



Assessing root traits associated with root rot resistance in common bean

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Abstract

Detecting differences in root architecture and growth patterns among common bean (*Phaseolus vulgaris* L.) genotypes may provide unique selection criteria for genetic resistance to *Fusarium* root rot. Genetic variation in root system architecture was quantified for 10 contrasting bean genotypes that represent four common bean classes (kidney, cranberry, black, and snap bean) under greenhouse conditions and under root rot disease pressure in the field. Genetic variation existed in root architecture among common bean classes and was highly significant under field conditions. Variation in root traits was minimal under environmentally controlled, greenhouse conditions. Results from the field evaluation suggest that a greater number of adventitious roots can contribute to root rot resistance, where the three most resistant genotypes accumulated large amounts of biomass in adventitious roots. In the field environment, total root system dry weight was correlated to fine ($r = 0.74$, $P < 0.001$) and intermediate ($r = 0.66$, $P < 0.01$) root classes. Plasticity of root system response was high, indicating the value of screening in the field environment.

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Keywords: *Phaseolus vulgaris* L.; Root system architecture; Disease resistance; *Fusarium* root rot; Breeding; Root environment

1. Introduction

A number of soil-borne, fungal pathogens are widespread throughout common bean (*Phaseolus vulgaris* L.) production areas. One such pathogen is *Fusarium* root rot (caused by *Fusarium solani* (Mart.) Sacc. f. sp. *phaseoli* (Burk.) W.C. Snyder and H.M. Hans.) which infects and colonizes common bean roots (Burke and Hall, 1991). Pathogen infection acts to reduce root density by killing roots and may attenuate the functional efficiency of the remaining infected roots. Seed yield losses from root rots in susceptible

kidney beans can be greater than 50% (Estevez de Jensen et al., 2002). The evaluation of root traits and root rot tolerance mechanisms is particularly challenging, due to high root plasticity in response to environment factors (Snapp et al., 1995).

Root disease becomes more severe when bean roots are unable to escape the pathogen due to edaphic factors. Low temperatures, drought, flooded or water logged conditions and soil compaction can hamper root growth and predispose bean plants to severe *Fusarium* root rot infection (Thung and Rao, 1999). Seed yield loss is especially severe when the disease occurs during flowering and pod fill (Schneider et al., 2001). When the primary root dies due to infection, its function could be replaced by roots that arise from the shoot–root transition zone and generally adopt a

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52 horizontal rather than a vertical orientation (Jackson, 100
 53 1955). These basal roots are frequently referred to as 101
 54 adventitious roots, although, by definition, adventi- 102
 55 tious roots arise only from hypocotyl tissue (Leskovar 103
 56 and Stoffella, 1995). A root system with many hori- 104
 57 zontal roots has been termed topsoil foraging archi- 105
 58 tecture with competitive advantage for phosphorus- 106
 59 acquisition in the topsoil (Rubio et al., 2003). Promot- 107
 60 ing lateral and adventitious roots may also contribute 108
 61 to plant survival in the presence of root rot organisms
 62 (Burke and Barker, 1966; Snapp et al., 2003). Inte-
 63 grated management strategies that combine vigorous
 64 rooting systems with bio-control seed treatments may
 65 be the most profitable and environmentally appropri-
 66 ate approach to controlling root rot in bean (Estevez de
 67 Jensen et al., 2002).

68 Limited knowledge on the relative importance and 111
 69 function of various root classes complicates the pro- 112
 70 spects of breeding for root traits in common bean 113
 71 (Lynch and van Beem, 1993; Kelly, 1998). Differences 114
 72 in root elongation and branching rate exist among 115
 73 different plant genera, among species within a genus, 116
 74 and among cultivars within a species (Gabelman et al., 117
 75 1986; Gallardo et al., 1996; Leskovar and Stoffella, 118
 76 1995; Lynch and van Beem, 1993; Jackson, 1995; 119
 77 Vercambre et al., 2003; Bingham and Bengough, 120
 78 2003; Zobel, 1995). Field studies suggest that root 121
 79 system traits pay a role in resistance to root rot (Burke 122
 80 and Barker, 1966; Snapp et al., 2003). Detecting 123
 81 genetic differences in root growth patterns and archi- 124
 82 tecture between genotypes may offer unique selection 125
 83 criteria for tolerance to root diseases enhanced by 126
 84 drought, flooding, and stressful root zone temperatures 127
 85 (Leskovar and Stoffella, 1995). 128

86 Understanding mechanisms of *Fusarium* root rot 129
 87 resistance in common bean, especially kidney beans, 130
 88 is a major goal of breeding programs. Breeding for 131
 89 resistance has been hampered by the high variability 132
 90 and scorer-bias associated with conventional rating 133
 91 systems, whether using hypocotyl lesion scoring or 134
 92 whole root system scoring (Beebe and Bliss, 1981; 135
 93 Schneider et al., 2001). Root architecture traits, such 136
 94 as secondary and tertiary root branches, adventitious 137
 95 roots, basal roots (arising from the basal region of the 138
 96 hypocotyl), root angles, and radii, should also be 139
 97 considered in evaluating root systems. Quantitative 140
 98 information on root system traits associated with root 141
 99 rot tolerance would improve selection criteria. More-

over, knowledge of the genetic determinants of root 100
 traits and how they influence yield would allow for a 101
 more targeted breeding approach utilizing technolo- 102
 gies such as QTL analysis. 103

The objectives of this study were to: (1) character- 104
 ize genetic variation of root architecture in contrasting 105
 bean classes types under field and greenhouse condi- 106
 tions and (2) identify root system characteristics that 107
 may be related to root rot resistance in common bean. 108

2. Materials and methods 109

2.1. Bean genotypes 110

Ten genotypes representing, four bean seed classes 111
 (kidney, cranberry, blacks, and snap beans) were 112
 evaluated for reaction to *Fusarium* root rot and root 113
 system traits. The characteristics and origin of geno- 114
 types chosen in each bean class are described in 115
 Table 1. Shoot growth habit of the germplasm was 116
 characterized according to Singh (1982). The bean 117
 genotypes included commercial cultivars grown by 118
 Midwestern farmers, recent variety releases (Kelly 119
 et al., 1998, 1999a,b) and black bean genotypes from 120
 Mexico, Colombia and Michigan with known resis- 121
 tance to root rot. An exception is FR266 (*Fusarium* 122
 Resistant 266), which is a non-commercial snap bean 123
 line that is closely related to kidney bean genotypes. 124
 FR266 was included as one of the few examples of a 125
 genotype with reported resistance to *Fusarium* root rot 126
 (Silbernagel, 1987). Earlier findings indicate that the 127
 FR266 root system is highly branched (Snapp et al., 128
 2003). 129

2.2. Plant growth and management 130

2.2.1. Greenhouse experiments 131

The study was planted on 30 June 2002 and har- 132
 vested on 9 August 2002 in a greenhouse at Michigan 133
 State University in East Lansing, MI. Greenhouse 134
 temperature was set to 25 °C at day and 20 °C at 135
 night. WatchdogTM temperature monitoring system 136
 (Spectrum Technologies, 23839 West Andrew Road, 137
 Plainfield, IL 60544) was used to monitor soil tem- 138
 perature at 3 cm of depth in the containers. Soil 139
 temperatures over the 30 days the experiment was 140
 conducted ranged from a low of 18 °C to a high of 141

Table 1
Characteristics of the common bean genotypes used to characterize bean roots during the summer 2002

Class	Genotype	Growth habit ^a	Origin ^b	Seed size ^c	Root rot reaction
Andean gene pool					
Kidneys	Red hawk	Type I	MSU	63.8	Susceptible
	Montcalm	Type I	MSU	61.3	Susceptible
	Beluga	Type I	MSU	64.0	Susceptible
	Chinook 2000	Type I	MSU	60.6	Moderately resistant ^d
Cranberries	C97407	Type I	MSU	54.5	Susceptible
	Taylor Hort	Type I	Michigan	56.8	Susceptible
Snap bean	FR266	Type I	ARS/USDA, WA	30.7	Resistant
Middle American gene pool					
Blacks	NSL	Type III	Mexico	38.5	Resistant
	TLP 19	Type III	CIAT	28.1	Susceptible
	B98311	Type II	MSU	29.8	Moderately resistant

^a Singh (1982).

^b MSU: Michigan State University; ARS: Agricultural Research Service; USDA: US Department of Agriculture; CIAT: International Center for Tropical Agriculture.

^c Seed size is expressed as weight in grams per 100 seeds.

^d Indicates those genotypes that had intermediate symptoms of *Fusarium* root rot compared to the resistant and susceptible genotypes.

22 °C during the first repetition and from 18 to 25 °C during the second repetition.

Genotypes were planted under greenhouse conditions in Treepots™ 40.6 cm in depth and 15.2 cm in width. The potting media consist of a mixture of coconut coir and perlite (1:2). Earlier research indicated the mixture produced representative root systems and root rot symptoms, and simplified root extraction to permit analysis of root growth patterns in the potting media (Snapp et al., 2003). Seeds were germinated 5 days prior to the initiation of the experiment to ensure uniform germination of all genotypes. A modified, low phosphorus half-strength Hoagland's solution was applied at planting and once a week thereafter as needed. Harvesting was conducted once, 30 days after planting (DAP) to minimize concern regarding restriction of root development in the containers.

The greenhouse experiment was arranged in a randomized complete block design. Two repetitions of the greenhouse experiments were conducted, one initiated on 30 June 2002 and the other on 8 July 2002. There were three replications of each genotype per experiment. Each replication had 10 homogeneous experimental units, each consisting of three treepots and a single seedling was transplanted per pot. One way analysis of variance using SAS was performed,

evaluating genotype effect (SAS Institute, Cary, NC). Where genotype was significant, a mean comparison was conducted using a preplanned non-orthogonal comparison by bean class. Pearson correlation coefficients were computed for all data collected.

2.2.2. Field experiment

The 10 genotypes were evaluated under field conditions at the Montcalm Research Farm located near Entrican, MI (43°20'N; 85°01'W), with an alfisol soil, series name Montcalm/McBride loamy sand. Plots were planted on 20 June 2002 and harvested on 27 July 2002. The Montcalm location was chosen, as the soil type is representative of bean producing areas in Michigan and the Upper Midwest where *Fusarium* root rot is a major problem, particularly for irrigated bean production sites. *F. solani* fsp. *phaseoli* is endemic to the Montcalm site.

The experimental design was a lattice design with three replications. Each experimental unit consisted of 20 plants per row (length of row was 5.0 m, 50 cm between rows and 20 cm between plants within rows). Harvests were conducted at 30 and 60 DAP. At each harvest, nine plants per genotype were randomly chosen from each experimental unit, making sure not to include border plants. Temperature for the field

193 trial varied from 20 to 26 °C. Precipitation at Mon-
 194 tcalm from the time of planting until the time of
 195 harvest was 23 mm during the month of June and
 196 28 mm during the month of July. Irrigation provided
 197 an additional 41 mm during the month of July.

198 2.3. Root system quantification

199 2.3.1. Greenhouse

200 Roots were harvested in the greenhouse as carefully
 201 as possible to assure the removal of the whole root
 202 system and minimize error due to loss at harvest.
 203 Roots were transferred to ice to prevent dehydration
 204 and taken to the laboratory where they were processed
 205 for analysis.

206 Roots were washed to remove excess coconut coir
 207 and perlite that was attached to the root system. Root
 208 architectural traits were analyzed following a slightly
 209 modified procedure of Yabba and Foster (2003) and
 210 Frahm et al. (2003) using the software WinRHIZO™
 211 (WinRHIZO, Regents Instruments Inc., 2001, Quebec,
 212 Canada). Individual root systems were transferred for
 213 scanning to a 30 cm × 20 cm plexi-glass plate where
 214 they floated in clear water and were carefully dis-
 215 persed into individual lateral roots and secondary roots
 216 with forceps as far as practicable to prevent over-
 217 lapping (Harris and Campbell, 1989). Care was taken
 218 to exclude the sides of the tray from the window area
 219 to avoid erroneous counts. Each root was scanned
 220 independently twice (front and back) to assure scan-
 221 ning of all roots and the average of two measurements
 222 were taken. Although root systems develop a three-
 223 dimensional form in the soil, roots were measured in
 224 two dimensions in this study. Dry weight (dried at
 225 60 °C for 72 h for dry weight determination) of above
 226 ground (vegetative area) and below ground (root
 227 system) sections of the plants were taken. The follow-
 228 ing root morphology parameters were measured: total
 229 root system length (cm), root system surface area
 230 (cm²), root system projected area (cm²), average root
 231 diameter (mm), total root volume (cm³), crossings,
 232 number of meristems (tips), and fractal dimension.
 233 Manual counting was conducted to determine the
 234 number of adventitious roots. Roots were divided into
 235 10 classes, based upon root length and diameter [class
 236 A (0–0.5 cm), class B (0.51–1.5 cm), class C (1.01–
 237 1.5 cm), class D (1.5–2.0 cm), class E (2.01–2.5 cm),
 238 class F (2.51–3.0 cm), class G (3.01–3.05 cm), class H

(3.51–4.0 cm), class I (4.01–4.5 cm), and class J
 239 (>4.5 cm)], previously described by Yabba and Foster
 240 (2003) and Frahm et al. (2003), with slight modifica-
 241 tion. The 10 root length classes classified as A–J,
 242 respectively, were grouped in three root diameter
 243 classes: fine roots or secondary roots (A–C), inter-
 244 mediate roots or laterals (D–G), and taproots (H–J). In
 245 this study lateral roots were defined as a major root
 246 axis originating at the taproot.
 247

248 2.3.2. Field

249 Because, field root harvesting is challenging, spe-
 250 cial care was taken to ensure that roots were dug up
 251 carefully and that root systems were as intact as was
 252 possible. These roots were harvested to an approx-
 253 imate depth of 0.31 m. After removing roots from the
 254 soil they were immediately put in a cooler with water
 255 and ice to prevent dehydration. At time of harvest,
 256 roots were rated in the field for *Fusarium* root rot
 257 symptoms using the root rating scale of 1–7, where 1
 258 denotes the root system completely free of disease and
 259 7 the root system severely affected by disease (Schnei-
 260 der and Kelly, 2000). The roots were taken to the
 261 laboratory and cleaned of excess soil. They were
 262 processed for image analysis following the procedures
 263 described for the greenhouse study.

264 3. Results and discussion

265 3.1. Root system variation: genotypes

266 There were marked differences in adventitious root-
 267 ing of genotypes, which varied from 4 to 43 adven-
 268 titious roots per plant among the bean genotypes
 269 screened in the field, and from 0 to 8 adventitious
 270 roots per plant under greenhouse conditions (Fig. 1A).
 271 The root rot resistant genotype Negro San Luís (NSL)
 272 exhibited a root system that accumulated biomass
 273 rapidly and had many adventitious roots, as did the
 274 moderately resistant genotypes B98311 and Chinook
 275 2000. Under greenhouse conditions, Chinook 2000
 276 had the highest number of adventitious roots followed
 277 by the susceptible TLP19 and the most resistant line,
 278 NSL, whereas some of the resistant genotypes had
 279 large diameter roots (Fig. 1A). B98311 had the highest
 280 number of adventitious roots under field conditions
 281 followed by TLP19, NSL, and Chinook 2000. B98311

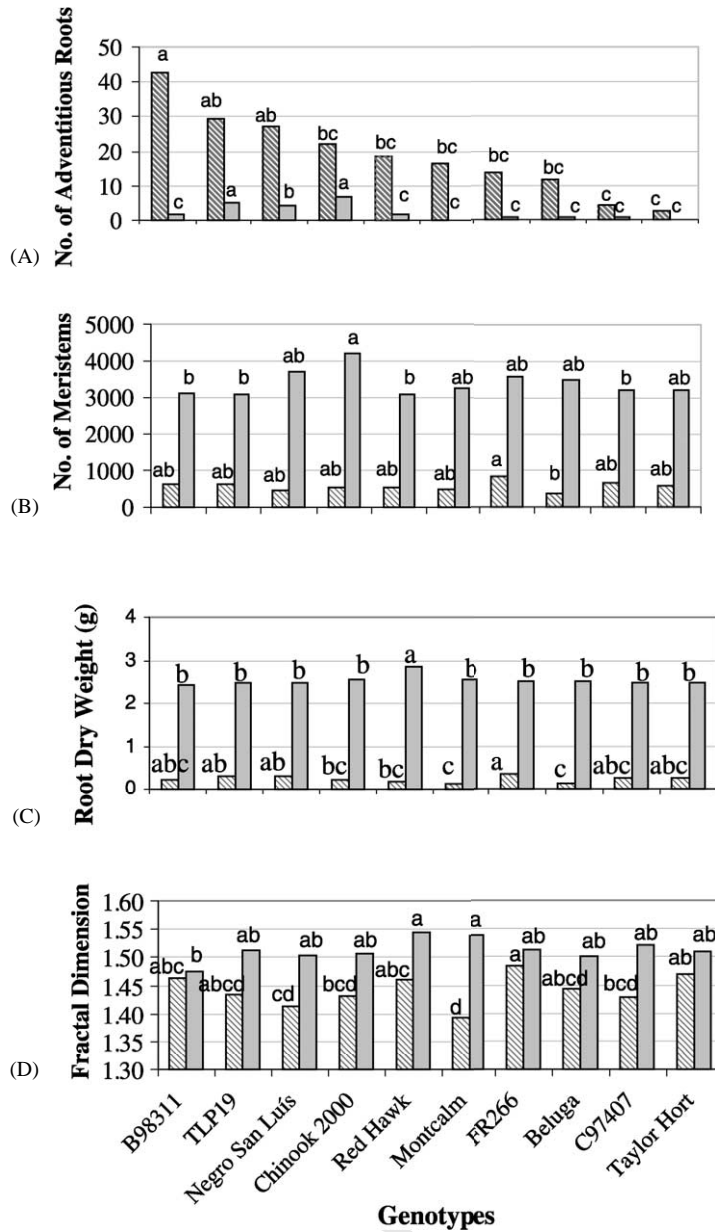


Fig. 1. Illustration of differences between genotypes 30 DAP under field (hatched boxes) and greenhouse conditions (solid boxes) for root traits such as adventitious rooting (A), number of meristems (B), root dry weight (C), and fractal dimension (D) (different letters on columns represent statistical differences at $P < 0.05$).

282 is a drought resistant line that has been reported as
 283 having a vigorous, deep-penetrating taproot (Frahm
 284 et al., 2003). Although shallow adventitious roots are
 285 more susceptible to drought, adventitious roots are

likely to persist under irrigation, and continue to
 function and contribute to the long-term development
 of the root system in soils infested with soil borne
 pathogens (Johnson et al., 2000).

286
 287
 288
 289

Fractal dimension provides a measure of root system size and density of root branching. Since research has shown that ontogeny is closely related to fractal dimension (Bertson et al., 1995), comparisons of genotypes should be at the same state of development. Fractal dimension values observed ranged from 1.40 to 1.55 (Fig. 1D) and were similar to the range in fractal dimension reported in an earlier study of bean root systems (Lynch and van Beem, 1993). In our study, the most root rot susceptible genotype, Montcalm, had a notably weak root system as characterized by limited branching which was reflected in the lowest level of fractal dimension observed for the field environment (Fig. 1D) and the limited amount of dry weight accumulated in the root system (Fig. 1C).

Plants were evaluated 30 DAP in both the field and greenhouse and developmental stage was similar in both environments, yet the genotype by environment interaction was substantial. Adventitious rooting was greatly enhanced under field conditions compared to greenhouse grown plants (Fig. 1A), whereas meristem number was high in the greenhouse trial (Fig. 1B). Chinook 2000 had the largest number of meristems compared to other kidney bean genotypes (Fig. 1B). Chinook 2000 was a plant selection made within 'Chinook' light red kidney cultivar (Kelly et al., 1999a,b), which was derived from crosses that included a black bean in its genetic background; black bean root systems may be associated with greater branchiness or root system meristem number (Kelly et al., 1992).

The reason for this phenomenon is not well understood, but the large number of lateral adventitious roots in the field may be related to the greater level of stress in the field environment, where nutrient and water supply is dynamic. In the greenhouse screen, root systems had many meristems, which may be related to proliferation of fine roots in low bulk density container systems or the disease stress in the field environment may have reduced the survival of fine roots. Roots in the field interact with indigenous soil-borne diseases and other soil microorganisms, which could potentially enhance initiation of adventitious roots by attacking the main tap root.

A large number of root meristems have been associated with acquisition of immobile nutrients such as phosphorus (Rubio et al., 2003). In both the greenhouse and field-based screens conducted here no

significant difference was observed for number of meristems between Chinook 2000 and the resistant genotype NSL, and between B98311, TLP19, C97407, and Red Hawk (Fig. 1B). TLP19 was previously selected as tolerant to low phosphorus, thus we hypothesized it would have multiple branched, top-foraging root architecture; however, this was not observed. These traits have been observed in lines resistant to low phosphorus (Bosner et al., 1996; Lynch and Beebe, 1995; Frahm et al., 2003). Other mechanisms such as root plasticity and rhizosphere acidification may contribute to low-phosphorus tolerance in TLP19 (Snapp et al., 1995; Yan et al., 1996).

3.2. Root system variation: bean classes

The four bean classes in this study varied significantly in plant growth habit and root system architecture (Table 2). Significance differences among bean classes were observed for all traits except root diameter in the field, whereas only root surface area, root volume, root dry weight, and fractal dimension were different in the greenhouse. Large differences between field and greenhouse data were observed for most traits except root diameter, and fractal dimension. Selection for root dry weight would appear to be useful in the greenhouse, but should be delayed to flowering around 45 DAP. The later harvest date would prevent the measurement of other root length, area and volume traits for which variability was limited in the greenhouse. Taproots contributed more than 1% of the total root length of kidney bean class in the greenhouse, whereas taproot length was less than 1% in cranberry, snap bean, and black bean classes. Across all bean classes, 95% of the final root length was contributed by the fine roots and ~4% by intermediate roots (data not shown).

Significant major contrasts for root dry weight were observed between kidney bean and all other classes (Table 3). Differences by bean market class appeared to be related to shoot growth habit and growth rate, as kidney beans (Type I shoot growth habit) exhibit a relatively shallow root system with lateral roots arising from the taproot at the base of the stem. This is similar to earlier observations of related bean root systems (Kelly, 1998; Stoffella et al., 1979), and the relationship of shoot to root growth habit in bean genotypes studied by Lynch and van Beem (1993).

Table 2

Bean class means for different root traits measured under greenhouse and field conditions at Entrican, Montcalm County, MI during the summer 2002^a

Class ^b	Length ^c (cm per plant)	Surface area ^c (cm ²)	Average diameter ^c (mm)	Root volume ^c (cm ³)	Root dry weight (g)	Fractal dimension ^c	Forks ^c	Tips ^c	Crossing ^c
Greenhouse									
K	1094 a	252.8 a	0.73 a	5.45 a	3.62 a	1.52 a	2984 a	3515 a	398.4 a
S	1127 a	240.6 a	0.68 a	4.12 ab	3.45 ab	1.52 a	3206 a	3584 a	450.1 a
C	1116 a	237.8 ab	0.68 a	4.09 ab	2.47 b	1.51 a	3014 a	3216 a	451.0 a
B	1094 a	228.9 b	0.70 a	4.06 b	2.46 b	1.40 b	2644 a	3258 a	354.0 a
Field									
K	277 b	72.0 b	0.83 a	1.50 b	0.17 c	1.43 a	411 b	493 a	38.9 b
S	461 a	120.8 a	0.85 a	2.54 a	0.34 a	1.51 b	841 a	816 a	78.2 a
C	377 ab	99.9 ab	0.85 a	2.11 ab	0.26 b	1.45 a	559 ab	613 a	54.0 ab
B	279 b	71.1 b	0.80 a	1.46 b	0.25 b	1.44 a	474 b	558 a	46.7 b

^a Different letters in the columns represent statistical differences at $P < 0.05$.

^b K: kidney bean class included four genotypes, C: cranberry bean class included two genotypes, B: black bean class included three genotypes, and S: snap bean class included one genotype.

^c Characteristics were determined using WinRHIZO software (WinRHIZO, Regents Instruments Inc., 2001, Quebec, Canada).

384 Similar to kidney bean, cranberry bean root systems
385 (Type I shoot growth habit) tended to be shallow
386 (length) and with limited branching (forks, crossing;
387 Tables 2 and 3). In contrast, root systems of the black
388 bean class (Types II and III shoot growth habit) tended
389 to have many adventitious roots and a dominant tap
390 root system (Fig. 1A). The black bean class exhibits
391 basal roots similar to those described by Stoffella et al.
392 (1979) in beans and by Zobel (1995) in tomatoes. The
393 black bean B98311 exhibits a deeper root system as

described by Frahm et al. (2003) compared to TLP19 394
and NSL, although the root rot resistant genotype NSL 395
has a highly branched root system similar to B98311. 396

The snap bean class had only one representative, 397
FR266 genotype, which is a root rot resistant breeding 398
line with a determinate bush growth habit (Silberna- 399
gel, 1987) and may not be typical of the level of root 400
rot resistance of this class. Thus no generalizations can 401
be made about snap beans. It was interesting to note, 402
however, that FR266 exhibits a root system similar to 403

Table 3

F-values for kidney bean class in contrast with black, snap, and cranberry bean classes for different root traits measured under greenhouse and field conditions at Entrican, Montcalm County, MI during the summer 2002

Class ^a	Length ^b (cm per plant)	Surface area ^b (cm ²)	Average diameter ^b (mm)	Root volume ^b (cm ³)	Root dry weight (g)	Fractal dimension ^b	Forks ^b	Tips ^b	Crossing ^b
Greenhouse									
K vs. B	0.42	3.10*	1.96	4.29*	5.52*	3.60*	1.43	0.58	0.65
K vs. S	0.13	0.21	1.78	1.46	0.88	0.31	0.28	0.03	0.42
K vs. C	0.10	0.63	2.80	2.74	4.82*	0.24	0.01	0.95	0.73
Field									
K vs. B	6.98*	8.86*	0.51	8.70*	31.22***	1.50	3.48	1.32	3.95
K vs. S	14.17**	16.32**	0.45	15.08**	46.66***	8.12*	17.64**	5.70*	16.03**
K vs. C	0.01	0.01	0.93	0.05	17.57**	0.11	0.82	0.50	1.34

^a K: kidney bean class included four genotypes, C: cranberry bean class included two genotypes, B: black bean class included three genotypes, and S: snap bean class included one genotype.

^b Characteristics were determined using WinRHIZO software (WinRHIZO, Regents Instruments Inc., 2001, Quebec, Canada).

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

404 Chinook 2000 at 30 DAP. The root system is highly
405 branched in the upper 12 cm and has a corresponding
406 higher root dry weight (Fig. 1C). FR266 is also similar
407 to B98311 in possessing deep laterals, but with less
408 secondary root branching in the lower portion of the
409 roots toward the root tips. The source of *Fusarium* root
410 rot resistance in FR266 was derived from PI 203958
411 (N203), an indeterminate prostrate vine black bean-
412 seeded line from Mexico that was used multiple times
413 as a parent during the crossing process (Silbernagel,
414 1987). A possible explanation for the similarity in root
415 systems between FR266, Chinook 2000 and B98311,
416 which represent different market classes (Table 1), is
417 that FR266 and Chinook 2000 both possess a black
418 bean in their genetic background and B98311 is a
419 black bean genotype.

420 Similar to the findings of Lynch and van Beem
421 (1993), the indeterminate Type II and Type III black
422 bean lines, tended to have more adventitious roots and
423 a deeper, more extensive root system. In our study a
424 larger number of genotypes were compared than in
425 previous research, and it appeared that beyond exten-
426 sive (deep, many laterals) and intensive (highly
427 branched, shallow) types of root systems we also
428 observed a vigorous, highly branched intensive root
429 system with a large number of extensive laterals. This
430 observation is consistent with it being possible to
431 combine an intensive and extensive root system type
432 from diverse genetic backgrounds. This combination
433 occurred in the black bean class, or in genotypes with
434 black bean parentage.

435 3.3. Root system screening methodology

436 Substantial differences in adventitious rooting and
437 other root traits were observed at 30 DAP in the field
438 compared to the greenhouse (Fig. 1). Genotypes with
439 smaller seed size are distinct and appear to generally
440 have a larger number of adventitious roots under field
441 conditions compared to the greenhouse environment.
442 Data collected in our greenhouse studies exhibited no
443 significant differences between bean classes for most
444 of the characteristics studied, perhaps due to root
445 restrictions imposed in a non-stressful environment
446 in the pots, or to differences in growth media and the
447 short evaluation period (Tables 2 and 3). Laboratory
448 screening systems for root growth response in rice
449 have also found limited correlation with field perfor-

450 mance (Clark et al., 2002). Plasticity may be enhanced
451 in a heterogeneous field environment where a range of
452 signals induce branching and root morphological
453 changes (Wraith and Wright, 1998). Root plasticity
454 is an adaptive variable that enhances resource acquisi-
455 tion and anchorage in a heterogeneous environment
456 (Campbell et al., 1991). Investigation of plasticity to a
457 specific constraint may require a controlled environ-
458 ment, whereas testing for general plasticity and ability
459 to overcome realistic stress encountered in the field
460 environment may require field-based evaluations.

461 Total root dry weight was significantly correlated
462 to fine ($r = 0.744$, $P < 0.001$) and intermediate
463 ($r = 0.657$, $P < 0.01$) root classes under field condi-
464 tions, but was not significantly correlated with average
465 diameter under greenhouse or field conditions (Table 4).
466 No significant correlation was observed for average
467 diameter and total root dry weight under greenhouse
468 conditions. The smaller taproot diameter in comparison
469 with the diameter of the intermediate roots is a result of
470 disease infection and environmental factors in the field.
471 Average root diameter was highly and significantly
472 correlated with intermediate and taproots root classes
473 both under greenhouse ($r = 0.795$ and 0.809 ,
474 $P < 0.01$, respectively) and field conditions
475 ($r = 0.605$ and 0.502 , $P < 0.01$ and < 0.05 , respec-
476 tively). The thickening of intermediate roots and tap-
477 roots appears to be associated with dry weight
478 accumulation of these root classes, for screening con-
479 ducted in both field and greenhouse environments.

480 There was a trend towards a greater number of
481 adventitious roots in plants with lower root rot scores
482 in the field environment although variation was high
483 ($r = -0.06$, $P < 0.05$). Root systems with many
484 adventitious roots may avoid some negative effects
485 of disease through replacement of the function of
486 disease-infected roots (Miller, 1986; Stoffella et al.,
487 1979). However, B98311, NSL, and FR266 varied
488 greatly in number of adventitious roots (Fig. 1A).
489 Our results are consistent with the partial replacement
490 by adventitious roots of roots eliminated by *Fusarium*
491 root rot in susceptible common bean genotypes. A
492 similar association of adventitious rooting with *Fusar-*
493 *ium* root rot tolerance was observed in an earlier study
494 involving inbred bean lines (Snapp et al., 2003). High
495 root plasticity may enhance plant growth and survival
496 through continuous alteration of the root system in
497 response to a varied soil environment (Smucker,

Table 4

Correlation coefficients (r) for root classes grouped in three categories, average diameter, and total root dry weight for greenhouse study and one field trial conducted during the summer 2002 in Montcalm, MI

	Average diameter	Root diameter classes ^a		
		Fine	Intermediate	Taproots
Greenhouse				
Total root dry weight	0.524	−0.251	0.390	0.465
Average diameter		−0.361	0.795**	0.809**
Field				
Total root dry weight	0.292	0.745***	0.657**	−0.009
Average diameter		0.156	0.605**	0.502*

^a Root classes were grouped in three major classes: fine roots (included A, B, and C root length in diameter classes) intermediate roots (included D, E, F, and G root length in diameter classes), taproots (included H, I, and J root length in diameter classes).

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

1993). To eliminate the interference of genetic differences among bean classes, a more effective method to study root plasticity would be to generate genetic populations consisting of recombinant inbred lines developed from parents contrasting only in root characteristics. These populations would provide the best opportunity to study root plasticity and the role of adventitious roots and root dry weight in root rot resistance given the wide genetic differences observed among the bean genotypes in this study.

4. Conclusions

Our results show that genetic variation for root architecture exists among different bean genotypes, and between common bean market classes. Results from this and previous research indicate that root traits such as adventitious roots (Snapp et al., 2003), total root dry weight (Kmieciak and Bliss, 1986), and lateral roots (Burke and Barker, 1966; Schneider and Kelly, 2000) can be quantified as part of a selection process by plant breeders interested in enhanced root rot resistance and over all root health of common bean. Classical methods for studying root systems involve excavation of whole root systems. This poses challenges in keeping root systems intact and extracting fine roots, yet it provides a realistic view of architectural changes that occur as root systems respond to environmental conditions and biotic stress caused by soil borne pathogens. In this study, markedly enhanced

adventitious rooting response was observed in a field-based screen compared to greenhouse screens. Greenhouse studies can be effective in understanding root system traits, but may be problematic in terms of container restrictions to growth and potentially providing a less stressed, unrealistic environment. Our study indicates that the potential exists to improve rooting characteristics of common bean and despite the genotypic differences between market classes, it would appear that breeders have been effective in introgressing desirable rooting traits from black bean into kidney and snap bean. These introgressed lines such as Chinook 2000 and FR266 would be valuable as parental lines to further enhance the root rot resistance of susceptible commercial kidney and snap bean varieties.

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