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Chapter 11

GROWTH PHYSIOLOGY

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Great progress has been made in acquiring knowledge of the physiology and biochemistry of plants. This basic information, along with that from other disciplines such as soil science, plant pathology, genetics, and entomology, provides a basis for improved crop management. Increased yields and better quality are the goals of agriculturists, but these are the complex end-products of a series of biological processes and reactions.

Until recently very little effort has been devoted to peanut physiology investigations. The effort has increased, but information on peanuts is deficient in comparison with other crops. However, progress is being made, and recent research developments will be discussed from the basic view to indicate their implications for improved peanut cultivars and crop management where applicable.

Major topics in this chapter are germination and seedling growth, photosynthesis and growth analysis, growth regulators, environmental factors, nitrogen fixation, and tissue culture. Also, some specific environmental effects on physiological processes discussed in this chapter will be included in their respective sections. Mineral nutrition was reviewed by Reid and Cox (1973) and in Chapter 6 of this volume. Early work on environmental factors was reviewed briefly by Gregory et al. (1973).

GERMINATION AND SEEDLING GROWTH

Life cycles in the plant kingdom begin and end with seed. Seed are the "thread of life" connecting successive plant generations. Continuity between generations is tenuous since seed are easily damaged physically and physiologically by unfavorable conditions during or after seed maturation. Gregory et al. (1973) previously reviewed peanut seed and seedling morphology. Only a brief description is given here. Reed (1924) described the mature peanut seed as a straight embryo, consisting of 2 fleshy cotyledons, a short hypocotyl, and a plumule all enclosed by a thin testa. Examination of the plumule by Yarbrough (1949) revealed a main axis and 2 cotyledonary lateral axes. He indicated that the mature seed contained 9 or more embryonic leaves on the main and lateral axes. In some recent research (Maeda, 1970, 1972, 1973) fewer leaf primordia were found in the embryo, indicating possible genotype differences in this characteristic of peanut seed. A dominant feature of peanut seed is the protruding tip of the hypocotyl-radicle axis. This protruding and relatively unprotected radicle is a major site of injury during harvesting and handling that may predispose the seed to subsequent physiological deterioration. Peanut seed are among the world's most delicate seed to handle in commerce.

Production Management

Preharvest cultural practices are essentially the same for commercial and seed peanuts. Especially significant are fertility and pest management in relation to seed yield. Many cultural practices tend to lessen or reduce harvest and postharvest problems with seed quality. For example, good weed control reduces impact injury to the seed during harvest since combine action can be reduced. Adequate field disease control reduces the probability that diseases will lead to deterioration of seed during storage (Christensen, 1964). There is little evidence, however, that these management practices influence the physiological quality of seed at maturity.

Cultural practices do influence the physiological changes that occur within each seed during development and maturation. Many seed are lost prior to harvest because of physiological deficiencies resulting from weakened plants (disease, fertility, etc.). Seed quality, however, is determined as it relates to the harvested, dried, and shelled seed population. Individual seed that are lost because of poor production management are never evaluated for seed quality because they are eliminated from the population prior to evaluating seed quality. This methodology makes it very difficult to determine the total impact of production management on seed quality.

Preharvest Conditions Influencing Germination Quality

The vitality of the parent plant is often assumed to affect the subsequent viability of the seeds produced. Such assumptions are not adequately documented in the literature. In most crops, the vitality of the parent plant impacts mostly on the quantity of seed produced. An unthrifty plant may produce only a few seed, but at physiological maturity the seed are usually of good germination quality.

Soil Fertility and Nutrition. Blackstone et al. (1954) did an exhaustive study of factors affecting the germination of seed from runner type peanuts. Neither geographic location nor soil type significantly affected seed quality. However, recent research has shown that both growing season and location affect peanut seed quality. Both seedling vigor and ethylene (an important regulator of peanut seed germination) production were altered by season and location (Ketring et al., 1978).

Fertilization treatments (N, P, and K) had little influence on the quality of spanish and runner type seed (Walker and Carter, 1971). Extensive field work in the mid-1940's showed that calcium and potassium levels in the fruiting zone seriously affected fruit quality (Brady and Colwell, 1945; Colwell and Brady, 1945; Colwell et al., 1945). Excessive potassium levels were detrimental to fruit quality, whereas high calcium levels improved fruit quality. Early ovule abortion was prevented by adequate calcium uptake. Adequate calcium in the fruiting zone overcame the detrimental effects of potassium and gave a marked increase in the calcium content of shells and seed.

Later investigations confirmed that peanut seed quality is significantly affected by calcium. Hartley and Bailey (1959) identified dark plumules in peanut seed as being associated with parent plants that were subjected to severe drought. Seed with a malady named stub-leaf gave normal root and hypocotyl development during germination, but no epicotyl developed and the pith of the hypocotyl and upper root eventually decayed.

Harris and Brolmann (1963) and Cox and Reid (1964) showed that plumule damage in peanut seed was due to a nutritional deficiency of calcium. The deficiency was eliminated by applications of gypsum. Sullivan et al. (1974) associated another seedling malady, watery hypocotyl, with calcium deficiency. Other investigators have confirmed the relationship between peanut seed quality and seed calcium (Harris and Brolmann, 1966; Hallock, 1980; Hallock and Allison, 1980). In addition to less calcium, low quality peanut seed contained less potassium and zinc, more phosphorus and manganese, and about the same amount of magnesium and copper as high quality seed (Ketring, 1971).

Cox et al. (1976) and Pallas et al. (1977) showed that soil moisture and soil calcium interact to influence pod uptake of calcium and thus affect peanut seed quality. Droughty conditions during pod development reduce seed quality. Higher calcium availability can partially offset the decline in seed quality caused by drought.

Harvest, Storage, and Handling Conditions that Influence Germination

Peanut seed are easily damaged by an impact to pods or seed. Present handling methods expose seed to numerous opportunities for impact damage. Most researchers agree, however, that damage is minimal if equipment is properly calibrated and operated.

According to Blackstone et al. (1954), harvesting practices did not affect the germination quality of runner type peanuts. Immature runner type seed, high in free fatty acids, did not germinate as well as more mature seed. Other factors that affected germination (such as combining, curing, and handling) followed digging. Curing methods affected seed quality, but the best curing methods changed from year to year because of climatic conditions. Norden (1975) obtained his best seed by digging seed peanuts early and curing on a stackpole. Turner et al. (1967) and Dickens and Khalsa (1967) found that impact damage during harvesting reduced seed quality and was related to seed moisture levels at harvest. Young et al. (1971) and Young and Moore (1972) found that early digging and careful combining, drying, and shelling resulted in the best quality seed.

Peanuts curing in the windrow may be exposed to unusually high or low temperatures. When seed moisture is high, excessively high or low temperatures may reduce seed quality. Norden (1975) reported that high temperatures increased the percent shriveled seed and reduced seed quality. Ketring (1979a) found that high moisture seed exposed to subfreezing temperatures while drying in the windrow had lower germination, vigor, and CO_2 and ethylene production. Enzymatic activity, particularly isocitric lyase, was also less than in control seed.

Mechanical shelling is generally believed to damage seed and reduce quality. Davidson (1974) found that sheller cylinder speed was the only operator controlled factor that affected seed quality during shelling. High cylinder speeds reduced seed quality. Davidson (1974) and Backman and Hammond

(1976) showed that the detrimental effects of mechanical shelling can be minimized by fungicide applications after shelling, but prior to seed storage.

Peanut seed (shelled or unshelled) deteriorate quickly in unfavorable storage conditions (high humidity and high temperature). Harrington (1960) proposed a direct relationship between seed longevity in storage and seed moisture and seed temperature. The lower the seed moisture and seed temperature, the greater the seed longevity. Peanuts are relatively short-lived in storage. Seed moisture near or below 7% and storage temperatures near 10 C are adequate for short-term storage of seed (Blackstone et al., 1954; Gavrielith-Gelmond, 1971b; Clark, 1972). At seed moisture levels above 7%, storage fungi may cause undesirable biochemical changes in seed quality (Ward and Diener, 1961; Christensen, 1964). Storage at high relative humidity (80 to 100%) even at cold temperatures (3 C) reduced germination, vigor, and ethylene production of stored seed (Ketring, 1971, 1973). Extractable lipids and nucleic acids were reduced by high storage relative humidity (Ketring, 1971). However, over extended storage periods with gradual reductions in germination and vigor, the earliest indication that changes in seed quality were occurring was ethylene production by the seed (Ketring, 1973; Ketring et al., 1974).

Imbibition and Germination

Water uptake is the first step in the resumption of active growth by quiescent seed after storage. Initial uptake is basically a physical process dependent on the characteristics of the seed, the degree of contact with the water substrate, and the content of water available on or in the substrate. Denny (1917a) studied the permeability of peanut seed coats to water and found increased permeability as temperature increased. He suggested that both physical and chemical processes are involved in the passage of water through peanut seed coats and later found increased permeability after extracting seed coat tannins and lipids (Denny, 1917a).

Peanut seed apparently imbibe water uniformly around the entire seed surface. Bewley and Black (1978) stated that most seed have a triphasic pattern of water uptake. Phase I is purely physical and is a result of matric forces of the water and seed. Phase II is a lag period during which little water is imbibed. During phase III, additional water is imbibed and is associated with cell metabolism and visible germination. During germination, hydration of cell walls and protoplasm of viable seed initiates a rapid return to metabolic activity. The resumption of active growth by the embryo results in the eventual rupture of the seed coat and emergence of the young plant.

The only external substances required by quiescent nondormant peanut seed for germination are water and oxygen. The oxygen available in air is usually adequate. Peanut seed require a seed moisture level greater than 35% for germination (Mixon, 1971b).

Favorable external temperature is also necessary for germination. Peanut seed will germinate in a temperature range of approximately 5 to 40 C, but this may depend upon the maximum temperature that the seed receive in an alternating temperature cycle. Alternating day-night cycles are usual under field conditions. The limiting factor at low temperature ranges is the slow growth rate of both hypocotyl-radicle and epicotyl. Seed quality also influences germination at cold temperatures and is an interfering factor in determining genetic differences in cold tolerance among peanut genotypes, but some tolerance seemed to exist (Branch, 1976). Recently, a few peanut plant introductions have been identified which are more tolerant of cold soil temperatures (Ablett, 1978). Minimum and maximum temperature requirements are not well established, but peanut seed germinate quickly within a temperature range of 20 to 35 C. Optimum temperature for most rapid germination and seedling development is approximately 30 to 33 C. Minimum, optimum, and maximum temperature conditions can be misleading since such values are established for a specific but arbitrary time interval. Also, soil temperatures are rarely near optimum at planting and vary over a wide range, particularly at northern latitudes.

Metabolism

Metabolism in quiescent peanut seed is very low at seed moisture levels below 10% but increases rapidly during water absorption and hydration of cell walls and protoplasm. Hydration of the seed tissues reactivates the protein-synthesis system and reactivates enzymes or leads to *de novo* synthesis of enzymes. Mayer and Poljakoff-Mayber (1975) stress that three main types of chemical changes occur in rehydrated seed. These are: (1) the breakdown of storage reserves; (2) the transport of materials to the embryonic axis; and (3) the synthesis of new materials from the breakdown products.

Seedling development is dependent on the food reserves in the cotyledons. The metabolic reserves in peanut seed are mainly lipids and proteins. The dry seeds contain 20 to 25% protein and 40 to 50% lipids (Pickett, 1950; Altschul, 1962). Jacks et al. (1967) characterized spherosomes as the principal site of lipid storage in peanut cotyledons. Bagley et al. (1963) reported that protein is stored in large bodies identified as protein bodies. Sugars and starches are found in peanut seed, but at relatively low levels. Hymowitz et al. (1972) found the disaccharide, sucrose, and the oligosaccharides raffinose and stachyose. Amuti and Pollard (1977) did not detect any free monosaccharides in peanuts, but also found the oligosaccharides raffinose, stachyose, and verbascose. In studies of the way that food reserves are accumulated and stored in peanut seeds, Pattee et al. (1974a,b) found that starch accumulates earliest in the pericarp, then seedcoats, and reached a constant level in the seed about mid-seed maturity. Sugar content maximized in the pericarp and seedcoats at later seed maturity stages and continued to steadily accumulate in the seed during development. Lipid slowly begins to accumulate at early stages of seed development, but did not reach maximum levels until late seed maturity. For further discussion of seed composition, refer to Chapter 17.

These storage reserves contain potential chemical energy that can be utilized during the germination process. The breakdown of storage reserves occurs through the glyoxylate cycle, tricarboxylic acid cycle, or pentose-phosphate pathway. In peanuts, where the metabolic reserves are largely lipids and storage protein, the final breakdown of the lipid reserves occurs through the glyoxylate cycle (Bradbeer and Stumpf, 1959). Marcus and Velasco (1960) showed that the enzymes malate synthetase and isocitric lyase are essential during the conversion of fats to carbohydrates. Gientka-Rychter and Cherry (1968) and

Longo (1968) found that malate synthetase and isocitric lyase are synthesized *de novo* after the onset of germination. Rapid fat breakdown begins after 3 to 4 days of germination (Yamamoto and Beevers, 1960) and is closely associated with a rapid increase in isocitric lyase and malate synthetase activity (Marcus and Velasco, 1960). Abscisic acid (ABA) inhibits germination and it also inhibits synthesis of isocitric lyase. Ethylene reversed the inhibitory effects of ABA on germination and isocitric lyase synthesis (Ketring, 1975). Since isocitric lyase is synthesized *de novo*, this suggests a fundamental role for ethylene, possibly at the RNA and/or protein synthesis level, in regulating peanut seed germination. But an action of ethylene or ABA prior to detectable effects on RNA or protein synthesis is not precluded. Allfrey and Northcote (1977) also found that ABA inhibited germination and induction of isocitric lyase synthesis, but not amylase activity and starch breakdown. Gibberellic acid and ethylene were promoters of germination and enzymatic activity. They suggested that isocitric lyase served as a control enzyme in maintaining the proper balance between fat and carbohydrate metabolism.

The degradation of storage protein occurs between 4 to 9 days of germination (Bagley et al., 1963). The degree of protein breakdown is related to the distance of the protein bodies from the nearest vascular bundle. In peanut seeds, only 22% of the original protein found in the cotyledons of dry seed remained after 15 days of germination.

The simpler chemical compounds resulting from the breakdown of storage materials are translocated to the growing points of the embryonic axis where they are utilized for seedling growth. During germination, the dry weight of the developing seedling decreases. Cotyledon dry weight decreases by 60% and protein is depleted by 70% (Cherry, 1963).

After imbibition, the structural integrity and functionality of cellular components returns to normal. The increase in respiratory activity has been correlated with an increase in mitochondria (Breidenbach et al., 1966). Cherry (1963) found few typical mitochronida in resting seed cotyledons. During the first 8 days of germination, the mitochondria increased in structure and internal organization. Marcus and Feeley (1965) found that the activity of the ribosome system increased to a maximum in imbibed seed whereas the system was barely functional in dry seed.

Seed Dormancy

Some seed upon imbibition do not germinate, and their metabolism remains at a low rate, although higher than dry seed. This phenomenon of seed dormancy is broadly defined as the failure of viable seed to initiate growth when placed in conditions favorable for development. Villiers (1972) discusses several types of dormancy, including embryo immaturity, seed coat impermeability to water or gases, and metabolic blocks within the embryo. Dormancy is generally viewed as a survival mechanism of wild plant species, but can cause less uniform germination of crop species.

Dormancy is an important factor in commercial peanut production. Peanut seed develop underground in conditions normally favorable for germination. Nondormant seed may germinate before harvest or crop maturity. Dormancy in peanut seed is absent or lasts only a few weeks for spanish and valencia type,

but may last up to 4 months or longer for virginia type peanut seed. The virginia type cultivar, NC13, has intense dormancy and is widely used as the seed source in dormancy related studies.

Seed dormancy in peanuts is apparently caused by endogenous metabolic barriers. Existing evidence discussed below suggests that the metabolic barriers are probably enzymatic in nature and prevent protein synthesis and/or the degradation and transport of food reserves to the embryo.

Intensity of dormancy in virginia type peanuts is affected by cultural practices. Toole et al. (1964) found that plants grown for a longer period produced seed with less dormancy than those harvested at an earlier time. In their studies, dormancy was reduced by leaching the seeds, removing seedcoats, increasing CO_2 concentrations, and treating with ethylene gas. Basal seed were always more dormant than apical seed. Gelmond and Nakamura (1965) found no differences in dormancy of seed grown in Japan or Israel. Bailey et al. (1958) reported that storage temperature influenced the period of dormancy. Seed are more dormant during dry than wet harvest seasons, indicating that germination inhibitors could be leached from the seed under wet conditions or the ratio of germination inhibitors to promotors is changed due to seasonal variations in climate.

Endogenous hormone levels are probable causal factors of dormancy in peanut seed. Gordin-Sharir and Wareing (1964), using bioassays and chromatography, found auxins and gibberellin-like substances in peanut seed. They did not conclude, however, that these hormones inhibited or promoted germination. In dormancy studies, ABA is a classic inhibitor of germination and gibberellic acid is a classic promotor of germination. Imbibition of NC13 peanut seed in ABA reduced the residual ethylene production and germination of dormant seed and also inhibited germination of nondormant, after-ripened NC13 peanut seed (Ketring and Morgan, 1971, 1972). Narasimhareddy and Swamy (1979) reported a decrease in ABA-like inhibitors during peanut seed storage and an increase in cytokinin levels as the stored seed lost dormancy.

Detailed studies have been completed elucidating the role of ethylene in dormancy regulation in peanuts (Ketring, 1970, 1973, 1975; Ketring and Morgan, 1970, 1971, 1972; Ketring et al., 1974). They have shown that kinetin, benzylaminopurine (BAP), ethylene gas, and 2-chloroethylphosphonic acid (Ethrel or Ethephon) stimulate germination of dormant peanut seed. Their results showed that ethylene production by dormant seed is nil, whereas nondormant seed produced ethylene. The inhibitory effects of ABA on germination were overcome by kinetin and BAP, which stimulated ethylene production by the seed, and most important, the effects of ABA were reversed by ethylene. This suggested an endogenous inhibitor-promotor type regulation of dormancy in these seed. The action of other hormones may be to stimulate ethylene production which then promotes germination of peanut seed by competing with an inhibitor(s) of germination.

Bear and Bailey (1970) suggested the use of Ethrel as a seed or germination towel treatment for breaking dormancy to determine seed viability. Ketring (1977a) used a dust formulation of Ethrel in combination with seed fungicides to break seed dormancy in field plantings. Dormancy can be confused with nonviability of peanut seed, and this can affect quality evaluations. For additional discussion of dormancy, refer to Chapter 16.

Evaluating Germination Quality

Peanut seed are planted under countless field conditions that vary in temperature, moisture, micro-organisms, edaphic characteristics, etc. Each seed is exposed to a unique microenvironment at some point in time during germination and seedling development. Everyone planting peanuts would like to accurately predict seed performance before planting. It is impossible with current technology to predict the performance of seed under all field conditions. Seed evaluation technology has thus developed on the principles of random sampling, statistical probability, and standardized testing conditions.

The most widely used method for evaluating peanut seed quality is the standard germination test. Procedures for conducting the test are specified by the Association of Official Seed Analysts (Copeland, 1978). Generally, 200 or 400 seed are placed on moist paper toweling (in replicates of 25 or 50 seed); the towels are rolled tight enough to keep the seed in place and put them to a germinator at a constant 25 C or an alternating 20 to 30 C environment. Tests are evaluated after 5 days. Seedlings are classified as normal or abnormal. If classification is not possible because of slow development, the seedlings are returned to the germinator for an additional 5 days and then evaluated.

The characteristics of normal and abnormal seedlings are detailed in the testing rules. A normal seedling must have a vigorous primary root or a set of secondary roots sufficient to anchor the seedling when grown in soil or sand, a sturdy hypocotyl with no open breaks or lesions extending into the central conducting tissue, at least 1 cotyledon attached, and an epicotyl with at least 1 primary leaf or an intact terminal bud. Seedlings not meeting these standards are classified as abnormal.

Gavrielith-Gelmond (1952) reviewed the problems associated with testing peanut seed. Although the procedures as specified are objective, many subjective decisions during evaluation are made by seed analysts. Complaints are often made that the standard germination test does not adequately predict field performance of peanut seed. Several researchers have compared the field performance of normal and abnormal seedlings and found that some abnormal seedlings develop under field conditions (Andersen, 1960; Gavrielith-Gelmond, 1971a; Sullivan and Perry, 1976). Pod yields of plants developing from these abnormal seedlings average less than pod yields of plants developing from normal seedlings.

Seed vigor tests are being evaluated for many crops as alternative or supplementary evaluation methods. Vigor tests are promoted as more reliable in predicting emergence of seed under adverse field conditions. Mixon (1971a) found that the promptness of radicle emergence in the germination test had good predictive value for field performance of seed. Moore (1972, 1976) proposed the use of tetrazolium tests for evaluating peanut seeds for quality and vigor. Crompton et al. (1978) found adenylate energy levels in peanut seed related to seed vigor.

Vigor tests for peanut seed are not well standardized. Adequate research in the area of seed vigor and field performance for peanuts is lacking, and it may be years before vigor tests are routine in peanut seed quality evaluations. The Association of Official Seed Analysts is currently compiling vigor testing methods with the objective of standardizing these procedures.

Seedling Development

The results of metabolic activities by rehydrated, high quality seeds are subsequent cell elongation and cell division. In peanut seeds, the first visible evidence of germination is the emergence of the radicle. Radicle emergence occurs by 24 hours or earlier for vigorous spanish type seed, but requires 36 to 48 hours in the virginia types. During the first few days of growth, the developing seedling is dependent upon the degradation of food reserves in the cotyledons for energy. Within 5 to 10 days, depending on the type of peanut and environmental conditions, the root is capable of absorbing minerals and the epicotyl is exposed to light and is capable of photosynthesis. At this point the next generation seedling becomes autotrophic, and an increase in growth begins.

PHOTOSYNTHESIS AND GROWTH ANALYSIS

Leaf Photosynthesis

General Characteristics. The tetrafoliate, pinnately compound leaf is the photosynthetic unit of the peanut plant. It ranges in size from about 4 cm^2 in the first seedling leaves up to 80 cm^2 in upper leaves of fully developed stands. The specific leaf weight is rather high compared to most legumes, ranging from 4.1 to 6.7 mg cm^{-2} in young fully expanded leaves (Pallas and Samish, 1974; Bhagsari and Brown, 1976a). Peanut leaves fold the 4 leaflets upon each other at night and unfold at sunrise, apparently in response to light (Pettit, 1895). A similar folding occurs in response to water stress (Il'ina, 1958; Allen et al., 1976).

The anatomy of the peanut leaf is rather typical of dicotyledonous plants with a well devoloped palisade parenchyma (Figure 1) which varies in thickness with light intensity under which it develops (Pallas, 1980). The lower epidermis is characterized by a layer of rather large, nonchlorophyllous cells.

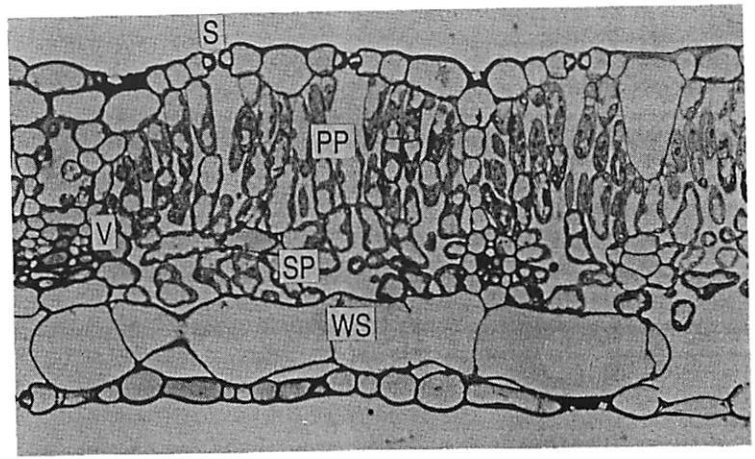

Fig. 1. A portion of a peanut leaf cross-section showing different cell and tissue types. Supplied by Dr. J. E. Pallas, Jr. PP - palisade parenchyma; SP - spongy parenchyma; WS - water storage cell; S - stoma; V - vein.

This layer accounts for about 25% of the leaf thickness (Il'ina, 1958; Maeda, 1970). Stomatal frequency is similar on the upper and lower surface, with the total for both ranging from about 300 to 400 per mm² (Bhagsari and Brown, 1976a).

Photosynthesis by peanut leaves is apparently typical of that for warm season dicotyledonous crop plants. Assimilation of CO_2 by reductive pentose phosphate (C_3) pathway is indicated by: (1) O_2 inhibition of photosynthesis (Pallas and Samish, 1974), (2) CO_2 compensation concentrations near 50 ppm (Bhagsari and Brown, 1976b), and (3) $\delta^{13}C$ ratios (Troughton et al., 1974), and also by leaf anatomy typical of that of C_3 dicotyledonous plants. The rate of light saturated apparent photosynthesis (AP) (Table 1) is also similar to values reported for C_3 crop species.

Table 1. Maximum Apparent Photosynthesis Rates for Peanut Leaves.

Growth & Measurement Conditions[1]	Apparent Photosynthesis ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)	Reference
Greenhouse ($1.2\ cal\ cm^{-2}\ min^{-1}$)	35	Alberte et al., 1976
Field or outdoors in pots (32 klux and outdoors at 70-100 klux, 30 C, young, fully expanded leaves)	41, 41, 30	Bhagsari and Brown, 1976a
Greenhouse & outdoors in pots ($1,000\ \mu E\ m^{-2}\ s^{-1}$, 30 C, youngest fully expanded leaf)	33, 43, 50	Bhagsari et al., 1976
Greenhouse (48.4 klux, 30C, second or third fully expanded leaf from tip of branch)	31, 23	Bhagsari and Brown, 1976b
Growth chamber at 25 C and $225\ \mu E\ m^{-2}s^{-1}$ ($1546\ \mu E\ m^{-2}s^{-1}$, 25 C, tops of 2 seedlings)	40, 41, 39, 43 44, 34, 52, 51	Pallas and Samish, 1974
Growth chamber at 28/21C & 32 klux (23 klux, 28 C, youngest fully expanded leaf)	21	Gallaher et al., 1976
Field grown ($1600\mu Em^{-2}s^{-1}$, 30C, third leaf from tip of branch)	22, 28	Henning et al., 1979
Field grown ($1600\mu Em^{-2}s^{-1}$, 26-35 C, 10 day old leaves)	65	Trachtenberg & McCloud, 1976
Growth chamber, 25/20 C, $340\ \mu E\ m^{-2}s^{-1}$ (25 C, 1150-1400 $\mu E\ m^{-2}s^{-1}$)	41	Pallas, 1980
Greenhouse (30 C, 4000 ft-c, young fully expanded leaves)	28	Daughtry, 1974
Mean	38.1 ± 10.6	

[1]Conditions during measurement given in parenthesis. Near atmospheric levels of CO_2 and O_2 were used during measurements.

Photosynthetic Capacity. The range in maximum AP of peanut leaves is from about 21 to 65 mg $CO_2\ dm^{-2}\ hr^{-1}$ (Table 1), so that even under near optimum conditions considerable variation exists in photosynthetic capacity. This wide variability is undoubtedly due in part to conditions under which plants were grown and to variation in experimental technique.

The values in Table 1 represent a range of cultivars, and some of the variation may be due to cultivar differences. Bhagsari and Brown (1976a) found considerable variation among 31 genotypes, with adapted cultivars having the highest AP rates and wild species of *Arachis* having the lowest. Pallas and Samish (1974) also found cultivar differences in AP, with the virginia type cultivars, NC4 and Cordoroy, having the highest rates and Tifton 8 the lowest. In a study by Bhagsari et al. (1976), Tifton 8 had a higher AP rate than Florunner, although the latter had the highest rate among many genotypes in other studies (Bhagsari and Brown, 1976a, b). It is unclear, therefore, whether photosynthetic capacity varies among recently developed cultivars.

Effects of Environmental Factors.

Temperature. As a subtropical legume crop, peanut attains its maximum leaf AP rates at about 30 C (Bhagsari, 1974). The rate decreases above and below this optimum so that at 40 C the rate is reduced about 25% and at 10 C by more than 65% (Figure 2). The temperature response curves were similar for 2 genotypes of *A. hypogaea* and 3 wild species, although the wild

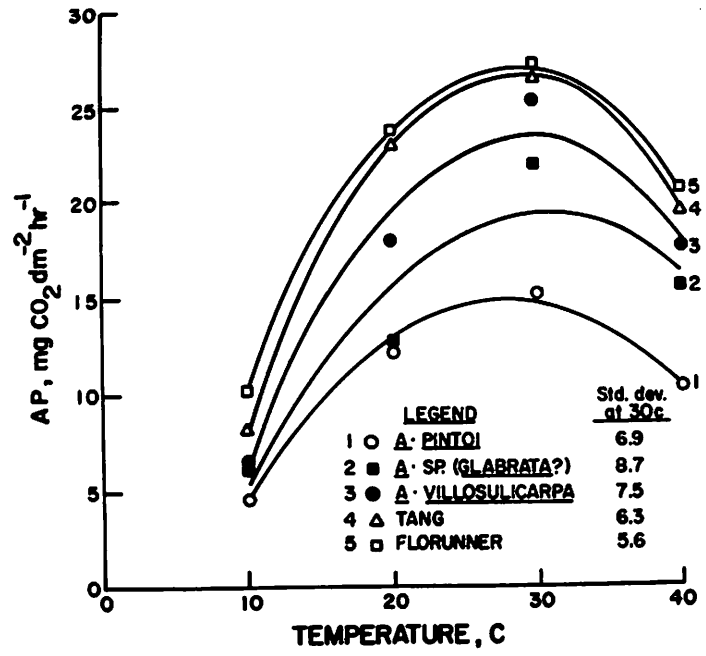

Fig. 2. The temperature response of apparent photosynthesis (AP) of leaves of two cultivars of *Arachis hypogaea* and three wild species of *Arachis*. Reprinted by permission from A. S. Bhagsari (1974).

species had lower AP rates. In contrast to the response reported by Bhagsari (1974), Pallas et al. (1974) showed a decrease in AP when leaf temperature was increased from 20 to 30 C. In their experiments the entire tops of young plants were enclosed in the measuring chamber, which may account for the lower optimum temperature.

Irradiance. The response of AP to irradiance depends on the conditions under which plants are grown. Therefore, the variability reported in response of peanut leaves may be due to the variable growth conditions. Bhagsari (1974) found one genotype of *A. hypogaea* to be saturated and another to be nearly saturated at irradiance of about 48 klux (Figure 3). These plants were grown in the greenhouse during spring and summer and had lower maximum AP (20 to

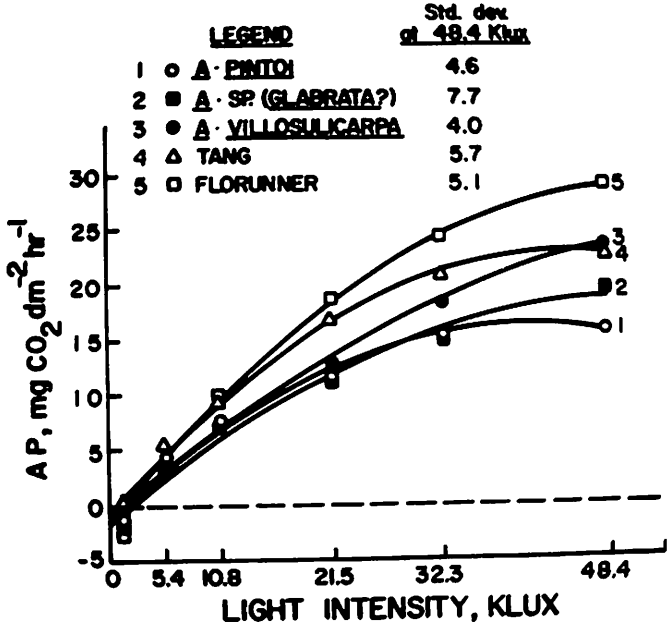

Fig. 3. Light response curves for apparent photosynthesis (AP) of leaves of two cultivars of *Arachis hypogaea* and three wild species of *Arachis*. Reprinted by permission from A. S. Bhagsari (1974).

30 mg CO_2 dm^{-2} hr^{-1}) than other studies have shown. Pallas and Samish (1974), however, grew plants at rather low irradiance (225 μE m^{-2} sec^{-1}) and found higher AP which was light saturated only at 1600 μE m^{-2} sec^{-1}. Young leaves of field grown plants have been found to have much higher maximum AP rates (65 mg CO_2 dm^{-2} hr^{-1}) and to require irradiances near full sunlight for light saturation (Trachtenberg and McCloud, 1976).

Very few measurements of dark respiration and AP at low light levels have been made. Bhagsari (1974) reported dark respiration of 1.7 to 2.6 mg dm^{-2} hr^{-1} for *Arachis* genotypes and found that 2.7 klux or less was needed for compensation by photosynthesis. Pallas et al. (1974) measured dark respiration rates ranging from 0.2 to 0.5 mg CO_2 dm^{-2} hr^{-1}.

Water Stress. Earlier reports of some xerophytic characteristics of peanut plants are not supported by response of AP to water stress. Reductions of

leaf water potential from about -7 to -30 bars, by withholding water from potted plants, caused AP of Florunner peanuts to decrease from 42.6 to 5.4 mg dm^{-2} hr^{-1} (Bhagsari et al., 1976). The decrease in AP was accompanied by an increase in diffusive resistance to water vapor of from 0.9 to 21 sec cm^{-1}. Similar results of water stress were observed for 3 other peanut genotypes and soybean. While the results are not conclusive with respect to adaptation to water stress, especially because the drying cycle was only 5 to 6 days, they indicate a response similar to other crop species. Although it has been suggested that leaf "water storage" cells (Figure 1) of peanut and folding of the leaves play a role in water stress avoidance (Il'ina, 1958; Allen et al., 1976), it is not certain that peanuts possess special characteristics which aid in maintaining photosynthesis under low moisture conditions.

During a rather long drying cycle (18 days) in a sandy field soil, Allen et al. (1976) found that minimum relative leaf water content had reached only about 85% compared to 30 to 40% in the experiments of Bhagsari et al. (1976). Likewise leaf diffusive resistance rose to a maximum of only about 10 sec cm^{-1} compared to 20 to 30 sec cm^{-1} in the pot experiments of Bhagsari et al. Therefore, AP may not normally be reduced by droughts in the field as severely as in the pot experiments of Bhagsari et al. (1976).

Carbon Dioxide and Oxygen. Although these 2 environmental factors are uncontrolled and show little variation in the field, response to them is informative about the nature of photosynthesis. As mentioned earlier, peanut is rather typical of the C_3 photosynthetic type. This is illustrated by the characteristics exhibited in Figure 4. Apparent photosynthesis increases in a linear manner with CO_2 concentration at least up to 600 ppm. The CO_2 compensa-

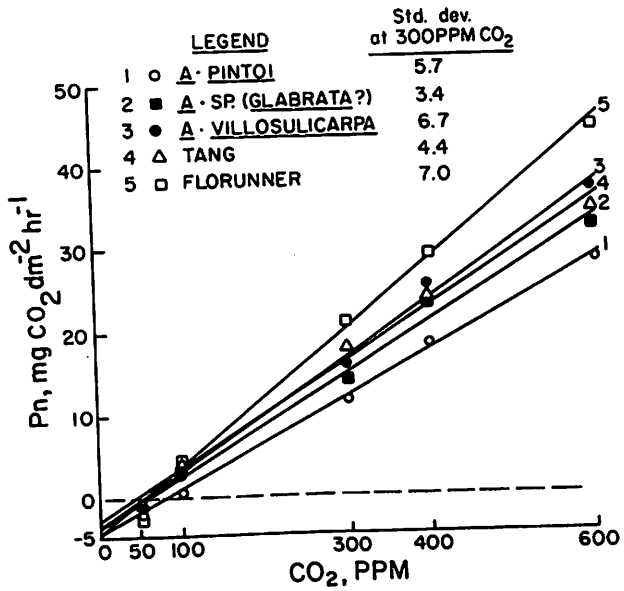

Fig. 4. The response of apparent photosynthesis (AP) of leaves of two cultivars of *Arachis hypogaea* and three wild species of *Arachis* to carbon dioxide concentrations. Reprinted by permission from Peanut Sci. 3:12 (1976).

tion concentration is about 40 to 60 ppm, typical of C_3 species. Extrapolation of the CO_2 response line to a CO_2 concentration of zero, or measuring CO_2 evolved from the leaf into CO_2-free air in the light, gives an estimate of photorespiration. In peanut this value is about 3 to 5 mg dm^{-2} hr^{-1} (Bhagsari and Brown, 1976b).

If peanut leaves are exposed to low O_2 concentrations (1 or 2 %), AP increases because O_2 both inhibits CO_2 uptake and stimulates photorespiration in C_3 plants. At atmospheric level of CO_2 and O_2, the reduction in AP by O_2 is about 30% (Pallas and Samish, 1974). Responses to CO_2 and O_2 characterize peanut as a C_3 species since C_4 plants, mostly tropical grasses, exhibit no photorespiration and are not sensitive to O_2.

Leaf and Plant Age. Leaves of peanut plants become less efficient with age after full expansion (Gallaher et al., 1976). This change is shown in Figure 5 in which AP rises during the time the leaf is expanding, but decreases thereafter. Full leaf size and maximum AP usually occur at about 10 to 15 days after the leaf appears. Beyond full leaf expansion, the rate at which AP declines is variable, probably depending on environment, nutrition, and disease. In leaves of plants grown in a growth chamber at an irradiance of 32 klux, AP dropped to near zero at about 40 days after unfolding (Figure 5), but leaves on field grown plants may photosynthesize for longer periods (Trachtenberg and McCloud, 1976). The field grown plants had leaf AP rates of 30 mg dm^{-2} hr^{-1} when leaves were 60 days old. Since maximum AP measured by Trachtenberg and McCloud (1976) was considerably higher than reported by others for field grown plants (Table 1), the AP rate of 30 mg dm^{-2} hr^{-1} for 60 day old leaves is probably not very representative.

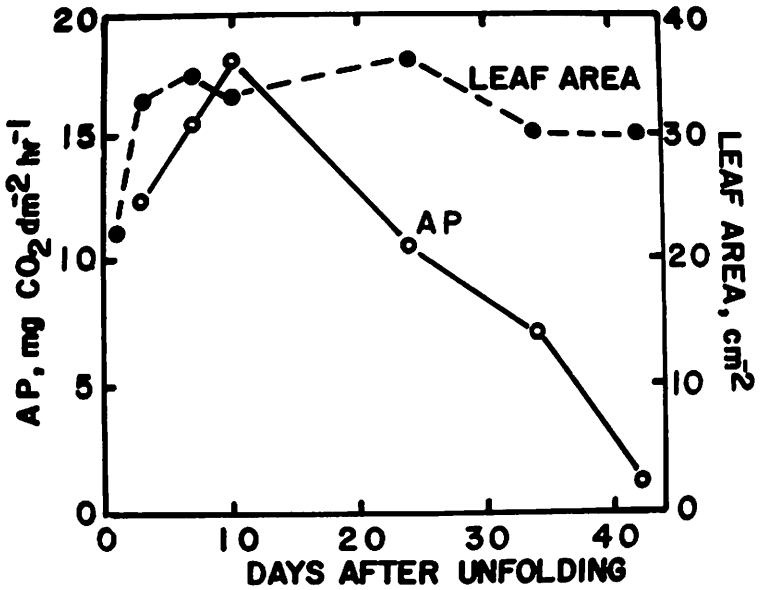

Fig. 5. Effects of age on apparent photosynthesis (AP) and area of leaves of Florunner peanuts. Leaves were selected from different positions on the plant to obtain the ages shown. Adapted from Gallaher et al., 1976.

Henning et al. (1979) showed a general decline in AP of peanut leaves as plants aged from 80 to 140 days in the field. Leaves at the third node from the tip of a branch decreased by 50 to 65% during this period. Leaves at node 8 had much lower AP, which decreased in a manner similar to that of the younger leaves.

Photosynthesis of Plant Canopies

Leaf Area Index and Light Interception. The leaf canopy of the peanut crop has not been very well defined. The density of the canopy measured as leaf area index (LAI = ratio of leaf area to soil area) increases from very low levels early in the season to maximum values which range from about 4 to 7 (Williams et al., 1975a, b; Enyi, 1977; Williams, 1979b; Yayock, 1979; Boote et al., 1980). Figure 6 shows changes in LAI for Starr spanish type peanuts planted at 100, 134, and 168 kg of seed per ha or populations of 207,000, 337,000, and 641,000 plants per ha. The increase in plant population raised the maximum LAI from about 4 to 7. A similar effect of plant population on LAI was reported by Enyi (1977). Maximum LAI occurs during the early-to mid-pod filling stage (Williams et al., 1975a, b; Enyi, 1977), and a decrease follows which varies depending on several factors, particularly leaf spot disease (Boote et al., 1980).

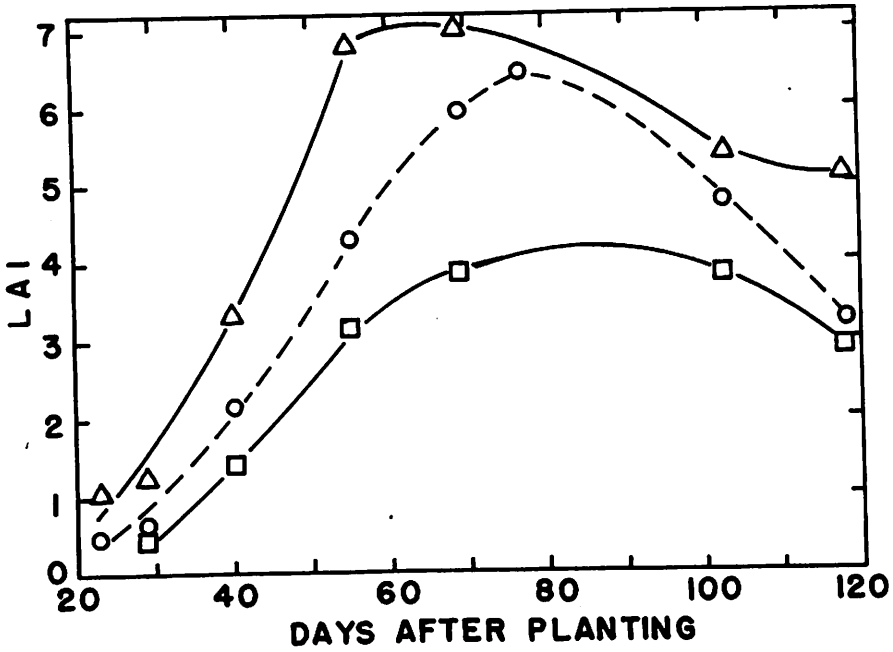

Fig. 6. Changes in leaf area index (LAI) for Starr spanish type peanuts during the growing season at plant populations per ha of 207,000 (squares), 337,000 (circles), and 641,000 (triangles), corresponding to seeding rates of 100, 134, and 168 kg ha^{-1}, respectively. Brown Unpub. data.

Duncan et al. (1978) observed that light interception was about 95% complete at an LAI of 3. From this observation an extinction coefficient can be calculated for visible radiation of about 1, a value typical of crops with near horizontal leaves. A value of 0.88 can be calculated from data of Boote et al. (1980) for nondefoliated plants, and the values were similar for 3 vertical canopy layers. Thus, while canopies may reach LAI values of 7 or 8, growth rate is probably near maximum at any LAI above 3. As shown in Figure 6, however, the highest plant population would have optimum or higher LAI for a longer period than the low population.

Carbon Dioxide Exchange. There are few published data concerning canopy photosynthesis in peanut. Boote et al. (1980) measured maximum AP rates of 2 to 4 g CO_2 m^{-2} ground area hr^{-1} in a study of leafspot disease damage. Daughtry (1974) observed AP rates as high as 7 and 8 g CO_2 m^{-2} hr^{-1} in Tifspan and Florunner cultivars, respectively. Unpublished data of Schubert and Brown in Figures 7 and 8 show maximum rates of 6 to 7 g CO_2 m^{-2} hr^{-1} for Florunner. It appears, therefore, that AP of well developed canopies of peanut may reach values of 6 to 8 g CO_2 m^{-2} hr^{-1}.

The response of canopy AP to irradiance is much more nearly linear than is leaf AP. Data in Figure 7 show that the response to light is nearly linear to irradiance of 1600 to 1800 μE m^{-2} sec^{-1}, which is near full sunlight. Extrapolation of the line to zero AP indicates that about 500 μE m^{-2} sec^{-1} is necessary for photosynthesis to compensate for respiration by the canopy. Curves presented by Boote et al. (1980) for Florunner peanuts with low leafspot damage are less steep than that in Figure 7 and show a somewhat lower light compensation point. Their canopy AP rates are also somewhat lower. They reported that respiration of the soil and plants was 1.4 g CO_2 m^{-2} hr^{-1}, or about 1/3 of maximum AP.

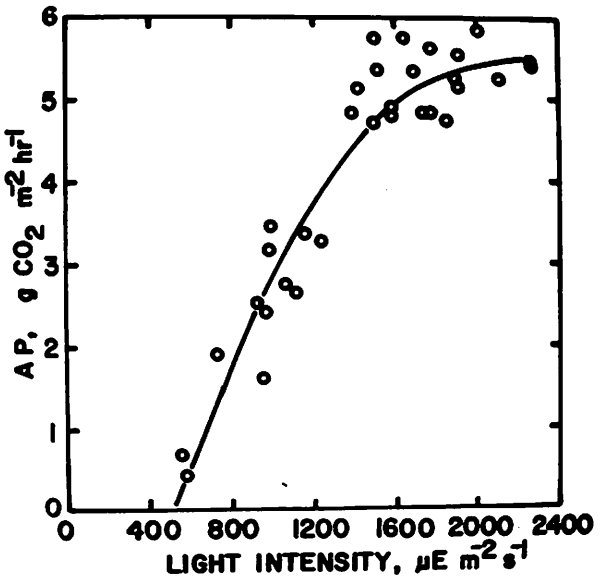

Fig. 7. Light response of apparent photosynthesis (AP) on a Florunner peanut canopy. AP is expressed on a soil area basis. Schubert and Brown Unpub. data.

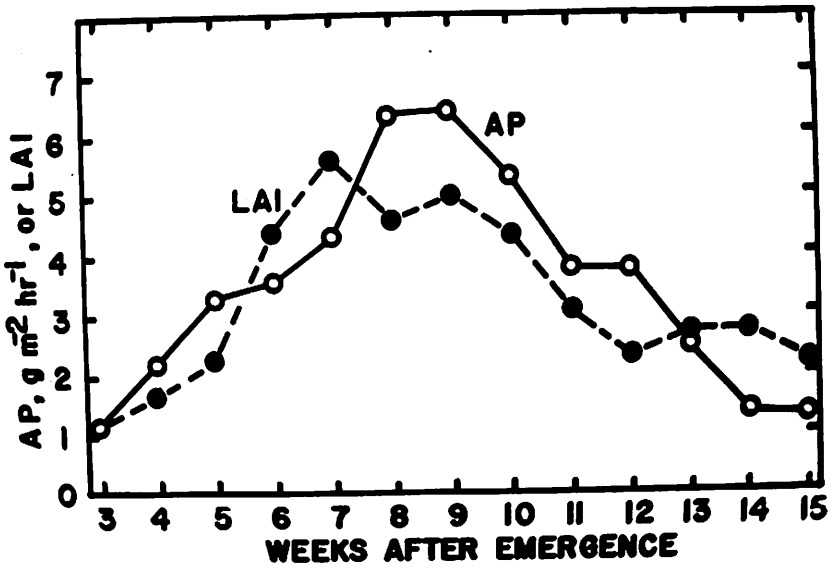

Fig. 8. Changes during the growing season in apparent photosynthesis (AP) and leaf area index (LAI) of a Florunner peanut canopy. Measurements were made near noon at high light intensities. Schubert and Brown Unpub. data.

In the work of Boote et al. (1980) leafspot damage substantially reduced canopy AP, increasing dark respiration and the light compensation intensity. At a light intensity of 1500 μE m^{-2} sec^{-1}, AP was reduced 35 and 65% when leafspot damage was 11 and 56%, respectively.

Seasonal Changes. Light interception is the major controlling factor in canopy AP and, therefore, AP is expected to follow the increase in LAI as the stand develops. The data in Figure 8 show that weekly maximum canopy AP for Florunner peanuts increases from about 1 g CO_2 m^{-2} hr^{-1} at 3 weeks after emergence to a value of 6.5 at 8 to 9 weeks. Thereafter, it drops steadily to nearly 1 g CO_2 m^{-2} hr^{-1} at 14 to 15 weeks. Leaf area index followed a similar trend with maximum values occurring slightly earlier than maximum AP. In the following year, 1976, leafspot control was better and the decline in LAI and AP was much more gradual.

Growth Analysis

Dry Matter Growth Rates. Total Plant Growth. Dry matter accumulation in a peanut crop follows the general pattern exhibited by most annual species. The pattern is characterized by: (1) a lag in early growth, (2) exponential increases in weight near the end of the lag phase, (3) a linear maximum growth rate during late vegetative growth and early pod filling, and finally (4) a leveling of weight during late pod filling (Figure 9). Early top growth is composed mostly of mainstem elongation and leaf production, but lateral branches account for the bulk of later growth. Maeda (1970) showed that for several cultivars mainstem leaves accounted for over one-half of the leaf area of the plant up to about 35 days after planting, but by 90 days mainstem leaves accounted for only about 10%. Late in the life of the plant, dry matter accumulation is

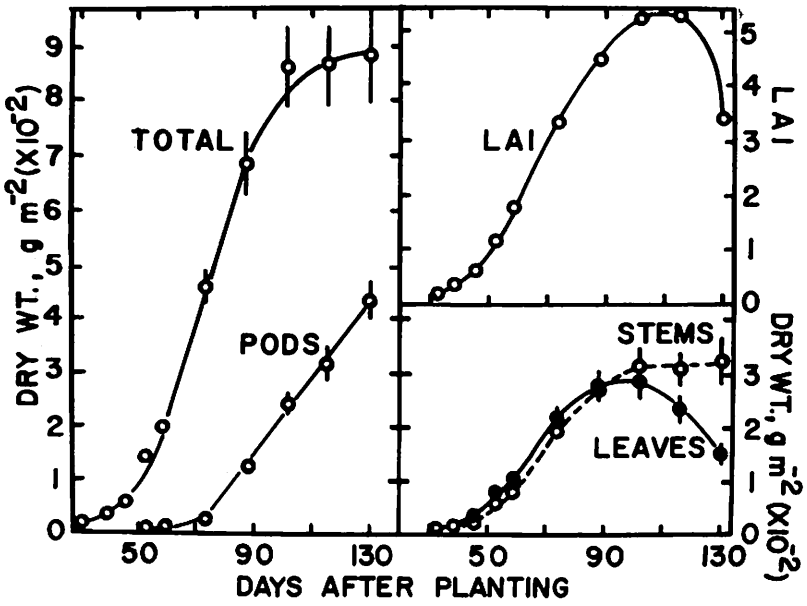

Fig. 9. Dry matter accumulation and changes in leaf area index (LAI) of a Florunner peanut crop. Vertical lines indicate one standard deviation. Brown Unpub. data.

mainly of reproductive structures, and estimates of growth are complicated by loss of leaves.

Crop growth rates (C) may be estimated from the slope of the total weight curve in Figure 9 and expressed as weight of dry matter accumulated per unit ground area per unit time (for example, g m^{-2} day^{-1}). The estimate, C, increases from a very low value early in the season to a maximum at about 60 to 90 days after planting. Maximum C estimated from published reports of 24 different experiments of cultivar comparisons averaged 19.6 ± 4.2 g m^{-2} day^{-1} (King, 1971; Cahaner and Ashri, 1974; Daughtry, 1974; Williams et al., 1975a, b; Enyi, 1977; Duncan et al., 1978; Young et al., 1979). This value is similar to those for other crops with the C_3 photosynthetic pathway.

Vegetative Growth. Early leaf and stem growth has been studied by Maeda (1970, 1972, 1973). He found that 5 or 6 leaf primordia existed in the embryo of the seed and that 5 were well developed in large seeded cultivars and 4 in small seeded ones. These primordia form the first leaves on the mainstem, and the rate of emergence was found to be more rapid for the first 3 or 4 leaves than later ones, apparently because of the higher degree of development for the first 3 or 4 primordia. Maeda (1973) also showed that leaf emergence rate on mainstems was strongly correlated with mainstem elongation rate over a range of temperatures.

Leaf and stem dry weights increase in a sigmoidal fashion up to maximum values which occur at about 90 to 100 days after planting (Figure 9). During this period leaves and stems accumulate weight at similar rates. Following maximum vegetative weight, leaf weight declines, whereas stem weight usually remains constant, although it sometimes decreases (Williams et al., 1975a). The loss of leaves during late pod filling may be nearly complete (Williams et al., 1975a; Enyi, 1977) or only slight (Cahaner and Ashri, 1974). The leaf loss from 100 to 130 days in Figure 9 was nearly 50%.

Very few studies have included measurements of root growth, but it appears that roots account for only a small percentage of the total plant weight, especially late in the growth cycle. Wood (1968) found that roots of plants growing in pots accounted for about 15% of total weight 32 days after planting, but only 2 to 4% at 88 days. Enyi (1977) observed lower percentages for root weight in field grown plants: the values being 5 to 7% at 1 month after planting and only 1 or 2% at 5 months after planting. Because of the difficulty in harvesting roots, the weights reported may not be very accurate. The low percentages of total dry weight in roots probably means that most reported crop growth rate values which do not include roots are not much in error because of this omission.

Reproductive Growth. Flowers begin to form at about 25 to 30 days after planting in most cases (Fortanier, 1957; Bolhuis and de Groot, 1959; Wood, 1968; Wynne et al., 1973), but Williams et al. (1975b) found considerable variation among cultivars, with Makulu Red beginning flowering as late as 55 days after planting. The number of flowers produced daily increases to a maximum at 2 to 4 weeks after flower initiation and then declines to nearly zero during pod filling (Smith, 1954; Ishag, 1970; Williams et al., 1975b; Young et al., 1979).

Pod number and weight become measurable at about 60 to 70 days after planting. Pod number rises rapidly to a maximum at about 100 to 120 days after planting (Daughtry et al., 1975; Williams et al., 1975b), then remains nearly constant until harvest. The increase in pod number is nearly linear until the maximum number is reached (Duncan et al., 1978; Williams, 1979b). Pod weight increases in a near linear fashion during pod filling after a short lag period (Figure 9). The linear growth rate continues until near harvest time in most cases, but may tend to level off during late pod filling (Williams et al., 1975b; Enyi, 1977).

The rates of pod dry matter accumulation during the linear growth phase range from about 5 to 10 g m^{-2} ground area day^{-1}. An average value for 24 separate experiments or cultivar comparisons from published reports was 8.3 ± 2.1 g m^{-2} day^{-1} (King, 1971; Cahaner and Ashri, 1974; Daughtry, 1974; Williams et al., 1975a, b; Enyi, 1977; Duncan et al., 1978; Young et al., 1979). Duncan et al. (1978) found cultivar differences in pod growth rates, but there do not appear to be consistent differences among botanical types.

Early growth of pods differs in relative weight of structures and chemical composition from later pod growth. Shells make up most of the weight of the fruit during early growth (Schenk, 1961; Williams et al., 1975b). For individual fruit Schenk (1961) observed that the shell had nearly reached its full weight before significant seed weight accumulated. The percentage of fruit weight accounted for by seed increased from about 5 to 10% at 2 weeks of age to 80% at maturity. Crude protein percentage decreased during fruit growth, but beyond about 3 weeks, protein in seed did not reach values lower than about 20 to 25% of dry weight. However, protein percentage in the shell and testa continued to decrease throughout development. Lipid content of seed increased from about 30% of dry weight at 2 weeks of age to 50% at 6 or 7 weeks.

The high lipid and protein percentages in peanut fruit means that more energy is required per unit of dry matter synthesized than is the case for vegetative organs. Watanabe (1975) found that the CO_2 equivalent in dry weight accumulation (change in dry weight/change in CO_2 equivalent) of the peanut plant decreased from 0.64 during vegetative growth to 0.29 near maturity. If the maximum C given earlier (19.6 g m^{-2} day^{-1}) is corrected for the reduced dry weight/CO_2 equivalent "transformation factor" (Watanabe, 1975) observed during early-to mid-pod filling, then C becomes 25 g m^{-2} day^{-1}.

Environmental Effects on Growth. Growth of peanuts is influenced by field environments in a manner similar to many other crops. Adverse environments reduce growth, but depending on the timing, vegetative and reproductive growth may not be influenced in the same way. For example, drought early in the growing season (36 to 70 days after planting) had a relatively small effect on pod yields (14% reduction), but drought during the 71 to 105 day period reduced yields 37% compared to control plots (Pallas et al., 1979). Vegetative yield was not significantly affected by drought during these periods. Since water relations are treated in Chapter 7, further discussion will deal with other environmental factors.

Temperature plays an important role in most aspects of plant growth. Response of photosynthesis to temperature was shown earlier (Figure 2) to be parabolic with an optimum near 30 C. It appears that dry matter production has a similar response (Fortanier, 1957), although some disagreement about the optimum exists. Optimum day/night temperatures for growth of whole plants has been reported at 35/25 C (Ono et al., 1974), 30/26 C (Cox, 1979), 35/20 and 30/35 C (Fortanier, 1957), and 25/25 C (Wood, 1968). Fortanier (1957) found that plants became less sensitive to temperature as they became older, and Cox (1979) confirmed this trend, finding very little effect on top growth of temperatures in the range of 22/18 to 34/30 C imposed after plants had grown for 28 days at a common temperature. However, plants grown for 21 days at a common temperature of 30/25 C and then exposed to 35/22 C for the remainder of the test had less total leaf area per plant than plants grown at 30/22 C (Ketring, unpublished). It is fairly clear from the several reports that the optimum mean daily temperature for the peanut plant is near 30 C, and some studies (Fortanier, 1957; Cox, 1979) show that growth ceases at about 15 C.

The initiation and growth of the various plant organs respond differently to temperature. Fortanier (1957) found, for example, that the optimum for stem extension and leaf expansion occurred at about 30 C, but flower number was greatest at 20 or 25 C. Wood (1968) also observed lower optimum temperatures for flowering than for growth, but Cox (1979) found vegetative growth and flowering to have the same optimum. Disparity also exists in the reports on relative temperature response of vegetative and pod growth. In some cases pod growth is reported to have a lower optimum temperature than top growth (Cox, 1979), but Ono et al. (1974) found maximum pod growth rates at 31 to 33 C, similar to the optimum for top growth.

Results thus far do not give a clear picture of temperature dependence of pod formation and growth. The number of developing pegs was found by Wood (1968) to be greater at 20 C daytime than at higher temperatures. Fortanier (1957) observed highest peg number at a day temperature of 32 C, when night temperature was 23 C. When night temperature was 32 C, the optimum day temperature was 26 C. Temperatures of 35/22 C reduced the number of subterranean pegs and weight of mature seed (Ketring, unpublished). Williams et al. (1975a) found the highest peg numbers in plants grown at an altitude of 900 m corresponding to a mean daily temperature of 23.2 C and the fewest pegs at 1620 m and a mean temperature of 17.9 C.

The percentage of pegs which bore pods was inversely related to temperature in the work of Williams et al. (1975a) so that high peg production did not insure high pod number or yield. The highest yield was at an intermediate altitude at which neither peg number nor individual kernel growth rate was maximum. Thus, the highest yield was obtained at a mean temperature, 20.1 C, which produced intermediate peg numbers and seed growth rates. This is in contrast to the optimum for pod growth of 26/22 C day/night temperatures in studies by Cox (1979) and 31 to 33 C soil temperatures observed by Ono et al. (1974).

Effects of environmental factors other than temperature are less well known. Fortanier (1957) stated that the irradiance requirements for normal growth was low for peanut compared to other crops, and Cox (1978) observed maximum growth of young plants at 25 E m^{-2} day^{-1} (equivalent to 463 μE m^{-2} sec^{-1} or about 23% of full sunlight over a 15 hr day). On the other hand, photosynthesis of leaves (Pallas and Samish, 1974; Trachtenberg and McCloud, 1976) and particularly photosynthesis of plant stands (Figure 7) does not light saturate except at irradiances near full sunlight. Growth and pod yield of field grown plants have also been found to be greatly reduced by shading to reduce sunlight by 50% or less (Ono and Ozaki, 1971; Brown, unpublished). Further discussion of this topic is given under "Environmental Factors" later in this chapter.

While environmental effects on growth and yield are profound, genetic effects may be more important because of the possibility for manipulation through breeding. Improvements in yield have been made through breeding as discussed in the following section.

Analysis of Yield Variation. In the simplest analysis, yield may be increased by producing a larger number of fruit per unit area or larger fruit. Both of these attributes are subject to environmental and genetic effects, but fruit number appears to be most variable for a given cultivar.

Although a small percentage of flowers result in pods, conditions which promote rapid flowering early in the season contribute to high yields. Temperatures which caused the largest flower numbers during a 12-day period in early flowering resulted in the greatest fruit weight for plants subsequently grown at a common temperature (Wood, 1968). However, because of the small percentage of flowers resulting in pods (Smith, 1954) and because flower number produced per day fluctuates widely (Young et al., 1979) while pod initiation appears nearly constant until a maximum is reached (Duncan et al., 1978), the total number of flowers is probably not closely related to yield.

The number of pods formed, however, is a strong determinant of yield. For a given cultivar fruit size is fairly constant at maturity, and the greatest yield determinant is pod number. In spacing trials, for example, variation in yield is accounted for almost entirely by pod number, with weight per pod being constant over a wide range of plant populations (Cahaner and Ashri, 1974; Enyi, 1977). In a comparison of cultivars differing in yield, Duncan et al. (1978)

found that the highest yielding cultivars were those which had the highest rate of increase in pod number. Florunner, the highest yielding of 3 runner type cultivars, had a daily pod initiation of 10.6 per m^2 compared to 6.6 per m^2 for the older, lower yielding Dixie Runner.

In the comparison by Duncan et al. (1978), the most influential physiological factor in yield determination was considered to be the partitioning of photosynthate to fruit during the pod filling period. Maximum vegetative growth rates were similar among the cultivars so that photosynthetic potential was considered to be equal. Figure 10 shows the relationship between pod yields and the "partitioning coefficient" for 5 cultivars (Duncan et al., 1978). The partitioning coefficients ranged from 40.5% to 97.8%. Since the crop growth rates (vegetative phase) were found to be similar, the partitioning of a higher percentage of photosynthate to pods gave higher pod growth rates. Therefore, plotting of pod growth rates against yield (Figure 10) shows a close relationship between these characteristics. Thus, highest yield among cultivars appears to be associated with rapid increase in pod number and near cessation of vegetative growth during pod filling.

A third plant characteristic which may influence yield, in addition to pod numbers and partitioning of photosynthate to pods, is the duration of pod fill. Duncan et al. (1978) considered length of the filling period to be 1 of 3 main factors influencing yield differences among cultivars. Makulu Red, a high yielding cultivar, was found by Williams et al. (1975b) to have a similar fruit growth rate to 2 lower yielding cultivars, but a longer filling period. In fact, Makulu Red fruit were still growing near harvest until complete defoliation caused growth to cease.

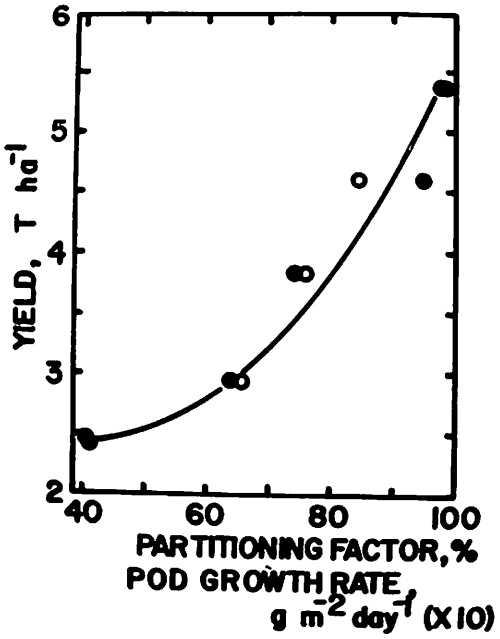

Fig. 10. Relationship between final pod yield and the partitioning of dry matter to pods (partitioning factor - closed circles) and pod growth rate during the linear phase (open circles). Calculated from data of Duncan et al., 1978.

The interaction of factors influencing yield is complex, and the importance of a given characteristic in yield determination depends on climate, cultural practices, and insect and disease problems. For this reason, high yielding cultivars bred for one area may not be successful in others.

GROWTH REGULATORS

Ontogenetic development and correlative growth of plants are controlled by balances between contents of natural endogenous phytohormones. The major well-known hormones are auxins (IAA), gibberellins (GA), cytokinins (Kinetin), ethylene, and abscisic acid (ABA). The exogenous application of natural substances as well as synthetic chemicals to alter plant growth and development has been extensively researched. Practical uses in agriculture have been most successful for production and processing of ornamental, vegetable, and fruit crops. Their successful use to increase yields of field crops has been more difficult to achieve, but the potential is there.

Vegetative Growth

The growth habit of peanut plants is under complex genetic control (Halevy et al., 1969; Coffelt, 1974; Levy and Ashri, 1978; Resslar and Emery, 1978) and is affected by light (Ziv et al., 1973) and plant growth regulators (Halevy et al., 1969). These factors apparently influence the balance between endogenous growth promoting and inhibiting substances. Halevy et al. (1969) found that contents of gibberellin-like substances were similar in both runner and erect type plants. However, runner type plants had an additional inhibitory substance(s) that antagonized gibberellin activity and they also had larger amounts of inhibitor in shoot tips and leaves from lateral branches than erect type plants. Thus, both genotype and environment determine endogenous levels and balances of plant hormones, but the concept of increasing the ratio of reproductive to vegetative growth by exogenous chemical means has not been very successful for field crops such as soybeans and peanuts.

The synthetic antiauxin, TIBA (2, 3, 5-triiodobenzoic acid), applied to peanut plants shortened internodes, reduced lengths of cotyledonary branches and main stems, and decreased shoot dry weight (Hallock and Alexander, 1970; Hartzook and Goldin, 1970; Bauman and Norden, 1971). Leaflets may be reduced in size and their morphology affected. However, vegetative growth of some cultivars was unaffected by TIBA.

The synthetic growth retardant SADH (succinic acid 2, 2-dimethylhydrazide), marketed under the trade names B-nine, Alar-85, and Kylar, affected vegetative growth similarly to TIBA (Brittain, 1967; Baumann and Norden, 1971; Brown et al., 1973; Brown and Ethredge, 1974; Hammerton, 1976). Another growth retardant CCC (2-chloroethyl) trimethylammonium chloride had no noticeable effect on vegetative growth (Gorbet and Whitty, 1973; Das Gupta, 1975).

Morphactins, derivatives of 9-hydroxyfluorene-(9)-carboxylic acid, inhibited shoot fresh weight (Ketring, 1977b), altered apical dominance, and promoted lateral branching of peanut plants (Krishnamoorthy and Khun, 1972). They also reduced stomatal frequency and aperture size, total chlorophyll con-

tent, and assimilatory capacity of peanut plants (Umapathi and Swamy, 1978). Spraying either runner or erect type plants with (2-chloroethyl) phosphonic acid (CEPA), marketed under the trade names Ethrel or Ethephon, caused lateral branches to grow more erect (Ziv et al., 1976). Natural ethylene evolution from branch tips of runner and erect type plants decreased and increased, respectively, as the lateral branches grew and assumed their usual growth habit (prostrate for runner type and vertical for erect type plants). Also, extracts from branch tips of Ethrel treated plants contained higher GA activity and less inhibitor activity than control plants, which corresponded with the erect growth habit. Ethrel applied to field grown peanuts at the early fruiting stage of a spanish type cultivar reduced vegetative growth (Wu, 1976). However, Ethrel treatments at earlier stages of vegetative growth (2-4 weeks postemergence) had no effect or stunted the plants in different years. But the stunted plants resumed growth and this effect was not noticeable at harvest (Ketring and Schubert, 1980).

On the other hand, ABA, which is generally considered as a natural growth inhibitor, increased shoot fresh weight without affecting dry weight of plants grown in the greenhouse (Ketring, 1977b).

Reproductive Growth

Flowering. All yields components (flowers, pegs, pods, and seeds) of peanut plants have been found to be affected by plant growth regulators. Flowering was increased or decreased by maleic hydrazide (MH) depending on the concentration used (Banks, 1971). Flowering was reduced by ABA, a growth retardant (4-chlorobenzyl-tri-n-butylammonium bromide) which had little effect on vegetative growth, and by a 1:1 mixture of picloram plus 2,4,5-T (4-amino-3,5,6-tri-chloropicolinic acid plus 2,4,5-trichlorophenoxy-acetic acid, Pic + T) (Ketring, 1977b). Ethrel also inhibited flowering. If applied before flowering began, it delayed flowering and reduced the number of flowers produced (Krishnamoorthy, 1972). Ethrel (Figure 11) or Pic + T, applied after flowering began, effectively blocked further flowering for a period of time and then flowering resumed (Ketring, 1977b; Ketring and Schubert, 1980).

Pegging. Pegs naturally produce ethylene during their growth. The highest rates occurred during initial stages of growth (first day) (Lee et al., 1972) and just after penetrating the soil (Hedges and Fletcher, 1979). Peg tip sections taken after 1 day of growth also had the highest GA content (Lee et al., 1972). Zamski and Ziv (1976) inhibited peg elongation with TIBA. Pegs with the ovary removed continued to grow more than controls (ovary removed without GA) if they were supplied with exogenous GA. Mnzava (1979) also found that GA partially reversed embryo removal and promoted intact peg elongation. This suggests that both auxins and gibberellins are involved in peg growth. Amir (1969) was able to induce pegging and pod formation from the upper nodes of erect plants by treatment with GA, but pod formation from the upper nodes reduced the number of pods from the lower nodes so that potential yield was not increased. Singh et al. (1978) also found increased pegging with sprays of GA, MH, and a napthaleneacetic acid (NAA) formulation. Pegging of peanut plants was enhanced by morphactins (Ketring, 1977b). Peg explant growth was enhanced by morphactin but it prevented their normal, positive

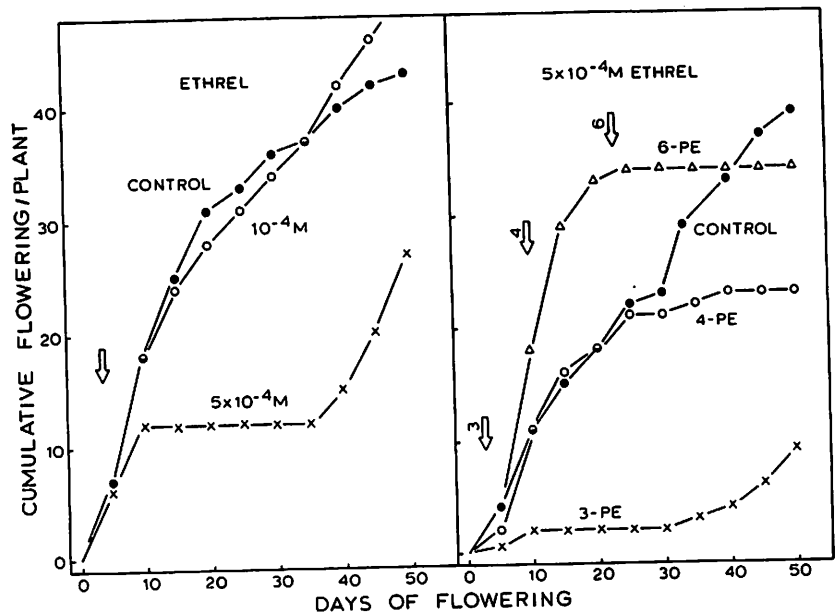

Fig. 11. Left: Effect of different Ethrel concentrations on flowering of Starr peanut plants. Treatment was applied at early flowering (28 days after planting). Indicated by arrow. Right: Effect of 5x10⁻⁴M ethrel applied 3 times at 2-week intervals beginning 3 and 4 weeks postemergence (PE) and once at 6 weeks PE on flowering of Tamnut 74 plants. Arrows indicate the day of treatment or start of multiple treatments. The first day of flowering was 25 days after planting for both tests. Reprinted by permission from Crop Sci. 20:329 (1980). Copyright 1980 by Crop Sci. Soc. of Amer., Inc.

geotropic growth (Mnzava and Flocker, 1978). This also implies a role for auxin in peg growth. Kylar tended to increase pegging of some cultivars (Bockelée-Morvan and Gillier, 1973; Daughtry et al., 1975) while decreasing it for others (King, 1971). Pod retention was better in 1 instance for a virginia type cultivar (Hodges and Perry, 1970), while neither Kylar nor TIBA significantly affected peg strength of other virginia type cultivars (Bauman and Norden, 1971; Troeger et al., 1976). Kylar reduced peg and pod lengths (King, 1971; Brown et al., 1973; Wynne et al., 1974; Daughtry et al., 1975). Early application times with Kylar tended to reduce seed size (Wynne et al., 1974; Daughtry et al., 1975; Hammerton, 1976), while later applications of Kylar (Daughtry et al., 1975) or TIBA (Hallock and Alexander, 1970) seemed to increase seed size.

Pod and Seed Formation. TIBA decreased pod weights of a virginia type cultivar and slightly increased pod weights of a spanish and valencia type cultivar, yet the total number of pods produced by all cultivars was reduced (Hartzook and Goldin, 1970). Kylar applications increased yield in only 1 growing season during 3 years of tests (Gorbet and Whitty, 1973) and increased yield in other tests (Bockelée-Morvan and Gillier, 1973). But no significant effects on yield were found for Kylar (Hammerton, 1976) or either TIBA or Kylar (Bauman and Norden, 1971). Similarly, TIBA applications did not produce consistent yields over seasons and cultivars and had small or no significant effects

on % sound mature kernels (Hallock and Alexander, 1970; Gorbet and Whitty, 1973). CCC applications have both depressed (Gorbet and Whitty, 1973) and increased yields (Das Gupta, 1975). However, these are 2 widely divergent systems: a runner type peanut grown in Florida, USA, and a bunch type peanut grown in Sierra Leone, W. Africa, respectively.

Yield of a spanish type cultivar planted in narrow rows (30 cm) was increased in one season by application of maleic hydrazide during later stages of growth (Krishnamurthy, 1971). Among growth regulators tested by Singh et al. (1978), also with narrow rows, maleic hydrazide provided the largest increase in weight of pods per plant. Brittain (1967) reported increased yields of virginia type cultivars when Kylar was applied to plants in narrow rows (45 cm) and compared with untreated plants at the same row spacing. Hodges and Perry (1970) found a similar row spacing effect, but otherwise yields were variable when Kylar was applied to virginia type cultivars at different treatment dates and row spacings. Other studies with virginia type cultivars at different interrow and intrarow spacings showed that Kylar applications had no effect or yields were reduced (Wynne et al., 1974). Brown and Ethredge (1974) also found a lack of consistent increase in pod yields of both virginia and spanish type peanut cultivars treated with Kylar. In combination with different irrigation treatments, Kylar seemed to aid retention of yield, but reduced crop value in some instances (Gorbet and Rhoads, 1975).

Other studies have also found that overall yields of spanish type cultivars have been affected in a variable manner by Kylar treatments (Morris, 1970; Brown et al., 1973; Daughtry et al., 1975). When yield increases have occurred, it seems to be due to an increase in number of pods per plant even though seed and pod size may be somewhat reduced (Brown and Ethredge, 1974; Daughtry et al., 1975).

Ethrel also has been used in attempts to increase peanut yields. As mentioned above, pegs naturally produce ethylene during initial stages of growth. Would an exogenous source of ethylene enhance pegging and, hence, yield? At concentrations (10^{-4} M) that had no effect on flowering in the greenhouse (Figure 11), the percentage of pegs formed was increased, but mature pods and seed were reduced. In addition, Ethrel applications had no effect or reduced yield and value of peanuts produced in the field (Ketring and Schubert, 1980). Other studies with Ethrel applications also have not improved yield (Azu, 1979).

The foregoing discussion deals with chemicals that retard plant growth. An opposite approach would be to use chemicals that promote growth, particularly fruit development. Plant cytokinins are one such group of chemicals. Cytex, the trade name of a water-soluble, cytokinin-containing material, was tested for its effects on peanut reproduction. It was sprayed on virginia and spanish type cultivars at different rates and growth stages over a 3 year period. Again, yield responses were inconsistent, and only in 1 year was a significant increase in yield obtained with a spanish type cultivar (Ketring and Schubert, 1981).

Others have had similar results with Cytex applications (Brown, Henning, Mixon, unpublished data). Yields were unaffected or, if increased, were not significantly different from the control. This new approach of using growth regulators to increase peanut yield warrants further research since it has had limited testing with only 1 material.

When treating peanuts or other seed crops with growth regulators, caution should be taken to insure that no detrimental residual effects occur to germination and vigor of the seed produced. Bauman and Norden (1971) reported reduced germination and vigor of seed from some of the cultivars treated with Kylar or TIBA. Seed from morphactin treated plants failed to emerge a radicle, and ethylene production by these seed was inhibited. Also, plants treated with abscisic acid or Pic + T produced seed with reduced hypocotyl-radicle growth (Ketring, 1977b).

In spite of the evidence reported above, some growers in the southeastern part of the USA peanut belt regularly include Kylar in their cultural system with apparent success (Cook, 1979; Hartwig, 1979; Henning, 1979). Their success may be due to reduced vegetative growth of the virginia type cultivars that are grown in this area. Control of excess vegetative growth probably allows better crop management by the grower rather than a stimulation of pod production per se. Further discussion of the use of Kylar in cultural practices is included in Chapter 5.

It is clear that peanut plants readily respond to exogenous application of plant growth regulators by changes in vegetative and reproductive growth. However, we have not yet developed the technology to increase fruit production using the chemicals that have been tried to date.

The Plant Growth Regulator Working Group, formed in 1973, is composed of individuals who are interested in using chemicals to beneficially modify the growth and development of plants. The 1979 chairman of this group, Dr. Page W. Morgan, had this to say in part of his address to the group, "Why then has the empirical approach not resulted in the use of many yield enhancers for major field crops? Visualize the number of problems involved: (a) one must select the proper chemical and the proper crop, (b) one must identify the proper stage of growth, concentrations, and method of application, (c) the response (yield increase) is much removed in time from the chemical treatment and can be influenced by a variety of other factors, and (d) the response may demand a combination of two or more compounds or two or more application dates." He not only indicates the problems involved, but also points out some approaches to solving them (Morgan, 1979). It is recommended reading for individuals pursuing research of plant growth regulators to increase crop yields.

ENVIRONMENTAL FACTORS

Light

The absorption of solar radiation by plants, in addition to being the energy source for photosynthesis, is a major factor in regulating plant growth and development. Light intensity (irradiance), quality, and photoperiod influence the way that plants grow.

Irradiance and Quality. In darkness peanut leaflets are folded closed. Blue light or far red irradiation cause the leaflets to open (Kadman-Zahavi, 1972). Ziv et al. (1973) showed that in darkness, or as solar radiation was decreased, the cotyledonary branches of runner type plants grew more erect and returned to horizontal growth in light. Also, with reduced irradiance or blue light the main axes and lateral branches were longer than at high irradiance or in blue

plus far red irradiation.

Shading treatments of peanut plants, begun shortly after emergence, not only reduced early growth but also inhibited subsequent growth (Ono and Ozaki, 1971; Hudgens and McCloud, 1975; Williams, 1979a). As less solar radiation was received and the treatment prolonged, plants produced less shoot dry weight and fewer mature pods and seed (Ono and Ozaki, 1971).

Shaded plants also had a slower rate of vegetative and reproductive growth. Maximum seed weight was achieved 2 weeks earlier under full sun or partially shaded plants, but seed weight at final harvest was not significantly different from fully shaded plants (Williams, 1979a). The shaded plants apparently compensated for the treatment by producing fewer seed which had the largest mean seed weight. This research agrees with the result that shading in the post-flowering period caused a reduction in the percentage of extra large kernels, but no significant difference in yield of individual shading treatments occurred (Hudgens and McCloud, 1975). An (1978) determined that a 21-day shading period during the pod filling stage caused the largest decrease in yield; however, shade increased oil percentage, starch, and reducing sugars in the seed.

Among the climatic factors tested by Gautreau (1973), total radiation received by the plants was a predominant factor in determining growth and fruiting. Cox (1978) reported that as photosynthetically active radiation was increased up to about 25 E m^{-2} day^{-1}, early seedling growth (shoot dry weight and leaf area) of a virginia type cultivar was increased. With less total irradiance, main axes and, to a lesser extent, lateral branches were elongated, in agreement with the work of Ziv et al. (1973). Ketring (1979b) found similar results with a spanish type cultivar grown for 21 days at 500 $\mu E\ m^{-2} s^{-1}$ followed by 300 $\mu E\ m^{-2} s^{-1}$. After 70 days the plants at the low irradiance had the same number of leaves, but larger total leaflet area per plant, and had longer main axes and cotyledonary lateral branches than plants grown at the higher irradiance. This research indicates that plants approaching the flowering stage of development can respond to different irradiances.

The way that light affects plant growth habit suggests that it may also alter endogenous levels of phytohormones. Gibberellic acid-like activity (activity obtained in bioassays of crude plant extracts containing unknown substances) was the same for extracts from the main axes and lateral branches of plants with a runner or erect type growth habit. However, bioassay indicated a higher content of growth inhibitors in extracts from runner type plants, particularly those under high irradiance where the runner type growth habit occurred (Ziv et al., 1973). Further studies showed that there was more ethylene production by branch shoot tips as irradiance was decreased or in blue light where runner type plants grew more erect (Ziv et al., 1976). Both erect growth and ethylene production were enhanced by red light or darkness and, as previously mentioned, Ethrel treated plants with erect growth habit had high GA activity and low inhibitor activity in shoot tip extracts. These results suggest that endogenous ethylene production and associated changes in other phytohormones may be involved in environmental and varietal regulation of the growth habit of peanut plants.

In relation to flowering and fertilization, Chhabra and Malik (1978) showed that red light hastened pollen tube growth and far red light reversed this effect. Blue light inhibited pollen tube growth, but this could be overcome by IAA.

Gibberellic acid increased pollen tube elongation in the dark and substituted for the red light effect.

In a study of light effects on pod development, Zamski and Ziv (1976) found that only in complete darkness was there normal pod development. Darkness was essential for induction of pod formation, and exposure to light inhibited further development. Also, in order for pods to assume their usual horizontal position, a mechanical stimulus such as entering the soil or some medium was necessary. Applying growth regulators (GA, NAA, Kinetin) to growing pegs did not overcome the dark requirement for pod development, and with GA and NAA abnormal peg growth occurred. But this may have been due to the high levels of GA and NAA used (0.1% in lanolin).

Other components of the reproductive phase of peanut plants are also affected by irradiance. Shading (Ono and Ozaki, 1971; Williams, 1979a) was mentioned above. In addition, flowering (Figure 12) and all subsequent reproductive components (pegs, mature pods, and seed) were decreased at low irradiance (300 $\mu E\ m^{-2} s^{-1}$) when compared to high irradiance (500 $\mu E\ m^{-2} s^{-1}$) (Ketring, 1979b). Yet flowering was not sufficiently reduced to account for the fewer mature pods and seed produced. There was no significant difference in immature reproductive components between the 2 irradiances. The low irradiance did not delay fruit formation, but the amount of fruit sustained by the plants to maturity was reduced. Concurrently, as mentioned above, vegetative growth, particularly leaf area, increased under low irradiance treatment. Since vegetative growth increased under low irradiance while reproductive components decreased, the plants quantitatively changed the proportion of vegetative to reproductive growth in response to irradiance. Leaf area was the

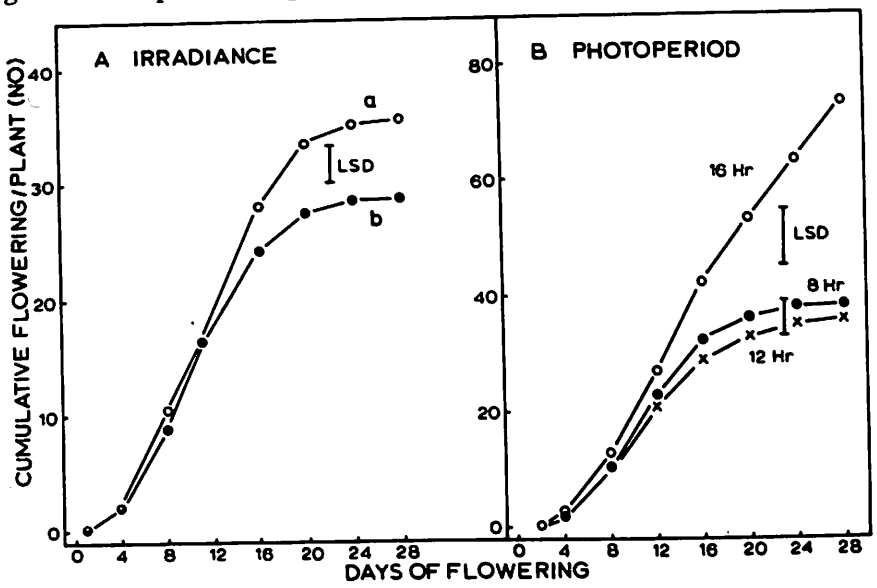

Fig. 12. Effect of irradiance (A) and photoperiod (B) on cumulative flowering of cv. Starr spanish type peanut plants. Irradiances were 500 $\mu E\ m^{-2} s^{-1}$ (a) and 300 $\mu E\ m^{-2} s^{-1}$ (b). Photoperiods were as shown. Day 1 of flowering was 23 to 26 days after planting. Reprinted by permission from Plant Physiol. 64:666 (1979). Copyright 1979 by Amer. Soc. of Plant Physiol.

main measurement of vegetative growth because in other work no relationship between shoot dry weight and seed formation was found (Ketring, 1977b).

Photoperiod. Early research cited by Gregory et al. (1973) showed that both vegetative and reproductive growth of peanut plants are influenced by photoperiod, that there is a photoperiod-temperature interaction, and that there are varietal differences in response to photoperiod.

Ketellapper (1969) showed that as photoperiod was increased from 8 to 20 hours at constant temperature dry weight and stem length of virginia type peanut seedlings increased. In 1973, Wynne et al. (1973) studied the effect of short- and long-day treatments on 6 peanut introductions (2 each of the 3 botanical types: virginia, valencia, and spanish). Plants grown under short-days (9 hour) were smaller and weighed less than plants under long-days when harvested at 64 days. Flowering was delayed, but more fruit was produced under short-days. The virginia type plants produced less vegetative and reproductive growth than the valencia and spanish types under both short- and long-days, but there was less difference under long-days. This may have been due to the naturally slower maturation rate of virginia type plants that was partially compensated for by the longer day lengths. Regardless of botanical type, plants under short-days at 30/26 C day/night temperatures had the highest fruit to shoot weight ratio. Similar results were found for hybrids among the 3 botanical types, but reciprocal crosses between spanish and valencia types had the highest fruit to shoot weight ratio under short-days (Wynne and Emery, 1974). Also, the ratios were higher when the spanish type was used as the female parent, and heterosis was expressed to a greater degree under short-days.

In a study of several peanut cultivars exposed to photoperiods from 6 to 24 hours, Sengupta et al. (1977) found that flowering occurred at all photoperiods. However, a 10-hour photoperiod was optimum for these cultivars under their conditions. Photoperiods shorter or longer than 10 hours delayed the initiation of flowering. This result differs from earlier research, and a more recent study shows a prolonged duration of flowering by a spanish type cultivar under a 16-hour photoperiod (Figure 12). Also, initiation of flowering was not delayed at any of the photoperiods (8-, 12-, or 16-hour) used (Ketring, 1979b). The 16-hour photoperiod also resulted in extensive vegetative growth. The plants had more leaves, larger total leaflet area, and longer main axes and cotyledonary laterals than plants grown at 8- or 12-hour photoperiods. However, as might be expected, the larger leaf area (photosynthetic surface) and long photoperiod did not result in more reproductive growth. Total pegs were the same for 12- and 16-hour photoperiods, but all subsequent reproductive components (mature pods, and number and weight of mature seed) of plants grown in 16 hours of light were reduced even below those of plants grown in 8 hours of light. A 12-hour photoperiod was optimum for reproductive growth in relation to total leaflet area (photosynthetic surface) produced (Ketring, 1979b) and was in the range of the 9 to 14 hours suggested to be optimum for fruit formation by the Schwarz 21 cultivar (Fortanier, 1957). The increased vegetative growth under long photoperiods and reproductive growth under short photoperiods agreed with the data of Wynne et al. (1973). Similar results also have been found for another spanish type cultivar (Emery et al., 1981). In addition, when plants were grown for 108 days and exposed to different photoperiod

treatments during 3 36-day periods, the 36- to 72-day period was most sensitive to photoperiod, and fruiting potential was highest when short-days were given during this period.

Thus, with respect to photoperiod, present peanut cultivars may not be very well adapted to the major peanut growing regions in the USA, where photoperiods exceed 14 hours during the season. However, Emery et al. (1981) mention that when the spanish genotype used in their study was grown in the field in North Carolina, USA, where it was exposed to 14-hour daylengths during fruiting, the yields per plant were similar to those of plants grown under short-days. The longer growing period in the field could certainly influence these results, but this plant, collected at 30° S latitude in Paraguay, may have previously adapted to longer photoperiods.

Temperature

Some additional aspects of temperature in relation to other environmental parameters are discussed here. Quantitative differences between genotypes can be induced by temperature treatments and, as mentioned above, there is a photoperiod effect. Also in combination with temperature is relative humidity. Perhaps due to the difficulty of strict control of intermediate levels of relative humidity, its effects have not been studied extensively. But comparisons between high (97%) and low (50%) relative humidity at 30 C have shown that flowering, pegging, and peg growth rate are increased by high relative humidity (Lee et al., 1972).

When plants grown at 26/22 or 22/18 C day/night temperatures were compared to those grown at 30/26 C, there was less vegetative and reproductive growth at the lower temperatures, and the fruit to shoot weight ratio was reduced. The ratio decreased further for all temperature regimes under long photoperiods (Wynne et al., 1973).

A bunch type cultivar was grown in Rhodesia at different altitudes. Mean radiation and relative humidity were the same, but temperature decreased with increasing altitude (Williams et al., 1975a). The most phytomass was produced at the lowest altitude (900 m), which had the highest mean daily maximum (29.7 C) and mean daily minimum (17.3 C) temperatures. The most pegs were also produced at these temperatures, but the proportion of pegs forming pods was greatest at the coolest temperatures (24.2 C mean daily max. and 13.6 C mean daily min.). However, the largest numbers of pods and seed (yield) were produced at the intermediate temperatures (27.0 C mean daily max. and 14.5 C mean daily min.), while the largest mean seed weight occurred at the coolest temperatures. Campbell and McCloud (1979) found that a runner type plant grown at a constant temperature of 26 C day/night produced the highest average seed weight, while a warmer regime (32/26 C) gave the highest number of seed, and a cooler regime (20/26 C) provided the highest yield of mature seed. Azu (1979) reported that in a cool climate with a short growing season for peanuts (Ontario, Canada), the warmer year produced the highest yields. This was attributed to a higher rate of pod filling at the warmer temperatures.

From the discussions of temperature thus far it seems that optima are different for each phase of peanut development and may not always occur in relation

to the present sequence of events from planting to harvest, i.e., vegetative growth occurs during the cool spring and early summer planting season while reproductive growth takes place during the hot summer relative to the latitude at which the crop is grown.

Since temperature is critical for peanut plant growth and development, attempts have been made to determine temperature requirements of peanut cultivars at different stages of their development. Using a heat unit method, Emery et al. (1969) estimated that a base temperature of 13.3 C could be used to determine the heat unit requirements of virginia type cultivars from planting to 50% flowering in North Carolina. Heat unit requirements were different for the 2 cultivars tested. Estimates of base temperature by curvilinear functions for planting to flowering of virginia type cultivars indicated a minimum base temperature of 6.1 C and a maximum base temperature of 21.7 C (Cox and Martin, 1974). The average of these 2 temperatures is near that of the base temperature estimated for use in the heat unit method. It was inferred from these estimates that planting at average minimum and maximum temperatures below these base temperatures would delay the rate of plant development. To minimize the time-to-flowering, optimum minimum and maximum temperatures at planting were estimated to be 16.1 and 30.5 C or 16.5 and 34.8 C, respectively, by alternate methods. Thus, temperature differences between daily minima and maxima could be in the range of 14 to 18 C at planting in North Carolina. Examination of research and weather station data for the United States southwest growing area indicated that differences between the mean daily or average monthly minimum and maximum temperatures during the major part of the growing season (May to September) ranged from about 8 to 13 C and were frequently greater than 13 C. In Rhodesia (Williams et al., 1975a) mean daily minimum and maximum temperature differences ranged from 10.6 to 12.4 C. Since field temperature measurements were used in all of these studies, it is clear that peanut plants are exposed to large temperature extremes during the growing season.

Evaluation of peanut cultivars for genotype x environment interactions on yield and yield components seems to indicate only minor effects of genotype x location and genotype x year interactions, but there were relatively large genotype and genotype x location x year interactions (Tai and Hammons, 1978; Wynne and Isleib, 1978). These interactions could occur if annual variations in weather are influencing yield components of genotypes. Some genotypes, with respect to pod yield, seed weight, and oil content, are apparently more stable across environments than others (Yadava and Kumar, 1978, 1979). Other studies of the effect of weather and genotype x environment interactions on yields of peanuts found that different components of the environment (temperature, radiation, and water stress) have significant effects on yield only at specific phases of growth and development (Williams et al., 1978). For instance, maximum temperature was significantly related to yield at all growth phases for 2 cultivars and most growth phases for a third cultivar. However, temperature range, radiation, and water stress were significantly related to yield only at specific growth phases. More genetic diversity in genotype x environment interactions was found when cultivars from the United States and Rhodesia were grown in environments for which they were not selected.

In studies of genotype x environment interactions for water-management systems (irrigated versus nonirrigated), there was a large portion of the variance due to genotype for yield components (Tai and Hammons, 1978). Other studies have found sufficient diversity between genotypes to make it possible to select cultivars better adapted to these environments. It appeared particularly advantageous to select for irrigated versus dryland conditions when harvesting at an earlier than normal date (Dashiell, 1979).

Soil temperature has received little attention, but it also affects peanut plant development. In a study of soil temperatures in the pegging zone, Ono et al. (1974) found an optimum temperature of 31 to 33 C for pod development. Treatment with high soil temperature (37 to 39 C) and low soil moisture (6 to 8%) indicated that a critical stage in pod development occurred 20 to 30 days after the peg entered the soil. The optimum temperature for pod development found in this study seems somewhat high when the atmospheric temperatures influencing pod and seed development mentioned above are considered. Cultivar differences might be an explanation, but it clearly is an area where research is needed.

Since temperature is a major environmental variable affecting both vegetative and reproductive growth phases of plants, it might be useful as a means of screening genotypes for their response to specific environments under controlled conditions. However, the temperatures (maxima, minima, and range) used must be based on those occurring under field conditions. One criticism of data obtained in most controlled environments thus far could be that the light/dark temperature regimes are too narrow, only differing by 4 to 5 C in many cases. As indicated above, greater differences often occur under field conditions.

NITROGEN FIXATION

Peanuts and other legumes can form symbiotic associations with soil bacteria of the genus *Rhizobium*. The bacteria infect the plant roots, proliferate, and invade the root cells (Dart, 1977). The root cells then proliferate to form the nodules where molecular nitrogen from the atmosphere is fixed. These nodules contain bacterial cells (bacteroids), host plant cells, and leghemoglobin. The leguminous plant by itself cannot fix nitrogen, but bacteroids and some free-living rhizobia can fix nitrogen under proper cultural and nutrient conditions (Burris, 1976; Bergersen, 1977). A general scheme for nitrogen fixation is:

$$N_2 \rightarrow H_2\,N\text{-}NH_2 \rightarrow 2NH_3 \rightarrow \text{amino acids}$$

(nitrogenase)

Rhizobium Strain

Symbiosis between plant and bacteria does not guarantee vigorous nitrogen fixation. Effective nitrogen fixation depends on a critical relationship between host plant and bacteria. In fact, bacteria can infect the roots, form nodules, but ineffectively fix nitrogen (Dadarwal et al., 1974; Weaver, 1974; Singh et al., 1976; Caldwell and Vest, 1977; Wynne et al., 1978).

Current research is attempting to overcome these ineffective host plant-bacteria associations. Different bacterial strains from nodules of both cultivated

and wild peanut genotypes are being isolated and tested for effective host-strain combinations (Van der Merwe and Strijdom, 1973; Dadarwal et al., 1974; Lopes et al., 1974; Weaver, 1974; Ayala, 1975, 1977; Staphorst et al., 1975; Singh et al., 1976; Schneeweis et al., 1978; Wynne et al., 1978). Kishinevsky and Bar-Joseph (1978) have developed a very sensitive method for identifying *Rhizobium* strains from *A. hypogaea* nodules.

Strain Evaluations

Isolated bacteria have been tested to determine physiological characteristics of effective nitrogen fixing strains. Vidhyasekaran et al. (1973) found 3 strains that produced large amounts of IAA in culture and also produced more and larger nodules on the host. However, Singh et al. (1976) found no correlation between physiological characteristics of *Arachis* rhizobium strains and their symbiotic efficiency.

Effectiveness of host-bacteria symbiosis has been evaluated by nodulation scores (number and weight formed); nodule leghemoglobin, nitrogen, and iron content; nodule nitrogenase and nitrate reductase activity; plant nitrogen content and color; and plant dry weight. Schiffman and Löbel (1973) found that leghemoglobin content of fresh peanut nodules from inoculated plants reached a maximum 2 to 3 months after planting, then declined, but remained relatively high until the end of the season. Dry weight of shoots and leaflets increased nearly to the end of the growth period, but nitrogen content of the leaflets was highest during the first 2 months after planting, then slowly declined. Nodule leghemoglobin and leaflet nitrogen content depended on planting date and plant age, and there was a plant age x planting date interaction. Correlation between leghemoglobin and nitrogen content was high and significant for later periods in the growing season. However, no correlation between specific nitrogenase activity or percent total nitrogen in the plant and nodule leghemoglobin content was found by Ayala (1977). But total nitrogenase activity and nodule leghemoglobin content were positively correlated. Also, nitrogenase activity and plant total nitrogen content were correlated with specific nitrate reductase activity of intact nodules. Nitrate reductase activity of intact nodules seemed to be the most promising test for comparative evaluation of effectiveness of peanut rhizobia (Ayala, 1977).

Dadarwal et al. (1974) found that rhizobia from wild species nodulated cultivated *A. hypogaea,* but based on nitrogen content of the shoots and nodules, isolates from *A. duranensis* were most effective. When isolates from *A. duranensis* were used to infect *A. hypogaea,* significant positive correlations between percentage nodule nitrogen and weight of shoots at flowering, weight of seed, percentage nitrogen in shoots at flowering, and percentage nitrogen in seed were found (Singh et al., 1976). However, a negative correlation was found between percentage nitrogen in the seed and percentage of fats.

Both nodule nitrogenase and nitrate reductase activities were highest at early stages of plant growth and declined as the plants aged (Ayala, 1975). However, Ratner et al. (1979) found that maximum nitrogenase activity occurred later in the season during pod-filling. In inoculation and inoculation plus nitrogen fertilization tests, Ratner et al. (1979) found that inoculation alone provided the highest pod and seed yields. Seed from inoculated plants had the highest crude protein and lower oil content than the controls, but on a kg/ha basis both protein and oil were highest from inoculated plots. The inverse relation between seed protein and oil contents agree with the data of Dadarwal et al. (1974) with respect to percentage nitrogen and fats in the seed. Estimation of the contribution of symbiotic nitrogen fixation to the total nitrogen accumulated in the plants was as high as 58% in the season when yields were highest. Comparing 2 seasons for nodule development (number and weight) and nitrogenase activity, it was found that nodule development was high while nitrogenase activity was low, and the opposite occurred in the second season (Ratner et al., 1979). However, maximum nitrogenase activity occurred about 90 days after planting in both seasons. One reason suggested for the decline of nitrogenase activity in the second season was exceptionally hot and dry weather.

Wynne et al. (1979) found changes in nitrogenase activity, nodule number, and nodule weights at different harvest dates during the season. These characteristics were different for cultivars, and there was a cultivar x harvest date interaction. Rhizobial strains also differed in their effects on host plant color and weight, nodule number and weight, plant nitrogen content, and nitrogenase activity (Wynne et al., 1980). The host genotype affected plant characteristics such as color, weight, and nitrogen content, while the bacterial strain affected these plant characteristics and nitrogenase activity as well. There were also interactions for nodule number and weight and nitrogenase activity.

These kinds of data for peanuts and other legumes have established that both the plant genotype (Caldwell and Vest, 1977) and the bacterial strain (Schwinghamer, 1977) determine an effective or ineffective host plant-bacteria symbiosis. Using grafting techniques, it was demonstrated that both the shoot and the root can influence nodulation (Caldwell and Vest, 1977). One of the major known contributions of the shoot to nitrogen fixation is photosynthate supplied to the nodule (Hardy et al., 1971; Hardy and Havelka, 1976; Pate, 1976). One of the environmental factors limiting photosynthesis and plant growth and development as discussed above is light. But other factors such as high temperature and drought also limit biological nitrogen fixation.

Environmental Factors

Light. Diurnal effects on nitrogen-fixing activities have been found with maxima occurring near the time of maximum light intensity (Hardy and Havelka, 1976; Pate, 1976). However, this may not be the case for peanut plants. Peanuts in the field showed 2 maxima: one near the end of the night period, and another toward the end of the day (Balandreau et al., 1974). Thus, it is possible to make measurements of nitrogen-fixing activity of peanuts in the field that could under- or overestimate their capability, particularly if only single measurements are made.

Few or no nodules develop on seedlings in the dark (Dart, 1977). Shading decreased nitrogen fixation, while supplemental light increased fixation, and nodule specific nitrogen-fixing activity was similarly affected (Hardy and Havelka, 1976; Pate, 1976; Sprent, 1976). Increasing the level of carbon dioxide in the peanut canopy increased nitrogen fixation by increasing nodule number and mass. This was attributed to increased photosynthesis and available photo-

synthate (Havelka and Hardy, 1976). Plants grown at low and high light intensities and then transferred to the opposite treatment showed an increase and decrease in nitrogenase activity, respectively (Gibson, 1976).

Photoperiod also affects legume nodulation, with long days promoting more and larger nodules than short days (Gibson, 1976; Pate, 1977). This result suggests a direct photosynthetic effect on symbiosis since this occurs regardless of the photoperiodic requirements of the host for flowering (Pate, 1977). However, as discussed above, peanut plants produce more fruit under comparatively short days.

There is also a nonphotosynthetic effect of light quality on nodulation. Exposure of the shoot or root of some legumes to far red light inhibits nodulation, while red light reverses this effect, which suggests the involvement of the phytochrome system (Gibson, 1976; Pate, 1977).

Temperature. Temperature effects on symbiosis are quite complex. Variables include the host, host age, rhizobium strain, and shoot and root temperatures. There are optimum temperatures for infection, nodule development, and nitrogenase activity, and these are host-strain dependent (Dart et al., 1976). However, nitrogen-fixing activity exhibits a rather wide temperature tolerance, and generally the optimum constant temperature promoting maximum yield of fixed nitrogen is close to the optimum for host plant growth (Dart, 1977; Pate, 1977). But the light/dark temperature regimes under which the plants are grown also influence their nitrogen-fixing activity. Such a response was found for peanut plants (Schneeweis et al., 1977). For other legumes, more activity occurred for plants grown at lower temperature regimes, and the temperature for maximum enzyme activity was also lower, while the opposite occurred for plants grown at higher temperature regimes (Gibson, 1976). At low root temperatures, nodule dry weight and nitrogen content were proportionately larger than at higher root temperatures. The point at which shoot and/or root temperatures becomes excessively high and nitrogen fixation is adversely affected depends on the rhizobium strain and host plant (Dart et al., 1976; Gibson, 1976; Lie et al., 1976).

Water Stress. When whole plants or detached nodules are subjected to water stress, there is a severe suppression of nitrogen fixation (Pate, 1976, 1977; Sprent, 1976). The effect may be direct since the nodule obtains a large portion of its water supply from the host root, or indirect due to inhibition of photosynthesis by the host. The pattern of nitrogen-fixing activity with respect to nodule fresh weight was similar for several legumes, and a 50% reduction in activity occurred at about 75% of maximum nodule fresh weight. Water stress affected nodulation, nodule growth and weight, as well as nitrogen-fixing activity (Sprent, 1976). Ratner et al. (1979) suggested that hot and dry weather caused cessation of nitrogenase activity in one year of their tests.

Many of the details concerning the effect of environment on nitrogen fixation by peanuts have not been elucidated, but the variability in host genotypes, rhizobium strains, and their interactions indicate that heritable factors in both host and bacteria are available for selecting to improve symbiosis of peanut plants for different climates, soil types, and agronomic practices. However, even when symbiosis is effective from indigenous rhizobium populations or improved strains that efficiently compete with native bacteria, factors (soil and atmospheric) other than nitrogen supply can limit yields (Staphorst et al., 1975).

TISSUE CULTURE

A discussion of peanut tissue culture seems particularly appropriate at this time. Most of the basic plant tissue culture techniques that have been used with other species have been partly successful for peanuts. Thus, there is reason to believe that peanuts may eventually be manipulated *in vitro* similarly to tobacco and alfalfa. On the other hand, published research on peanut tissue culture is small, and routine tissue culture techniques have not yet been developed. Only a few varieties have been tested *in vitro*, and it is likely that genotypic differences in *in vitro* performance will be found in peanuts just as they have been in other plants.

Within the next few years, progress in peanut tissue culture can be expected to accelerate. Since the first critical experiments have shown the potential for peanut tissue culture, the next step is to perfect these techniques so that they can be used to improve peanuts.

Banks (1976) pointed out that a number of agronomically desirable traits that are lacking in cultivated peanuts are found in wild *Arachis* species. These include resistance to diseases and pests. Species cross-incompatability factors have prevented the introduction of these traits into cultivated peanuts. However, these barriers may eventually be overcome by bridging schemes. *In vitro* techniques such as ovule or embryo culture, which have been used with other plants (Skirm, 1942; Smith, 1944; Keim, 1953; Inomata, 1968; Halberd, 1969), may be of use in circumventing embryo abortion or seed failure that occurs in wide crosses of *Arachis* (Johansen and Smith, 1956; Martin, 1970; Kubicek and Banks, 1971).

Culture of Vegetative Tissue

Leaf mesophyll cells have been cultured by several workers (Joshi and Noggle, 1967; Joshi and Ball, 1968; Jullien, 1970). In this instance, Joshi and Ball (1968) report that the minerals of either Murashige and Skoog (1962) or White (1963) are unsuitable. The authors do report a medium that is suitable for maintaining long-term suspension cultures. These cultures differ from those of most other plant species in that, even though the cells undergo dedifferentiation, they retain their chloroplasts and can be used in studies of photosynthesis.

Undifferentiated callus tissue has been derived from *Arachis* explants by several workers. Kumar (1974) used seedling hypocotyls as an explant source and cultured them on the minerals of Murashige and Skoog with various additives. He found that tissue growth and chlorophyll development was enhanced by the addition of thiamine hydrochloride, nicotinic acid, pyridoxine, inositol, and calcium pantothenate, either alone or in combination. Choline chloride impaired chlorophyll development, while folic acid and cyanocobalamin also had inhibitory effects. No differentiation was reported.

Russo and Varnell (1976) were able to culture peanut shoot tips that formed callus. The basal medium required 2,4-D (2,4-dichlorophenoxyacetic acid), and optimum concentrations were 3 to 4 ppm. Callus grown on 2,4-D continue to grow and produce shoots when transferred to a medium containing kinetin, but the shoots were produced from pre-existing meristems, not from

meristems formed *de novo* in culture. Some calli developed roots at the base of existing shoots. Illingworth (1968, 1974) propagated peanuts from cotyledons or cotyledonary fragments. In his initial work, peanut seed were kept in liquid nitrogen for at least 24 hours. They were fragmented by shaking, and the fragments were cultured. Auxin was found to promote root growth, while benzyladenine caused roots to turn green. No shoots differentiated with either growth regulator.

Heinis and Guy (1977) and Guy et al. (1978) also developed callus from peanut epicotyl, hypocotyl, and cotyledons. They used a modified Murashige and Skoog medium with 2 ppm each 2,4-D, NAA, and kinetin.

Culture of Reproductive Tissue

Peg explants with the tips pointing upward were induced to grow and orient positively geotropic in light when cultured on a basal medium or media containing kinetin and NAA. But no ovary growth occurred for light-grown explants. Only dark-grown explants supplied with kinetin and NAA grew positively geotropic and had ovary enlargement and pod formation (Ziv and Zamski, 1975).

Rangaswamy et al. (1965) cultured peanut pericarp tissue on modified White's medium (1963) with various additives. Explants grew only when the basal medium was supplemented with coconut milk. Roots differentiated, but no shoots formed.

Martin (1970) cultured ovules of *Arachis hypogaea* and obtained plants from ovules as small as 0.3 mm. The medium used included the major elements of Murashige and Skoog (1962) as well as kinetin (0.5 to 1.0 mg/l) at pH 5.5.

Using techniques similar to those of Saunders and Bingham (1972), Yung-ru and Yu-hung (1978) cultured peanut embryos and embryonic roots in a 2 step procedure. Callus was initiated on the medium of Murashige and Skoog with 2 mg/l 2,4-D. Suspension cultures were then made from callus using the medium of Liau and Boll (1970). When cell clumos had formed, they were plated out on modified Murashige and Skoog medium for differentiation. Roots formed on many of the calli, and 3 plantlets were obtained.

A low level of success in obtaining haploid cells from anther culture has been reported by 2 laboratories. Martin et al. (1974) and Martin and Rabechault (1976) found that 2,4-D, NAA, and kinetin in combination were the best growth regulators. Anthers cultured on medium with 60% sucrose showed slow callus growth and no differentiation. When callus started on that medium was transferred to differentiating medium with 20 g/l sucrose, it performed better than callus started on lower sucrose medium. Only 3 to 5% of the anther-derived calli differentiated. Roots formed fairly readily, but shoots formed only rarely. Only calli grown on medium containing coconut milk produced shoots and the few frail albino plants produced did not survive. Haploid cells were scarce in the callus while diploid or polyploid cells were common. Most of the callus was probably derived from diploid filament or connective tissue.

Mroginski and Fernandez (1979) cultured 3 species of *Arachis*. In addition to *A. hypogaea* L., *A. correntina* and *A. villosa* anthers were cultured. Callus formed on anthers from all 3 species and roots differentiated. Shoots did not form, although structures similar to shoot primordia were occasionally seen. The basic media of Nitsch (1969) and Murashige and Skoog were tested in combination with various growth regulators. Although callus formed on both media, performance was somewhat better on the medium of Nitsch.

Braverman (1975) cultured mature embryo axes and succeeded in producing pathogen free plants from seed that were contaminated with bacteria and fungi. One factor preventing the introduction of new peanut varieties into East Africa is pathogen contamination. Seed are routinely screened for contamination and those found to be contaminated are not introduced. As a result of the use of tissue culture, new varieties were released for use in East Africa.

Peanut embryos, anthers, seedling hypocotyl, and root tissue have been cultured in research at Oklahoma State University. Media tested have included those of Randolph and Cox (1943) as well as media previously reported for embryo culture (Keim, 1953; Halberd, 1969; Martin, 1970). These were supplemented with various additives including coconut milk, tomato juice, and the growth regulators NAA, IAA, GA, kinetin, and 2,4-D, either alone or in combination.

Plants have been produced from ovules or embryos as small as 2 mm. In a number of cases, rootless shoots have formed. In addition, profuse callus sometimes formed at the base of these shoots. In 2 instances, structures resembling shoot primordia formed from this callus. Upon transfer to other media, some of these reverted to callus production, while others showed no further development.

Genotype may well be a factor influencing the *in vitro* performance of peanut tissues and organs. Several cultivars have been used, and the strain EC-5, an early maturing spanish type peanut, performs best so far. It is quite possible that the "permissive conditions" to enable other varieties to perform *in vitro* will be found as various varieties are tested on growth media with different combinations and concentrations of growth regulators (Johnson and Banks, unpublished data).

SUMMARY AND CONCLUSIONS

Recent research concerning physiological aspects of peanut plant growth and development has revealed many facts about the nature of this plant. Cultural practices are adequate to produce quality peanut seed. Regulation of events in germination by phytohormones and metabolic processes of the seed are linked with seed quality. But evaluation of seed quality for better estimates of field emergence needs to be resolved. Growth patterns of the plants following seedling emergence are qualitatively similar, but differ quantitatively among genotypes. Photosynthesis and, perhaps as a consequence, both vegetative and reproductive growth are not very tolerant of temperatures above 30 C. Selection of genotypes more tolerant of high temperatures would seem to be a worthwhile endeavor. The 1980 growing season in the United States, with 40 or more days of maximum temperatures above 38 C in some areas, many days of 34 to 37 C, and the resultant drastic reductions in yield that were suffered by growers is evidence of this. Although variation exists in reports on the effects of environment (temperature, light) on reproductive growth, yield increases seem possible by selection for increased pod numbers, higher partitioning

coefficients, and longer pod filling periods. Environmental factors influence endogenous phytohormone levels that regulate growth and development, but exogenous application of chemicals to consistently increase yield components that result in a more marketable product needs an innovative approach that might use growth stimulating substances rather than inhibitors. The soil micro-environment also offers possibilities for improved peanut crop performance through better matching of peanut genotypes with new rhizobia strains that produce a more effective host plant-bacteria symbiosis for nitrogen fixation. Cross-incompatability factors have limited introduction of favorable genes from wild *Arachis* spp. into cultivated peanuts, but this may be circumvented through tissue culture techniques. Thus, several challenging physiological approaches are available in developing new and improved peanut cultivars.

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