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GENETIC ASPECTS OF SEED QUALITY[1]

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Quality seed is undamaged, has a high level of germination, and will produce uniform, vigorous seedlings without defects under various environmental conditions.

There has been much work on the physiology of seeds but relatively little on the genetics of various characteristics influencing seed quality. Physiologists have studied the attributes of seed that affect quality and quite often have reported differences among cultivars, but genetic studies are uncommon. However, the physiological studies were necessary before genetic studies could be made; for example, to identify differences among cultivars, to develop techniques which could be used to identify genetically different lines, and to identify characteristics affecting seed performance.

In this paper I will report on various characteristics affecting seed quality and discuss the inheritance of each character as far as possible.

Hard seed.

Seed vigor can be influenced by conditions at harvest, and there are genetic differences in ability of some lines to withstand inclement conditions prior to harvest and after the seed has matured. Hard seed in soybeans (42) has been suggested as a defense mechanism against conditions prevalent during delayed harvest for southern soybeans. Although hard seed is undesirable, its germination after a period of aging was much better than that of the permeable-seeded line.

Some cultivars of beans (*Phaseolus vulgaris* L.) are hard seeded. This character used to be a major problem in beans because it resulted in uneven germination, but it has been bred out of most commercial types, especially of snap beans. Ledebeff (32) indicated that, in crosses between soft-shelled lines and lines with various degrees of hard seededness, the F_1 was intermediate or approached the soft-seeded parent. In the F_2, seed permeability showed all possible degrees of variation between the extremes of the 2 parents. In 1 cross transgressive segregation occurred for both extremes. The data clearly indicated that the degree of hard-seededness was controlled by several genes.

Kyle (30) examined the nature of hard seed in 2 bean cultivars—'Great Northern' and 'Red Mexican'—and discovered that in 'Great Northern' the micropyle was the site of water imbibition while in 'Red Mexican' it was the raphae and hilum. The impermeability of the hilum and raphae was due to a simple recessive gene and was closely associated with the *p* gene for white seed. Gloyer (21), however, showed in a cross of red and white kidney beans that it was quite easy to select for soft seed in white segregants. Radiofrequency dielectric heating has been used for rendering hard seed of alfalfa permeable to water (39).

An advantage of the hard or semi-hard seeded character is that it protects the seed from aging, or, at least, slows the aging process. Selecting for semi-hard seed also may be a means to obtain seed with seedcoats which do not leak nutrients readily during imbibition. *Vivipary.* Seeds sprout in the fruits of some tomato cultivars because there is an insufficiency of the sprouting hihibitor abscisic acid (54); UF136 is an example of a severe case. The same problem occurs in beans (43).

Visible defects.

One of the most obvious visible defects in seed is the fish face, or seed coat rupture characteristic, evident in beans. Farooqui and McCollum (19) identified line differences which, under extreme conditions, ranged from 1.5–47.6% seed coat rupture. They observed that progeny of ruptured seed produced no more ruptured seed than progeny of unruptured seed within a given line. Dickson (9) observed a similar range of susceptibility to seed coat rupture, but concluded that there was a single incompletely dominant gene for susceptibility with 25 to 50% penetrance, the latter varying from season to season.

Transverse cotyledon cracking (TVC) occurs widely in large-seeded legumes. McCollum (35) reported that TVC in beans ranged from 0 to 48.3%. Resistant cultivars such as "Cherokee" became susceptible if imbibed with the seed coat removed. This event indicates that rapid imbibition of very dry seed induced rupture, and that a seed coat which only permitted slow imbibition prevented TVC. In other studies (15) the presence of a seed coat did not influence susceptibility to TVC.

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Dickson et al. (15) observed correlation of TVC with Ca and Mg content of the seed and also noted cultivar differences in snap beans in which TVC ranged from 5 to 94%. In a genetic study it appeared that inheritance was quantitative with narrow sense heritability of 26 to 46%, but with dominant genes for resistances (11). However, the most susceptible line, OSU 58, combined well to produce an unexpected number of resistant progeny. The study showed that with vigorous selection, resistant lines could be obtained.

Another factor that frequently affects seed quality is the presence of cross cracks of the seed coat. This character may be linked with the *By* gene for yellow bean mosaic virus resistance. However, the genetics of this character have not been studied.

Seed injury.

Large-seeded legumes are especially prone to thresher injury or mechanical damage. Thresher injury often results in cracked and loosened seed coats which then do not protect the cotyledons. This results in split seed and poor germination. Moisture level influences susceptibility to damage, and most screening is done on dry (5 to 8% moisture) seed. Selection has proven that damage-tolerant lines can be developed. Barriga (3) mechanically beat 41 strains of navy beans and showed differences did exist. Atkin (2) also screened a number of snap bean cultivars for tolerance to mechanical injury. Most of the tolerant lines had colored seed coats (herein colored seed refers to any seed color, except white) with the exception of the white-seeded 'Streamliner'.

Dickson et al (14) studied the inheritance of mechanical damage resistance (MDR). Inheritance was quantitative and resistance was associated with colored seed although resistant white-seeded selections could be obtained. Narrow sense heritability was 27 to 52%. Further, resistance to MDR was associated with resistance to TVC and loose seed coats (12). By means of vigorous selection, using simulated mechanical damage, in which 95% or more of the seed in a segregating population were destroyed, rapid improvement in MDR could be obtained (14).

Dorrell (16) found that, as seed density of navy beans increased, cotyledon splitting increased, whereas seed coat cracking declined. In MDR lines the shape of the seed was usually spherical, the thin parenchymatous layer was contiguous with the coat, and the seed was of high density.

Kannenberg (26) indicated that seed coat thickness in Lima beans directly affected the extent of seed coat cracking; however, in navy beans, there was no difference in seed coat thickness of tolerant and susceptible lines.

'Valencia A' peanuts had fewer split kernels than 'Starr' or 'Florunner', especially under conditions of extreme drying (22). The testae of 'Valencia A' were less compacted and more flexible than those of the other cultivars. Thin inner parenchyma, non-compact middle parenchyma, and relatively thick-walled outer sclerenchyma cell layers seemed to be the primary factors related to maintenance of testa integrity.

Green and Pinnell (23) studied visible seed defects in soybeans and found them all inherited quantitatively. They, along with Walters and Caveness (53), are among the few to specifically recognize the need for improved seed quality through improved breeding lines.

Cotyledon position.

Germination is influenced by the ease of emergence of the seedling and most dicotyledonous plants are epigeal in germination. This poses little problem for emergence of small seeded crops, but for large seeded crops, such as beans and soybeans, emergence of the cotyledons out of crusty soils can result in broken hypocotyls. In runner beans (*Phaseolus coccineus*) and peas the broken hypocotyls are avoided because they have hypogeal germination. By this arrangement the force required by the cotyledons for successful emergence from the soil is reduced.

Several researchers (20, 24, 31, 52) have tried to develop hypogeal *P. vulgaris* beans, but without too much success. Lamprecht (31) reported that the position of the cotyledons was controlled by 2 alleles of the interspecific gene *Epi* and *Hyp*. He concluded that these genes were part of the interspecific gene complex and could not be transferred from one species to the other. Freytag (20) indicated that, in the wild, the species *P. coccineus* and *P. vulgaris* intercross and thus result in natural intermediates with the cotyledons (52) that remain near the soil surface. Wall and York (52) made the most thorough genetic study of this character. The F_1 of a cross between epigeal *P. vulgaris* and hypogeal *P. coccineus* is intermediate between the parents and has the cotyledon at the soil surface. The F_2 mean tends toward the hypogeal type, but in succeeding generations the population veers towards the epigeal type. This tendency may occur because the epigeal character is linked to the *P. vulgaris* type which is self fertile and thus produces greater seed increases of the epigeal type.

Some breeders continue to try to overcome the association noted above. Ibrahim and Coyne (25) used *P. coccineus* as the seed parent, which is a more difficult cross but makes use of the effect of *P. coccineus* cytoplasm. The hypogeal characteristics will, I am sure, eventually be transferred successfully and will help improve germination in beans.

Seed conductivity and leakage.

The inadequacy of laboratory germination tests in relation to field germination under inclement conditions is well known. Several attempts to identify tests indicating the potential seed vigor have been made, but none are widely accepted at present.

Matthews and Bradnock (34) developed tests for peas and beans by measuring the electrical conductivity of leachates. The conductivity seems to correlate (negatively) better with field germination under adverse conditions than the standard laboratory roll towel tests for peas, but not for beans. However, even then the curvilinear regression of beans gives a true indication of weak seed. High levels of exudation may be an indication of susceptibility of the peas or beans to *Pythium* since this and other soil-borne organisms may be stimulated by exudates.

Rowland and Gusta (44) found a negative correlation of conductivity with germination in both peas and faba beans. Also TVC susceptible faba beans had more leachate, as might be expected, because cotyledonary damage will release nutrients. However, the system needs further perfecting before it can be used as a selection tool by breeders.

Levengood et al. (33) used seed conductivity as a tool for selection for seed vigor and found those seed with a minimum level of conductivity gave the best germination. They were able to use their system to select superior navy beans lines.

Seed color.

Colored seeds of many crops have been shown to be more resistant than white seed to organisms inciting root rot and seed rots. This is particularly a problem in peas and benas, where white seed is an otherwise desirable quality attribute. The resistance to these diseases has been due to several genes in each case and in beans the association has been with the *P* gene for colored seed. Dickson and Boettger (13) showed this linkage could be broken in beans for *Pythium* resistance and Muehlbauer and Kraft (37) have shown this for peas.

If alternate genetic systems of developing white seed can be used this problem may be more readily overcome. We are comparing 3 white seeded isogenic lines developed from a colored line. The white seed coat is due to 3 different gene systems.

Colored seed are often more resistant to mechanical damage (12). The resistance, which results in less seed coat cracking, presumably also results in less nutrient leakage from the seed during germination and consequently less attack by soil-borne fungi (55).

Vea and Eckenrode (51) found colored bean seed were more resistant to the seed corn maggot. Again, resistance is probably due to reduced leakage of nutrients during germination (46). A low level of leakage results in reduced activity of soil-borne fungi which stimulate oviposition by the female maggot flies (17).

Seed size.

Seed size would seem to be obviously related to seed vigor. However, this character has not been studied extensively in small vegetable seed and in large-seeded crops, increased size may be undesirable.

Large rapeseed (*Brassica campestris*) produced more fruit per plant, larger fruit, heavier seeds, and higher seed yield per plant than did plants grown from small seed (1). Essentially the same is true for soybeans (5) and snap beans (8). Smittle et al. (48) used air velocity to select out the heavy and dense seed of snap beans and found that the yield from such seed was significantly higher than that from ungraded seed.

With direct seeding being widely used for such vegetables as cabbage, selection for genetically large seed would be desirable, but has not yet been utilized in plant improvement.

Evans and Bhatt (18) studied seedling vigor in wheat and found that seed size and protein content were highly correlated with seedling vigor. However, it was also apparent that, when seed size and percent protein were held relatively constant, there was a genetic factor for seedling vigor. This study does emphasize though that use of graded seed that is typical for the cultivar is important in trials, as otherwise yields can be easily biased.

Townsend (49) used recurrent selection to obtain higher seed weight in 'Cicer' milkvetch, and obtained a 22 to 35% increase during 2 cycles of selection. Part of this gain was due to hybrid vigor. He pointed out that inbreeding depression could become a problem with additional selection and problems in other agronomic characters might develop if not selected against.

Chemical constituents.

Breeding of highly nutritious seeds, such as high lysine maize, has led to seed vigor problems. This is often due to the small, shrunken seed. Such small, incompletely developed seed are frequently of low vigor. Breeders are now trying to find genes controlling nutritional quality which do not result in reduced seed vigor.

Ullrich and Eslick (50) compared the effect of different shrunken endosperm genes on kernel weight of barley. The average mutant kernel wieght ranged from 38% ('Ingrid' seg 6) to 95% ('Glacier' amo 1) of normal. Thus, selection of those mutants that maintain a significantly higher percent lysine in the grain, even with added kernel weight or plumpness, would be the most desirable.

Nass and Crane (38) compared various endosperm genes with isogenic background in corn as they affect germination at 15° and 20 to 25°C. Seed with the fl_1 gene was superior to normal seed. Thus, mutants appear to produce changes in the component of the endosperm that are either favorable or unfavorable for germination and early seedling growth.

Ching et al. (7) correlated emergence in barley with various characters but concluded that seed weight was responsible for 61% of the variance in emergence rate. Inclusion of the ATP content of 3-day old seedlings increased the regression an additional 4%, the addition of total adenosine phosphates of hydrated embryos and dry weight of 7-day old seedlings added 4 and 2%, respectively. Thus seed weight was by far the most important criterion for selection for field emergence rate and vigor.

Some of the most interesting genetic factors correlated with seed vigor were mitochondrial respiration and efficiency in barley. McDaniel (36) correlated hybrid vigor with seedling respiration rate, and mitochondrial respiration and oxidative phosphorylation with yield. Growth rate was correlated with seed weight, but the large seed had much more mitochondrial activity than would be expected from size alone. Also, mitochondrial activity was successfully used to screen for hybrid vigor. Schneiter et al. (45) were able to correlate the ADP:0 ratio of 5-day old alfalfa seedlings with forage yield ($r = 0.81$).

Low-temperature seed germination.

Considerable effort has been made to select for the ability to germinate at low temperatures. Many crops have been studied and selected for this character but I will discuss only a few of them.

Smith and Millet (47) screened seed of various tomato lines for ability to germinate and identified wide differences in potential. The small-fruited 'Red Currant' and 'Tiny Tim' germinated better at 10°C than others. There was no correlation with low temperature germinability and time of fruit maturity. Ng and Tigchelar (40) studied the inheritance of low temperature sprouting and concluded that sprouting ability was polygenic, with dominance for inability to germinate at low temperatures. They indicated that 3 to 5 genes were involved. Others have made similar studies and found germination was additive and related to seed size.

Berry (4) found that the ability to germinate at high temperature was a characteristic of cold-germinating types, with the exception of 'Fireball'. The ability to germinate at high temperatures was independent of fruit maturity.

In large seed, such as corn or beans, seed moisture greatly influences response to imbibition at cold temperatures. Obendorf and Hobbs (41) showed differences in response among cultivars of soybeans to imbibition at low temperatures.

Kooistra (29) selected for cold germination ability in beans and found that the character was inherited quantitatively. Dickson (10) selected for cold tolerance in snap beans, and found that colored seed germinated better than white seed at low temperature and also that small-seeded cultivars from Central and South America germinated better at low temperatures than U.S. cultivars. However, ability to germinate at low temperatures is independent of the ability to grow at low temperatures. 'Comptess de Chambord' and some 'Blue Lake' beans will germinate at 7 to 9°C but growth at 10° is very slow; some other lines such as 'Limelight' and 'G5-161' will germinate at 9-10° but will also grow quite well at 10° (27).

In corn, the maternal parent influences tolerance to cold imbibition injury (6), possibly due to cytoplasmic inheritance of mitochondria. The same was observed in cotton.

Summary

There are many facets of seed vigor. We know something of the physiology and nature of many of these characteristics and have identified cultivar differences. Very few of the characters have been studied genetically, and those that have been studied frequently were found to be polygenic in inheritance.

It is time for breeders to study the genetics of seed characters, which, along with root characteristics, have been rather neglected. In many cases we now have the background knowledge essential to undertake such genetic studies. Genetic knowledge of the seed characters may well contribute greatly to improved yield and product quality.

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