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Ovule Number and Flower Size in Pea (*Pisum sativum* L.): Variation, Heritability, and Correlation with Some Components of Productivity

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Abstract: The seed yield in pea (*Pisum sativum* L.) depends on numerous environmental and genotypic factors. The ongoing climate changes draw one's attention to genetics and variation of underexplored reproductive traits. This study focuses on ovule number (ON) and flower size expressed as a length of flag petal (FL), in terms of their heritability, variability, and correlation with 1000 seed mass (TSM), seed number per pod, and seed/ovule ratio. A set of pea accessions was planted over several years in field conditions. Some of these accessions were also grown in a glasshouse. The chosen values were scored on living plants or while harvesting seeds. Nonparametric statistical methods were applied. Heritability of ON and FL was studied in five hybrid F_1/F_2 combinations. We found a relatively low (ca. 0.5) broad sense heritability of both ON and FL. Among other traits, TSM and ON reproduced best over the years. FL exhibited no reproducible correlations with other traits and cannot be used as a predictor of productivity. Water deficit and heat stress reduce seed yield in pea due to both seed abortion and development of fewer ovules. The differential and heritable ability to retain ON may become a basis for breeding pea cultivars adapted to changing climate.

Keywords: Leguminosae; reproducibility; seed set; stability; yield



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1. Introduction

The garden pea (*Pisum sativum* L., Leguminosae) is one of the most ancient legume crops in temperate latitudes [1]. Moreover, it was the first model object in genetics. That is why the correlation between and genetic control of different traits, especially agriculturally valuable ones, has been under thorough examination for decades. Even in several recent years, numerous works reported correlations between different morphological features and seed yield [2–10]. Only relatively strong ($r > 0.5$) and statistically significant correlations are discussed below. The seed yield in pea (i.e., mass of seeds produced by a single plant or a plot) was found predictably correlated with primary components of productivity, such as number of seeds [5,9] and pods [4–6] per plant or, to a surprisingly lesser extent, number of seeds per pod [3,6,9,10]. Data on the impact of 1000 seed mass on a yield are contradictory. While Shurkhaeva et al. [9] reported a negative correlation between seed yield and 1000 seed mass, some other authors [6,10] found these two traits to be positively correlated.

It is important to understand how seed yield is affected by the components of potential productivity. Among these, the ovule number (ON) is possibly the most significant, as seeds are directly derived from ovules, and ON can correlate with the number of seeds per pod (SN) [11]. There are not many works reporting how ON is inherited in pea and other legumes. Marx and Mishanec [12] stated that ON is controlled by approximately three loci with an additive effect in pea. A similar conclusion was drawn in a set of later papers [13–15]. A relatively low heritability (0.38) was reported for ON in pea [13]. Four loci with additive genetic effects were suggested to control ON in *Medicago* L. [16]. A partial

dominance of low ON over high was recorded in pea [13]. This agrees with fact that F_1 hybrids of interspecific and intergeneric crosses between *Cajanus cajan* (L.) Millsp. and *Atylosia* spp. had a lower average ON than the expected midparent value [17]. A simpler, probably monogenic, control of ON was reported in *Phaseolus vulgaris* L. [18].

Additionally, ON is partly dependent on pod length and shape, so genes controlling pod shape also affect ON in pea [2,7,12,19]. However, this association is not as tight as might be expected [19]. Some other morphological mutations may have a minor pleiotropic effect on ON (e.g., [20]). The works on model plant species such as *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) identified numerous genes involved in determination of ON [21], so in legumes the existing state of knowledge is in its initial state.

Observations on wild relatives of the pea, members of the tribe Fabeae, indicate that larger flowers tend to produce more ovules, i.e., there is a positive, although not very strong, correlation between flower size and ON [22]. This suggests that flower size may serve as a predictor of ON and overall productivity.

The present work aims to study whether ON correlates with more conventional traits of productivity in pea, viz. seed number per pod and 1000 seed mass. We also examined if flower size may serve as a predictor of a higher seed yield. Heritability and reproducibility of both ON and flower size were investigated.

2. Materials and Methods

2.1. Plant Material and Growing Conditions

The following accessions served as material for this study: Adagumskii, Alfa, Anvend, Chika, Fragment, Hurst Green Shaft, Izumrud, Kaira, Kelvedon Wonder, Kreiser, Lu Zhun, Pervenets, Pin Wan, Rannii Gribovskii 11, Senator, Sovershenstvo 65-3, Viking, Viola, Yantar (vegetable cultivars), Batrak, Filby, Frisson, Multik, Nemchinovskii 766, Orel, Orlan, Roi des Gourmands, Spartak (dry pea cultivars), Malinovka (fodder cultivar), A-agrimut 987/6, Az-23, B-agrimut type, B-agrimut 761/7, Novaya forma 42, Ras-tip, SGE, WL131, WL1132, and 5-listochkovaya Acacia (marker lines). More detailed characteristics of accessions are available in [23]. Seeds of all accessions are stored in the germplasm collection of the Dept. of Genetics, Lomonosov Moscow State University.

To study inheritance of quantitative features, we analyzed five F_1 and F_2 progenies from crosses between different accessions. Two of these hybrid combinations were sown in different conditions, viz., two field seasons and glasshouse. All cultivars, lines and hybrids were planted on the experimental plot of Skadovskii Zvenigorod biological station (Western Moscow District, Russia; N55.702134, E36.727971) in 2015–2017 and 2020–2022. Seeds were sown in the middle of May in a row with a space of ca. 5 cm between them. Rows were separated with gaps of 1 m. As far as plants were elongating, horizontal ropes were strung out to provide a support. Weeds were hoed manually in the course of the plants' growth. No fertilizers were applied. Pea plants with ripe pods were harvested in first ten days of August. Climatic conditions of growing periods are represented in Figure 1 and Table 1. Climatic data were obtained from the automated weather station located on the territory of Skadovskii biological station. In the case of incomplete observations, these were supplemented by records from the weather station in Novo-Ierusalim (N55.907419, E36.824343, ca. 23 km from the biological station) available on rp5.ru (accessed on 10 January 2023).

For comparison, selected accessions were planted in a glasshouse under long day conditions with artificial light (lamps DNa3, 46,000 lm; Reflux, Saransk, Russia). Ten pre-soaked seeds of each accession were sown in plastic pots of 24 cm × 24 cm × 20.5 cm filled with a mixture (1:1) of loamy soil and turf ground (Nevatorf, Saint Petersburg, Russia). Plants were watered manually every several days in the course of superficial drying of soil in pots. The temperature regime was not controlled nor recorded but in some periods it exceeded 30 °C.

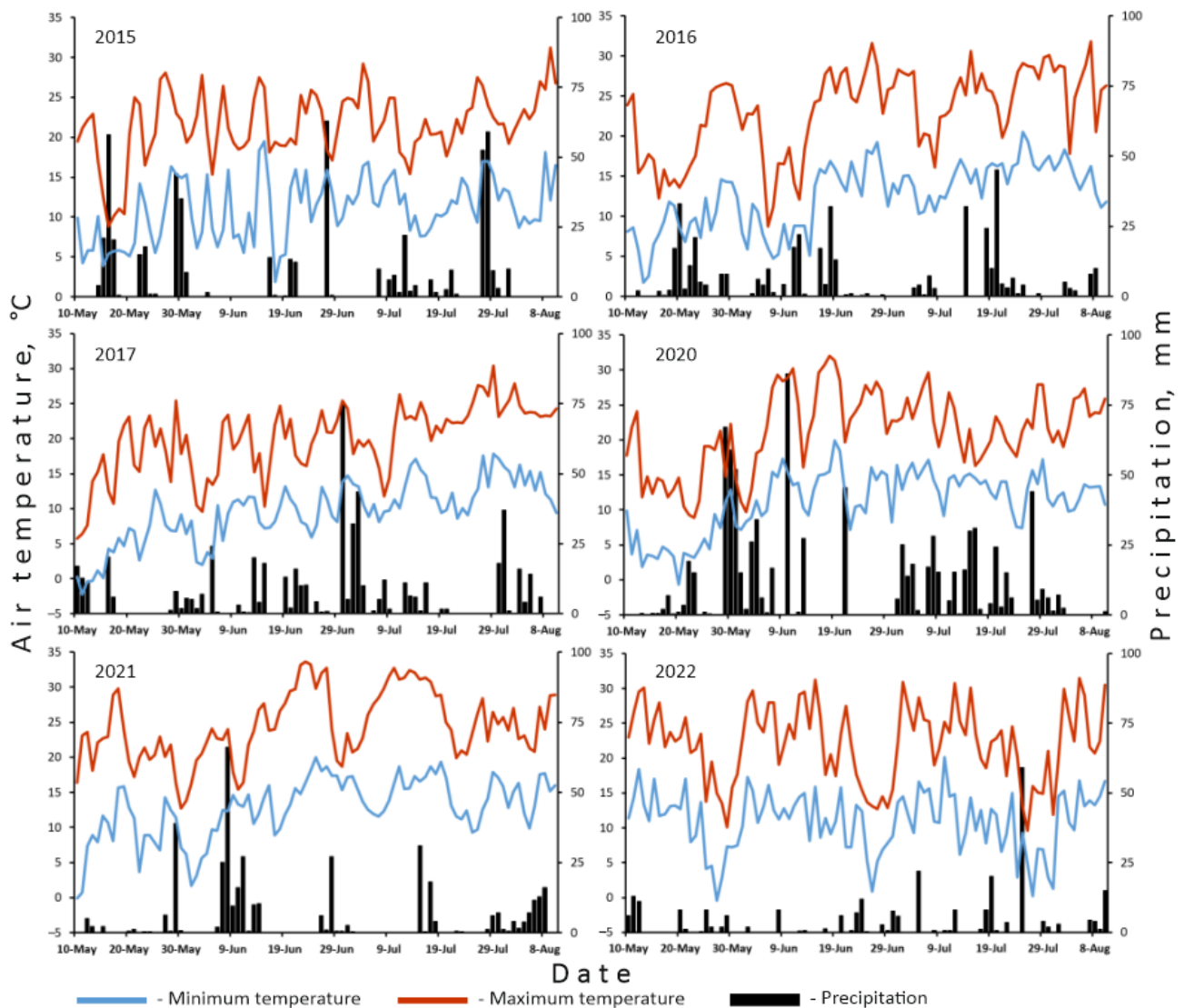


Figure 1. Daily air temperature (minimum and maximum) and precipitation during field seasons when plants were grown.

Table 1. Average air temperature (T , °C) and sum of precipitation (P , mm) in different periods of plant growth.

Year	10 May–31 May		01 June–30 June		01 July–31 July		01 August–10 August		Whole Season	
	T , °C	P , mm	T , °C	P , mm	T , °C	P , mm	T , °C	P , mm	T , °C	P , mm
2015	14.1	226.7	16.1	105.8	17.3	197.6	18.0	10.0	16.2	540.1
2016	14.4	116.0	17.0	136.5	20.2	149	20.3	27.8	17.8	429.3
2017	10.8	83.4	13.7	216.6	17.3	203.7	18.9	41.0	14.5	544.7
2020	10.4	228.4	18.3	260.1	17.8	341.6	17.9	10.4	16.2	840.5
2021	14.5	58.4	18.7	201.6	20.8	72.5	19.7	57.4	18.6	389.9
2022	15.9	57.3	16.4	49.2	16.1	135.8	19.6	27.3	16.5	269.6

2.2. Scored Parameters

Length of the flag petal (FL) served as a measure of flower size. Freshly collected or fixed in ethanol (70%) petals were spread under a glass and photographed with a 25 Mpx digital camera (Samsung, Seoul, Republic of Korea). All measurements were carried out in images using the program ImageJ 1.51 k (National Institutes of Health, Bethesda, MD, USA). To minimize imprecision, the length of each flag petal was measured three times.

With rare exceptions, a minimum of 20 petals randomly collected from ten or more plants was measured.

The number of ovules was counted either in ovaries of freshly collected flowers or in the course of harvesting mature seeds. Seeds to ovules (S/O) ratio was calculated as an average number of seeds divided by an average number of ovules. For most accessions, 20 pods/ovules were analyzed for SN and ON, although in several cases (especially in glasshouse conditions) sample size was lower (not fewer than five).

Seeds were weighed with an electronic scales Pioneer PA64 (Ohaus, NJ, USA). To obtain the commonly used value of 1000 seed mass (TSM), we usually weighed fewer seeds and then recalculated, as relatively small seed samples were available in most cases.

Not all features were recorded in all seasons for all accessions. For some years, only fragmentary data are available (Table S1).

In F₂ Filby × WL1132 and Filby × WL131 (2022), two pods or ovaries were sampled from each hybrid plant to count ovules. In other F₂ populations/trials, ovules and petals were sampled randomly from all flowering/fruitlet plants.

2.3. Statistical Analysis

All statistical procedures were carried out with usage of Statistica 12 (Statsoft, Tulsa, OK, USA) and Microsoft Excel (Microsoft, Redmond, WA, USA). As a relatively small number of cultivars was used in the comparison, nonparametric methods were applied.

To analyze possible genetic components of studied traits, we applied the method described by Sobolev [24]. Broad sense heritability was calculated according to the following formula:

$$H^2 = s^2_g / s^2_p, \quad (1)$$

where s^2_g stands for genotypic variance, s^2_p denotes phenotypic variance, s is a standard deviation. The two components of variance are connected as follows:

$$s^2_p = s^2_g + s^2_e, \quad (2)$$

where s^2_e stands for error variance resulting from spontaneous (non-heritable) fluctuations, ontogenetic variation, and imprecision of measurements. To assess H^2 in the second filial progeny, Formula (2) can be transformed as below:

$$s^2_p(F_2) = s^2_g(F_2) + [s^2_p(P_1) + s^2_p(P_2) + s^2_p(F_1)]/3, \quad (3)$$

where $s^2_p(P_1)$, $s^2_p(P_2)$, $s^2_p(F_1)$, and $s^2_p(F_2)$ are phenotypic variances of first parent, second parent, and hybrids of the first and second progenies, respectively. The Formula (3) is applied if $s^2_p(P_1) > s^2_p(F_1) < s^2_p(P_2)$, otherwise it is transformed in the following way:

$$s^2_p(F_2) = s^2_g(F_2) + [s^2_p(P_1) + s^2_p(P_2)]/2, \quad (4)$$

which was the prevailing case for our data. The Formula (4) was used to calculate $s^2_g(F_2)$ and H^2 for flower size (FL) and ON.

3. Results

The available values of ON, SN, S/O ratio, FL, and TSM of all trials for all accessions are available in Tables 2 and S1. These were used to evaluate heritability and correlations.

Table 2. Values and derived parameters for hybrid progenies and corresponding parental accessions.

Cross	Year	Average Value \pm s (Sample Size)				Calculated Parameters		
		P ₁ *	P ₂ *	F ₁	F ₂	MP	s ² _g (F ₂)	H ²
Ovule number								
Filby \times WL1132	2022	7.25 \pm 0.55 (20)	6.50 \pm 0.61 (20)	–	6.99 \pm 0.78 (157)	6.88	0.28	0.45
	2022	6.63 \pm 0.70 (41)	7.33 \pm 0.58 (21)	–	6.39 \pm 0.74 (150)	6.98	0.14	0.25
Ras-tip \times Az-23	2021 (field)	6.50 \pm 0.61 (20)	6.80 \pm 0.77 (20)	5.81 \pm 0.98 (26)	6.73 \pm 1.00 (98)	6.70	0.52	0.52
	2021 (glass.)	5.67 \pm 0.58 (3)	4.77 \pm 1.01 (13)	–	4.81 \pm 1.08 (31)	5.22	0.48	0.41
	2022	7.80 \pm 0.42 (10)	7.70 \pm 0.57 (20)	–	7.69 \pm 0.74 (98)	7.75	0.29	0.54
Filby \times WL131	2021 (field)	8.13 \pm 0.64 (15)	8.00 \pm 0.53 (15)	8.13 \pm 0.74 (15)	8.47 \pm 0.83 (15)	8.07	0.35	0.50
	2021 (glass.)	5.78 \pm 0.44 (9)	7.17 \pm 0.75 (6)	6.25 \pm 0.71 (8)	6.50 \pm 0.90 (26)	6.48	0.43	0.53
Flag length, mm								
	2022	16.42 \pm 1.37 (23)	17.80 \pm 2.10 (23)	14.62 \pm 1.45 (13)	15.79 \pm 1.76 (64)	17.11	0.30	0.10
Ras-tip \times Az-23	2021 (field)	13.54 \pm 1.50 (20)	13.26 \pm 1.14 (20)	13.19 \pm 1.27 (20)	13.45 \pm 2.00 (31)	13.40	2.24	0.56
	2021 (glass.)	13.99 \pm 1.14 (3)	12.89 \pm 1.10 (16)	15.97 \pm 2.04 (5)	14.58 \pm 1.99 (31)	13.44	2.71	0.68
Filby \times 5-list.	2016	13.36 \pm 1.27 (40)	19.37 \pm 1.48 (20)	–	13.97 \pm 1.75 (43)	16.37	1.17	0.38
Filby \times WL131	2021 (glass.)	12.35 \pm 0.48 (5)	13.72 \pm 0.71 (10)	13.69 \pm 0.52 (8)	12.18 \pm 0.83 (26)	13.04	0.32	0.47
N.f. 42 \times WL1132	2017	13.74 \pm 1.10 (19)	17.40 \pm 1.33 (20)	17.30 \pm 1.32 (20)	17.91 \pm 1.88 (61)	15.57	2.05	0.58

* P₁ and P₂ in this table are values of first and second parents in the order listed in column ‘Cross’. MP = midparent value. Dash = no data.

3.1. Heritability of Ovule Number and Flower Size

The calculated values of H^2 are presented in Table 2. They are relatively low: average H^2 for both ON and FL comprises 0.46, i.e., approximately 50% or less of observed phenotypic variation can be attributed to genotypic components. Surprisingly enough, in some hybrid combinations, the values of H^2 for ON have a relatively high reproducibility, e.g., in three trials of Filby \times WL131 (Table 2). Average ON of F₁ hybrids was usually lower than or close to the midparent value (Table 2).

For flower size expressed in terms of flag length, values of H^2 exhibited a weaker reproducibility (Table 2). Average FLs were either higher or lower than the calculated midparent value even in different replicates of the same hybrid combination, e.g., Ras-tip \times Az-23 (Table 2).

In F₂ populations Filby \times WL1132 and Filby \times WL131, ONs were compared between hybrid plants having different phenotypes, viz., normal (*LE*) vs. dwarf (*le*) stem, normal (*AF*) vs. afila (*af*) leaf, broad (*ST*) vs. narrow (*st*) stipules, green (*GP*) vs. yellow (*gp*) pods, and pigmented (*A*) vs. white (*a*) petals (see [25] for designation of genes). No reliable differences in ON were found between samples of hybrids having distinct phenotypes (Table S2).

Only three of nine accessions exhibited no reliable differences in ON between 2015 and 2021 (field) seasons, viz., Malinovka, SGE, and Viking (Table S1). Malinovka and SGE are accessions with pigmented flowers. One more purple-flowered accession, WL131, possessed no significant differences in ON between both 2021 trials (Table S1) and 2022 (not shown).

3.2. Within-Plant Variation of Ovule Number

To examine the degree of variation in ON within a single plant, we counted ovules in pods/ovaries on the main and lateral shoots separately in eight individual hybrid plants of F₂ Filby \times WL1132. Flowers of the main shoot produced 7.73 ± 0.49 ovules (average \pm s, $n = 51$), while fewer ovules, 6.84 ± 0.75 ($n = 76$), developed in flowers on lateral branches. Differences between these two groups are significant (Mann–Whitney test, $p < 0.01$).

3.3. Correlation between Studied Parameters and Their Reproducibility

As seen from Table 3, even correlations between the same parameters in two different trials (field and glasshouse) were weak. Climatic data for 2021 (Table 1, Figure 1) show that this season was quite dry, so both field and glasshouse conditions may be evaluated as stressful. As a result, although relatively small sets of cultivars were compared, reproducibility of studied parameters was found weak. The strongest correlation was found for ONs recorded in two trials (Spearman's $\rho = 0.523$). Stronger correlations between S/O ratio and ON and S/O ratio and SN (Table 3) seem trivial, as the S/O ratio is connected with ON and SN both ontogenetically and mathematically. To our surprise, SN and ON are correlated very weakly and unreliably (Table 3).

Table 3. Correlation (Spearman's ρ) between studied parameters in 2021 in field trial (lower left part of the matrix), glasshouse trial (upper right part of the matrix), and between two trials (diagonal). Numbers of compared accessions are given in brackets.

	SN	ON	S/O	TSM	FL
SN	0.504 (12)	−0.069 (16)	0.695 ** (17)	0.400 (5)	−0.252 (14)
ON	0.280 (17)	0.523 * (18)	− 0.731 ** (17)	− 0.900 * (5)	0.203 (19)
S/O	0.868 ** (17)	−0.127 (17)	0.360 (9)	0.900 * (5)	−0.275 (15)
TSM	0.047 (15)	−0.367 (14)	0.476 (12)	–	–
FL	0.371 (12)	0.151 (18)	0.441 (12)	0.670 * (13)	0.418 (13)

Significant correlations are marked with bold and asterisk: *, $p < 0.05$, **, $p < 0.01$. Dash = number of compared accessions is low (less than five).

In 2015, ON correlated positively and significantly with SN ($\rho = 0.636$; Table S3), while in other seasons these two parameters exhibited no reliable correlation. FL was measured only for two trials of 2021, and only in the field observations this parameter correlated reliably with TSM (Table 3). Notably, average FL and ON were significantly lower in the glasshouse than in field trials, although not for all accessions (Table S1).

Only fragmentary data are available for other seasons, but they may be informative for estimates of reproducibility of studied parameters (Table S4). TSM is reproduced (i.e., correlated) relatively precisely between different years of observation with Spearman's ρ nearing 0.600 or higher. For comparison, SNs correlated significantly only between data of 2015 and 2016, while S/O ratios appeared variable between seasons (Table S4).

4. Discussion

4.1. Ovule Number Is a Relatively Variable Trait Weakly Correlated with Seed Number

The whole set of correlations is only partly reproducible between years and trials (Tables 3 and S4) which agrees with the observations of Uhlarik et al. [10]. This may be also because the collection of accessions under study was not fully identical between years (Table S1). Similarly to the findings of Uhlarik et al. [10], TSM has the highest reproducibility between years.

In agreement with previous observations [12–15], our data provide evidence for a moderate heritability of ON, with approximately 50% of variation conditioned by genotype (Table 2). There is possibly no major locus which might affect ON significantly but numerous loci with a minor impact. At least some of well-known loci, such as *A*, *AF*, *GP*, *LE*, and *ST*, seem not to be influencing ON. This is of a special significance, as white flowers (*a*), dwarf stem (*le*) and 'afila' leaf type (*af*) are characteristic for many contemporary pea cultivars. On the other hand, two purple-flowered accessions, Malinovka and SGE, retained their ON best between years (Table S1). The exact role of different loci in heritable stability (not absolute value) of ON is yet to be investigated involving a much larger set of accessions.

On the way from ovules to seeds, the success of seed maturation is dependent on the position of the ovule in the pod [11] and environmental factors. Although pea is almost exclusively self-pollinated, the effectiveness of both pollination and seed maturation is

affected by temperature. As found by Jiang et al. [11], heat stress drastically reduces SN which should be taken into account considering the ongoing climate changes. Comparing S/O ratios for the same cultivars grown in relatively humid 2015, very dry 2021 and the stressful conditions of the glasshouse, one may find the S/O ratio decreasing in this series (Table S1).

Previously, differences of SN between control and heat-treated pea plants were reported as insignificant by Jiang et al. [11] who concluded that increased temperature negatively affects yield via acceleration of flowering and reduction of both pod number and seed size. However, our data evidence that not only SN but also ON is reduced under stress (most probably heat and water deficit, Table S1) in most cultivars (differences in ON between 2015 and 2021 are evident, Table S1), while accessions Malinovka, SGE, and Viking produce similar ONs in different conditions. Some cultivars (Fragment, Pervenets) exhibited slightly, although significantly, higher ONs in a glasshouse. It might be intriguing to study whether some genotypes are more resistant (in terms of ON) against various stresses compared with others. Differential response of SN and S/O ratio to heat stress was earlier described in different genotypes of pea [11].

A relatively low heritability together with a significant influence of environmental factors make a higher ON an unreliable goal in breeding. It is complemented with the fact that ON is a poor predictor of SN, one of the key components of yield. Indeed, these two traits are often weakly correlated (Table 3). This contradicts the results of Jiang et al. [11] but supports those of Semenova et al. [8] who reported a very low relation between maximum seed number per pod and both overall plant productivity and yield per plot. Our observations indicate that maximum SN is equal to the ON and achievable only in a small fraction of pods ($S/O = 1.00$). Those authors who studied the impact of average (not maximum) SN on productivity found them correlating significantly [6,9].

There is an ontogenetic component of variation of ON, as flowers on lateral branches usually produce fewer ovules than flowers on the main stem. There is possibly some difference between earlier and later flowers, although this phenomenon needs a deeper examination. Typically, a garden pea does not produce lateral branches actively but some of its crop relatives (*Lathyrus sativus*, *Vicia sativa*) develop a highly ramified seasonal shoot so this ontogenetic variation may matter in their case. Most pea cultivars are harvested with only several of the earliest pods on the main shoot fully mature. Kondykov et al. [26] reported that more than 90% of plant yield is brought by two first fruiting nodes, partly due to larger seeds. As data of Jiang et al. [11] indicate, the ovules in the oldest (basal-most) pod are more likely to develop into seeds successfully than the ovules in subsequent (distal) pods. Otherwise stated, S/O ratio has certain ontogenetic (or position-dependent) variation.

Taken together, these facts suggest that a higher ON may be beneficial for higher yield in optimal growing conditions when the potential productivity is realized to the maximum possible extent.

4.2. A Larger Flower Is Not Correlated with Higher Productivity

One of our initial hypotheses was that larger flowers produce more ovules, the phenomenon characteristic for the pea's wild relatives [22]. However, flower size expressed in terms of FL appears very unstable even for the same accession grown in different conditions (Table S1) and has no reliable correlations with any of studied traits except for TSM (field 2021, Table 3) which needs to be additionally examined in subsequent trials.

A relatively low and poorly reproducible heritability of FL (Table 2) also accords with its plasticity under different growing conditions. Although existing in wild-growing species as a result of their evolution, the relation between flower size and ON is disrupted under domestication. To our knowledge, flower size never was a matter of artificial selection in pea, so both large- and small-flowered cultivars exist having a relatively narrow range of ON variation. Numerous works on model plant species dissected a complex genetic and physiological regulation of flower size (reviewed in [27]) suggesting polygenic control of this trait.

5. Conclusions

Under stress (water deficit and heat), pea plants produce fewer seeds than in more favorable conditions. This phenomenon was previously attributed to a higher rate of abortion of seeds and immature ovules resulting in a lower seed/ovule ratio [11]. Our results indicate that stress also leads to initiation of fewer ovules, i.e., lower potential productivity. Ovule development is less responsive to environmental conditions in some genotypes compared with others. While the heritability of ON itself is not high (ca. 0.5), the differential and most probably heritable ability to retain ON under stress may become a basis for breeding pea cultivars better adapted to a warmer and drier climate. However, ON becomes a reliable determinant of SN only under best growing conditions.

The flower size in pea is also strongly dependent on environment and its heritability is therefore relatively low. In the course of evolution, floral size became more or less associated with ON [22] but this correlation seems not to exist in cultivated peas. The results reported here suggest that flower size cannot be used as a predictor of productivity.

However, the natural habit of the pea's wild relatives, such as the annual representatives of *Lathyrus* and *Vicia* inhabiting xeric conditions, may provide a clue to the appearance of future pea cultivars. Possibly forms with single-flowered inflorescences, few ovules, and, of utmost importance, short life cycle may be beneficial in the changed climate.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae9030371/s1>, Table S1: Values of studied parameters of examined accessions over different years and growing conditions; Table S2: Ovule number in plants of F₂ hybrids with different genotypes; Table S3: Correlations between selected parameters over different years; Table S4: Correlations between the same parameters over different years.

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Table S1. Values of studied parameters of examined accessions over different years and growing conditions.

Accession	Year, trait (average value \pm s)*																		
	2015				2016		2017	2020		2021 (field)					2021 (glasshouse)				
	SN	ON	S/O	TSM	SN	TSM	TSM	SN	TSM	SN	ON	S/O	TSM	FL	SN	ON	S/O	TSM	FL
Viola	6.87 \pm 0.70 ^a	7.28 \pm 0.64 ^a	0.94	161.28	5.29 \pm 1.74 ^b	-	-	-	-	3.00 \pm 1.93 ^c	-	-	206.95	-	-	5.33 \pm 0.50 ^b	-	-	13.60 \pm 1.16
Batrak	4.57 \pm 1.18 ^a	6.78 \pm 0.63 ^a	0.68	223.82	3.08 \pm 0.97 ^b	163.04	233.85	-	-	3.05 \pm 1.15 ^b	5.86 \pm 0.48 ^b	0.47	236.91	13.42 \pm 0.97 ^a	-	5.11 \pm 0.74 ^b	-	-	11.67 \pm 1.42 ^b
Orel	4.80 \pm 1.43 ^a	7.26 \pm 0.56 ^a	0.66	252.30	3.98 \pm 1.41 ^b	225.03	233.85	-	-	3.05 \pm 1.15 ^b	6.90 \pm 0.64 ^b	0.44	264.74	15.71 \pm 1.06 ^a	1.00 \pm 0.00 [†]	6.00 \pm 0.00 [†]	0.17	-	12.09 \pm 1.50 ^b
Sov. 65-3	5.72 \pm 1.40 ^a	6.95 \pm 0.65 ^a	0.85	222.39	3.75 \pm 1.60 ^b	191.59	207.47	3.52 \pm 1.81 ^b	91.15	1.50 \pm 0.84 [†]	6.20 \pm 0.52 ^b	0.24	148.15	12.57 \pm 0.92	1.50 \pm 0.55 [†]	7.00 \pm 0.00 [†]	0.21	-	-
Anvend	6.78 \pm 1.41 ^a	8.39 \pm 0.50 ^a	0.81	-	5.08 \pm 1.72 ^b	255.39	249.82	-	-	-	7.67 \pm 0.48 ^b	-	217.46	16.74 \pm 1.49 ^a	1.00 \pm 0.00 [†]	6.25 \pm 0.71 ^c	0.16	-	14.32 \pm 1.60 ^b
Malinovka	5.39 \pm 1.48 ^a	7.42 \pm 0.50 ^a	0.72	198.47	4.24 \pm 1.46 ^b	157.11	153.76	-	-	5.50 \pm 1.15 ^a	7.65 \pm 0.75 ^a	0.72	221.18	16.20 \pm 1.31	-	-	-	-	-
Roi des G.	4.97 \pm 1.33 ^a	7.19 \pm 0.40 ^a	0.69	-	2.91 \pm 1.00 ^b	219.08	233.99	-	-	3.00 \pm 1.22 ^b	-	-	224.42	-	-	6.55 \pm 0.60 ^b	-	-	19.89 \pm 1.14
Orlan	7.20 \pm 1.44 ^a	7.95 \pm 0.67 ^a	0.90	264.82	4.05 \pm 1.45 ^b	198.05	201.16	-	-	4.80 \pm 1.11 ^b	7.00 \pm 0.73 ^b	0.69	285.31	13.88 \pm 1.00	-	5.75 \pm 0.96 [†]	0.35	-	14.05 \pm 0.91 [†]
Viking	5.30 \pm 1.23 ^a	6.11 \pm 0.32 ^a	0.87	184.00	4.03 \pm 1.62 ^b	139.91	141.89	-	-	-	5.70 \pm 0.47 ^a	-	-	14.77 \pm 1.10 ^a	1.00 \pm 0.00 [†]	4.07 \pm 1.22 ^b	0.25	-	12.10 \pm 0.88 ^b
Multik	6.48 \pm 1.67 ^a	9.07 \pm 0.62 ^a	0.71	159.13	4.65 \pm 1.64 ^b	128.40	123.83	-	-	4.75 \pm 1.59 ^b	8.05 \pm 0.39 ^b	0.59	150.71	12.14 \pm 0.62 ^a	1.50 \pm 0.58 [†]	7.00 \pm 0.63 ^b	0.21	121.69	10.13 \pm 0.86 ^b
SGE	6.16 \pm 1.37 ^a	7.10 \pm 0.70 ^a	0.87	168.49	4.90 \pm 1.73 ^b	155.49	159.66	-	-	4.85 \pm 1.63 ^b	7.16 \pm 0.76 ^a	0.68	157.04	13.89 \pm 1.01	-	-	-	-	14.05 \pm 0.91 [†]
Frisson	-	-	-	-	5.31 \pm 1.44 ^a	-	118.19	-	-	3.80 \pm 1.58 ^b	7.45 \pm 0.69	0.51	120.03	12.14 \pm 1.00	-	-	-	-	-
Nem. 766	-	-	-	211.92	2.51 \pm 1.04 ^a	169.80	203.62	-	-	-	5.30 \pm 0.57 ^a	-	-	11.81 \pm 1.05 ^a	1.25 \pm 0.46 ^b	5.78 \pm 0.44 ^a	0.35	195.07	13.18 \pm 1.49 ^b
Filby	-	-	-	-	3.00 \pm 0.84 ^a	-	140.13	-	-	3.50 \pm 1.38 ^a	7.95 \pm 0.69 ^a	0.44	152.83	12.69 \pm 1.36 ^a	2.00 \pm 0.00 [†]	5.78 \pm 0.44 ^b	0.35	-	12.35 \pm 0.48 ^a
Kaira	-	-	-	-	5.13 \pm 1.59 ^a	144.91	162.85	3.83 \pm 2.27 ^{ab}	90.39	3.00 \pm 1.31 ^{ab}	8.15 \pm 0.80 ^a	0.37	136.26	13.06 \pm 1.11	1.40 \pm 0.55 ^{bc}	9.00 \pm 0.82 ^a	0.16	-	-
Kreiser	-	-	-	-	3.15 \pm 1.49 ^a	145.98	229.38	3.24 \pm 1.20 ^a	68.50	-	-	-	-	-	-	-	-	-	-
Chika	-	-	-	-	2.44 \pm 1.05 ^a	152.69	167.17	3.32 \pm 1.79 ^a	91.55	-	-	-	111.16	-	-	-	-	-	-
Hurst G.S.	-	-	-	-	4.93 \pm 2.23 ^a	-	217.48	3.00 \pm 2.16 ^b	-	-	-	-	-	-	-	-	-	-	-
Lu Zhun	-	-	-	-	4.43 \pm 1.12 ^a	-	172.07	3.17 \pm 1.83 ^a	72.13	-	6.33 \pm 0.58	-	-	-	-	-	-	-	-
Rannii Gr.	-	-	-	-	3.43 \pm 1.17 ^{abd}	202.48	192.67	5.00 \pm 2.20 ^{ab}	151.08	2.95 \pm 1.27 ^{abd}	-	-	181.58	-	1.17 \pm 0.39 ^c	7.97 \pm 0.72	0.15	-	15.83 \pm 0.91
Pin Wan	-	-	-	-	4.09 \pm 1.02 ^a	-	147.42	3.50 \pm 1.20 ^a	74.17	-	6.80 \pm 0.84 ^a	-	-	-	-	6.95 \pm 0.60 ^a	-	-	14.65 \pm 1.01

Fragment	-	-	-	-	5.35 ± 2.02 ^a	71.17	101.70	3.27 ± 1.72 ^b	75.13	-	7.50 ± 0.53 ^a	-	-	12.93 ± 0.89 ^a	1.22 ± 0.44 ^c	7.67 ± 0.52 ^b	0.16	85.10	12.16 ± 1.54 ^a	
Senator	-	-	-	-	6.63 ± 1.80 ^a	165.08	169.99	5.18 ± 2.13 ^b	133.61	-	-	-	162.43	-	-	5.45 ± 0.52	-	-	13.66 ± 1.23	
Yantar	-	-	-	-	6.54 ± 1.30 ^a	149.82	166.18	4.13 ± 1.26 ^b	62.26	-	-	-	-	-	-	-	-	-	-	
Kelv. W.	-	-	-	-	4.33 ± 1.22 ^a	155.69	177.97	4.69 ± 1.54 ^a	125.28	-	-	-	-	-	-	-	-	-	-	
Alfa	-	-	-	-	3.44 ± 1.36 ^a	-	195.63	4.22 ± 1.51 ^a	83.29	-	-	-	-	-	1.00 ± 0.00 [#]	5.83 ± 0.98	0.17	-	13.93 ± 1.14	
Izumrud	-	-	-	-	5.41 ± 1.66 ^a	195.30	185.80	5.75 ± 1.69 ^a	76.66	-	6.64 ± 0.50 ^a	-	170.64	13.97 ± 1.03 ^a	1.00 ± 0.00 [#]	6.69 ± 0.63 ^a	0.15	-	14.18 ± 2.10 ^a	
Adagum.	-	-	-	-	4.89 ± 1.93 ^a	138.43	176.98	3.29 ± 2.26 ^b	72.08	3.92 ± 1.80 ^b	7.62 ± 0.74	0.51	172.92	16.39 ± 1.06	-	-	-	-	-	
Pervenets	-	-	-	129.06	2.84 ± 1.04 ^a	138.45	145.37	2.00 ± 1.19 ^b	75.49	-	6.05 ± 0.60 ^a	-	-	11.49 ± 0.71 ^a	1.29 ± 0.49 ^b	6.86 ± 0.77 ^b	0.19	118.49	11.54 ± 1.17 ^a	
Az-23	-	-	-	-	-	127.28	-	-	-	3.05 ± 1.36	7.30 ± 0.66 ^a	0.42	-	13.26 ± 1.14 ^a	-	4.77 ± 1.01 ^b	-	-	12.89 ± 1.10 ^b	
Ras-tip	-	-	-	-	-	143.66	219.56	-	-	4.30 ± 1.56	6.50 ± 0.61	0.66	179.90	-	2.00 ± 1.00 [#]	5.67 ± 0.58 [#]	0.35	159.49	-	
Spartak	-	-	-	-	-	178.01	196.28	-	-	3.80 ± 0.62	6.20 ± 0.62	0.62	-	-	-	-	-	-	-	
5-list. Ac.	-	-	-	195.76	-	149.40	216.38	-	-	3.15 ± 1.18	6.30 ± 0.98	0.51	-	-	-	-	-	-	-	
A-ag. 987/6	-	-	-	-	-	-	-	-	-	3.20 ± 1.47	7.60 ± 1.14	0.42	-	-	-	-	-	179.76	-	
B-ag. type	-	-	-	-	-	-	-	-	-	3.48 ± 1.08	7.90 ± 0.62	0.44	-	-	-	-	-	-	-	
B-ag. 761/7	-	-	-	-	-	-	-	-	-	3.85 ± 1.42	8.00 ± 0.32	0.48	-	-	-	-	-	-	-	
WL131	-	-	-	-	-	-	-	-	-	-	8.00 ± 0.53 ^a	-	-	-	-	7.17 ± 0.75 ^a	-	-	13.72 ± 0.71	
Accession	SN	ON	S/O	TSM	SN	TSM	TSM	SN	TSM	SN	ON	S/O	TSM	FL	SN	ON	S/O	TSM	FL	
	2015				2016		2017	2020		2021 (field)				2021 (glasshouse)						
Year, trait (average value ± s)*																				

* As samples of different size were initially weighed and then recalculated to TSM, standard deviation and statistics on comparison are not provided for this parameter. Values of the same parameter (ON, SN or FL) with the same letter within each row differ insignificantly ($p < 0.05$; Mann-Whitney test for paired comparison, Dunn test for comparison of more than two groups).

Key: SN = seed number per pod, ON = ovule number per pod, S/O = seeds to ovules ratio, TSM = 1000 seed mass (g), FL = flag length (mm), dash = data absent, # = sample size too small for reliable conclusions.

Table S2. Ovule number in plants of F₂ hybrids with different genotypes. No reliable differences were found between dominant and recessive classes (Mann-Whitney test for paired comparison, Dunn test for comparison of more than two groups).

Trait (genotype)	Ovule number*		
	Dominant phenotype	Recessive phenotype	
F ₂ Filby × WL1132 (2022)			
Stem length: normal (<i>LE</i>)/ dwarf (<i>le</i>)	6.94 ± 0.73 (62)	7.14 ± 0.72 (14)	
Leaf type: normal (<i>AF</i>)/ afila (<i>af</i>)	6.93 ± 0.72 (53)	7.07 ± 0.72 (23)	
Stipule shape: broad (<i>ST</i>)/ narrow (<i>st</i>)	7.03 ± 0.72 (54)	6.86 ± 0.72 (22)	
Pod pigmentation: green (<i>GP</i>)/ yellow (<i>gp</i>)	6.93 ± 0.72 (59)	7.15 ± 0.72 (17)	
Flower color: purple (<i>AB</i>)/ pink (<i>Ab</i>)/ white (<i>a_</i>)	6.90 ± 0.72 (43)	6.97 ± 0.72 (17)	7.22 ± 0.72 (16)
F ₂ Filby × WL131 (2022)			
Stipule shape: broad (<i>ST</i>)/ narrow (<i>st</i>)	7.73 ± 0.69 (37)	7.47 ± 0.69 (17)	
Flower color: purple (<i>A</i>)/ white (<i>a</i>)	7.68 ± 0.68 (41)	7.58 ± 0.68 (12)	

*Ovule number is represented as average ± s. Sample size is provided in brackets. For designations and characteristics of genes, see PGene (<https://data.jic.ac.uk/pgene/>).

Table S3. Correlations (Spearman's ρ) between selected parameters in 2015 (for 2016-2017, data on SN and TSM were also analyzed). Numbers of compared accessions are given in brackets.

	SN	ON	S/O
Ovule number (ON)	0.636* (11)		
Seed to ovule ratio (S/O)	0.773** (11)	0.045 (11)	
	2015: -0.300 (9)		
1000 seed mass (TSM)	2016: -0.154 (22)	2015: -0.150 (9)	2015: -0.250 (9)
	2017: 0.575** (15)		

Significant correlations are marked with bold and asterisk: *, $p < 0.05$, **, $p < 0.01$.

Table S4. Correlations (Spearman's ρ) between same parameters over different years. Numbers of compared accessions are given in brackets.

		2015				2016		2017	2020		
		SN	ON	S/O	TSM	SN	TSM	TSM	SN	TSM	
2016	SN	0.755** (11)				/					
	TSM	0.927** (11)				/					
2017	TSM	0.682* (11)				0.651** (25)		/			
2020	SN	-				0.347 (15)		/			
	TSM	-				0.657* (12)		0.171 (15)		/	
2021 (field)	SN	0.326 (9)				0.386 (7)		/		-	
	ON	0.917** (9)						/			
	S/O	0.464 (7)						/			
	TSM	0.738* (8)				0.576* (16)		0.631** (18)		-	
2021 (glasshouse)	SN	0.365 (8)				-0.249 (11)		/		-0.649 (7)	
	ON	0.451 (10)						/			
	S/O	0.527 (8)						/			
	TSM	-				0.900* (5)		0.800 (5)		-	

Significant correlations are marked with bold and asterisk: *, $p < 0.05$, **, $p < 0.01$.