A Rapid Method of Evaluating Growth Rate in Pearl Millet and Its Weedy and Wild Relatives[1]

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ABSTRACT

Vegetative growth rate is a physiological trait that has been hypothesized to be useful in the improvement of grain yield in cereal crops. Usefulness of this physiological trait in a breeding program depends upon a rapid method that allows the evaluation of large numbers of lines. In this study, the objective was to determine if the rates of growth calculated from periodic samplings could be estimated by using only one or two dates of harvest relating to specific stages in the plant's development. Periodic samples of vegetative growth were made on 12 pearl millet (*Pennisetum americanum*) genotypes, plus three weedy (ssp. *stenostachyum*) and one wild (ssp. *monodii*) accession in two seasons once every 2 weeks starting at 21 days after emergence and continuing to maturity. With use of the rates calculated on these periodic samples as the actual growth rate, it was found that samples taken at either one or two dates of harvest could be used to adequately estimate this rate. The two dates of harvest were taken at either 10 days after flowering or at maturity. The rate was calculated as (vegetative dry weight at flowering + 10 days or at maturity)/(number of days to flowering + 10).

Additional index words: **Vegetative growth rate, Introgression, cumulative growth curves, periodic sampling.**

In CEREALS, grain yield can be expressed by the equation, Grain yield= growth rate × growth duration × harvest index (Takeda and Frey, 1977), because the components of growth rate and growth duration determine biological yield, and harvest index determines the proportion of biological yield that is deposited into grain yield. In cereal breeding, yield gains to date have been obtained almost entirely from increases in harvest index, but little possibility exists for further improvement of this trait. Takeda and Frey (1977) have proposed that when life cycles of cereal grains are restricted due to maturity constraints, direct attention must be given to selecting for increased growth rates as a basis for grain yield improvements.

The usual procedure for measuring growth rate in cereals is via sequential measurements of vegetative dry weight made throughout the growing season (Hughes and Freeman, 1967; Loomis et al., 1971). Fischer and Wilson (1975) used weekly samplings throughout the growth cycle of sorghum, a procedure that is accurate for measuring growth rate but so time consuming that only a few strains can be measured in one experiment. Thus, it cannot be used in a plant breeding program in which a large number of lines must be evaluated. For oats (*Avena sativa* L.), Takeda and Frey (1977); Takeda et al. (1979b); and Takeda et al. (1979a, 1980) found that vegetative growth rate could be estimated adequately by dividing straw weight at maturity by days to flowering. This method is rapid, thus permitting the evaluation of many strains for growth rate in a short time.

Our objective was to determine for pearl millet (*Pennisetum americanum*) whether the vegetative growth rates calculated by using frequent sampling could be estimated adequately by using sampling data from only one or two harvests that could be related to specific stages in the development of the plants.

MATERIALS AND METHODS

The materials for our study were 16 genotypes, including collections of cultivated, weedy, and wild pearl millet (Table 1). They included a diverse array of Indian hybrids and cultivars, African landraces, and weedy and wild millets.

Experimental Methods

Genotypes were evaluated in two experiments, one grown in January to April and the other in June to 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 of a randomized complete block design with four replicates. Genotypes were planted in whole plots that consisted of four rows of 9 m length with 75 cm between the rows and 10 cm between the plants within the row. Subplots were harvest dates and consisted of an area of 1.125 m^2 of competitive plants within the center two rows. The optimum size of a subplot was determined in a previous experiment (Bramel-Cox, unpublished data), and subplots were separated from one another by a border of 0.30 m^2. Harvest dates were randomized within each genotype. Plant population was 130 000 plants ha^{-1}. The dry-season (January-April) experiment was sown, irrigated, and emerged on 20, 21, and 26 January, respectively. Plots were watered by furrow irrigation once every 14 days until 1 March, after which they were irrigated at 10-day intervals until the last harvest. At each irrigation, ca. 30 mm of water was applied. Daylength during this experiment averaged 12.3 h. At sowing, day and night temperatures were 30 and 15°C, re-

Table 1. Origin and maturity of pearl millet genotypes.

Genotype	Origin	Group and maturity
ICH-162	India	Late hybrid
ICH-412	India	Late hybrid
MBH-110	India	Early hybrid
BJ-104	India	Early hybrid
WC-C75	India	Early variety
ICMS-7819	India	Early variety
ICMS-7703	India	Late variety
ICMS-7937	India	Late variety
P-242	Mali	Late landrace
M-70-1	Tanzania	Early landrace
Ankoutess	Niger	Late landrace
SAD-222	Malawi	Early landrace
P-2811I	Niger	Late weedy (ssp. *stenostachyum*)
P-946I	Oasis Niger	Early weedy (ssp. *stenostachyum*)
P-270I	Mali	Late weedy (ssp. *stenostachyum*)
Wild-Upper Volta	Upper Volta	Wild (ssp. *monodii*)

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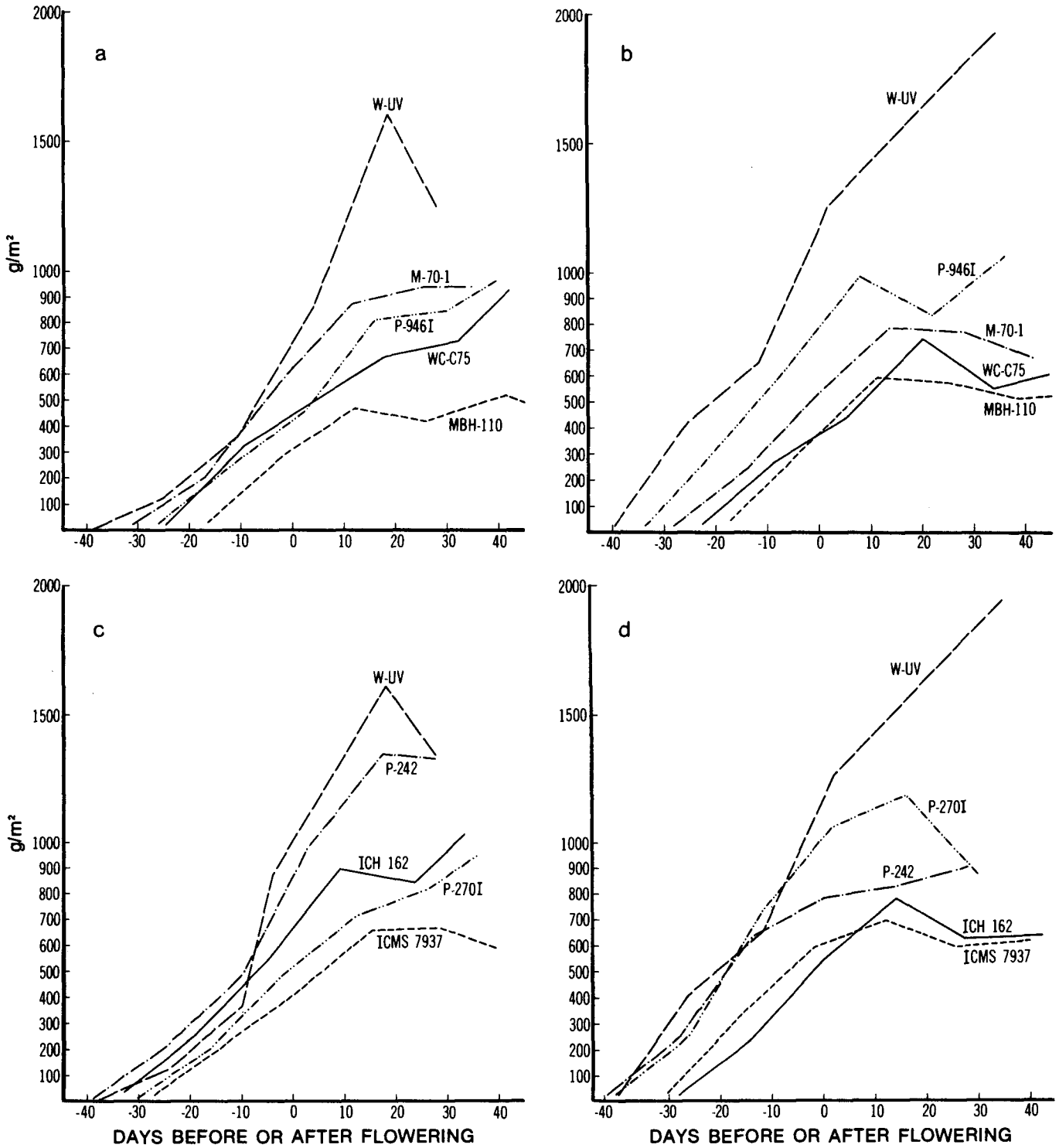

Fig. 1. Vegetative dry matter accumulation in *Pennisetum americanum* as related to flowering date and growth duration in each group, ssp. *monodii* and ssp. *stenostachyum* for (a) the early genotypes in the rainy season, (b) early genotypes in the dry season, (c) late genotypes in the rainy season, and (d) late genotypes in the dry season.

spectively, and near termination they averaged 38 and 23°C, respectively. The rainy-season (June–September) experiment was sown, irrigated, and emerged on 20, 21, and 24 June, respectively. Daylengths during this experiment averaged 13.4 h. Temperatures were fairly stable at 30°C for days and 22°C for nights. June to September, the normal production season for millet, usually is rainy, cloudy, and humid. During the 1981 season, no supplementary irrigation was needed.

Total-plant dry weight was determined by harvesting all plants in a subplot at ground level, drying the biomass at 75°C for 36 h, and weighing. After flowering, the biomass from a plot was divided into vegetative and reproductive portions, and dry weights were taken on the two portions

separately. All dry weights were converted to grams per meter^2 for analyses. 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. Harvests in both experiments were begun 21 days after seedling emergence and continued at 14-day intervals until physiological maturity. Physiological maturity of the main panicles was recorded as appearance of the black layer (in days after emergence). Sampling seasons were 16 February to 23 April for the dry-season experiment and 15 July to 18 to 28 September (depending on genotype) for the rainy-season experiment.

Residuals from the regression analysis were random, so regression coefficients and R^2-values were estimated from the original data.

RESULTS AND DISCUSSION

Growth Curve Characteristics

Cumulative growth curves from periodic samplings for four early pearl millet genotypes (WC-C75, MBH-110, M70-1, and P946I) and the wild ssp. are shown in Fig. 1a and 1b for the rainy- and dry-season experiments, respectively, and for four late genotypes (ICMS-7937, ICH-162, P-242, and P-270I) and the wild ssp. in Fig. 1c and 1d, respectively. Each group of genotypes shown in a figure contained a hybrid, a cultivar, a landrace, a wild subspecies, and a weedy subspecies. To determine whether the shapes of the cumulative growth curves were related to any particular stage of development, all harvest dates were arranged as plus and minus deviations from flowering date (Fig. 1). Mean flowering dates ranged from 49 to 63 days after emergence except for MBH-110 and BJ-104, both of which were earlier.

The growth pattern for pearl millet had two phases: Phase I—linear accumulation of dry weight until after flowering and Phase II—either a leveling off, an apparent decrease, or a continued increase. The change in growth between Phase I and II occurred ca. 10 to 15 days after flowering for most genotypes. Growth during the dry season was unique in that a slight lag period occurred during early growth of some genotypes; e.g., the wild entry (W-UV) and P-242. Also, growth of P-242 continued after flowering in the dry season but leveled off in the rainy season, whereas P-270 had a decrease in accumulation after flowering in the dry season but a continuation in the rainy season. Growth duration of the genotypes did not affect the morphological stage of change from Phase I to Phase II.

Frey et al. (1967) found that vegetative dry weight accumulation of oats (unit area basis) tended to terminate at flowering, whereas for pearl millet, the change from Phase I to Phase II occurred ca. 10 days after flowering except for the wild ssp. *monodii*.

Estimations of Growth Rate

The growth patterns in Fig. 1a to d suggested several methods to compute or estimate growth rates of the entries. The first and second actual growth rates were computed by regressing the vegetative dry weights on the harvest dates by using Phase I all harvests up to maturity (M) and Phase II all harvests up to the one closest to flowering plus 10 days (FL + 10). In the dry season, the M and FL + 10 growth rates were similar for some genotypes (e.g., P-242, Ankoutess, and P-2811I) but dissimilar for others (e.g., MBH-110, ICMS-7819, and M-70-1) (Table 2). In the rainy season, the FL + 10 growth rates were from 1.5 to 3.0 times greater than the M values for all genotypes except wild Upper Volta (Table 3). However, ranking of genotypes was similar for both computation methods, with rank correlation coefficients of 0.91** and 0.61** (**Significant at the 0.01 level.) for the dry and rainy seasons, respectively.

Table 2. Vegetative growth rates (g/m^2/day) of 16 pearl millet entries grown in the dry season computed by linear regression with data from all sampling dates (M) and sampling dates until flowering + 10 days (FL + 10) and estimated by three methods that use data from only one or two sampling dates.

	Growth rates (g/m^2/day)				
	By regression		By estimates†		
Entry	M	FL + 10	1	2	3
ICH-162	13.5 (7)‡	18.1 (6)	11.0 (10)	13.7 (4)	15.9 (11)
ICH-412	11.4 (10)	15.9 (9)	8.8 (13)	10.8 (9)	12.8 (15)
MBH-110	5.5 (16)	13.5 (12)	7.7 (15)	8.4 (14)	17.1 (9)
BJ-104	8.8 (13)	10.6 (15)	8.5 (14)	7.5 (15)	13.2 (14)
WC-C75	11.4 (10)	13.3 (13)	12.8 (6)	9.3 (12)	20.5 (3)
ICMS-7819	10.6 (12)	15.9 (9)	9.9 (12)	10.8 (10)	14.4 (13)
ICMS-7937	8.4 (15)	13.2 (14)	7.2 (16)	9.2 (13)	10.6 (16)
ICMS-7703	8.8 (13)	10.2 (16)	10.0 (11)	7.1 (16)	15.2 (12)
P-242	19.9 (2)	21.7 (2)	14.0 (3)	15.5 (2)	19.8 (4)
M-70-1	13.6 (6)	18.4 (5)	11.3 (9)	12.3 (7)	16.5 (10)
Ankoutess	18.4 (5)	17.6 (7)	13.1 (4)	12.6 (6)	18.2 (6)
SAD-222	18.6 (4)	20.5 (3)	13.0 (5)	14.5 (3)	18.6 (6)
P-2811I	19.7 (3)	19.1 (4)	15.0 (1)	13.1 (5)	21.8 (1)
P-946I	12.9 (8)	16.1 (8)	12.8 (6)	11.4 (8)	19.6 (5)
P-270I	12.8 (9)	14.8 (11)	11.5 (8)	9.9 (11)	17.2 (8)
Wild Upper Volta	22.1 (1)	24.9 (1)	14.8 (2)	18.6 (1)	21.2 (2)
$\bar{x}$			11.3	11.5	17.1

† See text for formulas used in Estimates 1, 2, and 3.
‡ Rankings within a column are given in parentheses.

Table 3. Vegetative growth rates (g/m^2/day) of 16 pearl millet (*Pennisetum americanum*) entries grown in the rainy season computed by linear regression by using data from all sampling dates (M) and sampling dates until flowering + 10 days (FL + 10) and estimated by three methods that use data from only one or two sampling dates.

	Growth rates (g/m^2/day)				
	By regression		By estimates†		
Entry	M	FL + 10	1	2	3
ICH-162	7.9 (9)‡	15.9 (10)	7.3 (11)	10.8 (9)	10.7 (13)
ICH-412	8.6 (8)	17.2 (7)	7.1 (13)	11.4 (7)	9.9 (14)
MBH-110	5.7 (16)	17.4 (6)	8.7 (5)	10.7 (10)	14.1 (4)
BJ-104	5.9 (15)	14.5 (14)	6.8 (14)	8.5 (16)	11.1 (10)
WC-C75	7.7 (10)	14.8 (12)	7.8 (9)	10.4 (11)	12.0 (6)
ICMS-7819	7.0 (12)	16.4 (8)	7.5 (10)	11.5 (6)	11.1 (10)
ICMS-7937	6.9 (13)	14.3 (15)	6.4 (16)	9.7 (13)	9.2 (16)
ICMS-7703	7.3 (11)	15.4 (11)	7.2 (12)	10.1 (12)	10.9 (12)
P-242	10.6 (5)	13.4 (16)	8.5 (6)	9.4 (15)	11.5 (9)
M-70-1	9.0 (7)	16.3 (9)	8.2 (8)	11.1 (8)	12.0 (6)
Ankoutess	6.9 (13)	14.8 (12)	6.7 (15)	9.7 (13)	9.9 (15)
SAD-222	10.1 (6)	18.8 (5)	8.8 (4)	12.1 (5)	12.4 (5)
P2811I	15.1 (2)	20.4 (3)	10.8 (3)	13.5 (4)	14.8 (3)
P-946I	12.9 (4)	20.3 (4)	12.2 (2)	13.8 (2)	18.0 (2)
P-270I	13.2 (3)	21.8 (2)	8.5 (6)	13.6 (3)	11.6 (8)
Wild-Upper Volta	23.5 (1)	26.8 (1)	21.2 (1)	18.2 (1)	29.6 (1)
$\bar{x}$			8.9	11.5	13.1

† See text for formulas used in Estimates 1, 2, and 3.
‡ Rankings within a column are given in parentheses.

Table 4. Percentages of variation among M and FL + 10 growth rates accounted for by growth rates computed by estimate methods 1, 2, and 3† and rank correlations between computed and estimated growth rates in pearl millet.

Comparison	Percentage of variation		Rank correlation	
	R^2 dry season	R^2 rainy season	Dry season	Rainy season
Growth rate (M) with				
Estimate 1	79	84	0.91**	0.72**
Estimate 2	79	85	0.93**	0.72**
Estimate 3	62	74	0.73**	0.55*
Growth rate (FL + 10) with				
Estimate 1	52	73	0.73**	0.73**
Estimate 2	97	94	0.97**	0.94**
Estimate 3	38	69	0.59*	0.66**

*,** Significantly different at 0.05 and 0.01 probability levels, respectively.
† See text fr formulas used in Estimates 1, 2, and 3.

Next, we estimated growth rates by using three procedures that used vegetative dry weights from only one or two harvests. The procedures were:

Estimate 1 = Straw weight (g/m^2) at final harvest/(number of days to flowering + 10)

Estimate 2 = Vegetative dry weight (g/m^2) at FL + 10/(number of days to flowering + 10)

Estimate 3 = Straw weight (g/m^2) at final harvest − dry weight at 21 days/(number of days to flowering + 10 −21) (i.e., number of days to flowering − 11).

Estimate 1 assumes that all net growth after flowering + 10 days was allocated to grain filling. Estimate 2 does not make that assumption and requires sampling at flowering + 10 days. Estimate 3 makes the same assumption as Estimate 1 but corrects for the slower dry-matter accumulation that usually occurs in the seedling stage. Estimate 3 requires a harvest at 21 days.

Estimates 1 and 2 gave similar growth rates for the different genotypes in the dry season, but Estimate 3 gave higher values than either of the other methods (Table 2). In the rainy season, growth rates were similar for Estimate 2 and Estimate 3, and they were generally higher than those from Estimate 1 (Table 3) whether based upon a comparison of the phenotypic values and their rankings only or upon the means for each estimate.

The relative worth of each of the three methods of estimating growth rate was evaluated in two ways. First, we computed the percentages of variability that could be accounted for in the dependent variables (M and FL + 10) by the independent variables (estimation procedures) (Table 4), and second, we correlated the ranks of the regression growth rates with the ranks of the estimation growh rates in all combinations. Estimates 1 and 2 accounted for 79 to 85% of the variation among M growth rates, but Estimate 3 accounted for only 62 to 74%. Estimate 2 accounted for 94 to 97% of the variability among FL + 10 growth rates. The other two estimates accounted for only 38 and 52% in the dry season and 69 and 73% in the rainy season (Table 4).

All rank correlations among methods of computing growth rates were significant at the 5 or 1% level in the dry and rain seasons. Correlations for Estimates 1 and 2 with M were > 0.9 and 0.7 in the dry and rainy seasons, respectively. These estimates were similar in both seasons, but Estimate 2 had the highest coefficient in both seasons with the FL + 10 actual growth rate.

Table 5. F-values and significances for tests of homogeneity of regression coefficients and intercepts with use of growth rate (FL + 10) for different germplasm comparisons in pearl millet for the dry and rainy seasons.

	Dry season		Rainy season	
	F-intercept	F-slope	F-intercept	F-slope
Within sources				
Indian hybrids (IH)	3.3	4.8**	2.7	0.9
Indian varieties (IV)	6.2	4.1*	1.0	0.4
African landraces (AL)	1.2	0.9	1.1	1.2
Weedy accessions (WA)	0.2	0.9	0.3	0.1
Among sources				
IH vs. IV	3.9	4.3**	0.4	1.4
IH vs. AL	1.6	2.8*	0.0	0.7
IH vs. WA	1.1	2.1	0.9	0.5
IH vs. Wild	0.7	2.8	4.2	22.5**
IV vs. AL	2.2	4.2**	0.9	0.8
IV vs. WA	1.5	2.6	1.5	1.1
IV vs. Wild	1.1	3.9**	1.8	5.7**
AL vs. WA	0.9	1.2	1.6	1.3
AL vs. Wild	0.5	1.0	2.1	5.1**
WA vs. Wild	0.3	1.7	0.1	0.8

*,** Significantly different at 0.05 and 0.01 probability levels, respectively.

The conclusion from Table 4 and those preceding, assuming that the regression coefficients accurately portray the actual growth rate, is that either the weight at final harvest or the weight at flowering + 10 days divided by the number of days to flowering + 10 days are good estimators of M and FL + 10 values.

Evaluation of Method of Estimation

Growth rate (FL + 10) and Estimate 2 each were used to evaluate growth rate differences of the 16 genotypes by using tests of homogeneity of regression coefficients and intercepts (Table 5) and specific orthogonal comparisons in the ANOVA for Estimate 2 (Table 6). Growth rates, both actual and estimated, for the wild and weedy accessions differed from those for the cultivated genotypes but not from each other, and growth rates for all cultivated genotypes were similar. None of the F-values (Table 5) of the among-group comparisons involving the weedy accessions and the cultivated groups or the weedy and the wild accessions were significant. Therefore, we conclude that the wild subspecies differs significantly from the cultivated groups for growth rate, but the weedy group falls between and does not differ significantly from the cultivated or wild group. The "among-sources-of-germplasm" component accounts for a greater proportion of the mean squares in Table 6, and is of greater importance as indicated by the number of significant F-values in Table 5, than does the "within-sources" component.

Results from the dry-season experiment were somewhat different from those for the rainy season. For example, when actual growth rates were compared for wild and weedy germplasm versus cultivated germplasm, the wild species differed from the

Table 6. ANOVA for dry weight at harvest date closest to flowering + 10 days/number of days to flowering + 10 (Estimate 2) in pearl millet for the dry and rainy seasons, with orthogonal comparisons.

Source of variation	df	Mean squares	
		Dry	Rainy
Replicates	3	10.6**	31.1**
Entries	15	46.3**	22.5**
Among	4	96.3**	71.9**
Wild vs. all others	1	338.4**	188.8**
Weedy vs. cultivated	1	34.1**	98.2**
Indian vs. African cultivated	1	2.9	0.6
Indian hybrids vs. varieties	1	9.3	0.2
Within	11	28.2**	4.5
Indian hybrids	1	93.6*	2.1
Indian varieties	1	17.2	3.1
African landraces	1	2.1	2.4
Weedy accessions	1	0.1	0.1
Residual	7	28.1**	5.9
Error	45 (41)	6.6	7.8

*,** Significantly different at 0.05 and 0.01 probability levels, respectively.

Indian varieties, whereas when estimated growth rates were used, both the wild accession and the weedy accessions differed from all the cultivated entries. Further, there was more or less equal importance for the "among-sources" and "within-sources" of germplasm components (Tables 5 and 6). Even with some differences in dry-and rainy-season results, it seems from Tables 5 and 6 that the formula (dry weight at flowering + 10 days)/(days to flowering + 10) adequately estimated actual growth rates and would lead to similar conclusions to those when three or more dates of harvest are used.

As would be expected, the wild and weedy subspecies were very inferior for grain yield and agronomic acceptability. However, if the high growth rate from these accessions could be incorporated into a cultivated pearl millet ideotype, it might improve grain yield in this grain crop of limited duration. Frey (1976, 1983) and Frey et al. (1984) have shown that the introgression of *Avena sterilis* into cultivated oats gave increases in grain yield of 10 to 29%. Takeda and Frey (1977) and Takeda et al. (1979b) have shown that these yield increases were due to increased growth rate. The wild and weedy accessions potentially could be used to improve grain yield of cultivated pearl millet by the transfer of their high growth rate. In fact, Frey et al. (1984), using backcross-derived lines from the mating of the cultivated and weedy millets, found that in segregates with high growth rate many exceeded the grain yield of the cultivated parent by at least one LSD. The agronomic potential of these segregates needs to be evaluated further to provide an accurate answer to the potential of ssp. *stenostachyum* and ssp. *monodii* to improve the grain yield of *Pennisetum americanum* via increased growth rate.

CONCLUSIONS

Actual vegetative growth rate of pearl millet grown in the rainy season, which is the normal season for this crop, can be estimated from one harvest of vegetative dry matter at either flowering + 10 days or at maturity. This method allows an estimate of the growth rate that is comparable to estimates made from three or more harvests. Estimated growth rates compared more closely with three or more harvest estimates in the rainy season than in the dry season, but this method would be adequate for a selection program in either season. Better growth rate estimates, as might be desired for segregates that contained genes from ssp. *monodii* or ssp. *stenostachyum*, could be obtained by using vegetative weights from harvest at both flowering date + 10 days and maturity. This method would allow one to distinguish between segregates whose growth pattern differs after the critical flowering + 10 days point. The period after flowering should have a vegetative growth rate near zero in those materials in which all growth after flowering + 10 days is reproductive, which does not seem to be the case in the wild and weedy accessions. Therefore, two harvests should be used when the evaluated material has wild and weedy germplasm in the background.

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