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SEED AND POD GROWTH AND DEVELOPMENT AND EFFECT ON SEED QUALITY IN DRY BEANS (Phaseolus vulgaris L.)

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IRVINE K. MARIGA

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L. O. Copeland
Major professor

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SEED AND POD AND DEVELOPMENT AND EFFECT ON SEED QUALITY IN DRY BEANS (*PHASEOLUS VULGARIS* L.)

By

Irvine Kwaramba Mariga

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ABSTRACT

SEED AND POD GROWTH AND DEVELOPMENT AND EFFECT ON SEED QUALITY IN DRY BEANS (PHASEOLUS VULGARIS L.)

By

Irvine Kwaramba Mariga

Seed and pod growth and development and effect on seed quality in navy and cranberry beans were studied over two growing seasons. Pod length, pod and seed fresh and dry weight changes in developing fruits were monitored and final yield components were recorded. Concentration and content of macro and micronutrients in the developing pods and seeds were determined. Seed germinability and vigor were evaluated during seed development and after physiological maturity (PM) under continued exposure to field conditions. Germination was evaluated using the standard germination test. Seed vigor was determined by a) warm germination test seedling classification, b) seedling growth rate, and c) hypocotyl length. Limited use of the accelerated aging test and cold soil test was made to evaluate seed vigor after PM.

Pod growth preceded seed growth in all varieties in both seasons. Time to reach full pod length and peak pod fresh and dry weight varied among varieties and with seasons but all varieties first reached maximum pod length before

peak fresh or dry weight. Pod dry weight loss during seed growth suggested pod dry matter remobilization to the developing seeds. Seed growth increased markedly after 22 days after anthesis in all varieties, with maximum growth rates achieved in the second week. Nutrients accumulated ahead, behind, or at the same rate as dry weight in both pods and seeds. Nutrient losses from the pod during seed growth accounted for 2 to 59% of the seeds requirement of different specific nutrients.

Germination of immature seeds occurred from 26 days after anthesis onwards and rapid increases in germination capacity were observed. Germination tests were initially dominated by high rates of abnormal seedlings but the level of normal seedlings increased as PM approached. Maximum levels of both total germination and normal seedlings were attained at PM. Hypocotyl length and seedling weight also increased with seed maturity. After PM, total germination, normal seedlings, hypocotyl length, and seedling weight decreased with time. The level of normal seedlings decreased earlier than total germination.

The results indicate that developing dry bean seeds develop germination capacity ahead of vigor but mature seeds lose vigor before losing germinability.

I dedicate this dissertation to my father, Moses Shonhiwa Mariga, who so willingly carried the burden of my initial schooling and showed me an exemplary life of honesty and hard work; and to my wife Kuda and son Nhamoinesu, who were such an essential ingredient in this undertaking.

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INTRODUCTION

The value of seed for purposes of propagation depends on its physiological and functional quality. The use of high quality seed is fundamental to the establishment of desired crop stands and production of stable yields. Physical purity and germination are the primary factors that determine seed quality. The Association of Official Seed Analysts (AOSA) (1981) defines germination as "the emergence and development from the seed embryo of those essential structures which, for the kind of seed in question, are indicative of the ability to produce a normal plant under favorable conditions." Although there is worldwide acceptance of the standard laboratory germination test, it has a major weakness in that it provides optimum conditions for seed germination whereas field conditions are often far from optimum. The laboratory germination and field emergence of a seedlot may thus vary widely (Isely, 1957). The germination test also fails to distinguish between strong and weak seedlings which may be important in terms of stand establishment, growth and yield.

Although there is almost universal acceptance of the standard warm germination test by both seed analysts and the seed industry, there is also widespread support for the need to determine the planting value of seed which is not dependant only on viability but also on the vigor of the seedlings. Additional vigor tests are therefore needed to supplement the laboratory germination test in order to improve the prediction of suitable field emergence. The International Seed Testing Association (ISTA) defines seed vigor as "the sum total of those properties of the seed which determines the potential level of activity and performance of the seed or seedlot during germination and seedling emergence" (Perry, 1978). The AOSA defines seed vigor as "those seed properties which determine the potential for rapid uniform emergence and development of normal seedlings under a wide range of field conditions" (McDonald, 1980). Both definitions deal with seed germination and seedling development.

Rate and duration of seed growth are dynamic components of seed yield. Only a few studies have been conducted on dry matter accumulation in dry bean seeds (Carr and Skene, 1961; Takao, 1962; Hsu, 1979). An understanding of dry matter accumulation and moisture status of the developing fruit may indicate the sensitive stages of fruit growth which could have agronomic significance.

Most of the studies that report on changes in chemical composition of developing dry bean seeds have focused on

storage products such as proteins (Loewenberg, 1955; Opik, 1968; Ma and Bliss, 1978; Sun et al., 1978; Brown et al., 1982) and starch (Opik, 1968). There is little published information on levels of nutrients in fruits of dry beans. In some legumes, pod walls have been shown to be an important source of nutrients during seed-filling (Hocking and Pate, 1977; Thorne, 1979). In a recent review, Goodwin and Siddique (1984) note that there is little work linking morphological, anatomical and chemical changes in bean seed development with the development of seed germination capacity and seedling vigor.

The main objective of this work was to study the relationship of dry matter and mineral nutrient accumulation to fruit growth and the development of germination capacity and vigor in dry bean seeds. Specific objectives were:

1) To study the moisture and dry matter status of developing seeds and dry matter redistribution between bean pod walls and seeds.
2) To follow changes in the content of major mineral elements in developing bean seeds and pods (fruits) and correlate these changes with the known biochemical events associated with growth and deposition of nutrient storage material in the seeds.
3) To monitor the germinability and seedling vigor of developing bean seeds.

4) To characterize the relationship between dry matter and mineral nutrient status of bean seeds and development of germination and vigor.

5) To monitor the effect of delayed harvesting on bean seed quality: germination and vigor.

LITERATURE REVIEW

Fruit Development

Pod Development

Pods of legumes attain maximum size early in fruit development. Several researchers have reported bean pod development to be completed by about two weeks after anthesis. Culpepper (1936) observed that pods attained full length between 10-15 days after flowering while pod diameter reached a maximum in 25-30 days after flowering (DAF). Carr and Skene (1961) observed completion of pod growth by 16-17 DAF. Watada and Morris (1967), Walbot *et al.* (1972) and Hsu (1979) reported attainment of maximum pod length after 13, 14 and 15 days, respectively.

Pods of Birdsfoot trefoil (*Lotus corniculatus* L) grew rapidly in the first 15 days and attained full length within 21 days (Anderson, 1956). Soybean pods attained maximum dry weight when seed had only 15-30% of their final weight (Egli, 1975). Fraser *et al.* (1982) recorded maximum pod length and width when the seed had reached a mere 4% of the final weight. These results generally agree with those reported on dry beans by Oliker *et al.* (1978) and on garden peas by Pate and Flinn (1977). Legume pod

development, together with the growth of seed testa and endosperm, occurs during the first phase of seed development which Dure (1975) described as the build-up of precursors for embryogenesis. Rapid elongation and inflation growth of the pod accounted for two of the three peaks in assimilate demand during legume fruit development, the last one being due to rapid growth of the seeds (Flinn, 1974).

The fact that pod growth was completed before any notable seed growth has taken place led to the hypothesis that the legume pod may at times serve as either a competing sink or as a source of assimilates for developing seeds (Thorne, 1979; Fraser et al., 1982). The latter role would be achieved through dry matter redistribution. Oliker et al. (1978) suggested that seed development does not depend on photosynthate from the pod but that growth of both the seeds and pod depends almost exclusively on photosynthate from outside the pod. They suggested that pod and seeds form a system of competing sinks. Either the pod reaches its maximum size and thus ceases to function as a sink, making assimilates available for the beginning of rapid seed development, or the events that start rapid seed growth also influence diversion of nutrients to the developing seed and in that way stop further pod growth.

Pods of dry beans have been observed not to redistribute any dry matter during seed development (Crookston et al., 1974), a negative attribute unless the beans are harvested for their fleshy pods. Pod dry matter

matter redistribution to developing seeds during late seed-filling has been observed in soybean (Thorne, 1979), peas (Pate and Flinn, 1977) and castor bean (Hocking, 1982). Pod development is therefore likely to influence the subsequent seed growth. In fact, Fraser et al. (1982) reported significant correlation of pod length and width to final seed size in soybean.

Seed Development

Studies of Hsu (1979) led him to suggest that legume seed development can be divided into two distinct processes: formation of basic cellular structure, and accumulation of storage material. Flinn (1974) indicated that rapid growth of seeds was the cause of the last of three well defined peaks of assimilate demand during legume fruit development. Seed growth in dry bean began nine DAF (Carr and Skene, 1961) and initial growth during pod extension was slow. Culpepper (1936) reported that seeds made up only 4% of the fruit weight at 15 DAF but accounted for 53.8% of the total weight at physiological maturity. He measured increase in seed length from 2.5 mm at 10 days to 15.8 mm at 30 DAF. Seed below 7 mm in length contributed 2% to total fruit weight but made up 57% at maturity (Hibbard and Flynn, 1945). Seed dry matter increased from 10 to 30% during the same period. Loewenberg (1955) reported a slow increase in seed dry weight, reaching 17% of the final weight in the first three weeks. The rates of fresh and dry weight gain then increased greatly in the next two weeks, reaching their

maxima 24 DAF while seed fresh weight reached a peak at 36 DAF.

The formation and development of the seed coat in legumes, as in most species, is completed considerably in advance of that of flowering, fertilization, and, thus, embryo formation and growth as shown for peas (Pate and Flinn, 1977) and beans (Hsu, 1979). Loewenberg (1955) found that in the very small seeds of about 2 mg, the seed coats accounted for 95% of the dry weight, whereas in mature seeds the seed coats accounted for only 10% of the seed weight. Hsu (1979) observed that the bean testa constituted a major part of the seed in the first two weeks of growth after which the embryo exceeded the testa in weight. Dure (1975) described the growth of the testa and endosperm during pod extension as precursors to embryogenesis. He stated that the legume endosperm developed in mass and served as a transient reservoir of sugars and amino acids before it was utilized by the developing embryo. Pate and Flinn (1977) illustrated that endosperm existence in garden peas was approximately seven days.

Cell division in the cotyledonary tissue of beans was completed three weeks after anthesis (Loewenberg, 1955). Generally, final cell number of the embryo was reached early in legume seed development (Dure, 1975).

Carr and Skene (1961) observed a diauxic pattern of seed growth in beans. The first phase of exponential growth was separated by a three day lag of very slow growth. The

next phase was characterized by rapid initial growth which later declined and stopped at maturity. The lag phase occurred from 20 to 23 DAF. Seed dry and fresh weights increased at about the same relative rate during the phase of exponential growth. Watada and Morris (1967) reported the growth pattern of snap bean seeds to be a double-sigmoid curve with a lag in growth from about 20 to 22 DAF. A similar biphasic pattern of seed growth separated by a lag phase of 3 days was reported for certain pea varieties (Pate and Flinn, 1977). The existence of a lag phase in the growth of legume seeds can easily be missed due to large sampling errors or when sampling is not frequent enough (Pate and Flinn, 1977). The occurrence of the lag phase in seed growth coincides with the completion of cell division in the cotyledonary tissue (Loewenberg, 1955).

The lag phase in seed growth may be caused by physical restriction imposed on the enlarging embryo by the testa once the embryo sac is filled (Carr and Skene, 1961). This is supported by work showing maximum volume of the seed coat at 23 DAF (Hsu, 1979). His studies also documented similar developmental patterns of weight and volume gain for the embryo and seed coat, suggesting that they are regulated as a single developing entity. Burrows and Carr (1970) suggested that the lag in growth may be nutritionally related to the disappearance of the endosperm with its high contents of cytokinins and other nutrients. Hsu (1979) observed the disappearance of the endosperm in bean seeds

after 13-15 DAF and Pate and Flinn (1977) showed the same time frame for field peas. It is thus possible that from 15 to 20 DAF, cell division in the cotyledons slows down until it stops by the onset of the lag phase. Smith (1973) contended that the lag marks some basic changes in cellular activity of the embryo. This is because it coincides with the end of cell division in the cotyledons and with a transition from a phase of expansion dominated by solute accumulation to a non-expansive one during which insoluble reserves start to accumulate as reported by Hall et al. (1972). A pause in the growth of pea seeds was associated with a decrease in the amount of sucrose per seed (Bisson and Jones, 1932). The control mechanism of the lag phase may involve several systems governing both growth and biochemical activities.

The embryos of the two varieties studied by Hsu (1979) generally followed similar weight change patterns until between day 18-20 when they both attained their peaks in dry weight gains. The difference in seed dry weight gain in those later stages determined the final differences in seed size. Hsu (1979) concluded that this later growth associated with seed-filling of storage material was more important in determining seed size in legumes than the initial growth during which basic cell structure is formed.

Chemical Composition

Nitrogen and Protein

Several workers have studied nitrogen and protein changes in developing fruits of dry beans and other legumes. Hall et al. (1972) observed that the bean pod has high protein content initially when seeds are very immature (2-10 mm in length) but it declines sharply as seeds become larger and increase in protein content. Similar results were reported for total nitrogen in bean pods by Culpepper (1936) in which nitrogen levels decreased from 25 DAF onwards. Total nitrogen in the bean fruit increased from .77% at 15 days to 1.58% by day 40, a sharp increase being noted after day 20 (Culpepper, 1936). This sharp increase begins just after the lag phase in seed growth described by Carr and Skene (1961), which is also the period of rapid dry matter accumulation in legume seeds.

Loewenberg (1955) recorded 6.5% seed nitrogen at 12 DAF which declined to 3.5% at 32 days where it remained until maturity. Opik (1968) reported an initial decrease in seed nitrogen content but the concentration remained constant at 3.8 % of the dry weight after 32 days. Most of the protein accumulation in bean cotyledons occured between 10 and 30 DAF, with sharp increases after 17 days (Sun et al., 1978). By 37 days the protein content in the cotyledons was 75 times the amount at 14 days. This agrees with Smith (1984) who stated that 95% of storage proteins are synthesized during cell expansion.

Protein content of mature bean seeds ranges between 20 and 30%. Leveille et al. (1978) reported an average of 22.3% for navy bean, Ma and Bliss (1978) a range of 25-28%, Sun et al. (1978) 20%, while Kay (1979) gave 22% protein as the approximate worldwide average. Globulin is the primary protein in pulses (Smith, 1984). Phaseolin is the major globulin storage protein of dry beans, the other being the lectin-containing globulin-2 and albumin protein fractions (Bliss and Brown, 1983). Phaseolin accounts for 36 to 46% of the total dry bean protein and is low in sulfur amino acids and has poor digestibility. The lectin proteins contribute to the poor nutritional value of raw bean flour but generally, the antinutritional factors, like trypsin inhibitor, can be inactivated by cooking. Globulin of garden pea, bean and soybean is composed of two fractions: vicilin and legumin (Bewley and Black, 1978). Beevers and Poulson (1972) reported that globulin, (legumin: vicilin ratio of about 3:1) comprized 85% of the total protein at maturity in garden peas. This is comparable to 80.7% of total nitrogen bound in reserve protein in mature field peas as reported by Pate and Flinn (1977).

Nutrient Elements

Little information has been published on changes in nutrient elements during fruit growth in dry beans but some detailed studies have been done on peas (Pate and Flinn, 1977; Hocking and Pate, 1977), lupins (Hocking and Pate, 1977) and castor bean (Hocking, 1982).

Loewenberg (1955) reported than nitrogen and phosphorus initially increased slowly in bean seeds, acquiring 17% of their final amounts after three weeks. Their rates of accumulation attained a maximum at 24 DAF. This indicates that the accumulation of nitrogen and phosphorus increased after the lag phase reported by Carr and Skene (1961) and is in general rhythm with the general seed growth. Phosphorus concentration in bean seeds decreased from 1.1% at 12 days to 0.4% by day 32 where it remained constant (Loewenberg, 1955). This agrees with Austin (1972) who noted that concentrations of simple nitrogen and phosphorus compounds are high in young seeds but decrease with maturity. The high initial levels are associated with active metabolism in the young tissue.

Pate and Flinn (1977) studied nutrient element changes in developing pea fruits. They reported that in the early phase of the fruit growth, zinc, phosphorus, iron and copper appeared to increase relatively in advance of dry weight. Manganese, magnesium and potassium paralleled dry weight gain, while calcium fell slightly behind dry weight. Similar results were observed by Hocking and Pate (1977) in the leaves, pods, seed coats and embryos of field peas, white lupin and narrow-leaved lupin. They found that phosphorus, nitrogen and zinc tended to increase ahead of dry matter; potassium, manganese, copper and magnesium increased concurrently with dry weight, but calcium and sodium increased at lower rates. Hocking (1982) observed that

concentrations of all nutrients except phosphorus were higher in young capsules of castor bean than in young seeds, but levels of nitrogen, phosphorus, magnesium, iron, zinc and copper were higher in mature seeds than in mature capsules. He noted that the rate of increase of most elements was out of phase with dry matter accumulation in the capsule but matched that in seeds.

There is a large build-up of phytic acid in cotyledons during the time of starch and protein deposition in dry beans (Makower, 1969) and in peas (Rowan and Turner, 1957). This indicates that legume cotyledons are a storage sink for phosphate. In mature seeds phytic acid content has been found to be highly correlated to total phosphorus in P. vulgaris (Lolas and Markakis, 1975) and in Vicia faba (Griffiths and Thomas, 1981).

Other Substances

The levels of starch, sucrose, protein, and soluble nitrogen are at their highest in the pod at maximum fresh weight (Bisson and Jones, 1932; Flinn and Pate, 1968). Free sugars achieve an early maximum in bean seed growth and then fall sharply once starch synthesis begins (Bisson and Jones, 1932). Yazdi-Samadi (1977) reported that sucrose concentration in soybean seeds decreased from 8 to 5% while galactose and fructose fell from 2 and 4%, respectively, to less than 0.6% between the start of seed development and maturity. Bisson and Jones (1932) speculated that the pool of sugars has a role in switching on or regulating the

synthesis of starch. Opik (1968) observed that starch synthesis starts ahead of protein synthesis in bean cotyledons. A marked increase of starch in bean seeds from 11.1% at 19 days to 39.0% at 43 DAF has been reported (Goodwin and Siddique, 1984). The level of starch then remained constant up to maturity. A comparable level of 45% has been reported for peas (Pate, 1975).

Mature soybean seeds have been reported to have little or no starch (Bils and Howell, 1963; Shibbles et al., 1975; Yazdi-Samadi, 1977). Shibbles et al. (1975) suggested that starch grains may be mobilized during dehydration of the seed. Smith (1984) supported the mobilization concept adding that the synthetic activities during late seed development consume the starch in the seed since there will be a reduction or termination of translocation of carbohydrates from the senescing leaves.

Hibbard and Flynn (1945) observed higher levels of ascorbic acid, thiamine, riboflavin and niacin in the seed than in the pod of dry beans but carotene concentration was higher in the pods throughout fruit development. Carotene levels in the pods decreased to less than a third of its peak level by the time the pod attained full length. Ascorbic acid, thiamine and riboflavin concentrations decreased with maturity in the pod but niacin levels remained constant. The four vitamins increased with maturity in seeds, and paralleled dry weight increase. Their results

suggested that green beans harvested as soon as the pod attained full length had the best balance of vitamins.

Nutrient Remobilization

Mckee (1955) reported translocation of starch from pods to seeds in dry beans and observed that the pod acted as a temporary reservoir of carbohydrates to be translocated to the seed. This is contrary to observations by Crookston et al. (1974) who stated that bean pods do not redistribute dry matter to developing seeds. A pronounced drop in pod nitrogen and phosphorus and their corresponding increase in the seed was observed during the last two weeks of growth of dry beans by Jantawat (1969), implying pod to seed translocation. Hall (1968) observed a similar pattern of transfer of protein in snap bean. Pate and Flinn (1977) reported that the pea pod could possibly supply 13.9% of the potassium, 12.6% of the phosphorus, 13.5% of the magnesium, 11.5% of the calcium, 9.2% of the iron, 6.6% of the zinc, 9.3% of the manganese and 5.2% of the copper required by the seeds during pod senescence. The pods also supplied 24.1% of the total seed nitrogen and 25% of the carbon requirements. The pod of the white lupin was shown to be a temporary reservoir of seed-bound solutes and provided 16% of the seed's nitrogen (Pate et al., 1977). The same study showed that the pea pod facilitated reutilization of the respiratory products of the seeds. In a study of garden peas, white lupin and narrow-leaved lupin, Hocking and Pate

(1977) estimated mobilization returns from pods to provide 4-39% of the seed's accumulation of specific minerals.

Significant losses of zinc, phosphorus, copper and manganese from capsules of castor bean during fruit ripening were reported by Hocking (1982), but dry matter, nitrogen, potassium, sulphur, calcium, magnesium, sodium and iron remained in the capsules. Egli et al. (1978) reported fairly substantial nitrogen redistribution from pods to seeds in soybean, while Thorne (1979) found starch, reducing sugars and nitrogenous compounds to be redistributed from pods of soybean.

Seed Maturation

Seed maturation refers to the last segment of development following a large increase in dry weight and the lag phase when seed desiccation occurs. Adams and Rinne (1980) noted that seed development and maturation are associated with an overall loss of moisture. Tekrony et al. (1979) suggested that the phenomenon of seed maturation can best be described in terms of physiological maturity and harvest maturity.

Physiological maturity (PM) is defined as the time of maximum dry weight accumulation in the seed (Harrington, 1972; Crookston and Hill, 1978; Tekrony et al., 1979). At this stage of development, movement of nutrients through the funiculus to the developing embryo ceases, making the seed an independent biological unit (Tekrony et al., 1979). Seed

is considered to have highest viability and vigor at PM (Wahab and Burris, 1971).

PM is therefore an important stage in seed development and the need to be able to define it can not be overemphasized. In cereals, the formation of a black layer at the base of the endosperm marks PM. Daynard and Duncan (1969) observed that formation of the black layer coincided with the completion of starch granule formation in the endosperm of corn. In sorghum it marked the termination of assimilate translocation into seeds (Eastin et al., 1973). In grain legumes, loss of green color by the pods seems to be the most reliable and practical determinant of PM. Crookston and Hill (1978) found initiation of seed shrinkage in the pod together with the loss of green color to be the most reliable indicators of PM for individual soybean seeds. Tekrony et al. (1979) concluded that when pods or seeds were completely yellow, soybean seeds have attained PM. While Spaeth and Sinclair (1984) reported color change at the periphery of the cotyledons, Gkipki and Crookston (1981) found loss of green color to be a satisfactory indicator of the end of soybean seed growth. Watada and Morris (1967) observed seed moisture content to be a reliable index of maturity in beans since environmental conditions varied among seasons making the chronological age of DAF unreliable. Egli et al. (1978) showed that moisture status of seed was directly related to its stage of development. This agrees with Crookston and Hill (1978) and Tekrony

et al. (1979) who found seed moisture content of soybeans at PM to be constant across cultivars and environments.

Seeds attain PM at high moisture levels which are unsafe for storage and when moisture levels in the other plant parts are too high for mechanical harvesting. Further desiccation is therefore necessary before harvest maturity (HM) is reached. HM was defined by Tekrony et al. (1979) as the first time seed moisture falls below 14%. The time from PM to HM varies with crops and environmental conditions during maturation (Tekrony et al., 1979) and seed quality can be adversely affected by severe weather during this period. Bishnoi (1974) reported less than a week for triticale seeds (Triticale hexaploid L.), Tekrony et al. (1979) reported a range of 10-20 days, while Gkikpi and Crookston (1981) found 9-10 days were required for soybeans to reach HM after first having attained PM.

Relationship between Seed Maturation and Germination

The ability of seeds to germinate before complete maturity is well known and this ability has been shown to be enhanced in dry beans by artificially drying the immature seeds (Inoue and Suzuki, 1962; Dasgupta et al., 1982) and soybeans (Burris, 1973; Adams and Rinne, 1981; Adams et al., 1983). Adams and Rinne (1981) and Adams et al. (1983) also showed that seeds that were allowed to dry slowly in intact pods had better viability than if dried faster outside the pod. Adams and Rinne (1981) germinated soybean seed at 30

DAF and obtained 2% germination from fast-dried seed and 86% germination from those air dried in the pod (i.e. slow-dried). Slow drying allowed degradation of chlorophyll, a characteristic of maturation, but fast-dried seed remained green (Adams et al., 1983). The same study showed that greater amounts of inorganic phosphate, sugars and soluble protein were leached from fast-dried seeds on subsequent rehydration than from slow-dried seeds. Slow-dried seeds contained specific enzymes necessary for germination: malate synthase and isocitrate lyase from as early as 33 DAF whereas the fast dried seed of the same age did not contain these enzymes which were found only in fresh seed 54 DAF or older. The results indicate that maturation facilitated by slow drying allowed the seeds to develop these enzymatic capabilities and seed coat integrity.

Although drying of immature seeds may enhance germination of immature seed, the seed must first become tolerant to desiccation. Dasgupta et al. (1982) reported some differences in cellular characteristics of immature seeds of varying ages which are likely linked to their germination ability. They suggested that desiccation tolerance in bean seeds may be associated with the integrity of the cell nucleus and its surrounding membrane or that some other fundamental changes must occur in the cells. Kermode et al. (1986) showed that premature drying of P. vulgaris and R. communis seeds permanently redirected metabolism from a developmental to a germination phase but

that the seed must first develop the ability to withstand the drying treatment. They speculated that this ability to tolerate desiccation is achieved simultaneously with the ability of the genome to change phases. They suggested that desiccation could switch the seed from developmental to a germination metabolism in one of two ways. Either loss of water triggers the cessation of development protein synthesis and the induction of germination protein synthesis or that messages for proteins essential for development may not be able to withstand drying whereas those necessary for germination can withstand drying. Furthermore, they suggested that after the compositional and conformational changes that make the seed desiccation-tolerant, premature or natural drying of developing seeds may affect hormonal balance of the seed favoring the germination process. Desiccation could either increase gibberellic acid sensitivity or decrease abscissic acid concentration or sensitivity.

It is quite possible that the genome controls maturation and triggers natural seed desiccation as a requirement to facilitate low moisture by the time the seed matures and thus ensure good seed quality and longevity. The seed may acquire desiccation tolerance when the genome has developed enough to survive unfavorable conditions, such as premature drying (an exogenous effect).

Seed Quality

Other than varietal purity, seed quality can be measured in terms of seed viability and vigor.

Seed Germination

Germination can be defined as "the resumption of active growth by the embryo resulting in the rupture of the seed coat and emergence" or, in the physiological sense, as "the emergence of the radicle through the seed coat" (Copeland and McDonald, 1985). In the seed industry, germination is defined as "the emergence and development from the seed embryo of those essential structures which for the kind of seed in question, are indicative of the ability to produce a normal plant under favorable conditions" (AOSA, 1981). Definitions of normal and abnormal seedlings are based on the development of essential structures and are found in the Rules of Seed Testing of both ISTA (1966) and AOSA (1981). Thus, a seedling can be classified as abnormal if it lacks certain essential structures, such as radicle, epicotyl or cotyledon, is twisted, has an abnormal shape or has greatly reduced growth (Copeland and McDonald, 1985). Standardized procedures of testing have made the standard warm germination test reliable and highly reproducible among laboratories. Germination test results are a requirement of seed labeling all over the world and are used to determine the suitability of a seed lot for sowing and to compare the value of different seed lots (Mackay, 1972).

Germination of immature seeds has been demonstrated by Inoue and Suzuki (1962), Walbot et al. (1972), Siddique (1980) quoted by Goodwin and Siddique (1984) and Dasgupta et al. (1982) in beans and by Burris (1973) and Adams and Rinne (1981) in soybeans. These studies also showed that germination of immature seed is enhanced by drying, the immature seed being tolerant to desiccation only after it has reached a certain stage of development. Dasgupta et al. (1982) suggested that desiccation tolerance in bean seeds may be associated with the integrity of the cell nucleus and its surrounding membrane. Adams and Rinne (1981) and Adams et al. (1983) demonstrated that the rate of drying influences germinability in immature seeds. Immature seeds of dry beans survived fast-drying but those of castor bean only tolerated slow-drying (Dasgupta et al., 1982).

Although the mechanism by which seeds develop germinability remains unclear, the review by Kermode et al. (1986) strongly suggested that desiccation plays a role. Siddique (1980), cited by Goodwin and Siddique (1984), found that the ability to germinate in dried immature beans was closely correlated with seed dry weight and lack of ion leakage on imbibition. That suggests that the development of the testa and other cell membranes could be associated with the development of germination ability which is considered to be highest at PM (Wahab and Burris, 1971).

Seed Vigor

Although testing for vigor is not yet a requirement for seed labeling, the concept of vigor and its importance to crop production are well recognized. Several reviews on the concept of vigor have been written (Isely, 1957; Heydecker, 1969; McDonald, 1975; McDonald, 1980).

Laboratory germination and field emergence of given seed lots have been reported to vary widely (Burris et al., 1969; Tekrony and Egli, 1977). These differences have been attributed to the vigor of the seeds. Heydecker (1969) noted that loss of seed vigor precedes loss in germinability and gave examples showing seeds with similar germination but different field emergence levels.

The detailed review by Suryatmana (1980) shows how perception of seed vigor developed and how the definition improved with time as more research was completed. Isely (1957) defined vigor as "the sum of all attributes which favor stand establishment under unfavorable conditions." Woodstock (1969) defined vigor as "that condition of active good health and natural robustness in seeds, which upon planting, permits germination to proceed rapidly and to completion under a wide range of environmental conditions." This was an improvement on Isely's definition in that Woodstock included the completion of germination and widened the range of environment. Ching (1973) defined seed vigor as "a potential for rapid and uniform germination and fast seedling growth under general field conditions." Her

definition added the important dimension of uniformity in germination which will result in uniform stands. She also stated that seed vigor involved germination and seedling growth, noting that establishment of early stands enabled the seedling to avoid or withstand the attack of micro-organisms, insects and competition of weeds. This shows that the idea of seed vigor can go well beyond just germination.

ISTA defined seed vigor as "the sum total of those properties of the seed which determines the potential level of activity and performance of the seed or seedlot during germination and seedling emergence (Perry, 1978). AOSA defined it as "those properties which determine the potential for rapid, uniform emergence and development of normal seedlings under a wide range of field conditions (McDonald, 1980)." McDonald (1980) considered the AOSA definition to be an operational one in that it focuses on what seed vigor does whereas the ISTA definition is considered academic because it conceptualizes seed vigor by discussing and describing it. It is important to note that both definitions mention emergence and performance of the seedling. Satisfactory as these definitions may seem, they still lack the precision required to lead to acceptable and reproducible procedures of evaluating seed vigor.

Factors Influencing Seed Vigor

Seed vigor is influenced by many factors which may act alone or collectively. Heydecker (1969) listed genetic, physiological, cytological, pathological, and mechanical

factors as possible causes of loss of seed vigor. Genetic constitution, environment during seed development, and seed storage environment were listed as the more important factors that influence seed vigor by Copeland and McDonald (1985). Barriga (1961) demonstrated varietal differences in the tolerance to mechanical abuse in navy beans. Hardseededness and hybrid vigor are also known to depend on genetic constitution. Inoue and Suzuki (1962) and Wijandi and Copeland (1974) demonstrated that premature harvesting of dry bean seeds resulted in loss of vigor. This loss in vigor may be related to seed size as prematurely harvested crops give smaller seeds and larger seed has been reported to produce larger seedlings (Ries, 1971). Seeds harvested before completion of seed-filling often exhibit low vigor which Thomson (1979) associated with permeability of cell membranes, since semi-permeability develops as the seed ripens. Ries (1971) reported a positive association between high vigor and high protein content of seeds. All major nutrients except phosphorus and iron have been shown to be important in the production of high vigor seeds (Goodwin and Siddique, 1984).

Vigor Tests

Reviews on vigor tests have been written by Moore (1968), McDonald (1975), McDonald (1980) and Suryatmana (1980). Laboratory evaluation of seed vigor is needed to assist farmers and seed traders in identifying high vigor seed lots (McDonald, 1975). The information also enables

farmers to make informed decisions on purchase of seeds, seeding rate and expected uniformity of stand. It helps seedsmen to make marketing decisions such as which seed lots to sell immediately, store, withdraw from the market or label and promote as high vigor seed (Suryatmana, 1980).

Isely (1957) divided vigor tests into direct and indirect tests while McDonald (1975) divided them into physical, physiological and biochemical categories. Direct tests such as the cold test attempt to measure the ability of seeds to emerge under simulated field stress conditions (Copeland and McDonald, 1985). The cold test exposes seeds to cold, wet soil and in that way put them under stress from temperature, moisture and micro-organisms. The major problem with the cold test is that reproducibility of the soil conditions, such as pH, moisture, microorganism content and temperature is difficult. Direct tests have also been criticized for not showing vigor differences when field conditions are near optimal.

Indirect tests measure some specific components of seeds such as cell membrane integrity in the conductivity test. The conductivity test measures leakage of electrolytes which is associated with degradation of cell membranes. This test has the weakness of averaging the leakage of all 25 seeds and thus fails to reflect the variation in a seed lot. New equipment that can monitor leakage of individual seeds has been developed and Copeland and McDonald (1985) cited

several examples that demonstrated its ability to assess seed vigor more accurately.

Physical tests measure physical characteristics of seeds, such as seed size, seed weight and seed density, and these have been shown to be correlated with vigor (McDonald, 1975). Physical tests have the advantage of being simple and are usually easy to perform.

Physiological tests measure some aspect of germination or seedling growth (Copeland and McDonald, 1985). These include speed of germination, standard germination and seedling growth rate tests. The speed of germination test is based on the fact that vigor differences in seed lots with similar total germination can be seen in differences in the rate of germination and growth. This test has the advantage of being performed along with the standard germination test but the evaluator must be sufficienty experienced to identify the earliest occurrence of germination. Edge and Burris (1970) found the 4-day count to be an effective vigor index for soybean seed. The seedling growth rate test assumes that differences in seed vigor are reflected in differences in seedling weight. This test also utilizes material for the standard germination test but it can be affected by variations in moisture and light.

Biochemical tests, such as the tetrazolium, respiration and glutamic acid decarboxylase activity (GADA) tests measure specific chemical reactions associated with the expression of germination. The tetrazolium test evaluates

potential germination level and soundness of embryo on the basis of tissue staining by formazan, an insoluble red pigment formed when dehydrogenase enzymes react with the tetrazolium molecule. This test is simple, quick and requires little equipment but the proper interpretation of the staining requires training and experience. The tetrazolium test has been reported to overestimate the potential of a seed lot (Burris et al., 1969) and fails to reveal dormancy (McDonald, 1980). The GADA test requires sophisticated equipment and presents opportunity for errors during measurements. Use of the respiration test assumes that vigorous seeds germinate and grow rapidly, thus requiring more energy which increases respiratory activity. This test is rapid and quantitative but requires a respirometer and some training. Mechanical damage may confuse the results as it results in increased respiration rates, though seed vigor may have been reduced. Kittock and Law (1968) reported high correlation of respiration with seedling vigor in wheat.

The accelerated aging test is an example of a stress test. Unimbibed seeds are subjected to high temperature (41°C) and high humidity (95-100%) for 3 days before being germinated under optimum conditions of the standard germination test. This test may become one of the most reliable vigor tests if initial seed moisture is standardized (McDonald, 1977, 1980).

Other tests which are less commonly performed include osmotic stress, brick-grit and polyethyleneglycol test.

Suryatmana (1980) reported very low correlations between seed vigor indices and crop yield in dry beans under both optimal and stress conditions. The standard germination test provided the best single estimate of field emergence under optimal field conditions but under less favorable conditions, field emergence was best estimated by a combination of standard germination and accelerated aging tests. He found the conductivity test to be the best single estimate of vigor and field emergence potential under stress conditions and suggested that a combination of two or three vigor indices may be required to predict field emergence.

Environmental Effects on Seed Quality

Although unfavorable environmental conditions during seed development and maturation have been reported to lower seed quality (Green et al., 1965; Kmetz et al., 1979), delayed harvesting seems particularly detrimental to seed quality of large seeded legumes (Pollock and Toole, 1964; Green et al., 1966; Nangju, 1977). Warm and wet conditions during seed development and maturation are known to cause infection of soybean seeds by Phomopsis (Kmetz et al., 1979). Spilker et al. (1981) found a combination of high temperature and high humidity during seed maturation to increase Phomopsis infection and lower germination in soybeans, but Tekrony et al. (1983) reported that the infection depends more on moisture than on temperature.

These reports indicate the need to choose varieties or times of planting that will ensure that maturity is attained in favorable weather.

Pollock and Toole (1964) reported that low vigor in lima bean was caused by bleaching which occured when the seeds were exposed to strong sunlight before harvest. Delayed harvest of beans under similar conditions results in over-dried seeds which are susceptible to mechanical or physical damage during harvesting, threshing, processing and planting operations (Schwartz, 1980). Delayed harvesting of soybeans has been reported to result in reduction of vigor (Green et al., 1966) as well as germination (Nangju, 1977). Thomson (1979) stated that delayed harvesting exposes seeds to weathering which causes deterioration in germination capacity and vigor of pulse crops when pods absorb water in a heavy storm and retain it for some time. In addition to enhancing microbial infections, rainfall can affect seed vigor by imposing physical stress caused by alternating swelling and contracting due to changing moisture content effected by wetting and drying. Mature seeds of large-seeded legumes such as dry beans expand when they absorb moisture but on rapid loss of water, the testa does not always fully shrink back to the embryo, thus creating a loose testa which is susceptible to damage during harvesting and processing (Moore, 1972).

MATERIALS AND METHODS

Planting

Certified seed of four varieties of Phaseolus vulgaris L was planted on the Michigan State University Botany and Plant Pathology farm during the 1985 and 1986 growing seasons. Included were two navy bean varieties, C-20 and Seafarer, and of two cranberry varieties, CRAN-028 and Michigan Improved Cranberry (MIC). Seafarer is an early maturing variety with bush (type I) growth and C-20, a full season variety with an upright short vine (type II) growth habit. CRAN-028 is a mid-season maturing bush type (type I) variety and MIC is a late maturing variety with a vine type (type III) growth habit (Copeland, 1984).

Experimental Design

In 1985, the four varieties were planted in four adjacent strips of 10 to 12 rows each, with one variety occupying each strip. Four adjacent rows with uniform growth were selected within each strip to become the experimental area. Three 10-meter plots were selected within each strip to comprise three replicated areas of study. Thus, each variety had three replicates occupying the same position in the three blocks as they progressed along one strip. In 1986, the experiment was laid out in a randomized complete

block design with three replicates. Each plot was 9 meters long with 9 rows.

Management

The experiments were planted on June 20 and June 21 in 1985 and 1986, respectively. Reseeding was done one week later for MIC in 1986. The rows were spaced 50 cm apart with an intra-row spacing of 7-8 cm for both years. The experiment was planted with a tractor-mounted planter in 1985 and a hand-operated planter in 1986. The standard fertilizer and herbicide practices recommended for bean production in Michigan were applied in both seasons. The 1986 crop received 100 kg/ha of urea (46%N) five weeks after planting, applied two days after cultivation to alleviate soil compaction.

Sampling Procedure

In 1985, the two middle rows of each plot were subdivided into 10 sampling units of one meter length which were randomly allocated numbers from one to 10. The subunits were later sampled from one upwards. In 1986, six of the middle rows were selected and divided into two units of three rows each. Each unit of three rows was subdivided into one meter segments, resulting in a total of 18 subunits, which were randomly allocated numbers from one to 18.

In each season, the plants were observed daily until 50% flowering (when 50% of the plants in a plot had at least one open flower). At that stage about 20-25 freshly opened

flowers were tagged per sampling subunit and the date was noted. Pod sampling began 12 days after flowering (DAF) in 1985 and 13-15 DAF in 1986. Sampling was always done in the morning between 8:00 and 10:00 AM. At each sampling, all pods formed on the tagged flowers in a sampling unit were removed from the plant, leaving a piece of the pedicel intact. Where the numbers of tagged pods were inadequate, due to abortion, additional pods which matched the tagged ones in size and appearance were selected from the sampling area. All pods which showed pronounced insect damage or other disorders were eliminated from the sample. The sampled pods were immediately placed inside plastic ziplock bags and kept in the shade until sampling was completed. The bean pods (fruits) were taken to the laboratory within one to one and a half hours from the beginning of sampling and refrigerated at about 5° C until processing as described below.

Sampling was done at three-day intervals for the first three or four samplings in 1985 and then at weekly intervals. All sampling was on a weekly basis in 1986. Sampling for fruit development was terminated at physiological maturity, when about 90% of all pods in a plot had changed color from green to yellow or brown. Sampling to monitor seed quality was continued after physiological maturity, roughly at weekly intervals, until the end of October in both years.

Laboratory Processing

Ten pods were randomly selected from each sample. These were measured for length (cm) after cutting off the pedicel. They were then opened with a razor blade and the seeds put in a labeled aluminum cup. The empty pods were cut into small slices and put into separate labeled aluminum cups. Both seeds and pods were immediately weighed on an analytical balance to determine their fresh weight and then dried in an oven at 65°C for 48 hours. After drying, they were cooled and weighed again to determine their dry weight. The dry samples were then sealed in paper bags for nutrient analysis. The ventral suture of the remaining fruits were carefully opened with a razor blade to avoid injuring the seeds which were removed, spread on paper, and allowed to air dry in the laboratory. As soon as the seeds were dry (after about a week) they were sealed in paper bags and immediately placed in air-tight plastic bags and stored in a cold room at 5°C for later evaluation for germination and vigor.

Harvesting Procedures

Harvesting to determine yield and yield components was done when 90 percent of the pods had obtained their mature pod color. All plants in the harvest area, except the two outermost plants in a row, if the harvest subunit was at the end of the plot, were removed and threshed by hand. At harvest, 10 representative plants were pulled and the number of pods/plant and seeds/pod determined. Weight per hundred

seeds was determined from each plot as an average of two 100-seed samples. In 1985, yield was estimated from 2.0 m^2 and in 1986, from 4.5 m^2 per plot. The threshed seeds were weighed and a 100-gram sample was dried at 65°C for 48 hours then weighed again to determine moisture content. Yields were adjusted to 12% moisture.

Percent seed and pod moisture were determined by the formula:

$$\frac{\text{Loss in weight (g)}}{\text{Weight before drying (g)}} \times 100 = \% \text{ moisture}$$

Final harvest yield was adjusted to 12% moisture by the formula:

$$\text{Weight at 12\% moisture} = \frac{\text{Weight before drying} \times (100 - \% \text{ moisture})}{88}$$

Plant Tissue Analysis

Dried samples of pods and seeds from the growth study were ground to pass through a 40 mm mesh sieve and immediately sealed into labeled plastic bags. These were later analyzed for total nitrogen and other nutrients.

Total Nitrogen

Total N in the plant tissue samples from 1985 was determined by the Kjeldahl method outlined by Bremner (1965). One hundred and fifty mg of plant tissue were digested for two hours with 3 ml concentrated H_2SO_4 and 1.3 g catalyst (a 100:10:1 mixture of K_2SO_4, $CuSO_4$ $5H_2O$ and Se) on digestion racks. Each sample was diluted with 10 ml of

distilled water as it cooled. About 12-15 ml of 10N NaOH was added to each flask to completely neutralize the acid. Distillation followed immediately and the distillate collected in a flask containing 5 ml 2% H_3BO_3 and methyl purple indicator. The samples were then titrated with H_2SO_4.

Percent nitrogen was calculated by the formula:

$$\frac{1400 \times N \times (\text{titration volume[ml]} - \text{blank[ml]})}{\text{Sample weight in milligrams}} = \%\text{Nitrogen}$$

(where N is the normality of the acid)

In 1986, a different procedure was used to determine the N percentage. One hundred and fifty mg of plant tissue were digested for one and a quarter to one and a half hours with 7 ml concentrated H_2SO_4 and 1.3 g of catalyst (a 100:10:1) mixture of K_2SO_4, $CuSO_4$ $5H_2O$ and Se). After cooling, the samples were diluted up to 75 ml with distilled water and put into vials. The N percentage was later determined on an automatic Technicon analyzer.

Total Spectrum of Mineral Nutrient Elements

Five hundred mg of plant tissue from each sample were weighed in a clean, numbered crucible, which was covered immediately. One standard (horticultural leaf material) and one blank were included for every 25 samples of experimental material. The covered crucibles were dry-ashed in a muffle furnace for five hours at 500° C. After cooling, the covered crucibles were transferred on trays to the hood for digestion. Twenty-five ml of digestion solution (3N HNO_3 in

1000 ppm LiCl) was added to each crucible. After a one-hour wait, the solution was filtered from the crucible into labeled vials which were capped with linerless caps. The sample solutions were then analyzed using a D.C. Plasma emission spectrophotometer to determine P, K, Ca, Mg, Mn, Zn, Fe, Cu, and B content.

Seed Quality Determination

Standard Germination Test

The standard warm germination test was conducted using procedures described in the AOSA "Rules for Testing Seeds" (1981). Three replications of 50 seeds each were germinated on moist Kimpac media at 25°C. Germination evaluations were made after seven days and recorded as normal seedlings, abnormal seedlings, hard seeds, and dead seeds.

Normal seedlings were classified on the basis of a) having a vigorous primary root or set of secondary roots sufficient to anchor the seedling in the growth media; b) well developed hypocotyl with no open breaks or lesions extending into the central conducting tissue; c) having one complete cotyledon or two broken cotyledons with half or more of the original tissue still attached to the seedling; and d) epicotyl having at least one primary leaf and an intact terminal bud.

Abnormal seedlings were those with the following characteristics: a) no primary root or well developed set of secondary roots; b) hypocotyls having deep open cracks extending into the central conducting tissue or showing

malformations such as markedly shortened, curled or thickened growth; c) both cotyledons missing; or d) epicotyl with no primary leaves or terminal bud (bald head).

The Cold Test

Seed vigor evaluation by the cold test was performed by planting a 100 seeds (two 50-seed replicates) in a soil medium composed of equal parts of sand and peat. Two centimeters of soil were placed on the bottom of a plastic box (31.0 cm x 16.0 cm x 8.5 cm) to form the base layer on which 50 seeds were evenly spaced. Another 2 cm layer of soil were placed over the seeds. Two hundred and eighty (280) ml of water was evenly applied on the soil to bring it to approximately 70% of its water-holding capacity. The plastic boxes were covered and put in a cold room at 10°C for three days after which they were transferred to a germination chamber at 25° C for seven days. The covers were removed as soon as the seedlings emerged. After seven days, normal seedlings were evaluated and put into vigor categories based on length of the hypocotyl. The hypocotyl lengths were separated into <5 cm, 5-13 cm, and >13 cm groups which were then multiplied by the index numbers one, two, and three, respectively. The total combined index of the two boxes (normal seedlings in each category expressed as percent of total x respective index number) categorized seedlings into the following vigor classes: <200, low; 201-400, medium; 401-600, high (Suryatmana, 1980).

Accelerated Aging Test

The accelerated aging test was only applied to C-20 and Seafarer seeds in 1986. The wire-mesh tray method described by McDonald and Phaneendranath (1978) was utilized. Plastic boxes (11.0 cm x 11.0 cm x 3.5 cm) were fitted with wire-mesh (10.0 cm x 10.0 cm x 3.0 cm) which formed a tray 2.0 cm above the bottom of the plastic box. Before fitting with the wire-mesh 80 ml of water was added to the box. About 250 seeds were placed in a single layer on the wire-mesh and the covers of the boxes were put in place, after which the boxes were sealed with tape. The sealed boxes were placed in an incubator at 41 ± 2° C for 72 hours. Care was taken during sealing and transfer to avoid contact between the seeds and the water at the bottom of the boxes. After incubation, the seeds were removed and allowed to dry at room temperature. Then two 100-seed replicates were germinated by the standard warm germination test. Germination evaluation was made after seven days and seedlings were classified into normal, abnormal, hard seeds, and dead seeds.

Hypocotyl Length

Hypocotyl length measurements were taken for 10 normal seedlings in the center row(s) of the warm germination test soon after germination evaluation. The seedlings were cut with a razor blade at the point where the primary root starts growing (i.e. base of stem) and the length of the stem to the point of cotyledon attachment was recorded.

Seedling Growth Rate

Cotyledons were carefully removed from the same 10 seedlings selected for hypocotyl length measurement. The seedlings were then cut into pieces, and put into a paper bag, and dried in an oven at 65° C for 48 hours. The weight of the seedlings was determined on an analytical balance soon after cooling.

Statistical Analysis

All statistical analyses were carried out using MSTAT, version 3 (Michigan State University, East Lansing, 1984). Analysis of variance was only applied to the 1986 data since the field layout for 1985 did not meet the requirements for analysis of variance.

RESULTS AND DISCUSSION

General Performance of the Crop

The 1985 dry bean crop was well established and had well developed plants and impressive stands for all of the four varieties. The crop had little foliage disease except for very mild white mold (*Sclerotinia sclerotiorum*) infestation late in the season on the two cranberry varieties. In 1986, dry soil conditions resulted in relatively poor emergence and stands, particularly for MIC which had to be partially replanted four days after 50% emergence. All four varieties showed foliage symptoms of common bacterial blight (*Xanthomonas campestris* pv. *phaseoli*) in the eighth week after emergence. Minimal blight occurred in C-20, Cran-028 and MIC but was relatively serious in Seafarer which was estimated to have 20% leaf infection. By the ninth week, the disease had induced premature senescence of lower leaves evident in Seafarer and C-20. Developmental details for the two seasons are given in Table 1. The latter part of the second season was very wet with excess moisture affecting the whole experiment, particularly one plot of MIC. Rainfall data for the two

Table 1. Developmental rate for four dry bean varieties.*

Variety	1985		1986	
	Days to 50% flowering	Days to Maturity	Days to 50% flowering	Days to Maturity
C-20	47	87	41	82
Seafarer	34	81	34	77
Cran-028	36	97	45	96
MIC	43	109	44	94

* Plant emergence on 25th June 1985 and 27th June 1986.

seasons and the 23 year mean for East Lansing are given in Appendix Table 29.

The 1985 crop generally had higher yields (Tables 2 and 3) higher numbers of seeds/pod and larger seeds, but in 1986, C-20 and Cran-028 had higher numbers of pods/plant. C-20 had higher yields in 1986 and the yields for Seafarer and Cran 028 in both seasons were fairly comparable, while MIC which had the highest yield in 1985 had the lowest yield in 1986, less than half the 1985 level. The navy varieties had more pods/plant and seeds/pod than the cranberries in both seasons, the differences over MIC being statistically significant in 1986. The differences in 1985 were larger than those in 1986. The cranberry varieties had much larger seed than the navy varieties in both seasons, the differences being statistically significant in 1986. The differences in seed size between the two bean classes were greater in 1985.

Correlations between yield and yield components are given in Table 4. With all varieties included, the correlations between pods/plant and seeds/pod, pods/plant and 100-seed weight, and between seeds/pod and 100-seed weight were highly significant (1%) in both seasons. Pods/plant and seeds/pod were highly positively correlated while the other two were highly negatively correlated. The latter result is as expected since an increase in number of pods/plant or seeds/pod would tend to result in smaller seeds. A look at the correlations between yield and yield

Table 2. Yield and yield components of four dry bean varieties (1985).

Variety	Yield (kg/ha)	Number of pods/plant	Number of seeds/pod	100-seed weight (g)
C-20	1680 (261.7)*	14.9 (2.1)	4.3 (0.1)	18.1 (0.12)
Seafarer	1600 (175.3)	20.9 (0.8)	4.2 (0.1)	19.4 (0.55)
Cran-028	1610 (77.8)	9.5 (1.1)	3.0 (0.02)	48.5 (3.67)
MIC	2070 (650.6)	11.6 (1.7)	3.1 (0.03)	52.7 (4.24)
Mean	1739.7	14.22	3.65	34.68

* Standard deviations given in brackets.

Table 3. Yield and yield components of four dry bean varieties* (1986).

Variety	Yield (kg/ha)	Number of pods/plant	Number of seeds/pod	100-seed weight (g)
C-20	1990 b	18.9 a	4.2 a	17.2 a
Seafarer	1570 ab	17.0 a	3.9 a	18.3 a
Cran-028	1690 ab	13.2 ab	2.6 b	40.9 b
MIC	1010 a	8.5 b	2.3 b	41.8 b
Mean	1566.6	14.39	3.24	29.55
L.S.D. (0.05)	697	6.54	0.52	4.25
C.V. (%)	22.27	22.73	8.05	7.20

* Values followed by the same letter in a column are not significantly different by the L.S.D. test at the 5% level.

Table 4. Associations between yield and yield components of four dry bean varieties.

Variety	Year	Yield and pods/plant	Yield and seeds/pod	Yield and 100-seed wt.	Pods/plant and seeds/pod	Pods/plant and 100 seed wt.	Seeds/pod and 100 seed wt.
		r	r	r	r	r	r
C-20	1985	.804	.753	.778	.214	.999	.173
	1986	.929	.109	.428	-.268	.733	-.852
Seafarer	1985	.280	-.966	.999*	-.024	.319	-.955
	1986	.456	.810	-.810	-.153	.153	-1.00**
Cran-028	1985	1.00	-.004	.999*	-.982	.999*	-.982
	1986	-.947	-.559	.987	.795	-.986	-.684
MIC	1985	.930	.939	.709	.999*	.919	.908
	1986	.816	.923	.282	.976	-.324	-.108
General (across varieties)	1985	-.001	-.236	.388	.743**	-.726**	-.971**
	1986	.716**	.640*	-.505	.836**	-.786**	-.963**

* Significant at the 5% level.

** Highly significant at the 1% level.

components, and among the yield components on a variety basis strongly suggests that the nature of these associations varies with varieties and seasons. However, some of the values reported in this study showed atypical reversal of correlations in the two seasons. Negative correlations between pods/plant and seeds/plant and between pods/plant and seed size have been reported in navy bean varieties (Adams, 1967). Adams also cited Camacho et al. (1964) who reported significant negative correlations between pods/plant and seeds/pod, pods/plant and seed size, and between seeds/pod and seed size. In this study the correlation between seeds/pod and 100-seed weight was mostly negative in all four varieties, but the correlation between pods/plant and seeds/pod was mostly negative and small in the navy varieties resulting from yield component compensation, as reported by Adams (1967). Correlation between pods/plant and 100-seed weight was positive in the navy varieties but variable with seasons in the cranberry varieties (Table 4).

Fruit Growth

Pod Development

Pods attained maximum size in the early stages of fruit development of all varieties in both seasons. The navy bean varieties C-20 and Seafarer attained maximum pod length between 15 and 18 days after flowering (DAF) in 1985 and by 21 days in 1986. The cranberry varieties Cran-028 and MIC attained maximum pod length by day 19 and 21 DAF in the

respective seasons. C-20 and Seafarer reached peak pod fresh and dry weight at the time of full pod length (Fig. 1) in 1985 but reached maximum fresh and dry weight 20 and 22 DAF in C-20 and Seafarer in 1986, (Fig. 2). Cran-028 attained maximum levels of both fresh and dry weight of the pod by 34 DAF and 28 DAF in the respective seasons (Figs. 3 and 4). MIC attained maximum pod fresh weight by 23 DAF and maximum pod dry weight by 29 DAF in 1985 (Fig. 3), while it reached maximum pod fresh weight by day 22 and maximum pod dry weight by 29 DAF in 1986 (Fig. 4). Fruit growth during the first 15 days was dominated by pod growth and pods accounted for about 95% of the total fruit weight by the end of that period in both seasons (Figs. 5-8). During the remaining bean fruit development the bean pod decreased substantially in both fresh and dry weight and more so in their contribution to total fruit dry weight (Figs. 5-8).

The early rapid growth of the bean pods in both length and weight in this study is in agreement with earlier reports by Culpepper (1936), Carr and Skeene (1961), Watada and Morris (1967), Walbot et al. (1972) and Hsu (1972) on beans; and Anderson (1955) on birdsfoot trefoil, and Fraser et al. (1982) on soybeans. The attainment of maximum pod weight after full pod length observed on MIC in both seasons has been previously reported on beans (Culpepper, 1936). In this study, the seeds of C-20, Seafarer, Cran-028 and MIC accounted for 3.4, 2.5, 2.7 and 2.9%, respectively, of the

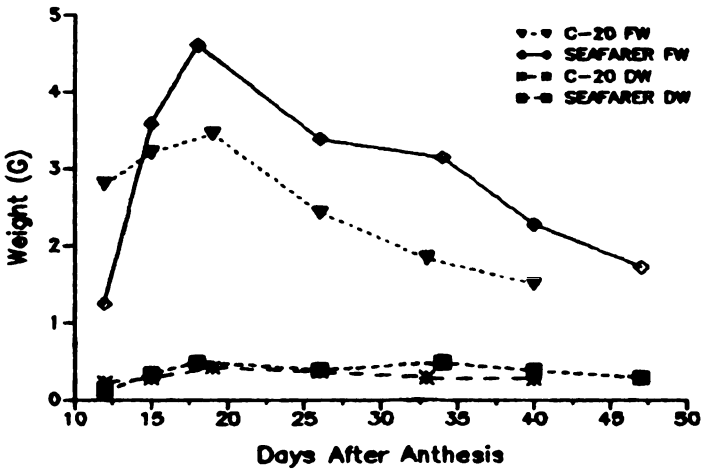

Fig 1: Pod fresh and dry weight during fruit development of navy bean varieties: C-20 and SEAFARER (1985).

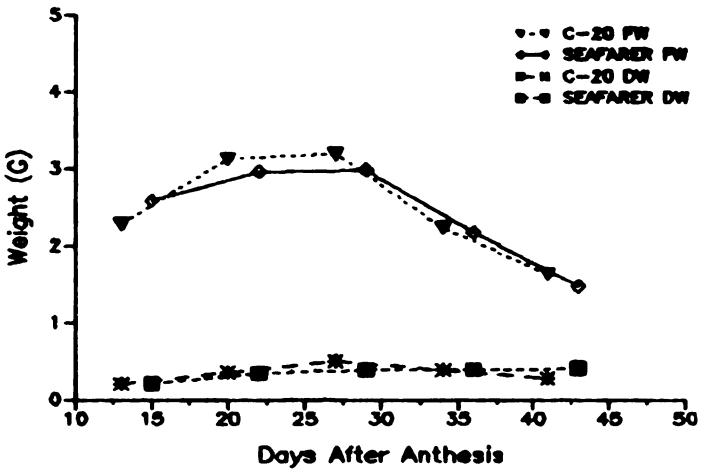

Fig 2: Pod fresh and dry weight during fruit development of navy bean varieties: C-20 and SEAFARER (1986).

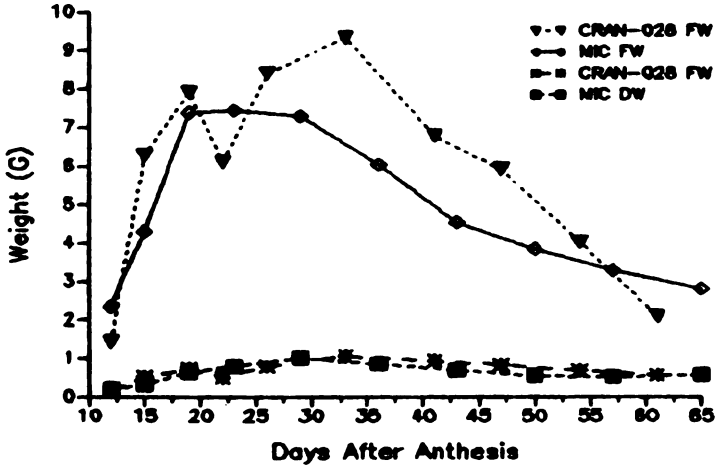

Fig 3: Pod fresh and dry weight during fruit development of cranberry bean varieties: CRAN-028 and MIC (1985).

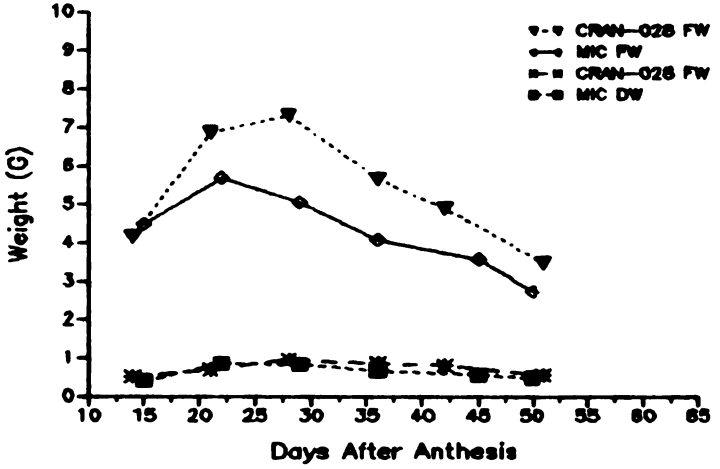

Fig 4: Pod fresh and dry weight during fruit development of cranberry bean varieties: CRAN-028 and MIC (1986).

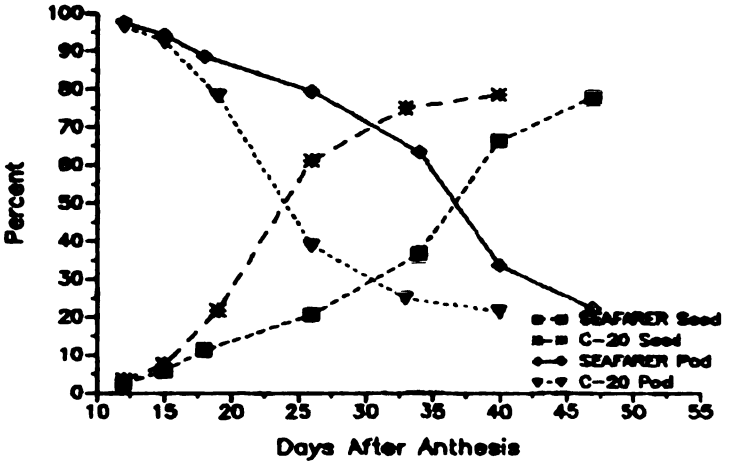

Fig 5: Relative distribution of dry matter between the developing pod and seeds of two navy bean varieties: C-20 and SEAFARER (1985).

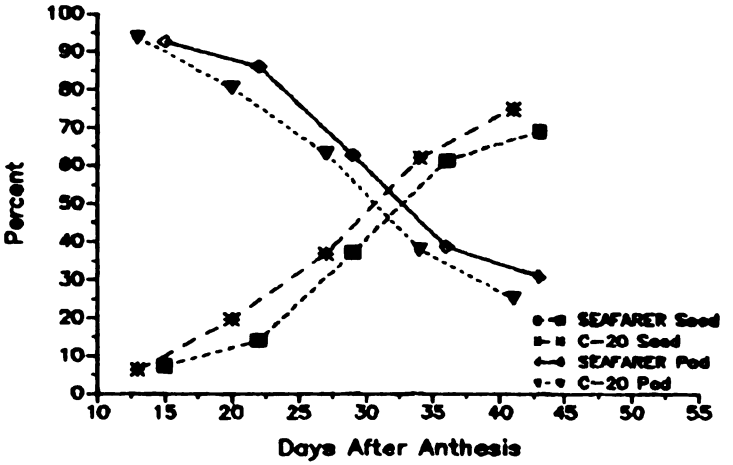

Fig 6: Relative distribution of dry matter between the developing pod and seeds of two navy bean varieties: C-20 and SEAFARER (1986).

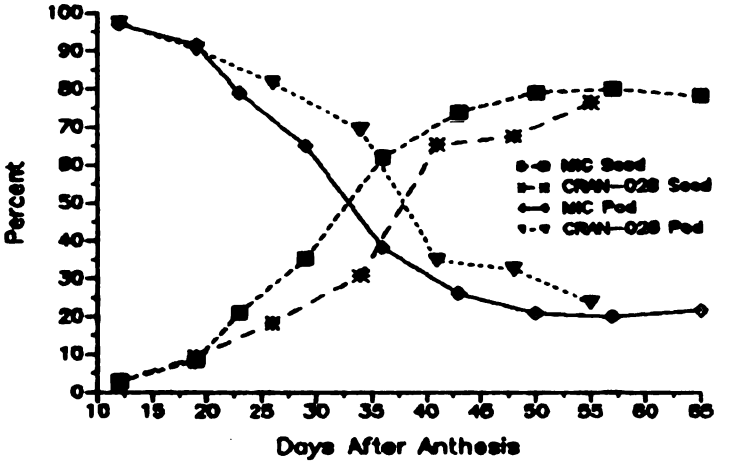

Fig 7: Relative distribution of dry matter between the developing pod and seeds of two cranberry bean varieties: CRAN-028 and MIC (1985).

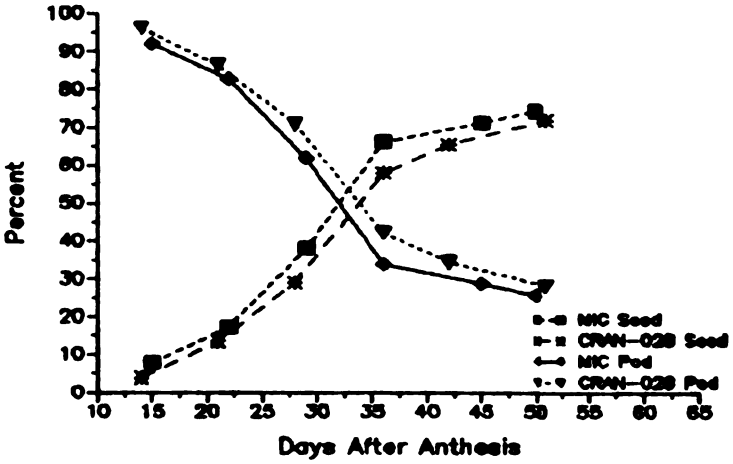

Fig 8: Relative distribution of dry matter between the developing pod and seeds of two cranberry bean varieties: CRAN-028 and MIC (1986).

total fruit weight by 12 DAF in 1985 and for 6.2% in C-20 after 13 days and 7.3, 3.9 and 7.9% in Seafarer, Cran-028 and MIC, respectively, at 15 DAF in 1986. The substantial difference between pod and seed contribution to fruit dry weight by the time maximum pod size is reached is typical of legumes. Soybeans have been reported to reach maximum pod size when the seed attains only 4% of its final weight (Fraser et al., 1982) and similar findings have been reported on garden peas (Pate and Flinn, 1977) and dry beans (Oliker et al., 1978).

In both 1985 and 1986, bean pods lost between 34 and 44% of their dry weight by the time they attained physiological maturity, except for Seafarer which exhibited no dry matter remobilization from the pod to the seed in 1986 (Table 5). Dry matter losses from the bean pod could supply between 14 and 28% of the seed dry matter within a fruit (Table 5), assuming all the dry matter the pod loses is remobilized to the developing seeds. Crookston et al. (1974) observed no dry matter redistribution from pods to developing bean seeds although this phenomenon had been reported in peas (Pate and Flinn, 1977), soybeans (Thorne, 1979) and castor bean (Hocking, 1982). Dure (1975) described the rapid early growth of the legume pod, concurrent only with the growth of seed testa and endosperm, as the build-up of precursors for embryogenesis. The results of this study support that view and provide evidence for the hypothesis that the bean pod may serve as a source of assimilates to

Table 5. Remobilization of dry matter from pods to seeds in senescing dry bean fruits.

Variety	Year	Maximum amount present in pod (mg)	Net loss during pod senescence (mg)	Loss from pod as proportion of final dry weight of seeds in fruit (%)
C-20	1985	419	146 (34.8)*	14.57
	1986	501	221 (44.1)	26.25
Seafarer	1985	493	193 (39.1)	19.05
	1986	406	0	0.00
Cran-028	1985	1052	369 (35.1)	16.71
	1986	960	401 (41.8)	28.06
MIC	1985	1008	436 (43.2)	21.15
	1986	852	368 (43.2)	26.38

* Net dry matter loss from pods expressed as % of pod maximum dry weight.

developing seeds as suggested by Thorne (1979) and Fraser et al. (1982) who worked with soybeans and by other researchers in work with other legumes. It was not possible to determine the actual contribution of the pod to the dry matter content of the seeds in one fruit since the seed increase in dry weight far exceeded pod losses right through to physiological maturity. Fraser et al. (1982) reported a significant correlation between pod size and final seed size in soybeans. Early pod development could thus affect final seed yield since seed size is one of the yield components. Adams (1967) stated that in navy beans the terminal components of yield are, in order of their development, number of pods per plant, number of seeds per pod and seed size. In this study, the number of seeds per pod was attained by the time of full pod size in all varieties, strongly linking pod development to final yield in dry beans.

Seed Development

In 1985, the seeds in the pods of C-20, Seafarer, Cran-028 and MIC had only accumulated 0.8, 0.3, 0.2 and 0.3% of their final seed weights, respectively, by 12 DAF (Table 6). In 1986, seeds of the four varieties accumulated 1.6, 1.8, 1.0 and 2.4% of their maximum seed weight, respectively, by 13 to 15 DAF (Table 7). By the onset of the lag phase (21-22 DAF), seeds of all four varieties still accounted for only 5-11% of their final dry weight. By the following week, the seeds of all varieties tripled their weights and in the

Table 6. Seed growth in four dry edible bean varieties (1985).

Variety	Age of seed (DAF)	Mean seed wt. (mg)	Seed wt. as % of maximum
C-20	12	1.36	0.77
	15	3.75	2.13
	19	19.67	11.14
	26	97.29	55.37
	33	137.20	78.08
	40	175.71	100.00
Seafarer	12	0.51	0.26
	15	3.50	1.76
	18	11.25	5.66
	26	17.12	8.62
	34	52.45	26.41
	40	136.18	68.56
	47	198.63	100.00
Cran-028	12	1.14	0.22
	15	6.32	1.23
	19	16.30	3.17
	26	35.40	6.89
	34	86.48	16.84
	41	373.83	72.80
	48	360.00	70.11
	55	513.49	100.00
MIC	12	1.58	0.28
	15	3.14	0.56
	19	13.49	2.40
	23	50.24	8.92
	29	123.86	22.00
	36	321.63	57.13
	43	481.95	85.61
	50	562.97	100.00
	57	501.95	89.16
	65	515.25	91.52

Table 7. Seed growth in four dry edible bean varieties (1986).

Variety	Age of seed (DAF)	Mean seed wt. (mg)	Seed wt. as % of maximum
C-20	13	2.49	1.65
	20	14.74	9.75
	27	50.31	33.28
	34	109.99	72.77
	41	151.15	100.00
Seafarer	15	3.08	1.85
	22	9.49	5.70
	29	36.82	22.13
	36	109.04	65.52
	43	166.41	100.00
Cran-028	14	3.89	0.99
	21	20.11	5.11
	28	78.20	19.85
	36	258.13	65.54
	42	348.14	88.39
	51	393.87	100.00
MIC	15	9.03	2.36
	22	44.80	11.69
	29	137.21	35.81
	36	335.91	87.67
	45	383.14	100.00
	50	374.12	97.65

second week after the 21-22 DAF mark also showed very high rates of dry weight accumulation, more than doubling within that week (Table 6 and 7). These accumulation rates subsequently slowed down towards maturity but considerable seed growth continued until PM. The increase in seed dry weight in the fruit relative to the pod is shown in Figures 5-8. There was a sharp rise in fruit dry weight in the seed after the 18-22 DAF period. In 1985, the seeds accounted for 76 to 78% of the total mature fruit weight and 69 to 75% in 1986. These results show little variation in the percent of total fruit dry weight retained in the pods in either of the two classes or varieties. Maximum fresh and dry seed weight of all four bean varieties were reached late in the growth cycle, with the latter mostly attained at PM (Figs. 9-12). Although seed fresh weight increased with seed growth until close to maturity, seed moisture content decreased continously from about 80-85% at 12 DAF and 74-79% at 13-15 DAF in 1985 and 1986, respectively, to about 54% at PM in both seasons.

Seed weight accumulation for whole seeds is shown in Tables 6-7 and daily growth rates in Table 8 and Appendix-Table 30. While the seed growth rates increased markedly in the first week after the lag phase (21-22 DAF), all varieties attained maximum seed growth rates in the second week (28-36 DAF), which is considerably later than 24 DAF reported by Loewenberg (1955). However, these results support reports by Hsu (1979) who observed that seeds of

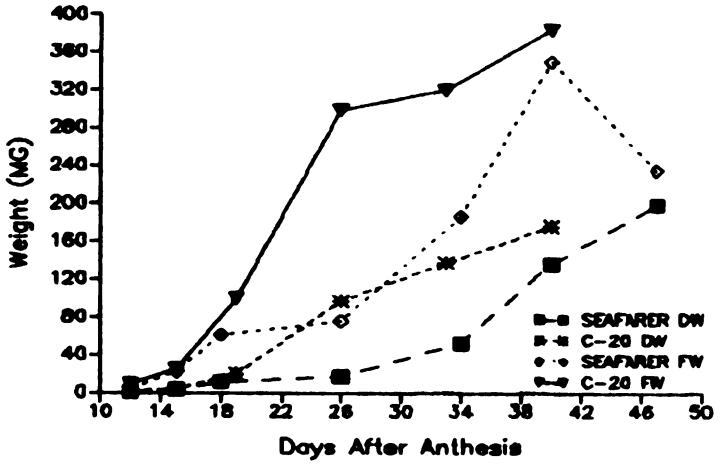

Fig 9: Fresh and dry weight of whole seeds during seed development of two navy bean varieties: C-20 and SEAFARER (1985).

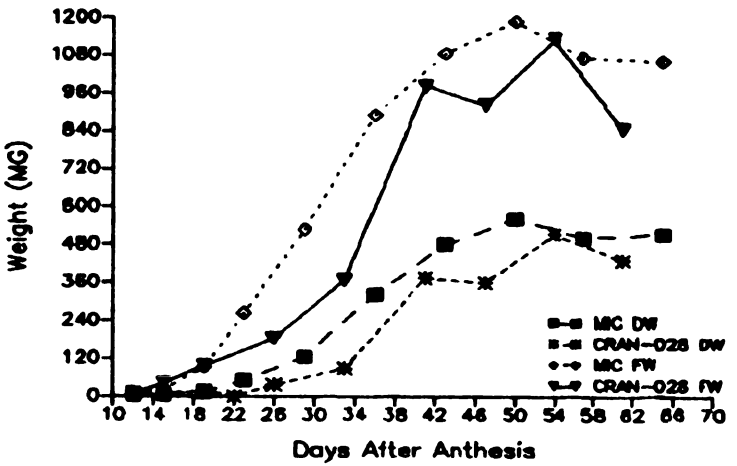

Fig 10: Fresh and dry weight of whole seeds during seed development of two cranberry bean varieties: CRAN-028 and MIC (1985).

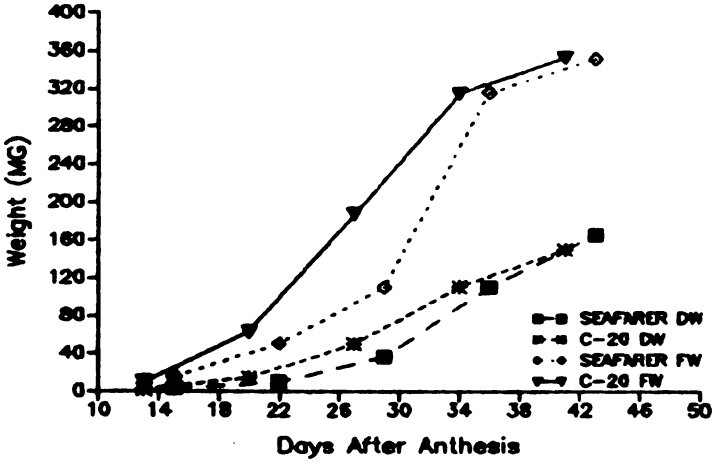

Fig 11: Fresh and dry weight of whole seeds during seed development of two navy bean varieties: C-20 and SEAFARER (1986).

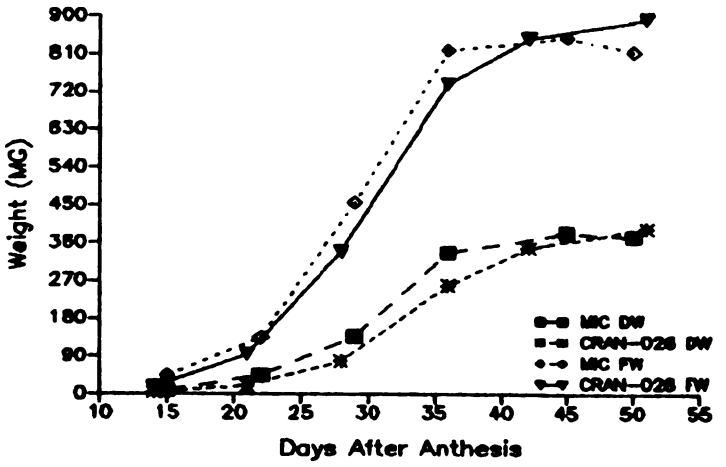

Fig 12: Fresh and dry weight of whole seeds during seed development of two cranberry bean varieties: CRAN-028 and MIC (1986).

Table 8. Average daily seed growth rates of four dry bean varieties (1986).

Variety	Period (DAF)	Mean daily weight gain (mg/day)
C-20	0-13	0.19
	13-20	1.75
	20-27	5.08
	27-34	5.53
	34-41	5.88
Seafarer	0-15	0.21
	15-22	0.92
	22-29	3.90
	29-36	10.32
	36-43	8.20
Cran-028	0-14	0.28
	14-21	2.32
	21-28	8.30
	28-36	22.49
	36-42	15.00
	42-51	5.08
MIC	0-15	0.60
	15-22	5.11
	22-29	13.20
	29-35	28.38
	36-45	5.25
	45-50	-1.80

bean varieties of different seed sizes had similar weight change patterns until just after the lag phase. He concluded that different seed dry weight gains in the later stage of growth influenced the final seed size. It is obvious from Tables 6-8 that the cranberry seeds were quite comparable in size to the navy bean seeds in early growth stages and their daily growth rates were within the same range, but that higher seed growth rates later accounted for massive seed size differences by PM. In this case Cran-028 and MIC had both larger growth rates during seed-filling and a longer seed-filling period than C-20 and Seafarer. Studies with soybeans have reported differences in final yields due to differences in duration of seed-filling rather than the growth rate (Hanway and Weber, 1971; Egli and Leggett, 1973).

Seed growth curves obtained in this study do not show the lag phase reported by Carr and Skene (1961) in beans or by Pate and Flinn (1977) in peas, probably due to the large sampling intervals employed. However, differences in seed growth rate after that stage are clear for all varieties (Figs. 9-12).

The varieties studied here exhibited the typical legume fruit development pattern of pod growth prior to seed development (Dure 1975). The main periods of growth of both pod and seed did not overlap (Fig 13-16). This suggests that the bean pod serves as a transitory reservoir of assimilates for the developing seeds as suggested for lupin by Pate et

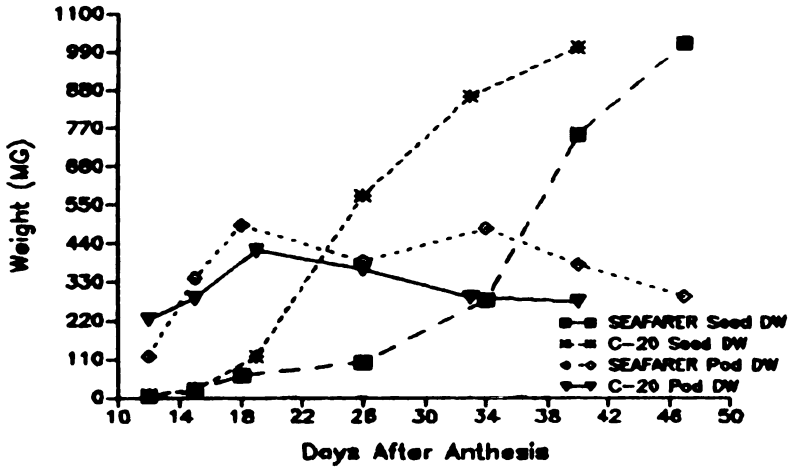

Fig 13: Dry weight accumulation in pod and seeds during fruit development of two navy bean varieties: C-20 and SEAFARER (1985).

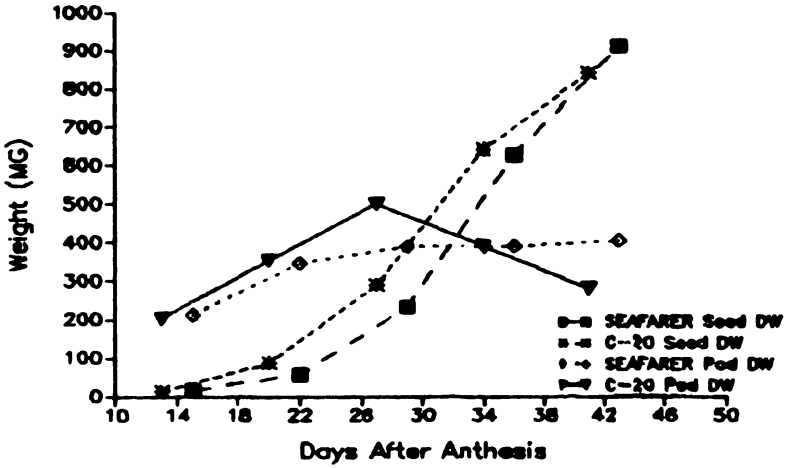

Fig 14: Dry weight accumulation in pod and seeds during fruit development of two navy bean varieties: C-20 and SEAFARER (1985).

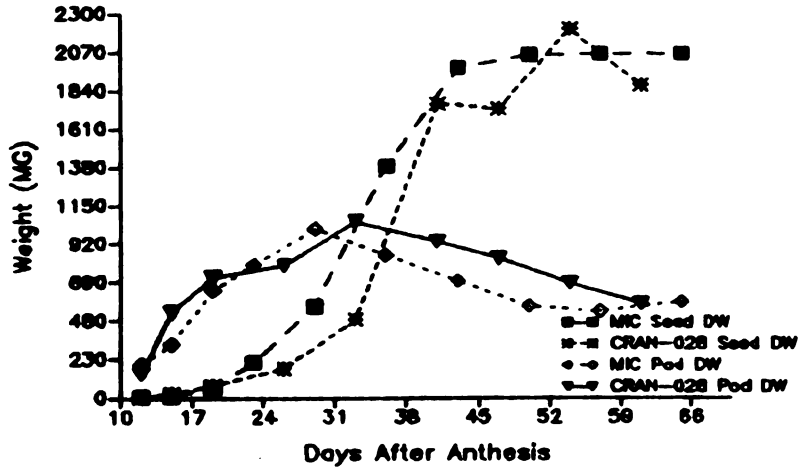

Fig 15: Dry weight accumulation in pod and seeds during fruit development of two cranberry bean varieties: CRAN-028 and MIC (1985).

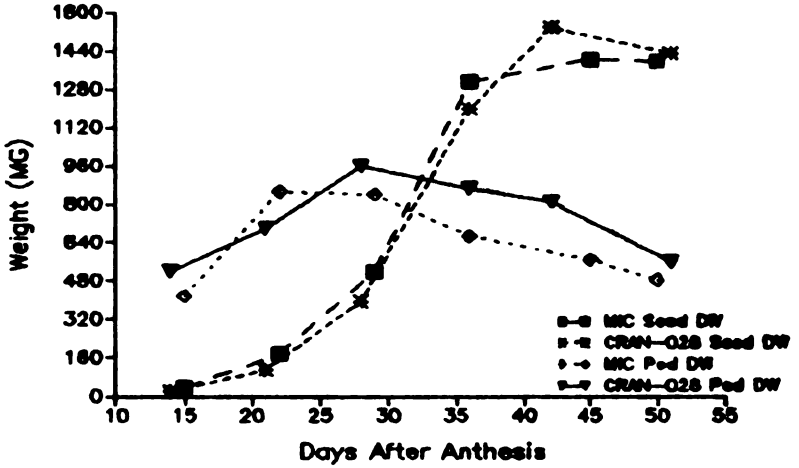

Fig 16: Dry weight accumulation in pod and seeds during fruit development of two cranberry bean varieties: CRAN-028 and MIC (1986).

al. (1977) and dry beans by Oliker et al. (1978). They do not support the role of the pod as a competing sink as suggested by Crookston et al. (1974). These results suggest that the assimilates from the pod can at best play a minor role in supplying the requirements of the seeds. Increase in seed weight per pod far surpassed weight losses from the pod (Table 5). This suggests that a good flow of photosynthate from the leaves remains necessary for full seed development, even after the pods attain full size. Optimum soil moisture and nutrient supply are necessary to maximize translocation of assimilates and sustenance of leaf area, particularly until after the two-week period following the lag phase during which most gains in seed dry matter and protein are made.

Nutrient Accumulation in Developing Dry Bean Fruit

Nitrogen and Protein

Pod nitrogen concentration was highest at 2.40 and 2.70% at 12 and 13 DAF in the respective seasons, then decreased continuously throughout fruit development, to levels of 0.64 and 0.75% at PM in the two respective seasons. Pod nitrogen content increased with dry matter in all varieties in both seasons. Pods contained the bulk of the dry bean fruit protein, representing 92.5, 77.2, 92.3 and 77.7% in C-20, Seafarer, Cran-028 and MIC, respectively, at 12-15 DAF in 1985. By 13-15 DAF, the total fruit protein in the pods in 1986 was 86.5, 86.8, 90.8 and 80.6% for C-20, Seafarer, Cran-028 and MIC, respectively. At PM, the pod

contained only 4 to 5% and 4 to 7% of the total fruit protein in the respective seasons. Accumulation of protein in the pod and seeds during fruit development is shown in Figures 17-20. Pod protein accumulated until about 18 DAF in 1985 in C-20 and Seafarer and until 22 and 26 days in the respective varieties during 1986 before starting to decline until maturity. Protein accumulation in the pods of MIC reached a peak 22 and 28 DAF in 1985 and 1986, respectively, while Cran-028 pods reached a peak at 26 and 28 DAF in the respective seasons. This trend of protein (nitrogen) accumulation generally agrees with that obtained by Culpepper (1936) who observed a decline in total bean pod nitrogen from 25 DAF onwards and Oliker *et al*. (1978) who reported peak pod nitrogen content at 20-24 DAF. Increase in pod nitrogen with increasing dry weight was also reported in *Lupinus albus* by Hocking and Pate (1977).

Seed nitrogen concentration was higher than that in the pod, ranging from 4.8 to 5.5% at 12-15 DAF in 1985 and 6.0 to 6.5% at 13-15 DAF in 1986 to between 3 and 4% by PM in both seasons. The seed and pod nitrogen concentration and protein content for 1986 are given in Table 9 and Appendix Table 31. The highest seed protein accumulation generally took place in rhythm to seed dry weight increase (Figs 17-20) and Table 9 clearly shows the pronounced changes in seed protein content per pod during seed-filling. In 1985, 86.3, 87.9, 89.9 and 96.6% of the total seed protein per fruit (pod and seed) and 86.5, 91.2, 90.4 and 84.9% of the same in

Table 9. Seed and pod nitrogen concentration and protein content during fruit development of four dry bean varieties (1986).

Variety	Age of Fruit (DAF)	Pod N (%)	Pod protein content (mg)	Seed N (%)	Seed protein content/fruit (mg)
C-20	13	2.70	34.08	6.55	5.32
	20	2.10	46.31	4.50	24.46
	27	1.70	53.21	4.05	73.40
	34	1.20	29.26	3.75	150.48
	41	0.75	13.13	3.45	181.54
Seafarer	15	3.17	41.80	6.00	6.37
	22	2.17	47.05	4.70	16.74
	29	1.65	40.21	3.92	57.08
	36	1.05	25.65	3.70	144.96
	43	0.60	15.22	3.35	190.76
Cran-028	14	2.60	84.66	6.50	8.53
	21	2.05	89.54	5.00	34.37
	28	1.62	97.15	4.97	122.69
	36	1.10	59.49	3.80	284.05
	42	0.77	38.91	3.70	355.35
	51	0.40	13.97	4.00	357.25
MIC	15	2.30	59.92	6.40	14.40
	22	1.72	91.59	4.65	51.44
	29	1.48	77.61	4.37	141.74
	36	1.00	41.62	3.85	315.67
	45	0.72	25.51	3.80	333.45
	50	0.54	16.31	3.90	339.96

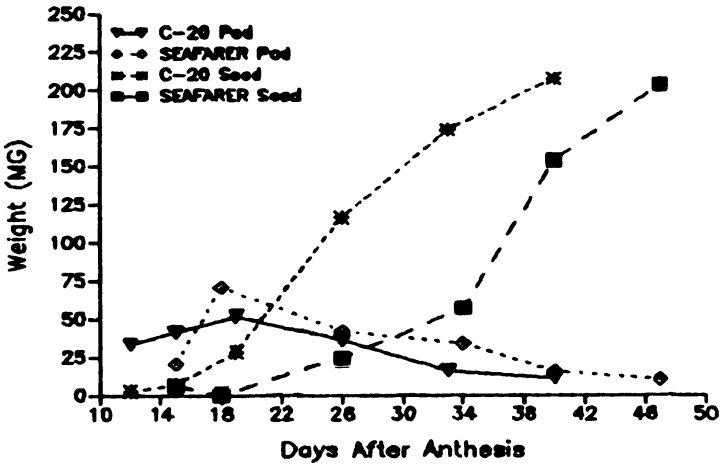

Fig 17: Protein accumulation in developing fruit of two navy bean varieties: C-20 and SEAFARER (1985).

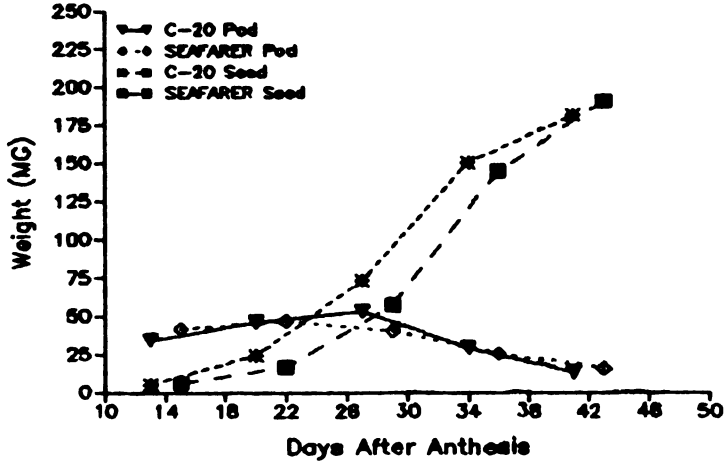

Fig 18: Protein accumulation in developing fruit of two navy bean varieties: C-20 and SEAFARER (1986).

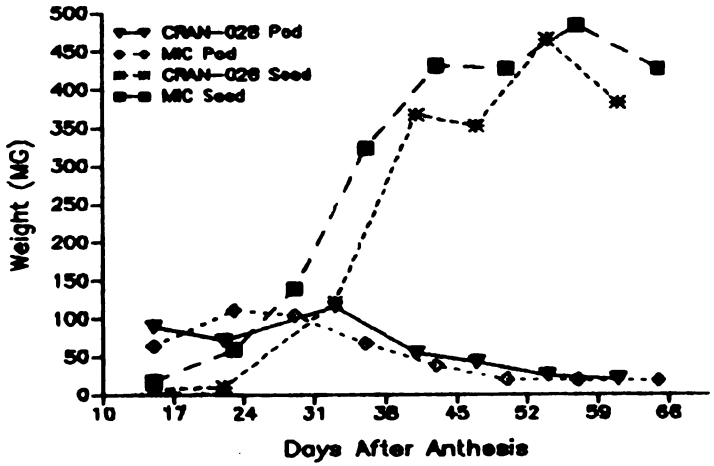

Fig 19: Protein accumulation in developing fruit of two cranberry bean varieties: CRAN-028 and MIC (1985).

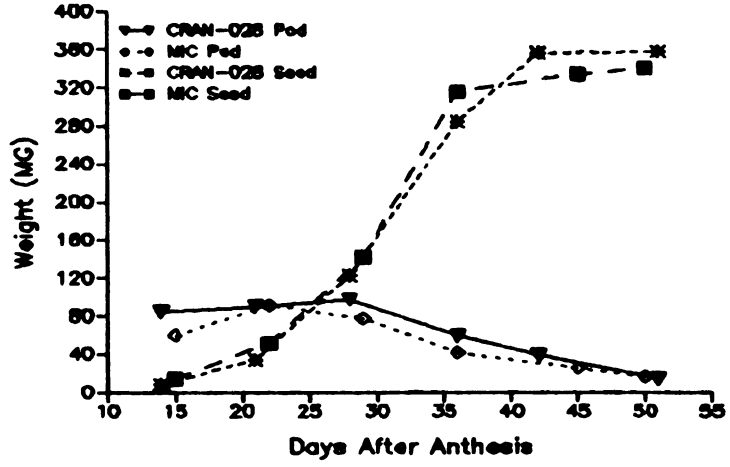

Fig 20: Protein accumulation in developing fruit of two cranberry bean varieties: CRAN-028 and MIC (1986).

1986 in C-20, Seafarer, Cran-028 and MIC, respectively, was accumulated after the lag phase. These figures are somewhat lower than the 95% Smith (1984) reported during cell expansion. They suggest that the two weeks following the lag phase are the most crucial period for the development of seed protein content. They are in agreement with observations by Sunny et al. (1978) who reported that most protein accumulation in dry bean cotyledons occurs between 10 and 30 DAF with sharp increases after 17 DAF and Oliker et al. (1978) who observed sharp increase in seed nitrogen during the third week after anthesis.

Seed protein concentrations at maturity were 20.7 and 21.6 % for C-20, 20.1 and 20.9% for Seafarer, 20.4 and 25.0% for Cran-028, and 20.7 and 24.4% for MIC in 1985 and 1986 respectively. A consistent but slight increase in seed protein concentration occurred in 1986 in the navy varieties but the increase was greater in the cranberry varieties. This was only expected for Seafarer and MIC since lower yields usually mean higher protein. Protein concentration results of this study compare well with a 22.3% average for navy beans reported by Leveille et al. (1978), 20% by Sun et al. (1978) and the approxmate world average of 22% by Kay (1979). However, they fall below the 25-28% reported by Ma and Bliss (1978).

Nutrient Elements

Macronutrient accumulation in dry bean pods is shown in Figures 21-24. Pod nitrogen (N), phosphorus (P) and calcium

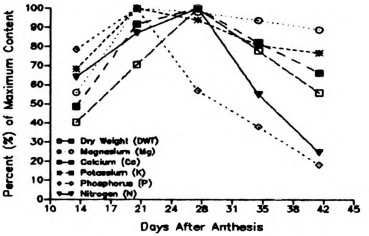

Fig 21: Relative accumulation of macronutrients and dry weight in developing pods of navy bean variety C-20 (1986).

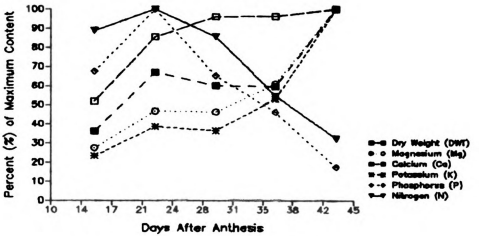

Fig 22: Relative accumulation of macronutrients and dry weight in developing pods of navy bean variety SEAFARER (1986).

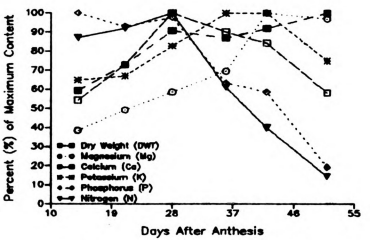

Fig 23: Relative accumulation of macronutrients and dry weight in developing pods of cranberry bean variety CRAN-028 (1986).

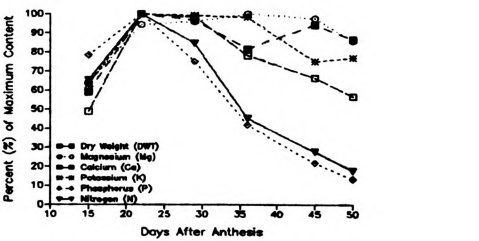

Fig 24: Relative accumulation of macronutrients and dry weight in developing pods of cranberry bean variety MIC (1986).

(Ca) accumulation preceeded dry matter accumulation although they reached a maximum at the same time as dry weight. Potassium (K) accumulation was generally behind dry weight increase but was quite variable. Magnesium (Mg) accumulation was consistently behind that of dry weight. Concentration and accumulation of P, K, Ca and Mg in 1986 are given in Table 10 and Appendix Table 32. Changes in P concentration during pod development in both years were fairly comparable for each variety. Phosphorus concentration in the pod fell from 0.266 and 0.314% at 12 and 13 DAF to 0.047 and 0.053% at maturity for C-20, 0.309 and 0.283% at 15 DAF to 0.029 and 0.038% at maturity in Seafarer, 0.372 and 0.228% at 14 and 15 DAF to 0.039 and 0.041% at maturity in Cran-028, and 0.406 and 0.258% at 15 DAF to 0.043 and 0.038% at maturity in MIC in 1985 and 1986, repectively. Potassium concentration in the pod was markedly higher in 1985 with the pattern of increase differing among varieties. Concentrations of K, Ca and Mg in the pod tended to dip between full pod growth and maturity whether the overall concentration between the two points increased or decreased (Table 10), however, P concentration decreased steadily up to maturity in both seasons. Phosphorus concentration in the pod declined to 8-10% of that at 13-15 DAF in both seasons but P content declined to roughly 20% of its level at 13-15 DAF. Potassium concentration showed little variation between the beginning and end of pod development (Table 10). Calcium

Table 10. Concentration and accumulation of P, K, Ca and Mg in developing pods of four dry bean varieties (1986).

Variety	Age of Fruit (DAF)	P		K		Ca		Mg	
		Concentration (%)	Content (mg)	Concentration (%)	Content (mg)	Concentration (%)	Content (mg)	Concentration (%)	Content (mg)
C-20	13	.314	.634	1.90	3.84	.387	.782	.249	.503
	20	.229	.808	1.59	5.61	.418	1.475	.255	.900
	27	.092	.461	1.05	5.26	.321	1.608	.176	.882
	34	.072	.308	1.16	4.52	.338	1.318	.216	.842
	41	.053	.148	1.54	4.31	.380	1.064	.285	.798
Seafarer	15	.283	.597	1.70	3.59	.393	.829	.246	.519
	22	.255	.885	1.71	5.93	.442	1.534	.254	.881
	29	.148	.577	1.44	5.62	.353	1.377	.224	.874
	36	.104	.407	2.08	8.13	.350	1.368	.295	1.153
	43	.038	.154	3.78	15.35	.564	2.290	.465	1.888
Cran-028	14	.228	1.188	1.66	8.65	.348	1.813	.188	.979
	21	.158	1.104	1.28	8.95	.319	2.230	.176	1.251
	28	.121	1.162	1.15	11.04	.289	2.774	.155	1.488
	36	.087	.753	1.54	13.34	.307	2.659	.204	1.767
	42	.086	.696	1.65	13.35	.348	2.815	.314	2.540
	51	.041	.229	1.79	10.01	.547	3.058	.441	2.465
MIC	15	.258	1.076	1.70	7.09	.540	2.252	.258	1.076
	22	.161	1.372	1.32	11.25	.448	3.817	.187	1.593
	29	.123	1.032	1.33	11.16	.440	3.692	.193	1.619
	36	.086	.573	1.66	11.06	.468	3.117	.253	1.685
	45	.053	.300	1.49	8.45	.634	3.595	.290	1.644
	50	.038	.184	1.79	8.66	.684	3.311	.299	1.447

showed a slight increase while the increase in Mg content as pod growth progressed was only fair.

The pattern of micronutrient accumulation in the pod is shown in Table 11. Micronutrients in the pod tended to either gradually increase or decrease with pod growth. Boron (B) concentration tended to increase slightly while those of manganese (Mn), iron (Fe), zinc (Zn) and copper (Cu) declined to between a third and half of their levels at 13-15 DAF. For the most part, Mn accumulated almost simultaneously with dry weight increase. Iron accumulation followed the same trend, but sometimes lagged behind or slightly ahead of increase in dry weight. Zinc consistently accumulated ahead of increase in dry weight, but reached a maximum almost concurrently with dry weight. Increase in Cu almost always lagged behind dry weight, while increase in B was consistently behind dry weight accumulation.

Interpretation of nutrient accumulation patterns in pods is difficult, since it is not consistent across species (Hocking and Pate, 1977). However, the fact that most nutrients attain maximum values before the beginning of seed growth suggests their possible use during embryogenesis, especially since the pod loses nutrients while they build up in seeds.

Nutrient Remobilization from Pods to Seeds

Nutrient losses from the pod during seed development are shown in Tables 12 and 13. These results indicate that the pods of dry beans could possibly supply between 13 and

Table 11. Micronutrient accumulation in the pod of four dry bean varieties (1986).

Variety	Age of seed (days)	Pod dry weight as % of maximum	Nutrient levels expressed as % of maximum				
			Mn	Fe	Zn	Cu	B
C-20	13	40.32	51.43	53.19	80.38	43.63	37.35
	20	70.46	100.00	100.00	100.00	66.88	71.90
	27	100.00	78.10	40.24	92.33	100.00	96.84
	34	77.84	48.33	34.00	59.00	47.77	100.00
	41	55.89	40.36	36.36	35.69	29.94	92.51
Seafarer	15	51.97	37.94	14.76	91.34	85.91	28.31
	22	85.47	81.03	47.90	100.00	94.09	42.88
	29	96.06	70.98	69.13	88.16	90.91	42.80
	36	96.31	53.52	41.95	56.71	100.00	62.36
	43	100.00	100.00	100.00	60.60	59.09	100.00
Cran-028	14	54.27	70.51	45.02	86.25	48.24	48.27
	21	72.81	83.04	69.43	87.63	79.40	58.92
	28	100.00	100.00	52.29	100.00	100.00	72.01
	36	90.21	79.49	54.43	71.44	63.01	92.29
	42	84.27	84.81	100.00	44.90	34.01	100.00
	51	58.23	76.46	98.38	32.21	23.71	85.88
MIC	15	48.94	54.78	56.75	81.83	52.12	56.23
	22	100.00	100.00	100.00	100.00	100.00	100.00
	29	98.47	98.43	71.03	78.48	70.34	68.52
	36	78.17	70.09	47.76	55.36	72.60	51.78
	45	66.55	56.17	34.21	43.98	59.46	46.31
	50	56.81	43.74	27.30	37.06	53.53	37.19

Table 12. Remobilization of nutrient elements from pod to seeds within a dry bean fruit during pod senescence (1985).

Nutrient	Maximum amount present in pod (weight/pod)				Net loss of element during pod senescence (weight/pod)				Loss from pod as proportion of final amount in seeds of fruit (%)			
	C-20	Seafarer	CRAN	MIC	C-20	Seafarer	CRAN	MIC	C-20	Seafarer	CRAN	MIC
Macronutrients (Amount in mg)												
N	8.29	11.29	13.86	14.25	6.55	9.64	10.04	11.73	19.75	29.65	13.90	17.22
P	.74	1.11	2.45	1.53	.61	1.03	2.23	1.29	18.07	28.97	28.76	16.04
K	6.78	13.11	29.42	20.16	0.00	3.03	0.00	.60	0.00	22.85	0.00	2.28
Ca	2.20	3.12	6.26	5.80	.96	.93	1.39	.77	54.82	44.25	41.90	16.62
Mg	.87	1.70	2.61	2.31	.22	.42	.20	.09	10.50	22.27	5.57	2.92
Micronutrients (Amount in ug)												
Mn	8.72	10.90	17.88	14.72	5.09	0.87	8.05	3.85	54.61	6.36	36.47	16.68
Fe	32.30	41.41	52.58	58.67	22.80	21.70	6.27	19.72	39.82	43.99	5.09	19.69
Zn	7.92	7.39	20.72	17.89	4.97	3.75	1.50	0.96	22.01	18.79	2.13	1.55
Cu	3.02	4.04	9.38	9.17	1.68	0.23	0.00	0.48	21.65	2.67	0.00	2.26
B	8.41	10.92	27.31	26.63	0.00	2.83	0.00	1.69	0.00	44.36	0.00	9.32

Table 13. Remobilization of nutrient elements from pod to seeds within a dry bean fruit during pod senescence (1986).

Nutrient	Maximum amount present in pod (weight/pod)				Net loss of element during pod senescence (weight/pod)				Loss from pod as proportion of final amount in seeds of fruit (%)			
	C-20	Seafarer	CRAN	MIC	C-20	Seafarer	CRAN	MIC	C-20	Seafarer	CRAN	MIC
Macronutrients (Amount in mg)												
N	8.51	7.53	15.54	14.65	6.41	5.09	13.31	12.04	22.07	1.68	23.20	22.13
P	0.81	0.88	1.16	1.37	0.66	0.73	0.93	1.19	22.53	18.67	170.00	25.65
K	5.61	8.13	13.35	11.25	1.30	0.00	3.34	2.59	11.52	0.00	16.93	12.63
Ca	1.61	2.29	3.06	3.82	0.54	0.00	0.00	0.51	34.00	0.00	0.00	17.35
Mg	0.90	1.89	2.54	1.68	0.10	0.00	0.07	0.24	6.81	0.00	3.00	10.53
Micronutrients (Amount in ug)												
Mn	8.40	7.96	7.90	11.50	5.01	0.00	1.86	6.47	41.03	0.00	12.64	44.59
Fe	33.50	54.61	57.28	76.42	21.32	0.00	0.00	55.56	35.26	0.00	0.00	92.42
Zn	6.78	5.66	18.91	39.45	4.36	2.23	12.82	24.83	18.56	9.83	29.22	58.94
Cu	3.14	2.20	7.38	7.08	2.20	0.90	5.63	3.29	29.18	12.84	51.18	30.13
B	8.54	12.22	19.33	12.61	0.64	0.00	2.73	7.92	9.41	0.00	18.55	58.54

29% of the N requirements of developing seeds, 16 to 29% of the P, 2 to 22% of the K, 16 to 55% of the Ca and 3 to 22% of the Mg. The pod could even supply a higher proportion of the micronutrient requirements of the seeds within the same fruit (Tables 12 and 13). These figures generally fall into the range reported by other workers such as Thorne (1979) on soybean and Hocking and Pate (1977) on lupins and peas. Even the large ranges in these figures are similar to those found in the classical studies of Hocking and Pate (1977) and Hocking (1982). In fact, Hocking and Pate (1977) reported that the contribution of minerals remobilized from pods may provide from 16 to 50% of an element laid down in the embryos and that the significance of this remobilization varies with species and elements. The results reported in this study show seasonal variability in the pod's potential to supply the developing seeds with nutrients. There could also be significant variation among varieties as suggested by the behavior of Seafarer in this study.

Nutrient accumulation in the seed

The macronutrients P, K, Ca and Mg generally increased in quantity as the seed gained in dry weight. Accumulation of P, K, Ca and Mg preceeded dry weight increase in C-20 in 1985. Phosphorus and Mg reached maximum accumulation at PM but maximum K and Ca were recorded one week before PM. In 1986, all four attained the maximum at PM in C-20. Nutrient elements accumulated at the same rate as dry weight up to 27 DAF after which K and Ca accumulated ahead of dry weight but

P and Mg increased at lower rates than dry weight. All P, K, Ca and Mg attained maximum content in Seafarer seeds at PM in both seasons. In 1985 P and K accumulated at the same rate as dry weight but Ca and Mg accumulated ahead of dry weight. In CRAN-028, the nutrient levels reached their maximum one week before PM in 1985 and at PM in 1986, except for Ca which reached its maximum one week before PM. In this variety all the nutrients accumulated ahead of dry weight except Mg which accumulated at the same rate as dry weight in 1985. In 1986 only Ca accumulated ahead of dry weight while P lagged behind and K and Mg increased at the same rate. In MIC, seeds attained maximum P, K, Ca and Mg well ahead of dry weight in 1985 but all reached maximum values at or 5 days before PM and increased at the same pace as dry weight in 1986. Macronutrient accumulation in seeds relative to seed dry weight are given in Table 14 and Appendix Table 33.

The data show some seasonal and varietal variations in the pattern of nutrient accumulation. Potassium and P have been reported by Hocking and Pate (1977) to accumulate in advance of dry weight in white lupin and pea while Mg and K were shown to accumulate simultaneously with dry weight. Considerable inconsistent differences in categorizing nutrient accumulation rates and/or patterns in several legumes are evident in their results. For example, Ca was reported to accumulate after dry weight in narrow-leafed lupin and pea but ahead of dry weight in white lupin.

Table 14. Macronutrient accumulation in growing seeds of four dry bean varieties (1986).

Variety	Age of seed (DAF)	Seed dry weight as % of maximum	Nutrient content expressed as % of maximum seed contents %			
			P	K	Ca	Mg
C-20	20	9.75	16.16	14.27	12.11	10.78
	27	33.28	36.50	34.52	31.83	30.11
	34	72.77	59.13	74.96	80.97	61.34
	41	100.00	100.00	100.00	100.00	100.00
Seafarer	15	1.85	5.17	4.06	1.96	2.55
	22	5.70	12.15	9.94	6.13	7.65
	29	22.13	33.80	29.14	25.25	24.08
	36	65.52	66.48	64.59	67.16	62.32
	43	100.00	100.00	100.00	100.00	100.00
Cran-028	14	0.99	2.65	2.04	1.59	1.74
	21	5.11	9.26	9.59	7.97	7.26
	28	19.85	26.19	28.63	24.60	22.93
	36	65.54	67.92	73.14	61.05	71.99
	42	88.39	77.58	85.83	100.00	86.36
	51	100.00	100.00	100.00	94.31	100.00
MIC	15	2.36	6.12	4.42	1.63	3.80
	22	11.69	18.60	16.55	6.96	16.01
	29	35.81	38.97	37.77	15.76	39.77
	36	87.44	82.53	88.87	62.83	91.42
	45	100.00	92.41	100.00	100.00	99.34
	50	97.65	100.00	97.66	85.00	100.00

Hocking and Pate (1977) also reported that the relative proportions of P:Mg:Ca remain constant during later embryo growth when phytate reserves are being laid down. They reported a P:Mg:Ca ratio of 3.7:1:1 for lupins and 11.8:1.7:1 for peas which suggested variation based on the chemical forms of phytate present or that different proportions of seed Ca, Mg and P become bound to phytin. The P:Mg:Ca ratio obtained in this study for seed a week before maturity and at maturity is presented in Table 15. These results show considerable consistency and therefore confirm the findings of Hocking and Pate (1977) but the ratios are quite different, possibly suggesting that relatively less of the seed P or more of the Mg and Ca are bound in phytate in beans. However, it may be important to note the P, Ca, and Mg concentration reported here involves whole seeds, including testa and embryo.

The micronutrients Mn, Fe, Zn, Cu, and B all attained maximum content a week before maturity in C-20 in 1985. All these elements accumulated ahead of dry weight in that season. In 1986, all five micronutrients reached maximum values at PM along with dry weight. Also in 1986, Mn and Fe accumulated behind dry weight and Zn at the same rate as dry weight, while Cu and B accumulated ahead of dry weight.

All five micronutrients studied reached maximum content in the seeds of Seafarer at PM in both seasons. In 1985, Mn increased concurrently with dry weight and Fe, Zn and B lagged behind slightly, while Cu was accumulated ahead of

Table 15. Ratio of P:Mg:Ca in maturing seeds of four dry bean varieties.

Variety	Year	Age of seed (DAF)	P:Mg:Ca
C-20	1985	33	1.39:0.88:1
		40 (PM)	1.93:1.20:1
	1986	34	1.32:0.70:1
		41 (PM)	1.78:0.91:1
Seafarer	1985	40	1.46:0.82:1
		47 (PM)	1.70:0.91:1
	1986	36	1.73:0.80:1
		43 (PM)	1.76:0.87:1
Cran-028	1985	54	2.96:1.43:1
		61 (PM)	2.34:1.08:1
	1986	42	2.66:1.35:1
		51 (PM)	3.65:1.67:1
MIC	1985	57	2.06:0.83:1
		65 (PM)	1.72:0.67:1
	1986	45	1.25:0.65:1
		50 (PM)	1.59:0.78:1

dry weight, particularly in the last two weeks. In 1986, Mn lagged significantly (10%) behind dry weight while Fe and Zn increased concurrently with dry weight, and Cu and B accumulation was significantly ahead of dry weight.

In CRAN-028, all five micronutrients reached maximum values at the same time as dry weight but only B increased concurrently with dry weight. All of the others accumulated ahead of dry weight. All micronutrients reached peak values at PM, along with dry weight in 1986. Manganese, Fe, and Cu increased concurrently with dry weight, B was slightly behind, and Zn significantly ahead of dry weight accumulation.

Micronutrients measured in this study attained maximum content in MIC seeds at varied times in both seasons. In 1985, Mn accumulated concurrently with dry weight until 36 DAF but surged to maximum values a week later. In 1986, Mn attained its maximum concurrently with dry weight although it accumulated ahead of dry weight. Fe accumulated ahead of dry weight in both seasons. Zinc also accumulated ahead of dry weight in both seasons, although it reached maximum values at the same time as dry weight in both years. Copper accumulation occurred in MIC seeds concurrently with dry weight in 1985 but reached peak values 3 weeks earlier. In 1986 it accumulated at the same rate as dry weight. Boron accumulated at the same rate as dry weight in both seasons. Micronutrient accumulation in the four varieties is shown in Table 16 and Appendix Tables 34-36.

Table 16. Micronutrient accumulation in developing seeds of four dry bean varieties (1986).

Variety	Age of seed (DAF)	Seed dry weight as % of maximum	Nutrient levels expressed as % of maximum				
			Mn	Fe	Zn	Cu	B
C-20	20	9.75	10.20	8.02	15.89	12.81	15.76
	27	33.28	26.13	18.58	36.28	34.17	41.47
	34	72.77	56.90	37.91	71.55	79.60	77.88
	41	100.00	100.00	100.00	100.00	100.00	100.00
Seafarer	15	1.85	3.59	3.88	6.80	2.97	4.39
	22	5.70	8.39	9.20	12.40	6.79	9.93
	28	22.13	24.04	28.38	25.14	24.59	30.40
	36	65.52	55.17	63.65	61.32	91.96	78.65
	43	100.00	100.00	100.00	100.00	100.00	100.00
Cran-028	14	0.99	2.02	2.97	3.19	1.37	1.77
	21	5.11	7.49	11.51	9.65	5.82	7.59
	28	19.85	25.07	26.78	29.35	21.41	22.75
	36	65.54	77.62	86.16	85.83	84.12	68.08
	42	88.39	89.25	89.98	100.00	88.30	81.69
	51	100.00	100.00	100.00	99.62	100.00	100.00
MIC	15	2.36	3.11	5.10	5.96	2.73	3.90
	22	11.69	13.85	21.83	18.36	12.70	16.80
	29	35.81	42.72	48.22	43.18	27.83	35.81
	36	87.44	93.06	100.00	93.98	88.53	83.43
	45	100.00	100.00	95.95	100.00	97.20	100.00
	50	97.65	89.08	87.60	96.37	100.00	91.97

These results show such varied patterns that generalizations are difficult. This agrees with reports by Hocking and Pate (1977) who reported that Fe, Zn, Mn and Cu accumulated ahead of dry matter in white lupin seeds, Fe in narrow-leafed lupin seeds, and Zn in pea seeds. Fe and Mn were reported to accumulate at the same rate as dry weight in the pea, as did Zn and Mn in the narrow-leafed lupin. However, Cu was found to lag behind dry weight in pea and narrow-leafed lupin. These complex variations in accumulation of various micronutrients compare well with results of this study. The data suggest that seeds have mechanisms to control the levels of micronutrients and macronutrients, according to the level needed. The early accumulation of some nutrients strongly suggests the existence of such a mechanism. The general increase in nutrient levels in the seeds with approaching maturity may imply that the seed requires increased levels to maintain developmental activities as growth occurs. It also implies that the seed increases nutrient levels as it approaches maturity to ensure adequate reserves required for the subsequent germination. These data also indicate that nutrient accumulation patterns are complex and likely to differ considerably between species and in response to different conditions.

Seed Quality

Germination development

Seed of C-20 became capable of germination from 26 and 27 DAF, Seafarer at 34 and 36 DAF, CRAN-028 at 33 and 28 DAF, and MIC at 36 and 29 DAF, in 1985 and 1986 respectively (Tables 17 and 18). Large increases in germination capacity occurred just one week after the first expression of germination ability in C-20 in both seasons, MIC in 1985 and CRAN-028 in 1986. These differences were significant (5%) for C-20 and CRAN-028 in 1986 and affected both total germination (radicle protrusion) as well as levels of normal seedlings. Significant gains in both total germination and level of normal seedlings occurred between the first onset of germination ability, a week later, and at PM (Table 19).

The number of abnormal seedlings generally decreased with increasing germinability. Abnormal seedlings in C-20 dropped from 16.7% to 6.7% as total germination increased from 24.0 to 67.3% between 26 DAF (first expression of germinability) and 33 DAF in 1985. Between 33 and 40 DAF the level of abnormal seedlings dropped even further to 5.3% when total germination and normal seedlings increased to 96.7% and 91.3% at PM. In 1986, a dramatic increase in total germination from 8.7 to 94.7% occurred, along with an increase in abnormal seedlings from 4.7 to 14.7%. Between 34 and 41 DAF, no further increase occurred in total germination, but normal seedlings increased from 80.0 to 87.3% while abnormal seedlings dropped to 7.3%. Tables 17

Table 17. Germination and seedling vigor development during seed growth of four dry bean varieties (1985).

Variety	Age of Seed (DAF)	Seed Dry Weight (mg)	Seed Moisture (%)	Total Germination (%)	% Normal Seedlings	% Abnormal Seedlings	Seedling Weight (mg)	Hypocotyl Length (cm)
C-20	26	97.3	67.2	24.0	7.3	16.7	27.3	4.7
	33	137.2	57.3	67.3	60.7	6.7	36.2	8.4
	40	175.7	54.2	96.7	91.3	5.3	57.6	12.0
Seafarer	34	52.4	71.8	74.7	36.7	38.0	47.3	9.9
	40	136.2	61.1	89.3	72.0	17.3	61.0	11.5
	47	198.6	24.1	97.3	94.0	3.3	68.8	13.0
Cran-028	33	86.5	76.5	37.3	16.0	21.3	41.6	3.6
	41	373.9	61.9	45.0	26.0	19.0	38.1	6.3
	47	360.0	61.0	59.3	48.7	10.7	74.5	9.0
	54	430.0	54.6	85.3	81.3	4.0	90.1	10.3
	61	513.4	49.2	90.7	88.0	2.7	98.8	11.0
MIC	36	321.6	63.9	11.3	5.3	6.0	30.1	4.6
	43	481.9	55.6	50.7	33.3	17.3	52.0	6.0
	50	550.0	53.3	53.3	27.3	26.0	61.1	6.8
	57	501.9	52.3	97.3	54.0	43.3	78.0	8.3
	65	515.2	51.5	96.0	92.7	3.3	99.6	10.3

Table 18. Germination* and seedling development during seed growth of four dry bean varieties (1986).

Variety	Developmental stage≠ (DAF)	Seed dry weight	Seed moisture %	Germination (%)			Seedling Parameters	
				Total	Normal seedlings	Abnormal seedlings	Mean dry weight (mg)	Hypocotyl length (cm)
C-20	27 (A)	50.3	73.3	8.7 a•	4.0 a	4.7 a	11.7 a	6.6 a
	34 (B)	110.0	64.9	94.7 d	80.0 de	14.7 ab	41.0 b	10.6 ab
	41 (C)	151.1	57.5	94.7 d	87.3 de	7.3 ab	48.3 bc	11.5 b
Seafarer	29	36.8	66.6	0.0	---	---	---	---
	36 (A)	109.0	65.3	88.7 cd	70.7 d	18.0 b	53.3 bc	11.8 b
	43 (C)	166.4	53.0	97.3 d	92.0 e	5.3 a	64.0 cd	12.4 b
Cran-028	28 (A)	78.2	76.8	18.0 a	10.0 a	8.0 a	19.2 a	6.3 a
	36 (B)	258.1	64.8	45.3 b	22.7 ab	22.7 c	46.8 b	9.7 ab
	51 (C)	393.9	55.5	83.3 cd	70.0 d	13.3 abc	98.0 e	9.9 ab
MIC	29 (A)	137.2	70.2	70.7 c	49.3 c	21.3 bc	55.8 bc	7.9 ab
	36 (B)	335.9	59.0	71.3 c	35.3 bc	36.0 d	70.7 cd	6.4 a
	50 (C)	374.1	53.6	87.3 cd	65.3 cd	22.0 bc	84.9 de	8.1 ab
L.S.D. (0.05)				19.97	19.26	13.30	16.10	4.39
C.V. (%)				16.32	20.31		17.25	26.92

* Determined by the 7-day warm germination test.

≠ A = time of first expression of germination, B = one week later, C = physiological maturity.

• Figures followed by similar letter in same column are not significantly different at the 5% level.

Table 19. Germination and seedling vigor development in growing seeds of four dry bean varieties (1986).

Development Stage	Germination (%)			Seedling Parameters	
	Total	Normal seedlings	Abnormal seedlings	Mean dry weight (mg)	Hypocotyl length (cm)
Earliest expression of germination	46.5 a≠	33.5 a	13.0 a	35.0 a	8.2 a
One week later	75.0 b	52.2 b	22.8 b	52.9 b	9.6 ab
Physiological maturity	90.7 c	78.7 c	12.0 a	73.8 c	10.5 b
S.E.±	3.31	3.21	2.217	2.68	0.73
L.S.D. (0.05)	9.99	9.63	6.65	8.05	2.20

* Determined by the 7-day warm germination test.

≠ Figures followed by same letter in a column are not significantly different at the 5% level.

and 18 show that once germination ability is attained, subsequent increases also show higher increases in level of normal seedlings, accompanied by reduced abnormal seedlings.

Thus Seafarer in 1985 (Table 17) had total germination and normal seedling levels of 74.7 and 36.7% respectively, and abnormal seedlings of 38.0% at 34 DAF. A week later (40 DAF) total germination had risen to 89.3% (a 19.6% increase) whereas the level of normal seedlings had risen to 72.0% (a 96.3% gain) while the level of abnormal seedlings dropped from 38 to 17.3%. Between 40 DAF and PM (47 DAF) the increase in total germination declined 9.0% to 97.3%, while the level of normal seedlings rose from 72 to 94.0% (a 30.6% increase). Abnormal seedlings decreased significantly from 17.3% at 40 DAF to 3.3% at PM. The same trend occurred for Seafarer in 1986 when total germination increased from 88.7% at 36 DAF to 97.3% at 43 DAF (PM), an increase of 9.8%, whereas normal seedlings increased from 70.7 to 92.0%, an increase of 30.2%, and level of abnormal seedlings fell from 18.0 to 5.3%. Similar patterns occurred for CRAN-028 and MIC. These results show that bean seeds first acquire the ability to germinate and then the ability to produce normal seedlings.

Seed of C-20 acquired germinability when the seed had accumulated 55.4 and 33.0 % of the final seed dry matter, Seafarer 26.4 and 65.0%, CRAN-028 16.9 and 19.9%, and MIC 58.4 and 36.7%, in the respective seasons. While this was not consistent across varieties, there was a definite trend

in the relationship between final seed dry weight and germination capacity. C-20 had 24.0% total germination and 7.3% normal seedlings at 55.4% of final seed dry weight at first germination in 1985. In 1986, the total germination was 8.7% and normal seedlings was 4.0% at 33.0% of final seed weight. Seafarer had 74.7% total germination and 36.7% normal seedlings at 26.4% of the total seed weight in 1985, but increased to 88.7 and 70.7%, respectively, at 65.0% of final seed weight in 1986.

In contrast, seed of CRAN-028 first germinated when less than 20% of the final seed dry weight had been attained in both seasons. Though positive correlation between seed dry weight and ability to germinate has been reported previously for dried immature beans (Siddique, 1980) cited by Goodwin and Siddique (1984), germination of immature bean seeds at very low percentage of the final seed weight has been previously reported. Inoue and Suzuki (1962) reported high germinability of bean seeds on plants harvested as early as 15 DAF. Even though considerable seed dry weight increase may have occurred as the plants dried, it is obvious that such seeds still had a very low percent of their potential final seed weight. Walbot *et al.* (1972) reported 30% germination from very young bean embryos at eight to 11 DAF, when the seed had accumulated only 2.5% of its final weight.

Seed moisture content showed high negative correlation with germination in all varieties in both seasons (Table 20) and had very high r^2 values. These negative correlations

Table 20. Relationship between seed moisture and germination≠ during seed development.

Variety	1985		1986	
	r	r^2	r	r^2
C-20	-0.903*	0.815	-0.938*	0.880
Seafarer	-0.911**	0.830	-0.789	0.623
Cran-028	-0.974**	0.949	-0.979**	0.958
MIC	-0.880**	0.774	-0.768	0.590
General	-0.870**	0.757	-0.847**	0.717

* Significant at the 5% level.

** Highly significant at the 1% level.

≠ Determined by the 7-day warm germination test.

were significant at the 5% level in C-20 in both seasons, and highly significant (1%) in Seafarer in 1985, MIC in 1985, and CRAN-028 in both seasons. The overall correlations, across varieties, were highly significant (1%) in both seasons. Seed moisture content at the time of first expression of germinability was 67.2 and 73.3% for C-20, 77.5% and 65.3% for Seafarer, 80.6 and 76.8% for CRAN-028 and 76.5 and 70.2 for MIC, in the respective seasons. At PM, seed moisture had decreased to about 50% for all varieties except Seafarer in 1985 (Tables 17 and 18). That agrees with Watada and Morris (1967) who found moisture to be a reliable index of maturity in dry beans and Tekrony et al. (1979) who found soybean seed moisture at PM to be constant across varieties and environments.

These results suggest that bean seeds acquire germination capacity at seed moisture of 80.0% and below. In this study seeds generally had slightly below 80.0% moisture after 22 DAF which indicates that the 80.0% observed for CRAN-028 is unusually high. Other reports in literature, such as those of Obendorf (1980) on soybeans and Kermode et al. (1986) on dry beans reported first expression of germinability at below 70% seed moisture.

All seeds used in this germination study were air-dried outside the pod. Adams and Rinne (1981) and Adams et al. (1983) have demonstrated that fast-drying outside the pod is detrimental to germination of immature seeds. Siddique (1980), cited by Goodwin and Siddique (1984), rapidly dried

immature beans harvested at 34 DAF using forced air for 12 hours, but still attained 50% germination. Adams et al. (1983) also reported that fast-drying delayed the appearance of germination-specific enzymes such as malate synthase and isocitrate lyase, however, the shear method of drying immature bean seeds has been reported to enhance their germination (Inoue and Suzuki, 1962; Dasgupta et al., 1982) as well as those of soybeans (Burris, 1973, and Adams and Rinne, 1981).

The results obtained in this study suggest that fast-drying did not adversely affect the evaluation of germination since they compare well with results of previous studies. Inoue and Suzuki (1962) obtained germination from seeds harvested as early as 25 DAF and Siddique (1980), cited by Goodwin and Siddique (1984), found germination at 31 DAF. Kermode et al. (1986) reported germination of 25% at 26 DAF, increasing to 70% and 100% at 32 DAF and 40 DAF (PM), respectively. They reported a pronounced increase in germination between the time of the first expression of germination and a week later, a phenomenon also observed in this study. It can thus be concluded that once the initial ability to germinate is acquired, germinability increases rapidly.

Almost all nutrients monitored in this study reached their maximum content at or near seed PM (refer to section on Nutrient Accumulation), thus there is a positive

correlation between their content in the seed and ability to germinate.

Dure (1975) characterized legume embryogenesis as beginning with a build-up of precursors, followed by the period of pod, testa and endosperm growth, towards the end of which rapid cell division occurs. Afterwards, there is a marked cessation of cell division during which DNA endoreduplication occurs, the period generally referred to as the lag-phase. Afterwards, a deposition of reserves occurs, followed by seed desiccation. Results presented earlier clearly show that nutrient accumulation in the dry bean pod fits this pattern, since peak values are mostly or nearly reached by 20-22 DAF. During the rapid growth phase of the embryo, isolation of any single nutrient becomes difficult.

Vigor Development

Vigor Development during seed development

Results discussed previously showed that germination capability was acquired ahead of the seeds capability to produce normal seedlings. Though total germination quickly reached maximum values, the increase in capacity to produce normal seedlings occurred only towards PM (Tables 17 and 18). Thus a seed needs more than just the ability to germinate to produce normal seedlings. The capacity for further development must occur for the production of normal seedlings. This not only provides a basis of the use of the standard AOSA germination test (AOSA, 1981) but also as a

basis for use of the level of normal seedlings as a measure of vigor (Burris, 1970), and specifically, the use of a 4-day count of normal seedlings (AOSA, 1983). In this study, development of normal seedlings in all varieties lagged behind total germination (protrusion of radicle) as discussed earlier, suggesting that development of vigor necessary for the development of a normal functional plant occurs after germination capacity is attained. Results in Tables 17 and 18 also suggest that seed vigor is highest at PM, evidenced by occurence of maximum normal seedlings.

Results of seedling dry weight and hypocotyl length (Tables 17 and 18) also show that seed vigor is maximum at PM. However, hypocotyl length values in Table 18 suggest a general lack of significant differences in seed vigor between the time of earliest germination capability, a week later, or at PM. Although hypocotyl length increased with time in both seasons, it appears to be less suited than dry weight as the sole basis for measuring vigor. Seedling dry weight changed markedly in some cases, and in seedlings of C-20 at the time of earliest germination, was less than one-half and one-fourth of that of mature seeds in both seasons. Similar results were obtained from CRAN-028 seeds. In fact, for all varieties, seedling dry weight differences reflected differences in germination capacity better than hypocotyl length.

Seedling weight and hypocotyl length values indicate that neither parameter can be used across varieties, even

those belonging to the same class. At PM in 1985, C-20 had 96.7% total germination, a mean seedling weight of 57.6 mg, and hypocotyl length of 12.0 cm, compared to 97.3%, 68.8 mg and 13.0 cm for the same parameters in Seafarer. At the same developmental stage, CRAN-028 had 90.7% total germination, 98.8 mg seedling weight and 11.0 cm hypocotyl length, while MIC had 96.0%, 99.6 mg, and 10.3 cm, respectively. Seedling weights of the navy bean varieties are much smaller than those of the cranberry varieties, mainly due to seed size differences. However, they have longer hypocotyls because they are generally longer and more slender, compared to the thick and relatively slow elongating hypocotyls of cranberry varieties. Even in the cranberry varieties, the difference in total germination is much more pronounced than that in the seedling weights, while hypocotyl lengths suggest that CRAN-028 seed is more vigorous than MIC seed. Although these tests are simple to perform and can be done on the same material used for the warm germination test, these results illustrate the limitations in their usefulness.

Post-Maturity vigor in bean seeds.

Delayed harvesting resulted in reductions of total germination, normal seedlings, seedling weight and hypocotyl length (Tables 21 and 22). The results also show that the rate of deterioration differs among varieties as well as seasons. This is expected since environmental conditions vary and different varieties mature at different times in the season. Very little differences occurred between total

Table 21. Germination* and seedling vigor of four dry bean varieties subjected to delayed harvesting (1985).

Variety	Days after maturity	Total germination (%)	% Normal seedlings	% Abnormal seedlings	Mean seedling weight (mg)	Mean hypocotyl length (cm)
C-20	0	96.7 (3.05)ƒ	91.3 (2.31)	5.3 (1.15)	57.6 (1.08)	12.0 (0.21)
	7	91.0 (1.41)	80.0 (0.00)	11.0 (1.41)	56.6 (0.71)	12.0 (0.26)
	24	94.0 (5.66)	90.0 (2.83)	4.0 (2.83)	57.8 (1.20)	11.3 (0.18)
	35	91.0 (1.41)	85.0 (1.41)	6.0 (0.00)	53.4 (0.21)	10.9 (0.19)
	40	85.0 (1.41)	75.0 (1.41)	10.0 (2.83)	51.6 (0.71)	10.4 (0.12)
Seafarer	0	97.3 (3.05)	94.0 (3.46)	3.3 (1.15)	68.8 (1.91)	13.0 (1.14)
	7	99.0 (1.41)	97.0 (1.41)	2.0 (0.00)	64.5 (5.80)	12.9 (0.13)
	15	95.0 (4.24)	83.0 (9.90)	12.0 (14.1)	59.4 (6.86)	12.2 (0.14)
	27	95.0 (4.24)	88.0 (8.48)	7.0 (4.24)	58.7 (4.81)	11.6 (0.73)
	34	92.0 (5.66)	77.0(15.56)	15.0 (9.90)	56.5 (5.23)	10.9 (0.20)
	43	90.0 (5.66)	63.0(18.38)	27.0(12.73)	48.7 (2.83)	11.3 (0.87)
Cran-028	0	90.7 (4.16)	88.0 (3.46)	2.6 (1.15)	98.8 (3.16)	11.0 (0.50)
	7	88.0 (2.83)	84.0 (2.83)	4.0 (5.66)	99.3 (3.75)	11.0 (0.64)
	14	78.0 (8.48)	76.0 (8.49)	2.0 (0.00)	98.6 (0.42)	10.7 (0.76)
	25	78.0 (2.83)	72.0 (5.66)	6.0 (2.83)	89.7 (3.82)	10.4 (0.45)
MIC	0	96.0 (4.00)	92.7 (5.03)	3.3 (1.15)	99.6 (4.18)	10.3 (0.28)
	14	97.0 (1.41)	82.0 (0.00)	15.0 (1.41)	107.7(13.36)	10.5 (0.13)
	18	81.0 (4.24)	64.0 (5.66)	17.0 (1.41)	91.7 (0.28)	10.0 (0.13)

* Determined by the 7-day warm germination test.

ƒ Standard deviation of the mean in parentheses.

Table 22. Germination* and seedling vigor of four dry bean varieties subjected to delayed harvesting (1986).

Variety	Time of harvest (days after PM)	Germination (%)			Seedling Parameters	
		Total	Normal seedlings	Abnormal seedlings	Mean dry weight (mg)	Hypocotyl length (cm)
C-20	0 (PM)ƒ	94.7 cd•	87.3 bc	7.3 ab	48.3 a	11.5 cd
	7 (HM)	94.7 cd	74.6 b	20.0 b	48.0 a	11.6 cd
	14	98.7 d	90.0 bc	8.7 ab	55.1 a	11.9 cd
	21**	84.0	46.0	38.0	43.5	8.6
Seafarer	0 (PM)	97.3 d	92.0 c	5.3 a	64.0 b	12.4 d
	7 (HM)	94.7 cd	89.3 bc	5.3 a	64.0 b	12.2 d
	14	95.3 cd	76.7 bc	18.7 ab	52.3 a	11.9 cd
	21**	98.7	68.7	30.0	45.1	8.7
	34**	74.0	24.0	50.0	32.0	6.8
Cran-028	0 (PM)	83.3 bc	70.0 ab	13.3 ab	98.0 cd	9.9 b
	7 (HM)	73.3 ab	68.0 ab	5.3 a	97.5 cd	10.9 c
	14	60.0 a	52.7 a	7.3 a	90.0 c	9.7 b
MIC	0 (PM)	87.3 bc	65.3 ab	22.0 b	84.9 c	8.1 a
	7 (HM)	89.0 c	74.0 b	15.0 ab	98.8 d	9.1 ab
	14	74.7 b	48.7 a	26.0 b	95.6 cd	9.0 ab
S.E.±		4.66	5.97	4.82	2.84	0.35
L.S.D. (0.05)		13.97	17.89	14.46	8.53	1.05
C.V. (%)		9.29	13.95	64.95	6.59	5.69

* Determined by the 7-day warm germination test.

** Data not included in the analysis of variance.

ƒ PM = physiological maturity, HM = harvest maturity (approximate).

• Figures followed by similar letter in a column are not significantly different by the L.S.D. test at the 5% level.

germination and number of normal seedlings at PM and those at harvest maturity (HM). However, delaying harvest beyond normal HM results in considerable loss in seed quality.

In 1985, germination of Seafarer decreased from 97.0 to 92.0% whereas percent normal seedlings decreased from 94.0 to 77.0% in the five weeks after PM (Table 21). In 1986 total germination was 97.3% at PM, 98.7% three weeks later, and 74.0% after a further two weeks but the corresponding levels of normal seedlings were 92.0, 68.7 and 24.0%. MIC had total germinations of 96.0, 97.0, and 81.0% at PM, after 14 days, and after 18 days, respectively in 1985, however, the levels of normal seedlings were 92.7, 82.0 and 64.0% respectively. In 1986, total germination was 87.3% at PM and 89.0 a week later, but dropped to 74.7% after the second week. Normal seedlings changed from 65.3% at PM, 74.0 a week later, and to 48.7% after the second week. The same trends occurred in C-20 and CRAN-028 (Tables 21 and 22), showing that dry bean seeds lose vigor before they lose ability to germinate, as noted by Heydecker (1969) and observed in soybeans by Miles (1985). The numbers of abnormal seedlings also increased markedly with delayed harvesting. Thus, loss in vigor becomes the major difference between germination in the physiological sense as discussed by Copeland and McDonald (1985) and germination as used in the seed industry (AOSA, 1981). The progressive decrease in germination ability results in capacity for radicle protusion without the vigor needed to develop into a normal seedling.

Although seedling dry weight and hypocotyl length reflect a general loss in vigor, they are not well correlated to the level of normal seedlings. Again, this limits their usefulness (Tables 21-23) as reliable indices in vigor, which also agrees with conclusions made by Woodstock (1969).

Results of accelerated aging tests on the two navy bean varieties, C-20 and Seafarer (Table 24) illustrate the relatively sharper decline in level of normal seedlings compared to total germination. With C-20 total germination decreased from 97.0% at PM to 43.5, 35.0 and 5.0% after one, two, and four weeks after PM while normal seedling percentage dropped from 82.5% at PM to 31.0, 9.5 and 0%, in the same period. The earlier reduction in number of normal seedlings relative to total germination is even more striking for Seafarer.

Cold test results on seed harvested following PM are shown in Tables 25-28. Across varieties, the cold test failed to detect any difference in seed quality up to two weeks after PM as shown by both numbers of normal seedlings and the cold test vigor index (Table 27). In 1985, the cold test indicated all C-20 seed at PM to three weeks after PM to be low in vigor, Seafarer seed at PM as medium vigor and everything later as low vigor. It indicated CRAN-028 as medium vigor at PM and a week later, but as high vigor two weeks after PM, and MIC as high at PM and medium in vigor after one and two weeks, but low after three weeks. In 1986,

Table 23. Seed germination* and seedling development at different times of harvesting dry beans after maturity (1986).

Time of harvest	Germination (%)			Seedling Parameters	
	Total	Normal seedlings	Abnormal seedlings	Mean dry weight (mg)	Hypocotyl length (cm)
Physiological maturity	90.7 b≠	78.7 b	12.0 a	73.8 a	10.5 a
Harvest maturity (1 week later)	87.9 ab	76.5 ab	11.4 a	77.1 a	11.0 a
2 weeks after PM	82.2 a	67.0 a	15.2 a	73.3 a	10.6 a
S.E.±	2.33	2.98	2.41	1.42	0.18
L.S.D. (0.05)	6.98	8.94	7.23	4.26	0.53

* Determined by the 7-day warm germination test.

≠ Values followed by same letter in a column are not significantly different by the L.S.D. test at the 5% level.

Table 24. Seed quality of navy beans after physiological maturity as evaluated by the accelerated aging test (1986).

Variety	Time of harvest (days after PM)	Total germination %	% Normal Seedlings	% Abnormal Seedlings	% Decayed Seed
C-20	0 (PM)	97.0 c*	82.5 c	14.5 ab	3.0 a
	7	43.5 b	31.0 b	12.5 ab	56.5 b
	14	35.0 b	9.5 ab	25.5 ab	62.5 b
	29	5.0 a	0.0 a	5.0 a	95.0 c
Seafarer	0 (PM)	96.0 c	68.0 c	28.0 b	3.0 a
	7	81.0 c	26.0 ab	55.0 c	17.0 a
	14	90.5 c	36.0 b	54.5 c	8.0 a
	21	6.0 a	0.0 a	6.0 a	94.0 c
S.E.		4.64	8.80	5.88	4.29
LS.D. (0.05)		16.07	30.46	20.34	14.83
C.V. (%)		11.6	39.4	33.1	14.3

PM = Physiological Maturity.

* Figures followed by the same letter in a column are not significantly different by the L.S.D. test at the 5% level.

Table 25. Evaluation of post-maturity seed quality of four dry bean varieties by the cold test (1985).

Variety	Time of Sampling* (Days after physiological maturity)	Cold Test Evaluation		
		% Normal seedlings	Vigor index	Vigor≠ category
C-20	0 (A)	32	168	Low
	7 (B)	22	118	Low
	24	24	108	Low
	35	29	148	Low
Seafarer	0 (A)	64	288	Medium
	7 (B)	34	140	Low
	15	16	66	Low
	27	11	46	Low
	34	14	62	Low
	43	8	32	Low
Cran-028	0 (A)	64	318	Medium
	7 (B)	76	340	Medium
	14	87	414	High
	25	65	232	Medium
MIC	0 (A)	94	432	High
	7 (B)	73	344	Medium
	14	82	362	Medium
	18	43	182	Low

* A = physiological maturity, B = approximate harvest maturity.

≠ Vigor indices: Low 0-200, Medium 201-400, High 401-600.

Table 26. Cold test evaluation of seed quality of four dry bean varieties subjected to delayed harvesting (1986).

Variety	Time of Harvest (Days after physiological maturity	Cold Test Evaluation		
		% Normal seedlings	Vigor index	Vigor≠ category
C-20	0 (PM)	9.0 a*	20.0 a	Low
	7	22.0 ab	52.0 a	Low
	14	9.0 a	17.0 a	Low
Seafarer	0 (PM)	34.0 b	67.0 a	Low
	7	29.0 ab	63.0 a	Low
	14	14.0 ab	34.0 a	Low
Cran-028	0 (PM)	73.0 c	167.0 bc	Medium
	7	79.0 c	193.0 bc	Medium
	14	73.0 c	180.0 bc	Medium
MIC	0 (PM)	86.0 c	219.0 c	High
	7	72.0 c	188.0 bc	Medium
	14	71.0 c	146.0 b	Medium
S.E.±		6.56	20.38	
L.S.D. (0.05)		21.41	66.46	

* Values followed by same letter in a column are not significantly diffferent by the L.S.D. test at the 5% level.

≠ Vigor indices: Low 0-100, Medium 101-200, High 201-300.

Table 27. Effect of delayed harvesting on seed quality of dry beans as determined by the cold test (1986).*

Time of harvest (days after PM)	% Normal Seedling	Vigor Index
0	50.2 a	118.2 b
7	50.5 a	124.0 b
14	41.7 a	94.2 b
S.E.±	3.28	10.19
L.S.D. (0.05)	10.70	33.23
C.V. (%)	19.54	25.70

* Values followed by the same letter in a column are not significantly different by the L.S.D. test at the 5% level.

Table 28. Varietal effect on dry bean seed quality evaluated by the cold test* (1986).

Variety	Cold Test Evaluation		
	% Normal Seedlings	Vigor Index	Vigor Category/
C-20	13.3 a	29.7 a	Low
Seafarer	25.7 a	54.7 a	Low
Cran-028	75.0 b	180.0 b	Medium
MIC	76.0 b	184.3 b	Medium
S.E.±	4.51	7.3	
L.S.D. (0.05)	12.4	38.4	
C.V. (%)	19.5	25.7	

* Values followed by same letter in a column are not significantly different by the L.S.D. test at the 5% level.

/ Vigor index: Low 0-100, Medium 101-200, High 201-300.

all the C-20 and Seafarer seed at PM, one week after and two weeks after PM was rated low in vigor while all the CRAN-028 at PM, one week later and two weeks later were classified as medium in vigor. Only MIC at PM was rated high, with the seed one and two weeks after PM rated as medium (Table 25 and 26). This does not agree with evaluation by the warm germination test (Tables 21 and 22) and also shows a varietal effect (Table 28). The navy bean varieties performed poorly in the cold test and most of the seedlings decayed at ground level soon after emergence. The cold test was more favorable to the cranberry varieties, as they developed more vigorously than in the warm germination test. This could have been due to better moisture absorption or positive response to the cold treatment. Although the cold test is widely used as a reliable vigor test, it was not very useful in these studies. Field emergence studies might have helped identify causes of this failure.

The purpose of evaluating seed quality of dry beans exposed to environmental stresses was not specifically to measure the effects of the environmental factors on seed quality as no systematic effects were applied to impose control. The seeds were simply harvested later than normal and the effects of delayed harvesting on large seeded legumes have been well documented (Pollock and Toole, 1964, Green et al. 1966, Moore 1971 and Nangju, 1977). An effort was made to evaluate bean seeds known to be deteriorating in

quality and use various methods to study the nature of that deterioration.

A combination of seed quality evaluation during growth and after PM strongly indicates that prior to full seed development, the seed first acquires the ability to germinate. With continued development, seed then gains the ability to produce normal seedlings, reaching a maximum at PM. After PM, loss of seed vigor precedes loss of germination capability. This pattern has been reported for soybeans by Miles (1985) and implies that the seed must acquire a certain level of development before it can produce normal seedlings and must maintain that level after maturity. Seed storage practices should be designed to keep the seed at or above that level of quality.

SUMMARY AND CONCLUSIONS

Fruit development and seed quality in navy and cranberry beans were studied in field and laboratory tests in 1985 and 1986. The 1985 growing season was near optimal but the 1986 crop was subjected to severe soil compaction before flowering and flooding and notable disease infestation in the later growth stages. Pod and seed fresh and dry weight, seeds/pod, and pod length were monitored during fruit development and final yield components were recorded. Nutrient status of the pod and seed of the developing fruit was determined. The nutrients evaluated were nitrogen (protein), potassium, phosphorus, calcium, magnesium, manganese, iron, zinc, copper and boron. Seed quality was monitored during seed development and after physiological maturity (PM) including prolonged exposure in the field. Seed germinability was evaluated by the standard germination test and vigor during seed development was evaluated by seedling classification, seedling growth rate, and hypocotyl length. Seed vigor after PM was evaluated as above, in addition to the cold soil test and accelerated aging test on the navy bean varieties.

Pod growth preceded seed growth in the navy and cranberry bean varieties in both seasons. The navy varieties

attained maximum pod length between 15 and 18 days after anthesis (Days after flowering - DAF) in 1985 and by 21 days in 1986. The cranberry varieties attained full pod length by 19 and 21 DAF in 1985 and 1986. The varieties differed in the time required to reach maximum pod length and peak pod fresh and dry weight but the pods in all varieties first reached maximum length before maximum fresh or dry weight. Loss in pod dry weight during seed development suggested pod dry matter remobilization to the developing seeds which could supply 14 to 28% of the seed dry matter requirements within a fruit. Seed growth was very slow initially but increased sharply from 22 DAF and maximum growth rates were reached in the second week. The seed had only accumulated 3-11% of its maximum dry weight by the onset of the lag phase (20-22 DAF).

Pod nitrogen concentration decreased from 2.40 and 2.70% at 12 and 13 DAF to 0.64 and 0.75% at PM in the respective seasons. By 12-15 DAF, pods contained 77 to 92% of total fruit protein but by PM they contained 4-7%. Peak pod protein content was reached between 22 and 28 DAF in the two seasons. Seed nitrogen was higher than that in the pod throughout fruit development and ranged from 4.8 to 6.5% at 12-15 DAF to between 3 and 4% by PM. Seed protein accumulation paralleled seed dry weight increase. The results showed that 85 to 96% of the total seed protein accumulated after the lag phase. Most mineral nutrient elements reached maximum levels in the pods by the time of

peak pod dry weight. Nutrient accumulation patterns in dry bean pods and seeds varied with both varieties and seasons. Nutrients accumulated ahead, behind, or at the same rate as dry weight. Nutrient loss from the pod during seed growth was noted which could supply 2 to 59% of the seed requirements of different elements.

The early completion of pod growth prior to seed development, and the loss of pod dry weight and nutrient supplies during seed development strongly suggest the role of the pod as a temporary reservoir of assimilates needed for embryogenesis and seed development. The data obtained however show that the pod can supply only a relatively small fraction of the seed nutrient requirements. The accumulation of some nutrients ahead of dry weight in both the pod and seeds suggests that the dry bean fruit has mechanisms to control the inflow of nutrients according to its needs. The data also indicated that nutrient accumulation patterns in dry beans are complex and likely to differ with varieties and in response to different conditions.

Immature dry bean seeds began to express ability to germinate from 26 DAF onwards in both years. There was variation among varieties and between seasons but the onset of germination in all cases occurred between 26 and 36 DAF. The seeds exhibited rapid increases in germinability after the first expression of the ability to germinate. Initial germination counts were dominated by abnormal seedlings but as the seeds approached PM, there was a reversal, with

normal seedlings dominating. Both total germination and normal seedlings attained maximum levels at PM. Hypocotyl length and seedling dry weight increased with seed maturity but their rates of increase were much smaller than that of total germination or level of normal seedlings. Seed quality generally deteriorated after PM and this was evidenced by a decrease in total germination, level of normal seedlings, hypocotyl length, and seedling dry weight with extended exposure in the field. The results showed that mature dry bean seeds lose the ability to produce normal seedlings before complete loss of germination per se.

Seed moisture contents showed high negative correlations with germination which were mostly significant. Seed moisture content at the time of first expression of germinability was between 65 and 80% and showed considerable variation with seasons.

The results demonstrated that developing dry bean seeds acquire the ability to germinate before acquiring the ability to produce normal seedlings. After PM the seeds gradually lose the ability to produce normal seedlings as they lose the ability to germinate. This implies that during development the seeds acquire germination capacity ahead of vigor but after PM they lose vigor ahead of germination ability. The results also confirm the ability of immature dry beans to withstand fast-drying.

It is suggested that future studies on fruit growth and seed quality development in legumes should consider the following points:

a) Utilize a shorter sampling interval of about three days to improve the sensitivity to detect changes in dry weight, moisture status, germinability, and nutrient status.

b) Tag as many open flowers as possible per sampling subunit to improve sampling precision and adequacy of test material.

c) Use at least four replications to reduce experimental error.

d) Use stress tests (accelerated aging, cold test) as additional tests for vigor evaluation during seed development.

e) Compare development of germination capacity in fast-dried and slow-dried seeds.

f) Use a variety x soil fertility or variety x soil fertility x soil moisture factorial arrangement if soil fertility and/or soil moisture are limiting.

APPENDIX

APPENDIX

Table 29. Rainfall data (Michigan State University farm, East Lansing) 1985-86.

Month	Year				23-year average rainfall (inches)
	1985		1986		
	Total rainfall (inches)	Days of rain	Total rainfall (inches)	Days of rain	
April	4.28	10	2.89	12	3.21
May	2.44	8	3.56	12	2.96
June	2.29	7	8.91	12	4.04
July	2.19	6	2.49	10	2.87
August	4.29	11	3.84	6	3.07
September	3.22	8	9.56	11	3.27
October	5.02	9	2.84	9	2.15
Total	23.73	52	34.09	72	21.57

Table 30. Average daily seed growth rates of four dry edible bean varieties 1985).

Variety	Period (DAF)	Mean daily weight gain (mg/day)
C-20	0-12	0.11
	12-15	0.80
	15-19	3.95
	19-26	11.10
	26-33	5.70
	33-40	5.50
Seafarer	0-12	0.04
	12-15	1.00
	15-18	2.58
	18-26	0.73
	26-34	4.42
	34-40	13.95
	40-47	8.92
Cran-028	0-12	0.09
	12-15	1.73
	15-19	2.49
	19-26	2.73
	26-34	6.38
	34-41	41.05
	41-55	9.98
MIC	0-12	0.13
	12-15	0.52
	15-19	2.59
	19-23	9.19
	23-29	12.27
	29-36	28.25
	36-43	22.90
	43-50	11.57
	50-65	-3.38

Table 31. Seed and pod nitrogen concentration and protein content during fruit development of four dry bean varieties (1985).

Variety	Age of fruit (DAF)	Pod N (%)	Pod protein content (mg)	Seed N (%)	Seed Protein content/pod (fruit)(mg)
C-20	12	2.40	33.60	5.47	2.74
	15	2.33	41.35	4.87	7.00
	19	1.98	51.83	3.89	28.44
	26	1.57	35.90	3.23	116.50
	33	0.89	15.90	3.23	173.63
	40	0.64	10.92	3.31	207.31
Seafarer	15	2.85	20.84	4.79	6.14
	18	2.29	70.55	--	--
	26	1.73	42.05	3.89	24.55
	34	1.12	33.74	3.27	56.82
	40	0.67	15.88	3.28	153.54
	47	0.57	10.29	3.21	203.21
Cran-028	15	2.81	89.56	4.97	7.45
	26	1.75	86.64	4.13	45.68
	34	0.94	61.75	3.34	97.46
	41	0.81	47.26	3.26	154.20
	48	0.58	30.12	3.37	363.92
	55	0.56	23.90	3.27	451.31
MIC	15	3.21	63.99	5.07	3.49
	23	2.23	89.08	4.49	16.27
	29	1.65	81.96	4.07	53.68
	36	1.26	79.33	3.73	127.04
	43	0.87	46.35	3.49	301.63
	50	0.57	24.81	3.33	411.21
	57	0.58	19.77	3.76	482.45
	65	0.49	15.76	3.31	425.80

Table 32. Concentration and accumulation of P, K, Ca and Mg in developing pods of four dry bean varieties (1985).

Variety	Age of Fruit (DAF)	P		K		Ca		Mg	
		Concentration (%)	Content (mg)	Concentration (%)	Content (mg)	Concentration (%)	Content (mg)	Concentration (%)	Content (mg)
C-20	12	.266	.596	1.868	4.184	.671	1.503	.244	.547
	15	.260	.738	1.673	4.751	.615	1.747	.234	.665
	19	.177	.742	1.593	6.675	.525	2.200	.207	.867
	26	.109	.399	1.709	6.255	.477	1.746	.229	.838
	33	.077	.220	2.251	6.438	.373	1.067	.189	.541
	40	.047	.128	2.482	6.776	.454	1.239	.236	.644
Seafarer	15	.309	.362	2.296	2.686	.665	.778	.295	.345
	18	.226	1.114	1.958	9.652	.632	3.116	.265	1.306
	26	.133	.517	2.147	8.352	.574	2.233	.237	.922
	34	.106	.511	2.264	10.912	.455	2.193	.300	1.446
	40	.044	.167	3.460	13.113	.653	2.475	.448	1.698
	47	.029	.084	3.490	10.086	.757	2.188	.441	1.274
Cran-028	15	.372	1.897	2.585	13.183	.724	3.692	.307	1.566
	22	.324	1.636	2.314	11.686	.687	3.469	.298	1.505
	34	.233	2.451	2.088	21.966	.595	6.259	.239	2.514
	41	.092	.859	2.341	21.865	.565	5.277	.280	2.615
	48	.074	.616	2.467	20.524	.606	5.042	.291	2.421
	55	.037	.253	3.026	20.668	.527	3.599	.378	2.582
MIC	15	.406	1.295	2.446	7.803	.960	3.062	.292	.931
	23	.251	1.995	1.712	13.610	.668	5.311	.232	1.844
	29	.152	1.532	1.468	14.797	.575	5.796	.196	1.976
	36	.124	1.066	2.007	17.100	.518	4.413	.222	1.891
	43	.070	.488	2.556	17.815	.684	4.767	.308	2.147
	50	.042	.229	3.330	18.182	.792	4.324	.423	2.310
	57	.045	.231	3.915	20.162	.754	3.883	.411	2.117
	65	.043	.246	3.420	19.562	.878	5.022	.388	2.219

Table 33. Macronutrient accumulation in growing seeds of four dry bean varieties (1985).

Variety	Age of seed (DAF)	Seed dry weight as % of maximum	Nutrient content expressed as % of maximum seed content			
			P	K	Ca	Mg
C-20	19	11.14	22.90	18.78	18.28	16.34
	26	55.37	63.53	65.84	87.47	60.31
	33	78.08	90.14	100.00	100.00	91.90
	40	100.00	100.00	80.16	79.32	100.00
Seafarer	15	2.07	5.43	4.94	5.25	3.62
	26	9.97	14.85	14.97	20.60	13.92
	34	27.44	27.53	30.63	39.39	31.41
	40	73.94	75.39	74.28	87.51	79.04
	47	100.00	100.00	100.00	100.00	100.00
Cran-028	15	1.08	2.51	3.50	2.23	1.57
	22	1.72	2.98	4.57	3.23	2.19
	34	21.15	34.39	42.50	37.48	25.70
	41	79.57	87.25	100.00	100.00	83.47
	48	78.26	84.53	93.79	94.80	78.66
	55	100.00	100.00	97.15	80.93	100.00
MIC	15	2.81	5.27	4.76	2.65	4.00
	23	10.24	15.03	14.11	10.26	13.82
	29	26.44	34.46	31.46	28.66	31.99
	36	67.10	70.48	58.85	64.52	69.91
	43	95.88	100.00	100.00	100.00	94.18
	50	99.61	96.63	79.95	80.75	100.00
	57	99.85	98.32	71.45	80.13	88.86
	65	100.00	94.57	67.39	92.07	81.94

Table 34. Micronutrient accumulation in developing seeds of four dry bean varieties (1985).

Variety	Age of seed (DAF)	Seed dry weight as % of maximum	Nutrient levels expressed as % of maximum seed content				
			Mn	Fe	Zn	Cu	B
C-20	19	11.14	16.24	19.88	19.28	11.16	17.20
	26	55.37	71.58	69.21	69.01	74.67	64.98
	33	78.08	100.00	100.00	100.00	100.00	100.00
	40	100.00	72.76	99.65	93.42	72.80	98.51
Seafarer	15	2.07	3.58	4.46	5.46	4.18	3.45
	26	9.97	13.16	14.09	14.18	10.34	13.79
	34	27.44	27.63	27.16	28.01	29.73	28.37
	40	73.94	70.10	67.87	66.43	84.44	65.67
	47	100.00	100.00	100.00	100.00	100.00	100.00
Cran-028	15	1.08	1.67	2.22	2.70	1.55	2.05
	22	1.72	2.44	3.13	2.80	2.24	2.75
	34	21.15	30.40	38.63	31.76	26.79	33.57
	41	79.57	94.25	98.96	90.54	81.88	83.66
	48	78.26	94.87	91.27	86.53	85.72	78.24
	55	100.00	100.00	100.00	100.00	100.00	100.00
MIC	15	2.81	3.08	4.66	5.76	2.67	4.39
	23	10.24	11.15	16.89	16.04	9.84	16.12
	29	26.44	28.20	41.09	36.99	26.03	36.33
	36	67.10	67.88	81.73	86.56	65.51	72.92
	43	95.88	100.00	100.00	98.93	100.00	90.90
	50	99.61	87.48	99.96	84.64	95.59	94.42
	57	99.85	93.99	94.43	100.00	90.81	100.00
	65	100.00	87.82	73.89	91.36	85.95	93.75

Table 35. Concentration and content of Mn, Fe, Zn, Cu, B in developing dry bean seeds (1985).

Variety	Age of Seed (DAF)	Mn		Fe		Zn		Cu		B	
		Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)
C-20	19	17.8	2.1	97.6	11.4	39.8	4.7	10.2	1.2	11.9	1.4
	26	15.9	9.2	68.9	39.8	28.9	16.7	13.8	8.0	9.1	5.2
	33	14.9	12.8	66.8	57.4	28.1	24.2	12.4	10.7	9.4	8.1
	40	9.3	9.3	56.8	57.2	22.4	22.6	7.7	7.8	7.9	8.0
Seafarer	15	23.3	0.5	105.0	2.2	51.8	1.1	17.2	0.4	10.5	0.2
	26	17.8	1.8	68.8	6.9	28.0	2.8	8.8	0.9	8.7	0.9
	34	13.6	3.8	48.2	13.4	20.1	5.6	9.2	2.6	6.5	1.8
	40	12.8	9.6	44.7	33.5	17.7	13.3	9.7	7.3	5.6	4.2
	47	13.5	13.7	48.7	49.3	19.7	20.0	8.5	8.6	6.3	6.4
Cran-028	15	18.5	0.4	142.7	3.4	84.6	2.0	15.1	0.4	18.5	0.4
	22	16.8	0.6	127.0	4.8	55.5	2.1	13.6	0.5	15.4	0.6
	34	17.1	8.0	127.5	59.5	51.2	23.9	13.3	6.2	15.4	7.2
	41	14.0	24.8	86.8	152.5	38.8	68.2	10.8	19.0	10.2	17.9
	48	13.6	23.5	81.4	140.7	37.7	65.1	11.5	19.9	9.7	16.8
	55	11.9	26.3	69.8	154.1	34.1	75.3	10.5	23.2	9.7	21.4
MIC	15	14.0	0.8	109.0	6.3	67.4	3.9	11.3	0.7	14.7	0.8
	23	13.9	2.9	108.5	22.9	51.6	10.9	11.5	2.4	14.8	3.1
	29	13.6	7.4	102.2	55.7	46.1	25.1	11.8	6.4	12.9	7.0
	36	12.9	17.8	80.1	110.8	42.5	58.8	11.7	16.2	10.2	14.1
	43	13.3	26.3	68.6	135.5	34.0	67.2	12.5	24.7	8.9	17.6
	50	11.2	23.0	66.0	135.5	28.0	57.5	11.5	23.6	8.9	18.3
	57	12.0	24.7	62.2	128.0	33.0	67.9	10.9	22.4	9.4	19.3
	65	11.2	23.1	48.6	100.2	30.1	62.0	10.3	21.2	8.8	18.1

Table 36. Concentration and content of Mn, Fe, Zn, Cu, B in developing dry bean seeds (1986).

Variety	Age of Seed (DAF)	Mn		Fe		Zn		Cu		B	
		Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)	Conc'n (ppm)	Content (µg)
C-20	20	15.2	0.2	59.5	0.9	45.6	0.7	11.5	0.2	13.1	0.2
	27	11.4	0.6	40.2	2.0	30.5	1.5	9.2	0.5	10.1	0.5
	34	11.6	1.2	37.5	4.1	27.4	3.0	9.8	1.1	8.7	1.0
	41	14.5	2.2	71.8	10.9	27.9	4.2	9.0	1.4	8.1	1.2
Seafarer	15	27.1	0.1	132.0	0.4	91.4	0.3	12.5	0.0	16.1	0.0
	22	20.4	0.2	101.7	1.0	54.2	0.5	9.1	0.1	11.9	0.1
	29	15.1	0.6	80.8	3.0	28.3	1.0	8.6	0.3	9.4	0.3
	36	11.7	1.3	61.2	6.7	23.3	2.5	10.8	1.2	8.2	0.9
	43	13.9	2.3	63.0	10.5	24.9	4.1	7.7	1.3	6.8	1.1
Cran-028	14	21.2	0.1	150.0	0.6	99.5	0.4	10.8	0.0	18.5	0.1
	21	15.1	0.3	112.5	2.3	58.3	1.2	8.8	0.2	15.3	0.3
	28	13.0	1.0	67.3	5.3	45.6	3.6	8.4	0.7	11.8	0.9
	36	12.2	3.1	65.6	16.9	40.4	10.4	10.0	2.6	10.7	2.8
	42	10.4	3.6	50.8	17.7	34.9	12.1	7.8	2.7	9.5	3.3
	51	10.3	4.1	49.9	19.7	30.7	12.1	7.8	3.1	10.3	4.1
MIC	15	15.1	0.1	104.0	0.9	77.4	0.7	8.8	0.1	17.0	0.2
	22	13.5	0.6	89.7	4.0	46.3	2.1	8.3	0.4	14.8	0.7
	29	13.6	1.9	64.7	8.9	36.9	5.1	5.9	0.8	10.3	1.4
	36	12.1	4.1	54.8	18.4	32.8	11.0	7.7	2.6	9.8	3.3
	45	11.4	4.4	46.1	17.7	30.6	11.7	7.4	2.8	10.3	3.9
	50	10.4	3.9	43.1	16.1	30.2	11.3	7.8	2.9	9.7	3.6

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