de, Oestry-Stidd LL, Cubero JL (1979) Origins and evolution of foxtail millets. J Agric Trad Bot Appl 26:53–63