GENETIC IMPROVEMENT OF YIELD AND NUTRITIVE VALUE OF TETRAPLOID POTATOES

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ABSTRACT

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by Erhard Meinzer-Clemons

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Genotypic, environmental and allometric control of potato yield and its components were studied in a breeding population. The inheritance of a number of developmental characteristics, yield, tuber protein, its "biological value," and processing characteristics were studied.

The first and second clonal generation of unselected F_1 seedlings consisting of 20 offspring from each of eight crosses between S. tuberosum and S. stoloniferum hybrids were grown in 1974 and 1975. The trials were conducted with 1-hill per plot in the first and 5-hills per plot in the second year.

Much of the genetic variability found was attributed to higher order genic interactions. The ratio of specific to general combining effects was, for most traits, larger than unity. The narrow sense heritability estimates were small: yield (.08), number of stems per hill (.07), number of tubers per stem (.31), average tuber size (.38), specific gravity (.24), date of emergence (.09) and flowering (.14), maturity (.24), rating of foliage vigor (.26), color of potato chips (.24), crude protein (.23), the ratio of non-protein N to total N (.37), and "biological value" (.26). The latter was assessed with Streptococcus zymogenes, using casein as standard.

The repeatabilities between the first and second clonal generation were determined: yield (.39), stems per hill (.10), tubers per stem (.16), tuber size (.26), specific gravity (.43), emergence (.35), flowering (.78), maturity (.69), and vigor (.20).

The correlations revealed strong interactions between developmental traits. Negative correlations exist between successive components of yield. Expression of the genotypic potential is confounded by developmental allometry, which partially accounts for the low repeatabilities.

A causal model for yield was proposed and analysed by Sewall Wright's path coefficient method. The effects attributable to genotype, clonal generations, and somatic correlations due to sequential development were separated. Compensation between the components of yield was observed. Fluctuations in preceeding components were not fully compensated for by subsequent ones.

Potato yield appears to be primarily limited by the strength of the tuber sink. Altering the genetic potential for tuber number, tuber size, or activity of tuber sinks would change the yield potential geometrically, since the strength of the tuber sink is the product of the three. Raising the genetic ceiling of one component will result in a yield increase to the extent that sink limitation occurring during the ontogeny can be removed. Heterotic effects may be produced by raising the genetic potential of complementary component traits.

In view of the low heritabilities, potato breeding must exploit the non-additive genetic variance, especially epistatic effects arising from interaction of physiological and morphological traits, since they may be predictable.

Breeding objectives to improve yield, the concentration and the "biological value" of tuber protein and chipping characteristics are compatible.

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By

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TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 3 page

CHAPTER 4

LIST OF FIGURES

CHAPTER 3 Page

1. INTRODUCTION

Optimism about the world food situation, generated by the green revolution of the late sixies, has reverted to pessimism. Improvements on all fronts of food production and utilization will be required to assure stable food supplies over periods of good and poor harvests. In view of limiting land, water, energy and fertilizer, improved yields of all crop plants becomes the major factor in alleviating food shortages and malnutrition that affect nearly 460 million people.

World wide, the increase in food production has failed to keep up with the population growth of the past twenty years. This increasing number of people will be forced to rely more on plant foods, with lower protein quality than foods from animal source. Encouraged by the success of the high lysine mutants that improve the protein quality of corn, scientists have screened most of the major crop species for varieties with a higher nutritional value. In plant breeding, higher nutritional value has become a new dimension to add to such characteris as yield, disease resistance, and processing qualities.

Great hopes lie with the potato for the production of future food supplies. Research to enhance and exploit the existing yield potential as well as the nutritional value of potatoes is necessary to ensure adequate nutrition for the growing world populations.

In the U.S., Potato yields have tripled within the last three decades. Despite this significant advance, the introduction of new varieties has contributed very little to yield improvement in North America (Horsfall, 1972) and Europe (Seiffert, 1957; Howard, 1963). It is possible that the narrow genetic base of cultivars in this hemisphere, derived from only a few introductions (Simmons, 1962), poses a limit to further improvement. The lack of improved yields from breeding could also be the result of the many efforts to breed for disease resistance and some quality factors, coupled with "good" yield. Recently several authors (Maris, 1966; Davis and Johnston, 1965 and 1974) have studied and questioned the effectiveness of both plant breeding and selection procedures presently utilized.

Attempts are being made to improve this situation in several breeding programs. Potato species other than Solanum tuberosum L. were used in the past mainly for their disease resistance. They are now used to improve such characters as yield and quality.

Plant breeding strategies and their success depend on the mode of inheritance of the traits under investigation and selection progress is proportional to the available genetic variance. The heretability of quantitative traits depends to a large extent upon the magnitude and the proportion of variance attributable to genes that act additively.

The cultivated potato is a tetrapoloid and highly heterozygous. It exhibits a high degree of inbreeding depression and loses its viability after only a few cycles of selfing. As a consequence, highly heterozygous parents are used in potato breeding. Much of the genetic variance may be attributable to dominance and genic interactions. Performance of offspring is difficult to predict and selection of superior genotypes becomes extremely important. Once a superior genotype has been identified, however, it can be propagated vegetatively.

Yield is a very complex phenomenon, involving in its development most of the physiological and morphological processes of the plant's growth. While selection for yield per se may be very difficult, selection of individual parameters that lead to the developmental-physiological network may render more progress. In cereal crops and legumes, the study of yield components has contributed much to the understanding of yield. In potatoes the components of yield are: (1) the number of stems per hill, (2) the number of tubers per stem, (3) tuber size, and (4) specific gravity, a measure of total solids.

A potato breeding program begins with a series of hybridizations among designated parental clones (cultivars and seedlings). The true seeds derived from these hybridizations are usually grown in the greenhouse to produce F_1 seedlings. Few small tubers are collected from an F_1 plant, and all the reserved F_1 tubers are then planted in the field with wide spacing between the adjacent plants. The number of seedlings grown in the first clonal generation is usually large.

Routinely, more than 90% of the population is eliminated through removal of obviously undesirable segregates. This aids in reducing the number of seedlings so that the merit of those selected can be evaluated more accurately in subsequent clonal generations. The criteria for selection at this stage are in most cases based on visual discrimination exercised by one or a group of selectors when the tubers of the individual seedlings are dug and exhibited on the ground. Stored tubers of the selected seedlings are cut into seed pieces and planted at a normal spacing for evaluation in the second clonal generation.

With the exception of research conducted by Maris (1969) and Davis and Johnston (1965 and 1974), only a few studies examined such visual selection procedures. Based on their results, the selection at the single hill stage is highly questionable. Duplicate selections of clones were made in only a few instances.

It is generally recognized that yield components of plants grown from a very small seed tuber in the first clonal generation differ considerably from plants grown in the following generation. Selection with respect to yield is often based only on tuber set and tuber size, ignoring the other yield components. It might, however, be possible to (1) evaluate each yield component with respect to the others, and (2) predict performance in the following years based on the knowledge of the average change in several yield components from the first to following clonal generations. Furthermore, emphasis for seedling selection should be placed on characters with high repeatability and for parental selection on characters with high heritability.

The inheritance of, and interaction between yield components is important in respect to improvement of yield. Tuber size is very important when determining the market value of a crop. Specific gravity influences both culinary and processing characteristics of the tuber. The pattern of development of a potato plant not only affects the morphological components of yield, but also the composition of the tubers. Clones with a large number, but smaller tubers had, on the average, a higher percent starch content (Swieszynski, 1965). The main objectives for genetic improvements of the nutritional value of potatoes are to raise the protein concentration and upgrade the biological value.

The potato tuber contains, on the average, 2% crude protein on a fresh and 10% on a dry weight basis. Approximately 10% of the dietary calories are provided by protein, which is adequate for healthy humans, possible exceptions being infants and small children. Net protein utilization and chemical scores are higher for potatoes than for the major cereals, navy, and soya beans (FAO, 1965). The sulfur containing amino acids are reported to be first limiting in potato protein (Schupan, 1958; Kies and Metzfox, 1972).

The crude protein is composed of 30 to 50% protein, the difference being non-protein nitrogen compounds, mostly free amino acids and amides. Although the protein has been classified according to solubility into only a few fractions, none of these represent a homogeneous protein. Most of the tuber protein is composed of a large number of enzymes. Potato protein is not compartmentalized as in cereals, where embryo, endosperms, and aleurone proteins can be clearly distinguished, which may make qualitative improvements more difficult.

It is the purpose of this research to investigate the relationship between the components of yield as they influence yield and to study the improvement of the nutritional value of the potato. Special emphasis is placed on the differences in yield components between the first and second clonal generation. Heritabilities and repeatabilities of yield and its components are assessed and selection of these and characters along with depth of eyes, chipping quality, and nutritional value are discussed.

2. REVIEW OF LITERATURE

The study of growth and differentiation of multicellular organisms is one of the most challenging and exciting fields of biological research. An understanding of the biological principles involved has become essential for the improvement of crop productivity and nutritional and agronomic characteristics. Equipped with the concept of limiting factors (Blackman, 1905), plant physiologists seek to single out limiting processes. With an increasing realization of the extent of feed-back between rates of anabolic and catabolic processes, translocation and storage, and the dynamic partitioning of assimilates, plant breeders must use an integrated approach to plant improvement. This review is an attempt to present some of the biological principles relevant to this tudy, and a review of potato yield and its nutritional value.

The cells as the production units of an organism, with enzymes as their tools, manufacture certain products such as protein and carbohydrates in a series of steps. The output of these products is controlled by (1) the number and kind of enzymes available for each step in the chains (activation and repression of genes) and (2) the rate of reaction (available energy, substrates, enzymic activation or inhibition, and cellular environment). Both structural and functional development of cells and organs is guided by sequential activation of genes and coordinated by hormones and genic response to external (e.g. light) and internal (e.g. substrate) environmental conditions.

Growth and differentiation, the outcome of cellular activity, is achieved through alteration in all cell composition, function, size and shape. While cells that participate in morphogenesis carry identical genetic information, the physiological environment of an individual cell is largely given by its neighbors. Its developmental fate depends primarily on its position (Driesch, 1908) The reasons are: competition for nutrients, and polar movement and gradients of nutrients and hormones.

External environmental factors affect various regions of the plant differently for they act on a variety of different and localized, yet strongly interdependent, systems. It is to be expected therefore, that the ideal external environment for "growth" varies with the particular plant characteristic under study and with the different phases of growth (Spiegelmann, 1945).

The phenotypic make-up of a complex trait corresponds to a complex genotypic make-up. Component analysis can both enhance our understanding and give simplified explanations of the formation of a complex trait (Watson, 1952). The idea of genetic analysis of subcharacteristics was advanced by Grafius (1956) and Williams (1959), and was found to lead to simpler genetic models and thus a better prediction of breeding behaviour. Duarte and Adams (1963) have shown that heterosis in the leaf area of field beans could be explained by the multiplicative relationship between number and size of leaflets, whose gene action is additive or shows partial to complete dominance. Heterosis in yield of barley (Grafius, 1959), tomato (Williams, 1959) and potatoes (Cubillos and Plaisted, 1976) could be explained similarly by the multiplicative interaction among yield components.

Phenotypic correlations may arise from the allometric relationship between morphological, physiological, or biochemical characteristics. Allometry is defined as the study of proportion changes correlated with variation in the size of either the total organism or the part under consideration. The definition may be extended to describe the effects of form or size upon function and upon the metabolic processes and vice versa. Allometry refers to relative differences between variates which arise in ontogeny, phylogeny, or in static comparisons of related forms differing in size (Gould, 1966).

All but the simples organisms reach their mature form by differential growth. In organisms which maintain geometric similarity with growth, surface area increases as the square of the length and volume as its cube. Since many functions (photosynthesis, respiration, transpiration, nutrient absorption, etc.) require that organ surfaces increase proportionately with size to maintain adequate efficiency, thus allometric growth becomes essential in evolution as well as in ontogeny.

Richards (1969) states that dry weight of a young organism increases in a nearly exponential manner, which implies an exponential increasing demand for nutrients. While the increase in cell number is controlled largely by the availability of such minerals as nitrogen and phosphorous supplied through roots, the relative growth rate in dry weight depends more on CO_2 assimilation. The authors suggest that the supply of nutrients through roots of an annual plant is outstripped at some stage by the increasing carbon-fixing capacity, so that the non-meristematic cells lose division power and carbohydrate content eventually rises.

Mutual conditioning and time coupling are expected to contribute significantly to the phenotypic correlation between component traits. Gene action is often limited to cell function in terms of ontogeny. Genes and environment, which influence preceding events set the state for both gene action and environmental stimuli for latter events. For example, the strength of both sinks and sources is the product of their respective size times activity (Wilson, 1972). Similarly, the rate of translocation will depend on the size and activity of the vascular system. Thus factors affecting the size of either one of these set the frame within which the different processes can take place. Size, as used by Wilson, should be broken down into number and size (surface area or volume) of cells or organs. Reasons being: (1) the relationship between form and function mentioned earlier, and (2) that the branching habit provides a means to increase the meristematic cell number (Richards, 1969), thus raising the production potential. Limited resources at certain stages of development, however, caused by either inter- or intraplant competition may result in negative correlation between morphological component traits of metabolic sinks (Adams, 1967). The meristematic, elongation, and storage sinks may compete within and between sink sites, if they depend simultaneously on the same sources.

The development of a potato plant. The number of mainstems developing from a seed tuber depends on variety, apical dominance, tuber size, storage environment, and treatment before planting (Burton, 1966). The number of mainstems per hill seems unaffected by spacing, but development of axillary branches usually decreases with the number of mainstems per hill (Toosey, 1963). Branching usually increases with lateness of maturity (Salaman, 1926). Svensson and Naglika (1975) found the rate of sprout growth to be a positive function of the initial seed piece weight. Multisprout tubers exhibited mutual interference for substrates from the tuber and competition between stems was apparent very early. The intensity of competition increased with temperature, but could be reduced and in some cases eliminated by supplying inorganic nutrients.

Chronologically, the development of potato tubers can be divided into periods of tuber formation and tuber growth. Tuber formation begins with stolon differentiation, starting at the basal nodes and proceding in acropetal succession (Plaisted, 1957). In S. tuberosum vars. stolon emergence occurs at the apex of the sprout at the time of flower differentiation. Stolons grow at different rates and growth rates change in relation to each other with time (Lowell and Booth, 1969). The number of stolon bearing nodes per sprout is an inverse function of the number of growing stems per hill (Toosey, 1963). Tuberization begins, in general, at about the end of flower bud development, for late varieties when the buds have started to open (Clark, 1921; Grosch, 1955). Potato plants may tuberize, however, over a wide range of developmental states (Burton 1966). Tuber induction is generally hastened by increasing physiological age of the plants, short days, low temperatures, high daily radiation, and low mineral supply (Slater, 1963, 1968).

According to Artschwager (1924), tubers grow as a result of cell division and subsequent cell enlargement, principally in the internal and external phloem areas. Booth (1963) states, however, that radially, expansion is initiated by cell enlargement before cell division is resumed. Plaisted (1957) concludes that cell division and cell enlargement continued concurrently throughout tuber growth and that cell multiplication was the factor most responsible for the increase in tuber size. Studying tuber histogenies, Reeve _et_. _al_. (1969, 1970), give evidence for the sequential origin of tuber tissue. Swelling of the stolon tip is initiated by cell enlargement. The young expanding tuber grows as a result of cell division at random planes and cell growth in the young pith. Although cell division continues at later stages, most of the tuber growth results from cell enlargement of procambial derivatives to form the starch-storage parenchyme around the internal and external phloem strand.

Starch granules are already abundant in young parenchyma cells which occasionally divide (Bradburg, 1955). The percent of both starch and dry weight per cell were low in young tubers but increased faster than fresh weight at late stages. The relationship was not linear but could be closely approximated by the allometric formula (Plaisted, 1957). This is in accordance with findings by Reeve _et_. _al_ (1970) that size differences between starch granules in different parts of the tuber become apparent by the time the young tubers are between two and three centimeters in diameter. A high proportion of large starch granules is associated with high specific gravity of tubers (Sharma and Thompson, 1956). With increasing size of developing tubers, the difference in specific gravity between the vascular and the pith region becomes more pronounced (Cole, 1975). Larger differences were found in varieties with a high specific gravity (Sharma _et_. _al_, 1958).

Leaf area and its duration. Photosynthesis provides the great bulk of dry matter for the growing tuber. Varietal differences between photosynthetic rates are extremely difficult to determine as rates of both photosynthesis and respiration of individual leaves are changing during their ontogeny. Net assimilation rates were similar for both early and late varieties when measured at the same stage of development (Meinl, 1967). A positive association between tuber bulking rate and leaf area was found when the leaf area index was lower than three. Above three, tuber growth rate declined, owing to mutual shading (Radley 1963). Mokronosov and Ivanova (1971) removed up to 30-50% of the leaf area without negative impact on tuber yield. Total dry matter production was determined mainly by the length of the growing season (Rijtema and Endroedi, 1970). Late maturing varieties have a higher yield potential (Howard, 1974). Maturity was positively correlated with plant height, tuber number and weight, specific gravity, and yield of potato seedlings (Maris, 1969). Late maturing and taller varieties generally produce a much deeper root system (Whitehead et. al., 1953). High specific gravity was observed more often in late varieties (Prokosev, 1939 and Akeley and Stevenson, 1943). Johannson et. al. (1967) found that earliness and high starch content were positively correlated at Baton Rouge, La., but the same cultivars produced no correlation at Grand Forks, N.D.

Maturity is polygenically inherited. Progeny means for maturity were slightly higher than mid-parent values (Harris, 1969). Heretability ranged from 76 to 92 percent.

Yield and its components. The number of main stems is the logical unit of plant population in the potato crop (Holliday, 1960); Bleasdale, 1965). Krijthe (1955) defined a main stem as a stem growing directly from the seed tuber. It is difficult, if not impossible, to record main stems in the growing crop. Gray (1971) has suggested that the number of main stems ten days after 50% emergence is a suitable density scale. Goodwin, et. al. (1969), Holmes, et. al. (1970) have shown a better relationship between yield or tuber number with the above ground stems than with main stems. While many authors assumed that secondary stems do not bear tubers, Krijthe (1955) and Holmes et. al. (1970) could demonstrate that they do. The essential difference between the two methods of counting is the presence of secondary stems in the above ground count. These are sub-surface branches and stolons which occasionally develop into leafy branches. They develop into virtually independent plants soon after emergence (Milthorpe, 1963). It would therefore appear that the count of the aboveground stems would be a suitable method of recording stem densities in a potato crop.

The number of tubers increased with the number of main and branch stems (Holmes et. al, 1970). Total yield was not affected, but yield of seed size tubers was increased by up to 70%. When thinned to one stem per plant, yields were below the controls (Davis, 1969). Of the two-stemmed plants, however, five out of thirteen cultivars gave greater yields than the checks, but specific gravities were lower in each case. Yields increased initially as stem density increased, tending to become constant at higher densities. Number of tubers per unit area increased asymptotically, while the number of tubers per stem declined to a constant value. While in absolute values, the yield structure was different for the varieties reported (Thompson and Taylor, 1974; Steineck, 1959), the response pattern was similar for all varieties investigated. The compensatory effect between the components of yield was studied by Steineck (1959), Maris (1969), and Tai (1975). All found similar correlation values. Steineck reported the following correlations for number of stems and tubers per hill, r = .70; or tubers per stems, r = -.58; and for number of tubers and tuber size, r = -.77. Correlations between these components and yield, although positive, were of a much smaller magnitude. Specific gravity was positively correlated with yield, tuber number and average tuber weight (Maris, 1969). It has to be remembered that tuber weight is the product of tuber size times specific gravity. Among others, Tikhonov and Demidovich (1935), Akeley and Stevenson (1944), and Hunnis (1969) conclude that high starch percentage usually correlated with small tubers and low yield, and is controlled by mainly dominant polygenes. Maris (1969) found, however, that progeny means were close to the parent with the lowest value. The mean specific gravity of selfing populations was lower than the mean of the parents Cunningham and Stevenson, 1963). Recurrent selection for high specific gravity proved to be successful (Plaisted and Peterson, 1963), but the authors encountered problems of maintaining high yielding ability. Heretability estimates given by all above authors were rather high, ranging from approximately 60-85%.

Riedl (1948) found tuber number to be an inherited characteristic. Wenk cited by Schick (1956) concluded from his observations on 5,000 progenies of different crosses, that selection for high tuber set is generally more successful than selection for high tuber weight to obtain a high tuber yield. Maris (1969) found a high correlation (+.97) between progeny means for tuber number per plant in a study of 1,116 seedlings from 12 crosses among 13 potato varieties. The tuber weight was considered more decisive in determining yield. But the correlation between mid-parent and progeny means was much lower, r = +.39, for tuber weight.

Akeley and Stevenson (1943) reported hybrid vigour for yield in some progenies. In contrast, Tikhonov and Demidovich (1935) had suggested that factors for low yield were dominant. Maris (1969) calculated heretability for yield to be approximately 67%. Population means approached mid-parent values or were below.

Nutritional value of the nitrogenous substances of the potato. Crude protein (N x 6.25) of the potato is composed of about 7-10% insoluble structural proteins, 25-50% true protein (Neuberger and Sanger, 1942), 8-12% nucleic acids (Levitt, 1954), and most of the remainder can be attributed to amides and free amino acids. Occasionally crystalline protein is found in small amounts (Hoelzl and Blancher 1959). Small, but often significant, amounts of anti-nutritional N compounds such as soladinine distract from the nutritive value of the potato.

The nutritional value of crude potato protein compares favorably with other plant proteins. For 258 samples examined, the biological value ranged from 61 to 89. The low values were caused by either deficiency or surplus of nitrogen fertilization (Schupan, 1959). Nitrogen balance studies with human adults showed that potato protein was superior to most major plant and animal protein and approached the value of whole egg (Kofranyi and Jekart, 1967).

According to Schupan (1958) the sulfur containing amino acids of potato protein are the first to limit growth of animals. Supplementing potato protein with methionine increased both digestibility and weight of growing voles (Rios et. al., 1972). By adding methionine, Kies and Metzfox (1972) improved nitrogen balance in human subjects who consumed dehydrated potato flakes.

Both quantitative and qualitative improvement of the potato protein have to be considered in a breeding program. The possibilities of genetic improvement of potato protein were discussed by Schwarze and V. Sengebush (1937), Siegle (1951), Reissig (1958), and Schupan (1970) and by a planning commission of the international potato center (CIP, 1973). Luescher (1972) found a range of crude protein from 7.5 to 18.8% in a segregating potato population. The biological value may vary considerably among wild potatoes (Schupan, 1959), a range of 61-81 was reported. (Schupan and Postel, 1957; Reissig, 1958; and Luescher, 1972).

Although the percent crude protein varies little with respect to fresh weight, a strong negative association is found between percent crude protein and specific gravity, dry matter, and starch content (Talley et. al., 1961; Luescher, 1972; and Verma et. al., 1975). High specific gravity is very desirable for processing and certain culinary qualities (Talburt and Smith, 1975). Using <u>Streptococcus</u> <u>zymogenes</u>, Luescher (1972) found the percent crude protein to be negatively correlated with both methionine (r = -.45) and the biolgical value (r = -.55). The variability in the essential amino acid index between true protein of different cultivars is very small (83-89). It is somewhat larger for the non-protein fraction (31-43). The EAA-Index among cultivars is influenced primarily by the ratio of protein-N to non-protein N (Reissig, 1958).

The results by Talley <u>et</u>. <u>al</u>. (1970) confirm varietal differences for crude protein, the ratio of free to total N and methionine, but all three are very subject to modifications by year, location, and very high genotype x environment interactions were found. Heavy nitrogen fertilization increased the percent crude protein mainly through an increase of aspartic and glutamic acids and their corresponding amides. The concentration of lysine, for example, increased proportionately, but the methionine content dropped from 2.2 to 1.6% (Hoff, <u>et</u>. <u>al</u>, 1971). Mineral nutrition had pronounced effects on the yield and protein content of the tubers, but did not influence the amino acid composition of the protein, wherease the amount and composition of the NPN was altered considerably (Mulder and Bakema, 1956). Deficiency or excess of either N, P, or K increased the free nitrogen pool.

Low temperature storage did not appreciably affect the free amino acid composition, but reconditioning resulted in a marked increase (Habib and Brown, 1957). Low temperature storage followed by reconditioning resulted in an increase of the free amino acids, but no change in true protein (Fitzpatrick and Porter, 1966). This apparent net increase in crude protein is explained by both respiratory and transpiratory losses, which primarily affect the carbohydrate and water content of tubers (Talley et. al., 1961).

During the growth of a tuber, the nitrogen content decreases gradually on a dry matter basis and the portion of protein is higher in the immature tuber Schupan (1970). Small tubers have a more favorable pattern of essential amino acids, primarily because crude protein increases with tuber size, with little change in true protein (Schupan, 1959). Of the essential amino acids, lysine and threonine increased with tuber weight, while most of the others showed little change or dropped slightly.

The compartmentalization of protein within the tuber has given hope to improvement through plant breeding. Nitrogen content is highest in the peel, decreases sharply in the cortex, and rises again towards the pith (Neuberger and Sanger, 1942). Monday and Riley (1964) found essentially the same distribution, but showed that throughout the tuber the percent crude and soluble N on a dry weight basis are inversely related to specific gravity. However, the EAA-Index is higher (74) in the cortex and the area near the apical and lateral buds than in the inner layers (61) (Schupan, 1970). The better balance of essential amino acids appears to be associated with the cell layers which are capable of cell division. It is noteworthy, that the protein crystals are also located in the outer layers.

Determination of protein content in foods is based on measurement of the nitrogen content. There are several methods available but the Kjeldahl method is most widely used and is standardized (AOAC, 1970). Crude protein is estimated by multiplying the amount of nitrogen by 6.25.

The nutritive value is determined by the amount and relative availability of the amino acids. Speedy and accurate methods are available for measuring amino acid composition (Speckmann et. al., 1956), but they do not indicate the availability. Micro-organisms have been used by Lueshcer (1972), voles by Rios et. al, (1972), rats by Peare (1973), and human subjects by Kofranyi and Jekart (1967) to assess protein quality of potatoes.

3. GENETIC IMPROVEMENT OF POTATO YIELD

3.1 Introduction

In a potato breeding program, following hybridization, F_1 plants are usually grown in the greenhouse from true seed. The small tubers obtained are subsequently vegetatively propagated in the field. In the first clonal generation, a rather large percentage of genotypes is eliminated. The plant type, however, developing from the small tubers in the first clonal generation differs considerably from later generations (Blomquist and Lauer, 1962). The reliability of visual selection procedures based on few hills in the first clonal generations was studied by Davis and Johnston (1965, 1974), Harris _et_. _al_. (1967), Maris (1969), and Tai (1975) and was found to be highly questionable.

Parent selection based on either yield, tubers per hill, or tuber weight resulted in populations with similar yields and yield structures (Plaisted and Cubillos, 1972). Hybrid vigor for yield was observed, however, in crosses of parental genotypes with large numbers of tubers and large numbers of tubers and large tuber sizes (Cubillos and Plaisted, 1976). Recurrent selection for high specific gravity proved to be successful (Plaisted and Peterson, 1963), but difficulties were encountered in maintaining high yielding ability. Parent and offspring selection, based on individual yield components was difficult because of the negative correlations between them (Steineck, 1959; Maris, 1969; and Tai, 1975). Interactions between sub-traits obscure expression of their genetic potential.

A greater understanding of the formation and structure of yield of potato plants is very important for both production and breeding of potatoes for a specific purpose. The complex quantity "yield" is the product of the number of stems per hill, the number of tubers per stem, and tuber weight (Steineck, 1959). Although total yield may be similar for different cultivars, the relative contributions of these components may vary within wide limits. For the producer, however, only a narrow range is desirable or ideal at best. But depending on environmental resources, emphasis may shift between yield components, which is very important if a stable yield potential is to be maintained. Optimal use of these resources can be made only if no genetic ceilings are encountered at any stage of development.

The analysis of crop yields entails the study of growth and differentiation. Yield is the manifestation of a long sequence of developmental events directed by segmental expression of the genome and by the environmental resources available in time and space. Both developmental and size allometry of phenotypic subtraits results from: interactions between form, or size, and function; mutual conditioning and time coupling; and physiological interactions between traits.

Yield components in potatoes develop in sequential fashion (Part 2 of this thesis), each affecting the following ones. A transformation technique was proposed by Thomas <u>et</u>. <u>al</u>. (1971) to remove the variance attributable to traits which are formed earlier in the developmental sequence. Tai (1975) applied path coefficient analysis to examine interactions between yield components of potatoes. In view of parent and early clonal selection in a potato breeding program, it would be extremely useful to know more about the relative contributions of genotype, environment and allometric factors to yield and its components.

The development of a potato plant is schematically portrayed in Figure 1. Tuber yield is the result of the rate and duration of tuber bulking. It is thus dependent on: (1) the size and duration of the foliage measured here by its height and width integrated over time from emergence to maturity; and (2) time of tuber initiation approximated by the time of flowering, until maturity. The components of yield are formed in a succession. They are: (X) the number of stems per hill, (Y), the number of tubers per stem, (Z) average tuber size, and (G) specific gravity. Yield (W) is thus the geometric production of these components.

$$W = X \cdot Y \cdot Z . G$$

The literature often refers to the total number of tubers per hill, which would correspond to the product of number of stems per hill and number of tubers per stem. The number of stems is considered an important trait since it is a varietal characteristic (Steineck, 1959; Thompson and Taylor, 1974) and it may be altered by seed treatment and storage (Burton, 1966). Number of tubers per stem is preferred to number of tubers per hill because of its direct and simpler functional relationships to the number of stems (Steineck, 1959). Tuber weight is broken down into tuber size and specific gravity because (1) tuber size is used in grading potatoes in most countries., (2) visual selection of the seedling is based on size rather than weight, (3) specific gravity influences cooking, processing, and culinary quality of tubers, and (4) specific gravity is closely associated with percent dry matter (r = .88) and percent protein (r = -.92) content (Verma et. al., 1975). Dry matter yield, the product of yield and dry matter content, was not considered as variable in the overall scheme, because it is almost entirely determined by total yield (r = .95; Tai and Young, 1972; Luescher, 1972).

Extensive investigations on photsynthesis and respiration of different potato genotypes (Winkler, 1971; Meinl, 1967) revealed relatively small differences between cultivars at the same physiological age compared to the variability encountered between physiological stages.

The leaf area at any point in time represents a conglomerate of leaves at different physiological stages. Net assimilation rate depends primarily on light intensity and leaf temperature. Both are subject to daily and seasonal fluctuations. Furthermore, light penetration and temperature exchange depend on the canopy structure. Winkler (1971) concluded that in productivity studies leaf area development and leaf area duration should be primarily considered because of the large varietal differences.

Most efforts in potato breeding have been directed towards clonal selection. The primary goal is to indentify superior genotypes which can be subsequently vegetatively propagated. Maris (1966) stated: "The number of seedlings required to breed a new potato variety, has very much increased in the past few decades. Selection ranges from fairly strict to strict in the first clonal generation. In the next few generations most of the clones do not come up to the expectations." It is suggested to use the repeatability of individual traits as a measure for the selection pressure which may be applied in clonal selection. The degree and direction of the modifiability from the first to later clonal generations may give an indication of the biases introduced by selection in the first clonal generation.

Only a few studies have been published about the inheritance of quantitative traits in autotetraploid potatoes. "The complications of tetrasomic inheritance have impeded the accumulation of basic genetic information concerning the cultivated potato (_S_. _tuberosum_) and no doubt has slowed genetic gains in breeding programs" (Rowe, 1967). Specific combining ability for yield was estimated to be two (Sanford, 1960) and four (Plaisted _et_. _al_., 1962) times larger than general combining ability. But no information is available for yield components.

The purpose of this investigation is to study the formation of the economic yield of potatoes. The genotypic and environmental control of the components of yield and of other selected traits was examined. Their relative importance in the determination of yield was evaluated. The paper is divided into four sections which examine: (1) the mode of inheritance and hertability, (2) clonal selection, repeatability, and modifiability, and (3) the genetic, environmental and allometric control of these traits. (4) The results are discussed in view of parent and early clonal selection.

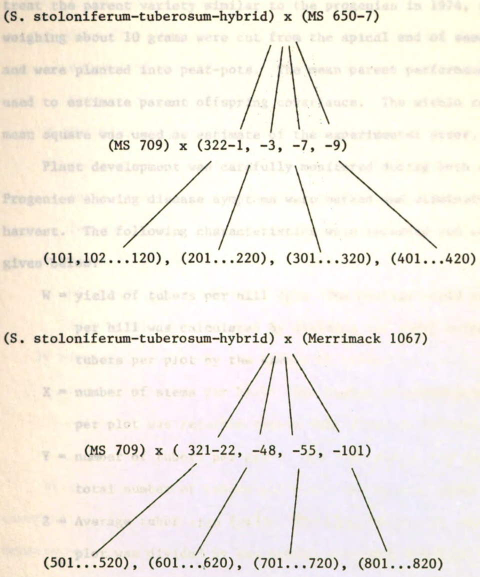
3.2 Experimental

Twenty offspring were selected at random from each of eight crosses of *S. stoloniferum-S. tuberosum* hybrids and an advanced *S. tuberosum* selection, excelling in yield, tuber size and shape and being medium early in maturity. (for pedigree see Table 1). The first and second clonal generation of the unselected progenies were grown in 1974 and 1975 on a sandy loam soil at the Montcalm Experiment Station. The trials were conducted in a randomized block design with two replications and 1-hill per plot in the first and 5-hill plots in the second season. In both seasons plants were spaced 30 cm. apart in 86 cm. rows. Cultural practices of fertilizer application, irrigation and pest control were followed as recommended for the location. Plants were harvested during the first week of September, after most progenies had reached maturity.

Seed tubers were kept in controlled storage and warmed for two weeks prior to planting. In the first season, seed tubers weighing approximately 10 grams were obtained from plants grown from true seed in the greenhouse the previous year. The tubers were planted in peat pots during the second week of May. In the second season, uniformly size tubers weighing about 60 grams were selected from the first season crop and planted directly to the field during the first week of May.

In both season, 16 plots within each replication were randomly

Table 1. Pedigree of the potato population under investigation. The progenies are identified by three digit numbers. The first digit indicates the cross and the last two the individual offspring.



assigned to the common parent of all progenies. In an attempt to treat the parent variety similar to the progenies in 1974, seed pieces weighing about 10 grams were cut from the apical end of seed tubers and were planted into peat-pots. The mean parent performance was used to estimate parent offspring covariance. The within replication mean square was used as estimate of the experimental error.

Plant development was carefully monitored during both seasons. Progenies showing disease symptoms were marked and eliminated at harvest. The following characteristics were recorded and coded as given below:

W = yield of tubers per hill (g): The average yield of tubers per hill was calculated by dividing the total weight of tubers per plot by the number of hills.

X = number of stems per hill: The number of above-ground stems per plot was recorded twenty days prior to harvest.

Y = number of tubers per stem: This represents the quotient of total number of tubers per plot and the stem count.

Z = Average tuber size (cm^3): The total weight of tubers per plot was divided by the number of tubers per plot and the specific gravity.

G = Specific gravity (g/cm^3): G was calculated from the air and under water weight of the tubers.

E = days from planting to emergence: The emergence date was recorded in three day intervals as the plants emerged in the first season and when three of the five plants had emerged in the second season.

F =days from planting to flowering: The flowering date was determined when the plants appeared to have reached fifty percent of full bloom.

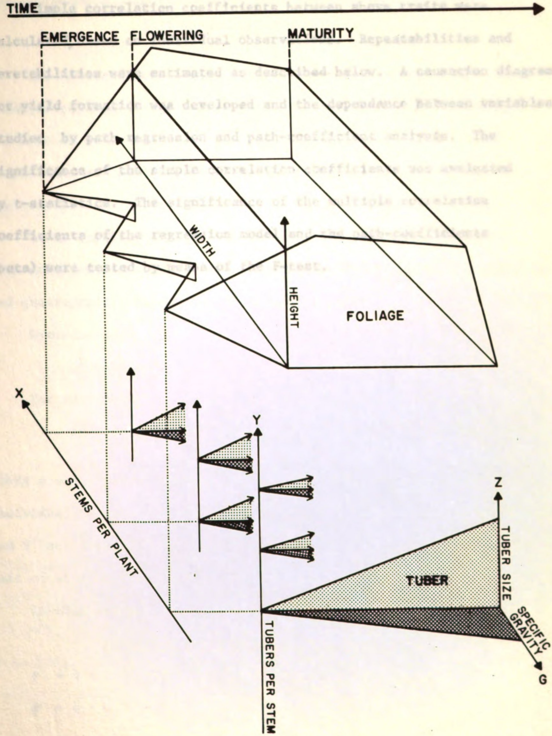
M =Maturity index: Maturity of the foliage was rated twenty and ten days prior to harvest on a 1 to 5 scale (very early, early, midseason, late, very late). The ratings were averaged for analysis.

V =vigor of the **foliage** (dm^2): Vigor was defined as the product of height times width of the foliage. Measurements were taken in ten day intervals.

IV =integral of vigor: The vigor ratings were integrated over time from emergence to flowering or maturity, by the trapezoidal method (IVEF, IVFM, IVEM).

Originally, attempts were made to estimate the leaf area by counting the leaf number and determining the mean leaf size from measurements of three leaves. The canopy structure was to be assessed by measuring plant height and spread of the leaves. Leaf area measurements were soon discontinued because of the variability in leaf size and the time involved in counting leaves. Future adventurers in this area should be warned that the number of leaves on a plant are almost innumberable, not to speak of the disturbance of the leaf

FIGURE 1. A SCHEMATIC REPRESENTATION OF THE DEVELOPMENT OF A POTATO PLANT



canopy that would be necessary to separate and measure the leaves.

Simple correlation coefficients between above traits were calculated, based on individual observations. Repeatabilities and heretabilities were estimated as described below. A causation diagram for yield formation was developed and the dependance between variables studied by path regression and path-coefficient analysis. The significance of the simple correlation coefficients was evaluated by t-statistics. The significance of the multiple correlation coefficients of the regression model and the path-coefficients (beta) were tested by means of the F-test.

3.3 Inheritance of yield, yield components and related traits

3.31 Mathematical Model

The heretability of quantitative characters measures the transmissable portion of the phenotypic variance. It is influenced by the mode of inheritance and the repeatability of the attributes. It provides an index of the potential for genetic improvement of the traits.

In tetrapolids the genetic variance can be partitioned into four components: variance due to additive effects, digenic, trigenic, and quadrugenic interactions (Kempthorne, 1955).

Symbolically:

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_T^2 + \sigma_Q^2$$

For relatives:

$$\sigma_G^2 = (\phi+\phi')1/4\ \sigma_A^2 + (\phi\phi'+\Psi+\Psi')1/6\sigma_D^2 + (\phi\Psi'+\phi'\Psi)1/4\ \sigma_T^2 + \Psi\Psi'\ \sigma_Q^2$$

where ϕ and ϕ' equal the sum of the probabilities that two related individuals receive the same sire or dam gene respectively, and Ψ and Ψ' equal the sum of the probabilities that they receive the same pair of sire or dam genes.

In this study,

Covariance among halfsib populations

$$\phi = 4 \cdot 1/2^2 = 1$$

$$\phi' = 4 \cdot 0 = 0 \qquad \mathrm{Cov(P)} = 1/4\ \sigma_A^2 + 1/36\ \sigma_D^2$$

$\Psi = 6 \cdot 1/6^2 = 1/6$

$\Psi' = 6 \cdot 0 = 0$

Covariance among families within populations

$\phi = 4 \cdot 1/2^2 = 1$

$\phi' = 4 \cdot 1/2^4 = 1/2$ $\quad$ $\mathrm{Cov(F)} = 3/8\ \sigma^2_A + 73/648\ \sigma^2_D + 5/216\sigma^2_T +$

$\Psi = 6 \cdot 1/6^2 = 1/6$ $\quad$ $1/648\ \sigma^2_Q$

$\Psi' = 6 \cdot 2 \cdot 1/6^4 = 1/108$

Covariance among offspring within families and populations (fullsibs)

$\phi = 4 \cdot 1/2^2 = 1$

$\phi' = 4 \cdot 1/2^2 = 1$ $\quad$ $\mathrm{Cov(O)} = 1/2\sigma^2_A + 2/9\sigma^2_D + 1/12\sigma^2_T + 1/36 + \sigma^2_Q$

$\Psi = 6 \cdot 1/6 = 1/6$

$\Psi' = 6 \cdot 1/6^2 = 1/6$

Covariance offsprings with male parent performance

$\phi = 4 \cdot 1/2 = 2$

$\phi' = 4 \cdot 0 = 0$ $\quad$ $\mathrm{Cov\ (OM)} = 1/2\sigma^2_A + 1/6\sigma^2_D$

$\Psi = 6 \cdot 1/6 = 1$

$\Psi' = 6 \cdot 0 = 0$

For each of the traits measured in the progeny population, the variance can be partitioned as given in Table 2. Note that the within family mean square is composed of the genetic variance among offspring plus the error mean square. The latter can be estimated from Table 3. Thus a clean estimate of the genetic variance within family is obtained:

$$\sigma^2_{O(PF)} = MS_O - \sigma^2_E$$

Since the offspring within families are full-sibs, it is evident that:

$$\sigma^2_{O(PF)} = \sigma^2_G - \text{Cov}(O) = 1/2\sigma^2_A + 7/9\sigma^2_D + 11/12\sigma^2_T + 35/36\sigma^2_Q \qquad 1)$$

The total covariance among families, Cov (F), equals the sum of σ^2_P and $\sigma^2_{F(P)}$, thus:

$$\sigma^2_P + \sigma^2_{F(P)} = \text{Cov}(F) = 3/8\sigma^2_A + 73/648\sigma^2_D + 5/216\sigma^2_T + 1/648\sigma^2_Q \qquad 2)$$

The covariance among populations is measured by:

$$\sigma^2_P = \text{Cov}(P) = 1/4\sigma^2_A + 1/36\sigma^2_D \qquad 3)$$

The parent-offspring covariance was obtained directly from the variance-covariance matrix:

$$\text{Cov}(OM) = 1/2\sigma^2_A + 1/6\sigma^2_D \qquad 4)$$

From 1), 2), 3), and 4) the genetic variance σ^2_G and its components can be readily estimated.

For parentage without inbreeding, the heretability in the narrow sense is estimated as follows:

$$h^2 = \frac{2\ \text{Cov}\ (OM)}{\sigma^2_G + \sigma^2_E} = \frac{\sigma^2_A + 1/6\ \sigma^2_D}{\sigma^2_A + \sigma^2_D + \sigma^2_T + \sigma^2_Q + \sigma^2_E}$$

NOTE: The numerator includes a portion of digenic interaction which is also transmittable.

General and specific combining ability are estimated according to **Levings and Dudley (1963).**

$$\sigma^2_{GCA} = 1/4\sigma^2_A + 1/36\sigma^2_D$$

$$\sigma^2_{SCA} = 1/6\sigma^2_D + 1/12\sigma^2_T + 1/36\sigma^2_Q$$

Table 2. Analysis of variance model for the potato population under investigation.

Source of variation	df	expected mean square
Season	1	
Reps. within season	2	
Populations	4	$\sigma^2_E + \sigma^2_{O(FP)} + 15.9\ \sigma^2_{F(P)} + 61.3\ \sigma^2_P$
Families within pops.	24	$\sigma^2_E + \sigma^2_{O(FP)} + 15.2\ \sigma^2_{F(P)}$
Offspring within fams.	460	$\sigma^2_E + \sigma^2_{O(FP)}$
Total	491	

Table 3. Analysis of variance model for estimation of the error mean square from multiple observations on the common male parent.

Source of variation	df	expected mean square
Season	1	$\sigma^2_E + 16\ \sigma^2_R + 32\ \sigma^2_S$
Reps. within season	2	$\sigma^2_E + 16\ \sigma^2_R$
Observ. within reps.	60	σ^2_E
Total	63	

3.32 Results and Discussion

The potato progenies under investigation were derived from eight crosses of non-inbred parents. They were grouped into two populations, which go back to a common ancestry (Pedigree, see Table 1). Twenty offspring were originally selected per family. Several of the progenies showing disease symptoms were discarded during the course of the study.

The number of offspring retained per cross is indicated in Table 4. This table also gives cross means and mean performance of all progenies in the first and second clonal generation. The mean squares for populations, families within populations, and offspring within families are summarized for all characteristics in Table 5. These values were used to compute the genetic variance components (Table 6), and subsequently estimates of heretability, general, and specific combining ability (Table 7).

Yield per hill. The mean performance in yield was similar for the progenies of all crosses. Most of the variability was found within families and only a comparatively small portion was accounted for by population and family within population. More than 80% of the within family variance, however, is attributable to genotypic differences among offspring. In this breeding material, the genetic variance due to additive effects was extremely small, compared to

Table 4a. Cross and seasonal means for yield per hill (W); number of stems per hill (X); number of tubers per stem (Y); number of tubers per hill (XY); average tuber size (Z); specific gravity (G).

Population	Cross	Offspring*	W (g)	X no.	Y no.	XY no.	Z (cm3)	G (g/cm3)
I	1	17	1131.4ab	2.81ab	5.68abc	12.73a	91.10ab	1.0760abc
	2	11	1295.3a	3.09a	4.48c	12.41a	103.83a	1.0731c
	3	12	1232.6a	2.39bc	5.69abc	10.89c	106.99a	1.0724c
	4	18	1207.6ab	2.61bc	5.30bc	11.24bc	107.81a	1.0732c
II	5	11	1141.8ab	2.39bc	6.19ab	11.95bc	99.96ab	1.0790ab
	6	18	1183.9ab	2.24c	6.84a	12.13abc	95.04ab	1.0752bc
	7	18	1055.2b	2.43bc	5.98abc	11.46bc	93.29ab	1.0762abc
	8	18	1086.9b	2.78ab	5.46abc	12.53a	89.75b	1.0796a
1974 means**		123	1024.5	1.75	7.78	12.07	87.75	1.077
1975 means***		123	1311.1	3.42	3.71	11.80	108.68	1.074

Duncan's multiple range test: values with the same letter are not significantly different at the 5% level.

*Number of offspring retained per cross: duplicate measurements for each offspring in the first and second clonal generation.

** 1-hill plots
*** 5-hill plots

the genic interactions. The specific combining ability is about 5.5 times greater than general combining ability. Thus, the transmittable genetic variance is very small, as indicated by the low heretability estimates. This suggests, that mass selection, as commonly practiced in a potato breeding program, is the most appropriate procedure to identify superior genotypes. This picture might change, however, if the yielding potential of the parents is widely different, or if the parentage was inbred.

The crosses made in this study are typical for a potato breeding program. The results indicate what might be expected in other programs. Although Sanford (1960) and Plaisted _et_. _al_. (1962) estimated combining abilities differently, they found that specific combining ability was, respectively, two and four times larger than general combining ability. In diploid potatoes, the magnitude of the dominance component was equal to the additive component in one experiment and much greater than the latter in another experiment (Rowe, 1969). Also in diploids, Morales (1968) found specific combining ability to be 2.3 times greater than general combining ability. Rowe suggested from his observations, that trigenic and quadrugenic interactions must be very important in tetraploids, which these results seem to prove.

Mendoza and Haynes (1974) postulated that increase in yield in potatoes might be directly related to the degree of heterozygosity.

Table 4b. Cross and seasonal means for days from planting to emergence and flowering (E,F); maturity ratings (M); vigour of foliage (V); integral vigour emergence to flowering (IVEF); flowering to maturity (IVFM); and emergence to maturity (IVEM).

Population	Cross	Offspring*	E	F	M	V	IVEF	IVFM	IVEM
I	1	17	25.94a	48.32c	2.56c	26.9a	424.5a	1743.9a	2184.4a
	2	11	25.91a	48.36c	2.66c	28.1a	443.0a	1796.4a	2239.4a
	3	12	26.96a	48.80abc	2.85abc	19.0bc	300.9b	1567.3ab	1868.2b
	4	18	26.72a	48.85abc	3.04ab	18.5c	294.5b	1552.3ab	1846.8b
II	5	11	26.50a	48.90ab	3.25a	20.5b	327.0b	1528.7ab	1855.7b
	6	18	26.89a	48.67abc	2.83abc	18.9bc	300.6b	1491.8b	1792.5b
	7	18	26.58a	48.95a	3.29a	19.4bc	311.6bc	1497.4b	1809.0b
	8	18	26.53a	48.65bc	2.82abc	18.9c	301.0b	1519.0b	1820.0b
1974 means**		123	27.12	49.90	2.89	19.1	303.5	1392.0	1695.0
1975 means***		123	25.95	47.55	2.94	22.9	363.5	1764.4	2127.9

Duncan's multiple range test: values with the same letter are not significantly different at the 5% level.

*Number of offspring retained per cross: duplicate measurements for each offspring in the first and second clonal generation.

** 1-hill plots

*** 5-hill plots

Increasing dissimilarities between the germplasm of the parents would thus maximize possibilities for genic interactions. In selfing studies, Krantz (1946) reported that yield of the S_1 was 81% of the F_1 and only 19% in the S_6. On the other hand, a high degree of heterosis for yield in tuberosum-andigena hybrids was demonstrated by Cubillos and Plaisted (1976).

In the present study, the segregation of _S_. _tuberosum_-_S_. _stoloniferum_ genomes of the female parents might have produced some very specific genic interactions in some progenies and thus could account for much of the large ratio of specific to general combining ability. Glendinning (1969) reported a much wider range of progeny-means for Andigena x Tuberosum crosses than for intra-group hybrids.

Components of yield. Much the same could be said for each component as was said for yield. To avoid redundency, the reader is referred to Tables 2, 3, 4, and 5, which can be interpreted analogously for these components as they were for yield. It is apparent that for all components the magnitude of the additive genetic variance is relatively higher than it was for yield. This in turn is reflected in a smaller ratio of specific to general combining ability and higher heretability estimates. It does suggest a simpler mode of inheritance of these less complex traits. Similar results were obtained for other crops (Williams, 1959; Grafius, 1959; Moll _et_. _al_, 1962), which lead these workers to suggest that the inheritance of yield components

Table 5. Mean squares for season, replication within season, population, family within population, offspring within family and population, and error mean square of 14 developmental traits

Source	Season	Rep	Pop	Family	Offs	Error*
W	.1793E+5	.3147E+3	.228E+4	.1417E+4	.9630E+3	.1534E+ 3
X	.6713E+2	.2470	.2287E+1	.1252E+1	.9902	.5194
Y	.1354E+3	.2665E+1	.1153E+3	.4631E+a	.1438E+2	.2455E+1
Z	.2165E+3	.1546E+2	.1377E+4	.3791E+4	.1700E+4	.5656E+3
G	.2629E-2	.2761E-3	.3421E-2	.1132E-2	.6207E-3	.1441E-3
XY	.2199E+2	.1780	.9672E+2	.2140E+2	.1509E+2	.8928E+1
ZG	.1041E+3	.1521E+2	.1407E+5	.4474E+4	.1970E+4	.6520E+3
E	.9736E+1	.6476	.6407E+1	.3659E+1	.2596E+1	.8326
F	.1372E+1	.1248	.3791E+1	.1878E+1	.1098E+1	.3476
M	.5679E+1	.8374E-1	.4304E+1	.1373E+1	.7631E+1	.1021
V	.3274E+3	.3249E+1	.7956E+1	.2585E+1	.1367E+1	.2568E+1
IVEF	.4123E+4	.9324E+2	.3578E+4	.1066E+4	.5160E+3	.1078E+3
IVFM	.9892E+5	.1729E+4	.7526E+5	.2022E+5	.8941E+4	.1743E+4
IVEM	.1483E+6	.3057E+4	.1245E+6	.2696E+5	.1293E+5	.2874E+4

* estimated from the common male parent.

rather than yield itself, should be studied.

Little information is available in the potato literature about the inheritance of yield components. However, Rowe's data (1969) on diploid potatoes seem to indicate, that the additive variance component is relatively larger for tuber number than for yield. In tetraploid potatoes, Riedel (1948) found that tuber-set (X.Y) is inherited and that it is transmitted by some varieties to a higher degree than by others. Wenk cited by Schick (1956) suggests that selection for high tuber number is more reliable than for a high tuber weight. High correlations were obtained between mid-parent values and progeny means for tubers per plant (.97) and specific gravity (.99), tuber weight (.39), and yield (.87) (Maris, 1969). Depending on the location, on the inter-group hybrids between _S. tuberosum_ ssp. Andigena and Tuberosa performed, on the average, intermediate or equal to the better intra-group population with respect to tuber number per hill and average tuber size. Since the genetic information available is very limited it is difficult to make direct comparisons. It appears, however, that the information available is consistent with the interpretation, that the mode of inheritance of the individual yield components is simpler than that of yield itself.

Emergence. The date of emergence gives some indication of the growth rate in early development. It is influenced by the size and physiological state of the seed tuber (e.g. dormancy, apical dominance) and environmental condition. (Burton, 1966). Early emergence would

Table 6. Genetic variance components due to additive effects, digenic trigenic, and quadrugenic interactions and error mean squares for 14 developmental traits.

Source		σ^2_A	σ^2_D	σ^2_T	σ^2_Q	σ^2_E
stems	X	.0626	.0377	.2550	.1815	.5194
tubers	Y	.3850E+1	.5013E+1	.3798E+1	.2697E+1	.2455E+1
size	Z	.5377E+3	.7740E+3	.1398E+3	.0945E+3	.5656E+3
gravity	G	.1312E-3	.1493E-3	.1892E-3	.1347E-3	.1446E-3
yield	W	.0325E+5	.1732E+5	.4551E+5	.2482E+5	.1534E+5
X·Y		.2112E+1	.1017E+1	.2675E+1	.1905E+1	.8928E+1
Z·G		.6131E+3	.9927E+3	.1486E+3	.1061E+3	.6520E+3
emergence	E	.1347	.3895	.8421	.6387	.8326
flowering	F	.1156	.1845	.3297	.2543	.3476
maturity	M	.1744	.1346	.2838	.2149	.1021
vigour	V	.3043E+1	.3857E+1	.3725E+1	.3245E+1	.2568E+1
IVEF		.1425E+3	.1773E+3	.1125E+3	.0987E+3	.1078E+3
IVFM		.3165E+4	.3542E+4	.1884E+4	.1166E+4	.1743E+4
IVEM		.4967E+4	.5192E+4	.2346E+4	.1757E+4	.2874E+4

allow a more rapid establishment of the leaf area.

Most of the genetic variance in earliness was due to genic interactions. The ratio of specific to general combining ability is very large and the heretability estimate is very small. It should be noted at this point, that emergence is also a complex trait similar to yield, since it is also the outcome of a long series of developmental events. Contrary to yield, however, emergence is not very stable, as indicated by the relatively large error mean square. The reader should be reminded though, that if the experimental error is properly estimated, a clean estimate of the genetic variance components is obtained.

Flowering. Stolon initiation occurs about at the time of flower differentiation, and tuber formation at about the end of flower bud development (Clark, 1921). The date of flowering provides an estimate of the beginning of the tuber bulking period.

The heretability estimate was rather small and specific combining ability was twice as large as general combining ability. This characteristic, presumable under photoperiodic control, could only be modified to a small degree by the environment.

Maturity. The time of leaf senescence, evaluated by the maturity ratings, indicates the termination of the tuber bulking period. While early varieties are very important to extend the duration of the potato marketing period and to fill demands for new potatoes early in the year, late varieties have a higher yield potential because of

Table 7. Estimates of heritability, general and specific combining ability for 14 developmental traits.

Source		h^2	$*h^2$	σ^2_{GCA}	σ^2_{SCA}	$\sigma^2_{SCA}/\sigma^2_{GCA}$
stems	X	.07	.14	.0167	.0326	1.96
tubers	Y	.31	.36	.1104E+1	.1227E+1	1.11
size	Z	.38	.52	.1559E+3	.1427E+3	.92
gravity	G	.24	.30	.3694E-4	.4439E-4	1.20
yield	Y	.08	.09	.1294E+4	.7369E+4	5.53
X·Y		.14	.32	.5563	.4453	.80
Z·G		.38	.51	.1806E+3	.1808E+3	1.00
emergence	E	.09	.13	.0449	.1528	3.43
flowering	F	.14	.20	.3403E-1	.6529E-1	1.92
maturity	M	.24	.27	.4733E-1	.5205E-1	1.10
vigour	V	.26	.31	.0867E+1	.1018E+1	1.17
IVEF		.32	.38	.4055E+2	.4167E+2	1.03
IVFM		.38	.45	.8896E+3	.7797E+3	.88
IVEM		.39	.47	.1581E+4	.0914E+4	.58

h^2 measures the ratio of transmittable genetic variance to phenotypic variance.

$*h^2$ measures the ratio of transmittable genetic variance to total genetic variance.

the longer growing period. Therefore, maturity ratings are very important in variety classification.

The variance accounted for by specific and general combining ability was approximately equal. The calculated heretability was about 24%. Maris (1969) found a close correlation (.98) between progeny means and mean parent performance. However, there was a wide range of maturity ratings within each cross indicating a high specific combining ability.

Vigor. It was found that the vigor rating (foliage height times width) at flowering time closely approximated the highest ratings, which were usually measured about a week later. If a single assessment of vigor were to be made, a physiological date, like flowering, would be preferable to a chronological date. Thus, it was felt that vigor at flowering was a useful and good measure of the size of the foliage of a plant or plot. Vigor ratings were also made at ten day intervals, allowing integration of vigor over time for different developmental time spans.

Surprisingly, all these measurements, which provide a rough estimate of leaf are and leaf area duration, showed a high heretability and reveal a high portion of additive genetic variance. General combining ability was equal or larger than specific combining ability. Morales (1968) measured the photosynthetic leaf area of haploid potato progenies at different stages of development and found general and specific combining ability to be about equal, although neither was significant.

Conclusion. The heretability in the narrow sense was extremely low for yield as was the general combining ability, due to the genic interactions. Therefore, mass selection, as presently practiced appears most suitable. Success will depend on the repeatability found between consecutive clonal generations. Several traits including the components of yield, showed a simpler mode of inheritance. Based on similar observations, in other crops, Moll et. al (1962) suggested, that the inheritance of the components of yield should be considered instead. Selection of potato parents based on either yield, tubers per hill, or tuber weight resulted in offspring populations with similar yields and yield structure (Plaisted and Cubillos, 1972). More recently, Cubillos and Plaisted, (1976) showed that hybrids between Andigena and Tuberosa were generally intermediate to the intra-group hybrids for the components of yield. For yield, however, a high degree of heterosis was found. Based on the results of this study, it is expected that progeny performance is more closely approximated by the mean parent value for the components of yield than it is for yield itself. The higher heretability for the components of yield is attributable to a relatively larger portion of additive to total genetic variance. The low predictability of yield from the parent performance does not rule out the possibility to predict yield of the progeny from the parental means of the components of yield.

3.4 Repeatability of yield and developmental traits in early clonal generations

3.41 Mathematical Model

Conceptually, the phenotypic value of an organism can be divided into components associated with the genotype and environment (P=G+E). The repeatability measures the relative importance of the genotype as the determinant of the phenotypic value and is given by the ratio of genotypic to phenotypic variance of σ^2_G/σ^2_P. In asexually propagated crops, successive performances of the same genotype can be measured through both temporal and spacial repetition of observations on genetically identical organisms. This gives an unbiased estimate of the genotypic and environmental variance components, which may be obtained only from identical twins in sexually propagated organisms.

In potatoes which are vegetatively propagated, the correlation among scores on plants of the same clone measures the equivalent of the repeatability ($\rho_R = \sigma^2_G/\sigma^2_P$). Thus, the magnitude of the repeatability between early clonal generations indicates the selection pressure that may be applied in clonal selection, with a minimal loss of potential valuable genotypes.

It was stated earlier that in the first clonal generation the plant type is distinctly different from later generations because of the small size of the seed tubers. The knowledge of the direction and magnitude of these differences in plant type would be valuable for potato selection. The modifiability of characteristics between the first and second clonal generations is indicated by the degree of association between individual observations and seasonal means. It can be measured by the intra-season correlations ($\rho_S = \sigma^2_S/\sigma^2_G+\sigma^2_S+\sigma^2_E$), where σ^2_E represents a residual environmental component.

3.42 Results and Discussion

The same fourteen traits were considered in this study as discussed in the previous section. Since the number of entries was too numerous to be tabulated, the reader is referred to Table 4, where the mean progeny performance for each cross and seasonal means for the first and second clonal generation are given. It should be kept in mind, that although the cross means were similar for most of these traits, the variability among offspring of each cross was considerable, due to high specific combining effects.

Repeatability estimates are given for all traits in Table 8. Logarithmic transformations were performed on some characteristics. The repeatabilities for the transformed variables were consistently higher than for the original variables, suggesting that the experimental error is independent and normally distributed with respect to the former. This seems to be confirmed by the generally higher correlations between the transformed variables in Table 9-b compared to values in the correlation matrix in Table 9-a. Both matrices are given, however, since most of the available literature deals with untransformed variates.

The repeatability estimates (ρ_R) represent the ratio of the total genotypic to phenotypic variance. It is equivalent to what is, in the potato literature, generally referred to as heretability (Maris, 1969; Tai, 1974). The repeatability measures the consistency in

Table 8. Repeatability estimates (ρ_R) and intra-season correlations (ρ_S) of 14 developmental traits for potato progenies grown in the first and second clonal generation.

Source		ρ_R	ρ_S	ρ_R'	ρ_S'
stems	X	.098	.556	.382	.354
tubers	Y	.161	.365	.463	.347
size	Z	.260	.100	.531	.232
gravity	G	.433	.056	.482	.175
yield	W	.388	.140	.463	.248
X·Y		.363	.001	.537	.247
Z·G		.259	.100	.522	.148
emergence	E	.351	.318	--	--
flowering	F	.785	.183	--	--
maturity	M	.693	.022	--	--
vigour	V	.198	.384	.352	.412
IVEF		.203	.411	.327	.447
IVFM		.312	.472	.473	.482
IVEM		.232	.461	.423	.436

ρ_R' and ρ_S' are repeatabilities and intra-season correlations for the transformed variables (eg. X' + ln (X)).

performance of the same genotype in different environments. In contrast, the modifiability (ρ_S) measures here the amount of common variation of all genotypes from the first (C1) to the second (C2) clonal generation. One would suspect an inverse relationship between repeatability and modifiability. The closeness of this association will depend, though, on the genotype times environment interaction.

Yield per hill. Repeatability estimates for yield were relatively high, ($\rho_R = .39$ and $\rho'_R = .46$), if compared to most other traits under investigation. This, however, corresponds to a degree of determination of only .15-.21, which makes selection for yield *per se* highly questionable. Tai (1974) published a similar repeatability of .31 for individual clones and .58 for cross means. The latter value is not very meaningful, since family selection appears to be out of question, because of the large genetic variability in the yielding potential between individual offspring. The repeatability reported by Maris (1969) was higher (.67), but based on later clonal generations. The correlation coefficient between yield in the seedling and clonal generations ranged from .17 to .65 (Pfeffer, 1963). In view of this wide range in correlation coefficients, it should be noted that some varieties inherently exhibit a higher degree of stability for yield between environments (Tai and Young, 1972).

In this study, yields were slightly higher on the average in the second season. This increase was not consistent for all genotypes as indicated by the low degree of modifiability. In view of these results,

Table 9a. Correlations among 14 developmental characteristics of 123 potato progenies grown in the first and second clonal generation.

		W	X	Y	Z	G	XY	ZG	E	F	M	V	IVEF	IVFM
yield	W													
stems	X	.32												
tubers	Y	.08	-.57											
size	Z	.45	.07	-.25										
gravity	G	-.03	.03	.09	-.15									
X·Y		.55	.44	.58	-.25	-.14								
Z·G		.46	-.09	-.25	.99	-.03	-.33							
emergence	E	-.20	.29	.13	-.12	.18	.32	-.05						
flowering	F	.12	.00	.12	.03	.14	.13	.02	.64					
maturity	M	.16	.01	.14	.02	.24	.14	.02	.26	.38				
vigour	V	.37	.49	-.12	.04	.01	.31	.04	-.34	.07	-.14			
IVEF		.38	.49	-.17	.05	.01	.32	.05	-.32	.32	-.07	.82		
IVFM		.48	.23	.10	.15	.11	.35	.16	-.18	-.14	.30	.55	.59	
IVEM		..49	.32	.05	.14	.10	.37	.14	-.28	.23	.24	.71	.73	.94

Probabilities for significance of correlation coefficients: P= .05,|r|= .09; P= .01,|r|= .12

it is not surprising that Maris (1966), Harris et.al. (1967), Davis and Johnston (1974), and Tai (1975) all found very poor agreements between hill selection made in early clonal generations and thus suggest that only the poorest performer should be discarded in the first generation. It would be desirable to have additional criteria to recognize potentially valuable genotypes.

Components of yield. The repeatabilities are consistantly higher for traits formed later in the developmental sequence. The number of stems per plant may be less stable than subsequent traits in the sequence, as indicated by the results of Steineck (1959), it is nevertheless a varietal characteristic as indicated by the results of Thompson and Taylor (1974) and by the fairly high repeatability of X'. The average number of stems per hill was two times larger in C_2 than C_1. This is believed to be the result of the smaller seed tuber size in C_1. The degree of apical dominance is expected to be higher in these small tubers and possibly the number of eyes might be reduced as well. Furthermore, fewer stems developed from small seed pieces because of increased competition between stems for nutrients from the mother tuber (Moorby, 1967). The C_1 plants did produce twice as many tubers per stem on the average. Thus the total number of tubers per plant was even slightly larger than in C_2 plants. The larger Y in C_1 clones, seems to have resulted in a smaller Z. This compensatory action between the yield components is indicated by the negative correlations between them (Table, 9).

Table 9b. Correlations among 11 transformed and three non transformed developmental traits of 123 progenies grown in the first and second clonal generations.

		W'	X'	Y'	Z'	G'	X'+Y'	Z'+G'	E	F	M	V'	IVEF'	IVFM'
yield	W'													
stems	X'	.47												
tubers	Y'	-.04	-.70											
size	Z'	.55	.14	-.45										
gravity	G'	-.04	-.09	.16	-.25									
X'+Y'		.53	.49	.63	-.48	-.30								
Z'+G'		.56	.15	-.48	.92	-.13	-.53							
emergence	E	-.40	.45	.23	-.17	.21	.61	-.01						
flowering	F	.17	.01	.22	.08	.10	.28	.14	.64					
maturity	M	.22	.01	.12	.07	.44	.16	.24	.26	.38				
vigour	V	.58	.48	-.04	.10	-.03	.46	.09	-.52	.06	.02			
IVEF'		.61	.49	-.06	.13	-.03	.42	.10	-.51	.63	.01	.06		
IVFM'		.68	.56	-.26	.36	.01	.34	.35	-.61	-.37	.39	.91	.63	
IVEM'		..65	.51	-.31	.42	.02	.38	.42	-.55	.11	.25	.83	.78	.92

' indicates logarithmic transformation (e.g. W'= ln(W)).
Probabilities for significance of correlation coefficients; P= .05, $|r|$= .09; P= .01, $|r|$= .12

The compensatory nature between yield components of potatoes was already pointed out by Steineck (1959). He also stressed the significance of this developmental plasticity in the attainment of stable yields. A high degree of developmental plasticity is expected to be especially important in vegetatively propagated crops. It was demonstrated by Adams (1967), however, that it is very important in other crops as well. The importance of this compensatory action can be fully realized only if one appreciates the degree of modifiability of X by the environment. Evidence in animals (Lerner, 1954) and corn, (Shank and Adams, 1960) suggests that this phenotypic buffering capacity may be associated with heterozygosity. Recalling the high degree of genic interactions in potatoes for most of these traits and the apparent close association between heterozygosity and yield or vigor, it is suggested that both heterozygosity and genetic interactions do provide the genetic resource for phenotypic homeostasis and thus stable yields of potatoes.

It must be stressed that the similar XY in C_1 and C_2 is achieved because of both individual and population buffering. In other words, the same clones do not have the highest XY in both seasons. Otherwise a much higher repeatability would have been obtained. The combination of low modifiability and low repeatability is the result of high genotype x environment interaction between and within clonal generations.

Repeatabilities were higher for X' and Y' than for X and Y indicating that these traits are altered exponentially with respect to seasonal differences. For example, clones with one stem in C_1 would have two in C_2, clones with two stems in C_1 tend to have four in C_2, etc.. We notice a significant correlation between X and W while the correlation between Y and W is not significant. This does not mean that one should select for high X in the C_1 since the genotypic potential for X cannot be accurately assessed, especially in the C_1. The selector should be aware that in selection for high W or XY in C_1, he is selecting primarily for high Y. This would be desirable in genotypes that are well buffered with respect to Y, but it would produce numerous XY and too small Z in the C_2 in clones with a low buffering ability, since X is expected to be greater in C_2. It is concluded that clones with a large XY, due to either an extremely large X or Y value or both can be safely rejected in C_1. Similarly plants with both a low X and Y value can also be eliminated. Clones with a moderate XY, due to either a high X or Y, and clones with a low X but moderate to high Y should be retained in C_1, although the latter may have a less than optimal XY and/or W.

The repeatabilities for tuber size and gravity are considerably higher than those for X and Y. The low modifiability indicates that there is only a small consistent change from C_1 to C_2. The within season variability is large, in part due to the compensatory interaction with XY. The selection pressure for Z applied in the C_1 should be very high for clones with both low X and Y, moderately high for medium to high X regardless of Y, and low for clones with low X but indicating that these traits are altered exponentially with respect to seasonal differences. For example, clones with one stem in C_1 would have two in C_2, clones with two stems in C_1 tend to have four in C_2, etc.. We notice a significant correlation between X and W while the correlation between Y and W is not significant. This does not mean that one should select for high X in the C_1 since the genotypic potential for X cannot be accurately assessed, especially in the C_1. The selector should be aware that in selection for high W or XY in C_1, he is selecting primarily for high Y. This would be desirable in genotypes that are well buffered with respect to Y, but it would produce numerous XY and too small Z in the C_2 in clones with a low buffering ability, since X is expected to be greater in C_2. It is concluded that clones with a large XY, due to either an extremely large X or Y value or both can be safely rejected in C_1. Similarly plants with both a low X and Y value can also be eliminated. Clones with a moderate XY, due to either a high X or Y, and clones with a low X but moderate to high Y should be retained in C_1, although the latter may have a less than optimal XY and/or W.

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but large Y. Fairly strong selection can be practiced for specific gravity for most clones in the C_1, except those with very large Z or large XY values, especially in combination.

The results reported for yield components in this study are consistent with the information in the available literature. Krug et. al. (1974) suggested that selection for XY is not possible. Agreements were very poor between clonal selections made at different locations, although XY was not significantly altered (Harris et. al 1967). From previous discussion it is clear that XY ought to be evaluated with respect to X or Y. Repeatability estimates given by Pfeffer (1963), Maris (1969), and Tai (1974) were .03-.22, .66 and .31 for XY and .24-.45, .64, and .38 for ZG. Among others, Geidel and Schuster (1965) and Harris et. al (1967) found specific gravity to be more stable than yield. Published repeatability estimates for G were .67 (Peterson and Plaisted, 1960), .63 (Cunningham and Stevenson, 1963), .39 (Johanson et. al. 1967) and .76 (Maris, 1969).

Emergence. The date of emergence is generally not considered in the selection of potato clones. Repeatabilities were measured in this study as .35 and by Maris (1969) as .47. Neither is very high and modifiability is also low. The correlation between E and W was significantly negative in both studies. Since the expected experimental error is very large for E, especially in C_1, where sprout and root development depend on a very small seed tuber, it might prove useful to the selector to take this criteria into consideration. Thus a stronger selection pressure for yield can be applied for early than for late emerging C_1 plants.

Flowering. The flowering date showed the highest repeatabilities, as would be expected for a trait under photoperiodic influence. F is positively associated with both E and M. The later flowering plants seem to produce more Y and a higher G.

Maturity. While the time of flowering may indicate the beginning of the tuberization, foliage maturity marks the decline of photosynthesis (Winkler, 1971). High repeatability and low modifiability was found for the maturity ratings. A positive correlation was found between maturity and yield. This association was not very strong, however, and does not preclude the possibility of finding early, high yielding clones. Maris (1969) reported a correlation between M and W of .75. The repeatability for maturity, as found in this study, of .69 is intermediate to the estimates of .52 (Tai, 1974) and .85 (Maris 1969), but all are high, indicating that a high selection pressure may be applied early in the selection program.

Vigor. The vigor ratings at the time of flowering were highly correlated with W. The plants with the higher X values were generally more vigorous. Since Y was only slightly influenced by V, plants with higher V and IVEF values produced more tubers per hill. Similarly if IVFM is high a larger Z and ZG value is expected. It is not surprising, therefore, that W is closely associated with IVEM.

Krug, *et. al* (1974) reported that yield was positively correlated with plant height in the first 60 days and the foliage duration. Plant height and maturity were positively correlated (Maris, 1969) with each other. Both gave a positive correlation with XY, ZG, G, and W. The repeatability for plant **height** was .67, which is considerably higher than in this study. It was obtained, however, from replicated trials in later clonal generations. The ρ'_R reported here does indicate that plant vigor can already be assessed fairly accurately in C_1. Foliage was more vigorous in C_2, which can be explained by the larger seed tubers employed and the more numerous stems found in C_2.

Conclusion. Clonal selection for yield in C_1 is highly questionable. The repeatabilities reported in this study agree well with the few reports in the past (Peterson and Plaisted, 1960; Cunningham and Stevenson, 1963; Johanson et. al, 1967; and Tai, 1974). Maris (1969) published generally higher values. They were obtained, however, from later clonal generations and more plants per replication. It seems possible though, to make negative selection even in C_1, if additional information to tuber set, tuber size, and appearance is included in the judgement. For some traits the high modifiability between C_1 and C_2 indicates a consistent trend, which could be taken into account by the selector or by covariance analysis. Much variability is unaccounted for as a result of the environment x genotype interactions.

Assessment of additional traits and knowledge of their contribution to yield and its structure promises to enhance the predictability of the desirability of a genotype. Correlations between traits may help to understand such relationship, but it does not imply causation and cannot measure the predictive value of a characteristic. The following section is devoted to studying the formation of yield in more detail.

3.5 GENETIC, ENVIRONMENTAL AND ALLOMETRIC CONTROL OF YIELD

Yield is the outcome of a long sequence of developmental events, presumably under genetic and environmental control. It is a complex characteristics, which can be logically divided into its components. Not only yield itself but its structure is important in potato breeding and production. The yield components interact physiologically and thus may limit full expression of the genotype and the available environmental resources (in a broad sense). Such interactions are commonly observed as negative correlations between these components. Examples for potatoes are given by Maris (1969), Tai (1975) and in Table 9 of this study. Tai used Sewall Wrights (1921) path coefficients to study this interaction.

The potato is an excellent organism in which to study these interactions and genetic control over the expression of sequential traits, since repeated measurement can be made on identical genotypes in different environments. Following, is a study of the significance of genotype and allometry in the expression of several traits in C_1 and C_2, which are believed to be important in the formation of yield.

3.51 Mathematical Model

The phenotypic expression of a character is the sum of genetic and environmental effects. The latter is further partitioned, since typical differences are anticipated between seasons in which C_1 and

C_2 are propagated.

Symbolically, $P = G + S + E$,

where P is the phenotype; G is the genetic effect and S is the seasonal effect typical to seasons in which the C_1 and C_2 **were grown, here** also confounded with effects specific to the two particular seasons; and E is the deviation of P from G + S. Since it is difficult to assess the genotype or environmental resources directly, their manifestation may be measured in phenotypic units instead. Then, if genotypes are randomly distributed relative to variations in environments and vice versa, phenotypic variance is:

$$\sigma^2_P = \sigma^2_G + \sigma^2_S + \sigma^2_E$$

where σ^2_G and σ^2_S are the variances of genetic and specific seasonal responses and σ^2_E is the residual environmental portion of σ^2_P.

The above result can be extended to sequential traits of a breeding population of potatoes. It was pointed out earlier that preceeding or contemporaneous events set the state (phenotype) for gene action and environmental stimuli which lead to subsequent or simultaneous events. Thus this state co-determines expression of successive traits. Based on the premise, that manifestation of a sequential trait Z is determined by the genotypic potential, the environmental resources available and the phenotypic state of the components X and Y, whose formation preceeds Z, the following dependence can be formulated:

$$Z = G_Z+S_Z+P_X+P_Y+E$$

where Z denotes the phenotypic value of the trait; G_Z, S_Z, P_X, and

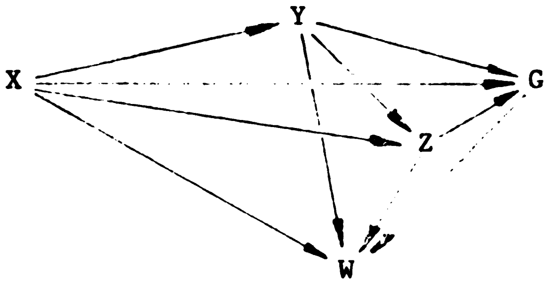
P_Y the phenotypic response attributable to genotype, season, and the allometric dependence between Z and the sequential traits X and Y; and E a residual environmental deviation. Thus, the following path regression model may be used to study their respective effects:

$$Z = a_Z+b_{GZ}\cdot G_Z+b_{SZ}\cdot S_Z+b_{XZ}\cdot X+b_{YZ}Y \qquad (1)$$

where X, Y, and Z are the phenotypic values of sequential traits; G_Z is the mean phenotypic value of a genotype measured over a range of environments, X's and Y's; S_Z is the mean phenotypic performance in the first and subsequent clonal generations measured over a range of genotypes X's and Y's; a_Z is the Z intercept; and the b's are the partial regression coefficients measuring the expected change in Z when either of the dependent variables change while the others remain constant.

NOTE: There are some potential dangers involved in the above approach: To estimate the use of environmental resources available for Z in different clonal generations by the mean phenotypic performance of Z may be valid only if the genotypes, X's and Y's are randomly distributed with respect to clonal generations. While the genetic potential may best be revealed in favorable environments, it seems reasonable to assess it based on the average phenotypic performance if the environmental conditions, the X's and Y's are divergent enough, to allow expression of the genetic differences. The power of this model is greatest if genotype-environment interactions are minimal or can be successfully reduced. Such interactions are believed to be largely the result of the influences which component traits exert on each other. Thus, the model should be valid for component traits after adjustment for their interactions.

The regression model (1) expresses the dependence between sequential traits analogously to the path coefficient model introduced by Sewall Wright (1921). The differences being, that the latter uses standardized variables. Thus the coefficients obtained by Wright's method would be identical to the standard partial regression coefficients (Beta) obtained by solving (1). The path coefficient model, however, does imply causal order, as may be defined in a diagram but the regression model may or may not. While each method has its merits and limitations, the path coefficient approach has a distinct advantage if the variates do not have equivalent scales and the relative contributions by the independent variables are to be assessed. It is thus extremely useful in studying the relationship between yield components and was used to this effect for potatoes (Tai, 1975). This author, however, calculated the path coefficients from the correlation matrix by methods, which become rather cumbersome for a large number of sequential traits. Also, Tai did not account for the influence of genotype or environment. It is shown below how the path coefficients may be obtained from beta by solving the regression equations (2) through (5). Suppose we have the causal relationship between yield (W) of potatoes and its components X, Y, Z, and G.



$$Y = a_Y + b_{XY} \cdot X \tag{2}$$

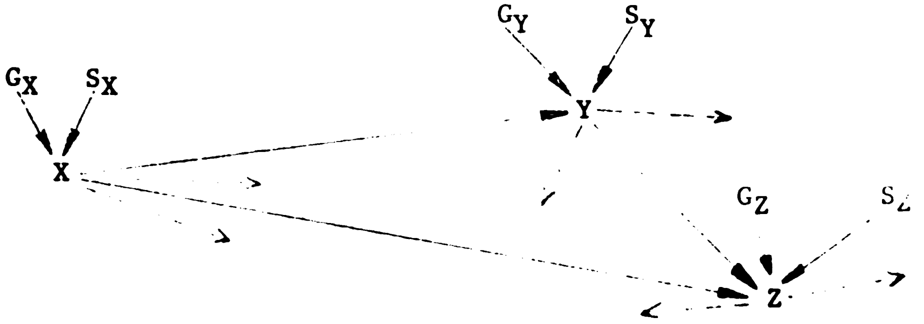
$$Z = a_Z + b_{XZ} \cdot X + b_{YZ} \cdot Y \tag{3}$$

$$G = a_G + b_{XG} \cdot X + b_{YG} \cdot Y + b_{ZG} \cdot Z \tag{4}$$

$$W = a_W + b_{XW} \cdot X + b_{YW} \cdot Y + b_{ZW} \cdot Z + b_{GW} \cdot G \tag{5}$$

The betas obtained from the above equations become path coefficients e.g. $p_{XY} \ldots p_{GW}$, because of the causal structure of the model.

Including the genotypic and seasonal components, the path diagram below and the path regressions (6, 7,...) are obtained.



$$X = a_X + b_{GX} \cdot G_X + b_{EX} \cdot E_X \tag{6}$$

$$Y = a_Y + b_{GY} \cdot G_Y + b_{EY} \cdot E_Y + b_{XY} \cdot X \tag{7}$$

$$Z = a_Z + b_{GZ} \cdot G_Z + b_{EZ} \cdot E_Z + b_{XZ} \cdot X + b_{YZ} \cdot Y \qquad (8)$$

'

'

'

etc.

NOTE: It is implied that the development of a plant is a process directed by timely and selective activation of genetic systems which are at least partially independent and by environmental resources which differentially and chronologically affect individual traits. Therefore, there are no direct paths from G_X or E_X to either Y or Z.

Data transformations. Full power of any statistical model is obtained only be selection of an appropriate scale of measurement. Both the regression and path coefficient model require linear dependance between variates. In this study logarithmic transformation was chosen for the following variables: yield, stems per plant, tubers per stem, tuber size, specific gravity, vigor, and integral vigor over time. It may be pointed out, that apart from the familiarity of the linear scale, there is really no scientific necessity for using it to measure variates. The logarithmic scale is preferred because the contributions to yield by its individual components are multiplicative. This relationship ($W = X \cdot Y \cdot Z \cdot G$) is not suitable for analysis by linear regression procedures. Upon transformation, however, it renders an additive model (9)

$$Z = a_Z + b_{GZ} \cdot G_Z + b_{EZ} \cdot E_Z + b_{XZ} \cdot X + b_{YZ} \cdot Y \qquad (8)$$

$$\vdots$$

etc.

NOTE: It is implied that the development of a plant is a process directed by timely and selective activation of genetic systems which are at least partially independent and by environmental resources which differentially and chronologically affect individual traits. Therefore, there are no direct paths from G_X or E_X to either Y or Z.

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$$\ln W = \ln X + \ln Y + \ln Z + \ln G \tag{9}$$

or

$$W' = X' + Y' + Z' + G' \tag{10}$$

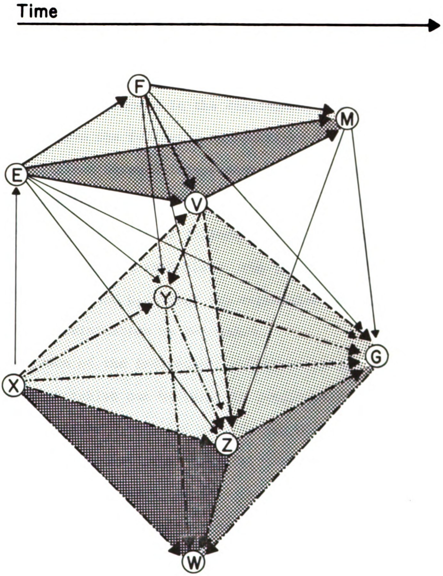
where the variable in (10) are transformed.

Experimental evidence given in the literature further seems to justify such a transformation. Total yield was found to increase asymptotically with increasing numbers of stems (Holliday, 1967; Thompson and Taylor, 1974). Tuber number per stem decreased asympototically with increasing stem density and tuber size decreases towards a constant value with increasing tuber numbers (Steineck, 1959; Thompson and Taylor, 1974). Plaisted (1957) showed that both ln(dry weight) and ln(starch content) increases linearly with ln(tuber weight). Also ln(shoot weight) was proportional to ln(stem per plant) Moorby (1967).

Note that the variables on the time scale were not transformed hence both leaf area and tuber weight appear to increase exponentially with time of development (Necas, 1965; Plaisted, 1957; and Gray, 1973). It must be emphasized, however, that the interactions between component traits, genotype, and environment depend on the scale of measurement. Also, it is implied that the error is normally and independently distributed with respect to the transformed variables, that is that the measurements on the log scale are unbiased. This seems to be a reasonable assumption since Cubillos and Plaisted (1976) found that population variances were positively associated with family means, for potato yield and its components.

The developmental model. The developmental model as schematically presented in Figure 1, was translated in a causation diagram (Figure 2), which indicates the assumed dependence between the traits under investigation. The single headed arrows represent paths along which a trait formed early during the sequential development influences a later one. W, X, Y, Z, and G were yield and its components, defined earlier. E and M measure together the leaf area duration and F and M duration of tuber bulking. The size of the foliage is estimated by V. The integrals of vigor over different developmental intervals were omitted, since they did not add any significant information in the regression model after E, F, M, and V were included. The significance level was generally higher though for IVEF, IVFM, and IVEM than for either E, F, M, or V individually. For simplicity, the genotypic and seasonal components contributing to each trait are omitted.

FIGURE 2. CAUSATION DIAGRAM INDICATING THE DEVELOPMENTAL RELATIONSHIP BETWEEN YIELD (W); ITS COMPONENTS: NUMBER OF STEMS PER PLANT (X), NUMBER OF TUBERS PER STEM (Y), AVERAGE TUBER SIZE (Z), AND SPECIFIC GRAVITY (G); DAYS FROM PLANTING TO EMERGENCE (E) AND FLOWERING (F); AND MATURITY RATINGS (M). THE ARROWS INDICATE THE PATH ALONG WHICH THE SEQUENTIAL TRAITS INFLUENCE EACH OTHER.



3.52 Results and Discussion

A separate path regression and path coefficient analysis was carried out for each variable. The determination of individual observations by the mean performance of an offspring, the mean performance of all offspring in the C_1 and C_2 and by the allometric relationship of variables which preceed in the development was measured. Tables 10a to 10i give the following information: (r_{21}) the correlation coefficient between independent and dependent variables; (p_{21}) the corresponding path coefficient (Beta); (P_{21}) the sum of the products of the path coefficients following all paths from the independent to the dependent variables; the indirect paths or the difference between P_{21} and p_{21}; (b_n) the regression coefficients; and R^2 the degree of determination by the model.

The importance of the independent variables in the determination of the dependent variables can be directly judged by relative magnitude of the path coefficients. Both the path or regression coefficients allow prediction of the dependent variable, whether or not the independent variables are standardized. The direct path (p_{21}) measures the expected change in the dependent variable by altering only one and keeping the other independent variable constant. The total path (P_{21}) measures the change in the dependent by altering one of the independent variables only, but accounting for changes it may have on other variables.

Table 10a. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits preceding in the development) and the dependent variable for the following trait: emergence.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance			Path Regression ($b_o \cdots n$)	Degree of Determination R^2
		direct (p_{21})	indirect ($p_{23} \cdot p_{31} + p_{24} \cdot p_{41} \cdots$)	total (P_{21})		
emergence/offspring	.351**	.389**	-	.389	.870**	
/season	.318**	.218**	-	.218	.679**	
/stems	.447**	.425**	-	.425	2.070**	
/constant					-18.662**	.43**

Emergence. The date of emergence is generally not considered in the evaluation of C_1 plants in a breeding program. However, both in this study and by Maris (1969) a negative correlation between emergence and the tubers per hill, or yield, was found.

The correlation coefficients and regression coefficients in Table 10a are of the same magnitude, thus indicating independence between the dependent variables. Both coefficients were low between the mean performance of each offspring and the actual emergence in each plot, indicating a weak control over emergence by the genotype. Recalling from Table 4, C_2 plants emerged more rapidly, which was expected because of the larger seed size in C_2. Also, the positive correlation between the number of stems and emergence indicate that the more stems that developed from a seed piece, the later they generally emerged. This is not surprising since early sprout development depends entirely on the nutrients available from the seed piece. Moorby (1967) showed, that due to early competition, the size of an individual sprout and its root system is smaller if more stems are developed from a seed piece. The magnitude of the path coefficients indicates that all three dependent variables are approximately equally important in the determination of emergence.

The information believed to be most significant is, that 57% of the variability could not be explained by the model. This genotype x environment interaction may occur from random deviations in the

Table 10b. Simple correlations,path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits preceding in the development) and the dependent variable for the following trait: flowering.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance direct (p_{21})	Causal Covariance indirect $(p_{23} \cdot p_{31} + p_{24} \cdot P_{41} \ldots)$	Causal Covariance total (P_{21})	Path Regression $(b_o \ldots n)$	Degree of Determination R^2
flowering/offspring	.784**	.835**	-	.835	.484**	
/season	.184**	.072*	-	.072	.195**	
/emergence	.643**	.393**	-	.393	.220**	
/stems	.011 ns	-	.167	.167	-	
/constant					12.093**	.81**

physiological state of the seed piece, differences in soil structure, and fertility, etc. Thus, most of the influence emergence has on later traits must be considered random and atypical for the offspring and should be taken into consideration in the evaluation of these traits.

Flowering. Potatoes are not grown for their flowers, however, since tuber development takes place underground, the flowering date does provide a mark in the physiological time table of a plant. If found closely tied to a less easily recognizable trait, flowering could be monitored instead. Tuberization was found to begin, in general, at about the time of flower bud development (Clark, 1921) or shortly prior to flowering (Grosch, 1955), and was used here as an index of tuber induction. Moorby (1967) found that neither seed tuber size nor number of stems influence time of tuber induction. Thus no path was drawn from X to F in the path diagram (Figure 2). This seems to be justified since no correlation between X and F was found (Table 10B). Late emergence did delay flowering somewhat, while there was hardly any difference between the season in which C_1 or C_2 were grown. From the relative size of the path coefficients, it can be seen that most of the variability was accounted for by offspring. Note, that the path coefficient between flowering and emergence is smaller than the correlation between emergence and flowering within each season, resulting in a decreased P_{SF} compared to r_{SF}. An

Table 10c. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits preceding in the development) and the independent variable for the following trait: vigor.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance direct (p_{21})	indirect ($p_{23} \cdot p_{31} + p_{24} \cdot P_{41} \cdots$)	total (P_{21})	Path Regression ($b_o \ldots n$)	Degree of Determination R^2
vigor/offspring	.403**	.314**	-	.314	.207**	
/season	.235**	.111*	-	.111	.482**	
/flowering	.060 ns	.151**	-	.151	.089**	
/emergence	-.516**	-.352**	.059	-.293	-.052**	
/stems	.455**	.349**	-.124	.225	.252**	
/constant					-2.174*	.66**

increasing number of stems is expected to delay the flowering slightly due to its effect on the retardation of emergence.

Vigor. The vigor ratings at flowering provide a rough estimate of the maximum size the foliage will attain. In a metabolic sense, both the foliage and the tuber are sinks, and compete for assimilates, thus the sink strength of the developing tubers might influence the final size of the foliage. Only the direction from V to Y, Z, and G, however, was considered (Figure 2) hence tuber sinks depend on imports of carbohydrates from leaves and stems, while the foliage does not rely on such imports from tubers. The number of stems was considered to influence the vigor ratings. Svensson and Naglika (1975) showed that the rate of sprout growth was a positive function of the initial tuber fresh weight. Multisprouts exhibited mutual interference for substrates from the seed tuber. The intensity of competition increased with temperature, but could be eliminated in some cases by supplying inorganic nutrients in the rooting medium.

Much of the variability in vigor was accounted for by the offspring (Table 10c). Later emergence reduced, and larger numbers of stems increased, the size of V. Moorby (1967) showed that the size of the sprout per hill was increased with the number of stems, although the size of individual sprouts decreased, due to competition between them. The earlier emergence in C_2 was most likely due to the larger seed tuber size. It was expected that plants which flower later and emerge earlier attain a larger size of the foliage, as a

Table 10d. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits proceding in the development) and the dependent variable for the following trait: maturity.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance			Path Regression $(b_o \ldots n)$	Degree of Determination R^2
		direct (p_{21})	indirect $(p_{23} \cdot p_{31} + p_{24} \cdot p_{41} \ldots)$	total (P_{21})		
maturity/offspring	.685**	.772**	-	.776	.765**	
/season	.018 ns	.058 ns	-	.058	3.319 ns	
/vigor	-.020 ns	-.203**	-	-.203	-.717**	
/flowering	.375**	.173**	-.030	.143	.361**	
/emergence	.260**	.128*	-.020	.108	.067**	
/stem	.011 ns	-	-.025	-.025	-	
/constant					15.706**	.71**

result of the prolonged growth period. Note, that later emerging plants reduce V, but through the delaying effect on F, V is increased indirectly by E. Similarly, a larger number of stems does increase V, but because it also delays emergence, the effect of X on V is lessened ($P_{XV}<p_{XV}$). Both types of compensation tend to stabilize the size of the foliage of a genotype, regardless of events occurring previously.

Maturity. The time of foliage senescence indicates the period when photosynthesis drops drastically in potato plants (Winkler, 1971) and is important in the classification of cultivars. Fortunately, it is very typical for each offspring (Table 10d). Plants which flower later also tend to mature later. Plots which emerged or flowered later senesced later. Plots which were more vigorous early in the season matured earlier. The latter was also found in another experiment (unpublished), which also showed that if vigor was greater due to increased nitrogen fertilization senescence was delayed. Radley et. al. (1961) have shown that early planting results in earlier tuber initiation, but is sometimes accompanied by earlier senescence.

Components of yield. The number of stems per hill was found to be typical for potato varieties (Steineck, 1959; Tai, 1975). In the previous section, the repeatability was found to be small based on observations on C_1 and C_2 clones. Accounting for these differences, which are easily explained by the small size of the seed tuber, and the genotypic variability between offspring, the degree of

Table 10e. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits proceding in the development) and the dependent variable for the following trait: number of stems per hill.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance			Path Regression ($b_o...n$)	Degree of Determination R^2
		direct (p_{21})	indirect ($p_{23} \cdot p_{31} + p_{24} \cdot P_{41} \cdots$)	total (P_{21})		
Stems/offspring	.441**	.441*	-	.441	.476**	
/season	.670**	.670*	-	.670	1.098**	
/constant					-1.068	.64**

determination for X is 64% (Table 10e). This indicates that the predictability is considerably better than indicated by the repeatability estimate (Table 8).

Good determination was obtained for the number of tubers per stem. Proportionately, a similar amount of the total variability was explained by offspring for Y' as was for X' (Table 10f). The more stems developed per hill, the fewer tubers were formed per stem. Similar results were reported by Steineck (1959) & Taylor and Thompson (1974). The results indicate that X' is at least as important in the determination of Y' as the genotype. Significantly more tubers were formed per stem by C_1 plants (Table 4, 10f), much of this is accounted for by the smaller X'. It is noteworthy also, that the more vigorous a plant at flowering and the longer the period between emergence and flowering, the larger Y will be. Both suggesting that number of tubers formed is dependent on the available assimilates during the period of tuber formation. An interesting experiment was carried out by Boerger _et_. _al_. (1956). Foliage of two varieties with similar leaf area indeces, but different potential for Y, Z, and G were grafted onto their own and each others stocks. Interestingly enough, the number of tubers produced was mostly determined by the shoot.

The average size of the tubers was determined to a similar extent by the genotype as were X' and Y' (Table 10g). The number of tubers per stem, however, accounted for a larger portion of the variability

Table 10f. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits preceding in the development) and the dependent variable for the following trait: number of tubers per stem.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance			Path Regression ($b_o...n$)	Degree of Determination R^2
		direct (p_{21})	indirect ($p_{23} \cdot p_{31} + p_{24} \cdot P_{41} \cdot\cdot\cdot$)	total (P_{21})		
tubers/offspring	.500**	.484**	-	.484	.803**	
/season	.623**	.324**	-	.324	.485**	
/stem	-.701**	-.529**	-.009	-.538	-.536**	
/vigor	-.036 ns	.204**	-	.204	.288**	
/flowering	.216**	.148**	.038	.186	.123**	
/emergence	.226**	-.141**	.012	-.129	-.029 ns	
/constant					-8.533**	.86**

than did offspring. Z' was larger the smaller Y' and X' were. $P_{X'Y'}$ was considerably smaller than $p_{X'Z'}$, mainly because the indirect paths over V' and Y' were positive. In other words, larger X' produced a larger foliage, hence more assimilates were available for tuber growth. Also, larger X' gave rise to fewer Y', hence less Y' were competing for these assimilates. The more vigorous plants would produce larger Z' if all the other variables were kept constant. A more vigorous plant was found to have more stems and produce more tubers, so that the net increase in size would be minimal (P_{VZ}). The grafting experiment (Boerger _et_. _al_, 1956) showed that tuber size was primarily determined by the stock. The direct path from emergence to size (p_{EZ}) indicates that later emerging plants do have a lower potential for tuber size. Most of the effect of late emergence, however, was compensated for already, primarily through a reduced number of tubers and a delay in maturity, that the net effect on tuber size is minimal. The results further show that the tuber size will be larger the longer the period from flowering to maturity.

Specific gravity seems to be primarily determined by the genotype (Table 10f). The high repeatabilities obtained here and by Maris (1969), and others seem to confirm this. The negative relationship between tuber size and gravity seems to indicate competition between growth (cell division and expansion) and storage sinks. The only other variable of importance is maturity. Later maturing clones do have higher potential for specific gravity. Interestingly enough,

Table 10g. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits preceding in the development) and the dependent variable for the following trait: average tuber size.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance direct (P_{21})	indirect ($P_{23} \cdot P_{31} + P_{24} \cdot P_{41} \cdots$)	total (P_{21})	Path Regression ($b_o \ldots n$)	Degree of Determination R^2
Size/offspring	.423**	.503**	-	.503	.432**	
/season	.318**	.221**	-	.221	.881**	
/tubers	-.446**	-.760**	-	-.760	-.585**	
/stems	.141**	-.740**	.456	-.284	-.518**	
/vigor	.102*	.277**	-.209	.068	.300**	
/maturity	.066 ns	.266**	-	.266	.082**	
/flowering	.028 ns	.046 ns	-.102	-.056	.0295 ns	
/emergence	-.169**	-.165**	.094	.071	-.0265**	
/constant					-2.960**	.71**

Table 10h. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits preceding in the development) and the dependent variable for the following trait: specific gravity.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance direct (p_{21})	indirect ($p_{23} \cdot p_{31} + p_{24} \cdot P_{41} \cdots$)	total (P_{21})	Path regression ($b_o \ldots n$)	Degree of Determination R^2
gravity/offspring	.308**	.448**	-	.448	.1038**	
/season	.181**	.175**	-	.175	.9642**	
/size	-.254**	-.258**	-	-.258	-.00158**	
/tubers	.156**	-.122**	.196	.074	-.00188 ns	
/stems	-.090*	-.054 ns	.100	.046	-.00084 ns	
/vigor	-.026 ns	.168**	-.077	.091	.00366**	
/maturity	.436**	.436**	-.068	.368	.00269**	
/flowering	.096*	-.036 ns	-.015	-.051	-.00047 ns	
/emergence	.210**	.129*	.027	.156	.00041*	
/constant					-.00464 ns	.65*

the grafting experiment (Boerger _et_. _al_., 1958) showed a very close relationship between gravity and the stock. The type of foliage appeared to have no influence as would be expected from these results.

Yield. From the correlation coefficients (Table 10i) one might conclude that neither gravity nor the number of tubers per stem were very important in the determination of yield. The b's and p's indicate, however, that if either component would be increased and the others kept constant, a corresponding increase in yield would be expected.

Because of the compensatory nature of the yield components, it appears that a high genetic potential and the availability of resources are especially important for later traits. If one of the components early in the developmental sequence is curtailed, it can be compensated at least in part by the others. Nevertheless, in this population, the components Y', Z', and G' could not account fully for the low X's. Similarly, compensation for late emergence, or flowering was almost complete for total yield, but the yield structures are expected to be altered. In the studied progeny, yield was generally higher for later maturing plants with more vigorous foliage.

The correlation matrix (Table 11) indicates the oscillatory nature of the yield components of potatoes as was discussed for other crops by Adams (1967). Notice the decreasing amplitude along the developmental sequence, which indicates that most of the compensation is achieved between the traits which follow each other immediately

Table 10i. Simple correlations, path coefficients, indirect and total paths and path regression coefficients between the independent variables (mean performance of each offspring, seasonal means of all offspring in C_1 and C_2, sequential traits preceding in the development) and the dependent variable for the following trait: yield.

Bivariate Relationship (var.1/var.2)	Simple Correlation (r_{21})	Causal Covariance direct (p_{21})	Causal Covariance indirect ($p_{23} \cdot p_{31} + p_{24} \cdot p_{41} \cdots$)	Causal Covariance total (P_{21})	Path Regression ($b_o \ldots n$)	Degree of Determination $\cdot R^2$
yield/gravity	-.043 ns	.018**	-	.018	1.00	
/size	.547**	.915**	-.003	.912	1.00	
/tubers	-.039 ns	1.188**	-.695	.493	1.00	
/stems	.466**	1.171**	-.861	.310	1.00	
/vigor	.583**	-	.290	.290	-	
/maturity	.223**	-	.252	.252	-	
/flowering	.074	-	.156	.156	-	
/emergence	-.105*	-	.053	.053	-	
					.00	1.00

and presumably compete for the same set of resources. The path coefficients (Table 12) adjust for such compensatory interaction. They measure the dependence between two variables by keeping the others constant. All the path coefficients are negative, indicating the competition for limiting resources, between different types of sinks. In other words, positive selection for one component implies negative selection for others, unless overall productivity can be raised.

Conclusion. A model was presented which allowed the study of effects due to genotype, seasons in which C_1 and C_2 clones were grown respectively, and allometric relationships between developmental traits. The model has great potential to study the dynamics of biological systems. The information obtained is similar in its content to results reported from defoliation experiments (Humphries 1969), removal of tubers (Noesberger and Humphries, 1965), grafting of tomato scions on potato stocks (Khan and Sagar, 1969) or reciprocal grafting of shoots on stocks of different varieties (Boerger *et. al*., 1956) and the numerous experiments conducted with altering stem density or tuber size. The limitations, however, which arise from these artificially induced modifications of plants do not apply to the approach presented in this study.

Yield is generally highest with increasing larger leaf area and duration. These relationships are not very strong, which indicate

Table 17. Simple correlation coefficients for yield and its components of 123 potato progenies grown in the first and second clonal generation.

Yield	1.0				
Gravity	- .043 ns	1.0			
Size	.547**	- .254**	1.0		
Tubers	- .039 ns	.156**	- .446**	1.0	
Stems	.466**	- .090*	.141**	- .701**	1.0
	Yield	Gravity	Size	Tubers	Size

ns: not significant at P = .05; *significant at P = .05;

** significant at P = .01

Table 12. Path coefficients between yield and its components of 123 potato progenies grown in the first and second clonal generation.

Yield	1.0				
Gravity	.018*	1.0			
Size	.915**	- .258**	1.0		
Tubers	1.188**	- .122*	- .760**	1.0	
Stems	1.171**	- .054 ns	- .740**	- .529**	1.0
	Yield	Gravity	Size	Tubers	Size

ns: not significant at P = .05; *significant at P = .05;

** significant at P = .01

that the potential for high economic yield is similar over a wide range of foliage size and duration, presumably because of a corresponding compensation in efficiency. A larger size of the foliage resulted primarily in a larger number of tubers per hill, while a delay in foliage senescence promoted sizing of the tubers and resulted in higher specific gravity. Within limits it can be expected that the plants can compensate for low numbers of stems by producing more tubers per stem, for low numbers of tubers by increasing tuber size, and for small tuber by increasing the solid content.

It was shown that traits formed later in the developmental sequence compensate for deviations in earlier ones. Although it is important that no genetic ceilings are encountered at any stage of development (Adams, 1967), it seems that these considerations are more important for later formed traits, since possibilities for compensation decrease along the developmental sequence.

The variability explained by offspring was about the same for all components of yield. Much of the variability of components formed later in the developmental sequence can be accounted for by their compensation for earlier ones. The large unexplained and generally not controllable variability in the number of stems, requires a large potential for compensation by both foliage and subsequent components of yield. Stable foliage size is achieved through either adaptible branching or by altering stem elongation (Lovell and Booth, 1969). Similarly, stable yields are obtained through adjustment of tuber number or tuber size.

Often the variables are not transformed for this type of study. The importance of linearization, however, was clearly demonstrated in this work. By definition W is completely determined by X·Y·Z·G and W' is equal to X'+Y'+Z'+G'. The regression model given in Table 101 reveals complete determination of yield by its components for the transformed variates as was expected. The regression coefficients are unity. Thus, if one were to increase either by keeping the others constant, yield would increase proportionately. When the identical regression model was applied, however, to the same data without transformation, only 72% of the variability in yield was explained by its components. Furthermore, both path and regression coefficients between gravity and yield were negative. Statistically speaking, this would mean, that if gravity was increased, and X, Y, and Z were kept constant, yield would be expected to decrease, which is mathematically and biologically impossible. These evidences point out the inadquacy of a linear regression model to explain the dependence between yield and its components.

3.6 Discussion of the Genetic Improvement of Yield

The estimate of the narrow sense heritability was found to be very low for yield in the population under investigation. The mean performance of each family was similar. Large differences, however, were found in the yielding ability between offspring. The wide segregation of the yielding potential within family was attributed to specific combining effects, believed to result from a high degree of genic interactions. These findings make parent selection extremely difficult and may have impeded the progress of producing higher yielding cultivars in the past. Difficulties stem from the tetrasomic mode of inheritance and the fact that highly heterozygous parents are generally employed. If the heterozygotes are indeed superior to homozygotes, as was suggested by Mendoza and Haynes (1976), selection of superior individuals as parents will merely reproduce an unselected progeny population similar to the one from which they were taken. Alternately, if superiority of parents arises from epistatic effects, offspring may, under many circumstances, contain none of these effects.

Most of the genetic variability in yield was due to genic interactions. The model used to estimate the genetic components in this study assumed linkage equilibrium and no epistasis. The former may be a reasonable assumption, but the latter cannot be ruled out. The heretability and genetic component estimates, however, are not expected to be considerably influenced by epistasis, since both are based on second degree statistics. Nevertheless, epistatic effects will influence the actual performance of individual offspring.

In the genetic analysis of self-fertilizing, sexually propagated crops the separation of intra- and inter-locus interaction is essential. In potato breeding this distinction is less important. Following hybridization both effects are fixable through vegetative propagation. Both are the result of specific gene combinations and may give rise to heterosis. Unfortunately, their predictability is low, especially when heterozygous parents are employed and if complex traits are studied. Nevertheless, if an attribute like yield is composed of complementary component traits, favorable epistatic effects (hybrid vigor) may be created.

In view of the low heretability it is essential that potato breeding exploits through asexual propagation all additivity, dominance, over-dominance, and epistasis. These expressions, however, are statistical terms for which biological explanations must be found to take advantage of these phenomenon.

It must be emphasized that many more possibilities exist for intra-locus interactions in tetraploids than in diploids. It was found that trigenic and quadrugenic interactions are very important in the determination of potato yield. This confirms the speculations of Mendoza and Haynes (1976) that high yield of potatoes is primarily due to a high level of genic interactions in highly heterozygous genotypes. It explains the observed inbreeding depression in tetraploid (Krantz, 1946), diploid (DeJong and Rowe, 1971), and vegetatively doubled diploid potatoes (Rowe, 1967) and the superiority of sexually produced tetraploids by means of unreduced gametes (Mendiburu and Peloquin, 1971), especially when tetraploids are obtained by first division restitution gametes (Mok and Peloquin, 1975).

Shank and Adams (1960) reported that the individual offspring capacity of corn plants is a varietal feature and is associated with heterozygosity. Griffin and Langridge (1963) showed that heterozygotes in Aribidopsis had a greater mean growth rate primarily because of a greater phenotypic stability over a wide range of temperature. Clausen and Hiersey (1958) demonstrated that F_1 hybrids of different ecotypes of Potenilla glandulosa were more adaptible than the parents and they were more vigorous than the best parent in its optimal environment. In potatoes, heterozygosity and polyploidy are means to store the genetic diversity necessary for high and stable yield. Phenotypic adaptation and individual buffering capacity are very important in potatoes. Population homeostasis is not possible because the asexually propagated plants represent a genetically identical clone. It was shown, however, that the number of stems emerging per plant is extremely variable, which affects the size of foliage and root systems and the potential sites for tuber formation. It becomes thus extremely important for plants to have an adaptible branching habitat of the above ground stems and stolons. Tai (1975) found that varieties with stable yields show great flexibility in the number of tubers formed per stem. Similarly here, the low correlation coefficient together with the high path coefficient between Y and W indicates that Y is highly variable yet very important. A high degree of compensation however, was shown also for the other components of yield, and some foliage characteristics.

In view of the interactions demonstrated between the studied attributes, epistatic effects cannot be ruled out. Epistasis was shown to influence yield in barley (Grafius, 1959), and wheat (Halloran, 1975), presumably because of the multiplicative interaction of yield components (Grafius, 1959).

The control of plant growth and differentation occurs at the physiological and morphological level, in as much as it is directed by the programmed, segmental unfolding of the genome and by the availability of environmental resources. Isolation of stimuli and responses are difficult because they are correlative and contemporaneous, with very short time lags and because of the feed-back observed in biological systems. What is clear, however, is that the effect of any stimulus, whether genetic, environmental, or physiological, will depend on the state of the receptor determined by previous events. Thus only a multivariate approach as used in this study can reveal the nature of control of developmental traits. The use of path coefficients allows the measurement of the magnitude of control by genotype, environment, and physiological, or morphological factors.

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Furthermore, the magnitude of epistatic effects arising from physiological interactions can be estimated. For example, the product $p_{GX} \cdot p_{XY}$ measures how much the variable Y is expected to change if the genetic potential of X would be raised by one standard unit. It is implied that developmental allometry and component compensation modualte, and often limit the realization of the genotypic potential <u>per se</u>, resulting in failure of prediction.

Photosynthesis, nutrient absorption, translocation, partitioning, and storage of assimilates contribute to the formation of yield. Either process may be limiting during certain phases of the ontogenic development or under specific environmental conditions. The evidence obtained from grafting experiments (Khan and Sager, 1969), removal of tubers (Noesberger and Humphries, 1965), partial defoliation, and measurements of the net assimilation rate over the growing season (Milthorpe, 1963) suggests, that the sink is limiting, especially during the middle part of potato development. During tuber bulking, the sink strength is equal to the product of number x size x activity of tuber sinks. Physiological and morphological plasticity allow compensation between these components and assure stable yield. In the population studied, however, compensation between yield components was incomplete, as indicated by the total paths to yield. Too few stems per hill and too few tubers per stem were generally formed to make optimal use of the environmental resources available. Sink strength is likely to be limited by the total size of the growing tuber tissue, as long as the tubers are small. As tubers grow very large, the efficiency of sinks is likely to drop since the proportion of meristematic tissue decreases, and gaseous exchange and assimilate diffusion may become impared. In either case, increasing the number of stems, thus the sites for stolon formation, and the number of tubers per stem would reduce these limitations.

The components X and Y are formed early in development before phenotypic adaptation to the environmental resources are possible. The number of stems established is controlled primarily by the degree of apical dominance. Although potato plants retain the potential of tuber formation throughout the growing season, only tubers formed within a two week period grow into harvestable tubers (Milthorpe and Moorby, 1966). The tubers formed later serve as temporary storage sites but do not surpass the threshold level which gives them the potency required to develop into permanent sinks. Genetic improvement must thus focus on genotypes with less apical dominance and a decreased level of competitive inhibition between developing tubers, which is presumably nutritionally and hormonally regulated.

Heterosis for potato yield was demonstrated in hybrids between andigena and tuberosum parents (Cubillos and Plaisted, 1976). The intra-andigena population out yielded the tuberosum population in Huancayo, Peru, while the tuberosum families yielded more in Ithaca, New York. The hybrid population, however, yielded more than the best intragroup population at both locations (Table 13). The heterosis in yield can be explained by the hybrid advantage for tuber number in Ithaca and tuber size in Huancayo, and the multiplicative interaction resulting from union of the heavier set of andigena and large tuber size of tuberosum. The authors speculate, that the mean day length may determine the extent of heterosis. This seems very unlikely, however, since Mendoza and Haynes (1976) showed that in similar hybrids shortening or prolonging the photoperiod affected primarily the growth of the foliage and had little influence on tuber yield or its components.

The data given in Table 13 show that the conditions are favorable for large tuber numbers in Huancayo and for large tuber size in Ithaca. Furthermore, the genetic potential is higher for the number of tubers in the andigena, and for tuber size in the tuberosum, population. The intragroup hybrids, however, are expected to be intermediate in both tuber number and tuber size. For tuber number, this was only the case in Peru and for tuber size, in Ithaca. This is compatible with the interpretation that the genetic differential is best expressed in the most favorable environment for the particular trait. Interestingly enough, in the less favorable environment for each component trait, the phenotypic values of the intragroup hybrids are equal to the intragroup population with the higher genetic potential.

The data in Table 13 support the evidence presented in this study that: (1) in potatoes, the inheritance of yield components is simpler

Table 13. Performance of selected andigena, tuberosum, and hybrid populations as spaced plant. Ithaca, New York and Huancayo, Peru.

Ithaca	Yield (gm) > 4.8 cm	Tubers per plant	Wt. (gms) per tuber
Adg x Adg	1254 ± 78	14.1 + 1.1	110 ± 8
Tub x Adg	2444 ± 101	14.5 + .6	197 ± 8
Tub x Tub	2162 ± 86	9.8 + .3	240 ± 9
Huancayo			
Adg x Adg	1073 ± 63	21.6 ± .87	70 ± 3
Tub x Adg	1231 ± 79	16.7 ± .70	100 ± 6
Tub x Tub	845 ± 90	9.0 ± .76	107 ± 10

Cubillos, A.G. and Plaisted, R.L., "Heterosis for yield in hybrids between S. tuberosum ssp. Tuberosum and S. tuberosum ssp. Andigena", American Potato J. 53(4): 146 (1976).

than yield itself; (2) yield of tuberosum material can be improved by raising the genetic ceiling for the number of tubers per hill and the number of tubers per stem, especially the former; (3) heterosis for yield is observed even if no heterosis for the components of yield is realized, because of their multiplicative interaction; and (4) the full genetic potential may not be expressed because of environmental limitations (Table 13) or because of the physiological interaction between traits (this study). This contributes to the low repeatabilities found and to the failure of prediction of the genotype from somatic analsysis. Nevertheless, both parent and progeny selection can be improved through better understanding of these dependencies.

Heterosis for yield through the multiplicative interaction between component traits is expected only if the sink strength is limiting during part, or the whole, period of tuber development. This implies that environmental resources are not utilized fully at one time or another. When the sink is limiting, raising the number of tubers per hill for example, would necessarily mean slower growth rates of tubers and would ultimately result in smaller tubers, and similar yield. It was demonstrated, however, that component compensation was not complete, and that competition between yield components is very strong only for those which follow each other immediately, shown by the decreasing magnitude of the negative path coefficients (Table 12). Contemporaneous components presumably draw on the same set or resources.

The positive, indirect path from vigor and maturity to yield indicates that on the average in the population studied, the plants with more vigorous foliage and longer foliage duration did yield more and that thus the source may be limiting.

4. INHERITANCE OF PROTEIN CONTENT, "BIOLOGICAL VALUE" AND CHIP COLOR

4.1 Introduction

Qualitative improvements of the potato focus on its nutritive value and processing characteristics. Recently, the topic of chip quality was extensively reviewed by Talburt and Smith (1976). Nevertheless, only few studies examined the inheritance of chipping characteristics. The main objectives in upgrading the nutritional value of potatoes are to increase the protein percentage on a dry weight basis, and to upgrade its biological value. The sulfur containing amino acids are first limiting in potato protein (Schupan, 1958; Kies and Metzfox, 1972).

Ford (1960) developed a microbiological assay procedure using Streptococcus zymogenes for several essential amino acids, including the S-containing ones. This organism grows rapidly, is powerfully proteolytic and was used to evaluate "available methionine" and a "biological" value of potato protein (Luescher, 1972).

The purpose of this study was to estimate heritabilities for protein content, "biological value", and chip color.

4.2 Material and Methods

Ten offspring were randomly selected from each of the eight families described in the previous chapter. Only tubers from the second clonal generation were studied. Following specific gravity determinations, five tubers per offspring were chosen at random from the two replications. Six longitudinal slices were cut from the middle of each tuber.

Three slices were rinsed in cold water and fried at 190°C until water evaporation ceased. The color of the potato chips was estimated using the standard color chart of the National Potato Chip Institute.

The other slices were quickly frozen, combined and freeze-dried. The samples were ground in a Wilely Mill with a sixty mesh screen. Crude protein (N x 6.25) and non-protein nitrogen (10% TCA soluble) were determined by Micro-Kjeldahl (CIP, 1973). The biological value of the crude protein was assessed with Streptococcus zymogenes (Luescher, 1972). Casein was used as standard. The mean of triplicate readings per flour sample were used for analysis.

Simple correlation coefficients, heritability estimates, and specific and general combining ability estimates were calculated analogously to those in the previous chapter.

4.3 Results and Discussion

The family means of ten progeny each are given for chip color ratings, crude protein, non-protein nitrogen and a "biological value" as determined in the microbiological assay in Table 1. Although there are significant differences among these family means for all these traits, they were small compared to the range found among genotypes.

Table 1: Cross means* for chip color (1- light to 10 - dark), crude protein (g/100g dry matter), NPH (g/100g N), and "biological value."

Population	Cross	Chip Color	Crude Protein	NPN	Biol. Val.
I	1	5.4b	11.54c	44.3bc	77.0c
	2	6.5a	12.38a	54.8a	76.8c
	3	5.0b	12.14ab	53.4a	78.5bc
	4	5.2b	11.94ab	52.1b	79.4b
II	5	5.1b	11.75abc	49.4ab	80.4b
	6	6.8a	11.90ab	50.4ab	77.8bc
	7	5.6b	11.68bc	48.9ab	78.3bc
	8	4.3c	10.87ab	38.8c	82.4a

Duncan's multiple range test: values with the same letter are not significantly different at the 5% level.

*mean of ten offspring per cross: duplicate observations for each offspring.

Chip color ratings ranged from 1.5 (very light) to 9 (very dark) with the bulk of the clones around 5, which would be unacceptable as a commercial product. Generally, lighter chips were obtained from potatoes with higher specific gravity (Table 2). Darkness increased slighlty with non-protein nitrogen. Nevertheless, these associations were not very strong. Fortunately, chip color appears to be independent of yield or the biological value, thus allowing improvement in either characteristic without negative impact on others. The heritability estimate of .24 is not very high, but it does indicate that breeders may make use of both general and specific combining ability. The family means for crude protein are very similar (Table 1). Nevertheless, the values for individual genotypes ranged from 8.6 to 15.7 percent, thus selection of clones with a protein content higher than the present cultivars would be possible. The heritability estimate of .23 falls in the range of 10-28% reported by Sanford et. al. (1971). Specific combining affects accounted for slightly more of the genetic variability than general combining affects. Although crude protein was independent of yield, raising the protein concentration may bring about a drop in the "biological value" of the protein (Table 2). Furthermore, crude protein was negatively correlated with specific gravity, which is a measure of some desirable culinary and processing characteristics. Most of the drop in the "biological value" of the protein stems from an increase in the non-protein nitrogen which has a lower "biological value" than true protein.

Table 2. Correlations between yield, specific gravity, chip color, crude protein, non-protein nitrogen, and "biological value."

Yield	1.0					
Spec. Gravity	-.08	1.0				
Chip Color	-.14	-.54	1.0			
Crude Protein	-.13	-.88	.17	1.0		
NPN	-.21	-.43	.31	.65	1.0	
Biol. Value	-.08	.16	-.09	-.58	-.73	1.0
	Yield	Spec. Grav.	Chip Col.	Cr. Prot.	NPN	Biol. Val.

Probabilities for significance of correlation coefficients:

P = .05, r = .154

P = .01, r = .204

Non-protein nitrogen accounted for almost half of the nitrogen in potato tubers analysed. The heritability estimates were higher than for the other quality attributes studied. Although its "biological value" is lower, its significance as a nitrogen source in the human diet should not be overlooked. The nitrogen balance studies by Kofranyi and co-workers clearly demonstrate this (Kofranyi and Jekart, 1967).

The high "biological values" measured clearly demonstrates the high quality of potato protein. Although the heritability estimates are not very high, progress through breeding should still be possible. Several genotypes supported growth of *Streptococcus* almost as well as casein. The "biological value" of potato protein is independent of both yield and processing quality, which would allow a combination of these objectives. Luescher (1972) reported estimates of narrow sense heritability for available methionine between 70 and 100% in a similar population. These estimates appear too high, based on the results given by the author and those presented in this study. Nevertheless, the genetic variability available makes the genetic improvement of the "biological value" possible.

Table 3. Mean squares for replication, population, family within population, offspring within population and error mean square of chip color, crude protein, percentage of non-protein nitrogen and "biological value."

Source	Rep.	Pop.	Family	Offspring	Error*
Chip Color	.2474E-1	.8603E+1	.2755E+1	.1426E+1	.2021
Crude Protein	.2892	.3763E+1	.1245E+1	.6828	.1585
NPN	.8247E-1	.7958E+1	.2586E+1	.1366E+1	.2571E+1
Biol. Value	.2456	.1381E+1	.3792E+1	.1721E+1	.5655

*estimated from common male parent.

Table 4. Narrow sense heritability and ratio of specific to general combining ability for chip color, crude protein percentage of non-protein nitrogen, and "biological value."

	Chip Color	Crude Protein	NPN	Biol. Value
h^2	.24	.23	.37	.26
SCA/GCA	1.10	1.20	.92	1.17

5. SUMMARY AND CONCLUSION

Breeding objectives to improve yield, processing characteristics, the quantity and quality of tuber protein are compatible. Estimates of the narrow sense heritability were moderately high for the qualitative characteristics. Improvements are possible by selection of parents with a high general combining ability.

The low heritability estimate for yield, partially due to heterozygous parent material, makes parent selection and the breeding of higher yielding cultivars extremely difficult. Higher order genic interactions are important in the determination of yield. A high degree of heterozygosity appears to be advantageous. This may best be exploited by crossing highly divergent genotypes.

Phenotypic traits, physiological and morphological, interact with each other. Heterotic effects may be produced by raising the genetic potential of complimentary component traits, since limitations in one may reduce the realization of the genetic potential of others. Both the nature of the limitations and its genetic basis must be further studied.

Sink limitations in potatoes must be eliminated to raise the yielding potential. Parent selection based on component traits, rather than yield *per se*, should make it easier to overcome these limitations. The components of yield have a simpler mode of inheritance than yield. Interactions between morphological and physiological component traits are predictable. Improvements in this progeny population are expected primarily by raising the genetic potential for stems per hill and tubers per stem, and maintaining the present selection pressure for tuber size.

Stable expression of traits late in the developmental sequence is achieved only by minimizing fluctuations in preceding traits. This may be accomplished by reducing random variability or imposing genetic ceilings upon early traits. For example, large tubers can be expected consistently only in varieties with a low tuber number, so that tubers do not compete for resources at later stages of development. Similarly, enlargement of tubers must be curtailed in favor of starch or protein deposition, if consistently high gravity tubers are desired. These limitations, however, imply a reduction of the yielding potential.

The size of the foliage was limiting yield in most of the progeny. Introduction of genotypes with more vigorous or efficient foliage would be advantageous. The population mean should be raised to a level where the total path from vigor to yield approaches zero. A higher proportion of progenies could then be expected to have and optimum foliage size.

Early maturing varieties are very important since they satisfy market demands early in the season. Nevertheless, their yielding ability is inferior to late varieties. Also, large tuber size and especially high specific gravity is more often associated with lateness.

In view of the low heritabilities the total genetic variability must be exploited through vegetative propagation. Clonal selection becomes therefore very important, but the repeatabilities between early clonal generations were found to be rather low. Developmental attributes formed in succession interact with each other. Their phenotype is co-determined by the genotype, environment, and by traits preceeding in the developmental sequence. Much of the described interactions occur at the physiological-morphological level. This confounds the expression of the genotype and must be kept in mind in clonal selection to avoid loss of valuable genotypes. These considerations are especially important when clonal selection is based on few plants.

Visual selection as influenced primarily by tuber size and tuber shape becomes highly questionable. C_1 plants develop fewer stems with large numbers of tubers, which will stay smaller. the only C_1 plants which can be safely eliminated are ones with very large X or Y, very low Y, estremely small tubers, medium sized tubers if $X \cdot Y$ is small. Fairly strong selection could be practiced for specific gravity.

LITERATURE CITED

Adams, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, Phaseolus vulgaris. Crop Sci. 7: 505-510.

Akeley, R.V. and Stevenson, F.J. 1943. Yield, specific gravity and starch content of tubers in a potato breeding program. Am. Potato J . 20: 203-17.

Akeley, R.V. and Stevenson, F.J. 1944. The inheritance of dry-matter content in potatoes. Am. Pot. J. 21: 83-89.

Artschwager, E. 1924 . Studies on the potato tuber, J. agric. Res. 27: 809-835.

AOAC. 1970. Association of Official Agricultural Chemists. 11th ed. Washington,D.C. p. 801.

Blackman, F.F. 1905. Optima and limiting factors. Ann. Botany (london) 19: 281-295.

Bleasdale, J.K.A. 1965. Relationships between sett characters and yield in main-crop potatoes. J. agric. Sci., Camb. 64; 361-366.

Booth, A. 1963. The role of growth substances in the development of stolons. Proc. 10th Easter Sch. agric Sci. Univ. Nottingham: 99-113.

Blomquist, A.W. and Lauer, F.J. 1962. First clonal generation potato progeny performance at two Minnesota locations. Am. Potato J. 39: 460-463.

Boerger, H., Huhnke, W., Koehler, D., and Schwanitz, F. 1956. Untersuchungen ueber die Ursachen der Leistung von Kulturpflanzen. Zuechter 26: 363-370.

Bradburg, D. 1953. Division of starch containing cells. Am.J. Bot. 40: 286-288.

Burton, W.G. 1966. The Potato. A survey on its history and of factors in influencing its yield, nutritive value, quality and storage. 2nd ed. H. Veenman and Zonen N.V. Wageningen. The Netherlands, pp. 623.

CIP. 1973. Potato Protein Quality. Report of the international potato center's planning conference on protein quality. Held at CIP-Lima, Peru. November 26-30, 1973, pp. 57.

Clark, C.F. 1921. Development of tubers in the potato. U.S.D.A. Bull. No. 958.

Clausen, J. and Hiersey, M.W. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Inst. Wash. Publ. 615.

Cole, S.C. 1975. Variation in dry matter between and within potato tubers. Potato Res. 18: 28-37.

Cubillos, A.G. and Plaisted, R.L. 1976. Heterosis for yield in hybrids between S. tuberosum ssp. Tuberosum and Tuberosum ssp. Andigena. Am. Potato J. 53 (4): 143-150.

Cunningham, C.E. and Stevenson, F.J. 1963. Inheritance of factors affecting potato chip color and their association with specific gravity. Am. Potato J. 40: 253-265.

Davies, H.T. 1969. The influence of stem thinning on tuber size. Am. Potato J. 46: 287-290.

Davies, H.T. and Johnston, G.R. 1965. First clonal generation potato seedling selections at two locations. Am. Potato J. 42: 186-189.

Davies, H.T. and Johnston, G.R. 1974. Reliability of potato selection in the first clonal generation. Am. Potato J. 51(1): 8-11.

DeJong, H. and Rowe, P.R. 1971. Inbreeding in cultivated diploid potatoes. Potato Res. 14: 74-83.

Driesch, H. 1908. The science and philosophy of the organism. I.Adam and C. Black, London. pp. 329.

Duarte, R. and Adams, M.W. 1963. Component interaction in relation to expression of a complex trait in bean cross. Crop Sci. 3: 185-186.

FAO/WHO Expert Group. 1965. Protein requirements. World Health Organization Technical Report Series No. 301. pp. 71.

Fitzpatrick, T.J., Akeley, R.V., White Jr., J.W., Porter, W.L. 1969. Protein, non-protein and total nitrogen in seedlings of potatoes. Am. Potato J. 46: 273-286.

Fitzpatrick, T.J. and Porter, W.L. 1966. Changes in the sugars and amino acids in chips made from fresh, stored and reconditioned potatoes. Am. Potato J. 43: 238-248.

Geidel, H. and Schuster, W. 1965. Untersuchungen ueber die oekologisch bedingte Variabilitaet bei verschiedenen Kartoffelsorten. Z. Acker -u. Pflanzenbau. 123:31-38.

Glendinning, D.R. 1969. The performance of progenies obtained by crossing Groups Andigena and Tuberosum of Solanum tuberosum. Eur. Potato J. 12:13-19.

Goodwin, P.B., Brown, A., Lennard, J.H. and Milthorpe, F.L. 1969. Effect of centre of production, maturity and storage treatment of seed tubers on the growth of early potatoes. II. Field growth. J. agric. Sci., Camb. 73: 167-176.

Gould, S.J. 1966. Allometry and size in ontogeny and phylogeny. Bio. Rev. 41:587-640.

Grafius, J.E. 1956. Components of yield in oats. A geometric interpretation. Agron. J. 48:419-423.

Grafius, J.E. 1959. Heterosis in barley. Agronomy J. 51:551-554.

Gray, D. 1971. The production of potatoes for canning. ADAS. Q. Rev. 1:24-30.

Gray, D. 1973. The growth of individual tubers. Potato Res. 16:80-84.

Griffing, B. and Langridge, J. 1963. Phenotypic stability of growth in self-fertilized species, Arabidopsis thaliana. In Statistical Genetics in Plant Breeding. Nat. Acad. Sci.-Nat. Res. Council Publ. 982:368-394.

Grosch, H.G. 1955. Weitere photoperiodische Versuche an Kulturkartoffeln. Z. Acker -u. Pflanzenbau. 101: 301-320.

Habib, A.T. and Brown, H.D. 1957. Role of reducing sugars and amino acids in the brown of potato chips. Food Techn. 11:85-91.

Halloran, G.M. 1975. Heterosis in wheat. Z.f. Pflanzenzuechtung 74: 18-27.

Harris, R.E., Davies, H.T. and Cannon, H.B. 1967. Selection of clonal potato seedlings at three widely separated locations. Am. Potato J. 44:24-29.

Hoelzl, J. and Blancher, E. 1959. Ueber Vorkommen und Sortenabhaengigheit der Eiweisskristalle in der Kartoffelknolle (Solanum tuberosum) Qual. Plant. Mater. Veg. 8:1-24.

Hoff, J.E., Jones, C.M., Wilcox, G.E. and Castro, M.D. 1971. The effect of nitrogen fertilization on the composition of the free amino acid pool of potato tubers. Am. Potato J. 48 (10): 390-394.

Holliday, R. 1960. Plant population and crop yield. Fld. Crop Abstr. 13: 247-254.

Holmes, J.C., Lang, R.W., and Singh, A.K. 1970. The effects of five growth regulators on apical dominance in potato seed tubers and on subsequent tuber production. Potato Res. 13: 342-352.

Horsfall, J.R. et.al. 1972. Genetic vulnerability of major crops. Nat. Acad. Sci. Washington, D.C., USA: pp. 190-203.

Howard, H.W. 1963. Some potato breeding problems. Plant Breed. Inst. Camb. Ann. Rep. 1961-1962: 5-21.

Howard, H.W. 1974. Factors influencing the quality of ware potatoes. I. The genotype. Potato Res. 17: 490-51.

Humphries, E.C. 1969. The dependence of photosynthesis on carbohydrate sinks: current concepts. Proc. Int. Symp. Tropical Root Crops, Univ. of West Indies 1, II: 34-45.

Hunnius, W. 1969. Zuechtungtrockensubstanzreicher Kartoffeln (Staerke und Eiweiss). Kartoffelbau 1969: 20: 46-51.

Johanssen, R.H., Miller, J.C., Newsom, D.W., and Fontenot, I.F. 1967. The influence of environment on the specific gravity, plant maturity and vigor of potato progenies. Am. Potato J. 44: 107-122.

Kempthorne, O. 1955. The correlation between relatives in a simple autotetraploid population. Genetics 40: 378-380.

Khan, A. and Sagar, G.R. 1969. Alteration of the pattern of distribution of photosynthetic products in the tomato by manipulation of the plant. Ann. Bot. 33: 753-762.

Kies, C. and Metzfox, H. 1972. Effect of amino acid supplementation of dehydrated potato flakes on protein nutritive value for human adults. J. Food Sci. 37: 378-380.

Kofranyi, E. and Jekart, F. 1967. Zur Bestimmung der biologisen Wertigheit von Nahrungsproteinen, XII. Die Mischung von Ei mit Reis, Mais, Soja, Algen. Hoppe Seyler's Z. Physiol Chem 348: 84-88.

Krantz,R,T.1946. Potato breeding methods. III. A suggested procedure for potato breeding. Techn. Bull. Minn. Agric. Exp. Sta. No. 173: p. 24.

Krijthe, N. 1955. Observation on the formation of growth of tubers of the potato plant. Neth. J. Agric. Sci. 3: 291-304.

Krug, H., Wriedt, G. und Weber, W.E. 1974. Untersuchungen zur Frueh-selektion in der Kartoffelzuechtung. I. Untersuchungen an der Saemlings Generation. Z. Pflanzenzuechtg. 73, 141-162.

Levings II, C.S. and Dudley, J.W. 1963. Evaluation of certain mating designs for estimation of genetic variance in auto-tetraploid alfalfa. Crop Sci. 3: 532-535.

Lerner, I.M. 1954. Genetic homeostasis. Oliver and Boyd, London.

Lovell, P.H. and Booth, A. 1969. Stolon initiation and development in Solanum tuberosum L. New Phytol. 68: 1175-1185.

Luescher, R. 1972. Genetic variability of "available" methionine, total protein, specific gravity and other traits in tetraploid potatoes. Ph.D. Thesis, Michigan State University, East Lansing, Michigan, USA.

Maris, B. 1966. The modifiability of characters important in potato breeding. Euphytica 15: 18-31.

Maris, B. 1969. Studies on maturity, yield, underwater weight and some other characters of potato progenies. Euphytica 18: 297-319.

Meinl, G. 1967. Assimilations vermoegen als Sortenmerkmal I.Vergleich der apparenten Assimilation von Kartoffelsorten verschiedener Reifezeit. Photosynthetica 1: 51-56.

Mendiburu, A. and Peloquin, S.J. 1971. High yielding tetraploids from 4x - 2x and 2x - 2x matings. Am. Potato J. 48: 300 (Abstract)

Mendoza, H.A. and Haynes, F.L. 1974. Genetic Basis of Heterosis for yield in the Autotetraploid Potato. Theoretical and Applied Genetics 45: 21-25.

Mendoza, H.A. and Haynes, F.L. 1976. Variability for photoperiodic reaction among diploid and tetraploid potato clones from three taxonomic groups. Am. Potato J. 53: 319-332.

Milthorpe, F.L. and Moorby, J. 1966. The growth of the potato. Proc. 3rd trienn. Conf. Eur. Ass. Potato Res. pp. 51-70.

Milthorpe, F.L. 1963. Some aspects of plant growth. Proc. 10th Easter. sch. agric. Sci. Univ. Nottingham: 3-16.

Mok, D. and Pelopquin, S.J. 1972. Three mechanisms of 2n pollen in diploid potatoes. Am. Potato J. 49: 362-363 (Abstract).

Mokronosov, A.T. and Ivanova, N.A. 1971. Photosynthesis under partial plant defoliation. Fiziologiya Rastenii 18: 668-676.

Moll, R.H. and Kojima, A. and Robinson, H.F. 1962. Components of yield and overdominance in corn. Crop Sci. 2: 78-79.

Monday, N.I. and Rieley , P.B. 1964. Relationship of specific gravity to the nitrogen and ascorbic acid content of potatoes. Am. Potato J. 41: 417-422.

Moorby, J. 1967. Inter-stem and inter-tuber competition in potatoes. Eur. Potato J. 10: 189-205.

Mulder, E.G. and Bakema, K. 1956. Effect of the nitrogen,potassium and magnesium nutrition of potato plants on the content of free amino acids and on the amino acid composition of the protein of tubers. Plant. and soil. 7: 135-166.

Mullin, R., Blomquist, A.W. and Lauer, F.I. 1966. Effect of seed tuber size on first clonal generation yield of potatoes. Am. Potato J. 43: 418-423.

Necas, J. 1965. Application of growth analysis to potatoes in field culture and some specific features of potato growth. Biol. Plant. 7: 180-193.

Neuberger, A. and Sanger, F. 1942. The nitrogen of the potato. Biochem. J. 36: 662-671.

Noesberger, J. and Humphries, E.C. 1965. The influence of removing tubers on dry-matter production and net assimilation rate of potato plants. Ann. Bot. 29: 579-588.

Peare, R.M. 1973. Potato protein as affected by: A. variety and environmental and B. air separation of the dried flour Master's Thesis. Michigan State University, East Lansing, Michigan, USA.

Peterson, L.C. and Plaisted, R.L. 1960. Recurrent selection for high specific gravity. 30th annual report to cooperatives, the National Potato Breeding Program, 1959.

Pfeffer, Ch., 1963. Vergleichende Untersuchungen ueber die Auslesemoeglichkeiten von im Freiland and in Toepfen kultivierten Kartoffelsaemlichen. Zuechter 33: 6-11.

Plaisted, P.H. 1957. Growth of the potato tuber. Pl. Physiol., Lancaster 32: 445-453.

Plaisted, R. and Cubillos, A. 1972. Selection of parents on the basis of components of yield. Am. Potato J. 49: 182-186.

Plaisted, R.L. and Peterson, L.C. 1963. Two cycles of phenotypic recurrent selection for high specific gravity. Am. Potato J. 40: 396-402.

Plaisted, R.L., Sanford, L., Federer, W.T., Kehr, A.E., Peterson, L.C. 1962. Specific and general combining ability for yield in potatoes. Am. Potato J. 39: 185-197.

Prokosev, S.M. 1939. Biochemistry of the potato. Biokhimia Kulturnykh Rastenii 4: 5-58. (M.S. Swanminathan and H.W. Howard 1953: Bibl. Genetica XVI:1-192).

Reeve, R.M., Hautala, E. and Weaver, M.L. 1969. Anatomy and compositional variations within potatoes. I, II. Amer. Potato J. 46, 361-373: 374-386.

Reeve, R.M., Hautala, E. and Weaver, M.L. 1970. Anatomy and compositional variation within potatoes. III. Gross compositional gradients. Am. Potato J. 47: 147-162.

Reissig, H. .1958. Ueber die Moeglichkeiten einer Zuechterischen Verbesserung der biologischen Wertigkeit von Kartoffeleiweiss. Zuechter 28: 51-60.

Richards, F.J. 1969. The quantitative analysis of growth: in plant physiology: F.C. Steward ed. vol. 5A. Academic Press, New York and London: 3-77.

Riedl, W.A. 1948. The inheritance of tuber set in _Solanum tuberosum_ L., Bull. Wyo. Agric. Exp. Sta. No. 287: p. 34.

Rijtema, P.E. and Endroedi, G. 1970. Calculation of production of potatoes. Neth. J. agric. Sci. 18: 26-36.

Rios Iriate, B.J., Thompson, N.R. and Bedford, C.L. 1972. Protein in potato flakes. Evaluating by the meadow vole (_Microtus pennsilvanicus_). Am. Potato J. 49: 255-260.

Rowe, P.R. 1967. Performance and variability of diploid and tetraploid potato families. Am. Potato J. 44(8): 263-271.

Rowe, P.R. 1969. Quantitative variation in diploid potatoes. Am. Potato J. 46: 14-17.

Simmonds, N.W. 1962. Variability in crop plants, its use and conservation. Biol. Rev. 37: 422-465.

Slack, E.B. 1948. Nitrogenous constituents of the potato. .Nature 4084: Febr. 7, 1958. Vol. 161: 211-212.

Slater, J.W. 1963. Mechanisms of tuber initiation. Proc. 10th Eastr. Sch. agric. Sci. Univ. Nottingham: 114-120.

Slater, J.W. 1968. The effect of night temperature on tuber initiation of the potato. Eur. Potato J. 11: 14-22.

Smith, O. 1968. Potatoes: Production, storing and processing. The AVI Publishing Compagny, Inc. Westpoint, Connecticutt.

Speckmann, D.H., Stein, W.H. and Moore, S. 1956. Automatic recording apparatus for use in chromatography of amino acids. Federation Procedings 15: 358.

Spiegelman, S. 1945. Physiological competition as a regulatory mechanism in morphogenesis. Q. Rev. Bio. 20: 121-146.

Steineck, V. 1959. Der Ertragsaufbau der Kartoffel. Bodenkultur 10: 231-245.

Svensson, B. and Naglicka, I. 1975. Development of potato stands in relation to stand density. Potato Res. 18: 105-108.

Swieszynski, K.M. 1965. Auslese von grossen Knollen als Selektionsmethode in der Zuechtung von staerkereichen Kartoffeln. Zuechter 35: 103-107.

Tai, G.C.C. 1974. A method of quantitative genetic analysis of early clonal generation seedlings of an asexual crop with special application to breeding population of the potato (Solanum tuberosum L.). Theoretical and Applied Genetics 45: 150-156.

Tai, G.C.C. 1975, Analysis of genotype-environment interactions based on the method of path coefficient analysis. Can. J. Genet. Cytol. 17: 141-150.

Tai, G.C.C. 1975. Effectiveness of visual selection for early clonal generation seedlings of potato. Crop Sci. 15: 15-18.

Tai, G.C.C. and Young, D.A. 1972. Genotypic stability analysis of eight potato varieties tested in a series of ten trials. Am. Potato J. 49: 138-150.

Salaman, R.N. 1926. Potato varieties. Cambridge University Press, London. p. 214.

Sanford, L.L. 1960. Comparative evaluation of clones as testers for yield, specific gravity and tuber appearance in potato. Ph.D. Thesis, Iowa State University, Ames Iowa, USA.

Sanford, L.L., Fitzpatrick, T.J. and Porter, W.L. 1971. Seleciton potential for tuber total nitrogen and total solids content in a tetraploid breeding population. Am. Potato J. 48: 428-437.

Schupan, W. 1958. Proteins et amino-acids. Teneurs en amino acids indispensables des vegetaux alimentaires et de leurs diverses organes. Qual. Plant. Mater. Veg. 3-4: 19-33.

Schupan, W. 1959. The influence of increasing nitrogen fertilizers on the content of essential amino acids and the biological albumine evaluation of potatoes. Z. Pflanzenernaeh. Dueng. Bodenk. 86: 1-14.

Schupan, W. 1970. Control of plant proteins: The influence of genetics and ecology of food plants. In "Proteins are Human Food," R.A. Lauwrie ed. The AVI Publ. Co., inc., Westport, Connecticutt: 245-265.

Schupan, W. and Postel, W. 1957. Ueber die biologische Wertigkeit des Kartoffeleiweisses. Die Naturwissenschaften 44: 40-41.

Schwartze, P. and v. Sengebusch, R. 1937. Eine Methode zur Bestimmung des Rohproteingehaltes in Zuchmaterial. Der Zuechter: pp. 256-266.

Seiffert, M. 1957. Die Bedeutung der Zuechtung fuer die Ertragsteigerung im Kartoffelban in den letzten 5 Jahrzehnten. Ein Beitrag aur Methodik der Eimittlung des zuechterischen Forschrittes. Zuechter: 27: 1-22.

Shank, D.B. and Adams, M.W. 1960. Environmental variability within inbred lines and single crosses of maize. Genet. 57: 119-126.

Sharma, M.K. Isleib, D.R. and Dexter, S.T. 1958. Specific gravity of different zones within the potato tuber. Am. Potato J. 35: 784-788.

Sharma, K.W. and Thompson, N.R. 1956. Relationshiop of starch grain size and specific gravity of potato tubers. Michigan Quarterly Bulletin: 38: 559-569.

Sigle, K. 1951. Das Kartoffeleiweiss, seine Steigerung und Verwertung. Z.f. Ackerbau-und Pflanzenbau 93: 208-258.

Talburt, W.F. and Smith, O. 1975. Potato Processing. The AVI Publishing Compagny, Inc., Westport, Connecticutt. p. 705.

Talley, E.A., Fitzpatrick, T.J., Porter, W.L. and Murphy, H.J. 1961. Chemical composition of potatoes. I.Preliminary studies on the relationship between specific gravity and the trogenous constituents. J. Food Sci. 26: 351-155.

Talley, E.A. and Porter, W.L. 1970. Chemical composition of potatoes VII.Relationship of the free amino acid concentrations to specific gravity and storage time. Am. Potato J. 47:214-224.

Thomas, R.L., Grafius, J.E. and Hahn, S.K. 1971. Transformation of sequential quantitative characters. Heredity 26: 177-178.

Thompson, R. and Taylor, H. 1974. Stem density and maturation studies with the potato cultivars Maris Peer and Pentland Marble. Potato Res. 17: 51-63.

Thorne, G.N. 1962. Survival of tillers and distribution of dry matter between ear and shoot of barley varieties. Ann. Bot. 26: 37-54.

Tikhonov, P.M. and Demidovich, A.F. 1935. (The inheritance of farming characters and results of potato selection). Izvestiga Agronomicheskogo Fakul'teta Saratovskogo Universiteta 93-117. (quoted by M.S. Swaminathan and H.W. Howard, 1953: Bibliographia Genetica 16: 1-192.

Toosey. R.D. 1963. Effect of number of sprouts per set on yield and grading of main crop production. Nature, 4630. July, 269-270.

Verma, S.C., Sharma, T.R., and Joshi, K.C. 1975. Relation between specific gravity, starch and nitrogen content of potato tubers. Potato Res. 18: 120-122.

Watson, D.J. 1952. The physiological basis of variation in yield. Adv. Agron. 4: 404-445.

Whitehead, T. McIntosh, T.P. and Finnay, U.M. 1953. The potato in health and disease. 3rd ed. Oliver and Boyd, Edinburgh. p. 744.

Williams, W. 1959. The isolation of "pure lines" from F_1 hybrids of tomato, and the problem of heterosis in inbreeding crop species. J. Agr. Sci. 53: 347-353.

Wilson, J.W. 1972. Control of crop pocesses. In crop processes in controlled environments, ed. A.R. Rees *et.al.*, London and New York, Academic Press. pp. 7-30.

Winkler, E. 1971. Kartoffelbau in Tirol II. Photosynthesevermoegen und Respiration von verschiedenen Kartoffelsorten. Potato REs. 14: 1-18.

Wright, S. 1921. Correlation and causation. J. Agric. Res. 20: 557-585.