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Inheritance of Pod Length and Other Yield Components in Two Cowpea and Yard-Long Bean Crosses

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Abstract: This study determined the gene effects involved in the inheritance of pod length and other yield-related traits and relationships among traits in crosses between two cowpea lines (TVu 2280 and TVu 2027) and a yard-long bean (TVu 6642) line with long pods. Plants of six generations (P_1, P_2, F_1, F_2, BC_1P_1, and BC_1P_2) derived from TVu 2280 × TVu 6642 and TVu 2027 × TVu 6642 were evaluated under field conditions. Data collected on 14 yield components of each cross were used for generation mean analysis. Gene effects and their magnitudes varied with the crosses; digenic epistatic gene effects were detected for 10 traits in TVu 2280 × TVu 6642 and 11 traits in TVu 2280 × TVu 6642. Only additive gene effect was significant for pod length in TVu 2280 × TVu 6642 while additive, dominant, and two of the three digenic epistatic gene effects were significant in TVu 2027 × TVu 6642. Models that incorporated only significant additive, dominant, and digenic epistasis were adequate for all 14 traits in TVu 2280 × TVu 6642 and eight of the 12 traits in TVu 2027 × TVu 6642 for which model-fitting was possible. Across segregating generation of the two crosses, pod length (PodLNT) was significantly ($p < 0.001$) correlated with three major yield components viz. pod weight (0.84, 0.77), number of seeds per pod (0.41, 0.30) and seed weight per pod (0.61, 0.29). Significant correlation of PodLNT with seed yield per plant was moderate and significant ($p < 0.01$–0.001) in the BC_1P_1 of the two crosses (0.31 and 0.41). An improvement in cowpea seed yield is feasible through selection for long pods in segregating generations involving crosses with yard-long bean.

Keywords: cowpea; yard-long bean; additive; dominance; epistasis; gene effects

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1. Introduction

Cowpea (*Vigna unguiculata* (L.) Walp.) is a well-adapted, multipurpose grain legume. Grains for human consumption is the most important product of the cowpea plant, although fresh and dried leaves [1,2], fresh peas, and fresh green pods, depending on preference, may be the most important in some local situations [3]. Cowpea also provides fodder for livestock and improves soil fertility by fixing atmospheric nitrogen through root nodule rhizobial symbiosis. Cowpea makes considerable contribution to food and nutrition security in developing countries, especially sub-Saharan Africa, as it is a cheap source of dietary protein and makes up for the low protein present in widely consumed cereals and tuber crop-based food [4,5]. Cowpea grains contain, on average, 25% protein, 53.2 mg/kg iron, 38.1 mg/kg zinc, 826 mg/kg calcium, 1915 mg/kg magnesium, 14,890 mg/kg potassium, and 5055 mg/kg phosphorus [5].

The species to which cowpea belongs has five sub-groups viz. *unguiculata*, *biflora*, *texilis*, *melanopthamus*, and *sesquipedalis* [6,7]. The *unguiculata* sub-group, commonly referred to as cowpea, black-eye pea, niebe, or southern pea, has seed size that ranges from medium to large while yard-long bean belongs to the *sesquipedalis* sub-group. The grain cowpea and yard-long bean are the most popular of the five sub-groups [8]. Yield is the expression of several characters that are considerably influenced by environment [9]. In breeding for increased yield, plant breeders require a good knowledge of the nature and magnitude of gene effects that moderate the characters that contribute to it. Inheritance of yield and its components have been reported in cowpea [10–15] and yard-long bean [16,17]. Yield-related traits are often correlated and selection for one may lead to negative or positive response in the other traits [18]. Correlation provides useful information on the association of plant traits that contribute to yield and are expected to be effective as selection indices for yield improvement, especially because yield is a complex trait usually with low heritability. Grain yield in cowpea has been reported to have a strong correlation with pod length [19,20], suggesting that an increase in pod length would result in increased yield.

Hybridization between genetically distant lines provides genetic variability that present opportunities for selecting plants with a combination of desirable traits from the parents. The transfer of valuable traits between genetically divergent genotypes has been explored extensively in the genus *Vigna* [21]. Efforts, which have met with little success, have been made to transfer genes between yard-long bean and cultivated cowpea or wild cowpea [22–25]. This indicates the existence of sexual barriers preventing such intra-species gene transfers [23,25]. Pod length in yard-long bean is one of the major morphological traits that differentiate it from grain cowpea [26]. The pod length of the yard-long bean varies from about 30 to100 cm, while that of the grain cowpea is about 15 to 30 cm [8]. The effect of the genes for increased pod length from yard-long bean on grain yield in cowpea is not known. Information on the genetics of yield and yield-related traits between cowpea genotypes and yard-long bean is fundamental to planning a breeding program to improve yield through increased pod length in cowpea. The objectives of this study were to determine the mode of gene action for pod length and other yield components in crosses between cowpea and yard-long bean and investigate the relationships among the traits.

2. Results

2.1. Variation in Means of Generations for Yield-Related Traits in TVu 2280 × TVu 6642

Significant differences were observed between the two parents in TVu 2280 × TVu 6642 for all considered traits, except number of days to first pod maturity (D1PMAT) and seed yield per plant (SYPP) (Table 1). The pod length (PodLNT) of the yard-long bean parent, TVu 6642, was higher than that of TVu 2280 by 28.2 cm (212%). TVu 6642 attained days to first flower (DFFL) 2.8 days later than TVu 2280 and had 15.9 (54.4%) fewer number of peduncles per plant (NpedPP) and 38.2 (186%) fewer number of pods per plant (NPosPP). Mean values of TVu 6642 were significantly higher than those of TVu 2280 by 3.4 (24.3%) for number of locules per pod (NLPP) and 1.79 g/plant (128%) for pod weight (PDWT). Pod length and NLPP for the F_1 were close to their mid-parental values, and the difference between F_1 and F_2 mean for each of these traits was not significant. These results suggest additive gene effect. The NPedPP value for their F_1 hybrid was significantly higher than that of TVu 2280, the parent with the higher value, by 10.3 (35.4%) (Table 1), indicating better-parent heterosis. The F_1 mean for PDWT was closer to that for the higher value parent TVu 6642 than TVu 2280, suggesting dominance for the trait. For DFFL, the means of the F_1 and F_2 were not significantly different. For NPosPP, the F_2 mean was 60% lower than that of the F_1. Similar results were obtained for NPedPP and NPosPP, with the F_2 mean significantly lower than values for the F_1 by 41.5% and 148.8%, respectively. These reductions in the F_2 mean values relative to the F_1 are indicative of dominant gene effects. The mean PDWT of the F_2 was not significantly different from that of the F_1. The values of BC_1P_1 and BC_1P_2 for PodLNT, NPedPP and PDWT converged on their respective recurrent parents, demonstrating the effectiveness of backcrossing for the genetic improvement of these traits. Although BC_1P_1 had a significantly higher NPosPP value than BC_1P_2, both values were lower than half the NPosPP for TVu 2280.

Of the seven seed traits studied, TVu 6642 was the better parent over TVu 2280 in four viz. number of seeds per pod (NSPP) by 2.7, seed weight per pod (SWPP) by 0.6 g/pod, 100 seed weight (100 SW) by 2.4 g and seed length (SL) by 4.3 mm. The cowpea parent, TVu 2280, was the better parent for the remaining three traits [seed width (SW) by 0.6 mm; seed thickness (ST) by 0.43 mm; and seed yield per plant (SYPP) by 13.23 g]. Difference between the two parents was significant for all traits, except SYPP. The F_1 mean values of NSPP and SL were similar to the mid-parent while the F_1 mean values for SWPP and 100 SW were higher than those of the higher value parent, TVu 6642, indicating heterosis for SWPP and 100 SW. The F_1 values for SW and ST were similar to that of TVu 2280, the better parent. Significant difference was observed between the F_1 and F_2 mean values for NSPP and SWPP, with the F_1 showing higher values over the F_2, also indicating dominance for higher NSPP and SWPP. The F_2 values for 100 SW, SL, SW and ST were not significantly reduced compared to those of the F_1, indicating additive effects. The backcross to TVu 2280 (BC_1P_1) for NSPP showed lower value (indicating convergence) but not significantly different from that of the recurrent parent. The mean values of the backcross to TVu 6642 (BC_1P_2), were also similar to values for the recurrent parent for NSPP, SWPP, 100 SW and SL and significantly different from BC_1 P_1 for each of the traits, suggesting effectiveness of backcross breeding method in improving these traits. The backcrosses converged on their respective recurrent parents for SW and ST. For ST, the convergence was complete for the BC_1 P_1 but partial for the BC_1 P_2. The F_1 mean value of SYPP was 69% and 130% higher than those of TVu 2280 and TVu 6642, respectively. The SYPP of the F_2 was reduced by 50.8% relative to that of the F_1. The reduction of the F_2 mean value compared to the F_1 was a demonstration of dominant gene effect, an inference similar to that made from the F_1 mean value relative to TVu 2280, the better parent.

2.2. Gene Effects for Yield-Related Traits in TVu 2280 × TVu 6642

Only additive gene effect was significant for PodLNT and PDWT. Chi-square values for a two-parameter model ('a' and 'd'), were 2.97 for PodLNT and 1.95 for PDWT, with both values indicating adequacy of the model. Among the six gene effects (m, a, d, aa, ad, and dd), only the mean effect was significant for DFFL (Table 2). At least one of the three digenic epistatic effects was significant for D1PMAT, NPosPP, and NLPP. For D1PMAT, the only significant main effect, in addition to 'm', was the dominant gene effect, and among the digenic epistatic gene effects, only additive × additive effect was significant (Table 2). In addition to significant additive and dominant gene effects for NPosPP and NLPP, dominant × dominant and additive × dominant digenic epistatic gene interactions were significant for these traits, respectively. Additive, dominant, and two epistatic gene effects, viz. additive × additive and additive × dominant gene effects, were significant for NPedPP. Models incorporating the significant additive–dominant and epistatic gene effects were also adequate in explaining the variation among the six generations for DFFL, D1PMAT, NPedPP, NPosPP, and NLPP in TVu 2280 × TVu 6642. For NPosPP, for which both dominant and dominant × dominant gene effects were significant, the former had a positive sign while the latter had a negative sign. The negative sign associated with the additive × additive gene effect for D1PMAT indicates that the cross was made in dispersion for this trait.

Only additive gene effect was significant for SWPP. The additive gene effect was also significant for the remaining seed traits except SYPP. The dominant gene effect was significant for SYPP and non-significant for the six other seed traits. Additive × additive gene effect was significant for all traits for which additive gene effect was significant except SWPP. Additive × dominant gene effect was significant only for NSPP; it was non-significant for the six other traits. Dominant × dominant gene effect was significant for NSPP and SYPP, and non-significant for the five other traits. A non-significant Chi-square value obtained for SWPP when an additive model was fitted showed that the model was adequate to explain the variation among the six generations for this trait (Table 2). For the remaining six traits, models incorporating significant digenic epistatic gene effects were adequate. The positive signs associated with estimates of additive × additive gene effect for NSPP indicate that the cross was made in association for this trait. For 100 SW and SYPP, the cross was made in dispersion as evidenced by the negative sign for estimates of additive × additive gene effect. Two of the 14 traits had opposite signs for dominant and dominant × dominant gene effect.

Narrow-sense heritability estimates of the four traits for which epistasis was absent showed considerable variation. It was 0.12 for PodLNT, 0.69 for DFFL, 0.75 for SYPP and 0.81 for PDWT.

2.3. Correlation among Traits in TVu 2280 × TVu 6642

Across the segregating generations, PodLNT showed moderate to high significant correlation with some agronomic traits contributing to yield, viz. PDWT (0.82), NLPP (0.33), NSPP (0.41), and SWPP (0.61), with some variation observed among the generations (Table 3). Although the correlation coefficient values of PodLNT with SYPP across the segregating generations (0.10), they were low and non-significant for F_2 (0.12) and BC_1P_2 (0.18), and the value for the BC_1P_1 was moderate and significant (0.31). Traits that showed significant correlation with SYPP across generations were NPedPP (0.78), NPosPP (0.89), NLPP (0.34), NSPP (0.39), and SWPP (0.30).

2.4. Variation in Means of Generations for Yield-Related Traits in TVu 2027 × TVu 6642

The parental lines showed differences for all traits in TVu 2027 × TVu 6642 except NPedPP, NLPP, NSPP, SL, and SYPP (Table 4). The pods of the yard-long bean parent TVu 6642 were, on average, longer than those of TVu 2027 by 17.9 cm (113.2%). TVu 6642 attained DFFL and D1PMAT earlier than the cowpea parent, TVu 2027, by 3.1 and 5.1 days, respectively. It had 1.9 (17.9%) fewer NPedPP than TVu 2027. TVu 6642 had higher mean value than TVu 2027 of 4.5 (44.7%) for NPosPP and 2.5 g/plant (45%) for PDWT. The F_1 mean values for PodLNT, NLPP, and PDWT were between the values for the parents but remarkably closer to the higher value parent, TVu 6642, suggesting dominant gene action for the traits. The F_1 of the cross attained DFFL and D1PMAT ahead of the earlier parent by 4.5 and 3.6 days, respectively, an indication of heterosis. The F_1 mean value for NPedPP was 2.4 (18.8%) higher than the mean value of the better parent, TVu 2027, although the difference was not significant. Better-parent heterosis was also manifested for NPosPP as evidenced by the significantly higher mean of the F_1 relative to that of the parent with higher value (TVu 6642) by 7.02 (48.8%). There was significant difference in the DFFL of the F_2 relative to the F_1. The F_2 mean values of NPedPP, NPosPP, and NLPP were similar to those of the $F_{1,}$ all indications of additive gene effect. For PodLNT, D1PMAT, and PDWT, the F_1 and F_2 showed significant differences. The means of the backcrosses for DFFL, D1PMAT, NLPP, PDWT, and PodLNT converged on their respective recurrent parents and were significantly different from each other, giving indication of the effectiveness of backcrossing for improving the traits. The BC_1P_1 mean for NPedPP was similar to that of the P_1 (higher value parent). For NPosPP, BC_1P_1 and BC_1P_2 did not converge on their recurrent parents, and their values were not significantly different from each other and from those of the F_1 and F_2.

The F_1 values for NSPP and SWPP were significantly higher than those of the better parent, TVu 2027, by 1.6 (14.6%) and 0.43 g (14.9%), respectively, indicating heterosis for both traits in TVu 2027 × TVu 6642. Mean F_1 value for 100 SW was higher than the mid-parental value and similar to the mean value of TVu 2027. The F_1 mean value was significantly higher than the F_2 mean by 1.8 (16.7%), 1.08 g (48.0%), and 3.19 g (18.7%) for NSPP, SWPP, and 100 SW, respectively. The F_2 mean value was similar to values of the P_1, P_2, BC_1P_1, and BC_1P_2 for NSPP (Table 4). Mean values of BC_1P_1 were lower and significantly different from that of the P_1 for SWPP and 100 SW but did not significantly differ from that of BC_1P_2. For SL, the F_1, F_2, BC_1P_1, and BC_1P_2 were not significantly different from one another and had similar values as the two parents. Seed width values for the F_1 and F_2 were not significantly different; the value for F_1 was similar to that of TVu 2027, the better parent. The SW of the backcrosses converged on those of their recurrent parents.

Mean F_1 value for ST was between those of the parents, but higher relative to mid-parental value. The F_1 value was significantly higher than the F_2 by 0.64 mm (13%). Each of the backcrosses converged on their respective recurrent parent and were significantly different from one another. The mean SYPP of the F_1 was significantly higher than the value for TVu 2027, the higher value parent, by 30.2 g (130%), indicating better-parent heterosis for the trait. The F_1 mean value for SYPP was significantly higher than that of the F_2 by 20.59 g (38%), an indication of dominance for higher SYPP in TVu 2027 × TVu 6642.

2.5. Gene Effects for Flowering, Pod, and Seed Traits in TVu 2027 × TVu 6642

All gene effects were significant for PodLNT except additive × dominant gene effect. Additive and dominant gene effects were significant NPosPP while only dominant gene effect was significant for NLPP. For NPosPP and NLPP, dominant × dominant gene effect was the only significant epistatic gene effect, while for NPedPP, only the additive × additive gene effect was significant in addition to the mean effect. Main and epistatic gene effects were adequate in explaining the variation among the six generations for PodLNT, NPedPP, NPosPP, and NLPP; for these traits, the Chi-square values were non-significant. The models that incorporated significant epistatic gene effects failed to adequately explain the variation among the generations for DFFL, D1PMAT, and PDWT; this was evidenced by the significant Chi-square values of 30.14, 16.36, and 4.47 for these traits, respectively (Table 5). The negative signs associated with the additive × additive gene effect for DFFL, D1PMAT, and NPedPP suggest that the cross was made in dispersion for these traits. For DFFL and D1PMAT, the negative sign was associated with dominant gene effect while the dominant × dominant gene effect had a positive sign.

The additive gene effect was significant for four of the seven seed traits studied in TVu 2027 × TVu 6642 viz. SWPP, 100 SW, SW, and ST. The dominant gene effect was significant for NSPP, SWPP, 100 SW, SW, ST, and SYPP. Among the six gene effects, only ‘m’ (mean effect) was significant for SL. Additive and dominant gene effects were significant for SW. None of the digenic epistatic gene effects were significant for SL, SW, and SYPP. While only the additive × additive gene effect was significant for NSPP and ST among the digenic epistatic effects, all three digenic epistatic gene effects were significant for SWPP and 100 SW. Dominant and additive × additive gene effects were significant for NSPP. The association of genes in the parents was indicated by the positive sign associated with the additive × additive gene effect for NSPP, SWPP, 100 SW, and ST.

Given the significance of all the gene effects for SWPP and 100 SW, a Chi-square analysis to fit the additive, dominant, and digenic epistatic model could not be carried out. A model incorporating only the main effects was adequate in explaining the variation among the six generations for SL and SW. This was evidenced by the non-significant Chi-square values (Table 5) of the deviations of observed from expected values for these traits. The additive–dominant and epistatic model could not explain the variation among the six generations for DFFL, D1PMAT, PDWT, and ST. This was indicated by the significant Chi-square value (Table 5). Apart from the mean effect, only the dominant gene effect was significant for SYPP. Eight of the 14 traits had opposite signs for dominant and dominant × dominant gene effects.

Narrow-sense heritability of the three traits for which epistasis was absent ranged from 0.75 for SYPP to 0.98 for SW.

2.6. Correlation among Traits in TVu 2027 × TVu 6642

Similar to the results obtained in TVu 2280 × TVu 6642, the correlation coefficient values of PodLNT with PDWT (0.77), NSPP (0.30), and SWPP (0.29) across the three segregating generations in TVu 2027 × TVu 6642 were significant ($p < 0.001$). However, unlike in TVu 2027 × TVu 6642, the correlation coefficient values of PodLNT with SYPP for each of the segregating generations and across them were significant; it was 0.20 for the F_2, 0.41 for BC_1P_1, 0.46 for BC_1P_2, and 0.19 across. Correlation coefficient between DFFL and most of the yield-related traits were negative and significant. The highest correlation coefficient values observed for SYPP in TVu 2027 × TVu 6642 were with NPosPP (0.77) and NPedPP (0.56) (Table 6). Both NPedPP and NPosPP (0.52) were also significantly correlated. Other traits with moderate correlation coefficient values with SYPP (0.37–0.48) were NLPP, NSPP, and SWPP.

Table 1. Means (± SE) of six generations for yield-related traits in TVu 2280 × TVu 6642.

	Generations								
Traits	**P_1 (TVu 2280)**	**P_2 (TVu 6642)**	**Mid-Parent**	**F_1**	**F_2**	**BC_1 P_1**	**BC_1 P_2**	**Range across Generations**	**LSD $_{(0.05)}$**
DFFL	41.7 ± 0.65 b	44.5 ± 0.82 a	43.1	40.7 ± 0.36 b	42.8 ± 0.40 ab	41.9 ± 0.44 ab	42.5 ± 0.50 ab	31.0–57.0	2.46
NPedPP	29.3 ± 1.89 b	13.3 ± 1.81 c	21.2	39.6 ± 2.96 a	23.0 ± 1.12 b	25.6 ± 1.69 b	14.7 ± 1.06 c	1.0–75.0	7.12
D1PMat	58.2 ± 0.63 bc	60.7 ± 1.28 ab	59.5	55.4 ± 0.75 c	61.8 ± 0.47 a	60.6 ± 0.61 ab	61.3 ± 0.62 ab	48.0–80.0	2.94
NPosPP	58.7 ± 3.45 a	20.5 ± 1.70 bc	39.6	66.9 ± 3.42 a	26.9 ± 1.35 b	29.3 ± 1.73 b	15.9 ± 0.96 c	2.0–101.0	8.41
NLPP	14.0 ± 0.30 d	17.4 ± 0.53 a	15.7	16.6 ± 0.36 ab	15.7 ± 0.15 bc	14.8 ± 0.17 cd	15.6 ± 0.17 bc	9.0–21.2	0.90
PodLNT (cm)	13.3 ± 0.30 e	41.5 ± 2.06 a	27.4	25.2 ± 0.52 c	26.9 ± 0.39 c	18.0 ± 0.34 d	33.8 ± 0.71 b	10.7–50.9	2.64
PDWT (g)	1.4 ± 0.07 d	3.2 ± 0.24 a	2.3	2.8 ± 0.08 b	2.6 ± 0.04 b	1.8 ± 0.05 c	2.9 ± 0.09 ab	0.6–5.4	0.33
NSPP	8.7 ± 0.49 cd	11.4 ± 0.40 a	10.1	10.2 ± 0.32 ab	9.1 ± 0.17 bcd	8.0 ± 0.24 d	9.5 ± 0.27 bc	2.0–16.2	1.15
SWPP (g)	1.1 ± 0.07 d	1.7 ± 0.12 b	1.4	2.0 ± 0.06 a	1.4 ± 0.03 c	1.2 ± 0.04 d	1.7 ± 0.06 b	0.2–3.2	0.21
100 SW (g)	13.2 ± 0.34 e	15.6 ± 0.56 d	14.4	18.7 ± 0.21 a	17.9 ± 0.18 ab	16.3 ± 0.25 cd	17.3 ± 0.24 bc	7.6–24.3	1.16
SL (mm)	7.5 ± 0.05 d	11.8 ± 0.19 a	9.6	11.0 ± 0.07 b	10.8 ± 0.07 b	9.0 ± 0.07 c	11.4 ± 0.07 a	7.0–13.4	0.40
SW (mm)	6.0 ± 0.05 a	5.4 ± 0.05 c	5.7	6.2 ± 0.04 a	6.2 ± 0.04 a	6.1 ± 0.03 a	5.8 ± 0.03 b	5.0–8.7	0.21
ST (mm)	4.5 ± 0.03 ab	4.1 ± 0.07 c	4.3	4.4 ± 0.05 ab	4.6 ± 0.05 a	4.6 ± 0.03 ab	4.3 ± 0.03 bc	3.5–9.0	0.24
SYPP (g)	50.0 ± 2.89 b	36.8 ± 2.60 bc	43.4	84.7 ± 2.81 a	41.7 ± 2.12 bc	31.3 ± 2.21 c	28.9 ± 1.96 c	0.6–168.1	14.00

Values with the same letters of the alphabet along each row are not significantly different by Duncan's multiple range test; DFFL = Days to first flower; NPedPP = Number of peduncles per plant; D1PMAT = Days to first pod maturity; NPosPP = Number of pods per plant; NLPP = Number of locules per pod; PodLNT= Pod length; PDWT= Pod weight; NSPP = Number of seeds per pod; SWPP = Seed weight per pod; 100 SW = Hundred seed weight; SL = Seed length; SW = Seed width; ST = Seed thickness; SYPP = Seed yield per plant.

Table 2. Estimates of gene effects (±SE) for yield-related traits in TVu 2280 × TVu 6642.

								Chi-Square		
Traits	**m**	**a**	**d**	**aa**	**ad**	**dd**	**Type of Epistasis**	**df**	**Value**	**Probability**
DFFL	44.8 ± 1.35 ***	−1.4 ± 0.82 ns	−4.1 ± 2.41 ns	−1.7 ± 1.58 ns	−2.2 ± 3.10 ns	0.8 ± 1.09 ns	-	5	0.02	>0.99
NPedPP	6.7 ± 3.90 *	8.0 ± 2.40 **	32.9 ± 6.94 ***	14.5 ± 4.58 **	−32.6 ± 8.74 **	3.0 ± 3.16 ns	-	1	3.68	0.05–0.10
D1PMat	68.1 ± 1.66 ***	−1.3 ± 0.97 ns	−12.7 ± 2.97 **	−8.7 ± 1.92 ***	4.1 ± 3.71 ns	0.6 ± 1.31 ns	-	3	0.25	0.95–0.99
NposPP	10.3 ± 0.33 *	−2.2 ± 0.08 *	25.0 ± 0.88 *	1.9 ± 0.31 ns	−1.2 ± 6.41ns	−13.9 ± 0.65 *	Duplicate	2	0.03	0.95–0.99
NLPP	14.8 ± 0.51 ***	−1.7 ± 0.30 ***	1.9 ± 0.91 *	0.9 ± 0.59 ns	−4.6 ± 1.13 ***	2.4 ± 2.21 ns	-	2	5.44	0.05–0.10
PodLNT (g)	28.5 ± 1.49 ***	−14.1 ± 0.87 ***	−3.3 ± 2.67 ns	−1.1 ± 1.73 ns	0.6 ± 3.33 ns	−1.7 ± 1.17 ns	-	4	2.97	0.50–0.75
PDWT (g)	2.4 ± 0.19 ***	−0.9 ± 0.11 ***	0.3 ± 0.33 ns	−0.1 ± 0.22 ns	−0.4 ± 0.42 ns	−0.2 ± 0.15 ns	-	4	1.95	0.50–0.75
NSPP	8.1 ± 0.65 ***	−1.3 ± 0.38 **	1.9 ± 1.15 ns	1.9 ± 0.75 *	−3.1 ± 1.45 *	6.9 ± 0.57 *	-	1	0.10	0.75–0.90
SWPP (g)	0.9 ± 0.12 ***	−0.3 ± 0.07 ***	1.1 ± 0.22 ns	0.6 ± 0.14 ns	−0.1 ± 0.27 ns	−0.2 ± 0.09 ns	-	4	6.03	0.10–0.25
100 SW (g)	17.2 ± 0.66 ***	−1.2 ± 0.38**	1.5 ± 1.18 ns	−2.8 ± 0.76 **	−2.1 ± 1.47 ns	0.2 ± 0.52 ns	-	3	0.14	0.95–0.99
SL (mm)	10.5 ± 0.22 ***	−2.1 ± 0.13 ***	0.5 ± 0.40 ns	−0.9 ± 0.26 **	−0.7 ± 0.50 ns	−0.3 ± 0.18 ns	-	3	4.77	0.10–0.25
SW (mm)	6.1 ± 0.12 ***	0.3 ± 0.07 ***	0.1 ± 0.21 ns	−0.3 ± 0.14 *	−0.6 ± 0.27 ns	0.0 ± 0.09 ns	-	3	0.52	0.90–0.95
ST (mm)	4.7 ± 0.13 ***	0.2 ± 0.08 **	−0.3 ± 0.24 ns	−0.4 ± 0.15 **	−0.3 ± 0.30 ns	0.0 ± 0.10 ns	-	3	0.51	0.90–0.95
SYPP (g)m	88.2 ± 5.76 *	3.7 ± 1.04 ns	−182.7 ± 13.95 *	−46.2 ± 5.60 ns	4.0 ± 84.80 ns	179.2 ± 8.85 *	Duplicate	3	0.29	0.95–0.99

DFFL = Days to first flower; NPedPP = Number of peduncles per plant; D1PMAT = Days to first pod maturity; NPosPP = Number of pods per plant; NLPP = Number of locules per pod; PodLNT = Pod length; PDWT = Pod weight; NSPP = Number of seeds per pod; SWPP = Seed weight per pod; 100 SW = Hundred seed weight; SL = Seed length; SW = Seed width; ST = Seed thickness; SYPP = Seed yield per plant. * = significant at 0.05; ** = significant at 0.01; *** = significant at 0.001; ns = non-significant at 0.05.

Table 3. Correlation among traits in segregating (F_2, BC_1P_1, and BC_1P_2) generations in TVu 2280 × TVu 6442 [n(F_2) = 195; n(BC_1P_1) = 95; n(BC_1P_2) = 93; n(across) = 383].

Traits		DFFL	NPedPP	D1PMat	NPosPP	NLPP	PodLNT	PDWT	NSPP	SWPP	100SW	SL	SW	ST
NPedPP	F_2	0.34 ***	-											
	BC_1P_1	0.25 **												
	BC_1P_2	0.39 ***												
	Across	0.30 ***												
D1PMat	F_2	0.78 ***	0.19 **	-										
	BC_1P_1	0.71 ***	0.02 ns											
	BC_1P_2	0.79 ***	0.24 *											
	Across	0.77 ***	0.14 *											
NposPP	F_2	0.35 ***	0.81 ***	0.20 **	-									
	BC_1P_1	0.29 **	0.83 ***	0.11 ns										
	BC_1P_2	0.27 **	0.74 ***	0.10 ns										
	Across	0.30 ***	0.82 ***	0.15 *										
NLPP	F_2	0.15 *	0.29 ***	0.12 ns	0.24 **	-								
	BC_1P_1	0.07 ns	0.23 *	0.03 ns	0.18 ns									
	BC_1P_2	0.10 ns	0.32 **	0.00 ns	0.31 **									
	Across	0.14 **	0.24 ***	0.09 ns	0.19 ***									
PodLNT (cm)	F_2	0.09 ns	0.12 ns	0.14*	0.04 ns	0.27 ***	-							
	BC_1P_1	0.08 ns	0.19 ns	−0.04 ns	0.23 *	0.31 **								
	BC_1P_2	0.04 ns	0.03 ns	0.03 ns	0.02 ns	0.43 ***								
	Across	0.08 ns	−0.11*	0.07 ns	−0.14 **	0.33 ***								
PDWT (g)	F_2	0.16 *	0.25 **	0.16 *	0.18 *	0.50 ***	0.75 ***	-						
	BC_1P_1	0.19 ns	0.41 ***	0.10 ns	0.45 ***	0.45 ***	0.70 ***							
	BC_1P_2	0.07 ns	0.21 *	−0.07 ns	0.19 ns	0.49 ***	0.80 ***							
	Across	0.14 **	0.10 *	0.10 ns	0.06 ns	0.49 ***	0.82 ***							
NSPP	F_2	0.15 *	0.30 ***	0.17 *	0.27 ***	0.73 ***	0.34 ***	0.60 ***	-					
	BC_1P_1	0.13 ns	0.34 ***	0.03 ns	0.33 **	0.56 ***	0.28 **	0.69 ***						
	BC_1P_2	0.07 ns	0.30 ***	−0.01 ns	0.27 **	0.87 ***	0.57 ***	0.52 ***						
	Across	0.14 **	0.24 ***	0.10 *	0.20 ***	0.73 ***	0.41 ***	0.60 ***						
SWPP	F_2	0.14 *	0.27 **	0.13 *	0.18 **	0.60 ***	0.48 ***	0.75 ***	0.66 ***	-				
	BC_1P_1	0.17 ns	0.38 ***	0.10 ns	0.39 ***	0.46 ***	0.53 ***	0.91 ***	0.74 ***					
	BC_1P_2	0.12 ns	0.29 **	0.06 ns	0.21*	0.66 ***	0.63 ***	0.81 ***	0.68 ***					
	Across	0.14 **	0.16 **	0.11*	0.09 ns	0.57 ***	0.61 ***	0.82 ***	0.69 ***					
100 SW (g)	F_2	0.05 ns	−0.17 *	0.05 ns	−0.25 **	−0.18 **	0.07 ns	0.14 *	−0.32 ***	0.17 *	-			
	BC_1P_1	−0.01 ns	−0.02 ns	0.01 ns	0.01 ns	−0.04 ns	0.47 ***	0.25 **	−0.32 **	0.12 ns				
	BC_1P_2	0.09 ns	0.19 ns	0.01 ns	0.23 *	0.16 ns	0.20 *	0.39 ***	0.00 ns	0.37 **				
	Across	0.06 ns	−0.08 ns	0.05 ns	−0.12 *	−0.03 ns	0.23 ***	0.30 ***	−0.17 **	0.24 ***				
SL (mm)	F_2	−0.05 ns	−0.19 **	−0.06 ns	−0.31 ***	−0.25 **	0.24 **	0.14 *	−0.30 ***	0.04 ns	0.54 ***	-		
	BC_1P_1	−0.13 ns	−0.06 ns	−0.20*	−0.07 ns	−0.13 ns	0.48 ***	0.19 ns	−0.33 **	0.02 ns	0.66 ***			
	BC_1P_2	0.09 ns	−0.03 ns	0.09 ns	0.02 ns	−0.08 ns	0.19 ns	0.28 **	−0.15 ns	0.16 ns	0.47 ***			
	Across	0.01 ns	−0.24 ***	0.00 ns	−0.30 ***	0.00 ns	0.63 ***	0.49 ***	−0.01 ns	0.30 ***	0.51 ***			

Table 3. *Cont.*

Traits		DFFL	NPedPP	D1PMat	NPosPP	NLPP	PodLNT	PDWT	NSPP	SWPP	100SW	SL	SW	ST
SW (mm)	F$_2$	−0.08 ns	−0.07 ns	−0.11 ns	−0.11 ns	−0.25 **	−0.28 ***	−0.18 **	−0.25 **	−0.13 ns	0.30 ***	0.52 ***	-	
	BC$_1$P$_1$	−0.02 ns	0.04 ns	−0.14 ns	−0.03 ns	−0.12 ns	0.12 ns	0.09 ns	−0.18 ns	0.06 ns	0.50 ***	0.37 **		
	BC$_1$P$_2$	0.06 ns	0.27 **	0.04 ns	0.25 *	−0.03 ns	−0.24 *	0.00 ns	−0.15 ns	0.07 ns	0.043 ***	0.39 **		
	Across	−0.05 ns	0.07 ns	−0.08 ns	0.04 ns	−0.19 **	−0.30 ***	−0.16 **	−0.22 ***	−0.14 **	0.32 ***	0.19 **		
ST (mm)	F$_2$	−0.05 ns	−0.15 *	−0.07 ns	−0.14 *	−0.21 **	−0.22 **	−0.14 *	−0.30 ***	−0.09 ns	0.40 ***	0.46 ***	0.77 ***	-
	BC$_1$P$_1$	0.10 ns	−0.05 ns	0.03 ns	0.01 ns	−0.14 ns	0.24 *	0.12 ns	−0.24 *	0.12 ns	0.48 ***	0.34**	0.51 ***	
	BC$_1$P$_2$	−0.06 ns	0.15 ns	−0.02 ns	0.02 *	−0.02 ns	0.14 ns	0.40 ***	−0.03 ns	0.32 **	0.54 ***	0.62 ***	0.49 ***	
	Across	−0.03 ns	−0.04 ns	−0.05 ns	−0.02 ns	−0.17 **	−0.19 **	−0.07 ns	−0.24 ***	−0.06 ns	0.38 ***	0.21**	0.74 ***	
SYPP (g)	F$_2$	0.36 ***	0.82 ***	0.22 **	0.93 ***	0.33 ***	0.12 ns	0.32 ***	0.39 ***	0.30 ***	−0.23 **	−0.29 ***	−0.14 *	−0.18 **
	BC$_1$P$_1$	0.28 **	0.81 ***	0.13 ns	0.95 **	0.27 **	0.31 **	0.58 ***	0.45 ***	0.52 ***	0.07 ns	−0.05 ns	0.00 ns	−0.03 ns
	BC$_1$P$_2$	0.34 ***	0.75 ***	0.15 ns	0.81 ***	0.43 ***	0.18 ns	0.38 **	0.43 ***	0.42 ***	0.28 **	0.00 ns	0.22 *	0.22 *
	Across	0.35 ***	0.78 ***	0.20 ***	0.89 ***	0.34 ***	0.10 ns	0.31 ***	0.39 ***	0.30 ***	−0.03 ns	−0.11 *	−0.02 ns	−0.08 ns

DFFL = Number of days to first flower; NPedPP = Number of peduncles per plant; D1PMAT = Number of days to first pod maturity; NPosPP = Number of pods. per plant; NLPP = Number of locules per pod; PodLNT = Pod length; PDWT = Pod weight; NSPP = Number of seeds per pod; SWPP = Seed weight per pod; 100 SW= 100 seed weight; SL = Seed length; SW = Seed width; ST = Seed thickness; SYPP = Seed yield per plant; Across = combined correlation for F$_2$, BC$_1$P$_1$ and BC$_1$P$_2$. * = significant at 0.05; ** = significant at 0.01; *** = significant at 0.001; ns = non-significant.

Table 4. Means (± standard errors) of seed yield and yield-related traits in TVu 2027 × TVu 6642.

	Generation								
Traits	**P$_1$ (TVu 2027)**	**P$_2$ (TVu 6642)**	**Mid-Parent**	**F$_1$**	**F$_2$**	**BC$_1$P$_1$**	**BC$_1$P$_2$**	**Range across Generations**	**LSD$_{(0.05)}$**
DFFL	44.0 ± 0.40 a	40.9 ± 0.44 b	42.5	36.5 ± 0.27 d	40.6 ± 0.26 b	44.4 ± 0.41 a	38.9 ± 0.29 c	33.0–61.0	1.55
NPedPP	12.5 ± 1.08 bc	10.6 ± 1.03 c	11.6	14.9 ± 0.93 ab	16.1 ± 0.46 a	13.0 ± 0.75 bc	14.3 ± 0.52 ab	1.0–39.0	2.81
D1PMat	64.3 ± 0.32 a	59.2 ± 0.61 bc	61.7	55.7 ± 0.45 d	60.5 ± 0.29 b	64.0 ± 0.43 a	57.9 ± 0.28 c	51.0–80.0	1.67
NPosPP	10.0 ± 1.18 c	14.4 ± 1.65 b	12.2	21.4 ± 1.82 a	19.3 ± 0.56 a	18.8 ± 1.13 a	20.8 ± 0.67 a	1.0–57.0	3.77
NLPP	13.0 ± 0.28 b	13.9 ± 0.72 ab	13.5	14.9 ± 0.35 a	13.9 ± 0.13 ab	13.1 ± 0.25 c	14.5 ± 0.22 a	4.0–22.0	0.98
PodLNT (cm)	15.8 ± 0.34 f	33.7 ± 1.79 a	24.7	27.4 ± 0.56 c	24.4 ± 0.30 d	18.6 ± 0.31 e	30.6 ± 0.49 b	9.5–54.4	2.00
PDWT (g)	5.6 ± 0.20 b	8.1 ± 0.42 a	6.9	8.0 ± 0.21 a	6.1 ± 0.11 b	5.5 ± 0.12 b	7.5 ± 0.15 a	2.1–13.8	0.67
NSPP	11.0 ± 0.31 b	10.8 ± 0.71 b	10.9	12.6 ± 0.41 a	10.8 ± 0.16 b	11.1 ± 0.26 b	11.3 ± 0.25 b	3.0–18.6	1.10
SWPP (g)	2.9 ± 0.11 b	1.8 ± 0.12 d	2.3	3.3 ± 0.14 a	2.2 ± 0.05 c	2.3 ± 0.08 c	2.0 ± 0.06 cd	0.5–4.7	0.30
100 SW (g)	24.9 ± 0.75 a	16.0 ± 0.44 d	20.4	24.9 ± 0.47 a	20.9 ± 0.47 b	19.3 ± 0.59 bc	17.7 ± 0.35 cd	2.1–60.9	2.54
SL (mm)	9.3 ± 0.11 a	10.8 ± 0.11 a	10.0	12.2 ± 0.17 a	12.1 ± 1.14 a	10.0 ± 0.13 a	11.2 ± 0.08 a	7.2–17.5	4.95
SW (mm)	7.1 ± 0.09 a	5.2 ± 0.05 d	6.2	7.0 ± 0.06 ab	6.4 ± 0.13 bc	6.7 ± 0.05 ab	5.9 ± 0.04 c	4.0–14.3	0.60
ST (mm)	6.2 ± 0.09 b	4.0 ± 0.04 e	5.1	5.5 ± 0.06 b	4.9 ± 0.05 c	5.4 ± 0.05 a	4.6 ± 0.04 d	3.1–6.7	0.26
SYPP (g)	23.2 ± 2.37 c	19.1 ± 1.94 c	21.1	53.4 ± 5.19 a	32.8 ± 1.05 b	31.6 ± 2.44 b	31.0 ± 1.31 b	0.6–115.3	7.67

Values with the same letters of the alphabet along each row are not significantly different by Duncan's multiple range test. DFFL = Days to first flower; NPedPP = Number of peduncles per plant; D1PMAT = Days to first pod maturity; NPosPP = Number of pods per plant; NLPP = Number of locules per pod; PodLNT = Pod length; PDWT = Pod weight; NSPP = Number of seeds per pod; SWPP = Seed weight per pod; 100 SW = Hundred seed weight; SL = Seed length; SW = Seed width; ST = Seed thickness; SYPP = Seed yield per plant.

Table 5. Estimates of gene effects (± SE) for yield-related traits in TVu 2027 × TVu 6642.

TRAITS	m	a	d	aa	ad	dd	Type of Epistasis	Chi-Square		
								df	Value	Probability
DFFL	44.7 ± 0.87 ***	1.6 ± 0.51 **	−8.3 ± 1.52 ***	−2.3 ± 1.01 *	−1.3 ± 1.95 ns	4.0 ± 0.70 ***	Duplicate	1	30.14	<0.0001
NPedPP	17.3 ± 1.57 ***	1.0 ± 0.92 ns	2.4 ± 2.76 ns	−5.7 ± 1.82 *	0.4 ± 3.56 ns	−2.2 ± 1.28 ns	-	4	2.90	0.50–0.75
D1PMat	65.4 ± 0.94 ***	2.5 ± 0.55 ***	−9.8 ± 1.64 ***	−3.7 ± 1.09 **	−1.9 ± 2.13 ns	3.6 ± 0.76 ***	Duplicate	1	16.37	<0.0001
NposPP	10.3 ± 0.33 ***	−2.2 ± 0.08*	25.0 ± 0.89 *	1.9 ± 0.31 ns	−1.2 ± 6.40 ns	−13.9 ± 0.65 *	Duplicate	2	0.01	>0.99
NLPP	12.8 ± 0.55 ***	−0.5 ± 0.32 ns	2.0 ± 0.97 *	0.6 ± 0.64 ns	1.1 ± 1.24 ns	−0.9 ± 0.44 *	Duplicate	3	0.74	0.75–0.90
PodLNT (cm)	21.5 ± 1.13 ***	−8.9 ± 0.65 ***	5.9 ± 1.99 **	3.2 ± 1.30 *	3.4 ± 2.52 ns	−3.0 ± 0.90 **	Duplicate	1	2.35	0.10–0.25
PDWT (g)	4.3 ± 0.38 ***	−1.3 ± 0.22 ***	3.6 ± 0.67 ***	2.5 ± 0.44 ***	0.4 ± 0.85 ns	−0.8 ± 0.30 *	Duplicate	1	4.47	0.01–0.05
NSPP	9.0 ± 0.62 ***	0.1 ± 0.36 ns	3.6 ± 1.10 **	1.9 ± 0.72**	0.5 ± 1.39 ns	−0.4 ± 0.50 ns	-	3	0.05	>0.99
SWPP (g)	1.2 ± 0.17 ***	0.6 ± 0.10 ***	2.2 ± 0.30 ***	1.2 ± 0.20 ***	−0.8 ± 0.38 *	−0.3 ± 0.14 *	Duplicate	-	-	-
100 SW (g)	17.0 ± 1.42 ***	4.4 ± 0.83 ***	7.8 ± 2.52 **	3.4 ± 1.65 *	−7.5 ± 3.19 *	−2.8 ± 1.15 *	Duplicate	-	-	-
SL (mm)	12.1 ± 2.80 ***	−0.8 ± 1.62 ns	0.0 ± 4.94 ns	−2.1 ± 3.23 ns	−3.1 ± 6.26 ns	−0.4 ± 2.24 ns	-	5	1.00	0.95–0.99
SW (mm)	5.8 ± 0.34 ***	1.0 ± 0.20 ***	1.2 ± 0.60 *	0.4 ± 0.39 ns	−0.6 ± 0.75 ns	−0.1 ± 0.27 ns	-	3	1.20	0.75–0.90
ST (mm)	4.3 ± 0.14 ***	1.1 ± 0.08 ***	1.3 ± 0.26 ***	0.8 ± 0.17 ***	−0.1 ± 0.32 ns	−0.2 ± 0.12 ns	-	2	6.82	0.01–0.05
SYPP (g)	12.2 ± 4.34 **	2.1 ± 2.51 ns	41.2 ± 7.66 ***	8.9 ± 5.01 ns	−12.2 ± 9.71 ns	−1.5 ± 3.48 ns	-	4	0.21	>0.99

DFFL = Days to first flower; NPedPP = Number of peduncles per plant; D1PMAT = Days to first pod maturity; NPosPP = Number of pods per plant; NLPP = Number of Locules per pod; PodLNT = Pod length; PDWT = Pod weight; NSPP = Number of seeds per pod; SWPP = Seed weight per pod; 100 SW = Hundred seed weight; SL = Seed length; SW = Seed width; ST = Seed thickness; SYPP = Seed yield per plant; * = significant at 0.05; ** = significant at 0.01; *** = significant at 0.001; ns = non-significant.

Table 6. Correlation among traits in segregating (F_2, BC_1P_1 and BC_1P_2) generations in TVu 2027 × TVu 6642 [n(F_2) = 186; n(BC_1P_1) = 84; n(BC_1P_2) = 92; n(across) = 362].

Traits		DFFL	NPedPP	D1PMat	NPosPP	NLPP	PodLNT	PDWT	NSPP	SWPP	100 SW	SL	SW	ST
NPedPP	F_2	−0.31 ***	-											
	BC_1P_1	−0.62 ***												
	BC_1P_2	0.00 ns												
	Across	−0.34 ***												
D1PMat	F_2	0.76 ***	−0.27 **	-										
	BC_1P_1	0.86 ***	−0.57 ***											
	BC_1P_2	0.74 ***	0.05 ns											
	Across	0.83 ***	−0.28											
NposPP	F_2	−0.33 ***	0.47 ***	−0.36 ***	-									
	BC_1P_1	−0.52 ***	0.67 ***	−0.52 ***										
	BC_1P_2	−0.04 ns	0.45 ***	−0.00 ns										
	Across	−0.33 ***	0.52 ***	−0.34 ***										
NLPP	F_2	−0.23 **	0.24 **	−0.27 **	0.31 ***	-								
	BC_1P_1	−0.43 ***	0.16 ns	−0.40 **	0.30 **									

Table 6. *Cont.*

Traits		DFFL	NPedPP	D1PMat	NPosPP	NLPP	PodLNT	PDWT	NSPP	SWPP	100 SW	SL	SW	ST
	BC_1P_2	−0.22 *	0.09 ns	−0.19 ns	0.12 ns									
	Across	−0.36 ***	0.18 **	−0.36 ***	0.27 ***									
PodLNT (cm)	F_2	−0.31 ***	0.01 ns	−0.12 ns	0.11 ns	0.40 ***	-							
	BC_1P_1	−0.41 **	0.07 ns	−0.31 **	0.26 *	0.58 ***								
	BC_1P_2	−0.19 ns	0.12 ns	−0.12 ns	0.22 *	0.63 ***								
	Across	−0.53 ***	0.07 ns	−0.47 ***	0.18 **	0.50 ***								
PDWT (g)	F_2	−0.18 *	0.02 ns	−0.11 ns	0.12 ns	0.27 **	0.58 ***	-						
	BC_1P_1	−0.26 *	0.07 ns	−0.19 ns	0.23 *	0.49 ***	0.85 ***							
	BC_1P_2	−0.17 ns	0.12 ns	−0.06 ns	0.17 ns	0.68 ***	0.93 ***							
	Across	−0.36 ***	0.50 ns	−0.31 ***	0.18 **	0.47 ***	0.77 ***							
NSPP	F_2	−0.14 ns	0.22 **	−0.28 ***	0.26 **	0.78 ***	0.24 **	0.17 *	-					
	BC_1P_1	−0.37 **	0.17ns	−0.39 **	0.33 **	0.90 ***	0.52 ***	0.48 ***						
	BC_1P_2	−0.18 ns	0.14 ns	−0.20 *	0.16 ns	0.85 ***	0.57 ***	0.60 ***						
	Across	−019 **	0.16**	−0.27 ***	0.26 ***	0.81 ***	0.30 ***	0.33 ***						
SWPP	F_2	−0.25 **	0.13 ns	−0.16 *	0.086 ns	0.40 ***	0.44 ***	0.48 ***	0.39 ***	-				
	BC_1P_1	−0.39 **	0.12 ns	−0.32 **	0.31 **	0.59 ***	0.79 ***	0.93 ***	0.61 ***					
	BC_1P_2	−0.20 *	0.06 ns	−0.13 ns	0.12 ns	0.72 ***	0.69 ***	0.80 ***	0.73 ***					
	Across	−0.18 **	0.12 *	−0.10 *	0.15 *	0.49 ***	0.29 ***	0.49 ***	0.51 ***					
100 SW (g)	F_2	−0.18 *	−0.04 ns	0.01 ns	−0.09 ns	−0.11 ns	0.26 **	0.34 ***	−0.31 ***	0.60 ***	-			
	BC_1P_1	−0.16 ns	0.07 ns	−0.04 ns	0.14 ns	−0.13 ns	0.45 ***	0.59 ***	−0.21 *	0.50 ***				
	BC_1P_2	−0.09 ns	−0.03 ns	0.08 ns	−0.03 ns	0.07 ns	0.29 **	0.44 ***	−0.05 ns	0.53 ***				
	Across	−0.11 *	0.03 *	0.04 ns	−0.03 ns	−0.10 ns	0.11 *	0.26 ***	−0.25 ***	0.56 ***				
SL (mm)	F_2	0.00 ns	0.00 ns	−0.00 ns	−0.07 ns	−0.03 ns	−0.04 ns	−0.03 ns	−0.04 ns	−0.05 ns	−0.03 ns	-		
	BC_1P_1	0.00 ns	−0.05 ns	0.15 ns	−0.04 ns	−0.21 ns	0.37 **	0.48 ***	−0.35 **	0.33 **	0.72 ***			
	BC_1P_2	0.05 ns	−0.11 ns	0.17 ns	0.06 ns	−0.15 ns	0.08 ns	0.16 ns	−0.19 ns	0.15 ns	0.49 ***			
	Across	−0.03 ns	0.02 ns	−0.02 ns	−0.05 ns	−0.02 ns	0.01 ns	−0.01 ns	−0.05 ns	−0.03 ns	0.01 ns			
SW (mm)	F_2	−0.07 ns	−0.08 ns	−0.02 ns	−0.09 ns	−0.05 ns	−0.01 ns	−0.09 ns	−0.08 ns	0.14 ns	0.19**	0.04 ns	-	
	BC_1P_1	−0.07 ns	0.09 ns	−0.05 ns	0.10 ns	−0.13 ns	0.25 *	0.47 ***	−0.18 ns	0.40 **	0.68 ***	0.63 ***		
	BC_1P_2	−0.15 ns	0.05 ns	−0.14 ns	−0.10 ns	0.09 ns	0.19 ns	0.30 **	0.05 ns	0.39 **	0.65 ***	0.49 ***		
	Across	0.06 ns	−0.05 ns	0.10 ns	−0.07 ns	−0.09 ns	−0.15 *	−0.12 *	−0.08 ns	0.18 **	0.26 **	0.04ns		
ST (mm)	F_2	−0.09 ns	−0.02 ns	0.06 ns	−0.10 ns	−0.18 *	0.13 ns	0.23 **	−0.35 ***	0.47 ***	0.65 ***	0.10 ns	0.21 **	-
	BC_1P_1	−0.12 ns	−0.03 ns	0.02 ns	−0.06 ns	−0.11 ns	0.29 **	0.50 ***	−0.18 ns	0.49 ***	0.75 ***	0.75 ***	0.80 ***	
	BC_1P_2	−0.09 ns	−0.00 ns	0.00 ns	−0.10 ns	−0.04 ns	0.07 ns	0.21 *	−0.07 ns	0.33 **	0.72 ***	0.53 ***	0.72 ***	
	Across	0.18 **	−0.05 ns	0.28 ***	−0.09 ns	−0.22 ***	−0.25 ***	−0.00 ns	−0.24 ***	0.44 ***	0.61 ***	0.07 ns	0.33 ***	
SYPP (g)	F_2	−0.40 ***	0.53 ***	−0.37 ***	0.73 ***	0.43 ***	0.20 **	0.25 **	0.36 ***	0.45 ***	0.28 **	−0.08 ns	−0.01 ns	0.10 ns
	BC_1P_1	−0.52 ***	0.65 ***	−0.52 ***	0.91 ***	0.37 **	0.41 ***	0.43 ***	0.41 **	0.50 ***	0.29 **	0.09 ns	0.24 *	0.21 *
	BC_1P_2	−0.24 *	0.49 ***	−0.06 ns	0.57 ***	0.34 **	0.46 ***	0.47 ***	0.42 ***	0.50 ***	0.32 **	0.05 ns	0.19 ns	0.16 ns
	Across	−0.35 ***	0.56 ***	−0.31 ***	0.77 ***	0.37 ***	0.19 **	0.27 ***	0.37 ***	0.48 ***	0.28 ***	−0.04 ns	0.04 ns	0.12 *

DFFL = Number of days to first flower; NPedPP = Number of peduncles per plant; D1PMAT = Number of days to first pod maturity; NPosPP = Number of pods. per plant; NLPP = Number of locules per pod; PodLNT = Pod length; PDWT= Pod weight; NSPP = Number of seeds per pod; SWPP = Seed weight per pod; 100 SW = 100 seed weight; SL= Seed length; SW = Seed width; ST = Seed thickness; SYPP = Seed yield per plant; Across = combined correlation for F_2, BC_1P_1 and $BC_1P_{2.}$ * = significant at 0.05; ** = significant at 0.01; *** = significant at 0.001; ns = non-significant.

3. Discussion

Improvement in seed yield is a major research objective for many tropical crops. Cowpea seed yield in farmers' fields in SSA ranges from 0.03 to 0.35 t ha^{-1} [27–29], while 1.5 to 2.5 t ha^{-1} have been reported for research stations [30]. Breeding programs aimed at increase in seed yield productivity in cowpea will benefit from information on the inheritance of agronomic traits that contribute to yield.

Several agronomic traits are associated with grain yield in cowpea, among which is pod length [22,31]. In the present study, pods of the yard-long bean TVu 6642 were, on average, 212% longer than those of the cowpea Line TVu 2280 in TVu 2280 × TVu 6642 and 113% longer than those of TVu 2027 in TVu2027 × TVu 6662. In TVu 2280 × TVu 6642, only the additive gene effect was involved in the inheritance of PodLNT. One of the advantages of generation mean analysis, the genetic analysis procedure used in this study, is that it provides a procedure for testing models with significant gene effects for adequacy. It has, therefore, been used extensively in the genetic analysis of several traits in cowpea [32,33], soybean [34], lentil [35], faba bean [36], wheat [37,38], and maize [39,40]. The non-significance of dominance and the three digenic epistatic gene effects for PodLNT in TVu 2280 × TVu 6642 as well as the adequacy of the additive model ('m' and 'a') clearly indicate that the trait was simply inherited in this cross. The importance of the additive gene effect was further demonstrated by the similar mean values for the F_1 (25.2 cm) and F_2 (26.9 cm) observed for this trait. This is in contrast to traits with predominant dominant gene effects for which superior performance in the F_1 are followed by a considerable reduction in performance of the F_2.

In TVu 2027 × TVu 6642, the significance of dominance and two of the three digenic epistatic gene effects ('aa' and 'dd') for PodLNT indicate that gene interactions made considerable contributions to the expression of this trait. The signs associated with estimates of dominant and dominant × dominant gene effects indicate the direction in which the gene effect influences the mean of the population [39]. The positive sign of the dominant gene effect and negative sign for the estimate of the dominant × dominant gene effect, as found for PodLNT in TVu 2027 × TVu 6642 in the present study, indicate duplicate interaction between dominant increasing alleles [41]. The non-significant Chi-square value for a five-parameter model showed that the digenic epistatic model was adequate in explaining the variation in PodLNT among the generations. This demonstrates, in contrast to the results obtained in TVu 2280 × TVu 6642, that the inheritance of PodLNT could be complex, depending on the cross and genetic background. It is plausible that the two cowpea lines have different alleles for PodLNT. In the present study, the pods of TVu 2027 were, on average, longer than those of TVu 2280 by 2.5 cm.

Epistasis was also important in the inheritance of other yield-related traits in the present study. Ten and 11 of the 14 traits studied in TVu 2280 × TVu 6642 and TVu 2027 × TVu 6642, respectively, had at least one significant epistatic gene effect. In traits for which digenic epistatic gene effects were not significant in one cross, at least one of them was significant in the other cross. The epistasis detected was mostly of the duplicate type as indicated by the opposite signs associated with the estimates of dominant and dominant × dominant gene effects. Inadequacy of models with digenic epistatic effects for some of the traits suggests the involvement of higher order gene interactions for those traits. The involvement of epistasis for yield components in cowpea has been reported [13,14,33]. Important contribution of epistasis to traits of economic importance implies that a significant component of performance for those traits derives from gene interactions. Favorable gene interactions are disrupted as individuals are advanced due to segregation and recombination. The additive × additive component of epistasis is fixable and can be exploited in crops cultivated as lines such as cowpea. Consequently, breeding programs aimed at cowpea seed yield improvement would require the advancement of large number of plants to later generations when individuals whose good performance for yield-related traits that are derived from fixed favorable additive × additive epistatic interaction can be identified.

The relationship between PodLNT and SYPP varied with segregating generations. The variation was higher for TVu 2280 × Tvu 6642, in which significant correlation between the traits was observed only in the BC_1P_1. The moderate and significant correlation between PodLNT and SYPP observed in the present study can be exploited in the introgression of genes for long pods into cowpea, since selection for traits being transferred from a donor parent is usually carried out in the backcross generation to the recurrent parent which, in this case, is the BC_1P_1. Pod length was also correlated with other yield components, viz. NLPP, PDWT, NSPP, and SWPP. Although SYPP was influenced more by NPosPP than any other trait in the present study, the moderate to high significant correlations of PodLNT with NLPP, PDWP, NSPP, and SWPP suggest that an intensive selection for plants with long pods would likely increase SYPP through these other yield components. Other studies have found significant correlation between PodLNT, on the one hand, and NLPP [42], PDWT [42,43], NSPP [10,19], and SWPP [43] on the other. Of the three genotypes used in this study, TVu 2280 had the highest SYPP, NPedPP, and NPosPP. Number of peduncles per pod (NpedPP) and NPosPP are both important yield components [19]. A breeding program in which TVu 2280 is used as a source of high NPedPP and NPosPP, while TVu 6642 is used as a donor of genes for high PodLNT, is promising for creating variability from which plants with superior combinations of genes for the important yield components can be selected. A backcrossing scheme with TVu 2280 as a recurrent parent, in which selection is carried out for the long pods of TVu 6642, will be effective in the transfer of the latter. The construction of a selection index that includes the yield-related traits would be most appropriate.

Digenic epistatic gene effects, as observed for many of the traits in the two crosses involved in the present study, often result in biases in variance estimates [44] which are, in turn, used for the estimation of heritability. In the present study, therefore, heritability was estimated only for traits for which epistasis did not make significant contributions. The low narrow-sense heritability obtained for PodLNT in the present study (0.12) involving cowpea and yard-long bean is indicative of a trait with a large environmental effect. A narrow-sense heritability of 0.25 was reported for PodLNT [15]. These results suggest that marker-assisted selection would be useful for the improvement of the trait. Several authors have reported the detection of QTLs for PodLNT in *Vigna unguiculata* [23,45,46]. Four QTLs were reported for pod length based on a study from restriction site associated DNA sequencing [47]. Using DArT markers, a major QTL (qPoL3) was reported for PodLNT on chromosome 3 and another (qPoL8) on chromosome 8 [46]. A total of 72 SNPs were detected to be associated with PodLNT in a study of recombinant inbred lines from a yard-long bean line and crosses with cultivated cowpea, landraces, cultivars, and breeding lines [45]. These markers can be tested for polymorphism in the developed populations derived from crosses of cowpea and yard-long bean. The clustering together of QTLs for PodLNT and 100-seed weight [46], another yield component, offers promise for the simultaneous improvement of these traits. Although previous attempts at crossing cowpea and yard-long bean have met with little success as a result of sexual barriers [22,24], the success achieved in the present study, especially with the production of a large number of seeds of the backcrosses, indicates that TVu 2280 and TVu 2027 could be used as bridge-genotypes for the transfer of desirable traits from yard-long bean to widely cultivated cowpea lines.

The highest better-parent heterosis in the two crosses was observed for SYPP. Heterosis results from dominant effects and their interaction [48,49]. It has been exploited commercially through hybrid breeding in several cross-pollinated crops, among which is maize, a crop in which the percentage of better-parent heterosis for yield ranges between 43.1 and 99.4 [50,51]. Self-pollinated crops in which heterosis has been reported for yield include rice (20–25%) [52], tomato (149%) [53] and cowpea (59%) [54,55]. The better-parent heterosis of 69–130% observed for SYPP in the present study was much higher than such values previously reported in cowpea [54,55]. The heterosis observed for yield in rice and tomato has been successfully exploited. However, the arrangement of the floral parts, poor seed set, and practical difficulty involved in hybrid seed production make the possibility of commercial hybrid exploitation in cowpea rather distant.

4. Materials and Methods

Seeds used in the study were generated in the screenhouse of the Cowpea Breeding Unit of the International Institute of Tropical Agriculture (IITA), Ibadan (7°30′ N, 3°54′ E and 213 m altitude), Nigeria. Parental lines and progenies (F_1, F_2, BC_1P_1, and BC_1P_2) of crosses of TVu 6642 (yard-long bean) with each of two cowpea lines, viz. TVu 2280 and TVu 2027, were evaluated for agronomic traits at the research field of IITA, Ibadan, located in the forest–savanna transition agro-ecological zone of Nigeria. The soil of the experimental field was sandy clay loam with a pH (of soil H_2O) of 6.2. Soil organic carbon (%) was 0.35. Total nitrogen was 0.085% and available p (ppm) was 614. Exchangeable bases (ppm) were 872 for Ca, 172 for Mg, 98 for K, and 118 for Na. Land was cleared, ploughed, and ridged prior to planting. Seeds were scarified and treated with fungicide (active ingredients: 20% w/w thiamethoxam, 20% w/w metalaxyl-M, and 2% w/w difenoconazole) to enable uniform seedling emergence. For each cross, a total of 200 F_2 plants, 100 each of the backcrosses and 20 each of the F_1, P_1, and P_2 were evaluated between 19 September 2017 and 16 January 2018 in a randomized complete block design with four blocks. Each block consisted of four rows, each 11.2 m long and spaced 0.75 m apart. Each block had 50 plants of the F_2, 25 each of the backcrosses, and 5 each of F_1, P_1, and P_2. Plants were spaced 0.40 m apart within rows.

The meteorological data of the location for the period the study was carried out are provided in Table 7. Total precipitation from 15 September 2017 to 22 October 2017, when the rains ceased, was 197.5 mm. Thereafter, 20 mm irrigation was supplied weekly in two equal split amounts of 10 mm in addition to 23.2 m of precipitation received in November. Irrigation was reduced to 10 mm per week from 30 November 2017 when the first pods were harvested. Minimum and maximum temperature over the duration of the study averaged 22.5 and 32.2 °C, respectively. Average minimum relative humidity was 35.8% (range = 0–80%), while average maximum relative humidity was 91.5% (range = 31–100%). No fertilizer was applied. Insecticide (active ingredient: 50 g/L lambda-cyhalothrin; imidacloprid 17.8% S.L. (soluble liquid) was sprayed at podding stage to control biting, chewing, and sucking insect pests. Plants were staked to prevent their long pods from making contact with the soil, and weeding was performed manually at regular intervals.

Data on individual plant basis were collected on flowering, maturity, pod, and seed traits, viz. number of days to first flower (DFFL), number of days to first pod maturity (D1PMAT), number of peduncles per plant (NPedPP), number of pods per plant (NPosPP), pod length (PodLNT), pod weight (PDWT), number of locules per pod (NLPP), number of seeds per pod (NSPP), seed weight per pod (SWPP), 100-seed weight (100 SW), seed yield per pod (SYPP), seed length (SL), seed thickness (ST) and seed width (SW). The last three seed traits were measured using vernier calipers.

Table 7. Meteorological data for September 2017 to January 2018 at International Institute of Tropical Agriculture (IITA), Ibadan.

Month	Year	Total Rainfall (mm)	Total Evaporation (mm)	Mean Minimum Temperature (°C)	Mean Maximum Temperature (°C)	Mean Minimum Relative Humidity (%)	Mean Maximum Relative Humidity (%)	Mean Daily Sunshine Hour (hr)
September	2017	221.2	80.0	21.98	28.82	65.47	93.10	3.32
October	2017	96.4	104.4	23.03	31.12	55.03	95.52	6.01
November	2017	23.2	111.9	23.60	32.97	30.50	93.63	7.71
December	2017	20.0	119.9	22.42	33.05	23.53	90.28	6.22
January	2018	0.0	133.2	20.00	33.00	10.00	82.70	6.89

Data Analysis

Data were analyzed using SAS 9.4 (2012) software. For generation mean analysis, data for each of the generations from the four blocks were pooled for the computation of the respective mean, variance, and standard error. Six gene effects were computed, viz. phenotypic mean of both parents [m], additive [a], dominant [d]; additive × additive [aa], additive × dominant [ad], and dominant × dominant [dd] gene effects [56–58]. Gene effects were related to means of the generations by the following equations:

$$\text{m} = \text{Mean} = \overline{F_2}$$

$$[\text{a}] = \overline{BC_1} - \overline{BC_2}$$

$$[\text{d}] = \overline{F_1} - 4\overline{F_2} - (1/2)\overline{P_1} - (1/2)\overline{P_2} + 2\overline{BC_1} + 2\overline{BC_2}$$

$$[\text{aa}] = 2\overline{BC_1} + 2\overline{BC_2} - 4\overline{F_2}$$

$$[\text{ad}] = 2\overline{BC_1} - 2\overline{BC_2} - \overline{P_1} + \overline{P_2}$$

$$[\text{dd}] = \overline{P_1} + \overline{P_2} + 2\overline{F_1} + 4\overline{F_2} - 4\overline{BC_1} - 4\overline{BC_2}$$

Each gene effect was tested for significance with its standard error. Significant gene effects were included in models to test the adequacy of the respective models using Chi-square analysis [56]. For traits without significant epistatic gene effects, narrow-sense heritability was computed as the ratio of additive (V_A) to total phenotypic variance (V_P). Additive variance was estimated as $2V_{F2} - V_{B1P1} - V_{B1P2}$, dominance variance ($V_D$) as $V_{B1P1} + V_{B1P2} - V_{F2} - V_E$, and phenotypic variance as $V_G + V_E$, where V_G is total genotypic variance and V_E is environmental variance [38,57]. Genotypic variance was the total of the additive and dominance variances while environmental variance was obtained as the mean of the variances of the three non-segregating generations (P_1, P_2, and F_1). Relationships among yield and its related traits in each and across all segregating generations were determined using Pearson's correlation analysis.

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