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Determination of plant traits that affect genotype × location (G×L) interaction in peanut using the CSM-CROPGRO-Peanut model

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Abstract

Genotype × environment (G×E) interaction complicates the identification of superior genotypes. An understanding its causes is needed for a more effective breeding strategy. The objective of this study was to determine the plant traits that cause genotype × location (G×L) interaction for pod yield in peanut using a modeling approach. The CSM-CROPGRO-Peanut model was used to simulate pod yield for 17 peanut genotypes for 14 locations representative of all peanut production areas in Thailand using 30 years of historical weather data. Sensitivity analysis was used to determine the effects of individual and combinations of plant traits on pod yield and yield response to environments by varying the value of one or more cultivar coefficients and then evaluating their effects. The results showed that the cultivar coefficients that showed major effects were the duration from first seed to physiological maturity (SDPM), maximum leaf photosynthesis rate (LFMAX), the maximum fraction of daily growth that is partitioned to seed and shell (XFRT), single seed filling duration (SFDUR) and the duration of pod addition (PODUR). Those having minor effects were the duration from emergence to first flower (EMFL), maximum leaf size (SIZLF) and maximum seed weight (WTPSD). The cultivar coefficients that caused the differences in both mean yield and yield response to locations between peanut genotypes in different pairs included LFMAX, XFRT, SDPM, SFDUR and PODUR, but the causal characters differed among pairs of genotypes. It was concluded that changing the degree of genotypic response to environments is possible through selection for a combination of some of these traits, and that model simulation could be used to identify those traits.

Keywords: G×E interaction; Cultivar adaptation; Yield stability; Crop model; Sensitivity analysis.

Introduction

Yield is generally the primary goal for the selection of superior genotypes in a plant breeding program. Crop yield has a high genotype × environment (G×E) interaction because it is an outcome of a complex integration of many growth and development processes. This makes the identification of superior genotypes difficult as the ranking for yield performance of the test genotypes may change for different environments (Allard and Bradshaw, 1964; Fehr, 1987; Kang, 1990; Cooper and Hammer, 1996; Kang, 2002). In general, G×E interaction is considered an obstacle to crop improvement (Kang, 1990). However, it could be considered as a reflection of the differences in genotypic adaptation, which might be exploited by selection and/or by adjustment of the testing strategy (Basford et al., 1996). A better understanding of the nature of the G×E interaction is needed to be able to use it effectively through appropriate breeding methodologies (Basford and Cooper, 1988). Knowledge of the physiological basis for the differential responses of genotypes to specific environments should improve the efficiency with which a breeder can characterize material for its G and G×E interaction and, hence, increase the speed at which superior genotypes can be identified (Wright et al., 1996). Information on plant traits that cause the G×E interaction for crop yield should lead to a more effective selection for improved genotypic adaptation to the target environment.

Several studies have been conducted to elucidate the causes of G×E interaction for crop yield based on analyzing yield trial data with various statistical methods, e.g., incorporating several covariates into a mixed model (Frensham et al., 1998), partial least squares regression (PLSR) (Vargas et al., 1998), factor regression analysis (Signor et al., 2001), site regression model (SREG) (Yan and Hunt, 2001) and the additive main effects and multiplicative interaction model (AMMI) (Motzo et al., 2001). These statistical models generally partition crop yield into the "statistical" components relating to genotype (G), environment (E) and G×E interaction. While these statistical models have yielded useful information, they can not elucidate the direct effect of each plant trait or each combination of traits on the G×E interaction for crop yield.

Separating yield into its components, such as number and weight of kernels or biomass and harvest index is one approach that can help with the interpretation of G×E interaction (Cooper et al., 1996). However, these

components are still the end product of a crop and they individually can not explain the processes that contribute to yield. Simple physiological models have also been used for analyzing multi-environment trial (MET) data. For example, Williams (1992) used the parameters of crop growth rate, partitioning and phenology for interpretation of yield data from METs of peanut genotypes. Wright et al. (1996) modeled yield as a function of amount of water transpired (T), transpiration efficiency (TE) and harvest index (HI). Its analog form in which yield was expressed as a function of intercepted radiation (R_i), radiation use efficiency (RUE) and HI has also been used (Bidinger et al., 1996). Although these approaches have contributed to a better understanding of the physiological basis of the G×E interaction, they too did not provide information on the effects of individual plant traits or each combination of traits on the G×E interaction for final crop yield.

Crop simulation models are one set of tools that have been used to answer complex questions related to crop production, economics and environmental impact (Tsuji et al., 1998; Hoogenboom, 2000; Jones et al., 2003). These models have also been used to study different aspects of G×E interaction (White and Hoogenboom, 1996; White and Hoogenboom, 2003; Chapman et al., 2002; Chapman et al., 2003; Messina et al., 2006; Phakamas et al., 2008; Phakamas et al., 2010). As these models can simulate yield of cultivars for different environments and agronomic practices (White et al., 1995; Boote et al., 1998; Chapman et al., 2002), they provide an opportunity to be used as a tool to help understand the direct effect of each plant trait or a combination of traits on the G×E interaction for crop yield.

The Cropping System Model (CSM)-CROPGRO-Peanut is a process-oriented model that is part of the Decision Support System for Agrotechnology Transfer (DSSAT) (Boote et al., 1998; Jones et al., 2003; Hoogenboom et al., 2004a). The model has been evaluated extensively in Thailand, particularly for assisting with multi-environment evaluation of peanut breeding lines (Banterng et al., 2006; Suriharn et al., 2008; Anothai et al., 2009), for determining the mega-environment for peanut breeding (Putto et al., 2008), for studying the dynamics of G×E interaction (Phakamas et al., 2008) and for designing a peanut ideotype for a target environment (Suriharn et al., 2011). Its design is a modular structure in which the model components separate along scientific discipline lines and are structured to allow replacement or addition of modules (Jones et al., 2003). A crop template is a module for crop processes that is defined and constructed based on the common processes of different crops. Species and cultivar input files in the crop template module contain information for

growth and development of individual species and genotypes. These files allow a user to modify values of parameters of the individual species and genotypes. By modifying the values of the cultivar coefficients in these files, many crop genotypes can be simulated with the same program source code under the main model. This feature of the model can be used as a tool in studying G×E interaction, particularly in determining the causal plant traits. The genotype × location (G×L) interaction is of special interest as it is the part of G×E interaction which is repeatable and is related to local adaptation of crop genotypes (Annicchiarico, 2002). Lately, there has been increasing interest to breed crop cultivars for specific areas to take advantage of local adaptation. Information on traits that affect G×L interaction would be useful to this breeding strategy. The objective of this study was to determine the plant traits that cause the G×L interaction for yield in peanut using the CSM-CROPGRO-Peanut model.

Materials and Methods

The approach used in this study consisted of (1) determining the yield performance and yield response to locations of the individual peanut genotypes as well as patterns of G×L interaction among peanut genotypes, (2) sensitivity analysis of cultivar coefficients for mean performance and yield response to locations utilizing the CSM-CROPGRO-Peanut model and (3) conducting sensitivity analyses for selected pairs of genotypes with different patterns of G×L interaction to determine the causal plant traits.

Determination of yield response to location and patterns of G×L interaction

This study is based on simulated pod yields for 17 peanut lines from 112 locations and three growing seasons, i.e., early-rainy, mid-rainy and dry seasons and 30 years similar to the studies conducted by Phakamas et al. (2008) and Putto et al. (2008). The procedures for generating this data set has been described in detail in these two papers (Phakamas et al., 2008; Putto et al., 2008) and are briefly presented here.

The 112 locations cover all peanut production areas in Thailand. They were identified by selecting districts with a considerable peanut acreage based on the crop production statistic of the Department of Agricultural Extension for the 2002-2003 cropping-year. A total of 43 districts in 24 provinces were identified. Questionnaires were sent to the district extension agents requesting information on the main peanut production villages in

their districts, the growing seasons and the range of planting dates in each season, the local soil characteristics and the irrigation practices. Once the production villages were identified, the soil types for the individual villages were determined from the soil map of the Department of Land Development. Twenty four weather stations that were located in or adjacent to the individual growing areas were also identified. The basic units for model simulation, designated as locations, were then determined by overlaying the area of influence of each weather station as determined by Thiessen polygons onto the soil series map, resulting in unique 112 locations. The 17 peanut lines used were breeding lines and released cultivars selected to provide diversity in yield level, seed size, plant type and maturity duration (Table 1).

Table 1. Peanut breeding lines and cultivars used in this study and sources of their respective cultivar coefficients.

Line No.	Line/cultivar	Seed type	Maturity duration	Source of cultivar coefficients
1	KK 5	Small-seeded	Early	Suriharn et al. (2007)
2	(Chico×GA 119-20) 8-3-12	Small-seeded	Early	Sujariya (2004)
3	KKU 1	Small-seeded	Medium	Suriharn et al. (2007)
4	(KK 60-3×(MGS9×Chico)-12-16-1)26-5-33	Small-seeded	Medium	Banterng et al. (2004)
5	(KK60-3 × (Ah 65 × NC Ac 17090))-3-11-7	Small-seeded	Medium	Banterng et al. (2004)
6	(KK 4 × NC8C)-33-6-21	Small-seeded	Early	Banterng et al. (2004)
7	A progeny of Tainan 9 × Moket	Small-seeded	Medium	Banterng et al. (2004)
8	(Luhua 11×KK60-3) F6-22	Large-seeded	Early	Suriharn et al. (2007)
9	(Luhua 11 × China 97-2) F6-11-3	Large-seeded	Early	Suriharn et al. (2007)
10	((Nc Ac 17090 × B1)-25 × Luhua 11) F5-14-2	Large-seeded	Medium	Suriharn et al. (2007)
11	(China 97-2 × Singburi) F6-13-1	Large-seeded	Medium	Suriharn et al. (2007)
12	((Nc Ac 17090 × B1)-25 × KK60-3) F6-2-2	Large-seeded	Medium	Suriharn et al. (2007)
13	((Nc Ac 17090 × B1)-25 × China 97-2) F5-11-2	Large-seeded	Late	Suriharn et al. (2007)
14	KKU 72-1	Large-seeded	Late	Suriharn et al. (2007)
15	KK 60-3	Large-seeded	Late	Suriharn et al. (2007)
16	(China 97-2×KK 60-3) F6-9-1	Large-seeded	Late	Anothai et al. (2008)
17	KKFC 4008-5	Large-seeded	Late	Anothai et al. (2008)

The CSM-CROPGRO-Peanut Model was used to simulate pod yield of the 17 peanut genotypes for the 112 locations. For each location, peanut yield was simulated for three growing seasons, i.e., early-rainy, mid-rainy and dry seasons and 30 years. The inputs required for model simulation included local weather and soil data, crop management practices and cultivar coefficients (Tsuji et al., 1994). The required soil characteristics of each soil type that included bulk density, percentage of sand, silt and clay, initial soil moisture, organic matter, pH, nitrate (NO_3^-) and (NH_4^+) concentrations and exchangeable P and K were obtained from the database of the Department of Land Development. Thirty years of historical data for daily maximum and minimum temperatures (^{o}C) and daily rainfall (mm) from 1972 to 2002 for the 24 weather stations were obtained from the Department of Meteorology. Daily solar radiation (MJ m^{-2} d^{-1}) was estimated based on the relationship between daily maximum and minimum temperature and solar radiation (Jintrawet et al., 2002). Crop management data for row spacing and plant population followed the standard procedure of the peanut yield trials, while the planting dates for each location were obtained from the questionnaires. The cultivar coefficients of the 17 peanut lines (Table 2) were obtained from previous studies of Banterng et al. (2004), Sujariya (2004), Suriharn et al. (2007) and Anothai et al. (2008). These cultivar coefficients have been validated with independent data in the respective studies and were found to generate simulated phenology, growth and yield of the peanut lines that agreed well with the corresponding observed values. For the model simulation, rainfed conditions were used for the early-rainy and the mid-rainy seasons and full irrigation was used for the dry season, utilizing the automatic planting feature of the model.

In the present study, the locations used were a sub-set of the 112 locations in order to be convenient for sensitivity analyses. They were derived by grouping the 112 locations based on their similarity in G×L interaction and then selecting a representative location from each group. Location grouping was performed with cluster analysis (Collaku et al., 2002) using the SAS Proc CLUSTER and TREE (SAS Institute, 1996). Ward's minimum variance method (Ward, 1963) was used in performing hierarchical cluster analysis, which was truncated at 14 groups for which over 99% of the total G×L interaction could be accounted for by the G×L-group interaction. A representative location was selected from each group to constitute a reduced set of 14 locations that was used for further analysis in this study. As in all groups, there were several locations that had a mean

yield that was close to the mean of their respective group. Therefore, selection of the representative locations was done in such a way that each selected location had a mean close to the mean of its group and that the 14 representative locations also had different soil types and were distributed in different geographical regions. The resulting 14 locations and their descriptions are listed in Table 3. Location, as used in this paper, includes not just the soil traits, but also the long-term climatology of a location to include temperature, rainfall and solar radiation effects.

The response of the peanut genotypes to different locations was determined with a conventional linear regression model (Eberhart and Russell, 1966):

$$Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$$

Where;

Y_{ij} = mean yield of the ith genotype at the jth location,

μ_i = mean yield of the ith genotype over all locations,

β_i = regression coefficient that measures the response of the ith genotype to varying performance of the test locations,

I_j = environmental index of the jth location expressed as a mean over all genotypes at the jth location reduced by a grand mean,

δ_{ij} = deviation from regression of the ith genotype at the jth location.

In general, multivariate techniques are thought to be more effective in explaining G×E interactions than linear regression models (Lin et al., 1986; Zobel et al., 1988; Nachit et al., 1992) and other methods for analyzing MET data are more popular, especially, the Additive Main Effects and Multiplicative Interaction (AMMI) and the genotype main effects and genotype × environment interaction biplot (GGE biplot) (Gauch, 2006; Yan et al., 2007). However, in the present study, the linear regression model was selected because it gives the responses of the test genotypes to locations and thus allows for the identification of patterns of G×L interaction which are needed for sensitivity analysis to determine the causal traits. Furthermore, our preliminary analysis showed that the relationships between the means of the individual genotypes at different sites with site mean yields were essentially linear.

Table 2. The cultivar coefficients of the individual peanut breeding lines and cultivars used in this study.

Entry[†] no.	Phenology-related coefficient[‡]					Growth-related coefficient[‡]							
	EMFL	FLSH	FLSD	SDPM	FLLF	LFMAX	SLAVR	SIZLF	XFRT	WTPSD	SDPDV	SFDUR	PODUR
	(Photothermal day, PD)					(mg CO_2 m^{-2} s^{-1})	(cm^2 g^{-1})	(cm^2)	fraction	(g)	(no. pod^{-1})	PD	PD
1	20.0	7.5	19.0	48.50	70.00	1.40	264	38.0	0.78	0.580	1.82	28.0	19.0
2	19.6	7.0	17.5	44.00	57.00	1.10	265	18.0	0.87	0.540	1.78	28.0	17.0
3	21.6	7.9	17.5	50.16	75.00	1.28	270	39.0	0.89	0.680	1.83	29.0	21.0
4	20.5	12.0	23.0	46.50	61.50	1.15	290	68.5	0.90	0.723	1.31	26.5	23.0
5	22.5	14.5	25.5	48.00	59.50	0.95	285	43.4	0.91	0.946	1.46	29.5	21.5
6	21.5	9.0	24.5	42.00	57.00	0.87	265	60.1	0.87	0.639	1.61	28.0	19.0
7	19.5	10.5	28.5	43.00	50.00	0.95	280	65.8	0.83	0.743	1.61	27.0	22.0
8	18.0	7.0	17.5	52.00	75.00	1.34	258	32.0	0.94	1.070	1.65	42.0	23.0
9	20.5	7.0	18.0	48.50	77.00	1.43	266	26.0	0.80	0.990	1.75	42.0	15.0
10	21.5	7.1	17.6	55.00	76.00	1.24	265	25.0	0.93	1.150	1.76	39.0	27.0
11	22.0	7.0	17.5	54.00	80.00	1.44	260	25.0	0.94	0.950	1.72	39.0	21.0
12	21.0	9.0	20.0	56.50	75.00	1.38	280	28.0	0.94	0.910	1.63	37.0	27.0
13	21.5	7.1	16.6	60.80	76.00	1.37	278	23.0	0.94	0.700	1.75	34.0	20.0
14	21.5	7.1	18.5	61.70	75.00	1.42	270	27.0	0.91	0.770	1.80	34.0	24.0
15	21.8	7.0	17.5	62.00	80.00	1.43	260	25.0	0.94	0.820	1.75	37.0	30.0
16	23.0	8.2	20.1	63.00	71.00	1.29	272	20.0	0.96	0.830	1.68	37.0	31.0
17	22.0	8.3	20.5	61.00	88.00	1.54	283	20.0	0.94	1.150	1.75	41.0	28.0
Range	18.0-23.0	7.0-14.5	17.5-28.5	42.00-63.00	50.00-88.00	0.87-1.54	258-290	18.0-68.5	0.78-0.96	0.540-1.150	1.31-1.83	26.5-42.0	15.0-31.0

[†] See Table 1 for entry description.
[‡] See Table 4 for cultivar coefficient description.

Table 3. Locations used in the present study and their description for soil and weather conditions.

Location no.	Province	District	Soil series	Great soil group	Soil texture	Plant extractable soil water (cm³ cm⁻³)	TAVG (°C)	SRAD (MJ m⁻² d⁻¹)	Rainfall (mm)
1	Phayao	Chiang muan	Ly, Lat Ya	Haplustults	Loam	0.10	26.7	17.4	649
2	Chaiyaphum	Chaiyaphum	Rn, Renu	Paleaquults	Silty loam	0.12	28.1	17.8	433
3	Udonthani	Kut chap	Kt, Korat	Kandiustults	Sandy loam	0.12	27.8	16.8	615
4	Nakhon Sawan	Krok phra	Sp, San Pa Tong	Paleustults	Loamy sand	0.12	29.1	18.4	421
5	Phare	Long	Li, Li	Haplustalfs	Silty clay	0.10	27.8	18.0	446
6	Phare	Long	Tp, That Phanom	Haplustalfs	Silty loam	0.13	26.8	17.1	651
7	Tak	Mae sot	Tk, Takli	Haplustolls	Silty clay loam	0.06	28.1	17.8	433
8	Lampang	Mae tha	Ty, Tha Yang	Haplustults	Loam	0.09	27.8	18.6	437
9	Roi et	Nong phok	Kyo, Khao Yai	Endoaqualfs	Clay loam	0.12	27.6	16.7	670
10	Roi et	Nong phok	Lk, Lom Kao	Paleustults	Sandy loam	0.12	27.6	16.7	669
11	Nan	Pua	Bg, Ban Chong	Paleustults	Clay loam	0.11	26.7	17.4	650
12	Chantaburi	Tha mai	Cp, Chumporn	Paleudults	Sandy loam	0.06	27.8	14.9	1.170
13	Uttaradit	Uttaradit	Ch, Chiang Khan	Kandiustults	Clay loam	0.04	28.5	18.4	571
14	Lampang	Wang nua	Hc, Hang Chat	Kandiustults	Sandy loam	0.11	26.0	17.6	792

† TAVG, SRAD, Rainfall=average daily temperature, average daily solar radiation and average rainfall, respectively, during the cropping period over the early-rainy, mid-rainy and dry seasons for 30 years (1972-2002).

The means for simulated pod yield of the 17 peanut lines over three seasons and 30 years were calculated for each of the 14 locations and for all locations (genotype mean yield), as well as the means over all genotypes, seasons and years for the individual locations (location mean yield). The genotype mean yields were used to indicate the mean performance of the individual genotypes. The yield response to locations of each peanut genotype was determined by regressing mean yield of the genotype for the individual locations against the location mean yield. The regression coefficient (b) value was used as an index to indicate the response of a genotype to different locations. Pairs of genotypes with different patterns of G×L interaction were identified by comparing the means and the b values of the individual genotypes. A pair of genotypes with the same b value will indicate no G×L interaction, while those with different b values will show G×L interaction. Genotypes with different b values will have the cross-over G×L interaction if their means are more or less the same, but will show the non-crossover G×L interaction if their means are significantly different.

Sensitivity analysis of cultivar coefficients for mean performance and yield response to locations

The CSM-CROPGRO-Peanut model requires 15 cultivar coefficients that define the growth and development characteristics or traits of a peanut cultivar (Table 4). Seven coefficients define the life cycle development characteristics and eight coefficients define the growth characteristics (Boote et al., 2003). In this study, only 13 candidate coefficients were evaluated for the effect of changing their values. These included five phenological development traits, three vegetative growth traits and five reproductive growth traits. The phenological development traits were the number of photothermal days from emergence to flowering (EMFL), from first flower to first pod (FLSH), from first flower to first seed (FLSD), from first flower to end of leaf expansion (FLLF) and from first seed to physiological maturity (SDPM). The three vegetative growth traits consisted of the maximum leaf photosynthetic rate (LFMAX), specific leaf area (SLAVR) and the maximum size of a full leaf (SIZELF). The five reproductive growth traits included the maximum fraction of daily growth that is portioned to seed and shell (XFRT), individual seed size (WTPSD), seed filling duration for an individual pod cohort (SFDUR), average seed per pod (SDPDV) and the photothermal time required for a cultivar to reach

final pod load (PODUR). Because peanut is insensitive to day length, the values of the remaining two coefficients, the critical short day length and the photoperiod sensitivity, were set to 11.84 h and 0.00, respectively (and coefficients are not listed in Table 4).

Table 4. Cultivar coefficients of the CSM-CROPGRO-Peanut model and the range of values and increment interval in varying the specific parameter during the sensitivity analysis.

Abbreviation	Definition	Unit[†]	Range		Increment interval
			Minimum	Maximum	
	Phenology parameters				
EMFL	Time between plant emergence and flower appearance (R_1)	PD	17.0	24.0	0.70
FLSH	Time between first flower and first pod (R_3)	PD	7.0	14.5	0.75
FLSD	Time between first flower and first seed (R_5)	PD	16.6	28.5	1.20
SDPM	Time between first seed (R_5) and physiological maturity (R_7)	PD	42.0	70.0	2.80
FLLF	Time between first flower (R_1) and end of leaf expansion	PD	50.0	88.0	3.80
	Growth parameters				
LFMAX	Maximum leaf photosynthesis rate at 30 °C, 350 vpm CO_2 and high light	$mg\ CO_2\ m^{-2}\ s^{-1}$	0.82	1.64	0.08
SLAVR	Specific leaf area of cultivar under standard growth conditions	$cm^2\ g^{-1}$	230	290	6.00
SIZLF	Maximum size of full leaf (four leaflets)	cm^2	15.0	67.5	5.25
XFRT	Maximum fraction of daily growth that is partitioned to seed and shell	fraction	0.72	0.96	0.024
WTPSD	Maximum weight per seed	g	0.36	1.15	0.08
SDPDV	Average seed per pod under standard growing conditions	no. pod^{-1}	1.31	2.50	0.12
SFDUR	Seed filling duration for pod cohort at standard growth conditions	PD	24.0	40.5	0.17
PODUR	Time required for cultivar to reach final pod load under optimal conditions	PD	13.0	31.0	1.80

[†] PD=photothermal day.

Sensitivity analysis was conducted to evaluate the effect of changing the value of each cultivar coefficient on mean yield and yield response to locations (b-value) of a peanut genotype. Entries 6, 10 and 16, representing the early maturing, medium maturing and late maturing peanut lines, respectively, were chosen to provide the initial values for the cultivar coefficients. For each entry, sensitivity analysis was performed by varying the value of a cultivar coefficient within the range of its ecotype or cultivar limits, creating a series of 11 synthetic genotypes that differed only in the value of the varying coefficient. The range of values and increment interval for each cultivar coefficient are given in Table 4. The range of values of cultivar coefficient for each trait was limited to 10% beyond the combined range of values published for that particular trait in the default file of DSSAT version 4.5 (Hoogenboom et al., 2010), in Banterng et al. (2004) and in Suriharn et al. (2007). Such a limit was based on the logic that the values of cultivar coefficients in these three sources were from a limited number of peanut lines and that values of 10% beyond these ranges should be available in the peanut germplasm. Simulated yield for 14 locations, three seasons and 30 years were obtained for each synthetic genotype and its mean yield and b-value were calculated. The derived mean and b-value for the individual synthetic genotypes were compared to determine the effects of varying that particular cultivar coefficient on mean yield and b-value. The process was repeated for all cultivar coefficients in three types of peanut genotype backgrounds.

Determination of plant traits causing G×L interaction

Six pairs of peanut genotypes showing the three patterns of G×L interaction, i.e., no interaction, crossover and non-crossover interactions, were selected for sensitivity analysis to determine the casual traits, two pairs for each pattern. Sensitivity analysis was performed for each pair by sequentially replacing the values of each cultivar coefficient and combinations of coefficients of the lower-yielding genotype with the values of the corresponding coefficients of the higher-yielding genotype. Pod yield of the synthetic genotypes with the modified cultivar coefficients was simulated for 14 locations, 3 seasons and 30 years and the mean yield and yield response to locations (b-values) was determined. The change in cultivar coefficients continued until the regression line of the synthetic genotype was more or less the same as that of the higher-yielding genotype. The minimum

cultivar coefficients that made the regression lines of the synthetic and high-yielding genotypes move closest together were considered the causal traits for G×L interaction for this pair of genotypes, particularly considering the singular trait shift that caused the most shift to agreement. The process was repeated for all selected pairs of genotypes.

Results

Response to location and patterns of G×L interaction

The 17 peanut genotypes used in the present study varied considerably in both phenological development and growth traits as shown by their ranges of values given in Table 2. The mean simulated pod yield for these peanut genotypes averaged over 14 locations, three seasons and 30 years also differed substantially, ranging from 1.63 to 3.32 t ha^{-1} (Table 5).

Table 5. Mean simulated pod yield and regression coefficient (b-value) against site mean yield for the individual peanut genotypes.

Entry No.	Line/cultivars	Mean yield[†] (t ha^{-1})		b-value[†]	
17	KKFC 4008-5	3.32	a	1.25	a
13	((Nc Ac 17090 × B1)-25 × China 97-2) F5-11-2	3.26	b	1.13	fg
11	(China 97-2 × Singburi) F6-13-1	3.22	c	1.15	ef
14	KKU 72-1	3.20	c	1.23	a
9	(Luhua 11 × China 97-2) F6-11-3	2.97	d	0.91	j
12	((Nc Ac 17090 × B1)-25 × KK60-3) F6-2-2	2.93	e	1.17	b
15	KK 60-3	2.92	e	1.16	cd
8	(Luhua 11 × KK60-3) F6-22	2.89	f	1.07	g
16	(China 97-2 × KK 60-3) F6-9-1	2.87	g	1.16	bc
10	((Nc Ac 17090 × B1)-25 × Luhua 11) F5-14-2	2.68	h	1.06	gh
3	KKU 1	2.37	i	0.98	i
1	KK 5	2.28	j	0.89	j
5	(KK60-3 × (Ah 65 × NC Ac 17090))-3-11-7	2.14	k	0.93	j
4	(KK 60-3 × (MGS9 × Chico)-12-16-1)26-5-33	2.00	l	0.86	jk
2	(Chico × GA 119-20) 8-3-12	1.86	m	0.68	l
6	(KK 4 × NC8C)-33-6-21	1.64	n	0.69	l
7	A progeny of Tainan 9 × Moket	1.63	n	0.69	l

[†] Numbers in the same column followed by the same letter are not significantly different at P≤0.05 by t-test.

The 14 locations used in the present study differed greatly in soil type, temperature, solar radiation and rainfall (Table 3). These locations were selected to represent the total environmental variation of the 112 peanut production locations across Thailand. The mean yield over all genotypes for the individual 14 locations also varied greatly, ranging from 1.20 to 3.56 t ha^{-1}. Differential cultivar responses to locations were found for the individual genotypes and all the responses were essentially linear. Examples are shown in Figure 1 for selected genotypes. The value of the regression coefficient (b) against site mean yield for the individual peanut genotypes varied from 0.69 to 1.25 (Table 5). A high correlation was observed between mean yield and b-value of the test genotypes (r=0.92, P<0.01), indicating the strong association between high yield and high b-value and vice versa. The combined analysis of variance for the full data set of 112 locations and for the reduced data set of 14 locations revealed that the reduced data set still maintained the same level of G×L interaction as the full data set (data not shown). Thus, the genotypic responses to locations obtained in the present study should reflect the G×L interaction prevailing over all peanut production areas in Thailand that can be accounted for by the CSM-CROPGRO Peanut model. Visual inspection of Figure 1 revealed all three patterns of G×L interaction, i.e., no-interaction, non-crossover and crossover interactions, among pairs of peanut genotypes. For all possible pairs of 17 genotypes in the present study, 28 pairs showed no G×L interaction, 93 pairs displayed non-crossover G×L interaction and 15 pairs exhibited crossover G×L interaction.
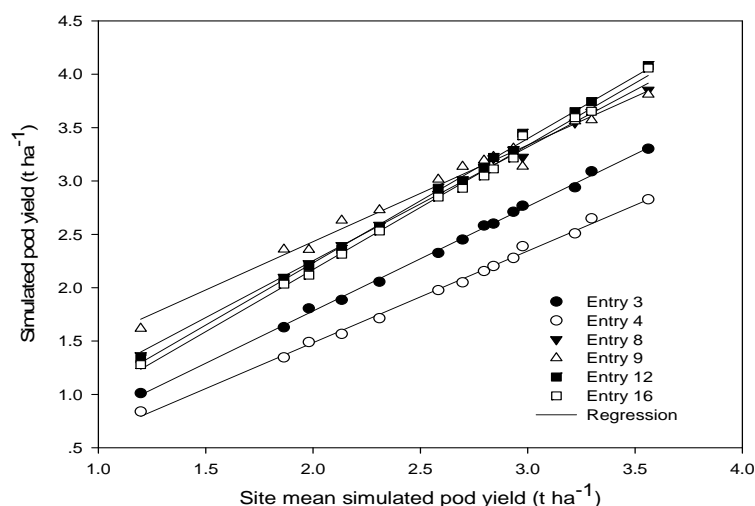

Figure 1. Response to location for simulated pod yield of selected peanut genotypes (see Table 1 for entry description).

Effect of changing the value of each cultivar coefficient

Model sensitivity analysis was used to determine the effect of a given cultivar coefficient on mean yield and yield response to locations (b-value) of a peanut genotype by varying the value of each coefficient and evaluating the effect of this change. The ranges of the values that were used for the individual cultivar coefficients are given in Table 4. The results of model sensitivity analysis showed that increasing the duration of phenological development for the number of days from first seed to physiological maturity (SDPM) resulted in a significant increase in both mean yield and yield response to locations (b-value) (Figure 2d), while changing the number of days from emergence to flowering (EMFL) and from first flowering to first seed (FLSD) resulted in only a slight increase in both mean yield and b-value (Figures 2a and 2c). On the other hand, changing the number of days from first flowering to first pod (FLSH) and from first flowering to end of leaf expansion (FLLF) did not have an impact on either the mean or b-value (Figures 2b and 2e). The effects of varying each of these phenological genetic parameters on mean yield and b-value were the same for the early maturing, medium maturing and late maturing peanut lines (Figure 3), except that the changes in both mean yield and b-value were greater for the medium and late maturing lines than for the early maturing lines (Figures 3g and 3h).

For the vegetative and reproductive growth traits, increasing the value of the maximum leaf photosynthesis rate (LFMAX), maximum fraction of daily growth that is partitioned to seed and shell (XFRT) and seed filling duration (SFDUR) resulted in considerable increases in both mean yield and b-value (Figures 2f, 2h and 2l, respectively). The responses to these parameters were the same for all three peanut maturity types (Figures 4a, 4b, 4g, 4h, 4m and 4n), except that the responses to changing SFDUR for both mean yield and b-value were less for the early maturing than for the medium and the late maturing lines (Figures 4m and 4n). However, increasing the maximum size of full leaf (SIZLF) and the maximum weight per seed (WTPSD) resulted in only a slight response (Figures 2g and 2j), while increasing the value of specific leaf area (SLAVR) and number of seeds per pod (SDPDV) did not show a response (Figures 2i and 2l). Similar responses to these three parameters were also observed for all the three maturity types (Figures 4e and 4f for SIZLF; 4i and 4j for WTPSD; 4c and 4d for SLAVR; and 4k and 4l for SDPDV). There was a negative response of mean yield to varying the

photothermal time required to reach final pod load (PODUR); increasing PODUR resulted in a significant decrease in mean yield (Figure 2m) and the responses were the same for all three maturity types (Figure 4o). However, differential responses to varying PODUR on the b-value were obtained among the three maturity types. Increasing PODUR gave an increase in b-value for both the medium and late maturing lines, although to a lesser extent for the medium maturing line, but increasing PODUR resulted in a significant decrease in the b-value for the early maturing line (Figure 4p). The above results indicated that, in many cases, the responses to individual cultivar coefficients were distinctly nonlinear, consistent with what was proposed by Boote et al. (2001) and Boote et al. (2003).

Based on the responses described above, the cultivar coefficients could be divided into three groups. The first group consisted of traits that showed a major effect on mean yield and b-value. These included SDPM, LFMAX, XFRT, SFDUR and PODUR; the former four parameters had a positive effect but PODUR had a negative effect on mean yield, while its effect on b-value could either be negative or positive depending on the maturity duration of the line. The second group consisted of the coefficients that had only a minor effect; these included EMFL, FLSD, SIZLF and WTPSD. The final group consisted of the coefficients that did not affect either the mean yield or b-value, i.e., FLSH, FLLF, SLAVR and SDPDV.

Causal plant traits for different patterns of G×L interaction

To determine the causal plant traits for G×L interaction, two pairs of genotypes were selected to represent each pattern of G×L interaction. The selected genotype-pairs were Entries 1 and 9 and Entries 3 and 8 for the no G×L interaction pattern (Figures 5a and 5g), Entries 7 and 14 and Entries 4 and 16 for the non-crossover G×L interaction (Figures 6a and 6e) and Entries 9 and 16 and Entries 9 and 12 for the crossover G×L interaction (Figures 7a and 7f). Sensitivity analysis was used to determine the plant traits that caused the yield difference between the two genotypes for the individual pairs. This was done by sequentially replacing one or more of plant traits of the lower yielding line with the corresponding value of the high yielding line until the line of the modified genotype came close to the line of the high yielding genotype. The minimum traits that resulted in the lines of the two genotypes being close together were considered the causal traits for G×L interaction for that particular genotype-pair.

Results of the sensitivity analysis revealed that, for the no G×L interaction pattern, the traits that caused the line of the lower yielding line to get close to that of the higher yielding line were SFDUR, PODUR, XFRT, LFMAX and WTPSD for the pair of Entries 1 and 9 (Figure 5f) and SFDUR, SDPM and LFMAX for the pair of Entries 3 and 8 (Figure 5j). For both pairs, SFDUR was the trait that had the greatest effect in increasing the yield level of the lower yielding lines (Figures 5b and 5h). However, the trait being second in its effect was PODUR for the pair of Entries 1 and 9 (Figure 5c), but was SDPM for the pair of Entries 3 and 8 (Figures 5i). While five traits were needed to move the line of Entry 1 close to that of Entry 9 (Figure 5f), only three traits were sufficient to move the line of Entry 3 close to that of Entry 8 (Figure 5j). For the non-crossover G×L interaction pattern, the traits that caused yield difference both between Entry 7 and Entry 14 and between Entry 4 and Entry 16 were SDPM, LFMAX and XFRT (Figures 6d and 6h). For both pairs, SDPM had the greatest effect (Figures 6b and 6f) followed by LFMAX (Figures 6c and 6g). Likewise, for the crossover G×L interaction pattern, the traits that caused the lines of the two genotypes to come close together were PODUR, SDPM, XFRT and LFMAX for the pair of Entries 9 and 16 (Figure 7d) and SDPM, PODUR and XFRT for the pair of Entries 9 and 12 (Figure 7h). While PODUR had the greatest effect followed by SDPM for the pair of Entries 9 and 16 (Figures 7b and 7c), SDPM had the greatest effect followed by PODUR for the pair of Entries 9 and 12 (Figures 7f and 7g). It appeared that the effect of an individual trait differed for different pairs of genotypes.

The above results also indicated that the plant traits that caused yield difference between the two genotypes of the individual pairs were among those that showed a major effect on mean yield and b-value in the previous sensitivity analysis (Figures 3 and 4), i.e., SDPM, LFMAX, XFRT, SFDUR and PODUR. Examination of the values of these parameters for the two genotypes in each pair revealed that the traits that caused yield differences between the two genotypes were those in which the two genotypes differed. On the other hand, if the two genotypes did not differ significantly for any of these traits it would not show up as a causal trait for G×L interaction in that particular genotype-pair. For instance, SDPM did not cause a yield difference between Entries 1 and 9 because both entries had the same value of SDPM, i.e., 48.5 photothermal days (PD). On the other hand, this trait was a cause of G×L interaction for the pair of Entries 4 and 16 and the pair of Entries 9 and

12 because the two genotypes in each pair differed significantly in this trait, the values being 46.5 and 63.5 PD for Entries 4 and 16, respectively and being 48.5 and 56.5 PD for Entries 9 and 12, respectively (Table 2). This also explained why LFMAX was the cause of the G×L interaction for the pair of Entries 9 and 16 but not for the pair of Entries 9 and 12.
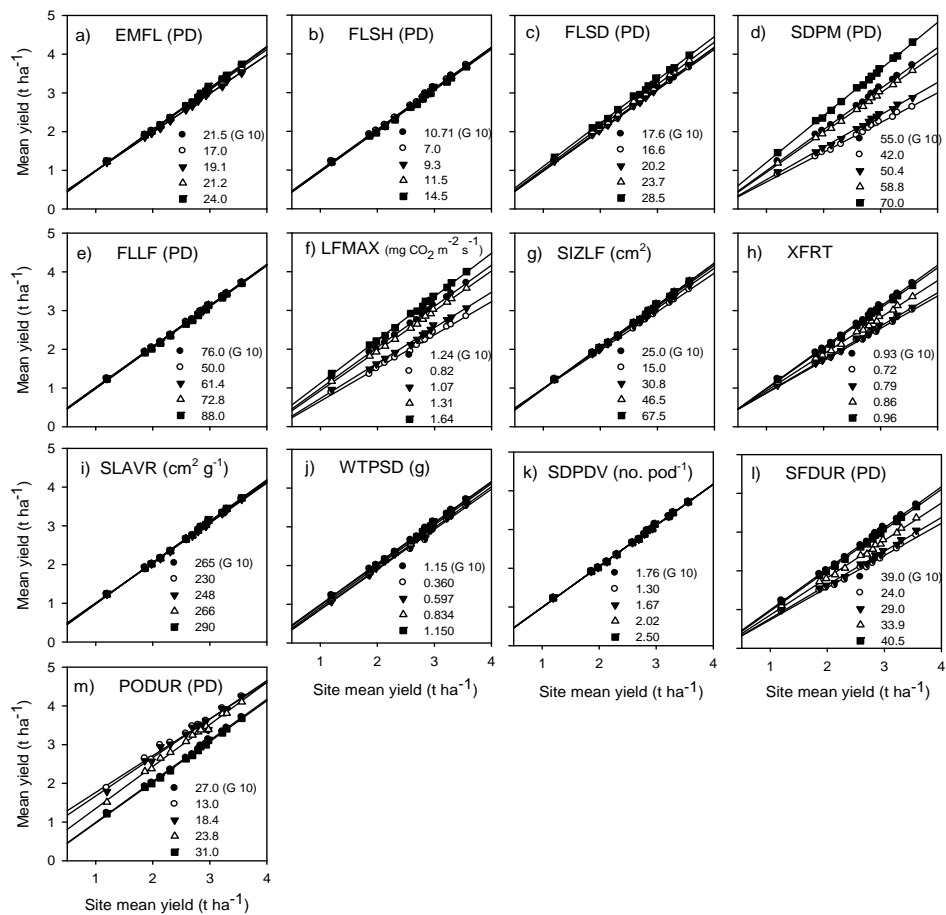

Figure 2. Effect of changing the value of each individual cultivar coefficient on mean yield and yield response to locations for Entry 10 (the medium maturing line).
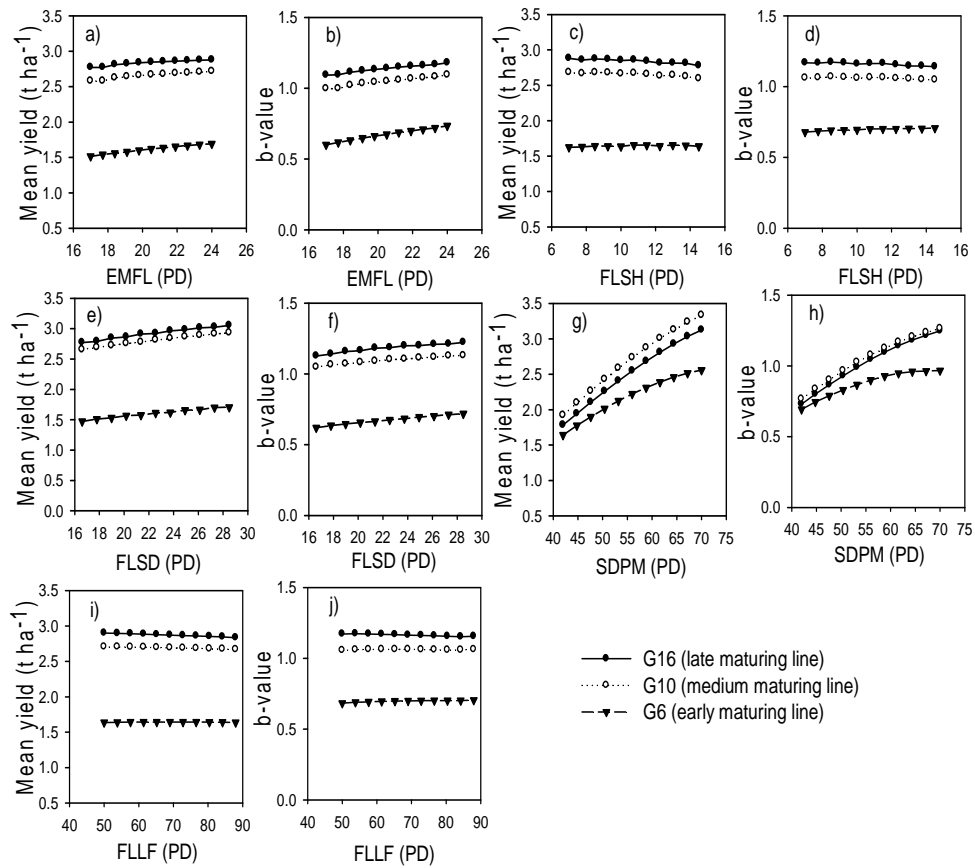
Figure 3. Effects of changing the value of each individual phenological genetic parameter on mean yield and yield response to locations (b-value) for the early maturing (G_6), the medium maturing (G_{10}) and the late maturing (G_{16}) peanut lines.
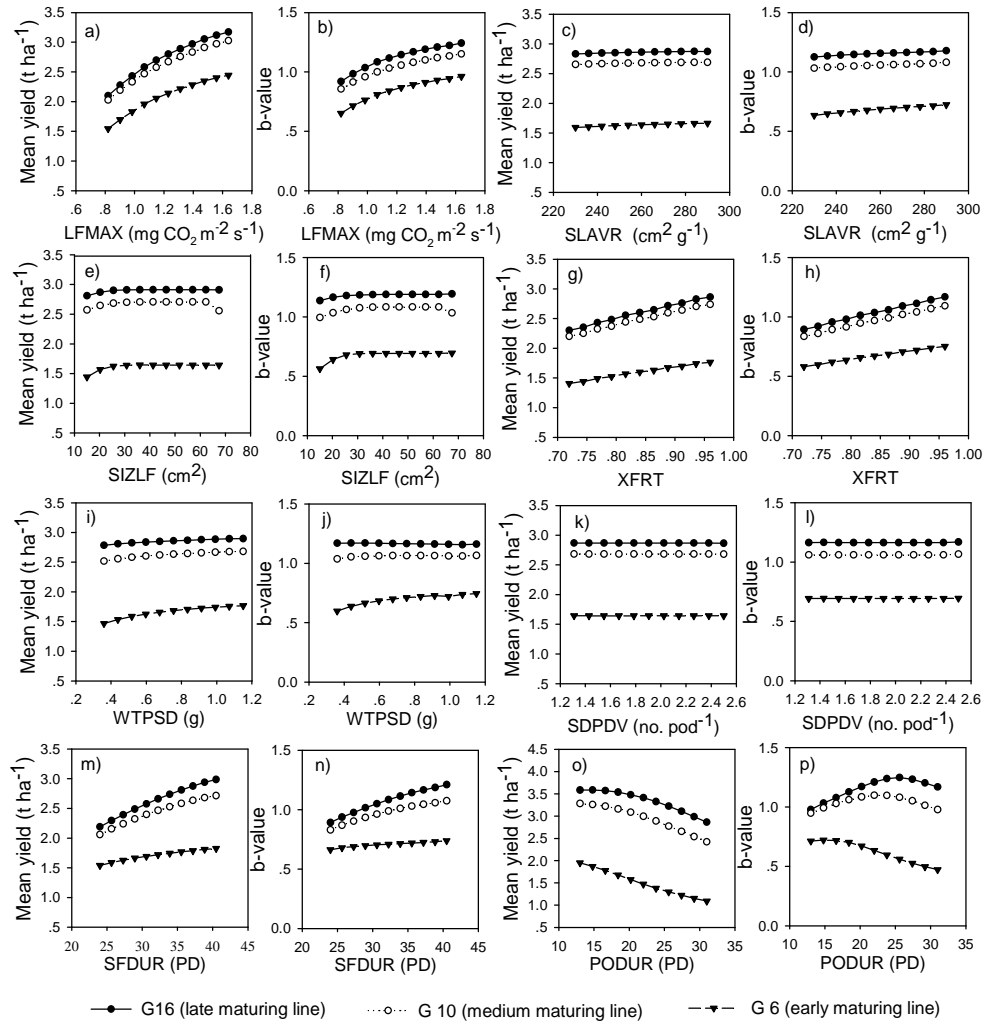
Figure 4. Effects of changing the value of each individual growth parameter on mean yield and yield response to location (b-value) for the early maturing (G_6), the medium maturing (G_{10}) and the late maturing (G_{16}) peanut lines.
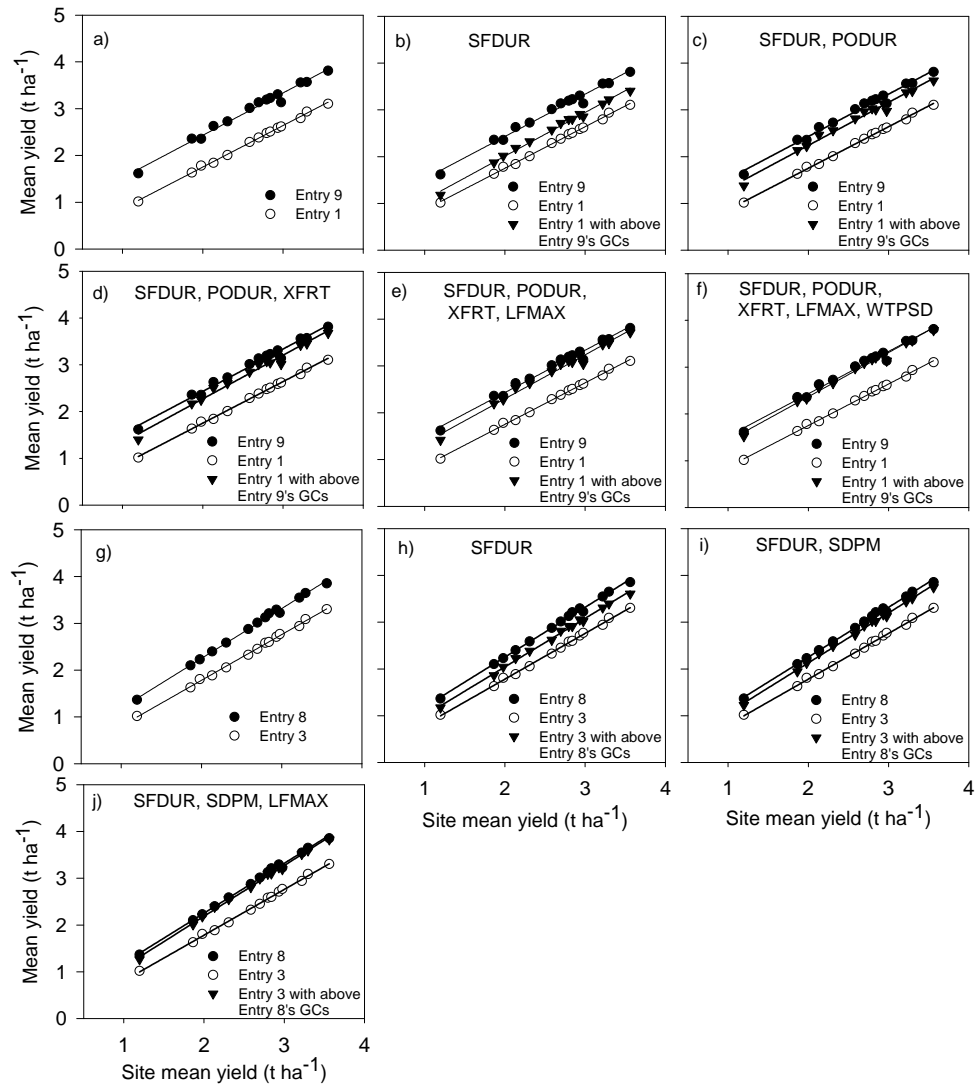
Figure 5. The no G×L interaction and the results after the specified cultivar coefficients of the low yielding line in each pair were adjusted to those of the corresponding high yielding line.
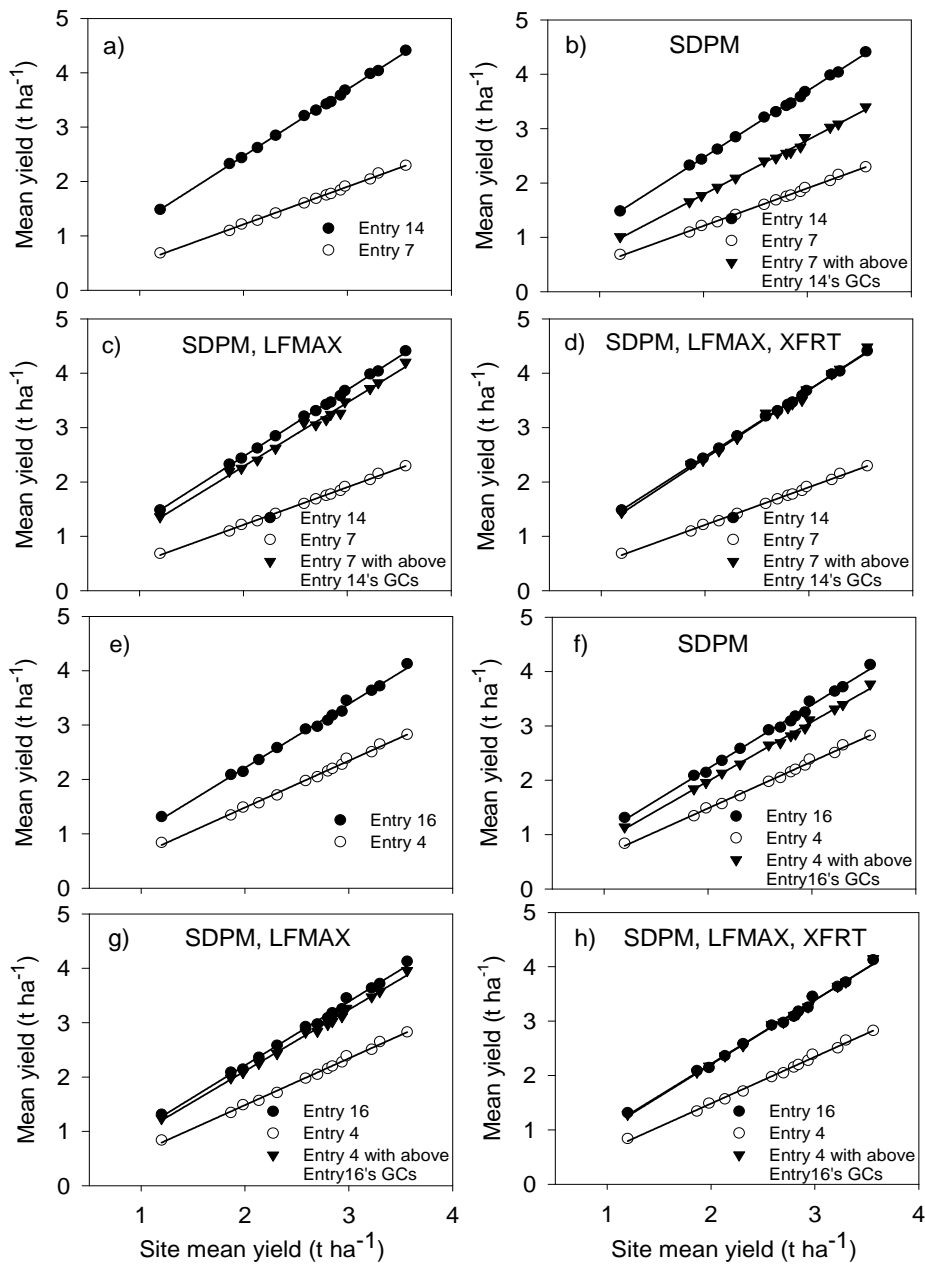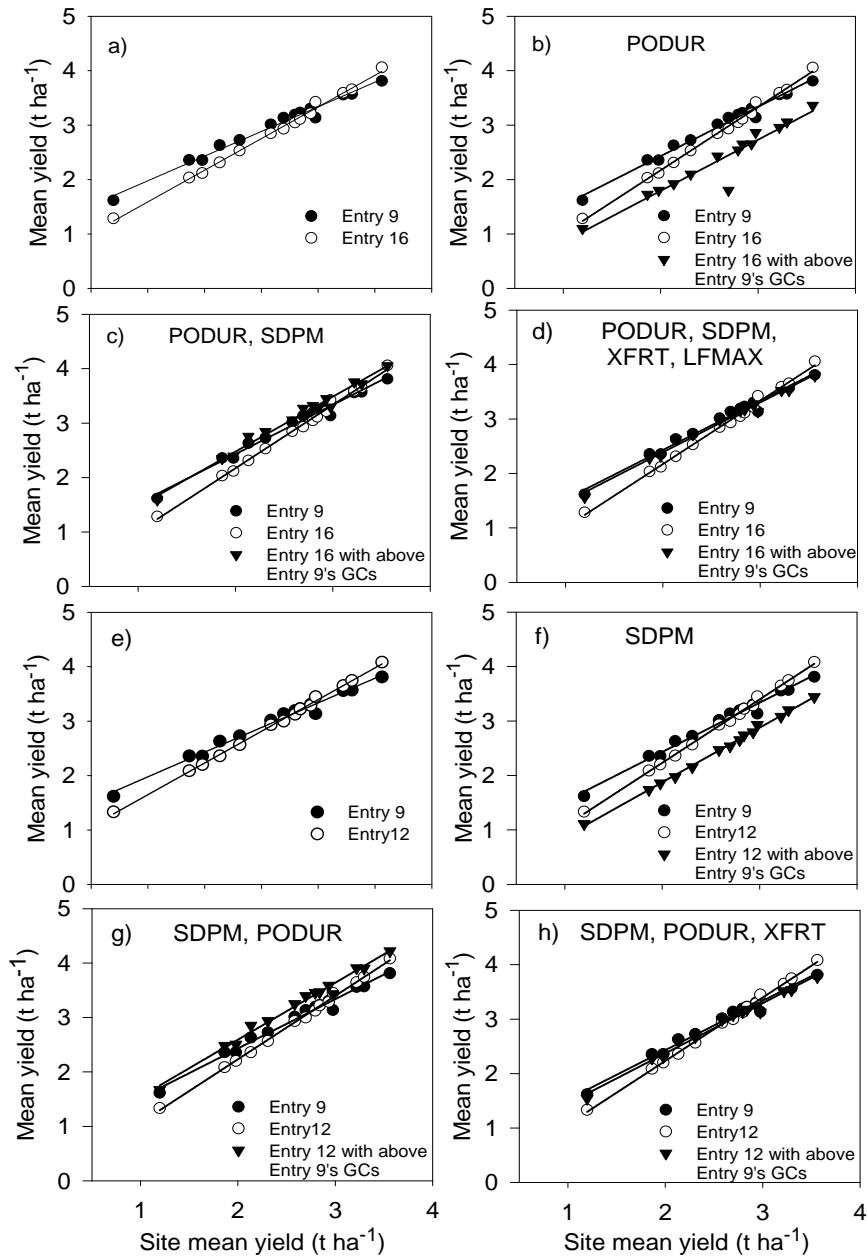
Figure 6. The non-crossover G×L interaction and the results after the specified cultivar coefficients of the low yielding line in each pair were adjusted to those of the corresponding high yielding line.

Figure 7. The crossover G×L interaction and the results after the specified cultivar coefficients of the low yielding line in each pair were adjusted to those of the corresponding high yielding line.

Discussion

This study aimed to identify plant traits that cause the G×L interaction for pod yield of peanut by using sensitivity analysis with the CSM-CROPGRO-Peanut model. The cultivar coefficients of the 17 genotypes used in the present study have already been validated with independent data in the respective studies from which they were taken (Banterng et al., 2004; Sujariya, 2004; Suriharn et al., 2007; Anothai et al., 2008) and the results showed good agreement between simulated and observed values of the corresponding traits. In additions, the cultivar coefficients of several peanut lines in the present study had also been shown to give good prediction of relative yield performances of the peanut lines in multi-environment trials (Banterng et al., 2006; Suriharn et al., 2008; Anothai et al., 2009). These studies have established that the CSM-CROPGRO-Peanut model is capable of predicting relative performances of the peanut lines across environments and that G×E interaction can be captured by model simulation. The latter was also shown in the present study in which all three patterns of G×L interaction, i.e., no interaction, non-crossover interaction and crossover interaction, were obtained.

The results of the present study showed that LFMAX, XFRT, SDPM, SFDUR and PODUR were the causal traits for the differences in yield potential and for G×L interaction between peanut genotypes. These traits are related to the production of photosynthates (LFMAX), the partitioning of assimilates to pods (XFRT), the phenological duration of pod and seed development (SDPM), single seed growth duration (SFDUR) and the rate of pod duration (1/PODUR), respectively. Changing the values of the above traits will affect these processes and, consequently, affect crop yield. In addition, they have an interactive effect in determining the yield potential and yield response to locations for a given peanut genotype.

Maximum leaf photosynthetic rate (LFMAX) is related to traits that maintain high photosynthesis, including high leaf N concentration and slow N mobilization (Boote et al., 2003). Increasing the value of this trait will result in an increase in crop growth rate (CGR), pod growth rate (PGR) and seed growth rate (SGR) and, as a result, an increase in biomass accumulation and ultimately final pod yield (Boote and Tollenaar, 1994).

The XFRT is the genetic parameter that limits the fraction of daily growth that is partitioned to seed and shell. Increasing XFRT increases the total rate of seed and pod dry weight accumulation (allowing more pods to be carried),

but it restricts vegetative growth during the pod filling phase because peanut cultivars may have differential determinacy in growth habit. In peanut, vegetative and reproductive growth occurs simultaneously under optimum conditions; although this is cultivar-dependent (Duncan et al., 1978). There is a strong competition for assimilates between vegetative and reproductive organs. The plant must produce sufficient assimilates in order to be able to continue to grow its vegetative organs as well as to provide assimilates for seed development, although the crop may already have some maturing seeds. A higher XFRT would mean a greater proportion of photosynthate is allocated to reproductive structures, resulting in a reduction in vegetative growth and a higher pod yield (Duncan et al., 1978; Gupta, 1992).

SDPM is the photothermal time between first seed to physiological maturity on a whole crop/plant basis (Boote et al., 1998). Increasing SDPM allows more time for biomass accumulation in seeds and pods and, consequently, an increase in pod yield. However, seed filling duration (SFDUR) is somewhat different, being the photothermal time required from the start to the end of seed filling for single pod cohorts (Boote et al., 1998). Increasing seed filling duration (SFDUR) will result in an increase in pod yield because the time of seed filling for a pod cohort is extended. On the other hand, increasing PODUR, which is the time required to reach final pod load, will result in a decrease in pod yield as the time required for rapid pod addition is increased and consequently a potentially lower number of pods are added (Boote et al., 1998). The reciprocal of PODUR can be thought of defining the pod addition rate in a normalized manner.

The interactive effects of these parameters can be seen by examining the causal traits for yield difference and G×L interaction for the individual pairs of genotypes. For example, Entries 3 and 8 have more or less the same b-value but a different mean yield, with SFDUR, SDPM and LFMAX being the causes for their yield difference (Figure 5j). Entry 3 has lower values than Entry 8 for all the three traits (Table 2). Changing the values of SFDUR, SDPM and LFMAX of Entry 3 to be the same as those of Entry 8 increased the yield for Entry 3 to the same level as that of Entry 8. As the two genotypes differed in all these three traits, to increase the yield level of Entry 3 to the level of Entry 8, thus, required a change in all three parameters simultaneously.

For the pair of Entries 9 and 16 in which PODUR, SDPM, XFRT and LFMAX were identified as the causal traits (Figure 7d). Entry 9 had a slightly higher mean yield but a slightly lower b-value than Entry 16 (Figure 7a).

Entry 9 had a higher LFMAX but lower SDPM, XFRT and PODUR than Entry 16 (Table 2). To increase the yield level for Entry 16 while lowering its b-value so that they were the same as those of Entry 9, the values for LFMAX of Entry 16 had to be increased and at the same time the values for SDPM, XFRT and PODUR had to be decreased to the corresponding values of Entry 9. Increasing LFMAX would increase the mean yield for Entry 16, which is desirable, but would also increase the b-value to be even higher, which did not cause the two lines to come together. Decreasing PODUR would increase the mean yield but decrease the b-value as Entry 16 is a late maturing line (Figures 4o and 4p). Decreasing SDPM and XFRT would bring about a decrease in both yield level and b-value of Entry 16. Decreasing SDPM, PODUR and XFRT would compensate for the increases of mean yield and b-value by increasing LFMAX. In this case, therefore, changing the causal traits in different directions is needed in order for Entry 16 to have the same yield level as well as the same adaptive response as Entry 9. It is noteworthy that PODUR was always among the causal traits found in the crossover pattern of G×L interaction.

The finding that LFMAX, XFRT, SDPM, SFDUR and PODUR are the causal traits for yield differences and for G×L interaction between peanut genotypes is quite useful for the determination of breeding strategies for improving yield and achieving the desirable adaptive response to environments. Unfortunately, changing these traits will affect not only the yield level but also the b-value. This could be a potential conflict, although these simulations also confirm the general finding in the literature that a high yield level is associated with a high b-value. This illustrates why the selection for both higher yield potential and yield stability is difficult. The present study, however, has demonstrated that model sensitivity analysis can be used in determining what traits should be changed and in what direction, i.e., either an increase or a decrease, in order to achieve the desirable yield level and adaptive response of a given genotype. This is particularly useful for practical applications as the normal goal of a breeding program is to develop new cultivars that are superior to the best current cultivar. The information obtained from model sensitivity analysis could be used in selecting parents for crossing and in defining selection criteria.

It should be pointed out that the CSM-CROPGRO-Peanut model is responsive to only certain abiotic factors that include air temperature, solar radiation, rainfall and irrigation and soil characteristics related to water availability in the profile and nitrogen in the soil. The model, however,

does not respond to biotic factors such as diseases, insects and weeds and other abiotic factors such as phosphorus, potassium, water logging and microvariability within the field (Boote et al., 1996; Hoogenboom et al., 1999; Jone et al., 2003). The G×E interaction in the present study is thus limited to the interaction of genotypes with the environmental factors that the model can account for and the causal traits identified are the traits that affect only this portion of G×E interaction. However, it is the portion of G×E interaction that is of great concern to breeders because of its association with the adaptability of genotypes to the inherent and persistent natural environments of different production areas. In reality, those factors that the model does not account for are also the major causes of G×E interaction, particularly, biotic factors. This part of G×E interaction also has significant effects on yield performance and stability of crop genotypes, but it needs to be dealt with by a different approach. For example, G×E interaction resulting from differential responses of genotypes to different levels of disease pressure in different locations (indicating different degrees of disease resistance of the genotypes) can be dealt with by breeding for disease resistance.

The results of the present study indicated that crop model sensitivity analysis can be a potential tool in assisting breeders to understand the relationship of plant traits and their interactions that contribute to a different yield potential and G×E interaction for a set of genotypes. It can also provide a potentially valuable tool for evaluation of the value of a given trait in a target environment that may aid breeders in the formulation of crop ideotypes and the evaluation of yield potential and yield stability of those ideotypes for target environments. This type of application of the crop simulation models is being used increasingly (Haverkort and Kooman, 1997; White, 1998; Yin et al., 2003; Hoogenboom et al., 2004b). However, more research is still needed for this type of model application, particularly in identification of plant traits contributing to adaptation to a specific environment (specific adaptation) and in the validation of the results from model simulation by actual breeding work.

Conclusions

This study demonstrated that model sensitivity analysis can be used as a breeding tool to study the causes of G×E interaction. The plant traits that affect both the differences in yield between peanut genotypes and the G×L

interaction for pod yield are maximum leaf photosynthesis rate (LFMAX), the maximum fraction of daily growth that is partitioned to seed and shell (XFRT), the number of day from first seed to physiological maturity (SDPM), single seed filling duration (SFDUR) and the duration of pod addition (PODUR). The study also showed that model sensitivity analysis can be used to hypothesize yield improvement likelihoods of a given peanut genotype for a peanut production environment such as Thailand based on improving single or multiple combinations of plant traits. This approach also has potential for other crops and for other target environments.

Acknowledgments

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