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INTEGRATING LEAF AND SEED PRODUCTION STRATEGIES FOR COWPEA (*VIGNA UNGUICULATA* (L.) WALP.)

By

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ABSTRACT

INTEGRATING LEAF AND SEED PRODUCTION STRATEGIES FOR COWPEA (VIGNA UNGUICULATA (L.) WALP.)

By

Robert Patrick Barrett

Cowpea is eaten both as a grain legume and a leaf vegetable in much of sub-saharan Africa. Three methods for harvesting leaves at flowering time, with and without apex removal at 28 days after planting, were compared using 6 diverse African cultivars. Apex removal did not change vegetative growth, and rarely altered seed yield. All methods of leaf harvest reduced seed yield, but increased edible dry weight when harvested leaves were added to seed weights. The average edible dry weight yields were 136%, 118%, and 104% of the control's seed weight for multiple harvest, single harvest, and pruning, respectively. The best treatment was 6 weekly harvests on 'Vita 7' with pinched apex, which yielded 209% of the control. Edible dry weight yield was higher in trailing cultivars than in bushy cultivars. The 2 traditional cultivars from Botswana yielded about the same seed weight and less edible dry weight than the best of 4 improved cultivars from Nigeria.

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TABLE OF CONTENTS

PAGE

LIST OF TABLES

INTRODUCTION

The cowpea is important in Africa as a grain legume and as a leaf vegetable, and sometimes both products are harvested from the same plants (14, 26). On a dry weight basis, the leaves are as nutritious as the seeds (14). Though partial defoliation usually reduces seed yield, increased seed yield has been recorded following leaf removal (34, 39, 82). Because past research has concentrated on the yield of only one product, this research focused on the production of both leaves and seeds. It was hypothesized that the total yield of edible products (dry weight) from cowpea could be increased by harvesting both leaves and seeds. Three factors were investigated: methods of leaf harvest, removal of apical bud at 28 days, and genotype. Six African cultivars representing a range of phenotypes were selected. Four were developed for high seed yields, and two were landraces consumed for leaves and seeds. The experiment was conducted in a greenhouse at Michigan State University from June-September, 1985.

LITERATURE REVIEW

Multiple uses of cowpea

The cowpea is usually considered as strictly a grain legume, but in the more humid parts of East Africa the crop is raised more for the leaves than the seeds (1). In Zimbabwe, the leaf and grain are given equal importance (79). The use of beans and cowpeas as both leaf vegetables and grain legumes has been documented in 14 African countries, especially in eastern and southern Africa (14). The young pods, stem tips, and unripe seeds are also eaten in the tropics, and even the roots are consumed in Ethiopia and Sudan (117). In Botswana, researchers have selected triple-purpose landraces for seed, forage, and leaf vegetable production (26).

Productivity for pods and hay

In India, it has been noted that harvesting immature cowpea pods for human consumption prevented leaf senescence, and the plants remaining after pod harvest were valuable for hay, containing 11-12% protein on a dry weight basis. Green fodder including pods was compared with hay yield plus separate pod harvest for 2 cultivars. Net profits showed that harvesting 2 products from the same plant can be more profitable (9).

Productivity of cowpea for hay

Cowpea is an important forage and hay crop, and its productivity under tropical conditions is well documented. Because the coarse stems of cowpea hinder rapid drying of the hay, cowpea is mainly grown for fodder where the shortage of water makes production of other species, such as alfalfa, too difficult (109). Cowpea plants continually produce new leaves if cut back regularly from an early stage. As early as 1907 it was reported that, weather permitting, cowpea pastures will regenerate vigorously if not severely damaged by grazing (30). In New South Wales, Australia, cowpea is used for strip-grazed pastures, and cattle graze the same crop 2 to 5 times (109). Many cultivars of cowpea are suitable for multiple harvests, which can be more productive on a kg/ha/day basis than when harvested once at the end of the season. Cutting forage cowpea 'E.C. 4216' once or twice gave dry weight yields of 1630-2110 kg/ha and 2560-3970 kg/ha, respectively. Average production for single harvests was 39.6 kg/ha/day, but 48.0 kg/ha/day if cut twice (80).

The highest reported cowpea fodder production is from India. Comparing 5 cultivars under irrigation in the dry season, yields ranged from 3557 to 4174 kg/ha of dry matter, with crude protein yields of 692 to 889 kg/ha (19.3-23.4% protein). In the monsoon (rainy) season, dry matter yields ranged from 3779 to 6249, and crude protein from 618 to 1210 kg/ha (15.3-20.2% protein). The highest yielder in the monsoon season (65 days) was 'Russian Giant', which gave dry weight and protein yields of 96.1 and 18.5 kg/ha/day, respectively (102).

Also in India, 26 cowpea cultivars were tested for fodder and nutrient production, but the number of days from sowing to harvest in the "pod-initiation stage" was not reported . Fodder dry weight ranged from 2090 to 6160 kg/ha, and crude protein from

374 to 998 kg/ha, averaging 4330 and 675 kg/ha, respectively. Protein content varied between 13.2% and 18.8% of dry weight, averaging 15.9% (121).

The effects of sowing date on fodder and seed production for 14 cultivars of cowpea were tested in Shika, Nigeria. The hay was harvested when the first yellow pod began to dry in half the plots, and the seeds when all pods were dry. Fodder dry weight (1048-5044 kg/ha) was divided into the components of leaves (244-1412 kg/ha), stems (413-2060 kg/ha), and pods (279-1715 kg/ha). Average crude protein content (dry weight basis) was 24.4% in leaves, 11.0% in stems, 21.7% in pods (averaging 17.5% for fodder), and 27.1% in mature seeds (4).

Protein productivity of leaves and seeds compared

The high productivity of leaf vegetables compared to grain legumes has been emphasized, not only for volume of food but for protein as well (8). Using U.S. yield averages, protein contents, and amino acid profiles, the yield of essential amino acids in cowpea was 3.5 times higher from forage than from seeds (3).

On a dry weight basis, the protein content of cowpea leaves has been measured at 28.5% (61) and 32.8-34.3%, with 88% retained after cooking (64). This is higher than the 23.3-30.0% of dry weight range for protein in seeds of 14 cultivars (4).

It was estimated that cowpea, under optimum conditions in a 60 day season, grown at 50 plants/m^2, would produce .5-1.5 kg/m^2 of fresh leaves, but only .06-.3 kg/m^2 of seeds (56). Cowpea seeds range from 19 to 35% crude protein (dry weight basis)(68), giving .01-.09 kg/m^2 of protein. With 4.2% protein in the leaves (94), they would produce .02-.06 kg/m^2 of protein. However, season length must also be considered. It has been calculated that 15 times as much protein would be produced per day from cowpea leaves (using an average of 1.0 kg/m^2 in 60 days) as from seeds (using a world average of .0212 kg/m^2 in 90 days) (14).

The above calculations consider seeds and leaves as mutually exclusive products, but some cropping practices yield both.

Cropping systems in Africa

African farmers sometimes broadcast cowpea seeds into a grain field when the plants are about 50 cm high. The seedlings are thinned according to the availability of soil moisture, and the thinnings are used as potherbs (69). In Uganda, cowpea plots are sown broadcast, thinned gradually during growth, and the thinnings boiled (125). In northern Cameroon, indeterminate cultivars are usually intercropped with cereals. They are harvested over a long period, first for leaves and green pods, and later for dry pods, as time permits while the farmers are primarily occupied with sorghum cultivation. The long vines are also valued for forage (119). Some African farmers reportedly believe that harvesting a moderate amount (about 2 tons/ha fresh weight) of stem tips and leaves at flowering time increases seed yield, but removing double that amount lowers it (94). In Botswana, any removal of leaves is considered to lower the seed yield, but long-season cultivars are valued for leaf harvesting during the vegetative stage. Short-season cultivars are unsuitable for double-purpose production in Botswana, because they do not produce excess leaves (27). In Kenya, cowpea plots are harvested for leaves starting in about 3 weeks when 5-10 leaves are present, and continuing up to flowering. Sometimes leaves are harvested during flowering as well, but not after pod filling begins (14).

Cowpea is sown thickly if grown only for the leaves, and is harvested in 3 weeks by uprooting the seedlings or cutting at ground level. This system is used year-round in West and Central Africa (94) and in western Kenya (14).

Marketing of cowpea leaves

In many parts of tropical Africa, cowpea leaves are among the top 4 leaf vegetables in terms of quantities eaten (14). The low price compared to other vegetables in the markets favors high consumption in southern Benin (127) and the highlands of Kenya, where cowpea leaves are the least costly (94). In parts of Kenya they are sold only in the rainy season (14, 64), but throughout much of the country they are available all year, and have become an important cash crop near urban areas (14).

Nutrient prices were calculated from market prices (surveyed for 2 years) in Bumbuli, Usambara, Tanzania. Mchicha, translated as "wild spinach", applies to 4 species of leaf vegetables, including cowpea, <u>Sonchus oleraceus</u>, and 2 species of <u>Solanum</u>. Beans and maize were cheaper sources of protein than mchicha, but mchicha was much cheaper than animal protein. Maize and beans were also the most important sources of nutrients and energy, but were deficient in vitamin A, which was best supplied by liver or mchicha. Of the 28 foods considered, liver was the cheapest source of all commonly deficient vitamins, but mchicha was a close second for riboflavin, vitamin A and iron, and third for vitamin C and niacin. For calcium, mchicha was 3 times cheaper than the second place source, beans (107).

In addition to Benin, Kenya, and Tanzania, cowpea leaves have been reported from markets in Ghana (137), Mali (29), almost all regions of Cameroon (138), Ethiopia (138), Uganda (82, 101), and Malawi (143).

Processing and storage

The Sukuma of Shinyanga district, northwest Tanzania, put leaves in the sun near the house for about 4 hr before placing in a pot with cold water, and cooking for about 3 hr, changing the water halfway through. Cooking is usually done at night, and then the pot is covered and left until morning when the leaves are pounded and sun dried until the early afternoon. Storage is in pots, for up to 1 year (48).

The Pedi of the northeast Transvaal, South Africa, prepare cowpea and other leaf vegetables for storage by boiling for about 1.5 hr. The drained leaves are kneaded into golf ball-sized pellets and set on a flat rock to dry in the sun. After 3 days the lumps are scraped into sacks and stored (135).

Cowpea leaves are also preserved by boiling and sun drying by the Venda, Ndebele, Shangaan (44), and the Kwena or Bakoni (45), all of the northern Transvaal, by the Shona of eastern Zimbabwe (17), and by the Tlokwa of eastern Botswana (55).

In Malawi, cowpea leaves picked in the morning are spread out in the sun to wither for 2 or 3 hr, before being put back into baskets. This reduces the bulk and preserves the flavor. The next morning they are packed into a large (16 liter) earthenware pot with a liter of cold water, and steamed 10-20 minutes until soft, and then spread on mats for drying in the sun 1-3 days. After 3-4 such batches have been dried, the leaves are packed into 1.5-2.5 kg balls, covered with large masuku (*Uapaca kirkiana*) leaves, bound tightly, and hung up in the hut until needed (143).

Fresh cowpea leaves are dried in Zambia without cooking (94). In Uganda, cowpea leaves may be dried in the sun with or without steaming them first, and are sometimes stored in powdered form (66). Storage as a dry powder is also recorded from northern Nigeria (24) and East Africa (1). Storage of dried leaves has been reported in Ghana (137), Cameroon (139), and Kenya (61).

Effect of sun drying on nutritional value

Excessive losses of beta-carotene often occur in sun drying fresh vegetable leaves, and in subsequent storage. Smaller losses occurred if the leaves were steamed first. Only 10-20% losses were recorded from cowpea and cassava leaves, showing remarkable stability of the B-carotene compared to other species (49). Cowpea leaves were shown superior to other leaf vegetables (cassava, sweet potato, and *Amaranthus*) in percentage and absolute retention of vitamin C and carotene under various solar drying treatments after minimal boiling. In full sun, cowpea leaves lost 89% and 71% of vitamin C and total carotene, respectively, but when dried in the shade they lost only 76% and 43%, respectively (76).

For human nutrition, the protein in fresh cowpea leaves was shown to be limiting in the S-containing amino acids. Lysine was found limiting for sun-dried leaves because a large proportion was destroyed by drying (75).

Cooking methods classified by country

Reported methods of cowpea leaf preparation vary by country. Boiling is the most popular, either as a potherb or alone as "spinach" or "greens". They may also be fried or combined with a starchy staple food, but nowhere are cowpea leaves consumed without cooking. Cowpea leaf consumption has been recorded from 24 countries in Africa, Asia, and the Pacific (table 1). It is probable that cowpea leaves are traditionally eaten in many other countries in the tropics, but they have not been reported in the diets of New World populations.

Place of cowpea leaves in African diets

Maize ugali, a stiff porridge,is an important staple in Kenya. Since most of the population consumes little food from animal products, leaf vegetables are crucial for many nutrients. Cowpea leaves are eaten as a side dish with ugali, and to a lesser extent cooked together with maize kernels, legumes, and either potatoes or green bananas (64). A Kenyan recipe for irio is given as follows: boil 1 kg each of maize and beans slowly for 2-4 hr. When almost ready, add 1 kg green bananas and .5 kg chopped cowpea leaves and boil for 20 minutes more (94).

Table 1. Cowpea leaf cooking methods classified by country, with citation numbers.

Country	As spinach^z	As potherb^y	Mixed in a starchy food	Fried
West Africa	(24)			
Senegal		(122)	(122)	
Ghana (137)^x				
Benin		(127)		
Mali	(88)			
Nigeria	(24)			
Cameroon	(139)			
Central Africa				
Zaire, Central African Republic, and Sudan				
(Azande)^w	(28)			
Sudan	(41)			
East Africa				
Ethiopia (Chako)		(138)	(138)	
Kenya	(14,64)	(14,64,94)	(14,49,64,94)	(14)
(Kikuyu)	(59)			(94)
Uganda	(66,101)	(101,125)		
(Ganda)	(14)	(14)	(14)	
(Northwestern)		(120)	(120)	(120)
Tanzania	(48,75,81,101)			(48)
(Sandawe)	(91)			

continued on next page

Table 1. continued.

Country	As spinach^z	As potherb^y	Mixed in a starchy food	Fried
Southern Africa				
Malawi	(143)	(14,143)		
Zambia	(94)	(40,87)		(94)
Zimbabwe	(17,79)			
Botswana	(26,55)	(26)		
South Africa	(44,45)	(44)		
(Pedi)		(135)	(135)	
Asia				
Hawaii	(83)			
Philippines	(15)			
Indonesia	(92)			
Bangladesh	(7)	(89)		
India	(123)	(89)		
Pakistan		(89)		

[z] "Spinach" is cooked alone by boiling or steaming, is consumed as a single item, and includes references to use as a "vegetable" or "greens".

[y] A "potherb" is boiled in a soup, stew, or sauce with other foods.

[x] Method of preparation not reported.

[w] Specific tribes or regions within a country shown in parentheses.

The Sandawe of central Tanzania consumed a diet based on ugali, supplemented with a wide variety of protein-rich relishes. Relishes from animal and vegetable sources were consumed with equal frequency. Gathered plants were eaten at 45% of all meals, but cultivated vegetables at only 9%. Leaves of crop plants (cowpea, bean, cassava, and sweet potato) were eaten at 4% of meals. Leaves of cowpea and other cultivated plants were dried and saved for the dry season, when they became more prominent in the diet (91).

In the northeastern Transvaal, the Pedi people have a proverb: "Meat is a visitor, but spinach is a daily food". Their normal diet consists of maize porridge, cowpeas, some cucurbits, and a wide variety of leaf vegetables. The most common spinaches are morogo, translated as "wild green leaves", and cowpea leaves. Morogo can include wild plants and cultivated cowpea and cucurbits. During the dry season, dried morogo is crushed and sprinkled over the porridge (135).

The Kikuyu of Kenya consume various grain legumes and starchy staple foods, but rarely eat meat. The most frequently eaten vegetables are the leaves of cowpea, pumpkin, cabbage, and kale (59).

A large number of leaves and fruits are eaten by several ethnic groups in northwestern Uganda. Leaves of cultivated cowpea were commonly eaten, and less often the wild cowpea (ssp. dekindtiana). Cowpea leaves, dried for storage, were found equal in protein content (22.6%) and "overall food value" to dry cowpea seeds, except the leaves had more vitamin C (120). In addition to northwestern Uganda, leaves from wild cowpeas are gathered for food in Kenya (67), Tanzania (78, 106, 107), and South Africa (135).

Traditional African vegetables

The displacement of traditional African vegetables, both gathered and cultivated, by "exotic" or European vegetables has been noted by many authors. This trend has alarmed some, who point out that the traditional vegetables are generally more nutritious, better adapted to the local environment, better able to compete with weeds or in mixed culture, and less subject to pests and diseases (78). With respect to vitamin A, lettuce, cabbage, Swiss chard, and even carrots were shown inferior to traditional East African leaf vegetables such as cowpea, bean, cassava, and *Amaranthus* (49, 78). Cowpea leaves had over 4 times the protein of cabbage grown in Tanzania (78).

The usefulness of annual leaf vegetables is limited in most areas of Tanzania. Because of a shortage of water, they can be grown only during the rainy season when alternate sources of leaves are most abundant. Rural families gather nutritious leaves of weeds and crop plants to eat, including cowpea (129).

Nutritional value of cowpea leaves

The nutritional value of cowpea compares favorably with other leaf vegetables commonly eaten in Africa. It is a good source of minerals, especially iron, calcium, phosphorus, and zinc (table 2). Available iron was measured at 14% of total iron (64).

Table 2. Nutrient content/ 100g edible portion of cowpea leaves.

	Preparation method					
	Fresh-Uncooked			Fresh-Cooked		Dried
Source^{z}	(83)	(65)	(70)	(68)	(65)	(70)
calories (KCAL)	30	-	44	-	-	227
water (g)	-	85.7	85.0	86.8	89.3	10.6
protein (g)	4.8	-	4.7	-	-	22.6
vitamin A (IU)	712	13500	4000	333	10833	45000
vitamin C (mg)	36	-	56	12	5.8	86
niacin (mg)	1.1	-	2.1	-	-	-
riboflavin (ug)	175	-	370	43	-	-
folacin (ug)	-	288	-	-	73	-
thiamine (ug)	354	-	200	.04	-	-
calcium (mg Ca)	73	217	256	-	133	1556
potassium (mg K)	-	446	-	-	128	-
phosphorus (mg P)	106	88	63	-	42	348
iron (mg Fe)	2.2	5.5	5.7	-	4.7	12.0
zinc (mg Zn)	-	2.8	-	-	2.1	-

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[z] Reference cited.

The fluoride content of common leaf vegetables grown in different parts of Kenya was highest in cowpea, from 10 to 115 mg F/kg (96).

Vitamin C content in cowpea leaves was reduced by 76% by boiling for 15-20 minutes, from 91 to 19 mg/100 g. An extreme range of 56-123 mg/100 g was recorded for fresh leaves. Boiling with trona, a crude hydrated sodium carbonate formula commonly used by Kenyans to soften fibrous leaf vegetables, reduced the vitamin C content to "a mere trace" (50).

Vitamin C content in cowpea leaves was reduced 90% by continued cooking for 30 minutes after boiling, from 59 down to 6 mg/100 g (not counting an additional 2 mg/100g leached into the cooking water) (64, 65). While Kenyans usually consume the cooking water from vegetables, they use trona for its flavor even with young tender cowpea leaves that need no softening (14). Thus it appears that even more than 90% of the vitamin C would be destroyed when trona is used.

Vitamin C content in cowpea leaves was reduced by 91% when boiled for 50 seconds and dried in full sun, but only by 76% when the drying was done under shade (76).

An international unit (IU) of vitamin A equals 0.6 micrograms of B-carotene or 0.3 micrograms of retinol. Vitamin A occurs as retinol only in animal products, but the B-carotene eaten in vegetables is converted to retinol at the ratio of 6:1. Vitamin A and carotene are not soluble in water or destroyed by cooking, but rapidly decompose when exposed to air (142). Drying cowpea leaves greatly reduces the availability of vitamin A, but the amount remaining may still be large. The wide range of concentrations reported for B-carotene in cowpea leaf samples probably reflects differences in freshness, water content, cooking, and analytical techniques. Differing cultivars and growing conditions in the various locations could also be involved.

B-carotene concentration in cowpea leaves from the highlands of Kenya ranged between 332-345 IU/100g (67).

When the nutrient content of various common foods of northeast Tanzania was determined, vitamin A was shown to be one of the most deficient nutrients in the diet. Yellow maize was presumed to supply about 50% of the vitamin A requirement. It had the second-highest concentration of all foods analyzed, with about 400 IU/100g. Cowpea leaves were highest, with 3000 IU/100g (6).

The carotene content of fresh cowpea leaves declined by 47% when boiled for 1 hr, from 9500 IU to 5000 IU Because eye diseases from vitamin A deficiency were common in Tanzania, more consumption of leaf vegetables and fish livers was recommended (79).

Total carotene in cowpea leaves was measured at 13,500 IU/100g before and 10,833 IU/100g after cooking 30 minutes, for a decline of only 20% (64, 65).

A mean of 15,693 IU/100g B-carotene was recorded in fresh cowpea leaves, with a range of 13,750-17,500 IU/100g. When measured on a dry weight basis, B-carotene content increased 70% with 15 minutes of boiling, from 91,845 to 156,322 IU/100g. In other leaf vegetables, B-carotene increases of 24-88% were observed under the same treatment, presumably due to better extraction by the acetone solvent. For Kenya, dried cooked cowpea leaf proved economical and culturally acceptable as a vitamin A supplement. As little as 10-20 g of dried leaf per day would give an adequate intake (51). Cowpea leaves were still an excellent source of vitamin A, even after the concentration had been reduced by drying.

On a dry weight basis, fresh cowpea leaves contained 114,000 IU/100g, which was reduced 58% to 48,000 IU/100g by boiling 50 seconds and sun-drying (76).

Introduction to leaf and seed yield in bean and cowpea

In many parts of Africa, bean (*Phaseolus vulgaris*) and cowpea (*Vigna unguiculata*) plantings are harvested for 2, 3, or even 4 edible products. Tender pods with immature seeds and the full-sized "shell beans" or "green peas" are eaten as vegetables, and the dried seeds are soaked and boiled before eating. The young leaves are also cooked and eaten (14). Harvesting leaves is not often seriously considered by western scientists, as it is believed to reduce seed yields, erroneously considered to be the only economic product. However, yield increases following leaf removal have been reported (34, 39, 82). Most of the reports reviewed here cover defoliation in the laboratory as part of basic research, or try to quantify insect damage in the field.

Many factors are involved in the effect of leaf removal on seed yield in nitrogen-fixing legume crops. The following discussion will examine the role of the leaves in providing, through photosynthesis and translocation, the carbohydrates and nitrogen (N) required for seed production, and will examine the processes that defoliation affects. An empirical formula for relating yield loss to defoliation percentage is worthless if it does not consider the age of the foliage and the plant's stage of development (60). Because cultivars differ in the time required to mature and weather is so variable, reporting treatments relative to the plant's growth stage is much more useful than the number of days from planting.

Cowpea leaf initiation, expansion, and area

In cowpea, many processes that affect leaf area are influenced by temperature. High or low temperatures during vegetative growth can greatly accelerate or retard leaf area and reproductive growth (71, 116).

The final size of each leaf and rates of leaf appearance and expansion increase with temperature, while the duration of expansion for each leaf decreases, because a constant number of leaves on each apex are expanding at any given time (71). Others also found cowpea leaf appearance rate highly dependent on temperature (12).

Cowpea leaves are initiated about twice as fast at 30 C as at 20 C average temperatures (116). The base temperature for leaf appearance is estimated at 16 C and for leaf expansion at 21 C (71). Since cowpea leaves expand mostly at night, daily minimum rather than average temperatures would be critical for leaf area expansion (116). Higher daytime temperatures following partial defoliation would therefore be expected to speed up leaf initiation (but not leaf expansion) on branches below the canopy, speeding up replacement of the lost leaves.

Leaf initiation is slowed by cool temperatures, moisture stress, and dense planting (which can promote moisture stress) (116). Dense plantings of 50-100 plants/m^2 reduced the leaf appearance rate (71). Leaf appearance rate was not related to leaf water potential, but was closely related to stomatal conductance (r=.80**). Stomatal conductance declined as vapor pressure deficit increased (141).

Leaf dry weight/area tended to decrease with rising temperature (in controlled environments but not in the field) and decrease with time. Leaves continued to increase in dry weight after full expansion (73).

In cowpea, as in fava bean (Vicia fava) and soybean (Glycine max), final leaf size increases with node number for a time, and then decreases in the last leaves that develop. The variation is mainly due to the rate, rather than duration of expansion. This can be explained by source-sink relations. The earliest, lowest leaves expand more slowly because so little active leaf surface supports the new growth, but this constraint gradually diminishes. The latest leaves become ever smaller as assimilates are diverted to growing seeds (71). For this reason, harvested leaves would be replaced most easily when they are largest, at or before anthesis.

In cowpea, nutrient translocation, leaf senescence, and death begin sooner at higher temperatures. Corrected for temperature, the time of the start of leaf death divided by the time of the end of leaf growth gives a constant of 0.86. These appear to be 2 ends of a single process, which is accelerated by higher mean temperatures, but is not influenced at all by time of flowering. Apparently, flowering is influenced by minimum, rather than mean temperature. Once leaf senescence starts, the overall rate of leaf area loss depends on the pod-filling pattern rather than temperature (71).

Leaf Area Index (LAI) is the ratio of a plant's leaf area divided by the area of ground the plant shades at noon. The LAI depends on the balance between the rates of expansion in young leaves and abscission in senescent old leaves. Maximum light interception is reached at a LAI of about 3 in cowpea, regardless of growth habit or leaf shape. At LAI values below 3, the dry matter accumulation rate increases linearly with LAI. Peak LAI is normally reached in cowpea at flowering time, but the number of days required and the LAI reached depend on genotype, temperature, and water supply (116). The greatest LAI was observed during the 2 weeks after first flower in 3 cowpea cultivars (116), and 18 days after blooming in 'Caloona' (58).

Peak LAI values above 5 are typical for indeterminate cowpeas. Determinate cultivars frequently have a maximum LAI of 3, but the time needed to develop it has ranged from 30 to 60 days for various cultivars, spacings, locations, and weather conditions. Generally, cowpeas attain a larger LAI and reach a given value sooner at closer spacings (116).

In a determinate and an indeterminate cultivar of cowpea at 2 planting densities ($12/m^2$ and $24/m^2$), plants at the low density had greater leaf areas and leaf, stem, and total dry weights per plant. The difference was relatively greater for the indeterminate cultivar which had double the leaf area/plant at half the density, compared with only 50% greater for the determinate cultivar (19).

The canopy temperatures of well-watered plants were 2-7 C below ambient air temperatures. But drought-stressed leaves could not maintain lower temperatures in the middle of the day by evaporative cooling. The stressed plants adapted by limiting the expansion of new leaves, so that maximum LAI was 3, compared with 5 in the control (141).

Photosynthesis and growth rates

Leaf photosynthesis rates are known to vary between cowpea cultivars, but a wide range of measurements is often reported for the same cultivar. The maximum photosynthetic rate for each cowpea leaf occurs at full expansion, when light-saturation is reached at about 66% of full sunlight in the tropics. As leaves age the rate declines gradually, but plunges suddenly as they begin to senesce (116).

Maximum photosynthetic rates/area for leaves increase during leaf expansion. High maximum rates were recorded for a span of about 20 days in each leaf, with the peak usually reached just after expansion ceased. Photosynthetic rates and leaf areas declined thereafter, as the leaves senesced. The earliest leaves have lower maximum rates, which increase with leaf number up to about the fifth leaf, and then remain constant. The mean values for maximum photosynthetic rate were about 1.2mg $CO_2/m^2/sec$ for the third leaf, and about 1.5mg CO_2/m^2/sec for leaves 5, 7, and 9 (72).

The net photosynthesis rate of 'Caloona' cowpea plants rose to a peak at 70 days after planting (10 days after anthesis), but before the greatest leaf area was measured at 78 days. Net photosynthesis then declined rapidly as leaves abscised (58).

In a field experiment, the crop growth rates (mg/cm^2/day) of 3 cowpea cultivars were linearly related to the leaf area index (which never exceeded 3 because of wide spacing). The mean net assimilation rate (crop growth rate) for 3 cultivars in the field and greenhouse varied only between 4.6 and 5.2 g/m^2/day. The maximum leaf area and crop growth rate occurred during the first 2 weeks after first flower (93).

The crop growth rate (g/m^2/week) of cowpea cv. 'Morod' from 4-6 weeks after planting was directly related to LAI ($r=1.00$) in the range of 0.2-2.0. The relationship was also close for 6-8 weeks with LAI below 2.0. A peak growth rate of about 85g/m^2/week (or 12g/day) was recorded at a LAI of about 1.6 (36).

Maximum growth rates of 98g/m^2/week (14g/day) were measured at a LAI of about 2.5, with no differences between broad and narrow leaf cowpea types (140).

During early growth in cowpea, dry weight increase was proportional to intercepted radiation. Weight differences between trials at different seasons were due equally to variations in sunlight, the proportion intercepted, and net photosynthetic efficiency (73). The mean radiation conversion efficiency has been measured at 3.8% (73) and 3.4% (126).

Some have concluded that declining photosynthesis with age limits seed yield in cowpea. During rapid seed growth, carbohydrate use was greater than production (19).

In the dark, cowpea leaves respire and give off CO_2 at rates equivalent to about 5-10% of the CO_2 uptake during maximum photosynthesis (116).

The CO_2 compensation point for cowpea has been measured at 62 ppm CO_2, at a temperature of 22-25 C (62).

Photosynthesis of pods

Cowpea pods and peduncles did not show a net export of carbohydrates, but were shown to contribute 80-85% of their respiration requirements (72). In beans under field conditions, 76-97% of 14CO2 fixed by the pods was retained in the pod 24 hr later. At earlier stages of pod growth, a higher percentage of labeled material was exported, but the proportion sent to other pods steadily increased with time (74).

Effects of heat and drought on photosynthesis

Even when adequately watered, fruits and leaves exposed to the sun commonly reach temperatures above 30 C that inhibit photosynthesis. Shading can reduce surface temperatures by up to 4 C (116). Canopy temperatures of well-watered cowpea plants were 2-7 C below ambient air temperatures. Although moisture stress reduced the water potential in cowpea leaves, stomatal conductance showed a close negative correlation with vapor pressure deficit (VPD). Despite stomata closing as VPD rose, evaporative cooling of leaves increased with VPD (141).

Gas exchange measurements indicated that photosynthesis is not seriously impaired by moisture stress at constant temperature (27% reduction at full irradiance). But, drought-stressed cowpea leaves could not stay below the ambient air temperature by evaporative cooling in the middle of the day. Less photosynthesis would occur in the short term from high temperatures, and in the long term due to limited expansion of new leaves. (115, 143).

In field-grown 'Michelite' beans, there was little relation between LAI and seed yield. For various planting dates, the effect of a large leaf area could be either helpful or harmful, depending on the weather at anthesis. When the weather was hot and dry, a large leaf area was a liability (25).

Thus, if leaves become too hot and less productive when moisture is limiting, removing a number of leaves could make the available water supply adequate to cool the remaining leaves, allowing full production. Under such conditions, partial defoliation may not reduce net photosynthesis. Because most plants grow rapidly early in the season when competition for water and light is minimal, they often acquire more leaf area than can be utilized in hot dry weather later. Since net photosynthesis declines more or less linearly with reduced turgor pressure, the loss of a few leaves under drougÒv conditions (which occurs naturally through more rapid senescence) would benefit the plant by allowing greater water supplies to the remaining leaves, and greater photosynthesis (57). The labor cost of trimming leaves during drought may or may not be justified by the value of the additional seeds produced, but when the harvested leaves are assigned a fair market value as vegetables, this practice can be profitable.

Photosynthesis rate, hormones, and reversal of senescence

Photosynthetic rates in cowpea leaves decrease with age (71, 60). Chlorophyll, protein, carotenoid, and RNA levels and leaf weight/area decline as leaves senesce. Plant hormones including auxins, gibberellins, and cytokinins have been shown to delay these symptoms of senescence (128). Greater photosynthetic efficiency and reversal of senescence have been documented in bean and cowpea following defoliation (5, 108, 110, 128, 132).

In a series of defoliation experiments with urd bean (*Vigna mungo*), photosynthetic rates increased in remaining leaves, which varied directly with defoliation severity (98).

During defoliation experiments with beans, the remaining leaves in the defoliated plots were much darker green than in the control plots. This suggests that chlorophyll content increased to compensate for the leaves removed (33).

In mung bean (*Vigna radiata*), pod number was not affected by applied NAA, GA3, or the cytokinin 6-benzylaminopurine (BAP) during bud swelling, blooming, or pod setting, though BAP applied through all 3 stages significantly increased pod number. It was hypothesized that pod set and development are limited by photosynthate supply, either directly to the pods, or indirectly. Because the root system was a major sink, especially during flowering and pod setting, it is possible that root-synthesized

hormones (either gibberellins or cytokinins) regulate reproductive yield (22).

Removing the upper leaves from a cowpea plant significantly increased photosynthesis and dry weight accumulation in the primary leaves and the second trifoliate, reversing the symptoms of senescence. Continued removal of new leaves maintained a high photosynthetic rate in remaining lower leaves (108).

Treating bean plants with the synthetic cytokinin benzyladenine (BA) or decapitating the plants above the primary leaves produced marked increases in DNA, RNA, protein, carotenoid, and chlorophyll levels. Senescence was reversible by either treatment even after the primary leaves had begun to yellow and the carotenoids and protein had been largely depleted 35 days after planting, but severing the upper part of the plant was shown to be more effective than BA. This was attributed to a continuous supply of endogenous cytokinins to the leaves with no competition from other plant parts (128).

Decapitation of bean seedlings induced additional chlorophyll formation, greater expansion, and a longer life span in the primary leaves (110). In partially defoliated bean plants (all younger leaves and buds above the second trifoliate removed), the remaining leaves became darker green, thicker, and leathery. Compared with measurements (per area of leaf) on the control plants, which showed only minor fluctuations, the photosynthesis rate and the in-vitro ribulose bisphosphate carboxylase activity both increased in the treated plants until 8 or 10 days after defoliation, and then leveled off. Total

chlorophyll, however, continued to increase for the duration of the experiment (132).

In defoliated bean plants (all leaves above the first trifoliate removed as they emerged), the photosynthetic rate of the first trifoliate slowly increased. It was always above the control, but the difference was not significant until the final measurement at 45 days. These results place doubt upon the hypothesis that photosynthetic capacity of leaves is proportional to the demand placed upon them by the rest of the plant (the source-sink ratio). The photosynthetic rate would be expected to stay below rather than above the rate for the control. But if the photosynthetic rate and chlorophyll content vary with endogenous hormone levels, they could be increased by defoliation or other damage which removes the competitive demand of other plant parts (5). This hypothesis fits the present evidence, and is supported by other results (16).

In another experiment, 3 treatments on bean seedlings left the primary leaves intact. Some plants were decapitated and totally debudded, others were heat-girdled above the primary leaves to seal off the phloem and then debudded below the wound, and the third group was defoliated (all leaves were pinched off before they could expand) but not debudded. Heat-girdled plants continued normal vegetative growth and defoliated plants continued growing stems and branches (16).

The primary leaf area, thickness, chlorophyll content, and photosynthesis rate increased similarly after the decapitation and defoliation treatments. Decapitated plants also had 80-85%

greater ribulose bisphosphate carboxylase activity than the heat-girdled plants and the control. In the control and the heat-girdled plants, primary leaf area and thickness did not increase with time. In the decapitated plants, photosynthetic activity did not increase in the first 4 days, but did so within 7-8 days, and was even higher 16 days after treatment. Photosynthetic activity did not increase in the primary leaves of the heat-girdled plants where translocation of assimilates downward was blocked, even though the primary leaves obtained no assimilates from above just as in the decapitated group. The defoliated plants had a much greater demand placed on the primary leaves to support continued stem growth, yet the measured increases were equal to those in the decapitated plants (16).

Thus, it is unlikely that photosynthesis is regulated by source-sink relationships. Neither is it likely that factors regulating photosynthesis are transmitted from younger leaves through the phloem or against the flow through the xylem, nor from the buds (16). To maintain photosynthesis in primary leaves, it is not even necessary to remove the leaves above. Bean primary leaves that have started to senesce can be rejuvenated by preventing transpiration from the upper leaves, as by greasing them or covering with a plastic bag (144).

An explanation for these observations has been suggested. Increased photosynthesis in leaves remaining after partial defoliation may result from an increased supply of endogenous cytokinins, which are synthesized in the root and transported in the xylem (136). Applying cytokinins to bean primary leaves has

increased chlorophyll content, leaf area and thickness, ribulose bisphosphate carboxylase activity, and photosynthesis rate. It has been further hypothesized that the flow rate of water through the roots and xylem does not change the production rate for the regulating factor. Thus, the endogenous regulation of each leaf's photosynthetic capacity depends on the amount of the hormone arriving in the transpiration stream. Defoliation increases the amount received by the remaining leaves (16).

There is further evidence that cytokinins are involved in promoting photosynthesis and delaying leaf senescence. Cytokinins are mainly synthesized in roots, and are carried through the xylem to the leaves in the transpiration stream (46, 122, 144). Senescence in detatched leaves can be reversed if the leaves are induced to form roots (144). Since removing buds or fruits (and presumably other organs) increases the cytokinin concentration in the remaining parts, endogenous cytokinins probably travel to all parts of the shoot (124).

To confirm the cytokinin hypothesis would require that endogenous cytokinin levels be correlated with the physical changes in the leaves that resulted from the treatments. This was not done in any of the experiments on bean and cowpea reviewed here.

The self-destruction hypothesis

In most annual legume crops (including cowpea but not peanut, Arrachis hypogaea) the N demand by growing seeds is greater than can be fulfilled by current uptake, requiring translocation from vegetative parts. Metabolizing proteins to export N from the vegetative tissues eventually halts photosynthesis, induces senescence, terminates the seed-filling period and restricts yield. Seed yield in such self-destructive species depends on the N uptake rate during pod-filling, since the deficit must be met by internal translocation. A low assimilation rate means more rapid senescence, a shorter duration of seed growth, and lower yield (111).

Later researchers concluded that the decline in photosynthesis following early fruit development limited seed yield in cowpea, since carbohydrate consumption during rapid seed growth outpaced production. It was hypothesized that indeterminate cultivars which continue vegetative growth while producing pods would be higher-yielding, as would those with a longer duration of pod development (19).

Others claim that more recent data do not support the hypothesis of self-destruction, but do not elaborate (116). The evidence presented in the next section supports the self-destruction hypothesis.

Carbon and N metabolism and translocation

The proportions of seed N content derived from current uptake (from soil and symbiotic fixation) and translocated from leaves and stems varied in different experiments (table 3), influenced by the cultivar and experimental conditions (table 4). Generally, about 50% of seed N came from current uptake, 35% from leaves, and 15% from stems.

Table 3. Proportions of seed N content from current uptake and translocation.

	% Translocated			
% Current	From leaf	From stems	Total	Reference
56	25	19	44	(58)
50[z]	-	-	50	(73)
47	40	13	53	(32)
78	13	10	23	(90)[y]
50	34	16	50	(32)
47	37	16	53	(115)
53	33	14	47	(85)[x]
31	36	33	69	(85)[w]

[z] Estimated values.

[y] Numbers given add up to 101%.

[x] Nodulated; no added N.

[w] Not nodulated; fertilized with nitrate.

Table 4. Experimental conditions for N translocation analysis.

Cultivar	Det?[z]	N[y]	Rhiz?[x]	FF[w]	H[v]	Reference
Caloona	No	None	Yes	62	120	(58)
TVu-4552	Yes	30kg/ha	Yes	30-37	83-87?	(73)
TVu-4552	Yes	30kg/ha	Yes	35-40	56-61	(32)
TVu-1503	?	None	Yes	35?	87	(90)
K-2809	Yes	25ppm	Yes	48	90	(32)
K-2809	Yes	30ppm	Yes	45-47	88-94	(115)
K-2809	Yes	None	Yes	37	77	(85)
K-2809	Yes	200ppm	No	37	77	(85)

[z] Determinate cultivar.

[y] Applied N.

[x] Rhizobial nodules present.

[w] Days to first flower.

[v] Days to final harvest.

The percentages of N in plant parts at anthesis were also measured. Leaves contained 3-6%, stems 1-3%, roots 1-2%, and rhizobial nodules 6-7% (table 5).

The percentages of N in plant parts at final harvest was lower than at anthesis for leaves and stems, and about the same for roots and nodules. Seeds contained 3.5-4.3% N, and pod husks 0.9-1.5% (table 6). Other authors reported 0.9% N in husks of mature pods (105), and an average figure of 4.0% N for mature cowpea seeds (117). The N contents of leaves, stems, and pods (with seeds) were 3.9%, 1.8%, and 3.5%, respectively, when harvested for fodder at near maturity (4).

In annual legumes the leaves abscise after exporting much of their nutrient reserves to the seeds. The dynamics of C and N metabolism and transfer during the cowpea life cycle have been reported in detail for a determinate cultivar 'K-2809' (32, 85, 115, 118) and for an indeterminate fodder cultivar, 'Caloona' (58), which exhibits the "self-destruction syndrome" (90).

The net photosynthesis rate of 'Caloona' plants rose to a peak during early flowering (70 days), and then declined rapidly as leaves abscised. The greatest leaf area was at 78 days. Maximum N fixation was measured shortly before anthesis (60 days), but it also dropped sharply as nodules abscised so that fixation ceased by day 92. During the seed-filling stage (79-120 days), all vegetative parts lost C, N, and dry weight. All the N given up was assumed to have been derived from protein breakdown, but no evidence was offered. Before leaflets abscised, 31% of their N content was exported, and 32% was mobilized from

Table 5. Percentage of N in parts of cowpea plants at anthesis.

Leaves	Stems	Roots	Nodules	Reference
5.2-5.6	1.7-1.8	1.7-1.9	6.8-7.0	(86)
4.1-4.4	1.3-1.5	1.2-1.3	6.2-7.1	(84)
4.5	1.5	0.8	6.1	(32)
4.0-4.6	1.7-2.0	1.0-1.2	5.9-6.8	(118)[z]
3.2-4.4	1.2-2.6	1.1-1.5	---	(118)[y]

[z] Nodulated; no N added.

[y] Not nodulated; nitrate fertilizer added.

Table 6. Percentage of N in parts of cowpea plants at final harvest.

	Nodule dependent		NO_3 dependent
Plant part	[z]	[y]	[y]
Green leaves	-	2.8-3.0	2.6-2.9
Dead leaves	2.1-2.2	1.7-1.8	1.7-2.0
Main stem	0.6-0.9	0.6-0.8	0.6-1.1
Side branches	1.4-1.7	1.0-1.3	0.9-1.3
Peduncles	-	0.8-1.2	1.1-1.6
Roots	-	1.1-1.2	0.9-1.3
Nodules	7.2	5.6-5.8	-
Pod husks	0.9-1.3	1.3-1.5	1.3-1.5
Seeds	3.8-4.3	3.5-3.6	3.5-3.8

[z] Reported in (86).

[y] Reported in (118).

senescing stems. Assuming 100% efficient transfer of these reserves to the growing pods, 25% of the N needed for the seeds would have been met by leaflets and 19% by the stems. The remaining 56% would have come from senescing roots, rhizobial fixation and uptake from the soil. Current photosynthesis provided 80% of the seeds' carbohydrate requirement; only 20% was mobilized from stems and leaves. The conversion efficiency of imported organic substances to seed dry matter was calculated at 67% (58).

Plant N was accumulated at 28 mg/plant/day during both vegetative and late reproductive stages. During early reproductive growth over half of total plant N was accumulated, and the rate rose to 111 mg/plant/day. Translocation from the stems and leaves formed before anthesis accounted for 30% of the N content of developing fruits at mid pod-fill, and for 12% of final content in seeds. Translocation from all vegetative parts after mid pod-fill contributed 62% of the increase in seed N content (44% of final content), with 37% from leaves, 18% from stems and peduncles, and 7% from nodules, with the remaining 38% of the increase from current uptake (table 7). Source of total N in the seeds at harvest is shown in table 4. At the final harvest on day 90, seeds comprised 48% of total dry weight and contained 63% of total plant N. Redistribution and N proportions very close to these results, despite differences in growing period, plant size, and total N content, were obtained with "TVu 4552" cowpeas in the field in Nigeria (32).

Table 7. N concentration and distribution in components of cowpea 'K-2809' at 3 growth stages. (32)

Days after planting	48		67		90	
Growth stage	Anthesis		Mid podfill		Maturity	
Component	%N	% of all	%N	% of all	%N	% of all
Leaves						
Pre-bloom	4.49	69	2.81	19	2.48	4
Post-bloom			4.51	26	2.72	8
Total green		69		45		12
Abcised					1.61	9
Total		69		45		21
Stems						
Pre-bloom	1.46	23	0.76	6	0.53	2
Post-bloom			1.73	9	0.84	4
Peduncles			1.85	5	0.96	3
Total		23		20		9
Roots	0.75	2	1.18	1	0.97	1
Nodules	6.07	6	7.04	6	5.27	2
Vegetative total		100		72		33

continued on next page

Table 7. continued.

	48 days		67 days		90 days	
	Anthesis		Mid podfill		Maturity	
Component	%N	% of all	%N	% of all	%N	% of all
Pod husks			1.40	2	1.22	4
Seeds			3.60	22	3.33	63
Young pods			4.35	4		
Reproductive total				28		67
Total N content (g)	1.329		3.664		4.318	
% from each stage	31		54		15	
N gain mg/plant/day	28		111		28	

The cultivar "K-2809" is normally determinate, but under long day (13-16 hr) conditions vegetative growth continued after flowering. Over 76% of plant dry weight at maturity (including dead leaves) was accumulated after flowering began at 48 days. Between first flower and mid pod-fill at 67 days, fruits (pod husks and seeds) composed only 32% of the weight increment, but by final harvest at 90 days they comprised 63% of the post-bloom weight increase (32).

Between mid pod-fill and maturity, the total dry weight of vegetative components declined by 7%. Almost all of the decline was accounted for by the weight loss in stems and branches produced before flowering, reflecting the mobilization of reserves for peduncle and fruit growth. Total leaf weight (green + senesced) declined only 2% between 67 and 90 days, showing that the export of nutrients from senescing leaves was nearly balanced by new leaf growth at the youngest nodes. Total peduncle weight increased only 18% after day 67, while their average weight decreased by 52%, due to translocation to fruits rather than a change in morphology. At the final harvest on day 90, seeds comprised 48% of total dry weight and contained 63% of total plant N (32).

"K-2809" cowpea was tested in an adverse fluctuating temperature regime known to diminish seed yields. Plants were either nodule-dependent or were fed 200 ppm inorganic N which suppressed nodulation. All plants first bloomed 37 days from sowing, matured the first pods 17 days later, and were ready for harvest at 77 days. The C and N contents of leaves, stems, and

roots were the highest at 49 days in non-nodulated plants, and peaked about a week later in the nodulated plants. Remobilization of N from leaves and stems was detected a week earlier in the non-nodulated plants than the rest, but for both treatments the rate of N translocation to the pods increased rapidly until day 63, and then declined as the seeds ripened (85).

The N and total dry weights of cowpea seeds were negligible for 7 days after anthesis, but increased continuously until maturity at 19 days. The dry weight of the pod husks increased steadily, then leveled off. Pod husk N content increased, then declined, suggesting translocation to the growing seeds. Nitrogen analysis showed that doubling the density from 12 to 24 plants/m^2 also doubled the proportion of total plant N found in the seeds at harvest from about 15% to about 30%, but seed yield was not changed (19).

Cowpea plants with and without rhizobial nodules were given different concentrations of nitrate N. Nodulated plants had higher N concentrations above ground at flowering time, compared to non-nodulated plants over all fertilizer levels: 1.8% vs. 1.4% in stems and branches, and 4.4% vs. 3.8% in leaves. Concentrations declined as the seeds grew, and all differences were minor by harvest time. Senesced leaves averaged only 1.8% N, regardless of nodulation. At harvest, N concentrations for pod husks and seeds averaged 1.4% and 3.6%, respectively, again unaltered by N nutrition. In all treatments, about 1/3 of the

plant's total protein N content remained in vegetative components at harvest, with 2/3 in the pods (118).

Moisture stress for 2 weeks altered the N distribution pattern in cowpea. At final harvest (63 days) stressed plants put higher proportions of dry weight and N (55% and 70%) into fruits than did controls (45% and 64%). Even though total dry weight was reduced by moisture stress, sometimes significantly, cowpea seed yield was not altered by any of the treatments. Pod number decreased by 7-19%, seeds per pod remained unchanged, and seed weight increased by 9-15%. (141).

Nitrogen fixation after anthesis was inhibited by 76-79% in nodule-dependent 'Vita 3' cowpea plants by flushing the root systems daily with 100% oxygen. This induced N starvation, resulting in significantly higher seed abortion and lower seed size and total weight, and more efficient mobilization of N from vegetative parts to seeds. Seed weight/plant declined by 33% and seed N weight/plant declined by 52%, giving a lower N concentration in seeds. However, seeds accounted for a similar proportion of dry weight at harvest (32-33%) regardless of treatment, but 59% of plant N was in the seeds at harvest in the starved plants compared to 55% in the control (99).

In summary, the N and dry weight harvest indexes have been increased in cowpea by increasing planting density or through moisture stress, but not by adding nitrate fertilizer. Actual N harvest index ranged from 15% to 65-70%.

Constraints to N fixation

Some have concluded that breeding or agronomic practices which prolong symbiotic fixation during reproductive growth, and thus delay senescence, could potentially improve the yield of field-grown cowpeas (32, 90). Photosynthate availability is the major limiting factor on symbiotic N fixation in cultivated legumes (20).

Maintaining leaves on the plant for as long as possible after anthesis is crucial for high seed yields because the seeds need both the carbohydrates they produce and the N contained in the leaves. There is also an indirect effect of leaf removal, since reducing the supply of photosynthate to the root nodules hinders symbiotic N fixation, cutting off the other main source of N (58).

Carbohydrate availability to nodules will often limit N fixation in bean and cowpea. In beans, climbing cultivars appear to supply a greater proportion of their carbohydrates to nodules, mainly at the expense of the roots. Nodule growth and N fixation are normally reduced as photosynthate is diverted to growing pods (52).

In mungbean (Vigna radiata) a continuous 33% defoliation significantly reduced nodule fresh weight per plant. This resulted in significant reductions in per plant N fixation, nodule H evolution, and nodule O uptake (respiration). Defoliation did not change the relative efficiency of N fixation expressed as: 1 - (H evoluted / acetylene reduced). The respiratory cost of fixing a unit of N was calculated to be significantly higher with 33% defoliation, though the cost declined by 60-70% from the vegetative stage to pod filling regardless of treatment (20).

In 'K-2809' cowpea the N source (nodules or inorganic fertilizer) made no difference in the reduction of dry weight of the total plant (by 50%) and the seeds (by 48%) due to waterlogging during vegetative growth. Waterlogging after flowering was less damaging to seed yield. All waterlogging treatments delayed leaf senescence in the nodule-dependent plants, but senescence was unaffected in the non-nodulated group. Nitrogen concentration in green leaves measured much lower in waterlogged plants (3.2%) than in the control (3.7%), but dead leaves were very similar (2.1-2.2%). Nitrogen source differences did not affect the N content of green or dead leaves (86).

Various authorities agree that yield of the symbiotic combination cowpea cv. 'K-2809' and Rhizobium 'CB 756' can not be increased by higher levels of inorganic N (32, 86, 118). Vegetative growth, except for roots, was markedly stimulated by added nitrate, but the number of branches was unaffected, and each peduncle produced fewer open flowers and mature pods than on the smaller nodule-dependent plants (86). Thus, other strategies must be used to raise production.

Chemical reactions of N in the plant

Nitrate reductase activity in cowpea roots is very much lower than in leaves (86). In 'K-2809' cowpea plants, nitrate reductase activity in roots was low and declined throughout growth, amounting to only 9% of the total for leaves. In the stems, nitrate reductase activity was detected only in the extreme apical portions. Though it remained relatively constant, it was also minor compared to leaves. Leaf activities were very high in young plants, but plunged after 21 days to about 25% of the former level around flowering time (35-40 days). Foliar activities later recovered to about 50% of the maximum, before suddenly declining during senescence (85).

Evidence suggests intense metabolic conversion of root-derived N (nitrates and ureides) to amino acids by vegetative plant parts before translocation to pods. Severe defoliation might hinder the metabolic conversion through a shortage of sites for it to take place (99).

Influence of temperature on reproduction

According to genotype, cowpea fruits may be borne above or below the leaf canopy. Those that are shaded by the canopy can remain 4 C cooler than fruits exposed to direct sun (116). Because many processes are influenced by temperature, the sudden change in sunlight penetration through the canopy due to defoliation may be cause for concern. Within normal temperature ranges, however, the minimum (night) temperature, which is probably not affected by shading, appears more important than maximum (day) temperature. Too low night temperatures result in delayed growth, flowering, and pod development, while excessively high night temperatures 5-7 days before anthesis will cause pollen sterility and flower abortion (73, 129).

In cowpea, translocation of nutrients out of leaves, and leaf senescence and death begin earlier at higher temperatures

(71). The timing of the start of pod filling depends on mean temperature, rather than on time from first flower. The rate and duration of pod-filling were not related to temperature, though the duration of filling of individual pods at particular nodes was found related to temperature. Pods tended to fill simultaneously, rather than sequentially, and pod weight was a relatively constant proportion of total dry weight, unaffected by temperature variations (73).

Seed growth and components of yeild in cowpea

In cowpeas, the number of leaves, peduncles, and pods are related to the number of nodes on the plant, and all vary directly with total plant weight. Within a single genotype, seed yield is strongly correlated with number of mature pods, while number of seeds per pod and weight of individual seeds seldom contribute to yield variations. The effects on yield from differing locations, weather conditions, soil factors, crop mixtures, pest attacks, and dependency on rhizobial or inorganic N supply have all been strongly correlated with pod number (116).

In extensive testing, pod weight was shown to be a relatively constant proportion of total dry weight, unaffected by temperature variations. Final pod number was reached after considerable pod abortion in most trials, and was proportional to total plant dry weight. Seed weight per pod did not change (73).

Components of yield were analyzed for 5 cowpea cultivars with rhizobial inoculation and nitrate fertilization (100 kg/ha $CaNO_3$). Among the 3 major seed yield components (pods/plant, seeds/pod, weight/seed), only pods/plant was influenced by all

treatments. Regression analysis showed that pods/plant accounted for the greatest proportion of the variability in seed yield among inoculated plants of the same cultivar. This component has low heritability and is greatly influenced by individual plant physiology and morphology and environmental factors, so is highly unstable. There were no differences observed in seeds/pod or weight/seed, which were quite stable and cultivar specific. These components are known to have high heritability in cowpea (42).

In the cowpea cultivars 'Adzuki', 'New Era', and 'Mala' in the greenhouse and the field, 70-87% of flower buds abscised before anthesis, and 45-64% of fruits set aborted before maturity. The proportion of ovules producing seeds in each fruit was inversely related to the proportion of flowers producing fruits. This negative correlation between seeds/pod and pods/plant was not always significant. Mean weight/seed has also been found to decline as both seed number/pod and pod number/plant increased in various cowpea cultivars (93). Because environmental conditions were not mentioned, it may be that the negative correlations were due to stress, rather than genetics.

Effects of stress on seed growth and components of yield

It remains to be seen exactly what causes flower and pod abortion in bean (11), Vigna radiata (21, 22), and other annual legumes. Failure of some blossoms to produce seeds may be due to a lack of photosynthate, a lack of other nutrients, hormonal influences, or a combination of these factors. Much evidence suggests that photosynthate supply determines pod number, either directly, or indirectly through the roots. The root system is a strong sink for photosynthate, especially during the flowering and pod setting stages. It is possible that seed growth in the earliest pods diverts assimilate from the root system, diminishing hormone synthesis there, and that a shortage of the necessary hormones (such as cytokinnins or gibberellins) curtails pod growth (11).

The growth rate, duration of growth, and final weight of soybean seeds were influenced by variation in the assimilate supply at a critical time. This was at the linear stage of seed development during the pod-filling stage, when existing cells expand at a constant rate. However, rather large variations in source-sink ratios were required to disrupt seed growth (35).

This suggests that, for legume crops, assimilate shortage for an individual seed is not normally a constraint in the field. Plants tend to maintain a relatively constant source-sink ratio by aborting or abscising flowers, fruits, and immature seeds in response to reduced assimilate supplies. Also, changes in assimilate levels are buffered by the storage capacity in vegetative plant parts. Both processes work to minimize fluctuations in the growth and final weight of seeds (35).

Bean seed yield involves negative correlations between pod number, seeds per pod, and seed size, so that one increases at the expense of the others. To adjust to a limited nutrient supply, reproductive growth is regulated according to a hierarchy. The most recently formed pods abscise first, then unopened flowers. This is followed by abortion of some ovules in the next older pods, until the pods with expanding seeds are reached. Next the open flowers and finally flower buds abscise, preserving the pods with the most resources already invested in seeds. In operation, this hierarchy means that the components of yield are allowed to vary at different times. Pod number is adjusted at the start of the reproductive phase, but after all buds have bloomed or aborted, it can not increase. At the end of the reproductive stage, only seed weight can be changed. In between and overlapping the other components, seed number is adjusted according to nutrient availability. Fertilized ovules may abort at any time until near maturity (2).

Seed yield and pod number were found closely related ($r=0.98$), as were seed yield and 100 seed weight ($r=0.72$), after repeatedly defoliating bean plants. Reduced leaf area was blamed for a shortage of carbohydrates which increased pod abortion and decreased seed weight. Successive defoliations appear to disrupt individual seed growth and final weight more than single defoliations (33).

When various defoliation and decapitation treatments were performed on 2 bean cultivars before anthesis, yield on inflorescences at the second mainstem node was mainly determined by pod number (10).

A fruiting cowpea plant responds to a shortage of metabolites (carbohydrates and/or N) by abscising flowers to keep the source-sink ratio from worsening, by abscising immature pods to restore a balance, and if that fails, by aborting seeds in the remaining pods (98).

Although moisture stress reduced total dry weight in cowpea, seed yield was not significantly altered. Pod number decreased significantly by 7-19%, seeds per pod remained unchanged, and seed weight increased significantly by 9-15% (141).

Waterlogging stress during the vegetative stage results in a smaller plant, so the reproductive load would be proportional to the number of nodes (86).

In summary, stresses on annual legume plants may affect different components of yield depending on the stage of reproductive growth. Since flowers and immature fruits are aborted first under stress, most observed yield reductions are due primarily to fewer pods. If the stress continues to restrict the nutrient supply to growing pods, some ovules will abort. Ultimately, the weight of individual seeds may be reduced, but this is rare. Weight per seed may increase if the plant recovers after all remaining flowers have aborted.

Effect of amount and timing of defoliation

Defoliation beyond some threshold level reduces total photosynthesis, allowing fewer pods and seeds to form. With all leaves removed, a plant must depend on the limited photosynthetic surface of green stems, pods, and petioles to regenerate new leaves and to produce seeds (98). The threshold for damage depends on the developmental stage of the plant.

Complete leaf removal at 7, 14, 21, and 35 days after first flowering reduced seed yield in S-5269 cowpea by 57%, 50%, 46%, and a non-significant 3%, respectively. Pandey gave considerable additional evidence that seed yield in cowpea and many other grain legumes depended mainly on photosynthesis after flowering. Defoliation later in the reproductive phase reduced yield less and less; removing leaves that have already exported the bulk of their substance depressed yield slightly (98).

Defoliation of bean plants was most damaging to yield during anthesis and podsetting in 'McCaslan 42' (133) and 'S-182-N' (130). Removing leaves 10-20 days after anthesis (during pod-filling) gave the lowest yield in 'Carioca'. Treatment later when the seeds were large, or earlier before blooming, had less effect (130).

Removing 1 of the 2 primary leaves at the seedling stage did not significantly influence the yield of pods in 'McCaslan 42' pole bean. Removing both primary leaves (100% defoliation) reduced yield by 59% and 71% in separate plantings. The loss of all trifoliate leaves when the plants were 1 week old did not influence yield, but yield was reduced significantly by various levels of defoliation 3, 5, and 7 weeks after emergence. At 5 weeks, during anthesis and podsetting, the loss was the most severe. Continuous weekly removal of 50% of the leaves (in relation to control plants) reduced pod yield by approximately 40% in the fall and 28% in the spring (133).

By removing a portion of each leaf with scissors, 2 cultivars of beans were defoliated at 4 growth stages at 5 levels of severity. The determinate cultivar 'ICA-Guali' has large leaves, while the semi-indeterminate cultivar 'Porrillo Sintetico' has medium-sized leaves. The timing of defoliation was at the stages of 3 trifoliate leaves (15 days from planting), first flower (30 days), the start of pod-filling (45 days), and maturity of the seeds (60 days). The seeds reached full physiological maturity after 75 days. The semi-indeterminate 'Porrillo Sintetico' cultivar showed a greater ability to regenerate lost leaf area, thus reducing yield loss, with 20 to 60% defoliation. In both cultivars, regrowth was vigorous before flowering, intermediate after flowering, and very slight after pod-filling began (table 8) (47).

It was shown that 'Harvester' and 'Early Harvester' snapbeans could lose 66% of their leaflets prior to anthesis with no significant reduction in the harvest of green pods (53). At flowering time, over 33% of the leaflets could be removed without reducing green pod yield (54). Based on these results, it was recommended that snapbeans be sprayed with insecticide only if pests consume over 20% of the leaf area before blooming, or 10% after (134).

Two determinate bean cultivars were defoliated at 3 intensities at 20 days (vegetative), 30 days (anthesis) and 40 days (pod formation). In 'Manteigao 977', 33% defoliation lowered yield by 19% at 40 days, 66% defoliation lowered yield by 35% at 30 and 40 days, and removing all leaves reduced yield by 71-85% at each growth stage. In 'Manteigao Fosco II', only 100% defoliation gave large yield reductions, of 78-85% at each growth stage. 'Manteigao 977' requires about 70 days to mature, while 'Manteigao Fosco II' has very large leaflets and needs about 80 days. The difference in response between the 2 cultivars was attributed to the larger leaflets of 'Manteigao Fosco II', which

Table 8. Seed yield as percent of control (intact) in 'Ica-guali' and 'Porrillo sintetico' beans with various levels of defoliation (47).

Defoliation level	20%	40%	60%	80%	100%
			Ica-guali		
Growth stage					
3 leaves	80	80	75	73	51
First flower	84	76	72	61	41
Pod-filling	86	72	67	52	23
Mature seed	99	95	88	92	78
			Porrillo sintetico		
Growth stage					
3 leaves	94	88	76	71	66
First flower	88	80	72	62	40
Pod-filling	87	82	72	52	27
Mature seed	95	92	90	87	82

No indication of the statistical significance of these figures was given, except for the comment that the yield reduction of "around 20%" observed for both cultivars at the mature seed stage with 100% defoliation was not significant. More severe reductions may have been significant.

permit less light to reach the lower leaves. Assuming that the lower leaves were not functional, their loss would have less effect (18).

Bean cultivars 'Jalo EEP 558' and 'Rico-23' were defoliated by 33% and 66% at 30, 45, and 60 days from planting using planting densities of 100,000 and 300,000 plants/ha. 'Jalo EEP 558' had fewer and larger leaves compared to 'Rico-23', and showed a greater reduction in yield from defoliation at 45 days because the seeds were almost mature at 60 days. On the average, 33% and 66% leaf removal gave 83% and 79% of the control seed yield, respectively, in 'Jalo EEP 558', and 95% and 93% respectively, in 'Rico-23', where the reduction in yield was linear with advancing age. At 100,000 plants/ha, 33% and 66% defoliations averaged 94% and 88% of the control seed yield, respectively. At 300,000 plants/ha, 33% and 66% defoliations both gave 87% of control (104).

In 4 legume species defoliated by 50% and 100% at various growth stages, the greatest reductions in seed yield occurred during the early podding stage. At this stage in cowpea, peanut, soybean, and green gram (<u>Vigna aureus</u>), 50% defoliation resulted in yields 86%, 57%, 58%, and 54% of control, respectively. Complete leaf removal gave yields 21%, 40%, 14%, and 5%, of the control, respectively. With yields reduced only 3-25% depending on growth stage, cowpea 'Iran gray' tolerated the loss of half its leaf area much better than the other species. This was attributed to better light penetration into the canopy. Total defoliation in the vegetative stage or at the start of flowering gave 33% and 55% of the control seed yield, respectively, and increased the number and weight of pods per peduncle. Complete defoliation during early and late podfilling, and near maturity gave yields of 21%, 40%, and 64%, respectively, showing that damage decreases as the seeds mature (37).

In a series of defoliation experiments with urd bean (*Vigna mungo*), complete defoliation during the reproductive period at 7, 14, and 35 days after anthesis reduced seed yield to 21%, 10% and 64% of control yield, respectively (98).

Effect of the age of the leaves removed

In urd bean, partial defoliations of 33%, 67%, and "basal leaves removed" (which was not described) gave seed yields of 74%, 41%, and 95% of control, respectively, when performed weekly from 15 to 55 days after sowing (98).

Removing 60% of the leaf surface from the upper or lower portions of bean plants decreased yield by 20% and 6%, respectively, during vegetative growth, and reduced yield by 27% and 13%, respectively, during pod formation (40 DAP). There was no difference between the treatments at 60 days, but the effect on yield was not reported (47).

Determinate '600/1' beans were subjected to 3 levels of defoliation at 3 fertilizer levels over 2 seasons. The 3 top fully expanded leaves were removed by pinching the petiole by hand, starting at 21 days. Leaves were removed 0, 1, 2, and 3 times at weekly intervals. The last defoliation at 35 days corresponded with full bloom. New leaves formed after the first and second defoliations were smaller. Average leaf areas of the

3 leaves from the second and third defoliations were 63% and 25% of the first defoliation. No new leaves grew after the third defoliation. Remaining leaves on the defoliated plants were much darker green than on the control plants. In 1974 heavy rains promoted a higher incidence of halo blight in the defoliated treatments, which did not occur in the drier growing season of 1975. Averaged over N levels, removing 3 leaves 1, 2, or 3 times reduced yields by 8%, 50%, and 63% in 1974 and by 3%, 10%, andst12vp10 43% in 1975, respectively. Reduced leaf area was blamed for a shortage of carbohydrates which increased pod abortion and decreased individual seed weight, lowering seed yield (33).

Other researchers pinched all buds from 'K-2809' cowpea plants with 6 trifoliate leaves, the youngest 2 not fully expanded, and removed various leaves. Removing the 4 oldest leaves, which reduced leaf area by 86%, reduced subsequent weight gain by only 45%, and expansion of new leaf area by only 3%. Selective removal of young leaves had a much more drastic effect. Taking off the 2 youngest leaves decreased the new leaf area by fully 90%. Removing only the youngest leaf reduced new leaf area by just 34% because the second youngest leaf was able to compensate. Weight gain was also seriously affected. Removing the 1, 2, 3, or 4 youngest leaves, which reduced the existing leaf area by only 10%, 17%, 39% and 59% respectively, decreased the weight increment compared to the control by 5%, 45%, 54%, and 81%. The loss of the 2 youngest leaves affected plant weight as much as the loss of the 4 oldest leaves, although the loss of leaf area was 17% compared with 86%. Fully expanded leaves which were only 2-3 weeks old made very little contribution to growth, implying that the photosynthetic capacity of the cowpea leaf is rather short-lived. They hypothesized that leaves would endure less time in the field with the added stresses from insects, wind damage, and tropical heat. They further speculated that under certain conditions removing old leaves could increase growth and yield by improving the distribution of endogenous hormones (60).

Defoliating 'K-2809' cowpeas at first flower by removing the oldest 80% of trifoliate leaves gave the same yield reduction (60%) as taking off the youngest 50% of the leaves. On the average, 50% defoliation was twice as deleterious to yield when biased to young leaves rather than old leaves (115).

Removing cowpea leaves or parts of leaves that have been fully expanded for about 2 weeks was seen as unlikely to significantly affect growth or yield. Losing parts of young leaves would likewise have no major effect since compensating expansion would occur. However, selectively removing several young leaves from a single shoot would drastically reduce future growth, impairing the seed production by stunting the plant (60).

In 'Mezed' cowpea, removing all young leaves produced after flowering lowered yield by 16%. Taking off the 4 or 5 oldest leaves (which subtended branches) raised yield by 22%. The presence of old leaves after flowering appeared to depress yield, since their removal raised yield. The net contribution of such leaves may be minimal or negative (39).

Leaves of annuals show declining photosynthetic rates with age, so the oldest ones would contribute little as they continued to respire carbohydrates. Leaves in warm climates reach maturity and senesce more rapidly than in cooler environments. Finally, cowpeas typically have a dense canopy which shades the lower older leaves, further retarding photosynthesis (39).

In 3-week-old bean plants, it made no difference if the upper or lower leaves were selectively removed. Later in the season, yields were reduced less when older lower leaves were removed than when younger leaves were taken (133).

Photosynthetic efficiency of different zones of the bean plant was analyzed by selectively defoliating zones A (top 1/3, youngest), B (middle 1/3), and C (bottom 1/3, oldest) in all possible combinations (table 9). Cultivar '373' was grown in Malawi and treated by pinching off the petiole by hand, at 21 and at 35 days from planting (34).
Zone B was the most efficient single zone and zone C was the least efficient. This was attributed to age and the fact that zone C had the least light. Plants treated at 35 days produced new leaves at a slower rate and had much less time to recover before leaf growth ceased (34).

Defoliations at 21 days removed fewer leaves than at 35 days, and the height and number of leaves would have increased proportionally more after the early treatment. All defoliations at 21 days removed leaves that probably would have been located in zone C at maturity. This would give an added advantage by reducing the number of parasitic leaves in zone C. The only treatment at 35 days which surpassed the effect at 21 days was the defoliation of zone C alone, which left fewer leaves in zone

Table 9. Seed yields expressed as percentage of the control resulting from defoliation of zones A (upper 1/3), B (middle 1/3), and C (lower 1/3) in bean cv. '373' at 2 growth stages (34).

Zones		Yield as percentage of control		
Defoliated	Intact	21 Days	35 Days	Mean
A	BC	115%	89%	102%
B	AC	103%	78%	91%
C	AB	109%	116%	113%
AB	C	91%	50%	70%
AC	B	125%	101%	114%
BC	A	95%	68%	81%
ABC	None	54%	30%	42%
Mean		99%	76%	----

C at maturity than the earlier treatment. The only combinations that augmented yield at both dates (and gave the highest average increases) involved removing zone C and leaving the most efficient zone B intact (table 9) (34).

All researchers found the lowest (oldest) leaves to be the least valuable to the plant. Actual increases in yield following removal of the oldest leaves have been reported (34, 39). When old leaves lose so much of their photosynthetic ability or become so shaded that the amount of carbohydrate they produce is less than that needed to keep them alive, they become parasitic. Apparently, the only functions they provide are the storage of N for future translocation to the seeds, and acting as spare leaves in case something destroys the upper foliage. When the top of the plant is removed, remaining old leaves can rejuvenate and return to peak production (107, 128, 132). If the hormones responsible for rejuvenating old leaves act to stimulate photosynthesis in leaves generally, then per leaf production of carbohydrates should increase after partial defoliation, regardless of age. Under normal conditions, it appears that removing the correct number of old leaves at the right time will increase yield.

Effects of plant size on seed yield

Larger plants, whether influenced by growing conditions or heredity, should have a higher threshold level for damage before seed yield decreases since they have greater reserves and leaf areas. For example, indeterminate bean cultivars may tolerate more defoliation than determinate cultivars. The same leaf removal treatment (not described) lowered yield in a determinate bean by 22% and 41% when done once or twice. In an indeterminate cultivar, defoliation 1, 2, or 3 times reduced yield by 12%, 20%, and 34%, respectively (33). However, after comparing yield losses from identical treatments in 2 determinate and 2 indeterminate bean cultivars, it was concluded that defoliation tolerance bears no relation to growth habit. Instead, leaf size, number, and orientation appeared to determine the level of tolerance to defoliation (130).

In 'Michelite' beans the correlation between seed weight and "straw" weight was highly significant in 14 of 18 trials. The components of "straw" were not indicated, nor how dry it was when weighed, but these results support the view that seed yield is related to plant size (25).

Bean yields are often limited, especially in determinate cultivars, by too few nodes on the plant, and poor leaf area development and duration. These attributes result from early flowering and curtailment of vegetative growth (51). In cowpeas, the number of leaves, peduncles, and pods are related to the number of nodes on the plant, which all vary directly with total plant weight (116).

In 20 determinate cowpea accessions, growth rate and size before flowering had little effect on seed yield. Seed yield per pod, and harvest index, did not vary with plant size and varied little within genotypes. Thus, seed yield is related to above-ground biomass at maturity, but not during vegetative stages.

This explains the much lower sensitivity to defoliation in younger plants (63).

Compensatory growth following defoliation

Compensatory leaf expansion has been observed in defoliated bean plants. All leaves above the first trifoliate were removed as they emerged, so that only 1 leaf was allowed to expand. The control plants were not defoliated. All measurements were taken on the center leaflet of the first trifoliate. Leaf area expanded throughout the sampling period giving a final area about 50% greater than the control. The dry weight increase was continuous but even more dramatic, so that the weight per unit of area was about 2/3 greater. At the end of the experiment (45 days) the leaflets' mean dry weights were 150% above the control's. Defoliation also increased the photosynthetic rate in this experiment (5).

Defoliated Vigna mungo plants compensated for foliar loss by growing new leaves, increasing areas of remaining leaflets, and increasing photosynthetic rates in remaining leaves (98).

Pruning the side shoots from cowpea plants before they produced leaves increased leaf size and number on the main stem. Total yield decreased slightly, but greater reproductive efficiency resulted (38).

When 'Harzgruss' bean seedlings were decapitated by removing all buds above the primary leaves 15 days after sowing, the primary leaf area and chlorophyll concentration continued increasing until 24 days, 15 days longer than in the control (110).

Summary and conclusions

The effect of defoliation on seed yield in annual legumes such as bean and cowpea depends on the growth stage, and the quantity and age of the leaves. Minor defoliation does not cause significant yield reduction, but the threshold level is lower after anthesis. Lost leaf area can be replaced during vegetative growth by expansion of both remaining and new leaves, but after flowering the necessary resources are diverted to reproduction, preventing compensatory growth. Increased rates of photosynthesis in leaves remaining after defoliation result in compensation even without restored leaf area.

Continued production of carbohydrates during the reproductive stage is vital for high seed yields, to feed the symbiotic N-fixing bacteria in the root nodules and also to fill the seeds. Leaf removal while pods and seeds are forming is the most damaging to yield, but as the seeds approach maturity they become less vulnerable. Stored carbohydrates and N are exported from stems and leaves to the growing seeds, so defoliation late in the reproductive stage is relatively harmless; the nutrients are already in the seeds and the leaves will soon abscise.

When nutrients are insufficient for all the potential seeds to mature, the source-sink ratio is adjusted by aborting flowers, young pods, and young seeds. Individual seed weight is reduced only if these actions fail to restore a balance.

High planting densities and/or moisture stress will reduce plant size but increase harvest index. Adding N fertilizer to nodulated cowpea plants can increase size but not harvest index, and may even promote vegetative growth at the expense of seeds.

Larger plant size, which increases storage capacity and leaf area, generally increases seed yield. However, not all leaves make a positive contribution to yield. Photosynthetic capacity declines with age and shading reduces illumination so that lower leaves become parasitic. Removing the oldest leaves can increase seed yield by reducing carbohydrate losses to respiration, and possibly also by improving efficiency of fuctional leaves through increased hormone supplies. Endogenous hormones, possibly cytokinins produced in the roots, may regulate photosynthesis and senescence in bean and cowpea leaves. Leaf functions apparently depend on the total hormone supply per leaf, since both defoliation and applied hormones rejuvenate old leaves.

Additional leaves beyond a leaf area index of about 3 are surplus in cowpea. Their cost in carbohydrates and hormones may exceed their value as storage organs. Under drought conditions they promote wilting and hinder photosynthesis until shedding restores a balance between uptake and transpiration. If excess leaves were harvested the moisture stress could be relieved more rapidly.

To maximize the harvest of edible bean or cowpea leaves without significantly reducing the yield of seeds, defoliation must be performed early and lightly enough (generally 33% or less) for the plant to recover before vegetative growth ceases. The older lower leaves should be selected because they will be shaded later and will contribute less to yield. Although a greater number of old inactive leaves could be picked later in the life cycle, which would probably increase the seed yield as well, such leaves would be too fibrous for eating.

MATERIALS AND METHODS

The Cultivars

'Vita 7' is a hybrid from Nigeria, and has narrow leaves typical of many traditional cultivars in Nigeria, where leaves are not eaten except in the far north. Leaves are commonly eaten in Botswana, where cultivars generally have wide leaves. The 2 traditional Botswanan cultivars tested, 'B-138' and 'B-162', have unusually large leaves, which speed the harvest of single leaves by hand. An improved cultivar from Nigeria with equally large leaves, 'TVu-1948', was also tested. The other 2 improved Nigerian selections, 'TVu-3662' and 'Vita 5', have small leaves on smaller plants and a more compact habit than the others, which are trailing types. All the Nigerian types were bred at the International Institute for Tropical Agriculture, while the Botswanan cultivars were collected from peasant farmers for a germplasm project assisted by Colorado State University.

Experimental Design

The treatments were applied as a 6 x 2 x 4 factorial in a split plot design with 6 blocks. Cultivars were the main plots; apex removal at 28 days and leaf harvest method were the subplots. The experimental unit was 1 plant. Leaf harvest methods were: the control, with no leaves removed; multiple harvest with weekly removal of 1 or 2 leaves from each stem (the 3rd and 4th fully expanded leaves counted from the apex) starting at 35 days and continuing for 4-6 weeks depending on the cultivar; single harvest with removal of all leaves from all stems down to the 3rd or if possible 4th fully expanded leaf at or soon after anthesis for each cultivar (46-60 days after planting); pruning, which was identical to the single harvest except that it also removed the stem just below the lowest leaf picked, to represent a more rapid harvesting process. Leaves on stems with only 1 or 2 fully expanded leaves were not harvested under any treatment. The multiple harvest procedure was based on the method reported by Mehta (82).

Growing conditions

The experiment was conducted in a greenhouse at Michigan State University. Day temperatures were usually 28-38^{o}C and night temperatures 18-22^{o}C, with an extreme range of 13-48^{o}C. Seeds were sown May 31, 1985, in Bacto potting mix in flats with compartments 2.5 by 5.0 cm. Seedlings emerged in 3 days after planting. At the 2-3 trifoliate leaf stage (21 days), seedlings were transplanted to 25 cm diameter 8 liter black plastic pots. The media was 60% peat moss, 20% vermiculite, and 20% sterilized sand.

Before transplanting, the seedlings grew under the natural photoperiod of 15 hr. After transplanting, day length was limited to 13 hr by shading with black cloth.

Each plant was allowed .18 m^2 of space, or 5.7 plants/m^2. Trailing branches that grew over other plants or beyond the edge of the greenhouse bench were tied to vertical stakes.

The cowpeas were not inoculated with rhizobial culture, but were uniformly given 20-20-20 and 20-5-30 N-P-K fertilizer. The total amounts per plant were 1.80 g N, 0.46 g P, and 1.91 g K. These amounts are equivalent to 102 kg/ha N, 26 kg/ha P, and 108 kg/ha K.

The plants were treated with Malathion, nicotine smoke, Orthene, and Pentac, about every 2 weeks to control thrips and two-spotted spider mites.

Least significant differences at 1% and 5% levels were calculated with the analysis of variance in the "Factor" subroutine of the MSTAT microcomputer software program.

Leaf measurements

Changes in leaf area were calculated weekly by recording length and width for each leaflet on each trifoliate on each of the 48 plants in block 1. The areas of all leaves in block 1 were measured on a LI-COR leaf area meter, either when harvested, upon abscission, or at the end of the season when the plants were dismembered for weighing.

The product of the length and maximum width measurements of the center leaflet (LxW) of the trifoliate cowpea leaf is a useful indicator of leaf area (95). The LxW products were added together for each plant, and the total was divided by the leaf area measured on the LI-COR meter for those same trifoliates. This gave a ratio (generally between 0.4 and 0.6) of LxW to actual area, which was unique for each plant. Then LxW for each leaf was divided by this ratio to give an estimate of each trifoliate leaf's area. From the weekly measurements the number and estimated areas of leaves on each plant could be calculated for all leaf harvest dates.

The actual leaf area recorded from each harvest was divided by the estimated area of the mature leaves on the plant at the time, giving a defoliation percentage (DP)(table 10). With multiple harvests, each plant had 4-6 separate DPs, plus a cumulative DP (representing the proportion of leaf area removed in all harvests, not counting leaves produced after the last harvest). In cases where the single and pruning harvests were conducted 3 or more days after the newest mature leaves were last measured, the estimated areas for the leaves measured the next week (if any) were assumed to have been present at harvest time, and were included in the calculations. Leaflet length and width measurements were always recorded the same or next day after the multiple harvests, providing more accurate estimates for this treatment.

Because of the variability of the small samples, DP averages for all 6 blocks were estimated (table 11). Harvested leaf areas from the other blocks were assigned DPs according to the proportions in block 1, and the 6 DPs were averaged. It was assumed that all plants of the same cultivar and harvest treatment had the same total leaf area at the same time. Because single harvest and pruning treatments used the same procedure to select leaves for harvest, at the same time, their estimated average DPs were combined.

Weighing

Leaf and stem samples were sealed in plastic bags and refrigerated upon harvest to avoid weight losses. After fresh weight and leaf area were measured, samples were placed in a

Table 10. Defoliation percentages for each of the multiple leaf harvests, and cumulative total defoliation percentages for multiple, single and pruning leaf harvest methods, as measured for each of the plants in block 1.

		Harvest number						Cumulative totals		
Cultivar	Apex	1	2	3	4	5	6	Multi	Single	Pruned
B138	+	26	12	31	45			64	86	66
B138	-	20	9	45	0			45	92	95
B162	+	38	31	38	37	30		76	58	53
B162	-	18	13	42	44	36		70	59	72
TVu3662	+	19	32	39	56			79	61	60
TVu3662	-	10	30	34	50			73	61	64
TVu1948	+	29	34	15	47	53	41	85	66	64
TVu1948	-	28	21	50	32	49	54	88	--	--
Vita 5	+	15	19	49	34			77	81	71
Vita 5	-	9	30	58	46			78	73	78
Vita 7	+	24	22	33	40	20	20	72	55	45
Vita 7	-	19	22	30	35	31	16	77	66	40

+ = apex intact, - = apex removed at 28 days.

Table 11. Estimated defoliation percentages for leaf harvest methods, averaged from all blocks.

	Harvest number						Cumulative totals	
Cultivar	1	2	3	4	5	6	Multi	S & P[z]
B138	21	14	29	29			56	85
B162	29	22	32	37	35		69	60
TVu3662	16	29	36	46			71	60
TVu1948	30	20	44	35	37	45	80	70
Vita 5	14	19	39	51			73	75
Vita 7	22	27	27	33	27	25	77	50

[z] Single and pruning harvest methods had the same procedure for selecting the leaves to be harvested, so they have the same estimated average defoliation percentages for each cultivar.

drying oven at 60°C for at least 4 days until constant weight was reached. At the end of the season when all pods on a plant were dry, the seeds were removed. The husks, abscised parts, and all remaining vegetative parts were then oven-dried. In order to maintain viability, the seed was air-dried. Based on samples that had been pulverized and oven-dried, the dry weight of the seeds was calculated at 90% of the air-dry weight. A factor of 56.5 was used to convert g/plant weights to kg/ha.

Seed weight (yield) and pod number per plant were measured for all 6 blocks. Weight per seed was determined for 4 blocks by counting and weighing 50 seeds from each plant.

Missing data

Chipmunks ate some seeds and pods at maturity. To estimate the weights of the missing seeds and pod husks, the average weights of seeds and husks were calculated for intact plants in each of the 24 cultivar by harvest method combinations. The numbers of missing pods on the plants were multiplied by these averages, and the products were added to the weights of the remaining pod husks and seeds.

RESULTS

Harvest index for leaves, seeds, and total edible products

Harvest index as discussed here is the percentage of the plant's above-ground dry weight (not including the parts that abscised before harvest) that was harvested as edible. Although the stems removed in the pruning treatment and the harvested leaves were absent at the end of the experiment, they are included in the plant's total weight. The harvest index does not indicate that the remainder of the plant is useless or is never harvested for fodder, but only that it is not harvested for human food.

For edible leaves, harvest index values ranged from 14-30%, and both extremes were reached by 'Vita 7' (table 12). Apex removal generally caused no change or gave a higher harvest index, but caused decreases in 'TVu-3662'. Multiple harvest gave the highest efficiency of leaf production in most cultivars, but the lowest efficiency in 'B-138'. 'TVu-3662' showed no response to leaf harvest method.

The average harvest index for seeds was 36% for the controls, 27% for multiple and single harvests, and 22% for pruning. 'TVu-3662' had the highest efficiency, with 52% in the control (table 13). 'Vita 7' had the lowest measurement, with 15% for pruning. 'Vita 5' required a longer time to mature the pods on the new growth produced after pruning, resulting in its improved efficiency for that treatment.

The harvest index for both products was increased by multiple and single harvest treatments in all cultivars (table 14). The effect of pruning was either positive or negative, depending on the cultivar. The greatest responses were seen in 'Vita 5' and the smallest in 'TVu-3662'. Cultivars with a low harvest index in the control group showed the most improvement from leaf harvesting. The differences between the harvest treatments were unusually large for 'Vita 7'. 'TVu-3662'

Table 12. The effect of cultivar, apex removal, and leaf harvest method on the harvest index for leaves (edible leaf wt/total wt, x 100).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Multi	15	24	23	25	20	30
Apex cut	15	24	21	27	21	28
Single	19	18	25	21	18	15
Apex cut	19	25	20	23	18	17
Pruned	14	17	23	18	18	14
Apex cut	21	20	22	21	18	16

LSD for means in the same row or column	
5%	3
1%	4

Table 13. The effect of cultivar, apex removal, and leaf harvest method on the harvest index for seeds (seed wt/total wt, x 100).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	35	40	51	38	23	28
Apex cut	37	48	52	33	27	27
Multi	30	29	36	29	20	20
Apex cut	29	29	38	25	20	22
Single	27	32	33	28	21	24
Apex cut	28	29	34	22	24	23
Pruned	27	24	23	18	27	15
Apex cut	23	21	26	20	23	16

LSD for means in the same row or column

5%	5
1%	6

Table 14. The effect of cultivar and leaf harvest method on the harvest index for edible products (seed wt + harvested leaves wt/total wt, x 100).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	36	44	51	36	25	27
Multi	44	53	59	53	41	50
Single	46	51	55	47	40	40
Pruned	42	41	47	38	44	30

LSD for means in the same row or column	
5%	5
1%	6

had the highest harvest index in all treatments, but had the lowest above-ground dry weight in the control.

Edible products yield

All leaf harvesting treatments yielded more than the control, except in TVu-3662 with single harvest and pruning, and TVu-1948 with pruning (table 15). The dry weight of edible products was highest with multiple harvests in all cultivars. All leaf harvest methods lowered seed yield, but increased the yield of edible products an average of 4% for pruning, 18% for single harvest, and 36% for multiple harvest. In 'Vita 7', multiple harvest almost doubled the control yield. The seed yields in the controls ranged from 700-1220 kg/ha, while the maximum seed and leaf yield was 1690 kg/ha (table 16).

The yield per square meter per day is the total seed and leaf yield divided by the length of the growing season. It is an average rate for the entire season and not the same figure for each day. The season length was recorded for each individual plant, being the number of days required to dry all the pods. Multiple harvests gave the highest yield in all cultivars, with 'TVu-1948' and 'Vita 7' yielding above 2.0 g/m2/day (table 17). Pruning gave the lowest yields in 4 cultivars, and the control was lowest in 'Vita 5' and 'Vita 7'. The low values in the pruning treatment were due to both reduced yields and more days.

Seed yield

All leaf harvest treatments reduced seed yield (table 18). Multiple harvest decreased seed yield the least for 3 cultivars,

Table 15. The effect of cultivar and leaf harvest method on the dry weight of edible products (seeds and leaves combined) (g/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	21.1	20.9	21.6	19.8	12.4	15.6
Multi	25.8	26.4	22.1	28.9	18.5	30.0
Single	24.0	25.0	20.9	22.9	15.4	23.1
Pruned	21.9	22.2	19.1	19.7	16.0	18.0

LSD for means in the same row or column

5%	2.1
1%	2.8

Table 16. The effect of cultivar and leaf harvest method on the dry weight of edible products (seeds and leaves combined) (metric tons/hectare).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	1.19	1.18	1.22	1.12	0.70	0.88
Multi	1.46	1.49	1.25	1.63	1.05	1.69
Single	1.36	1.41	1.18	1.29	0.87	1.31
Pruned	1.23	1.26	1.08	1.11	0.90	1.01

LSD for means in the same row or column	
5%	0.12
1%	0.16

Table 17. The effect of cultivar and leaf harvest method on the daily dry weight production rate of edible products (seeds and leaves combined) ($g/m^2/day$).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	1.57	1.53	1.56	1.43	0.93	1.11
Multi	1.92	1.92	1.62	2.14	1.35	2.12
Single	1.74	1.82	1.53	1.68	1.10	1.65
Pruned	1.46	1.48	1.41	1.29	1.07	1.20

LSD for means in the same row or column	
5%	.15
1%	.20

Table 18. The effect of cultivar and leaf harvest method on the estimated seed yield (g dry weight/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	21.1	20.9	21.6	19.8	12.4	15.6
Multi	17.1	14.4	13.9	14.6	9.1	12.7
Single	14.3	14.8	12.6	12.3	8.6	13.6
Pruned	12.9	12.4	10.0	9.6	9.5	9.3

LSD for means in the same row or column	
5%	1.9
1%	2.5

and was close behind another treatment for the other 3. Apex removal had a minor effect on seed yield on the average, but gave some large changes in yield depending on the cultivar and harvest treatment (table 19). Because of chipmunk damage, the averages include some estimates.

Components of seed yield

Generally, the controls had the highest numbers of peduncles with pods (table 20). Pruning reduced seed yield due to fewer peduncles on the stems that remained. Usually all peduncles on the pruned plants had mature pods, while in the other treatments all pods aborted on the younger outermost peduncles which bloomed last.

All treatments reduced the number of pods per plant (table 21). Generally, pruning gave the greatest losses and multiple harvest the least.

The harvest treatments generally increased seed number per pod, except for 'TVu-1948' (table 22). Extreme increases of over 10% were associated with the largest reductions in pod number. This inverse relationship was not observed in 'B-138', where seeds per pod was remarkably stable, nor in 'TVu-1948', where both pod and seed numbers declined.

Multiple and single harvest always reduced the weight per seed, but pruning increased it in 3 of the cultivars (table 23). The weight per seed declined an average of 9% in response to multiple and single harvests, and dropped 1% with pruning.

Table 19. The effect of cultivar and leaf harvest method on the percent change in seed yield with apex removal compared to apex intact.

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	1	21	0	-14	21	-11
Multi	2	9	7	-14	2	15
Single	3	-25	16	-22	20	-2
Pruned	-16	-9	10	13	-23	10

Table 20. The effect of cultivar and leaf harvest method on the number of pod-bearing peduncles per plant.

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	12.9	12.5	15.8	10.6	9.3	10.4
Multi	11.9	10.8	12.4	10.1	8.3	9.3
Single	11.2	9.3	10.9	10.4	6.0	10.5
Pruned	6.9	6.1	8.0	6.1	6.3	4.9

LSD for means in the same row or column

5%	1.6
1%	2.2

Table 21. The effect of cultivar and leaf harvest method on the number of pods per plant.

Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
	Cultivars					
Control	13.6	20.3	25.8	14.1	14.6	11.9
Multi	12.4	15.0	18.9	12.1	12.8	10.9
Single	11.6	13.1	16.4	12.8	8.9	11.3
Pruned	8.6	9.3	13.3	8.2	9.4	6.3

LSD for means in the same row or column

5%	2.0
1%	2.7

Table 22. The effect of cultivar and leaf harvest method on the number of seeds per pod.

Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
	Cultivars					
Control	14.2	6.9	8.7	11.7	7.8	9.1
Multi	14.8	7.1	9.0	11.6	7.0	9.4
Single	14.1	8.6	9.0	9.8	8.3	9.6
Pruned	14.3	9.5	10.1	9.9	8.6	10.1

LSD for means in the same row or column

5%	1.6
1%	2.2

Table 23. The effect of cultivar and leaf harvest method on the dry weight per 100 seeds (g/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	10.63	15.12	9.26	11.99	11.49	14.62
Multi	9.70	13.76	8.57	10.73	11.20	12.80
Single	9.12	13.80	8.45	10.36	11.38	13.13
Pruned	10.17	15.48	8.42	12.40	11.73	14.03

LSD for means in the same row or column

5%	0.75
1%	1.04

Relationships between components of seed yield

The seed yield losses resulting from all 3 harvest treatments were mainly due to a reduction in pod number. Seed number per pod was usually the same or higher than the control, except in 'TVu-1948'. Weight per seed usually changed little, and always declined except in the pruning treatment. Yield losses in 'B-138' and 'Vita 7' with multiple and single harvests were about equally due to fewer pods and to reduced weight per seed (table 24). The percentages of control yield shown in table 21 were based on all 6 blocks, and do not always agree with the products of the 3 components which are the means of 4 blocks.

Leaf growth, abscission, and harvest

Except for 'Vita 5', all cultivars produced new leaves to replace those harvested (table 25). 'Vita 5' and 'TVu-3662' both have a distinctly determinate habit, so their growth type is a poor indicator of suitability for leaf harvest.

Apex removal resulted in 20% higher dry weight of abscised leaves, but it was 65% and 69% higher for 'B-138' and 'B-162', respectively (table 26). The trend was reversed for 'Vita 5' (16% lower). The control group had more abscised leaves than any of the treatments, except in 'TVu-1948' with apex removed, where the weight was 77% higher in the pruned treatment. After the control, pruned plants dropped the most leaves, which was due to delayed blooming and ripening of the last pods. During the longer season, more leaves senesced. Removing the ends of the stems in this treatment also deprived the plants of an important reserve of mobilizable nutrients, so more had to be translocated

Table 24. The effect of cultivar on components of yield for the controls, and on the percentage of each cultivar's control values for the leaf harvest methods.

			Cultivars			
Control	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Yield (g/plant)	21.1	20.9	21.6	19.8	12.4	15.6
Pods/plant	13.6	20.3	25.9	14.1	14.6	11.9
Seeds/pod	14.2	6.9	8.7	11.7	7.8	9.1
100 S Wt(g/plant)	10.63	15.12	9.26	11.99	11.49	14.62
Multi		% of control				
Yield	81	69	64	74	73	82
Pods/plant	91	74	73	86	87	92
Seeds/pod	104	102	103	98	90	103
100 Seed Wt	91	91	93	89	97	88
Single		% of control				
Yield	68	71	58	62	69	89
Pods/plant	85	65	64	91	61	94
Seeds/pod	99	123	103	83	106	105
100 Seed Wt	86	91	91	86	99	90
Pruned		% of control				
Yield	61	59	46	48	76	60
Pods/plant	63	46	52	58	65	52
Seeds/pod	101	136	116	84	111	111
100 Seed Wt	96	102	91	103	102	96

Table 25. The effect of cultivar and leaf harvest method on the dry weight of all leaves (harvested, abscised, and remaining) (g/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	12.54	10.63	9.70	13.86	15.17	16.82
Multi	17.06	17.03	12.09	19.03	16.92	23.26
Single	17.01	17.41	14.22	17.98	14.06	19.28
Pruned	17.06	18.20	14.81	20.47	13.43	21.41

LSD for means in the same row or column

5%	1.45
1%	1.92

Table 26. The effect of cultivar, apex removal, and leaf harvest method on the dry weight of senesced abscised leaves (g/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	2.62	4.79	6.59	5.80	1.85	6.80
Apex cut	3.75	8.64	6.57	3.97	1.68	7.87
Multi	0.88	1.18	2.08	0.99	0.26	1.83
Apex cut	0.80	1.60	2.14	0.72	0.40	1.64
Single	0.29	2.19	3.21	1.80	0.92	3.90
Apex cut	1.32	3.40	3.48	1.66	0.27	3.58
Pruned	1.09	2.86	1.76	4.35	1.24	4.30
Apex cut	2.16	4.98	2.09	7.04	1.25	5.25

LSD for means in the same row or column

5%	1.72
1%	2.27

out of leaves, also increasing senescence. The dry weight of abscised leaves was generally least in the multiple harvest treatment because fewer leaves remained on the plants and proportionally fewer senesced during podfilling.

'Vita 5' dropped a very small proportion of its leaves and remained vigorous after the pods ripened, which matches previous observations of this cultivar in the greenhouse. In a preliminary trial of 130 days, 'Vita 5' plants produced 3 progressively smaller crops of pods with very little senescence of the oldest leaves. New growth after each crop was overwhelmingly reproductive, with only a few small leaves. The plants may have produced more crops of pods, but they had to be disposed of because of spider mite infestation.

On the average, apex removal increased both the number (table 27) and dry weight (table 28) of harvested leaves by 7%. In general, multi-harvest was most productive and pruning was least productive, with the yield directly related to the amount of labor required for picking. The decision of which harvesting practice to use thus depends on local economic factors. The number and/or dry weight of harvested leaves in the multi-harvest treatment reached a peak 2 weeks before vegetative growth ceased in each of the cultivars. This characteristic may be useful in scheduling farming operations, as it could predict how much longer the leaf harvesting season will continue.

The harvested leaf area was 9% greater on the average with apex removal, but increased 22% in 'B-162' and declined 8% in 'TVu-3662' (table 30). Multiple harvest averaged 24% above the

Table 27. The effect of cultivar and leaf harvest method on the mean number of leaves harvested, with means for each of the multiple harvests.

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	0	0	0	0	0	0
Apex cut	0	0	0	0	0	0
Multi	12.5	15.5	26.7	26.5	20.5	40.3
Apex cut	12.7	19.5	25.7	30.8	22.3	40.8
Single	14.3	12.2	22.5	20.5	17.5	22.3
Apex cut	16.7	14.5	19.8	20.5	19.8	26.2
Pruned	11.7	11.0	24.2	18.8	19.5	23.2
Apex cut	16.8	15.5	21.2	21.2	16.0	24.7

LSD for means in the same row or column

5%	2.7
1%	3.6

Each harvest	B138	B162	TVU3662	TVU1948	VITA5	VITA7
1st	2.0	2.0	2.2	2.0	2.1	2.0
2nd	1.4	1.6	7.3	2.8	3.8	5.2
3rd	5.2	4.8	9.2	6.4	7.8	7.7
4th	4.0	4.8	7.6	5.8	6.3	8.3
5th	0	4.3	0	6.1	0	8.9
6th	0	0	0	5.6	0	5.3

Table 28. The effect of cultivar and leaf harvest method on the dry weight of harvested leaves (g/plant), with means for each of the multiple harvests.

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	0	0	0	0	0	0
Multi	8.70	12.01	8.18	14.27	9.42	17.24
Single	9.66	10.20	8.34	10.61	6.74	9.26
Pruned	8.94	9.86	9.10	10.14	6.54	8.68
LSD for means in the same row or column						
5%			1.10			
1%			1.46			
Each harvest						
1st	0.83	0.78	0.49	0.94	0.56	0.72
2nd	1.24	1.50	1.54	1.41	1.54	1.83
3rd	3.28	3.02	3.19	2.90	3.75	3.12
4th	3.36	3.40	2.96	3.21	3.57	4.22
5th	0	3.31	0	3.48	0	4.38
6th	0	0	0	2.33	0	2.95

Table 29. The effect of cultivar and leaf harvest method on the total area of harvested leaves (m^2/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Single	.257	.234	.216	.326	.191	.261
Apex cut	.289	.301	.206	.357	.201	.319
Pruned	.220	.216	.245	.322	.202	.265
Apex cut	.302	.310	.211	.361	.171	.292
Multi	.221	.343	.246	.428	.217	.466
Apex cut	.208	.355	.237	.470	.237	.476
LSD for means in the same row or column						
5%			.037			
1%			.049			
Each harvest						
1	.024	.029	.015	.033	.017	.025
2	.032	.045	.050	.047	.045	.058
3	.086	.105	.100	.106	.093	.103
4	.073	.096	.077	.099	.072	.111
5	0	.074	0	.093	0	.101
6	0	0	0	.070	0	.073

mean of the other 2 harvest methods, which were very close, but was 66% higher in 'Vita 7' and 20% lower in 'B-138'.

Weight of various above ground plant parts

Because pod and seed weights had to be reconstructed for some plants, the averages for total above-ground plant dry weight also include estimates. Only in 'B 162' and 'Vita 7' did a treatment (pruning) give a higher weight than the control (table 30). The differences between treatments were less for these 2 cultivars. Beyond the general superiority of the control, there was no clear pattern for harvest treatments. 'Vita 7' had the greatest weight in every treatment, which resulted from a longer period of vegetative growth. 'TVu-3662' and 'Vita 5' had the least weight, due to their compact bushy growth habit and shorter period of vegetative growth.

Pod husk weight was estimated for some plants because of chipmunk damage, but was highest in the control and lowest with pruning for all cultivars (table 31). Weight was higher for multiple harvest than for single harvest except with 'Vita 7'.

All cultivars except 'B-138' and 'Vita 5' produced new stems to compensate for the pruned branches. Stem and petiole weight was higher in the control than for multiple and single harvest treatments, because of impaired vegetative growth and/or because of greater translocation of reserves from stems to compensate for fewer remaining leaves (table 32).

Table 30. The effect of cultivar and leaf harvest method on the estimated dry weight of all the above ground plant parts (g/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	62.6	54.5	49.3	60.3	52.4	64.4
Multi	59.5	51.7	40.2	55.2	46.0	62.1
Single	53.1	52.1	41.5	50.9	39.3	62.4
Pruned	53.6	58.3	42.8	57.5	38.0	64.8

LSD for means in the same row or column

5%	3.7
1%	4.8

Table 31. The effect of cultivar and leaf harvest method on the estimated dry weight of pod husks (g/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	7.2	5.4	4.3	6.4	3.7	5.0
Multi	6.2	4.2	3.1	5.0	2.9	4.3
Single	5.1	3.9	2.8	4.3	2.7	4.6
Pruned	4.8	3.2	2.5	3.5	2.9	3.4

LSD for means in the same row or column

5%	0.6
1%	0.8

Table 32. The effect of cultivar and leaf harvest method on the dry weight of stems and petioles (g/plant).

	Cultivars					
Method	B138	B162	TVU3662	TVU1948	VITA5	VITA7
Control	21.67	17.40	13.44	20.26	20.98	27.07
Multi	19.13	15.92	10.76	16.64	16.94	21.66
Single	16.56	15.75	11.49	16.30	13.87	24.60
Pruned	18.84	24.48	15.37	23.92	12.19	30.65

LSD for means in the same row or column

5%	1.78
1%	2.36

Days to first flower, first dry pod, and to ripen and dry all pods

The overall average date of flowering was 50.9 days after planting, with a range of 45-71 days. Most cultivars averaged 49.4-50.9 days, except 'Vita 7' with 55.0 days (table 33). The harvest treatments made little difference.

The pruning treatment delayed the first dry pod by 4.2 days, but multiple and single harvests had no effect (table 33). The overall average first dry pod date was 69.5 days after planting, with a range of 62-92 days.

While the other harvest treatments varied from the control by less than 1 day, pruning delayed ripening of the last pod by 6.6 days (table 33). This was because some of the pruned plants produced new branches, on which flowers formed. The resulting pods ripened much later. The overall average was 79.2 days after planting, with a range of 73-99 days.

DISCUSSION AND CONCLUSIONS

Effects of cultivars

The dry weights of all plant parts were affected by leaf harvest methods and cultivar differences. Apex removal affected harvested leaf weight, number, and harvest index, and weight of abscised leaves. The cultivars did not react similarly to treatments, except for apex removal.

Table 33. The effect of cultivar (averaged across treatments) and leaf harvest method (averaged across cultivars) on number of days between planting and anthesis, first dry pod, and last dry pod.

	Number of days from planting		
Cultivar	Anthesis	1st Pod	Last Pod
B138	50.1	67.3	78.8
B162	50.9	69.4	79.3
TVu3662	50.5	69.6	77.2
TVu1948	49.5	70.9	79.7
Vita 5	49.4	67.4	79.3
Vita 7	55.0	72.8	80.9
LSD for cultivars			
5%	1.3	1.4	2.3
1%	1.7	1.9	3.1
Leaf harvest method			
Control	50.7	68.5	77.4
Multi	50.7	68.5	77.4
Single	50.3	68.5	78.1
Pruned	51.9	72.7	84.0
LSD for leaf harvest methods			
5%	0.8	1.1	1.5
1%	1.1	1.4	2.0

Of the 6 cultivars tested, 'Vita 5' was the least responsive to treatments. It had a shorter period of vegetative growth, did not produce more leaf or stem material to replace what had been removed, and did not allow many leaves to abscise. 'Vita 5' had the lowest seed yield, seed harvest index, and edible harvest index in the control and multiple and single harvest treatments. It also had the lowest leaf yield with pruning and single harvest treatments, and the lowest edible products yield in all cases. However, this indeterminate bush type cultivar has the potential to produce multiple crops of pods. Most 'Vita 5' plants had flowered a second time before being cut for weighing.

'TVu-3662' had the highest seed yield in the control and the highest harvest index in all cases, but had the greatest yield loss due to defoliation. The 2 Botswanan cultivars, 'B-138' and 'B-162', had relatively high seed yields from all treatments. They would probably yield more than the other cultivars at wider spacings because their trailing vines would rapidly cover the ground. 'TVu-3662' is smaller and more determinate, and would probably give the highest yield at higher planting densities. Since it had the smallest seeds of all cultivars tested, a higher planting density would not necessarily require more total seed weight.

The multiple harvest treatment of 'Vita 7' resulted in the highest yield of leaves. 'TVu-1948' was second highest for leaf yield with multiple harvests and highest with pruning and single harvest treatments. These 2 cultivars had the longest periods of vegetative growth, allowing 6 weekly leaf harvests, and had large leaves which facilitate picking by hand. The 2 bushy cultivars, 'Vita 5' and 'TVu-3662', had the smallest leaves and the shortest leaf production seasons, though 'TVu-3662' actually had the highest harvest index for leaves with pruning and single harvests.

For total yield of edible products, multiple leaf harvests were most productive in all cultivars, and 'Vita 7' had the highest yield, closely followed by 'TVu-1948'. 'TVu-3662' had the highest harvest index in every treatment, but also had the lowest average above-ground weight. Therefore, if space is not limiting, larger cultivars like 'Vita 7' and 'TVu-1948' would appear to be ideal. When limited by space rather than labor availability, small cultivars like 'TVu-3662' with a high harvest index would probably be most productive provided the seeds were planted close together.

The origin of the cultivar does not appear useful for predicting yield levels or efficiency for leaves or seeds. Contrary to expectations, some Nigerian high-yield cultivars produced more edible leaves and less weight of seeds than the traditional cultivars from Botswana (in a greenhouse environment). Growth habit was a poor indicator of seed yield level and harvest index efficiency. The larger trailing cultivars produced more weight of harvested leaves than the smaller bushy cultivars, but a bushy cultivar sometimes had the highest harvest index.

Effects of treatments

This study showed that apex removal at 28 days after planting had little effect on seed yield, but tended to increase leaf production and accelerated leaf senescence. All leaf harvesting methods reduced seed yield. Lower yields were mainly due to fewer pods, as noted by others (10, 33, 86, 97). Because single harvest and pruning treatments were performed near the time of first flowering, pod number was usually reduced with little effect on other components of yield. In some cultivars the pruning treatment greatly increased seeds/pod, indicating that the number of pods had been reduced excessively by removing the ends of the branches. Multiple leaf harvests were shown to reduce weight/seed in bean (33). Yield reductions in 3 of the 4 large-leafed trailing cultivars under both multiple and single harvest treatments were about equally due to fewer pods and smaller seeds. Nutrients may have been limiting at both the start and the end of reproductive growth (2, 35). In the other large-leafed cultivar, 'B-162', and both small-leafed cultivars the magnitude of the reduction in pod number was much greater than the reduction in weight/seed (table 24).

All leaf harvest methods lowered seed yield, but increased the total yield of edible products an average of 4% for pruning, 18% for single harvest, and 36% for multiple harvest. In 'Vita 7' with apex removal, multiple harvest yielded 209% of the control.

In this study the defoliations ranged from 50-85% depending on cultivar, and significant reductions in seed yield resulted.

Less severe defoliations would give higher yields of seeds and lower yields of leaves. Although lower defoliation levels were not tested, earlier researchers have observed that large reductions in seed yield rarely occur with 33% defoliation, but are usually obtained with 50-67% leaf removal (18, 34, 37, 47, 54). If a 30-50% defoliation does not reduce a cultivar's seed production, the total yield of edible products could possibly be greater than measured in this experiment. More testing is needed to clarify this matter.

Practical applications

Since the increases in food production were related to the amount of labor required, recommendations for farmers would depend on local economic factors, such as labor availability and market prices of leaves and seeds. Harvesting and drying cowpea leaves does not require great strength or any tools other than baskets, so it can be done by children while the adults concentrate on more strenuous farming tasks. In addition, leaf harvesting has the advantage of producing food earlier in the season than mature seeds or even immature pods would be available. Kenyan farmers harvest cowpea leaves from 3 weeks after planting up to the start of podfilling (14).

Cowpea leaves are nutritious fresh or dried, are easily stored when dry, and are already marketed and consumed in many parts of Africa. It appears that intensive cultivation of cowpea for both leaves and seeds would become more important as the population and food requirements of Africa continue to increase.

Before new cowpea cultivars are distributed to farmers in regions where leaf harvesting is practiced, their responses to leaf removal should be determined, because this is as much a part of the local crop environment as the soil, daylength, and prevalent diseases. Ideally, such testing would occur during selective breeding, with the goal of developing multi-purpose cultivars.

Because of the variability of local environments, improved alien cultivars often do not perform as well as traditional local cultivars which are better adapted. In such places, a better strategy might be to cross the local cultivars with improved introduced cultivars, and to select the hybrids with qualities that the farmers desire (119).

Insecticides may be used safely on cowpea if reasonable precautions are taken (100). Pyrethrum daisies (<u>Chrysanthemum pyrethrum</u>) are grown in great quantities in East Africa, to produce the insecticide pyrethrin, which is not poisonous to humans or livestock (1). This locally produced insecticide is likely to be safer and cheaper for African farmers than imported oil-based products. Breeding for resistance to leaf-eating pests might make cowpea leaves unpalatable to people as well.

Generations of African farmers have managed cowpea plantings for multiple products. However, harvesting edible leaves requires proper timing and minimal damage so that seed production is not greatly reduced. Leaves are replaced most readily during the vegetative stage when plants are small. Plants are larger in the reproductive stage, but defoliation during pod growth is harmful to seed yield, and after the seeds are grown the leaves tend to wither and abscise. The time period at anthesis appears to be optimal for leaf harvesting, but the harvest season can be extended by removing a few leaves at a time.

Other tropical regions with inadequate food resources may also benefit by combining seed and leaf production. Over 185 legume species are consumed as leaf vegetables. In addition to cowpea, annual legume crops which have edible leaves include bean, lima bean (*Phaseolus lunatus*), winged bean (*Psophocarpus tetragonolobus*), lablab bean (*Dolichos lablab*), fennugreek (*Trigonella foenum-graecum*), and pea (*Pisum sativum*)(14).

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