INHERITANCE OF SPEED OF GERMINATION IN SUGAR BEETS (BETA VULGARIS, L.)

Thesis for the Degree of Ph. D.
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Thomas E. Sedlmayr

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AN ABSTRACT

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ABSTRACT

With the advent of monogerm and polyploid sugar beet varieties the demand for seed having both rapid and high total germination has become urgent. The objective of this study was to determine whether speed of germination in sugar beets is controlled by genetic factors, and to what degree selection can be effective in improving this characteristic.

The seedlots were harvested from individual plants and from clones of a multigerm variety. Speed of germination was determined by germinating the seedballs in contact with a mineral nutrient solution of 10 atmospheres osmotic pressure.

Genetic-statistical methods were used to determine the degree of heritability of speed of germination. Heritability ratios were estimated on the basis of: (a) between half-sib family variances, (b) within half-sib family variances, (c) parent-offspring correlations, (d) variances within clones to estimate environmental variance, and (e) the gains obtained in a selection experiment. The heritability estimates demonstrated that speed of germination is a highly heritable trait, averaging 91 percent for the 2-, and 3-day germination data. Dominance was found to be insignificant in the inheritance of this characteristic. A sizable gain in speed of germination was obtained through mass selection. Fi hybrids of seedlings are cured to be inherited and affected speed of [illegible]mination.

The data re-confirmed that speed of germination is controlled mainly by the maternal parts of the seedcoat. Thus selection for rapid germination must be based on the original plants producing rapidly germinating seed, rather than on seedlings (embryos) of the rapidly germinating seedlots. (These seedlings represent a different generation than the maternal tissues of the seedcoat which surrounded them.) Speed of germination was improved considerably through simple mass selection, by interpollinating a small number of plants that had produced the fastest germinating seeds.

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By

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The seeds* of sugar beets possess unsatisfactory germination characteristics from the agronomic point of view. Thus it is not too surprising that 5-10 percent of the planted sugar beet acreage is lost annually, largely because of irregular or poor seedling emergence (Agricultural Statistics, 1958), and many acres have to be replanted (COKE 1947, NICHOL 1955). Unsatisfactory germination and slow field emergence also account for beet stands considerably thinner than the optimum, causing reduced yield and sucrose content (DEEM, 1946, NICHOL 1955). Although rapid emergence may not be the crucial factor every year, in some years and in certain fields it may become one of the most important factors determining yield.

With the increasing use of monogerm and polyploid sugar beet varieties, the demand for high quality seed is becoming extremely urgent. Seeds of polyploid sugar beet varieties generally have a lower germination capacity and a slower rate of germination than do the equivalent

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*The term sugar beet "seed" will refer to either monogerm or multigerm fruits. For multigerm fruits the term "seedball" will be used, for monogerm fruits the term "fruit". The sugar beet seed, as defined in the botanical terminology (frequently referred as to "germ" in the sugar beet literature), will be consequently designated as "true seed" to avoid possible confusion with fruits and seedballs.

diploids (PETO and HILL 1942, SEDIMAYR 1957). To fulfill their intended purpose, i.e. space planting to a perfect stand, seeds of monogerm varieties require better germination characteristics than do multigerm varieties. With monogerm seeds, a high percent of germination combined with rapid and uniform emergence is a virtual necessity.

Rapid emergence is especially important where low temperature, poor aeration, critically low soil moisture, or soil crusting create temporarily unfavorable environmental conditions. Slow emergence may delay prompt cultural operations, causing disadvantageous competition between the sugar beet seedlings and weeds. The severity of certain diseases may also be considerably decreased by rapid emergence and vigorous subsequent growth (AFANASIEW 1942). Since a direct correlation exists between the length of growing season and yield and also sucrose content(NUCKOLS 1946), earlier emergence provides a longer period of growth for beets, and consequently a higher sugar yield.

The agronomic value of the sugar beet seed has been determined largely on the basis of the germination capacity (percent of seedballs producing at least one seedling), or on the basis of the total number of seedlings per 100 seedballs, under certain laboratory conditions. Recently, however, more and more emphasis has been placed on rate and vigor of germination (DEXTER 1951, SNYDER 1955).

As a most obvious approach, different chemical and physical treatments of the seedball have been used to accelerate germination in sugar beets (HUNTER 1951, DEXTER and MIYAMOTO 1959). However, very little has been done to improve speed of germination or other seed

characteristics by plant breeding methods. This was a logical consequence of the generally accepted assumption that germination characteristics of the sugar beet seed are innately poor and are influenced largely by environmental factors (seedball maturity, storage conditions, temperature, etc.).

The main purpose of this thesis is to determine whether speed of germination in sugar beets is genetically controlled and to what degree selection can be effective in improving this characteristic.

LITERATURE REVIEW

A number of factors are thought to be responsible for the rapid or slow emergence of sugar beet seeds. These factors can be classified conveniently into two main groups: (1) Internal factors, inherent in the sugar beet seed (seedball or true seed) itself, and (2) External environmental factors, affecting the emergence of the planted sugar beet seed under field conditions.

Numerous external factors, such as soil moisture, soil temperature, aeration, soil structure and compaction, tillage practices, various seedbed preparation techniques, fertilizer application, crop rotation, etc. have important roles in obtaining early and uniform emergence, as have been shown by ARCHIBALD (1951), HARVEY (1958), HUNTER (1951), HUNTER and DEXTER (1951), HUNTER and ERICSSON (1952), STOUT, et al. (1957), WOFFORD (1953), WOFFORD and DEXTER (1953). Because of the scope of this thesis, we will limit the detailed review and discussion, however, solely to the internal factors.

Environmental conditions during the development and ripening of seeds can have a great influence on the subsequent germination and growth of the resulting plant (KIDD and WEST 1918). In sugar beets, PENDLETON (1954) found that under field conditions phosphate and heavy nitrogen fertilizer application increased the germination capacity of the seed by 8-10 percent. Nitrogen alone had a less pronounced effect.

In pot culture experiments, using different nutrient solutions, [illegible] (1956b) could demonstrate no detrimental effect on germination from applying excess nitrogen.

According to JAHN-DIEDRICH (1957), improved germination capacity as well as faster germination were found, when seed producing sugar beet stecklings were grown on heavy humic soils rather than on light, sandy soils. Seed production on saline soils decreased germination percentages in the subsequent generation (PUCHNER 1948). Chipping the seedstalk tips when they were about 60 cm high was also shown to be detrimental to the germination of the harvested seed (PFEIFFER, 1954).

Weather conditions during the development and ripening of seeds have been regarded as very important for good germination characteristics of the sugar beet seed (KNAPP 1958). STEDET and HOGAN (1960) demonstrated that seeds which developed and matured at approximately 25° C mean temperature were significantly more rapid in germinating than those produced at 18° C mean temperature.

Very little is known about the effect of maturity of the true seeds and fruits on germination in sugar beets, although relatively early harvest generally did not affect germination adversely (PUCHNER 1957). Rumanian researchers (ANGHEL et al. 1957) reported that sugar beet seedballs containing less than 30 percent of water must be regarded as fully ripe and would germinate immediately. Seedballs harvested with [illegible] percent water content attained their full germination capacity only after a certain period of storage. According to FISCHER et al. (1959) no significant differences could be detected in germination percentage when the seedballs had less than 60 percent water content, but germination

capacity dropped considerably (10 percent reduction) when seedballs contained 75 percent water when harvested.

In some cases insect damage, due to different Lygus species, was observed to be responsible for a reduction of germination capacity (HILLS, 1942). This occurred during the early stages of seed development (HILLS and TAYLOR 1950), but could be controlled effectively by the application of 5 percent DDT (HILLS et al. 1946).

Apparently sugar beet seeds maintain their germination capacity for a long time when stored under dry and cool conditions. Seedballs stored for 22 years around 0° F still germinated 75 percent, only about 10 percent less than the original material. The resulting seedlings showed normal vigor and the roots had normal sucrose content at harvest (PACK and OWEN 1950). At room temperature the germination capacity dropped rapidly after 15 years of storage (after 10 years 96 percent, after 15 years 59 percent, after 19 years 27 percent germinated). On the other hand, FILUTOVICZ and BEJNAR (1954) observed that seedlings from seeds older than four years emerged 1-2 days later than plants from younger seeds. Under storage conditions of high moisture and relatively low temperature the viability of the sugar beet seed is quickly diminished (PETO 1950, HUNTER 1951).

Different seed processing methods (shearing, segmenting, decortication), used to decrease mechanically the number of true seeds per seedball, can also have an influence on the germination characteristics of the sugar beet seed. TOLMAN and STOUT (1944) observed that sheared seedballs have a lower field germination capacity than the

normal ones, because 11-15 percent of the smeared seed germinated abnormally due to the exposure of the true seeds to air. Whole seedballs and segmented seedballs processed to the same size gave about the same germination percent and emergence results under comparable field conditions (BUSH 1948, SCHWERTDT et al. 1949). Decorticated and non-decorticated seedballs were reported (BUSH 1950) to have essentially the same field germination capacity, although LEACH et al. (1946) found that decorticated sugar beet seedballs germinated and emerged faster at low soil moistures. This beneficial effect was attributed to the increased water absorption of decorticated seedballs. At high soil moisture, only slight differences could be demonstrated.

Polyploid sugar beet varieties produced artificially by colchicine treatment possess generally a lower germination capacity and slower field emergence than the corresponding diploid ones (ETTO and HILL 1942, MATSUMURA 1953, SADLAYA 1957, KÖRNEY 1957, SAATL et al. 1957). Tetraploid seedballs, although larger than diploid seedballs, contain fewer viable seeds. MATSUMURA (1953) suggested that the inferior germination of polyploids is due to meiotic irregularities. SAATL et al. (1957) could not confirm this finding; they suggested instead that the relatively lower number of seed chambers and the larger number of empty seed cavities are responsible for the inferior germination of polyploids.

For several decades, intensive investigations have been made on the influence of seedball size on germination. This great interest was due to an early report of BALL (1900, cited by ARCHIBALD 1956), who claimed that larger seedballs produced not only better field germination

results, but gave rise to more vigorous plants and higher yield than the smaller seedballs. Although HULL's findings could not be confirmed (SCHMIDT 1938, BUSH and [illegible] 1946, ORLOVSKY et al. 1957), a positive correlation between seedball size and germination capacity could be demonstrated. The experiments have also clearly shown that this correlation is due mainly to the poorer germination of the smallest seedball classes (diameter smaller than 2 mm.). Very large seedballs have no advantage over middle-sized ones (HULL 1945, SAVITSKY and DEXTRASE 1956, PRICE and CARSNER 1946).

In multigerm fruits the problem of seedball size is very much complicated by the fact that larger seedballs contain proportionally more true seeds than smaller ones, and that the size of the true seeds within the same seedball is also variable (ORLOVSKY et al. 1957). According to STAHL (1957), true seeds have approximately the same germination capacity whether they come from one, two, or multiseeded seedballs. However he observed, that true seeds in the same seedball do not germinate independently, but that there exists a certain "community of fate" between their germination i.e., when seedballs containing two true seeds germinate, they produce either 2 seedlings or none in greater proportions than would be expected theoretically. This was true for laboratory as well as for field conditions. According to ORLOVSKY et al. (1957), larger true seeds produced seedlings with better vigor and heavier roots than did small seeds from the same seedball.

SAVITSKY et al. (1954, Table 2) used true breeding monogerm sugar beet lines to study the effect of fruit size on germination. While no significant differences were demonstrated between germination of the

different monogerm fruit classes, smaller fruits started to germinate somewhat earlier than large ones. They also reported that, under field conditions, large monogerm fruits gave a thinner stand than medium or small sized ones, although the opposite conclusion was drawn in the summary of the same paper on the basis of other non-presented experiments. WESTERLUND (1957) demonstrated clearly that larger monogerm fruits possessed a lower germination capacity and a slower rate of emergence than smaller fruits. Rubbing off some of the pericarp material improved germination considerably. He concluded, therefore, that the greater amount of pericarp material decreased germination capacity and seedling vigor. He suggested developing monogerm sugar beet varieties with large true seeds and with less pericarp material as a means of improving germination. Working with monogerms, MANN et al and SNYDER (1960) found also that, except for the very smallest sized fruits, speed of germination was inversely correlated to the size of fruit (including both diameter and thickness). The fruits of medium classes contained the highest proportion of viable seeds.

The relationship between seedball size and germination is further complicated by inhibitory substances present in the fruit. According to DUYK, et al. (1947), JANTYS in 1942 prepared an extract from sugar beet seedballs and recognized its inhibitory effect on the true seeds. He also gave the first analyses of the inorganic components of these extracts. FROSCHEL (1939) demonstrated that the water soluble inhibitor(s) are not specific to the species, but retarded the germination of at least 29 other species as well.

Independent of JANTYS and FROSCHEL, TOLMAN and STOUT (1920)

proved conclusively that the corky material of the sugar beet seedball (pericarp and perianth) contains water soluble substances retarding germination and sometimes even killing the radicles of the seedlings in laboratory tests. Extract from the seedballs of slowly germinating seed-lots retarded the germination of the true sugar beet seeds in comparison with true seeds germinated in water. The great differences in the percent germination of seedballs of various varieties or seed-lots almost completely disappeared when true seeds were used as a basis of comparison. They concluded that the inhibitory substances, which were present in the seedball, must have been responsible for the differences in speed and total germination, at least in laboratory tests.

They suggested also that the water soluble germination inhibitors vary not only with varieties, but are influenced by climate, soil and seedball maturity as well. TOLMAN and STOUT (1940) assumed that the toxic substances interfere especially with the forecast of potential field germination as measured by a laboratory test, because under field conditions the absorptive power of the soil removes these substances. On this basis they recommended the washing of seedballs in running water before testing them on a blotter for germination (STOUT and TOLMAN 1941b). This procedure also decreased the percentage of "browned seedlings" (injured radicles ?) (ABBASOW 1948). According to the official seed testing methods of the United States (TESTING AGRICULTURAL AND VEGETABLE SEEDS, 1952), sugar beet seedballs should be soaked for 2 hours and washed in running water to remove water soluble inhibitors, which may interfere with the laboratory germination test on blotter.

Very confusing results have been published in the literature on

the nature of the presumed inhibitory substances. STOUT and TOLMAN (1941a) claimed that in dry seedballs the germination is inhibited largely by the toxic action of free ammonia, which is liberated from nitrogenous substances present in the seedball by enzymatic hydrolysis. However, in fresh seeds they suggested osmotic pressure to account for germination inhibition. KERN (1953), using garden beet seed, also claimed that free ammonia acts as an inhibitor during germination; but he found that the ammonia was formed mainly through the action of bacteria. Therefore, he concluded that this type of germination inhibition takes place only in laboratory dishes, but not in the field and may be prevented simply by the use of seed disinfectants.

DUYM, et al. (1947) reported that osmotic pressure, due to the presence of inorganic substances in the seedball, retarded germination, but they were unable to obtain any specific substance, which inhibited germination.

On the other hand, as early as 1940, GILLIS found a strikingly high concentration of oxalate ions in the beet seedball extracts. He demonstrated an inhibitory effect of an 0.03 normal potassium oxalate solution on germination (cited by DUYM et al. 1947). Independent of GILLIS, NAKINO and MIYAMOTO (1954) found that the most remarkable inhibitory substance in the sugar beet seedball was water soluble oxalate. This was demonstrated by MIYAMOTO (1957) for both dry and fresh seedballs. He claimed that only 50 mg percent oxalate is toxic for the germination of the sugar beet seed, while he found that the seedball of the investigated diploid and polyploid varieties contain about 2 percent oxalate (40 times higher than the toxic dose). Seedballs of diploid and

polyploid varieties did not differ significantly in oxalic acid content.

DE KOCK, et al. (1950, 1952) obtained from the water extract of the beet seedball an unsaturated yellow oil, which acted as a powerful germination inhibitor when tested on both sugar beet and other seeds. Although FRÖSCHEL (1955) admitted that the germination inhibition in Beta is largely osmotic in nature, nevertheless he could demonstrate that the demineralizated extracts of the seedballs also inhibit germination. He concluded that at least some of the inhibitory effect, therefore, must be attributed to a specific organic substance.

By the use of paper- and electrochromatographical methods MASSART (1956, 1957) found that p-oxybenzoic, vanillic, p-oxycinnamic and ferulic acids in sugar beet seedball extracts inhibit germination. He also isolated ferulic and vanillic acid from the fruits of the other species of Chenopodiaceae. Recently, similar results have been reported by Hungarian investigators (KÖVES and VARGA 1959), who found p-oxybenzoic, ferulic, p-coumaric, caffeic and salicylic acids in the pericarps of sugar beet seedballs. They also recovered these compounds from numerous other fresh fruits, as well.

On the other hand, SAYDA (1960a) presented evidence that, in some cases, sugar beet seedballs may stimulate germination and early seedling growth.

Although it is generally assumed that inhibitory substances are important in preventing a premature germination of the seed, nothing definitive is known concerning the importance or role of the presumed germination inhibitors in the sugar beet seedball. According to DE KOCK, et al. (1952) the presence of a water soluble germination inhibitor in the

sugar beet seedball may be advantageous in preventing germination until the soil has attained a sufficient moisture content, by which time the inhibitor would be washed out. On the other hand, they speculated that the function of the inhibitor may be to maintain the seed only partially dormant. The wide distribution of certain types of germination inhibitors, as those demonstrated by HABART (1957) and KÖVES and VARGA (1954) would suggest that the presence of germination inhibitors in fruits is a general phenomenon, which may have an essential role in the biology of the plant.

The presumed importance of germination inhibitors has overshadowed somewhat the long recognized fact that the physical properties of the seedball itself may hinder germination in the cultivated sugar beets. The tough woody pericarp and the tightness of the seedcaps were suggested as the cause of non-germination in certain Beta subspecies (STEWART 1950, GEORGIA 1957). From this it is logical to suspect that in Beta vulgaris similar difficulties may exist. SAVDAN (1955) in a search for factors responsible for the delayed germination of sugar beet seeds, observed marked differences between and within varieties in the thickness of the dense inner layers of the seedballs, as well as in the tightness of the seedcaps. He also demonstrated that notched seedballs have a faster germination than the non-notched seedballs (SAVDAN 1956a). On the other hand, BARTL et al. (1957) found no differences in the structure of the seedball or in the tightness of the seedcaps between the seed of polyploid and diploid sugar beet varieties.

The generally recognized beneficial effect of concentrated acid treatments on the germination of sugar beet seeds can be regarded also as an indirect evidence for the physical hindrance of the seedball.

Germination could be significantly improved by concentrated H_2SO_4 treatment, which corroded away much of the hard pericarp material and increased its permeability (HENLEY and WOODMAN 1930, ANONYM 1931, GARNER and SANDERS 1932). Concentrated acid treatments were shown to have also a great effect on the loosening of the seedcaps, which are cemented to the seedballs by hemi-cellulose (LACKEY 1943). Due to the above effects, the concentrated acid treatments increased germination capacity, hastened emergence, and produced a greater plant population at harvest, which sometimes increased sugar yield (FALLADA and GREISENEGGER 1916, GRACANIN 1928, HENLEY and WOODMAN 1930, ANONYM 1931, GARNER and SANDERS 1932, BARTL et al. 1957). However, according to TOLMAN and STOUT (1940), the beneficial effect of concentrated acid treatments may also be explained by the removal of an inhibitory substance from the seedballs.

Besides concentrated acid treatments, which are somewhat dangerous to use in the practice, a great variety of seed treatments have been proposed in an attempt to stimulate sugar beet seed germination. MIYAMOTO (1957) found that soaking the sugar beet seedballs in water solutions of different inorganic and organic salts increased significantly the germination capacity and speed of germination in soil tests in the laboratory. A 1:1 mixture of M/1000 $Hg(CH_3COO)_2$ and 0.5 percent $MgSO_4$ gave the best results, especially in the case of a tetraploid sugar beet variety. MIYAMOTO (1957) assumed that this effect was due to the inactivation of the oxalic acid content of the seedballs. MÁNDY and PÁL (1958) reported that the application of 0.25-1.00 percent KNO_3 solution improved considerably the germination capacity of polyploid sugar beet seed. But generally it was found that soaking sugar beet seedballs in water alone

was as effective as various inorganic salt solutions in increasing or hastening the germination of the sugar beet seed (TOLLENAAR and SMIT 1940, SATO-ICHI 1947, HUNTER 1951). However, in field experiments no significant beneficial effect of the soaking could be demonstrated when the seedballs were planted dry. Soaking wet seedballs increased the rate of emergence considerably (HUNTER 1951, HUNTER and DEXTER 1951).

Treating the seedballs with different hormones had no beneficial effect on germination, seedling emergence, or seedling vigor (DEXTER 1942, 1943; STOUT and TOLLENAAR 1944). Gibberellic acid treatment of the seedballs similarly had no effect on germination, vigor or yield in sugar beets (DEXTER 1958, PETERSON 1958, SAVITSKY 1959a).

Coating the surface of sugar beet seedballs with hydrophilic colloids (gelatin, agar, and "algin") accelerated water uptake from sand and accelerated emergence under field conditions (MIYAMOTO 1959, DEXTER and MIYAMOTO 1959, MIYAMOTO and DEXTER 1960).

Relatively few attempts have been made to improve the germination of the sugar beet seed by plant breeding methods. This is not too surprising, since almost no definitive evidence exists for assuming that germination characters in sugar beets are genetically controlled.

WOOD, et al. (1950) and WOOD (1952) have shown that under low temperature conditions (2-3° C) varieties differ with respect to the ability of their seed to germinate. By simple mass selection germination was improved 20-30 percent, showing that sufficient genetic variability existed between and within lines of sugar beets to permit selection for this characteristic. Differences between varieties and inbred lines,

which had the same total germination and speed of germination at room temperature, were noted when they were kept around 2-3° C temperature. On the basis of selection experiments SMITH (1958) concluded that under low temperature conditions both rate of germination and vigor of seedlings seem to be heritable traits.

MATSUURA (1955) and BAHL et al. (1957) demonstrated that the inferior germination characteristics of polyploid sugar beet seed can be improved by selection and that germination similar to the seed of diploid varieties can be obtained.

SNYDER observed large differences in rate of germination of seeds of different varieties (1945) and in emergence of such seedlings from sand (1954) or soil (1957). There was great difference between seedballs harvested from individual plants of the same variety when germinated in contact with nutrient solution of 10.1 atmospheres osmotic pressure (SNYDER 1957). He has suggested that the major factors contributing to speed of germination reside in the maternal tissues surrounding the true seed (SNYDER 1960a).

SNYDER (1960b) selected rapid and slow germinating seedlings from the seed of a broad-base, open-pollinated variety. Plants within the two groups were allowed to inter-pollinate and seedballs from 72 of the rapid and 72 of the slow germinator plants were compared for speed of germination using a liquid-contact germination technique. On the average, the seed of the rapid germinating plants showed somewhat faster germination than those from the slow germinating plants. On the basis of these limited results he suggested that genetic factors may be responsible for the observed difference between selection groups.

Using an inositol solution, which produced about 10 atmospheres osmotic pressure, DOXTATOR and FINK et al (1958) made selections and re-selections for early sprouting and late sprouting seedlings in four commercial sugar beet varieties. The early sprouting reselections from all the four varieties germinated significantly faster than the late ones, when tested in inositol solution. Due to the improved speed of germination, the yield in one out of two years increased significantly in comparison to the original parental varieties (DOXTATOR, et al. 1958).

To avoid repetition, literature citations pertaining to the applied techniques are given in the appropriate sections.

MATERIALS AND METHODS

<u>Germination methodology</u>:

A laboratory germination technique ([illegible]) was used throughout this investigation to determine speed of germination of sugar beet seeds. The essential feature of this method is that sugar beet seedballs are germinated in contact with a salt solution. Due to the osmotic pressure of this solution, germination is considerably delayed, thus making the detection of differences in speed of germination easier ([illegible] 1955). (Hereafter in this paper the method will be designated as the "liquid-contact" method of germination.)

FRYXELL (1954) summarized the early European investigations, in which osmotic solutions were employed successfully. More recently, similar methods have been used to improve germination and emergence of alfalfa ([illegible] and [illegible] (1959), of grasses ([illegible] 1957), of wheat ([illegible] and [illegible] 1958), and of sugar beets ([illegible], [illegible] and [illegible] 1958). [illegible] (1930), [illegible] (1957) and [illegible] ([illegible]) further reported that by germinating seeds in salt or sugar solutions and selecting the best seedlings in cold and drought hardiness, seedling vigor, and yield were also indirectly improved.

[illegible] (1957) found very good agreement between emergence from soil in the greenhouse and speed of emergence as determined by the liquid-contact method. According to [illegible] (1957), "this technique

appears to offer a reliable test for selecting seedlots, which will emerge rapidly when planted in soil. It also provides a greater degree of control of environmental conditions during germination than would be possible in soils."

In the liquid-contact method (SAYLOR 1965), the seeds were germinated in closed plastic boxes. In each box a piece of saran screen was supported on five pieces of glass tubing. Twenty seedballs were placed in each quarter of the box in contact with the surface of approximately 180 milliliter of a balanced mineral nutrient solution (Figure 1.). The molar composition of the nutrient solution was as follows: $CaCl_2.2H_2O$, 0.0255; $Ca(NO_3).4H_2O$, 0.0240; KCl, 0.0445; KH_2PO_4, 0.0744; $MgSO_4.7H_2O$, 0.0240; $NaSO_4.10H_2O$, 0.0295. The osmotic pressure of this solution is 10.1 atmospheres. To avoid variation in germination within and between boxes, the level of the solution was carefully adjusted to maintain uniform contact with the seedballs. (The level of the liquid is a critical factor in this technique.)

For all experiments uniformly ripe seedballs (straw color prior to harvesting) were used. After harvest the seedballs were immediately dried in a plant drier at 30-35° C, and threshed on a combination thresher and drier designated to handle small samples (WILLIAMS and STANFORD 1943). After threshing the seedballs were stored at room conditions for at least 8 weeks before they were tested for germination.

Unprocessed seedballs were used in all the germination studies. The seedballs were not treated with a fungicide. ALLEN and FIELD (1958) reported that larger seedballs were less affected by osmotic solutions than smaller ones. Therefore, only seedballs were used

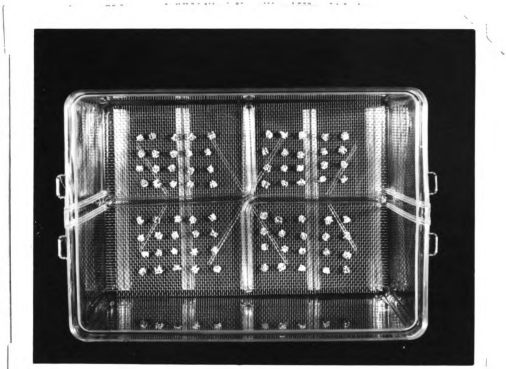

Figure 1.

Top view of plastic box used in liquid contact germination technique, showing arrangement of seedballs, saran screen, and glass rods supporting the screen. The glass tubings on top of the screen separates four different seedlots within a box. Each seedlot in a germination box is represented by 20 seedballs.

11/64 - 13/64 inch (4.4 - 5.1 mm) diameter were used. Total germination percent was also determined for each seedlot, so that those with poor viability (less than 85 percent germination capacity) could be excluded from the results.

All germination experiments, except as noted, were conducted at room temperature (22-25° C). Germination counts were made 48, 72, and 100 hours after the seeds were placed in contact with the nutrient solution. A seedball was considered as germinated when the radicle of at least one true seed extended beyond its seedcoat. This could be decided only by a careful examination of each seedball, and often only by the removal of the loose seedcap.

Genetic-statistical methods:

JOHANNSEN (1909) demonstrated that both environmental and genetic factors may contribute to the observed phenotypic variation between the individuals of a segregating population. FISHER (1918) found it useful to express this relationship in the following linear form: $\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{GE}^2$; where σ_P^2 represents the total observed phenotypic variance, σ_G^2 is the part of the phenotypic variance due to genetic effects, σ_E^2 is the part of the phenotypic variance due to environmental factors, and σ_{GE}^2 is the variance due to genotype-environmental interactions. FISHER (1918) further partitioned the genetic variance into three components: (1) an additive genetic part, associated with the average effects of genes (σ_D^2), (2) a dominance part, arising from the interactions of alleles (σ_H^2), (3) and an epistatic part, attributable to the interactions of non-alleles (σ_I^2). He also showed how additive genetic and dominance variance contribute to correlations among relatives in randomly breeding populations.

MATHER (1949) pointed out the difference between fixable and unfixable genetic variance. Unfixable additive genetic variance arises due to the presence of dominance when the allelic gene frequencies are not equal to one-half. Recently, epistatic variance has been further partitioned (COCHERHAM 1954, KEMPTHORNE 1954) into factorial components (additive x additive, additive x dominance, dominance x dominance, etc. interactions) to estimate its importance compared to additive genetic and dominance variance.

LUSH and PAIGE (1940) proposed the ratio of the additive genetic component of variance (σ^2_D) to the total phenotypic variance (σ^2_P), as a measure of the degree of heritability. Later, LUSH (1943) referred to this as to "heritability in the narrow sense"; whereas for the ratio of the total genetic variance ($\sigma^2_G = \sigma^2_D + \sigma^2_H + \sigma^2_I$) to the total phenotypic variance (σ^2_P) he used the term "heritability in the broad sense".

Heritability values are expressed usually in percent. If the estimated heritability value (h^2) is high (close to 100 percent), the observed variability must be largely due to genetic factors. If the heritability value is low, the observed variation is mainly due to environmental factors, and little gain can be expected for the given characteristic from selection in the particular population.

In the way heritability is defined, it is implied that - strictly speaking - any h^2 estimate of a certain characteristic is valid only for a particular population and for a specific environment. Also, at present no satisfactory method is available to attach confidence intervals for heritability estimates (KEMPTHORNE 1957, HANSON 1959). Despite these shortcomings, heritability estimates can give the plant breeder very valuable information to predict the gain from selection, and to determine the most effective method of improvement in quantitative characteristics. This is especially true where, for the same trait, more than one h^2 value can be estimated using different populations and different statistical techniques.

Several different methods have been used to calculate heritability values for a certain characteristic. These methods vary according to the applied statistical techniques (regressions, covariances, variance

components, etc.) and according to the nature of the population, from which the data were used to estimate heritability (inbred lines, randomly breeding populations, etc.). With the exception of one method (estimating h^2 on the basis of a selection experiment), all estimation methods are based on relationships among relatives (parents contrasted with offsprings, half-sibs, F_2's, F_3's, etc.). No attempt is made in this thesis to review all the existing methods of obtaining heritability estimates.

The sugar beet is a cross-pollinating crop with natural barriers to self-fertilization and controlled crossing. Therefore, the classical method of estimating variance components (MATHER 1949) could not be applied directly. Instead of this it was assumed that a commercial sugar beet variety is a randomly interbreeding (panmictic) population. Genetic variances and heritability ratios were estimated (Experiment B) from such a population using parent-offspring regressions and between and within (maternal) half-sib relationships. The parent-offspring regressions and the between half-sib family variances can contain only additive genetic variances (σ^2_D) and some epistatic variance (σ^2_I) (COCKERHAM 1956, KEMPTHORNE 1957); the within half-sib family variances may contain a certain amount of dominance variance (σ^2_H) as well (HUSH 1948, 1949, MATHER 1949). Following FREY and HORNER (1957), instead of parent-offspring regressions parent-offspring correlation coefficients were used to estimate heritability.

As a different method to estimate heritability for speed of germination, the variance between clonal plants was used to estimate the environmental variance (Experiment C). Comparing the variance obtained between these genetically uniform plants with the total variance

between the plants of segregating populations, heritability values could be estimated for those populations. However, only total genetic variances ($\sigma^2_G = \sigma^2_D + \sigma^2_H + \sigma^2_I$) can be estimated by this method, and the calculated h^2 values will correspond to heritability in the broad sense.

As another method, h^2 ratios were estimated on the basis of a selection experiment (Experiment D). To calculate h^2, the gain from selection was divided by the selection differential (Lush 1949). In this case, selection was made in the two opposite directions, thus making the comparison between the means of the two selected groups and the original population unnecessary. To estimate heritability by this method, the absolute difference between the means of the two selected groups after interpollination (polycross) was divided by the absolute difference between the means of the original two selected populations.

EXPERIMENTAL RESULTS

Experiment A

To determine whether the large differences observed in speed of germination between seedlots* are due to factors residing in the maternal tissues, or to factors present in the true seed itself, the germination of seeds in seedballs and true seeds of the same seedlot were compared using the liquid-contact germination technique.

The seedlots (harvested in 1957) used in this experiment came from individually harvested plants of US 401, a commercial, multigerm sugar beet variety. The seedlots were previously evaluated for speed of germination by Snyder. Out of this material, two extremely slow (118 and 123) and two rapid (528 and 547) germinating seedlots were chosen for the experiment. From each of the four seedlots, 80 true seeds with the brown outer seedcoat (testa) and 80 true seeds without the brown outer seedcoat were obtained. (The true seeds were removed from the seedballs with the aid of a fingernail clipper.)

The experiment was arranged as a split-split plot experiment, the main plots being the four germination counts (made after 24, 48,

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*The term "seedlot" will refer to seeds harvested from a single plant.

72, and 120 hours); the subplots, the three different seed types (seedballs, true seeds with brown seedcoats, true seeds without brown seedcoats); and the sub-subplots, the four different seedlots. Seed types within replications and seedlots within seed types (germination boxes) were completely randomized. One basic unit (sub-subplot) consisted of either 20 seedballs or [illegible] true seeds, and was replicated four times.

The germination results, expressed in percent germination, are shown in Table 1. The analysis of variance data are presented in Table 2. Least significance differences (LSD values) were calculated to test the differences between seedlots within a certain seed type (Table 1).

The germination percentages of seeds embedded in seedballs differed greatly between seedlots, but for the excised true seeds (with or without the brown outer seedcoat) the germination between seedlots was similar (Table 1). For true seeds the germination differences between seedlots were not significant (Table 2), although it is possible that a more elaborate experiment might have revealed small real differences. Similarly, no significant differences were found between the germination of the true seeds with and without the brown seedcoats (Table 2).

The data also indicate that the surrounding maternal tissues may in some cases hinder and in other cases stimulate the germination of the true seeds. However, this observation cannot be valid, since the technique compares the germination of the true seeds with the fastest germinating seed in the seedball.

These results confirm the earlier findings of TOL[illegible] and STO[illegible]T (19[illegible]) and [illegible] (19[illegible]), who found that in sugar beets the rate of

TABLE 1. PERCENT GERMINATION VALUES OF SEEDS IN SEEDBALLS AND EXCISED TRUE SEEDS OF FOUR SEEDLOTS OF US 401. (EXPERIMENT A)

SEED LOT	SPEED OF GERMINATION	Germination of seeds in seedballs after 24 hours	48 hours	72 hours	120 hours	Germination of true seeds with brown seedcoat after 24 hours	48 hours	72 hours	120 hours	Germination of true seeds without brown seedcoat after 24 hours	48 hours	72 hours	120 hours
119	slow	0.00	16.25	47.50	61.25	5.00	58.75	78.75	88.75	0.00	62.50	80.00	88.75
123	slow	0.00	7.50	32.50	43.75	1.25	60.00	85.25	91.25	0.25	68.75	82.75	87.50
519	rapid	21.25	87.50	95.00	96.25	2.50	60.00	81.25	90.00	1.25	58.75	77.50	87.50
553	rapid	17.50	92.50	97.50	98.75	3.75	63.75	86.25	93.75	0.00	65.00	91.25	92.50

LSD 5% between seedlots within seedtypes and hours	7.60	NS[1]	NS
LSD 1% between seedlots within seedtypes and hours	10.10	NS	NS

Percent germination values are based on 80 seedballs or true seeds.

[1] No significant differences between seedlots according to F-test (Table 2).

TABLE 2. ANALYSIS OF VARIANCE FOR THE GERMINATION DATA OF EXPERIMENT A.

S O U R C E	D. F.		M. S.	F
Replications	3		6.40	
Germination counts	3		2503.20	785.41**
Error (a)	9		3.19	
Seed types+ within germination counts	8		32.43	8.91**
Seed type 2 versus seed type 3		4	1.09	
Seed type 1 versus seed type 2 & 3		4	48.79	12.20**
Error (b)	24		3.64	
Seedlots within germination counts and within seed types	36		54.19	45.92**
Within seed type 1		12	159.97	135.57**
Within seed type 2		12	1.04	
Within seed type 3		12	1.56	1.32
Error (c)	108		1.18	
Total	191			

+Seed type 1 refers to seeds in seedballs
Seed type 2 refers to excised true seeds with brown outer seedcoat
Seed type 3 refers to excised true seeds without brown outer seedcoat

**Significant at 1% level

germination was mainly influenced by factors present in the maternal tissues of the seedball. Therefore, for the purpose of this study, speed of germination will be considered to be a typical maternal characteristic.

Experiment 3

Seeds from 518 plants of the broad-base, multigerm sugar beet variety, US 401, were harvested in 1957. In the fall of 1957, Snyder tested the seedlots individually for speed of germination, using 20 seedballs per seedlot. Of the 518 seedlots, 60 seedlots with good total germination capacity were randomly selected for further studies.

Ten seedballs taken at random from each of the 60 seedlots (which will be designated as "half-sib families") were planted in pots in the greenhouse in September 1958. Plants were allowed to grow for three month, after which they were photothermally inducted for 10 weeks at 50° F (10° C) mean temperature and under continuous light (GASKILL 1952) in a plastic induction chamber (HOGAN 1960) in the greenhouse. After induction the plants were left for post-induction (66°F mean temperature, continuous light) in the same chamber, until they were transplanted to the field. All 600 plants of the 60 half-sib families showed good growth and vigor. Before transplanting them to the field, the plants were distributed according to their relative size into two equal groups of five plants, each group being planted as a separate field replication. The first replication was planted on May 5, the second on May 6, 1959. Within a field replication the plants were distributed at random, being planted in rows 3 feet (90 cm) apart, and spaced 2 feet (60 cm.) apart within the row.

All plants showed excellent seedstalk and seed development.

Before harvest 1-2 percent of the plants were lodged off and had to be discarded. Nevertheless for each of the 60 half-sib families in each of the two field replications, four healthy plants were available at harvest. Harvesting was made individually as the grain ripened, that is between July 19 and August 5.

After drying, threshing, cleaning, and sizing of the seeds the percent of lost seedcaps* was determined (see Table 14). A test of germination for all 480 (60 x 8) seedlots was tested in the late fall of 1959. To secure uniform conditions, the seedballs were germinated in a temperature control chamber at a constant temperature of 78±1° F (25° C). For each seedlot, two germination replications were used, each consisting of 50 seedballs.

From the germination data of the experiment it was possible to calculate heritability estimates for speed of germination in two different ways, i. e. from half-sib family means and from plants within half-sib families. Variance components were estimated, in the first case, from the family mean squares and from the families x field replications mean squares; in the second case, from the plants within families within field replications mean squares, and from the plants x germination replications mean squares (Table 3). Differences, significant at the 1% level, were obtained between families, and between plants within families within field replications (Table 3).

The genetic and environmental components of variance, assuming

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*The term "percent of lost seedcaps" refers to the percent of seedballs in a seedlot that had at least one of their seedcaps (covering the true seed) missing.

TABLE 3. ANALYSIS OF VARIANCE FOR THE GERMINATION DATA OF 480 SEEDLOTS OF US 401. (EXPERIMENT B)

SOURCE		2-day germination		3-day germination		5-day germination	
	D. F.	M. S.	F	M. S.	F	M. S.	F
Families	59	122.60	4.02**	76.90	3.77**	35.46	3.17**
Families x Field Replications	59	30.48		20.40		11.17	
Plants within Families and Field Reps.	360	37.90	13.88**	23.59	7.94**	15.75	6.40**
Plants within x Germination Replications	360	2.73		2.97		2.46	
Total	959						

**Significant at 1% level

perfect cross pollination in the original population, may be estimated (GATHER 1949, COCKERHAM 1956) as follows:

Between half-sib family variance (σ^2_F) = 1/8 D

Within half-sib family variance (σ^2_W) = 3/8 D + 1/4 H

Families x field replications variance (σ^2_1) = E_1

Plants x germination replications variance (σ^2_2) = E_2 ; where

D is the additive genetic variance

H is the dominance variance

E_1 is the environmental variance for family means

E_2 is the environmental variance for individual plants

The variance component σ^2_F was estimated as follows (Table 3):

$$\sigma^2_F = \frac{\text{(Between Families M.S.)} - \text{(Families x Field Replications M.S.)}}{r} ;$$

where r is the number of field replications.

The variance component σ^2_W was estimated as follows:

$$\sigma^2_W = \frac{\text{(Between Plants within Families M.S.)} - \text{Families x Germ. Reps, M.S.)}}{n};$$

where n is the number of germination replications.

The environmental variance for family means (σ^2_1) was estimated (FREY and HORNER 1955, JOGI 1966) as follows:

$$\sigma^2_1 = \frac{\text{(Families x Field Replications M.S.)}}{r}$$

The environmental variance for individual plants within families (σ^2_2) was estimated as follows:

$$\sigma^2_2 = \frac{\text{(Plants within Families x germination replications M.S.)}}{n}$$

The heritability ratio for between half-sib family means (Table 4) was estimated by means of the following formula:

$$h_a^2 = \frac{\sigma_F^2}{\sigma_1^2 + \sigma_F^2}$$

The heritability ratio for plants within half-sib families (Table 5) was estimated using the following formula:

$$h_a^2 = \frac{\sigma_W^2}{\sigma_2^2 + \sigma_W^2}$$

Heritability values are also given in relation to the original randomly interbreeding population (US 401), using both between and within family variances to estimate genetic variance components, and assuming that linkage and epistasis do not play an important role. In this case, heritability ratios may be estimated from between family variances as follows:

$$h_b^2 = \frac{1/2\ D}{1/2\ D + E} = \frac{4\ \sigma_F^2}{4\ \sigma_F^2 + \sigma_1^2}$$

and from within family variances as follows:

$$h_b^2 = \frac{1/2\ D + 1/3\ H}{1/2\ D + 1/3\ H + E} = \frac{4/3\ \sigma_W^2}{4/3\ \sigma_W^2 + \sigma_2^2}$$

The h^2 values estimated on the basis of between family variances correspond to heritability in the narrow sense; while h^2 values estimated on the basis of within family variances correspond to heritability in the broad sense.

E, 1/8 D, and heritability percentages for the 2-, 3-, and 5-day germination data, estimated by using half-sib family variances, are given

TABLE 4. CALCULATED VALUES OF E*, 1/8 D**, AND HERITABILITY PERCENTAGES FOR 2-DAY, 3-DAY, AND 5-DAY GERMINATION DATA USING BETWEEN HALF-SIB FAMILY VARIANCES.

	E	1/8 D	h_a^2 #	h_b^2 ##
2-day germination	15.24	46.05	75.1	94.4
3-day germination	10.20	28.45	73.6	91.7
5-day germination	5.58	12.15	68.5	88.8

* E is the estimate of the environmental variance

** 1/8 D is the estimate of the additive-genetic variance

\# h_a^2 is the heritability percentage calculated for between half-sib families, according to the formula (1/8 D)/(1/8 D + E)

\#\# h_b^2 is the heritability percentage calculated for the original randomly interbreeding population (US 401) according to the formula (1/2 D)/(1/2 D + E)

TABLE 5. CALCULATED VALUES OF E*, (3/8 D + 1/4 H)**, AND HERITABILITY PERCENTAGES FOR 2-DAY, 3-DAY, AND 5-DAY GERMINATION DATA USING WITHIN HALF-SIB FAMILY VARIANCES.

	E	3/8 D + 1/4 H	h_a^2 #	h_b^2 ##
2-day germination	1.37	17.59	92.3	94.5
3-day germination	1.49	10.31	87.4	90.2
5-day germination	1.23	6.15	83.3	87.0

* E is the estimate of environmental variance

** (3/8 D + 1/4 H) is the joint estimate of additive and dominance variance

\# h_a^2 is the heritability percentage (in the broad sense) calculated for within half-sib families, according to the formula (3/8 D + 1/4 H) / (3/8 D + 1/4 H + E)

\#\# h_b^2 is the heritability percentage (in the broad sense) calculated for the original randomly interbreeding population (US 401), according to the formula (1/2 D + 1/3 H) / (1/2 D + 1/3 H + E)

in Table 4. E, (3/8 D + 1/4 H), and heritability percentages, estimated by using within half-sib family variances, are presented in Table 5.

To estimate heritability using the parent-offspring relationship, the mean germination values of the 60 (maternal) half-sib families in 1959 were correlated with the germination values of the 60 mother plants, from which the half-sib families originated (Table 6). These parent-offspring correlations correspond to parent-offspring regressions expressed in standard deviation units (FALCONER and MORRIS 1955). Assuming perfect cross pollination in the original population, heritability estimates may be obtained for the original US 401 population by multiplying the estimated r values by two (Table 6). These heritability values may contain a certain amount of epistatic variance (COCKERHAM 1956), but they will not contain any dominance variance (IMSH 1943, MATHER 1949).

TABLE 6. PARENT-OFFSPRING CORRELATION COEFFICIENTS AND HERITABILITY PERCENTAGES FOR 2-DAY, 3-DAY, AND 5-DAY GERMINATION DATA USED TO PROGENIES FROM US 401.

	r value	h^2_{b} %
2-day germination	0.465**	93.0
3-day germination	0.451**	90.2
5-day germination	0.287*	57.4

*Significant at 5% level

**Significant at 1% level

%Heritability for the original randomly interbreeding population (US 401) calculated by multiplying the r values by 2, and expressing heritability in percentage.

Experiment C

In April 1958, controlled crosses were made in the greenhouse between certain plants from the sugar beet variety, US 401, which produced either extremely slow or extremely rapid germinating seed in 1957. This was possible by using the original seed-producing roots along with some clones of these plants, which Snyder had propagated in the greenhouse.

The plants were photothermally induced in the winter of 1957-1958 and produced seedstalks in early spring. The plants were paired according to their germination characteristics and their hypocotyl color. Control of pollination was accomplished by means of white paper craft bags. The plants with the rapid germination characteristic (528, 547) had dominant-red hypocotyls, and the plants with the slow germination characteristic (318, 357) had recessive-green hypocotyls. Hence the hybrid plants (318 x 547 and 357 x 528) could be identified by hypocotyl color. After the seed obtained from the plants with green hypocotyls was germinated, the seedlings with green hypocotyls were eliminated and only true hybrid plants were saved for further propagation. Reciprocal crosses (where the mother plant had the rapid germination characteristic) could not be performed, because no plants were available showing slow seed germination and having red hypocotyls.

The true hybrid seedlings were planted in separate pots in June 1958. Some of these seedlings were photothermally induced in an attempt to produce second and backcross generations. However, the

crosses made in November 1958 failed to produce any viable seed.

For each of the four genetically different plants, used in the crosses, clones or vegetative cuttings were made from the seedstalks (CHILDS 1941). The clones were kept for two months in a mist chamber (HILGARD 1960), and then for four weeks under short photoperiod (8 hours light daily), to promote good rooting and vegetative development.

The clones and the remaining hybrid plants were inducted photothermally along with the 48 plants of a rapid and 48 plants of a slow germinating polycross population (Experiment D) in the winter of 1958-1959. The plants were transplanted in the field on May 7, 1959.

The field experiment was arranged as a modified randomized complete block design (POWERS 1955), in that two entries ("slow" and "rapid" polycross) appeared four times in each block, two entries (318 x 547 and 357 x 528 crosses) appeared twice in each block, and four entries (the four clonal populations) appeared only once in each block. All plots (entries and duplicate entries) were distributed at random in each of the two field replications. A plot consisted of 6-8 plants, from which only the seed of the 6 most healthy plants was used in the germination experiments.

The plants were planted in rows 3 feet (90 cm) apart and were spaced 2 feet (60 cm) apart within the row. Fairly uniform seedstalk development and blooming was obtained for the different populations. Seedballs were harvested at approximately the same stage of ripeness, between July 19 and August 5.

After drying, threshing, cleaning, sizing of the seedballs, and determining the percent of lost seedcoats, speed of germination for

all 192 seedlots (32 plots x 6 parents) was tested in the fall of 1969. Each seedlot was tested in two germination replications. A replication included 20 seedballs from each seedlot.

Means, total variances, and genetic variances for 4-, 5-, and 6-day germination data and for different populations are listed in Tables 7, 8, and 9. The four clonal populations provided an excellent measure of the environmental variability, since plants within a clone are genetically identical and can contain no genetic variability. Since the between plant variances of the four clonal populations were similar, they were pooled to provide a general estimate for the environmental variance in this experiment.

The genetic variances for the segregating populations (Table 7, 8, and 9) were obtained by subtracting the pooled environmental variance (estimated from the total variance between clonal plants) from the total variance of the segregating populations. By comparing genetic and total variances, heritability estimates (in the broad sense) may be obtained as follows:

$$h^2 = \frac{\sigma_G^2}{\sigma_P^2} \quad ; \text{ where}$$

σ_P^2 is the total observed phenotypic variance,

σ_G^2 is the genetic variance, estimated from the difference between the total phenotypic variance and the environmental variance.

Heritability values calculated according to this formula and expressed in percent are shown in Table 7, 8, and 9.

The actual and theoretically expected mean germination values of

TABLE 7. MEANS, TOTAL PHENOTYPIC VARIANCES, AND GENETIC VARIANCES FOR 2-DAY GERMINATION DATA OF DIFFERENT NON-SEGREGATING AND SEGREGATING POPULATIONS FROM US 40L.

POPULATION	NO. OF PLANTS	MEAN %	VARIANCE Total	VARIANCE Genetic	HERITABILITY
NON-SEGREGATING POPULATIONS (CLONES):					
Clone No. germination type					
218 slow	12	16.46			
257 slow	12	12.50	4.80		
528 rapid	12	93.12	(pooled)		
547 rapid	12	87.08			
SEGREGATING POPULATIONS:					
218 x 547 cross	24	49.49	23.40	18.60	79.5
257 x 528 cross	24	41.04	43.28	38.48	88.8
Polycross of slow selection*	48	30.31	52.17	48.37	91.0
Polycross of rapid selection*	48	76.25	30.10	25.30	84.1
LSD at 5% level between population means		8.96			
LSD at 1% level between population means		13.01			

* obtained by interpollination of 9 of the slowest or 9 of the fastest germinating plants from a population of US 40L.

TABLE 8. MEANS, TOTAL PHENOTYPIC VARIANCES, AND GENETIC VARIANCES FOR 3-DAY GERMINATION DATA OF DIFFERENT NON-SEGREGATING AND SEGREGATING POPULATIONS FROM US 401.

POPULATION	NO. OF PLANTS	MEAN %	VARIANCE Total	VARIANCE Genetic	HERITABILITY
NON-SEGREGATING POPULATIONS (CLONES):					
Clone No. germination type					
318 slow	12	49.79			
357 slow	12	42.08	2.31		
528 rapid	12	98.75	(pooled)		
547 rapid	12	96.04			
SEGREGATING POPULATIONS:					
318 x 547 cross	24	74.90	17.79	15.48	87.0
357 x 528 cross	24	66.04	31.32	29.01	92.6
Polycross of slow selection*	48	59.95	48.69	46.38	95.3
Polycross of rapid selection*	48	88.75	14.45	12.14	84.0
LSD at 5% level between population means		6.40			
LSD at 1% level between population means		9.33			

* obtained by intercrossing of 9 of the slowest or 9 of the fastest germinating plants from a population of US 401.

TABLE 9. MEANS, TOTAL PHENOTYPIC VARIANCES, AND GENETIC VARIANCES FOR 5-DAY GERMINATION DATA OF DIFFERENT NON-SEGREGATING AND SEGREGATING POPULATIONS FROM US 401.

POPULATION	NO. OF PLANTS	MEAN %	VARIANCE Total	VARIANCE Genetic	HERITABILITY
NON-SEGREGATING POPULATIONS (CLONES):					
Clone No. Germination type					
218 slow	12	69.38			
257 slow	12	59.48	3.34		
528 rapid	12	99.17	(pooled)		
547 rapid	12	96.67			
SEGREGATING POPULATIONS:					
218 x 547 cross	24	81.98	9.99	5.65	66.4
257 x 528 cross	24	76.14	16.22	12.88	79.4
Polycross of slow selection*	48	72.60	30.60	27.96	89.5
Polycross of rapid selection*	48	97.49	5.69	1.75	34.4
LSD at 5% level between population means		8.19			
LSD at 1% level between population means		11.90			

* obtained by intermatings of 9 of the slowest or 9 of the fastest germinating plants from a population of US 401.

the two hybrid populations are shown in Table 10. The theoretical means were calculated as the arithmetic means of the germination values obtained for those two clonal populations, which were used as parents for the particular hybrid. Only one of the actual mean values differed significantly from the theoretically expected germination value (Table 10).

TABLE 10. OBTAINED AND THEORETICAL MEANS AND THEIR STANDARD ERRORS OF TWO HYBRID POPULATIONS FOR 2-DAY, 3-DAY, AND 5-DAY GERMINATION DATA.

GERMINATION	POPULATION	MEAN AND STANDARD ERROR Obtained	MEAN AND STANDARD ERROR Theoretical	DIFFERENCE (O-T) AND ITS STANDARD ERROR
2-day	318 x 547	49.69 ± 3.88*	51.77 ± 2.74**	- 2.08 ± 4.75#
	357 x 528	41.04 ± 3.88	52.82 ± 2.74	- 11.78 ± 4.75
3-day	318 x 547	74.90 ± 2.78	72.92 ± 1.97	+ 1.98 ± 3.41
	357 x 528	66.04 ± 2.78	70.42 ± 1.97	- 4.38 ± 3.41
5-day	318 x 547	81.98 ± 3.55	82.03 ± 2.51	- 1.05 ± 4.34
	357 x 528	76.46 ± 3.55	79.38 ± 2.51	- 2.92 ± 4.34

Means and standard errors are expressed in germination percents

* Standard error of the mean, calculated from the populations x field replications interaction mean square.

** Standard error of the theoretical mean, calculated by the formula $\sqrt{(s_1^2 + s_2^2)/4}$; where s_1^2 and s_2^2 are the populations x field replications interaction mean squares of the two parental populations, from which the theoretical mean was calculated.

\# Standard error of the difference between obtained and theoretical F_1 means, calculated by the formula $\sqrt{s_o^2 + s_t^2}$; where s_o is the standard error of the observed mean, and s_t is the standard error of the theoretically expected mean.

Experiment D

To estimate the gain from selection, and also indirectly heritability, a rapid and a slow germinating population were selected from the 615 plants of a panmictic interbreeding population of PS 401. The "slow" group was composed of 9 plants, which produced extremely slow germinating seeds in 1957; the "rapid" group was composed of 9 plants, which produced extremely rapid germinating seeds in 1957. The mean germination values obtained for these two selected populations are shown in Table 11.

The clones of the original seed-producing plants were photothermally inducted in the winter of 1957-1958, and produced seedstalks in the spring of 1958. Before blooming, the plants of the "rapid" group were placed in one greenhouse room and the plants of the "slow" group in another to allow interpollination within groups. All plants within a group started to bloom at approximately the same time. Adequate quantities of seedballs were obtained from all the 18 plants. A composite sample was formed, by taking the same number of seedballs from each of the 9 plants of a group. A random sample of the composite sample was taken to represent a group.

Each seedball was planted in a pot in the greenhouse in March 1958. Fifty plants from each of the selection groups were photothermally inducted in the winter of 1958-1959. Fortyeight healthy plants from the "slow" and 48 from the "rapid" population were transplanted to the field,

TABLE 11. [illegible], [illegible] [illegible] [illegible]D.

[illegible]	[illegible]	[illegible] rapid A	[illegible]P slow B	A - B	(A-B)/2	[illegible]
[illegible]-day	Average of 9 selected plants in 1957	9[illegible]	[illegible].5	[illegible]	[illegible]	[illegible] ± [illegible]"
	Polycross progeny in [illegible]	7[illegible]	[illegible]	[illegible]	[illegible]	
3-day	Average of 9 selected plants in 1957	95.2	[illegible]	58.6	29.3*	9[illegible].0 ± [illegible].2
	Polycross progeny in [illegible]	[illegible]	[illegible]	[illegible]	17.[illegible]	

TABLE 11. - Continued

5-day	Average of 9 selected plants in 1957	95.9	52.6	43.3	21.7*	96.4 ± 36.5
	Polycross progeny in 1959	93.5	72.6	20.9	10.4//	

* Selection differential (i)

// Gain from selection (ΔG)

@ Heritability estimates, calculated by the formula $\frac{2 \times \Delta G}{i}$; e. g. heritability for 3-day germination = $\frac{28.8}{29.3} = 98.0$

" Standard error for the heritability ratio, calculated by means of a formula for estimating the standard error of a ratio.

together with some of the populations of experiment C. One plot consisted of six plants. Seeds were obtained and tested for speed of germination as described in Experiment C.

Mean germination values for the two selected populations ("slow" and "rapid" groups in 1957) and for the progenies derived from these two populations by random interpollination within the two groups (polycross progenies in 1959) are shown in Table 11. The differences in percent germination between the slow and rapid groups in 1957 and 1959 are also given. Since selection was practiced in opposite directions one-half of the germination difference between the two selection groups in 1957 will correspond to the selection differential: "i"; and one-half of the difference in percent germination between the two populations in 1959 will correspond to the gain from selection: "ΔG", assuming no asymmetrical selection response. Since $\Delta G = i \times h^2$ (Lush 1958), heritability ratios may be estimated in the following indirect way: $h^2 = \Delta G/i$. However, in this experiment, the mother plants, which were allowed to interpollinate within the two groups, originated from a randomly interbreeding population. Thus the expected gain from selection can be only one-half of that, which could be expected in a self-pollinating crop, or in crops where pollination from both parents can be controlled (corn). Therefore, to obtain heritability estimates for a cross-pollinating crop, which has natural barriers to self fertilization and controlled crossing (i. e. sugar beets), the gain obtained from selection (ΔG) has to be multiplied by two and divided by the selection differential (i).

This is expressed in the following formula:

$$h^2 = \frac{\text{(Gain from selection) x 2}}{\text{Selection differential}} = \frac{2\Delta G}{i}$$

Standard deviations (σ values) were estimated for the numerator and the denominator of the above formula. These values were used to calculate a σ value for the h^2 ratio, according to a formula for estimating the standard deviation of a quotient (ANDERSON, 1958, pp.268).

Experiment E

To determine the influence of environment in different years on speed of germination, and to disclose whether genetically different plants react in the same way to the differing environment of the two years, clones of the 23 plants, from which seed was obtained in 1957, were planted in the field for seed production in 1959.

The plants were propagated vegetatively in the greenhouse for 18 month, inducted in the winter of 1958-1959, and transplanted to the field on May 7, 1959. The plant were distributed at random in one field location. The seedballs, along with the remnant seedballs from the genetically identical plants, were germinated simultaneously in a laboratory experiment. Two germination replications, each consisting of 20 seedballs, were used for each seedlot. The germination data, expressed in percent germination, are listed in Table 12. The analysis of variance data are given in Table 13.

Although the germination of the seed from the 23 plants differed significantly in the two years, the plants did not react differently to the environments of the two years. This can be seen from the non-significant Years x Plants interactions (Table 13).

TABLE 12. [illegible] PERCENTAGES OF [illegible] (EXPERIMENT E)

PLANT NO.	2-day germination 1957	1959	3-day germination 1957	1959	5-day germination 1957	1959
1	0	0	23	25	43	43
2	0	0	40	43	65	75
3	0	0	28	35	45	73
4	3	3	30	40	40	53
5	3	5	65	60	88	83
6	20	13	65	58	78	85
7	43	40	73	73	75	83
8	83	78	93	95	95	100
9	85	73	90	90	93	93
10	85	78	90	95	90	90
11	88	73	98	95	98	95
12	88	75	93	95	93	98
13	88	75	98	98	98	95
14	90	73	90	88	93	90
15	90	75	95	88	95	88
16	95	93	95	98	98	98
17	95	95	95	100	95	100
18	98	70	98	90	98	100
19	98	85	100	95	100	98
20	98	88	100	98	100	98
21	98	88	100	100	100	100
22	98	90	98	98	98	98
23	98	95	98	95	98	98
Average of all plants	66.9	59.1	81.1	79.5	85.7	88.2
LSD 5% between plants	11.8	11.8	10.5	10.5	11.4	11.4
LSD 1% between plants	15.7	15.7	13.8	13.8	15.1	15.1
LSD 5% between years	2.5		2.2		2.4	
LSD 1% between years	3.3		2.9		3.2	

TABLE 13. ANALYSIS OF VARIANCE FOR THE GERMINATION DATA OF SEED PRODUCED ON THE SAME CLONES OF US 401 IN TWO YEARS. (EXPERIMENT E).

S O U R C E	D. F.	2-day germination M. S.	F	3-day germination M. S.	F	5-day germination M. S.	F
Replications	1	6.79		0.38		13.31	
Plants	22	227.37	156.60**	91.64	82.56**	45.66	34.79**
Years	1	54.79	38.53**	2.45	2.21	5.75	4.38*
Plants x Years	22	2.21	1.56	1.04		2.13	1.61
Error (Remainder)	45	1.42		1.11		1.32	
Total	91						

* Significant at 5% level

** Significant at 1% level

Effect of tightness of seedcase on speed of germination

In 1957, a marked relationship was observed between the number of lost seedcases+ and speed of germination of the sugar beet seed. On the basis of the seedcalls of 60 plants ("mother plants" in Expt. B), a correlation coefficient of +0.47** (significant at the 1% level) was obtained between the number of lost seedcases and the 2-day germination values (Table 14). Although all the seedlots were threshed and hackled in approximately the same way, the percent of lost seedcases for different seedlots ranged between 0 and 73.5%.

In 1959, the percent of lost seedcases was recorded for all the seedlots, which were used in the genetic studies (Experiments A, C, and D). Two to three weeks after transplanting, the percent of lost seedcases was determined for each seedlot on the basis of two random samples, each containing 100 seedcalls. The mean values for the different crosses and populations in 1959 were compared with the corresponding data for 1957 (Table 14). Although the percent of lost seedcases was lower in 1959 than in 1957, the corresponding values for the 2 years were similar in relative magnitude. This indicates that in addition to the influence of environmental factors, genetic factors also control this characteristic. This conclusion is supported by the high parent-offspring correlation

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+ The term "lost seedcase" will refer to seedcalls, on which at least one of the seedcases (lids), covering the true seeds, is missing.

obtained from the mean values for last seedcount of the 60 half-sib families in 1958 and air-dry loss in 1957. The parent-offspring correlation was estimated as +0.42**, which corresponds to a heritability estimate of 84 percent. For calculating the parent-offspring correlation coefficient, the data were transformed, using a square root transformation ($\sqrt{X + 1}$; SNEDECOR 1957). A correlation coefficient of +0.46** was obtained in 1959 between the last seedcount and the 2-day germination values using the mean values of 60 half-sib families (Table 14).

These results indicate that a close relationship exists between speed of germination and tightness of the seedcaps; and also that the tightness of the seedcaps is genetically controlled. When the percent of seedballs, which have missing seedcaps is relatively high, this characteristic may indirectly indicate rapid germination potential. Further experiments are required to determine the specific environmental factors causing a clone (e.g. Clone 54, Table 14) to react differently in different years.

TABLE 14. PERCENT OF SEEDBALLS HAVING LOST SEEDCAPS AND CORRELATIONS BETWEEN PLANTS AND PROGENIES FOR THE 2-DAY GERMINATION TEST AS APPLIED TO AOI IN 1957 AND 1959.

	YEAR 1957			YEAR 1959	
	No. of Plants	Lost caps %		No. of Plants	Lost caps %
Clone 318 (slow+)	1	0.0		12	0.0
Clone 357 (slow)	1	0.0		12	0.0
Clone 523 (rapid++)	1	10.5		12	15.3
Clone 547 (rapid)	1	73.5		12	14.6
			318 x 547 hybrid	24	1.2
			357 x 523 hybrid	24	2.3
Slow selection group	9	0.1	Progenies of slow group	48	0.6
Rapid selection group	9	29.9	Progenies of rapid group	48	4.8
Plants with seedballs having no lost seedcaps	22	0.0	8 progenies of each plant having no lost seedcaps in 1957	176	0.8
Plants with seedballs having at least 10% lost seedcaps	22	29.5	8 progenies of each plant having at least 10% lost seedcaps in 1957	176	5.9

Correlation between the number of lost seedcaps and the 2-day germination counts on the basis of 60 plants (1957) :

$$r = 0.67^{**}$$

Correlation between the number of lost seedcaps and the 2-day germination counts, on the basis of 60 family means (1959) :

$$r = 0.60^{**}$$

+ "slow" refers to plants producing extremely slowly germinating seeds.
++"rapid" refers to plants producing extremely rapidly germinating seeds.
**Significant at the 1% level

DISCUSSION

Large differences have been observed in speed of germination of sugar beet seedlots harvested from individual plants. The experimental results (Experiment A) re-confirm previous observations that the differences are due largely to the characteristics of the maternal tissues of the seedball, surrounding the true seed. Both physical and chemical attributes of the seedball have been demonstrated to influence rate and precent germination. Although it is possible that some differences may exist between the germination of the true seeds, these differences must be relatively unimportant when compared to the effect of the seedball on germination.

A marked positive relationship was found between speed of germination and tightness of seedcaps, when the latter was measured by the percent of seedballs having missing seedcaps (Table 14). This suggests that the physical characteristics of the seedball may play a relatively important role in determining speed of germination.

The results of the genetic experiments (A, C, and D) give definitive evidence that the germination rate of the sugar beet seed is under genetic control. The heritability ratios (h^2), obtained by different statistical techniques, for the 1-, 3-, and 5-day germination counts are summarized in Table 15. They are consistently very high, especially for the 2-, and 3-day germination counts. The heritability

TABLE 15. SUMMARY TABLE OF HERITABILITY PERCENTAGES FOR 2-DAY, 3-DAY, AND 5-DAY GERMINATION DATA ESTIMATED FOR DIFFERENT POPULATIONS USING DIFFERENT STATISTICAL TECHNIQUES.

POPULATION	HERITABILITY PERCENTS FOR 2-day germination	3-day germination	5-day germination	ESTIMATED FROM	EXPERIMENT
US 401 variety	92	92	90	between half-sib family variances	3
US 401 variety	95	93	87	within half-sib family variances*	4
US 401 variety	92	96	57	parent-offspring correlations	5
US 401 variety	100"	93	96	gain obtained from selection	6
318 x 547 cross	80	97	67	variances within clones*	8
257 x 523 cross	90	93	80	" " "	8
slow polycross/	91	95	90	" " "	9
rapid polycross/	84	94	34	" " "	8

* The heritability percents so estimated from within half-sib family variances and within clone variances can include dominance variance in addition to additive genetic variance and epistatic variance.

/ Obtained by interpollinating 9 plants of the US 401 population which produced the fastest or slowest germinating seed.

" The actually obtained h^2 estimate was 112 percent (Table 11), which is impossible by definition, and was therefore reported as an estimate of 100 percent heritability.

estimates, obtained for the different segregating populations using different statistical techniques, agree already well with each other.

The heritability estimates obtained from the between half-sib family variances, parent-offspring correlations, and from the gains of selection do not include dominance variance. The heritability estimates calculated on the basis of within family variances and within clone variances may include a certain amount of dominance variance in addition to additive genetic and epistatic variance. Since these two types of heritability estimates were similar and uniformly high, the results indicate that dominance cannot play an important role in the inheritance of speed of germination. This conclusion also is confirmed by the results of the slow x rapid crosses, since the germination values of the hybrid populations were not significantly different from the average germination of the two parental populations (Table 10). Epistasis (interallelic gene action), also, already plays a minor role, as can be inferred from the high heritability values and from the results of the selection experiment (Experiment D).

Because of the lack of plants with marker genes, no reciprocal crosses could be performed to exclude the possibility of maternal effects, however the hybrid values obtained in Table 10 indicate strongly that cytoplasmic inheritance is not involved in this characteristic. It can be also assumed from the high heritability values, and from the size of the gain obtained in the selection experiment, that the number of effective genetic factors determining speed of germination must be relatively low.

High heritability values in [illegible] selection. The results of the selection experiment (Experiment D) were in agreement with the obtained high heritability values, since gain from selection was high. The data in Table 7, 8, and 9 showed that after one selection cycle sufficient genetic variability (high h^2 values) was left in the selected population to allow further effective selection. This was especially valid for the 5-, and 9-day germination data. The lower heritability value (34 percent) obtained for the selected rapid population in the 5-day germination count, indicates that the characteristic had approached its physiological limit. The selected population had a mean germination value of 91.5 percent (Table 9), which is not far from the maximum limit of 100 percent.

The results of Experiment A demonstrated that speed of germination is controlled mainly by the maternal tissues of the seedballs. Since these maternal parts of the seedballs have the same genetic constitution as the mother plants, selection must be based on the generation represented by the original mother plants. Because the seedlings (embryos) represent a different generation than the maternal tissues of the seedball which control speed of germination, selection of seedlings could not be very effective. [illegible] (1960b) in 1955, selected seedlings instead of the original seed-producing plants; as a result, he obtained only a slight gain from selection for rapid germination. Using a similar selection procedure through two generations, [illegible] and [illegible] (1963) obtained a larger gain, because they compared reselections of early and late sprouting seedlings with each other and with the original population.

Because of the material available, the seedballs of a multigerm variety were used in these studies. However, it is logical to assume that the rate of germination of the seeds of monogerm fruits also is heritable and controlled by the maternal parts of the fruit. HOGABOOM and SAYLOR (1940) recently have observed similar large differences in speed of germination between the seedlots of monogerm plants; however, the most rapid germinating monogerm seedlots were slower than many of the rapidly germinating multigerm seedlots. Therefore it appears that speed of germination in monogerm varieties also can be improved by breeding methods.

SUMMARY AND CONCLUSIONS

The plant material for this study was derived from the multigerm, commercial sugar beet variety US 401. Seeds from 318 individually harvested plants as well as from certain clones that produced either slowly or rapidly germinating seeds were used. Field and laboratory experiments were conducted to determine whether speed of germination is a heritable trait; and if heritable, in what manner and to what degree selection can be effective in improving this characteristic.

The major conclusions of this study are summarized as follows:

1. Speed of germination was found to be a highly heritable trait. The heritability estimates, obtained for different populations using different statistical techniques, ranged between 80 and 100 percent for the 2-, and 3-day germination data. Dominance apparently played no important role in the inheritance of speed of germination.
2. The observation that speed of germination is controlled mainly by the maternal parts of the seedball was re-confirmed by comparing the speed of germination of excised seeds and seeds intact in the seedball.
3. The influence of the physical character of the seedball on speed of germination was indicated by a high positive correlation obtained between speed of germination and tightness of seedcaps. Seedcap tightness appeared to be a heritable trait.

4. Since speed of germination is controlled mainly by the maternal parts of the seedball, selection for rapid germination must be based on the original plants producing rapidly germinating seed, rather than on the seedlings (embryos) of the rapidly germinating seedlots. These seedlings represent a different generation than the maternal tissues of the seedball which surrounded them.
5. Speed of germination was improved considerably through a single mass selection, by intermollinating a small number of plants that had produced the fastest germinating seeds. (Fortunately, in sugar beets this can be easily accomplished, since seed-producing roots can be saved and vegetative propagation is relatively simple.)

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