IN PURSUIT OF pal

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Few reports concerning the genetics of seed coat color and pattern in Pisum have appeared in recent years, perhaps in part because the complex and seemingly inscrutable inheritance patterns reported in the past may have discouraged fresh attacks on the problem.

Gene pal (pallens) is one of a number of the so-called "part1y coloured" — seed genes extensively investigated by Lamprecht (1-6). In A Z seeds, pal is said to have a "slight and often uncertain" effect whereas "In A z seeds the effect is distinct" (6). Moreover, in "A z mp dem cal seed[,] pal causes the entire disappearance of seed-coat colour", and the seeds appear as if they were borne on a plants. This implies that, by itself, pal cannot effect a disappearance of seed coil color but instead requires the simultaneous presence of at least four additional recessive genes. With this many genes affecting the expression of the pal, it would seem that most crosses would result in a confusing array of phenotypes, a situation that might thwart straightforward Mendelian analysis. If, however, the parental lines of crosses had several genes in common, then the complexities would be minimized. Apparently this was the case when Lamprecht used his line 607 (Le A z mp dem Cal Pal str S Wb K) and line 989 (Le A z mp dem pal Str s wb k), to determine the linkage relations of pal on chromosome 2 (4). Presumably cal was also present in L-989, although Lamprecht doejs not so state in his 1960 paper.

Murfet (7) described a recessive gene that mapped to chromosome 2 in the vicinity of k and wb. Segregation could be followed in F2 on the basis that the gene in question diluted the expression of M.

In 1976 I made a series of crosses between WL 578, the type Line for pal, and a number of my own lines. Blixt lists WL 578 as having the following genotype: A D^{co}, dem, cal, mp, z, pal, (also pre, ins, td, gri, wb, k, s, mifo st). My lines carrLed one or more of the following: U, oh, M, F, or Fs, and one line was f fs. These crosses revealed that WL 578 evidently is f and fs since the seed of F. plants from crosses in which the second parent was known to be f fs were unspotted but the....d of F^'s from crosses in which the second parent was F or Fs exhibit tot typical anthocyanin spots.

Because many of the F_2 plants derived from these crosses exhibited poor seed set and because the seed color patterns were variable and, at the time, unfamiliar and difficult to classify, no definite ratios werfe obtained. Still, a significant portion of the A plants bore seeds which were colorless or very nearly so, i.e. resembling seeds for a plants. Selection was practiced among the progenies and eventually a number >i fully fertile A lines with colorless seed (pal) were available. One of these, an F _ (A1082-34), was then used in a new cross made in 1982.

1/ As Blixt points out in his 1972 monograph (p. 174), these genes would more appropriately be described as "partly de-coloring".

cross made in 1982. The second parent In this cross was an F8 with the genotype A f Fs (A882-35). Of twenty-five F1 seeds from this cross planted in the field in 1982, twenty-three produced seed. Most F1 plants were robust and prolific; all were fully fertile. Unexpectedly, though explicably, all F1 plants produced purple, self-colored seed, a manifestation of U. The U gene had been introduced in the original crosses and its expression in line A1082-34 had been masked by pal or by a combination of genes which includes pal.

A population of 200 F2 plants was grown and scored in the greenhouse in the fall of 1982 and additional F2 populations from the same cross were grown in the field in 1983. Table I summarizes the results. The seed produced by the individual F2 plants could be placed into five rather distinct categories: self purple; self pink; spotted; partly de-colored; and "colorless". The pink seed can be explained by the fact that the pal parental line also carried b, the pink coloration being merely an expression of the interaction between U and b. Some of the seeds In the "colorless" category had a faint trace of color but in general they readily could be distinguished from those in the partially de-colored class. In the latter class, while much of the color had disappeared, the pigment was incompletely inhibited and the background was somewhat dull in contrast with bright seeds in the colorless class. The plants with spotted seeds were typical of plants carrying F, Fs or F Fs, the color of the spots being diluted on the seeds from b segregants.

The simplest interpretation of the results is that the parents of the cross differed at three loci: U-u, Z-z and Pal-pal. Since A1082-34 was the parent with colorless seed (like a seed), its presumed genotype is A, Fs, U, z, pal. Completely de-colored seed apparently requires recessivity at, minimally, two loci, z and pal. This combination is epistatic to both Fs and U. The genotype of the second parent evidently was A, Fs, u, Z, Pal. Note that both parents are presumed (on grounds not discussed here) to be homozygous dominant at Fs and therefore did not segregate in F2. Seed spotting only appeared to segregate because this phenotype can only be observed in plants recessive for u and dominant for Z. It is suggested that both pa u is rrents may have been homozygous recessive at mp. The partially de-colored class is attributed to the action of z/z in combination with Pal/Pal or Pal/pal, only z/z pal/pal plants bearing colorless seed. This scheme also implies that some of the plants containing partially de-colored seed would be heterozygous Pal/pal and would, when progeny tested, produce segregants with colorless seeds. F3 and F4 progeny tests verified this expectation. The putative genotypes and observed phenotypes may be summarized as follows:

	Genotype			
	U	Z	Pal	Seed Phenotype
27	+	+	+	Self purple or pink
9	+	+	−	Self purple or pink
9	+	−	+	Partially de-colored
3	+	−	−	Colorless
9	−	+	+	Spotted
3	−	+	−	Spotted
3	−	−	+	Partially de-colored
1	−	−	−	Colorless

Clearly, this scheme is far less complex than that proposed by Lamprecht, but it in no way invalidates his extensive analyses. Applying Lamprecht 'a scheme to the present results would mean that both parents had certain other genes such as dem and cal in common. It is difficult to assess the probability of that occurrence. The participation, if any, of other genes such as ca, cat, den, disp, lob, str and ve are even more problematical. Nor is it possible accurately to assess the involvement of complicating factors such as multiple heterozygosity, modifier genes behaving in a quantitative manner, or environmental influences. The discussion and illustrations provided by the Tedins (8) emphasize the variation that can be encountered.

In the present case the distinction between classes was remarkably clear. The partially de-colored class (resulting from z z) was the only moderately variable class and even so there was unquestionably a greater affinity between the partly de-colored and colorless classes than between the two remaining classes, i.e. self purple or pink and spotted. Also, whatever the interpretation, the present data show that it is possible to effect the conversion (in A plants) from self purple to colorless with segregation at only two Mendelian loci.

Coincidental to these studies segregation occurred for a difference in axil color. In addition to the normal wild-type axil color associated with wild-type flowers and to the diluted, pink axil color associated with b/b, there appeared in these populations plants bearing wild-type flowers with an axil color similar to that conferred by b/b. This difference was followed only in the glasshouse populations where it was observed that of the 134 B/- segregants, 107 had wild-type axil color and 27 had orangy pink axils. In the remaining 66 b/b plants, orangy pink axils could not be distinguished from the pink color normally associated with b. This matter will be pursued further but at the moment there appears to be no relationship between the orangy pink axil color and pal, or with any other segregating locus.

Table 1. Seedcoat color phenotypes observed in F_2 of cross between parental lines with following putative genotypes: **A z pal U (Fs) b** and **A Z Pal u Fs B.**

Population identity	Self-colored (Purple/pink)	Spotted (Speckled)	De-colored Partial	De-colored Complete	Total
C282-151-153	115	43	29	13	200
B283-154-155	170	59	57	19	305
Observed	285	102	86	32	505
Exp. (36:12:12:4)	284.1	94.7	94.7	31.6	505.1

1. Lamprecht, H. 1956. Agrl Hort. Genet. 14:34-44.
2. Lamprecht, H. 1957. Agrl Hort. Genet. 15:48-57.
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7. Murfet, I. C. 1978. PNL 10:53-54.
8. Tedin, H. and 0. Tedin. 1928. Hereditas 11:1-62.