

CIAT Research Online - Accepted Manuscript

Sowing density effect on common bean leaf area development

The International Center for Tropical Agriculture (CIAT) believes that open access contributes to its mission of reducing hunger and poverty, and improving human nutrition in the tropics through research aimed at increasing the eco-efficiency of agriculture.

CIAT is committed to creating and sharing knowledge and information openly and globally. We do this through collaborative research as well as through the open sharing of our data, tools, and publications.

Citation:

Ricaurte, José Jaumer; Clavijo Michelangeli, Jose A.; Sinclair, Thomas R.; Rao, Idupulapati Madhusudana; Beebe, Stephen. 2016. Sowing density effect on common bean leaf area development. *Crop Science*. 56: 1-9.

Publisher's DOI:

<http://dx.doi.org/10.2135/cropsci2016.01.0056>

Access through CIAT Research Online:

<http://hdl.handle.net/10568/76271>

Terms:

© 2016. CIAT has provided you with this accepted manuscript in line with CIAT's open access policy and in accordance with the Publisher's policy on self-archiving.



This work is licensed under a [Creative Commons Attribution-NonCommercial 4.0 International License](https://creativecommons.org/licenses/by-nc/4.0/). You may re-use or share this manuscript as long as you acknowledge the authors by citing the version of the record listed above. You may not use this manuscript for commercial purposes.

For more information, please contact CIAT Library at CIAT-Library@cgiar.org.

Sowing Density Effect on Common Bean Leaf Area Development

Jaumer Ricaurte^a, Jose A. Clavijo Michelangeli^b, Thomas R. Sinclair^{*b} and Idupulapati M. Rao^a

Author Affiliations

^a Centro Internacional de Agricultura Tropical (CIAT), A. A. 6713, Cali, Colombia

^b Crop Sciences Department, North Carolina State University, Raleigh, USA

Abstract

Sowing density is a major management factor that affects growth and development of grain crops by modifying the canopy light environment and interplant competition for water and nutrients. While the effects of sowing density and plant architecture on static vegetative and reproductive growth traits have been explored previously in the common bean, few studies have focused on the impacts of sowing density on the dynamics of node addition and leaf area development. We present the results from two sites of field experiments where the effects of sowing densities (5, 10, 15, 20, 25 and 35 plants m⁻²) and genotypes with contrasting plant architectures (two each from growth habits I through III) on the dynamics of node addition and leaf area were assessed. Analysis of the phyllochron (°C node⁻¹) indicated genotype and density effects (but no interaction) on the rate of node addition. While significant, these differences amounted to less than two days of growth at either site. In terms of leaf area development, analysis using a power function reflected large differences in the dynamics and final size of individual plant leaf area between the lower density (<15 plants m⁻²) treatments and commonly used values (>20 plants m⁻²) at the growth habit, but not genotype level. These differences in node addition and leaf development dynamics translated to marked differences between growth habits and sowing densities in estimated leaf area indices, and consequently, in the estimated fraction of intercepted light at lower densities.

Introduction

Interception of light by plant canopies and its use in carbon assimilation to accumulate plant mass is the key driver of crop growth. Leaf area development is critical for light interception, and entails several related physiological processes such as leaf addition, expansion and senescence. In grain legumes, these processes have been found to vary by genotype (Nienhuis and Singh, 1985; Parvez et al., 1989; Ball et al., 2000;), and affected by management factors such as sowing density (Purcell et al., 2002; Bell et al., 1987; Lovett-Doust, 1992; Soltani et al., 2006). In the common bean (*Phaseolus vulgaris* L.), higher sowing densities tend to limit individual plant branch formation (Nienhuis and Singh, 1985; Hampton et al., 1997), plant node numbers (Nienhuis and Singh, 1985; Lovett-Doust, 1992), and consequently individual plant leaf area and vegetative mass (Lucas and Milbourne, 1976). However, the lower leaf area per plant at higher density may be more than compensated by increased plant numbers leading to overall higher leaf area, node numbers and consequently, higher yields per unit land area (Lucas and Milbourne, 1976; Nienhuis and Singh, 1985; Redden et al., 1987; Xu and Pierce, 1998; Hampton et al., 1997). Moreover, previous work has shown effects of increased sowing density can vary depending on genotype (Nienhuis and Singh, 1985).

While the impacts of sowing density and crop genotype on crop yields and yield components has been explored previously in the common bean (e.g. Redden et al., 1987; Lovett-Doust, 1992; Lucas and Milbourne, 1976; Daniells and Wilson, 1987; Hampton et al., 1997; Crothers and Westermann, 1976), their impact on leaf area development over time has received less attention. To our knowledge, no studies have looked at the effects of genotype and sowing density on the rate of leaf addition or the expansion of crop leaf area. Previous work in soybean (*Glycine max* (Merr.) L.) indicated that the rate of node addition increases with increasing sowing densities (Barthou and Buis, 1991), although studies in other legumes such as pigeonpea (*Cajanus cajan* L.) (Ranganathan et al., 2001), cowpea (*Vigna unguiculata* L.) (Craufurd et al., 1997) or chickpea (*Cicer arietinum* L.) (Soltani et al., 2006) have failed to

identify such a relationship. In terms of leaf area, while studies have observed differences in plant areas in common beans grown under contrasting densities (Kueneman and Wallace, 1976; Lovett-Doust, 1992; Lucas and Milbourne, 1976), few have focused on studying differences in the dynamics of leaf area development.

In this study, leaf area development is determined based on a two-step calculation. In the first step, the number of main stem nodes is calculated as a function of phyllochron (thermal period between emergence of successive leaves), which has been commonly done in grain legumes (e.g. Sinclair, 1984; Soltani et al., 2006; Craufurd et al., 1997; Turpin et al., 2002). Once the phyllochron is defined then main stem node number (MNN) at any time can be estimated from phyllochron (β , °C node⁻¹) and cumulative temperature units (CTU, °C).

$$MNN = \alpha + CTU / \beta \quad (\text{Eq. 1})$$

where α is the intercept from the linear regression.

The second step is to use an allometric relationship to calculate plant leaf area (PLA, typically cm² plant⁻¹) as a function of MNN. In this analysis we used a power function for this relationship as suggested by Soltani et al. (2006).

$$PLA = PLACON \times MNN^{PLAPOW} \quad (\text{Eq. 2})$$

where PLACON is a regression term that approximates PLA when the plant has one node, and PLAPOW is the exponent obtained from the regression. Previous studies have suggested that the PLAPOW parameter can vary as a function of sowing density in chickpea (Soltani et al., 2006).

The objective of the study was to explore the effects of sowing density on vegetative growth and development of six common bean genotypes of growth habits I, II and III grown in two locations with contrasting temperature regimes. Specifically, we explored differences in the

rate of node addition and in leaf area development over time, and assessed their impacts on leaf area index and light interception.

Materials and Methods

Sites and Plant Material

Two field experiments were conducted to obtain the data for this study. The first experiment was sown on 13 October 2013 in a fertile Mollisol at CIAT Palmira-Valle del Cauca (PAL, 965 masl). The second was sown on 29 May 2014 in a low phosphorous soil (Inceptisol) at Darién-Valle del Cauca (DAR, 1570 masl). Average minimum and maximum temperatures (°C), solar radiation ($\text{MJ m}^{-2} \text{ day}^{-1}$) and daily temperature units are presented in Table 1. Daily temperature units (DTU) used in describing plant development were calculated using a Beta-type function (Yan and Hunt, 1999) with base, optimum and critical temperatures were set at 10, 25 and 36 °C based on data from Wallace et al. (1991).

Non-limiting growth conditions were maintained throughout the experiment, including irrigation as needed. Plants were established from seeds protected with fungicides and inoculated with *Rhizobium tropici* CIAT 899. P was supplied as 60 kg P ha⁻¹ at sowing at both sites and micronutrients were applied as foliar sprays.

Genotypes in the experiments were chosen to represent two major gene pools (Andean and Mesoamerican) and the three most widely grown growth habits of the common bean. Growth habit I genotypes are determinate with bush-type architecture, while Growth habits II and III are both indeterminate, with bush and prostrate architectures, respectively (Debouck et al., 1986). Information on the origin, growth habits and seed weights of the genotypes sown are presented in Table 2.

Experimental Design and Data analysis

In both experiments, treatments were arranged as split plots in a completely randomized block design, with sowing density (6 levels) as main plots and genotypes (6 levels) as subplots, with three and four replicates in DAR and PAL, respectively. Experimental units in PAL were 4-m long, with 7 (DAR) and 8-row (PAL) plots, spaced at 0.6 m. The six density treatments were obtained by varying distance between plants in the row, with final sowing densities equivalent to 5, 10, 15, 20, 25 and 35 plants per m⁻².

Data collection and analysis

Data collected included destructive samples and non-destructive phenological measurements collected every 2 to 3 days. Phenology measurements were emergence (V1), and reproductive stages pre-flowering (R5, bud formation) and flowering (R6). Destructive samples consisted of 0.3 m⁻² of each plot (1-12 plants), initially at 14 (PAL) or 18 (DAR) days after sowing (DAS), then weekly from 28 to 56 DAS, and then bi-weekly until 105 DAS. Measurements from destructive samples included main stem node numbers and leaf area (cm²) to obtain plant averages. For analysis of phyllochron, data were limited to that collected between V1 and R6, since the rate of node addition tended to decline shortly before or just after the onset of flowering. For the analysis of the leaf area – node number relationship, data from all harvests up to flowering time were used.

Analysis of phyllochron

The effects of density, sites and genotypes on the phyllochron (°C) were explored using a linear mixed effect model using average main stem node numbers as the response variable. The analysis was conducted according to a split-plot design with the whole-plot factor arranged in a randomized complete block design using the *nlme* package (Pinheiro and Bates, 2006) in the R statistical software (R Core Team, 2015), following the guidelines in Zuur et al. (2009). In the

analysis pipeline, plant density was used as a factor (Density.f, as a categorical variable with 6 levels) or as continuous covariate centered at the 25 plants m⁻² level (Density.c) to facilitate model parameter interpretation and reduce collinearity between interacting model terms (Schielzeth, 2010). Similarly, centered cumulative temperature units (CTU) were estimated by accumulating the daily temperature units calculated previously, and subtracting the average across sites.

Initially, a full model was fitted that included random effects of site, repetition and density within repetition within site and fixed effects for Site, Density.f, Genotype, CTU and their interactions. The full model was then used to identify the appropriate variance and covariance structures by testing different weights and correlation functions within *nlme*, using Akaike's information criteria corrected for sample size (AICc) to select the most parsimonious forms (data not shown), calculated using the *AICcmodavg* package (Mazerolle, 2011). Additionally, ΔAICc values were calculated as the difference between the model with lowest AICc and every other model, and were used to select the most parsimonious, with those having $\Delta\text{AICc} < 2$ having strong support, those with ΔAICc between 4-7 substantial support, and any model with $\Delta\text{AICc} > 10$ discarded from consideration (Burnham and Anderson, 2002). The final variance-covariance structure selected had an exponential function of the fitted values to model the increasing variances with increasing node numbers by site, while the covariance was modeled using an continuous time autoregressive correlation structure of order 1 (estimated by site), to capture the repeated nature of the data collection over time.

With the appropriate variance-covariance structure, the full model was compared to an identical model that had density as a centered continuous variable (Density.c) using AICc, which suggested that the model with Density.c was preferable to the full model ($\Delta\text{AICc} = 27.81$). Subsequently, all non-significant three- and four-way interaction terms ($P < 0.05$) were then dropped from the full model with Density.c. The remaining higher-order terms were evaluated by dropping each two-way interaction term and comparing them with the model containing all two-

way interactions using AICc. Only the Site \times CTU interaction was dropped, with the final model consisting of Site \times Genotype, Genotype \times Density.c, Genotype \times CTU and Density.c \times CTU interactions and all corresponding main effects (Table 4). From this model, the inverse of the sum of the regression coefficients for CTU, CTU \times Genotype and CTU \times Density.c correspond to the phyllochron. The standard errors for the phyllochron estimates were estimated using the approach in Schielzeth (2010). Goodness-of-fit measures root mean squared error (RMSE) were also estimated for each of the final models.

Analysis of the leaf area - node number relationship

The relationship between node number and leaf area was modeled using the power function described in Eq. 2 following similar procedures to those used for the analysis of phyllochron. First, full models were fit with both PLACON/PLAPOW parameters estimated as functions of Site, Genotype, Density.f and the Genotype \times Density.f interaction to estimate the correct variance-covariance structure using AICc as described previously. Subsequently, simpler models were fit to tease out the need for Genotype \times Density interactions or Site, Genotype or Density main effects, and compared to the full model using AICc. Goodness-of-fit measures root mean squared error (RMSE) were also estimated for each of the final models.

Estimation of leaf area index and light interception

The impact of density and genotype on light interception dynamics was assessed by estimating leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$) as the product of density (plants m^{-2}) and plant leaf area (PLA, $\text{m}^2 \text{plant}^{-1}$) obtained from fitted models. Using the estimated LAI, the fraction of the incident radiation intercepted by the leaves (FINT) was estimated using an exponential radiation-interception equation (Eq. 3) analogous to the Beer-Bouguer-Lambert Law (Sinclair, 2006; Thornley, 1976)

$$FINT = 1 - e^{-KPAR \times LAI} \quad (\text{Eq. 3})$$

where KPAR is the light extinction coefficient. While KPAR has been found to vary with LAI and Density (Flénet et al., 1996; Wells, 1991) and time of day (Tsubo et al., 2001), we used a single KPAR value of 0.70 for all calculations, which is in line to previously obtained values for the common bean (Tsubo et al., 2001).

Results

Node addition

Average main stem node number (MNN) exhibited a linear increase over cumulative temperature units (CTUs, Figure 1 and S1). Across sites and genotypes, lower plant densities (< 20 plants m⁻²) tended to exhibit higher variability in responses, particularly at later harvests. Model comparisons (Table 3) indicated that the intercept of the MNN to CTU relationship was affected by genotype, site, density and Site × Genotype, Density × Genotype interactions, with varying slopes for genotypes and densities across genotypes. While the effect of a Site × CTU could not be discarded (see Model 2, Table 3), we opted to use the simpler model for inference, since it also had equal RMSE=0.95. Observations from DAR were also more variable than those in PAL across genotypes and densities (Fig 1).

Phyllochron increased linearly with plant density at a rate of 0.26 °C plants⁻¹ m⁻². Together with the Genotype × CTU interaction, this resulted in phyllochron intervals that ranged from 51.3 °C node⁻¹ for genotype G 21212 at the 5 plants m⁻² density to 72.5°C node⁻¹ for CAL 96 at the 35 plants m⁻² density (Table 4). However, while there was enough power to detect small differences in phyllochron, the differences between densities amounted, at most, to half a day based on average daily temperature units (Table 1).

Leaf area expansion

Overall, model comparisons indicated that leaf area expansion, assessed via the allometric relationship between node number and leaf area was affected by Growth Habit, Site, Density and a Growth Habit \times Density interaction (Table 5). As with the addition of main stem nodes, observations at lower densities (< 20 plants m^{-2}) across genotypes and sites exhibited higher variability in responses than those at higher densities (> 20 plants m^{-2}) (Figures 2 and S2). Observations from DAR were also more variable than those in PAL across genotypes and densities.

In terms of the parameters, PLACON increased linearly with density at 0.40, 0.46 and 0.27 $\text{cm}^2 \text{plant}^{-1}$ for growth habits I, II and III, respectively (Table S2). On average, genotypes in Palmira had PLACON values 19.5 $\text{cm}^2 \text{plant}^{-1}$ lower. Together with the growth habit main effects, this leads to PLACON parameter values that ranged from 17.4 $\text{cm}^2 \text{plant}^{-1}$ (SE = 4.2) for growth habit II genotypes grown at 5 plants m^{-2} , to 57.8 $\text{cm}^2 \text{plant}^{-1}$ for growth habit I genotypes at the 35 plants m^{-2} densities (Table 6).

In contrast to the PLACON parameter, densities reduced PLAPOW estimates by 0.011, 0.009 and 0.007 per unit plant m^{-2} increase in density (Table S2). Across growth habits and densities, genotypes grown in Palmira tended to have PLAPOW values -0.074 lower. Combined with the growth habit main effects, PLAPOW estimates ranged from 1.40 for growth habit I at the 35 plants m^{-2} density in PAL to 1.79 (SE = 0.07) for growth habit I at the 5 plant m^{-2} density in DAR, respectively (Table 6).

Impacts on light interception

Given the previously described effects, the combined factors of node addition rate and leaf area expansion lead to markedly different leaf area indices (LAI) and light interception dynamics for each density \times genotype and site in the study. For instance, genotypes varied widely in the time they took to reach an LAI ~ 3 across densities and sites (Figure 3). For instance, the latest that

any genotype reached LAI ~ 3 was 69 DAS at the 5 plants m⁻² density (ICA Quimbaya at PAL), while at a density of 20 plants m⁻², genotypes reached LAI ~ 3 between 36 and 49 DAS. Consequently, the calculated fraction of intercepted light reached values reaching near unity occurred at differing times. For instance, genotypes CAL 96, DOR 364 and Carioca grown at the 5 plants m⁻² density reached FINT >0.95 at 13, 13 and 11 DAS later, respectively, than the 20 plants m⁻² treatment (Figure 4). However, when compared to the 35 plants m⁻² level, the 20 plant m⁻² reached FINT >0.95 between 1 DAS (SER 118 at DAR, data not shown) to 7 DAS (DOR 364 at PAL, Figure 4) later.

Discussion

This common bean study using genotypes from two gene pools and three contrasting growth habits was undertaken to explore the effects of plant density, genotypes and sites on the dynamics of main stem node addition and plant leaf area development, as well as their impacts on light interception. Analysis of the phyllochron indicated effects of genotype and density, but no genotype x density interactions. Across genotypes, phyllochron increased linearly with density, which is consistent with previous findings by Nienhuis and Singh (1995). These results indicated lower node numbers (and likely slower addition rates) may occur as a result of at higher plant densities used for indeterminate genotypes. Moreover, the phyllochron values obtained of 51.3 to 72.5 °C are consistent with previously reported values for diverse common bean genotypes, such as 2.9 to 4.0 days per leaf (or 55 to 73°C per node), for five indeterminate genotypes of growth habits II and III (Yourstone and Wallace, 1990), or 68.9 °C per node reported by Marrou et al. (2014). In practice the observed differences have little impact on leaf area development as illustrated by the two most contrasting genotype x density combinations in which phyllochron differed by ~ 21°C, which amounts to little more than one day at either site. Given the weekly harvest interval, it is likely that this difference is not biologically meaningful.

In terms of leaf area dynamics, the lowest densities ($< 15 \text{ plants m}^{-2}$) tended to have plants that developed larger leaf areas (up to 1.5 to 2x larger), particularly after 6-7 nodes. This finding coincides with previous studies in the common bean that up to 34% fewer leaves and 40-42% fewer branches per plant when sowing density was increased from ~ 13 to 40 plants m^{-2} across genotypes of growth habits I-III (Keuneman and Wallace, 1979). Similarly, Nienhuis and Singh (1985) also found a marked decrease of up to 50% in branches per plant and nodes per branch with increases in density from 5 to 30 plants m^{-2} across growth habits I-III. However, differences between usual planting densities ($> 20 \text{ plants m}^{-2}$) are small in our study, as predicted using estimated parameters (Table 6) from Equation 2.

In terms of the parameter estimates, given that the estimates of PLACON are, by definition, closely related to individual leaf size and the timing of the initial data collection, the larger values reported for genotypes of growth habit I coincides with previous findings in density trials reported by Keuneman and Wallace (1979) and Nienhuis and Singh (1985). PLAPOW values, on the other hand, showed more variation between densities within a given growth habit (up to $\sim 18\%$), and were negatively correlated with PLACON values, with an average correlation coefficient between comparable components of the parameter estimates > -0.90 (data not shown).

These differences in phyllochron and leaf area expansion dynamics translate to marked differences in leaf area index and light interception throughout the growing seasons. While Keuneman and Wallace (1976) found growth habit I genotypes tend to have $\sim 50\%$ of the LAI at flowering than either growth habit II-III genotypes, which tend to have similar LAI values at flowering. However, in our study, growth habit I genotypes had lower LAI (approximately 60%) than growth habit II-III genotypes only under lower densities ($< 20 \text{ plants m}^{-2}$), while at higher densities growth habits I and II had similar LAI (~ 4.7 to 5.1 , data not shown), both being lower than those of growth habit III genotypes (LAI ranging from 6.2 to 7.4 , data not shown). It is important to note that, while these differences appear important, they only appear meaningful at

the lower densities levels. For instance, the fraction of intercepted radiation at the lowest two densities at flowering in our study average 55% for growth habits I-II and ~64% for growth habit III, while at the two highest densities they average 90, 89 and 94%, for growth habits I-III, respectively.

In spite of the (small) differences between genotype x density levels in the analysis of phyllochron, and those detected at the growth habit levels for leaf expansion rates, care should be taken when assuming common patterns of all phonological traits within growth habits, since there is substantial variation within each growth habit set for many vegetative and reproductive traits (Nienhuis and Singh, 1985; Keuneman and Wallace, 1979).

Conclusions

The results of these analyses offer insights into two critical components of crop vegetative development, node addition rate and leaf area expansion, as affected by density, site and genotype effects. Overall, significant effects of genotype and density on the phyllochron were detected, although the magnitude of the differences appear small and likely not biologically meaningful. Stronger differences were observed between leaf area estimates obtained from the analysis of Equation 2, where larger individual plant areas were obtained at lower densities across growth habits. However, the differences between them appear insignificant at higher densities that are common plant densities ($> 20 \text{ plants m}^{-2}$). Overall, these differences in phyllochron and leaf area expansion translated to markedly different light interception capacities between canopies grown at low and high densities, across growth habits. However, all growth habits had reached close to 100% light interception at flowering time under the higher densities.

Acknowledgements

Funding from TLI project from BMGF through ICRISAT. Technical support from Martin Otero and Jarden Molina.

References

- Ball, R.A., L.C. Purcell, and E.D. Vories. 2000. Optimizing soybean plant population for a short-season production system in the southern USA. *Crop Sci.* 40:757-764.
- Barthou, H., and R. Buis. 1991. Kinetics of apical phyllogenesis of the main stem of soybean (*Glycine max* (L.) merr.): Effects of stand density. *Environ. Exp. Bot.* 31:59-66.
- Bell, M.J., R.C. Muchow, and G.L. Wilson. 1987. The effect of plant population on peanuts (*Arachis hypogaea*) in a monsoonal tropical environment. *Field Crops Res.* 17:91-107.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer Science & Business Media.
- Craufurd, P.Q., M. Subedi, and R.J. Summerfield. 1997. Leaf appearance in cowpea: Effects of temperature and photoperiod. *Crop Sci.* 37:167-171.
- Crothers, S., and D. Westermann. 1976. Plant population effects on the seed yield of *Phaseolus vulgaris* L. *Agron. J.* 68:958-960.
- Daniells, J., and G. Wilson. 1987. Effects of plant spacing on uniformity of pod maturity in french beans. *Scientia Horticulturae* 32:1-8.
- Debouck, D., R. Hidalgo H, F. Fernandez O, A. Correa E, and J. Smithson. 1986. Morphology of the common bean plant *Phaseolus vulgaris*.??????????????
- Doust, J.L. 1992. The influence of plant density on flower, fruit, and leaf demography in bush bean, *Pphaseolus vulgaris*. *Canadian Journal of Botany* 70:958-964.
- Flénet, F., J.R. Kiniry, J.E. Board, M.E. Westgate, and D.C. Reicosky. 1996. Row spacing effects on light extinction coefficients of corn, sorghum, soybean, and sunflower. *Agron. J.* 88:185-190.
- Hampton, J., F. Mesquita and M. Hill. 1997. The effect of genotype and plant density on grain yield and cooking quality in common bean (*Phaseolus vulgaris* L.). p. 109-114. *In Proceedings of the agronomy society of New Zealand*, 1997.

- Kueneman, E., and D. Wallace. 1979. Simplified growth analysis of non-climbing dry beans at three spacings in the tropics. *Exp. Agric.* 15:273-284.
- Lucas, E., and G. Milbourn. 1976. The effect of density of planting on the growth of two *Phaseolus vulgaris* varieties in England. *The Journal of Agricultural Science* 87:89-99.
- Marrou, H., T. Sinclair, and R. Metral. 2014. Assessment of irrigation scenarios to improve performances of lingot bean (*Phaseolus vulgaris*) in southwest France. *Eur. J. Agron.* 59:22-28.
- Mazerolle, M. 2011. AICcmodavg: Model selection and multimodel inference based on (Q) AIC (c). R Package Version 1:???
- Nienhuis, J., and S.P. Singh. 1985. Effects of location and plant density on yield and architectural traits in dry beans. *Crop Sci.* 25:579-584.
- Parvez, A., F. Gardner, and K. Boote. 1989. Determinate-and indeterminate-type soybean cultivar responses to pattern, density, and planting date. *Crop Sci.* 29:150-157.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2011. R development core team. 2010. nlme: Linear and nonlinear mixed effects models. R package version 3.1-97. R Foundation for Statistical Computing, Vienna.
- Pinheiro, J., and D. Bates. 2006. Mixed-effects models in S and S-PLUS. Springer Science & Business Media, .
- Purcell, L.C., R.A. Ball, J. Reaper, and E.D. Vories. 2002. Radiation use efficiency and biomass production in soybean at different plant population densities. *Crop Sci.* 42:172-177.
- Ranganathan, R., Y. Chauhan, D. Flower, M. Robertson, C. Sanetra, and S. Silim. 2001. Predicting growth and development of pigeonpea: Leaf area development. *Field Crops Res.* 69:163-172.
- Redden, R., T. Usher, D. Younger, R. Mayer, B. Hall, A. Fernandes, and D. Kirton. 1987. Response of navy beans to row width and plant population density in Queensland. *Animal Production Science* 27:455-463.

- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103-113.
- Sinclair, T.R. 2006. A reminder of the limitations in using Beer's law to estimate daily radiation interception by vegetation. *Crop Sci.* 46:2343-2347.
- Sinclair, T. 1984. Leaf area development in field-grown soybeans. *Agron. J.* 76:141-146.
- Soltani, A., and T. R. Sinclair. 2012. Modeling physiology of crop development, growth and yield. Publisher?
- Soltani, A., M.J. Robertson, Y. Mohammad-Nejad, and A. Rahemi-Karizaki. 2006. Modeling chickpea growth and development: Leaf production and senescence. *Field Crops Res.* 99:14-23.
- Team, R.C. 2015. R: A language and environment for statistical computing. vienna, austria; 2014. URL <http://www.R-Project.Org>.
- Thornley, J.H. 1976. Mathematical models in plant physiology. Academic Press (Inc.) London, Ltd.
- Tsubo, M., S. Walker, and E. Mukhala. 2001. Comparisons of radiation use efficiency of mono-/inter-cropping systems with different row orientations. *Field Crops Res.* 71:17-29.
- Turpin, J., M. Robertson, N. Hillcoat, and D. Herridge. 2002. Fababean (*Vicia faba*) in Australia's northern grains belt: Canopy development, biomass, and nitrogen accumulation and partitioning. *Crop and Pasture Science* 53:227-237.
- Wallace, D., and G. Enriquez. 1980. Daylength and temperature effects on days to flowering of early and late maturing beans (*Phaseolus vulgaris* L.). *Journal of American Society for Horticultural Science* 105:583-591.
- Wallace, D., P.A. Gniffke, P. Masaya, and R. Zobel. 1991. Photoperiod, temperature, and interaction effects on days and nodes required for flowering of bean. *J. Am. Soc. Hort. Sci.* 116:534-543.

- Wells, R. 1991. Soybean growth response to plant density: Relationships among canopy photosynthesis, leaf area, and light interception. *Crop Sci.* 31:755-761.
- Xu, C., and F.J. Pierce. 1998. Dry bean and soil response to tillage and row spacing. *Agron. J.* 90:393-399.
- Yan, W., and L. Hunt. 1999. An equation for modelling the temperature response of plants using only the cardinal temperatures. *Annals of Botany* 84:607-614.
- Yourstone, K., and D. Wallace. 1990. Application of plastochron index to common bean grown in controlled environments. *J. Am. Soc. Hort. Sci.* 115:820-823.
- Zuur, A., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media, .

Table 1. Average minimum and maximum temperatures (standard deviation), daily temperature units and solar radiation at the Darien and Palmira, Colombia, study sites.

Site	Temperature		DTU	Solar Radiation
	Min (°C)	Max (°C)	(°C)	(MJ m ⁻² day ⁻¹)
DAR	16.6 (0.92)	25.5 (1.2)	12.5 (0.6)	18.6 (3.1)
PAL	19.1 (0.93)	31.1 (1.9)	14.6 (0.4)	14.2 (3.2)

Table 2. 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 3. Model selection table for average main stem number over time, including the three best models within those tested.

No.	Model Form	K	AICc	Δ AICc	wAICc	LL	RMSE
1	Site \times Genotype + Density \times Genotype + Genotype \times CTU + Density \times CTU	31	3052.4	0	0.68	-1494.4	0.95
2	Site \times Genotype + Density \times Genotype + Genotype \times CTU + Density \times CTU + Site \times CTU	32	3053.9	1.49	0.32	-1494.1	0.95
3	Site \times Density \times Genotype \times CTU	54	3069.9	17.44	0	-1478.3	0.92

Table 4. Estimated phyllochron (temperature units of °C per leaf appearance, SE) for six common bean genotypes grown under six sowing densities in combining data from experiments conducted in Palmira and Darien, Colombia.

Genotype	Sowing Density (plants m ⁻²)					
	5	10	15	20	25	35
CAL 96 (I)	62.9 (6.9)	64.3 (6.9)	65.8 (6.9)	67.4 (6.9)	69.0 (6.9)	72.5 (6.9)
ICA Quimbaya (I)	59.1 (5.4)	60.4 (5.4)	61.7 (5.4)	63.0 (5.4)	64.5 (5.4)	67.5 (5.4)
DOR 364 (II)	57.4 (5.6)	58.6 (5.6)	59.8 (5.6)	61.1 (5.6)	62.4 (5.6)	65.3 (5.6)
SER 118 (II)	52.3 (5.7)	53.3 (5.7)	54.3 (5.7)	55.4 (5.7)	56.5 (5.7)	58.8 (5.7)
Carioca (III)	55.4 (5.9)	56.5 (5.9)	57.7 (5.9)	58.9 (5.9)	60.1 (5.9)	62.7 (5.9)
G 21212 (III)	51.3 (5.6)	52.3 (5.6)	53.2 (5.6)	54.2 (5.6)	55.3 (5.6)	57.5 (5.6)

Table 5. Model selection table for the plant leaf area vs. main stem node number relationship.

Model	Model Form	K	AICc	Δ AICc	wAICc	LL	RMSE
1	Growth habit \times Density + Site	20	-8886	0	0.88	4463.3	0.29
2	Genotype \times Density + Site	32	-8881	4.46	0.10	4473.5	0.29
3	Genotype + Trt + Site	16	-8878	7.50	0.02	4455.4	0.29

Table 6. Estimated parameters for the allometric relationship between node number and leaf area (cm²) for six common bean genotypes grown under six sowing densities in experiments conducted in Palmira and Darien, Colombia.

Parameter	Site	GH	Sowing Density (plants m ⁻²)					
			5	10	15	20	25	35
PLACON	DAR	I	46.8 (4.8)	48.6 (4.8)	50.4 (4.8)	52.3 (4.8)	54.1 (4.8)	57.8 (4.8)
		II	36.9 (4.2)	39.0 (4.2)	41.2 (4.2)	43.3 (4.2)	45.5 (4.2)	49.7 (4.2)
		III	43.8 (4.3)	45.0 (4.3)	46.2 (4.3)	47.4 (4.3)	48.5 (4.3)	50.9 (4.3)
	PAL	I	27.3 (4.8)	29.1 (4.8)	31.0 (4.8)	32.8 (4.8)	34.6 (4.8)	38.3 (4.8)
		II	17.4 (4.2)	19.6 (4.2)	21.7 (4.2)	23.9 (4.2)	26.0 (4.2)	30.2 (4.2)
		III	24.4 (4.3)	25.5 (4.3)	26.7 (4.3)	27.9 (4.3)	29.1 (4.3)	31.4 (4.3)
PLAPOW	DAR	I	1.79 (0.07)	1.74 (0.07)	1.69 (0.07)	1.63 (0.07)	1.58 (0.07)	1.48 (0.07)
		II	1.73 (0.07)	1.69 (0.07)	1.65 (0.07)	1.61 (0.07)	1.56 (0.07)	1.48 (0.07)
		III	1.74 (0.07)	1.7 (0.07)	1.67 (0.07)	1.64 (0.07)	1.61 (0.07)	1.54 (0.07)
	PAL	I	1.72 (0.07)	1.67 (0.07)	1.61 (0.07)	1.56 (0.07)	1.51 (0.07)	1.40 (0.07)
		II	1.66 (0.07)	1.62 (0.07)	1.57 (0.07)	1.53 (0.07)	1.49 (0.07)	1.40 (0.07)
		III	1.66 (0.07)	1.63 (0.07)	1.60 (0.07)	1.57 (0.07)	1.53 (0.07)	1.47 (0.07)

Figure 1. Average node number over time plotted versus cumulative temperature units for three common bean genotypes grown at 5, 20 and 35 plants m⁻². Symbols represent observed values, while lines represent predicted values from the best linear regression model.

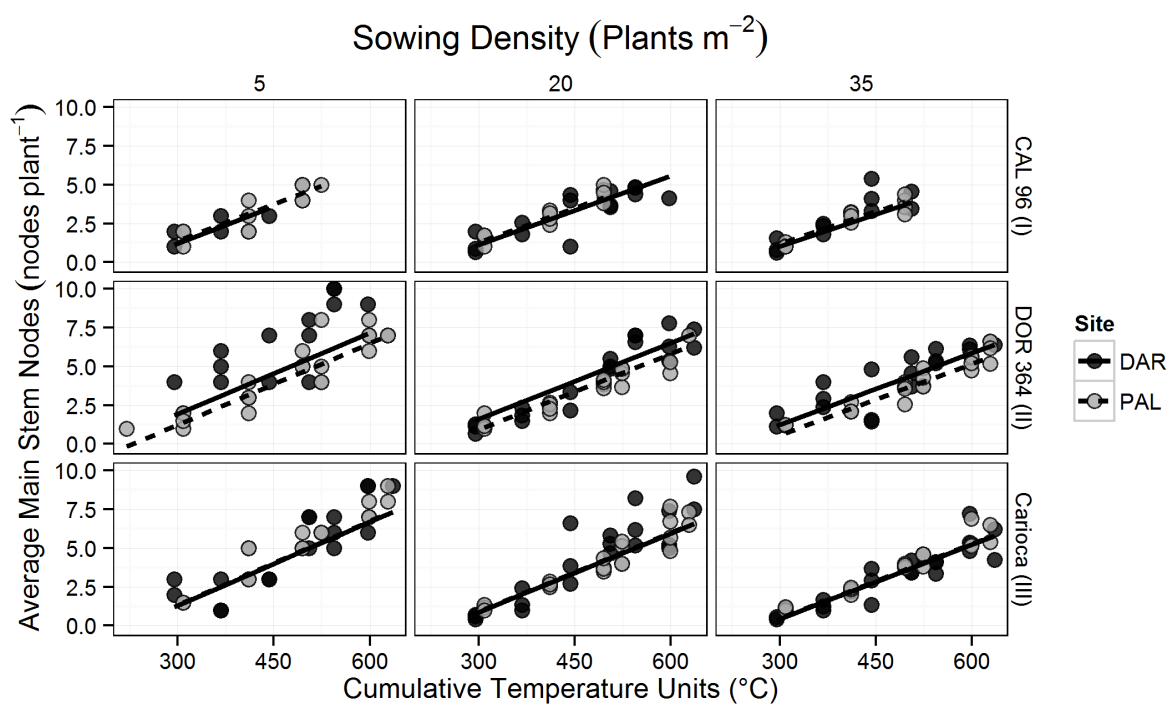


Figure 2. Plant leaf area as a function of node number for three common bean genotypes grown at 5, 20 and 35 plants m^{-2} . Symbols represent observed values, while lines represent predicted values from the best model.

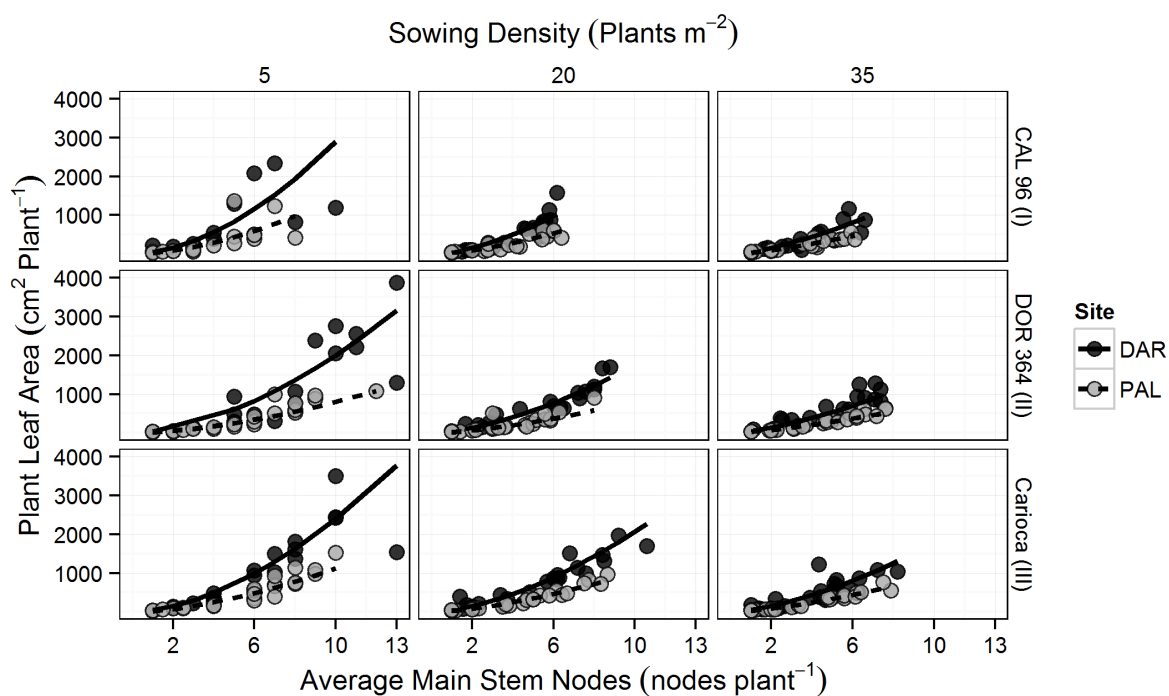


Figure 3. Leaf area index over time for three common bean genotypes grown at 5, 20 and 35 plants m^{-2} . Symbols represent observed values, while lines represent predicted values from the best model.

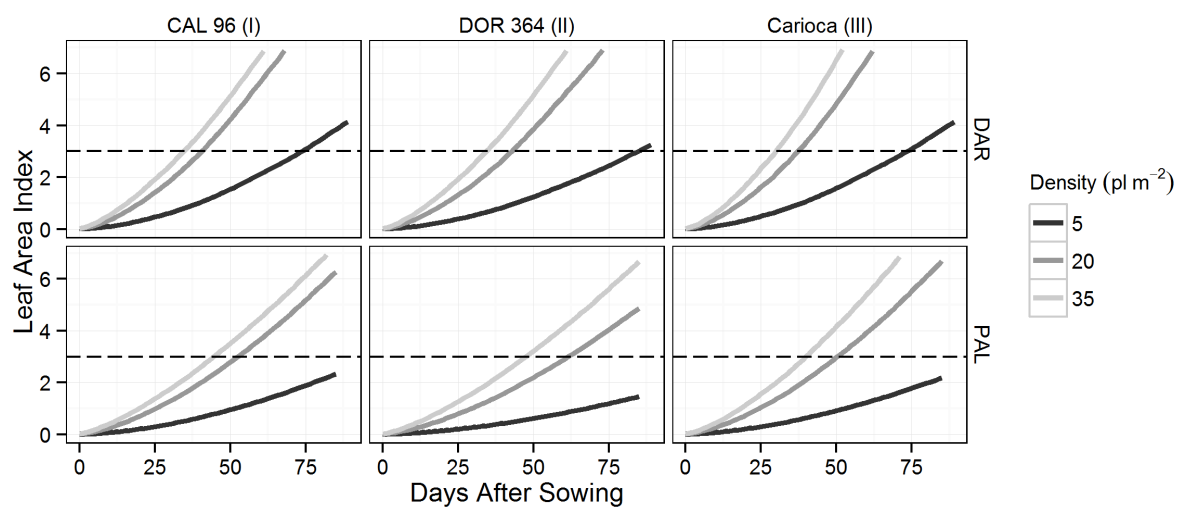
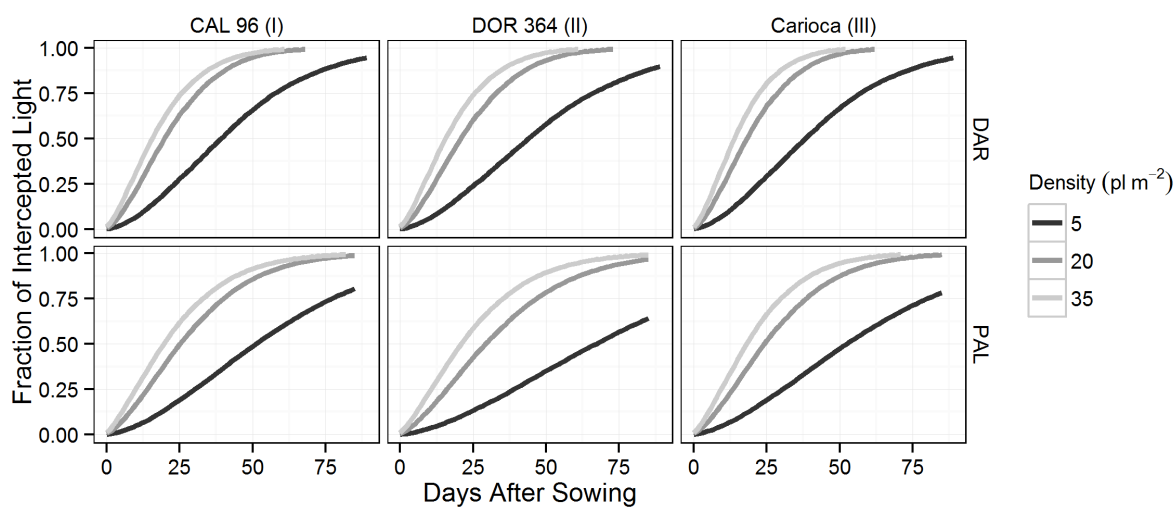


Figure 4. Fraction of intercepted light over time for three common bean genotypes grown at 5, 20 and 35 plants m^{-2} . Symbols represent observed values, while lines represent predicted values from the best model.



Supplemental figures and tables

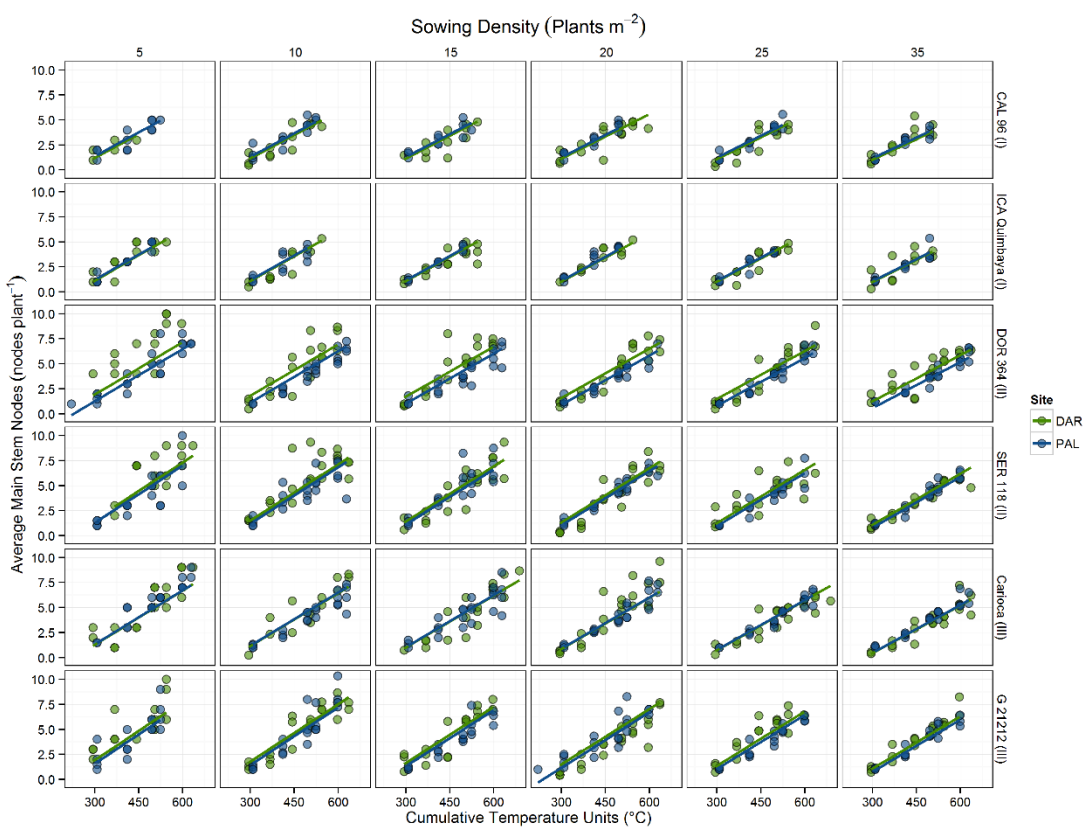


Figure 5. Average main stem nodes (nodes plant⁻¹) as a function of accumulated temperature units (°C) for six common bean genotypes (plot rows) grown under six sowing densities (plot columns) in Palmira (blue symbols/lines) and Darien (green symbols/lines), Colombia. Lines represent predicted value from selected model in table 1.

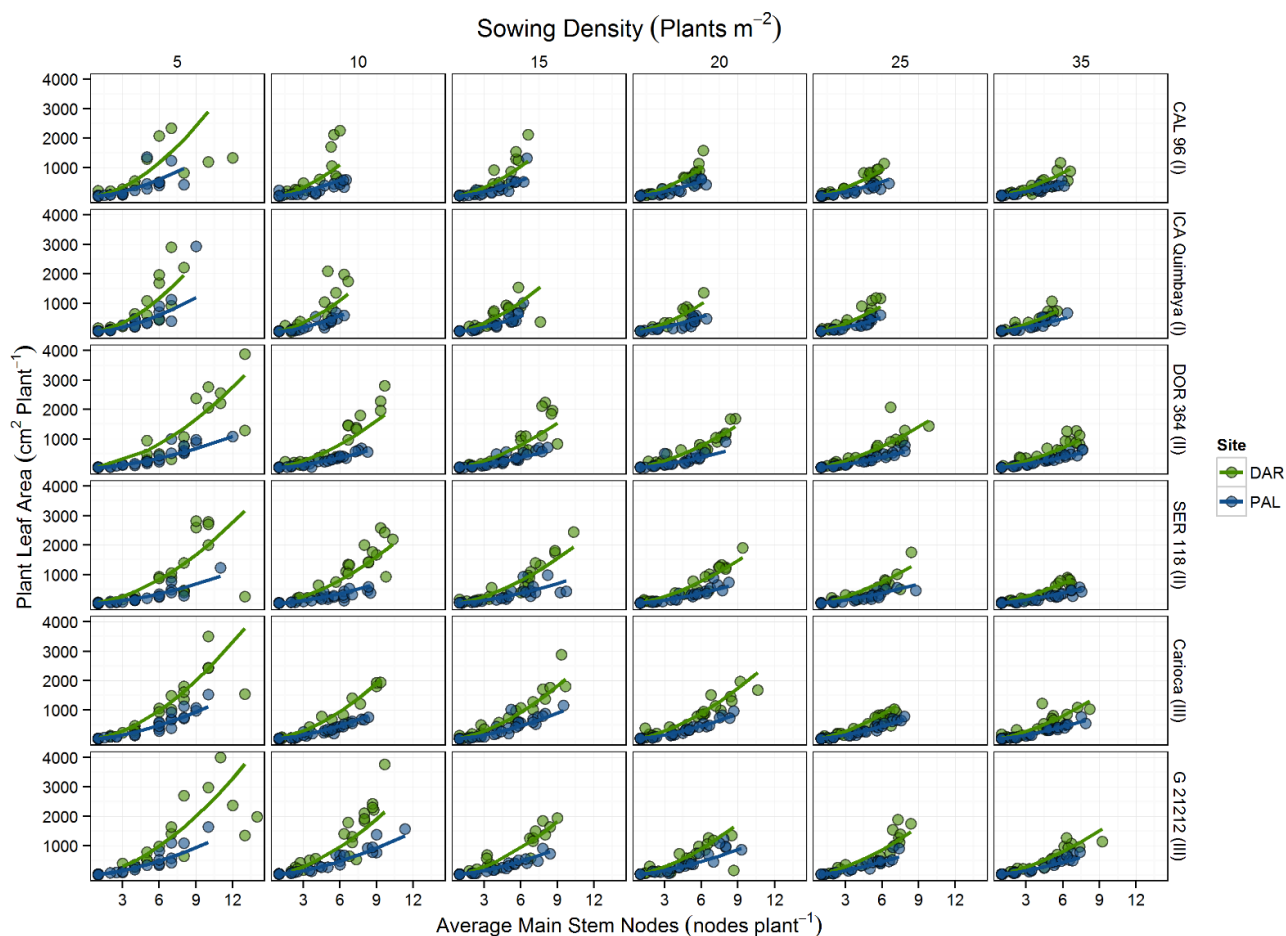


Figure 6. Plant leaf area ($\text{cm}^2 \text{ plant}^{-1}$) as a function of accumulated temperature units ($^{\circ}\text{C}$) for six common bean genotypes (plot rows) grown under six sowing densities (plot columns) in Palmira (blue symbols/lines) and Darien (green symbols/lines), Colombia. Lines represent predicted value from selected model in table 1.

Table 3. Fixed-effects of the selected mixed-effects model for the average number of main stem nodes from six genotypes of the common bean grown under six densities in Darien (DAR) and Palmira (PAL), Colombia.

Parameter	Value	SE	DF	t-value	p-value
(Intercept)	3.43265	0.14401	1130	23.84	0.00
SitePAL	0.16494	0.15276	5	1.08	0.33
Genotype Carioca	-0.02153	0.16993	1130	-0.13	0.90
Genotype DOR 364	0.63869	0.17712	1130	3.61	0.00
Genotype G 21212	0.85907	0.17852	1130	4.81	0.00
Genotype ICA Quimbaya	0.09643	0.18673	1130	0.52	0.61
Genotype SER 118	0.68560	0.17520	1130	3.91	0.00
Density.c	-0.01724	0.00794	34	-2.17	0.04
CTU.c	0.01449	0.00075	1130	19.42	0.00
SitePAL:Genotype Carioca	-0.12585	0.18506	1130	-0.68	0.50
SitePAL:Genotype DOR 364	-0.84970	0.18947	1130	-4.48	0.00
SitePAL:Genotype G 21212	-0.50064	0.18689	1130	-2.68	0.01
SitePAL:Genotype ICA Quimbaya	-0.07509	0.19022	1130	-0.39	0.69
SitePAL:Genotype SER 118	-0.46856	0.18563	1130	-2.52	0.01
Genotype Carioca:Density.c	-0.02217	0.00917	1130	-2.42	0.02
Genotype DOR 364:Density.c	-0.01652	0.00923	1130	-1.79	0.07
Genotype G 21212:Density.c	-0.02147	0.00913	1130	-2.35	0.02
Genotype ICA Quimbaya:Density.c	0.00142	0.00942	1130	0.15	0.88
Genotype SER 118:Density.c	-0.01048	0.00906	1130	-1.16	0.25
Genotype Carioca:CTUby2.c	0.00215	0.00091	1130	2.36	0.02
Genotype DOR 364:CTUby2.c	0.00153	0.00090	1130	1.69	0.09
Genotype G 21212:CTUby2.c	0.00360	0.00096	1130	3.76	0.00
Genotype ICA Quimbaya:CTUby2.c	0.00102	0.00106	1130	0.96	0.34

Genotype SER 118:CTUby2.c	0.00321	0.00094	1130	3.41	0.00
Density.c:CTUby2.c	-0.00007	0.00002	1130	-2.98	0.00

Table 4. Effects of the selected nonlinear regression model for the leaf area and average main stem node number power function fit to six genotypes of the common bean grown under six densities in Darien (DAR) and Palmira (PAL), Colombia.

Parameter	Effect	Value	SE	t-value	P-value
PLACON	(Intercept)	54.1	3.7	14.55	0.00
	Growth.Habit Type II	-8.6	3.0	-2.91	0.00
	Growth.Habit Type III	-5.6	3.1	-1.81	0.07
	Density.c	0.4	0.2	1.95	0.05
	SitePAL	-19.5	3.2	-6.08	0.00
	Growth.Habit Type II:Density.c	0.1	0.2	0.27	0.79
	Growth.Habit Type III:Density.c	-0.1	0.2	-0.54	0.59
PLAPOW	(Intercept)	1.582	0.054	29.25	0.00
	Growth.Habit Type II	-0.020	0.054	-0.37	0.71
	Growth.Habit Type III	0.025	0.054	0.47	0.64
	Density.c	-0.011	0.003	-3.07	0.00
	Site PAL	-0.074	0.047	-1.58	0.11
	Growth.Habit Type II:Density.c	0.002	0.004	0.45	0.65
	Growth.Habit Type III:Density.c	0.004	0.004	0.91	0.37