REVIEW PAPER

Drought Tolerance in Oil Palm (*Elaeis guineensis* Jacq.)

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In tropical regions, rainfall /water is one of the main limiting factors for growing oil palm or at least for obtaining higher yields. The best areas for growing oil palm have well-distributed rainfall throughout the year. Typical monthly rainfall associated with the best yields is around 150 mm (Hemptinne and Ferwerda, 1961). Despite its origin as a species of wet soils on riverbanks, the oil palm is a drought tolerant crop, surviving in parts of West Africa with a dry season of several months. However, in the most severe dry seasons, death, particularly of young palms may occur. In less severe climates, the effect of drought on bunch yield may be large.

In Benin, where palm death in the dry season is common, tolerance is being equated with survival (Houssou *et al.*, 1989) but in less severe environments, a more useful definition would be the ratio of yield under drought to yield without drought. Though oil palm is being grown in India under irrigated conditions, the palms are often subjected to harsh environments *viz.*, temperatures go as high as 40-45°C and relative humidity as low as 15-20% during the summer months, creating atmospheric drought. Under these conditions, it is imperative that a thorough knowledge of the understanding of the basic physiological processes, when the palms are subjected to drought assumes paramount importance.

Leaf characters associated with drought tolerance

Some very well known indicators of water deficit in oil palm are the accumulation of unopened leaves (spears), bending and breakage of lower leaves that yellow and eventually become desiccated, and bunch failure (Umaña and Chinchilla, 1989). Villalobos and Rodriguez (1998) have reported that the accumulation of unopened leaves (spears) was a symptom consistently associated with water deficit. As water stress becomes more severe, yellowing of leaves developed and some necrotic zones appeared at the tips of the leaflets. Eventually, some of the lower leaves dried out and the rachis would bend or break.

Luibis et al. (1993) also described the effect of drought on the growth of the palms and have divided into five stages. During the first stage i.e., when the water deficit is less than 200 mm/year, the palms do not show any serious problem. The second stage occurs when the water deficit is 200-300 mm/year. The symptoms like sticking of the frond and immature leaves together and may not open. Also the old fronds become defective. The third stage occurs when the water deficit is 300-400 mm/day and the common symptoms are the number of sticked and unopened leaves increases to 4-5 and the number of defective old fronds will be seen in 1-1.5 spirals and fronds become dry. Subsequently when the water deficit increases to 500 mm/day, the young fronds will not open and leaf bud cracks, becomes defective and breaks.

Maillard et al. (1974) measured a drought sensibility index (SI), which was a numerical assessment of the drought effects recorded in a population or progeny with a formula: $SI = (10M + 5S_{o})$ + $3S_2$ +2 S_1)/N, Where N is total number of palms, M is number of dead palms, ${\rm S}_{\rm s}$ is palms showing an accumulation of unopened spears, S₂ is palms with four to six leaves broken or collapsed and S, is palms with all the leaves withered. The progenies obtained from the Angola dura population (1.8 spears/palm) and the Tanzania teneras (1.7 spears/palm) showed fewer spears accumulated during the dry season. Those progenies descending from the Deli dura lines, particularly when combined with AVROS, Ekona and Calabar parents (2.5-2.8 spears/palm) showed more spears accumulating. The Deli origin showed more tolerance when crossed with palms from the Tanzania, Yangambi and La Mé populations.

Villalobos and Rodriguez (1998) have indicated that the mean number of dried lower leaves varied between progenies from 1 to 21. Those crosses of Bamenda and Angola origins, as well palms from the wild Malawi population showed fewer desiccated leaves (4-7.2/palm). Descendants from the Deli dura lines and Tanzania (dura) had more bent and dried leaves (11-15.5). Differences were not so marked between parent lines and the Mobai source (6.4 dry leaves). Asemoto *et al.* (1996) has screened oil palm genotypes in the nursery for stress tolerance using polyethylene Gycol 6000 and reported significant differences in leaf area and leaf elongation.

Root system and drought tolerance

Observations on the root system of several oil palm families showed that tolerant crosses have a better-developed root system than susceptible crosses. In effect, for an equivalent yield, the cross that can withstand drought is that with the densest root system. Better soil penetration by the roots facilitates water and nutrient uptake, making the plant better able to withstand water stress. However it is important to bear in mind that root density is not the only parameters to be taken into account, since yields vary considerably between different resistant and moderately resistant families with comparable root densities (1.1 t/ha for L430T X L404D to 1.8 t/ha for L13T X D8D). However tolerant families manage water reserves more economically, due to better water supply through a more developed root system and to reduced water losses via more efficient stomatal regulation. In the event of the stress, these characteristics make it possible to maintain high turgidity, which leads to better preservation of tissue turgidity and metabolic functioning.

Maillard *et al.* (1974) tried to develop methods for measuring drought tolerance in younger palms and they have looked at root growth of seedlings under high osmotic pressure using polyethylene glycol and tolerance to high temperature. But the agreements between these two methods were not very positive. Cornaire *et al.* (1989) found that progenies with better root development tended to have greater drought resistance. Some of the morphological and physiological characteristics associated with better tolerance to water deficit are large stem volume (water storage), an extensive radical system, and very efficient stomatic control (Maillard *et al.*, 1974; Villalobos *et al.*, 1991, 1992).

Plant water status and drought tolerance

Villalobos *et al.* (1991) had studied water status of oil palm in response to drought in Costa Rica and found that during the dry season, non-irrigated palms which were 11 or 17 years old showed leaf water potentials and relative water contents similar to or greater than those in irrigated palms. They also observed a negative correlation between stomatal conductivity and leaf water potential measured at midday in adult palms, which is unusual in cultivated plants and indicates a strong stomatal control of leaf water status. Young palms at 10 months after planting were unable to maintain a high leaf water status, possibly due to the absence of a voluminous stem and extensive root system. In young palms subjected to 75 days of drought, the relative water content and leaf water potential at midday were lower than in those with a good water supply.

An analysis of the leaf tissue water retention in adult trees has shown that these tissues possessed high apoplastic volume, but did not provide a classification that tallied with drought tolerance of different families. A study of the relationship between water potential and relative water content failed to reveal any differences between susceptible and resistant families, which suggest that the osmoregulation mechanism is common to all varieties. Similarly, an explanation of the pressure/volume curve showed that the oil palm leaflet tissue characteristics differ significantly from those of seedlings and that neither set of characteristics enables classification of families according to their drought tolerance. However it did show that during water stress, osmotic adjustment mechanisms come into play in all the families. In effect, tissue plasmolysis occurs at lower potentials when plants are under stress.

Stomatal regulation and drought tolerance

Cornaire et al. (1989) considered stomatal opening, leaf water potential and membrane breakdown as possible selection criteria for drought tolerance in oil palm. Reduced transpiration due to stomatal closure in response to water deficit well before wilting interferes with photosynthesis, and hence, drought resistance mechanisms based on stomatal sensitivity and reduced transpiration are generally opposed to the maintenance of a higher yield potential. Stomatal activity per se is an imperfect criterion of resistance, unless it is related to both carbon fixation and transpiration under stress. Oil palm stomatal regulation is particularly delicate and enables the plant to minimize water losses in the event of water stress. However tolerant crosses regulate losses more effectively than susceptible crosses, leading to a greater reduction in stomatal opening during the dry season. At the seedling stage, there are no differences between families as regard to stomatal opening and it is not therefore possible to predict drought tolerance or susceptibility of the same adult material in the field.

K. Suresh and R.K. Mathur

Carvalho (1991) showed that the leaf tissues in oil palm could withstand to major falls in water potential with no proportional effects on their relative water contents. Rees (1990) have reported the mid day closure of stomata in oil palm occurs only during the later half of the dry season when the soil moisture is low and air temperature is high. Cornaire et al. (1989) found that a low yielding palm but drought tolerant cross had fewer open stomata, higher leaf water potential and less membrane damage under drought than high yielding but susceptible crosses. Adiahossou et al. (1984) studied correlations between stomatal resistances of oil palm cultivars and drought tolerance at Benin. Leaf resistance (as a measure of stomatal opening) following suspension of watering differed among the lines, particularly in the period between 10 and 20 days from the beginning of the treatment. The studies on these two lines on the relationship between leaf conductance and photosynthesis suggested that stomatal closure occurs more slowly in high-yielding lines than in low-yielding ones.

Smith (1993) found significant differences between families in stomatal opening and photosynthetic rate during the dry season in Congo and suggested that these parameters might be used to select for drought tolerance. The stomatal response to water deficit is rather fast, which implies a reduction in photosynthesis, and therefore in yield potential; so producing genotypes resistant to water deficit seems incompatible with commercial objectives (Villalobos and Rodriguez, 1998). Lamade *et al.* (1989b) also studied photosynthetic rate and other physiological parameters for three different oil palm clones under drought conditions.

Membrane structural resistance and drought tolerance

Maintenance of membrane structure integrity is a major factor in water stress tolerance. Maintenance of membrane integrity to measure dehydration tolerance is usually determined by the leakage of solutes (electrolytes, sugars, amino acids, organic acids, hormones, etc) from cells. The capacity for stem reserve mobilization/ translocation appears to be related to drought tolerance or resistance, and could be due to accumulation of ABA in response to water stress. However experiments on leaf tissue membrane stability carried out on both seedlings and adult trees showed that an assessment of protoplasmic resistance cannot be used as a sole early test when breeding for drought tolerance. In effect, sometimes the results obtained on seedlings do not tally with adult trees. Hence membrane observations are to be done in comparison with membrane lipid composition and changes in the event of drought.

Reserves and their mobilization during drought tolerance

Although the effect of stomatal regulation on photosynthetic activity has not been guantified, the stomatal closure during water stress occurs to the detriment of carbon nutrition. Hence the palm has to compensate for this deficit. Carbohydrate reserves could play an important role as a source of carbon. It has been shown on seedlings that not only are these reserves larger in resistant families, but mobilization is also better due to the increase in certain enzyme activities (invertase, b amylase). All the organs are seen to use reserves during water stress, which helps to lessen the demand for carbon that results from stomatal opening and can, also play a role in osmoregulation. Adiahossou (1983) has shown that the leaf starch is hydrolyzed during the dry season and that there is an increase in soluble sugar concentration in oil palm. Initially the soluble sugar levels in the stem falls as the sugars are used for the palm's metabolism and then rise again in a second phase probably due to starch hydrolysis. On adult trees, although starch hydrolysis and carbohydrate accumulation occurred during the dry season, no differences were observed among the families.

Another way of solving the oil palm demand for carbon is to regulate the photosynthetic capacity. Results have indicated that the resistant families have higher assimilation rates than susceptible crosses, but the reduction in the event of stress is smaller. The difference can be explained by higher Ribulose 1,5 bi phosphate carboxylase-oxygenase (Rubisco) activity that is also less sensitive to stress, in tolerant crosses. Ollagnier (1985) studied the ionic reactions and fertilizer management in relation to drought resistance of oil palm. Fertilizers acted positively on plant development and a yield components such as weight and number of bunches. Drought during the bunchforming cycle i.e., 26-28 months reduces the efficiency of fertilizers. Accumulation of large amounts of proline contributes to osmotic adjustment and serves as cytoplasmic osmotic balance for potassium accumulation as the main osmoticum in the vacuole. Harun (1997) studied the proline accumulation in the leaves of water stressed oil palm seedlings and reported that increased stomatal resistance was related to increased water deficits as indicated by a reduction in leaf water potential. Proline began to accumulate after stomatal resistance reached a peak and this led to a recovery in leaf water potential followed by a similar reduction in stomatal resistance. The proline level eventually fell to the control level after watering was resumed.

Yield and drought tolerance

There are important differences among oil palm genetic materials, and some of them could be selected for high tolerance to stress without losing much of their yield potential (Maillard et al., 1974). Furthermore, the ability to abort some of the developing inflorescences and mobilize reserves, and the large annual variation in yield during the year, helps compensate for lower photosynthetic rates caused by stomata closure (Nouy et al., 1999). Houssou et al. (1989, 1992) demonstrated genetic differences in survival between progenies in Benin. He showed that Deli X La Me crosses, although potentially high yielding, suffered a significantly higher death rate than Deli X Yangambi crosses. The yield from surviving palms was not much higher from Deli x La Mé than Deli X Yangambi. However, important differences were also found among progenies of this latter cross.

Nouy et al. (1999) had similar results when these two crosses were evaluated in two sites with annual water deficits ranging from 400 to 700 mm. These results create a problem with breeding for drought tolerance, when severe drought is an irregular occurrence. A compromise may have to be made between drought tolerance and yield in years with less severe drought. Houssou et al. (1989) did find few progenies that both yielded well and had low mortality. Villalobos and Rodriguez (1998) have reported that the bunch production during the first two years gives an estimate of yield potential of these genotypes planted in very extreme conditions. The wild palms originated in Malawi (14.2 bunches/palm), and the progenies derived from the female parents Bamenda and Tanzania (11.8 and 9.5 bunches/palm) were the best. At the other extreme, the Deli dura palms performed poorly. With respect to parent lines, the original Mobai (14.2 bunches) and Tanzania lines (17 bunches) were the best.

Foo (1998) reported that the moisture stress suppresses female inflorescence formation and increases abortion of female inflorescences. The inadequate water supply to meet such high evapotranspiration demand during the dry period would severely affect sex differentiation and the subsequent inflorescence development process and this will eventually reduce the ultimate yield. Adequate irrigation and fertilizer application has achieved 59 t FFB/ha at a palm age of 19 years. An irrigation trial on a semi-commercial scale in a dry area has achieved 38.8 t FFB/ha at the third year of irrigation as compared with only 14.1 t FFB/ha without irrigation. At 8-10 years old, the irrigated palms could sustain a yield of 30-35 t FFB/ha as compared with 16-18 t FFB/ha of the nonirrigated palms. Thus the photosynthetic efficiency, frond and bunch production was also higher during water areas. Villalobos and Rodriguez (1998) have reported that the commercial progenies derived from the Deli dura population performed poorly, and were severely affected by water stress. Only the Deli x La Mé progenies, and to a lesser degree, those of Deli x Yangambi origins, had acceptable behavior, which is in accord with the findings of others (Maillard 1974, Houssou et al., 1992). The appearance and yield of the Malawi wild palms indicate that they carry genes that make them tolerant to water stress. The most promising populations were Angola, Tanzania and La Mé, as well as some Deli lines. The best crosses were Angola x Tanzania and Angola x La Mé, which had better appearances, higher water potentials at dawn and higher leaf specific weights.

Screening of African dura germplasm based on physiological markers has been completed (Mathur *et al.* 2001, Suresh *et al.*, 2008). Based on these results, superior drought tolerant duras have been identified. ZS-1 was the most drought tolerant dura compared to that of other duras, while TS-9 was most susceptible one. Among Guinea Bissau duras, GB-25 was the most tolerant one, while GB-21 was most susceptible. ZS-1 and ZS-2 were most tolerant and susceptible duras respectively among Zambian duras. Studies on membrane susceptibility indices (MSI) indicated that ZS-2 recorded highest value closely followed by TS-9 indicating their better tolerance to drought.

Studies at Benin have classified the oil palm crosses according to their drought tolerance. Four main groups were identified. The first contained crosses with high production potential and good drought resistance, as they showed little sign of damage in the event of water stress. The second also contained high yielding crosses, but suffered severe drought damage, even the death of some individuals. The trees in the third group were low yielding and showed little sign of damage, and the last group contained families with a low production potential and highly susceptible to drought (very few families fell into this group).

Fourteen dura (Africa) x pisifera crosses were screened for drought tolerance in nursery by undertaking studies on membrane stability indices (MSI). Highest MSI was recorded in 34CD X 110P closed followed by 124CD X 17P and 66CD X 129P, indicating their better tolerance to drought. 254CD X 14P and 435CD X 14P recorded lower MSI indicating their poor tolerance to drought.

To understand plant stress responses in the form of sap flux and transpirational adjustments made by

K. Suresh and R.K. Mathur

oil palm under Indian conditions, sap flow studies have been undertaken (Suresh *et al.*, 2006; Suresh and Nagamani, 2007) and results revealed that sap flux increased gradually from 9.00 AM reaching a peak during 1.00 to 2.00 A.M and decreased as day progressed. Evapo-transpiration and vapor pressure deficit also showed similar trend as that of sap flux. Seasonal variations in sap flux indicated higher sap flux during February and March and lower flux during May and June. The lower flux during dry months could be due to closure of stomata after mid day as atmospheric vapor pressure deficit increased.

Drought tolerance phenomenon is complex, since it involves varied mechanisms, which are often antagonistic to each other. These different factors lead to a balance that enables the plant to withstand water stress to varying degrees. To date research has been concentrated on plant water status and on carbon molecule supplied in the event of water stress.

Under the Indian Context, Agronomic techniques for achieving better water reserves at plantation level (through irrigation and erosion control), ensuring more effective distribution of available water to oil palm (by reducing competition with weeds, bare soil cropping, anti-transpirants, cropping with other palms) and lessening water consumption by palms during dry seasons through ablation of bunches are effective, but becomes limited due to technical or economic reasons. The use of drought tolerant planting materials will be another option for overcoming drought in the long run.

Future Strategies

- The new research options should primarily concentrate on the knowledge of adult oil palm and seedlings functioning under water stress. These studies should enable the "Physiological characterization" of all the available crosses and parents and provide new tools for genetic improvement programmes.
- 2. The research on drought tolerance should integrate factors like assimilate partitioning (source-sink relationship), photosynthetic capacity, stomatal regulation and resistance or rigidity of cell membrane integrity in the seedlings and field stages for the same planting materials in order to develop performance tests.
- 3. The research developed on the above aspects should lead to new strategies for developing planting materials more closely adapted to the climatic conditions of that particular agro-climatic zone.

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