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Economy of Water, Carbon, and Nitrogen in the Developing Cowpea Fruit[1]

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ABSTRACT

The nutritional economy of the fruit of cowpea (*Vigna unguiculata* (L.) Walp cv Vita 3) was assessed quantitatively from intake and utilization of carbon, nitrogen, and water. Fruits failed to make net gains of CO_2 from the atmosphere during daytime, although pod photosynthesis did play a role in the fruit's carbon economy by refixing a proportion of the fruit's respired CO_2. Of every 100 units by weight of carbon entering the fruit, 70.4 were finally incorporated into seeds, 10.3 remained as nonmobilizable material in pod walls, and the remaining 19.3 were lost in fruit respiration. Phloem supplied 97% of the fruit's carbon and 72% of its nitrogen. The xylem contribution of nitrogen occurred mainly in early growth. Ninety-six% of the fruit's nitrogen was incorporated into seeds, approximately 10% of this mobilized from the senescing pod. The mean transpiration ratio of the fruit was very low—8 milliliters water transpired per gram dry matter accumulated. Models of carbon, nitrogen, and water flow were constructed for the two consecutive 11 day periods of fruit development, and indicated a considerably greater entry of water through xylem and phloem than could be accounted for in changes in fruit tissue water and transpiration loss. This discrepancy was greater in the second half of fruit growth and was interpreted as evidence that a significant fraction of the water entering the fruit through phloem cycled back to the parent plant via the xylem.

A number of experimental observations are required when relating the water economy of a developing fruit to its uptake and utilization of C and N. These include the amounts of water lost in fruit transpiration or gained or lost by fruit tissues during growth and metabolic activity, the net atmospheric exchanges of CO_2 by the fruit in respiration and photosynthesis, the amounts of C and N incorporated into fruit dry matter, and the C:N weight ratios and absolute concentrations of solutes delivered to the fruit in xylem and phloem. Proportional intake of C and N by the fruit through xylem and phloem can then be determined, and the amounts of water predicted to have flowed into the fruit through these channels compared with the fruit's transpiration loss and changes in water content.

Due to absence of information on phloem sap composition, models of fruit economy of C, N, and water have so far been restricted to only two species, white lupin (*Lupinus albus* L.) (18) and soybean (*Glycine max* [L.]Merr.) (8). This paper reports on the fruit of a third legume species, cowpea (*Vigna unguiculata* [L.] Walp), exploiting a recently developed cryopuncture technique (16) to examine fruit phloem sap composition. Budgets for water, C, and N exchange between fruit and parent plant are related to the utilization, storage, and mobilization of C and N and the CO_2 exchanges of pod wall and seeds during growth and development.

MATERIALS AND METHODS

Plant Material and Harvests of Fruits. Cowpea seed (*Vigna unguiculata* [L.] Walp cv Vita 3), originating from the International Institute of Tropical Agriculture, Ibadan, Nigeria, was inoculated with *Rhizobium* CB756 and grown in sand culture in a naturally lit, temperature-controlled (28–32°C day, 20–22°C night) glasshouse. Plants were watered daily and received adequate N-free mineral nutrient solution throughout growth (15). Plants were tagged at anthesis of the first flower (around 60 d after sowing: see Ref. 15), thus enabling the age of the first fruit to be determined. Harvests of 30 fruits were taken at daily, or 2 or 3 d intervals after anthesis, for measurement of growth and contents of C and N.

Analysis of Growth and Accumulation of C and N by Fruits. Fruits were separated into pod walls and seeds and fresh weights and dry weights recorded. C content of dry matter was measured by a Shoniger combustion technique, N in dry matter by standard Kjeldahl analysis (16).

Carbon Dioxide Exchange and Transpiration of Fruits. Net CO_2 exchange of attached fruits was measured continuously throughout growth by enclosing individual fruits of known age into glass cuvettes and monitoring sequentially the effluent gas streams (2.5 l/min) for CO_2 using an IRGA operating in the differential mode (15). Transpiration of the enclosed fruits was measured simultaneously by following changes in RH of the effluent stream using a temperature-controlled Vaisala humicap humidity probe (Helsinki, Finland). An empty cuvette flushed with ambient air was included as a reference stream against which changes in CO_2 or water content in the assay gas streams could be assessed.

Fruit transpiration was also determined gravimetrically by passing the effluent air from the cuvettes through individual freezer traps and comparing the amount of water collected over a 24 h period from cuvettes enclosing fruits with that from empty cuvettes through which ambient air was passing. A good agreement (±10%) was found between the two methods of measuring transpiration. Data for the humidity probe were used in the assessments of fruit water balance since this technique measured transpiration continuously.

A new set of fruits was enclosed in the cuvettes every 3 or 4 d over the period during which the gas exchange and transpiration of the population of fruits was being studied. All measurements were made using a water screen above the plants to restrict temperature changes within the cuvettes to within 4°C of ambient. Enclosure did not appear to affect subsequent growth or development of the fruits.

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Gas Exchange of Isolated Seeds. Net CO_2 exchange of detached seeds was measured under conditions simulating those within the pod. Seeds were daily removed from the fruits at regular intervals throughout the 24 h period, weighed, and 2 to 3 g samples quickly placed in serum vials (34 ml capacity). The vials were then gassed with, and sealed to contain, a humidified CO_2-air mixture of composition similar to that of the fruit gas space (0.3–2.6% [v/v] CO_2) from which the seeds had been removed (see Ref. 4 for the methodology of collection and analysis of the fruit's internal gas space). The vials were then incubated at ambient glasshouse temperature. Samples of gas (0.5 ml each) were taken at 10 min intervals over a 1 h period after enclosure in the vial to monitor the increase in CO_2 content with time and thus measure the respiration rate of seeds. Nighttime measurements of seed respiration were made in total darkness, daytime measurements while exposing seeds to the same radiant flux that they were estimated to have been receiving through the pod wall (310–340 $\mu E \cdot m^{-2} \cdot s^{-1}$). This was assessed by using the pod wall as a filter for ambient daylight and measuring the transmitted PAR (400–700 nm) by means of a small quantum sensor (Lambda Instruments Corp.). The measurements of seed respiration made throughout any one diurnal cycle were integrated to estimate the total CO_2 exchange of the day/night cycle.

Collection and Analysis of Xylem Sap and Phloem. Xylem sap was collected daily as root bleeding sap or tracheal sap collected by vacuum extraction of inflorescence stalks (peduncles) (see Ref. 11 for discussion of relevant techniques). A sample of 15 plants was used for each collection, and at least three nighttime and three daytime collections were pooled to represent each 3 d interval of fruit growth. Phloem sap was obtained by cryopuncturing the fruit stalk (pedicel) with a needle cooled in liquid N_2, applying the puncture close to (within 2 mm) the point of attachment of the fruit (see Ref. 16). Phloem exudate was collected for a 1 h period from sets of 15 fruits during each 24 h period of the 22 d growth cycle of the fruit, sampling times being evenly distributed throughout night and day.

Sap samples (xylem and phloem) were assayed for ureide, amino acids, amides, sugar, and organic acids and C:N weight ratios determined as described elsewhere (16).

RESULTS

Growth of Fruit Parts (Fig. 1). The pod comprised the main sink for C and N during the first half of fruit development, after which all of the fruit's increases in dry matter, C, and N were attributable to growth of seeds (Fig. 1). Pods reached maximum contents of N at 11 d and of C at 13 d, after which they lost 67% of their N and 37% of their C. Seeds showed maximum rates of accumulation of C and N over the period 12 to 18 d after anthesis. Seed maturity (full dehydration) was achieved by day 21 or 22.

CO_2 Exchange of Intact Fruits with the External Atmosphere and Respiration of Seeds (Fig. 2). Photosynthesis of the fruit failed to maintain it above CO_2 compensation point during any photoperiod of its development (Fig. 2A). However, CO_2 fixation was clearly of significance to the fruit C balance, since CO_2 losses between days 4 and 11 were consistently lower in the 14 h photoperiod than in the 10 h night. Seed respiratory output (Fig. 2B) paralleled growth of seeds over the period 5 to 18 d but declined steadily after this as the seeds matured. Detached seeds always showed greater CO_2 loss in the day than at night due to the complete absence of the photosynthetic enzyme, ribulose-1,5-bisphosphate carboxylase (EC 4.1.1.39), from the tissues of the seed (data not shown), and the day/night temperature differential. The bulk of the CO_2 output of the older fruits was clearly attributable to seed respiration (*cf.* Fig. 2, A and B).

Transpiration and the Water Balance of Fruits (Fig. 3). Fruit transpiration rate increased with increasing fruit size over the first 8 d and then remained constant at 1.6 to 1.8 ml/fruit/d until the fruits dried out at 18 to 20 d (Fig. 3A).

Tissues of the pod accumulated 8 ml water over the first 13 d of development and then lost water steadily until fruit maturity. Seeds increased in water to a maximum of 4.8 ml at 19 d and then dehydrated (Fig. 3B). Almost half of the water lost from the fruits over the second half of development could be accounted for as changes in fruit tissue water. Transpiration ratios (ml water

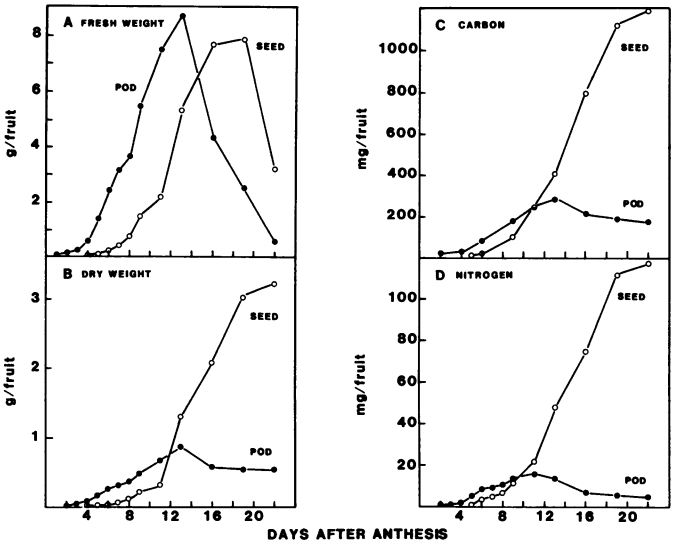

FIG. 1. Changes during development of fruits of cowpea (*V. unguiculata* [L.] Walp cv Vita 3). (A) Fresh weight; (B) dry weight; (C) carbon content; (D) nitrogen content. Total C determination of dry matter varied with a SE of between ± 2 and 7%, while total N measurements varied with a SE of around ± 2 to 3%. All values as amounts per fruit.

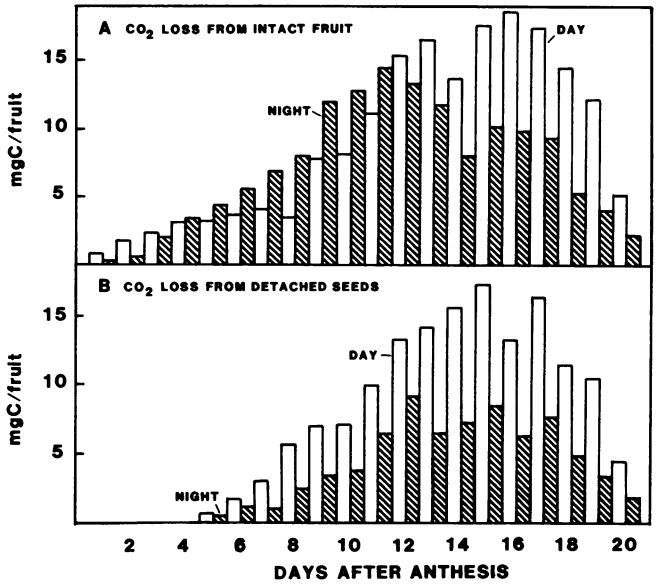

FIG. 2. Changes during development of fruits of cowpea (*V. unguiculata* [L.] Walp cv Vita 3) in (A) net CO_2 exchange of whole fruits and (B) net CO_2 exchange of detached seeds. All values as amounts (mg C) per fruit per day or night period. Net CO_2 exchange measurements of whole fruits varied with a SE of ±10% at any one age, those for seed respiration by ±6%. Respiration of freshly detached seeds was measured over the first 1 h after detachment, under conditions of CO_2 concentration, radiant flux, and temperature simulating those currently experienced by seeds within the intact fruit.

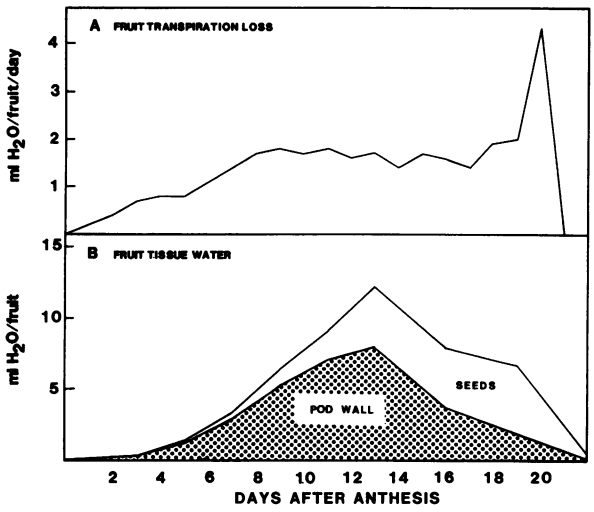

FIG. 3. Changes during development of cowpea (*V. unguiculata* [L.] Walp cv Vita 3) fruits in (A) rate of transpiration and (B) amounts of water in tissue of pod wall and seeds. Data of B plotted cumulatively.

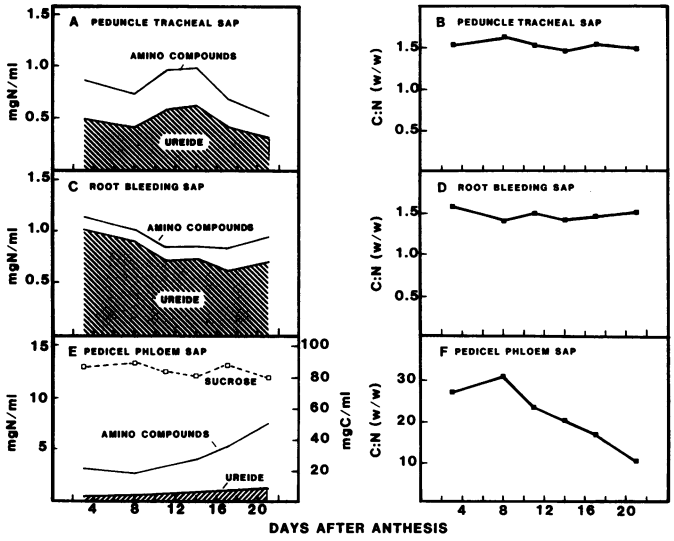

FIG. 4. Changes during fruit development of cowpea (*V. unguiculata* [L.] Walp cv Vita 3) in concentrations of major organic solutes and the C:N weight ratios of xylem and phloem fluids serving the fruit. Solutes (A) and C:N ratios (B) of fruit stalk tracheal (xylem) sap; solutes (C) and C:N ratios (D) of root bleeding xylem sap; major organic solutes (E) and C:N ratios (F) of pedicel cryopuncture phloem exudate. Ureide and amino N contents are plotted cumulatively.

transpired per g dry matter gain) for the fruit were 11 ml/g for the period 0 to 11 d, 7 ml/g for 12 to 22 d, and 8 ml/g for the whole 22 d period of fruit maturation (*cf.* data for dry weight [Fig. 1B] and transpiration [Fig. 3A]).

Changes in Composition and C:N Mass Ratio of Xylem Sap and Phloem Exudate (Fig. 4). Changes during fruit development in the concentrations of major organic N compounds of xylem root bleeding sap and peduncle tracheal xylem sap were as shown in Figure 4, A and C. Total measured N content (weight of amino compounds + ureides per ml) did not differ greatly between the two classes of xylem sap, but the peduncle tracheal samples showed a lower concentration of N during late fruit growth and a consistently higher proportion of amino acid N to ureide N than in corresponding age samples of root bleeding sap. Organic acids (malate, malonate, succinate, and tartarate) comprised, on average, 27% of the total C of root bleeding sap and 15% of the C of tracheal peduncle sap. Sugars were not detected in xylem sap. C:N weight ratios (based on organic acid, amino acid, and ureide contents) averaged 1.49 for root bleeding xylem sap (Fig. 4B) and 1.54 for tracheal sap of peduncles (Fig. 4D).

Sucrose was the major organic constituent of the cryopuncture phloem exudate of the pedicel (Fig. 4E). Its concentration in phloem (80–100 mg C/ml) did not change significantly during fruit growth. Organic acids (see Ref. 16) at 13 to 16 mg C /ml represented on average 12% of the total C of the samples. Unlike xylem sap, phloem exudate contained several times more N as amino compounds than as ureides (Fig. 4E) and this disparity was accentuated in late fruit development. Total N in phloem (as amino compounds + ureides) increased from 3 to 8 mg N/ml over the period from 8 to 20 d. C:N weight ratios of phloem (Fig. 4F) accordingly decreased from 36:1 to 10:1 over this same period, largely reflecting the altered balance between sucrose and nitrogenous solutes.

Assessment of the Relative Importance of Xylem and Phloem in Delivery of C and N to the Fruit (Table I). As in earlier studies (8, 13, 14, 18), it was assumed that the fruit acquired all of its C and N by unidirectional intake through xylem and phloem and that these channels furnished C and N in the proportions (C:N weight ratios) shown in Figure 4. Calculations were based either on the C:N weight ratios of root bleeding or of peduncle tracheal sap, and gave almost identical results in view of the closely similar balance between C and N in the two classes of sap. The

Table I. *Consumption of Carbon and Nitrogen by Developing Fruits of Cowpea (V. unguiculata [L.] Walp cv Vita 3) and Estimates of Delivery by Xylem and Phloem*

Item of Budget	Interval of Fruit Development (d)		
	0–11	12–22	0–22
1. C gain in dry matter of seeds (mg C/fruit)[a]	250	940	1190
2. C gain or loss (−) in dry matter of pod (mg C/fruit)[a]	241	−67	174
3. C loss to atmosphere as CO_2 (mg C/fruit)[b]	95	231	326
4. C intake through fruit stalk (1 + 2 + 3) (mg C/fruit)	586	1104	1690
5. N gain in dry matter of seeds (mg N/fruit)[c]	21.8	95.2	117.0
6. N gain or loss (−) in dry matter of pod (mg N/fruit)[c]	15.6	−10.5	5.1
7. N intake through fruit stalk (5 + 6) (mg N/fruit)	37.4	84.7	122.1
8. Average C:N ratio of pedicel phloem sap (w/w)[d]	27.2	16.0	18.6
9. Average C:N ratio of penduncle tracheal (xylem) sap (w/w)[d]	1.57	1.51	1.54
10. Proportional intake of C through phloem (%)[e]	95.4	97.6	96.9
11. Proportional intake of C through xylem (%)	4.6	2.4	3.1
12. Proportional intake of N through phloem (%)	55.1	79.5	72.0
13. Proportional intake of N through xylem (%)	44.9	20.5	28.0

[a] Data from Figure 1C.
[b] Data from Figure 2A.
[c] Data from Figure 1D.
[d] Data from Figure 4.
[e] Assumes xylem and phloem deliver all of C and N to fruit at C:N ratios given in items 8 and 9.

data presented in Table I refer to peduncle sap. The equations employed to calculate the mixture of xylem and phloem streams which met precisely the fruit's recorded consumption of C and N were reported earlier (14). Applied to the two consecutive 11 d periods of fruit growth (Table I), the experimental data indicated an almost total dependence (95–98%) of the fruit on phloem for C, an approximately equal dependence on phloem (55%) and xylem (45%) for N in the first half of fruit development, and a much higher dependence on phloem (80%) than on xylem (20%) for N in the second half of fruit growth.

A net loss of 67 mg C (Table I, item 2) and 10.5 mg N (Table I, item 6) occurred from the pod during the second half of fruit development. These losses were equivalent to 7% and 11% of the seed's intake of C and N, respectively, during the 12 to 22 d interval of growth. The C:N ratio of this mobilized translocate from pod wall to seed was estimated to be 6.4, a value approaching to the C:N ratio of protein and substantially less than the mean C:N value of 16.0 recorded for the phloem stream currently entering the fruit stalk (Table I, item 8). Seeds then may have received a translocate relatively more rich in N than suggested from analysis of fruit stalk phloem sap.

Assessment of the Significance of Pod Photosynthesis in the C Economy of the Fruit (Table II). Estimates of the contributions of the pod wall in refixation of CO_2 were computed as shown in Table II, using experimental data on the fruit's CO_2 economy abstracted from Figure 2. Assuming that respiratory behavior of detached seeds reflected their true behavior in the pod, the capacity of the pod wall in reassimilating CO_2 during the photoperiod (Table II, item 7) was assessed as: measured CO_2 loss by detached seeds during the photoperiod (Table I, item 3) + gross daytime respiration of the pod wall (Table II, item 6) − net CO_2 loss from fruits in the photoperiod (Table II, item I). The estimates (item 7) indicated a refixation by the pod of 79 mg C over the period 0 to 11 d, 40 mg over 12 to 22 d, and a total of 119 mg C over the whole maturation period of the fruit. These amounts of C were equivalent to 13, 4, and 7% of the total net C intake by the fruit from the parent plant during these respective times of development (*cf.* Table I, item 4 and Table II, item 7).

Table II. *Carbon Dioxide Exchange of Whole Fruit, Seeds, and Pod of V. unguiculata (L.) Walp cv Vita 3 and Estimations of Photosynthetic Contribution of Pod Wall to Fruit Carbon Economy*

Budget Item (mg C/fruit)	Period of Fruit Development (Days after Anthesis)		
	0–11	11–22	Total
1. CO_2 loss from fruits in photoperiod[a]	38.5	142.2	180.7
2. CO_2 loss from fruits in night period[a]	56.2	88.6	144.8
3. CO_2 loss from seeds in photoperiod[b]	25.1	126.8	151.9
4. CO_2 loss from seeds in night period[b]	12.2	62.1	74.3
5. Net CO_2 loss from pod wall in night period (2–4)	44.0	26.5	70.5
6. Estimated gross daytime respiratory loss by pod wall[c]	92.4	55.5	147.9
7. Estimated contribution of pod wall photosynthesis to carbon economy of fruit (6 + 3) − 1	79.0	40.1	119.1

[a] Derived from Figure 2A.
[b] Derived from Figure 2B.
[c] Estimated by using night CO_2 loss of pod (item 4) and assuming a Q_{10} value of 2 for respiration of pods during a 14 h photoperiod at an average temperature of 27°C compared with a night period of 10 h at 21°C.

DISCUSSION

The principal aim of this investigation was to examine quantitatively the relationship between the water economy of a cowpea fruit and its intake of C- and N-containing solutes from the parent plant by xylem and phloem. This can be achieved by comparing the measured consumption of water by the fruit in transpiration (Fig. 3A) or in incorporation or loss of water in its tissues (Fig. 3B) with estimates of water intake through xylem and phloem associated with the acquisition of C and N. Relevant data are found in Table III in which it is assumed that C and N solutes enter exclusively by mass flow through xylem and phloem, and are delivered in the proportions indicated in Table I and at the concentrations (mg C or mg N/ml) suggested from analyses of peduncle tracheal sap and fruit cryopuncture phloem exudate (Fig. 4). The data indicate that in both halves of fruit development more water enters through xylem and phloem than can be accounted for in changes in tissue water or transpirational activity. The discrepancy is much greater in the second half (26 ml) than in the first half (6 ml) of fruit growth, reflecting the greater intake of water through phloem, and the lower transpirational ratio and higher proportional involvement of dehydration losses of water in transpiration during the later period of fruit growth.

Delivery of such a large excess of water (over 2 ml/d per fruit over the period 12–22 d) is difficult to ascribe to experimental error or to incorrect assumptions when modeling C and N flow into the fruit. For instance, if some form of non-mass flow delivered C and N but not water to the fruit through phloem in the 12 to 22 d period, one would still have to account for how the fruit had rid itself of an excess of 13 ml of water acquired through the xylem. Similarly, assuming mass flow in xylem and phloem had taken place, C:N weight ratios and concentrations of C and N in the transpirational stream and in the phloem would have to be greatly different from the values predicted by peduncle tracheal sap and cryopuncture pedicel exudate before achieving the situation in which the water intake of the fruit

Table III. *Water Economy of Fruits of Cowpea (V. unguiculata [L.] Walp cv Vita 3) for Different Periods of Development*

Items of Budget (ml/fruit)	Period of Fruit Development (Days after Anthesis)		
	0–11	12–22	0–22
1. Tissue water gain or loss (−) by pod wall[a]	7.0	−6.9	0.1
2. Tissue water gain or loss (−) by seeds[a]	2.2	−1.8	0.4
3. Transpiration loss of water[b]	11.2	19.7	30.9
4. Total water consumption (1 + 2 + 3)	20.4	11.0	31.4
5. Estimated water intake through phloem[c]	6.5	12.9	19.4
6. Estimated water intake through xylem[c]	20.0	24.2	44.2
7. Apparent excess delivery by xylem and phloem (5 + 6) − 4	6.1	26.1	32.2

[a] Derived from Figure 3B.
[b] Derived from Figure 3A.
[c] Assumes C and N supplied to fruit in xylem and phloem in proportions indicated in Table I and at concentrations in xylem and phloem given in Figure 4.

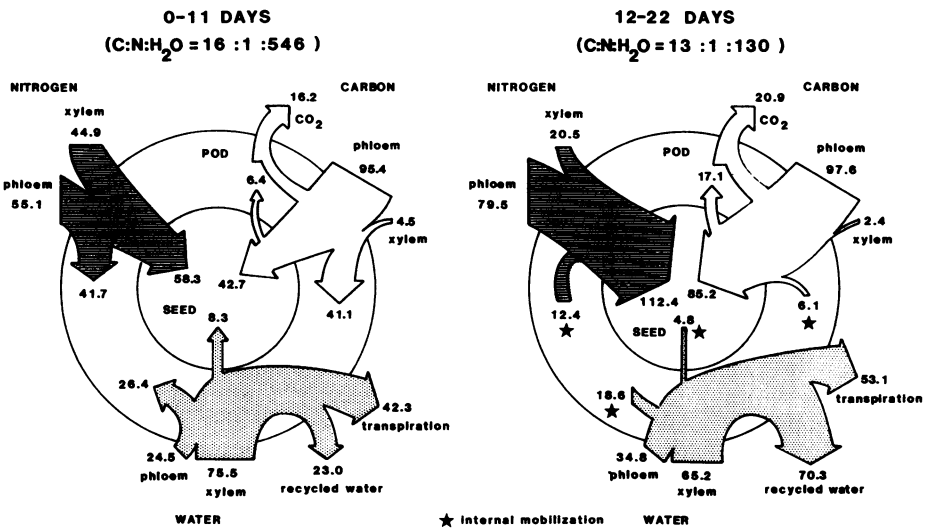

FIG. 5. Proportional intake of carbon, nitrogen, and water through xylem and phloem during (A) early (0–11 d) and (B) late (12–22 d) development of a cowpea fruit. All components of the fruit's budget are expressed relative to a net intake of 100 units of C, N, or H_2O through xylem and phloem. Values for mobilization of C, N, or H_2O (★) are given for the second half of development and estimates of the hypothetical 'recycled' components of the water budget given for both stages of fruit growth. Ratios of absolute amounts by weight of C, N, and H_2O consumed by fruits are given.

equalled its measured consumption of C, N, and water. Finally, the discrepancy might be resolved if some form of nonvascular transport contributed C and N, but not water, to the fruit. Again, this component would have to be of great magnitude were the anomaly to be resolved in this way.

The more logical interpretation is to accept the experimental observations and conclude that the measured excess of water entering the fruit stalk returns in some manner to the parent plant. This could be achieved if certain xylem strands continued importing water while others engaged simultaneously in back flow of water to the parent plant. Alternatively, the whole flux of water in the xylem between fruit and plant might reverse periodically.

Quantitative relationships between the economies of C, N, and water of the Vita 3 cowpea fruit are shown diagrammatically in Figure 5. These utilize all experimental observations on the water economy, CO_2 exchanges, and C and N increments or losses of pod and seed, and companion observations on concentrations of C and N in phloem and xylem sap. Excess water delivered to the fruit in xylem and phloem (Fig. 5, 'recycled water') is pictured as returning to the parent plant through xylem. The role of the pod in providing mobilized C and N to seeds in the second half of development is indicated. Values for proportional intake of C, N, and water are expressed on a percentage basis, that is, in relation to 100 units by weight of each entering in xylem and phloem through the fruit stalk. The two stages of fruit development can then be readily compared by partitioning of C and N to pod and seed; by the extent of involvement of phloem and xylem in transport of C, N, and water; and by losses of C as CO_2 from pod and seed relative to C intake from the parent plant. Figure 5 also indicates the ratios by weight of intake through the fruit stalk of C:N:water, the water component including that cycled back to the plant as well as that committed to tissue water or transpiration.

Many investigations on a number of aspects of the utilization of C, N, and water by developing fruits have been conducted on legumes, including bean (*Phaseolus vulgaris*) (3), pea (*Pisum sativum*) (4–7, 12), soybean (*Glycine max*) (1, 8, 10, 20–22), white lupin (2, 12, 18) as well as cowpea (9, 15, 19). In all instances, fruits are reported to exhibit good economy in water usage (transpiration ratios less than 28 mg/g) to achieve high final yields of C and N in seeds as opposed to pod wall dry matter, to exercise measurable economy of C in terms of photosynthetic refixation of daytime respiratory losses of C from pod and seed, and to depend more heavily on phloem than on xylem for intake of C and N from the parent plant. The present evidence (see discussion in Ref. 12) suggests that the cowpea fruit is particularly economical in water usage and in partitioning C and N to seeds, but relatively inefficient in photosynthetic CO_2 fixation.

Associated with the cowpea fruit's unusually low transpiration ratio (8 ml/g) is an apparent capacity to return the equivalent of up to 70% of its water intake back to the parent plant, probably *via* the xylem. The validity of these suggestions is tested in a companion paper (17) in which anatomical observations are combined with a series of tracer studies examining patterns of solute and water movement into the fruit at different stages of its development.

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