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CYTOGENETICS OF THE VEGETABLE CROPS

III. LEGUMES. A. GARDEN PEAS, *PISUM SATIVUM* L.

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ORIGIN

Cultivated garden peas appear to be of considerable antiquity. Wade (308) cites C. Pickering for the statement that they can be traced back to the Stone Age. A wild species from which the crop may have been developed remains unknown. Vavilov (302) gives four centers of origin. For three of them, Central Asia, the Near East and Abyssinia, *P. sativum* is listed as a cultivated grain crop, while the Mediterranean area produced a variety with large seeds.

According to Bailey (4) there are three botanical varieties—*humile* Poir. the Early Dwarf Pea, *macrocarpon* Ser. the Edible-podded Pea, and *arvense* Poir. the Field Pea. Both *P. humile* Boiss. (not Mill.) and *P. arvense* L. were first described as distinct from *P. sativum.* Crosses between *P. sativum* and the other two forms are fertile (128, 218, 284) where chromosomal interchange has not occurred. Nine characters regarded as specific behave the same genetically in the second generation of *P. humile* × *P. sativum* as in *P. sativum* (128). Similar results have been obtained in crosses between Asiatic and European varieties of *P. sativum* (111, 250). The genetic evidence thus supports the treatment of *humile* and *arvense* as botanical varieties of *P. sativum.* Lamprecht (153) feels that *P. sativum* has developed from *P. arvense* through mutations, mainly *A* to *a, Le* to *le, V* to *v,* and *R* to *r,* selected in cultivation. Since *P. arvense* is so widespread geographically and may antedate *P. sativum* he would keep *P. arvense* L. as the major species name and place the cultivated varieties of peas in *hortense,* as a botanical variety of *P. arvense.*

CHROMOSOMES

Number and Morphology

Numerous investigators (1, 35, 274, 296) are listed as reporting seven haploid and 14 diploid chromosomes. Three independent descriptions of the somatic chromosomes appeared in 1931 (210, 223, 250). Their size is relatively small; the early reports give 1.0 to 4.4 μ (223), 4.0 to 6.1 μ (210), and later (25) 3.8 to 5.4 μ. In the last report mentioned the chromosomes were treated with an oxyquinoline derivative and measured with a screw ocular micrometer.

There is disagreement in regard to the number of chromosomes having "secondary constrictions." Lewitsky (210) illustrates one pair of medium length with a satellite and one homolog of the next to

longest pair with a satellite. Sansome (250) found three pairs with one secondary constriction, one pair having two. Marshak (223) reports four pairs with one secondary constriction and one pair having two. Koller (88) lists one chromosome with a satellite and one with a secondary constriction. Morrison and Lin (231) observed only two chromosomes with secondary constrictions (satellites). Caroli and Blixt (25) report that three pairs—III, IV and VI—have secondary constrictions producing terminal portions that differ in size, but in a later publication Blixt (12) illustrates chromosome III without a satellite. Atabekowa (1) finds two chromosomes with satellites and two with terminal constrictions. Differences in cytological technique and material used probably account for these discrepancies of observation.

Recently (13) an improved technique wherein root-tips are treated with an aqueous solution of 5-7-dibromo-8-hydroxyquinoline (bromoq) for 16 hours at 3° C. has been adopted. They are then hydrolysed for nine minutes in normal HCl and given a Feulgen stain, after which the root-tips are squashed on a slide. Such treatment gives maximum contraction of the chromosomes consistent with useful preparations. Fifty plates of Lamprecht's normal Line 110 together with a few plates from nine additional normal lines were studied in detail. The data presented in Table 1a were compiled from this report (14). Data from a later report (15) are presented in Table 1b.

Features aiding in the identification of some of the somatic chromosomes are the length of I, the subterminal centromere of VII, the shorter satellite of IV, and the longer satellite of VI. A secondary constriction can sometimes be seen in III.

The resting nucleus is without chromocenters (69), although they are present in the interphase nucleus. More chromocenters are found in the interphase nucleus of wrinkled than of round seeded peas.

MEIOSIS

Seven pairs are observed in the pollen mother cells and meiosis proceeds normally through both divisions (280). All points of association between homologs are the result of chiasmata (250). The nucleolus is a sphere 4.5 μ in diameter at early prophase (56). At pachytene it flattens out on the periphery of the nucleus but again becomes spherical at diakinesis, disappearing at early AI. At late anaphase I or telophase each chromosome forms a small nucleolus at the region of the centromere. These nucleoli begin to fuse at inter-

kinesis when they become reduced to one or two per nucleus. In *uni* plants one or more extra-nuclear nucleoli are commonly seen (250). Similar nucleolar development has been observed during mitosis.

TETRAPLOIDY

On the whole the tetraploid form is not especially larger than the diploid, although the lateral leaflets and stipules are somewhat larger, wider and relatively shorter, which tends to give the leaves an ovate form. Edges of the petals are scalloped instead of entire as in the diploid. The $2x$ pollen has a greater diameter than haploid pollen and some grains are poorly filled. Both stomata and cells of the tetraploid are somewhat larger than those of the diploid (281).

CHROMOSOMAL INTERCHANGE

The gene linkage groups as determined from a study of commercial varieties are regarded as representing the normal chromosomal arrangement. Interchanges between non-homologous chromosomes have been discovered, which involve all seven linkage groups (267). Discussion of individual interchanges follows the section on linkage.

Lines homozygous for an interchange are fertile and have seven pairs of chromosomes at MI. Such plants crossed with normals usually produce plants that exhibit about 50 percent pollen sterility and ordinarily have five pairs and a chain or ring of four chromosomes. Either adjacent or alternate chromosomes of the ring go to opposite poles. Cells receiving both interchange chromosomes develop normally since they have a full complement of genes. Cells receiving only one interchange chromosome and the normal homolog of the other abort because one part of the interchange chromosome duplicates the normal, while essential genes attached to the other interchange chromosome are missing. In some cells there is a six-and-eight division at AI.

Crosses between plants having distinct chromosomal interchanges involving the same two chromosomes also have an association of four chromosomes at meiosis. When two interchanges have one chromosome in common there is an association of six chromosomes, and when the two interchanges involve distinct chromosomes two groups of four chromosomes plus three pairs are found (265).

INTERCHANGE AND STERILITY

Several degrees of sterility have been observed in interchange materials (105, 129, 144). The 50 percent sterility found in crosses between

plants homozygous for a single interchange and the normal type has been mentioned. When plants with distinct interchanges having one chromosome in common are crossed the ring of six chromosomes results in about 62.5 percent sterility. If two interchanges involving four distinct chromosomes are crossed the two associations of four chromosomes result in about 75 percent sterility. Plants have also been observed in which there was approximately 25 or 32.5 percent sterility, and one in which the pollen was normal but there was 50 percent seed abortion. Where sterility is less than expected there are three possible explanations: (a) interchanges that involve only small terminal portions whose absence in certain situations is not lethal; (b) interchanges, while large in comparison with those in (a), that do not include genes essential to gametic fertility; (c) simple translocation, resulting in duplication that can substitute for the missing portion of the chromosome.

Other Structural Types

In a discussion of polymeric genes Lamprecht (135) suggests "It is characteristic of the seven chromosomes of *Pisum* that each of them contains at least one—sometimes two—smaller or greater parts which are homologous with corresponding parts in other chromosomes." These sections are apparently too short to influence pairing and the normal course of meiosis but might rarely lead to an interchange between nonhomologous chromosomes.

One plant from a cross between *P. sativum* and its variety *humile* was found to have a chromosome with duplicate ends (268). From 20 to 30 percent of the nuclei had two univalents because of the failure of this chromosome to pair with its normal homolog.

Two plants of *P. sativum* var. *humile* had chromosomes structurally distinct from the normal. One was heterozygous for two inversions. The other plant had reduced chiasma formation as a result of several structural changes for which it was heterozygous (286).

Various chromosomal changes that result in the relocation of both centromeres and satellites may reduce pairing as much as 30 percent (88). The resulting univalents divide during any of several meiotic stages. A single short terminal inversion was observed in this case. Polyploid areas in root tips of this plant were common. The multiple microspores varied greatly in size. Only 9–14 percent of the pollen was considered to be good. The seedlings obtained did not reflect the degree of chromosome irregularity observed (88).

TRISOMICS

The eight-chromosome gametes resulting from unequal division in the heterozygous interchange plants have led to the production of 15-chromosome plants. Some of these have a normal diploid complement plus an extra normal chromosome; others have an extra interchange chromosome. One plant of the latter type had an association of six chromosomes (264). The primary trisomics have six pairs and a group of three chromosomes or seven pairs plus a univalent (55). Division is often seven plus eight, but the extra chromosome is sometimes excluded.

Tertiary trisomics and trisomic interchange heterozygotes have been obtained from Hammerlund's K-line, which is homozygous for a single interchange (287). A trisomic interchange heterozygote is a plant that is heterozygous for the interchanged chromosomes and that has an extra interchange chromosome. The extra chromosome is thus primary for its interchange homolog but tertiary with respect to its normal homolog.

INFLORESCENCE

MORPHOLOGY

A simple recessive gene, *sup,* results in two additional wings, giving a total of seven petals (107, 137). The supplemental wings can attain normal size but are usually small to very small. Recessive *k* produces a keel on the wing (251). In some families *K* is not fully dominant which results in intermediate wing types (187). Another recessive, *nap,* causes the petals to be broader than normal and to have a thick, broad keel at the upper end (137). Several genes reduce the width of the sepals and sometimes the petals as well. Their principal effect may be on the stipules and often on the leaves. Three of these, *fo, fob,* and *fol,* for folium oblongum, affect sepals, stipules and leaflets (67). They are independent in inheritance. The partially recessive *ten* (tenuifolia), causing a small leafy plant with narrow rounded leaflets and stipules, has a similar but greater effect on the sepals than do *fo, fob,* or *fol* (125, 137).

In the recessive mutant *aph,* called aphacoides, both sepals and petals are narrow and pointed. The standard is lance-like and the keel petals have an extended point (115, 137, 243). Plants recessive for *trip* (tripistillum) have lance-like leaves and sepals. Both standard and wing are narrow, and the keel is upright with two lateral lanceolate leaflets (112, 137). Unifoliate plants (*uni*) have a small proportion of both

bi- and trifoliate leaves. The inflorescence is repeatedly branched and compressed, with very short internodes. The flower elements are more or less pistilloid and resemble somewhat a small head of broccoli (99, 137, 139).

Recessive *re* reduces the size of the flower (237). The lethal *red* also reduces the size of the flower, which remains in the bud stage. The greenish petals are poorly developed. Both stamens and pistils are abnormal in shape; the latter become hooked (107, 137, 346). The recessive *sti* (stipuloides) produces a pair of small triangular accessory leaves on the flower stalk and two small white leaflets in the flower. There are no petals or sepals (137).

The inflorescence is modified to branchlets by *inc* (inflorescentia conversa). The plants may develop terminal flowers followed by pods with a few seeds, although seed production is greatly reduced (178). An X-ray mutant *siv* (sine-vexillum) in Lamprecht's interchange Line 58 causes the early flowers to lack a standard (169). Such flowers are completely sterile.

Bracteoles are due to the nearly dominant *Br* (209). A second gene, *Bra,* is also required (135). Largest bracteoles occur in plants homozygous dominant for both genes. An abnormal condition of the floral bracts that takes the form of a green collar is reported to have bred true for three generations (18).

Sterility

A recessive gene, *pe,* causes stamens to develop as petals (237). Such petaloidy is highly variable. Another gene, *brev,* shortens the length of the filament, which hinders self-pollination (100, 137). Recessive *com* has a similar effect (100). A rogue-producing gene, *ang,* for angustifolia, causes sterility as well (8, 107, 137). The aphacoides mutant is female-sterile (243). Branched plants, caused by *bri* (breviramosus), are male-sterile (112, 137).

The leaves of plants recessive for *lac* (laciniata) have only one pair of leaflets, which are abnormal in shape. The inflorescence is unbranched and the terminal bud does not open completely. The sepals are only 10–12 mm. long. The anthers are small and about 80 percent of the pollen is empty. Stigma and style are small but appear normal otherwise. Such plants are fully sterile (159).

Plants with obovate leaves (obovatus) due to *obo* have a small androecium and gynoecium. The flowers open only silghtly and are sterile

(115, 137). The *trip* plants mentioned in the preceding section are partially pollen sterile (112). Unifoliate plants (99), as well as plants heterozygous for *re* (237) and the lethal *red* (107, 137), are completely sterile. In some genetic backgrounds recessive *re* frequently mutates to *Re,* which restores fertility to the upper portions of *re* plants (191, 194). Homozygous *sti,* described above, causes the flowers to be female sterile (137).

Pollen Tube Growth

A gene has been observed to stimulate growth of the pollen tube (275). Linkage with other genes increases their ratio in the progeny. The amount of increase is related to the closeness of the linkage. A dominant factor, *Pt,* accelerating pollen tube growth, is mentioned by Wellensiek (319).

Number of Flowers

In spite of reports (30, 299) that higher flower number is dominant to lower, most workers (119, 228, 305, 325, 341) agree that low number is dominant. The gene symbol *Fn* was proposed by White (341). It was later shown (119) that two genes are involved; *Fn Fna* together produce a single flower. Either *Fn fna* or *fn Fna* cause two flowers to develop, and *fn fna* are responsible for three or more flowers. Environmental conditions that favor vigorous growth may cause an *Fn Fna* plant to produce some 2-flowered peduncles. Poor growing conditions have the reverse effect, but do not reduce the higher numbers to two (119). X radiation has produced a mutation with proliferating inflorescence (43).

Spacing

Relative distance between the first and second flowers is determined by three independent pairs of genes (124). Two of these affect the total length of the inflorescence. *Dt* is a flower-distance gene, while *Pr* and *Pre* also determine length of the peduncle. In crosses between extremes the distance between flowers in the first generation is nearer the closer spaced parent, while the longer flower stalk tends to be dominant. A distance index is obtained by dividing the length of the stalk to the lowest flower by its total length and multiplying by 100. Crosses between plants having indices 81.71 and 61.97 had an F_1 index of 77.42. Extreme indices are 54 and 86. *Dt Pr Pre* produce an index of 83 to 86

with a total peduncle length of 135 to 160 mm. Index for the triple recessive is 54 to 60 with a total stalk length of 50 to 70 mm. Index and flowering-stalk lengths for selected genotypes are *Dt pr pre* 72 to 78, and 90 to 110 mm.; *dt Pr pre* 54 to 70, and 90 to 110; *dt pr Pre* 54 to 70, and 70 to 90 mm. *Pr* has more influence than *Pre* on the length of the flowering stalk.

Season will be discussed as a plant character. Flower colors are considered in the section on anthocyanin pigments.

SEEDS

FORM

In 1908, Lock (216) added the F_2 data of Mendel, Tschermak, Bateson, and Hurst to his own to get a total of 19,106 round to 6,297 wrinkled seeds. In 1917 White (341) obtained a total for all investigators of 24,290 smooth to 8,029 wrinkled. The gene pair is designated *Rr*. Round (smooth) seeds have a simple "potato" type of starch grain while wrinkled seeds have a smaller compound (33, 44) or, more accurately, split (80) grain. Both types of seeds also have a few small round grains. The F_1 has modifications of both forms (33). Smooth seeds average 46.3 percent starch, of which 38 percent is amylose, while the wrinkled seeds average 33.7 percent starch of which 69 percent is amylose (85).

Indent differs from smooth by two dominant genes, designated L_1 and L_2 by Tschermak (298). L_1 has since been found to be the equivalent of the basic color factor *A*, and L_2 has been redesignated *L* (185, 332). When either *A* or *L* is recessive in plants with round seeds, crosses between round and indent give a 3:1 F_2 ratio (48, 291). When both are recessive there is a 9:7 ratio. Since indent is a pericarp and therefore plant character all seeds on a plant are the same and the character is determined by the genotype of the plant, not of the endosperm.

In contrast to those of most other varieties, seeds of 'Chenile' adhere to each other when removed from the pod (305). The character takes its name from this variety, but it has been found in other material (36). The condition is recessive (228, 299) and has been designated *s* (341). It is subject to environmental influence (228). A second gene, *miv*, has a similar effect (131). The two genes are in different linkage groups (I and II). Both genes compress the seed.

The radicula becomes deeply sunken with *fov*, from foveatus (184).

Dimpled seed is due to *di,* which is hypostatic to *A* and so requires *a* for expression. Recessive *di* is also hypostatic to *r*. This gives in the F_2 9 *R Di*: 3 *R di*: 4 *r* (*Di* + *di*) (76, 328).

Four additional recessive genes are concerned with the shape of seed resulting from crowding in the pod. The sides of *pla* seeds are slightly flattened; *qua* is ineffective with *Pla,* but *pla qua* seeds are cubical. The sides of *com* seeds are considerably compressed or flattened. Recessive *sul* produces a "sulciform" impression at the radicula, similar to the effect produced by *fov* (185). A dominant gene *Ro* is also proposed for seeds flattened in the pod (328); this is later questioned (185).

Size

Seed size depends upon several genetic factors. When plants with large seeds are crossed with plants having small seeds the first generation has seeds of intermediate size. Four factors are mentioned (298). Wellensiek (318) redesignated Tschermak's four *Sg* size factors S_1, S_2, S_3, and S_4. Four genes for length of seed, *Lo*, Lo_1, Lo_2, and Lo_3 are also listed (224, 308). The recessive *ma* increases size of the seed in a variable amount (169).

Seed Coat

The inner surface of the testa may be coated with traganth, due to *Tra,* formerly *Tram.* In round seeds the traganth is limited to two spots, but with *r* the locations are less definite. With *I* the spots appear a greasy yellow, but with *i* the spots are green. The character is difficult to classify in dark-colored seeds but can be identified by examining the inside of the testa with a microscope. *Tra* lies between *Fa* and *Td* in linkage group IV (152, 157).

A bilaterally symmetrical stripe 1 to 2 mm. wide appears below the hilum as a result of *gri.* With *A* the stripe is clear green; with *a* it is gray. *Gri* is linked with the gene *I* in chromosome group I (113, 120, 166).

Thickness of the seed coat is determined by two genes, Ep_1 and Ep_1' (224, 308).

Protein

The protein content of the 'Golden' variety is 19 to 26 percent and that of 'Wonder of America' is 22 to 34 percent. Varieties that are morphologically homozygous may be heterozygous for protein content. Its inheritance is Mendelian (353).

VITAMINS

Highly significant varietal differences have been found over several seasons for ascorbic acid, carotene, riboflavin and thiamin (68). Thiamin has the least seasonal variation. The range in ascorbic acid content obtained for different varieties of 29.0 to 44.4 mg. per 100 g. on a fresh-weight basis, with an LSD of 5.7 mg. at 1 percent, is similar to results obtained by other workers (219). Data obtained in 1944 in terms of mg. per 100 g. fresh weight and LSD at 1 percent follow: (early varieties) carotene 383 to 560 (LSD 57), riboflavin 78 to 117 (LSD 23), thiamin 116 to 370 (LSD 93); (late varieties) carotene 338 to 714 (LSD 100), riboflavin 84 to 117 (LSD 12), and thiamin 305 to 447 (LSD 62) (68).

ABORTION

The abortion of seeds in the pod is evident from obvious constriction. The condition is dominant in the F_1. The gene designation is *Q* (335). This gene is questioned by Lamprecht (114) because of so much chromosomal interchange and other abnormalities in *Pisum*. A somewhat similar gene *Fe* is proposed by Sverdrup (288). The recessive *fe* causes female sterility and splitting of the pod.

PODS

BREADTH

Early work (216) suggests that several genes are involved in diameter of pod, although Clay (30) later reports a single major factor. The effect of *Te* on width of pod follows: *TeTe* 13.5 to 14 mm., *Tete* 12.5 to 13 mm., and *tete* about 10 mm. A cross between plants having pods 10 and 14 mm. in diameter gave an F_1 with pods 12.5 to 13 mm. wide and a second generation with pods 9.4 to 17.8 mm. wide (133, 145). In order to explain the widest pod a new gene, *Laf*, is postulated (145). Combined, the two genes give breadth of pod about as follows (mm.): *TeLaf* 15.4, *Telaf* 13.8, *teLaf* 11.8, and *telaf* 10.0. A third gene, *Lt*, that increases breadth of pod about 25 percent, is linked with *P* and *Wlo* in linkage group VI (167). The gene *n*, in addition to giving a thick pod wall, reduces breadth of pod 25 percent. Recessive *teu* gives with *te* a very narrow pod (196).

WALL THICKNESS

Thin pod wall due to *N* is dominant to thick wall (298, 318). This gene also affects the type of pod apex as well as pod shape (114, 234). The recessive *n* produces a smaller pod than *N* (104).

FORM

The dominance of blunt over pointed apex has long been recognized (216). Rasmusson (253) obtained an F_2 segregation of 9 blunt to 7 acute. He designated the two genes involved *Bta* and *Btb*. In a cross between the two types Nilsson (234) secured 3 blunt to 1 acute in the second generation. Lamprecht (114) recognizes only one gene *Bt*. The sugar variety 'Roi des Gourmands' is a special pointed type which, crossed with normal pointed, produces in the F_2 9 blunt to 3 Roi pointed to 4 pointed. It is concluded that *Bt* can produce a blunt point only in the presence of *N*, the gene for thin wall. "Roi des Gourmands" is thus *Bt Bt n n*, which give Roi acute point, and the cross is *Bt Bt n n* × *bt bt N N* (234). This may explain the observations of Rasmusson.

Pods may be straight, convex or concave. Concave pod was named scimitar pod by White (344), who found various degrees of curving, the F_1 between curved and straight being slightly curved. However, scimitar × 'Acacia' gave straight F_1 and 45 straight to 13 curved in the F_2. White suggests *Ss ss* as the symbol. This was redesignated *Cp* by Wellensiek (320) and adopted by Lamprecht (101) because of the similarity of *Ss ss* to *S s*, the gene for adherent seed. The combination *N Cp* gives a completely straight pod (114).

Convex pod *con* is also essentially recessive (101). The recessive *n* favors concave pod, while *con* causes curving in the opposite direction. The combinations *n con* and *N Con* give pods that are approximately straight, while *n Con* produce concave and *N con* convex pods (104, 114, 135). Only one variety, 'Pois Sabre,' is said to have a convex pod. Lamprecht (135) crossed *N Con* × *n Con* (straight × curved pod) and obtained in the second generation a 3:1 ratio for thin to thick pod wall and a 15:1 segregation for straight to curved pod. He therefore assumes a second recessive gene *co* for curved pod. He regards *con* and *co* as polymeric genes. Lamprecht (156) later mentions another recessive gene for curved pod, which he designates *cpa*. This is based on a 15:1 ratio secured with heterozygous *Cp* and is reminiscent of von Rosen's cp_1 and cp_2 (260).

TEXTURE

Most varieties grown in America have a pod that is inedible because of a tough membrane, which is dependent for expression upon two dominant genes. One of these was discovered by Mendel (226). Vilmorin (304) crossed two varieties with membraneless pods which produced an F_1 with pod membrane and an F_2 segregating 9:7 for this character. Pods having a membrane are referred to as smooth (325), hard (244), inflated or parchmented (341). The two genes are *P* and *V*. *P v* give a thin membrane over the entire inner surface of the pod (236, 325). *V p* produce a heavier layer or "string" along each edge of the pod. Lamprecht (101, 108) describes the *P v* membrane as flecked and the *p V* membrane as striped. It has been observed (108, 325) that in the combination *P v* the recessive *v* mutates rather frequently to *V*.

PLANT CHARACTERS

HEIGHT

Early reports (216, 226, 305) indicate a single gene pair governing height, tall being dominant to short. Differences were observed in both number and length of internodes. A series of alleles was later described for each (83, 253, 343). *Le* (originally *L*) gives long internodes, Le_1 very long, and *le* short internodes with a zigzag stem. A series of four alleles for internode number with suggested range in number is T_1, 40 to 60; T_2, 20 to 30; *T*, 20 to 40; and *t*, 10 to 20 (83, 343). *Le* T_1 produce the tallest plant and *le t* the shortest. Long × short internode gave in the F_2 434 long and 134 short (292). A second cross with less difference in internode length segregated 386 long to 136 short in the second generation. It should be noted that T was originally named for thick stem (83) and was later considered to influence internode number as well (292, 343). Two additional genes for internode length are *coe* (20 to 32 mm.) and *cot* (33 to 64 mm.) (206). Lamprecht (206) proposes the gene *mie* (minuere) for 10 to 16 internodes, based on the work of Keeble and Pellew (83).

In spite of the obvious relationship between the number of nodes and the number of internodes on the same plant, a second series of alleles affecting the number of nodes is proposed (292, 319). Sn_1 Sn_2 produce a high node number, while sn_1 sn_2 or sn_1 Sn_2 give a low number and Sn_1 sn_2 an intermediate number. Comparisons need to be made under the same growing conditions, as plant height is considerably

affected by the environment (319). Hybrid vigor has also been observed in crosses and needs to be taken into account.

Genes for height have been found in all linkage groups but IV (206).

X-radiation has produced two recessive point mutations that reduce size of the plant. These are *min* (minutus) and *cov* (coeruleovirens), which also cause a deep bluish-gray-green plant (169).

Other genetic factors involved in height of plant give special plant types or have other effects. Gene *brev,* mentioned as reducing the length of the filament (100), also reduces internode length. Compact branches in the leaf axils result from a single gene, *com* (100). Several instances are known in which the double recessive of a cross between two dwarf forms results in a "slender" plant.

Recessive genes for dwarf are designated cry_1 and cry_2 by Rasmusson (253), who calls the double recessive "crypto-dwarf." The slender type of de Haan (45) is *la lb.* Lamm (89) considers that cry_1 is the equivalent of *la* and renames it cy_1. He believes that *lb* has two alleles, cy_2^c and cy_2^s. Crypto-dwarf is thus $cy_1\ cy_2^c$ and slender is $cy_1\ cy_2^s$. There are four types of dwarf plants according to this scheme: $Cy_1\ cy_2^c$, $Cy_1\ cy_2^s$ $cy_1\ Cy_2$, and $Cy_1\ Cy_2$. Von Rosen (261) finds three dominant genes for dwarf plant that are allelic to cry_2. They are Cry_2^{dw} dwarf, Cry_2^{lw} low dwarf, and Cry_2^{na} nana. Each of these functions with *le* Cry_1. These dominant dwarfing genes are thought to "promote enzymes which inhibit growth in length." Lamprecht (206) redesignates cy_2^c as cry^c and cy_2^s as cry^s, retaining *la* for cry_1 and cy_1. Crypto-dwarf then becomes *la* cry^c *le* and slender *la* cry^s *Le* or *le.*

Wellensiek (329) reports a slender type, which he calls "springers," segregating from crosses between two dwarf forms. They appear in both 3:1 and 15:1 ratios. No gene designation was made, although springers are considered to be distinct from both slender and crypto-dwarf. A very small dwarf "micro" appears when its gene, *lm,* is in combination with *le,* cy_1, and cy_2 (212, 256). Other combinations give three additional types: *lm Le* Cy_1 Cy_2—microtall, *lm, le* cy_1 cy_2^c—microcrypto-dwarf, and *lm le* cy_1 cy_2^s—microslender (212). The new types are similar to their corresponding *Lm* types but smaller.

Screwball, a dwarf type with poorly shaped leaves of reduced size, can be recognized at an early stage of growth (84). Lamprecht (158) proposes to change the original designation of screwball, *sb,* to semi-pumilio, *sp.*

Dwarf mutations have resulted from radiation treatments (42, 206, 333). One bears pods at the fourth to sixth node; another has very short internodes.

HABIT

Certain plants of var. *humile* are semi-prostrate, the stem twisting to about a 45° angle. The character behaves as a simple recessive in crosses with *P. sativum.* The gene is named *asc* for ascendens (128).

TOP-ROOT RATIO

The variety 'Knott's Excelsior' growing to a height of 19 inches, had a root length of 28 inches and a top-to-root ratio of 1:1.4. The 46-inch "Telephone" variety had roots 36 inches long and a ratio of 0.7. The second generation of a cross between these varieties had 209 tall to 68 short plants. The top-root ratios for these segregates were 1.5 and 0.9, respectively. Pruning did not change the top-root ratio (74).

BRANCHING

The degree of branching is controlled by two independent genes, *fr* and *fru.* When both are recessive, plants have 5 to 10 branches instead of 1 to 4 when both genes are dominant. A second-generation ratio of 362 normally branched to 20 with increased branching was obtained (126). The number of branches increases somewhat when either gene is recessive. The character is subject to environmental influnce. Pleiotropic effects of *fru* include a reduction of plant height, bloom at a lower node, and pods about 20 percent shorter than normal with a corresponding reduction in seed production. This gene resulted from X-radiation (179). Another gene, *bri* (breviramoses), produces branches with short, thick internodes. The stems later become more normal and bear sterile flowers (112, 137). Recessive *inc* changes the inflorescence to branchlets (178).

FASCIATION

In fasciated plants the stem gradually flattens towards the tip, where the flowers are borne in a cluster or umbel instead of being axillary. The condition is a simple recessive (216, 226). The degree of fasciation varies under different environmental conditions. "Mummy peas" are fasciated. The gene is *fa* (341). A second, polymeric, gene *fas* also causes fasciation (132). Plants heterozygous for either gene or both exhibit hybrid vigor.

ROGUES

Certain varieties, such as 'Telegraph,' produce a small proportion of plants resembling a "wild type." The leaflets, stipules and petals are narrow and the leaflets are pointed. These plants are known as rabbit-ear rogues. Normal plants may produce both typical rogues and plants that are intermediate. The first generation between normal and rogue at first appears normal but later develops the rogue characteristics. The rogue type breeds true. Intermediates give different proportions of rogue, intermediate and normal (8, 9). Some intermediates give only rogue plants. The increased proportion of rogues produced with advancing maturity of the plant may be explained by a development of genetic particles, or plasmagenes, in the cytoplasm of the pollen. Entrance of such self-propagating particles into the cytoplasm of the egg would account for the intermediate type of rabbit-eared rogue and the increasing genetic potency of plants to produce rogues (34).

A second type of narrow-leaved rogue appeared in the second generation of a cross between 'Early Giant' and 'Sugar Pea.' The plants have low pollen and seed viability. This condition is due to a single recessive gene *n* (247). This gene is reported as *nr* by Matsuura (224), to avoid confusion with the gene for thick pod wall.

The rogues developing from American varieties of canning peas differ from those described by Bateson and Pellew (8), although their genetic behavior is similar (19). In such varieties the true rogue develops early in the life of the plant, but the intermediates are at first normal (20). The latter give different proportions of rogues in their progeny. These rogues have 10 or more characters modified. These include the stem, leaves, flower envelopes, pods and seeds. The F_1 between rogue and normal is highly variable, especially in early development. Change toward the rogue condition is gradual but always shows up in the pods. The F_1 rogues breed true. Intermediates throw a higher proportion of rogues as the plants become older. The chromosome number is normal (20, 23).

Primary rogues from the 'Gradus' variety result from the mutation of *x* to *X*. *X x* always becomes *X X*. This accounts for the true-breeding behavior of the first generation of the cross between rogue *X* and normal *x*. Mutation also accounts for the increasing proportion of rogues with advancing age of the plants. A third allele, *x'*, found originally in Mummy peas, is relatively stable in the presence of *Yr* (originally *Y*). It gives a length to width ratio of 2 for the stipule, but

mutates to *X* in the presence of *yr*. This produces a ratio of 1.7 (21).

Two additional types somewhat resembling rogue plants in appearance, but genetically distinct, are reported. One, listed as *Pisum aphicoides,* is female sterile and gives normal plants with *P. sativum.* Later generations are normal. The gene is *aph* (243). A small-leaved type has rounded instead of pointed leaflets. Both leaflets and stipules are narrower than normal. It is controlled by a simple recessive gene, *ten.* The character is affected by the environment (125). Lamprecht (137) refers the gene *ang,* greatly reducing leaf-size and causing sterility, to the rabbit-eared rogue described by Bateson and Pellew (8).

Stipules

A reduced form of stipule is characteristic of rogue plants. The behavior of genes *x, x′,* and *Yr* is discussed under rogues. The variety 'Rice's 330,' which does not produce rogues, has a stipule width intermediate between the stipule widths of normal 'Gradus' and its rogue. The length-width ratio of the normal 'Gradus' stipule is 1.69, of its rogue 2.34, and of 'Rice's 330' is 1.99. The ratio of the F_1 between normal 'Gradus' and 'Rice's 330' is 1.82, and of the F_1 between 'Gradus' rogue and 'Rice's 330' is 2.18. F_2 results of the latter cross depend upon the rate of mutation of *x* or *x′* to *X* (22). Another recessive gene, *st,* reduces the size of the stipules (251, 319). It originated in the 'Duke of Albany' variety. Another recessive, *stim,* for stipula imminuata, gives a broader stipule than does *st,* with an irregular margin (195). Several genes, discussed in the paragraph on leaf size, affect the size of both leaves and stipules.

Emergences

A slow-growing type having elliptic first leaves that are a dull green has emergences or protuberances on the stem, which correspond anatomically to leaf tendrils. The plants are highly sterile; 41 plants total only five seeds. The cross first producing this condition gave a 3:1 ratio of normal to emergence plants, but other crosses produced 15 normal to one emergence in the second generation. The two genes responsible are designated em_1 and em_2 (47).

Leaves

A mutation that produces obovate leaflets as well as stipules appeared in the fifth generation of a cross between 'Extra Rapid' and 'Badenia.'

It is governed by a single recessive gene, *obo,* for obovatus (115). Some lines are considerably deficient in the homozygous recessive because of selective fertilization (137). The gene *ten,* discussed under rogues, produces narrower leaflets and stipules than normal (125). Genes increasing length-breadth ratios of leaflets with rounded apex have a similar effect on stipules and sepals. Four independent genes, *fo, fob, fol* (67), and *Fom* (188) are involved. *Fo* has a close linkage with *N,* which affects thickness of the pod wall. Effects are independent of those produced by *ten* (67). Breadth of leaflets, stipules and pods is increased by recessive *lat* (latifolium), which, like *fo,* is linked with *N* (96). The normal length-breadth ratio in 'Withem Wonder' (*Lat*) is 1.5 for leaflets and 1.9 for stipules. Comparable figures for *lat* are 1.2 and 1.6. For all the genes inheritance is additive with incomplete dominance and little interaction among non-allelic genes (211).

The recessive *red,* mentioned in connection with a reduction of size of flower, also reduces the size of the leaflets (100).

Lack of tendrils as observed in the variety 'Acacia' tends to be recessive to their presence (237, 304, 305, 334, 341). A third allele has petiolules of increased length but no tendrils (96). The three alleles are *Tl, tl^w,* and *tl^{pet}.* Both *Tl* and *tl^w* (White's acacia) are completely dominant to *tl^{pet}.*

Leaf margins may have medium or very slight indentation. The former condition, due to *Td,* is dominant to the latter (114, 207, 283, 319). Recessive *un* produces undulating leaflets (173).

Crisp or folded leaves are simple recessive to normal; the gene is *cri* (92). Crinkled leaves are due to *cr,* which mutates rather frequently to *Cr.* For this reason *cr* plants ultimately attain normal leaves (338). Lamprecht (173) notes that the illustrations of crinkled leaves indicate that they are also variegated and for this reason proposes *vac* (variegatocrispus) as a substitute for *cr.*

Td produces the scalaris type with five coarse saw-tooth indentations on each side. The indentation of *Ser* the serratus type is more pointed. *Int* adds to the degree of indentation. The combination *Td Int Ser* is most indented (207).

Unifoliate leaves gave an F_2 ratio of 1167 normal to 382 unifoliate in crosses with normal. The gene is *uni* (99, 139). The number of pairs of leaflets is determined by *Up,* which produces two or three pairs, *up* giving one pair (260).

Laciniated leaflets have a single lateral lobe on each side and a

terminal notch ending in a single tendril. The base of some leaflets is funicular. The condition is ordinarily a simple recessive (*lac*), but the number of recessives is sometimes deficient on this basis. Such plants are sterile (159, 178). Recessive *ins* (insecatus) also produces a notch at the tip of the leaflet (183).

A type of leaf in which the base forms a funnel is illustrated by Delwiche and Reynard (36). It was found in an emerald strain. It is due to a recessive gene *ff* (256). The plants are sterile. Secondary effects of *inc*, changing inflorescence to branchlets, and of *lac*, laciniated leaflets, produce a similar funnel at the base of the leaflets (159, 178).

Small flat air blisters beneath the epidermis cause a gray spotting of the leaves (293) and stipules (336). This condition is a simple dominant. The gene designation is *Fl*. An allele Fl^w causes more intense spotting and Fl^v is intermediate. The series in descending order is Fl^w, Fl^v, *Fl*, *fl* (203).

Number of stomata is controlled by three genes Sa_1, Sa_2, and Sa_3 (289). The triple recessive gives approximately 54 stomata per sq. mm. on the under surface and 160 on the upper surface. Each dominant multiplies these numbers by four and five, respectively.

WAX (BLOOM)

Vilmorin (304) obtained a 9:7 ratio in the second generation of a cross between "glauque" (waxy) and "emeraude." *Bl* is a basic factor for wax. *Bl Bl w w* produce some wax (341). Wellensiek (323) later established a second *W* gene and a three-gene allelic series at the loci of *Wa* and *Wb*. The following results are indicated:

Bl Bl Wa_2 Wa_2 Wb_2 Wb_2—most wax
Bl Bl Wa_2 Wa_2 Wb_1 Wb_1—intermediate wax
Bl Bl Wa_2 Wa_2 *wb wb* —little wax
Bl Bl Wa_1 Wa_1 Wb_2 Wb_2—little wax
Bl Bl wa wa Wb_2 Wb_2—very little wax
bl bl Wa_2 Wa_2 Wb_2 Wb_2—no wax

The recessive *wlo* (wachslos) has no wax on the upper surface of the leaves (113, 150, 238). In contrast to this *wsp* (wax pars superior) causes wax to form only on the upper surface of the leaves (106, 143). A new waxless mutant has appeared in the variety 'Alnarps Stens.' Similar to *wa*, it is designated *was* (similis). It is linked with *N* (96). Two recessive waxless mutants found in the varieties 'Early Badger' and 'Asauji' are associated with short plant and poorly filled pod (76).

SEASON

Flowers of early varieties are produced on lower nodes than flowers of late varieties. Early varieties begin flowering at the fifth to eighth node; late varieties begin at the twelfth to eighteenth node or later (6, 292, 319). It has been calculated that each sterile node accounts for two additional days to time of first bloom (62). Tschermak (297) proposed two factors. *A* was intermediate, and when homozygous, reacted with *Bb* or *BB* to give increasing earliness. Recessive *a* was late. A similar proposal (70) made *A* very late, *a* very early, *B* late, and *b* early. Both schemes are superseded by one devised by Wellensiek (318, 319), who adopts the designation *Lf* of White (341) as *Lf'* primarily responsible for late flowering, but not White's gene *Ef*, modifying *Lf* toward earlier flowering. Wellensiek (318) adds *If'* for intermediate flowering and its recessive allele *if'* for early flowering. *Lf'* functions only in the presence of the homozygous dominant *If'*. The accents for Wellensiek's genes are now dropped. *If Lf* plants are thus late, *If if Lf* intermediate, and *if Lf* and *if lf* early.

Rasmusson (255) confirms the tendency of lateness to be dominant and finds one factor linked to the color gene *A* and the other closely linked to or identical with *le* for internode length. Von Rosen (260) found a factor for early bloom in *P. abyssinicum,* linked with *A* with about 12 percent crossing-over, which he identifies as *xa.* Peas that bloom earliest—at the third node—are recessive for *ib* (inflorescentia basalis). A second gene, *iba,* is responsible for bloom at the fifth or sixth node (161). Irradiation has produced a mutation blooming 10 days earlier than untreated material (42).

In general, crosses between early- and late-flowering varieties are intermediate in flowering in the first generation and give various dihybrid ratios in the second generation (83, 297, 319).

Grafting studies have demonstrated a material in the seedling stage of late varieties that retards the time of first bloom (6, 245). 'Massey,' an intermediate variety, grafted on 'Telephone,' a late variety, blooms later than when on its own roots. 'Telephone' grafted on 'Telephone' blooms a little earlier than when on its own roots, apparently because of an interruption in the translocation of the retarding, or "inhibiting," material 'Telephone' grafted on 'Massey' flowers earlier than on its own roots. A dominant gene, *Sn,* is postulated for the production of the flower-delaying substance (278). Its relation to *Lf* has not been determined.

It should be pointed out that there is a relation between night temperature, length of day and variety in the determination of flowering time (5, 257). Varieties such as "Alderman," "Greenfeast" (*Sn*) and "Telephone" (*Sn*) flower quickest under long days when night temperatures are up to 60° F. while varieties such as "Alaska" (*sn*) and "Massey" (*sn*) are neutral with respect to day-length at 60° but at 50° bloom only during periods of long days. Gibberellic acid delays flowering, especially of varieties carrying *le* (5).

Life Span

Duration of life varies among varieties of each season (early, intermediate, and late). Botanic variety *abyssinicum* has the shortest life span and variety *asiaticum* the longest. According to Lamprecht (118) life span is determined by progenes rather than by genes. The fewer the progenes the shorter is the life span. In contrast, times of flowering and of the first green pod are determined by genes, as discussed in the preceding section.

ANTHOCYANIN PIGMENTS

Flower Color

A basic color gene, *A*, first proposed in 1912 by Tschermak (298), is necessary for color in the flower, in the seed coat and such color as may be in the epidermis. It is the equivalent of Lock's *C* (215, 216), and the *R* of Kajanus and Berg(79). *A* alone gives only faint color (120). A rather large number of genes affecting color in some part of the plant depend upon *A* for their expression. Some of these genes, as proposed, have similar effects and may be identical.

A_1 and A_2 were first proposed by Wellensiek (319) to replace the *A* and *B* factors of Tedin (290) to give a_1 A_2 *B*—white, A_1 a_2 *B*—violet, A_1 A_2 *b*—pink, A_1 a_2 *b*—light purple, and A_1 A_2 *B*—purple. Later de Haan (46) uses A_1 for cryptopurple, a purple bicolor, and A_2 for a purple mosaic, or "purple patch." De Haan considers his A_1 and A_2 to be allelic to *A a*. Lamprecht (170) lists this series in a review of genes for flower color. Another allele A^{ma}, called maculosa, results in splashes of lighter color on the wings (204).

Because a good many of the color genes are complementary, some of the effects ascribed to known genes in earlier work were actually due to factors not yet identified. This was recognized in 1930 by de Haan

(46), who states that *A* produces a light bicolor purple flower and that it has different effects on different botanical varieties. He proposes a second color factor *Am,* which with *A* gives purple flower. The cross *a Am* (white) × *A am* (pinkish white) gave in the second generation 583 purple: 188 pinkish white: 262 white, a 9:3:4 ratio. Wellensiek's *Aw* (330) is similar in effect and both *Aw* and *Am* are linked with *I* within a range of 15 to 48 percent of crossing-over (140). There appear to be two distinctions: *Am* is required for purple axil ring and *Aw* is not; *A am* gives a pinkish white flower while the *A aw* flower is white. The *am am* class is usualy deficient (46).

Ar is a reddening factor with *A* (290, 294, 295) and with *Am* gives a pink or rose flower (39). According to Fedotov (39) *Ar* determines the intensity of various red tints by increasing the acidity of the sap. *Ar* is usually present with *a* in white-flowered commercial varieties (46). *Ar* replaces Tedin's *B* (290).

Tschermak (298) crossed a "*Pisum arvense*" having a rose-colored flower with a white-flowered *P. sativum* and obtained a red-flowered first generation. The second generation segregated 407 red: 104 rose: 155 white. This was regarded as a 9:3:4 ratio. The cross was represented as *A b* × *a B*. Wellensiek (332) later classifies *A cr b* as crimson rose and *A cr B* as crimson, and identifies his *B* with the *B* originally proposed by Tschermak, to which the *C* of Tedin (290) is referred. *B* is generally recognized as a bluing factor and is included as such by White (341) in his list of genes published in 1917.

Another factor, B_1, is required for purple flower (39). Thus flower color with *A* and *Am* is *b* b_1—white, *b* B_1—pink, *B* b_1—bluish rose, and *B* B_1—purple. *B* and B_1 are reported to be linked with 5.4 percent crossing over (39). Lamprecht (120) calls *A*, *Am* and B_1 the three 'Grundgene,' or basic factors. B_1 also contributes to color of the seed coat. Lamprecht (170) recently proposes to substitute *Paf* (particular and fundamentum) for B_1.

Cr crimson was mentioned in connection with the discussion of *B*. In addition to crimson and crimson rose *A Cr B* produce purple and *A Cr b* pink (332). *Cr* has been identified with the *Ap* apple blossom of de Haan, although the two terms do not suggest quite the same color (39, 46, 140, 332).

Ce cerise functions with *A B Ar Aw* and *Cr* (331). When *ce* is recessive the flower color is cerise; when both *cr* and *ce* are recessive the color is described as "light" with clear spots of color on the wings. *Ce*

is linked with *Cr* with about 26.5 percent crossing over. The combination *A Am ar B cr Ce* produces a light mauve flower (170).

Cv acts as an intensifier with *A* (39). It also requires *B* B_1 and *Am*. *Cv* was found in an Afghan pea. *Kp* produces a purple color in the keel (39). It was found in a Transcaucasian weedy *Pisum*, and is incompletely dominant. It requires *A B* B_1 and *Cv*. *Kp* is said to "enhance" flower color.

Two genes affect the color of the standard. The serenum type is lighter than the normal purple for some distance from the edge, due to *sre*. The centrobscurum type is darker than normal in the central portion of the standard. It is also recessive, *ceo* (204).

Blixt (17) in reviewing color mutations of peas lists the combined color effect on the wings of the flower of 6 genes:

A Am Ar B Cr Ce—purpureus, a dull dusky purple (highly variable). Modified in *P. arvense humile* to griseo-purpureus or Argyle purple.
A Am ar B Cr Ce—coeruleoviolaceus, nigrosin violet
A Am Ar b Cr Ce—clariroseus, deep rose pink
A Am ar b Cr Ce—roseialbus, pale rose pink
A Am Ar B cr Ce—fuscopurpureus, Indian lake
A Am Ar B Cr ce—roseus, cerise
A Am Ar B cr ce—palleopurpureus, pale rose purple
A Am ar B cr Ce—malvaceous, light mauve

The cream-colored flower of the Afghan pea is not an anthocyanin color and does not depend upon *A* for expression. It depends upon a single dominant gene, *Cm* (308). Lamprecht (201) considers the yellow-flowered *P. fulvum* Sibth. & Sm. to be *P. arvense* L. oect. *fulvum* Sibth. & Sm. In addition to *Cm* the yellow color requires *Cit* (citron yellow).

Color of Seed Coat

Genes reported as influencing the color or color pattern of the testa are more numerous than genes affecting flower color. Some genes influence both flower and seed color; for example, *A* is basic for color in both corolla and testa (120, 298). *B* and B_1 will be mentioned as required for the expression of other genes affecting seed coat color. *Z* is also necessary for seed coat color (77, 120), although *z* produces a faint or pale brown seed coat. Both *Ar* and B_1, in addition to *A* and *Z*, are considered to be essential for color in the seed coat (120).

Several seed colors are possible with recessive *a*. In review Lamprecht (180) lists the combined effect of *a I* and *O*:

a I O—pale ochraceous buff, testa colorless
a I o —same
a i O—irisgreen, testa "Eisgrun"
a i o —cream, testa colorless

These seed colors are modified by a gene pair *Gla gla* (glaucescens) as follows:

a I O Gla—pale greenish ochraceous buff
a I O gla —pale ochraceous buff
a i O Gla—irisgreen, testa "Eisgrun"
a i O gla —greenish blue

Recessive *gla* thus changes the "Eisgrun" testa to colorless.

The testa may have any of several self colors. Recessive *och* produces an ocher yellow (181), *H* an orange or orange-brown (298), *J* a dark brown (298), and *sal* (salmoneus) a pinkish salmon (197). *Oh* was proposed as a dilution factor, which changes red to reddish brown (77, 78, 79, 294). It was later found that the color may vary from clear brown to gray-green (319). Fedotov (39) refers gray-green to dominant *Oh* and reddish-brown to recessive *oh*. Lamprecht (120) assigns brownish-red (mineral red) to *A Ar B oh* and brown-rose (ocher red) to *A Ar b oh*. Ruby seed coat *Ru* is expressed only in immature seed (37). It is masked in mature seed by *A Oh*.

Deep purple, caused by *U* (341), is sometimes referred to as black (39), violet black (120), and violet (318). There are two alleles, *Ust*, causing violet striping and *u*, which is neither violet self nor striped (134). *Ust* was earlier reported as *Ast* (102). V_1, found in a pea from the Urals (39), also produces a deep purple testa, but the color is less intense than that resulting from *U*. V_1 requires B_1 for its expression (120).

Pattern of Seed Coat

There are two independent speckling genes, *F* and *Fs* (39, 109, 298). They require *A Am Ar B* B_1 *Z* for complete expression (39, 120, 140, 319, 346). The pattern varies somewhat and is referred to as speckling (298), spotting (341, 346), stippling (321), dotting (120), and streaking (39). *Fs* has two alleles, Fs_{ex}, which has larger dots, and *fs*, which has no dots (110, 120).

Under some environmental and genetic conditions the purple color of the dots diffuses partially or completely throughout the seed coat. The character is highly variable and is called obscurantum. The work of early investigators is discussed by Wellensiek (319), by von Rosen (260) and by Lamprecht (155). The latter (176) has recently obtained evidence that, subject to environmental and genetic background effects, the condition is dependent upon recessive *obs.* The character is said to be unsatisfactory for most genetic studies.

Dominant *Ca* (caneo) requires *A z mp cal* to produce drab-gray (172). It does not color the entire testa. It is in linkage group III (189). Dominant *Cal* inhibits the action of *Ca.*

A marbled or mottled seed coat, due to *M,* also called maple, has long been studied (7, 216, 298). It is a pattern gene and the color depends upon the presence of color genes. For example, *M Oh* is rusty-red while *M oh* is a red-brown, both marbled (39). *M* is dependent upon both *A* and *Z* for full expression. *M a Z* produce a faint pattern referred to as ghost marbling (215) and *M A z* give a very faint marbling (79).

Black hilum is due to dominant *Pl* with either *A* or *a* (320, 322). Brown hilum is *A pl* and colorless hilum *a pl* (227, 341).

Several genes give a bilaterally symmetrical pattern that is oriented with respect to the hilum and the funiculum, which is a triangular spot of medium size near to and directly in line with the hilum. The corona immediately surrounds the hilum and extends to the apex of the radicula. Both intensity of color and area covered vary widely. Because of their complexity these patterns are difficult to describe briefly. The interested reader is referred to Lamprecht's illustrations (120, 141, 142, 162, 164, 190) and those of Blixt (17).

The small white area between hilum and radicula in *A z Mp Mp* plants becomes a white corona with *Mp mp* and this is increased further in size in the double recessive (120). The deminutio design is *A z mp dem Cal.* Calvitium is *A z mp Dem cal,* and triangulatum is *A z mp dem cal.* Each design has progressively less pigment (120). Lobata *A z mp Dem Cal lob* is pigmented except for an inverted V pattern surrounding the hilum and a portion of the radicula. Adversus, *A z mp Dem cal lob,* and intermissa, *A z mp dem Cal lob,* are distinctive designs with less pigment. Heterozygous *Cal* is distinct from either homozygous type (120, 142, 162). *Ve ve* affect the size and number of shields around the hilum (142).

A yellow-orange radicula results from *A Z gl* (103, 294). Recessive *cor* adds a yellow-orange shield around the hilum. The two genes are not allelic (141). Brown radicula results from the presence of *A Rf z*. The color varies widely from pale to distinct brown even in seeds from the same plant (136). *A Rt z mp* produce a rusty color over the radicula (294), and *rag* a gray shield (196).

Recessive *pal* bleaches colors of the seed, especially with *A z*. It eliminates all color in the triangulatum combination (208). The gene *str* produces a caruncula stripe (190), and *gri* a clear green stripe near the hilum (113, 120, 166).

Plant Color

Green pod × green pod may give purple pod (303), and purple versus green pod may segregate either in a 3:1 or a 9:7 ratio. The genes have been designated P_1 and P_2 (341, 346). Lamprecht (104, 116) distinguishes three degrees of pod color: *Pur*—full anthocyanin, pur_a and pur_b—progressively less color, and *pur*—without color. Further, *Pur Gp Oh* give violet and *Pur Gp oh* red-lilac. Lamprecht (135) still later identifies his *Pur* with White's P_1 and Winge's P_2, and *Pu*, a second gene for purple pod, with White's P_2 and Winge's P_1. *Pur* and *Pu* are regarded by Lamprecht as polymeric. Purple pod may mutate to green by as much as 40 percent (135).

Purple splashing of the pod in *P. arvense* L. oect. *fulvum* Sibth. is due to the dominant *Astr*, astriatus (199).

Purple color in the axil may take the form of a fleck (spot), a double or a single ring, or be absent. There are four alleles: *Dw*—double ring, *Dco*—single ring, *Dma*—fleck, and *d*—colorless (81, 111, 293, 330). Dominance is from double ring to ringless. The *co* refers to corona and the *ma* to maculatum.

CHLOROPHYLL DEFICIENCIES

Cotyledons

The combined F_2 data of all workers to 1925 totaled 42,117 yellow cotyledons to 13,948 green (319). The shade of yellow varies rather widely and may be darker in the F_1 (73), or it may be greenish yellow (229). The dominant *G* (green) is epistatic to *Y* (yellow) (340). There is also a recessive yellow (235, 340). When the inhibiting gene *I* suppresses *G*, *Y* functions as a dominant. *Y g i* is Goldkönig yellow, recessive to *Y G i* green, while *Y G I* is dominant yellow because green

is inhibited by *I* (340). Nilsson (235) considers *G* to be identical with *O*, a gene for green foliage discussed later. He supposes that an allele, *or*, gives pale green. According to Nilsson's scheme *I O* is dominant yellow, while *i O* is green and *i or* light green.

Blaringhem (10, 11) reports what appears to be a variegation of green and yellow, although it was not interpreted this way. He considers the variety "Pariser Gold" to have an unstable gene. Yellow is constant but the mixed or variegated and the green seeds from different parts of the plant give different proportions of mixed, yellow and green cotyledon. More green seeds are obtained from the base and the top of the plant than from other parts.

PLANT

Several types of chlorophyll deficiencies have been observed. Classification is based on color, stage of development of the plant at which the deficiency is first apparent, the part or parts affected, and what might be termed pattern, where only certain areas are deficient. Lamprecht (130) proposes names from the literature for several types: Chlorina is a greenish yellow that may become increasingly yellow as plants approach maturity. Chlorescens is green in the seedling stage but later becomes greenish-yellow. Virescent plants reverse this process. Xanthina is a straw yellow in contrast to aurea, which is a golden yellow. Lutescens is at first green and later yellow. Chlorina-terminalis is green except for a greenish-yellow growing point. Albino is white. Variegated may be spotted or striped, green and yellow or green and white. Except for albino, which is always lethal, the degree of handicap resulting from the deficiency varies with the causal gene. Many chlorophyll-deficient plants die before blooming. Non-genic factors that may play a role in variegated deficiences are the maternal cytoplasm and the environment. Fewer than expected numbers are common for the recessive class, especially where the entire plant is affected (130).

Yellow pod was first reported by Mendel (226) to be a simple recessive. The gene was later designated (340) *Gp gp* (green pod). A chlorina type was reported (341) as due to a single gene *O o*. This proved to have two additional alleles to function with *Gp* (233, 345) as follows:

O Gp—green foliage and immature pods
O gp—green and canary yellow
or Gp—lemon yellow

or gp—lemon canary yellow
oy Gp—golden yellow
oy gp—golden canary yellow.

Usually fewer *gp gp* plants are obtained than expected (121). The pod color factor, *pa,* produces pale pod (346) with dark green leaves in contrast to the clear green with *Pa* (131), and dark seed (242). Another recessive, *Vim* (viridis medium), results in a somewhat darker green pod than does *pa* (152).

Rasmusson (256) reports ten chlorophyll deficiencies affecting the plant, each inherited as a simple recessive. Three are of the chlorina type. Recessive *cha* plants die after 4–6 weeks. The other two genes are designated chc_1 and chc_2. Lamprecht (130) regards these three genes as polymeric, and in the interest of uniformity redesignates them ch_1, ch_2, and ch_3, respectively. Four more deficiencies are of the xanthina type. Recessive *chd* has yellow leaves with an orange tint. The leaves of *che* are lemon yellow. Both *chd* and the third gene, *chh,* are inviable. Lamprecht proposes to substitute for these genes xa_1, xa_2, and xa_3 respectively. The fourth xanthina reported by Rassmusson is *chj.* It is also inviable. Rasmusson's *chg* and *chr* are at first green but turn to yellow after one or two weeks (256). As this places them in the lutescens type Lamprecht (130) proposes to substitute lu_1 and lu_2, respectively. Rasmusson's tenth chlorophyll deficient *chl* is a chlorina-terminalis type (256); for this reason it is redesignated *cht* by Lamprecht (130). Lamprecht's *au* is a golden yellow, an aurea type (130). Apparently there has been no opportunity for a study of a possible relationship between *au* and *oy,* and xa_2 (*che*) and *or.* The upper internodes of alba-terminalis *alt* are white. The plants die before blooming (148, 182).

Various other cases of chlorophyll deficiency have been reported. Recessive cl_2 has light green leaves and pods. In contrast cl_3 plants have light green growing points only (337). This second chlorina-terminalis type has been redesignated cht_2 (163). Both of these were found in the Alaska variety. The cl_4 designation refers to a phenotype of the xanthina-terminalis classification. It is not simply inherited (230). Radiation treatment has produced a series of chlorophyll-deficiencies. X-28 is an ivory lethal, and X-33 is a yellowish-green lethal (230). Yellow-green *yg* seedlings later become green (84). This is renamed virescent, vi_1, by Lamprecht (135). Plants homozygous for yg_2 are green the first week, then become "almost pure yellow," only

to return to a normal green later (84). Another chlorophyll-deficient type has narrow green and yellow stripes with yellow veins. The leaves at the growing point may be almost completely yellow. The plant becomes a nearly normal green at maturity. Direct and reciprocal crosses with green gave in the first generation 38 normal and 35 yellow and green. The green bred true, while the chlorophyll-deficient plants produced 228 normal, 314 green and yellow, and 21 albino (84). As with many other plants variegation appears to be primarily cytoplasmic. The chlorophyll-deficient areas may be yellowish or white (130). Recessive genes have been mentioned in connection with studies of variegation—w_2 (308), *wb* (319), and *wv* (224).

Combinations of different chlorophyll-deficient types are possible. There is a chlorina-virescens, due to *chves* that is at first chlorotic and later becomes a virescent green (193). Another recessive gene, *cvit* produces chlorina-virescens-chlorotica-terminalis (193). This is a chlorina-virescens that has a pale green tip.

Von Rosen (259) obtained a series of chlorophyll mutations from X-irradiation: *chr-w*—albo-viridis chimaera, semi-lethal, plants small; *chr-y*—a lutescens type; *chr-d*—a xanthina type; *chr-a*—lutescens; *chr-l*—described as like Rasmusson's *chl,* which would indicate a chlorina-terminalis type; *chr-o*—listed as chlorina type; *chr-g*—leaves at first green, later becoming a watery gray-green with an increasing tendency to roll. All mutations are regarded as simple recessive, but usually deficient in the number of homozygous recessive.

An X-ray mutant, *auv* (aureovirescens), in Lamprecht's interchange Line 680 is at first normal green, then produces golden yellow leaves and later returns to normal green in the upper portion of the plant (169, 171).

The irradiation of Lamprecht's interchange Line 21 produced a dark bluish gray-green mutant, due to recessive *cov* (coeruleovirens). Blue-green plants are shorter than normal (169). Two radiation-induced mutants are reported by Wellensiek (333, 334).

Blixt (16) reviews in detail both the chlorophyll-deficient and the anthocyanin color types of peas, based largely on Lamprecht's (192) comprehensive system of classification of these types alone and in combination.

RESISTANCE TO DISEASE

APHANOMYCES

Resistance is reported to a root rot caused by *Aphanomyces euteiches* Drechs. There appear to be two races of the organism. Two Plant Introduction numbers 166159 and 167250 are most resistant. Five other PI numbers also exhibit resistance (217).

ASCOCHYTA

Resistance to leaf and pod spot caused by *Ascochyta pisi* Lib. has been observed in a few varieties. It is suggested that there probably are several races of the causal organism (40, 72). 'Austrian Winter' is most resistant (316). Resistance is due to three dominant genes, and modifiers are possible (316). In crosses betwen 'Austrian Winter' and susceptible varieties the first generation is usually as resistant as the resistant parent. Resistant segregates have small pods and dark seed coat. Most of them are also late.

Plants from colored seed of the field pea did not become infected by a spore suspension of *Ascochyta pinodella* Jones, the cause of foot rot, while seedlings of the garden pea did become infected (279). The results suggest that a plasmatically conditioned resistance to the foot rot stage of the disease probably does not exist. 'Austrian Winter' is most resistant (317).

FUSARIUM

Resistance to *Fusarium* root rot (*Fusarium martii* Appel & Wr. f. *pisi* Jones) is being developed through field selection of plants growing in infested soil. Crosses between selected lines, which are further selected for several generations, have greater resistance than either selected parent (86, 314).

A good many varieties of peas carry resistance to wilt caused by *Fusarium oxysporum* Schlecht. f. *pisi* (Linford) Snyder & Hansen race 1 (24, 32, 213, 313). Varieties originating in Ethiopia (311), India and Turkey (87) are resistant. Resistance is due to a single dominant gene, *Fw* (307). It is believed that resistance is largely confined to the root system (214).

Commercial varieties resistant to wilt were found to be susceptible to near-wilt, caused by race 2 of *F. oxysporum* f. *pisi* (315). Resistance to near-wilt behaves as a simple dominant (63). The genes for re-

sistance to wilt, *Fw,* and near-wilt, *Fnw,* are linked with about 40 percent crossing-over (339).

MARSH SPOT

A lack of manganese contributes to marsh spot. Some varieties are immune to the disease; others may have up to half of the plants affected. Resistant or immune varieties include 'Union Jack,' 'Earliest of All,' 'Early White Seedling,' 'First and Best,' and 'William the Conqueror.' Varieties with less than 10 percent marsh spot include 'American Wonder' and 'Laxton's Superb.' Early varieties are less affected than late ones (41).

MILDEW

Certain varieties developed from peas introduced into Peru by the early Spaniards are immune to powdery mildrew resulting from infection by *Erysiphe polygoni* DC. Immunity is due to a single recessive gene, *er,* which has a 35-percent linkage with *A,* responsible for purple flower (64). 'Stratagem' has been found to be highly resistant. Resistance also behaves as a simple recessive (252). Other material appears to have up to three additional dominant genes for susceptibility (58).

PYTHIUM

Resistance to pre-emergence damping-off, caused by *Pythium ultimum* Trow., is influenced by several known genes. Plants carrying the basic color factor *A* are more resistant than those having *a.* Among *a* plants those with *R,* responsible for round seed, are more resistant than plants with wrinkled seed. Plants having both *a* and *r,* but carrying *I,* producing yellow cotyledon, are more resistant than *a r i* plants. *B* and *Mp* may also be involved. The presence of tannin-like, phenolic compounds in the seed coat is found to confer resistance to Pythium (38).

SEPTORIA

In a test of the resistance of 134 varieties and strains of peas to *Septoria pisi* West. only a single strain of 'Perfection' and a line from Puerto Rico exhibited a high degree of resistance. In general, canning varieties of the 'Perfection' type were most resistant (351).

VIRUSES

Varieties reported to be immune to pea "mosaic" include 'Little Marvel,' 'Hundredfold,' 'William Massey,' 'Autocrat,' 'English Won-

der' (29), and 'Canner's Perfection' (312). Immunity results from the presence of recessive *mo* (349).

Symptoms of the Alsike clover virus 1 are similar to those of common pea virus and some varieties are resistant to both viruses, but others, such as 'Blue Bantam' and 'Surprise,' are resistant to the Alsike clover virus but susceptible to common mosaic (310). Two strains of Alsike clover virus have since been identified. 'Little Marvel,' 'Perfection,' 'Surprise,' and 'Wisconsin Early Sweet' are resistant to both Alsike clover viruses 1 and 2 (350).

Most varieties are susceptible to pea virus 1 (pea enation virus), although several varieties, including 'Alderman,' 'Creole,' 'First and Best,' 'Improved Gradus,' 'Laxton's Progress,' and 'Little Marvel,' have some tolerance (276). Resistance, or tolerance, is caused by a single dominant gene (270).

'Perfection,' 'Hundredfold,' 'Nott's Excelsior,' 'Giant Wonder,' and 'Abundance' are resistant to the 3 strains of pea virus 2 (282). Twenty-one of 44 varieties of peas were found to be resistant to pea virus 3. These include 'Perfection,' 'Hundredfold' and 'Nott's Excelsior' (232). 'Little Marvel,' 'Perfection,' 'Surprise,' and 'Wisconsin Early Sweet' are resistant to pea virus 4 and to pea virus 5 (350). A good deal of resistance to pea streak virus 1 is shown by 'Little Marvel' and 'Nott's Excelsior' (352).

Considerable resistance is found among 'Perfection'-type peas to bean virus 2 (225). Some 'Perfection'-type varieties are susceptible and there are differences in the reaction of such varieties to independent isolates of bean virus 2 (49). Resistance behaves as a simple recessive (75). The heterozygote has some delayed symptom expression, and is affected by temperature. At 80° F the gene for resistance is recessive, but is dominant at 65° (271).

Top yellows, formerly referred to as foot rot, and thought to be caused by a *Fusarium,* is a virus disease transmitted by aphids. Resistance is due to one or a few dominant genes. Many varieties exhibit some resistance; some show only weak symptoms. Certain varieties are resistant to both top yellows and *Fusarium* wilt: 'Alderman,' 'Morse's Market,' 'Perfectah,' 'Perfection,' 'Pride' ('Wisconsin'), 'Stratagem,' 'Giant-Stride' and several European varieties (71).

RESISTANCE TO INSECTS

APHID

Significant differences among varieties in resistance to the pea aphid, *Macrosiphum pisi* Harr. (*Illinoia pisi* Kalt.), have been found (66, 220), but no variety is highly resistant. The more resistant varieties have lighter green foliage than do the susceptible varieties (2, 31, 272). Height of plant is not a factor in resistance. A test of third-generation families from a cross between varieties having light-green and dark-green foliage showed that selections with light-green foliage were more resistant than those with dark-green leaves (272). Both the dwarf 'Onward' variety and the tall 'Admiral' are resistant (273).

It is possible that the susceptible varieties, which have higher proportions of nitrogenous materials (amino acids except proline) in the sap, are those with dark-green foliage (2, 221). Resistant varieties have a definite unfavorable effect upon the aphids feeding on them. Aphids on the resistant variety 'Pride' were reduced in development by 3.1 percent, in reproduction by 12.5 percent, and in longevity by 20 percent as compared with aphids on the susceptible variety 'Perfection' (65).

The 13-year average number of aphids per tip: 'Perfection' 39.6, 'Daisy' 32.6, 'Lincoln' 35.0, 'Laurier' 9.8, 'Champion of England' 11.8, and 'Melting Sugar' 16.8 (3). The susceptible varieties again have more nitrogenous material and less sugar (222).

MOTH

Apparently "resistance" to the pea moth, *Laspeyresia nigricana* Steph., is a secondary effect of differences in earliness and size of vine. The shorter, earlier varieties are less affected by this insect. Later, tall varieties with a heavy vine provide shelter for the adults, which results in more egg-laying. While the differences are genetic, the effect is indirect (277, 348).

WEEVIL

Resistance to the pea weevil, *Bruchus pisorum* L., does not yet seem to be well established. As early as 1880 the 'Prussian Blue' pea was reported to be immune from the weevil, although doubt was expressed as to the accuracy of this statement (28). Late varieties have been observed to escape attack (262). The possibility of breeding for resistance has been considered favorably by Tschermak-Seysenegg (300) and

apparent differences among selections within a single variety found (301).

RESISTANCE TO COLD

The garden pea is a cool-weather crop. To secure the advantage of a cool growing season, especially in southern areas of the northern hemisphere, early planting is desirable. Hardiness in the seedling stage is especially important for this reason. For practical considerations two things are important: (a) amount of damage and (b) rapidity of recovery. The 'Progress' variety is highly tolerant to field temperatures as low as 19° F. and recovers rapidly. 'World Record' is very susceptible to low temperature and does not recover from cold damage. Selections in the fifth to eighth generations of crosses between tolerant and susceptible varieties are more tolerant to cold than 'Progress,' the tolerant parent (309). It was noted that 30-degree frost during the blooming period was more damaging to lines with white flowers than to those having colored flowers.

POLYMERIC GENES

Several cases of duplicate genes in peas are listed by Lamprecht (132, 135). The following characters are dependent upon the action of two independent genes: bracteoles—*Br* and *Bra,* wax bloom on plant—*wa* and *wb* (distinction difficult), slender plant with long internodes—*cry* and *la* (distinction difficult), fasciation—*fa* and *fas,* number of flowers per peduncle—*fn* and *fna,* ramification of the stem —*fr* and *fra,* convex pods—*co* and *con,* pod membrane—*P* and *V* (distinction rather easy), purple pod—*Pu* and *Pur,* violet speckling of seed coat—*F* and *Fs* (with *A*).

Except for the three cases noted, a distinction between the phenotypic effects of the polymeric genes can not be made with certainty. Lamprecht offers two explanations for the occurrence of polymeric genes: They may be due either to crossing between non-homologous chromosomes (133, 135) or to polyploidy (119). Both involve crossing with selection during an extended period and result in stable diploid lines. Such lines contain two essentially homologous genomes with small portions of non-homologous chromosomes. Because of the several known structural types, evidence seems to be better for the first explanation than for the second.

GENES LISTED ALPHABETICALLY

A—Basic for anthocyanin color in plant, flower and seed (298). Alone *A* produces only a faint color (120). Required also for dimpled seed (48, 298, 332). Confers resistance to *Pythium* (38).

A^{ms}—Gives splashes of lighter color on the wings (204).

a—White flower.

A_1 and A_2—Basic color genes proposed by Wellensiek (319).

A_1—Cryptopurple flower color (46).

A_2—Purple patch flower color (46). *A*, A_1 and A_2 for flower color, and *a* are alleles.

alt—Alba-terminalis chlorophyll deficiency; upper internodes white (148).

Am—Basic complementary color factor; required with *A* and *B* for purple flower and for axil ring (46).

am—Pinkish-white flowers with *A*.

ang—Leaves very small; flowers sterile, a rogue type (8, 107).

ap—Apple blossom flower color (39, 46), synonym of *cr*.

aph—Sepals and petals narrow and pointed; female-sterile (243).

Ar—A reddening factor with *A* and *Am* (39, 294).

ar—Light mauve flower color with *A Am B cr Ce* (170).

Asc—Semi-prostrate growth (128).

Ast—See *Ust*.

Astr—Purple splashing of pod (199).

au—Golden-yellow chlorophyll deficiency (130).

auv—Golden-yellow chlorophyll deficiency of lower leaves (169).

Aw—Similar in effect to *Am*, it has a similar position in linkage group I. Not required for axil ring (330).

aw—Flower white with *A*.

B—A bluing factor with *A* and *Am* or *Aw* (298, 332).

B_1—Also needed for purple flower (39). Certain genes affecting pigmentation of the seed coat are dependent upon B_1 (120). Not allelic to *B* (170).

Bl—Basic gene for wax bloom of foliage (323, 341).

bl—Waxless (emerald).

Br—With *Bra*, a nearly dominant gene producing bracteoles (209).

Bra—Polymeric with *Br* (135).

brev—Shortens length of filament, which hinders self-pollination; reduces internode length (100).

bri—Causes plants to branch and induces male-sterility (112, 137).

Bt—Blunt apex of pod (234, 341).

Bta and *Btb*—Two genes for blunt apex have been reported (253).

bt—Pointed apex of pod (234).

Ca—Drab gray seed coat pattern with *A Am Ar b M z mp cal* (172, 189).

cal—Seed-coat pattern gene with *A z mp*; reduces area of color on side opposite to hilum (120, 208).

ce—Cerise flower color with *A Am Ar B Cr* (331).

ceo—Increases depth of color in central part of standard (204).

ch_1, ch_2, ch_3—Redesignation of *cha*, *chcl* (*chal*), and *chc_2* (*cha_2*) (130, 256). Chlorina type of chlorophyll deficiency in which greenish-yellow seedlings become increasingly yellow with advancing maturity.

cht—Chlorina-terminalis chlorophyll deficiency in which only the growing point is greenish-yellow; a redesignation of *chl* (130, 256).

cht_2—Redesignation of *cl_3* (163, 193).

chves—Chlorina-virescens type of chlorophyll defect (193).

Cit—With *Cm* produces yellow flowers (201).

cl_2—Light green leaves and pods (337).

cl_3—Light green growing points only (337).

Cm—Cream-colored flower of the Afghan pea; does not depend upon *A* (308).

co—Convex pod; a polymer of *con* (135).

coe—Internodes 20 to 30 mm. long (206).

com—Like *brev,* reduces the length of the filament and so reduces self-pollination. Also produces compact branches in the leaf axils (100).

com—Sides of seeds considerably flattened (185).

con—Convex pod. Balances the effect of *n* for concave pod to produce a straight pod (both *n con* and *N Con*). *N con* is convex and *n Con* is concave (101).

cor—With *A Z gl* produces a yellow-orange shield around the hilum (120, 141).

cot—Internodes 33 to 64 mm. long (206).

cov—Deep bluish gray-green plant that is shorter than normal (169).

cp—Curved pod; a redesignation of White's *ss* (320, 344).

cpa—With *cp* curved pod (156).

cr—Crinkled leaves; mutates frequently to *Cr* (338). Lacks priority. (See *vac.*)

cr—With basic color factors, crimson or "fusco-purple" flower; *b cr* crimson rose (332). Appears to be the equivalent of de Haan's *ap* (39).

cri—Folded or crisp leaves (92).

cry—With *la le* dwarf (202, 253).

cry cry^{c} (*cry*$_1$, *cry*$_2$)—Rasmusson's dwarfing genes (253); double recessive is "crypto-dwarf" (89, 206).

cry cry^{s}—Slender (89, 206).

Cry$_2$^{dw}—Dominant dwarf (261). Should be *Cry*^{dw}.

Cry$_2$^{lw}—Low dwarf (261). Should be *Cry*^{lw}.

Cry$_2$^{na}—Nana (261). Should be *Cry*^{na}.

cvit—Chlorina-virescens-chlorotic-terminalis type of plant (193).

cy$_1$—The equivalent of *la* (89).

cy$_2$—The equivalent of *lb* (89).

Cv—Flower color intensifier, requiring *A Am B B*$_1$ (39).

d—Green leaf axils (293, 298, 330, 341).

Dco—With *A Am* gives a single anthocyanin ring on the leaf axil (293).

Dma—Colored spot at axil (111).

Dw—Double ring on leaf axils (293). These four genes are alleles; decreasing dominance: *Dw, Dco, Dma, d* (111).

dem—Affects pattern of the seed coat by reducing the colored area on the side opposite to the hilum (120).

di—Dimpled seed, hypostatic to *A* (76, 328).

Dt—Flower-distance gene (124).

em$_1$, *em*$_2$—The double recessive causes emergences on the stem (47).

Ep$_1$, *Ep'*$_1$—Factors for thickness of the seed coat. Listed by Matsuura (224) and Wade (308).

er—Resistance to mildew (64).

F—With basic color factors, purple spotting of the seed coat (298, 341).

fa, fas—Either recessive gives fasciated stem with terminal inflorescence; polymeric (132, 216, 341).

fe—Split pods; female-sterile (288).

ff—Funicular leaf base; viable but sterile (256).

Fl—Gray spotting on leaves (293), stipules (336).

Fl^{v}—Intermediate gray spotting of the leaves (203).

Fl^{w}—Intense gray spotting of the leaves (203).

Fn—One flower per peduncle (341).

Fna—With *fn* produces two flowers per peduncle, as do *Fn* and *fna* (119).

fn, fna—Together give three flowers per peduncle (119).

Fnw—Resistance to near-wilt (63, 339).

fo—Reduces width of sepals, stipules, and leaflets (67).

fob—Effect similar to but not so pronounced as with *fo* (67).

fol—Effect similar to that of *fob* (67). These three genes are not alleles. Each has some effect when heterozygous.

fom—Effect similar to that of *fob* (188).

fov—Radicula deeply sunken (184).

Fr, Fru—Together produce 1–4 branches (126). They are independent in inheritance.

fr, fru—Together produce 5–10 branches. Either recessive alone increases branching somewhat.

Fs—With basic color factors, purple spotting of the seed coat (39, 298, 346).

Fs_{ex}—Larger or very dark spots (110).

fs—Testa not spotted (110); a 3-gene allelic series.

Fw—Resistance to *Fusarium* wilt (307).

G—Green cotyledon, epistatic to *Y* for yellow cotyledon (340). *G* is suppressed by *I* permitting *Y* to function. Considered by Nilsson (235) to be identical with *O*.

g—Yellow cotyledon (234).

gl—Ochre-yellow or yellow-orange radicula (103, 294).

gla—Greenish blue testa (180).

Gp—Green pod (226, 340).

gp—Canary-yellow pod.

gri—Clear-green stripe near the hilum (113, 120, 166).

H—With basic color factors gives orange seed coat (298).

I—Inhibits action of *G*, giving dominant yellow cotyledon (340).

ib—Causes plants to bloom at the third node (161).

iba—Responsible for bloom at the fifth or sixth node (161).

If, if—With *Lf* determine time of flowering. If *Lf* late; *If if Lf* intermediate; *if Lf* and *if lf* early (318).

inc—Modifies inflorescence into branchlets; causes base of leaves to funnel (178).

ins—Produces insecatus notch in apex of leaflet (183).

Int—Increases degree of leaf indentation (207).

J—With basic color factors gives dark chocolate-brown seed coat (298).

k—Keeled wings (251).

Kp—Colored keel (with basic factors); may also intensify color of corolla; incompletely dominant (39).

L—With *A* or *R* gives dimpled seed (48, 298, 332). Dimpled seed may be *A l R, a L R* or *A L R.*

la, lb—de Haan's genes for slender type of growth (45, 46). Both recessives are required; considered to be the equivalent of cy_1 and cy_2 (89).

lac—Abnormal leaflets and sepals; reduces pollen fertility (159).

Laf—Broad pod (145).

lat—Increases width of leaflets, stipules, and pods (96).

Le—Long internodes. The *Le* genes find expression in conjunction with series of *T* genes (83, 253, 343).

Le_1—Very long internodes (343).

le—Short internodes with a zigzag stem (253).

Lf—Causes *lf* to flower later (318, 341).

lf—Early flowering.

lm—Microdwarf; functions in conjunction with *le, la lb* (cy_1 cy_2) (212, 256).

Lo, Lo_1, Lo_2, Lo_3—Genes for seed length listed by Matsuura (224) and Wade (308).

lob—Inverted-V pattern around hilum (120).

lt—Increases breadth of pod (167).

lu_1, lu_2—Lutescens type of seedlings (130); proposed to supersede *chg* and *chr* (256).

M—Marbling pattern of the seed coat (39, 216, 298).

ma—Increases seed size in a variable amount (169).

mie—Gives 10 to 16 internodes (206).

min—Reduces plant height (169).

miv—Close spacing of seed in pod; simulates effect of *s* for adherence (131).

mo—Confers immunity from mosaic (349).

Mp—Narrow white hilum band; not fully dominant (120, 294).

mp—Broad white hilum band.

N—Thin pod wall (298, 318).

n—Thick pod wall; pod smaller than with *N* (104). Favors concave pod; *n con* produce a straight pod.

nap—Broad petals with a broad thick keel at upper end (137).

nr—Narrow-leaved rogue (224, 247); originally *n*.

O—With *gp*, green foliage and canary-yellow pod (233, 235, 341).

obo—Obovate leaflets and stipules; sterile flowers (115).

obs—A color distribution gene causing the dark purple of speckled seeds to spread out over the testa; subject to environmental and residual genetic effects (155, 176).

och—Ocher yellow seed coat (181).

Oh—Dilution factor converting *A B Z* red seed coat to a reddish brown (79, 294, 319).

ob—Changes *A b Z* brown seed coat to gray-green (39). With *A B Z Ar* gives purple or pink flowers and red seeds (120, 294).

or—With *gp*, lemon canary-yellow pod (233).

oy—With *Gp*, gold pod; with *gp*, gold canary-yellow pod (223). *O*, *or* and *oy* form an allelic series.

P—Thin parchmented membrane in pod wall (236, 325, 341).

p—No pod membrane with *v*.

P_1, P_2—Identical with *Pur* and *Pu*; both genes are required for purple pod (341, 346).

pa—Pale green pod, dark green leaves and seed (131, 242, 346).

Paf—The equivalent of B_1 (170).

pal—Bleaches seed-coat colors, especially with *A* and *z* (208).

pe—Causes a variable petaloidy (237); has priority.

pe—Pearl pod (346); should be redesignated.

Pl—Dark to black hilum with either *A* or *a* (320, 322, 341).

pl—Brown hilum with *A* and colorless with *a* (227, 341).

pla—Sides of seeds somewhat flattened (185).

Pr, *Pre*—Affect length of the peduncle and distance between flowers (124).

Pt—Accelerates pollen tube growth (319).

Pu, *Pur*—Polymeric genes giving purple pod (104, 109, 116, 135). (See P_1 and P_2.)

pur_a—Gives color to larger portion of the pod (135).

pur_b—Produces less color on pod or may limit color to the funiculus (135).

pur—No anthocyanin on pod.

Q—Aborted seeds (335).

qua—With *pla* seeds cubical (185).

R—Round seed (216, 226, 341); with *a l*, smooth seed; with *A* or *L* dimpled seed (322).

r—Wrinkled seed.

rag—With *A z mp* produces a gray shield over the radicula (196).

re—Reduced size of flower; sterile (237).

red—Leaflets and flowers reduced in size; sterile; originally *re* (100, 107, 346).

Rf—Radicula pale to distinct brown, with *A z Mp* or *mp* (136).

Ro—Seeds flatten in the pod; not well established (185, 328).

Rt—Rusty color over radicula, with *A z mp* (294).

Ru—Ruby color of immature seed; masked by gray of mature seed (37).

s—Seeds adhere in pod; called chenille (341).

S_1, S_2, S_3 S_4—Factors for size of seed; originally Sg_1, Sg_2, Sg_3, and Sg_4 (298, 318).

Sa_1, Sa_2, Sa_3—Cumulative genes for high number of stomata (289).

sal—Pinkish cinnamon seed coat (197).

sb—Screwball, a form of dwarf plant (84). (See *sp*).

Ser—Gives serratus type of leaf indentation (207).

siv—Causes early flowers to lack a standard; accompanied by sterility (169).

Sn—Produces substance that delays flowering (278).

Sn_1—Intermediate number of nodes (292, 319).

sn_1—Low node number.

Sn_2—Increases node number over that of Sn_1 (292).

sp—Half dwarf; proposed to replace *sb* by renaming the character semi-pumilio (84, 135, 158).

sre—Dilutes color around edge of standard (204).

st—Reduces size of stipules (251, 319).

sti—Produces a pair of small leaves on peduncle; two small white leaflets in the flower; no petals or sepals; female-sterile (137).

stim—Gives broader stipula than *sti*, with irregular margin (195).

str—Caruncula stripe (190).

sul—Sulciform impression on radicula, similar to effect of *fov* (185).

sup—Adds two small wings to flower, resulting in seven petals (108).

T, T_1, T_2, *t*—Genes for number of internodes. *T* originally named for thick stem (83, 292, 341, 343).

Td—Leaves dentate (114, 207, 283, 319).

Te, te—Broad vs. narrow pod (133, 145).

ten—Narrow rounded leaflets and stipules (125).

Teu—Medium pod breadth (196).

teu—Much narrower.

Tl—Tendril leaves (96, 237, 304, 341).

tl^{w}—Leaves without tendrils.

tl^{pet}—Leaves with long petiolules (96). The *tl* genes form a series of alleles.

Tr—Affects pattern of the seed coat with *A z mp* (294).

Tra—Produces traganth flakes on the inside of the seed coat; orange yellow with *I*; green with *i* (113, 157); originally *Tram.*

trip—Narrow leaflets, stipules, and petals; partially pollen-sterile (112, 137).

U—Purple seed coat (39, 120, 341).

un—Undulating leaflets (173).

uni—Unifoliate leaves and branched inflorescence; flowers tend to be pistiloid (99).

Up—Two or three pairs of leaflets (260).

up—One pair.

Ust—Purple striping of seed coat (39, 102). Lamprecht (134) considers this gene to be identical with *Ast* (102), which he proposes to supplant by *Ust.* Allelic to *U.*

V—Strong pod membrane; with *P* gives parchmented, smooth pods (236, 325, 341).

v—With *p*, no pod membrane.

V_1—Purple seed coat; functions only with B_1 (39, 120).

vac—Proposed as a substitute for *cr*, crinkled leaves (173).

Ve, ve—Affect the size and number of shields around the hilum (142).

vi_1—Virescent, a redesignation of *yg* (130, 135).

vim—Somewhat darker than *pa* in affecting shade of green of pod (152).

W—With B_1, glaucous stem and foliage (304, 323).

wa—Very little wax (323).

Wa_1, Wa_2—Increase the amount of wax, or bloom, on plant (323).

was—Similar to *wa* (96).

Wb_1, Wb_2—Increase the amount of wax; polymeric to *Wa* (150, 238, 323).

wlo—Waxless upper surface of leaves (150, 238).

wsp—Waxless lower surface of leaves (106, 143).

w_2, wb, wv—Designations for white variegated foliage (224, 308, 319, respectively).

X—Rogue gene; reduces size of stipule (21).

x—Normal allele of *X*; always mutates to *X* in plants heterozygous for *X*.

x'—From Mummy pea; reduces size of stipules; mutates to *X* in presence of *yr* (21).

xa—Induces early flowering in *abyssinicum* (260).

xa_1, xa_2, xa_3—Yellow leaves of different shades; proposed to supplant *chd, che* and *chh* respectively (130, 149, 256).

Y—Dominant yellow cotyledon (340).

yg—Yellow-green seedlings becoming green (84). (See *vi_1*.)

yg_2—Seedlings normal, then yellow and later green (84).

Yr—Stipule length-breadth ratio of 2 (21).

yr—Stipule length-breadth ratio of 1.7.

Z—Basic gene, with *A*, for colored seed coat (77).

z—Partial coloring of the testa.

LINKAGE

The establishment of firm values for percentage of cross-over between genes has been at least as difficult in *Pisum* as in other organisms that have been as intensively studied. The different structural types account for some of the difficulty, especially in the earlier work, and must of course still receive careful attention. Wide variability in cross-over values among genes located towards the ends of the chromosomes has been an important factor in later investigations (121). For example, cross-over values between *S* and *K* in Lamprecht's linkage group II have ranged between 2.3 and 39.1 (163).

Because of the large number of papers on this subject published by Lamprecht it is convenient to introduce the groups as presented by him, followed by additional data not already included. Linkage groups are sometimes referred to as "chromosomes" in the literature. It should be pointed out that the numbers assigned to linkage groups are distinct from the numbers given chromosomes as studied cytologically. The numbers appearing between genes in the linkage groups are cross-over values.

GROUP I. *-A*-10-*Vi_1*-16-*Au*-9-*Lf*-9-*Y*-10-*Miv*-20-*Pur*-8-*D*-10-*Re*-25-*Fom*-20-*Lac*-18-*Cor*-4-*Am*-19-*Sal*-5-*O*-3-*Sp*-11-*Red*-6-*I*-30-*Gri-* (144, 160, 198, 202). *A* is linked to a gene for late flowering (255, 330).

-A-11.8-*Vi*$_1$- (98). *-A*-0.5-*Miv-* (131). *-A*-11-*Yg-* (84). *-A*-12-*Lf-* (249). *-A*-12-*Nr*-5-*Lf-* (247). *-A*-13-*Au*-14-*D-* (158). *-A*-16-*Lf-* (158, 342). *-A*-20-*Yr-* (21). *-A*-22-*Cr-* (338). *-A*-35-*Er-* (64). *-D*-27.3-*Fom-* (188). *-A*-39-*D*-32-*Lac*-40-*I-* (160). *-D*-0.7-*P*$_2$-31-*Red-* (346). *-Pur*-15-*Cor-* (158). *-P*$_2$-32-*I-* (346). *-Aw*-26-*I-* (330). *-O*-11-*G-* (319, 337). *-O*-9-*I-* (249). *-Sb*-12-*I-* (84). *-Red*-3-*I-* (346). *A* is on short arm (15).

GROUP II. *-La*-2-*Wa*-3-*Oh*-11-*Ar*-25-*Ve*-37-*S*-12-*Wb*-18-*K*-30-*Fn*-5-*Pal*-31-*Str-* (117, 131, 144, 163, 190, 202). *Oh-Ar-Bl* are considered to be in IV and *S-Wb*$_2$-*K* in V by Winge (346). *-Cy*$_2$-close-*Wa-* (90). *-Ar*-12-(*Bl*) *Wb-* (346). *-Ve*-36-*Wb*-29-*Bl-* (142). *-Ve*-39-*Wb-*, *-Ve*-46-*K-* (162). *-C*-13 to 31-*S*-15-*Bl*-19-*K-* (337). *-S*-0.8-*Wb*-15.6-*K-* (327). *-S*-15.7-*K-* (327). *-S*-2.4-*W-* (320). *-inc*-27-*Wb-* (261).

GROUP III. *-Uni*-4-*M*-24-*Rf*-29-*Mp*-14-*Lob*-5-*Alt*-8-*F*-6-*Pu*-4-*Cry*-2-*St*-26-*Pla*-16-*Fov*-6-*Och*-8-*Ca*-4-*L*-17-*B*-22-*Gl*-10-*Rag-* (116, 136, 144, 164, 184, 196, 198, 202, 294, 321). Centromere between *St* and *B* (98). *-M*-37-*F-* (261). *-M*-33-*F*-13-*B-* (324). *-Mp*-15-*F-* (135). *-Alt*-25.4-*St-*, *Alt*-35.2-*B-* (182). *-Kp*-31.9-*B-* (205). *-Lob*-27-*St*-29-*B-* (164). *-Pu*-4.7 to 6.9-*St-* (347). *-F*-8 to 18-*B-* (327). *-St*-28-*B-* (98, 251). *-St*-31 to 34-*B-* (347). *-L*-11 to 23-*B-* (332). *-L*-?-*St-*(144). *Pu, Cry, St, B, Gl* are on the short arm (15).

GROUP IV. *-Lat*-14-*N*-13-*Z*-10-*Was*-10-*Dem*-9-*Fo*-16-*Tra*-6-*Fa*-28-*Fna*-10-*Td*-14-*Fw*-9-*Br*-20-*Con*-15-*Vim*-28-*Le*-13-*V*-40-*Un-* (114, 144, 146, 160, 164, 174, 198, 202). *-Lat*-10-*N*-19-*Was-* (96). *-N*-17-*Q-* (335). *-N*-4.3 to 15-*S-* (326). *-N*-21 to 23-*Tra-* (157). *-Z*-17-*Fa-* (157). *-Z*-15- to 18-*Fa-* (346). *-Con*-25-*Tra*-29-*Le*-8.5-*V-* (160). *-Tra*-44-*V-* (157). *-Cl*$_2$-35-*Le-* (337). *-Cl*$_2$-45-*V-* (337). *-Fw*-40-*Fnw-* (339). *-Fw*-35-*Le-* (339). *-Le*-8-*V-* (243). *-Le*-8.5-*V-* (160). *-Le*-13.8-*V-* (324). *Le, V, Un* are on the short arm (15).

GROUP V. *-Cp*-7-*Teu*-14-*Gp*-12-*Cri*-9-*Cr*-15-*Te*-10-*Com*-12-*Cal*-16-*Laf*-9-*Sul*-15-*Ce*-10-*Fs*-23-*U*-30-*Ch-* (127, 144, 160, 165, 186, 196, 197, 198, 200, 202). Centromere near *Gp* (98). *-Cp*-3.2-*Gp-* (109). *-Cp*-9.7 to 13-*Gp-* (332). *-Cp*-12-*Gp*-33-*Fs*-18-*Ust-* (121). *-Cp*-16-*Te-* (133). *-Cp*-26-*Cal-* (156). *-Cp*-32-*Fs-* (109). *-Cp*-34-*Laf-* (145). *Gp*-12-*Cri-* (92). Some plants carry a short inversion whereby *-Cp-Teu-Gp-* becomes *-Gp-Teu-Cp-* (196, 200). *Gp*-13.6-*Te*-46-*Ust-* (145). *-Gp*-20-*Cal*-34-*Ust-* (156). *-Gp*-26-*Laf-* (145). *-Gp*-29-*Fs-* (160).

-Gp-42-*Fs-* (249). *-Gp*-34-*Ust-* (160). *-Y*-5.5-*Gp-* (288). *Gp* linked with *R* (98). *-Cr*-18-*Fs*-22-*U-* (127). *-Cr*-26-*Ce-* (286). *-Laf*-38-*Ust-* (145).*-Fs*-22-*Ust-* (160). *Cp* is on the short arm; *U* is on the long arm. (15).

GROUP VI. *-Wlo*-6-*Lm*-4-*P*-25-*Lt*-15-*Pl*-7-*Fl-* (168, 202, 240, 336). *-Fl*-32-*P-* (336). *-Pl*-32 to 33-*P-* (330). *-Pl*-31-*P*-10-*Wlo-* (241). *-Pl-* 33 to 37-*Pe-* (346). *-Pl*-32 to 37-*Wlo-* (240, 241). *-P*-16-*Wlo-* (156). *-Lt*-25.5-*P*-11-*Wlo-* (167).

GROUP VII. *-Wsp*-35-*Xa*$_1$-15-*Pa*-10-*R*-5-*Tl*-37-*Obo*-8-*Bt-* (82, 143, 149, 152, 202, 240, 246, 306, 342). *-Wsp*-34-*R*-5-*Tl*-36-*Bt-* (151). *-Wsp*-34-*R*-34-*Bt-* (143). *-Wsp*-34-*R*-5-*Tl*-13-*Pa*-33-*Bt-* (143). *-Xa*$_1$-15-*R-* (149). *-Pa*-9.6-*R-* (241). *-Pa*-6.4-*Tl*-3.2-*R*-35-*Btb-* (241). *-Pa-* 20-*Tl-* (240). *-Tl*-35-*Btb-* (241). *R* linked with *Gp* (95). *R* linked with *Obo* (175). *-R*-31-*Bt-* (249). *R, Tl, Bt* are on the short arm (15).

A point still in debate is the independence of Lamprecht's linkage groups V and VII, which Lamm regards as a single group (95, 98), referred to as chromosome 1 (97). Evidence for the single grouping comes from linkage between *Gp* of Lamprecht's group V and the point of interchange in the K-line, Thibet-7 and the Winge reciprocal translocations, and in these same interchanges a linkage between *R* of Lamprecht's group VII and the point of interchange (see Table 1). More convincing evidence comes from a cross between Lamprecht's translocation Line 21 (VII-I) and Line 379 (V-III). If these four chromosomes are distinct, two groups of four chromosomes plus 3 bivalents should be found in the F_1 hybrid. If chromosomes V and VII are parts of a single chromosome one group of six and four bivalents should appear at meiosis. The latter was found, and the plants were 63 percent sterile (97). 'Extra Rapid N' may also contribute some evidence, although the linkage value for *R* and the point of interchange in this case is large (46.2 percent) and not statistically significant (98).

Lamprecht (175) points out that this conclusion leaves only six linkage groups, which would indicate that one chromosome has no active genes. He also cites the cytological work of Caroli and Blixt (27) demonstrating a translocation from V to VII in his Line 680. The work of Blixt (15) identifying the seven somatic chromosomes with Lamprecht's seven linkage groups is also cited (200). It is hardly surprising that work on the abundance of genetic materials in *Pisum* might lead to conflicting conclusions by different workers.

Dr. R. Lamm has very kindly supplied by correspondence a comparison of linkage group numbers as used by him and by Lamprecht:

Linkage group number		Important marker genes
Lamm	Lamprecht	
1	V and VII	*Ust-Gp* and *R-Bt*
2	I	*A-I*
3	III	*St-B-Gl*
4	—	—
5	IV	*Fa-Le-V*
6	VI	*Pl-P-Wlo* (probably)
7	II	*Ob-Wb-K* (probably)

Present status of the identification of linkage group with somatic chromosomes studied cytologically follows:

Linkage group no. (Lamprecht)	Chromosome no. (Caroli and Blixt)	References
I	III	(12, 15, 144)
II	II	(15)
III	VII	(12, 15, 26)
IV	IV	(15)
V	I	(12, 15, 26, 27)
VI	V	(15)
VII	VI	(15)

INTERCHANGE TYPES

Designation

Several plans for the designation of interchange types have been used by different workers. Structural lines under study have been named by letter, number, or a combination of these. Nilsson (239) designates five "prime types" by letter, A being the normal commercial type, and Sansome (265, 267) refers to eleven "structural types" by number. Lamprecht (144) mentions "line" numbers, which are a part of his pedigree system. It is not always clear whether two of his line numbers represent identical or distinct translocations. He (177) later adopts a system of naming the chromosomes involved—"Interchange III/V *Fs-St*" (Line 379) and "Interchange III/V *B-Gp*" (Line 582), or "Interchange I/V" (K-line).

TABLE 1.
NORMAL SOMATIC CHROMOSOME COMPLEMENT IN *Pisum*

a. Compiled from report of Blixt (14)

Chromosome number	Chromosome length (microns)	% 2n	Long arm-Short arm	Position of constriction
I	4.4	8.6	1.5	submedian
II	3.1	6.0	1.1	median
III	3.4	6.6	1.2	nearly median
IV	3.6	7.1	1.9	satellite 0.4 μ
V	3.6	7.0	1.7	submedian
VI	4.0	7.6	2.2	satellite 0.6 μ
VII	3.6	7.0	2.8	subterminal

b. Compiled from report of Blixt (15)

Chromosome number	Length in microns	
	short arm	long arm
I	1.5	1.9
II	1.5	1.6
III	0.9	2.7
IV	1.2	2.0 + 0.4 (satellite)
V	1.8	2.6
VI	1.3	2.3
VII	1.2	2.2 + 0.6 (satellite)

Lamm and Miravalle (98) propose a system patterned after work with maize in which a particular interchange is designated by T followed by the numbers of the involved linkage groups in parentheses and a letter indicating the order in which a reciprocal translocation between these chromosomes was discovered. The K-line thus becomes T (1-2)a. The success of this system depends upon general agreement on details and designation of the linkage groups. An attempt to correlate the various designations is included with Table 2.

INTERCHANGES

Additional information on the genes involved in each exchange, location of the point of interchange, and other items of interest are summarized in Table 2, which should be considered in connection with this section. In discussing interchanges it is convenient to disregard distinctions between chromosome in the cytological sense and linkage group in a genetic concept since the two represent different aspects of the same physical entity. In this discussion the linkage-group numbers adopted by Lamm, based on the work of Sansome (265), are given in Arabic numerals, while those of Lamprecht are presented in Roman

numerals. When all linkage groups are identified with their respective chromosome, a single numerical designation for each chromosome-linkage group can be adopted. Several interchanges will now receive brief mention. Additional citations to the literature will be found in Table 2.

The K-line of Hammarlund (57, 59) was the first to receive extensive study. When crossed with normal the semi-sterile F_1 may have a ring of four chromosomes at MI (50) or a chain of four (61). The ring does not have a zigzag arrangement, and alternate or adjacent chromosomes go as separate entities to the same pole at random (50, 51). 'Early Giant Rogue' has an interchange between the same two chromosomes, but the point of interchange lies farther from *A* than in the first case (98, 267).

One plant of a race of peas from Thibet, when crossed with 'Duke of Albany,' produced semi-sterile plants, which had a ring of four chromosomes at MI (250, 258). Thibet-7 was the first to involve Sansome's linkage group numbers 1 and 3 (265). The point of interchange is rather close both to *Tl* of linkage group 1 and to *B* of group 3 (94, 95).

The variety 'Extra Rapid' seems to have been the source of several reciprocal translocations. One found by Hammarlund and subsequently studied by Hakansson (51, 53) in the cross 'Early Rapid N' × 'Soloärt' and other crosses has an interchange between chromosomes 1 and 3, while the 'Extra Rapid S' interchange studied by Sansome (269) involves 3 and 5. These two interchanges were at first thought to be identical. Lamprecht has also studied interchanges from 'Extra Rapid' in his Line 379 (116, 171), which concerns the same chromosomes (III and V) as 'Extra Rapid N' but may have a different point of interchange. His Line 582 (144) also concerns III and V and has a point of interchange distinct from Line 379 (Table 2). In addition, Line 582 has a slight chromosomal deficiency that results in dwarf plants. It is thought that this deficiency may often be covered by a duplication in lines ordinarily considered to be of normal chromosome structure. Line 118, also from 'Extra Rapid,' has a IV-VI interchange (144).

Line 379 has been studied cytologically by Caroli and Blixt (26). They found that the exchange occurred between the long arm of chromosome I and the short arm of chromosome VII. The long arm of I thus became shorter than its normal short arm and the short arm of VII became longer than its normal short arm.

TABLE 2.
SUMMARY OF INTERCHANGES IN *Pisum*

Name	Source	Designations		Linkage groups of Lamprecht	Genes involved	% X-over, gene and point of interchange	Notes	References
		Other	Sansome					
K-line	Hammarlund	B[a], S2[b]	T(1-2)a	V-I	*Gp, Fs, R, Tl-A, Vi*$_1$	*Gp*-1; *Fs*-20; *R*-40; *A*-3.8-7.7; *Vi*$_1$-3.2-11.8	10 to 18% trisomics	50, 51, 57, 60, 61, 200, 248, 249, 265, 287
'Thibet 7'	Pellew	C, S3	T(1-3)a	V, VII-III	*Gp, Fs, R, Tl-St, B*	*Gp*-16.9; *Tl*-2.4-4.5; *R*-5-11; *B*-1-5.9	Fig-8 IV common	93, 95, 98, 250, 258, 263, 265
'Extra Rapid N'	Hammarlund (Weibull)	D. N IV[c]	T(1-3)b	V-III	*Gp, Fs, Ust, St, B*	*Gp*-6.5; *Fs*-12-21; *Ust*-10-24; *St*-8; *B*-8-17	Trisomics (elatius) More rings	51, 53, 55, 91, 92, 238, 239
N III (E x A)	'Bohnenerbse' × 'Automobile'	E	T(3-5)a T(3-5-6?)	III-IV-VI	*St, B-Le, V, N, -Wlo, P, Pl*	*St*-22.4; *B*-8-17; *Le*-21-36; *V*-15; *N*-38; *Wlo*-32; *P*-34	Kite conformation	52, 53, 98, 238, 239, 241, 254
'Extra Rapid S'	Sansome	S4	T(3-5)b	III-IV			Chain of 4	265, 269
DeWinton	DeWinton	S5	T(4-5)a					265

TABLE 2 (cont.)

Name	Source	Designations: Other	Designations: Sansome	Linkage groups of Lamprecht	Genes involved	% X-over, gene and point of interchange	Notes	References
Winge	Winge	S6	T(1-4)a	V-VII	*Gþ,-R*	*Gþ*-28; *R* 1.4	IV or Fig. 8 Small terminal segment	95, 98, 248, 265, 285
Merton 1	'Duke of Albany' × 'Tibet' normal	S8	T(3-4)a	III-VII?	*St, B-*	*B*-8.5; *St*-4-10.8;	Linkage p.i.- *R* probably accidental	98, 267
'Early Giant'	'Early Giant'	S9	T(1-2)b	V?-I	*-A*	*A*-10.8		98, 267
G-line	'Sabre' variety	S10 (N II)	T(6-7)a	VI-II	*Wlo*			52, 53, 98, 239, 267
F-line	Nilsson	S11 (N I)	T(5-6)a	IV-VI	*Le-Pl*			52, 53, 98, 239, 267
Line 379[d]	'Ambrosia' × 'Extra Rapid'		T(1-3)c	V-III	*Cþ, Gþ, Fs,U-Mþ, F, St, B, Gl*	*Gþ*-18; *Fs*-8-12; *B*-9 to 17; *St*-8	P.i. between *Fs, U* and *F, St*	91, 116, 121, 129, 138 144, 177
Line 118	'Extra Rapid' (Weibull)		T(5-6)	IV-VI-VII	*Le, V*	*V*-3.2. Both interchange + translocation probably	⅔ 32% sterile ⅓ 62% sterile in cross	105, 123, 129, 144, 177

TABLE 2 (cont.)

Name	Source	Designations: Other	Designations: Sansome	Linkage groups of Lamprecht	Genes involved	% X-over, gene and point of interchange	Notes	References
Line 582	'Extra Rapid' (England)		T(1-3)d	V-III	*St, B-Gp, U*	*Gp*-23; *U*-36; *St*-32; *B*-7.9	x normal gave 20% dwarf plants, due to deficiency	91, 144
Line 761	'Brechmarkerbse'		T(5-6)	IV-VI	*Le, V-*		Small deficiency is covered by duplication	144
Line 936	*P. sativum* var. *humile*		T(1-5)	V-IV	*Fs-V*	*Fs*-7.8 *V*-close		200
Line 21	Tedin 01001		T(1-2)c	VII-I	*Bt, Tl, R-A, I*	*R*-0.4-10; *Tl*-5.9; *Bt*-26	P.i. between *Bt, Tl* Line 11 is similar	105, 129, 144, 151
Line 58	Grave Posthornchen		T(5-6)	IV-VI	*Le, V-P, Lm, Wlo*	*Le*-6.5; *V*-12.8; *P*-34.6	Interchange to normal type after mutation *v* to *V*	105, 123, 129, 144, 168
Line 690	'Early Dwarf'			IV-VI	*P*		Interchange after mutation *p* to *P*	123

TABLE 2 (cont.)

Name	Source	Designations: Other	Designations: Sansome	Linkage groups of Lamprecht	Genes involved	% X-over, gene and point of interchange	Notes	References
'Abyssinian'	von Rosen		T(1-7?)	VII-I + IV-VI?	*R, Tl* *R*		1 IV + an inversion. 42 and 75% pollen st.	129, 144, 177, 260
humile × arvense	Håkansson		T(3-5)	III-			1 IV. Second cross has inversion and bridge	54
humile	*P. sativum* var. *humile*		T(1-3)	V-III	*Y*		Probably 2 interchanges. More chains.	128, 266, 286
abyss. fulvum × asiaticum	von Rosen		T(1 or 3-?)				1 IV. 52% sterility	260

a Prime type of Nilsson
b Structural type of Sansome
c Heterozygous interchange designation
d Pedigree number of Lamprecht

N III is the heterozygous interchange of prime type E ('Bohnenerbse' × 'Automobile'). Listed by Lamm and Miravalle (98) as T(3-5)a, it has a kite-like formation of the chromosomes during first division of meiosis and appears to involve a third linkage group (52, 53, 238, 239, 241) and to need further study.

Information on the interchanges listed by Sansome (265, 267) as S 4 through S 11 are presented in Table 2. These include the DeWinton, Winge and Merton interchanges as well as the F-line (N I) and G-line (N II).

Lamprecht's Line 58 holds especial interest because of a mutation from *v* to *V* concurrent with the appearance of an interchange between linkage groups IV and VI. The point of interchange is very close to *V* (0.44 percent). While the discussion (123, 144) is on the basis of an association between the mutation of *v* to *V* and the appearance of a IV-VI interchange, it seems that Line 58 is a IV-VI interchange recessive for *v*, and the mutation to *V* is associated with a change to the "normal" chromosome structure of Line 59. The structural status of each line was established by numerous crosses with normal lines. The mutation of *v* to *V* thus seems to be associated with a return of this IV-VI interchange to a normal condition rather than the reverse. This indicates that the point of interchange, when the chromosome structure returns to normal, remains the same as when the interchange first appeared. This point is shown to be 6.5 cross-over units from *Le* in linkage group IV and 34.6 units from *P* in group VI (168).

Line 690 (IV-VI) is also associated with a mutation, in this case from *p* to *P*. Lamprecht (144) considers the *v* and *p* to be polymeric genes, whose distinctive effect is the result of their position in different chromosomes.

Line 118 is similar to Line 58 in that the point of interchange is also close to *v* (3.2 percent), but it carries, in addition, a simple translocation. In crosses with normal two-thirds of the plants are 32 percent sterile and one-third are 62.9 percent sterile. Line 761 may represent the same interchange found in Line 118. In addition it has a deficiency (144).

Lamprecht's Line 21 has a close association between the genes *R* and *Tl* of his linkage group VII and sterility (105, 151, 171). Gene *A* of his linkage group I is also associated with segregation into fertile-sterile. The cross-over value in this case was 27.3 percent. This interchange has been studied cytologically by Blixt (12). Chromosome IV,

which corresponds to linkage group VII, has a distinct satellite. An exchange has occurred between the short arm of chromosome IV and the long arm of chromosome III at a point to increase the long arm of III and decrease by an equal amount the short arm of chromosome IV. It is concluded that linkage group I corresponds to chromosome III.

Lamprecht's Line 680 was originally reported to be a simple translocation when studied both genetically (147) and cytologically (27). A portion of the long arm of chromosome I, carrying the gene *Cp* of linkage group V, became attached to the long arm of chromosome IV, which resulted in close linkage with the gene *Bt* of linkage group VII. This simple translocation is later listed as a reciprocal translocation "Interchange V/VII" (177).

In his cross No. 1276 Lamprecht (177) found linkage between genes in linkage groups I, IV, and VII and sterility as follows:

Linkage group	Gene	Cross-over values
I	*I*	31.5 +4.62 percent
IV	*Tra*	23.5 + 3.64 percent
IV	*Con*	29.8 + 4.23 percent
VII	*R*	29.8 + 4.23 percent

Points of interchange between *Tra* and *Con* to either the left or the right of *R* are indicated.

Crosses Between Interchange Types

The first generation of crosses between a fairly large number of interchange types has been examined cytologically. The results are summarized in Table 3. The chromosomal associations found are with a single exception those to be expected from previous study of the original interchange types and so confirm the validity of the earlier studies. For example, where the same two chromosomes have interchanged, such as in K-line × 'Early Giant Rogue,' only one association of four chromosomes results, and where the interchanges have one chromosome in common, as in K-line × 'Thibet-7,' an association of six chromosomes is found. If all four chromosomes of the two interchanges are distinct, as is found in Prime type E × K-line, two groups of four chromosomes appear in the F_1. In similar manner, S7 × Winge, which is T(1-2-3) × T(1-4), gives an association of eight chromosomes. In addition to the multivalent groups the appropriate number

TABLE 3.

CROSSES BETWEEN INTERCHANGE TYPES IN *Pisum*

Cross		Chromosomal groupings	% sterility	Notes	References
Name	Type				
Translocation × Normal	—	1 IV + 5 II	50	% sterility varies	See Table
K-line × Thibet 7 (S7)	T(1-2)a × T(1-3)a	1 VI + 4 II	70	Structural type 7	
				78% fig.-8, Trisomics	263, 264, 265
'Extra Rapid N' × K-line	T(1-3)b × T(1-2)a	1 VI + 4 II	68	T(1-3)b has 2 long arms	
				T(1-2)a has 2 short arms	94
Prime type E × K-line	T(3-5)a × T(1-2)a	2 IV + 3 II	70	10 + "frying pan"	94
'Extra Rapid S' × K-line	T(3-5)b × T(1-2)a	2 IV + 3 II			269
K-line × Winge	T(1-2)a × T(1-4)a	1 VI + 4 II	75		98, 285
K-line × Merton 1	T(1-2)a × T(3-4)a	2 IV + 3 II	75		98
K-line × 'Early Giant' reg.	T(1-2)a × T(1-2)b	1 IV + 5 II		Distinct translocations	265, 267
K-line × F-line (N I)	T(1-2)a × T(5-6)a	2 IV + 3 II		Håkansson unpublished	98
K-line × G-line (N II)	T(1-2)a × T(6-7)a	2 IV + 3 II	77		98
'Extra Rapid N' × Thibet 7	T(1-3)b × T(1-3)a	1 IV + 5 II	65	Sometimes 7 II	94, 95
				Pecular configuration	
Prime type E × Thibet 7	T(3-5)a × T(1-3)a	1 VI + 4 II			94, 98
'Extra Rapid S' × Thibet 7	T(3-5)b × T(1-3)a	1 VI + 4 II			269
Thibet 7 × Winge	T(1-3)a × T(1-4)a	1 VI + 4 II	75		98, 285
'Extra Rapid N' × Prime type E	T(1-3)b × T(3-5)a	1 VI + 4 II	50	Sometimes 1 IV + 5 II	53, 98
'Extra Rapid N' × Merton 1	T(1-3)b × T(3-4)a	1 VI + 4 II	59		98
'Extra Rapid N' × F-line	T(1-3)b × T(5-6)a	2 IV + 3 II	71		53
'Extra Rapid N' × G-line	T(1-3)b × T(6-7)a	2 IV + 3 II			98
Winge × Prime type E	T(1-4)a × T(3-5)a	2 IV + 3 II	71		98
Merton 1 × Prime type E	T(3-4)a × T(3-5)a	1 VI + 4 II	61		98
F-line × Prime type E	T(1-3)b × T(3-5)a	1 VI + 4 II	50		53, 98
G-line × Prime type E	T(6-7)a × T(3-5)a	2 IV + 3 II	67		98

TABLE 3 (cont.)

Cross		Chromosomal groupings	% sterility	Notes	References
Name	Type				
'Extra Rapid S' × *DeWinton*	T(3-5)b × T(4-5)a	1 VI + 4 II			269
'Extra Rapid S' × Winge	T(3-5)b × T(1-4)a	2 IV + 3 II			269
Winge × F-line	T(1-4)a × T(5-6)a	2 IV + 3 II	78		98
Winge × G-line	T(1-4)a × T(6-7)a	2 IV + 3 II	77		98
Merton 1 × F-line	T(3-4)a × T(5-6)a	2 IV + 3 II			98
Merton 1 × G-line	T(3-4)a × T(6-7)a	2 IV + 3 II	66		98
F-line × G-line	T(5-6)a × T(6-7)a	1 VI + 4 II		Chain or ring	53, 98
S7 × Winge	T(1-2-3) × T(1-4)	1 VIII + 3 II		Largest association	265
Abyssinicum × Tibetinicum	T(1-3) × T(1-3)	1 IV + 5 II	68		260
L21 × L58	T(1-2)c × T(5-6)	1 VI + 4 II	69.7	Association unexpected	106, 144
Line 582 × Line 379	T(1-3)d × T(1-3)c		62.5	1 IV + 5 II (?)	144
Line 582 × Abyssinicum	T(1-3)d × T ?		75		144
Line 379 × Line 21	T(1-3)c × T(1-2)c	1 VI + 4 II	63	Ring or figure eight	97
Line 379 × Line 936	T(1-3)c × T(1-5)		62.3	Linkage groups V/III/IV	200

of paired chromosomes was observed. The degree of sterility found in crosses between interchange types may vary from expectation in different amounts. Proportions of sterility reported are noted in Table 3.

SPECIES RELATIONSHIPS

In 1930 Lutkov (218) crossed *Pisum humile* Boiss. with *P. sativum.* The plants exhibited hybrid vigor, but he reports "a considerable degree of sterility." Some second generation plants were normal and fertile. Meiosis was normal in both generations. Apparently some of the chromosomes of the two forms are interchangeable, while others are not. This accounts for the sterility observed. The author regards the two species as "quite independent." Lamprecht (128) finds greater fertility in this cross and considers the sterility to be the result of reciprocal translocation in *humile.* For this reason he considers *P. humile* to be a race of *P. sativum.*

Von Rosen (260) crossed *Pisum abyssinicum* A. Braun with *P. sativum* and found both an inversion and a reciprocal translocation in *abyssinicum* as compared with *sativum.* The order of linkage of *xa* and *A* was reversed in the former species. The author thinks that the essential difference between the two species "consists of a certain difference in the stock of small quantitative genes (polygenes)." He would keep the two species distinct.

Crosses between *Pisum arvense* L. and both *P. elatius* Bieb. and *P. jomardi* Schrank demonstrate that the last two should be regarded as synonymous with *P. arvense* (154), which is herein treated as *P. sativum* var. *arvense.* This conclusion is based upon the high degree of fertility found in the crosses, upon similarities in linkage, and upon segregation ratios obtained.

A weak-stemmed wild pea with a solid magenta flower and olive-green mottled seeds, found in Palestine, was crossed by Sutton (283) with a white-flowered *P. sativum.* The F_1 was partially sterile and had a bi-colored flower. The Palestine pea was not considered to be the ancestral source of *P. sativum* or *P. sativum* var. *arvense.*

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