10 Finger Millet

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10.1 Introduction

Finger millet, *Eleusine coracana* Gaertn L., is a cereal grown for food in Africa and Southern Asia, mainly India (the states of Uttar Pradesh, Bilhar, Tamil Nadu, Karnataka, and Andhra Pradesh) and Nepal. In Africa, the crop is principally grown in the eastern regions, mainly in Uganda, Kenya, and Tanzania and, to a lesser extent, in Ethiopia, Rwanda, Malawi, Sudan, Zambia, and Zimbabwe.

10.1.1 Brief History of the Crop

Finger millet originated and was domesticated in Africa. Archeological and linguistic evidences show that around 5,000 years ago, farming communities in eastern Africa were already cultivating this millet (Klichowska 1984). The exact area of domestication is unknown, and it has been suggested that it may have occurred anywhere between western Uganda and the Ethiopian highlands of Eastern Africa (de Wet 1995). From Africa the crop was transported to India about 3,000 years ago, whereupon the subcontinent became its secondary center of diversity.

Cultivated finger millet (*Eleusine coracana* subsp. *coracana*) is likely to have been derived from selection and domestication of a large-grained mutant of the wild *E. coracana* subsp. *africana*. Evidence for the ancestry of cultivated millet has been provided by cytological (Hiremath and Salimath 1992), morphological (Hilu and de Wet 1976), and molecular data (Dida 1998; Hilu 1988).

10.1.2 Botanical Descriptions

Finger millet (*E. coracana*) and related species belong to the subfamily Chloridoideae within the Poaceae family. The crop belongs to the genus *Eleusine*, which contains eight species, both annuals and perennials. Finger millet is a tufted annual growing from about 40 to 150 cm tall and takes from 3 to 6 months to mature. The stems are erect, compressed, and glabrous. The leaf blades are linear and taper to an acute point, folded, and striated and often have ciliated margins (Rachie and Peters 1977). The inflorescence consists of a variable number of spikes ranging from 3 to 20 arranged in a bird's foot style. It resembles fingers on a hand, hence its common name "finger millet". Each spike contains about 70 spikelets arranged alternately on the rachis, and each spikelet carries 4 to 7 seeds. The seeds vary in diameter from 1 to 2 mm. The caryopsis (seed) is globose and smooth, and the color can be brown, reddish brown, black, orange red, purple, and white (J. Duke, 1983, Handbook of Energy Crops. Unpublished, Purdue University).

The morphology of the finger millet inflorescence is highly variable and may be a consequence of farmers' selection preferences (de Wet 1995). Based on the inflorescence morphology, finger millet can be grouped into five races. The race *coracana* resembles the subspecies *africana* and has well-developed central spikes numbering from 5 to 20. The spikes are straight, slender, and up to 11 cm in length. The race *vulgaris* has inflorescences with incurved or straight spikes (Fig. 1). The *compacta* race (Cockscomb finger millet) has incurved spikes with lower finger branches divided in compacta. The lower inflorescence branches usually present in Indian cultivars may not be present in some African cultivars (Fig. 1). The race *plana* has large spikelets arranged in two even rows along the rachis, giving the head a ribbonlike appearance, and the *elongata* race has long slender spikes that are incurved at maturity, with lengths of up to 24 cm.

Finger millet (*Eleusine coracana* subsp. *coracana*) and the weedy wild relative *E. coracana* subsp. *africana* are allotetraploids with $2n = 4x = 36$

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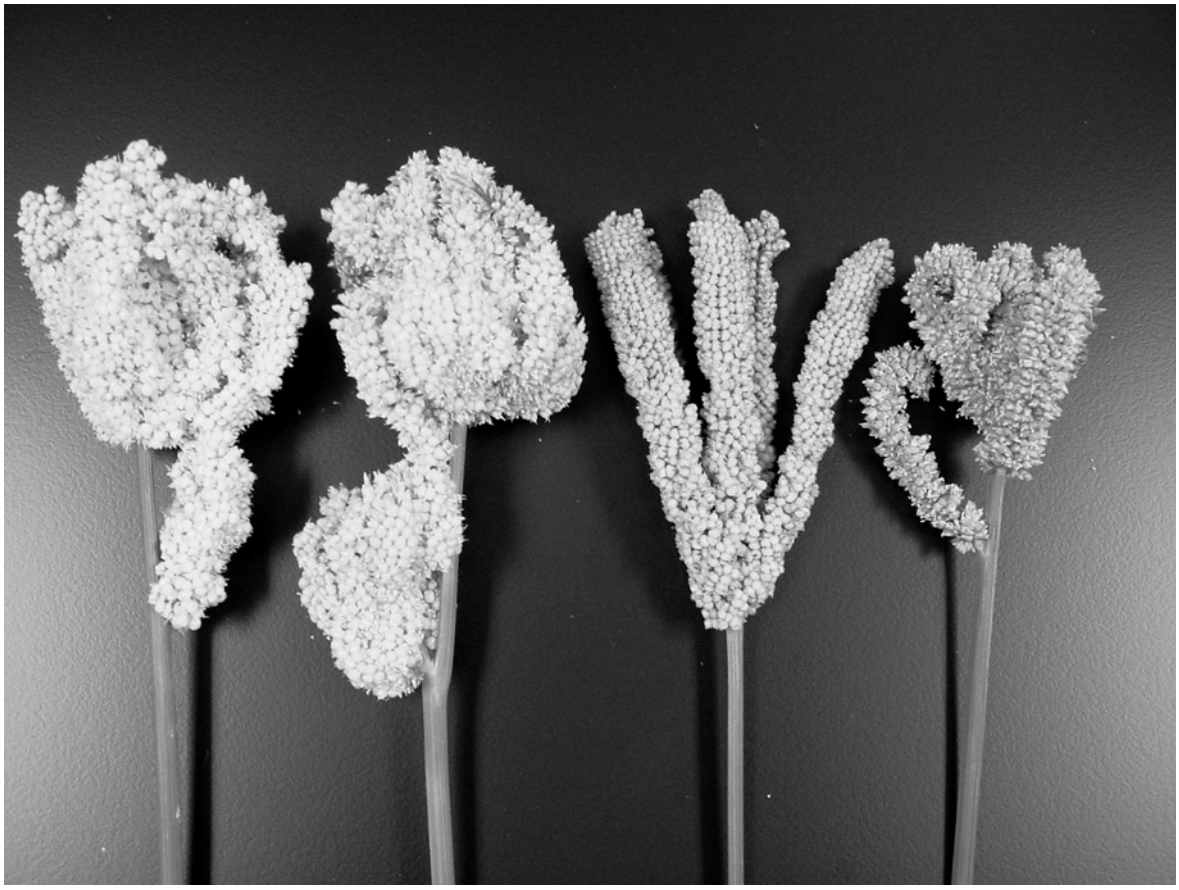


Fig. 1. Variation of finger millet head shapes. The first and second from *left* belong to the race Compacta, the third and fourth belong to races Coracana and Vulgaris, respectively

chromosomes. These two subspecies have been assigned the genomic notation AABB (Chennaveeriah and Hiremath 1974; Hiremath and Salimath 1992). It has been established that the diploid *E. indica* (wild goosegrass) is the source of the A genome in finger millet (Hilu 1988; Hiremath and Salimath 1992; Dida 1998; Bisht and Mukai 2001a). The source of the B genome, however, has not been unequivocally established. The results of recent genomic in situ hybridization studies suggest that the perennial *E. floccifolia* may be the B genome donor to both cultivated finger millet and the subspecies *africana* (Bisht and Mukai 2001a,b). Cultivated finger millet is cross-compatible with the wild subspecies *africana* and with another allotetraploid, *E. kigeziensis* ($2n = 4x = 38$) (Hiremath and Salimath 1991). These two wild allotetraploids are confined to the African continent with *E. kigeziensis* being endemic to southwestern Uganda (Kabale district) and Rwanda (Phillips 1974).

There are limited reports on the DNA content of finger millet and related species. A review by Bennett and Leitch (1995) reported that cultivated finger millet had a 2C (diploid) nuclear DNA content of 5.5 picograms (pg), whereas the wild subspecies *africana* had a value of 5.1 pg. These values were determined on root nuclei using a microdensitometry method with onion (*Allium cepa*) as standard (Hiremath and Salimath 1991). Later, another report of DNA contents of *Eleusine* species using laser flow cytometry and chicken red blood cell nuclei as standard gave comparatively lower values (Mysore and Baird 1997). Mysore and Baird reported 2C nuclear DNA value of 3.6 pg and 3.3 pg for *E. coracana* and *E. africana*, respectively. These authors further postulated that the earlier reported DNA values may have been overestimated owing to the use of onion with higher DNA content as standard and a frequent occurrence of root endopolyploidy. Based on these reports,

the finger millet 2C nuclear DNA content translates into ca. 3.6×10^9 base pairs.

10.1.3 Economic Importance

Finger millet is adapted to a wide range of environments. It is often grown from sea level up to 2,400 m on the slopes of the Himalayas in Nepal and in the Kabale district in Uganda. Finger millet can be grown as a dryland crop in areas with as little as 500 mm of annual rainfall. The crop is also adapted to a wide range of tropical soils, ranging from red lateritic to sandy loams and black heavy vertisols.

Table 1. Major nutrient composition of finger millet (per 100 g) (Sources: Rao 1994; FAO 1995; National Research Council 1996; Vandivoo et al. 1998)

Major component	Content
Proteins (g)	7 to 14
Fats (g)	1.5
Ash (g)	2.6
Crude fiber (g)	3.6
Carbohydrates (g)	73
Calcium (mg)	160 to 490
Iron (mg)	4 to 12
Phosphorus (mg)	200 to 320
Magnesium (mg)	140
Zinc (mg)	1.5 to 2.4
Copper (mg)	0.5
Manganese (mg)	1.9 to 5.5
Molybdenum (μg)	2
Potassium (mg)	314
Sodium (mg)	49
Iodine (μg)	10
Thiamine (mg)	0.24
Riboflavin (mg)	0.11
Energy (Kcal)	335

Finger millet is a staple food for millions of people in Africa, India, and Nepal. The estimated global annual production of finger millet is about 4.5 million tons of grain, of which approx. two million tons is produced in Africa while the Asian continent (mainly India and Nepal) produces the remainder (FAO 1996). African finger millet is grown mainly in eastern Africa, where the finger millet cultivation area encompasses at least one million hectares (ha), with ca. 405,000 ha in Uganda, 320,000 ha in Tanzania, and 90,000 ha in Kenya (FAO 1996). In Nepal, finger millet, locally known as kodo, is the fourth staple food crop after rice, maize, and wheat. Here the crop is grown on about 26,000 ha of land with an average productivity of 1,100 kg/ha (Joshi and Joshi 2002). In this country finger millet is popular, mainly due to its adaptation to growing on marginal lands where subsistence farmers live. Its popularity is also due to its good response to low levels of fertilizer applications and the crop's tolerance to cold temperatures.

Finger millet is an outstanding subsistence food crop. Its small seeds can be stored for many years with minimal insect damage and with little loss of viability. Finger millet grain can be used in many ways. The ground flour is made into porridge or bread that represents nutritious and wholesome foods for diabetics and the elderly (Duke 1983). The grains can also be fermented into malt, which is highly nutritious and recommended for infants and the elderly (National Research Council 1996). The malted grains are also used to brew beers. Among the tropical cereals, finger millet provides the best malt for beer making and is better than either maize or sorghum. Finger millet straw makes good fodder for animals and contains up to 61% total digestible nutrients (Duke 1983).

The nutrient content of finger millet grain is given in Table 1. It has a protein content ranging from about 7 to 14%. Brown and red seeded cultivars generally have protein levels in the lower range, whereas levels in the white seeded cultivars and the wild subspecies *africana* are at the higher end of the spectrum (10 to 14%) (Rachie and Peters 1977; Rao 1994; FAO 1995; Vadivoo et al. 1998). Finger millet protein has a very favorable amino acid composition and is particularly rich in the essential amino acids tryptophan and methionine (National Research Council 1996). Compared to other cereals, finger millet grains also have a relatively higher content of minerals such as calcium, phosphorus, iron, and manganese. The calcium content, for example, is 16 times that of maize.

10.1.4 Breeding Objectives

Finger millet hybridization and breeding are often hampered by the crop's high rate of self-fertilization, coupled with extremely small flowers that are difficult to emasculate. However, this challenge can be

overcome by employing hot water emasculation and a contact method of crossing (Rachie and Peters 1977; Dida 1998). Some finger millet lines with male sterility have been discovered (Gupta et al. 1997; National Research Council 1996), and the availability of male sterile lines in finger millet should greatly facilitate cross breeding of different lines or cultivars. Most finger millet cultivars tend to lodge under high fertility and moisture conditions. Tall lines with heights of more than 120 cm tend to lodge more compared to shorter genotypes, and the ideal plant height for grain and fodder production is around 80 cm. Therefore, selection for reduced plant height and incorporation of dwarf and semidwarf genes into adapted lines are important breeding goals. Other major breeding objectives include the development of genotypes with profuse basal tillering and reduced number of nodal tillers. Developing genotypes with more and longer digits is required since there is a positive correlation between length, number of digits, and grain yield. For drier semiarid areas, early maturing genotypes that flower within 80 to 90 d after planting are the best adapted and, hence, the farmers' choice.

Breeding for improved grain quality is also a major objective. Most pearly white seeded grains of finger millet have been found to have high protein content and to be low in tannins compared to most brown and red seeded types. The tannins may have protective functions against fungi, birds, and other predators. However, they impart an astringent taste to the grains and reduce their palatability and nutritional quality. Therefore, the development of high protein and low tannin varieties should be emphasized.

A major biotic constraint on finger millet production in moist mid-altitude and higher elevations of East Africa is infection by the blast pathogen *Pyricularia oryzae*. Blast epidemics can result in significant losses in crop yields in susceptible varieties. In eastern Africa, only a few finger millet varieties with blast resistance have been developed. Identification and development of varieties with blast resistance should be a priority in eastern Africa.

Grain yield improvement is a major breeding objective in finger millet. Most current finger millet lines, particularly those grown in eastern Africa, are landraces or landrace selections with average grain yields of one to two tons per hectare. Breeding and improvement in agronomic practices can substantially raise the grain yields, potentially to 5 tons per hectare (Duke 1983).

Other breeding efforts in eastern Africa should be directed toward the development of drought and striga weed tolerance. For marginal and semiarid regions, shade-tolerant genotypes for relay and intercropping should be useful. These should fit in well in farming systems where farmers are already practicing relay and intercropping.

10.1.5 Classical Breeding Achievements

In India, finger millet breeding has been carried out mainly in the southern states of Tamil Nadu, Karnataka, and Andhra Pradesh. Breeding progress has been remarkable. In Tamil Nadu alone, more than 15 improved cultivars have been developed and released (Rachie and Peters 1977). In Nepal, examples of high-yielding varieties developed are Okhale I and Dalle I (Joshi and Joshi 2002).

In eastern and southern Africa, major breeding efforts have been reported in Uganda, Malawi, Zimbabwe, Kenya, Tanzania, and Ethiopia. In Uganda, several improved varieties have been developed including Gulu E, Serere 1, P283, Engeny, and P224 (PESE1). In Kenya, evaluation and screening of local collections and introductions have resulted in the identification of high-yielding cultivars such as Gulu E, P224, KA2, and KATFM1 (KARI 1990). In Ethiopia, screening of introductions has identified varieties with high yield potential such as KNE 409, KNE 1098, Acc 100057, and KNE 479 (Mulatu et al. 1985). Multilocation yield trials in eastern Africa have indicated that these improved lines have a yield potential of two tons per hectare (Mukuru and Guiragossian 1990). In Zimbabwe, a variety SDEV 87001 that yields up to 3.5 tons per hectare has been developed (Gupta and Mushonga 1994). However, there is still scope to further improve finger millet yields to attain the five-metric-tons-per-hectare target.

In India and Nepal, the area under finger millet production has been expanding. In Nepal, a growth rate of 8% per year has been reported (National Research Council 1996). In Africa, on the other hand, a general decline of the area under finger millet production has taken place within the last 50 years. This has been attributed to changing farming systems and competition with maize and other cereals (Oryokot 1990). It is believed that the decline may have stabilized (National Research Council 1996). Moreover, in eastern Africa, the crop is regaining its importance

and popularity. In Uganda, finger millet occupies 50% of the land area under cereal crops. In Kenya, finger millet grain fetches a premium price that is more than twice that of maize and sorghum.

Currently, in East Africa, there are a number of finger-millet-flour-based formulations for adult and infant porridge on the market. To satisfy the demands of diverse growers and users of this crop as a specialty food, current breeding efforts should be holistic. The integration of classical, molecular, and participatory breeding approaches will lead to the development of revolutionary finger millet lines that are adapted to local environmental niches and stresses, with nutritionally superior characteristics that are culturally acceptable.

10.2 Genetic Mapping in Finger Millet

10.2.1 Brief History of Mapping Efforts

Genetic mapping in finger millet is in its infancy. Although finger millet is an important food crop in regions of Africa and India, based on the limited interest from the research community and funding agencies, finger millet most definitely can be classified as a "neglected crop". The first partial finger millet genetic maps were produced in 1998 (Dida 1998). In early 2000, mapping efforts were renewed with funding from the McKnight Foundation, and maps covering 18 linkage groups, each larger than 20 cM, in addition to several smaller linkage groups have recently been constructed (MM. Dida, Srinivasachary, K.M. Devos, unpubl. obs.).

10.2.2 First-Generation Genetic Maps

Before embarking on a genetic mapping study, it is useful to have information on the extent of variation present within the target crop. Because such information was not available for finger millet, a small survey was conducted on the level of restriction fragment length polymorphism (RFLP) present within *E. coracana* germplasm. Eight *E. coracana* subsp. *coracana* lines from Kenya, Uganda, Ethiopia, and Nepal together with five Kenyan *E. coracana* subsp. *africana* accessions were evaluated using 30 RFLP probes. Polymorphism levels within cultivated finger millet were limited to 15% despite the diverse origins of the lines. This may be a reflection of the relatively recent (some 2,000 to 3,000 years ago) introduction of finger millet into Asia. Variation between the wild accessions amounted to 28% (Dida 1998). Polymorphism levels between the two subspecies, however, were 72%. Therefore, a mapping population consisting of 151 F_2 progeny was generated from a cross between the cultivar Okhale I and the wild accession MD-20. In the first mapping phase, a total of 126 RFLP probes were placed onto the genetic map. In addition to the 182 RFLP loci, 15 amplified fragment length polymorphism (AFLP) markers, generated using the restriction enzyme combination *Pst*I/*Mse*I, were incorporated into the map (Dida 1998). The second mapping phase was conducted using finger millet expressed sequenced tags (ESTs) (Srinivasachary and K.M. Devos, unpubl. obs.). Primers were generated to the ESTs and amplification products were checked for single strand conformation polymorphisms (SSCP). This technique detects mainly single nucleotide polymorphisms (SNPs) and small insertion/deletions (indels). Polymorphism levels in the intersubspecific *coracana* × *africana* population were around 55%.

A preliminary analysis of the current mapping data set (RFLP, AFLP, and SSCP markers) has grouped the 379 loci into 18 large linkage groups (each exceeding 20 cM and containing a minimum of seven markers). In addition, several smaller linkage groups were formed, and 85 loci, including 27 AFLP markers, remained unlinked. The large number of unlinked markers is due to the fact that the maps were constructed at LOD (log of the odds ratio) 10 to avoid spurious linkages, and this precluded the inclusion of markers that link at distances of >25 cM. A more thorough analysis of the mapping data is required to incorporate at least a subset of the currently unlinked markers into the genetic maps.

Of the 18 major linkage groups, 9 belong to the B genome, 7 to the A genome and 2 are, as yet, unassigned. In wheat, linkage groups can be located to genomes and, indeed, chromosomes using sets of aneuploid lines. No such lines exist in finger millet. However, we can take advantage of the relatively low level of variation that exists between *E. indica*, the A genome donor of finger millet, and the present-day A genome of *E. coracana*. Following hybridization of RFLP probes to digested DNA of an *E. indica* accession, and of Okhale I and MD-20, the parents

of the mapping population, it is possible, at least for a number of probes, to identify common A genome fragments (Fig. 2). A fragment that is monomorphic between *E. indica*, Okhale I, and MD-20 will, most likely, belong to the A genome. A second, polymorphic fragment present only in the tetraploid *E. coracana* therefore represents a B genome locus (Fig. 2; PSE143). Alternatively, a fragment that is polymorphic between Okhale I and MD-20, but monomorphic either between Okhale I and *E. indica* or between MD-20 and *E. indica*, can be allocated to the A genome (Fig. 2; PSE84).

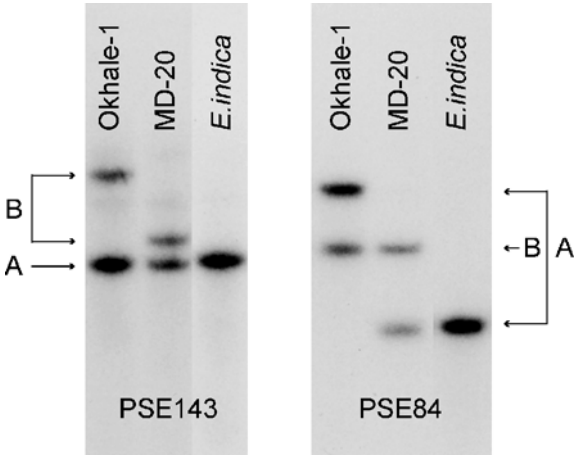


Fig. 2. Hybridization of RFLP probes PSE143 and PSE84 to digested DNA of tetraploid (AABB) *E. coracana* accessions Okhale I and MD-20, and to *E. indica*, the A genome donor

Homoeology between the A and B genome chromosomes has been established for seven pairs of linkage groups. Two examples of homoeologous linkage groups are presented in Fig. 3. In addition, one B genome linkage group shows homoeology with two A genome linkage groups. Although this may be an indication that the two genomes are rearranged with respect to one another, it is possible that the two A genome linkage groups will link when new markers are added to the genetic map.

One such further source of markers is microsatellites or simple sequence repeats (SSRs). Screening of some 18,000 *Hind*III, *Sal*I, and *Pst*I finger millet genomic clones containing insert sizes of 1 to 1.5 kb with selected di- and trinucleotide repeats has yielded 111 SSR sequences to which primers were designed (K.M. Devos, unpubl.). Some 70 primer pairs gave consistent amplification against a panel of eight finger millet varieties, including Okhale I and MD-20. Fifty SSRs that are polymorphic between Okhale I and MD-20 are being mapped.

10.2.3 Comparative Genetic Maps

The incorporation of heterologous RFLP markers that had previously been mapped in rice into the finger millet genetic maps allowed the construction of a rice–finger millet comparative framework. A further source of comparative markers was provided by mapped finger millet ESTs. Priority was given to mapping those ESTs for which a putative homolog could be identified in the rice genomic sequence produced by the International Rice Genomic Sequencing Project (IRGSP) (http://rgp.dna.affrc.go.jp/IRGSP/). Since the IRGSP sequenced the rice genome using a BAC by BAC approach of physically mapped BACs, many of which were anchored to the genetic map, the location of the putative homologs of the finger millet ESTs in the rice genome could be established.

Many of the preliminary established finger millet linkage groups correspond to a single rice chromosome, indicating that few rearrangements have taken place at the map level in the finger millet genome since its divergence from a common ancestor with rice (Fig. 3). Nevertheless, considering that rice has $2n = 2x = 24$ chromosomes and finger millet has $2n = 4x = 36$ chromosomes, one would expect at least some finger millet linkage groups to have orthology to two or more rice chromosomes. Two such linkage groups were identified among the current data set. One finger millet linkage group contained loci orthologous to both rice chromosome 5 and rice chromosome 12 (Fig. 3). A second linkage group showed orthology to both rice chromosomes 2 and 10.

A comparison with other grass genetic maps suggests that the observed rearrangements occurred either in the Chloridoideae lineage or in finger millet itself. The only other comparative map constructed in a species belonging to the Chloridoideae subfamily is *Eragrostis tef* (Zhang et al. 2001). However, due to the incompleteness of the tef maps, it is not possible to infer whether any of the putative rearrangements detected in finger millet are common to tef. No tef linkage groups with orthology to rice chromosomes 5, 10, and 12 were identified by Zhang and colleagues (Zhang et al. 2001).

The availability of rice–finger millet comparative maps should enhance the efficiency with which agronomic traits can be mapped and tagged in finger millet. This is particularly true for traits such as maturity and plant height for which QTLs are often conserved across species (e.g., Lin et al. 1995; Peng et al. 1999). However, blast resistance may be another trait that can benefit greatly from the available data in rice. Blast is caused by the fungus *Pyricularia oryzae*, which has a wide host range including rice and finger millet (Kato et al. 2000). In rice, some 30 genes for blast resistance have been identified, several of which have been isolated (e.g., Wang et al. 1999; Bryan et al. 2000; Jiang and Wang 2002; Zheng et al. 2004). It will be interesting to investigate whether homologous genes underlie QTL for blast resistance that map to orthologous positions in finger millet and rice. Particularly encouraging in this respect is a recent report by Chen and colleagues who identified four QTLs contributing resistance to *P. grisea* in orthologous positions in rice and barley. The orthologous QTLs had complete or partial conserved isolate specificity Chen et al. 2003).

10.3 Future Scope of Work

Finger millet genetic studies lag considerably behind those of major cereal crops. Nevertheless, a first step, the construction of genetic maps and establishment of their relationship to other cereal genomes, in particular the rice genome, has been accomplished. These maps will form the foundation for targeted improvement of finger millet. Being a recent polyploid, finger millet has a very narrow genetic base. It is envisioned that in the future, the genetic base of this crop can be widened using the wild relative gene pool. This strategy has been used successfully in other cereals, where wild species have been donors of novel genes, in particular to confer resistance to biotic stresses but also to enhance quality traits (Friebe et al. 1996; Tanksley and McCouch 1997). A systematic analysis of the biodiversity existing within cultivated and wild finger millet germplasm has not yet been conducted. However, a small-scale biodiversity study is under way, and some *E. coracana* subsp. *africana* accessions have been identified with relatively good levels of resistance to the blast fungus *P. oryzae* (M.M. Dida, N. Wanyera, K.M. Devos, unpubl.). Furthermore, in an analysis of protein and calcium content of the finger millet grain, it was found that some of the highest values were present in the wild *E. africana* (Barbeau and Hilu 1993). Screening large collections of wild and cultivated germplasm therefore will most likely lead to the identification of lines containing high levels of protein, lysine, and minerals, in particular, calcium and iron. These efforts should also concomitantly aim at reducing the levels of grain tannins that are antinutritional factors. *E. africana* alleles could thus contribute to the improvement of finger millet for resistance to blast disease and the nutritional quality of the grain. Through hybridization, backcrossing, and selection, useful traits could be transferred from subspecies *africana* and, potentially, *E. kigeziensis* to the cultivated finger millet. However, gene introgression is carried out most efficiently in conjunction with marker-assisted selection. This requires knowledge of the location of quantitative trait loci (QTLs) conferring the phenotype and the availability of linked markers.

Remarkable yield improvements have occurred in other cereals such as wheat over the last 50 years. This was achieved in large part through the introduction of semidwarf genes. A similar approach could be applied to finger millet. Application of a combination of conventional and molecular breeding techniques will allow for a rapid development of high-yielding crop ideotypes adapted to specific environments and ecological niches and has the potential to more than double the current finger millet yields.

Finger millet improvement will require collaborative efforts between breeders, biotechnologists, and, importantly, funding agencies. Unfortunately, finger millet has been stigmatized as a food for the poor, and this negative label has contributed to the decline of finger millet production in recent decades. However, the elimination of finger millet has had serious health implications. In households where rice has replaced finger millet as the staple diet, anemia caused by nutritional unbalance has become widespread. It is clear that finger millet has a very important contribution to make to satisfy current and future nutritional needs in human food. The most important prerequisites to improve finger millet are a change in attitude, in particular by governments and funding agencies, toward finger millet as a famine food and a growth in interest of researchers and breeders to work on this underresourced crop.

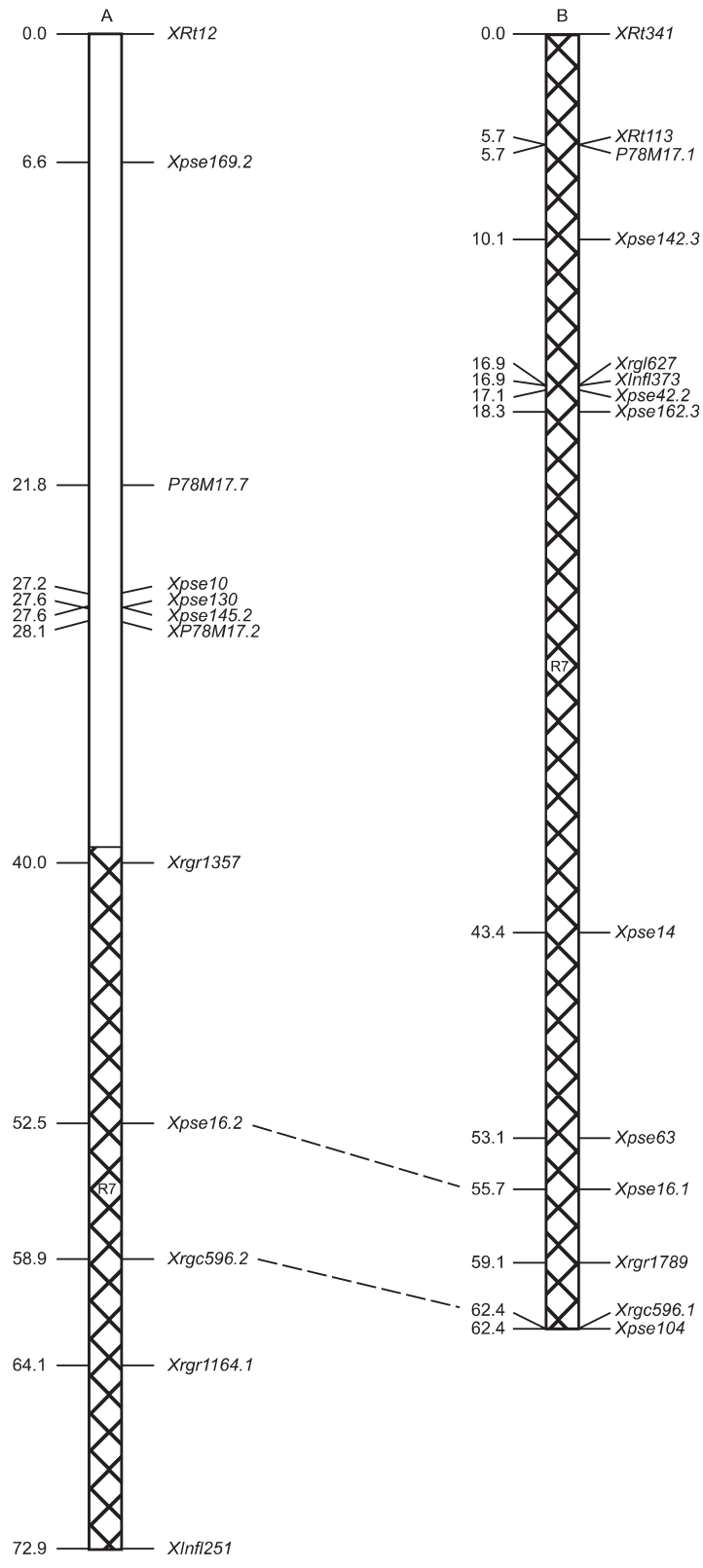
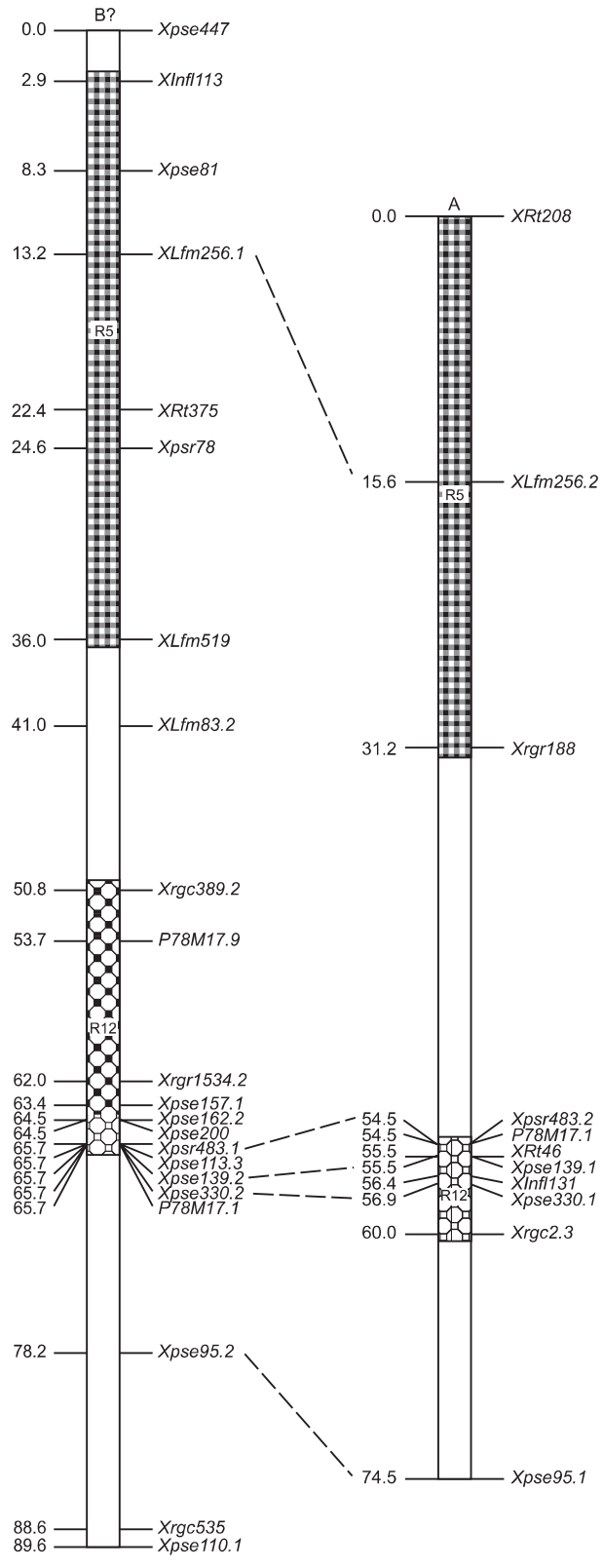


Fig. 3. Two sets of homoeologous finger millet linkage groups. Markers are on *right-hand side*, genetic distances on *left-hand side*. A and B indicate whether the linkage groups belong to the A or B genome, respectively. *Dotted lines* between homoeologous groups connect homoeologous loci. The relationship with rice is shown by a *hatched bar*

Fig. 3. (continued)



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