CHANGES IN FREE AMINO ACIDS, CARBOHYDRATES, AND PROTEINS OF MATURING SEEDS FROM VARIOUS PEANUT (*ARACHIS HYPOGAEA* L.) CULTIVARS

S. M. M. BASHA[1], J. P. CHERRY, and C. T. YOUNG, Department of Food Science, University of Georgia Experiment Station, Experiment, GA 30212

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ABSTRACT

Maturing seeds harvested from plants of six peanut cultivars (*Arachis hypogaea* L.) grown for 17 and 20 weeks from time of planting were analyzed for dilute buffer (sodium phosphate; I = 0.03, pH 7.9) and total (1*N* NaOH)-soluble proteins, free amino acids, and carbohydrates. Based on morphological characteristics, the developing seeds were conveniently classified into four major stages of development, including immature, low and high intermediate, and mature. Based on the total protein content of defatted meals of mature seeds, each of the six cultivars included in this study could be placed in one of two groups (instead of the high, intermediate, and low classification of earlier findings) as follows: (a) 42–52%: Argentine, Tennessee Red, and Florida Jumbo; and (b) 30–38%: NC5, F 334-A-B-14, and Virginia Bunch 67. Quantities of free amino acids and carbohydrates in seeds of all six cultivars first decreased rapidly during immature and low- and high-intermediate stages, and then the rate of decline of these constituents slowed as the seeds reached maturity. Individual free amino acids of maturing seeds from different cultivars disappeared quantitatively at various rates. The rate at which these biochemical changes occurred in developing seeds of high-protein cultivars differed from that of the low-protein group. Soluble and total protein content in these maturing seeds increased simultaneously, with these increases occurring more rapidly in the high-protein maturing seeds than in the low-protein group. Levels of free amino acids in immature cotyledons were higher in the high-protein than in the low-protein cultivars. However, a much more rapid decline in free amino acids occurred in the high-protein cultivars during the immature and low-intermediate stages, resulting in comparable levels of these constituents within the two groups at maturity. Electrophoretic studies revealed that nonarachin proteins were deposited early in cotyledon development, and arachin, the major storage globulin of peanut seeds, rapidly became the predominant component synthesized during the high-intermediate and mature stages.

Morphological changes during development of cotyledons and embryonic axis of peanut seeds (*Arachis hypogaea* L.) are well known (1–5). The physiological and biochemical changes accompanying maturation of these seeds have recently become a major interest of a number of investigators (4,6–13). In general, these studies have shown that during the first 8 to 12 weeks after pegging, immature peanut seeds rapidly increase in fresh weight and contain high amounts of various enzymes. Further, these developments are accompanied by various compositional changes such as synthesis of nucleic acids, proteins, lipids, carbohydrates, and organic volatiles. Recently, Cherry (11) used gel electrophoretic techniques to show that the large molecular-weight storage globulins were rapidly deposited between 9 and 12 weeks after pegging and were found to vary quantitatively among mature seeds grown in different environments. Young and Hammons (14) showed that the total crude protein content of mature seeds from 105 genotypes grown under similar agronomic

[1]Postdoctoral Research Associate.

conditions ranged from 23 to 28%; seeds of certain cultivars were shown to consistently contain higher amounts of total protein than others. Thus, qualitative and quantitative protein variations of peanut seeds appeared to be related to both genetic and agronomic conditions.

Understanding the biochemistry of protein deposition in maturing seeds of various peanut cultivars may yield useful information for understanding the genetic and environmental factors affecting these constituents. This information is necessary in the development of methods to improve protein quality in peanut seeds. At the immature stage, high-protein rice grains were shown to have larger amounts of free amino nitrogen and a greater capacity to deposit proteins during maturation than low-protein seeds (15). Beevers and Poulson (16) demonstrated that the free amino acid incorporating capacity of ribosomal preparations from maturing pea (*Pisum sativum* L.) cotyledons was related to their polysome content. Ribosomal extracts of peas undergoing rapid protein synthesis contained a higher percentage of polysomes than monosomes, while those with a declining capacity for polypeptide formation contained amounts of these genetic materials in reverse. Thus, increased protein deposition in maturing seeds could be genetically related to transcription of messenger ribonucleic acid and/or translation of these components, or to incorporation of free amino acids into polypeptides at the ribosomal level.

Despite detailed information on biochemical changes occurring during peanut seed maturation, there is limited data correlating free amino acid and carbohydrate changes to protein deposition. Moreover, studies are needed to examine differences in the rate and extent of protein accumulation in maturing seeds of various peanut cultivars. Knowledge of protein deposition relative to free amino acid and carbohydrate levels in developing seeds of various cultivars may be useful in determining agronomic and genetic factors affecting protein composition in these storage organs at maturity.

MATERIALS AND METHODS

Six cultivars of peanuts *Arachis hypogaea* L. (Tennessee Red, Florida Jumbo, Argentine, Virginia Bunch 67, NC5, and F 334-A-B-14) were grown during the 1974 season in experimental plots at the Southwest Georgia Experiment Station at Plains; Florida Jumbo and F 334-A-B-14 are experimental strains (14). The plots were prepared under standard recommended cultural practices and irrigated as needed during the growing period. Randomly selected plants were collected at 17 (digging 1) and 20 (digging 2) weeks after planting, fruits were harvested, and seeds were separated into four stages of maturity as follows: Mature—seeds having black splotches throughout the pericarp, and brown, tightly bound testa; High Intermediate—seeds having brown splotches only on the inner pericarp, and dark pink testa; Low Intermediate—seeds with a white pericarp, and thick, light pink to white testa; Immature—seeds with water, soft and spongy pericarp, and very thick white testa. To ensure proper age differentiation of maturing seeds within cultivars, the conventional size screening technique for peanuts was used along with this method of determining maturity levels according to certain morphological characteristics. After the seeds were classified into respective groups, they were freeze-dried and ground with a mortar and pestle, and the resulting meals were defatted with diethyl ether. The

defatted meals were stored at −18°C until used.

Free Amino Acids

Defatted meals were extracted with methanol:chloroform:water (60:25:15, v/v/v) according to the method of Young *et al.* (17). These extracts were centrifuged and the resulting supernatants evaporated to dryness at 4°C. The residue was suspended in citrate buffer, pH 2.2, and assayed for free amino acid content on a Durrum D-500 amino acid analyzer.

Total Protein

A quantity (100 mg) of defatted meal was washed with 30 ml of cold 10%

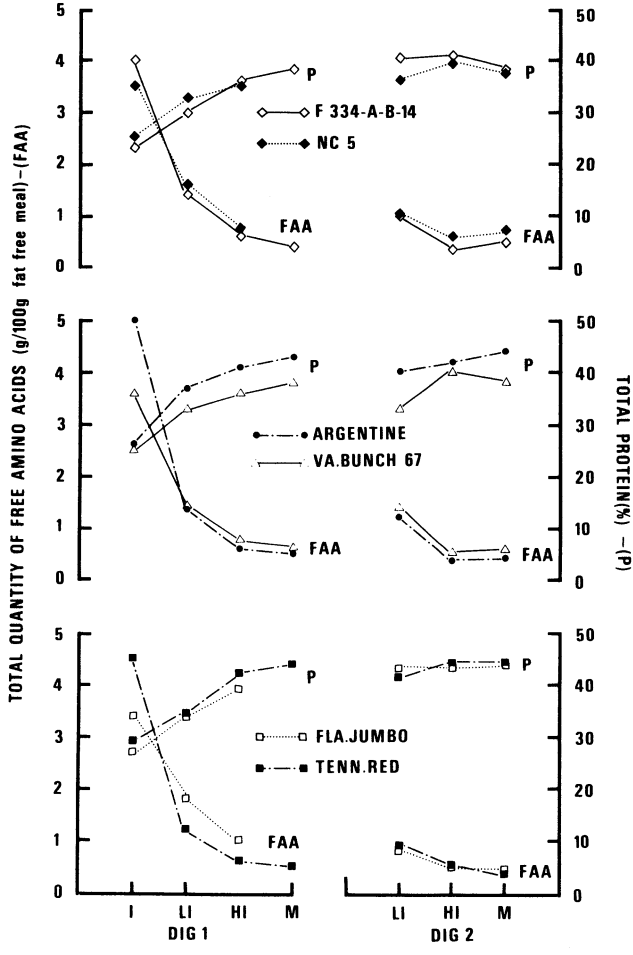

Fig. 1. Quantitative changes of total free amino acids and proteins during peanut seed development. Maturity stages include: immature (I), low-intermediate (LI), high-intermediate (HI), and mature (M).

trichloroacetic acid (TCA) and centrifuged at 20,000 × *g* for 15 min. This process was repeated and the resulting TCA-washed pellet was resuspended twice in ethanol (15 ml), centrifuging after each treatment, and finally air-dried. This material, less free amino acids, was suspended in 5 ml of 1*N* NaOH and incubated at 40° C for 16 hr. The resulting hydrolysate was centrifuged at 20,000 × *g* for 20 min. The pellet was re-extracted with 2.5 ml of 1*N* NaOH and centrifuged. The two supernatants were pooled and the protein content was determined by the method of Lowry *et al.* (18), using bovine serum albumin as standard.

Soluble Protein

Defatted meal was ground in pH 7.9, I = 0.03 sodium phosphate buffer (1:20, w/v) with a mortar and pestle. The homogenate was centrifuged at 20,000 × *g* for 20 min at 22° C and the supernatant analyzed for protein content as described above.

Total Carbohydrates

Peanut meal (500 mg) was heated with 20 ml of 0.01*N* H_2SO_4 in a boiling-water bath for 1 hr following the procedure of Watschke and Waddington (19). The insoluble material was removed by centrifugation and the resulting pellet re-extracted with 5 ml of 0.01*N* H_2SO_4. The supernatants were pooled and made up to 30 ml, and their carbohydrate content was determined by the method of Yemm and Willis (20). Other analytical methods involving hydrolysis of meals with 1*N* H_2SO_4 at 100° C for 40 min showed that the former method was efficient in recovering more than 95% of the total seed carbohydrates.

Gel Electrophoresis

Soluble protein extracted with sodium phosphate buffer (I = 0.03, pH 7.9) from seeds grouped into the four maturity levels was examined by polyacrylamide disc-gel electrophoresis (7.5% gels) as described by Canalco (21) and Cherry *et al.* (22). All samplings and chemical analyses of these collections were evaluated in duplicate.

RESULTS AND DISCUSSION

Total Free Amino Acids and Proteins

Changes in percentage of total free amino acids and proteins in defatted meals of peanut seeds classified into immature, low- and high-intermediate, and mature stages are shown in Fig. 1. In digging 1, the samplings of NC5 and Florida Jumbo contained no mature seeds, and at digging 2 all cultivars had few or no immature seeds. The cultivars were separated into three groups according to total or crude protein (Kjeldahl analysis) levels of mature seeds reported by Young and Hammons (14). These include: (a) low-protein group—NC5 and F 334-A-B-14; (b) intermediate—Argentine and Virginia Bunch 67; and (c) high—Tennessee Red and Florida Jumbo. In the present study, however, mature seeds of cultivars classified earlier (14) as having intermediate protein levels in *A. hypogaea* instead contained amounts of these components similar to either those grouped as storing high (Argentine) or low (Virginia Bunch 67) quantities of proteins. Differences in protein levels such as these are not surprising since their quantities

in mature peanut seeds were shown to be sensitive to fluctuations in seasonal and agronomic conditions (11,23–25). On the other hand, some of these variations may be partially due to variance among the cultivars of the morphological characteristics used for the four maturity classes of seeds.

Defatted meals of immature seeds collected in digging 1 from cultivars classified in high-, intermediate-, and low-protein groups contained approximately 3.5–4.5, 3.5–5.0, and 3.5–4.0% free amino acids, respectively (Fig. 1). Similar preparations of immature seeds of two cultivars which exhibited the highest levels of total proteins in defatted meals of mature seeds (about 45%), Tennessee Red (high-protein group) and Argentine (intermediate) contained the greatest amounts of free amino acids (4.5 to 5.0%), while those of other cultivars (averaging less than 40% total protein in mature seeds) showed free amino acid levels between 3.5 and 4.0%. During development, seed meals of all cultivars exhibited a rapid decline in percentage of free amino acids to similar levels of approximately 1.5 and 0.5% in low- and high-intermediate stages, respectively, and then leveled off to 0.4% at maturity. Mature seeds of the two cultivars exhibiting the highest free amino acid levels initially showed a much more rapid decline in these components between immature and low-intermediate stages than the other cultivars.

In conjunction with the decline in free amino acid content, there was a steady increase in total protein deposition in cotyledons from approximately 25 to 30% at the immature stage to 35 to 45% at maturity. Increases in protein content were rapid between immature and high-intermediate stages, corresponding with the rapid decline in free amino acid content noted during this same period. Moreover, developing seeds of the two cultivars, Argentine and Tennessee Red, which showed the fastest rate of decline in free amino acids during this period of maturation, also accumulated storage protein more rapidly at this time than those of the other cultivars.

Free amino acid levels of high-intermediate and mature cotyledons from all cultivars in digging 2 were similar to those of digging 1. However, in most cases, the protein content of seeds from low- and high-intermediate stages of cultivars in the various protein groups was greater in digging 2 than that of digging 1. Since peanuts are considered to be indeterminate in their rate of growth, the seeds produced late in the growing season may be physiologically more mature in the intermediate stages of development than those grown earlier.

The data suggest that very early in the development of peanut seeds (possibly at the time of pegging) free amino acids are rapidly synthesized. As seeds mature, these stored free amino acids are converted to storage proteins and/or nonprotein constituents. These latter changes were especially conspicuous between the immature and low-intermediate stages of seed maturation, when fresh weight rapidly increased. In addition, the precursor role of free amino acids during protein deposition in peanut seeds is evident; *i.e.*, maturing seeds containing high amounts of free amino acids deposited protein more rapidly than those with low content of these constituents. High levels of free amino acids in maturing seeds have been shown by others to contribute to a faster and greater accumulation of protein in protein bodies (8,15,16,26). This occurs even if levels of enzymes involved in protein synthesis are similar in seeds of both low- and high-protein-containing cultivars. Our results are consistent with these observations, showing that the amino acid incorporating capacity of cotyledons

TABLE I
Changes in the Individual Free Amino Acids of Maturing Peanut Seeds[a] from Three Cultivars

Maturity Stage	Free Amino Acids (g/100 g fat-free meal)																	
	ASP	THR	SER	GLU	GLY	ALA	VAL	MET	ILE	LEU	TYR	PHE	HIS	LYS	NH_4	TRY	ARG	Others
									Tennessee Red									
Mature	0.065	0.012	0.046	0.156	0.004	0.019	0.011	0.004	0.011	0.008	0.009	0.098	0.017	0.012	0.004	0.026	0.030	0.076
H-Inter[b]	0.075	0.014	0.054	0.273	0.005	0.031	0.015	0.005	0.010	0.013	0.013	0.050	0.030	0.014	0.005	0.032	0.033	0.026
L-Inter	0.092	0.019	0.094	0.443	0.009	0.077	0.019	0.006	0.016	0.015	0.017	0.094	0.029	0.036	0.010	0.058	0.235	0.048
Immature	0.190	0.070	0.379	0.819	0.026	0.237	0.081	0.024	0.057	0.073	0.063	0.360	0.112	0.130	0.027	0.201	1.398	0.234
									Argentine									
Mature	0.061	0.008	0.031	0.137	0.004	0.017	0.011	0.004	0.010	0.008	0.009	0.105	0.016	0.011	0.003	0.026	0.023	0.074
H-Inter	0.074	0.010	0.064	0.231	0.007	0.030	0.018	0.005	0.011	0.013	0.010	0.030	0.029	0.014	0.005	0.034	0.034	0.031
L-Inter	0.110	0.022	0.145	0.456	0.008	0.083	0.029	0.008	0.017	0.017	0.014	0.094	0.032	0.037	0.010	0.066	0.308	0.056
Immature	0.235	0.125	0.454	0.772	0.024	0.299	0.085	0.023	0.052	0.059	0.053	0.026	0.162	0.132	0.027	0.204	1.814	0.236
									F 334-A-B-14									
Mature	0.056	0.009	0.032	0.131	0.003	0.012	0.012	0.004	0.010	0.011	0.009	0.037	0.016	0.013	0.003	0.031	0.020	0.043
H-Inter	0.101	0.011	0.056	0.201	0.004	0.018	0.015	0.004	0.011	0.013	0.011	0.034	0.035	0.016	0.003	0.037	0.035	0.027
L-Inter	0.159	0.027	0.133	0.378	0.006	0.048	0.025	0.012	0.017	0.018	0.015	0.086	0.033	0.042	0.006	0.072	0.354	0.043
Immature	0.273	0.158	0.399	0.512	0.024	0.193	0.076	0.040	0.040	0.062	0.053	0.175	0.214	0.125	0.017	0.208	1.346	0.179

[a]From digging 1.
[b]H-, L-Inter = high-, low-intermediate.

is greatest during the early stages of peanut seed development, although protein deposition continues until seeds mature and dehydrate. In addition, data from at least two cultivars, Tennessee Red and Argentine, suggested that a high level of free amino acids early in seed development will contribute to a rapid as well as an increased accumulation of storage proteins, as was shown in developing rice seeds (15). However, it should be noted that free amino acids are not exclusively incorporated into protein. In certain instances, the carbon skeletons of these constituents serve as precursors of carbohydrates, organic acids, growth regulators, alkaloids, cyanogenic glucosides, porphyrins, etc. (27,28).

Individual Free Amino Acid Changes

Quantitative changes in individual free amino acids of maturing seeds from

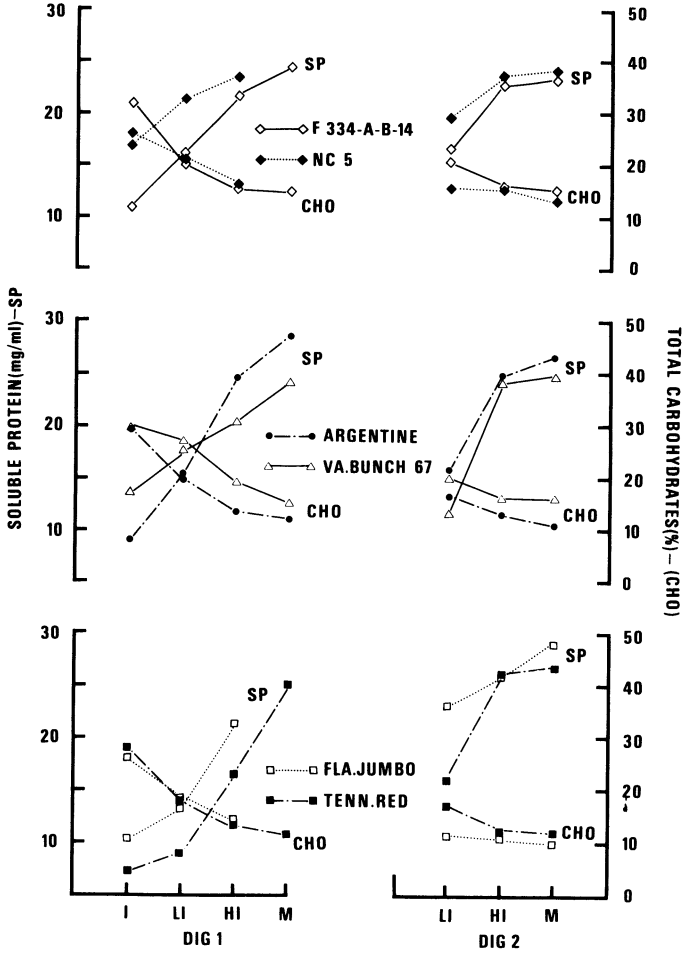

Fig. 2. Quantitative changes of carbohydrates and soluble proteins during seed development. Maturity stages include: immature (I), low-intermediate (LI), high-intermediate (HI), and mature (M).

Tennessee Red and Argentine (high-protein group) and F 334-A-B-14 (low) are presented as examples in Table I. In general, quantities of all free amino acids were highest in immature seeds, declining rapidly as the cotyledons developed to maturity. The period in which most free amino acids showed the greatest decline was between the immature and low-intermediate stages. Individual free amino acids differed quantitatively in seeds from these cultivars at the immature stage. For example, asp, thr, met, his, and try contents were higher in the immature seeds of the low-protein cultivar than those of the high-protein group. Immature cotyledons of both high-protein cultivars, on the other hand, contained more glu, ala, val, ile, lys, phe, and the unidentifiable components. Although immature seeds from these cultivars differed in free amino acid content, in most cases, these variations were less distinct in mature seeds. These data suggest that during maturation peanut seeds from different cultivars incorporate various free amino acids into proteins and/or nonprotein material at different rates. Thus, these data imply that certain proteins or polypeptides (or portions of these constituents) are deposited in the maturing seed at different time intervals; the rate at which this occurs can differ among various cultivars. This information may be important for future studies to alter levels of certain amino acids during maturation which may result in changes in the rate at which certain proteins are deposited. Such changes could be accomplished by altering certain agronomic or genetic variables at appropriate stages of peanut seed development.

Carbohydrates

Content of total carbohydrates in immature seeds of all cultivars included in this study ranged between 25 and 35%, and declined continuously thereafter to levels of approximately 10% at the mature stage (Fig. 2). These changes were similar for seeds from both digging 1 and digging 2. These observations agree with the findings of others (6,12,13,29), which showed that immediately after pegging, carbohydrate content in maturing seeds increased and then declined. Thus, maturing seeds probably used stored, nonstructural carbohydrates as a source of energy for synthesis of lipids and protein. This is further supported by the observation that maturing peanut seeds using free amino acids and depositing proteins at a very rapid rate (especially evident in the high protein cultivars Tennessee Red and Argentine) also showed a faster decline in carbohydrate content during the immature and low-intermediate stages than those of the other cultivars. Thus, quantitative changes in free amino acids, carbohydrates, and total proteins in maturing peanut seeds may be closely related to one another but may vary among cultivars. This type of information can become valuable in future studies to regulate the quantity of these constituents in maturing seeds by possibly altering certain genetic and agronomic factors.

Soluble Proteins

The relative amounts and types of protein deposited in maturing seeds were shown to vary (11,16,30–32). For example, studies using radioisotopes showed that albumins were synthesized early in developing pea cotyledons, whereas globulin synthesis was predominant during the later stages of maturation (16). Cherry (11) showed that nonarachin components were mainly deposited early in seed development and arachin predominantly synthesized between 6 and 12

weeks after pegging. In the present study, maturing seeds collected in both diggings from all cultivars showed increases in soluble protein content ranging from 4.0 to 18.0 mg/ml at immaturity and from 24.0 to 30.0 mg/ml at maturity (Fig. 2). In digging 1, quantities of soluble proteins remained consistently higher in maturing seeds of NC5 than those of F 334-A-B-14 (low-protein cultivars: 17.0 *vs.* 11.0 mg/ml at the immature stage, 22.0 *vs.* 16.0 mg/ml at the low-intermediate stage, and 24.0 *vs.* 22.0 at the high-intermediate stage). In contrast, the maturing seeds of these cultivars from digging 2 showed only minor differences in soluble protein content at each developmental stage (19.0, 23.0, and 24.0 mg/ml at low- and high-intermediate, and mature stages, respectively). Maturing seeds of Virginia Bunch 67 (intermediate protein group) from digging

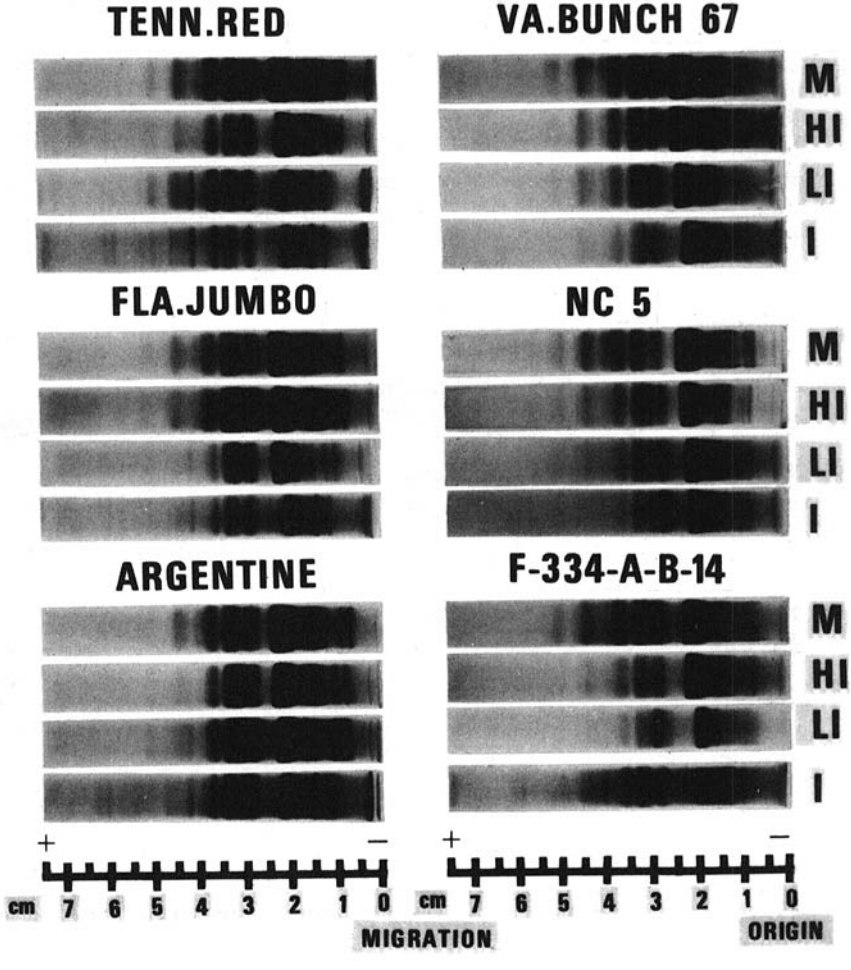

Fig. 3. Polyacrylamide disc-gel electrophoretic patterns of changes in soluble proteins during seed development. Maturity stages include: immature (I), low-intermediate (LI), high-intermediate (HI), and mature (M).

1 showed increases in soluble protein similar to those of the low-protein group. On the other hand, soluble protein content in maturing seeds of Argentine (intermediate protein group) from digging 1 was lower than that of Virginia Bunch 67 at the immature (9.0 *vs.* 14.0 mg/ml, respectively) and low-intermediate (16.0 *vs.* 18.0 mg/ml) stages, but afterwards increased rapidly to higher values during the high-intermediate (25.0 *vs.* 22.0 mg/ml) and mature stages (28.0 *vs.* 24.0 mg/ml). In fact, maturing seeds of Argentine attained the highest amount of soluble protein when their values were compared among all cultivars examined in this experiment. In digging 2, protein levels were similar for all cultivars, increasing more rapidly than those from digging 1 between the low- and high-intermediate stages (approximately 14.0 to 25 mg/ml), but changing very little afterwards during the mature stage. The cotyledons from high-protein cultivars (*e.g.*, Tennessee Red, Florida Jumbo) showed slow rates of protein deposition between the immature and low-intermediate stages. However, deposition rapidly increased afterwards to the mature stage. The soluble protein levels at all stages examined in digging 2 were higher than those of digging 1 and, as shown with the other cultivars, the rate of deposition decreased between the high-intermediate and mature stages. Other than the differences noted in the rate at which soluble proteins were deposited, these data did not distinguish the three protein groups of cultivars (14).

In digging 1, levels of soluble protein in developing seeds of all cultivars increased continuously between the immature and mature stages. However, in digging 2 the rate of protein deposition decreased between the high-intermediate and mature stages. These data show that peanut seeds considered morphologically mature and harvested early in the growing season are still actively depositing soluble proteins, whereas those harvested 3 weeks later seem to have attained a greater degree of biochemical dormancy. Other studies with seeds from various sources have shown that enzymatic activity and protein deposition proceed even after harvesting, and continue until moisture levels become too low for the metabolic activities to continue (1,6,26,33).

Polyacrylamide-Gel Electrophoresis

Qualitative changes in protein components of soluble extracts from developing peanut seeds of the cultivars included in this study were characterized by polyacrylamide disc-gel electrophoresis (Fig. 3). The soluble extracts of immature seeds from all cultivars contained mainly nonarachin components. The two components of arachin (region 1.5–2.5 cm) were present in small amounts in immature seeds. As the seeds matured, the arachin levels shown in the gel patterns increased quantitatively, becoming the dominant components in extracts of mature seeds. These data support earlier findings showing that during peanut seed development nonarachin proteins are primarily synthesized shortly after pegging, and in the later periods of maturity, arachin deposition becomes predominant (11).

Although mature seeds of the different cultivars examined in this study showed no major qualitative differences in the soluble protein composition, variations were noted among gel patterns of immature seed extracts. Extracts of immature seeds of Tennessee Red, Florida Jumbo, Argentine, and F 334-A-B-14 produced numerous bands in the gel patterns where arachin is normally located (region 1.5–2.5 cm). The arachin components were clearly (11) distinguished in

the gel patterns of extracts from immature seeds of Virginia Bunch 67 and NC5. These observations may be valuable in future studies in the development of techniques to determine the quality of proteins in peanut seeds at different maturity levels during the harvesting period. Moreover, protein variability in maturing seeds of various cultivars may be used in agronomic and genetic studies to improve uniformity in the synthesis of these constituents and/or to select for improved quality.

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