INTRODUCTION

Compartmentation is a term often used in metabolism studies to describe the differential localization of metabolites among various areas or structures within a particular plant tissue. For the discussion of mineral nutrient compartmentation within the developing cotton boll, the boll itself will be considered as the unit tissue of interest. The major structural components of the boll—the carpel walls (the bur), the seeds, and the fiber—will be defined as the compartments within the boll.

During the first few weeks after anthesis, the boll enlarges rapidly. After a major increase during the first 3 weeks of development, the fresh weight of the boll remains relatively constant until dehiscence, when it declines rapidly. Various descriptive parameters, such as boll length, diameter, surface area, and volume, have been used as measures of boll size; each provides a similar pattern. The first 3 to 4 weeks of boll development, the enlargement phase, is the time that maximum volumes of the boll and seeds are established and most of the fiber elongation occurs. The next period of boll development, the filling phase, begins during the fourth week postanthesis. Fresh weight plateaus during this phase, but dry weight continues to increase linearly with time. The true endosperm of the seed is consumed by the developing cotyledons and embryo, while fiber development is characterized by the termination of elongation and the initiation of secondary wall formation (Schubert et al., 1973). The filling phase continues into the sixth week of development, when the final period of boll development, the maturation phase, begins.

Most of the discussion of mineral compartmentation will be directed toward a description of the mineral nutrient complements of the three boll fractions and the shifting relationships among them during the filling and maturation phases of boll development. The distributions of minerals among the fractions will be
described individually first, then generally in the final section. (Additional discussions on minerals may be found in Chapters 9, 20 and 24.)

As a general reference, the dry weights of the various fractions are illustrated in Figure 1, as are the approximate times of the three phases of boll development. The seed and fiber were separated at the demarcation between the inner and outer integuments of the seedcoat. Consequently, the weights of the fiber fraction were very slightly overestimated because parts of the outer integuments were included with the fiber. Fiber samples used for chemical determinations were, however, contaminant-free.

Most of these data are taken from the earlier reports of Leffler (1976) and Leffler and Tubertini (1976). The levels of mineral nutrients found in these studies agree, in general, with those reported in other studies (Bassett et al., 1970; Bartee and Krieg, 1974).
Nitrogen

The carpel walls and the seeds were analyzed for nitrogen (N) content (Figure 2). While there would surely be some N in the fiber, especially during early development, our efforts to measure it were not successful. Therefore, the discussion of boll N will be restricted to the pools of N in the bur and in the seeds. During early boll development, most of the boll's N is in the vegetative tissue. This bur N content peaks around the end of the third week of development, then declines throughout subsequent development.

The decrease in bur N coincides with the acceleration of N accumulation by the seeds. Between the third and sixth weeks of boll development, the accumulation of N by the seeds was nearly linear. Even though seed N accumulation slows at the end of the filling phase, it remains significant well into the maturation phase. In fact, over one-third of the seed N accumulates during boll maturation. (Other aspects of N may be found in Chapter 10).

Phosphorus

The accumulation of phosphorus (P) by the boll fractions follows much the same pattern as does N accumulation (Figure 3). There are, however, two major
Figure 3. Compartmentation of P in developing bolls.

differences in the accumulation patterns of these two major nutrients. First, significant transient accumulation of P by the fiber was observed, with fiber P content reaching a maximum about 21 days postanthesis—this is the period of maximum fiber elongation. Phosphorus content of the fiber decreased during the period of secondary wall formation. Second, the P content of the bur does not peak until about the fifth week of development, and subsequent loss of P from the bur is not nearly so great as that for N.

As was the case with N, though, the seeds are the primary sites of P compartmentation within the developing boll. Additional accumulation during the maturation phase amounts to almost one-fourth of the total seed P. Similarly, three-fourths of the P present in the fiber fraction at the beginning of maturation is lost during that phase.

POTASSIUM

The accumulation and distribution of potassium (K) in the developing boll are markedly different from those patterns described above for N and P (Figure 4). The bur, not the seeds, is the primary sink for boll K. With only minor fluctuations, the accumulation of K by the bur is nearly linear throughout the three phases of boll development. At maturity, the bur contains over 5 percent K.

The fiber is the second greatest sink for K through the fifth week of development, which suggests that K may be required for both elongation and secondary
Figure 4. Compartmentation of K in developing bolls.

Although some K moves from the fiber during the sixth week, most of the K is exported later in the maturation phase. Accumulation of K by the seeds is essentially complete by the end of the sixth week; only about one-eighth of the total seed K accumulates during seed maturation.

MINOR ELEMENTS

CALCIUM

Calcium (Ca) is often considered to be a mineral nutrient with more structural than metabolic function. As such, fluctuations of Ca contents of the various components of the cotton boll would be expected to relatively approximate their changes in dry weight. This is essentially the pattern that is found (Figure 5). Again, the seeds ultimately contain more of the boll Ca than do either the bur or the fiber, accounting for almost all of the accumulation after the third week of development. The Ca in the bur increases only during the enlargement phase, then remains constant at about 2.5 mg. The bur, however, contains more Ca than the other boll components through the first 5 weeks of development. Then, beginning during the transition into the maturation phase, the Ca content of the seeds exceeds that of either the bur or the fiber. The Ca content of the fiber remains low throughout development, increasing only during fiber elongation (Benedict et al., 1973; Schubert et al., 1973).
Figure 5. Compartmentation of Ca in developing bolls.

Figure 6. Compartmentation of Mg in developing bolls.
MAGNESIUM

The magnesium (Mg) in the developing boll is representative more of a metabolic nutrient than of a truly structural nutrient (Figure 6). Once again, most of the Mg content of the boll is partitioned into the seeds. As with K, Mg appears to be associated with both fiber elongation and secondary wall formation. The Mg contents in the bur and the fiber are dynamic, increasing to peaks early or midway in the developmental period, then decreasing until maturity. The bur exports 46 percent of its Mg between 21 days postanthesis and maturity; the fiber moves out 49 percent of its Mg during the final two weeks of development.

DYNAMIC RELATIONSHIPS OF NUTRIENT COMPARTMENTATION

By separating developing bolls into components and then analyzing the mineral nutrient complement of each component separately, it has been possible to generate significant information about the physiology of boll formation. Boll development has been considered to cover three separate but overlapping phases: enlargement, filling, and maturation (see Chapter 20). The enlargement phase begins at anthesis and lasts for 3 to 3½ weeks. During this time, the seed volume is established, much of the fiber elongation occurs, and the structural housing for the boll grows to final dimensions. This structure, the bur, is also the predominant sink for mineral nutrients during this phase of development. Some of the minerals accumulated in the first 3 weeks are required strictly for boll enlargement; others, however, appear to be accumulated as a ready reserve from which the demands of other growing components can be met later.

During the second, or filling, phase, the predominant growth is inside the boll; the seeds and the fiber continue growth through about the sixth week of development. Each acquires a significant complement of mineral nutrients during this phase. Although most of the mineral nutrients acquired by these internal structures are newly arrived to the boll, a lesser but significant proportion of the total may be derived from nutrients that are exported from the bur. The potential contribution of the bur to the other boll components appears to be greatest for nitrogen and magnesium and lower for phosphorus. It appears not to be significant for either potassium or calcium.

The maturation phase of boll development may yet prove to be the most interesting of the three, especially from the standpoint of mineral compartmentation. This is the phase that has generally been overlooked when only dry weight measurements have been made; yet, there are relatively massive shifts in the compartmentation of mineral nutrients during this final fortnight of formation. Similarly, both the quantity and the quality of cotton seed proteins shift significantly during the final two weeks of boll development (King and Leffler, 1979).

The importance of the maturation period may be better understood when the degree of nutrient import to the seed is more fully identified. During this phase,
the seeds accumulate about one-third of their nitrogen, one-fourth of their phosphorus, one-eighth of their potassium, one-seventh of their calcium and two-fifths of their magnesium. Simultaneously, the fiber loses three-fourths of its phosphorus, three-fifths of its potassium, one-fourth of its calcium and half of its magnesium. These changes, coupled with those in the bur, demonstrate the relative magnitudes of mineral nutrient redistribution among the components of the boll within a comparatively short time (Figure 7). Further, these data strongly suggest that the several boll components remain physiologically interconnected and interdependent as long as the boll remains closed, and that normal boll development continues through boll opening. For these reasons and because seeds harvested just before boll opening have been found to be of poor quality (Leffler, 1980b; Halloin, 1981b), the maturation process must be regarded as an important ontogenetic period, not simply a relatively quiescent one.

![Figure 7. Relative changes in mineral nutrient contents of the boll components during the maturation phase.](image-url)
Published data describing the distribution of mineral nutrients in developing cotton bolls were recalculated on a mass basis to illustrate the internal relationships among boll components. The major components of the boll, the carpel walls (bur), the seeds and the fiber, were considered as the compartments of interest in this evaluation. During early boll development, the carpel walls accumulate significant amounts of all nutrients examined: once secondary boll development is initiated, however, further accumulation occurs only for potassium and, to a limited degree, phosphorus. During secondary boll development, nitrogen and magnesium move from the carpel walls, presumably to the seeds, which comprise the major nutrient sink of the boll. The most striking changes in mineral compartmentation occur during maturation, a two-week interval immediately preceding boll opening which was once considered to be a relatively quiescent period. It is during this period of maturation that the major movement of mineral nutrients occurs that result in the mature boll distribution of nutrients. This redistribution of minerals among the various compartments of the boll indicates that the boll retains physiological integrity and activity at least until dehiscence occurs.