ASSIMILATION, TRANSLOCATION AND GROWTH IN SOME ONION CULTIVARS

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Z A R I A

ASSIMILATION, TRANSLOCATION AND GROWTH IN SOME ONION CULTIVARS

To

My Dad

Mr. Akaahar Yuwa

Member of Order of the Niger (M.O.N.).

THESIS RECOMMENDATION PAGE

We hereby recommend that the thesis prepared by

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S U M M A R Y

Three onion cultivars namely, Red-Kano, Eclipsel-Bermuda and Texas-Grano were used in this study.

Individual leaves of the plants were labelled with $^{14}CO_2$ 59, 81, 101 and 123 days after transplanting. The distribution of the labelled photosynthates in different plant parts was determined 24 hours after labelling by qualitative (autoradiography) and quantitative (counting) techniques. In general, the translocation efficiency of the source leaves increased with leaf and plant age. Mature leaves retained considerable proportion of fixed ^{14}carbon. At 101 days after transplanting, mature leaves of cv. Red-Kano retained up to 38% (L2) of the fixed ^{14}carbon.

The bulb was the dominant sink for photosynthates and its importance increased with plant age, importing up to 94% of the fixed assimilates at 101 days after transplanting. Each mature leaf was responsible for filling up its bulb scale and the youngest initiated bulb scale. The pseudostem and roots were important sinks in the early stage of plant growth but later on they became unimportant sinks.

Varietal differences were observed as to the efficiency of the leaves in exporting assimilates. Cultivar Red-Kano

exported significantly higher percentage of assimilates than the other two cultivars ($P < 0.05$). Leaf position was significant at the early stage ($P < 0.01$) but as the plants matured it became insignificant.

The growth characteristics comprising of plant height number of leaves, diameter and fresh weight of the bulbs the dry weights of the component plant parts, the chlorophyll content and minerals (P, K, Ca, Mg and Zn) were measured weekly starting from 35 days after transplanting up to plant maturity.

Cultivar Red-Kano had significantly more leaves, greater leaf area and larger bulbs than cv. Eclipsel-Bermuda and cv. Texas-Grano ($P < 0.001$). The plants of cv. Red-Kano had a final diameter of 7.88 cm and fresh weight of 171.25 g. Plants of cv. Eclipsel-Bermuda had a diameter of 4.07 cm and fresh weight of 28.29 g while cv. Texas-Grano achieved a diameter of 4.3 cm and fresh weight of 55.38 g. Cultivar Red-Kano had higher dry matter than the other two cultivars with the bulb contributing the highest percentage.

Phosphorus accumulated more in the bulb and least in the pseudostem. Phosphorus concentration in the bulbs of cv. Eclipsel-Bermuda and cv. Texas-Grano was significantly higher than in that of cv. Red-Kano ($P < 0.001$). Potassium concentrated more in the leaves and least in the bulb. Potassium concentration in the plant parts decreased with increasing plant age ($P < 0.001$). Calcium concentration was generally lower in cv. Red-Kano than cv. Eclipsel-Bermuda and cv. Texas-Grano. At any sampling the concentration of calcium was lowest in the bulbs and tended to decrease with increasing plant age ($P < 0.001$).

Magnesium accumulated more in the leaves and least in the bulb. Magnesium concentration in the leaves increased with increasing plant age ($P < 0.01$). Zinc accumulated most in the pseudostem and least in the leaves. Zinc concentration in cv. Texas-Grano was higher than in cv. Red-Kano and cv. Eclipsel-Bermuda. Zinc concentration in the leaves decreased with increasing plant age ($P < 0.01$).

There was no significant difference in the chlorophyll a and b content of the onion cultivars. The change in Chl.a with plant age and cultivar was significant ($P < 0.001$).

The Chl.a/Chl.b ratio was 2 on the average for all cultivars but its change with age of the plant was significant ($P < 0.001$).

Varietal differences were observed. Cultivar Red-Kano showed better growth characteristics, photosynthetic efficiency and produced larger bulbs than cv. Eclipse1-Bermuda and cv. Texas-Grano but these latter two cultivars had higher concentration of phosphorus, calcium and zinc in the bulb.

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ABBREVIATIONS USED IN THIS THESIS

Ca	Calcium
cm	Centimeter
Chl.a	Chlorophyll a
Chl.b	Chlorophyll b
CGR	Crop Growth Rate
cv.	Cultivar
^{o}C	Degrees Celcius
g, gm	gram gramme
hr	Hour
Kg/ha	Kilogram per hectare
LAR	Leaf Area Ratio
L	Leaf
Mg	Magnesium
u Ci	Micro currie
mg/l	Milligram per litre
mg/g	Milligram per gram
ml.	Millilitre
NAR	Net assimilation rate
N	Nitrogen
ppm	Parts per million
%	Percentage
day^{-1}	per day

ABBREVIATIONS CONTINUED

dm^{-2}	per decimetre square
g^{-1}	per gram
gm^{-2}	per grame square
wk^{-1}	Per week
P	Phosphorus
K	Potassium
RGR	Relative Growth Rate
RLGR	Relative Leaf Growth Rate

CHAPTER 1
INTRODUCTION

Onion (Allium capa L.) is one of the most important vegetable crops of the world. The use of species of Allium for food, far exceeds their other uses by man. Many are important as range crops, ornamental plants, for medicine and as weeds. According to Vavilov (1926) the cultivated onion originated from 'The Central Asiatic Centre of Origin,' an area which includes North Pakistan, Afghanistan and Eastern U.S.S.R. It was cultivated in Egypt during the period of the Pharoahs and there is evidence that it is more ancient than that. Today it is in universal demand and is widely grown (Jones and Mann, 1963).

China is the world's largest producer of onions (2,331,000 metric tons) and Africa's largest producer and exporter is Egypt (670,000 metric tons) (F.A.O. Trade report, 1977). The average annual output of onions in Nigeria is 77,000 tons, with an estimated average annual increase in production of 2.6% (Fed. Min. of Agric. and Nat. Res. Plan. Comm., 1974). There are, however, no accurate dependable records on onion acreage in Nigeria. The crop is usually grown on stream banks and managed by family labour. The bulk of the crop in Nigeria is grown in the Northern part of the country, north of Latitude

$9^{o}30'N$. The crop is cultivated during the dry season (October _ May) and irrigated (as the crop is essentially a dry season crop). The wet season is associated with disease problems (Green, 1973).

The interaction of the environment and crop physiological processes needs to be better understood inorder to find solutions to problems of onion crop productivity. The onion plant exhibits a delicate balance between vegetative and reproductive phases of growth, which is greatly affected by environmental conditions. The pattern of organ formation and development varies not only among different species of the onion plant but also within one species depending upon the conditions under which the plant is grown. The developing onion plant goes through a sequence of distinct morphological phases (vegetative and reproductive) which occur in response to environmental conditions. The two most important of these conditions are daylength, and temperature (Abdalla and Mann, 1963), but the response of a plant to environmental conditions may also depend on the stage of growth, growth characteristics of the cultivars and the plant constituents (Adedipe and Ormrod, 1975).

The primary function of the leaves as food synthesizers and subsequent distribution of photosynthates to other

parts of the plant follows well defined patterns for each crop. Leaf growth has been postulated to be the main yield determinant in a crop (Watson, 1956). Broughman (1960) presented evidence indicating that plant productivety is actually more related to the amount of chlorophyll exposed to light than the leaf area. The total chlorophyll content of certain leaves is however, known to vary with developmental stage and to some extent with growing conditions (Jahn and Young, 1976).

The correlation between the activity and efficiency of the leaves and the subsequent supply of phtosynthates to other parts of the plant (especially the main storage organ) needs to be better understood to be able to postulate the productivity of the onion crop. Export of assimilates may not be governed principally by proximity of the leaf to a given organ, but also in response to demands by specific 'sinks', the magnitude of which may depend on dry weight gain and leaf expansion. The total dry matter production by a crop may vary through changes in the activity of the photosythetic system or in the length of the growth period (Adedipe, 1975a.).

Butt (1968) established that growth in weight of the entire onion plant and it's various organs (i.e., roots, leaf blades, neck and bulb) increased with increasing light

intensity (up to the highest one applied). After 126 days, reduced leaf emergence, caused by bulb development resulted in decreased leaf dry weight, even at full light intensity. El-Habbasha and Shaheen (1976) showed that in onion seedlings, water deficit affected their growth. After depletion of 55% available soil moisture, irrigation resulted in the production of onion seedlings of suitable size for transplanting. Seedling size was shown to be a function of dry matter content, chlorophyll a and b and the net assimilation rate.

Steer and Darbyshire (1979), under Australian condition, limited their carbon economy study of the onion plant (c.v. Creamgold), to the first six leaves of the plant's life. They found that the onion plant grown from seed is adapted to bulb formation and the sinks for carbon translocation were roots, newly initiated leaves and leaf bases. They also found that in young onion plants up to the 3-leaf stage, actively growing leaves supply carbon to roots and unemerged leaves, but in older plants, young emerged leaves do not export carbon. Within such leaves the carbohydrate moved basipetally, primarily to the leaf base. Khan (1981) and Khan and Asif (1981) studied the carbon economy of onion (c.v. Red-Kano) and found that the export of assimilates from a leaf increased with increasing age of the plant

They also observed that the bulb became an increasingly dominant sink as the plant grew, importing assimilates from all the leaves but mostly from basal and middle leaves. The stem and mature leaf blades were unimportant sinks, while roots were weak sinks.

It is possible that there are differences in the carbon economy between cultivars, especially if they have different lengths of growing period. It is also possible that there is some relation of cultivar and length of growing period to the mineral accumulation and other growth characteristics of the bulb onion. Although some work (Jones and Mann, 1963; Butt, 1968) has been carried out on the development of the onion plant in relation to photoperiod and temperature, photosynthesis and mineral nutrition, detailed information on the changes in growth and mineral accumulation during the life history of the plant is still of interest, especially under Nigerian environmental conditions.

Morphogenesis and carbohydrate accumulation (resulting from assimilate translocation from the leaves) are the main features of onion bulb development. This study tries to assess these changes and their efficiency. In view of the limited information available, the present work was

undertaken to compare a local strain of onion (c.v. Red-Kano), which is late maturing and two imported early maturing cultivars (c.v. Eclipse1 Bermuda and c.v. Texas-Grano). Attempts were made:

1. To study qualitatively and quantitatively the translocation of photosynthates from individual leaves and the relative importance of the leaves in the formation of the bulb.
2. To analyse the growth of the onion plant by measuring chlorophyll content and calculating photosynthetic efficiency.
3. To study the mineral content of the various plant parts at different stages of growth and development.

CHAPTER 2

LITERATURE REVIEW

2.1. TRANSLOCATION OF LABELLED ASSIMILATES FROM LEAVES.

2.1.1. MOVEMENT OF ASSIMILATES.

Living cells of the plant are dependent upon the photosynthetic cells of the leaves for their carbohydrate supply. The use of radioactive tracers in the study of the mechanism of the transport of the leaf assimilates to various plant organs has unveiled some of the mystery. These studies have covered a wide range of plants and different aspects.

Aronoff (1955) reported no activity in the rest of the leaflet lamina of soybean if only a limited area of the leaf was exposed to $^{14}CO_2$, nonetheless, activity moved out of the leaflet. Mayer and Porter (1960) also reported no activity in leaves other than those treated and only traces in the leaf sheaths of rye. At this time evidence accumulated to show that assimilates move from a fed leaf depending on the age and stage of development of that leaf e.g., Jones et al. (1959); Shiroya et al. (1961) in tobacco, Thrower (1962) in soybean and Joy (1964) in sugar beet. These studies showed that a young leaf retained all the assimilates it produced and imported from older leaves until it was about 30 percent of fully expanded

size (Thrower, 1962). Thrower (1962) further observed that when a leaf was 30 - 50 per cent of its mature size it imported and exported simultaneously and after this stage it exported predominantly.

In Cucurbita melopepo, translocation started within 15 minutes of assimilation and export reached a maximum within the next 10-15 minutes. After 3 hours, 55 per cent of the total assimilated ^{14}C was exported and there was no further net-output (Webb and Gorham, 1965).

Hofstra and Nelson (1969) observed that assimilates moved rapidly down from a fed area of corn leaf, with no detectable lateral movement. They reported that 50 per cent of the assimilates moved out of the fed leaf in the first 30 minutes and about 80-90 per cent of the assimilate was translocated in 24 hours. The amount of assimilates remaining in the fed area decreased with time. However, in tomato, only 17% of the assimilated carbon moved out of a mature leaf in the first 24 hours. At the time of fruit development, leaves retained more than 80 per cent of the carbon they fixed (Khan and Sagar, 1966). These workers were able to increase the export of the ^{14}C from a source leaf by 30-50 per cent by reducing the number of sources of photosynthates and by increasing the physiological

activity of the sinks (Khan and Sagar, 1969a).

The age and position of the leaf is a major factor influencing the retention and export of assimilated $^{14}CO_2$ in both vegetative and reproductive plants. Ryle and Powell (1972) reported that export from a fully expanded leaf of Lolium temulentum increased from 65% to 85% when a new leaf expanded above it. Further ageing decreased export and a slightly greater percentage of assimilate was retained. They further noted that the sheath of a newly expanded leaf blade, keeps on growing after the expansion of the lamina is complete, but whether this sheath or base is still growing or not, ^{14}C moved out of the fed zone of the lamina.

2.1.2. DIRECTION OF MOVEMENT OF ASSIMILATES.

Mason and Maskell (1928) showed that in cotton plants, the movement of sugars followed a "diffusion pattern." That is, a correlation existed between the rate of transport and sugar gradient in the bark. They observed that the direction of translocation was always from a region of high concentration to a region of low concentration. Defoliation caused this sugar gradient to disappear (Mason and Phillis, 1937).

In grapevine upward translocation was very rapid but slower in the opposite direction (Swanson et al. 1958). Aronoff (1955) in soyabean and Mayer and Porter (1960) in rye reported a predominantly donward movement. Thaine et al. (1959) and Thrower (1962) showed that in soybean there was a change of direction of assimilate movement from a leaf as the leaf position changed from being upper to being lower on the shoot. In the upper position the leaf exported upwards to the shoot apex, but when it was lower on the shoot it exported mainly downwards to the roots. Hale and Weaver (1962) further presented evidence in Vitis vinifera to show that translocation of assimilates could be either upwards or downwards depending on the stage of development and where the strongest sinks were situated, relative to the treated leaf. One of the important economic crops which has received considerable attention is sugar cane. Hartt et al. (1963), after several years of study, reported movement of photosynthate made in one lamina to be mainly down that blade and sheath to the stalk in the parallel veins of the leaf. On reaching the stalk, the photosynthate first moved down before it was found in an upward moving stream. Biddulph and Cory (1965) observed the movement of organic materials in bean plants to be

bidirectional in separate phloem bundles.

2.1.3. PATTERN OF ASSIMILATE DISTRIBUTION AMONG THE PLANT PARTS AT DIFFERENT GROWTH STAGES.

Mayer and Porter (1960) in their experiments with rye, found large amounts of labelled ^{14}C in the roots, but little activity in adjacent tillers. Studies with wheat revealed that the movement of ^{14}C within the wheat plant was extensive in the early stages of growth but gradually became more localized until, after ear emergence, there was little transference of ^{14}C between tillers in 24 hours (Quinlan and Sagar, 1962). They showed that meristematic regions and tillers became dependent on their own leaves which also supplied assimilates to associated young tillers. Doodson et al. (1964) observed how the distribution pattern of assimilates in wheat varied with age, using the 3rd leaf as source of ^{14}C. They showed that old leaves imported only small amounts of photosynthates. The youngest leaf imported small quantities of assimilates, which increased with an increase in its growth rate, after which it fell rapidly as the leaf became mature. They recorded large quantities of translocates in the roots and stem with the proportion in the roots increasing considerably as the movement to the leaves decreased.

In an elegant study of phloem transport in bean plants, Biddulph and Cory (1965) using $^{14}CO_2$ feeding, and fluorescence techniques, have shown that those leaves nearest to the root, transport metabolites primarily to the root, leaves nearest to the top of the plant transport to the stem apex, while leaves in an intermediate position translocated metabolites in both directions. At this time, evidence accumulated from different workers on different plant species, to show that young growing leaves utilize assimilated carbon for their own growth and do not export carbon to the rest of the plant, while fully expanded leaves export most of their photosynthate to roots and young leaves, but with the half expanded leaf, a bidirectional flow occurred (Belikov, 1955; Aronoff, 1955); and Thrower, 1962 in soyabean; Jones et al. 1959 in tabacco, Joy, 1964 in sugarbeet; Webb and Gorham, 1964 in straight necked squash; Khan and Sagar, 1966; 1967 and 1969b in tomato). Hale and Weaver (1962) showed by autoradiography that there was no translocation out of the source leaf of grapevine which was still growing actively at the time of treatment. Assimilates from a treated leaf in the grapevine moved to areas of meristematic activity (i.e. the shoot tip) and to the parent vine. Thrower (1967) reported

that as a leaf ages, there was a decline in it's photosynthetic efficiency and contribution to other parts. There was a changing pattern of assimilate distribution from a leaf as the plant developed. Webb and Gorham (1964) further showed that partly yellowed senescent leaves were still able to synthesize stachyose and sucrose and contributed to the translocation stream. Khan and Oritsejafor (1980) made a similar observation in maize. In young corn plants, Hofstra and Nelson (1969) observed each leaf to be an importer and exported of assimilates to all other parts of the plant.

Rawson and Hofstra (1969) studied the movement of ^{14}C assimilated by each leaf of the wheat plant at successive stages of development from sowing to maturity. Each leaf exported in a specific direction with the lower leaves exporting downwards to the tillers and roots and the upper leaves supplying the stem and ear. They also showed that as the plant grew, the function of supplying the developing leaves passed successively from one expanded leaf to another. But on the contrary, in the vegetative tomato plant, Khan and Sagar (1966) observed that the lower leaves exported more carbon upwards than downwards, while the upper leaves exported a larger proportion down than up.

In the age series experiments of Nelson et al. (1961) in soybean, the total amount of ^{14}C assimilated was observed to be relatively constant, inspite of changes in leaf size and age, but the amount translocated was variable, Shiroya et al. (1961) reported that the seventh leaf of tobacco, at different stages of growth ranging from 68 days to 135 days, distributed labelled metabolites to roots and stems but areas of high metabolic activity such as the actively growing stem tip and young leaves were strong sinks for the translocated carbohydrate. The seventh leaf of maize has been shown to increase its exporting capacity from 3% when it is one day old, to 45% when it was 21 days old. The bulk of its exported assimulates were recovered from the young leaves which constituted strong sinks, and to other important sinks such as stems and roots, to which this leaf however supplied inconsistent amounts of assimilates (Khan and Oritsejafor, 1980). Adedipe (1975a) concluded from his experiments on Okra plants that the export of ^{14}C assimilates was not controlled by the proximity of any particular organ but was in response to temporal requirements by specific sinks.

Recent work on onions indicated that carbon was rapidly translocated from the leaf blade to the leaf base

where it accumulated, even before bulb induction. To a lesser extent carbon was also translocated to roots and unemerged leaves. In the mature plant, young emerged leaves did not export carbon, but within the leaf the carbon tended to move basipetally (Steer and Darbyshire, 1979). Khan (1981) and Khan and Asif (1981) showed that the export of assimilates from an onion leaf increased with increasing age of the plant; the bulb, which imported assimilates from all the leaves, became an increasingly dominant sink as the plant grew, being supplied mostly from the basal and middle region leaves. They also indicated that the stem and mature leaf blades were unimportant sinks for ^{14}C throughout the life of the plant.

2.1.4. EFFECT OF PHYLLOTAXIC PATTERN.

Several studies have shown that very little tangential movement of metabolites takes place and in most cases it is absent. That is, very little movement of metabolites occur between leaves phyllotaxily opposite each other. Distribution patterns in the tobacco plant showed both bidirectional and tangential movements of assimilates (Shiroya et al. 1961). The labelled metabolites in tobacco moved up and down the stem, and as tangential distance from fed leaf increased, there was a

progressive decrease in radioactivity found in the young leaves. The question is whether it is a problem of distance from source leaf or vascular connections. Thrower (1962) showed that export of assimilates from an expanded leaf to the apex and root was inversely proportional to it's distance from these sinks i.e., as the distance of the 'sink' from the source leaf increased, the amounts of assimilates supplied to it decreased.

When $^{14}CO_2$ was fed to a leaf of sugar-beet, ^{14}C metabolites were found only in leaves directly above or in the root directly below the supplying leaf, indicating the absence of tangential movement (Joy, 1964). However, if all fully expanded leaves from one side of the plant were removed and a mature leaf on the intact side of the plant was fed, tangential movement could be induced as labelled metabolites were then found not only below and above the supplying leaf but also in the young leaves left intact on the defoliated side. The young leaves on the otherwise defoliated side constituted such a great 'sink' as to induce tangential movement having being deprived of photosynthate from mature leaves, on their side, by defoliation. These defoliation experiments suggest that the pattern of assimilate movement is the net result of a complex

interaction between sources and sinks and do not depend on intervascular connections alone (Thaine et al. 1959; Thrower, 1962). Tangential movement has also been shown in other plant species such as Red Kidney Bean (Biddulph, 1956) and Willow (Peel, 1964 and 1966).

2.1.5. INFLUENCE OF STORAGE ORGANS AND REPRODUCTIVE STRUCTURES ON ASSIMILATE DISTRIBUTION.

The influence of reproductive structures on the pattern of assimilate distribution is varied. In wheat (Doodson, et al. 1964) and in young plants of Lolium multiflorum (Marsha and Sagar, 1968) up to half the labelled carbon which left the source leaf was present in the roots, but in flowering cereals the proportion was less (Wardlaw and Porter, 1967). In the flag leaf of wheat, 15-20 days after antheis movement of assimilates upwards was twice as fast as downwards, but removal of grains decreased upward movement in favour of downward movement (Wardlaw, 1965). He concluded that storage organs have a polarizing effect on assimilate movements.

It is well established that there is frequently a characteristic pattern of assimilate movement within the shoot system and that individual 'sinks' may derive assimilates from fairly specific groups of leaves. Thus, all

leaves on a young fruiting tomato plant supplied assimilates to the developing fruits but as more and more fruits were produced, groups of leaves nearest to developing fruits became responsible for their food supply (Khan and Sagar, 1966; 1967). The sink strength of the tomato trusses caused the stem to gain more carbon from upper and lower leaves other than from those leaves nearer the trusses. In wheat also, the developing ear obtained most of its assimilates from the uppermost (flag) leaf, the lower leaves supplying little to the developing grains (Quinlan and Sagar, 1962; Wardlaw, 1968). These studies showed the polarizing effect that major 'sinks' could have on the direction of assimilate movement. They also showed which leaves were responsible for filling up the developing grains.

Initially, most of the assimilates exported from a young leaf are transported to the adjacent shoot apex. However, with time and the development of leaves above it, an increasingly greater proportion of assimilates from a leaf, move to the roots. Thus a fairly universal pattern of assimilate distribution within whole plant has emerged from the many investigations of these processes. That is, the lower leaves act as the main source of assimilates for roots, whereas the upper leaves supply the shoot apex,

and leaves in an intermediate position may supply assimilates in both directions (Wardlaw, 1968).

Eastin (1969) reported that photosynthate distribution patterns from various leaves of a corn plant were affected by metabolic activity in the sink as well as spatial relationships between photosynthate source and sink. The direction of export from a given leaf was found to change as development progressed (Tripathy et al. 1972). They reported that the transport of ^{14}C from the upper leaves was predominantly downwards while direction of export from lower leaves changed from downward to upward as the ear became the dominant sink, indicating that sink-demand strongly influenced the direction in which the photosynthate moved. Presumably, photosynthate from upper leaves of corn was used first in seed development than that generated by the lower leaves.

Export from expanded leaves was much greater in reproductive shoots than from comparable leaves on vegetative shoots (Ryle and Powell, 1972). They showed that in Lolium temulentum, increased demand of assimilates was caused by reproductive structures. Ryle (1972) reported no change in photosynthates in the main shoot of L. temulentum, when it developed an inflorescence. He attributed

this to the absence of change in the level of meristematic activity. He associated the movement of carbon with meristematic activity. He observed that the supply of carbon to the stem when it was meristematic at its internodes, increased in both vegetative and reproductive shoots of Lolium temulentum. This was at the expense of the roots which received a reduced export of less than 10 per cent.

Some plants can be propagated by planting stem cuttings, bulbs or leaves. In most of such cases, these parts of the plant acted as storage organs during the life of the plant. The food reserves were remobilized to sustain new growth of roots, shoots and leaves, until these were fully established. The bulb scales of Tulip supplied significant amounts of ^{14}C reserves to the new leaves and roots in the first three months of replanting. The partitioning of the reserves to various organs was related to the timing of their development and growth, their sink strength and to their position relative to source organs (Ho and Rees, 1976).

2.1.6. FORM OF ASSIMILATES TRANSLOCATED.

Analysis of phloem exudates of sixteen tree species by Zimmermann (1957) have shown that sucrose was by far

the most dominant carbohdrate translocated. Swanson and El-shishiny (1958) and Swanson (1959), reported that hexoses were not translocated in beans but glucose and fructose sugars were found as a result of hydrolysis. Burley (1961) also reached the same conclusion, in soybean and Raspberry. However, sucrose was found to remain intact while moving in sugar cane (Hartt, 1965). Hartt, et al. (1963) also found sucrose to be the only translocated compound in sugar cane.

Hofstra and Nelson (1969) reported sucrose to be the only translocated compound in corn. They also found that lowering of temperature only delayed changing of ^{14}C into sucrose but had no effect on the distribution of ^{14}C among the sucrose intermediates,malate and aspartate, thereby starting the process of conversion to sucrose. In tulip, Ho and Rees (1975) found sucrose to be the main translocatory sugar remobilized from the mother to the daughter bulbs. The conversion to starch and insoluble fractions progressed with time in the daughter bulbs, but in other growing organs sucrose and glucose were the substances remobilized from the mother bulb.

Translocation of products of assimilation was selective in soybean. Nelson et al. (1961) reported sucrose

and serine as the principal translocatied products but under suitable conditions of growth, malic acid and other compounds were translocated.

In Cucurbita melopepo, stachyose with a trace of raffinose and sucrose were found to be the principal compounds translocated to all parts of the plant (Burley (1961). Similar results were obtained in tobacco Jones et al. 1959).

In onions (cv. Creamgold) after 10 minutes of exposure to $^{14}CO_2$, 80% of the ^{14}C was found to exist as sucrose which was evidently its major photosynthetic product (Steer and Darbyshire, 1979).

2.1.7. VELOCITIES AND RATES OF ASSIMILATE TRANSPORT.

When one estimates the amount of material needed to maintain the rapid growth of storage organs, one becomes aware of the importance of translocation rates for the movement of substances. These rates used to be obtained by noting the increase in dry weight of fruits, tubers, storage roots and other organs that import large amounts of materials. Corrections had to be made for local synthesis of metabolites if photosynthetic tissues were used. Losses due to respiration, condensation and retranslocation of metabolites had to be calculated. These

factors presented difficulties as in most cases these losses could not be measured directly, causing certain assumptions to be made. This suggested that translocation rates obtained in this manner were only indicative of the actual rates occuring (Devlin, 1969).

With the advent of radioactive tracer techniques however, fairly accurate translocation rates were obtained. Usually these methods involved the feeding of the leaf or leaves with $^{14}CO_2$ which was assimilated in the photosynthetic process. The progress of the radioactive metabolites so formed was followed by detection of radioactivity at different distances along the stem. Using this method Vernon and Aronoff (1952) reported that the soybean translocated assimilates at the rate of 100cm/hr while Swanson (1959) reported a translocation rate of 60cm/hr. for Concordgrapes. Translocation rates of 84cm/hr (Hartt et al. 1963) and 270cm/hr (Hatch and Glasziou, 1964) were observed in Sugar cane. In straight-necked squash, translocation rates were as high as 290cm/hr (Webb and Gorham, 1964).

The variable translocation rates depend on the type of metabolites translocated as well as other physical factors affecting translocation. Biddulph and Cory (1957) observed

that when a solution containing tritiated water (THO), ^{32}P and ^{14}C-sucrose was fed to a 12-day old bean plant, the ^{14}C-sucrose moved considerably faster (107cm/hr) than either THO or ^{32}P, both of which moved at the rate of 87cm/hr.

Nelson et al. (1961) listed a number of sequential processes whose rates of action alone or in group, influence the translocation rate of photosynthates from its site of synthesis in the leaf into and down the stem. The processes were CO_2 assimilation, synthesis of the labelled compound, mixing of the labelled compound with unlabelled compounds and local utilization of the mixed endogenous compounds.

Troughton et al. (1974) compiled comprehensive data on maize, tomato and wheat plants and described a technique for measurement of the rate of carbon-transport in vivo. They noted two stages of efflux from the fed area with an initial fast but later slower rate varying from 0.012 - 0.3% min^{-1}. Recently, Ho (1978) reported that the rate of carbon transport from a mature leaf in a single photoperiod was regulated not by the current rate of carbon fixation, but by the quantity of carbohydrate reserve in the leaf. This reserve was a result of previous carbon fixation and transport.

2.1.8. FACTORS AFFECTING TRANSLOCATION.

Factors affecting translocation are many and vary from external physical to internal physiological. They have received considerable attention. The major environmental factors which are known to influence the translocation of ^{14}C assimilates are temperature and light while internal factors influencing translocation are mineral nutrition, growth inhibitors and promoters, water stress and other minor factors.

2.1.8.1. TEMPERATURE:

The influence of temperature on other processes, such as photosynthesis, respiration and auxin synthesis that may directly or indirectly affect the movement of solutes, complicates an analysis of the effect of temperature on translocation rates (Devlin, 1969). Nevertheless a definite relationship between temperature and rate of translocation has been demonstreated. By varying the temperature of a plant and measuring the increase or decrease in the dry weights of different organs, indirect measures of translocation were obtained using the assumption that the dry weight of an organ reflected the rate of movement of solutes into that organ. Using this method, Hewitt and Curtis (1948) demonstrated that the optimum temperature for translocation

in bean plants was between 20°C and 30°C. Swanson and Bohning (1951) used localized temperature treatment in order to circumvent the problem of subjecting whole plant to a range of temperatures and thus influencing its whole metabolism. They hoped to be able to measure the effects of temperature on translocation per se. They took the increase in length of a stem after a given time as a measure of the rate of movement of sucrose through the treated petiole to the stem. Their results agree remarkebly well with those of Hewitt and Curtis (1948), where the whole plant was subjected to fluctuations in temperature. Both studies show that the translocation of solutes was influenced by temperature in the same manner as other physiological processes. That is, the rate of translocation increases with temperature to a maximum and then decreases due to the detrimental effects of high temperature.

Sugar-cane plants fed with $^{14}CO_2$ showed translocation rates that increased with increase in temperature. Thus sugar-cane plants subjected to air temperatures of 20, 24.5 and 33°C had translocation rates 84, 93.6 and 120 cm hr^{-1} respectively (Hartt, 1965).

It appears that the difference in the temperature of the root as compared to the shoot may influence the

direction of movement of sugars (up or down) from a $^{14}CO_2$ supplied leaf. Hartt (1965) observed that in sugar-cane when root temperature was kept higher than shoot temperature, translocation to root increased, and to the top decreased. When the situation was reversed (i.e. shoot temperature was kept higher than root temperature), translocation to the top increased and that to the root decreased.

The influence of temperature on source. (e.g. leaf blade) and sink (e.g. storage organ) regions primarily reflected the influence of temperature on the rate of translocation. This was demonstrated in the sugar beet plant (Geiger, 1966; Swanson and Geiger, 1967). When the sink regions were cooled to about 1°C there was a drop, in the translocation rate of ^{14}C-labelled photosynthate, to a new steady rate approximately 35-45% of the original rate, but rapid recovery of the original rate occurred when cooling was stopped (Geiger, 1966). The continued translocation at a steady low rate, even though the sink regions were cooled to 1°C was due to the likely active secretion of photosynthate into the sieve tubes at the uncooled and therefore uninhibited source region (Devlin, 1969).

Swanson and Geiger (1967) obtained different results with this plant, when low temperatures of 1-2°C were applied

to areas other than the source and sink regions e.g., petiole. When a 2cm petiole zone was cooled to about 1°C, holding the rest of the plant at 30°C, they found a rapid drop in the translocation rate of ^{14}C-photosynthate. However, after a suitable thermal adaptation period, recovery to the origional rate occurred.

2.1.8.2. LIGHT:

Vernon and Aronoff (1952) observed that high and low light intensity or absence of light had no effect on the rate of translocation of photosynthate in soybean stems. Nelson and Gorham (1957), however, found the movement of assimilates to be affected by light. They observed that after 15 minutes of photosynthesis, 30-day old soybean plants transported 2.0% of their total radioactivity to the top of a shoot and 4.4% to the roots in a 3 hour period. In the absence of light, in a similar period, the shoot received 5% of the assimilates and the roots 16.5%. Only 1% of the radioactivity disappeared from the leaves in a 14 hour period of illumination while 49% of the deposited sugar moved towards the roots in 14 hrs. of darkness. It can be postulated from such data that root translocation was favoured over shoot translocation in the dark.

The root/shoot dry weight ratio of wheat was found to increase with increasing light intensity indicating that the ratio of translocation to the root as compared to the shoot also increased with light intensity (Nelson, 1963). He also showed that in Pinus strobus, light intensity did not have any effect on the movement of material through the stem or on the activity of the root but rather on the physiological state of the shoots. Thus low light intensity during translocation had little or no effect on translocation to roots, but during growth, there was considerably reduced flow of organic material to the roots.

Quality of light may also influence translocation of photosynthates in plants. Hartt (1966) reported that translocation of ^{14}C-photosynthate in detached blades of sugar-cane was accelerated in the presence of red or blue light. Hartt's observations were supported in part by the discovery that red light also enhanced the uptake of ^{14}C-sucrose by the plumules of etiolated pea seedlings (Goren and Galston, 1966 and 1967). Under high light intensity (2,000 ft. candles), 58-68% of the assimilates were exported from the source leaf of Lolium temulentum in 24 hours, but in low ligh higher amounts were retained (Ryle, 1970b). This showed that high light intensity enhanced movement of

assimilates from the source leaf. Ryle (1970) further noted that the terminal meristem was the largest sink for assimilates in both annual and perennial grasses under high light intensity.

2.1.8.3. MINERAL NUTRITION

Gauch and Dugger (1953) reported that the absorption and translocation of sourose by the leaf of a bean or tomato plant immersed in a solution of ^{14}C-sourose were greatly facilitated when boron was added to the solution. They suggested that an ionizable complex was formed between boron and sucrose which moved through cell membranes much more readily than non-borated sucrose. These results were supported by Sisler et al.(1956) in tomato and Lee et al. (1966) in sun-flower plants. In both studies fixed ^{14}C was translocated in plants supplied with boron. Sucrose was not the only substance aided in its translocation by boron. Mitchell et al. (1953) observed that the growth regulators 2, 4, 5-trichlorophenoxy acetic acid and 2, 4-dichlorophenozy acetic acid when applied with sucrose to the leaves of a bean plant were translocated more efficiently in the presence of boron.

Supplying combined nitrogen decreased the proportion of photosynthate translocated to nodules in nodulated legumes. However, a corresponding increase in the proportion going to

the roots was noticed (Small and Leonard, 1969). They took this change in translocation pattern to be a contributing factor in the inhibition of nitrogen fixation by combined Nitrogen. Nutritional elements such as phosphorus and nitroge are known to have comparable effects on the translocation pattern of sucrose in plants like Hibiscus esculentus. Adedipe (1975b) compared the effects of these nutritional elements in an old and young leaf. He found the effects of nitrogen to be opposite to those of phosphorus as regards distribution of ^{14}C to the leaves, stem and root. The direction of transport of photosynthates was similarly affected. That is, in the old leaf while high and medium levels of N and P (100, 20 and 2 mg/l) enhanced export of assimilates, in the young leaf, high levels of P decreased ^{14}C export. In the old leaf stage, high leves of N enhanced ^{14}C distribution to the leaves while high levels of P decreased it. High levels of N decreased and that of P increased the distribution to the stem and root.

2.1.8.4. ROLE OF GROWTH INHIBITORS AND PROMOTERS ON TRANSLOCATION.

Certain compounds which have an inhibitory effect on some physiological processes may also enhance, retard or prevent translocation. Metabolic inhibitors have been shown

to inhibit carbohydrate translocation; some of these inhibitor include 2, 4 dinitrophenol (D N P), arsenite, azide, fluoride and hydrogen cyanide (Willenbrink, 1957; Ullrich, 1961; Harel & Reinhold, 1966; Kriedemann & Beevers, 1967). Studies with soyabean (Harel & Reinhold, 1966) and castor bean seedlir (Kriedemann & Beevers, 1967) strongly indicate that DNP inhibition of translocation was due to the effect of DNP on the metabolic processes involved in the movement of photosynthate into and out of the sieve tubes. In these studies, translocation in the sieve tubes did not appear to be affecte by DNP. Leanard et al. (1967) also reported that both 2, 4-D and picloran applied to the shoots of grape prevented an export of assimilates from such shoots, but transport within the shoots continued.

Cellular and tissue growth stimulated by growth hormones puts a heavy demand on translocated metabolites for building materials and energy. It is believed that the metabolism of these growth centres (sinks) have a strong influence on translocation (Devlin, 1969). Experiments by De Stigter (196 with Cucumis melo and Cucurita ficifolia suggest a direct hormonal influence on phloem translocation. Application of auxin, cytokinins or mixtures of auxin, cytokinins and Gibberellic acid to decapitated internodes or pedicels promo

the accumulation of labelled assimilates in the stump (Booth et al, 1962; Seth and Wareing, 1964, 1967 and Davies and Wareing, 1965). Booth et al. (1962) observed that there was accumulation of radioactivity when IAA was applied to stumps of Solanum andigena after decapitation. They made a similar observation in Meteor pea bearing 4 - 5 expanded leaves. Although Kinetin and Gibberellic acid were ineffective in this respect, in later experiments it was observed that Kinetin and Gibberellic acid (GA) when applied with Indole - 3-acetic acid (IAA) to the decapitated plants of Phaseolus vulgaris var. 'Canadian wonder', greatly enhanced the effect of IAA by doubling the accumulation of radioactivity (^{32}P) in the internode (Seth and Wareing, 1964). Davies and Wareing (1965) showed that IAA induced accumulation of ^{32}P in decapitated intenodes, was reduced if IAA and triiodobenzoic acid (TIBA) were applied in combination and they suggested that basipetal transport of IAA was involved in regulating the ascent of assimilate into the treated tissue. Khan and Sagar (1969) observed an increase of 30 - 50% in export of $^{14}_{1}C$ in 24 hours in tomato plants when growth regulators were applied 48 hours before supply of $^{14}CO2$. They used 1-naphyl-acetic acid (NAA) and 2,4,5-trichlorophenoxy acetic acid (2, 4, 5-T).

Application of ethylene, Indole - 3 - acetic acid (IAA), 6 (Benzylamino)-9-(2-tetra - hydropyranyl)- 9 - H-purine (SD_{8339}) or mixtures of IAA, GA and cytokinins increased the accumulation of ^{14}C-activity in decapitated internodes of Phaseolus vulgaris seedlings (Mullins, 1970). He observed the differences between treated and untreated tissues with respect to import of labelled assimilates only 3 hours after the application of mixtures of IAA, Ga and SD_{8339}. Mullins (1970) also noted that the inhibitory effects of abscisic acid on import of assimilates were counter-acted by SD_{8339}. There have been several interpretations of the hormone directed transport. One interpretation of this effect is that growth regulators increase the demand for assimilates by stimulating synthetic activities in the treated tissues, that is, by creating a sink,(Mullins, 1970). Booth et al. (1962), however proposed that the effect of IAA on transport of metabolites was not primarily to create a metabolic 'sink' by stimulating synthesis but may be rather to stimulate active uptake and accumulation by the tissues to which it is applied. Davies and Wareing (1965) also proposed the theory that growth regulators may have direct effects on translocation by stimulating the activity of the phloem transcellular strands (Thaine, 1961 and 1962),

Mullins (1970), however, could not make any distinction as to the mechanism of the effect of growth regulators on assimilate translocation. According to him it could be due to one of two reasons. Either: there may be effects on sink potency through stimulation of synthetic activities in all tissues of the internode and thereby increasing the demand for assimilates (e.g., mass flow hypothesis). Alternatively, the influence of growth regulator may be more specific and have greatest effect on phloem metabolism (transcellular strand hypothesis).

2.1.8.5 WATER STRESS AND OTHER FACTORS

The retention and transport out of the fed leaf of applied ^{14}C-sucrose and ^{32}P, the distribution patterns of ^{14}C to the plant parts and direction up or down, were found not to be influenced by moisture stress in Hibiscus esculentus (Adedipe, 1976). He concluded that this was an indication of marked drought tolerance by Hibiscus esculentus. Normal growth was observed to be associated with the distribution of ^{14}C and if soil moisture stress was not enough to influence growth, the latter was not affected.

Tomato leaves grown under a carbon dioxide enriched environment have been found to have a higher rate of carbon

fixation, transport and consequently a greater supply of mobile leaf assimilate than those under atmospheric carbon dioxide. This suggests a higher rate of photosynthesis in a carbon dioxide enriched environment (HO, 1977).

2.2 GROWTH ANALYSIS

2.2.1. GROWTH OF THE ONION PLANT

Onions are grown mostly by transplanting the seedlings when they are about four weeks old, but when seeds are required, then the bulbs are planted since onions are biennial. Ideally, onions are transplanted before bulbing begins. After the seedling is established, the young onion seedling continues to produce new foliage and roots and the stem slowly elongates and broadens (Jones and Mann, 1963).

At the centre of the shoot stem, on its upper surface, is the apex where new leaves are formed. Each leaf arises from the stem tip as a ring which is somewhat higher on one side. This ring, as it grows upwards forms a tube (the sheathing leaf base) and the higher side of the ring elongates into the leaf blade (Jones and Mann, 1963). The shoot apex is thus left within and at the bottom of the youngest tubular leaf blade and gives rise to next leaf so that each leaf surrounds the successively younger leaves which follow it.

The leaves alternate along the stem, each leaf blade extending from the side of the plant opposite the leaf blade which preceded it, so that the leaves are disposed in two ranks. As the internodes do not elongate, the leaves appear compact. The true stem (disc) lies underground but the false stem (pseudostem), a firm structure to which the leaf blades are attached, projects above the ground (Jones and Mann, 1963).

2.2.2. GROWTH OF THE BULB

Even though Rey (1973) indicated that bulbing started at the 7 - leaf stage in onions, its onset has been found to be a function of daylength and temperature. When conditions of daylength and temperature are favourable, the leaf bases above the stem enlarge and food reserves are stored in them. As bulbing progresses, leaves near the bulb centre abort their blades and become storage structures which remain within the bulb and enlarge (Abdalla and Mann, 1963). Bulb formation is generally accompanied by carbohydrate accumulation. This accumulation indicates an excess of carbohydrate production over current consumption (Butt, 1968).

The need for a continuous supply of sugars in large quantities to support bulb growth has been shown by Heath and Holdsworth (1948) in their defoliation experiments.

They observed that defoliation delayed bulbing until after the emergence of new leaves. Even though short day conditions do not favour bulbing, as shown by Manuel and Velasco (1962), onions grown from sets (small onion bulbs) under short day conditions (8 hours) developed bulbs when supplied with sugars (Heath and Holdsworth, 1948).

Onions are very sensitive to daylength and temperature. Each variety or group of varieties has a well defined minimum daylength requirement for bulb formation (Jones and Mann, 1963). As the photoperiod stimulus is received by the leaves, some foliage must be present in order that the plant may respond to daylength, but at any stage of its life, even as a dormant bulb the onion may respond to temperature. Walker (1921) working with 'Red globe' and Yellow Bermuda onion varieties found that the optimum temperature for germination was 25°C. Rapid growth of tops as compared with roots occurred at 20°C or higher, while root growth was best at lower temperatures (12 - 20°C). Thompson and Smith (1938) with Ebenezer onion plants grown under long days and at three different temperatures found that the plants under different temperatures did not react in the same way. Plants at 50 - 60°F did not bulb; those at 60 - 70°F developed

mature bulb with still green tops; those at 70 - 80°F had mature bulbs and the tops were dead. High temperature under short days, however, was not effective in causing bulbing, indicating that bulbing is determined by the interaction of long day and high temperature. Heath (1943) Heath and Holdsworth (1943) and Clark and Heath (1962) found that bulbing is speeded up by rise in temperature and greatly delayed or prevented by low temperature. Butt (1968) observed that 25°C was optimal for bulb growth and development.

Length of photoperiod has been shown to exert an effect on bulb formation and subsequent development which was opposite to that exerted on top growth (Manuel and Velasco, 1962). They showed that short days promoted top growth but inhibited bulb formation and development, while long days had the reverse effects. Butt (1968) observed a clear positive correlation between plant size at the time at which bulbing is induced by long days, and the final bulb size and weight. He therefore showed that in bulb production it is important to grow the onion plant under short day conditions in the early stages of growth in order to develop a considerable leaf area before bulb induction in cv. Wijbo. Bulb size of white Grano has been found to be greatly reduced if plants

were grown after the daylength requirement is exceeded, but if the plants reached appreciable size before the daylength requirement was met, the bulbs were large. If plants grown after the daylength requirement was exceeded were provided with the minimum temperature requirement, bulbs were formed but were small even though mature (Jones and Manm, 1963).

Bulb production has been shown to be related to seedling vigour. There was a greater bulb production from onion plants grown from seedlings with high vigour (Moursi and El-Habbasha, 1967).

Soluble solids have been found to be unequally distributed both radially (center to outer periphery) and vertically (bottom to top) in the bulbs of cultivars Yellow Globe and Sweet Spanish. The soluble solids were highest at the basal end of the bulb and decreased toward the top. The centre of the onion bulb (younger fleshy scale leaves) was found to have the highest soluble solids which decreased radially toward the periphery (outer scale leaves) (Dehlavi, 1971). He also showed that soluble solids varied with the age of the plant, increasing rapidly when the plants were 20 - 40 days old but the subsequent increase was not as rapid. This study indicated differential accumulation of soluble solids in the fleshy scale leaves during growth

of the onion bulb.

2.2.3. ROOT GROWTH

Onion roots are continually added, arising from the younger stem tissue; the onion plant is known to have one of the most limited root systems among the vegetable crops (Jones and Mann, 1963). Sideris (1925) reported that there are two periods of root production. The first set of new roots produced at the time of germination gradually died and a new set was produced at the time of bulbing, which functioned until the plant died. Jones and Mann (1963) did not confirm the existence of two main periods of root production, but showed new roots being added at a uniform rate. As the plant died, the rate of death of roots was faster than production of new roots.

2.2.4. OTHER ASPECTS OF ONION GROWTH AND DEVELOPMENT

Growth analysis represents a promising experimental approach in the initial stages of analysing the complex character of yield capacity (Sestak et al. 1971). Estimation of the surface area of leaves and other assimilating plant organs, and measuring the resulting biomass accumulation, expressed as the dry weights of whole plants or parts, is an essential part of classical growth analysis. It is

necessary in many plant physiological studies. Growth analysis has been shown to be more suitable for some types of plants than others e.g., sunflower, tobacco and maize have been observed to be suitable (Kostkova, 1968). Plants with bulky roots, tubers and corms (e.g., potato) show large variations in their underground dry weight so that pairing of individuals based on shoot parameters has been found to be ineffective (Nosberger and Humphries, 1965). These plants are not suitable for growth analysis. Many plants show large variation in leaf area and tend to be highly susceptible to damage to the leaves by pests e.g., sugar beet (Sestak et al., 1971). This risk can be reduced by chemical treatment. Sestak et al. (1971) reviewed the principal methods suitable for estimating the area of all plant assimilating surfaces indicating which methods are suitable for the different shapes of leaves. Specific or varietal differences in various growth characteristics have been described e.g., differences between three spring wheat varieties were examined by Stoy (1965). He observed that the seasonal changes in the assimilatory surface area had two peaks associated with tiller growth. The main factors determining the photosynthetic production seemed to be the

size and arrangement (to avoid self shading) of the leaves as well as the time over which the leaves were photosynthetically active.

On the basis of reports mentioned earlier, it seems likely that onion growth could be affected by temperature, photoperiod, water stress and mineral nutrition. These affect the plant through its photosynthetic system and thereby affecting assimilate production and distribution among the plant parts to facilitate growth.

2.2.4.1. PHOTOSYNTHETIC SYSTEM

In most higher plants chlorophylla (chl.a) is usually the major pigment component by weight and is always accompaired by chlorophyll b (chl.b). The absorption spectrum of Chl.b is almost half that of Chl.a and this is also reflected in their composition by weight. Magnesium is tied up in the structural ring of both chlorophylls and Zinc is also related to chlorophyll formation (Nason, 1958) and leaf chlorosis has been established to be one of Zinc deficiency symptoms (Ajakaiye, 1975).

The total chlorophyll content of citrus leaves and fruits were found to vary with the developmental stage and to some extent with the growing conditions (Turrell et al, 1961).

They also observed that within a given plant, the chlorophyll a/b ratio may also change. Jahn and Young (1976) found that in the rind of citrus fruits, as they ripened, the relative concentration of chlorophylls a and b changed and there was a decrease in the a/b ratio as total chlorophyll levels decreased Chlorophyll b was found by these workers to have a greater resistance to degradation.

Variations in chlorophyll content are recognised within and between species and have been correlated with agronomic performance. Boyd and Walker (1972) showed that the variation of chlorophyll a in nineteen varieties of wheat appeared to be independent of all other parameters that they assessed. Whilst lower leaf canopy senescence was greater at low nutrient levels, flag leaf chlorophyll content increased slightly. In contrast, as light intensity improved, chlorophyll content increased markedly. Thomas and Gausman (1977) reported that chlorophyll concentration of eight crops varied from 4.67 mg/g in Sorghum to 14.48 mg/g in lettuce with cocumber, cotton, contaloupe, maize, spinach and tobacco coming in between in that order.

Vega et al. (1972) observed that water stress led to a decrease in the dry weight of the leaves and bulbs of onion. The number of leaves decreased during the drought period at first but this effect latter disappeared. The lower yield of plants subjected to drought was found

by these workers to be due to a reduction of the photosynthetic system since leaves could not complete their growth before the critical period of rapid bulb growth.

Prometryne (a herbicide) applied at a rate of 1.5 or 3 kg/ha was found to reduce the chlorophyll and pigment contents of onion leaves, compared with untreated controls, in a dry year, but in a wet year it increased the chlorophyll and pigment contents (Sivtsev and Kuznetsova, 1973). They also reported a reduction in bulb yield by 75% in a dry year.

2.2.4.2. NET ASSIMILATION RATE (NAR)

Gregory (1926) showed that in Barley, up to the time of maximum leaf area (which coincides approximately with the first differentiation of flowers), the net assimilation rate (NAR) was independent of time. He made the generalization that the mean net assimilation rate was constant for different species in the most diverse environments. Heath and Gregory (1938) later presented data to support this, but since then many variations have been observed by other investigators.

Watson (1952) found the NAR of kale to decrease linearly with increase of leaf area index (LAI) but that of sugarbeet was less affected by change in LAI. Because of the link

between NAR and L/I, the rate of dry-matter production per unit area of land (Crop growth rate, CGR) was found to show a curved relation to LAI for kale. He asserted that defoliation in plants where NAR is in excess of the optimum, can increase the total dry-matter as could be the case in Kale.

Robinson (1973) found short-day onion plants (De Wildth and Texas Grano) of similar chronological age, but differing in weight, to have a constant ratio of bulb to leaf dry matter at any particular stage of growth. There was little variation in leaf area and dry matter during the growing season when plants were sown from February - May. In June sown crops the leaf area and dry matter had lower values due to premature rapid bulb swelling and arrested leaf growth, both attributable to high temperatures. The mean NAR was also found to rise with successive sowing dates.

Water deficit has been observed to depress the NAR of onion seedlings (El-Habbasha and Shaheen, 1976). They attributed this to a reduction in the water content of the plants, which resulted in reduction in enzymatic activity and stomatal closure; the latter in turn caused a reduction in the supply of carbon dioxide to the plant. This consequently caused a reduction in assimilate production.

2.2.4.3. MINERAL NUTRITION

Several investigators have studied the effects of mineral nutrition on onion growth and bulb production and it is generally agreed that mineral nutrition has marked effects on onion growth (Pande et. al. 1969; Asif et al. 1976). Mineral nutrient content of the plants have also been shown to vary with development stage, position of leaves and part of the plant (Jones, 1964; Gorshine et.al., 1965 and Jones, 1970).

The translocation of nutrients necessarily represents an interphase, it follows and depends on uptake and precedes assimilation or perhaps storage in distant tissues. The availability of plant nutrients is closely related to soil pH. The optimum pH for most plants is about 6.0 to 6.8 but crops on organic soils often grow better at somewhat lower pH values. Such soils have much higher amounts of calcium and magnesium than mineral soils of the same pH (Mortvedt et al., 1972)

A relationship between nutrient concentration and growth has been shown. In peas it was observed that as the nutrient solution concentration was decreased, dry matter production

decreased but not proportional to the dilution. There was a somewhat more pronounced drop in chlorophyll content but this too was not proportional to the degree of dilution (Lastavka and Minar, 1970).

Onions supplied with nitrogen as nitrate, have been found to grow significantly more in respect of their height, number of leaves and fresh weight of tops. The best results were obtained when 400 kg/hectare of nitrogen was applied as nitrate (Verma et al., 1974). NPK fertilizer increased tissue content of zinc, phosphorus, calcium and magnesium in 'Sweet Spanish' onion (Ajakaiye, 1975).

Zinc deficiency symptoms occur in many plants when the leaf concentration is less than 20 ppm in the dry matter. The normal concentration range is 25 - 150 ppm with toxicities occuring when the zinc levels exceed 400 ppm. Ajakaiye and Greig (1976) found the optimum zinc rate for bulb onion growth to be 6 ppm with $ZnSO_4$ as source, but this concentration depressed leaf calcium and magnesium concentration, while that of the bulb was increased. The depression of leaf tissue concentration of calcium and magnesium at high rates of Zn application led these workers to suggest some interactions within the plant.

In a study of the interaction of temperature and phosphorus levels, Martin et al. (1965) observed that in soils moderately low in available Zn, high levels of phosphorus induced Zn deficiency in tomatoes at low but not at high temperatures. Soils that were very low in Zn, however, produced Zn deficient plants at both low and high temperatures. Asif & Ajakaiye (1974) presented data from field experiments in Nigeria which indicated that high levels of soil phosphorus (P) induced Zn deficiency in onions thereby reducing growth and yield. Ajakaiye and Greig (1976) however, reported increase in Zn content of the bulb to be followed by consequent decrease in Zn content of the leaf. They suggested that Zn translocation to the onion leaf was apparently impeded by detrimental or enhanced by favourable P/Zn ratios. An increase in bulb magnesium and calcium was accompanied by a decrease in Zn content of the leaf for which they suggested difficulties in translocation.

CHAPTER 3

MATERIALS AND METHODS

3.1. PLANT CULTURE

Three cultivars of onion used were Red-Kano (a popular red skinned local onion), Eclipsel-Bermuda and Texas-Grano (imported white early maturing types).

The seedlings were raised in sterilized soil in trays. The soil was steam sterilized in a "camplex" soil sterilizer following the manufacturer's directions. The soil used was a moderately well-drained sandy-loam soil with a pH of 6.5.

When the seedlings were four weeks old, 400 plants of each cultivar were transplanted into clay pots (22 x 26 cm) on 27th February, 1978 for the 1978 experiment and 2nd March, 1979 for the 1979 experiment. The plants were watered daily until the seedlings were well established after which they were watered every other day. A 1:1 mixture of ammonium sulphate and super phosphate was supplied at the rate of 7g per pot in two split doses when the plants were two and six weeks old after transplanting. The plants were sprayed twice (at four and eight weeks after transplanting) with DDT/BAC solution to control thrips.

3.2 TRANSLOCATION STUDY

3.2.1. AGE AND POSITION OF THE LEAF SUPPLIED WITH $^{14}CO_2$

Experiments were carried out on the following stages of development of the plants:

STAGE 1

59 days after transplanting (on 27th April for the 1978 experiment and 1st May for the 1979 experiment), the bulbing had just started. Plants were selected for uniformity of size and with 5 - 6 leaves. Leaves 1 - 5 were treated with ^{14}Carbon dioxide.

STAGE 2

81 days after transplanting (on 19th May for the 1978 experiment and 23rd May for the 1979 experiment), leaves 1, 3, 5 and 7 were treated, on plants with an average of 8 - 9 leaves. These were selected for uniformity of size.

STAGE 3

101 days after transplanting (on 12th June, 1979), leaves 2, 4, 6 and 8 were treated with ^{14}C on plants of cv. Red Kano with an average of 11 leaves. Leaves 3 and 5 were treated in cv. Eclipsel-Bermuda and cv. Texas-Grano on plants with an average of five leaves.

STAGE 4

123 days after transplanting (on 4th July, 1979), leaves 5, 6 and 7 of cv. Red Kano were treated. Plants of cv. eclipsel Bermuda and cv. Texas Grano had no more green leaves on that date and most of the plants of cv. Red Kano had dry basal leaves.

3.2.2. LABELLING THE PLANTS WITH $^{14}CO_2$

At each of the four growth stages, four replicates (individual onion plants) of each treatment were selected and treated. In each treatment one leaf blade to be treated was selected and enclosed in a polyethylene bag (34cm x 9cm) in which a small glass tube was adhered (towards the closed upper end). The open end of the bag was lined with a layer of thin foam and it was closed with bull-dog clips, after inserting the treated leaf in the bag (Fig.1). The polyethylene bag was pierced, near the place of attachment of the glass tube, to facilitate the entry of a hypodermic needle fitted to an 'Agla' micrometer syringe. The enclosed portion of each plant (leaf blade) was then supplied with 25 μCi of $Na_2{}^{14}CO_3$ (specific activity 0.5 mCi/ml) obtained from 'The Radiochemical Centre' Amersham, England. Labelled carbon dioxide was released by the addition of excess normal

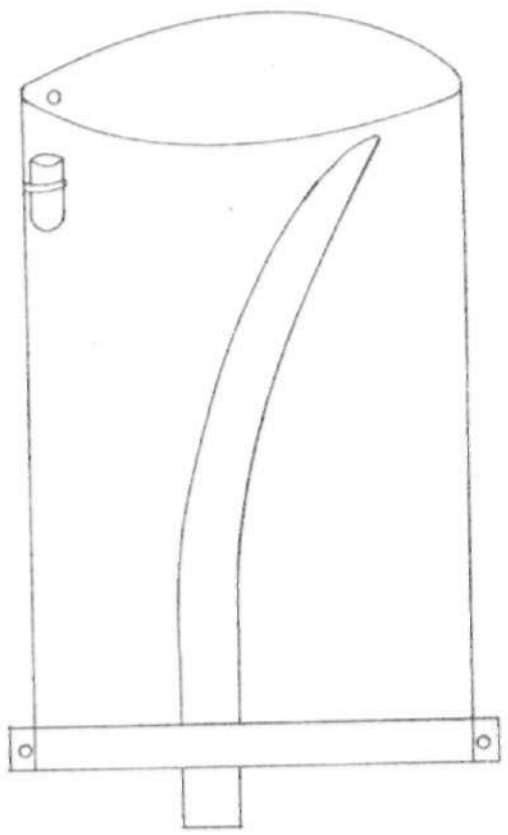


FIGURE 1 Diagram showing Assimilating Chamber in which leaf was supplied with $C^{14}O_2$

Hydrochloric acid from a hypodermic syringe through the same hole which was immediately sealed with cellotape. The experiments were done on a bright sunny day between 10 a.m. to 1 p.m.

The plants were allowed to photosynthesize in the $^{14}CO_2$ enriched atmosphere for one hour after which the bags were removed. The plants were then left to photosynthesize in the normal atmosphere for a further 23 hours, after which they were harvested. The roots were washed free of soil and rinsed with distilled water. The plants were then quickly divided into the following components to avoid further translocation:

Roots

Bulb

Pseudostem (PS)

Leaf blades below treated leaf (LBTL)

Treated leaf (TL)

Leaf blades above treated leaf (LATL)

The fresh weights and diameters of the bulbs were recorded and two plants from each treatment were selected for autoradiography, and later they were included in the radio-assay.

3.2.3. AUTORADIOGRAPHY

The bulb was cut transversely into thin slices, and the

pseudostem divided longitudinally into two. The leaves, pseudostem, roots and bulb slices were pressed between newspapers and kept in an oven at 50°C for 24 hours. They were then mounted on white art papers using masking tape strips to hold the plants in place and dried in the oven at 55°C until they were dry. The mounted sheets were exposed to kodirex X-ray films, using the method described by Yamaguchi and Crafts (1958). In the dark room, the paper with mounted onion plant was placed in contact with an X-ray film, and the two were pressed between two flat wooden boards. The boards were tied tightly with string and wrapped in black polyethylene sheet and left in the dark room for a week.

The exposed X-ray films were developed according to the manufacturers instructions, washed in running water and dried. Photographs were taken of the mounted plants and their respective autoradiographs. The mounted plants were then carefully removed and prepared for radio-assay.

3.2.4. METHOD OF ASSAY

The plant parts were dried at 70°C and then weighed. Each sample was first ground coarsely in a blender, then passed through a micro-Wiley mill to pass through a 40 mesh sieve. About 10 mg of the powder was ground finely in a mortar with

80% alcohol and made up to 5 ml with the same solvent. This was shaken and 1 ml of it pipetted onto a weighed planchet. The sample was dried by overhead heating and kept in a dessicator. It was later weighed to determine the amount of material deposited on the planchet. The sample was assayed for radioactivity with a Panax Autoscaler using MX123 GM tube. The background count was subtracted from the gross count of each sample. The count per mg/minute (Specific activity) was calculated. The specific activity multiplied by the total dry weight of the individual plant part in mg gave the total count. The relative distribution of the ^{14}C-labelled products was then expressed as the proportion of the total radioactivity in the plant.

3.3. GROWTH ANALYSIS

The experiment was carried out between April and June 1979. Every week, four plants were randomly selected and uprooted, washed free of soil, rinsed with distilled water and the following observations made:

1. Number of mature leaves per plant.
2. Fresh weight of whole plant
3. Fresh and dry weights of leaves bulbs, roots and pseudostem.

4. Diameter of fresh bulb

5. Leaf area.

3.3.1. DETERMINATION OF LEAF AREA

The leaf area was measured using a portable leaf area meter (model LI-3000) fitted to a transparent belt conveyor accessory (Model LI-3050 A/3) manufactured by Lambda Instrument Corporation Ltd. of the U.S.A. Since this instrument was designed for measuring area of flat surfaces, it was necessary to open out the cylindrical leaves of the onions and spread them out flat. To avoid folding up of leaves and giving inaccurate results, the leaves were traced out on sheets of paper. These were cut out and their area measured. This area was equivalent to that of the leaves. Sestak et al. (1971) stated that most of the methods of estimating leaf area are applicable not only to fresh leaves but also their images whether drawn, recorded photographically on film or paper or as blue-prints or colour images. Such recording allows the area measurements which are usually relatively time-consuming to be postponed to a more convenient time.

3.3.2 PREPARATION OF MATERIAL FOR MINERAL ANALYSIS

The plants used for leaf area determination were dried at 70°C until dry, their dry weights taken and then they were

ground in a cassella mill. The ground material was oven dried overnight at 100°C and 1 g of it weighed out and wet digested in a Kjeldahl flask as described by Sandel (1950). This was done by adding 20 ml of digestion mixture (made up of 650 ml of nitric acid, 20 ml of sulphuric acid and 80 ml of Perchloric acid) to 1g of the plant material in a digestion flask. The flask was heated at 100°C in a fume cupboard until all the yellow fumes of the nitric acid were expelled and the plant material was properly combusted. The temperature was then reduced to 30°C and the heating continued until all white fumes of perchloric acid and sulphuric acid were expelled and a clear liquid or white substance was left in the flask. The flask was allowed to cool. The digest was then washed with distilled water into a 100 ml volumetric flask and made up to the mark.

3.3.2.1. QUANTITATIVE DETERMINATION OF Ca, Mg, K, Zn and P

The concentrations of Ca, Mg, K and Zn were determined with a Perkin Elmer model 250B atomic absorption spectrophotometer.

3.3.2.1.1. CALCIUM AND MAGNESIUM

The reagent was prepared by dissolving 30.43 g strontium chloride in one litre of distilled water giving

a 10,000 ppm concentration of strontium. 5 ml of the reagent was added to 50 ml of sample to give a 1,000 ppm concentration of strontium. The addition of the strontium reagent was to prevent the interference of alluminium and phosphorus when readings of calcium and magnesium are being taken. The concentrations of calcium and magnesium were read at a wavelength of 4227Å for calcium and 2852Å for magnesium.

3.3.2.1.2 POTASSIUM AND ZINC

The reagent was prepared by dissolving 61.1 g of lithium chloride in one litre of distilled water to give a 1,000 ppm lithium solution; 5 ml of this reagent was added to 50 ml of sample to give a final concentration of 100 ppm lithium. The reagent was added in order to prevent the ionization of potassium in the hot acetylene flame, when readings are being taken, otherwise lower results would have been obtained. Potassium was read at a wavelength of 7665Å .

Zinc was read, without addition of any reagent, at a wavelength of 2138Å .

3.3.2.1.3 PHOSPHORUS

Phosphorus was determined by the vanadomolybdate colorimetric method. The reagent was prepared by dissolving 50g ammonium molybdate in 500 ml of water and 2.5g ammonium

vanadate in 500 ml of water. The latter was heated to dissolve the ammonium vanadate. 700ml of concentrated perchloric acid were added to the mixture and made up to 2 litres with distilled water. 10ml of the reagent were added to 10 ml of the digest (sample) in a 50ml volumetric flask and made up to the mark; a yellow colour developed. The colour developed was read on a Bausch and Lomb spectronic 20 model 33-31-72 at a wavelength of 440 nm. The instrument was previously set between zero and 100 using the standard.

3.3.3. QUANTITATIVE DETERMINATION OF CHLOROPHYLL CONTENT

Chlorophyll was determined by the method of Witham, Blaydes and Devlin (1971). One gram of small freshly-cut pieces of fully-expanded leaves were placed in a mortar. 40ml of acetone: water (80:20, v/v) was added and the tissue ground to a fine pulp. The resulting green liquid was transferred to a Buchner funnel and filtered by suction through No.1 Whatman filter paper. The grinding of the pulp was repeated with a 30ml aliquot of 80% acetone and filtered. Using another 20ml of the acetone, the grinding was repeated until the tissue was devoid of chlorophyll. The mortar and funnel were rinsed with 10 ml of the acetone. The final volume of the filtrate was adjusted to 100ml with 80% acetone.

The optical density of the chlorophyll extract in a 10mm cell was read with a Corning colorimeter (model 253) set at 645 & 663. Acetone (80%) was used as the blank. The amount of chlorophyll present in the extract was calculated on the basis of mg of chlorophyll per gm of leaf tissue using the following equations:

mg chlorophyll a/g tissue

$$= \left[12.7\ (D_{663}) - 2.69\ (D_{645})\right] \times \frac{V}{1000 \times W}$$

mg chlorophyll b/g tissue

$$= \left[22.9\ (D_{645}) - 4.68\ (D_{663})\right] \times \frac{V}{1000 \times W}$$

mg total chlorophyll/g tissue

$$= \left[20.2\ (D_{645}) + 8.02\ (D_{663})\right] \times \frac{V}{1000 \times W}$$

v = final volume of chlorophyll solution

w = weight in grams of fresh leaf tissue

D = Absorbance at the given wavelengths.

3.3.4. GROWTH INDICES

The data on leaf area and dry weights were used for calculating some growth indices using the following equations after Watson (1952):

1. Net Assimilation rate (NAR) $= \frac{(W_2-W_1)(\text{In } A_2 - \text{In } A_1}{(A_2-A_1)(t_2-t_1)}$

2. Leaf area ratio (LAR)

$$= \frac{A_2-A_1\ (\text{In } W_2-\text{In } W_1)}{(\text{In } A_2-\text{In } A_1)(W_2-W_1)}$$

3. Relative growth rate (RGR)

$$= \frac{(\text{In } W_2-\text{In } W_1)}{(t_2-t_1)} \times 100$$

4. Relative leaf growth rate (RLGR)

$$= \frac{\text{In } A_2-\text{In } A_1}{(t_2-t_1)} \times 100$$

5. Crop growth Rate (CGR)

$$= \frac{W_2-W_1}{t_2-t_1}$$

A = green leaf area (dm^2)

W = dry wt. of tops (g)

t = time in weeks.

3.3.5. STATISTICAL ANALYSIS

Analysis of variance was carried out to determine if there was any significant difference between the cultivars, and the effect of leaf position and plant age on the accumulation of carbon assimilates in the plant parts.

Analysis of variance was also carried out to see if there was any significant difference between the cultivars in the accumulation of minerals, and in other growth parameters.

CHAPTER 4

RESULTS

4.1. DISTRIBUTION OF ^{14}C-LABELLED PRODUCTS

4.1.1. AUTORADIOGRAPHIC STUDY

4.1.1.1. $^{14}CO_2$ SUPPLIED TO LEAVES 1-5 59 DAYS AFTER TRANSPLANTING

At this stage L1 supplied ^{14}C-labelled assimilates to all the leaves above the treated leaf in all the three cultivars. However, the two youngest leaves on the plants were more heavily labelled than the rest of the leaves in cv. Eclipsel-Bermuda and cv. Texas-Grano (Plates 2A and 3A), while in cv. Red-Kano there was less labelling of the youngest leaves (Plate 1A). When L2 was the source of radio-carbon, little activity appeared in L1 in cv. Red-Kano and cv. Eclipsel-Bermuda (Plates 1B and 2B) but in cv. Texas-Grano L1 did not show any activity (Plate 3B). Leaf 2 supplied labelled compounds to all the younger leaves in cv. Red-Kano and cv. Eclipsel-Bermuda but in cv. Texas-Grano only the youngest leaf was labelled (Plate 3B). From L3 no activity moved to the older leaves (Leaves 1 and 2) in any of the cultivars but all the younger leaves were labelled, the two youngest leaves being more heavily labelled than the others (Plates 1C, 2C, and 3C). When L4 was supplied

with $^{14}CO_2$, only a trace appeared in L3 in cv. Eclipsel-Bermuda and cv. Texas-Grano (Plates 2D and 3D), while in cv. Red-Kano there was no labelling in the older leaves (Plate 1D). In cv. Eclipsel-Bermuda and Texas-Grano, the youngest leaves imported the labelled assimilates from source leaf 4, the lower part of these leaves were more heavily labelled than the tips. In cv. Red-Kano, no activity appeared in the younger leaves (Plate 1D). Leaf 5 supplied no labelled assimilates to older leaves (Leaves 1-4) but the younger L6 and the emerging L7 in all the three cultivars were heavily labelled (Plates 1E, 2E and 3E).

The root system was extensively labelled with radiocarbon in all the treatments in each cultivar although some roots were more heavily labelled than others (Plates 1, 2 and 3). In cv. Red-Kano, less labelling of the root was observed from leaves 4 and 5 (Plates 1D and 1E). In each case activity accumulated in the root tips.

The pseudostem was heavily labelled in all the treatments. The corresponding fold of the treated leaf in the pseudostem was heavily labelled (note displaced pseudostem fold of the treated leaf in plate 2D).

The bulb imported ^{14}C-labelled assimilates in all treatments (Plates 1, 2 and 3). The radiocarbon in the bulbs

was localised in the bulb scale of the leaf supplied with $^{14}CO_2$ and that of the youngest leaf.

In each treatment, considerable amount of radiocarbon was retained by the source leaves.

PLATE 1: Photographs of the treated plants (above) and their autoradiographs (below) showing the pattern of distribution of ^{14}C from leaves 1(A), 2(B), 3(C), 4(D) and 5(E) respectively, from left to right, in cv. Red-Kano at 59 days after transplanting. The arrows indicate the position of the leaf that was exposed to $^{14}CO_2$ for one hour.

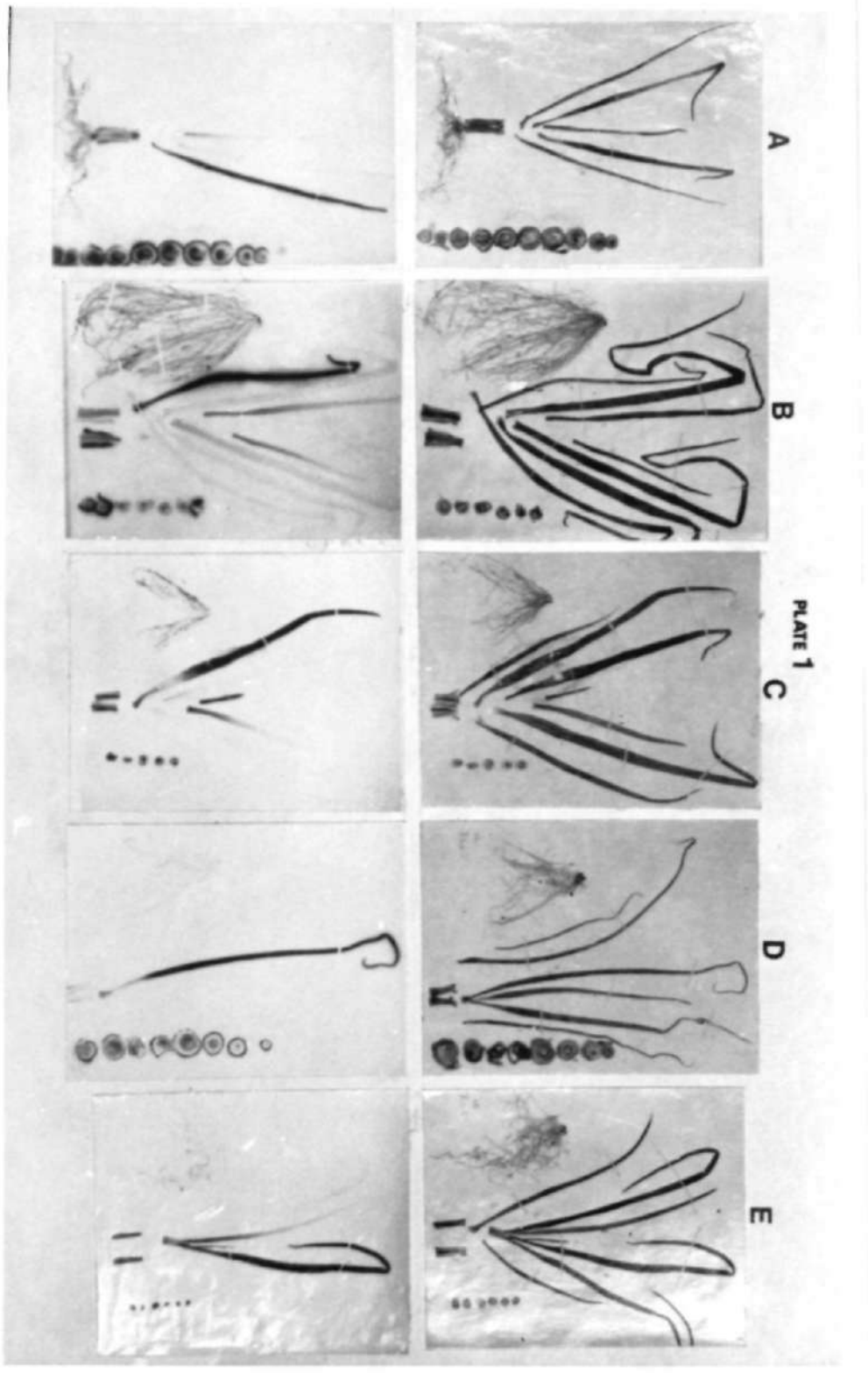


PLATE 1

PLATE 2: Photographs of the treated plants (above) and their autoradiographs (below) showing the pattern of distribution of ^{14}C from leaves 1(A), 2(B), 3(C), 4(D) and 5(E) respectively, from left to right, in cv. Eclipsel-Bermuda at 59 days after transplanting. The arrows indicate the position of the leaf that was exposed to $^{14}CO_2$ for one hour.

PLATE 2

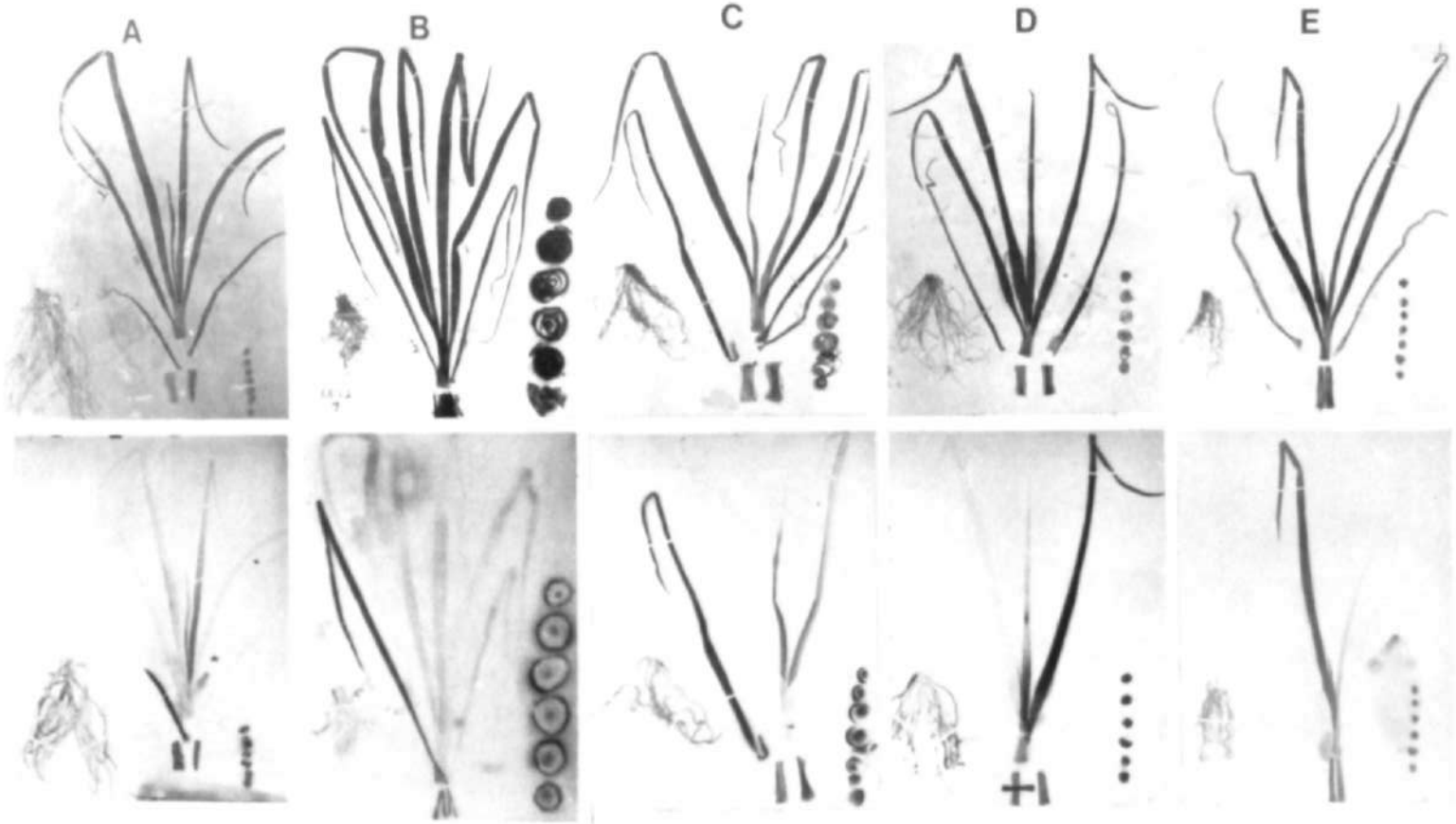
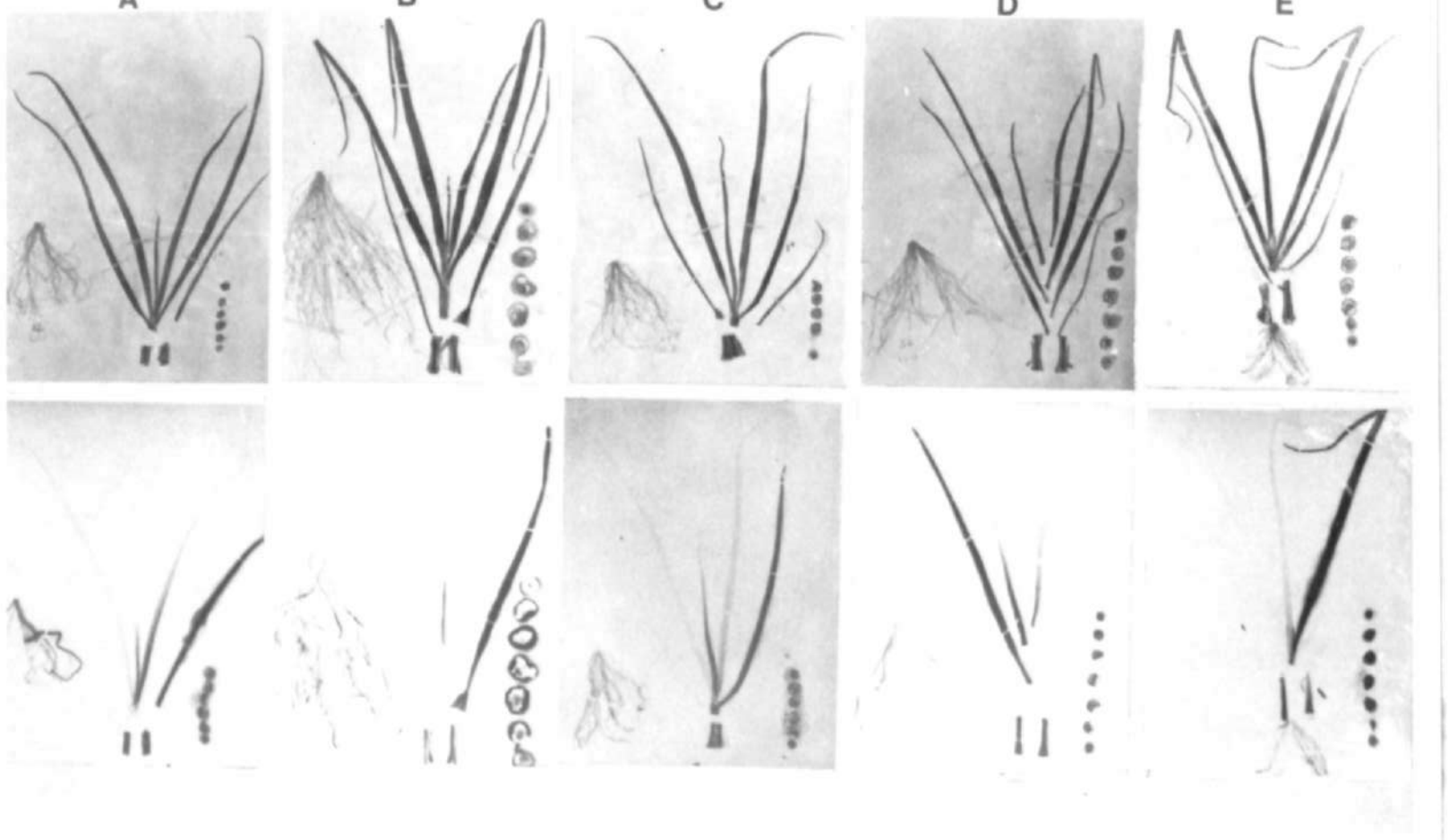


PLATE 3: Photographs of the treated plants (above) and their autoradiographs (below) showing the pattern of distribution of ^{14}C from leaves 1(A), 2(B), 3(C), 4(D) and 5(E) respectively, from left to right in cv. Texas-Grano at 59 days after transplanting. The arrows indicate the position of the leaf that was exposed to $^{14}CO_2$ for one hour.

PLATE 3



4.1.1.2. $^{14}CO_2$ SUPPLIED TO LEAVES 1, 3, 5 AND 7, 81 DAYS AFTER TRANSPLANTING

Leaf 1 supplied some labelled assimilates to the younger leaves. All the leaves showed same activity and labelling (Plates 4A, 5A, and 6A). When L3 was labelled with $^{14}CO_2$, no activity appeared in the older leaves (Leaves 1 and 2) in cv. Eclipsel-Bermuda and cv. Texas-Grano (Plates 5B and 6B). From L3 only a small amount of labelling was noticed in the upper leaves in cv. Red-Kano. The amount of ^{14}C-labelling present was much less in cv. Eclipsel-Bermuda and cv. Texas-Grano.

Leaf 5 of cv. Eclipsel-Bermuda and cv. Texas-Grano supplied labelled assimilates to all the upper leaves and to a lesser extent to the leaves below the source leaf (Plates 5C and 6C) but in cv. Red-Kano activity appeared in these two groups of leaves (Plate 4C). No activity moved out of the source leaf 7 in any of the cultivars (Plates 4D, 5D and 6D).

The pseudostem was less heavily labelled than in experimer one but in this case also the pseudostem fold of the treated leaf was more heavily labelled than that of other leaves.

In all the three cultivars, leaves 2, 3 and 5 supplied the radiocarbon products to the roots but L7 supplied negligible amounts which were not visible (Plates 4D, 5D and 6D). At this stage, the roots were less labelled than in the previous experiment.

The bulb imported ^{14}C-labelled assimilates from all the treated leaves at this stage. The bulb scale of the leaf supplied with $^{14}CO_2$ and the youngest bulb scales imported more radiocarbon. Older bulb scales did not show any activity.

There was close agreement in all the replicates in 1978 and 1979 experiments.

PLATE 4: Photographs of the treated plants (above) and their autodiographs (below) showing the pattern of distribution of ^{14}C from leaves 1(A), 3(B), 5(C) and 7(D) respectively from left to right, in cv. Red-Kano at 81 days after transplanting. The arrows indicate the position of the leaf that was exposed to $^{14}CO_2$ for one hour.

PLATE 4

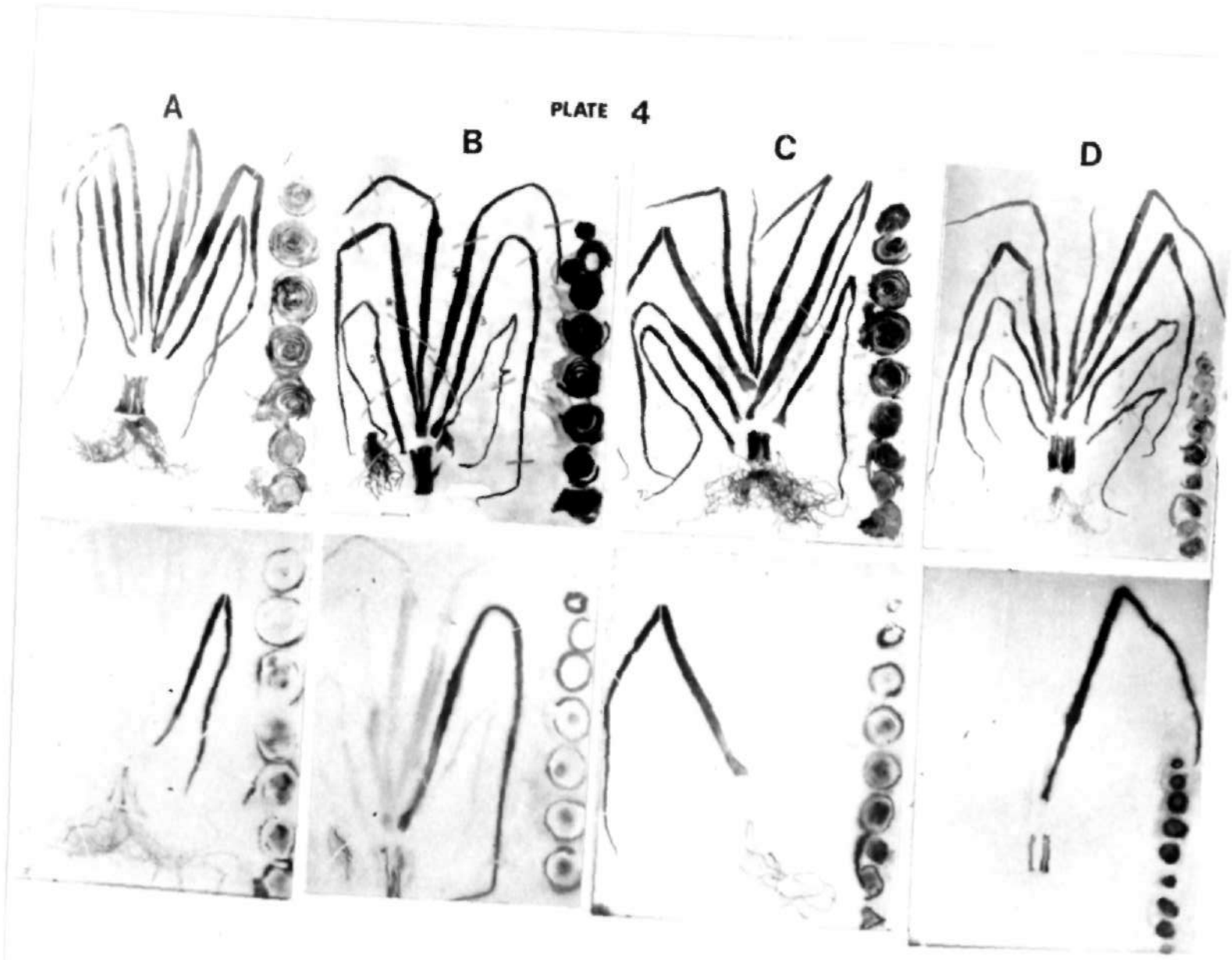


PLATE 5: Photographs of the treated plants (above) and their autoradiographs (below) showing the pattern of distribution of ^{14}C from leaves 1(A), 3(B), 5(C) and 7(D) respectively, from left to right, in cv. Eclipsel-Bermuda at 81 days after transplanting. The arrows indicate the position of the leaf that was exposed to $^{14}CO_2$ for one hour.

PLATE 5

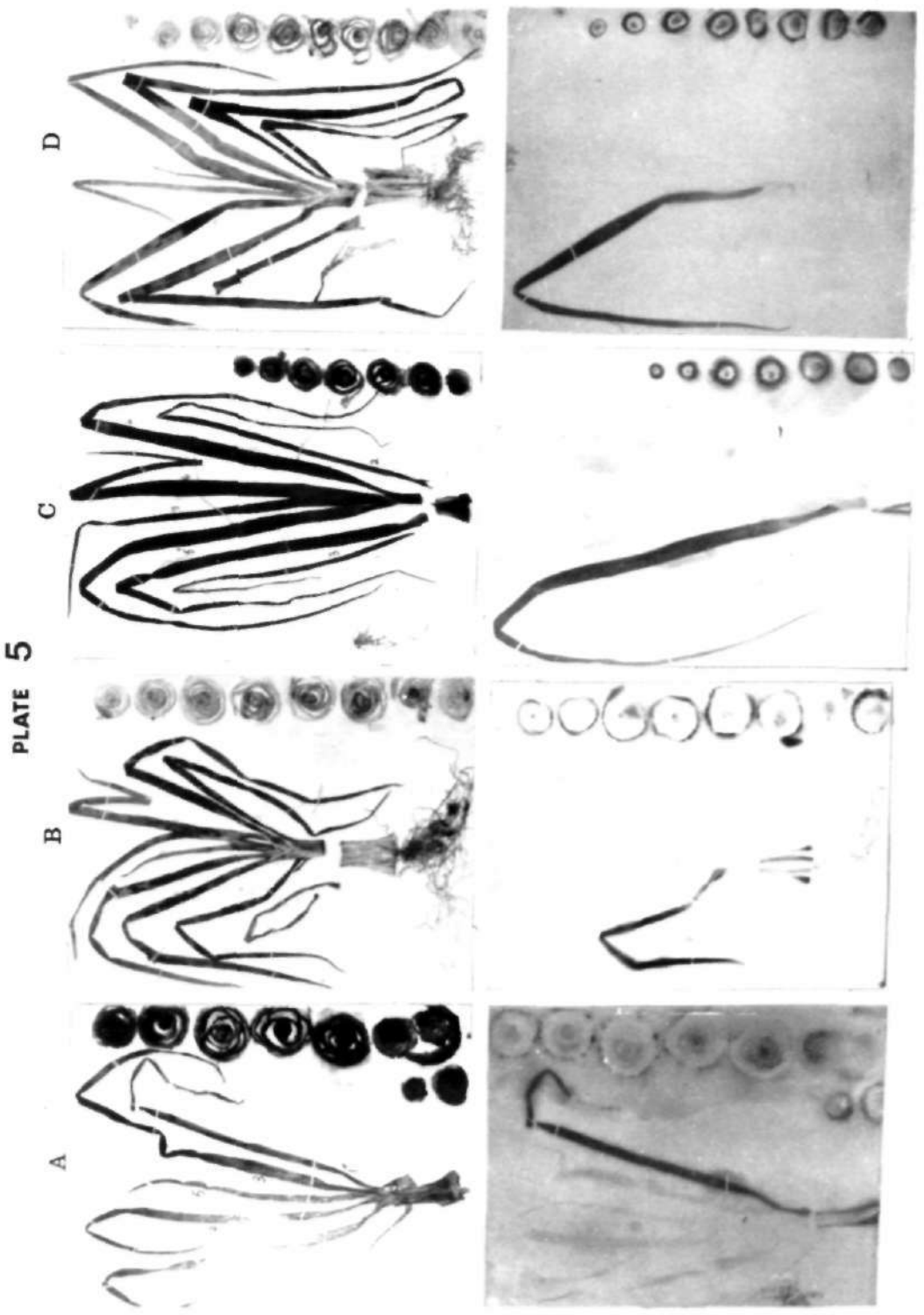
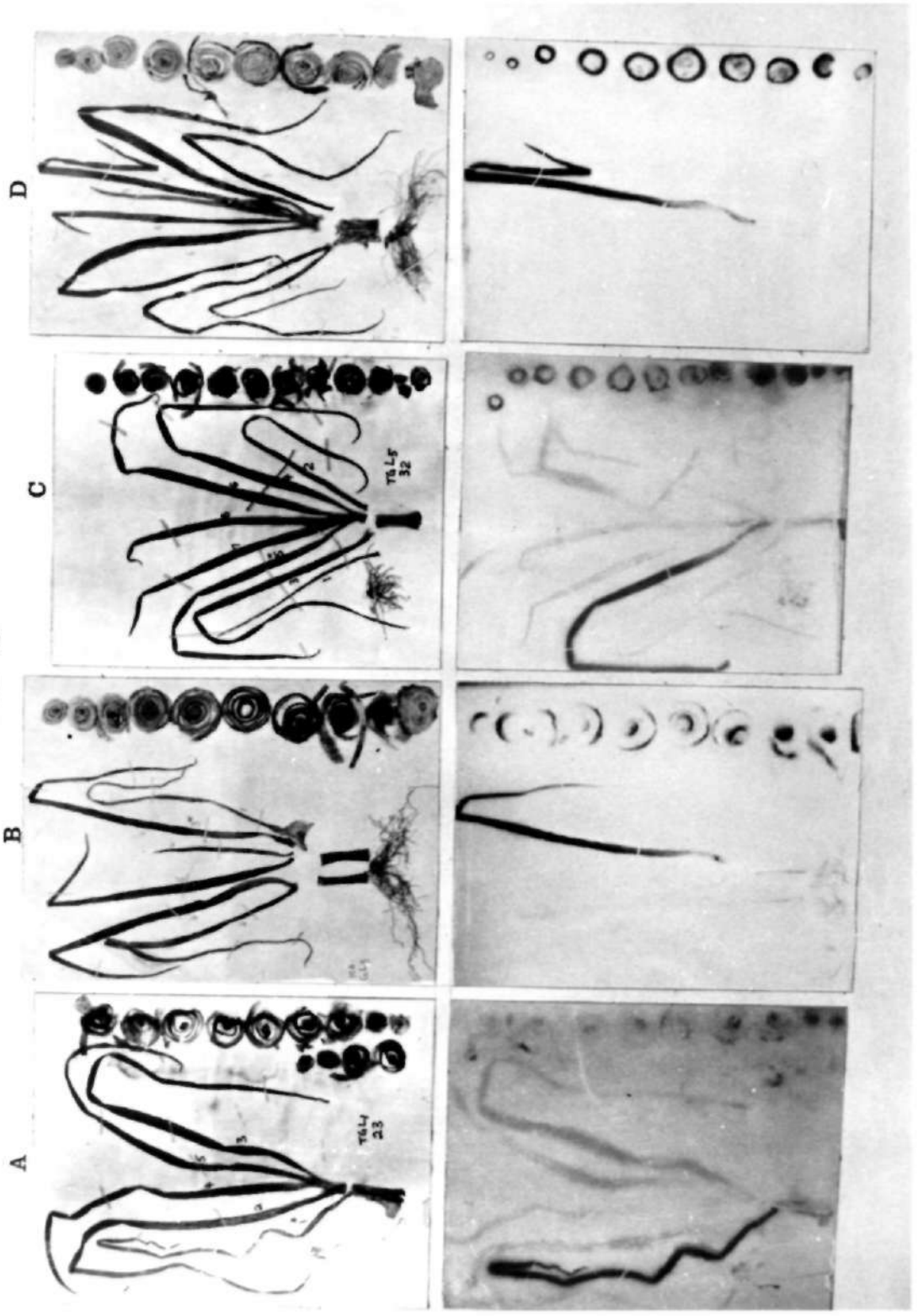


PLATE 6: Photographs of the treated plants (above) and their autoradiographs (below) showing the pattern of distribution of ^{14}C from leaves 1(A), 3(B), 5(C) and 7(D) respectively from left to right, in cv. Texas-Grano at 81 days after transplanting. The arrows indicate the position of the leaf that was exposed to $^{14}CO_2$ for one hour.

PLATE 6



4.1.2. QUANTITATIVE ASSAY

4.1.2.1. $^{14}CO_2$ SUPPLIED TO INDIVIDUAL LEAVES 59 DAYS AFTER TRANSPLANTING (EXPERIMENT I)

4.1.2.1.1. EXPORT OF LABELLED ASSIMILATES FROM THE TREATED LEAVES

The general pattern of export by leaves of cv. Eclipsel-Bermuda and cv. Texas-Grano in experiment I, 1978 was similar to that found in 1979 (Figs, 2 and 3), except for some slight differences from leaves 1 and 5, In 1978, L1 and L5 of cv. Eclipsel-Bermuda exported higher quantities (90.3% and 70.1% respectively) of ^{14}C-labelled assimilates than same leaf positions of cv. Texas-Grano (51.1% and 42.3% respectively). In 1979 experiment L1 and L5 of cv. Eclipsel-Bermuda exported lesser quantities (51.6% and 58.9% respectively). Export values from leaves 1, 3 and 5 of cv. Eclipsel-Bermuda in 1978 was much higher than the corresponding leaves of cv. Texas-Grano (Figs. 2 and 3).

In 1979 experiment, leaves 1 and 2 of cv. Red-Kano exported more assimilates than the corresponding leaves of the other two cultivars (81.5% and 98.6% respectively, Fig.3). Leaf 1 of cv. Eclipsel-Bermuda exported the least quantity of assimilates (51.6%), which increased to 71.5% from L2.

The export values in cv. Texas-Grano from these leaf positions was between those of cv. Red-Kano and cv. Eclipsel-Bermuda with a value of 66.6%. The export value from L2 of this cultivar was similar to L1. Leaves 1 and 2 of cv. Red-Kano and cv. Eclipsel-Bermuda showed a similar trend and in these cultivars export was initially low from L1 which then increased considerably from L2 by 17.1% and 19.9% respectively (Fig.3).

In all the three cultivars, L3 exported less assimilates than L2. Cultivars Red-Kano and Eclipsel-Bermuda exported similar quantities (72.8% and 70.2% respectively), while cv. Texas-Grano exported much lesser quantity (58.2%).

Leaves 3 and 4 of cv. Red-Kano exported similar quantities of labelled assimilates (72.8% and 73.8% respectively) but cv. Eclipsel-Bermuda and cv. Texas-Grano behaved differently. Leaf 4 exported more assimilates than L3 in cv. Texas-Grano (70.1%) and lesser quantities than L3 in cv. Eclipsel-Bermuda (64.8%).

Leaf 5 of cv. Red-Kano exported the least quantity of labelled assimilates (47.4%) while that of cv. Texas-Grano exported the largest quantity (68.3%). The value of cv. Eclipsel-Bermuda was (58.9%) (Fig.3). The total radioactivity recovered from the different plant parts when the leaves supplied with $^{14}CO_2$ are shown in tables 1 - 5.

4.1.2.1.2. PATTERNS OF ASSIMILATE DISTRIBUTION IN DIFFERENT PLANT PARTS

4.1.2.1.2.1. EXPORT TO THE LEAVES ABOVE THE TREATED LEAF (LATL)

The results of 1978 experiment are shown in Fig.7. The export of labelled assimilates to the LATL ranged from 15.6% to 34.6% in cv. Eclipsel-Bermuda and 12.2% to 32.7% in cv. Texas-Grano. Lower leaves (L1 - L3) exported higher quantities of the radiocarbon to the younger leaves in both cultivars. Leaf 2 exported 34.6% in cv. Eclipsel-Bermuda and 32.7% in cv. Texas-Grano. The cv. Texas-Grano showed a continuous decrease in export to the LATL from leaf 3 to leaf 5 (24.9% to 12.2%). A similar pattern was observed in cv. Eclipsel-Bermuda but in this case L5 exported higher quantities to this sink (23.5%) (Fig.7).

In 1979, in cv. Eclipsel-Bermuda the amount recovered from this sink was much lower than 1978. It ranged from 9.6% from L2 to 17.1% from L1. In cv. Texas-Grano, the largest percentage export to the LATL came from L1 (35.2%), followed by L4 (32.6%) but export from L2 and L3 was only 16.7% and 21.5% respectively. The contribution of L5 of this sink organ was only 7.7%. In cv. Red-Kano the highest

percentage export to these leaves was from L2 (39%) and the least from L4 (9%) while leaves 1, 3 and 5 exported 17.7%, 19.2% and 25.1% respectively, (Fig.9).

4.1.2.1.2.2. EXPORT TO LEAVES BELOW THE TREATED LEAF (LBTL)

In 1978, export to the LBTL in cv. Eclipsel-Bermuda ranged from 3% (from L2) to 7.7 (from L5). In cv. Texas-Grano, it ranged between 5.2% (from L2) to 14.2% (from L5). In 1979, a lower percentage was exported to this sink generally in all the cultivars. This ranged from 1.9 (from L2) to 8.9% (from L5) in cv. Eclipsel-Bermuda and 1.2 (from L3) to 5.6% (from L5) in cv. Texas-Grano. In cv. Red-Kano export of fixed ^{14}carbon to these leaves ranged between 0.9% (from L2) to 8.5% (from L4) (Fig.9).

4.1.2.1.2.3. EXPORT OF THE PSEUDOSTEM

In 1978, the highest percentage export of labelled assimilates to the pseudostem was from leaves 1 and 4 of cv. Eclipsel-Bermuda which exported 10.6% and 16% respectively while the amount exported by other leaves ranged between 7-12%. In cv. Texas-Grano higher quantities of radiocarbon was recovered from the pseudostem from source L1, which supplied 20.5%. Leaf 2 and 4 supplied 13% of ^{14}C while L3 and L5 exported 9-11% respectively to the pseudostem (Fig.7).

In 1979, percentage export of labelled carbon to the pseudostem was highest from L1 (14.2%) in cv. Texas-Grano while cv. Eclipsel-Bermuda and cv. Red-Kano exported 12.1% and 10.7% respectively. The amount of ^{14}C recovered from the pseudostem was 7% in cv. Eclipsel-Bermuda while in cv. Texas-Grano and cv. Red-Kano it was only 4.3% ard 2.2% respectively from source L2. The pseudostem imported more labelled assimilates from L3 in cv. Red-Kano (18.6) while in cv. Eclipsel-Bermuda and cv. Texas-Grano the amount recovered from this sink was only 14.8% and 11.7% respectively. When leaf 4 was supplied with $^{14}CO_2$, cv. Eclipsel-Bermuda exported a higher percentage (18.5%) of fixed ^{14}carbon to the pseudostem than cv. Texas-Grano and cv. Red-Kano which exported 8.8% and 12.7% respectively. Leaf 5 of cv. Red-Kano exported 22.9% of its fixed carbon to the pseudostem while cv. Eclipsel-Bermuda and cv. Texas-Grano exported 7% and 8.9% respectively (Fig. 9).

4.1.2.1.2.4. EXPORT TO THE BULB

The bulb imported a significant proportion of the labelled assimilates from all the leaves at this stage. In 1978 experiment, leaves 1 and 5 of cv. Eclipsel-Bermuda exported 59.4% and 47.5% respectively while those of cv. Texas-Grano

exported 44.3% and 57.8% respectively (Fig.5). Leaves 2 and 4 of cv. Texas-Grano supplied more labelled assimilates to the bulb (41% and 62.3%) than the corresponding leaves of cv. Eclipsel-Bermuda. The bulb imported more labelled assimilates from L3 of cv. Eclipsel-Bermuda (49.5%) than from the corresponding leaf of cv. Texas-Grano (46.3%)(Fig.5).

In 1979, the quantity of ^{14}C-assimilates recovered from the bulbs was higher than in 1978 (Figs. 7 and 8) from all the source leaves. Export of labelled assimilates to the bulb in 1979 was not less than 30% of the assimilated carbon in all the leaves except from L5 of cv. Red-Kano which exported 28.8% but even this amount was higher than that exported to other parts of the plant by this leaf (Fig.9). Import of labelled assimilates by the bulb from the leaves ranged from 28.8% to 56.9% in cv. Red-Kano; 59.8% to 78.3% in cv. Texas-Grano. Generally, the amount of radiocarbon recovered from the bulb showed an increasing trend from L^1, reaching a peak from L2 and decreasing from L3 (for all the 3 cultivars) and up to L4 (in cv. Eclipsel-Bermuda). From L4 (in cv. Red-Kano and cv. Texas-Grano) there was a gradual increase which continued from L5 (in cv. Texas-Grano and cv. Eclipsel-Bermuda) but dropped off sharply in cv. Red-Kano (Fig. 6).

4.1.2.1.2.5. EXPORT TO THE ROOTS

Both in 1978 and 1979, lower leaves were the main source of radiocarbon. In 1978, leaves of cv. Eclipsel-Bermuda exported larger quantities of ^{14}C-labelled assimilates to the root and was in the range of 7.4% (from L4) to 23% (from L2) than the leaves of cv. Texas-Grano which supplied quantities ranging from 3.6% (from L4) to 9.9% (from L1) (Fig.7). In 1979 however, these cultivars supplied comparable percentages of radiocarbon to the roots which were less than those of the previous year (Fig. 9). These were in the range of 2.1% (L3) to 4.1% (L1) in cv. Eclipsel-Bermuda while in cv. Texas-Grano the values were 1.3% to 6.7% (L5 and L1). Import of labelled assimilates from the leaves of cv. Red-Kano ranged from 9.2% (L5) to 8.4% (L1) and these values were higher than those supplied by the leaves of cv. Eclipsel-Bermuda and cv. Texas-Grano to the roots.

4.1.2.2. $^{14}CO_2$ SUPPLIED TO INDIVIDUAL LEAVES 81 DAYS AFTER TRANSPLANTING (EXPERIMENT 2)

4.1.2.2.1. EXPORT OF LABELLED ASSIMILATES FROM THE TREATED LEAVES

Results of these are illustrated in Figs. 2 and 4. Export of ^{14}C-assimilates from all the leaves were higher in

cv. Eclipsel-Bermuda than cv. Texas-Grano in both years (1978 and 1979). In 1978, export from the leaves of cv. Eclipsel-Bermuda ranged from 66.8% (L7) to 94.8% (L1) but leaves of cv. Texas-Grano exported 59.6% - 80.7% (leaves 7 and 5) of the fixed carbon. In cv. Eclipsel-Bermuda export of labelled assimilates was lowest by the youngest leaf (L7) and increased as the leaves increased in age i.e., increasingly higher percentages were exported from leaves 5, 3 and 1 in that order (Fig.2). No definite pattern of export was observed in cv. Texas-Grano but alternate leaves still on same side of the plant exported similar quantities of radiocarbon during both years. That is, in 1978, leaves 1 and 5 exported 76.4% and 80.7% respectively while leaves 3 and 7 exported 57.7% and 59.6% respectively while in 1979 leaves 1 and 5 exported 56.7% and 44.4% while leaves 3 and 7 exported 74.4% and 59.2% respectively (Figs. 2 and 4).

In 1979 leaves 1 and 7 of Red-Kano exported higher percentage of fixed ^{14}carbon (83.5% and 91.5%) than leaves at same position of cv. Eclipsel-Bermuda and cv. Texas-Grano. Leaf 3 of all the three cultivars exported similar percentages which was 79.3% in cv. Eclipsel-Bermuda, 74.4% in cv. Texas-Grano and 72.5% in cv. Red-Kano while L5 of cv. Red-Kano and

cv. Eclipsel-Bermuda exported similar proportion of the fixed carbon (75.1% and 71.1% respectively), a lesser percentage was exported from the leaf of cv. Texas-Grano (44.4%) (Fig.4).

4.1.2.2.2. PATTERNS OF ASSIMILATE DISTRIBUTION IN DIFFERENT PLANT PARTS

Results are shown in Figs. 8 and 10.

4.1.2.2.2.1. EXPORT TO THE LEAVES ABOVE THE TREATED LEAF (LATL)

Export of labelled assimilates to the LATL from leaves supplied with $^{14}CO_2$ 81 days after transplanting was higher from the lower leaves in all the three cultivars. Export of fixed carbon to these leaves was generally less at this stage of the plant development than at 59 days after transplanting.

In 1978, the LATL imported 3% - 14.7% from leaves 5 and 1 of cv. Eclipsel-Bermuda while in cv. Texas-Grano 1.6% - 23% were recovered from this sink when L7 and L3 were the source (Fig.8). Leaves 3 and 7 of cv. Eclipsel-Bermuda supplied 11.6% and 6.4% of their assimilated carbon respectivel while leaves 1 and 5 of cv. Texas-Grano supplied 20.5% and 13.6% respectively to these leaf blades.

In 1979 leaves of cv. Red-Kano supplied higher amounts of ^{14}C to the LATL (0.4% - 22.8% from leaves 7 and 1 respectively) than leaves of cv. Eclipsel-Bermuda and cv. Texas-Grano. Labelled leaves of cv. Eclipsel-Bermuda exported assimilates in the range of 0.7% (from L7) to 15.6% (from L5) while those of cv. Texas-Grano exported lesser quantities of radiocarbon, 1.4% (from L7) to 7.4% (from L1) to the leaves above the treated leaves (Fig.10).

4.1.2.2.2.2. EXPORT TO LEAVES BELOW THE TREATED LEAF (LBTL)

Individual leaves supplied with $^{14}CO_2$ at 81 days after transplanting supplied generally lesser quantity of assimilates to the LBTL than at 59 days. In 1978, export of fixed carbon to the LBTL from leaves of cv. Eclipsel-Bermuda varied from 3% (from L5) to 11.7% (from L7). These values were higher than those of cv. Texas-Grano which exported 1.5% (from L3) to 4.5% (from L7). In each case, however, the higher percentage import by these leaves came from L7 (Fig. 8).

In 1979, leaves of cv. Texas-Grano exported much lesser proportion of ^{14}C-assimilates to the LBTL than those of cv. Eclipsel-Bermuda and cv. Red-Kano. In cv. Texas-Grano, percentage export of labelled assimilates to the LBTL ranged

from 1.2% (from L5) to 2.9% (from L7) while in cv. Eclipsel-Bermuda it ranged from 0.9% (from L3) to 4.8% (from L5). In cv. Red-Kano radiocarbon exported to the LFTL varied from 2.9% (L7) to 7.1% (L5). All the leaves however, supplied insignificant percentage of assimilated radiocarbon to this sink organ (Fig.10).

4.1.2.2.2.3. EXPORT TO THE PSEUDOSTEM

In 1978, imports of radiocarbon by the pseudostem from L1 was 9.4% in cv. Texas-Grano and 8.9% in cv. Eclipsel-Bermuda, while the amount recovered from L3 was 8.4% in cv. Eclipsel-Bermuda and 5.7% in cv. Texas-Grano. Leaf 7 which was the youngest leaf supplied 14.1% in cv. Texas-Grano and 8.7% in cv. Eclipsel-Bermuda respectively to the pseudostem. Leaf 5 which was an older leaf supplied only 2% and 3.7% in cv. Eclipsel-Bermuda and cv. Texas-Grano respectively (Fig. 8).

In 1979, import of fixed ^{14}carbon by the pseudostem was highest from L5 in cv. Eclipsel-Bermuda (12.8%), L1 in cv. Texas-Grano (14.7%) and L3 in cv. Red-Kano (8%). In all the three cultivars, percentage export to the pseudostem was lowest from L7 which exported 1.1% in cv. Red-Kano, 2.1% in cv. Eclipsel-Bermuda and 2.3% in cv. Texas-Grano (Fig.10).

4.1.2.2.2.4. EXPORT TO THE BULBS

At this stage the amount of ^{14}carbon recovered from the bulbs increased in all the cultivars during both years. In 1978, leaves of cv. Eclipsel-Bermuda exported higher percentage of fixed ^{14}carbon to the bulb (62.6% from L7 to 90.3% from L5) than leaves of cv. Texas-Grano which exported assimilates in the region of 59.1% (from L1) to 79.5% (from L7) Leaf 3 of both cultivars exported similar percentages of assimilates to the bulb (67.5% in cv. Eclipsel-Bermuda and 63.3% in cv. Texas-Grano)(Fig. 5).

In 1979, percentage export of ^{14}C-assimilates from all the similar source leaves to the bulbs was almost the same in all the three cultivars. The pattern of export from the individual leaves of cv. Red-Kano decreased with increasing leaf age up to L3 but increased again from L1. The highest export of assimilates to the bulb in cv. Red-Kano was from L7 (95.1%) while L3 (54.1%) showed the lowest export. In cv. Eclipsel-Bermuda export of assimilates to the bulb varied from 91.2% (frol L7) to 61.8% (from L5) while in cv. Texas-Grano it varied from 93% (from L7) to 74.8% (from L1). In all the three cultivars, L7 exported the highest amount of the labelled assimilates (Fig.6).

4.1.2.2.2.5. EXPORT TO THE ROOTS

Generally, the lower leaves (leaves 1 and 3) supplied a larger percentage of the fixed carbon to the roots than the upper leaves (leaves 5 and 7) in 1978 in cv. Eclipsel-Bermuda and cv. Texas-Grano but L7 of cv. Eclipsel-Bermuda also supplied comparably a high percentage of 10.6% to the roots. Leaves 1 and 3 of cv. Eclipsel-Bermuda supplied 7.3% and 4.5% respectively while those of cv. Texas-Grano supplied 11% and 6.5% respectively to the roots. Upper leaves of Eclipsel-Bermuda supplied negligible quantities to the roots (Fig. 8).

In 1979, export of fixed carbon to the roots was higher from leaves of cv. Red-Kano than those of cv. Eclipsel-Bermuda and cv. Texas-Grano. Import of ^{14}C-assimilates by the roots was mostly from leaves 1 and 3 in cv. Red-Kano and cv. Texas-Grano and from leaves 3 and 5 in cv. Eclipsel-Bermuda. Leaf 7 of all the cultivars contributed only negligible quantities (Fig. 10).

4.1.2.3. $^{14}CO_2$ SUPPLIED TO INDIVIDUAL LEAVES 101 DAYS AFTER TRANSPLANTING (EXPERIMENT 3, 1979 ONLY)

4.1.2.3.1. EXPORT OF LABELLED ASSIMILATES FROM THE TREATED LEAVES

At this stage, more than 50% of the plants of cv. Eclipsel-Bermuda and cv. Texas-Grano had dry tops which had fallen over. Most of the plants of cv. Red-Kano were still growing well with luxuriant green tops. The two leaves treated (Leaves 3 and 5) in cv. Eclipsel-Bermuda and cv. Texas-Grano exported over 58% of the fixed carbon. The amount exported from leaves of cv. Eclipsel-Bermuda were much higher than from leaves of cv. Texas-Grano. Leaf 3 of cv. Eclipsel-Bermuda exported 75% while that of cv. Texas-Grano exported only 58.8%. Leaf 5 of cv. Eclipsel-Bermuda exported 73% and that of cv. Texas-Grano 67.7%. In cv. Red-Kano leaves 2 and 6 exported more radiocarbon (61.8% and 78.2% respectively) than leaves 4 and 8 which exported 46.2% and 55.4% respectively. In all the three cultivars the amount exported from the respective leaf positions was almost the same (Fig. 11).

4.1.2.3.2. PATTERNS OF ASSIMILATE DISTRIBUTION IN DIFFERENT PLANT PARTS

4.1.2.3.2.1. EXPORT TO LEAVES ABOVE THE TREATED LEAF (LATL)

The amount recovered from this sink organ was less than 2% in all the three cultivars from most of the source leaves. The only exception being L2 and L3 of cv. Eclipsel-Bermuda which supplied 21.5% and 16.5% respectively (Fig.11).

4.1.2.3.2.2. EXPORT TO THE LEAVES BELOW TREATED LEAF (LBTL)

The amount of ^{14}C-labelled assimilates recovered from these leaves increased considerably 101 days after transplanting, particularly from the upper leaves. In cv. Eclipsel-Bermuda and cv. Texas-Grano L5 exported 13% (cv. Eclipsel-Bermuda) and 10.7% (cv. Texas-Grano). Leaf 3 however, contributed less than 2.5% in cv. Eclipsel-Bermuda and cv. Texas-Grano. In cv. Red-Kano there was an almost uniform percentage export of assimilates to these leaves from all the treated leaves which ranged between 2.7% (from L6) to 5.2% (from L8), while leaves 2 and 4 exported 4.3% and 3.2% respectively (Fig. 11).

4.1.2.3.2.3. EXPORT TO THE PSEUDOSTEM

The pseudostem in cv. Eclipsel-Bermuda imported about 2.8% from both the leaves. In cv. Texas-Grano, L5 exported a higher percentage (12%) of its fixed ^{14}carbon to the pseudostem than L3 (3.8%). In cv. Red-Kano the amount recovered from this sink organ was between 1 - 4% only (Fig.11).

4.1.2.3.2.4. EXPORT TO THE BULB

At 101 days after transplanting, more than 60% of the fixed ^{14}carbon was imported by the bulb from leaves of the three cultivars. The leaves of cv. Eclipsel-Bermuda exported 79.2% and 81.5% from leaves 3 and 5 respectively, while 91% and 73.5% was recovered from same leaf positions of cv. Texas-Grano. In cv. Red-Kano, the highest percentage export of the bulb was from L6 which exported 94% and the least came from L2 which supplied only 66.9%. Leaves 4 and 8 of this cultivar exported 91.2% and 90.8% of radiocarbon respectively to the bulb.

4.1.2.3.2.5. EXPORT TO THE ROOTS

At this stage (101 days after transplanting), roots were unimportant sink organs and in the three cultivars the amount of ^{14}C recovered from this sink was only between 1 - 4% (Fig. 11).

4.1.2.4. $^{14}CO_2$ SUPPLIED TO INDIVIDUAL LEAVES 123 DAYS AFTER TRANSPLANTING (EXPERIMENT 4, cv. RED-KANO ONLY)

At this stage of development, the export of radiocarbon was above 50% from the source leaves. Labelled assimilates were distributed to all parts of the plant. The bulb was the most significant sink, importing between 70.3% to 81.8% of the fixed ^{14}carbon. The amount recovered from the lower leaves was between 9.8 - 15.2% while from the upper leaves it was only 2-1 - 6% (Fig.11).

More labelled assimilates were recovered from the pseudostem when upper leaves were supplied with $^{14}CO_2$ (5.2% from L6 and 4.2% from L7).

There was a slight increase in export of ^{14}C-assimilates to the roots with the highest proportion coming from L7, the uppermost leaf treated, which supplied 7.5% to the roots. Leaves 5 and 6 supplied only 3.8% and 3.2% respectively to the roots (Fig. 11).

TABLE 1: Total ^{14}C-radioactivity recovered from various plant parts when individual leaves of two onion cultivars were supplied with $^{14}CO_2$ 59 days after transplanting in 1978 (Expt.1). Results as means of four plants.

ECLIPSE L-BED UDA						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	21408	37165	23504	-	10409	11432
L2	19985	17577	4692	1837	48791	23112
L3	18973	108483	15748	6967	47019	68231
L4	5424	71319	10486	3635	47814	10155
L5	6968	24501	19139	5214	36788	17846
Standard error	3451	16964	3141	1095	7288	10803

Table 1 continued

TEXAS-GRANO						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseudo-stem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	2739	21695	11304	-	57736	11049
L2	3325	21774	6558	959	2727	22438
L3	9196	42818	7664	17988	71047	22704
L4	3641	56800	14100	156532	33864	12348
L5	2737	28657	5356	5034	76117	5816
Standard error	1232	8824	1622	33463	9800	3337

TABLE 2: Total ^{14}C-Radioactivity recovered from various plant parts when individual leaves of two onion cultivars were supplied with $^{14}CO_2$ 81 days after transplanting in 1978 (Expt.2). Results as means of four plants.

ECLIPSE-BERMUDA						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	11304	149437	1[illegible]331	-	11698	39634
L3	10262	152324	20789	15181	16482	32885
L5	5444	459228	8340	13232	61510	11463
L7	15661	174077	25028	28225	170192	11831
Standard error	2097	75354	3732	4712	36824	7237

TEXAS-GRANO						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	10106	47354	6327	-	47433	11372
L3	5679	120901	4927	915	85693	11493
L5	2877	386539	7483	5276	43124	16973
L7	1574	402412	5975	25923	380969	9153
Standard error	1887	90896	19439	7721	81120	1664

TABLE 3: Total ^{14}C-radioactivity recovered from various plant parts when individual leaves of three onion cultivars were supplied with $^{14}CO_2$ 39 days after transplanting in 1979 (Expt.1). Results as means of four plants.

RED-KARO						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated leaves TL	Leaves above TL
L1	15107	43619	8632	-	7329	14577
L2	18944	155191	1797	2288	2322	204448
L3	12670	65210	17194	5504	43763	17584
L4	9789	116835	10774	7029	33125	7222
L5	5167	20125	15400	8872	83778	15127
Standard error	2344	24702	2725	1392	14683	38207

Table 3 continued

ECLIPSEL-BERMUDA						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	3798	69045	10956	-	95339	13931
L2	2389	72777	5123	1532	32161	7190
L3	2122	80753	10307	1708	38497	8098
L4	4071	76248	25237	5496	56883	11374
L5	3349	69737	6961	7482	69314	7851
Standard error	384	2166	3555	1463	11367	1287

TEXAS-GRANO						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	3416	23484	7748	-	29449	19644
L2	3958	120288	6121	4076	84162	29053
L3	4795	91328	18207	2121	111549	36991
L4	2478	115823	16977	5918	84269	70574
L5	2102	136091	9386	9241	7041	10982
Standard error	490	19879	2479	1514	19435	10288

TABLE 4: Total ^{14}C- Radioactivity recovered from various plant parts when individual leaves of three onion cultivars were supplied with $^{14}CO_2$ 81 days after transplanting in 1979 (Expt.2) Results as means of four plants.

RED-KANO						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated Leaf (TL)	Leaves above TL
L1	563682	105699	7126	-	23944	32662
L3	16358	71951	11092	4642	52817	27119
L5	4978	1777456	4949	11019	77771	9159
L7	3388	822607	5069	24953	76141	3852
Standard error	138890	400360	1274	6004	12603	6930

ECLIPSEL-BERMUDA						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	2088	175959	8769	-	77280	6524
L3	96305	702920	54724	4925	114503	67694
L5	5867	70116	12237	22886	31369	14393
L7	5012	386116	7919	13162	233205	2613
Standard error	23009	139472	11309	5196	43191	15161

Table 4 continued

TEXAS-GRANO						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseudo-stem	Leaves below TL	Treated leaf (TL)	Leaves above TL
L1	8515	411362	36239	-	185754	15061
L3	5456	488304	7971	4706	114165	6662
L5	4953	401847	21659	4573	8337019	9675
L7	1346	342602	8514	9929	250660	4812
Standard error	1469	926160	6678	1765	2038563	2239

Table 5: Total ^{14}C-Radioactivity recovered from various plant parts when individual leaves of three onion cultivars were supplied with $^{14}CO_2$ 101 days (Expt.3) and 123 days (Expt.4) after transplanting.

RED-KANO						
Leaf supplied with $^{14}CO_2$	Root	Bulb	Pseud-ostem	Leaves Below TL	Treated leaf (TL)	Leaves above TL
Expt.3 L2	7031	129735	6964	8308	13045	36955
L4	6521	351524	7086	10712	517312	7837
L6	6053	3[illegible]603	4682	11018	113855	2131
L8	2215	337623	4598	14071	373365	3287
Standard Error	1106	58300	634	1181	97871	8226
Expt.4 L5	8355	254136	1741	28808	163919	5035
L6	5[illegible]86	148[illegible]91	9561	25534	220266	12024
L7	9284	148932	4793	23413	44002	6113
Standard Error	1092	35116	2278	1571	52036	2174

Table 5 contd.

ECLIPSE--BERMUDA						
Leaf supplied with $^{14}CO_2$	Roots	Bulb	Pseudostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
Expt.3 L3	3883	248086	9453	6866	185389	2635
L5	3849	488825	58219	29668	329187	4599
Standard error	682	57043	3612	38130	20646	41563

[illegible]-GRANO						
Leaf supplied with $^{14}CO_2$	Roots	Bulb	Pseudostem	Leaves below TL	Treated leaf (TL)	Leaves above TL
Expt.3 L3	3883	248086	9453	6866	185389	2635
L5	3849	488825	58219	29668	329187	4599
Standard error	17	12072	24455	11435	72113	984

TABLE 6: The diameter, fresh and dry weights of the bulbs of the plants supplied with $^{14}CO_2$ in different treatments in 1978.

Experiment 1, 59 days after transplanting

ECLIPSEL-BERMUDA				TEXAS-GRANO		
Position of leaf supplied with $^{14}CO_2$	Bulb fresh weight (g)	Bulb dry weight (g)	Bulb diameter (cm)	Bulb fresh weight (g)	Bulb dry weight (g)	Bulb diameter (cm)
L1	3.4	0.22	1.49	2.68	0.35	1.42
L2	7.06	0.49	2.1	2.78	0.17	1.46
L3	4.69	0.26	2.31	2.42	0.13	1.31
L4	5.54	0.41	1.98	4	0.24	1.62
L5	1.68	0.12	1.16	2.81	0.14	1.44
S.E.	0.91	0.06	0.21	0.27	0.04	0.04

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Table 6 continued

Experiment 2, 81 days after transplanting

Position of leaf supplied with $^{14}CO_2$	ECLIPSSL-BERMUDA			TEXAS-GRANO		
	Bulb fresh weight (g)	Bulb dry weight (g)	Bulb diameter (cm)	Bulb fresh weight (g)	Bulb dry weight (g)	Bulb diameter (cm)
L1	27.91	4.39	4.06	7.95	0.81	3.22
L3	34.46	3.5	4.41	26.88	5.36	3.64
L5	32.59	6.19	4.28	32.32	5.44	4.07
L7	20.57	2.0	3.41	19.89	2.01	2.25
S.E.	3.09	0.87	0.22	5.25	1.27	0.38

TABLE 7: The diameter, fresh and dry weights of the bulbs of the plants supplied with $^{14}CO_2$ in different treatments in 1979.

Experiment 1 (59 days after transplanting)

RED-KANO				ECLIPSEL-BERMUDA			TEXAS-BRUC		
Position of leaf supplied with $^{14}CO_2$	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh Bulb diameter (g)	Bulb fresh weight (g)	Bulb dry weight (g)	fresh bulb diameter (cm)	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh bulb diameter (cm)
L1	1.87	0.26	1.56	3.41	0.22	1.49	2.58	0.16	1.42
L2	5	0.56	2.08	7.06	0.50	2.10	2.78	0.17	1.46
L3	4.64	0.41	1.96	8.45	0.71	2.31	2.42	0.13	1.31
L4	6.88	0.56	2.17	5.54	0.41	1.98	4.00	0.24	1.62
L5	1.52	0.13	1.17	1.67	0.12	1.16	2.61	0.14	1.44
S.E.	1.01	0.08	0.18	1.22	0.10	0.21	0.27	0.01	0.04

TABLE: 7 continued

Experiment 2 (81 days ater transplanting)

	RED-KANO			ECLIPSEL-BERMUDA			TEXAS-GRANO		
Position of leaf supplied with $^{14}CO_2$	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh bulb diameter (cm)	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh bulb diameter (cm)	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh bulb diameter (cm)
L1	19.69	2.31	3.65	27.91	4.34	4.06	7.95	0.56	3.22
L3	39.20	1.02	4.60	34.46	3.50	4.41	19.89	2.01	2.25
L5	28.91	1.39	4.13	32.59	6.19	4.28	26.88	5.36	3.64
L7	16.30	4.45	3.19	20.57	1.65	3.41	32.32	5.44	4.07
S.E.	5.13	0.76	0.30	3.09	0.94	0.22	5.25	1.22	0.38

TABLE 7 Continued

EXPERIMENT 3 (101 days after transplanting)

	RED-KANO			ECLIPSEL-BERMUDA			TEXAS-GRANO		
Position of leaf supplied with $^{14}CO_2$	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh bulb diameter (cm)	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh bulb diameter (cm)	Bulb fresh weight (g)	Bulb dry weight (g)	Fresh bulb diameter (cm)
L2	52.94	3.71	5.44						
L3				48.14	3.61	4.94	52.84	2.16	4.63
L4	82.02	7.28	6.30						
L6	84.72	8.34	6.35						
L8	88.46	6.83	5.97						
S.E.	7.29	0.99	0.21	2.29	0.35	0.08	1.58	0.32	0.06

Table 7 continued

Experiment 4 (123 days after transplanting)

RED-KANO			
Fosition of leaf supplied with $^{14}CO_2$	Bulb fresh weight (-)	Bulb dry weight (-)	Fresh Bulb diameter (-)
L5	64.12	8.69	5.86
L6	91.98	8.69	6.47
L7	100.95	8.90	6.45
S.E.	11.10	1.27	0.20

TABLE 8: Analysis of variance for percentage export of assimilated labelled ^{14}carbon recovered from the different plant parts in Experiment 1, 1978.

Source of variation	DF	F					
		Roots	Bulb	Pseud-ostem	Leaf blades below TL	Leaf blades above TL	Percentage exported
Leaf position (LP)	4	3.83	1.45	1.11	2.20	1.61	1.71
Cultivar (Cul)	1	9.80**	0.05	0.83	1.16	0.05	13.02***
LP x Cul	4	1.62	0.59	0.90	0.20	0.42	5.61**

Legend

*** - significant at 0.1% level ($P < 0.001$)

** - significant at 1% level ($P < 0.01$)

* - significant at 5% level ($P < 0.05$).

Blank - not significant

TL - Treated leaf

TABLE 9: Analysis of variance for percentage export of assimilated labelled ^{14}carbon recovered from the different plant parts in Experiment 2, 1978.

Source of variation	DF	F					
		Roots	Bulb	Pseud-ostem	Leaf blades below TL	Leaf blades above TL	Percen-tage exported
Leaf position (LP)	3	1.39	1.78	1.54	6.68**	2.48	1.11
Cultivar (Cul)	1	0.22	0.23	0	1.58	2.12	1.74
LP x Cul	3	2.16	0.97	0.13	0.67	0.44	0.86

Legend

***	-	significant at 0.1% level ($P < 0.001$)
**	-	significant at 1% level ($P < 0.01$)
*	-	significant at 5% level ($P < 0.05$)
Blank	-	not significant
TL	-	Treated leaf

TABLE 10: Analysis of variance for percentage export of assimilated labelled ^{14}carbon recovered from the different plant parts in Experiment 1, 1979.

Source of variation	DF	F					
		Roots	Bulb	Pseud-ostem	Leaf blades below TL	Leaf blades above TL	Percen-tage exported
Leaf position	4	1.14	0.67	2.57	16.46***	0.90	3.98**
Cultivar (Cul)	2	15.36***	7.59***	1.21	5.94**	3.95*	4.27*
LP x Cul	8	0.30	1.66	1.21	1.74	2.62	3.15**

Legend

DF	-	Degrees of freedom
***	-	significant at 0.1% level ($P < 0.001$)
**	-	Significant at 1% level ($P < 0.01$)
*	-	significant at 5% level ($P < 0.05$)
Blank	-	not significant
TL	-	treated leaf

TABLE 11: Analysis of variance for percentage export of assimilated labelled ^{14}carbon recovered from the different plant parts in experiment 2, 1979

Source of variation	DF	F					
		Roots	Bulb	Pseud-ostem	LBTL	LATL	Percen-tage export-ed
LP	3	6.58***	4.22*	1.92	4.50**	4.40*	0.76
Cul	2	13.88***	3.89*	1.13	2.24	5.43**	5.09*
LP x Cul	6	7.65***	4.56**	1.91	1.13	4.23**	1.04

Legend

*** - significant at 0.1% level ($P < 0.001$)

** - significant at 1% level ($P < 0.01$)

* - significant at 5% level ($P < 0.05$)

Blank - not significant

TL - Treated leaf

TABLE 12;

Analysis of variance for percentage export of assmilated labelled ^{14}carbon recovered from the different plant parts in Experiment 4.

Source of variation	DF	F					
		Root	Bulb	Pseud-ostem	Leaf blades below TL	Leaf blades above TL	% exported
LPOS	2	1.06	1.20	2.40	0.78	1.62	1.09

FIG. 2

The Percentage of the fixed ^{14}C exported by Leaves of Eclipsel-Bermuda and Texas-Grano after 24 hrs of fixation in 1978. Vertical Lines indicate LSD at 5% Level of significance.

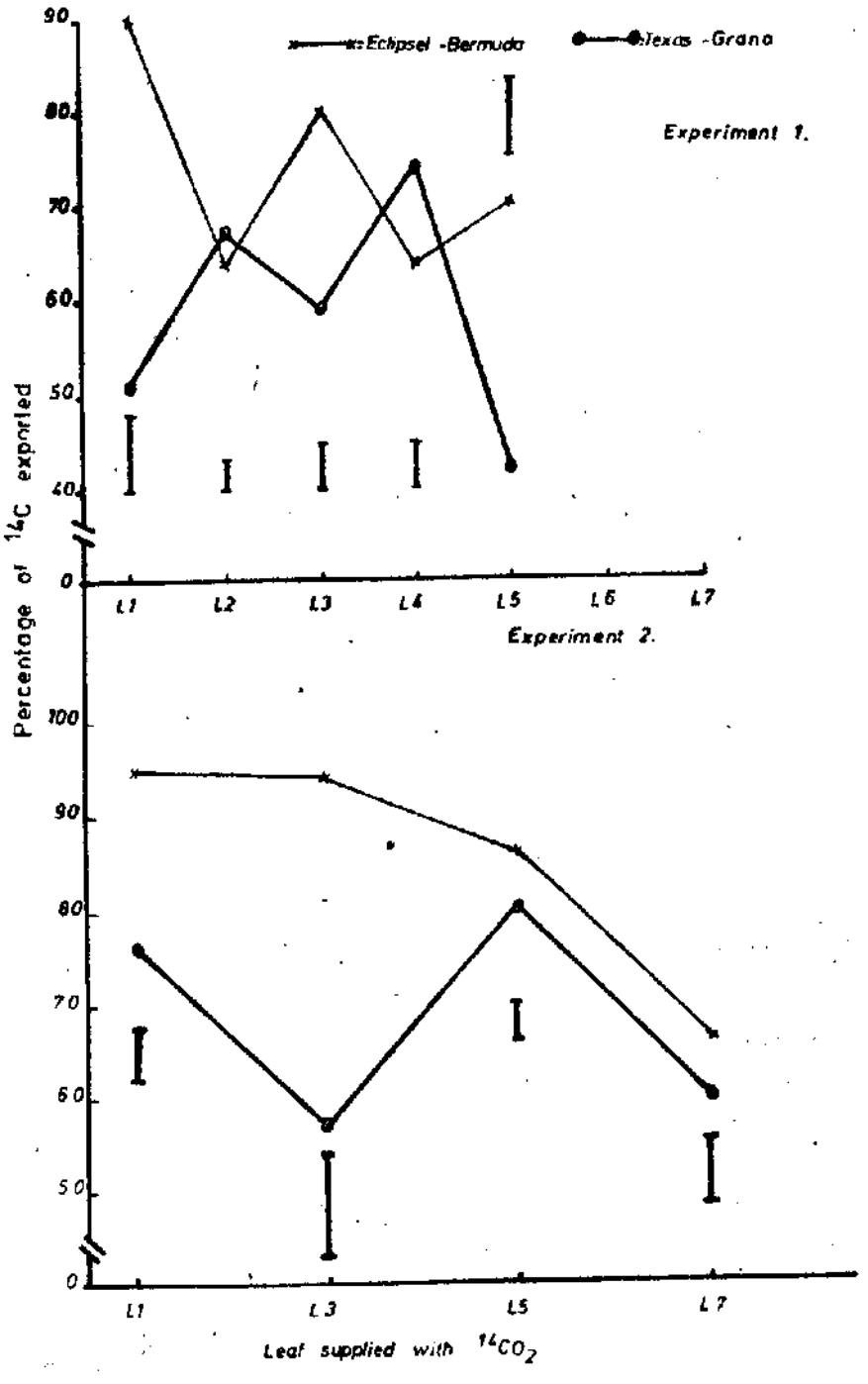


FIG. 3

The percentages of the fixed ^{14}C exported by Leaves 1,2,3,4, and 5 after 24 hrs of fixation, 59 days after transplanting (**Exp**eriment 1, 1979). Vertical Lines indicate LSD at 5 % level of significance.

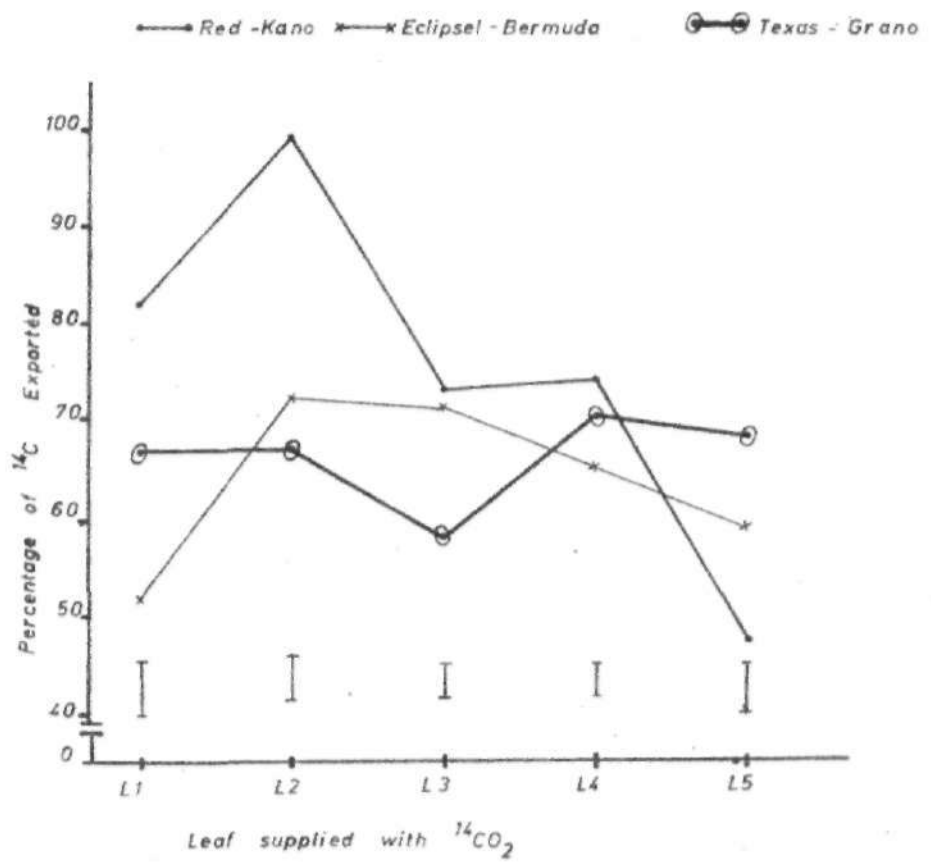


FIG. 4

The percentage of the fixed ^{14}C exported by leaves 1,3,5 and 7 after 24 hrs of fixation, 81 days after transplanting (Experiment 2,1979)
Vertical lines indicate LSD at 5% level of significance

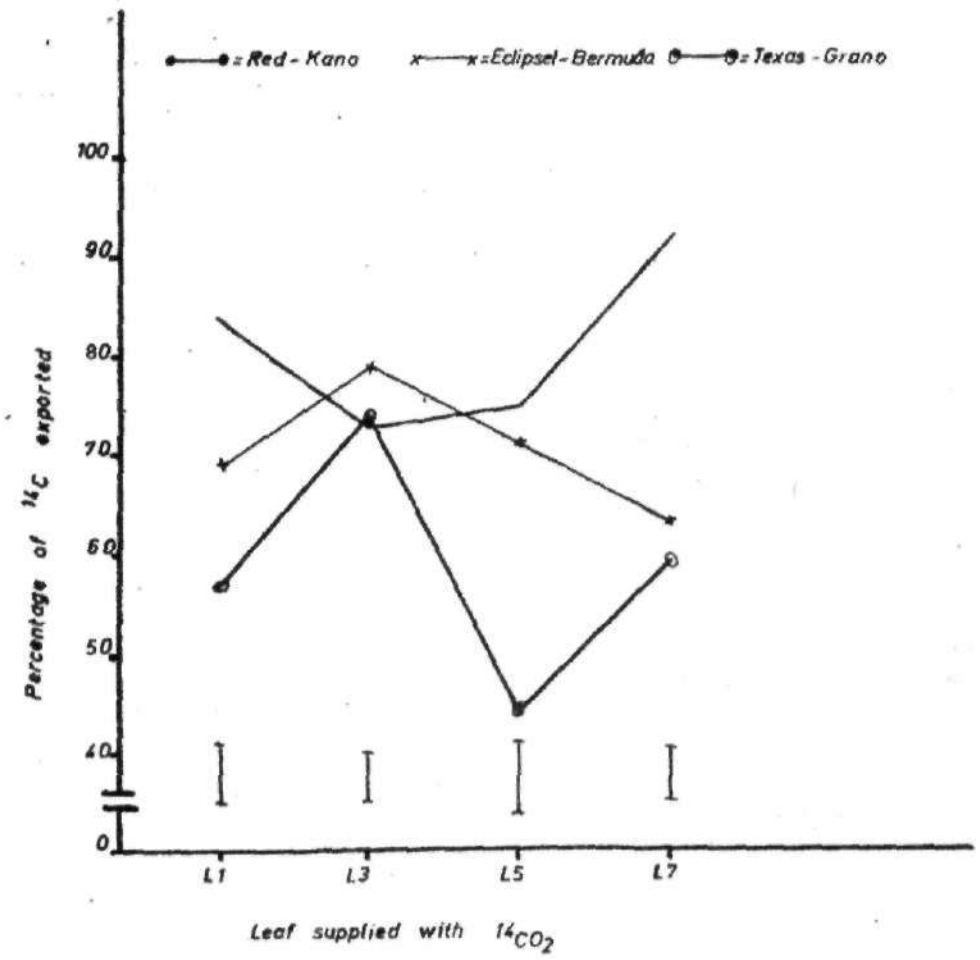


FIG. 5

Changing patterns of percentage export of assimilated ^{14}C to the bulb by different Leaves of Eclipsel - Bermuda and Texas - Grano in 1978. LSD at 5 % Level of significance.

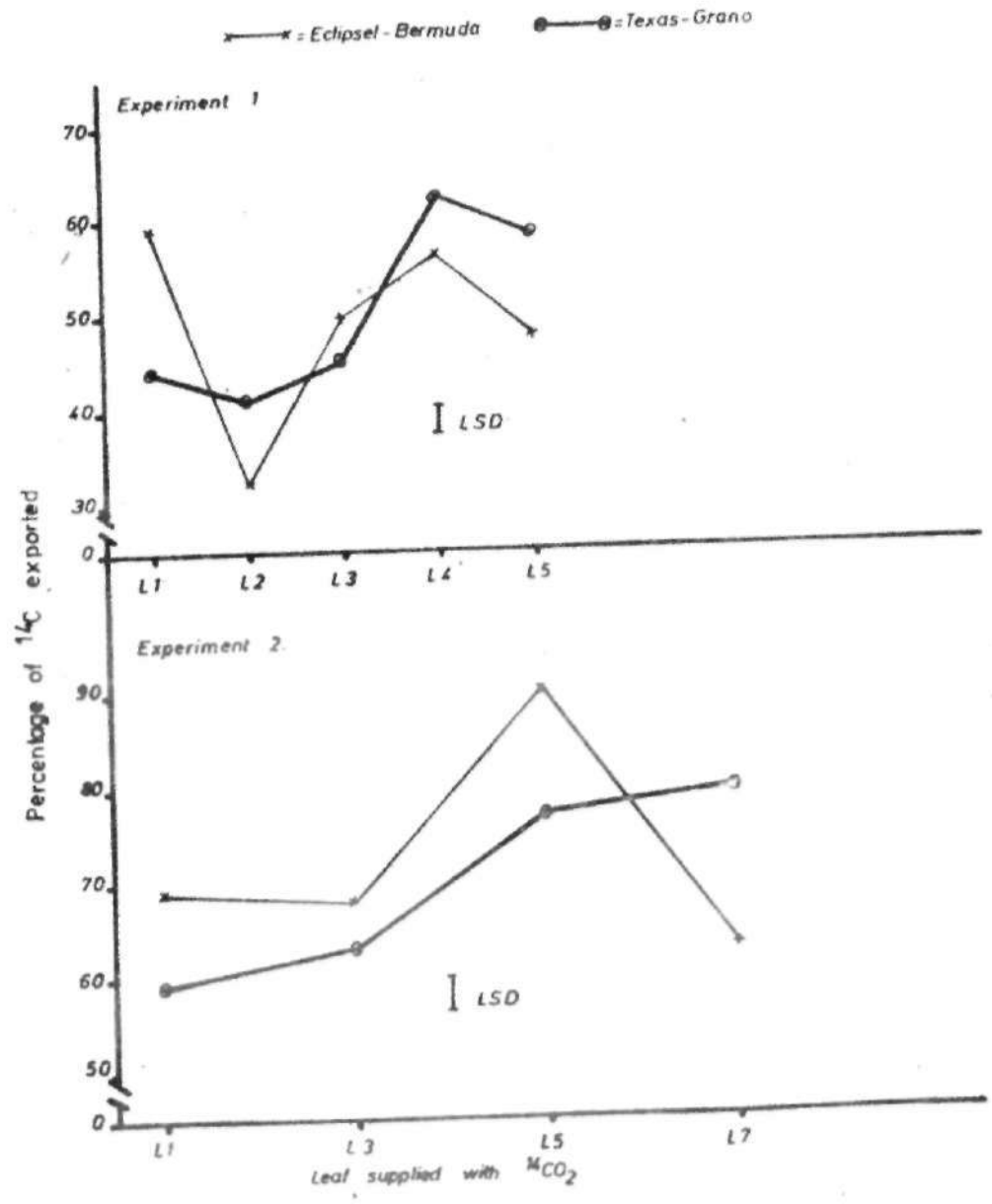
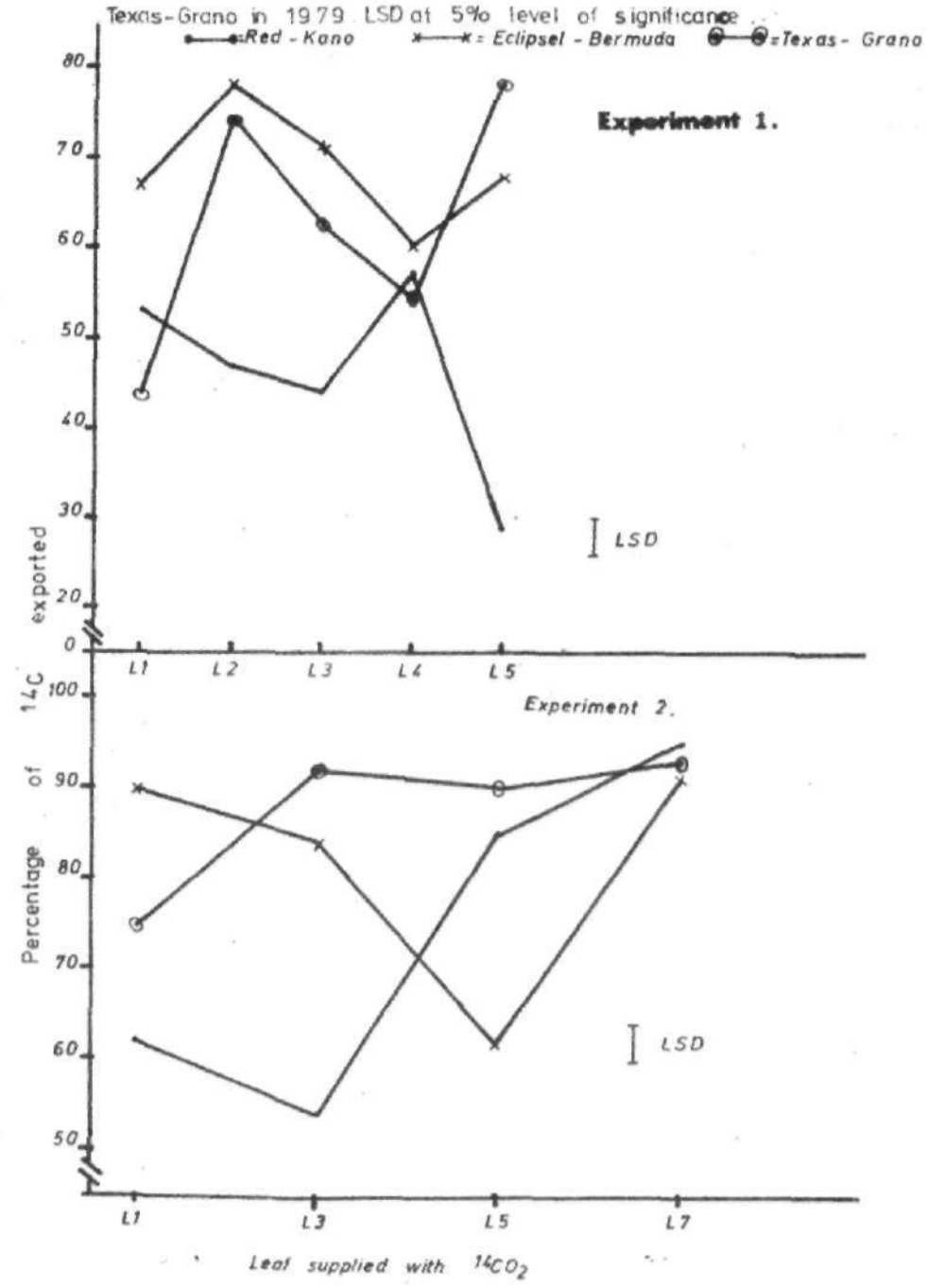


FIG. 6

Changing patterns of percentage export of assimilated ^{14}C to the bulb by different Leaves of Red-Kano, Eclipsel - Bermuda and Texas-Grano in 1979. LSD at 5% level of significance.



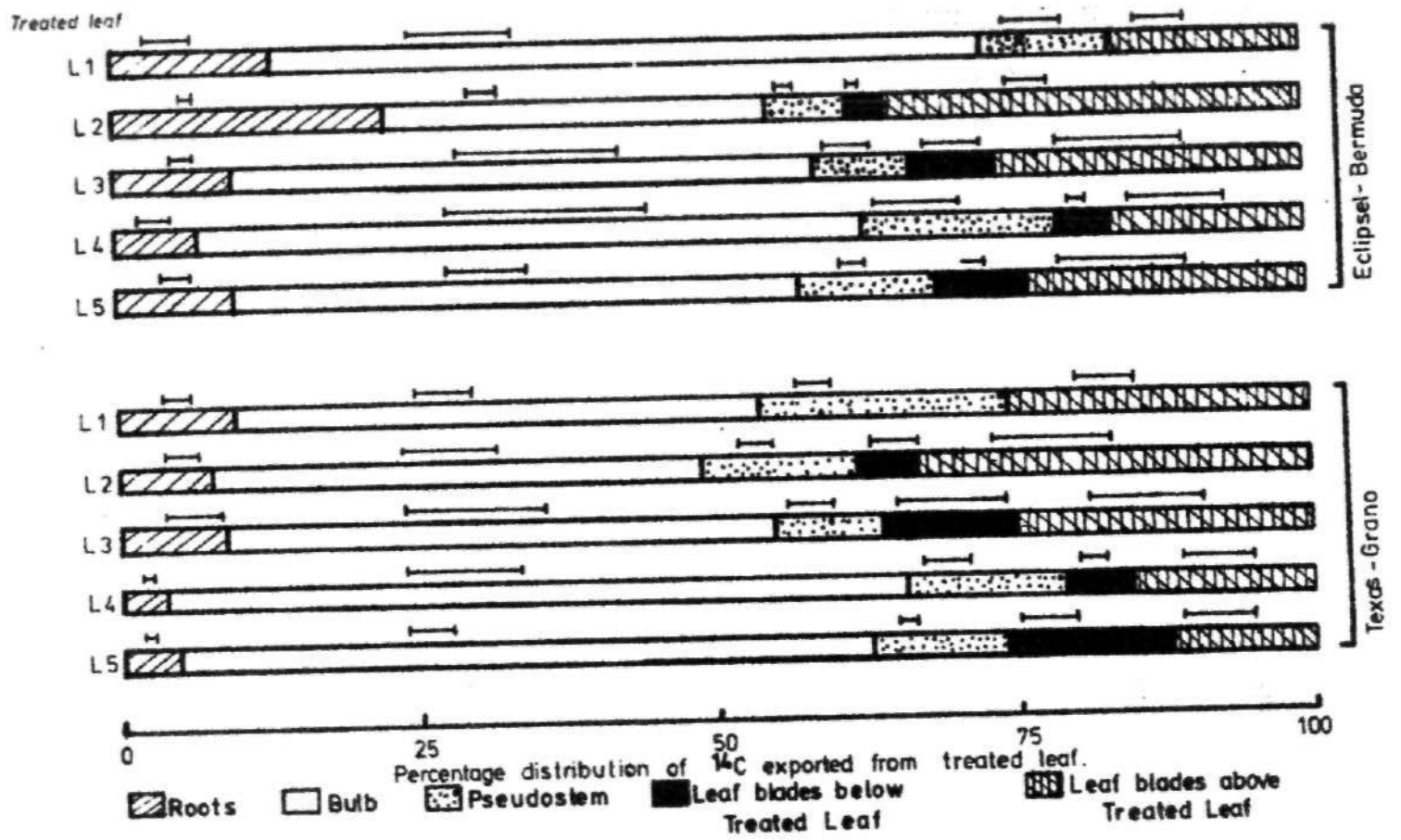


Fig.7 Patterns of distribution of ^{14}C - Labelled Assimilates in different plant parts 24 hrs after the supply of ^{14}C to individual leaves of Eclipse1 - Bermuda and Texas-Grano in expt. 1, 1978. Results are expressed as percentage of the total radioactivity exported and recovered in different plant parts (mean of 4 plants ± s.e.) Leaves 1-5 were Supplied with $^{14}CO_2$ 59 days after transplanting.

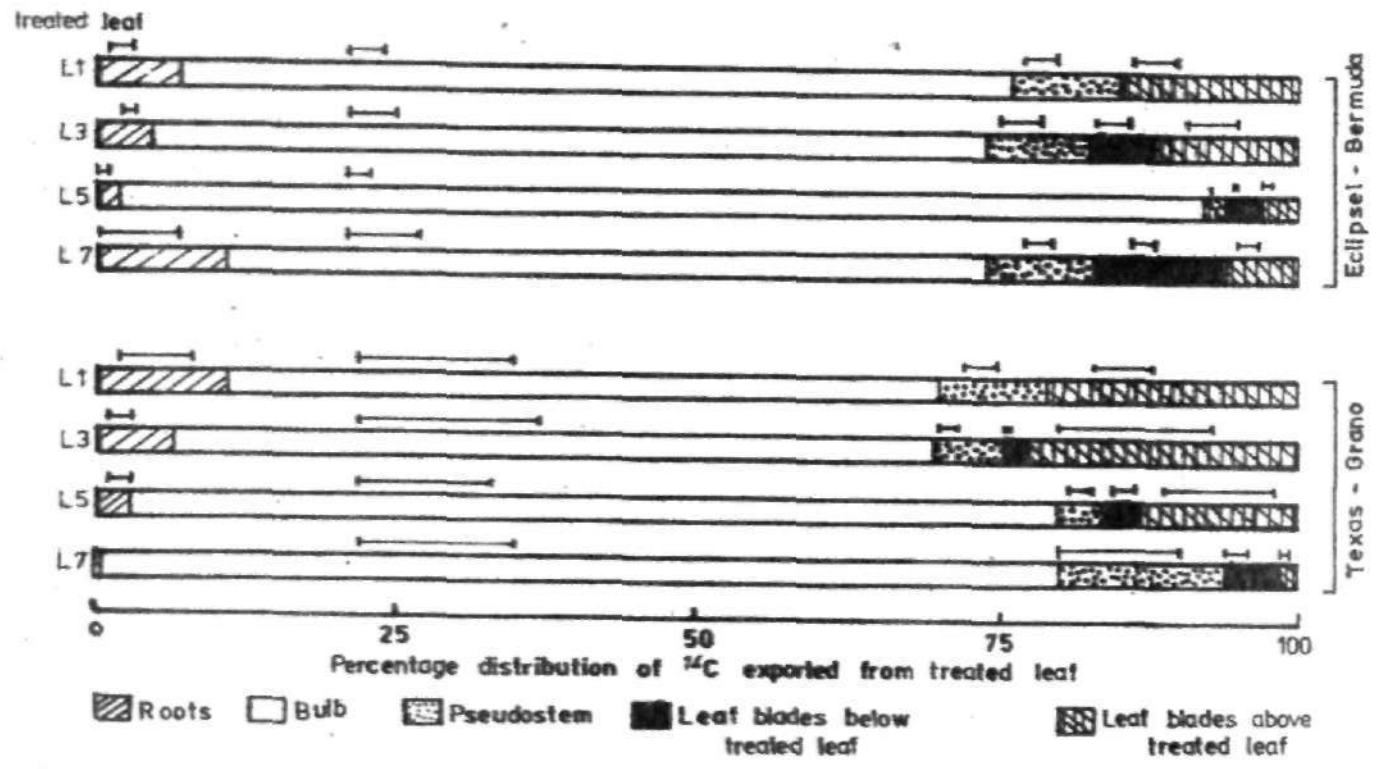


Fig.8 Patterns of distribution of ^{14}C - **Labelled Assimilates in different** plant parts 24hrs after the supply of $^{14}CO_2$ to individual leaves of Eclipse!- **Bermuda and Texas**- Grano in expt. 2, 1978. Results are expressed as percentage of the total radioactivity **exported and recovered** in different plant parts (mean of 4 plants ± S.E.) Leaves 1,3,5, and 7 were supplied with $^{14}CO_2$ **81 days** after transplanting.

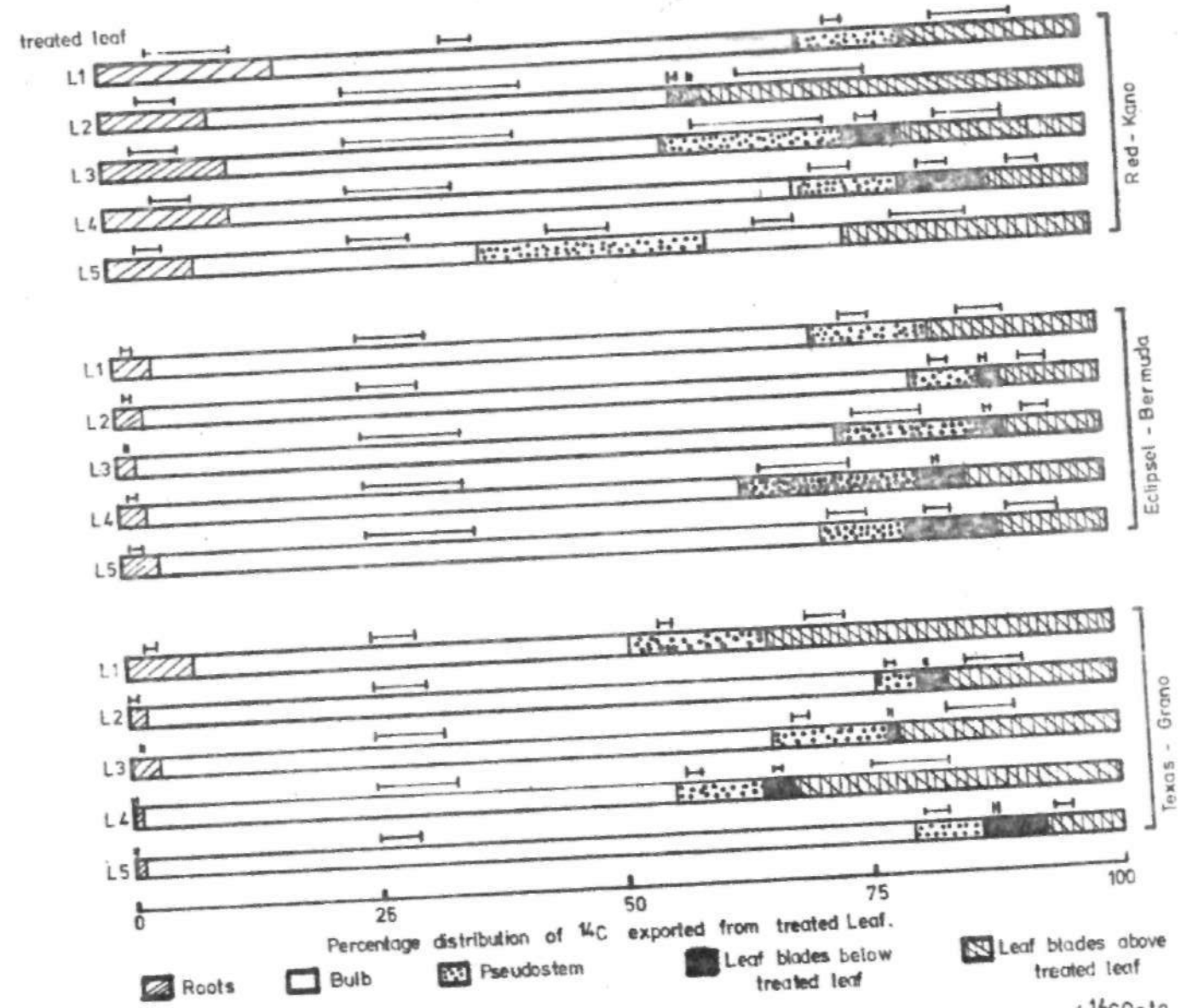


Fig. 8 Patterns of distribution of ^{14}C-Labelled assimilas in plant parts 24hrs after the supply of $^{14}CO_2$ to individual leaves of Red-Kano, Eclipse! -Bermuda and Texas-Grano in expt 1.1979. Results are expressed as percentage of the total radioactivity exported and recovered in the different plant parts (mean of 4 plant ± s.e.) Leaves 1-5 were supplied with $^{14}CO_2$ 59 days after transplanting.

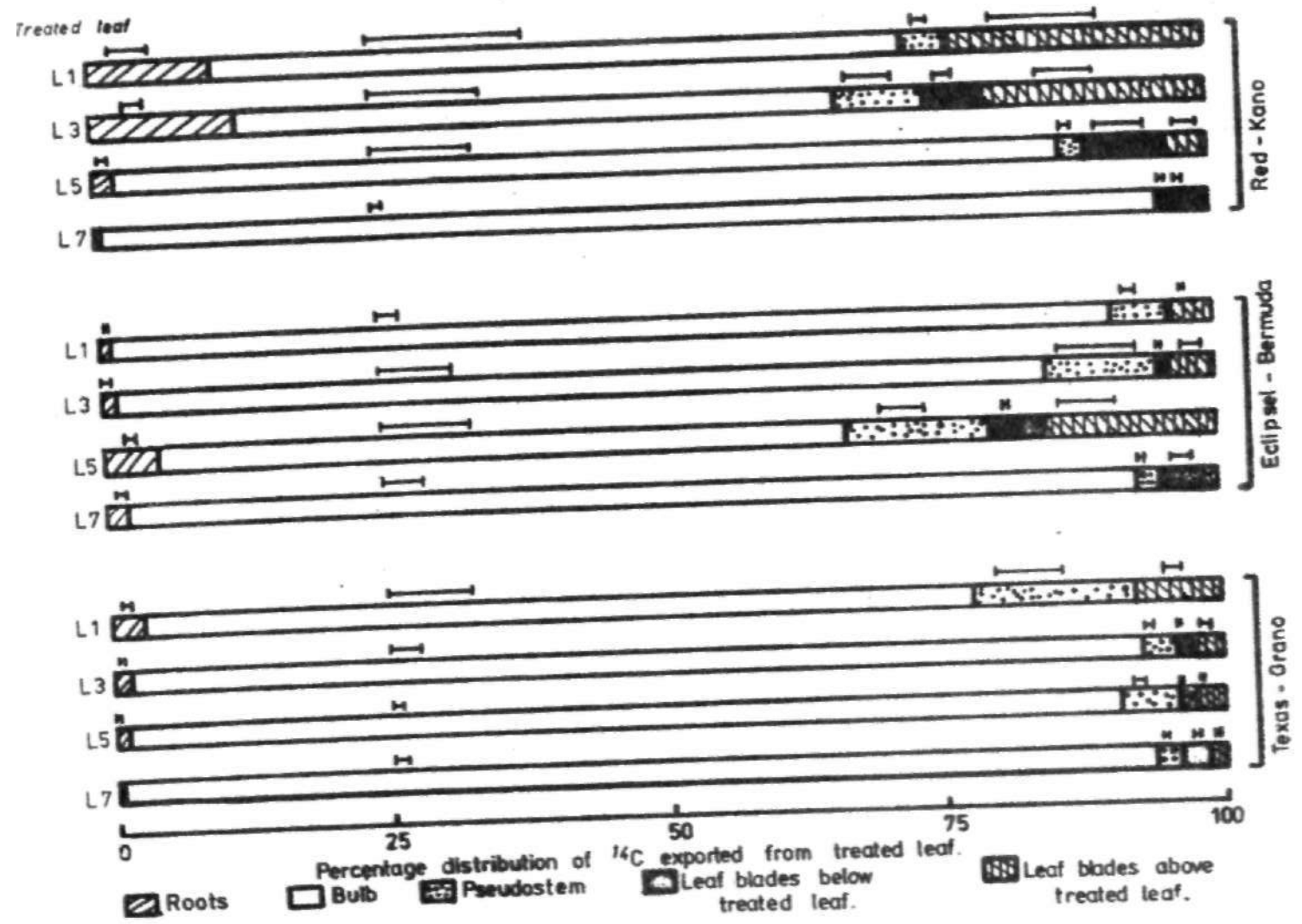


Fig.10 Patterns of distribution of ^{14}C - Labelled assimilates in different plant parts 24 hrs after the supply of $^{14}Co_2$ to individual leaves of Red - Kano, Eclipsel - Bermuda, and Texas - Grano in Expt. 2, 1979. Results are expressed as percentage of the total radioactivity exported and recovered in the different plant parts (mean of 4 plant ± s.e.). Leaves 1, 3, 5 and 7 were supplied with $^{14}CO_2$ at 81 days after transplanting.

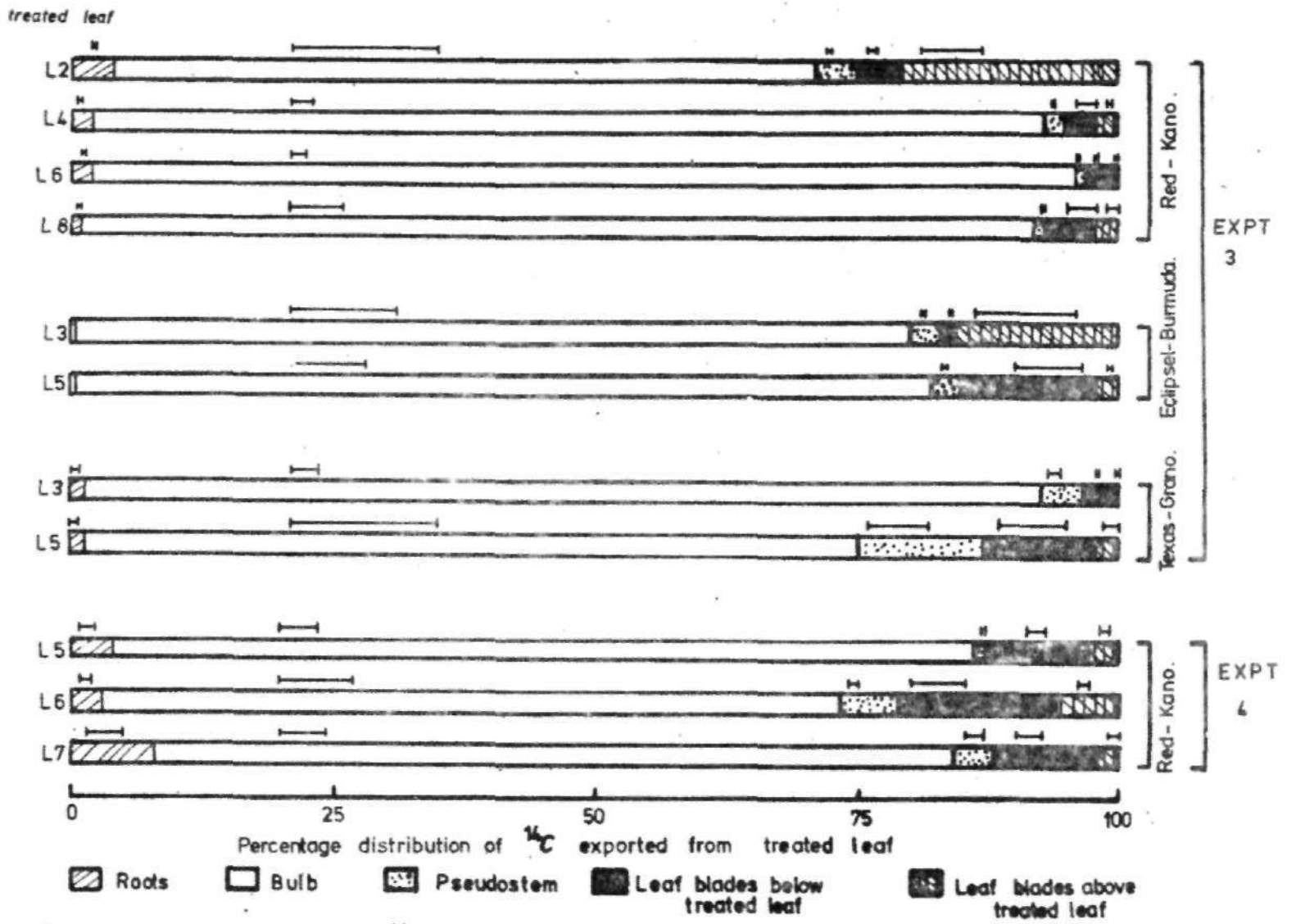


Fig-11 Patterns of distribution of ^{14}C - Labelled assimilates in different plant parts 24hrs after the supply of $^{14}CO_2$ to individual leaves of Red-Kano, Eclipse!- Bermuda and Texas-Grano in Expt_3 and 4 1979. Results are expressed as percentage of the total radio activity exported and recovered in different plant parts (means of 4 plants ± s.e.). Leaves were supplied with $^{14}Co_2$ 101 days (expt 3) and 123 days (Expt 4) after transplanting.

4.2. GROWTH ANALYSIS

The results of some growth characteristics, RGR, CGR, RLGR, NAR and LAR chlorophyll content and distribution of minerals (P, K. Ca, Mg and Zn) of the three onion cultivars are illustrated in tables 13-17 and figures 12 - 23.

4.2.1. GROWTH CHARACTERISTICS

In all the three onion cultivars studied, maximum growth in height, leaf area, number of leaves, dry weight of leaf and pseudostem were achieved between 61 and 75 days after transplanting. The dry weight of bulbs showed a continuous increase and reached to its peak at maturity. There was no consistent increase in root development but showed three definite and equal peak periods of growth on days 54, 75 and 97 (App., 1). The differences in the average values between cultivars are shown in table 17.

4.2.1.1. DRY WEIGHT

The total dry matter of cv. Red-Kano increased with increasing age of plant up to 97 days after transplanting and thereafter decreased by 35.7%. The pattern of total dry weight gain was similar in cultivars Eclipsel-Bermuda and

Texas-Grano but Texas-Grano reached its maximum dry weight a week earlier (68 days) than cv. Eclipsel-Bermuda (75 days). The decrease in dry weight thereafter was 26% in cv. Texas-Grano and 39% in cv. Eclipsel-Bermuda. In both these two cultivars, their maximum total dry weight was of same value (5.4g), but that of cv. Red-Kano was much higher (23.8g), (Fig. 13).

In cv. Red-Kano, the increase in bulb dry weight with time followed the same pattern as that of the total dry weight, both reaching their maximum dry weight at the same time (97 days after transplanting) and decreasing by similar amounts (37% for bulb). Eclipsel-Bermuda showed similar results. In cv. Texas-Grano, however, the bulb continued to increase in dry weight up to the last date of sampling but the pattern again followed that of total dry weight (Fig. 13).

The leaf dry weight increased up to 61 days after transplanting in cv. Eclipsel-Bermuda and thereafter decreased gradually. Cultivars Eclipsel-Bermuda showed similar results, but in this cultivar the leaf dry weight remained near the highest value up to 75 days after transplanting and then decreased. Leaves of cv. Texas-Grano

reached its maximum dry weight a week later than both cv. Red-Kano and cv. Eclipsel-Bermuda (at 68 days) and thereafter decreased (Fig. 13).

The dry weight gain of the pseudostem in all the three cultivars was very small. It showed almost a stable value in cv. Eclipsel-Bermuda and cv. Texas-Grano and the small increases correspond with the increase in number of leaves. The slight increase of the pseudostem dry weight with time in cv. Red-Kano may be due to the additional number of leaves and consequently leaf sheaths (Fig. 13).

4.2.1.2. LEAF AREA

There was a rapid increase of leaf area in cv. Red-Kano and cv. Texas-Grano, reaching its maximum at 61 days after transplanting and then it decreased. In cv. Eclipsel-Bermuda the maximum leaf area was attained at 75 days after transplanting. Cultivar Red-Kano attained a significantly higher leaf-area than both cultivars Eclipsel-Bermuda and Texas-Grano (Fig. 12).

4.2.1.3. NUMBER OF LEAVES

Leaves less than half the mature size were not counted. Results are illustrated in Table 13. Cultivar Red-Kano had the largest number of leaves. The leaves were added gradually at an average rate of two per week.

After the maximum number was attained at 75 days after transplanting, there was no addition, but decrease due to either death of old leaves or due to faster rate of death of older leaves than addition of new ones. The number of leaves however, seemed to increase again at maturity. Cultivars Eclipsel-Bermuda and Texas-Grano had a lower number of mature leaves per plant than cv. Red-Kano Table 13).

4.2.1.4. PLANT HEIGHT

Cultivar Red-Kano showed much higher plant-height than cultivars Eclipsel-Bermuda and Texas-Grano. Cultivar Red-Kano attained a maximum plant height of 63.6cm at 75 days after transplanting and this decreased towards maturity. Cultivars Eclipsel-Bermuda and Texas-Grano attained a maximum height of 18 - 22cm at 61 - 68 days after transplanting. The plant height did not change much during the sampling period (Table 13).

4.2.2. RGR, CGR, RLGR, NAR AND LAR

Some growth indices comprising the Relative Growth Rate (RGR), Crop Growth Rate (CGR), Relative Leaf Growth Rate (RLGR), Net assimilation rate (NAR) and Leaf area ratio (LAR) calculated for the three cultivars namely Red-Kano,

Eclipsel-Bermuda and Texas-Grano are presented in Table 14 (see methods page 62 for equations used).

The RGR was generally highest at early stages of growth and development but declined to negative values towards maturity. In cv. Red-Kano, the RGR decreased with time up to the sixth week after which it showed fluctuations. In cv. Eclipsel-Bermuda, the RGR decreased with time up to the last week of sampling but in cv. Texas-Grano it increased again during the last week of sampling (72 - 82 days) at which stage cv. Eclipsel-Bermuda showed the lowest RGR.

The RLGR was also highest initially in cv. Red-Kano while cultivars Eclipsel-Bermuda and Texas-Grano had similar but much lower values. The RLGR of all the three cultivars decreased as the plants advanced in age, but cv. Eclipsel-Bermuda and cv. Texas-Grano showed a higher rate of decrease than cv. Red-Kano which showed fluctuating values during the last three weeks.

The CGR of the tops of all the three cultivars showed a similar trend to the RGR. It was positive in cv. Red-Kano during the first three weeks and then declined to negative values a week earlier than cv. Eclipsel-Bermuda and cv. Texas-Grano. In cv. Red-Kano, the CGR increased to its

maximum value in the third week, after which it gradually decreased but during the last three weeks it increased again. The CGR of cv. Eclipsel-Bermuda and cv. Texas-Grano was highest in the first week but these values were much lower than that for cv. Red-Kano. The CGR of these two cultivars, Eclipsel-Bermuda and Texas-Grano showed a continuous decline as the plant increased in age. The growth rate of the bulb component was highest in cv. Red-Kano initially and continued to increase up to the sixth week after which it declined, showing fluctuating values during the last three weeks as in RGR, RLGR and CGR of the onion tops. In cv. Eclipsel-Bermuda, the growth rate of bulb increase for the first two weeks and then showed a continuous decline with increasing age of the plants. The bulbs of cv. Texas-Grano showed a uniform growth rate for the first three weeks followed by a sharp decline during the fourth week. During the last week it again increased to the former values. In all the three cultivars, the bulb growth rate was always higher than the growth rate of the tops.

The NAR generally decreased with increasing age of the plants in all the three cultivars with cv. Red-Kano showing higher NAR. In cv. Red-Kano, the NAR showed a continuous

decline till the fifth week (68 - 75 days) after which it again increased up to maturity. On the whole cv. Texas-Grano had the lowest NAR, whereas cv. Eclipsel-Bermuda and cv. Texas-Grano had negative values of NAR during the last two weeks, in cv. Red-Kano it was positive up to the last harvest.

The LAR of cv. Red-Kano remained constant throughout, except in the fifth week when it was zero. In cv. Eclipsel-Bermuda the LAR was $20dm^{-2}\ g^{-1}$ and then showed a sharp decline to $0.3dm^{-2}\ g^{-1}$ in the third week after which it again showed a rapid increase and was $22dm^{-2}$ at the last harvest. In cv. Texas-Grano, the LAR showed a slow continuous decline for the first four weeks, then it dropped rapidly during the last week.

4.2.3. CHLOROPHYLL CONTENT

The amount of chlorophylls a and b and the ratio of chl.a/chl.b at different dates of sampling are shown in table 15. In cv. Red-Kano chl.a increased with age of plant reaching a maximum between 82 and 97 days after transplanting and then decreased, but chl.b reached its maximum value earlier, at 68 days after transplanting. Chlorophyll a reached its maximum value in cultivars

Eclipsel-Bermuda and Texas-Grano between 47 - 54 days and thereafter decreased. In these two cultivars, the highest chl.a /chl.b ratio was attained at 61 - 68 days while in cv. Red-Kano; it was attained within the time chl.a reached its maximum value i.e., at 90-97 days after transplanting.

In both cv. Eclipsel-Bermuda and cv. Texas-Grano, the values of chl.a and chl.b were high from the first sampling but decreased at maturity. For cv. Red-Kano, however, these values were low at the beginning and end of sampling.

4.2.4. DISTRIBUTION OF P, K, Ca, Mg AND Zn

4.2.4.1. PHOSPHORUS

The phosphorus (P) concentration in the bulb of cv. Red-Kano increased with age up to 61 days after transplanting and thereafter decreased gradually. In the leaves, the P concentration was highest at 47 days but decreased to a lower value at plant maturity and this pattern was similar to that of the pseudostem. In cv. Eclipsel-Bermuda, the concentration of P in the bulb decreased to its lowest value at 68 days after transplanting, increased to its maximum value at 75 days and then decreased. The leaves of cv. Eclipsel-Bermuda however, had their maximum P concentration at 54 days,

it then decreased but increased again at maturity. This pattern was similar to that of the pseudostem in this cultivar. The pattern of P accumulation in cv. Texas-Grano was inconsistent. The accumulation of P in the bulb of cultivars Eclipsel-Bermuda and Texas-Grano was significantly higher than in cv. Red-Kano. In all the three cultivars, the general pattern of P accumulation in the plant parts was B > L > PS (Figs. 14 and 19).

4.2.4.2. POTASSIUM

The highest concentration of potassium (K) in leaves of cv. Red-Kano was observed at 75 days after transplanting while the highest K concentration of the pseudostem and bulb were at 90 and 47 days respectively. In the bulb the K concentration decreased from 2.4% per gm at 47 days to 1.5% per gm and then remained almost constant up to maturity. In the leaf and pseudostem, the pattern of K accumulation was incosistent. Whereas the K value in leaves of cv. Texas-Grano was almost constant up to 68 days before it decreased slightly, in cv. Eclipsel-Bermuda the highest value of K in all the three plant parts was observed at 54 days and this decreased gradually so that at maturity the concentration of K was lower than at the beginning of the experiment.

Generally, the pattern of K accumulation in the plant parts for all the three cultivars was the same:
Leaves > Pseudostem > Bulb (Figs. 15 and 20).

4.2.4.3. CALCIUM

In all the three cultivars, calcium (Ca) concentration was lowest in the bulbs and its concentration at maturity was lower than at the start of sampling. In the leaves and pseudostem of cv. Red-Kano, Ca concentration first decreased with age up to 61 - 68 days after transplanting and then increased so that at maturity the concentration in the leaves was higher than that in the bulbs. In cultivars Eclipsel-Bermuda and Texas-Grano, the concentration of Ca in the leaves and pseudostem was such that when one was high, the other was low. (Figs. 16 and 21).

4.2.4.4. MAGNESIUM

The concentration of magnesium (Mg) was generally lowest in the bulb and highest in the leaves of all the three cultivars. The concentration of magnesium in cultivars Eclipsel-Bermuda and Texas-Grano was highest in the leaves up to 75 days, but decreased to a lesser value than that in the pseudostem at 82 days after transplanting.

In cv. Red-Kano however, Mg continued to increase with age in the leaves up to maturity, attaining values higher than that in the pseudostem and the pattern of Mg concentration was Leaves > Pseudostem > Bulb (Figs. 17 and 22).

4.2.4.5. ZINC

Zinc (Zn) concentration in bulbs, pseudostem and leaves was high initially but decreased to lower values at plant maturity in cultivars Red-Kano and Texas-Grano. Zn concentration was generally lowest in the leaf and highest in the pseudostem while the concentration in the bulb was intermediate in these two cultivars (Fig. 23). The same was true in cv. Eclipsel-Bermuda at maturity even though between 61 and 68 days the Zn concentration in the bulb dropped to values lower than that in the leaf. In cv. Eclipsel-Bermuda, the Zn concentration in the bulb and pseudostem continued to increase from 68 days up to maturity while that in the leaf decreased to lower values.

The difference in accumulation of Zn in bulb, pseudostem and leaf with age in the three cultivars was highly significant ($P < 0.001$ and 0.01 respectively, Table 16). The difference in concentration of Zn in the pseudostem between cultivars was also significant; Zn was highest in

cv. Texas-Grano and lowest in cv. Red-Kano. Zn accumulated more in the leaves of cv. Eclipsel-Bermuda than the other two cultivars and this was significant. There was no significant difference however, between the cultivars in the concentration of Zn in the bulbs (Table 16).

Table 13

Effect of age on plant height and number of leaves in three onion cultivars. Results as means of 4 plants.

Plant age (days)	RED-KANO		ECLIPSEL-BERMUDA		TEXAS-GRANO	
	Plant height (cm)	No.of mature leaves	Plant height (cm)	No. of mature leaves	Plant height (cm)	No. of mature leaves
36	31.6	5.25	-	-	-	-
47	38.5	6.5	16.5	3.5	15.75	4
54	47.7	8.5	17.4	4.5	20.7	5.25
61	59.8	10.25	16.8	4.5	21.75	5.75
68	57.2	10.75	18.3	4.75	19.75	5.5
75	63.6	12	16.6	4.25	16.1	5.5
82	60.9	11.5	16.4	4	16.1	3.5
90	50.3	9.75	-	-	-	-
97	50.3	8.75	-	-	-	-
104	49.2	10.75	-	-	-	-
111	48.2	11.25	-	-	-	-

TABLE 14: Growth attributes of three onion cultivars at different stages of growth.

Age of plants after trans-planting	Red-Kano	Eclipsel-Bermuda	Texas-Grano
	Relative Growth Rate (RGR) % wk^{-1}		
36 - 47	104	-	-
47 - 54	76	63	42
54 - 61	66	28	3
61 - 68	-16	3	31
68 - 75	0	-9	-82
75 - 82	-40	-35	-3
82 - 90	-22	-	-
90 - 89	5	-	-
97 -104	-36	-	-
104-111	50	-	-
Relative Leaf Growth Rate (RLGR) % wk^{-1}			
36 - 47	100	-	-
47 - 54	93	35	34
54 - 61	53	7	4
61 - 68	26	0	-10
68 - 75	1	19	-33
75 - 82	-14	-47	-3
82 - 90	-46	-	-
90 - 97	22	-	-
97- 104	-29	-	-
104-111	32	-	-

TABLE 14 Continued

CROP GROWTH RATE (CGR) gm^{-2} day^{-1}						
Age of plants after trans-plant-ing	Red-Kano		Eclipsel-Bermuda		Texas-Grano	
	Tops	Bulb	Tops	Bulb	Tops	Bulb
36 - 47	0.19	0.10	-	-	-	-
47 - 54	0.37	0.16	0.10	0.09	0.09	0.10
54 - 61	0.58	0.33	0.07	0.21	0.01	0.10
61 - 68	-0.18	0.38	-0.01	0.10	0.10	0.11
68 - 75	-0.0014	0.30	-0.03	0.03	-0.21	0.01
75 - 82	-0.33	0.51	-0.16	-0.04	-0.04	0.09
82 - 90	-0.14	-0.38	-	-	-	-
90 - 97	0.03	1.29	-	-	-	-
97 -104	-0.18	-1.03	-	-	-	-
104-111	0.26	0.002	-	-	-	-

Net Assimilation Rate (NAR)g dm^{-2} wk^{-1}

	Red-Kano	Elcipsel-Bermuda	Texas-Grano
36 - 47	0.05	-	-
47 - 54	0.05	0.03	0.02
54 - 61	0.04	0.02	0.0017
61 - 68	0.01	0	0.02
68 - 75	0.00013	-0.0049	-0.05
75 - 82	0.02	-0.04	-0.04
82 - 90	0.01	-	-
90 - 97	0.003	-	-
97 -104	0.02	-	-
104-111	0.03	-	-

TABLE 14 Continued

Leaf Area Ratio (LAR) dm^{-2} g^{-1}

Age of plants after trans-plant-ing	Red-Kano	Eclipsel-Bermuda	Texas-Grano
36 - 47	17	-	-
47 - 54	18	20	20
54 - 61	19	14	18
61 - 68	17	0.3	17
68 - 75	0	18	16
75 - 82	18	22	2
82 - 90	18	-	-
90 - 97	15	-	-
97 -104	19	-	-
104-111	18	-	-

Table 15

Effect of plant age on chlorophyll content of onion leaves. Results as mean of 4 plants.

Onion Cultivar	Plant age in days after trans-planting	Chlorophyll Content (Mg/g fresh plant material)			Ratio Chla/Chlb
		Ch/a	Ch/b	Total	
Red-Kano	36	0.36	0.19	0.55	1.89
	47	0.39	0.21	0.60	1.86
	54	0.46	0.24	0.70	1.92
	61	0.42	0.25	0.67	1.68
	68	0.50	0.31	0.81	1.61
	75	0.38	0.22	0.60	1.73
	82	0.51	0.29	0.80	1.76
	90	0.39	0.17	0.56	2.29
	97	0.51	0.23	0.74	2.22
	104	0.32	0.17	0.49	1.88
	111	0.33	0.18	0.51	1.83
S.E.		0.02	0.01	0.03	0.06

TABLE 15 Continued

Onion Cultivar	Plant age in days after trans-planting	Chlorophyll Content (Mg/g fresh plant Material)			Ratio
		Ch/a	Ch/b	Total	Cla/Chlb
Eclipse1-Bermuda	47	0.50	0.37	0.87	1.35
	54	0.57	0.31	0.88	1.84
	61	0.43	0.21	0.64	2.05
	68	0.45	0.18	0.63	2.50
	75	0.40	0.30	0.70	1.33
	82	0.30	0.18	0.48	1.67
S.E.		0.04	0.03	0.06	0.18
Texas-Grano	47	0.49	0.31	0.80	1.58
	54	0.50	0.29	0.79	1.72
	61	0.45	0.19	0.64	2.37
	68	0.44	0.21	0.65	2.10
	75	0.46	0.24	0.70	1.92
	82	0.36	0.23	0.59	1.57
S.E.		0.02	0.02	0.03	0.13

TABLE 16: Analysis of variance for P, K, Ca, Mg and Zn distribution in pseudostem bulb and leaves of three onion cultivars as influenced by plant age and cultivar.

	Source of variation	Age x cultivar	Cultivar	Age
	DF	10	2	10
Phospherus	Pseudostem	1.27	1.26	0.64
	Bulb	9.28***	6.37**	3.51***
	Leaves	2.61	0.08	1.62
Potassium	Pseudostem	1.52	7.94***	1.54
	Bulb	1.54	10.92	5.51***
	Leaves	2.53*	0.37	0.68
Calcium	Pseudostem	5.13***	22.69***	1.10
	Bulb	1.79	5.01**	5.75***
	Leaves	2.33*	23.77***	4.34**
Magnesium	Pseudostem	3.64***	0.55	1.69
	Bulb	3.13**	0.47	1.86
	Leaves	2.13*	4.87*	2.79**
Zinc	Pseudostem	1.56	8.32***	2.93**
	Bulb	8.31***	1.35	4.24***
	Leaves	1.02	4.83*	2.90**

Legend

*** - significant at 0.1% level ($P < 0.001$)

** - significant at 1% level ($P < 0.01$)

* - significant at 5% level ($P < 0.05$)

Blank - not significant

TABLE 17: Analysis of variance for growth characteristics in three onion cultivars as influenced by plant age and cultivar.

	Source of variation	Age	Cultivar	Age x cultivar
	DF	10	2	10
Dry-weight	Leaves	24.89***	212.46***	10.27***
	Pulb	42.97***	45.68***	5.81***
	Pseud-ostem	10.60***	50.69***	9.34***
	Roots	6.74***	20.07***	3.28**
	Leaf area	3.44***	2.03**	1.53**
	Chloro-phyll a	8.64***	1.30	6.82***
	Chloro-phyll b	0.63	1.28	1.27
	Chlo.a/Chl.b ratio	7.15***	1.64	6.33***
	Plant height	18.01***	749.54***	9.04***
	No. of leaves per plant	11.31***	174.08***	4.10***

Legend

*** - significant at 0.1% level ($P < 0.001$)

** - significant at 1% level ($P < 0.01$)

* - significant at 5% level ($P < 0.05$)

Blank - not significant

Fig. 18 *Changes in Leaf area with plant age in three onion Cultivars. Vertical lines indicate the standard error.*

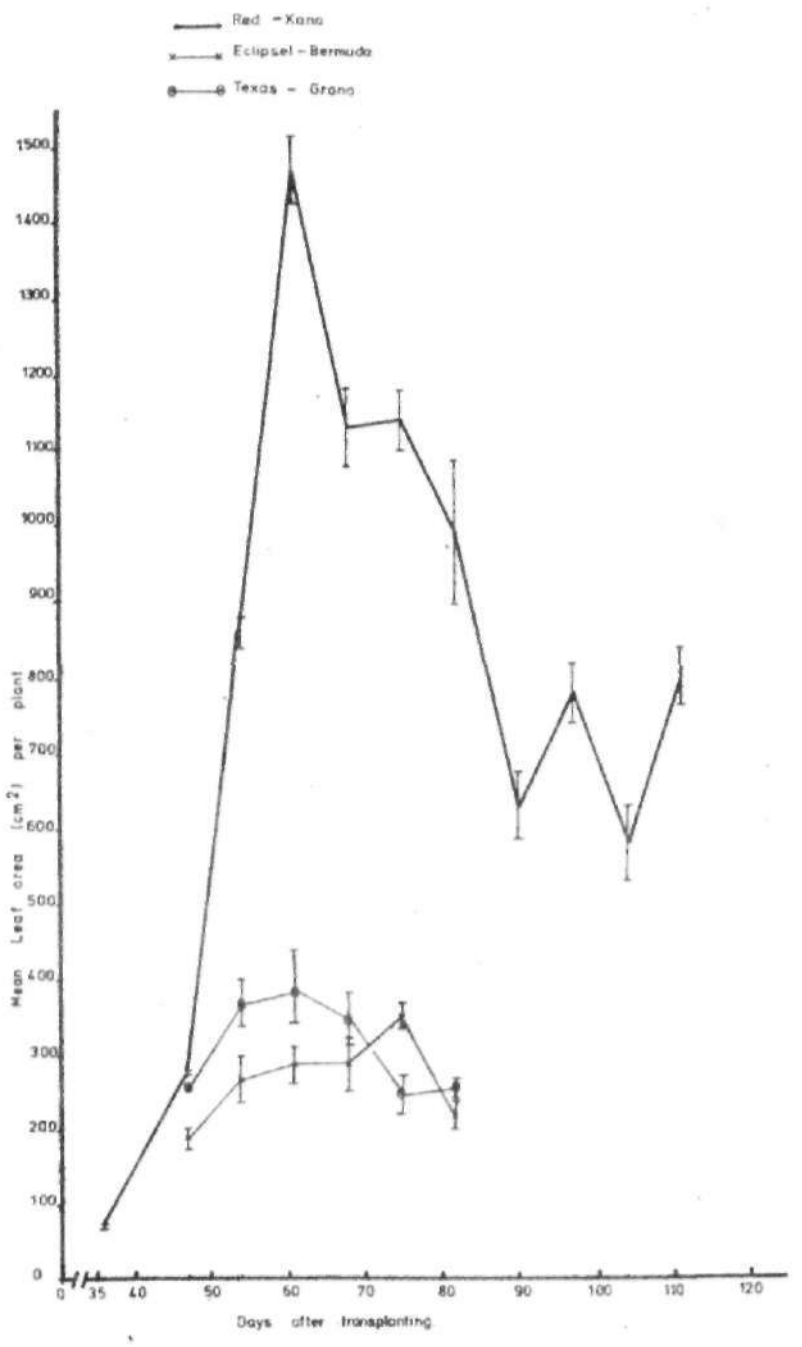


Fig.13 *Relationship Between Total Dry Weight, Weight of the bulb, Pseudostem and leaves as influenced by age.*

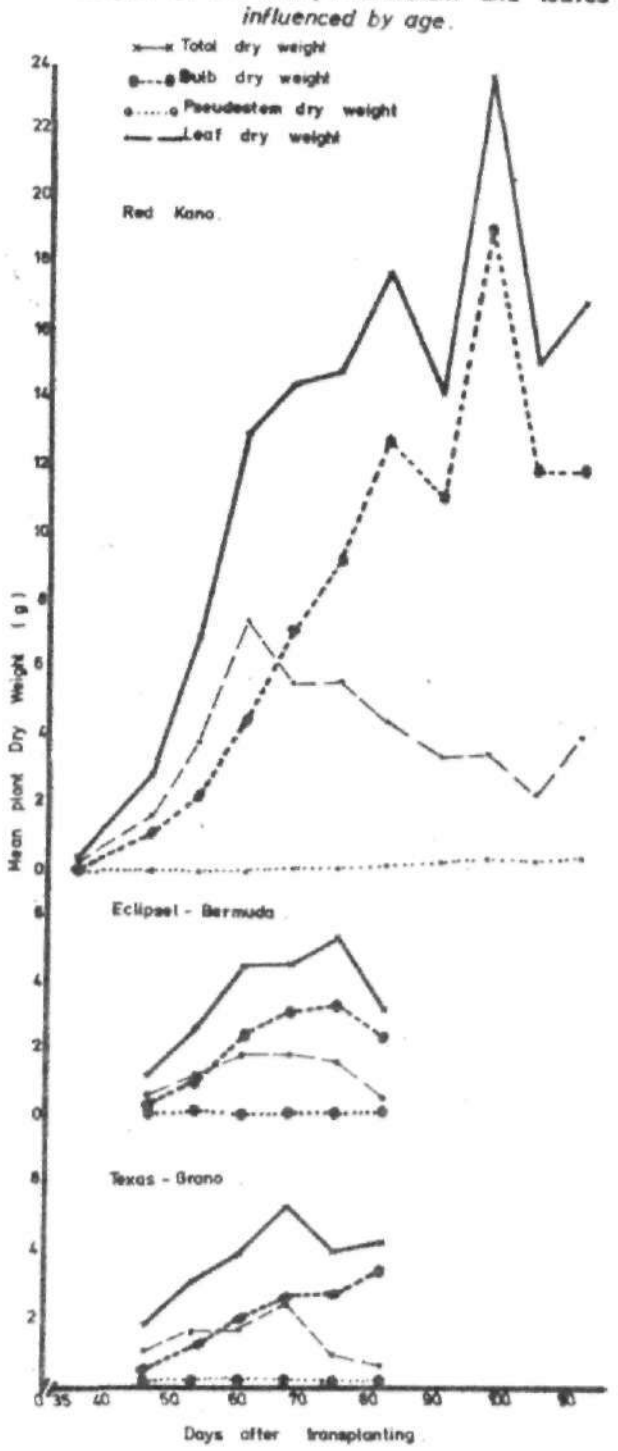


Fig. 14 *Phosphorus concentration in three onion cultivars as influenced by plant part and age (s.e. given)*

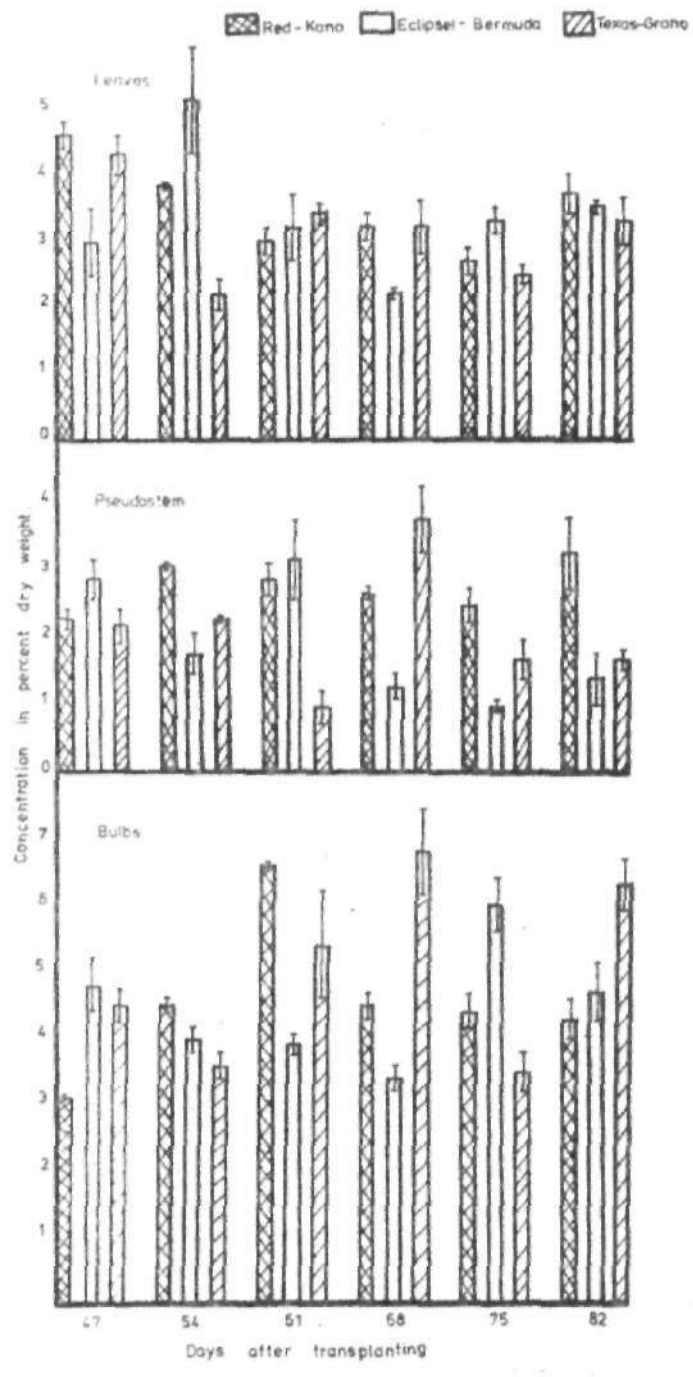


Fig. 15 *Potassium concentration in three onion cultivars as influenced by plant part and age (s.e given)*

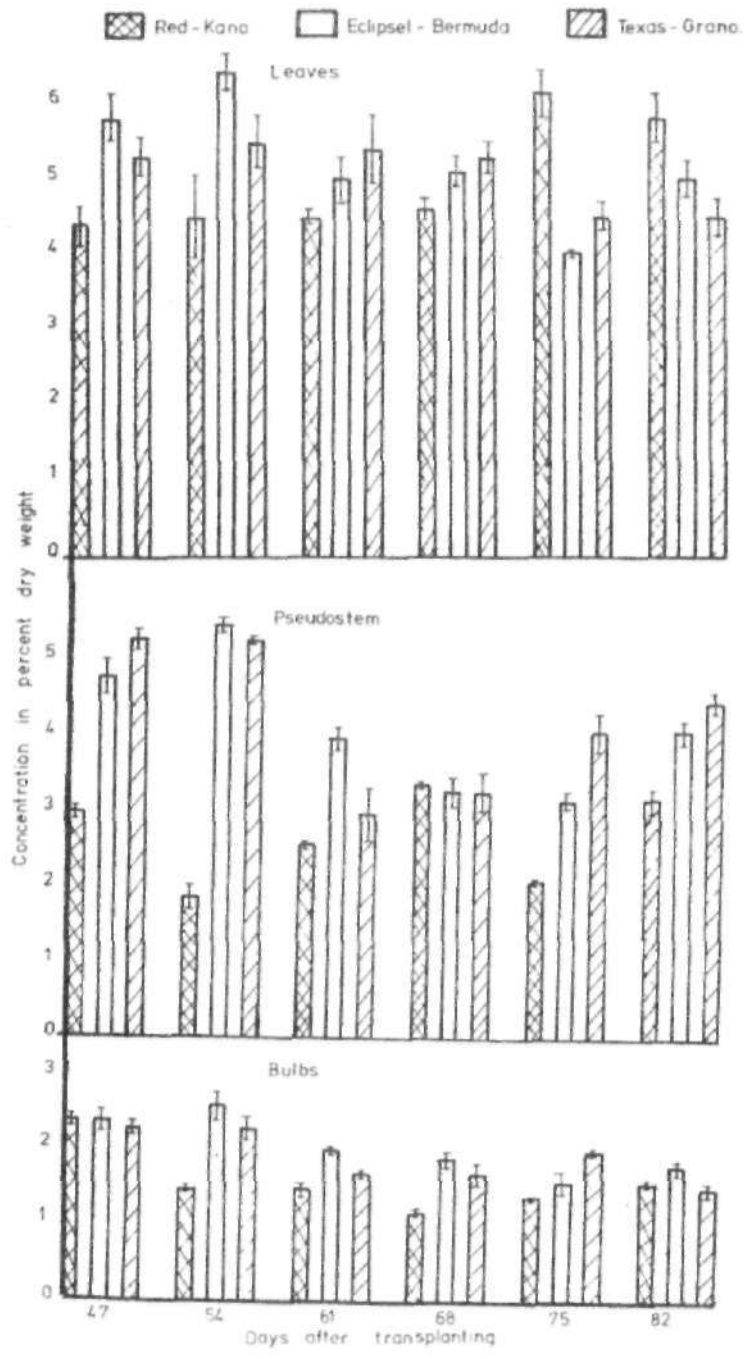


Fig.16 *Calcium concentration in three onion cultivars as influenced by Plant part and age(s.e. given).*

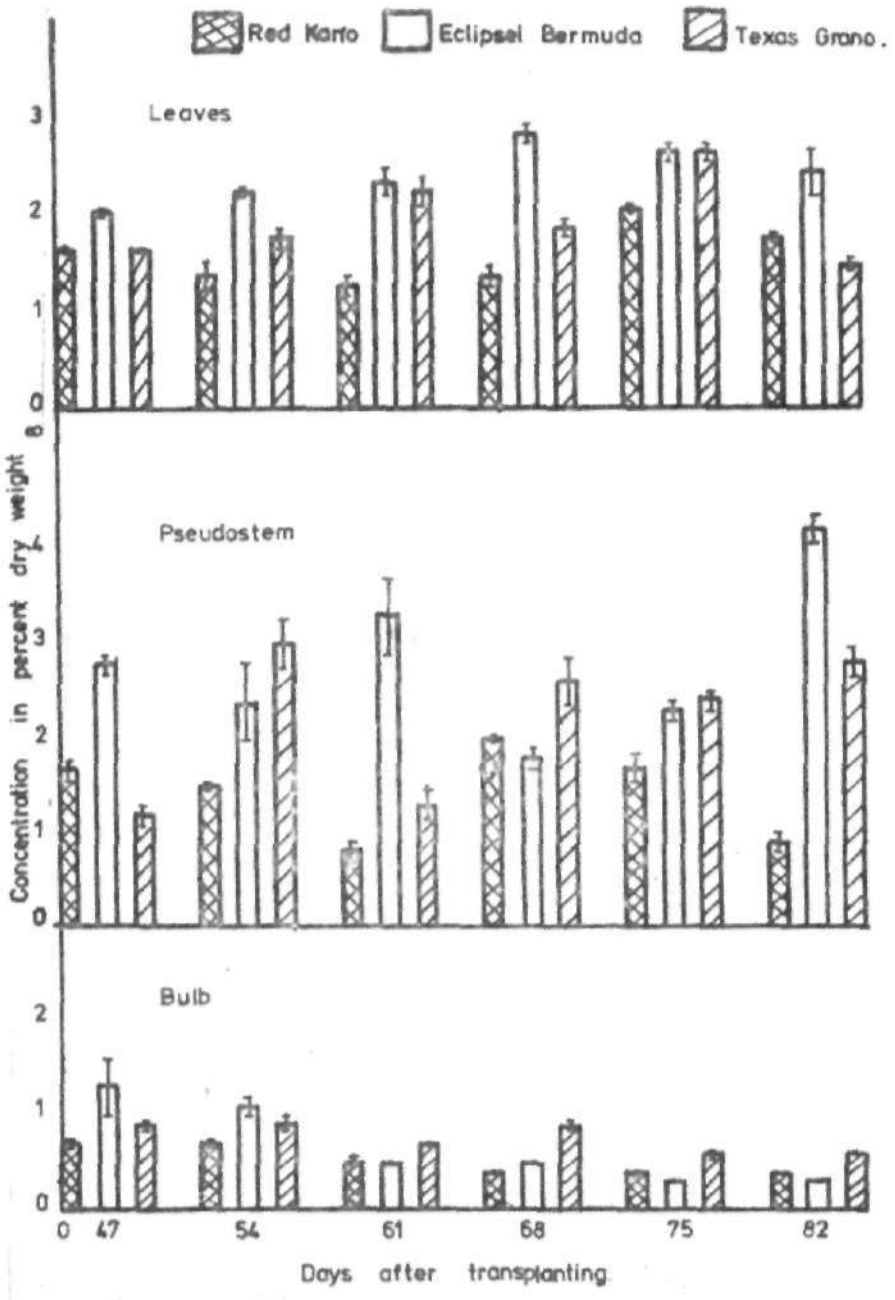


FIG. 17

Magnesium concentration in three onion cultivars as influenced by plant part and age (s.e. given).

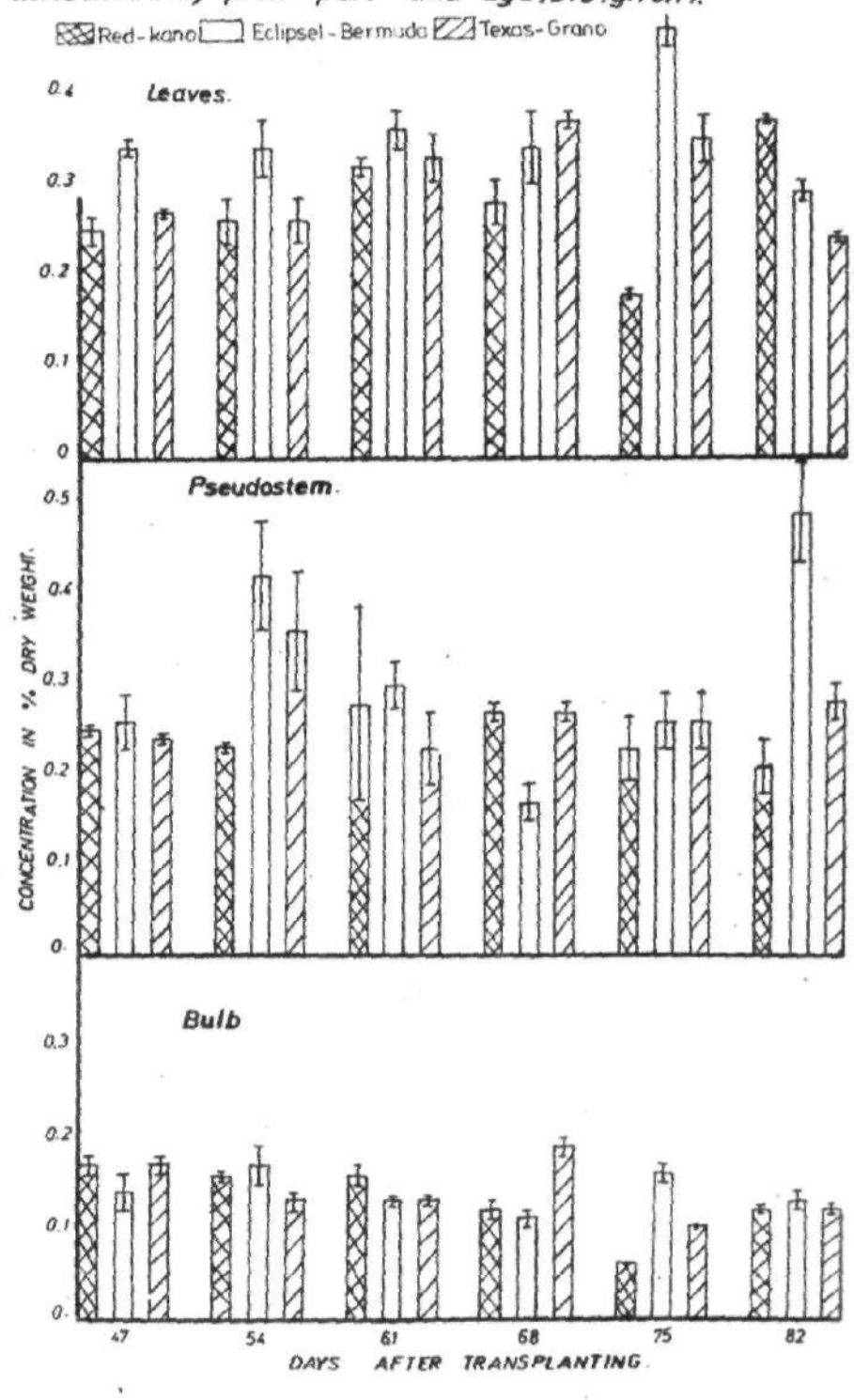


FIG. 18 *Zinc concentration in three onion cultivars as influenced by plant part and age (s.e. given).*

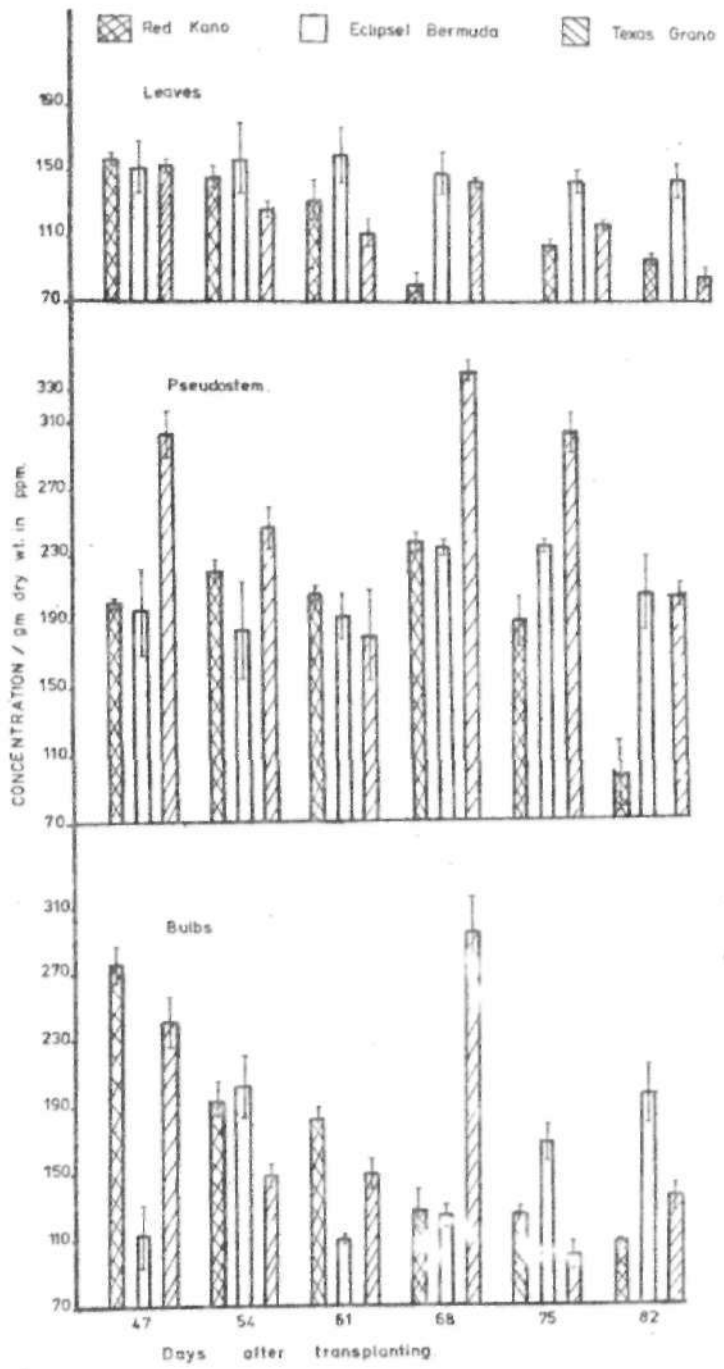
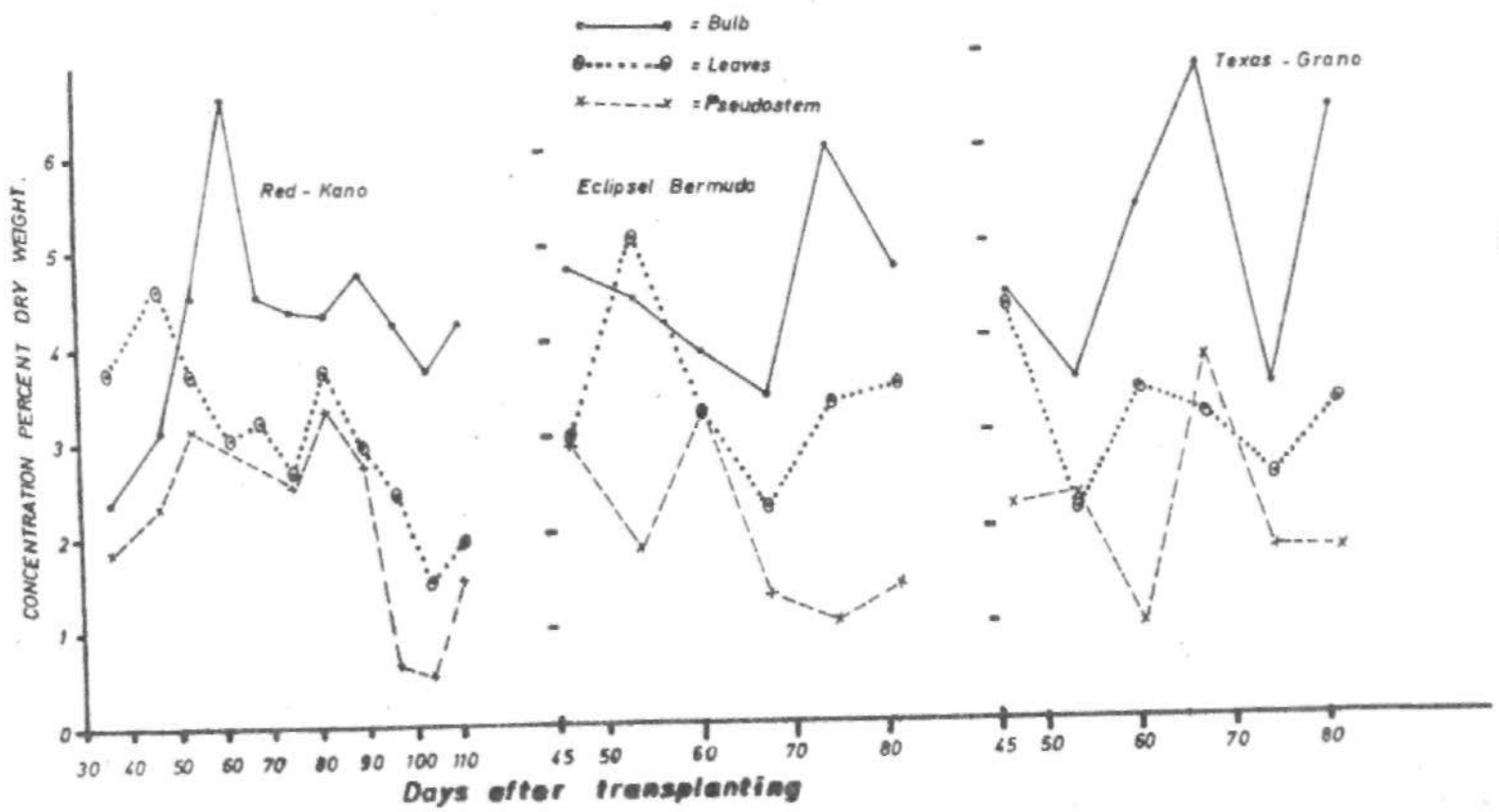


FIG. 19

ACCUMULATION OF PHOSPHORUS IN RED – KANO, ECLIPSEL–BERMUDA AND TEXAS – GRANO AS INFLUENCED BY PLANT PART AND AGE



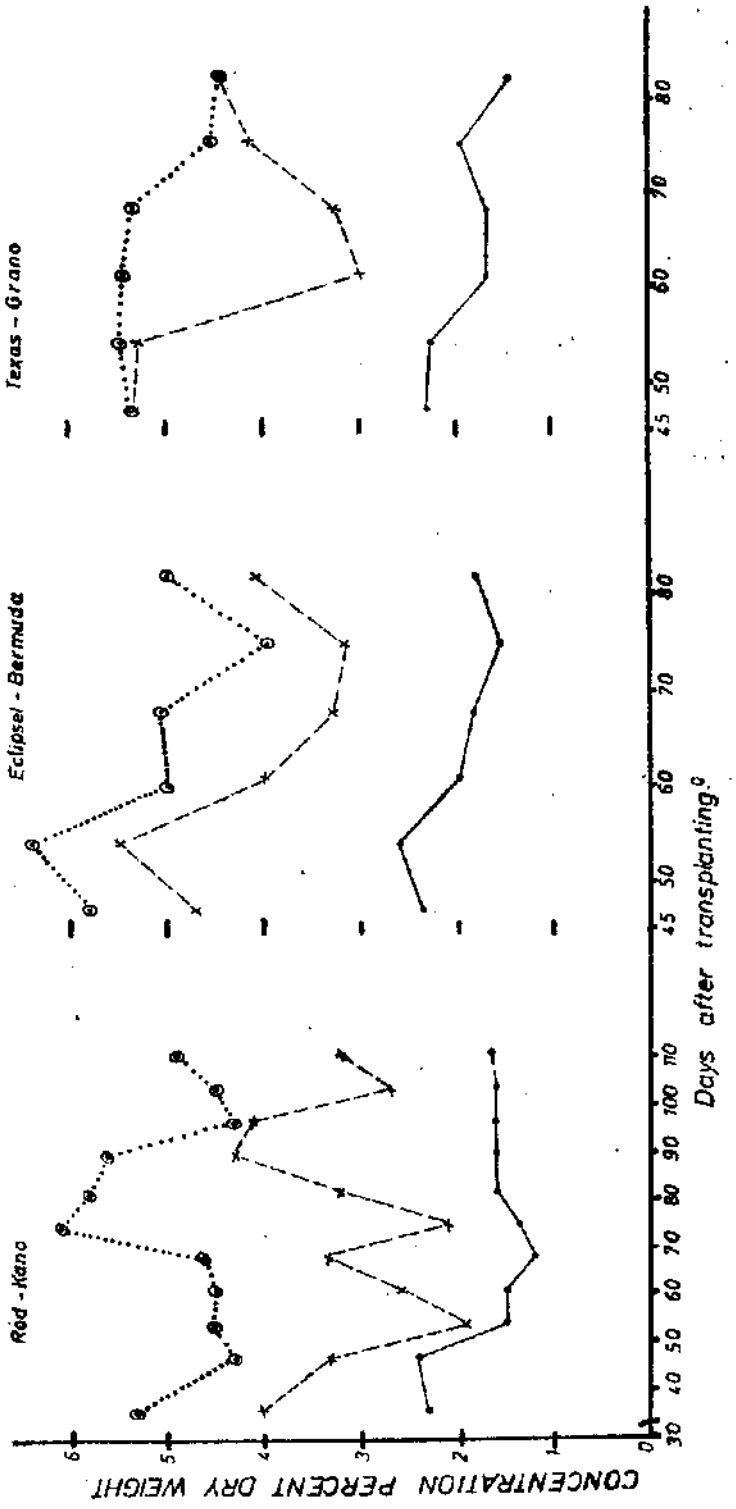
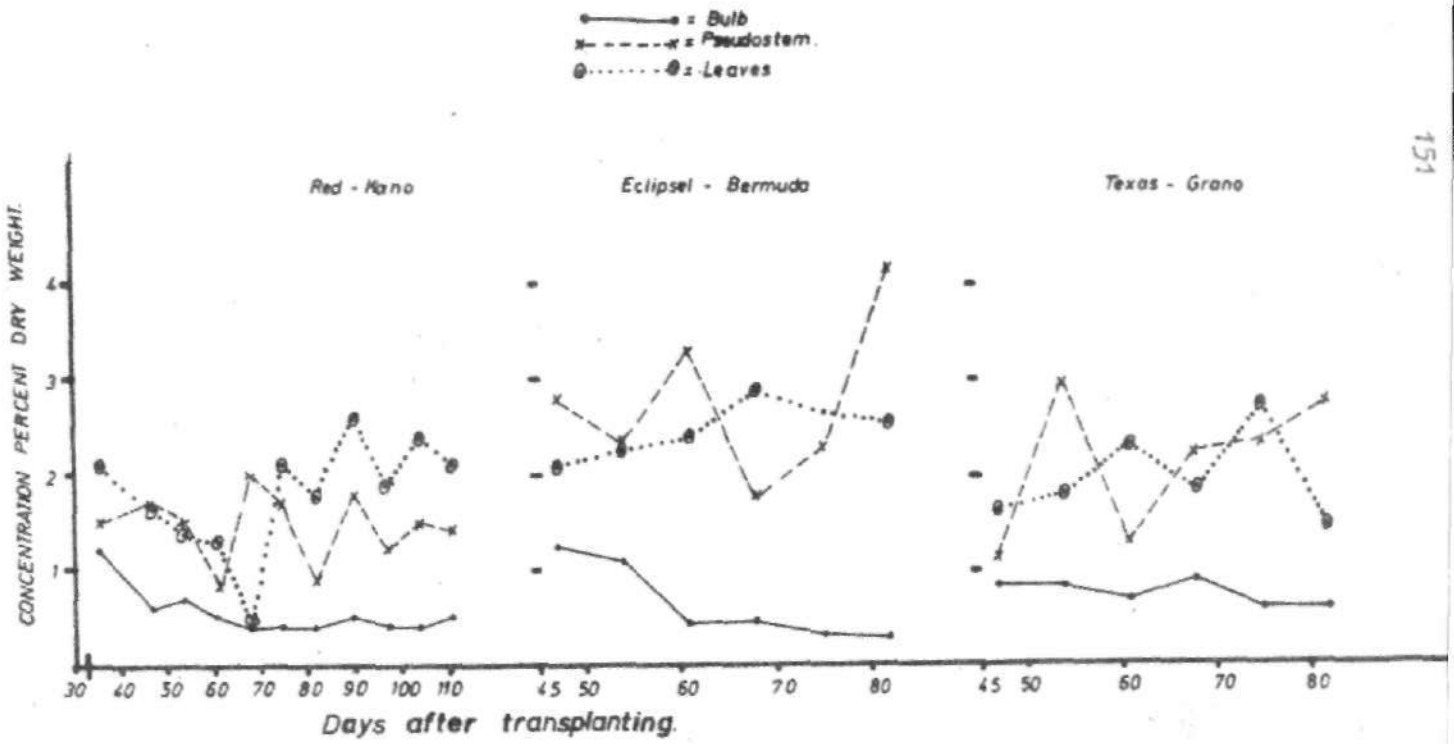


Fig. 20 ACCUMULATION OF POTASSIUM IN RED-KANO, ECLIPSEL - BERMUDA AND TEXAS-GRANO AS INFLUENCED BY PLANT PART AND AGE

Fig.21
ACCUMULATION OF CALCIUM IN RED-KANO, ECLIPSEL - BERMUDA AND TEXAS-GRANO AS INFLUENCED BY PLANT PART AND AGE.



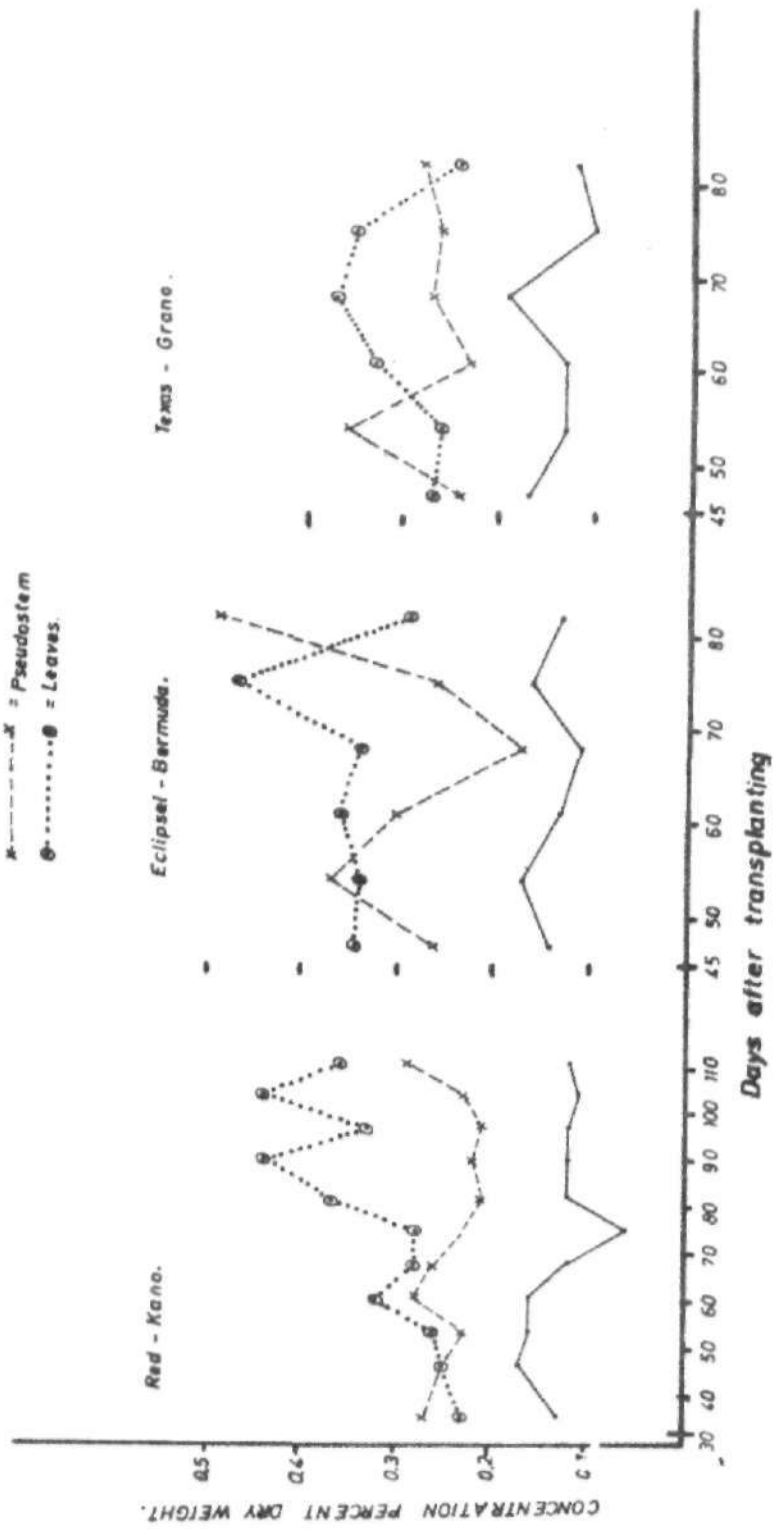


Fig. 22 *Accumulation of magnesium in Red - Kano, Eclipse! - Bermuda and Texas - Grano as influenced by plant part and age.*

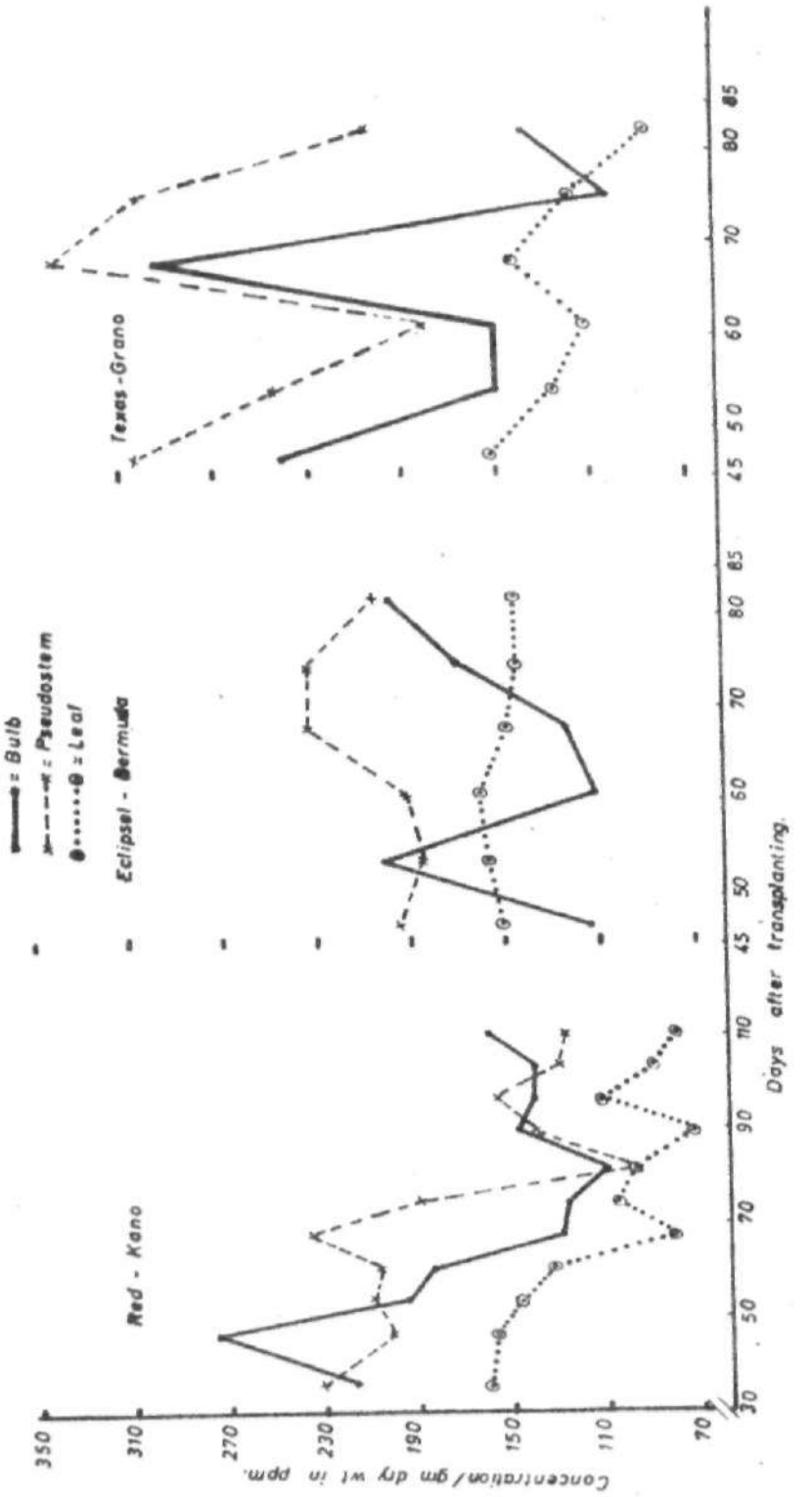


FIG. 23 *Accumulation of Zinc in three onion cultivars as influenced by plant part and age.*

CHAPTER 5

DISCUSSION

5.1. TRANSLOCATION OF ^{14}C-ASSIMILATED

From the experiments carried out, the following main features have emerged:

1. The translocation efficiency of source leaves increased with plant age to a certain extent.
2. Mature leaves retained a considerable proportion of ^{14}carbon,
3. The bulb was the dominant sink for photosynthates and its importance increased with plant age.
4. The pseudostem and roots were important sinks in the early stage of plant growth but later on they became unimportant sinks.

5.1.1. THE EFFICIENCY OF THE SOURCE LEAVES

In experiment 1 export from L1 to L5 of cv. Red-Kano increased with increase in leaf age, reaching a maximum from L2 and then decreased. The results were similar to soyabean (Thrower, 1962), sugarbeet (Joy, 1964) and tomato (Khan and Sagar, 1969), where the export of assimilates increased with increase in age of leaf. In Lolium temulentum the leaves exported less after the passing

of full expansion period.(Ryle and Powell, 1972). The concept of assimilate export and photosynthetic activity of a leaf is closely linked. The reduced photosynthetic activity from L1 as a result of ageing may have resulted in reduced export.

In cv. Eclipsel-Bermuda, export of labelled assimilates from L1 - L5 in experiment 1 increased with increasing age of leaf but the young source leaf (L5) in this experiment still exported a higher percentage of assimilates than the oldest leaf (L1) (Figs. 2 and 3). In cv. Texas-Grano, export from the younger treated leaves (L4 and L5) in this experiment was higher than the oldest leaves (L1 and L2). It would appear that in these two cultivars, the young leaves started to export very early in their life and after emergence they quickly reached maturity because the plants were early maturing. Net export of assimilates from leaves have been shown to start when the leaf was between one-third and one-half of its final size (Wardlaw, 1968). Since the final size of the leaves of these two cultivars was smaller than that of cv. Red-Kano, it seems that the leaves attained the status of a net exporter earlier than those of cv. Red-Kano. The higher export

from the younger leaves than the older leaves in cv. Eclipsel-Bermuda and cv. Texas-Grano was similar to the finding of Ryle (1972) in Lolium temulentum, where the youngest leaves supplied two to five times more carbon than the lower old leaves, due to their higher photosynthetic activity. The analysis of variance of experiment 1, 1978 showed that there was significant difference between cv. Eclipsel-Bermuda and cv. Texas-Grano as regards the percentage of ^{14}C exported ($P < 0.001$, Table 8). Plants of cv. Eclipsel-Bermuda exported much higher percentage of the assimilates they fixed which ranged from 63.5 - 90.3%. Leaves of cv. Texas-Grano exported significantly lower percentage of assimilates, ranging from 42.3% to 74.4%. The effect of leaf position on the percentage of ^{14}C exported was not significant but the effect of leaf position and cultivar was significant ($P < 0.01$, Table 8).

In 1979 when the three cultivars were tested, there was significant difference between the three cultivars in the percentage of ^{14}C exported ($P < 0.05$, Table 10). Export of assimilates from leaves of cv. Red-Kano was significantly higher than from those of cv. Eclipsel-Bermuda and cv. Texas-Grano and ranged from 47.3% to 98.6%. Percentage export of assimilates from the other two cultivars was of

similar value and ranged from 58.2% to 71%. There was also significant difference between the leaf positions ($P < 0.01$, Table 10). This showed varietal differences in onion. Little information is available on translocation efficiency in different varieties. Lupton (1966, 1968) did not notice any varietal difference in the translocation behaviour in wheat but Khan (unpublished) found varietal differences in millet.

Export of assimilates at this stage of plant development (59 days after transplanting) was generally high from all treated leaves. The assimilates were mobilised to support the newly formed leaves and the developing bulb. Steer and Darbyshire (1979) also found only 22.3% of labelled assimilates remained in the fed leaf after 24 hours when the upper segment of the leaf of onion cv. Creamgold at the 6th leaf stage were exposed for 1 hour to $^{14}CO_2$. Other workers have also recorded such high export values in other species (Hartt et al. 1963 in sugarcane, Hofstra and Nelson, 1969 and Eastin 1970 in maize).

At the time of the second experiment, export of labelled assimilates was above 40% in both years. In 1978, the percentages of fixed ^{14}carbon exported by cv. Eclipse1-Bermuda

and cv. Texas-Grano were not significantly different (Table 9). There was no significant difference between the leaves treated as regards the percentage of fixed ^{14}carbon they exported. The youngest leaf retained most of its fixed assimilates. It exported 66.8% in cv. Eclipsel-Bermuda and 59.6% in cv. Texas-Grano. Export of assimilates was higher from the lower older leaves. In 1979 the percentage of fixed carbon exported in cv. Red-Kano was significantly higher than the other two cultivars ($P < 0.05$, Table 11). Export of assimilates from all the treated leaves in the subsequent experiments was over 46% in all the cultivars and was not significant (Table 12). All the leaves must have reached maturity by then and were mainly exporters. Khan (1981) also found that in cv. Red-Kano at 112 days after transplanting the leaves exported up to 92.7% of the fixed carbon. Khan and Asif (1981) further showed that even the fixed carbon left in the leaves at the time of senescing may be re-exported to the bulbs.

5.1.2. PATTERNS OF DISTRIBUTION

5.1.2.1. IMPORT OF RADIOCARBON BY LEAVES

Import of labelled assimilates by the younger leaves was mainly from the lower older leaves during both years

and it varied from 9% to 39% (Figs 7 and 9). Most of the carbon was imported mainly by the youngest emerging leaves (Plates 1, 2, 3). Steer and Larbyshire (1979) found no labelling in the next leaf above the treated leaf in onion cv. Creamgold with 13 leaves when this younger leaf had an emerged blade. The pattern of assimilate distribution in onion changed with plant age. That is, when the plant was very young all the leaves were still expanding, the emerging blade was not supported by other expanding leaves. But when the leaves became fully expanded they exported assimilates to the emerging blades. In Lolium temulentum export of assimilates from an expanded leaf increased from 65% to 85% when a new leaf expanded above it (Ryle and Powell, 1972). Most of the photosynthate translocated to the younger leaves was present in the base (Plates 1E, 2E, and 3E). In onion leaf the meristematic region is at the leaf base. Shiroya et al. (1961) and Wardlaw (1968) showed that areas of high metabolic activities like the stem and young leaves were strong sinks for translocated carbohydrates.

Import of labelled assimilates by the younger leaves at 81 days after transplanting was higher from the lower leaves in all the three cultivars ($P < 0.05$, Table 11).

In 1978 leaves of cv. Eclipsel-Bermuda and cv. Texas-Grano imported more than in 1979. As the leaf aged the import by this sink declined. This may be due to the fact that in cv. Eclipsel-Bermuda and cv. Texas-Grano no new leaves were being formed while in cv. Red-Kano new leaves were still forming.

Import of labelled assimilates by mature leaves was insignificant and ranged from 0.9% to 14.2% but leaf position had a significant effect (Figs. 7 and 9, Tables 8 and 10). Both the antoradiographic and quantitative assay showed that old mature leaves imported an unsignificant quantity of assimilates. Thrower (1962), Doodson et al. (1964), Khan and Sagar (1969) and Nyahoza et al. (1973) have reported that older leaves imported some photosynthates. Export of assimilates to the older leaves was higher from the upper leaves but this may be a cumulative effect. In the first experiment percentage export of labelled assimilates to the older leaves was significantly different in 1979 ($P < 0.001$). The percentage contribution by the different cultivars to this sink was also significantly different ($P < 0.05$, Table 10). With the ageing of the plant there was less export of

assimilates to the leaves but at plant maturity import by these leaves increased slightly. This may be so because at the time of the second experiment the leaves constituting this sink had fully expanded and were actively photosunthesizing and exporting assimilated photosynthates. At maturity they imported a slightly higher percentage of ^{14}C to support their metabolic activities due to delayed senescence so as to fill up the bulb scales with aborted leaf blades.

5.1.2.2. IMPORT OF RADIOCARBON BY PSEUDOSTEM

Most assimilates found in the pseudostem were in transit from the leaf blades to the stem (where there were the bulb, roots and other leaves). The pseudostem is the immediate section below the leaf blade through which assimilates from the leaf blades pass. The leaf folds that form the pseudostem are usually not very fleshy and not adapted for storage. Assimilates recovered from the pseudostem were of higher percentage than that recovered from the mature leaf blades below the treated leaf but were insignificant (Tables 8 and 9). Generally, export of labelled assimilates to the pseudostem was high from L1, decreased from L2 and increased again from the middle and upper

leaves in experiment 1. Leaf position at this stage was significant and important in determining the percentage of assimilates exported to this sink ($P < 0.05$, Table 10).

As the plant matured the pseudostem became an unimportant sink. At maturity however, higher amounts of photosynthates were recovered from the pseudostem when upper leaves were labelled. This shows that these leaves were actively exporting more assimilates to the bulb than other leaves. Khan (1981) also found that the upper leaves of onion cv. Red-Kano contributed 14.2% while lower leaves contributed only 1.4% to the pseudostem at 112 days after transplanting and the proportion of photosynthates recovered from the pseudostem decreased as the plant aged.

The fact that the pseudostem was mainly a translocatory path was further supported by the fact that the leaf fold (pseudostem) of the leaf supplied with $^{14}CO_2$ was more extensively labelled than that of other leaves and in most instances little or no activity appeared in the fold of other leaves, (Plates 1, 2, 3). Mayer and Porter (1960) recorded only traces of activity in the leaf sheaths of rye. The sheath of sugarcane has also been found to act only as a translocatory path of photosynthates from the leaf

lamina to the stem (Hartt et al. 1963)

5.1.2.3. IMPORT OF RADIOCARBON BY THE BULB

Wardlaw (1965) showed the polarizing power of assimilate movement caused by the presence of storage organs. Unlike the tomato plant where groups of leaves had primary responsibility for supplying single trusses when the number of trusses increased (Khan and Sagar, 1966), in the onion plant all leaves at all stages of growth supplied radiocarbon to the bulb. Export of photosynthates to the bulb increased with increasing age of the plant and the bulb became an increasingly significant sink between 59 and 81 days after transplanting (Table 9 & 11). Towards maturity, however, export of assimilates to the bulb decreased slightly as the bulb scales were almost completely filled (Figs. 5 and 6).

The period between 59 and 81 days after transplanting was the period of rapid bulb swelling since it was at this time that the bulb reached a stage of maximum import of assimilates. The maximum leaf area was also attained at this time. The plants of cv. Red-Kano and cv. Texas-Grano reached their maximum leaf area at 61 days after transplanting while those of cv. Eclipsel-Bermuda attained it at 75 days

(Fig. 12). With the attainment of maximum leaf area and subsequent decrease due to reduced leaf emergence, there was reduced competition for assimilates by the leaves. Root growth was also slowed down at this stage and less assimilates were mobilized to them. The bulbs were increased considerably in weight at this stage (Table 6 & 7) and their growth rate was also increased (Table 14). Warren Wilson (1972) indicated that the sink strength of an organ was a product of sink size (dry weight) x sink activity (its relative growth rate). Increase in sink strength as the plant grows may make the growth of the sink source-limited. Furthermore, decreasing source-sink ratios (by reduced leaf area) causes assimilate accumulation to operate below its maximum potential (Wareing and Patrick, 1975). This implies that at the early stages of onion bulb growth, the rate of accumulation of photosythates was sink limited but later as the bulb increased in size and its growth rate increased, it became source limited. In a single plant of artichoke, the larger the tuber, the relatively more receptive it was to translocated carbon. On the other hand with similar experiments on potato, no obvious relationship was found between size of tuber and amount of labelled photosynthate absorbed (Edelman, 1963).

The relationship between the growth rate of the sink and the source size was further demonstrated in tulips when partial defoliation reduced relative growth rate of daughter bulbs approximately in proportion to the area of leaf removed. Tulips are also similar to onions in a sense that they also show a period of rapid bulb growth (Rees, 1972). Khan (1981) also found that the bulbs of onion cv. Red-Kano showed a rapid increase in size and weight and became the dominant sink at 71 days after transplanting.

At the first sampling in 1978, leaves of cv. Eclipsel-Bermuda and cv. Texas-Grano exported similar amounts of assimilates to the bulb which were not significantly different (Table 8), but in 1979 these two cultivars exported higher amounts of labelled photosynthates to the bulb than cv. Red-Kano at this stage ($P < 0.001$, Table 10). In cv. Red-Kano more assimilates were imported by the bulb from the lower mature leaves. This is in agreement with Khan (1981). In cv. Eclipsel-Bermuda and cv. Texas-Grano, L4 and L5 exported more to the bulb (Fig. 6) which confirmed the earlier view that the leaves of these cultivars quickly attained maturity after emergence. At the second sampling, leaf position became an increasingly important factor in the mobilization of assimilates to the bulb ($P < 0.05$, Table 11).

The newly fully expanded leaf (L7) exported the highest percentage of assimilates to the bulb (91.2% - 95.1%) in all the three cultivars.

At the early stage all the leaves translocated labelled assimilates to all the young bulb scales but as the plant increased in age, labelled assimilates from mature leaves were mainly translocated to the bulb scale of the source leaf and the youngest bulb scale initiated. At this stage no activity was detected in bulb scales below that of the source leaf and those inbetween those of source leaf and the youngest scales (Plates 4, 5 and 6). This showed that each leaf blade was responsible for the formation of its bulb scale once the leaf is mature. Assimilates from mature leaves also supplied the youngest bulb scale. This was in agreement with the observation of Steer and Darbyshire (1979) in young onion plants of cv. Creamgold where they detected activity in young bulb scales without emerged lamina when an older leaf was labelled. In potato tubers however, radio activity spread evenly throughout the tuber after the tops were exposed to $^{14}CO_2$ but the periderm became most highly labelled. Activity was also localized in the periphery of its starch grain.

Similar results were obtained with the tuber forming artichoke plant (Edelman, 1963). These works show that activity was localised in growing regions as was observed in the onion.

Killing of flowers in tulip increased the weight of the daughter bulbs due to reduced competition (Rees, 1972). The bulb of onion became an increasingly dominant sink because of its high meristematic activity, increasing sink strength as well as reduced competition from other sinks. The daughter bulbs of tulip also became an increasingly dominant sink for newly fixed carbon with the completion of flower and stem growth and hence reduced competition for assimilates from these sinks (Ho and Rees, 1976).

5.1.2.4. IMPORT OF RADIOCARBON BY ROOTS

Although all leaves supplied some radiocarbon to the root, the lower leaves supplied higher qunatity of photosynthates to the root in both years in all the three cultivars (Table 11). In 1978, at the first sampling, leaves of cv. Eclipsel-Bermuda supplied higher amount of assimilates to the root (23% from L2) than leaves of cv. Texas-Grano but in the following year, cv. Red-Kano supplied higher quantities (18.4% from L1) and had a more profuse

root system ($P \leq 0.001$, Table 10). It has been reported that lower leaves were the main source of assimilates for the roots (Belikov, 1955, Jones et al., 1959; Wardlaw and Porter, 1967 and Khan, 1981).

At the second sampling, there was decreased import of assimilates by the roots and they became an increasingly unimportant sink during subsequent samplings and imported negligible quantities of assimilates (1 - 4%). Most of the assimilates imported by the roots accumulated at the root tips (Plates 1, 2, 3). These are the areas of meristematic activity in the roots. However, with ageing of the plant, the labelling of the root was more uniformly distributed (Plates 4, 5, 6). The decrease in movement of assimilates to the roots may be associated with the increase in the sink strength of the bulb as more assimilates were translocated to the bulb with the growth of the plant. Steer and Darbyshire (1979) and Khan (1981) have also found that the sink strength of the roots decreased with increasing sink strength of the onion bulb and its size. Ho and Rees (1976) also found that in tulip the roots were major sink organs in the early period of growth but became unimportant sink as the daughter bulbs became the major sink in the second period of growth.

5.2. GROWTH ANALYSIS

5.2.1. GROWTH CHARACTERISTICS

Onion bulbs need a continuous sugar supply for growth and this links leaf size and number, which amount to sugar production, with bulb growth (Heath & Holdsworth, 1948). Abdalla and Mann (1963) presented further evidence to show that leaf size was related to bulb growth. If leaves emerged but remained small, translocation of sugars, leading to bulb growth was also retarded. Partial defoliation of tulip plants reduced RGR of daughter bulbs approximately in proportion to the leaf area removed (Rees, 1972). In the present investigation, cv. Red-Kano had more [illegible] leaves, greater leaf area and produced corresponding larger bulbs than cv. Eclipsel-Bermuda and cv. Texas-Grano (Fig. 12 & 13). Bulb size increased with increasing age of plant. The bulbs of cv. Red-Kano on each sampling date were larger (in terms of diameter, fresh and dry weight) than those of cv. Eclipsel-Bermuda and cv. Texas-Grano ($P < 0.001$, Table 17). The plants of cv. Red-Kano attained a diameter of 7.88 cm and fresh weight of 171.25 g. Plants of cv. Eclipsel-Bermuda had a diameter of 4.07 cm and fresh weight of 28.29g while cv. Texas-Grano achieved a diameter of 4.3 cm and fresh weight of

55.38g (Append.1). There was no significant difference in the bulb size of cv. Eclipsel-Bermuda and cv. Texas-Grano. The bulb of cv. Red-Kano continued to increase in size even after the number of mature leaves and the leaf area started to decrease (Fig. 13 and Table 13). This showed that the bulb growth did not stop for sometime after the maximum leaf area was attained. This showed that the leaves after attaining maximum size were supporting new expanding leaves. Moreover, there was further increase in the translocation of carbohydrates for the bulb growth. In cv. Eclipsel-Bermuda and cv. Texas-Grano, decrease in leaf area did not affect bulb growth much, since the increase (for cv. Texas-Grano) or decrease (for cv. Eclipsel-Bermuda) in bulb size after the maximum leaf area was attained was only of a small proportion. This showed that there was not much increase (or no increase at all) in the rate of translocation of assimilates to the bulbs of these two cultivars, following the decrease in assimilate transport to the leaves to support their growth.

The increase in the number of leaves at maturity resulted in bulb scales with aborted leaves to swell up. Rees (1966) found that tulips showed a rapid growth in

leaf area followed by a slowing down of leaf growth followed in turn by a rapid senescence and loss of leaf area until none remained. This was similar to the observation in onions. Whereas, there was a rapid growth of leaf area in all the three cultivars, followed by a slowing down of leaf growth, senescence was not rapid and at the time of lifting of the bulb even when the necks had fallen over, some leaf area was still recorded.

The pattern of total dry matter followed closely that of dry weight of bulbs. The bulbs contributed the highest percentage to the total dry matter of the plants (Fig.13). Watson (1947) reported that the size of the leaf surface determined the dry matter production. Cultivar Red-Kano had the largest leaf surface and also produced the maximum dry matter (Fig.13).

More root growth was observed in cv. Red-Kano than cv. Eclipsel-Bermuda and cv. Texas-Grano, but all showed peaks of root production at 54, 75 and 97 days after transplanting but that of cv. Red-Kano was more significant ($P < 0.001$, Table 17). This agrees with the observations of Jones and Mann (1963) that in onions new roots were added few at a time at intervals but at the time of plant death

the rate of death of roots was faster than addition.

The pseudostem is not a storage organ in onions and contributed only a small proportion to the total dry matter of the plant. The small rise in its dry weight with time, corresponded with increased number and thickness of leaves and consequently leaf sheaths. This agrees with the observation of Butt (1968). The dry weight of the pseudostem of the three cultivars and its variation with age of plant was significantly different with that of cv. Red-Kano being higher ($P < 0.001$, Table 17).

5.2.2. GROWTH ATTRIBUTES (RGR, RLGR, CGR, NAR, LAR)

Measurement of all the growth attributes (Table 14) studied showed that the cv. Red-Kano had the highest values as compared to cv. Eclipsel-Bermuda and cv. Texas-Grano. The latter two cultivars showed similar values in respect of relative leaf growth rate (RLGR) and leaf area ratio (LAR) but cv. Texas-Grano had the lowest relative growth rate (RGR), crop growth rate (CGR) and net assimilation rate (NAR). Generally, all the growth attributes decreased with time i.e., as the plant increased in age.

The lowest value of NAR in cv. Red-Kano was achieved between 68 - 75 days after transplanting and this corresponded

to the time the RGR and LAR had zero values i.e., there was no appreciable change in leaf dry weight. At this stage the leaf area and dry weight has started to decline after achieving highest values at 61 days after transplanting. The reduction in leaf area at this stage also caused a decline in the RLGR to the negative values (75 - 82 days period).

In cv. Red-Kano, an increase in NAR at 75 - 82 days was accompanied by a decrease in RGR and CGR but in cv. Texas-Grano, a decrease in NAR at this time was accompanied by an increase in RGR and CGR. In cv. Eclipsel-Bermuda, however, NAR, RGR and CGR simultaneously decreased as the plant matured. This was due to the efficiency of the leaf in producing photosynthates and was not accompanied by a subsequent increase in the dry matter of the above ground parts, because the carbohydrates were mainly transported for the building up of the dry matter content of the bulb. The dry matter of the bulb continued to increase even when the leaf area and weight were not increasing. Thorne & Evans (1960) also found that when the potato plants failed to produce tubers (probably due to long photoperiod or high night temperature) the NAR of sugarbeet was higher than that of potato. They explained

that rapid transport of carbohydrates to a storage organ, as in sugarbeet plants, might permit a higher rate of photosynthesis by decreasing the carbohydrate content of the leaves.

The CGR of the tops was positive in the early stages for all the three cultivars but decreased to negative values towards maturity. This was due to the decrease in the dry weight of the leaves caused by the decrease in leaf number and size. The CGR for bulbs was higher than the CGR for tops in all the three cultivars. The CGR for bulbs of cv. Red-Kano and cv. Texas-Grano was positive throughout the experimental period but cv. Eclipse1-Bermuda showed a negative value during 75 - 82 day period. Cultivar Red-Kano showed a progressive increase in bulb growth rate up to the 8th week, with low negative rates occuring during the 7th and 9th weeks after transplanting. At the last date of sampling, the CGR for the bulbs of cv. Red-Kano were very low but still positive. Cultivar Texas-Grano had a constant CGR for bulbs except at 68-75 days after transplanting when there was a sharp decline but then recovered its original rate. The higher CGR for bulbs of

cv. Red-Kano over cv. Eclipsel-Bermuda and cv. Texas-Grano may explain why the bulbs of the latter two cultivars did not attain a large size while those of cv. Red-Kano attained a large size. The highest CGR for bulbs for cv. Red-Kano was $1.3g^{-2}$ day^{-1} while for cv. Eclipsel-Bermuda it was $0.2g^{-2}$ day^{-1} and for cv. Texas-Grano it was $o.1g^{-2}$ day^{-1}. The higher CGR for bulbs compared with the leaves was due to larger quantities of carbohydrates which were translocated to the bulbs.

Rees (1965) showed that bulb plants, especially tulips, suffer a loss of potential dry-matter production because of their short growing season and early senescence. Examining the CGR of three tulip cultivars in comparison with an estimate of potential growth rate derived from de Wit (1959), he concluded that as the peak CGR occured earlier than the potential rate and then fell. The relatively poor efficiency of the tulip plant on an annual basis was due to inefficient dry matter production during the growing season. Onion plants also showed a similar pattern of leaf growth. This may explain why cv. Red-Kano with its longer growing duration, more numerous leaf blades and leaf area and increasing bulb growth rate, attained larger bulb size and dry weight than cv. Eclipsel-Bermuda and cv. Texas-Grano.

The increase in NAR at 75 - 82 days in cv. Red-Kano may be due to a response of the photo-synthetic apparatus to increased demand for assimilates which was in turn due to rapid growth of the bulb (9.3 - 12.9g). There was considerable increase in the bulb growth rate at this time ($0.5g^{-2}$ day^{-1}) (Table 14). Koller et al. (1970) also found a similar increase in NAR of soyabean which was due to rapid growth of the seed fraction.

The leaf area and dry matter rapidly increased at the early stages of bulb growth to meet the heavy demand for the carbohydrates by the bulb. At this stage the RGR and RLGR were highest in all the three cultivars. The constant LAR in cv. Red-Kano was due to the concurrent increase in leaf area and dry weight of the leaves. At 68 - 75 days after transplanting there was no appreciable change in leaf area and weight. The LAR of cv. Texas-Grano declined with time and more sharply at 75 - 82 days, indicating that the dry weight of the tops increased more rapidly than the leaf area even during earlier stages when the leaves were rapidly expanding. In cv. Eclipse1-Bermuda the two peaks in the LAR at 47 - 54 days and 75 - 82 days after transplanting were due to the fact that initially the dry weight of the leaves was

increasing more rapidly than the leaf area and towards maturity there was a more rapid decrease in the dry weight than the leaf area. Power et al. (1967) also found that the leaf area ratios of barley tops reduced with time. They attributed this to the fact that dry weight of the barley tops increased more rapidly than the leaf area even during early growth stages when the leaf areas were rapidly expanding.

5.2.3. MINERAL DISTRIBUTION

The general pattern of phosphorus (P) accumulation in the three cultivars was B > L > PS (Fig. 19). The concentration of P in the bulb of cv. Eclipsel-Bermuda and cv. Texas-Grano was significantly higher (P 0.01, Table 16) than in cv. Red-Kano. This was probably so because the bulbs of the early maturing cultivars (i.e., cv. Eclipsel-Bermuda and cv. Texas-Grano) were growing at a faster rate and hence their meristematic activity was greater. The higher P values observed in the bulbs (Fig. 14) may also be an indication of their higher meristematic activity than the leaves and pseudostem. Phosphorus has been found to be essential for development of meristematic tissue and seems to increase leaf area without affecting the power of the leaves to

transport carbohydrates (Russell, 1961). The changes in P concentration with age of plant was generally inconsistent in cv. Texas-Grano but in cv. Eclipsel-Bermuda, P increased at maturity while in cv. Red-Kano it decreased (Fig. 19). This observation in cv. Red-Kano was in agreement with the observation of Lastavka and Minar (1970) in peas. In rice the greatest uptake of the nutrients NPK took place between 14 - 70 days after transplanting (Mehrotra et al., 1968).

In cv. Red-Kano, the highest potassium (K) concentration in the plant parts was at different times after transplanting. In the bulb it was at 47 days, leaf at 75 days and pseudostem at 90 days. In cv. Eclispsel-Bermuda and cv. Texas-Grano, the maximum concentration of K in the plant parts was at 54 days. However, in all the three cultivars K concentration in the plant parts decreased at maturity (Fig. 15 and 20). Widdowson et al. (1965) found that the concentration of K in grass dropped with increasing maturity. The pattern of K accumulation in plant parts was slightly different from that of P. Potassium concentrated more in the leaves ($P < 0.05$, Table 16) and least in the bulb while concentration values in the pseudostem were intermediate. Potassium is important for photosynthetic process because

shortage of K in the leaf lead to low rates of carbon dioxide assimilation (Russell, 1961). The variation in the concentration of K in the bulb as the plants increased in age was significant ($P < 0.001$). There was significant difference in the concentration of K in the pseudostem and bulbs of the three cultivars ($P < 0.001$),(Table 15).

Calcium concentration was generally lower in cv. Red-Kano than cv. Eclipse1-Bermuda and cv. Texas-Grano. In cv. Red-Kano the general pattern of calcium accumulation in the plant parts was more apparent and first it decreased with increasing plant age and then increased at maturity so that the pattern was L>PS>B. At all times however, the calcium concentration in the bulb was lowest for all the cultivars (Figs. 16 and 21). Calcium has been reported to accumulate more in the leaves and is essential for the growth of meristems (Russell, 1961). The alternating values of calcium concentration in the leaves and pseudostem evident in cv. Eclipse1-Bermuda and cv. Texas-Grano may mean that the calcium in the pseudostem was in a transitory stage to the leaves. This was why if the concentration in one was high then it was low in the other. Onion compared with other vegetables have been reported to be rich in calcium (Jones and Mann, 1963).

Magnesium (Mg) accumulated more in the leaves and least in the bulb (L ⩾ PS ⩾ B) in all the three cultivars (Figs. 17 and 22). This conforms with the agreed behaviour of Mg, that it is tied up with the structural ring of the chlorophylls (Nason, 1958, Hill, 1963). Magnesium concentration increased in the leaves with increasing age of the plants in all the cultivars and was significant ($P < 0.01$). (Table 16). This may be associated with the increase in the concentration of chlorophyll (Table 15). The decrease in Mg concentration in the leaves of cv. Eclipsel-Bermuda and cv. Texas-Grano at 82 days after transplanting may be due to the decrease in chlorophyll content at maturity.

Zinc (Zn) accumulated most in the pseudostem and least in the leaves in all the three cultivars (PS ⩾ B ⩾ L) (Figs. 18 and 23). This was in agreement with the findings of Ajakaiye (1975) when he supplied $ZnSO_4$ to onion plants (cv. Sweet Spanish) but was at variance with his general conclusion that the leaves had the highest Zn concentration and the pseudostem the lowest. Studies by other workers have also shown variation in Zn concentration in plant parts. Jones (1964) found that the Zn concentration of sugarbeet leaf lamina was about three times that found in petioles.

He later observed that Zn concentration in the upper leaves of corn was higher than that in the lower leaves and the Zn concentration of the midrib was about half that found in the leaf blades (Jones, 1970). Generally, cv. Texas-Grano accumulated more Zn than either cv. Red-Kano and cv. Eclipsel-Bermuda. The normal concentration range for Zn in the leaf has been stated to be 25 - 150ppm with toxicities occuring when the leaf Zn levels exceed 400ppm (Mortvedt et al. 1972). In the present study, the concentration of leaf Zn was found to range from 72ppm (in cv. Red-Kano at 90 days) to 159ppm (in cv. Eclipsel-Bermuda at 61 days). This is within the the usual range but at variance with the finding of Ajakaiye (1975) who obtained higher concentrations of Zn (up to 179ppm) and where the concentration was 131ppm at 108 days after sowing, causing a significant decrease of dry matter and eventually death of the plants. This may be due to the effects of time of sampling, cultivar or hybrid and environmental factors (e.g. soil moisture, temperature, light quality and intensity) which may significantly affect the relationship between element concentration and plant response.

Zinc concentration in the leaf decreased with age of plants in all the three cultivars and this change in

concentration with age varied significantly ($P < 0.01$), (Table 16). Gorshine et al. (1965) also found that Zn in corn leaves decreased with plant age.

5.2.4. CHLOROPHYLL CONCENTRATION

The total chlorophyll content increased with plant age but decreased at maturity in cv. Red-Kano. In cv. Eclipsel-Bermuda and cv. Texas-Grano, it was high from the start of the experiment but decreased at maturity (Table 15). Turrell et al. (1961) also found that the total chlorophyll content of citrus leaves and fruits varied with the developmental stage. The decrease in chlorophyll content towards maturity may be associated with loss of photosynthethic capacity of the leaves due to age. The leaves at this stage lose their deep green colour. It would appear that cv. Eclipsel-Bermuda and cv. Texas-Grano attained a high photosynthetic capacity earlier than cv. Red-Kano and this may be associated with their short growing period. The chl. a/chl. b ratio of the three cultivars did not change much but was two on the average. Jahn and Young (1976) suggested that a low ratio of chl.a/chl.b (less than 3) in citrus rinds would make them resistant to de-greening.

For onions, chl.a/chl.b ratio of about two may make them difficult to degreen and hence the leaves in the markets are still green long after removal from the farm. There was no significant difference in the chlorophyll a and b in the three onion cultivars but the variation of chlorophyll a concentration with age of the plant was significant ($P < 0.001$, Table 17).

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APPENDIX 1: Total dry weights of the plant parts, fresh weights of leaf and bulb and fresh bulb diameter of the three onion cultivars as influenced by age.

Onion cultivar	Plant Age (days)	fresh bulb diameter(cm)	Fresh bulb weight(g)	Leaf fresh weight(g)	Dry Weights (g)			
					Leaves	Pseudostem	Bulb	Root
RED-KANO	36	0.71	0.9	1.9	0.4	0.02	0.06	0.02
	47	1.73	4.6	12.2	1.7	0.05	1.2	0.02
	54	2.15	6.3	30.2	3.9	0.4	2.3.	0.5
	61	3.72	26.4	61.8	7.5	0.9	4.6	0.2
	68	5.29	59.9	62.6	5.6	1.6	7.2	0.1
	75	6.16	91.9	63.2	5.7	1.5	9.3	0.5
	82	6.83	94.5	60.7	4.5	0.3	12.9	0.2
	90	6.28	92.9	43	3.5	0.4	10.2	0.2
	97	7.08	171.3	37.1	3.6	0.5	19.2	0.5
	104	6.88	113.6	22.9	2.4	0.4	12	0.4
	111	6.42	97.9	36.9	4.1	0.6	12	0.4
	S.E.	0.73	16.45	6.47	0.59	0.15	1.76	0.05

Appendix 1 continued

Onion cultivar	plant age (days)	Fresh Bulb diameter (cm)	Fresh Bulb weight(g)	Leaf fresh weight(g)	Dry Weights (g)			
					Leaves	Pseudo-stem	Bulb	Root
ECLIPSEL-BERMUDA	47	1.64	3.9	7.0	0.7	0.1	0.4	0.03
	54	2.72	12.7	18.3	1.3	0.2	1.1	0.08
	61	3.94	29.3	12.7	1.9	0.1	2.5	0.04
	68	4.43	37.5	18.7	1.9	0.2	3.2	0.04
	75	3.75	21.3	9.6	1.7	0.2	3.4	0.05
	82	4.07	28.3	8.3	0.6	0.2	2.4	0.03
	S.E.	0.42	5.0	2.07	0.24	0.16	0.48	0.007
TEXAS-GRANO	47	1.5	7.2	12.4	1.1	0.2	0.5	0.05
	54	2.8	17.9	25.3	1.8	0.2	1.3	0.007
	61	3.4.	28.1	16.0	1.7	0.2	2	0.06
	68	4.5	55.4	17.3	2.5	0.2	2.7	0.04
	75	3.9	38.8	12.8	1	0.2	2.8	0.05
	82	4.3	47.8	10.5	0.7	0.2	3.5	0.04
	S.E.	0.44	7.49	2.17	0.21	0	0.44	.004