

INFORMATION TO USERS

This reproduction was made from a copy of a document sent to us for microfilming. While the most advanced technology has been used to photograph and reproduce this document, the quality of the reproduction is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help clarify markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure complete continuity.
2. When an image on the film is obliterated with a round black mark, it is an indication of either blurred copy because of movement during exposure, duplicate copy, or copyrighted materials that should not have been filmed. For blurred pages, a good image of the page can be found in the adjacent frame. If copyrighted materials were deleted, a target note will appear listing the pages in the adjacent frame.
3. When a map, drawing or chart, etc., is part of the material being photographed, a definite method of "sectioning" the material has been followed. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again—beginning below the first row and continuing on until complete.
4. For illustrations that cannot be satisfactorily reproduced by xerographic means, photographic prints can be purchased at additional cost and inserted into your xerographic copy. These prints are available upon request from the Dissertations Customer Services Department.
5. Some pages in any document may have indistinct print. In all cases the best available copy has been filmed.

**University
Microfilms
International**

300 N. Zeeb Road
Ann Arbor, MI 48106

8514375

Bramel-Cox, Paula Jean

**EVALUATING THREE POTENTIAL SOURCES OF GERMPLASM TO IMPROVE
GROWTH RATE, GRAIN YIELD, AND HARVEST INDEX IN PEARL MILLET**

Iowa State University

Ph.D. 1985

**University
Microfilms
international** 300 N. Zeeb Road, Ann Arbor, MI 48106

**Evaluating three potential sources of germplasm to
improve growth rate, grain yield, and
harvest index in pearl millet**

by

Paula Jean Bramel-Cox

**A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY**

**Department: Agronomy
Major: Plant Breeding and Cytogenetics**

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

**Iowa State University
Ames, Iowa**

1985

TABLE OF CONTENTS

	Page
GENERAL INTRODUCTION	1
SECTION I. GROWTH ANALYSIS OF PEARL MILLET AND ITS WEEDY AND WILD RELATIVES	13
ABSTRACT	14
INTRODUCTION	15
MATERIALS AND METHODS	17
RESULTS	22
DISCUSSION	33
REFERENCES CITED	37
SECTION II. GROWTH CHARACTERISTICS OF GENOTYPES OF CULTIVATED PEARL MILLET AND ITS WEEDY AND WILD RELATIVES	39
ABSTRACT	40
INTRODUCTION	41
EXPERIMENTAL PROCEDURES	43
RESULTS AND DISCUSSION	47
CONCLUSIONS	65
ACKNOWLEDGEMENT	65
REFERENCES CITED	66
SECTION III. EXOTIC GERMPLOSM FOR IMPROVING GRAIN YIELD AND GROWTH RATE IN PEARL MILLET	67
ABSTRACT	68
INTRODUCTION	69
MATERIALS AND METHODS	71
RESULTS	76

	Page
DISCUSSION	90
REFERENCES CITED	94
SECTION IV. TRAIT ASSOCIATIONS IN INTROGRESSED POPULATIONS OF PEARL MILLET	96
ABSTRACT	97
INTRODUCTION	98
MATERIALS AND METHODS	100
RESULTS AND DISCUSSION	104
SUMMARY	122
REFERENCES CITED	123
 GENERAL CONCLUSIONS AND DISCUSSION	 124
ADDITIONAL REFERENCES CITED	128
ACKNOWLEDGEMENTS	133

GENERAL INTRODUCTION

Grain yield can be expressed by the formula: Grain yield = Growth rate x Growth duration x Harvest index (Takeda and Frey, 1977). Growth rate x growth duration determines biological yield, and harvest index measures the proportion of biological yield in the grain. Interspecific matings of oats (Avena sativa L.), barley (Hordeum spontaneum L.), and sorghum (Sorghum bicolor (L.) Moench) have been useful for improving grain yield and because the growth duration of some high yield segregates is no greater than current cultivars, this improvement in yield was caused indirectly through either higher harvest index and/or growth rate.

Singh and Stoskopf (1971) found that harvest index was positively correlated with grain yield in all cereals except oats, and Chaudhary et al. (1977) showed that it varied among cultivars of wheat (Triticum aestivum L.), was highly heritable, and positively correlated with grain yield. In the latter study, low soil fertility caused expression of high harvest index, but this trait was subject to genotype x environment interaction.

Rosielle and Frey (1975) found that oat lines selected for high harvest index were superior to those selected for grain yield only. Nass (1980) and Bhatt (1977) stated that this trait was a good selection criterion for improving grain yield of wheat, especially during early generations.

When Takeda et al. (1980a) predicted grain yields from growth rate and harvest index they found a coefficient determination of 0.94.

However, selection for very high harvest index in A. sativa x A. sterilis matings resulted in poor grain yields, which suggested that an optimum harvest index does exist (Takeda and Frey (in preparation)). A harvest index above optimum resulted in a constant grain yield and reduced straw yield (Takeda and Frey, 1977). Takeda et al. (1980b) postulated that for cereal crops with a long growth duration, harvest index was the limiting trait in grain production, whereas for crops with a limited duration, growth rate was the limiting trait. Oats grown in the midwestern U.S.A. have a short growth duration (Takeda et al. (1979). Thus, increasing growth rate is the most appropriate route to obtain greater productivity.

Pearson et al. (1977) found that pearl millet (Pennisetum americanum L.) had greater vegetative dry-matter production during the three weeks following emergence than did maize (Zea mays L.) or hybrid Pennisetum, but the highest rate of dry-matter production for all three crops occurred during silking and early grain filling.

Interspecific matings have been useful for transferring genes for resistance to disease from exotic, weedy, or wild relatives to the cultivated forms, but few matings have shown value for increasing vigor traits, such as biological or grain yield, growth rate, etc.

Gupta and Singh (1973) used exotic germplasm sources to improve general and specific combining ability of pearl millet lines, and Ahluwalia and Patnaik (1963) showed that genes from exotic genotypes increased heterosis and specific combining ability of this crop.

Takeda et al. (1979) studied intraspecific oat matings classified as adapted x adapted, adapted x semi-exotic, and adapted x exotic, and found that the first mating type gave the greatest proportion of

vigorous segregates. Heritabilities of vigor traits were similar in all three types of matings. Harvest index and growth rate were genetically related to yield, but were inherited independently. A negative error correlation between harvest index and growth rate indicated that they acted compensatorily to make grain yield adjustments to minor environmental changes. Interspecific oat matings (a) gave greater grain yield increases via growth rate than did intraspecific ones, (b) gave greater heritability for growth rate, and (c) produced a greater number of positive transgressive segregates for this trait.

The general objective of this study was to determine whether matings of cultivated pearl millet with weedy and wild strains would produce high yielding, high growth rate segregates. The specific objectives were to:

- (1) Evaluate adapted cultivated, unadapted cultivated, weedy, and wild strains of pearl millet for variation in growth rate, harvest index, grain yield, and growth patterns;
- (2) Compare unadapted cultivated, weedy, and wild strains for improving growth rate, grain yield, harvest index, and other traits in matings with pearl millet inbreds;
- (3) Compare the associations of physiological traits and traits of domestication when unadapted cultivated, weedy, and wild strains were mated with pearl millet inbreds.

Review of Literature

Evaluation of wild and weedy relatives

A few studies have compared a cultivated crop with its wild and weedy relatives for such traits as grain characteristics, growth patterns,

salt tolerance, and ripening behavior.

Evans and Dunstone (1970) compared hexaploid wheat with its tetraploid and diploid progenitors, and found as the level of ploidy and domestication increased, grain size, seedling establishment rate, and leaf size increased. Final dry weight/plant was similar for all wheats, however. Domestication and higher ploidy increased apical dominance of the inflorescence, and resulted in fewer tillers and more grains per plant. Mobilization of photosynthate from the stems and leaves probably increased with an increase in culm phloem capacity. Rate of photosynthesis at high light intensities was greater in wild diploids, but flag leaf area was reduced by domestication: The resulting lower flag leaf photosynthesis in domesticated wheat was compensated by a delayed flag leaf senescence. The authors concluded that increases in grain size, leaf size, and translocation of assimilates to the grain have been the dominant physiological changes that increased grain yield during the domestication of wheat.

According to El-Sharkawy et al. (1965), the greater yield of cultivated cotton (Gossypium hirsutum L.), compared with its wild relative, was the result of larger seeds and cotyledons, but not an increased photosynthetic rate. However, Elmore et al. (1967) reported significant differences between the primitive and cultivated cottons for photosynthetic rates. Bramel-Cox et al. (1984), in a comparison of cultivated, weedy, and wild pearl millet strains, found no variation for growth rate among cultivated genotypes, but on average, they were significantly inferior to wild and weedy accessions.

Rush and Epstein (1976, 1981) reported that some ecotypes of the wild tomato (Lycopersicon cheesmanii L.) could grow successfully in full seawater, whereas the cultivated tomato (L. esculentum Mill) died when grown in 50% seawater. The cultivated tomato could not withstand salinity because of its inability to keep Na below toxic levels in leaf tissue, whereas because the wild tomato could not distinguish between Na and K ions, it accumulated Na in the leaf tissue where Na substituted for K in metabolic functions. Grumet et al. (1981) found ripening patterns in tomato species that could be useful in cultivated strains.

Use of introgression to improve quantitative traits

The weedy and wild relatives of a crop may have potential to improve qualitatively inherited traits such as disease resistance and quantitatively inherited traits such as grain yield, fodder yield, drought resistance, etc. Coons (1975) found the wild Beta species were useful for improving disease resistance, yield, and other traits in Beta vulgaris (L.). Oldemeyer (1975) introgressed high yield genes from fodder beets into cultivated sugar beets, but little progress resulted. Meredith (1977) found fiber strength was increased with little reduction of yield in the cross of a tri-species Gossypium hybrid with G. hirsutum.

Rajhathy et al. (1963) postulated that interspecific hybrids in Hordeum may extend the growing area of barley via improved winter hardiness and drought tolerance. Wild Saccharum species have been introgressed with cultivated sugar cane (Saccharum officinarum L.) to improve drought and cold tolerance, erectness, vigor, sugar content, and tillering since the late 1800s. (Panje, 1972; Dunckelman and Breaux, 1972a, b;

Walker, 1972). Efron and Everett (1969) found teosinte (Zea mexicana) tended to reduce the vigor of corn hybrids as the proportion of teosinte germplasm increased, but teosinte and Mexican corns were excellent sources of genes for improving stover dry-matter production.

Rick (1974) increased the soluble-solids content of the cultivated tomato by 40% by introgression of genes for high-solids content from L. chmielewski (L.). Epstein et al. (1979) found that a cross between domesticated tomato and a salt-tolerant L. cheesmanii (L.) produced fruit at 70% seawater.

Hammons (1970) registered 'Spancross', a selection from a cross of Arachis hypogaea (L.) var. Argentine with the wild species, A. monitcola (L.), which yielded 3.5% more than the cultivated parent. Stalker et al. (1979) selected four lines with yields 56-68% more than the cultivated parent in a cross of a low-yielding peanut cultivar with a wild diploid relative.

Reeves (1950) recovered lines from a cross of teosinte with a maize inbred that yielded 20% more than the inbred parent, and Reeves and Buckholdt (1964) selected lines from a cross of maize and Tripsacum that had higher yields than the maize inbred. No lines had a higher testcross and two of the high-yielding lines showed the influence of Tripsacum genes on morphological traits.

Campbell and Frey (1972) increased the genetic variation for protein content in oats via interspecific crosses. Lawrence and Frey (1976), in a study of the inheritance of yield in A. sativa x A. sterilis matings, found that the weedy parent contributed about one-third of the plus

factors segregating for grain yield. Bloethe and Frey (1978) showed that increased grain yield of A. sterilis-derived lines was due to greater leaf area and leaf-area duration. She postulated that A. sterilis contributed either leaf growth and/or growth rate genes. Takeda et al. (1979) found greater genetic variation for growth rate index in interspecific matings of A. sativa and A. sterilis than in intraspecific matings. Interspecific matings generally gave transgressive segregates with higher growth rates, but there was specific nicking among parents in either intraspecific or interspecific matings. Murphy and Frey (1984) found means and genetic variances for grain yield were lower in multiple-parent oat populations with 12.5% wild germplasm than in populations derived from cultivars only. About 15% and 26% of lines from interspecific and intraspecific populations exceeded the highest-yielding parent. They concluded that for short-term use, a breeder should use only adapted oat lines as parents, but for long-term goals, the wild relatives were useful as gene sources.

Cox (1979) and Frey (1977) introgressed high-protein content and Thro (1982) introgressed high groat-oil content from A. sterilis into A. sativa. Kuenzel (1982) found high-protein lines of oats with improved yield and acceptable agronomic characters from interspecific crosses as well. Thomas et al. (1980) crossed A. magna (L.), a tetraploid, with A. sativa, a hexaploid, to improve protein content of A. sativa. There was good chromosome pairing in the backcrosses to A. sativa, and 80% of the backcross progeny had protein similar to A.

magna (32.4%). One plant had seeds 10% heavier than A. magna, with the desirable hull percentage of A. sativa.

Rodgers (1982) introgressed Hordeum spontaneum germplasm into H. vulgare to produce a population of random BC_0F_2 - through BC_4F_2 -derived lines. Transgressive segregation among BC_2 - BC_4 lines for high yield ranged from 1.7% to 9.6% for nine H. spontaneum parents. Some matings produced high-yielding lines despite having low means. BC_0 breeding value predicted the percentage of high-yielding progeny in the BC_2 to BC_4 quite well.

Interracial matings of sorghum in the BC_2 to BC_4 were shown by Cox et al. (1984a) to produce 1% transgressive segregates. One line from a mating involving race verticilliflorum had a 15% yield advantage and comparable plant height but earlier maturity than the cultivated parent. The greatest number of high-yielding lines were found in the BC_4 . Cox and Frey (1984) postulated that a regulatory mechanism in the wild sorghums may influence the value of wild x cultivated crosses. Therefore, the plant breeder must evaluate progeny from matings rather than the wild accessions per se when choosing parents for interspecific matings. Back-crossing or recurrent selection would be necessary to lower the frequency of regulatory alleles.

Overall, the wild and weedy relatives have been useful sources of genes for improving cereal crops. Because wild sorghums have a regulatory mechanism to maintain gene complexes necessary for survival (Cox and Frey (1984), the complexes of traits associated with domestication on one hand and survival in the wild on the other must undergo recombination to obtain acceptable introgressed progeny.

Trait associations in wild and cultivated populations and their hybrids

Oka and Morishima (1971) grew perennial and annual wild rices (Oryza sativa L.), hybrids between O. perennis and O. sativa, and indica and japonica cultivars to study the process of domestication in cultivated rice. The wild population contained desirable alleles for cultivation that increased in frequency when selected. They coined the term "cultivation pressure" to denote selection for these alleles. The bulk method of plant breeding asserted greater "cultivation pressure" than the pedigree method. The bulk population caused rapid change to cultivated types, especially for the nonshattering trait and domestication scores; however, grain weight did not change, even though the intra-population genetic variability decreased. Progeny derived via pedigree breeding gradually resembled either the wild or the cultivated types, whereas the bulk method eliminated the wild traits, and rapidly produced a homogeneous population. Oka and Morishima (1971) found that hand sowing increased cultivated traits while naturally sown populations remained wild.

Cox et al. (1984b) concluded that grain yield could be improved independently of "wild" or "cultivated" trait complexes in interracial matings of sorghum. specific traits that Belliard et al. (1980) found that distinguished between cultivated and wild forms of pearl millet were tillering rate, tiller numbers, rate of leaf senescence, certain flag leaf characteristics, diameter of the peduncle, 100-grain weight, grain hardness, grain shape and color, rachis length, number of bristles, and length of bristles.

Pernés et al. (1980) used principal component analysis on data from F_2 families of the matings made by Belliard et al. (1980). The primary axis was weighed heavily by traits associated with photoperiodic sensitivity. The secondary component was the axis of domestication, with high and low component scores associated with wild and cultivated type spikelets. The tertiary axis was composed of grain and tillering characters. Introgressed F_2 progeny had normal fertility and development. One parent, 'Massua', had diverged further from the wild than the other two. They grouped the traits into four gene structures: Morphological structures, photoperiodic sensitivity, spike and grain characteristics, and tillering organization. Shedding, aristation, presence of glumes, and the threshing ratio were determined by four independent genes. Domestication traits were disseminated on several axes with most of the variance accounted for by parental combinations.

Marchais and Tostain (1984) crossed two wild millets and two cultivated pearl millets, and found a distorted segregation of the wild floral traits and esterase genes had resulted from pollen with wild alleles being more competitive than pollen without wild alleles. Linkage occurred between the esterase allele for G.O.T. allozyme, pubescence, and pedicel length of the floral involucre.

Problems inherent in the introgression of genes from wild species into cultivated gene pools may be the association between desirable and undesirable alleles. During domestication, these undesirable alleles were eliminated without concurrent elimination of the desirable ones. The traits changed with domestication have been identified in a number

of crops and in most crops the alleles determining these traits were not found to be linked with desirable alleles from the wild populations.

Organization of the *Pennisetum americanum* subspecies

The *Pennisetum americanum* species has been organized into three subspecies by Brunken et al. (1977). The wild progenitor is *P. americanum* subsp. *monodii* (Maire) Brunken, which produces fully sterile hybrids with cultivated millet. It is characterized by the absence of the involucreal stalk, small seed size, elliptical seed shape, long fertile lemmas, and short inflorescences. It grows in the Sahel zone of West Africa, from Senegal to central Sudan, and the central highlands of the Sahara, where it is a natural colonizer.

P. americanum subsp. *stenostachyum* (Klotzsch) Brunken is a "mimic" weed called "shibra" which cannot be distinguished from cultivated types before flowering. Shibras disperse seed through callus formation. They resemble cultivated millets in gross morphological characteristics, but are intermediate for seed traits. Shibras are found with cultivated millets except in zones where millets were introduced recently.

Cultivated pearl millet, *P. americanum* subsp. *americanum* (L.) Leake, differs from wild types and shibras in the absence of callus formation at maturity. During domestication seed and inflorescence sizes have increased, but floral bracket length has decreased. Cultivated pearl millet grows from Senegal to South Africa, northeast India, portions of the Arabian Peninsula, Spain, southwestern U.S.A., and Australia, but greatest variation is found in the Sahel zone. Hybrid swarms occur at the margins of cultivated fields where crosses and

backcrosses between wild and cultivated millets give shibras. Shibras are stabilized and cannot survive without the crop.

The cultivated millet is a myriad of highly variable and locally restricted races. This variation resulted from domestication, migration, and local selection in the Sahel zone of West Africa.

Explanation of Thesis Format

This thesis contains five sections. Section I is a comparative growth analysis of cultivated pearl millet and its weedy and wild relatives. Section II is a summary of the association of certain physiological traits within cultivated pearl millet and its weedy and wild relatives. Section III is a study of the means, variances, and frequency distributions of grain yield, growth rate, and a number of physiological traits in matings of two pearl millet inbreds with an exotic accession, a weedy accession, and a wild accession. Section IV presents a study of trait associations in these populations.

Each section is in the form of a complete paper that will be submitted to a professional journal. Appendices to all sections appear at the end of the dissertation. Appendices and any reference to them will not be included in the published papers. A General Conclusion and Discussion will follow Section IV. References cited in the General Introduction and the General Conclusion and Discussion are listed in Additional References Cited, which follows the General Discussion. This format is authorized on p. 6 of the 1981 edition of the Iowa State University Thesis Manual.

**SECTION I. GROWTH ANALYSIS OF PEARL MILLET AND ITS WEEDY AND WILD
RELATIVES**

ABSTRACT

In a study of pearl millet (Pennisetum americanum (L.)) and its weedy and wild relatives (ssp. stenostachyum (Klotzch) Brunken and ssp. monodii (Zaire) Brunken), respectively, Bramel-Cox et al. (1984) found that the wild relative had a significantly higher growth rate than 15 cultivated or weedy genotypes. The latter 15 genotypes did not differ significantly for growth rate. In this study, these same 16 genotypes of pearl millet were examined for traits associated with growth rate, namely, crop growth rate, relative growth rate, net assimilation rate, relative leaf-area growth rate, and leaf-area ratio. The 16 genotypes were assigned to five groups according to origin, and group means were examined for these traits in five growth periods from 21 days after emergence to physiological maturity in each of two seasons. In the dry season, the greater growth rates of the wild relative and the African landraces resulted because leaf-area development extended longer into the season. The greater growth rate of the wild relative in the wet season was caused by extensive early leaf-area development and rapid growth of the shoot before flowering.

INTRODUCTION

Bramel-Cox et al. (1984) found that growth rates of cultivars, hybrids, and relatives of pearl millet (Pennisetum americanum L.) were similar, but a wild pearl millet accession had growth rate significantly higher than those of the other entries. Differences in growth rate (CGR) of crop plants can be due to differences in leaf-area index (LAI), net assimilation rate (NAR), leaf-area ratio (LAR), relative growth rate (RGR), and leaf-area duration (LAD).

Watson et al. (1963) found that winter wheat (Triticum aestivum L.) had higher CGR and LAI than spring wheat until ear emergence, but at ear emergence, they did not differ, and after emergence, leaf senescence was slower in spring wheat. Davidson (1965) suggested that leaf photosynthetic activity and distribution of assimilates before ear emergence in wheat determined the potential grain yield of the crop, whereas events after ear emergence determined the degree to which this potential was realized.

Williams et al. (1965, 1968), and Duncan and Hesketh (1968) concluded that CGR in the vegetative growth phase was directly related to LAI in maize (Zea mays L.). In a study by Muramoto et al. (1965), a high rate of leaf-area development led to an early attainment of maximum LAI and greater growth duration and grain yield in two species of cotton (Gossypium hirsutum L.) and their hybrid. And Baker and Gebeyehou (1982) found that high CGR during early growth and high LAD after anthesis gave high grain yield in spring wheat and barley (Hordeum vulgare L.). Bloethe-Helsel and Frey (1978) studied oat

cultivars and lines selected from matings of Avena sativa and A. sterilis L. and found no differences in CGR during early growth; however, after anthesis, the selected lines had LAD superior to the recurrent parent, which resulted in greater grain yield.

Gibson and Schertz (1977) concluded that the sorghum (Sorghum bicolor (L.) Moench) hybrid RS610 had a higher CGR than its parents due to greater LAI up to 45 days after emergence and greater NAR during grain filling. Watson and Witts (1963) concluded that current sugar beet (Beta vulgaris L.) cultivars produce high dry matter as a result of the introgression of genes for high LAI and NAR from their wild relatives.

Buttery and Buzzell (1972) found that soybean (Glycine max (L.) Merrill) lines selected for increased yield had greater NAR and decreased LAR, LAI, dry weight, and shoot/root ratio than did the discarded ones. Selection showed no effect on RGR and relative leaf-area growth rate (RLAR). Wallace and Munger (1966) showed distinct differences for RGR among dry bean (Phaseolus vulgaris L.) cultivars, and no physiological trait was correlated with biological or economic yield.

Generally, variation in CGR can be explained by differences in LAI, LAD, or NAR, and occasionally, increased CGR contributes to increased economic yield. The objective of this study was to compare CGR and its component traits, RGR, NAR, LAR, and RLAR for cultivated pearl millet with its weedy and wild relatives.

MATERIALS AND METHODS

The material for this study consisted of 16 cultivated, weedy, and wild genotypes of pearl millet (Table 1). They belong to four groups: four Indian hybrids (HYB), four Indian varieties (VAR), four African landraces (AFR), and one wild and three weedy accessions (NW).

Experimental Methods

Genotypes were evaluated in two experiments, one grown in January-April and the other in June-September, 1981, at the International Crops Research for the Semi-Arid Tropics (ICRISAT) near Hyderabad, India. Each experiment was conducted in a split-plot arrangement of a randomized complete-block design with four replicates. Genotypes were planted in whole plots that each consisted of four rows 9 m long with 75 cm between the rows and 10 cm between plants within rows. Subplots were harvest dates and each consisted of an area of 1.125 m^2 of competitive plants within the two center rows. Subplots were separated from one another by a border of 0.30 m^2 . Plant population was 130,000 plants per ha.

The dry-season (January-April) experiment was sown, irrigated, and emerged on 20, 21, and 26 January, respectively. Plots were watered by furrow irrigation every 14 days until 1 March, after which they were irrigated at 10-day intervals until final harvest. At each irrigation, ca. 30 mm of water was applied. Daylength during this experiment averaged 12.3 hr. At sowing, day and night temperatures were 30 and 15C, respectively, and near termination they averaged 38 and 23C,

Table 1. Area of adaptation or origin, maturity, and group for 16 genotypes of Pennisetum americanum

Genotype	Adaptation or origin	Maturity and group	
ICH-162	India	Late hybrid	(ssp. <u>americanum</u>)
ICH-412	India	Late hybrid	(ssp. <u>americanum</u>)
MBH-110	India	Early hybrid	(ssp. <u>americanum</u>)
BJ-104	India	Early hybrid	(ssp. <u>americanum</u>)
MC-C75	India	Early variety	(ssp. <u>americanum</u>)
ICMS-7819	India	Early variety	(ssp. <u>americanum</u>)
ICMS-7703	India	Late variety	(ssp. <u>americanum</u>)
ICMS-7937	India	Late variety	(ssp. <u>americanum</u>)
P-242	Mali	Late landrace	(ssp. <u>americanum</u>)
M-70-1	Tanzania	Early landrace	(ssp. <u>americanum</u>)
Ankoutess	Niger	Late landrace	(ssp. <u>americanum</u>)
SAD-222	Malawi	Early landrace	(ssp. <u>americanum</u>)
P-28111	Niger	Late weedy	(ssp. <u>stenostachyum</u>)
P-9461	Oasis	Early weedy	(ssp. <u>stenostachyum</u>)
	Niger		
P-2701	Mali	Late weedy	(ssp. <u>stenostachyum</u>)
Wild-	Birkina	Wild	(ssp. <u>monodii</u>)
Upper Volta	Fasso		

respectively. The rainy-season (June-September) experiment was sown, irrigated, and emerged on 20, 21, and 24 June. Daylengths averaged 13.4 hr. Temperatures were fairly stable at 30C for days and 22C for nights. No irrigation was needed for the wet-season experiment.

Plant dry weight at a given harvest date was determined by cutting all plants in a subplot at ground level, drying them at 75C for 36 hr, and weighing them. After flowering, the harvested biomass was divided into vegetative and reproductive portions, and dry weights were taken

on the two portions separately. All dry weights were converted to g/m^2 for analyses.

Leaf area was determined on the harvested sample at each harvest date. First, leaves and stems from all culms were separated, and a subsample of green leaves or green portions of leaves, amounting to ca. one-quarter of the total sample, was measured on a Lambda LI3000 leaf-area meter with a LI3050A conveyer belt assembly. To convert a subsample to subplot leaf area, the subsample value was multiplied by the ratio of subsample:subplot dry weights. LAI was computed as leaf area in m^2 divided by 1.125 m^2 , the land area of a subplot.

Harvests in both experiments were begun 21 days after seedling emergence and continued at 14-day intervals until physiological maturity, which gave five harvests for each genotype. Physiological maturity of primary panicles was recorded (in days after emergence) when the grain black layer appeared. Sampling seasons were 16 February to 23 April for the dry-season experiment and 15 July to 18-28 September (depending on genotype) for the rainy-season experiment.

Days to flowering was recorded as number of days from emergence to the date when 50% of the panicles on primary culms in a plot had stigmas completely emerged.

Statistical Analysis

The dry weights and leaf areas were used to compute crop growth rate (CGR), relative crop growth rate (RGR), net assimilation rate (NAR), and leaf-area ratio (LAR) by using the methods of Radford (1967).

Relative leaf-area growth rate (RLAR) was calculated by using the method of Buttery and Buzzell (1972).

Variance analyses for the data collected during the dry and wet seasons were conducted separately because a strong genotype x season interaction occurred.

Profile analyses (Johnson and Wichern, 1982) were conducted on CGR, RGR, NAR, LAR, and RLAR over growth periods. This analysis was used to determine whether differences among growth patterns of genotypes were significant. The basic model for each trait was:

$$x_{ij} = \mu_{ij} + \beta_i G_j + \delta_i G_j^2 + e_{ij}$$

x_{ij} = value of the i th entry in the j th growth period

μ_{ij} = overall mean

G_j = growth period number

e_{ij} = error deviation

β_i = linear coefficient for the i th entry

δ_i = quadratic coefficient for the i th entry

The analysis was conducted within groups of genotypes to test the significance of the linear and quadratic coefficients, and among groups to test the significance of differences between coefficients of different groups. The null hypothesis $H_0: \beta_1 = \beta_2 = \beta_3 = \beta_4 = 0$ and $\delta_1 = \delta_2 = \delta_3 = \delta_4 = 0$ was tested first. This H_0 may be written in matrix form as

$$H_0: \underline{C}_{k \times r} \underline{\beta}_{r \times p} \underline{M}_{p \times u} = \underline{0}_{k \times u}$$

where $\underline{C}$ and $\underline{M}$ are contrast matrices and $\underline{\beta}$ is the parameter matrix. $\underline{C}$ compares rows of the $\underline{\beta}$ matrix, and $\underline{M}$ compares columns of the $\underline{\beta}$ matrix.

To calculate an F-value to test the significance of the null hypothesis, a Wilk's Lambda, which is related to a likelihood ratio criterion, was calculated. Wilk's Lambda is equal to:

$$W = |\underline{E}|/|\underline{H} + \underline{E}| ,$$

where $\underline{E}$ and $\underline{H}$ are the error and model sums of squares and cross products matrices, respectively. This Wilk's Lambda can be converted to an F-value by:

$$F = \left(\frac{1 - W}{W} \right) \left(\frac{d + 1}{m + 1} \right) , \text{ where}$$

$$m = \frac{(k - u) - 1}{2} \quad \text{and} \quad d = \frac{p - r - u - 1}{2}$$

with $(2m + 2, 2d + 2)$ d.f.

If the quadratic term was not significant it was deleted from the model and a new hypotheses, $H_0: \beta_1 = \beta_2 = \beta_3 = \beta_4 = 0$ was tested; if the quadratic term was significant the model including both terms was used to test the significance of the linear term. Once the degree of significance for both terms was determined, a test of slope differences was conducted with the null hypotheses $H_0: \beta_1 = \beta_2 = \beta_3 = \beta_4$ and $\delta_1 = \delta_2 = \delta_3 = \delta_4$. Whether the quadratic term was included in the model depended upon whether it was significant or not.

RESULTS

The linear and quadratic coefficients were significantly different from zero for all genotypes for all traits. The within-group F-values for models 1 and 2 applied to CGR, RGR, NAR, RLAR, and LAR from the dry and wet seasons are presented in Table 2. A significant F-value indicated slope heterogeneity among the entry regressions for a trait within a group. Heterogeneity of regressions was found in the dry season for all traits in the VAR group, for CGR, RGR, and LAR in the HYB group, for LAR in the AFR group, and for RGR, RLAR, and LAR in the MW group (Table 2). In the wet season, heterogeneity was found for RGR, RLAR, and LAR in the HYB group, for LAR in the AFR group, and for CGR, NAR, RLAR, and LAR in the MW group.

CGRs of HYB and VAR groups were similar in the dry season and changed little over growth periods (Fig. 1). CGR for the NEED group increased to a maximum in period 3, decreased in period 4, and increased again in period 5. AFR and MILD groups had the lowest CGR in period 1 and increased gradually to a maximum at period 4, when they had the highest CGRs recorded. In the among-group comparisons (Table 3), there were significant differences for MILD vs. other entries for periods 1 and 4. AFR differed significantly from HYB and VAR in periods 1, 3, and 4.

In the wet season, AFR, NEED, and VAR groups had similar patterns for CGR over growth periods (Fig. 1). Their CGRs increased to period 3, and decreased in period 4, and remained constant in period 5. CGR of the MILD group, which was the lowest of any group in period 1, was the highest of all groups in periods 2 through 5. HYB group had a

Table 2. F-value and significance of Model 1 (linear coefficient homogeneity) and Model 2 (quadratic coefficient homogeneity) for CGR, RGR, NAR, RLAR, and LAR in the wet and dry seasons

Traits	Dry season							
	Model 1 ^a				Model 2 ^b			
	HYB	VAR	AFR	WM	HYB	VAR	AFR	WM
CGR	3.6*	3.8*	1.3	0.1	2.9	5.8*	0.7	2.9
RGR	6.3**	8.8**	0.6	4.5*	5.2**	9.9**	0.4	0.1
NAR	0.6	10.7**	1.2	2.6	0.5	16.7**	0.9	2.8
RLAR	1.8	5.8**	3.3	4.1*	1.9	6.8**	0.6	4.2*
LAR	3.7*	3.4*	10.5**	11.8**	0.6	1.1	2.2	0.9
	Wet season							
	HYB	VAR	AFR	WM	HYB	VAR	AFR	WM
CGR	0.6	0.3	0.7	5.3*	0.8	1.1	0.3	2.1
RGR	4.1*	0.1	0.6	2.9	3.4	1.0	0.5	2.8
NAR	0.8	1.2	2.2	1.8	2.4	2.1	1.0	3.9*
RLAR	4.4*	0.3	0.1	4.7*	5.6**	2.9	0.7	3.9*
LAR	7.4*	1.6	10.8**	3.6*	3.8*	1.5	0.9	0.7

^a Model 1 = $H_0: \beta_1 = \beta_2 = \beta_3 = \beta_4$.

^b Model 2 = $H_0: \delta_1 = \delta_2 = \delta_3 = \delta_4$.

*, ** Significance at 0.05 and 0.01 levels, respectively.

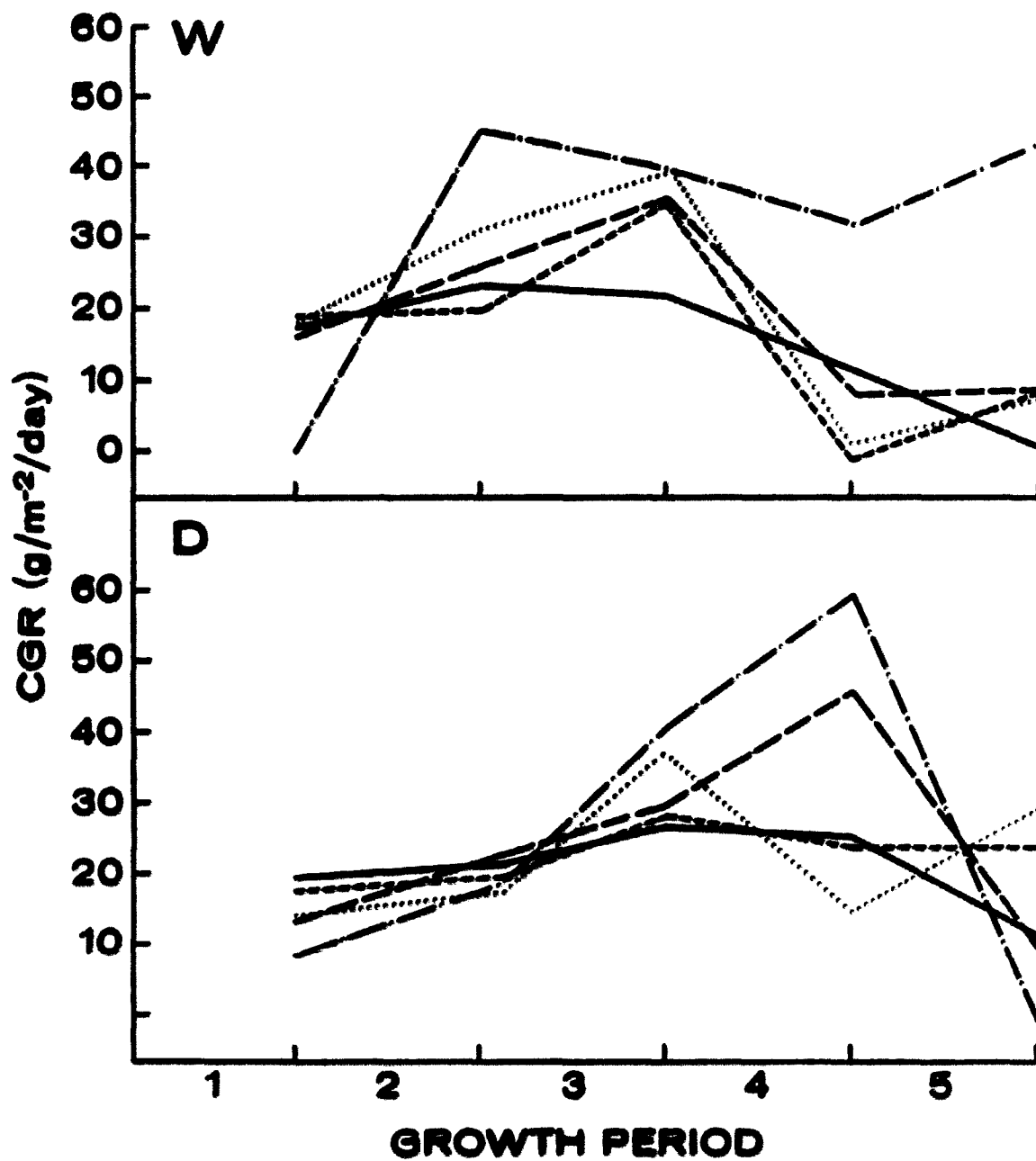


Figure 1. Mean CGRs for the five groups of pearl millet during five growth periods when evaluated during the wet (W) and dry (D) seasons. HYB —, VAR ---, AFR — —, WEED, WILD — . —

nearly constant CGR in periods 2 through 4. In the between-group comparisons (Table 3), the only significant differences for CGR were between WILD vs. others in periods 1, 2, and 5.

HYB, which showed similar CGR profiles in both seasons, had a relatively constant CGR in all periods. WEED and VAR groups had maximum CGRs in period 3 in both seasons; AFR reached maximum CGRs in periods 3 and 4 in the wet and dry seasons, respectively.

RGRs of all groups were similar over the entire dry season (Fig. 2), with a gradual decrease from one period to the rest. WILD, WEED, and AFR differed significantly from HYB and VAR and from each other in period 1 (Table 3). In periods 3 and 4, AFR differed significantly from HYB and VAR. In the wet season, WEED, AFR, HYB, and VAR groups had similar RGR profiles, whereas WILD was very different, especially in the early growth periods. This group had the lowest RGR in period 1, and the highest in period 2. After that, its pattern was similar to those of the other groups. This pattern difference is verified by between-group comparisons (Table 3) where the RGR profiles of AFR, HYB, and VAR were similar, but differed significantly from WILD in periods 1 and 2.

For NAR, RLAR, and LAR, no data could be computed for period 1 the dry-season experiment because leaf-area measurements were not taken at that sampling date. In the dry season, the patterns for NAR, RLAR, and LAR were similar except in period 5, when NARs of VAR, HYB, and WILD increased but those of AFR and WEED decreased (Fig. 3). No significant differences occurred for NAR in the dry season (Table 3). In the wet

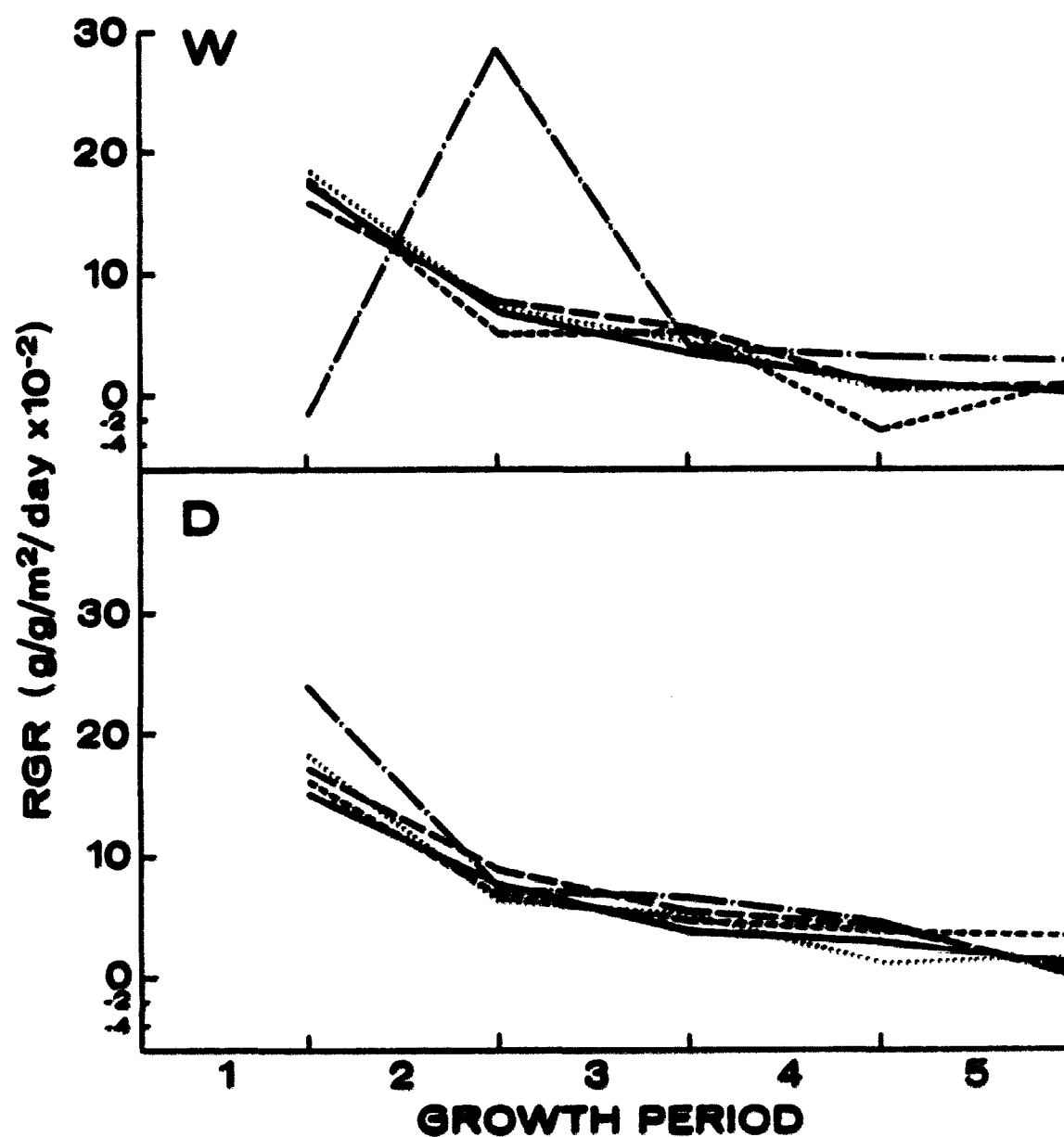


Figure 2. Mean RGRs for the five groups of pearl millet during five growth periods when evaluated during the wet (W) and dry (D) seasons. HYB —, VAR ---, AFR — —, NEED, WILD — . —

Table 3. Significance of the among-group comparisons for CGR, RGR, NAR, RLAR, and LAR for each growth period and season separately

Trait	Comparison	Dry season					Wet season				
		Growth period					Growth period				
		1	2	3	4	5	1	2	3	4	5
CGR	WILD vs. Rest	**	n.s. ^a	n.s.	*	n.s.	**	**	n.s.	n.s.	**
	WEED vs. Cult.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	HYB, VAR vs. AFR	**	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	HYB vs. VAR	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
RGR	WILD vs. Rest	**	n.s.	n.s.	*	n.s.	**	**	n.s.	n.s.	n.s.
	WEED vs. Cult.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	HYB, VAR vs. AFR	**	n.s.	**	*	n.s.	*	n.s.	n.s.	n.s.	n.s.
	HYB vs. VAR	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
NAR	WILD vs. Rest	--	n.s.	n.s.	n.s.	n.s.	**	**	n.s.	n.s.	n.s.
	WEED vs. Cult.	--	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	HYB, VAR vs. AFR	--	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.
	HYB vs. VAR	--	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
RLAR	WILD vs. Rest	--	n.s.	*	**	**	**	**	**	n.s.	n.s.
	WEED vs. Cult.	--	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	HYB, VAR vs. AFR	--	**	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.
	HYB vs. VAR	--	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LAR	WILD vs. Rest	--	*	**	**	**	*	n.s.	n.s.	**	n.s.
	WEED vs. Cult.	--	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	HYB, VAR vs. AFR	--	**	**	**	**	n.s.	n.s.	**	*	n.s.
	HYB vs. VAR	--	*	*	**	**	n.s.	n.s.	n.s.	**	n.s.

^a Nonsignificant.

*, ** Significant at the 0.05 and 0.01 levels, respectively.

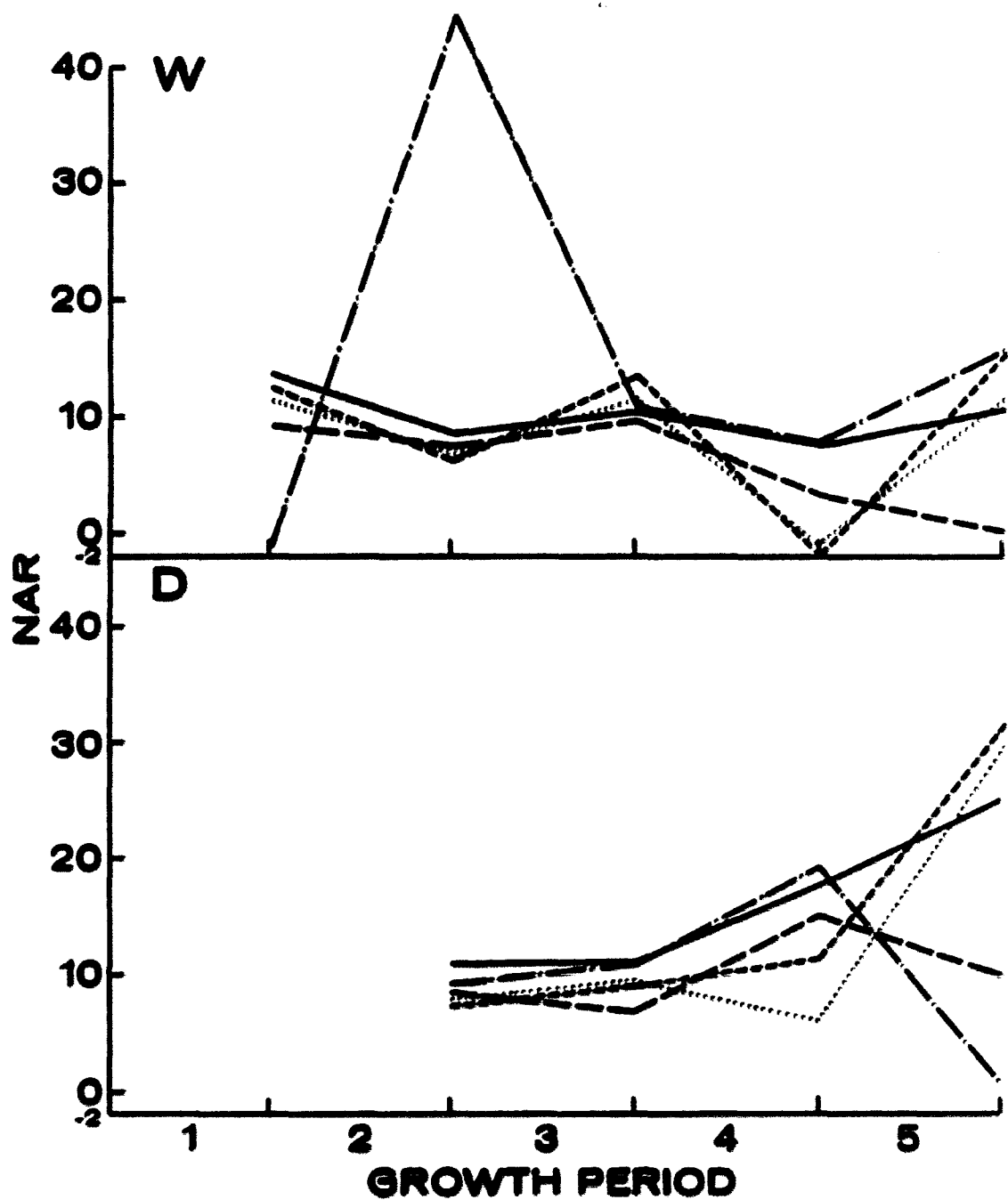


Figure 3. Mean NARs for the five groups of pearl millet during five growth periods when evaluated during the wet (W) and dry (D) seasons. HYB —, VAR ---, AFR — —, WEED, WILD — . —

season, all groups except WILD had similar profiles for NAR at all harvests. HYB and WILD showed a leveling-off of NAR in periods 3 through 5. The WILD entry had the lowest NAR in period 1 but its NAR increased greatly in period 2. Between-group comparisons (Table 3) verified that the difference between WILD and other entries was significant in periods 1 and 2. Also, AFR showed a significantly lower NAR than HYB and VAR in period 1. In both seasons, all groups except WILD had similar profiles for NAR.

In the dry season, RLAR decreased gradually to minimum values in period 4 or 5 for all groups of entries (Fig. 4). Between-group comparisons (Table 3), however, did show some cases of significant differences at individual growth periods. WILD was significantly different from other entries in the last three periods, whereas NEED was significantly different in period 4. AFR differed significantly from HYB and VAR in periods 2, 3, and 5. In the wet season, NEED, VAR, HYB, and AFR had maximum RLARs in period 1, followed by gradual decreases over the remaining periods. WILD had a relatively constant RLAR over all periods. Between-group comparisons (Table 3) showed that differences in RLAR profiles were significant in periods 1 through 3. In both seasons, the profiles were similar over periods 2 through 5.

In the dry season, LAR profiles were similar for all groups of entries, i.e., there were gradual decreases over all periods (Fig. 5). Between-group comparisons (Table 3) showed that WILD had a significantly greater LAR in all periods and that AFR, HYB, and VAR differed significantly. In the wet season, all groups except WILD had gradual and

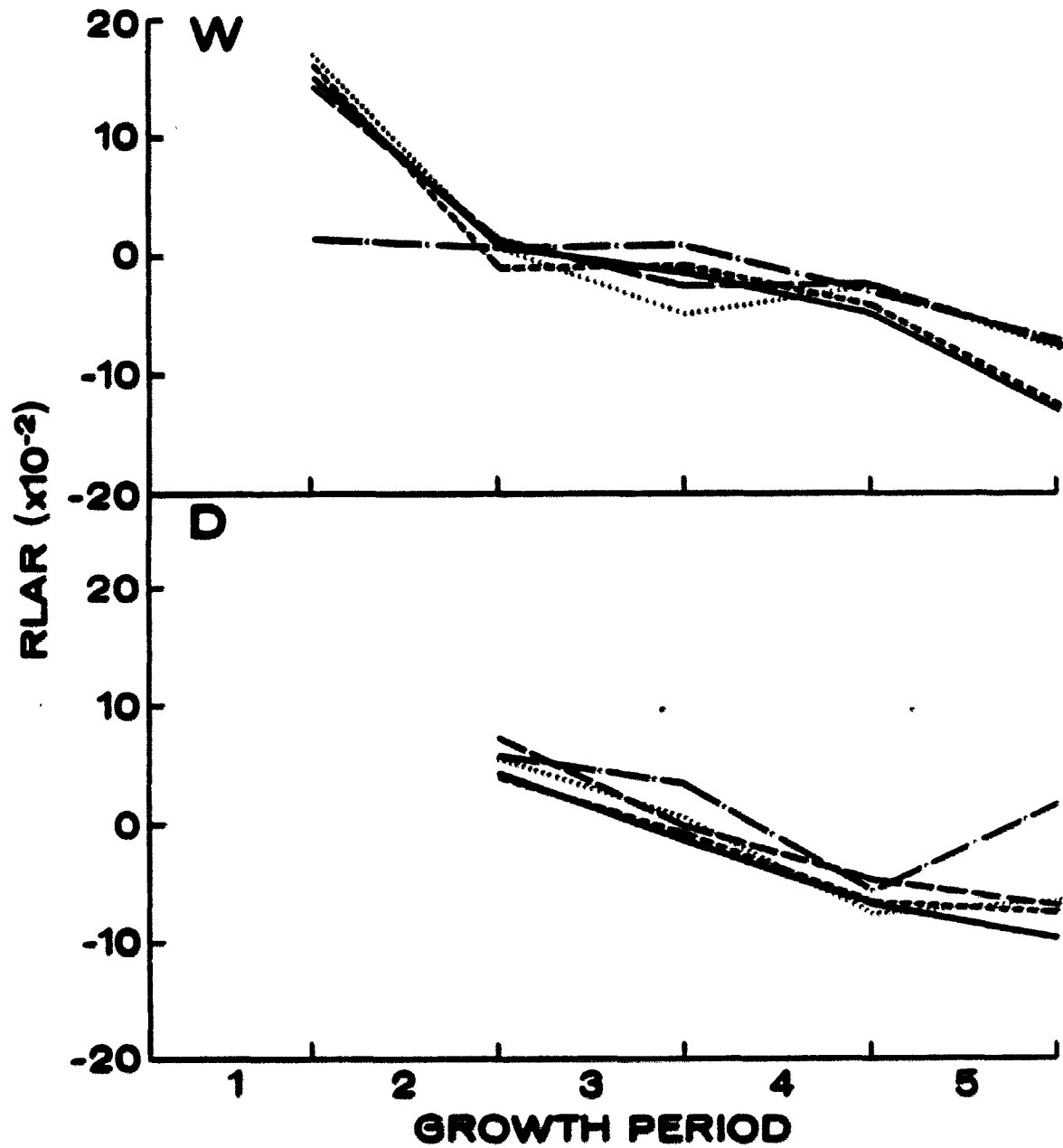


Figure 4. Mean RLARs for the five groups of pearl millet during five growth periods when evaluated during the wet (W) and dry (D) seasons. HYB —, VAR ---, AFR —, WEED, WILD — . —

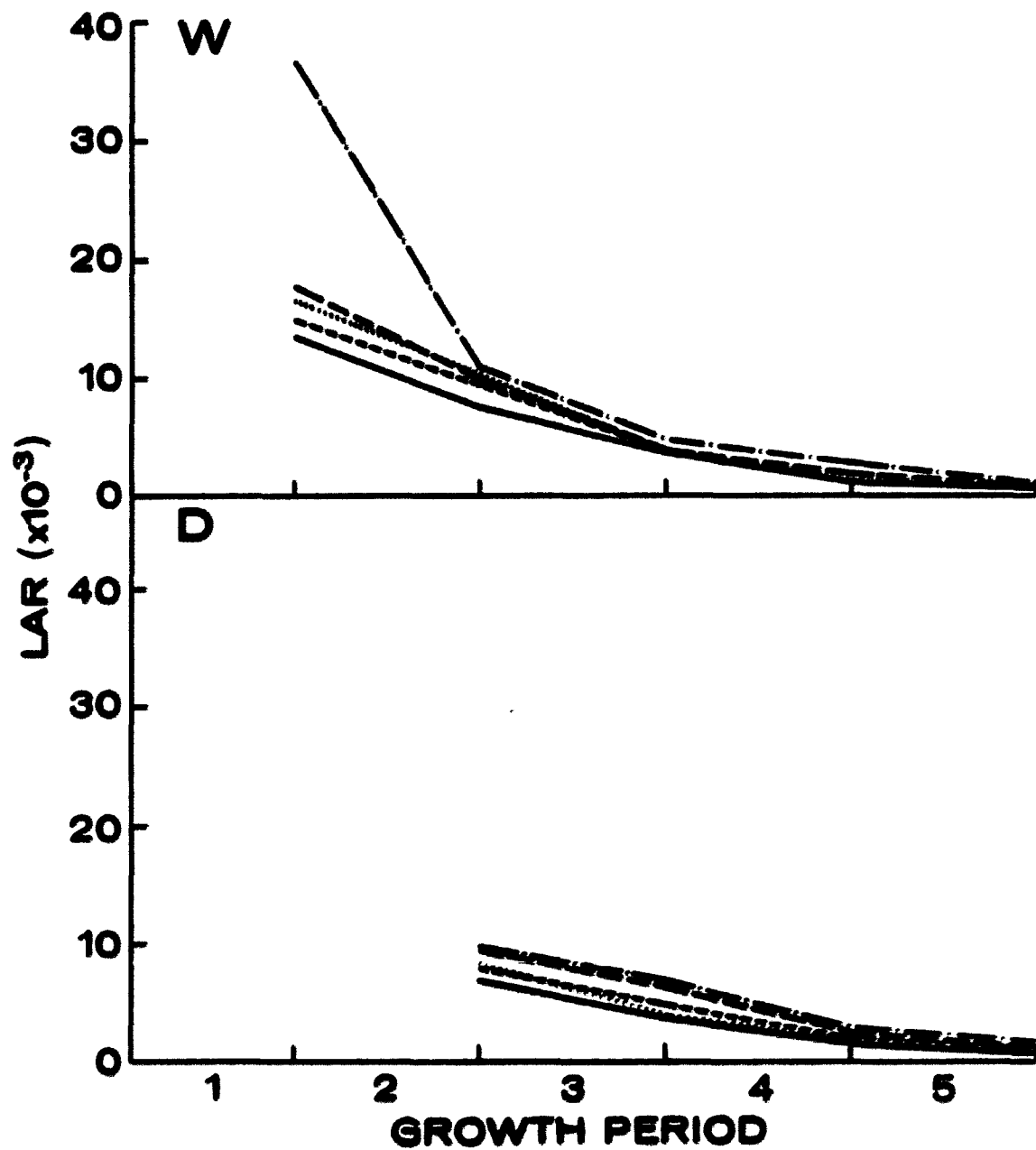


Figure 5. Mean LARs for the five groups of pearl millet during five growth periods when evaluated during the wet (W) and dry (D) seasons. HYB —, VAR ---, AFR — —, WEED, WILD — . —

similar decreases in LAR. WILD had the same profile as other groups for periods 2 through 5, but in period 1 it had a much greater LAR. Between-group comparisons (Table 3) verified that WILD had a significantly higher LAR in periods 1 and 4. Although the differences in LAR were small, AFR did differ significantly from HYB and VAR in periods 3 and 4, and HYB differed significantly from VAR in period 4. For periods 2 through 5 all groups had similar profiles in both seasons. WILD had the highest LAR in all periods.

In summary, the WILD group tended to have a pattern of development different from those of all other groups of entries, as exemplified by differences in CGR, RGR, and NAR in the first two periods and in LAR and RLAR in period 1. VAR, HYB, AFR, and NEED groups had similar profiles for all traits.

DISCUSSION

Whereas significant differences occurred among groups of pearl millet entries for profile patterns of CGR, RGR, NAR, RLAR, and LAR over the growing seasons, the only major difference was between WILD and other groups. The WEED group closely resembled the cultivated groups, HYB, VAR, and AFR, probably because it grows pannictically with the cultivated crop, and thus has opportunity for gene flow between between the two groups. Also, a weedy millet's survival may depend upon its ability to mimic the cultivated crop. These results corroborate those of Bramel-Cox et al. (1984), who showed that the WILD entry differed significantly in overall growth rate from all other entries in both wet and dry seasons. They found, however, that significant variation occurred among the other groups for growth rate in the dry season.

The WILD relative develops in a mixed stand where early seedling establishment may be critical to its survival. Rapid establishment would require that an extensive root system be established early to meet vegetation requirements for water and nutrients later in the growing season. Once the root system has been adequately established, a rapid vegetative growth can be supported with water and nutrients. This growth pattern might not be selected for in the cultivated crop, which is grown in pure stands: thus the WILD and cultivated pearl millets would be expected to differ in their growth patterns, especially in the early periods in the wet-season experiment. The results of this study give strong evidence that growth patterns of the WILD entry closely

resembled the scenerio postulated as necessary for its survival in the natural environment.

In the wet season, the measurements for CGR, RGR, NAR, and RLAR indicate that the WILD entry did not increase its vegetative dry weight and leaf area proportionately in period 1. CGR, RGR, and NAR of the WILD were greater in period 2 than in period 1, but LAR was lower and RLAR was the same. So in period 2, there was a rapid accumulation of vegetative dry matter without a proportionate increase in leaf area. RLAR remained the same over all harvests, which means that high leaf area was established early in the growth cycle and its rate of development was constant over the entire season; thus, the WILD entry had a greater assimilatory capacity per unit of time or per unit of dry weight in the second period when there was competition for assimilate between stem and reproductive organ development.

Rapid vegetative growth ceased for all millets when the reproductive stage occurred. And all traits that measured vegetative development nearly ceased in periods 3, 4, and 5 for all groups of entries. However, note that the WILD entry always had the highest values for these traits in periods 3, 4, and 5. Therefore, one can hypothesize that the greater growth rate and final biological yield of the WILD entry resulted because it had greater early leaf area and root establishment, which permitted greater vegetative growth during the critical period before flowering, when the "fixed capital" (Bramel et al., 1984) of the plant was established. The greater "fixed capital" provided more capacity for reproductive growth.

The pattern of development in the WILD pearl millet could be useful in cultivated varieties and hybrids in which seedling establishment often limits grain yield. Rapid root growth coupled with accelerated vegetative growth before flowering would result in a greater assimilatory capacity before reproductive growth. This greater assimilatory capacity coupled with efficient partitioning to the reproductive organs could result in a greater economic yield despite the limited growth duration of this crop.

The differential patterns for CGR and its component traits in the wet and dry seasons must have resulted from environmental differences between the two seasons. In the dry season, the early part was cool and no differential photoperiodic response would have occurred among entries. The greatest differential between seasons for CGR occurred between AFR and WILD. The AFR and WILD groups had similar growth patterns in the dry season, but in the wet season they differed greatly.

The differential patterns of the WILD entry in the two seasons were a product of environmental differences in the wet and dry seasons. The dry season is characterized by cool early season temperatures which may have slowed early vegetative and root growth with consequent limitation on water, nutrients, and assimilates. As a result, CGR showed a steady increase to a maximum in period 4. In the wet season, when temperatures were warm and water abundant, its maximum occurred by period 2. These differences in growth patterns of the WILD in the two seasons could explain the results of Bramel-Cox et al. (1984) where the WILD differed significantly from all the other genotypes for growth

rate in the wet season but was similar to the AFR genotypes in the dry season.

The results of the dry season experiment may be applicable only in an irrigated environment where it is possible to extend the growing season and take advantage of high solar radiation. Since most millet production is in the wet season under rainfed conditions, the dry season results may not be applicable for the normal production of pearl millet.

REFERENCES CITED

- Baker, R. J., and G. Gebeyehou. 1982. Comparative growth analysis of two spring wheats and one spring barley. *Crop Sci.* 22:1225-1229.
- Bloethe-Helsel, D., and K. J. Frey. 1978. Grain yield variations in oats associated with differences in leaf area duration among oat lines. *Crop Sci.* 18:765-769.
- Bramel, P. J., P. N. Hinz, D. E. Green, and R. M. Shibles. 1984. Use of principal component analysis in the study of three stem termination types of soybeans. *Euphytica* 33:387-400.
- Bramel-Cox, P. J., D. J. Andrews, F. R. Bidinger, and K. J. Frey. 1984. A rapid method of evaluating growth rate in pearl millet and its weedy and wild relatives. *Crop Sci.* 24:1187-1191.
- Buttery, B. R., and R. I. Buzzell. 1972. Some differences between soybean cultivars observed by growth analysis. *Can. J. Plant Sci.* 52:13-20.
- Davidson, J. L. 1965. Some effects of leaf area control on the yield of wheat. *Aust. J. Agric. Res.* 16:721-731.
- Duncan, W. G., and T. D. Hesketh. 1968. Net photosynthetic rates, relative leaf growth rates and leaf numbers of 22 races of maize grown at eight temperatures. *Crop Sci.* 8:670-674.
- Gibson, P. T., and K. F. Schertz. 1977. Growth analysis of a sorghum hybrid and its parents. *Crop Sci.* 17:387-391.
- Johnson, R. A., and D. W. Wichern. 1982. Applied multivariate statistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.
- Muramoto, H., J. Hesketh, and M. El-Sharkawy. 1965. Relationships among rate of leaf area development, photosynthetic rate and rate of dry matter production among American cultivated cottons and other species. *Crop Sci.* 5:163-166.
- Radford, P. J. 1967. Growth analysis formulae--their use and abuse. *Crop Sci.* 7:171-175.
- Takeda, K., and K. J. Frey. 1977. Growth rate inheritance and associations with other traits in backcross populations of *Avena sativa* x *A. sterilis*. *Euphytica* 26:309-317.

- Wallace, D. H., and H. M. Munger. 1966. Studies of the physiological basis for yield differences. II. Variations in dry matter distribution among aerial organs for several dry bean varieties. *Crop Sci.* 6:503-507.
- Watson, D. J., and K. J. Witts. 1963. The net assimilation rates of wild and cultivated beets. *Ann. Bot. N.S.* 23:431-439.
- Watson, D. J., G. N. Thorne, and S. A. M. French. 1963. Analysis of growth and yield of winter and spring wheats. *Ann. Bot. N.S.* 27:1-21.
- Williams, W. A., R. S. Loomis, and C. R. Lepley. 1965. Vegetative growth of corn as affected by population density. II. Components of growth, net assimilation rate, and leaf-area index. *Crop Sci.* 5:215-219.
- Williams, W. A., R. S. Loomis, W. G. Duncan, A. Dourat, and F. Munez A. 1968. Canopy architecture at various population densities and the growth and grain yield of corn. *Crop Sci.* 8:303-308.

**SECTION II. GROWTH CHARACTERISTICS OF GENOTYPES OF CULTIVATED PEARL
MILLET AND ITS WEEDY AND WILD RELATIVES**

ABSTRACT

The potential of a germplasm source for improving production in a crop may be assessed in two ways. With one, representative genotypes of the potential sources are mated to the crop species to assess their value as parents for improving certain traits. The second makes a comparison by measuring traits on the various entries per se. This latter method was used to evaluate 16 genotypes of pearl millet representing four groups of genotypes--adapted-cultivated genotypes, unadapted-cultivated genotypes, weedy relatives, and wild relatives--in two different seasons. Traits measured were growth rate, biological yield, grain yield, harvest index, days to flowering, two measures of tillering type, seed weight, and threshing percentage. Means and mean squares were compared and the correlations among these traits were assessed with their degrees of relationship of genotypes held constant.

It was found that little variation occurred among adapted-cultivated genotypes for any trait. The wild and weedy relatives were greater than the cultivated entries for certain traits and lower for other traits. These relatives may serve as sources of genes for improving biological yield, grain yield, and growth rate of cultivated pearl millet. Few significant correlations occurred between grain yield and the other traits in the 16 genotypes.

INTRODUCTION

The potential of exotic sources of germplasm, i.e., unadapted populations or wild or woody relatives, for improving adapted, desirable cultivars of a crop species, makes use of two experimental procedures. With one, matings between adapted and exotic types are evaluated (Frey et al., 1984). With the other, exotic sources per se are compared with the adapted, cultivated type for traits of interest.

Evans and Dunstone (1970) compared hexaploid wheat with its tetraploid and diploid progenitors, and found that increased grain and leaf size and higher harvest index were the dominant physiological changes that caused increased grain yield during the evolution of cultivated wheat (Triticum aestivum). El-Sharkawy et al. (1965), who studied Gossypium species with different genomes and ploidy levels, found that all species had similar photosynthetic rates, but those with higher dry weight production had greater leaf areas.

From an evaluation of a salt-susceptible cultivated tomato (Lycopersicon esculentum) and four wild ecotypes (L. spp.) that were salt tolerant, Rush and Epstein (1976) found that the wild accessions had a common, but unique, mechanism for controlling the effect of Na in the leaves. Further, nine species of wild tomatoes had a different pattern of ripening than did the cultivated tomato (L. esculentum) (Grumet et al., 1981).

In this study, a number of growth characteristics were measured on four types of millet; two were cultivated (Pennisetum americanum ssp. americanum), one adapted and one unadapted to India; one was a weedy

relative (P. americanum ssp. stenostachyum (Klotzch) Brunken), and one was a wild relative (P. americanum ssp. monodii (Maire) Brunken), adapted to the drier regions of Africa. The objective was to compare and evaluate several growth characteristics, including growth rate, of genotypes of these four millet types, to assess their value as sources of improvement for grain yield and these associated traits.

EXPERIMENTAL PROCEDURES

Materials

The materials for this study were the 16 genotypes of pearl millet given in Table 1. The millet genotypes included eight Indian hybrids and cultivars, four African landraces, and one wild and three weedy accessions. These categories of genotypes generally exhibited the characteristics given by Brunken et al. (1977) and Belliard et al. (1980).

Experimental Methods

The pearl millet genotypes were evaluated in two experiments, one grown in January-April and the other in June-September, 1981, at the International Crops Research Institute for the Semi Arid Tropics, near Hyderabad, India. Each experiment was conducted in a split-plot arrangement using a randomized complete-block design with four replicates. Genotypes were grown in whole plots, each consisting of four rows 9 m long, with 75 cm between rows and 10 cm between plants within a row. Subplots were harvest dates and each consisted of an area of 1.125 m^2 of competitive plants harvested from the center two rows of the whole plot. Subplots were separated from one another by a border of 0.30 m^2 . Harvest dates were randomized among subplots within a whole plot. The plant population for all experiments was 130,000 plants per ha.

The dry-season (January-April) experiment (hereafter denoted D) was sown, irrigated, and emerged on 20, 21, and 26 January, respectively. Plots were watered by furrow irrigation every 14 days until 1 March. after which they were irrigated at 10-day intervals until the last

Table 1. Area of adaptation or origin, maturity, and group for
16 genotypes of Pennisetum americanum used in our study

Genotype	Adaptation or origin	Maturity and group	
ICH-162	India	Late hybrid	(ssp. <u>americanum</u>)
ICH-412	India	Late hybrid	(ssp. <u>americanum</u>)
MBH-110	India	Early hybrid	(ssp. <u>americanum</u>)
BJ-104	India	Early hybrid	(ssp. <u>americanum</u>)
WC-C75	India	Early variety	(ssp. <u>americanum</u>)
ICMS-7819	India	Early variety	(ssp. <u>americanum</u>)
ICMS-7703	India	Late variety	(ssp. <u>americanum</u>)
ICMS-7937	India	Late variety	(ssp. <u>americanum</u>)
P-242	Mali	Late landrace	(ssp. <u>americanum</u>)
M-70-1	Tanzania	Early landrace	(ssp. <u>americanum</u>)
Ankoutess	Niger	Late landrace	(ssp. <u>americanum</u>)
SAD-222	Malawi	Early landrace	(ssp. <u>americanum</u>)
P-28111	Niger	Late weedy	(ssp. <u>stenostachyum</u>)
P-9461	Oasis	Early weedy	(ssp. <u>stenostachyum</u>)
	Niger		
P-2701	Mali	Late weedy	(ssp. <u>stenostachyum</u>)
Wild-	Birkina	Wild	(ssp. <u>monodii</u>)
Upper Volta	Fasso		

harvest. At each irrigation, ca. 30 mm of water was applied. Day-length during this experiment averaged 12.3 hr. At sowing, day and night temperatures were ca. 30 and 15C, respectively, but they gradually increased until harvest, when they averaged ca. 38 and 23C, respectively. The rainy season (June-September) experiment (hereafter denoted N) was sown, irrigated, and emerged on 20, 21, and 24 June. Daylengths during this experiment averaged 13.4 hr., and temperatures were fairly stable at 30C for days and 22C for nights. No irrigation was needed for this experiment.

The traits measured in this experiment, their abbreviations, methods used to measure the traits, and their units of measurement are listed in Table 2. The number of effective basal tillers, total basal tillers, and aerial tillers were counted on a plot basis from plants harvested for yield determination. To be classified effective, a tiller had a mature head at harvest.

Analyses of data were conducted separately for each season because a strong genotype x season interaction existed. For analysis, the 16 genotypes were divided into five groups: Indian hybrids (HYB), Indian varieties (VAR), African landraces (AFR), weedy relatives (NEED), and wild relative (WILD).

Table 2. Abbreviations and method of measurement and units of measurement for the traits measured in this study

Trait measured	Abbreviation	Method used	Units of measurement
Growth rate	GR	method used in Bramel-Cox et al. (1984)	$\text{g/m}^2/\text{day}$
Grain yield	GY	g/m^2 converted to kg/ha	kg/ha
Biological yield	BY	g/m^2 converted to kg/ha	kg/ha
Harvest index	HI	grain yield/ biological yield	--
Threshing percentage	TH	grain yield/weight of heads unthreshed	--
Days to flowering	FLW	number of days from seedling emergence to the date when 50% of the panicles in a plot had stigmas completely emerged	DAE
Seed weight	SW	weight of 500 seeds	g/500 seeds
Effective basal tiller ratio	ETP	number of effective basal tillers/total number of basal tillers	--
Aerial tillers per basal tiller	NDP	number of aerial tillers/total number of basal tillers	--

RESULTS AND DISCUSSION

Means and Variances

Means and ranges for nine traits measured in the wet- and dry-season experiments are presented in Table 3 for the five groups of pearl millet, and degrees of significance of mean squares for the various sources of variation in the analyses of variance are given in Tables 4a and 4b for the dry- and wet-season experiments, respectively. The wet season is the normal growing season for pearl millet in most areas of its production.

In the dry-season experiment, the only source of significant variation among group means for BY was for AFR vs. IND (HYB and VAR) (Tables 3 and 4a). Despite the large ranges within groups, no within-group mean square was significant. In the wet season, all cultivated entries (both adapted and unadapted) had similar means for BY of ca. 10,000 kg/ha, but the NEED group had 25% greater BY and the WILD entry had a BY more than twice as large as the mean of the cultivated entries. The WILD entry differed significantly from the mean of all other entries, and the NEED group differed significantly from the cultivated group means. No significant variation occurred among cultivated entries within groups (Table 4b) for BY, but the NEED group had significant variation within the group.

In the dry season, mean GY showed a progressive reduction from the Indian hybrids, which yielded 4791 kg/ha, down to the WILD accession, with 721 kg/ha. Mean squares for among group means were significant for all comparisons except HYB vs. VAR, and significant variation occurred

Table 3. The means and ranges for the five groups of genotypes of pearl millet for BY, GY, HI, GR, SW, TH, ETP, NDP, and FLW when calculated in the dry and wet seasons

Group	Season		BY	GY	HI
			(kg/ha)	(kg/ha)	
Indian hybrid (HYB)	D	Mean	13128	4791	0.37
		Range	6129-18335	2439-5856	0.31-0.47
	W	Mean	10192	3561	0.35
		Range	6055-14869	2120-7001	0.28-0.38
Indian variety (VAR)	D	Mean	12519	4162	0.33
		Range	8056-21026	2775-7634	0.32-0.35
	W	Mean	9891	3622	0.36
		Range	8374-11118	2445-5025	0.35-0.38
African landrace (AFR)	D	Mean	15438	3435	0.22
		Range	12315-22176	1913-8264	0.14-0.30
	W	Mean	10301	2914	0.29
		Range	7491-14439	1804-4605	0.21-0.34
Weedy relative (WEED)	D	Mean	13184	1798	0.15
		Range	7665-20869	265-2703	0.07-0.19
	W	Mean	12632	2301	0.18
		Range	8375-15895	146-366	0.12-0.22
Wild relative (WILD)	D	Mean	15597	721	0.04
	W	Mean	21941	1561	0.07
LSD	D		4110	1340	0.06
	W		1832	1389	0.06

Traits					
GR (g/m ² /da)	SW (g/500 seeds)	TH	ETP	NDP	FLW
10.12 5.52-14.83	8.12 5.79-11.31	0.73 0.71-0.75	0.39 0.19-0.62	0.20 0.15-0.23	47 35-55
10.34 8.01-17.44	7.95 4.56-12.15	0.75 0.69-0.78	0.42 0.01-0.81	0.20 0.00-0.64	46 38-58
9.14 6.91-13.66	8.18 6.95-9.46	0.74 0.70-0.77	0.30 0.21-0.39	0.31 0.21-0.41	48 40-51
10.44 7.34-13.16	7.33 4.36-8.94	0.80 0.78-0.82	0.27 0.01-0.50	0.25 0.00-0.71	47 42-53
13.71 7.67-25.17	8.26 6.11-10.52	0.72 0.62-0.87	0.24 0.11-0.39	0.43 0.18-0.96	53 49-61
10.61 7.45-17.28	6.57 2.7-11.71	0.77 0.65-0.83	0.34 0.09-0.56	0.64 0.00-1.92	58 42-64
11.45 8.08-16.04	6.64 3.22-9.07	0.52 0.36-0.62	0.37 0.21-0.48	1.64 0.81-2.35	51 45-60
13.65 9.57-14.83	5.62 3.41-7.87	0.64 0.48-0.74	0.45 0.01-0.75	1.95 0.26-5.00	60 50-64
18.56	3.25	0.19	0.72	3.71	59
16.94	3.36	0.32	0.66	2.83	61
4.75	1.42	0.17	0.15	0.50	--
3.63	1.19	0.08	0.27	0.71	--

Table 4a. Degrees of significance for mean squares from the ANOVA for eight traits measured on the 16 genotypes in the dry-season experiment

	d.f.	Trait							
		BY	GY	HI	GR	SW	TH	ETP	NDP
Entry	15	*	**	**	**	**	**	**	**
Among	4								
WILD vs. rest.	1	n.s. ^a	**	**	**	**	**	**	**
WEED vs. cult.	1	n.s.	**	**	**	**	**	n.s.	**
AFR vs. IND	1	**	**	**	n.s.	n.s.	n.s.	**	n.s.
HYB vs. VAR	1	n.s.	n.s.	**	n.s.	n.s.	n.s.	*	n.s.
Within	11								
HYB	3	n.s.	n.s.	**	**	**	n.s.	**	n.s.
VAR	3	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
AFR	3	n.s.	**	**	n.s.	**	*	**	*
WEED	2	n.s.	n.s.	**	**	**	**	*	**

^a Nonsignificant.

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Table 4b. Degrees of significance for mean squares from the ANOVA for eight traits measured on the 16 genotypes in the wet-season experiment

	d.f.	Trait							
		BY	GY	HI	GR	SW	TH	ETP	NDP
Entry	15	**	*	**	**	**	**	**	**
Among	4								
WILD vs. rest.	1	**	**	**	**	**	**	**	**
WEED vs. cult.	1	**	**	**	**	**	**	*	**
AFR vs. IND	1	n.s. ^a	*	**	n.s.	**	n.s.	n.s.	**
HYB vs. VAR	1	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	n.s.
Within	11								
HYB	3	n.s.	n.s.	n.s.	n.s.	**	*	**	n.s.
VAR	3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
AFR	3	n.s.	n.s.	*	n.s.	**	**	n.s.	**
WEED	2	**	n.s.	**	n.s.	*	**	**	**

^a Nonsignificant.

*, ** Significant at the 0.05 and 0.01 levels, respectively.

within the VAR and AFR groups. In the wet season, the same comparisons among group means showed significance as in the dry season, but no significant variation occurred among entries in any group. Mean GYs were lower in the wet season than in the dry season for both the Indian and the African groups, but they were greater for the WEED and WILD groups.

The progressive reduction in the group means was similar for GY and HI within both seasons. However, differences in the means for HI were significant for all groups, whereas for GY, there were no significant differences between the two adapted types in the dry season. In the wet season, there was significant variation for all comparisons among group means except HYB vs. VAR, and the within-group variation was significant for all groups except HYB.

The WILD entry had the largest GR in both seasons, whereas the AFR group in the dry season and the WEED group in the wet season had intermediate GRs. In both seasons, the only significant among-group comparisons were between the WILD vs. rest and WEED vs. cultivated (Tables 4a and 4b). Significant within-group mean squares occurred for the HYB and WEED groups in the dry season. The significant relationships among groups were similar for GR and BY in the wet season.

Takeda and Frey (1977) showed that biological yield was the product of growth rate and growth duration: Therefore, an increase in GR when growth duration is held constant would be expected to increase BY. This relationship was found to exist for the cultivated groups in both seasons, but for the WEED and WILD groups there were inverse

associations between GR and BY when compared across seasons.

All cultivated groups had similar means for SW in the dry season, whereas WEED was intermediate between the cultivated and WILD groups. The small seeds produced by the wild and weedy relatives would be an undesirable trait for varieties and hybrids. Both the AFR and HYB groups had significant within-group mean squares, but the largest-seeded entry was in the HYB group. In the wet season, the SW means of the AFR, WEED, and WILD groups were significantly smaller than those of the HYB and VAR groups.

The weedy and wild relatives had low threshing percentages. In the wet season, the WEED and WILD groups had higher mean THs than in the dry season, but they were still at an undesirable level. This lower TH was indicative of the presence of bristles and small seeds in these two groups.

Brunken et al. (1977) have described the African landraces as having one primary spike with several noneffective tillers, and the Indian varieties and hybrids as having a primary spike with several effective tillers. In this study, the proportion of effective basal tillers was only slightly, though significantly, different between the Indian and African types. The mean ETP of the wild entry was high, which may indicate that this entry had a better partitioning of resources between the primary spike and tillers, so that a greater proportion of the basal tillers contributed to yield. The WILD entry might contribute genes that could improve this trait in cultivated millet, where only 20-40% of the tillers contribute to yield. The ranges for ETP were

greater in the wet season than in the dry season for all groups, indicating a more variable response among entries in the June-September season.

In both seasons, the HYB and VAR groups had similar and low values for NDP, as shown by the nonsignificant mean square for HYB vs. VAR, and the group means (Table 3), respectively. The AFR group did not differ from the HYB and VAR groups in the dry season, but it differed significantly in the wet season. The WEED and WILD groups had the largest NDP. Aerial tillers are not desirable except when the sink is limited by a low number of basal tillers or when a long and favorable growing season occurs. In the cultivated types, only 20-40% of the basal tillers contribute to yield, therefore increasing the ETP might be a more efficient method of increasing grain yield than increasing NDP. The development of aerial tillers indicates a low apical dominance of the terminal spike on the basal tiller. In the WEED and WILD groups, the spikes and seeds are both small, so any one spike does not provide a strong "sink" for the "sources" of that tiller. Nodal buds develop into spikes as the sink strength is reduced, and they may contribute to grain yield in these groups.

There is an association between growth duration and FLW in pearl millet. A difference in FLW between the dry and wet seasons was due to photoperiodic sensitivity of the entries making up groups. The adapted types had similar FLW means in the two seasons as expected when the genotypes were photoperiodic insensitive. The AFR and WEED groups differed between the two seasons for both FLW mean and range, indicating

photoperiod sensitivity, as hypothesized by Brunken et al. (1977) and Belliard et al. (1980).

Overall, the WILD group was at the extreme of the 16 entries for most traits, and the WEED group was intermediate between the WILD and cultivated groups. Since the phenotypes and therefore probably genotypes of these two relatives were so different from the cultivated types, they might be sources of genes for modifying and hopefully improving BY, GR, and ETP in the cultivated varieties and hybrids. Generally, the HYB and VAR groups had homogeneous BYs and GRs in both growing seasons: The only exception was the significant variation within HYB entries for GR in the dry season. For ETP, the HYB were significantly superior to VAR in both seasons, but neither group was very elite for this trait when compared to the WILD entry. The adapted strains (HYB and VAR) were the least variable, whereas the entries in the AFR and WEED groups were more variable. The adapted Indian cultivars were products of intense breeding effort to similar production environments, which may account for the lower variation within these groups, while the African landraces together with the weedy relatives were products of local selection for specific adaptation. This specific adaptation for both groups was for a number of highly variable environments, which may explain the increased variation within the groups.

Trait Associations

Grain yield of cereals is a product of biological yield and harvest index, whereas in turn, biological yield is a product of growth rate and growth duration (Takeda and Frey, 1977). Various associations

among these four traits were important to manipulating them genetically to improve grain yield of oats, and the same situation may occur for pearl millet. The relationships of GR with GY, BY, and HI for the dry season are presented in Fig. 1a, 2a, and 3a, respectively, and for the wet season in Fig. 1b, 2b, and 3b, respectively.

The scatter diagrams provide visual evidence of the associations among the four traits for the 16 genotypes; however, to quantify these associations and to reduce the effect of the extreme trait values shown by the wild and weedy relatives, a type of partial correlation was computed for each trait pair in each season. The influence that these extreme values would have on the magnitudes of correlations can be visualized from Figs. 1, 2, and 3. For computing a partial correlation, scores were assigned to accessions according to their potential degrees of genetic relationship to the Indian cultivated types, i.e., scores of 1 to 4 were assigned to Indian varieties and hybrids, African landraces, weedy entries, and the wild accession, respectively. The partial correlation was computed between two traits holding the degree of relationship score constant. The partial correlations computed in this way are given for the dry and wet seasons in Table 5.

No plus or minus relationship was found between GR and GY in either season (Fig. 1 and Table 5). However, there were significant positive associations between GR and BY in both seasons (Fig. 2 and Table 5). The scatter diagram between GR and HI (Fig. 3) indicated a positive relationship between these traits; but the correlation between them (Table 5) was not significant in either season.

Figure 1. Scatter diagrams of GR plotted against GY for the HYB and VAR group ● , AFR group ▲ , and WEED group and wild entry ■ in the dry (a) and wet (b) seasons

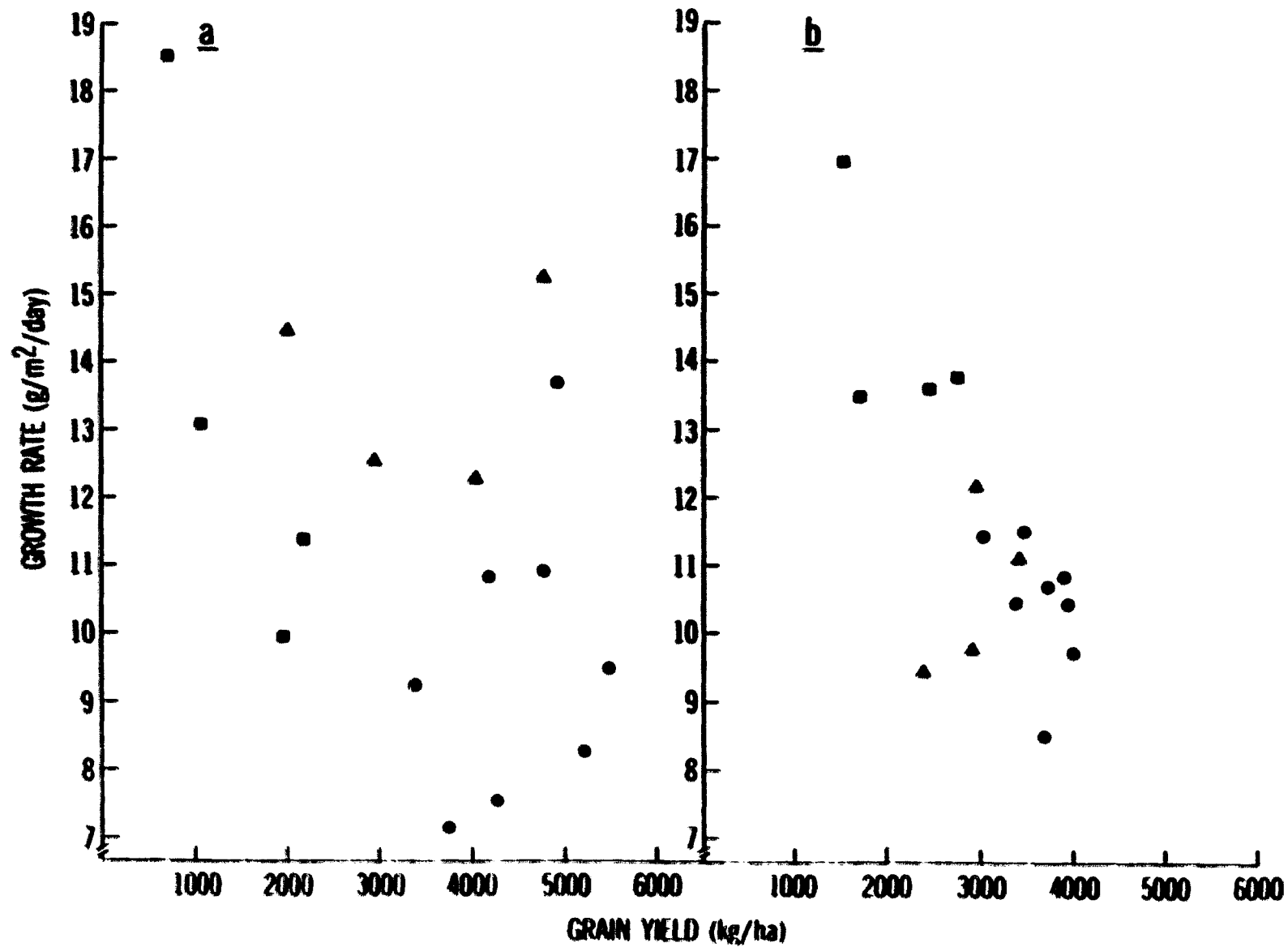


Figure 2. Scatter diagrams of GR plotted against BY for the HYB and VAR group ● , AFR group ▲ , and WEED group and WILD entry ■ in the dry (a) and wet (b) seasons

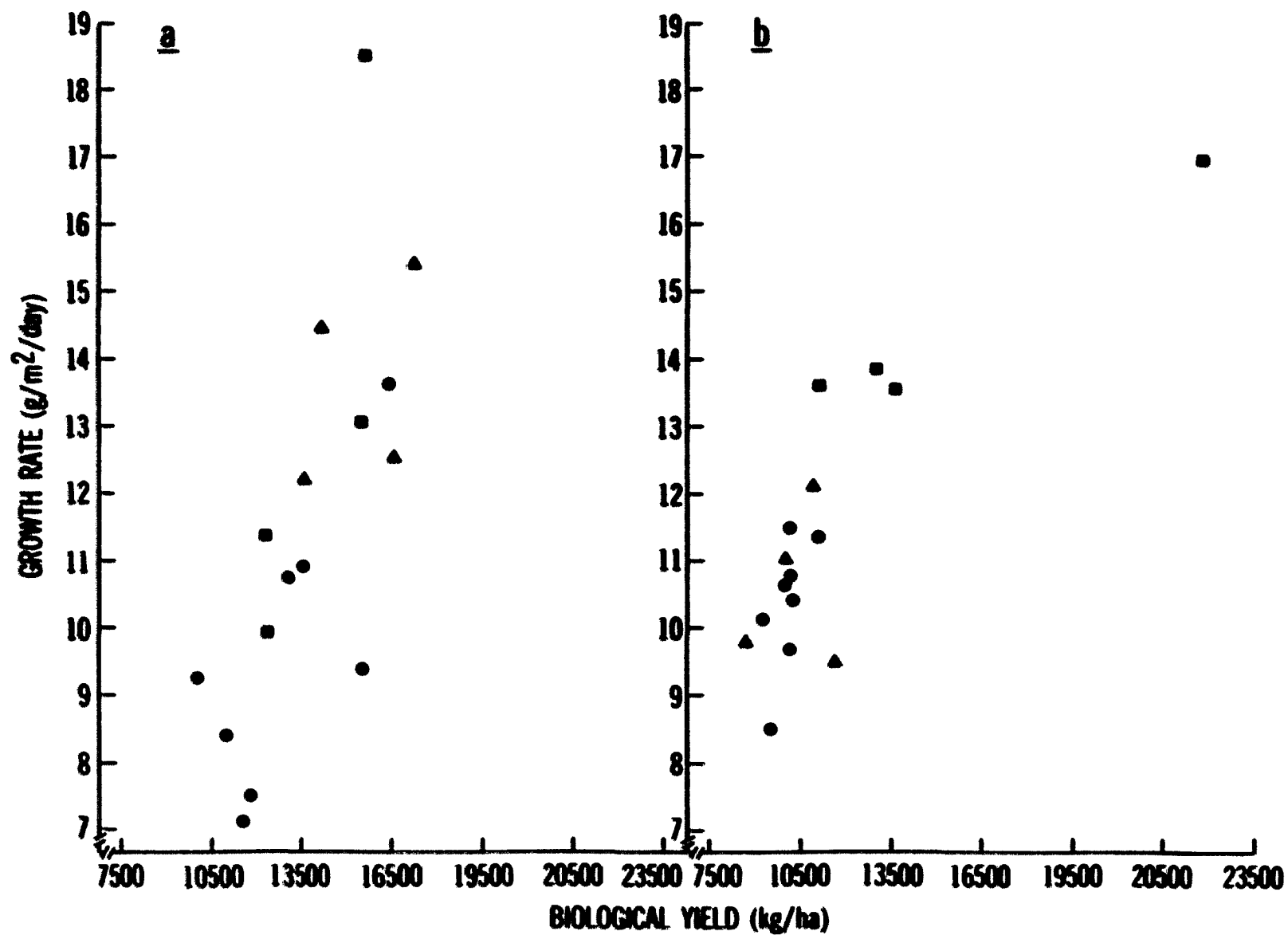


Figure 3. Scatter diagrams of GR plotted against HI for the HYB and VAR group ● , AFR group ▲ , and WEED group and WILD entry ■ in the dry(a) and wet (b) seasons

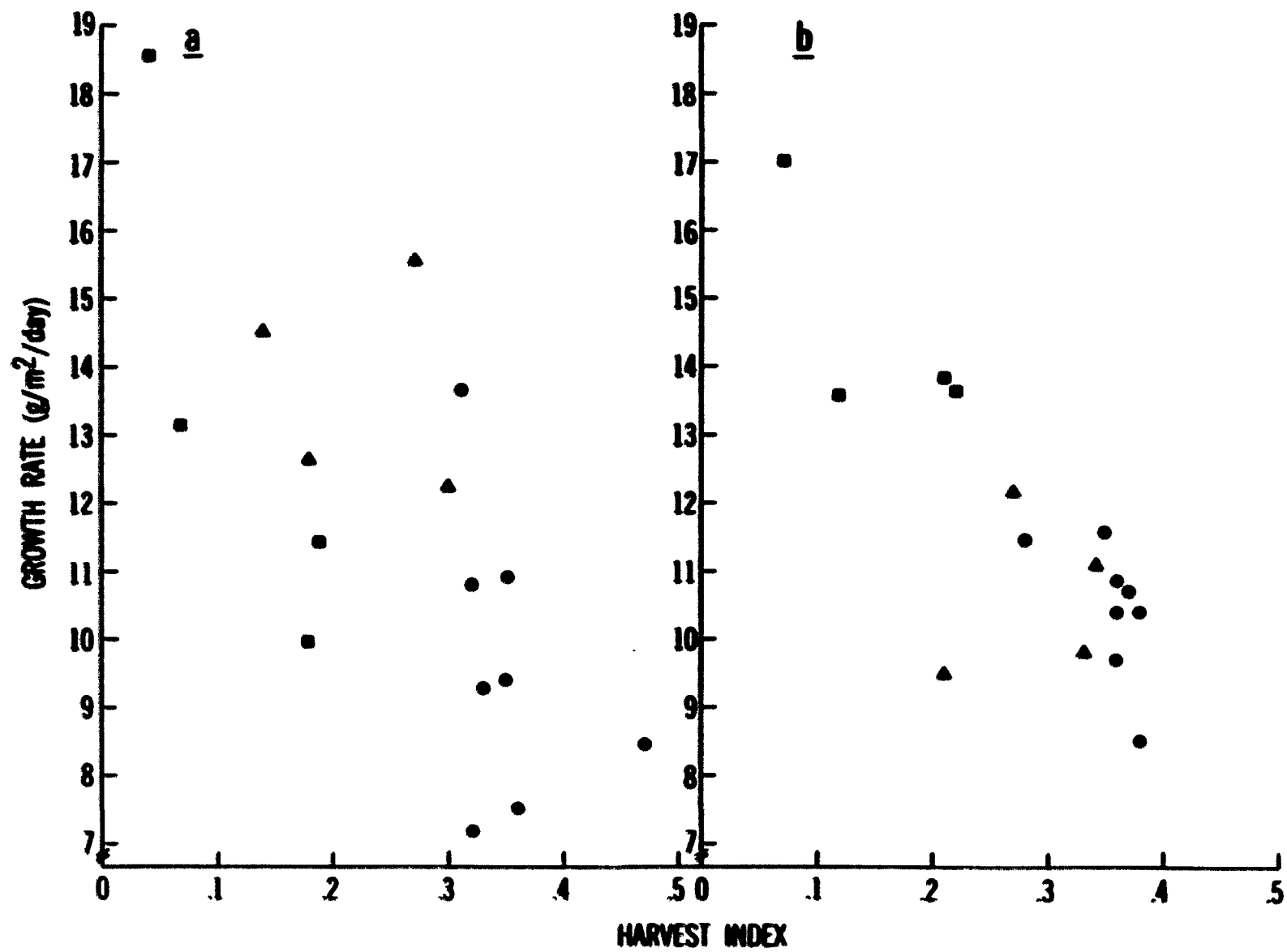


Table 5. Partial correlations among traits with scores for relationships among genotypes held constant for the dry and wet seasons

Wet Dry		BY	GY	GR	HI	SW	TH	ETP	NDP	FLW
		BY	GY	GR	HI	SW	TH	ETP	NDP	FLW
	BY	--	-0.22	0.56*	-0.59*	-0.23	-0.76**	0.26	0.26	0.09
	GY	0.33	--	0.07	0.86**	0.53	0.62*	0.12	-0.47	-0.61*
	GR	0.74**	0.22	--	-0.39	0.00	-0.33	0.10	0.17	-0.01
	HI	-0.44	0.68**	-0.36	--	0.47	0.69**	0.02	-0.57*	-0.69**
	SW	-0.11	0.59*	-0.19	0.66**	--	0.23	0.19	-0.28	-0.56*
	TH	-0.01	0.69**	-0.04	0.58*	0.73**	--	-0.33	-0.40	-0.26
	ETP	-0.37	-0.22	-0.28	0.16	-0.28	-0.49	--	-0.48	-0.59*
	NDP	-0.23	-0.34	-0.08	-0.14	-0.51*	-0.54*	0.71**	--	0.14
	FLW	0.73**	-0.18	0.74**	-0.76**	-0.31	-0.08	-0.56*	-0.22	--

*, ** Significant at the 0.05 and 0.01 levels, respectively.

The other traits were included in Table 5 not only to study the relationships between GR, GY, BY, and HI, but also their relationships to the other traits measured in this experiment. GR and FLW were highly significantly correlated with each other and both were positively correlated with BY in the dry season. In the wet season, GR and BY were significantly and positively correlated, but neither was correlated with FLW. In the dry season, GY was significantly and positively correlated with HI, SW, and TH, and all three traits were significantly and positively correlated with each other. In the wet season, only HI and TH had a significant, positive correlation with each other and with GY. FLW was significantly and negatively correlated with HI, SW, and GY in the wet but not in the dry season. FLW had a nonsignificant association with NDP, but was significantly negatively correlated with ETP in both seasons.

The correlations suggest that for the genotypes of pearl millet tested, and perhaps for pearl millet accessions in general, high GY was associated with high HI, large SW, and high TH in the dry season, and early FLW in the wet season. In both seasons, high BY was associated with a high GR, but high BY did not manifest itself in a high GY because of the negative association between HI and BY. The relationship of GY and FLW depended upon season apparently because of a different degree of photoperiod response in the adapted and nonadapted materials. ETP and NDP were not related to GY; but in both seasons, the ETP was higher in the earlier flowering genotypes, indicating either a reduction in basal tillers with early flowering or less competition among tillers in the early flowering types.

CONCLUSIONS

In this study, 16 genotypes of pearl millet were evaluated for a number of growth traits and especially biological yield, grain yield, and growth rate. The differences in means for most traits show that these genotypes were representative of the different types described by Brunken et al. (1977) and Belliard et al. (1980). The wild and weedy relatives had extreme phenotypes for all traits, and the entries within the African landrace and weedy relative groups were highly variable. The wild relative differed significantly from the cultivated groups for all traits, and the weedy relative differed from the cultivated groups for most traits. The wild and weedy genotypes were undesirable for most traits, but they may be potential sources of genes for improving BY, GR, and ETP in hybrids and varieties. Little variation exists for any trait among the adapted, cultivated genotypes. Because of the nature of the materials used in this study, higher GR or BY was not associated with higher GY. The associations (or lack thereof) among these traits, HI, and others, however, suggest that it may be possible to develop breeding populations utilizing germplasm sources of higher growth rate, biomass, and improved basal tiller ratio in which selection for higher grain yield should be possible.

REFERENCES CITED

- Belliard, J., E. Nguyen Van, and J. Pernés. 1980. Analyse des relations génétiques entre formes spontanées et cultivées chez le Mil à chandelle. I. Etude des parents et hybrides de première génération (F_2) entre un ecotype de Pennisetum mollissimum Hoehst. (forme spontanée) et différentes formes cultivées de Pennisetum americanum (L.), Leeke. Ann. Amélior. Plantes 30:229-251.
- Bramel-Cox, P. J., D. J. Andrews, F. R. Bidinger, and K. J. Frey. 1984. A rapid method of evaluating growth rate in pearl millet (Pennisetum americanum) and its weedy and wild relatives (ssp. stenostachyum and ssp. monodii). Crop Sci. 24:1187-1191.
- Brunken, J., J. M. J. De Wet, and J. R. Harlan. 1977. The morphology and domestication of pearl millet. Econ. Bot. 31:163-174.
- El-Sharkawy, M., J. Hesketh, and H. Muramoto. 1965. Leaf photosynthetic rates and other growth characteristics among 26 species of Gossypium. Crop Sci. 5:173-175.
- Evans, L. T., and R. L. Dunstone. 1970. Some physiological aspects of evolution in wheat. Aust. J. Biol. Sci. 23:725-741.
- Frey, K. J., T. S. Cox, D. M. Rodgers, and P. Bramel-Cox. 1984. Increasing grain yields with genes from wild and weedy species. Proc. XV Intl. Genet. Congr., New Delhi, India. (In press)
- Grumet, R., J. F. Fobes, and R. C. Herner. 1981. Ripening behavior of wild tomato species. Plant Physiol. 68:1428-1432.
- Rush, D. W., and E. Epstein. 1976. Genotypic response to salinity: Differences between salt sensitive and salt tolerant genotypes of the tomato. Plant Physiol. 57:162-166.
- Takeda, K., and K. J. Frey. 1977. Associations among grain yield and other traits in Avena sativa and A. sterilis backcross populations. Euphytica 26:309-317.

**SECTION III. EXOTIC GERMPLOSM FOR IMPROVING GRAIN YIELD AND GROWTH
RATE IN PEARL MILLET**

ABSTRACT

Pearl millet is a grain and forage crop that has received little attention in genetic improvement programs. In this study, three exotic strains of pearl millet were compared for their potential for improving grain yield, growth rate and a number of associated traits. The three exotic strains, a primitive landrace, a weedy relative, and a wild relative were mated with two pearl millet inbred lines in a mating scheme designed to evaluate both the variability within the exotic strains and the progeny from their matings with the inbred lines. The experiment was evaluated in the rainy season of 1982 at the International Crops research Institute for the Semi-Arid Tropics (ICRISAT), near Hyderabad, India. The results of the study indicated that the best exotic parent had the best mean progeny but in all the matings it was possible to select lines with transgressively increased grain yield and growth rate. The exotic strain with the most potential to improve growth rate in pearl millet inbreds was the wild accession. The best exotic parents for improving grain yield (based upon a number of criteria) were the primitive landrace and the weedy relative.

INTRODUCTION

Pearl millet (Pennisetum americanum ssp. americanum L. Leake) is grown for grain and forage on about 26 m ha annually, principally in the tropical and subtropical areas of Africa and the Indian subcontinent. It has received little attention in genetic improvement programs despite its importance as a human food and the availability of extensive germplasm collections of cultivars, lines, and wild accessions. Primitive landraces have been used to improve grain productivity but their potential for improving other attributes has not been explored (Andrews et al., 1984).

P. americanum ssp. monodii L. (Maire) Brunken, a wild relative of cultivated pearl millet, has been evaluated in several studies (Brunken et al., 1977; Belliard et al., 1980; Pernds et al., 1980). Bramel-Cox et al. (1984) suggested that weedy and wild relatives may have genes for improving growth rate of cultivated pearl millet. Cox et al. (1984) reported on the potential benefits of introgressing germplasm from wild into cultivated sorghum (Sorghum bicolor (L.) Moench). Frey et al. (1984) reviewed the use of wild relatives of oats (Avena sativa L.), barley (Hordeum vulgare L.), sorghum, and pearl millet to improve grain productivity of those cereals.

Takeda and Frey (1977) expressed grain yield of cereals as the product of growth rate, growth duration, and harvest index. Lawrence and Frey (1976), Rodgers (1982), and Cox et al. (1984) have shown that interspecific matings have resulted in quantum improvements in yielding ability of oats, barley, and sorghum, respectively. For oats, this

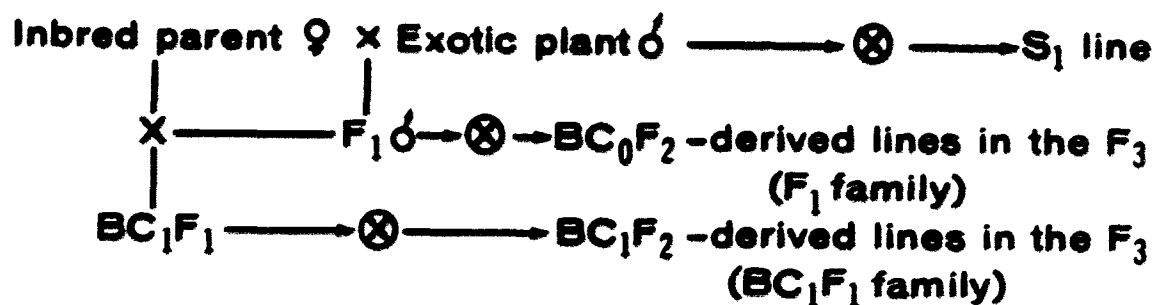
yield increase has been shown to be due to increased growth rate (Takeda and Frey, 1977). Growth durations and harvest indexes of most high-yielding segregates were the same as those of the cultivated parents. The primary objective of this study was to evaluate wild, weedy, and exotic cultivated strains of P. americanum for their potential to improve growth rate and grain yield of pearl millet.

MATERIALS AND METHODS

Genetic Materials

Two inbred pearl millet lines (recurrent parents) were used as females in matings with three exotic parent accessions. The origins of the five parents were as follows: (a) J104 was an inbred line used extensively in Indian hybrids, (b) MS81B (81B) was an experimental inbred line developed at ICRISAT, (c) M-70-1 (designated AL) was a landrace collected from the wet region of Tanzania, (d) P-28081 (designated NEED) was a weedy accession (*P. americanum* ssp. *stenostachyum* L. (Klotzch) Brunken) collected from a farmer's field in Niger, and (e) the wild relative (ssp. *monodii*) was represented by an accession from Burkina Fasso (designated WILD).

The exotic parents were heterozygous, heterogeneous, and open-pollinated populations, whereas the adapted parents were inbred lines. The heterogeneity in the exotic parent collections required a mating design that allowed for separation of genetic variation within the exotic population from variation generated by the exotic x cultivated matings. Eight to ten crosses were produced per mating, with each cross being made between one plant from the exotic parent and one plant from the inbred, as diagrammed below:



All plants to be crossed or selfed were taken at random. Thus, approximately 200 entries were evaluated per mating (8 to 10 S_1 lines from the exotic parent, 8 to 10 F_1 families, ca. 80 F_2 -derived lines, 8 to 10 BC_1F_1 families, ca. 80 BC_1F_2 -derived lines, the exotic parent (S_0) and the cultivated parent).

Experimental Methods

An experiment to evaluate the entries from the six matings was conducted at the International Crops Research for the Semi-Arid Tropics (ICRISAT) near Hyderabad, India in 1982. The experiment was conducted in a split-split-plot arrangement using a randomized complete block design with two replications. Main plots were matings, subplots were backcross generations, and sub-subplots were entries. S_1 lines were included in BC_0 subplots, and parents were included in subplots for backcross generations of a mating. Each sub-subplot consisted of four rows 3 m long, spaced 75 cm apart and a 10-cm spacing between plants within a row. An area of 1.125 m^2 containing competitive plants was harvested from the center two rows of each sub-subplot twice during the growing season. Harvest dates were randomized within each sub-subplot, and they were separated from one another by a border of 0.25 m^2 . The plant population in the experiment was 130,000 plants per ha.

The experiment, which was conducted in the 1982 rainy season, was sown on 19 June, and seedlings emerged on 22 June. Normal temperatures in the rainy season are 30C and 22C for day and night, respectively, and normal rainfall is 700 mm at Hyderabad. No irrigation was used, and downy mildew (Scleropora graminicola) was controlled by hand spraying

affected plants with metalaxyl.

Traits Measured

Growth rate (GR) was measured by using the formula

$$GR = \frac{\text{sample dry weight at days to anthesis} + 10}{\text{days to anthesis} + 10}$$

(Bramel-Cox et al., 1984), and this trait was expressed in g/m²/da. Grain yield (GY), head yield (HY), and biological yield (BY) were measured in g/m². Harvest index (HI), expressed in %, was the ratio (GY/BY) 100. Days to flowering (FLW) was recorded as days from seedling emergence to the date when 50% of the panicles in a plot had stigmas completely emerged (DAE). Seed weight (SW) was the mean weight in g of two 100-seed samples, and threshing percentage (TH) was the ratio (GY/HY) 100.

Statistical Analysis

All trait values for an exotic parent were the means of the S_1 lines representing that parent. Each backcross generation within a mating was analyzed separately because the experiment was not balanced. The entry mean square was subdivided into a set of orthogonal comparisons as shown in Table 1. In the BC_1 there were no S_1 lines so $\underline{S}$ was deleted from those sources of variation where it occurred. Genetic variance (σ_g^2) was calculated as a linear function of the appropriate mean squares.

A least significant difference (LSD) between a progeny and recurrent parent mean was

$$LSD = t_{0.05} \sqrt{\frac{1}{2b} + \frac{1}{2a}} MS_E$$

Table 1. ANOVA for original cross or backcross of a mating

Source of variation	Degrees ^a of freedom
Replication	$r-1$
Entry	$(s + x + c + f + fv) - 1$
Parents vs. Progeny	1
Parents	$(s + x + c) - 1$
Cultivated vs. Exotic	1
Within cultivated	$c-1$
Within exotic	$(s + x) - 1$
S_0 vs. S_1	1
Within S_1 lines	$s-1$
Progeny	$(f + fv) - 1$
F_1 vs. F_2	1
F_1	$f-1$
F_2 -derived lines	$fv-1$
Among F_1 'families'	$f-1$
Within F_1 'families'	$f(v-1)$
Error	$((s + x + c + f + fv) - 1)(r-1) - 1$

^a r , s , x , c , f , and v equal numbers of replications, S_1 lines, S_0 entries, recurrent parent entries, F_1 families, and F_2 -derived lines within an F_1 family, respectively.

where $t_{0.05}$ is the tabular value of t at the 5% level of significance, b and a equal the number of entries in a progeny mean and number of entries in a recurrent parent mean, respectively, and MS_E is the error mean square. A transgressive segregate was defined as a progeny with a grain yield or growth rate one or more LSD above the high or below the low parent.

RESULTS

Comparisons of Means

The two recurrent parents, J104 and 818, did not differ for GY, GR, or BY, but J104 was significantly earlier and higher in HI. The three exotic parents did not differ for GR, BY, and FLW but they did differ significantly for GY and HI. The recurrent parents differed significantly from the exotic ones for all traits except that J104 and AL did not differ for GY and AL and 818 did not differ for HI (Table 2).

Means of F_2 -derived lines for each mating for five traits are given in Table 3. The J104 matings were earlier and gave higher GY, but lower GR and BY than did the 818 matings. AL matings were earlier and had higher mean GY and HI, but lower GR and BY than did the WEED or WILD matings.

For two matings, AL x 818 and WEED x 818, the GY means for F_2 -derived lines were significantly greater than the recurrent parent, 818. AL x 818 was significantly earlier and higher in GR than 818, and WEED x 818 was significantly later and higher in GR and BY but lower for HI than was 818. The WILD x J104 mating had a significantly lower mean GY than that of J104. WEED x J104 was significantly later in FLW, higher in GR and BY, and lower in HI than J104, but had the same GY. The six matings differed significantly in the BC_0 for GY and GR and in both backcrosses for the other three traits (Table 4). J104 and 818 matings did not differ for GY in either backcross but they were significantly different for the other four traits in both backcrosses. The AL, WEED, and WILD matings differed significantly for all traits in

Table 2. Means of recurrent and exotic parents for GY, GR, BY, FLW, and HI

Parent	Trait				
	GY	GR	BY	FLW	HI
	(kg/ha)	(g/m ² /da)	(kg/ha)	(DAE)	(%)
J104	2521	9.5	7495	52.3	.34
81B	1816	8.9	7099	63.6	.26
AL	3132	16.9	10792	68.9	.29
NEED	1504	17.3	10873	68.7	.15
WILD	468	18.9	10329	71.8	.05
LSD ^a	939	3.2	2454	5.8	.04

^a At 0.05 level.

Table 3. Means of BC₀F₂- and BC₁F₂-derived lines from six pearl millet matings for GY, GR, BY, HI, and FLW

Exotic parent	GY		GR		BY		FLW		HI	
	J104	818	J104	818	J104	818	J104	818	J104	818
	----kg/ha----		--g/m ² /da--		---kg/ha---		-----DAE-----		-----%-----	
AL	2562	2513**	10.4	12.1**	7936	7829	55.6	66.5**	.32	.26
WEED	2533	2287*	12.3**	13.0**	9419**	10382**	61.5**	68.9**	.28**	.22**
WILD	1859**	1907	12.8**	13.9**	9513**	10414	60.1**	68.8**	.20**	.18**

*, ** Significantly greater than the recurrent parent at the 0.05 and 0.01% levels, respectively.

Table 4. Significance levels for mating mean squares and for specific orthogonal comparisons for the BC_0 (1) and BC_1 (2) for GY, GR, BY, HI, and FLW

Source of variation	Degrees of freedom	GY		GR		BY		HI		FLW	
		1	2	1	2	1	2	1	2	1	2
Matings	5	*	n.s. ^a	*	n.s.	*	*	**	**	**	*
Among adapted	1	n.s.	n.s.	*	**	**	**	**	**	**	**
Among exotic	2	**	n.s.	*	n.s.	**	n.s.	**	**	**	**
Adapted x exotic	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.

^a Nonsignificant.

*, ** Significantly greater than the recurrent parent at the 0.05 and 0.01 levels, respectively.

the BC_0 , but they differed only for HI and FLW in the BC_1 . There was a significant interaction between the adapted and exotic parents in only one trait, HI, and in only one backcross generation, BC_0 .

As a further assessment of the value of AL, WEED, and WILD as donors of genes for improving cultivated pearl millet, the best 10% of F_2 -derived lines in each mating-backcross combination for GY were evaluated for seven traits including GY. To provide easy comparison, the sample means were expressed relative to the recurrent parent of a mating (Table 5).

In all mating-backcross combinations, the selected lines had a significantly greater GY, GR, and BY. No mating-backcross combination differed significantly from the recurrent parent for TH and only the AL matings differed significantly for SW. The BC_0 of J104 x AL had a significant 21% increase in HI but the BC_0 of J104 x WILD had a significant 21% decrease from the recurrent parent for this trait.

There were a number of mating-backcross combinations where the FLWs of the selected lines were significantly later than the recurrent parents.

The relative values for GY of the selected samples were greater when 818 was a recurrent parent than when J104 was; however, the lines with the highest actual GYs occurred in the J104 x WEED mating. Selected lines with the lowest actual GYs occurred in the J104 x WILD mating. In each mating involving AL or WEED as a donor, the relative GY of the selected sample was greater in the BC_1 than in the BC_0 , which indicates the nobilizing value of the first backcross. In the BC_0 , the WILD accession was not as good a donor for increasing GY as the other

Table 5. Means of GY, GR, BY, HI, FLW, SW, and TH for the top 10% of the lines for each mating selected for GY expressed as a percentage of the recurrent parent in the $BC_0(1)$ and $BC_1(2)$ generations

Mating	Generation	GY	GR	BY	HI	FLW	SW	TH
J104 x AL	1	148**	112*	123**	121*	103	124*	116
	2	157**	125**	129**	124	103*	116*	119
J104 x WEED	1	155**	134**	147**	106	111*	98	111
	2	158**	117**	151**	106	107*	110	103
J104 x WILD	1	127**	146**	154**	79**	111*	105	95
	2	124**	135**	130**	97	111**	89	101
818 x AL	1	189**	139**	150**	115	102	122*	112
	2	214**	153**	185**	112	105	128*	110
818 x WEED	1	177**	141**	174**	112	110**	91	112
	2	188**	144**	175**	112	108*	102	107
818 x WILD	1	183**	174**	170**	108	107*	100	109
	2	161**	173**	164**	96	108*	88	109

*, ** Significantly greater than the recurrent parent at the 0.05 and 0.01 levels, respectively.

exotic sources when J104 was the recurrent parent, but all donors were about equal when 818 was the recurrent parent. The WILD matings were unique, however, in that the GY of the selected sample regressed from BC_0 to BC_1 . In fact, however, all matings produced sizable numbers of segregates with very high GY.

Takeda et al. (1979) analyzed transgressive yielding lines from interspecific matings of oats and found that the high grain yields were due to increased growth rates. A similar situation seems to have occurred in the matings of pearl millet. In general, the FLWs of the high GY samples of lines were increased only from 2 to 11%, and HI, another component of GY, of the selected samples were only significantly different from the recurrent parents in the BC_0 of two matings where they differed by 21%. However, the third yield component, GR, of the samples selected for high GY was significantly greater for all matings. Thus in most of the matings in the BC_0 and all the matings in the BC_1 , the increased GY resulted from an increased GR with FLW and HI being similar to the recurrent parents.

The highest-yielding selected lines were found in the J104 x WEED mating and the lowest-yielding selected lines were found in the J104 x WILD mating. The highest growth rates were in 818 x WILD and the lowest in J104 x AL.

Comparison of Variances

There are several sources of genetic variability for GY and GR that were of importance to this study. For example, genetic variability among F_2 -derived lines could arise as a result of recombination among

genes within matings, from the gametic sample used in making the BC_1 , and genetic heterogeneity in the AL, WEED, and WILD accessions. The mean squares for GY and GR needed to discuss this subject are presented in Tables 6 and 7, respectively. In the BC_0 of all matings except J104 x WILD, the GY and GR mean squares for F_1 vs. F_2 were significant, which indicates the occurrence of significant inbreeding depression for these traits. In the BC_1 , the pattern of significant inbreeding depression was the same for GR as it was in the BC_0 , i.e., all matings except J104 x WILD showed a significant F_1 vs. F_2 mean square. However, for GY, there was no significant inbreeding depression for any mating in the BC_1 .

The accessions of AL, WEED, and WILD used as exotic parents were expected to be genetically heterogeneous, so F_1 crosses between different pairs of individual plants in a mating were accessioned and tested separately. This permitted the assessment of whether genetic heterogeneity within exotic parent accessions was important for GY and GR. Of six matings, the mean squares for "among F_1 's" was significant in only one (i.e., J104 x AL) for GY (Table 6) and one (i.e., 81B x AL) for GR (Table 7). Another estimate about the presence or absence of genetic heterogeneity in the exotic accessions was obtained from comparisons among sets of F_2 -derived lines within F_1 families in BC_0 . For GY, five of six matings showed significant variation among F_1 families and for GR four of six matings had significant mean squares for this source of variation. Thus, F_1 crosses per se indicate that genetic heterogeneity within exotic accessions was not great, whereas the F_1 families of F_2 -derived lines indicate that it was an important source of variation. The better estimate of this genetic heterogeneity was among F_1 families

Table 6. Mean squares^a for GY for sources of variation among progeny within the BC₀ and BC₁ of six matings of pearl millet

Source of variation	Mean squares					
	AL x		NEED x		WILD x	
	J104	81B	J104	81B	J104	81B
-----BC ₀ -----						
F ₁ vs. F ₂	164.1**	341.6**	17.4	115.6**	0	348.7**
F ₁ 's	144.9**	14.2	14.0	14.6	8.1	15.2
F ₂ -derived lines	120.1**	9.2	14.8**	6.8	13.2**	11.9**
Among F ₁ families	43.6**	7.3	25.5**	18.0*	14.0	34.6**
Within F ₁ families	8.9**	9.4	13.5**	6.0	9.2*	9.1
-----BC ₁ -----						
F ₁ vs. F ₂	110.6**	196.4**	116.0**	181.8**	.2	43.3**
F ₁ 's	8.3	6.9	11.5	15.7	18.8**	3.1
F ₂ -derived lines	10.8	10.2**	17.1	9.1	11.3**	6.8*
Among F ₁ families	23.4*	13.7**	55.9**	7.7	23.8**	20.3**
Within F ₁ families	9.3	9.8**	12.3	9.3	9.7	5.0

^a x 10³.

*, ** Significance at the 0.05 and 0.01 levels, respectively.

of F₂-derived lines because (a) it would be less affected by dominance relationships than would F₁ crosses per se and (b) it provided more replication with which to estimate the variance.

The F₂-derived line variance was subdivided into two sources, (a) F₂-derived lines within F₁ families and (b) among F₁ families of F₂-derived lines. For GY, the greater, and in most cases the only significant, mean square was that among F₁ families. For GR, this result was

Table 7. Mean squares for GR for sources of variation among progeny within the BC_0 and BC_1 of six matings of pearl millet

Source of variation	Mean squares					
	AL x		NEED x		WILD x	
	J104	81B	J104	81B	J104	81B
----- BC_0 -----						
F_1 vs. F_2	29.4**	185.7**	56.9*	56.0**	30.4	174.1**
F_1 's	5.4	17.9**	14.9	10.2	21.5	6.1
F_2 -derived lines	7.4**	8.7*	14.2	7.3	22.4**	13.0*
Among F_1 families	10.7**	4.4	37.2**	12.3	38.1**	29.8**
Within F_1 families	7.1**	9.3*	11.4	6.4	20.2**	10.9
----- BC_1 -----						
F_1 vs. F_2	13.8	1.5	1.0	8.2	0.3	9.5
F_1 's	8.6	6.6	26.7*	5.4	2.0	12.0
F_2 -derived lines	5.7	7.8	14.0	11.3*	9.4**	13.7**
Among F_1 families	7.7	9.0	44.6**	29.4**	28.9**	52.0**
Within F_1 families	5.4	7.7	10.2	8.9	1.4	8.9

*, ** Significance at the 0.05 and 0.01 levels, respectively.

even more evident, especially in the BC_1 , where no within F_1 families' mean squares were significant. The only matings with significant variance among F_1 families in both backcrosses were the J104 matings and 81B x WILD for GY and the WILD matings and J104 x WEED for GR. No mating had significant variance within F_1 families in both backcrosses for either GY or GR.

The distribution of the F_2 -derived lines mean squares among and within the F_1 families and its significance has important implications

when breeding for improved GR and GY in populations from these exotic sources. The greater importance of the among F_1 families source of variation indicates it would be best to topcross onto as many plants as possible from the exotic population. Then, testing a large number of F_1 families as bulk F_2 and F_3 progenies would evaluate the variability within the exotic population and determine which family or families should be saved. Selection should then be made for high GR among lines within the F_1 families with high GR, these progenies could be used in a recurrent selection program, or for continued backcrossing to improve the adaptation of the selected crosses. Since the variance among F_1 families was greater than that within F_1 families of both the BC_0 and the BC_1 , the primary reason for backcrossing would be to raise the adaptation of the progeny from the matings.

Intrageneration means, genetic variances, and numbers of high and low transgressive segregates for GY and GR are given in Table 8. None of the differences between backcross generation means for GY and GR was significant. Genetic variation among F_2 -derived lines for GY in the BC_0 was significant for four of six matings and three of these had J104 as one parent. In the BC_1 , three of six showed significant genetic variances and two of these were the matings involving WILD. Genetic variance among F_2 -derived lines for GY changed in both directions with backcrossing. In three of the six matings, there was a decrease to nonsignificance, and one mating, 81B x WEED, did not have significant genetic variance in either backcross generation. 81B x AL had an increase to significant genetic variance with backcrossing. The WILD matings were the only ones with significant genetic variance in

Table 8. Mean ($\bar{x}$), genetic variance (σ_g^2), and percentages of transgressive segregates (T.S.) above the high parent (H) and^a below the low parent (L) for GY and GR for the BC₀ (1) and BC₁ (2) from six pearl millet matings

Mating	Genera- tion	GY				GR			
		$\bar{x}$ kg/ha	σ_g^2	T.S.		$\bar{x}_2$ g/m ² /da	σ_g^2	T.S.	
				H	L			H	L
J104 x AL	1	2466	3464 ^a	26	38	10.8*	2.1	1	6
	2	2659	n.s.	32	25	10.9*	n.s.	2	6
J104 x WEED	1	2608	4044	49	5	12.8**	n.s.	6	2
	2	2457	n.s.	23	6	11.8**	n.s.	0	9
J104 x WILD	1	1792**	2098	6	5	13.8**	6.1	11	2
	2	1929**	2935	6	0	11.8**	2.2	2	8
81B x AL	1	2323*	n.s.	13	5	11.5**	1.3	5	3
	2	2703**	2789	39	3	12.7**	n.s.	9	1
81B x WEED	1	2352*	n.s.	65	3	13.2**	n.s.	1	1
	2	2224	n.s.	54	3	12.7**	2.0	5	1
81B x WILD	1	1768	2711	16	0	14.3**	2.2	11	2
	2	2046	1436	41	0	13.6**	2.4	9	0

^a Nonsignificant.

*, ** Significantly different than the recurrent parent at the 0.05 and 0.01 levels, respectively.

both the BC_0 and BC_1 . The genetic variance decreased to one-half in the 81B x WILD mating and increased by one-half in J104 x WILD.

Genetic variance among F_2 -derived lines for GR was significant for the AL and WILD matings in the BC_0 and the WILD matings and 81B x WEED in the BC_1 . In the AL matings, genetic variance decreased to nonsignificance with backcrossing; in the WEED matings, the genetic variance among F_2 -derived lines remained nonsignificant or increased to significance with backcrossing, and only in the WILD matings did both backcross generations have significant genetic variance for GR.

In all matings except J104 x AL, there was a much greater percentage of high transgressive than low transgressive segregates for GV in both BC_0 and BC_1 . In fact, in seven of the 12 mating-backcross combinations, more than 25% of the segregates were transgressively high for this trait. And in 81B x WEED, 65% and 54% of the F_2 -derived lines were transgressively high in BC_0 and BC_1 , respectively. Across all matings, the BC_0 and BC_1 produced 29% and 33%, respectively, high transgressive segregates for GV. In this study, the adapted parent had a very low GR, whereas the exotic parent had a very high GR. The percentages of high transgressive segregates for GR were quite low, i.e., the means for BC_0 and BC_1 were 4% and 3%, respectively. The percentage of low transgressive segregates was not very high, either, but in one mating in the BC_0 and three matings in the BC_1 , there were more low than high transgressive segregates. For traits, such as GR, where the parents are so extreme, most of the plus genes for the trait should come from one parent with no or very few from the other parent. This may be the

explanation why so few lines were transgressive for GR. After all, for a line to be transgressive it would need to have all the plus genes from the exotic parent and some from the adapted parent. Most transgressive segregates for GR occurred in the BC_0 of the WILD matings, but matings which had either an increase or a slight decrease upon backcrossing were those which involved the 81B adapted parent. Thus, 81B may have had some plus genes for GR, whereas J104 did not.

DISCUSSION

The proportion of positive transgressive segregates for grain yield averaged 21 and 35% in the BC_0 and BC_1 of AL matings, 52 and 37% in the BC_0 and BC_1 of WEED matings, and 11 and 23% in the BC_0 and BC_1 of WILD matings. Overall, there was 18% high transgressive segregation in the WILD matings, 44% in the WEED matings, and 24% in the AL matings. The frequencies of high transgressive segregates for GY in the WILD and WEED matings were much greater than those reported for interspecific and interracial matings of sorghum, oats, and barley (Frey et al., 1984). In the BC_1 , the WEED matings had greater numbers of high transgressive segregates and means for GY equal to means for AL matings, and they were superior to the WILD matings in both backcrosses. In both J104 x AL and J104 x WEED, mean GY in the BC_0 were equivalent to that of J104, but the genetic variances for GY decreased to zero in BC_1 . Only 818 x AL differed significantly from 818 for mean GY in both backcrosses, and the genetic variance increased from BC_0 to BC_1 for this mating. The AL and WEED parents were equivalent as sources for GY improvement in pearl millet, and were better than the WILD parent when judgement was based on BC_0 and BC_1 .

Positive transgressive segregates for GR were judged against the exotic parents, which had extremely high GRs. However, GR would not need to be higher than the exotic parent to improve GY potential in the adapted parent. As a way of judging the significance of this statement, the following table gives the percentage of high transgressive segregates when the adapted parents are used as the basis for judgement:

Backcross generation	Mating					
	J104 x AL	818 x AL	J104 x WEED	818 x WEED	J104 x WILD	818 x WILD
BC ₀	43	56	75	89	89	91
BC ₁	46	84	55	80	65	83

From 43 to 91% of the mating progenies were transgressive segregates with GR at least one LSD above the adapted parent. In the J104 matings, the percentage of high transgressive segregates decreased from 69 to 55 for BC₀ to BC₁, whereas in the 818 matings, percentages were similar at 79 and 82, respectively. Thus, most progeny lines were superior to J104 and 818 for GR, and by combining any of these GR values with the FLW and HI of the adapted J104 and 818, should produce adapted pearl millet lines with superior GY, irrespective of whether the GR were as high as the exotic parents or not.

The exotic parent with the highest mean, progeny mean, percentage of transgressive segregates above the high parent and the adapted parent, and a significant genetic variance for GR was WILD. The highest-yielding line occurred in J104 x WEED and the largest number of positive transgressive segregates for GY occurred in 818 x WEED. The only matings with significant genetic variance in both backcrosses for both GY and GR were the WILD ones.

Overall in this study, matings with the best parents for a trait produced the best progeny for that trait. For example, the GYs of the exotic parents were directly reflected in the means of their progenies. In all matings it was possible to select for increased BY,

and the samples of 10% highest GY lines were not inferior for HI, SW, or TH. The WEED and WILD parents have low values for these traits (Bramel-Cox et al., 1984). Therefore, it might be possible to select lines transgressive for high GY and that had satisfactory agronomic traits directly from the populations of segregates evaluated in this study.

Takeda and Frey (1977) expressed grain yield of cereals as a product of growth rate, growth duration, and harvest index. The high GY of the selected sample of lines from the J104 matings resulted from increased GR without an accompanying negative change in HI or FLW (except in the BC_0 of J104 x WILD). In the 81B matings, the high GY in the selected sample resulted from increased GR and increased FLW. In each set of matings, the result was a BY greater than the recurrent parent accompanied by a HI similar to the recurrent parent.

Among the exotic parents used in this study, the best source of genes to improve GR in cultivated pearl millet would be the WILD parent, but the WEED parent was nearly equivalent. The best sources of genes to improve GY directly were the AL and WEED parents. The WILD and WEED matings had high BY but low HI. Selection for increased HI in these high-GR populations or populations derived from them via additional backcrossing or recurrent selection may further improve GY and lead to new high-GR, high-GY lines of pearl millet. The study shows that the WILD and WEED accessions can be important sources of genes for improving GR and GY of cultivated pearl millet, and certainly additional sources of these exotic types should be explored. However, AL was the source

of germplasm with the most desirable agronomic traits and probably would provide the best short-term results.

REFERENCES CITED

- Andrews, D. J., S. B. King, S. D. Singh, K. N. Rai, R. P. Thakur, B. S. Taluadar, S. M. Charvan, P. Singh, and J. R. Witcombe. 1984. Breeding for disease resistance and yield in pearl millet at ICRISAT. *Field Crops Res.* (in review).
- Belliard, J., É. Nguyen Van, and J. Pernés. 1980. Analyse des relations génétiques entre formes spontanées et cultivées chez le mil à chandelle. I. Etude des parents et hybrides de première génération (F_2) entre un écotype de Pennisetum mollissimum Hoehst. (forme spontanée) et différentes formes cultivées de Pennisetum americanum (L.), Leeke. *Ann. Amélior. Plantes* 30: 229-251.
- Bramel-Cox, P. J. 1985. Part II. Growth characteristics of genotypes of cultivated pearl millet and its weedy and wild relatives. In *Evaluating three potential sources of germplasm to improve growth rate, grain yield, and harvest index in pearl millet*. Ph.D. dissertation. Library, Iowa State University, Ames, Iowa.
- Bramel-Cox, P. J., D. J. Andrews, F. R. Bidinger, and K. J. Frey. 1984. A rapid method of evaluating growth rate in pearl millet and its weedy and wild relatives. *Crop Sci.* 24:1187-1191.
- Brunken, J., J. M. J. De Wet, and J. R. Harlan. 1977. The morphology and domestication of pearl millet. *Econ. Bot.* 31:163-174.
- Cox, T. S., L. R. House, and K. J. Frey. 1984. Potential of wild germplasm for increasing yield of grain sorghum. *Euphytica* 33: (in press).
- Frey, K. J., T. S. Cox, D. M. Rodgers, and P. Bramel-Cox. 1984. Increasing grain yields with genes from wild and weedy species. *Proc. XV Intl. Genet. Congr., New Delhi, India* (in press).
- Lawrence, P. K., and K. J. Frey. 1976. Inheritance of grain yield in oat species crosses. *Egypt. J. Genet. Cytol.* 5:400-409.
- Pernés, J., É. Nguyen Van, M. Beninga, and J. Belliard. 1980. Analyse des relations génétiques entre formes spontanées et cultivées chez le mil à chandelle (Pennisetum americanum (L.) Leeke, P. mollissimum Hoehst). II. Etude de trois familles F_2 issues d'hybrides entre une plante d'un écotype de Pennisetum mollissimum Hochst et trois lignées de mil cultivé, Pennisetum americanum (L.) Leeke. *Ann. Amélior. Plantes* 30:253-269.

Rodgers, D. M. 1982. Improvement of cultivated barley (Hordeum vulgare) with germplasm introgressed from H. spontaneum. Ph.D. dissertation. Iowa State University. Ames, Ia. Univ. microfilm no. 82-21223.

Takeda, K., and K. J. Frey. 1977. Growth rate inheritance and associations with other traits in backcross populations of Avena sativa x A. sterilis. Euphytica 26:309-317.

Takeda, K., K. J. Frey, and D. Bloethe-Helsel. 1979. Growth rate inheritance and associations with other traits and contributions of growth rate and harvest index to grain yield in oats (Avena sativa L.). Z. Pflanzenzuchtg. 82:237-249.

**SECTION IV. TRAIT ASSOCIATIONS IN INTROGRESSED POPULATIONS
OF PEARL MILLET**

ABSTRACT

Principal component analysis has been used in this study to describe the trait associations between 17 traits measured on progenies developed from the matings of two adapted pearl millet inbreds with three exotic pearl millets. These exotic parents were a primitive land-race, a weedy relative, and a wild relative. The first three components were calculated for these matings and the associations defined. The correlations between these components and grain yield and growth rate were also determined. The first principal component described a hybrid index in five of the six matings and a number of other complexes of traits were determined by the other components. Some of these complexes were determined by the other components. Some of these complexes were common in a number of matings. The first three components only accounted for 50-60% of the total variability, thus no strong association of traits was found that would hinder recombination of parental types to select agronomically desirable segregates with high grain yield or growth rate.

INTRODUCTION

Principal component analysis has been used in several studies involving introgression between species or races of plants. Anderson (1949) stated that the distribution of progeny from interspecific or interracial matings would fall on a narrow recombination spindle between the two parents; therefore, only a small fraction of the total range of trait combinations was possible in introgressed populations. Cox et al. (1984) used the first principal component score as a hybrid index to determine whether a recombination spindle existed in progeny of matings between the wild and cultivated sorghums (Sorghum bicolor L. Moench). A recombination spindle existed, but it was more a result of differences in gene frequency in the different backcross generations than of linkage or pleiotropy within backcross generations.

Marchais and Tostain (1984) and Pernés et al. (1980) used principal component analysis of introgressed progeny to study the process of domestication of pearl millet (Pennisetum americanum L. Leake). Pernés et al. (1980) found that F_2 progeny scores for the first principal component segregated between the wild and cultivated parent and that a large proportion of the total variability was accounted for by the first component. The first four principal components were associated with photoperiodic sensitivity, domestication for spike structures, characteristics of the grain and tillers, and tiller proliferation, respectively. Traits associated with domestication were distributed on several axes, independent of the cultivated or wild phenotype. The other traits were disseminated throughout several components but parental combinations

accounted for most of the variability. Marchais and Tostain (1984) found that the first component was an orthogonal linear combination of two independent groups of traits, while the second component represented a gradual flow from the wild to the cultivated phenotype.

In this study, principal component analysis was used to study trait associations within introgressed populations of pearl millet developed from three exotic sources: primitive landraces, weedy, and wild relatives. The first component score was used as a hybrid index to determine whether a recombination spindle existed and to estimate the proportion of the total variability accounted for by it. The axes defined by the principal components were determined and studied for trait associations that might interfere with introgression of genes from any of the exotic sources into cultivated pearl millet.

MATERIALS AND METHODS

Genetic Material

Two pearl millet lines were used as females in matings with three exotic accessions. The origin of the five parents were as follows: J104 was an inbred line used in Indian hybrids, MSB1B (designated 81B) was an experimental inbred developed at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), M-70-1 (designated AL) was a primitive landrace collected from the wet areas of Tanzania, P2808I (designated NEED) was a weedy accession (Pennisetum americanum ssp. stenostachyum (Klotzsch) Brunken) collected from a farmer's field in Niger, and the wild relative (P. americanum ssp. monodii (Maire) Brunken) was an accession from Burkina Fasso (denoted WILD). The parental material was represented in evaluation experiments by the inbred lines of the cultivated parents and S_1 lines of the exotic parents. BC_0 and BC_1 progenies were F_2 derived lines in the F_3 and they were developed as described in Bramel-Cox (1985).

Experimental Procedures

The pearl millet entries were evaluated at ICRISAT near Hyderabad, India in the rainy season of 1982. An experiment was conducted in a split-split-plot arrangement using a randomized complete-block design with two replications. Main plots were matings, subplots were backcross generations, and sub-subplots were lines. Entries consisted of the inbred parents, S_1 lines of the exotic parents, and F_2 -derived lines in the F_3 . A sub-subplot consisted of four rows 3 m long, spaced 75 cm

apart, and plants were spaced 10 cm apart within a row. Two samples, each consisting of a random land area of 1.125 m^2 with a competitive stand of plants, were taken from the center two rows of a plot. Harvest areas were separated from one another by a border of 0.25 m^2 . The first sample was taken at 10 days after flowering and the second at maturity. The population density for the experiment was 130,000 plants per ha.

The rainy season of 1982 was normal with about 700 mm of rainfall and mean temperatures of 30C and 22C for day and night, respectively. The experiment was planted on 19 June and seedlings emerged on 22 June. No irrigation was used, and downy mildew (Sclerospora graminola) was treated by spraying affected plants with metalaxyl. Pearl millet is typically grown in the rainy season in India and Africa.

Traits Measured

Traits measured, their abbreviations, and methods for measuring them are given in Table 1. All dry weights were taken on oven-dried samples. SL, SG, SD, PH, and LL were taken on samples of 10 plants using the methods described in IBPGR and ICRISAT (1981). GR was measured by using the method of Bramel-Cox et al. (1984). FLW, GR, PH, and LL were measured on the first harvest sample. SD, PH, and LL were measured on samples harvested at dough stage. All other traits were measured on the final harvest sample at final harvest.

Statistical Analysis

An analysis was performed on a combined array of BC_0F_2 - and BC_1F_2 -derived lines for each mating for traits listed in Table 1. Principal

Table 1. Traits measured, their abbreviations, and method used for their measurement or calculation

Trait	Abrevia- tion	Method of measurement or calculation
Days to flowering	FL	Days after emergence when 50% of heads in a plot had completely emerged stigmas (DAE)
Growth rate	GR	Vegetative dry weight at (L + 10)/(FL + 10), (g/m ² /da)
Grain yield	GY	Dry weight of threshed grain, (g/m ²)
Spike yield	SPY	Dry weight of spikes before threshing, (g/m ²)
Straw yield	SY	Dry weight of straw, (g/m ²)
Biological yield	BY	SPY + SY, (g/m ²)
Change in dry weight	CD	Dry weight of straw at final harvest - dry weight of straw at FL + 10, (g/m ²)
Threshing percentage	TH	(GY/SPY) x 100, (%)
Harvest index	HI	(GY/BY) x 100, (%)
Seed weight	SW	g/200 seeds
Aristation	AR	Score for type of aristation: 1= mono-aristation, short; 3=mono-aristation, long; 5=poly-aristation, sparse; 7=poly-aristation, dense
Shedding	SH	Score for spikelet shattering: 1=spontaneous shattering; 2=shattering at touch; 3=nonshattering and free threshing; 4=nonshattering and difficult to thresh
Percentage of effective tillers per plant	EFT	Number of basal tillers with mature spikes at final harvest/ number of basal tillers at final harvest
Percentage of early tillers effective	CBT	Number of basal tillers with mature spikes at final harvest/ number of basal tillers at 35 days
Aerial tillers per basal tiller	AT	Number of aerial tillers at final harvest/number of basal tillers at final harvest
Spike length	SL	Base to tip of spike on the primary tiller, (cm)
Spike girth	SG	Maximum diameter of spike, excluding bristles, (mm)
Stem diameter	SD	Internode above 4th node below spike on main tiller, (mm)
Plant height	PH	Ground level to tip of spike, (cm)
Leaf length	LL	Ligule to tip of leaf on 4th node below spike on main tiller, (cm)

component analysis (Karson, 1982) was applied to the array of BC_0F_2 - and BC_1F_2 -derived line means by using the phenotypic correlation matrix. Eigenvalues (γ_n , $n=...3$) were calculated for the first three components of each mating. Total variance was equated to k , the number of traits; thus, the proportion of the total variance accounted for by each component was γ_n/k . The spindle width, R , (Cox et al., 1984) was calculated as $(k - \gamma_1)/(k - 1)$. Eigenvectors were computed and a component score was calculated for each progeny line as the product of the eigenvectors and the standardized values of the vectors.

RESULTS AND DISCUSSION

The adapted parents were different from the exotic ones for most traits (Table 2). In general, the inbred parents had low values and the exotic parents had high ones for most traits. For the traits that were exceptions to this generality, the trait values for the progeny lines were multiplied by -1 to assure that the exotic parent traits had the high and the adapted parent traits the low values. Because the adapted parents had the low values for all traits and the exotic parents high values, large positive associations between traits in a progeny implied a low level of recombination among exotic and cultivated traits (Cox et al., 1984). Here, recombination refers to the occurrence of traits of both the adapted and exotic parents in the same progeny line, not to genetic linkage.

The eigenvectors, proportions of total variance (γ_i/k) explained by the component, and correlations of components with GY and GR are shown in Table 3, 4, and 5, for principal components one, two, and three, respectively. The spindle width (R) was calculated for the first component (Table 3).

Components of AL Matings

In the J104 x AL mating (Table 3), 50% of the total variability was accounted for by the first three principal components. The first principal component defines a hybrid index when it measures the closeness of the line's phenotype to either the exotic or adapted parent. This index is constructed by summing the products of the eigenvectors multiplied by standardized values for the corresponding traits. A high

Table 2. Means for 20 traits measured on the inbred and exotic pearl millet parents

Trait	Parent				
	J104	81B	AL	NEED	WILD
FLW (DAE)	52.6	62.2	68.9	68.7	71.9
GR (g/m ² /da)	9.1	8.9	14.3	15.7	15.2
GY (g/m ²)	283.9	201.1	290.1	189.6	88.6
SPY (g/m ²)	377.9	297.3	369.9	332.2	199.1
SY (g/m ²)	440.6	446.9	844.2	890.0	962.9
BY (g/m ²)	818.5	744.2	1214.1	1222.2	1162.0
CD (g/m ²)	30.7	92.4	176.2	253.0	120.9
TH (%)	75.0	68.0	77.0	54.0	37.0
HI (%)	34.0	27.0	24.0	15.0	8.0
SW (g/200 seeds)	0.6	0.6	0.8	0.5	0.5
EFT	2.8	.9	.9	1.2	3.3
CBT	0.5	0.1	0.2	0.2	0.4
AT	0.3	0.1	0.1	0.4	3.6
SL (cm)	15.1	19.5	19.9	34.9	19.4
SG (mm)	3.3	3.1	3.9	2.9	2.6
SD (mm)	1.2	1.4	1.7	1.7	1.4
PH (cm)	147.9	138.0	231.5	241.5	234.8
LL (mm)	45.5	51.4	62.5	65.6	59.1
AR	1.0	1.0	1.0	7.0	7.0
SH	4.0	4.0	4.0	1.0	1.0

Table 3. Eigenvector values for the first principal component, the proportion of the total progeny variance accounted for by this component (γ_1/k), R , spindle width (R), and the correlation of component scores with GY (r_{GY}) and GR (r_{GR}) for six pearl millet matings

Traits	Matings					
	AL		WEED		WILD	
	J104	81B	J104	81B	J104	81B
EFT	0.22	0.13	0.25	-0.24	-0.21	-0.28
CBT	0.20	0.11	0.30	-0.23	-0.18	-0.31
SS	-0.18	-0.11	-0.07	-0.02	-0.07	0.07
AT	-0.08	0.03	-0.04	0.04	-0.18	-0.24
AR	-0.06	0.06	-0.04	-0.07	-0.06	-0.28
SH	0.02	0.01	0.03	-0.05	-0.16	-0.24
SPY	-0.08	0.24	-0.16	0.13	0.09	-0.14
SY	0.23	0.45	0.29	0.36	0.31	0.19
FL	0.42	0.35	0.36	0.35	0.34	0.25
CBD	0.05	-0.27	0.09	-0.14	0.05	-0.12
BY	0.12	0.44	0.19	0.34	0.30	0.24
TH	-0.29	-0.08	0.24	-0.08	-0.05	0.20
HI	-0.36	-0.22	0.35	0.12	0.06	0.10
SL	0.20	0.26	0.16	0.25	0.35	0.33
SG	0.18	-0.11	0.01	0.14	0.11	0.12
PH	0.42	0.20	0.34	0.32	0.36	0.22
LL	0.30	0.28	0.35	0.37	0.39	0.32
SD	0.23	0.25	0.33	0.38	0.36	0.33
γ_1/k	0.22	0.22	0.28	0.25	0.25	0.27
R^1	0.82	0.82	0.76	0.79	0.79	0.77
r_{GY}	0.42**	0.31**	-0.49**	0.29**	0.19*	0.51**
r_{GR}	0.35**	0.16*	0.57*	0.23**	0.52**	-0.02

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Table 4. Eigenvectors of the second principal component in each mating, the proportion of the total variance accounted for by this component (γ_2/k), and the correlation of the component score with GY(r_{GY}) and GR (r_{GR})

Variables	Matings					
	AL		WEED		WILD	
	J104	81B	J104	81B	J104	81B
EFT	-0.16	0.33	0.41	0.32	0.10	0.22
CBT	-0.14	0.33	0.29	0.30	0.04	0.16
SS	0.15	0.21	0.17	-0.20	0.21	-0.24
AT	-0.04	0.18	-0.13	0.19	0.28	0.16
AR	-0.13	0.04	-0.13	-0.09	0.28	0.19
SH	-0.03	0.08	-0.20	-0.09	0.28	0.11
HY	0.45	0.44	-0.01	0.47	-0.30	0.23
SY	0.46	0.07	-0.36	0.23	0.16	0.40
FL	-0.05	-0.26	-0.17	-0.16	0.13	0.29
CD	-0.40	-0.18	0.35	-0.30	0.02	-0.22
BY	0.55	0.23	-0.33	0.38	0.02	0.28
TH	0.06	0.24	-0.13	-0.23	0.44	-0.15
HI	0.04	0.39	-0.22	-0.31	0.51	-0.42
HL	-0.02	-0.01	0.28	-0.11	-0.08	-0.05
HG	0.13	0.16	0.31	-0.03	-0.24	-0.22
PH	-0.02	-0.17	0.07	-0.04	0.21	0.25
LL	-0.05	-0.19	0.05	-0.06	0.04	0.22
SD	0.10	-0.19	0.10	-0.14	0.08	0.09
γ_2/k	0.16	0.13	0.14	0.14	0.18	0.21
r_{GY}	0.67**	0.76**	0.06	0.75**	-0.81**	-0.48**
r_{GR}	-0.03	-0.08	0.08	-0.09	0.27**	0.19*

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Table 5. Eigenvectors of the third principal component in each mating, the proportion of the total variance accounted for by this component (γ_3/k), and the correlation of the component score with GY (r_{GY}) and GR (r_{GR})

Variables	Matings					
	AL		MEED		WILD	
	J104	818	J104	818	J104	818
EFT	0.50	-0.39	0.04	0.29	0.38	0.25
CBT	0.49	-0.35	0.06	0.28	0.39	0.23
SS	0.25	0.39	0.34	0.32	-0.25	0.31
AT	-0.39	-0.03	0.04	0.04	0.15	0.16
AR	-0.14	0.15	-0.02	0.13	0.26	0.24
SH	0.07	-0.01	0.02	0.04	0.07	-0.11
HY	0.11	0.15	0.54	-0.08	0.36	-0.47
SY	-0.06	0.01	0.25	0.25	0.31	0.23
FL	-0.06	0.06	-0.09	0.03	-0.15	-0.22
CO	0.08	0.18	-0.23	-0.24	-0.33	-0.21
BY	0.02	0.06	0.47	0.16	0.39	0.40
TH	0.14	0.35	-0.26	0.44	0.02	-0.01
HI	0.18	0.33	-0.23	0.53	-0.02	0.14
HL	-0.25	0.21	0.14	0.00	0.03	-0.07
HG	0.29	0.24	0.26	-0.27	0.20	0.36
PH	-0.12	0.16	0.14	0.06	-0.03	-0.07
LL	-0.11	0.21	0.03	-0.04	-0.06	-0.03
SD	0.11	0.29	0.10	-0.07	0.04	0.04
γ_3/k	0.12	0.12	0.12	0.11	0.16	0.11
r_{GY}	0.22**	0.44**	0.81**	-0.43**	0.38**	0.48**
r_{GR}	0.07	0.31**	0.15	-0.03	0.11	0.13

** Significant at the 0.01 level.

index would show that a progeny line was similar to one parental phenotype and a low score that it was similar to the other parental phenotype. In the J104 x AL mating, a high score would show that a line was similar to the AL phenotype. Eigenvectors for the first component in this mating were high for those traits by which the J104 and AL parents differed most. It accounted, however, for only 22% of the progeny variability. The R -value was 0.82 in this mating, which indicates that there was no restriction to recombination between adapted and exotic parent traits. A low value for R would have indicated a restriction on recombination. The first principal component was significantly and negatively correlated with GY and significantly and positively correlated with GR. Thus, there were definite and important associations of the exotic phenotype with low GY and high GR, but they were not strong. Eigenvectors for the second component of the J104 x AL (Table 4) indicated that this component was associated with those traits that contribute to efficiency of biomass production before flowering. A high progeny score for this component was associated with the high biomass characteristics of AL and the efficient partitioning of assimilates between vegetative and reproductive growth of J104. The second component was significantly and positively correlated with GY but noncorrelated with GR. This indicated that GR was not associated with BY in this mating. Eigenvectors for the third component of J104 x AL (Table 5) indicated it was associated with traits related to partitioning of assimilates between basal and aerial tillers. Low EFT was associated with low AT. This component had a small but significant positive correlation with GY and no association with GR, so high GR was not associated with a high EFT or AT.

In the 81B x AL mating, the proportion of total variance accounted for by the first three principal components was 48%. The first component (Table 3) had large eigenvectors for the productivity traits SPY, SY, BY, FL, HL, PH, LL, and SD. This component was heavily weighted by measurements of photoperiodic response or biological habit, so a high component score was associated with the exotic parental phenotype for these traits. This finding corroborated the results of Pernés et al. (1980). There were low but significant positive correlations of this principal component with GY and GR. Large eigenvectors for the second component for 81B x AL were associated with traits that measured the efficiency of partitioning of assimilates: A progeny with high EFT, CBT, SPY, HI, SS, BY, TH, and early flowering would be representative of a desired pearl millet ideotype. That is, an adequate supply of assimilates partitioned efficiently between basal tillers, panicles, and individual seeds in an early genotype should produce a high grain yield. This component was significantly and positively correlated with GY but was noncorrelated with GR. High eigenvectors for the third principal component were associated with high values of SS, TH, and HI but low values of EFT and CBT (Table 5). Thus, this component represented the compensatory relationship between spike number and seed weight. It was significantly and positively correlated with both GY and GR. The correlation with GR indicated that some lines with both high GR and high HI occurred in this mating.

Components of WEED Matings

For the J104 x WEED and 81B x WEED matings, the first three principal components accounted for 50 and 55% of the total variance, respectively. The eigenvectors of the first principal component (Table 3) in both matings indicated that a high scoring progeny was associated with the weedy phenotype. No recombination spindle was defined for either mating. The first principal component for J104 x WEED was significantly and negatively correlated with GY and significantly and positively correlated with GR. This was expected since low GY and high GR are characteristic of the WEED phenotype. In the 81B x WEED mating, this component was significantly and positively correlated with both GY and GR.

The eigenvectors for the second component of the J104 x WEED mating (Table 4) were high for traits associated with partitioning between spike number and size. High second component scores contained high positive weights for BY, SY, EFT, and CBT and negative weights for CD, SL, and SG, so in plant development a high biomass and efficient partitioning to basal tillers were associated with low vegetative/reproductive competition and small heads. This component was not correlated with either GY or GR in J104 x WEED. Interestingly, eigenvectors for the second component for the 81B x WEED mating (Table 4) and the third component for the J104 x WEED mating (Table 5) were similar in magnitude. A high score was associated with high TH, SS, HI, EFT, CBT, and biomass traits (SY, SPY, and BY) but low competition between vegetative and reproductive growth after flowering (CD). That

is, these two components were related to partitioning of assimilate between vegetative and reproductive growth and structures. Component scores were significantly and positively correlated with GY but non-correlated with GR. Eigenvectors for the third principal component for 81B x WEED were similar in size to those for 81B x AL, but opposite in sign (Table 5). The correlation of this component with GY was significant and negative in 81B x WEED but significant and positive in 81B x AL. The traits associated in this component tended to be higher in AL than in 81B; thus a high-scoring line in the 81B x AL mating had high SS, TH, and HI, but in 81B x WEED, a high-scoring line had a low SS, TH, and HI. Correlations of this component with GR were nonsignificant.

Components of WILD Matings

In each mating involving WILD, the first three principal components accounted for about 60% of the total variance. In the J104 x WILD mating, a high score for the first principal component was associated with the WILD parental phenotype. It was significantly and positively correlated with both GY and GR. The second principal component for this mating had high eigenvectors for traits affected by the domestication process (Pernés et al., 1980). This association occurred only in J104 x WILD, a mating that involved the two most diverse parents. That is, J104 was developed from lines of Indian origin, whereas WILD was of African origin. This component was significantly and negatively correlated with GY and significantly and positively correlated with GR, indicating that traits for domestication and productivity in the wild

parent were associated.

The third component of J104 x WILD (Table 5) defined a similar axis for the progeny as did the third component for J104 x WEED and the second component for 81B x WEED (Table 4). These components were heavily weighted by traits that measured the efficiency of partitioning of assimilates between vegetative and reproductive growth. In both WILD matings, this component was positively and significantly correlated with GY and noncorrelated with GR. It accounted for less of the variance in the 81B x WILD mating than in J104 x WILD.

The 81B x WILD mating was the only one for which the first principal component did not define a hybrid index (Table 3). A hybrid index was defined if the eigenvectors were such that the component score could be used to determine how closely a progeny line was to the exotic or adapted parent's phenotype. But in this mating, a high score was associated with a recombinant type having the values for EFT, CBT, AT, TH, and SH from 81B and the values for SY, BY, FL, HL, PH, LL, and SD from WILD. The component score was significantly and positively correlated with GY but noncorrelated with GR. The eigenvectors of the second component in 81B x WILD (Table 4) were large for SY and HI. A high score for this component was associated with the wild parent phenotype but also with large seeds. It was significantly and negatively correlated with GY and significantly and positively correlated with GR.

In summary, the first principal component score defined a hybrid index in five of the six matings. In J104 x AL, J104 x WEED, and 81B x

NEED, this index involved all the traits in which the parents differed, but in 81B x AL and J104 x WILD, all the productivity traits were involved. In one mating (81B x WILD), the first component was associated with a recombinant type. In five matings, the first-component hybrid indexes had significant and positive correlations with GR, but the correlations with GY, although significant, were both positive and negative. A complex of traits measuring efficiency of partitioning between vegetative and reproductive growth was associated with the second component of J104 x AL and 81B x NEED and the third component of J104 x NEED and the two WILD matings. These components had similar significant and positive correlations with GY and were noncorrelated with GR. There were a number of components in the different matings which defined compensatory relationships between two competing structures in the plant. For example, there was competition between basal and aerial tillers in J104 x AL, between spike number and seed weight in 81B x AL and 81B x NEED, and between spike number and spike size in J104 x NEED. Further, the second components of the WILD matings defined complexes of traits that were not defined in any other mating. In J104 x WILD, it defined a group of traits associated with domestication, and in 81B x WILD, it defined a complex of traits that characterized the wild phenotype with large seeds.

Contrast of First Two Components

Plots of the first vs. the second principal component scores for the parents and their BC_0 and BC_1 progenies are shown in Figs. 1 through 6 for J104 x AL, 81B x AL, J104 x NEED, 81B x NEED, J104 x WILD, and

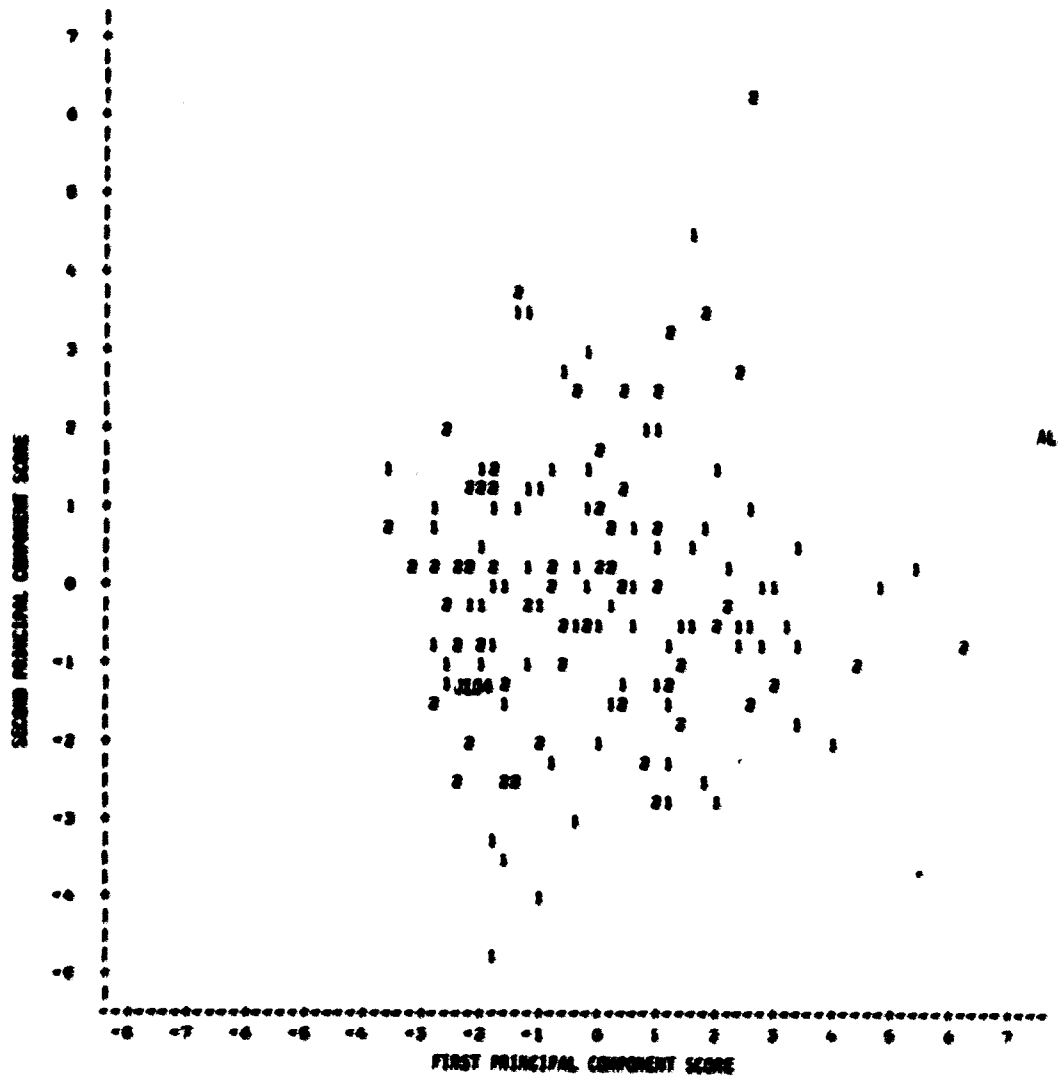


Figure 1. Plot of first vs. second principal component scores for J104, AL, and their introgressed progeny (1 = one BC_0F_2 -derived line, and 2 = one BC_1F_1 -derived line)

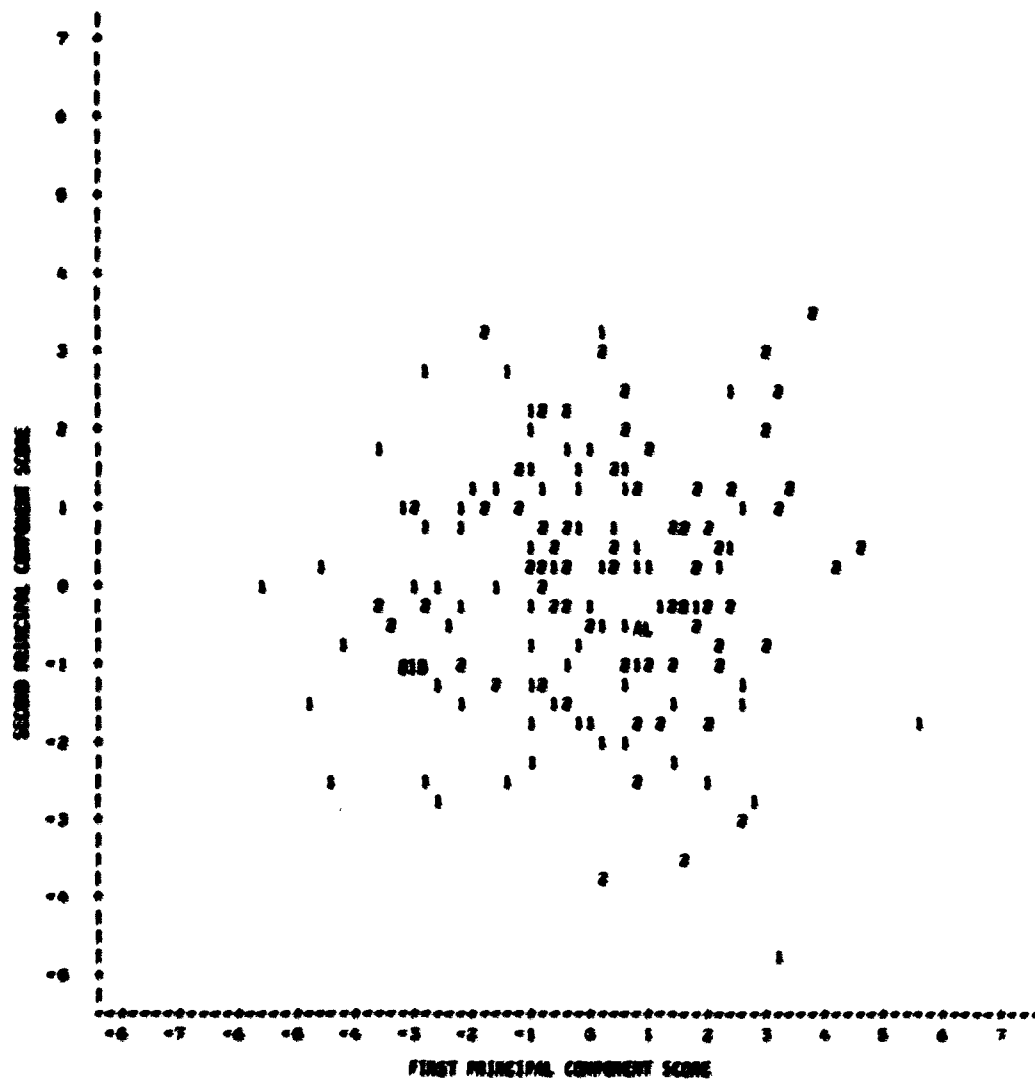


Figure 2. Plot of first vs. second principal component scores for 81B, AL, and their introgressed progeny (1 = one BC_0F_2 -derived line, and 2 = one BC_1F_2 -derived line)

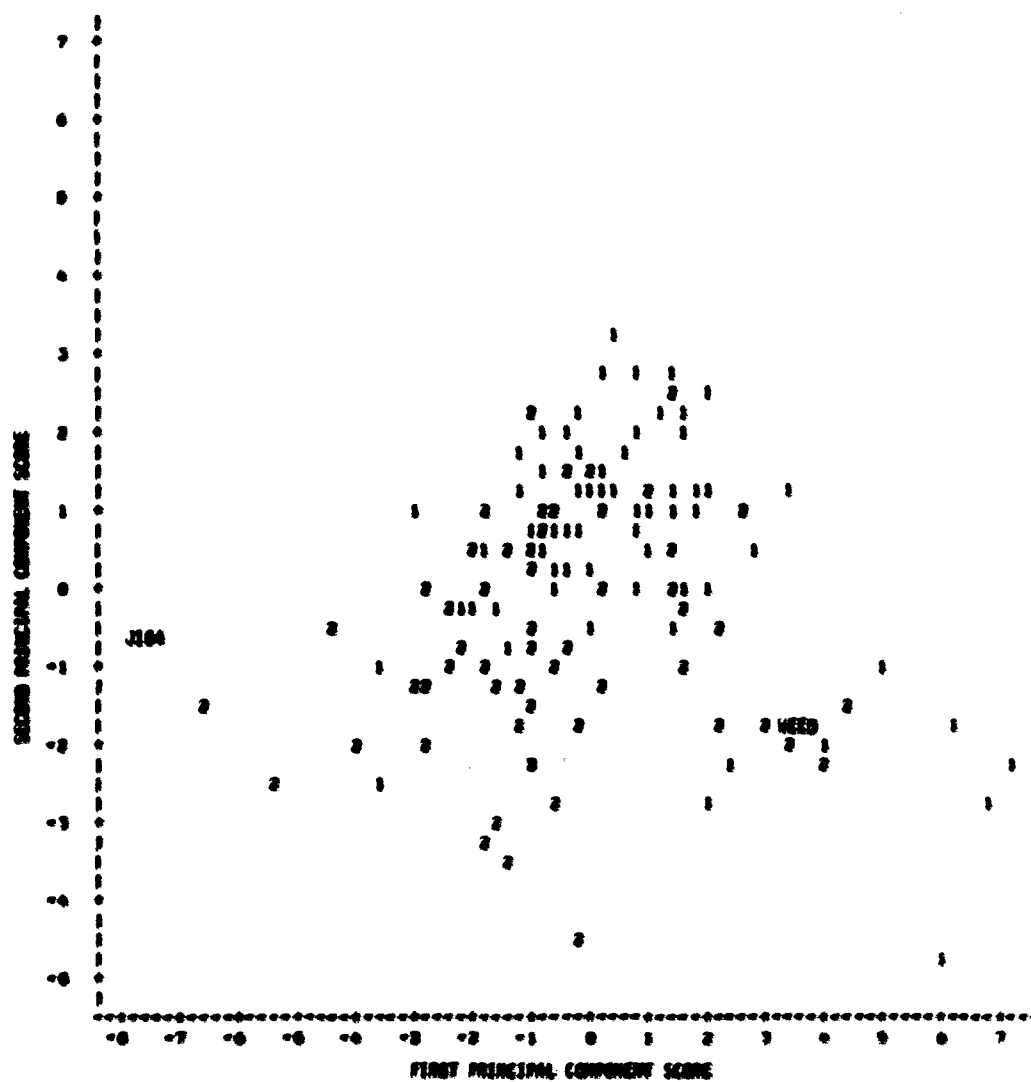


Figure 3. Plot of first vs. second principal component scores for J104, WEED, and their introgressed progeny (1 = one BC_0F_2 -derived line, and 2 = one BC_1F_2 -derived line)

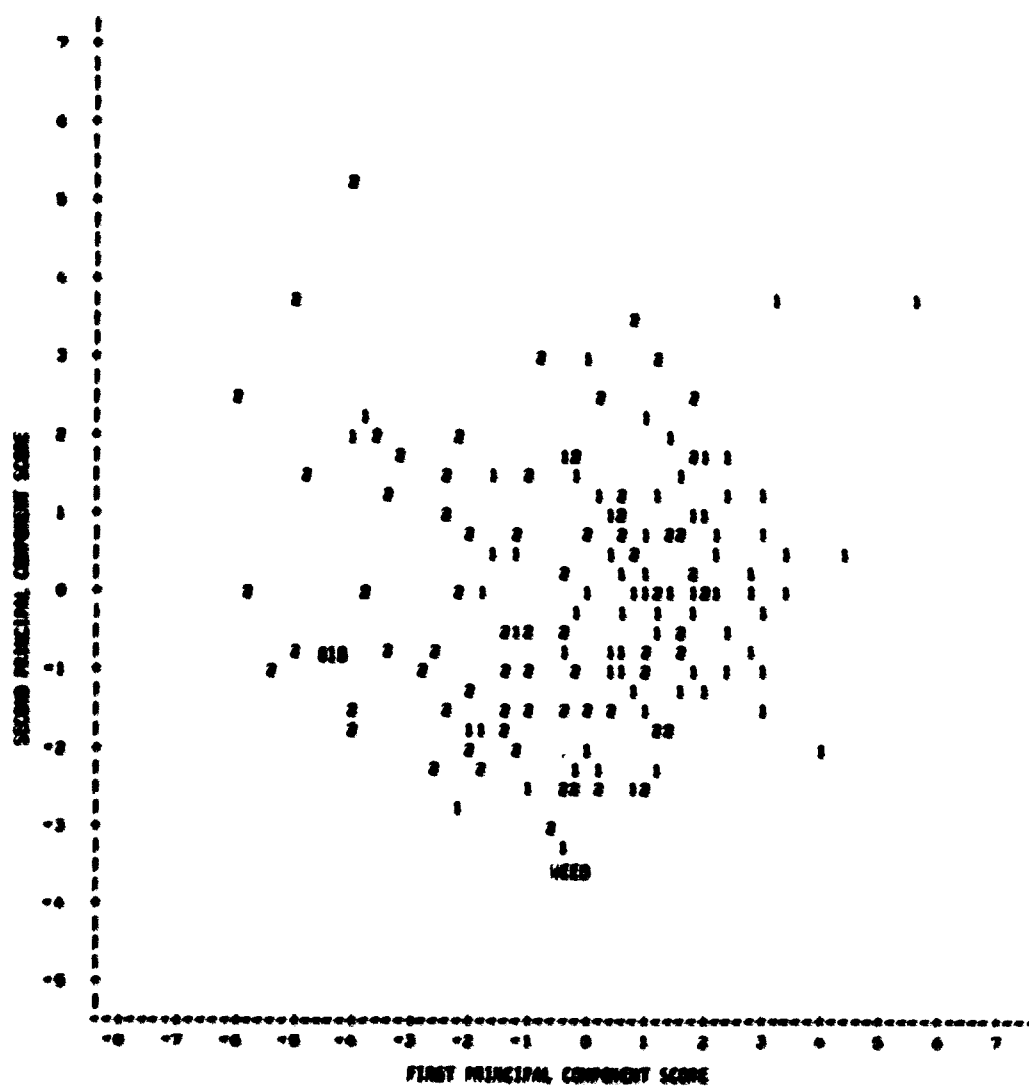


Figure 4. Plot of first vs. second principal component scores for 81B, WEED, and their introgressed progeny (1 = one BC_0F_2 -derived line, and 2 = one BC_1F_2 -derived line)

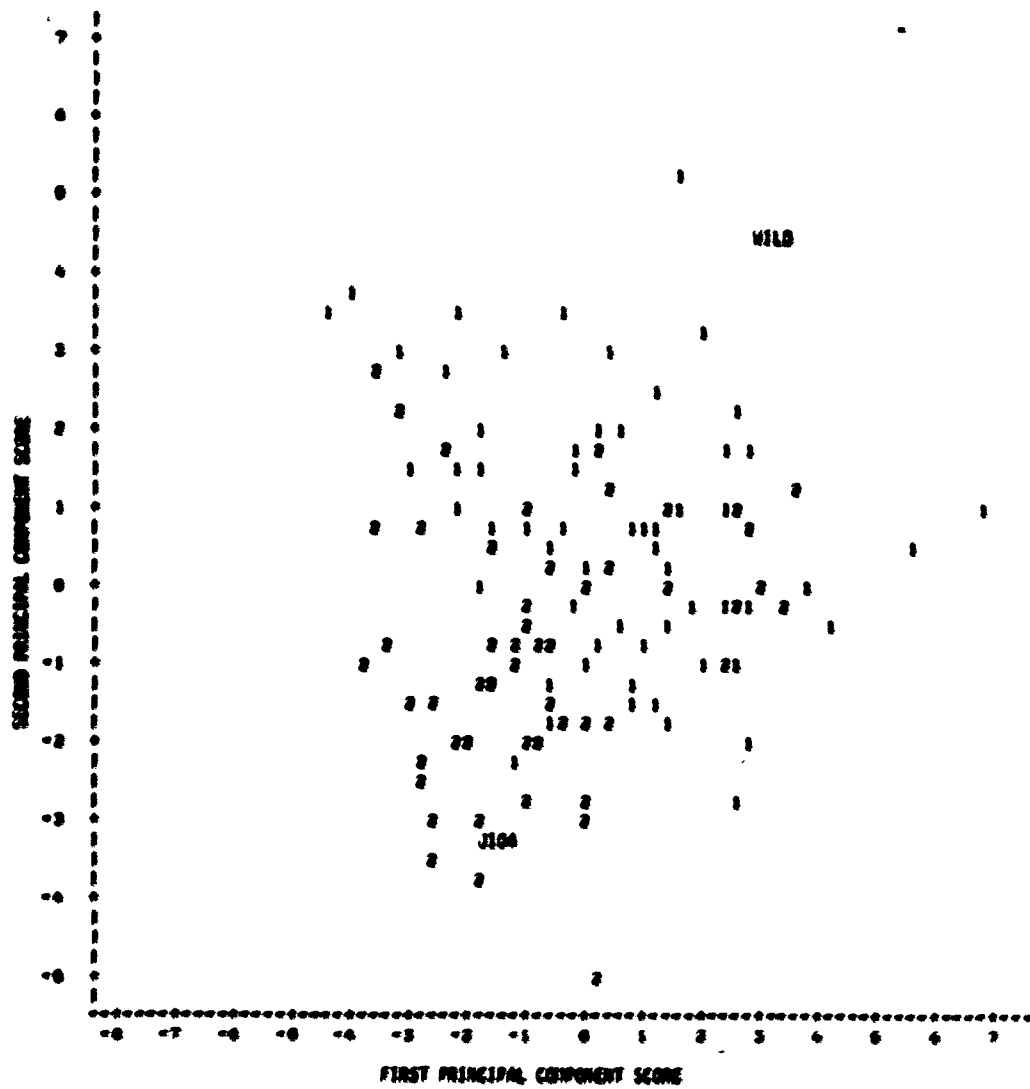


Figure 5. Plot of first vs. second principal component scores for J104, WILD, and their introgressed progeny (1 = one BC_0F_2 -derived line, and 2 = one BC_1F_2 -derived line)

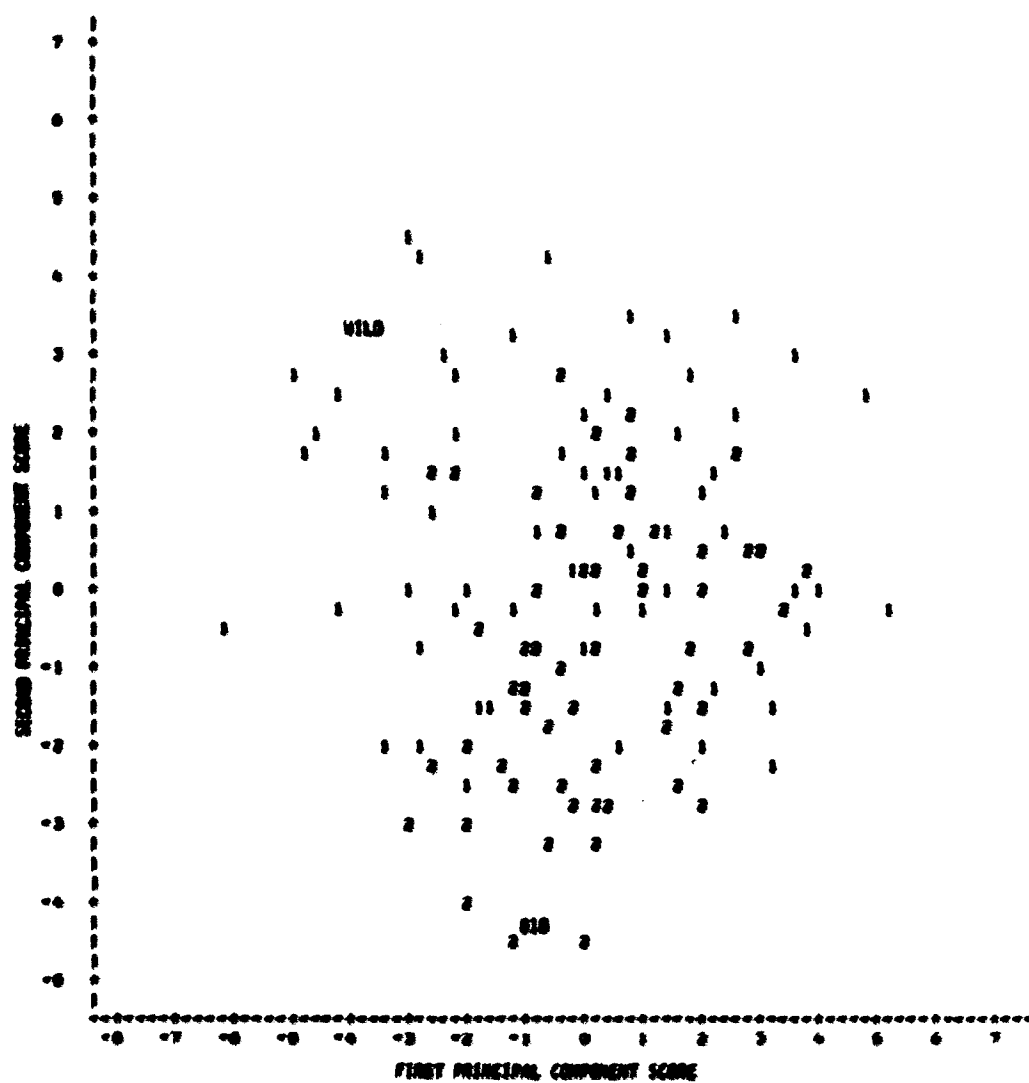


Figure 6. Plot of first vs. second principal component scores for 81B, WILD, and their introgressed progeny (1 = one BC_0F_2 -derived line and 2 = one BC_1F_2 -derived line)

81B x WILD, respectively. In the AL and WEED matings, the parents differed more for the first component scores than for the second component scores. In all the WILD matings, the two parents differed more for the second component score than the first component score. In one mating (81B x WEED), the parents differed nearly equally for both component scores. In J104 matings, few progeny exceeded the exotic parent for hybrid index, which means that few offspring in these matings were more exotic than the exotic parent. In 81B matings, many progeny of both backcross generations exceeded the exotic parent for the hybrid index. In 81B x WILD, many backcross progeny exceeded both parents for the first component; this was not unexpected, since the first component did not define a hybrid index in this mating. In J104 x WILD, only one progeny line exceeded the WILD parent's second component score. This indicated only one progeny line was more nondomesticated than the WILD parent. The progenies from BC_0 and BC_1 did not differ for principal component scores in three matings (J104 x AL, 81B x AL, and 81B x WILD). In contrast, Cox et al. (1984) found that backcross generations of introgressed progeny from interracial matings of sorghum did differ in mean hybrid index scores. The fact that BC_1 progeny were not phenotypically closer to the recurrent parent than were the BC_0 progeny was unexpected. In only one mating (J104 x WEED) was there strong differentiation of generations. In all matings except J104 x WILD, the progeny were offset from a line connecting the two parents, which indicated either intra- or interlocus interactions of adapted and exotic genes (Sneath, 1976).

SUMMARY

The first principal component described a hybrid index of traits in five of six matings, and some common complexes of traits were defined by the other components in these matings. However, only 50 to 60% of the total variances in the six matings were accounted for by the first three principal components. Because there were no strong correlations among traits, from adapted parents on the one hand or exotic parents on the other, selection for recombinant progeny from matings involving the three exotic germplasm sources should be possible. Grain yield was significantly correlated with several of the principal components in the six matings, indicating that the complexes of traits that the components defined may offer routes for improving GY of pearl millet. GR was also significantly correlated with several of the components but none of the correlations of GY or GR with the principal components indicated the occurrence of undesirable associations that would hinder selection of high GY or GR in agronomically desirable segregates.

REFERENCES CITED

- Anderson, E. 1949. Introgressive hybridization. John Wiley and Sons, New York.
- Bramel-Cox, P. J. 1985. Part III. Exotic germplasm for improving grain yield and growth rate in pearl millet. In Evaluating three potential sources of germplasm to improve growth rate, grain yield, and harvest index in pearl millet. Ph.D. dissertation. Library, Iowa State University, Ames, Iowa.
- Cox, T. S., L. R. House, and K. J. Frey. 1984. Trait associations in introgressed populations of sorghum. Z. Pflanzenzuchtg. (In press).
- International Board for Plant Genetic Resources (IBPGR) and International Crops Research Institute for the Semi-arid Tropics (ICRISAT). 1981. Pearl millet descriptors. IBPGR Secretariat, Rome, Italy.
- Marchais, L. and S. Tostain. 1984. Genetic divergence between wild and cultivated pearl millets (Pennisetum typhoides). II. Characters of domestication. Z. Pflanzenzuchtg. (In press).
- Pernés, T., É. Nguyen Van, M. Beninga, and J. Belliard. 1980. Analyse des relations génétiques entre formes spontanées et cultivées chez le mil à chandelle (Pennisetum americanum (L.), Leake, P. mollissimum Hochst). II. Etude de 3 familles F₂ issues d'hybrides entre une plante d'un ecotype de Pennisetum mollissimum Hochst et 3 lignées de mil cultivé, Pennisetum americanum (L.), Leake. Ann. Amélior. Plantes 30:253-269.
- Sneath, P. H. A. 1976. Some applications of numerical taxonomy to plant breeding. Z. Pflanzenzuchtg. 76:19-46.

GENERAL CONCLUSIONS AND DISCUSSION

The results presented in the four sections of this dissertation have important implications relative to the utilization of exotic germplasm for improving the productivity of pearl millet, either directly by breeding for higher grain yield or indirectly by manipulating growth rate. The first two sections dealt with the differences between the exotic strains and the adapted inbred lines. The last two sections dealt with evaluation of three exotic parents as sources of desirable genes for improving grain yield and growth rate of adapted pearl millet without destroying the adaptability and agronomic type of this crop plant.

Section I concluded that the wild accession had an unusual early-season growth pattern that may have contributed to its greater growth rate as reported by Bramel-Cox et al. (1984). This wild strain had seedling establishment and early development patterns that could be desirable for pearl millet produced in regions where seedling establishment limits production. Section II characterized adapted and unadapted hybrids and cultivars and weedy and wild accessions of pearl millet for grain yield, growth rate, biological yield and several other traits. In this section, it was concluded that the weedy and wild strains may be sources of genes that could improve growth rate, biological yield, and effective basal tiller percentage of cultivated pearl millet, but these accessions possessed a number of undesirable traits.

In both Section I and Section II, primitive landraces and weedy and wild accessions were tested per se, but this was not an appropriate

method to determine the potential of these germplasm sources for improving grain yield or growth rate in breeding programs where these sources would be used as gene donors. Section III evaluated the breeding potential of these exotic strains for improving grain yield or growth rate while Section IV evaluated trait associations that might hinder the usefulness of them as germplasm sources.

Section III concluded that the best parent for improving growth rate in cultivated pearl millet would be the wild accession but the weedy strain was nearly equivalent. For short-term improvement, the primitive landraces would be the best source of genes for increasing grain yield because the agronomic quality of the progeny from matings involving them was not altered by introgression. However, it was possible to select segregates with increased grain yield, growth rate, and biological yield and the harvest index and maturity of the adapted parent from matings involving any of the exotic parents. Cox et al. (1984a) studied the use of wild sorghum to improve grain yield of cultivated sorghum. Less than 1% of the progeny were high transgressive segregates for grain yield of sorghum, but with pearl millet, there were 18% high transgressive segregates for grain yield from the wild accession matings, 44% from the weedy strain matings, and 24% from the primitive landrace matings. Cox et al. (1984a) found that the mean grain yield of the top ten progeny lines selected for grain yield significantly exceeded the recurrent parent in only five of the six interracial matings and only by 12-15%. In this study, the mean of grain yield of the top 10% of the pearl millet lines selected for grain yield exceeded

the recurrent parent by 24-119%. So the grain yield improvements via introgression were very different in sorghum and pearl millet, but in neither crop was there any trait association which would hinder the use of genes from exotic strains for increasing the productivity potential of adapted sorghum and pearl millet (Section IV and Cox et al., 1984b). In Section IV, it was shown that certain groups of traits were correlated significantly with grain yield and growth rate. Such a group of traits usually was associated with a common physiological process and some were common to several matings. If such a group of traits could enhance grain yield and growth rate, it might be beneficial to select for the group to increase grain yield and/or growth rate.

This study evaluated different exotic strains as donors of genes for improving pearl millet inbreds per se, but to utilize genes for higher grain yield or growth rate, the combining ability of derived lines with these enhanced traits needs to be evaluated. Pearl millet normally is grown as a hybrid or synthetic. Lines developed in this study and the inbred parents could be evaluated for combining ability simultaneously. BC_0F_2 - and BC_1F_2 -derived lines, and the original adapted parents, could be crossed to a number of inbred lines, and any difference in grain yield or growth rate of the sets of hybrids would result from alleles contributed by the exotic parents.

This study has implications for long-term population improvement of pearl millet. Section III showed that backcrossing would not be necessary to improve growth rate in the adapted parent but it may be needed to improve adaptation of derived lines. It would be best to make a number of crosses between single plants in an exotic population

and adapted inbreds. These single-plant crosses would be selfed to develop F_1 families that would be tested for growth rate per se and/or as families of F_2 -derived lines to assess variability for growth rate. The families with high growth rate and variability for growth rate would be recombined to develop a base population. This high growth rate base population could be improved for adaptation by backcrossing and/or population breeding. And, the improved populations could be a source of inbred lines with high growth rate and grain yield. These lines conceivably could have good combining ability for high grain yield.

This study was part of a larger research program designed to evaluate the potential of wild and weedy relatives of cultivated crops for improving quantitatively inherited traits in both allogamous and autogamous crops. Pearl millet is different from oats, barley, and sorghum, the other crops studied, in that it is cross-pollinated and thus probably has a constant gene exchange with its weedy and wild relatives in nature. But like sorghum, pearl millet possesses a large untapped reservoir of genes in the primitive landraces and weedy and wild relatives.

ADDITIONAL REFERENCES CITED

- Ahluwalia, M., and M. C. Patneik. 1963. A study of heterosis in pearl millet. *Ind. J. Genet.* 23:34-38.
- Belliard, J., É. Nguyen Van, and J. Pernès. 1980. Analyse des relations génétiques entre founes spontanées et cultivées chez le Mil à chandelle. I. Etude des parents et hybrides de première génération (F_2) entre un écotype de Pennisetum mollissium Hoehst. (formé spontané) et différentes formes cultivées de Pennisetum americanum (L.), Leake. *Ann. Amélior. Plantes* 30:229-251.
- Bhatt, G. M. 1977. Response to two-way selection for harvest index in two wheat (Triticum aestivum L.) crosses. *Aust. J. Agric. Res.* 28:29-36.
- Bloethe, D. G., and K. J. Frey. 1978. Grain yield variation in oats associated with differences in leaf area duration among oat lines. *Crop Sci.* 18:765-769.
- Bramel-Cox, P. J., D. J. Andrews, F. R. Bidinger, and K. J. Frey. 1984. A rapid method of evaluating growth rate in pearl millet and its weedy and wild relatives. *Crop Sci.* 24:1187-1191.
- Brunken, T., J. M. J. DeMet, and J. R. Harlan. 1977. The morphology and domestication of pearl millet. *Econ. Bot.* 31:163-174.
- Campbell, A. R., and K. J. Frey. 1972. Inheritance of groat protein in interspecific oat crosses. *Can. J. Plant Sci.* 52:735-742.
- Chaudhary, B. S., O. P. Luthra, and V. P. Singh. 1977. Studies on harvest index and related characters in wheat. *Z. Pflanzenzüchtg.* 79:336-339.
- Coons, G. H. 1975. Interspecific hybrids between Beta vulgaris L. and the wild species of Beta. *J. Am. Soc. Sugar Beet Technol.* 18: 281-304.
- Cox, T. S. 1979. Inheritance and complementarity of genes for high groat protein from two Avena species. M.S. Thesis. Library, Iowa State University, Ames, Iowa.
- Cox, T. S., and K. J. Frey. 1984. Genetic variation for grain yield and related traits in sorghum introgressed populations. *TAG* 68: 145-148.
- Cox, T. S., L. R. House, and K. J. Frey. 1984a. Potential of wild germ-plasm for increasing yield of grain sorghum. *Euphytica* 33: In press.

- Cox, T. S., L. R. House, and K. J. Frey. 1984b. Trait associations in introgressed populations of sorghum. *Z. Pflanzenzuchtg.* In press.
- Dunckelman, P. H., and R. D. Breaux. 1972a. Breeding sugarcane varieties for Louisiana with new germplasm. *Proc. Int. Soc. Sugarcane Technol.* 14:233-239.
- Dunckelman, P. H., and R. D. Breaux. 1972b. Evaluation of germplasm in the USDA program in Hoama, Louisiana. *Proc. Int. Soc. Sugarcane Technol.* 14:888-892.
- Efron, H., and H. L. Everett. 1969. Evaluation of exotic germplasm for improving corn hybrids in Northern United States. *Crop Sci.* 9:44-47.
- Elmore, C. D., J. D. Hesketh, and H. Muramoto. 1967. A survey of rates of leaf growth, leaf aging, and leaf photosynthetic rates among and within species. *Ariz. Acad. Sci.* 4:215-219.
- El-Sharkawy, M., J. Hesketh, and H. Muramoto. 1965. Leaf photosynthetic rates and other growth characteristics among 26 species of Gossypium. *Crop Sci.* 5:173-175.
- Epstein, E., R. W. Kingsbury, J. D. Norlyn, and D. W. Rush. 1979. Production of food crops and other biomass by seawater culture. In Hollaender, A., J. C. Allen, E. Epstein, A. S. Pietro, and O. R. Zaborsky (eds.), *The biosaline concept*. Plenum Press, New York, New York.
- Evans, L. T., and R. L. Dunstone. 1970. Some physiological aspects of evolution in wheat. *Aust. J. Biol. Sci.* 23:725-741.
- Frey, K. J. 1977. Protein of oats. *Z. Pflanzenzuchtg.* 78:185-215.
- Frey, K. J., T. S. Cox, D. M. Rodgers, and P. J. Bramel-Cox. 1984. Increasing grain yields with genes from wild and weedy species. *Proc. XV Intl. Genet. Congr., New Delhi, India.* In press.
- Grumet, R., J. F. Fobes, and P. C. Herner. 1981. Ripening behavior of wild tomato species. *Plant Physiol.* 68:1428-1432.
- Gupta, V. P., and T. P. Singh. 1973. Combining ability for grain yield and its components in pearl millet. *Ind. J. Genet. Plant Breed.* 33:183-188.
- Hammons, R. O. 1970. Registration of Spancross peanuts. *Crop Sci.* 10:459.

- Kuenzel, K. A. 1982. Grain yield and groat-protein percentage relationships in oats (Avena sativa L.). Ph.D. dissertation. Iowa State University, Ames, Ia. Univ. microfilm no. AD682-21197.
- Lawrence, P. K., and K. J. Frey. 1976. Inheritance of grain yield in oat species crosses. Egypt. J. Genet. Cytol. 5:400-409.
- Marchais, L., and J. Tostain. 1984. Genetic divergence between wild and cultivated pearl millets (Pennisetum typhoides). II. Characters of domestication. Z. Pflanzenzüchtg. In press.
- Meredith, W. R. 1977. Backcross breeding to increase fiber strength of cotton. Crop Sci. 17:172-175.
- Murphy, J. P., and K. J. Frey. 1984. Comparisons of oat populations developed by intraspecific and interspecific hybridization. Crop Sci. 24:531-536.
- Nass, H. G. 1980. Harvest index as a selection criterion for grain yield in two spring wheat crosses grown at two population densities. Can. J. Plant Sci. 60:1141-1146.
- Oka, H., and H. Morishima. 1971. The dynamics of plant domestication: Cultivation experiments with Oryza perennis and its hybrid with O. sativa. Evolution 25:356-364.
- Oldemeyer, R. K. 1975. Introgression hybridization as a breeding method in Beta vulgaris. J. Am. Soc. Sugar Beet Technol. 18:269-273.
- Panje, R. R. 1972. The role of Saccharum spontaneum in sugarcane breeding. Proc. Int. Soc. Sugarcane Technol. 14:217-233.
- Pearson, C. J., F. M. Dawbin, D. R. Muldoon, and L. C. Campbell. 1977. Growth and quality of tropical forages in a temperate climate. Aust. J. Exp. Agric. and Anim. Husb. 17:991-994.
- Pernés, J., É. Nguyen Van, M. Beninga, and J. Belliard. 1980. Analyse des relations génétiques entre formes spontanées et cultivées chez le mil à chandelle (Pennisetum americanum (L.), Leake, P. mollissimum Hochst). II. Etude de 3 familles F₂ issues d'hybrides entre une plante d'un ecotype de Pennisetum mollissimum Hochst et 3 lignées de mil cultivé, Pennisetum americanum (L.), Leake. Ann. Amélior. Plantes 30:253-269.
- Rajhathy, J., J. W. Morrison, and S. Symko. 1963. Interspecific and intergenetic hybrids in Hordeum. Barley Genet. Wageningen, p. 195-212.
- Reeves, R. G. 1950. The use of teosinte in the improvement of corn inbreds. Agron. J. 42:248-251.

- Reeves, R. G., and A. J. Buckholdt. 1964. Modification and improvement of maize by crossing it with Tripsacum. Crop Sci. 4:7-10.
- Rick, C. M. 1974. High soluble-solids content in large-fruited tomato lines derived from a wild green-fruited species. Hilgardia 42: 493-510.
- Rodgers, D. M. 1982. Improvement of cultivated barley (Hordeum vulgare) with germplasm introgressed from H. spontaneum. Ph.D. dissertation. Iowa State University. Ames, Ia. Univ. microfilm no. 82-21223.
- Rosielle, A. A., and K. J. Frey. 1975. Estimates of selection parameters associated with harvest index in oat lines derived from a bulk population. Euphytica 24:121-131.
- Rush, D. W., and E. Epstein. 1976. Genotypic responses to salinity: Differences between salt-sensitive and salt-tolerant genotypes of the tomato. Plant Physiol. 57:162-166.
- Rush, D. W., and E. Epstein. 1981. Comparative studies on the sodium, potassium, and chloride relations of a wild halophytic and a domestic salt-sensitive tomato species. Plant Physiol. 68:1308-1313.
- Singh, I. O., and M. C. Stoskopf. 1971. Harvest index in cereals. Agron. J. 63:224-226.
- Stalker, H. T., J. C. Mynne, and M. Company. 1979. Variation in progenies of an Arachis hypogaea x diploid wild species hybrid. Euphytica 28:675-684.
- Takeda, K., and K. J. Frey. 1977. Associations among grain yield and other traits in Avena sativa x A. sterilis backcross populations. Euphytica 26:309-317.
- Takeda, K., and K. J. Frey (in preparation). Grain yield improvement through increase of harvest index and vigor traits by a method of independent culling level in Avena sativa x A. sterilis backcross populations. Agronomy Dept., Iowa State University.
- Takeda, K., K. J. Frey, and T. B. Bailey. 1980a. Contribution of growth rate and harvest index to grain yield in F₂-derived lines of oats (Avena sativa L.). Can. J. Plant Sci. 60:379-384.
- Takeda, K., K. J. Frey, and T. B. Bailey. 1980b. Correlations among grain yield, protein yield, and related traits of oats (Avena sativa) cultivars. Egypt. J. Genet. Cytol. 8:283-294.
- Takeda, K., K. J. Frey, and O. Bloethe-Helsel. 1979. Growth rate inheritance and associations with other traits and contributions of growth rate and harvest index to grain yield in oats (Avena sativa L.). Z. Pflanzenzuchtg. 82:237-249.

- Thomas, H., J. M. Haki, and S. Arangzeb. 1980. The introgression of the wild oat Avena magna ($2N = 4x = 28$) into the cultivated oat A. sativa ($2n = 6x = 42$). *Euphytica* 29:391-399.
- Walker, P. I. T. 1972. Utilization of Noble and Saccharum spontaneum germplasm in the West Indies. *Proc. Int. Soc. Sugarcane Technol.* 14:224-232.

ACKNOWLEDGEMENTS

I would like to thank David Andrews, my advisor in India, for his guidance, advice, and assistance in the planning of my experiments, the actual technical conductance of the research, and its interpretation. He was always ready to lend assistance in getting land, supplies, and labor whenever it was necessary. I feel I not only learned a lot about pearl millet and general experimentation under his guidance, but also about the daily administration of a research program. His guidance further heightened an excellent experience I gained at ICRISAT. I also would like to thank Dr. F. R. Bidinger for his help.

I would like to acknowledge the research scholarship from the training program at ICRISAT, and in particular Dallas Oswalt, who was always there for advice, also. The opportunity to do research at ICRISAT has been very rewarding and will undoubtedly influence any research I do in the future. There were many programs and subprograms at ICRISAT that were helpful, and I wish to thank all of them. I especially wish to thank my two field assistants, Mr. A. Ganapathi and Mr. K. P. Reddy. Mr. A. Ganapathi taught me, a novice, about the actual breeding of pearl millet, and Mr. K. P. Reddy helped introduce me to the many administrative decisions involved in conducting this type of research with a large labor force. I also would like to thank Mr. B. P. Reddy for his advice and help.

My major advisor was Dr. K. J. Frey, and I would like to thank him for his support and advice, both in India and at Iowa State University. I would also like to thank the members of my committee for putting up

with meeting at strange times to get around my need to travel from Kansas.

It would not be possible to adequately express to the reader of this dissertation the contribution made by my companion and partner in life, my husband Stan Cox (alias T. Stanton Bramel-Cox). His contributions included advice on the research, taking up household duties and baby-sitting, and general morale boosting when the juggling of responsibilities seemed overwhelming to this student, mother, and wife. His love and encouragement helped me through the bad times and added immensely to the good. I would also like to thank my daughter, Sheila, a source of distraction and sometime assistance during the last three years of this degree. I want to especially thank my son Paul, whose untimely arrival during the final stretch of this dissertation could have complicated it even further had he not been such a good companion during those long hours when one sits and writes. I finally must thank Mary Jo Vivian for being my typist, housemate, and most importantly, friend.