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Assimilate partitioning in pigeonpea under two levels of drought and during recovery

A.S.NANDWAL, S.BHARTI and I.SINGH

Department of Botany, Haryana Agricultural University, Hisar 125004, India

Abstract

The partitioning of ^{14}C-assimilates was studied in pigeonpea (*Cajanus cajan* L.) at vegetative and flowering stages (40 and 70 d after sowing, respectively) exposed to moderate and severe drought induced by withholding the irrigation. At vegetative stage, the ethanol soluble fraction in shoot decreased from 99 to 43.16 % between 0 and 120 h, whereas in underground part it increased from 1% to 56.84 % with maximum amount in nodules (35.51 %). Similar trend was observed in ethanol insoluble fraction. At moderate drought, a significant increase in soluble fraction (11.31 %) in nodules was observed. Stem showed significant reduction of assimilates (13.09 %). After flowering, the assimilates produced in leaves were exported to reproductive parts, especially under drought. In plants recovering from severe drought, ^{14}C in soluble and insoluble fractions in reproductive parts was reduced to 85 % and 43 %, respectively, whereas leaf and nodules showed a significant increase. Thus the assimilate partitioning to different plant parts was dependent on growth stage and affected by drought.

Introduction

The influence of water deficit on distribution of assimilates depends on the stage of growth (Turner and Begg 1981, Huck *et al.* 1986). The organ which grows most rapidly at the time of stress is the most affected (Aspinall *et al.* 1964). Under water stress, root growth increases due to higher carbon allocation to roots (Constable and Rawson 1982). An increased photosynthate transport to legume root and nodules has been observed by Finn and Brun (1982), however, an opposite response was found during reproductive stage (Silvius *et al.* 1977). Thus water stress results in smaller carbon source, leading to a modification of growth and dry matter partitioning and accumulation (Snyder and Carlson 1984). According to earlier reports a related work has been done either on long-term effect of water stress or under controlled conditions and the partitioning of ^{14}C has been studied till the harvesting of crops.

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A short-term water deficit generally occurs at anytime of crop growth and development. In pigeonpea, which is an important tropical legume, no information is available on this aspect. Therefore, the changes in ^{14}C partitioning under two levels of drought were studied in this work.

Material and methods

Growing crop. Pigeonpea crop (*Cajanus cajan* L., cv. ICPL-151, a determinate type) was raised in earthen pots (30 cm in diameter) filled with 5.5 kg of dune sand, in screen house under natural conditions. Seeds were surface-sterilized with 1 % sodium hypochlorite and inoculated with standard *Rhizobium* culture. The pots with two plants each were irrigated with nitrogen-free nutrient solution. The plants were subjected to drought stress by withholding the irrigation at vegetative stage, *i.e.* 35 - 45 d after sowing, and at flowering stage, *i.e.* 65 - 75 d after sowing. Depending upon the soil moisture content (SMC %) and soil water potential the levels of drought were regarded as moderate (SMC = 5.5 % and soil Ψ_w = -0.77 MPa) and severe (SMC = 3.0 % and soil Ψ_w = -1.34 MPa). The control plants receiving normal irrigation were sampled at the SMC of 10 %, *i.e.* 50 % of soil saturation, corresponding to soil Ψ_w of -0.37 MPa. For the recovering after stress (RAS) half of the plants from severe drought were irrigated and sampled after two days at the same SMC and soil Ψ_w as that of the control. SMC was determined gravimetrically while soil Ψ_w was measured with Dewpoint Microvoltmeter, HR-33T (*Wescor*, USA) using the sensor PT 51-05. Variations in the time interval of moderate and severe stress at two stages was due to change in temperature and daylength. Average maximum and minimum temperature at vegetative stage was 39.4 °C and 28.2 °C and at the flowering stage was 28.7 °C and 11.5 °C. The irradiance was 1150 ± 50 μmol m^{-2} s^{-1} and 1020 ± 30 μmol m^{-2} s^{-1}, respectively. Five replications were used to calculate per cent distribution of ^{14}C.

$^{14}CO_2$ feeding. Two plants per pot were exposed to $^{14}CO_2$ on sunny day between 09.00 and 10.00 local time at vegetative stage, and between 10.00 and 11.00 at flowering stage. Each set of plants was allowed to assimilate for 20 min and the remainder of $^{14}CO_2$ was absorbed using a NaOH trap (Luthra *et al.* 1983).

Harvesting. One set of the control plants was harvested at 0, 24, 48, 72, 120 and 168 h . They were separated into leaves, stem, root, nodules and reproductive parts. Another set of treated plants was subjected to drought and then harvested at moderate and severe stress. Half of the severely stressed plants were reirrigated and harvested after two days.

^{14}C assay. For measuring radioactivity, the oven dried samples were milled and extracted with 80 % ethanol and 6 M HCl to prepare the ethanol soluble and ethanol insoluble fraction (Luthra *et al.* 1983). The radioactivity of the two fractions was measured separately in a Liquid Scintillation Counter (*Beckman LS-1801, Irvine*

USA) using scintillation composition given by Brey (1960). Count rates [s^{-1}] in different plant parts were added to give total count rate; distribution of $^{14}CO_2$ in plant parts was expressed as per cent of total.

Results and discussion

Vegetative stage:

Ethanol soluble fraction: Immediately after feeding, at 0 h, the highest portion of ^{14}C (82.23 %) was estimated in leaf followed by 16.68 % in stem, 0.67 % in root and 0.33 % in nodules. After 24 h, ^{14}C portion significantly dropped to 33.99 % in leaf, whereas in stem, root and nodules it significantly increased to 26.23 %, 16.28 % and 23.47 %, respectively (Table 1). Significant increase in ^{14}C amount was observed in stressed nodules in comparison to respective controls sampled after 48 h, however, in stem 13.09 % decline was observed. Although ^{14}C amount in leaf further declined to 26.63 %, yet in root and nodules increased up to 19.33 and 30.40 % after 72 h. A significant decline of 14 % in stem and an increase of 19 % in root was noticed when plants were subjected to severe stress as compared to their respective controls (Table 1). No differences were observed in partitioning of ^{14}C in different components between the plants RAS and their respective controls. In control plants the total ^{14}C in shoot decreased from 99 % to 43.16 % between 0 and 120 h, whereas it increased simultaneously in underground part from 1 % to 56.84 %, with the highest value in nodules (35.51 %).

Ethanol insoluble fraction: ^{14}C amount estimated at 0 h in this fraction (Table 1) was lower in leaf (75.84 %) and stem (12.73 %) as compared to soluble fraction, whereas in root and nodules it was 4 - 5 % higher. After 24 h, a significant decline of 2.5 times in leaf and 3 times increase in stem was observed whereas in root and nodules ^{14}C content increased significantly by 6 % and 14 %, respectively. After 48 h, *i.e.* at moderate stress, ^{14}C content increased significantly by 13.46 % in root with simultaneous 8.05 % decline in stem as compared to their respective controls. Under severe drought, leaf and root significantly accumulated ^{14}C, in ethanol insoluble fraction by 12.26 % and 33.00 % whereas in stem and nodules there was a decline of 12.55 % and 10.65 %, respectively (Table 1). When the plants relieved from severe stress, nodules showed significant enhancement from 26.60 % to 33.50 %. In shoot ^{14}C amount declined from 88.57 % at 0 h to 49.56 % after 120 h and increased simultaneously in underground part from 11.43 % to 55.44 % with highest value of 34.45 % in nodules (Table 1). An increase in large amount of ^{14}C in nodules and root of controlled plants showed that they were the actively growing organs of the plants at vegetative stage. Stem has shown to act as a temporary storage site of ^{14}C.In chickpea, also Hooda *et al.* (1989) suggested that the greatest amount of ^{14}C present in both the fractions of leaves decreased during subsequent growth and increased in nodules. Similar reports are available for lupin (Pate and Herridge 1978)

Flowering stage:

Ethanol soluble fraction: More than 98 % of ^{14}C was received in the aerial parts of the plant. Leaf showed the highest amount of 82.84 % and reproductive parts just

Table 1. Effect of drought on partitioning of ^{14}C-assimilates (in % of total) in pigeonpea at vegetative stage. Values are the mean of 5 observations ± standard deviation. Plants were harvested at 0, 24, 72 and 120 h after $^{14}CO_2$ feeding.

	Control	Control	Control	Moderate stress	Control	Severe stress	Control	Rehydration
	0	24	48	48	72	72	120	120
(Ethanol soluble fraction)								
Leaf	82.29±6.10	33.99±3.70	30.46±4.10	31.75±2.80 (4.23)	28.63±3.60	29.40±2.80 (2.68)	25.12±2.70	25.21±3.40 (0.35)
Stem	16.63±1.40	26.23±2.80	24.66±2.40	21.43±2.90 (-13.09)	21.64±2.80	18.51±1.70 (-14.46)	18.04±1.40	18.02±1.70 (-0 11)
Root	0.70±0.03	16.28±1.50	17.61±1.30	18.67±2.00 (6.01)	19.33±1.80	23.08±2.10 (19.39)	21.33±1.90	20.62±2.00 (-3.32)
Nodules	0.33±0.01	23.47±2.20	25.27±2.50	28.13±2.00 (11.31)	30.40±3.10	28.98±3.40 (-4.67)	35.51±2.70	36.12±3.10 (1.71)
(Ethanol insoluble fraction)								
Leaf	75.84±5.60	29.53±2.8	28.3±2.10	28.93±3.00 (3.21)	22.38±3.10	25.19±1.90 (12.55)	18.26±1.40	20.00±1.70 (10.07)
Stem	12.73±1.10	37.33±2.60	36.12±2.90	33.21±3.10 (-8.05)	35.05±3.30	30.75±2.80 (-12.26)	31.29±2.50	29.28±2.30 (-6.42)
Root	5.26±0.70	12.56±1.10	12.85±0.90	14.58±1.30 (13.46)	13.42±1.50	17.98±2.00 (33.97)	15.94±2.10	17.21±1.80 (7.96)
Nodules	6.17±1.20	20.55±2.30	23.00±2.40	23.26±1.80 (1.13)	29.15±2.60	26.06±2.30 (-10.60)	34.45±2.70	33.50±3.20 (-2.75)

Values in parentheses are percentage decrease or increase over respective controls.

Table 2. Effect of drought on partitioning of ^{14}C assimilates (in % of total) in pigeonpea at flowering stage. Values are the mean of 5 observations ± standard deviation. Plants were harvested at 0, 24, 72, 120 and 168 h after $^{14}CO_2$ feeding.

	Control	Control	Control	Moderate stress	Control	Severe stress	Control	Rehydration
	0	24	72	72	120	120	168	168
(Ethanol insoluble fraction)								
Reproductive parts	2.01±0.06	21.55±2.80	23.07±3.00	26.79±3.20 (16.12)	24.85±2.70	23.46±2.70 (-5.59)	27.57±3.00	4.14±1.10 (-84.98)
Leaf	82.84±6.30	26.50±3.10	25.72±2.90	20.67±2.30 (-19.63)	25.34±2.70	21.62±1.90 (-14.68)	23.54±1.80	37.43±3.40 (59.00)
Stem	13.77±1.30	17.45±1.70	17.25±1.20	16.89±2.00 (-2.08)	17.02±1.70	16.46±1.90 (-2.23)	15.69±1.20	20.02±2.30 (27.59)
Root	0.86±0.01	17.88±1.80	15.25±1.90	13.68±1.60 (-10.29)	12.85±1.70	13.17±1.60 (6.69)	10.67±1.80	10.31±1.70 (-3.37)
Nodules	0.52±0.02	16.59±2.10	18.71±1.90	21.94±2.30 (17.26)	19.94±2.10	25.09±2.30 (25.82)	22.53±1.90	28.08±2.60 (24.63)
(Ethanol insoluble fraction)								
Reproductive parts	11.44±1.70	23.54±2.30	24.11±2.70	30.80±2.10 (27.74)	24.68±2.30	32.20±3.10 (30.89)	26.49±2.60	15.01±2.00 (-43.33)
Leaf	53.77±6.20	17.24±2.10	17.15±1.90	15.63±1.40 (-8.86)	17.10±1.70	19.37±1.90 (13.27)	17.41±1.70	19.53±1.50 (12.17)
Stem	15.25±1.40	20.51±1.90	20.61±2.30	23.06±2.70 (11.88)	20.85±2.10	19.73±2.10 (-5.37)	21.39±2.40	23.03±2.50 (7.66)
Root	10.69±1.40	17.24±1.80	16.42±1.70	11.02±1.20 (-32.88)	15.40±1.80	10.95±1.10 (-31.81)	11.83±1.30	15.74±1.90 (33.05)
Nodule	8.85±1.00	21.44±2.80	21.72±2.60	19.46±2.10 (10.40)	22.05±2.40	17.70±2.30 (-19.72)	22.88±2.40	26.67±2.60 (16.56)

2.01 % only. After 24 h (Table 2), a significant increase of ten times in reproductive parts, nineteen times in root and thirty-two times in nodules was found, while in leaf it dropped down to three times. Comparing the vegetative stage, leaf, stem and nodules received the smaller portion of ^{14}C due to the presence of reproductive parts. After 168 h, ^{14}C declined significantly to 23.54 % in leaf, 15.69 % in stem and 10.17 % in root but in reproductive parts and nodules it increased up to 27.25 % and 22.53 %, respectively. After 72 h of moderate drought, there seemed to be a ^{14}C transport towards reproductive parts (27 %) and nodules (22 %) resulting in significant decline of ^{14}C in leaf and root by 20 % and 10 % against their respective controls (Table 2). Under severe drought (Table 2), *i.e.* after 120 h, maximum ^{14}C was estimated in nodules (25.09 %) followed by reproductive parts (23.46 %). A significant decrease of ^{14}C in leaf (14.68 %) was observed in severely stressed plants as compared to its respective control. However, in plants RAS the maximum ^{14}C recovered from the leaf (37.43 %) followed by nodules (28.08 %) and stem (20.02 %) and the values were significantly higher (*i.e.* 59.00, 24.63, and 27.59 %, respectively) than their respective controls. Reproductive parts showed 84.98 % decrease in ^{14}C as compared to its respective control.

Ethanol insoluble fraction: 80.46 % of total ^{14}C was retained in the shoot at 0 with maximum 53.77 % in leaf (Table 2). This value decreased linearly with time interval and reached 17.41 % after 168 h, whereas in reproductive parts it enhanced from 11.44 % to 26.49 %, thus clearly indicating the translocation of assimilates towards them. A rapid accumulation of ^{14}C from 8.85 % was observed in nodules.

Under moderate drought, there was a maximum accumulation of ^{14}C in reproductive parts (30.80 %) followed by stem (23.06 %) and which were significantly higher by 27.74 % and 11.88 % as compared to their respective controls. A significant decrease of 32.88 % was observed in root (Table 2). At moderate stress there was a decline in ^{14}C content in leaf, root and nodules, whereas at severe stress ^{14}C declined in stem, root and nodules (Table 2). Root and nodules showed significant decline in ^{14}C content by 31.81 % and 19.72 % respectively. However, at severe stress reproductive parts and leaf significantly increased in their ^{14}C content by 30.89 % and 13.27 % as compared to their respective controls. It means all the five components behaved differently at moderate and severe stress for ^{14}C content in ethanol soluble and insoluble fractions, this is related to sensitiveness and degree of a stress for a specific component of the plant. In plants RAS a significant reduction of 43.33 % in ^{14}C was evinced in reproductive parts (Table 2) whereas in leaf root and nodules increased significantly by 12.17 %, 33.05 % and 16.86 %, respectively as compared to their respective controls. While comparing the partitioning of ^{14}C at two stages, the maximum amount was retained by leaf and nodules at vegetative, whereas by reproductive parts and nodules at flowering. Two reasons may be assigned for a drastic decrease in ^{14}C amount in both the fractions of leaf at vegetative stage. Firstly due to active growth of the leaves during this period, utilizing most of assimilates for own growth and development and secondly a major portion of the labelled ^{14}C mobilized from leaves to nodules and root as they were the major sinks. Under moderate stress ^{14}C was diverted to root and nodules estimated in soluble fraction, might be due to extra growth of root in soil (Nandwal 1989) to meet the water requirement of the plant. Accumulation of ^{14}C in insoluble fraction under severe stress in leaf was due to check of translocation and active growth of leaf and non-utilization of assimilates for their own growth. In plants RAS least ^{14}C estimated in retained reproductive parts, because most of the flowers were abscissed on reirrigation.The results suggest that assimilates produced in leaves after flowering were transported mainly to the growing reproductive parts and by that time leaves had also little growth. In soybean (Pearen and Hume 1981) and chickpea (Hooda *et al.* 1989) reported similar reports in control plants. Most of the ^{14}C was moved from leaves, stem and root to the reproductive parts and least from nodules. When stress was created a high content of ^{14}C was estimated in reproductive parts. Except in chickpea (Hooda *et al.* 1989), no familiar information is available. Stem again showed a temporary storage at flowering stage by increasing ^{14}C amount in RAS plants.

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