II.5 Pearl Millet

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1 Introduction

"We are talking about a crop that is virtually unimprovable – a crop that grows where not even weeds can survive; a crop that has been improved by farmers and through natural selection for thousands of years; a crop that produces nourishment from the poorest soils in the driest regions in the hottest climates; a crop that grows straight out of sand dunes; a crop that survives sand storms and flash floods" (ICRISAT 1996).

2 Species Origin and Economic Importance

Pearl millet (*Pennisetum glaucum* [L.] R. Br.) is the sixth most important cereal world-wide and is the main food source in the poorest regions of India and the African continent. It is a high-yielding, diploid C4 summer grass with $2n = 14$ chromosomes. Amongst the major cereals, pearl millet is highly tolerant to heat and drought, to saline and acid soils and is easy to grow in arid regions where rainfall is not sufficient for maize or even sorghum (FAO 2004). Pearl millet is descended from wild grasses native to the central Saharan plateau region of Niger, from where it spread to East Africa and India. Developing countries, mainly in Asia and Africa, account for about 94% of the global output of millet, where annual production exceeds 10×10^6 t, to which India contributes nearly half. In 2003, world-wide millet production was estimated at 29.8×10^6 t harvested on 36.3×10^6 ha, an area larger than that used for wheat production in the USA (FAOSTAT 2004). Five countries in West Africa (Nigeria, Niger, Mali, Burkina Faso, Senegal) produce 85% of the continent's total pearl millet crop. Almost all millet is produced by small-scale farmers for household consumption and localised trade.

Pearl millet is used for food, feed, brewing and as a building material. It is consumed primarily as a thick porridge ("toh"), but it is also milled into flour to prepare unfermented breads and cakes ("roti"), steam-cooked dishes

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("couscous"), fermented foods ("kisra and gallettes"), non-alcoholic beverages and snacks. Roasted young ears are a popular food for children. Furthermore, it is the most preferred cereal grain grown in the Sahelian countries, Senegal, Mali, Niger and Burkina Faso and is consumed in preference to sorghum. In northern Nigeria, pearl millet is used in making a popular fried cake known as *masa*.

Feeding trials conducted in India have shown that millet is nutritionally superior to maize and rice. It is a "high-energy" cereal with starch amounts of 70% in the dry grain. Its protein content of 16% is higher than in maize with a good balance of amino acids. Further, it contains 5–7% fat, which is greater than the values in most maize varieties; and it is particularly high in calcium and iron. It has low contents of fibre and most vitamins, whereas it is rich in vitamin A (NRC 1996; DeVries and Toenniessen 2001).

Although resistant to many diseases, pearl millet is susceptible to several pathogens, amongst which *Sclerospora graminicola*, the causal agent of downy mildew, is economically the most important, causing high annual yield losses. Smut, caused by *Moesziomyces penicillariae*, and top rot, caused by *Fusarium moniliforme*, present further fungal pathogens of pearl millet. The root parasite *Striga hermonthica* and the stem borer *Coniesta ignefusalis* also belong to its important pests (Wilson 2000; FAO 2004).

3 Pearl Millet Biotechnology

The African continent is dominated by agriculture and about 70% of its population live off farming. Africa has the highest percentage of agriculturally working population and the second highest cultivated area world-wide. Nevertheless, yields are the world's lowest (DeVries and Toenniessen 2001). In the past decades, impressive advances have been achieved in the productivity of the major three cereal crops, wheat, rice and maize, which helped to mitigate the disasters of population explosion. In the years to come, considering global warming and overpopulation, Africa's native grains will dominate, having the greatest untapped potential, since they still retain many of the robust properties of their wild ancestors.

Pearl millet is considered a "lost" crop of Africa (NRC 1996). Its available gene pool with traditional breeding methods is restricted by sexual incompatibility in many interspecific and intergeneric crosses. Most pearl millet cultivars are grown in Africa using minimal levels of purchased input. Breeding is aimed towards the capacity of surviving harsh conditions rather than increasing yield. Like other native African crops, pearl millet is still poorly supported by both science and politics; and biotechnology research in this field remains an underdeveloped resource for improved crop production in African agriculture. Also, the practical utilisation of biotechnological advances has been limited. A large number of African scientists have acquired skills and knowledge in

biotechnology but they are often unable to apply the techniques on local crops due to a lack of facilities and research funding. Furthermore, most African countries do not possess legal requirements and need consumption regulations for genetically modified organisms (GMOs). Biotechnological products aimed at Africa and improved in foreign laboratories await only the appropriate regulatory licences for importation (DeVries and Toenniessen 2001).

To date, the improvement of plants by means of genetic transformation and in vitro culture has been successfully implemented. Most activities on pearl millet, such as molecular breeding for downy mildew resistance, stover quality, increased beta-carotene content, drought and salinity tolerance (ICRISAT 2004), are localised at the International Crops Research Institute for the Semi–Arid Tropics (ICRISAT) in India. Applications of biotechnology to pearl millet are being investigated regarding methods of in vitro culture, such as micropropagation through tissue culture, genetic engineering and marker-assisted selection (DeVries and Toenniessen 2001).

There is an urgent need for an increased focus on crops relevant to the small farm holders and poor consumers in the developing countries of the humid and semi-arid tropics (Sharma et al. 2002). Pearl millet is the only major staple cereal that reliably produces both grain and forage on poor, sandy soils under the hot, dry conditions of Africa and Asia (Goldman et al. 2003), yet fungal phytopathogens such as *Sclerospora graminicola* have devastating effects on grain production. Genetic manipulation and in vitro culture provide a means for the plant gene pool to be broadened. Besides eliminating time-consuming back-crossing procedures in the field, gene technology offers transfer methods for specific genes controlling well-defined traits which are not available by classic breeding. Thus, the improvement of the native crops of Africa could directly benefit the people in greatest need. Transgenic pearl millet, conferring increased resistance to fungal invasion and developed through biotechnological methods, could complement current breeding programmes. Nevertheless, transgenic pearl millet will have to be tested as stringently as any other cultivars released. The World Health Organisation/Food and Agricultural Organisation (WHO/FAO) have protocols for a rigorous assessment and testing of genetically modified (GM) foods (Halsberger 2003) which would be applicable to transgenic pearl millet expressing selected valuable transgenes. Furthermore, it is essential to exclude gene flow from GM pearl millet to non-GM pearl millet. The pollen-mediated flow of transgenes can be controlled by cytoplasmic or nuclear male sterility. As cytoplasmic male sterility is a maternally inherited trait (Budar and Pelletier 2001; Feil and Stamp 2002), it can minimise the possibility of gene flow to non-GM pearl millet, which might otherwise present the threat of contaminating the gene pool of pearl millet. Furthermore, cytoplasmic male sterility systems already contribute significantly to increasing the productivity in pearl millet breeding (Thakur et al. 2001).

Finally, the gains in food production provided by the "Green Revolution" have reached their climax, while the world population continues to grow (Wisniewski et al. 2002). A new "Green Revolution" will necessitate the application

of recent advances in plant breeding, including new tissue culture techniques, marker-assisted selection and genetic modification (Wisniewski et al. 2002), in order to aid mankind's increasing food requirements, with cereal grains playing a pivotal role (Hoisington et al. 1999). The affluent nations can afford to adopt elitist positions and pay more for food produced by the so-called natural methods; the one billion chronically poor and hungry people of this world cannot (Wisniewski et al. 2002). Therefore, despite the diverse and widespread beneficial applications of biotechnology products, there remains a critical need to present these benefits to the general public in an understandable way that stimulates an unbiased and responsible public debate (Sharma et al. 2002) and pro-GMO government policies.

3.1 Somatic Embryogenesis and Plant Regeneration

An efficient transformation system has to be available in order to enhance the genetic pool of pearl millet and to apply recombinant DNA technology. Furthermore, high frequency plant regeneration from cultured explant material is a prerequisite for the successful transformation of this crop, as the limiting step in the development of genetic engineering technologies for the improvement of selected cereal genotypes lies in the in vitro culture step. Cultures of cereals, in general, show strong genotypic dependency and development of appropriate cultures is generally restricted to certain genotypes (Lambé et al. 1999). The improvement of efficient in vitro regeneration systems for pearl millet is therefore a major precondition to achieve applicable plant transformation.

Different in vitro regeneration systems for pearl millet have been reported within the past 20 years, such as regeneration of plants from protoplasts (Vasil and Vasil 1980), immature embryos and inflorescences (Vasil and Vasil 1981a; Swedlund and Vasil 1985) and from suspension cultures derived from immature zygotic embryos (Vasil and Vasil 1981b) or shoot apical meristems (Devi et al. 2000). Recently, efficient regeneration systems targeting selected pearl millet genotypes, based on shoot apices and immature zygotic embryo-derived embryogenic tissue, were developed by Oldach et al. (2001) and O'Kennedy et al. (2004a). These studies tasked the optimisation of explant source, culture media including carbon sources, and phytohormone concentrations and ratios (Fig. 1).

The duration needed to obtain mature pearl millet regenerants averages up to six months and is long compared with that of other cereals. Furthermore, the culture of certain pearl millet genotypes is characterised by an extensive production of phenolic substances, that oxidise and provoke browning of the culture medium and the plant tissue. Their accumulation slows down plant growth and increases mortality, leading to retarded plant regeneration. The addition of particular compounds to the culture medium, such as silver nitrate, can antagonise and thus mitigate this effect. Furthermore, callus induction medium supplemented with L-proline improved regeneration efficiencies to

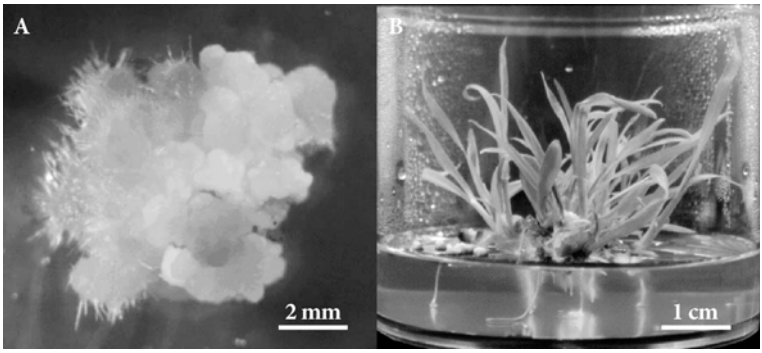

Fig. 1. Regeneration of pearl millet from immature zygotic embryos, according to Oldach et al. (2001). **A** Callus induction and early regeneration. **B** Root induction on regenerating plants

nine plants per immature zygotic embryo, six plants per shoot apex (Oldach et al. 2001) and 80 plants per immature zygotic embryo (O'Kennedy et al. 2004a).

3.2 Genetic Transformation

Although successful in vitro regeneration and transformation systems for pearl millet have been published (Lambé et al. 2000; Goldman et al. 2003), transformation of this crop is still limited by relatively low and erratic stable transformation efficiencies. Until recently, reports were restricted to transient reporter gene expression (Taylor and Vasil 1991) and expression of selectable marker genes in long-term callus cultures which often could not be regenerated to transgenic plants (Lambé et al. 1995, 2000). Establishing an efficient routine transformation protocol for pearl millet would therefore form the technological basis for the genetic enhancement of this crop and provide the means of introducing commercially important genes. Lately, transgenic, fertile pearl millet plants were regenerated from scutellum cells of cultured immature zygotic embryos, the cells being transformed with either the PDS 1000/He gun (BioRad) or the particle inflow gun (PIG) devices, using the herbicide selectable marker gene, phosphinotricin acetyltransferase from *Streptomyces hygroscopicus* ("*bar*") or *Streptomyces viridochromogenes* ("*pat*"; Girgi et al. 2002). Transformation rates ranged between 0.04% and 0.7%, requiring a regeneration period of 10–12 months for the various genotypes used.

It is well documented that only a minor fraction of the treated cells will integrate the foreign DNA during the transformation process, while the majority of the untransformed cells need to be eliminated by selection. During negative selection by herbicides or antibiotics, most of the cells in the cultured tissue die. These dying cells release toxic substances, which in turn affect the regeneration of transgenic tissue and may form a barrier between the medium and the transgenic cells, thereby preventing or slowing the uptake of nutrients. Although the stable integration of such selection genes makes it possible

to identify and select transgenic plant cells, their lingering presence in crops complicates the regulatory process and negatively affects public acceptance of the final product. Thus, positive selection systems, based on enzymes from sugar metabolism, favour the regeneration and growth of the transgenic cells, while the non-transgenic cells are starved but not killed. Finally, transgenic plants expressing these enzymes have no potential risk to animals, humans or environmental safety, which is essential since pearl millet is indigenous to Africa. Recent investigation resulted in significantly higher transformation frequencies in other cereal crops when the phosphomannose isomerase gene *pmi* from *E. coli* was used for selection, in maize (Negrotto et al. 2000) and rice (Lucca et al. 2001). Similarly, fertile, transgenic pearl millet plants were produced using *manA*, also encoding a phosphomannose isomerase, resulting in a higher transformation efficiency of 0.7–3.0% (O'Kennedy et al. 2004b).

Beyond the establishment of pearl millet transformation, first approaches concerning genetic enhancement of pearl millet towards fungal resistance were published recently. Selected genes, like the chemically synthesised *pin* gene (Latha et al. 2006), and the *afp* gene encoding the anti fungal protein from the mould *Aspergillus giganteus* (Girgi et al. 2006) were successfully transformed into different pearl millet cultivars and showed significant enhancement in fungal resistance against downy mildew and rust infection.

3.3 Genomics in Pearl Millet Breeding

During the past ten years, resources have been established for the genetic analysis of pearl millet (Qi et al. 2004). Among these are detailed genetic maps containing both homologous and heterologous restriction fragment length polymorphism (RFLP) markers, and simple sequence repeats (SSRs). In 1994, the first genetic map of pearl millet was generated by Liu et al. (1994). It contained 181 RFLP markers covering the seven pearl millet chromosomes and spanning a genetic distance of 303 cM. Subsequently, a subset of these markers was transferred to a series of different crosses that segregate for agronomically important traits. Quantitative trait loci (QTL) for downy mildew resistance (Jones et al. 1995, 2002), drought tolerance (Yadav et al. 2002, 2003, 2004) and characteristics involved in domestication (Poncet et al. 2000, 2002) have been mapped. The integration of markers, previously mapped in other grass species, enables the alignment of the pearl millet linkage groups to other cereal genetic maps, including the model species rice (Qi et al. 2004). The pearl millet genome appears to be highly rearranged compared to rice. Nevertheless, regions of colinearity between the two species can be clearly identified (Devos et al. 2000). These regions present a framework for utilising rice genomic sequences as a source of new markers and candidate genes underlying traits in pearl millet. The maps and markers provide a base for future genomic and comparative analysis of pearl millet and for the application of marker-assisted selection in breeding programmes (Qi et al. 2004).

4 Conclusions

There is an urgent need to increase nutritional supplies to help attain food security, especially in developing countries. Due to their high adaptation to environmental conditions, the improvement of local crops presents a capable strategy for small farm holders and poor consumers. Pearl millet is the only major staple cereal that survives under the hot and dry climate in Asia and Africa (Sharma et al. 2002). Nevertheless, its gene pool can be broadened towards economically important traits such as resistance to fungal pathogens, higher yields and nutritional properties. Besides classic breeding, gene- and biotechnology offer promising strategies for the selective genetic enhancement of crops. Until recently, plant breeding relied solely on the sexual transfer of genes between plant species. Today, advances in plant molecular biology and genomics now give access to the knowledge and understanding of plant genomes and genetic engineering (Job 2002). Research on in vitro technologies, genetic transformation and molecular techniques have to be intensified for pearl millet. In order to achieve this purpose, more scientific and political investigations are required. Supporting technology transfer and the development of the legal requirements to handle GMOs will help to establish the needed prerequisite for an autonomous research base to match the demands in those countries where pearl millet is cultivated as a major crop.

References

Budar F, Pelletier G (2001) Male sterility in plants: occurrence, determinism, significance and use. CR Acad Sci III 324:543–550

Devi P, Zhong H, Sticklen MB (2000) *In vitro* morphogenesis of pearl millet (*Pennisetum glaucum* (L.) R. Br.): efficient production of multiple shoots and inflorescences from shoot apices. Plant Cell Rep 19:251–260

Devos KM, Pittaway TS, Reynolds A, Gale MD (2000) Comparative mapping reveals a complex relationship between the pearl millet genome and those of foxtail millet and rice. Theor Appl Genet 100:190–198

DeVries J, Toenniessen G (2001) Securing the harvest: biotechnology, breeding and seed systems for African crops. CAB International, Wallingford

FAO (2004) *Pennesitum americanum* (L.) Leeke: species description. Food and Agriculture Organization of the United Nations, Rome. Available at: www.fao.org/ag/AGP/AGPC/doc/Gbase/DATA/Pf000297.htm

FAOSTAT (2004) FAOSTAT statistical database. Food and Agriculture Organization of the United Nations, Rome. Available at: apps.fao.org/faostat/form?collection=Production.Crops.Primary&Domain=Production&servlet=1&hasbulk=0&version=ext&language=EN

Feil B, Stamp P (2002) The pollen-mediated flow of transgenes in maize can already be controlled by cytoplasmic male sterility. AgBiotech Net 4:1–4

Girgi M, O'Kennedy MM, Morgenstern A, Mayer G, Lörz H, Oldach KH (2002) Stable transformation and regeneration of pearl millet (*Pennisetum glaucum* L.) R. Br. via microprojectile bombardment of scutellar tissue. Mol Breed 10:243–252

Girgi M, Breese WA, Lörz H, Oldach KH (2006) Rust and downy mildew resistance in pearl millet (*Pennisetum glaucum*) mediated by heterologous expression of the *afp* gene from *Aspergillus giganteus*. Transgenic Res 15:313–324

Goldman JJ, Hanna WW, Fleming G, Ozias-Akins P (2003) Fertile transgenic pearl millet [*Pennisetum glaucum* [L.] R. Br.] plants recovered through microprojectile bombardment and phosphinothricin selection of apical meristem-, inflorescence-, and immature embryo-derived embryogenic tissues. Plant Cell Rep 21:999–1009

Halsberger AG (2003) GM food: the risk assessment of immune hypersensitivity reactions covers more than allergenicity. Food Agric Environ 1:42–45. Available at: www.biotech-info.net/hypersensitivity.html

Hoisington D, Khairallah M, Reeves T, Ribaut J-M, Skovmand B, Taba S, Warburton M (1999) Plant genetic resources: what can they contribute toward increased crop productivity? Proc Natl Acad Sci USA 96:5937–5943

ICRISAT (1996) Improving the unimprovable: succeeding with pearl millet. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh. Available at: africancrops.net/crops%20millet.html

ICRISAT (2004) International Crops Research Institute for the Semi–Arid Tropics. Data available at: www.icrisat.org/web/index.asp; www.icrisat.org/gt1/pest.pdf;www.icrisat.org/gt1/drought.pdf; www.icrisat.org/gt1/disease.pdf;www.icrisat.org/gt1/agronomic.pdf

Job D (2002) Plant biotechnology in agriculture. Biochimie 84:1105–1110

Jones ES, Liu CJ, Gale MD, Hash CT, Witcombe JR (1995) Mapping quantitative trait loci for downy mildew resistance in pearl millet. Theor Appl Genet 91:448–456

Jones ES, Breese WA, Liu CJ, Singh SD, Shaw DS, Witcombe JR (2002) Mapping quantitative trait loci for resistance to downy mildew in pearl millet: field and glasshouse screens detect the same QTL. Crop Sci 42:1316–1323

Lambé P, Dinant M, Matagne RF (1995) Differential long-term expression and methylation of the hygromycin phosphotransferase (*hph*) and beta glucuronidase (*gus*) genes in transgenic pearl millet (*Pennisetum glauccum)* plants. Plant Sci 108:51–62

Lambé P, Mutambel HSN, Deltour R, Dinant M (1999) Somatic embryogenesis in pearl millet (*Pennisetum americanum*): strategies to reduce genotype limitation and to maintain long-term totipotency. Plant Cell Tissue Organ Cult 55:23–29

Lambé P, Dinant M, Deltour R (2000) Transgenic pearl millet (*Pennisetum glaucum*). In: Bajaj YPS (ed) Transgenic crops I. (Biotechnology in agriculture and forestry, vol 46) Springer, Berlin Heidelberg New York, pp 84–108

Latha AM, Rao KV, Reddy TP, Reddy VD (2006) Development of transgenic pearl millet (*Pennisetum glaucum* (L.) R. Br.) plants resistant to downy mildew. Plant Cell Rep (in press). DOI 10.1007/s00299-006-0141-6

Liu CJ, Witcombe JR, Pittaway TS, Nash M, Busso CS, Hash CT, Gale MD (1994) An RFLP-based genetic map of pearl millet (*Pennisetum glaucum*). Theor Appl Genet 89:481–487

Lucca P, Ye X, Potrykus I (2001) Effective selection and regeneration of transgenic rice plants with mannose as selective agent. Mol Breed 7:43–49

Negrotto D, Jolley M, Beer S, Wenck AR, Hansen G (2000) The use of phosphomannose-isomerase as a selectable marker to recover transgenic maize plants (*Zea mays* L.) via *Agrobacterium* transformation. Plant Cell Rep 19:798–803

NRC (1996)Lost crops of Africa, vol 1: grains. National Research Council/National Academy Press, Washington, D.C.

O'Kennedy MM, Smith G, Botha FC (2004a) Improved regeneration efficiency of a pearl millet (*Pennisetum glaucum*) breeding line. S Afr J Bot 70:502–508

O'Kennedy MM, Burger JT, Botha FC (2004b) Pearl millet transformation system using the positive selectable marker gene phosphomannose isomerase. Plant Cell Rep 22:684–690

Oldach KH, Morgenstern A, Rother S, Girgi M, O'Kennedy M, Lörz H (2001) Efficient in vitro plant regeneration from immature zygotic embryos of pearl millet (*Pennisetum glaucum* (L.) R: Br.) and *Sorghum bicolor* (L.) Moench. Plant Cell Rep 20:416–421

Poncet V, Lamy F, Devos KM, Gale MD, Sarr A, Robert T (2000) Genetic control of domestication traits in pearl millet (*Pennisetum glaucum* L., Poaceae). Theor Appl Genet 100:147–159

Poncet V, Martel E, Allouis S, Devos KM, Lamy F, Sarr A, Robert T (2002) Comparative analysis of QTLs affecting domestication traits between two domesticated × wild pearl millet (*Pennisetum glaucum* L., Poaceae) crosses. Theor Appl Genet 104:965–975

Qi X, Pittaway TS, Lindup S, Liu H, Waterman E, Padi FK, Hash CT, Zhu MD, Gale MD, Devos KM (2004) An integrated genetic map and a new set of simple sequence repeat markers for pearl millet, *Pennisetum glaucum*. Theor Appl Genet 109:1485–1493

Sharma HC, Crouch JH, Sharma KK, Seetharama N, Hash CT (2002) Applications of biotechnology for crop improvement: prospects and constraints. Plant Sci 163:381–395

Swedlund B, Vasil IK (1985) Cytogenetic characterization of embryogenic callus and regenerated plants of *Pennisetum americanum* (L.) K. Schum. Theor Appl Genet 69:575–581

Taylor GM, Vasil IK (1991) Histology of, and physical factors affecting, transient GUS expression in pearl millet (*Pennisetum glaucum* [L.] R. Br.) embryos following microprojectile bombardment. Plant Cell Rep 10:120–125

Thakur RP, Rai KN, Rao VP, Rao AS (2001) Genetic resistance of pearl millet male-sterile lines to diverse Indian pathotypes of *Sclerospora graminicola*. Plant Dis 85:621–626

Vasil V, Vasil IK (1980) Isolation and culture of cereal protoplasts. Part 2: embryogenesis and plantlet formation from protoplasts of *Pennisetum americanum*. Theor Appl Genet 56:97–99

Vasil V, Vasil IK (1981a) Somatic embryogenesis and plant regeneration from tissue cultures of *Pennisetum americanum* and *P. americanum* × *P. purpureum* hybrid. Am J Bot 68:864–872

Vasil V, Vasil IK (1981b) Somatic embryogenesis and plant regeneration from suspension cultures of pearl millet (*Pennisetum americanum*). Ann Bot 47:669–678

Wilson JP (2000) Pearl millet diseases: a compilation of information on the known pathogens of pearl millet (*Pennisetum glaucum* [L.] R. Br.). (Agriculture Handbook 716) United States Department of Agriculture Agricultural Research Service, Washington, D.C.

Wisniewski JP, Frangne N, Massonneau A, Dumas C (2002) Between myth and reality: genetically modified maize, an example of a sizeable scientific controversy. Biochimie 84:1095–1103

Yadav RS, Hash CT, Bidinger FR, Cavan GP, Howarth CJ (2002) Quantitative trait loci associated with traits determining grain and stover yield in pearl millet under terminal drought stress conditions. Theor Appl Genet 104:67–83

Yadav RS, Bidinger FR, Hash CT, Yadav YP, Yadav OP, Bhatnagar SK, Howarth CJ (2003) Mapping and characterization of QTL × E interactions for traits determining grain and stover yield in pearl millet. Theor Appl Genet 106:512–520

Yadav RS, Hash CT, Bidinger FR, Devos KM, Howarth CJ, Skot K (2004) Genomic regions associated with grain yield and aspects of post-flowering drought tolerance in pearl millet across stress environments and testers background. Euphytica 136:265–277