

The Genetic Driving Force for the Grain-Vegetable Cowpea Diversification: A Focus on the Pod Length

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Commentary

The formation/loss of characterized traits in a given cultivated species is strongly affected by long-term artificial selection. Cowpea (*V. unguiculata* L. Walp.) is an important legume crop for many residences in the tropics and subtropics of the world, being consumed as either a grain, fodder or vegetable crop depending on local cultivation and consumption habits. Cowpea is believed to have originated from African and be brought to India and East Asia later [1]. Nowadays, cultivated cowpea has well diverged into two main subspecies, which is the ssp. *sesquipedialis*, known as yard-long bean or asparagus bean, and the ssp. *unguiculata* well known as common cowpea or African cowpea [2]. The ssp. *unguiculata* has undergone through intensive selection for seed characteristics, including particularly high protein content and grain yield, in addition to the 'bush'-type plant architecture and short (20-30 cm in length) and crisp pods usually with a high fiber content [3,4]. On the contrary, the ssp. *sesquipedialis* was most often consumed as a vegetable [5]. This subspecies is characterized by long (30-90 cm in length) succulent pods that tastes tender and crisp. The pods are often harvested when immature, and are stewed, fried or preserved for eating. When grown in the field, the ssp. *sesquipedialis* develops characteristic climbing and twining stems.

Genomic studies, particularly population genomic studies have cast insight into the genetic driving force for the grain-vegetable cowpea diversification. Population structure analysis and genome-wide linkage disequilibrium assay demonstrated that yard-long bean could be classified into the 'non-standard' vegetable type and the 'standard' vegetable type [6], suggesting the the vegetable cowpea is derived from the grain type of cowpea ancestors. Quantitative trait loci (QTL) analysis targeting traits related to vegetable use of cowpea further revealed the genetic architecture of pod length, pod number and the node position of the first flower in yard-long bean [7]. In this study, an F_{810} recombinant inbred line population derived from a cross between a long-podded vegetable cowpea cultivar, zhijiang 282, and a medium-podded landrace accession, ZN016, were used for mapping. QTLs for traits including Pod Length (PL), Flowering Days (FLD), Node of First Flower (NF), Pod Number per plant (PN) and Plant Senescence (PS) were identified [8]. A total of four QTLs for Pod Length were detected, which all together explained nearly a half of the phenotypic variation. This study also explicitly demonstrates the feasibility of marker-assisted selection (MAS) in early generations selection of pod length, as the broad-sense heritability (h^2) calculated for Pod Length was high as 70.9% [9]. Moreover, intragenic or intergenic interactions were found to play a role in determining pod length in cowpea, based on the observation of transgressive segregation in some RILs exhibiting a pod length outside the parental value range. QTL co-localization analysis has helped understanding the co-domestication of different traits, either favorable or unfavorable for vegetable use. For example, QTLs controlling pod number per pod and pod length are co-localized but in

different directions in terms of effect [10-12], explaining the paradox of pod quality and yield that has long been faced by cowpea growers [13-14]. Co-localizations of QTLs governing pod tenderness and pod length were also reported, which well explained why cowpea varieties with longer pods are often more soft [15,16].

More clues of the genetic driving force of grain-vegetable diversification came from the investigation of natural variations of pod length. Population stratification analysis of 299 cowpea accessions including both long and short podded germplasm revealed that there were two major subpopulations, while pod length distributions looked well consistent with the subpopulation classification. A subsequent PCA analysis clearly showed that the major principal component between the two subspecies was the pod length, indicating that pod length is the main character being subject to long-term selection in breeding history. Seventy-two SNPs associated with pod length were determined through a genome-wide association analysis (GWAS) then.

Through a genomic scan of population differentiation index (F_{ST}) and nucleotide diversity (π) between the two subgene pools, as well as between the landraces and cultivars/breeding lines of the long-podded subpopulation [10], serious loss of genetic diversity in the vegetable cowpea gene bank was found, leading to the conclusion that the domestication of yard-long bean was accompanied by selection of pod traits and other characters. Pod length then became the only primary trait being selected during further improvement of vegetable cowpea. In a cellular assay trying to elucidate the growth kinetics of pods with different length, cell diameters for pods from three varieties i.e. the Zhijiang282, ZN016 and G314, which bears long, medium and short pods, respectively, were measured at three different stages of post-anthesis (1, 5, 10 dpa). The results pointed to the conclusion that cell size/elongation had no major impact on the pod length differentiation, while the longer-podded genotypes displayed a longer duration of cell division. Lush et al. also reported that duration of photosynthetic activity has increased after cowpea is domesticated [11]. Transcriptomic analysis suggests that sugar metabolism, gibberellin and nutritional signalling are involved in pod length regulation in cowpea [10].

To summarize, the recent work for the grain-vegetable cowpea diversification has provided solid evidence for the long-term assumption that the yard-long bean is a uniquely domesticated subspecies from the ancient grain cowpeas [17,18]. During this process, level of genetic diversity has remarkably decreased in the yard-long bean germplasm. Such lack of broad genetic diversity within domesticated vegetable cowpeas calls for a need of introgression of grain cowpea genetic components to critically enhance the morphological/disease resistance traits plasticity. The more general scientific significance of the afore-mentioned cowpea work is that they would provide insights into the understanding of domestication and

improvement of closely related species, such as the vegetable/grain types of soybeans, garden pea and faba bean.

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