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Influence of plant density and growth habit of common bean on leaf area development and N accumulation

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ABSTRACT

Crop yield requires leaf area to intercept solar radiation and to undertake photosynthesis, both of which depend on nitrogen (N) accumulation. Further, the amount of accumulated plant N at the beginning of seed fill serves as the reservoir for N required in synthesizing the proteins in developing seeds. For common bean (*Phaseolus vulgaris* L.), resolution of the basic characteristics limiting production is challenging ~~due to~~because of variation in plant growth-habit and in wide ranging plant spacing. Field experiments were undertaken at two low-latitude locations with three plant growth-habit types and six plant densities to measure canopy leaf area and leaf N accumulation at the beginning of seed fill. Plant spacing of 20 plants m^{-2} or more was sufficient to result in equal leaf area and N accumulation for all six plant types at each location. However, the low-altitude, higher-temperature location had lower accumulated leaf N and yield than the high-altitude, cooler-temperature location. These results indicate attention needs to be given to physiological or agronomic approaches to overcome the negative impact of high temperature on N accumulation by common bean.

Introduction

Leaf area development and nitrogen (N) accumulation in leaves prior to the initiation of seed fill are ~~each~~ both essential processes impacting, respectively, the interception of solar radiation and the synthesis of photosynthesis components in the leaves to support high carbon accumulation rates. The balance between the use of newly acquired N between formation of new leaf area and accumulation of leaf N concentration to support photosynthesis influences the productivity of a crop (Sinclair and Horie, 1989). Further, once seed-fill is initiated, N in the leaves and stems is transferred to the seeds contributing directly to yield formation. The total amount of the N available in the leaves for transfer to the seeds can be quantitatively linked to seed yield as part of the 'self-destruction' process during seed growth (Sinclair and deWit, 1976). In common bean (*Phaseolus vulgaris* L.), Saberali et al. (2016) found a linear relationship between seed yield and accumulated N.

Evaluating the use of N to support leaf area development and ~~in~~ increas~~ing~~ing leaf N concentration is challenging in common bean because of the confounding influence of differences in growth habit among genotypes and a range of plant densities under which the crop is grown. In particular, four distinct growth habits have been identified in common bean: type I, determinate bush; type II, indeterminate upright; type III indeterminate prostrate; and type IV indeterminate climbing (Singh, 1981). Kueneman and Wallace (1979a) found leaf area index of common bean ~~was~~ to be lower in Type I genotypes than in Types II and III. They also included plant density in their experiments, and found lower leaf area index at a plant density of 13.5 plants m^{-2} than for canopies grown at densities of 18 and 38 plants m^{-2}. Their conclusion was that "leaf area index was positively correlated with yield" at the highest plant density but the correlation was more variable at lower plant densities.

In a subsequent study, Nienhuis and Singh (1985) found similar results. Type I genotypes had fewer main stem nodes, i.e., fewer main stem leaves, and lower yield than Type II and III. Maximum seed yield was not achieved in their study until plant density was 22 plants m^{-2} or more. In our previous report (Ricaurte et al., 2016) during the development of main stem node number and leaf area, leaf area index of two genotypes of Type I was slightly less than that of genotypes of Types II and III. The node number increased linearly with cumulative temperature units, and leaf area index increase was predicted to increase exponentially with increase in node number.

While several studies have documented N in leaves at the beginning of vegetative growth, the results were only for leaf concentration, not for total accumulated N (Soratto et al., 2017; Nascente et al, 2017; Pias et al., 2017; Barros et al., 2018). Further, these studies were

70 often focused on a single cultivar or a single plant density so the impact of these variables even

71 on leaf N concentration could not be fully evaluated. In the study by Saberali et al. (2016), for

72 example, the plant density was 40 plants m^{-2}, which is high for many cases of common bean

73 production. Therefore, the objective of the current study was to compare at the end of

74 vegetative develop~~ment~~ leaf area and leaf N amount of six common bean genotypes

75 representing three growth habits grown at six plant densities. A key analysis of this study was

76 the relationship between accumulated leaf N prior to seed fill and final seed yield across

77 genotypes and plant densit~~ies~~~~y~~.

78

79 **Materials and methods**

80

81 ***Experimental*** ~~***Design***~~***design***

82

83 Two field experiments as previously described by Ricaurte et al. (2016) were conducted in

84 southwestern Colombia. The first experiment was sown in a fertile mollisol (Typic Pellustert) soil

85 at the Centro Internacional de Agricultura Tropical (CIAT) in Palmira-Valle del Cauca (999 masl,

86 3.54° N, 76.30° W) on 13 October 2013, wh~~ereas~~~~ile~~ the second experiment was sown in an

87 inceptisol (Typic Fulvudands) soil at an experimental station in Darién-Valle del Cauca (1570

88 masl, 3.92° N, 76.60° W) on 29 May 2014. Prior to sowing, seeds were inoculated with

89 *Rhizobioium tropici* CIAT 899 and treated with fungicide. Application of 60 kg ha^{-1} phosphorus

90 was ~~applied~~ made to the soil at both locations at sowing. Non-limiting management was used

91 throughout the experiment, including irrigation.

92 Two genotypes were selected for the experiment from each of growth habit type~~s~~ I, II,

93 and III, so that six genotypes were included in the study. Table 1 ~~gives~~ contains information on

94 origin, growth ~~habits~~ habit- and seed size of the studied genotypes.

95 At both locations, a completely randomized block design was employed with treatments

96 arranged as split plots, where sowing density (5, 10, 15, 20, 25, 35 plants m^{-2}) and the six

97 genotypes were main and subplots, respectively. Individual plots were 4-m long, with 7 rows at

98 Darien and 8 rows at Palmira. The rows were spaced 0.6 m apart. There were three replicates

99 at Darien and four replicates at Palmira. The plots were irrigated as needed.

100

101 ***Data collection***

102

103 Visual observations were made every 2 to 3 d on phenological development to assess whether
104 the plant density treatments impacted the duration to reach initiation of seed fill. The initiation of
105 seed fill was identified as Developmental Stage 8, i.e., p: Pod filling, which begins when 50% of
106 the plants in a plot are observed to be filling seeds in the first pod (Fernandez et al., 1986). To
107 assess a possible difference in development between the two experimental locations,
108 cumulative temperature units from date of sowing were calculated as the basis for comparing
109 occurrence of stage R8. Cumulative temperature units were obtained by summing daily
110 temperature units, which were determined using a Beta function described by Yan and Hunt
111 (1999). The base, optimum, and critical temperatures in these calculations were set at 10, 25
112 and 36 °C, respectively, based on data from Wallace *et al.* (1991).
113   Destructive sampling of 0.3 m^2 area was done biweekly within all plots (Ricaurte et al.,
114 2016). For each plant, mainstem node number, branch number, leaf number, leaf area, and leaf
115 weight were measured. In the results presented here, only data collected at the harvest prior to
116 seed fill are presented.
117   A final harvest for seed yield was done at pod maturity. A length of 3 m was harvested
118 from two adjacent rows in the center of each plot for a total harvest area of 3.6 m^2. Seeds were
119 removed from the pods and weighed. The seed water content was measured (MT-16 Grain
120 Moisture Tester, Agratronix, Streetsboro, OH, USA) and seed weight adjusted to 0.14 g H_2O g^{-1}
121 mass.
122   For measurement of leaf N content, leaf samples excluding petioles were processed at
123 the University of Florida's Forage Evaluation Lab. Ground samples were digested using a
124 modification of the aluminum block digestion procedure of Gallaher et al. (1975). N analysis
125 was done by semi-automated colorimetry using the procedure described by Hambleton (1977).
126 Results were expressed as leaf N per unit leaf area (g N m^{-2}, i.e. specific leaf N) by multiplying
127 N mass concentration of N (g N g^{-1} mass) by the ratio of leaf mass to leaf area for each sample.
128 Total plant leaf N per unit ground area (g N m^{-2}) was calculated by multiplying leaf N per unit
129 leaf area by leaf area index.
130
131 ***Data analysis***
132
133   The effects of density, sites and genotypes on all variables were explored using data
134 collected from all six genotypes that were studied. Linear models were used to conduct an
135 analysis according to a split-plot design with the whole-plot factor arranged in a randomized
136 complete block design using the *nlme* package (Pinheiro and Bates, 2000) in the R statistical

137 software (R Core Team, 2015), following the guidelines in Zuur et al. (2013). In the analysis,

138 density was used as a factor (Density.f, as a categorical variable with 6 levels) or as continuous

139 covariate centered at the 25 plant m^{-2} level (Density.c) to facilitate model parameter

140 interpretation and reduce collinearity between interacting model terms (Schielzeth, 2010).

141 Initially, a full model was fitted that included random effects of site, density, and genotype within

142 site and fixed effects for Site, Density.f and Genotype and their interactions.

143   The full model for each variable was then used to identify the appropriate variance

144 structure within *nlme*, using Akaike's information criteria (AICc) corrected for sample size (AICc)

145 to select the most parsimonious form (data not shown), calculated using the *AICcmodavg*

146 package (Mazerolle, 2011). Model selection was done using ΔAICc values, which were

147 calculated as the difference between the model with lowest AICc and every other model.

148 Assessment of these differences indicated that those models having ΔAICc < 2 having strong

149 support, those with ΔAICc between 4-7 substantial support, and any model with ΔAICc > 10 not

150 considered (Burnham and Anderson, 2002). The final variance structure selected had an

151 exponential or a power function of the fitted values to model the increasing variances with

152 increasing node numbers by site. In a second step, a full model without random terms using

153 generalized least squares was fit and compared using likelihood ratio tests to determine if the

154 random terms were necessary in the model. In the current study, only variable-specific leaf N

155 was analyzed using the random term formulation described previously.

156   With the appropriate variance structure, the final fixed-effect or regressor structure was

157 selected by fitting all possible models with 2nd and 3rd-order interactions and main effects, with

158 density either as a factor or continuous, and genetic effects by genotype, growth habit or

159 determinacy levels. Model selection was carried out using the procedure described previously

160 based on ΔAICc values, and the top three models reported in each case. Finally, goodness-of-fit

161 measure root mean squared error (RMSE) were was also estimated for each of the final

162 models.

163

164 **Results**

165

166 The environments at the two sites were different as expected. At the higher altitude of Darien,

167 minimum and maximum temperatures were cooler and solar radiation during the growing

168 season was higher than at Palmira (Table 2). For Type I genotypes, the same cumulative

169 temperature at both locations was required to reach Stage 8. However, for Type II and Type III

170 genotypes Stage 8 was delayed by about an additional 100 °C cumulative temperature units at

171 Palmira as compared ~~with~~ Darien. A result of the difference between the two locations in

172 cumulative temperature units during the vegetative stages of ~~type~~ Type II and Type III growth

173 ~~habits~~ plants was that the plants had about two more nodes at Stage 8 at Palmira than at

174 Darien.

175

176

177 *Leaf area*

178 Comparison of leaf area development at the beginning of seed fill across growth habits and

179 plant ~~density~~ densities was a major objective of this study. As illustrated in Figure 1, with one

180 genotype for each of the three growth habits, the results for the two locations were quite similar.

181 Leaf area per plant decreased with increasing plant density for each of the genotypes. Leaf

182 area per plant was highest at a plant density of 5 plants m^{-2}, with mean values greater than 0.3

183 m^2 plant^{-1}. At the lower plant densities, leaf area per plant tended to be greater for ~~types~~ Types

184 II and III than for ~~type~~ Type I. At higher plant densities the leaf area per plant decreased linearly

185 with increasing plant density. All genotypes at the highest plant density had similar plant leaf

186 areas of less than 0.1 m^2 plant^{-1}. Model selection indicated the most parsimonious model for

187 plant leaf area included interaction terms ~~for~~ of Site × Density.f, Growth Habit × Density.f and

188 Site × Growth Habit and their respective main effects.

189   Leaf area per unit ground area, i.e., leaf area index, increased from approximately 1.5 at

190 low plant densities to mean values of about 2.5 to 2.8 at high plant densities (as illustrated in

191 Figure 2). An increase in leaf area index of less than two-fold represents much less variation in

192 leaf area index across plant densities than found for plant leaf area. At plant densities of 20

193 plants m^{-2} and greater, leaf area was ~~approximately~~ about constant. Leaf area index was

194 slightly greater for growth habit ~~types~~ Types II and III as compared ~~with~~ ~~to type~~ Type I in these

195 Stage R8 data. Model selection indicated the best model for leaf area index included interactive

196 effects of Site × Density.f + Site × Genotype, and all lower-order terms (Table 3).

197   Leaf weight per unit ground area at both locations was lowest at the 5 plants m^{-2} density

198 but tended to be stable at sowing densities of 10 plants m^{-2} and above (Figure 3). However, leaf

199 weight per ground area was different between the two locations. For growth habit types II and

200 III, the leaf weights per ground area for the high densities at Palmira were about 60 to 70 g m^{-2}

201 and at Darien about 100 to 110 g m^{-2}. The leaf weight per ground area was slightly less for the

202 type I genotypes as compared to types II and III. Model selection indicated the most

203 parsimonious model for plant leaf weight included genotype, Site and Density.f main effects, as

204 well Site × Density.f interaction term (Table 4).

205

Leaf N

207 Except for differences between locations, there was general stability in leaf N per unit leaf area

208 across growth habit types and plant density (Figure 4).   However, leaf N per unit leaf area was

209 somewhat elevated for the 5 plants m^{-2} density at Darien as compared ~~to~~ with the other plant

210 densities at that location. Mean leaf N per unit leaf area at Darien was commonly about 2.0 g N

211 m^{-2}. ~~while~~ whereas at Palmira it was roughly about 1.3 g N m^{-2}. The difference between the two

212 locations in leaf N per unit leaf area for each plant density was generally in the range of 0.4 to

213 1.0 g N m^{-2}. Model selection criteria indicated that a model containing main effect~~s~~ terms for

214 Site, Density.f and Growth Habit, as well as ~~a~~ for Site × Growth Habit interaction was the most

215 parsimonious.

216 Given the approximate stability in the leaf N per unit leaf area at each location at plant

217 density of 10 plants m^{-2} and above, the pattern in total leaf N per unit ground area (Figure 5) is

218 roughly the same as the pattern in leaf area index. That is, the two lowest plant densities (5 and

219 10 plants m^{-2}) tended to have somewhat lower leaf N per unit ground area than the high plant

220 densities. At the high plant densities at each location, N per unit ground area had fairly stable

221 values. Differences in leaf N per unit ground area existed between the two locations with an

222 ~~average~~ mean of 2.11 g N m^{-2} lower at Palmira as compared ~~to~~ with Darien. This is in spite of

223 the fact that the vegetative period for Type II and III genotypes was 100 TU longer at Palmira

224 than at Darien. Model selection criteria indicated that a model containing main effect~~s~~ terms for

225 Site, Density.f and Growth Habit, as well as ~~a~~ Site × Growth Habit interaction was the most

226 parsimonious (Table 5).

227

Discussion

229

230 Carbon assimilation is required for seed development and the production of crop yield, and is

231 dependent of the interception of solar radiation by the leaves and the photosynthetic activity of

232 the leaves. However, in common bean these two variables associated with carbon

233 accumulation have not been found to be consistently associated with yield. Kueneman and

234 Wallace (1979a) only found a consistent correlation between yield and leaf area in common

235 bean at a 38 plants m^{-2} density. In the study by Kueneman and Wallace (1979b), ~~l~~Leaf

236 photosynthesis rate measured at one time during pod filling showed no correlation with yield for

237 the growth habits and plant densities tested ~~by Kueneman and Wallace (1979b)~~.

238   N accumulation by a crop is also essential ~~in~~ for producing yield because both leaf area

239 development and photosynthesis rate are dependent on N availability in the plant, and crucially,

240 during yield formation N is quantitatively required in the formation of the components of the

241 growing seeds. No previous studies have, however, investigated N accumulation in common

242 bean to offer information about the N resource needed in seed yield formation. The lack of

243 insight in common bean about the N influence on yield may have resulted because of the

244 challenge to account for the influence of plant growth habit and plant density, which are two

245 common variables in common bean production. This study was targeted to explore the variation

246 in leaf area development and N accumulation at the beginning of seed fill by genotypes

247 representing three growth types of common bean and plant densities of 5 to 35 plants m^{-2}.

248   The results of leaf N measurements indicated a sensitivity of leaf N accumulation to

249 location. While leaf N per unit leaf area was fairly stable across all plant densities (Figure 4),

250 leaf N per unit leaf area at Palmira was less than that at Darien. The explanation of this

251 difference in leaf N concentration is likely to result from differences in N accumulation rates

252 between the two sites.

253   ~~Figure 6 shows t~~The correlation between final seed yield and the amount of leaf N per

254 unit ground area accumulated prior to seed fill is shown in Figure 6. The results for Palmira

255 emphasize the importance of leaf N accumulation per unit ground area being positively

256 associated with increasing yield. That is, low leaf N accumulation per unit ground area was

257 associated with low yield. The correlation between increasing yield and accumulated N per unit

258 ground area is consistent with the results reported by Saberali et al. (2016) for an experiment in

259 which N fertilizer treatment accounted for differences in accumulated N. In the experiment at

260 Palmira, results from low plant density were the source of low leaf N per unit ground area(< 3 g

261 N m^{-2}) and low yield. On the other hand, at Darien leaf N accumulation per unit ground area

262 was greater than ~~about~~ 3 g N m^{-2} at all plant densities and yield was stable with increasing

263 accumulation of leaf N per unit ground area. These results indicate that a threshold of N

264 accumulation per unit ground area is required to maximize yield.

265   There are two possible bases for the difference in N accumulation between sites. One

266 basis may be the lower soil organic matter content at Palmira than at Darien so the smaller

267 reservoir for soil uptake may have provided less N to developing leaves. ~~A~~ The second basis

268 for the lower leaf N accumulation at Palmira may result from the temperature difference

269 between the two locations and possible sensitivity of soil N accumulation and/or symbiotic N_2

270 fixation in common bean to high temperature. Palmira is a lower altitude location with an

271 average maximum temperature of 31.1 °C during the experiment (Table 2) as compared ~~to~~ with
272 average maximum temperature of 25.5 °C at Darien.
273   Published ~~experiments~~ reports have show~~ned~~ decreases in N_2 fixation rates in
274 Phaselous when temperature exceeded about 30 °C. Pankhurst and Sprent (1976) found
275 maximum N_2 fixation rate ~~of~~ in French bean occurred at 20 °C and virtually no N_2 fixation was
276 found when temperature was increased to 35 °C. Hernandez-Armenta et al. (1989) found N_2
277 fixation rate at 32 °C was substantially less than the rate at 26 °C. Similarly, Piha and Munns
278 (1987) found a very large decrease in N_2 fixation rate by common bean at 34 °C daytime
279 temperatures as compared ~~to~~ with 28 °C. Therefore, high temperature a Palmira may have
280 resulted in less N_2 fixation, low leaf N per unit leaf area (Figure 4), low leaf N accumulated per
281 unit ground area (Figure 5), and lower yield (Figure 6).
282   Overall, growth habit type had little impact on the leaf area index and plant N content at
283 the initiation of seed fill ~~for cases where~~ when plant density was 20 plants m^{-2} or more.
284 Therefore, growth-habit type based on these field studies did not appear to be a major factor for
285 direct physiological improvement ~~for~~ in carbon and N accumulation in common bean as long as
286 plant density was at least 20 plants m^{-2}. However, a major finding from these field ~~results~~
287 experiments was the deficiency in N accumulation at Palmira as compared ~~to~~ with Darien was
288 associated with lower seed yields. These results indicate attention may need to be given to the
289 negative impact of high temperature on N accumulation by common bean, at least for the six
290 genotypes included in this study. Lower leaf N per unit area is likely associated with lower leaf
291 photosynthesis rate and radiation use efficiency (Sinclair and Horie, 1989). Crucially, the lower
292 total leaf N means that less N is available for transfer to the seeds during seed-fill to achieve
293 higher ~~yield~~ seed yields (Sinclair and deWit, 1976).
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Table 1. Information on common bean genotypes sown in both experiments.

Genotype	Gene pool	Growth habit	Seed size (g 100 seeds^{-1})
CAL 96	Andean	I	Large (56.5)
ICA Quimbaya	Andean	I	Large (47.3)
DOR 364	Mesoamerican	II	Small (20.4)
SER 118	Mesoamerican	II	Medium (29.2)
G 21212	Mesoamerican	III	Medium(29.8)
Carioca	Mesoamerican	III	Small (23.4)

Table 2. Average minimum and maximum temperatures, daily temperature units (DTU), and solar radiation during the experimental period at the Darien and Palmira, Colombia, study sites. Standard error of the mean is given in ~~paranthesis~~parenthesis.

	Temperature		DTU	Solar Radiation
Site	Min (°C)	Max (°C)	(°C)	(MJ m^{-2} day^{-1})
Darein	16.6 (0.92)	25.5 (1.2)	12.5 (0.6)	18.6 (3.1)
Palmira	19.1 (0.93)	31.1 (1.9)	14.6 (0.4)	14.2 (3.2)

Table 3. Model selection table for leaf area index at the onset of seed fill (R8). The columns present number of estimated parameters for each model (K), Akaike's information criteria corrected for sample size (AICc), difference in AICc of model with lowest AICc and other modelts (ΔAICc), Akaike's weights (wAICc), log likelihood (LL), and root mean square error (RMSE).

| Form	K	AICc	ΔAICc	wAICc	LL	RMSE
Site*Genotype + factor(Density)*Site	24	470.51	0	0.95	-208.61	0.62
Site*Genotype + factor(Density)	19	477.84	7.33	0.02	-218.28	0.63
Site*factor(Density) + Genotype	19	478.26	7.75	0.02	-218.49	0.65

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Table 4. Model selection table for plant leaf weight per unit leaf area at the onset of seed fill (R8). The columns present number of estimated parameters for each model (K), Akaike's information criteria corrected for sample size (AICc), difference in AICc of model with lowest AICc and other modelts (ΔAICc), Akaike's weights (wAICc), log likelihood (LL), and root mean square error (RMSE).

Form	K	AICc	ΔAICc	wAICc	LL	RMSE
Site*factor(Density) + Genotype	18	2264	0	0.76	-1112.5	24.9
Site*factor(Density) + Growth.Habit	15	2267.7	3.78	0.12	-1117.9	25.1
Site*factor(Density) + Site*Genotype	23	2268.7	4.71	0.07	-1108.9	24.6

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Table 5. Model selection table for plant leaf N weight per unit ground area at the onset of seed fill (R8). The columns present number of estimated parameters for each model (K), Akaike's information criteria corrected for sample size (AICc), difference in AICc of model with lowest AICc and other modelts (ΔAICc), Akaike's weights (wAICc), log likelihood (LL), and root mean square error (RMSE).

| Form	K	AICc	ΔAICc	wAICc	LL	RMSE
Density.f + Site × Growth.Habit	12	784.73	0	0.54	-379.71	1.35
Density.f + Site × Genotype	18	787.23	2.5	0.15	-374.15	1.34
Density.f + Site × Determinacy	10	787.92	3.19	0.11	-383.5	1.37

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386   Figure 1. Leaf area per plant at each plant density for one genotype of each growth habit type

387   at both experimental locations. The datum for each replicate is presented. The line in the bars

388   represents the estimate for the value from the best fit of the model and the bars are the

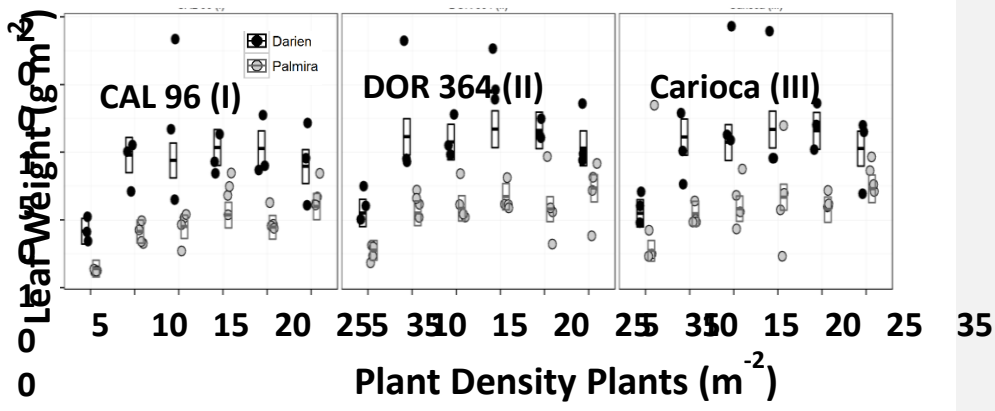389   standard error of this value.

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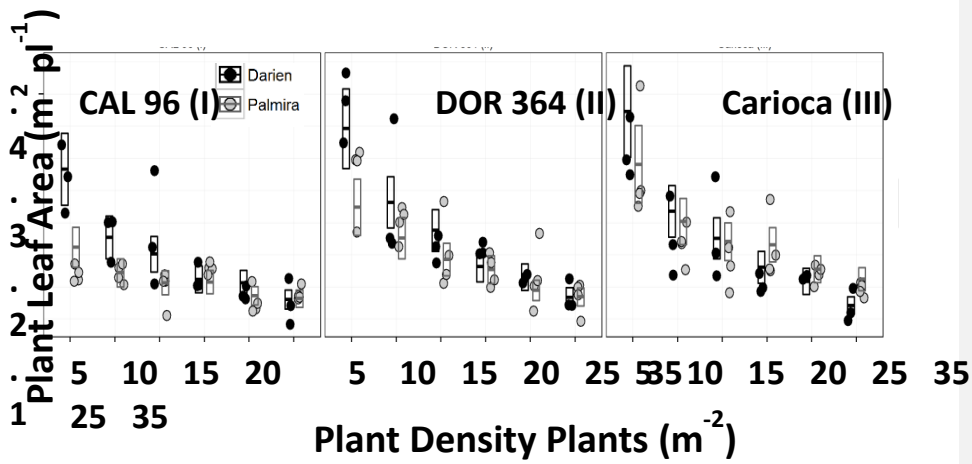
395   Figure 2. Leaf area index at each plant density for one genotype of each growth habit type at
396   both experimental locations. The datum for each replicate is presented. The line in the bars
397   represents the estimate for the value from the best fit of the model and the bars are the
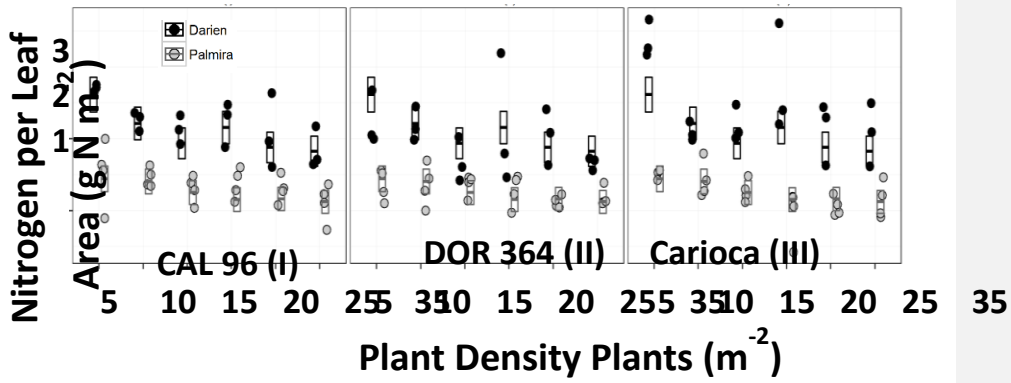398   standard error of this value.
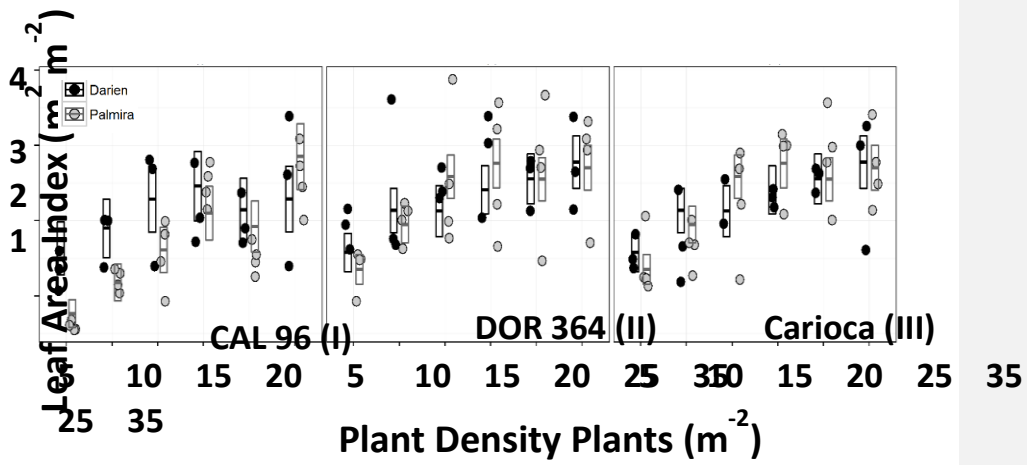
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402   Figure 3. Total leaf weight per ground area at each plant density for one genotype of each

403   growth habit type at both experimental locations. The datum for each replicate is presented.

404   The line in the bars represents the estimate for the value from the best fit of the model and the

405   bars are the standard error of for this value.

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411   Figure 4. Leaf N per leaf area at each plant density for one genotype of each growth habit type

412   at both experimental locations. The datum for each replicate is presented. The line in the bars

413   represents the estimate for the value from the best fit of the model and the bars are the

414   standard error of for this value.

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422 Figure 5. Total leaf N per ground area at each plant density for one genotype of each growth
423 habit type at both experimental locations. The datum for each replicate is presented. The line
424 in the bars represents the estimate for the value from the best fit of the model and the bars are
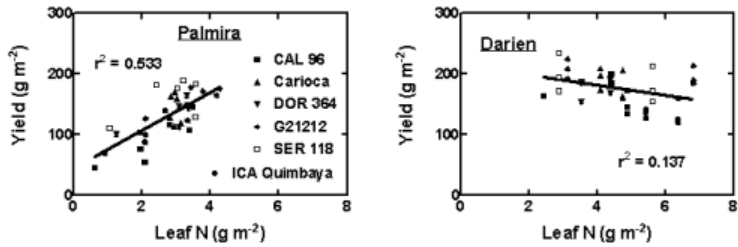425 the standard error of for this value.

426
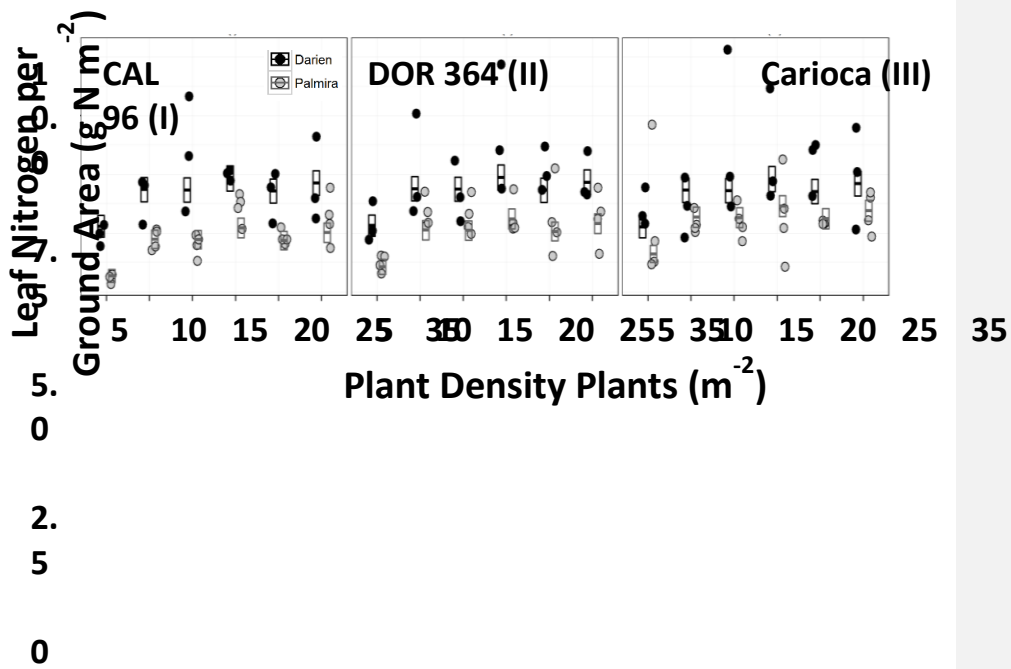
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430   Figure 6. Graph of final bean yield vs. accumulated leaf N per ground area for each of the two

431   locations and six genotypes.

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