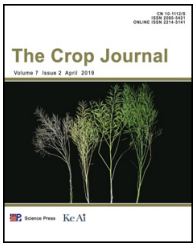
Available online at www.sciencedirect.com

ScienceDirect



Identification of major QTL for seed number per pod on chromosome A05 of tetraploid peanut (*Arachis hypogaea* L.)

*Yuning Chen, Zhihui Wang, Xiaoping Ren, Li Huang, Jianbin Guo, Jiaojiao Zhao, Xiaojing Zhou, Liying Yan, Huaiyong Luo, Nian Liu, Weigang Chen, Liyun Wan, Yong Lei, Boshou Liao, Dongxin Huai, Huifang Jiang**

Oil Crop Research Institute, Chinese Academy of Agricultural Sciences/Key Laboratory of Biology and Genetic Improvement of Oil Crops, Ministry of Agriculture and Rural Affairs, Wuhan 430062, Hubei, China

ARTICLE INFO

Article history:
Received 5 May 2018
Received in revised form 22 August 2018
Accepted 30 September 2018
Available online 6 January 2019

Keywords:
Peanut
Number
Pod
Seed
QTL

ABSTRACT

The inheritance of pod- and seed-number traits (PSNT) in peanut (*Arachis hypogaea* L.) is poorly understood. In the present study, a recombinant inbred line (RIL) population of 188 lines was used to map quantitative trait loci (QTL) for number of seeds per pod (NSP), number of pods per plant (NPP), and numbers of one-, two-, and three-seeded pods per plant (N1PP, N2PP, and N3PP) in four environments. A total of 28 consensus QTL and 14 single QTL were identified, including 11 major and stable QTL. Four major and stable QTL including *qN3PPA5.2*, *qN3PPA5.4*, *qN3PPA5.5*, and *qN3PPA5.7* each explained 12.3%–33.0% of phenotype variation. By use of another integrated linkage map for the A5 group (hereafter referred to as INT A5 group), QTL for PSNT were located in seven intervals of 0.73–9.68 Mb in length on chromosome A05, and candidate genes underlying N3PP were suggested. These findings shed light on the genetic basis of PSNT. Major QTL for N3PP could be used as candidates for further positional cloning.

1. Introduction

The cultivated peanut is an allotetraploid ($2n = 4x = 40$) legume crop used either for edible oil or as food, owing to its high oil and protein content [1,2]. It is derived from a cross of diploid ancestor species ($2n = 2x = 20$) originating primarily in South America and is cultivated in >100 countries worldwide. Peanut is also an important crop in China, with >17 Mt of annual production. Yield is always the predominant objective in peanut breeding and is determined by seed number per unit area and seed weight. Some quantitative trait loci (QTL) associated with yield components have been identified [3,4]. Many QTL for yield traits, especially seed weight, have been identified [3–12]. However, there have been few reports of research on pod- and seed-number traits (PSNT). Peanut plants produce four main types of pods, with one to four seeds. Seed number per unit area is the product of plant density, number of pods per plant (NPP), and number of seeds

* *Corresponding author.*
E-mail address: peanutlab@oilcrops.cn (H. Jiang).
Peer review under responsibility of Crop Science Society of China and Institute of Crop Science, CAAS.

https://doi.org/10.1016/j.cj.2018.09.002

per pod (NSP). NPP and NSP are determined by the number of each type of pod, including numbers of one-, two-, and three-seeded pods per plant (N1PP, N2PPn, and N3PP) and the number per plant of pods containing more than three seeds. NSP is the sum of N1PP, N2PPn, N3PP and number of pods containing more seeds. To date, there has been little information in the literature about the genetic components of PSNT.

As an important criterion of peanut taxonomy, pod type is stable across years and environments [13]. Limited classical genetic analysis resulted in conflicting genetic models for control of pod type. Seshadri [14] reported that one- and two-seeded pods was dominant to multiple-seeded pods. However, other authors [15,16] found that multiple-seeded pods was dominant to fewer-seeded pods. The latest report [13] states that one-seeded pods is controlled by two of three recessive genes. No further molecular research on the PSNT has been reported, and the relationship among PSNT remains unclear.

PSNT are also important yield traits in other dicotyledonous crops, and some achievements have been obtained in other legume crops and rapeseed. Co-localizing QTL and genes associated with these traits have been observed and the relationships among them have been well characterized in some cases. A typical example of research on PSNT is the map-based cloning of the *Ln* gene in soybean [17]. The pleiotropic *Ln* encoded Gm-JAG1, which regulated leaf shape and pod type, and an amino acid substitution in the ERF motif of Gm-JAG1 increased the number of multiple-seeded pods per plant, thereby increasing NSP and the total number of seeds per plant and in turn, seed yield [18]. The *GmCYP78A10b* gene was selected artificially during soybean breeding because it was associated with large seed size and lower NPP; however, the selection of *GmCYP78A10b* did not affect the seed yield of individual plants [19]. The pentatricopeptide repeat (PPR) gene was identified as a candidate underlying NPP in chickpea [20]. An SSR marker associated with NSP was also identified in common bean [21]. In broad bean, NSP was a component of yield and was NSP was negatively correlated with NPP [22]. Co-localization of QTL for NPP, flowering date, and seed development was also observed in soybean [23]. QTL for NPP and seed yield were co-located in chickpea [24]. Markers associated with flowering date, NPP, and NSP were identified in common bean [25]. Liu et al. [26] reported that eight metabolic pathways were involved in the formation of pods with four or more seeds in soybean. In rapeseed, the pleiotropic major QTL *qSN.A6* exerted an effect on NSP and seed yield [27]. In another study in rapeseed, tight linkage accounted for the co-localization of QTL for NPP and NSP [28]. Investigation of the genetic basis of PSNT and the relationship among these traits could be valuable for further understanding the complexity of peanut yield components.

Multivariable conditional analysis methods have been developed [29] to dissect the genetic relationships among different traits at the QTL level. In peanut, conditional QTL mapping was used to identify genetic interdependencies among QTL for different traits that co-localized in the same genome region [3,30]. By conditional mapping, Luo et al. [3] showed that pod length contributed more to 100-pod weight than pod width as a yield component of peanut, and Zhou et al. [30] found that resistance to late leaf spot was influenced strongly by the total number of branches. Thus, it is possible to dissect the genetic interrelationships among QTL for PSNT.

Recently released genome sequences of wild species of *Arachis* [1,31] have afforded a rough picture of the genes located in the genomic physical intervals of QTL for PSNT. Luo et al. [3,12] identified candidate genes for QTL controlling pod size and weight by comparing their locations on the genetic and physical maps of *A. duranensis*.

The objectives of the present study were as follows: (1) to dissect the genetic architecture of PSNT components in peanut by linkage mapping, (2) to identify QTL for PSNT, and (3) to identify candidate genes for PSNT.

2. Materials and methods

2.1. Plant material

A RIL population including 188 lines from a cross between the peanut cultivars Fuchuan Dahuasheng and ICG6375 has been previously [11] well characterized. Fuchuan Dahuasheng (subsp. *hypogaea* L. var. *hirsuta* Kohle) is a landrace of southwest China, and bears 15–20 pods per plant, approximately 50% three-seeded and 45% two-seeded. ICG6375 (subsp. *fastigata* Waldron var. *vulgaris* Harz) was introduced from ICRISAT, and bears >45–50 pods per plant, of which approximately 95% are two-seeded (Fig. 1).

2.2. Field trials and trait phenotyping

The population was grown in the 2013 (F_5), 2014 (F_6), and 2015 (F_7) seasons. Ten plants of each line were phenotyped for one-, two-, and three-seeded pods. The F_5 RIL population was phenotyped in Wuchang (114°34′ E, 30°59′ N, environment 1, E1) and Yangluo (114°52′ E, 30°59 N, E2) in 2013, and the F_6 and F_7 RIL populations were phenotyped in Wuchang in 2014 and 2015 (E3 and E4) for two replicates each year. Five traits, NSP, NPP, N1PP, N2PP, and N3PP were scored, and they were calculated as the total number of corresponding seeds or pods divided by the number of plants.

2.3. Statistical analysis

Phenotypic data were tested for normality using the PROC UNIVARIATE procedure of SAS 9.3 (SAS Institute, Cary, NC, USA). Correlation coefficients among the five traits were calculated using the PROC CORR procedure of SAS. Broad-sense heritability was estimated for each trait following Wu et al. [32].

2.4. Molecular-marker and QTL mapping

QTL analysis was performed using the trait values from single replicates or the average trait values of each environment and existing map reported previously [11]. An INT A5 map was constructed by integration of maps reported previously [11,33]. The INT A5 group is described in Table S1. Conditional phenotypic values of T1|T2 were calculated by the mixed-model approach for the conditional analysis of complex traits