ELSEVIER

Field Crops Research 80 (2003) 33–56

Field Crops Research

www.elsevier.com/locate/fcr

A yield architecture framework to explain adaptation of pearl millet to environmental stress

E.J. van Oosterom[a,b,*], F.R. Bidinger[a], E.R. Weltzien[a,1]

[a]International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India
[b]CSIRO Sustainable Ecosystems/Agricultural Production Systems Research Unit, Long Pocket Laboratories, 120 Meiers Road, Indooroopilly, QLD 4068, Australia

Received 29 May 2002; received in revised form 9 August 2002; accepted 16 August 2002

Abstract

Functional knowledge of the physiological basis of crop adaptation to stress is a prerequisite for exploiting specific adaptation to stress environments in breeding programs. This paper presents an analysis of yield components for pearl millet, to explain the specific adaptation of local landraces to stress environments in Rajasthan, India. Six genotypes, ranging from high-tillering traditional landraces to low-tillering open-pollinated modern cultivars, were grown in 20 experiments, covering a range of non-stress and drought stress patterns. In each experiment, yield components (panicle number, grain number, 100 grain mass) were measured separately for main shoots, basal tillers, and nodal tillers. Under optimum conditions, landraces had a significantly lower grain yield than the cultivars, but no significant differences were observed at yield levels around 1 ton ha^{-1}. This genotype × environment interaction for grain yield was due to a difference in yield strategy, where landraces aimed at minimising the risk of a crop failure under stress conditions, and modern cultivars aimed at maximising yield potential under optimum conditions. A key aspect of the adaptation of landraces was the small size of the main shoot panicle, as it minimised (1) the loss of productive tillers during stem elongation; (2) the delay in anthesis if mid-season drought occurs; and (3) the reduction in panicle productivity of the basal tillers under stress. In addition, a low investment in structural panicle weight, relative to vegetative crop growth rate, promoted the production of nodal tillers, providing a mechanism to compensate for reduced basal tiller productivity if stress occurred around anthesis. A low maximum 100 grain mass also ensured individual grain mass was little affected by environmental conditions. The strategy of the high-tillering landraces carries a yield penalty under optimum conditions, but is expected to minimise the risk of a crop failure, particularly if mid-season drought stress occurs. The yield architecture of low-tillering varieties, by contrast, will be suited to end-of-season drought stress, provided anthesis is early. Application of the above adaptation mechanisms into a breeding program could enable the identification of plant types that match the prevalent stress patterns in the target environments.

Keywords: Breeding; Landraces; Stability; Tillering; Yield components

1. Introduction

Genotype × environment (G × E) interactions for grain yield generally reduce the rate of progress in yield improvement in breeding programs (Basford and

---

[*] Corresponding author. Present address: School of Land and Food Sciences, University of Queensland, Brisbane, Qld 4072, Australia.
E-mail address: erik.van.oosterom@uq.edu.au (E.J. van Oosterom).

[1] Present address: International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), B.P. 320, Bamako, Mali.

PII: S0378-4290(02)00153-3

Cooper, 1998). In programs targeting general adaptation, cross-over G × E interactions complicate selection of superior genotypes from multi-environment trials (Basford and Cooper, 1998), because of the difficulty of selecting test environments that adequately represent the entire target population of environments (TPE) (Cooper and Chapman, 1996). This becomes a greater problem as the frequency of contrasting environments in the TPE increases (Cooper and Chapman, 1996). Such a situation is particularly common in regions where the occurrence of stress is unpredictable, because the effect of stress on growth and yield depends on its timing (Craufurd and Peacock, 1993; Mahalakshmi et al., 1987). Breeding programs targeting specific adaptation can only exploit G × E interactions effectively, if the physiological causes of the interaction are well understood (Basford and Cooper, 1998).

The above impediments of G × E interactions to the efficiency of breeding programs are particularly valid for pearl millet (*Pennisetum americanum* L.) in Rajasthan, the major semi-arid/arid millet producing area in India (FAO and ICRISAT, 1996). Timing and intensity of stress occurrence in this region are highly variable, both between locations and years (Sharma and Pareek, 1993; van Oosterom et al., 1996). The wide variety in pearl millet landraces that have evolved in Rajasthan (Appa Rao et al., 1986; Saxena et al., 1978) is testimony to this. The farmers' choice of cultivar depends heavily on the probability of favourable growing conditions (Kollavalli, 1997). In the arid areas of western Rajasthan, where drought stress is likely to occur but its timing is highly unpredictable (van Oosterom et al., 1996), farmers predominantly grow high-tillering local landraces (Kelley et al., 1996; van Oosterom et al., 1996). In the wetter eastern parts, by contrast, the probability of favourable growing conditions is much higher and drought stress occurs predominantly past-anthesis (van Oosterom et al., 1996). In these areas, farmers prefer genotypes with fewer, larger panicles (van Oosterom et al., 1996; Christinck, 2002) and predominantly grow higher yielding F_1-hybrids or advanced generation hybrids (Kelley et al., 1996; vom Brocke et al., 2002). These geographical differences reflect the common perception among farmers that local landraces are better adapted to harsh conditions, but are unable to capitalise on the additional resources available in good years (Kelley et al., 1996; Kollavalli, 1997; Christinck, 2002). Indeed, Bidinger et al. (1994) and Yadav and Weltzien (2000) demonstrated that germplasm accessions from western Rajasthan on average yielded more grain than low-tillering control cultivars in arid zone environments, but not in more favourable environments. In addition, preferences for plant types (fertile tiller number, panicle size) depend on the importance of fodder for livestock (quantity and quality), competition for human resources (labour for hand-harvesting), and the need to manage multiple objectives of a farm household (risk management), as illustrated by Byerlee and Husain (1993) for farming systems in Pakistan. A high degree of specificity of adaptive traits to environmental stress patterns thus exists.

The development of plant types that are adapted to the prevalent stress patterns of the TPE, while simultaneously meeting farmers' requirements for plant types, is therefore a major thrust of breeding programs targeting specific adaptation (Richards, 1989; Ceccarelli et al., 1991). However, the physiological knowledge of specific genotype responses to environmental stress is often lacking (Boote et al., 2001; Jackson et al., 1996). This is certainly the case for the difference in adaptation pattern between traditional landraces and modern cultivars in pearl millet. van Oosterom et al. (2002) found no difference in radiation use efficiency and biomass partitioning prior to anthesis between contrasting plant types of pearl millet, indicating that a difference in plant type per sé does not explain the low grain yield of landraces under high-input conditions. This is in accordance with results of Craufurd and Bidinger (1988b) that two hybrids with contrasting tillering habit had similar grain yields under conditions without water or nutrient stress. Similarly, Bidinger and Raju (2000) observed across a range of N-treatments and plant densities that plant type of pearl millet was not related to the G × E interaction for grain yield, although contrasting plant types had different ways to adjust yield components to changes in assimilate availability. A better understanding of the crop physiological causes of adaptation of landraces to resource-poor conditions could increase the efficiency of breeding programs targeting specific adaptation.

The objective of this paper is to (1) analyse the observed repeatable G × E interactions for grain yield between traditional landraces and modern cultivars, grown in both favourable and stressed environments and (2) to develop a physiological framework to explain the relationship between plant type and adaptation to specific stress patterns.

2. Materials and methods

2.1. Genotypes

The experiments included six cultivars that were selected for contrasting plant type (production of fertile tillers) and comparable phenology. Three were entirely based on landraces originating from Rajasthan (referred to as landraces), whereas the other three were partly or entirely based on exotic (to western Rajasthan) germplasm (referred to as modern varieties).

The landraces included Nokha Local, ERajPop, and WRajPop. Nokha Local is a pure landrace, collected from a farmer's field in western Rajasthan. It is a high-tillering, dual-purpose open-pollinated population with small seed size, variable seed set, indeterminate growth and extremely high-tillering ability, but is highly susceptible to downy mildew (*Sclerospora aminicola*). ERajPop (Early Rajasthan Population) and WRajPop (Western Rajasthan Population) are breeding populations derived from a small number of selected landrace accessions from Rajasthan (Yadav and Weltzien, 1998): ERajPop has been selected for early flowering, whereas WRajPop is based on populations collected from the dry western part of Rajasthan (Yadav and Weltzien, 1998). Both populations have undergone several cycles of full-sib progeny-based recurrent selection for grain yield. They have a plant type comparable to Nokha Local (high-tillering with small seed size), although panicle size is generally larger, due to selection for seed set and grain yield.

The modern varieties comprised of three open-pollinated cultivars: RCB-IC 911, WC-C 75, and CZ-IC 922. RCB-IC 911 is the product of three generations of modified mass selection in the Bold Seeded Early Composite, carried out in Jaipur, Rajasthan (Yadav and Weltzien, 1998). It is entirely based on *Iniadi* germplasm from Togo and Ghana, which is characterised by thick stems, large leaves and grain size, but low-tillering capacity (Andrews and Anand Kumar, 1996) and thus represents a plant type opposite to that of the landraces. WC-C 75 was selected at Coimbatore (south India) from seven full-sib progenies of the World Composite (Andrews et al., 1985). It is based largely on early flowering Nigerian landrace material and has a low-tillering, large panicle plant type similar to RCB-IC 911. CZ-IC 922 was bred from 14 S_1-progenies of EC-C6 (Early Composite Cycle 6), selected at the Central Arid Zone Research Institute (CAZRI) at Jodhpur (Rajasthan, India). CZ-IC 922 is largely based on North Indian material, although not only from Rajasthan. Its plant type and tillering habit are intermediate between landrace-based genotypes on the one hand and RCB-IC 911 and WC-C 75 on the other.

Although the six cultivars were selected for comparable phenology, ERajPop was generally the first and WC-C 75 the last to reach anthesis. Across all experiments, the average number of days from emergence to the median anthesis date of the main shoot was 45.3 for ERajPop, 53.6 for WC-C 75, and 48–49 for the other four cultivars.

2.2. Experimental details

The cultivars were grown in 20 experiments (location × year × management combinations), conducted at Patancheru (17°53′N) in central India and at Jodhpur (26°18′N), Mandore (26°18′N), Fatehpur-Shekawati (27°17′N), and Pali (25°50′N) in Rajasthan, northwest India (Table 1).

Most experiments were grown during the rainy season. They were sown at the start of the rainy season in June or July (Table 1) and were generally rainfed. At Patancheru 1994, two additional experiments were carried out in a rain-out shelter. One was protected from rain soon after emergence until anthesis, whereas the other was protected from anthesis onwards. In addition, experiments were conducted during the dry seasons of 1994 (two experiments) and 1995 (one experiment) at Patancheru (Table 1). The two 1994 experiments were fully irrigated and included a normal and extended daylength, which mimicked daylength encountered in Rajasthan during the rainy season. In the 1995 dry season, drought stress was imposed 4 weeks after emergence, and was only temporarily relieved by irrigation and some rain around anthesis. Irrigation (when used) was applied

Table 1

Date of sowing, rainfall before anthesis (period from 5 days before sowing until average date of anthesis of the main shoots) and after anthesis (20-day period), plus the mean biomass, grain yield (total and nodal tillers), 100 grain mass, grain number, number of fertile basal tillers per plant, grain number per panicle, and plant density, averaged over six pearl millet cultivars, grown in 20 experiments across India

	Date of sowing	Rainfall			Grain yield		100 grain mass (g)	Grain number (per square metre)	Basal tiller (per plant)	Grain number (per pan)[a]	Plant number (per square metre)
		Pre-anthesis (mm)	Post-anthesis (mm)	Biomass ($g\ m^{-2}$)	Total ($g\ m^{-2}$)	Nodal ($g\ m^{-2}$)					
Patancheru no stress (17°53′N)											
1994 dry season	25 January 1994	121.2[b]	154.0[b]	908	364	42	0.78	46474	3.07	1822	6.7
1994 dry season ext. daylength	25 January 1994	171.2[b]	160.8[b]	1135	350	46	0.79	44089	2.00	2162	7.1
1994 rainy season	15 June 1994	281.3[c]	100.5	1025	426	62	0.84	51403	2.80	2029	7.0
1995 rainy season	20 June 1995	385.6	175.2	1026	414	36	0.90	45838	2.53	2145	6.2
Patancheru drought stress (17°53′N)											
1994 rainy season early stress	22 June 1994	98.1[c]	169.7	538	241	19	0.78	30413	1.77	1148	10.1
1994 rainy season late stress	22 June 1994	164.6[c]	0.0	495	214	8	0.75	28659	0.97	1520	10.1
1995 dry season	26 January 1995	192.0[b]	94.4[b]	461	181	13	0.67	27028	1.63	1310	8.3
Jodhpur, Rajasthan (26°18′N)											
1994 rainy season	03 July 1994	415.6	107.7	855	221	2	0.77	29642	1.34	2553	5.3
1995 rainy season	21 July 1995	309.9[d]	0.0	409	147	2	0.70	20866	0.71	1774	7.3
1996 rainy season	01 July 1996	409.5	14.3	519	170	3	0.68	24752	0.22	2113	9.7
1997 rainy season low fertility	27 July 1997	284.9[e]	13.9[e]	358	76	3	0.78	9713	0.72	948	6.5
1998 rainy season	2 August 1998	145.4	26.4	434	166	6	0.74	22574	1.23	1684	6.8
Mandore, Rajasthan (26°18′N)											
1998 rainy season	3 July 1998	98.4	83.2	356	70	2	0.48	14501	0.84	1199	6.8
Fatehpur, Rajasthan (27°17′N)											
1994 rainy season	14 July 1994	323.1	39.3	496	157	8	0.82	19184	1.10	1909	4.9
1995 rainy season	20 July 1995	278.4	0.0	506	182	5	0.65	27098	1.69	2122	5.0
1995 rainy season low fertility	20 July 1995	278.4[e]	0.0[e]	331	119	5	0.78	15520	1.09	1807	4.4
1996 rainy season	29 June 1996	197.1	65.2	756	220	12	0.89	25286	0.90	2460	5.7
1996 rainy season	27 June 1996	217.0	86.8	1008	264	14	0.87	31085	1.62	2176	5.7
Pali, Rajasthan (25°50′N)											
1996 rainy season	10 July 1996	517.3[e]	12.0[e]	420	160	7	0.86	18939	0.53	2004	6.4
1997 rainy season	21 July 1997	N/A[f]	N/A[f]	575	154	5	0.71	21336	1.23	1170	8.5

[a] Calculated as total grain number (including nodal tillers), divided by the number of plants and productive basal tillers.

[b] Predominantly irrigation. Amount of water applied estimated from duration of irrigation, assuming a rate of $17.5\ mm\ h^{-1}$ for sprinkler irrigation and $50\ mm\ h^{-1}$ for furrow irrigation.

[c] Includes 8 mm irrigation around anthesis.

[d] Includes 10 mm of irrigation, applied 1 week before emergence.

[e] Date of flowering was not observed, and was estimated from other experiments.

[f] N/A = not available.

by overhead sprinklers during the first weeks after sowing, and by furrow irrigation thereafter. For all experiments (except Pali 1997) daily weather records on temperature and rainfall were available. Pre-anthesis (from 5 days prior to sowing until anthesis) rainfall (including irrigation) ranged from <100 to >400 mm, whereas post-anthesis rainfall (first 20 days after anthesis) ranged from 0 to 175 mm (Table 1).

At Patancheru, experiments were sown on an alfisol (clayey-skeletal mixed isohyperthermic Udic Rhodustalf) on ridges 60–75 cm apart; the only exceptions were the two experiments in the rain-out shelter, where, due to limited space, row-spacing was 50 cm, and no ridges were used. Experiments generally received a pre-sowing basal application of 150 kg ha^{-1} di-ammonium phosphate (28:28:0 NPK) and a top dressing of 100 kg ha^{-1} urea at the start of rapid canopy growth. In Rajasthan, experiments were sown on predominantly sandy soils (Psamment) at a row spacing of 60–65 cm, without ridges. Most experiments in Rajasthan received a pre-sowing basal application of 100 kg ha^{-1} mono-ammonium phosphate (18:46:0 NPK) and a topdressing of 50 kg ha^{-1} urea, providing a total of 41 kg N ha^{-1}. Actual fertiliser applications, however, varied with moisture conditions and nitrogen applications ranged from 26 to 62 kg ha^{-1}. In two experiments, however, fertility was kept at a low level (Table 1): at Fatehpur 1995, only a topdressing of urea (15 kg N ha^{-1}) was applied, whereas the experiment at Jodhpur 1997 was sown in a low-fertility field and did not receive any additional fertiliser. All crops were sown at a high seed rate, and thinned back to the desired plant density around 10–14 days after emergence (DAE). Because of the differences in row spacing, plant density ranged from approximately 5–10 plants m^{-2}. The plot size was two (Patancheru) or four (Rajasthan) rows of 4 m length, the difference reflecting the higher probability of poor plant establishment in Rajasthan. All experiments were laid out as a randomized complete block design with three replications, although in a few cases only two replications could be harvested.

Prior to sowing, seeds at Patancheru were treated with metalaxyl (Ridomil) against downy mildew. No such treatment was done at Rajasthan, because of the generally low disease pressure. Weeds were controlled manually, and no significant outbreak of any pest or disease occurred in any of the experiments. At Patancheru, plants were supported by ropes during grain filling to avoid negative effects of lodging on grain yield formation.

2.3. Observations and data analyses

2.3.1. Tiller appearance, final leaf number, and anthesis date for individual axes

Observations on the time of tiller appearance and final leaf number per axis were done in the rainy season of 1995 at Patancheru and Fatehpur. Five plants per plot were labelled soon after thinning, and the date of appearance of each primary basal tiller was estimated through regular (three times a week) inspections of the plants. For the main shoot, the date of crop emergence was used as the appearance date. For each productive axis the date of anthesis (stigma's visible from 50% of the florets) and the final number of leaves were recorded.

For each cultivar, the maximum number of primary basal tillers that appeared per plant and the fraction that produced a panicle were calculated, to determine if genotypic and environmental differences in tillering were associated with differences in tiller appearance or in tiller survival. The anthesis dates were used to analyse the phenology of the nodal tillers in relation to that of the main shoot and basal tillers, to assess their importance as a stress escape mechanism. The timing of anthesis was expresses in degree days (°C d) from emergence, using 10, 33, and 47 °C as the minimum, optimum, and maximum temperature, respectively (Garcia-Huidobro et al., 1982; Ong, 1983a,b; Mohamed et al., 1988).

2.3.2. Yield components

In all but four of the experiments, the anthesis date of individual panicles was estimated from observations three times per week and recorded on colour-coded tags (to distinguish main shoots, basal tillers, and nodal tillers) that were tied around the peduncle. Due to the high number of nodal tillers produced under optimum conditions at Patancheru, nodal tillers were not tagged in some of the experiments at this location.

At maturity, panicles were hand-harvested and panicles were grouped by type (main shoot, basal tillers, and nodal tillers) and anthesis date. For experiments where individual panicles were not tagged at anthesis, panicles were grouped by type only. In general, the entire plot was harvested, except for areas with poor plant stand and parts of rows that were not properly bordered. The number of panicles per sample was counted and samples were then oven-dried for at least 2 days at 80 °C. After obtaining panicle dry weight, panicles were threshed and grain yield determined. Individual grain mass was determined from three counts of 100 grains, or from all grains if the sample contained <300 grains. Grain number was derived from grain yield and grain mass.

After all panicles were harvested, a stover sample was taken from each plot. Fresh weight was measured, and a subsample was taken to obtain the dry matter percentage. Total biomass was calculated as the sum of stover weight and panicle weight.

The vegetative crop growth rate (CGR) of each genotype in each experiment was calculated from biomass and grain yield at maturity and anthesis date (Bramel-Cox et al., 1984):

$$\mathrm{CGR} = \frac{\mathrm{biomass_{mat}} - \mathrm{grain\ \ yield_{mat}}}{\mathrm{days\ \ from\ \ emergence\ \ to\ \ anthesis} + 10} \tag{1}$$

To evaluate genotypic differences in relative sink size at anthesis, panicle weight (excluding grain) at maturity was used to represent panicle sink strength at anthesis. Observations on sorghum (*Sorghum bicolor* L.) (van Oosterom, unpublished data) show that this structural panicle weight (hereafter referred to as chaff) is relatively constant once grain growth starts. The ratio between grain number and chaff weight was used as a measure of efficiency of grain number production per unit of mass invested in panicle structure (hereafter referred to as seed set). This ratio was constant for wheat (*Triticum aestivum* L.) cultivars across environments (Demotes-Mainard et al., 1996) and hence provides a simple but effective measure of seed set.

All analyses were performed in SAS. The GLM-procedure was used for analyses of variance, using Type I sum of squares (SS) to partition the genotype SS into plant type (three high-tillering versus three low-tillering genotypes) and genotype within plant type SS. Variance components were estimated from the ANOVA using the REML option in the VARCOMP procedure, assuming all factors to be random. The TTEST procedure was used for pair wise comparisons between the means of the two genotype groups to determine significance of differences between group means across experiments.

3. Results

3.1. Effects of genotype, environment, and their interactions on yield and yield components

Mean biomass ranged from 331 g m^{-2} (Fatehpur 1995, low fertility) to 1135 g m^{-2} (Patancheru in 1994 extended daylength) (Table 1). Genotypic differences in average biomass were small in most of the environments (Table 2). Nokha Local generally produced the least biomass, which appeared to be a consequence of its low grain yield (Table 2). The significant differences in biomass among the other genotypes under optimum conditions at Patancheru were associated with differences in phenology, with WC-C 75 (highest biomass) having the longest time to anthesis and ERajPop (lowest biomass) the shortest. Environments explained most of the SS, while the genotype SS was small compared with the G × E SS (data not shown). The environmental variance (s^2_{E}) was >60 times larger than the genotypic variance (s^2_{G}) and nearly 20 times the G × E variance ($s^2_{\mathrm{G\times E}}$). The effect of grouping genotypes (into landraces and modern cultivars) on the SS of biomass was just significant. However, the genotype groups explained 35% of the G × E SS (data not shown).

Mean grain yield ranged from 70 g m^{-2} at Mandore in 1998 to 426 g m^{-2} at Patancheru in 1994 (Table 1). Under optimum conditions at Patancheru, the high-tillering landraces had significantly lower grain yield than the low-tillering modern cultivars, but in most other environments, differences in grain yield were small, particularly in Rajasthan (Table 2). The s^2_{E} was about 10 times $s^2_{\mathrm{G\times E}}$, and $s^2_{\mathrm{G\times E}}$ in turn was 1.75 times s^2_{G}. The genotype grouping explained 71% of the genotype main effect SS and 60% of the G × E interaction SS for grain yield. As genotypic differences in total biomass were relatively small, differences in mean grain yield between the two groups of plant types were predominantly due to differences in the partitioning of dry matter to the grain.

These differences in partitioning were a result of genotypic differences in 100 grain mass, rather than

Table 2
Biomass, grain yield, 100 grain mass, grain number, number of fertile basal tillers per plant, grain number per panicle, and dry weight per main shoot panicle for six pearl millet genotypes, averaged over four groups of experiments[a]

	Biomass ($g\ m^{-2}$)	Grain yield ($g\ m^{-2}$)	100 grain mass (g)	Grain number (m^{-2})	Basal tillers (per plant)	Grain number (per pan)	Main shoot weight ($g\ pan^{-1}$)
Patancheru no stress (four experiments)							
ERajPop	918 c	345 b	0.75 d	45800 bc	3.39 a	1608 d	17.0 d
Nokha Local	961 bc	275 c	0.68 e	40732 d	2.49 b	1731 d	15.4 d
WRajPop	1047 ab	359 b	0.77 cd	46657 bc	3.57 a	1598 d	17.5 d
RCB-IC 911	1041 ab	475 a	1.08 a	43878 cd	1.64 c	2456 b	38.1 a
CZ-IC 922	1062 ab	438 a	0.80 c	54888 a	2.69 b	2167 c	27.3 c
WC-C 75	1114 a	440 a	0.88 b	49751 b	1.82 c	2677 a	33.6 b
Patancheru drought stress (three experiments)							
ERajPop	467 ab	193 bc	0.70 c	27344 ab	2.08 a	982 c	11.0 c
Nokha Local	426 b	150 c	0.62 d	24026 b	1.69 a	1019 c	10.4 c
WRajPop	543 a	224 ab	0.69 cd	32380 a	1.97 ab	1101 c	12.7 c
RCB-IC 911	522 ab	247 a	0.86 a	28025 ab	0.78 c	1662 a	23.6 a
CZ-IC 922	524 ab	240 ab	0.74 bc	32281 a	1.42 b	1459 b	18.1 b
WC-C 75	508 ab	221 ab	0.78 b	28143 ab	0.79 c	1734 a	21.6 a
Rajasthan, mean biomass >450 $g\ m^{-2}$ (seven experiments)							
ERajPop	641 ab	193 a	0.73 c	26468 a	1.48 a	1746 c	20.0 d
Nokha Local	674 ab	177 a	0.65 d	27191 a	1.71 a	1793 c	16.9 e
WRajPop	726 a	200 a	0.73 c	27359 a	1.76 a	1694 c	19.1 de
RCB-IC 911	604 b	206 a	0.98 a	21291 b	0.43 c	2452 a	35.2 a
CZ-IC 922	645 ab	205 a	0.79 b	25772 a	0.93 b	2264 b	27.8 c
WC-C 75	726 a	196 a	0.77 bc	24815 ab	0.56 c	2616 a	30.8 b
Rajasthan, mean biomass <450 $g\ m^{-2}$ (six experiments)							
ERajPop	372 a	124 a	0.69 b	17884 a	1.17 a	1369 cd	14.2 d
Nokha Local	357 a	113 a	0.62 c	18010 a	1.38 a	1271 d	11.4 e
WRajPop	410 a	121 a	0.69 b	17550 a	1.31 a	1196 d	13.3 de
RCB-IC 911	392 a	133 a	0.88 a	14997 a	0.32 c	1892 b	26.1 a
CZ-IC 922	368 a	124 a	0.73 b	17205 a	0.67 b	1567 c	18.1 c
WC-C 75	408 a	125 a	0.72 b	16928 a	0.29 c	2140 a	23.0 b

[a] Values followed by the same letter are not significantly different at $P < 0.05$ according to Tukey's test for pair wise comparisons.

grain number. For 100 grain mass, s^2_G was larger than s^2_E and the importance of the genotype main effect was illustrated by the fact that genotype grouping explained over 50% of the SS for the genotype main effect. For grain number, however, s^2_G was small compared with s^2_E. Although genotypic differences in grain number were significant (Table 2), they were not associated with plant type, as the genotype grouping explained <0.5% of the SS for the genotype main effect. The relative magnitude of the G × E interaction also differed for grain mass and grain number. For grain mass, s^2_G was three times $s^2_{G\times E}$, but for grain number s^2_G was smaller than $s^2_{G\times E}$. Consistent with this, the genotype grouping explained >50% of the G × E SS for 100 grain mass, but only 37% of the G × E SS for grain number.

The yield architecture (panicle number and size) differed between the two groups of plant types. For both fertile basal tiller number per plant and grain number per fertile axis, over 85% of the cultivar differences was explained by their grouping, with the landraces having higher tiller number and the cultivars higher grain numbers per panicle. In addition, the small size of $s^2_{G\times E}$ compared with s^2_G for these two parameters indicated that these differences were consistent across environments. In fact, the weight of the main shoot panicle was a good parameter to distinguish the plant types, as the grouping explained 86% of its genotype SS and 63% of its G × E SS.

Table 3
The number of plants observed, number of leaves per main shoot, number of primary basal tillers per plant that emerged and produced seed, and the percentage of emerged tillers that produced seeds, for three landraces and three modern varieties of pearl millet, grown in the rainy season of 1995 at Patancheru and Fatehpur

		High-tillering landraces			Low-tillering exotic varieties		
		ERajPop	Nokha Local	WRajPop	RCB-IC 911	CZ-IC 922	WC-C 75
Number of plants	Patancheru	19	18	20	18	20	19
	Fatehpur	29	25	28	30	28	29
Leaf number main shoot	Patancheru	15.9	16.5	16.3	16.9	15.9	18.3
	Fatehpur	17.2	17.9	18.0	18.1	17.3	20.0
Produced tillers per plant	Patancheru	5.68	5.72	6.35	5.44	5.90	5.00
	Fatehpur	5.21	6.20	6.79	6.03	6.29	5.55
Fertile tillers per plant	Patancheru	3.26	3.06	3.00	1.61	2.75	1.89
	Fatehpur	2.03	3.28	3.04	0.77	2.04	0.83
Survival %	Patancheru	57	53	47	30	47	38
	Fatehpur	39	53	45	13	32	15

3.2. Tiller appearance and panicle number

3.2.1. Basal tillers

Tiller appearance started around 150 °C d after emergence at Patancheru 1995 (data not shown). Genotypic differences in the rate and duration of tiller appearance were small: the maximum number of basal tillers that appeared per plant ranged from 5.0 for WC-C 75 to 6.4 for WRajPop and was on average 5.9 for the landraces and 5.4 for the modern cultivars (Table 3). The absence of major genotypic differences in tiller appearance was confirmed by the results from Fatehpur 1995, where the landraces on average produced 6.1 basal tillers per plant and the modern varieties 6.0. The higher tiller number at Fatehpur was consistent with a higher leaf number on the main shoot (Table 3), indicating a longer vegetative period due to the higher latitude.

The number of fertile tillers per plant, by contrast, differed consistently between both genotypes and locations, due to differences in the tiller survival rate. For landraces, about half the basal tillers that appeared at each location ultimately produced a panicle; the only exception was ERajPop at Fatehpur 1995, which had a survival rate of only 39% (Table 3). RCB-IC 911 and WC-C 75, by contrast, had a tiller survival rate between 30 and 40% at Patancheru 1995, but of only 13–15% at Fatehpur 1995. These results indicate that the effects of cultivar, environment, and their interaction on fertile basal tiller number per plant are predominantly due to an effect on tiller survival.

The number of fertile basal tillers per plant was negatively correlated with the dry weight per main shoot panicle at maturity, if experiments with similar overall grain yields were compared (Fig. 1). This negative correlation was significant across groups of environments in which grain yield ranged from 70–76 g m^{-2} (Fig. 1a), 148–166 g m^{-2} (Fig. 1b), 182–264 g m^{-2} (Fig. 1c), to 350–426 g m^{-2} (Fig. 1d). The slope of the regression of basal tiller number on main shoot panicle weight was similar across a wide range of yield levels, with on average one additional fertile basal tiller produced for each 12–14 g decrease in main shoot panicle weight (Fig. 1b–d).

At Patancheru 1995, anthesis on the basal tillers commenced at the same time as on the main shoot, but extended for a longer period on the basal tillers (Fig. 2). The higher number of basal tillers in WRajPop, compared with RCB-IC 911, did not result in a significant increase in the overall spread of flowering dates among basal tillers. A detailed analysis of anthesis dates in two rainy season experiments at Patancheru and seven experiments at Fatehpur and Jodhpur showed that on average, basal tillers reached anthesis 2–4 days later than the main shoot, whereas differences between main shoot and basal tillers in the standard deviation for anthesis were minor under

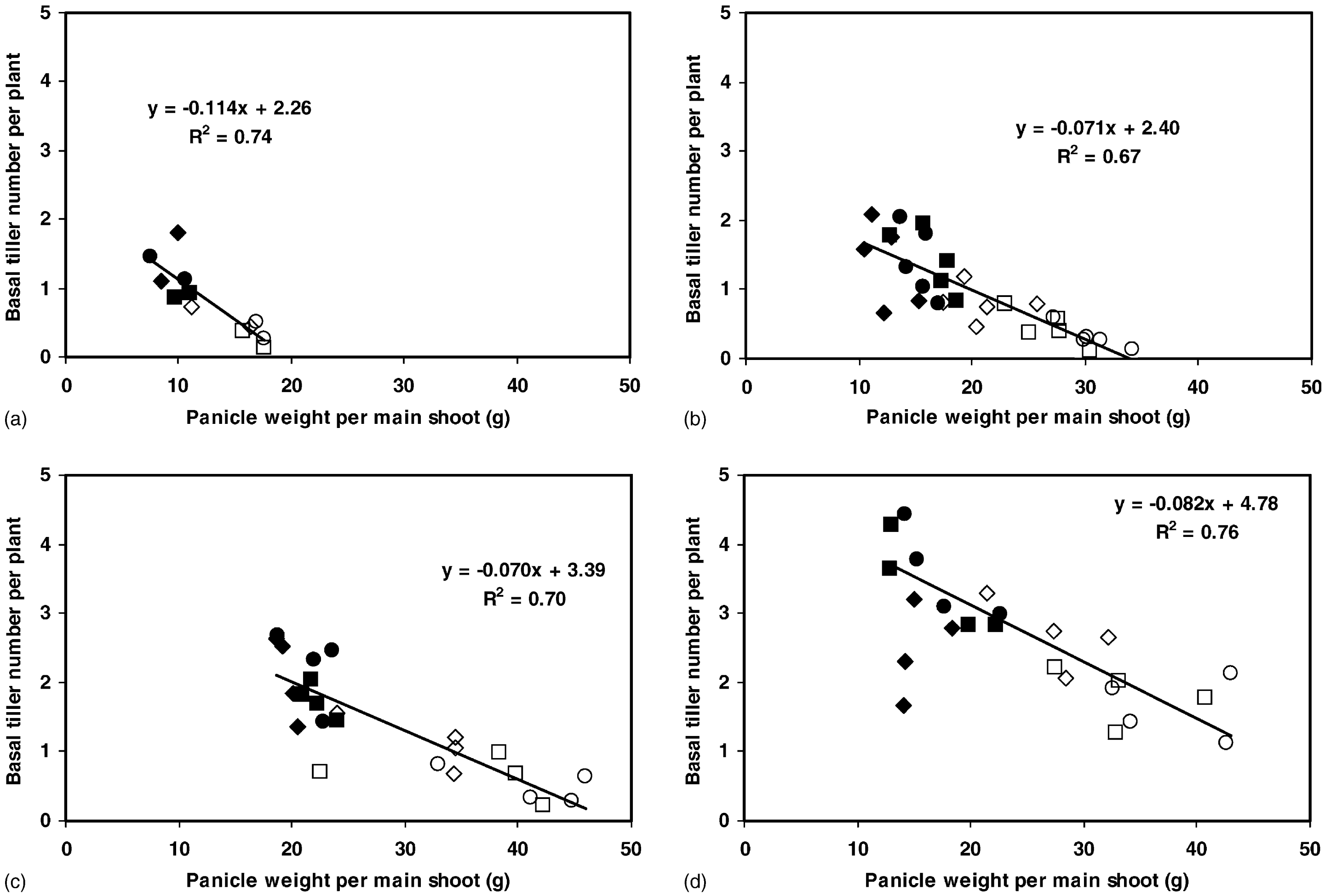

Fig. 1. Number of primary basal tillers per plant as a function of the panicle weight per main shoot for ERajPop (■), Nokha Local (◆), WRajPop (●), RCB-IC 911(○), CZ-IC 922 (◇), and WC-C 75 (□) across four levels of grain yield: (a) 70–76 g m^{-2} (Mandore 98, Jodhpur 97); (b) 148–166 g m^{-2} (Jodhpur 1995 + 1998, Pali 1996 + 1997, Fatehpur 94), 182–264 g m^{-2} (Fatehpur 1995 + 1996 (two experiments), Jodhpur 94), and 350–426 g m^{-2} (Patancheru dry season 94 (two experiments), Patancheru rainy season 1994 + 1995). The two off-points for Nokha Local in Fig. 2d not included in the regression line.

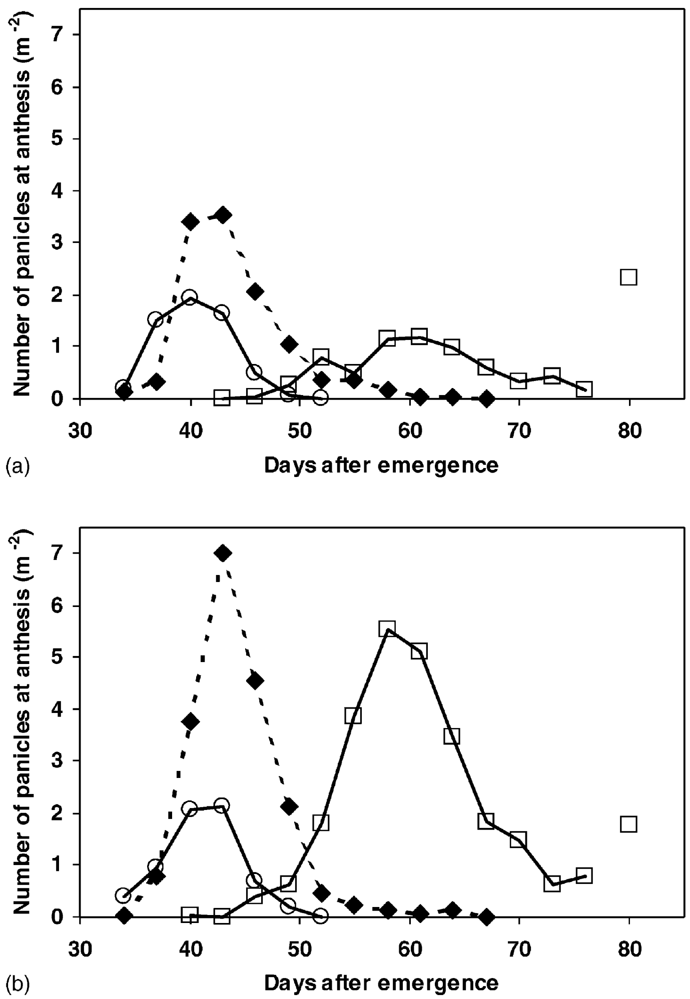

Fig. 2. The number of panicles per square metre reaching anthesis at a certain number of DAE at Patancheru rainy season 1995 for (a) RCB-IC 911 and (b)WRajPop for main shoot (○—○), basal tillers (◆…◆) and nodal tillers (□—□). Panicle numbers are pooled for 3-day intervals. Nodal tiller numbers at 80 DAE represent panicles for which the anthesis date was not known.

optimum conditions at Patancheru in the rainy season and absent in Rajasthan.

3.2.2. Nodal tillers

At Patancheru 1995, nodal tillers on the main shoot started to emergence around 120 °C d (1 week) prior to anthesis of the main shoot panicle (Table 4), approximately coinciding with the appearance of the flag leaf (data not shown). Nodal tillers generally appeared acropetally, beginning in the fourth or fifth leaf axil below the flag leaf, with the uppermost nodal tillers appearing from the penultimate leaf axil, just after anthesis of the main shoot panicle (Table 4). They generally reached anthesis 250–300 °C d (nearly 3 weeks) after anthesis of the main shoot panicle (Table 4), coinciding with mid-grain filling (van Oosterom et al., 2002). Most of the period between emergence and anthesis of nodal tillers thus coincides with the period between the end of leaf growth and the start of grain filling of the main shoot, when the chaff of the panicle and the upper internodes of the stem are the main sinks for carbon.

To test the hypothesis that nodal tiller appearance is a consequence of assimilate surplus around anthesis,

Table 4
Appearance and anthesis of nodal tillers on the main shoot (expressed in °C d, relative to the anthesis date of the main shoot panicle) and the duration of appearance to anthesis, averaged for nodal tillers appearing at a common leaf position, counted from the flag leaf (Flag Leaf = Leaf 0) for plants grown in the rainy season of 1995 at Patancheru[a]

Leaf number	Appearance			Anthesis			Duration		
	Mean	Standard deviation	*N*	Mean	Standard deviation	*N*	Mean	Standard deviation	*N*
1	30.3	64.7	32	284.4	92.7	32	245.6	48.7	16
2	−32.9	59.6	50	264.0	83.5	36	289.2	56.7	28
3	−63.2	52.2	46	282.5	83.1	23	349.2	73.7	22
4	−63.0	69.8	35	303.8	89.3	5	417.3	86.9	5
5	−73.0	66.2	18	198.9	–	1	332.5	–	1
6	−101.0	54.6	8	313.6	–	1	447.2	–	1
7	−122.1	63.2	3						

[a] Number of observations and standard deviation are also given.

due to limited demand by the growing stem and panicle, we calculated the ratio between the chaff weight at maturity (of the main shoot and basal tillers) and the vegetative CGR (see Section 2). A low ratio indicates a relatively low demand for assimilates by the growing panicle during the period that nodal tillers appear, which would indicate that more assimilates are available to sustain the production of nodal tillers. Using mean values for the two cultivar groups, the ratio was on average 20% lower for landraces than for the modern cultivars, what was significant ($P < 0.001$) according to a *t*-test for paired comparisons across individual experiments. Hence, the prolific nodal tiller production by the landraces is associated with a relatively small investment in panicle growth.

Across experiments conducted at Patancheru, there was a significant negative relationship between productive nodal tiller number and the ratio between chaff weight and vegetative growth rate (Fig. 3; $R^2 = 0.47$, $n = 14$, $P < 0.01$). The relatively low R^2 was due to the rainy season experiment of 1995, when nodal tiller numbers were low; exclusion of that

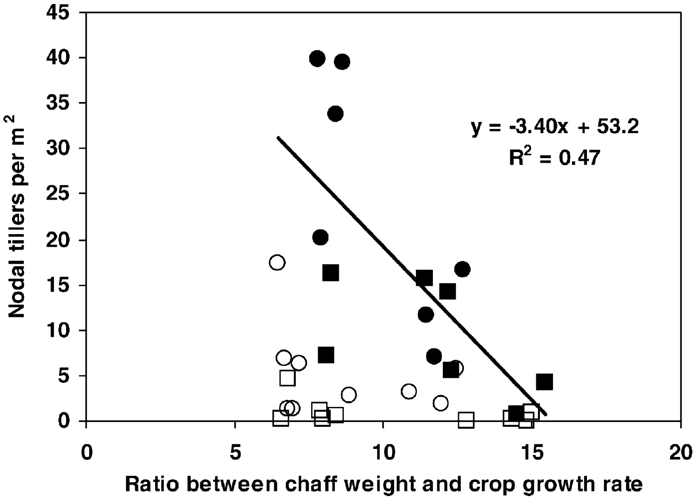

Fig. 3. The number of productive nodal tillers per square metre as a function of the ratio between chaff weight (of the main shoots and basal tillers) at maturity and vegetative growth rate at Patancheru (closed symbols) and in Rajasthan (open symbols), averaged for three landraces (circles) and three varieties (squares). The regression line is for the Patancheru data only (seven experiments).

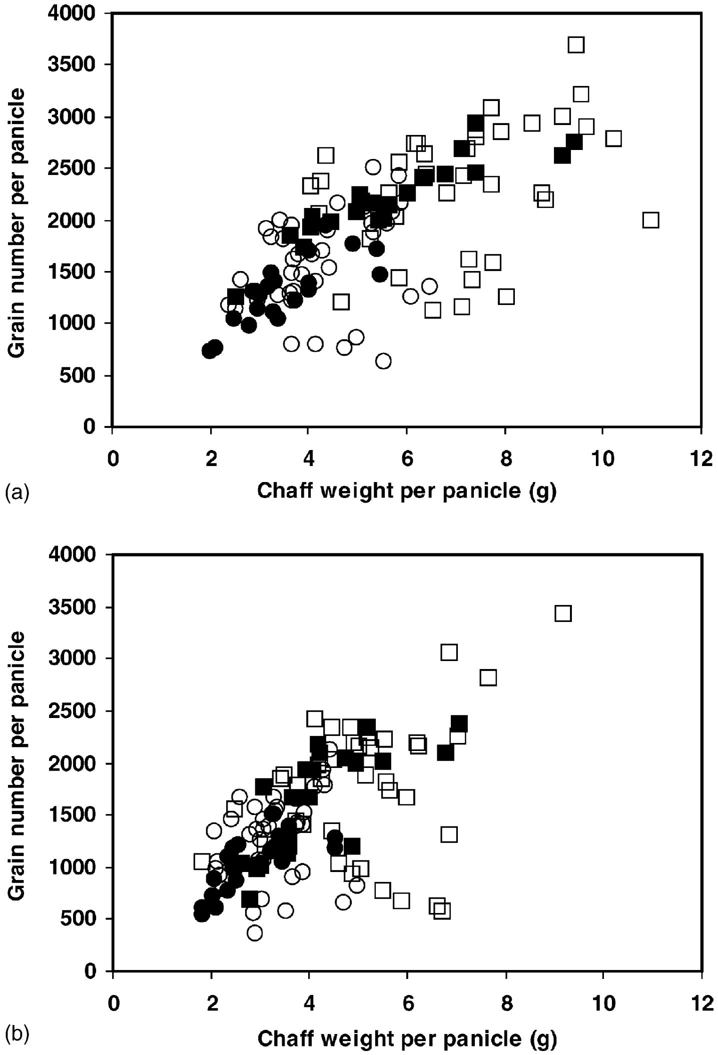

Fig. 4. Grain number per panicle as a function of chaff weight per panicle at maturity for (a) main shoots and (b) basal tillers at Patancheru (closed symbols) and in Rajasthan (open symbols), averaged for three landraces (circles) and three varieties (squares).

experiment increased the R^2 to 0.70. In Rajasthan, however, the relationship was weak, as several experiments produced few nodal tillers, despite a low ratio between chaff weight and vegetative growth rate. Presumably, in these experiments productive nodal tiller number was reduced by other factors, like drought stress during grain filling (Table 1). Importantly, the triangular configuration of the data points in Fig. 3 indicates an upper limit to nodal tiller production as a function of relative assimilate requirement by the panicle (chaff) under non-limiting growing conditions. Such an upper limit supports the hypothesis that nodal tiller production is a consequence of assimilate surplus.

3.3. Grain number per panicle

3.3.1. Relationship between grain number in main shoot and basal tillers

At Patancheru, grain number per panicle was closely related to the chaff weight per panicle (Fig. 4). The relationship was not affected by axis type (main

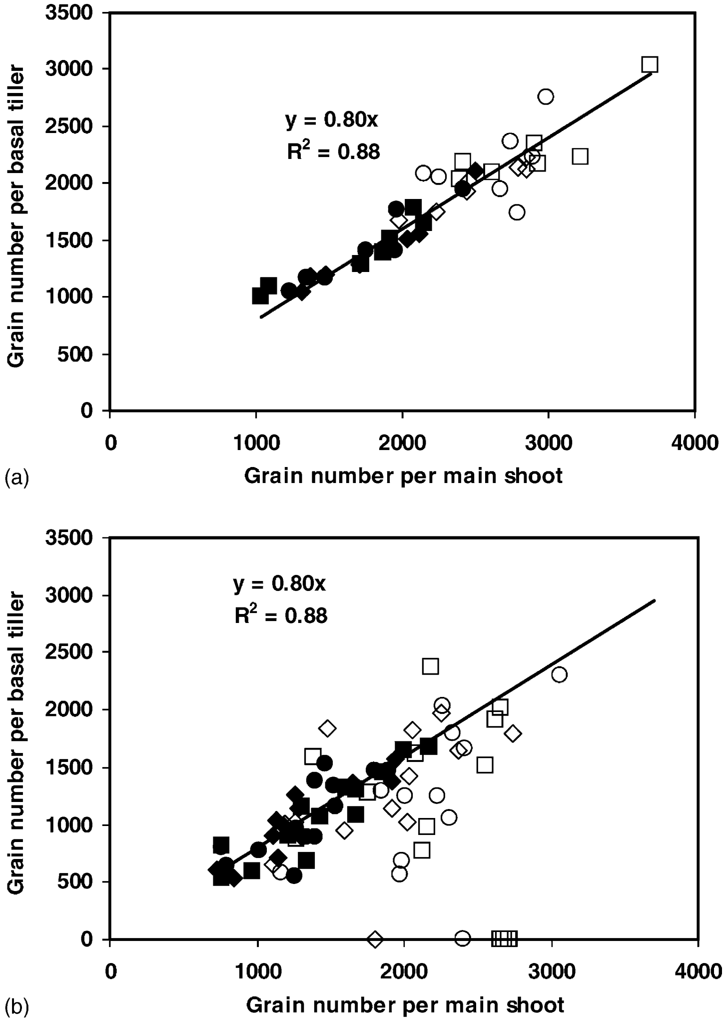

Fig. 5. Grain number per basal tiller as a function of grain number per main shoot in (a) experiments without drought stress and (b) experiments with drought stress for ERajPop (■), Nokha Local (◆), WRajPop (●), RCB-IC 911(○), CZ-IC 922 (◇), and WC-C 75 (□). Experiments in (a) include Patancheru dry season 1994 (two experiments) and rainy season 1994 + 1995, Jodhpur 1994, and Fatehpur 1996 (two experiments). The regression line for non-drought experiments has been added to (b) for comparison.

shoot versus basal tiller) or cultivar, although grain number levelled off for larger panicles. Similar results were obtained for the experiments conducted at Rajasthan, with the exception of three experiments (Jodhpur 1997, Mandore 1998, Pali 1997), where grain numbers were low relative to chaff weight. Two of these experiments experienced severe stress during grain filling (nutrient stress at Jodhpur 1997, drought stress at Mandore 1998, Table 1). Exclusion of these three experiments yielded a strong relationship (Edmeades and Daynard, 1979) between grain number and chaff weight per panicle, which was independent of cultivar, axis, or experiment:

$$\text{grain\_nr} = \frac{6026(\text{chaff\_wt} - 0.485)}{9.11 + (\text{chaff\_wt} - 0.485)}, \qquad (2)$$
$$R^2 = 0.77, \quad n = 204$$

In environments without drought stress, grain number per basal tiller was closely related to grain number per main shoot (Fig. 5a). As the intercept of the regression was not significantly different from zero, the regression was forced through the origin. On average, basal tillers contained approximately 80% of the grain number in the main shoot. According to Eq. (2), this lower grain number in the basal tillers was a consequence of a lower chaff weight.

Under drought, grain number in basal tillers varied from 94% of the grain number in the main shoot (averaged over all genotypes) under low-fertility at Fatehpur 1995, to 47% at Pali 1997 (Fig. 5b). In some experiments, the modern cultivars with large main shoot panicles (RCB-IC 911 and WC-C 75) even failed to produce any productive basal tillers at all. Across 10 drought-stressed experiments where all genotypes produced productive basal tillers, the average grain number per basal tiller was 79% of that of the main shoot for the landraces, but only 68% for the modern cultivars. This difference was significant at $P < 0.05$ according to a t-test for paired comparisons across experiments. Hence, under stress the landraces are better able to maintain the size of the basal tiller panicles (relative to the main shoot) than the modern cultivars.

3.3.2. *Consequences for flowering under stress*

Panicle size had a consistent effect on the ability of the crop to reach anthesis under pre-anthesis drought stress. In the two experiments that were conducted simultaneously in the rain-out shelter at Patancheru 1994, the delay in anthesis following pre-anthesis drought stress was strongly linearly related ($R^2 = 0.94$, $n = 6$) to sink size, represented by the number of grains per main shoot panicle (Fig. 6a). A similar effect of panicle size on the ability to reach anthesis under pre-anthesis drought was obtained for the experiments at Jodhpur and Mandore in 1998. At Jodhpur, only 39 mm of rain fell during the 10 days prior to anthesis of the earliest genotype, with an additional 14 mm during the 2 weeks that separated anthesis of the earliest and latest genotype; at Mandore, only 11 mm of rain was received during the 3 weeks preceding anthesis of the earliest genotype. Under these severely drought-stressed conditions, the landraces reached anthesis on average 9.1 days (Jodhpur 1998) and 14.6 days (Mandore 1998) earlier than the modern cultivars. By contrast, in seven other experiments in Rajasthan, where pre-anthesis drought stress was less severe, the difference in mean anthesis date between the two groups never exceeded 4 days, and on average was only 2.4 days. Thus, differences in anthesis between the two groups were small, except following severe pre-anthesis drought stress, when anthesis was more delayed in genotypes with larger panicles.

In the dry season of Patancheru 1995, where drought stress was temporarily relieved around anthesis, there was a bimodal distribution in the anthesis date of the basal tillers (Fig. 6b). The first cohort of basal tillers reached anthesis around 40–44 DAE, during a dry spell. The number of panicles reaching anthesis then declined as drought rapidly increased due to high levels of incoming radiation. Anthesis had virtually stopped when drought was relieved by irrigation on 52 DAE, but resumed once plants had a chance to recover. The ability to produce fertile panicles after drought stress was relieved was strongly related to phenology, rather than panicle size: the fraction of the total number of fertile basal tillers that reached anthesis during the second cohort was a linear function of the anthesis date of the main shoot (Fig. 6c). As the average anthesis date of the two cohorts of basal tillers differed by 24 days, small differences in phenology of the main shoot resulted in large differences in phenology of the basal tillers.

3.4. *Grain mass*

The significant G × E interaction for 100 grain mass (Table 2) was due to genotypic differences in the response of grain mass to environment. For Nokha Local, 100 grain mass was largely independent of grain yield per plant (Fig. 7) and 100 grain mass ranged from 0.55 to 0.71 g, except in Mandore, 1998 (0.44 g). For RCB-IC 911, by contrast, 100 grain mass ranged from 1.0 to 1.2 g under high-yielding conditions to 0.54 g in Mandore 1998.

Within crops, there was a close relationship between the grain mass of the main shoot and basal tiller panicles, particularly in environments without drought stress (Fig. 8). The intercept of the relationship with the y-axis was significantly positive ($P < 0.001$). Combined with a slope which was significantly less than 1, the results indicate that the difference in grain mass between the main shoot and basal tillers was relatively bigger for large-seeded than small-seeded cultivars.

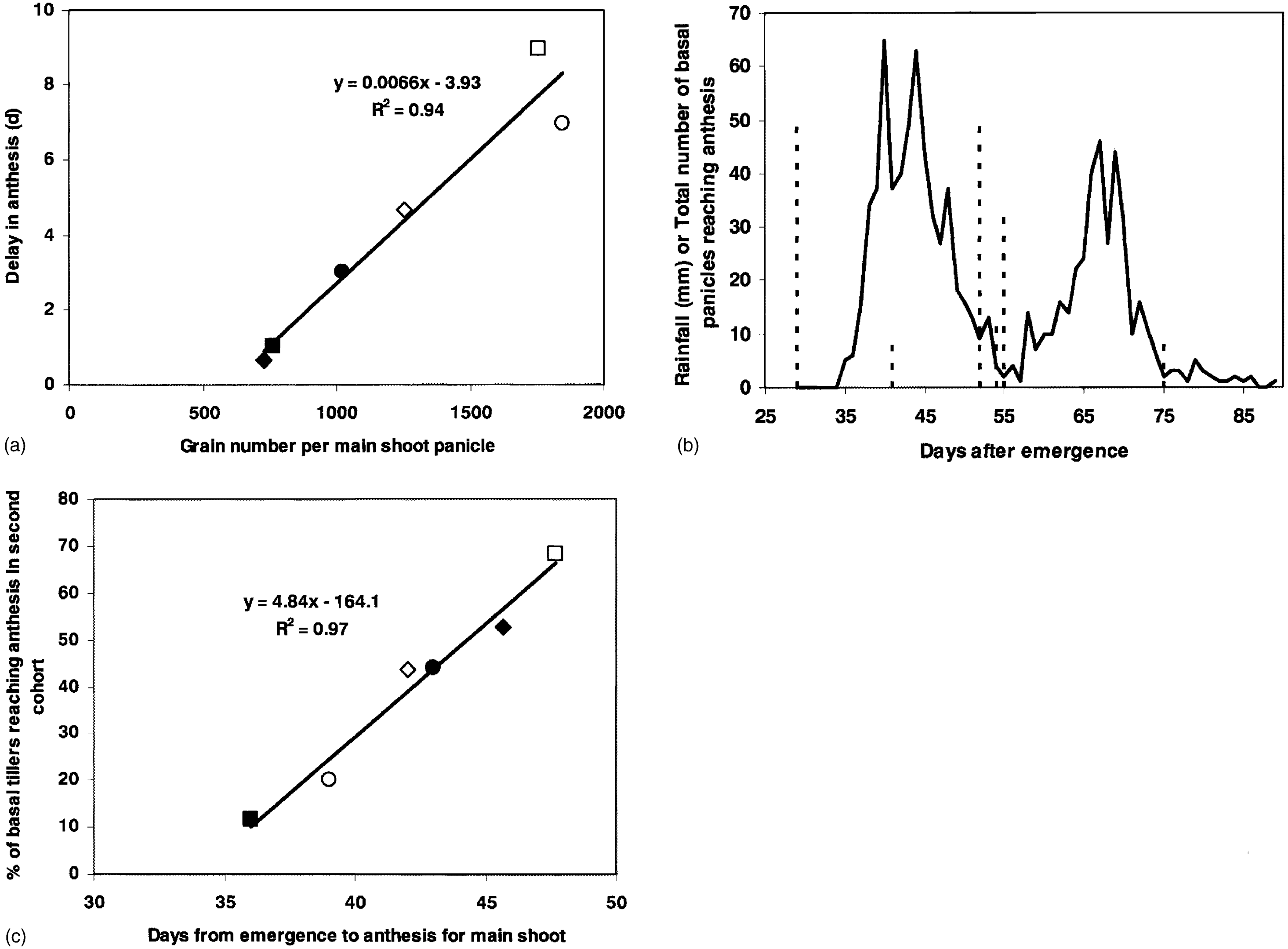

Fig. 6. (a) Effect of grain number per main shoot panicle on the delay in anthesis date following pre-anthesis drought stress (compared with no pre-anthesis drought) at Patancheru during the rainy season of 1994; (b) total number of basal tiller panicles across genotypes that reached anthesis each day (solid line) and daily rainfall (mm, dotted line) for Patancheru dry season 1995; and (c) the fraction of productive basal tillers that reached anthesis in the second cohort as a function of anthesis date of the main shoot for Patancheru dry season 1995. ERajPop (■), Nokha Local (◆), WRajPop (●), RCB-IC 911(○), CZ-IC 922 (◇), and WC-C 75 (□).

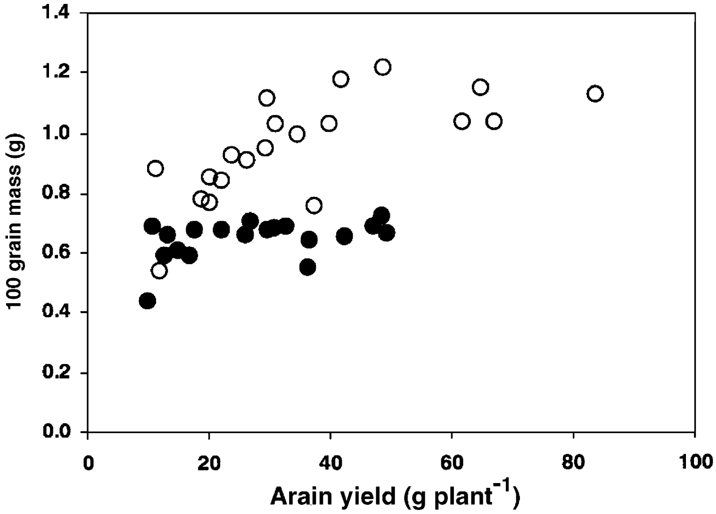

Fig. 7. Hundred grain mass as a function of grain yield per plant for Nokha Local (●) and RCB-IC 911 (○).

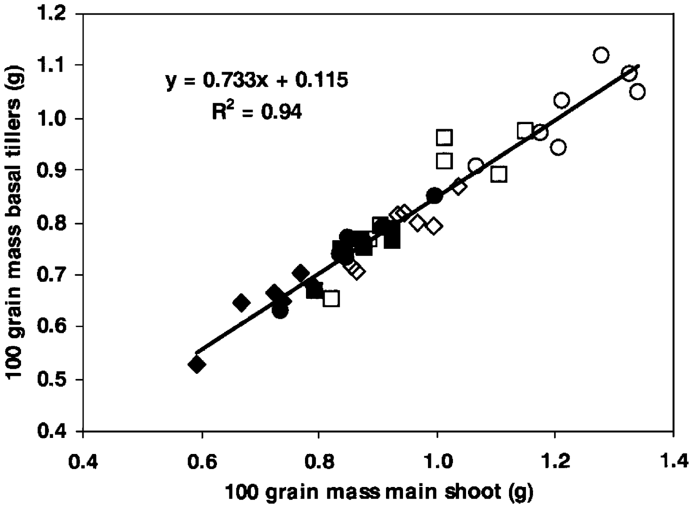

Fig. 8. Hundred grain mass in the basal tiller panicle as a function of 100 grain mass in the main shoot panicle for ERajPop (■), Nokha Local (◆), WRajPop (●), RCB-IC 911(○), CZ-IC 922 (◇), and WC-C 75 (□), across seven experiments without drought stress: Patancheru dry season 1994 (two experiments) and rainy season 1994 + 1995, Jodhpur 1994, and Fatehpur 1996 (two experiments).

4. Discussion

The results of this paper support the hypothesis that differences in yield architecture between the high-tillering landraces and low-tillering modern cultivars represent a difference in adaptation strategy. The yield architecture of the landraces is aimed at survival in the arid zone through minimising the risk of a crop failure, whereas the yield architecture of the modern cultivars is aimed at survival in breeding fields by maximising yield potential. The small size of the main shoot is a key component of the adaptation strategy of the landraces, while features like low investment in structural panicle weight and low maximum grain size provide additional adaptation mechanisms. The adaptation framework that is developed in this paper can be a useful tool to assist farmers and breeders in the identification of (mixtures of) plant types that maximise adaptation and yield stability in variable stress environments.

4.1. Differences in main shoot size as key to differences in yield architecture

The significant negative correlation between dry weight per main shoot panicle and the number of fertile basal tillers in Fig. 1 is not causal, but rather reflects that both panicle dry weight and tiller number are determined by the size and growth rate of the main shoot prior to anthesis. Our results on the appearance of primary basal tillers confirm previous results (van Oosterom et al., 2001a) that, despite consistent genotypic differences in the number of fertile tillers at maturity (Table 3), there is little difference in the rate and duration of basal tiller production. Hence, differences in productive tiller number are not due to genotypic differences in tilllering ability, but rather to differences in growing conditions, experienced by the tillers during stem elongation. Lafarge and Hammer (2002) observed for sorghum that tiller appearance ceased when crop LAI was approximately 0.6, whereas the rate of loss of potentially fertile tillers was related to the ratio of realised to potential leaf area. Similarly, van Oosterom et al. (2001a) reported for pearl millet a significant positive association between the rate of decline in viable tiller number during stem elongation and the maximum LAI of the main shoot. Thus, both genetic and environmental factors affect tiller survival. Such a causal relationship between LAI and tiller survival accounts for the observation in our experiments that the cultivar with few productive tillers (RCB-IC 911) has large leaves (van Oosterom et al., 2001b). Similar results have been reported for tall fescue (*Festuca arundinacea* Schreb.) (Jones et al., 1979) and rice (*Oryza sativa* L.) (Tivet et al., 2001). This relationship would also explain the low number of productive tillers in Rajasthan (Table 1), where the longer daylength (compared with Patancheru) delayed floral initiation and increased final leaf number on the main shoot (Table 3), resulting in a higher main shoot LAI (van Oosterom et al., 2001b) and hence a higher rate of loss of tillers (van Oosterom et al., 2001a). In addition, Craufurd and Bidinger (1988a) reported a significantly positive linear relationship between maximum leaf area per axis and the growth rate of its stem or panicle. As the duration of panicle growth is relatively constant across daylengths (Craufurd and Bidinger, 1988a), a larger maximum leaf area per axis will result in larger panicles. Genotypic and environmental differences in productive tiller number and in panicle size are thus both associated with differences in main shoot LAI, resulting in a significant, but non-causal, relationship between the two.

If differences in fertile tiller number are related to differences in the size of the main shoot leaves (and hence the size of the main shoot in general), then genotypic differences in plant type are already established early in the life cycle of the crop by genetic factors that determine leaf size. Differences in leaf size can be accounted for by differences in the duration and rate of leaf elongation. Genotypic differences in the leaf expansion rate (LER) have been reported for tall fescue (Volenec and Nelson, 1981, 1983). In our study, RCB-IC 911 (low-tillering) has larger leaves than WRajPop (high-tillering) (van Oosterom et al., 2001b). As there are no significant differences in the appearance rates of either leaf tips or leaf ligules between these two cultivars (van Oosterom et al., 2001a), it is likely that these differences in leaf size are a result of differences in LER, which in turn can be a consequence of differences in the size of the apical dome. It has been hypothesised (Pieters and van den Noort, 1988) that the mature size of an individual leaf is determined at its initiation. As the first leaf initials are already present in the embryo in the seed, the larger leaf size may thus already be established in the seed. López-Castañeda et al. (1996) indeed showed that embryo weight explained 92% of the variation in early leaf area between four temperate cereals, whereas within species, embryo weight was significantly and linearly correlated to seed weight. A relationship between early vigour and seed size has also been observed for pearl millet (Manga and Yadav, 1995). In tall fescue, cultivars with a high LER tend to have a high yield per axis and low tiller number (Jones et al., 1979; Volenec and Nelson, 1981; Skinner and Nelson, 1994). These observations are consistent with the negative correlation between size of the main shoot and tiller number that we observed (Fig. 1). Similar results were obtained by Craufurd and Bidinger (1988a) for pearl millet and by Kirby and Riggs (1978) for the contrast between two-row and six-row barley. This supports the view that a low number of productive tillers in cultivars with a large main shoot is a consequence of restricted assimilate availability to the tillers, due to increased competition from the main shoot.

4.2. G × E interactions for grain yield

The significant interaction for grain yield between genotypes and environments was due to the relatively low grain yield of landraces under optimum conditions at Patancheru (Table 2). These differences were not caused by differences in grain number per square metre, but rather by the inability of the landraces to capitalise on the increased resource availability under high-yielding conditions through increasing individual grain mass (Fig. 7). Bidinger and Raju (2000) also observed limits to the increase in grain size of high-tillering genotypes that are not operating in low-tillering ones. As there was no lack of available assimilates in the high-tillering genotypes in our study, as judged from the abundance of nodal tillers, this restriction appears to be genetic and is likely to operate through a low maximum grain growth rate. Previous results (van Oosterom et al., 2002) indicated grain growth rates were nearly 30% higher for the low-tillering cultivars than the high-tillering ones, while the duration of grain filling was very similar. Genotypic differences in the grain growth rate of pearl millet have also been observed by Fussell and Pearson (1978) and accounted for most of the variation in grain mass in an analysis of grain growth in pearl millet by Bieler et al. (1993). The low grain yield of the landraces under optimum conditions at Patancheru thus appears to be due to genetic constraints on maximum grain growth rate, which prevent a complete use of available assimilates by the grains.

Genetic constraints on the maximum grain growth rates for high-tillering genotypes do not automatically result in low grain yields under optimum conditions. Bidinger and Raju (2000) did not observe a significant interaction for grain yield between plant type and either fertility or density in a comparison of modern high- and low-tillering pearl millet cultivars and hybrids. Similarly, Craufurd and Bidinger (1988b) found that high- and low-tillering pearl millet hybrids had similar grain yields under high-yielding conditions. In both cases (Bidinger and Raju, 2000; Craufurd and Bidinger, 1988b), the high-tillering cultivars had higher grain numbers per square metre than the low-tillering genotypes, but lower grain mass. In our experiments, CZ-IC 922 showed this type of compensation under optimal conditions at Patancheru, where its grain number was significantly higher than that of any of the other cultivars (Table 2). The high grain number per square metre of the high-tillering hybrid (BJ 104) in the study of Craufurd and Bidinger (1988b) could be explained by a high grain number per unit of structural panicle weight, as illustrated by a direct comparison with WRajPop and RCB-IC 911 (Table 5). As grain number per unit area and 100 grain mass are generally negatively correlated (Craufurd and Bidinger, 1989), with about 50% of the variation in 100 grain mass explained by differences in grain number (Bidinger et al., 2001), it is unclear whether the low 100 grain mass in the high-tillering genotypes of the studies by Bidinger and Raju (2000) and Craufurd and Bidinger (1988b) is a consequence of increased competition from the higher grain number, or the result of a low maximum grain growth rate per sé. In our study, however, the low 100 grain mass of the landraces under optimum conditions at Patancheru, relative to their grain number, suggests they have a poor grain filling ability (Bidinger et al., 2001), as opposed to being affected by competition for assimilates due to a high grain number.

Under stress conditions in Rajasthan, the low maximum grain growth rate of the landraces did not result in major grain yield penalties. This can be explained by the strong likelihood that assimilate availability during grain filling was so low, that even the low maximum grain growth rate of the high-tillering landraces was

Table 5
Ratio of grain number per square metre and structural panicle weight (g m^{-2}) at maturity for three pearl millet genotypes, grown at four plant densities under well-watered and well-fertilised conditions at Patancheru in the dry season of 1996

Plant density (per square metre)	BJ 104	RCB-IC 911	WRajPop
4	419	280	283
11	372	237	247
15	332	221	242
20	303	239	222
Density effect	$P = 0.012$		
Genotype effect	$P < 0.001$		
Interaction	$P = 0.439$		

not a limitation to the complete utilisation of all available assimilates for grain growth. This hypothesis is supported by the low contribution of nodal tillers to grain yield in Rajasthan (Table 1). The main exception was Nokha Local, the unimproved landrace, which tended to have the lowest grain yields under low-yielding conditions at Rajasthan (Table 2), although differences were not significant. This lower grain yield was entirely due to a low 100 grain mass (Table 2). The lack of response of 100 grain mass to assimilate availability in Nokha Local (Fig. 7, Table 2) indicates that its potential grain growth rate is so low, that even in most of the low yielding experiments in Rajasthan it could not translocate all available assimilates into the grains. This hypothesis is supported by the observation that across the 13 Rajastan experiments, Nokha Local on average produced 67% more nodal tillers per square meter than the other two landraces (ERajPop and WRajPop), whereas its grain yield from nodal tillers was twice that of ERajPop and WRajPop. This excessive nodal tillering is a symptom of assimilate surplus. The large-seeded cultivar RCB-IC 911, by contrast, had a considerably smaller grain size in Rajasthan than under optimum conditions at Patancheru (Fig. 7, Table 2), presumably because carbon availability under stress in Rajasthan was unable to maintain the high grain growth rate. The repeatable interaction for grain yield between landraces and modern cultivars in optimum versus stressed environments is consistent with results for barley landraces under dry conditions in west Asia (Ceccarelli et al., 1998) and supports the conclusion that the adaptive mechanisms of the landraces are as important in determining grain yield under stress as the ability to produce high grain yield under optimum conditions.

4.3. *Stress-adaptation strategy of the landraces*

4.3.1. *Small size of the main shoot panicle*

The small size of the main shoot and its panicle was a key component in the adaptation to stress of the landraces. Under optimum conditions, the mean grain number in basal tillers was on average about 80% of that in the main shoot (Fig. 5a). Under stress conditions, however, landraces were, compared with modern varieties, generally better able to maintain the normal grain number and 100 grain mass (and hence the grain yield) of the productive tillers relative to the main shoot. Grain yield of individual axes is linearly related to their growth rate (Craufurd and Bidinger, 1988a); hence, maintenance of grain yield of the tillers under stress conditions indicates maintenance of their growth rate. This is likely to be due to a reduced competition with the main shoot for limited resources (water, light, nutrients), resulting from the smaller size of the main shoot. The low grain number per individual axis (but not per unit area) ensured that the sink demand per panicle during grain filling was small, thus providing a mechanism to stabilise grain number per basal tiller panicle in the landraces under stress.

The small panicle size of the landraces also enhanced the stability of grain yield through minimising the detrimental effects of drought stress on timing of anthesis. In environments with pre-anthesis drought stress, the delay in anthesis increased linearly with the size of the main shoot panicle (Fig. 6). This was likely to be caused by the higher sink demand (amount of structural panicle weight) of the larger panicles. Delayed anthesis can be a useful developmental mechanism to escape mid-season drought stress, provided there is adequate moisture to complete development (Bidinger et al., 1982). In many of the environments in Rajasthan where pearl millet landraces are grown, however, rainfall events are few and far between (Sharma and Pareek, 1993) and delayed anthesis increases the probability that the growing season extends well beyond the occurrence of the last significant rainfall (van Oosterom et al., 1996). This can result in small grains, as illustrated in Fig. 9 by the negative relationship within genotypes between late anthesis and 100 grain mass in experiments that experienced end-of-season drought stress. Extremely small grains constitute a waste of assimilates, as they are often lost during winnowing of the harvested seeds. Moreover, small grains are not used by farmers as a seed source for next crop (Dhamotharan et al., 1997), because of the likelihood of poor early growth vigour (Manga and Yadav, 1995; López-Castañeda et al., 1996). The small panicle size of the landraces thus provides an additional mechanism to maximise yield stability if stress occurs around anthesis.

4.3.2. *Low investment in structural panicle dry matter*

The low investment in structural panicle weight, relative to growth rate, provides the landraces with a

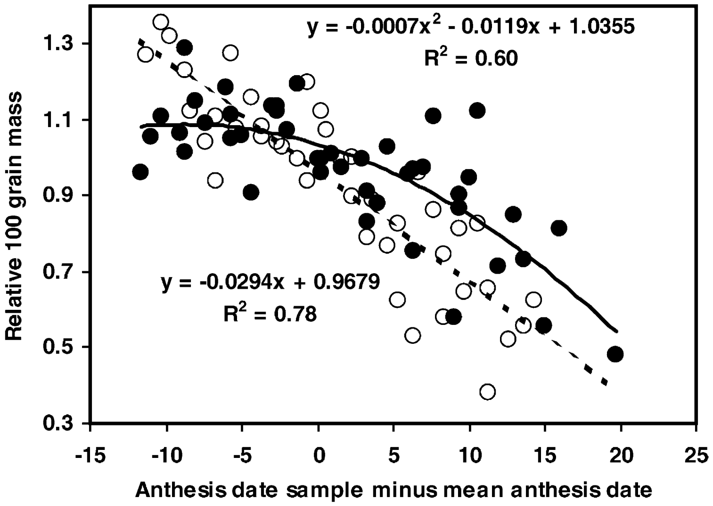

Fig. 9. Relative 100 grain weight for main shoot panicles as a function of their anthesis date for RCB-IC 911 (○···○) and WRajPop (●—●), grown in experiments which experienced end-of-season drought stress. Individual data points are means for panicles with a similar anthesis date within an experiment. Anthesis is expressed as the difference between the anthesis date of the sample and the mean anthesis date for the genotype in a particular experiment (positive value indicates later than average anthesis). Relative 100 grain mass is 100 grain mass of sample, relative to the average 100 grain mass of the variety in that experiment. As the anthesis date of panicles is in general normally distributed, samples close to the average anthesis date have the highest number of panicles and thus tend to have a relative grain mass close to unity.

mechanism to escape stress around anthesis of the main shoot through the production of nodal tillers. It has been suggested that asynchronous tillering in pearl millet provides phenological plasticity, allowing a fraction of the tillers to escape stress (Mahalakshmi et al., 1987). However, our results and those of a related study (van Oosterom et al., 2001a) show that an increase in the number of productive basal tillers does not substantially increase the range in anthesis dates. In addition, Craufurd and Bidinger (1988a) showed that basal tillers reach panicle initiation soon after the main shoot, suggesting limited options for stress-escape through basal tillers. However, even the small asynchrony between main shoots and basal tillers can cause substantial differences in anthesis, as illustrated by the bimodal distribution of anthesis date of the basal tillers in Fig. 6. Asynchrony is therefore not a genotype effect per sé, but also a result of tiller × stress interactions. Nodal tillers increase asynchrony, as they generally appear during the period between flag leaf emergence and mid-grain filling, and reach anthesis approximately 3 weeks later than the main shoot (Table 4). They first appear when the structural part of the panicle and the upper stem internodes are the main sinks in the plant. The significant relationship, under optimum conditions, between nodal tiller number and the size of the panicle sink, relative to the CGR, supports the hypothesis that the production of nodal tillers is a consequence of assimilate surplus. Therefore, their contribution to grain yield will generally decline as assimilate supply becomes more limited (Table 1). However, even under the low-yielding conditions of Jodhpur 1997, 1998, the contribution of nodal tillers to the grain yield of Nokha Local was 20 and 13%, respectively, and results of vom Brocke et al. (2001) confirm that prolific nodal tiller production can occur at yield levels well below 1 ton ha^{-1}. Presumably, even under these low-yielding conditions, the potential grain growth rate is too low for all available assimilates to be translocated to the grains. The modern cultivars, by contrast, produce few nodal tillers, as they have generally been selected for maximum grain yield under favourable conditions, where this insurance policy is of little use. Results of Mazaredo et al. (1996) on nodal tillering in deep water rice, showed that crops with a large proportion of nodal tillers always had lower grain yield than crops without nodal tillers. This is consistent with the low grain yield and prolific nodal tillering of the landraces under optimum conditions at Patancheru (Tables 1 and 2). If extensive nodal tillering is a symptom of assimilate surplus, then the high contribution of nodal tillers to grain yield at Patancheru (up to 25% for Nokha Local) indicates an inefficient use of available assimilates. As stress escape is of no importance under such conditions, the ability of landraces to produce nodal tillers (as a result of a relatively small investment in structural panicle weight) provides a specific adaptation to stress (particularly around anthesis when nodal tillers are produced) while carrying a yield penalty under optimum conditions.

4.4. Tailoring plant type to stress pattern

The yield architecture of the high-tillering landraces is aimed at minimising the risk of a crop failure under stress conditions. But as some of the adaptation strategies are particularly aimed at minimising the detrimental effects of stress around anthesis, this strategy assures maximum stability in environments where timing of stress is unpredictable and mid-season drought stress is likely to occur. This is consistent with the high probability of occurrence of pre-anthesis drought stress in western Rajasthan, where the landraces have evolved (van Oosterom et al., 1996). As landraces are the product of both natural and deliberate (by local farmers) selection, the plant type of landraces included in our study reflects the importance of risk avoidance to farmers in the drier areas of western Rajasthan (vom Brocke et al., 2001). The concept of an adapted plant type supports the conclusion of Ceccarelli et al. (1991) that yield stability in environments with unpredictable occurrence of stress is conferred by a combination of traits or even a mixture of plant types.

The low-tillering, large-seeded modern cultivars, by contrast, have been bred for high yield potential through a greater investment of assimilates into structural panicle weight and individual grain mass. However, the absence of significant differences in grain yield in the low-yielding environments (Table 2) illustrates that this plant type is not necessarily unadapted to stress. If stress only occurs after anthesis, the conservative strategy of the high-tillering landraces may have little advantage. Under such conditions, grain yield is negatively correlated with time to anthesis (Bidinger et al., 1987), but in the absence of drought around anthesis, the phenology of large panicles will not be delayed. Moreover, the number of productive tillers is reduced under post-anthesis drought stress (Bidinger et al., 1987), reducing the potential for high-tillering landraces to compensate for the small panicle size. Consistent with this is that in Eastern Rajasthan, where drought stress is likely to occur after anthesis, farmers prefer early varieties with large panicles and large grains (van Oosterom et al., 1996). Similarly, in the West African environments where low-tillering *Iniadi* germplasm (from which RCB-IC 911 is derived) is traditionally grown, the risk of post-anthesis drought stress is considerably higher than the risk of pre-anthesis drought stress (Sivakumar, 1988, 1992; Andrews and Anand Kumar, 1996). The low-tillering plant architecture might thus provide better adaptation to environments with predictable timing of drought stress.

The high-tillering plant type of the landraces had no obvious advantage under the stress conditions in our experiments (Table 2). This could partly be explained by the prevalence of post-anthesis drought stress in the experiments conducted in Rajasthan (Table 1). The effect of yield architecture on adaptation to specific stress patterns was clearer in selected experiments if RCB-IC 911 and WRajPop, which have similar phenology, are compared (Table 6). Under the post-anthesis drought stress of Jodhpur 1995, RCB-IC 911 yielded significantly more grain than WRajPop. The reduction in productive basal tiller number in the landrace was too much to adequately compensate for the smaller panicle size, while sufficient carbon was available to allow higher grain mass in RCB-IC 911. Hence, the high-tillering plant type had no advantage. In the dry season of 1995 at Patancheru, however, where pre-anthesis drought was temporarily relieved around anthesis, WRajPop had a non-significant yield advantage over RCB-IC 911, as the stress adversely affected the production of basal tillers in RCB-IC 911, but not in WRajPop. This resulted in a significantly higher grain number for the landrace, which compensated for the lower grain mass (Table 6). Recent analyses on a large population of Rajasthan landraces with contrasting yield architecture (van Oosterom, Weltzien, Bidinger, unpublished data) also show that high-tillering landraces that produce small

Table 6
Grain yield and yield components (per square metre) of WRajPop and RCB-IC 911 in three experiments with contrasting occurrence of drought stress[a]

	Drought stress		
	None (Patancheru 1995 rainy season)	Post-anthesis (Jodhpur 1995 rainy season)	Pre- and post-anthesis (Patancheru 1995 dry season)
Main shoot number			
RCB-IC 911	5.8 a	6.6 a	8.5 a
WRajPop	6.4 a	8.0 a	8.5 a
Basal tiller number			
RCB-IC 911	12.3 b	1.9 b	5.5 b
WRajPop	19.3 a	8.3 a	20.3 a
Grain yield (main shoot)			
RCB-IC 911	210 a	149 a	156 a
WRajPop	114 b	89 b	85 b
Grain yield (basal tillers)			
RCB-IC 911	248 a	25 b	23 b
WRajPop	225 b	56 a	99 a
Grain yield (all axes)			
RCB-IC 911	488 a	174 a	189 a
WRajPop	387 b	147 b	200 a
Grain number (all axes)			
RCB-IC 911	43506 a	19207 a	22608 b
WRajPop	45428 a	22093 a	33618 a
100 grain mass (average)			
RCB-IC 911	1.12 a	0.91 a	0.84 a
WRajPop	0.86 b	0.66 b	0.60 b
Biomass			
RCB-IC 911	1094 a	428 a	431 a
WRajPop	984 a	443 a	522 a

[a] Values followed by a different letter are significantly different at $P < 0.05$ according to Tukey's test for pair wise comparisons.

panicles yielded significantly more than low-tillering ones with large panicles and similar phenology under extreme mid-season drought stress in Rajasthan, but significantly less under post-anthesis drought stress at Patancheru. The existence of such significant cross-over interactions for grain yield would support the framework developed here that high-tillering and small panicles are particularly advantageous if drought stress occurs both before and after anthesis, but have little advantage if only post-anthesis drought stress occurs.

5. Conclusions

This paper developed a crop physiological framework to explain the repeatable G × E interaction for grain yield between high-tillering pearl millet landraces and modern low-tillering cultivars across favourable and stressed environments. It is concluded that these interactions are the result of two different yield strategies: avoidance of a crop failure in environments where the timing of stress is unpredictable (landraces) versus maximising yield potential (modern cultivars). It is hypothesised that the second strategy may also be useful in environments where the timing of stress occurrence is predictable (e.g. prevalence of post-anthesis drought). Although the adaptation strategy of the landraces carried a yield penalty under optimum conditions, this is of little concern to subsistence farmers in arid zones where favourable growing conditions are unlikely to occur. This framework could be a useful tool in a breeding program, targeting specific adaptation by identifying plant types that best match the prevalent stress patterns in a geographical area.

Acknowledgements

Staff of the cereals physiology and pearl millet breeding units at ICRISAT are acknowledged for conduction the experiments. Dr. N.L. Joshi of the CAZRI, Jodhpur, and staff at the Rajasthan Agricultural University, Fatehpur, are thanked for facilitating the experiments at their research station. Drs. M.J. Robertson and P.S. Carberry are thanked for reviewing earlier versions of the manuscript.

References

Andrews, D.J., Anand Kumar, K., 1996. Use of the west-African pearl millet landrace Iniadi in cultivar development. Plant Gen. Res. Newslett. 105, 15–22.

Andrews, D.J., Gupta, S.C., Pheru Singh, 1985. Registration of WC-C75 pearl millet. Crop Sci. 25,199–200.

Appa Rao, S., Mengesha, M.H., Vyas, K.L., Rajagopal Reddy, C., 1986. Evaluation of pearl millet germplasm from Rajasthan. Indian J. Agric. Sci. 56, 4–9.

Basford, K.E., Cooper, M., 1998. Genotype × environment interactions and some considerations of their implications for wheat breeding in Australia. Aust. J. Agric. Res. 49, 153–174.

Bidinger, F.R., Raju, D.S., 2000. Mechanisms of adjustment by different pearl millet plant types to varying plant populations. J. Agric. Sci. Camb. 134, 181–189.

Bidinger, F.R., Mahalakshmi, V., Talukdar, B.S., Alagarswamy, G., 1982. Improvement of drought resistance in pearl millet. In: Drought Resistance in Crops with Emphasis on Rice. International Rice Research institute, Los Baños, The Philippines, pp. 357–375.

Bidinger, F.R., Mahalakshmi, V., Rao, G.D.P., 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. I. Factors affecting yield under stress. Aust. J. Agric. Res. 38, 37–48.

Bidinger, F.R., Weltzien, R.E., Mahalakshmi, V., Singh, S.D., Rao, K.P., 1994. Evaluation of landrace topcross hybrids of pearl millet for arid zone environments. Euphytica 76, 215–226.

Bidinger, F.R., Chandra, S., Raju, D.S., 2001. Genetic variation in grain-filling ability in dwarf pearl millet [*Pennisetum glaucum* (L.) R. Br.] restorer lines. Theoret. Appl. Genet. 102, 387–391.

Bieler, P., Fussell, L.K., Bidinger, F.R., 1993. Grain growth of *Pennisetum glaucum* (L.) R. Br. under well-watered and drought-stressed conditions. Field Crops Res. 31, 41–54.

Boote, K.J., Kropff, M.J., Bindraban, P.S., 2001. Physiology and modeling of traits in crop plants: implications for genetic improvement. Agric. Syst. 70, 395–420.

Bramel-Cox, P.J., Andrews, D.J., Bidinger, F.R., Frey, K.J., 1984. A rapid method of evaluating growth rate in pearl millet and its weedy and wild relatives. Crop Sci. 24, 1187–1191.

Byerlee, D., Husain, T., 1993. Agricultural research strategies for favoured and marginal areas: the experience of farming systems research in Pakistan. Exp. Agric. 29, 155–171.

Ceccarelli, S., Acevedo, E., Grando, S., 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56, 169–185.

Ceccarelli, S., Grando, S., Impiglia, A., 1998. Choice of selection strategy in breeding barley for stress environments. Euphytica 103, 307–318.

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. Margraf Verlag, Weikersheim, Germany.

Cooper, M., Chapman, S.C., 1996. Breeding sorghum for target environments in Australia. In: Proceedings of the Third Australian Sorghum Conference, February 20-22, 1996, Tamworth, Australia.

Craufurd, P.Q., Bidinger, F.R., 1988a. Effect of duration of the vegetative phase on shoot growth, development and yield in pearl millet (*Pennisetum americanum* (L.) Leeke). J. Exp. Bot. 39, 124–139.

Craufurd, P.Q., Bidinger, F.R., 1988b. Effect of the duration of the vegetative phase on crop growth, development and yield in two contrasting pearl millet hybrids. J. Agric. Sci. Camb. 110, 71–79.

Craufurd, P.Q., Bidinger, F.R., 1989. Potential and realized yield in pearl millet (*Pennisetum americanum*) as influenced by plant density and life cycle duration. Field Crops Res. 22, 211–225.

Craufurd, P.Q., Peacock, J.M., 1993. Effect of heat and drought stress on sorghum (*Sorghum bicolor*). II. Grain yield. Exp. Agric. 29, 77–86.

Demotes-Mainard, S., Doussinault, G., Meynard, J.M., Gate, Ph., 1996. Is it possible to diagnose at harvest a problem of pollen sterility in wheat? Eur. J. Agron. 5, 169–180.

Dhamotharan, M., Weltzien R.E., Whitaker, M.L., Rattunde, H.F.W., Anders, M.M., Tyagi, L.C., Manga, V.K., Vyas, K.L., 1997. Seed Management Strategies of Farmers in Western Rajasthan in their Social and Environmental Contexts: Results from a Workshop using New Communication Techniques for a Dialogue between Farmers and Scientists, February 5–8, 1996, Digadi village, Jodhpur district, Rajasthan, India. Integrated Systems Project Progress Report No. 9. ICRISAT, Patancheru, India, pp. 47.

Edmeades, G.O., Daynard, T.B., 1979. The relationship between final yield and photosynthesis at flowering in individual maize plants. Can. J. Plant Sci. 59, 585–601.

FAO and ICRISAT, 1996. The World Sorghum and Millet Economies. Facts, trends and outlook. Food and Agriculture Organization (FAO) of the United Nations, Via delle Terme di Caracalla, 00100 Rome, Italy, and International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India, 68 pp.

Fussell, L.K., Pearson, C.J., 1978. Course of grain development and its relationship to black region appearance in *Pennisetum americanum.* Field Crops Res. 1, 21–31.

Garcia-Huidobro, J., Monteith, J.L., Squire, G.R., 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.). J. Exp. Bot. 33, 288–296.

Jackson, P., Robertson, M.J., Cooper, M., Hammer, G.L., 1996. The role of physiological understanding in plant breeding—from a breeding perspective. Field Crops Res. 49, 11–37.

Jones, R.J., Nelson, C.J., Sleper, D.A., 1979. Seedling selection for morphological characters associated with yield of tall fescue. Crop Sci. 19, 631–634.

Kelley, T.G., Parthasarathy Rao, P., Weltzien, R.E., Purohit, M.L., 1996. Adoption of improved cultivars of pearl millet in an arid environment: straw yield and quality considerations in western Rajasthan. Exp. Agric. 32, 161–171.

Kirby, E.J.M., Riggs, T.J., 1978. Developmental consequences of two-row ands six-row ear type in spring barley. 2. Shoot apex, leaf and tiller development. J. Agric. Sci. Camb. 91, 207–216.

Kollavalli, S., 1997. Water and nutrient management: farmers' practices, perceptions, and researchable issues. In: Seeling, B., Joshi, N.L. (Eds.), From Research Station to Farmer's Fields: Nutrient Management Research for Millet-based Cropping Systems of Western Rajasthan Proceedings of a Planning Workshop, May 20–22, 1996, Jodhpur, India, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India, and Central Arid Zone Research Institute, Jodhpur, Rajasthan, India, pp. 71–77.

Lafarge, T.A., Hammer, G.L., 2002. Tillering in grain sorghum over a wide range of population densities: modelling dynamics of tiller fertility. Ann. Bot. 90, 99–110.

López-Castañeda, C., Richards, R.A., Farquhar, G.D., Williamson, R.E., 1996. Seed and seedling characteristics contributing to variation in early vigor among temperate cereals. Crop Sci. 36, 1257–1266.

Mahalakshmi, V., Bidinger, F.R., Raju, D.S., 1987. Effect of timing of water deficit on pearl millet (*Pennisetum americanum*). Field Crops Res. 15, 327–339.

Manga, V.K., Yadav, O.P., 1995. Effect of seed size on development traits and ability to tolerate drought in pearl millet. J. Arid Environ. 29, 169–172.

Mazaredo, A.M., Laureles, E.V., Setter, T.L., 1996. Growth and yield of modern deepwater rice: Comparisons with modern irrigated rice. Field Crops Res. 46, 105–116.

Mohamed, H.A., Clark, J.A., Ong, C.K., 1988. Genotypic differences in the temperature responses of tropical crops. III. Light interception and dry matter production of pearl millet (*Pennisetum typhoides* S.H.). J. Exp. Bot. 39, 1137–1143.

Ong, C.K., 1983a. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). 1. Vegetative development. J. Exp. Bot. 34, 322–336.

Ong, C.K., 1983b. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). 4. Extension of individual leaves. J. Exp. Bot. 34, 1731–1739.

Pieters, G.A., van den Noort, M.E., 1988. Effect of irradiance and plant age on the dimensions of the growing shoot of poplar. Physiol. Plant. 74, 467–472.

Richards, R.A., 1989. Breeding for drought resistance—physiological approaches. In: Baker, F.W.G. (Ed.), Drought Resistance in Cereals. CAB International, Wallingford, UK, pp. 65–79.

Saxena, M.B.L., Subba Rao, G.V., Gupta, G.K., Verma, R.C., 1978. *Bajra* germplasm of arid areas of Rajasthan. Ind. J. Genet. Plant Breeding 38, 390–395.

Sharma, P.C., Pareek, R.S., 1993. Variability of southwest monsoon in west Rajasthan during last two decades. Mausam 44, 389–391.

Sivakumar, M.V.K., 1988. Predicting rainy season potential from the onset of rains on southern Sahelian and Sudanian climatic zones of West Africa. Agric. For. Meteor. 42, 295–305.

Sivakumar, M.V.K., 1992. Empirical analysis of dry spells for agricultural applications in West Africa. J. Clim. 5, 532–539.

Skinner, R.H., Nelson, C.J., 1994. Role of leaf appearance rate and the coleoptile tiller in regulating tiller production. Crop Sci. 34, 71–75.

Tivet, F., Pinheiro, B.D., De Raissac, M., Dingkuhn, M., 2001. Leaf blade dimensions of rice (*Oryza sativa* L. and *Oryza glaberrima* Steud.). Relationships between tillers and the main stem. Ann. Bot. 88, 507–511.

van Oosterom, E.J., Whitaker, M.L., Weltzien Rattunde, E., 1996. Integrating genotype × environment analysis, characterisation of drought patterns, and farmer preferences to identify adaptive plant traits for pearl millet. In: Cooper, M., Hammer, G.L. (Eds.), Plant Adaptation and Crop Improvement. CAB International, Wallingford, UK, pp. 383–402.

van Oosterom, E.J., Carberry, P.S., Hargreaves, J.N.G., O'Leary, G.J., 2001a. Simulating growth, development, and yield of tillering pearl millet. II. Simulation of canopy development. Field Crops Res. 72, 67–91.

van Oosterom, E.J., Carberry, P.S., O'Leary, G.J., 2001b. Simulating growth, development, and yield of tillering pearl millet. I. Leaf area profiles on main shoots and tillers. Field Crops Res. 72, 51–66.

van Oosterom, E.J., O'Leary, G.J., Carberry, P.S., Craufurd, P.Q., 2002. Simulating growth, development, and yield of tillering pearl millet. III. Biomass accumulation and partitioning. Field Crops Res., S0378-4290(02)00156-9.

Volenec, J.J., Nelson, C.J., 1981. Cell dynamics in leaf meristems of contrasting tall fescue genotypes. Crop Sci. 21, 381–385.

Volenec, J.J., Nelson, C.J., 1983. Responses of tall fescue leaf meristems to N fertilization and harvest frequency. Crop Sci. 23, 720–724.

vom Brocke, K., Presterl, T., Christinck, A., Weltzien, R.E., Geiger, H.H., 2001. Farmers' seed management practices open up new base populations for pearl millet breeding in a semi-arid zone of India. Plant Breeding 121, 36–42.

vom Brocke, K., Christinick, A., Presterl, T., Weltzien, R.E., Geiger, H.H., 2002. Effects of farmers' seed management on performance and adaption of pearl millet in Rajasthan, India. Euphytica, unpublished data.

Yadav, O.P., Weltzien, R.E., 1998. New Pearl Millet Populations for Rajasthan, India. Integrated Systems Project Report Series No. 10. ICRISAT, Patancheru, Andhra Pradesh, India, 88 pp.

Yadav, O.P., Weltzien, R.E., 2000. Differential response or landrace-based populations and high yielding varieties of pearl millet in contrasting environments. Ann. Arid Zone 39, 19–45.