ACCUMULATION AND PARTITIONING OF CARBOHYDRATES IN TWO CULTIVARS OF NAVY BEANS (PHASEOLUS VULGARIS L.) AS INFLUENCED BY GRAFTING AND SOURCE-SINK MANIPULATION

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By

Mohamed Bouslama

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For this study, two experiments were conducted. In Experiment I, a series of grafts (reciprocal, check and double grafts) were made on greenhouse-grown plants to determine whether varietal differences are controlled by the genotype of the scion or the root. Varietal differences in plant dry weight, reducing sugar and total nonstructural carbohydrate in root, stem and leaves are apparently controlled by the above-ground portion of the plant (scion). The effect of the graft *per se* appeared to be negligible although some effects were observed on certain agronomic characteristics.

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In Experiment II, a series of source-sink manipulations were imposed on field-grown plants by removing ca. 33 per cent of the leaf area (one leaflet from each trifoliolate leaf) and all pods at weekly intervals, starting from the end of the flowering period. This study was undertaken to determine quantitative changes in carbohydrate levels under the imposed conditions.

Nep-2 accumulated high amounts of reducing sugar and total nonstructural carbohydrate throughout the growing season as compared with Seafarer.

Treatments designed to reduce the source-sink ratio (partial defoliation) decreased yield, total plant dry weight, reducing sugar and total nonstructural carbohydrate in all plant parts in both cultivars. Partial defoliation was more detrimental to Nep-2 (54 per cent reduction of pod dry weight) than Seafarer (27 per cent reduction of pod dry weight). Such stress conditions could constitute an important factor limiting yield in bean cultivars such as Nep-2 since the amount of previously stored carbohydrate mobilized to the sink was insufficient to compensate for loss in leaf area. In Seafarer, the stem and branches were important storage areas for carbohydrate, and under such stress conditions (reduced source supply) there was sufficient remobilization and/or free sugars to sustain pod and seed dry weight increases.

Conversely, treatments designed to enhance the photosynthetic source-sink ratio (depodding) maintained total plant dry weight, reducing sugars and total nonstructural carbohydrates above control levels. This indicates that both cultivars could be induced to store carbohydrate in stem and branches in response to a reduced sink demand.

Information gained from the last experiment indicates that storage carbohydrate could constitute a buffer between seed growth and photosynthate production in certain varieties but not in all.

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DEDICATION

TO MY PARENTS AND MY WIFE FAOUZIA

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INTRODUCTION

In recent years attention has been given to carbohydrate production and partition in plants as factors related to crop yield; carbohydrate mobilization may be especially important under stress conditions.

Varietal differences in carbohydrate accumulation or partitioning may be related to maintenance of a high rate of seed filling during periods of temporary environmental stress when photosynthesis is adversely affected.

A previous study established that two cultivars of the navy bean (Phaseolus vulgaris L.), Nep-2 and Seafarer, differed in the type and amount of carbohydrate stored (Martinez and Adams, 1975).

Source-sink manipulations and grafting techniques provide simple and useful methods for investigating varietal differences in carbohydrate storage. They may also add to our understanding of the regulation of carbohydrate accumulation or partitioning.

With these possibilities in mind, the experiments of this thesis were conducted to answer the following questions:

1. Is differential accumulation and form of carbohydrate between two varieties controlled by the genotype of the root or shoot?
2. How does source-sink manipulation affect the pattern and form of accumulation of carbohydrate stored in root and stem?
3. Do varieties that differ in starch-sugar storage patterns under normal conditions respond similarly when source-sink manipulations are imposed?

LITERATURE REVIEW

Thorpe and Murashige (1968) noted that the physiological significance of starch accumulation in organ initiation requires further elucidation. They postulated that the accumulation of starch functions in the initiation of organized structures in plants. When primordia elongate as shoots, stored starch decreases in cells of the no-longer meristematic region of the newly formed organs; for example, initial cells of the leaf and stem in the shoot apex continue to store starch but the level of storage activity is diminished.

Thorne and Koller (1974) suggested that starch levels may not be regulators of photosynthetic rates. They also reported that increasing sink demand (i.e., increasing the number of pods) increases the concentration of sucrose but decreases the concentration of starch in source (photosynthesizing) leaves. Their data, however, do not conclusively eliminate the role of starch as a regulator.

Neales and Incoll (1968) reported that detached leaves and leaf disks represent systems in which the assimilation source is isolated from sinks of the products of assimilation. Here starch formation constitutes a sink for assimilates. Throwes (1962) and Maggs (1965) demonstrated that when a portion of the leaf area of an intact plant is removed or shaded, translocation of assimilates is altered. The remaining functional leaf area is capable of supplying a proportionate number of sinks.

Johnston and Pendleton (1968) showed that defoliation of the top third of the soybean plant resulted in significantly lower seed yield than from corresponding nodes on non-defoliated plants. In their experiment they reported that removal of leaves from a certain area of the soybean plant generally decreased seed yields of other areas on the plant. Egli and Leggett (1976) suggested that removal of 66 per cent of the leaf area in soybeans had no significant effect on pod number, however complete defoliation reduced pod and seed yield by 93 and 96 per cent, respectively, compared with the control.

Graber et al. (1927), Cooper and Watson (1968) and Reynolds and Smith (1962) reported that frequent defoliation of alfalfa decreased the percentages of carbohydrates in storage organs. Also, low carbohydrate percentages have been associated with losses in stand and reduced yields (Graber et al., 1927; Bryant and Blaser, 1964). This is why carbohydrate reserves are essential for regrowth and survival.

Egharevba et al. (1976) indicated that after defoliation of the stalk in corn (Zea mays L.) the measurements of the mobilization of sugar in the fifth internode showed 75 per cent was removed within 48 hours after defoliation. They also reported that regardless of severity, defoliation within 30 days after silking significantly reduced total accumulated dry matter and these losses varied with time of treatment application.

Egli and Leggett (1976) reported that defoliation lowered the concentration of sugar in the stem sap compared with the control and reduced the growth rate of the seed only near the end of the filling period.

McAllister and Krober (1958) reported a decrease in stem sugars as a result of 80 per cent leaf removal although there was no effect on leaf sugar levels of remaining leaves. Eastin (1969) reported that under some conditions inhibition of photosynthesis in the ear brought about an increased rate of photosynthesis in the flag leaf of corn (Zea mays L.). In this system, then, there are relatively rapid interactions, and the photosynthetic rate of the source appears to be closely regulated by the demand of the sink.

Yoshida (1972) concluded that the grain carbohydrates of high yielding crops are derived foremost from photosynthesis after heading, thus minimizing the importance of stored carbohydrates. Evans (1975) reported that photosynthesis during the storage phase can be an important determinant of yield, but photosynthesis prior to that contributes to the determination of storage capacity and generates reserves that may be mobilized during the storage phase.

Stritzke et al. (1976) noticed that as shade levels increased, there was a reduction in forage production of wheat, and a concurrent reduction of water soluble carbohydrate contents of both tall fescue and wheat. They also observed an effect of low intensity light on the reduction of sugar production in Poa pratensis L.

Sinclair and de Wit (1976) think that the ability of plants to fix atmospheric CO_2 into carbohydrates places the initial restriction on yield. They assume that carbon translocated within the plants contributes insignificantly to seed development and that the rate of seed production is not greater than the current rate of material produced by photosynthesis. The lower leaves act as the main source of assimilates for roots whereas the upper leaves perform this function for the shoot apex; leaves in an intermediate position may supply assimilates in either or both directions. This pattern has been well substantiated for tomato by Bonnemain (1965, 1966) as well as for soybean by Belikov and Kostetsky (1958).

Egli and Leggett (1973) concluded that the combination of high rates of grain filling and low yield in soybean in one year (1970) indicate that sink size may have been a limiting yield factor. During the next year, greater seed set plus a lower rate of filling over a longer time period resulted in higher grain yields. If in fact this is true, one could suggest that effective filling periods (EFP) are influenced by pod set, which is a function of environmental conditions during flowering. One could also suggest that duration of filling is more important than rate.

Wallace and Munger (1965) reported that higher overall relative growth rate and leaf growth rate of the navy bean varieties were accompanied by a much higher leaf area ratio. They suggested that this may have been the factor chiefly responsible for differences in growth rates.

Wallace and Munger (1966) indicate that leaf area, leaf area ratio and relative growth rate vary among the dry bean varieties studied. Wein et al. (1973) reported that leaf area duration for red kidney in the reproductive period is longer for deflowered plants.

Hale and Weaver (1962) noticed that during early growth in _Vitis vinifera_ (grape vine), a young leaf will require carbohydrate from other parts of the plant for its development; however, once a leaf is fully expanded it is no longer capable of importing assimilates even when placed in darkness. They think they can predict, to a certain degree, from leaf position, leaf area and the growth rates of individual organs, the likely distribution of assimilates from any one source of supply.

Evans and Wardlaw (1964) reported that when leaf area is large relative to the growth requirements for carbohydrate, the demand for assimilate per unit leaf area will be small. They reported also that in Lolium temulentum L., removal of the upper part of the leaf, thus reducing leaf area available for growth, stimulated the movement of assimilates from the remaining basal leaf area.

In sugar cane, however, the opposite effect was obtained; removal of the upper part of the leaf reduced the flow of assimilates from the remaining leaves (Hartt, Kortschak and Burr, 1964).

An added complication is the ability of a leaf to temporarily store excess carbohydrate as sugars (Mortimer, 1965) or starch (Porter, 1966), thus modifying the pattern of carbohydrate movement from the leaf.

Regrowth of corn following removal of the cob (Loomis, 1935 and 1945) and the cessation of root growth during fruit development in tomato (Van Doblen, 1962) suggests that fruits develop at the expense of vegetative growth (Leonard, 1962).

Complete dominance of reproductive over vegetative organs has been illustrated many times by the pattern of assimilate distribution or changes in pattern following leaf or fruit removal (Maggs, 1964 and 1965; Wardlaw, 1965; Wardlaw, Carr and Anderson, 1965; Bonnemain, 1966; Hansen, 1967; Khan and Sagar, 1967).

Although in cereals there may be some movement of assimilates from the ear to the developing stem during the initial stages of grain development (Carr and Wardlaw, 1965), this movement ceases as stem development stops and grain growth becomes more active (Buttrose and May, 1959; Carr and Wardlaw, 1965). Although the same restriction in movement is evident in the pods of bean plants, Wanner and Bachofen (1961) noted that up to half the assimilates can be exported from a green pod if this is the only part of the plant illuminated. The exported carbon, then, moves to other pods on the plant. McAllister and Krober (1958) also reported an increase in sugar and starch in soybean leaves and stems near maturity in response to a high rate of pod removal. Egli and Leggett (1976) reported that altering the source-sink ratio in favor of the source by pod removal did not result in an immediate increase in growth rate of the remaining seed of soybean; however, 15 to 20 days after pod removal, the rate of growth of the remaining seed did increase.

Hale and Weaver (1962) suggested that flowers are a 'weak' sink and fruits are a 'strong' sink in grapes. Wein et al. (1973) reported data which suggest that in beans the stems, leaves and roots collectively function as efficiently as sinks for photosynthates as do developing pods. They think that the dry weight decrease of vegetative tissue at the end of the growing season results from translocation of carbohydrates to the pods. Balasko and Smith (1973) reported that at initiation of stem elongation, roots and leaves in grasses are the primary sinks of photosynthate. The stem bases which accumulate carbohydrates at anthesis did not appear to be strong sinks at any other growth stage.

Kollman et al. (1974) presented data which showed that 64 per cent of the carbohydrate (starch and sugars) content of soybean leaves and forty per cent of the stem and petiole carbohydrate decrease as the number of pods per node increase from 0 to 2.7.

Neales and Incoll (1968) reported that one method of investigating the relationship between leaf assimilation rates and the rate of withdrawal of assimilates from them is to excise the whole or a portion of the main sink to which assimilates are moving. They also suggested that root-growth rate is a better measure of sink size than is the mass of the root system. Increased sink size in sugar beet and spinach beet have been reported by Thorne and Evans (1964). After observing that sugar beet has a larger net assimilation rate than spinach beet, they cross-grafted roots and shoots of each specie. Spinach beet leaves on sugar beet roots showed higher net assimilation rates than the corresponding intraspecific graft of spinach beet. Thus, the rate of photosynthesis of spinach beet leaves can be influenced by the type of sink available.

Studies of the cause of variation in yield among crops can be directed toward the control of starch accumulation and the efficiency of sinks for storage of assimilates. Hume and Criswell (1973) demonstrated that stems accumulate considerable amounts of ^{14}C while they are growing, but relatively little ^{14}C disappears by maturity. The implication is that stems serve as permanent storage sites for photosynthates. If the same were true for 'Nep-2', there would seem to be little advantage to its accumulating carbohydrates unless they could be remobilized under stress conditions. Hume and Criswell (1973) reported that stems of soybeans do not act as temporary storage sites for carbohydrates as frequently occurs in corn.

In sugar cane, Glasziou (1961) concluded that the maturation of storage tissue, which is accompanied by a marked increase in sucrose content and concomitant decreases in glucose and fructose, occupies a key position in the storage of sucrose in the inner space, and that the rate of inversion must decline as the tissues mature. He noted also that immature internodes of sugar cane stalks, to which the photosynthetically active leaves are attached, contain considerable quantities of reducing sugars. Sacher (1966) reported that in bean endocarp tissue sugar is stored almost entirely in the form of glucose and fructose rather than sucrose. Reynolds (1971) has shown that the concentration of nonstructural carbohydrates (TNC) in alfalfa roots decreases for a time after forage harvest and then increases as photosynthate is translocated to the roots. His data showed that carbohydrate fluctuations were rather regular, decreasing after defoliation and then increasing toward maturity. Balasko and Smith (1973) reported that changes in the concentration of total nonstructural carbohydrate in grasses are due primarily to fluctuations in fructosan. A later study by Jung et al. (1976) showed that concentrations of TNC reach high levels in spring herbage before extensive stem tissue development and are generally minimal at flower-head emergence. They also reported that the concentration of TNC is affected much more by harvest date than by maturation of the herbage.

Glasziou (1960) noted that all sugars in sugar cane diffuse slowly from the storage compartment, reducing sugars diffusing more rapidly than sucrose. He reported that the immature storage tissue contains an invertase and the mature tissue contains a higher total sugar concentration but lower reducing sugar.

A later paper published by the same author (1961) established that sucrose is virtually the sole sugar transferred from the metabolic to the storage compartment. Reducing sugars in the storage compartment are derived from hydrolysis of accumulated sucrose. A possible explanation for the presence of glucose and fructose in relatively high concentration in immature tissue is that these sugars are not stored when the concentration of the photosynthate moving from the leaves exceeds the capacity of the tissue to store carbohydrate as sucrose.

Sacher (1965) reported that in bean pod tissue, over a wide range of concentrations of exogenous glucose, the sucrose-reducing sugar ratio of accumulated sugars remained unchanged at about 20. Synthesis of sucrose appears to be requisite to initial accumulation from glucose or fructose, since free hexoses do not increase at the apparent saturating concentration for uptake. He also reported that sucrose accumulation from exogenous hexose represents a steady-state value in which sucrose is transported across the tonoplast into the vacuole at a rate equivalent to the rate of synthesis. Within 16 hours after a period of accumulation, practically all the sugar occurs as glucose and fructose. Porter and May (1955) concluded from their data that fructose and glucose, whether supplied free or combined as sucrose, are equally available for starch synthesis. Williams et al. (1948) noted that in fresh cut tissue the endogenous sugars consist largely of glucose and fructose and only trace amounts of sucrose. If this is true, storage of the samples may create variations in the quality of the sugars. Grant and Beevers (1964) concluded that glucose uptake is increased more than ten-fold by increasing the temperature from 3° to 25° C. Withholding O_2 strongly depresses the uptake of glucose, fructose, galactose and xylose.

Saleem and Buxton (1976) reported that higher carbohydrate levels were found in debudded cotton plants than in control plants and in plants grown under high illumination than in plants grown under low illumination. Thus, by limiting photosynthesis (light stress), carbohydrates are mobilized. They also suggested that total available carbohydrate (TAC) level is not a major factor in determining differences in plant growth rates among population densities. However, other factors, such as free sugars, which were not investigated in their study, may have a more important effect. Upon the same plant one can find different positions of leaves, consequently, solar radiation interception is different. Furthermore, Saleem and Buxton (1976) noticed that high levels of TAC at the cotton plant top reflected the favorable position of leaves for solar radiation interception and high photosynthetic activity, with a relatively low sink demand by developing fruiting forms for these carbohydrates. However, low levels near the middle of the stem probably result from the effect of shading and effective utilization of carbohydrate by rapidly developing bolls in this region. They also reported that TAC variability was more pronounced in leaf blades than in petioles. This seems logical since leaf blades are major photosynthetic structures while petioles are primarily conducting channels.

Extensive reviews by Deinum (1966), Sullivan (1969) and more recently by Smith (1973) stated that environment greatly affects nonstructural carbohydrate concentrations in herbage. Thus, one may encounter different results between greenhouse and field experiments. Changes in the amount of carbohydrates also are associated with the time of season. Thus, Saleem and Buxton (1976) suggested that high TAC levels at the end of the season probably reflect a reduction in growth rate and translocation of photosynthates to the roots and stems for active accumulation of carbohydrate reserves. On the other hand, reduction in TAC levels at mid-season is related to the development of a strong sink for TAC by developing cotton bolls demonstrated by the same authors in 1971 and 1972. Their data showed that maximum dry weight incremental changes were associated with minimum TAC levels during both years. Egli and Leggett (1976) presented data about the variation in pods weight and stem sugar levels which suggested that storage carbohydrates serve as a buffer between photosynthesis and seed growth. McAllister and Krober (1958) and Kollman et al. (1974) have noted a similar phenomenon.

Several studies have been conducted on the effect of genotype on nutrient uptake by utilizing reciprocal grafts. Grafting studies have indicated that genotypic differences in accumulation of Sr and Ca are controlled almost exclusively in the scion (Kleese, 1967).

Brown et al. (1958), working on two varieties of soybean, found the genotype of the root to be more important than the stem in Fe accumulation although there was some scion effect.

The effect of the graft per se on mineral accumulation has been shown by Kleese and Smith (1970) and Cardwell and Polson (1972) to be negligible. However, Lawn and Brun (1974) reported that differences between the respective ungrafted and self-grafted were not small for total plant yield of 'Chippewa 64' soybean.

Many of the previous studies dealing with the effect of genotype on nutrient uptake have utilized reciprocal grafts. The shoot and root of different cultivars were used to test if nutrient uptake is governed by the scion or the root by several workers: Brown et al. (1958); Caldwell and Hanson (1968); Kleese (1967); Kleese (1968); Kleese and Smith (1970); and Polson and Smith (1972).

Sanders and Brown (1976) stated, "despite the substantial progress made in these areas, the data do not clearly differentiate between the contribution of shoots and roots in nutrient uptake . . ."

However, Polson (1968) concluded that reciprocal scion-root grafts in beans grown in high zinc established that tolerance to this level of zinc is mediated by the genotype of the scion.

MATERIALS AND METHODS

Two cultivars of *Phaseolus vulgaris* L., Nep-2 (indeterminate, with late maturity) and Seafarer (determinate, short life cycle), were grown in two experiments. The first experiment was conducted in a greenhouse at East Lansing, Michigan during October-November, 1975; the second was conducted in the field at the Bean-Beet Research Farm near Saginaw, Michigan during June-September, 1975.

Experiment I: Seeds were planted October 7 in large (9") and also small (2") sterile pots. On October 22, approach grafts NO were made in all self and reciprocal combinations. Plants grown in small pots served as scions and those grown in large pots as stocks. The scion was cut half-way between the cotyledon and the soil surface, shaped into a wedge and placed into a slit made through the growing point of the stock. The union was secured by wrapping a small piece of pressure-sensitive, vinyl-coated tape around the graft. Time between making a cut and joining the scion to a new stock varied from 1 to 5 minutes.

Two weeks after grafting, the leaves on the stock were excised. Afterwards, any axillary buds that grew on the stock were removed. Three days later, the tape was removed and successful grafts were chosen for further experimentation. A short length of greenhouse wire-tie was wrapped around each grafted plant to support it. In the greenhouse, plants were watered periodically with nutrient solution. ✓

Throughout the remainder of this thesis the graft combination will be expressed as a fraction, the numerator being a scion and the denominator a stock. For example, $\frac{N}{S}$ represents a graft in which a Nep-2 scion was grafted onto a Seafarer stock. $\frac{N + /S/}{\underline{N}}$ represents a double graft in which a Seafarer scion was the tissue of interest. In addition to the self-grafted controls ($\frac{N}{N}$ and $\frac{S}{S}$), ungrafted controls of Nep-2 and Seafarer were also grown. ✓

✓ Ten replications of ten treatment combinations were grown in a randomized block. On November 22, freshly harvested plants were divided into three parts (leaves, stems and roots). Flowers were present in some graft combinations.

At the sampling time, total leaf area was measured. Roots were washed free from soil and their diameters were measured. The three plant parts were dried to constant weight at 70 C, weighed and ground to pass a 40 mesh screen using a Wiley Mill. Leaf areas, root diameters and leaf, stem and root dry weights were recorded to provide an estimate of plant size and dry matter distribution.

Only material from six replication of the original ten were prepared for the analysis of reducing sugars and total nonstructural carbohydrates. These were analyzed according to the procedure outlined by Smith (1969). Some modifications as described by Subhadrabandhu (1976) were also used.

Optical densities were determined colorimetrically at 620 nm using the anthrone-reagent technique (Yemm and Willis, 1954).

Experiment II: A field experiment was conducted near Saginaw, Michigan during the summer of 1975. Seeds were planted in 70 cm rows, and plant populations of approximately 285,000 per hectare were obtained.

Four replications of three treatment combinations were grown in split-plot arrangement. Navy bean cultivars were the main plots and harvest dates the sub-plots. Treatments were applied at weekly intervals from the end of flowering (August 16) to maturity (October 2). Treatments consisted of: 1) weekly defoliation of the central leaflet at each node; 2) weekly flower removal and; 3) plant intact as a control.

Samples of twelve plants were removed from each plot on the following dates: August 6, August 27, September 10 and October 2 which will be designated as H_1 (end of flowering), H_2, H_3 and H_4, respectively.

Plants were divided into their component parts as leaves, stems (main stem, branches and petioles), root and reproductive material (pods and seeds) for dry weight determination, once oven-dried to constant weight at 70 C. Fresh leaf area of the plants was also measured for ten leaflets. For the analysis of reducing sugars and total nonstructural carbohydrate, the same procedure was followed as in Experiment I.

A combined analysis of variance across sampling dates was used to evaluate the significance of differences in dry weights of roots, stems, leaves, pods (including seeds) and soluble and insoluble carbohydrate. The least significant difference (LSD) test was used for comparisons among treatment means.

RESULTS AND DISCUSSION

Greenhouse Experiment

Effect of Grafting on Weight Characteristics of Two Navy Bean Cultivars

Significant varietal differences in dry weight were found in all plant organs (Table 1). The total dry weight of ungrafted Nep-2 was significantly greater than that of Seafarer, which was expected.

To determine the effect of the graft *per se* on dry weight accumulation, data from self-grafts of each cultivar were compared--root, stem and leaf dry weights. The Nep-2 self-graft was somewhat different from the respective ungrafted plant. Comparisons of ungrafted Seafarer with its respective self-graft exhibited significant differences in accumulation of dry weight in all tissues. Comparisons of ungrafted plants with their respective self-grafts for root diameter and leaf area revealed significant differences, but only with Seafarer (Table 2).

Although the comparisons between ungrafted and the respective self-grafts were not significantly different in Nep-2, data for Seafarer were taken as evidence that grafting may have some effect on plant dry weight accumulation. Lawn and Brun (1974) reported that differences between the respective ungrafted and self-grafted control were small except for total plant yield for Chippewa 64.

Root and leaf dry weights of grafted plants having Nep-2 as the shoot (N/N and N/S) were generally greater than those with a Seafarer shoot (S/N and S/S). Results for root diameter, date to flowering and leaf area are essentially the same as those reported for dry weight. Where Nep-2 served as the root in graft combinations, all growth characteristics ranged from high to low values depending upon the scion used.

Table 1. Dry weights of ungrafted and grafted plants of two navy bean cultivars: Nep-2 (N) and Seafarer (S)

Treatments	Root		Stem		Leaf	
			gm			
1. N	.411	BD*	.70	BC	1.53	BC
2. S	.285	EF	.48	C	1.03	DE
3. N/N	.361	DE	.72	BC	1.70	B
4. S/S	.495	B	1.02	A	1.72	B
5. N/S**	.555	B	.94	AB	2.23	A
6. S/N	.211	F	.72	BC	1.14	DE
7. $\frac{\text{N+/S/}}{\text{N}}$***	.489	B	.70	BC	0.96	E
8. $\frac{\text{/N/+S}}{\text{S}}$	1.02	B	.47	C	1.02	DE
9. $\frac{\text{N+/S/}}{\text{S}}$			1.21	A	1.74	B
10. $\frac{\text{/N/+S}}{\text{N}}$			.72	BC	1.33	CD

* Means followed by the same letter within columns are not significantly different at the 5% level.

** N/S indicates Nep-2 (N) shoots grafted on Seafarer (S) roots.

*** $\frac{\text{N+/S/}}{\text{N}}$ indicates Seafarer (S) shoots are analyzed.

Table 2. Root diameter, date to flowering and leaf area of ungrafted and grafted plants of two navy bean cultivars: Nep-2 (N) and Seafarer (S)

Treatments	Root Diameter (mm)		Date to Flowering (days)		Leaf Area (cm^2)	
1. N	4.34	BC*	28.4	A*	847.16	BC*
2. S	3.38	E	22.1	D	473.55	FG
3. N/N	3.98	CD	28.0	A	910.54	AB
4. S/S	3.81	D	22.2	D	692.68	CDE
5. N/S**	4.66	AB	28.2	A	1090.00	A
6. S/N	3.38	E	22.1	D	502.70	DEFG
7. $\frac{N+/S/}{N}$	4.86	A	20.9	E	384.85	G
8. $\frac{/N/+S}{S}$	4.36	BC	26	C	479.27	EFG
9. $\frac{N+/S/}{S}$			20	F	678.23	CDEF
10. $\frac{/N/+S}{N}$			27.6	B	694.10	CD

* Means followed by the same letter within columns are not significant different at the 5% level.

** N/S indicates Nep-2 (N) shoots grafted on Seafarer (S) roots.

*** $\frac{N+/S/}{N}$ indicates Seafarer (S) shoots are analyzed.

A comparison of scion means with the respective ungrafted plants of each cultivar supports the conclusion that the scion has more effect on the growth of the plant than does the root. However, there appear to be some root contribution to genotype differences in growth characteristics.

The data of the double-grafted plants in many cases indicated that the scion is dominant in determining the growth of the plant. For instance, the root diameter of $\frac{N + S}{S}$ was 4.36 mm while that of $\frac{S}{S}$ was 3.81 mm, which indicates the strong influence of N in determining diameter.

In the same double-grafted plant $\frac{/N/+S}{S}$, the date to flowering of the shoot N was only 26 days while that of the shoot $\frac{N}{S}$ was 28.2 days. Thus, the decrease from 28.2 to 26 days was probably due to the effect of the shoot S. Furthermore, other data show that ungrafted N registered 28.4 days while ungrafted S only 22.1 days. An analogous conclusion can be drawn from leaf area data from the same plant, $\frac{/N/+S}{S}$.

Several other changes in dry weight lead one to assert that the scion predominates the root.

Effect of Grafting on Reducing Sugar Concentration (RS)

Significant varietal and treatment differences for concentration of reducing sugar (RS) were found in roots, stem and leaves (Tables 3, 4 and 5). Ungrafted plants were not significantly different in RS accumulation from the respective self-grafted plants, indicating the absence of any graft effect per se in this case. The absence of specific grafting effects has been reported by Cardwell and Polson (1972).

In all simple grafts involving a Seafarer scion, a high concentration of RS was found in roots, stem and leaves. Where Seafarer served as the

Table 3. Reducing sugar (RS) and total nonstructural carbohydrates (TNC) concentrations in roots of ungrafted and grafted plants of two navy bean cultivars: Nep-2 (N) and Seafarer (S)

Treatments	Reducing Sugar (mg/g dry wt)		Total Nonstructural Carbohydrate (mg/g dry wt)	
1. N	21.25	B*	88	A
2. S	27.04	A	41.0	C
3. N/N	21.75	B	93	A
4. S/S	26.33	A	43.17	C
5. N/S**	20.38	B	69.3	B
6. S/N	25.63	A	29.67	C
7. $\frac{N+S}{N}$	19.08	B	88.17	A
8. $\frac{N+S}{S}$	21.17	B	83.00	AB

* Means followed by the same letter within columns are not significantly different at the 5% level.

** N/S indicates Nep-2 (N) shoots grafted on Seafarer (S) roots.

Table 4. Reducing sugar (RS) and total nonstructural carbohydrates (TNC) concentrations in stems of ungrafted and grafted plants of two navy bean cultivars, Nep-2 (N) and Seafarer (S).

Treatments	Reducing Sugar (mg/g dry wt)		Total Nonstructural Carbohydrate (mg/g dry wt)	
1. N	49.17	D*	117.67	EF
2. S	119.12	AB	188.50	C
3. N/N	49.25	D	140.83	DE
4. S/S	132.46	A	222.83	B
5. N/S**	50.00	D	107.33	F
6. S/N	123.83	A	226.83	B
7. $\frac{\text{N+/S/}}{\text{N}}$***	102.42	B	171.00	CD
8. $\frac{\text{/N/+S}}{\text{S}}$	74.92	C	152.33	DE
9. $\frac{\text{N/S/}}{\text{S}}$	118.79	AB	367.67	A
10. $\frac{\text{/N/+S}}{\text{N}}$	59.04	CD	169.17	CD

* Means followed by the same letter within columns are not significantly different at the 5% level.

** N/S indicates Nep-2 (N) shoots grafted on Seafarer (S) roots.

*** $\frac{\text{N+/S/}}{\text{N}}$ indicates Seafarer (S) shoots are analyzed.

Table 5. Reducing sugar (RS) and total nonstructural carbohydrates (TNC) concentrations in leaves of ungrafted and grafted plants of two navy bean cultivars: Nep-2 (N) and Seafarer (S)

Treatments	Reducing Sugar (mg/g dry wt)		Total Nonstructural Carbohydrate (mg/g dry wt)	
1. N	53.75	D*	76.75	E
2. S	115.00	B	137.50	D
3. N/N	52.92	D	81.25	E
4. S/S	116.23	B	149.25	CD
5. N/S**	54.95	D	82.75	E
6. S/N	115.67	B	135.25	D
7. $\frac{N+/S/}{N}$***	104.00	BC	235.75	A
8. $\frac{/N/+S}{S}$	90.42	C	180.00	C
9. $\frac{N+/S/}{S}$	130.58	A	176.75	BC
10. $\frac{/N/+S}{N}$	96.67	C	145.50	D

* Means followed by the same letter within columns are not significantly different at the 5% level.

** N/S indicates Nep-2 (N) shoots grafted on Seafarer (S) roots.

*** $\frac{N+/S/}{N}$ indicates Seafarer (S) shoots are analyzed.

root in simple grafts, accumulation of RS in roots, stems and leaves ranged from high to low depending upon the scion used. Nep-2 self-grafts accumulated the lowest amount of RS in roots, stems and leaves and simple grafts with Nep-2 as scion also showed low RS accumulations in all three plant parts. Thus, there is consistent indication that RS accumulation is determined largely by the shoot of the plant.

In the double grafts there is also an indication of scion control in RS accumulation. The root of $\frac{N+S}{S}$ accumulated only 21.17 mg of RS/g dry weight while the root of $\frac{S}{S}$ accumulated 26.33 mg/g. This decrease is probably due to the influence of the Nep-2 scion.

Results of double grafting for stems and leaves are essentially similar to those reported for roots. For instance, in plant $\frac{N+/S/}{N}$ where S stem was analyzed, the accumulation of RS was 102.42 mg/g dry weight while that of $\frac{S}{N}$ stem was 123.83 mg/g. So as ungrafted N accumulated less concentration of RS than ungrafted S, this suggests, then, that the N scion is responsible for decreasing the concentration of RS from 123.83 mg/g to 102.42 mg/g. In the same way, in $\frac{/N/+S}{S}$, the stem S increases the concentration of RS and therefore creates the net difference.

Predominance of scion control was further illustrated in other cases (i.e., RS in leaves). The accumulation of RS in the double-grafted plants did not show as striking an effect of scion control as did the simple grafted plants mentioned above; however, the general pattern of scion control can be accepted as evident.

The previous data consistently illustrate that differences in the accumulation of reducing sugars in the root, stem and leaves of these navy bean cultivars are controlled primarily by the above-ground portion of the plant. Evidence obtained by other researchers (Thorne and Evans, 1964; Klesse, 1967; and Polson, 1972) suggests that genotypic differences in the accumulation of minerals also are determined by the scion and not the root.

The data of this thesis suggest that the genotype of the shoot has an effect on production of reducing sugars and upon translocation, since the scion was dominant in all of the measured factors. Furthermore, the higher concentration of sugar in stem and root of Seafarer may provide a more readily available pool of short-chain carbohydrates for amino-acid synthesis and other metabolic processes.

Effect of Grafting on Total Nonstructural Carbohydrates (TNC)

Accumulation of total nonstructural carbohydrates in roots, stems and leaves (Tables 3, 4 and 5) are similar to those reported for reducing sugars. However, the root of Nep-2 accumulated a higher amount of TNC than the root of Seafarer, possible because Seafarer was at the end of the flowering stage (for translocation into the reproductive organs) and Nep-2 at the vegetable stage.

There were significant varietal and treatment differences in accumulation of TNC in root, stem and leaves. In this case, the only significant difference between the ungrafted and self-grafted plants was found in TNC accumulation in Seafarer where stems of the self-grafted plants (S/S) had a significantly higher concentration of TNC than the ungrafted plants. Similar results were found with root, stem and leaf dry weight and leaf area. In addition, although there was no significant difference between the ungrafted and self-grafted plants of Nep-2, there was a general pattern which suggested that grafting may have some effect on TNC accumulation. Scion control of TNC accumulation in the root, stem and leaves was found in this case, too. The level of accumulation of

TNC in root and leaves was similar to that for RS of plants which have the same genotypes as scion. The accumulation of TNC in stems did not show as striking an effect of scion control. When plants of Seafarer were used as root stocks, the accumulation of TNC in the stem and leaves was similar to that of ungrafted plants having the genotype of the scion. For the accumulation of TNC in the root, when plants of Nep-2 were used as root stocks, the accumulation was the same as the ungrafted plants having the genotype of the scion. Similarly, when cultivars which were relatively low in accumulation of TNC in root, stem and leaves were used as scions, accumulation in these plant organs was, in all cases, low.

In the case of the accumulation of TNC in the double grafted plants, there was a similarity to the results reported for RS. For instance, the accumulation of TNC in the root of $\frac{N+S}{S}$ was 83.0 mg/g while $\frac{S}{S}$ accumulated only 43.17 mg/g, which suggests that N contributes to the difference. In the same way, the genotype of N influenced the reduction of TNC in the stem of $\frac{N+/S/}{N}$, while the genotype of S influenced the relative increase of TNC in the stem of $\frac{/N/+S}{S}$. In leaves, the genotype of S influenced the greater amounts of TNC in plant $\frac{/N/+S}{S}$. Although the data of the double grafted plants were not as consistent as those for simple grafted plants, a general trend of scion influenced on accumulation and translocation of total nonstructural carbohydrates continues to be manifest.

With Nep-2 and Seafarer, the top genotype seems to be mainly responsible for varietal differences in production and accumulation of total nonstructural carbohydrates in root, stem and leaves while the root genotype seems to have a lesser or no effect.

Conclusion

It is concluded that the genotype of the shoot controls the accumulation of carbohydrates in the various plant organs. The principal influence of the shoot is upon production and translocation of reducing sugars (RS) and total nonstructural carbohydrates (TNC).

The mechanism involved in scion control could be due to carbohydrates translocation into reproductive organs rather than into vegetative tissues. Furthermore, there might be an influence of the scion on the photosynthesis rate during the flowering stage and, therefore, on carbohydrate synthesis.

The higher sugar concentration in stem and root of Seafarer may provide a more accessible available pool of short-chain carbohydrates for amino-acid synthesis.

Grafted plants with Seafarer tops had greater accumulation of soluble and insoluble carbohydrates during the flowering stage, less leaf area and a lower concentration of total nonstructural carbohydrates in root than did plants grafted with Nep-2 tops.

It is concluded that the effect of the graft *per se* appeared to be negligible although some effects were observed on certain agronomic characteristics.

Field Experiment

Root Dry Weight

Root dry weights of Nep-2 and Seafarer for all treatments during the four harvest dates are given in Figure 1 and Table 6. There was a highly significant difference between the two cultivars (Appendix table 1). The root dry weight of Nep-2 averaged 2.36 gm compared to 1.10 gm for that of Seafarer.

Although there was no significant difference among the harvest dates, root dry weight in control plants of Nep-2 showed a seasonal pattern of low level at mid-season and high level at the end of the season. This may suggest that Nep-2, retaining active photosynthetic leaf area to the end of the growing season, had a greater amount of photosynthate to partition than would be stored in only the reproductive sinks. The excess was consequently stored in the root and not withdrawn. However, for Seafarer, there was no such trend, the level remaining essentially constant from H_1 to H_4 (Fig. 1). The slight decrease of root dry weight of Seafarer at the end of the season probably reflects the development of a strong sink by developing seeds and pods on control plants.

Although differences in root dry weight due to partial defoliation or pod removal treatments were not statistically significant, there were noticeable effects in harvests 2, 3 and 4; this was more evident in Nep-2.

The treatment designed to reduce the source-sink ratio (partial defoliation) resulted in root dry weights below the control in both varieties. In contrast, the treatment designed to enhance source-sink ratio (depodding) resulted in root dry weights above those of the controls; this seems reasonable.

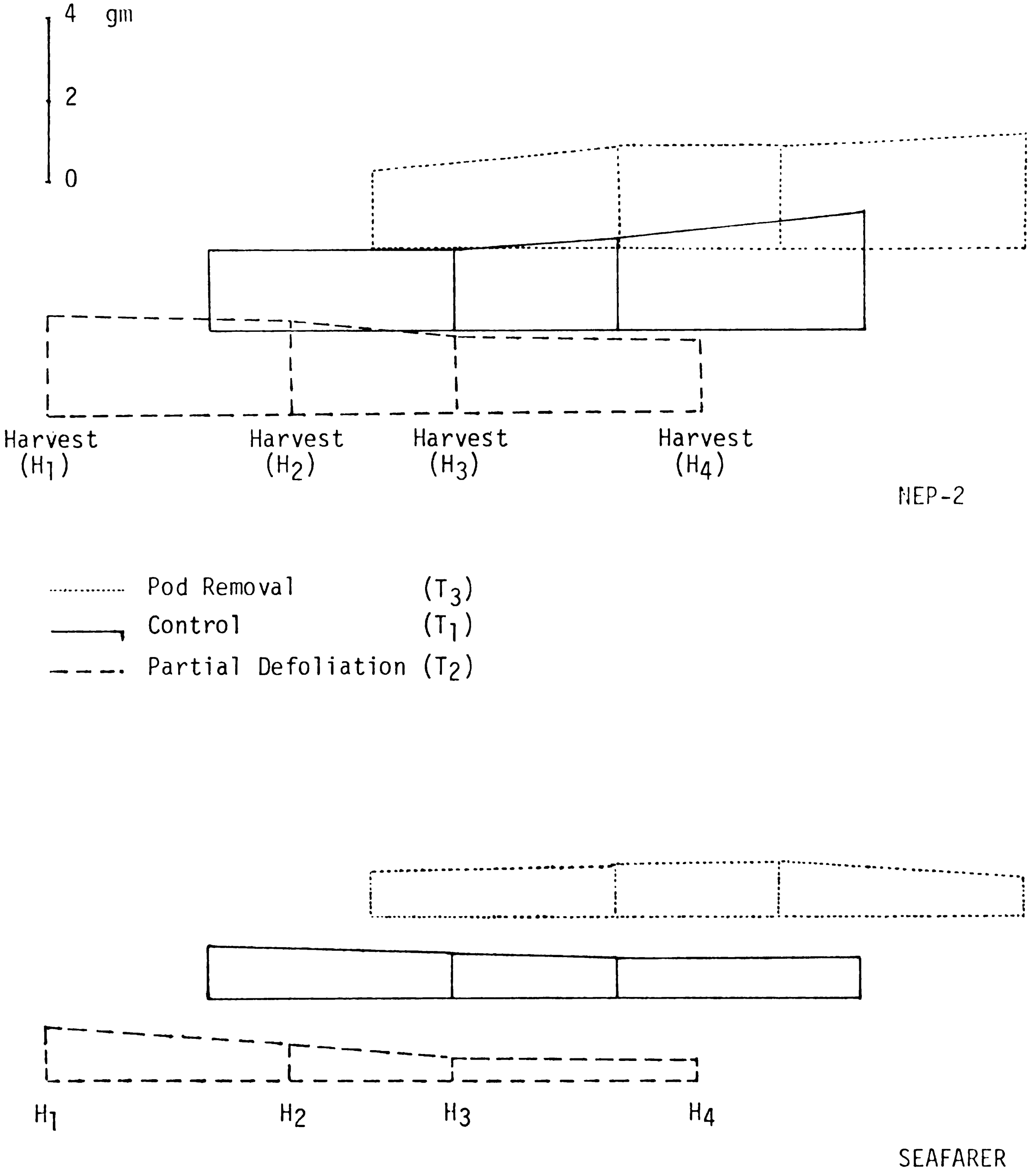


Figure 1. Effect of photosynthetic source-sink manipulation treatments on root dry weight in two navy bean varieties.

Table 6. Effect of photosynthetic source-sink manipulation treatments on root, stem and leaf dry weight of two navy bean varieties.

Harvest	Treatment	Root (gm)		Stem (gm)		Leaf (gm)	
		Nep-2	Seafarer	Nep-2	Seafarer	Nep-2	Seafarer
H_1	Control	2.15 DEFG*	1.40 AB	9.15 E	4.50 EF	6.79 B	4.02 C
	Partial Defoliation	2.42 BCD	1.45 A	8.40 E	5.37 CDE	5.83 B	3.86 C
	Pod Removal	2.00 EFG	1.10 AB	8.40 E	4.20 EF	6.14 B	4.70 BC
H_2	Control	2.07 DEFG	1.23 AB	11.05 BCD	9.13 A	9.56 A	7.45 A
	Partial Defoliation	2.37 CDE	1.05 ABC	9.25 E	6.95 BC	6.82 B	3.90 C
	Pod Removal	2.67 ABC	1.32 AB	13.42 A	8.53 AB	10.69 A	7.11 A
H_3	Control	2.27 CDEF	1.00 BCD	12.05 AB	6.75 CD	10.45 A	4.55 BC
	Partial Defoliation	1.92 FG	.60 D	9.6 DE	3.90 EF	5.91 B	1.55 D
	Pod Removal	2.67 ABC	1.40 AB	12.65 AB	8.70 AB	10.05 A	5.55 B
H_4	Control	3.0 A	1.05 ABC	9.63 CDE	5.13 DEF	1.19 C	.477 D
	Partial Defoliation	1.8 G	.65 CD	4.85 F	3.42 F	.60 C	.455 D
	Pod Removal	2.87 AB	1.00 BCD	11.38 BC	6.75 CD	1.60 C	.800 D

* Means followed by the same letter within columns are not significantly different at the 5% level.

Stem Dry Weight

Highly significant varietal differences in stem dry weight were found (Appendix table 1). Nep-2 averaged 10.0 gm/plant and Seafarer only 6.1 gm/plant. Maximum stem dry weight occurred at H_3 for Nep-2 and at H_2 for Seafarer (Table 6). This is due to the different rates of development of the two cultivars. In all cases, Nep-2 had greater stem dry weights as compared to Seafarer.

At H_4, stem dry weights declined in both varieties (Fig. 2). This is probably due primarily to carbohydrate translocation to pods (including seeds). The loss of some petioles by abscission, which were supposed to be included in stem dry weight, probably also contributed to the decrease.

The treatment effect was highly significant relative to stem dry weight. Leaf removal caused a definite and similar decrease in stem weight in both cultivars. It was consistently lighter than the control at harvests 2, 3 and 4. The lighter weight of stem due to this treatment was a reflection of a smaller leaf area supplying carbohydrates to a larger amount of stems, roots, and pods. Figure 2 shows the range in surfaces of the stem dry weights due to the various treatments.

Pod removal treatment increased the stem dry weight in both cultivars. In fact it was consistently heavier than the controls' at H_2, H_3 and H_4, although the differences were not always significant ($P = 0.05$). This is illustrated by the differences of the slopes between the control and the pod removal treatment for the two cultivars. The decrease of the slopes of pod removal treatments at the end of the season suggests that since there were no pods (sink), there may have been some conversion of assimilates to other plant organs such as new roots, new leaves, etc. The slopes of control plants were much steeper than those of the pod removal

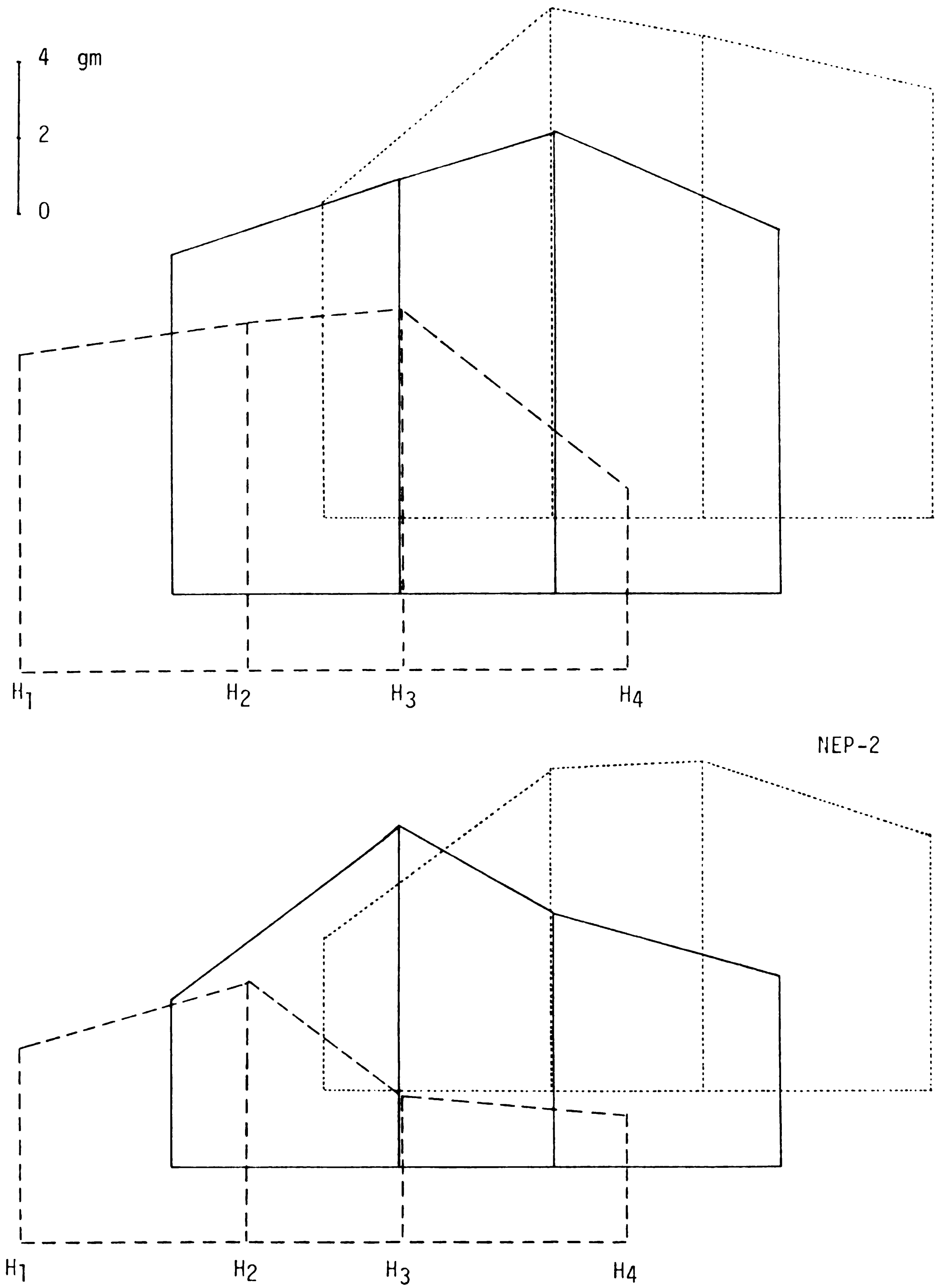


Figure 2. Effect of photosynthetic source-sink manipulation treatments on stem dry weight in two navy bean varieties.

treatment from H_3 and H_2 for Nep-2 and Seafarer, respectively. Thus, by enhancing the source-sink ratio (depodding), stems became alternate and permanent storage sites for photosynthate.

Leaf Dry Weight

Highly significant differences were observed between the two cultivars for dry weight of leaves (Appendix table 1). The overall average was 6.3 gm/plant for Nep-2 and 3.7 gm/plant for Seafarer. Leaf dry weight displayed a seasonal pattern of intermediate levels early in the season, high levels during the pod-filling period and low levels at the end of the season (Fig. 3). The great loss of leaf dry weight is probably due to high sink demand, leading to mobilization of protein from leaves to pods.

The pod removal treatment did not result in any significant increase in either variety. This might be due to the fact that at the time of treatment the leaves had already reached their full size, and most of the carbohydrates available were mobilized to stems and roots by the end of the season.

Leaf Area

Highly significant varietal differences in leaf area were found also (Appendix table 1). Maximum leaf areas were reached at H_2 for Seafarer, long before those of Nep-2 were attained at H_3 (Fig. 4 and Table 7).

The reduced amount of leaf area due to the leaf removal treatment during pod filling was, as expected, one-third compared with control plants for Nep-2. However the reduction in Seafarer was more pronounced with 50 percent instead of 33 percent. This is due mainly to the fact that the central leaflet, which was removed, is larger than any of the

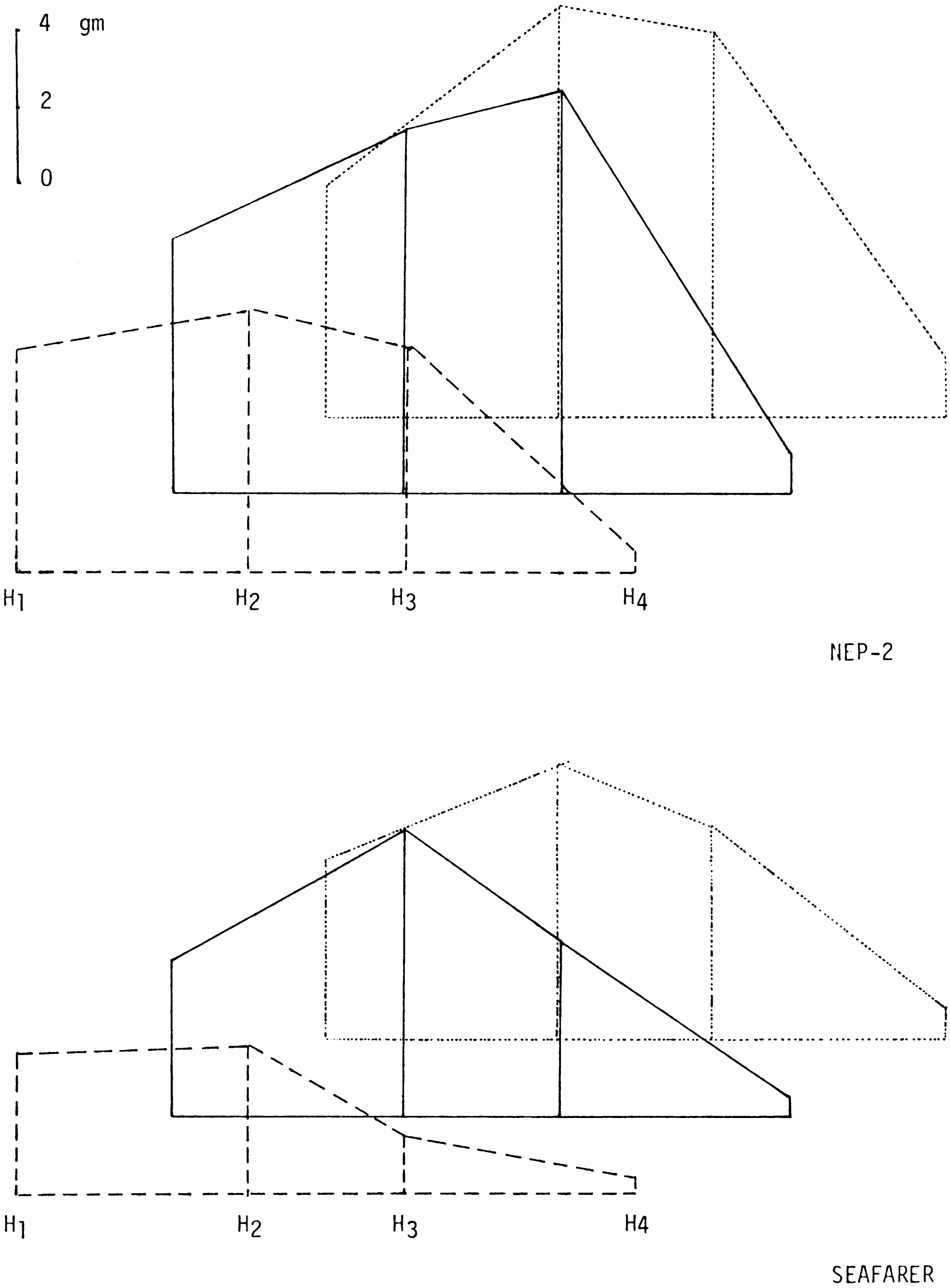


Figure 3. Effect of photosynthetic source-sink manipulation treatments on leaf dry weight in two navy bean varieties.

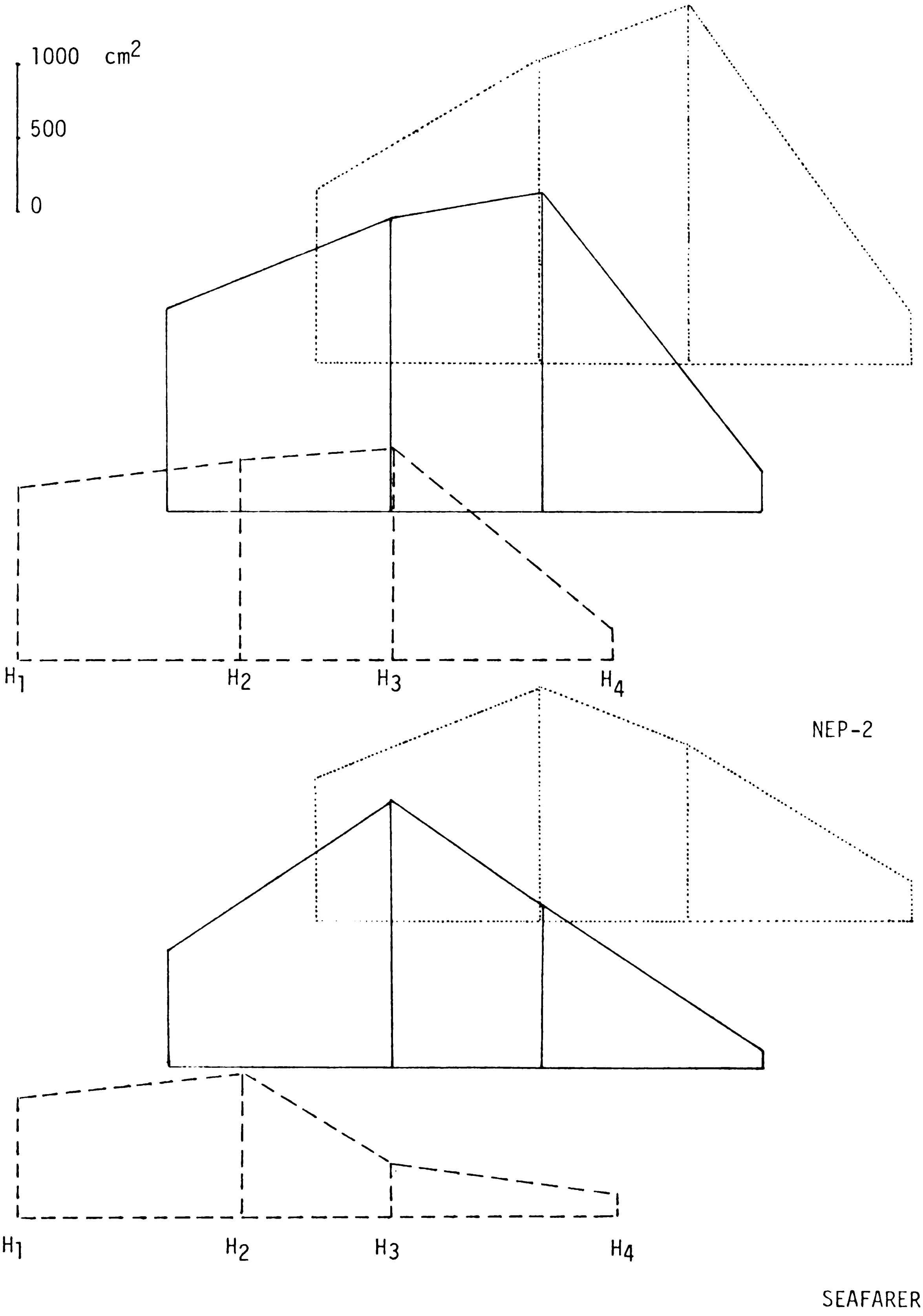


Figure 4. Effect of photosynthetic source-sink manipulation treatments on total leaf area in two navy bean varieties.

Table 7. Effect on photosynthetic source-sink manipulation treatments on leaf area of two navy bean varieties.

Harvest	Treatment	Leaf area (cm^2) Nep-2		Leaf area (cm^2) Seafarer	
H_1	Control	1384.25	C*	810.35	C
	Parial Defoliation	1162.86	C	808.05	C
	Pod Removal	1190.01	C	977.98	BC
H_2	Control	1968.56	B	1839.65	A
	Partial Defoliation	1363.80	C	959.71	BC
	Pod Removal	2044.54	AB	1561.43	A
H_3	Control	2144.90	AB	1106.84	BC
	Partial Defoliation	1433.34	C	357.39	D
	Pod Removal	2408.90	A	1187.65	B
H_4	Control	264.45	D	135.87	D
	Partial Defoliation	205.42	D	160.72	D
	Pod Removal	349.84	D	255.69	D

* Means followed by the same letter within columns are not significantly different at the 5% level.

remaining leaflets. Only a small increase in leaf area occurred in both cultivars as a result of pod removal, probably due to the same reason suggested above.

Specific leaf dry weights were significantly different between cultivars and among harvest dates. The data indicate that there was a slightly high level of specific leaf dry weight during the pod-filling period compared to the end of the season for the control Seafarer. However, for Nep-2, the control did not show a significant difference (Table 8).

There was no significant difference in specific leaf weight due to treatment effect. However, there was a slight difference due to pod removal for Seafarer during harvests 2 and 3.

Yield--Pod Dry Weight Including Seeds

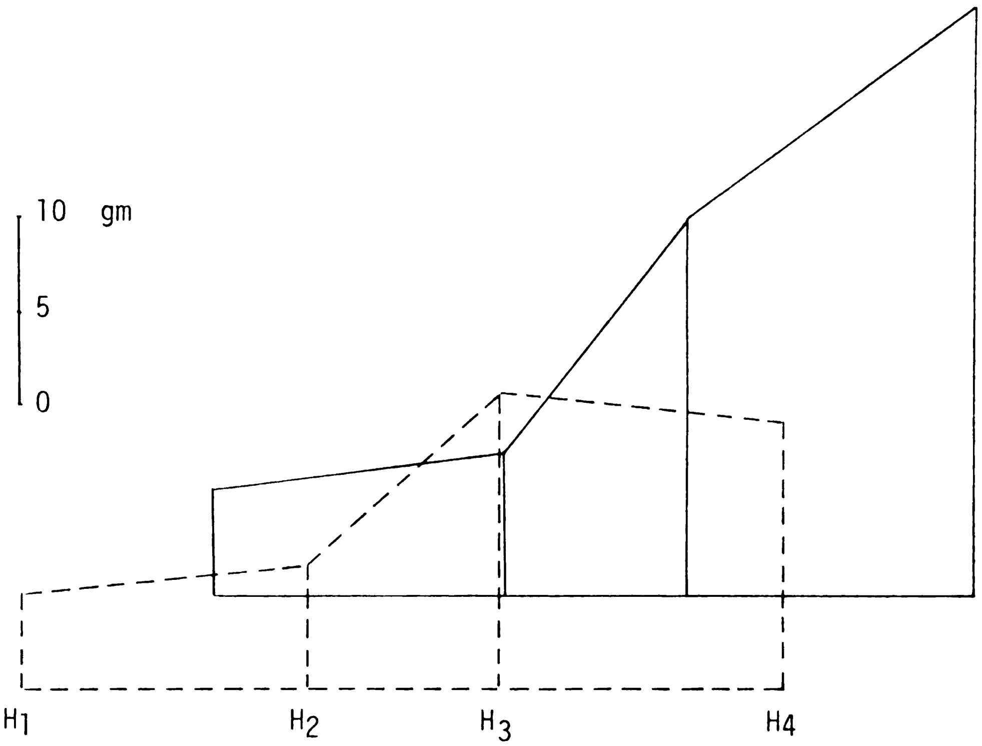
The largest increase in pod dry weight (including seeds) occurred at the end of the season for both varieties (Fig. 5). The pod dry weights differed significantly between varieties and averaged 13.3 gm/plant for Nep-2 and 7.3 gm/plant for Seafarer (Appendix table 1). The latter had lower yield (pods and seeds) at the four harvest dates when compared with Nep-2 (Table 9).

After H_3, the yield of Nep-2 control plants continued to increase until H_4; however, with Seafarer control plants, the increase was slower. This was expected because Seafarer matures earlier than Nep-2. Differences in source-sink balance between the cultivars Nep-2 and Seafarer at different growth stages could probably account for these findings. Moreover, Evans (1975) suggested that photosynthetic rates may parallel yield late in the storage phase, reflecting differences between varieties in their duration of photosynthesis and storage rather than in photosynthesic capacity.

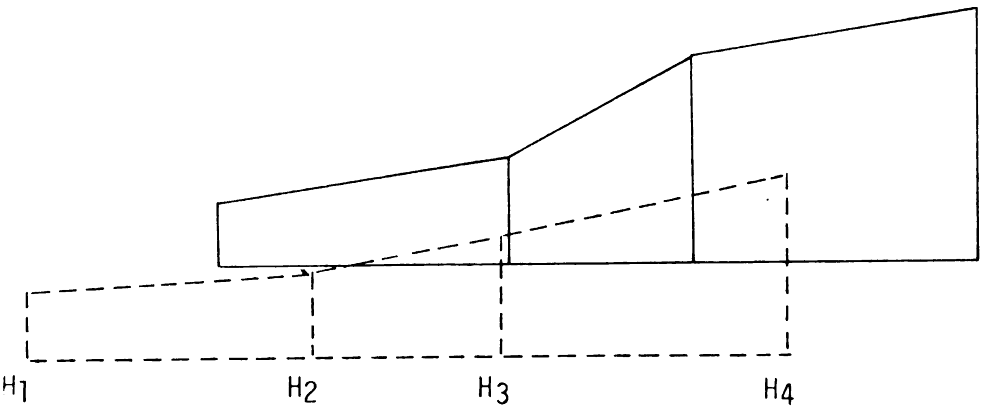
Table 8. Effect of photosynthetic source-sink manipulation treatments on specific dry weight of leaves of two navy bean varieties.

Harvest	Treatment	Nep-2 (mg/cm^2)		Seafarer (mg/cm^2)	
H_1	Control	4.95	ABC*	5.05	A
	Partial Defoliation	5.12	A	4.80	ABC
	Pod Removal	5.25	A	4.92	AB
H_2	Control	4.90	ABC	4.06	DE
	Partial Defoliation	5.03	AB	4.11	DE
	Pod Removal	5.22	A	4.57	ABCD
H_3	Control	4.95	ABC	4.22	CDE
	Partial Defoliation	4.19	D	4.41	BCD
	Pod Removal	4.41	CD	4.73	ABC
H_4	Control	4.47	BCD	3.73	EF
	Partial Defoliation	3.04	E	2.86	G
	Pod Removal	4.77	ABCD	3.31	GF

* Means followed by the same letter within columns are not significantly different at the 5% level.



NEP-2



SEAFARER

Figure 5. Effect of photosynthetic source-sink manipulation treatments on pod + seed dry weight.

Table 9. Effect of photosynthetic source-sink manipulation treatments on pod dry weight of two navy bean varieties.

Harvest	Treatment	Pods (gm) Nep-2	Pods (gm) Seafarer
H_1	Control	5.48 IHG*	3.47 I
	Partial Defoliation	5.02 IHG	3.65 IH
H_2	Control	7.85 GFE	5.77 IGH
	Partial Defoliation	6.85 HGF	4.90 IHG
H_3	Control	20.03 B	10.97 DE
	Partial Defoliation	15.80 C	6.60 IHGF
H_4	Control	31.05 A	13.40 CD
	Partial Defoliation	14.33 CD	9.73 DEF

* Means followed by the same letter are not significantly different at the 5% level.

As can be seen from Figures 1-5, dry weight of various plant organs decreased after pod filling, while the sink size (pod dry weight) increased.

The data reported here for stem, leaf and pod dry weight suggest that there were changes in dry weight that occurred mainly during pod filling from leaves to stems and then to pods. Similar observations were reported by Adams (1975).

Treatments that should decrease total plant photosynthesis (partial defoliation) caused a significant decrease in yield for the two cultivars at the last two harvest dates. This effect was significantly greater for Nep-2 (Nep-2 decreased 54 percent and Seafarer, 27 percent). Several factors could be responsible for this difference:

- Because the partially defoliated plants of Seafarer retained at least 50 percent of their total leaf area at the pod-filling stage (Table 7), the remaining leaves along with the carbohydrate reserves stored in the relatively greater number of branches on Seafarer (Table 10) provide carbohydrate to the pod and seed at a level almost comparable to that of the non-defoliated plants. Thus, plants of Seafarer were not severely damaged by partial defoliation.
- For Nep-2, the lighter seed weight due to leaf removal was a reflection of less leaf area supplying food to a large number of seeds (sink demand). Thus, the plants of Nep-2 that were defoliated seemed to abort their pods more easily and to exhibit a more severe reduction in yield (50%). The limited pod number of Seafarer probably explains why the partial defoliation treatment caused a lesser reduction in yield (30%).

Table 10. Effect of photosynthetic source-sink manipulation treatments on stem dry weight over stem dry weight and leaf dry weight of two navy bean varieties.

Harvest	Treatment	$\frac{\text{Stem dry weight}}{\text{stem dry weight + leaf dry weight}}$ (means of 4 replicates) - gm - Nep-2	Seafarer
H_2	Control	0.54	0.55
	Partial Defoliation	0.57	0.64
	Pod Removal	0.56	0.55
H_3	Control	0.54	0.60
	Partial Defoliation	0.62	0.72
	Pod Removal	0.56	0.60

- Evans (1975) reported that a greater rate of photosynthesis in remaining leaves may compensate for leaves removed.
- Since Seafarer has a shorter life cycle and therefore a faster rate of development, the leaf removal treatment during the last two harvest dates would not substantially reduce the yield of Seafarer.

The data suggest that stress at the pod-filling stage, whether it be from natural or man-imposed causes, may reduce yield significantly in Nep-2. However, reduction of leaf area during the period of storage sometimes reduces yield substantially, and at other times slightly, as Evans (1975) has suggested.

Carbohydrates

Reducing Sugars (RS)

Root RS

Variation in the concentration of reducing sugars in roots during the four harvest dates is shown in Figure 6 and Table 11. The concentration of RS in control plants increased from the first to the second harvest in each cultivar. Maximum concentration occurred at H_2. There was a significant difference between cultivars only for the total amounts of RS. In fact, on a total amount basis, Nep-2 averaged 260.0 mg/plant and Seafarer only 131.0 mg/plant, whereas for the concentration of RS, Nep-2 averaged 107.44 mg/g dry weight and Seafarer 106.75 mg/g dry weight (Appendix tables 2 and 3).

Reduction in RS levels from the middle to the end of season is related to the development of a strong sink represented by developing pods.

Treatment effects were highly significant for both RS concentration and total amounts. The concentrations of RS in the root from the partial

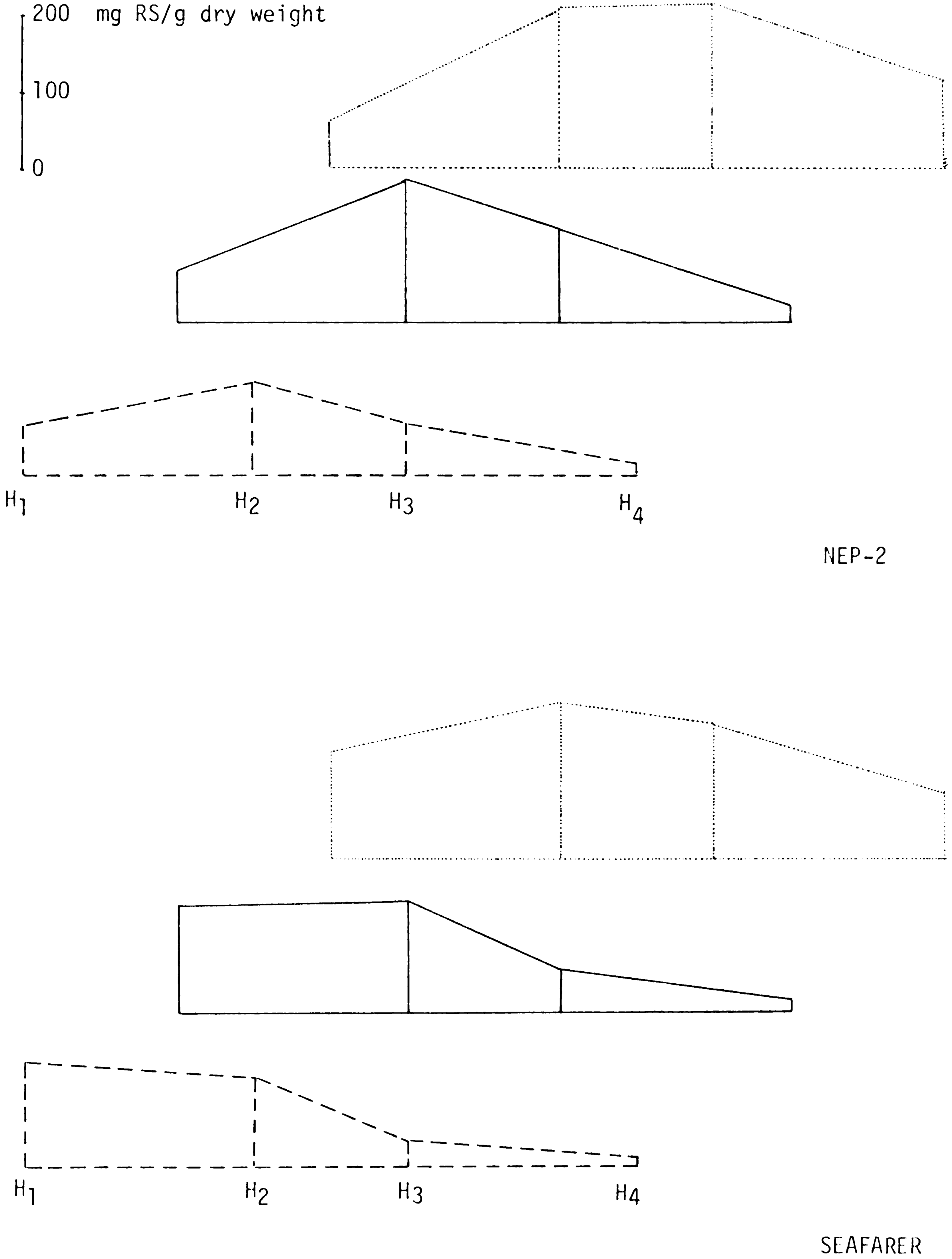


Figure 6. Effect of photosynthetic source-sink manipulation treatments on concentration of reducing sugar in roots of two navy bean varieties.

Table 11. Effect of photosynthetic source-sink manipulation treatments on concentration of reducing sugar and total nonstructural carbohydrates in root of two navy bean varieties.

Harvest	Treatment	Reducing Sugar		Total Nonstructional Carbohydrate	
		mg/g dry wt			
		Nep-2	Seafarer	Nep-2	Seafarer
H_1	Control	70.50 H*	140.87 CD	195.0 C**	152.5 EF
	Partial Defoliation	70.50 H	139.13 CDE	190.75 CD	149.0 EF
	Pod Removal	68.88 H	142.62 CD	189.75 CD	150.75 EF
H_2	Control	188.25 B	147.25 C	267.25 B	152.5 EF
	Partial Defoliation	125.37 DEF	118.5 F	156.25 DEF	132.75 F
	Pod Removal	207.25 A	207.12 A	341.75 A	244.0 B
H_3	Control	121.00 EF	57.63 H	147.25 EF	59.25 GH
	Partial Defoliation	69.25 H	34.75 I	78.5 G	49.25 GHI
	Pod Removal	217.25 A	174.87 B	270.0 B	251.0 B
H_4	Control	21.12 IJ	16.0 J	46.75 GHI	41.5 HI
	Partial Defoliation	14.62 J	13.25 J	25.0 I	38.25 HI
	Pod Removal	115.0 F	89.0 G	173.75 CDE	146.0 EF

* Means followed by the same letter for RS are not significantly different at the 5% level.

** The same format applies to TNC means.

defoliation treatment were consistently and significantly lower than those of the control in both cultivars at harvests 2 and 3. At harvest 4, however, the differences, though still observed, were less significant (Figure 6 and Table 11). The variation of RS for total amounts shows the same trend (Figure 7 and Table 12).

Pod removal had a significant effect on sugar levels (concentration and absolute amounts) at harvest 2, 3 and 4. At the last sampling date both concentration and total amounts in plants with the pods removed were greater than those of the control by almost five-fold in both varieties. In the control plants, the sugars from the leaves presumable moved principally into stems and then into the pods, whereas in the depodded plants a greater part of the sugar that otherwise would have moved into the pods was utilized in relatively greater proportion for development of the roots. It appears from the above data that much of the decline in reducing sugar of plants having pods can be attributed to the increased movement of sugar to the roots. There was probably some conversion of sugar in pod removal plants to new development (observe slopes on pod removal curve in Figure 6). Beevers (1969) reported that developing buds and meristematic regions in roots place demands on the available assimilate and compete successfully as sinks with developing leaves.

Stem RS

Variation of reducing sugar concentrations in stems is shown in Figure 8 and Table 13. Highly significant varietal differences in stems were found only on a total amount basis where Nep-2 averaged 1479.0 mg/plant and Seafarer only 974.2 mg/plant (Appendix table 3). Stem RS had the highest level at H_2 for both varieties, although there were

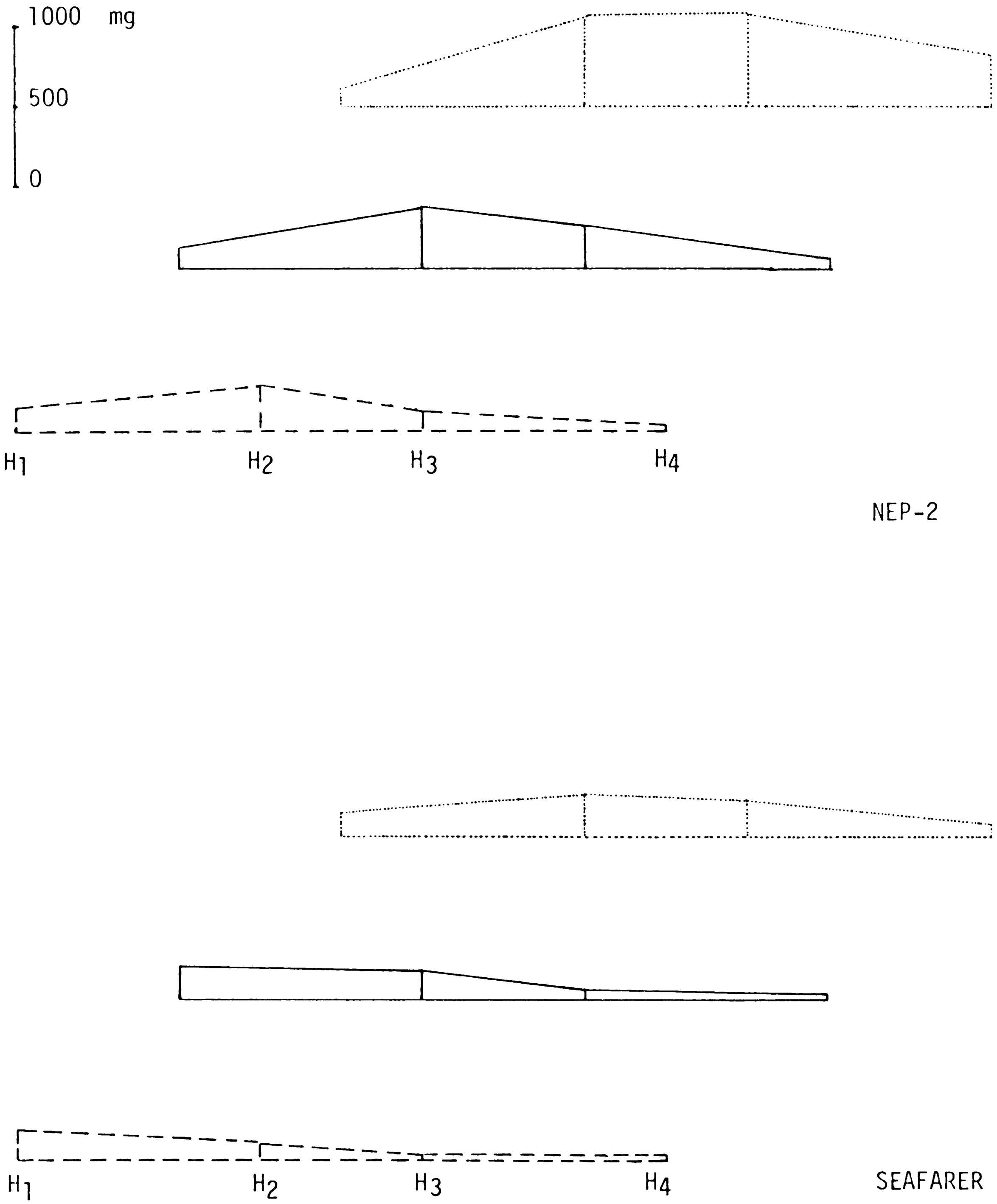


Figure 7. Effect of photosynthetic source-sink manipulation treatments on total amount of reducing sugar in root of two navy bean varieties.

Table 12. Effect of photosynthetic source-sink manipulation treatments on total amount of reducing sugar (RS) and total nonstructural carbohydrates (TNC) in root of two navy bean varieties.

Harvest	Treatment	Reducing Sugar Content		Total Nonstructural Carbohydrate Content	
		mg			
		Nep-2	Seafarer	Nep-2	Seafarer
H_1	Control	151.77 D*	190.80 BC	422.47 DEF	212.90 B
	Partial Defoliation	170.76 D	200.74 BC	464.25 CDE	216.57 B
	Pod Removal	135.86 D	156.56 CD	378.75 EF	164.40 B
H_2	Control	393.70 B	177.95 CD	558.22 C	185.00 B
	Partial Defoliation	299.62 C	121.61 DE	374.12 EF	138.37 BC
	Pod Removal	544.66 A	279.11 A	906.77 A	313.75 A
H_3	Control	280.02 C	57.24 EF	336.30 F	60.45 CD
	Partial Defoliation	131.21 D	20.95 F	152.42 G	29.30 D
	Pod Removal	584.90 A	249.24 AB	719.25 B	347.02 A
H_4	Control	63.79 E	17.22 F	138.07 GH	41.07 D
	Partial Defoliation	26.20 E	8.60 F	46.02 H	24.52 D
	Pod Removal	332.61 BC	90.71 E	503.30 CD	150.70 BC

* Means followed by the same letter within columns are not significantly different at the 5% level.

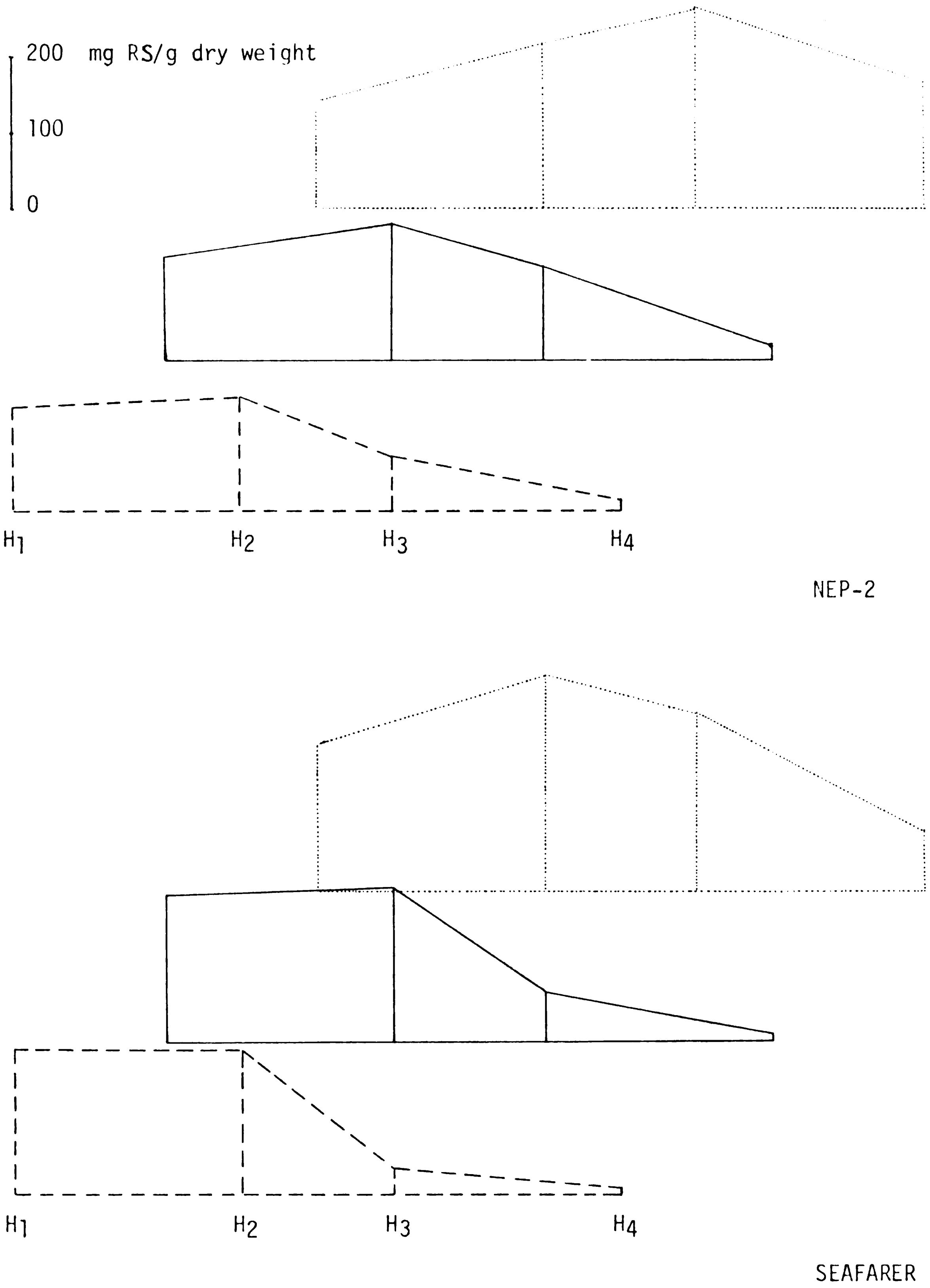


Figure 8. Effect of photosynthetic source-sink manipulation on concentration of reducing sugar in stem of two navy bean varieties.

Table 13. Effect of photosynthetic source-sink manipulation treatments on concentration of reducing sugar and total nonstructural carbohydrates in stem of two navy bean varieties.

Harvest	Treatment	Reducing Sugar (RS)		Total Nonstructural Carbohydrate (TNC)	
		mg/g dry wt			
		Nep-2	Seafarer	Nep-2	Seafarer
H_1	Control	143.62 FG*	193.12 D	223.00 FG	236.00 EF
	Partial Defoliation	140.25 FG	196.62 CD	223.50 FG	228.25 F
	Pod Removal	142.50 FG	194.87 CD	214.5 FG	228.5 F
H_2	Control	183.00 DE	205.87 CD	325.00 C	266.25 DE
	Partial Defoliation	155.62 F	191.25 D	195.50 G	245.25 EF
	Pod Removal	219.50 BC	286.75 A	440.00 A	344.25 BC
H_3	Control	128.00 G	68.25 H	221.00 FG	73.25 IJ
	Partial Defoliation	72.87 H	37.50 I	144.50 H	41.25 K
	Pod Removal	264.37 A	235.87 B	369.00 B	284.00 D
H_4	Control	21.50 IJ	11.75 IJ	52.50 JK	36.50 K
	Partial Defoliation	17.50 IJ	10.00 J	47.75 JK	22.00 K
	Pod Removal	164.12 EF	79.12 H	264.00 DE	96.50 I

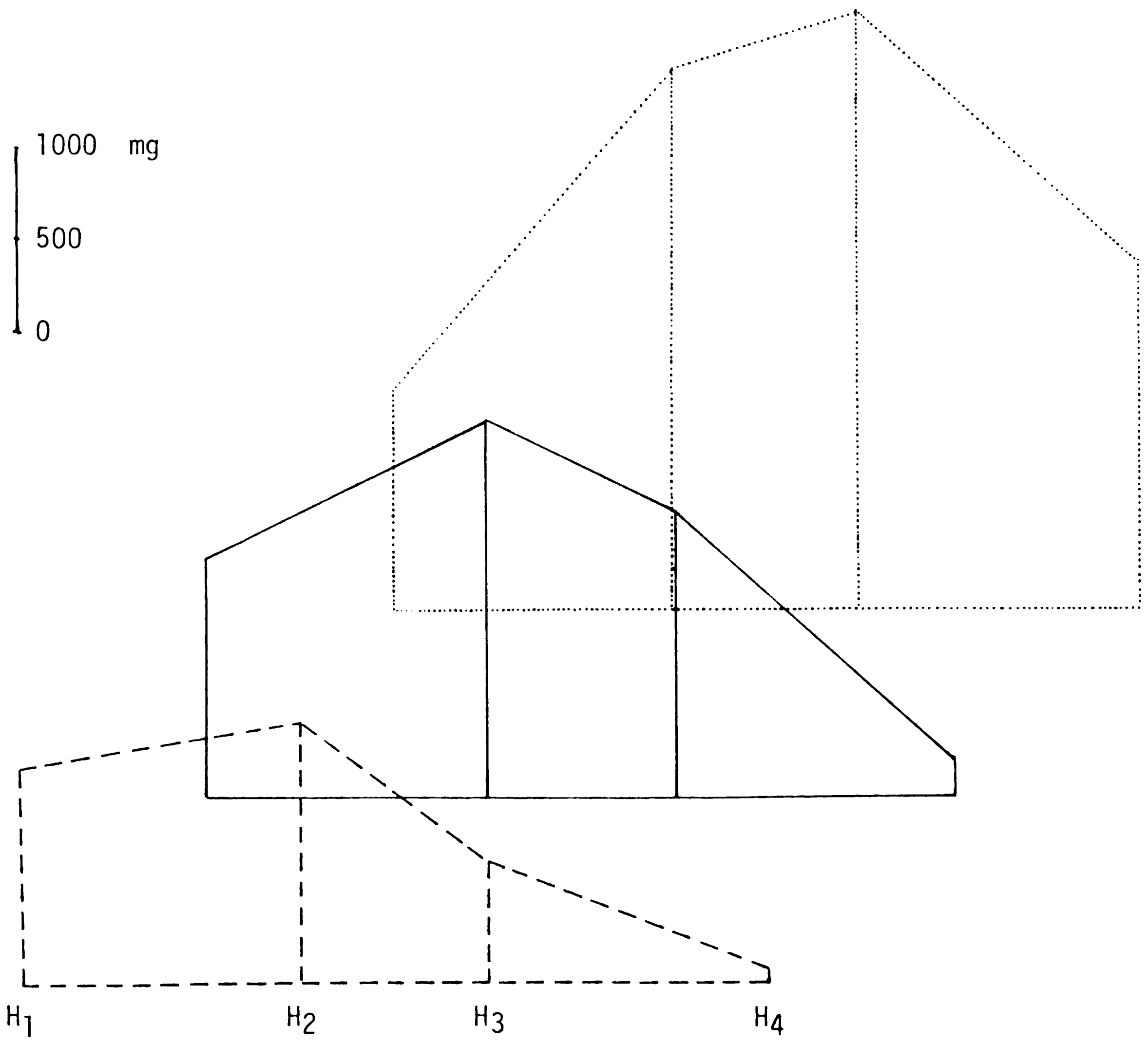
* Means followed by the same letter for RS (or TNC) are not significantly different at the 5% level.

slight differences between H_2 and H_3 in Nep-2. Reduction at mid-season is related to the development of strong sinks for carbohydrates by developing pods and seeds. Between H_3 and H_4 there was no change in RS in Seafarer, while in Nep-2 there was some decrease (note slopes on control plant curves). This may be due to the different rate of development for the two varieties. Thus, any environmental stress that occurred after H_3 could cause a severe reduction in yield for Nep-2 but not necessarily for Seafarer.

Treatment effects were highly significant. Partial defoliation affected the concentration of RS in stem at H_2 and H_3 in Nep-2 but only at H_3 in Seafarer. The data on total amounts reflected almost the same response for each variety, except that Nep-2 accumulated a greater amount of sugar since it had a greater stem dry weight (Figures 9 and 9' and Table 14). Thus, the treatment designed to alter the photosynthate supply to various plant organs was also consistent with the expectation of a limitation to carbohydrate formation (or fixation) for photosynthate for the developing pods.

Removing pods initially increased levels of RS at harvests 2, 3 and 4 compared to the control. The concentration of RS, though decreased from H_1, was almost eight-fold greater at H_4 in both varieties, comparing the pod removal treatment with control. The data on absolute amounts reflected almost the same response for each variety. The observed reduction in RS levels of control plants is minimized by enhancing the source-sink ratio (depodding). (Note the slopes of control plant curves that are greater than those of pod removal plant curves.)

The data reported here suggest that carbohydrate storage in stem and branches probably provides most of the reservoir of readily labile



NEP-2

Figure 9. Effect of photosynthetic source-sink manipulation on total amount of stem reducing sugar in Nep-2.

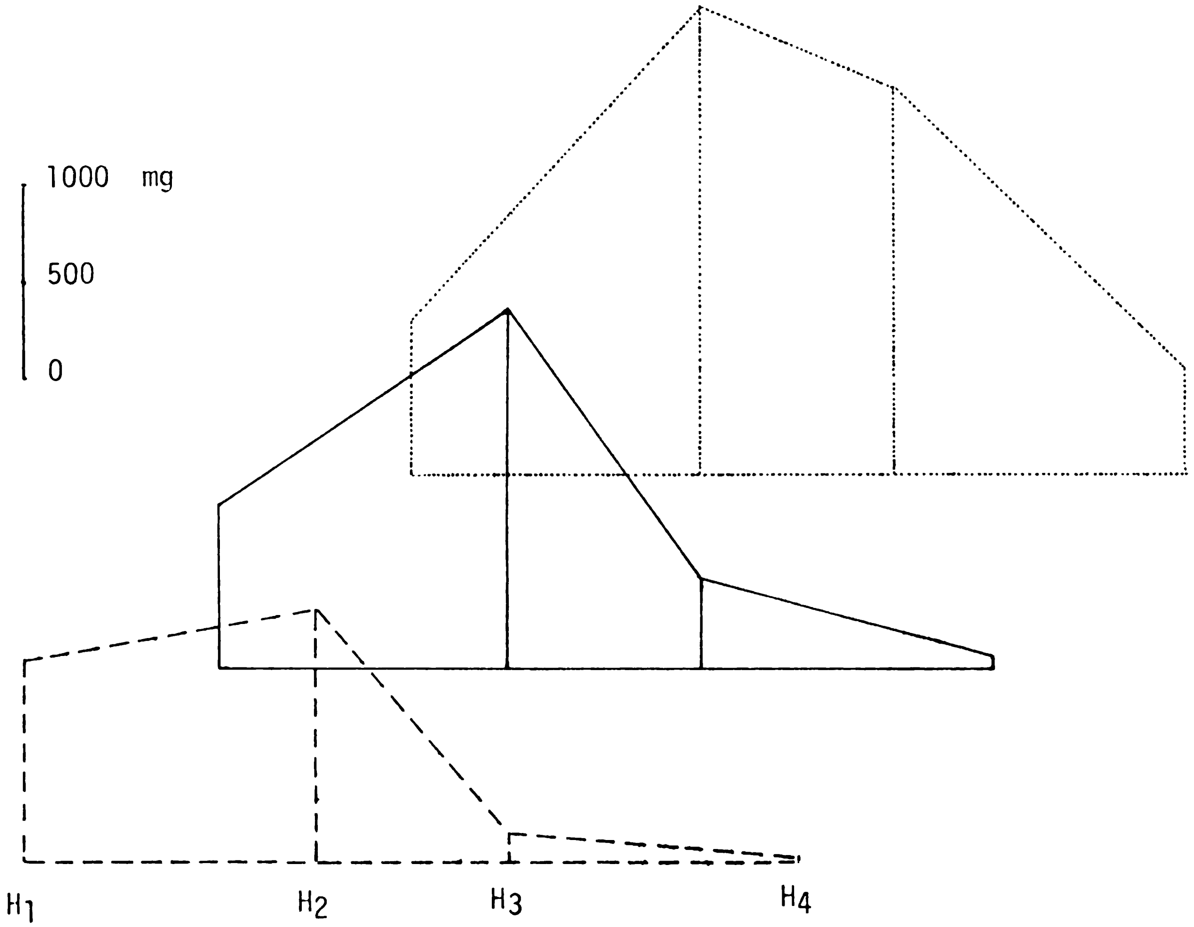


Figure 9'. Effect of photosynthetic source-sink manipulation on total amount of stem reducing sugar in Seafarer.

Table 14. Effect of photosynthetic source-sink manipulation treatments on total amount of sugar (RS) and total nonstructural carbohydrate (TNC) in stems of two navy bean varieties.

Harvest	Treatment	Reducing Sugar Content		Total Nonstructural Carbohydrate Content	
		mg			
		Nep-2	Seafarer	Nep-2	Seafarer
H_1	Control	1311.51 F*	871.14 DE	2039.02 EFG**	1057.42 IJKL
	Partial Defoliation	1180.35 F	1063.11 CD	1873.40 EFGH	1210.47 HIJKL
	Pod Removal	1198.40 F	818.59 DEF	1870.30 EFGH	962.82 JKLM
H_2	Control	2029.64 C	1875.79 B	3595.05 C	2443.52 DEF
	Partial Defoliation	1418.96 EF	1336.24 C	1760.15 FGHI	1695.87 FGHIJ
	Pod Removal	2909.60 B	2434.30 A	5909.85 A	2945.15 CD
H_3	Control	1538.47 DE	461.59 FG	2655.15 DE	495.27 LMN
	Partial Defoliation	674.07 G	152.27 GH	1438.70 GHIJK	163.32 N
	Pod Removal	3319.54 A	2015.67 B	4592.75 B	2480.17 DEF
H_4	Control	208.34 H	62.02 H	507.85 LMN	189.47 MN
	Partial Defoliation	84.66 H	34.40 H	233.45 MN	75.07 N
	Pod Removal	1874.11 CD	565.15 EF	2988.45 CD	684.45 KLMN

* Means followed by the same letter within columns for RS are not significantly different at 5% level.

** Means followed by the same letter for TNC are not significantly different at 5% level.

carbohydrates (reducing sugars) required to maintain relatively constant pod and seed growth under stress conditions (i.e., defoliation). This was especially true for Seafarer. In fact, the increase in pod dry weight of the defoliated plants was associated with a corresponding decrease in the dry weight of the stem and branches and at the same time a decrease in Seafarer's sugar content. This suggests that most of the weight loss of the stem and branches was caused by translocation of reducing sugars. If this is true, it would appear that storage carbohydrates in stems and branches and probably in roots may serve as a buffer between reduced photosynthesis and bean seed growth, as Egli and Leggett (1976), Kollman et al. (1974) and McAllister and Krober (1958) have earlier suggested for soybeans.

Leaf RS

There was a highly significant difference between cultivars for total amounts of RS in leaves. Nep-2 averaged 999.07 mg/plant and Seafarer 556.28 mg/plant (Appendix table 3). Intermediate levels were observed early, followed by high levels at H_3 for Nep-2 and at H_2 for Seafarer, and very low levels at the end of the season. It is possible that high sink demand, leading to mobilization of protein and therefore dry weight from leaves to pods and seeds, may cause senescence. The reduction of RS levels occurred earlier in Seafarer (Note slope differences between the two varieties in Figures 10, 11 and 11'.) It could be that Nep-2 and Seafarer differ in the way in which they fill pods. Nep-2 may depend mainly on current photosynthesis and Seafarer not as much.

Partial defoliation caused significant reductions mainly in total amounts of RS at H_2 and H_3 (Table 16). However, for the concentration

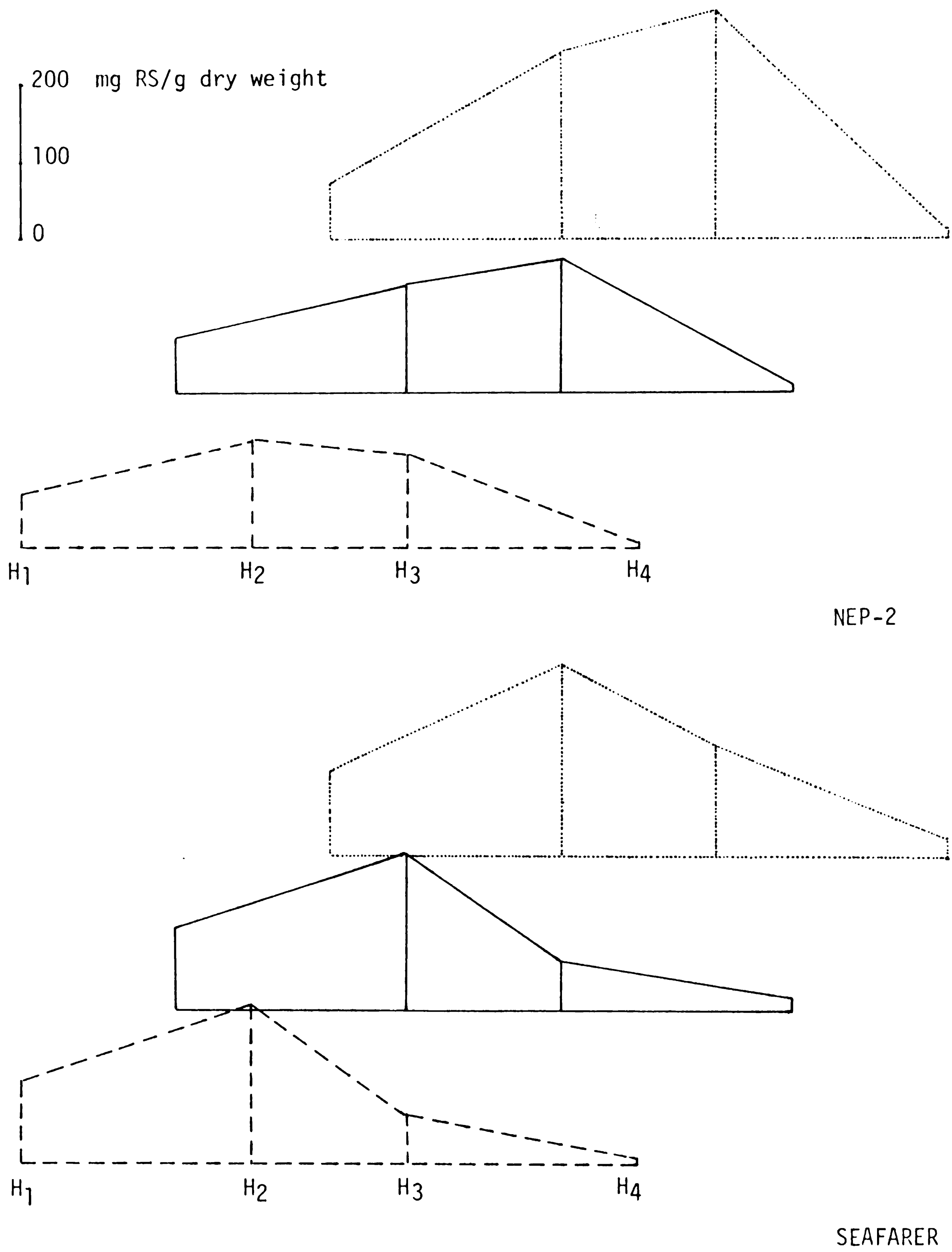


Figure 10. Effect of photosynthetic source-sink manipulation treatments on concentration of reducing sugar in leaves of two navy bean varieties.

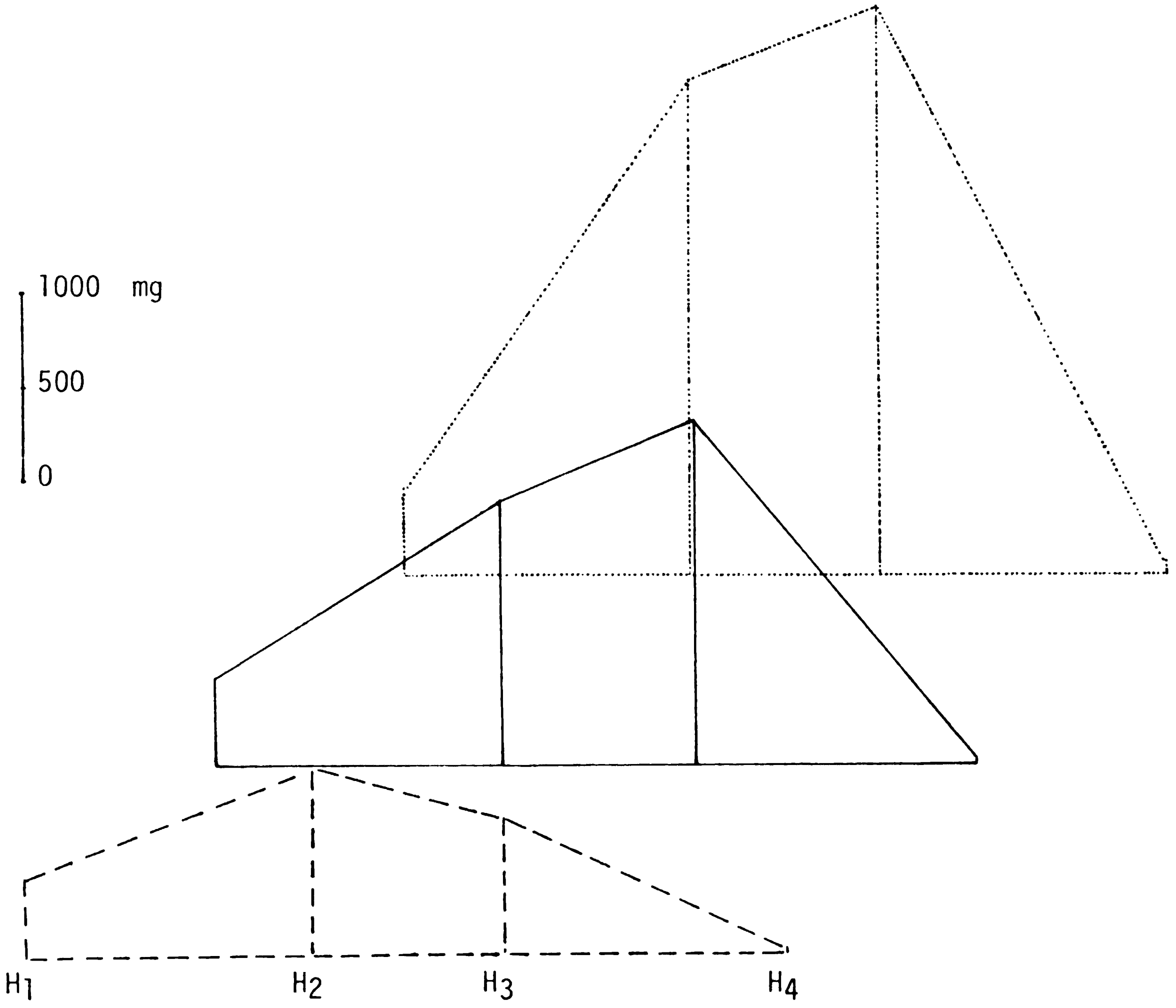


Figure 11. Effect of photosynthetic source-sink manipulation treatments on total amount of reducing sugar in leaves of Nep-2.

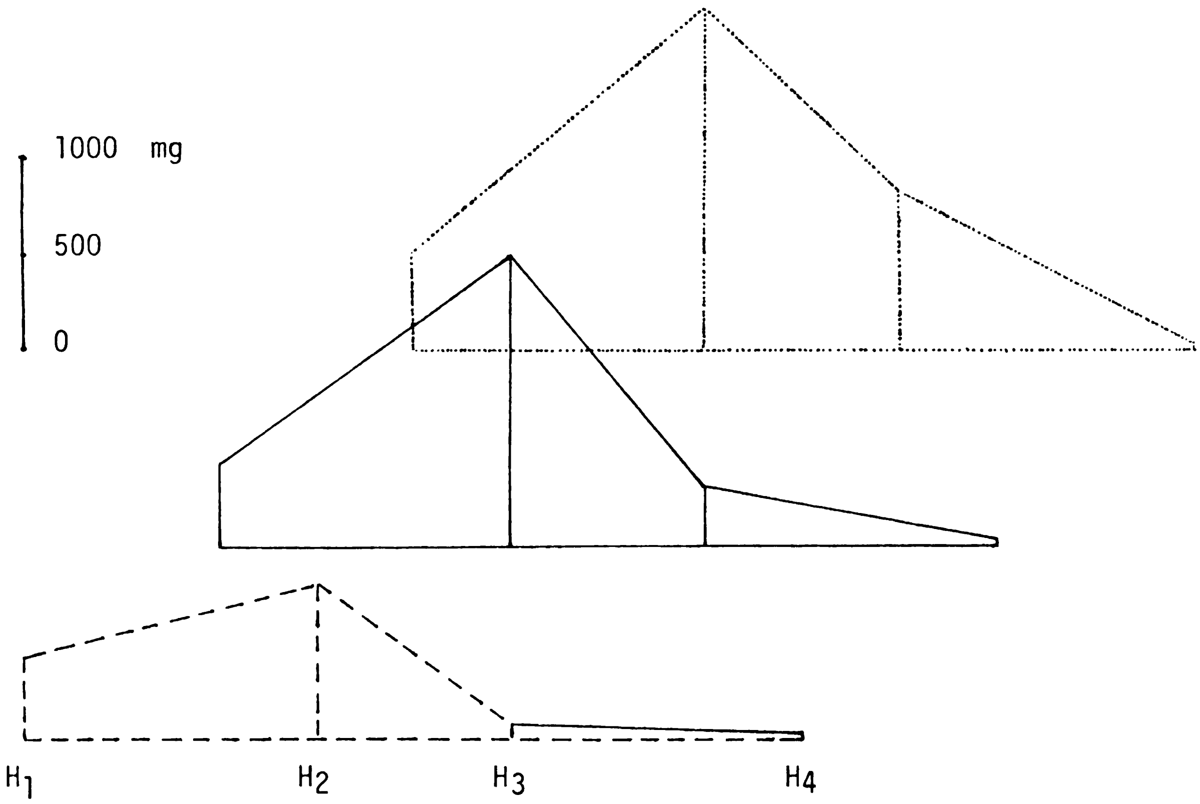


Figure 11'. Effect of photosynthetic source-sink manipulation treatments on total amount of reducing sugar in leaves of Seafarer.

Table 15. Effect of photosynthetic source-sink manipulation treatments on concentration of sugar (RS) and toal nonstructural carbohydrates (TNC) in leaf of two bean varieties.

Harvest	Treatment	Reducing Sugar (RS)		Total Nonstructural Carbohydrate (TNC)	
		mg/g dry wt			
		Nep-2	Seafarer	Nep-2	Seafarer
	Control	73.62 G*	107.50 F	216.75 D	265.88 C
H_1	Partial Defoliation	73.37 G	108.62 F	216.00 D	263.25 C
	Pod Removal	71.50 G	110.25 F	214.50 D	262.87 C
	Control	145.37 E	200.50 CD	155.12 EF	206.25 D
H_2	Partial Defoliation	146.12 E	209.87 C	186.75 DE	212.25 D
	Pod Removal	248.00 B	249.12 B	288.37 C	349.87 B
	Control	177.12 D	64.00 G	351.75 B	65.62 HI
H_3	Partial Defoliation	126.25 EF	63.75 G	180.75 DE	123.75 FG
	Pod Removal	299.00 A	145.25 E	413.62 A	279.75 C
	Control	12.87 H	17.12 H	93.37 GH	37.13 I
H_4	Partial Defoliation	5.37 H	7.12 H	39.00 I	27.38 I
	Pod Removal	14.75 H	20.25 H	151.87 EF	163.50 E

* Means followed by the same letter for RS (or TNC) are not significantly different at the 5% level.

Table 16. Effect of photosynthetic source-sink manipulation treatments on total amount of reducing sugar (RS) and total nonstructural carbohydrate (TNC) in leaf of two navy bean varieties.

Harvest	Treatment	Reducing Sugar Content		Total Nonstructural Carbohydrate Content	
		mg			
		Nep-2	Seafarer	Nep-2	Seafarer
	Control	493.200 EFG*	432.91 EFGH	1487.53 DE	1069.98 DE
H_1	Partial Defoliation	423.73 EFGH	417.98 EFGH	1265.67 DE	1010.94 DEF
	Pod Removal	437.57 EFGH	515.12 EFG	1325.41 DE	1225.42 DE
	Control	1401.27 BC	1494.00 B	1485.51 DE	1555.08 DE
H_2	Partial Defoliation	1007.64 CD	819.11 DE	1275.34 DE	823.71 EFG
	Pod Removal	2621.61 A	1763.89 B	3076.05 BC	2512.24 C
	Control	1834.85 B	300.70 FGH	3705.67 AB	300.90 FGH
H_3	Partial Defoliation	737.37 DEF	99.10 GH	1039.88 DE	189.19 GH
	Pod Removal	2992.35 A	804.80 DE	4232.66 A	1580.93 D
	Control	15.37 H	7.35 H	110.47 GH	17.46 H
H_4	Partial Defoliation	3.29 H	3.17 H	23.84 H	12.74 H
	Pod Removal	20.60 H	16.25 H	240.71 GH	131.47 GH

* Means followed by the same letter for RS (or TNC) are not significantly different at the 5% level.

level, this treatment affected only Nep-2 during the third harvest (Table 15). McAllister and Krober (1958) reported that there was no effect on leaf removal on leaf sugar levels. The data for Seafarer suggest that pod and seed growth are probably not directly related to the short-term photosynthate supply as reported earlier by Egli and Leggett (1976).

The pod removal treatment caused a significant increase in concentration of RS during H_2 and H_3 in both cultivars. Peaks in concentration and absolute amounts of RS for pod removal were measured at H_3 in Nep-2 and at H_2 for Seafarer (note the slopes in Figures 10, 11 and 11'). The pod removal treatment stimulated vigorous leaf growth during the pod-filling stage. A great part of RS that would otherwise have moved into pods was apparently utilized in relatively greater proportion in the development of the leaves.

The data reported on reducing sugar indicate a more pronounced effect of pod removal on RS of stems and branches than on RS of leaves (Table 13, 14, 15 and 16). Similar relationships have been noted previously by McAllister and Krober (1958). However this was in contrast to Kollman et al. (1974) where the opposite relationship was observed. Data of this thesis affirm that stems and branches can act as storage sites for carbohydrates in contrast to leaves.

Pod RS

The amount of reducing sugar found in seed and pod are summarized in Figure 12 and Table 17. Highly significant differences between cultivars were found in total amounts of RS. Nep-2 averaged 2255.53 mg/plant and Seafarer 1226.22 mg/plant (Appendix table 3).

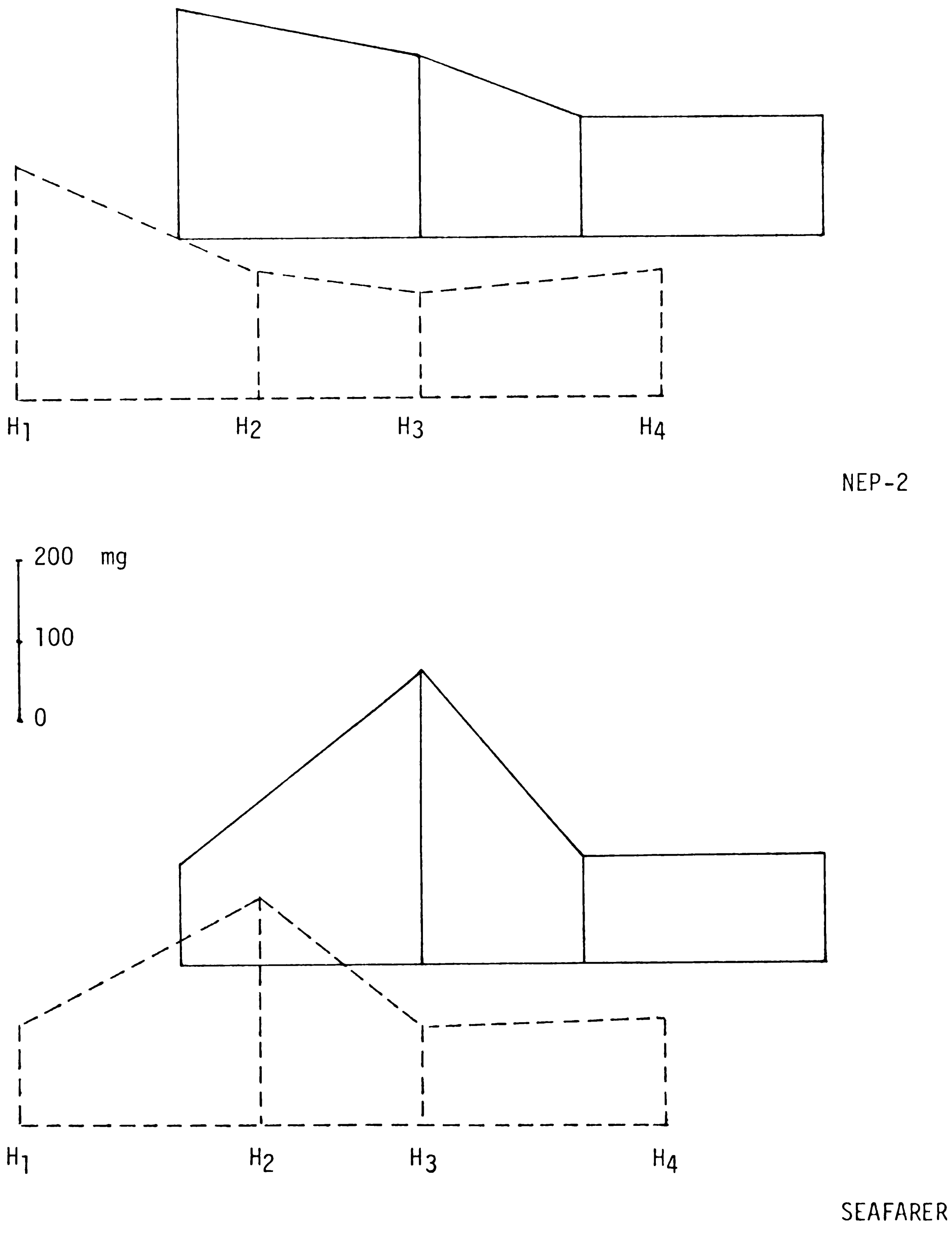


Figure 12. Effect of photosynthetic source-sink manipulation treatments on concentration of reducing sugar in pods of two navy bean varieties.

Table 17. Effect of photosynthetic source-sink manipulation treatments on concentration of sugar (RS) and total nonstructural carbohydrates (TNC) in pods of two bean varieties.

Harvest	Treatment	Reducing Sugar (RS)		Total Nonstructural Carbohydrate (TNC)	
		mg/g dry wt			
		Nep-2	Seafarer	Nep-2	Seafarer
H_1	Control	285.00 A*	126.12 C	556.25 C	494.25 D
	Partial Defoliation	292.00 A	129.25 C	552.00 C	493.75 D
H_2	Control	225.25 B	365.12 A	320.25 F	372.25 EF
	Partial Defoliation	161.12 C	282.12 B	340.50 F	422.50 E
H_3	Control	510.37 CD	135.00 C	623.75 B	541.25 CD
	Partial Defoliation	131.00 D	124.75 C	546.25 CD	554.25 C
H_4	Control	150.00 CD	135.50 C	820.75 A	594.25 BC
	Partial Defoliation	166.25 C	135.87 C	589.50 BC	550.50 CD

* Means followed by the same letter within columns for RS are not significantly different at the 5% level, and means followed by the same letter for TNC are not significantly different at the 5% level.

A highly significant harvest effect was also evident. The main differences are due to cultivars, treatments and harvests. In all harvests except the second, Nep-2 accumulated a greater amount of RS than Seafarer. RS decreased rapidly in pods of control plants of Nep-2 from 285 mg/g dry weight at harvest 1 to 150 mg/g dry weight at harvest 4. However, in Seafarer, the highest RS accumulation was during the second harvest, after which the amount of RS in the pods diminished from 365.12 mg/g dry weight at harvest 2 to 135.50 mg/g dry weight at harvest 4.

There was an increase in RS concentration between H_1 and H_2 in Seafarer. This sugar reserve could probably omit plant recovery during stress conditions (e.g., defoliation) during pod storage. However, for the cultivar Nep-2, there was only a decrease in RS concentration from H_1 to H_4, indicating some sugar was consumed by respiration. This may leave the plant without enough reserve during pod filling, and therefore, unable to recover readily from stress conditions. This could be a limiting factor in the variety Nep-2.

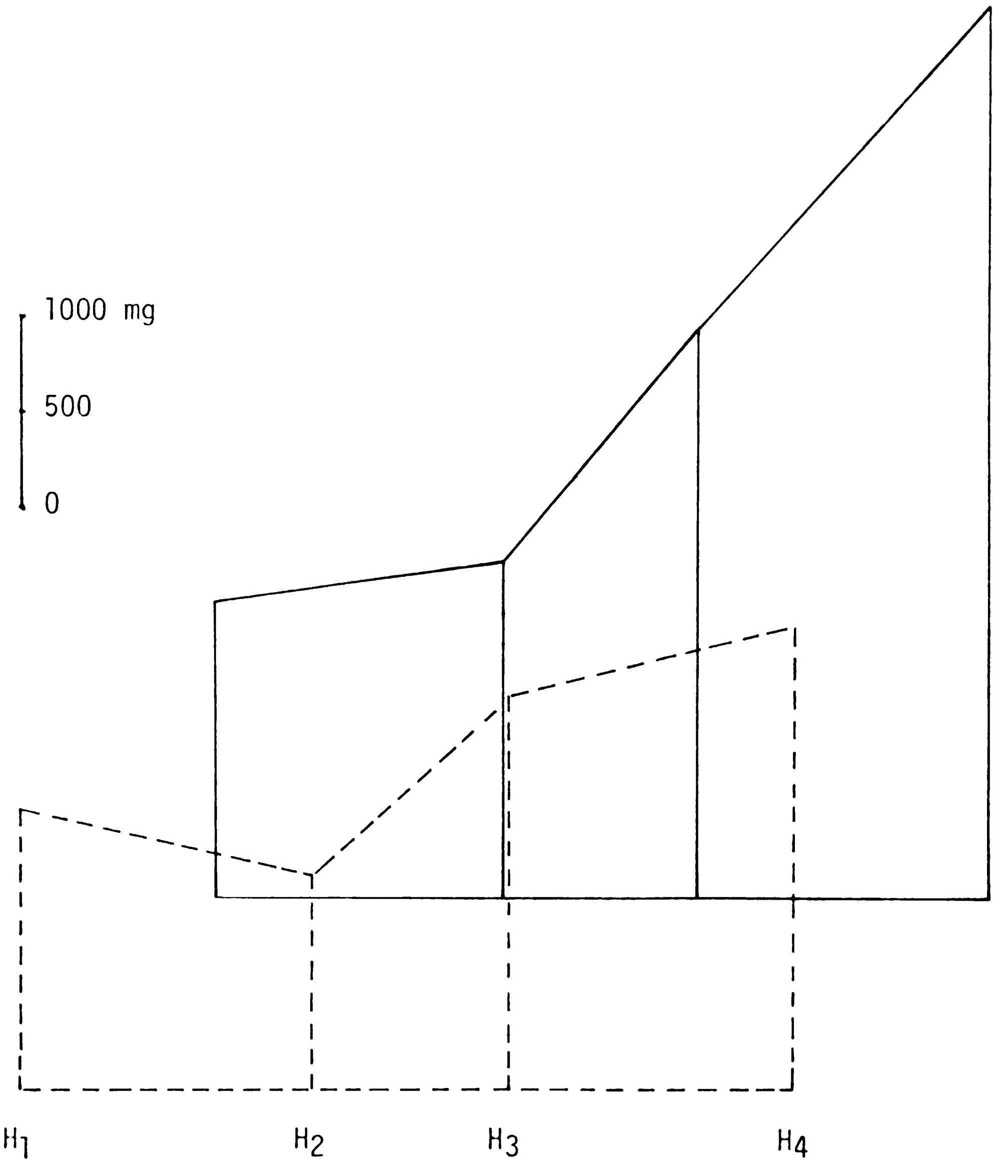
This differential response in the early stage may be due in part to the length of the pod-filling period which is different in the two varieties.

Partial defoliation significantly reduced the concentration of RS only in harvest 2 for varieties as compared to the control. However, in total amounts, the effect of defoliation is stronger from H_2 to H_4 as shown in Figure 13 and Table 18. Cultivar patterns in defoliated plants are rather distinct when compared with control plants (Figures 13 and 13'). Although the effect of defoliation was not very clear for both cultivars, there was a depressing effect concerning the total amounts of RS. This could have been due to removal of central leaflets which were probably

Table 18. Effect of photosynthetic source-sink manipulation treatments on total amount of reducing sugar (RS) and total nonstructural carbohydrate (TNC) in pod of two navy bean varieties.

Harvest	Treatment	Reducing Sugar Content		Total Nonstructural Carbohydrate Content	
		mg			
		Nep-2	Seafarer	Nep-2	Seafarer
H_1	Control	1544.95 DEF*	445.54 H	3042.10 FG	1716.57 G
	Partial Defoliation	1464.96 EFG	478.06 H	2763.30 FG	1809.40 FG
H_2	Control	1766.42 CDEF	2107.66 CD	2512.05 FG	2157.75 FG
	Partial Defoliation	1127.82 FGH	1338.20 EFG	2292.10 FG	2099.70 FG
H_3	Control	2982.91 B	1471.87 DEFG	12471.68 B	5975.15 D
	Partial Defoliation	2063.29 CD	822.77 GH	8586.32 C	3662.90 EF
H_4	Control	4683.56 A	1837.86 CDE	25292.80 A	7929.20 C
	Partial Defoliation	2410.30 BC	1307.76 EFG	8500.20 C	5375.57 DE

* Means followed by the same letter for RS (and TNC) are not significantly different at the 5% level.



NEP-2

Figure 13. Effect of photosynthetic source-sink manipulation on total amount of reducing sugar in pod of Nep-2.

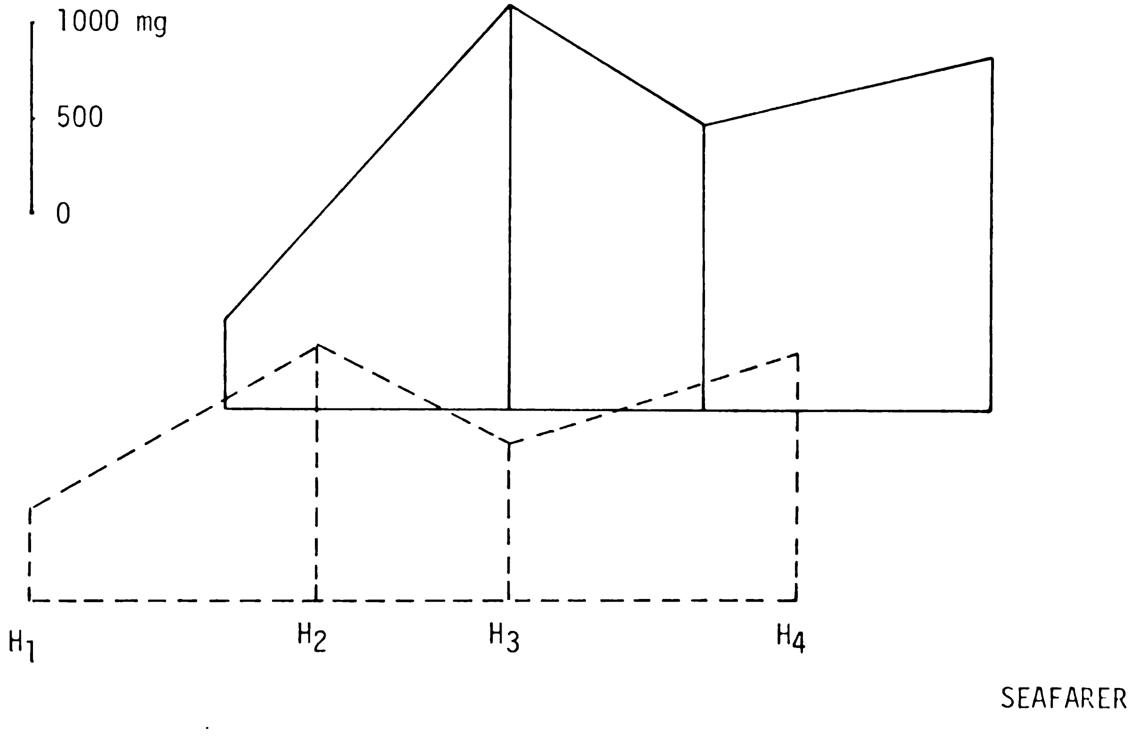


Figure 13'. Effect of photosynthetic source-sink manipulation on total amount of reducing sugar in pod of Seafarer.

photosynthetically very active. The reduction of RS induced by defoliation during the pod-filling stage made the cultivar Nep-2 more responsive to defoliation and reduced its capabilities to store carbohydrate.

Total Nonstructural Carbohydrates (TNC)

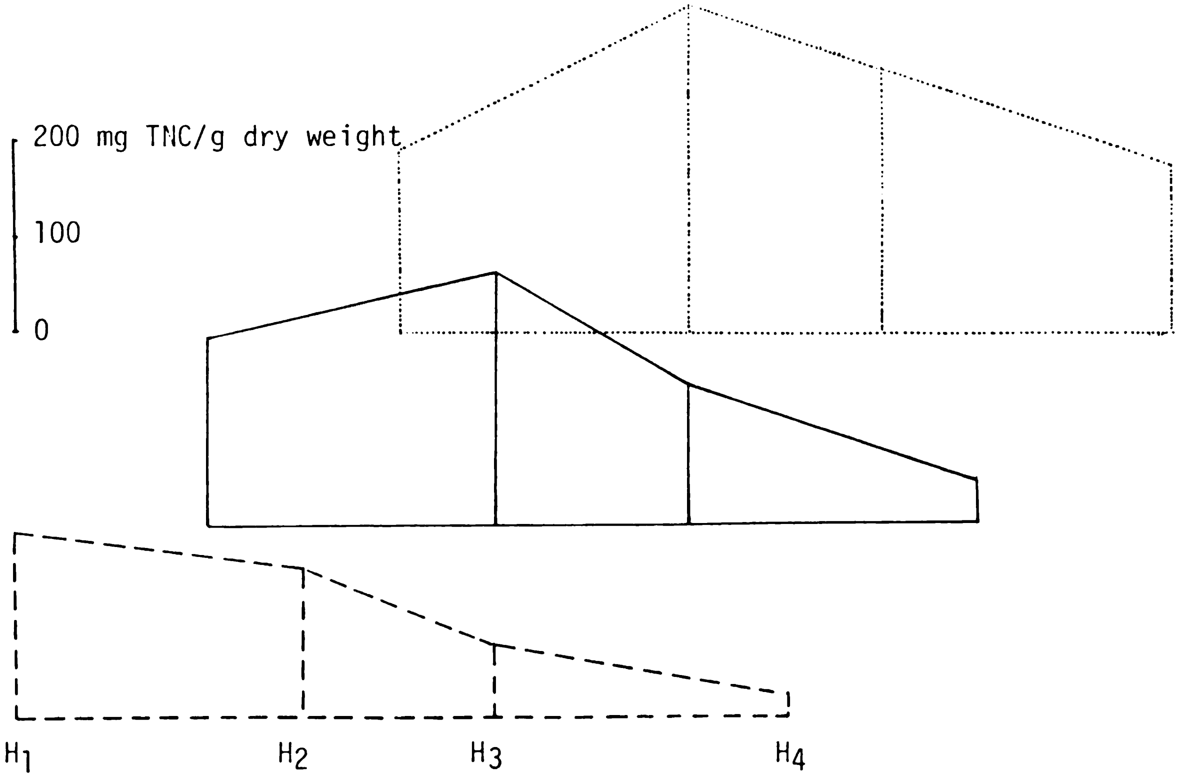
Root TNC

There were highly significant differences due to cultivars, treatments and harvests. Nep-2 averaged 173.5 mg TNC/g of dry weight, while Seafarer averaged 130.6 mg TNC/g dry weight (Appendix table 4). For total amounts Nep-2 averaged 416.66 mg TNC/plant and Seafarer 157.0 mg/plant (Appendix table 5). The greatest level of TNC was measured at H_2. After that there were decreases until the end of the season which was related to the development of a strong sink for TNC by developing pods and seeds. In all cases, Nep-2 accumulated a greater amount of TNC as compared to Seafarer.

The general effect of source-sink manipulation treatment on total nonstructural carbohydrates in roots was similar to that of reducing sugar. Significant treatment effects were generally evident at H_2, H_3 and H_4, as illustrated by Figure 14 and Table 11 for concentration levels and Figure 15 and Table 12 for total amounts.

Partial defoliation treatments had more effect on TNC concentration in Nep-2 than in Seafarer. This was even more marked in total levels. Thus, Seafarer does not seem to be as affected by partial defoliation, probably for the same reasons given earlier (see reducing sugar section).

Pod removal had significant effects on TNC levels at harvest 2, 3 and 4. At the end of the season the concentration of TNC for the pod removal treatment in both cultivars was approximately three and one-half



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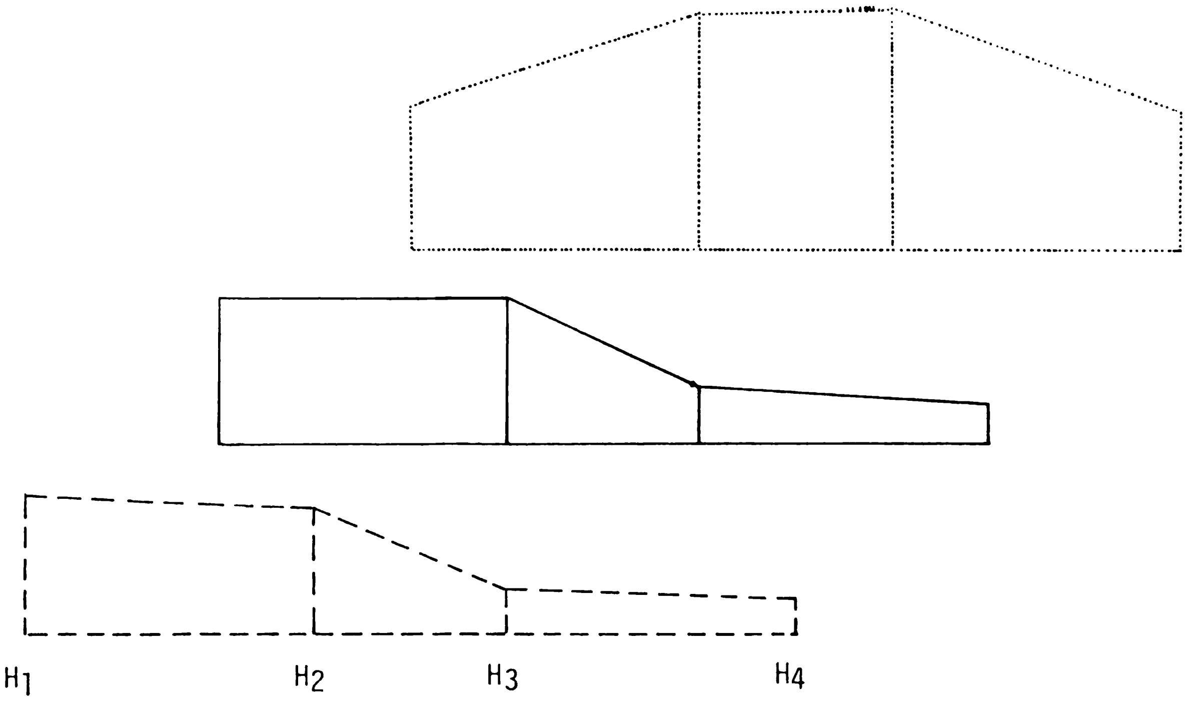


SEAFARER

Figure 14. Effect of photosynthetic source-sink manipulation on concentration of total nonstructural carbohydrate in root of two navy bean varieties.

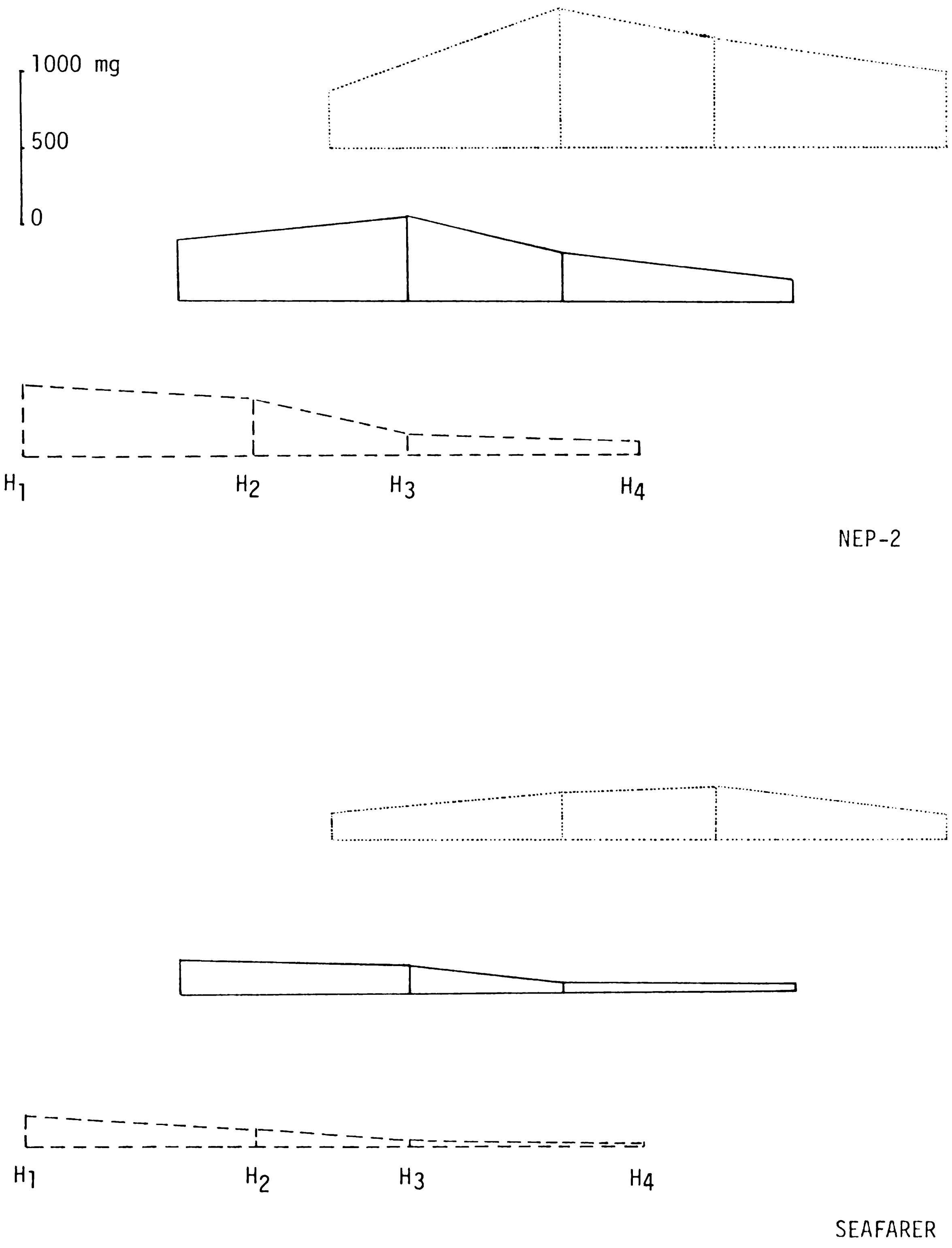


Figure 15. Effect of photosynthetic source-sink manipulation on total amount of nonstructural carbohydrate in root of two navy bean varieties.

fold greater than the TNC concentration of control plants. Thus, it appears that the Seafarer cultivar, which seems to be a non-starch storing genotype under ordinary field conditions, can be induced to store carbohydrate in response to a reduced sink demand. The decline of TNC levels following pod removal treatment, between the last two harvest dates, may be attributed either to the conversion of stem carbohydrate or to new root development. There was a substantial amount of TNC stored in roots of pod-removal plants as compared to control plants, as illustrated in plates I and II.

Stem TNC

Highly significant varietal differences were found. Nep-2 accumulated a greater amount of TNC than Seafarer (Nep-2 averaged 227.35 mg of TNC/g dry weight and Seafarer 175.16 mg/g dry weight) (Appendix table 4). The greatest amount of TNC in stem was also registered at H_2 (Figures 16, 16', 17 and 17'). The low level of TNC at the end of the season reflected its conversion to the pods. For Seafarer this conversion was made by the end of H_3 since this variety had already reached maturity. However, for Nep-2 at H_3, translocation was still occurring, since Nep-2 had not reached normal maturity.

As expected, defoliation decreased while pod removal increased total nonstructural carbohydrate in the stems, branches and petioles (Tables 13 and 14). The treatment designed to reduce the source-sink ratio (partial defoliation) resulted in TNC levels below the control in both varieties. However, as for roots, the levels of TNC in stems under partial defoliation were more affected for Nep-2 than Seafarer. This is due probably to reasons discussed earlier (i.e., greater number of branches, photosynthetic efficiency, smaller sink size and therefore

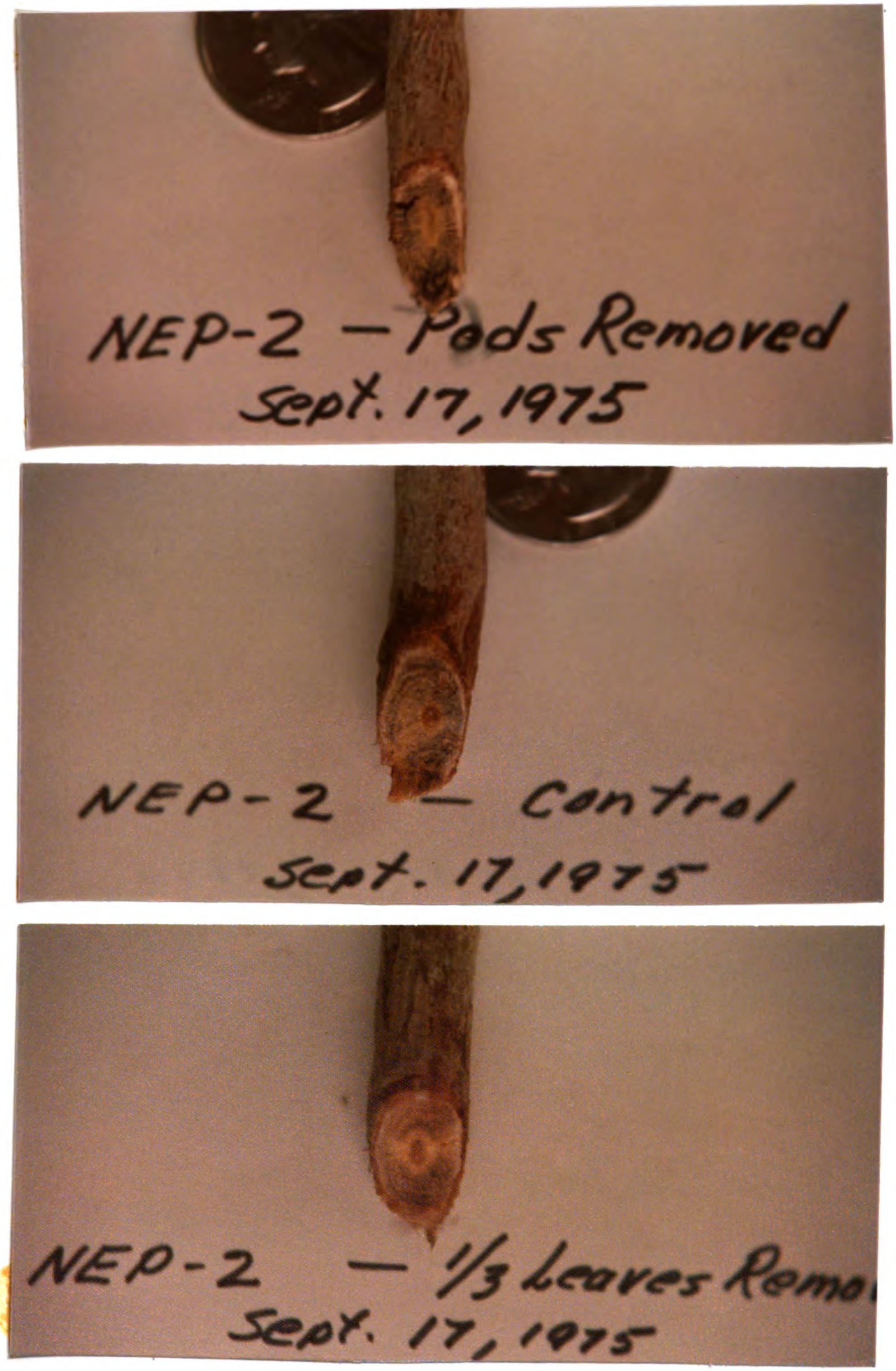


PLATE I. Effect of source-sink manipulation on starch accumulation in root of Nep-2

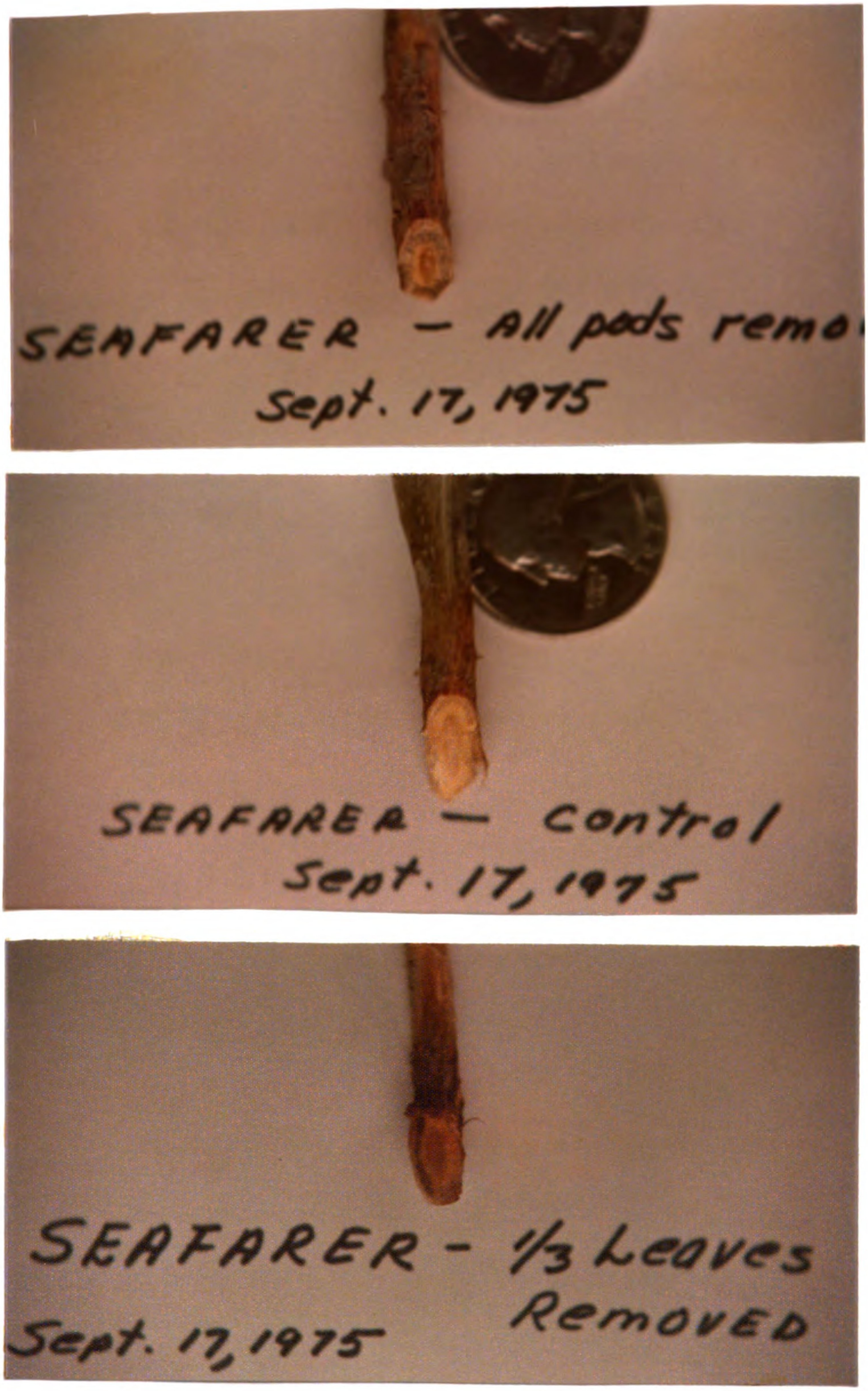
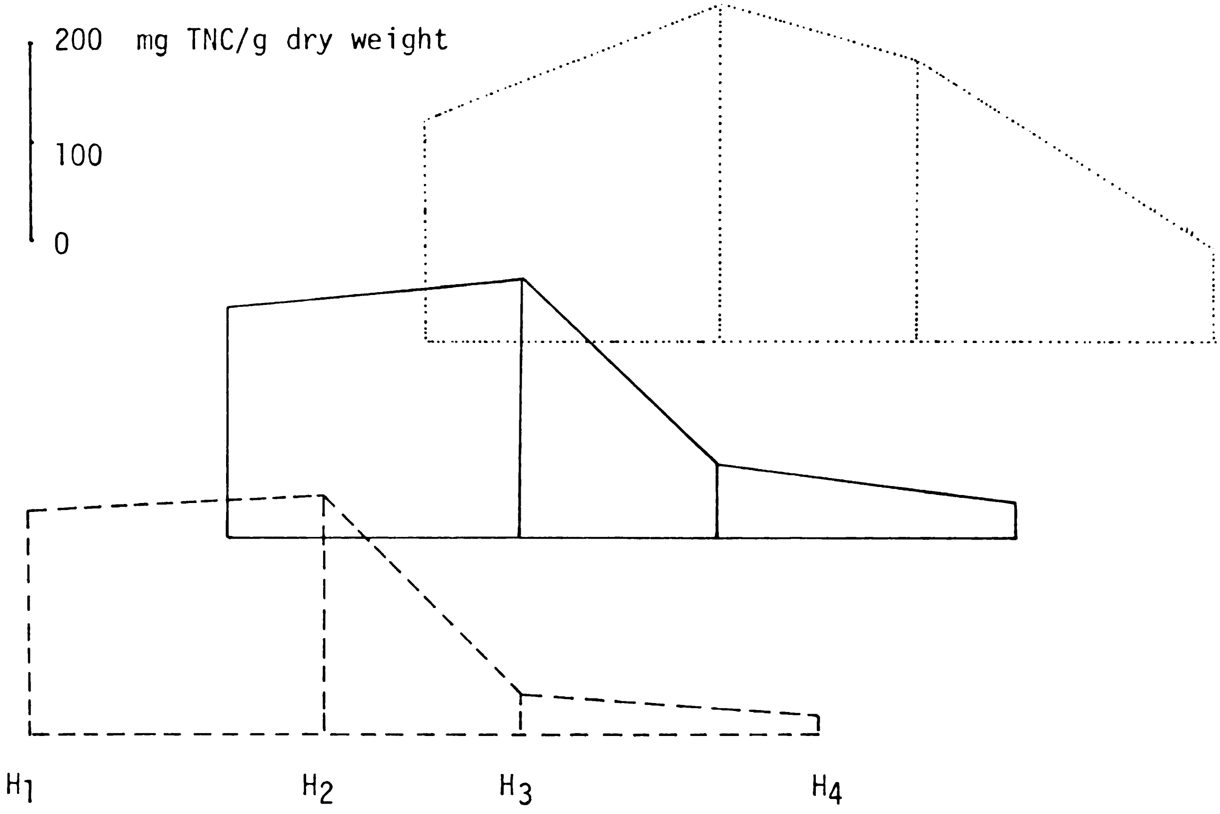
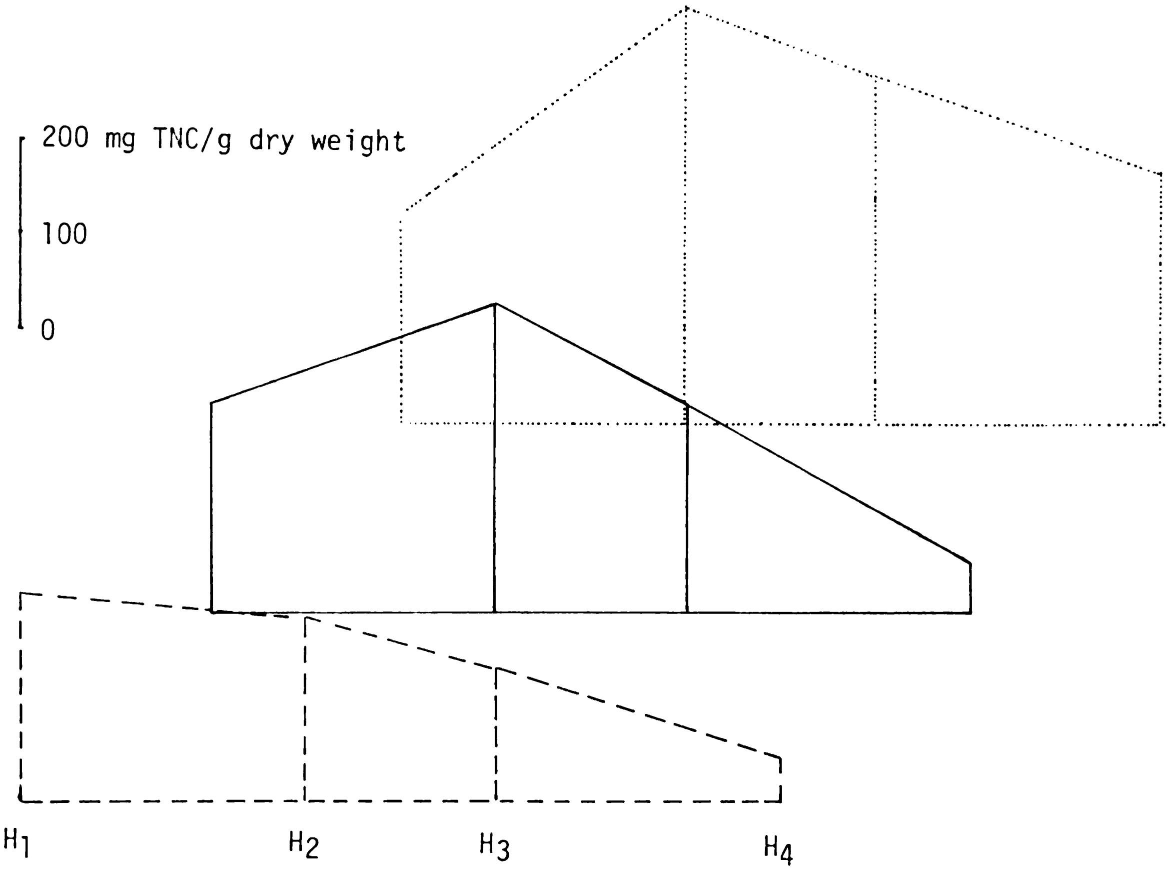


PLATE II. Effect of source-sink manipulation on starch accumulation in root of Seafarer



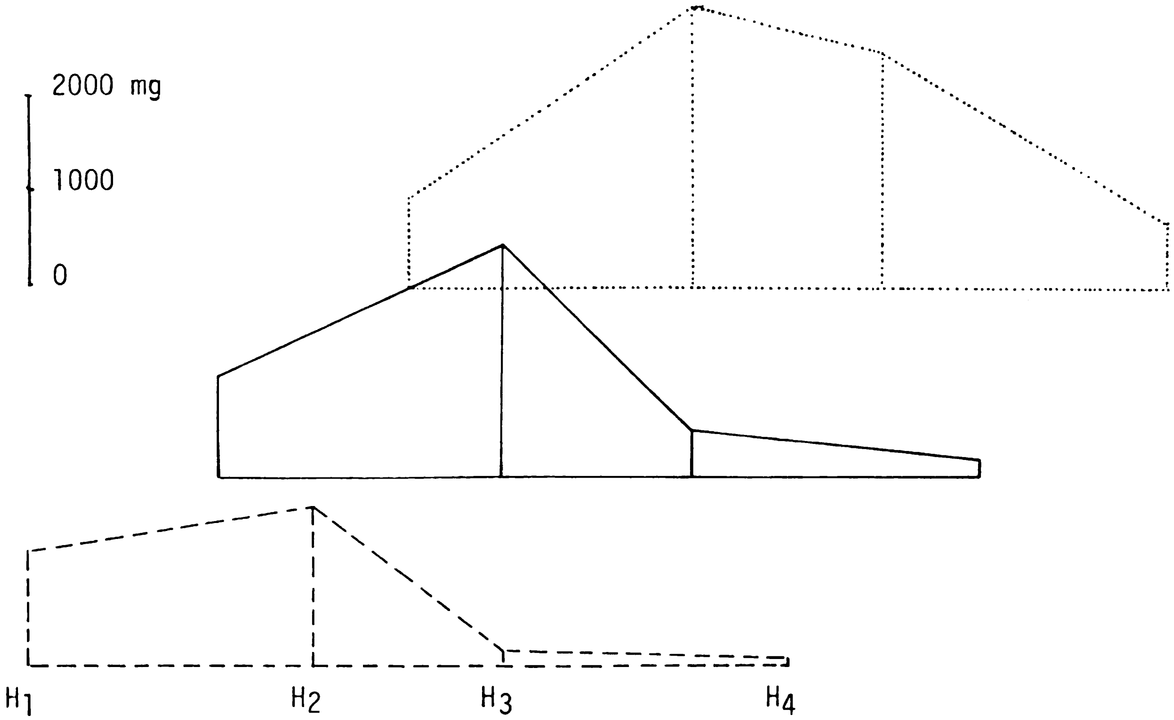
SEAFARER

Figure 16. Effect of photosynthetic source-sink manipulation on concentration of total nonstructural carbohydrate in stem of Seafarer.



NEP-2

Figure 16'. Effect of photosynthetic source-sink manipulation on concentration of total nonstructural carbohydrate in stem of Nep-2.



SEAFARER

Figure 17. Effect of photosynthetic source-sink manipulation on total amount of nonstructural carbohydrate in stem of Seafarer.

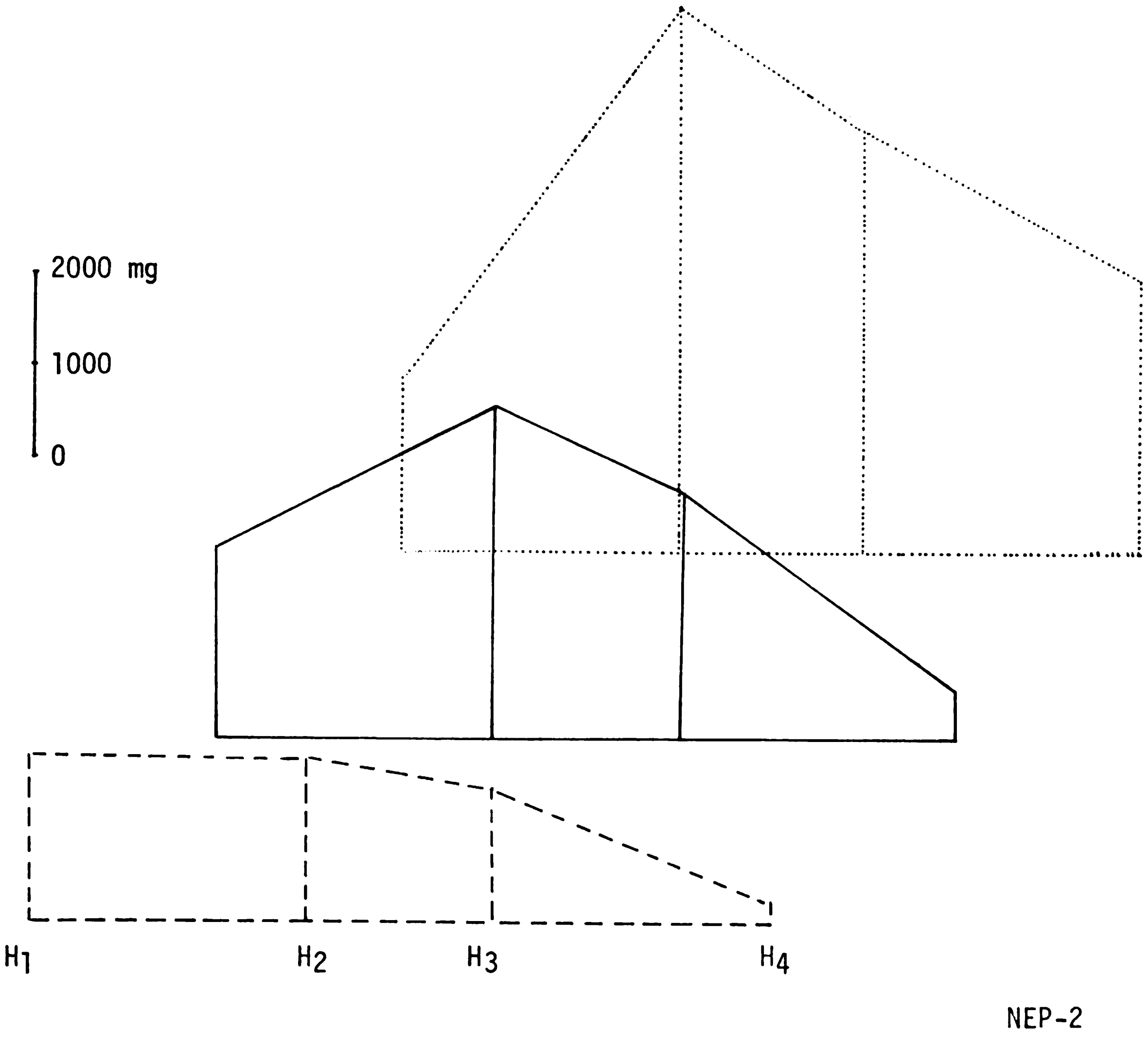


Figure 17'. Effect of photosynthetic source-sink manipulation on total amount of total nonstructural carbohydrate in stem of Nep-2.

no demand for a large leaf area and early maturity for the variety Seafarer).

The effect of pod removal was manifested during harvests 2, 3 and 4. The levels of TNC had increased at the end of the season by approximately five-fold in Nep-2 and three-fold in Seafarer (Tables 13 and 14). Note the differences of the slopes in both varieties between control and pod removal plants during H_1 and H_2. The slopes are more accentuated on graphs of pod removal as compared to those of control plants (Figures 16 and 17).

On control plants the TNC is converted to the development of pods, while on pod removal plants there is a strong sink for TNC by developing vegetative growth. The change of slopes between H_3 and H_4 on graphs of pod removal plants probably reflected the conversion of TNC into fibers. There was a large significant difference between the amount of TNC in control and pod removal plants (Figures 16, 16', 17 and 17'). At the end of the season, quantities of carbohydrate in pod removal plants translocated from leaves to petioles, illustrated by the declination of the slopes. However during the treatment and harvest dates, a number of petioles may have fallen off. This could also explain the declination of the slopes for total nonstructural carbohydrate on pod removal plants between H_3 and H_4.

Leaf TNC

Variation in the concentration of TNC is shown in Figure 18 and Table 15. Cultivars showed significantly different (Nep-2 averaged 209.0 mg of TNC/g dry weight and Seafarer 188.1 mg/g dry weight) (Appendix table 4). This was more evident for the total amounts where Nep-2 averaged 1605.73 mg/plant of TNC and Seafarer 868.34 mg/plant

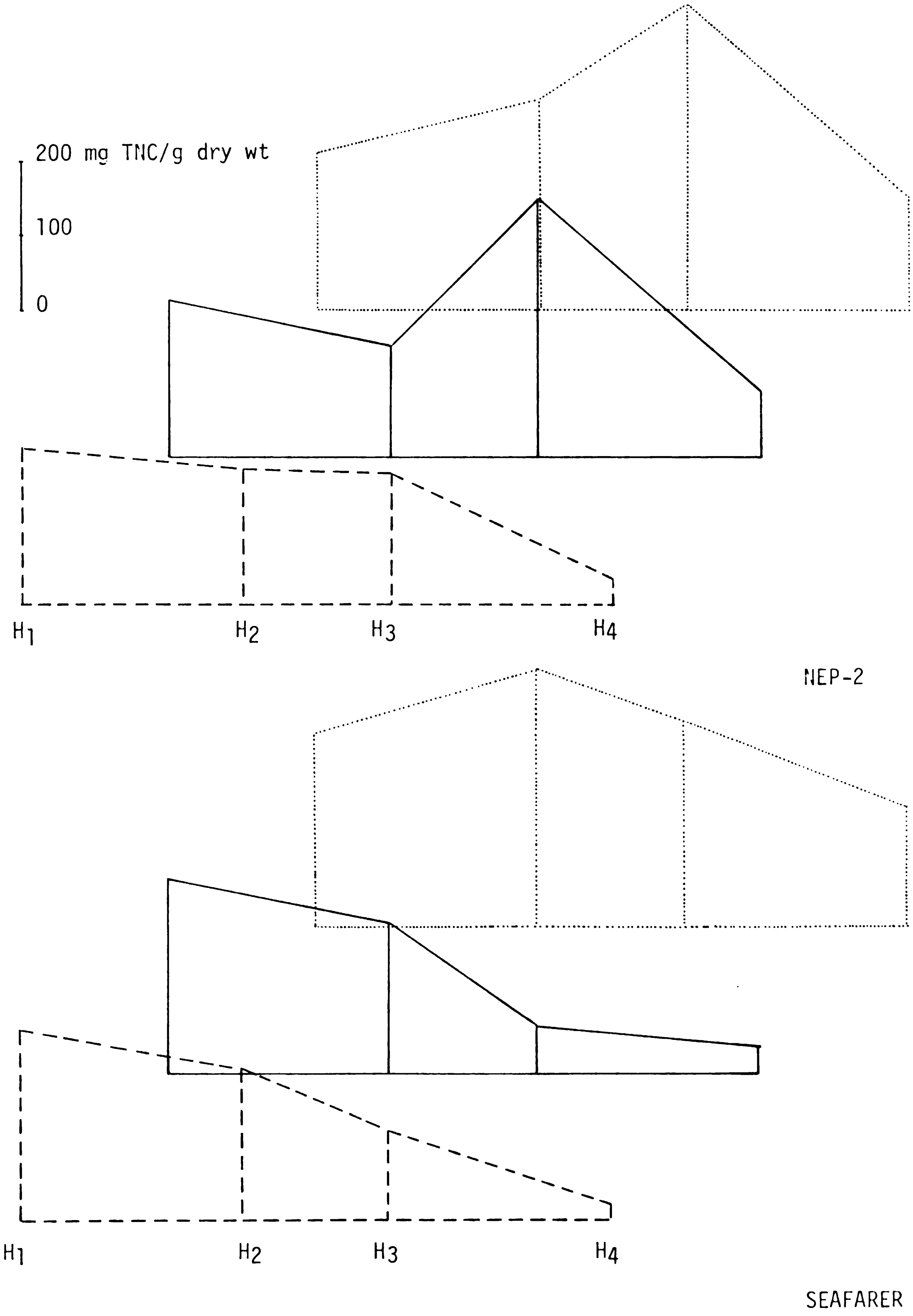


Figure 18. Effect of photosynthetic source-sink manipulation on concentration of total nonstructural carbohydrate in leaves of two navy bean varieties.

(Appendix table 5). Peak accumulation of TNC occurred at H_3 for Nep-2 and H_2 for Seafarer as indicated in previous cases. Between H_2 and H_3, the slope of the graph for control plants of Nep-2 was very accentuated (Figures 18 and 19), possible due to low level transport out of leaves as the pods are developing. Furthermore, the continuous increase of TNC in leaves of Nep-2 control plants during that stage may also indicate that translocation of soluble carbohydrate from leaves to pods and seed is a limiting factor in navy bean production. This was discussed previously in the section on reducing sugar of the variety Nep-2 (Figure 12).

The defoliation effect was highly significant. However, this was more evident in Nep-2 than in Seafarer (i.e., at H_4 there was a 60% decrease in the concentration of TNC in Nep-2 and only 26% in Seafarer). Thus, and as noted before, Seafarer does not seem to be severely affected by partial defoliation. The data of TNC for total amounts reflected almost the same responses (Figure 19 and Table 16).

The pod removal treatment increased both concentration and total amounts of TNC in leaves in both varieties from H_2 to H_4 (Figures 18 and 19). At the end of the season, the concentration of TNC from the pod removal treatment was 60 percent greater than that of the control of Nep-2 and four-fold greater in treatment plants of Seafarer vis-a-vis Seafarer's control. Thus, it is evident that Seafarer, again, can be induced to store carbohydrate in response to a reduced sink source. On the other hand, the excess carbohydrate stored by Nep-2 can be mobilized to vegetable organs in response to a reduced sink demand (i.e., reduced pods).

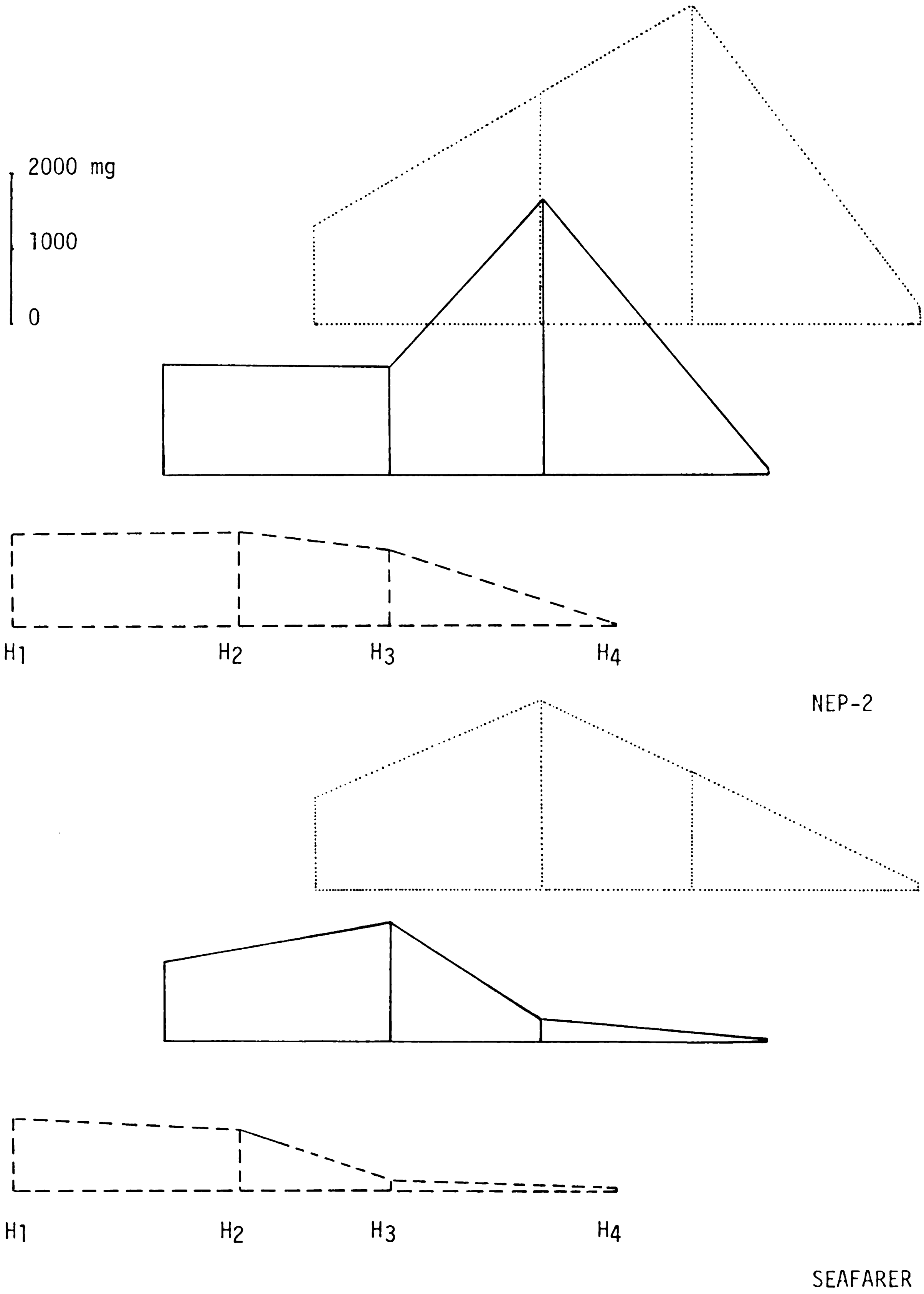


Figure 19. Effect of photosynthetic source-sink manipulation on total amount of total nonstructural carbohydrate in leaves of two navy bean varieties.

The declination of the slope between H_3 and H_4 in the pod removal treatment is probably due to the conversion to fibers or to another sink source such as new leaves since most reserve storage occurred only after meristematic sinks had been satisfied. In summary, there was a great difference between the surfaces formed between H_2 and H_4 of control and pod removal plants as exhibited in Figures 18 and 19. Thus, these responses to the pod removal treatment are due in large part to the accumulation of TNC in leaves which normally would have been destined for the pods.

As indicated in the section on reducing sugar, the TNC data suggest that there is a more pronounced effect of pod removal on stem, branch and petiole TNC than on leaf TNC. This suggests that carbohydrate storage in the stem and branches probably provides most of the reservoir of carbohydrate needed by the plant under stress conditions.

Pod (including seed) TNC

Main differences were due to variety, treatment and harvest effects, especially for the absolute amounts of TNC. Nep-2 averaged 8195.1 mg/plant and Seafarer 3841.0 mg/plant (Appendix table 5).

The concentration of TNC in pods displayed a seasonal pattern of intermediate levels at the end of the flowering stage (H_1), low levels at H_2 and high levels at H_3 and H_4 (Figures 20 and 20'). Reduction of TNC at H_2 is probably due to low level transport out of leaves until pods begin development as previously explained in the section on TNC of leaves (Figure 18). Once pods are formed, the level of TNC in the pods increases, forming a strong sink for carbohydrates. These trends are similar to those of pod dry weight, reflecting translocation of photosynthates to pods for inactive accumulation of carbohydrate reserves.

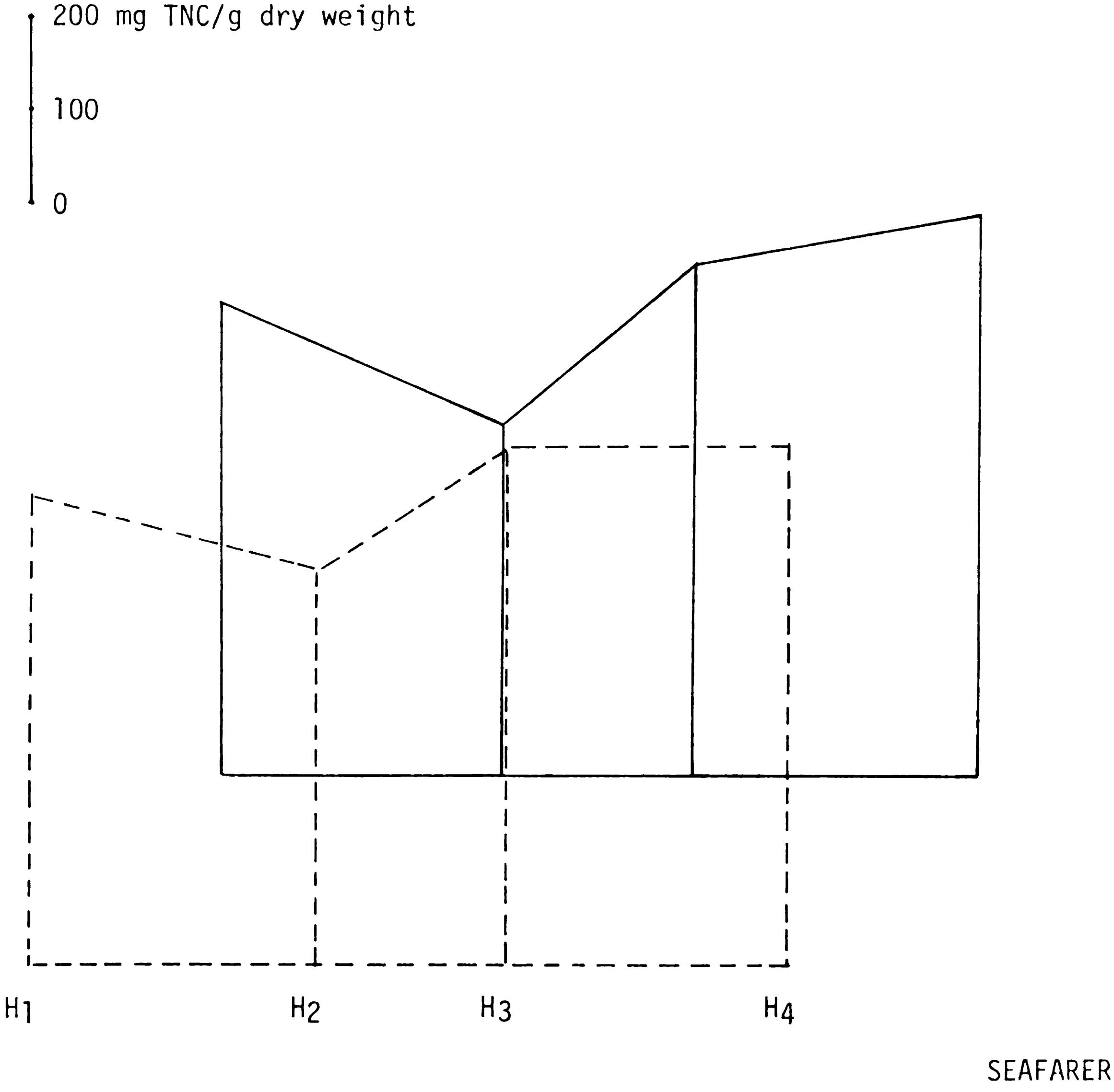
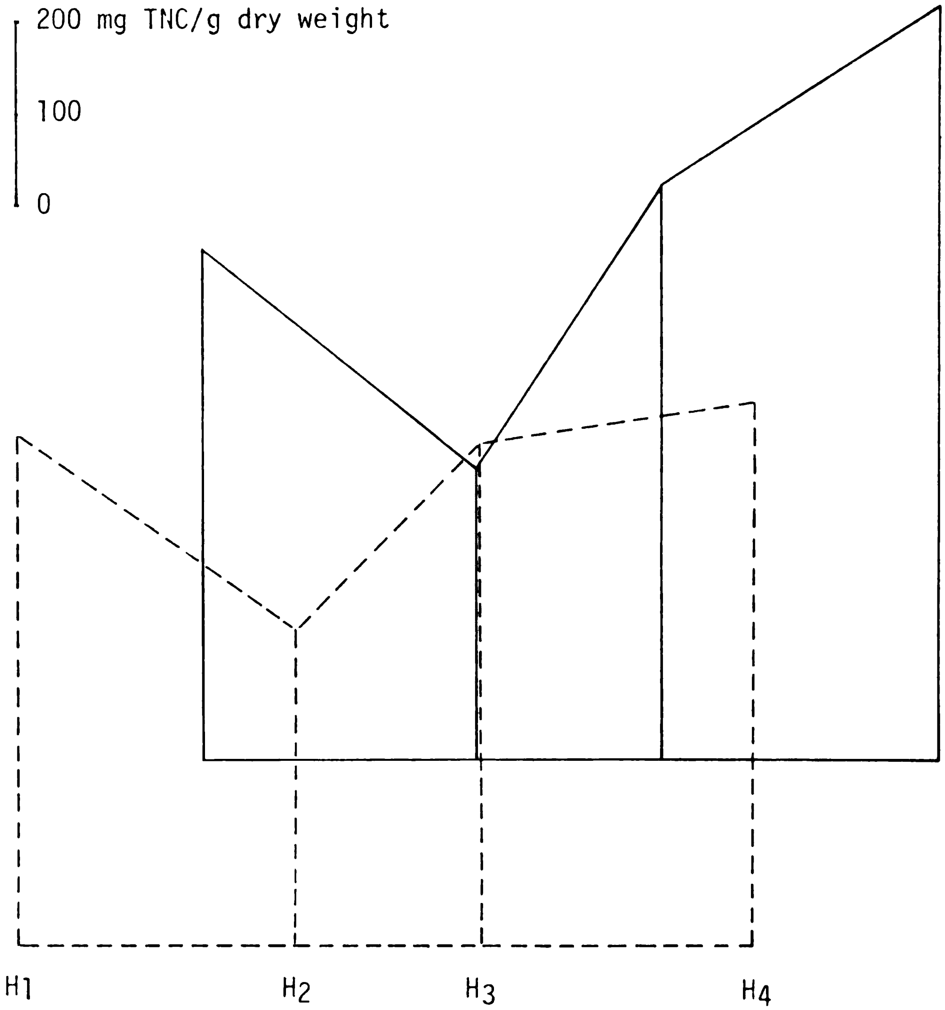


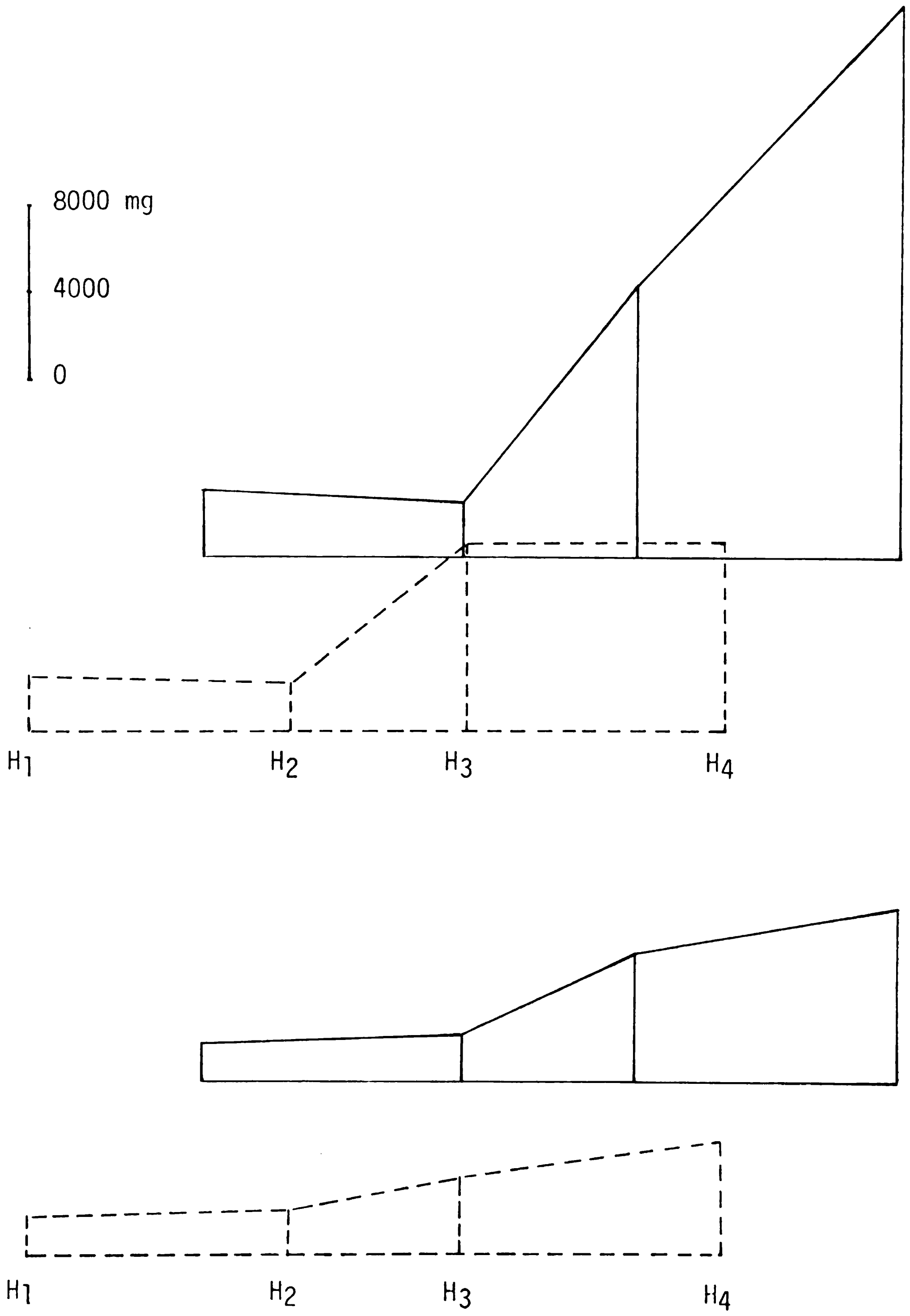
Figure 20. Effect of photosynthetic source-sink manipulation on concentration of total nonstructural carbohydrate in pods of Seafarer.



NEP-2

Figure 20'. Effect of photosynthetic source-sink manipulation on concentration of total nonstructural carbohydrate in pods of Nep-2.

The partial defoliation treatment significantly reduced the concentration of TNC in only Nep-2 as compared to the control. In fact, Nep-2's that were defoliated exhibited a great reduction in concentration of TNC (28%) while Seafarer reduced only 7 percent at the end of season (Table 17). During H_2 this treatment effect had only negligible effects on TNC concentration in Nep-2; significant effect of treatment was evident at H_3 and H_4. However, there was no treatment effect on the concentration of TNC in Seafarer. For the total amounts of TNC, there was a significant treatment effect during the last two harvest dates in both cultivars (Figure 21 and Table B11). Here again the treatment effect was consistently greater in Nep-2 than in Seafarer. In fact, the data show a 67 percent reduction for Nep-2 and only 32 percent reduction for Seafarer at H_4. Thus, the general effect of partial defoliation on TNC in Seafarer suggests that, as such, TNC is not a major determining factor of differences in carbohydrate reserves. Therefore, partial defoliation does not seem strongly to affect Seafarer's total nonstructural carbohydrate levels.



NEP-2

SEAFARER

Figure 21. Effect of photosynthetic source-sink manipulation on total amount of total nonstructural carbohydrate in pods of two navy bean varieties.

CONCLUSIONS

1. The cultivar Nep-2 yielded more dry weight and more total nonstructural carbohydrate than the cultivar Seafarer.

2. Partial defoliation seems to be highly detrimental to Nep-2 as compared to Seafarer. Frequent defoliation, by reducing the plant's ability to assimilate carbon, reduced growth and carbohydrate accumulation. Translocation of assimilates was altered and the remaining leaf area was capable of supplying only a proportional number of sinks as suggested by Trowes (1962) and Maggs (1965). Such stress, from natural or man-imposed causes, could constitute an important factor limiting yield or adaptation of the cultivar Nep-2.

3. Data reported in this study suggest that the excess carbohydrate stored by Nep-2 could be mobilized in response to a reduced source but not sufficiently to replace concurrent photosynthesis required for pod filling. However, under the conditions of this experiment, the branches of Seafarer were the important storage organ for carbohydrate which can be translocated to maintain dry weight growth of pod and seed for an extended period after defoliation. This supports Egli and Leggett's (1976) suggestion that storage carbohydrate serves as a buffer between photosynthesis and bean seed growth.

4. By altering the source-sink ratio in favor of the source, various dry weights, reducing sugars and total nonstructural carbohydrate were significantly affected in both varieties. Other workers have reported similar observations for soybeans (McAllister and Krober, 1958; Egli and Leggett, 1976). The data suggest that excess photosynthate produced by both varieties can be mobilized to the stem in response to a

reduced sink demand since sink manipulation has exhibited marked changes of carbohydrate reserves. The stem appears to act as a storage site in response to a reduced sink in the plant.

Under the conditions of defoliation in this experiment, Seafarer appeared to recover from the imposed stress and to be capable of normal bean production. However, similar environmental stresses (such as frost, hail, insects, wind or foliage diseases) would limit productivity and cause the cultivar Nep-2 to be more prone to post-defoliation injury.

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BIBLIOGRAPHY

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APPENDIX

APPENDIX TABLE 1. Summary of analysis of variance of dry weight and leaf area for two navy bean cultivars subjected to source-sink manipulations.

	Root	Stem	Leaf	Pod	Leaf area cm^2
Nep-2	2.36	10.0	6.3	13.3	13.3
Seafarer	1.10	6.1	3.7	7.30	7.3
Variety (V)	**	**	**	**	**
Treatment (Tmt)	**	**	**	**	**
V x Tmt	ns	ns	ns	**	ns
Harvest (H)	ns	**	**	**	**
V x H	*	ns	**	**	**
Tmt x H	**	**	**	**	**
V x Tmt x H	ns	ns	ns	**	ns

* significant at 5%

** significant at 1%

ns not significant

APPENDIX TABLE 2. Summary of analysis of variance of the concentration of reducing sugar for two navy bean cultivars subjected to source-sink manipulation.

	Root	Stem	Leaf	Pod
	-------- mg-RS/gm dry wt ------			
Nep-2	107.44	137.74	116.11	195.2
Seafarer	106.75	142.6	108.61	179.2
Variety (V)	ns	ns	ns	**
Treatment (Tmt)	**	**	**	**
V x Tmt	ns	ns	**	ns
Harvest (H)	**	**	**	**
V x H	**	**	**	**
Tmt x H	**	**	**	**
V x Tmt x H	*	**	**	ns

* significant at 5%

** significant at 1%

ns not significant

APPENDIX TABLE 3. Summary of analysis of variance of the total amount of reducing sugar for two navy bean cultivars subjected to source-sink manipulation.

	Root	Stem	Leaf	Pod
	------------- gm RS ----------			
Nep-2	260.0	1479.0	999.07	2255.53
Seafarer	131.0	974.2	556.28	1226.22
Variety (V)	**	**	**	**
Treatment (Tmt)	**	**	**	**
V x Tmt	**	**	*	**
Harvest (H)	**	**	**	**
V x H	**	**	**	**
Tmt x H	**	**	**	**
V x Tmt x H	ns	ns	**	*

* significant at 5%

** significant at 1%

ns not significant

APPENDIX TABLE 4. Summary of analysis of variance of the concentration of total nonstructural carbohydrate for two navy bean cultivars subjected to source-sink manipulation.

	Root	Stem	Leaf	Pod
	--------- mg-TNC/gm dry wt ----			
Nep-2	173.5	227.35	209.0	543.66
Seafarer	130.6	175.16	188.1	502.87
Variety (V)	**	**	*	**
Treatment (Tmt)	**	**	**	*
V x Tmt	*	**	**	**
Harvest (H)	**	**	**	**
V x H	**	**	**	**
Tmt x H	**	**	**	**
V x Tmt x H	*	**	**	ns

* significant at 5%

** significant at 1%

ns not significant

APPENDIX TABLE 5. Summary of analysis of variance of the total amount of total nonstructural carbohydrate for two navy bean cultivars subjected to source-sink manipulations.

	Root	Stem	Leaf	Pod
	mg TNC			
Nep-2	416.66	2455.3	1605.73	8195.1
Seafarer	157.0	1201.1	868.34	3841.0
Variety (V)	**	**	**	**
Treatment (Tmt)	**	**	ns	**
Harvest (H)	**	**	**	**
V x H	**	**	**	**
Tmt x H	**	**	**	**
V x Tmt x H	ns	**	**	**

* significant at 5%

** significant at 1%

ns not significant