PATTERNS OF PARTITIONING AND REMOBILIZATION OF NON-STRUCTURAL CARBOHYDRATES IN COMMON BEAN AND OTHER SELECTED GRAIN LEGUMES

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ABSTRACT

PATTERNS OF PARTITIONING AND REMOBILIZATION OF NON-STRUCTURAL CARBOHYDRATES IN COMMON BEAN AND OTHER SELECTED GRAIN LEGUMES

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Levels of non-structural carbohydrates (NSC) were examined in root, stem, leaf beans (Phaseolus vulgaris L.) and other selected grain legumes. Samples were taken weekly from 50% flowering until physiological maturity. IKI solution was used to monitor the amounts of starch and a hand refractometer served to determine concentrations of soluble solids (mostly sugars).

Genotypic and environmental differences in partitioning of NSC between plant tissues were observed in all entries except in Vicia faba L.

Analysis of source-sink relationships indicated that: (a) flowers of grain legumes studied constitute a weak sink for assimilates, and (b) high seed growth rates were correlated with important decreases in levels of NSC. High yields were associated with more tissues being involved in remobilization. In dry beans, soluble solids were preferentially remobilized as compared to starch.

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INTRODUCTION

Photosynthesis or "carbon assimilation" is commonly defined as the manufacture of simple carbohydrate (sugar) from carbon dioxide and water by chloroplasts of green plants in the presence of light. With respect to this process, the growing plant consists anatomically of the assimilatory surface of leaves, conducting pathways, i.e., the phloem in which assimilates are transported, and storage sites which are parenchymatous cells in specialized organs such as tubers, roots, fruits, seeds, internodes, and so forth. As plant growth proceeds, such organs become repositories for organic compounds derived from photosynthesis. In many storage sites the entering sugar is converted to starch.

Adams et al (1978) reported undetectable to large levels of starch in roots and stems of twenty-three dry bean cultivars. Amounts of starch varied with the three developmental stages (first flowering, mid-pod filling, and physiological maturity) at which samples were taken.

One may question the role of large amounts of non-structural carbohydrates in non-economic vegetative tissues of a grain crop such as dry beans. It would

appear more reasonable that such carbohydrates should be diverted to seed production.

If, in fact, the sink was large enough to accept carbon assimilates their presence in roots and stems would rather constitute one of the yield limiting factors, and therefore the opportunity of diverting them to the economic part of the plant should be examined.

Donald suggested (1968) that the plant breeder should take the initiative in identifying morphological and physiological characteristics that would lead to achieving spectacular yields. In other words, analysis of the source-sink relationship is also pertinent in common beans and requires that the relation existing between these stored non-structural carbohydrates (NSC) and seed production be investigated.

The study herein reported was intended to monitor the content of non-structural carbohydrates in dry beans and other selected grain legumes during reproductive development. More explicitly, the study is aimed at identification of characteristic partitioning patterns of starch and soluble solids (mostly sugars) among genotypes of common beans (Phaseolus vulgaris L.), soybeans (Glycine max (L.) Merr.) cowpeas (Vigna unguiculata Walp.), some Asian beans (Vigna spp.) and a broad bean (Vicia faba L.).

The study was carried out to answer the following major questions:

1. Do differences in carbohydrate partitioning exist in different tissues, i.e., roots, stems, petioles and pod walls of each genotype?
2. Is there any difference in carbohydrate partitioning between species and between cultivars within species?
3. How does the change of these non-structural carbohydrates relate to seed production?

LITERATURE REVIEW

The seed consists of three structurally different tissues: the seed coat (2N), the embryo (2N) that comes from the embryonic tissue, and the endosperm (3N). In dry beans the liquid endosperm disappears at about two weeks after anthesis (Hsu, 1977). These three structural entities, together with the maternal plant, the environment, and their complex interactions regulate seed size. Hsu (1979) used two dry bean cultivars of contrasting seed size, a small and a large, to analyze seed development in Phaseolus vulgaris L. The pod and seed length, the weight and the volume of the seed were size variables. It was found that both cultivars yielded mature seeds after a period of seed development of about 36 days, and Hsu (1979) concluded that their differences in seed size was accounted for by their growth rates and not the duration of development. At the cellular level, an increase of about seven-fold in the number of cotyledon cells per seed of the cultivar Black Valentine bush beans can be calculated from Loewenberg's data (1955) between twelve and twenty days after flowering. Loewenberg (1955) reported that cell division in the cotyledons had ceased

three weeks after flowering and cells achieved their maximal growth rates twenty-four days after flowering, the same period at which the seeds also achieved their maximal growth rates.

Both investigators noted that although both embryo and seed coat contributed significantly to final seed size, cotyledons were the most determinant organs at nearly all stages of seed development.

Two distinct phases of seed development may be inferred from these studies, the first being the formation of the basic cellular structure completed half way through the period of seed development (Hsu, 1979), and the second, filling of seed with storage materials. Furthermore, Egli et al (1978) designed experiments to investigate the relationship between final seed size and the rate of seed growth in five soybean cultivars of varying seed sizes. The large-sized seed was reported to have the highest growth rate (7.96 mg seed^{-1} day $^{-1}$) whereas the smallest-sized seed had the lowest rate (3.64 mg seed^{-1} day^{-1}). The other cultivars occupied intermediate positions between these two values.

Seed development depends upon photosynthesis and the import of organic compounds from the leaves or storage areas. Relative to photosynthesis, ribulose -1-5-bisphosphate (RuBP) carboxylase was shown to be the key

enzyme in the CO_2-assimilation process of beans (Wareing et al, 1968). It is the principal component of "Fraction I" protein of the leaves. Fraction I protein appears synonymous with RuBP carboxylase (Kawasaki and Wildman, 1970). The dehydrogenation of malate is well-established as one of the energy yielding steps in the Krebs cycle, i.e., dark respiration (Salisbury and Ross, 1978). Jackson and Volk (1970) produced evidence that glycolate oxidase is operative in the production of CO_2 released in photorespiration. The three enzymes named or referred to above respectively characterize photosynthesis, respiration, and photorespiration of plants.

The transport of compounds, however, requires energy. The energy is provided or created through respiration. The dry weight of crops is considered as the algebraic sum of the assimilates produced by photosynthesis and lost by respiration. Thus, yield = photosynthesis - respiration. Ishizuka (1969) suggested that high yield may be achieved by increasing the photosynthetic efficiency and maintaining respiration as low as possible. However, since respiration provides energy and carbon compounds that are utilized in many biosynthetic pathways that occur in plant cells, a right balance between photosynthesis and respiration should be found for optimum yield.

Gaastra (1963) suggested that, at light saturation, photosynthetic rate is determined primarily by physical

resistance to CO_2 diffusion in mesophyll tissue of the leaf. The mesophyll resistance (r_m) is the sum of the biophysical and biochemical resistances to CO_2 movement between the mesophyll cell wall and the site of carboxylation in the chloroplast (Prioul et al, 1975). Wareing et al (1968) noted high levels of RuBP carboxylase activity per unit leaf area in the leaves of "Canadian Wonder" bean plants three days after defoliation. They were also able to demonstrate an increase in photosynthetic rate at saturating light intensities after spraying with hormones such as indole-3-acetic acid, gibberellic acid, and cytokinin.

Their studies led to the conclusion that partial defoliation leads to the increase of photosynthetic rates due to increased levels of carboxylating enzymes. Wareing et al (1968) implied that under normal field conditions photosynthetic rates are limited by levels of carboxylating enzymes and not only by physical resistance to carbon dioxide exchange.

Peet et al (1977) found photosynthetic rates during pod set in dry beans to be significantly correlated with RuBP carboxylase activity; both photosynthetic rates and RuBP carboxylase activity were significantly correlated with yields. Correlations of malate dehydrogenase activity with seed yield and harvest index, and of glycolate

oxidase activity with biological yield were also observed (Peet et al, 1977). On the other hand, Dornhoff and Shibles (1970) measured leaf net CO_2 exchange of twenty varieties of soybeans and found that net photosynthesis of most varieties began to increase at the beginning of seed filling.

Thus, while the relationship between photosynthetic rate and yield appear to be a function of developmental stage, high yields are not necessarily associated with high photosynthetic rates which, for instance, may result from a greater demand for assimilate by higher yielding varieties (Peet et al, 1977). Tanaka and Fujita (1979) concluded that in bean varieties, whether determinate or indeterminate, the photosynthetic rate per unit leaf area increases with the growth of a leaf, reaches a maximum when the area of the leaf reaches its maximum, maintains the high rate for some time, and then decreases with age due to accumulation of carbohydrates or a slower removal of photosynthates from the leaf by translocation (Liu et al, 1973) or due to translocation of nitrogen from the leaf (Tanaka and Fujita, 1979). For beans, Tanaka and Fujita (1979) noted a maximum photosynthetic rate of about 40 mg CO_2 dm^{-2} hr^{-1} which they consider to be in the same range as that of C-3 plants such as rice, but lower than that of C-4 plants such as corn.

Crookston et al (1974) reported that the bean pod contributes photosynthetically to its own yield. Their measurements of the CO_2 - fixing capacity of the red kidney dry bean "Redkote" showed that the pod had 40 percent as much RuPB carboxylase activities per unit area as did the leaf. Over 700 percent as much malate dehydrogenase activity and a substantial glycolase oxydase activity were also recorded per unit area as the leaf. The activity of these two enzymes indicates a high respiratory potential per unit area as compared to the leaf. Crookston and colleagues (1974) also counted 25 percent as many stomata per unit area of the lower surface of the leaf but some stomata of the pod were found to be partially or completely obstructed. Furthermore, Tanaka and Fujita (1979) recognize the photosynthetic ability of pod walls but consider that the rate is generally less than the respiratory rate except at very early stages. Tanaka and Fujita (1979) ruled out the possibility that pods can continue growth on their own photosynthetic products.

Translocation (transport) of photosynthate involves three aspects: those affecting assimilate supply (source of assimilate), the polar transfer of assimilate through the phloem, and those concerned with the storage capacity of assimilate (sink). A sink exists wherever in the plant the products of photosynthesis are utilized.

Neals and Incoll (1968) have summarized factors that may influence the leaf net photosynthesis rate. Their paper, in fact, revolves around the idea that the rate of translocation from the leaf is controlled by the demand for assimilates. Thus, one consequence is that the rate of growth (or demand for assimilates) may control the rate of photosynthesis of a leaf surface. The papers they reviewed and later works (Hanson and Yeh, 1979; Coggeshall and Hodges, 1980) do not show any unequivocal experimental evidence that the accumulation of assimilates in a leaf causes a decrease in leaf assimilation. All kinds of manipulations used by investigators: manipulation of the source of assimilate, manipulation of translocation from source to sink (e.g., by ringing, barking, or petiole chilling) and manipulation of the sink to which assimilates move do, indeed, influence the leaf assimilation rates and leaf carbohydrate content. However, this is correlational evidence and not positive proof of causal relations between the assimilation rate and the concentration of carbohydrate content in the leaf.

Most plants have a common pattern of assimilate distribution (Wardlaw, 1967). The lower leaves serve as main source of assimilates for the roots, whereas the upper ones feed the shoot apex. Leaves in intermediate

position may supply assimilates in either or both directions. This pattern has been substantiated in field beans by Tanaka and Fujita (1979) and Waters et al (1980). A field bean is considered to be composed of nutritional units (Adams, 1967; Tanaka and Fujita, 1979). These source-sink units are composed of a leaf, an internode, a raceme and/or a branch. When actively growing, grains within pods on a raceme of a unit receive photosynthates mostly from the leaf within the nutritional unit (Tanaka and Fujita, 1979).

Physiologically, the nutritional unit constitutes at the same time the source of assimilates, a pathway through which the assimilates move, and utilization or storage sites. Hartt and Kortschak (1964) noted that the translocation of ^{14}C-photosynthate takes place in detached sugar cane blades. They observed that the translocation of photosynthate does not require a sink, but the amount translocated is greatly increased by supplying one. Even though the movement of leaf assimilates away from the site of assimilation is greatly enhanced and given direction by growing tissues and storage organs, tissues do differ in their demand for assimilates. The mechanism that accounts for these differences is referred to variously as the sink capacity, sink strength, or sink size. In grapes, Hale and Wever (1972) refer to flowers as a

weak sink and to fruits as a strong sink. Yoshida (1972) suggested that the movement of assimilates may be regulated by proximity and the size of the sink. The importance of sink size with regard to translocation was noted in soybean (Kenny et al, 1980) and in wheat (Bingham, 1969).

Many compounds such as different sugars and their derivatives, nitrogenous compounds and even steroids are known to be translocated (Wardlaw, 1967; Beevers, 1969) but by far the most important and general constituent is the disaccharide sucrose (Kursanov, 1963; Hartt and Kortschak, 1964; Sacher, 1966; Hanson and Yeh, 1972; Galsziou, 1961). Translocation occurs in the sieve tubes of the phloem. Under experimental conditions blades of sugar cane (Sacher et al, 1963; Hartt and Kortschak, 1964), and bean pod tissue (Sacher, 1966) continue translocation against the gradient in sucrose which implies the existence of a regulating factor other than continued photosynthesis of sucrose and the expenditure of cellular energy (Beevers, 1969). Hartt and Kortschak (1964) postulated that the translocation of photosynthate in sugar cane depends upon the strong basipetal polarity within the phloem of the blade. The mechanism of sugar accumulation against concentration gradients seems to be not clearly understood. Beevers (1969) believes that at the terminus

of a transport pathway exists some finishing reaction which lowers the concentration of the moving photosynthate under the concentration of 0.2 M sucrose. When assimilates move out of phloem the first reaction seems to be the hydrolysis of sucrose by invertase (Sacher, 1966), but in castor bean sucrose is absorbed intact (Kriedman and Beevers, 1966).

Beevers (1969) discussed the biosynthesis of starch. There is much indication that when provided as uridine diphosphate-glucose or adenosine diphosphate-glucose units of glucose are added to pre-existing starch or smaller molecules by starch synthetases. Starch may also be synthesized directly from sucrose.

Duncan et al (1978) define partitioning as the division of daily assimilate between reproductive and vegetative plant parts. The partitioning of assimilate appears to be a function of sink capacity and proximity (Yoshida, 1972; Bingham, 1969; Kinny et al, 1980). Of ^{14}C fed to the leaf at node 8 of a bean plant by Waters et al (1980), 80 percent was found in the middle and upper stem sections at flowering, but over 85 percent moved into the pod during pod-fill. The radioactivity from node 4 translocated mostly to the roots during both flowering and pod-fill. Besides, they noted that nodules sequestered the radioactivity of the lower stem.

Hume and Campbell (1972) reported that soluble solids accumulated in corn stalks after anthesis declined rapidly during the grain filling period and the most part was found in internodes below the ear. They also indicated that the prevention of pollination and grain development caused the soluble solids to accumulate in stalks until the end of the growing season.

The use of $^{14}CO_2$ has contributed a great deal to the identification of the direct source of grain carbohydrate. An experiment, involving labelling with $^{14}CO_2$, by Kenny et al (1980) showed that the size of available sink was the important determinant of translocation rate in six soybean genotypes, Hume and Crisswell (1973) fed soybean plants with $^{14}CO_2$ at different stages of development. Plants that have been labelled later during ontogeny showed decreasing amounts of ^{14}C and more ^{14}C accumulated in seeds by the maturity period. Furthermore, they noted a little accumulation in roots and nodules after seed development had begun.

It is clear from these reports that an active mobilization of metabolites from vegetative parts of the plants to the seed takes place during grain-filling.

Depending on variety, bean roots and stems accumulate undetectable to abundant amounts of starch. This

accumulation is generally followed by a decline during the seed fill period (Adams et al, 1978). Waters et al (1980) reported a decline in the concentration of starch in the middle and upper sections of bean stems where most pods are concentrated, whereas the concentration raised in the lower sections of stems with few pods as pod fill proceeded.

Waters et al (1980) suggested that the accumulation of starch in stems during pod-filling may indicate that beans are inefficient in their use of photosynthate or provide inadequate sink capacity for the source present. This seems quite plausible since McAllister and Krober (1958) found that 80 percent depodding increased sugar and starch concentrations in leaves and starch levels in stems of soybean.

Experiments involving depodding are throwing some light on mobilization and translocation of previously stored assimilates from other parts into pods. Those by Lawn and Brun (1974) led to the conclusion that the excess of the growth rate of soybean pods over that of the total tops at midpod fill were due to mobilization of material previously stored as non-structural carbohydrate (NSC) in the plant. Ciha and Brun (1978) found that the concentration of NSC in soybean stems, leaflets, and petioles remained fairly constant in control plants, whereas it

increased markedly in depodded plants. That difference was mostly due to starch accumulation.

Tanaka and Fujita (1979) consider the abortion of excessive flowers and pods as a unique characteristic of dry beans to adjust the sink size to the source in order to keep the 1000-grain weight (seed size) relatively stable.

For rice, Yoshida (1972) reported that under normal field conditions, 68 percent of stored carbohydrate was translocated into grain (i.e., 21 percent of the grain carbohydrate), 20 percent was respired during the ripening period, and 12 percent remained in vegetative parts. In addition, the evidence gathered by Yoshida (1972) shows that stored carbohydrates are able to support the grain growth of rice and corn at almost a normal rate at least for some time when photosynthesis is restricted during the ripening period. Furthermore, from references cited by Yoshida (1972), it seems that under heavy nitrogen fertilization the grain carbohydrates derive mostly from photosynthesis after heading, for in these conditions the storage of carbohydrates is reduced.

Donald (1968) stressed the importance of morphological features that could lead to high yields in breeding for crop ideotypes. Although he described only the

morphological requirements that a wheat crop should meet, characteristics that ascribe superiority to certain plants vis-a-vis the others within a species are basically accounted for by physiological differences.

Since the photosynthetic rate is known to vary genotypically, Wareing et al (1968) suggested its use in search of high yields. Although genotypic differences affecting carbon exchange rate (CER) have been reported in dry beans (Peet et al, 1977) and in soybeans (Dornhoff and Shibles, 1970; Dreger et al, 1969), the work by Curtis et al, (1967) does not seem to confirm the association of photosynthesis rate and high yielding ability in soybean. Furthermore, Hanson and Yeh (1979) did not find genotypic differences for maintaining CER with assimilate accumulation in leaves of six soybean genotypes. One can then wonder whether there is conclusive evidence that increase in yield potential of a variety is associated with increase in photosynthesis rate.

In dry beans, Robitaille, 1978, and Wien et al, 1973, and in soybeans, Hanway and Weber, 1971, found similar dry matter accumulation patterns between determinate and indeterminate cultivars. Thus, yield seems not to be influenced by the degree of indeterminacy in these legumes. Therefore, the degree of indeterminacy should be taken into account only upon consideration of factors

such as maturity date and specialized cultural practices, e.g., spacing, mechanical harvest, or crop association (Hanway and Weber, 1971). On the other hand, Westerman and Crothers (1977) found that seed yield per unit area was relatively constant over a wide range of plant populations for the indeterminate bean cultivars, but decreased at the smaller plant populations for the determinate cultivars. They postulated that the determinate bean cultivars have the greatest potential for seed yield increases in high plant populations.

Shibles and Weber (1966) suggested that one possible approach to maximize soybean yields would be to select for a high harvest index. Harvest index is the ratio of the grain yield (economic yield) to the total yield of plant material (biological yield)(Donald, 1962). Wilcox (1974) indicated that selections of genotypes that would maintain a high harvest index under high populations should help to maximize yields. In field beans, Wallace and Munger (1966) observed varietal differences with regard to harvest index. Yet Buzzel and Buttery (1977) did not record any change in soybean harvest index in response to increasing population within hills. They also noted that harvest index was negatively associated with yield. Hence, harvest index seems to be of little value as an indicator of yielding ability in soybean. If, however, a high bio-yield can be maintained while selection

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is practiced for harvest index then it would be worthwhile. Donald and Hamblin (1976) reported instances in which harvest index had real predictive value.

Wallace and Munger (1965, 1966) indicated that NAR, LAR, AND RGR are genetically controlled physiological factors, but their contribution to both biological and economic yield was masked by various environmental influences and tendency of inverse correlations existing among yield components and among physiological factors themselves. They concluded that the determination of bases for genetic differences in economic yield is extremely difficult and suggested that all genetic, physiological, and environmental factors capable of influencing seed production should be integrated in the breeding for high yields. Where a source limitation prevails, Tollenaar and Daynard (1978) suggested that, in corn, grain yield can be improved by increasing leaf area per plant, or by extending leaf area duration after flowering. Yet Jones et al (1979) pointed out that usual physiological variables such as NAR, LAI, and so forth are laborious and difficult for screening large populations. Therefore, plant breeders currently have found the study of grain filling rates and duration an easier way to measure physiological performance.

In non-competitive populations correlations between components of yield capacity are practically nil. Adams

(1968) emphasized that such correlations are developmental rather than genetical. Thus, yield components are predominantly genetically independent and their inverse variations will tend toward stabilization of yields under a given set of conditions. Furthermore, Williams and Gilbert (1960) stressed the irrelevancy of speaking about genes for complex characters such as crop yield. Their data showed that variation in tomato yields resulted from gene systems governing individual yield components (i.e., number of fruit per plant and fruit weight).

Daynard et al (1971) defined the yield of a grain crop as the product of the average rate of grain production (dry weight increment per unit ground area per unit time) and duration of grain formation (units of time). Both the duration of vegetative period and grain-filling period are important to achieving high yield in wheat (Bingham, 1969). Rasmusson et al (1979) suggested that the modification by selection of vegetative period and grain filling period should be used in breeding crops showing heritable differences. In rice, Jones et al (1979) indicated that the grain-filling rate was more important than its duration. In wheat, however, Rasmusson et al (1979) pointed out that it is more straightforward to modify by selection the duration of the vegetative period than it is for the grain-filling period. Egli et al (1978) concluded that the rate of seed growth is

partially determined by the genetic make-up of the soybean seed. They also observed a direct relationship between the seed growth rate and seed size.

Duncan et al (1978) reported that yield variation in five Florida peanut cultivars was explained by differences in three physiological processes, namely, the partitioning ratio of assimilate between vegetative and reproductive parts, the length of the filling period, and the rate of fruit establishment. Of these, the partitioning ratio of assimilate was found to have the greatest effect on fruit yield.

MATERIALS AND METHODS

Three experiments have been carried out, two in 1978 and one in 1979. Ten grain legume entries (Table 1) were planted in Saginaw Valley Bean and Sugar Beet Research Farm on May 25, 1978, and 14 entries on June 23. At the Bean and Sugar Beet Farm water stress occurred during the last week of July and the first two weeks of August 1978. The 1979 experiment consisted of 12 entries planted on June 14 at the Michigan State University (MSU) Crops Research Farm in East Lansing, Michigan. The list of all the entries is given in Table 1. These experiments will be referred to respectively as A78, B78, and 79.

In all three experiments, rows were 5 meters long, 50 centimeters apart, and seeds were sown at 7.5 centimeters apart within rows. Individual plots made up of 4 rows were arranged in a randomized complete block design with four replications. Each entry was sampled on a weekly basis, but due to disturbing circumstances the 7 day interval was sometimes longer or shorter. Four randomly selected plants were uprooted from each plot from 50 percent flowering until physiological maturity. Fifty percent flowering was the time when about 50 percent of

TABLE 1.--List of entries and their growth types

Entry Name and Type	Growth Type	CIAT Type	Experiment		
			A78	B78	79
A. Common beans (*Phaseolus vulgaris* L.)					
Navy					
1. Seafarer	det.	I	+	+	+
2. California Small White	indet.	III	+	+	+
3. Nep-2	det.	II	+	+	+
Kidney					
4. Redkloud	det.	I	+	+	+
5. Redkote	det.	I	+	+	+
Tropical black					
6. Black Turtle Soup (BTS)	indet.	II	+	+	+
Swedish Brown					
7. Swedish Brown	det.	I		+	+
B. Soybeans (*Glycine max* (L.) Merr.)					
8. Evans soybean	indet.		+	+	+
9. Beeson soybean	indet.		+	+	+
C. Asian beans					
10. *Vigna radiata*	det.			+	
11. *Vigna angularis* type I (Adzuki)	det.		+	+	+
12. *Vigna angularis* type II (Adzuki)	indet.		+		
D. Cowpeas (*Vigna unguiculata* Walp.)					
13. Cowpea F-51	indet.			+	+
14. Cowpea 10R-61	indet.			+	
15. Cowpea Pink Eye Purple Hull	indet.				+
E. Fava beans (*Vicia faba* L.)					
16. *Vicia faba*	det.			+	

Note: det., indet.: determinate, indeterminate types of growth.
+: planted

the plants had at least one open flower and physiological maturity was considered reached when about 95 percent of the pods were tan to brown for dry beans, soybeans, and Vigna angularis type I and blackish for cowpeas, Vigna radiata and Vicia faba. Vigna angularis strain II was damaged by frost before maturity.

For each of the four plants, amounts of starch were monitored by means of an IKI solution made by mixing 1 gm potassium iodide, 1 gm iodine and 100 CC of distilled water (Sass, 1958). A visual scale of 8 classes from 1.0, 1.5, 2.0 to 5 was used (Adams et al, 1978), with a score of 1 indicating no detectable starch and 5 indicating a dark blue color of the entire slanted cross section of the organ (root, stem, leaf petiole, and pod wall). Roots were sectioned in their middle and stems at the V_1-V_2 internodes, i.e., internodes between the first and the second trifoliate leaves (Lebaron, 1974; Fehr and Caviness, 1980). Petioles were picked from branches at the V_2 nodes and only one petiole and one pod per plant were assayed. The same material was used for soluble solids quantification.

Total soluble solids (mostly sugars) were determined from the sap squeezed out of the above-named plant sections by using a pair of modified pliers. One or two drops of sap were dropped on the window of the temperature

compensated Hand Refractometer model 10431 of the American Optical Corporation, having an inner scale which reads from 0 to 50 degrees Brix.

The modified pliers used were found to be suited only to extract sap from roots, stems, petioles, and relatively young pod walls. They were not successful in extracting sap from thin and fiberous soybean, cowpea, and Asian bean pod walls. Soybean pod walls crumbled under pressure and released no juice. Thus, the soluble solids data for the pod wall tissue were not available for soybean and most of the data are insufficient for statistical analysis for cowpeas, early maturing dry bean cultivars, and other non-dry bean entries.

At each sampling date the dry weights of roots, stems, and leaf petioles, pod walls and seeds (separately), of the four plants (plot sample), were taken, after being heated in forced-air dryers for at least 48 hours at 65° Centigrade. At harvest the economic yield (seed weight) for 1 m^2 from a non-sampled area of inner rows was measured per plot and the moisture content was determined. Final seed yields reported herein are standardized at 16 percent moisture.

With regard to data analysis, tissue means across all developmental stages have been compared between and within entries using the Statistical Package for the Social

Science (SPSS) (Nie et al, 1970). In order to isolate interactions the Michigan State University Stat 4 package was used for analysis of variance for NSC and seed yields. To visualize trends in changes of non-structural carbohydrates, we needed to plot the amounts of starch (IKI scores) and soluble solids (refractometer readings) as functions of days of reproductive period (the first observation date was referred to as day 1). About 250 polynomial functions were derived and only 78 that satisfied the criterion $R^2 \geq 0.50$ and four others were reported. For the sake of easy interpretation, however, there was no interest in polynomial functions beyond the fourth order. Data were first analyzed on the Hewlett Packard System 984B Desktop Computer to generate polynomial models of the form

$$Y = \beta o + \beta_1 X + \ldots + \beta_4 X^4$$

where y represents the amount of starch or soluble solids,

β_o is the y-intercept, and

$\beta_{1,2,3,4}$ are the constants respectively for the first order, the quadratic, the cubic, and the quartic terms .

The selected polynomial is the one which could not be significantly improved at the 0.05 level of significance by fitting the next highest order. Subsequently, using

the MSU CDC 750 computer and a Fortran program the equations were used to generate points for curves which were plotted together by using the SPSS plotting routine, and the observed values were manually added to the graphs from compute scatter diagrams.

RESULTS

Description of Partitioning Patterns In Non-Structural Carbohydrates

Comparisons Between Tissues Within Entries

Comparisons among tissues within varieties, with respect to their mean starch scores and soluble solids mean readings for various tissues, computed over the entire period of reproductive growth, are given in Tables 2 and 3. The Tukey Honestly Significant Difference (HSD) at the 0.05 level of probability was used for these comparisons. Since our data are naturally unbalanced, the Tukey HSD is expected to be approximate. However, the procedure yielded almost the same results as LSD at 0.01. LSD is known to be exact for unequal groups sizes (Nie et al., 1975).

Starch Scores.--From data in Table 2 for Experiment A78, it appears that roots and stems of most dry beans and Vigna angularis II showed significantly greater levels of starch than leaf petioles or pod walls. Roots of Vigna angularis Type I had significantly higher starch scores than the other tissues. Higher starch scores were observed for leaf petioles of Beeson soybean than for the other

tissues whereas leaf petioles, stems, and roots of Evans soybean showed equivalent levels of starch.

One may infer from this experiment that grain legumes, especially common beans but not soybeans, tend to store relatively higher amounts of starch in roots and stems than in leaf petioles and pod walls. Furthermore, dry beans tend to show equivalent amounts of starch in roots and stems and the amounts of starch in leaf petioles tend to be similar to those found in pod walls. Although the soybeans have barely detectable amounts of starch in roots and stems, leaf petioles seem to accumulate relatively higher levels of this carbohydrate.

In Experiment B78 the dry bean cultivars California Small White and Swedish Brown, the cowpeas F-51 and 10R-61, a broad bean and Vigna radiata were included in this experiment. No seeds were available for the late maturing Vigna angularis Type II. Since Cowpea 10R-61 and V. radiata set only few pods the IKI mean scores for the pod wall tissue were excluded from statistical analysis. The broad bean's petiole is indistinguishable from the leaf and therefore its mean score is lacking.

Roots and stems had equivalent mean starch scores (means across all stages of reproductive growth), except for Nep-2 whose mean starch score for root tissue was higher than that of stem tissue. On the other hand, leaf

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The observation made in the preceding experiment (A78) that roots and stems store greater amounts of starch than in leaf petioles or pod walls and that the latter organs store similar levels, also prevails in these data.

In Experiment 79 from the two cowpeas planted in B78, only cowpea F-51 was retained and cowpea Pink Eye Purple Hull was added. Neither Vigna angularis Type I used in A78 nor Vicia faba planted in B78 were part of the material planted in Experiment 79.

Again, roots and stems tended to show similar levels of starch, but the data showed roots of the dry beans California Small White and Nep-2 having higher levels of starch than the stem tissue. In addition, stems of cowpea F-51 and Cowpea Pink Eye had higher mean starch scores than for roots. The pod wall tissue showed equivalent levels of starch as either root or stem, except for Redkloud and Swedish Brown in which it had higher starch

scores than the other tissues. Soybean leaf petioles showed higher starch levels than those of other tissues which had similar mean starch scores.

Summary.--The IKI staining technique used to monitor the amounts of starch in roots, stems, petioles, and pod walls together with the Tukey HSD procedure used in the ranking of mean scores allow us to draw some tentative conclusions pertaining to the starch partitioning patterns for each group of legumes studied.

It appears that most dry beans tend to store more starch in roots and stems than in leaf petioles or pod walls. The amounts of starch stored in roots were, however, significantly different from those stored in stems only in a few cases. This exception is exemplified by Nep-2 whose mean starch scores for roots remained significantly higher than those for stems in Experiment A78 and 79. Results of the two experiments conducted at the Bean and Sugar Beet Research Farm show the pattern of equality between starch amounts in leaf petioles and pod walls, whereas those of the MSU Crops Farm experiment show the pod walls of Redkloud, Swedish Brown as having higher levels of starch than the other tissues.

For soybean cultivars, leaf petioles had numerically higher starch scores. In two experiments mean

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Cowpeas tend to have equal amounts of starch in root and stems but either organ may have significantly higher amounts, depending on the environment, as in the case for the stem in Experiment 79.

Vigna radiata and Vicia faba were only used in experiment B78. Starch was undetectable in tissues of Vicia faba. Vigna radiata showed relatively high levels of starch but no variation was found among tissues.

Vigna angularis Type II was only examined in experiment A78. Both roots and stems showed the same levels which were found to be significantly greater than those in leaf petioles. The pod wall showed significantly lower levels than other tissues.

Total Soluble Solids.--In most cases in experiment A78, the leaf petiole tissue had a significantly higher concentration of soluble solids than the other tissues assayed (Table 3). Of 9 cultivars, 6 were found

with significantly higher concentrations of soluble solids in leaf petiole than in root or stem. Mean refractometer readings (means across all stages of reproductive growth) were not statistically different from those of the other tissues only in Redkote and Adzuki beans (Vigna angularis). Besides, the stem tissue tended to have numerically higher concentrations than roots and stems of Nep-2. Those of Evans soybean had significantly higher concentrations of soluble solids than the root.

In experiment B78 also the leaf petiole showed numerically higher concentrations of soluble solids than the root or stem. Significant differences with other tissues were found for leaf petioles of Seafarer, Redkloud, and both soybeans. Although roots and stems tended to show equivalent concentrations of soluble solids, roots of Seafarer and California Small White had higher concentrations than stems. Stems of Evans soybeans had a higher concentration of soluble solids than roots. Roots and leaf petioles of Nep-2 had similar concentrations as did the stems and leaf petioles of Vigna anguluris I.

In experiment 79 pod walls showed higher concentrations of soluble solids than other tissues, except in Redkote and Vigna angularis I in which the amounts of soluble solids were respectively similar to those in stems and in stems and roots. Leaf petioles had similar levels as stems, except in soybeans in which concentrations of

the MSU CDC 750 computer and a Fortran program the equations were used to generate points for curves which were plotted together by using the SPSS plotting routine, and the observed values were manually added to the graphs from compute scatter diagrams.

RESULTS

Description of Partitioning Patterns In Non-Structural Carbohydrates

Comparisons Between Tissues Within Entries

Comparisons among tissues within varieties, with respect to their mean starch scores and soluble solids mean readings for various tissues, computed over the entire period of reproductive growth, are given in Tables 2 and 3. The Tukey Honestly Significant Difference (HSD) at the 0.05 level of probability was used for these comparisons. Since our data are naturally unbalanced, the Tukey HSD is expected to be approximate. However, the procedure yielded almost the same results as LSD at 0.01. LSD is known to be exact for unequal groups sizes (Nie et al., 1975).

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In experiment 79 pod walls showed higher concentrations of soluble solids than other tissues, except in Redkote and Vigna angularis I in which the amounts of soluble solids were respectively similar to those in stems and in stems and roots. Leaf petioles had similar levels as stems, except in soybeans in which concentrations of

soluble solids were higher than those found in stems and roots. The root tissue seemed to have the lowest amounts of soluble solids for all entries.

Summary.--From the Saginaw Valley experiments the leaf petiole emerged as the most important storer of soluble solids in comparison with root and stem tissues. The early season planting (A78) consistently showed numerically higher amounts of soluble solids in stem than in root tissues, whereas this situation was reversed in the B78 planting. In the MSU Crops Farm experiment carried out in Summer 1979, entries showed more soluble solids in pod walls followed by the stem, than the petiole. Root tissues seemed to have the lowest amounts of soluble solids.

As far as soybeans are concerned, the highest concentrations of soluble solids were observed in leaf petioles and the lowest amounts in roots. All tissue means were found to be significantly different in Evans and this situation occurred for Beeson soybean only in the experiment at the MSU Crops Research Farm. At the Bean and Sugar Beet Research Farm, roots and stems of Beeson soybean showed statistically similar amounts of soluble solids.

These results pertaining to soluble solids reflect the complex interactions that may exist between sink demand and environmental variables. Some environmental

factors that influenced plant growth and grain production in both locations will be discussed on page 129.

Comparison Between Entries

Analyses of variance (ANOVA) on data of three stages of reproductive growth (50% flowering, middle of reproductive growth and physiological maturity), across all three experiments, were run for both root and stem IKI scores and refractometer readings. Only the dry bean cultivars Seafarer, Redkloud, Redkote, BTS, and Nep-2 were analyzed. For both root and stem, IKI scores and refractometer values, the interaction term "Stages x Varieties" was statistically highly significant. This interaction is essentially the subject discussed in the next section. The interaction "Varieties x Experiments" was only significant for IKI scores for both root and stem tissues. Data for other tissues caused the design matrices to be singular, and therefore, Stat 4 and the SPSS MANOVA procedure could not process them.

It appears that levels of soluble solids for root and stem in these cultivars were not affected by different planting times and locations.

Table 4 shows the ANOVA for stem IKI scores. Table 5 gives IKI score averages for stem per stage of reproductive growth and per experiment. When they were plotted per stage with IKI scores as a function of average

TABLE 4.--Analysis of variance for stem IKI scores, taken at three stages[1] of reproductive growth, of 5 dry bean cultivars grown in two locations in Michigan: Saginaw, 1978 and East Lansing, 1979

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F Values
Total	178	139.22		
Experiments	2	6.20	3.1	20.8**
Rep. within Exp.	9	0.80	0.09	0.59 ns
Varieties	4	32.64	8.16	36.4**
Var. x Exp.	8	4.22	0.53	3.5**
Rep. x Var. + Rep. x Var. x Exp. = Error 1	36	5.38	0.15	
Stages	2	24.19	12.10	54.1**
Stages x Exp.	4	10.46	2.6	11.7**
Stages x Var.	8	18.18	2.3	10.2**
Stages x Exp. x Var.	16	17.14	1.1	4.8**
Residual Error	89	19.9	0.22	

[1]Stage 1: 50% flowering; stage 2: middle of reproductive period; stage 3: physiological maturity

**Statistically significant at 0.01 level.

ns: Non-significant

TABLE 5.--Stem IKI scores, for three stages of reproductive growth, of 5 dry bean cultivars grown at two locations in Michigan--Saginaw (Exp. A78 and B78), 1978, and East Lansing (Exp. 79), 1979

Variety and Experiment	Stages of Reproductive Growth		
	1	2	3
Seafarer			
A 78	1.3	3.4	3.2
B 78	1.1	2.4	1.2
79	1.0	2.9	1.6
Redkloud			
A78	1.6	1.8	1.6
B78	1.4	1.6	2.6
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Redkote			
A78	3.5	2.9	2.8
B78	2.6	3.4	3.3
79	1.7	3.4	2.9
Black Turtle Soup			
A78	3.6	3.7	1.8
B78	3.1	3.2	1.2
79	1.8	3.3	1.6
Nep-2			
A78	3.2	3.2	2.7
B78	1.6	3.1	2.6
79	1.6	3.1	2.5

Note: Stage 1: 50% flowering; Stage 2: middle of reproductive period; stage 3: physiological maturity.

seed yields (environmental indices) per experiment for all varieties, data of Table 5 did not suggest any clear explanation of the interaction, i.e., Variety x Experiment.

It should be remembered that Experiment A78 and B78 were planted at different times and they faced different moisture stresses (discussed in the next section). It is also to be realized that Experiments A78, B78, and Experiment 79 were planted at different locations and in different years. Taking all these variables into account and genotypic differences, it is not possible to pinpoint variable(s) among these which caused differences in patterns of starch accumulation in root snd stem tissues of the above-named dry bean cultivars.

The mean starch scores and soluble solid means reported respectively in Tables 2 and 3 are the same as given in Tables 6 and 7. In the latter, however, comparisons are made between entries on the basis of individual tissue means. Means are averages across all developmental stages of reproductive growth. Again, means were separated by Tukey's HSD at the probability = 0.05.

With respect to starch accumulation (Table 6) in roots and stems, Tukey's criterion distributed entries into three groups. In order of decreasing magnitude of IKI scores, the groups are cowpeas together with Vigna angularis type II and Vigna radiata, the dry bean group,

and the soybeans together with Vicia faba. Vigna angularis I whose mean scores ranked among dry beans in the Saginaw Valley experiments was found to be the most important starch storer for both root and stem in the MSU Crops Farm experiment.

In general, entries showed lesser amounts of starch in leaf petioles as compared to roots and stems. Not many differences were found between entries for this organ; this is particularly the case for the Saginaw Valley experiment.

Redkote, Nep-2, Swedish Brown, and BTS often appeared as the most important starch storers of the common bean group.

Because so few pods were formed, pod wall means for cowpeas are not reported. Even where available, however, this thin and fiberous tissue did not exhibit much starch, by contact with IKI solution. The dry beans showed greater amounts of starch in pod walls and were found to be significantly different from soybeans.

As far as total soluble solids are concerned (Table 7) the grouping mentioned above for roots and stems holds true. Vigna radiata was found to be the highest of the soluble solids storers in these two organs. For leaf petioles, however, the order is completely reversed. The soybeans were found to have the highest amounts.

They were followed by the group of those other cultivars than the dry beans which appeared to have the lowest amounts of soluble solids in their petioles. The dry bean group had the lowest concentration of soluble solids.

Analysis of Characteristic Patterns of Remobilization of Non-Structural Carbohydrates (NSC) During Reproductive Growth

In this section curves are presented describing changes in non-structural carbohydrates of each entry in all experiments during the period of reproductive growth. Curves of a given genotype, relative to each type of NSC, are plotted together per each experiment. In addition to the information usually provided in graphs, i.e., equations of the curves, R^2 values and number of observed values plotted, the graphs contain average seed growth rates given in terms of grams per 0.0375 m^2 (area occupied by a single plant) per day.

Seafarer

Curves describing certain patterns of remobilization of NSC have been found for Seafarer in all experiments (Figures I.1-7). Figures I.1, 3, 5, 7 show changes in starch (IKI Scores) and Figures I.2, 4, 6 show changes in soluble solids (refractometer readings) in roots, stems, leaf petioles and pod walls from mid-flowering to physiological maturity. Mid-flowering and full bloom were periods

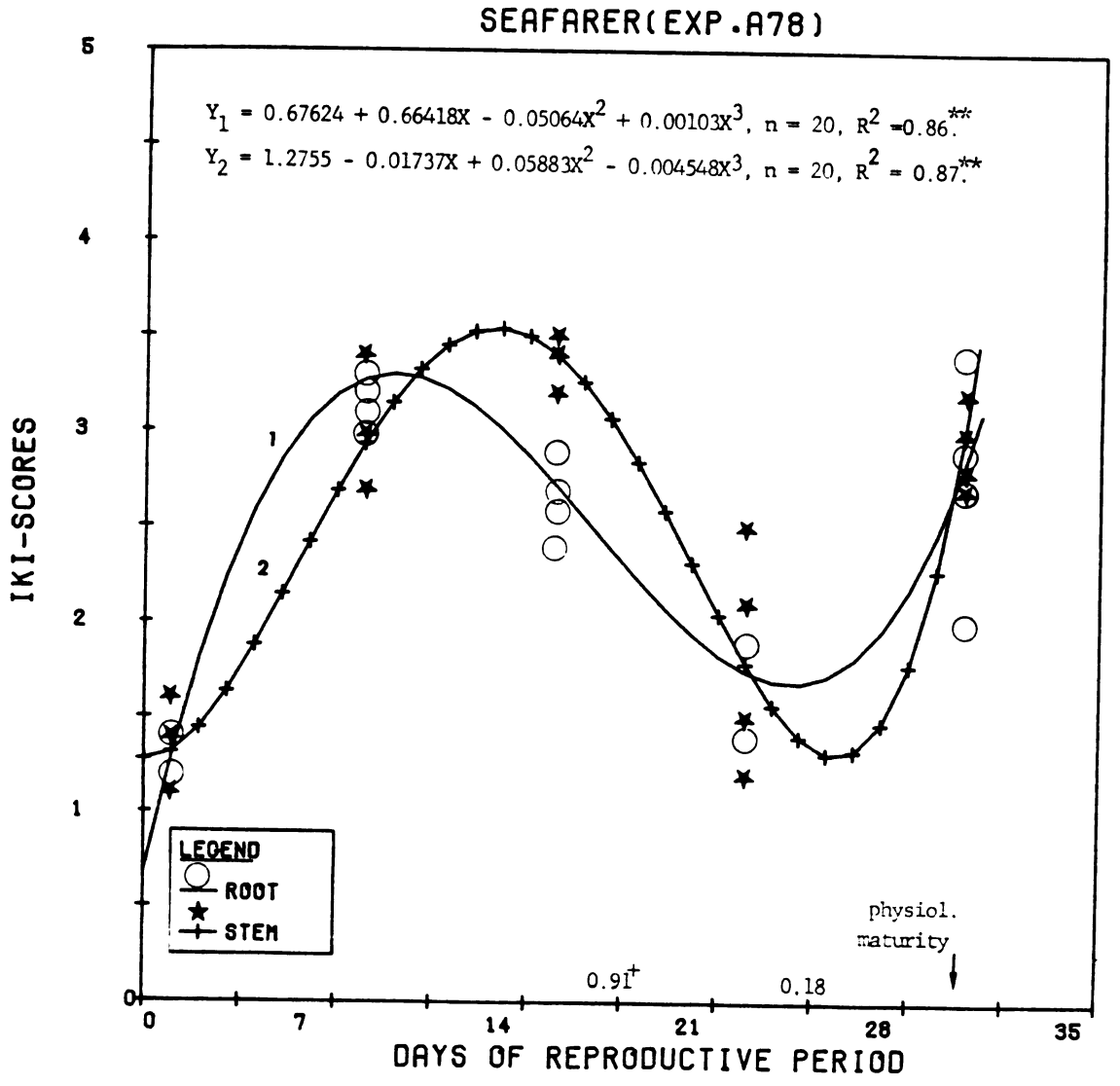

Fig. I.1: Trend of starch (IKI score) accumulation in roots and stems of Seafarer beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

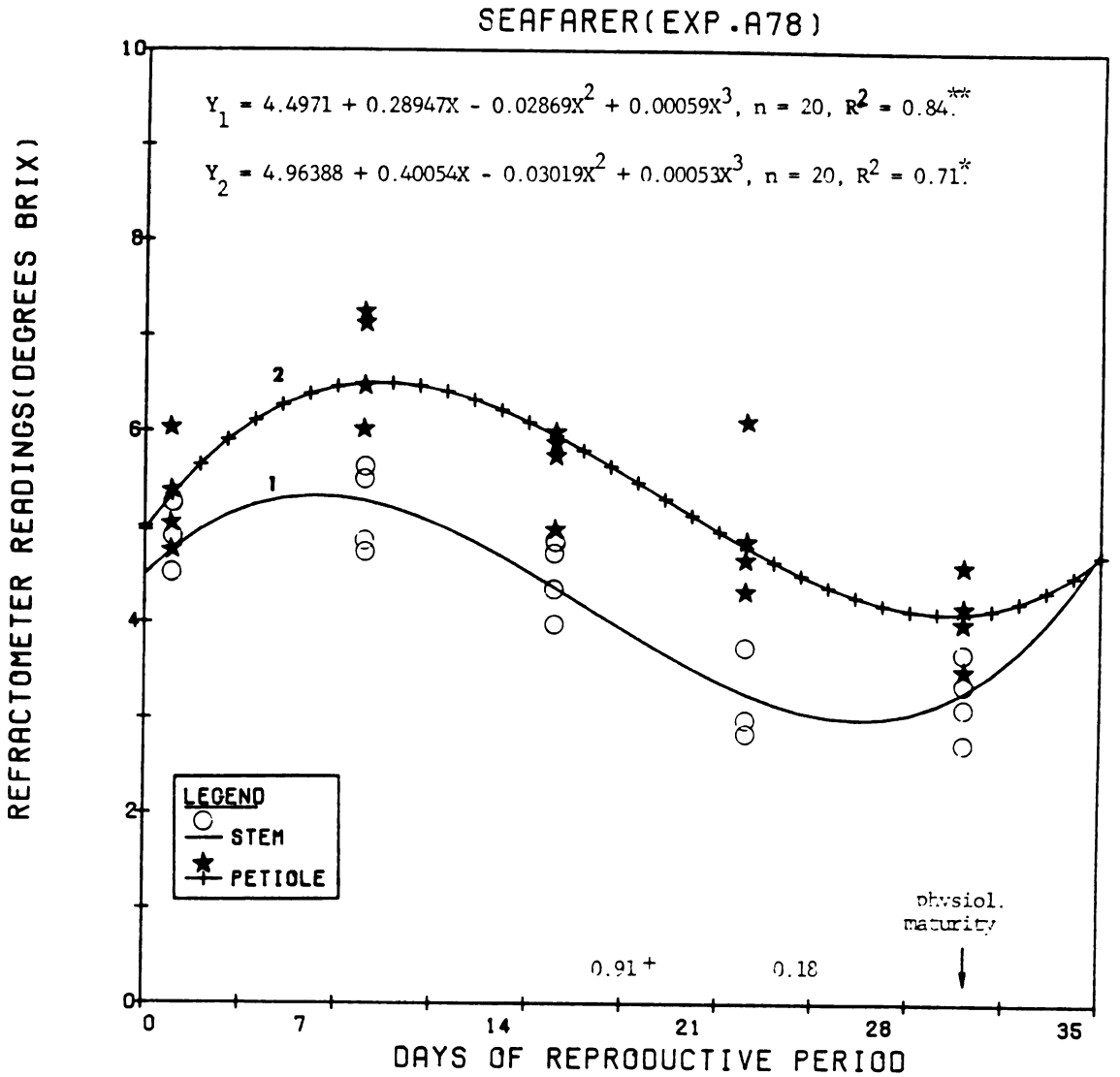

Fig. I.2: Trend of soluble solids (refractometer values) accumulation in stems and leaf petioles of Seafarer beans during reproductive growth, Bean and Beet Farm, Experiment A, 1978.

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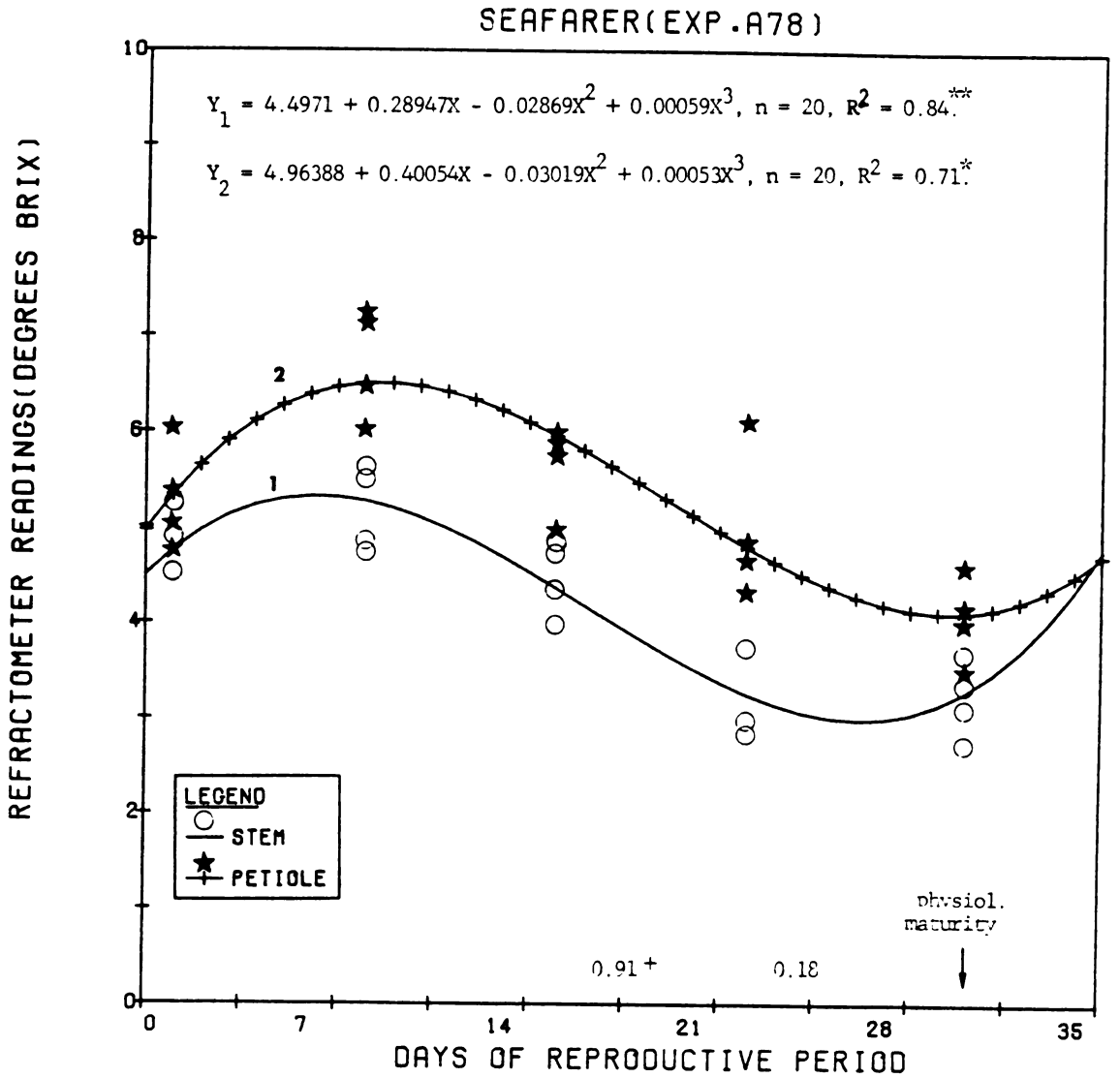

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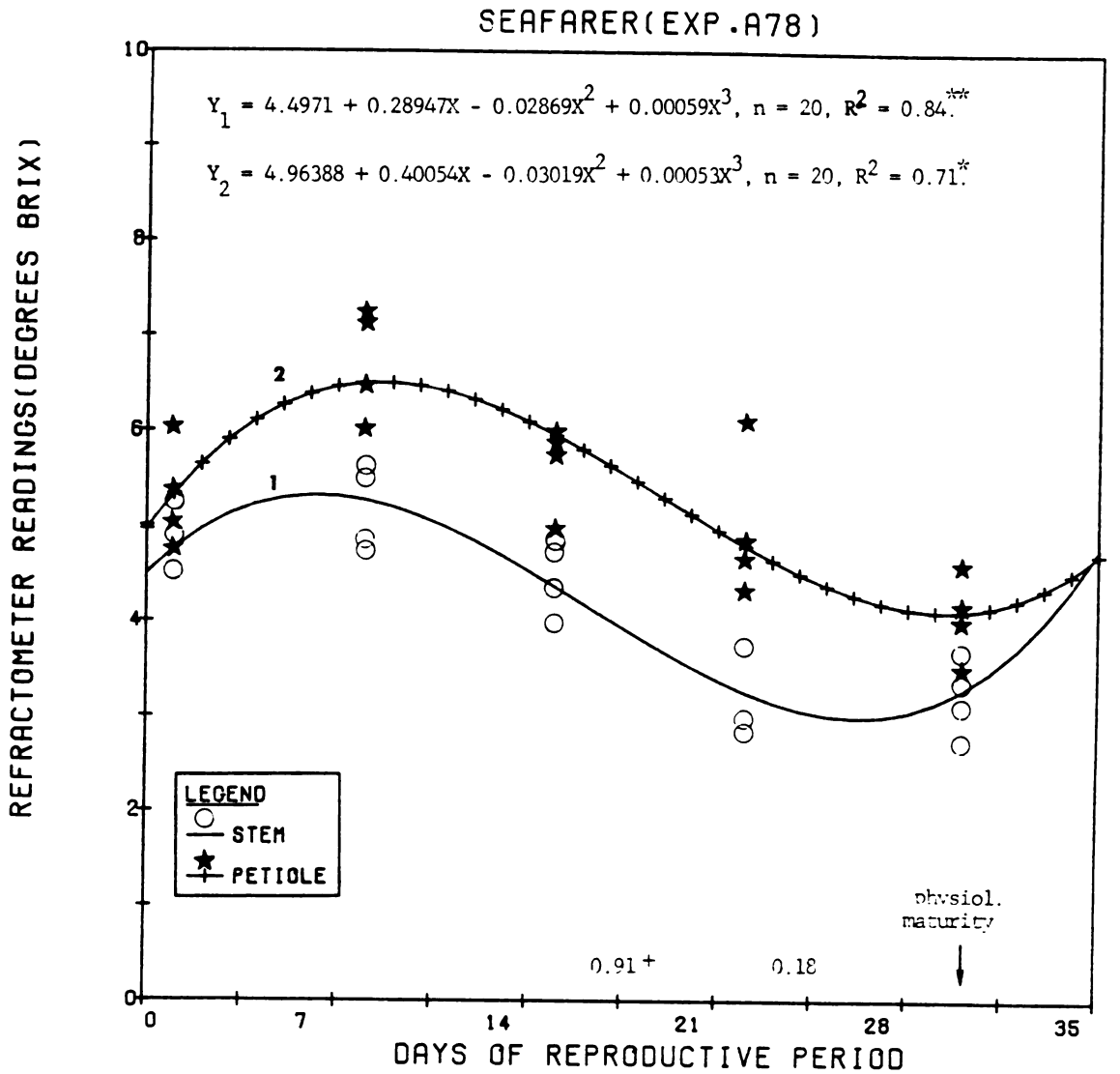

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Redkote, Nep-2, Swedish Brown, and BTS often appeared as the most important starch storers of the common bean group.

Because so few pods were formed, pod wall means for cowpeas are not reported. Even where available, however, this thin and fiberous tissue did not exhibit much starch, by contact with IKI solution. The dry beans showed greater amounts of starch in pod walls and were found to be significantly different from soybeans.

As far as total soluble solids are concerned (Table 7) the grouping mentioned above for roots and stems holds true. Vigna radiata was found to be the highest of the soluble solids storers in these two organs. For leaf petioles, however, the order is completely reversed. The soybeans were found to have the highest amounts.

They were followed by the group of those other cultivars than the dry beans which appeared to have the lowest amounts of soluble solids in their petioles. The dry bean group had the lowest concentration of soluble solids.

Analysis of Characteristic Patterns of Remobilization of Non-Structural Carbohydrates (NSC) During Reproductive Growth

In this section curves are presented describing changes in non-structural carbohydrates of each entry in all experiments during the period of reproductive growth. Curves of a given genotype, relative to each type of NSC, are plotted together per each experiment. In addition to the information usually provided in graphs, i.e., equations of the curves, R^2 values and number of observed values plotted, the graphs contain average seed growth rates given in terms of grams per 0.0375 m^2 (area occupied by a single plant) per day.

Seafarer

Curves describing certain patterns of remobilization of NSC have been found for Seafarer in all experiments (Figures I.1-7). Figures I.1, 3, 5, 7 show changes in starch (IKI Scores) and Figures I.2, 4, 6 show changes in soluble solids (refractometer readings) in roots, stems, leaf petioles and pod walls from mid-flowering to physiological maturity. Mid-flowering and full bloom were periods

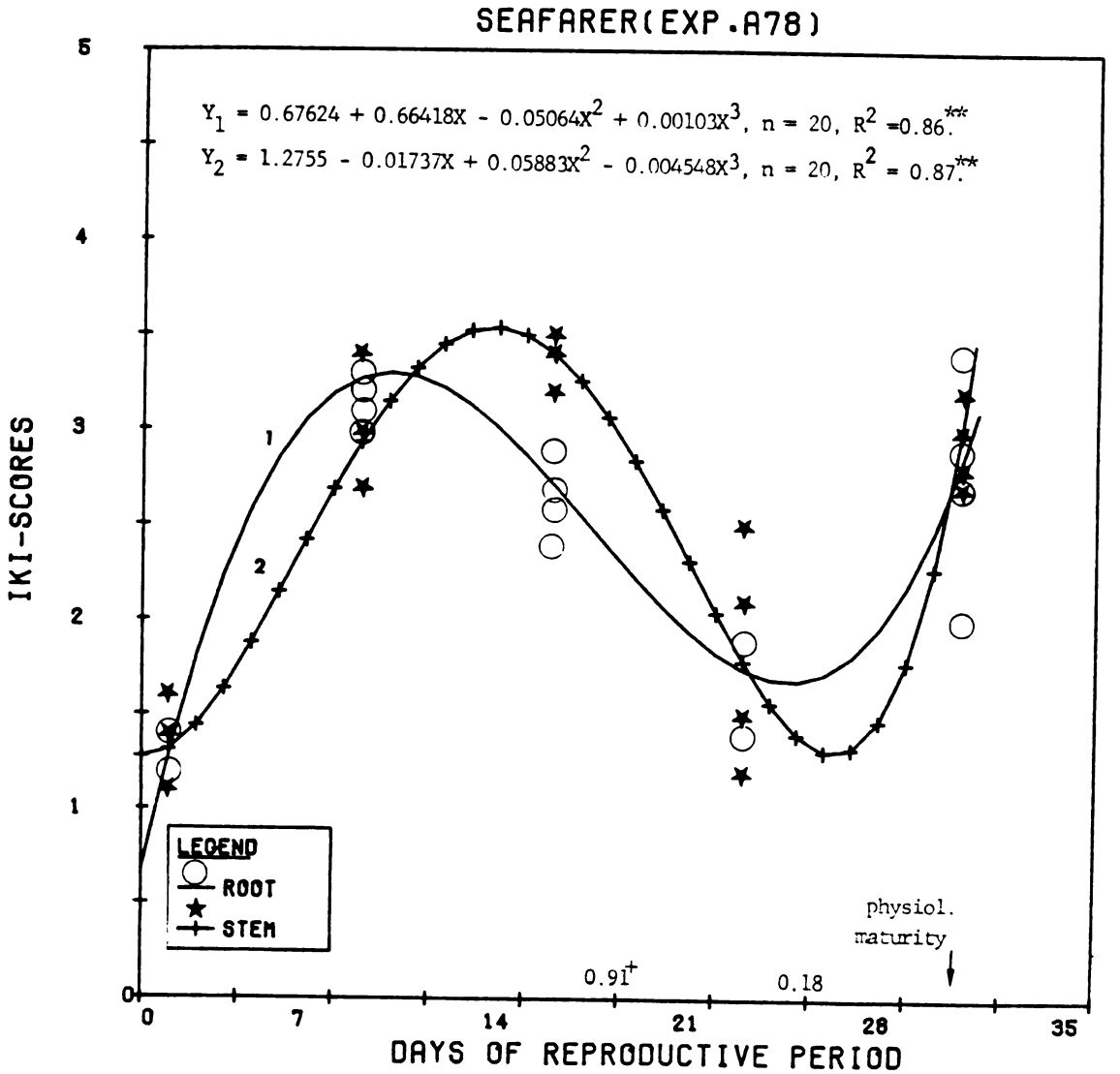

Fig. I.1: Trend of starch (IKI score) accumulation in roots and stems of Seafarer beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

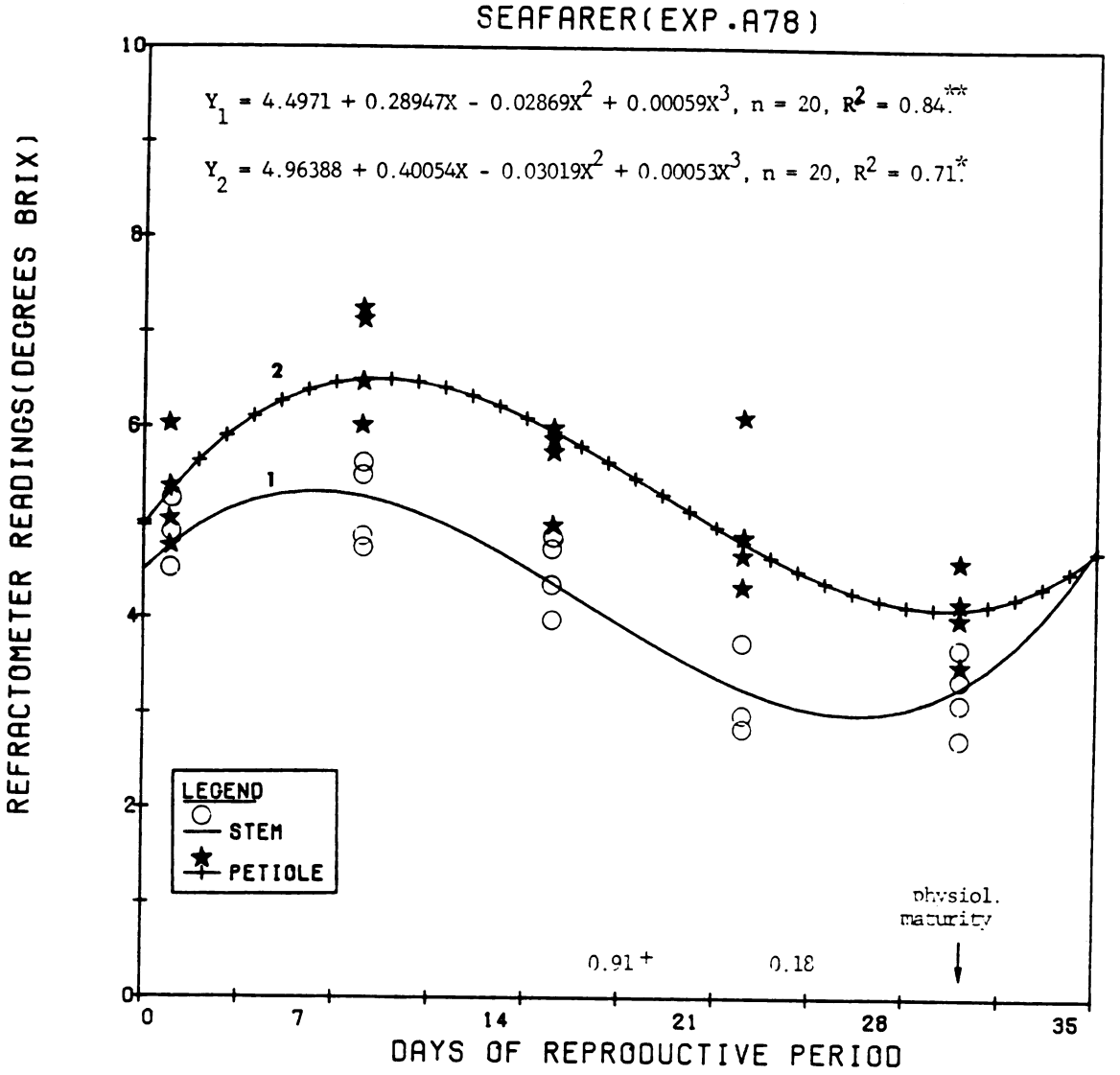

Fig. I.2: Trend of soluble solids (refractometer values) accumulation in stems and leaf petioles of Seafarer beans during reproductive growth, Bean and Beet Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

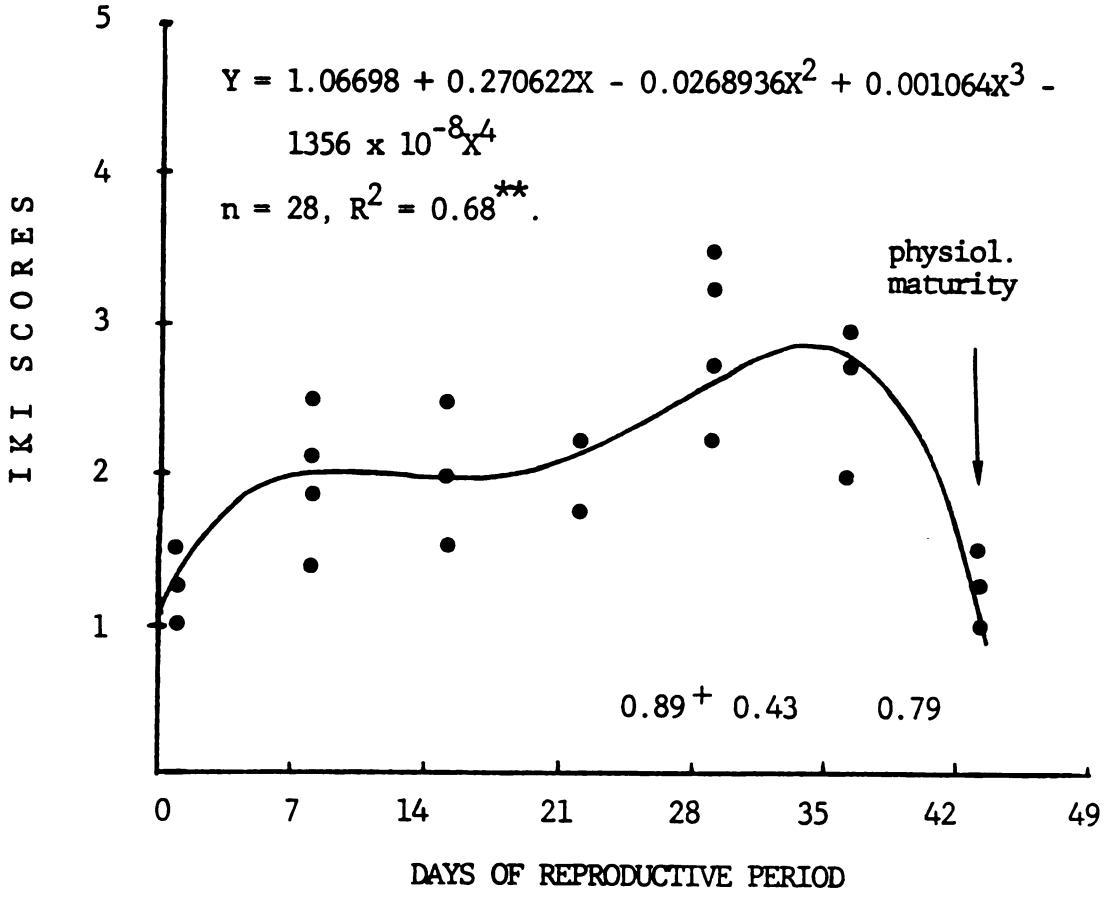

Fig. I.3: Trend of starch (IKI score) accumulation in roots of Seafarer beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

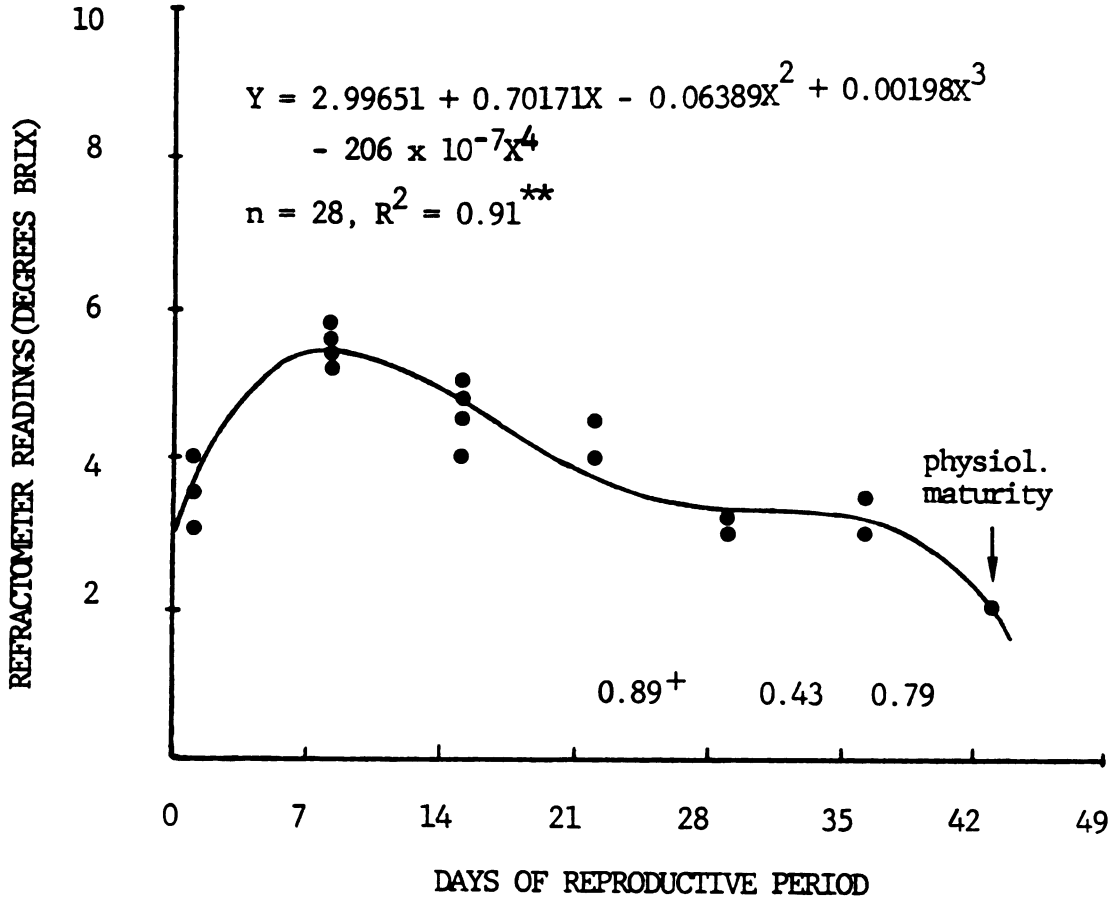

Fig. I.4: Trend of soluble solids (refractometer values) accumulation in stems of Seafarer beans during reproductive growth, Bean and Sugar Beet Farm Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

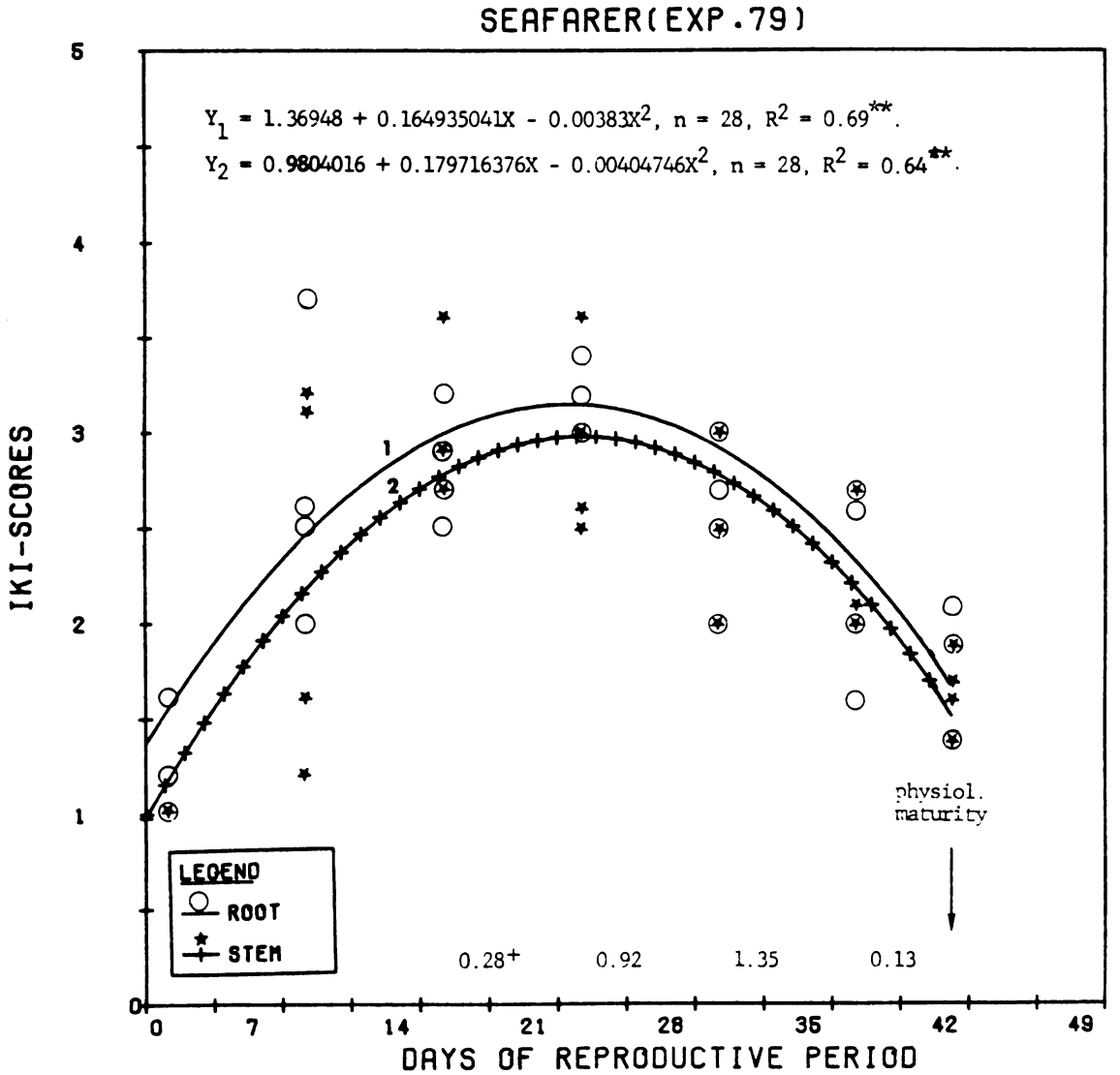

Fig. I.5: Trend of starch (IKI score) accumulation in roots and stems of Seafarer beans during reproductive growth, MSU Crops Research Farm, 1970.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

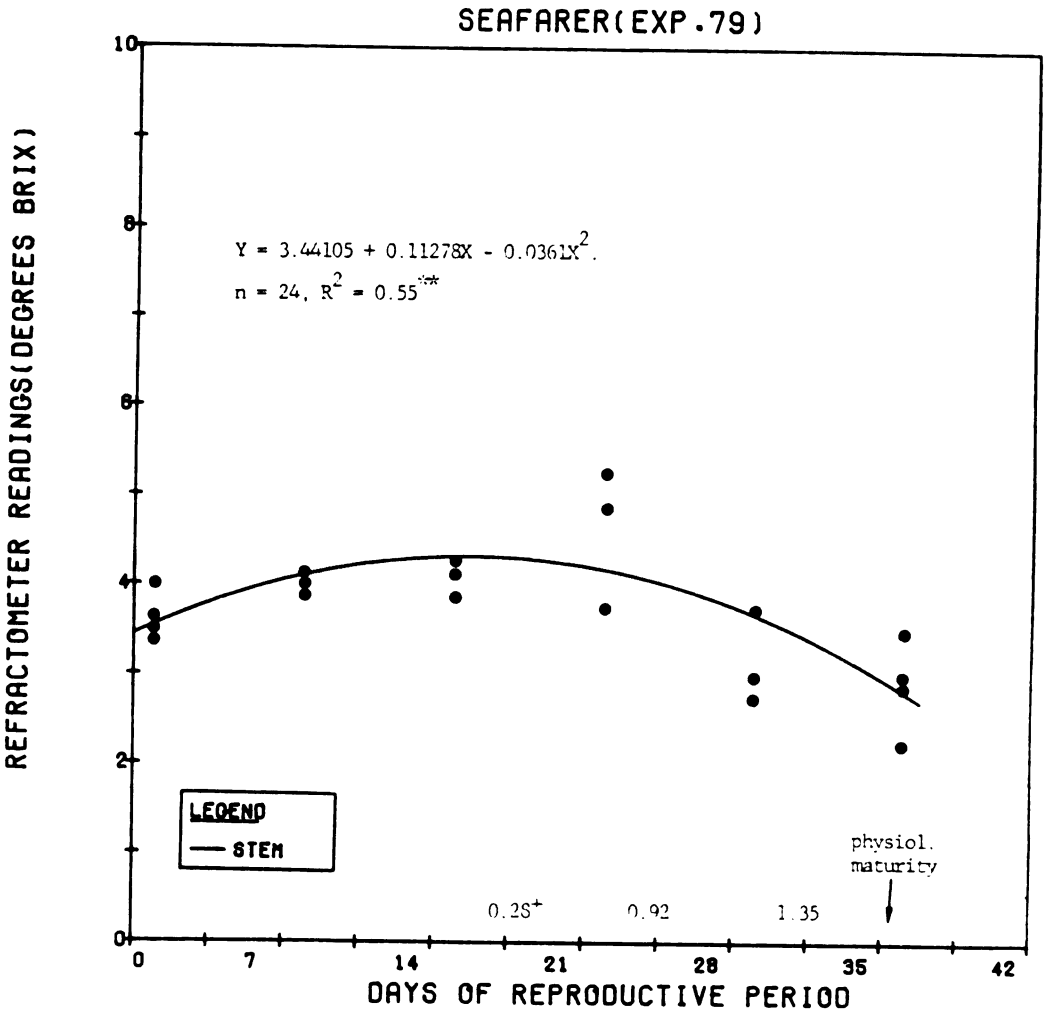

Fig. I.6: Trend of soluble solids (refractometer values) accumulation in stems of Seafarer beans during reproductive growth, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

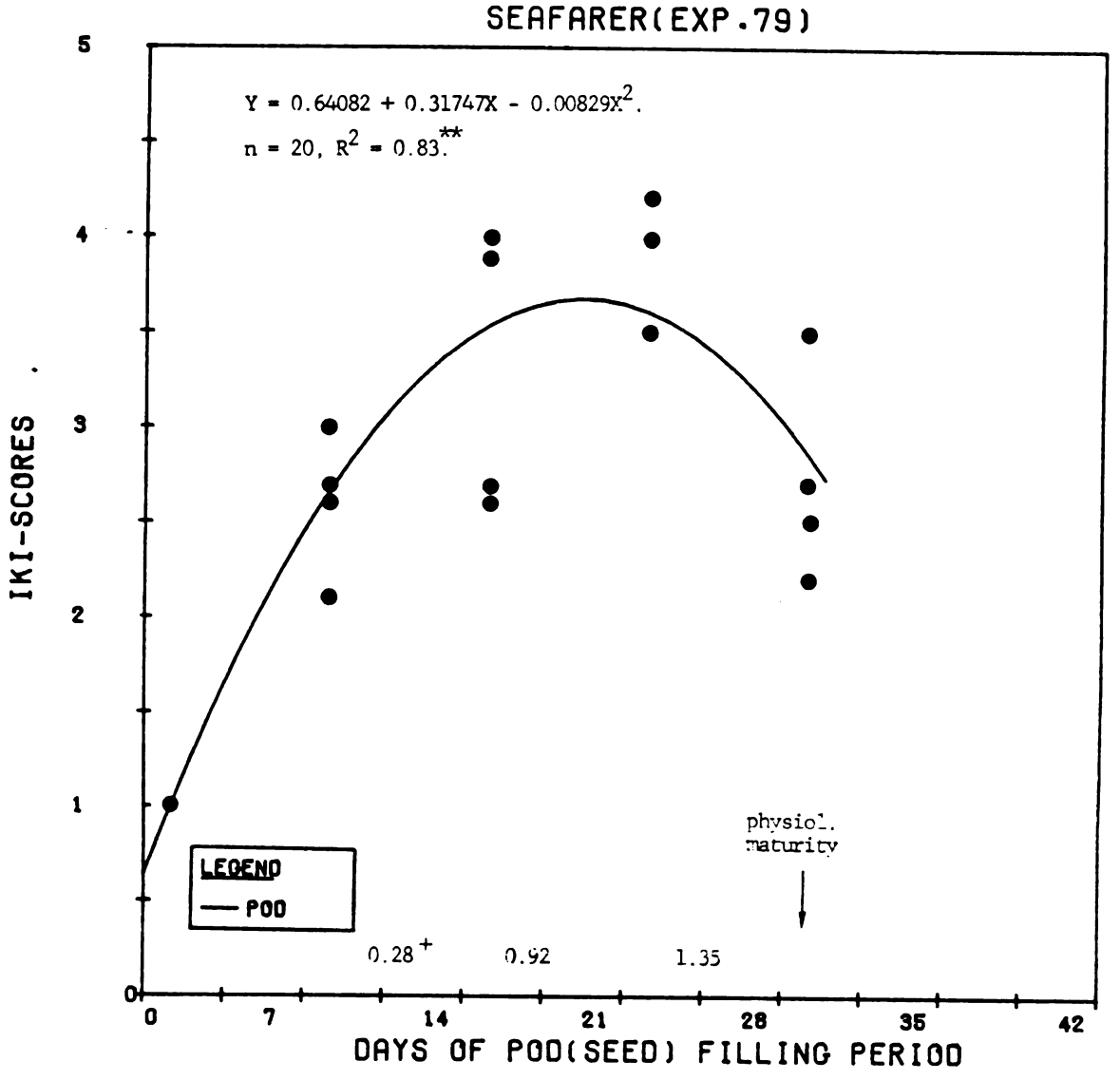

Fig. I.7: Trend of starch (IKI score) accumulation in pod walls of Seafarer beans, MSU Crops Research Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

when respectively about 50 to 95 percent of plants had at least one open flower. Seafarer flowered 35 days after planting and mid-flowering occurred 2 days later. Full bloom was recorded at day 38.

The curves relative to Experiment A78 (Fig. I.1, 2) indicate that the amounts of starch and soluble solids increased during the flowering period and reached their maxima during the period of early seed development, i.e., between 7 and 15 days after flowering. In Experiment B78, however, the amounts of starch stored in roots (Fig. I.3) increased and subsequently decreased from day 33 to day 44 whereas amounts of soluble solids in stems (Fig. I.4) decreased almost linearly from the 8th day after 50 percent flowering to physiological maturity. The curves relative to the MSU Crops Farm experiment indicate that the highest amounts of non-structural carbohydrates in roots and stems (Fig. I.5 and 6) were reached at about 20 days after 50 percent flowering. The highest daily seed growth rates per plant were 0.91 gms between 15 and 22 days (Experiment A78), 0.89 gms between 22 and 29 days (Experiment B78), and 1.35 gms for the 29-36 days after mid-flowering period (Experiment 79).

The mid-seed fill periods for Seafarer (period in which half of the physiological maturity seed weights were reached) occurred between 15 to 22 days (A78), at about

day 22 (Experiment B78), and at about day 29 after mid-flowering in Experiment 79.

It appears from the curves, Figures I.1-7, that the periods in which NSC decreased agree with the periods of the highest seed growth rate which coincide with the linear phase of seed growth. This implies that in Seafarer during the period of the highest seed growth rate, the sink demand greatly exceeded the rate of current production of carbohydrates and, therefore, the stem and root storage sites became the alternative source of carbohydrates to support the growing seed.

Seafarer planted at the MSU Crops Farm, as well as many other entries, matured late and, in general, had higher yields (Table 9) in comparison with the Bean and Sugar Beet Farm experiments. In addition, from day 15 or so after 50 percent flowering to physiological maturity, the overall daily seed growth rate in Experiment 79 was equal to that in Experiment A78 (0.71 gms per plant) and was equivalent to the daily seed growth rate in Experiment B78 (0.67 gms per plant). From day 15 after mid-flowering (end of pod wall growth) physiological maturity was reached at about 15, 28, and 26 days later in Experiments A78, B78, and 79, respectively.

From the above-mentioned seed growth rates and seed yields reported in Table 9, it appears that in

Experiments B78 and 79 Seafarer gave higher yields than in Experiment A78 due to relatively high seed growth rates maintained for a longer period. Thus, for this early-maturing dry bean cultivar, an extended seed filling duration is also important in achieving high yields.

Curves relative to Experiment 79 (Fig. I.5, 6, 7) indicate that levels of NSC decreased in Seafarer tissues for about 20 days (from day 21 to day 41), but were remobilized for only 15 days (between 10 and 25 days after mid-flowering) in Experiment A78. In Experiment B78 starch (Fig. I.3) in storage was remobilized from root only during the last eight days of reproductive growth, whereas levels of soluble solids decreased in stem tissue for 35 days from day 8 after mid-flowering (Fig. I.4).

These data based on IKI staining of starch and refractometer readings for soluble solids do not allow a quantitative assessment of NSC diverted to seed production. However, the straightforward decrease of NSC in three tissues as revealed by Fig. I.5-7 could lead to the suggestion, as compared with the Bean and Sugar Beet Farm Experiments, that higher amounts of previously stored carbohydrates were diverted to the growing seed and contributed significantly to a greater grain production in the experiment conducted at the MSU Crops Farm.

Redkloud

Figures II.1-7 are curves describing the behavior of NSC in roots, stems, leaf petioles, and pod walls of the red kidney bean cultivar Redkloud.

This cultivar flowered at day 33 after planting, mid-flowering was recorded at day 35 and full bloom at day 39.

Curves, except those relative to soluble solids, show an increase in carbohydrates from 50 percent flowering to the period of early seed development or beyond. Curves from data of the Saginaw Valley experiments (A78 and B78) (Fig. II. 1-4) show a decrease of NSC from the beginning of seed development to the time when the pod reaches its maximum elongation (at about day 15 after 50 percent flowering). Mid-seed fill and the highest rate of seed growth (1.59 gms day^{-1} per plant) were recorded between 15 and 22 days after mid-flowering (Experiment A78). This is the very period when a sharp decrease in NSC was observed in roots and stems. In Experiment B78, however, the highest daily seed growth rate (0.79 gms per plant) was recorded between 28 and 35 days after 50 percent flowering.

Again, as was observed for Seafarer, it was clear that the high seed growth rates for this cultivar were supported by the ability to divert carbohydrates from storage sites to the developing seed.

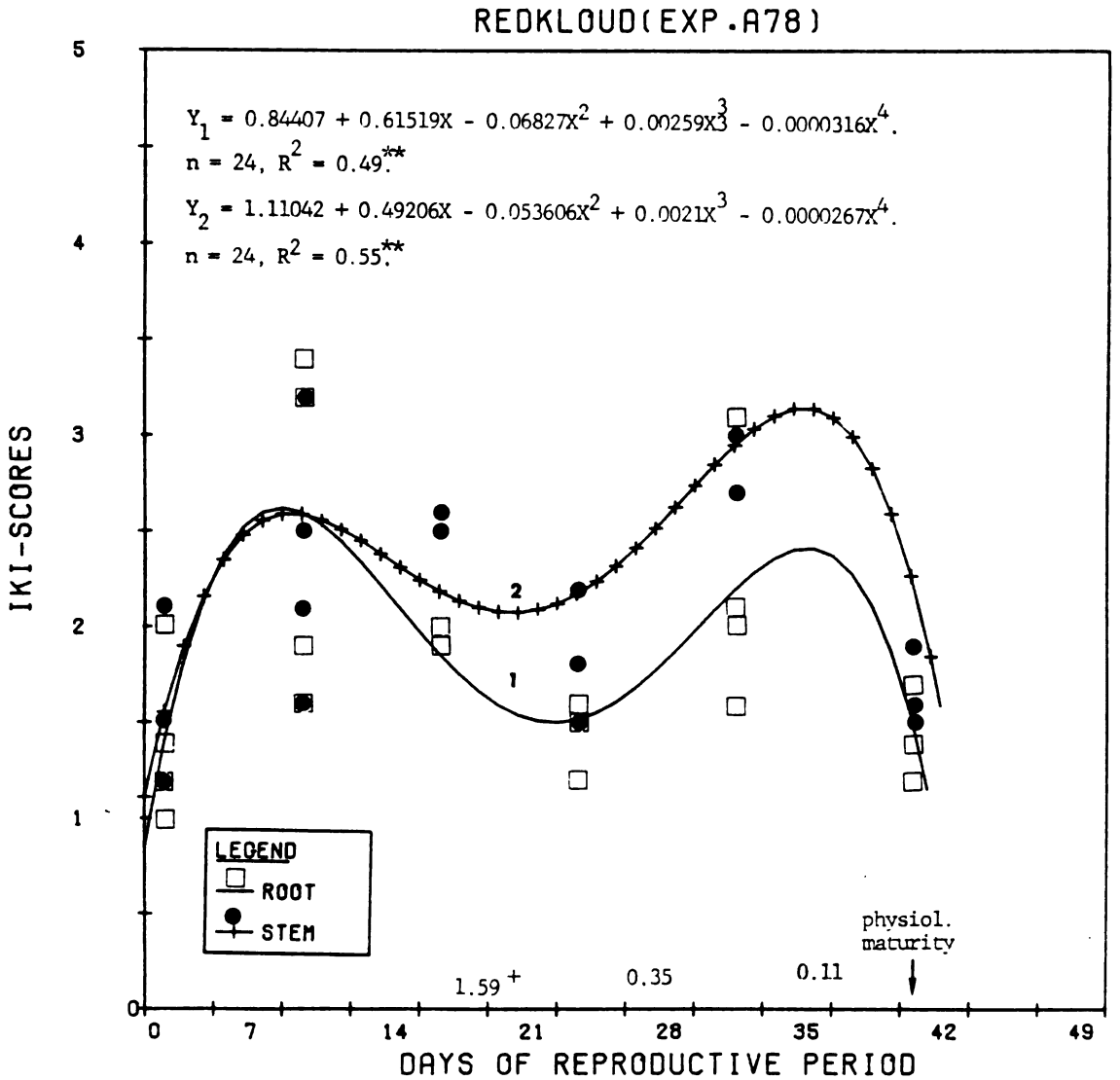

Fig. II.1: Trend of starch (IKI score) accumulation in roots and stems of Redkloud beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

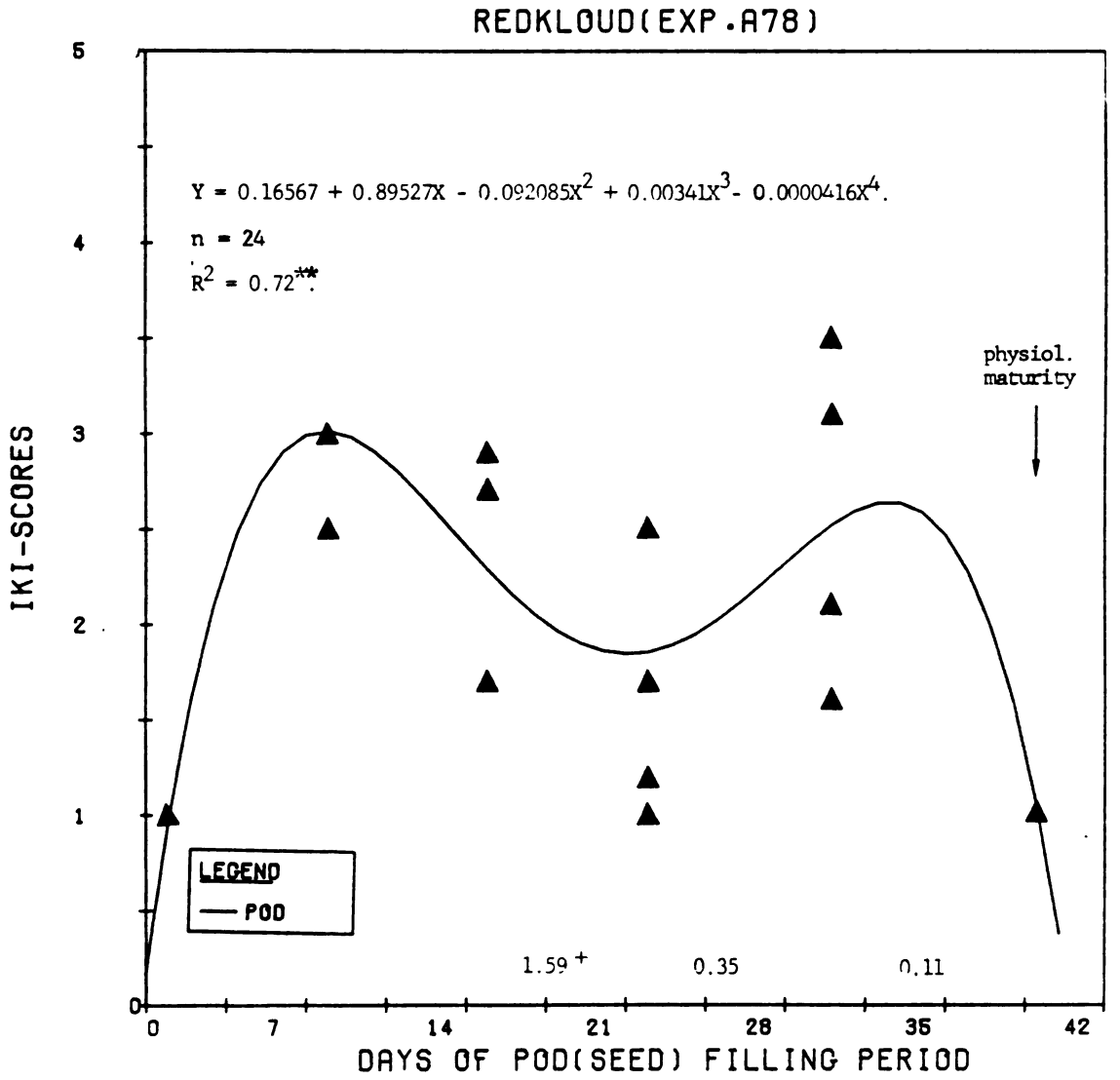

Fig. II.2: Trend of starch (IKI score) accumulation in pod walls of Redkloud beans, Bean and Sugar Beet Research Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

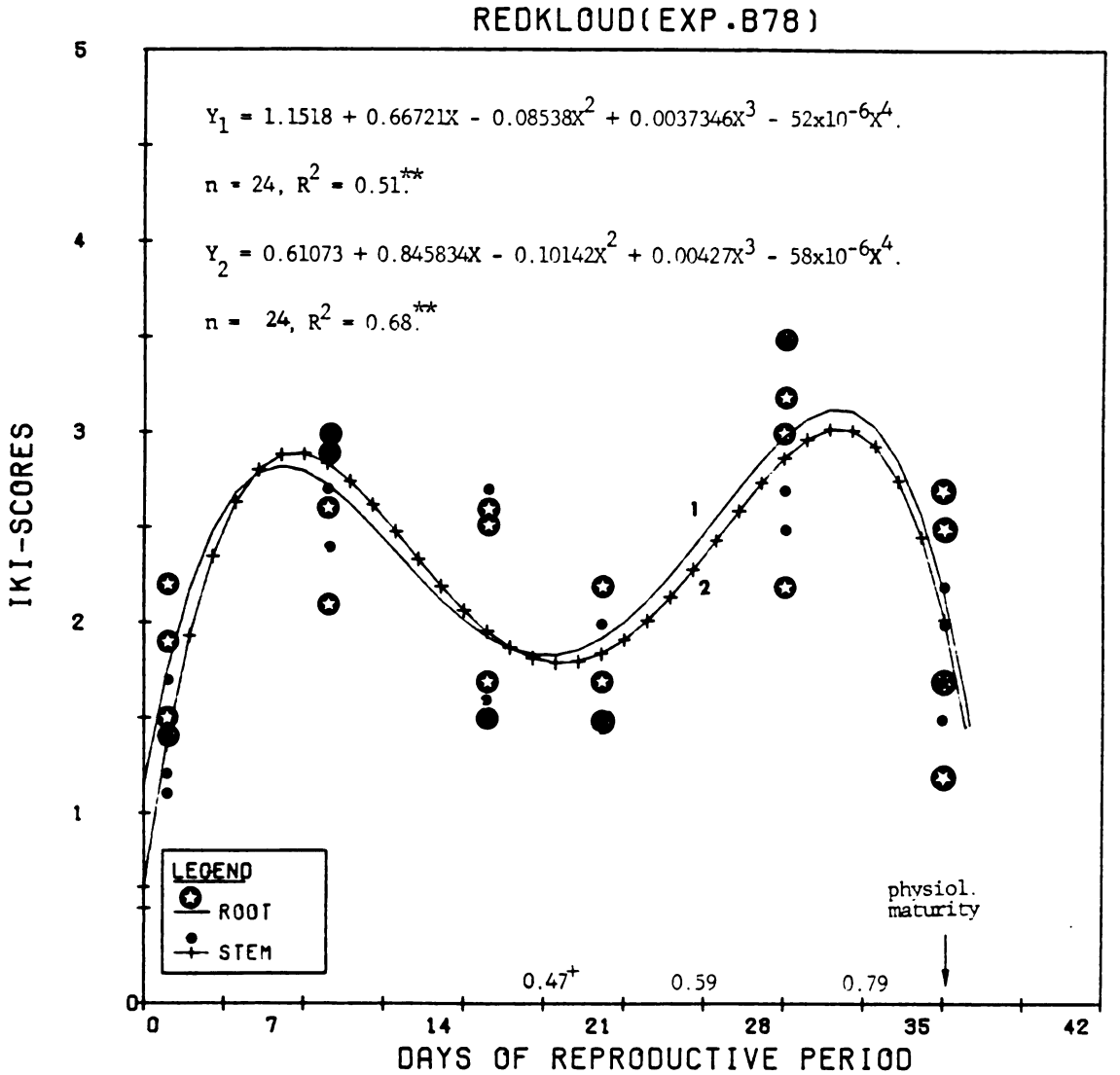

Fig. II.3: Trend of starch (IKI score) accumulation in roots and stems of Redkloud beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

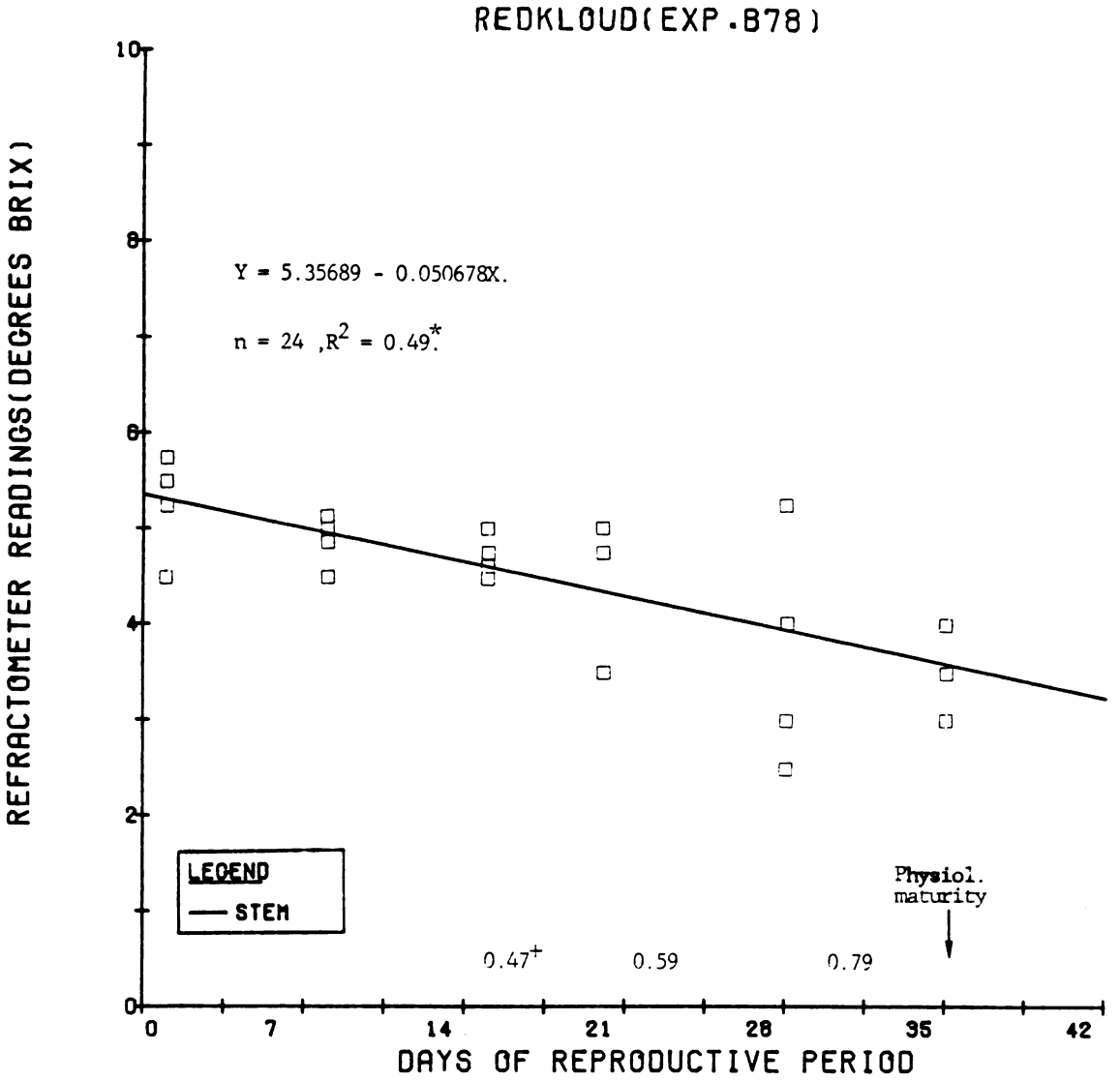

Fig. II.4: Trend of soluble solids (refractometer values) accumulation in stems of Redkloud beans during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

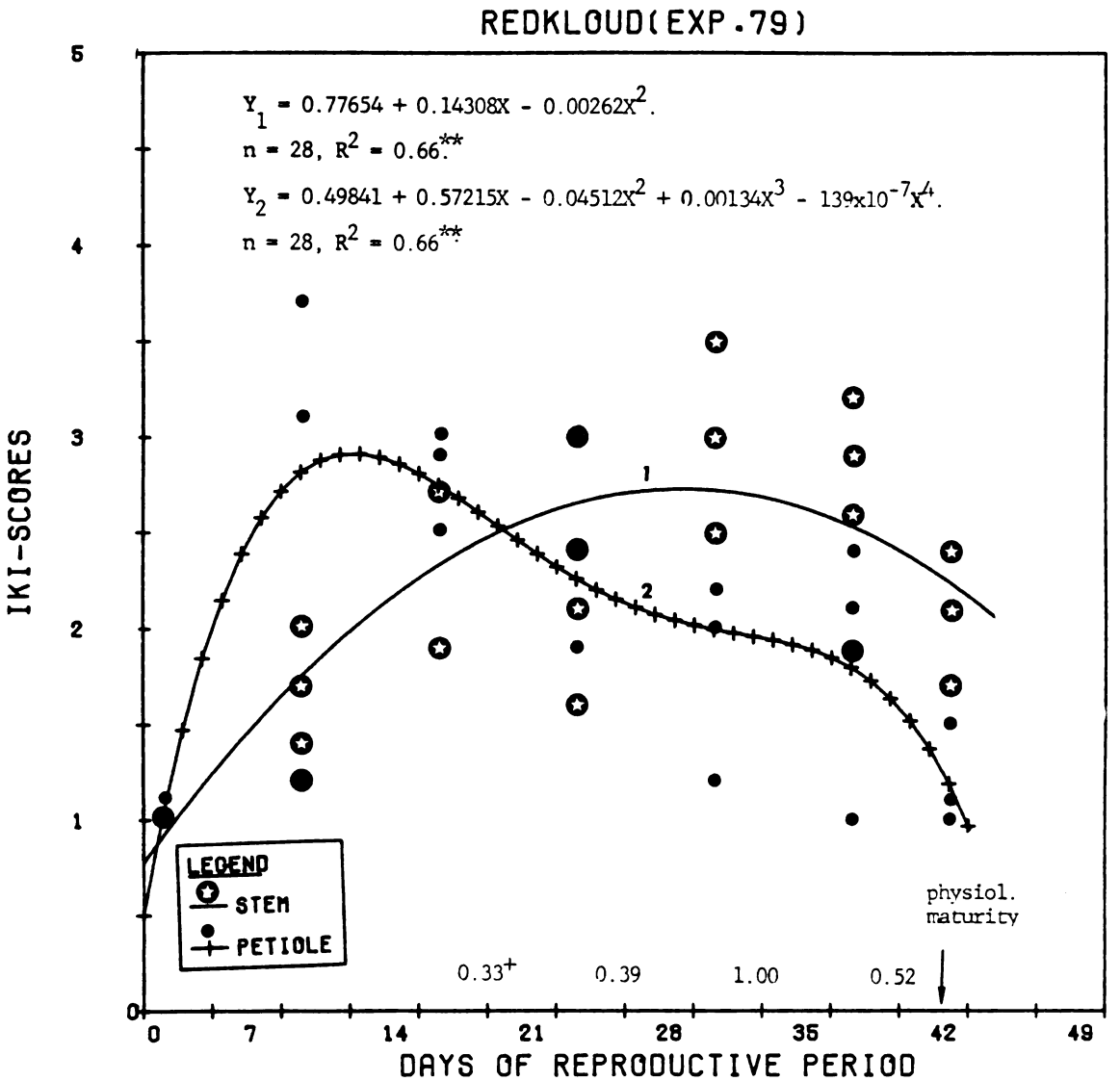

Fig. II.5: Trend of starch (IKI score) accumulation in stems and leaf petioles of Redkloud beans during reproductive growth, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

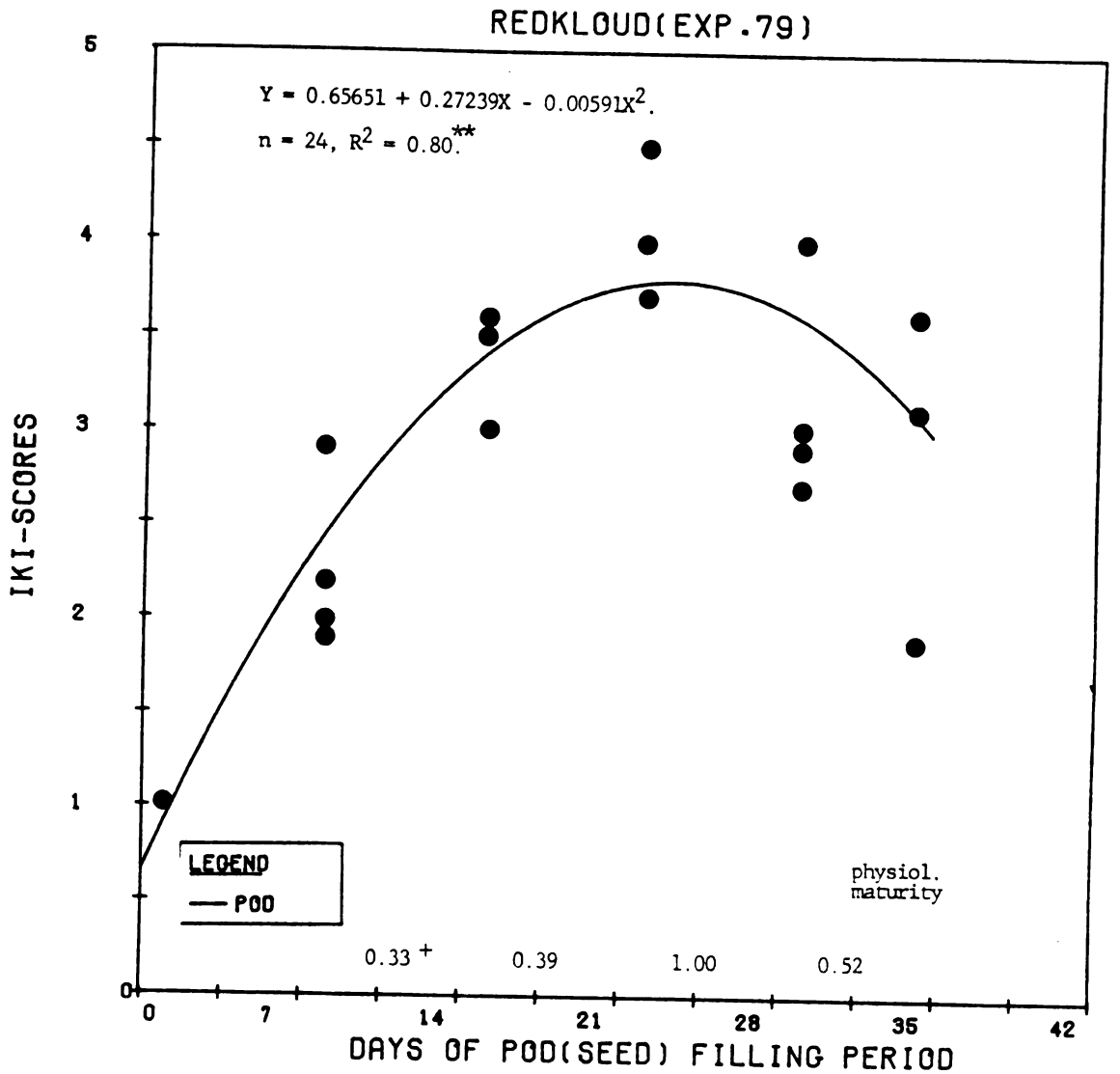

Fig. II.6: Trend of starch (IKI score) accumulation in pod walls of Redkloud beans, MSU Crops Research Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

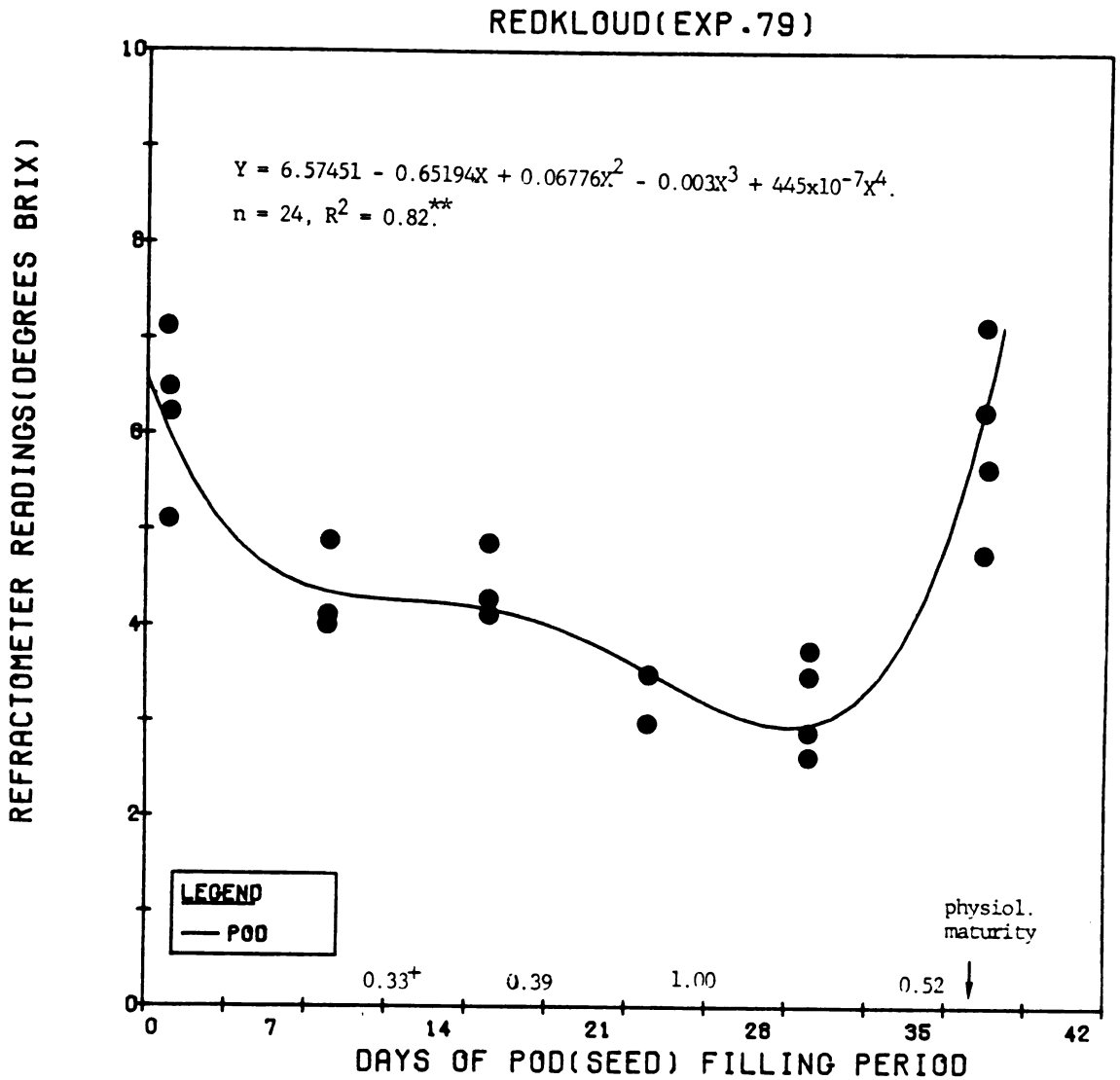

Fig. II.7: Trend of soluble solids (refractometer values) accumulation in pod walls of Redkloud beans, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

The 1979 planting overwhelmingly yielded more for this cultivar than the 1978 Saginaw Valley plantings. The 1979 curves look different and suggest a higher remobilization rate of NSC. At the MSU Crops Farm, Redkloud gained daily and successively 0.33, 0.39, 1.0, and 0.52 gms per plant, respectively, in the periods 15-22, 22-29, 29-36, and 36-41 days after mid-flowering. The remobilization occurred in order to support the rate of 1.0 gm day^{-1} per plant and the gain of 0.52 gms day^{-1} per plant was still high in comparison with those when the amounts of carbohydrates were still increasing in tissues.

Although Redkloud seems to be an inefficient remobilizer of NSC, the general remobilization pattern described by the curves derived from the MSU Crops Farm data agree with the above-mentioned rates. It can be seen that whereas the petiole starch and the pod wall soluble solids supported seed growth at the beginning of seed development, the stem and pod wall starch intervened when the seed was in its highest growth rate phase, i.e., 1.0 gm day^{-1} per plant between and beyond 29-36 days after mid-flowering.

With respect to the low coefficients of multiple determination (R^2) for the curves and remobilization patterns just described, Redkloud offers a picture of an inefficient remobilizer of NSC. This also may be supported

by data of Peet et al (1977) which indicate an increase of 408 percent in photosynthesis from flowering to early pod set. Hence, it seems that in this cultivar the manufacture of photosynthate exceeds the demand and, therefore, there is no need to remobilize the stored carbohydrates unless it is in critical periods.

From 15 days after mid-flowering, the overall seed growth rates calculated until physiological maturity were 0.57, 0.63, and 0.56 gms per plant, for A78, B78, and the 79 experiments, respectively. The lengths of reproductive periods were same for the B78 and 79 experiments. Although the remobilization of NSC in Experiment 79 seems to have been more effective than in previous experiments (Figures II), the reason underlying that higher remobilization and the higher yield is not clear. It might be clearer, however, if we had measured the yield components, i.e., the number of pods per plant, the number of seeds per pod, and the single seed weight.

Redkote

After planting, 37, 45, and 47 days were, respectively, days at which first flowering, 50 percent flowering, and full bloom were observed for Redkote. Curves describing changes in its NSC are presented in Figures III.1-5.

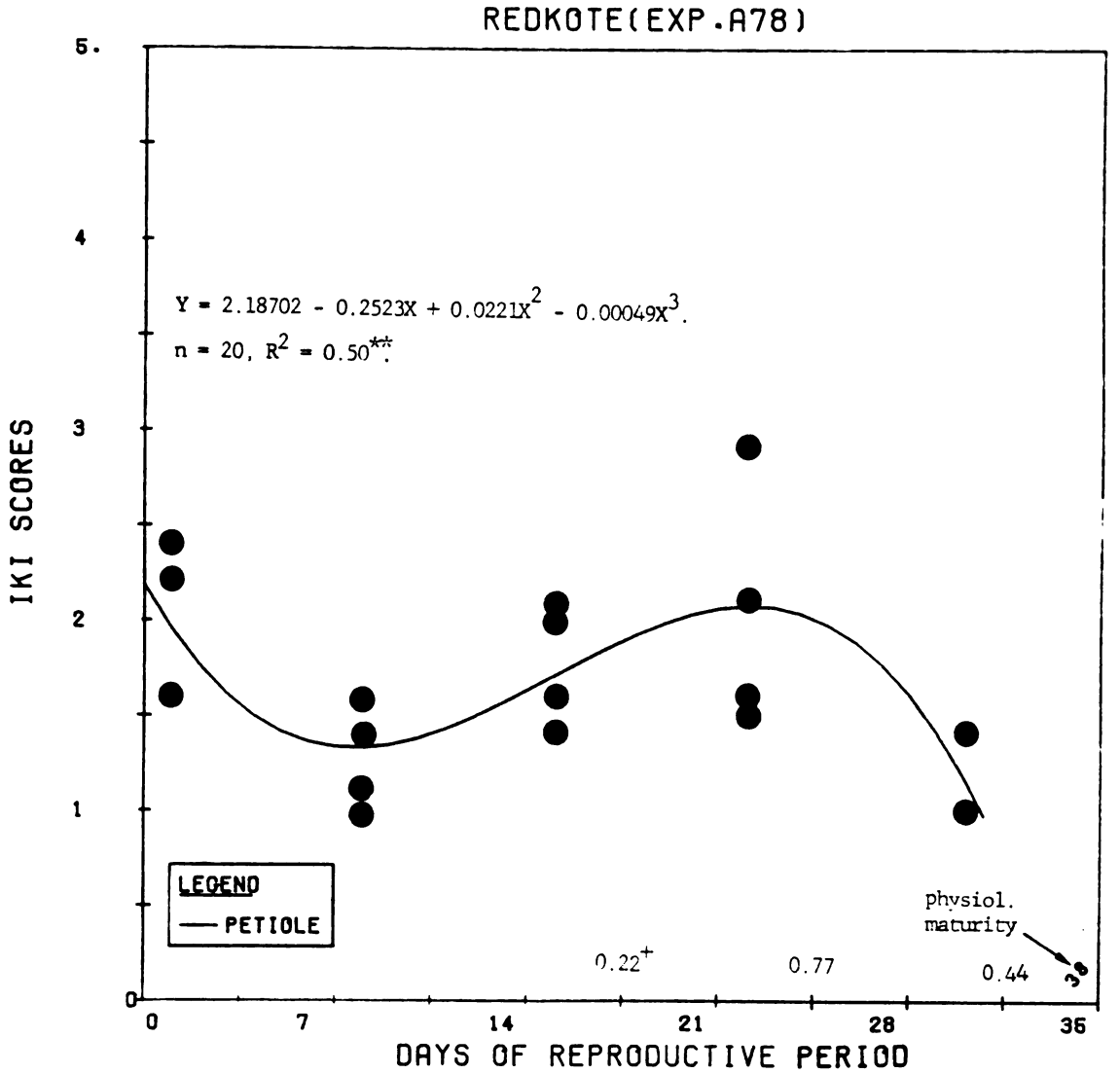

Fig. III.1: Trend of starch (IKI score) accumulation in leaf petioles of Redkote beans during reproductive growth, Bean and Sugar Beet Farm, Experiment A, 1978.

+: seed growth (grams day^{-1} per plant) calculated for two successive sampling dates.

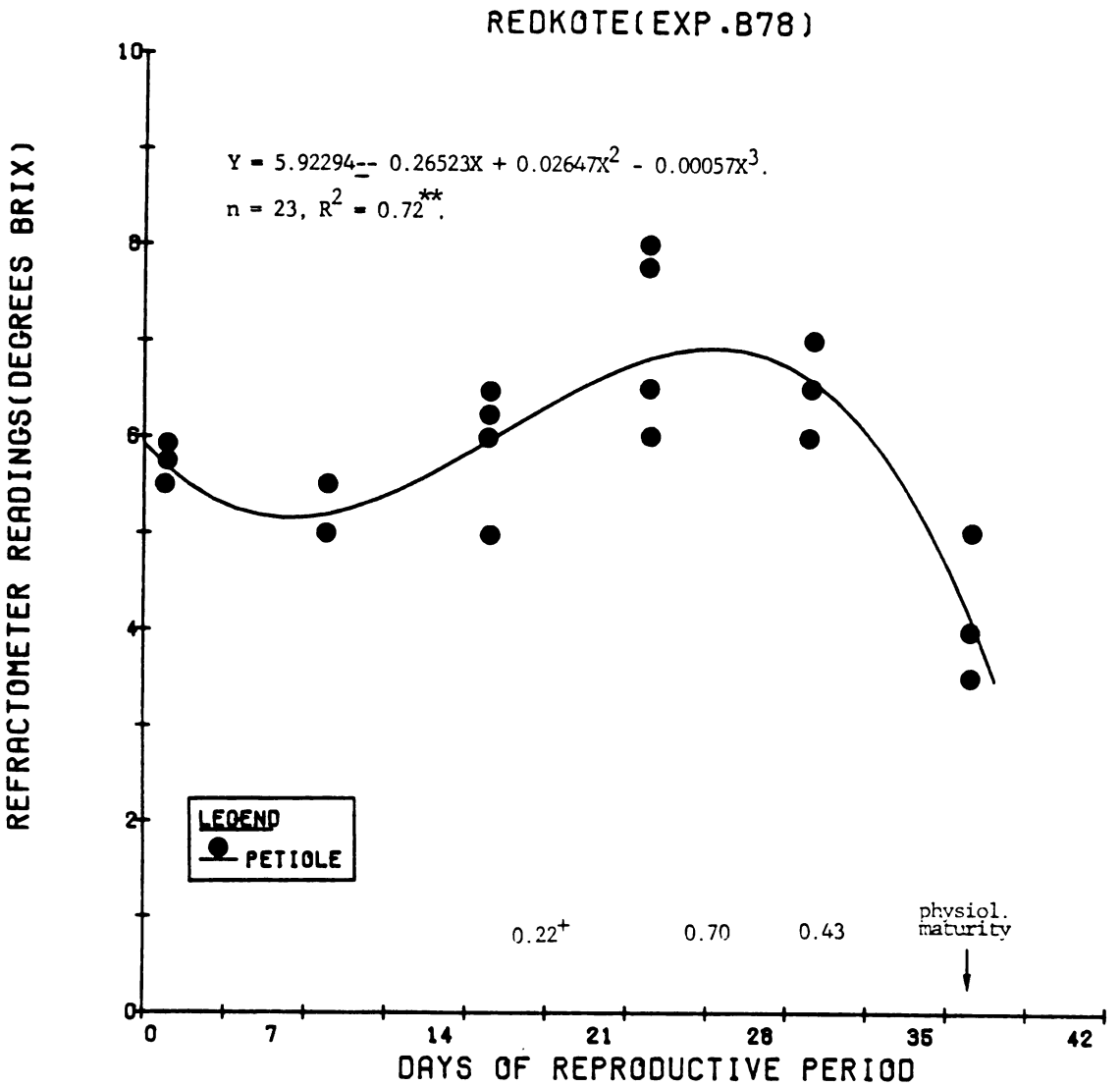

Fig. III.2: Trend of soluble solids (refractometer values) accumulation in leaf petioles of Redkote beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

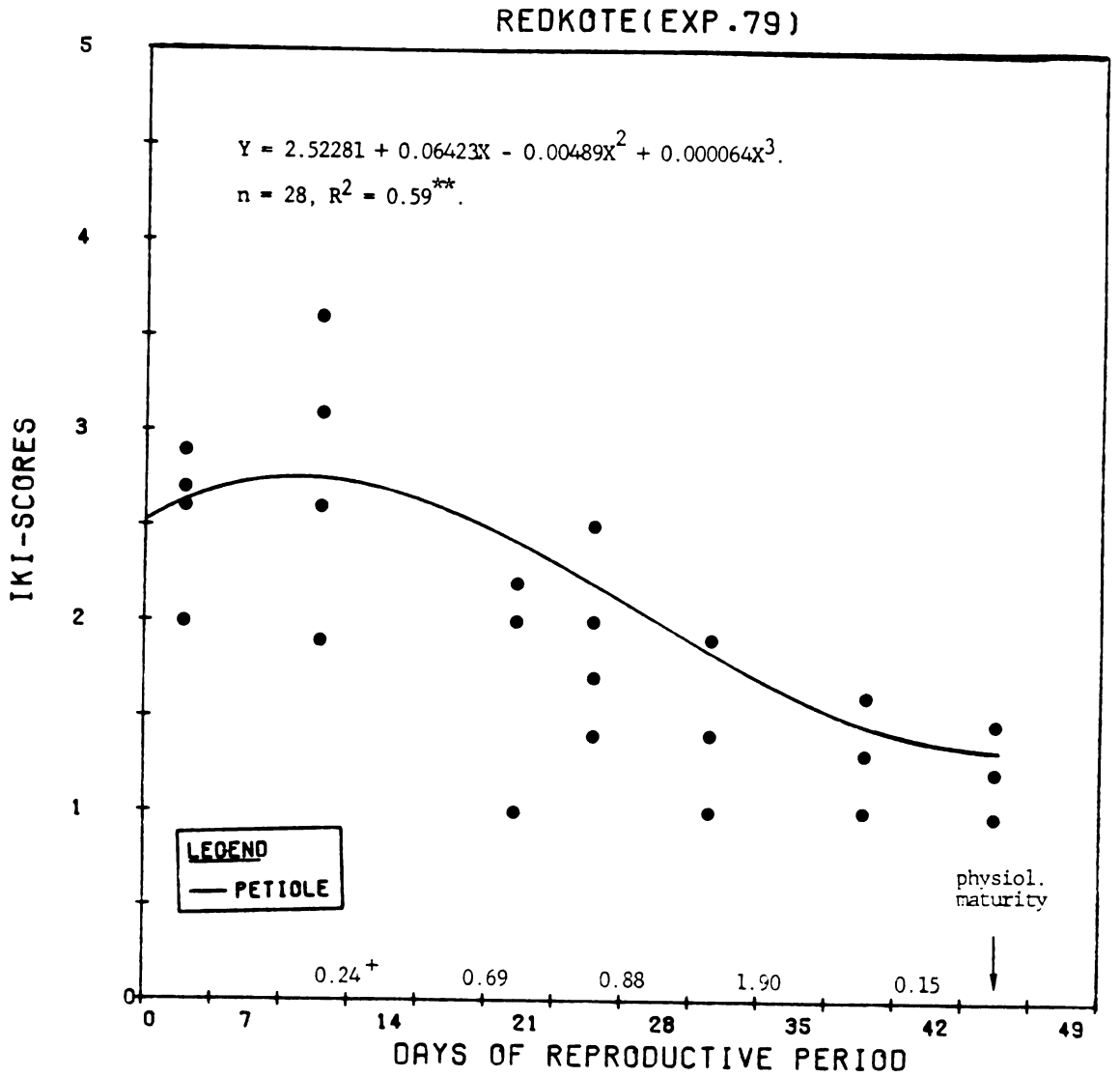

Fig. III.3: Trend of starch (IKI score) accumulation in leaf petioles of Redkote beans during reproductive growth, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

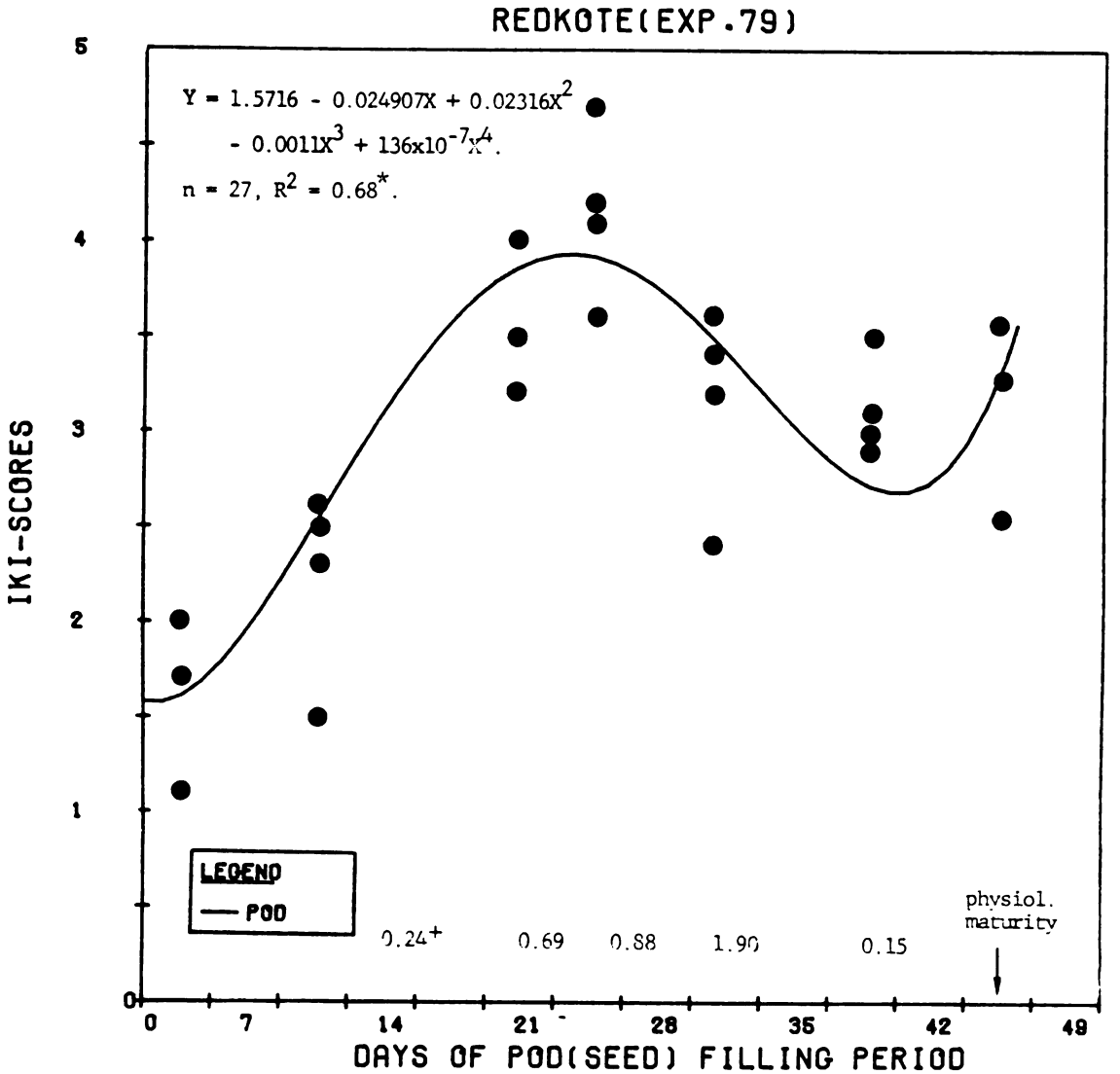

Fig. III.4: Trend of starch (IKI score) accumulation in pod walls of Redkote beans, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

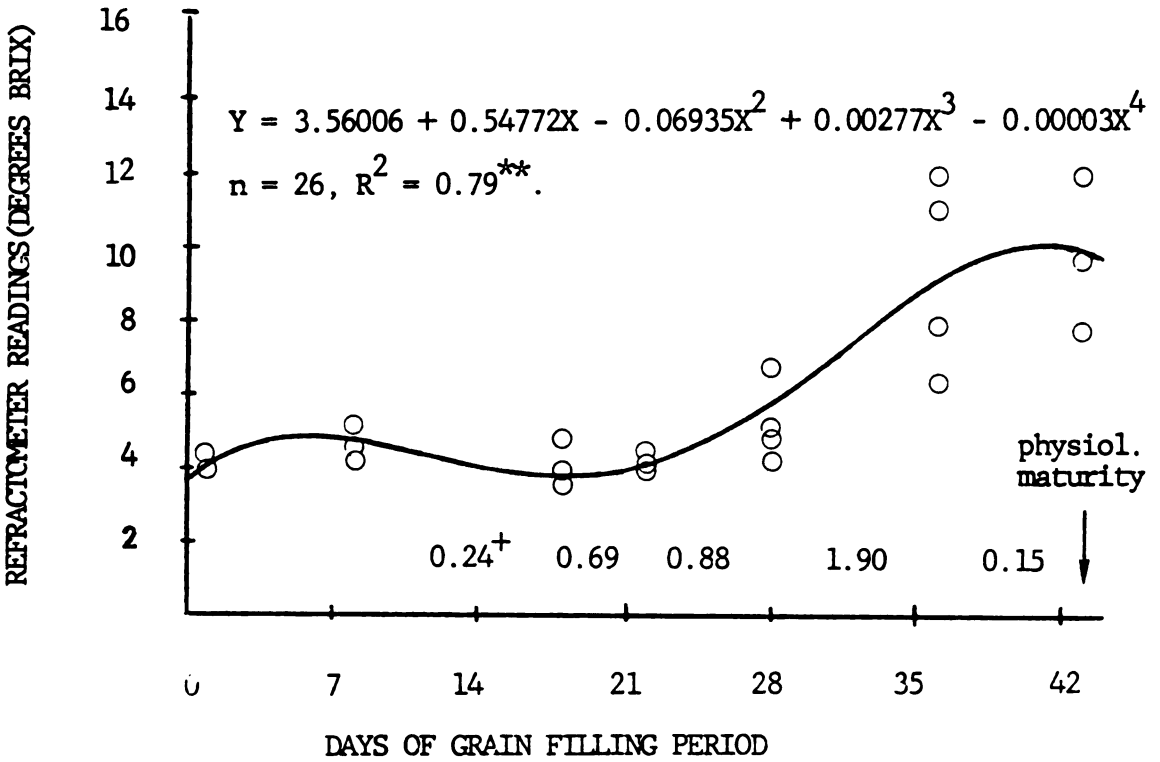

Fig. III.5: Trend of soluble solids (refractometer values) accumulation in pod walls of Redkote beans, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

The amounts of starch (Experiment A78) (Fig. III.1) and soluble solids (Experiment B78)(Fig. III.2) in leaf petioles decreased during the flowering period then rose and reached their peaks at day 22 (A78) and day 26 (B78) after mid-flowering. The highest daily seed growth rates were recorded between 22 and 30 days (Experiment A78) and 22 and 29 days after mid-flowering (Experiment B78).

A continuous remobilization of starch from pod walls of Redkote (Experiment 79) was observed between 28 and 45 days after mid-flowering, i.e., between 2 and 39 days from the day when first data on pod wall were taken. In graphs pertaining to pod wall, days from the first sampling of pod wall (day 15 after mid-flowering in the majority of cases) are referred to as days of seed filling period. On the other hand, Fig. III.5 indicates that amounts of soluble solids in pod wall tissue increased until physiological maturity, whereas after a slight increase during the active period of flowering and pod wall growth levels of starch in leaf petioles (Fig. III.3) decreased almost linearly until physiological maturity. In the MSU Crops Farm experiment, the highest daily seed growth rate of 1.90 gms per plant was noted between 36 and 44 days after 50 percent flowering.

The decrease in the amounts of starch and soluble solids shown by the curves corresponds with the period of

higher demand for assimilates by the growing seed. Again these decreases may be viewed as a diversion of carbohydrates from vegetative tissues to the reproductive organs.

Furthermore, Tables 2, 3, 6, and 7 indicate that this red kidney dry bean holds high amounts of NSC in roots and stems. It is likely that the photosynthetic products always exceed the seed storage capacity. In fact, Peet et al (1977) observed photosynthesis rates of 7.61, 17.66, and 17.81 mg CO_2 dm^2 hr^{-1} for the periods of first flowering, early pod set, and late pod development, respectively. That is, from first flowering to early pod set the photosynthesis rate of Redkote leaves increased by 132 percent and this performance remained unchanged during the remaining period of seed filling. We may speculate also that, CO_2 uptake being efficient, every nutritional unit is self-sufficient and this is why the leaf petiole and pod wall seem to be more involved in remobilization phenomena than the other tissues. Of course, this efficient photosynthetic performance, together with the large amounts of NSC stored in roots and stems readily demonstrate lack of an adequate sink for assimilates.

Black Turtle Soup (BTS)

Remobilization patterns of NSC in the black tropical dry bean "Black Turtle Soup" are described by curves presented in Figures IV.1-5. All tissues assayed, including roots, stems leaf petioles, and even pod walls, were deprived of their carbohydrates in storage to supply the growing seed. Both starch and soluble solids were, indeed, remobilized. In both Experiments A78 and 79 BTS has recourse to the petiole in which starch amounts decreased linearly from flowering to maturity. Days to first flowering, mid-flowering, full bloom, and end of the flowering period were respectively, 41, 43, 45, and 65.

In addition, both stem and leaf petiole appear to be the first order sites of remobilization because as it can be seen from curves of the first two experiments (Fig. IV.1-4), carbohydrates were not allowed to increase substantially in these tissues during the flowering period. Also, the downward linear trend indicating changes in stem soluble solids (Fig. IV.2 and 4) is corroborative of this observation.

In comparison with all cultivars already discussed and discussed later, this tropical dry bean seems to offer the best example of remobilization of previously stored non-structural carbohydrates. The explanation of the remobilization patterns described by the curves may be

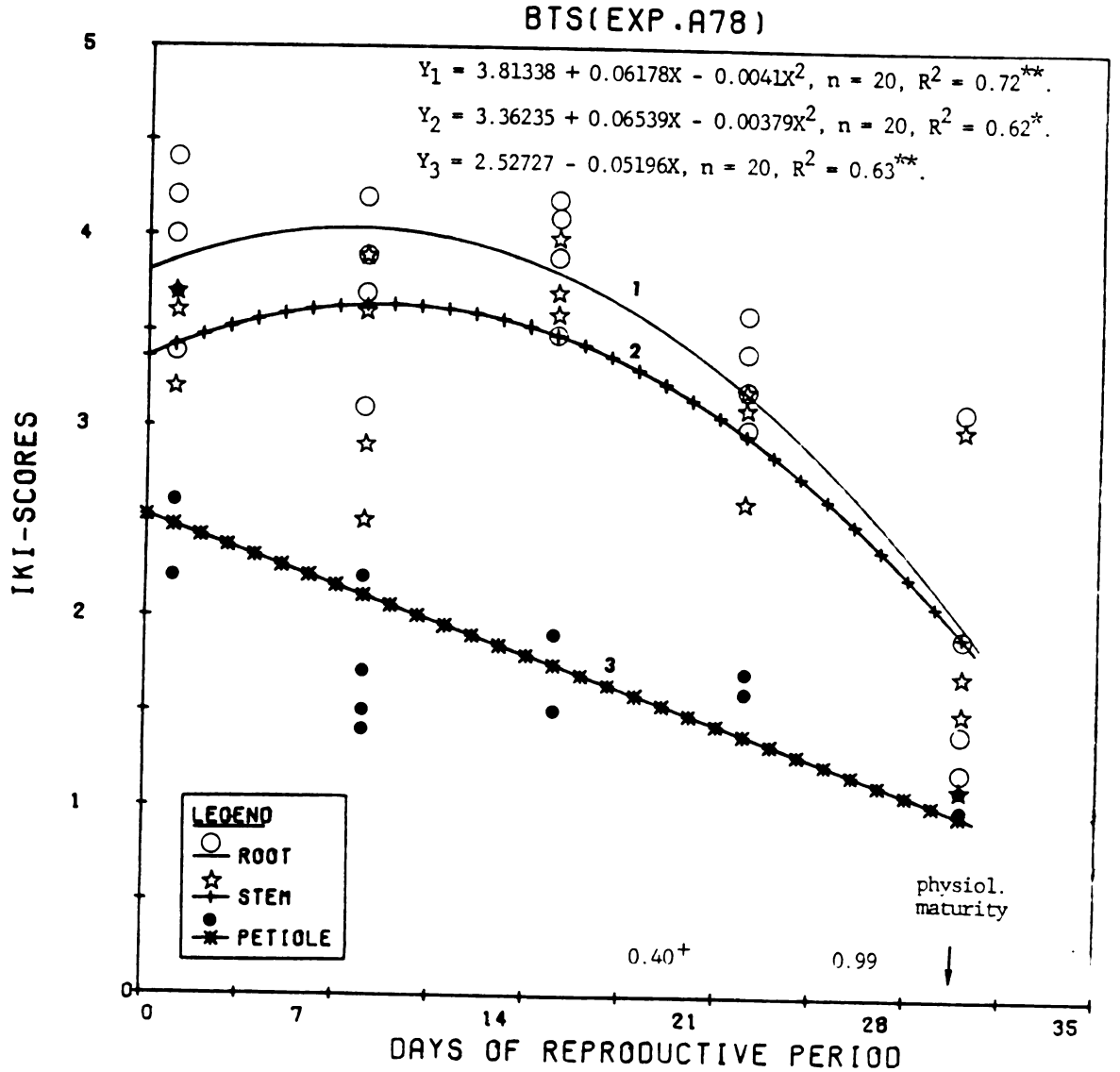

Fig. IV.1: Trend of starch (IKI score) accumulation in roots, stems and leaf petioles of Black Turtle Soup beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

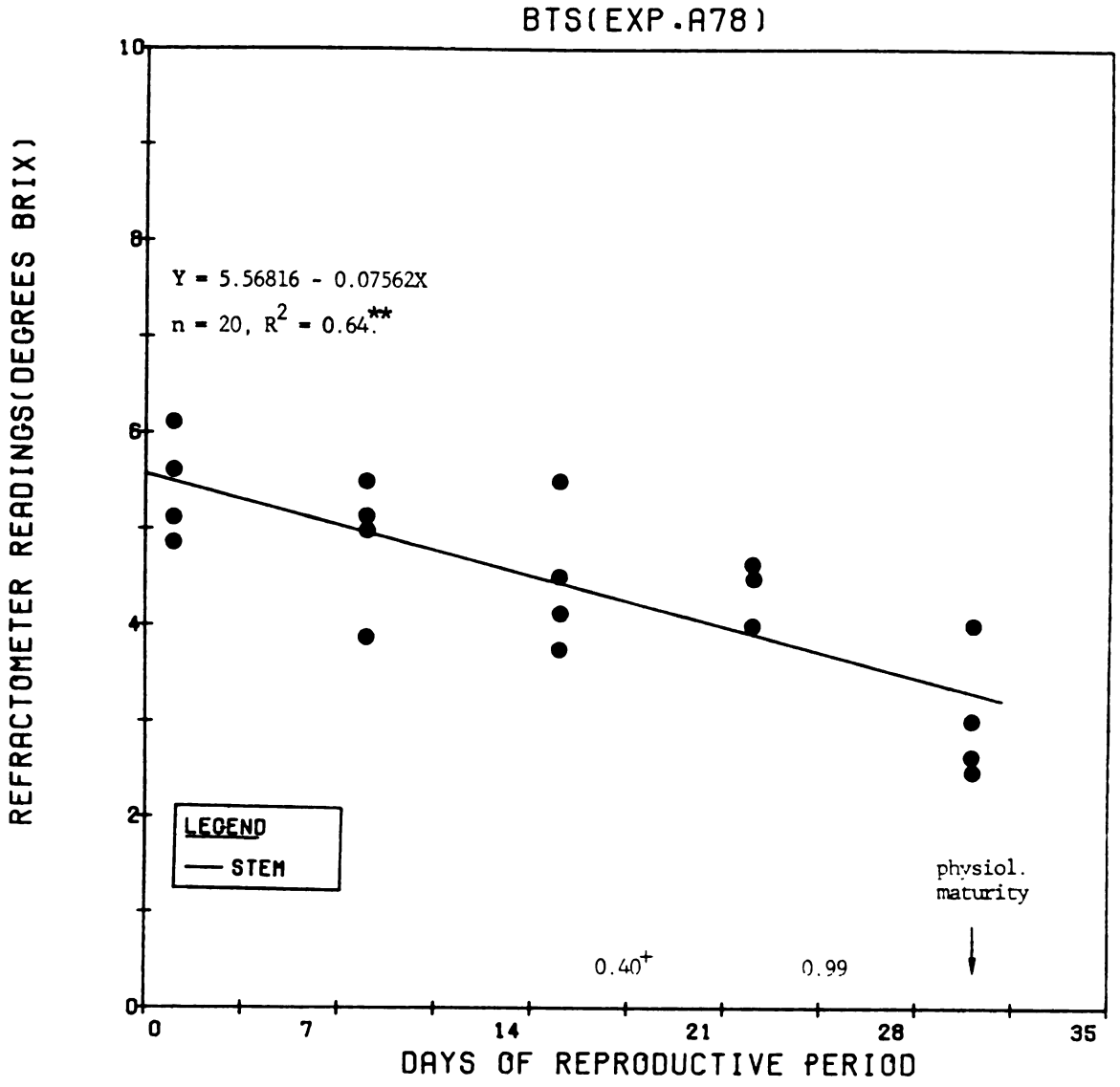

Fig. IV.2: Trend of soluble solids (refractometer values) accumulation in stems of Black Turtle Soup beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

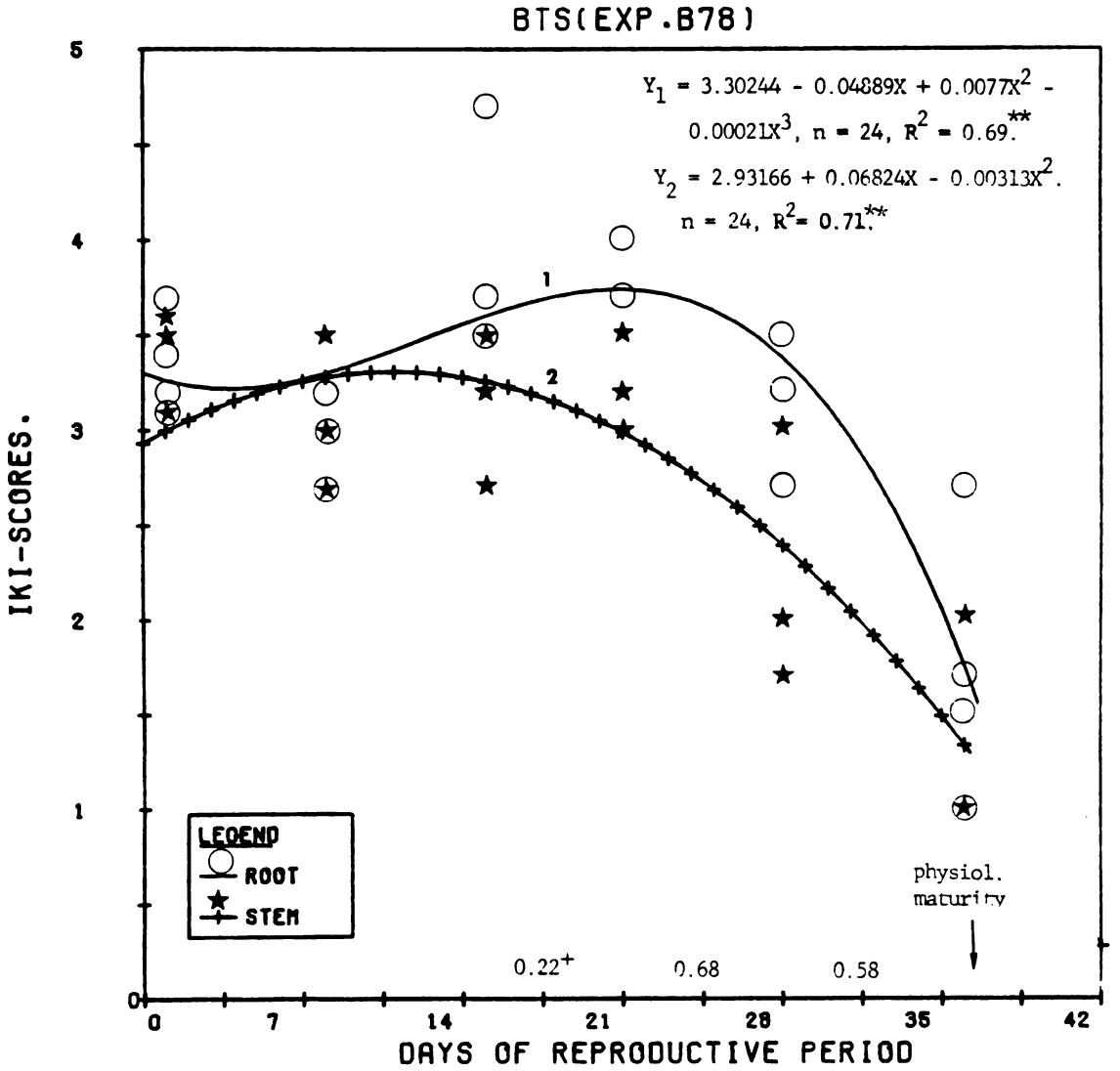

Fig. IV.3: Trend of starch (IKI score) accumulation in roots and stems of Black Turtle Soup beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

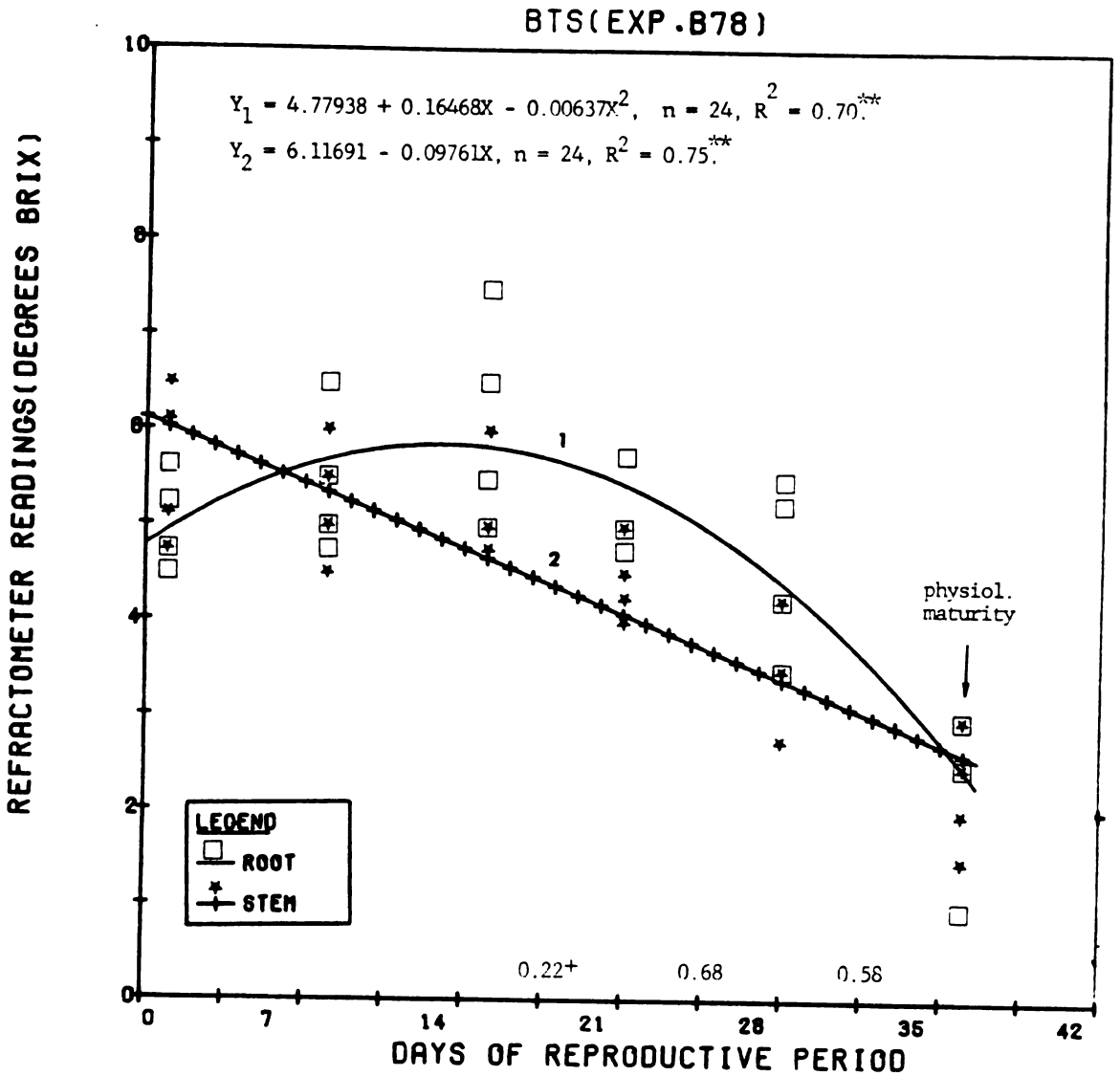

Fig. IV.4: Trend of soluble solids (refractometer values) accumulation in roots and stems of Black Turtle Soup beans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

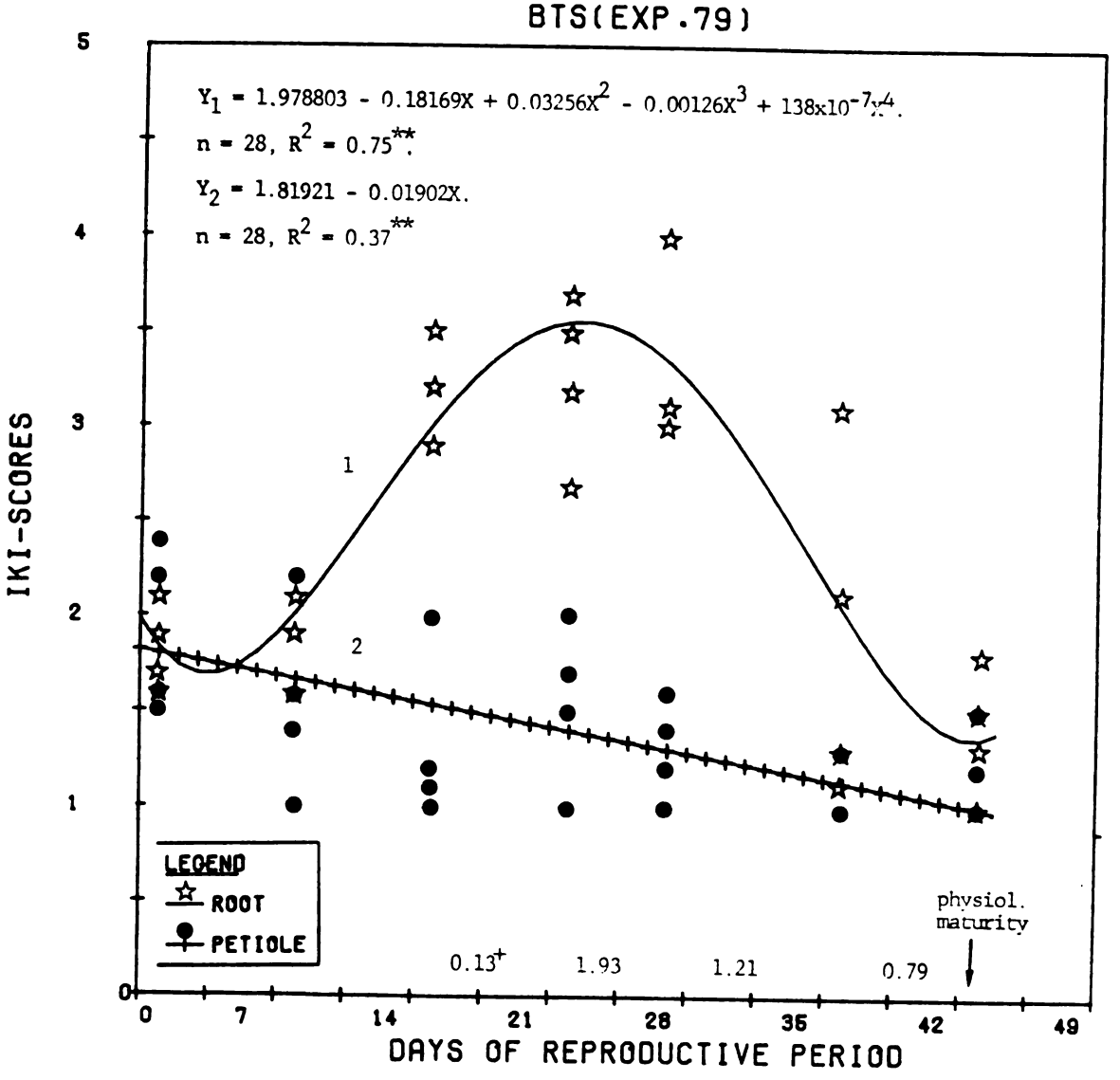

Fig. IV.5: Trend of Starch (IKI score) accumulation in roots and leaf petioles of Black Turtle Soup beans during reproductive growth, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

found partly in seed growth rates. The overall daily seed growth rates were 0.71, 0.50, and 0.96 gms per plant, respectively, for the Saginaw Valley Experiments (A78 and B78) and the MSU Crops Farm Experiment.

The highest daily seed weight increased per plant occurred between 22 and 28 days after 50 percent flowering in all experiments. They were 0.99 gms, 0.68 gms, and 1.93 gms respectively for Experiments A78, B78, and 79.

The overall seed weight increase per day and per plant for the experiments B78 and 79 (0.71 and 0.96 gms day^{-1} per plant, respectively) were higher than that for the other experiment (0.05 gms). The yields for Experiment 79 was significant greater (Table 9). On the other hand, if we consider the A78 and B78 low yields and the active simultaneous remobilization of both types of non-structural carbohydrates from the major storage tissues which are the root and stem, it seems that Black Turtle Soup responded to water stress (discussed in the next section) by remobilization in order to maintain the 100-seed weight (I did not measure this character). As compared to the other two experiments, the yield from the MSU Crops Farm planting was spectacular (Table 9) even among all entries, but the tropical bean seems to have utilized only small amounts of its stored carbohydrates. The root was no longer involved in supplying material to

the growing seed. Neither was remobilization from the stem and the leaf petiole as extensive as in previous plantings. Indeed, it can be seen (Fig. IV.5) that the amounts of starch only decreased in the stem during the period of highest demand, that is, the period of the highest seed growth rate. Besides, the slope of the line describing the changes in levels of starch in the leaf petiole is weak and the $R^2 = 0.37$ is small.

Thus, the MSU Crops Farm was better than the Bean and Sugar Beet Farm for the growth of BTS. Data by Peet et al (1977) indicate a 30 percent increase in the photosynthesis rate of BTS from first flowering to late pod development. Possibly the MSU Crops Farm environment did allow this performance. By comparing the yields and the overall seed growth rates for the Bean and Sugar Beet Farm experiments, it appears that the higher the seed growth rate, the higher the yield. The lower the seed growth rate, the more difficult it would have been for BTS plants to maintain the specific seed weight, therefore, the more stored carbohydrated would have been withdrawn from storage tissues. The fact that the BTS population required time and a higher daily seed growth rate to achieve a spectacular yield corroborates once more the shared importance of both growth rate and duration in achieving higher yields in common beans.

Nep-2

The remobilization patterns of NSC are shown in Figures V.1-5 for root, stem, leaf petiole, and pod wall. Nep-2 showed its first flowers on day 43 after planting, 50 percent of the population had flowered on day 45 and the full bloom was observed two days later. Nep-2 is a late maturing dry bean cultivar.

Like Redkote in Experiment A78, the amounts of starch in leaf petioles of Nep-2 decreased during the flowering period then remained almost at the same level before they decreased again in the period of the highest seed growth rate (0.78 gms per plant) between 21 and 30 days after mid-flowering. During the following week, leaf petioles were already dry prior to the next sampling (Experiment A78). The remobilzation of soluble solids in stems can be noted for the period of the highest seed growth rate, i.e., between 26 and 29 days after mid-flowering (Experiment B78). From data on Experiment B78, second degree polynomial equations for starch in roots, soluble solids in roots and leaf petiole were fitted and did show a tendency to remobilization, but are not reported because their coefficients of multiple determination were too small; they were respectively, 0.33, 0.27, and 0.44. Both Figures V.3 and 4 (Experiment 79) indicate that the remobilization of starch did take place in roots and stems

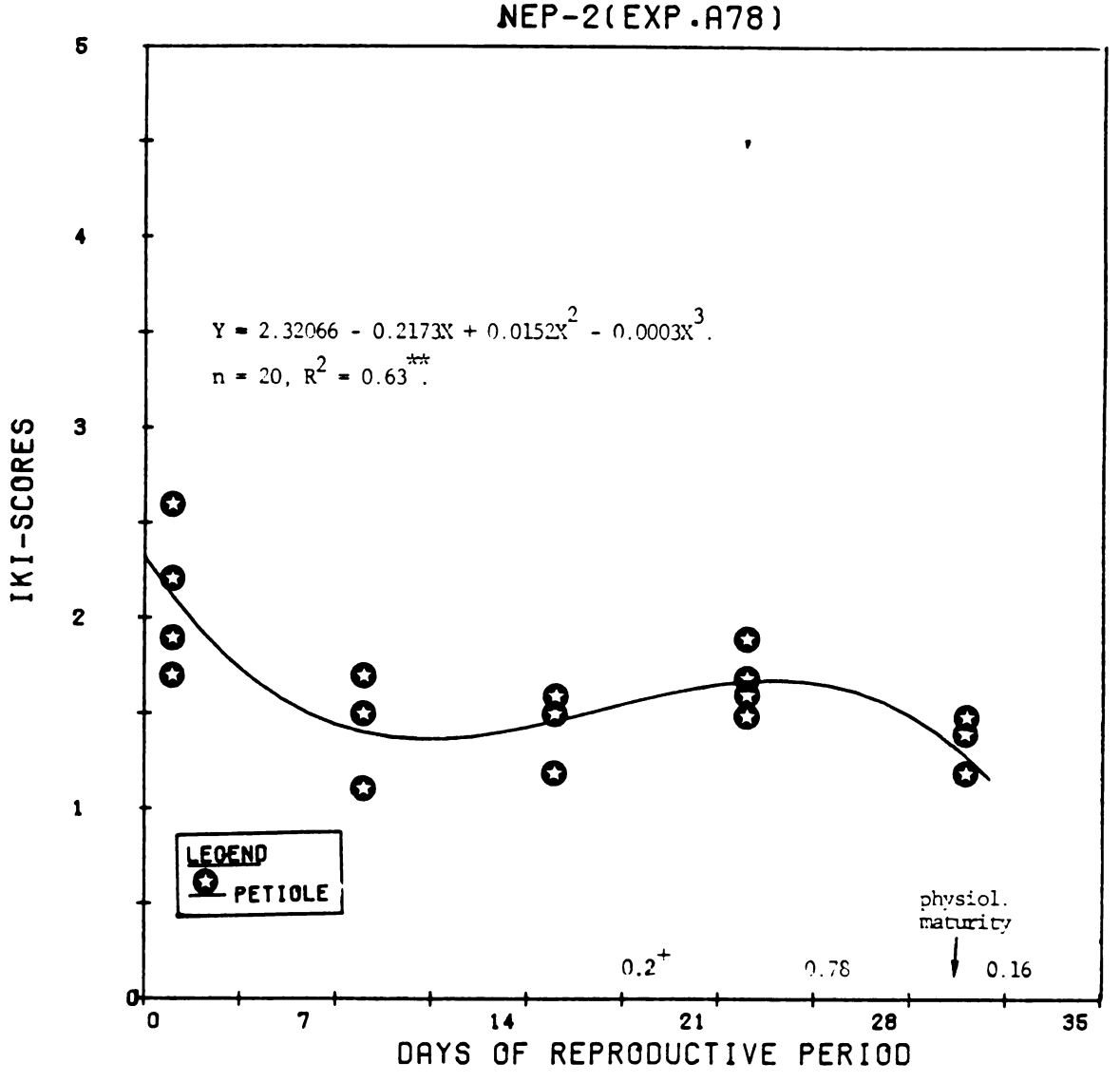

Fig. V.1: Trend of starch (IKI score) accumulation in leaf petioles of Nep-2 beans during reproductive growth, Bean and Sugar Beet Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

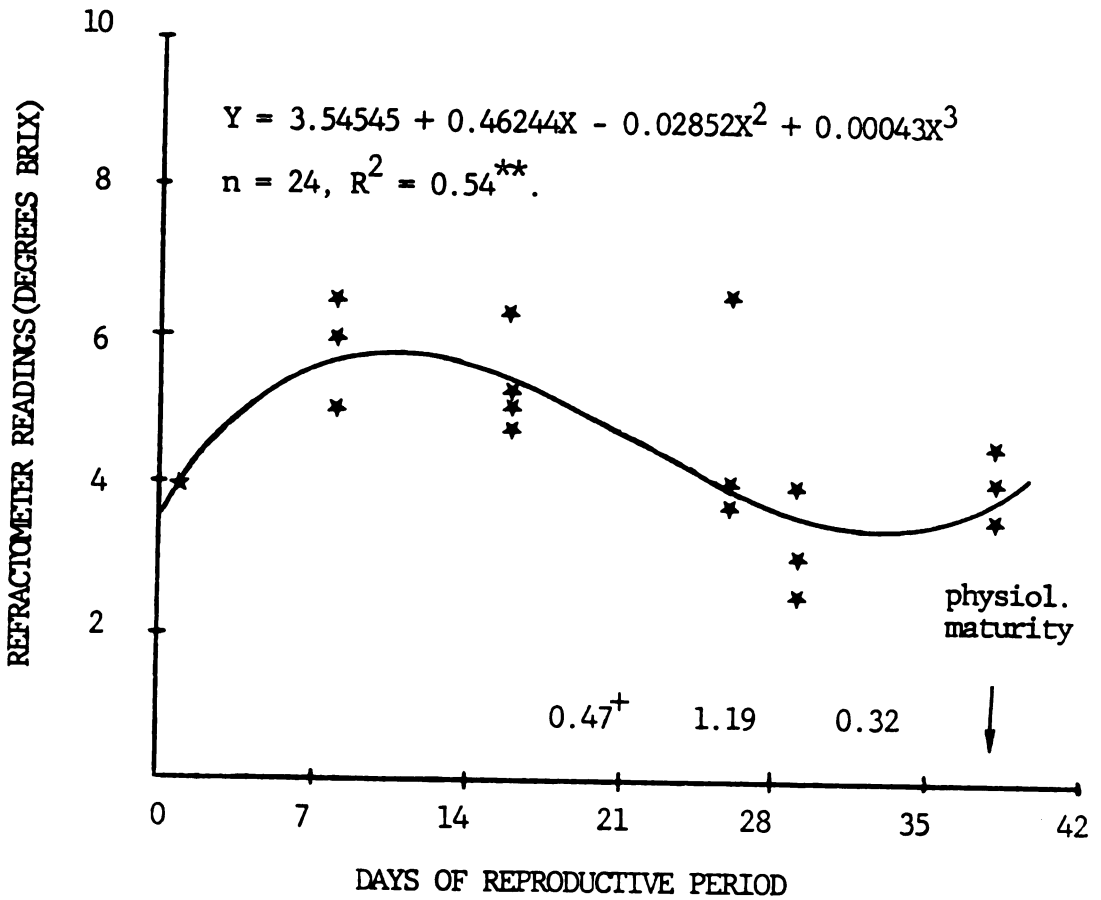

Fig. V.2: Trend of soluble solids (refractometer values) accumulation in stems of Nep-2 beans during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

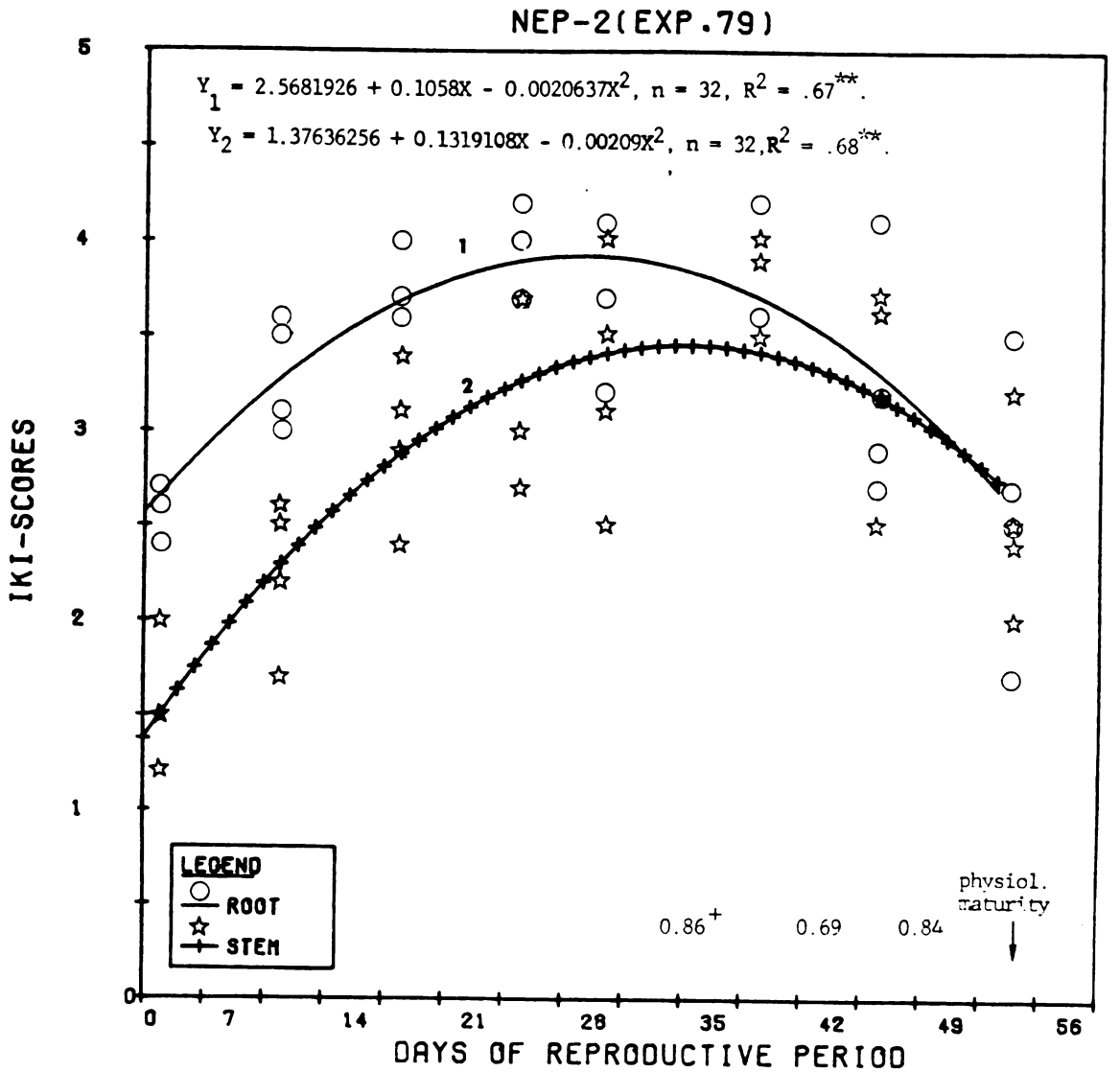

Fig. V.3: Trend of starch (IKI score) accumulation in roots and stems of Nep-2 beans during reproductive growth, MSU Crops Research Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

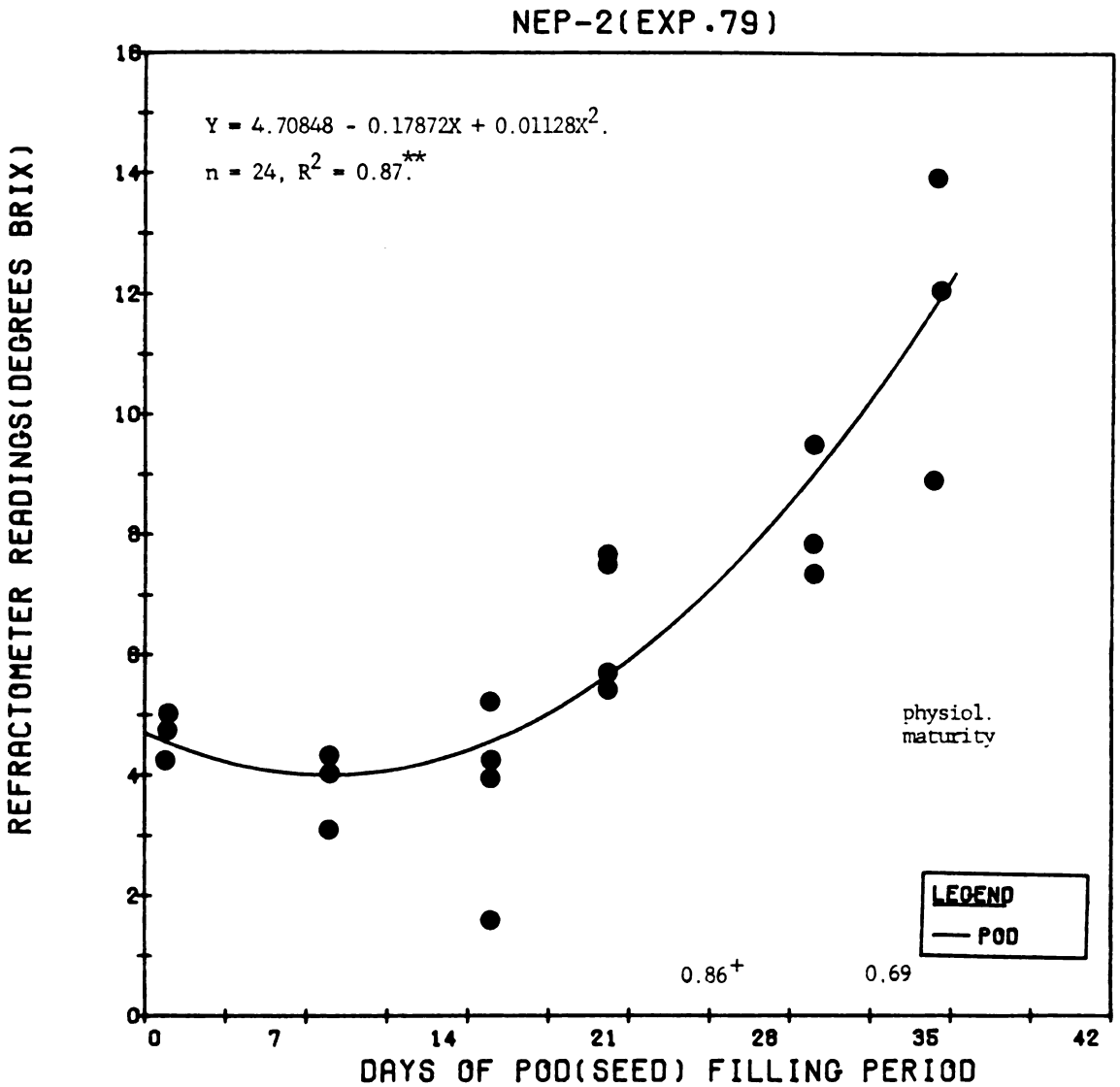

Fig. V.4: Trend of soluble solids (refractometer values) accumulation in pod walls of Nep-2 beans, MSU Crops Research Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

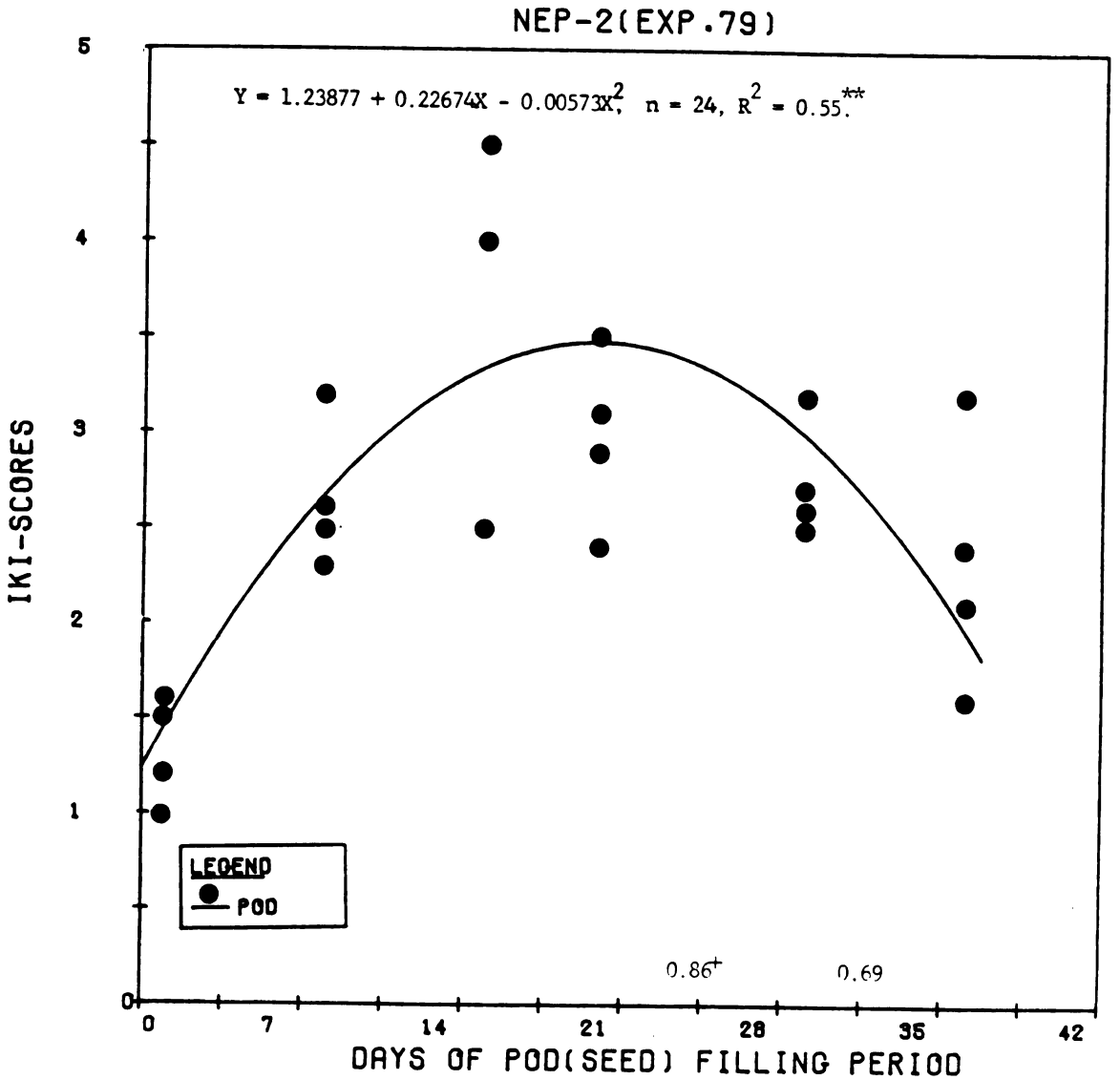

Fig. V.5: Trend of starch (IKI score) accumulation in pod walls of Nep-2 beans, MSU Crops Research Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

from about day 28, and from pod walls from day 35 after mid-flowering until physiological maturity. By that time, however, the amounts of soluble solids in pod walls were increasing (Fig. V.5).

Yield performances (Table 9) suggest that Nep-2 needed to withdraw carbohydrates from storage sites in order to complete a relatively high yield. Indeed, where the yield was the lowest (Experiment A78), only the petiole had contributed to the support of seed growth. Where it was higher (Experiment B78), roots, stems, and leaf petioles contributed, but poorly (small R^2). Experiment 79 gave the highest yield and therefore the root, the stem, the leaf petiole and pod wall had to remobilize their starch for the sake of seed development.

Nevertheless, the overall picture presented by the patterns under discussion suggest that Nep-2 is a poor remobilizer of previously stored non-structural carbohydrates.

Carlos Burga (1978) compared the photosynthetic capacity of Seafarer and Nep-2 during their reproductive periods. The minima CO_2 uptake were 12.9 and 5.75 mg CO_2 dm^{-2} hr^{-1} and the maxima were 16.31 and 10.77, respectively, for Seafarer and Nep-2. It appears that Seafarer is more efficient in CO_2 uptake as it is for remobilization of NSC. In all experiments seed filling durations

for Nep-2 were one week longer than those of Seafarer. But overall daily seed filling rates per plant were higher for Seafarer than for Nep-2 in the Bean and Sugar Beet Farm experiments. Overall daily seed filling rates for both cultivars were equal (0.50 gms day^{-1} per plant) in the MSU Crops Farm experiment. In this experiment, total seed filling durations were 42 for Seafarer and 50 days for Nep-2 and these extended durations contributed to increased yields for both cultivars (Table 9). Nevertheless, in all experiments Seafarer had higher yields than Nep-2 but without a significant difference. In most cases yields of Nep-2 are relatively higher than those of Seafarer; however, Adams (Research Report, 1978) reported significantly higher yields in favor of Seafarer for two tests conducted at the Bean and Sugar Beet Research Farm. The 1978 dry bean yields at that location were affected by severe weather (discussed in the next section) and this impaired more the normal development of the late-maturing Nep-2 than that of Seafarer.

Thus, compared to the early-maturing dry bean, navy-type "Seafarer," the cultivar Nep-2 has a lower photosynthetic efficiency, an extended grain filling period, but has an inefficient pattern of remobilization of NSC.

Swedish Brown

Swedish Brown was only planted in the last two experiments. Curves describing the behavior of stored assimilates in its tissue are presented in Figures VI.1-7.

Curves relative to the 1978 experiments show that the amounts of starch kept increasing in roots and stem from flowering to near maturity. As for soluble solids, curves (Fig. VI-2) show that they remained at almost comparable levels in roots, stems, and petioles throughout the reproductive period. Nevertheless, amounts of starch (Fig. VI.3) in pod walls decreased sharply during the period of the highest daily seed growth rate between 28 and 38 days after mid-flowering (Experiment B78). This situation was also observed for starch in the same tissue (Experiment 79) (Fig. VI.6) between 29 and 61 days after mid-flowering. In Figures VI.3 and VI.6, the above-mentioned periods of reproductive growth correspond, respectively, with 13-23 (Experiment B78) and 14-36 (Experiment 79) days from the first sampling of pod wall at day 15 after mid-flowering. These days are referred to, in the graphs, as days of grain filling period. The slight deflections in curves may denote the demand that all developing tissues imposed on the sites of stored assimilates, for this insignificant remobilization took place when pods, leaves, stems, and roots were reaching their maximum weights.

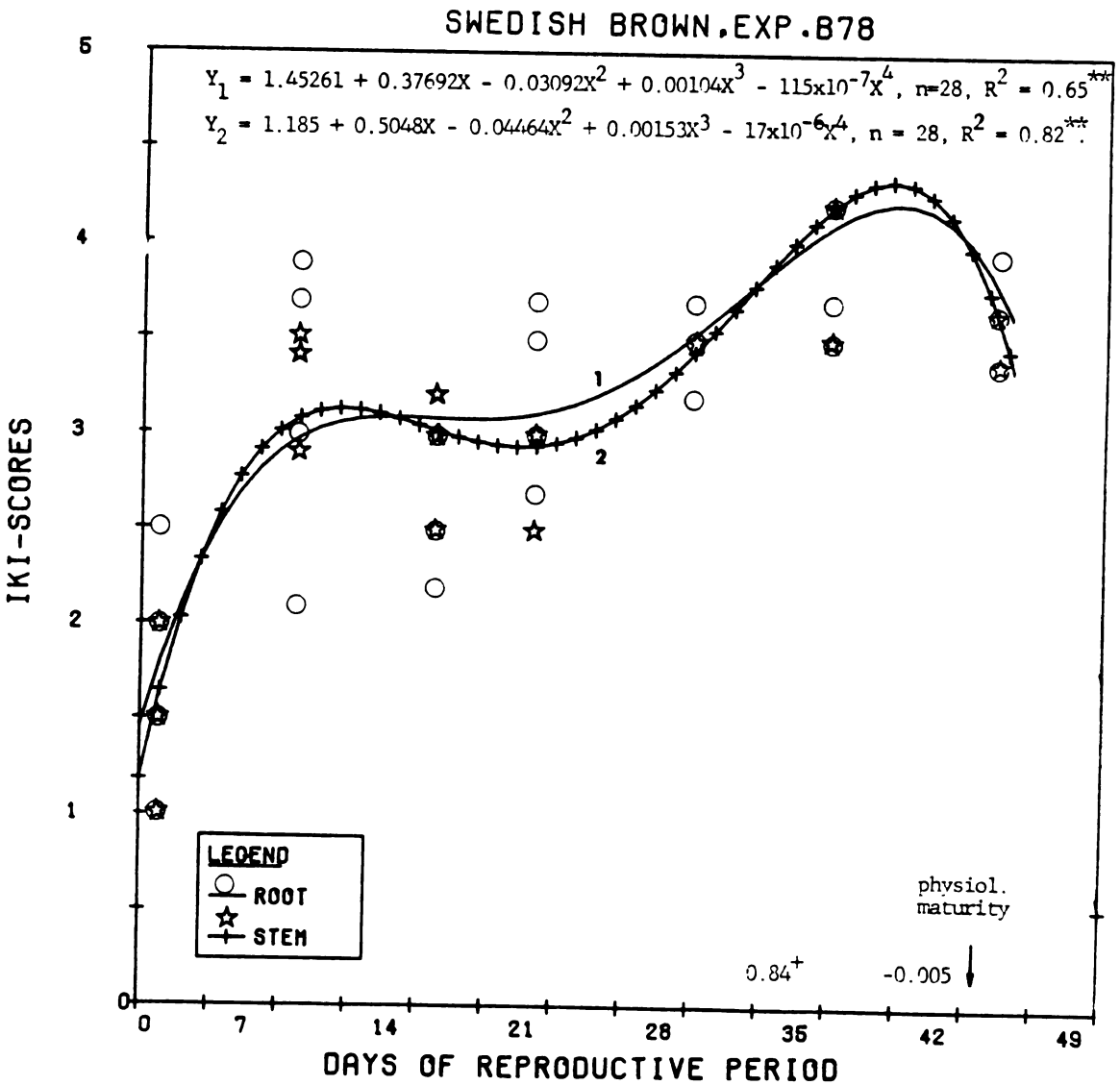

Fig. VI.1: Trend of starch (IKI score) accumulation in roots and stems of Swedish Brown beans during reproductive growth, Bean and Sugar Beet Research Farm Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

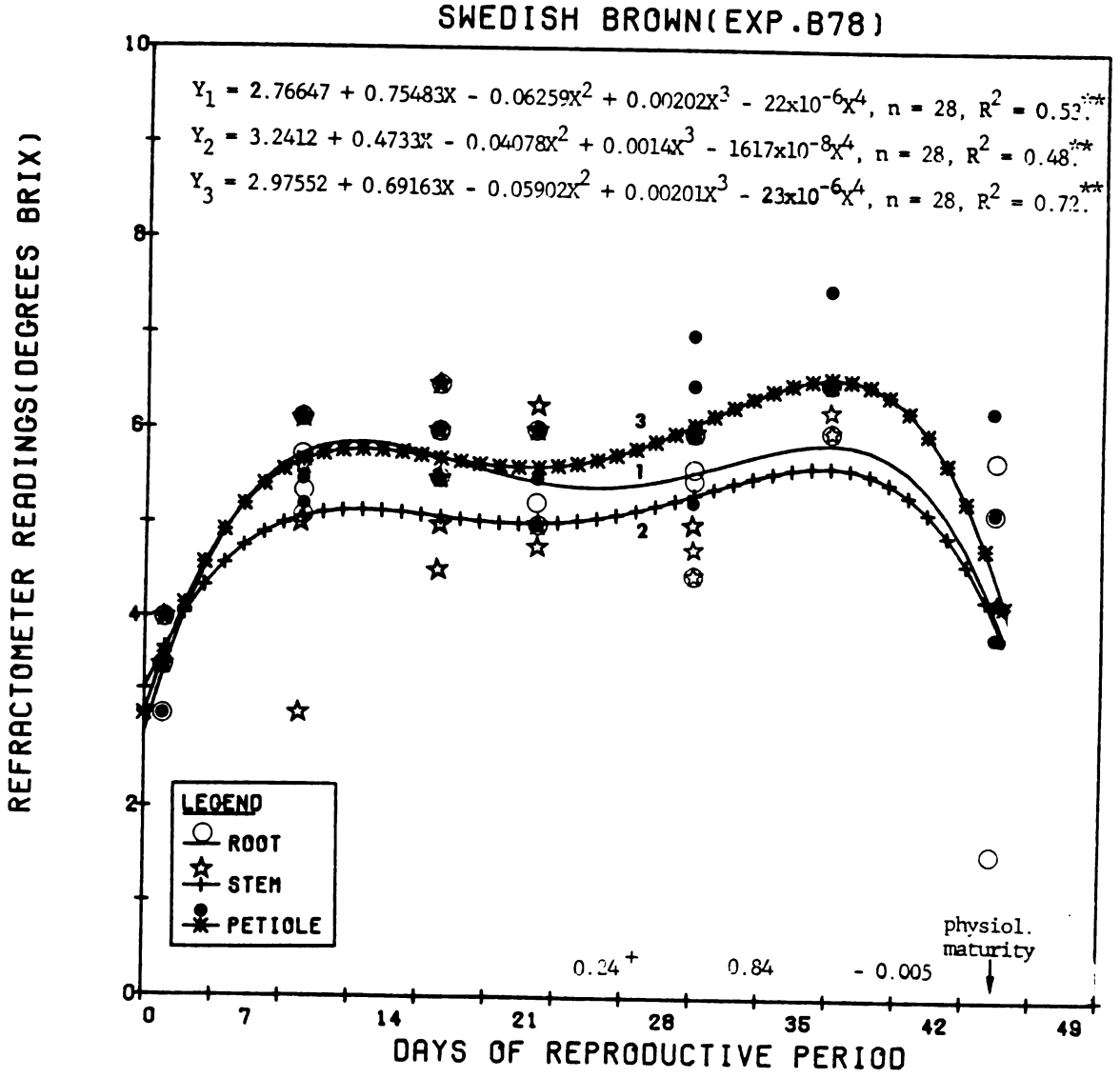

Fig. VI.2: Trend of soluble solids (refractometer values) accumulation in roots, stems, and leaf petioles of Swedish Brown beans during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

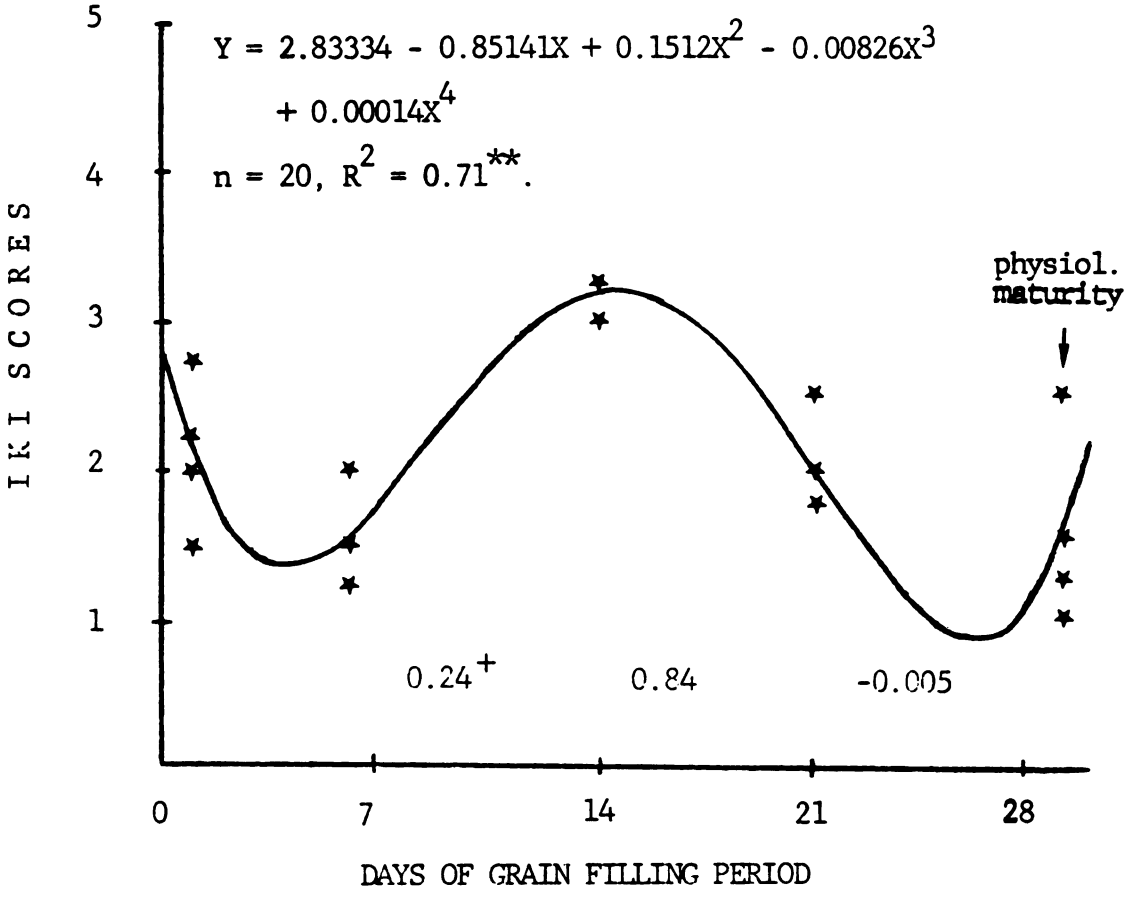

Fig. VI.3: Trend of starch (IKI score) accumulation in pod walls of Swedish Brown beans, Bean and Sugar Beet Farm, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

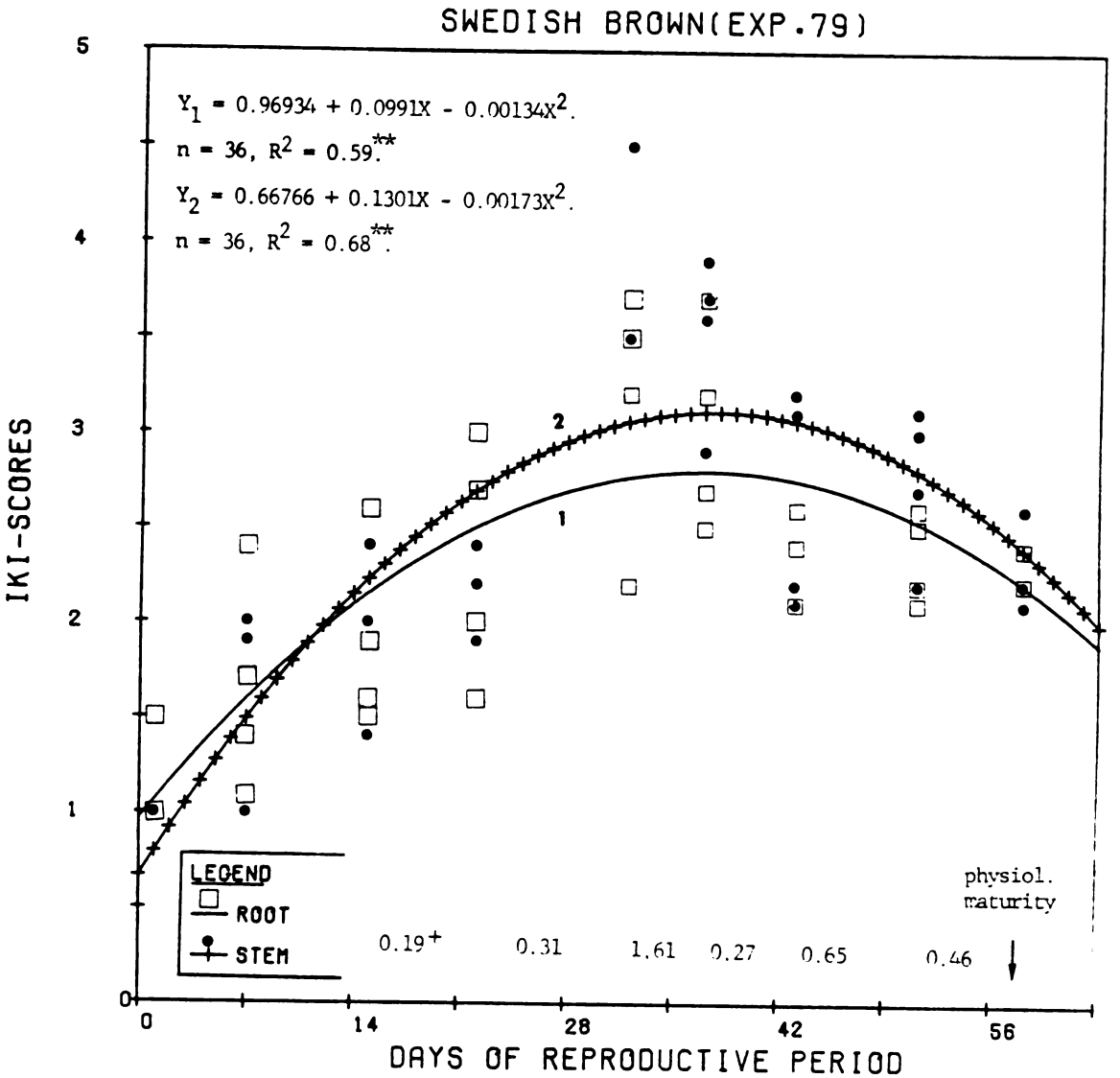

Fig. VI.4: Trend of starch (IKI score) accumulation in roots and stems of Swedish Brown beans during reproductive growth, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

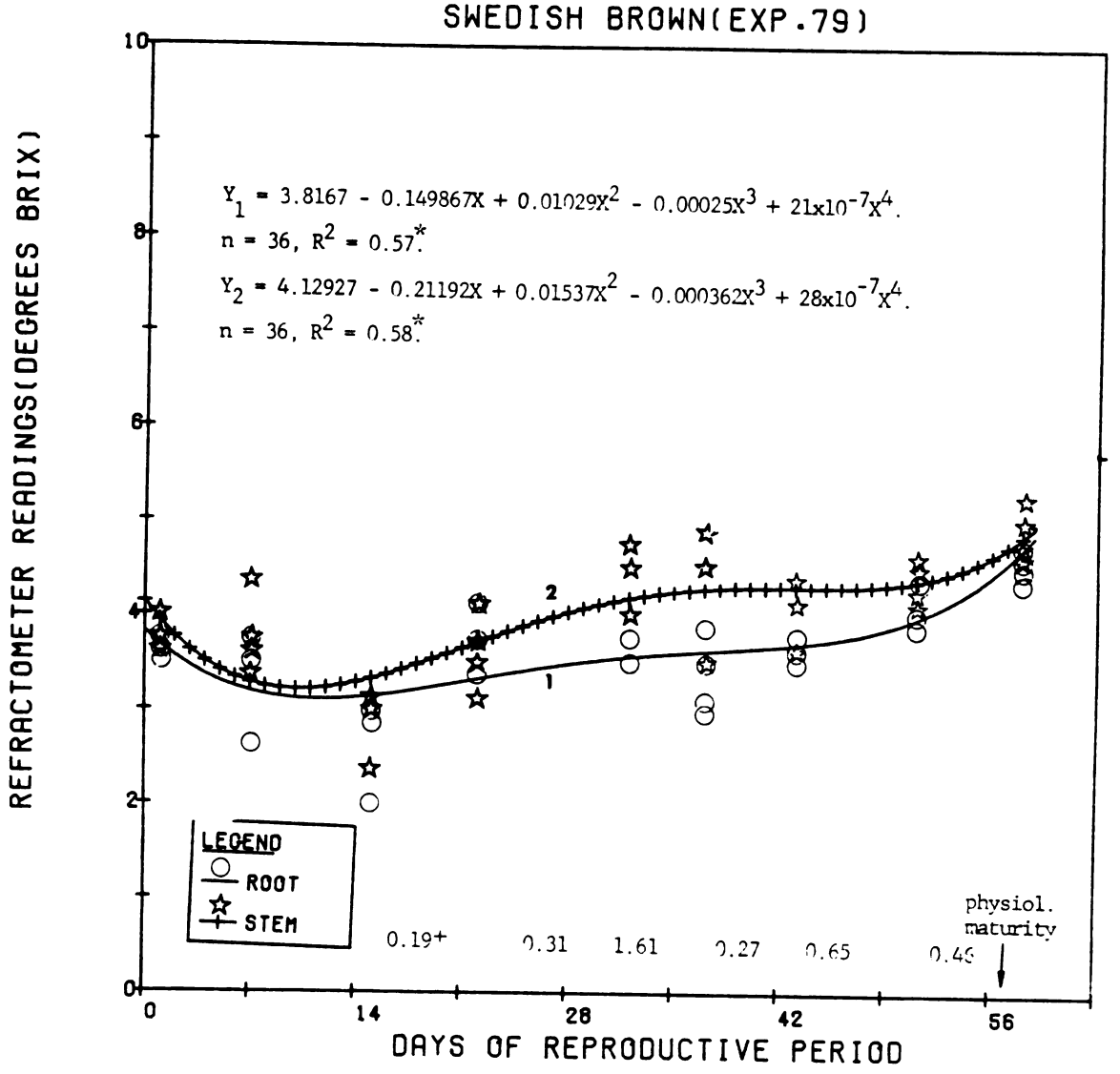

Fig. VI.5: Trend of soluble solids (refractometer values) accumulation in roots and stems of Swedish Brown beans during reproductive growth, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

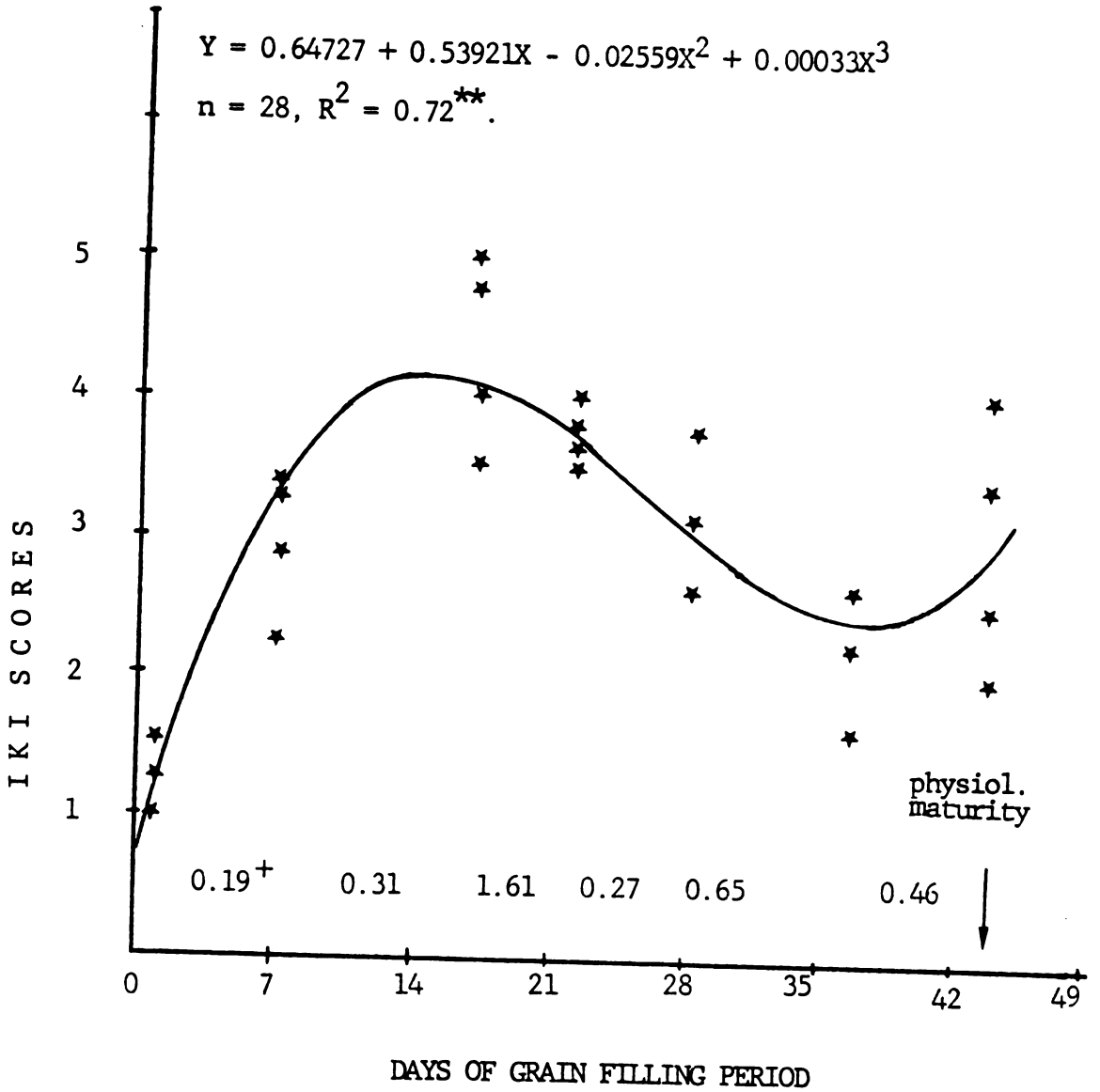

Fig. VI.6: Trend of starch (IKI score) accumulation in pod walls of Swedish Brown beans, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

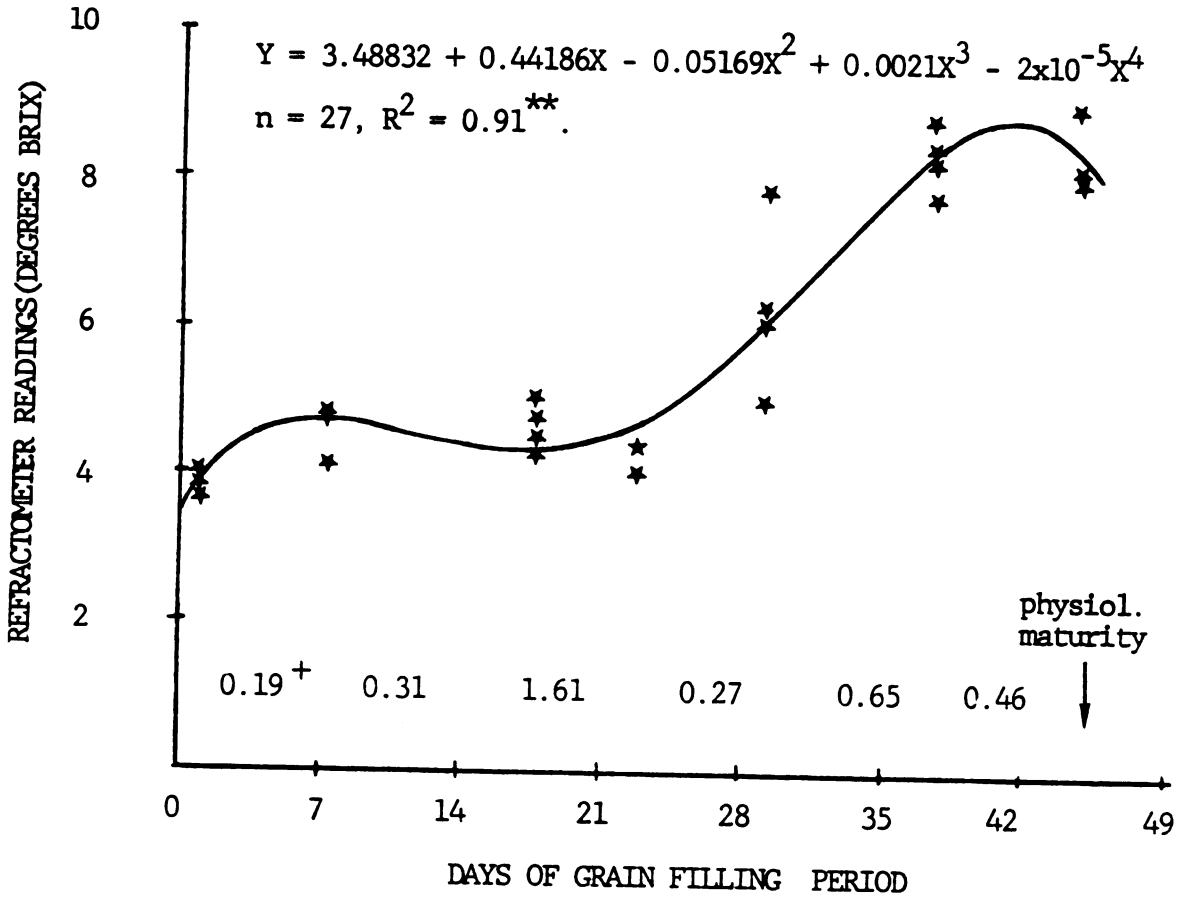

Fig. VI.7: Trend of soluble solids (refractometer values) accumulation in pod walls of Swedish Brown beans, MSU Crops Farm, 1979.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

The highest seed daily growth rate (0.84 gms per plant) occurred between 28 and 35 days after mid-flowering in Experiment B78, that is, the period when the highest levels of stored starch and soluble solids were observed in tissues. Possibly, during this time (28-35 days) LAI and Co_2-uptake were greatest exceeding the capacity of the sink to absorb photosynthetic products.

Experiment 79 offers a somewhat different, but yet similar, pattern in that the amounts of starch began declining in roots and stems in the period of the highest daily seed growth rate (1.6 gms per plant) between 32-37 days after mid-flowering, and in that amounts of soluble solids in the same tissues remained at almost the same levels during the period from mid-flowering to physiological maturity. The remobilization is possibly accountable, in part for the higher yield obtained in the 1979 season.

The remobilization pattern described for Swedish Brown is to a great extent similar to that of the red kidney bean cultivar "Redkloud." In another connection, Peet et al (1977) reported increases in photosynthesis of 873 percent for Swedish Brown and 408 for Redkloud from flowering to early pod set. Unfortunately, they did not provide data for the period of late pod development. Nevertheless, it seems that during the reproductive period the photosynthesis of these dry bean cultivars always exceeds the capacity of the seed to accumulate assimilates.

Swedish Brown is also similar to Redkloud in flowering patterns. First flowers appeared 33 days after planting, mid-flowering occurred 2 to 3 days later, full bloom was observed at day 38 and both cultivars stopped flowering at day 56 after planting.

California Small White

Due to day-length California Small White was very late in my experiments. Even for Experiment A78 which was planted May 25th completely mature seeds were not harvested because frosts occurring in September had damaged the leaves and non-mature pods. Second and third degree curves had very small coefficients of multiple determination.

Vigna angularis I
(Adzuki beans)

Polynomial functions describing changes in starch levels of roots, stems and leaf petioles are shown in Figures VII.1 and 2. Vigna angularis I had an extended flowering period. In the 1979 planting, the first flowers of Vigna angularis I appeared at day 45 after planting. Days when 50 percent flowering, full bloom, and end of flowering occurred, were 48, 55, and 99 days after planting respectively. It was even difficult to determine the physiological maturity for Adzuki beans because while old pods shattered and lost their seeds many young pods were

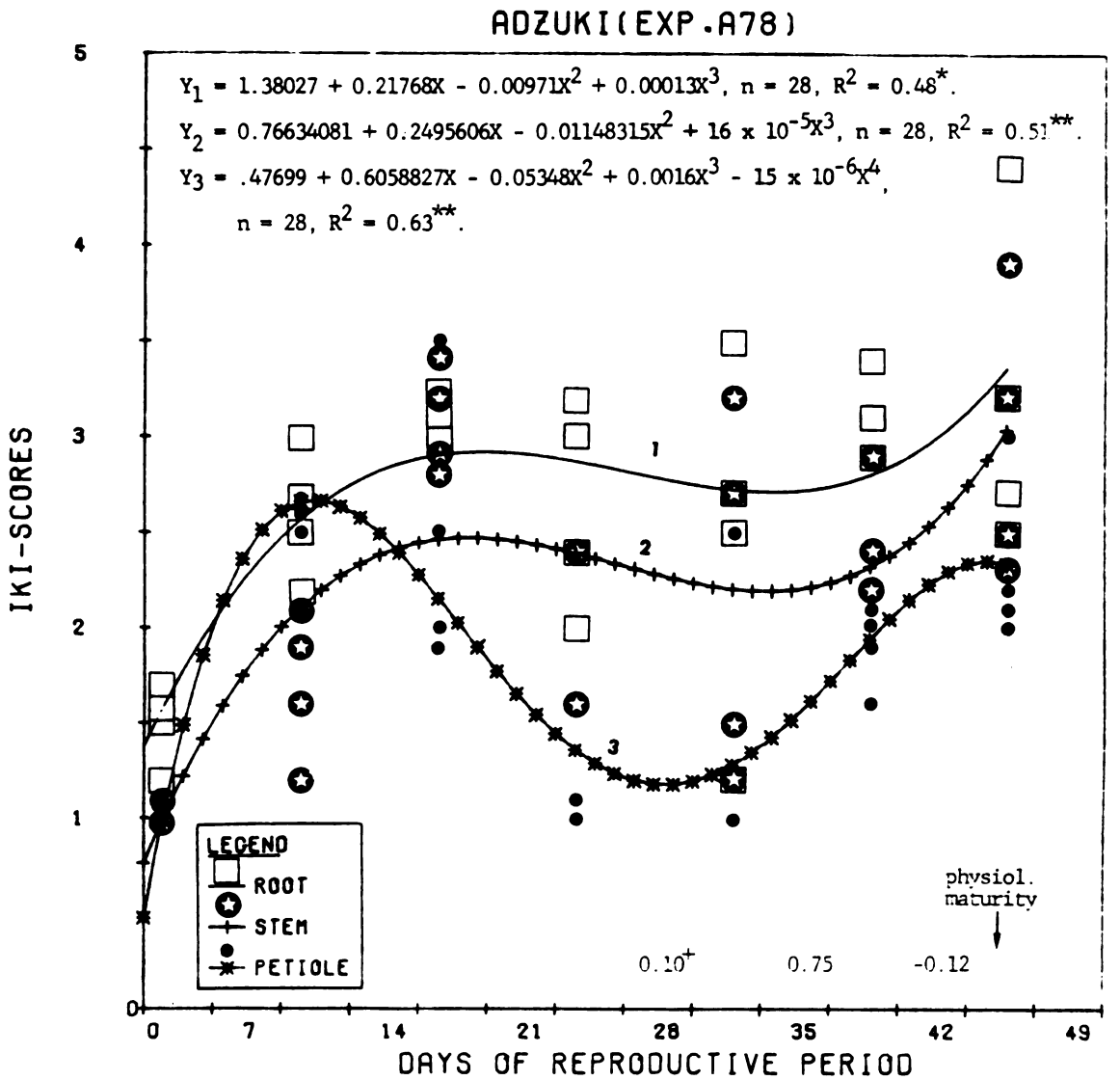

Fig. VII.1: Trend of starch (IKI score) accumulation in roots, stems, and leaf petioles of Vigna angularis (Adzuki beans) type I during reproductive growth, Bean and Sugar Beet Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

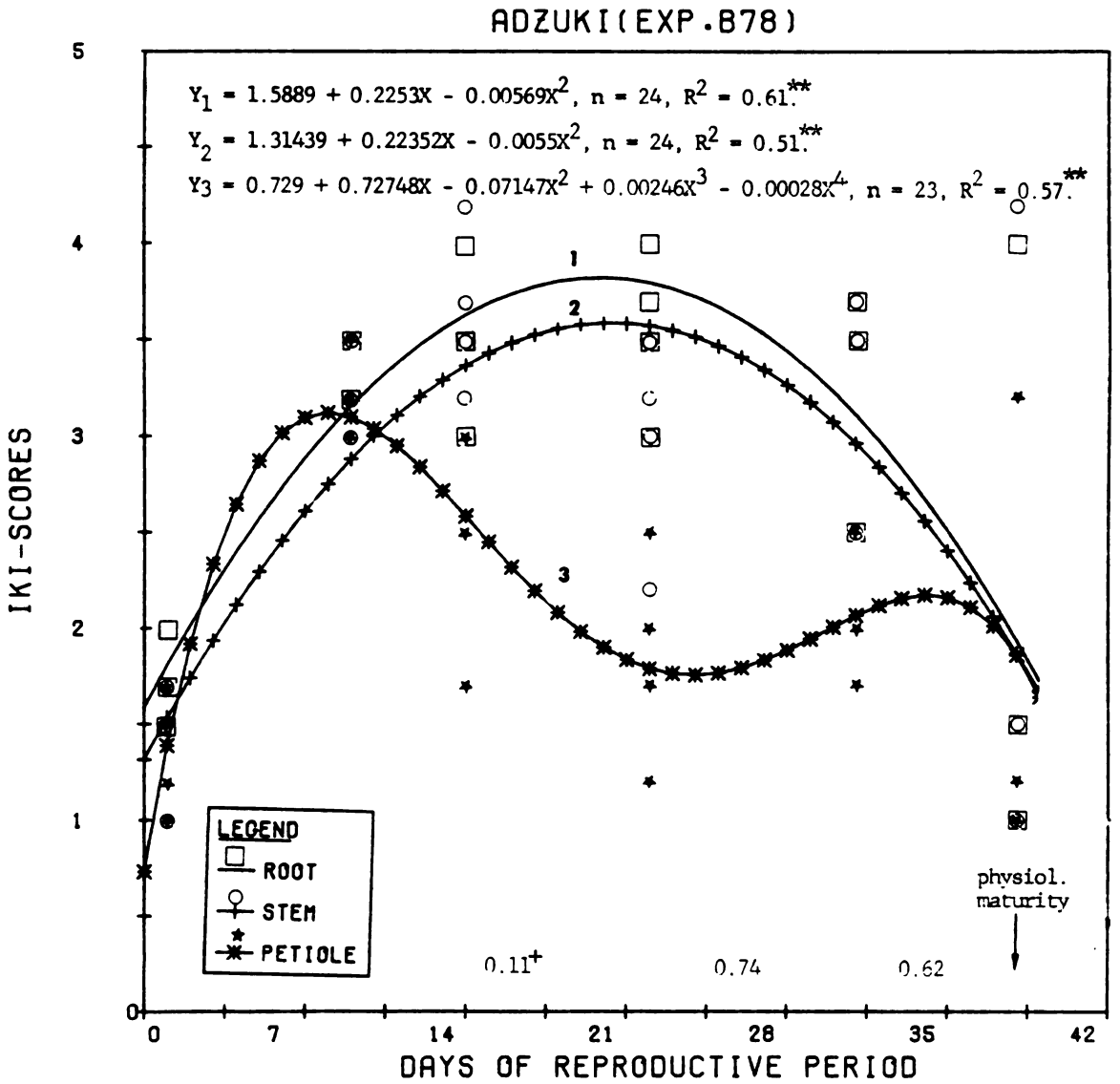

Fig. VII.2: Trend of starch (IKI score) accumulation in roots, stems, and leaf petioles of Vigna angularis (Adzuki beans) type I during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

still green and developing. The leaves of plants in Experiment A78 maintained their deep green color throughout the reproductive period. Those in Experiment B78 were damaged by frosts which occurred at the end of September and beginning of October. The graphs relative to Experiment B78 (Fig. VII.2) show that samples from 2 replications had higher amounts of starch than the two other replications. If these replications with higher values were plotted alone, they would yield curves similar to those of the previous planting (A78).

In Experiment A78 and for both roots and stems, levels of starch increased from 50 percent flowering until the period when the seed began its development. The slight deflections seen in curves correspond with the linear phase of seed growth in which the highest daily seed growth rate was 0.75 gms per plant between 30 and 37 days after mid-flowering. Between 37 and 44 days the seed was no longer growing.

In the B78 experiment Vigna Angularis I utilized starch in storage to support the growing seed. The highest daily seed growth rate (0.74 gms per plant) occurred between 22 and 31 days after mid-flowering. By that time, the decrease in the amounts of starch in roots and stems had already started, from the 18th day after mid-flowering.

Starch in leaf petioles behaved as in Redkloud. In the early seed development period levels of starch in

leaf petioles decreased substantially, but recovered by the time when the root and stem began to remobilize their stored products.

It seems that the compensation phenomenon takes place in this Asian bean cultivar. It may be that the proximity law requires the petiole initially to nourish the young seed of the same nutritional unit, but this is supplemented greatly from assimilates stored in root and stem when the sink demand becomes stronger as the seed develops.

The MSU Crops Farm (Experiment 79) did not favor the vegetative development of Adzuki beans. One replication had dwarf plants and plants in two other replications did not develop normally. The data from this experiment did not fit a regression line of any order. That is, the amounts of NSC practically remained at the same levels throughout the reproductive period.

It appears from the Bean and Sugar Beet Farm experiments that Vigna angularis I needs to use only small amount of stored NSC to support seed growth. From curves, it seems also that when old leaves remained green and younger ones grew their photosynthetic capacity remained relatively constant or may even have increased during the seed development period.

Evans soybean

Evans soybean, as compared to Beeson, is an early-maturing variety. The first flowers appeared 35 days after planting and 4 days later 50 percent flowering occurred. Full bloom occurred at day 41 and flowering continued until day 60 after planting. Plants did not develop well in three replications at the MSU Crops Farm. Data from this location did not show any changes in NSC. Besides, the yield (Table 9) was numerically the lowest of the three experiments.

Soybeans store NSC in leaf petioles (Table 2 and 3) and are known to be photosynthetically more efficient than dry beans. Indeed, Bhagsari et al (1977) reported data in which the apparent photosynthesis of 16 soybean cultivars ranged from 23 to 37 mg CO_2 $dm^{-2}hr^{-1}$. In addition, Scott et al (1980) observed carbon exchange rates ranging from 17.9 to 26.8 mg CO_2 dm^{-2} hr^{-1} 80 days after emergence.

In Experiment A78, Evans remobilized small amounts of starch from leaf petioles during the seed growth period (Fig. VIII.1) but in Experiment B78 (Fig. VIII.2 and 3) the remobilization of both starch and soluble solids seems to have been greater since in addition to leaf petioles, root and stem tissues were also involved. In this planting, the highest seed increase rate (0.83 gm day^{-1} per plant) occurred between 28 and 35 days after

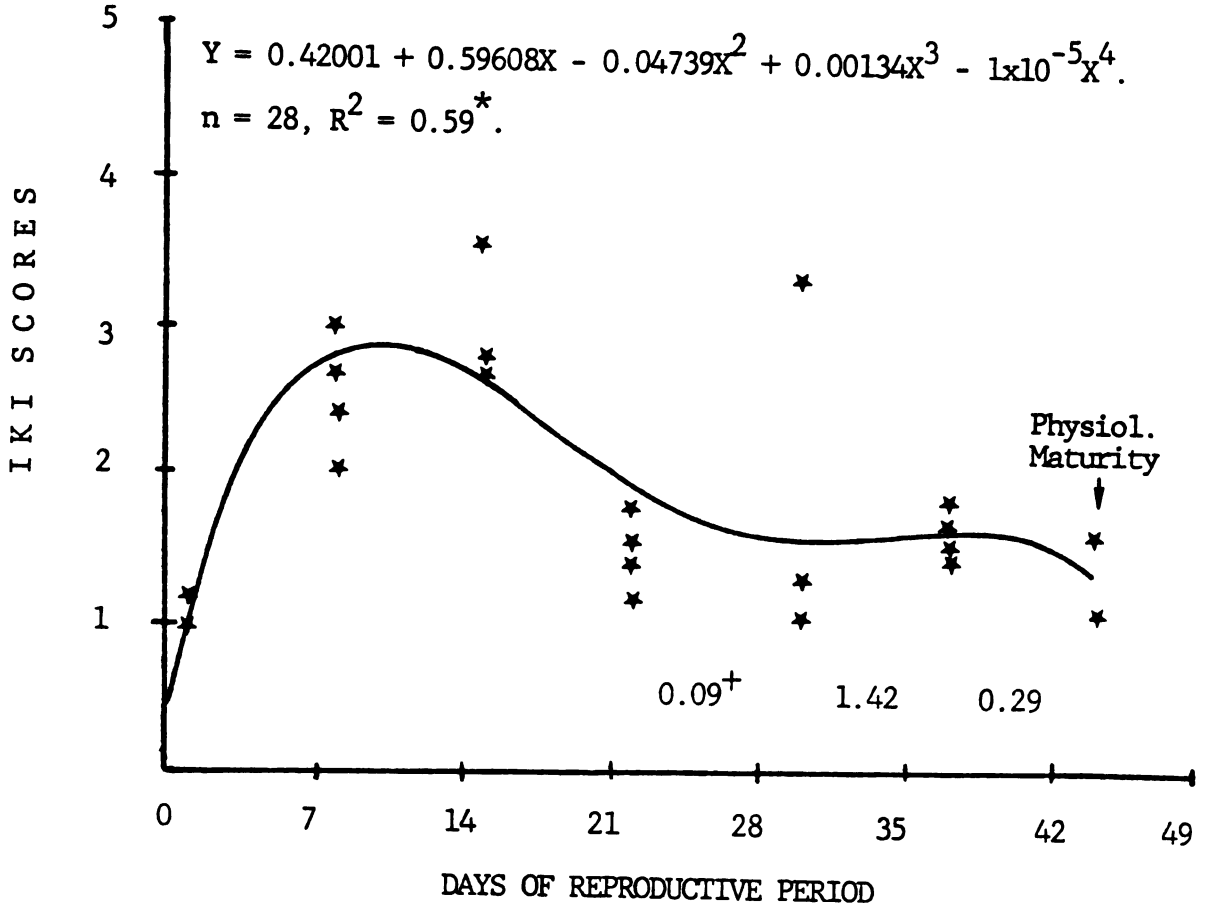

Fig. VIII.1: Trend of starch (IKI score) accumulation during reproductive growth in leaf petioles of Evans soybean grown at the Bean and Sugar Beet Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

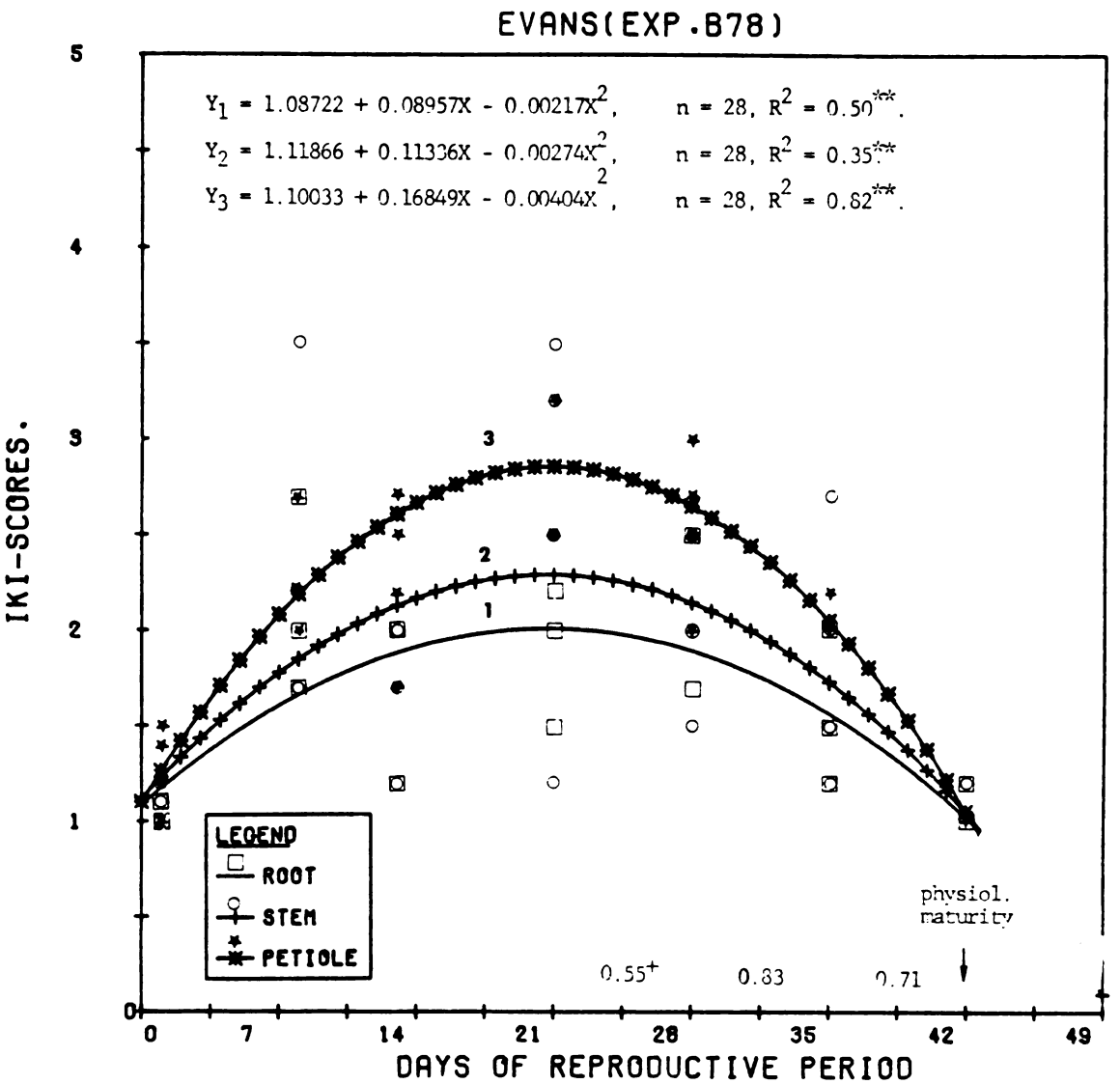

Fig. VIII.2: Trend of starch (IKI score) accumulation in roots, stems, and leaf petioles of Evans soybeans during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

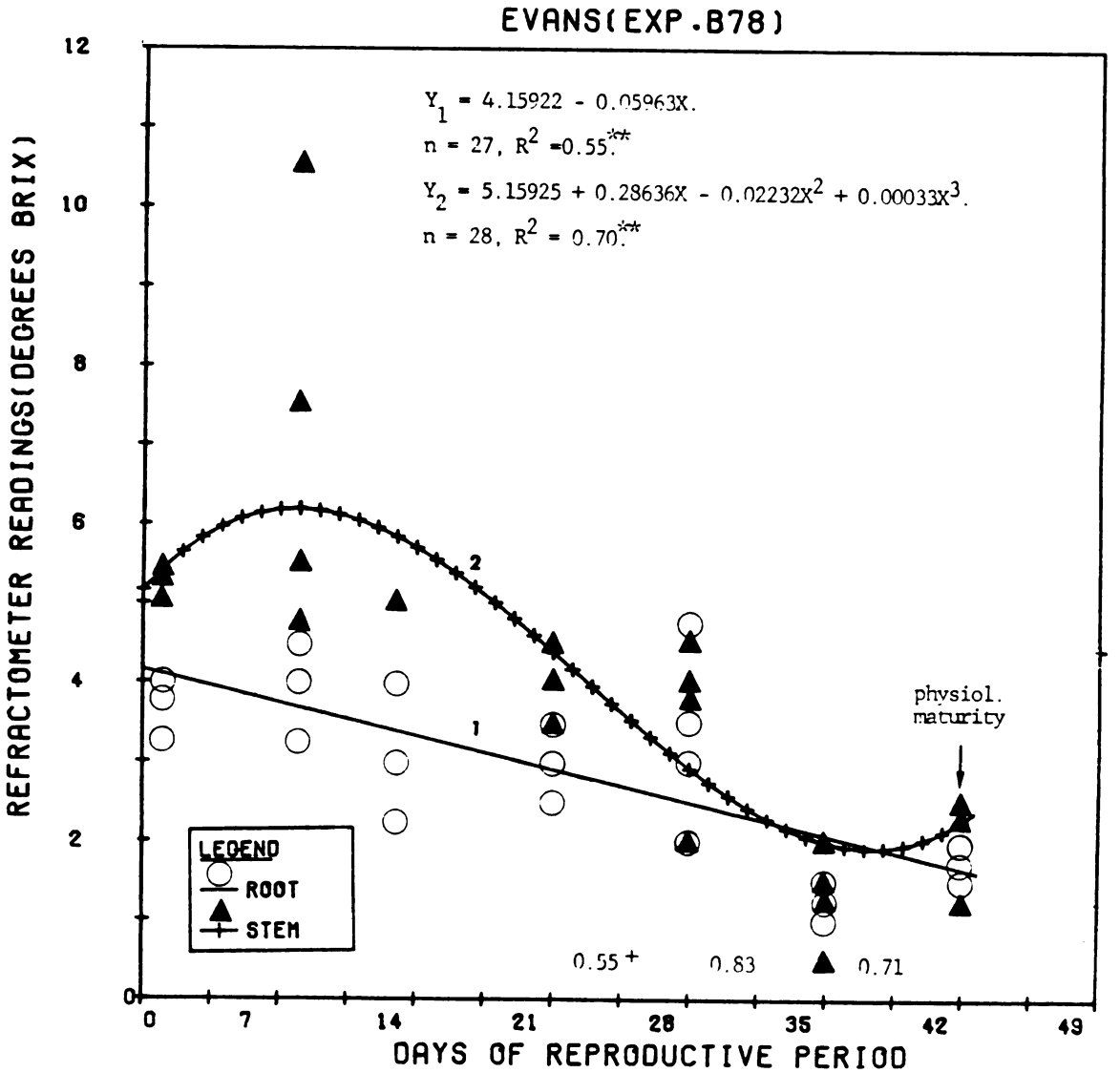

Fig. VIII.3: Trend of soluble solids (refractometer values) accumulation in roots and stems of Evans soybeans during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

mid-flowering. From day 28 to physiological maturity, the overall seed growth rate was also high (0.71 gm day^{-1}) and this was supported by the active remobilization which took place in root, stem, and leaf petiole.

Coefficients of multiple determination for curves describing changes in NSC in roots, stems, and leaf petioles indicate that remobilization of starch was more important in leaf petiole than in root and stem tissues (Experiment B78) which instead used their soluble solids in storage to support seed growth (Fig. VIII.3). This is logical since not much starch was observed in roots and stems (Table 2).

Beeson Soybean

Beeson soybean is a very late variety that reaches physiological maturity about 70 days after flowering in Michigan. In all experiments its growth was curtailed by severe frosts of late September and early October. The first experiment (A78), however, was planted early enough (May 25th) and the frosts came when seed development was almost completed. This was the only experiment in which Beeson soybean reached its physiological maturity. From the data of that experiment, polynomial functions describing changes in the amounts of starch in roots, stems, and leaf petioles (Fig. IX) were derived. The midseed fill was completed about 38 days after

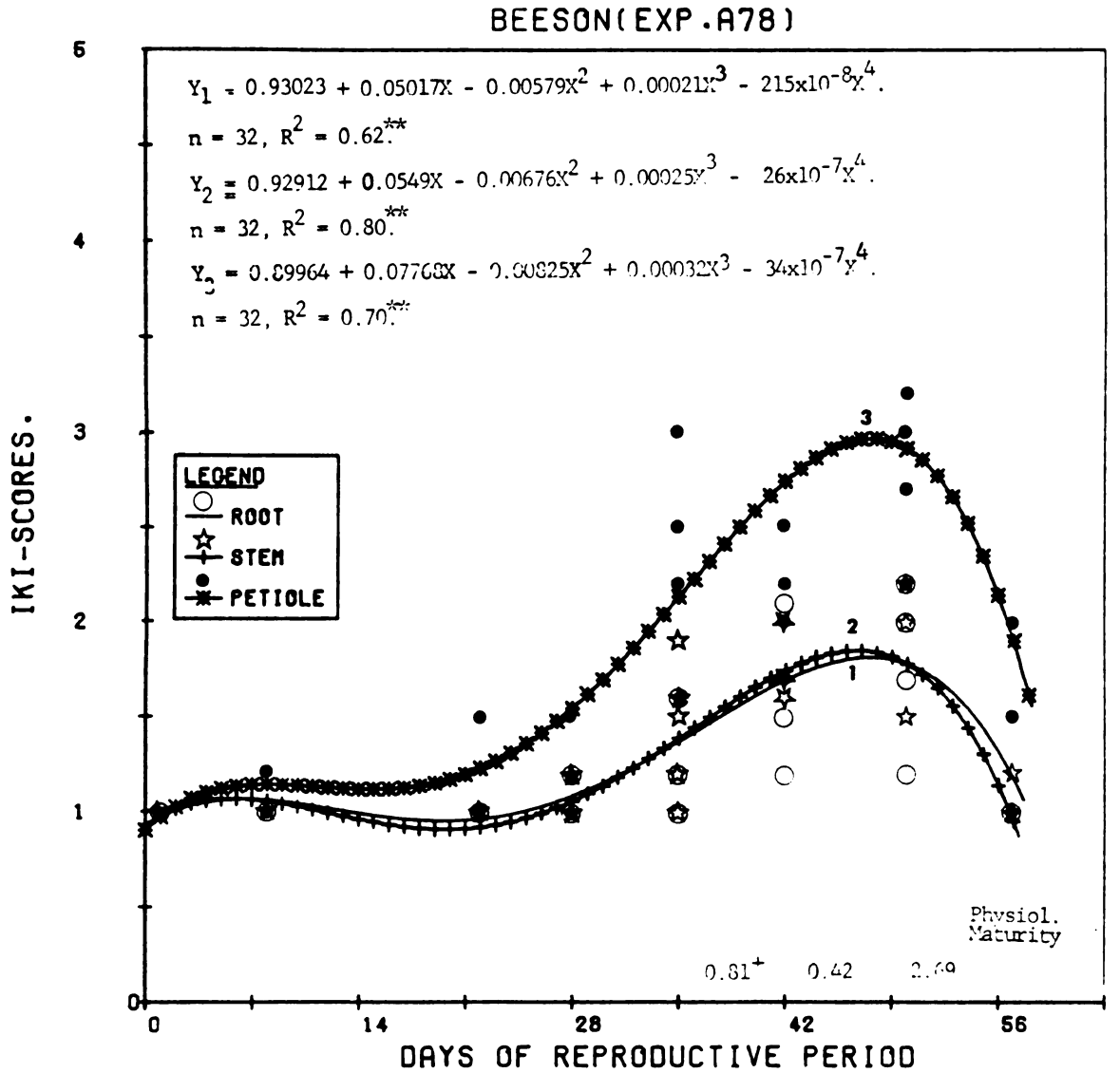

Fig. IX: Trend of starch (IKI score) accumulation in roots, stems, and leaf petioles of Beeson soybeans during reproductive growth, Bean and Sugar Beet Research Farm, Experiment A, 1978.

+: seed growth rate (grams day^{-1} per plant) calculated for two successive sampling dates.

mid-flowering and the highest daily seed weight increase (2.69 gm per plant) occurred between 50 and 57 days after mid-flowering. The first flowering date was day 39 after planting. Mid-flowering and full bloom occurred 6 and 8 days later, respectively. The end of flowering was recorded at day 85 after planting. As for the Experiment A78 the physiological maturity was noted within the week between 57-64 days. In addition, the leaf dry weight measured at day 57 after mid-flowering was the highest of the growing season. The seed growth rate day^{-1} calculated per plant for the period between 35 and 57 days after mid-flowring was 1.27 gms per day per plant.

Graphs (Fig. IX) indicate that the amounts of starch increased from day 21 and began to decline at day 48 after mid-flowering, just when the seed entered the phase of highest growth rate. That is, indeed, the time when the storage sites were needed to supplement the leaves in supplying assimilates to the seed sink.

Cowpeas

Four cowpea cultivars have been planted. Cowpea F-51 was the only one which was planted twice (Experiments B78 and 79). The others were not repeated due to lack of sufficient seed. This legume species was characterized by extensive flower abscission. Because of the limited pod bearing, it was impossible to determine the seed growth

rate per plant by sampling four plants per plot as was done for other entries. Likewise, the mid-flowering data could not be determined.

In Experiment B78, cowpea F-51 had partial yield and plants were less etiolated and less twining than they were at the MSU Crops Farm where this cowpea did not bear any pod because all flowers abscised. Figures X.1 and X.2 indicate that the amounts of starch in stems of cowpea F-51 increased during reproductive growth in both locations and so did soluble solids in roots, stems, and leaf petioles (Fig. X.4). In Experiment B78 (Fig. X.3) in which cowpea F-51 bore pods, levels of sugars remained almost constant in root and decreased slightly from 50 percent flowering until about day 30 after mid-flowering and thereafter increased. Likewise, soluble solids in roots, stems, and leaf petioles of cowpea Pink Eye (Experiment 79, Fig. X.7) increased during reproductive growth whereas levels of starch in stems (Fig. X.6) decreased during the pod ripening period. Dry matter of vegetative tissues accumulated in the same fashion (Table 8 and Fig. Xl.3).

Despite its insignificant yield, soluble solids in tissues of cowpea 10R-61 (Fig. X.5) decreased from flowering until the 21st day after flowering and, thereafter, increased sharply. The decrease in NSC during that

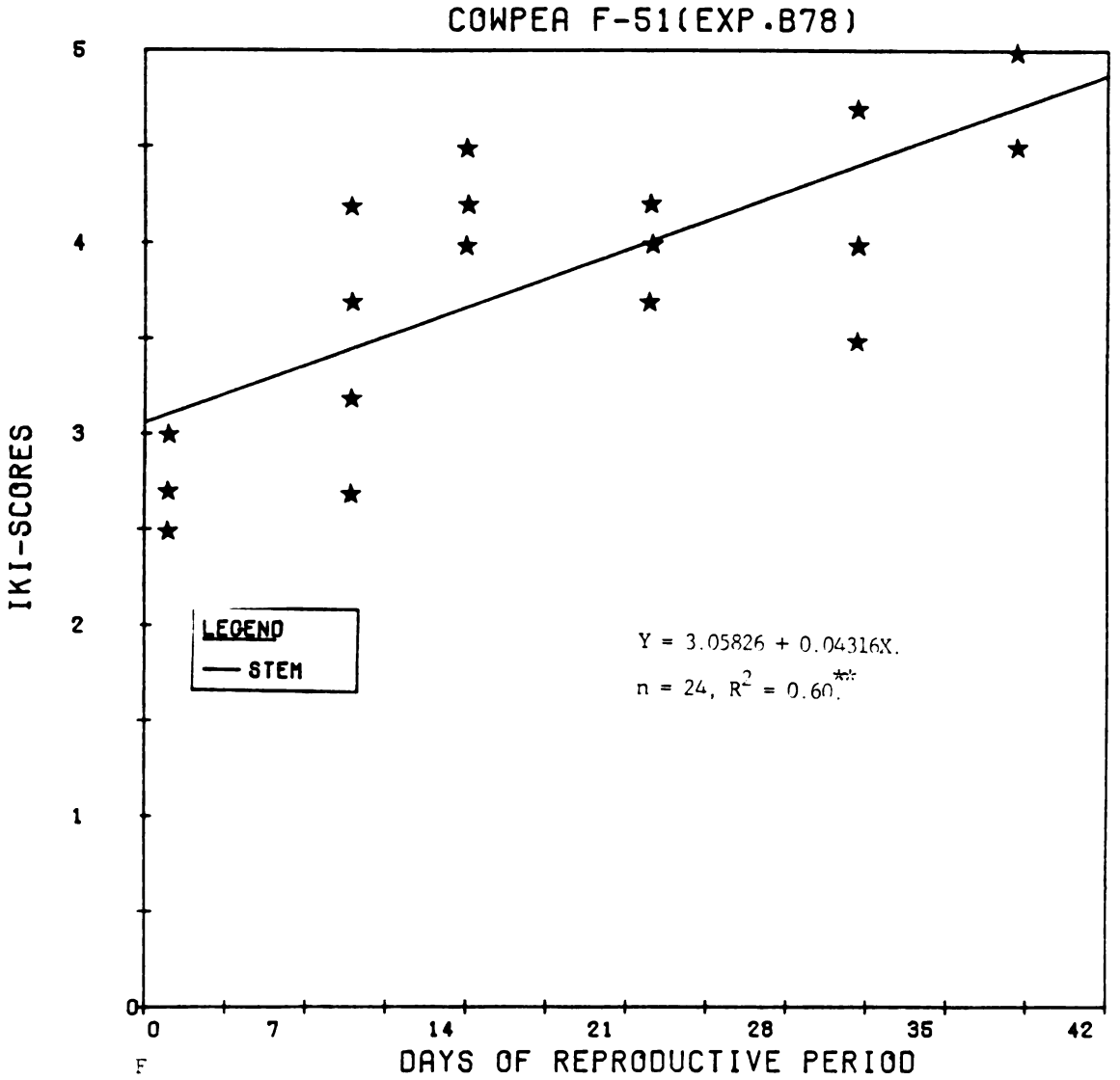

Fig. X.1: Trend of starch (IKI score) accumulation in stems of cowpea F-51 during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

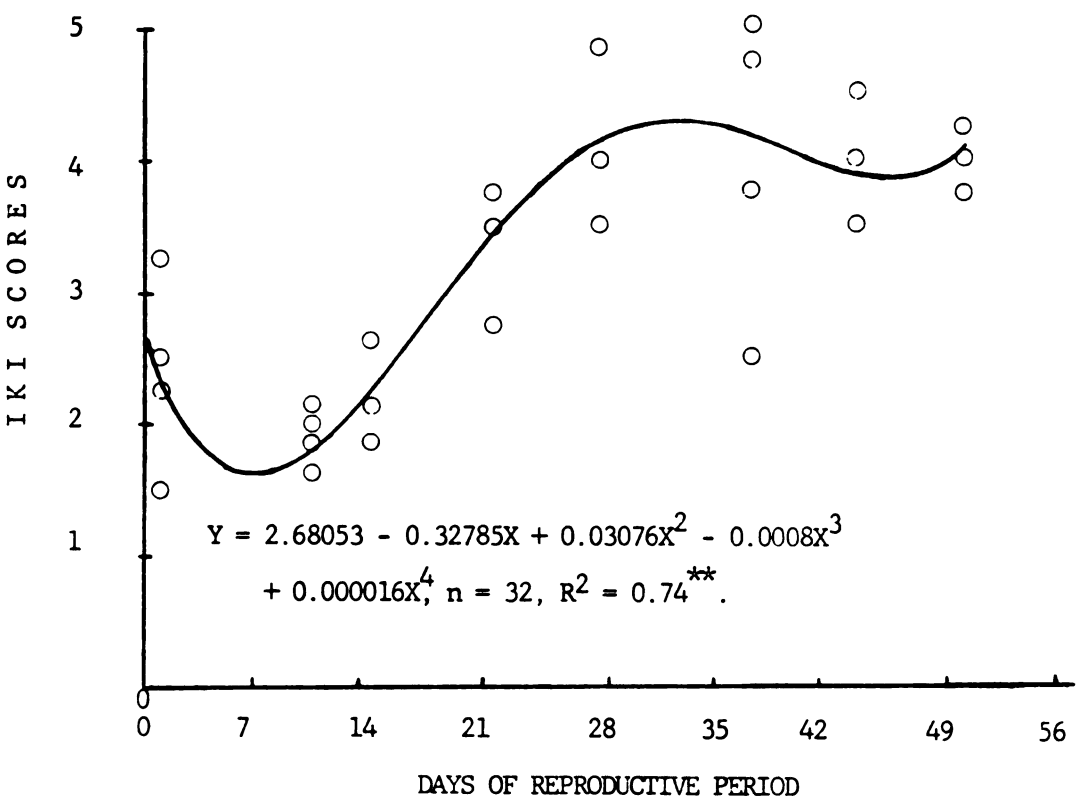

Fig. X.2: Trend of starch (IKI score) accumulation in stems of cowpea F-51 during reproductive growth, MSU Crops Farm, 1979.

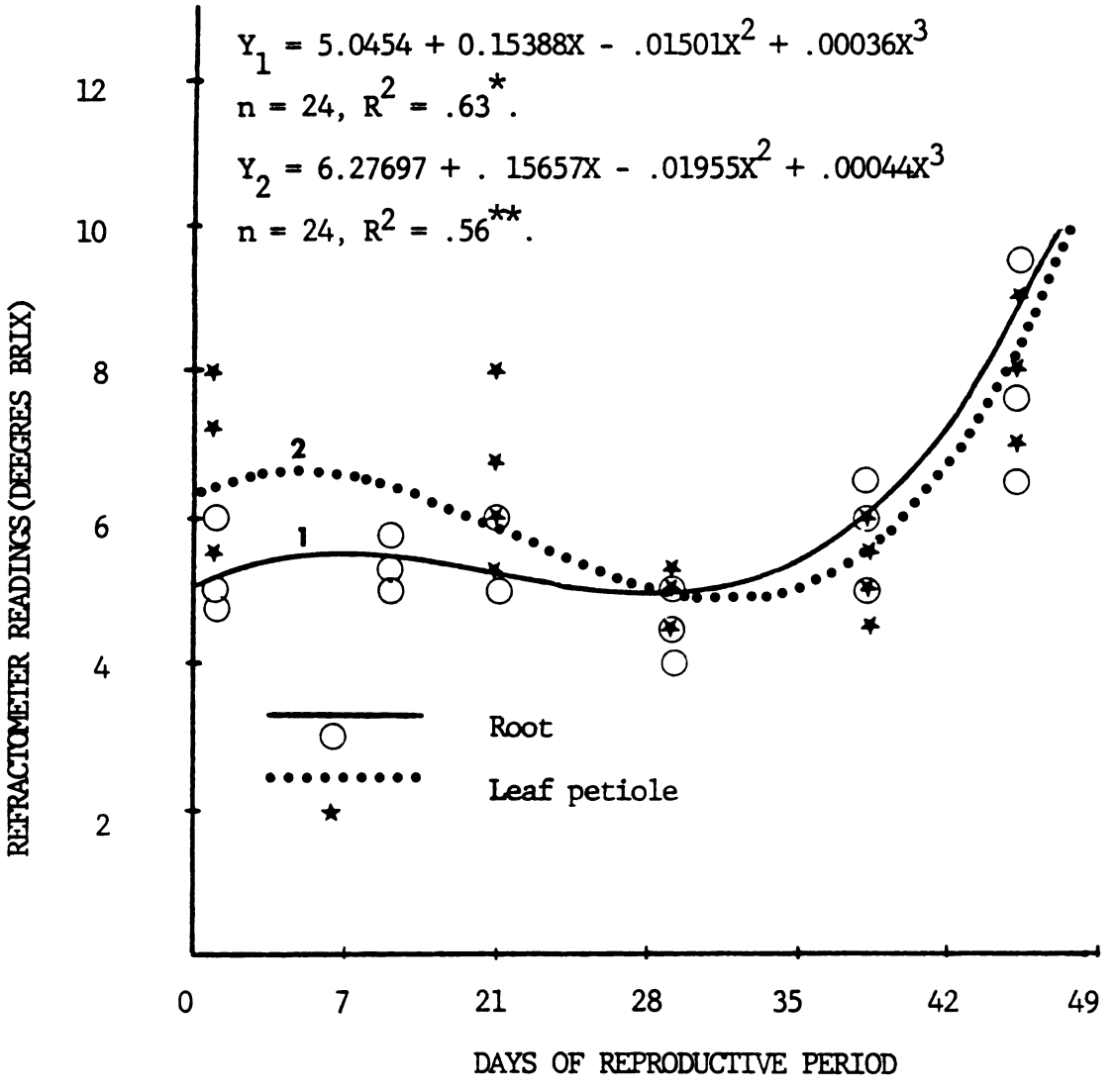

Fig. X.3: Trend of soluble solids (refractometer values) accumulation in roots and leaf petiolès of cowpea F-51 during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

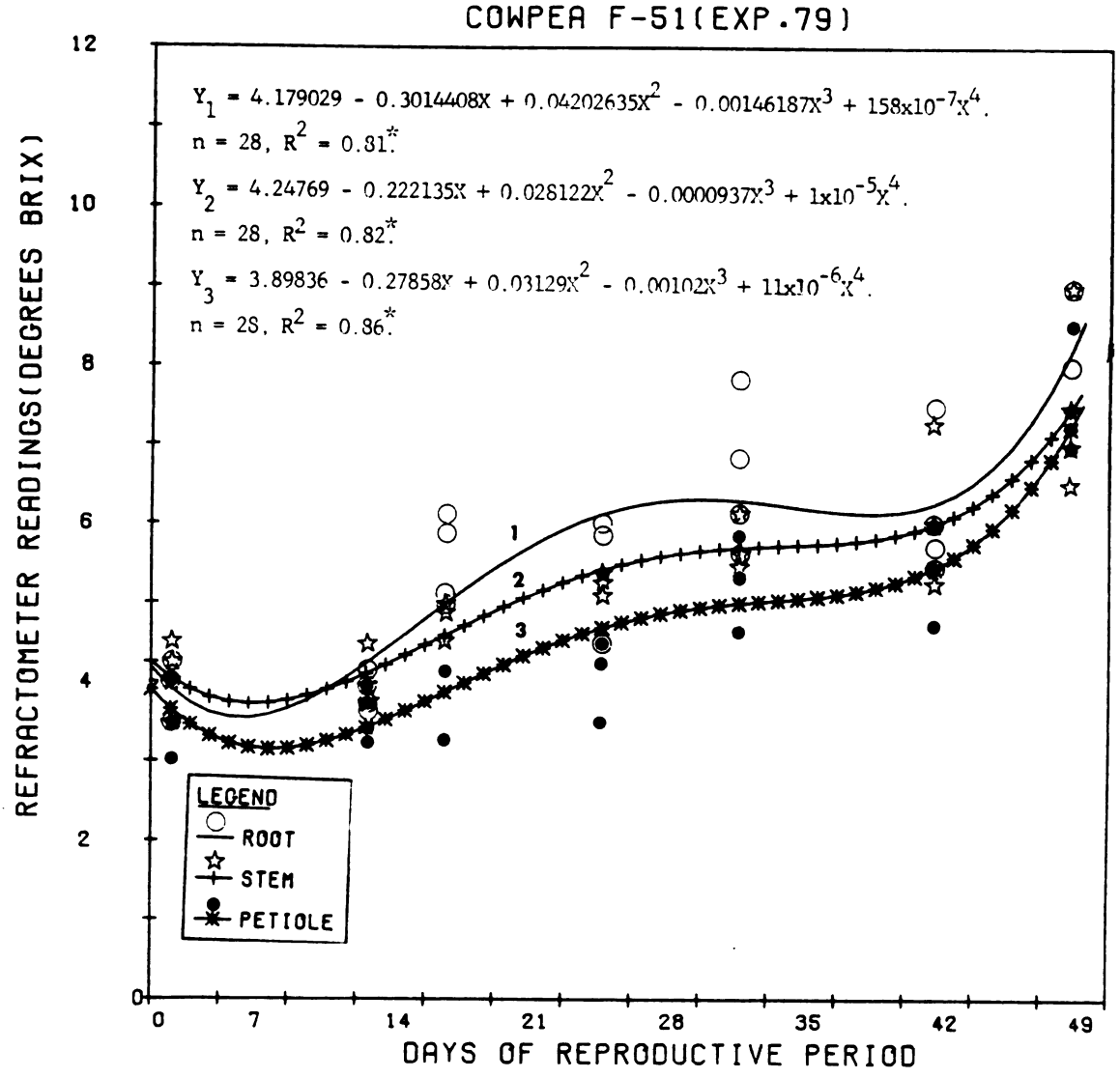

Fig. X.4: Trend of soluble solids (refractometer values) accumulation in roots, stems, and leaf petioles of cowpea F-51 during reproductive growth, MSU Crops Research Farm, 1979.

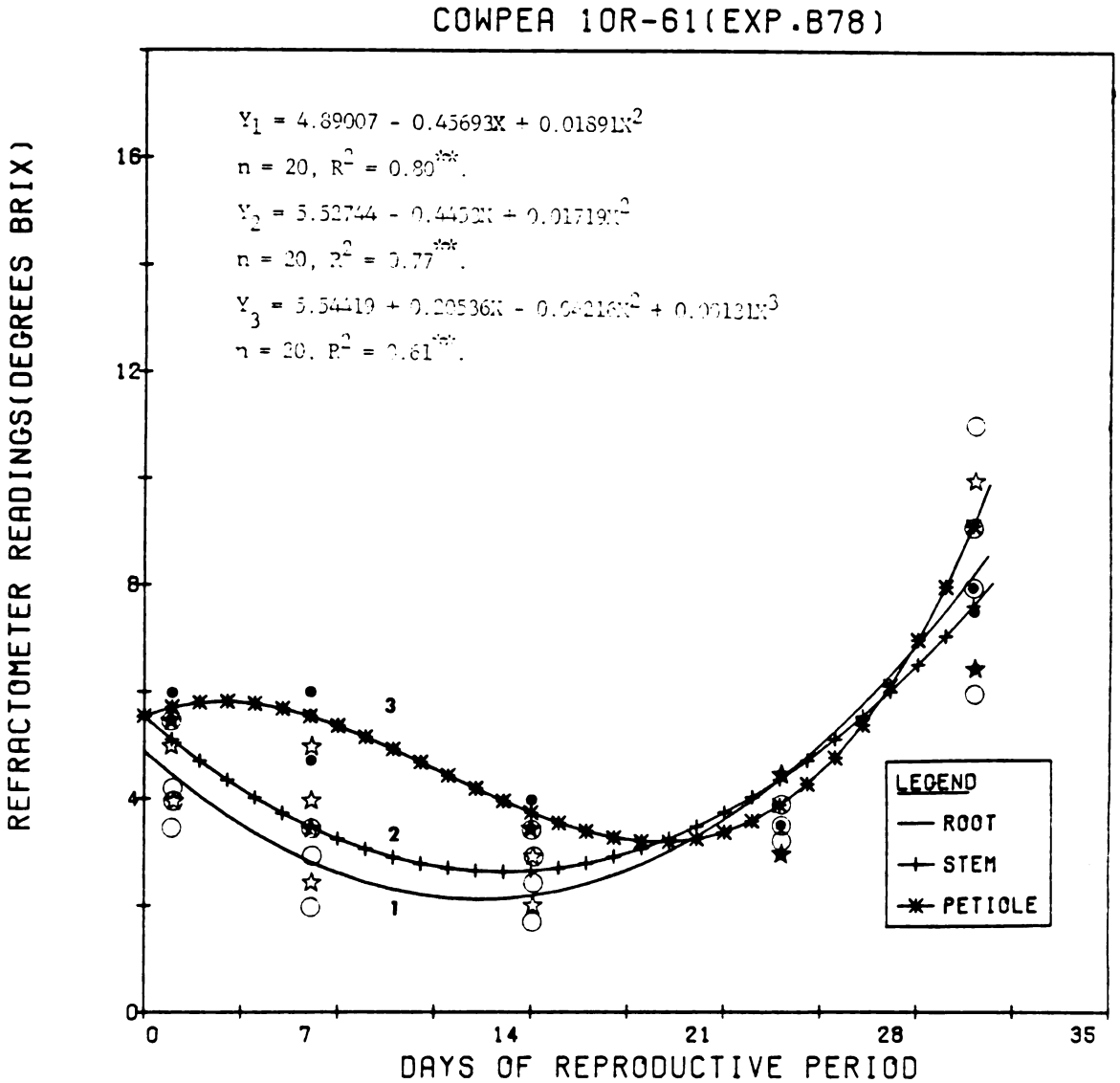

Fig. X.5: Trend of soluble solids (refractometer values) accumulation in roots, stems, and leaf petioles of cowpea 10R-61 during reproductive growth, Bean and Sugar Beet Farm, Experiment B, 1978.

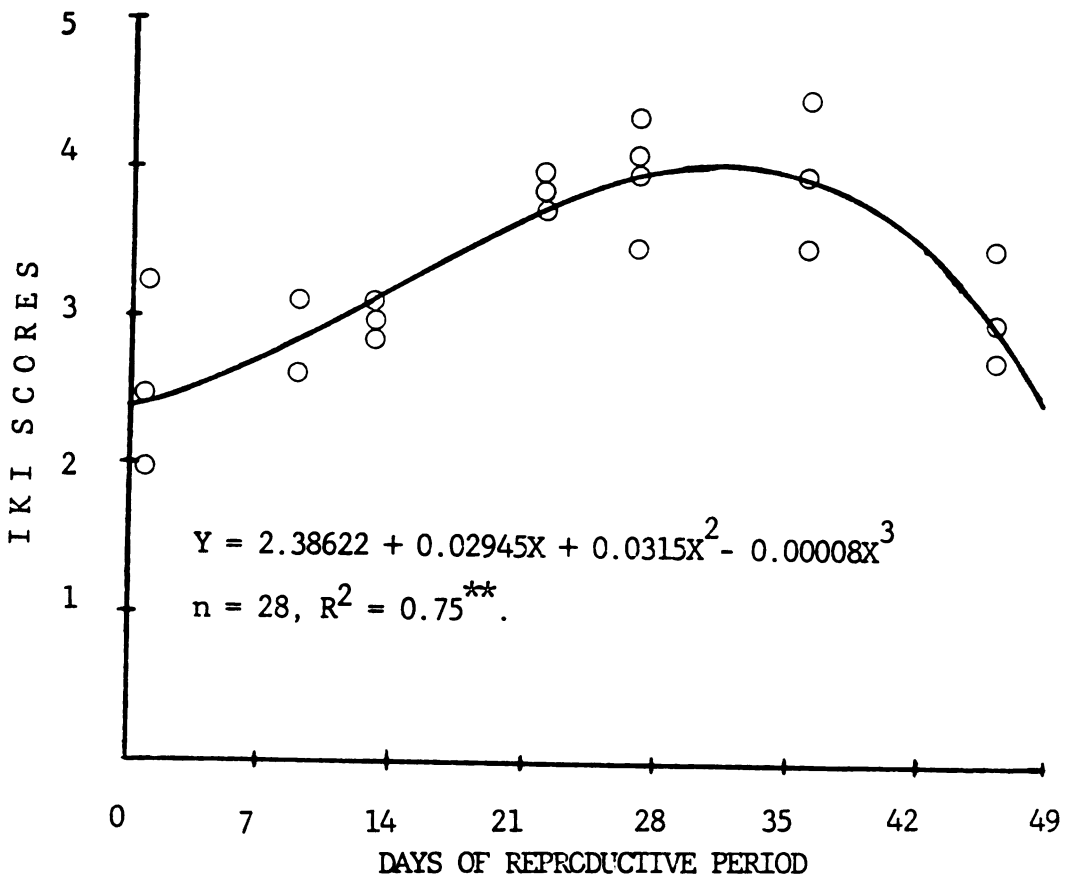

Fig. X.6: Trend of starch (IKI score) accumulation in stems of cowpea Pink Eye Purple Hull during reproductive growth, MSU Crops Farm, 1979.

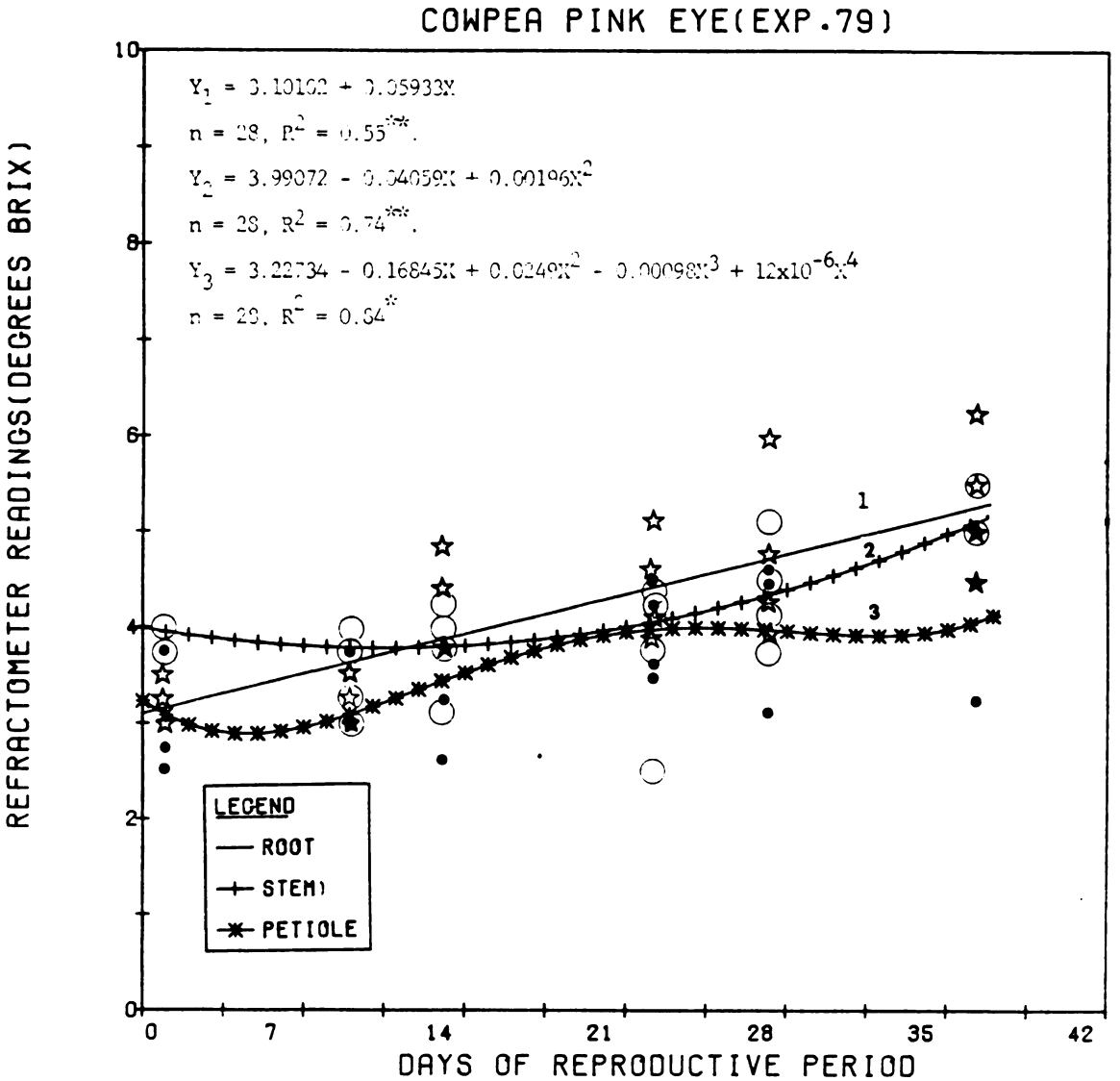

Fig. X.7: Trend of soluble solids (refractometer values) accumulation in roots, stems, and leaf petioles of cowpea Pink Eye Purple Hull during reproductive growth, MSU Crops Research Farm, 1979.

period corresponds with the active growth of all plant tissues.

Cowpeas are known to be predominantly a hot-weather crop adapted to tropical conditions. They are believed to have originated in Central-West Africa and that is where seeds of cultivars I planted came from. In this study they were the only entries that showed a linear increase in stored carbohydrates. Furthermore, their excessive vegetation to the detriment of grain yield is a sign of lack of adaptation and the few or no pods borne is an obvious lack of an adequate sink.

The Remaining Entries

The mung bean (Vigna radiata), Vigna angularis type II and the broad bean (Vicia faba) did not exhibit any pattern in the status of their non-structural carbohydrates. This means that the levels of these carbohydrates remained constant throughout reproductive growth. Furthermore, Tables 2, 3, 6 and 7 show high amounts of NSC in tissues of Vigna radiata and Vigna angularis type II, but starch levels in tissues of Vicia faba were barely detectable.

Dry Matter Production

Vegetative Growth

Table 8 contains dry matter values for roots, stems, and pod walls combined together; values given in

terms of grams per 0.375 m^2 (area occupied by a single plant) are averages of 16 plants. Dry matter for leaves has been left out because the abscised ones were not picked up from soil to be dried and weighed with those found on plants on sampling days. Although all roots were not recovered, especially in soybeans, much effort had been made to extract most root material.

Dry matter values of four cultivars representing 3 major patterns in changes of NSC during reproductive growth are plotted in Figures XI.1-3. Data in Table 8 indicate that, always, dry matter content in grain legumes increases from flowering until the end of pod wall development at about 15 days after flowering. After that period the dry matter content may continue increasing (e.g. Nep-2 in Experiment A78, Fig. XI.2, and cowpeas in Figure XI.3) or may decline (e.g. BTS in Experiment A78, Figure XI.1) or may remain almost constant (BTS and Nep-2 in Experiment B78, Fig. XI.2). A perusal of Table 8 indicates that the plotting of all data of all experiments per entry would distribute entries within these 3 classes represented by BTS, Nep-2, and cowpeas.

As it was seen from remobilization curves discussed in the preceding section, BTS appeared to be the best remobilizer of previously stored non-structural carbohydrates. Indeed, curves describing changes in dry matter

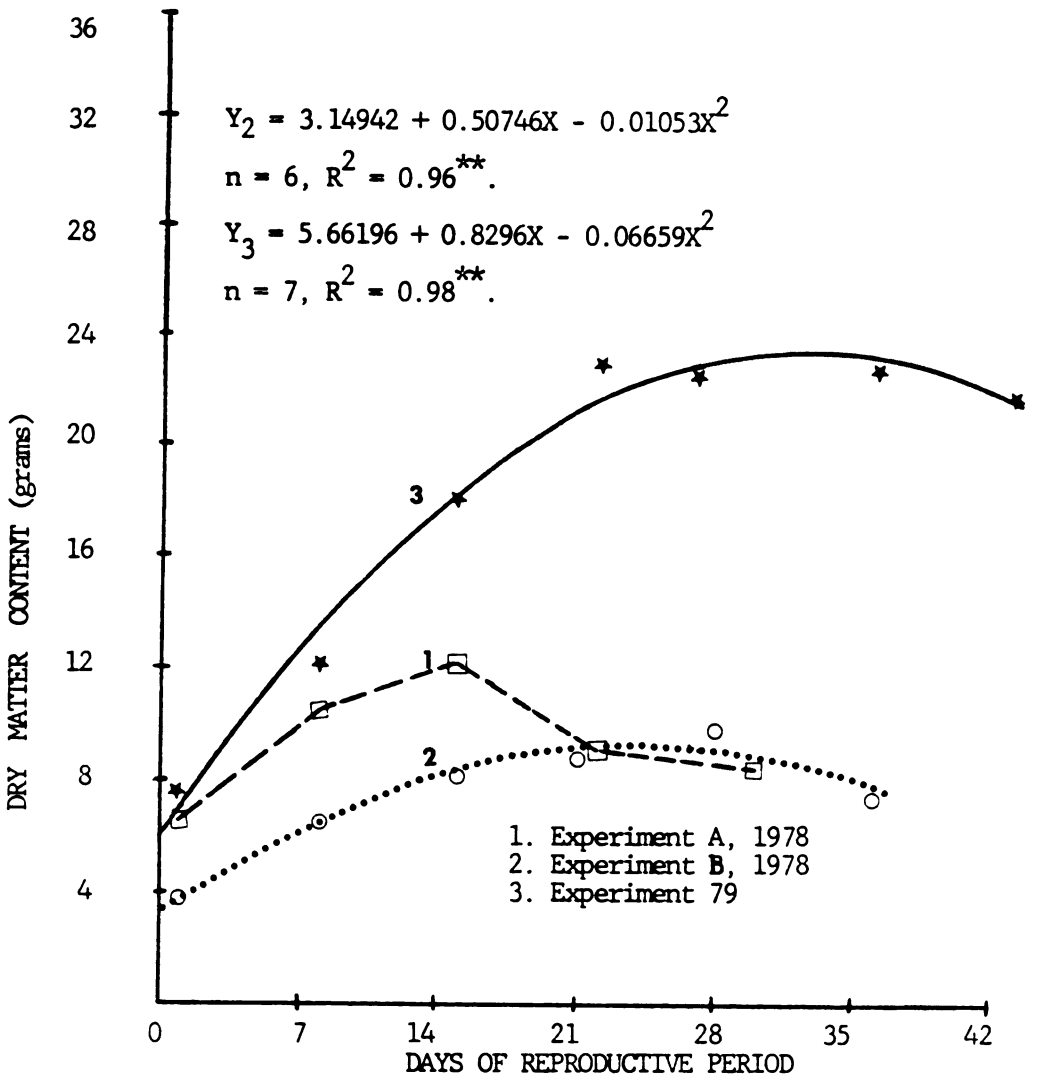

Fig. XI.1: Trends of dry matter (gms per 0.0375 m^2) accumulation (roots, stems, and pod walls) during reproductive growth in Black Turtle Soup beans, Bean and Sugar Beet Farm, 1978; MSU Crops Farm, 1979.

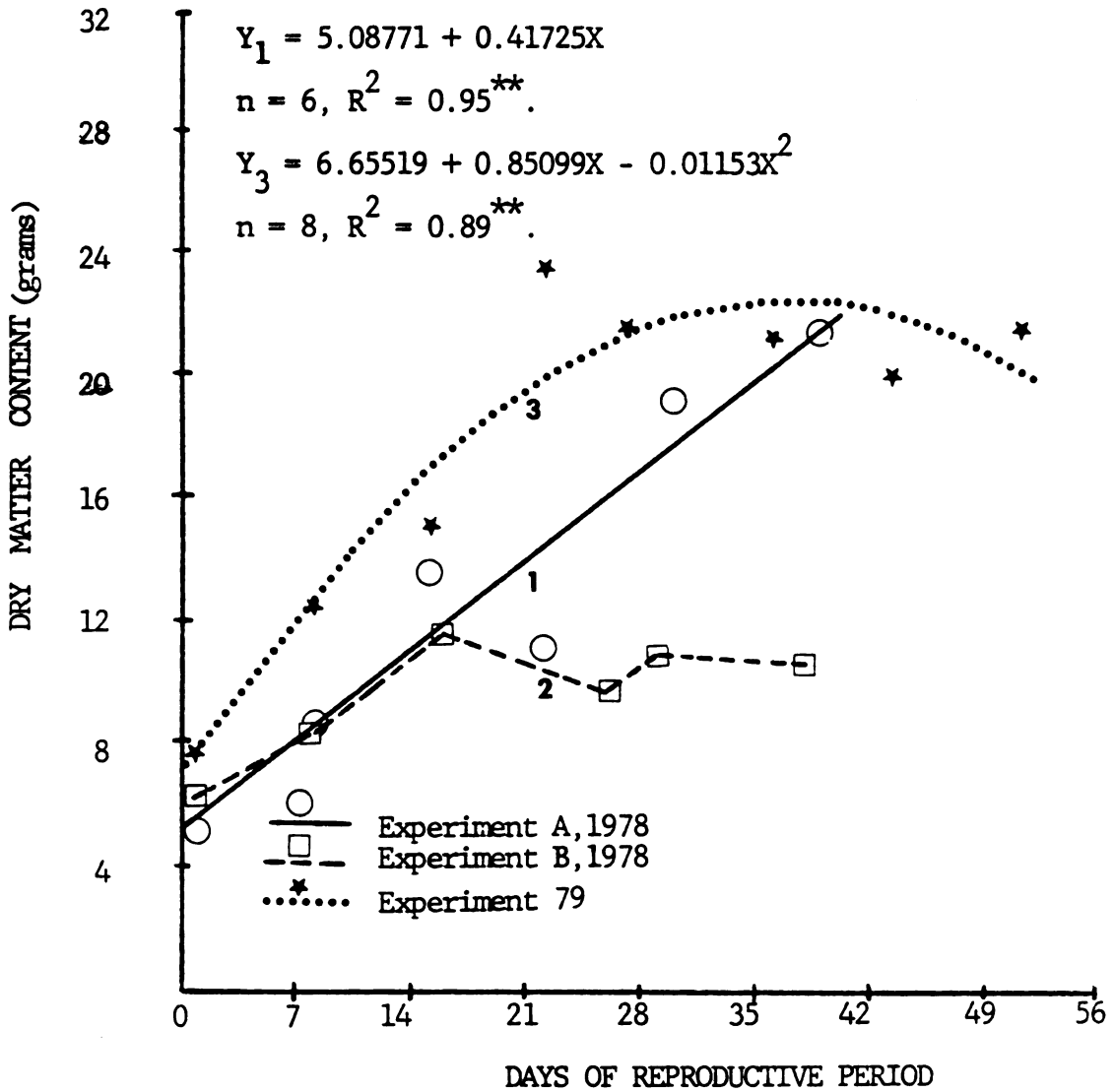

Fig. XI.2: Trends of dry matter (gms per 0.0375 m^2) accumulation (roots, stems, and pod walls) during reproductive growth in Nep-2 beans, Bean and Sugar Beet Farm, 1978; MSU Crops Farm, 1979.

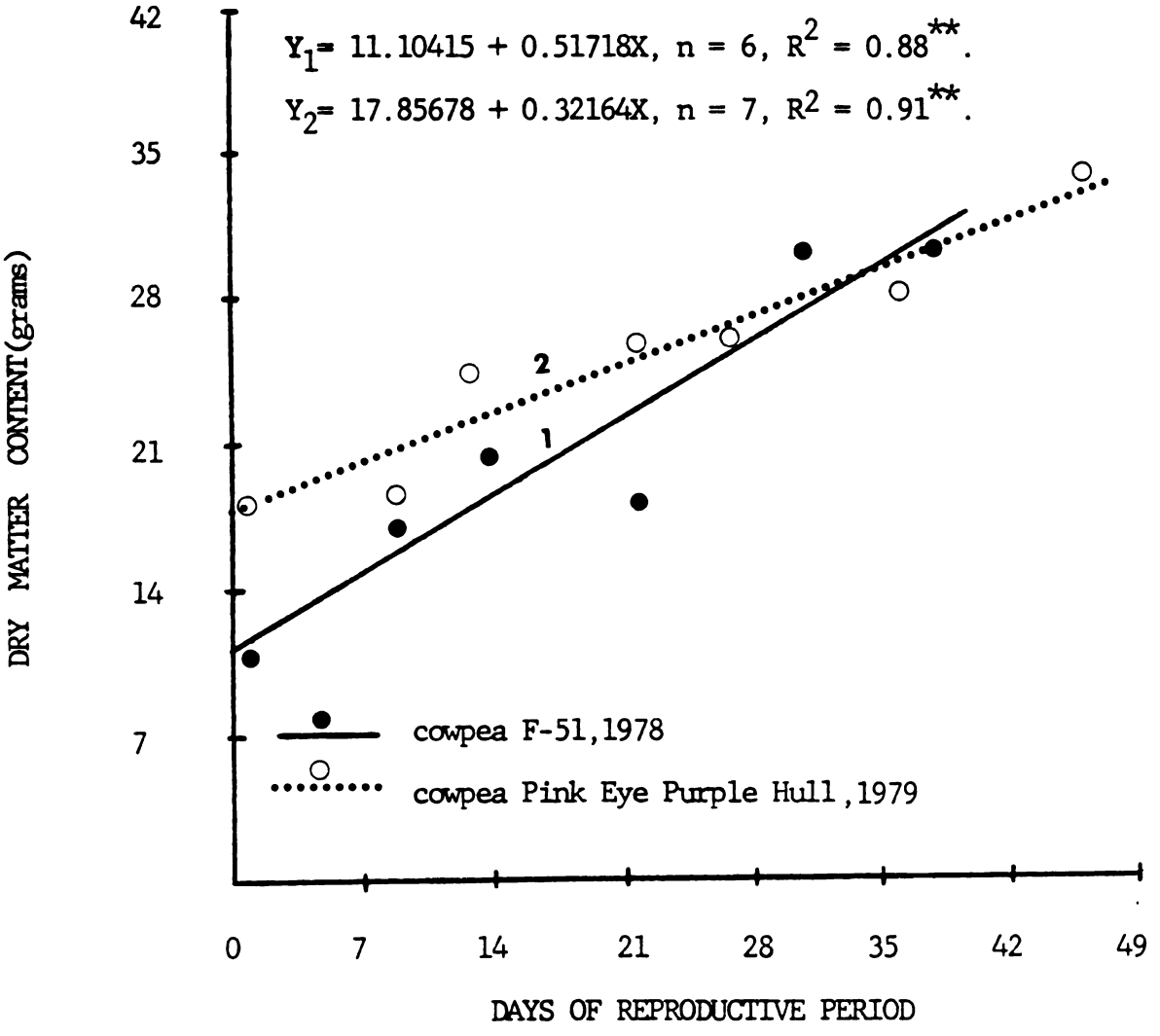

Fig. XI.3: Trend of dry matter (gms per .0375 m^2) accumulation (roots, stems, and pod walls) during reproductive growth in cowpea F-51, Bean and Sugar Beet Farm, Experiment B, 1978 and cowpea Pink Eye, MSU Crops Farm, 1979.

content agree perfectly with remobilization patterns. In Experiment A78 in which BTS had to respond to water stress by diverting its NSC in storage to grain production (Fig. XI.1) vegetative organs lost their weight from day 15 after mid-flowering until physiological maturity. At that stage the dry matter content remained constant in Experiment B78. In Experiment 79, however, the same figure indicates that the dry matter content remained constant from day 21 after mid-flowering until physiological maturity. That is the period in which the seed grew actively; the daily seed growth rate was 1.13 grams per plant between 21 and 43 days after 50 percent flowering. BTS supported this growth rate by remobilizing starch mostly from root tissue (Fig. IV.5).

The dry bean navy-type "Seafarer" is the closest to BTS in dry matter accumulation patterns.

Since no important decreases occurred in levels of NSC in major storage sites (root and stem), Nep-2 was considered to be a poor remobilizer of previously stored NSC. In Experiment B78, however, a significant remobilization of soluble solids from stems (Fig. V.2) was observed between 10 and 30 days after mid-flowering. Fig. XI.2, on the other hand, indicates that in Experiment B78 the dry matter content of Nep-2 remained almost constant from day 15 after mid-flowering until physiological maturity. Dry matter accumulated throughout reproductive growth in

Experiment A78 in which only starch from leaf petioles supported seed growth at the end of reproductive growth. It can also be seen from Fig. XI.2 that the dry matter content of Nep-2 in Experiment 79, decreased from day 21 until 50 percent flowering, but remained almost constant from day 27 after mid-flowering until physiological maturity. Figure V.2 indicate that remobilization of starch from roots and pod walls took place in that period.

Nep-2, Redkote, Redkloud, and Swedish Brown belong to the same category of poor NSC remobilizers.

Cowpeas produced excessive vegetation to the detriment of grain production. This is reflected in dry matter accumulation patterns. Indeed, curves (Fig. XI.3) indicate that vegetation accumulated linearly throughout reproductive growth.

Grain Production

Seed yields (grams per m^2) are reported in Table 9. In analyzing yields, only dry beans, soybeans, and adjuki beans were considered. The analyses of variance (Tables 10 and 11) indicate a highly significant "times of planting (Exp.) x variety" interaction. In fact, apart from Beeson soybean and the dry bean Redkote, the Saginaw Valley experiments gave similar grain yields among entries although, in general, numerically they were higher in the first than in the second experiment. The reason is that

TABLE 9.--Comparisons of mean seed yields (gms per m^2) for several grain legumes grown in three plantings in Michigan--Saginaw, 1978 and East Lansing, 1979

Entry Name	Within Entries			Between Entries
	Exp. A78	Exp. B78	Exp. 79	
Seafarer	143 a	179 ab	244 b	188 bc
California S.W.	64 a	94 a	51 a	73 a
Nep-2	107 a	148 a	237 b	164 abc
Redkloud	163 a	124 a	303 b	194 bc
Redkote	191 b	120 a	309 c	206 bc
BTS	142 a	130 a	345 b	206 bc
Swedish Brown	--	88 a	225 b	156 abc
Evans Soybean	215 a	219 a	179 a	204 bc
Beeson Soybean	352 b	212 a	142 a	235 c
Vigna angularis I	131 a	104 a	106 a	114 ab
Cowpea F-51 (1)		51	0	
Cowpea 10R-61 (1)		4.25		
Cowpea Pink Eye (1)			51	
Vigna radiata (1)		3.25		
Vicia faba (1)		30.5		

(1) not included in comparisons.

Yield means with the same letter are not significantly different by Tukey's HSD procedure at 0.05 level.

TABLE 10.--Analysis of variance for seed yields[1] of several dry seeded grain legumes grown in three plantings in Michigan--Saginaw, 1978 and East Lansing, 1979

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	Observed F Value
Total	107	877622		
Times of Planting (Exp.)	2	83203	41602	15.93**
Replications within times of planting (Exp.) (Error 1)	9	22117	2457	
Variety	8	257619	32202	12.72**
Times of planting (Exp.) x Variety	16	332477	20780	8.21**
Residual Error	72	182205	2531	

[1]The analysis only includes cultivars whose yields were estimated in the three experiments.

**Statistically significant at 0.01 level.

TABLE 11.--Analysis of variance for seed yield[1] of 6 dry bean cultivars grown in three plantings in Michigan--Saginaw, 1978 and East Lansing, 1979

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	Observed F Value
Total	71	563591		
Times of planting (Exp.)	2	215680	107840	51.4**
Replications within times of planting (Exp.) (Error 1)	9	18879	2098	
Variety	5	157801	31560	20.84**
Times of planting (Exp.) x variety	10	103101	10310	6.81**
Residual Error	45	68129	1514	

[1]Swedish Brown not included.

**Statistically significant at 0.01 level.

the first experiment benefitted from the adequate moisture of June and early July, whereas entries of the second experiment faced dryness in early August (this was also true for the first experiment) and frosts of late September to early October, which impaired seed maturity.

The entries planted at the MSU Crops Farm in Summer 1979 gave significantly higher yields than in previous experiments, except for California Small White (which as usual was killed by frosts before maturity), soybeans and Adzuki beans. In this experiment, the lack of rain during the germination period was unfavorable to the normal development of soybean and adzuki bean populations.

The most prominent factor which influenced yields at the Bean and Sugar Beet Farm was dry weather. Minor effects could be attributed to zinc and manganese deficiency, to soil compaction, the latter a problem on the fine-textured soil of the Bean and Sugar Beet Research Farm. For about 3 weeks from July 27 to August 15, 1978, the Sugar Beet and Bean Research Farm received only 0.17 inches of rainfall in two passing showers (0.11 inches on August 2nd and 0.08 inches on August 9th). Besides, daily temperatures during this period were in the middle 80s (degrees Fahrenheit or 30°C) (Research Report, 1978).

For dry bean entries planted on May 25th the physiological maturity was invariably reached on August 15th,

except Seafarer whose physiological maturity occurred a week earlier. Water stress, among other things, is known to be able to reduce photosynthesis below the dark respiration rate, to alter carbohydrate metabolism and reduce the rate of translocation of photosynthates (Laude, 1971).

The 1979 experiment, conducted at the MSU Crops Research Farm in East Lansing, received, after germination, a good rainfall which even made the proliferation of weeds difficult to control during the sampling period. In that experiment, entries required more time to reach physiological maturity than in the previous experiments. Thus, higher yields were due partly to longer duration of the grain filling period.

Cowpeas originated in Central and West Africa. Of the Wrold's cowpea production, 85 percent is found in the Savannah Zone of West Africa between 10 and 20°N latitude (FAO, 1972, cited by Wien et al, 1979). Currently, cowpeas are predominantly a hot-weather crop adapted to semi-arid and forest-margin tropics (Rachie and Roberts, 1974). In the United States of America cowpeas are found in the South with some production in California.

From information gathered by Rachie and Roberts (1974), it seems that under favorable conditions, cowpea yields range from 1600 to 2500 kg per hectare. Results from research indicate that 6 to 16 percent of the total

flower buds produce mature fruits (Ojehoman, 1972; Rachie and Roberts, 1974). Ojehomon (1968) cited by Ojehomon (1972), pointed out that abscission in cowpeas limits grain production. Ojehomon (1972) concluded that the primary cause of flower abscission in cowpeas may be found in internal factors which control vital processes related to the embryo development, whereas the nutrient availability for flowers in the upper part of the peduncle is just a secondary cause. Summerfield et al (1973), cited by Rachie and Roberts (1974), indicated that flowers do not constitute a very large sink in cowpeas.

Short-day and day-neutral cultivars exist in cowpeas (Rachie and Roberts, 1974). Day-neutral cultivars are the ones grown in low tropical latitutdes and in long day temperate regions. Since in this study cowpea seed yields were insignificant (Table 9), it may simply be said that the cowpea as represented by these entries is not adapted to Michigan conditions.

DISCUSSION AND CONCLUSIONS

Literature (Wardlaw, 1968; Yoshida, 1972; Evans, 1980) indicates that the pattern of assimilate distribution is largely dependent on the relative strength and proximity of regions of utilization, and on the supply of assimilates from leaves, is susceptible to modification by the pattern of vascular connections, and is dependent on environmental conditions. Data of this study show genotypic differences in pattern of assimilate distribution in different tissues of grain legumes and also reflect the control that environmental conditions can have on transport and distribution of photosynthetic products. Although only in deliberately designed experiments can a single environmental cause and effect be clearly isolated,water stress, p. 124, limited yield production at the Bean and Sugar Beet Research Farm in 1978. Factors of environment control distribution of assimilates in various ways. In this study, however, this control was clearly mediated through changes in rate of growth of developing organs and has been emphasized for seed growth (pp. 44-117). Wardlaw (1968) believes that changes in growth rate are in turn due to hormonal control.

The IKI staining technique showed that dry bean roots and stems tend to show similar amounts of starch, and amounts usually higher than those found in other tissues. The cultivar Nep-2, however, consistently showed significantly higher amounts of starch in root than in stem tissue in Experiments B78 and 79 (Table 2). Results indicated also that cowpeas tend to show equal amounts of starch in root and stem tissues, but either tissue may have significantly higher amounts depending on the environment, as was the case for the stem in Experiment 79. In addition, leaf petioles of dry beans were found to be the least important starch storers whereas the pod wall tissue of those entries other than the dry beans, *viz.*, cowpeas, *Vigna angularis* (Adzuki beans) and *Vigna radiata* was least important as starch storing tissue. Soybeans showed barely detectable amounts of starch in roots and stems, but the leaf petiole was found to be the best storer of this photosynthetic product. Remobilization curves indicated also that the soybean leaf petiole was the best remobilizer of starch. *Vicia faba* appeared to be a non-starch storer in roots, stems, and pod walls. Nevertheless, the staining of starch by IKI being specific for amylose the possibility that amylopectin could be stored in tissues of *Vicia faba* cannot be excluded.

Environmental influences mediated through changes in growth rates were also reflected in the distribution

patterns of non-structural carbohydrates in plant tissues.

The dry bean leaf petioles of the Bean and Sugar Beet Farm experiments (A78 and B78) showed practically the same amounts of starch as pod walls, whereas at the MSU Crops Farm (Experiment 79) mean IKI scores for pod walls of the majoirty of dry beans (Seafarer, Redkote, BTS and Nep-2) were equivalent to those of the major storage tissues (root and stem).

As far as soluble solids are concerned, at the Bean and Beet Farm (Experiment A78 and B78, Table 3), the leaf petiole emerged as the tissue with the highest concentration of soluble solids as compared with root and stem tissues. Pod wall appeared to be the most important storer of soluble solids at the MSU Crops Research Farm (Experiment 79, Table 3), followed by stem and leaf petiole. The root had the lowest amounts of soluble solids. In soybeans, however, the highest smounts of soluble solids were found in leaf petiole (Table 3) and the lowest in roots; stem tissue occupied an intermediary position. The inventory of curves showing remobilization of soluble solids indicates that dry beans preferentially remobilize stem soluble solids and often the level of these compounds decreases in a linear fashion. In fact, of 11 curves showing changes in content of soluble solids, 6 pertain to stem tissue, 3 to the root and 2 to pod wall. Rawson and Evans

(1971) noted that 2.7 to 12.2% of final weight of wheat grain came from assimilates previously stored in stems.

The Tukey Honestly Significant procedure is considered a conservative statistical test in that, unlike LSD, it is less likely to declare small differences as signifiant when, in fact, they are not truly different. The comparison between genotypes by this procedure yielded 3 groups ranked according to their storage capacity for starch and soluble solids in root and stem tissues. Cowpeas were found to be the most important starch storers followed by dry beans and then soybeans. Vigna angularis II fell in the cowpea group. Vigna angularis I ranked with dry beans in the Saginaw Valley experiments but emerged as the most important storer in the MSU Crops Research Farm experiment.

It appears that the status of carbohydrates found in tissues is related to remobilization patterns. This relationship seems to be straightforward. Those entries other than the dry beans which showed high levels of NSC also appeared to be inefficient remobilizers of previously stored NSC. This is revealed by no change (no polynomial function fitted to the data of some tissues) or by the curves showing increases in the levels of NSC throughout reproductive growth. This is clearly the case for cowpeas and Vigna radiata which did not bear enough pods (inadequate sink) to cause the diversion of these carbohydrates.

It is also the case for Vigna angularis II and California Small White which did not reach completion of seed development. For them too, the sink remained weak. In addition, the dry beans Redkote, Redkloud and Swedish Brown, which retained higher amounts of NSC in their tissues, did not show the expected decreases of stored carbohydrates as pod wall and seed development proceeded. In another connection, the reported data suggest that perhaps these cultivars did not need to divert their NSC in storage to the growing reproductive organs because their leaf photosnythetic rate increased to match or else to exceed sink demand. In fact, Peet et al (1977) showed that the leaf photosynthetic rates increased by 132, 408, 873, and 21 percent, from flowering to early pod set, respectively, for Redkote, Redkloud, Swedish Brown and Black Turtle Soup.

The tropical dry bean "Black Turtle Soup" appears in this study to be the quintessence of remobilization of previously stored non-structural carbohydrates, especially where drought stress occurred during the active period of pod wall and seed growth, i.e., in Saginaw Valley experiments. Indeed, all tissues assayed showed remobilization of starch and both types of non-structural carbohydrates, viz., starch and sugars, were found to be decreasing during almost the entire period of reproductive growth. As a

matter of fact, starch in leaf petiole and soluble solids in stem tissues decreased linearly. On the contrary, at the MSU Crops Farm without water stress, levels of starch only decreased in roots during the period of the highest seed growth rates. The slope describing the linear decrease of starch in leaf petioles was very weak, indicating thereby a low rate of remobilization. Hence, environmental factors being favorable, BTS does not need to divert its stored carbohydrates to seed growth. The highest yield of BTS was achieved at the MSU Crops Farm; the overall daily seed growth rate was 0.96 grams per plant during 6 weeks whereas those of the previous experiments were 0.71 gms day^{-1} per plant (A78) and 0.50 gms day^{-1} (B78) per plant during 4 weeks. The A78 experiment had numerically higher yield than the B78 experiment. This illustrates the equal importance of both duration and rate of grain filling in achieving high yields in BTS.

Important decreases in both types of NSC (starch and soluble solids) were noted in all tissues of Seafarer (Fig. I.1-7). In Experiment 79 where a significantly higher yield than in Experiments A78 and B78 (Table 9) was obtained, the second degree curves describing changes in NSC suggest a high rate of remobilization of starch from root, stem and pod wall tissues (Fig. I.5 and 7). Thus, in this study, the dry bean navy-type Seafarer appears to

be the second best remobilizer of previously stored NSC as compared to Black Turtle Soup.

Gates (1964) reviewed previous papers and concluded that effects of water stress on distribution of photosynthetic assimilates was only partially understood. Wardlaw (1967) noted that during the development of wheat grain a water stress of 15-20 days after anthesis reduced photosynthetic efficiency and resulted in an increased movement of assimilates from the lower leaves to the ear. This observation was considered (Wardlaw, 1968) as being similar to the compensation that takes place when photosynthesis is reduced under low light intensities. McWilliam (cited by Wadlaw, 1968) observed a translocation of assimilates, due to drought stress, from stems to roots and buds of the perennial grass, Phalaris tuberosa L. when the plant was dormant. Thus, it appears that the transport system of assimilates is able to function under conditions of plant dessication and possibly under other kinds of stress, such as lodging, flooding, soil compaction, high temperature, etc.

In the light of this discussion it appears that Black Turtle Soup could be used in breeding programs where stress resistance is required.

In comparison with dry beans, soybeans have higher photosynthetic rates. Bhagsari et al (1977) presented data

for 16 soybean cultivars in which the apparent leaf photosnythetic rates ranged from 23 to 37 mg CO_2 dm^{-2} hr^{-1}. Likewise, rates from 17.9 to 26.8 mg CO_2 dm^{-2} hr^{-1} were reported by Scott et al (1980) for soybeans 80 days after emergence. Intense IKI staining of starch and high concentrations of soluble solids (Tables 2 and 3) were only observed in leaf petioles for soybeans as compared to other tissues. Important decreases of NSC during seed development were also found in this tissue.

However, Evans soybean appears to have achieved a higher yield by diverting soluble solids to the seed from root and stem tissues (Experiment B78) (Fig. VIII.3). It is surprising, however, to see that the amounts of soluble solids in leaf petioles did not show any change during reproductive growth although they were the highest of all tissues in all genotypes. Possibly, levels of sugars were kept in a steady state to maintain the internal cell osmotic levels and avoid plasmolysis, for the osmotic pressure due to non-electrolytes (e.g. sucrose) is known to be directly proportional to the solute concentration.

The reproductive growth of grain legumes involves three stages, namely, blooming, pod wall extension, and grain growth. Tanaka and Fujita (1979) have already described some physiolgocial processes involved in these growth phases. In this study, it was also noticed that

pod wall growth is completed in about 15 days after flowering but grain development starts about one week earlier. The initiation of grain development was determined simply by touching tagged developing pods at two days interval from day 7 after flowering. Data summarized in Table 8 indicate that during blooming and pod wall development all vegetative parts including roots, stems and leaves continue growing.

The patterns of changes found in NSC during ontogenetic development of the plant may be categorized as follows:

1. No changes observed in NSC in tissues throughout reproductive growth, i.e., data of some tissues did not fit polynomial functions of any order, e.g., NSC in roots and stems of Redkote.

2. The decrease in amounts of NSC in tissues starts during the development of pod wall, e.g., starch in roots of Seafarer (Fig. I.1).

3. Decrease in levels of NSC commences during the flowering period, followed subsequently by the highest seed growth rates. This case was found for starch levels in leaf petioles of Nep-2 (Fig. V.1) and for the amounts of starch and soluble solids in leaf petioles of Redkote (Fig. III.1 and III.2).

4. Decrease in amounts of NSC during periods of the highest seed growth rates only. Typical examples are found in starch levels of BTS roots (Fig. IV.5) and in stems of Seafarer (Fig. I.1).

5. Continued (linear) decrease in amounts of NSC throughout the entire reproductive period, e.g., amounts of soluble solids in stems of Black Turtle Soup and starch in leaf petioles of the same genotype.

6. Increase in the amounts of NSC during ontogenetic development of the plant, e.g., NSC in cowpeas, amounts of starch in roots and stems of Swedish Brown (Fig. VI.1).

Most curves show increases in the amounts of NSC especially starch in root and stem tissues during the most active periods of flowering and pod wall growth. Thus, results of this study do not support Tanaka and Fujita's view (1979) according to which the blooming flowers constitute a sink larger than the source of assimilates. On the contrary, this study is corroborative of the idea that in dry beans, soybeans and Adzuki beans, as in grapes (Hale and Weaver, 1972) and in cowpeas (Summerfield, 1973, cited by Rachie and Roberts, 1974), flowers constitute a weak sink for assimilates. In addition, Tanaka and Fujita (1979) consider the abortion of flowers and pods to be a specific process by which dry beans tend to adjust sink

size to source capacity. It was noticed, however, that the dry bean cultivars Redkote, Nep-2, Swedish Brown and BTS shed important quantities of their flower and pods during the most active periods of flowering and pod wall development. These are stages in which increases in amounts of NSC were mostly observed in tissues and, to be acceptable, Tanaka and Fujita's hypothesis would require that photosynthetic products decrease in storage sites and, as a consequence of that, reallocation of carbon assimilates abscission of reproductive structures should not occur. Moreover, Izquierdo and Hosfield (1981) noted that 66.5 and 67 percent of reproductive structures abscised in Black Turtle Soup and Nep-2, respectively, even as these cultivars display a great capacity to store NSC.

Leopold (1971) indicated that the physiology of abscission can be considered as a sequence of five morphological stages, in which hormones play a key role in regulating two of them, namely, stage 1 of abscission which is insensitive to the promotive effect of applied ethylene and stage 2 in which applied ethylene becomes a stimulator. Auxin appears to be a major agent inhibiting abscission development (Webster, 1970; Cracker et al, 1970; Abeles and Rubinstein, 1964) and ethylene appears as the major agent promoting abscission (Leopold, 1971; Abeles et al, 1971; Pooviah, 1973). In cotton, Varma (1976, a and b)

believes that the abscission of a flower bud or a boll is not a matter of concentration of endogenous abscissic acid alone but may rather be determined by a relational balance between growth regulators.

Thus, it seems that in dry beans, in cowpeas and other grain legumes, the abortion and shedding of reproductive structures may be due rather to the imbalance of endogenous hormones than the failure of the source to manufacture carbon assimilates in sufficient quantities needed for the growth of reproductive structures.

Hence, we should emphasize with Waters et al (1980) that the accumulation of important amounts of NSC in roots, stems and other plant tissues during ontogenetic development indicates that beans are inefficient in their use of photosynthates or provide inadequate sink capacity. From results of this study the hypothesis of inadequate sink seems to be the most plausible. In fact, the status of NSC found in cowpeas, Vigna radiata, Vigna angularis, Swedish Brown, Redkote and Redkoud demonstrates the consequences of inadequate sink. By depodding plants of Seafarer and Nep-2, Bouslama (1977) noted that the amounts of total non-structural carbohydrates were maintained above control levels in stems and branches in response to a reduced sink demand. Likewise, the report by McAllister and Krober (1958) that 80 percent depodding increased the

amounts of sugars and starch in leaves and stems of soybean is corroborative of this idea.

This study was able to answer the questions raised in the introduction.

1. Differences in partitioning of NSC between plant tissues were found in all genotypes except Vicia faba which did not show starch and which also showed the lowest amounts of soluble solids in its tissues.

2. The partitioning of NSC was found to vary genotypically.

3. Of 82 curves presented in this report, 50 pertain to starch and only 32 to soluble solids. Thus, starch was preferentially remobilized and the same type of judgment leads to mention that dry beans preferentially remobilized stem soluble solids. Environmental factors reflected themselves in seed growth rates and duration and were found to influence the pattern of assimilate distribution. High seed growth rates were found to be correlated with important decreases of NSC and accumulation of dry matter in tissues. Higher yields were associated with more tissues being involved in the diversion of NSC to seed production. In some instances both types of NSC were remobilized. Thus, sink strength is an important determinant of translocation patterns, of the partitioning of dry matter, and therefore of grain yield. Flowers of dry

beans as well as those of other grain legumes appeared to be a weak sink for assimilates. Black Turtle Soup appeared to be the best remobilizer of NSC in a stress situation. Of all genotypes used it appears to be the most suited to be used in breeding for stress resistance.

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TABLE 2.--Comparison of tissue starch mean[1] scores (IKI scores) within entries, by experiments, for several grain legumes, grown at two locations in Michigan, 1978 and 1979. (R = Root; S = Stem; LP = Leaf Petiole; PW = Pod Wall).

Entry Name	Experiment A78				Experiment A78				Experiment 79			
	R	S	LP	PW	R	S	LP	PW	R	S	LP	PW
Seafarer	2.3^{a}	2.5^{a}	1.9^{a}	2.1^{a}	2.3^{b}	2.4^{b}	1.4^{a}	2.3^{b}	2.5^{b}	2.3^{b}	1.5^{a}	2.7^{b}
California Small White					2.5^{b}	2.3^{b}	1.5^{a}	2.2^{b}	2.9^{c}	2.4^{b}	1.1^{a}	3.2^{c}
Nep-2	3.4^{b}	3.2^{b}	1.5^{a}	1.8^{a}	3.4^{c}	2.8^{b}	1.5^{a}	2.0^{a}	3.4^{c}	2.8^{b}	1.4^{a}	2.7^{b}
Redkloud	1.8^{ab}	2.1^{b}	1.5^{a}	1.9^{ab}	2.2^{b}	2.1^{b}	1.5^{a}	1.8^{ab}	1.8^{a}	2.1^{a}	1.9^{a}	2.8^{b}
Redkote	3.1^{b}	3.2^{b}	1.6^{a}	1.7^{a}	3.0^{c}	2.9^{c}	1.6^{a}	2.4^{b}	3.0^{b}	2.9^{b}	2.1^{a}	3.1^{b}
Black Turtle Soup	3.4^{b}	3.1^{b}	1.7^{a}	2.1^{a}	3.1^{b}	2.7^{b}	1.4^{a}	2.0^{a}	3.1^{c}	2.8^{bc}	1.4^{a}	2.5^{b}
Swedish Brown					3.0^{b}	2.9^{b}	2.3^{a}	2.2^{a}	2.2^{a}	2.4^{ab}	2.1^{a}	2.9^{c}
Averages	2.8	2.8	1.6	1.9	2.8	2.6	1.6	2.1	2.7	2.5	1.6	2.8
Evans Soybean	1.5^{ab}	1.8^{ab}	1.8^{b}	1.3^{a}	1.6^{a}	1.7^{a}	2.1^{a}	1.7^{a}	1.3^{a}	1.7^{a}	2.2^{b}	1.4^{a}
Beeson Soybean	1.2^{a}	1.3^{a}	1.6^{b}	1.4^{ab}	1.1^{a}	1.2^{ab}	1.6^{b}	1.3^{ab}	1.3^{a}	1.6^{a}	2.4^{b}	1.6^{a}
Averages	1.3	1.5	1.7	1.3	1.3	1.4	1.8	1.5	1.3	1.6	2.3	1.5
Cowpea F-51					4.0^{c}	3.9^{c}	3.2^{b}	1.5^{a}	2.6^{a}	3.2^{b}	2.0^{a}	--
Cowpea 10R-61					3.8^{b}	3.8^{b}	2.4^{a}	--				
Cowpea Pink Eye P.H.									1.8^{a}	3.3^{b}	1.8^{a}	--
Averages					3.9	3.8	2.8	--				
Vigna angularis I	2.6^{c}	2.1^{b}	1.7^{ab}	1.2^{a}								
Vigna angularis II	3.6^{c}	3.4^{c}	2.5^{b}	1.8^{a}								
Vigna radiata					3.0^{a}	3.3^{a}	2.8^{a}	--				
Averages	3.1	2.7	2.1	1.5	2.9	3.0	2.4					
Vicia faba					1.0^{a}	1.1^{a}	--					

[1]Means across all stages of reproductive growth.

For each entry in each experiment tissue means with the same letter are not significantly different by Tukey's HSD procedure at 0.05 level.

TABLE 3.--Comparison of tissue soluble solids mean[1] readings (refractometer values) within entries, by experiments, for several grain legumes, grown at two locations in Michigan, in 1978 and 1979. (R = Root; S = Stem; LP = Leaf Petiole; PW = Pod Wall.)

	Experiment A78			Experiment B78			Experiment 79			
	R	S	LP	R	S	LP	R	S	LP	PW
Seafarer	4.0^{a}	4.2^{a}	5.3^{b}	4.8^{b}	4.1^{a}	5.3^{c}	2.9^{a}	3.8^{b}	3.5^{ab}	5.4^{c}
California Small White				4.8^{b}	3.8^{a}	5.4^{c}	3.4^{a}	3.7^{a}	3.6^{a}	5.5^{b}
Nep-2	4.6^{a}	5.1^{b}	5.6^{c}	4.8^{ab}	4.4^{a}	5.3^{b}	3.9^{a}	4.4^{a}	3.9^{a}	5.5^{b}
Redkloud	4.3^{a}	4.3^{a}	5.8^{b}	4.6^{a}	4.4^{a}	5.5^{b}	3.4^{a}	4.0^{b}	4.0^{b}	4.5^{c}
Redkote	5.0^{a}	5.2^{ab}	5.5^{b}	5.2^{a}	5.2^{a}	5.8^{a}	3.4^{a}	4.5^{bc}	4.0^{ab}	5.3^{c}
Black Turtle Soup	4.0^{a}	4.4^{a}	5.6^{b}	4.8^{a}	4.3^{a}	5.2^{a}	3.5^{a}	3.9^{a}	3.8^{a}	5.0^{b}
Swedish Brown				5.4^{a}	5.0^{a}	5.6^{a}	3.6^{a}	4.0^{a}	4.0^{a}	5.7^{b}
Averages	4.4	4.6	5.6	4.9	4.4	5.4	3.4	4.0	3.8	5.3
Evans Soybean	2.9^{a}	4.2^{b}	7.4^{c}	2.9^{a}	4.0^{b}	7.8^{c}	4.0^{a}	5.8^{b}	6.9^{c}	--
Beeson Soybean	3.2^{a}	3.2^{a}	6.7^{b}	3.1^{a}	3.0^{a}	6.6^{b}	4.6^{a}	5.6^{b}	6.4^{c}	--
Averages	3.0	3.4	7.0	3.0	3.5	7.2	4.3	5.4	3.3	--
Cowpea F-51				5.8^{a}	5.7^{a}	6.3^{a}	6.1^{a}	5.9^{a}	5.7^{a}	--
Cowpea 10R-61				4.4^{a}	4.6^{a}	5.6^{a}				
Cowpea Pink Eye P.H.							4.4^{a}	4.4^{a}	4.2^{a}	
Averages				5.1	5.1	5.4	5.2	5.1	4.9	
Vigna angularis I	5.1^{a}	5.4^{a}	5.4^{a}	4.9^{a}	5.0^{ab}	5.8^{b}	5.1^{ab}	5.6^{ab}	4.9^{a}	5.9^{b}
Vigna angularis II	4.8^{a}	4.7^{ab}	5.0^{b}							
Vigna radiata				6.0^{a}	6.0^{a}	7.0^{a}				
Averages	4.9	5.0	5.2	5.5	5.5	6.4				
Vicia faba				3.2	3.5					

[1]Means across all stages of reproductive growth.

For each entry in each experiment tissue means with the same letter are not significantly different by Tukey's HSD procedure at 0.05 level.

TABLE 6.--Comparison of entry starch mean[1] scores, by experiments, for several grain legumes, grown at two locations in Michigan, in 1978 and 1979. (R = Root; S = Stem; LP = Deaf Petiole; PW = Pod Wall)

	Experiment A78				Experiment B78				Experiment 79			
	R	S	LP	PW	R	S	LP	PW	R	S	LP	PW
Seafarer	2.3^{cd}	2.5^{cd}	1.9^{ab}	2.1^{bc}	2.3^{bc}	2.4^{bcd}	1.4^{a}	2.3^{c}	2.5^{cd}	2.3^{bc}	1.5^{abc}	2.7^{b}
California Small White					2.5^{bcd}	2.4^{bcd}	1.5^{ab}	2.2^{c}	2.9^{def}	2.4^{bc}	1.1^{a}	3.2^{b}
Nep-2	3.4^{f}	3.2^{e}	1.5^{a}	1.8^{abc}	3.4^{ef}	2.8^{de}	1.5^{ab}	2.0^{bc}	3.4^{fg}	2.8^{cd}	1.4^{ab}	2.7^{b}
Redkloud	1.8^{bc}	2.1^{bc}	1.5^{a}	1.2^{abc}	2.2^{b}	2.1^{bc}	1.5^{ab}	1.8^{abc}	1.8^{ab}	2.1^{ab}	1.9^{bcd}	2.7^{b}
Redkote	3.1^{ef}	3.2^{f}	1.6^{a}	1.7^{abc}	3.0^{de}	2.9^{be}	1.6^{ab}	2.4^{c}	3.0^{def}	2.9^{cd}	2.1^{cde}	3.1^{b}
Black Turtle Soup	3.4^{f}	3.1^{de}	1.7^{a}	2.1^{c}	3.1^{de}	2.7^{cde}	1.4^{a}	2.0^{bc}	3.1^{efg}	2.8^{cd}	1.4^{ab}	2.5^{b}
Swedish Brown					3.0^{de}	2.9^{de}	2.3^{cd}	2.2^{c}	2.2^{bc}	2.4^{bc}	2.1^{be}	2.9^{b}
Averages	2.8	2.8	1.6	1.9	2.8	2.6	1.6	2.1	2.7	2.5	1.6	2.8
Evans Soybean	1.5^{ab}	1.7^{ab}	1.8^{a}	1.3^{a}	1.6^{a}	1.7^{ab}	2.1^{bc}	1.7^{abc}	1.3^{a}	1.7^{ab}	2.2^{de}	1.4^{a}
Beeson Soybean	1.2^{a}	1.3^{a}	1.6^{a}	1.4^{a}	1.1^{a}	1.2^{a}	1.6^{ab}	1.3^{ab}	1.3^{a}	1.6^{a}	2.4^{de}	1.6^{a}
Averages	1.3	1.5	1.7	1.3	1.3	1.4	1.8	1.5	1.3	1.6	2.3	1.5
Cowpea F-51					4.0^{g}	3.9^{f}	3.2^{e}	1.5^{ab}	2.6^{cd}	3.2^{de}	2.0^{cde}	--
Cowpea 10R-61					3.8^{fg}	3.8^{f}	2.4^{cd}	--				
Cowpea Pink Eye P.H.									1.8^{ab}	3.3^{de}	1.8^{bcd}	--
Averages					3.9	3.8	2.8	--				
Vigna angularis I	2.6^{de}	2.1^{bc}	1.7^{a}	1.2^{a}	2.9^{cde}	2.7^{ced}	2.1^{bc}	1.6^{abc}	3.7^{g}	3.8^{e}	2.6^{de}	2.6^{b}
Vigna angularis II	3.6^{f}	3.4^{e}	2.5^{b}	1.8^{abc}								
Vigna radiata					3.0^{de}	3.3^{ef}	2.8^{de}	1.7^{abc}				
Averages	3.1	2.7	2.1	1.5	2.9	3.0	2.4					
Vicia faba					1.0^{a}	1.1^{a}		1.1^{a}				

[1]Means across all stages of reproductive growth.

For each tissue in each experiment entry means with the same letter are not significantly different by Tukey's HSD procedure at 0.05 level.

TABLE 7.--Comparison of entry soluble solids mean[1] readings (refractometer values), by experiments, for several grain legumes, grown at two locations in Michigan, 1978 and 1979

	Experiment A78			Experiment B78			Experiment 79			
	R	S	LP	R	S	LP	R	S	LF	PW
Seafarer	4.0^{bc}	4.2^{ab}	5.3^{a}	4.8^{b}	4.1^{abc}	5.3^{ab}	2.9^{a}	3.8^{a}	3.5^{a}	5.4
California Small White				4.8^{b}	3.8^{ab}	5.4^{ab}	3.4^{ab}	3.7^{a}	3.6^{a}	5.5
Nep-2	4.6^{bcde}	5.1^{bc}	5.6^{a}	4.8^{b}	4.4^{bc}	5.3^{a}	3.9^{bcd}	4.4^{a}	3.9^{ab}	5.5
Redkloud	4.3^{dcd}	4.3^{bc}	5.8^{ab}	4.6^{b}	4.4^{bcd}	5.5^{ab}	3.4^{ab}	4.0^{a}	3.9^{ab}	4.5
Redkote	5.0^{de}	5.2^{bc}	5.5^{a}	5.2^{b}	5.2^{cde}	5.8^{abc}	3.4^{ab}	4.5^{a}	4.0^{ab}	5.3
Black Turtle Soup	4.0^{b}	4.4^{bc}	5.6^{a}	4.8^{b}	4.3^{bc}	5.2^{a}	3.5^{ab}	3.9^{a}	3.8^{ab}	5.0
Swedish Brown				5.4^{bc}	5.0^{cde}	5.6^{ab}	3.6^{abc}	4.0^{a}	4.0^{ab}	5.7
Averages	4.4	4.6	5.6	4.9	4.4	5.4	4.3	4.0	3.8	5.3
Evans Soybean	2.9^{a}	4.2^{ab}	7.4^{c}	2.9^{a}	4.0^{abc}	7.7^{d}	4.0^{dcd}	5.8^{b}	6.9^{d}	
Beeson Soybean	3.2^{a}	3.2^{a}	6.7^{bc}	3.1^{a}	3.0^{a}	6.6^{bcd}	4.6^{cde}	5.6^{b}	6.4^{d}	
Averages	3.0	3.7	7.0	3.0	3.5	7.2	4.3	5.7	6.6	--
Cowpea F-51				5.8^{bc}	5.7^{cde}	6.3^{ab}	6.1^{f}	5.9^{b}	5.7^{cd}	
Cowpea 10R-61				4.4^{b}	4.6^{bcd}	5.6^{abc}				
Cowpea Pink Eye P.H.							4.4^{cde}	4.4^{a}	4.2^{ab}	
Averages				5.1	5.1	5.9	5.2	5.1	4.9	
Vigna angularis I	5.1^{e}	5.4^{c}	5.4^{a}	4.9^{b}	5.0^{cde}	5.8^{bc}	5.1^{e}	5.6^{b}	4.9^{bc}	5.9
Vigna angularis II	4.8^{ade}	4.7^{bc}	5.0^{a}							
Vigna radiata				6.0^{c}	6.0^{e}	7.0^{cd}				
Averages	4.9	5.0	5.2	5.5	5.5	6.4				
Vicia faba				3.2^{a}	3.5^{a}					

[1]Means across all stages of reproductive growth.

For each tissue in each experiment entry mean with the same leter are not significantly different by Tukey's HSD procedure at 0.05 level.

TABLE 8.--Averages of dry matter production (grams per .0375 m^2) from mid-flowering to seed maturity for roots, stems, and pod walls of selected several grain legumes grown at two locations in Michgian, 1978 and 1979

Entry	Seafarer			BTS			Nep-2			Redkote			Redkloud		
Experiment	A78	B78	79	A78	B78	79	A78	B78	79	A78	B78	79	A78	B78	79
Days of Rep. Gr.															
1	4.7	3.6	4.0	6.6	3.7	7.3	5.0	6.2	7.7	8.5	5.7	6.8	7.9	4.5	3.0
7-9	7.4	5.4	6.6	10.6	6.5	12.0	8.6	8.3	12.3	14.5	6.6	11.7	16.9	6.8	6.4
13-16	11.0	5.8	11.9	12.1	8.1	18.0	13.5	11.6	15.0	18.4	11.6	17.1	15.4	9.4	10.9
20-23	12.3	14.3	17.0	9.2	8.8	22.9	11.0	9.7	23.4	14.1	11.6	23.6	19.6	11.0	20.0
27-32	9.5	14.8	17.4	8.5	9.9	22.4	19.1	10.8	21.4	12.2	12.8	31.1	16.3	16.4	22.2
35-38		14.3	17.8		7.4	22.6	21.2	10.6	21.2	12.6	10.3	33.8	14.8	11.0	20.2
41-44		13.5	13.8			21.7			20.0			35.1			20.4
50						19.4			21.5			31.0			
57												28.0			
64															

Table 8.--Continued

Entry	Swedish Br.		V. ang. I			Evans soyb.			Beeson soyb.		Cowpea F-51		Cowpea P.E.
Experiment	B78	79	A78	B78	79	A78	B78	79	A78	79	B78	79	79
Days of Rep. Gr.													
1	2.8	3.4	5.6	4.7	5.7	7.1	6.4	6.8	9.4	9.5	10.8	17.8	18.4
7-9	3.4	4.8	9.2	9.6	6.0	10.6	9.1	13.7	11.7	19.0	16.9	22.1	18.6
13-16	5.9	11.9	10.5	7.9	8.5	14.4	13.2	24.4	--	27.3	20.3	28.0	24.4
20-23	5.8	13.3	9.9	10.2	12.2	17.0	17.3	33.8	20.8	44.1	18.0	28.0	25.6
27-32	7.1	23.4	11.4	13.7	12.3	16.0	16.1	27.0	21.0	46.6	30.0	31.3	25.9
35-38	8.3	15.3	13.2	--	9.9	24.4	16.2	30.5	28.0	45.9	30.0	26.7	28.0
41-44	6.5	19.2			8.5	17.0	25.4	26.0	32.5	44.8		29.5	33.5
50		14.2							27.8	53.4			
57		15.5							48.4	41.0			
64		17.0							45.1	--			

ABSTRACT

PATTERNS OF PARTITIONING AND REMOBILIZATION OF NON-STRUCTURAL CARBOHYDRATES IN COMMON BEAN AND OTHER SELECTED GRAIN LEGUMES

By

Kabonyi Sebasigari

Levels of non-structural carbohydrates (NSC) were examined in root, stem, leaf beans (Phaseolus vulgaris L.) and other selected grain legumes. Samples were taken weekly from 50% flowering until physiological maturity. IKI solution was used to monitor the amounts of starch and a hand refractometer served to determine concentrations of soluble solids (mostly sugars).

Genotypic and environmental differences in partitioning of NSC between plant tissues were observed in all entries except in Vicia faba L.

Analysis of source-sink relationships indicated that: (a) flowers of grain legumes studied constitute a weak sink for assimilates, and (b) high seed growth rates were correlated with important decreases in levels of NSC. High yields were associated with more tissues being involved in remobilization. In dry beans, soluble solids were preferentially remobilized as compared to starch.