Parawilt/sudden wilt of cotton – a perspective on the cause and its management under field condition

K. B. Hebbar[1,2,*] and C. D. Mayee[1,3]

[1]Central Institute for Cotton Research, Shankar Nagar, Nagpur 440 010, India
[2]Present address: Plant Physiology, Biochemistry and Post Harvest Technology Division, Central Plantation Crops Research Institute, Kasargod 671 124, India
[3]Present address: Agricultural Scientists Recruitment Board, Krishi Anusandhan Bhawan, New Delhi 110 012, India

There are several reasons why plants wilt. Some of them are over-watering, lack of water, too much sun, not enough sun, too many/much fertilizers, diseases caused by infection, etc. Wilt due to lack of water or other environmental factors generally occurs gradually and hence, the cause of those can be studied and accordingly it can be controlled by devising appropriate management strategies. Moreover, plants recover with appropriate control measures and continue to yield. In this review, we discuss a typical wilt which is sudden and occurs within a few hours. Hence, understanding the cause and devising a control measure are difficult. Its sporadic distribution and untimely occurrence further complicate the effort to find the cause of this wilt. Unlike the wilt mentioned above which occurs due to lack of water, sudden wilt occurs when the soil is suddenly saturated by a downpour of rain and the sun later shines bright and hot. Paradoxically, the physiological responses, i.e. wilt symptoms to those induced by either drought or flooding are similar. However, the causal mechanism is different. Here, we demonstrate that the imbalance in uptake and loss of water under flooding is the cause of sudden/parawilt of cotton. We also discuss how plants with rapid growth rate and climate factors like bright sunshine and high temperature accentuate the problem of parawilt in cotton.

Keywords: *Bt* hybrids, cotton, flooding, parawilt, root respiration, transpiration.

Background

SUDDEN wilt is common in field-grown crops like tomato[1,2], tobacco[3], pigeon pea[4], vegetable crops like cucurbits[5] and herbaceous perennials like *Dendrathema* species[6]. In cotton, it was first reported in the rainy season of 1978 in an intra hirsutum hybrid JKHY-1 from Adilabad District of Andhra Pradesh[7]. Its rapid spread to many cotton-growing states and to the newly released hybrids and varieties of cotton, and the scale of its destruction caused havoc among cotton growers across the country. Initially, it was viewed as a pathological disorder. However, when none of the measures used to control pathological wilts worked on this, a group discussion was convened at Nagpur to review the problem[8]. Interestingly, the proceedings highlighted the possibilities of causes as diverse as biotic, abiotic and genetic. There was more disagreement on etiology than the agreement on other facets of the disorder. Since it was a mysterious wilt, it was called by different names like sudden wilt, new wilt, and often termed as parawilt by cotton researchers[9].

Efforts to find the cause of sudden wilt over the years are slow, mainly because of uncertainty of its occurrence and its inability to simulate under artificial conditions. Considerable research has been done on the causes of sudden wilt. Detailed study on isolation, distribution pattern and pathogen transmission proved that fungi, bacteria and nematodes were not involved in this malady[10–12]. Though earlier workers did observe unconventional pathogens like flagellate protozoan in the phloem of wilted plants, their association in causing wilt is yet to be proved through research tools. Unlike pathogenic wilt, which occurs in groups of plants in fields, this malady was noticed to be sporadic (random) in distribution[10].

During the same period, some workers[13] reported to have seen 'xylem emboli' in wilted plants. However, they did not prove if that could be the cause of parawilt, as embolism generally occurs under extreme water-deficit stress or freezing condition[14], whereas parawilt occurs under heavy inundation. Similarly, the wilt-like symptoms observed with the exogenous application of ethylene[15] also did not have sufficient experimental proof to confirm that ethylene could be the primary causative agent of parawilt. It was later established that wilting occurs well before increase in ethylene production in petioles of flooded tomato plants[2], confirming non-involvement of ethylene in parawilt. Several biotic and abiotic agents have been proposed as probable causes of this malady from time to time, however, the actual cause was not clear. The details of these agents with possible

*For correspondence. (e-mail: kb_hebbar@rediffmail.com)

evidences in their support are discussed in detail by later reports[12,16].

Meanwhile, parawilt is suddenly in the news again, with the inception of *Bt*-cotton for commercial cultivation. Large-scale wilting was often observed in *Bt* fields of Andhra Pradesh, Karnataka, Maharashtra, Madhya Pradesh, Gujarat and the northern cotton belts. A probe conducted by the Genetic Engineering Approval Committee on wilting in Madhya Pradesh[17], and Gene Campaign in Andhra Pradesh and Maharashtra reported that wilting was more in *Bt* fields compared to non-*Bt* fields[18]. The greater occurrence of wilting in *Bt* fields over non-*Bt* fields prompted this team to conclude that the insertion of foreign *Bt* gene into host genome made the plants vulnerable to adversities[19].

A close watch on the sequence of events leading to the occurrence of parawilt in farmers' fields in different cotton-growing areas and the subsequent successful simulation of this disorder in experimental fields and the detailed research work carried out at Central Institute for Cotton Research (CICR), Nagpur, have adequately established that it is a physiological disorder[20,21]. It is a disorder in which the soil–plant–atmosphere continuum is broken due to adverse environmental factors like flooding or soil saturation. High air temperature and bright sun accentuate this sudden wilting and its occurrence is much more severe if the cotton has been growing rapidly. In this review we describe the symptoms, the mechanism of cause of sudden or parawilt, and cotton species and genotypic variability in sudden wilt tolerance. We also discuss, why *Bt*-cotton is more sensitive to sudden wilt compared to non-*Bt* cotton.

Symptoms

The sudden wilt in cotton is characterized by a premature death of top leaves followed by collapse of the plant (Figure 1). Wilting of leaves can be seen within a few hours of heavy rainfall or soil saturation. If the sun shines bright and hot, leaves may dry immediately. Young plants are generally not affected and the symptoms typically occur from flowering onwards (Figure 2). Wilted plants eventually shed all their leaves and are left with small immature fruits. If parawilt occurs just prior to harvest, bolls may forcefully open but will not ripen fully, leading to poor quantity and unmarketable quality. Under cloudy weather, leaves often turn yellow and die with little or no wilting. Anthocyanin pigment content goes up. Epinasty also is common, it is more in the top leaves compared to the lower leaves. The root system of affected plants is typically smaller with few fine, healthy rootlets.

At times wilt spreads like a wild fire and can cover the whole field within a few hours of its initiation. Hardly any time is left to think of control measures. All the plants in a row may not wilt. Similarly, in a hill if there are two plants, one plant may wilt whereas the other plant may remain normal. Upon the resumption of normal conditions, the recovery of the wilted plant depends on the stage at which it occurs. Plants wilted at early squaring or flowering may recover to a certain extent, however, the yield is drastically reduced. On the other hand, if wilting occurs at boll development, hardly any recovery is seen.

Severity of the problem

Wilting is observed in all the different agro-climatic zones of cotton cultivation. In North India, where more than 95% of the crop is irrigated, plants wilt both due to excessive irrigation and late-season rains. In Central India, where more than 70% of the crop is rainfed, quite often it suffers from wilting due to heavy rains during August–October. In South India, where part of the crop is cultivated under irrigated condition and the rest under rainfed condition, wilting at some stage of its life cycle is common. The wilt menace is more in ill-drained soils such as deep and heavy clay soils compared to shallow and light soils.

Figure 1. Typical view of a sudden/parawilt affected field. Wilt started in the morning and the photograph was taken around noon.

Figure 2. Severity of parawilt damage under field condition. Parawilt at early stage (left) and at advanced stage (right). At advanced stage all the leaves are dried and shed, and only green bolls are retained on the plant.

Cause

Sudden/parawilt is the generic term used for any plants that suddenly dies at or around flowering and fruit filling. The exact cause of sudden wilt is not known, nor why the disorder is more severe than others. Severe onset seems to usually follow a period in which the soil environment is unfavourable to root growth. Research over the years has established that the disorder is caused by several factors, which leads to poor root development and function. Three factors have been implicated with the cause of the disorder complex, i.e. agronomic, pathogen and plant factors. The interaction between these factors seems to be responsible for the seasonal occurrence of the disorder.

Though the cause of the malady is not clear, one thing is common across the species for the occurrence of parawilt/sudden wilt. The sudden wilt occurs where drainage is slow and the soil remains saturated at least for a few hours after rainfall. High air temperature and bright sun accentuate sudden wilting. Its occurrence may also depend on the condition of the plants, apparently being much more severe if the cotton has been growing rapidly. The wilting is more common and severe on clayey soils because they drain more slowly than sandy soils, but injury sometimes occurs even on sandy soils, if poorly drained.

From the above it is clear that the following three prerequisites are essential for the occurrence of sudden/parawilt.

(1) Soil saturation/waterlogging.

(2) Rapid growth rate of plants at grand growth stage.

(3) Bright sunshine and hot air temperature.

The first prerequisite is associated with the soil, the second to the plant and the third to the atmosphere. Thus, it is a problem typically related with the soil–plant–atmosphere continuum.

Effect of soil saturation/waterlogging

In waterlogged soils, the diffusion of gases through soil pores is so strongly inhibited by their water content that it fails to match the needs of growing roots. A slowing of oxygen influx is the principal cause of injury to roots and the shoots they support[22]. The maximum amount of oxygen dissolved in the floodwater in equilibrium with the air is a little over 3% of that in a similar volume of air itself. This small amount is quickly consumed during the early stages of flooding by aerobic microorganisms and roots.

Earlier workers[23] reported wilting of tobacco growing in sand culture deficient in O_2. Further, the reaction of flooded plants was studied with and without aeration treatment[3]. Plants in a flooded soil without aeration severely wilted at midday, whereas with aeration they did not wilt. In an unflooded soil if air is displaced with either N or CO_2, then too plants wilt. Similarly, application of chemicals such as cyanide (a respiratory inhibitor which blocks the cytochrome oxidase of the oxidative phosphorylation chain in mitochondria and inhibits respiration similar to the respiratory inhibition brought about by O_2 deficit) to the rooting medium degenerates the root apices and root hairs immediately and elicits wilting symptoms in cotton[20]. These observations confirm that soil depletion of O_2 is the main cause of root injury.

An absence of oxygen usually arrests the root growth and death arises principally because (i) demand for ATP exceeds the supply and (ii) self-poisoning by products of anaerobic metabolism. In the case of (i) anaerobic roots generate ATP mainly by glycolysis through the ethanolic fermentative pathway. This pathway yields only two ATPs from each glucose molecule, which is only about 6% of the ATP generated by mitochondria-based aerobic respiration. The small yield of ATP in anaerobic cells is insufficient for survival beyond a few hours and decreases the membrane integrity and viability of root cells[24]. In the case of (ii) the most notable toxin being excess protons that acidify the cytoplasm and vacuole[25]; others include acetaldehyde, reactive oxygen species[26] and gases such as ethylene and carbon dioxide[27].

It was further demonstrated that the rate of water intake fell by 60% within 1 h of flooding and continued to decrease steadily until the rate levelled off after 3 h of flooding at about 25% of the rate after 15 min of flooding[3]. This experiment showed that flooding of the soil results in a rapid decrease in permeability to water, which causes the sudden wilting often observed in the field. Cotton is one of the most susceptible of crop plants to injury from flooding or saturation of the soil with water. Cotton roots survive less than 30 min of O_2 deprivation[28]. Soon after flooding, the primary roots and root hairs are damaged. In hydroponically grown cotton plants, the roots and root hairs become discoloured (brownish) without aeration as against fresh roots and root hairs with aeration (Figure 3 *a* and *b*) confirmed cotton is sensitive to lack of oxygen. Prolonged waterlogging in addition to degenerating primary roots and root hairs, also damaged the taproot and formed black spots in the conducting

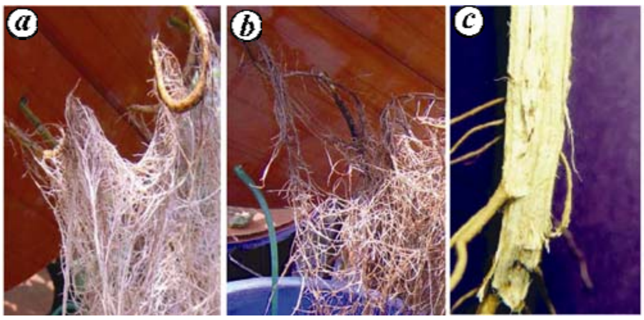

Figure 3. Cotton roots under hydrophonic and field conditions, ***a***, Hydrophonics grown in normal aeration; ***b***, Damaged root after aeration, withheld for two days; ***c***, Blackening of conducting tissues of a wilt-affected plant under field.

Table 1. Temporal measurements of photosynthesis and transpiration in normal and continuously waterlogged plants under field condition

	Transpiration (mol/m^2/s)			Photosynthesis (μmol/m^2/s)		
		Waterlogging			Waterlogging	
Days after waterlogging	Control	Wilt-tolerant	Wilt-sensitive	Control	Wilt-tolerant	Wilt-sensitive
1	7.2 (0.09)	7.3 (0.34)	8.09 (0.78)	26.5 (0.71)	25.5 (0.71)	29.0 (1.41)
2	7.0 (0.21)	6.9 (0.25)	3.49 (0.12)	27.0 (1.41)	27.0 (1.41)	11.5 (0.71)
4	7.4 (0.13)	6.3 (0.46)	0.04 (0.01)	27.5 (0.71)	21.0 (1.41)	0.3 (0.42)
9	7.2 (0.15)	6.2 (0.56)	–	27.0 (1.41)	15.0 (0.83)	–
13	7.0 (0.46)	5.7 (0.34)	–	25.5 (2.12)	15.5 (0.71)	–
28	7.3 (0.51)	6.1 (0.29)	–	27.0 (1.41)	14.5 (2.12)	–

Values in the parenthesis are SE.

Figure 4. Effect of waterlogging on pot-grown cotton plants under shade (left) and bright sunlight (right). Under sun, cotton plants suffer from wilting.

vessels (Figure 3 *c*). Waterlogging for longer duration could lead to the formation of adventitious root system in waterlogging-tolerant varieties. The newly formed adventitious roots usually contain aerenchyma and these roots can replace the stress-damaged roots that are formed before waterlogging. Secondly, new laterals completely replace the existing degenerated roots in cotton if waterlogging is prolonged beyond 5–6 days[29].

Association between parawilt and rapid growth rate of plants

At initial stages, plants have relatively slower growth rate and this gradually increases and peaks at flowering and early fruiting stage (Table 1). At this stage plants have high metabolic rate. With optimum light, temperature and soil moisture, plants exhibit high transpiration (T_r), stomatal conductance (g_s) and photosynthesis (P_N). There are several studies which have emphasized that leaf photosynthesis can be influenced by the presence of developing fruits. A positive effect of crop load on P_N has been reported in many plant species, including *Citrus unshiu*[30], *Prunus cerasus*[31], *Vitis vinifera*[32,33], soybean[34] and cotton[35,36]. Cotton plants show higher metabolic activity at grand growth stage, i.e. at flowering and early boll development stages. There is a strong association between P_N and stomatal conductance and hence, these plants would lose water through transpiration at a faster rate. If water uptake from the soil is not commensurate with the water loss through the leaves, then the plants will wilt.

Highly photosynthesizing plants require higher uptake of nutrients for the assimilation of photosynthates into proteins and other macromolecules. The nutrient uptake through the roots is an active process requiring respiration for ATP generation and hence, plants with higher root respiration as in the case of rapidly growing plants, consume the limited O_2 available in waterlogged soil at a fast rate. This lack of O_2 in the root zone causes root injury. Thus, the rapidly growing plants are more vulnerable to flooding injury.

How do bright sunshine and hot air temperature accentuate sudden/parawilt?

Soil saturation due to rains or excessive irrigation followed by bright sunshine leads to sudden wilting in rapidly growing plants. The intensity of light has a direct effect on photosynthesis. Generally speaking, the higher the intensity faster is the rate of photosynthesis until a maximum rate is reached. On a cloudy day, the rate would be slower. Plants growing under cloudy weather or shade, if waterlogged, do not wilt because of low g_s, T_r and P_n. On the other hand, sudden wilt occurs in plants that are waterlogged under bright sunlight (Figure 4). Thus, under bright sunlight plants will have high stomatal conductance, transpiration and photosynthesis, which is an important prerequisite for sudden wilt.

High soil temperature would be expected to increase the rate and severity of flooding injury, because it can act in several ways. Root respiration increases with increasing temperature, causing an increase in O_2 requirement which probably results in more rapid injury than would occur with a low O_2 requirement. It was further observed that a higher O_2 concentration is required for root growth at high temperatures than at low temperatures[37], and the same relation probably holds for the survival of roots. High temperature also increases the activity of microorganisms, speeding up the depletion of O_2 and the accumulation of CO_2. Perhaps equally important is the increased severity of injury to the root systems and bases of stems of flooded plants. At 20°C soil temperature, the root systems showed little damage, but at 34°C soil temperature the roots and stem bases were dead and decaying[3].

Wilting mechanism

From the above evidences, the cause of parawilt/sudden wilt of cotton can be represented in a flowchart as shown in Figure 5.

In general, plants with rapid growth, apparently, those with large canopy and high boll load have high transpiration loss of water, stomatal conductance and photosynthesis under bright sunlight. High photosynthesis demands greater uptake of nutrients through the roots, which is an active process involving respiration for ATP synthesis. Respiration depletes the limited O_2 available in waterlogged soil, which is faster in plants with rapid growth. This lack of oxygen leads to death of roots and root hairs, and thus restricts the uptake and transport of water through the roots. These plants otherwise have a high transpiration loss of water through the leaves, and as a consequence the soil–plant–atmosphere continuum collapses. Thus, the mismatch between the uptake of water through the roots and transpiration loss of water through the leaves causes sudden wilt/parawilt of cotton.

Species and varietal variation for flooding tolerance

Wide genetic variation for sudden wilt tolerance has been documented both between species within a taxon, and to some extent, within species[38]. In cotton too, there is wide variability for parawilt tolerance. Generally, species like *Gossypium arboreum* and *G. herbaceum* do not wilt, whereas within *G. hirsutum* species there is good variation between the genotypes for parawilt tolerance (Figure 6 *a* and *b*). The acclimatization of some of the varieties or species has been attributed to one or more adaptive mechanisms, including compensation for poor aeration in the normal root system by production of hypertrophied lenticels or adventitious roots, better stomatal regulation or metabolic adaptation. In a germplasm evaluation field trial at CICR, it was observed that the sudden wilt tolerance species of *G. arboreum* and *G. herbaceum* have lower stomatal conductance, transpiration and photosynthesis at flowering compared to *G. hirsutum* lines and hybrids (Table 2), suggesting that the slow metabolic rate of diploids could be one of the adoptive traits for sudden wilt tolerance. On the other hand, *G. hirsutum* and hybrids lose water through transpiration at a faster rate because of higher stomatal conductance, thus making these species more vulnerable to flooding.

Another important primary causative factor responsible for sudden wilt is a shortfall of oxygen availability in a

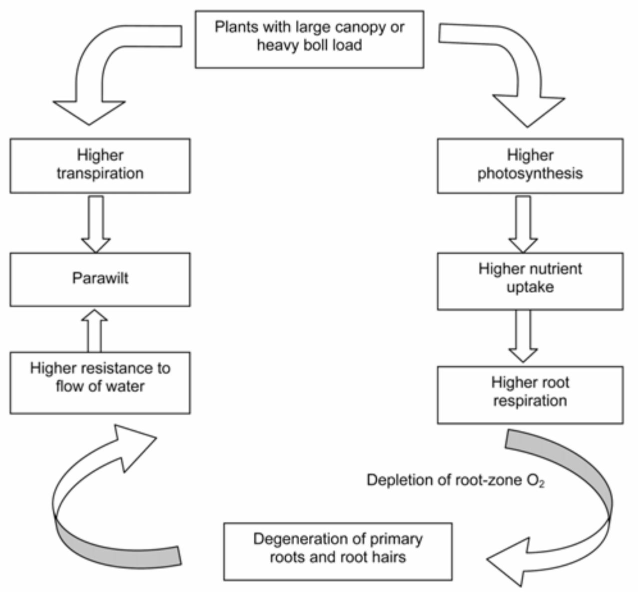

Figure 5. Flowchart showing the various processes involved in causing wilt.

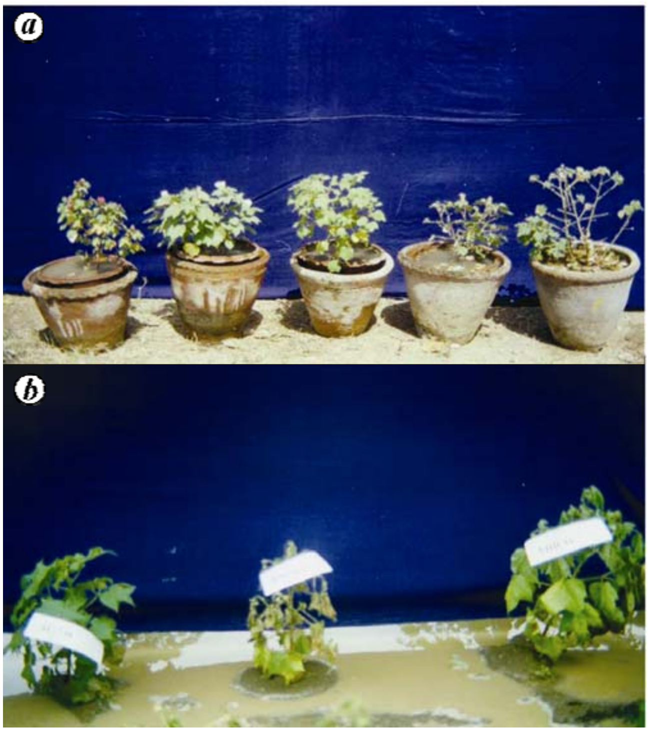

Figure 6. ***a***, Species and genotypic responses of cotton to parawilt. Pot-grown 60-day-old plants were submerged under bright sunlight. Pot in the extreme left is *Gossypium arboreum* and the rest are of *G. hirsutum* varieties. *G. arboreum* is tolerant while in *G. hirsutum* two varieties in the extreme right are sensitive and the others are wilt-tolerant. ***b***, Sudden wilt tolerance of a hybrid (extreme right) and its parents (left and centre) under field condition. Field was waterlogged when the crop was 55 days old. Photograph was taken one day after waterlogging.

Table 2. Stomatal conductance, transpiration and photosynthesis of germplasm lines of *G. arboreum*, *G. herbaceum*, *G. hirsutum* and cotton hybrids measured during early boll development (authors' unpublished data)

Species	Transpiration (mol/m^2/s)	Stomatal conductance (mol/m^2/s)	Photosynthesis rate (μmol/m^2/s)	No. of genotypes (*n*)
G. arboreum	3.94	245	18.11	50
G. herbaceum	3.73	230	17.25	3
G. hirsutum	4.35	280	20.29	100
Hybrids	4.71	320	23.65	6

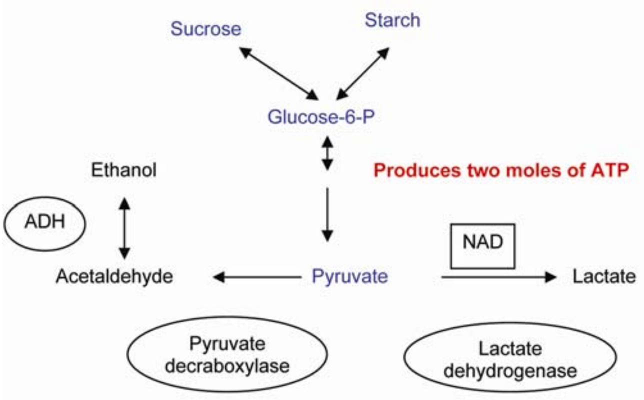

Figure 7. Depiction of various pathways from starch and sucrose that generate ATP anaerobically.

Figure 8. ***a***, Hypertropied lenticels on submerged stem portions of 70-day-old pot-grown cotton plant after 6 days of waterlogging. ***b***, Above-ground and below-ground parts of 70-day-old *Bt*-cotton hybrids, RCH 2 and MECH 184. Plants were grown in brick structure. To excavate the roots, the brick structure was dismantled and roots removed intact from the soil with a jet of water.

flooded soil, and its impact is felt both directly by the root system and indirectly by the shoots. In tissues suffering hypoxia or anoxia (low or no O_2 respectively), oxygen-dependent processes are suppressed, the functional relationships between roots and shoots are disturbed, and both carbon assimilation and photosynthate utilization are inhibited[22]. Adaptation to low oxygen levels in plants occurs in three stages[39]. Initially, the plant induces a set of signal transduction components. This is followed by metabolic adaptation involving fermentation pathways, and finally depending on the tolerance of the plant species, by morphological changes such as hypertrophied lenticels, aerenchyma and/or adventitious root formation.

At the metabolic level, under anaerobic condition plants shift their carbohydrate metabolism from an oxidative to a fermentative pathway and ATP is generated not by the Krebs cycle, but by alcoholic fermentation (Figure 7). Alcohol dehydrogenase (ADH) is the terminal enzyme in the ethanolic fermentation pathway, which plays a major physiological role in converting acetaldehyde to ethanol and regenerating NAD^+ in the process[40]. Thus, in waterlogged plants ADH helps produce at least two ATPs instead of 38 ATPs produced under normal conditions. Tolerant genotypes possessed higher enzyme content and activity in roots and leaves[41].

Sudden flooding also stimulates the accumulation of reactive oxygen species (ROS), superoxide (O_2^-), hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH^-) in the leaf, all of which damage the cell constituents, among which the chloroplasts are highly sensitive[42]. The scavenging of ROS is carried out by a number of well-characterized enzymes, primarily superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT). High levels of SOD, CAT and APX have been identified as being important for the survival of a number of species in the event of prolonged waterlogging[43,44].

The most common morphological and anatomical (morphoanatomical) responses to root hypoxia include the formation of adventitious roots, aerenchyma and hypertrophied lenticels, all of which improve the capacity of the plant for oxygen capture and its transfer to submerged tissues[45–47]. They facilitate the transport of O_2 from the shoots to the roots, and also encourage rhizosphere oxidation and the removal of toxic products[48]. As a result of its extensive network of air spaces, aerenchyma tissue helps maintain a low oxygen tolerance for the storage and exchange of gases within the plant[49]. In cotton, hypertrophied lenticels are formed at the zone of submergence at the stem base within 3–4 days of waterlogging (Figure 8 *a*). Hence it cannot be a first line of defence against a sudden wilt. In case of sudden wilt which occurs immediately after flooding, the first line of defence could be metabolic adaptation, better stomatal

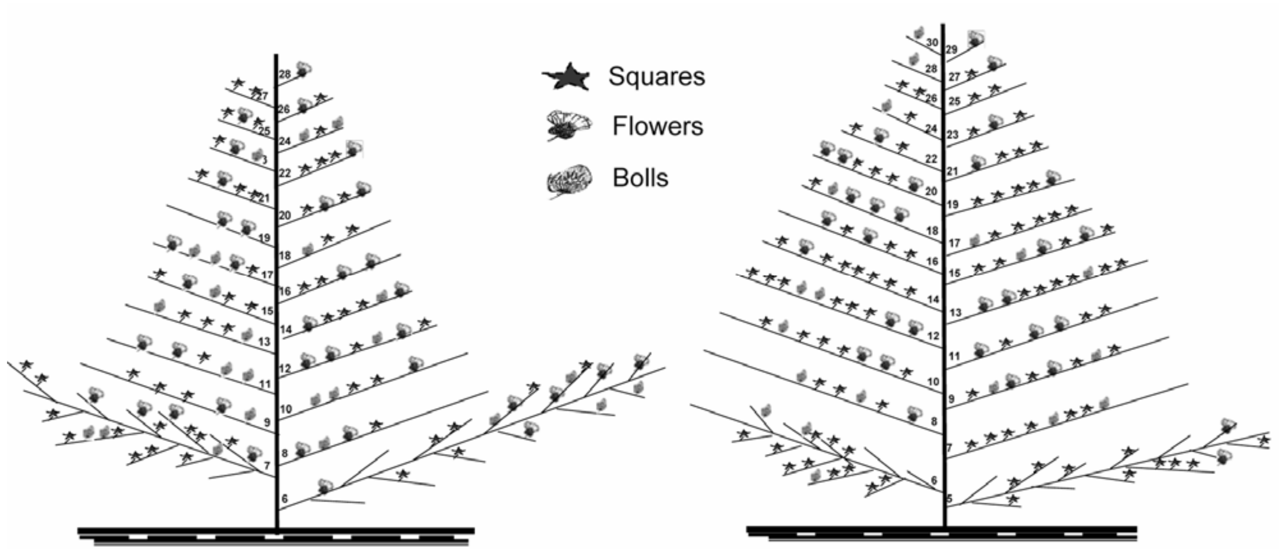

Figure 9. Temporal and spatial distribution of squares, flowers and open bolls of a typical *Bt* and non-*Bt* plant grown under field condition[52].

regulation or ability to survive better under oxygen deprivation. Sudden wilt tolerance showed a positive association with root volume and depth of the different cultivars, as it would get O_2 from larger areas. From Figure 8 *b*, it is evident that cultivar RCH 2 with a large volume of roots, in relation to the above ground parts, is more tolerant compared to shallow rooted cultivar MECH 184. If the plant is able to survive sudden flooding, subsequent survival under prolonged water-logging could be either through the production of hypertrophied lenticels[46] or adventitious roots[50,51]. Hypertrophied lenticels production is more and early in *G. hirsutum* and hybrids compared to *arboreum* and *herbaceum*.

Bt-cotton versus non-*Bt*-cotton

Parawilt/sudden wilt is in the news for the last few years because of its higher occurrence in *Bt*-cotton (*Bacillus thuringiensis* transgenic cotton) compared to non-*Bt*-cotton. Thus cotton workers believed that the introduction of *Bt* gene made the cotton plants more susceptible to parawilt at the genetic level. Our observations, however, clearly showed that it is not because of *Bt* gene insertions, rather the retention of early-formed squares and bolls in *Bt* plants, that makes it more susceptible to parawilt. There was no marked difference in growth, physiological processes and square production of *Bt* and non-*Bt* hybrids up to 80 days after sowing (DAS) (Table 3). Because of better bollworm control in *Bt* plants there was greater retention of early-formed bolls on the lower canopy, whereas they were intermittently distributed in non-*Bt* plants (Figure 9). Photosynthesis and growth during boll development have a positive association with boll load in *Bt* plants[36,52]. Thus, the higher metabolic activity and rapid growth of a *Bt* plant at reproductive phase make it more vulnerable to any environmental abnormalities like sudden floods. But for this growth difference, the *Bt* gene has nothing to do with the occurrence of wilt in transgenic *Bt* plants, as claimed by earlier workers[9]. On the other hand, non-*Bt* plants show lower g_s and P_N during the same period. Therefore, if both *Bt* and non-*Bt* plants are waterlogged with heavy rains or excessive irrigation under bright sunlight, the sudden wilt/parawilt occurrence is likely to be more in *Bt* compared to non-*Bt* plants.

Control

With the above understanding certain guidelines for managing and minimizing the impact of parawilt on cotton can be formulated. These are mostly practices that favour the growth of strong, healthy root systems and better regulation at above-ground level so as to keep the soil–plant–atmosphere continuum intact under higher incidence of extreme rainfall events as projected by the scenarios of climate change. Some of the issues to consider for the control of sudden wilt in cotton are: (i) Proper irrigation: In irrigated areas, over irrigating in the early life of a crop forces the roots to grow on the surface and can support the plants till flowering. At flowering, the heavy demands for moisture and the tendency to apply more irrigation water results in soil anaerobiosis which in plants with shallow roots, leads to sudden wilt. Over irrigating, under hot and bright sun, particularly at flowering and early boll set, should be avoided. Accurate management of irrigation is essential to minimize the disorder. (ii) Adequate drainage: Cotton crops grown in well-drained soils are less at risk of developing parawilt than those grown in poorly drained soils. Green manure crops grown during the off-season can help improve the soil structure and drainage. (iii) Choice of cultivars: Past research has

Table 3. Plant growth and physiological processes: transpiration rate (*E*), stomatal conductance (g_s), and net photosynthetic rate (P_N) of field grown *Bt* and non-*Bt* hybrids measured at 50, 80, and 110 DAS. Means of three hybrids[36]

DAS	Treatment	Main stem node number	Plant height (cm)	Dry matter per plant (g)	*E* (mol/m²/s)	g_s (mol/m²/s)	P_N (µmol m²/s)
50	*Bt*	11	23	55	5.76	474	26.8
	Non-*Bt*	11	20	57	6.56	466	26.7
	SEM	0.20	0.41	0.61	0.03	0.35	0.20
	LSD ($P < 0.05$)	NS	NS	NS	NS	NS	NS
90	*Bt*	20	57	87.80	6.56	488	31.2
	Non-*Bt*	20	56	83.42	6.59	487	31.8
	SEM	0.37	0.13	1.94	0.12	45.72	0.16
	LSD ($P < 0.05$)	NS	NS	NS	NS	NS	NS
110	*Bt*	27	66	107.46	7.23	673	33.6
	Non-*Bt*	29	78	94.6	6.63	493	29.2
	SEM	0.14	1.48	0.65	0.02	0.35	0.20
	LSD ($P < 0.05$)	NS	9.17	3.96	0.62	6.40	2.56

DAS, Days after sowing; NS, Non-significant.

clearly shown that some species and cultivars are more resistant to the disorders than others. *G. arboreum* and *G. herbaceum* are more resistant compared to *G. hirsustum*. This has been associated with the root volume of the different cultivars. Cultivars with a large volume of roots, in relation to the above ground parts, tend to be more resistant and should be selected for disorder-prone fields. The short-duration, fast-growing cultivars are more vulnerable compared to slow-growing, long-duration cultivars. (iv) Optimum vegetative growth of the crop: Excessive use of farmyard manure and fertilizers results in high vegetative growth and relatively faster growth rate. Under adverse conditions like flooding by inundation or soil saturation by excessive irrigation, this depletes the soil oxygen at a fast rate and leads to wilting. The excessive growth can be curbed using growth retardants like lihocin, planofix, etc. (v) Better stomatal regulation: Wide variability is seen in stomatal response to climatic variables like flooding. Some species are believed to have strong communication between roots and shoot. In such plants, the roots can sense any changes in the root zone and immediately send a signal to the shoot to close the stomata under adverse conditions. Such a mechanism would reduce water loss and metabolic processes like photosynthesis which is indirectly involved in the cause of parawilt. Stomatal regulation is one of the most important traits that needs to be incorporated while evolving newer varieties for sudden/parawilt tolerance so as to make them adapt to the anticipated flood due to climate change.

The above controlled strategies can be more effective when implemented in an integrated disorder management programme in which one option complements the other. This is largely the direction that needs to be undertaken in future research for the sustainable management of sudden/parawilt of cotton.

1. Bradford, K. J. and Hsiao, T. C., Stomatal behaviour and water relations of waterlogged tomato plants. *Plant Physiol*., 1982, **70**, 1508–1518.
2. Else, M. A. and Jackson, M. B., Transport of 1-aminocyclopropane-1-carboxylic acid (ACC) in the transpiration stream of tomato (*Lycopersicon esculentum*) in relation to foliar ethylene production and petiole epinasty. *Aust. J. Plant Physiol*., 1988, **25**, 453–458.
3. Kramer, P. J. and Jackson, W. T., Causes of injury to flooded tobacco plants. *Plant Physiol*., 1954, **29**, 241–245.
4. Jackson, M. B., Rapid injury to peas by waterlogging. *J. Sci. Food Agric*., 1979, **30**, 143–152.
5. Cohen, C., Elkind, Y., Burger, Y., Offenbach, R. and Nerson, H., Variations in the response of melon genotypes to sudden wilt. *Euphytica*, 1996, **87**, 91–95.
6. Yin, D., Chen, S., Chen, F., Guan, Z. and Fang, W., Morpho-anatomical and physiological responses of two *Dendranthema* species to waterlogging. *Environ. Exp. Bot*., 2010, **68**, 122–130.
7. Srinivasan, K. V., The new wilt disease affecting cotton. In Proceedings of the Group Discussion on New Wilt of Cotton, Central Institute for Cotton Research (CICR), Nagpur, 6–7 November 1984, pp. 9–13.
8. Anon., In Proceedings of the Group Discussion on New Wilt of Cotton, CICR, Nagpur, 6–7 November 1984.
9. Mayee, C. D. and Choular, A. B., Parawilt of cotton. In National Seminar on 'Changing Pest Situation in Current Agricultural Scenario in India', Indian Agricultural Research Institute, New Delhi, 1988.
10. Mayee, C. D., Choulwar, A. B. and Acharya, H. S., Distribution pattern of parawilt of cotton (*Gossypium* species). *Indian J. Agric. Sci*., 1990, **60**, 777.
11. Mayee, C. D., Indian Council of Agricultural Research Adhoc Scheme on Etiology and Epidemiology of Parawilt of Cotton, Marathwada Agricultural University, Substation, Aurangabad, Final Report, 1991.
12. Mayee, C. D., Parawilt of cotton: nuances and the challenges. *J. Mycol. Plant Pathol*., 1997, **27**, 28.
13. Shastry, P. P., Balasunramanya, R. H., Paralikar, K. M., Krishna, A., Mishra, U. S., Mandloi, K. C. and Nayak, M. L., Xylem embolism in new wilt of cotton. *Indian Phytopathol*., 1995, **48**, 308–313.

14. Tyree, M. T. and Sperry, J. S., Vulnerability of xylem to cavitation and embolism. *Annu. Rev. Plant Physiol. Plant Mol. Biol*., 1989, **40**, 19–38.
15. Sahay, R. K., Bhale, N. L., Pundarikakshudu, R. and Rao, M. R. K., Involvement of ethylene with new wilt of cotton. *Indian J. Agric. Sci*., 1988, **58**, 885–887.
16. Shastry, P. P., Mandloi, K. C. and Koutu, G. K., New wilt of cotton. *Natl. J. Plant Improv*., 2001, **3**, 49–55.
17. Anon., Third World Network, 2 April 2003.
18. Nair, K. P., *Business Line*, 30 March 2005.
19. Banerji, D., *Bt* cotton in India. Barking up the wrong tree. In Third World Network Biosafety Information Service, 2 April 2003, pp. 1–5.
20. Hebbar, K. B. and Mayee, C. D., Parawilt of cotton: Is inhibition of root respiration a causal factor? *Indian J. Agric. Sci*., 2004, **74**, 48–51.
21. Hebbar, K. B. and Khadi, B. M., A process patent filed entitled 'The cause of parawilt/sudden wilt in cotton'. Patent No. 1404/MUM/2006 dated: 01/09/2006.
22. Vertapetian, B. B., Andreev, I. N., Kozlova, G. I. and Agapova, L. P., Mitochondrial ultrastructure in roots of mesophyte and hydrophyte at anoxia and after glucose feeding. *Protoplasma*, 1977, **91**, 243–256.
23. Hopkins, H. T., Specht, A. W. and Hendricks, S. B., Growth and nutrient accumulation as controlled by oxygen supply to plant roots. *Plant Physiol*., 1950, **25**, 193–209.
24. Rawyler, A., Arpagaus, S. and Braundle, R., Impact of stress and energy availability on membrane stability of plant cells. *Ann. Bot*., 2002, **90**, 499–507.
25. Gerendás, J. and Ratcliffe, R. G., Root pH control. In *Plant Roots: The Hidden Half* (eds Waisel, Y., Eshel, A. and Kafkafi, U.), Marcel Deker Inc, New York, 2002, pp. 553–570.
26. Van Toai, T. T. and Bolles, C. S., Postanoxic injury in soybean (*Glycine max*) seedlings. *Plant Physiol*., 1991, **97**, 588–592.
27. Arshad, M. and Frankenberger, W. T. J., Production and stability of ethylene in soil. *Biol. Fertil. Soils*, 1990, **10**, 29–34.
28. Huck, M. G., Variation in taproot elongation as influenced by composition of the soil air. *Agron. J*., 1970, **62**, 815–818.
29. Hebbar, K. B., Effect of long duration waterlogging on growth and yield of *G. hirsutum* and arboreum genotypes of cotton at early seedling and flowering stages. *Indian J. Agric. Sci*., 2003, **73**, 172–174.
30. Iglesias, D. J., Lliso, I., Tadeo, F. R. and Talon, M., Regulation of photosynthesis through source: sink imbalance in citrus is mediated by carbohydrate content in leaves. *Physiol. Plant*., 2002, **116**, 563–572.
31. Layne, D. R. and Flore, J. A., End-product inhibition of photosynthesis in *Prunus cerasus* L. in response to whole-plant source–sink manipulation. *J. Am. Soc. Hortic. Sci*., 1995, **120**, 583–599.
32. Edson, C. E., Howell, G. S. and Flore, J. A., Influence of fruit loads on photosynthesis and dry matter partitioning of Seyval grapevines. 2. Seasonal changes in single leaf and whole vine photosynthesis. *Am. J. Oncol. Viticult*., 1995, **46**, 469–477.
33. Naor, A., Gal, Y. and Bravdo, B., Crop load affects assimilation rate, stomatal conductance, stem water potential, and water relations of field-grown Sauvignon Blanc grapevines. *J. Exp. Bot*., 1997, **48**, 1675–1680.
34. Setter, T. L., Brun, W. A. and Brenner, M. L., Stomatal closure and photosynthetic inhibition in soybean leaves induced by petiole girdling and pod removal. *Plant Physiol*., 1980, **65**, 884–887.
35. Jasoni, R., Cothren, T. and Fernandez, C., Carbon dioxide exchange rate of cotton after complete removal. *J. Cotton Sci*., 2000, **4**, 91–96.
36. Hebbar, K. B., Perumal, N. K. and Khadi, B. M., Photosynthesis and plant growth response of transgenic *Bt* cotton (*Gossypium hirsutum* L.) hybrids under field condition. *Photosynthetica*, 2007, **45**, 254–258.
37. Cannon, W. A., Physiological feature of roots, with special reference to the relations of roots aeration of the soil. Carnegie Institute of Washington Publication, 1925, **368**, 1–168.
38. Kreuzwieser, J., Forniss, S. and Renennber, H., Impact of waterlogging on the N-metabolism of flood tolerant and non-tolerant tree species. *Plant Cell Environ*., 2002, **25**, 1039–1049.
39. Denis, E. S. *et al.*, Molecular strategies for improving waterlogging tolerance in plants. *J. Exp. Bot*., 2000, **51**, 89–97.
40. Davis, D. D. (ed.), Anaerobic metabolism and the production of organic acids. In *The Biochemistry of Plants*, Academic Press, New York, 1980, vol. 2, pp. 581–611.
41. Hebbar, K. B., Physiological and biochemical basis of waterlogging tolerance in cotton. Annual Report, CICR, 2000.
42. Yordanova, R. Y., Kristov, K. N. and Popova, L. P., Antioxidative enzymes in barley plants subjected to soil flooding. *Environ. Exp. Bot*., 2004, **51**, 93–101.
43. Hurng, W. P. and Kao, C. H., Lipid peroxidation and antioxidative enzyme activities in senescing tobacco leaves following flooding. *Plant Sci*., 1994, **96**, 41–44.
44. Hwang, S. Y., Lo, H. F., Shao, C. K. and Chen, L. F., Changes in antioxidative enzyme activities in two leafy vegetable sweet potato cultivars subjected to waterlogged conditions. *J. Chin. Soc. Hortic. Sci*., 2000, **46**, 287–296.
45. Colmer, T. D., Long distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ*., 2003, **26**, 17–36.
46. Hebbar, K. B., Prakash, A. H. and Rao, M. R. K., Lenticel – a morphological adaptation of cotton plant to waterlogging. *J. Plant Biol*., 2001, **28**, 119–121.
47. Malik, A. I., Colmer, T. D., Lambers, H. and Schortemeyer, M., Aerenchyma formation and radial O_2 loss along adventitious roots of wheat with only the apical root portion exposed to O_2 deficiency. *Plant Cell Environ*., 2003, **26**, 1713–1722.
48. Visser, E. J. W., Colmer, T. D., Blom, C. W. P. M. and Voesenek, L. A. C. J., Changes in growth, porosity and radial oxygen loss from adventitious roots of selected mono and dicotyledonous wetland species with contrasting types of aerenchyma. *Plant Cell Environ*., 2000, **23**, 1237–1245.
49. Pang, J. Y., Newman, I., Mendham, N., Zhou, M. and Shabala, S., Microelectrode ion and O_2 fluxes measurements reveal differential sensitivity of barleyroot tissues to hypoxia. *Plant Cell Environ*., 2006, **29**, 1107–1121.
50. Gill, C. J., The ecological significance of adventitious rooting as a response to flooding in woody species, with special reference to *Almus glutinosa*. *Gaertn Flora*, 1975, **164**, 85–97.
51. Sena Gomes, A. R. and Kozlowski, T. T., Growth responses and adaptations of *Fraximus pennsylvanica* seedlings flooding. *Plant Physiol*., 1980, **66**, 267–271.
52. Hebbar, K. B., Rao, M. R. K. and Khadi, B. M., Synchronized boll development of *Bt* cotton hybrids and their physiological consequences. *Curr. Sci*., 2007, **93**, 693–695.

Received 6 September 2010; accepted 24 March 2011