

Expl Agric. (2009), volume 45, pp. 107–115 © 2008 Cambridge University Press
doi:10.1017/S0014479708007059 Printed in the United Kingdom

GENETIC IMPROVEMENT OF PEARL MILLET FOR THE ARID ZONE OF NORTHWESTERN INDIA: LESSONS FROM TWO DECADES OF COLLABORATIVE ICRISAT-ICAR RESEARCH

By F. R. BIDINGER^{†, ¶}, O. P. YADAV[‡] and E. WELTZIEN RATTUNDE[§]

[†]*International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502
324, Andhra Pradesh, India, ‡Central Arid Zone Research Institute (CAZRI), Jodhpur 342 003
Rajasthan, India and §ICRISAT, BP 320, Bamako, Mali*

(Accepted 15 August 2008)

SUMMARY

The arid zone of northwestern India is a unique adaptation zone for crop plants because of its pervasive severe moisture stress and high temperatures. Pearl millet (*Pennisetum glaucum*) is a major cereal in this zone as it represents approximately 25% of the total acreage of the crop in the country. Pearl millet hybrid cultivars, which have gained widespread acceptance from farmers elsewhere in the country, have not been adopted in the arid zone. Farmers continue to sow their traditional landraces because the yield advantage of current hybrids is not expressed in this zone, and the risk of failure in poor years with the hybrids is unacceptably high. The International Crops Research Institute for the Semi-Arid Tropics and the Indian Council of Agricultural Research have been collaborating to understand the unique nature of pearl millet in the arid zone since the late 1980s. This collaboration has produced a better understanding of how arid zone farmers manage their germplasm, of the unique features of this invaluable resource and of a range of ways of using this germplasm to produce well-adapted new varieties and hybrids that will meet the requirements of the farmers of the arid zone. It has been shown that new cultivars for the arid zone need to be based on parental materials, including traditional landraces that are specifically adapted to the arid zone. This paper summarizes the main lessons of nearly 20 years of this collaborative research.

INTRODUCTION

Selection for improved yields under marginal environmental conditions is a continuing challenge for plant breeders (Ceccarelli, 1994). Differences in grain yield in such environments are as likely to reflect differences in adaptation to one or more of the yield limiting factors in a specific environment as they are to reflect differences in yield potential itself. Unfortunately, much less is known about the genetic basis of, and methods to select for, improved adaptation (yield under stress) than is known about improving yield potential in favourable environments where control over environmental factors is better. In addition, in many marginal environments, especially drought-prone ones, specific traits conditioning adaptation can change from one environment to another as the seasonal pattern of moisture

[‡]Corresponding author: opyadav@cazri.res.in

[¶]Deceased.

availability/deficiency changes (van Oosterom *et al.*, 2003). Thus differences among experimental materials in single experiments are as likely to be the consequences of genotype \times environment interaction as they are a reflection of generalizable genetic differences.

The arid zone of the western part of Rajasthan State in northwestern India (Barmer, Jodhpur, Jaisalmer and Bikaner districts) is one of the most marginal environments for arable agriculture in the world. Rainfall in the arid zone averages between 150 and 350 mm per year, with a very high degree of annual variability and not infrequent crop failures. Average rainy season maximum and minimum temperatures ($^{\circ}\text{C}$) are in the mid-30s and the mid-20s, respectively, and potential evaporation equals or exceeds rainfall even in the rainy season. Despite the severely limited environmental resources, the zone has a relatively high population density, mainly supported by the traditional system of mixed arable cropping, and both small and large ruminant husbandry. Pearl millet (*Pennisetum glaucum*) is the staple cereal and is widely rotated/ intercropped with several arid zone grain legume species, and these crops form the basis of the human diet. The straw of both pearl millet and the legumes forms the basis of the diet of the ruminant population for much of the year.

For the All-India Co-ordinated Pearl Millet Improvement Programme (AICPMIP), the arid (A1) zone represents an unmet and urgent challenge. Single-cross pearl millet hybrids bred by AICPMIP and private seed companies are widely grown in the rest of the country, with coverage of new cultivars greater than 90% in some areas. In the arid zone, in contrast, there has been very limited adoption of new cultivars (apart from the occasional irrigated field) and yield increases have been much less than those achieved nationally, with mean yields still in the range of 100–300 kg ha⁻¹ (Directorate of Millets Development, 2006). The arid zone represents about 25% of the total acreage of pearl millet area in India (>2 million of 9 million hectares), and one where farmers have no alternative to pearl millet.

There is increasing evidence that the lack of adoption of currently available pearl millet hybrids by arid zone farmers is due to their inadequate adaptation to the marginal environmental conditions of the arid zone (Bidinger *et al.*, 2006; Dhamotharan *et al.* 1997; Kelley *et al.*, 1996; Yadav and Bidinger, 2008). The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and the Indian Council of Agricultural Research (ICAR) have been collaborating with various organizations with a shared interest in the arid zone since the late 1980s. These partners include AICPMIP, Central Arid Zone Research Institute (CAZRI), Rajasthan Agricultural University, National Bureau of Plant Genetic Resources and a range of local non-governmental organizations. This collaboration has produced a better understanding of the ways in which farmers use and manage the traditional landrace pearl millet germplasm of the arid zone and of the opportunities for the use of this germplasm in breeding new and higher yielding cultivars for the arid zone. Our objective here is to summarize the main lessons of 20 years of collaborative research on pearl millet in the arid zone so that they are useful to others working in similar environments, such as the Sahelian zone of west and central Africa, where the

production constraints of pearl millet are similar to those encountered in northwestern India.

FARMERS' MANAGEMENT OF THEIR GENETIC RESOURCES

The farmers' concepts of a variety is different from that commonly used by plant breeders (Christinck, 2002). Rajasthan farmers subdivide all pearl millet into two main categories, the *desi* or local landrace plant type, and the *sankar*, the plant type common in modern varieties. Farmers with better land tend to diversify their seed sources regularly every 2–4 years with purchased seeds, thus continually increasing the diversity (vom Brocke *et al.*, 2003a) and expanding the range of adaptation in their seed stocks (vom Brocke *et al.*, 2003b). The majority of farmers with poorer land prefer to use pure *desi* types, which are better adapted to extremely harsh and variable growing conditions (Yadav, 2008; Yadav and Weltzien, 2000). Traditional seed markets serve as an important source of seed in both eastern and western Rajasthan especially in drought periods (Weltzien, 2000). Seed is traded from farmer to farmer, without the involvement of intermediate traders ensuring a high degree of transparency with regard to origin, environmental conditions, cultivation practices and quality of seed (Dhamotharan *et al.*, 1997).

Farmers also have a comprehensive concept of the food and fodder qualities, including culinary qualities, grain storability and health aspects of their varieties (Christinck, 2002). Traditional varieties are considered superior to modern varieties for most of the grain quality traits, especially in western Rajasthan, where pearl millet is consumed throughout the whole year. Farmers in Rajasthan tend to select and keep their own seed, even when they grow both *desi* and *sankar* varieties, quite often in the same fields. Responsibility for seed management often relies on the older women of the family.

EVALUATION OF ARID ZONE GENETIC RESOURCES

Multi-environment evaluation over a wide range of arid and semi-arid environments of more than 100 arid zone germplasm accessions selected by sub-sampling the full collection of arid zone pearl millet accessions contained in the Genebank at ICRISAT showed good genetic diversity in arid zone germplasm for grain and stover productivity and several phenotypic traits (Yadav *et al.*, 2004a). However, phenotypic diversity was less in arid zone pearl millet germplasm than that reported among landraces from Africa (Wilson *et al.*, 1990). Specific accessions with parental value for improving drought tolerance (Yadav *et al.*, 2003a) and better responsiveness to improved environments (Yadav and Bidinger, 2007) were identified. A number of the accessions identified in this exercise have been used as parental materials in a collaborative open-pollinated variety breeding programme at CAZRI, which has a specific mandate for the arid zone.

In addition, the entire data set from drought and non-drought environments was used to better understand the plant yield processes associated with adaptation to the most drought stressed of the evaluation sites, which suggested an ideotype (resource

allocation pattern) that combined maximum yield under severe (especially pre-flowering) stress conditions with the ability to respond to improved moisture conditions. The successful ideotype in severe pre-flowering stress environments combined a high tillering capacity, a large dry matter investment in reproductive structures (per unit land area) and a maximum grain number per unit of dry matter invested in reproductive structure (van Oosterom *et al.*, 2006).

BREEDING OPEN-POLLINATED VARIETIES FROM ARID ZONE GERMPLASM

The breeding of better adapted and higher yielding open-pollinated varieties based on arid zone germplasm has been the ultimate objective of the collaborative research. This has included both basic studies on breeding for the arid zone, as well as applied breeding programmes based on the research findings. A number of research studies confirmed that the more marginal the conditions, the better was the relative performance of landrace-based materials compared with that of conventionally bred materials (Yadav and Bidinger, 2007; 2008; Yadav and Weltzien, 2000; Witcombe and Weltzien, 1989) supporting the need for basing breeding programmes for the arid zone on landrace germplasm (Figure 1).

The most successful example of the use of landraces in cultivar breeding is the composite variety CZP 9802, which was bred from the landrace-based Early Rajasthan Population. This population was synthesized from four early maturing Rajasthan landraces, and underwent a number of cycles of recurrent selection for both adaptation to arid zone conditions and for downy mildew resistance under glasshouse conditions. In AICPMIP A₁ zone tests, the mean grain yield of CZP 9802 across years and sites was 25–58% greater than that of the standard AICPMIP trial checks in drought environments and equal to them in favourable environments, but superior in stover (straw) yields in both kinds of environment. CZP 9802 is thus unique in that it combines a high level of adaptation to drought stress, in addition to being as responsive to improved conditions as were the national controls (Yadav, 2004). As a result, CZP 9802 was released by the Government of India for cultivation in drought-affected pearl millet growing areas in the states of Rajasthan, Gujarat and Haryana, and has been received very well by farmers.

The performance of populations bred by introgressing non-landrace germplasm into landrace backgrounds (both by farmers and plant breeders) increased the responsiveness of landrace germplasm to better-endowed arid zone environments (Presterl and Weltzien, 2003; Yadav, 2007; 2008; Yadav and Weltzien, 1997), but indicated that selection in such materials needed to be done in both good and poor (typical arid zone) environments to retain the adaptation of the landrace parent (Weltzien, 1990). One key lesson learned was the clear superiority of full-sib over self-pollinated progenies for recurrent selection with landraces in arid zone environments (Weltzien, 1995; Weltzien and Hash, 1995). It proved to be vital to evaluate only heterozygous materials under these harsh growing conditions, as progenies with a significant degree of inbreeding, e.g. S₁ lines, showed much higher error variances, and as a consequence differentiation between progenies was less effective.

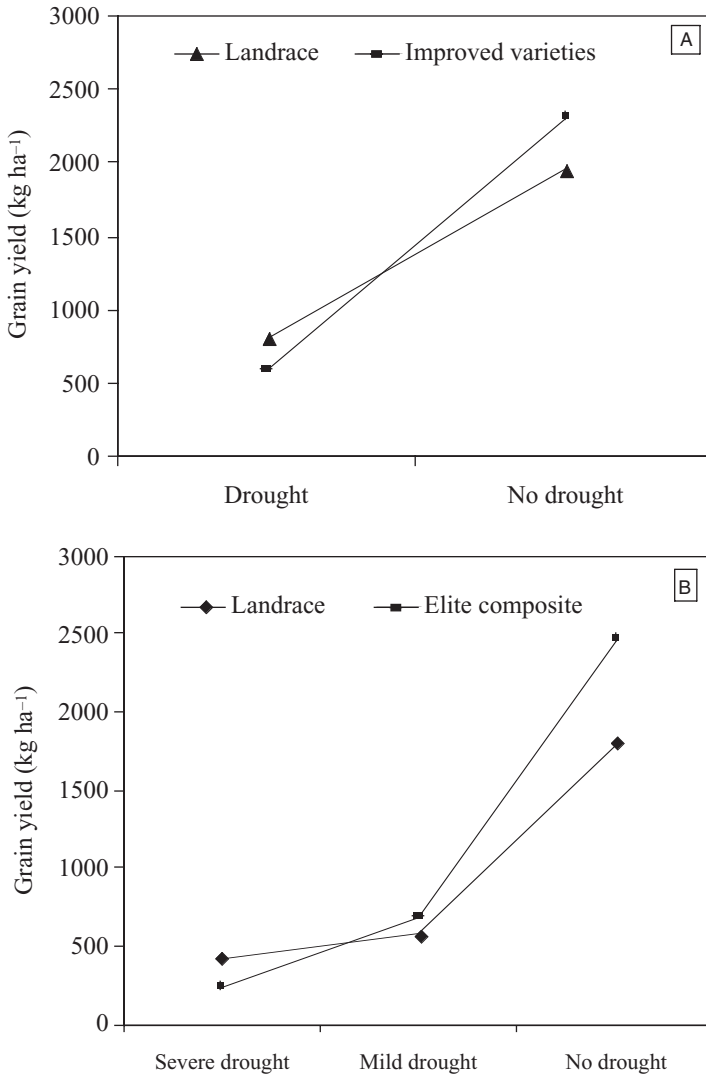


Figure 1. Grain yield performance of group of pearl millet landraces and elite improved materials under different drought intensities in arid zone of India. The differences between two groups of material is significant ($p < 0.05$) under severe drought and non-drought conditions. Source: A – Yadav and Weltzien (2000); B –Yadav and Bidinger (2007).

Full-sib progenies' performance is also a better predictor than S_1 progenies of general combining ability (GCA) which determine the performance of varieties made from selected progenies.

OPPORTUNITIES FOR HYBRIDS IN THE ARID ZONE

The lack of adoption of hybrids in the arid zone does not necessarily mean that hybrids as a cultivar type are not adapted to this zone. Currently available hybrids do not meet farmer requirements, particularly for the ability to produce a grain yield in

the poorest years and to produce an adequate stover yield to maintain animals during the dry season. This is because hybrids were bred from the parental lines with little adaptation to the climatic constraints of the arid zone and/or to farmers' requirements in this zone. Early research assessed the performance of topcross hybrids made with conventional seed parents and adapted landrace pollinators in the arid zone. Results indicated that it is clearly possible to exploit heterosis in such combinations (Bidinger *et al.*, 1994; Yadav *et al.*, 2000), but obviously additional work was required to identify seed parents with acceptable adaptation to the arid zone, and to breed disease resistant restorers, with good GCA, from adapted landrace sources.

Subsequently a large scale assessment of all publicly available male-sterile lines was undertaken to assess their combining ability for grain and stover yields, stability, responsiveness to improved environmental conditions, drought tolerance, downy mildew resistance and plant type of their hybrids (Bidinger *et al.*, 2002; 2003a) to identify sets of seed parents with characteristics necessary for arid zone environments, ranging from low-input subsistence environments to supplemental irrigated ones (Yadav *et al.*, 2003b). The key trait for seed parents for the arid zone was a positive GCA for biomass under arid zone conditions (Bidinger *et al.*, 2003b) which can be combined with good adaptation to arid zone environments from pollinators bred from landrace sources to increase both grain and stover yields and to maximize yield stability. Specific seed parents possessing good GCA for biomass have been identified. We are currently testing a number of B \times B line combinations to identify maintainer crosses with a positive GCA for biomass that can be used to develop new maintainers with this ability.

A set of arid zone adapted populations with a range of phenotype and origin (pure landrace, diversified landrace and exotic selected in the arid zone) were used as source material for breeding adapted restorer lines for the arid zone (Bidinger and Yadav, 2008; Yadav and Weltzien, 1998). The lines derived from two landrace-based populations showed differences in their combining abilities for adaptation to arid zone conditions and produced hybrids that comprehensively out yielded the best available checks under typical arid zone drought environment (unpublished data). A further advantage with adapted hybrids is that they have more chances of being delivered to farmers through well-established seed delivery system of both private and public sectors. We have begun developing inbreds from a number of other restorer populations based on germplasm, selected from AICPMIP programmes in the arid zone and ICRISAT, which was reasonably adapted to the arid zone.

Because of a history of limited success in breeding for drought adaptation by conventional phenotypic selection (Barker *et al.*, 2005; Blum, 1988), this field has become a prime focus for molecular marker-assisted breeding. Identification of genomic regions determining drought tolerance of arid zone adapted landraces is underway at CAZRI. Other research at ICRISAT has identified quantitative trait loci (QTL) which had significant effects on pearl millet yield in drought stress environments (Bidinger *et al.*, 2005; Yadav *et al.*, 2002; 2004b). Comparison of hybrids with and without these QTL showed that QTL-based hybrids were significantly, but modestly, higher yielding in a series of terminal drought stress environments

(Bidinger *et al.*, 2005). However, this gain under stress was achieved at the cost of a lower yield in the non-drought environments. A major QTL mapped on linkage group 2 determining grain yield in post-flowering drought stress environments (Yadav *et al.*, 2002) has been transferred to drought sensitive pearl millet lines through marker-assisted backcross breeding and its effect on yield performance under arid zone droughts is being investigated.

CONCLUSION

The collaborative research between ICRISAT and ICAR was able to document the procedures used by arid zone farmers to maintain their traditional pearl millet germplasm. Evaluation of germplasm and other breeding materials suggested that the more marginal the conditions, the better was the relative performance of landrace-based materials than that of conventionally bred materials. Plant yield processes associated with adaptation to drought conditions suggested that successful ideotypes in severe pre-flowering stress environments combined a high tillering capacity with a large dry matter investment in reproductive structures and a maximum grain number per unit of this investment. Research also suggested that it was possible to exploit heterosis in the arid zone environments through topcrossing adapted landrace pollinators with conventional seed parents. The key trait for seed parents for the arid zone was a positive general combining ability for biomass under arid zone conditions that could be combined with good adaptation from pollinators bred from landrace sources. A set of arid zone adapted populations with a range of phenotype and origin has been used as source material for breeding adapted restorer lines for the arid zone.

REFERENCES

- Barker, T., Campos, H., Cooper, M., Dolan, D., Edmeades, G., Habben, J., Schussler, J., Wright, D. and Zinselmeier, C. (2005). Improving drought tolerance in maize *Plant Breeding Review* 25:173–226.
- Bidinger, F. R. and Yadav, O. P. (2008). Biomass heterosis as the basis for grain and stover yield heterosis in arid zone pearl millet (*Pennisetum glaucum* (L.) R. Br.) hybrids. *Crop Science* (in press)
- Bidinger, F. R., Weltzien, R. E., Mahalakshmi, V., Singh, S. D. and Rao, K. P. (1994). Evaluation of landrace topcross hybrids of pearl millet for arid zone environments. *Euphytica* 76:215–226.
- Bidinger, F. R., Yadav, O. P. and Sharma, M. M. (2002). Male-sterile seed parents for breeding landrace-based topcross hybrids of pearl millet (*Pennisetum glaucum*) for the arid zone. I. Productivity, responsiveness and stability. *Indian Journal of Genetics and Plant Breeding* 62:121–127.
- Bidinger, F. R., Thakur, R. P., Yadav, O. P. and Sharma, M. M. (2003a). Male-sterile seed parents for breeding landrace-based topcross hybrids of pearl millet (*Pennisetum glaucum*) for the arid zone. II. Downy mildew resistance, plant type, fertility restoration and terminal drought tolerance. *Indian Journal of Genetics and Plant Breeding* 63:99–105.
- Bidinger, F. R., Yadav, O. P., Sharma, M. M., van Oosterom, E. J. and Yadav, Y. P. (2003b). Exploitation of heterosis for simultaneous improvement in both grain and stover yields of arid zone pearl millet (*Pennisetum glaucum* (L.) R. Br.). *Field Crops Research* 83:13–26.
- Bidinger, F. R., Serraj, R., Rizvi, S. M. H., Howarth, C., Yadav, R. S. and Hash, C. T. (2005). Field evaluation of drought tolerance QTL effects on phenotype and adaptation in pearl millet [*Pennisetum glaucum* (L.) R. Br.] topcross hybrids. *Field Crops Research* 94:14–32.
- Bidinger, F. R., Bhasker, Raj, A. G. and Hash, C. T. (2006). Zonal adaptation in pearl millet cultivar types. *Indian Journal of Genetics and Plant Breeding* 66:207–211.
- Blum, A. (1988). *Plant Breeding for Stress Environments*, Boca Raton: CRC Press.
- Ceccarelli, S. (1994). Specific adaptation and breeding for marginal environments. *Euphytica* 77:205–219.

- Christinck, A. (2002). This seed is like ourselves. A case study from Rajasthan, India, on the social aspects of biodiversity and farmers' management of pearl millet seed. *Kommunikation und Beratung Volume 47*, Weikersheim, Germany: Margraf Verlag.
- Dhamotharan, M., Weltzien, E., Whitaker, M. L., Rattunde, H. F., Anders, M. M., Taigi, Manga, V. K. and Vyas, K. L. (1997). Seed management strategies of farmers in western Rajasthan in their social and environmental contexts: Results from a workshop using communication techniques for a dialogue between farmers and scientists, Digadi Village Jodhpur District, Rajasthan, India. *Integrated Systems Project Report No. 9. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.*
- Directorate of Millets Development. (2006). State wise area, production and yield of coarse cereals. [online] http://dacnet.nic.in/millets/state_wise_main.htm.
- Kelley, T. G., Parthasarathy Rao, P., Weltzien, R. E. and Purohit, M. L. (1996). Adoption of improved cultivars or pearl millet in an arid environment: Straw yield and quality considerations in western Rajasthan. *Experimental Agriculture* 32:161–172.
- Presterl, T. and Weltzien, E. (2003). Exploiting heterosis in pearl millet population breeding in arid environments. *Crop Science* 43:767–776.
- van Oosterom, E. J., Bidinger, F. R. and Weltzien R., E. (2003). A yield architecture framework to explain adaptation of pearl millet to environmental stress. *Field Crops Research* 80:33–56.
- van Oosterom, E. J., Weltzien, E., Yadav, O. P. and Bidinger, F. R. (2006). Grain yield components of pearl millet under optimum conditions can be used to identify germplasm with adaptation to arid zones. *Field Crops Research* 96:407–421.
- vom Brocke, K., Christinck, A., Weltzien, E., Presterl, T. and Geiger, H. H. (2003a). Farmers' seed systems and management practices determine pearl millet genetic diversity patterns in semi-arid regions of India. *Crop Science* 43:1680–1689.
- vom Brocke, K., Weltzien, E., Christinck, A., Presterl, T. and Geiger, H. H. (2003b). Effects of farmers' seed management on performance and adaptation of pearl millet in Rajasthan, India. *Euphytica* 130:267–280.
- Weltzien, E. (1990). Effect of selection under natural drought conditions in pearl millet. *Agronomy Abstracts 1990*. p. 115.
- Weltzien R., E. (1995). Ertragssteigerungen unter marginalen Bedingungen – züchterische Ansätze und Erfahrungen – gen mit Perlhirse. (Productivity increases under marginal conditions: breeding approaches and experiences with pearl millet). *Vorträge für Pflanzenzüchtung* 31:116–128.
- Weltzien R., E. (2000). Supporting farmers' genetic resources management: Experiences with pearl millet in India. In *Encouraging Diversity: the Conservation and Development of Plant Genetic Resources*, 189–193 (Eds. C. Almekinders and W. de Boef) London: Intermediate Technology Publications.
- Weltzien R., E. and Hash, C. T. (1995). Co-operative breeding of open-pollinated varieties. In *Eighth EARSAM Regional Workshop on Sorghum and Millets, 30 Oct–5 Nov 1992, Wad Medani, Sudan*, Patancheru, India: International Crops Research Institute for the Semi-arid Tropics, 73–76
- Wilson, J. P., Burton, G. W., Zongo, J. D. and Dicko, I. O. (1990). Diversity among pearl millet landraces collected in Central Burkina Faso. *Crop Science* 30:40–43.
- Witcombe, J. R. and Weltzien, E. (1989). Population improvement in pearl millet (*Pennisetum glaucum* (L.) R. Br.) in India. Paper presented at *Sixth International Congress of SABRAO. August 21–25, 1989, Tsukuba, Japan.*
- Yadav, O. P. (2004). CZP 9802 – a new drought-tolerant cultivar of pearl millet. *Indian Farming* 54:15–17.
- Yadav, O. P. (2007). Genetic diversification of landrace-based populations of pearl millet (*Pennisetum glaucum* L. R. Br.) to enhance productivity and adaptation to arid zone environments. *Indian Journal of Genetics and Plant Breeding* 67:358–364.
- Yadav, O. P. (2008). Performance of landraces, exotic elite populations and their crosses in pearl millet (*Pennisetum glaucum*) in drought and non-drought conditions. *Plant Breeding* 127:208–210.
- Yadav, O. P. and Weltzien, R., E. (1997). Performance of two introgressed populations of pearl millet in contrasting environments. *International Sorghum and Millets Newsletter* 38:110–112.
- Yadav, O. P. and Weltzien R., E. (1998). New pearl millet populations for Rajasthan, India. *Integrated Systems Project Report Series no. 10. International Crops Research Institute for the Semi-Arid Tropics, Patancheru India.*
- Yadav, O. P. and Weltzien, R., E. (2000). Differential response of pearl millet landrace-based populations and high yielding varieties in contrasting environments. *Annals of Arid Zone* 39:39–45.
- Yadav, O. P. and Bidinger, F. R. (2007). Utilization, diversification and improvement of landraces for enhancing pearl millet productivity in arid environments. *Annals of Arid Zone* 46:49–57.

- Yadav, O. P. and Bidinger, F. R. (2008). Dual-purpose landraces of pearl millet (*Pennisetum glaucum*) as sources of high stover and grain yield for arid zone environments. *Plant Genetic Resources: Characterization and Utilization* 6:73–78.
- Yadav, O. P., Weltzien R., E., Bidinger, F. R. and Mahalakshmi, V. (2000). Heterosis in landrace-based topcross hybrids of pearl millet across arid environments. *Euphytica* 112:285–295.
- Yadav, R. S., Hash, C. T., Bidinger, F. R., Cavan, G. P., and Howarth, C. J. (2002). Quantitative trait loci associated with traits determining grain and stover yield in pearl millet under terminal drought stress conditions. *Theoretical and Applied Genetics* 104:67–83.
- Yadav, O. P., Weltzien, R., E. and Bidinger, F. R. (2003a). Genetic variation in drought response of landraces of pearl millet (*Pennisetum glaucum*). *Indian Journal of Genetics and Plant Breeding* 63:37–40.
- Yadav, O. P., Bidinger, F. R. and Sharma, MM. (2003b). Male-sterile seed parents for breeding landrace-based topcross hybrids of pearl millet (*Pennisetum glaucum*) for the arid zone. III. Matching A-lines and specific target environments. *Indian Journal of Genetics and Plant Breeding* 63:106–114.
- Yadav, O. P., Weltzien R., E. and Bidinger, F. R. (2004a). Diversity among pearl millet landraces collected in northwestern India. *Annals of Arid Zone* 43:45–53.
- Yadav, R. S., Hash, C. T., Bidinger, F. R., Devos, K. M., and Howarth, C. J. (2004b). 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.