Lack of Monocarpic Senescence in Florunner Peanut

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ABSTRACT

Essential to understanding any plant is basic knowledge of its life cycle. This investigation was designed to determine if the Florunner cultivar of peanut (*Arachis hypogaea* L.) is an annual or perennial from a strictly botanical standpoint. In order to investigate this aspect of the life cycle, it was necessary to determine if signs of monocarpic senescence were evident at the end of the customary growing season, and to determine how long Florunner specimens would live when disease, temperature and water were not permitted to become fatally stressful. To monitor for signs of senescence, shoot growth and N content were measured until the best harvest date (146 days after planting, DAP). Carbon assimilation and distribution, flower and fruit development also were determined at the best harvest date. No signs of monocarpic senescence were noted. Shoot N concentration was found to initially decline and then level off to a steady state of 28 mg N g^{-1} of tissue. At harvest, proportions of recently assimilated carbon were measured in root, shoot and fruit tissue. In the longevity portion of the experiment, individual Florunner plants were field-grown for 1158 days under protection from disease and cold injury. At 1158 DAP, the plants still showed no sign of senescence. Fruit of all maturity classes were present on every plant from 90 DAP until the experiment ended (1158 DAP). Throughout the experiment, most of the plant's assimilate appeared to go into fruit production. Tissue samples examined throughout the experiment showed considerable secondary phloem and xylem in older shoot and root tissue. Cork, derived from the phellogen, formed around older portions of the stem and root. Growth of xylem, phloem and phellogen were similar to other perennial herbaceous dicots.

Key Words: *Arachis hypogaea*, life cycle, groundnut, growth and development, perennial, carbon partitioning.

The genus *Arachis* contains 22 described and possibly 40 or more undescribed herbaceous species (14). Cultivated peanut, *A. hypogaea* L., is thought to have originated as a natural hybrid allotetraploid of quasi-annual *A. batizocoi* and perennial *A. cardenasii* (14).

Although *Arachis hypogaea* L. is cultivated as an annual, the botanical life cycle of the species is still unclear. Hammons (16) stated that *Arachis hypogaea* is an annual in agricultural practice but many *Arachis* species are perennial. Small (24) characterized the genus *Arachis* as perennial low herbs. Hoehne (17) described the peanut as perennial or at least biennial and noted that earlier classifications of *Arachis* as an annual herb were made on immature specimens. Ames (1), Bailey (2), Bentham (3), Bunting and Elston (7), and Radford *et al.* (22) however, all classify *Arachis hypogaea* L. as an annual.

If *Arachis hypogaea* were an annual species then it would be expected to undergo monocarpic senescence. Nitrogen exhaustion of vegetative organs, recently fixed carbon allocated almost completely to the developing fruit, and the lack of new fruit initiation are all signs of monocarpic senescence (21).

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Materials and Methods

Certified Florunner peanut (*Arachis hypogaea* L.) seed were planted 10 May 1983 at the Univeristy of Georgia Coastal Plain Experiment Station near Tifton, Georgia on a Tifton loamy sand, (fine-loamy, siliceous, thermic Plinthic Paleudults). Florunner was chosen because it is the most widely grown cultivar in the USA and typical of the runner market type peanut.

Plants were grown using cultural practices consistent with Georgia Cooperative Extension Service recommendations (27). Before planting, the land was turned (to 20 cm) and bedded with a tillivator. Plots were irrigated to maintain a soil moisture content at or above -50 kPa (15 cm depth) soil water pressure, and gypsum 550 kg ha^{-1} was applied to supplement soil calcium. Early and late leafspot diseases [*Cercospora arachidicola* Hori. and *Cercosporidium personatum* (Berk. & Curt) Deighton, respectively] were controlled with biweekly applications of 400 g of active ingredient (ai) ha^{-1} chlorothalonil (tetrachloroisophthalonitrile). White mold (*Sclerotium rolfsii* Sacc.) infection was suppressed with monthly applications of 36 g ai ha^{-1} diniconazole [(E)-1-(2, 4-dichlorophenyl)-4, 4-dimethyl-2-(1,2,4-triazol-1-yl)-1-pentane-3-ol]. Weeds were controlled with preplant incorporated applications of benefin (1.4 kg ai ha^{-1}) and alachlor (3.3 kg ai ha^{-1}), one postemergence application of bentazon (1.1 kg ai ha^{-1}), cultivation and hand weeding.

Nitrogen Content and Carbon Assimilation Studies

At 20, 38, 56, 74, 92, 110, 128 and 146 days after planting (DAP), 10 plants were harvested from each of seven replications. Each 10-plant sample was separated into fruit and shoot, oven dried at 65 C for three days, weighed and ground in a Wiley mill (Arthur H. Thomas, Philadelphia, PA) to pass a 1-mm screen. Total nitrogen (N) concentration of each plant fraction was measured by the method of Nelson and Sommers (20).

Carbon assimilation and distribution of labeled carbon by field-grown plants was determined at the normal harvest date [(determined by the hull-scrape method to be 146 DAP) (25)]. To follow movement of newly fixed carbon, the main stem of each sampled plant was enclosed in a plexiglass photosynthesis chamber (18 cm by 25 cm by 4 cm deep). Air inlets and outlets were located at opposite ends of the chamber. A piston pump (3 L min^{-1}) was used to circulate air through the 5 L closed system containing the sample chamber and a cooling coil located in a refrigerated water bath held at 6 C. A metal plate with copper coils filled with circulating cold water (6 C) formed the base of the photosynthesis chamber. With these precautions, temperature rise during the labeling process was less than 5 C. The main stem was labeled by injecting 10 μCi of $^{14}CO_2$ directly into the air stream entering the chamber, thus the specific activity of the $^{14}CO_2$ was 2 μCiL^{-1} in the air stream. Each plant was exposed to the label for 10 minutes after which the air stream was diverted through a series of 2N solutions of KOH to trap any $^{14}CO_2$ remaining in the system. A total of 21 plants were labeled over a three day period, all labeling was conducted between 1100 and 1300 h. At 0.5, 2, 8, 24, 48, 120 and 216 h after the radiolabel was applied, three plants were individually harvested and divided into fruit, shoot and root (extracted from a soil cylinder 30cm in diameter and 30cm deep). Plant fractions were dried, weighed and ground to pass a 1-mm screen.

One-gram subsamples of each plant fraction were oxidized in a Beckman Biological Material Oxidizer. In this apparatus the sample is combusted in a hot, oxygen rich chamber maintained at 538 C. The gases are passed over a copper oxide catalyst to assure complete oxidation. The liberated $^{14}CO_2$ was then trapped in ethanolamine (19). The carbamate of ethanolamine was solubilized in ethyleneglycol monomethyl ether, added to a toluene-PPO solution and counted in a Beckman LS-150 liquid scintillation

counter.

Fruit maturity class distribution was determined at 146 DAP using the endocarp color and morphology characteristics as described by Williams and Drexler (25). Maturity classes correspond to six major classes as defined by endocarp color. White endocarp (class 1) generally occurs 0-13 days after the peg enters the ground (DAE), light yellow (class 2) 14-27 DAE, dark yellow (class 3) 28-41 DAE, orange (class 4) 42-55 DAE, brown (class 5) 56-66 DAE, and the black endocarp (class 6) indicates physiological maturity which occurs 67-87 DAE.

All experiments were conducted using a randomized complete block design with 3 ($^{14}CO_2$ experiment) to 7 (nitrogen + dry matter accumulation) replications. Data were analyzed using a general linear model procedure (PROC-GLM) of Statistical Analysis Systems (23). Means were separated with least significant differences calculated at the 0.05 level of probability.

Perenniality Study:

At 146 DAP two rows of Florunner were thinned to a denisty of one plant per 800 cm^2. To assure plant identity, each plant was labeled with a plastic ribbon loosely tied just below the cotyledonary lateral branch. A temporary, heated greenhouse was built over the experimental area during each 1 November through 15 April period for each of the three winters of the experiment to shelter plants from cold injury. Two resistance-type heaters were placed in the greenhouse to prevent the temperature from dropping below +5 C. Twelve 200-liter water-filled drums were placed inside the greenhouse to buffer against temperature changes and to provide a reserve heat source if power failed.

Volunteer seedlings from seed produced by the test plants were periodically removed to prevent confusion with test plants and to decrease disease potential. Disease, insects, and fungal pathogens were controlled during the entire 1158 days of the experiment using cultural practices consistent with the Georgia Cooperative Extension Service recommendations (27) as discussed earlier in the opening of the materials and methods section. Irrigation was applied as needed to prevent severe wilting of test plants.

Three plants were harvested at each of three sampling dates (30, 390 and 750 DAP) and notes on vegetative and reproductive growth were taken. Anatomical differences related to plant age were determined for root tissue (first lateral coming off the taproot) and shoot tissue (first lateral branch off cotyledonary lateral branch). Tissue was fixed with 4% formaldehyde in phosphate buffer (100 mM, pH 7.2), dehydrated in a graded ethanol/tertiary butanol series, infiltrated first with paraffin oil and then with melted paraplast. Cross sections were cut (8 µm thick), stained with toluidine blue and examined.

The experiment was terminated at 1158 DAP (14 October 1986) with five of the 30 original plants surviving (sampling and disease eliminated the rest).

Results

Nitrogen Content and Carbon Assimilation Studies

Individual Florunner plants (fruit + shoot) increased in

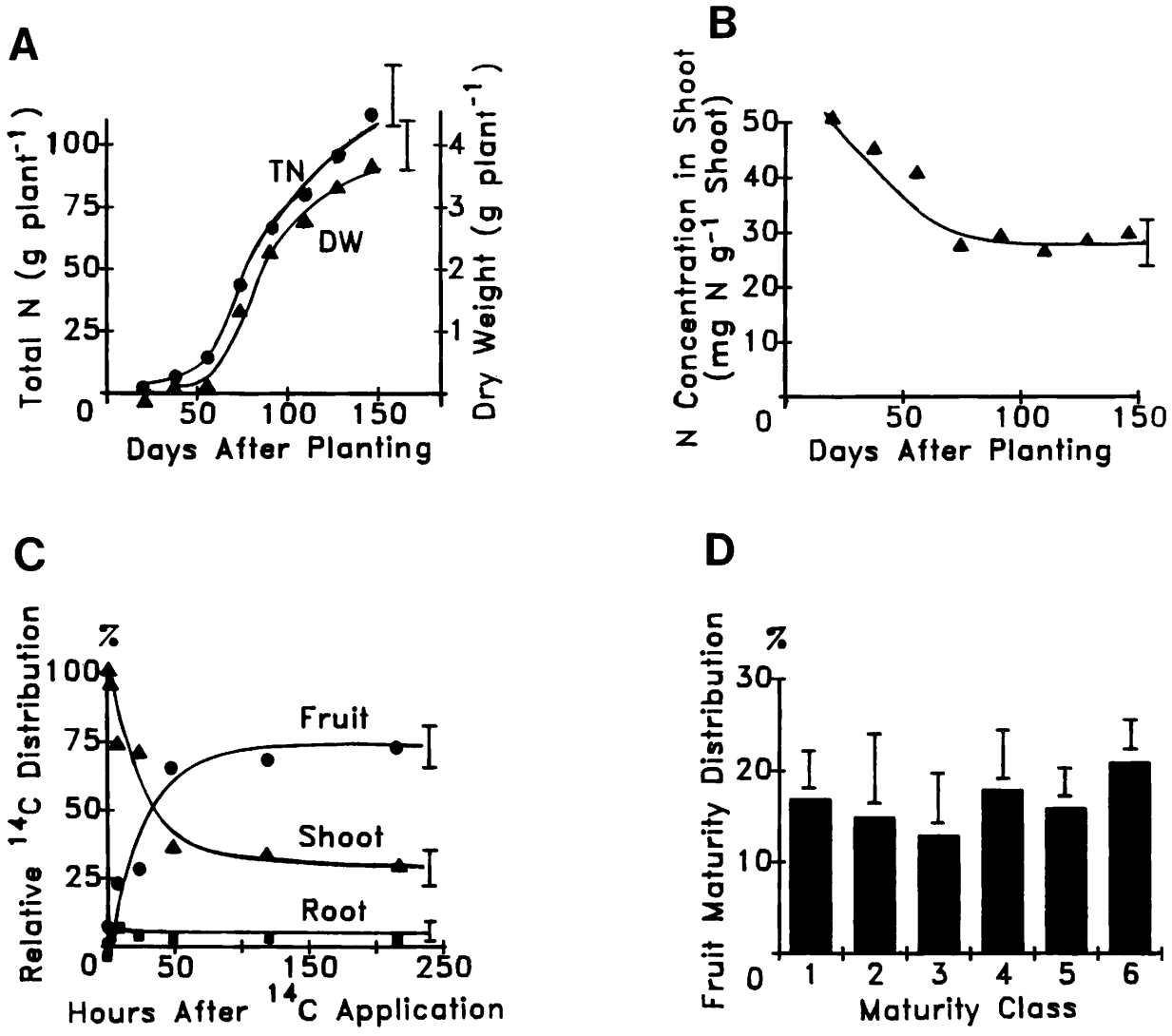

Fig. 1. Nitrogen, carbon and dry weight accumulation and distribution in Florunner peanut. (A) Total nitrogen (TN) and dry weight (DW) accumulation during the first 146 days after planting (DAP). (B) N concentration in the shoot (stem + leaf tissue) during the first 146 DAP. (C) Time course for partitioning of ^{14}C after $^{14}CO_2$ was applied to plants at 146 DAP. (D) Fruit maturity class distribution on plants 146 DAP. Class 1 is least mature and Class 6 fully mature. Bars indicate an LSD (P=.05) value.

total dry matter and N mass throughout the 146-day sampling period (Fig. 1a). Shoot N concentration declined during the first 70 DAP and then leveled off at 28 mg N g^{-1} shoot tissue (Fig. 1b).

Plants were still actively fixing $^{14}CO_2$ at 146 DAP. Proportions of radiolabel measured in root, shoot and fruit tissue at 48 h after application and beyond were 1, 27, and 72% respectively (Fig. 1C). Flowers were observed and new fruit were also being set at 146 DAP as indicated by the presence of all major fruit maturity groups (Fig. 1d).

Perenniality study:

Peanut plants did not exhibit natural senescence associated with the end of life cycle during any part of the 1158 days of the experiment. Several test plants died during the experiment as a result of disease (mostly caused by *Sclerotium rolfsii*). A power failure to the heaters during the first winter resulted in the loss of several other plants due to frost.

Shoot growth continued throughout the entire experimental period. Numbers of nodes present on the cotyledonary lateral branch at 146 DAP and 390 DAP were 22 and 42, respectively. Internode length ranged from 5 mm to 80 mm and was positively related to the soil and air temperatures during the internode expansion period. Lateral branches up to 3 m in length were measured at 1158 DAP.

After a mild frost (-2 C) occurred inside our temporary greenhouse eliminating a large portion of the canopy during the first winter, new braches sprouted from the crown area and from the lateral branches. Flower and fruit development began 30 DAP and continued throughout the entire 1158-day experimental period. Pods matured approximately 65 days after the peg entered the ground. After the pod reached maturity the pod stem weakened at or slightly below the soil surface. Within 30 to 40 days after reaching full maturity, the pod stem had degraded to the point that it was no longer attached to the plant. The seeds in these pods germinated 10 to 40 or more days after detachment. Both flower and fruit formation decreased with increasing fruit load and decreasing temperature. At 1158 DAP, flowers and pods were present on new branches in the crown area and on the lateral branches.

Anatomical changes in stem tissue included formation of a central cavity from breakdown of pith cells, development of secondary xylem and phloem, collapse of cortical cells, and development of a periderm in the outer cortical cells (Fig. 2a-2f). Phellogen developed as a series of tangential arcs rather than as a continuous ring.

Ray parenchyma divided the root's axial xylem, cambium, and phloem into four main sectors (Fig. 2e). The diffuse porous arrangement of the secondary xylem contained vessels of varying diameters accompanied by fibers and parenchyma cells (Fig. 2f). Old sieve tubes were crushed leaving only fibers and storage parenchyma in the outer phloem tissue. Merging with outer phloem was the pericyclic parenchyma. Occasionally, an additional periderm formed, surrounding necrotic root tissue which had been invaded by pathogenic fungi. Active N-fixing nodules (nodules containing the red pigment leghemoglobin) were also present on the oldest portions of the roots, 750 DAP (Fig. 2e).

Discussion

In Boote's (5) descriptive growth stages of peanut, no vegetative death phase was included. The most mature physiological stage described by Boote (5) was a harvest maturity stage (designated R8) defined as two-thirds to three-fourths of all developed pods having pericarp coloration. Williams *et al.* (26) divided the peanut life cycle into ten arbitrary phases of development. The tenth stage was described as "50 to 70 percent of the pods mature; defoliation rapid and crop lifted at the end of this phase." Despite lack of a described vegetative death stage, the cultivated peanut is still widely considered to be an annual plant (7, 10, 18). We saw no evidence of a vegetative death phase in Florunner peanut during the 1158 days of our experiment.

Like other studies (18), our study also found the peanut to exhibit the following general growth pattern: (a) a lag in early growth, (b) exponential increase in weight near the end of the lag phase, (c) a constant growth rate during early pod set and (d) a slowing of vegetative weight gain during pod filling. Often associated with this leveling of vegetative weight gain during late pod fill is loss of leaves which could be nearly complete (12) or only slight (8). We believe this type of leaf loss in peanut is associated with poor control of early and late leafspot diseases. Severe leafspot damage can reduce leaf area index by 80% and canopy carbon-exchange rate by 93% (6). By controlling leafspot with plant protective chemicals we found no association of leaf drop with harvest maturity.

Growth analysis during the first 145 DAP revealed that once canopy closure was complete (60 DAP), most of the assimilate was partitioned to fruit. Carbon assimilate partitioning rates to fruit as high as 98% have been reported for Florunner (11). High assimilate partitioning rates to fruit slows vegetative development. However, our studies showed that total dry matter production (vegetative + reproductive) continued to increase. Plants were still actively fixing $^{14}CO_2$ at the best harvest date for high seed yield (146 DAP) with portions of fixed carbon distributed to root, shoot and fruit tissue. If the plant were an annual near the end of its life cycle, carbon fixation would have been minimal and partitioned almost exclusively to the fruit.

During the 1158-day study, a majority of the plant's net assimilate (dry matter) went towards fruit development. However, when a mild freeze eliminated much of the canopy during the first winter, reproductive growth slowed until the canopy recovered. Throughout the experiment, old leaves (especially in the lower portion of the canopy) were lost as new leaf and stem tissue continued to form. As did Bunting and Elson (7), we found Florunner to be day-neutral (with respect to flowering), to have an indeterminate branching pattern and its phenology to be determined primarily by temperature.

Monocarpic senescence often is associated with N exhaustion from vegetative organs by developing fruit (21). Our studies measured an initial decline in vegetative N concentration, followed by a stable and apparently non-limiting (to CO_2 fixation) level of 28 mg N g^{-1} shoot. Thus the peanut does not "self destruct" by translocating most N from the leaves to the fruit as do annual crops such as soybean.

Temperature decreases associated with the oncoming of fall can reduce dry matter accumulation and confound temperate-climate studies of tropical mesophiles such as peanut. Bhagsari (4) noted that as temperature decreased from 30 C to 10 C, peanut photosynthetic rates decreased by 65%. Cox (9) reported that growth ceased at 15 C, and death has been reported to occur between 5 C and -5 C, depending

on cultivar (15).

Slowing of vegetative and reproductive growth during winter months was evident in our experiments. Loss of several experimental plants during a mild freeze (-2 C) proved Florunner's sensitivity to cold. Our temporary greenhouse was designed to prevent a killing frost and not to simulate summer conditions. Cool temperatures and short days associated with winter months slowed both reproductive and vegetative growth.

Microscopic examination of shoot and root tissue revealed formation of considerable secondary phloem and xylem. Cork, derived from the phellogen, formed a protective

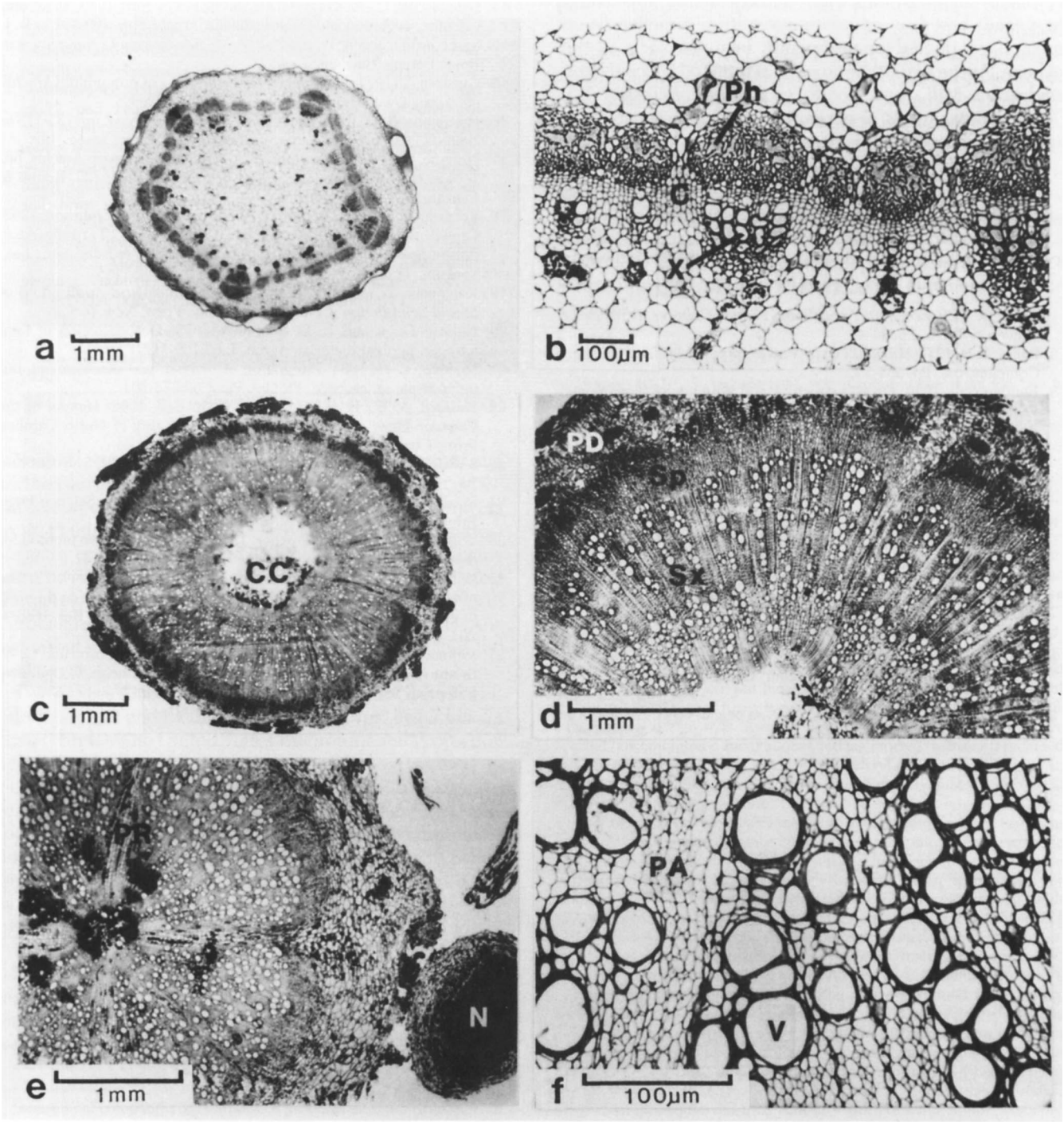

Fig. 2. Shoot and root cross sections. (a) Cross section of a cotyledonary lateral stem showing largely primary growth. (b) Enlargement of a section of (a) showing vascular bundles and early secondary growth. Ph indicates phloem tissue, C cambium and X xylem. (c) Cross section of stem showing largely secondary growth (this portion of the stem was approximately 750 days old) cc marks the central cavity. (d) Enlargement of a section of (c) showing development of a periderm (PD) and extensive secondary xylem (Sx) and secondary phloem (Sp). (e) Cross section of a root in secondary state of growth (this portion of the root was approximately 750 days old). Note four parenchyma rays (PR) dividing the root into four main sectors and a nitrogen fixing nodule (N) on the right side of the section. (f) Enlargement of a section of (e) showing the diffuse-porous vessel (V) arrangement accompanied by fibers and parenchyma (PA) cells. Figs. a-f prepared by C. Styer.

barrier around older portions of the stem and root. Growth of xylem, phloem and phellogen in Florunner peanut was similar to that found in other perennial herbaceous dicotyledons such as alfalfa (*Medicago sativa* L. Medick) (13). In summary, the Florunner peanut behaves as a perennial herb. Our study with one cultivar does not prove all cultivated peanut are perennial. However, it does remind the reader to be cautious when making assumptions about the peanut based on common agricultural practice or on research conducted on temperate legumes such as the soybean. As are two other crops, the tomato (*Lycopersicon esculentum* Mill.) and potato (*Solanum tuberosum* L.), Florunner peanut is a perennial South American herb cultivated as an annual.

Acknowledgments

Assistance provided by F. Barnes and D. Cheek in caring for plants is appreciated. We thank W. Hanna and C. Styer for preparation of plant sections in Fig. 2. This work was supported by state and Hatch funds and grants from the Georgia Agricultural Commodity Commission for Peanuts.

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Accepted May 17, 1991