Low Soil Fertility Tolerance in Landraces and Improved Common Bean Genotypes

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ABSTRACT

Soil mineral deficiencies or toxicities adversely affect common bean (*Phaseolus vulgaris* L.) production worldwide. Cultivars tolerant to low soil fertility (LF) should support sustainable farming systems and reduce production costs and farmers' dependence on fertilizers. Our objective was to identify LF tolerant landraces and improved common bean genotypes. We systematically screened 5000 to 5500 landraces and improved genotypes for LF tolerance at Popayán and Quilichao, Colombia, between 1978 and 1998. Mean LF intensity index across locations for seed yield ranged from 0.35 to 0.68. Average seed yield reduction over five cropping seasons was 53%. Seed yield, biomass, and HI were positively associated in LF and high soil fertility (HF). LF tolerance was identified in eight landraces and 14 improved genotypes. All landraces were from Middle America (MA), belonging to common bean races Durango, Jalisco, and Mesoamerica. All improved genotypes except one (A 36) also possessed characteristics of and involved one or more LF tolerant MA landraces in their pedigree. There was considerable variation for seed, plant, and maturity characteristics among LF tolerant genotypes. In LF, mean seed yield for landraces ranged from 856 kg ha^{-1} for 'Apetito' to 332 kg ha^{-1} for G 19833. Among improved genotypes, A 774 had the highest (948 kg ha^{-1}) and CAP 4 the lowest (651 kg ha^{-1}) seed yield. Reduction in seed yield due to LF ranged from 31% for A 36 to 63% for CAP 4. All landraces and seven improved genotypes had either a below average or average LF susceptibility index. Use of these LF tolerant landraces and improved genotypes should be maximized in breeding and genetic studies to enhance sustainable farming systems.

Deficiencies or toxicities of minerals in soils in common bean production regions occur throughout the world. For common bean, general symptoms of mineral deficiency or toxicity may include poor emergence; slow growth; seedling and adult plant stunting; leaf yellowing, chlorosis, and bronzing; early seedling death; reduced overall growth and dry matter production; delayed and prolonged flowering and maturity; excessive flower and pod abortion; low harvest index; reduced seed weight; deformed and discolored seeds; and up to 100% yield loss. Root growth may also be adversely affected (Cumming et al., 1992; Fawole et al., 1982a). These symptoms may vary with the type, severity, and duration of mineral stress.

To overcome mineral deficiencies and toxicities, common bean growers must use corrective soil amendments such as lime (Fageria et al., 1995; Westermann, 1992), manure or composted manure (Tarkalson et al., 1998), and fertilizers rich in macro- and micronutrients such as N, P, B, Fe and/or Zn (Edji et al., 1975; Henson and Bliss, 1991). Identification and use of cultivars tolerant to mineral deficiencies and/or toxicities are essential for reducing production costs and dependence of farmers on soil amendment inputs.

Greenhouse, growth chamber, and/or field screening methods have been used to identify crop germplasm tolerant to mineral deficiency or toxicity (Duncan et al., 1983). Large genotypic differences among crops also have been reported (Dwivedi, 1996; Fageria et al., 1995). Within-species variation in common bean for P (Whiteaker et al., 1976) and Zn deficiency and response (Westermann and Singh, 2000) and Al tolerance (Foy et al., 1972; Noble et al., 1985) have been documented. At the Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia, extensive research was conducted on N_2 fixation (Graham, 1981) and tolerance of P deficiency (Lynch and Beebe, 1995; Thung, 1990; Yan et al., 1995a, b; Youngdahl, 1990) and Al and Mn toxicity (Ortega and Thung, 1987). In each of these cases, large genotypic differences were found.

In real farming situations, deficiencies and toxicities of two or more mineral elements often occur simultaneously (Sanchez and Salinas, 1981; Wortmann et al., 1995). Furthermore, there can be strong interactions among different minerals (Bache and Crooke, 1981) and other abiotic and biotic factors. Therefore, a more holistic approach was adapted at CIAT to develop low-input, environmentally sensitive technologies for common bean and other species (Nickel, 1987). In regard to LF, multiple deficient or toxic mineral stresses were applied to screen common bean germplasm (Ortega and Thung, 1987; Singh et al., 1995) and conduct genetic (Urrea and Singh, 1989) and breeding studies (Singh et al., 1989a, b). It was believed that germplasm and cultivars thus developed would be better suited for poor farmers in the tropics and subtropics. Such LF tolerant cultivars with higher yield potential would also be valuable for environment-friendly, sustainable farming systems in other production regions and increase profit margins for growers. Our objective was to identify LF tolerance among landraces and improved common bean genotypes.

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Abbreviations: A, March to June growing season; B, September to December growing season; CIAT, Centro Internacional de Agricultura Tropical; HF, high soil fertility; HI, harvest index; LF, low soil fertility; LFII, low soil fertility intensity index; LFSI, low soil fertility susceptibility index; MA, Middle America; PR, percent reduction in seed yield due to LF.

MATERIALS AND METHODS

Common bean and other *Phaseolus* species germplasm have been systematically screened for abiotic and biotic stresses under field conditions at CIAT. For example, as many as 20 000 germplasm accessions were screened for anthracnose [caused by *Colletotrichum lindemuthianum* (Sacc. & Magn.) Lams.-Scrib.] at Popayán (Pastor-Corrales et al., 1995; Schwartz et al., 1982) and for angular leaf spot [caused by *Phaeoisariopsis griseola* (Sacc.) Ferr.] (Pastor-Corrales et al., 1998), and common bacterial blight [caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye] (Singh and Muñoz, 1999) at Quilichao, Colombia. Both Popayán [with a fine loamy, mixed, isothermic, typic (Andic) Dystrandept (Inceptisol) soil, pH of 4.3; 18°C mean growing temperature; elevation 1750 m; and 1925 mm rainfall] and Quilichao (with a very fine kaolinitic, isohypothermic, plinthic Kandiudox soil, pH of 4.5; 24°C mean growing temperature; elevation 990 m; and 1750 mm rainfall) have high levels of exchangeable Al and Mn, thereby causing toxicity. Also, these soils are deficient in N, P, B, Ca, and Mg (Table 1). Because disease nurseries often were grown in residual soil fertility, in addition to identifying disease resistant genotypes, these field environments also permitted retention of genotypes that had a better overall plant performance. A similar evaluation scheme, including use of complementary nurseries for different abiotic and biotic stresses, was used each year for evaluation of improved genotypes (Singh, 1992). Thus, more than 5000 landraces and improved genotypes with potential for LF tolerance were assembled for screening for their response to LF.

Common bean could not be grown on newly cleared native pastureland at Popayán and Quilichao without added lime and nutrients. Therefore, in HF plots, up to 5000 kg dolomitic lime and 90 kg N, 39 kg P, 90 kg K, 10 kg Zn, 20 kg Mg, and 1 kg B ha^{-1} were applied at the beginning in 1978–1979. The LF plots received half that amount. Additional lime and fertilizers were regularly applied for the first 5 to 7 yr to homogenize the fields and ensure adequate crop growth. Dolomitic lime and fertilizer applications were gradually reduced such that the LF plots did not receive any fertilizer and lime between 1990 and 1998 at either location. Chemical fertilizers were applied in HF plots in each cropping season at the rate of 45 kg N, 20 Kg P and 45 kg K ha^{-1}. Results from soil analyses showed that LF plots at Quilichao remained deficient in B, Ca, Mg, and P and had toxic levels of Al (Table 1). B, P, and Zn were deficient in both HF and LF plots at Popayán. Moreover, the average yield potentials of LF and HF plots were similar to that of bean production areas in tropical and sub-tropical Latin America. At both sites, trials were grown during the main cropping seasons (A = March to June, and B = September to December), following the bimodal rainfall distribution common throughout tropical Latin America. At Popayán trials were always treated as rain fed, and supplemental sprinkler irrigation was used at Quilichao whenever necessary.

More than 5000 promising germplasm accessions and improved genotypes of common bean were systematically evaluated in LF plots at Popayán and Quilichao between 1978A and 1994B (Singh et al., 1995). Each plot consisted of a single row, 3.0 to 5.0 m long without replication. The distance between rows at Popayán was 0.5 m and at Quilichao 0.6 m. Visual appraisal of the vegetative growth before flowering and overall performance (including pod load) at maturity were recorded on a 1-to-9 scale, where 1 = excellent and 9 = very poor. All genotypes receiving scores of 7 and higher were discarded. Selected genotypes (approximately 500) were again evaluated in LF at both locations in 1994B and 1995A. Each plot consisted of four rows without replication. The length of the rows and spacing between rows were similar to the previous experiment. Visual appraisal before flowering and at maturity and seed yield were used to select the 81 highest-yielding genotypes.

Thirty-five landraces and 46 improved genotypes were evaluated in LF at Popayán and Quilichao in 1995B. A 9-by-9 partially balanced lattice design with four replicates was used. Each plot consisted of four rows, each 3.4 m long. The 33 highest yielding landraces and 31 improved genotypes were selected for further evaluations in 1996A. The trial was planted at Popayán and Quilichao under both HF and LF. An 8-by-8 partially balanced lattice design with four replicates was used. Plot size and row spacing were similar to the 1995B experiment. Mean seed yield in HF and LF and percent reduction (PR) due to LF were used as selection criteria. The selected 17 landraces and 19 improved genotypes were again evaluated under both HF and LF at Popayán and Quilichao in 1996B by means of 6-by-6 partially balanced lattice design with four replicates. Plot size, row spacing, and agronomic management of the nursery were similar to the previous year. However, in addition to seed yield, data were also recorded for biomass yield and harvest index (HI). In 1997A and 1998A, 11 selected landraces and 14 improved genotypes were evaluated in similar conditions at both Popayán and Quilichao by means of a 5-by-5 partially balanced lattice design with four replicates. Only seed yield was recorded for all genotypes.

Seed and biomass yields were adjusted to 140 g kg^{-1} moisture by weight. Formulae from Fischer and Maurer (1978) were adopted to calculate low soil fertility intensity index (LFII) for each growing season (and location) as LFII = 1 − Xlf/Xhf, where Xlf and Xhf are the mean of all genotypes under LF and HF environments, respectively. LF susceptibility index (LFSI) for each genotype was calculated as follows: LFSI = (1 − Ylf/Yhf)/LFII, where Ylf and Yhf are mean yields of a given genotype under LF and HF environments,

Table 1. Soil characteristics at Quilichao and Popayán, Colombia, between 1978 and 1999 used to evaluate common bean genotypes for low soil fertility tolerance.

Location and year	pH	Organic matter	P	Al saturation rate	Al	Ca	Mg	K	Zn	B
		%	g kg^{-1}	%	cmol$_c$ kg^{-1}				g kg^{-1}	
Popayán										
1978LF	5.3	24.7	1.0	45.8	1.4	1.1	0.3	0.25	1.00	0.24
1991LF	6.4	19.8	5.3	0.5	0.1	9.6	4.0	0.11	0.48	10.10
1999LF	6.4	13.0	4.2	1.7	0.1	13.7	4.3	0.32	0.49	0.23
1999HF	6.5	14.8	5.7	0.0	0.0	15.9	4.8	0.40	0.58	0.30
Quilichao										
1979LF	4.2	7.0	4.0	84.6	4.4	0.4	0.2	0.17	2.20	0.22
1991LF	5.1	7.3	11.8	8.5	0.5	3.7	1.4	0.25	0.50	0.04
1999LF	4.2	5.5	2.6	69.3	3.9	1.2	0.4	0.20	1.20	0.38
1999HF	5.2	5.4	17.2	10.6	0.7	4.9	1.7	0.30	2.10	0.43
Critical levels	<5.5	<1.5	<15.0	>20.0	>1.1	<4.5	<2.0	<0.15	<0.80	0.50

Table 2. Number of genotypes (N), range, and mean seed yield for 81 common bean genotypes evaluated in low soil fertility at Popayán and Quilichao, Colombia, in September to December 1995.

		Popayán		Quilichao		Mean	
Genotype	N	Range	Mean	Range	Mean	Range	Mean
		kg ha^{-1}					
Landrace	35	968–1991	1487	6–724	364	620–1313	926
Improved	46	341–2212	1410	82–959	423	342–1310	917
Mean	81		1449		394		922
LSD (0.05)		630	99	229	36	334	53

respectively. For further data analysis, years and replications were considered as random effects, and genotypes and fertility levels as fixed effects. Simple phenotypic correlation coefficients among seed and biomass yields and HI were determined for the trials conducted in 1996B. All data were analyzed with a SAS PROC GLM statistical package (SAS Institute, 1985).

RESULTS AND DISCUSSION

Fields at Popayán and Quilichao possessed deficient or toxic levels of two or more minerals (Table 1). No fertilizer or other amendments were applied in LF plots, and only 45 kg N, 20 kg P, 45 kg K ha^{-1} were applied in HF plots in each growing season between 1996 and 1998. Growth and development of common bean, like other crops, remove mineral nutrients from soil (Thung, 1990). Hence, the composition of mineral deficiency and toxicity changed over years at the two locations (Table 1). Furthermore, B, Ca, Mg, and P deficiencies and Al toxicity in LF at Quilichao, and deficiencies of B, P, and Zn in both LF and HF at Popayán still persisted at the end of our experiments. Thus, for identifying superior common bean landraces and improved genotypes tolerant to a range of mineral deficiencies and toxicities sequential screening in nonreplicated trials between 1978 and 1995A (Singh et al., 1995) and in replicated trials from 1995B to 1998 (Tables 2–8) were essential.

Because the amount of fertilizers and other soil amendment inputs used in this study were considerably lower, the seed yields (especially in HF) were not as high as those reported by Singh et al. (1989a) and Yan et al. (1995b). The LF intensity index (LFII) ranged from 0.02 in 1996A (Table 3) to 0.81 in 1996B (Table 4). However, the LFII varied between 0.43 and 0.66, suggesting that a relatively more consistent and moderately high stress due to LF occurred at Popayán and Quilichao during the final trials in 1997 and 1998 (Table 7). Thus, the mean seed yields in HF and LF, and PR due to LF within and across locations were used as the principal selection criteria. Consequently, some of the highest yielding genotypes across both locations in the early stages such as 'Porrillo Sintetico' (1313 kg ha^{-1}), MAM 13 (1310 kg ha^{-1}), and Amarillo 154 (1152 kg ha^{-1}) in 1995B got excluded from 1996B (Table 4) and subsequent trials (Tables 7 and 8). Nonetheless, in the final trials, significant interactions among genotype, soil fertility level, year, and location still occurred (Table 6). Consequently, significant changes in rankings among genotypes were observed for seed yield at both soil fertility levels and locations over the cropping seasons and years (Tables 4, 7, and 8). Yan et al. (1995b) also recorded significant interactions among genotypes, P levels applied, and locations. Because temperature fluctuations over the cropping seasons and years near the equator often are minimal, changes in the rankings of genotypes could largely be due to differences in soil fertility levels, rainfall, and their interactions with the common bean genotypes at the two sites. While supplemental sprinkler irrigation was applied at Quilichao, Popayán trials were always grown as rain-fed or dryland crops. Thus, despite relatively higher rainfall at Popayán, occasional moisture stress, especially during the pod and seed development phases, could not be ruled out. Water stress is known to affect P uptake and utilization in common bean (Al-Karaki et al., 1995).

The type and number of minerals considered, level of stress applied, screening environment (field versus greenhouse or growth chamber), selection criteria, and diversity of germplasm used for screening drastically affect the outcome of experiments. For example, Yan et al. (1995a,b), interested in genotypic differences and understanding the physiology of specific mineral uptake and utilization, screened six common bean genotypes each of Andean and Middle American evolutionary origins for P deficiency tolerance, P-use efficiency, and response. Popayán was one of the sites included in their experiment. They reported that Andean genotypes, including G 16140 and G 19833, were more tolerant to P deficiency and were more efficient in P use in both Andosol (Popayán) and Ultisol (Mondomo) soils (located at approximately 1300 m elevation between Popayán and Quilichao) compared with Middle American genotypes such as 'Carioca'. The genotypes G 16140, G 19833, G 2333, Carioca, and 'Rio Tibagi', common to

Table 3. Number of genotypes (N), range, and mean for seed yield for 64 common bean genotypes evaluated in high and low soil fertility at Popayán and Quilichao, Colombia, in March to June 1996.

		Popayan				Quilichao						
		HF†		LF		HF		LF		Mean		
Genotype	N	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	PR
		kg ha^{-1}										
Landrace	33	68–1115	583	101–941	548	78–1082	490	6–412	186	143–677	447	26
Improved	31	152–1593	538	169–1060	555	127–1317	742	73–416	247	263–818	519	32
LSD (0.05)		547	96	392	69	300	53	171	30	188	33	
LFII‡			0.02				0.65			0.35		

† LF = low soil fertility, HF = high soil fertility, and PR = Percent reduction in seed yield due to low soil fertility stress.
‡ LFII, low soil fertility intensity index = 1 − Xlf/Xhf, where Xlf and Xhf are the mean of all genotypes in low and high soil fertility environments, respectively.

Table 4. Origin, growth habit, seed color, 100-seed weight, maturity, seed yield, percent reduction, low soil fertility susceptibility index, biomass yield, and harvest index for 36 common bean genotypes evaluated in high and low soil fertility at Popayán and Quilichao, Colombia, in September to December 1996.

Genotype	Origin	Growth habit	Seed color	100-seed weight	Maturity	Seed yield: Popayán HF†	Popayán LF	Quilichao HF	Quilichao LF	Mean HF	Mean LF	Mean	PR	LFSI	Biomass yield HF	Biomass yield LF	Harvest index HF	Harvest index LF
Landrace (17)				g	d	kg ha⁻¹							%		kg ha⁻¹			
Apetito (G 1759)	Mexico	III	Light purple	23	79	2925	781	2545	835	2735	817	1776	70	1.0	3890	1263	0.71	0.64
J 117	Mexico	III	Pink stripped	28	84	2793	679	2577	905	2685	830	1758	69	1.0	3981	1310	0.68	0.62
Carioca (G 4017)	Brazil	III	Cream stripped	23	80	2689	567	2527	1009	2608	862	1735	67	1.0	3807	1320	0.69	0.63
Flor de Mayo IV (G 22036)	Mexico	IV	Pink speckled	30	81	2027	502	2908	1017	2468	845	1656	66	1.0	3600	1302	0.70	0.63
Garbancillo Zarco (G 22041)	Mexico	IV	Beige	32	86	2183	453	2395	1297	2289	1016	1652	56	0.8	3631	1680	0.64	0.58
Garrapato (G 2402)	Mexico	III	Pinto	32	80	2486	602	2373	850	2430	767	1598	68	1.0	3505	1153	0.70	0.65
De Celaya (G 13614)	Mexico	III	Pink	33	81	2702	144	2319	900	2511	648	1579	74	1.1	3988	1078	0.63	0.52
Kabenga (G 22263)	Rwanda	III	White	31	80	2595	516	1954	820	2275	719	1497	68	1.0	3571	1233	0.64	0.57
Compuesto Chimaltenango 2 (G 5711)	Guatemala	III	Black	22	86	2348	393	2348	731	2348	618	1483	74	1.1	3924	1098	0.61	0.54
Rio Tibagi (G 4830)	Brazil	II	Black	17	80	2433	310	2065	835	2249	660	1454	71	1.0	3365	1025	0.67	0.60
Ojo de Cabra 24 MU (G 22079)	Mexico	III	Brown	29	80	2791	556	1219	797	2005	717	1361	64	0.9	2821	1037	0.69	0.67
Amarillo 169 (G 8142)	Mexico	III	Yellow	25	81	2446	682	1473	641	1960	655	1307	67	1.0	2783	998	0.69	0.64
Rosinha G2 (G 21703)	Brazil	III	Pink	19	79	1287	349	1853	680	1570	570	1070	64	0.9	2303	915	0.68	0.60
Colorado de Teopisca (G 2333)	Mexico	IV	Red	21	88	1824	108	1113	452	1469	338	903	77	1.1	2975	868	0.51	0.36
G 16140	Peru	III	Gray stripped	42	86	2188	165	667	363	1428	297	862	79	1.2	2923	728	0.45	0.35
Tostado (G 20554)	Rwanda	I	Yellow mottled	42	84	970	420	1395	433	1183	429	806	64	0.9	2236	854	0.54	0.48
Chaucha Chuga (G 19833)	Peru	III	Yellow mottled	29	88	1705	293	70	159	888	204	546	77	1.1	2272	563	0.32	0.32
Improved (19)																		
A 321	CIAT	III	Cream	27	79	3674	556	2829	1049	3252	885	2068	73	1.1	4518	1361	0.72	0.63
MAM 46	CIAT	III	Beige	31	81	2687	608	3258	922	2973	818	1895	72	1.1	4591	1314	0.65	0.62
FEB 190	CIAT	II	Cream	27	82	2568	520	3085	1165	2827	950	1888	66	1.0	4274	1569	0.67	0.59
A 774	CIAT	III	Cream	24	80	2745	220	2916	1277	2831	924	1877	67	1.0	4193	1503	0.68	0.54
MAM 38	CIAT	III	Pink speckled	27	81	2701	714	2648	1207	2675	1042	1858	61	0.9	4088	1667	0.66	0.62
A 445	CIAT	III	Cream stripped	29	80	3108	155	2557	1143	2833	814	1823	71	1.0	4145	1296	0.68	0.53
APN 115	CIAT	III	Red	28	79	2788	486	2589	1018	2689	841	1765	69	1.0	3948	1314	0.68	0.61
DICTA 17	Honduras/CIAT	III	Red	29	80	2699	492	2603	1037	2651	855	1753	68	1.0	3929	1353	0.68	0.62
ARA 14	CIAT	III	Pinto	29	81	2236	591	2858	1015	2547	874	1710	66	1.0	3563	1294	0.73	0.66
DICTA 11	Honduras/CIAT	III	Red	24	79	2538	422	2667	992	2603	802	1702	69	1.0	3851	1219	0.68	0.64
A 752	CIAT	IV	Purple speckled	32	86	2649	599	2193	1117	2421	945	1683	61	0.9	3827	1610	0.64	0.57
FEB 192	CIAT	II	Cream	25	79	1906	410	2832	1121	2369	884	1627	63	0.9	3410	1335	0.70	0.64
CAP 2	CIAT	II	Beige	24	81	2391	499	2585	789	2488	692	1590	72	1.1	4177	1245	0.60	0.56
A 750	CIAT	IV	Purple speckled	27	88	2797	427	2066	757	2432	647	1539	73	1.1	4068	1283	0.60	0.48
CAP 4	CIAT	III	Beige	23	80	1707	440	2534	890	2121	740	1430	65	1.0	3624	1283	0.60	0.58
SEA 12	CIAT	II	Brown	28	81	2484	314	1863	711	2174	579	1376	73	1.1	3033	994	0.72	0.61

Continued next page.

Table 4. Continued.

Genotype	Origin	Growth habit	Seed color	100-seed weight	Maturity	Seed yield: Popayán HF†	Popayán LF	Quilichao HF	Quilichao LF	Mean HF	Mean LF	Mean	PR	LFSI	Biomass yield HF	Biomass yield LF	Harvest index HF	Harvest index LF
				g	d	kg ha^{-1}							%	—	kg ha^{-1}			
Catrachita	Honduras/CIAT	III	Red	27	79	1743	388	2115	813	1929	671	1300	65	1.0	2964	1105	0.66	0.59
A 36	CIAT	II	Red mottled	37	80	1265	481	1646	849	1456	726	1091	50	0.7	2345	1231	0.63	0.56
PVA 800A	CIAT	II	Red mottled	33	80	1247	377	1634	597	1441	524	982	64	0.9	2327	941	0.62	0.51
Overall mean				28	82	2342	451	2202	866	2273	728	1500	68	1.0	3512	1204	0.64	0.57
Landrace mean				28	83	2258	442	1871	748	2065	647	1355	69	1.0	3269	1084	0.62	0.55
Improved mean				28	81	2417	458	2499	972	2459	801	1629	67	1.0	3730	1311	0.66	0.59
LSD (0.05) ‡				0.4	1.2	151	64	95	64	89	57	17			131	83	0.17	0.02
LSD (0.05) §				2	5	683	297	434	397	378	240	71			555	350	0.02	0.07
LFII¶						0.81		0.61		0.68					0.66		0.11	

† LF = low soil fertility, HF = high soil fertility, PR = percent reduction due to LF, and LFSI = low soil fertility susceptibility index: LFSI = (1 − Ylf/Yhf)/LFII, where Ylf and Yhf are mean yields of a given genotype under LF and HF conditions, respectively.
‡ To compare means between landraces and improved genotypes.
§ To compare among 36 genotypes.
¶ LFII = low soil fertility intensity index = 1 − Xlf/Xhf, where Xlf and Xhf are the mean of all genotypes in LF and HF environments, respectively.

experiments by Yan et al. (1995a, b) were also included in this study. Contrary to their findings, G 16140 and G 19833 were the lowest yielding, and all other genotypes had significantly higher seed yields in both LF and HF environments despite their comparatively low PR and LFSI values (Tables 4, 7, and 8). Thus, these two landraces should be classified as highly LF susceptible.

Over the last 25 yr, large-seeded Andean common beans consistently had significantly lower yield than their small- to medium-seeded Middle American counterparts in Colombia and elsewhere (Singh, 1991; White and Gonzáles, 1990; White et al., 1992). Similar yield differences between the two groups of germplasm have been recorded across dozens of locations in the Cooperative Dry Bean Nursery that is evaluated each year in the USA and Canada (Singh and Powers, 2000). Yan et al. (1995a, b) used 2000 kg dolomite lime, 180 kg N, 203 kg K, 2.5 kg B, and 10 kg Zn ha^{-1} at Popayán irrespective of the P levels. In contrast, between 1990 and 1998 no lime and fertilizer were applied in LF, and only 45 kg N, 20 kg P, and 45 kg K ha^{-1} were applied in HF plots. Thus, differences in type and levels of mineral stresses imposed in the two studies could be largely responsible for these contrasting results.

Subsistence farmers in Latin America seldom apply fertilizer for common bean that is grown on residual soil fertility, as was the case for LF in this experiment. Moreover, farmers rarely apply >50 kg ha^{-1} each of N, P, and/or K, and they almost never use micronutrient fertilizers containing B, Fe, and/or Zn. Seed yields recorded in LF and HF environments in this study were similar to those reported for contrasting environments in the Americas and elsewhere in the world. For common bean germplasm screening and breeding for low-input sustainable farming systems in Latin America, the USA, and elsewhere, an integrated approach whereby combined stress to multiple mineral elements are simultaneously imposed should be preferred over stress for specific minerals at specific times. Of course, the latter might be essential for understanding the physiology and genetics of specific mineral uptake and utilization.

Considerable variability for LF tolerance exists among landraces and improved genotypes identified in this study. Among the landraces, Apetito, Carioca, Garbancillo Zarco, Garrapato, and J 117 were consistently higher yielding in both LF and HF environments (Tables 4, 7, and 8). While they had similar PR and LFSI values, they also had considerably higher biomass yields and harvest index, especially compared with large-seeded Andean landraces such as G 16140, G 19833, and G 20554 (Table 4). Among the improved genotypes, A 321, A 445, A 774, FEB 190, MAM 38, and MAM 46 often had slightly higher seed and biomass yields than the highest yielding landraces, especially in HF. The large-seeded A 36 had the lowest yields. Nonetheless, its yields in both LF and HF were significantly higher than G 16140, G 19833, and G 20554. Mean seed yield reduction due to LF was 53% (Table 8). On average, landraces had slightly lower PR than improved genotypes. All landraces including G 16140 and G 19833 and improved genotypes had an average to below average LF susceptibility index.

Table 5. Simple phenotypic correlation coefficients between seed yield, biomass yield, and harvest index for 36 common bean genotypes evaluated in high and low soil fertility at Popayán and Quilichao, Colombia, in September to December 1996.

	Harvest index HF†	Harvest index LF	Biomass HF	Biomass LF	Seed yield HF	Seed yield LF
Harvest index HF	–	0.91**	0.41*	0.58**	0.69**	0.76**
Harvest index LF		–	0.36*	0.56**	0.63**	0.76**
Biomass HF			–	0.72**	0.93**	0.68**
Biomass LF				–	0.76**	0.95**
Seed yield HF						0.81**

* Significant at $P < 0.05$.
** Significant $P < 0.01$.
† HF = high soil fertility and LF = low soil fertility.

In addition to LF tolerance, landraces possess many other useful traits. For example, landrace cultivars Apetito, Flor de Mayo IV, and Garbancillo Zarco also have high levels of resistance for drought stress (Terán and Singh, 2002). De Celaya and J 117 have high levels of resistance to bean pod weevil (*Apion godmani* Wagner) (Garza et al., 1996, 2001); Carioca is highly resistant to root-knot nematode (*Meloidogyne chitwoodi* Golden et al.) (S. Hafez and P. Sundararaj, personal communication, 2001); Garrapato has a high level of resistance to *Bean golden yellow mosaic virus* (Morales and Niessen, 1988; Urrea et al., 1996); Colorado de Teopisca has three independent dominant genes for resistance to many races of *C. lindemuthianum* (Pastor-Corrales et al., 1994; Young et al., 1998); and Compuesto Chimaltenango 2 has a broad-based resistance to rust [caused by *Uromyces appendiculatus* (Pers.) Ung.] (Stavely and Grafton, 1989). Moreover, Garbancillo Zarco has been a popular cultivar, grown on hundreds of thousands of hectares in association with corn (*Zea mays* L.) in moderately infertile soils in the state of Jalisco, Mexico. Similarly, Carioca has been the most popular cultivar for decades occupying more than two million hectares in infertile soils in Brazil. Owing to its high and stable yield, Carioca's cultivation has also been extended to Argentina, Bolivia, and Africa. Because these landraces were domesticated under subsistence farming systems in the absence of chemical fertilizers, herbicides, pesticides, and irrigation, they may possess resistance to many abiotic and biotic stresses. These useful intrinsic landrace characteristics therefore should be introgressed in cultivars destined for low-input sustainable farming systems.

No yield gains in LF and HF environments would be expected from intraracial common bean populations lacking genetic variation (Singh et al., 1989b). A 752 was specifically selected in the LF environment at Popayán (Singh et al., 1989a). It also exhibited good levels of tolerance to LF in this study. LF tolerant Carioca and 'Flor de Mayo' were among the parents used in the interracial population from which A 752 was derived. These two cultivars also are in the parentage of MAM 38. Like MAM 38, all other improved genotypes except APN 115, CAP 4, DICTA 11, and DICTA 17 were bred at Popayán and Quilichao under moderate biotic and abiotic stresses, and exhibited comparatively high LF tolerance. Moreover, LF tolerant landraces identified in this study or similar genotypes were used in broad-based interracial populations that were often subjected to the mass-pedigree method of selection (Singh et al., 1989a) with (Singh et al., 1990) or without early generation yield tests across locations (Singh et al., 1991b, 1992, 1993). For pedigree of improved genotypes refer to Rodríguez et al. (1995). A 321 exhibited LF tolerance in Africa (Wortmann et al., 1995). A 774 has out yielded most genotypes, including Carioca, in Brazilian national trials since it was introduced in the country in 1989 (Thung et al., 1993). MAM 38 was the highest yielding genotype in its market class across environments in the Mexican highlands (Acosta-Gallegos et al., 1995).

Because rigorous selection was applied over a period of several years for the identification of most promising LF tolerant landraces and improved genotypes, researchers interested in a much broader range of LF tolerant germplasm may wish to evaluate an additional portion or all 81 genotypes included in the 1995 and 1996 trials. In addition, root growth in P deficient conditions (Fawole et al., 1982a), P-use efficiency (Fawole et al., 1982b; Lindgren et al., 1977), K-use efficiency (Shea et al., 1967), resistance to chlorosis induced by Fe (Coyne et al., 1982; Zaiter et al., 1987a, b) and Zn (Singh and Westermann, 2002) deficiencies, seed Zn accumulation (Forster et al., 2002), and tolerance to LF as measured by seed yield (Urrea and Singh, 1989) are heritable traits in common bean and other crops (Clark and Duncan, 1991). Thus, much larger gains and higher levels of LF tolerance should be expected from the broad-based interracial populations involving landraces and improved genotypes identified in this study (Singh et al., 1989a). Moreover, owing to the fact that for N_2 fixation considerably higher levels of P are required (Graham and

Table 6. Analysis of variance for seed yield for 25 common bean genotypes evaluated in high and low soil fertility at Popayán and Quilichao, Colombia, in March to June 1997 and 1998.

Source	DF	Mean square
Year (Y)	1	11 061 926.5*
Location (L)	1	33 557 708.9**
Fertility level (F)	1	180 880 199.9**
Y × L	1	126 169 789.5**
Y × F	1	4 997 857.3
L × F	1	13 086 728.0*
Y × L × F	1	48 467 919.7**
Rep (Y × L × F)	24	1 891 650.4
Block (Rep × Y × L × F)	128	207 717.6
Genotype (G)	24	2 885 519.4**
G × Y	24	269 392.6**
G × L	24	1 027 286.3**
G × F	24	879 716.1*
G × Y × L	24	584 019.1**
G × Y × F	24	119 338.3
G × L × F	24	420 415.5**
G × Y × L × F	24	383 597.8**
Error	448	130 357.0

* Significant at $P < 0.05$.
** Significant $P < 0.01$.

Table 7. Means for seed yield, percent reduction, and low soil fertility susceptibility index for 25 common bean genotypes evaluated in high and low soil fertility at Popayán and Quilichao, Colombia, in March to June, 1997 and 1998.

	Popayán				Quilichao								
	1997		1998		1997		1998		Mean				
Genotype	HF†	LF	HF	LF	HF	LF	HF	LF	HF	LF	Mean	PR	LFSI
Landrace (11)	kg ha^{-1}											%	
Apetito (G 1759)	635	729	2728	950	2878	1387	1240	580	1870	912	1391	51	0.9
Carioca (G 4017)	652	264	2348	1066	3443	727	1641	802	2021	715	1368	65	1.1
Garrapato (G 2402)	1078	518	2246	778	3155	1003	934	541	1853	710	1282	62	1.0
J 117	1114	821	2113	1015	2178	690	1019	549	1606	769	1188	52	0.9
Garbancillo Zarco (G 22041)	948	812	1585	953	2541	1183	692	406	1442	839	1141	42	0.7
De Celaya (G 13614)	794	797	2436	1286	1726	933	764	340	1430	839	1135	41	0.7
Flor de Mayo IV (G 22036)	532	387	2229	532	2718	1087	947	562	1607	642	1125	60	1.0
Compuesto Chimaltenango 2 (G 5711)	960	342	2234	590	1543	728	697	555	1359	554	957	59	1.0
Colorado de Teopisca (G 2333)	790	304	1239	436	1138	791	235	195	851	432	642	49	0.8
G 16140	613	154	1645	592	342	142	150	58	688	237	463	66	1.1
Chaucha Chuga (G 19833)	921	134	1390	381	0	74	68	31	595	155	375	74	1.3
Improved (14)													
FEB 190	559	466	3445	733	4340	1175	1857	1042	2550	854	1702	67	1.1
A 774	498	357	2043	837	4555	1396	2202	1282	2325	968	1647	58	1.0
A 445	1272	786	3854	757	3371	869	1544	620	2510	758	1634	70	1.2
MAM 38	1444	752	3248	968	3395	1121	1334	734	2355	894	1625	62	1.1
A 752	1775	1183	3015	1342	2778	623	888	523	2114	918	1516	57	1.0
ARA 14	796	722	2014	1458	3791	1123	1454	473	2014	944	1479	53	0.9
FEB 192	310	171	2198	913	4191	1178	1774	949	2118	803	1461	62	1.1
MAM 46	1021	604	2479	697	3826	1272	1195	550	2130	781	1456	63	1.1
A 321	668	492	2768	658	3530	1213	1486	702	2113	766	1440	64	1.1
DICTA 17	1153	300	2650	1112	3462	841	1300	617	2141	718	1430	66	1.1
CAP 4	491	304	2494	857	3734	894	1706	497	2106	638	1372	70	1.2
DICTA 11	902	178	2261	658	3187	917	1503	678	1963	608	1286	69	1.2
APN 115	725	343	2011	828	2154	1285	905	525	1449	745	1097	49	0.8
A 36	468	174	2295	1006	1942	837	388	201	1273	555	914	56	1.0
Overall mean	845	484	2359	856	2797	939	1117	560	1779	710	1245	59	1.0
Landrace mean	821	478	2017	780	1969	795	762	420	1393	618	1006	56	0.9
Improved genotype mean	863	488	2627	916	3447	1053	1395	671	2083	782	1433	62	1.1
LSD (0.05) ‡	421	324	670	576	612	611	308	272	242	258	177		
LSD (0.05) §	113	88	178	161	175	157	86	71	69	74	50		
LFII¶	0.43		0.64		0.66		0.50		0.60				

† LF = low soil fertility, HF = high soil fertility, PR = percent reduction due to LF, and LFSI = low soil fertility susceptibility index: LFSI = (1 − Ylf/Yhf)/LFII, where Ylf and Yhf are mean yields of a given genotype under LF and HF conditions, respectively.
‡ To compare among 25 genotypes.
§ To compare means between landraces and improved genotypes.
¶ LFII = low soil fertility intensity index = 1 − Xlf/Xhf, where Xlf and Xhf are the mean of all genotypes in LF and HF environments, respectively.

Rosas, 1979), LF tolerant genotypes identified in this study might be useful for N_2 fixation at low P levels.

All LF tolerant landraces originated in tropical and subtropical Latin America and improved genotypes were developed at locations close to the equator. It is therefore likely that many genotypes identified in this study are sensitive to long summer days in the temperate environments of North America (White and Laing, 1989). Thus, it would be essential first to test these genotypes for photoperiod response and general adaptation before their use in breeding programs in the USA. Sensitive genotypes would need to be grown in short-day (≤12 h light) conditions for hybridization with adapted elite parental germplasm and cultivars. Furthermore, because most genotypes possess undesirable sprawling or climbing, indeterminate growth habit Type III or IV (Singh, 1982), and have noncommercial seed types in the USA, some form of backcrossing or recurrent selection may need to be used for introgression of LF tolerance and other useful traits into North American cultivars.

Association between seed and biomass yields often are positive, and both are negatively correlated with harvest index (White et al., 1992). However, in this study, all three traits were positively correlated among themselves in both LF and HF environments (Table 5). This would suggest that the three traits were interdependent and that similar mechanisms were largely involved in their expression in both LF and HF environments. Despite these findings, the high expenses associated with conducting yield trials, and the significant interactions existent among genotypes, fertility levels, locations, and years (Table 6 and Yan et al., 1995b), the use of biomass yield and vegetative organs at any growth stage and/or HI as indirect selection criteria for LF tolerance in common bean are not proposed. Similarly, the use of LFSI or PR alone as selection criteria for LF tolerance is not advocated. Exceptions occurred such that genotypes with high biomass yields did not always have the highest seed yield and/or HI (A 750 and CAP 2) and genotypes with high HI did not always have the highest seed yield (Ojo de Cabra 24 MU and SEA 12). Moreover, these are highly selected genotypes, and even in the HF environments moderate stress due to low soil fertility existed. Thus, a positive correlation among the three traits might be expected. The proposed exclusive reliance on seed yield as the selection criterion for LF tolerance is contrary to the earlier proposal by Lynch

Table 8. Mean seed yield, percent reduction, and low soil fertility susceptibility index for 25 common bean genotypes evaluated in high and low soil fertility at Popayán and Quilichao, Colombia, from 1995 to 1998.

Genotype	1995B	1996A†		1996B		1997A		1998A		Mean		Overall mean	PR	LFSI
	LF‡	LF	HF	LF	HF	LF	HF	LF	HF	LF	HF			
Landrace (11)	kg ha^{-1}												%	
Apetito (G 1759)	1107	634	880	817	2735	1058	1757	663	1613	856	1746	1252	51	0.9
Carioca (G 4017)	969	539	463	862	2608	496	2048	871	1818	747	1734	1186	57	1.0
J 117	898	490	865	830	2685	756	1646	653	1293	725	1622	1124	55	1.0
Garbancillo Zarco (G 22041)	1140	491	707	1016	2289	998	1745	545	916	838	1414	1094	41	0.7
Garrapato (G 2402)	903	449	537	767	2430	761	2117	605	1262	697	1587	1092	56	1.0
Flor de Mayo IV (G 22036)	1091	493	498	845	2468	737	1625	551	1268	743	1465	1064	49	0.9
De Celaya (G 13614)	930	303	741	648	2511	865	1260	561	1182	661	1424	1000	54	1.0
Compuesto Chimaltenango 2 (G 5711)	1048	475	653	618	2348	535	1252	561	1082	647	1334	952	51	0.9
Colorado de Teopisca (G 2333)	785	158	571	338	1469	548	964	262	486	418	873	620	52	0.9
G 16140	959	367	195	297	1428	148	478	196	524	393	656	510	40	0.7
Chaucha Chuga (G 19833)	1011	219	337	204	888	104	461	120	399	332	521	416	36	0.7
Improved (14)														
A 774	1221	536	762	924	2831	877	2527	1183	2163	948	2071	1447	54	1.0
A 321	1284	320	1316	885	3252	853	2099	696	1807	808	2119	1390	62	1.1
A 445	1161	711	773	814	2833	828	2322	654	2122	834	2013	1358	59	1.1
FEB 190	829	379	699	950	2827	821	2450	970	2254	790	2058	1353	62	1.1
MAM 38	1080	544	795	1042	2675	937	2420	801	1813	881	1926	1345	54	1.0
MAM 46	1005	456	888	818	2973	938	2424	601	1516	764	1950	1291	61	1.1
DICTA 17	1281	510	973	855	2651	571	2308	745	1638	792	1893	1281	58	1.1
FEB 192	941	486	829	884	2369	675	2251	951	1880	787	1832	1252	57	1.0
A 752	878	370	999	945	2421	903	2277	728	1420	765	1779	1216	57	1.0
ARA 14	902	491	554	874	2547	923	2294	721	1594	782	1747	1211	55	1.0
DICTA 11	1158	505	667	802	2603	548	2045	670	1693	737	1752	1188	58	1.1
CAP 4	841	508	823	740	2121	599	2113	568	1903	651	1740	1135	63	1.1
APN 115	893	421	586	841	2689	814	1440	606	1182	715	1474	1052	51	0.9
A 36	1279	489	381	726	1456	506	1205	390	865	678	977	811	31	0.6
Overall mean	1024	454	700	774	2404	712	1821	635	1428	720	1588	1106	53	1.0
Landrace mean	986	420	587	658	2169	637	1396	508	1077	642	1307	937	49	0.9
Improved genotype mean	1054	480	789	864	2589	771	2155	735	1704	781	1809	1238	56	1.0
LSD (0.05)§	99	38	55	57	89	96	105	99	103					
LSD (0.05)¶	334	213	310	240	378	338	370	346	361					
LFII#		0.35		0.68		0.61		0.56		0.55				

† Growing season A = March to June and B = September to December.
‡ LF = low soil fertility, HF = high soil fertility, PR = percent reduction due to LF, and LFSI = low soil fertility susceptibility index: LFSI = (1 − Ylf/Yhf)/LFII, where Ylf and Yhf are mean yields of a given genotype under LF and HF conditions, respectively.
§ To compare means between landraces and improved genotypes.
¶ To compare among 25 genotypes.
# LFII = low soil fertility intensity index = 1 − Xlf/Xhf, where Xlf and Xhf are the mean of all genotypes in LF and HF environments, respectively.

and Beebe (1995) who advocated selection for mechanisms of tolerance or their linked markers. The latter may be of some use in the early stages of a germplasm-screening program when researchers do not have access to dependable field screening facilities. Nevertheless, seed yield testing across contrasting environments must be an integral part of any successful LF tolerant breeding program, should seed remain the principal harvestable product. After all, seed yield is the final product resulting from integration of all physiological processes controlling growth and development during the entire crop cycle (Wallace, 1985).

A positive correlation between seed yields in LF and HF environments would not justify a separate breeding program for each environment (Atlin and Frey, 1989). Singh et al. (1989a) found that the amount and type of genetic variation among common bean populations were more important than selection in high- versus low-input environments. The highest seed yield gains were realized in interracial populations among Middle American common bean races Durango, Jalisco, and Mesoamerica (Singh et al., 1991a). The Andean × Middle American intergene pool population resulted in the lowest yielding genotypes regardless of selection environment (Singh, 1995; Singh et al., 1989a). Yield testing of early generation broad-based populations involving high yielding parents with positive general combining ability in both LF and HF environments, development of advanced generation lines in HF only from promising populations that do well in both environments, followed by yield testing in both LF and HF environments might be a worthwhile breeding strategy for development of high yielding common bean cultivars for sustainable farming systems.

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