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CROP PRODUCTION

Character of Inheritance of the Number of Fertile Nodes in Determinate Forms of Garden Pea

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Abstract—The character of inheritance of the determinate stem growth type in a garden pea form having four productive nodes (cv. Pervenets with a dwarf stem) has been first studied. The analysis of first-generation hybrids obtained from crosses between indeterminate forms and determinate samples (DTR-2 and DTR-4) showed that the phenotype of all plants was characterized by a usual stem growth type and formation of buds in the stipule axiles. In the case of DTR crosses between themselves, all plants corresponded to the DTR-2 phenotype. In the case of the cross combination (indeterminate form × DTR-2), segregation at a 3 : 1 ratio was observed in the second generation. In the case of the (indeterminate form × DTR-4) variant, phenotypes of resulting plants were segregated into four classes indicating the presence of two genes. For the (DTR-2 × DTR-4) cross, a 3 : 1 segregation was observed in relation to the early bud production. The inheritance of the "number of productive nodes" trait in the cv. Pervenets is determined by two genes, one of which is not related to the determination. This fact was confirmed by the test crossing with the further evaluation of the deviation of the actual segregation from the expected one using the χ^2 (chi-square) method. According to the obtained data, the crossing [DTR-2 × (Voronezhsky zeleniy × Ranniy 28-11-early budding)] resulted in a new variety characterized by a limited stem growth type and four fertile nodes that is suitable for mechanical harvesting.

Keywords: pea, *Pisum sativum* L., hybridization, inheritance, DTR, gene, phenotype, fertile node number

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INTRODUCTION

Garden pea (*Pisum sativum* L.) is one of the main prevernal crops representing an important component of sustainable agriculture [1–3]. Due to a wide range of use, pea cultivars are characterized by a wide diversity of forms and types of cultivation adapted to various environmental conditions and agricultural systems [4].

Garden pea cultivars bred for agricultural production differ in genes controlling phenotypic traits. The main problem in the breeding of garden pea cultivars for canning included limitation of their growth functions with the simultaneous improvement of seed productivity; this resulted in the creation and introduction of dwarf and semidwarf cultivars with strong shortened internodes determined by the action of *le*, *lm*, and some other genes [5, 6]. However, a high yield potential was combined with a prolonged reproductive period, nonuniform ripening, and a tendency to prolification.

A short flowering period and simultaneous yield formation can be provided by the determinate type (DTP) of a stem growth [7] characterized by a complete transformation of the apical meristem into the apex inflorescence [8]. The *det* gene controlling the determinate type of stem growth is recessive and monogenically inherited [9, 10]. This gene is localized in the group VII and is closely linked to the *r* (*rugosus*) gene determining a wrinkled surface of seeds [11, 12].

Breeding studies on field pea made it possible to obtain a number of mutations providing a limited stem growth [13, 14]. A study of DTP mutations showed not only the prospects for use of such morphotypes in the breeding of highly productive garden pea cultivars, characterized by a simultaneous ripening due to the formation of generative buds instead of apical vegetative ones, but also its disadvantages [8, 15]. Industrial cultivars of garden pea with the determinate type of stem growth, such as the cvs. Atlant (Crimean Experimental Station) and Cruiser (All-Russia Research Institute of Vegetable Breeding and Seed Production (VNIISSOK)), are uncompetitive because of an imbalance of the seed productivity elements [16]. Though the number of beans per a productive node and their plumpness are high, which does not compensate the number of productive nodes per a plant, so the resulting productivity is not too high. DTP-type pea cultivars are promising for use in breeding for the creation of initial breeding material with the optimal reproductive zone (3–5 productive nodes) [17].

Table 1. Genetic analysis of the F_2 hybrids with DTP participation

Hybrid combination	Phenotype, number of plants				
	DTP-1-2 nodes	DTP-3-4 nodes	usual stem growth type		total number of plants
			1*	2*	
P1, Kreiser	30				30
P1, Pervenets		30			30
P3, Voronezhskiy zeleny			32		32
1. F_2 (Voronezhskiy zeleny × Kreiser)	23		74		97
2. F_2 (Voronezhskiy zeleny × Pervenets)	27	8	65	24	124
3. F_2 (Kreiser × Pervenets)	93	28		6	127

1*, usual stem growth type and bud formation in the stipule axiles;
2*, usual stem growth type, early bud production, and simultaneous flowering of four nodes.

This work was aimed at studying the character of inheritance of the DTR-4 trait and creating constant and simultaneously ripening determinate forms of garden pea, characterized by four productive nodes and suitable for mechanical harvesting, using a composite crossing technique.

MATERIALS AND METHODS

The study was carried out at the Laboratory of Breeding and Seed Growing of Legumes of the Federal Research Center of Vegetable Breeding (VNIISSOK). The objects of the study were garden pea cultivars from the collection of the Vavilov All-Russia Research Institute of Plant Industry and the above-mentioned laboratory (cvs. Pervenets, Ranniy VIR, Ranniy 28–11, Voronezhskiy zeleny (k-8925), Kreiser (k-9589), and Wenson (k-7985)). The hybridization and evaluation of the obtained material was carried out in 2011–2016 using common methods and techniques.

The determinate form of garden pea with four reproductive nodes (cv. Pervenets) was obtained at the VNIISSOK headquarters by recurrent crossing [(DTP × Ranniy VIR) × Ranniy VIR] [8]. Since the determinate stem growth type actually changes growth and generative processes controlled by different genetic systems, cv. Pervenets is interesting as the object of study intended to create and obtain a new determinate model of a cultivar with the optimum ratio between the reproductive and vegetative spheres. However, the character of the DTP-4 trait inheritance is not completely studied, though it is important for the planning of the selection in hybrid populations and obtaining of productive constant determinate forms with four productive nodes and elongated internodes.

RESULTS AND DISCUSSION

Garden pea is characterized by an acropetal flowering type, i.e., the flowering starts from the bottom node and continues upwards to the apex; the buds are formed in stipule axiles. At the same time, the cv. Pervenets produces unformed buds (so-called flower tubercles) that, according to the plant physiology, corresponds to stage V of the organogenesis; thus, the opening of flowers occurs simultaneously at 3–4 nodes [18].

A comprehensive study of the cv. Pervenets in relation to productivity elements allowed us to reveal two traits (limited number of productive nodes (3–5) and simultaneous flowering of four nodes) distinguishing this cultivar from cultivars with a simple stem growth type and determinate cultivars with two productive nodes.

The analysis of first-generation hybrids obtained by crossing of forms characterized by the usual stem growth type with determinate forms [F_1 (Voronezhskiy zeleny × Kreiser) and F_1 (Voronezhskiy zeleny × Pervenets)] showed that the phenotype of all obtained plants was characterized by a usual stem growth type and bud formation in stipule axiles. The second generation from the first combination showed segregation at a 3 : 1 ratio, and the number of productive nodes in DTP was 1–3 (Table 1).

Distribution of phenotypic classes strictly corresponded to the stem growth types, which agreed with the earlier-published data on the monogenic inheritance [9]. In the case of the second combination [F_2 (Voronezhskiy zeleny × Pervenets)], plants with the number of productive nodes varying from one to five were observed in the DTP class; some of these plants were characterized by early bud production. Among plants with the usual stem growth type, we also observed forms with a simultaneous flowering of four productive nodes. These plants were characterized by early flowering (the number of unproductive nodes was 6–8) and a larger number of fertile nodes (8–11) that indicated the presence of a second gene controlling the early bud production trait. As a result, plants segregated into four phenotypic classes.

Table 2. Deviation of the actual segregation from the expected one in the hybrids F_2 (Voronezhskiy zeleny × Pervenets)

Data	Phenotype, number of plants				
	DTP		usual stem		total number of plants
	1–2	3–5	1*	2*	
Experimental	27	8	65	24	124
Expected (q)	23.25	7.75	69.75	23.25	124
Deviation (d)	3.75	0.25	−4.75	0.75	0
d^2	14.06	0.06	22.56	0.56	
d^2/q	0.6	0.01	0.32	0.02	0.95

1*, usual stem growth type and bud formation in the stipule axiles;
2*, usual stem growth type, early bud production, and simultaneous flowering of four nodes.

To confirm a hypothesis of a dihybrid inheritance of the "number of productive nodes" (NPN) trait in the cv. Pervenets, we calculated the deviation of the actual segregation from the expected one using the χ^2 (chi-square) test. Since χ^2 calculated for the F_2 (Voronezhskiy zeleny × Pervenets) was 0.95, then $0.80 < P < 0.95$. Therefore, in this case, the revealed deviation is rather accidental (Table 2).

To prove the independent inheritance of the "early bud production" trait and the "determinate" trait, we performed a hybridological analysis of hybrids obtained by crossing of two determinate forms (Kreiser × Pervenets). All first-generation plants demonstrated the determinate phenotype with modifications in 1–3 productive nodes and bud formation in stipule axiles. This fact indicated the domination of the parental form with two productive nodes, i.e., the inheritance is directed to the parent characterized by the lower value of the analyzed trait. The performed test revealed the allelism of the mutation in the *det* gene. No plants with early bud production were observed, so the corresponding trait was recessive.

In the case of the F_2 population (crossing 3, Table 1), we revealed divergence in relation to the early bud production trait; the observed segregation was the following: 93 DTP-1-2 plants, 28 DTP-3-4 plants, and six plants with the normal stem growth type. Indeterminate plants were characterized by 5–9 productive nodes and a simultaneous flowering of four nodes.

Actually, the dominant in relation to the stem growth type was observed among recessive forms. Similar cases were also observed for other vegetable crops (carrot, lettuce) [19].

All F_2 plants characterized by a simultaneous flowering of four nodes were combined into one group. The segregation among these plants was 3 : 1. Therefore, one can assume that the inheritance of the NPN trait in the cv. Pervenets is determined by two genes, neither of which is related to the determination. This assertion agrees with the segregation of two phenotypes in relation to the "early bud production" trait observed in the F_a test cross [F_a(Radar × Pervenets) × Pervenets]. Among 58 obtained plants, 31 belonged to the DTP-1-2 group with the bud formation in stipule axiles, while 27 plants belonged to the DTP-2-6 group with the early bud production.

To check the correspondence between the experimental and theoretical segregation, we calculated the χ^2 significance: for F_2 (Kreiser × Pervenets, $\chi^2 = 0.21$ (actual.); for F_a [(F_1 Kreiser × Pervenets) χ^2 Pervenets], $\chi^2 = 0.28$; $\chi^2_{50} = 0.455$. Therefore, the observed deviation was accidental, and an increased number of productive nodes (3–5) in the cv. Pervenets is inherited by two genes, one of which is the *det* gene. The second gene is inherited independently and is manifested in a certain type of bud formation.

For better understanding of the genetic determination of this trait, we analyzed the genealogy of garden pea lines and cultivars characterized by a large number of productive nodes as well as their parental cultivars. The cultivars Ranniy VIR, Ranniy 28–11, Wenson, and Pervenets are characterized by a high and stable number of productive nodes. Along with this trait, they are also characterized by early bud production with a simultaneous flowering of four fertile nodes and also by early ripeness. After investigation of complex hybrids obtained with the participation of these cultivars, we revealed the same pattern of inheritance.

Based on the obtained data, a hybridization of two breeding samples was performed to confirm the character of the DTP-3 inheritance. One of these samples was DTP-2, while another one [DTP-2 × (Voronezhskiy zeleny × Ranniy 28–11)] was characterized by the usual stem growth type and early bud production. In the third-generation DTP plants, we selected forms with four productive nodes. These plants kept these traits in the further generations, were characterized by a prolonged stem (40–45 cm) compared to the cv. Pervenets (28–30 cm), and were suitable for mechanical harvesting.

Thus, we first studied the character of inheritance of the determinate garden pea form with four produc-

tive nodes. The inheritance of this trait is determined by two genes, one of which represents the *det* gene. The second gene is connected with the early bud production and genetically determined increased number of productive nodes. After the crossing of two breeding samples (DTP-2 and the carrier of the gene determining early bud production), the constant determinate plants with four productive nodes have been selected among the third-generation plants. The selected productive specimen with the limited stem growth type, four fertile nodes, and semidwarf stem is suitable for mechanical harvesting.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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