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Breeding beans for resistance to terminal drought in the lowland tropics

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Summary

In the lowland regions of Latin America, a large proportion of beans are sown at the beginning of a dry season where a guaranteed terminal (end-of-season) drought will reduce yields. This study was undertaken to identify lines within two black bean recombinant inbred line (RIL) populations with resistance to terminal drought. The two RIL populations were developed from crosses between a drought resistant line, B98311 from Michigan, with TLP 19 and VAX 5, two lines from CIAT with improved disease resistance and adaptation to growing conditions in Latin America. The RIL populations were evaluated in experiments conducted in Zamorano, Honduras and Veracruz, Mexico under drought stress and well-watered (non-stress) treatments. Yields were reduced in each experiment by drought and the fungal pathogen, *Macrophomina phaseolina*. Drought stress, disease pressure and low yields contributed to high coefficients of variation (CV), which made it difficult to select superior lines. Selection was based on rank of geometric mean (GM) yield calculated from the yield in the stress and non-stress treatments. One RIL, L88-63, ranked first in GM yield at both locations. Subsequent testing in Honduras and Michigan confirmed the high yield potential and broad adaptation of L88-63. Breeding beans for drought resistance in lowland tropical environments should also include breeding for resistance to *M. phaseolina*.

Introduction

Terminal drought constrains common bean (*Phaseolus vulgaris* L.) production in Central America. The lowland tropic environments of Central America have a bimodal rainfall pattern that permits two seasons of crop production. The first season (Primera) has the greatest rainfall (720 mm), whereas the second season (Postrera) has limited rainfall (560 mm) that rapidly diminishes. More than 60% of the area cultivated to bean in Honduras is planted in the second cropping season under a relay system after maize (*Zea mays*) has been harvested (Rosas et al., 1991). The short life cycle of common bean makes it an ideal crop to grow at the end of the first cropping season but diminishing soil moisture ultimately creates a terminal drought stress. The bean production area in Honduras is signficantly greater during the second season than during the first season despite an overall yield reduction of 50% due to terminal drought (Cotty et al., 2001). Since irrigation is unrealistic due to socio-economic constraints, genetic improvement for drought resistance provides the main opportunity to increase the productivity of beans grown under terminal drought stress in Central America and Mexico.

Two types of drought are described for the semi-arid tropics (Ludlow & Muchow, 1990). Terminal (end-of-season) drought occurs in lowland tropical environments when crops are planted at the beginning of a dry season. The crop relies on stored soil moisture for growth during the critical flowering and pod-fill periods as the terminal drought stress intensifies. Intermittent drought is due to climatic patterns of sporadic rainfall that cause intervals of drought at varying intensities. The nature of this rainfall is unpredictable and leads to marginal yields in potentially valuable land. This type of rainfall pattern is endemic to the semiarid highlands (1800 masl) of Mexico (Singh, 1995). Different breeding strategies and bean archetypes may be needed to confer adaptation to terminal and intermittent drought.

The most drought resistant germplasm reported in *P. vulgaris* comes from the Durango race in the Middle American gene pool (Terán & Singh, 2002). Moderate success in breeding beans for intermittent drought resistance has been achieved in diverse bean genotypes from the Durango race (Acosta-Gallegos & Adams, 1991; Acosta-Gallegos & Kohashi-Shibata, 1989; Ramirez-Vallejo & Kelly, 1998; Rosales-Serna et al., 2004; Schneider et al., 1997). In Central American countries, however, mainly race Mesoamerican beans are planted. Interracial populations have been suggested as the most effective way to combine high yield with drought resistance within the Middle American gene pool of common bean (Singh, 1995; Terán & Singh, 2002). The ideal genotype for terminal drought stress may be one that combines the drought resistant traits of Durango race beans with the archetype of Mesoamerican beans (Kelly et al., 1999). This archetype was bred into the drought resistant Michigan breeding line, B98311 by crossing the Mesoamerican cultivar Raven (Kelly et al., 1994) with the drought resistant line T-3016 from Mexico. T-3016 was derived from a cross of Sierra/AC1028 and is a non-commercial Durango race breeding line previously identified as being drought resistant based on high GM yield in Mexico and Michigan (Schneider et al., 1997). B98311 was selected as the highest yielding genotype under severe drought stress in Michigan in 1998 (Kolkman & Kelly, 1999).

Drought resistance is defined based on the relative yield of a genotype compared with other genotypes subjected to the same drought (Hall, 1993). Yield measured under moisture stress (Yd) and non-stress conditions (Yp) can be used to calculate the GM = $(Yp*Yd)^{1/2}$ yield for individual genotypes. GM yield has been shown to be an effective selection criterion for drought resistance in common bean (Abebe et al., 1998; Samper, 1984). Since drought resistance must be developed in a genetic background of high Yp (Blum, 1988), breeding for drought resistance in common bean should first consist of selection for high GM yield, followed by selection for high yield under stress (Schneider et al., 1997).

In addition to lower yields caused by terminal drought, performance can be reduced by attacks from *Macrophomina phaseolina* (Tassi) Goid., the causal organism of charcoal rot disease of bean. This disease proliferates in hot, dry environments and will inevitably attack and kill susceptible bean genotypes grown in terminal drought stress environments (Mayek-Pérez et al., 2002). Resistance to charcoal rot has been reported in bean genotypes BAT 477 and TLP 19 (Mayek-Pérez et al., 2001a; Olaya et al., 1996) and should be incorporated into cultivars for production in lowland regions where the disease occurs. Currently, TLP 19 is the most resistant genotype in a differential set created to distinguish between isolates of *M. phaseolina* from Mexico (Mayek-Pérez et al., 2001b).

The objective of this study was to use performance data to identify genotypes from two black bean RIL populations segregating for resistance to terminal drought in Central America and Mexico, and determine the reaction of individual selections to charcoal rot and their broader adaptation in temperate regions.

Materials and methods

Parents and population development

Three black bean genotypes, B98311, TLP 19 and VAX 5, were crossed to generate two RIL populations segregating for drought resistance and possessing commercial quality black bean seed. The drought resistant genotype, B98311 from the Michigan State University (MSU) breeding program possesses a type II growth habit and a deep vigorous taproot (Frahm et al., 2003). TLP 19 was developed for tolerance to low phosphorus at the International Center for Tropical Agriculture (CIAT). Phosphorus-efficient bean genotypes have a shallow root system that spreads superficially through the topsoil, limiting basal root competition (Rubio et al., 2003). Under terminal drought stress in Mexico, TLP 19 has shown resistance to charcoal rot (Mayek-Pérez et al., 2001a). The third genotype, VAX 5, was developed at CIAT from an interspecific hybridization of common bean and tepary bean (*P. acutifolius* A. Gray) and selected for resistance to common bacterial blight (CBB) caused by *Xanthomonas axonopodis* p.v. *phaseoli* (Singh & Munoz, 1999). TLP 19 and VAX 5 were selected as parents for their adaptation to the lowland tropics and superior combining ability with B98311, which is adapted to temperate conditions. Additional traits such as commercial seed type, upright growth habit and disease resistance were considered in the selection of parents in order to hasten utilization in the Central American and Caribbean region of any beneficial black genotypes resulting from this work.

The original crosses made in 1998 were B98311/TLP 19 and B98311/VAX 5, which generated populations L88 and L91 respectively. Single pods from individual F_2 plants were harvested in both populations and a single F_3 seed was advanced to the F_4 generation. The last single plant selection was made in the F_3 generation so the seed from each $F_{3:4}$ genotype was harvested in bulk. This $F_{3:5}$ seed was planted in Michigan in 2000 to increase the quantity of seed without selection, and the $F_{3:6}$ seed was shipped to Honduras for testing in 2001. A total of 81 RILs in L88 and 69 RILs in L91 population were produced for testing. Data on growth habit, flowering and maturity dates and seed weight and size were collected on the individual 150 $F_{3:5}$ RILs.

Zamorano, Honduras 2001

The 150 $F_{3:6}$ RILs, three parents and seven checks were planted by hand on January 23rd, 2001 in Zamorano, Honduras (14°00' N, 87°02' W, 800 masl) in collaboration with scientists from the Programa de Investigaciones en Frijol (PIF). The seven checks included the local red-seeded check cultivar Tio Canela-75 and the PIF breeding line EAP 9510-77 from Honduras, the black-seeded cultivar, Negro Tacaná (DOR 390) and the genotype Negro 8025 from Mexico, two drought resistant genotypes BAT 477 and SEA 5 from CIAT and the drought resistant black bean cultivar Rio Tibagi from Brazil (Table 3). Two experiments with different moisture treatments and 160 entries were planted as completely randomized designs (CRD) with three replications. The soil is a sandy-loam, isohyperthermic Mollic Ustifluvent. Plots were single rows 5 m long and 0.7 m wide. Moisture stress and non-stress treatments were applied through control of irrigation. Since furrow irrigation was applied after planting, data on the quantity of water applied could not be measured. Thirty plants were harvested per row to record yield. Data were collected on days to flower and maturity, plant height, lodging, adaptation rating, plant stand, seed size after harvest and disease incidence (DI), rated 75 days after planting as the number of dead plants among 50 plants due to charcoal rot.

Montcalm, Michigan 2001

Using data on GM yields from Zamorano as the selection criteria, the top and bottom 10% of 150 RILs were selected for testing in a temperate environment at Michigan. RILs from population L88 had higher average yield than those from L91 in Zamorano. An equal number of RILs from each population was represented in the selections. Eleven drought resistant and five drought susceptible RILs were selected from population L88 and five drought resistant and ten drought susceptible RILs were selected from population L91 (Table 4). Local black bean cultivars, Phantom and T-39 and the three parents were included to complete two 36-entry, square lattices, which were planted at the Montcalm Research Station (43°40' N, 85°20' W, 244 masl) on June 16th, 2001. The soil type is a McBride sandy loam (coarse-loamy, mixed, mesic Alfic Fragiorthods). An early drought began seven days after planting where less than 5 mm of rain fell during the next 30 days. Water stressed and non-stressed plots were irrigated by overhead sprinklers and the irrigated plots received 38 mm more water than stressed plots. Weeds were controlled with recommended herbicides. Plots were two rows 5.8 m long and 0.5 m apart and a 4.6 m^2 section was hand harvested to calculate yield. Data were collected on days to flower, maturity, plant height, lodging and seed size.

Veracruz, Mexico 2002

The 150 RILs, two parents (B98311 and TLP 19) and one drought resistant check (SEA 5) were planted at the Cotaxtla Research Station (18°44' N, 95°58' W, 16 masl) in Veracruz, Mexico on January 24th, 2002. A factorial experimental design was randomized with four treatment regimes and two replications each treatment. Both populations were exposed to terminal drought stress and non-stress treatment. The soil type is a typical udifluvent (FAO-UNESCO). The second treatment involved inoculation with isolates of *M. phaseolina* compared to non-inoculated natural field infection. Plots were inoculated with 8 g of rice seeds colonized with *M. phaseolina* using an isolate obtained from bean plants at the Cotaxtla Research Station. The non-stress treatment was irrigated by furrow irrigation, so data on the quantity of water applied could not be measured. Plots were 4 m long and 0.61 m apart and a 2.44 m^2 section was harvested to calculate yield. Field data were collected on days to flowering and maturity, plant stand, seed yield, seed quality, rust, angular leaf spot, senescence and charcoal rot disease ratings using a 1–9 scale (Abawi & Pastor-Corrales, 1990).

Zamorano, Honduras and Saginaw, Michigan 2002

Advanced yield tests of a selected group of RILs and local checks were evaluated under moisture stress in an 11-entry trial in Zamorano, Honduras and in a 42-entry rectangular lattice grown under rainfed conditions in Saginaw, Michigan (43°41' N, 84°08' W, 183 masl) in 2002. Plots in Zamorano consisted of a single 5 m row with 4 replications and were planted on January 28th, 2002. Insects and diseases were controlled chemically and irrigation was applied 8-times for a total of 200 mm as no precipitation occurred during the experiment. Data were collected on Yd, days to flower and maturity. Plots in Michigan consisted of 4 rows (including a common 2-row border), 5.8 m long and 0.5 m apart and were planted on June 9th, 2002. Rainfall during the 4-month growing season was 255 mm and no additional irrigation was applied. The soil type in Saginaw, MI is a Misteguay (fine, mixed (calcerous), mesic Aeric Endoaquepts). Data were collected on days to flower and maturity, lodging, plant height and seed size. Plots were direct harvested and a 4.6 m^2 section of 2-row plots was used to calculate yield.

Statistical analysis

Analysis of variance (ANOVA) was calculated for each experiment. PROC GLM was used in the Zamorano experiment with the number of harvested plants per plot as the covariant to adjust yield estimates (SAS Institute Inc., 2000). The stress and non-stress treatments were analyzed as two CRDs with three replications each. Means, least significant differences (LSD) values and CV values were calculated after being adjusted for the covariant. In the Montcalm experiment, data from 36 genotypes were analyzed as a square lattice design. Mean yield, LSD and CV values were calculated. In the Veracruz experiment, the inoculation and control treatments were combined to give four replications within the stress and non-stress treatments. Each population was analyzed separately as a CRD. The number of plants per plot was used as the covariate to adjust plot yield. Mean yield for individual RILs of the stress treatment were used with the corresponding yield means of the non-stress treatment to calculate GM. The drought intensity index [DII = 1-(Xd/Xp)] was calculated for each experiment, where Xd is the mean yield under drought and Xp is the mean yield under non-stress for each experiment (Fischer & Maurer, 1978).

Results

The 150 RILs ranged in yield from 2 to 842 kg/ha grown under moisture stress at Zamorano, while in the non-stress conditions, yield ranged from 1130 to 2922 kg/ha (Table 1). In Veracruz, the same 150 RILs ranged in yield under stress from 210 to 1365 kg/ha and from 461 to 2402 kg/ha for yield under non-stress conditions. Significant genotypic effects were recorded in both populations for each treatment in the Veracruz and Montcalm experiments (Table 2), whereas, significant genotypic differences were only recorded in the stress treatment for population L88 at Zamorano in 2001 due to high variability at this location.

The magnitude of stress at all locations is represented in the DII values for each experiment. The experiment in Zamorano experienced a severe terminal drought stress with DII = 0.82. This stress was more severe than the Veracruz experiment (DII = 0.48) and previous experiments conducted with beans under rain-fed conditions in the Mexican highlands (DII = 0.49; Schneider et al., 1997) and under a rain-shelter controlled drought treatment in Michigan (DII = 0.63; Ramirez-Vallejo & Kelly, 1998). The Montcalm experiment did not experience the desired level of stress in 2001 as reflected by a low DII value (0.02) and similar mean yields under stress (2961 kg/ha) and non stress (3006 kg/ha). Lowland tropical areas experience decreasing soil moisture and increasing temperatures, both of which contributed to the substantial reduction in Yd in Zamorano and Veracruz. In non-stress conditions, the mean yield for population L88 was 200 kg/ha greater than the L91 mean yield in Zamorano and 700 kg/ha greater in Veracruz (Table 1). Under moisture stress conditions, the mean for population L88 averaged 150 kg/ha more in all locations except the Veracruz experiment inoculated with charcoal rot where it was 400 kg/ha greater than the mean of population L91.

One factor that significantly contributed to variability in yield in the lowland tropical regions was the variable plant stand. Plant stand was significantly different in all stress conditions in Zamorano and Ver-

Table 1. Range of yields from high to low and means for populations L88 and L91 grown under stress and non-stress in Zamorano, Honduras in 2001, Montcalm, Michigan in 2001 and Veracruz, Mexico in 2002

	Population L88				Population L91			
			Veracruz				Veracruz	
Range	Zamorano	Montcalm	Inoculated*	Control	Zamorano	Montcalm	Inoculated	Control
	——- $kg{\cdot}ha^{-1}$ ——-				——- $kg{\cdot}ha^{-1}$ ——-			
Yd**	842	3870	1365	1120	599	3646	775	854
	77	1928	465	332	2	1975	210	265
Mean	320	3050	857	671	207	2844	442	533
Yp	2922	4646	2240	2402	2587	4379	1367	1368
	1441	1987	631	799	1130	1467	461	548
Mean	2057	3251	1430	1624	1858	2791	875	898

* Inoculated with *Macrophomina phaseolina*; Control was not inoculated.
** Yd – Yield under drought stress, Yp – Yield under non-stress.

Table 2. ANOVA for seed yield for populations L88 and L91 with mean squares and significance levels for different sources of variation, grown in three locations in Zamorano, Honduras, Montcalm, Michigan and Veracruz, Mexico

Pop L88	Zamorano, 2001			Montcalm, 2001[a]			Veracruz, 2002		
Source	DF[b]	S	N	DF	S	N	DF	S	N
Block	–	–	–	15	62***	131***	–	–	–
Replication	2	102574	755201	2	2334***	121***	3	1471137****	1416776****
Genotype	80	72989*	304003	35	69***	105***	80	72891****	308982****
Stand	1	840106****	461861	–	–	–	1	1607054****	459439*
Error	159	49863	320694	55	19	27	239	31041	96838
CV (%)		70.2	27.6		16.7	19.5		22.9	20.2
Pop L91	**Zamorano, 2001**			**Montcalm, 2001**			**Veracruz, 2002**		
Source	DF	S	N	DF	S	N	DF	S	N
Block	–	–	–	15	62***	131***	–	–	–
Replication	2	96906	654273	2	2334***	121***	3	247125****	35533
Genotype	68	49461	357196	35	69***	105***	80	53978****	160596****
Stand	1	158990*	682311	–	–	–	1	619994****	1639751****
Error	135	35870	330826	55	19	27	203	14429	30122
CV (%)		90.4	30.9		16.7	19.5		24.8	19.7

[a] Montcalm data represents selected lines from both populations.
[b] DF – degrees of freedom, CV – coefficient of variation, S – Drought stress, N – Non-stress.
* $p < .05$, ** $p < .01$, *** $p < .001$, **** $p < .0001$.

acruz (Table 2). Stand problems in Zamorano were a direct result of charcoal rot infestation antagonized by drought stress, as the number of dead plants resulting from infection with charcoal rot varied greatly between treatments, replications and experiments. The reaction to *M. phaseolina* was similar in Veracruz, where population L91 showed less disease incidence (0.21) than population L88 (0.29; Figure 1). Despite heavy charcoal rot pressure, population L88 had a greater yield in Zamorano and Veracruz (320 and 764 kg/ha) than population L91 (207 and 491 kg/ha; Figure 1). Reaction of the parents to *M. phaseolina* was not always reflected in yield differences. As expected TLP 19 showed the highest resistant response to charcoal rot among the three parents (0.15; Figure 1), even though it had the lowest mean yield under stress (169 kg/ha; Table 3). VAX 5 had a higher mean yield (249 kg/ha) under stress than TLP 19, whereas the drought resistant parent B98311, yielded 375 kg/ha under severe drought stress despite a high charcoal rot rating (0.42) in Zamorano (Table 3). In Veracruz, B98311 performed in a similar fashion, exhibiting broad adaptation and stability under different stress levels, whereas TLP 19 had a greater GM yield

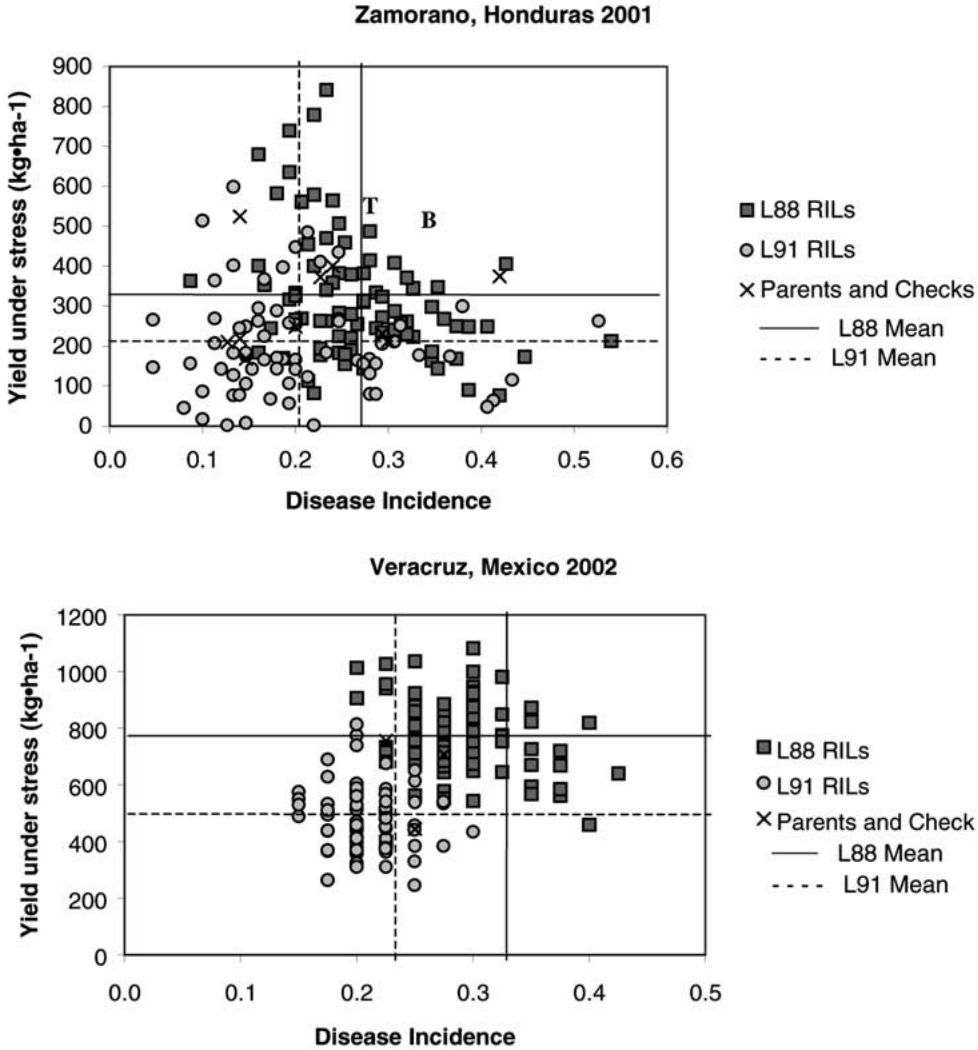

Figure 1. Scatter plot of yield under drought stress and disease incidence of charcoal rot in the 150 RILs of populations L88 and L91, including parents B98311 (B), TLP 19 (T), VAX 5 (V) and local checks grown at Zamorano, Honduras in 2001 and Veracruz, Mexico in 2002.

(1046 kg/ha) than B98311 (991 kg/ha) demonstrating its ability to yield under a moderate drought stress.

A number of RILs from L88 and L91 yielded more than the drought resistant genotypes and local checks in the different experiments (Tables 3 and 4). Drought resistant checks, Rio Tibagi, BAT 477 and SEA 5, and the local check, Tio Canela 75, were out-performed in GM, Yd, and Yp by several RILs from L88 and L91 at Zamorano (Table 3). SEA 5, the only check to be tested in both Zamorano and Veracruz, produced an average Yd and GM yield in Zamorano, yet performed below average in every treatment in Veracruz. The absence of moisture stress in Montcalm resulted in only a few RILs with greater yields than the local black bean check cultivars, Phantom and T-39 (Table 4).

One RIL, L88-63, ranked first in GM yield among 153 common entries tested in both lowland tropical locations. The superiority of L88-63 was further validated in two other tests where it consistently yielded above the test mean (Table 5). In 2002, L88-63 ranked fourth in Saginaw, Michigan against elite MSU breeding lines and local checks, where the top three lines in the test were unrelated genetic material. It ranked first among the other RILs in the test and all local checks including Phantom and T-39 (Table 4). In Zamorano, Honduras in 2002, L88-63 also ranked first under

Table 3. Yield comparisons of the top six and bottom one RIL from populations L88 and L91, parents and checks grown in Zamorano, Honduras in 2001 and Veracruz, Mexico in 2002

Line	Zamorano, 2001			Veracruz, 2002		
	GM[a]	Yd	Yp	GM	Yd	Yp
	—— kg·ha^{-1} ——			—— kg·ha^{-1} ——		
L88-63	1473 (1)[b]	842 (1)	2576 (6)	1468 (1)	1036 (2)	2080 (3)
L88-30	1328 (3)	779 (2)	2263 (30)	1264 (10)	947 (8)	1687 (22)
L88-69	1286 (4)	680 (4)	2432 (18)	1120 (34)	711 (60)	1765 (16)
L88-13	1285 (5)	565 (9)	2922 (1)	1182 (27)	873 (18)	1600 (37)
L88-66	1205 (6)	561 (10)	2589 (4)	1235 (16)	849 (24)	1797 (12)
L88-61	1050 (11)	507 (13)	2173 (39)	1329 (5)	839 (25)	2105 (2)
L88-18	368 (146)	90 (144)	1501 (148)	907 (76)	733 (52)	1122 (87)
L91-30	1073 (9)	599 (6)	1922 (83)	593 (123)	410 (133)	856 (115)
L91-25	1064 (10)	514 (12)	2202 (34)	490 (147)	373 (141)	644 (146)
L91-3	1023 (14)	435 (20)	2406 (21)	531 (139)	495 (114)	569 (152)
L91-59	1016 (15)	486 (15)	2126 (46)	816 (90)	588 (84)	1131 (86)
L91-10	1004 (16)	448 (19)	2250 (31)	597 (122)	437 (129)	815 (123)
L91-33	976 (18)	368 (36)	2587 (5)	655 (112)	447 (124)	959 (109)
L91-69	60 (160)	2 (160)	1534 (142)	588 (125)	411 (132)	840 (117)
B98311(p)	951 (22)	375 (33)	2411 (20)	991 (63)	706 (62)	1392 (61)
SEA 5	893 (30)	524 (11)	1521 (145)	643 (115)	444 (125)	931 (110)
Rio Tibagi	886 (31)	372 (34)	2108 (51)	–	–	–
BAT 477	784 (54)	400 (27)	1536 (141)	–	–	–
VAX 5 (p)	663 (90)	249 (82)	1765 (110)	–	–	–
TLP-19 (p)	637 (95)	169 (118)	2399 (22)	1046 (55)	756 (44)	1446 (56)
Tio Canela 75	602 (105)	218 (95)	1657 (129)	–	–	–
Mean		275	1517	1077–661[c]	764–491	1527–896
LSD (0.05)		333	933		245–167	433–242
CV (%)		77	30		23–25	20–20

[a] GM – Geometric Mean, Yd – Yield under drought stress, Yp – Yield under non-stress.
[b] Rank shown in parenthesis, (p) designates parent; Mean of 160 entries in Zamorano and 153 entries in Veracruz.
[c] Population L88 values – Population L91 values.

drought stress conditions yielding 1128 kg/ha or 123% of the site mean that included the drought resistant line SEA 5 and local checks. Consequently, L88-63 out-competed local elite checks and drought tolerant lines under a range of environmental conditions in Honduras, Mexico and Michigan. Apparently, L88-63 has broad adaptation and high yield potential in both drought stressed and irrigated environments.

Discussion

Breeding crops for drought resistance has traditionally involved the use of stress and non-stress treatments. However, a consistent stress is needed between experiments, which can only be accomplished through a careful selection of test sites. The Zamorano and Veracruz test sites were selected because a natural terminal drought stress is an annual occurrence that substantially reduces bean production. Rainfall at both locations is generally negligible during the January to April period. Drought resistance is an integral part of the local breeding programs. Both breeding programs are faced with the challenge to invest in large experiments with contrasting moisture treatments to identify drought resistant bean cultivars.

The scale of drought experiments may be a limitation for many small breeding programs, as two treatments are needed for screening which doubles the size of the experiment. If resources limit the evaluation to one treatment, only the stress treatment is generally performed. Yet theory has shown that selection in the

Table 4. Advanced yield testing results of top yielding RILs, parents and checks grown in the temperate climate of Michigan at Montcalm in 2001 and Saginaw in 2002

Entries	Montcalm 2001			Saginaw 2002
	GM[a]	Yd	Yp	Yp
	—— kg·ha^{-1} ——			kg·ha^{-1}
L91-10	4056 (1)[b]	3791 (3)	4340 (1)	3802 (15)
L88-69	3849 (2)	4015 (1)	3690 (5)	3892 (7)
L88-63	3596 (3)	2995 (16)	4318 (2)	4105 (4)
T-39	3533 (4)	3544 (4)	3522 (8)	3432 (34)
TLP 19 (p)	3527 (5)	3466 (6)	3589 (6)	–
B98311 (p)	3495 (6)	3903 (2)	3129 (15)	–
Phantom	3493 (7)	3466 (7)	3522 (9)	3219 (37)
L88-30	3398 (9)	3432 (8)	3365 (12)	3869 (9)
L88-61	3387 (10)	3432 (9)	3342 (13)	3129 (40)
L88-66	3333 (12)	3488 (5)	3185 (14)	3600 (27)
VAX 5 (p)	2244 (32)	2097 (34)	2400 (31)	–
Mean		2961	3006	3667
LSD (0.05)		819	953	460
CV (%)		17	19	8

[a] GM – Geometric Mean, Yd – Yield under drought stress, Yp – Yield under non-stress.
[b] Rank shown in parenthesis, (p) designates parent; Mean of 36 entries in Montcalm and 42 entries in Saginaw.

stress treatment could result in a reduced yield in the non-stress treatment (Rosielle & Hamblin, 1981). Alternatively, a large set of lines could be evaluated for yield under non-stress and only test those lines with high Yp under two moisture treatments. Additional yield data under stress could be collected later to support or refute the potential of individual lines. There is a risk of losing potential drought resistant lines using this approach, but those genotypes with an overall low Yp typically are not desirable (Blum, 1988). In this study, the consistent performance of the best lines across diverse stress and non-stress environments suggests that such a strategy should work.

Higher variability among genotypic data under stress (Yd) makes it difficult to identify superior lines. Since drought stress reduces yield and generates an additional level of variability, the statistical power of most stress experiments is low due to high values for error variance and CV. Also, the inability to randomize treatments for each genotype prevents an accurate analysis for comparison of genotypes. More replications could be included as a possible solution, but the added resources that would be required could make this solution impractical. Placing reliance solely on statistical differences between genotypes could dramatically limit the identification of superior lines that may demonstrate superiority when experimental CV's are lower. Ranking genotypes based on performance provides an opportunity to identify the highest yielding entries in an individual test and continue to evaluate the same genotypes through additional testing. For example, genotypes like L88-63 that consistently demonstrate the highest ranking regardless of statistical significance need to be given special attention by breeders, as they may possess the desired combination of performance-based characteristics that are required for stress environments (Table 3).

Diseases that are unique to stress environments have a confounding antagonistic interaction with performance-based traits that can complicate the efforts of breeders to identify superior lines based soley on yield. Pathogens that attack susceptible genotypes can mask the expression of the desired performance-based traits and interfere with the interpretation of results. Soil borne pathogens such as *Fusarium* and *Rhizoctonia* (Navarrete-Maya et al., 2002) complicate breeding for resistance to intermittent drought in common bean, as root health is vital to sustain plant growth through extended periods of stress typical of intermittent drought. In the case of terminal drought, *M. phaseolina* is the pathogen that is favored by the extended dry conditions and can result in premature leaf loss, reduced vigor and death of susceptible plants (Mayek-Pérez et al., 2002). A strong correletion has been observed between the occurrence of drought and susceptibility to *M. phaseolina* (Mayek-Pérez et al., 2001a). Genotypes lacking adequate levels of resistance to charcoal rot or healthy root structures will not express their true yield potential under drought due to the negative effects of the invading pathogen that results in stand losses and lower yields (Figure 1).The confounding effect of disease incidence in this study resulted in plant stand being significantly different and lower in every stress treatment (Table 2). Bean genotypes evaluated for Yd under terminal drought should be rated for their reaction to *M. phaseolina*, but the stress should be sufficient to induce adequate disease pressure as no significant differences in disease were noted between the inoculated and control treatments in Veracruz (Table 1).

Yield potential and disease reactions of populations L88 and L91 appears to result from the different genetic make-up of the populations. Germplasm from race Mesoamerica is recognized as a source of yield genes for stressed or non-stressed environments in Central America (White et al., 1994), whereas B98311

Table 5. Rank and percent test mean of RIL L88-63 grown in five different experiments in Honduras and Michigan in 2001 and 2002 and Veracruz, Mexico in 2002

Location	Year	No. of entries	GM[a]		Yd		Yp	
Zamorano, Honduras	2001	160	1st	153%	1st	168%	6th	124%
Montcalm, Michigan	2001	36	3rd	119%	16th	102%	2nd	130%
Veracruz, Mexico	2002	153	1st	134%	2nd	133%	3rd	136%
Saginaw, Michigan	2002	42	–	–	–	–	4th	111%
Zamorano, Honduras	2002	11	–	–	1st	123%	–	–

[a] GM – Geometric Mean, Yd – Yield under drought stress, Yp – Yield under non-stress.

is the progeny of an interracial cross with a Durango race breeding line. One contrast between B98311 and TLP 19 was in total root length (Frahm et al., 2003). Root architecture is vitally important in beans since a deep penetrating root system is needed to reach and mine the lower soil levels for moisture. The shallow root system of TLP 19 (Frahm et al., 2003) may have resulted in low yield under severe stress (Table 4). Shallow root systems may be suited for production in soils with low P (Rubio et al., 2003) but may not be ideal under drought stress where a deeper root system is favored. The inconsistency between the contrasting root characteristics may prevent the development of bean genotypes with tolerance to terminal drought and low P. Despite these differences, breeders should not be reluctant to cross parents with contrasting phenotypic characteristics. The frequency of drought adapted progeny in L88 suggests that breeding for drought resistance can be accomplished through two generations of simple crossing and selection from the original drought resistant Durango line T-3016 (Schneider et al., 1997). The same characteristics that were functional for intermittent drought appear to be important in conditoning resistance to terminal drought in common bean. Apparently, the best drought resistant genotype should combine the high yield and archetype of the Mesoamerican race and the drought resistance from the Durango race.

Selection for drought resistance favored the L88 RILs, which combined Durango and Mesoamerican backgrounds that include adequate levels of disease resistance for the stress environment. One RIL, L88-63, ranked first in GM among all lines tested in Zamorano and Veracruz and yielded 153% and 134% above the respective site means (Table 5). Selection of L88-63 was based on GM yield using only Zamorano 2001 data. Additional testing in 2002 of potential drought resistant RILs in the non-stress environment of Saginaw, Michigan and the drought stress environment of Zamorano, Honduras gave contrasting mean yields, 3667 kg/ha and 871 kg/ha respectively. Despite these dramatic differences in yield potential, L88-63 ranked first among the RILs and checks and outyielded the site mean in the respective locations by 111% and 123%, respectively (Table 5). The performance of this line indicates it should continue to be tested in other environments where terminal drought is pervasive.

Conclusions

The ranking system for GM yield used in this study permitted the identification of L88-63 as a highly drought resistant genotype with broad adaptation in lowland tropical and temperate regions. Despite the complexity of breeding for drought resistance in common bean, resistance was effectively transferred through simple crossing and selection methods in appropriate test locations. Breeding for terminal drought in Central America and Mexico will require the incorporation of additional levels of resistance to *M. phaseolina* to meet the needs of the production area. The commercial black seed quality of L88-63 should expedite its use in breeding black beans, the major commercial bean class grown in lowland tropical regions of Latin America and the Caribbean.

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