Environmental physiology of the bananas (*Musa* spp.)

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The bananas are thought to be particularly sensitive to changes in the environment. This review considers some historical and recent investigations into the response of the leaf, root and reproductive system to the environment. Monteith's analysis of the response of plants to intercepted radiation is appropriate for analyzing the productivity of bananas and plantains. The banana is sensitive to soil water deficits, and expanding tissues such as emerging leaves and growing fruit are among the first to be affected. As soil begins to dry, stomata close and leaves remain highly hydrated, probably through root pressure. Productivity is affected because of the early closure of stomata. We find the common belief that bananas use large amounts of water does not have a strong physiological basis. Improvements in water-use efficiency in irrigated plantations could come from a closer match between plant water use and the amount of water applied. We examine recent data on water-use efficiency of different banana cultivars and propose that agronomists, physiologists and breeders could quantify the amount of water available in each rain-fed environment and work towards directing more of that water through the plant. The banana is day neutral for floral induction, but photoperiods of less than 12 h are associated with a slowing in the rate of bunch initiation that is independent of temperature expressed as growing degree days. This may contribute to seasonal variations in banana flowering, even in more tropical environments with moderate temperatures.

Key words: crop yield, leaf system, light, photoperiod, photosynthesis, reproductive system, root system, temperature, water supply

Ecofisiologia de bananeiras (*Musa* spp.): Bananeiras são particularmente sensíveis a mudanças no ambiente. Nesta revisão, exploram-se alguns estudos clássicos e recentes sobre as respostas ao ambiente da folha, raiz e sistema reprodutivo dessa espécie. A análise de Monteith sobre as respostas das plantas à radiação interceptada mostrou-se apropriada para a análise da produtividade de bananeiras. Bananeiras são sensíveis ao déficit hídrico do solo, particularmente tecidos em expansão tais como as folhas em formação e os frutos em crescimento. Na medida em que o solo começa a secar, os estômatos se fecham e as folhas se mantêm altamente hidratadas, provavelmente devido à pressão radicular. A produtividade é afetada, em função do fechamento estomático. A crença geral de que bananeiras usam grandes quantidades de água não tem forte embasamento fisiológico. O aumento na eficiência do uso da água em cultivos irrigados pode advir de aumentos na densidade de plantio e quantidade de água aplicada. Examinam-se dados recentes sobre a eficiência do uso da água em diferentes cultivares de banana e propõe-se que agrônomos, fisiologistas e melhoristas possam quantificar a quantidade de água disponível nos vários ambientes de sequeiro, de modo a maximizar a eficiência do uso da água pela planta. A bananeira é uma espécie neutra para a indução floral, porém fotoperíodos inferiores a 12 h são associados a uma redução na taxa de iniciação do cacho, que é independente da temperatura quando expressa em graus-dia durante a fase de crescimento. Isso pode contribuir para variações sazonais na floração da banana, mesmo em ambientes tipicamente tropicais com temperaturas moderadas.

Palavras-chave: fotoperíodo, fotossíntese, luz, produção, sistema foliar, sistema radicular, suprimento hídrico, temperatura

INTRODUCTION

People have been using bananas for at least 7,000 years in Papua New Guinea (Denham et al., 2003), possibly 6,000 years in Uganda (Lejju et al., 2006) and 2,500 years in Cameroon (Mindzie et al., 2001). Today, most people of the world are familiar with this delicious fruit. Edible clones of bananas and plantains, based on landraces, are derived from hybrids of the wild sub-species of *Musa acuminata* (A genome) and *M. balbisiana* (B genome). The wild bananas occur within the tropics from India to Oceania but there is a distinction between the distribution of *M. acuminata* and *M. balbisiana* within that range. *Musa balbisiana* overlaps the northern part of the range of *M. acuminata* and extends beyond it to the west and north (Simmonds, 1962). The edible clones are now grown more widely including in the subtropics of both hemispheres. Triploids (AAA, AAB and ABB) are most common among the edible bananas with the plantains belonging to the AAB group. A special feature of the edible clones is the parthenocarpic development of sterile fruit (Simmonds, 1959). The cultivars of the Cavendish sub-group (AAA) currently dominate the international banana trade that is only 15% of the world's annual production of 105 Mt (FAO, 2006). In recent years, the world production of bananas has grown 3.3% annually. In countries such as Brazil, a major producer, and Australia, a minor producer, bananas grow in tropical and subtropical environments and on a wide range of soils.

Simmonds (1962) summarized the features of the wild bananas, based on observations in the field, as being a group of broadly opportunistic plants that are intermediate in ecological succession, distributed by animals, and requiring high temperature, humidity and light. They do not tolerate competition or poor soil drainage and tend to be short-lived. Within the wild bananas, Simmonds noted significant differences between species in their ecological demands and tolerances. Early comments on bananas, particularly of the cv. 'Gros Michel' (AAA group) used by the international trade early in the 20th century, focus on the sensitivity of the plant to changes in the environment (Popenoe, 1941). Most of the research on the effect of environment on *Musa* species has been on members of the edible bananas. There is a need to know more about the responses of the wild species that provide the genetic basis for the edible genotypes.

LEAF SYSTEM

The banana is a monocotyledon with an underground main axis that is a sympodium and is commonly called a 'corm'. The corm supports a series of leaves the sheaths of which form the 'pseudostem'. The leaves arise in sequence from the apex of each vegetative shoot. In ratoon plants the first leaves on the shoot are scale like, subsequent leaves are lanceolate, and later in development laminate leaves are produced. The petiole is an extension of the sheath and this leads to the midrib that supports the lamina. In total, 30 to 50 or more leaves may be produced on a shoot but at any one time only 10 to 14 living leaves are present. As each leaf develops within the pseudostem the lamina increases in area until it begins to emerge from the top of the pseudostem. It may take 7 to 14 d for one leaf to emerge. During that time, increase in area ceases for those parts of the lamina that have emerged. Each laminate leaf is larger than its predecessor except for the last couple of leaves that emerge before the inflorescence which are smaller in area than their predecessors. The maximum amount of leaf area on a shoot coincides with the emergence of the bunch (inflorescence) from the top of the pseudostem. After this, no new leaves are produced on that shoot because the bunch is terminal and the leaf area then begins to decline over time as the older leaves senesce. During the development of a single shoot, lateral shoots or suckers develop from buds on the corm and these begin to grow, each producing their own sequence of leaves and an inflorescence. In commercial plantations, most suckers are removed to allow a single shoot to develop on each plant. The capacity of a canopy of leaves in a plantation to intercept light and fix carbon is measured by the leaf area index, LAI. The LAI includes the area of all green leaves on all shoots present. It is the area of leaf (single side) divided by the area of land occupied by the plants. It varies with location, planting density and a number of other factors, including season, and ranges from 2 to 5. This is not large compared with an apple tree that may have an LAI of 7 or more (Proctor et al., 1976), but even apple trees normally have LAI within the range of 3.5 to 4.6 when the leaves are fully grown (Jackson, 2003). The individual leaves on bananas can be quite large, up to 2 m^2, and this gives the impression that LAI must be high, compared with other crops, but measurements suggest this is not the case. In a banana plantation with LAI of

4.5, about 90% of the ground will be shaded at noon on a sunny day. This implies that about 90% of the incoming radiation is being intercepted by the leaf canopy. Thus increasing LAI beyond this value is of little benefit to the plantation because most of the incoming radiation is already being intercepted.

Interception of radiation, photosynthesis and productivity: Leaves intercept radiant energy from the sun and use it to fix carbon dioxide and synthesise carbohydrates that are used for plant function and growth. Several authors have reported measurements for banana of the relationship between light received and the rate of net photosynthesis (*A*) of individual leaves. These data were summarized by Turner (1998a,b). There is considerable variation in the form of light response curves between experiments, cultivars and environmental conditions, mainly in the maximum rate of *A*, that may vary from 5 to 25 μmol CO_2 $m^{-2}s^{-1}$, and the saturation value for the photosynthetic photon flux density, that may vary from 700 to more than 2,000 μmol quanta m^{-2} s^{-1}. In addition, the experiments of Robinson et al. (1992) show that *A* is increased by the presence of growing organs on the plant and this may be a reason why Thomas and Turner (2001) found that *A* of leaves on rapidly growing vegetative plants of cv Williams (AAA, Cavendish subgroup) did not reach light saturation, even at full sunlight. There is a need to use the data available on light response curves to simulate carbon fixation by a canopy of banana leaves. In this way the significance of differences in the light response curve for functioning of the canopy could be evaluated. One may expect that while an individual leaf saturates for photosynthetic photon flux density, a canopy does not and so the primary production (CO_2 fixed per unit ground area) of a canopy tends to increase the more light it receives (Jones, 1992). This analysis assumes the canopy cover is complete. Furthermore, if LAI is low (< 3) then the light saturation of all leaves in the canopy is more likely to be reached and the canopy will show saturation for light (Thornley and Johnson, 2000). Added to this for a canopy of banana leaves is the ability of leaves to fold as incoming net radiation increases, resulting in more radiant energy being shed to lower leaf levels or to the ground.

The relationship between leaf *A* and its internal CO_2 concentration, C_i, can give clues about the factors limiting photosynthesis. Recently Sharkey et al. (2007a,b) proposed a curve fitting procedure for analyzing A/C_i curves. Schaffer et al. (1996) measured the effect of root restriction and high ambient CO_2 concentration on the A/C_i response of leaves of cv Gros Michel (AAA group). We subjected their published data to the curve fitting procedure of Sharkey et al. (2007b) which has five outputs: the maximum carboxylation rate allowed by Rubisco, V_{cmax}; the rate of photosynthetic electron transport, *J*; triose phosphate use, TPU; day respiration rate, R_d; and mesophyll conductance, g_m. The procedure standardizes the values of these parameters to 25ºC for comparison. Root restriction reduced plant growth by 25% and it affected the biochemistry of photosynthesis by reducing V_{cmax} 46% and increasing R_d by 44% (Table 1). The changes in *J*, TPU and g_m were smaller in magnitude. Increasing ambient CO_2 concentration from 350 to 1,000 μL L^{-1} more than doubled plant growth and it changed the biochemistry of photosynthesis. It more than halved V_{cmax} and increased R_d by five fold (Table 1). There were smaller effects on *J*, TPU and g_m. This analysis of the data of Schaffer et al. (1996) complements their findings and quantifies the five parameters of the A/C_i curves.

At the level of the crop, two approaches have been used to analyse the response of bananas to incoming solar radiation. The first approach is the effect of shading. This is sensible to investigate because increasing plant density reduces the amount of sunlight available per plant and in gardens bananas may be grown as an understory. Turner (1998b) summarized the findings of shading experiments and these show that in deep shade, the increase in yield is proportional to the increased amount of light received. At higher levels of radiation, other factors begin to limit yield and so there is no further response to increased radiation (Figure 1). The second approach is that proposed by Monteith (1981) where, for plants in general, the amount of growth is proportional to the intercepted radiation, irrespective of the amount incoming radiation. This approach has been widely accepted among crop physiologists and in bananas has been used to estimate the seasonal demand for nitrogen (Turner, 1990) and the productivity of bananas in a range of environments (Turner, 1998b). The equation of Monteith has been modified for bananas to

Table 1. The parameters of the photosynthetic carbon dioxide response curve for banana cv. 'Gros Michel' (AAA group). The A/C_i response curves come from the experiments of Schaffer et al. (1996) who applied treatments of root restriction (container volume, 20 or 200 L) and ambient CO_2 concentration (350 or 1,000 µl L^{-1} CO_2). The A/C_i parameters were derived from the curve fitting procedure of Sharkey et al. (2007b). V_{cmax} = maximum carboxylation rate allowed by Rubisco; J = rate of photosynthetic electron transport; TPU = triose phosphate use; R_d = day respiration; and g_m = mesophyll conductance. * container volume and ambient CO_2 concentration both significantly affected total plant dry weight ($P \leq 0.05$).

Parameter		Treatments			
	Units	20 L pot	200 L pot	350 CO_2	1,000 CO_2
V_{cmax}	µmol m^{-2} s^{-1}	539	996	1249	539
J	µmol m^{-2} s^{-1}	268	290	252	296
TPU	µmol m^{-2} s^{-1}	19.1	20.6	18.0	20.9
R_d	µmol m^{-2} s^{-1}	13.9	9.6	3.4	17.7
g_m	µmol m^{-2} s^{-1} Pa^{-1}	1.21	1.14	1.22	0.91
Total plant dry weight	g	1,686	2,272*	1,142	2,731*

include the effects of temperature and plant vigour, expressed as the cycling time of ratoon crops (Turner, 1994, 1998b). Data are needed to determine the coefficients, especially the radiation use efficiency. It is possible using this approach to estimate the potential yield for a site (Turner, 1998b) and, despite the number of assumptions, this is a good base for further discussions about what factors might be limiting yield in a given situation.

Monteith's approach gives insights into the effect of protected cultivation on banana yield. In that situation there is an increase in productivity (20-30%) but a reduction in the amount of solar radiation (20%) beneath the protective cover (Galan Sauco et al., 1992). The model in Figure 1 would indicate that such a reduction in incoming radiation would either reduce yield or have no impact. Monteith's model accounts for the observed response because protected cultivation increases LAI and changes the extinction coefficient such that the plants intercept more incoming radiation than their counterparts growing in an open plantation (Turner, 1998b). The plants in the open do not have enough leaf area to intercept as much radiation as their counterparts under cover, and the arrangement of their leaves magnifies this effect.

Water relations of the bananas: Knowledge of the water relations of a plant, particularly its leaves, has long been associated with understanding the physiological responses of the plant to soil and atmospheric water deficits. This knowledge can assist in management decisions concerning irrigation, water use and productivity. While extensive gains in our knowledge of plant responses have been achieved for many plants, the more unusual morphology and anatomy of bananas has hindered the rate of achievement. Water relations of plant tissues are described using changes in volume (usually the amount of water present, since water is incompressible) and changes in the thermodynamic

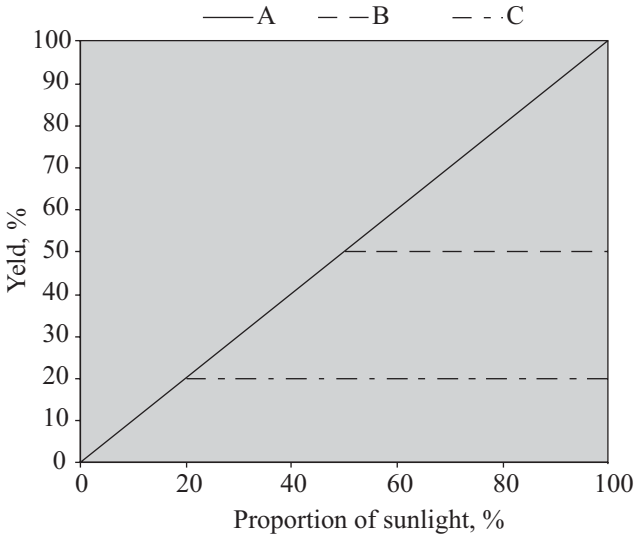

Figure 1. A schematic diagram of the response of banana yield to shade. Line **A** is the expected response of yield based on the efficiency of growth of well-shaded plants. Lines **B** and **C** show no response to increased light because factors other than light now limit yield.

status of the water in the tissues. It is the presence of large air pockets within the leaves, and laticifers containing latex within the leaves, fruit and corm that hinders the use of standard methods of measuring water relations. In banana leaves it is thought these air pockets could fill when volumetric methods of measuring water status are used (Kallarackal et al., 1990), especially when leaf tissues are being rehydrated. Exuding latex makes it difficult to distinguish water exuding from xylem when using the standard pressure chamber for measurements of leaf water potential. The laticifers in the lamina are several centimeters long and those in the midrib and leaf sheath can be several metres long. The laticifers contain fluids at a lower potential than the surrounding tissues and this is why when banana leaves or fruit are cut, their contents exude as they are replaced by water from the surrounding tissues. If no latex exudes, then the leaf is most likely to be lacking in water.

Despite these challenges of anatomy and morphology, water relations of bananas have been measured using both volumetric and thermodynamic methods. Additionally the plant morphological technique of measuring the extent of leaf folding has been used. Each of the thermodynamic, volumetric or morphological techniques has its strengths and weaknesses and can indicate different aspects of the water status of leaf tissues. Early studies that assess leaf water status in bananas used mainly volumetric methods such as leaf water content (g H_2O per g leaf dry matter), specific leaf water content (g H_2O per m^2 leaf surface) (Shmueli, 1953; Chen, 1971) or relative leaf water content (Turner and Lahav, 1983). These studies typically show large responses in plant behaviour within a very narrow and high (moist) range of values of leaf water status measured by these techniques. In a later study Turner and Thomas (1998) confirmed this finding and showed air spaces within the leaf were not biasing volumetric measurements. In fact the high values for volumetric techniques (relative water content) indicate water does not fill the air spaces and furthermore, in banana, high vacuum is needed to fill these air spaces with water (Turner and Thomas, 1998). Volumetric measurements of leaf water status indicate that banana plants remain very hydrated even when showing other signs of water deficit.

Methods of measuring the thermodynamic status of leaf water, such as with a pressure chamber, have been used for bananas (Hegde and Srinivas, 1989; Thomas and Turner, 1998). Milburn et al. (1990) developed a technique to measure plant water status based on the osmotic potential of exuding latex. This technique avoids the dangers of differentiating xylem water, which has to be forced from the leaf, and latex fluid that exudes freely from severed leaves. Despite a lack of similarity in water potential measured by the latex based method and xylem water based measurements both methods showed declining leaf water status in droughted plants which could be linked to other plant functions (Hegde and Srinivas, 1989; Kallarackal et al., 1990). This contrasts with the findings of Thomas and Turner (1998) and Turner and Thomas (1998) who showed measurements of leaf water potential using either the exuding xylem or relative leaf water content could not be reliably linked to plant functions such as stomatal aperture, net photosynthesis or leaf folding. Water potential measured by the exuding latex method appeared the best for determining leaf water status, but even this shows a small change in plants experiencing soil water deficit (Thomas and Turner, 1998; Turner and Thomas, 1998) supporting the hydrated status of banana leaves although the soil is dry.

The laminae of banana leaves fold in response to environmental stimuli. This movement does not reflect wilting of the leaf because if the leaf is excised and inverted, the laminae do not flop apart. These leaf movements are due to differential turgor of cells within the pulvinar bands caused by water movement accompanying ion movements (Satter, 1979; W. Robertson, unpublished data). The folding of banana leaves typically follows a diurnal rhythm with the leaves more horizontal during the night, and early morning, becoming more vertical during periods of bright sunlight, and returning to more horizontal positions in late afternoon. These changes in turgor within the cells of the pulvinar bands are similar to changes in stomatal aperture that is controlled by the turgor of guard cells. In addition, the laminae of banana leaves fold in response to soil drought (Milburn et al., 1990; Thomas and Turner, 1998; Turner and Thomas, 1998) suggesting leaf folding may reflect leaf water status, albeit somewhat unreliably. However, Lu et al. (2002) did not find any link between leaf folding and soil water deficit. Lu et al. (2002) measured water use of banana plants using a sap flow

system calibrated against gravimetrically determined water loss. This system measured water use by insertion of heat sensing probes into the central cylinder of the banana corm that conducts water from the root system to the shoot. It is a widely used technique to measure water use of trees, and has the advantage over other systems that measure whole plant water use in that the water sensing unit (typically heat based) is localized thus causing less damage to the plant being measured and hence greater reliability of data. Alternate systems can overheat and greatly damage or kill banana plants thus rendering measurements useless (D.S. Thomas, unpublished data).

Despite our best efforts, there is not a straightforward link between leaf scale gas exchange and leaf water status in bananas. Often, turgor-based changes within leaves such as changes in stomatal aperture or leaf folding or leaf elongation in response to soil water deficit or to high vapour pressure deficit do not correspond with changes in leaf water status measured by classical methods based on either thermodynamics or volumetric water content. On first thoughts this is a concern as it indicates our knowledge is not complete. However, hypotheses to explain these relationships can be developed.

Stomatal aperture, which greatly influences net photosynthesis through its effect on the diffusion of CO_2 into the leaf and its more tenuous link to productivity, is controlled by turgor of the guard cells. It is possible for the turgor of guard cells to operate reasonably independently of the water relations of the plant or bulk leaf. Extreme examples include stomatal responses to light or concentration of CO_2, but stomata also respond to the amount of water vapour in the air, in addition to more classical 'within plant' controls such as leaf water potential or changes in plant growth regulators such as abscisic acid. Localised water loss from the stomatal region is thought to be the mechanism by which stomata respond to vapour pressure deficit. This creates a gradient in water potential between the guard cells and stomatal subsidiary cells and affects guard cell turgor. If stomata respond directly to vapour pressure deficit it becomes clear why the relationship between stomatal aperture and bulk leaf water status is variable (Schulz et al., 1972; Turner et al., 1985). A decrease in stomatal aperture and/or stomatal conductance will reduce leaf transpiration but should not decrease water flow to the leaf from the plant and soil, therefore the net water balance of the leaf should increase. Models of the response of stomata to vapour pressure deficit suggest that guard cells are at or near the end of the water potential gradient and thus a change in leaf water potential is likely to affect the guard cells to a greater extent than the remainder of the leaf (Shackel and Brinckmann, 1985). This means guard cells will close even if the leaf is hydrated. The findings of Thomas et al. (1998) in banana (cv. 'Grand Nain', AAA, Cavendish subgroup) and Thomas and Eamus (1999) in tropical eucalypts that leaf transpiration can decline in direct response to low humidity supports the idea that leaf water status can increase and leaves appear well hydrated when stomatal aperture is independently restricted by these same environmental conditions. Additionally the observations of Thomas and Turner (1998) and Turner and Thomas (1998) that stomatal responses can be independent of plant water status can be explained by this mechanism. The independent measurements of whole plant water use using sap flow technology (Lu et al., 2002) show plant water use follows a diurnal pattern with greater water use in sunnier conditions and periods of higher vapour pressure deficit. This is consistent with earlier reports of patterns of stomatal conductance measured on small leaf sections. The 'feed-forward' response of stomata to humidity described above is not mutually exclusive from the feed-back response to low leaf water potential/low plant hydration. Both mechanisms could be operating in unison to maintain a hydrated leaf, yet one where stomatal aperture and water loss are controlled by soil, plant and atmospheric water content.

The use of water: There is a conundrum in our knowledge of the link between water and productivity in bananas. Anecdotal evidence, based on experience in plantations, supports the view that bananas require 'abundant and constant supplies of water' (Popenoe, 1941). On the other hand, physiological investigations suggest that bananas are remarkably tolerant of soil water deficit (Kallarackal et al., 1990) and can evaporate less water than other crops (Lu et al., 2002).

The notion that bananas require abundant and constant supplies of water is supported experimentally by numerous investigations into the water use of

bananas and their response to irrigation in a range of environments in the tropics (Meyer and Schoch, 1976; Meyer, 1980; Holder and Gumbs, 1983; Hegde and Srivinas, 1989) and subtropics (Kebby and Eady, 1956; Trochoulias, 1973; Lahav and Kalmar, 1981; Robinson and Alberts, 1986, 1987). Robinson (1996) summarizes these and other observations by pointing to the high sensitivity of banana to soil water deficit and that in practice, the 'little and often' approach to scheduling irrigation is the best strategy, in addition to the large amount of water that is needed for high production.

So, why might investigations into the physiology of the plant suggest a different outcome, that banana plants do not use a lot of water and that they might be quite hardy? To explain the need for large amounts of water to be applied as irrigation, several features of the banana plant have been highlighted over a number of years and are widely believed (Van Vosselen et al., 2005; Opfergelt et al., 2006). Robinson (1996) summarized these features.

1. A high potential for transpiration because of the large, broad leaves and a high LAI.

2. Shallow roots in comparison with other fruit crops.

3. A poor ability to withdraw water from drying soil.

4. A rapid physiological response to soil water deficit.

What physiological evidence exists to support these features? Large, broad leaves do not mean a high rate of transpiration per unit of leaf area. Water vapour moves from inside to the outside of the leaf in the direction of the leaf-to-air vapour pressure difference. Water vapour diffuses through the stomata and the leaf boundary layer, which is the layer of unstirred air adjacent to the leaf surface, before it reaches the atmosphere. Low wind speed and large leaf area increase the depth of the boundary layer, slowing the movement of water vapour from the leaf to the air. Thus, all things being equal, we could expect less evaporation per unit of leaf area from large leaves than small leaves. In reality the situation is more complex because sensible heat also diffuses across the boundary layer. Thus large leaves will be warmer than smaller leaves, as demonstrated clearly by Taylor and Sexton (1972). An increase in wind speed will reduce the boundary layer thickness, cool the leaf and consequently reduce the leaf-to-air vapour pressure difference, which drives evaporation from the leaf. The reduced gradient and the thinner boundary layer will both influence evaporation rate but will operate in different directions, making the prediction of water loss from the leaf difficult to generalize. A feature of banana leaves is their ability to 'shed' solar radiation by folding the lamina downwards (Thomas and Turner, 2001). In dense plantations this allows more radiation into the lower leaf layers and distributes the intercepted radiation more evenly across the canopy. Where LAI is low, the effect is to allow more radiation to reach the ground. In addition, under the influence of wind, the laminae tear into strips, making the leaves 'smaller' and the experiments of Eckstein et al. (1996) show that this changes the physiology of the leaves.

Transpiration from sections of leaves is often measured with a gas analysis system where a small section of leaf is enclosed in a chamber through which there is a flow of air (Robinson and Bower, 1986; Schaffer et al., 1996; Thomas and Turner, 2001). The boundary layer in the chamber is determined by the flow rate of the air stream and the size of the chamber. It is standardized so that stomatal conductance can be estimated. The boundary layer in these chambers is very different in size to that encompassing a whole leaf that influences evaporation from the whole leaf or plant. Lu et al. (2002) measured the water use of whole banana plants cv. 'Williams' (AAA, Cavendish subgroup) by using gravimetric and sap flow techniques. Water flowing from the root system to the leaves must flow through the corm and sap flow sensors placed there can give an estimation of the water use by the whole plant. In this case the boundary layer of the leaves is not modified by the instrumentation used to measure transpiration, such as it is when a gas exchange system is used. Lu et al. (2002) compared the maximum sap flux density they measured in the corm of banana plants at 15 g cm^2 h^{-1} with published values for spruce (19 g cm^2 h^{-1}), mango (35 g cm^2 h^{-1}) and tropical rainforest tree species (40 g cm^2 h^{-1}). They pointed out that the value for banana was lower than for other species and they attributed this to the low leaf area/ sapwood area ratio in banana compared with other species. Thus large leaves can be misleading as banana has large leaves but the sap flux density in the corm is less than that measured for tree species with small individual leaves.

A canopy with a high LAI could be expected to evaporate more water than a smaller canopy with lower LAI. In the longer term, the amount of water evaporated

from a leaf canopy will be proportional to the amount of radiation intercepted because energy is needed to convert water from a liquid to vapour. About 90% of the incoming radiant energy is intercepted at an LAI of 4.5 to 5.0 for bananas, although under protected cultivation this may reach 94% (Tanny et al., 2006). Thus LAI beyond about 5.0 is unlikely to contribute greatly to increased evaporation. As we have already seen, the LAI of banana plantations is similar to that of other fruit crops.

The impact of a shallow root system is to reduce the amount of water available to the crop. Robinson (1995) summarized a number of studies of soil water extraction by bananas and concluded that for irrigation purposes, the effective rooting depth falls in the range of 0.3 to 0.4 m, which could be regarded as shallow. However, there are instances where banana plants (cv. 'Valery', AAA, Cavendish subgroup) growing in clay soils have not responded to irrigation (Madramootoo and Jutras, 1984) and in this case it was thought that the dry-land plants were able to obtain water from below 0.3 m depth. The root system is strongly modified by the soil environment. Popenoe (1941) thought that oxygen supply, related to soil texture, was a major factor in determining the depth of the root system of cv. 'Gros Michel' (AAA), with shallow root systems reflecting a reduced supply of oxygen at depth. In deep soils roots of bananas can be found down to 1.5 to 1.8 m. More recently, Lecompte et al. (2002) found that the mean angle of exit of roots from the corm of cv. 'Grand Naine' (AAA, Cavendish subgroup) was 30º. This would mean that at 1 m from the corm many roots should reach 0.58 m depth, considerably further than the 0.3 to 0.4 m that is a working depth for irrigation. The 'shallow' nature of banana root systems may be more a reflection of edaphic factors than an inherent quality of the crop. Whatever the reason for the shallow root system, this needs to be taken into account when applying irrigation.

The capacity of banana roots to withdraw water from drying soil has not been evaluated, to our knowledge. The issues here are the gradient in water potential between the soil at the root surface and the stele and the capacity of the root to conduct water across the cortex to the stele. The hydraulic conductivity of banana roots cv. 'Williams' (AAA, Cavendish subgroup), when well supplied with water, is somewhat higher but of the same order of magnitude as that of maize (Gibbs et al., 1998; Aguilar et al., 2003) and so is not unique. Root hydraulic conductivity may fall as soil dries, as is the case for many plants, but this situation is not universal (Bramley et al., 2007). The magnitude and significance of changes in root hydraulic conductivity in bananas has yet to be established.

For water to flow into roots, the water potential in the root needs to be less than that in the soil. Several investigations have shown that banana leaves remain quite hydrated as soil dries (Shmueli, 1953; Kallarackal et al., 1990; Turner and Thomas, 1998). Leaf water potentials as high as -0.1 to -0.5 MPa occur in banana plants cv. 'Grand Nain' (AAA, Cavendish subgroup) where the soil has dried sufficiently to stop leaf emergence and leaf gas exchange. In roots, in soil dry enough to stop leaf emergence, Turner and Thomas (1998) found the osmotic potential was -1.0 MPa. The soil had a matric potential of -0.06 MPa. Thus the banana root should be able to withdraw water from soil even when leaf gas exchange and leaf emergence have ceased because there is a negative gradient in water potential from the soil to the root. If the roots were unable to withdraw water from drying soil, then it would not be possible for the banana plant to remain highly hydrated as the soil dries. It is therefore unlikely that the capacity of banana roots to withdraw water from dry soil is a reason for the sensitivity of the plant to soil water deficit.

Robinson (1996) points out that bananas have rapid physiological responses to soil water deficit and this is the feature that is most likely to determine the response of the crop to irrigation. The most sensitive indicator of soil water deficit in banana is the rate of emergence of the new leaf (Kallarackal et al., 1990; Hoffmann and Turner, 1993; Turner and Thomas, 1998). If the soil dries rapidly, the leaf may stop emerging after 2 to 10 d and if it dries slowly, leaves may stop emerging after 23 d. In the experiments of Hoffmann and Turner (1993) a 21 kPa reduction in soil water potential halved the rate of leaf emergence but a 40 kPa reduction in soil water potential was needed to halve transpiration rate. Thus the rate of emergence of the new leaf is a sensitive indicator of drying soil, more so than the closing of stomata.

Bananas remain highly hydrated even when the soil is dry and so there needs to be a mechanism by which this occurs. Thomas (1995) grew bananas cv. 'Williams' (AAA, Cavendish subgroup) with a split root system and showed that if half of the roots were exposed to drying

soil, then the stomata closed, even though the leaves were well hydrated. Severing the roots that were exposed to the dry soil opened the stomata, indicating a signal from roots to shoots that closed them. By this mechanism the banana would be able to sense drying soil and begin to close its stomata. This would reduce water loss from the leaves, but it does not explain why the plant remains highly hydrated because the data of Bananuka et al. (1999) show that if a leaf is severed from a banana plant then it will lose from 24 to 76% of its weight (primarily water) after 48 h of drying, depending on the genotype. This is a high rate of water loss considering that in the field the loss of water from intact leaves on banana plants (cv. 'Dwarf Cavendish', AAA, Cavendish subgroup) was only 10% even though they were subjected to a reduction of 70% in available water in the soil over 10 d (Shmueli, 1953). This implies that the root system has an important role to play in keeping the plant hydrated even when the soil is drying. The mechanism by which this might occur is that once the stomata are closed, root pressure becomes the dominant force supplying water to the shoot. Bananas have strong root pressure (Davis, 1961). With this drought tolerance mechanism the banana is able to survive long periods of soil water deficit but the disadvantage is that production is very sensitive to soil drying. Whether this mechanism applies across the genetic diversity of *Musa* species needs to be established. If genetic variation can be detected then there is the possibility of developing cultivars that are less sensitive to soil drying, from the point of view of production, but which might not survive long periods of drought. From a practical perspective it would be useful to determine the relationship between soil water potential and stomatal conductance for a range of cultivars in different environments.

We conclude that neither the large leaves, high leaf area index, shallow roots systems or the poor ability of banana roots to extract water from the soil can be invoked to account for the sensitivity of the crop to soil drying. However, the sensitivity of the root system to drying soil, the ability of the plant to send this information to the leaves so that stomata close and once the stomata are closed, the capacity of root pressure to maintain the plant in a hydrated state are consistent with the widely observed sensitivity of the plant to soil drying supported by anecdotal and experimental evidence in the field. Experimental evaluation of this hypothesis is required.

In addition to pointing to a physiological mechanism that might be modified in the plant to produce cultivars more adapted to dry conditions, knowing that the banana plant itself is not substantially different from other plants in its use of water leads to questions about the technology of applying water to bananas. Lu et al. (2002) pointed out the large difference between the amount of water evaporated by the plant compared with the amount of water recommended for irrigation at Darwin, Australia. They suggested that water-use efficiency at the level of the plantation could be improved by paying attention to the technology of irrigation. Robinson (1995, 1996) presents useful discussions of these issues and some mathematical aspects are presented by Turner (1995) and recently, and in more detail, by Van Vosselen et al. (2005).

Water-use efficiency: With anticipated reductions in water available for cropping in many countries, water-use efficiency has aroused interest. Water-use efficiency has different definitions depending on the problem being investigated and the level of organization of the plant. At the level of the leaf it can be expressed as the amount of CO_2 fixed per unit of H_2O evaporated per kPa of vapour pressure deficit. These data can be obtained from instantaneous measurements of leaf gas exchange. They are not necessarily correlated with the water-use efficiency of the whole plant or the plantation. At the whole plant level, water-use efficiency may be expressed as the amount of dry matter increase in the plant per unit of water evaporated from the plant. At the crop level, the economic yield is important and the water-use efficiency may be expressed as kilogram of fresh fruit per unit of water used. In this last case it is necessary to take account of the water lost from the soil or trash to the atmosphere as well as that lost in deep drainage because the water lost from the plant is only a proportion of that lost from the system. In this last case, water-use efficiency can be increased by increasing the proportion of water in the system that flows through the plant.

Farmers are interested in plants that have high yields whether they are irrigated or rainfed. Plant breeders need a simple method of evaluating large numbers of progeny from breeding schemes so that promising genotypes can be rapidly selected. For bananas, Bananuka et al. (1999) used leaf water retention capacity to evaluate the

tolerance of several *Musa* genotypes to drought. The ability of a leaf to retain water is determined very simply by severing the leaf, weighing it, allowing it to dry for 48 h, reweighing and determining dry weight of the leaf. Clarke and McCaig (1982) investigated this technique for use in wheat breeding schemes in the Americas and concluded that the leaf water loss rate was a suitable method for distinguishing between genotypes of wheat that were tolerant of drought. Drought tolerance was evaluated by comparing the yield of genotypes in rainfed plots with yields from irrigated plots. We examined the published data of Clarke and McCaig (1982), expressed drought resistance as the yield from rainfed plots divided by the yield from irrigated plots and plotted these data against the rate of drying of excised leaf segments, a measure of the leaf water retention capacity. We found no significant correlation ($P = 0.13$, $n = 8$) between these two parameters. Since leaf water retention was not related to drought tolerance in wheat, but had been used by Bananuka et al. (1999) in a range of *Musa* genotypes, we undertook a similar analysis on their data. We assumed firstly, that all cultivars had a similar leaf number at the beginning of drying, and secondly, that the number of live leaves at the end of 32 d of drying reflected the drought resistance of the six banana cultivars investigated and plotted this against the published values of leaf water retention capacity. There was no significant correlation ($P = 0.19$, $n = 6$) between the two parameters for the banana genotypes. Both Clarke and McCaig (1982) and Bananuka et al. (1999) found that the rate of leaf drying was different between cultivars and based their conclusions on this difference. Our analyses would suggest that leaf water retention capacity, as a proxy for drought resistance or water-use efficiency, should be treated very cautiously. In bananas, there is a need to have yield data for irrigated and rainfed plots so that drought tolerance can be quantified in these terms as well as yield from rainfed plots.

An alternative approach to water-use efficiency is to evaluate the amount of water available in the system and then work out how best to arrange for most of it to flow through the banana plant. This would involve management strategies, in addition to new germplasm, and may be a more rewarding way forward than simply evaluating germplasm for drought resistance or tolerance in a range of environments.

Tanny et al. (2006) used the energy balance and eddy covariance approach to measure water use of bananas, cv. 'Grand Nain' (AAA, Cavendish subgroup), growing under protected cultivation in Israel in the summer (June). The value of this work in the current context is the separation of evaporation from the soil from that of the canopy, as this provides a measure of plant transpiration at the crop level. The plants were drip irrigated with 7 or 8 mm d^{-1} and 28% of the land area was 'wet' from the irrigation water from the drippers. Mean water use was 5.6 mm d^{-1} with almost no evaporation from the soil (0.1 mm d^{-1}). Net radiation was 14.65 MJ m^{-2} d^{-1} which would provide enough energy to evaporate 6.0 mm water d^{-1}. Since little water was evaporated from the soil, the measured evaporation was taken as transpiration. An increase in water application from 7 to 8 mm d^{-1} during the study did not change the evaporation from the crop. The amount of water applied to the plants under protected cultivation was about 70% of that applied in the field. In this environment, the use of protected cultivation produced considerable savings in irrigation. It would be of considerable interest to compare water use of bananas grown as an understory crop, especially if the root zones of the bananas and overstory did not overlap to a large extent.

Variation in stomatal conductance between genotypes: Ekanayake et al. (1994) investigated the ability of different genotypes of *Musa* to adapt to drought in the field by measuring the stomatal conductance (g_s) in the morning and afternoon. In this case, the soil water content is unlikely to change significantly between measurements but the leaf-to-air vapour pressure difference will increase as temperature rises. It is therefore a strategy for detecting the sensitivity of the stomata to vapour pressure deficit, which may or may not be related to drought tolerance.

Genotypic differences in this character are evident in a number of plant species, with differences apparent between and within species (Jones, 1992). Ekanayake et al. (1994) found differences among *Musa* genotypes. Those genotypes that tended to restrict stomatal opening in the afternoon were classed as 'water savers' and could therefore be expected to tolerate short periods of soil water deficit in contrast to those whose stomata remained open in the afternoon. The cvs. 'Bluggoe'

(ABB) and 'Fougamou' (ABB) showed the greatest differences in leaf conductance between morning and afternoon while cvs. 'Bobby Tannap' (ABB) and 'Valery' (AAA, Cavendish subgroup) maintained their g_s throughout the day. They concluded that there was variation in response to drought among the genotypes in the ABB genomic group that was worth further investigation.

Thomas et al. (1998) used controlled conditions to separate the effects of vapour pressure deficit and temperature on g_s of cvs. 'Williams' (AAA, Cavendish subgroup), 'Lady Finger' (AAB) and 'Bluggoe' (ABB). Their data clearly show that g_s of cv. 'Williams' is much more sensitive to leaf to air vapour pressure difference than that of cv. 'Bluggoe', decreasing as the vapour pressure deficit increased. At a vapour pressure difference of 5 kPa, there was no difference in g_s between either cultivar with differences increasing under more humid conditions. The work of Ekanayake et al. (1994) and Thomas et al. (1998) remind us that the stomata of bananas respond to the aridity of the air as well as to soil drying and that there is genetic variation in this trait.

ROOT SYSTEM

Architecture: The architecture of the root system is its arrangement in the volume of the soil occupied by the plant and so it has a plant and edaphic component. In the bananas, roots arise in groups of 2 to 4 from primordia at the inner edge of the cortex of the corm. These main or primary roots give rise to secondary roots that support tertiary roots. Each class of root is thinner than the root that supports it, grows more slowly (Lecompte et al., 2001) and is much shorter in length. Main or cord roots may be several metres long, secondary roots are usually less than 1 m and tertiary roots are several centimetres long. The extension of the main roots provides new sites for the development of secondary roots that have a much shorter life than that of the main roots. The same pattern exists between secondary and tertiary roots. Thus, for banana the main or primary roots emerging from the corm provide the framework of the root system that extends well out from the plant. The secondary and tertiary roots explore the volume of soil adjacent to the primary roots. Studies of the banana root system have therefore focused on the development and extent of the primary roots and the factors affecting the growth and development of the secondary and tertiary roots.

Draye (2002a) reviewed the architecture of the banana root system especially in relation to the genetics of the plant. Root architecture has been studied using soil excavation (Araya, 2005), simulation (Draye et al., 2005) and manipulative experiments (Lecompte et al., 2001, 2005). Soil excavation is laborious but it provides data on the distribution of the root system at a point in time and is useful for informing management practices. Over the years numerous studies of this type have been undertaken, some more comprehensive than others, depending on the objectives of each study. For simulation, conceptual and mathematical relationships among the components of the root system need to be established to explore the simulated changes in time and space. The advantages of simulation lie in the ability to ask 'what if' and then change a mathematical relationship or concept and see what happens. Thus many 'thought experiments' can be done in a short time. The difficulty is relating the precise calculations of the simulation to the field where there is considerable variation in space and time in the soil in which roots grow. Nonetheless, if simulations are used to complement field and laboratory work, then useful progress can be made.

To reduce the amount of effort needed to undertake excavations of whole root systems, Blomme et al. (2005) investigated a number of methods for indirectly measuring the root system of 31 genotypes of *Musa* in southeastern Nigeria. The methods included early screening, that sought a relationship between the root system of nursery plants and mature plants in the field; allometric relationships between root and shoot characters in field-grown plants; soil core sampling; and electrical capacitance. Only the soil core sampling gave useful predictive power, with two samples per plant giving 80% accuracy. The soil core sampling was 20 times faster than complete excavation of the root system. Draye et al. (2005) used their simulation model of the banana root system to evaluate different parameters of soil core methods for measuring banana root systems. Of crucial importance are the distance of the cores from the plant, the number of cores taken and the size of the cores. Precision in estimating the size of the root system is increased by sampling close to the plant (20 cm) and having a large number (8) of large cores (25 cm). Draye et

al. (2005) point out that their calculations are indicative and should not be taken as firm recommendations but it is the proximity to the plant that has the greatest impact on accuracy and precision.

The paper of Araya (2005) provides data on the root distribution of several *Musa* genotypes in Central America. The total excavated fresh weight of roots varied from 0.8 kg for cv. 'Valery' (AAA, Cavendish subgroup) to more than 3.5 kg for cv. 'Yangambi km5' (AAA), showing the large difference in size of the root system between genotypes. His paper also provides data on the changes in the root system during development of the plant and thus has a 'dynamic' component.

Lecompte et al. (2001) proposed a method for reconciling the 'static' components of root growth, measured at the one time, with the 'dynamic' components that change over time. They used cv. 'Grande Naine' (AAA, Cavendish subgroup) for their studies in rhizotrons (using two soil types) and in the field. The distance from the root cap to the appearance of the first lateral on any root, termed the length of the unbranched zone, was positively correlated with the growth rate of the root up to the time of measurement. For roots with an unbranched zone that varied from 4 to 24 cm, the growth rate increased linearly from 0.5 to 3.5 cm d^{-1}, an increase of 0.15 cm d^{-1} in growth rate for each centimetre of unbranched root length. The apical diameter indicated the potential for the root to grow, with large roots growing more rapidly than smaller roots. However, for any root class (primary, secondary or tertiary) the length of the unbranched zone was the indicator of actual growth. Armed with this knowledge it is possible to interpret the growth of roots in different situations, whether between cultivars, fields, plants or stages of growth.

Structure: Since there is a relationship between the diameter of the root tip and other properties of the root, Lecompte et al. (2005) explored the relationship between the diameter of the root tip and the class of root, the variation of root tip diameter within classes and the effect of soil compaction on this variability. The diameter of the root tip is easy to measure and, as Lecompte et al. (2005) point out, across a number of plant species has been related to the size of the root meristem, axial growth and its duration, root anatomy, water transport and capacity of the root to penetrate media. For the primary roots of cv. 'Grande Naine' (AAA, Cavendish subgroup) growing in an andosol, the apex ranged from 0.6 to 2.1 mm diameter, for secondary roots from 0.09 to 0.52 mm and for tertiary roots from 0.06 to 0.27 mm. The mean apical diameters and their coefficients of variation were 1.46 mm (23%) for primary roots, 0.21 mm (40%) for secondary roots and 0.12 mm (35%) for tertiary roots. Increasing soil compaction from 0.66 to 0.81 g cm^{-3} had no effect on the variability in root diameter in a field experiment but there were some effects in a glasshouse experiment. Across the different classes of root there was a relationship between the diameter of the root and the diameter of the roots arising from it but the relationship was not linear. Lecompte et al. (2005) brought together data for 12 different plant species, including monocots and dicots, annuals and perennials and showed that the data for banana fitted within the general picture. Roots with an apical diameter of 0.5 to 2.0 mm produce laterals that have a diameter in the range of 0.1 to 0.4 mm. Roots with a larger apical diameter of 5 to 13 mm produce laterals with diameters in the range of 0.45 to 0.90 mm.

The lateral roots are the main interface between the plant and the soil and so it is important to know about their structure and function. Lateral roots arise from primordia at the pericycle. The primordia are laid down acropetally at the root apex and in a series of files, lines or poles that are based in the proto-xylem and run along the axis of the root. To account for the variable distances between lateral roots one possibility is that there is variation in the initiation of root primordia. Another view is that the primordia are laid down regularly, but it is whether or not they develop into a lateral root that explains the variability. Draye (2002b) investigated the effects of root growth and vascular structure on the initiation and development of lateral roots. Using the banana genotypes 'Agbagba' (AAB), 'Grande Naine' (AAA, Cavendish subgroup) and 'Pisang Lilin' (AA) he found that the distance between files (vascular structure) of lateral root primordia around the circumference of the pericycle was very stable across classes of root and genotypes. The average distance between files was 63 μm in roots grown in water and slightly further apart at 76 μm in roots grown in sand. Thus roots of greater diameter had more files of lateral root initials around their larger steles. Within a file there was a strong positive

relationship between the diameter of the root apex and the distance between laterals in that file (root growth factor). In a file the distance between laterals ranged from 1 to 4 mm and this was almost directly proportional to the apical diameter of the root, with some differences between genotypes. Because there are a large number of files in each root the distance between laterals on the root irrespective of the file ranged from 0.05 to 0.14 mm and was independent of the size of the root apex. Draye (2002b) proposed a model framework to differentiate the effects of root growth (lateral root initiation and cell number and size influencing the distance between laterals in each file) and vascular structure (stellar diameter and distance between files on the pericycle) on the distance between laterals on a root. This analysis suggested that root growth would be the major, but not only, influence on the density of branching in roots.

Roots depend entirely on the shoots for their carbon supply for growth. Manipulation of the carbon supply changes root growth and architecture. Under conditions of reduced carbon supply within a root. the allocation of carbon would be between the growth of the main apex, where primordia for new laterals would be laid down, and the growth of lateral roots. Since carbon flows along the primary root before reaching the first and then the second order laterals, one may expect those roots closest to the source would benefit most. Lecompte and Pagès (2007) grew banana cv. 'Grand Naine' (AAA, Cavendish subgroup) under high (field, 29 mol quanta m^{-2} d^{-1}) and low (shaded glasshouse, 6 mol quanta m^{-2} d^{-1}) light regimes and studied the effect on root growth and architecture. Shading reduced the number of primary roots arising from the corm by 12% but had no effect on the elongation rates of those roots. Shading reduced branch density of the first order lateral roots by 32%, their diameter by 14% but increased their growth rate by 16%. The effect of shading was much greater on the second order laterals whose diameter was reduced by 31%, growth rate by 23% and branching by 11%. So, while the general principle of those organs closest to the source being best served, was evident, the allocation of carbon among the different functions within the root orders differed qualitatively and quantitatively. Since the second order laterals are the most affected, and these have the greatest interface with the soil, then the impact of changes in their structure and function can be expected to have considerable impact on the capacity of the plants to absorb water and nutrients.

Bananas and plantains grow in areas where solar radiation varies seasonally and spatially. Solar radiation on an overcast day is about 20% of that on a clear day. Extended cloudiness could affect the amount of carbon fixed by the canopy and this may have consequences for root growth and function. It is possible in extended periods of cloudy weather that the root system would be affected and these roots that remain would face different challenges when the cloudy weather ended.

Function: Plant roots have a number of functions including the uptake of nutrients and water. Lahav (1995) summarised the work on banana nutrition, mainly from the perspective of nutrient use in a plantation. Johns and Vimpany (1999a), using cv. 'Williams' (AAA, Cavendish subgroup), investigated the effect of lime and high potassium (K) application on soil and plant chemistry and plant growth, including roots. With their data they were able to construct models of the relationship between chemical composition and plant performance. They show the empirical nature of such relationships and the need to take considerable care in extending them to locations different from the one in which they were established. Delvaux et al. (2005) reviewed ion absorption by banana roots, including for a range of triploid genotypes. For banana, K and nitrogen (N) are the elements absorbed in greatest amounts. Bananas require a large amount of K compared with other species because the plant holds a high amount of water per unit area of land. For example, a standing crop of bananas at anthesis will contain the equivalent of 30 mm of water, whereas a forest may contain 15 mm and a crop of wheat at anthesis about 3 mm. If the molar concentration of K in the plant tissues is the same in all three situations then to establish, bananas need to absorb 10 fold more K than wheat, for example. In ratoon situations a proportion of K is recycled to the next crop either by redistribution within the plant or through the return of organic matter from the plant to the soil. Roots require energy to absorb K from the soil and protons are excreted from roots into the rhizosphere to maintain the cation/anion balance of the root (Delvaux et al., 2005). The excreted protons may react with clay minerals, changing the chemistry of the rhizosphere making available elements such as calcium and

magnesium that are beneficial to the plant or aluminium that may become toxic. In addition, bananas roots are able to absorb NH_4^+ in preference to NO_3^- and this further contributes to the net excretion of protons. Delvaux et al. (2005) point out the importance of the rhizosphere for the plant and the need for greater knowledge of its role. It is important not only for water and nutrient uptake but for interaction of the plant with soil biota, organic constituents, gases and minerals.

Recently there has been interest in the silicon (Si) uptake of bananas because of its perceived benefits summarized by Henriet et al. (2006) who addressed several questions. Does an increased supply of Si improve plant growth in banana under optimal conditions? What is the mechanism of Si uptake? Is the transpiration stream the dominant factor controlling uptake of Si and its distribution within the plant? Is there genetic variation in the response of bananas to increased supply of Si? Henriet et al. (2006) examined the response of cv. 'Grande Naine' (AAA, Cavendish subgroup) and selections of *M. acuminata* subsp. *banksii* (AA) and *M. balbisiana* (BB, Tani) to Si supply under controlled conditions. Silicon, at concentrations normally found in soil solutions, did not influence the growth of any of three genotypes. The amount of Si absorbed by the plant was a function of the concentration of Si in the nutrient solution and the amount of water transpired by the plants. However, this relationship was influenced by the Si concentration in the solution. At lower concentrations (0.02 to 0.83 mM Si) there was evidence that more Si was absorbed than might be expected by the water uptake and so at these concentrations an energy-dependent mechanism may be involved. There was no evidence that genotype affected Si uptake, but there were differences in the way Si was distributed within the plants, especially at lower concentrations of Si. In this case the *M. acuminata* subsp. *banksii* plants sequestered more Si in the tissues closer to the source than did the *M. balbisiana* (Tani) genotype.

The supply of oxygen to banana root systems in the field has long been a concern (Popenoe, 1941) and is dealt with by extensive drainage systems when growing bananas for export (Stover and Simmonds, 1987). Turner (2005) summarized recent research on the effects of oxygen deficiency on the nutrient uptake and hydraulic conductivity of banana roots. This work (Aguilar et al., 2003) showed that the gradient in oxygen concentration from the bathing solution to the stele was quite high and that only a small decrease in oxygen concentration (3 kPa) external to the root would induce anoxia in the stele and reduce nutrient transfer to the stele. This work has been done on primary roots arising directly from the corm. What happens in lateral roots has yet to be determined. It is likely that the principles established by Aguilar et al. (2003) for primary roots will apply but the lateral roots are thinner and their connection to the shoot is more remote and more tortuous. The significance of aerenchyma in primary roots (Aguilar et al., 1999) for supplying oxygen to lateral roots needs to be evaluated.

Oxygen deficiency quickly kills the root apex that even in aerated soils has very low oxygen concentrations because of its high metabolic activity. Death of the root tip causes several lateral roots to arise not far behind the dead apex and in the field this symptom is referred to as 'chicken feet' or 'witches broom'. This symptom was thought to be caused by dry soils and high concentrations of nutrients, especially K, in soils in New South Wales, Australia (Johns and Vimpany, 1999b). Experiments that included a range of soil water deficits and K applications in excess of that normally applied to bananas, failed to link the 'witches broom' symptoms with these factors. Any increase in root death caused by these factors tended to affect the whole root system rather than just the root tip (Johns and Vimpany, 1999b).

REPRODUCTIVE SYSTEM

Bunch initiation: In banana, the inflorescence (bunch) is initiated at the apex of the vegetative plant and subsequently the nodes of flowers that become the hands of fruit begin to differentiate. The first three to 18 nodes of the inflorescence form female flowers that become the fruit of commerce. At the time of bunch initiation about 11 leaves are present within the pseudostem (Summerville, 1944). After these leaves emerge the bunch appears at the top of the pseudostem at anthesis. Day-neutral plants do not depend on photoperiod for floral induction (Lincoln et al., 1982) and banana falls into this category. Bunches emerge (anthesis) at any time of the year where the plant is grown, although the number of bunches emerging may be influenced seasonally by environmental and edaphic

factors. If photoperiod does not influence bunch initiation then the development of the plant can be described by growing-degree-days (GDD, with units of C° days). This can be demonstrated in planting date experiments where, for each planting date the GDD from planting to bunch emergence is expected to be the same, other things being equal. However, Turner and Hunt (1987) pointed out that for banana cv. 'Williams' (AAA, Cavendish subgroup) growing in the subtropics, the GDD was not the same for three different planting dates suggesting some other factor, perhaps photoperiod, was involved in bunch initiation.

Lassoudière (1978a,b) conducted planting date experiments with banana cv. 'Poyo' (AAA, Cavendish subgroup) over five years in Ivory Coast (5º30'N). In 1971/1972 suckers were planted in a ferralitic soil on four occasions at Azaguié. At Nieky, corm pieces with buds were planted on six occasions in 1973/1974 in a virgin organic soil and on five occasions in 1974/1975 in an organic soil that had been subjected to agriculture for some time. Using these data from Ivory Coast we calculated the GDD from planting until bunch emergence of the plant crop for each planting date (Figure 2). There was variation in the GDD for the different locations, soils and planting material, which may be expected. More importantly there was variation in the GDD between planting dates within locations where the crops planted earliest in the year had the least GDD. From these data we can say that it is likely that a factor other than temperature is influencing bunch initiation in bananas, a similar conclusion reached by Turner and Hunt (1987) for cv. 'Williams' in a sub-tropical environment.

Herndl et al. (2008) proposed a method for identifying factors that contribute to early or late flowering in cereals. In this method the GDD of the early planting date is plotted on the *x* axis against the GDD of the later planting dates, for a range of cultivars. The 1:1 line indicates no effect of photoperiod or temperature (independent of GDD) on plant development, and is the 'earliness per se' line (Figure 3). Points falling above or below the 1:1 line indicate an effect of temperature on earliness per se. Points below the 1:1 line indicate sensitivity to photoperiod where the GDD of later planted crops is less than that of earlier planted crops. The larger the difference between the GDD sums of the early and later planted crops the greater the sensitivity to photoperiod. We used this method of analysis for crops

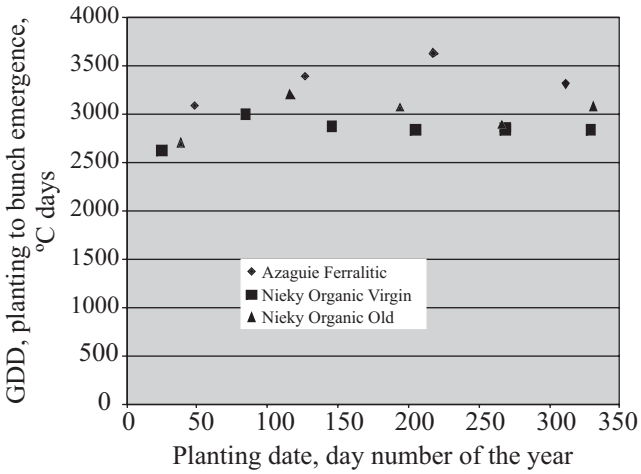

Figure 2. The effect of planting banana cv. 'Poyo' (AAA, Cavendish sub-group) at different times of the year at three sites in Ivory Coast (Lat 5ºN) on the growing-degree-days (GDD) from planting until bunch emergence of the plant crop. Data from Lassoudière (1978a,b).

of bananas planted at different times in Ivory Coast, a tropical location (Lat 5ºN) (Lassoudière 1978a,b), and in New South Wales, Australia, a sub-tropical location (Lat 29ºS) (Turner and Hunt, 1987) (Figure 3).

The crops grown in Ivory Coast matured more rapidly (fewer GDD) than those in Australia as they had lower values of GDD for all planting dates (Figure 3). Within a planting series (Azaguie, Nieky, Alstonville), the later planting dates took longer to mature because they had more GDD from planting until bunch emergence, and these points are located above the 1:1 line (Figure 3). In these crops, this implies an effect of temperature that is independent of GDD, on earliness per se. For Alstonville, with its subtropical environment, the cooler temperatures experienced in the winter may delay plant development more than expected by the fewer GDD accumulated at this time of year. However, a similar delay is observed in Ivory Coast but the mean daily temperatures experienced there (23-28ºC) are above those at Alstonville (13-24ºC). For the data from Turner and Hunt (1987) at Alstonville, we explored this further by plotting the cumulative bunch initiation (taken as the appearance of the 11th last leaf, (Summerville, 1944)) against GDD and superimposing the photoperiod upon these graphs. Data were available for three crop cycles (plant, ratoon 1 and 2) at three planting dates. Here we present the data for the November planting date (Figure 4) since a similar pattern appeared in

the data for the January and March planting dates. During the time when the photoperiod was less than 12 h, there is a change in the slope of the cumulative curves indicating a slowing of the rate of initiation of bunches in each of the three crop cycles. The change of slope is more marked in the ratoon crops than in the plant crop. These periods correspond to the cooler seasons of the year and may indicate an effect of temperature on the 'earliness per se' factor in banana cv. 'Williams'. This is consistent with the data in Figure 3 suggesting that temperature, other than GDD, influences 'earliness per se' in banana. However, it is not clear what factor(s) might have the same effect in the tropics of Ivory Coast.

In Honduras (15ºN) Dens et al. (2008) found that removal of the bunch and leaves on the parent hastened the development of the ratoon crop in long days but the same treatment had no effect on development when conducted during short days. They concluded that an environmental factor was contributing to floral induction in banana because the effect of the treatment in hastening development of the ratoon was overridden in the season with shorter days.

While banana is currently regarded as day-neutral for floral induction because it does not depend on photoperiod for flowering, there is evidence that environmental factors delay floral development, independent of growing-degree-days. If this factor was short photoperiod, then bananas may be classified as quantitative long day plants.

Flower development: The inflorescence is a terminal spike comprising of a series of nodes of flower clusters (hands) that are subtended by bracts. The female flowers occupy the basal nodes and the male flowers the apical nodes. The female ovary is inferior with three locules that each contain an axile placenta. The ovules are in two or four rows in each locule. The megasporogenesis and megagametogenesis of *Musa* spp. are typical of angiosperms. The ovule is anatropous, bitegmic and crassinuclear. Both integuments form the micropyle. The megaspore is monosporic and gametogenesis is polygonal. The nucellus is massive. The megasporocyte undergoes the usual meiotic division to form a linear tetrad of four cells. The embryology is of the Asterad type (White, 1928; Bouharmont, 1963; Dahlgren et al., 1985; Goldberg, 1989; Johri et al., 1992).

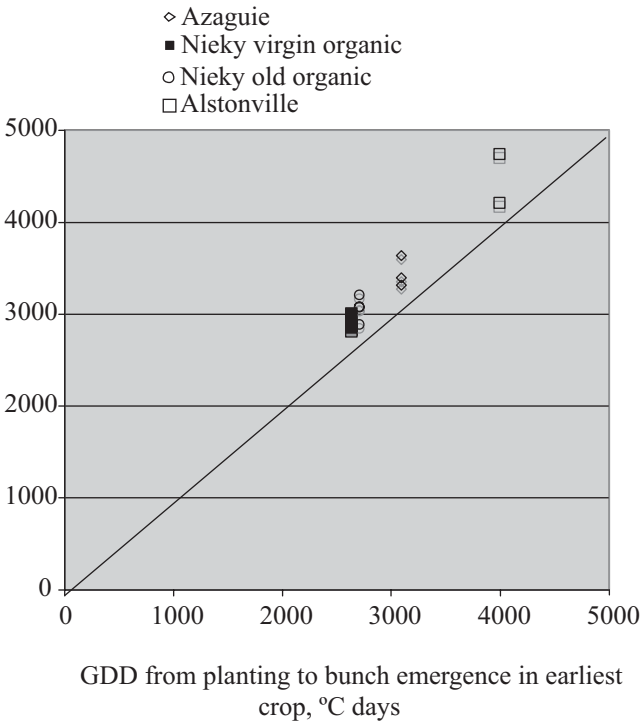

Figure 3. The relationship between the growing-degree-days (GDD) of the time from planting until bunch emergence of the plant crop in planting date experiments in Ivory Coast (Azaguie, Nieky, 5ºN) and Australia (Alstonville, 29ºS). The 1:1 line represents earliness per se. Data for Ivory Coast from Lassoudière (1978a,b) and for Australia from Turner and Hunt (1987).

Floral initiation begins when the indeterminate vegetative apex is transformed into a determinate reproductive apex; the shoot apex ceases to produce leaves and starts to produce floral parts. The inflorescence bears five to 15 or more clusters of female flowers and 150 to 300 clusters of male flowers. Summerville (1944) proposed that the upper limit of inflorescence size was set by the size of the meristem at the time of transformation, thus at floral initiation environmental conditions that affect general vegetative development will affect fruit production. This notion has yet to be tested experimentally although within a cultivar, large plants produce large bunches of fruit. Within the inflorescence the transformation from female to male flowers is marked by a sudden decline in ovary length that is first noticeable when the inflorescence is midway up the pseudostem and the female ovaries have reached approximately 10 mm in length.

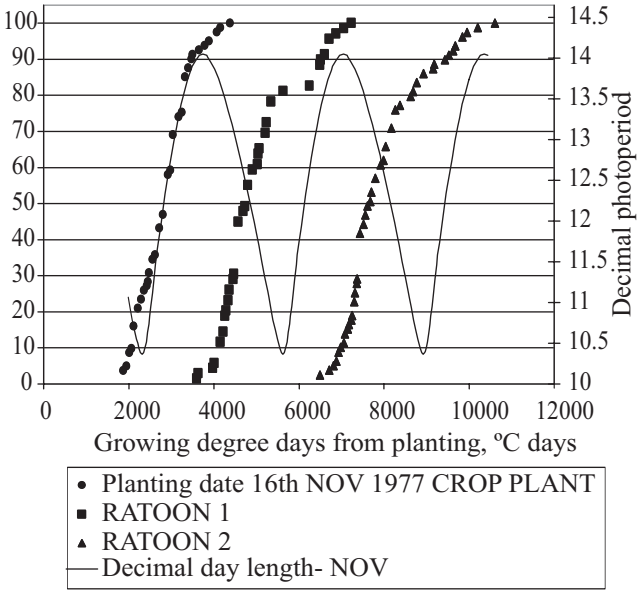

Figure 4. The cumulative (%) bunch initiation of three crop cycles of cv. 'Williams' banana planted in November 1977 at Alstonville, NSW (Lat 29ºS). Curves are plotted against growing-degree-days (GDD) from planting date. The oscillating line is the photoperiod (decimal hours) and the horizontal line describes the 12 h photoperiod. Data from Turner and Hunt (1987).

The sequence of floral initation, formation of the ovule primordium and the megaspore mother cell occurs while the inflorescence is inside the pseudostem. Consequently, when the inflorescence emerges they are almost at anthesis. When the inflorescence is midway up the pseudostem the megasporangium (ovule) is differentiating, it appears as a rounded protuberance growing at right angles from the placental wall. It is at first atropus and by differential growth becomes anatropous with its micropyle pointing towards the placental wall. The inner integuments have already formed when the archesporium arises from any sub-epidermal cell near the summit of the nucellus. It is easily distinguished from the surrounding cells by its relatively large size and becomes the megaspore mother cell. The differentiation of the archesporium takes place before the differentiation of the outer integument and when the megasporangium is half anatropous. The ovules have almost attained maximum size when the megaspore mother cell begins to divide. When the inflorescence protrudes from the pseudostem the gametophyte or embryo sac has differentiated and the nuclei are in their respective positions ready for fertilization (Fortescue and Turner, 2005b).

The development of the female flowers inside the pseudostem spans 12-13 weeks in the tropics and is up to twice as long in the sub-tropics. Any effect of environmental conditions during this time will be reflected in the shape and anatomy of the fruit. Morphological and anatomical evidence suggests that the development of the flower in banana is sensitive to low temperature when the ovary is differentiating (Fahn et al., 1961), when the perianth and stamens are forming (White, 1928) and when the megasporangium is differentiating (Fortescue and Turner, 2005a). These studies have been conducted mainly on triploid AAA clones of the Cavendish subgroup. Low temperature when the ovary is differentiating is associated with deformed fruit that are not suitable for marketing. Internally these fruits are characterized by a reduced number of locules in the ovaries and in some flowers there are no locules at all. Flowers with reduced locules develop into undersized fruit while those with no locules form very small fruit no larger than the ovaries of neuter or male flowers (Fahn et al., 1961).

Cool temperatures at the time of megasporogenesis and embryo sac formation can lead to malformations in the ovule itself. Low temperature (3-18ºC) reduced the size of ovules and caused them to have a rounder shape than normal ovules. In addition, the nucellus and nucellar cap protruded through the micropyle. These deformations were observed in ovules in bunches growing in the autumn, winter and spring in the subtropics. Fortescue and Turner (2005a) suggested that megasporangium formation was particularly sensitive to low temperature and that low temperatures need not last for more than a night or two.

There are three critical times in the reproductive biology of *Musa* when it is sensitive to damage by low temperature. Firstly, low temperature affects the differentiation of the ovaries and associated tissues soon after floral initiation. Secondly it affects the ovaries, when the carpels and stamens are forming midway up the pseudostem. Thirdly, it affects the differentiation of the megasporangium three to six weeks before anthesis.

Fruit growth and soil water deficit: Mahouachi (2008), in a field study on cv. 'Grand Nain' (AAA, Cavendish

subgroup), examined the effects of soil water deficit on the growth and nutrient concentrations of fruit during the first two months after bunching and then for a further three weeks after the plants had been re-watered. Soil water content at 15 cm depth and 40 cm from the irrigation drip line decreased exponentially from 33 to 15% during 63 d of drying. Upon re-watering, the soil water content did not increase instantaneously, but increased linearly and did not reach field capacity until 20 d later. From the data of Mahouachi (2008) we calculated the effects of the soil water deficit on rates of fruit growth and rates of accumulation of K in the fruit. In well-watered plots the fruit grew (fresh and dry weights) exponentially for the 83 d of measurement. For the first 63 d the relative growth rate (FW) was 1.1 % per day and in the last 20 d it increased to 1.6% per day. This pattern of growth was similar in the fruit on plants subjected to soil drying, but the rate was reduced by 30% during soil drying (0-63 d) and by 11% during re-watering (63-83 d). Even so, the fruit was still growing after 63 d of drying. The net photosynthesis of the leaves had been reduced by 80% at this time. Soil water deficit reduced the rates of accumulation of fresh weight and dry weight by 39% and the accumulation of K by 57%. Soil drying reduced the accumulation of water and K in the fruit and the K concentration fell by 19%, from 186 to 151 mmol K per 'cell sap' volume. Re-watering fully restored the rate of K uptake by the fruit but the accumulation of dry matter was 17% less than control and the fresh weight was 30% less. These data suggest that the fruit adjusts its growth rate to the supply of water available and that some of this adjustment may be related to maintaining a sufficient concentration of K in the fruit tissues. This mechanism allows the fruit to increase its absolute growth rate and complete its development, despite dwindling supplies of water. Commercially, soil drying reduces fruit size, which is often a criterion for markets, and this effect begins soon after soil drying commences. Nonetheless, the fruit continues to grow, albeit at a slower rate, whereas in a similar situation, the emerging leaf on vegetative plants is likely to stop elongating. For fruit to grow as the soil dries it must be able to attract water by having a more negative water potential than other organs of the plant. This might be achieved by decreasing its osmotic potential through the accumulation of solutes. Since soil drying reduced the amount of K entering the fruit in the experiment of Mahouachi (2008), any decrease in osmotic potential is not caused by K and must be attributed to other osmolytes, perhaps sugars.

CONCLUDING REMARKS

Physiology is about how things work. We can also put physiology to work to improve management and productivity of one of the world's most important crops, the bananas. Much of the research on physiology has been on a narrow group of cultivars (Cavendish subgroup) that are currently important for the international trade. There is a need to expand our interests to establish genotypic variation in physiological responses of the bananas to the environment. For this work we can build on what is known about the Cavendish subgroup as well as our knowledge of plant science, aspects of which we have considered in this review. Steady progress is being made and the foundations for this work have been laid in studies of the genetic diversity within *Musa* spp., briefly reviewed by Heslop-Harrison and Schwarzacher (2007). The triploid nature of many cultivars, their parthenocarpy and sterility have slowed genetic improvement in this crop species compared with other plants important for human sustenance. Complementary progress in bananas might be made if physiological knowledge was applied to the cultural techniques used to manage different cultivars in a range of environments. The question then becomes: how can we best match the cultivar with the environment to meet market requirements? *Musa* spp. are difficult to manage in experiments partly because of their size. Nonetheless, we need to take up the challenge of using more experimental manipulation to discover physiological mechanisms, rather than relying on the correlative studies that are the basis of much of our current beliefs and knowledge. We lack knowledge of environmental controls on the reproductive system and the functional aspects of the root system. Exploring the physiology of a group of plants as fascinating as the bananas is imperative. For those who take up the challenge, the work will be intellectually satisfying and productive, perhaps mixed with a little frustration.

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REFERENCES

Aguilar EA, Turner DW, Sivasithamparam K (1999) Aerenchyma formation in roots of four banana (*Musa* spp.) cultivars. Sci. Hort. 80:57-72.

Aguilar EA, Turner DW, Gibbs DJ, Armstrong W, Sivasithamparam K (2003) Oxygen distribution and movement, respiration and nutrient loading in banana roots (*Musa* spp. L.) subjected to aerated and oxygen-depleted environments. Plant Soil 253:91-102.

Araya M (2005) Stratification and spatial distribution of the banana (*Musa* AAA, Cavendish subgroup, cvs 'Valery' and Grande naine') root system. In: Turner DW, Rosales FE (eds), Banana Root System: Towards a Better Understanding for its Productive Management, pp.83-103. INIBAP, Montpellier.

Bananuka JA, Rubaihayo PR, Tenywa MM (1999) Reactions of *Musa* genotypes to drought stress. Afr. Crop Sci. J. 7:333-339.

Blomme G, Teugels K, Blanckaert I, Sebuwufu G, Swennen R, Tenkouano A (2005) Methodologies for root system assessment in bananas and plantains (*Musa* spp.). In: Turner DW, Rosales FE (eds), Banana Root System: Towards a Better Understanding for its Productive Management, pp.43-57. INIBAP, Montpellier.

Bouharmont J (1963) Evolution de l'ovule feconde chez *Musa acuminata* Colla subsp. *burmannica* Simmonds. La Cellule 63:261-283.

Bramley H, Turner DW, Tyerman SD, Turner NC (2007) Water flow in the roots of crop species: the influence of root structure, aquaporin activity and waterlogging. Adv. Agron. 96:133-196.

Chen CY (1971) Study on the water relations in banana. J. Agric. Assoc. China 76:24-38.

Clarke JM, McCaig TN (1982) Evaluation of techniques for screening for drought resistance in wheat. Crop Sci. 22:503-506.

Davis T (1961) High root pressure in palms. Nature 192:277-278.

Dahlgren RMT, Clifford HT, Yeo PF (1985) The Families of the Monocotyledons. Springer Verlag, Berlin.

Delvaux B, Rufuikiri G, Dufey J (2005) Ion absorption and proton extrusion by banana roots. In: Turner DW, Rosales FE (eds), Banana Root System: Towards a Better Understanding for its Productive Management, pp.114-121. INIBAP, Montpellier.

Denham TP, Haberle SG, Lentfer C, Fullagar R, Field J, Therin M, Porch N, Winsborough B (2003) Origins of agriculture at Kuk Swamp in the highlands of Papua New Guinea. Science 301:189-193.

Dens KR, Romero RA, Swennen R, Turner DW (2008) Removal of bunch, leaves, or pseudostem alone, or in combination, influences growth and bunch weight of ratoon crops in two banana cultivars. J. Hort. Sci. Biotechnol. 83:113-119.

Draye X (2002a) Banana roots: Architecture and genetics. In: Waisel Y, Eshel A, Kafkafi U (eds), Plant Roots: The Hidden Half, 3rd ed. pp.261-277. Marcel Dekker, New York.

Draye X (2002b) Consequences of root growth kinetics and vascular structure on the distribution of lateral roots. Plant Cell Environ. 25: 463-1474.

Draye X, Lecompte F, Pagès L (2005) Distribution of banana roots in time and space: new tools for an old science. In: Turner DW, Rosales FE (eds), Banana Root System: Towards a Better Understanding for its Productive Management, pp.58-74. INIBAP, Montpellier.

Eckstein K, Robinson JC, Fraser C (1996) Physiological responses of banana (*Musa* AAA; Cavendish sub-group) in the subtropics 5. Influence of leaf tearing on assimilation potential and yield. J. Hort. Sci. 71:503-514.

Ekanayake IJ, Ortiz R, Vuylsteke DR (1994) Influence of leaf age, soil moisture, VPD and time of day on leaf conductance of various *Musa* genotypes in a humid forest-moist savanna transition site. Ann. Bot. 74:173-178.

Fahn A, Klarman-Kuslev N and Ziv D (1961) The abnormal flower and fruit of May-flowering Dwarf Cavendish bananas. Bot. Gaz. 123:116-125.

FAO (2006) http://www.fao.org/docrep/004/ad452e/ad452e1q.htm.

Fortescue JA, Turner DW (2005a) The association between low temperatures and anatomical changes in preanthetic ovules of *Musa* (Musaceae). Sci. Hort. 104:433-444.

Fortescue JA, Turner DW (2005b) The anatomy of ovule ontogeny of banana, plantain and enset (Musaceae). Sci. Hort. 104:479-492.

Galan Sauco V, Cabrera J, Hernandez Delgado PM (1992) Phenological and production differences between

greenhouse and open-air bananas (*Musa acuminata* Colla AAA cv, Dwarf Cavendish) in Canary Islands. Acta Hort. 296:97-111.

Gibbs DJ, Turner DW, Armstrong W, Sivasithamparam K, Greenway H (1998) Response to oxygen deficiency in primary maize roots. 2. Development of oxygen deficiency in the stele has limited short-term impact on radial hydraulic conductivity. Aust. J. Plant Physiol. 25:759-763.

Goldberg A (1989) Classification, Evolution and Phylogeny of the Families of Monocotyledons. Smithsonian Institution Press, Washington DC.

Hegde DM, Srivinas K (1989) Irrigation and nitrogen fertility influences on plant water relations, biomass and nutrient accumulation and distribution in banana cv. Robusta. J. Hort. Sci. 66:91-98.

Henriet C, Draye X, Oppitz I, Swennen R, Delvaux B (2006) Effects, distribution and uptake of silicon in banana (*Musa* spp.) under controlled conditions. Plant Soil 287:359-374.

Herndl M, White JW, Hunt LA, Graeff S, Claupein W (2008) Field-based evaluation of vernalisation requirement, photoperiod response and earliness *per se* in bread wheat (*Triticum aestivum* L.). Field Crops Res. 105:193-201.

Heslop-Harrison JS, Schwarzacher T (2007) Domestication, genomics and the future for banana. Ann. Bot. 100:1073-1084.

Hoffmann HP, Turner DW (1993) Soil water deficits reduce the elongation rate of emerging banana leaves but the night/day elongation ratio remains unchanged. Sci. Hort. 54:1-12.

Holder GD, Gumbs FA (1983) Effects of irrigation on the growth and yield of banana. Tropical Agriculture, Trinidad 60:25-30.

Jackson JE (2003) Biology of Apples and Pears. Cambridge University Press, Cambridge.

Johns GG, Vimpany I (1999a) Interaction of pH amendment and potassium fertilizer on soil chemistry and banana plant growth. Aust. J. Agric. Res. 50:199-210.

Johns GG, Vimpany I (1999b) Effect of high rates of potassium chloride fertilizer on banana leaf conductance, plant growth, nutrient concentration and root death under contrasting watering regimes. Aust. J. Exp. Agric. 39:211-219.

Johri BM, Ambegaokar KB, Srivastava PS (1992) Comparative Embryology of Angiosperms. Vols 1 & 2, Springer Verlag, Berlin.

Jones HG (1992) Plants and Microclimate, a Quantitative Approach to Environmental Plant Physiology. Cambridge University Press, Cambridge.

Kallarackal J, Milburn JA, Baker DA (1990) Water relations of the banana 3. Effects of controlled water stress on water potential, transpiration, photosynthesis and leaf growth. Aust. J. Plant Physiol. 17:79-90.

Kebby RG, Eady CA (1956) Supplementary watering of bananas. Division of Horticulture Bulletin 7457, Department of Agriculture New South Wales, Sydney.

Lahav E (1995) Banana nutrition. In: Gowen S (ed), Bananas and Plantains, pp.258-316. Chapman and Hall, London.

Lahav E, Kalmar D (1981) Shortening the irrigation interval as a means of saving water in a banana plantation. Aust. J. Agric. Res. 32:465-467.

Lassoudière A (1978a) Quelques aspects de la croissance et du développement du bananier Poyo en Côte d'Ivoire. 1. Matériel vegetal et méthodes d'études. Fruits 33:293-313.

Lassoudière A (1978b) Quelques aspects de la croissance et du développement du bananier Poyo en Côte d'Ivoire. 4. L'inflorescence. Fruits 33:457-491.

Lecompte F, Pagès L (2007) Apical diameter and branching density affect lateral root elongation rates in banana. Environ. Exp. Bot. 59:243-251.

Lecompte F, Ozier-Lafontaine H, Pagès L (2001) The relationships between static and dynamic variables in the description of root growth. Consequences for field interpretation of rooting variability. Plant Soil 236:19-31.

Lecompte F, Pagès L, Ozier-Lafontaine H (2005) Patterns of variability in the diameter of lateral roots in the banana root system. New Phytol. 167:841-850.

Lecompte F, Vaucelle A, Pagès L, Ozier-Lafontaine H (2002) Number, position, diameter and initial direction of growth of primary roots in *Musa*. Ann. Bot. 90:43-51.

Lejju BJ, Robertshaw P, Tayler D (2006) Africa's earliest bananas? J. Archaeol. Sci. 33:102-113.

Lincoln RJ, Boxshall GA, and Clark PF (1982) A Dictionary of Ecology, Evolution and Systematics. Cambridge University Press, Cambridge.

Lu P, Woo K-C, Liu Z-T (2002) Estimation of whole-plant transpiration of bananas using sap flow measurements. J. Exp. Bot. 53:1771-1779.

Madramootoo CA, Jutras PJ (1984) Supplemental irrigation of bananas in St Lucia. Agric. Water Manag. 9:149-156.

Mahouachi J (2008) Growth and mineral nutrient content of developing fruit on banana plants (*Musa acuminata* AAA, 'Grand Nain') subjected to water stress and recovery. J. Hort. Sci. Biotechnol. 82:839-844.

Meyer JP (1980) Besoins en eau et irrigation des bananiers aux Antilles Françaises. Fruits 35:95-99.

Meyer JP, Schoch PG (1976) Besoin en eau du bananier aux Antilles. Mesure de l'evapo-transpiration maximale. Fruits 31:3-19.

Milburn JA, Kallarackal J, Baker DA (1990) Water relations of the banana. I. Predicting the water relations of the field-grown banana using the exuding latex. Aust. J. Plant Physiol. 17:57-68.

Mindzie CM, Doutrelepont H, Vrydaghs L, Swennen R, Swennen RJ, Beekman H, de Langhe E, de Maret P (2001) First archaeological evidence of banana cultivation in central Africa during the third millennium before present. Veg. Hist. Archaeobot. 10:1-6.

Monteith JL (1981) Does light limit light production? In: Johnson CB (ed), Physiological Processes Limiting Plant Productivity, pp.23-38. Butterworths, London.

Opfergelt S, Cardinal D, Henriet C, Draye X, André L, Delvaux B (2006) Silicon isotopic fractionation by banana (*Musa* spp.) grown in a continuous nutrient flow device. Plant Soil 285:333-345.

Popenoe W (1941) Banana culture around the Caribbean. Tropical Agriculture, Trinidad 18:8-12 and 33-38.

Proctor JTA, Watson RL, Landsberg JJ (1976) The carbon budget of a young apple tree. J. Am. Soc. Hort. Sci. 101:579-582.

Robinson JC (1995) Systems of cultivation and management. In: Gowen S (ed), Bananas and Plantains, pp.15-65. Chapman and Hall, London.

Robinson JC (1996) Bananas and Plantains. CAB International, Wallingford.

Robinson JC, Alberts AJ (1986) Growth and yield responses of banana (cultivar Williams) to drip irrigation under drought and normal rainfall conditions in the subtropics. Sci. Hort. 30:187-202.

Robinson JC, Alberts AJ (1987) The influence of under-canopy sprinkler and drip irrigation systems on growth and yield of bananas (cultivar Williams) in the subtropics. Sci. Hort. 32:49-66.

Robinson JC, Bower JP (1986) Transpiration characteristics of banana leaves (cultivar 'Williams') in response to progressive depletion of available soil moisture. Sci. Hort. 30:289-300.

Robinson JC, Anderson T, Eckstein K (1992) The influence of functional leaf removal at flower emergence on components of yield and photo-synthetic compensation in banana. J. Hort. Sci. 67:403-410.

Satter RL (1979) Leaf movements and tendril curling. In: Haupt W, Felnleib ME (eds), Encyclopedia of Plant Physiology - New Series, pp.442-484. Springer-Verlag, Berlin.

Schaffer B, Searle C, Whiley AW, Nissen RJ (1996) Effects of atmospheric CO_2 enrichment and root restriction on leaf gas exchange and growth of banana (*Musa*). Physiol. Plant. 97:685-693.

Schulz ED, Lange OL, Buschbom U, Kappen L, Evenari M (1972) Stomatal response to changes in humidity in plants growing in the desert. Planta 108:259-270.

Shackel KA, Brinckmann E (1985) *In situ* measurement of epidermal cell turgor, leaf water potential, and gas exchange in *Tradescantia virginiana* L. Plant Physiol. 78:66-70.

Sharkey TD, Bernacchi CJ, Farquhar GD, Singsaas EL (2007a) Fitting photosynthetic carbon dioxide response curves for C_3 leaves. Plant Cell Environ. 30:1035-1040.

Sharkey TD, Bernacchi CJ, Farquhar GD, Singsaas EL (2007b) In practice: Fitting photosynthetic carbon dioxide response curves for C_3 leaves. Plant Cell Environ. 30: XX-XX, version 2007.1.

Shmueli E (1953) Irrigation studies in the Jordan Valley. 1. Physiological activity of the banana in relation to soil moisture. Bull. Res. Counc. Isr. 3:228-247.

Simmonds NW (1959) Bananas. Longmans, Green and Co. Ltd., London.

Simmonds NW (1962) The Evolution of the Bananas. Longmans, Green and Co. Ltd., London.

Stover RH, Simmonds NW (1987) Bananas. 3rd ed. Longman Scientific and Technical, Harlow.

Summerville WAT (1944) Studies on nutrition as qualified by development in *Musa cavendishii* Lamb. Queensland J. Agric. Sci. 1:1-127.

Tanny J, Haijun L, Cohen S (2006) Airflow characteristics, energy balance and eddy covariance measurements in a

banana screenhouse. Agric. For. Meteorol. 139:105-118.

Taylor SE, Sexton OJ (1972) Some implications of leaf tearing in Musaceae. Ecology 53:143-149.

Thomas DS (1995) The influence of the atmospheric environment and soil drought on the leaf gas exchange of banana (*Musa* spp.). The University of Western Australia. PhD thesis.

Thomas DS, Eamus D (1999) The influence of predawn leaf water potential on stomatal responses to atmospheric water content at constant C_i and on stem hydraulic conductance and foliar ABA concentrations. J. Exp. Bot. 50:243-251.

Thomas DS, Turner DW (1998) Leaf gas exchange of droughted and irrigated banana cv. Williams (*Musa* spp.) growing in hot, arid conditions. J. Hort. Sci. Biotechnol. 73:419-429.

Thomas DS, Turner DW (2001) Banana (*Musa* sp.) leaf gas exchange and chlorophyll fluorescence in response to soil drought, shading and lamina folding. Sci. Hort. 90:93-108.

Thomas DS, Turner DW, Eamus D (1998) Independent effects of the environment on the leaf gas exchange of three banana (Musa sp.) cultivars of different genomic constitution. Sci. Hort. 75:41-57.

Thornley JHM, Johnson IR (2000) Plant and Crop Modelling. A Mathematical Approach to Plant and Crop Physiology. The Blackburn Press, Caldwell.

Trochoulias T (1973) The yield response of bananas to supplementary watering. Aust. J. Exp. Agric. Anim. Husb. 13:470-472.

Turner DW (1990) Modelling demand for nitrogen in the banana. Acta Hort. 275:497-503.

Turner DW (1994) Bananas and plantains. In: Schaffer B, Andersen PC (eds), Handbook of Environmental Physiology of Fruit Crops, vol. 2. Sub-tropical and Tropical Crops, pp.37-64. CRC Press, Boca Raton.

Turner DW (1995) The response of the plant to the environment. In: Gowen S (ed), Bananas and Plantains, pp.206-229. Chapman and Hall, London.

Turner DW (1998a) Ecophysiology of bananas: The generation and functioning of the leaf system. Acta Hort. 490:211-221.

Turner DW (1998b) Influencia de los principales factores ambientales (temperatura, humidad, luminosidad y suelo) sobre crecimiento y producción en banano y plátano. In: Proceedings of the 13th ACORBAT Meeting, Guayaquil, Ecuador, pp.635-663. CONABAN, Ecuador.

Turner DW (2005) Factors affecting the physiology of the banana root system. In: Turner DW, Rosales FE (eds), Banana Root System: Towards a Better Understanding for its Productive Management, pp.107-113. INIBAP, Montpellier.

Turner DW, Hunt N (1987) Planting date and defoliation influence the time of harvest of bananas. Sci. Hort. 32:233-248.

Turner DW, Lahav E (1983) The growth of banana plants in relation to temperature. Aust. J. Plant Physiol. 10:43-53.

Turner DW, Thomas DS (1998) Measurements of plant and soil water status and their association with leaf gas exchange in banana (*Musa* spp.): a laticiferous plant. Sci. Hort. 77:177-193.

Turner NC, Schulze ED, Gollan T (1985) The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. 2. In the mesophylic herbaceous species *Helianthus annuus*. Oecologia 65:348-355.

Van der Vorm PDJ, van Diest A (1982) Redistribution of nutritive elements in a 'Gros Michel' banana plant. Neth. J. Agric. Sci. 30:286-296.

Van Vosselen A, Verplancke H, Van Ranst E (2005) Assessing water consumption of banana: traditional versus modelling approach. Agric. Water Manag. 74:201-208.

White PR (1928) Studies on the banana. An investigation of the floral morphology and cytology of certain types of the genus *Musa* L. Z. Zellfors. Mikroskop. Anat. Bd. 7:673-733.