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Studies on the etiology of the crown disease / spear rot syndrome in oil palm

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ABSTRACT

The crown disease/common spear rot (CD/CSR) syndrome is the most common disorder in young oil palm plantations worldwide. Diseased and healthy plants were compared in their nutrient content, water status and type of soil in which they were growing. Disease progress curves were adjusted to either the monomolecular or Gompertz equations.

The most frequently isolated microorganisms from necrotic lesions on leaves and rachises were species of *Erwinia* spp and *Fusarium* spp. These are probably common inhabitants of the phylloplane. Attempts to reproduce the CSR symptoms through the inoculation of isolated microorganisms normally failed. Typical CSR symptoms were reproduced only once, with at least three isolates of *Erwinia* sp. in 19 months-old nursery palms.

The Gompertz equation was adequate to describe the disease progress curve for several of the most susceptible progenies. However, disease progress tended to follow the monomolecular equation for the more resistant progenies.

Plants with the CD/CSR symptoms usually had higher nutrient contents in their younger leaves than healthy plants. The genotype showed to be the main determinant of susceptibility to the disorder. However, conditions that favor a vigorous growth could make more susceptible the plant by causing abnormal lignification of young tissues and allowing opportunistic microorganisms enter.

INTRODUCTION

The syndrome known as crown disease/common spear rot (CD/CSR) is the most common disorder found in young (1-2 year) oil palm plantations throughout the world. Incidence is normally low (less than 0.5%), but in some susceptible progenies may be up to 5% or more (Turner, 1981; Chinchilla, 1987; Breure and Sebagjo, 1991). Common spear rot and crown disease are normally mentioned as two different disorders, however in Central America they are consistently associated. This work objective was to gather evidence to support the hypothesis that both symptoms have indeed a common cause.

Symptoms of CSR include the development of necrotic lesions on the leaflets and rachises of the elongating spears. Once the young leaves open the lesions stop growing. However, occasionally a soft bad-smelling rot may progress deep into the whorl sometimes causing the plant death. The most striking symptom CD is the bending of young rachises. Accompanying these symptoms, there develop necrotic lesions on the still unfolded leaflets of the spears (Duff, 1963; Turner, 1981). The presence of plants showing CSR symptoms without crown disease is common, however the opposite is rarely seen.

The causes that lead to the presence of this disorder are not clear. It has been assumed that CD is a genetic disorder which means that there is no transmissible agent involved. At least two genes

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may be implicated in these symptoms (De Berchoux and Gascon, 1963; Gai, 1969; Blaak, 1970; Breure and Saebagjo, 1991). So far, the study of the physiological and anatomical causes for the bending of the rachises has received little attention (Heusser, cited by Turner, 1981; Monge et al, unpublished).

There are at least two microorganisms consistently isolated from the necrotic lesions on the rachis and leaflets of plants with either CD or CSR symptoms. These are *Erwinia* spp and *Fusarium* spp. Nevertheless, the attempts to prove the pathogenicity of these microorganisms have not been conclusive (Duff, 1962, 1963; Robertson et al, 1968; Ochoa and Bustamante, 1974; Turner, 1981). Most failures to prove pathogenicity are probably due to the lack of knowledge on factors that predispose to the disease. The role of mineral nutrition and other environmental factors as determinants of the susceptibility to the disorder have not been studied well (Kovachich, 1957; Robertson, 1962; Duff, 1962,1963; Robertson et al, 1968; Turner, 1981; Breure and Sebagjo, 1991) and the results have been contradictory.

Other two objectives of this study were: 1. Reproduce the symptoms of the CD and CSR disorders through the inoculation of microorganisms isolated from infected tissue and the application of several growth regulators. 2. Compare the growth conditions and some physiological aspects of diseased plants.

MATERIALS AND METHODS

Field work was carried out in a commercial oil palm plantation (Cia. Palma Tica) in the South Pacific coast of Costa Rica (8m over the sea level. Mean annual rainfall = 4,118 mm. Dry season from January to March. Max. temperature 31.8°C, min. 21.2°C). The life zone corresponds to a very humid, low tropical forest. Laboratory and greenhouse work was done in the of the University of Costa Rica Plant Pathology laboratory and the laboratory of the Palm Research Program, ASD de Costa Rica /Palma Tica.

Isolation tests

<u>Methodology #1</u>. Leaves on position -1 and -2 of the phyllotaxis, of two-year old infected field plants showing CD/CSR symptoms were cut and superficially disinfected with sodium hypochlorite (0.5%). Leaflet pieces (0.5 x 0.5 cm) from the border of actively growing lesions were again superficially disinfected and put in incubation on standard PDA media. A total of 119 isolates were done.

<u>Methodology #2</u>. Similar to #1, but after the second sterilization groups of three pieces of tissue were placed in sterile test tubes with 2 ml of sterile distilled water and incubated at 30°C for 24h. Petri dishes with nutrient agar (NA) were seeded with the content of a microbiological loop from each tube. A total of 146 isolates were obtained from this methodology.

<u>Methodology #3</u>. Similar to #1, but 40 pieces of tissue (0.5 x 0.5 cm) were macerated in a sterile mortar with 10 ml of sterile water. Nine successive dilutions were done by adding 1 ml of the more concentrated solution to 9 ml of distilled water in test tubes. The content of four loops from each dilution was seeded in Petri dishes with NA. 36 isolates were obtained this way.

Pathogenicity tests

<u>Methodology #1</u>. A solution (pH = 7.06) of macerated infected tissue and distilled water was filtered in cheese cloth and poured (50 ml) in the whorl of eight 18 month-old nursery plants. Half of the plants were injured in the inoculation area with a dissecting needle. A second group

of 11 plants were similarly inoculated, all received injuries and a humid piece of cotton was placed in the inoculation area to keep it wet.

Methodology #2. A suspension of three of the most commonly isolated bacteria (isolates 110-1, 112-2 and 115-1 grown for four days in PDA) were poured (6 ml) into the whorl of 19 month-old nursery plants from a progeny (C9570) know for its susceptibility to CD/CSR. Two of the bacterial isolates were *Erwinia* sp. identified as such in the D-3 differential medium (Kado and Heskel, 1970). A total of 21 plants were inoculated with the *Erwinia* isolates and only three with the unknown isolate. All plants received injures at the base of the youngest leaves (position -1 to -3). A wet piece of towel paper was placed in the whorl after the inoculation, and the area was then covered with aluminum foil to keep it moist.

Typical symptoms of CSR were reproduced as a result of these inoculations, but plants recuperated after one month. The possibility that the previous infections were caused by organisms resident on the phylloplane was evaluated on 14 of these plants. For this purpose, a humid chamber (wet towel paper and aluminum foil) was placed again around the whorl of the plants. Half of the plants were injured with a dissecting needle at the base of the spears. No further inoculation was done on these plants.

Also using progeny C9570, it was attempted to make the plants susceptible by spraying them with glyphosate (100, 500, 2000 and 8000 mg a.i./l) previous to the bacteria inoculation. Three plants were treated with each doses of glyphosate, two inoculated with an Erwinia isolate (112-2) and the other one was kept as control.

Methodology #3. Healthy leaflets from leaf -2 of in two-year old field plants were collected from a large group of progenies varying greatly in susceptibility to CD/CSR. Two plants per progeny were sampled taking six leaflets from each plant. Leaflets were inoculated with one of six isolates (5 bacteria: 110-1, 112-2, 115-1, 127, 136 and a *Fusarium* sp.) directly on three injures made with a dissecting needle. The leaflets were then put in semi-hermetic plastic boxes with a wet paper towel on the bottom.

The procedure was repeated for other five bacterial isolates (3 of them were *Erwinia* sp.: 165-1, R-2 C-2-1 and R-5-2-1), one *Fusarium* sp. isolate (106-1), and a mixture of *Erwinia* sp. (isolates R-5-2-1 and 106-1). A control with no wounds was included in each case.

Methodology #4. Six leaflets on each side of the rachis from a spear in position -2 of a two year-old plants (progeny C9688) were detached and wounded with a dissecting needle (three equidistant injures at 0.5 cm). Leaflets on one side of the rachis were inoculated with one of six bacterial isolates (231, 233, 235, 245, 247, 248) and the opposite leaflets on the rachis were left as controls. All treatments were placed in a humid chambers kept inside a greenhouse. Each isolate was inoculated on three leaflets from different plants.

Methodology #5. Severe transplanting shock was caused on 64 and 24 month-old nursery plants (progeny C9570) by moving them to a greenhouse. Since these were quite old plants, a lot of the roots had grown through the bottom of the polybag and were pruned when they were moved.

Groups of four plants received one of 16 treatments: Inoculation of wounded tissue (needle injures at the base of the spear leaves) with one of seven bacterial isolates (205, 247, 254, 255, 265, 266, 273). Placement of a wet piece of cotton in the whorl (7 treatments) with *Fusarium* sp. (isolate 257) inoculated in a similar way that the bacteria (one treatment). Mixture of a bacterial isolate (205) and *Fusarium* sp. inoculated with and without wounds at the whorl region and putting a wet cotton after inoculation (2 treatments) and with no wounds or the wet cotton (one treatment). Five controls were included: Three treatments with wounds and distilled water with and without a wet cotton in the whorl. Two treatments without wounds and distilled water and the wet chamber, and finally an control with no treatment at all.

Methodology #6. Detached spears (position -1 and -2) from plants of a susceptible progeny (C9688) were superficially disinfected with ethanol 95%. The basal and distal portion of the leaflets were cut off, and the central portion (ca. 20 cm) was inoculated with either a bacteria or a fungus, on the abaxial surface on each side of the central vein. Three drops of a bacterial (10^8 cells ml^{-1}) or fungal (10^6 spores/ml) suspension were placed on the unwounded tissue, near one end of the leaflet piece. On the opposite end, three needle injures were made before the inoculation. A disc of filter paper was placed on top of each inoculation site, which was kept wet for as long observations were made (six days). All leaflets were placed in plastic boxes on top of a wire screen under which a wet sponge was placed. A total of 70 different bacterial and 10 fungal isolates were tested, with six replications (leaflets) for the bacteria and three for the fungi. The procedure was repeated for other 71 bacterial isolates and 14 fungi, but only three leaflets per isolate were inoculate.

Methodology #7. Twenty six bacterial isolates were inoculated on the leaflets of spears at -2 position of 12 month-old nursery plants from progeny C9570. Attempts were made to force a bacterial suspension (0.02-0.03 ml: 10^8 bacteria ml^{-1}) inside the leaflet parenchyma with the help of a hypodermic syringe. This was achieved in only 20 % of the cases. After the inoculation, a humid chamber (wet towel paper and aluminum foil) was placed around the plant whorl. Three plants were inoculated with each bacterial isolate.

One month after this test (which gave negative results), the same plants were inoculated again with another 27 bacterial isolates. This time it was possible to force the suspension in 35% of the cases. Another group of 15 month-old nursery plants was inoculated with 5 fungal isolates (10^6 spores/ml^{-1}) by making wounds on the base of the spears in position -1, -2 and -3. Negative results were again obtained, and one month later three wounded leaflets (spear -3) on these plants were inoculated with eight *Fusarium* isolates. In these tests, three plants were inoculated with each isolate and a wet piece of towel paper was placed on the base of the inoculated spears.

Methodology #8. Two bacterial suspensions (10^8 bacteria ml^{-1}) and a *Fusarium* isolate (6.5 x 10^6 spores ml^{-1}) were inoculated on 14 month-old nursery plants of progeny C9570. Four methods were tried:

a. injection of the bacterial suspension between the two epidermis of some internal leaflets in leaf one
b. same as "a" but using the external leaflets
c. inoculation on 3-6 wounds on both the internal and external leaflets of leaf one
d. same as c
e. on 50 needle wounds made on both the internal and external basal leaflets of spears -1, -2 and -3.

Methodologies "d" and "e" were repeated again on plants of the same progeny, but 18 month-old. All plants were covered with a humid chamber around the inoculation site.

Methodology #9. Three *Fusarium* isolates (H-4: *F. lateritium*; H-353: *F. oxysporum*; H-377: *F. moniliforme* f. sp. *subglutinans*), seven bacterial isolates (B-270, B-339, B-356, B-365, B-369, B-385, B-390), and a mixture of H-377 and B-390 were inoculated on nursery plants of three ages: 92 plants of the progeny C9570 (16 month-old = 69 plants; 18 month-old = 23 plants) and 29 plants (14 month-old) belonging to different related progeny.

Tests with growth regulators

The herbicide glyphosate is known for its inhibitory action of the synthesis of phytoalexins, phenols and lignin by blocking the shikimic acid pathway. This effect could make the plants more susceptible to an infection (Hahlbrock and Grisebach, 1979; Arheim et al, 1980; Duke et al, 1980; Hollander and Arheim, 1980; Lee, 1982; Rubin et al, 1984). The application of indolebutyric acid (IBA) and ethephon to plants causes an unbalance of these growth regulators, and also may interfere with the biosynthesis of lignin (Sequeira, 1973; Aloni, 1980; Pegg, 1981; Misaghi, 1982; Aloni, 1987; Ke and Saltveit, 1988). Other growth regulators (gibberellic acid, benzylaminopurine etc), calcium and nitrogen could also predispose plants to the attack by some microorganisms by interfering with the biosynthesis of lignin (Graham, 1983).

Several of these growth regulators were applied to young oil palms in an attempt to make them more susceptible to CSR and reproduce the rachis bending symptom, which probably occur due to an abnormal lignification of these tissues (Heusser, cited by Turner, 1981; Monge et al, unpublished data).

Three groups of 12 nursery plants (progeny C9570, 19 month-old) received one of three treatments:

a. glyphosate: Round Up (480 g a.i l^{-1}); rates of 100, 500, 2000 and 8000 mg a.i. l^{-1}
b. ethephon: Ethrel (399 g a.i. l^{-1}) at the rates of 100, 250, 500 and 1000 mg a.i l^{-1}
c. indolebutyric acid (reagent quality, dissolved in alcohol 95%) at the rates of 25, 50, 100 and 200 mg a.i. l^{-1}.

The sticker SandovitR^{E} (0.1 ml l^{-1}) was added to all solutions, that were sprayed (50 ml) directly on the whorl of the plants. One month later no symptoms had appeared, so the plants were again sprayed with ethephon and IBA at higher doses: 1000, 2500, 5000, 20000 and 200, 500, 800, 1000 mg a.i. l^{-1} respectively.

Another group of nursery plants (C9570, 14 month-old) were treated with the following substances:

a. 6-benzylaminopurine (6-BAP, 26 mg a.i. l^{-1})
b. ethephon (Ethrel, 239 mg a.i. l^{-1})
c. indolebutyric acid (IBA, 1.3 mg a.i. l^{-1})
d. gibberellic acid (AG3,1.4 mg a.i. l^{-1})
e. calcium chloride bihydrated ($CaCl_2.2H_2O$, 2 g a.i. l^{-1})
f. potassium nitrate (KNO_3, 3 g a.i. l^{-1})
g. glyphosate (Round Up, 576 mg a.i. l^{-1})

h. distilled water a control.

Each treatment was applied to three plants through root absorption or wounds. For the first method, the nursery bag was cut laterally and two primary roots were selected. The distal part of the root was cut and placed inside a plastic bag (15 x 6 cm) with 50 ml of the solution at the chosen concentration. For the second procedure, 20 wounds were made with a dissecting needle at the base of the spears in position 0, -1 and -2 and a piece of cotton was placed in these areas before pouring the solution. Another test consisted in spraying a solution of calcium chloride (5 g a.i l^{-1}) to four plants, and glyphosate (8000 g a.i l^{-1}) to five plants.

Nutritional studies

Spears (position -1 and -2) from healthy and affected (crown disease) 12 month-old nursery plants (progeny, C9570) were collected at the beginning of the rainy season in May. Tissue with necrosis was not included. The rachises and leaflets were cut in small pieces, dried in a convection oven (70°C, 48 h) and ground in a mill. Samples were sent for nutrient analysis to the Institut de Recherches pour les Huiles et Oléagineux (IRHO) in France.

Four weeks later, when the rainy season was already established new leaf samples were taken from three progenies (C9650: very susceptible; C9570: susceptible; C9590: resistant). Samples were leaflets from the middle region of a leaf in position #9 (12 leaflets per frond) and the rachises of leaf 0. Both types of tissue were obtained from healthy and crown diseased infected two-year old field plants. Except for progeny C9590 where only healthy plants could be sampled. Nutritional analysis was done at the IRHO as well. At the sane time soil samples (0-30 cm depth) were taken around each plant (circle) and in the inter-row. Each sample was formed from eight sub-samples and was analyzed at the Centro de Investigaciones Agronómica (CIA), University of Costa Rica

Leaf sampling was repeated again in December, late in the rainy season. Four soil samples (8 sub-samples) were also taken: circle and inter-row of affected and healthy plants. Leaf tissue was sent to the IRHO for analysis, and soil samples to the CIA.

Leaf samples (leaf #9) were also taken from affected palms (CD/CSR) in a commercial lot during August. Each sample came from eight plants. Analysis was done at the Laboratorio de Suelos de la Compañia Costarricense de Café in Costa Rica.

Water status

Water vapor conductivity was determined in healthy and diseased plants (CD/CSR) with an automatic porometer (MK-ll, Delta Morris, England). Ten three-year old field plants (progeny C9650) were selected in each category. Data were taken on the abaxial surface of four leaflets on leaves 9 and 17 on a sunny day in August between 9:30 and 11:00 a.m.

Soil water potential was estimated with several tensiometer placed at a depth of 20 cm in the circle of five healthy and five affected plants. Data were taken every other day between November 24 and December 15.

Disease progress curves

Four experimental plots were selected; two had planted in 1985 (experiment 85-04: 8 progenies and experiment 85-05: 10 progenies), and two in 1987 (experiment 87-06: 7 progenies and experiment 87-10: 6 progenies). These plots were visited every three months quantifying the number of diseased plants and the type of symptoms present in each case. The following information was obtained:

> Incidence = Percentage of plants with symptoms during each visit. Since recurrence of symptoms is a common phenomenon, the accumulated incidence only considers those plants that appear with symptoms for the first time in each date.
>
> CSR = Plants that only showed common spear rot symptoms (no bent fronds) in all the surveys conducted.
>
> CSR/CD = Plants that presented crown disease symptoms combined with common spear rot in at least one evaluation.
>
> CSR+CSR/CD = This is the addition of the previous categories.
>
> Recurrence = Percentage of plants that appear with symptoms in more than one survey.

Disease progress curves for the different symptoms were obtained. Data on incidence was transformed using Gompertz and monomolecular equations in order to estimate disease increase rate (Madden, 1980; Berger, 1981; Park and Lim, 1985).

RESULTS AND DISCUSSION

Symptoms

Two types of lesions were observed on the leaflets of plants with both symptoms CD and CSR:

a. Very extensive wet, soft and bad smelling lesions with well defined margins. The lesions tended to advance preferentially along the margins of the leaflet
b. Lesion frequently localized near the central vein, with a "ring" that marked the beginning of the infection. In this case lesions were not very soft or extensive and had an ammonia smell.

The border was reddish in coloration and not well defined. In both cases, the first symptoms observed were small translucent stains that became circular lesions with a dark spot in the center. In spite of the different lesions appearance the microorganisms isolated from both of them were similar.

Lesions normally progressed to contiguous still unfolded leaflets in the same spear. In a group of affected leaflet the oldest lesion was more extensive and the tissue appeared more disintegrated. The lesion size decreased with the distance from what seemed to be the point where infection started. The youngest lesions were small translucent stains on the leaflet farthest point. This situation may be taken as evidence for the presence of a transmissible agent that caused the necrosis of the tissue, which advanced from one leaflet to the next while they were in close contact in the spear. Several groups of such lesions may appear in one particular spear.

The type of necrotic lesion on the leaflets of plants with CD symptoms was identical to that observed on the leaflets of plants with typical symptoms of CSR (absence of bent rachises).

Furthermore, in many CD cases the first symptom observed was the rotting of leaflets on the emerging spears. A close look of the basal section of the spear of these plants showed a tissue which was unusually soft and flaccid, indicating an abnormal lignification. In mature leaves the rachis could appear bent at any point and not necessarily at the central portion, as sometimes indicated in the literature (Turner, 1981).

There was not a clear relationship between the portion of the rachis that appeared curved and the position of the leaflets that showed necrosis. The leaflets opposite to the bent portion of the rachis were not necessarily the ones that presented necrotic lesions. Also, the relationship between the number and severity of the lesions on the leaflets and the number of rachises that developed curvature, and the severity of this last symptom was not clear either. In a particular plant, some leaves may appeare with only necrotic lesions and others with both lesions and rachis bending. The presence of plants with only bent rachises and without necrotic lesions on the leaflets was a rare event.

Associated arthropods

The arthropods most frequently found associated to diseased tissue were millipedes (Diplopoda), isopods (Isopoda), spiders (Arachnida), ants, cockroaches (Orthoptera), Otitidae larvae (Diptera), fireflies (Lampyridae) and leafhoppers (Cicadellidae). None of these arthropods was consistently associated to any of the symptoms observed.

Isolates

From more than 300 isolates near half of them yielded bacteria. From those, about one fourth were *Erwinia* spp. The more frequently found fungi were: *Fusarium lateritium*, *F. moniliforme* f. sp. *subglutinans*, *F. oxysporum* and *Fusarium* spp. (Table 1). Again, there were no differences in the types of microorganisms isolated from plants with CD and CSR symptoms.

Inoculations

The inoculation methodologies 1 and 2 did not produced any specific symptom on the inoculated plants. When bacteria isolates were inoculated on wounds on detached leaflets a small lesion (usually less than 0.5 cm in length) developed at the inoculation point. The *Fusarium* species inoculated normally caused larger lesions, particularly *F. moniliforme* f. sp. *subglutinans*, but these were also less than 1 cm in length. The "humid chamber" favored the development of lesions when wounds were made. This kind of response was probably due to tissue oxidation, since the lesions were very different from those associated to CSR. No lesion of any type developed on unwounded leaflets.

The other methodologies of inoculation tried (detached tissue or whole plants) also failed to reproduce the characteristic necrotic lesions of plants with CSR symptoms. Nevertheless, the results obtained using the so called methodology # 4 were somehow unexpected. Here, three bacterial isolates were directly inoculated on wounds made in the whorl of 19 month-old nursery plants. These palms were etiolated because nursery bags were close spaced. In 23 out of 24 plants, lesions identical to those found on CSR naturally infected plants were obtained. Some lesions on the spear leaflets were larger than 5 cm in length and in some plants the rotting extended to the rachis base.

Table 1. Type and frequency of microorganisms isolated from tissue with symptoms of common spear rot/crown disease)

Fungi	**%**
Alternaria sp	0.29
Fusarium lateritium	1.45
F. moniliforme f. sp. *subglutinans*	1.16
F. oxysporium	3.78
Fusarium spp.	7.56
White growth	0.87
Gray growth	0.87
Brown growth	1.45
Other fungi	4.94
Bacteria	
Erwinia sp.: Clover-shaped colony	5.23
Erwinia sp.: Fast growing convex colony.	1.16
Erwinia sp.	0.29
Bacilli Gram Fast growing colony, similar to *Erwinia* spp	6.1
Bacilli Gram -: Clover-shaped, similar to *Erwinia* spp	4.94
Bacilli Gram -:	26.16
Bacilli Gram -: . Mixed with Gram +.	0.87
Bacilli Gram -: Mixed with coccus Gram +	12.21
Cocos Gram -: -*Coccus Gram*.	9.88
Colonies not characterized	10.76

Since more than one isolate was used, and all symptoms observed were similar, it can be concluded that this type of response can be obtained with different microorganisms. Bacteria isolated from the inoculated plants were similar to those inoculated and some belonged to the genus *Erwinia*. However, there is also the possibility that infection was caused by some resident microorganisms on the phylloplane, which behaved as a opportunistic pathogen. This hypothesis was tested by making wounds on the tissue and placing the "humid chamber" previously used around the whorl, but skipping the inoculation with external microorganisms. The results were negative. Whatever it was the factor that made the plants susceptible to the first inoculation remains unknown.

Negative results were obtained with stressed plants in the greenhouse (methodology 5), as well as with the use of glyphosate prior to the inoculation with isolated microorganisms. The leaf bending symptom associated with crown disease was not reproduced either.

Growth regulators

Typical symptoms of CD or CSR could not be reproduced with any of the chemical substances applied. However, when glyphosate was applied to 14 month-old nursery plants (576 mg a.i. l^{-1}) it caused the formation of rounded lesions on the leaflets and rachises. The same type of response was obtained regardless of the type of application: root absorption, spraying on the foliage or on the base of the spears after wounding. One of the treated plants showed one spear bent near its base.

The application of glyphosate on seven month-old field palms (8,000 mg a.i. l^{-1}) caused the bending of some young rachises (position +1 to +3) in 25 % of the treated plants. When a fertilization (33-0-0: 750 g $plant^{-1}$) was followed after 15 days by the application of glyphosate (8,000 mg a.i. l^{-1}) on 13 month-old field palms, all treated plants showed at least one bent spear two weeks later. The basal portion of the rachis was flaccid, very similar to what is observed in plants with crown disease. Many plants also developed a wet and bad smelling rot in the whorl. On the leaflets, the lesions where rather dry localized and with a chlorotic halo. The most severely affected plants recuperated through the production of several verticils of short and deformed leaves. This leaf malformation was very similar to that observed when oil palm recovers from a severe CSR attack.

Nutritional analysis

There were not important differences in soil fertility between healthy and diseased plants. Some differences found in the December soil sampling seem not to be relevant (Table 2). However, it was very clear that diseased palms (CD/CSR) had a higher leaf nutrient content compared to healthy neighboring plants (Tables 3-5). In general, the elements that frequently reached a high concentration in the leaflets and rachises of affected palms were Mn, N, Mg, K, Ca, Cl and B. No differences were apparent among progenies.

Several authors have reported an abnormal accumulation of nutrients in the leaves of coconut palms affected by Cadang-Cadang and Root Wilt diseases. This nutrient accumulation, particularly in the late stages of the disease, could be caused by a reduction in total leaf biomass and reduced nut yields (Cecil et al, 1991).

A nutritional sink effect in the area of the lesion may be caused by some pathogens (Livne and Daly, 1966) but this seems not to be the case with the CD/CSR syndrome. The authors suspect that the high concentration of nutrients in the affected tissue could well be part of the cause for the disorder. Other pieces of evidence so far accumulated indicate that more actively growing plants may be more susceptible to the CD/CSR disorder than stressed plants (Monge y Chinchilla, 1992). Active growth implies a high metabolic activity, and the absorption and transport of metabolites to the young growing tissues (Barceló et al, 1983).

Field observations also indicate that an increase in disease incidence frequently follows nitrogen fertilization in young plants. The fertilization would trigger the mechanism that leaded to CD/CSR. Nitrogen has been involved in increasing susceptibility to many diseases (Graham, 1983). It is also known that most plants with excessively high levels of this element present poor tissue lignification, which is probably due to the use of nitrogen to synthesize primarily amino acids and proteins, and not phenols and lignin (Graham, 1983).

Table 2. Chemical characteristics of the soil where diseased (common spear rot\crown disease), and healthy plants were growing, Costa Rica

	Sep-89		Dec-89				Aug-90	
	Diseased*		Healthty		Diseased		Healthy	Diseased
	I**	C	I	C	I	C	C	C
pH (w	5	5	5.4	5.1	5.6	5.4	6.9	6.4
P (mgl)	12	13	14	6	5	6	10	14
Ca cmol\l)	34.8	38.1	34.4	33.5	40.1	34.1	19.3	17.9
Mg (cmol\l)	5.1	5.5	6.3	5.8	6.6	5.3	2.4	2.5
K (cmol\l)	0.25	0.25	0.42	0.36	0.36	0.23	0.44	0.48
Acidy exchan-geable (cmol\l)	2.9	2.9	1.9	2.1	0.6	0.5	0.1	0.1
Fe (mg\l)	132	131	139	130	84	94	55	65
Cu (mg\l)	64	91	143	182	104	89	27	66
Zn (mg\l)	6	11	12	11	10	8	1	3
Mn (mg\l)	208	267	228	227	356	283	24	47
Sum of cations (cmol\l)	40.2	43.8	41.1	39.7	47.1	39.6	22.1	20.9
CICE (cmol\l)	43	46.8	43	41.8	47.7	40.1	22.2	21
Acid saturation (%)	6.74	6.2	4.42	5.03	1.26	1.25	0.45	0.48
Ca/Mg	6.8	6.9	5.5	5.8	6.1	6.4	8.2	7.2
Ca/K	139.2	152.4	81.9	93.1	111.4	148.3	43.8	37.3
Mg/K	20.4	22	15	16.1	18.3	23	5.3	5.2
(Ca+Mg)/K	159.6	174.4	96.9	109.2	129.7	171.3	49.2	42.5

*. Diseased= sample taken within the palm circle; Healthy= sample from the circle of healthy palms).

**. I= sample from the interrow; C= sample from the palm circle).

Other elements like Ca, Mn, B, Cu, Mg, Fe and Zn, also take part during the synthesis of lignin (Grahan, 1983; Lipetz, 1962). It is also clear that symptoms of rachis bending characteristic of palms with the crown disease are associated to an abnormal tissue lignification during rachis elongation (Heusser, cited by Turner, 1983; Monge *et al,* in preparation).

Water status

Diseased plants tend to have their stomata slightly closer than healthy neighbor palms (Table 6). Furthermore, there were more palms with symptoms of CSR in a soil with a high water potential than with less water availability. Some field observations indicate that the CD/CSR disorder tend to be common in imperfectly drained soils. Soil anaerobiosis normally causes an increase in the level of endogenous auxins and abcisic acid, and a decrease of gibberellic acid and cytokinins in the xylem, and a high production of ethylene (Bradford and Yang, 1981). An unbalance in the content of these substances in the plant may interfere with the xylem differentiation process and with the normal pattern of lignin deposition in the tissues (Roberts, 1969).

Table 3. Nutrient content in leaf Nº 9 of healthy and diseased (common spear rot\crown disease) commercial oil palms planted in 1989)

Element	Healthy palms	Diseased palms
N(%)	2.46	2.63
P (%)	0.17	0.18
K (%)	1.24	1.29
Ca (%)	0.67	0.69
Mg (%)	0.22	0.27
B (ug/g)	11	18
Fe (ug/g)	86	91
Cu (ug/g)	9	9
Zn (ug/g)	22	18
Mn (ug/g)	57	90

1. Sampling done in August, 1990.

Table 4. Rachis nutrient content in leaf zero healthy and diseased (common spear rot\crown disease) oil palms planted in August, 1987; Coto, Costa Rica)

	Percent							**ug/g**					
	N	**P**	**K**	**Ca**	**Mg**	**Cl**	**S**	**B**	**Fe**	**Cu**	**Zn**	**Mn**	**Al**
May, 1989[1]													
Healthy	0.583	0.202	1.948	0.288	0.217	0.8	0.075	7.5	38.7	12.9	10.3	10.7	19.7
Diseased	1.238	0.347	2.92	0.794	0.509	1.597	0.205	0.3	52.2	19.7	24.8	20.4	27.9
September, 1989													
Healthy													
C9650[2]	0.595	0.154	1.194	0.33	0.163	0.06	0.074	7.9	61.3	9.6	10.5	48.4	-
C9590	0.445	0.135	1.405	0.217	0.129	0.054	0.049	7.4	86.5	8.1	7.6	38.8	-
Diseased													
C9650	0.887	0.136	1.417	0.408	0.206	0.111	0.073	9.1	71.6	8.9	11.8	67.7	-
December, 1989													
Healthy													
C9650	0.604	0.147	1.248	0.331	0.164	0.08	0.056	8.2	25.9	9.5	8.3	63.2	17.4
C9590	0.599	0.136	1.902	0.232	0.142	0.06	0.056	8	39.2	9.5	10.1	58.4	25
Rachis with no symp-toms*	0.793	0.124	1.788	0.448	0.198	0.222	0.05	8.6	32.6	9.2	11.2	79	10.7
Rachis with symptoms*	1.155	0.157	1.92	0.195	0.347	0.286	0.077	8.7	58.8	11.3	15.7	75.6	43

1. May= beginning of rainy season; September= rainy period; December= end of rainy season. 2. C9650= susceptible. progeny; C9590= resistant progeny. Diseased C9650

Table 5. Leaf nutrient content in leaf Nº 9 of healthy and diseased (common spear rot\crown disease), oil palms planted in August, 1987; Coto, Costa Rica)

	Percent							ug/g					
	N	**P**	**K**	**Ca**	**Mg**	**Cl**	**S**	**B**	**Fe**	**Cu**	**Zn**	**Mn**	**Al**
September, 1989 (wet season)													
Healthy palm													
C96501	2.66	0.168	1.234	0.515	0.316	0.071	0.182	8.3	68.7	6.6	13.5	204.1	-
C9570	2.844	0.188	1.392	0.565	0.329	0.057	0.191	9.7	65.7	9.1	14.9	168.7	-
C9590	2.764	0.171	1.239	0.565	0.36	0.065	0.191	9.3	52.8	7.2	14.2	187.1	-
Recovered palm													
C9570	2.994	0.188	1.248	0.636	0.327	0.065	0.195	9.4	60.2	6.9	12.8	174.6	-
Diseased palm													
C9650	3.251	0.192	1.171	0.528	0.272	0.092	0.225	8.6	72.5	7.7	17.5	238.7	-
	2.993	0.179	1.077	0.609	0.346	0.061 0.198	8.7	60	6.8	12.2	183	-	
December, 1989 (end of rainy season)													
Healthy palm													
C9650	2.721	0.177	1.496	0.471	0.279	0.148	0.183	9.6	63.2	9.5	17.5	247.1	25
C9570	3.046	0.198	1.469	0.634	0.349	0.085	0.2	9	70.8	11.2	18.5	259.1	23.6
C9590	2.926	0.189	1.464	0.542	0.367	0.098	0.198	9.1	78	9.8	20.8	263.3	32
Recovered palm													
C9570	3.076	0.194	1.368	0.673	0.347	0.069	0.205	8.6	77	10.3	18.4	260.1	27.2
Diseased palm													
C9650	3.15	0.2	1.28	0.546	0.345	0.145	0.22	8.6	70.7	9.3	18.3	269	25
C9570	2.957	0.196	1.465	0.609	0.289	0.08	0.203	10.2	60	9.8	19.5	235.4	25

1. C9650= very susceptible progeny; C9570= susceptible progeny; C9590= resistant progeny)

Table 6. Stomatal resistance in healthy and diseased (common spear rot\crown disease) oil palms)

(condition)	**Stomatal resistance**		
	leaf position	**mean**	**Standard deviation**
Healthy)	9	104.4	13.1
	17	163.5	41.3
Diseased	9	119.0	28.9
	17	171.8	72.2

1. Data taken between 9:30 and 11:00 a.m, August 31, 1990. Stomatal resistance in sec\cm; each number is the mean from 10 plants

Disease progress in time

The accumulated incidence of CD, CSR and CD/CSR varied in each of the four experiments evaluated (plantings of 1985 and 1987) and seemed to depend primarily on the genotype planted (Table 7 and Table 8). Differences among progenies were found in the highest level of incidence reached, rate of disease increase, and types of symptoms (Fig. 1 and Fig. 2). Unfortunately, only two of the progenies studied appeared in two experiments making impossible to evaluate the environmental effect of the environment on the incidence and type of predominant symptom. Nevertheless, incidence in these two progenies (C9208 and C9236) varied greatly between experiments. Other observations by the second author indicate that disease incidence can be very different in one particular genotype planted in different areas. Breure and Sebagjo (1991) and Turner (1981) also found a strong effect of the environment on the presence and incidence of the disease.

Table 7. Variables of the Gompertz equation for the disease progress curves of common spear rot / crown disease in several oil palm progenies

Progeny	Type of symptom	Gompertz Model Components² Variables				
		Yo	B	A	r	R
C9198	PCF (CSR)	0.013	4.343	0.227	0.32	0.98**
	PCF\AF	0.027	3.612	0.04	0.7	0.61*
	PCF+PCF\AF (CSR+CSR\CD)	0.04	3.219	0.24	0.28	0.98**
C9208	PCF\AF	0.013	4.343	0.04	0.09	0.74**
(Exp. 85-04)[3]	PCF+PCF\AF	0.013	4.343	0.093	0.09	0.80**
C9208	PCF\AF	0.008	4.828	0.025	0.12	0.68**
(Exp. 85-05)	PCF+PCF\AF	0.008	4.828	0.117	0.09	0.78**
C9210	PCF	0.006	5.116	0.118	0.12	0.97**
	PCF\AF	0.006	5.116	0.024	0.16	0.81**
	PCF+PCF\AF	0.006	5.116	0.13	0.11	0.97**
C9650	PCF	0.012	4.423	0.185	0.23	0.99**
	PCF\AF	0.049	3.016	0.333	0.18	0.97**
	PCF+PCF\AF	0.062	2.781	0.333	0.23	0.95**
C9688	PCF	0.014	4.269	0.1	0.42	0.97**
	PCF\AF	0.071	2.645	0.56	0.19	0.98**
	PCF+PCF\AF	0.071	2.645	0.57	0.19	0.98**

1. CSR= common spear rot (no bent rachises CSR\CD= common spear rot associated to crown disease (bent rachises). 2. Yo= Gompertz; A= Yo= initial amount of disease; B= constant; A= asymptote; r= rate of disease increase). 3. Same progeny planted in two different. *: P= 0.05; **: P= 0.01experiments).

The predominant symptom on progenies planted in 1985 was that of common spear rot, and on those planted in 1987 was the combination of crown disease and CSR (Table 7). The presence of plants with rachises bent without apparent necrosis of leaflets was a very rare event.

Table 8. Recurrence of symptoms of common spear rot\crown disease in several oil palm progenies; Coto, Costa Rica)

Progeny	Type of symptoms[2]	Times symptoms recurrent							% palms with recurrent symptoms	
		0	1	2	3	4	5	6/more		
C9198	PCF (CSR)	41.2	29.4	17.6	5.9	0	0	5.9	58.8	(n=17)[3]
PCF\AF	(CSR\CD)	44.4	27.8	16.7	0	5.5	0	5.6	55.6	(n=18)
C9199	PCF	50	25	0	12.5	12.5	0	0	50	(n=8)
	PCF\AF	50	25	0	12.5	0	0	12.5	50	(n=8)
C9205	PCF	87.5	12.5	0	0	0	0	0	12.5	(n=8)
	PCF\AF	87.5	12.5	0	0	0	0	0	12.5	(n=8)
9206	PCF	54.5	9.1	18.2	9.1	0	0	9.1	45.5	(n=11)
	PCF\AF	53.8	15.4	15.4	0	7.7	0	7.7	46.2	(n=13)
C9208	PCF	100	0	0	0	0	0	0	0	(n=4)
(Exp. 85-04)[4]	PCF\AF	100	0	0	0	0	0	0	0	(n=7)
C9208	PCF	63.6	36.4	0	0	0	0	0	36.4	(n=11)
(Exp. 85-05)	PCF\AF	71.4	28.6	0	0	0	0	0	28.6	(n=14)
C9210	PCF	45	40	5	5	0	5	0	55	(n=20)
	PCF\AF	50	27.3	9.1	4.6	4.5	4.5	0	50	(n=22)
C9226	PCF	40	50	10	0	0	0	0	60	(n=10)
	PCF\AF	60	20	13.3	6.7	0	0	0	40	(n=15)
C9229	PCF	100	0	0	0	0	0	0	0	(n=6)
	PCF\AF	75	25	0	0	0	0	0	25	(n=8)
C9234	PCF	83.4	8.3	0	0	0	0	8.3	16.6	(n=12)
	PCF\AF	75	16.7	0	0	0	0	8.3	25	(n=12)
C9246	PCF	88.9	11.1	0	0	0	0	0	11.1	(n=9)
	PCF\AF	64.7	17.7	17.6	0	0	0	0	35.3	(n=17)
C9570	PCF	85.7	14.3	0	0	0	0	0	14.3	(n=7)
	PCF\AF	76.9	15.4	7.7	0	0	0	0	23.1	(n=13)
C9650	PCF	80	6.7	13.3	0	0	0	0	20	(n=15)
	PCF\AF	14.8	3.7	3.7	26	11.1	14.8	25.9	85.2	(n=27)
C9688	PCF	100	0	0	0	0	0	0	0	(n=7)
	PCF\AF	30	12.5	12.5	7.5	20	10	7.5	70	(n=40)
C9721	PCF	88.9	11.1	0	0	0	0	0	11.1	(n=9)
	PCF\AF	77.8	22.2	0	0	0	0	0	22.2	(n=18)

1. Progenies were evaluated every three months during a period of 27 months. 2. CSR= common spear rot (no bent rachises); CD= crown disease. 3. Number of plants with symptoms in parenthesis. 4. Same progeny in two different experiments

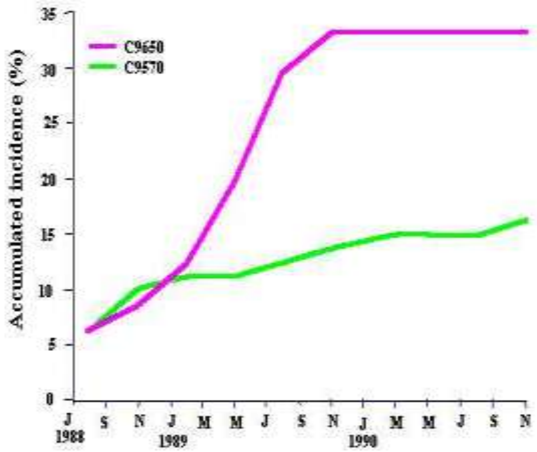

Fig. 1. Accumulated incidence of common spear rot / crown disease in two oil palm progenies field planted in August, 1987

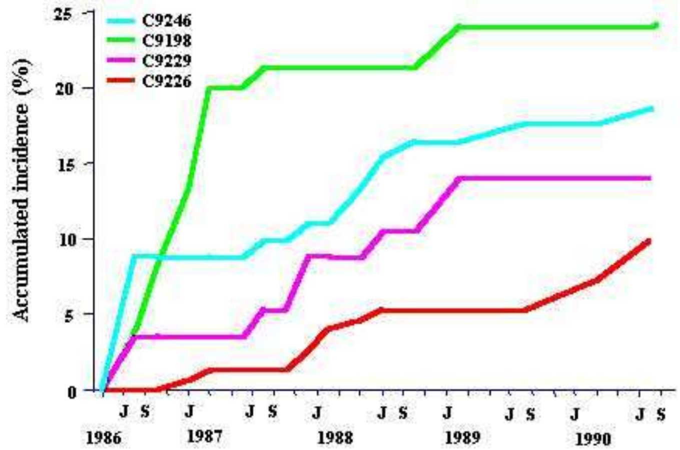

Fig. 2. Accumulated incidence of common spear rot / crown disease in four oil palm progenies field planted in May, 1985.

The highest increase in disease incidence (CD/CSR) was observed after 13-16 month from field transplanting in most progenies, and this peak normally coincided with the beginning of the rainy season, and frequently occurred after the plots were fertilized. After this peak, there were others (at least two) of smaller magnitude that commonly coincided with the end of the present rainy season and the beginning of the following. However, the relationship between climatic data and disease incidence was not always apparent. Some climatic factors could trigger the reaction of susceptibility in the plant but, after the onset of the attack, this seemed to continue with apparent independence of the climatic factors. Disease severity was more affected by climate, and it was normally higher during the rainiest spells of the year. This is probably due to more favorable conditions for secondary microorganisms to gain access to the affected tissue. The situation is probably more complicated than this, since the time of reaction of the different progenies to these alleged predisposing factors is probably not the same.

The leaf emission rate is very sensitive to changing conditions in the environment. A higher leaf emission rate was related in one experiment to an increase in disease incidence (Monge and Chinchilla, 1992). A low rate of lignin deposition in a fast elongating rachis, may favor the attack of the many opportunistic microorganisms inhabiting the phylloplane, such as *Erwinia* spp and *Fusarium* spp.

The association between crown disease and the so called common spear rot in Central America was clear; the type of necrotic lesions on the leaves for both disorders could not be visually differentiated, and the microorganisms isolated were also similar. Both types of symptoms are also commonly present in the same plant, and either symptom may precede a future attack of the other disorder several month later. However, the percentage of plants with both symptoms at any moment depends on the genotype, and the time of the year when a survey is done. There were also differences among genotypes in the percentage of plants with recurrence of symptoms (Table 8). The more susceptible progenies were also those that had a higher percentage of plants with recurrent symptoms; the progeny C9650 presented at least six different attacks during the first three years of observations.

Disease progress curves for the different genotypes do not always follow a pattern that can be identified as associated to the presence of a transmissible agent. However, a sigmoid curve was obtained for some progenies (Fig. 1). In general, a good fit to the Gompertz equation was obtained when only plants with the CSR disease (or this symptom combined with crown disease) were considered. When only the variable CD/CSR was considered, part of the original fit was lost (lower R value) (Table 7). This may indicate that there exists the possibility that the inoculum potential of the microorganisms that cause rotting of tissues might increase in some areas of the plantation. The presence of definite foci of the disorder in both the nursery and the field is frequently observed.

CONCLUSIONS

Two types of necrotic lesions were observed and described on the leaflets of plants with symptoms of common spear rot. Despite the differences in appearance, the microorganisms isolated from both were similar. The necrotic lesions on fronds of plants with the crown disease were identical to those described on plants with common spear rot. It was noted on plants with crown disease, that one or several fronds showed both symptoms of tissue rotting and rachis bending, but other fronds only had evidence of rotting with no deformed rachises. Furthermore, one particular plant that overcame an attack, and appeared as healthy for some time, could present either symptom (CD, CSR or a combination of both) in a recurrent attack. The predominant symptom in most progenies evaluated was that of rotting on leaflets and sometimes on the base of the young spears. If both symptoms of CD and CSR correspond to manifestations of the same disorder, then the bending of the rachises was a symptom that could or not develop on some plants. However, the "escape" of the opportunistic microorganisms that caused the rotting of the young tissues occurred only in a very low percentage of the affected plants.

It was not possible to reproduce consistently the symptoms of rotting on the leaflets associated to the common spear rot disease. A lot of microorganisms were isolated from diseased palms and inoculated on healthy tissue. In only one opportunity, symptoms identical to those found on naturally infected plants in the field, were obtained through the inoculation of three bacterial isolates. Two of these isolates were *Erwinia* sp. Most frequently isolated organisms from diseased tissue were several species of *Fusarium* (*F. lateritium*, *F. moniliforme* f. sp. *subglutinans*, *F. oxysporum* and *Fusarium* spp) and bacteria (about one forth were *Erwinia* spp).

It was evident that some microorganisms isolated from diseased tissue (particularly *Erwinia* sp.), could reproduce the symptoms of rotting on the leaflets, which were associated to the common spear rot disease. The results obtained by Duff (1962, 1963), and those from one of our inoculations proved it. The common failure to consistently reproduce the symptoms probably lays in the lack of knowledge of the several factors that predispose the susceptible palm to infection. Future research on this disease must identify these factors.

The flaccidity at the base of the spear is characteristic of palms with crown disease. This has been shown is due to a abnormal lignification of these tissues. The final result of the lack of mechanical support at this point is the breakage of the spear near its basal section. Many opportunistic microorganisms that invade this area cause rotting of tissues and facilitate the process. However, it is also common that the spear does not break, but continued its growth, and due to its own weight, it bends as it elongates. When lignification is eventually completed, it has as a final result a mature bent frond. A high leaf emission rate in an actively growing palm could be an indication that conditions are right for the onset of an attack of the common spear rot/crown disease.

Plants with crown disease/common spear rot, frequently had higher concentrations of mineral nutrients in their tissues (leaflet and rachis) than neighboring healthy palms. Mn, N, Mg, K, Ca, Cl and B were particularly high in affected palms. An unbalance of some of these nutrients could affect the normal pattern of lignification of the young elongating tissues, such as the rachises. It has been shown for many diseases that, when high doses of N are applied, the tissue becomes more succulent and susceptible to the attack by some opportunistic microorganisms.

A tendency for diseased plants to be grouped in an area with high soil water potential was observed. Diseased plants had a higher stomatic resistance than healthy ones. The reasons by which an imperfectly drained soil could predispose the plants to the disease are not known. The role of other environmental conditions as predisposing factors could not be determined in this study. In general, disease incidence and particularly severity tended to increase early and late in the rainy season. The genotype effect was fairly clear. This seems to determine:

a. the initial level of the disease
b. the highest incidence reached
c. the predominant symptom (tissue rotting with or without bending of fronds)
d. percentage of plants with recurrent infections
e. rate of disease increase over time

The Gompertz equation was adequate to describe the disease progress curves for many of the progenies tested, in particular the most susceptible ones. This could be taken as an indication of the presence of a transmissible agent. However, fitting was poor for other progenies, particularly those considered as fairly resistant. In these situations, the monomolecular model fit better fit.

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