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Effect of the *n* Gene on Pea Pod Characteristics¹

T. C. Wehner and E. T. Gritton^{2,3}

Department of Agronomy, University of Wisconsin, Madison, WI 53706

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Abstract. Fifteen pod characteristics were measured on parents and on F₁ and F₂ progeny of 14 crosses involving 9 cultivars or experimental lines of peas segregating for the *n* gene. In the F₂ generation, pods of *nn* plants were 17% shorter, 32% narrower, and 17% lighter in weight than normal (*N-*) pods. Pod walls of *nn* plants were 54% thicker, primarily the result of an increase in the number of parenchyma cells, though cell size also tended to be greater. Variation among F₂ progeny indicated that plants with thicker and heavier pod walls can be developed.

Pea plants homozygous recessive for the *n* gene have pods with thick walls (10, 12), while plants with the dominant allele have the normal, thin-walled pods. Lamprecht (5) reported that *nn* plants had pod walls with larger parenchyma cells, and the walls were 1.3 to nearly 2 times as thick as those of *N-*plants. He found that width and length of the pods of *nn* plants were 21.4 and 27.2% less, respectively, and that pod cross-section was circular rather than flat (6). Using a pod-curvature index, Nilsson (8) reported that pods of *nn* plants were 10 to 15% more curved than those of *N-*plants. Lamprecht (3, 4), Yarnell (14), and Blixt (1) provide further discussion on the effect of the *n* gene on pod characteristics.

Fiberless pods were reported as early as 1537 by Ruel (reported by Lamprecht and Svensson, 7). This trait is controlled by 2 genes (11) designated *p* and *v* (13). Normal (*P-V-*) plants have sclerenchyma on the inside of the pod walls which makes them unpalatable. The other 3 genotypes produce pods with reduced amounts of fiber. The genotype *pp V-* has sclerenchyma along only the pod wall sutures. *P-vv* types have small patches of fiber over the en-

tire inner pod wall surface, and *pp vv* plants are fiberless (12). Rasmusson (9) presented photographs of dry pods to show differences in wall fiber content and fiber location in the 3 types of pods which he called parchmented (*P-V-*), semi-parchmented (*P-vv* or *pp V-*), and non-parchmented (*pp vv*).

The objective of this study was to compare the pods of *NN* and *nn* parental lines or cultivars, and their F₁ and F₂, to quantify the effect of the *n* gene on pod length, width, area, volume, weight, moisture content, and wall thickness. Pea pod anatomy was studied to determine whether the thicker pod walls (developing ovarian walls) of *nn* plants were the result of more or larger parenchyma cells, or both. For edible podded peas, both pod wall thickness and wall fiber are factors contributing to quality.

Materials and Methods

Field study. Two edible-podded cultivars, 'Dwarf Grey Sugar' (DGS) and 'Mammoth Melting Sugar' (MMS), were each crossed with 7 *nn* lines of the Lamprecht collection obtained from Dr. Stig Blixt, Landskrona, Sweden. The genotype of the parental lines differed with respect to the genes *p* and *v*; this permitted evaluation of the *n* gene over 4 levels (phenotypes) of pod fiber. Both *NN* parents had fiberless pods, while the *nn* parents were as follows: 862 and 1514 had fibered pods (*PP VV*); 110, 462, 761, and 1143 had partially fibered pods (*PP vv*); and 1255 had fiberless pods (*pp vv*).

Parents, F₁s, and F₂s were grown along wire trellises in the field nursery at the Arlington, Wisconsin, Agronomy Farm. The experimental design was a split-split plot in a randomized complete block with 3 replications. The 2 whole plots contained crosses involving only DGS, or only MMS. Subplots were the 7 crosses involving each of the 7 Lamprecht lines as crossed to either DGS or MMS. Sub-subplots consisted of the 5 populations within a cross: *NN* parent, *nn* parent, *Nn F₁*, *N-F₂*, and *nn F₂*. The sub-

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²Former graduate research assistant (presently Assistant Professor of Horticulture, North Carolina State University, Raleigh, NC 27650), and Professor of Agronomy.

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subplots for parents and F_1 s were 0.9 m in length and had an average of 36 plants grown along both sides of the trellis. The F_2 plots were 2.4 m long and contained approximately 96 plants to provide a sufficient number of the recessive nn types for study. Statistical analyses were performed on plot means, each mean based on measurement of from 2 to 9 pods, with an average of 5 pods per plot. No more than 1 pod was harvested from each plant.

To assure that all pods were sampled at the same stage of development, flowers were tagged on the day of anthesis and pods collected from each plot 12 days later. Data were recorded for total fresh weight (pod with ovules), pod fresh weight, pod length and width, and pod wall thickness. Pod wall surface area, volume, and density were calculated from the data on pod weight, length, width, and wall thickness. Pods and ovules were dried separately at 60°C to determine dry weight and moisture content.

Anatomical study. Pod anatomy was studied in 6 selected families obtained from crossing the NN cultivars, DGS and MMS, with each of the nn Lamprecht lines, 462, 862, and 1255. Three pods from each plot were collected from the field for the NN parent, nn parent, $Nn F_1$, $N-F_2$, and $nn F_2$ of each cross. Free hand, transverse sections were cut from fresh pods of the first 2 field replicates. Pods from the third replicate were fixed in formalin-ace-toalcohol, dehydrated in tertiary butyl alcohol, and embedded in Paraplast. Transverse sections were cut on a rotary microtome at 10 μ m and stained with safranin O, crystal violet, and light green SF yellowish (2). Pod transverse sections from fresh and embedded materials were examined under a light microscope, and the number of cells across 5 pod wall sections was counted. The diameter of 16 cells selected at random in the same 5 sections was measured on the 2 replicates of fresh material only, using an ocular micrometer.

Results and Discussion

Field study. Comparison of population means averaged over all crosses for the 15 pod characteristics shows that the pods of the NN parent had the greatest length, width, surface area, wall volume, and weight (Table 1). Pods of the $Nn F_1$ and $N-F_2$ were similar for all characters measured, being significantly different only for percent moisture of the pod. Pods of the nn parent and $nn F_2$

were similar for length, width, wall thickness, surface area, and wall volume but differed in pod density, weight, and percent moisture. Pods of the $Nn F_1$ had values intermediate to those of the parents for all characters except wall thickness and percent moisture, for which the $Nn F_1$ pods measured significantly lower than either parent. In most cases, pods of the $N-F_2$ more closely resembled those of the NN parent than of the nn parent.

To further assess the effect of the n gene, the $N-F_2$ and $nn F_2$ were compared, under the assumption their genetic backgrounds were random since they were segregating for many genes. Results show that pods of $nn F_2$ plants averaged 53.8% thicker walls than those on $N-F_2$ plants (Table 1). This agrees with the findings of Lamprecht (5), who found 30–100% thicker walls on nn pods. In addition, nn pods were shorter, narrower, and had lower fresh and dry weights. Depending on whether pod yield was measured as wall volume, fresh, or dry weight, plants with thick-walled pods yielded 82–88% that of plants with thin-walled pods. The reduction in length (16.8%) and width (31.7%) in pods of nn plants is somewhat different from the 27.2 and 21.4% reductions obtained by Lamprecht (6), who used different experimental lines.

A frequency distribution of plants for fresh weight of pods with ovules indicated that thin-walled pods from $N-$ plants tended to be heavier than thick-walled pods from nn plants. This is due to the greater length and width of pods on $N-$ plants compared to those of nn plants. However, some thick-walled pods were among the heaviest, indicating that the weight of thick-walled pods might be increased through selection in a breeding program.

Anatomical study. Thick-walled pods generally had more and larger parenchyma cells than thin-walled pods (Table 2). However, differences in cell diameter were not significant according to the analysis of variance. This is due to the wide range in cell size: cells near the inner and outer epidermis were small, and the more internal cells were larger.

The effect of cell number on pod wall thickness was much greater than that of cell size. Single-degree-of-freedom comparisons between pods of all $N-$ and nn plants, as well as between pods of the $N-$ and $nn F_2$ plants, showed no significant difference between thick-walled and thin-walled pods with respect to cell

Table 1. Means of 15 crosses for pea pod characteristics measured in the field study.²

Characteristic	NN parent	$Nn F_1$	$N-F_2$	$nn F_2$	nn parent	($nn F_2$ / $N-F_2$) x 100
Pod length (mm)	86a ²	78b	78b	64c	62c	83.2
Pod width (mm)	20a	18b	18b	13c	12c	68.3
Pod wall thickness (μ m)	1050a	1008c	1036bc	1594a	1622a	153.8
Pod surface area (mm ²)	1239a	1034b	1044b	591c	523c	56.6
Pod wall volume (mm ³)	2685a	2100b	2185b	1915c	1797c	87.6
Pod wall density (mg/mm ³)	1.19a	1.18a	1.20a	1.16a	1.01b	96.3
Total ³ fresh wt (g)	4.73a	3.88b	4.06b	3.38c	2.52b	83.2
Pod fresh wt (g)	3.20a	2.48b	2.63b	2.22c	1.82d	84.4
Ovule fresh wt (g)	1.53a	1.40a	1.43a	1.16b	0.70c	81.1
Total dry wt (g)	0.78a	0.69b	0.69b	0.57c	0.39d	82.7
Pod dry wt (g)	0.52a	0.45b	0.46b	0.37c	0.28d	82.1
Ovule dry wt (g)	0.26a	0.24a	0.24a	0.20b	0.11c	83.7
Total % moisture	83b	82c	83b	83b	85a	100.0
Pod % moisture	84b	81d	82c	83bc	85a	100.5
Ovule % moisture	83a	83a	83a	83a	83a	99.1

²All pods measured 12 days after anthesis.

³Mean separation (within rows) by Fisher's LSD test, 5% level.

⁴Total = pod + ovules.

Table 2. Generation means within crosses for cell number^a and cell diameter^b in pea pod walls.

Generation	Cross						Mean
	DGSx462	DGSx862	DGSx1255	MMSx462	MMSx862	MMSx1255	
	<i>Cell number</i>						
<i>NN</i> Parent	10.6a [*]	10.6b	10.6b	9.7a	9.7a	9.7a	10.2a
<i>Nn</i> F ₁	9.9a	9.0a	9.0a	10.8a	9.4a	10.1a	9.7a
<i>N-</i> F ₂	10.3a	9.6ab	9.9ab	10.1a	9.6a	9.9a	9.9a
<i>nn</i> F ₂	13.4b	13.2c	12.2c	12.8b	13.9b	14.5b	13.4b
<i>nn</i> Parent	14.5b	14.5c	13.1c	14.5c	14.5b	13.1b	14.1c
	LSD 5% = 1.5 (col. 1-6)						0.6
	<i>Cell diameter (μm)</i>						
<i>NN</i> Parent	128.2b	128.2a	128.2a	139.5bc	139.5a	139.5a	133.9ab
<i>Nn</i> F ₁	99.5ab	131.0a	111.4a	105.6ab	142.6a	111.9a	117.0a
<i>N-</i> F ₂	99.9ab	131.3a	114.8a	128.5bc	126.1a	114.0a	119.1a
<i>nn</i> F ₂	136.3b	149.4a	105.9a	151.6c	160.7a	131.4a	139.2b
<i>nn</i> Parent	66.5a	152.1a	127.2a	66.5a	152.1a	127.2a	123.6ab
	LSD 5% = 44.8 (col. 1-6)						17.9

^aAvg number of cells between the epidermal layers of the pod wall.^bAvg diameter of parenchyma cells in the pod wall.^{*}Mean separation within columns by Fisher's LSD test, 5% level.

size ($F = .01$ and $.16$, respectively). Differences for cell number, however, were highly significant ($F = 32.99^{**}$ and 9.44^{**} , respectively).

Conclusions

The major effect of the *n* gene when homozygous recessive was to produce plants with curved pea pods, round in transverse section, having thick pod walls. The *nn* plants also had pods with less length, width, area, volume, and weight than pods of *N-* plants. Thicker pod walls were mainly the result of an increase in the number of pod wall parenchyma cells, although an increase in cell size was partially responsible. Plant breeders with the goal of developing cultivars with fiberless, thick-walled pods exemplified by 'Sugar Snap' may profit by selecting for both thick pod walls and greater pod weight.

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