1464

Pearl millet *(Pennisetum glaucum)* — a cereal of the Sahel

J. M. J. DE WET, F. R. BIDINGER AND J. M. PEACOCK

Cereals Program, International Crops Research Institute for the Semi-arid Tropics, Patancheru P.O., Andhra Pradesh 502 324, India

DE WET, J. M. J., BIDINGER, F. R. and PEACOCK, J. M., 1991. Pearl millet *(Pennisetum glaucum)* — a cereal of the Sahel. In considering the role of grasses in the containment and retrieval of deserts it is clear that pearl millet has been selected by farmers on the fringes of the Sahara for its adaptability to drought and high temperature. As a consequence, landraces are characterized by wild-type adaptations such as the production of large numbers of small seeds, long seed viability and seed dormancy under conditions of low humidity and high temperatures, rapid seed germination and growth when sufficient moisture becomes available, seedling survival under high temperatures, completion of a life cycle in as little as 60 days, and the ability to fill grain under extreme heat and drought stress, all of which allow for survival in this harsh environment. Many plant breeders would argue that these rather conservative ecological traits should be selected against. This is not to say we should not develop millets that are more resistant to insects and diseases and are higher yielding than the traditional varieties, but the emphasis must be on the retention of the high stability of yield under low inputs. We believe that this can be done, ensuring that pearl millet remains one of the most important crop species in the desert regions of the tropics.

KEYWORDS:— Adaptation — domestication — drought stress — heat stress — pearl millet — *Pennisetum glaucum*.

CONTENTS

INTRODUCTION

The genus *Pennisetum* L. Rich is distributed throughout the tropics and subtropics of the world. The African *P. glaucum* (Linn.) R. Br. was domesticated as pearl or bulrush millet. It is adapted to areas of the Old World arid and semi-arid tropics where no other cereal will consistently produce a harvest

Desertified Grasslands: Their Biology and Management
ISBN 0-12-168570-5

because of the low annual rainfall and the high temperatures during the growing season. Pearl millet is sown on c. 14 million ha in Africa and 11 million ha in India and Pakistan where annual rainfall varies from 300 to 800 mm during the growing season. Where annual rainfall exceeds 600 mm, pearl millet is usually replaced by *Sorghum bicolor* (Linn.) Moench (sorghum), and where rainfall is above 1200 mm *Eleusine coracana* (Linn.) Gaertner (finger millet) or *Zea mays* Linn. (maize) becomes the common cereal under rainfed agriculture in the tropics of Africa and Asia. Nevertheless, average yields of pearl millet compare favourably with those of sorghum or finger millet. The origins, distribution and mechanisms of adaptation to extreme heat and drought of this remarkable cereal are discussed in this paper.

TAXONOMY

Pennisetum glaucum is extensively variable. Stapf & Hubbard (1934) recognized the complex to include 13 cultivated, 15 weed (intermediate between cultivated and wild) and six wild annual taxa. Clayton (1972) combined the 15 cultivated taxa into *P. americanum* (Linn.) Leeke, divided the 15 weedy taxa between *P. stenostachyum* (Klotzsch ex A. Br.) Stapf & Hubbard and *P. dalzielii* Stapf & Hubbard, and included the six wild taxa in *P. fallax* (Fig. & de Not.) Stapf & Hubbard and *P. violaceum* (Lam.) L. Rich. Brunken (1977) demonstrated that the five taxa recognized by Clayton (1972) are conspecific. He recognized *P. americanum* subsp. *americanum* to include all cultivated taxa, subsp. *monodii* (Maire) Brunken to include close wild relatives, and subsp. *stenostachyum* (Klotzsch ex A. Br. & Bouche) Brunken to include plants that are morphologically intermediate between wild and cultivated taxa. Clayton & Renvoize (1986) indicated that *P. americanum* is not a taxonomically valid name for cultivated pearl millet. The correct name is *P. glaucum* (Linn.) R. Brown.

MORPHOLOGY AND DISTRIBUTION

Pennisetum glaucum is native along the southern fringes of the Sahara. Since domestication pearl millet has been distributed across the semi-arid tropics of Africa, and was introduced as a cereal into the South Asian continent.

The species is characterized by involucres composed of bristles that each enclose one to nine spikelets. Wild *P. glaucum* is distinguished from weed and cultivated taxa by its small, elliptic grains, and sessile involucres. Weedy taxa grade morphologically into wild or cultivated taxa. The agricultural weeds known as shibras in West Africa often resemble cultivated pearl millet except for their ability of natural seed dispersal. The involucres of cultivated pearl millet do not, in comparison, disarticulate at maturity.

Wild taxa are widely distributed in the Sahelo-Sudanian (350–600 mm rainfall) zone of West Africa and extend into the Sudanian (600–800 mm) bioclimatic zone from coastal Senegal and Mauritania to north-eastern Ethiopia (Brunken, 1977). They also occur along the foothills of mountains in the Central Sahara (Clayton, 1972). Wild taxa are aggressive colonizers of disturbed habitats. They are common weeds around villages and along the edges of cultivated fields. Clayton (1972) distinguished between *P. fallax* and

P. violaceum on the basis of bristle pubescence. Brunken (1977), however, demonstrated that bristle pubescence is often a continuously variable trait in large populations.

The weedy shibras are a complex of hybrids between cultivated pearl millet and its close wild relatives, genetic segregants of such hybrids, and their stabilized derivatives. Shibras are confined to Africa. They are common in the cultivated pearl millet zone of West Africa and the Sudan. They also occur in southern Angola and Namibia, but did not accompany pearl millet to Pakistan or India.

Cultivated pearl millet is extensively variable morphologically (Brunken, 1977; Clement, 1985; Marchais & Tostain, 1985). Inflorescences range from cylindrical to broadly elliptic, and from 5 to 200 cm long. Large inflorescences are commonly produced on plants with single culms, while small- to medium-size inflorescences are produced on plants that tiller.

Brunken, de Wet & Harlan (1977) recognize four races of pearl millet. Race typhoides is widely distributed, and morphologically the most variable cultivated race of pearl millet. It is characterized by obovate caryopses that are obtuse and terete in cross section. Inflorescences are variable in length, but usually several times longer than wide, and more or less cylindrical. Less common are plants with short inflorescences that are almost elliptic. Race typhoides extends across the range of pearl millet cultivation in Africa, and into the Indian subcontinent. Race nigritarum differs from typhoides primarily in having obovate caryopses that are angular in cross section. It is the dominant pearl millet of the eastern Sahel from Sudan to Nigeria. The principal pearl millet west of Nigeria is race globosum with large, globose caryopses, and commonly large, candle-shaped inflorescences. The common pearl millet in Sierra Leone, Senegal and Mauritania has oblanceolate caryopses with the apex acute. It is recognized as race leonis.

DOMESTICATION

Botanical evidence suggests that the *P. fallax–P. violaceum* complex is the progenitor of domesticated pearl millet. These wild taxa are distributed across the Sahel and along the central highlands in the Saharan desert (Clayton, 1972). They probably had a more northern distribution at the time when pearl millet was domesticated. Analyses of pollen samples suggest that the Sahara is presently in a dry phase that started about 5000 years ago (Clark, 1976). Pearl millet could have been domesticated anywhere along the southern fringes of the Sahara.

Clark (1962) suggests that cereal cultivation spread from the Near East to North Africa during the 5th millennium BC, and subsequently became widely established across North Africa. Cereals grown were wheat and barley adapted to the winter rainfall regime that dominates the region. With the onset of a dry phase in North Africa, cultivation of these Mediterranean cereals eventually became confined to the coastal belt, and those farmers forced south by the expanding desert abandoned wheat and barley, and domesticated tropical grasses as cereals (Clark, 1964). The first tropical grass species encountered along the southern fringes of the expanding desert that lend itself to domestication was *P. glaucum*.

Wild *P. glaucum* is an aggressive colonizer of disturbed habitats, and preadapted to man-disturbed habitats. Its colonizing ability resulted in large, continuous populations that facilitated harvesting as a wild cereal. Munson (1976) presents archaeological evidence of its use as a wild cereal by people along the southwestern fringes of the Sahara dating as far back as 3000 years, and Davies (1968) reports archaeological remains of cultivated pearl millet in northern Ghana dated about the same time. Race typhoides includes relics of the oldest cultivated pearl millets. It was the progenitor of the West African cultivated races, became widely distributed across the semi-arid tropics of Africa, and probably reaching India some 2500 years ago (Rao *et al.*, 1963).

Pearl millet owes its success as a cereal to the original adaptation of its wild progenitors to heat and drought stress. Wild pearl millet is a typical desert grass. It produces large numbers of caryopses that can withstand extreme heat and drought, and will remain dormant in the soil until conditions become favourable for germination. Caryopses germinate rapidly after the first good rains of the season, and the seedling quickly extend roots into the subsurface soil layers. Plants tiller profusely, can go dormant under severe stress, and will produce new tillers when conditions again become favourable for growth and reproduction. Cultivated *P. glaucum* retained these adaptations to heat and drought stress.

The strategy for adaptation in cultivated pearl millet is opportunism with respect to moisture availability, and tolerance with respect to high temperature. The cereal is characterized by rapid growth and development at the elevated temperatures characteristic of the Sahel. This combined with its heat tolerance allows it to take advantage of the short growing season, to survive short periods of severe drought stress, and to resume growth when water again becomes available. Specific characteristics such as seed viability, seed germination, seedling survival, rapid vegetative and reproductive development, and good seed set under moisture and heat stress contribute to the success of the cereal in the harsh agricultural environment where it is grown.

SEEDLING ESTABLISHMENT AND SURVIVAL

Caryopses of pearl millet landraces have a dormancy period of up to three months (Burton, 1969). This is rare in domesticated cereals (Harlan, de Wet & Price, 1973). In wild genotypes dormancy prevents germination before adequate moisture for seedling survival becomes available. As a cultivated cereal it prevents germination when planted before adequate rains to sustain growth.

When adequate moisture is available, pearl millet germinates rapidly, and emergence rate is fast in comparison with other cereals. The caryopses require *c.* 18°Cd from imbibition to radicle emergence (Garcia-Huidobro, Monteith & Squire, 1982), and 29°Cd from imbibition to established seedling (Ong & Monteith, 1985). At the characteristic temperatures of the Sahel, this occurs in two days. Optimum temperatures for germination vary little across pearl millet genotypes or races, averaging about 34°C with a base temperature between 8 and 13.5°C, and an upper limit of between 47 and 52°C (Mohamed, Clark & Ong, 1988a). This wide range of germination temperatures allows germination to proceed over the range of soil temperatures to which the caryopses are likely to be exposed. More importantly, it allows for germination to proceed quickly under high soil temperatures, where evaporation of moisture from the seed zone is rapid and survival depends upon rapid extension of the radicle into the lower soil zones which have adequate moisture. Similarly, as soil crust strength increases progressively with surface soil drying, rapid elongation of the hypcotyl/coleoptile allows for successful emergence from the soil (Soman, Peacock & Bidinger, 1984).

Farmers conventionally plant millet with the first good rains of 20 mm or more. This takes advantage of the flush of mineralized nitrogen that occurs on the first wetting of the soil. If the initial rain proves to be an isolated event, soils dry rapidly under the high levels of radiation characteristic of the end of the dry season, and soil surface temperatures rise to as high as 55°C at midday (Soman & Peacock, 1985). Such temperatures combined with the lack of moisture in the root zone to sustain transpiration and plant cooling, can result in high levels of seedling mortality. Although pearl millet has relatively better thermotolerance than other cereals, failure of crop stands because of heat stress is not uncommon in arid regions.

High soil surface temperatures affect the movement of carbohydrates to the root, and death is probably caused by the inability of the root to maintain growth and water uptake. There is considerable genetic variation in pearl millet to tolerance of high soil surface temperatures, with landraces from arid environments possessing the greatest tolerance. This may be related to their superior ability to synthesize a special set of heat shock proteins (Howarth, 1989). Although the role of these heat shock proteins is not fully understood, a current hypothesis is that they protect the protein synthetic machinery of the cell. It is thought that heat stress causes denaturing and precipitation of proteins, which in some way obstructs the normal phloem transport of carbohydrates from the leaves to the root, leading to the reduction and the eventual cessation of root growth (Peacock *et al.*, 1990). Research is underway to characterize these heat shock proteins and to identify the genes that control their synthesis.

Absolute growth rates during the seedling stage (the period between emergence and secondary root emergence) in pearl millet are lower than in some other tropical cereals (Siband, 1979), primarily because of smaller seed size. For the same reason the crop is completely dependent upon the soil for its mineral nutrition from five days after germination (Siband, 1979) and this is one of the most vulnerable periods for the crop. Not until tillers appear and the adventitious root system is initiated, does the crop begin to have either a canopy or a root system capable of supporting sufficient crop growth rates to assure survival. Farmer strategy is customarily to use very high sowing rates in the hope that sufficient seedlings will survive to assure an adequate plant stand, analogous to the high seed production and poor seed dispersal strategy of wild pearl millet (Soman *et al.*, 1984).

VEGETATIVE GROWTH

Maximum leaf growth rates (7–10 mm h^{-1}) occur between 32 and 35°C and are invariably linear between the base temperature and this optimum. These high leaf growth rates are important adaptations in overcoming early seedling death. A vigorously growing seedling seems to acquire the ability to survive high soil temperatures. There is a strong correlation between the rate of germination and the rate of leaf production (Mohamed, Clark & Ong, 1988b). At later stages of growth, a vigorous vegetative phase is less important for survival than rapid seedling growth, but it does influence final grain yields.

Another adpatation for survival in the hot semi-arid tropics that pearl millet inherited from its wild ancestors is the ability to tiller. This is particularly important to compensate for a reduction in population size due to seedling mortality, or to compensate for a loss of production on the main shoot due to water stress (Mahalakshmi & Bidinger, 1986). Tillers can account for 60–70% of the total leaf area and more than 50% of the grain production. Temperature influences tiller production. In Indian cultivars tiller number is closely related to thermal time, the first tiller merges at about 200°Cd and each subsequent tiller at a rate of one per 47°Cd. Cessation of tiller development occurs at about 430°Cd (Ong, 1984). Genetic variation in these rates has been demonstrated (Ong & Monteith, 1985). During reproductive development, axillary tillers may form on the upper nodes of the main stem. These tillers are of considerable practical importance as they allow rapid new growth after periods of dormancy induced by severe heat and drought stress.

Pearl millet has a typical graminaceous root system. The caryopsis produces one seminal root or radicle which supports the plant until the secondary root system becomes effective about 20 days after emergence. The secondary roots develop from primordia at the base of each tiller and these begin to appear 10–14 days from emergence. Root penetration is rapid, reaching a maximum velocity of 3.4 cm day^{-1}, and by 33 days after emergence roots reached a depth of 1 m (Chopart, 1983). Pearl millet not only has a very deep primary root system, it also has an extensive secondary surface root system close to the surface, with between 3 and 10 m of root dm^{-3} in the top 30 cm of the profile (Chopart, 1983). Maximum rooting depth in this study was 1.8 m, but there are reports of maximum rooting depths of more than 3.0 m in mature plants pearl millet (Begg, 1965). This allows the plant to extract deep accumulations of moisture and nitrate nitrogen under conditions of terminal drought stress, and to harvest water from small showers that occur in the arid tropics.

REPRODUCTIVE DEVELOPMENT

The initiation of reproductive structures on the shoot apex in landraces of pearl millet is under photoperiodic control (Ong & Everard, 1979). This provides an effective mechanism to continually adjust the crop to the risks of flowering either too early or too late across a broad range of season lengths (60–180 days). Early flowering increases the risk of poor seed yield, insect attack and bird damage. Late flowering increases the risk of drought and heat stress during grain filling.

A study of the time of flowering of local sorghum landraces in southern Nigeria indicated that there was a close relationship between onset of flowering and the time of ending of the rains across a range of latitudes and season lengths (Curtis, 1968). Pearl millet appears to have evolved a similar adaptation. An early initiation of the reproductive phase limits the ability of a genotype to adjust to the effects of possible early season droughts (Mahalakshmi & Bidinger, 1985), but it is effective in assuring that the grain will mature in short-season environments. It also reduces total biomass production, but does not necessarily reduce grain yield potential (Craufurd & Bidinger, 1988).

The rates of spikelet initiation and development in pearl millet are under temperature control, as is the length of the developmental period between floral initiation and flowering. High temperatures result in faster rates of development, but often a reduction in total growth (and yield) because of a reduced reproductive growth period. Under arid conditions the ability of the crop to complete this critical growth phase in 20–25 days is highly advantageous.

The effects of intermittent drought stress during the reproductive development phase on grain yield are largely dependent on the time of onset and termination of the stress. The later the stress is terminated, the greater is the reduction in yield on the main shoot panicle, and the smaller is the potential for compensation for this loss by an increase in production by tillers (Mahalakshmi, Bidinger & Raju, 1987). The development of tillers is arrested by stress during either the vegetative or early reproductive stage, but the species retains the potential to resume normal development when conditions again become favourable (Mahalakshmi & Bidinger, 1985). Complete compensation is possible when the stress is terminated before flowering, and when there is adequate moisture available to complete grain filling on these tillers. Stress during the reproductive period is a serious limitation to grain yield, primarily when the total length of the period of available moisture is substantially reduced. In such a situation, it is the lack of moisture during grain filling on the tillers that is responsible for yield reduction, and not the mid-season stress *per se*.

FLOWERING AND GRAIN FILLING

Flowering in pearl millet is protogyneous, with the stigmas emerging several days before anther emergence and pollen shed. This assures a high degree of cross pollination. Flowering in genotypes with synchronous tiller development takes place over a period of 10–15 days, and is considerably longer in genotypes with asynchronous development of tillers (Ramond, 1968). These adaptations provide pearl millet with considerable buffering against stress occurring at flowering. Pollen shed occurs early in the morning, avoiding the harsh midday conditions. Pollen viability and pollination does not seem to be sensitive to the temperature stress normally encountered by pearl millet.

The grain filling period normally requires about 300°Cd. This is accomplished in about 20 days at an average (25°C) mean temperature. However, pearl millet is capable of producing viable, if only small grains (4–5 g per 100 grains) in 15 days from flowering. The effects of both high temperature stress (Fussell, Pearson & Norman, 1980), and drought stress (Bieler & Fussell, 1989) on grain fill seem to be almost entirely on the duration of grain growth, not on growth rate. The crop has evolved adaptations to assure the production of a large number of viable seed, at the expense of a large seed size, under stress conditions. This rapid grain filling ability is undoubtedly one of the major adaptive features of the crop to arid environments.

Grain yields are significantly reduced by drought and temperature stress during flowering and grain filling (Mahalakshmi et al., 1987). Comparisons among genotypes indicate that differences in time of flowering under stress during grain fill are a major reason for yield differences among cultivars (Bidinger et al., 1987). This suggests that the high degree of variability in time to flowering in landrace populations is due to natural selection for earlier flowering and drought escaping in dry years, and farmer selection for later flowering and plants with large inflorescences in wet years. Also under such terminal stress conditions, asynchronous tillering that provides adaptation to stress before flowering, becomes a liability. The main grain loss is in tillers that flower late and are exposed to an increasing moisture deficit.

REFERENCES

BEGG, J. E., 1965. The growth and development of a crop of bulrush millet (*Pennisetum typhoides* S. & H.). *Journal of Agricultural Sciences, 65:* 341–349.

BIDINGER, F. R., MAHALAKSHMI, V. & RAO, G. D. P., 1987. Assessment of drought resistance in pearl millet (*Pennisetum americanum* (L.) Leeke). I. Factors affecting yields under stress. *Australian Journal of Agricultural Research, 38:* 37–48.

BIELER, P. & FUSSELL, L. K., 1989. Screening pearl millet (*Pennisetum glaucum* (L.) R. Br.) for post flowering drought response in West Africa. *Paper presented at Regional Pearl Millet Workshop*, Sadore (Niamey) Niger, 4–7 September 1989. Niamey, Niger: International Crops Research Institute for Semi-arid Tropics.

BRUNKEN, J. N., 1977. A systematic study of *Pennisetum* sect. *Pennisetum* (Gramineae). *American Journal of Botany, 64:* 161–167.

BRUNKEN, J. N., DE WET, J. M. J. & HARLAN, J. R., 1977. The morphology and domestication of pearl millet. *Economic Botany, 31:* 163–174.

BURTON, C. W., 1969. Breaking dormancy in seeds of pearl millet, *Pennisetum typhoides. Crop Science, 9:* 659–664.

CHOPART, J. L., 1983. Etude du système racinaire du mil *(Pennisetum typhoides)* dans un sol sableux du Senegal. *Agronomique Tropicale, 38:* 37–51.

CLARK, J. D., 1962. The spread of food production in sub-Saharan Africa. *Journal of African History, 3:* 211–228.

CLARK, J. D., 1964. The prehistoric origins of African culture. *Journal of African History, 5:* 161–183.

CLARK, J. D., 1976. Prehistoric populations and pressures favoring plant domestication in Africa. In J. R. Harlan, J. M. J. de Wet & A. B. L. Stemler (Eds), *The Origins of African Plant Domestication,* 67–105. The Hague: Mouton Press.

CLAYTON, W. D., 1972. Gramineae. *Pennisetum.* In F. N. Hepper (Ed.), *Flora of West Tropical Africa, 3,* part 2: 170–465. London: Crown Agents.

CLAYTON, W. D. & RENVOIZE, S. A., 1986. *Genera Graminum. Grasses of the World.* London: H.M.S.O.

CLEMENT, J. C., 1985. *Les Mils Penicillaires de L'Afrique de L'Ouest.* Rome: I.B.P.G.R.-O.R.S.T.O.M.

CRAUFURD, P. Q. & BIDINGER, R. F., 1988. Effect of the duration of the vegetative phase on shoot growth, development and yield in pearl millet (*Pennisetum americanum* (L.) Leeke). *Journal of Experimental Botany, 39:* 124–139.

CURTIS, D. L., 1968. The relationship between date of heading of Nigerian sorghums and the duration of the growing season. *Journal of Applied Ecology, 5:* 215–226.

DAVIES, O., 1968. The origins of agriculture in West Africa. *Current Anthropology, 9:* 479–482.

FUSSELL, L. K., PEARSON, G. J. & NORMAN, M. J. T., 1980, Effect of temperature during various growth stages on grain development and yield of *Pennisetum americanum* (Pearl millet). *Journal of Experimental Botany, 31:* 621–633.

GARCIA-HUIDOBRO, MONTEITH, J. L. & SQUIRE, G. R., 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.). III. Inhibition of germination by short exposure to high temperature. *Journal of Experimental Botany, 36:* 338–343.

HARLAN, J. R., DE WET, J. M. J. & PRICE, E. G., 1973. Comparative evolution of cereals. *Evolution, 27:* 311–325.

HOWARTH, C., 1989. Heat shock proteins in *Sorghum bicolor* and *Pennisetum americanum*. I. Genotypic and developmental variation during seed germination. *Plant, Cell and Environment, 12:* 471–477.

MAHALAKSHMI, V. & BIDINGER, F. R., 1985. Flowering response of pearl millet to water stress during panicle development. *Annals of Applied Biology, 106:* 571–578.

MAHALAKSHMI, V. & BIDINGER, F. R., 1986. Water deficit during panicle development in pearl millet: Yield compensation by tillers. *Journal of Agricultural Sciences, 106:* 113–119.

MAHALAKSHMI, V., BIDINGER, F. R. & RAJU, D. S., 1987. Effect of timing of water deficit on pearl millet *(Pennisetum americanum)*. *Field Crops Research, 15:* 327–339.

MARCHAIS, L. & TOSTAIN, S., 1985. Genetic divergence between wild and cultivated pearl millets *(Pennisetum typhoides)*. II. Characters of domestication. *Zeitschrift für Pflanzenzuchtung, 95:* 245–261.

MOHAMED, H. A., CLARK, J. A. & ONG, C. K., 1988a. Genotypic differences in the temperature responses of tropical crops. I. Germination characteristics of groundnut *(Arachis Hypogaea L.)* and pearl millet (*Pennisetum Typhoides* S. & H.). *Journal of Experimental Botany, 39:* 1121–1128.

MOHAMED, H. A., CLARK, J. A. & ONG, C. K., 1988b. Genotypic differences in the temperature responses of tropical crops. II. Seedling emergence and leaf growth of groundnut (*Arachis hypogaea* L.) and pearl millet (*Pennisetum typhoides* S. & H.). *Journal of Experimental Botany, 39:* 1129–1135.

MUNSON, P. J., 1976. Archaeological data on the origins of cultivation in the southwestern Sahara and its implications for West Africa. In J. R. Harlan, J. M. J. de Wet & A. B. L. Stemler (Eds), *The Origins of African Plant Domestication*, 187–210. The Hague: Mouton Press.

ONG, C. K., 1984. Response to temperature in a strand of pearl millet (*Pennisetum typhoides* S. & H.). V. Development and fate of tillers. *Journal of Experimental Botany, 35:* 83–90.

ONG, C. K. & EVERARD, A., 1979. Short day induction of flowering in pearl millet (*Pennisetum typhoides*) and its effect on plant morphology. *Experimental Agriculture, 15:* 401–410.

ONG, C. K. & MONTEITH, J. L., 1985. Response of pearl millet to light and temperature. *Field Crops Research, 11:* 141–160.

PEACOCK, J. M., MILLER, W. B., MATSUDA, K. & ROBINSON, D. L., 1990. Role of heat girdling in early seedling death of sorghum. *Crop Science, 30:* 138–143.

PEARSON, C. J., 1985. Editorial: research and development for yield of pearl millet. *Field Crops Research, 11:* 113–121.

RAMOND, C., 1968. Pour une meilleure connaissance de la croissance et du development des mils Pennisetum. *Agronomique Tropicale, 23:* 844–863.

RAO, S. R., LAL, B. B., NATH, B., GHOSH, S. S. & LAL, K., 1963. Excavation at Rangpur and other explorations in Gujarat. *Bulletin of the Archeological Survey of India, 18/19:* 5–207.

SIBAND, P., 1979. Nutrition minerale des plantudes de mil, mais et sorgho au cours des premier jour de vegetation. *Agronomique Tropicale, 34:* 242–249.

SOMAN, P. & PEACOCK, J. M., 1985. A laboratory technique to screen seedling emergence of sorghum and pearl millet at high soil temperatures. *Experimental Agriculture, 21:* 335–341.

SOMAN, P., JAYACHANDRAN, R., BIDINGER, F. R. & PEACOCK, J. M. 1984. Factors affecting seedling emergence and stand establishment — studies in farmer's fields in Aurepally and Dhandhan during 1981, 1982 and 1983. *I.C.R.I.S.A.T. Internal Report.* Patancheru, India: I.C.R.I.S.A.T.

SOMAN, P., PEACOCK, J. M. & BIDINGER, F. R., 1984. A field technique to screen seedling emergence of pearl millet and sorghum through soil crusts. *Experimental Agriculture, 20:* 327–334.

STAPF, O. & HUBBARD, C. E., 1934. *Pennisetum*. In D. Prain (Ed.), *Flora of Tropical Africa, 9:* 954–1070. London: Crown Agents.