The cotton leaf cuticle and absorption of foliar-applied agrochemicals

Derrick M. Oosterhuis
University of Arkansas, Department of Crop, Soil, and Environmental Sciences, Fayetteville AR UNITED STATES OF AMERICA
Correspondence author oosterhu@uark.edu

ABSTRACT

Inconsistent results are often experienced with foliar-applied agrochemicals in cotton (Gossypium hirsutum L.) production. It has been speculated that this may be associated with environmental conditions, the nature of the chemical applied, the water status of the crop, and the nature of the cuticle. The studies summarized here were designed to study the characteristics of the cotton leaf surface, the effects of water deficit stress, and the absorption of foliar-applied chemicals. The cuticle constituted a continuous waxy covering over the underlying epidermis, interspersed with numerous stomates and glandular trichomes. Superimposed on this was the epicuticular layer of predominantly lipid material. Also noted was the presence of waxy ledges extending partially over the stomatal pore, and the presence of an internal cuticle extending through the stomatal pore and covering some of the substomatal mesophyll cells. Water deficit stress increased the cuticle thickness by 33% and also changed the qualitative composition of cuticular waxes. The leaf wax from water stressed cuticles contained more long chain molecular waxes of greater hydrophobicity. The thickness of the leaf cuticle was shown to increase with leaf age from 20 to 60 days after leaf unfolding. This was negatively associated with a decrease in absorption of foliar-applied ^{15}N-urea. In related studies, the uptake of foliar-applied plant growth regulators as well as defoliants were significantly decreased by increased leaf wax due to water deficit stress. Subsequent studies showed that the uptake of foliar-applied chemicals, e.g., KNO_3 could be increased by the use of adjuvants. These studies showed the dynamic nature of the leaf cuticle and indicated that this needs to be taken into consideration for efficient foliar application of chemicals.

Introduction

Foliar-application of chemicals, including fertilizers, defoliants and plant growth regulators, is a common practice in crop production and reviews on the subject have been published (e.g. Kannan, 1986; Witter *et al*., 1963). However, the performance of some of these foliar-applied chemicals, in cotton for example, has often been disappointing with inconsistent results experienced. The reasons for this have been associated with environmental conditions (Zhu, 1989), crop conditions (Oosterhuis *et al*., 1991a), and the nature of the chemical applied (Chang and Oosterhuis, 1995). However, little attention has been given to the dynamic nature of the leaf surface and how this affects the uptake of foliar fertilizers.

The outer surface of all crop leaves consists of the cuticle situated immediately above the epidermal cell layer. These two structures constitute the first line of defense against adverse environmental stresses including chemical penetration of foliar-applied agrochemicals. The cuticle is composed of cutin impregnated with wax and forms a waxy covering over the epidermis (Franke, 1967). Genotypic variation in epiculticular wax exists (O'Toole *et al*., 1983; Mosely, 1983). Environmental factors such as radiation, temperature, humidity and water stress have been shown to affect the amount of surface wax in plants. Leaf glaucousness (waxiness) is a characteristic that has been cited as a plant adaptation to drought (Johnson *et al*., 1983; Shantz, 1927). The importance of glaucousness in wheat in drought conditions was suggested by Fisher and Wood (1979). Wax content of sorghum increases under drought conditions (Jordan *et al*., 1992). Details of the cotton cuticle and its impact on evaporative water loss have been documented (Wullschleger and Oosterhuis, 1997). Weete *et al*. (1978) reported that wax synthesis in cotton leaves was inhibited by water stress (-2.4 MPa), and that after a suitable period of rehydration, previously stressed leaves in cotton produced more wax than leaves prior to stressing. Studies have been done on cotton fiber wax and its constituents, but relatively little work has been done on cotton leaf wax (Hanny and Guelder, 1976) though it has been shown to effect the efficacy of foliar fertilization.

Foliar application of N to cotton is used in the US Cotton Belt (Gerik *et al*., 1999; Hake and Kerby, 1988; Miley and Maples, 1988) although some scepticism has arisen as to the benefit of this procedure (Keisling *et al*., 1995) with some negative results reported (Bednarz *et al*., 1997). Chokey and Jain (1977) suggested that the recommended growth stages in cotton for foliar-applied N were at the pinhead and first flower stages, and at peak boll development. Whereas, Maples *et al*. (1977) suggested that cotton was more responsive to foliar fertilization with N during the boll development period. The developing boll load has a high requirement for N, which is apparently not completely met by the subtending leaves (i.e., from soil uptake), thereby indicating a requirement for additional N from foliar applications (Zhu and Oosterhuis, 1992; Maples *et al*., 1977). Urea is the most popular form of N for foliar application, and it has also been widely used as a foliar fertilizer in various crops, because of costs as well as the greater effectiveness of N in urea when applied to foliage resided in its non-polar organic properties (Yamada, 1962). Foliar-applied N may serve as a supplement to alleviate N deficiency caused by low soil N availability, to meet the high demand for N by the rapidly developing bolls, and to avoid the possible hazards of rank growth from excessive soil N (Hake and Kerby, 1988; Zhu and Oosterhuis, 1992). However, there is insufficient research to fully explain and support the practice of foliar feeding cotton with N.

Widespread potassium (K) deficiency has been reported across the US Cotton Belt. These K deficiencies have been associated with the introduction of faster-fruiting varieties with higher fruit loads (Oosterhuis, 1995b). Research in Arkansas has shown that these deficiencies can be partially corrected by soil or foliar applications of K (Oosterhuis *et al*., 1990; Snyder *et al*., 1995). However, the response to foliar fertilization with K has been generally inconsistent (Oosterhuis *et al*., 1994). This was related to the chemical nature of the foliar K salt (Miley and Oosterhuis, 1993) and the pH of the foliar K solution (Chang and Oosterhuis, 1995; Howard *et al*., 1993). The latter authors showed that decreasing the pH of the foliar K solution from about eight to less than six significantly increased leaf absorption of the foliarly applied K, while decreasing phytotoxicity. It has been speculated that inconsistent responses to foliar fertilization was related to inadequate attention being paid to crop condition, specifically the nature of the leaf surface, and environmental conditions at the time of application. However, inadequate information exists on the effect of environmental conditions, solution pH, leaf wax content, or adjuvants on foliar absorption of agrochemicals.

The objectives of these studies were: (a) to determine the nature of the cotton leaf cuticle, (b) to study the effects of water-deficit stress on leaf cuticle characteristics, (c) to observe the effect of adjuvants and pH on the efficacy of foliarly-applied KNO_3, and (d) to study changes in the leaf cuticle with ontogeny and the effect on the uptake of foliar-applied nitrogen, potassium nitrate, defoliants and plant growth regulators. The results should provide valuable information for improving the efficiency of foliar-applied fertilizers.

Experimental procedure

The nature of the cotton leaf cuticle

Cotton (*Gossypium hirsutum* L. cv. Stoneville 506) was grown in a field with a Captina silt loam soil (Typic Fradiudalt) using recommended production practices. Leaf samples were taken from uppermost, fully expanded leaves for anatomical studies (Oosterhuis *et al*., 1991a). Scanning and transmission electron microscopy were used to observe the nature of the leaf surface and changes in cuticle thickness (Oosterhuis *et al*., 1991a; Oosterhuis *et al*., 1991b). Interveinal tissue was excised from well-watered and water-stressed plants and placed immediately in fixative. The samples were dehydrated and infiltrated with Spurr's medium. Tissue was subsequently embedded and sectioned with a LKB ultramicrotome. Ultra-thin sections were viewed and photographed using a Siemens Elmiskop 1A transmission electron microscope at 75 kV and cuticle thickness recorded from the electron micrographs.

Effects of water deficit stress on the cotton leaf cuticle

Field trials were conducted at the Northeast Research and Extension Center in Keiser, Arkansas, on a Sharkey clay (Vertic Haplaquept) soil (Oosterhuis *et al*., 1991a). The cultivar Stoneville 506 was planted in 1-m rows during the first week in May each year. Irrigation was applied from an overhead lateral-move system and the soil-water status monitored using tensiometers installed at 0.3 m depths. The well-watered treatment was irrigated at a 2.5 cm soil-water deficit, while the water-stressed plots were managed in a dryland production regime. Both treatments were irrigated to field capacity two weeks prior to defoliation to remove potential stomatal effects on chemical penetration. A growth chamber study, using the same cultivar grown in 2 l pots of the same soil, was conducted to confirm the results from the field trial, and to allow more detailed observation of the effects of water stress on leaf waxes. Prior to defoliant application, leaf samples were taken from uppermost fully expanded leaves for anatomical and biochemical studies. Leaf area was determined, and the epicuticular waxes were extracted with chloroform and dried. Total wax content was determined by weighing the residue. Separation and identification of wax constituents was achieved using gas chromatography. Identification of cuticle constituents was accomplished by comparison of retention times of the separated waxes with known standards. Changes in cuticle thickness were recorded from anatomical studies using transmission electron microscopy as previously described (Oosterhuis *et al*., 1991a; Wullschleger and Oosterhuis, 1987).

Uptake of defoliants by water-stressed leaves

The effect of drought induced alterations in the cotton leaf cuticle on the uptake of the defoliants Harvade, Dropp, and Folex were investigated in a field study in 1987 (Oosterhuis *et al*., 1991). The defoliants were applied at labeled rates to well-watered and water-stressed plants in a split plot design with four replications, and the resulting effect on defoliation recorded. In a separate experiment the penetration of the ^{14}C-labeled defoliant Harvade into well-watered and water-stressed leaves was determined.

Penetration of nitrogen applied to water-stressed leaves

The effect of water-deficit stress on the absorption and translocation of foliar-applied ^{15}N-urea was studied on field-grown cotton using well-watered and water-stressed cotton as previously described. Individual sympodial leaves at the first fruiting positions of mainstem node 10 sympodial branches were treated with ^{15}N-labeled urea at 2.5 atom percent two weeks after flowering at a rate equivalent to the recommended 10 kg N ha^{-1}. Leaves and associated bolls were harvested at 1, 6 and 24 hours after N application and the ^{15}N

content determined by mass spectrometry. The severity of the water stress was measured using end-window thermocouple psychrometers (84 Series, JRD Merrill Specialty Equipment, Logan, UT) (Oosterhuis and Wullschleger, 1989).

Changes in the leaf cuticle with ontogeny and the effect on the uptake of foliar nitrogen

Leaf age studies were conducted at the Agricultural Experiment Station, Fayetteville, AR, on a moderately well-drained Captina silt loam soil (Typic Fragiudalt) (Bondada *et al*., 1994). The cotton cultivar, Stoneville 506 was planted on May 10, 1990 and May 16, 1991. Plots consisted of six 5 m rows spaced 0.9 m apart. The experimental design was completely randomized with three replications. Treatments consisted of 4 different leaf-age groups, 20, 30, 40, and 60 d old leaves. ^{15}N (5 atom percent ^{15}N-urea) was applied to each leaf-age group using a paintbrush at a rate of 10 kg N/ha (Bondada *et al*., 1996). To record leaf physiological activity (Wullschleger and Oosterhuis, 1990) photosynthesis measurements were made from each leaf-age group using a LI-6000 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) equipped with either a 0.25 l or 1 l stirred cuvette. Leaf wax content and thickness were determined as previously described (Oosterhuis *et al*., 1991a). Total N in the leaf was determined on a 0.2 g sample by the $KMNO_4$-Fe^{2+} modification of the semi-micro-Kjeldahl procedure.

The effect of adjuvants on the efficacy of foliarly-applied KNO_3

A field study was conducted in Fayetteville, AR in summer 1993 on a Captina silt loam (Typic Fragiudalt) soil using recommended cotton production practices. The design was a randomized complete block with five replications. Plot size was three rows, 5 m long spaced 0.9 m apart. All treatments were applied with a CO_2 backpack sprayer using 90 l water per hectare. The potassium study consisted of a control sprayed with water only, KNO_3 at 5.6 or 11.2 kg/ha applied four times at 2, 4, 6, and 8 weeks after flowering, with and without the adjuvants Penetrator Plus™ (Helena Chemicals, Memphis, TN) or LI-700™ (Loveland Industries, Greeley, CO). To assess the treatments effects in the K study measurements were made of the K concentration in upper canopy petioles.

Results and Discussion

The nature of the cotton leaf cuticle

The cuticle constituted a continuous waxy covering over the underlying epidermis, interspersed with numerous stomates and glandular trichomes (Plate 1A). Superimposed on this was the epicuticular layer (Plate 1B) of predominantly lipid material (Oosterhuis *et al*., 1991a). Scanning electron microscopy revealed that epicuticular wax occurred as ridges or striations, which increased with leaf age (Bondada *et al*., 1994). Also noted was the presence of waxy ledges extending part way over the stomatal pore (Plate 2), and the presence of an internal cuticle extending through the stomatal pore and covering some of the substomatal mesophyll cells (Plate. 2) first reported by Wullschleger and Oosterhuis (Wullschleger and Oosterhuis, 1989). The cuticle leaf was about 0.46 μm thick (Plate 1B).

Effects of water deficit stress on the cotton leaf cuticle

Our earlier work using electron micrographs indicated that water stress caused a significant increase in cuticle thickness as compared to well-watered plants (Oosterhuis *et al*., 1991a). The thickness of the leaf cuticle of the water-stressed leaves increased approximately 33%, from 0.46 μm in the well-watered control to 0.59 μm in the stressed treatment (Table 1). There was also a significant increase in the total wax content of the water-stressed leaves in the growth room compared to the well-watered leaves. In the field studies, differences were non-significant, although a trend toward more chloroform-extractable compounds in water-stressed plants was found in both years. Gas-chromatographic separation of the chloroform extracts revealed qualitative differences in epicuticular wax composition between well-watered and water-stressed treatments (Table 2). Leaf cuticles of well-watered plants contained the shorter-chain n-alkanes, tricosane, n-tetracosane, pentacosane, hexacosane, and octocosane. In contrast, in the water-stressed plants the first three lower molecular weight waxes were absent, while more higher molecular weight waxes, e.g. fucosterol and n-nonacosane, were present. This trend towards longer-chain waxes would result in a more hydrophobic cuticle and thereby contribute to a reduced defoliant penetration. This potential reduction was supported by a 34% decrease in penetration of a labeled defoliant (data not shown) (Oosterhuis *et al*., 1991a).

Penetration of a defoliant applied to water-stressed leaves

Visual ratings of percent defoliation two weeks after application in the field showed that significantly less defoliation occurred in the water-stressed plants (Table 1). Vegetative regrowth was much greater in the water stressed treatment presumably because of fewer chemicals entering the plant due to the altered cuticular characteristics. The efficiency of defoliation under water-stressed conditions was reduced similarly for Dropp and Folex in 1989 (data not presented). Furthermore, there were significant differences in defoliation and regrowth between the chemicals in the drought treatment. The penetration of ^{14}C-labeled defoliant Harvade was decreased by 34% in water-stressed leaves (Oosterhuis *et al*., 1991a).

Penetration of a nitrogen applied to water-stressed leaves

For well-watered control plants, the results indicated that there was no significant difference in the absorption of foliar-applied urea by the leaf between the applications made early morning (0600 h) and late evening (1950 h) (Figure 1). However, the absorption from applications made at midday (1300 h) was significantly reduced when compared with those made early morning or late evening. The percentage recovery of ^{15}N-urea at 0600 and 1950 was 40% and 38%, respectively, and only 34% for the mid-day treatment. The applications made late evening and midday to water-stressed plants resulted in significantly less absorption than from the early morning application (Figure 1). Absorption was reduced by water stress from 35% in the early morning, to 7% at midday and 23% in the late evening (Zhu, 1989).

The absorption of foliar-applied ^{15}N by the sympodial leaf at the first fruiting position was significantly reduced by water stress by 45%, 34% and 23% after 1, 6 and 24 h post urea application, respectively (data not shown)(Zhu, 1989). The translocation of foliar-applied ^{15}N to the developing bolls was also reduced by water stress (data not shown). Twenty-four hours after foliar-urea application in the control, 11% of the ^{15}N applied was present in the boll at the first fruiting position, whereas less than 7% of the ^{15}N applied was present in the boll in the water-stressed treatment. This was in conjunction with a 27% and 23% reduction in water potential after 24 hours in the first and second fruiting position, respectively. Water stress reduced the amount of ^{15}N absorbed as well as the amount translocated, suggesting that water stress was not only affecting the uptake of the ^{15}N but also the translocation process.

Leaf water status is thought to play an important role in the absorption of foliar-applied nutrients (Kannan, 1986; Witter *et al*., 1963). These researchers suggested that the leaf water status affected the physical structure of the leaf cuticle, such that when the leaf was dry, the structure of the cuticle constricted and impeded the penetration of foliar-applied nutrients. Oosterhuis *et al*. (1991a) showed that water deficit increased cotton leaf cuticular thickness, quantity of epicuticular wax, and cuticle chemical composition.

The effect of changes in the leaf cuticle with ontogeny on the uptake of foliar-applied nitrogen

Epicuticular wax content increased with increasing leaf age (Figure 2A). In contrast, maximum absorption of ^{15}N (79%) was achieved by the 20 d old leaves and decreased with progressively increasing leaf age as exhibited by 30, 40 and 60 d old leaves (Bondada *et al*., 1996). The 20 d old leaf was the most photosynthetically active (Wullschleger and Oosterhuis, 1990). The negative relationship between ^{15}N absorption and total epicuticular wax content of leaves of different ages suggested epicuticular wax as a major barrier to ^{15}N absorption in the older leaves (Figure 2B). The subsequent translocation and distribution of ^{15}N within the boll were dependent upon the developmental stage of the boll and independent of leaf age. Initially, most of the ^{15}N was retained in the young 20 d old leaf. As the leaves aged, more ^{15}N was translocated to the subtended boll. The study demonstrated that increased wax content during leaf ontogeny reduced ^{15}N absorption and subsequent translocation to the subtended boll. Furthermore, the foliar absorption of N decreased throughout the season (Figure 3) in conjunction with the overall increase in leaf wax content in the canopy (Bondada *et al*., 1996) (Figure 2A) as the average leaf age increased.

The effect of adjuvants on the efficacy of foliarly applied KNO_3

Foliar KNO_3 at both the 5 kg/ha and 10 kg/ha rates did not significantly (P=0.05) increase leaf K concentration (Table 3). However, when adjuvants were added to the foliar K fertilizer, leaf K concentrations increased by an average of about 10%. Unfortunately yields were not recorded. These results are in agreement with Howard *et al*. (1993) who also showed that addition of a surfactant (Penetrator Plus) increased leaf K concentrations.

Conclusions

The anatomical, morphological and biochemical nature of the cotton leaf cuticle has been described. Furthermore, the cuticle has been shown to have a dynamic response to leaf aging and water-deficit stress through an increase in cuticle thickness and a change in lipid composition resulting in an increase in hydrophobicity. This needs to be taken into consideration when foliar-applying fertilizers. The use of adjuvants has been shown to improve the uptake of foliar-applied fertilizers such as fertilizers and defoliants.

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Table 1. *Leaf cuticular thickness of adaxial epidermal cells, gravimetric comparison of chloroform-extractable (wax) compounds on leaf surfaces, percentage defoliation, and visual ratings of percentage regrowth 14 days post-application for well-watered and water-stressed cotton plants[1].*

Treatment	Cuticular thickness (μm)	Chloroform-extractable wax (mg g^{-1} dwt)	Defoliation (%)	Regrowth (%)
Well-watered	0.46 b[2]	5.0 a[1]	78 a	23.8 a
Water-stressed	0.59 a	6.3 a	60 b	78.3 b

[1] From Oosterhuis *et al.* (1991a).

[2] Means within a column followed by the same letter are not significantly different (P=0.05).

Table 2. *Composition of the chloroform extracts from the adaxial cuticles of well-watered and water-stressed cotton leaves as determined by gas chromatography[1].*

Epicuticular constituent	Molecular formula	Epicuticular wax composition: Well-watered	Water-stressed
Tricosane	$C_{23}H_{48}$	+[2]	-
n-Tetracosane	$C_{24}H_{50}$	+	-
Pentacosane	$C_{25}H_{52}$	+	-
Hexacosane	$C_{26}H_{54}$	+	+
Octocosane	$C_{28}H_{58}$	+	tr
n-Nonacosane	$C_{29}H_{60}$	tr	++
Decasane	$C_{30}H_{62}$	tr	++
Octocosanol	$C_{28}H_{58}O$	+	++
Fucosterol	$C_{29}H_{48}O$	+	++

[1] From Oosterhuis *et al*. (1991a).

[2] - = wax absent, + wax present, ++ = increased quantity, tr = trace present.

Table 3. *Effect of foliar KNO_3 alone and in combination with two adjuvants on leaf potassium concentration of field grown cotton.*

Treatment	Adjuvant rate (ml/ha)	Potassium Concentration (% K): Low K soil[1]	High K soil[2]
Untreated control	---	1.01	1.01
Foliar KNO_3[3]	---	1.01	1.05
Foliar KNO_3 + Penetrator Plus	585	1.09	1.15
Foliar KNO_3 + LI-700	282	1.08	1.10
LSD(0.05)		0.07	0.09

[1] Applied at 5.6 kg KNO3/ha in 92 l water/ha.

[2] Applied at 11.2 kg KNO3/ha in 92 l water/ha.

[3] No adjuvant applied.

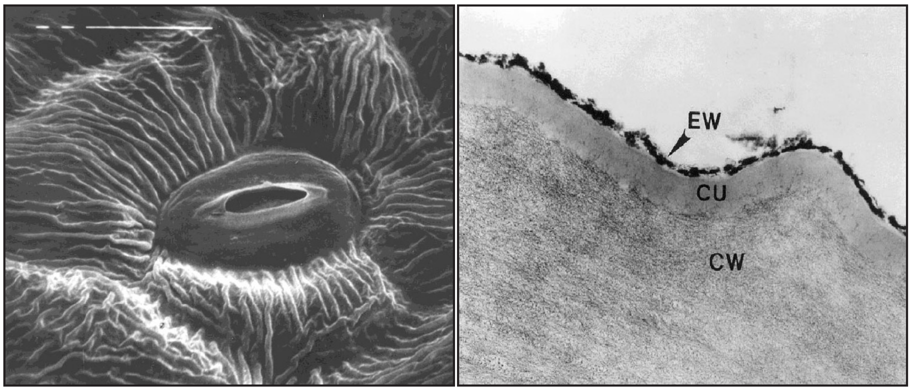

Plate 1.
A. The cuticle on the adaxial leaf surface as a continuous waxy covering over the underlying epidermis, interspersed with numerous stomates and glandular trichomes (x450). B. Cross section of the cuticle (CU) with epiculticular wax layer (EW) on the outside and the underlying epidermal cell wall (CW) on the inside (x 8000). (From Oosterhuis et al.*, 1991).*

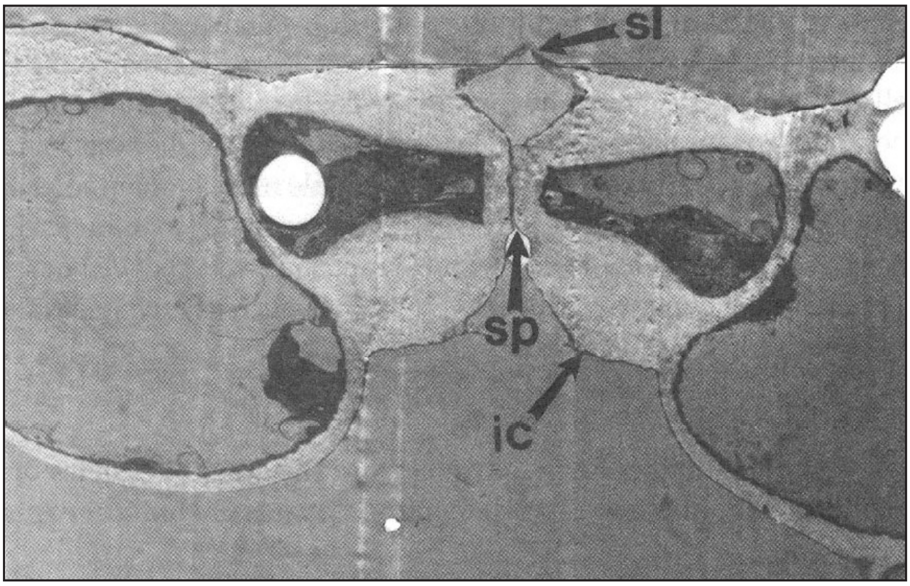

Plate 2.
Cross section of an abaxial cotton leaf stomate showing the cuticular covering and internal cuticle (x5000). Note the presence of waxy stomatal ledges (sl) extending over the stomatal pore (sp), and the presence of an internal cuticle (ic) extending through the stomatal pore and covering some of the substomatal mesophyll cells (From Wullschleger and Oosterhuis, 1989).

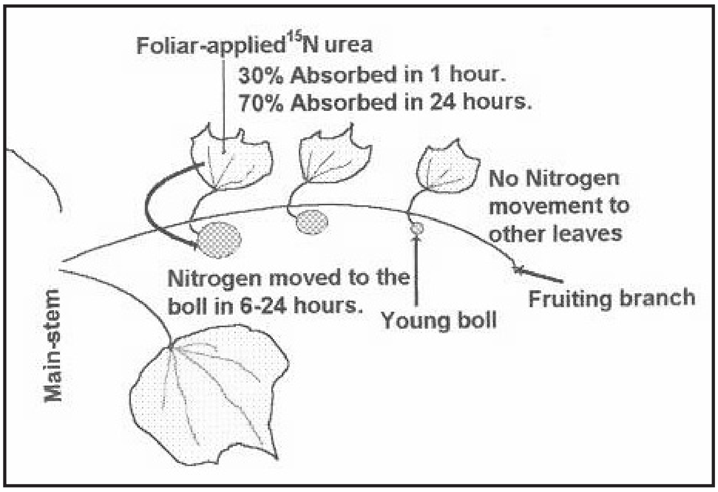

Figure 1. *The uptake of foliar-applied* ^{15}N *six hours after application as affected by water deficit stress and timing of the applications during the day. Values within the same treatment with the same letter are not significantly different (P=0.05). (From Zhu, 1989).*

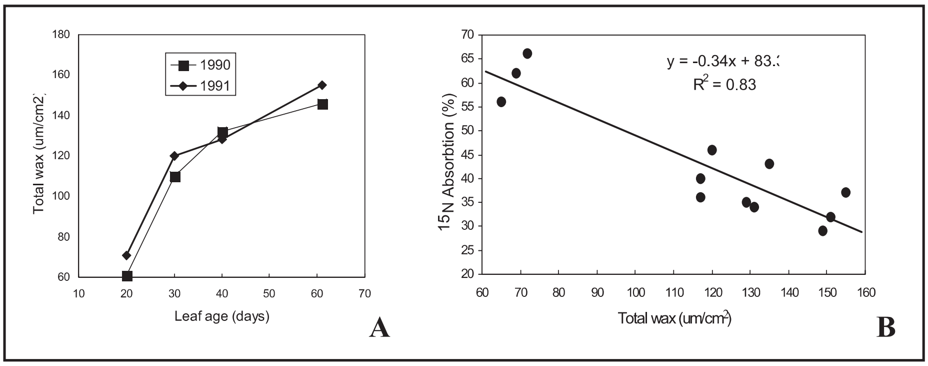

Figure 2. *A.Change in leaf epicuticular wax content with increase in leaf age of field-grown cotton. B. Relationship between leaf* ^{15}N *absorption and total wax content during leaf ontogeny for field-grown cotton. (From Bondada et al., 1996).*

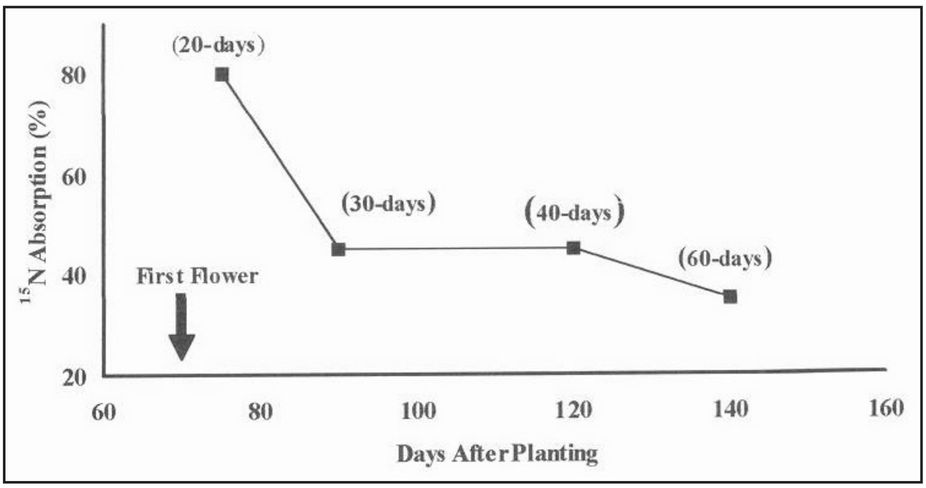

Figure 3. *Foliar* ^{15}N *absorption by the cotton crop during a growing season as average age of the leaves and wax content increases. The values in parentheses indicate average canopy leaf age. (From Bondada et al., 1994).*