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A RESEARCH NOTE

PLANTAIN LEAF BIFURCATION

Godwin Norense Osarumwense Asemota
Department of Electrical and Electronics Engineering
Kigali Institute of Science and Technology, Kigali, Rwanda

ABSTRACT

Bifurcation and phyllotaxy are common and important processes in plants. Plantain leaf bifurcation occurs naturally in Lagos, Nigeria, especially for double-bunching plantains. Plantain leaf bifurcation studies are important because of the perceived special qualities impacted to the plantain pseudostem. Quasi-quantitative techniques were used for this study. As a result, both the physical presentation of the divided leaflets and bunches overhang characteristics were used to predict the most likely positioning of the plantain bunches overhang based on the work done by the plantain pseudostem itself. The results showed that the divergence angle of about 10° between the divided leaflets does not seem to agree with the tenets of the Fibonacci sequence of using the golden mean. The 90° bunches overhang can be used to predict at least two overhang positions. That is, in the same direction and also at 180° out of phase with each other. Similarly, the bifurcated leaflets presentation with four edges to the atmosphere seems to confer some compensatory adaptation to the environment. The thermodynamic implication of the four edges in the bifurcated leaflets ensure increased random mixing and transfer of greater amounts of carbon dioxide, water vapour and energy for improved photosynthate production. Consequently, plantain leaf bifurcation is an efficient self-organising method for coping with more food production under nutrients constraints.

Keywords: Adaptation, divergence angle, double-bunching, fibonacci, pseudostem.

INTRODUCTION

Leaves have been shown to originate from the shoot apical meristem (Puja *et al.,* 2005; Reinhardt *et al.,* 2000), which is a small mound of undifferentiated tissue at the tip of the stem. Reinhardt *et al.* (2000) have further stated that leaf formation begins with the selection of a group of founder cells in the peripheral zone at the flank of the meristem, followed by the initiation of local growth and finally morphogenesis of the resulting bulge into a differentiated leaf. While lateral organ emergence in plant embryos and meristems depends on spatially coordinated auxin transport and auxin response (Ploense *et al.,* 2009) the way some of the tissues of the *Arabidopsis* fruit are moulded indicates how plants may sculpt plant form by modulating the degree of meristematic properties (Girin *et al.,* 2009).

Whereas the mechanisms controlling the switch between meristem propagation and leaf initiation have been identified by genetic and molecular analyses, the radial positioning of leaves, known as phyllotaxis are poorly understood (Reinhardt *et al*., 2000). Phyllotaxy is the arrangement of petals around a flower, leaves around branches, and seeds on seed-heads and pinecones, and are present in many fruits and vegetables (Knott, 2009). Knott has further stated that the appearances which we see in nature relates to the divergence angle represented by phi. This divergence angle lies in the packing, which gives the best arrangement of objects that minimizes wasted space for optimal resource utilization. Shipman and Newell (2004) demonstrated how phyllotaxis, which is the arrangement of leaves on plants and the deformation configurations seen on plant surfaces, as the energy-minimizing buckling pattern of a compressed shell of the plant's tunica on an elastic deformation. In addition, the strain energy developed is minimized by configurations consisting of special triads of almost periodic deformations. SIAM (2004) has suggested that the origin of external stress in plants is differential growth near the tip of the plant's shoot, which causes an annular region of the plant's tunica (its hardened skin) to undergo compressive stresses. Smith *et al.* (2006) defined phyllotaxis in plants as the regular arrangement of lateral organs around a central axis, where the plant hormone auxin was linked to the molecular mechanisms of morphogenesis and the geometry of phyllotaxis.

Plants are generally made up of branches, leaves, petals, stamens, sepals, florets and trunks (Selvam, 1998), while phyllotaxy or phyllotaxis is the arrangement of leaves on the stem of plants (Korn, 2008; Wikipedia, 2008; Nisoli *et al.,* 2009), which can be arranged in alternate, opposite, whorled or spiral patterns. These leaves branching

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Corresponding author email: asemotaegno@yahoo.co.uk

arrangement and architecture are to optimize access to moisture, rainfall, carbon dioxide and sunlight. Seaweed for example, grows with dichotomous branching from an unbranched frond by repeated bifurcations. Naturally, this plant growth is uneven because some branches get out of step with each other and some others cease to divide altogether (Burton, 1998).

Many monocotyledons have leaves of peculiar form. The lamina in a palm arises as a continuous but pleated sheet of tissue, and then, as it expands, it spontaneously tears along the folds so as to form a set of apparent "leaflets". A rather similar result can be achieved when a banana-leaf is torn by the wind, but the palm-leaf is distinctive in tearing automatically to look like compound leaf when mature (Simon *et al.,* 1990). Similarly, the leaves of the banana and other *Musaceae* are split by winds to form what are essentially pinnately compound leaves (Eames and MacDaniels, 2001). The banana (*Musa paradisiaca* subsp. *Sapientum; Musaceae*) is one of the tallest herbaceous plants. Its treelike stem is composed of the sheathing spiral leaf bases, which contain fibres of sufficient strength to make possible the erect habit (Hill and Sharma, 2000; Nelson *et al.,* 2006). Additionally, the plantain, which is a close relative of the banana, is one of the great food plants of the tropics and it is usually eaten cooked or made into powder. Tivy (1998) explained that among the few species of plants which have attained an almost world-wide range in both tropical and temperate latitudes are some of the notorious weeds of domestication and cultivation, such as the plantain (*plantago* spp.). Tivy (1998) further stated that because bananas have been vegetatively propagated for so long, their seed producing capacity has been drastically reduced. This is so because the domestication was the selection of a sterile hybrid able to produce attractive fruit but unable to develop seeds necessary for its perpetuation. Bananas are picked and shipped when green (Nelson *et al.,* 2006). When they are thoroughly ripe, as revealed by their brown blotches on yellow skin; they constitute one of the most healthful and nourishing foods. Bananas have a high content of carbohydrates with some fats and proteins. Indeed, their food value is about three times that of wheat (Hill and Sharma, 2001).

Physiological studies of three plantains in the laboratory, *Plantago major, P. media* and *P. lanceolata* supplied with equal quantities of seeds in three different plots, were given a replicated series of treatments to the soil surface. The different treatments had markedly different selective effects on the emergence of the three species depending upon the type of microenvironment each treatment had created. Quantitative inheritance, being able to measure how much of the phenotypic variation is genetic, as opposed to environments to which different individual plantains are exposed or to random perturbations arising during development, are necessary (Silvertown and Charlesworth, 2001). However, it is impossible as yet, to tell how much of the phenotypic value of any individual plantain is genetic vs environmental.

Therefore, *Ex post facto* (after the fact) research and hypothesising were the main recourse in this study. These are important research alternatives, which supply the missing links to characteristics and phenomena that occur naturally without the researcher's intervention.

The main objectives of this study include: (i) detailed and systematic examination of plantain leaf midrib division for pattern recognition; (ii) to identify special and specific characteristics of *false horn* plantain leaf division *in situ*. However, only two relevant plantain bunch types are distinguished (Swennen and Vuylsteke, 1987): (1) *False horn* plantain: inflorescence is incomplete at maturity (hands consisting of large fingers followed by few hermaphrodite flowers); (2) *Horn* plantain: inflorescence is incomplete (few hands consisting of few but very large fingers; no hermaphrodite flowers and no male inflorescence; inflorescence axis is terminated by a tail or a deformed glomerule); (iii) to focus on the visual and presentational aspects of plantain leaf bifurcation and its bunches for analyses and possible explanation.

Therefore, *ex post facto* plantain leaf midrib bifurcation was studied from clay soil acidification, ion exchange balance, absorption of available nutrients from soil, effect of calcium deficiency and other ions in the cleavage of middle lamella. Furthermore, enzymatic action on cell wall and separation layers, formation of organometallic complexes, mutations and chromosome abnormalities, and gene-expression, which is correlated with compensatory adaptation to environment have been used for this study.

As a result, literature search, review and soil sample analyses were used to account for the plantain leaf division *in situ*. However, the assumption in the uniform spread of acidity over large neighbouring areas, that ranged from pH 6 to 7 (like neighbouring Oko-Oba and Oke-Aro villages, in Lagos, Nigeria), as reported by Van Wambeke (1992), for south West Africa, was used and this constitutes a major weakness of the research.

MATERIALS AND METHODS

There were two *ex post facto* double-bunching plantain subjects observed to possess bifurcating leaflets in their leaf midribs at Oko-Oba village (August, 2000, Fig. 1) and Oke-Aro village (December, 2001) respectively, near Lagos, Nigeria, which are about 5 Km apart. Photograph of the Oko-Oba village sample (Fig. 1) was taken and a protractor used to measure the angle between the bifurcating (separating) plantain leaflets. The pH of the Oke-Aro soil sample very close to the bifurcating plantain leaf site was determined later in May 2003 to examine if there were any relationships between plantain leaf bifurcation and pH of soil. Whereas the flaky Oke-Aro soil sample had a pH of 7.5; the clay was mainly composed of Ca^{2+} and Na_2SO_4 (Leached).

But, neither the photograph nor the angle of divergence between the bifurcating plantain leaflets could be obtained for the Oke-Aro plantain pseudostem. This was so because one of the bifurcating leaflets (left hand side) fell over the un-separated leaf portion. And unfortunately, the plantain bunches were harvested soon after this visual observation by the plantains garden owners, before a photograph could be taken.

Because these unpredictable plantain leaf bifurcations occurred naturally, it was thought that *ex post facto* design should be the most appropriate method of study. A weakness of the design was the inability to obtain soil pH soon after the respective visual observations of *false horn* plantain leaf midrib division.

As a result of the peculiar nature of *ex post facto* research, this study was preceded with a review of some factors that could impact on plantain leaf midrib division and analyse the plantain photograph in conjunction with the soil sample, to enable us draw some conclusions about *false horn* plantain leaf bifurcation advantages for enhancing more food production.

Clay soils in tropical regions

Hillel (1998) suggested that the most prevalent minerals in clay fractions of tropical regions are hydrated oxides of iron, and aluminium. The absorbed cations Na^+, K^+, H^+, Mg^{2+}, Ca^{2+} and Al^{3+}, which are not part of the lattice structure could be replaced or exchanged by other cations in the soil solution. This is important in soils as it affects the retention and release of nutrients and other salts as well as for flocculation. Russel (1950) explained that acid soils with displaceable aluminium leach out aluminium compounds when leached with a neutral salt to act as an exchangeable base, which contributes to calcium "exchange acidity". If the pH rises above 5, aluminium hydroxide ($Al(OH)_3$) are so precipitated that aluminium cations are washed out of acid soils in appreciable quantities (Hillel, 1998). In places with high rainfall and leaching (like Lagos, Nigeria) kaolinite is formed where silica and alkali are removed from soil to form minerals rich in alumina.

Soil leaching and microbial action

Van Wanbeke (1992) related the 11 months (800-1200 mm/year) rainfall of southern parts of West Africa having a pH range of 6 to 7 with a stable and persistent kaolinite soil structure. Leaching of soluble salts, which is formed (Russel, 1950; Van Wanbeke, 1992) during oxidation offers alternative reclamation procedures with technical and environmental difficulties, caused by soil acidity. This may spread over large neighbouring areas. Allen (1993) explained that some ectomycorrhizal fungi produce calcium oxalate in high concentrations to increase the weathering rates of phosphorous (P) in soils (due to increased cycling rates of cations like Ca, Fe and Al). Because these oxalates preferentially bound Ca, Fe, and Al to phosphates (Russel, 1950), ectomycetes degraded oxalates could enhance soil CO_2 by further weathering P from the clay matrix while maintaining the solution P through binding Ca with secreted oxalates (Allen, 1993). These actions undoubtedly reduce the binding capabilities of Ca and Al and hence (Russel, 1950 and Allen, 1993) increase actively cycling P in the ecosystem. In addition, Russel (1950) explained that leached alkaline soils, with low Ca and high Na, cause accumulation of Sr, which either compromises the vigour of the plant or harm it altogether; these are also important for understanding plantain leaf bifurcation.

Plantain biology

The aerial shoot of bananas and plantains are cylindrical pseudo-stems of overlapping leaf bases, which are tightly rolled around each other to form rigid bundles about 30cm across. New leaves continuously grow up through the centre of the pseudo-stem such that laminas tightly rolled, expand at the top into large, oblong blades with pronounced supporting midrib and well marked, pinnately arranged parallel veins. In addition, each plant carries a crown of ten to fifteen leaves with new ones appearing every 1 or 2 weeks to replace old ones, which have died (Cobley and Steele, 1989). Another study, Norman *et al.* (1996) explained that plantain pseudo-stem commonly have 11 unexpanded leaves within it and carry about 10 expanded leaves for which more than half may have been non-functional, owing to wind damage, senescence and disease. Although both Cobley and Steele (1989) and Norman *et al*. (1996) agreed that when pseudo-stems grown from suckers are about 5.5-10 months old and have produced between 30 and 50 leaves, the apical growing points of the corm becomes reproductive and instead of leaves, it produces an inflorescence which grows up inside the pseudostem on a long un-branched axis.

Because plantain has a free assortment of genes, it cannot remain indefinitely unaffected by mutation of its genes. Simon *et al.* (1990) continued by stating that instances exist where *Plantago coronapus* showed clear evidence that contrasting genes are segregating amongst the population and it is possible to see variations in a whole catalogue of characters such that there is no constant one-to-one relationship between leaf and branch. This is so because a leaf may have no axillary branch or it may have leaves of peculiar form and in some larger ones of warm climates (like that in Lagos, Nigeria), development of the leaf involves an actual separation and destruction of tissue (Fig. 1) like the lamina "leaflets" in palm.

Other literature reviewed, relate symmetry and bifurcation with visual phenotypic patterns and nonlinear mathematical modelling (Golubitsky *et al.*, 2003). Branching with binomial distribution (Mohlenbrock, 2000; Weisstein, 2004), shows a bifurcation as a period doubling, quadrupling, etc, that accompanies the onset of chaos (Khammash and El-Samad, 2004). It could also mean the sudden appearance of a qualitatively different solution as some parameter is varied which in general, is a separation of a structure into two branches or parts.

RESULTS AND DISCUSSION

Two different plantain *false horn* bifurcating leaves were observed at separate time periods in Oko-Oba August 2000 (Fig. 1) and Oke-Aro December, 2001 villages near Lagos, Nigeria that are about 5km apart. The Oko-Oba *false horn* plantain, presented with about 10° angle of divergence between the bifurcating leaflets while the two plantain bunches were pointing approximately in the same direction at about 90° to the horizontal (Fig. 1). Similarly, the Oke-Aro village *false horn* had its bunches approximately at right angles to the horizontal, but about 180° out of phase with each other (pointing in opposite directions).

The angle of divergence between the bifurcating leaflets could not be estimated nor measured because one of the bifurcating leaflets fell over the left hand side of the un-separated region of the bifurcating leaf (probably confirming the a priori assumption of a weak middle lamella of plantain leaf midrib: Allen, 1993; Jones, Jr., 1998; Strafford, 1970). Additionally, before a photograph could be taken soon after the visual observation, these plantain bunches were harvested.

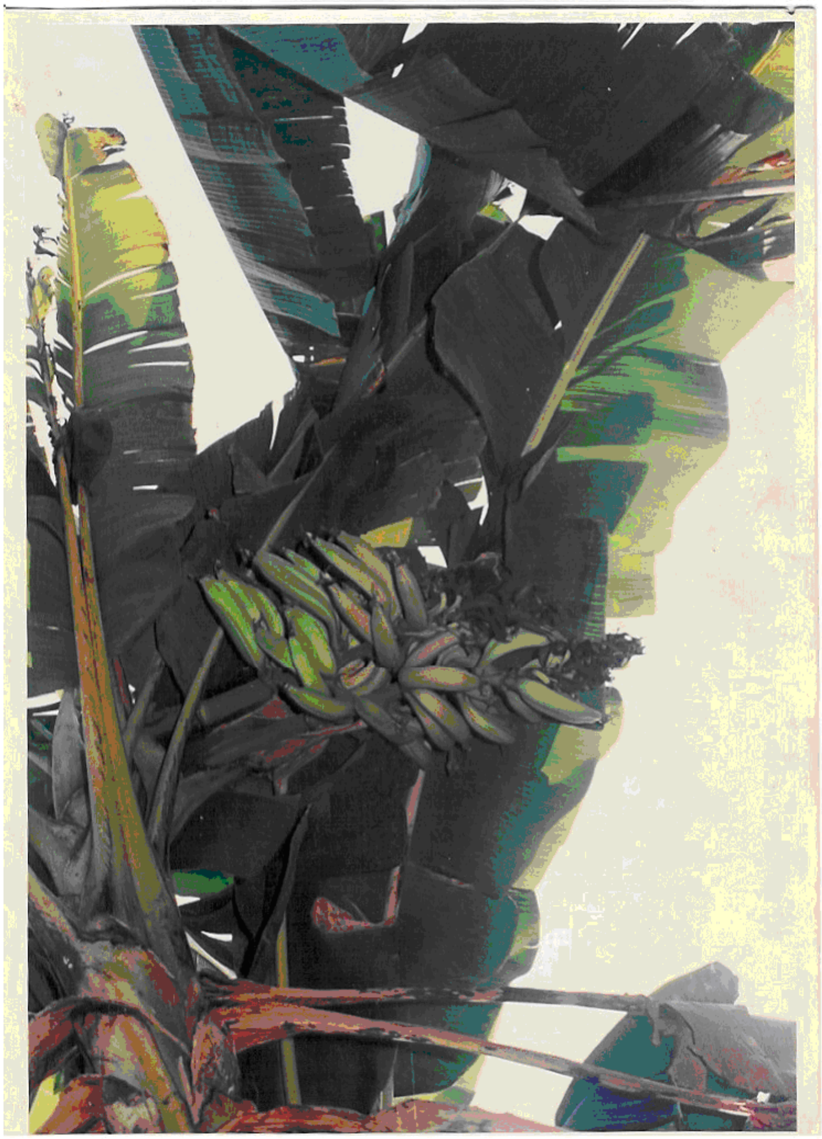

Fig. 1. Plantain Leaf Bifurcation Photograph of Oko-Oba Sample (August 2000).

Although the divergence angle between the bifurcating Oke-Aro plantain leaflets could not be determined, both the cleavage line that seems to derive from the corm and the second right-hand half of bifurcating leaflet were visible, coupled with the 90° bunch overhang. Also, each bifurcating plantain leaf in the two samples was seen to be among the subsisting leaves until bunch harvest. Therefore, we could infer that these subsisting bifurcating leaves until bunch harvest should have positive correlation with fruit formation, maturity as well as genetic compensation for the *false horn* "double bunching" double leafing plantain.

Determinacy of plantain leaf division and bunches overhang

It is, however, not known if there is any regularity or otherwise in determining which leaf sheath would bifurcate or at what angle each bunch would hang, because two samples are not sufficient for generalisation. But, the realisation that such characteristics do exist in plantain pseudo-stems should be instructive for biologists and especially to banana and plantain researchers. This is so because, the bifurcating leaf sheath from the Oko-Oba sample and that from Oke-Aro showed plantains bunches overhang characteristic. Whereas both plantain bunches pointed almost to the same direction for the Oko-Oba sample at about 90° to the horizontal (Fig. 1), those from Oke-Aro lay in the east-west directions and each at about 90° to the horizontal. The 90° bunch overhang observed in these two cases may have been a coincidence, when this overhang phenomenon is placed besides that established fact of plantain bunch direction pointing indeterminacy (Norman *et al.,* 1996). The biophysical, biochemical and/or physiological explanations to confirm or disprove the "double bunching double leafing" 90° bunch overhang is subject to further investigation. It could, also be, a Fibonacci process (Simon *et al*., 1990).

Plant hormones

It has been shown that indole-3-acetic acid (IAA) has been the only receptor with a multiplicity of effects like stimulation of cell division, shoot growth, control of vascular bundle system differentiation, control of apical dominance, senescence delay, promotion of flowering and fruiting which could be explained from knowledge of secondary messengers (Bandurski and Nonhebel, 1989; Jones and MacMillan, 1989; Wilkins, 1989). Thus, the IAA receptor complex could act through a transducer on a Ca^{+2} gate, which in turn affects intracellular calcium and calmodulin-controlled enzymes like the plant NAD kinase. Consequently, the physiological events observed would depend on the most step limiting pathways mediated by calmodulin (Bandurski and Nonhebel, 1989), like media acidification, longer range enzyme changes resulting in the plasticity of cell wall protein matrix, cellulosic matrix, and hemicellulosic matrix. These metabolites act on cell wall, which makes it to divide through newly synthesised wall polymers. These inserted cell wall polymers act as loosening agents that break bonds within or between the cell wall (Jones and MacMillan, 1989).

Wilkins (1989) explained that of the known growth regulators, only IAA initiated growth in the vertical node (Fig. 1). This growth can be initiated in the leaf sheath bases by lowering the pH of the tissue to 3 and terminated by raising the pH to 5 or 7. In addition, the possibility of electrical signal propagation through the tissue during proton transport in apoplasts is known to gravitropically stimulate at least one enzyme system in wheat (possibly plantain) nodes. Horgan, (1989) suggested that growth in a complex multicellular organism like plantain is usually the result of interrelated cell division and cell expansion processes: such that cytokinins respond in the redifferentiation of certain plantain leaf tissue and in combination with auxin, for the regulation of morphogenesis. Furthermore, cytokinins in combination with gibberellins markedly modify the shapes of plantain leaves in intact plantains as to suggest that normal leaf development can be controlled by gibberellins/cytokinins ratio. Milborrow (1989) explained that phytoalexins, which are compounds synthesised in response to attack by a pathogen or damage to plantain tissue, could cause drastic changes in a plantain leaf physiology. Because, IAA can be oxidised by a plantain tissue homogenate, the reaction may be brought about by an unspecific oxidase released from ruptured plantain pseudostem tissues (Allen, 1993; Swanson *et al.,* 1967; Van den Broek, 2002).

Ethylene action

Climateric fruits like banana are characterised by low rates of ethylene production during the pre-climateric or unripe stage, followed by the climacteric stage of sudden increase in ethylene production and respiration, accompanied by other biochemical changes of ripening. Beyer *et al.* (1989) have stated that the purpose of stress ethylene as a "second messenger" is to communicate the effect of stress to the plantain in a way that facilitates a response, such that the synthesis of Acc-synthase results in the accumulation of Acc and onset of stress-ethylene production. Consequently, ethylene-mediated events in the abscission zone of the plantain pseudostem could result in dissolution of the middle lamella of the plantain leaf sheath (Russel, 1950; Strafford, 1970), hydrolysis of the cell walls, and a localised cell enlargement, which facilitates separation by providing shearing action in the plantain leaf. Hilman (1989) related multicellular terrestrial plants and bifurcating plantains with a scissile mode of life and how they have developed strategies to exploit and adapt to their changing environment over time. Because they are continuously developing organisms, their shape is a product of their differential action and activity in regions of their apices; for which, the cells remain in an embryonic condition called meristems. Mansfield and Snaith (1989) explained that Fusaric acid produced by a fungus causes wilt disease because it impairs the semi-permeability of the plasma membrane by changing the conformational properties of the constituent plantain phospholipids. The theophylin formed, could change the binding of Ca^{2+} and affect plantain membrane function. Sprent (1989) stated that curling and sometimes branching of *plantain leaves* and root hairs are known to precede infection (Allen, 1993), and the way in which such root hair or leaf growth has been modified is not yet, understood.

Enzymatic action and pH-mediated activities

Furthermore, wall-dissolving enzymes such as pectinases, glycosyltransferases, and polygalacturonases act as lectins and are sensitive to Ca^{2+}. Also, wherever bacteria penetrate root hairs (plantain *corm*), Ca^{2+} distribution is altered in the plantain leaf sheath (Bandurski and Nonhebel, 1989; Jones, 1989; Wilkins, 1989). Therefore, the proper amounts of both enzymes and substrate must be present for the curling reaction to occur. But, if there is a problem of ionic balance with more cations (K^+, Ca^{2+}, Mg^{2+}, etc.) being taken up than anions ($H_2PO_4^-$, SO_4^{2-}, Cl^-) as in nitrogen leaving roots for shoots in xylem sap, the plantain must synthesise anions to balance the excess cations in the sap. Consequently, (Clarkson, 1989; Strafford, 1970) the pH balance discrepancies may take biophysical and biochemical pH stats where excess OH^- is neutralised by H^+ from strong organic acids like malate or oxalate made from neutral precursors.

Also, oxalate could be precipitated in plantains as its insoluble Ca^{2+} salt, where malate is transported in the phloem with K^+ to the roots and ultimately to the soil. This process causes soil acidity and reduces the available Molybdenum ($Mo^{-2 \text{ to } +6}$), which is a constituent element of Nitrogenase, Nitrate reductase, and Xanthine dehydrogenase (Clarkson, 1989; Sprent, 1989; Song, 1989; Strafford, 1970). The effects of reduced Mo in soil, which drastically reduces Cd^{2+} availability include poor nitrogen fixation capacity, highly reduced soil fertility and seriously hampered crop production. Hence, the occurrence of plantain leaf bifurcation is to compensate for these adverse effects.

Plant needs and organometallic complexes

Water, reduced carbon, reduced nitrogen, phosphate, potassium, and a diminishing indefinite list of other elements (Canny, 1989) in lesser amounts of magnesium, calcium, sodium, etc. form the general need of all plant cells. Although (Jones, Jr., 1998; Canny, 1989) only reduced carbon and reduced nitrogen are not obtained from the soil, the reduced carbon is made in abundance where the cells are green and remote from the soil. Canny (1989) added, by showing that anions in the sap are principally phosphate and occasionally chloride and organic anions like malate, which has a sap of pH between 7.5 and 8.5. Clarkson (1989) explained that the packing capacity of plantain phospholipid headgroups when disturbed showed protrusions of intrinsic membrane proteins, which float and displace the headgroups as they do so. Additionally, calcium ions control leakage of plantain solutes through the formation of linkages with negatively charged ions or headgroups. Stronger plantain headgroup linkages result in more rigid headgroup packing when formed with some other divalent (Van den Broek, 2002), like, Cd^{2+} and trivalent, La^{3+} and Al^{3+} cations. These cations inhibit plantain membrane bound enzymes like ATPase and compromise the integrity of plantain cell wall (Russel, 1950; Strafford, 1970).

Bond cleavage and wall weakening

Thomas and Vince-Prue (1989) stressed that plantain leaf perception, transmission and floral evocation are three independent components in a chain; leading to flowering. There is, therefore, a requirement for a number of favourable cycles before the plantain leaves are induced. Sometimes, non-inductive cycles interpolated into a series of inductive cycles do cause flowering. This “fractional induction” has been shown to persist over several weeks of non-inductive cycles as in *Plantago lanceolata*, long day plant (LDP). Jones and MacMillan (1989) stated that transglycosylation in the plantain cell wall results in the cleavage of a glycosyl bond, which causes a weakening of the wall followed by transfer of the polysaccharide terminus to a new position. The formation of a new glycosylic bond in plantain is catalysed by transglycosylases, which serves the dual purpose of plantain glycosylic bond cleavage and synthesis. It has been shown by Beyer *et al.* (1989) that because ethylene participates in all phases of plantain behaviour, like the binding of olefins to metals, it is generally accepted that plantain in vivo ethylene receptor site should contain a metal (Ca, at least), based on the principles of organometallic chemistry.

False horn compensatory adaptation to the environment

Hilman (1989) explained that the plantain apex is a self-determining region, which controls cell differentiation. It also affects those processes that culminate in the non-determinate growth habits of most perennial and vegetative monocarpic plants (*plantain*), reflecting the interplay between gene-expression in cells derived from the plantain meristem and responses to the environment (Fig. 1). Therefore, the successful existence of a plantain leaf bifurcation depends on its sensitivity and responsiveness to environmental changes. This includes adaptive changes that result in compensatory growth effects (plantain leaf bifurcation) as well as, its attendant correlative relationships. Clarkson (1989) explained that physiologically active plantain gibberellins could reduce plantain headgroups reordering, increase ionic conductance and bilayer fluidity. Therefore, plantain nutrient deficiencies may bring about major changes in the abscisic acid and gibberellins content of plantain shoots and roots, which ultimately affects plantain membrane permeability when interacting with plantain lipid headgroups (Fig. 1).

Chromosome abnormalities

Van den Broek (2002) suggested that many proteins deform plantain DNA when bending, which equally involves, stretching, kinking and/or unwinding of the double helix. The plantain energy cost, if not provided by ATP, is obtained from the contacts between plantain DNA and enzymes. Therefore, whenever the plantain DNA forms a left-handed super helix around the nucleosomes, it must be bent under a constant angle (Fig. 1). During plantain cell division, duplicated chromosomes are pulled apart (Fig. 1) by semi-flexible polymers called microtubules. Overstretching of the plantain DNA structure is only possible when the plantain DNA is not torsionally constrained or when a single strand break is present. Alternatively, the plantain DNA could have its two strands separated as shown in Fig. 1.

Lester and Bohlin (1984) explained plantain leaf bifurcation as chromosomal alterations, regulatory gene mutations and developmental bifurcations caused by an accumulation of minor plantain mutations with reverse patterns of gene expression. This is so because certain plantain gene complexes have been broken and new ones formed with their structural genes changed and expressed phenotypically in plantain leaf bifurcation (Fig. 1).

Simiarti *et al.* (2001) explained near mirror-image plantain leaf bifurcation architecture arising during leaf development from shoot apical meristem (SAM). These results in plantain leaf primary vein bifurcation at the tip to form secondary veins, which elongate basipetally toward the primary vein (Fig. 1). In cases where the cells of the SAM resemble plantain pseudostems that have the capacity for self-regeneration in undifferentiated state, the plantain leaf primordia is generated from its peripheral zone (Fig. 1). Similarly, Tsiantis *et al.* (1999) suggested that disturbed auxin gradient transport both within the plantain leaves and across the plantain vegetative axis could mediate in certain facets of the mutant phenotype. This situation occurs when signals involved in ligular differentiation originate near the plantain leaf midrib during embryogenesis of the plantain leaf sheath (Fig. 1).

Nutrient availability

Hilman (1989) related correlative phenomena with nutrient availability and competition in consonance with compensatory growth effects in apical dominance, coupled with the nutritive state of the plantain. Similarly, Baker (1989) suggested that plantain leaves normally present a very large surface area (Fig. 1) to the surrounding air to facilitate CO_2 assimilation and transpiration as a consequence of the structural organisation of plantains growing in air (Woodward and Sheehy, 1983). As a result, bifurcated plantain leaves in air further presents a much larger surface area and four leaf edges to the atmosphere to better optimise resources made available to it. Schopfer (1989) related factors such as light interference with the realisation of plantain leaf genetically determined bifurcation patterns by selectively stimulating the expression of defined parts of the genetic information and inhibiting the expression of others. This goes to show that enzyme activities are essential elements in plantain leaf bifurcation due to photo-morphogenetic control (Fig. 1).

Further, Gregory (1978) and Sexton and Woolhouse (1989) explained that the breakdown of chlorophyll and dissolution of the plantain thylakoid membrane may proceed almost to completion with the plantain chlorophyll envelope, mitochondria and plasma membrane remaining intact or showing little signs of plantain leaf midrib disruption (Fig. 1).

Infection and gene modification

Allen (1993) showed mycorrhizal infection to increase the number of vascular bundles, and morphological changes in host plantains and consequently alter the ability of plantains to survive stress and gain access to resources that ultimately improve plantain fitness (Fig. 1). Swanson *et al.* (1967), Simon *et al.* (1990) and Sengbusch (2002) explained plantain leaf diakinesis as the continuation of plantain leaf diplotene where four plantain leaf chromatids are separated into twos, and the bivalent is held together by one or more plantain leaf chiasmata at points in which neighbouring plantain leaf chromatids have broken and rejoined into new arrangements at plantain leaf crossover.

Consequently, particular pairs of plantain leaf-linked genes (Theurer, 1984) (Pl_1 and Pl_2) may be separated (Fig. 1) or combined at different frequencies (Swanson *et al.* 1967), which may be dependent on the physical distance between these plantain leaf genes on their common chromosomes.

Additionally, Swanson *et al.* (1967) suggested plantain leaf fibrils about 40Å in diameter to be the basic longitudinal unit of the plantain leaf chromosome in division, with each plantain leaf chromatid quadripartite and each plantain leaf chromosome, possibly octipartite. Where, of course, plantain leaf ruptured cells are enzymatically relaxed for each plantain leaf chromatid to bifurcate still further (Fig. 1).

Effects of calcium and other cations on plantain leaf division

Strafford (1970), Simon *et al.* (1990) and Russel (1950) explained how Ca^{2+} combines with pectic acid to form calcium pectate which is a constituent of the middle lamella of the plantain leaf cell wall, such that, a shortage of calcium weakens the plantain leaf cell wall, and causes it to bifurcate (Fig. 1). Similarly, a high number of chromosome abnormalities could be traceable to the roles calcium ions play in plantain leaf chromosome structure in tending to connect protein and plantain leaf DNA components together. Jones, Jr. (1998) suggested four categories of nutrient requirements for banana (and possibly, plantains) whose quantities of supply have implications for plantain leaf bifurcation, and plantain and banana pseudostems survival. So, very high requirements are for $N^{-3 \text{ to } +5}$, $P^{-3,0,+3,+5}$, K^{+}; high for: Mg^{+2} and B^{+3}; medium for: $S^{-2,-4,-6}$ and low for: Ca^{+2}, $Cu^{+1,+2}$, $Fe^{+2,+3}$, $Mn^{+4 \text{ to } +7}$ and Zn^{+2}.

In addition, ammonium toxicity could lead to lesions in plantain pseudostems, cupping of leaves and, decay of conductive tissue at the base of pseudostem (Fig. 1). Magnesium deficiency may also occur while high Phosphorus (P) may interfere with normal Ca nutrition and consequently Ca deficiency in plantain leaf midrib lead to bifurcation (Russel, 1950; Strafford, 1970; Van Wambeke, 1992; Allen, 1993; Kanwal *et al.,* 2008).

Soil analyses

Van Wambeke (1992), Allen (1993) and Russel (1950) explained that calcium deficiency can also occur in alkaline soils low in calcium but high in sodium (Na), especially on highly leached soils that lead to boron (B) deficiency as exemplified by the Oke-Aro soil sample pH. As a consequence, both calcium and boron deficiencies may indirectly interfere with the plantain leaf midrib by allowing other substances like strontium (Sr) to accumulate in the plantain leafsheath tissues so as to either compromise the vigour or actually harm the plantain leaf midrib (Strafford, 1970; Russel, 1950; Smit and Combrink, 2004). In addition, the presence of free calcium carbonate in alkaline calcareous soils can affect the availability of B to plantains. Also, the Ca/B ratio in plantain leaf tissues can be used to assess B deficiency, sufficiency and toxicity in plants. In addition, genotypic variation in crop plants (possibly, plantains) can be related to the quality of B and Ca uptake (Kanwal *et al.,* 2008).

Similarly, Srivastava and Gupta (1996) suggested that boron deficiency affects the activity of the cambium tissue, such that longitudinal plantain leaf midrib cell walls give a serated appearance due to irregular thickening and disorganisation of the middle lamellae with longitudinal lesions appearing along the plantain pseudostem vesicular tissues (as in plantain leaf bifurcation, Fig. 1). Whereas molybdenum (Mo) deficiency results in "whiptail symptom", the appearance of chlorosis in the plantain leaf basal interveinal areas of young leaves progresses toward the leaf margin or midrib as in Fig. 1, (www.gov.nf.ca/agric/pubfact/Fertility/nutrition.htm, 2003), to cause plantain leaf midrib bifurcation.

Strafford (1970) related mottling of leaves along the plantain leaf midrib middle lamella with Ca and Mo deficiency. Jones Jr. (1998), Allen (1993) and www.gov.nf.ca/agric/pubfact/Fertility/nutrition.htm, (2003) explained that the middle lamella of the plantain leaf cell wall will not be completely formed with Mo deficiency (Fig. 1). This is so because Mo is strongly absorbed by Fe and Al oxides. This Mo absorption is pH dependent coupled with that fact that, P and Mg enhance Mo uptake while sulphate (SO_4) reduces Mo uptake. The cumulative effects reduce soil fertility, reduce availability of useful cations and anions for good food production, which ultimately leads to dismal harvest.

Heavy metals binding mechanisms

Harborne (1997) explained that heavy metals binding (like Pb, Zn, and Ni) to plantain leafsheath tissues in the plantain root cell wall could result in the accumulation/detoxification of peptide chelates, which show themselves in a divergence (Fig. 1) of biochemical adaptive responses, that are dependent on metals present for both primary and secondary metabolism.

Biochemical factors

Avigad and Dey (1997) suggested plantain frutans to be linear or branched polymers of β-fructofuranosyl-fructose linkages of oligosaccharides where the plantain leaf tetrasaccharides may be cleaved into a linear inulin type structure and a branched (Fig. 1), bifurcose (1 and 6-kestotetraose) levan type structure by invertase enzymes. Lam (1997) explained that plantain leaf genes encode protein kinases with calcium as a signal transduction intermediate, especially with calmodulin as it could change plantain leaf membrane permeability. Consequently, these types of gene regulation appear in naturally occurring plantain leaf tissue differentiation (bifurcating plantain leaflets, Fig. 1), and have their genetic loci controlled by developmental processes. So, plantain leaf midrib mutations at these loci alter the form of plantain leaf organs in both the early and late steps of their phenotypic developments. These occurrences represent the causes and effects between plantain leaf cell linkages and environmental factors for meristematic cells development (Fig. 1).

Whereas other elements like vanadium, tungsten, titanium, nickel, cobalt, copper and chromium (Strafford, 1970 and Hydroponicsbc, 2003) play their parts as participants in enzymatic reactions and DNA synthesis, the genes which differ among themselves and are revealed in phenotypic expression seem to be organised along the length of the chromosome in linear fashion (Swanson *et al*., 1967) which bears resemblance to the longitudinally length-wise plantain leaf midrib bifurcation observed in the December 2001 and August 2000 plantain leaf (shown in Fig. 1).

Similarly, Lester and Bohlin (1984) explained plantain leaf developmental bifurcation as the small genetic mutations which may accumulate to the point where a new developmental pathway may emerge resulting in drastic morphological changes, where in fact, the difference between evagination (to turn inside plantain leafsheath out or like inverted "vagina") and invagination (to dent or force a plantain leafsheath inwards, or form a hollow in-growth) could be small, but the phenotypic effect is quite noticeable (Fig. 1).

Clay soil acidification, enzymatic dissolution of separation layers, effect of photo-morphogenesis and burden to bear more food, seem responsible for plantain leaf phenotype. Also, the parts ions play in connecting and binding proteins and DNA components together, were equally implicated in plantain leaf bifurcation of two leaflets on a midrib along the cleavage line, which derives from the corm in genetic compensation. Analysis also show that turbulence at leaf-free air interface, results in greater heat, water vapour and carbon dioxide mixing and transfer due to random eddies, for more photosynthate production. These deductions were so because these bifurcated leaflets subsisted until plantain bunch harvest. It was also observed that plantain leaf midrib division seems to give special strength and stability to the plantain pseudostem. This is especially so because the pseudostem was able to carry the plantain bunches as cantilever. The Physics of the work done by the two peduncles carrying the plantain bunches, at right angles to the horizontal is zero. This is so because the value of cosine 90^0 equals zero (Force x distance x cos 90° = 0). As a consequence, two directions are possible for the plantain peduncles to overhang at about 90° to the horizontal. That is, either in the same direction as in Fig. 1 or diametrically opposite directions at about 180° out of phase, to each other. Additionally, the divergent angle between the divided leaflets was about 10° (±0.5°), while the plantain bunches were hanging at about 90° to the horizontal. From literature it was reported that only about 5% of the sunlight is converted by a leaf for photosynthesis (Woodward and Sheehy, 1983). So, the divided leaf of the plantain under study is able to use about 10% of the sunlight available to it. As a result, this plantain midrib leaf division mechanism represents a genetic improvement. It is also able to acquire and convert about twice the quantity of sunlight available for more food production when compared to other undivided plantain leaves. Therefore, bifurcated plantain leaf is about 100% more energy efficient and has higher capacity of resources utilisation, for enhanced food production, compared to the undivided leaf.

CONCLUSION

Despite all the enumerated weaknesses of the *ex post facto* research and hypothesising, the special strengths impacted to the plantain pseudostem and peduncle coupled with the thermodynamic implications of a plantain leaf presenting four edges to the air in the atmosphere, confers some interesting characteristic properties and also nouvelle plantain leaf symmetry. This above plantain leaf symmetry ensures that at least twice the amount of water vapour, carbon dioxide, sunlight energy and other nutrients is transferred into the plantain and converted into photosynthate for more food production, than it would have been without this leaf midrib division. Therefore, plantain leaf midrib bifurcation is both advantageous and important to the plantain form, function, strength and stability. These characteristic phenomena have, thus far, been observed with the "double-bunching" plantain species, which could have arisen principally from Ca^{2+} and Mo deficiencies, thereby leading to genetic improvement. Most importantly, this plantain leaf bifurcation phenotype discussed in this study should be a reliable guide to the genotype, at least, where dominant genes are concerned.

Abbreviations

IAA, indole acetic acid; LDP, long day plant; SAM, shoot apical meristem

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