ORIGINAL ARTICLE

Heritability and phenotypic correlation of resistance to *Peanut bud necrosis virus* (PBNV) and agronomic traits in peanut

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Abstract

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Heritability and phenotypic correlation of resistance to *Peanut bud necrosis virus* (PBNV) and agronomic traits in peanut
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Peanut bud necrosis virus **(PBNV) is a potential threat to peanut production in Thailand. Therefore, the improvement of peanut lines, which are resistant to PBNV and maintain acceptable agronomic traits, is important. The objective of this study was to estimate broad sense heritability and phenotypic correlation in 16 crosses of the F_2 populations derived from cross of four resistant parents with four large-seeded peanut cultivars. A randomized complete block design with four replications was used. Peanut bud necrosis disease (PBND) incidence, PBND score and agronomic data were recorded. Estimates of heritability for PBND score on F_2 individual plants were low at 60 days after sowing (DAS) and seemed to be improved at 70 DAS. Esti-**

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mates of heritability for agronomic traits varied over crosses and traits and were generally low. However, high heritability estimates were observed for 100 seed weight in cross KKU 72-1 × IC 10 and for shelling percentage in crosses KKU 72-1 × IC 34 and Luhua 11 × ICGV 86388. High positive correlation coefficients were found among PBND score, PBND incidence and area under disease progress curve (AUDPC) but all PBNV resistance parameters had low correlation with all agronomic traits. High positive correlation coefficients were found among pod weight per plant, pod number per plant and seed weight per plant. Because of low heritability estimates for PBNV resistance and agronomic traits, selection among individual plants in the F_2 generation will be ineffective. Selection should be carried out in advanced generations or on the progeny performance as family mean basis.

Key words : *Arachis hypogaea* L., disease score, disease incidence, area under disease progress curve

บทคัดย่อ

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อัตราพันธุกรรมและสหสัมพันธ์ของลักษณะความต้านทานโรคยอดไหม้และลักษณะทางการเกษตรของถั่วลิสง

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ไวรัสยอดไหม้ของถั่วลิสงมีแนวโน้มว่าจะเป็นปัญหาสำคัญในการผลิตถั่วลิสงในประเทศไทย การปรับปรุงพันธุ์ถั่วลิสงให้ต้านทานต่อโรคยอดไหม้และมีลักษณะทางการเกษตรดีจึงมีความสำคัญ การทดลองนี้มีวัตถุประสงค์เพื่อประเมินอัตราส่วนพันธุกรรมแบบกว้างและสหสัมพันธ์ระหว่างลักษณะความต้านทานต่อโรคยอดไหม้และลักษณะทางการเกษตร ในลูกผสมชั่วที่ 2 จำนวน 16 คู่ ซึ่งเกิดจากการผสมข้ามระหว่างถั่วลิสงสายพันธุ์ต้านทานและพันธุ์เมล็ดโต ใช้แผนการทดลองแบบสุ่มสมบูรณ์ภายในกลุ่มมี 4 ซ้ำ บันทึกข้อมูลลักษณะเปอร์เซ็นต์ต้นที่เป็นโรค ความรุนแรงของโรคและลักษณะทางการเกษตร พบว่าอัตราพันธุกรรมของลักษณะความรุนแรงของโรคที่ประเมินจากแต่ละต้นเมื่อ 60 วันหลังปลูก มีค่าต่ำและส่วนใหญ่มีค่าเป็น 0 และสูงขึ้นเมื่อ 70 วันหลังปลูก อัตราพันธุกรรมของลักษณะทางการเกษตรแตกต่างกันไปในแต่ละคู่ผสมส่วนใหญ่มีค่าต่ำถึงปานกลาง คู่ผสมที่มีค่าอัตราพันธุกรรมของลักษณะน้ำหนัก 100 เมล็ดสูง คือ KKU 72-1 × IC 10 และคู่ผสมที่มีค่าอัตราพันธุกรรมของลักษณะเปอร์เซ็นต์กะเทาะสูง คือ KKU 72-1 × IC 34 และ Luhua 11 × ICGV 86388 เปอร์เซ็นต์ต้นที่เป็นโรค ความรุนแรงของโรคและพื้นใต้กราฟการพัฒนาของโรคมีสหสัมพันธ์ต่อกันสูง แต่มีสหสัมพันธ์ต่ำกับลักษณะทางการเกษตร ลักษณะทางการเกษตรที่มีสหสัมพันธ์กันสูง คือ น้ำหนักฝัก/ต่อต้น จำนวนฝัก/ต้น และน้ำหนักเมล็ด/ต้น เนื่องจากอัตราพันธุกรรมของลักษณะความต้านทานโรคและลักษณะทางการเกษตรต่ำ การคัดเลือกเป็นรายต้นในประชากรชั่วที่ 2 จะไม่ได้ผลดี ควรคัดเลือกโดยอาศัยค่าเฉลี่ยของครอบครัว หรือมีการทดลอบลูกในชั่วหลัง ๆ จะมีประสิทธิภาพมากกว่า

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Peanut bud necrosis disease is caused by peanut bud necrosis virus (PBNV). It is a distinct member of tospoviruses, which cause diseases of many crops worldwide, and is transmitted by *Thrips palmi* Karny (Reddy *et al*., 2000). Distribution of the disease seems to be limited to peanut producing countries in South and Southeast Asia, including India, Nepal, Pakistan, China, Vietnam

and Thailand. Since the first report on PBNV occurrence in Thailand in 1987, the disease incidence increased at alarming rate and appeared to have potential threat to peanut production, particularly in dry season. No complete management strategy is available to control the disease and to protect peanut crop from severe losses. Although many breeding lines introduced from the International Crops Research Institute for Semi-Arid Tropics (ICRISAT) represent a source of PBNV resistance, they have small seed size and give lower yield than released cultivars. It would be advantageous to develop large-seeded, high yielding and resistant peanut cultivars from the crosses of high yielding cultivars with lines resistant to PBNV.

Very limited information of quantitative resistance to PBNV in peanut has been reported (Buiel, 1996; Pensuk, 2002, Pensuk *et al*., 2002a). Poldate (2002) reported that narrow sense heritability estimates evaluated at different dates by variance components for peanut bud necrosis disease (PBND) incidence ranged from 0 to 1.0 and for PBND score ranged from 0 to 0.63. Phudenpa (2002) reported highly significant negative phenotypic correlation coefficient (-0.54**) between PBND score and leaf color score. Significant negative correlation coefficient (-0.27*) was observed between PBND score and pod weight per plant, but correlation coefficient between PBND score and shelling percentage was highly significant positive (0.38**). However, the materials used in these studies were crosses of small-seeded peanuts with lines resistant to PBNV. To our knowledge, no heritability estimates and phenotypic correlation for PBNV resistance parameters and agronomic traits from crosses of large-seeded peanuts with lines resistant to PBNV are available in the literature.

As part of the on-going confectionery peanut breeding program at Khon Kaen University, this study was conducted to determine the potential for selecting large-seeded, high yielding and PBNV resistant peanut lines from F_2 generation crosses of large-seeded peanuts with lines resistant to PBNV. The objective of this study was to estimate broad-sense heritabilities and phenotypic correlation coefficients for PBNV resistance parameters and agronomic traits.

Materials and Methods

Development of breeding population

Four peanut cultivars (KK 60-3, KKU 72-1, KKU 72-2 and Luhua 11) selected for large seed and high yield were used as female parents to cross with four PBNV resistant lines (IC 10, IC 34, ICGV 86031 and ICGV 86388) used as male parents in a four × four factorial mating design (well known as North Carolina Design II) to generate 16 crosses of F_1 hybrids at Khon Kaen University (KKU)'s agronomy farm. Description of these lines was reported by Kesmala (2003). Briefly, KK 60-3, KKU 72-1 and KKU 72-2 are large-seeded virginia-type released cultivars in Thailand and Luhua 11 is a large-seeded and early maturing germplasm line from China. IC 10 and IC 34 are germplasm lines from insect screening in Thailand which are resistant to thrips and PBNV under greenhouse and field conditions. ICGV 86031 and ICGV 86388 are PBNV resistant germplasm lines from ICRISAT. Sixteen crosses of F_1 hybrids were allowed to self-pollinate to produce ample F_2 seeds for evaluation.

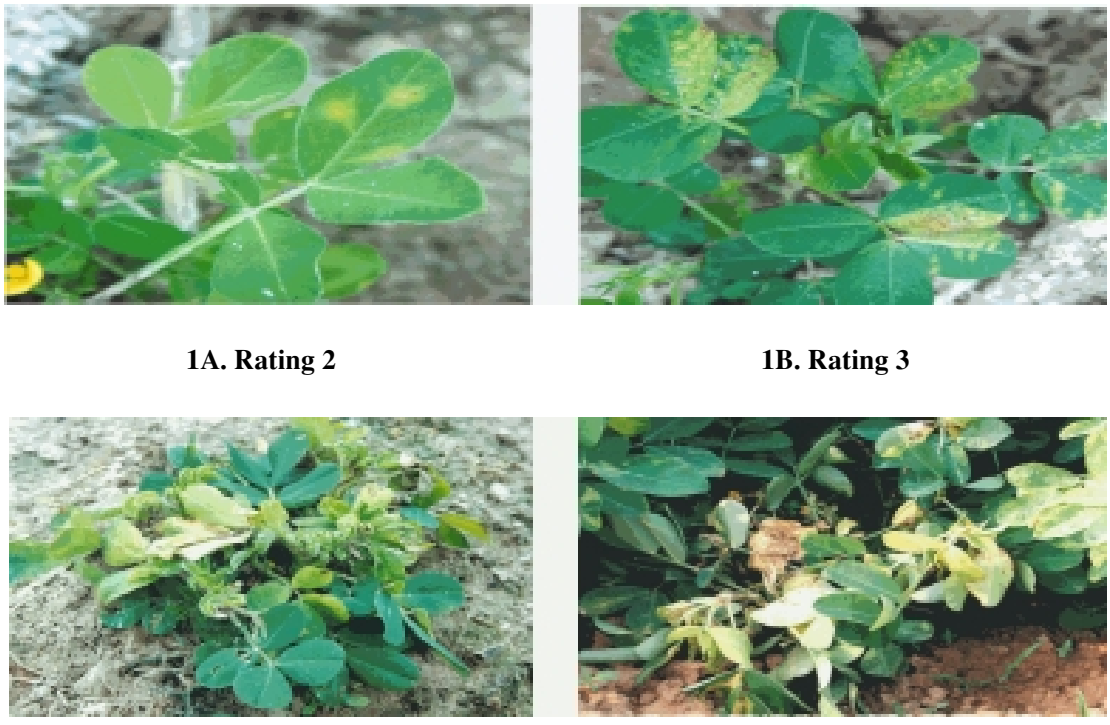
Evaluation of peanut bud necrosis virus resistance

Twenty six entries consisting of F_2 seeds of 16 crosses, eight parents and two susceptible checks (Tainan 9 and JL 24) were planted on 11 January 2001 in Kalasin province in Northeast Thailand. A randomized complete block design with 10 replications was used. Seeds for each entry were over-planted on raised bed in a single-row plot, 7.5 m long with 30 cm spacing between plants and 50 cm spacing between rows and then thinned to obtain 1 plant per hill at 20 days after planting. Neither fungicides nor pesticides were applied during the crop cycle. Other cultural practices were followed according to the recommendation for irrigated peanut in Thailand (Department of Agriculture, 1994). Tainan 9 was planted in border rows surrounding the experimental site to ensure

secondary spread of the disease.

Ten plants in each plot were randomly selected and recorded for disease scores, 1-5 for PBNV symptoms with 1 = healthy plant, 2 = spots on some leaves but no systemic symptoms, 3 = systemic symptoms without stunting, 4 = systemic symptoms with stunting and 5 = severe necrosis or die as described by Pensuk *et al*. (2002b) (Figure 1.) at 30, 40, 50, 60 and 70 days after sowing (DAS). For different evaluation dates, bamboo sticks with different colors were used as markers and placed near main stems of diseased plants to facilitate succeeding evaluations. Disease incidence was determined as percentage of infected plants in each plot. Plants showing local lesions were considered putatively susceptible and only local lesions confirmed by systemic symptoms in succeeding evaluations were considered diseased.

Because the standard deviations for PBND score were proportional to their corresponding means, disease score data were log-transformed (log(X+1)) and disease incidence data were arcsine-transformed (asin(sqrt(X*0.01))*57.3) in order to stabilize error variance before analysis of variance was performed (Snedecor and Cochran, 1980). Sixty and 70 day data were used for evaluation of PBNV resistance because of their low CV values and high F-ratios. Previous study also supported these suitable times (Pensuk, 2002). For arcsine transformation, zero values were substituted by (¼)/n and 100 values were substituted by 100-(¼)/n, where n is the number on which the percentage of infected plants is based. The arcsine formula gives the values being identical to



1A. Rating 2 **1B. Rating 3**

1C. Rating 4 **1D. Rating 5**

Figure 1. Typical symptoms of peanut bud necrosis disease: 1A. Spots on some leaves but no systemic symptoms; 1B. Systemic symptoms without stunting; 1C. Systemic symptoms with stunting and 1D. Severe necrosis or death. Healthy plant (rating 1) is not presented.

the arcsine tabular values and also facilitates the calculation in the Microsoft Excel program. Area under disease progress curve (AUDPC) was also calculated for each genotype using disease incidence (transformed data), which was the proportion (0-1.0) of symptomatic plants in the plot, using the formula:

$$AUDPC = \sum_{i=1}^{n} [Y_{i+1} + Y_i] / 2[T_{i+1} - T_i] \qquad [Eq. 1]$$

where: Y_{i+1} = apparent incidence (0-1.0) at the i^{th} observation, T_i = time (days) at the i^{th} observation, n = total number of observations (Shaner and Finney, 1977)

Broad-sense heritability (h^2_{bs}) estimates of each cross based on individual plants in the plot were calculated for PBND score, using relationships as follows:

$$\sigma^2_P = \sigma^2_G + \sigma^2_E \qquad [Eq. 2]$$

$$h^2_{bs} = \sigma^2_G / \sigma^2_G + \sigma^2_E \qquad [Eq. 3]$$

$$h^2_{bs} = [\sigma^2_{F2} - (\sigma^2_{P1} + \sigma^2_{P2})/2] / \sigma^2_{F2} \qquad [Eq. 4]$$

where: σ^2_{F2} = Variance among F_2 plants of any cross = phenotypic variance (σ^2_P)
σ^2_{P1} = Variance among plants of female parent
σ^2_{P2} = Variance among plants of male parent

Variances of crosses and parents are obtained from analysis of variance according to a completely randomized design, assuming that replications are classes. Therefore, variation within classes is the variance among plants of each entry as shown in Table 1. The variances after elimination of block effects were used for calculating heritability estimates. Estimate of environmental variance (σ^2_E) for any cross was calculated as ($\sigma^2_{P1} + \sigma^2_{P2}$)/2 and total genetic variance (σ^2_G) was obtained by subtracting σ^2_P.

Evaluation of agronomic traits

Because the disease incidence at the Kalasin experimental site was very high in the previous three consecutive years (Pensuk, 2002), evaluation for agronomic traits at this site was impossible, and thus it was conducted at Khon Kaen University (KKU)'s agronomy farm under rainfed conditions with supplemental irrigation during July to October in 2001. Treatments and experimental procedures were the same as those used in PBNV evaluation at the Kalasin site. At KKU site, the standard cultural practices followed the Department of Agriculture's recommendation (1994). Harvest time (60-75% of mature pods) was determined by pod scrape technique. Pods that showed blackening of inner shells were considered mature (Williams and Drexler, 1981). Ten plants in the plot were selected randomly and six important agronomic traits were determined from these samples. Pods were air-dried to obtain approximately 8% moisture content and data were recorded for pod number per plant, pod weight per plant, seed number per pod, seed weight per plant, 100 seed weight and shelling percentage.

Analysis of variance was done for testing significance of cross effects and heritability esti-

Table 1. Analysis of variance of crosses and parents.

Sources of variation	df.	MS		
		F_2	P_1	P_2
Among classes (block)	t-1	MST	MST	MST
Among plants within class	t(r-1)	MSE = variance F_2	MSE = variance P_1	MSE = variance P_2

t = Number of replications of each entry
r = Number of plants within replication

mates were calculated as described previously.

Evaluation of phenotypic correlation

Simple phenotypic correlation coefficients (based on plot means of 16 F_2 crosses) among PBNV resistance parameters as well as agronomic traits were calculated using correlation function of MSTAT-C (Bricker, 1989) and the method for hand calculation is available in standard statistics textbooks such as Gomez and Gomez (1984).

Results and Discussion

Evaluation of peanut bud necrosis virus resistance

Evaluation of parent lines for PBND score and PBND incidence indicated that the parents differed in the expression of PBNV resistance. IC 10, IC 34, ICGV 86031 and ICGV 86388 were resistant, whereas KK 60-3, KKU 72-1, KKU 72-2 and Luhua 11 were susceptible (data not reported). PBND incidence and AUDPC data were recorded based on plot means and were not used to estimate heritabilities. Sixty and 70 days data were used to estimate broad sense heritability for PBND score. Theoretically, negative values of heritability estimates were assumed to be zero and were expressed as zero values. The majority of heritability estimates in 16 crosses evaluated at 60 days after sowing (DAS) were zero and the rest had very low values (Table 2). The highest heritability estimate was in the cross KKU 72-1 × ICGV 86031 (0.33).

Heritability values at 70 DAS were zero for most crosses. The crosses KKU 72-1 × ICGV 86031, KKU 72-1 × ICGV 86388, KKU 72-1 × IC 34 and KKU 72-2 × ICGV 86388 had low heritability estimates and no cross had heritability estimates larger than 0.5. Similar results were reported recently by Poldate (2002) who found that narrow-sense heritability estimates for PBND score in cross ICGV 86388 × IC 10 were zero at 30, 40 and 50 DAS but the value become 0.63 at

Table 2. Broad-sense heritability estimates for PBNV score and agronomic traits of F_2 peanut population.

Cross	PBND score[2/]		Agronomic trait[3/]					
	60 DAS	70 DAS	Pod weight/ plant	Seed weight/ plant	Pod number/ plant	Seed number/ pod	100 seed weight	Shelling percentage
KK 60-3 × IC 10	0[1/]	0[1/]	0.16	0.32	0.55	0[1/]	0[1/]	0[1/]
KK 60-3 × IC 34	0	0	0.40	0.46	0.18	0.48	0.27	0.10
KK 60-3 × ICGV 86031	0	0	0.14	0.24	0.41	0.02	0.49	0
KK 60-3 × ICGV 86388	0	0	0.54	0.44	0.63	0	0	0.65
KKU 72-1 × IC 10	0	0	0[1/]	0[1/]	0.24	0.39	0.90	0.65
KKU 72-1 × IC 34	0	0	0	0	0.01	0.61	0.44	0.89
KKU 72-1 × ICGV 86031	0.33	0.30	0.08	0.04	0.27	0	0.54	0
KKU 72-1 × ICGV 86388	0	0.37	0.20	0.21	0.43	0.13	0.64	0.60
KKU 72-2 × IC 10	0	0.03	0	0	0[1/]	0.27	0.60	0
KKU 72-2 × IC 34	0.03	0.23	0	0	0	0.25	0.50	0.48
KKU 72-2 × ICGV 86031	0.06	0	0.46	0.49	0.59	0	0.52	0
KKU 72-2 × ICGV 86388	0.07	0.24	0.65	0.43	0.46	0.33	0.49	0.58
Luhua 11 × IC 10	0	0	0.30	0.52	0.73	0	0	0
Luhua 11 × IC 34	0	0	0.31	0.68	0.63	0.61	0	0.23
Luhua 11 × ICGV 86031	0	0.06	0.54	0.54	0.53	0.07	0	0
Luhua 11 × ICGV 86388	0	0	0.34	0.32	0.32	0.59	0.03	0.78

[1/] **Negative values are expressed as zero.**
[2/] **Data from Kalasin site and** [3/] **data from KKU site.**

60 DAS. In the cross ICGV 86388 × KK 60-1, the heritability estimates were zero at 30, 40, 50 and 60 DAS and in the cross IC 10 × KK 60-1, the heritability estimates were zero at 30, 40 and 50 DAS and become larger at 60 DAS (0.35). Poldate (2002) also found similar patterns of heritability for PBND incidence (percent infected plants) in these crosses. The heritability estimates were zero at 30, 40 and 50 DAS and larger than zero at 60 DAS. This indicated that assessments for PBNV resistance in peanut under field conditions should be done at 60 or 70 DAS, when PBNV symptoms were fully expressed and more variation among plants occurred. Assessments earlier than 60 DAS may be too soon to get an accurate estimation. The low heritability estimates found in this experiment indicated that environmental effects played major role in the variation of disease score and could mask genetic variation. This trait may not be useful for selection for PBNV resistance in peanut and another alternative disease parameters such as percent infected plants would be recommended. The advantage of PBND incidence compared to PBND score is that it is easier to evaluate especially when only systemic symptoms are considered. The systemic symptoms of PBNV are different from those of other viruses. Therefore, the coincidence of other viruses in the fields will not confound PBNV symptoms. Pensuk (2002) reported that 90% of PBND visual symptoms were confirmed by ELISA test. Culbreath *et al*. (1992) also reported for spotted wilt (caused by tomato spotted wilt virus (TSWV), a related species of PBNV) in peanut that 95 % of visual symptoms were confirmed by ELISA test. Considering the high accuracy of visual symptom evaluation, there is no need to confirm the symptomatic plants by ELISA test.

Tonsomros (2003) used F_4 generation of the crosses of small-seeded parents with lines resistant to PBNV (Some of his resistant lines was common to this study.) and reported that broad-sense heritability estimates for PBND score and PBND incidence were moderate to high. The contrasting results from this study may be due to the differences in population size, levels of PBND occurrence, environmental factors and generations used for evaluation. Larger population size is required for accurate evaluation and the evaluation should be based on family means in F_3 or more advanced generations rather than individual plants in F_2 generation. However, evaluation in F_2 generation can provide information on the general performance of the crosses.

Evaluation of agronomic traits

Analysis of variance among parent lines and crosses for agronomic traits revealed significant variation for most traits except for seed number per pod (data not reported), indicating sufficient genetic variation. Broad-sense heritability in the F_2 population was estimated based on individual plant observations to evaluate promising crosses that should be retained for generation advance and line development. In general, heritability estimates for agronomic traits in the F_2 population were low to moderate (Table 2). However, heritability estimates exceeding 0.5 were obtained for pod weight per plant in three crosses. For seed weight per plant, heritability estimates larger than 0.5 were found in three crosses. For pod number per plant, there were five crosses that showed moderate heritability estimates. Moderate heritability estimates were also observed for seed number per pod in three crosses, although variation component of this trait was not significant. Moderate to high heritability estimates were found for 100 seed weight in seven crosses. For shelling percentage, there were six crosses that had moderate to high heritability estimates.

Our results were in agreement with Jogloy *et al*. (1999). They found that estimates of heritability for agronomic traits were consistently low for most traits except for seed size, shelling percentage, pod weight and seed weight in some crosses in which high heritabilities were observed. In the parallel study, Kesmala (2003) found that additive gene effects were significant for all traits and non-additive gene effects were significant only for pod number per plant, pod weight per plant and seed weight per plant but smaller than additive gene effects.

Selection of breeding populations was gen-

erally based on population performance, genetic effects and genetic variation in the populations. Broad-sense heritability provides information of genetic variation but does not provide indication for the progress expected from selection. Considering low heritability estimates and the presence of non-additive gene effects that could hinder the progress of selection, selection of superior genotypes in the F_2 generation will be ineffective. Selection in more advanced generations will be more effective and modification in selection should be done such as selection based on progeny performance.

Correlation

Phenotypic correlation coefficients among traits studied were calculated based on plot means (Table 3). Significant positive correlation coefficients were found among PBNV resistance parameters with values of 0.91**, 0.87** and 0.84** for PBND score and PBND incidence, PBND score and AUDPC and PBND incidence and AUDPC, respectively. The results indicated that the same genetic systems regulated the expression of PBNV resistance traits. Any PBNV resistance parameter can be used for evaluation of peanut genotypes if it is more effective than the others. All PBNV resistance parameters showed low correlation coefficients with pod weight per plant, seed weight per plant, pod number per plant, seed number per pod, 100 seed weight and shelling percentage.

Highly significant and positive correlation coefficients were observed among pod weight per plant, seed weight per plant and pod number per plant with values of 0.93**, 0.93** and 0.80** for seed weight per plant and pod weight per plant, pod number per plant and pod weight per plant, and pod number per plant and seed weight per plant, respectively. Weight of 100 seeds had moderate correlation coefficient with pod number per plant (0.57**) and seed weight per plant (0.50**). Shelling percentage was significantly correlated with seed number per pod (0.28**). Ideally, data for calculating correlation coefficients should be recorded on the same population or the same plants.

For PBND, primary spread of the disease is more important than secondary spread and infected plants at early growth stages usually die and yield no pod (Buiel, 1996). Furthermore, there was high disease pressure at Kalasin site in the previous 3 consecutive years. In the pioneer work, experimental plots with 100% infected plants were observed (Pensuk, 2002). The evaluation of agronomic traits in the same population would not be

Table 3. Phenotypic correlation coefficients among 3 PBNV resistance parameters and 6 agronomic traits in the F_2 peanut populations of 16 crosses.

	PBNV resistance parameter[1/]		Agronomic trait[2/]					
	AUDPC	PBND score	Pod weight per plant	Seed weight	Pod number per plant	Seed number per pod	100 seed weight	Shelling percentage
PBND incidence	0.84**	0.91**	0.16*	0.05	0.05	0.02	0.14	-0.16
AUDPC		0.87**	0.19*	0.17*	0.17*	0.06	0.10	0.19*
PBND score			0.15	0.14	0.14	0.07	0.11	0.18*
Pod weight per plant				0.93**	0.93**	-0.04	0.57**	0.02
Seed weight per plant					0.80**	0.02	0.50**	0.10
Pod number per plant						0.01	0.18*	0.07
Seed number per pod							0.04	0.28**
100 seed weight								-0.09

***,** Significant at 0.05 and 0.01 probability levels, respectively.**
[1/]Data from Kalasin site and [2/]data from KKU site.

possible. Therefore, we evaluated PBNV resistance and agronomic traits in different environments that favored disease expression in one site and agronomic trait performance in another, using duplicated materials. The results indicated that genetic systems controlling the inheritance of PBNV resistance and agronomic traits were not associated. Selection of superior genotypes with reduced PNBD incidence and good agronomic traits will be possible because genes conditioning PBNV resistance and agronomic traits segregate independently in these populations. However, the conclusion is based on data of one experiment and further investigation is still required.

In conclusion, PBND score is not a useful parameter for estimating heritability in the F_2 generation of peanut because environmental effects are more important in the expression of PBNV symptoms. Selection of individual plants in the F_2 generation based on severity of PBNV symptoms will be ineffective. Selection for PBNV resistance should be based on family means in advanced generations of inbreeding. PBND incidence should be used rather than PBND score as it is easy to evaluate, especially when only systemic symptoms are considered. Low association between PBND resistance and agronomic traits provides the possibility to simultaneously select peanut genotypes with reduced PNBD incidence and good agronomic traits. For agronomic traits, low heritability estimates indicate that selection should be carried out in more advanced generations of inbreeding. Seed size should be used as criteria to improve pod weight per plant, seed weight per plant and yield. Selection for high pod number per plant may improve yield but not seed size.

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