Morpho-physiological monitoring of oil palms (*Elaeis guineensis* Jacq.) affected by spear rots (PC)

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Abstract

The morphology, growth and physiology of oil palms (*Elaeis guineensis* Jacq., Deli x Nigeria variety) was characterized at different stages of development of the condition known as 'dry spear' or FS (for 'flecha seca' in Spanish), and some morpho-physiological indicators associated with a predisposition for the disorder were identified. In Costa Rica, 'FS' has symptomology very similar to spear rot or PC (pudrición del cogollo), as it was described in South America. 'PC' is a dynamic disorder of complex etiology that affects the development and physiology of palms. The symptomology ('yellowing', drying and rotting/) occurs in young leaves and in tissues near the meristem. The aerial symptoms are associated with a deteriorated fine root system.

During the initial stages of the disorder in the season with the least precipitation (3.8-73 mm/month), the palms presented low water potential in the leaves, increases in stomatic conductance, reduction in foliage temperature, higher chlorophyll content and reduction of vegetative development. The loss of the fine root system was possibly the cause of the interruption of hormonal 'signals' toward the aerial part; which caused the loss of stomatic control of transpiration that led to a hydric, nutritional and energetic imbalance.

The anomalous behavior of stomatic conductance and other variables (root density and petiole cross-section), described in a previous article (this journal), is an indicator that could signal conditions of predisposition to a syndrome like PC.

Introduction

The disorder known locally as 'flecha seca' (dry spear), which is considered similar in its causes and effects to the so-called spear rot or PC (for 'pudrición del cogollo' in South America) (Franqueville 2001, Chinchilla 2010, Corley and Tinker 2003), has affected some plantations in Costa Rica, which have recovered, but not before suffering losses in productivity, according to the incidence and severity of the disorder.

The etiology of PC is complex and the intents to associate it with a unique pathogenic agent have not yielded conclusive results nor contributed to the management of the problem. In some regions of South America, such as Tumaco, Colombia, the presence of PC associated with problems of low productivity have even caused the abandonment of plantations.

In general, the aerial symptoms of PC include the appearance of a yellow coloration (chlorosis) on the basal sections of some of the youngest leaves and rotting and/or drying of the spear leaves (unopened leaves) (Chinchilla 2010). Invariably, these aerial symptoms are associated with a deterioration of the fine root system of the plant (Albertazzi et al. 2005). The deterioration of the plants can be very great with a halt in bunch production of fruits. Nevertheless, it is possible to recover most of the plants, whose recovery period is associated with the degree to which it is possible to improve soil aeration

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conditions and the health of the root system (Chinchilla and Durán 1998). However, some affected palms can die apparently due to inanition (inability to recover the root system) and also because they could be attacked by some pests such as the South American palm weevil (*Rhynchophorus palmarum*), root miners such as *Sagalassa valida* (in South America) and/or opportunistic pathogens (endophytic or external).

The variation in symptomatology, the possible causes, the presence or absence of pathogenic agents associated with the plants affected by different types of rots that encompass the young tissues and the management strategies available have been described elsewhere (Chinchilla 1998, 2008, 2010, Franqueville 2001, Laing 2009, Turner 1981, Akino and Kondo 2012).

The different stress factors that induce susceptibility to pests and diseases of the plants in the tropics have been well documented (Henson et al. 2005, Ayres 1974, Yarwood 1976). Noteworthy among these stress factors are the low availability of solar radiation, hypoxia conditions in the soil, water deficit, high temperatures and deficiencies of non-structural carbohydrates.

The objective of this work was to characterize the morphology, growth and physiology of oil palms in different stages of development of the 'flecha seca' syndrome in Costa Rica in an attempt to identify indicators of predisposition to the disorder.

Materials and Methods

Location of the study and plant material

The study was carried out in oil palm plantations of the southern Pacific of Costa Rica, at an elevation of 24 to 30 masl. The climate of the region is very wet, with less than three months of low precipitation. Annual average precipitation oscillates between 3800 and 4500 mm and the highest precipitation occurs between the months of March and November, with records of 800 mm per month or more during some months (July and November). In these conditions the soil moisture regime is *udic*.

The evaluations were done between April 2011 and August 2012, but prior information was available on climatic variables for the area, its soils and morpho-physiological measurements of the plants. During the evaluation period there were two periods with high rainfall (> 374 mm/month); the first between May and December 2011 and the second between April and December 2012. Between January and March 2012, a relatively dry period (3.8 mm - 73 mm/month) was recorded.

Palms of the commercial variety Deli x Nigeria (*Elaeis guineensis*) were used in the study, grouped into three categories: healthy, with initial PC symptoms, and recovered from the disorder (Table 1). Each category was found/placed in separate plots at the start of the evaluations. In addition, and as a point of reference, evaluations were done on Amazon hybrid palms (*E. oleifera x E. guineensis*) with two years in the field considered tolerant to the disorder.

Table 1. Categories of palms according to their reaction to PC at the onset of the morpho-physiological characterization of the disorder

Plot	Genetic material	General description of palms at the start of observations
Palms with initial PC symptoms	Deli x Nigeria Six years in the field	-Initial symptoms that included chlorotic leaflets or with limited drying, accumulation of spear leaves that were shorter. *PxS* values lower than normal in young leaves
Palms initially healthy (first cases in this plot appeared 11 months later)	Deli x Nigeria Five years in the field	-Absence of symptoms associated with PC - Absence of drastic changes in leaf or *PxS* size
Palms in the symptom recovery phase	Deli x Nigeria Five years in the field	-Recovered from the disorder following surgery of the damaged spear leaves. -Normal *PxS* values in older leaves -At least 8 healthy expanded leaves
OxG tolerant hybrid	Amazon Two years in the field	-Without symptoms. The information for this hybrid is included as a reference point only; but many data are not comparable due to differences in age with palms in other categories evaluated

Physiological variables

Physiological evaluations were done on basal, medial and distal leaflets of leaves No. 1 and 17 from five plants in each category (Table 1). Three rounds of one week duration each were carried out during the months of May and July 2011 (average precipitation: 494 mm/month) and March and May 2012 (average precipitation: 198 mm/month). Measurements were repeated during the morning and the afternoon.

The water potential of the leaves (MPa) was determined using a Scholander pressure chamber (Mod. PMS 1000, plant moisture stress, Oregon) between 5:00 and 6:00 am and 11:00 am and 1:00 pm. Stomatic conductance (mmol $m^{-2}s^{-1}$), temperature (°C) and transpiration (µmol m^{-2} s^{-1}) were measured using an auto-porometer (Li-Cor 1600), equipped with a sensor for photosynthetically active radiation (µmol photons m^{-2} s^{-1}), to characterize the light microenvironment. Measurements were taken between 8:00 and 10:00 am and 11:00 am and 1:00 pm.

Fluorescence (Fv/Fm) was measured using a *fluorometer* (Mod. OS-30p, Opti-Sciences) between 8:00 and 10:00 am, under real light conditions, without exposing the leaf to darkness before the measurement. The Fv/Fm index is an indicator of stress when this deviates significantly from the low values of 0.7-0.8. The chlorophyll content index, which is a quantitative indicator of leaf color, was measured with a SPAD sensor (Mod. Minolta 502), between 8:00 and 10:00 am, following the protocols indicated.

The relative water content (RWC, %) and specific leaf weight (g/cm^2) were determined in December 2011 only (end of the rainy season: 362 mm). Thirty discs, 7 mm in diameter, collected from the basal, medial and distal leaflets of leaves No. 1 and 17 between 10:00 and 11:00 am in the four categories of plants were used for this purpose.

Specific leaf weight, which is an indicator of the quality of the leaves, represents the inversion of dry material per surface unit and it enables assessment of acclimation to the light or water regime. It is calculated as the quotient between the area and the dry weight of the leaf discs used for the measurements of relative water content (Gutiérrez and Villalobos 1996).

RWC = (FW - DW)/(SFW - PS) X 100, where RWC is the relative water content, FW is the fresh weight, SFW is fresh weight at saturation, and DW is the dry weight of the sample.

The change in the severity of PC was evaluated in 1295 palms (between March and October 2011, January and July 2012 and January 2013) using a scale between 0 and 5, where 0: healthy palm; 1: palm with leaflets of young leaves with chlorosis and often with the accumulation of spear leaves; 2: palm with chlorosis and necrosis in young leaves and accumulation of spears; 3: palm with rotting and drying in the packet of spears and necrosis and chlorosis in young leaves; 4: palm with very severe symptoms including drying and widespread chlorosis on young leaves.

For the interpretation of the data an analysis of variance (Info Stat, P > 0,05) was done and the multiple comparison of all the pairs of medias was done using the DGC test. The results are the means of 360 evaluations for each leaf number in each season.

Results and Discussion

Geographic and climatic characteristics

The four categories of palms evaluated (Table 1) are located within the geomorphological unit known as the alluvial floodplain of the Coto-Colorado River in the southern Pacific of Costa Rica. Annual precipitation in 2011 was 5937 mm (higher than the historic average due to the influence of the La Niña phenomenon). In 2012, accumulated precipitation was 3343 mm due to the influence of the opposite phenomenon El Niño. Between the second week of December 2011 and the middle of March 2012, a rather dry period occurred, which is referred as the dry season in the rest of the document. The highest solar radiation and evapotranspiration values and the lowest relative humidity values occurred between January and April 2012. In the dry season, the maximum temperature reached 37 ˚C and the minimum was 17.9 ˚C (35.3 ˚C and 20.2 ˚C in the rainy season).

Between April and December (the rainiest period), the water table level fluctuated between 0.4 and 1.5 m and volumetric humidity in the first 85 cm of soil remained near 48%, particularly at sites with fine texture and low hydraulic conductivity. The high bulk density at the site aggravated the problem of low oxygen content in the soil during most of the rainy season, a phenomenon that was documented earlier by Durán and Ortiz (1995).

Water potential

During the rainy season, the youngest open leaf (No. 1 in the phyllotaxy) of the affected palms showed a higher water potential than the palms in the three other categories. On leaf 17, no significant differences were found between healthy, affected and recovered palms. Water potential in the leaves of the Amazon hybrid (of younger age) was significantly lower. In the dry season, the affected plants showed water potentials significantly lower in leaf No. 1 than in the other categories of palms. The leaves in position 17, for affected plants as well as healthy ones, showed significantly lower water potentials with respect to the recovered palms and the Amazon hybrid. These results could indicate a lower capacity for the regulation of the water potential of the leaves on the plants with PC and a loss of capacity for responding to a high evaporative demand from the atmosphere through stomatic closure (Fig. 1).

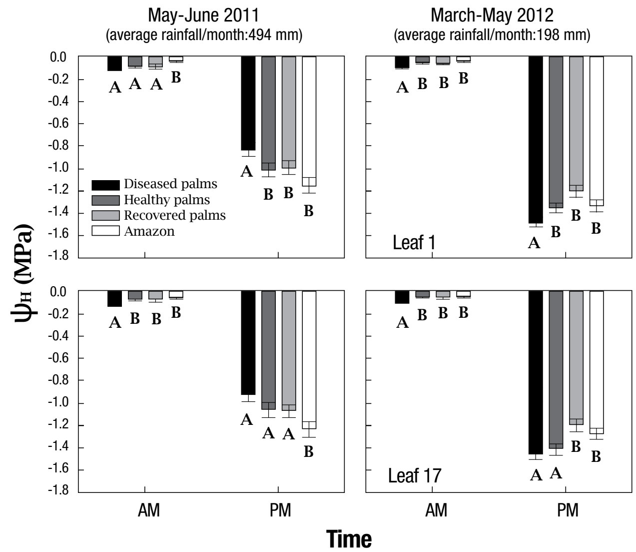

Fig. 1. Water potential in leaves No. 1 and 17 in three categories of palms (*E. guineensis*: Deli x Nigeria variety) with distinct responses to PC. The initially healthy palms and the recovered ones had 5 years in the field, and the affected ones had 6 years, when data collection began. The OxG Amazon hybrid plants are tolerant and they were younger (2 years in the field), and are included as a reference only. AM: 5:00-6:00 am; PM: 11:00 am-1:00 pm. Southern Pacific of Costa Rica. The same palms in each category were measured on both occasions (May-June 2011 and March-May 2012), therefore they were in different physiological stages (symptoms or recovery more advanced at the second measurement). Multiple comparison of pairs of means using the DGC test. The data are the means of 360 samples for each season. Palm categories with the same letters denote non-significant differences, $P < 0.05$.

Relative water content and specific leaf weight

Measures for these variables were taken in December 2011 only (362 mm of rainfall). The relative water content in leaves No. 1 and 17 of the affected palms was significantly higher than the values found in palms in the other categories. This kind of response has been observed in some bacterial infections (Beattie 2011). However, there are no data for this variable during the dry season for comparative purposes.

Specific leaf weight explains many of the variations in growth between the species and the cultivars (Roderick et al. 1999, Poorter et al. 2009). The value for the variable on leaf one was significantly higher in the affected palms and lower in the healthy and recovered ones (Fig. 2).

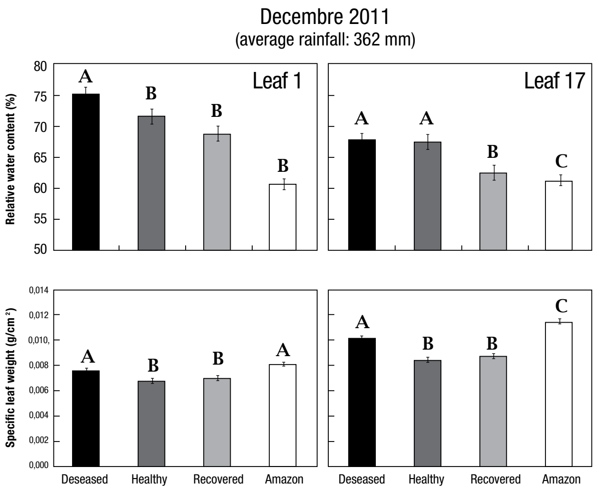

Fig. 2. Relative water content and specific leaf weight in leaves No. 1 and 17 in three categories of palms (*Elaeis guineensis*, variety Deli x Nigeria), according to their response to PC. The initially healthy and recovered palms had 5 years in the field, and the affected ones had 6 years, when data collection began. The OxG Amazon hybrid is tolerant and the plants were younger (2 years in the field), and included as a reference. Southern Pacific of Costa Rica. The multiple comparison of all the pairs of means in the analysis of variance was done using the DGC test. The data are the means of 360 samples. Same letters denote non-significant differences, $P < 0.05$.

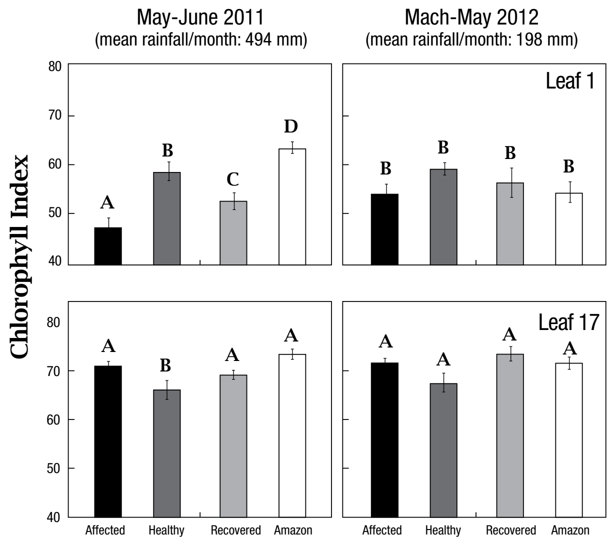

Fig. 3. Chlorophyll index in leaves No. 1 and 17 in three categories of palms (*Elaeis guineensis*, variety Deli x Nigeria) according to their response to PC. The initially healthy palms and the recovered ones had 5 years in the field, and the affected ones had 6 years, at the beginning of data collection. The OxG Amazon hybrid is tolerant and it was younger (2 years in the field), and it is included as a reference. Southern Pacific of Costa Rica. The same palms in each category were measured on both occasions (May-June 2011, average precipitation: 494 mm/month) and (March-May 2012, average precipitation: 198 mm/month); therefore they were in different physiological stages (symptoms or recovery more advanced in the second measurement). Multiple comparison of pairs of means using the DGC test. The data are the means of 195 samples in each season. Palm categories with the same letters denote non-significant differences, $P < 0.05$.

One way of interpreting these results is to assume that the first visible aerial symptoms of PC in reality correspond to the last phases of a disorder that began several months earlier and that at the time of the observations the palm was found in an attempted recovery phase. The data for high stomatic conductance indicate higher photosynthetic rates that allowed the accumulation of larger amounts of photosynthetic products and biomass per unit of leaf area.

Chlorophyll index

No differences were detected in the green color of leaf 17 between categories of plants nor between measurements over time. As expected, the young leaves (No. 1) of the affected palms were less green at the onset of the symptoms. According to the measurements during the ‘dry season’ (March-May 2012, average precipitation: 198 mm/month), the leaves showed a greener color, possibly associated with the recovery process for these plants, since the measurement was taken approximately one year after the appearance of the first symptoms. This response occurred even though the water potential was lower (Fig. 3).

Fluorescence (Fv/Fm)

The optimum value of the Fv/Fm index varies between 0.7 and 0.8 in most of the plants, and changes throughout the day in response to environmental conditions (light, temperature) and in response to different biotic and abiotic stresses during which the Fv/Fm index decreases. In the months of March-April 2012, during the drier period (198 mm/month), this value was higher in leaf No. 1 of the affected plants, apparently indicating that the palms with PC suffered less water stress than plants belonging to other categories, or that there may be mechanisms that tried to prevent water loss. In leaf 17 (without apparent symptoms), this did not occur (Fig. 4).

The favorable Fv/Fm values in adult leaves of palms with PC could be indicating that these do not have the capacity to respond to environmental stimuli that can generate stress during the dry season, such as high radiation and the atmospheric drought. The color and the hydric relations in these leaves (which remained reasonably green and showed lower water potential values) corroborate this idea.

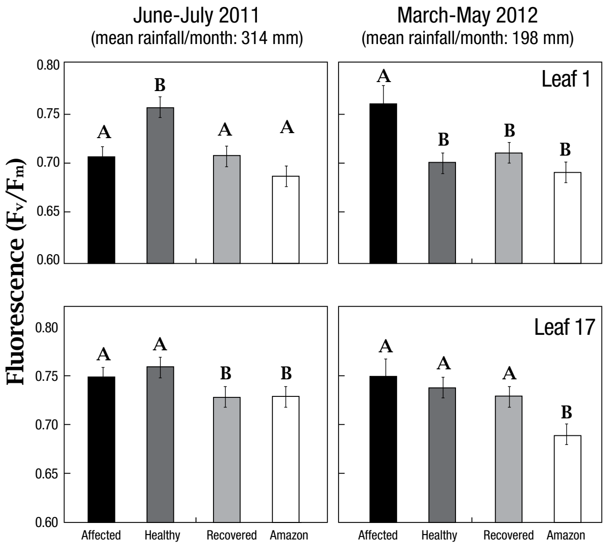

Fig. 4. Variable fluorescence/maximal fluorescence index (Fv/Fm) in leaves No. 1 and 17 in three categories of palms (*Elaeis guineensis*, Deli x Nigeria variety), according to their response to PC. The initially healthy palms and the recovered ones had 5 years in the field, and the diseased ones had 6 years, at the start of data collection. The OxG Amazon hybrid is tolerant and it was younger (2 years in the field), and it is included for reference. June-July 2011: 314 mm/month; March-April 2012: 198 mm/month. Southern Pacific of Costa Rica. The same palms in each category were measured on the two occasions, therefore they were in different physiologic stages (symptoms or recovery more advanced in the second measurement). Multiple comparison of pairs of means using the DGC test. The data are the means of 360 samples in each season. Palm categories with the same letters denote non-significant differences, P < 0.05.

Stomatic conductance, transpiration and temperature

During the second measurement of stomatic conductance (March-April 2012, average precipitation: 198 mm) of the recently opened leaves (one in the phyllotaxy), this value was notoriously higher in the palms that had been showing symptoms at least since April 2011. The transpiration of the leaves in the plants affected by PC was significantly higher and the temperature of the leaves significantly lower (Fig. 5). Similar responses and loss of stomatic control have been seen in coconut trees affected by rooting of the roots associated with potential pathogens present in the soil (Rajagopal et al. 1986).

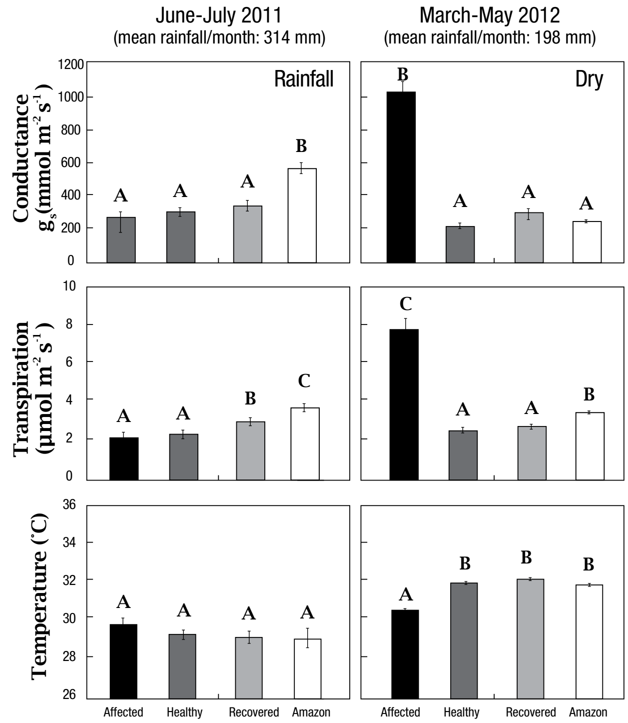

Fig.5. Stomatic conductance, transpiration and temperature in leaves No. 1 and 17 in three categories of palms (*Elaeis guineensis*, variety Deli x Nigeria) according to their response to PC. The initially healthy palms and the recovered ones had 5 years in the field, and the affected ones had 6 years, at the onset of data collection. The OxG Amazon hybrid is tolerant and had 2 years in the field; it is included for reference. The same palms were used to take measurements in the two periods, such that physiological status changed in the period (due to the progress of the symptoms and the process of recovery). June-July 2011: 314 mm/month; March-May 2012: 198 mm/month. Southern Pacific of Costa Rica. Multiple comparison of pairs of means using the DGC test. The data are means of 720 samples in each season. The same letters denote non-significant differences, P < 0.05.

Nutrients in the leaves

The content of most of the elements in the leaf was medium to high, but Fe and Mn were above what is considered normal. The Fe/Mn relation was low (<2:1), indicating that Fe content could be deficient in comparison to that for Mn. The imbalances between Fe and Mn have been associated with an unhealthy appearing root system or 'corchosis' in the roots, which has also been observed in other plants (Vargas 1996, 1999).

The young leaves had higher contents of N, P, K, Zn and Cu and the older leaves had more Ca, Mg, B, Fe and Mn. Nitrogen showed a special behavior in the affected palms, which was higher in the rainy season (July 2011, precipitation: 603 mm) in adult leaves. The chlorophyll index also indicated that the adult leaves were greener than the young ones.

The affected palms had relatively high contents of K, in the rainy season as well as the dry season, probably due to the additional applications of KCl (this was done in an attempt of reducing the severity of the symptoms). Extra fertilizer applications possibly altered the relations between bases and between nitrogen and potassium that could have been present at the beginning.

Despite the above, some trends can be seen as indicating that some ratios between elements could be associated with the appearance of some PC symptoms. For example, during the ‘dry season’ (April 2012, precipitation: 210 mm), intermediate leaves (16-17) of the palms with symptoms had the maximum value observed (3.0) for the N/K relation. It can also be noted that the Mg/K ratio in young leaves as well as ones of intermediate age in the plot with the initially healthy palms (but where palms with symptoms eventually appeared) was consistently higher. In affected palms that had already recovered, this relationship was similar. On the other hand, the Ca/Mg relation was always higher in palms in the process of recovery from the symptoms. Some of these possible imbalances were observed in other studies of PC-affected palms or ones that eventually showed symptoms (Chinchilla and Durán 1999) (Table 2).

Table 2. Content of nutrients in young (1, 2 and 3) and adult (15, 16 and 17) leaves in three categories of palms (*E. guineensis*, variety Deli x Nigeria): healthy, with symptoms, and recovered from PC. The OxG hybrid was younger (two years in the field) and is include for reference only. Each value is the average of the analysis of basal, medial and distal leaflets from three palms for each category of plant

		July 2011 (603 mm, rain)								April 2012 (210 mm, rain)							
		Young				Adults				Young				Adults			
		Affected	Healthy	Recovered	Amazon	Affected	Healthy	Recovered	Amazon	Affected	Healthy	Recovered	Amazon	Affected	Healthy	Recovered	Amazon
(%)	N	2,75	3,01	3,03	3,14	2,83	2,94	2,74	2,87	2,63	2,79	2,51	2,82	2,61	2,68	2,74	2,58
	P	0,17	0,18	0,17	0,21	0,16	0,17	0,16	0,16	0,20	0,19	0,18	0,17	0,14	0,16	0,16	0,15
	K	1,49	1,47	1,34	1,49	1,31	1,23	1,29	1,17	1,79	1,49	1,67	1,50	0,87	1,25	1,27	1,12
	Mg	0,25	0,37	0,27	0,23	0,25	0,31	0,23	0,16	0,21	0,30	0,23	0,27	0,18	0,27	0,24	0,22
	Ca	0,58	0,67	0,79	0,65	0,79	0,84	0,99	0,85	0,46	0,66	0,90	0,52	1,03	0,87	1,11	1,00
(mg/Kg)	B	14	15	13	16	19	18	18	18	25	43	44	29	32	42	37	41
	Zn	18	23	23	25	17	21	23	17	22	20	22	17	14	18	20	17
	Fe	48	50	51	47	64	59	56	63	43	65	56	68	81	73	64	95
	Mn	87	288	115	83	108	363	125	129	61	176	137	99	89	231	158	136
	Cu	7	8	8	11	6	7	6	10	6	8	7	5	5	6	6	5
	S	0,17	0,19	0,19	0,19	0,19	0,18	0,17	0,16	0,16	0,17	0,16	0,18	0,17	0,17	0,18	0,17
	Fe/Mn	0,55	0,18	0,45	0,56	0,61	0,17	0,45	0,50	0,70	0,41	0,44	0,69	0,93	0,35	0,41	0,73
	N/K	1,96	2,29	2,32	2,31	2,21	2,59	2,16	2,65	1,48	2,16	1,96	1,90	3,00	2,35	2,18	2,41
	Ca/Mg	2,26	1,78	2,96	2,84	3,20	2,78	4,24	5,65	2,14	2,17	4,02	1,92	5,71	3,31	4,92	4,71
	Ca/K	0,42	0,52	0,62	0,49	0,63	0,78	0,81	0,81	0,26	0,55	0,70	0,36	1,20	0,87	0,92	0,96
	Mg/K	0,18	0,28	0,21	0,17	0,19	0,27	0,19	0,14	0,12	0,24	0,15	0,18	0,21	0,24	0,19	0,20

Conclusions

The appearance and severity of PC in oil palm cannot be separated from a series of situations that cause stress in the plant due to imbalances in the soil-plant-environment continuum, and that can trigger a morpho-physiological syndrome, which apparently begins primarily with the death of the fine tertiary and quaternary roots. In the particular case of the Southern Pacific of Costa Rica, much stress is created due to the combination of excess water in the soil (high rainfall), soil characteristics, and the related anaerobiosis and low solar radiation during some periods.

High volumetric humidity is associated with the saturation of soils, low availability of oxygen for the roots, and nutritional imbalances (Durán and Ortiz 1995, Peralta et al. 1985). The rainy seasons of 2010 and 2011 were very intense, with months with 800 mm or more of rain; but the 'dry period' of 2012 was abnormally dry.

Apparently the deterioration of the root system of the palms affected by PC and its effects on the crowns was also associated with a problem of absorption and abnormal translocation of nutrients. This resulted in the development of the symptoms of progressive chlorosis in the youngest leaves. These symptoms can be associated with the deficiency of non-mobile elements such as iron and calcium; in the necrosis of the spear leaves and of the leaves in expansion, which receive sub-optimal quantities of essential nutritive elements. The uptake and abnormal transport of some elements can lead to the presence of imbalances between them; particularly between Fe and Mn, Ca, Mg and K, nitrogen and potassium, and possibly others where calcium and boron intervene.

The leaves of the palms affected by PC showed a loss of stomatic control of transpiration and reductions of the water potential, probably due to the absence of chemical or hydric signals that, in healthy palms, come from functional root systems (Davies and Zhang 1991). Indeed, some of the physiological symptoms that characterize the palms affected by PC manifested during the dry season, during which the palms are induced to transpire excessively in proportion to the evaporative demand of the atmosphere and high solar radiation, thereby reducing their water potential.

Physiological predisposition can make the palms susceptible to opportunist microorganisms (Ayres 1974); some of which can live as endophytes of healthy plants (*Pseudomonas, Fusarium, Phytium*) (Porras and Bayman 2011, Zamioudis et al. 2013). *Pseudomonas* sp., can live as an endophyte of plant roots and promote their growth and health (Zamioudis et al. 2013), but they can become pathogenic under conditions of stress, releasing toxins into the transpiration current that inhibits stomatic closure in the leaves (Beattie 2011). Similarly, diverse bacterial pathogens of foliage release 'effectors' on leaf surfaces that interfere with stomatic functioning and impede their closure in response to the infection (Melotto et al. 2008).

The plants with PC in the initial stages can show transitory increases in stomatic conductance, lower foliage temperature, and higher chlorophyll content that initially makes them appear greener. However, in the absence of fine roots capable of absorbing soil water and minerals in sufficient quantity, a hydric, nutritional and energetic imbalance is generated during the dry season, which is overcome by the reserves of water and nutrients in the palm trunk; these reserves meet structural and functional needs, but they are limited by the size of the trunk, such that their depletion in the advanced stages of PC lead to the relatively rapid collapse of the structure and functioning of the palms, which lose the shine on the leaves and their physical and mechanical stability (Rajagopal et al, 1986; Henson and Haniff, 2005).

Several indicators of stress and predisposition to the appearance of a disorder like PC were validated, such as changes in the PxS index, the sex ratio and stomatic behavior. Another indicator, one that is much more labor-intensive to measure, is the periodic evaluation of the abundance, quality and health of the roots (Albertazzi et al. 2005).

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