PULSE PHYSIOLOGY

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PART I

PIGEONPEA PHYSIOLOGY

by

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Pulse Physiology

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Preface

This report covers the first season's research carried out at ICRISAT on Pigeonpea Physiology. Very little work has been done on the physiology of this crop before, and so we have been proceeding on a broad front in order to obtain background information for future investigations and to provide a perspective within which the physiological problems can be seen and more clearly defined. Much of the work reported here is descriptive rather than experimental.

The research being carried out at present, during the second season (1975/6), follows up some of the findings reported here. However, in the following pages we have confined ourself to presenting results, including some of a very preliminary nature, which were obtained before May 1975.

A comprehensive anatomical study of pigeonpeas was begun in late 1974 and is continuing, but the results are not reported here; they will be presented separately and systematically within a year or two.

This report is not in any way a formal publication or an official document of the Institute. It is intended for limited circulation only and should not be cited.

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Abbreviations

HI = Harvest Index = $\frac{\text{Grain Dry Weight}}{\text{Total Plant Dry Weight at Harvest}} \times 100$

LAI = Leaf Area Index = $\frac{\text{Total Leaf Area of Crop}}{\text{Ground Area Occupied by Crop}}$

LAD = Leaf Area Duration = Sum of Weekly Average LAI throughout the Growing Season.

NAR = Net Assimilation Rate = $\frac{\text{Dry Weight gained in time } t_2 - t_1}{\text{Average Leaf Area during } t_2 - t_1}$

CGR = Crop Growth Rate = Dry Weight gained by Unit Area of Crop in Unit Time.

RGR = Relative Growth Rate = $\frac{\text{Increase in Dry Weight in time } t_2 - t_1}{\text{Dry Weight at time } t_1}$

SLW = Specific Leaf Weight = $\frac{\text{Leaf Dry Weight}}{\text{Leaf Area}}$

CHAPTER I

Analysis of Growth and Yield

1. GROWTH ANALYSIS

Introduction

In order to lay the foundations for an understanding of the growth and development of pigeonpeas, a detailed investigations was carried out using the methods of classical growth analysis. These methods enable the net photosynthetic productivity and the distribution of dry matter to be estimated at different stages of the plants' development.

Five cultivars of different durations and growth habits were selected for this study. They were in order of decreasing earliness: T-21, Pusa Ageti, ST-1, ICRISAT-1 and HY-3C.

Methods

The cultivars were planted in black and red soils on 26-6-74 and 4-7-74 respectively, after fertilizing the soil with 50 Kg. P_2O_5/ha and 45 Kg. Zn SO_4/ha (broadcast and incorporated). No nitrogenous fertilizer was applied. A randomised block design with two replicates was employed. The plot sizes were 9 x 40 M. Two seeds were planted per hill on ridges 75 cm apart and thinned to one after a week. The plant-to-plant spacing was 30 cm. The crop was raised entirely under rainfed condition. The weekly rainfall, maximum and minimum temperatures were averaged according to sampling date and are given in Fig. 3.

Destructive growth analysis was carried out at weekly intervals on all five cultivars from black soil and only on ICRISAT-1 from red soil. Five plants per replicate were harvested and separated into leaves, petioles, stems, root nodules (only at the early stages), buds flowers, pods and peduncles (at later stages). Leaf area was measured on all the five plants at the early stages and later on one plant and calculated for the rest on the basis of dry weight of leaves. Leaves were outlined on square paper and the squares were counted to calculate the area. This was done at the early stages. Later on, leaves were either blue-printed and the area was measured with planimeter or area was directly measured by means of an leaf area meter. The plant parts from each plant weighed separately and dried at 80°C for dry weight determination. At each sampling, the length of main stem, number of leaves on the main stem and branches, total number of leaf scars, number of leaves on the main stem and branches, total number of leaf scars, number of primary and secondary branches, length of branches node by node on the main stem and number of pods were recorded.

Non-destructive growth analysis was also carried out weekly on 6 marked plants per cultivar. Each week, the height of the plants, number of leaves, leaf scars, branches, buds, flowers and pods were recorded. In addition to these observations, two marked plants of each cultivar were photographed every week.

Nitrogen analysis was performed by micro-and macro-Kjeldhal methods.

Results

A. Morphological observations.

Branching Pattern:

A diagram showing the distribution of primary branches on the main stem at the maturity of some representative plants has been given in Fig.1A. The lengths of the primary branches are plotted on the main stem node by node. The lower branches were longer than the upper branches except in ICRISAT-1 grown in red soil where the middle branches were longer than the lower and upper branches. It can clearly be seen from this figure that the branches were produced in flushes.

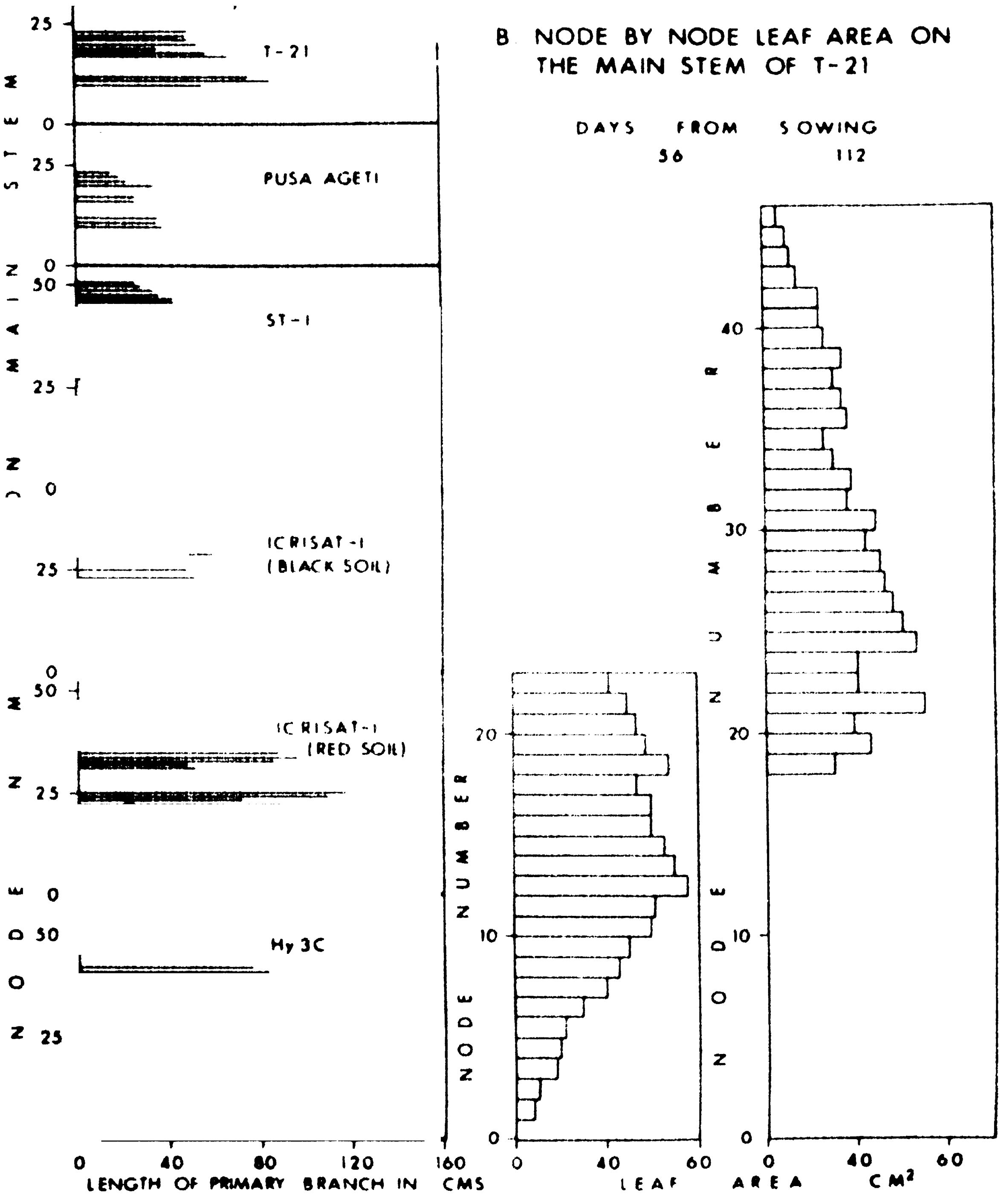
Variation of leaf size on the main stem:

In order to understand the distribution of leaf size on the main stem, the areas of individual trifoliate leaves were determined node by node on the main stem of all the cultivars at different sampling times. Fig.1B shows the data taken on T-21 at 56 and 112 days from sowing. The lower and upper leaves on the main stem were smaller than the middle ones. This was true of all the cultivars and a smaller pattern was found on the branches too. It may be noticed that the primary branches were mostly growing from nodes 10 to 25 on the main stem in this cultivar (see Fig. 1A).

Leaves at maturity:

The number of green leaves, their area and dry weight, and the number of leaf scars were determined at maturity and are presented in Table 1.

FIGURE 1



A. DISTRIBUTION OF PRIMARY BRANCHES ON THE MAIN STEM

B. NODE BY NODE LEAF AREA ON THE MAIN STEM OF T-21

The early cvs T-21 and Pusa Ageti had a small number of green leaves whereas the medium cultivars had more green leaves retained at the time of maturity. On the basis of leaf area, T-21 was the lowest but on the basis of leaf dry weight, Pusa Ageti was the lowest. Among the medium cvs ICRISAT-1 (Red soil) had the highest leaf area but the dry weight was similar to HY-3C whose leaf area was only half of ICRISAT-1.

The total number of leaves produced up to the time of maturity is shown in Table 1. The percentage of leaves which had fallen off by the time of maturity was lowest in HY-3C.

Mean specific leaf weight during vegetative and reproductive phases:

SLW was calculated by dividing leaf area by leaf dry weight at every sampling time. The mean SLW during the vegetative phase varies for cvs as ICRISAT-1 > ICRISAT-1 (Red soil) > HY-3C > ST-1 > Pusa Ageti > T-21 and during the reproductive phase as:

HY-3C > ICRISAT-1 > ST-1 > Pusa Ageti > ICRISAT-1 (Red soil) > T-21 (Table 2).

It is interesting to note that the mean SLW during the reproductive phase was more than during the vegetative phase for all cultivars except ICRISAT-1 (Red soil).

Stem:

The height of the main stem and dry weight of stem, including branches, at different sampling times are given in Fig.2.

Table 1. Leaves at maturity in five Pigeonpea cultivars.

Cultivars	Per Plant					
	No. of green leaves	Dry weight of green leaves in g.	Leaf area cm^2	No. of leaf scars.	Total No. of leaves produced	% leaf fall
T-21	41.6	5.3	311	146.1	187.7	78
Pusa Ageti	18.3	1.9	534	103.5	121.8	84
ST-1	153.2	9.5	1734	440.8	598.0	74
ICRISAT-1	136.4	9.2	1593	356.3	492.7	72
ICRISAT-1 (Red soil)	198.4	13.9	2643	434.6	633.0	69
HY-3C	116.9	13.7	1830	260.0	376.9	31

Table 2. Mean specific leaf weight (SLW) during the vegetative and reproductive phases of growth.

Cultivars	SLW (mg/cm^2) during	
	Vegetative phase	Reproductive phase
T-21	3.74	4.05
Pusa Ageti	3.80	4.31
ST-1	4.04	4.54
ICRISAT-1	4.42	5.03
ICRISAT-1 (Red soil)	4.32	4.15
HY-3C	4.20	6.37

In all five cultivars the height of the main stem increased rapidly up to the time of flower bud initiation. Thereafter it remained constant in cvs Pusa Ageti and HY-3C whereas in others there was a slow increase in height. In all cultivars the dry weight of the stem increased after flower bud initiation reflecting the continued production of new branches (Table 3) and also a continued growth in thickness of the previously existing stems.

Preliminary observations indicated that in the medium duration varieties the diameters of the stems (main stems measured half-way up) increased by 30-65% between flower initiation and maturity.

The early cultivars T-21 and Pusa Ageti produced a greater proportion (73-86%) of their total stem dry weight after flower bud initiation than the medium duration cultivars (35-55%). The latter produced fewer, or in the case of ICRISAT-1, no new primary branches during the reproductive phase; but in all cultivars the production of new secondary branches continued during the reproductive phase (Table 4)

Cvs ST-1 and ICRISAT-1 produced a greater total number of primary and secondary branches than the other cultivars.

FIGURE 2
PLANT HEIGHT AND DRY WEIGHT OF STEM

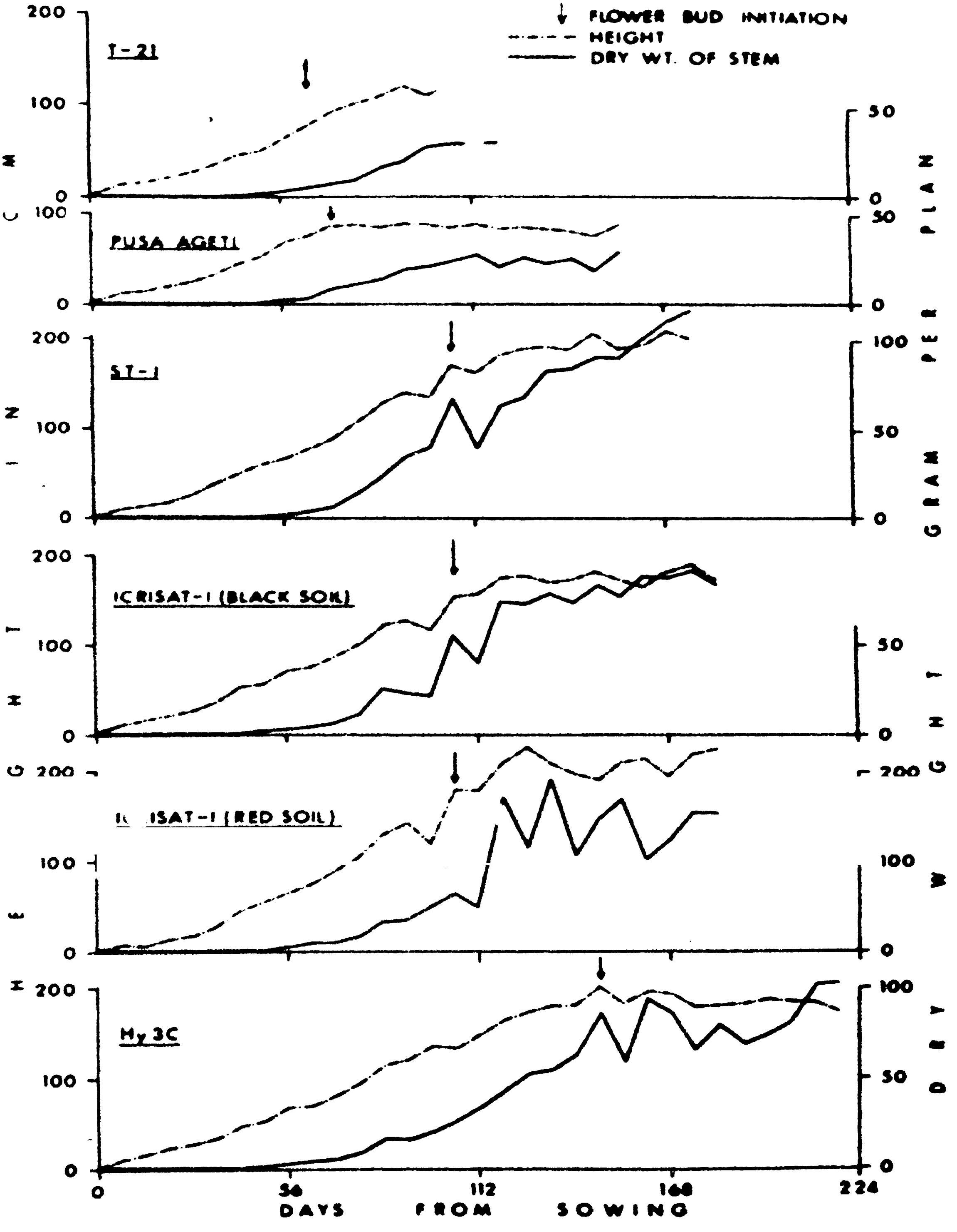


Table 3. Mean plant height, stem weight and number of branches after flower bud initiation (on per plant basis).

Cultivar	At maturity		After flower bud initiation		% after flower bud initiation		No.of branches produced after flower bud initiation.	
	Height cm.	Dry wt. of stem g.	Height cm.	Dry wt. of stem g.	Height cm.	Dry wt. of stem g.	Primary	Secondary
T-21	125.8	30.6	75.1	4.2	40	86	4.5	9.0
Pusa Ageti	86.0	28.9	86.0	7.7	0	73	4.4	3.1
ST-1	203.8	116.4	172.1	65.6	15	44	1.9	5.3
ICRISAT-1	176.1	85.0	149.5	55.5	15	35	0	2.5
ICRISAT-1 (Red soil)	226.0	152.1	180.4	67.9	20	55	0	6.2
HY-3C	184.5	103.0	181.1	62.2	2	40	2.6	5.0

Table 4. Leaf area development in five pigeonpea cultivars.

Cultivars	Max. LAI	Days from sowing	
		For Max. LAI	For flower bud initiation
T-21	1.34	98	63
Pusa Ageti	1.68	112	70
ST-1	3.60	119	105
ICRISAT-1	3.68	119	105
ICRISAT-1 (Red soil)	12.70	119	105
HY-3C	3.58	126	140

B. Dry matter

The dry matter distribution from germination to maturity for all the five cultivars is given in Fig. 3. Since the sampling dates for ST-1, ICRISAT-1 and ICRISAT-1 (Red soil) differed by 3 days from the other cultivars the mean rainfall and temperature were averaged according to the sampling week. They are also shown in Fig.3.

Three phases of growth can be discerned:

The initial "lag" phase (extending up to 56 days from sowing), a rapid growth phase (lasting up to 112 to 125 days depending on the duration of the cultivars) and a final phase of slow net accumulation of dry matter.

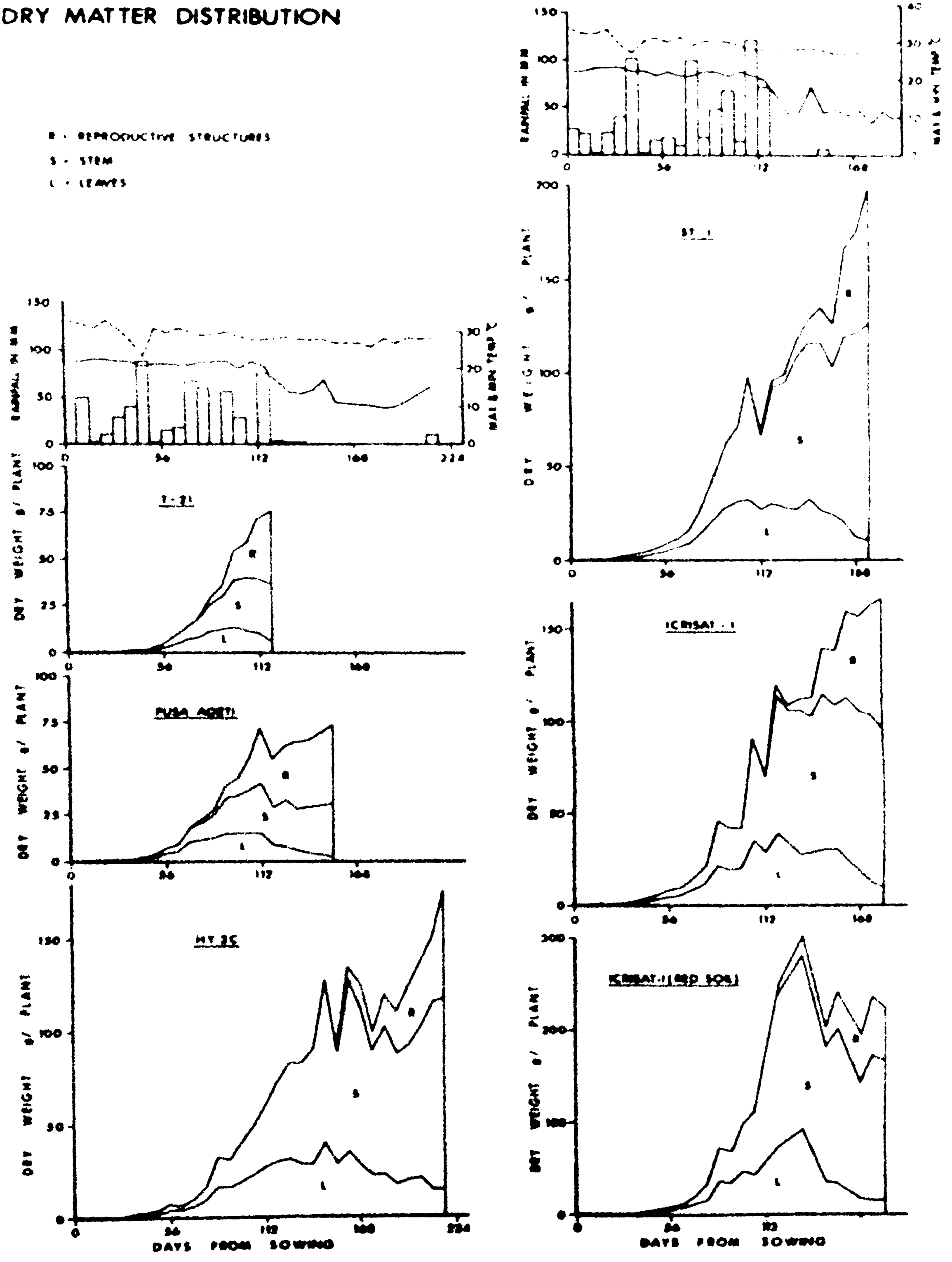
During the initial "lag" phase, the leaf fraction contributed more to the total dry matter than the stem. After this phase of growth the leaves made up a smaller proportion of the total dry matter than the stem or reproductive structures.

Leaves:

The leaf fraction included both laminae and petioles. It can be seen from Fig. 3 that there was a net decline in leaf dry weight during the reproductive phase of all cultivars.

The short duration cvs T-21 and Pusa Ageti reached their maximum Leaf Area Index (LAI) much earlier than the medium and late medium cultivars (Table 4). The maximum LAIs for T-21 and Pusa Ageti were 1.3 and 1.7 respectively, whereas for ST-1, ICRISAT-1 and HY-3C,

FIGURE 3
DRY MATTER DISTRIBUTION



they were about 3.6. In the case of ICRISAT-1 grown in red soil, the maximum LAI was the highest, 12.7, although the number of days taken to reach this LAI was the same as that of plants in black soil. Considering the physiological stage of the crop, T-21 and Pusa Ageti took about 35 to 42 days after flower bud initiation to attain the highest LAI. ST-1 and ICRISAT-1 took only 14 days but HY-3C reached its maximum LAI 14 days before flower bud initiation.

The trend of LAI, leaf dry weight and total number of green leaves over time showed a close similarity (Fig. 4).

In order to study the remobilization of nutrients from senescent leaves, branches from cvs ST-1, ICRISAT-1 and HY-3C were selected which had yellow leaves at the base, mature leaves in the middle and young leaves at the top. The leaves were collected node by node and their area and dry weight were determined and nitrogen analysis were carried out. The SLW and nitrogen content of these leaves are shown in Fig. 5. There was a progressive decline in SLW as the leaf age increased on a given branch of ST-1 and ICRISAT-1 whereas in HY3C, this trend was not observable. The nitrogen content of the senescent leaves was much lower than that of the mature and maturing leaves in all cultivars. The low SLW of senescent leaves may be accounted for in part by respiration but mainly by the mobilization of compounds like carbohydrates, nitrogen etc. towards the growing parts of the plant. The analysis of nitrogen clearly indicated that the senescent leaves had lost substantial quantities of nitrogen

FIGURE 4 LAI, LEAF DRY WEIGHT AND NUMBER OF LEAVES OF PIGEONPEA CULTIVARS

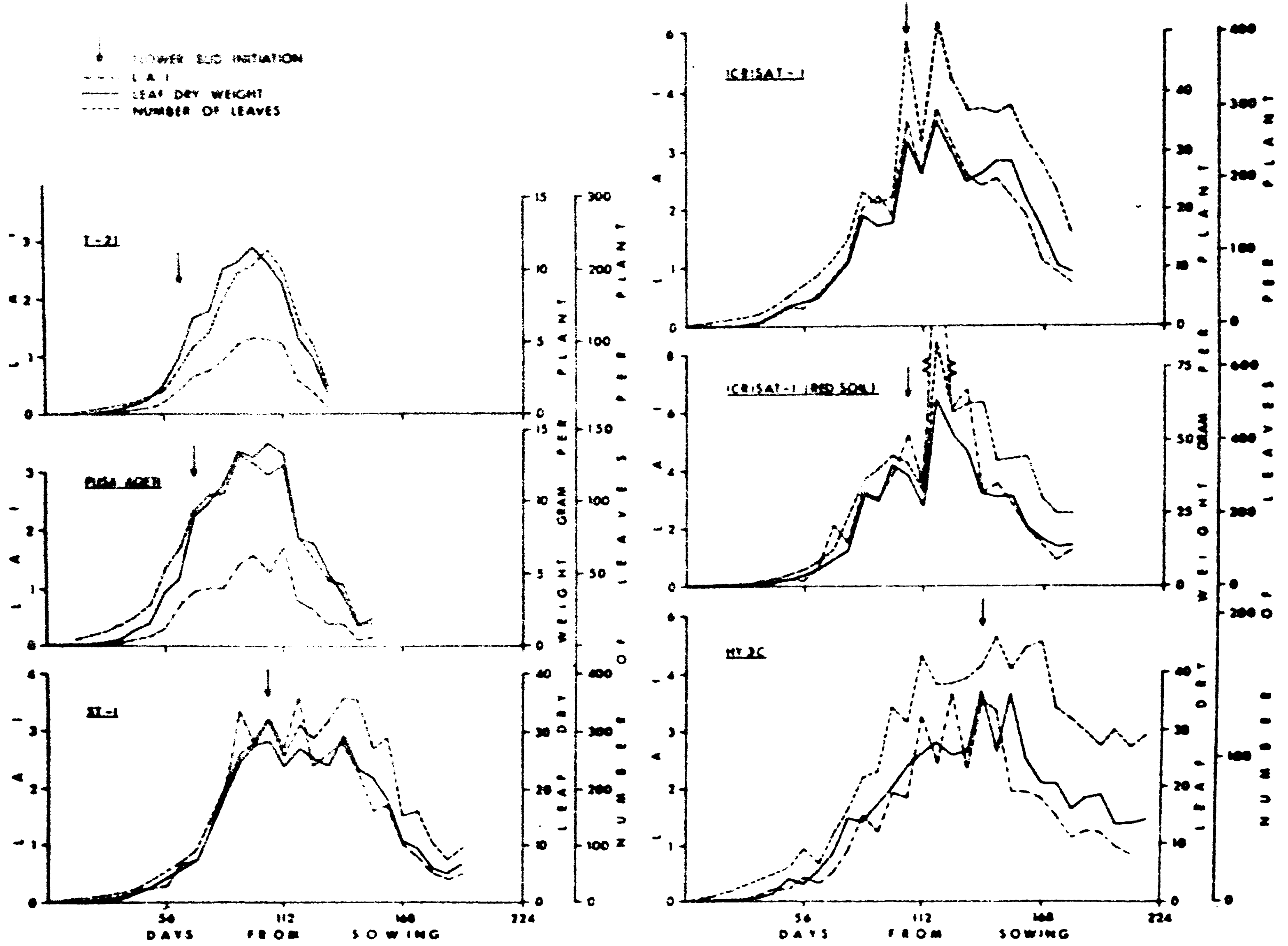
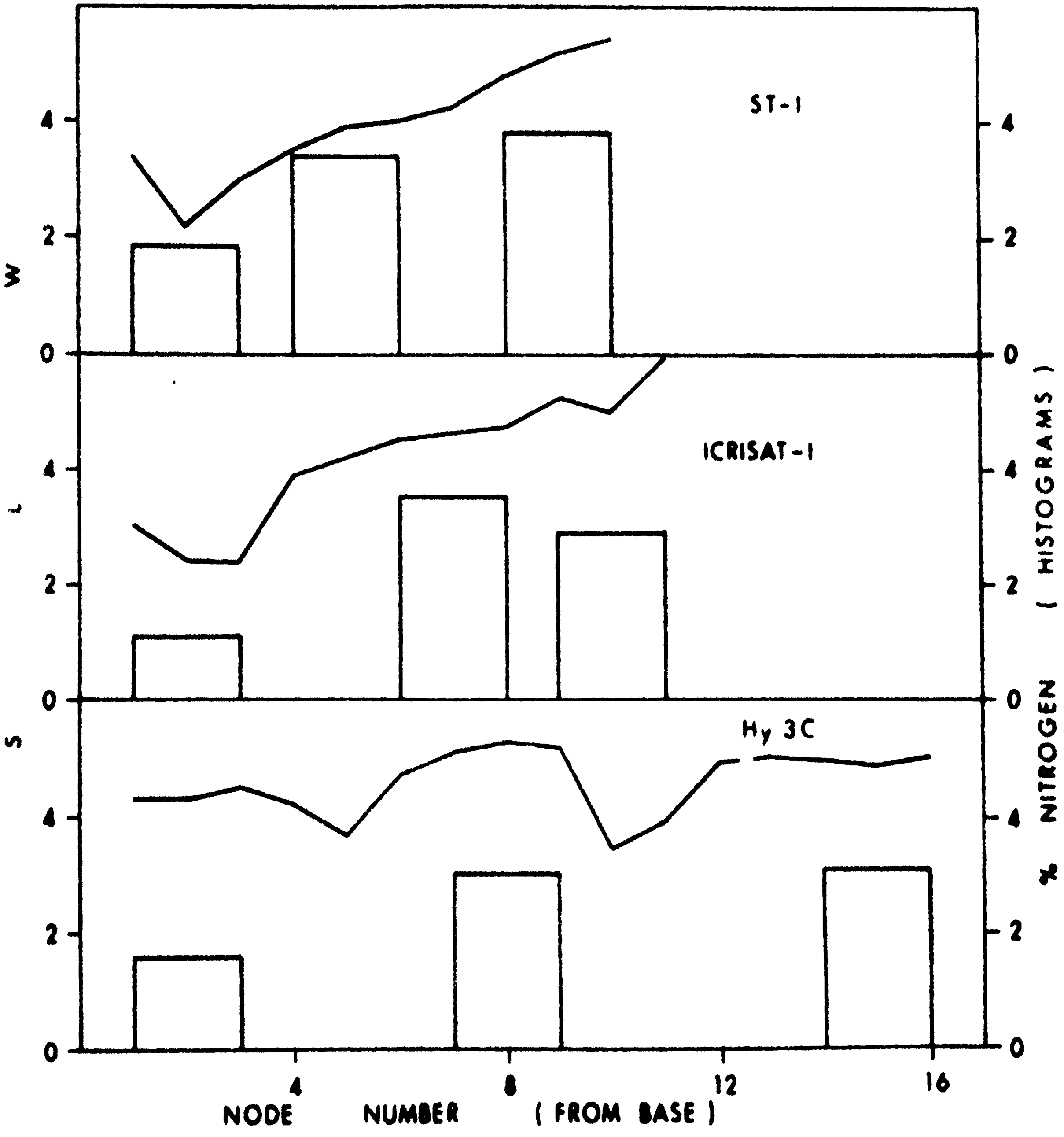


FIGURE 5

SPECIFIC LEAF WEIGHT (SLW) AND NITROGEN PERCENTAGE OF SENESCENT, MATURE AND YOUNG LEAVES ON A BRANCH



which must have been translocated to other parts of the plant.

Stem:

During the initial "lag" phase, the majority of the dry matter was in the main stem only. Later on, a greater contribution was due to primary and secondary branches. The production of branches was not uniform over the individual plants and consequently introduced sampling errors which were reflected in the growth curves where instead of a smooth curve at later stages, we ended up with a zig zag trend. The ratio of stem to leaf went on increasing as the plant approached the reproductive phase. The dry weight of stem in ICRISAT-1 grown in red soil was much higher than the same cultivar grown in black soil.

In order to get an approximate estimate of the surface area of the stem compared with the leaf area, the stem diameter at the middle of main stem and primary branches and the length of main stem and primary branches were taken. The area was calculated for three sampling dates for all cultivars and the results are given in Table 5. (The total stem area was divided by two since the leaf area was recorded for only one side of the leaves). From 91 to 105 days from sowing, the surface area of stem was between 17 and 29% of the leaf area present at that particular time. Later on, this population increased until it was equal to or greater than the leaf area, owing to the growth of the stem and branches and to the senescence and loss of leaves. The photosynthetic contribution of this stem surface may be of considerable significance for the plant.

Reproductive structures:

Reproductive structures consisted of peduncles, pedicels, buds, flowers, green and mature pods. The fraction of dry matter going to the reproductive structures started when flowering began and soon this fraction increased rapidly.

The time taken for flower bud initiation and for maturity by different cultivars in relation to the vegetative and reproductive crop growth rates are presented in Table 6.

Table 5. Stem area (cm^2) of pigeonpea cultivars at different stages of growth.

Cultivars	Days from sowing.	Surface area of stem, cm^2	Leaf area cm^2	Stem area over leaf area (%)
T-21	91	259	1770	15
	126	365	1060	34
Pusa Ageti	91	285	2518	11
	119	356	1386	26
	161	364	411	89
ST-1	105	615	5700	11
	140	1313	4229	31
	175	1583	1557	102
ICRISAT-1	105	738	7609	10
	140	693	3115	22
	182	1015	1843	55
ICRISAT-1 (Red soil)	105	724	6672	11
	140	1339	4764	28
	182	1159	1647	70
HY-3C	91	261	3101	8
	140	510	3882	13
	217	1579	2361	67

Table 6. Vegetative and reproductive crop growth rates of pigeonpea cultivars.

Cultivars	Crop growth rate Kg./ha/day		Days from	
	During vegetative phase.	During reproductive phase	Sowing to flower bud initiation	Flower bud initiation to maturity
T-21	6.0	33.5	63	56
Pusa Ageti	11.3	21.3	70	84
ST-1	41.3	44.4	105	70
ICRISAT-1	38.6	41.7	105	77
ICRISAT-1 (Red soil)	47.0	33.1	105	77
HY-3C	29.0	31.8	140	77

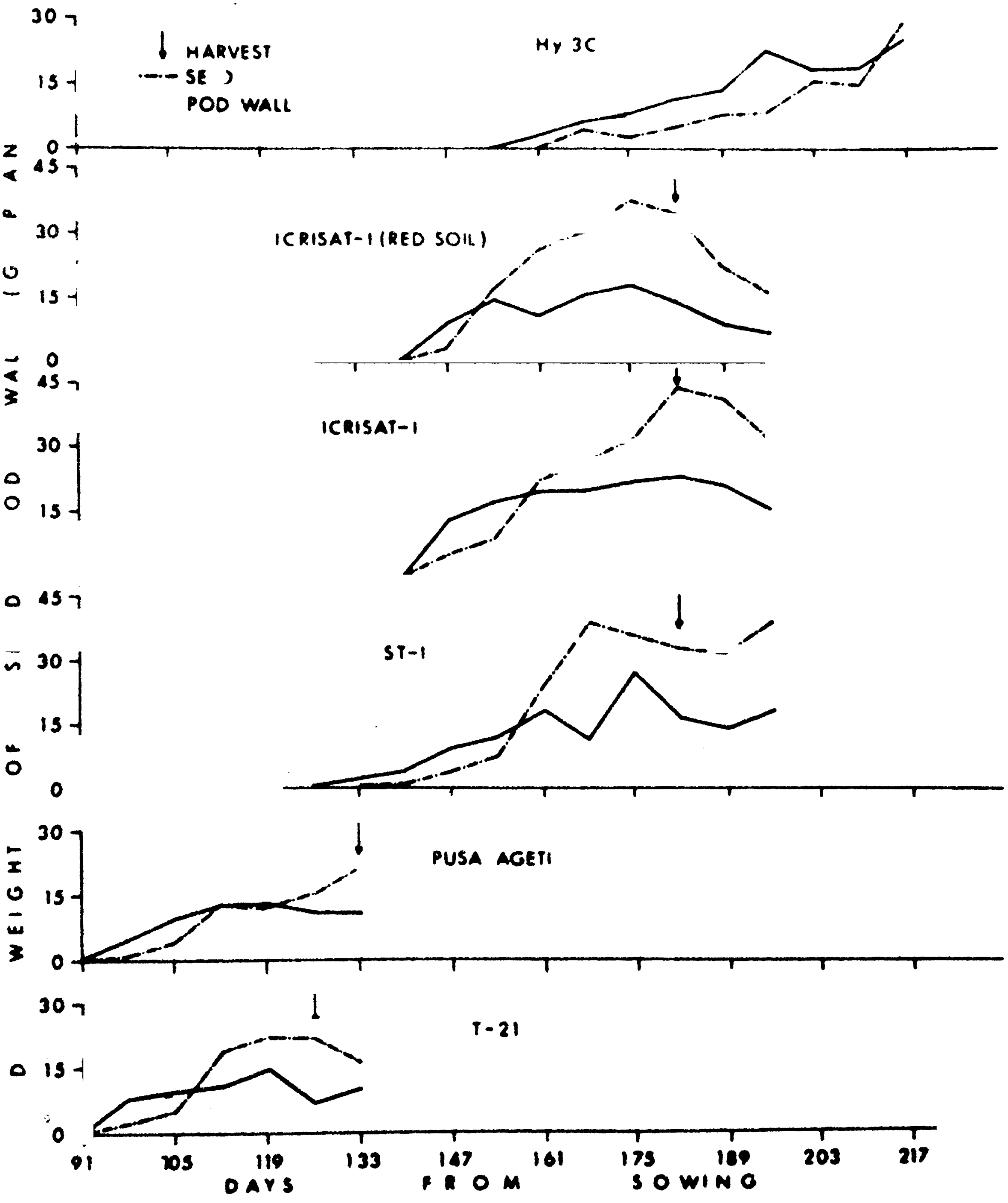
The number of days to flower initiation were related to the duration of the cultivars. On the other hand, the medium (ST-1, ICRISAT-1) and late-medium (HY-3C) cultivars took almost the same time to complete their reproductive growth. Cv T-21 completed its reproductive phase by 56 days, whereas Pusa Ageti took about 84 days, which was a fortnight longer than the duration of vegetative growth phase. Therefore the crop growth rate during the reproductive phase of this particular cultivar was much less than other cultivars. The reproductive crop growth rate of T-21 was 5.6 times more than the vegetative crop growth rate probably owing to the fewer number of days for reproductive growth. This ratio for Pusa Ageti was 1.9. For cvs ST-1, ICRISAT-1 and HY-3C the ratio tended to 1, and was less than 1 in the case of ICRISAT-1 grown in red soil, although the number of days for reproductive growth was the same as that of the other medium cultivars.

The dry weights of the separated seeds and pod walls are plotted against time in Fig. 6. In all cultivars except HY-3C, the dry weight of pod wall reached its maximum when the seed dry weight started increasing rapidly. This agrees well with the pod development studies (Chapter IV). In the case of cv HY-3C, both pod wall and seed dry weight increased side by side. Also the rate of increase of seed dry weight was slower in this cultivar.

In some cultivars a fall in the dry weight of pods and seeds took place after maturity, i.e., after the time at which the crop would normally have been harvested (Fig. 6). This fall was particularly striking in the case of cv ICRISAT-1 and was observed on both red and black soils. The fall in dry weight was associated with a fall in total pod and seed number per plant. This was owing to the dehiscence and/or shattering of pods and the loss of pods from the plant by the breaking of the pedicels which became very brittle.

FIGURE 6

DEVELOPMENT OF SEEDS AND POD WALLS ON PLANT BASIS



2. YIELD ANALYSIS

Introduction

An analysis of yield and yield components i.e. pod number/plant, seed number/pod and 100-seed weight, was carried out on each of the five cultivars grown both in black and red soils. The relative importance of these yield components in different cultivars was investigated.

Methods

At maturity, 50 plants of each cultivar were cut at the ground level and tagged. Pods were removed from the plant, dried at 80°C for 48 hrs and weighed. Seeds were separated, counted and weighed. From these records, yield components were calculated. The stem was also dried and weighed.

Another set of 100 plants of cvs ST-1, ICRISAT-1 (black and red soils) and HY-3C (red soil only) were tagged in the field after harvesting the pods from each plant. The plants were allowed to stay in the field where they produced a second flush of pods. Yield and yield components were determined as before.

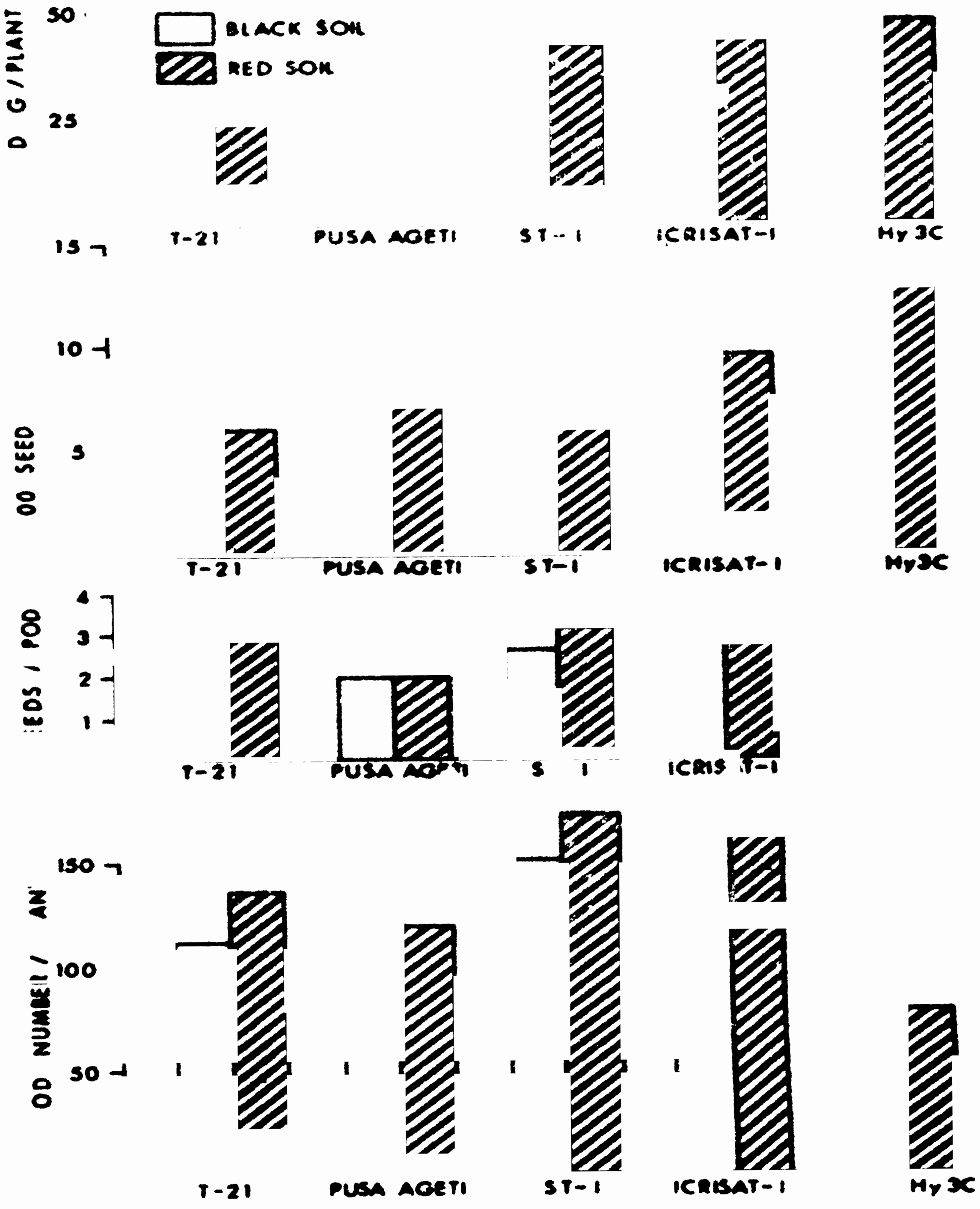
Results

Yield and yield components of cvs T-21, Pusa Ageti, ST-1, ICRISAT-1 (black and red soils) HY-3C (red soil) are represented in Fig. 7. The grain yield per unit area and productivity per day are shown in Table 7.

The grain yield of T-21, Pusa Ageti, ST-1 and ICRISAT-1 was

FIGURE 7

YIELD AND YIELD COMPONENTS OF PIGEONPEA CULTIVARS



34%, 34%, 31% and 19% respectively more in red soil than in black soil, and the productivity per day was also considerably higher in red soil than in black soil. In black soil the lower yield, particularly of HY-3C may in part have been owing to water-logging.

The main yield component contributing yield was pod number per plant both in early and medium cultivars, but in HY-3C it seemed to be the seed size. Pusa Ageti had the minimum seeds/pod.

The harvest indices of the cultivars grown in black and red soils are given in Table 8. The calculated harvest index (HI) was not a true harvest index because the roots and the fallen leaves were not taken into account for the calculation. There was practically no difference in HI between soils except for cv ICRISAT-1. For cv HY-3C we had no data for black soil owing to the damage caused by water-logging.

There was a variation in grain to pod wall ratio among cultivars (Table 9). ST-1 had the highest ratio both in black and red soils. Cultivars grown in red soil showed a higher ratio compared with those grown in black soil. The average weight of the pod walls on red and black soils was not very different and so most of this change in grain to pod wall ratio was owing to the higher seed number per pod and higher seed weight on red soil (Table 10, First Flush data). The seed numbers per pod are the <u>net</u> seed numbers at harvest. There may have been different degrees of insect attack on red and black soils, and hence a differential loss of seeds before harvest.

The relationships between first and second flush yield of cvs ST-1, ICRISAT-1 (black and red soils) and HY-3C (red soil only) were calculated on the basis of percentage over the first flush and shown in Fig. 8.

Table 7. Grain yield of Pigeonpea cultivars

Cultivars	Grain yield Kg./ha		Grain yield Kg./ha/day	
	Black soil.	Red soil.	Black soil.	Red soil.
T-21	768	1176	6.4	9.9
Pusa Ageti	824	1188	5.3	7.7
ST-1	1790	-	10.2	-
ICRISAT-1	1702	2440	9.3	13.4
HY-3C	518	-	2.4	-

Table 8. Harvest Index of Pigeonpea cultivars.

Cultivars	Harvest Index (Percent)	
	Black soil	Red soil
T-21	34	36
Pusa Ageti	33	32
ST-1	20	19
ICRISAT-1	23	15
HY-3C	--	26

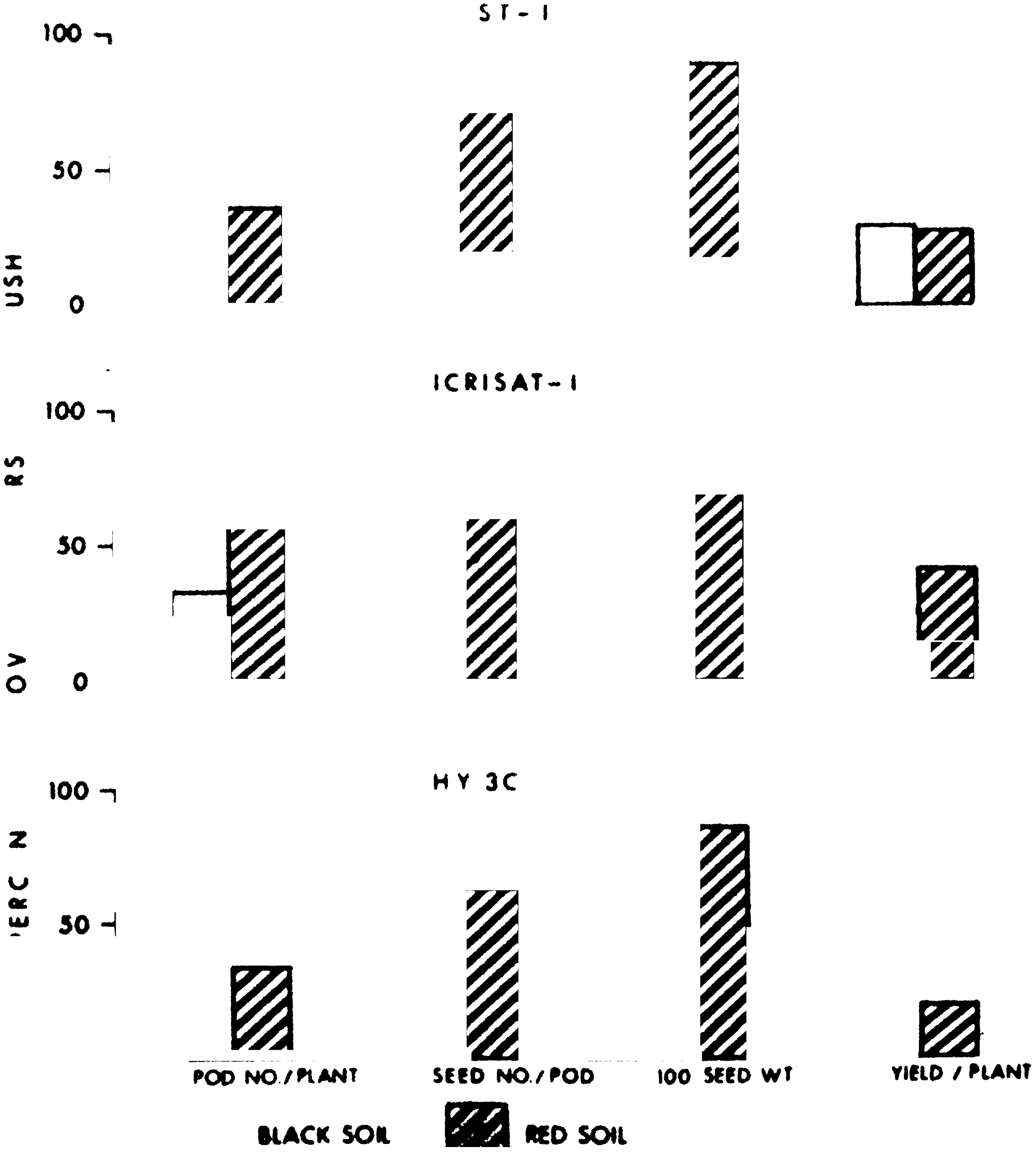
Table 9. Variation in grain to pod wall ratio.

Cultivars	Grain weight/pod wall weight	
	Black soil	Red soil
T-21	1.56	1.80
Pusa Ageti	1.75	1.79
ST-1	2.31	2.88
ICRISAT-1	1.87	2.26
HY-3C	-	2.18

Table 10. Yield analysis of first and second flush harvests.

Cultivars	Harvested on	Number of pods/plant		Number of seeds/pod		Weight of 100-seeds in g.		Yield/plant	
		Black soil	Red soil	Black soil	Red soil	Black soil	Red soil	Black soil	Red soil
I Flush									
ST-1	23-12-74	169.6	175.5	2.9	3.1	7.8	7.9	38.2	42.6
ICRISAT-1	30-12-74	176.3	163.1	2.6	3.2	9.1	9.7	42.2	50.8
HY-3C	30-1-75	-	78.4	-	3.9	-	15.4	-	47.8
II Flush									
ST-1	6-3-75	59.8	63.2	2.7	2.6	7.1	7.1	11.6	11.9
ICRISAT-1	14-3-75	58.2	114.7	2.2	2.4	8.5	7.9	11.0	21.4
HY-3C	4-3-75	-	27.8	-	2.5	-	13.3	-	9.4

FIGURE 8
YIELD AND YIELD COMPONENTS OF SECOND FLUSH (EXPRESSED AS PERCENTAGE OF FIRST FLUSH YIELD AND YIELD COMPONENTS)



The yield/plant from first flush was more in red soil than in black soil for ST-1 and ICRISAT-1; in the second flush the yield of ICRISAT-1 followed the same trend whereas ST-1 yielded almost same in both soils (Table 10). The second flush yield was almost 20% of the first flush yield for HY-3C, 30% for ST-1 and for ICRISAT-1 it was 42% in red soil and 26% in black soil.

It was surprising that the yield of the second flush of ICRISAT-1 was higher on the red soil which has a lower water-holding capacity than black soil, but perhaps this was owing to the better growth of the plants in red soil which might have continued to give a good second flush yield. The time taken for a second flush yield was over 2 months for ST-1 and ICRISAT-1 and over one month for HY-3C (Table 10).

The number of pods per plant in the second flush was about 30% of the first flush for all the three cvs except for ICRISAT-1 grown in red soil which had 70%. There was a reduction in the number of seeds per pod and weight of 100 seeds in the second flush in all cultivars (Table 10), but the yield component which underwent the greatest reduction was the number of pods per plant.

3. NITROGEN UPTAKE

Introduction

The investigation carried out with five cultivars was in soil which was not fertilized with nitrogen. The plants did not show any visual deficiency for this nutrient. Apart from the residual nitrogen of the soil, the rest would have come from the fixation of atmospheric nitrogen by the root nodules. A major portion of the nitrogen found in the plant may be coming from this process.

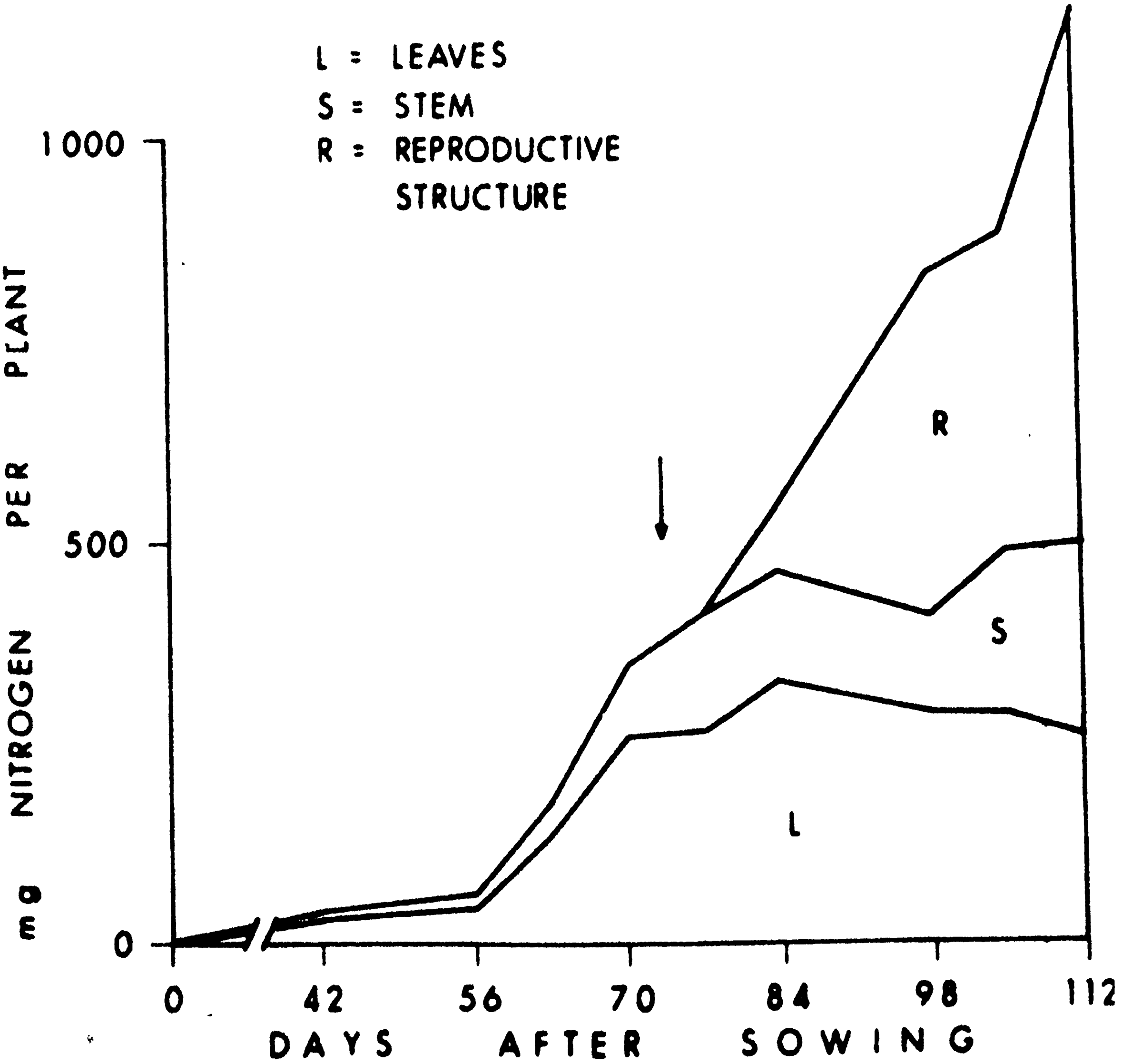
Methods

To study the pattern of nitrogen uptake at different phases of growth, the samples taken for the growth analysis study was ground to powder and analysed for nitrogen by micro or macro-Kjeldhal's method (depending on sample size). This analysis has so far been carried out on one cultivar, namely T-21.

Results

The amounts of nitrogen in the leaves, stems and reproductive structures at different times are shown in Fig. 9. The total amount of nitrogen in the leaves went on increasing upto flower bud initiation and remained constant thereafter. The amount of nitrogen in the stems increased slightly after flower bud initiation. The total uptake of nitrogen by the reproductive structures was much more than by the leaves and stems.

FIGURE 9
DISTRIBUTION OF NITROGEN _CV T-21



4. DISCUSSION

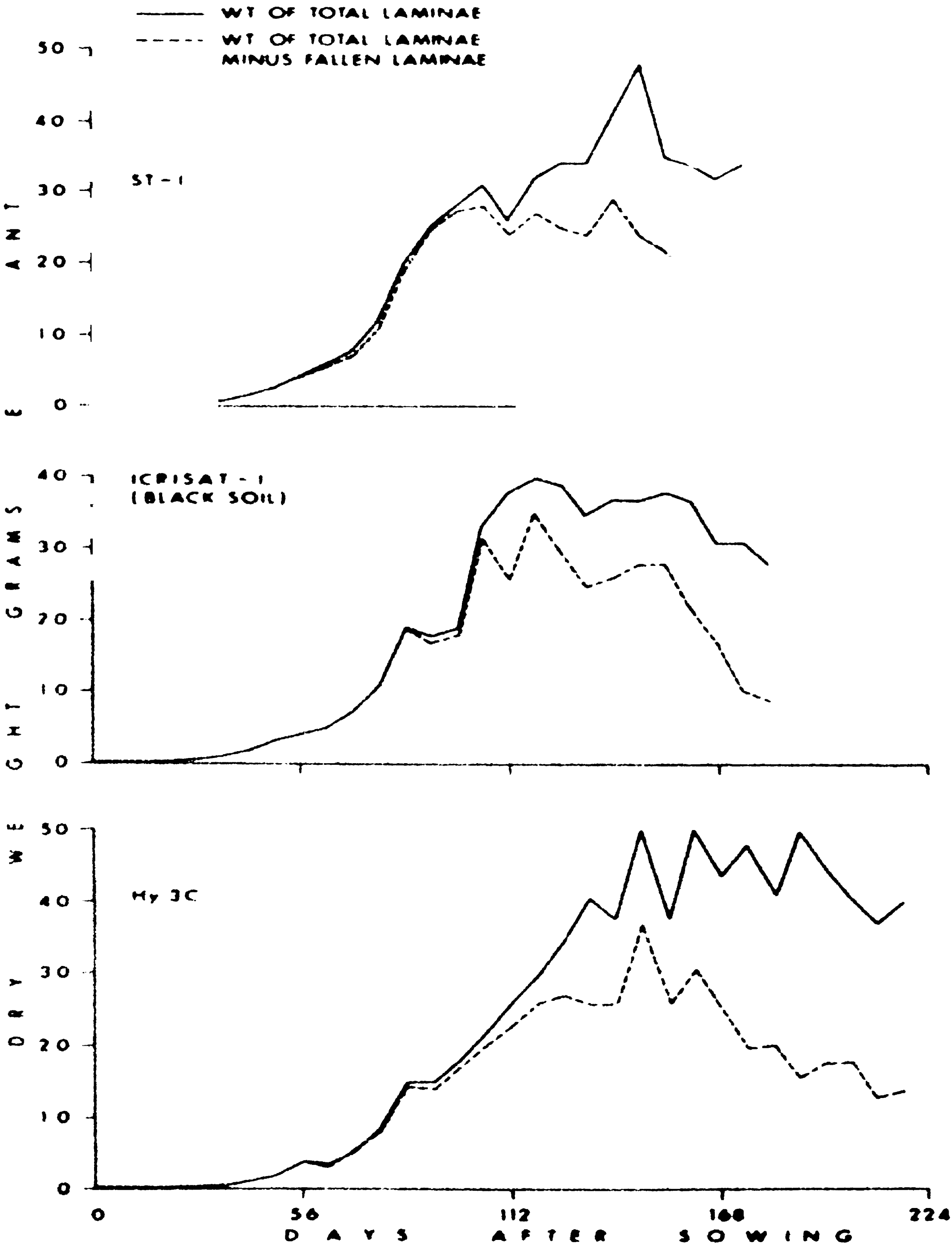
The data collected in the growth analysis give a quantitative picture of the accumulation and partitioning of dry matter throughout the growth of the crop, but this picture is not complete for two reasons. Firstly, data on root dry weights have been omitted because of the difficulty of measuring them quantitatively, and this omission has to be borne in mind when considering the direct and derived data from the growth analysis. (Studies on the development of roots and nodules are reported separately in Chapter II). Secondly, like many other dicotyledonous crops, pigeonpeas lose leaves as they grow and mature; the dry matter lost in the fallen leaves is not recorded in the growth analysis. Some dry matter is also lost as a result of flower and pod drop, but the amount is relatively small (see Chapter IV).

In order to correct for dry matter lost by leaf-fall the fallen leaves could have been collected and weighed, but this was not done. An indirect method of correcting for this loss was adopted instead. In the growth analysis data the number of leaves which has been lost at each time of sampling was measured (by counting the leaf scars). Since the younger leaves drop off first, the area of the leaves which had fallen could be calculated from the measurements of leaf area on plants at an earlier stage, when the total leaf number corresponded approximately to the number of fallen leaves in the older plants. The data shown in Fig. 5 give the specific leaf weight of senescent leaves; and so the total dry weight lost by the abscission of a given number of senescent leaves could be calculated. In Fig. 10 the total leaf dry weight in cvs ST-1, ICRISAT-1 and HY-3C is shown with and without the calculated corrections for leaf-fall. In both ICRISAT-1 and HY-3C total leaf dry weight reached a plateau shortly after flowering whereas in ST-1, it continued to increase for a longer time. The total leaf dry weight fell towards maturity, a fall which probably reflects the decrease in SLW during leaf senescence.

The leaf area index (LAI) in all varieties was less than one up to about 70 days after sowing (Fig. 4); thereafter the grand period of growth began. A more effective use of the light would be achieved if a higher LAI could be achieved earlier. One way of doing this might be by providing more nutrients, such as nitrogen, to give an initial 'push'. An increase in the plant population may not be a solution because the plants require a wider spacing later on for better branching and pod set. This slow development of LAI is not, however, such a disadvantage in the intercropping situation in which pigeonpea is commonly grown; the companion crops are generally faster growing and develop a larger leaf area more rapidly so that a more efficient utilization of light by the whole system is achieved.

The five cultivars varied in their LAI and for ICRISAT-1 a big difference was found in LAI on red and black soils (Fig. 4). The low LAIs in the early cultivars simply reflect in part their earlier maturity; they were planted at the same spacings as the other cultivars. A higher population-density would have been more appropriate for such

FIGURE 10. DRY WEIGHT OF LEAF LAMINAE CORRECTED AND UNCORRECTED FOR LEAF FALL



varieties; and at higher population-density they would have had higher LAIs.

The early cultivars reached their maximum LAI during the flowering and podding stage; on the other hand in the medium cultivars the LAI was declining during the reproductive phase. The patterns of leaf senescence and leaf fall varied with the cultivars (Fig. 4). The proportions of the total leaves produced still present at maturity are shown in Table 1. Furthermore, the loss in dry weight during leaf senescence and the remobilization of nitrogen from the leaves showed striking differences when cultivars were compared (Fig. 5). Less dry weight was lost by the leaves of HY-3C and also less nitrogen was remobilized from these leaves.

Although in the early stages pigeonpeas grow slowly, giving the impression of a 'lag phase' (Fig. 3) in fact it is in this period that they have the highest <u>relative</u> growth rate (RGR) (Fig. 11). The fall in relative growth rate with time is a common feature in many crops. The decline in RGR occurs as the proportion of non-growing but respiring times in the plant increases; one reason for the fall in RGR is that a higher and higher proportion of photosynthetic assimilates have to be used for maintenance respiration.

While RGR gives some idea of the 'sink' activity of the whole plant, the net assimilation rate (NAR) can be used as a measure of 'source' activity. Like RGR, NAR declines with time (Fig. 11) but in the medium and medium-late cultivars, it rises again shortly before maturity. The initial decrease in NAR may be attributed to the progressive shading of the lower by the upper leaves and/or to the decreasing photosynthetic efficiency of the earlier-formed leaves as they grow older. The rise as the plants approach maturity could be explicable in one or more of the following ways:

(i) An increase in photosynthetic efficiency towards the end of the reproductive phase.

(ii) A reduced partitioning of dry matter into the roots giving an apparent increase in photosynthetic efficiency which, in these calculations, takes into account only the weight of the shoot system. But this effect would have to be large to explain more than a small part of the rise in NAR, and it may be more than offset by another source of error, namely the loss of leaves. Leaf fall will lead to an underestimate of the dry weight of the shoot system and hence to an underestimate of NAR. However, when the NAR is recalculated taking into account the correction for leaf fall, the overall pattern remains much the same (Fig. 12).

(iii) An increase in the proportion of total photosynthesis carried out by organs other than leaves. Only leaf area is taken into account in calculating NAR, and if the proportion of total photosynthesis carried out by organs other than leaves increases the leaves will be credited with progressively more photosynthetic assimilation than they have actually carried out and hence the calculated NAR will rise. There is indeed a large increase in the

FIGURE 11

RELATIVE GROWTH RATE (RGR) AND NET ASSIMILATION RATE (NAR) OF PIGEONPEA CULTIVARS

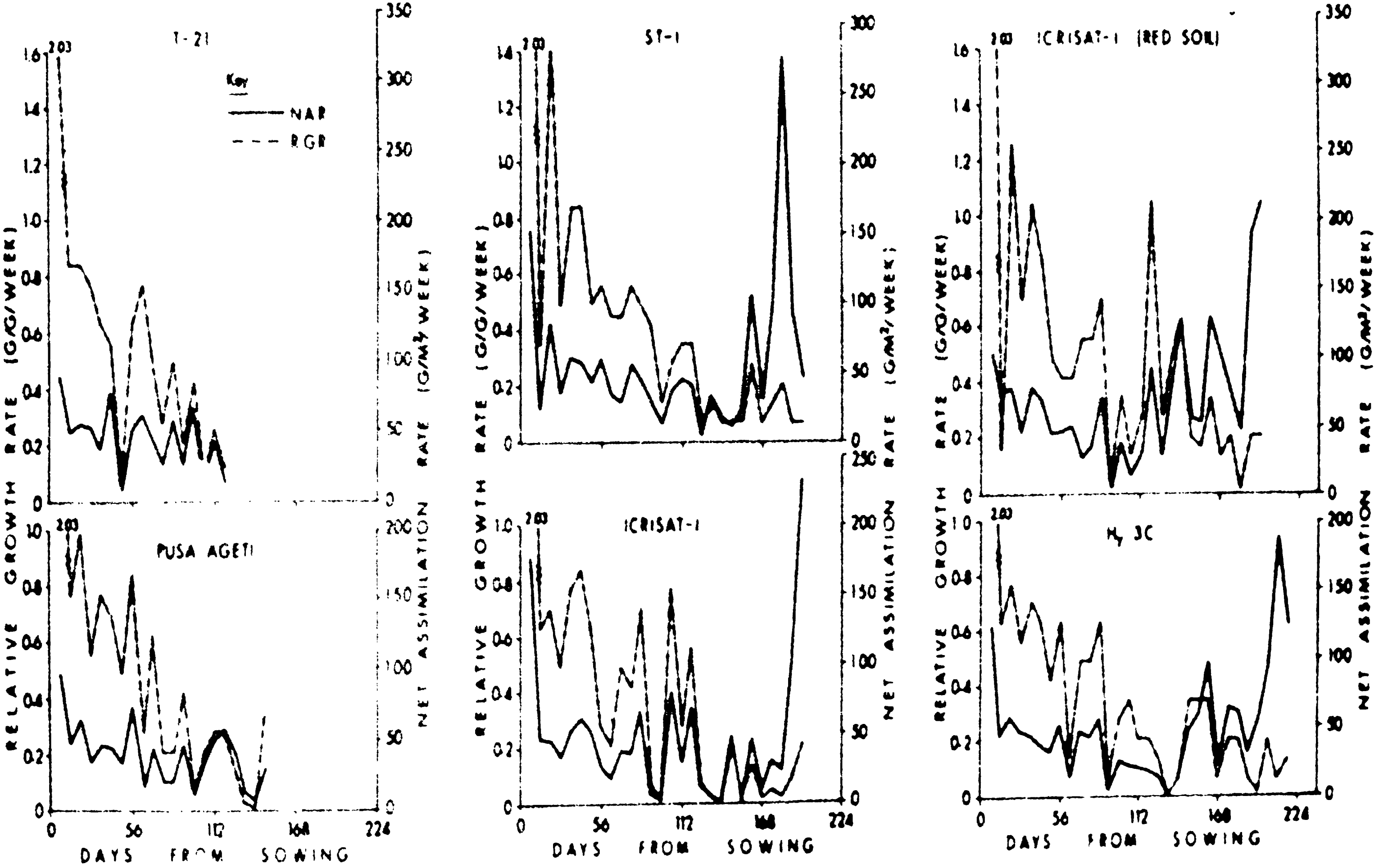
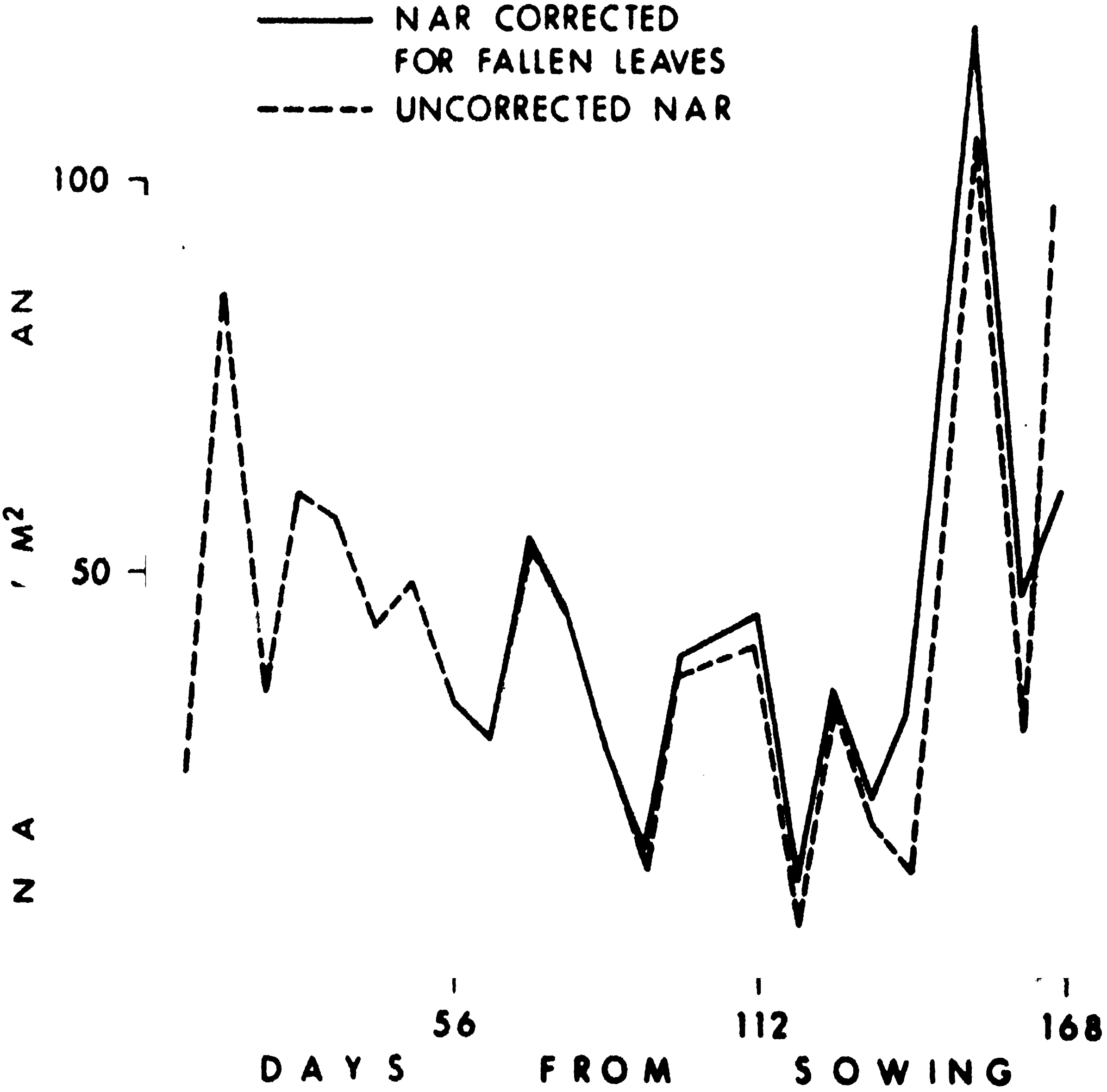


FIGURE 12
NET ASSIMILATION RATES CORRECTED AND UNCORRECTED FOR FALLEN LEAVES (CV.ST-1)



proportion of non-leaf photosynthetic surface during the reproductive period. The stem area (divided by two to make it comparable to leaf area where only one side of the leaves is taken into account) rises from around 10% of the leaf area at the time of flowering to as much as 102%, in the case of ST-1, at the time of maturity (Table 5). This relative change is a result both of an increase in stem area and a reduction of leaf area owing to leaf fall. Furthermore the photosynthetic activity of the stems may increase as leaf fall takes place; they are subjected to less shading. During the reproductive phase there is probably also a significant photosynthetic contribution from the pods.

Of these explanations the third seems likely to be the most important and it highlights the probable significance of the stems and pods as photosynthetic organs. However, it is difficult to know why a comparable rise in NAR was not found with T-21 and Pusa Ageti. One possible reason is that during their reproductive phases the weather was cloudy for most of the time (late rains occurred throughout October; see Fig. 3) and the soil was waterlogged intermittently. These factors might well have reduced the rate of photosynthesis per unit area and hence reduced NAR.

The first possibility, that part of the rise in NAR in the medium duration varieties might be due to a rise in photosynthetic efficiency of their leaves during the reproductive phase, cannot be excluded. Such effects have been claimed to occur in certain other crops as a response to increased demand from 'sinks'.

For many years, the possibility of increasing crop yields by increasing photosynthetic efficiency has been discussed. The best integrated measure of net photosynthetic efficiency in the field is NAR. This varies considerably throughout the growing season as can be seen from Fig. 11. In other crops, where significant varietal differences in NAR have been detected, little or no correlation has been found between NAR and total dry matter production. The variation in leaf area frequently accounts for much more of the difference in dry matter production than varietal differences in the photosynthetic efficiency per unit area of leaf surface.

In this connection, not only the LAI is relevant but the persistence of leaf area over time. This is given by the leaf area duration (LAD) which is an integral of the LAI over the growth period. In a wide variety of crops LAD has been found to be correlated with total dry matter produced. We also found that this was the case (Fig. 13; $r = .844^{**}$).

Although the wood of the pigeonpeas has some economic value, the most important aspect of yield is of course the grain. The yield of seeds depends both on total dry matter production and on the proportion of this dry matter which is partitioned into seeds.

This proportion is given by the harvest index (HI). Data from the yield on a plot basis have been given in Table 8. The low

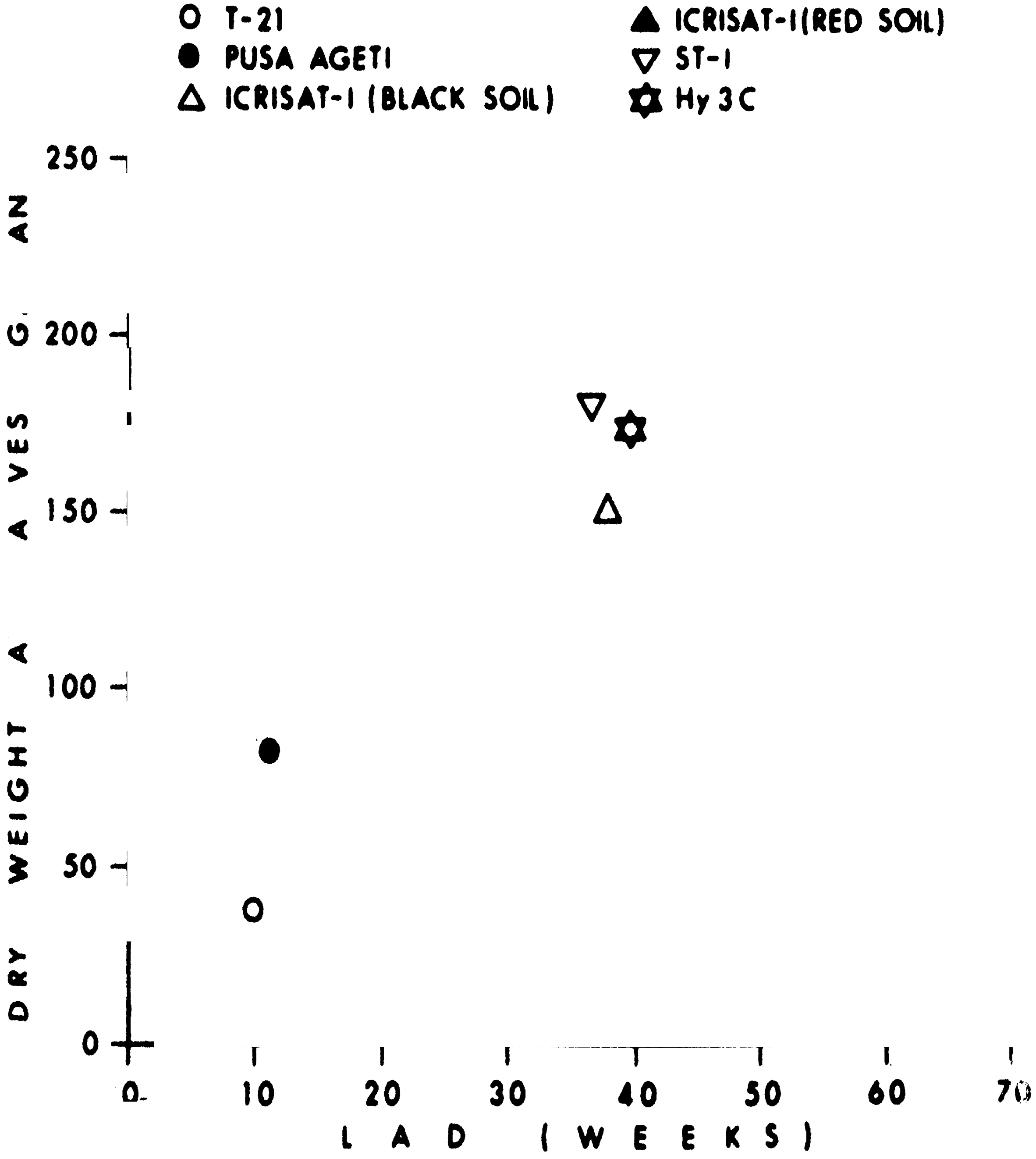


FIGURE 13. RELATION BETWEEN LEAF AREA DURATION (LAD) AND DRY MATTER PRODUCTION

value for HY-3C may largely be a consequence of poor and abnormal growth in the plots of this cultivar owing to bad patches of soil and water-logging. The HI of HY-3C calculated from the growth analysis data was not so low (Table 11 column A).

One problem in measuring HI in non-cereal crops is that the total dry matter produced by the plant is greater than the total dry matter present at harvest because of leaf-fall. Therefore a comparison of HIs involves error owing to differential leaf-fall before harvest; to obtain the true harvest index a correction would have to be made for the weight of the leaves and petioles. Alternatively the effects of differential leaf fall could be eliminated by removing all leaves before measuring the total dry matter at harvest, which would then represent the ratio of seed weight to stem weight+pod wall weight+seed weight. The effect of these corrections on the HI can be seen in Table 11. The HI is of course lower after for correction for fallen leaves and higher if leaves are eliminated together, but the differences are not very great, and most important, the ranking of HI is not altered by these corrections in spite of the fact that there were considerable differences in leaf fall before harvest (see Fig. 4; Table 1). This indicates that for a comparison of harvest indices a good idea of the relative values can be obtained simply by taking the ratio of seed weight to total dry weight at harvest, ignoring the error owing to differential leaf fall.

In the column D of Table 11 the ratio of seed weight to seed weight + stem weight is shown. Pod walls were not taken into account this makes a considerable difference to the HI, but again the ranking is not affected. In practice this is not a convenient index to use, since it involves removing leaves and pods from the stem and then threshing the separated pods, and it has no particular advantage. It is included here only for purposes of comparison.

In Tables 8 and 11 differences in HI between cultivars are quite marked. However, HI is also strongly influenced by the environment, In the case of ICRISAT-1, the HI was much lower on red soil than on black soil (Tables 8 and 11) while the soil type had less effect on the HI of the other cultivars (Table 8). One surprising effect of the soil type on a component of the HI was the difference in the ratio of grain weight to pod wall weight (Table 9). But we do not know to what extent this represents differential insect damage. (Pod borers, for example, reduce grain weight by eating seeds but have relatively little effect on pod walls). However, if differential insect attack (greater on black soil than red) were responsible, a correction for this would give an increased HI on black soil and increase further the difference in HI of ICRISAT-1 on red and black soils. Harvest index was also influenced by the cultural practice. The seed to stem+seed index calculated from the data in Table 18 on pigeonpeas inter-cropped with cereals or legumes was for HY-3C, 7.8% with pearl millet and 12.5% with cowpea and for ICRISAT-1, 19.5% with setaria and

Table 11. Harvest Index of Pigeonpea cultivars (calculated from growth analysis data).

Cultivars	A Seed wt.x 100 / Total plant wt.	B Seed wt. x 100 / Total plant wt. corrected for fallen leaves.	C Seed wt.x 100 / Stem wt. + Pod wall wt. + Seed wt.	D Seed wt.x 100 / Seed wt. + Stem wt.
T-21	28.6	-	31.0	39.5
Pusa Ageti	32.1	-	33.1	41.8
ST - 1	18.4	16.4	19.4	22.7
ICRISAT-1	26.6	23.9	28.3	33.1
ICRISAT-1 Red soil	15.7	-	16.8	18.1
HY-3C	16.9	14.8	18.5	22.0

Table 12. Percentage of Dry Matter Accumulated During Reproductive Phase Partitioned into Seeds

i.e. $\frac{\text{Seed Weight}}{\text{Total dry weight produced after flowering}} \times 100$

Cultivars	Not corrected for fallen leaves	Corrected for fallen leaves
T-21	34.9	-
Pusa Ageti	46.4	-
ST-1	28.3	23.9
ICRISAT-1	45.8	38.9
ICRISAT-1 Red soil	31.1	25.8
HY-3C	62.8	49.3

26.6% with soyabeans. These figures again differ from those for the same cultivars grown in mono-culture (see Table 11, column D).

The environmental effects on HI discussed above refer to plants grown in the same season, but the effects of different times of planting are even more striking. The harvest indices of cvs Mukta and ST-1 grown in the monthly planting trial increased progressively from the January planting onwards. To a large extent this represents the effect of photoperiodic sensitivity, since the length of the vegetative growth period, and also the height of the plant, declined progressively in plants planted between January and September (see p 81 of ICRISAT Pigeonpea Breeding Annual Report 1974/5).

The effect of the time of planting on HI is not only a consequence of the photoperiodic response. This is shown by comparing the HI of short duration cultivars Pusa Ageti and T-21 planted in June and in December when these cultivars show no photoperiodic response and the length of the vegetative phase is practically the same in both seasons (see Chapter VII). The harvest indices, derived in both cases from the growth analysis data, were for T-21 29% and 44% and for Pusa Ageti 32% and 41% for June and December plantings respectively (Table 19).

These observations serve to emphasize that HI is strongly affected by environment. To some extent in actual agricultural practice yield might be increased by increasing the HI of existing varieties by agronomic practices. One possibility is in exploiting the ability of the plants to produce a second flush of pods. Even if the plants are simply left untouched in the field after plucking the first flush of pods, up to 40% more yield can be obtained from the second flush (Table 10; Fig. 8). Preliminary observations suggest that the second flush yield can be increased further by ratooning after the first harvest. There may also be a possibility of reducing excessive vegetative growth and increasing seed yield in medium and long duration varieties by pruning or ratooning before flowering begins.

Varietal differences in HI may be influenced both by the relative duration of the vegetative and reproductive phases and by the proportion of dry matter partitioned into seeds in the latter. The higher HI of the early than of the medium duration varieties in the kharif season (Table 8) may be in part owing to the relatively higher proportion of their whole growth period which was occupied by the reproductive phase (Table 6).

During the reproductive phase itself, the cultivars differed in the proportion of accumulated dry matter which was partitioned into seed (Table 12). A correction for the dry weight lost in falling leaves did not change the overall pattern of the results which was that HY-3C partitioned the highest proportion of dry matter into seeds, or in other words re-invested the lowest proportion of dry matter in vegetative growth. On black soil, ST-1 partitioned a lower proportion of dry matter into seeds than ICRISAT-1.

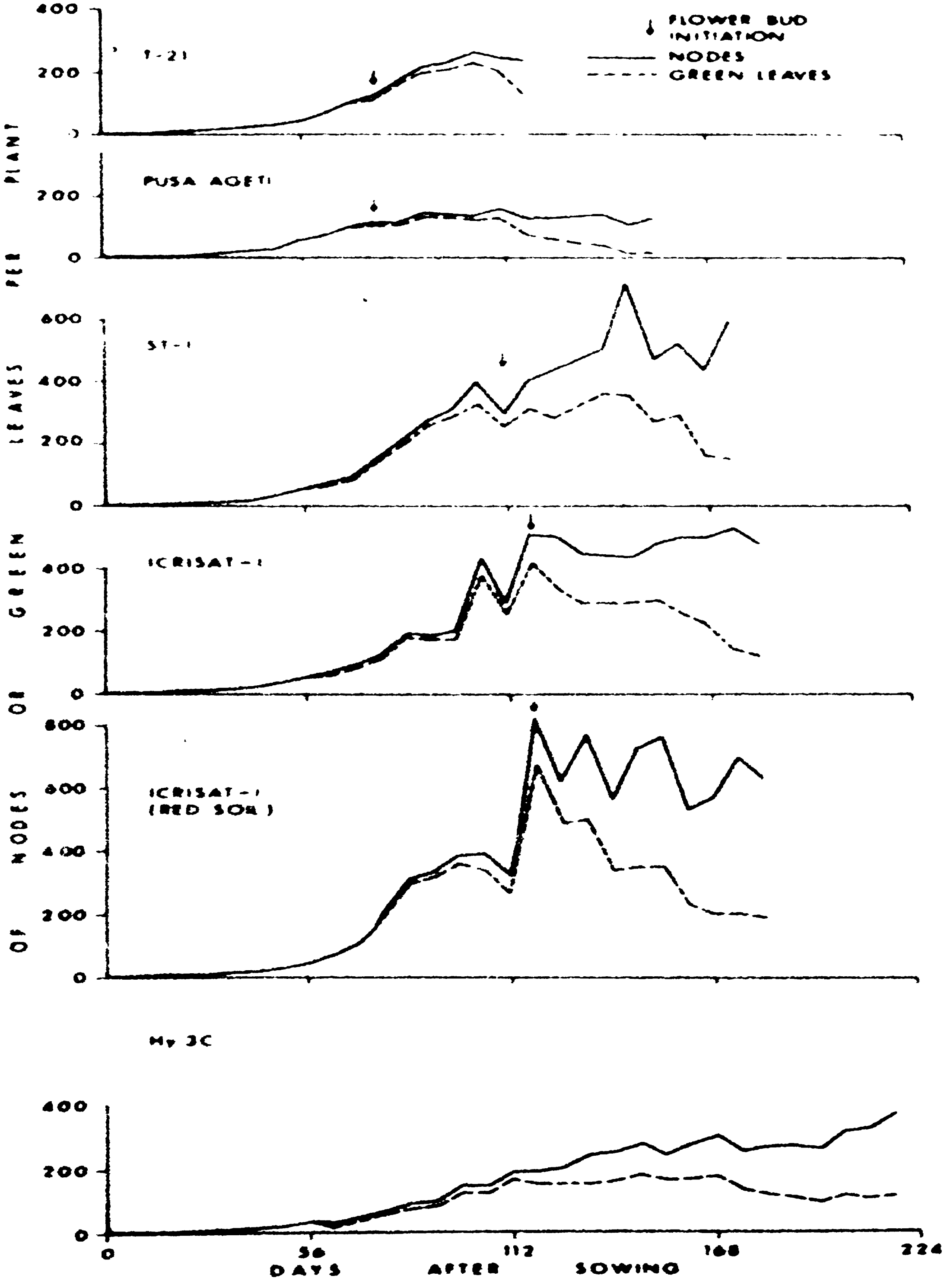
When considering the partitioning of dry matter during the reproductive phase in more detail we can use two indices of continued vegetative growth. One is the increase in the weight of stem and branches and the number of new branches (see Table 3) and the other is the number of new nodes produced by the vegetative meristems. This is given by the sum of the number of leaves and the number of fallen leaves (i.e. the number of leaf scars) and is shown in Fig.14.

Although the determinate cv Pusa Ageti stopped growing in height after the beginning of the reproductive phase and produced relatively few new leaves, the weight of the stem and the number of branches continued to increase almost as much as in T-21 which, being indeterminate, continued to grow in height and formed many new leaves. The HI of T-21 was slightly higher than that of Pusa Ageti (Table 8).

Among the other varieties HY-3C behaved in a semi-determinate manner in that after the beginning of flowering relatively few new leaves were formed and there was not much increase in height. However, here again the increase in stem weight and branch number was considerable. The cvs ST-1 and ICRISAT-1, both indeterminate and of similar duration to each other, continued to grow in height during the reproductive period but showed interesting differences in that ST-1 produced more primary and secondary branches and considerably more new leaves than ICRISAT-1 on black soil.

The results of the nitrogen analysis of cv T-21 indicate that net nitrogen uptake continued throughout the reproductive period (Fig.9)

FIGURE 14. MEAN NUMBER OF NODES AND GREEN LEAVES PER PLANT



There was little net loss from the leaves or stems, and the remobilization of nitrogen from leaves to pods cannot account for more than a small proportion of the nitrogen in the latter. The continued uptake of nitrogen into the shoot during the reproductive phase while nodule numbers were declining (see Chapter II) is surprising and, if confirmed with other cultivars, needs further investigation.

CHAPTER II

The Development of Roots & Nodules

Introduction

The purpose of these investigations was to obtain basic descriptive data on the growth and development of the root system and of the nodules.

Methods

Regular observations were carried out on two cultivars, Pusa Ageti and ST-1, growing in the experimental plots in black soil.

Samples were taken as described in the section on chickpea root and nodule studies (see Chickpea Physiology Report, Chapter II). The procedure differed only in the following respects:

(i) the soil cores were divided in 15 cm intervals only for the first 30 cm depth of soil, and thereafter 30 cm intervals were taken.

(ii) nodules were on the whole small and discrete, and nodule numbers in different size categories were recorded. The nodule mass was too small for accurate weighings to be made.

1. ROOTS

Results & Discussion

There was a good correlation between root lengths and root numbers in the various samples. Root length data are presented here. Root dry weights were very variable and bore little relation to root numbers or root lengths, probably because of the high error caused by the adherence of soil particles.

Regular observations were made on cvs Pusa Ageti and ST-1, both of which germinated on 27-6-1974. Owing to heavy rains the soil was in such a condition that soil cores could not be taken between the middle of September and the end of October. The results are shown in Figs. 15 and 16.

For the early cv Pusa Ageti, the water content of the surface zones of the soil remained well above permanent wilting point (15%) up to the time of maturity, and at this time there was also a high water content in the lower parts of the soil profile. Root development seems to have continued to some extent after flowering, and there may have been a decline in the root system in the few weeks preceding maturity. However, the root data show a number of inexplicable fluctuations, especially in the surface regions, suggesting that large sampling errors may have been involved.

Cv ST-1, a medium duration variety, matured under conditions of progressive water depletion from the top 90 cm or so of the soil. After flowering, root development continued for some time but declined a few weeks before maturity (i.e. the stage at which the plants are normally harvested). However, if the plants are left in the field, a second flush of growth takes place and this was associated with a resumption of root development in the lower zones of the soil where a considerable amount of moisture was still available.

Flowers were removed continuously from plants of cvs T-21, ST-1, ICRISAT-1 and HY-3C to prevent the development of pods.

These plants showed continued vegetative growth. Soil cores were taken after 6-8 weeks of flower removal, and in controls after 6-8 weeks of pod development. In all varieties more root development had taken place in the plants without developing pods than in controls, especially in the lower zones of the soil. These results indicate that during the reproductive phase there is competition between pod development and root development.

A small number of cores were taken between, rather than immediately over, the position of the main stems and tap-roots. The pattern of root development was found to be somewhat different: the cores taken between the rows contained a lower proportion of roots in the surface zones.

Measurements were made of the water content of the soil inside and outside the plots to obtain an indication of the pattern of water depletion owing to the activity of the roots. The data for cv ICRISAT-1 on 11-2-1975 during the second flush of growth indicate that water extraction by the roots had been taking place down to 120 cm (Fig. 17).

FIGURE 15

CULTIVAR PUSA AGETI (GERMINATED 27-6-74; BLACK SOIL) ROOT DEVELOPMENT AND WATER CONTENT OF SOIL AT DIFFERENT DEPTHS; AND NODULE NUMBERS PER PLANT

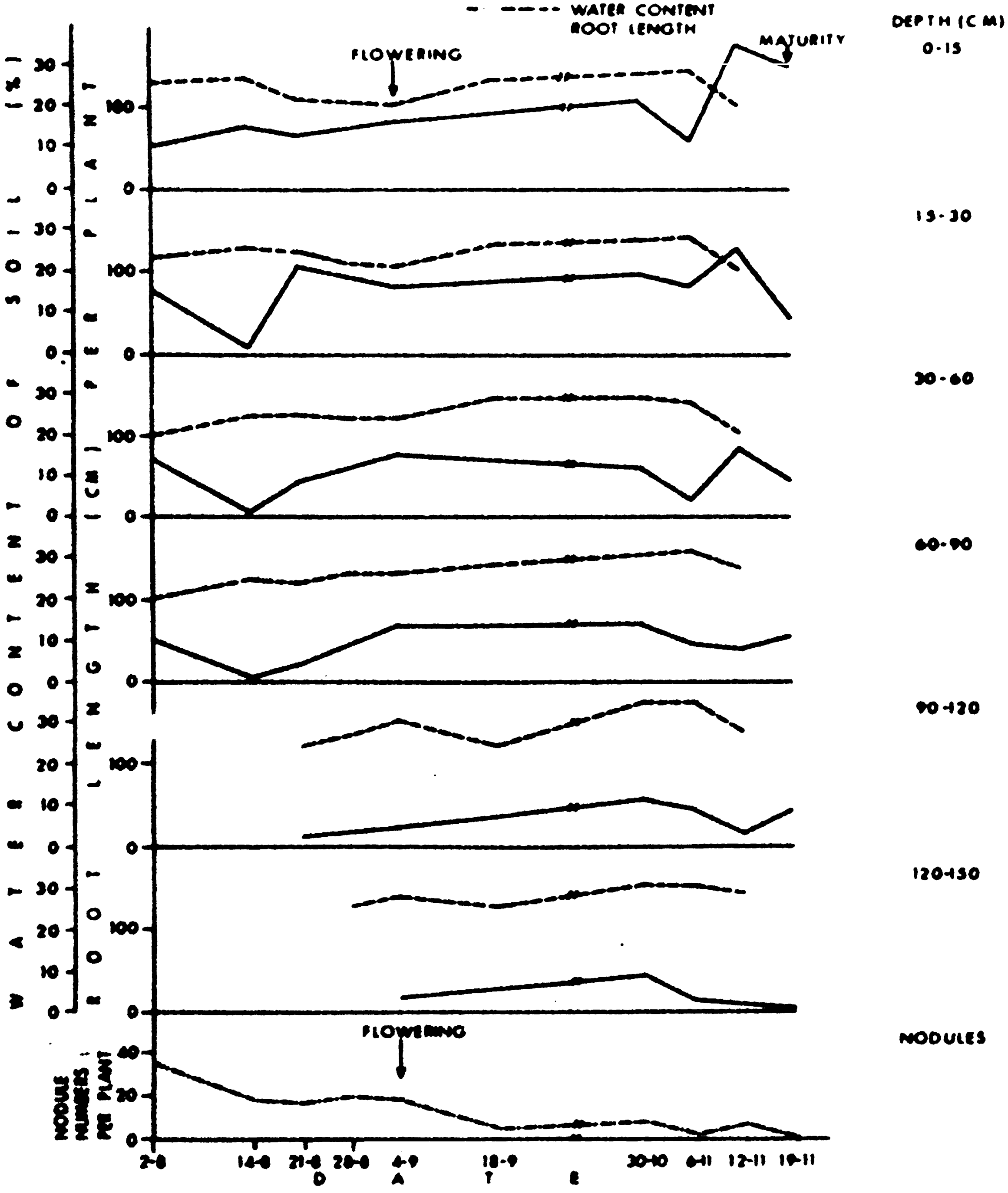


FIGURE 16

CULTIVAR ST-1 (GERMINATED 27-6-74; BLACK SOIL) ROOT DEVELOPMENT AND WATER CONTENT OF SOIL AT DIFFERENT DEPTHS; AND NODULE NUMBERS PER PLANT

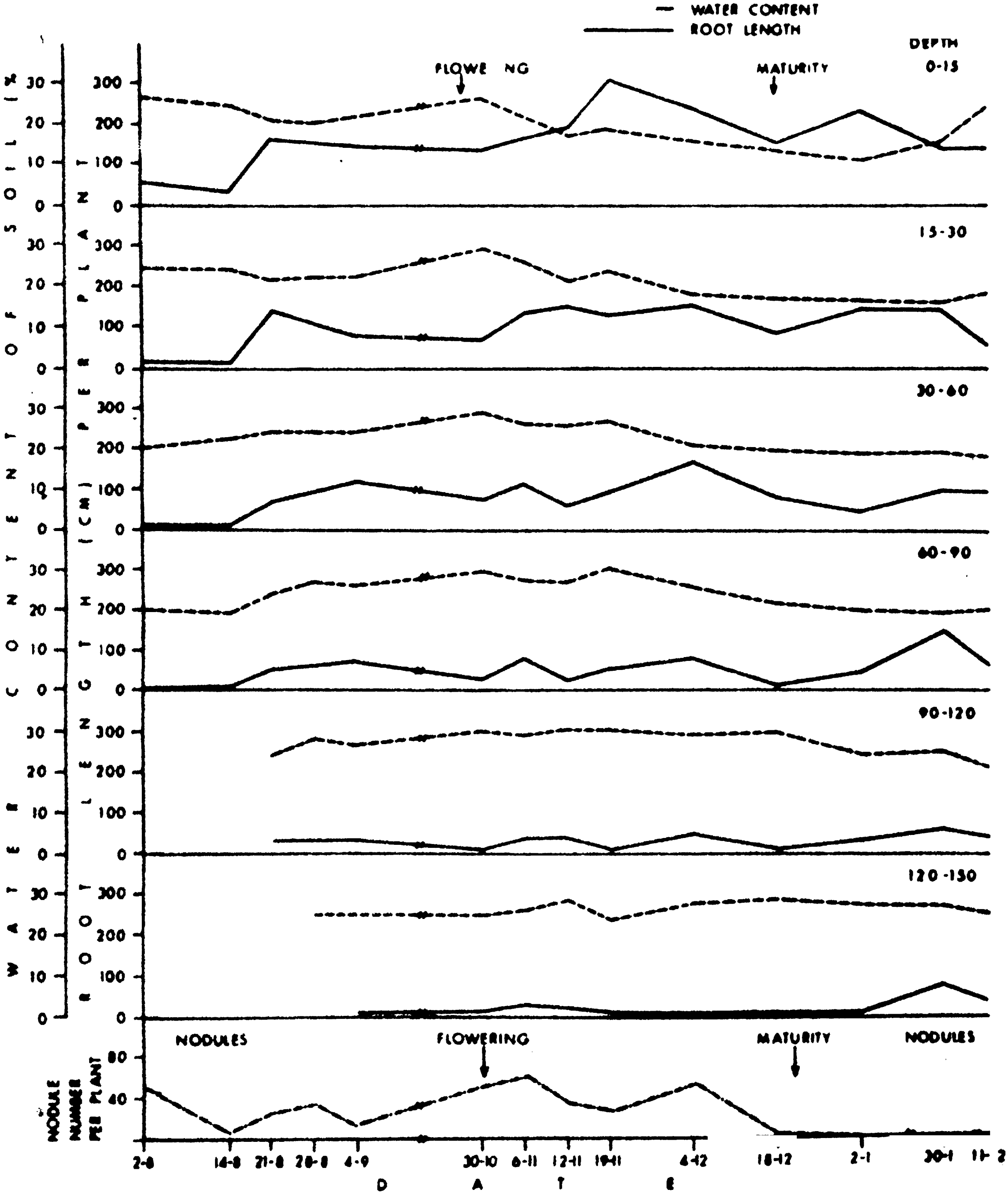
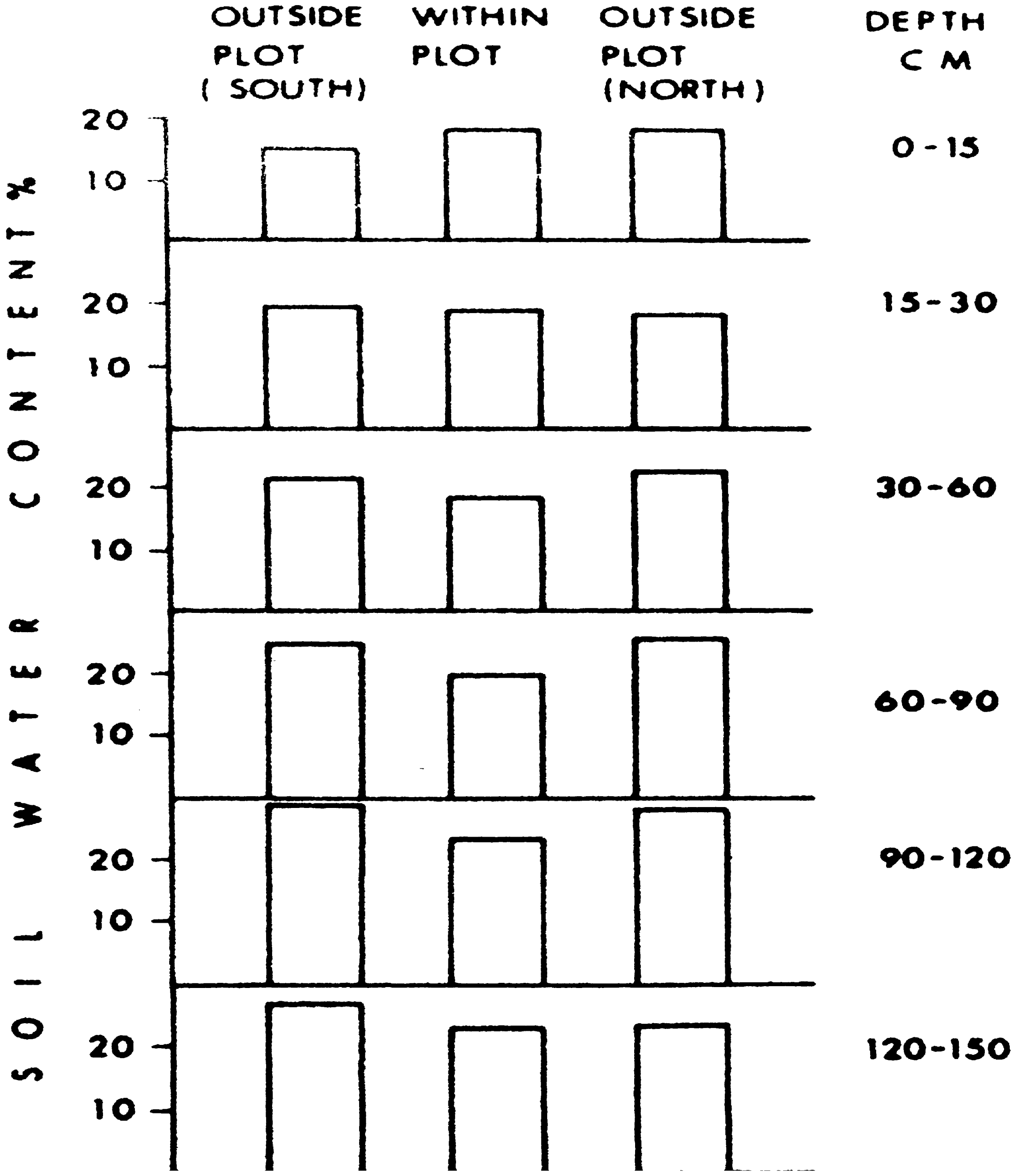


FIGURE 17

WATER CONTENT OF SOIL AT DIFFERENT DEPTHS WITHIN AND 1.5 m OUTSIDE PLOT OF ICRISAT-I ON 11-2-75



2. NODULES

Results and Discussion

Nodulation was observed within 10 days of germination on all five cultivars in the field. Nodule growth and development in red soil and black soil followed a very different pattern. In the red soil elongated, occasionally branching nodules developed and continued to grow to a large size ($>$ 1 cm in length). In the black soil relatively small, spherical nodules were found and degenerating nodules were frequently observed, suggesting that the life-span of these nodules was relatively short and that new nodules were initiated and older nodules died throughout the growth of the plants.

Regular observations of nodule numbers were made only in the black soil on cvs Pusa Ageti and ST-1. The average number of nodules per plant (i.e. in the soil core) at different dates is shown in Figs. 15 and 16. Unfortunately it is difficult to know to what extent the fluctuations in nodule numbers reflect sampling errors or real fluctuations. The plant-to-plant variation was high, and the core method employed would have meant that nodules on the larger lateral roots were missed. The small size and mass of the nodules meant that accurate dry weights could not be taken, owing to the high error caused by adhering soil particles.

In spite of these disadvantages, two fairly clear conclusions could be drawn. One is that the nodule numbers decline before the period of maturity, though in ST-1 at least, by no means immediately after flowering began. The other clear-cut finding was that nodules are not confined to the surface 15 cm or so of the root system. Small nodules were not uncommon in the 120-150 cm zone and were sometimes found even below 150 cm. Some representative data are shown in Fig. 18. Although the majority of the nodules were found in the first 30 cm up to 35% were present in the lower zones.

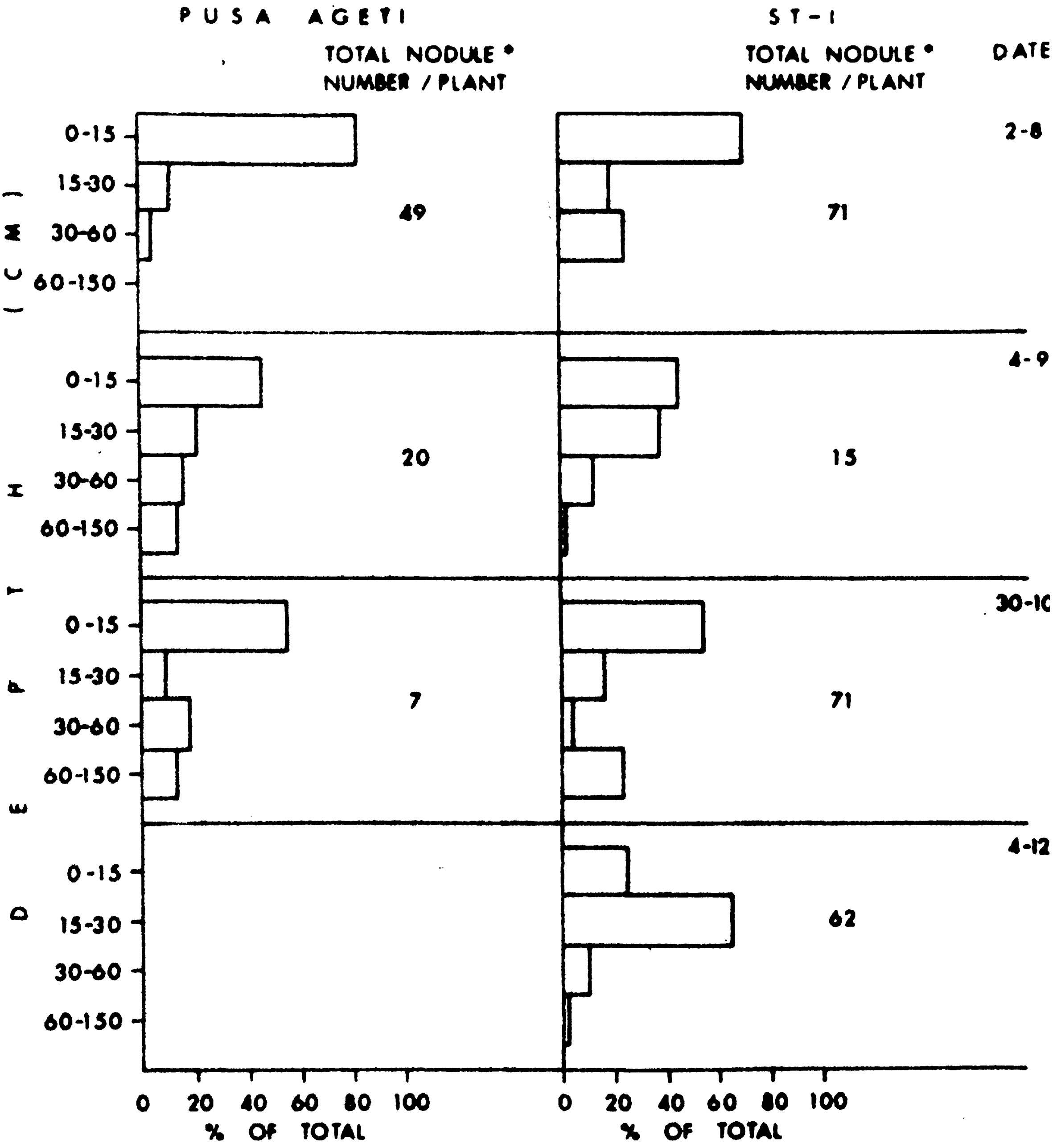
In plants where pod development was presented by flower removal, no clear evidence was obtained that the removal of competition by the developing pods enhanced nodule development. On the contrary, the nodule numbers progressively declined both in controls and in plants from which flowers had been removed (Table 13). In chickpeas also, although the continuous removal of flowers led to enhanced nodule development at first, the nodules thereafter declined (see Chickpea Physiology Report Chapter II). These results indicate that competition from developing pods for photoassimilates cannot be the only reason for the regression of nodules during the reproductive phase.

Table'13. Nodule numbers (average per plant) after the onset of flowering.

Cultivars	Date flowering began.	Sampling date.	Nodule numbers per plant	
			Control	Continuous flower removal
Pusa Ageti	12-9-74	4-9-74	20	
		30-10-74	8	13
		19-11-74	0	6
ICRISAT-1	21-10-74	12-12-74	8	15
		26-12-74	19	13
		30-1-75	1	0
ST-1	21-10-74	30-10-74	52	
		12-11-74	38	62
		19-11-74	30	22
		4-12-74	57	31
		2-1-75	0	6
HY-3C	21-11-74	9-1-75	0	1
		16-1-75	0	0
		23-1-75	0	1

FIGURE 18

PERCENTAGE OF NODULES AT DIFFERENT DEPTHS



* NODULE NUMBER WEIGHTED ACCORDING TO NODULE SIZE (SMALL NODULES COUNTED AS ONE; NODULES 10-20 MM^2 COUNTED AS 2; > 20 MM^2 AS 3) RESULTS SHOWN ARE AVERAGES FROM THREE PLANTS

CHAPTER III

Effects of Seed Size on the Growth of Seedlings

Introduction

There are considerable varietal differences in seed size in pigeonpeas. Hundred seed weights range from about 5 to 22 gms. There are also variations in seed size within the seed lots of a given cultivar. Some preliminary experiments were carried out to investigate the effects of seed size on seedling growth.

Methods

Seeds were sown in plant-pots containing sand to which a small amount of soil taken from a field in which pigeonpeas were growing had been added to serve as a source of Rhizobial inoculum. They were grown outdoors and watered regularly. Those grown in darkness were placed under cardboard boxes in a shaded place. For experiments involving half seeds, seeds were soaked in water overnight and then bisected with a scalpel in such a way that the cotyledons were cut, but not the plumule or radical. Controls were similarly soaked but not bisected. At the timeof harvest the roots of the plants were carefully washed out of the pots with a jet of water. The seedlings were measured and separated into seeds (cotyledons plus testa) roots, stems and leaves for weighing. Ten plants were taken per sample. The first experiment was carried out by MissCarol Green during her vacation from High School.

Results

(i) In the first experiment, the growth of seedlings of ICRISAT-1 (100 seed weight = 9.5 g) and HY-3C (100 seed weight = 18.5 g) was compared in both light and darkness. The seedlings of the larger seeded cultivar grew faster in both light and darkness, roots and shoots were longer and more nodules developed, although the smaller seeded variety had more nodules at first in both light and darkness (Table 14). In darkness the seedlings of both cultivars had a higher shoot : root ratio.

(ii) A study of the effects of seed size within a cultivar was made by selecting large and small seeds of cv ICRISAT-1: again it was found that the larger seeds produced larger seedlings, which grew faster.

(iii) In a third experiment seedlings of cvs T-21 (100 seed weight = 6.5 g) and HY-3C (100 seed weight = 18.5 g) were grown from whole and from half seeds. Again the larger seeded variety produced larger seedlings than the smaller seeded variety, with more and larger roots, larger shoots, larger leaf area and more nodules. Within each variety, the half seeds gave rise to seedlings that were approximately half the size and weight, with approximately half the leaf area, of controls. Data for dry weights and nodule numbers are shown in Fig. 19. There was a tendency for the seedlings from half seeds to form more nodules at first, but soon this initial advantage was lost and the nodules followed the same trend as the other parameters measured, with more nodules on the larger seedlings which had developed from the larger seeds.

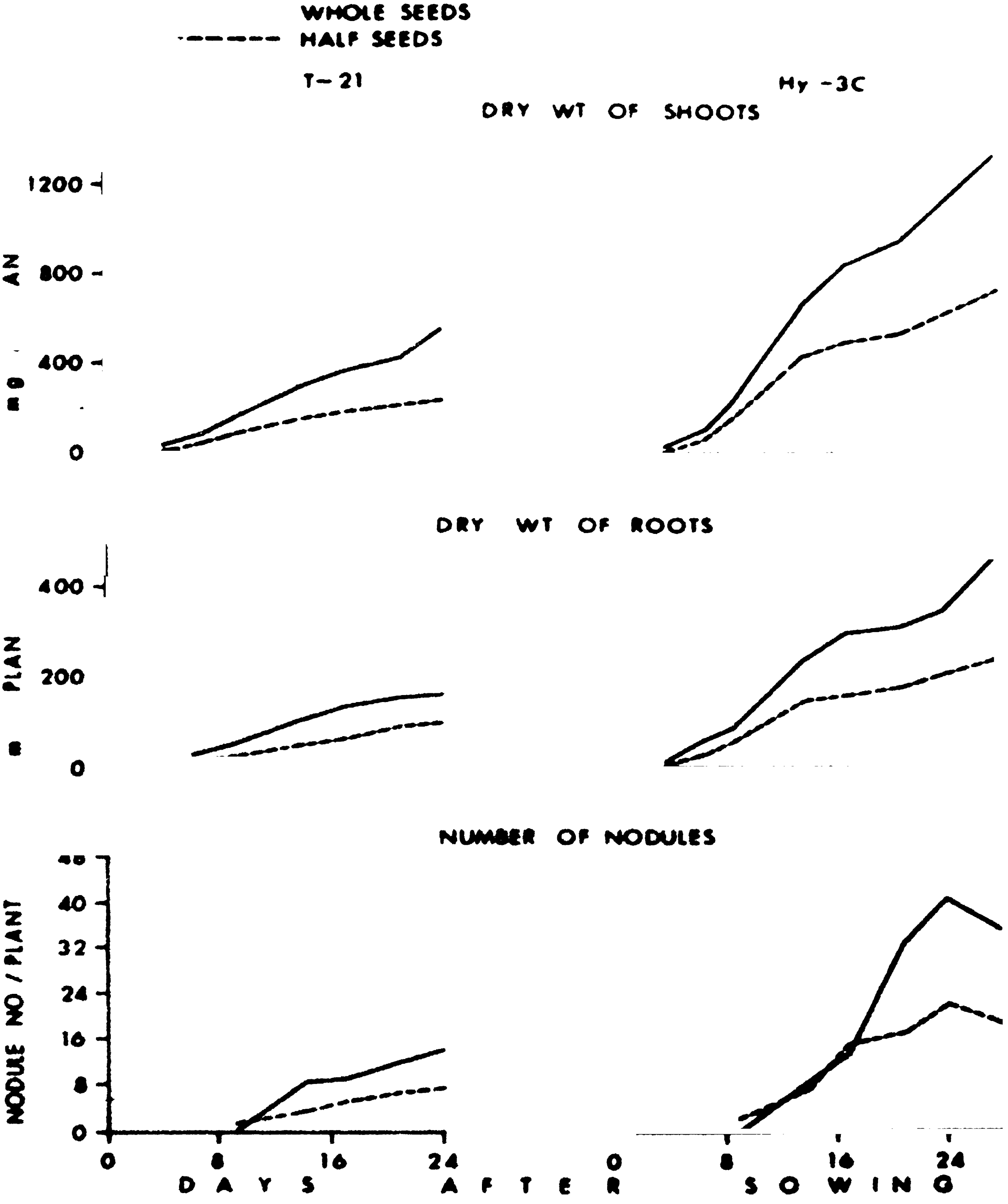
Discussion

The relatively large size of pigeonpea seeds with relatively large supplies of reserve materials enables them to make an important contribution to the early growth of the seedlings. Seedlings continued to grow in darkness at the expense of the reserve materials in the cotyledons for about two weeks (Table 14).

Table 14. Dry weights of seeds, roots and shoots and nodule numbers of seedlings of ICRISAT-1 and HY-3C - Average results on per plant basis.

Day	ICRISAT-1 Dry weight (mg) Seeds	ICRISAT-1 Dry weight (mg) Roots	ICRISAT-1 Dry weight (mg) Shoots	ICRISAT-1 Nodule number	HY-3C Dry weight (mg) Seeds	HY-3C Dry weight (mg) Roots	HY-3C Dry weight (mg) Shoots	HY-3C Nodule number
				LIGHT				
0	95	-	-	0	185	-	-	-
4	84	3	6	0	158	5	6	0
7	55	5	17	0	119	13	20	0
11	22	12	49	5.1	37	16	61	2.2
14	21	15	63	4.0	28	18	99	3.1
18	15	6	91	9.4	24	28	120	4.4
21	16	37	144	14.7	-	67	295	19.9
				DARK				
0	95	-	-	-	185	-	-	-
4	87	2	4	0	159	4	9	0
7	64	5	17	0	114	9	29	0
11	30	6	31	6.0	38	11	59	2.6
14	11	7	38	6.4	17	10	63	4.5
18	9	24	29	6.5	7	12	58	5.1
21	11	3	19	5.0	-	12	52	10.0

FIGURE 19
DEVELOPMENT OF SEEDLINGS FROM WHOLE AND HALF SEEDS OF CVS T-21 AND Hy-3C



The weight of the seedlings produced was roughly proportional to the weight of the seeds either when cultivars were compared (HY-3C with ICRISAT-1 and T-21) or large and small seeds of the same cultivar (ICRISAT-1) or whole and half seeds of the same cultivars (HY-3C and T-21). The simplest explanation of these findings is that the most important factor which affected seedling growth in these cultivars was the amount of reserve material in the seeds. The comparison between whole and half seeds shows that larger seeds were not giving rise to larger seedlings simply because they had larger embryos.

The slight initial advantage in nodulation of the seedlings developing from smaller seeds or half seeds may be explicable in terms of a lower internal supply of nitrogenous compounds. It is known that nodulation can be inhibited by external sources of nitrogen; internal nitrogen supplies from the cotyledonary reserves may have the same effect. However these initial effects were soon superceded and, later on, nodulation was roughly proportional to seedling size: the faster growing seedlings with more leaf area had more nodules.

Similar effects of seed size on seedling growth are also observable in the field. In the growth analysis, the ranking of seedling weight, leaf area and nodule numbers closely followed the ranking of seed size of the five varieties for at least 6 weeks.

The selection of larger seeds by seed-grading for planting in the field is likely to give larger seedlings; but whether or not higher yields will be obtained as a consequence remains to be seen.

CHAPTER IV

Flower Drop, Pod Set and Pod Development

Introduction

Pigeonpeas generally flower profusely, but the majority of the flowers simply drop off the plant and wither on the ground. Of the young pods which develop from the remaining flowers a considerable number abort and fall off. And even before they develop into flowers, many floral buds are lost.

The pattern of flowering, flower-drop and pod-set was studied in the same five cultivars used in our other investigations. In addition, the course of pod and seed development, once pod-set had taken place, was investigated.

Methods

The pattern of pod set and flower drop could conveniently be studied by examining the plants at the time of maturity. The positions at which pods had developed were simply indicated by the presence of pods; the positions at which flowers, buds or young pods had abscinded were indicated by scars. 30-80 branches were used in each sample, and for the study of racemes 75-200 were taken.

The time-sequence of flowering and pod development was given by the data collected in non-destructive growth analysis.

The net effect of seed position within the pod on seed development was studied by collecting pods at maturity and separating the seeds from all pods of a given category (e.g. 4-seeded pods) in sequence, so all the first, second, third and fourth seeds were collected together.

For the study of pod development, a large number of flowers which were open on a given day were tagged and pods which developed from these flowers were sampled at approximately weekly intervals. They were separated into pedicels, seeds and pod walls. The lengths of the pedicels and pod walls were measured, and the components were weighed separately, before and after drying.

The Nitrogen content of ground-up seed samples was determined by the micro-Kheldahl method. The values were multiplied by 6.25 to give the protein percentage.

Results

1. Pattern of flowering and pod set

(a) In the determinate cultivar Pusa Ageti, flowering and pod set began and continued more or less synchronously in axillary and terminal inflorescences. In the indeterminate cvs T-21, ST-1 and ICRISAT-1 flowering and pod set began on the lower & middle branches and later spread to the (younger) upper branches. In HY-3C flowering and pod set were more or less synchronous on upper and lower branches.

On the given branch of cvs T-21, ST-1 and ICRISAT-1 flowering and pod set progressed acropetally, and growth of the branches and the consequent production of new flowering nodes contained for some time after flowering began. In HY-3C the acropetal progression of flowering and pod-set was less clear-cut, the whole process was condensed into a shorter period of time, and the cessation of vegetative growth was more rapid than in the other indeterminate varieties. In all varieties the main stem behaved in a similar way to the branches. Some representation results for individual branches of ICRISAT-1 and HY-3C are shown in Table 15.

Table 15. Pods set at different flowering nodes (numbered from the most basal flowering node on the branch) on individual branches of ICRISAT-1 & HY-3C plants at different times.

ICRISAT-1 (Plant B-2, Black Soil)

POD NO/NODE

Date	BRANCH 5 Node No. 1	2	3	4	5	6	7	8	9	10	11	12	13	14
23/10	0	0	0	0	0	0	0	0	0	0				
29/10	1	1	1	0	0	0	0	0	0	0	0	0		
5/11	2	3	1	1	1	3	0	0	0	0	0	0	0	
12/11	2	3	1	1	1	4	2	0	0	0	0	0	0	
19/11	2	3	1	3	1	5	3	0	2	0	1	0	0	
26/11	2	3	1	2	1	5	3	0	2	1	0	2	1	0
17/12	1	3	1	2	1	4	3	0	2	0	0	1	0	0
	BRANCH 6													
29/10	0	0	0	0	0	0	0	0						
5/11	1	1	2	0	0	0	0	0	0					
12/11	1	2	2	0	0	0	0	0	0	0				
19/11	1	2	4	0	2	3	1	1	0	0				
26/11	1	2	4	0	2	3	1	1	0	0				
17/12	1	2	4	0	2	3	1	1	0	0				

HY-3C (Plant B-1, Black soil)

Date	1	2	3	4	5	6
	BRANCH 5					
3/12	0	0	0			
10/12	2	0	0	0	0	0
17/12	3	4	2	3	1	0
7/1	3	1	2	1	0	0
	BRANCH 6					
3/12	0	0	0			
10/12	6	2	3	3	2	0
17/12	6	2	2	3	2	0
7/1	1	1	1	3	2	0

Within a given inflorescence, flowering began at the lower nodes of the raceme and progressed acropetally. The same pattern was observed ih all varieties.

Some of the pods which started developing aborted. This phenomenon was particularly pronounced in HY-3C (see Table 15).

(b) The distribution of pods which both set and developed was studied at the time of maturity.

Branchwise: This was studied by pooling all branches and inflorescences subtended by the first 12 nodes of the main stem, then the second 12 nodes and so on. The total number of pods, seed number per pod and 100 seed weights are shown in Fig. 20 for cvs ST-1 and ICRISAT-1 grown on black soil (see also Fig. 29). Comparable results were obtained with plants grown on red soil. The lower and middle branches (which were longer and older) bore more pods than the upper ones, but there were no consistent differences between upper and lower branches in seed number per pod or 100 seed weight.

Nodewise within the branches: The average pod number per node declined acropetally in all 4 indeterminate varieties (Figs. 21-3). However, the seed number per pod and hundred seed weight remained more or less the same from node to node in cvs T-21, ST-1 and ICRISAT-1 (Figs.21-3). These parameters were not measured in HY-3C.

Nodewise within the racemes there was also an acropetal decline in the number of pods. In racemes from the lower parts of the branches

FIGURE 20 DISTRIBUTION OF YIELD COMPONENTS BRANCHWISE : CVS ST-I AND ICRISAT-I

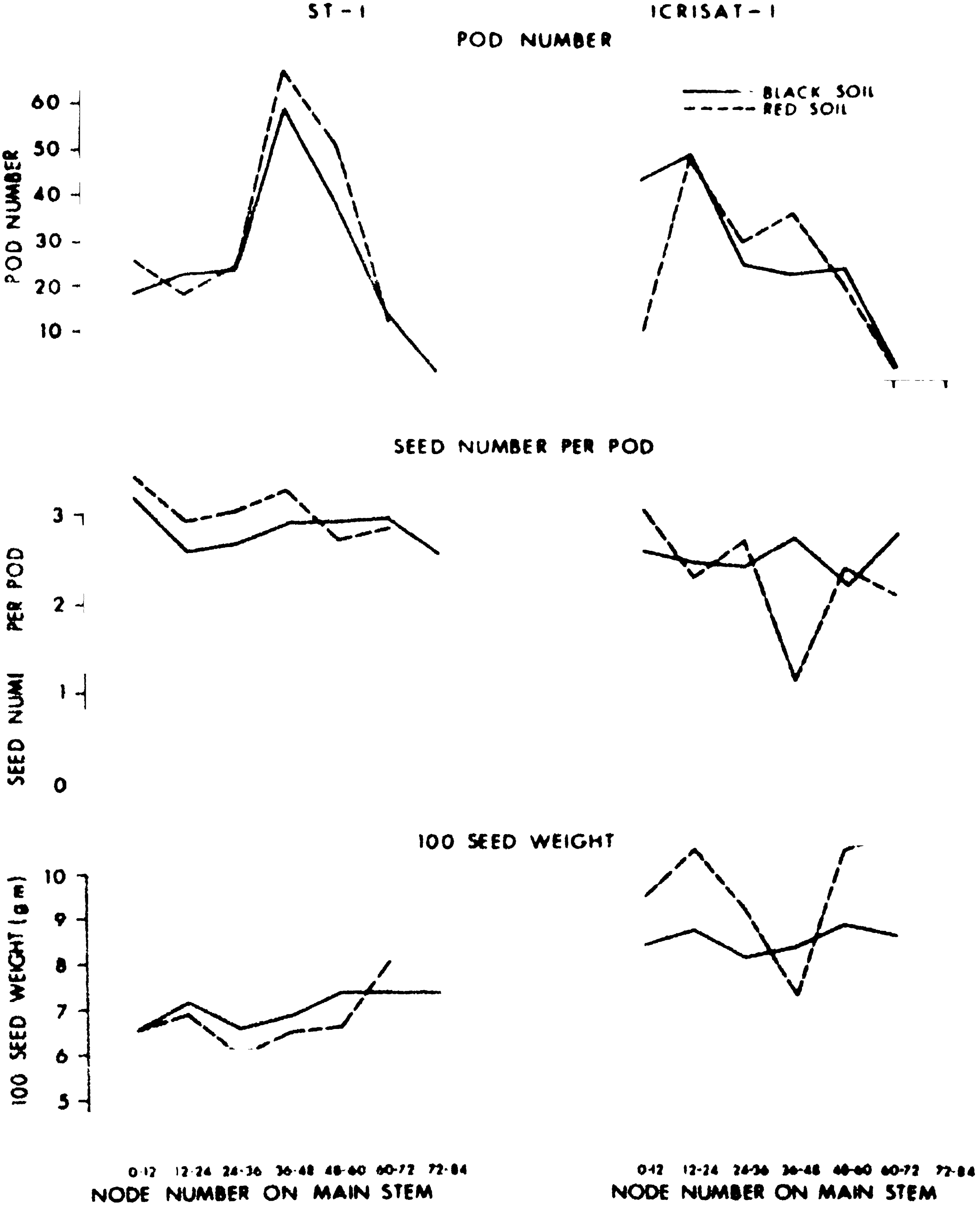


FIGURE 21 NODEWISE ANALYSIS OF YIELD WITHIN BRANCHES: CV. ICRISAT-I

(AVERAGE OF 30 BRANCHES)

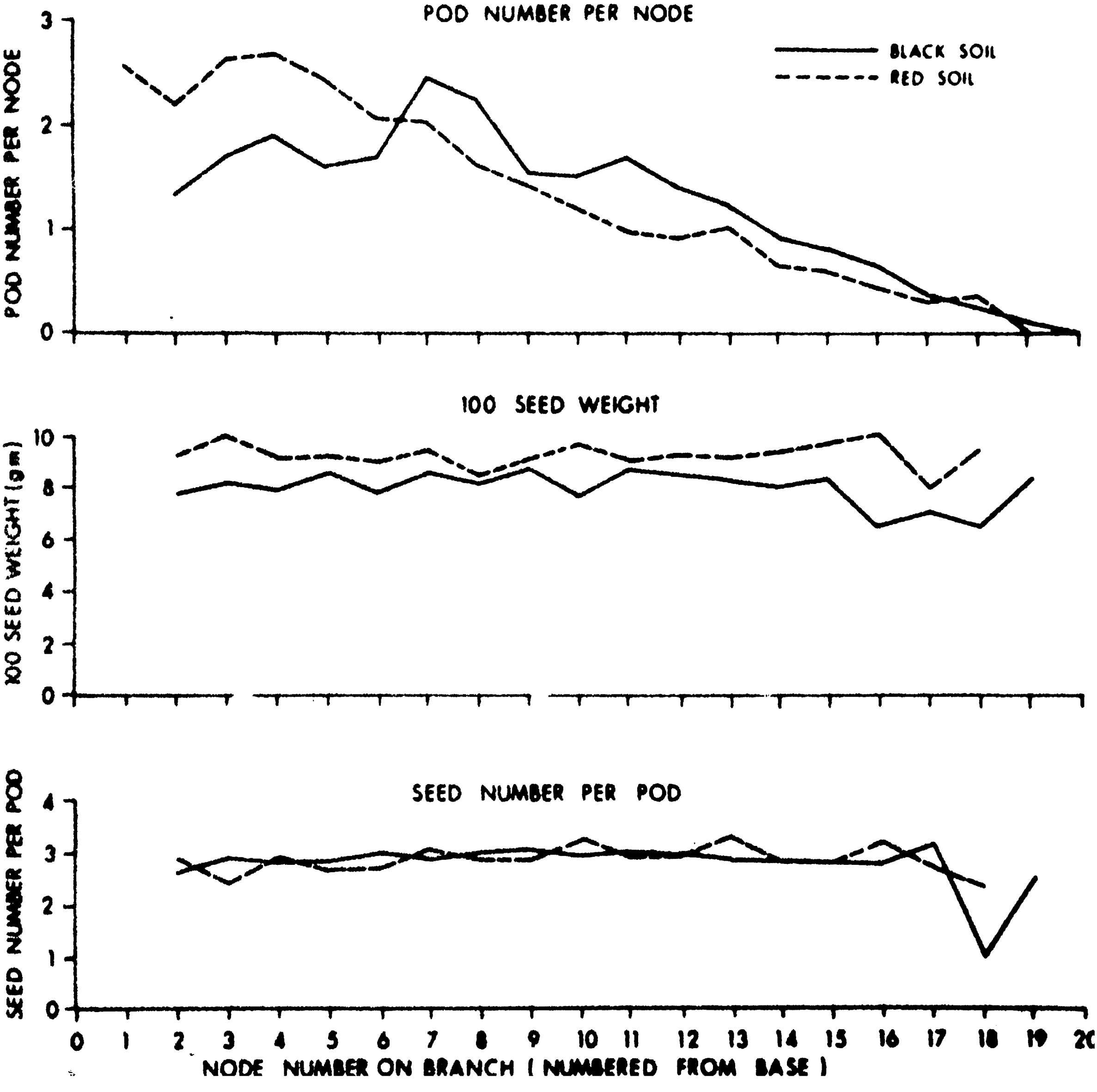


FIGURE 22 NODEWISE ANALYSIS OF YIELD WITHIN BRANCHES

ST-1 (AVERAGE OF 30 BRANCHES)

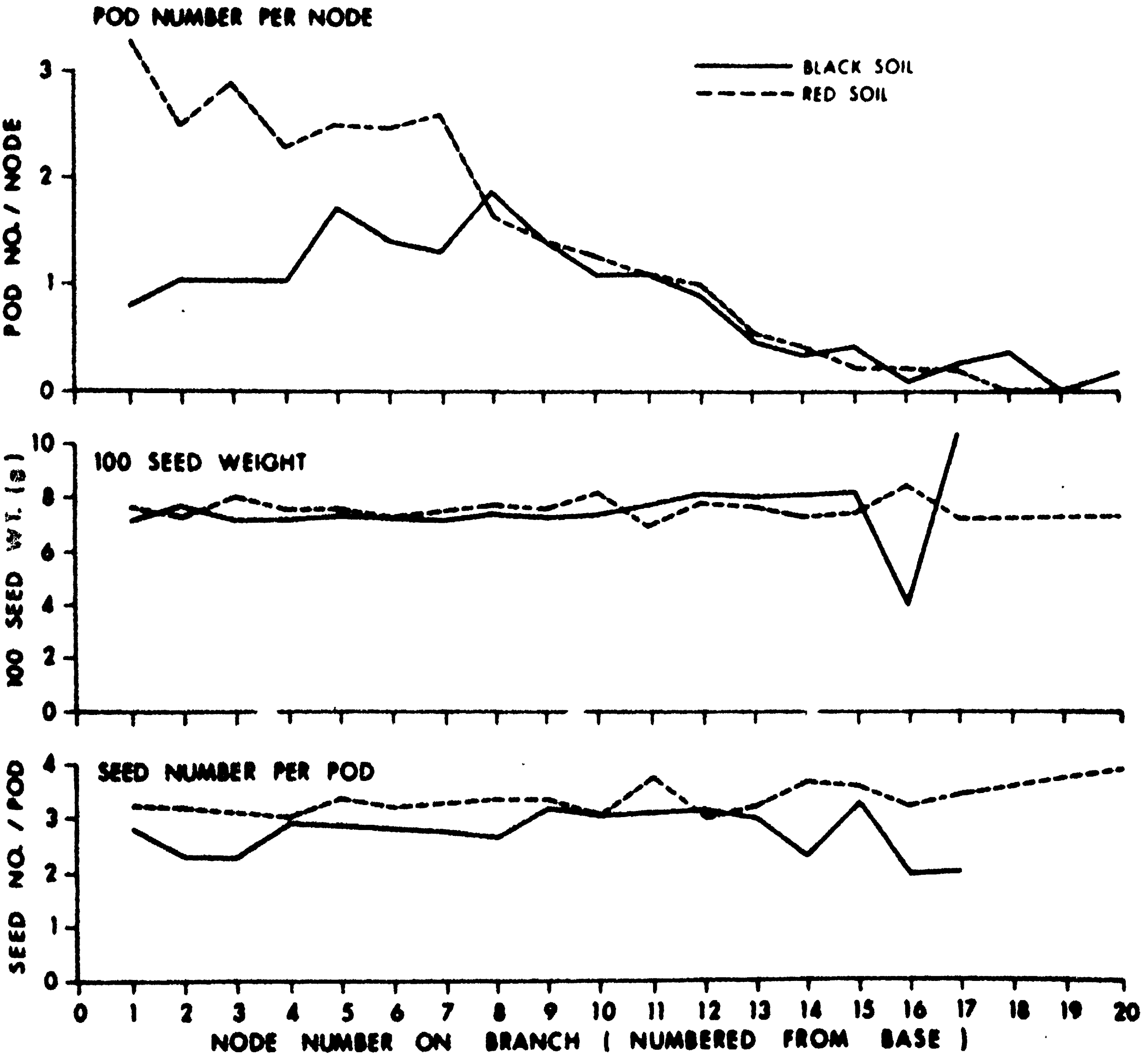
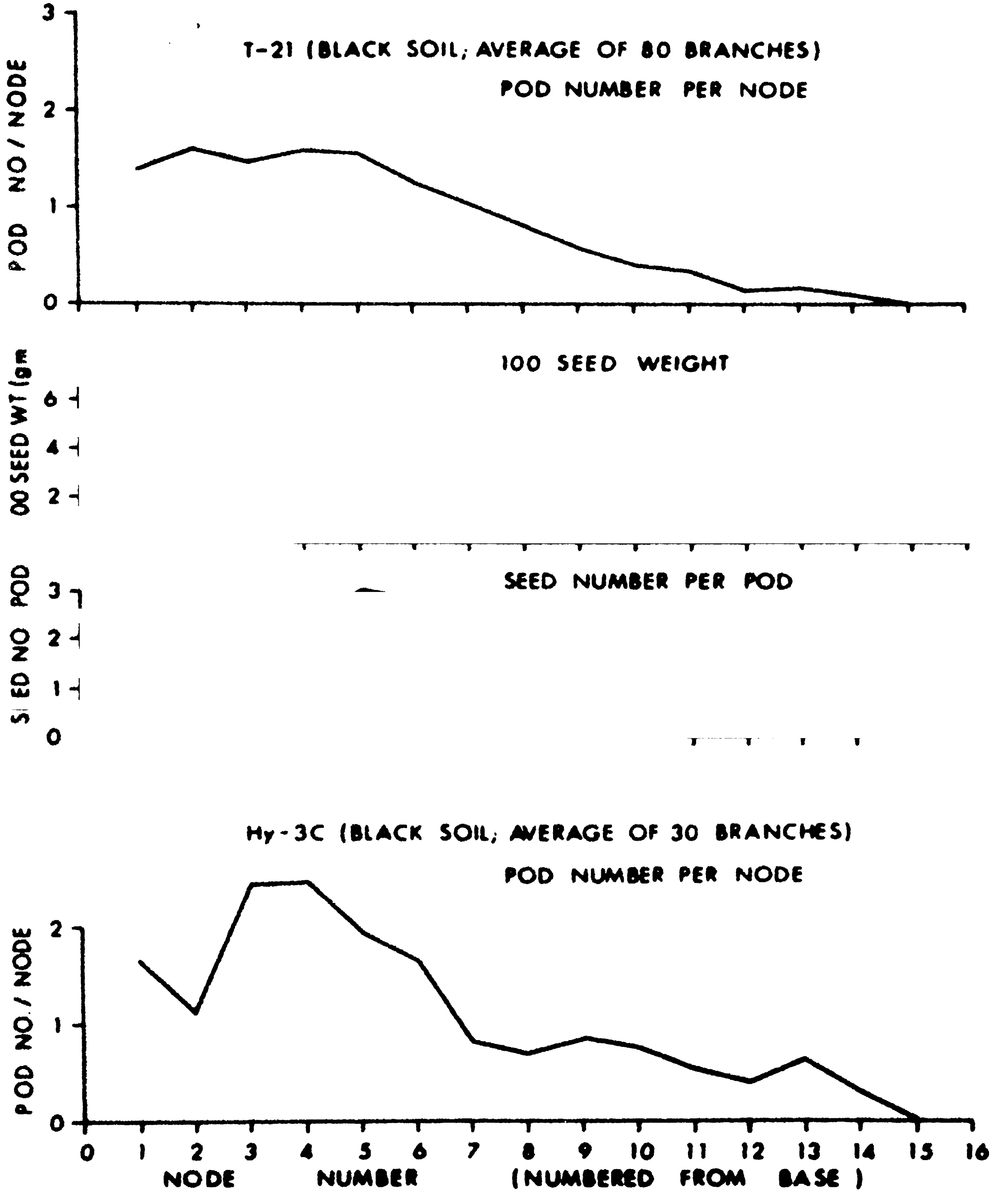


FIGURE 23
NODEWISE ANALYSIS OF YIELD WITHIN BRANCHES



of ST-1 and ICRISAT-1 and also in the terminal inflorescences of the determinate cv Pusa Ageti the maximum pod number was found just above the basal end of the raceme; in racemes from the upper part of the branches of ST-1, ICRISAT-1 the maximum pod number occurred on the most basal node. The same pattern was found in T-21 (racemes from both upper and lower parts of branches mixed) and HY-3C (Fig.24).

(c) Young developing pods were either completely removed, or partially removed by bisecting them transversely, from the lowest nodes of racemes of ICRISAT-1. After this treatment a higher proportion of flowers at more apical nodes within the raceme gave rise to pods which were retained and matured (Fig. 25).

2. Pod and Seed Development:

(a) In all three cultivars studied, ST-1, ICRISAT-1 and HY-3C, a similar pattern of pod wall and seed development was found (Figs.26 & 27). The pod wall grew rapidly at first and reached its final size while the seeds were still at an early stage of their development. Thereafter the pod wall began to dry while the seeds continued their development. The seeds themselves began to lose fresh weight while their dry weight was still increasing.

Cv HY-3C had larger pods and more and heavier seeds than the other two cultivars; in this cultivar pod development took place at a higher rate and also over a longer period (Fig. 27).

The nitrogen percentage of pod wall and seeds was measured in cv ICRISAT-1. The nitrogen content of pod walls fell as they

FIGURE 24 POD DISTRIBUTION ON RACEMES

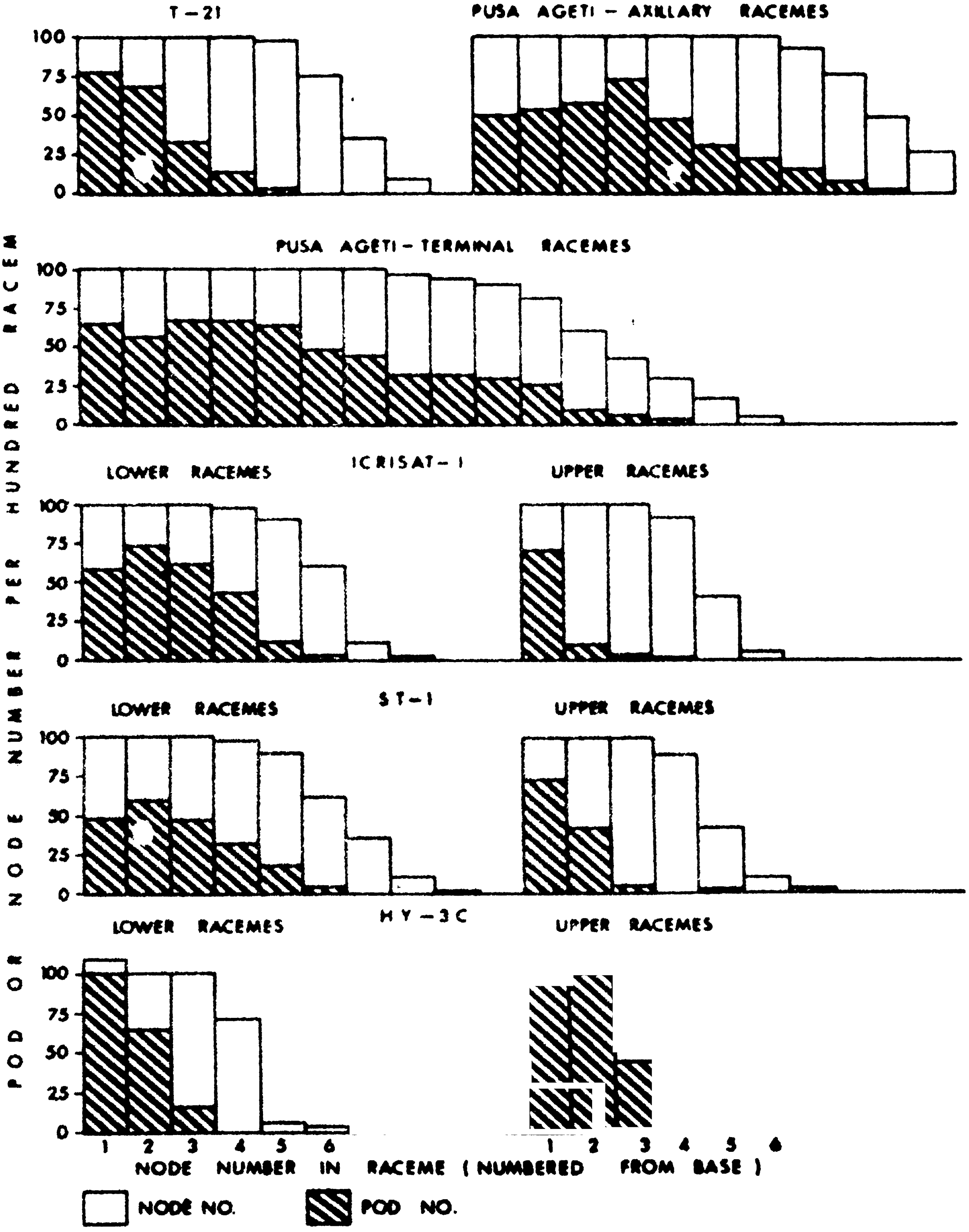


FIGURE 25

POD DISTRIBUTION ON RACEMES OF ICRISAT-1 AFTER PARTIAL OR COMPLETE REMOVAL OF YOUNG PODS FROM BASAL NODE

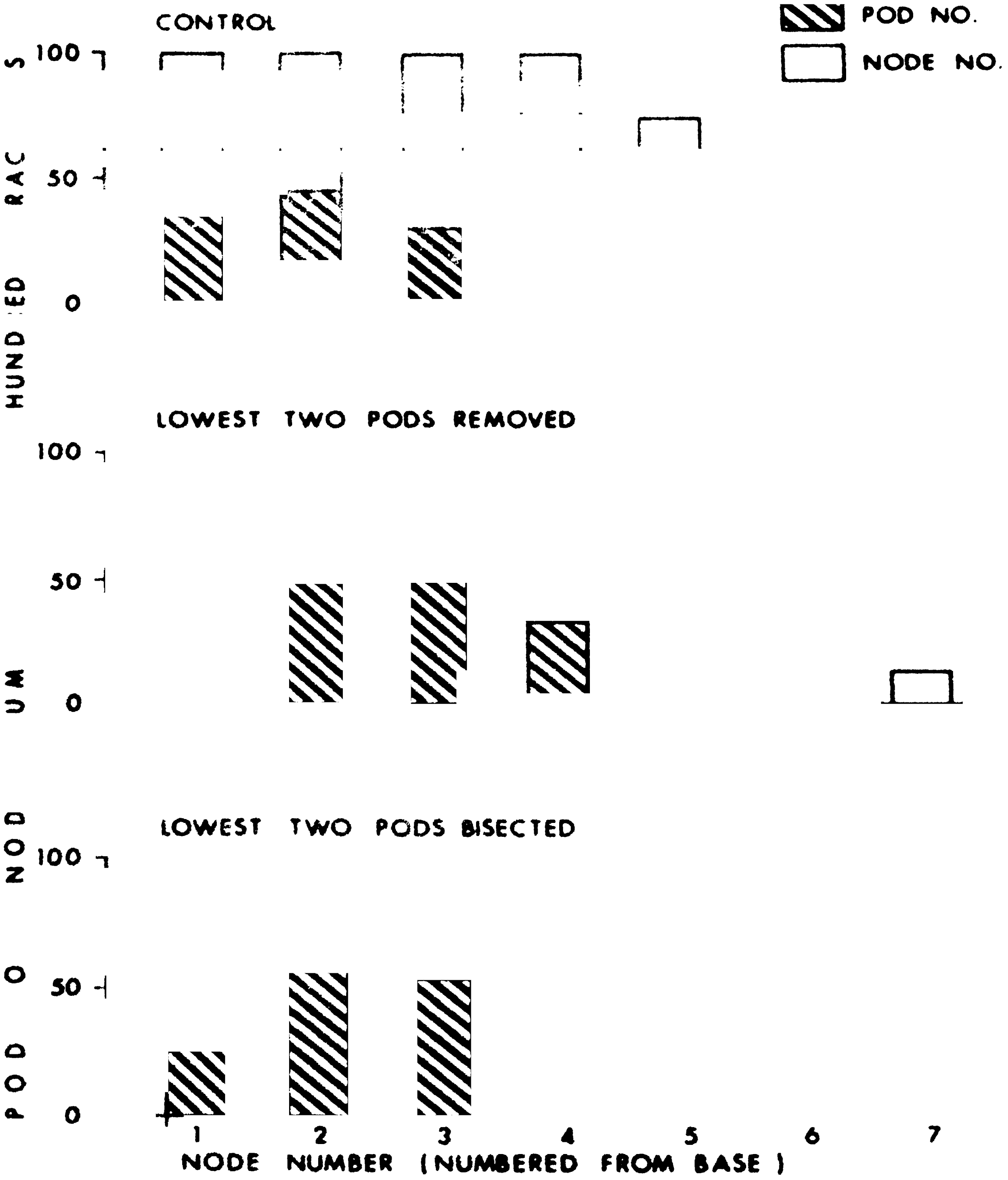


FIGURE 26. POD WALL AND SEED DEVELOPMENT

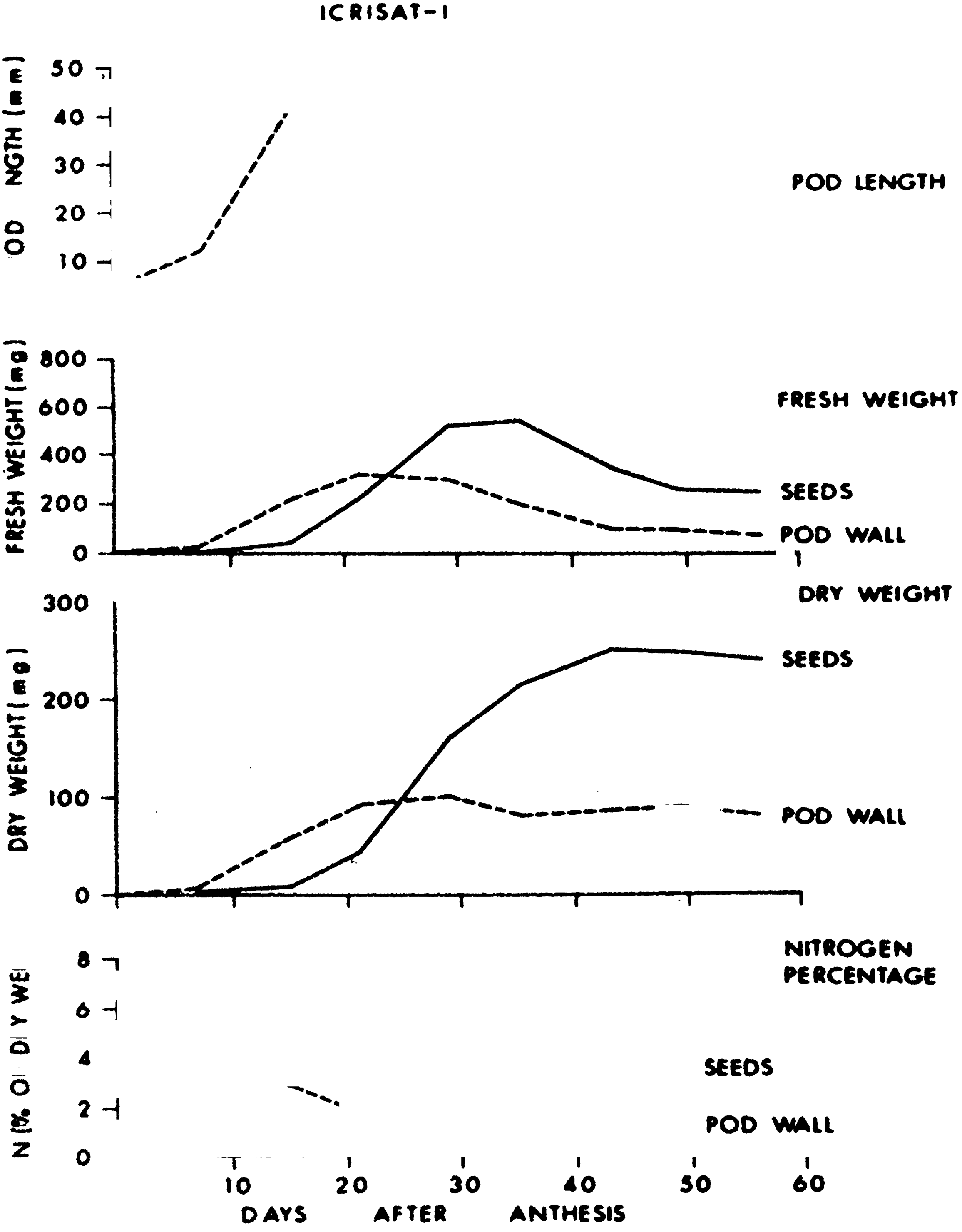
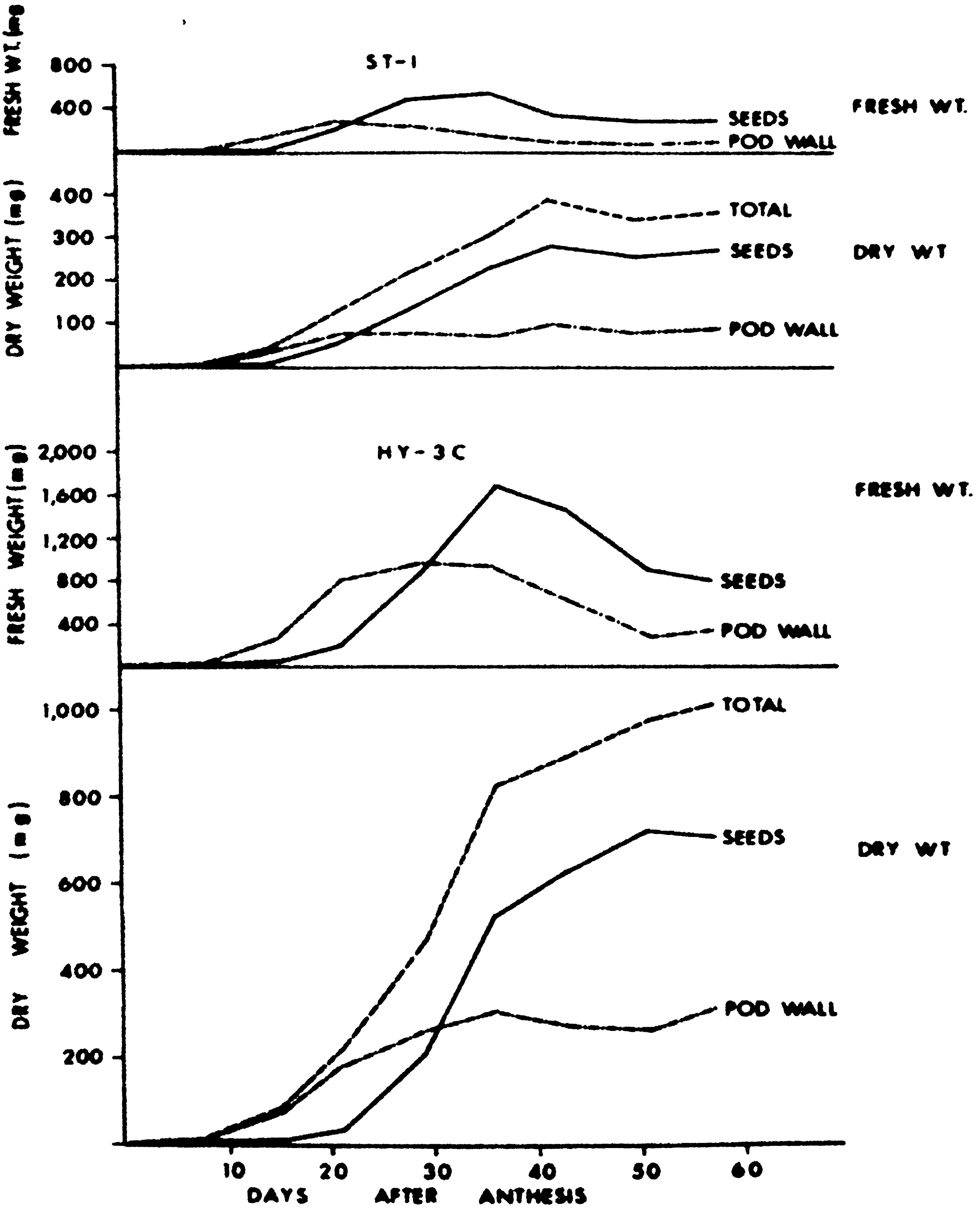


FIGURE 27
POD WALL AND SEED DEVELOPMENT CVS ST-1 AND HY-3C



developed and then remained fairly steady at about 1%. The percentage of nitrogen in the developing seeds declined until the later stages of development when it remained more or less constant (Fig. 26).

(b) An effect of seed position within the pod on seed development was observed in all cultivars studied. The first (i.e. most proximal) seeds were smaller than the seeds in the middle of the pod, and the last seeds also tended to be smaller (Table 16). However there were no consistent differences in the protein percentages of the seeds taken from different parts of the pods (Table 16).

Discussion

In the cultivars studied here the great majority of the flowers dropped off. Only 10-20% gave rise to pods. If all the flowers had developed into pods, could the yields have been increased proportionately, i.e., five-to ten-fold? The answer to this question is : no. The harvest indices of these cultivars lay in the range 20-34% (see Table 8). A five-to ten-fold increase in seed production would give harvest indices of over 100%, which is impossible since the seed yield cannot exceed the total dry matter produced by the plants. It is therefore inevitable that the only a relatively small percentage of the numerous flowers could give rise to mature pods of normal size.

Table 16. Weight and protein content of seeds at different positions within the pods. (Results are the average of between 40-100 pods in each category).

Cvs	Year harvested	Soil type	Seed No/pod	100 seed wt, & % protein content(in brackets) Seed position (numbered from basal, i.e. proximal end of pod) 1	2	3	4	5	6
ICRISAT-2526	1974	Black	4	7.09 (17.6)	8.02 (17.9)	7.93 (17.1)	7.82 (18.5)		
	"	"	3	7.88 (17.9)	8.35 (18.7)	8.19 (18.5)			
ICRISAT-4613	"	"	4	9.10 (18.6)	9.39 (19.2)	9.25 (18.6)	8.87 (19.1)		
ICRISAT-2518	"	"	4	8.62 (18.2)	9.32 (18.9)	8.84 (18.6)	8.88 (19.1)		
	"	"	3	9.35 (17.3)	9.52 (18.4)	9.54 (17.7)			
ICRISAT-4665	"	"	4	7.00 (18.3)	7.57 (18.3)	7.46 (17.8)	7.06 (17.7)		
	"	"	3	7.30 (18.1)	8.03 (18.0)	7.19 (18.8)			
ICRISAT-25	"	"	4	10.03 (20.0)	11.32 (20.6)	11.30 (20.2)	10.68 (20.3)		
			3	10.22 (20.6)	10.89 (21.0)	10.00 (19.8)			
ICRISAT-1	"	"	4	9.25 (21.6)	10.20 (20.7)	10.28 (21.3)	9.88 (21.5)		
			3	10.05 (20.4)	10.60 (20.1)	10.20 (20.4)			
ICRISAT-1	1975	Red	4	10.05	11.10	11.07	10.95		
			3	(10.13	10.56	10.60			
			2	11.22	11.33				
ST-1	"	"	4	8.12	8.45	8.37	8.15		
			3	8.97	9.53	9.37			
			2	8.44	8.50				
HY-3C	"	"	6	17.42	18.35	18.50	18.54	18.42	17.50
			5	16.17	16.69	16.65	16.82	16.50	
			4	16.44	16.78	17.00	16.96		
			3	16.25	16.87	16.56			

In the indeterminate cultivars the progress of flowering was acropetal. The lower branches began flowering before the upper branches; within a branch the lower part of the branch began flowering before the upper part; and within an inflorescence, in all cultivars, the lower nodes began flowering before the upper nodes. A higher proportion of the earlier-formed, more basal, flowers formed pods; there was an acropetal decrease of pod set from lower branches to upper branches (Fig. 20), from lower nodes within the branch to upper node (Figs. 21-23) and from the lower nodes of the inflorescence to the upper nodes (Fig. 24).

From a practical point of view this information indicates that in making crosses for breeding purposes, a higher rate of success could be achieved by using the earlier-formed, more basal flowers. From a theoretical point of view, the acropetal decline in pod set suggests that pods developing from the earlier-formed flowers tend to inhibit the development of pods from later formed flowers. This suggestion is supported by the finding that the partial or complete removal of the earlier-formed pods from a raceme leads to a compensatory increase in pod-setting from later-formed flowers which would otherwise has dropped off (Fig. 25).

The simplest interpretation of this inhibition of effective pod set by already developing pods is in terms of competition for nutrients such as photoassimilates. In preliminary experiments it was found that complete defoliation of the plants led to a reduction in pod set, which is hardly surprising (see Chapter V). What is perhaps surprising is that while a reduction in the nutrient supply either by defoliation or by competition from earlier-formed pods reduces the numbers of pods which are set, it has little effect on the size of the pods or the size of the seed produced. The pods formed on lower and upper branches (Fig. 20) and lower and upper parts of the same branch (Figs. 21-23) show no consistent trend towards a reduction in either average seed number per pod or average 100 seed weight. Comparable preliminary results have obtained in the defoliation experiments: even total defoliation which led to a considerable reduction in the numbers of pods set had relatively little effect on seed number per pod or 100 seed weight (see Table 17 and Fig. 28).

It therefore seems likely that the setting and development of a pod is not unlike an "all or none" process and that whether or not this takes place depends on whether or not the nutrient (e.g. photoassimilates) supply available to the flower and/or young pod during a critical period is above or below a threshold level. The continued development on the one hand, or on the other hand the formation of an abscission layer and the abortion of the flower or young pod no doubt depend on the levels of hormones locally produced in the more or less rapidly developing ovules. But while these hormonal balances are involved in the control of pod development or pod abscission and are part of a chain of causality, hormonal factors alone cannot "explain" the phenomena.

It is possible to disturb the internal hormonal balances within the plant by spraying the plant with various chemical analogues of Hormones or anti-hormones. But too little is known about the internal hormonal balances or the distribution within the plant of the natural hormones or of the artificially applied chemicals for this to be done on any other basis than trial-and-error. Emperical investigations of this type are being carried out at a number of centres in India and sometimes stimulatory effects on pod set and yield have been reported. However, attempts to increase yield by the use of such sprays in a number of co-ordinated trials throughout the country have not so far met with any consistent success.

A point that may be of some importance emerges from the study of pod development. From Figs. 26 & 27 it can clearly be seen that the pod walls attain their final size while the seeds are still small. This pod size is therefore not determined by the final size of the seed; it may be under a more or less independent control. On the one hand some cultivars may develop pods considerably larger than the seeds which they contain; on the other hand other cultivars may produce pods too small which may physically restrain the seeds and prevent them for reaching their full potential size. This could impose a limitation on yield.

So far only the physiological aspects of flower drop, pod set and pod development have been discussed. The problem takes on an extra dimension when we consider the real world in which the plants grow.

Under conditions of variable climate (e.g. periods of bad weather) and pest attacks on either flowers or developing pods, or even on individual seeds within developing pods, would inevitably lead to a reduction in yield if the "sink" capacity of the plant were fixed. However, the continued production of flowers which can set pods if earlier formed flowers or pods are damaged or lost provides the plant with an insurance, and also means that it is able to take advantage of more favourable conditions which may arise after the onset of the reproductive period (e.g. late rains).

A more "determinate" reproductive period, confined to a shorter period of time, would necessarily result in a loss of this potential to adapt to an unpredictable environment.

The only apparent disadvantage of the excessive production of flowers is that it is wasteful of the plants' resources. A measure of this wastefulness in terms of dry weight can be obtained by calculating the proportion of the total maximum dry weight attained by the plants which is lost by flower drop. The results for the five cultivars studied are:
Pusa Ageti: 5.5%; T-21: 5.9%! ST-1: 3.9%; ICRISAT-1: 4.4%; HY-3C: 1.8%.
So the waste is small, although not negligible.

In considering whether yields could be increased by breeding for a reduction in flower drop, we have to bear in mind the potentially adverse effect on yield stability under varied conditions which might result from a reduction in the extent and duration of flowering. This is not to say that an increase in effective pod set would be impossible; in fact the indications are that pod set may be a major limiting factor for yield (see Chapter V). But even if effective pod set were to be increased by 100%, the majority of the flowers would still drop off infructuously. Breeding for increased pod set and breeding for reduced flower drop are not necessarily the same thing, since it may be possible to reduce the latter without increasing the former simply by reducing the extent and duration of flowering. So the best selection criterion for more effective pod set would be pod set itself; there may be little to be gained and perhaps something to be lost in terms of yield stability by selecting for reduced flower drop *per se*.

CHAPTER V

Effects of Defoliation

Introduction

Some investigations were made of the effects of defoliation at the time of flowering on pod set and pod development. Although these experiments were only of a preliminary nature and carried out on a small number of plants, the results were fairly consistent.

Methods

The plants were defoliated shortly after flowering began by plucking off the leaves. Thereafter new leaves which appeared were also removed at regular intervals in a manner appropriate to the defoliation treatment. The treatments were, in the first experiment : total defoliation (all leaves removed) and 50% defoliation (alternate leaves removed); and in the second experiment total defoliation (all leaves removed) and 50% defoliation by removal of alternate leaves, or by removal of all the leaves from the upper half of the plant, or by removing all the leaves from the lower half of the plant. A further defoliation treatment was the removal of the two side leaflets from all the leaves; this resulted in a reduction of the leaf area by approximately 60%. Untreated plants were used as controls.

The first experiment was conducted with late duration cultivars in the breeders' ACT-3 trial on black soil. Four plants per treatment were used. Defoliation began on 13-12-1974.

The second experiment was carried out on the early cultivars

Pusa Ageti and T-21 sown in January 1975 in grey-black soil in the RA-25 area and irrigated at regular intervals. Defoliation began on 11-3-1975. The experiment was carried out in three replicates and five plants were sampled from each replicate.

In both experiments yield and yield components were measured on individual plants at maturity. The averaged results are expressed below on a per plant basis.

Results

(i) Experiment 1

The yield per plant and average pod weight of control, totally defoliated and 50% defoliated plants of 10 cultivars are shown in Table 17.

Table 17. Effects of 50% and total defoliation at the time of flowering on yield and average weight per pod in ten late-duration cultivars.

	Yield/plant (gm)			Average weight/pod (gm)		
Cultivars	Control	50% defoliated.	Totally defoliated.	Control	50% defoliated.	Totally defoliated.
T-17	34.1	32.2	7.2	0.21	0.29	0.25
NPWR-15	35.3	37.0	6.6	0.23	0.24	0.20
AS-29	35.0	55.6	9.8	0.31	0.33	0.25
7-S	10.9	10.7	2.4	0.25	0.23	0.25
1234	9.6	6.1	0.7	0.22	0.20	0.22
GW-3	24.0	17.6	2.0	0.26	0.20	0.20
KWR-1	19.2	11.9	2.8	0.23	0.22	0.21
K-23	14.8	13.0	2.4	0.25	0.24	0.21
K-16	28.4	22.3	7.9	0.26	0.24	0.22
T-7	31.1	31.5	3.5	0.28	0.26	0.23
MEAN	21.2	23.7	4.5	0.25	0.25	0.22

Because of the small samples involved it is not possible to know whether the different responses of different cultivars are significant. But the general tendency is summarized in the average results from all cultivars : the removal of half the leaves had little or no effect on yield or pod size, while total defoliation reduced the yield by about 80% but again had little effect on pod size. A more detailed analysis of the yield components confirmed that total defoliation had only a slight effect on seed number per pod and seed weight.

(ii) Experiment 2

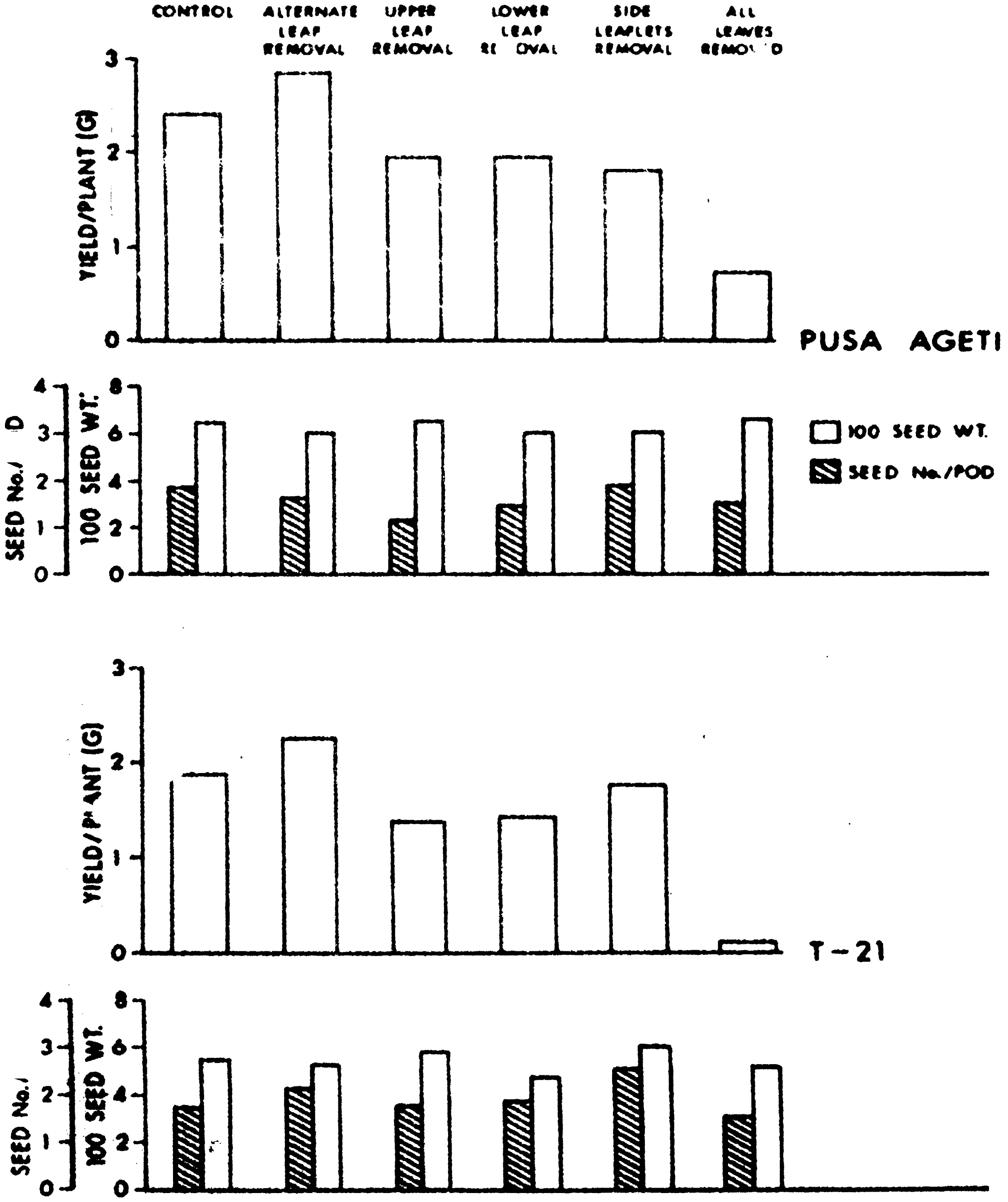
The total grain yields per plant, and the average 100 seed weight and seed numbers per pod after the various defoliation treatments are shown in Fig. 28. The results from the two cultivars are in reasonable agreement with each other and show that alternate leaf removal far from depressing yield may even have stimulated it. Removal of 50% of the leaves by removing all upper or all lower leaves gave some depression of yield compared with controls, as did the removal of side leaflets from all leaves (leading to a reduction in leaf area of about 60%). Total defoliation had a markedly depressing effect on yield, more so in T-21 than Pusa Ageti. There was, however, relatively little effect of any of these treatments on weight per pod, 100 seed weight or seed number per pod.

Discussion

Because of the small sample sizes the varietal differences in response to defoliation in Experiment 1 and the differences between

FIGURE 28

EFFECT OF DEFOLIATION AT THE TIME OF FLOWERING ON YIELD AND YIELD COMPONENTS OF CVS PUSA AGETI AND T-21 (GROWN IN THE OFF SEASON)



different methods of partial defoliation in Experiment 2 can be regarded as nothing more than indications that such differences may exist. However, the consistent results which emerge from both experiments are that the removal of half of the leaves had little or no effect on yield or yield components, while total defoliation depressed yield but again had relatively little effect on seed size or seed number per pod. This consistency is remarkable because of the very different types of plants used in the two experiments : in Experiment 1, large, fully grown, late-maturing varieties; in Experiment 2 early varieties which were even smaller than usual since they were grown in the off-season.

It is not surprising that total defoliation of the plants led to a reduction in yield but what is perhaps surprising is that there was any yield at all; in Experiment 1 the average yield was 20% of the control. The carbohydrates which supplied the developing pods must have come from reserves within the stems and/or from current photosynthesis by the stems and pod walls themselves; the nitrogen must have come from reserves in the stem and/or from root or nodules. The yield obtained after total defoliation gives some idea of the extent of these processes since the photosynthetic contribution of the leaves and also the remobilization of nitrogen from senescent leaves (see Fig. 5) are completely eliminated.

By contrast, the lack of effect of 50% defoliation indicates that the remaining 50% of the leaves were able to provide as much photosynthetic assimilate as was necessary for normal pod development; and also either directly (by remobilization from senescent leaves) or indirectly (by providing assimilates to power nitrogen fixation by nodules or uptake by roots) as much nitrogen as was needed for pod development in controls. This unexpected conclusion further suggests that neither nitrogen supply nor photosynthesis are the limiting factors for pod set and development in controls but that some other factors, internal or environmental, are involved.

The small effect of partial or even complete defoliation on seed number per pod or seed size shows that the number of pods which set and developed was either approximately equal to, or less than, the number which the plant was capable of supporting to maturity. If <u>more</u> pods had set and developed than the plant was able to supply with carbohydrates, nitrogen or other nutrients, then this supply would have run out before the pods reached maturity, resulting either in seed abortion (leading to fewer seeds per pod) and/or to a reduction in seed size.

Therefore in some way the plant must adjust the amount of pod-set to a level equal to or lower than its capacity to support the pods to maturity. The lack of effect of 50% defoliation suggests that in control plants the amount of pod-set is in fact considerably lower than the capacity of the plant to fill the pods; the plant leaves itself a large margin of safety; the result is that the only component of yield that shows a major variation in these experimental treatments is pod number per plant, and not seed number per pod or 100 seed weight. A similar conclusion is suggested by the branchwise and nodewise analyses discussed in Chapter IV; on later-formed inflorescences on upper branches or on the upper inflorescences of a given branch the pod number declined, but not the number or size of seeds within the pods. This is in striking contrast to the situation in chickpeas where later-formed flowers produce pods with fewer and smaller seeds (see Chickpea Physiology Report, Chapter I). A decline in the size and number of seeds in later-formed pods may be a good indication that what is limiting yield is the ability of the plant to supply the developing pods with nutrients (Chickpea Physiology Report, Chapter I) Conversely, a relative constancy of average seed size and number both in later-formed pods on normal plants (Figs. 20-23) and after defoliation (Table 17; Fig. 28) suggests that the limiting factor for yield is effective pod-set.

CHAPTER VI

Intercropping in relation to plant morphology and yield

Introduction

Intercropping is one of the cropping patterns adopted in the semi-arid tropics where pigeonpea may be intercropped with pearl millet, sorghum and/or other crops. Preliminary investigations were carried out on pigeonpeas intercropped with pearl millet, setaria, soyabeans and cowpeas by sampling material from trials conducted by the Farming Systems group. The effects of intercropping on the morphology and yield of pigeonpea were observed. The Pigeonpeas were shaded when grown with pearl millet or setaria, butwhen grown with cowpea and soyabean they were not shaded.

Methods

Plant samples for this investigation was collected from the intercropping experiments carried out by Farming System groups in black soil. Fifty to hundred plants of pigeonpea cvs ICRISAT-1 and HY-3C grown either with cereals (setaria, pearl millet) or with legumes (cowpea, soyabean) were sampled at the time of harvest. The main stem of each plant was divided into a series of 12-node segments, starting from the base, and the dry weight and grain yield of the branches borne on these segments were measured.

Results & Discussion

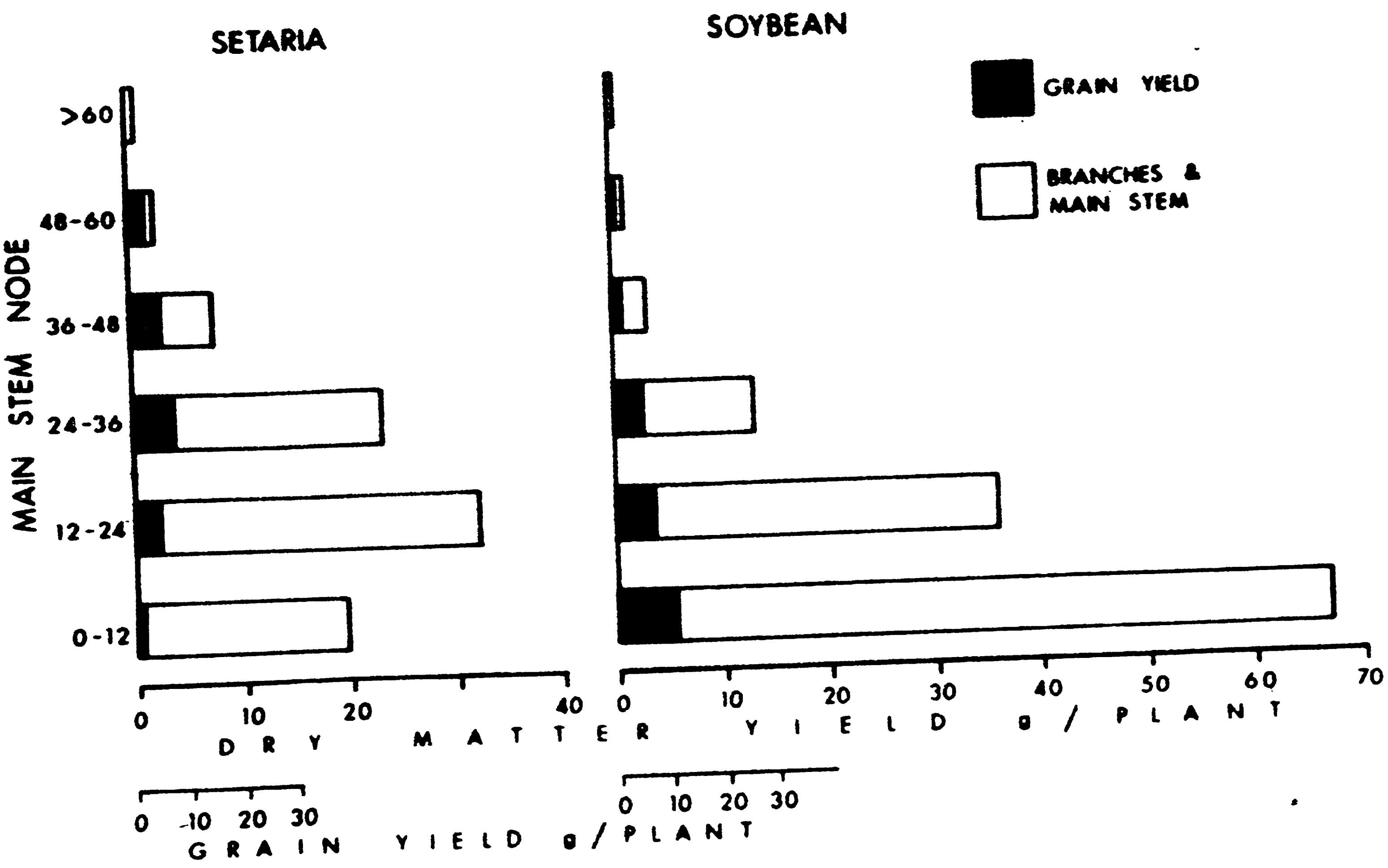
The dry weight of main stem, branches and grain yield segment-wise are presented in Table 18 and Fig.29. The 0-12 node segment of the main stem was thicker and had a higher dry weight in pigeonpea grown with cowpea or soyabean compared with the cereal combination, and the dry weight of branches borne at the basal nodes of the main stem was more in pigeonpea grown with cowpea and soyabean. This was due to the supression of branching by the shading caused by the vigorously growing, early-maturing cereals. In the case of cowpea and soyabean enough light was available to the pigeonpea for development of branches from the early stages onwards. When we consider the total dry weight of the main stem after these two treatments there was not much difference, but there was a considerable difference in the total dry weight of the branches. The total grain yield per plant was reduced when pigeonpea was grown with the millet or setaria. This reduction in part have been owing to competition for nutrients, water and space, but light was probably the major limiting factor.

The suppression of basal branching as a result of shading by the cereals was striking in both cultivars even though one of them, ICRISAT-1, under unshaded conditions usually branches profusely. This physiological suppression of branching by shading suggests that there is no need to breed special cultivars with little or no basal branching for use in intercropping systems with cereals.

Table 18. Effect of intercropping on branching and yield of two pigeonpea cultivars.

Plant part.	Node number on the main Stem 0 - 12	13-24	25-36	37-48	49-60	61-72	73-84	Total
	Dry weight g/plant							
	HY-3C with Pearl millet (HB-3)							
Main stem	35.2	35.4	23.0	11.8	5.8	2.8	1.1	115.1
Branches	0	11.1	23.1	18.5	7.4	1.5	0	61.6
Seeds	0	0.8	2.9	4.5	3.0	0.9	3.0	15.1
	HY-3C with Cowpea (C-152)							
Main stem	46.5	36.7	20.7	14.0	8.3	3.5	1.3	131.0
Branches	36.4	54.5	17.3	15.4	9.1	1.6	-	134.3
Seeds	4.1	8.1	2.8	9.4	10.7	2.5	0.2	37.8
	ICRISAT-1 with Setaria (H-1)							
Main stem	16.3	16.2	8.4	3.2	0.2			44.3
Branches	3.3	15.7	14.1	3.9	0.1			37.1
Seeds	0.3	4.3	7.3	4.8	3.0			19.7
	ICRISAT=1 with Soyabean (UPSS 38)							
Main stem	20.2	12.2	5.6	2.2	0.8	0.1		41.1
Branches	46.9	24.0	10.8	1.1	0.5	0		83.3
Seeds	11.0	6.6	24.8	1.6	1.1	0		45.1

FIGURE 29 PIGEON PEA. (ICRISAT-1): BRANCH DISTRIBUTION AFTER INTERCROPPING WITH SETARIA AND SOYBEAN



CHAPTER VII

Some observations on an off-season crop

Introduction

In Hyderabad the early cultivars Pusa Ageti and T-21 have a vegetative phase whose duration is almost the same after planting at any time between June and March (see ICRISAT Pigeonpea Breeding Annual Report 1974/5 pp 79-81). In other words, unlike the medium-duration cultivars, during this period the number of days from planting to flowering is independent of day-length and these cultivars behave as if they are "photo-insensitive".

The growth and development of the plants is, however, very different in the different seasons. This year we made observations on an off-season crop planted in December.

Methods

Cvs T-21 and Pusa Ageti were sown on 4-12-1974 in the grey-black soil in the RA-25 region of the farm. The soil was fertilized with zinc sulphate and single superphosphate at the same rates used for the main-season crop (Chapter I). The seeds were planted on ridges 75 cm apart and at a plant-to-plant spacing of 30 cms. The crop was irrigated in the furrows at regular intervals.

Results

Although the duration of the vegetative phase was much the same as in the normal season, the off-season plants grew more slowly, were far smaller had fewer leaves, the leaves were smaller (but had a higher specific leaf weight) and the total dry weight per plant and yield were much less (Table 19). The harvest index was higher. 100 seed weights were more or less the same.

Table 19. Comparison of characters of pigeonpea cultivars grown in normal and off-season (sown on 27-6-74 and 4-12-74 respectively).

Characters	T - 21		Pusa Ageti	
	Normal season	Off-season	Normal season	Off-season
Days to flower bud initiation	70	70	70	70
Days to maturity	120	120	154	120
Plant height at maturity (cm)	126	45	86	41
Total number of leaves at flowering	94	11	94	9
SLW in vegetative phase (7 weeks) (mg/cm^2)	3.9	7.0	3.8	7.7
Average area of single leaf in vegetative phase(7 weeks) (cm^2)	3.0	2.1	4.4	2.7
Total dry weight/plant at maturity (g)	76.4	12.1	72.6	14.2
Total seed yield/ plant (g)	21.8	5.3	23.3	5.8
100 seed wt. (g)	5.7	6.0	7.8	7.8
HI (%)	29	44	32	41

Discussion

The far smaller size and yield of the off-season plants were not surprising since similar effects are well-known in other crops grown in the off-season. It is probable that the size of the plant is reduced because of the lower temperatures prevailing during the earlier part of the off-season. In the monthly planting data (ICRISAT Pigeonpea Breeding Report 1974/5, pp 79-80) there was a reduction in height (measured at the time of flowering) of cvs T-21 and Pusa Ageti in plantings after September, increasing again only after the February plantings. All or part of the vegetative phase of the plants planted during this period would have been spent at lower temperatures than those encountered during the summer and monsoon seasons. The day-lengths are also somewhat shorter (at Hyderabad, latitude 17°N, the shortest day in December is 10 h 56 m, the longest day in June 13 h 4 m) but in spite of the shorter days the irradiation is greater in the off-season than in the monsoon because the sky is far less cloudy. (This greater irradiation may have been responsible for the reduction in leaf area and increase in SLW, in a manner similar to the effect of irradiation on "sun-leaves" compared with "shade-leaves"). So the reduced growth in the off-season was not a result of reduced irradiation. Nor was it likely to be a consequence of water-shortage in the soil since irrigations were frequent.

In spite of the reduction in plant size in the off-season, probably because of the lower temperatures, the number of days to flowering were unaffected; and the same is true of the time taken from flowering to maturity in cv T-21. This suggests that the duration of the juvenile or vegetative phase was not determined by "degree-days", nor by the plant size reaching a threshold level, nor by node number, but simply by the passage of a given number of days. "Biological Clocks" are usually considered to be concerned with measuring time on the scale of hours, but the concept of a Biological Clock is not really appropriate in thinking about phenomena on a much longer time scale; these pigeonpeas appear to have a "Biological Calendar" which enables them to count the number of days. If this is indeed the case it is extremely interesting from a physiological point of view.

The small size of the plants suggests that if pigeonpeas are grown as an off-season or rabi crop they should be planted at much higher population-densities than those used in the normal season.

CHAPTER VIII

Some Preliminary Observations

In this chapter we present a number of preliminary observations on different aspects of the physiology of the plants.

1. The secretory ducts of the pigeonpea

After pigeonpea plants are wounded, the wound becomes covered with a reddish substance. This is particularly evident in damaged stems and pods. In some cultivars after harvest quite large amounts of this substance appear on the cut stamp, and solidified, transparent lumps of it can be collected.

The chemical nature of this substance is not known. The red colouration, however, is not initially present but appear after some time perhaps as a result of oxidative reactions.

When a young shoot tip is cut, a drop of colourless liquid rapidly appears on the cut surface. If it is placed on the tongue even in very small amounts, it has an unpleasant, bitter taste. If it is collected on filter paper it turns red or reddish brown within a day or two. The same occurs when it gets onto clothing, which inevitably happens when one is working in the field. The stains which develop on shirts etc. cannot be washed out by any method yet tested.

An anatomical examination of sections of pigeonpea tissues revealed that there is a system of secretory ducts which are present near the phloem tissue and also in the pith region of the stem; these ducts are also present in petioles, leaves and pods. In fresh sections the contents of these ducts are colourless; but in fixed, sectioned material, a reddish-brown colouration is present.

It seems very probable that the bitter fluid which exudes from wounded tissues comes from these secretory ducts and that this fluid contains a substance or substances which undergo oxidation on the wounded surfaces.

The function, if any, of this secretory system is unknown; it seems possible that it may have a role in providing a mechanism of resistance to pests and/or diseases.

2. Preliminary Observations on the Incidence of the Wilt Disease.

The wilt disease commonly affects pigeonpeas during the reproductive phase and leads to the death of the plants before pod-filling can take place. The plants relatively rarely show signs of the disease during the vegetative phase.

During the off-season, in a crop planted in December, a very high incidence of wilt disease occurred during the reproductive phase of the plants both in the breeders' plots and in the physiology plots in RA-25.

In both sets of plots it was observed that plants with the sterility mosaic disease, which prevents or greatly inhibits flowering, were unaffected by wilt while all around them other plants were killed.

Moreover, in our experimental plots, plants which were prevented from forming pods by the regular removal of flowers were almost unaffected by wilt. This is illustrated by the results shown in Table 20, which refer to rows of plants from which flowers were removed, and the neighbouring rows of control plants.

Table 20. Incidence of wilt of plants from which flowers were removed at regular intervals compared with controls growing in adjacent rows.

Cultivars	Treatment	No.of plants observed.	No.wilted	Percentage wilted
PANT-A2	Control 1	77	31	40
	Control 2	84	35	42
	Flowers removed	89	0	0
Prabhat	Control 1	92	28	30
	Control 2	103	34	33
	Flowers removed	97	1	1

A further observation which seems relevant is that the incidence of wilt was higher in plants which had been ratooned than in non-ratooned plants.

One possible explanation of these results is that the wilt disease can affect the plant only if the root system is weakened. This may be brought about by competition from developing pods, which may reduce the supply of assimilates to the roots, or by a sudden reduction of the leaf area by ratooning which may also reduce the supply of assimilates to the roots. It may be that this situation leads to the death of some of the roots and nodules which could enable the pathogen to enter more easily; or alternatively the pathogen may already be present within the plant but be kept in check until the ability of the roots to resist the pathogen is weakened by a shortage of assimilates. Preliminary results obtained by the plant pathology section indicated that the wilt pathogen was not present in the plants from which flowers had been removed or which were affected by the sterility mosaic disease.

3. Morphological Effects of Wind

Throughout the monsoon season there are relatively strong winds which here at ICRISAT, Patancheru are almost invariably Westerly. The wind of course has immediate effects on the plants which are bent by it; but this bending leads to permanent anatomical and morphological changes which persist even when the wind is not blowing. The bending of the stem leads to an asymetric distribution of wood, with more on the side towards the wind. A microscopical examination revealed that the structure of the xylem fibres was altered on the windward side and the cell walls were thick and gelatinous. These features are characteristic of dicotyledenous "tension wood".

Morphologically the major effect of the wind was on the development of the branches, the majority of which appeared on the windward side of the plant. Since these early-formed branches in time become the largest of the primary branches of the plant, the morphological effects of the wind persist right throughout the life of the plant, and are clearly visible in the asymmetrical morphology of the plants many months later. In this way the prevailing direction of the wind during the monsoon season has a permanent effect on the structure of the crop canopy; and, consequently, this structure differs according to the orientation of the rows.

4. Preliminary Observations on the Angles of the Leaves

The angles of the leaves and leaflets are not fixed but change continuously depending on the time of day or night and on the environmental conditions. These changes are brought about by the pulvini. One pulvinus is located at the base of the petiole and controls the petiolar angle; the other pulvini are located between the petiole and the leaflets and control the angles of the leaflets.

The alterations of these angles were observed both by day and night, and in the day-time a number of leaves were photographed at regular intervals.

The results of observations made at different times throughout the growing season can be summarized as follows:

Around sunset the petioles and leaflets move towards a vertically upright position with the side leaflets folded inwards in such a way that their upper surfaces are apposed. If the angle of the branches is then changed, e.g. by tying them down, so that the leaves project from the branches at an angle to the vertical, within an hour or so the pulvini change their position such that the leaves are once again hold vertically upright. This upright "sleep" position of the leaves therefore appears to involve a gravitational response.

The leaves remain in this upright position throughout the night. Shortly before sunrise they begin to open up again, and the leaflets swivel round so that their surface faces the rising sun i.e., they at right angles to the rays of the sun. As the sun moves higher in the sky the leaflets follow it at first with their surfaces facing the sun, but later in the morning they fold upwards until they are more or less parallel to the rays of the sun. The petioles and leaflets move to maintain this parallel orientation well into the afternoon. It is only in the early evening that the leaflets once again open out until they are at right angles to the sun. Around sunset once again they assume their upright "sleep" position.

Only leaves which are exposed to the sunlight respond to the direction of the sun as described above. Leaves which are shaded assume a more or less horizontal position. Individual leaflets can behave independently and it is not uncommon to find within the canopy one leaflet of a leaf illuminated by a sunfleck facing the sun, while the other leaflets are in the shade and remain horizontal. On heavily overcast days all the leaves assume a more or less horizontal position.

The movements of the leaves also appear to be influenced by the water status of the plant. After rain when there is plenty of water available to the plant the leaves tend to remain horizontal even under bright sunlight, and at night, on some occasions, at least the petioles and leaflets have been observed to point donward, rather than upwards. Conversely if the plants are subjected to water stress, the tendency for the leaves to assume an upright position during the day is accentuated. A similar response is found in plants subjected to stress by waterlogging.

The diurnal rhythms of sleep movements of the leaves in other legumes such as Phaseolus have been found to be endogenous and to persist for several days even if the plants are kept in a constant environment. It seems probable that the pulvinar movements of pigeonpeas may also be controlled by an endogenous rhythm. In addition they are influenced by the direction and intensity of light, by gravity, and by the water status of the plant. Their physiology is both interesting and complex.

Unfortunately very little is known about the functional significance of pulvinar movements. The reason why the leaves of so many species assume a sleeping position at night is very obscure. However, the significance of the daytime movements may be simpler to explain. In low light intensities the orientation of the leaflets at right angles to the incident light will achieve maximum light interception, while at high light intensities the orientation of the upper leaves of the canopy parallel to the sunlight will allow a greater penetration of light to the lower leaves and a more efficient use of the incident radiation. Under conditions of stress the stronger orientation of the leaves parallel to the sunlight will result in a reduction in the surface area exposed to radiant energy and thus to a reduction in heating of the leaves and a reduction in transpiration. But at present such explanations are merely speculative.

Some attention is being paid by cereal physiologists and breeders to leaf angle as a heritable character influencing yield. On theoretical grounds, in crops with a high leaf area index, a vertical orientation of the leaves, especially the upper leaves, would be expected to give a more efficient use of light and thus a higher net assimilation rate. There is some evidence that at least in the case of rice this is true. But for a legume crop such as pigeonpea where the leaf angle is not fixed but changes continuously it would clearly be impossible to breed for a given leaf angle. There may be varietal differences in pulvinar response, but until more is known about leaf movements and their physiological significance, little can be done about the angles of the leaves in a practical plant breeding programme.

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