TABLE DES MATIERES

INTRODUCTION GENERALE

La palmeraie mondiale couvre plus de 12 millions d'hectares, localisés dans la zone intertropicale et essentiellement en Asie du sud-est. Avec 41 millions de tonnes produites par an, l'huile de palme est la première source d'huile végétale produite dans le monde (Esteulle and Perennes, 2007). Les deux pays leaders, en 2007, sur ce marché sont respectivement l'Indonésie (avec 78 millions de tonnes de fruits) et la Malaisie (avec 77.7 millions de tonnes de fruits) assurant plus de 85% de la production mondiale (FAOSTATS, 2008).

Depuis maintenant deux décennies, le marché des huiles végétales et de l'huile de palme en particulier est en pleine expansion. Leur consommation, associée à une demande accrue et à un engouement pour ces produits naturels, est six fois plus importante aujourd'hui qu'il y a 20 ans (19,8 kg consommés par an et par personne en 2007 ; Perennes and Mercier, 2007). A cette demande alimentaire, se rajoute un intérêt grandissant pour les biocarburants.

Parmi les plantes oléagineuses cultivées, le palmier à huile est une plante à très haut rendement. Des rendements supérieurs à six tonnes d'huile à l'hectare sont couramment enregistrés sur des plantations de plusieurs milliers d'hectares. Lors de conditions climatiques favorables, la production est relativement bien répartie sur l'année, montrant toutefois des variations saisonnières (entre 8 et 12% de la production annuelle). En conditions moins favorables, les variations saisonnières s'accentuent (entre 1 et 25% de la production annuelle) ; elles sont généralement accompagnées de variations interannuelles de plus de 50%.

Afin de répondre à la demande croissante, les planteurs se voient contraints d'étendre les zones de culture à des zones moins favorables (contraintes agro-environnementales accrues) voire à des zones considérées marginales pour cette plante. Enfin, ce contexte est, en Asie du sud-est notamment, aggravé par l'apparition d'évènements météorologiques extrêmes, connus sous le nom de « El Niño », pour l'instant spasmodiques, mais qui provoquent des périodes intenses et longues de sécheresse entraînant systématiquement des chutes drastiques de production (Mialet-Serra, 2005). Devant cette situation complexe, il devient fondamental pour les producteurs d'appuyer leurs décisions et leurs prévisions sur une bonne analyse des mécanismes et des facteurs qui participent à l'élaboration de la production du palmier à huile.

De nombreux auteurs (Ziller *et al.*, 1955, Bredas and Scuvie, 1960, Michaux, 1961, Dufrêne *et al.*, 1990) ont étudié le comportements de différents matériels végétaux dans des conditions agro-climatiques données et, en particulier, en fonction de l'alimentation hydrique, en scrutant principalement les composantes du rendement. Cette approche a démontré son efficacité d'une part pour montrer que l'eau est un des principaux facteurs limitant le rendement du palmier à huile et, d'autre part, pour évaluer les matériels étudiés vis-à-vis de leur tolérance à la sécheresse. Cependant l'absence de prise en compte des mécanismes en jeu ne permet pas d'extrapoler ces diagnostics à de nouvelles situations et de nouveaux matériels.

Par ailleurs, les processus physiologiques les plus largement étudiés sur palmier à huile portent sur les échanges gazeux, avec des études sur la photosynthèse et la régulation stomatique (Hong and Corley, 1976, Dufrêne and Saugier, 1993, Smith, 1993, Haniff, 2006), et la croissance au sens large (De Berchoux and Gascon, 1965, Corley *et al.*, 1971, Chang *et al.*, 1988, Corley and Breure, 1992, Gerritsma and Soebagyo, 1999). Ces connaissances alimentent les premiers modèles de fonctionnement (Van Kraalingen, 1985, Dufrêne, 1989, Henson, 2007) dont la robustesse reste à prouver.

Fonder, dans une situation quelconque, un diagnostic sur une analyse générique intégrant, non seulement, l'importance et les raisons des fluctuations du rendement du palmier à huile mais aussi et surtout les mécanismes mis en jeu dans l'impact des variations agro-environnementales, représente une question fondamentale qui intéresse à la fois agronomes, sélectionneurs et améliorateurs. Ce travail tente d'y apporter des éléments de réponse.

L'objectif de la présente étude, est de développer une théorie cohérente du fonctionnement du palmier à huile afin de dégager les principaux processus d'ajustement mis en jeu par cette plante en fonction des conditions agro-environnementales rencontrées. Ces ajustements peuvent être de natures diverses : phénologiques, morphologiques, liés à la croissance et au développement de la plante, physiologiques (régulation de l'assimilation carbonée, gestion de réserves carbonées). Notre hypothèse de travail suppose que, ces ajustements peuvent se traduire par une régulation de la demande à l'échelle de la plante entière voire de certains organes en croissance par une régulation de l'assimilation et/ou par le jeu du stockage et de la mobilisation des réserves carbonées. Par ailleurs, compte tenu des longs cycles de développement des organes du palmier à huile (quatre années entre l'initiation d'une feuille et la maturité du régime qu'elle axille), ces ajustements peuvent apparaître de manière différée dans le temps ce qui rend leur analyse d'autant plus ardue.

Les grandes questions posées dans le cadre de cette étude sont :

- Face à des conditions agro-environnementales changeantes, quels sont, chez le palmier à huile, les paramètres les plus plastiques ?
- Quels sont les mécanismes d'ajustement mis en place en situations de déséquilibres source-puits naturels ou provoqués ?
- Peut-on établir des relations explicatives simples entre conditions environnementales et paramètres décrivant la croissance végétative, la phénologie, la gestion du carbone dans la plante et les composantes du rendement ? Si oui, quelles sont-elles ? Ces relations varient-elles en fonction du matériel végétal étudié ?
- Une modification du rapport source : puits influe-t-elle sur les relations précédemment établies ? Quels sont les paramètres les plus affectés ?

Nous exposerons, dans le chapitre qui suit, l'état de l'art permettant de décrire le cadre scientifique dans lequel cette étude se déroule, le contexte socio-économique lié au palmier à huile est tout d'abord décrit. Sa morphologie, sa phénologie, sa croissance et sa productivité en conditions optimales et sub-optimales sont ensuite détaillées. Les principaux principes de gestion de carbone pour les plantes supérieures, en général, et pour le palmier à huile en particulier sont brièvement abordés. Pour finir, la problématique et les principaux objectifs de ce travail sont exposés.

CHAPITRE I :

CONTEXTE SCIENTIFIQUE

PHOTO 1. Plantation de palmier à huile à Kandista, Indonésie.

PHOTO 2. Ensemble de régimes matures en attente de ramassage.

I. CONTEXTE ET ENJEUX ECONOMIQUES

Les plantations de palmier à huile sont réparties sur trois continents : africain, asiatique et américain (Photo 3). L'essentiel de la production est le fait de grandes exploitations industrielles de plusieurs centaines de milliers d'hectares d'un seul tenant, qui possèdent des unités locales de transformation des principaux produits destinés à l'exportation vers de gros marchés étrangers. Les exploitations villageoises, allant de quelques palmiers à quelques hectares autour de la ferme familiale, restent marginales. Elles sont regroupées en coopératives.

PHOTO 3. Localisation des principaux pays producteurs d'huile de palme en 2007.

Source: www.fedepalma.org

Le palmier à huile est originaire de la forêt tropicale humide des régions d'Afrique de l'Ouest (Corley and Tinker, 2003e). Au milieu du XIX^{ème} siècle, quatre palmiers issus de cette région ont été introduits en Asie du sud-est, donnant par la suite naissance aux « *Deli Dura* » d'Indonésie et de Malaisie. Trois variétés de palmiers à huile existent (Fig. 1) (i) les *Pisifera*, très souvent stériles, qui, à ce titre, sont utilisés comme géniteur mâle et dont les fruits se caractérisent par l'absence de coque, (ii) les *Dura*, dont les fruits se caractérisent par une coque épaisse et une pulpe (ou mésocarpe) peu épaisse et enfin, (iii) les *Tenera*, issus du croisement entre un *Dura* × un *Pisifera*, présentant un ratio pulpe sur noix élevé, intéressant sur le plan commercial. La palmeraie mondiale se compose majoritairement d'hybrides de type *Tenera*.

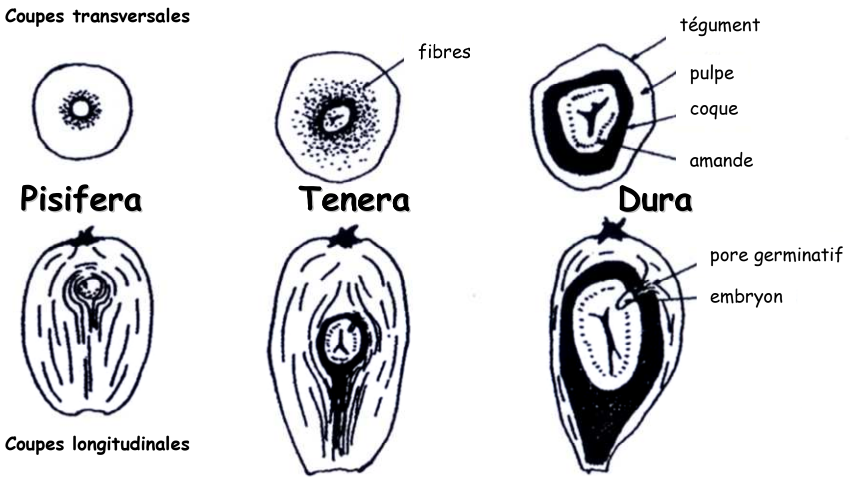

FIG. 1. Représentation schématique des trois variétés de palmier à huile.

Le principal produit industriel du palmier à huile est l'huile de palme. Elle est consommée dans plus de 130 pays du monde (Fold, 2003) et représente depuis peu l'huile végétale la plus consommée. L'huile de palme est extraite de la pulpe (ou mésocarpe). De couleur rouge ambrée, elle est riche en caroténoïdes. Elle peut être utilisée non raffinée comme ingrédient dans des plats traditionnels locaux, leur apportant son goût unique. Elle est exportée raffinée. Sa grande stabilité aux températures élevées en fait une des huiles les plus prisées pour la friture. Elle entre, par ailleurs, dans la composition d'une large gamme de produits courants tels que la margarine, les barres chocolatées, les plats préparés, les crèmes glacées, les chips… L'huile de palmiste (extraite de la noix) ainsi qu'une petite part de la production d'huile de palme (10%) sont utilisées dans l'industrie non alimentaire, entrant dans la composition de savons, de cosmétiques ou encore de détergents. L'émergence des biocarburants offre, aujourd'hui, de nouvelles opportunités de valorisation de l'huile de palme.

L'huile de palme ne représente que 10% de la biomasse totale d'un palmier à huile adulte, les 90% restants représentant une source de fibres et de cellulose qui peut également être exploitée (Basiron, 2007). Les régimes vides peuvent être épandus dans les champs ou transformés en compost afin de créer un nouvel apport de matière organique (Caliman *et al.*, 2005) ; la sève du palmier à huile, une fois fermentée et distillée, donne du vin ou de l'alcool (Noël, 2003), les fibres et la cellulose pourraient être, à terme, utilisés dans la fabrication de biocarburants.

II. EXIGENCES AGRO-ECOLOGIQUES

II.1. Conditions optimales

Le palmier à huile est une culture équatoriale qui, comme le cocotier, est très exigeante en eau. Pour atteindre une production maximale, la culture doit bénéficier d'une quantité d'eau égale ou supérieure à l'évapotranspiration potentielle (ETP) (Olivin and Ochs, 1978). La pluviosité minimale doit être de 2000 mm par an (Caliman, 1992, Corley and Tinker, 2003b), bien répartie sur toute l'année (soit un minimum de 150 mm mois^{-1}).

L'optimum thermique moyen est proche de 26°C. Les limites des moyennes annuelles de température sont situées entre 22°C et 33°C. La culture du palmier reste, cependant, possible dans des zones présentant des températures inférieures à 22°C (régions d'altitude comme à Nord Sumatra, au Honduras ou en Afrique de l'Ouest). Le palmier à huile supporte des températures élevées (38°C) à condition que l'humidité de l'air reste élevée (Jacquemard, 1995). L'humidité relative de l'air doit être supérieure à 85% afin d'éviter des déficits de pression de vapeur (VPD) élevés (Dufrêne, 1989, Smith, 1989).

Pour différents auteurs (Ong, 1982, Corley and Tinker, 2003b), une durée moyenne du jour de 5 à 7 heures et un taux de rayonnement d'environ 15 MJ m^{-2} j^{-1} semble être une bonne combinaison pour le palmier à huile. Un palmier à huile adulte, à densité classique de 143 plants ha^{-1}, intercepte 70% du rayonnement global et 90% du rayonnement photosynthètiquement utilisable (RPU) (Henson, 1995, Corley and Tinker, 2003b).

Le palmier à huile supporte une large gamme de type de sols (Corley and Tinker, 2003b). Pour permettre une croissance générale optimale de la plante, le système racinaire du palmier à huile doit être bien développé afin de faciliter l'alimentation en eau et sels minéraux et permettre un bon ancrage de l'arbre dans le sol. Les sols argileux bien structurés, argilo-sableux ou argilo-limoneux permettent ainsi un développement des racines en profondeur mais également en surface, ils sont considérés comme idéaux pour le palmier à huile. Au contraire, les sols hydromorphes ou encore les tourbières (très fréquentes en Malaisie et en Indonésie), présentant une couche imperméable à la pénétration des racines, limitant leur croissance, ou une nappe phréatique en surface saturant le profil et provoquant une asphyxie racinaire, sont peu recommandés. Le palmier à huile s'accommode de sols chimiquement pauvres mais bien structurés ; il est relativement aisé, dans de pareils cas, de corriger les carences par un apport d'engrais approprié. Les sols à pH neutre sont bien adapté, cependant, le palmier à huile peut également supporter des pH plus acides allant jusqu'à 4.

Les éléments essentiels au palmier à huile sont (i) pour les éléments majeurs, l'azote, le phosphore, le potassium, le magnésium, le calcium, le chlore et le soufre, impliqués dans la croissance et la production (Corley and Tinker, 2003d), (ii) pour les éléments mineurs, l'aluminium, le bore, le cuivre, le fer, le manganèse, le molybdène et le zinc, impliqués le plus souvent dans les processus physiologiques. Une déficience minérale peut entraîner, à l'échelle cellulaire, une chute des concentrations principalement dans les feuilles les plus âgées, les mécanismes de translocation interne se faisant prioritairement vers les organes les plus jeunes. Le calcium et le fer sont des éléments moins mobiles, qui ne peuvent être transportés par le phloème et dont la carence s'observe principalement au niveau des points de croissance. Les principaux besoins en minéraux s'élèvent, par an, à 190, 25, 270, 90 et 60 kg ha^{-1} respectivement pour l'azote, le phosphore, le potassium, le calcium et le magnésium (Corley and Tinker, 2003d). Cependant, ces valeurs peuvent varier selon le type de sol, le lieu de plantation et la méthode de mesure. Le niveau de nutrition minérale du palmier à huile est déterminé par le stock initial des éléments minéraux dans le sol, les exportations dues aux récoltes, les pertes par lessivage et érosion, les prélèvements par les plantes adventices et de couverture, le recyclage des éléments contenus dans la matière organique qui retourne au sol (minéralisation des feuilles, inflorescences, racines) et les apports en fertilisants. L'état de nutrition minérale est apprécié par un diagnostic foliaire.

II.2. Principales contraintes en Asie du sud-est

Les facteurs limitant la production du palmier à huile dans le sud-est asiatique sont principalement d'ordre climatique et parfois édaphique. Les contraintes climatiques sont la température (dans les zones d'altitude de nord Sumatra), le rayonnement solaire et, principalement, l'alimentation hydrique ; l'eau apparaissant, comme le facteur principal, limitant la production du palmier à huile.

Le rayonnement solaire reçu est fonction de la latitude, de la période de l'année et de la couverture nuageuse. Le niveau de rayonnement en Asie du sud-est diminue à certaines périodes de l'année. Les causes de cette diminution sont de natures diverses, liées aux feux de forêts, aux éruptions volcaniques ou encore à l'augmentation de la pollution industrielle et automobile (Caliman and Southworth, 1998, Henson, 2000). Ainsi, en Indonésie, pendant plusieurs semaines consécutives, des 'brouillards' ou 'fumées' recouvrent les principales zones de production. Les conséquences sont encore mal connues, mais ces évènements coïncident avec des périodes de sécheresse intense et s'atténuent à la reprise des pluies.

De nombreux sites de plantations de palmier à huile en Asie du sud-est, e.g. le Lampung et l'ouest de l'ile de Bornéo, subissent des distributions de la pluviosité intra et interannuelles très variables (Caliman and Southworth, 1998) entrainant des déficits hydriques marqués pouvant aller de 200 à 500 mm an^{-1} pour les années les plus sèches. Les rendements peuvent alors chuter de 10 à 40% en dessous du potentiel normal de production. De plus, le réchauffement climatique entraîne depuis plusieurs années l'apparition d'évènements météorologiques extrêmes, très marqués en Asie du sud-est, spasmodiques mais qui tendent à devenir de plus en plus fréquents, liés au phénomène « El Niño » et qui provoquent d'intenses périodes de sécheresse. Au cours de ces périodes, se rajoutent un rayonnent intense et des déficits de pression de vapeur élevés affectant grandement la physiologie et la phénologie de la plante. Les conséquences peuvent être dramatiques ; à court terme, des chutes drastiques de production ou un arrêt de la croissance voire dans les pires situations la mort des palmiers, s'observent.

Sur le plan édaphique, les terres identifiées pour les futures plantations ont des sols très pauvres. Il s'agit majoritairement de sols tourbeux situés à l'ouest de la Malaisie, à l'est de Sumatra et sur les côtes nord et sud de Bornéo dans lesquels les nappes phréatiques affleurent. Dans de pareils cas, la mise en place de dispositifs de drainage ainsi qu'une attention particulière portée sur la nutrition minérale sont nécessaires.

III. MORPHOLOGIE, PHENOLOGIE ET CROISSANCE DU PALMIER A HUILE

III.1. Morphologie du palmier à huile en conditions optimales

Le palmier à huile appartient à la famille des *Arecaceae*. C'est une monocotylédone pérenne, arborescente, monoïque et allogame.

PHOTO 4. Appareil aérien du palmier à huile.

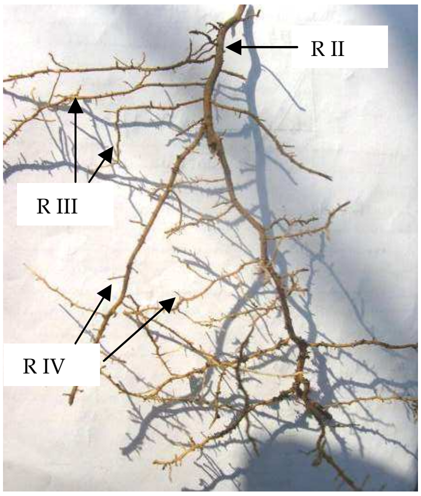

PHOTO 5. Racine secondaire portant des racines tertiaires et quaternaires.

Le *système racinaire* du palmier est de type fasciculé. Il se présente sous la forme d'un organe volumineux hémisphérique d'environ 80 cm de diamètre. Trois voire quatre types de racines se distinguent (Photo 5). Plus d'un millier de racines primaires (diamètre supérieur à

5 mm et constant sur toute la longueur de la racine) sont directement attachées à la base du stipe ou plateau racinaire (Photo 6). Les racines secondaires, insérées directement sur les racines primaires, ont un diamètre compris entre 1 et 4 mm et se développent aussi bien en surface qu'en profondeur. Ces deux types de racines ont principalement un rôle d'ancrage au sol et permettent la circulation des sèves brutes et élaborées. Les ramifications suivantes donnent les racines tertiaires (densité de une racine par cm de RII) et quaternaires (densité de une racine par mm de RIII) de diamètre compris entre 0,2 et 1,5 mm, elles sont considérées comme absorbantes et principalement localisées dans les horizons de surfaces (Jourdan and Rey, 1996). La biomasse racinaire d'un palmier à huile adulte dans un sol africain de type sableux profond est de l'ordre de 30 à 40 t_{MS} ha^{-1} (Jacquemard, 1995) et est estimée à 10 t_{MS} ha^{-1} en Indonésie (Legros *et al.*, 2006).

PHOTO 6. Bulbe racinaire d'un palmier à huile adulte sur lequel sont insérées les racines primaires.

Le palmier à huile possède une *tige* unique dépourvue de branche et de croissance secondaire (Photo 4). Cette tige, appelée stipe, fortement scléreuse et très épaisse (Henry, 1955a), est constituée de tissus parenchymateux. Sa hauteur peut atteindre 30 m pour les palmiers les plus âgés. Son diamètre est constant à partir de 1 m de hauteur ; il est d'environ 80 cm à la base et varie entre 45 et 60 cm au delà de 1 m de hauteur (Corley and Tinker, 2003a). Il peut varier en fonction de l'origine génétique et des conditions pédoclimatiques. A l'extrémité (haute) du stipe se situe l'unique point de croissance de la plante ou méristème apical. De forme conique, il est situé au fond d'une petite cavité, protégé par la couronne foliaire (Corley and Gray, 1976a). Les bases pétiolaires (bases des pétioles des feuilles élaguées lors des récoltes des régimes) restent attachées au stipe au moins jusqu'à l'âge de 12 ans puis commencent à se détacher, pour des raisons encore mal connues. Le stipe perd alors son aspect écailleux et devient gris foncé et lisse ; laissant apparaitre les cicatrices des bases pétiolaires. La biomasse du stipe à l'âge adulte atteint plus de 300 kg (Legros *et al.*, 2006) représentant environ 50% de la biomasse totale de l'arbre, faisant de ce compartiment végétatif et pérenne, un compartiment de stockage idéal et imposant.

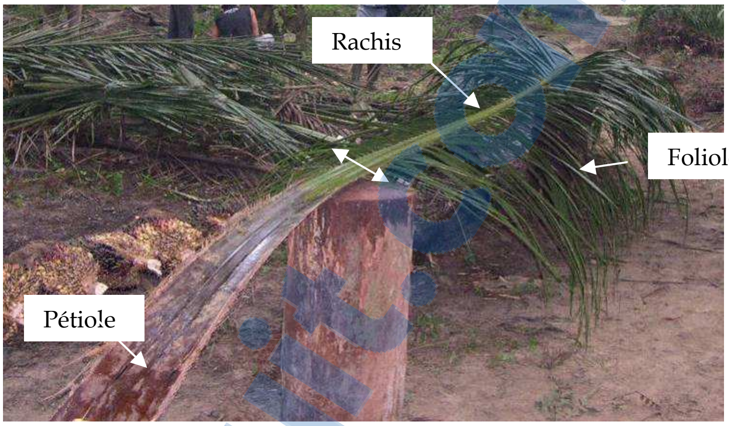

PHOTO 7. Une feuille et ses différents compartiments.

La *couronne foliaire* est constituée d'environ 40 feuilles. La surface d'une feuille varie entre 10 et 12 m² ; la longueur totale moyenne est comprise entre 6 et 7 mètres et sa masse sèche varie entre 5 et 8 kg. La feuille se compose d'un pétiole, d'un rachis et de 350 à 400 folioles assimilateurs (Photo 7). La densité de stomates est d'environ 146 mm^{-2} ; ils sont situés exclusivement sur la face inférieure de la foliole. La biomasse de l'appareil foliaire représente 26% de la biomasse totale de l'arbre (Legros *et al.*, 2006). Le poids de la feuille, la longueur et la largeur du pétiole et du rachis et le nombre de folioles sont beaucoup plus élevés pour certaines variétés indonésiennes et le nombre de feuilles dans la couronne est inférieur aux variétés africaines (De Berchoux and Gascon, 1965). L'organisation des feuilles dans la couronne (phyllotaxie) suit un agencement régulier et constant (Rees, 1964) ; 135,7 à 137,5° séparent deux feuilles consécutives (Hirsch, 1978). Huit spires apparentes se déroulent ainsi sur la droite ou sur la gauche du stipe ; le déterminisme du sens de rotation est encore inconnu (Henry, 1955a) mais ne semble pas être génétique (Rees, 1964).

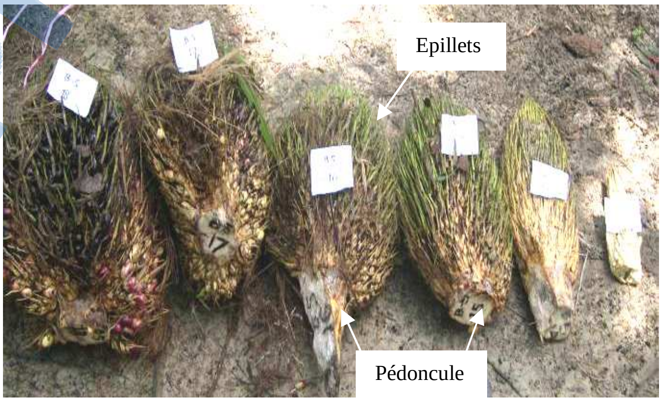

PHOTO 8. Stades de développement des inflorescences femelles sans leur spathe pour des feuilles de rang 13 à 18 (droite à gauche).

Chaque *inflorescence* est composée d'un pédoncule de 30 à 45 cm de long sur lequel sont positionnés environ 150 épillets. Le nombre de fleurs par épillet varie entre 10 et 30 pour les inflorescences femelles d'un arbre adulte, le nombre de fleurs est d'environ 780 par épillet pour les inflorescences mâles. Sur les inflorescences femelles, des fleurs dites infertiles sont localisées à la base des régimes. A maturité, l'inflorescence est appelée régime (Photo 9).

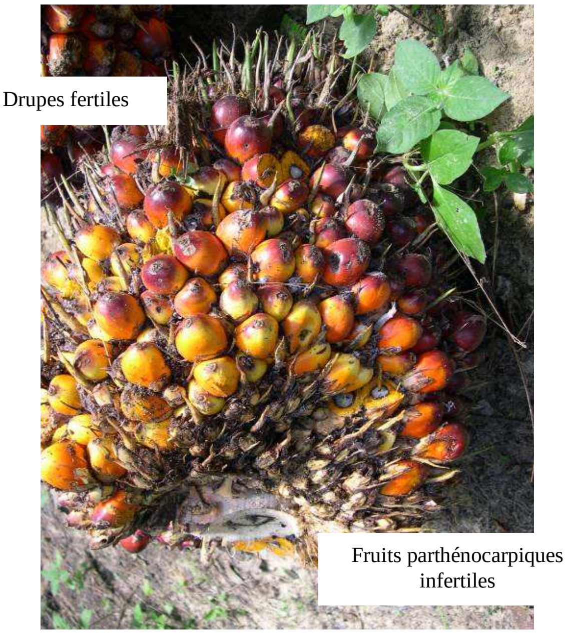

PHOTO 9. Régime mature de palmier à huile adulte.

Le *fruit* du palmier est une drupe dont la taille et la forme varie selon l'origine de l'arbre. Il est composé d'un péricarpe recouvert par un éxocarpe, d'un mésocarpe (ou pulpe) et d'un endocarpe (ou coque) entourant l'amande (l'amande + la coque sont communément appelés noix) (Photo 10). La longueur d'un fruit varie entre 2 et 5 cm et son poids entre 3 et 30 grammes. Les principales distinctions entre variétés se font sur la taille du fruit et principalement sur le rapport pulpe sur noix. La couleur du fruit évolue avec son stade de maturation. A maturité et selon l'origine de l'arbre, l'extrémité du fruit est foncée (violet à noir) (Photo 9 et 10) alors que sa base est plutôt orangée ; mais ces paramètres varient selon les variétés. Un fruit mature stocke environ 65% de lipides dans son mésocarpe et sa noix.

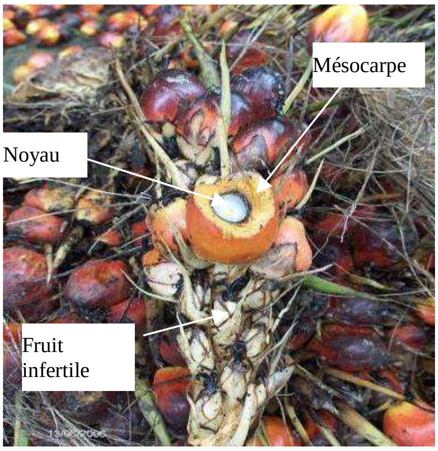

PHOTO 10. Epillet portant une drupe mature et des fruits infertiles.

III.2. Phénologie et croissance du palmier à huile en conditions optimales

Le système racinaire du palmier est en perpétuel renouvellement. La majeure partie de ce système se développe en surface : 50 à 66% des racines totales et des racines fines se trouvent dans le premier mètre de sol (Nouy *et al.*, 1999), puis peuvent descendre jusqu'à 6 mètres de profondeur. La colonisation verticale des racines dépend principalement du type de sol et de la présence ou non de nappe phréatique (Reyes *et al.*, 1988, Jourdan and Rey, 1996). La densité des racines tertiaires et quaternaires, qui représentent l'essentiel de la partie absorbante du système racinaire, évolue de 1 g_{MS} dm^{-3} en surface à 0.3 g_{MS} dm^{-3} à un mètre de profondeur. Les croissances racinaires sont estimées entre 1,5 et 3, 0,75 et 2 et 0,3 et 0,8 mm jour^{-1}, respectivement, pour les racines primaires, secondaires et tertiaires (Jourdan and Rey, 1997a, Corley and Tinker, 2003a).

Lors des deux premières années de croissance de la plante, le stipe croît en diamètre, formant un empattement pouvant atteindre jusqu'à 80 cm de diamètre. La croissance en hauteur s'accélère ensuite alors que la croissance en diamètre devient quasiment nulle. Un arbre adulte croit de 35 à 75 cm par an (Corley and Gray, 1976a). La variation de croissance en hauteur du stipe dépend principalement des conditions agro-environnementales, de l'âge du palmier et du matériel végétal (Henson, 2006a). Ce caractère est très héritable et important pour la gestion de la culture ; la croissance en hauteur ne doit pas être trop forte afin de faciliter la récolte des arbres les plus âgés. La longueur d'un entrenœud peut varier de 14 à 23 mm pour différents génotypes en Afrique (De Berchoux and Gascon, 1965) alors que les variations sont entre 15 mm et 25 mm pour des arbres de 4 et 10 ans en Malaisie (Corley and Gray, 1976a).

Le méristème apical initie en continu, selon un plastochrone supposé constant, les nouvelles feuilles et inflorescences. Le rythme d'émission d'un phytomère (feuille + inflorescence + entrenœud) est d'environ deux semaines pour un arbre adulte (Rees, 1964) dans des conditions optimales de culture. Il varie avec l'âge de la plante ; 40 feuilles par an sont émises pour un jeune palmier à huile, 20 à 24 feuilles par an sont émises pour les palmiers adultes (De Berchoux and Gascon, 1965). Le nombre de feuilles émises par an est un caractère phénotypique héréditaire ; cependant, son observation montre qu'il est relativement constant selon le lieu et le génotype considérés (Corley and Gray, 1976a, Gerritsma and Soebagyo, 1999). Une feuille encore non épanouie et visible est, par convention, appelée flèche ; la feuille suivante dont les folioles sont totalement épanouies est, par convention, appelée feuille de rang un. Le rachis atteint sa longueur définitive lorsque la feuille est au stade de flèche, les folioles lorsqu'elle est au rang 1, en revanche le pétiole s'allonge encore quelque temps après (jusqu'à une feuille de rang 8) (Henry, 1955b).

Au sein du méristème (phase cachée du développement d'une feuille), il s'écoule deux années entre l'initiation d'une feuille et son épanouissement (Henry, 1955b). Au cours de cette période, la jeune feuille connait d'abord une période de croissance lente qui s'accélère au cours des quatre mois précédant son épanouissement (Gerritsma and Soebagyo, 1999). Elle est ensuite photosynthétiquement active jusqu'à son élagage lié aux récoltes (Corley and Gray, 1976a).

PHOTO 11. Succession d'inflorescences et de régimes dans une couronne foliaire de palmier à huile adulte.

Parallèlement à l'émission des feuilles, en conditions favorables, le palmier à huile émet en continu des inflorescences mâles et femelles à l'aisselle de chaque feuille (Photo 11). Des séries d'inflorescences mâles puis femelles et ainsi de suite se suivent consécutivement. La maturité sexuelle de ces séries ne se recouvrant pas, il y a nécessairement allogamie. La longueur des cycles mâles ou femelles dépend du génotype, de l'âge du palmier, de son état trophique, des conditions écologiques et des techniques culturales (Corley, 1976). L'émission des inflorescences est totalement liée au rythme d'émission des feuilles (Corley and Tinker, 2003c). Pendant 2 ans ½ à 3 ans, l'inflorescence encore immature se développe au sein du méristème (Corley and Gray, 1976a) ; elle passe par une phase lente de croissance puis par une phase rapide jusqu'à l'anthèse (Corley and Tinker, 2003c). Elle traverse, alors, des étapes clés qui vont, à terme, déterminer le nombre et la biomasse des régimes récoltés. La différenciation sexuelle (ou détermination du sexe mâle ou femelle de l'inflorescence) intervient environ 26 à 30 mois avant la récolte (Nouy *et al.*, 1999, Corley and Tinker, 2003c). Le sex-ratio (ratio entre inflorescences femelles et nombre total d'inflorescences (femelles+mâles+avortées)) (Corley, 1976) est un facteur important de la variation saisonnière du nombre de régimes. Au début de la croissance rapide de l'inflorescence sexuellement différenciée, celle-ci peut avorter (10 à 14 mois avant la récolte), cela se traduira, à la floraison, par l'absence d'inflorescence à l'aisselle de la feuille axillante (Hemptinne and Ferwerda, 1961). Peu après l'ouverture de l'enveloppe ou spathe qui entoure l'inflorescence, l'anthèse se produit (sur les feuilles axillantes de rang 17 à 20, Photo 8). Les inflorescences femelles après nouaison (qui intervient peu après l'anthèse) ou régimes, se développent pendant une phase de maturation qui dure 6 mois. L'oléosynthèse, très consommatrice en énergie, débute 2 mois avant la maturité du régime (ou récolte) (Corley and Tinker, 2003a).

III.3. Impact de conditions contraignantes

De nombreuses études ont été menées pour étudier le comportement du palmier à huile en conditions hydriques limitantes (Caliman 1992, Wormer 1959, Cornaire 1994) Les périodes de sécheresses récurrentes (saisonnières) ou inopinées (mais sévères) liées au phénomène El Niño ont des effets immédiats ou différés dans le temps, touchant aussi bien l'appareil végétatif que reproducteur.

Sur l'appareil végétatif. Très rapidement, la croissance végétative est diminuée voire stoppée (Bredas and Scuvie, 1960) lors de périodes de déficit hydrique. La croissance en hauteur du stipe ralenti ou s'arrête selon l'intensité de la sécheresse. Le rythme d'apparition des feuilles est modifié ; la durée du phyllochrone augmente, l'épanouissement des feuilles se produit avec un délai de 2 à 3 mois (Ochs and Daniel, 1976). Les feuilles non épanouies (ou flèches) s'accumulent alors au centre de la couronne foliaire. Lors de périodes prolongées de sècheresse, la teneur en eau des tissus diminue rapidement entrainant un dessèchement visible des folioles, voire une casse des feuilles encore vertes et assimilatrices (Photo 12). A la reprise de la saison des pluies, l'ensemble des feuilles à l'état de flèche s'épanouit dans un intervalle de temps très court. Les dégâts que provoque une sécheresse peuvent être limités par un bon développement du système racinaire permettant une meilleure gestion de l'eau dans le sol et donc une optimisation de l'alimentation hydrique de la plante. De plus, une régulation osmotique efficace permet au palmier à huile de traverser ces périodes sèches sans chute du potentiel hydrique foliaire (Cornaire *et al.*, 1994, Nouy *et al.*, 1999). Des adaptations structurelles des cellules peuvent également s'observer : les concentrations en amidon et en glucides solubles (Adjahossou, 1983) ainsi que les teneurs et le degré d'insaturation des acides gras membranaires sont modifiés pour permettre aux cellules de garder une hydratation suffisante et augmenter ainsi leur résistance (Cornaire *et al.*, 1994).

PHOTO 12. Impact de la sécheresse sur l'appareil foliaire d'un palmier à huile adulte.

Sur l'appareil reproducteur. Les retards observés sur l'épanouissement des feuilles entrainent des retards sur l'émission des inflorescences. Une sexualisation mâle des inflorescences (Bredas and Scuvie, 1960, Caliman and Southworth, 1998) s'observe alors, entrainant une diminution du sex-ratio, et à terme une baisse significative du nombre de régimes récoltés. Des avortements précoces d'inflorescences, dont la croissance se situe 7 à 13 mois avant la récolte (Frere, 1986, Nouy *et al.*, 1999) se rajoutent à cela. La durée de maturation des régimes est par ailleurs modifiée ; en Afrique, un décalage pouvant aller jusqu'à 100 jours (Michaux, 1961) peut s'observer. Une maturation incomplète peut également s'observer dans certains cas (Ochs and Daniel, 1976). Le ratio huile sur pulpe est diminué et le taux d'extraction d'huile des régimes peut être réduits de 30 à 40%. Compte tenu des longs délais qui caractérisent le palmier à huile entre la phase de différenciation sexuelle, d'avortement et la récolte proprement dite, les impacts de la sécheresse sur le nombre de régimes récoltés seront encore visibles plusieurs mois après la fin de celle-ci.

IV. PRODUCTIVITE DU PALMIER

IV.1. Composantes du rendement

Les principales composantes du rendement chez le palmier à huile sont le nombre, le poids de régimes récoltés et le taux d'huile sur pulpe par régime. Nous rappellerons que le nombre de régimes, paramètre très variable est corrélé au rythme d'émission des feuilles, au sex-ratio et au taux d'avortement des régimes (Corley, 1977, Jones, 1997). Le poids des régimes, déterminé environ 3 à 4 mois avant la récolte, est fortement corrélé au taux de nouaison, lui-même corrélé au taux de pollinisation (5 mois avant la récolte) (Corley, 1977). Le rendement en huile des régimes dépend du nombre de fruits fertiles, du nombre de fruits infertiles, du poids unitaire d'un fruit, du ratio pulpe sur noix et du ratio pulpe sur régime. Ces caractères sont généralement spécifiques d'un génotype considéré mais peuvent également varier en fonction des contraintes rencontrées (Harun and Noor, 2002) et notamment en fonction de l'alimentation hydrique.

IV.2. Rendements moyens et variabilité

Dès la troisième année après plantation, les premiers régimes matures sont récoltés. Les rendements du palmier à huile augmentent alors et atteignent un maximum vers l'âge de 10 ans, se stabilisent puis déclinent progressivement (Corley and Gray, 1976b). Les rendements du palmier peuvent atteindre plus de 10 tonnes d'huile par hectare et par an pour les meilleurs matériels végétaux ; le rendement moyen du palmier à huile est de 4 tonnes d'huile par hectare et par an, très supérieur à la majorité des cultures oléagineuses et, en particulier, au soja dont les rendements en huile se situent autour de 0,4 tonnes par hectare et par an (Basiron, 2007). Le rendement en poids frais de fruit est généralement situé autour de 13 t ha^{-1}. Ce rendement enregistre d'importantes fluctuations (Fig. 2) intra et inter annuelles. Sur des sites subissant de sévères saisons sèches, la distribution mensuelle de la production peut varier entre 1 et 25% de la production annuelle (Nouy *et al.*, 1996). Un El Niño peut entrainer une diminution de plus de 13% des rendements par rapport à une année normale (FAOSTATS, 2008).

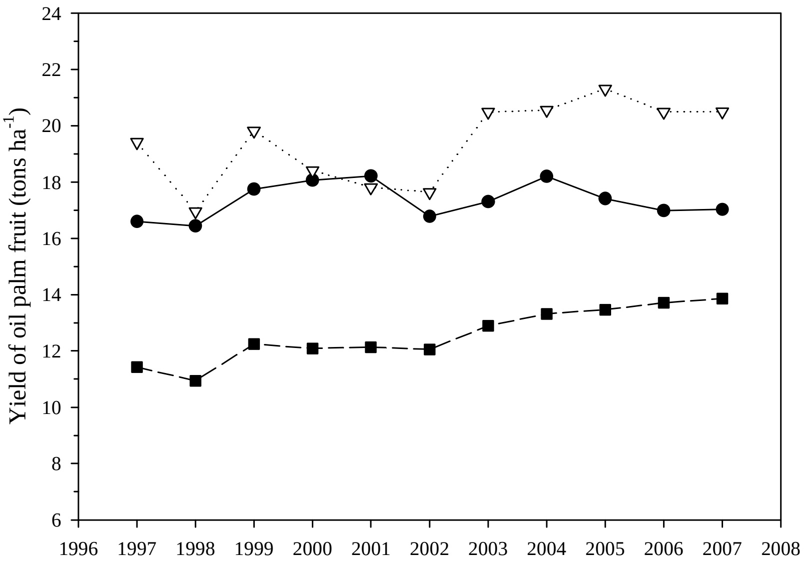

FIG. 2. Surface cultivée, production et rendement du palmier à huile en Indonésie, Malaisie et dans le monde entre 1997 et 2007. *Source : http://faostat.fao.org*

IV.3. Evolution de la productivité : moyens mis en œuvre

Les rendements du palmier à huile ont très nettement augmenté au cours des cinquante dernières années grâce à la sélection de matériels plus performants (Basiron, 2007), à une meilleure protection des cultures, à des techniques d'extraction d'huile plus performantes (Caliman *et al.*, 2005) ou encore à des pratiques culturales raisonnées et durables (Cochard *et al.*, 2005).

Une meilleure gestion de la disponibilité en eau du sol peut passer par la mise en place de systèmes d'irrigation, par une étude préalable du terrain de plantation (présence ou non de nappe phréatique peu profonde), par une adaptation du schéma de plantation en fonction de la pente pour limiter le ruissellement, par une amélioration de la structure du sol (sous-solage) (Caliman, 1992) mais aussi par la mise en place de plantes de couverture en estimant avec soin leur densité (Ochs and Daniel, 1976, Caliman, 1992, Cornaire *et al.*, 1994). Ochs (1976) identifie des variétés de plantes de couverture qui ont pour spécificité de réduire leur métabolisme en période sèche afin d'éviter une trop grande compétition avec les palmiers mais tout en gardant un sol protégé. D'autres auteurs (Ochs and Daniel, 1976, Caliman, 1992, Henson and Mohd Tayeb, 2003, 2004) préconisent une diminution de la densité de plantation, afin de réduire la compétition entre arbres et permettre ainsi une augmentation de la production de biomasse. La densité de plantation se réfléchit, notamment en fonction du type de sol et de l'architecture du matériel végétal utilisé (Henson and Mohd Tayeb, 2003). Par ailleurs, l'ablation systématique de toutes les inflorescences au jeune âge des palmiers permet aux plantes de développer un système racinaire important (Nouy *et al.*, 1999) et de favoriser le développement de l'appareil végétatif. Cependant cette pratique est à manier avec précaution même si elle est toujours utilisée au Benin, elle peut induire une plus grande vulnérabilité des arbres les années suivant l'arrêt de l'ablation (Nouy *et al.*, 1999). Sur les arbres adultes, une diminution de la charge en fruits permettrait de les aider à affronter les périodes de sécheresse intense (Daniel and De Taffin, 1976) en limitant la demande interne de la plante.

L'adaptation des techniques culturales peut s'avérer difficile à mettre en place à grande échelle (Cornaire *et al.*, 1994). Un choix raisonné du matériel végétal est donc également nécessaire, notamment avec la recherche de génotypes tolérants à la sécheresse. Ce choix doit, au préalable, s'appuyer sur la caractérisation des caractères phénologiques et physiologiques d'adaptation à la sécheresse des variétés (Cochard *et al.*, 2005).

V. GESTION DU CARBONE DANS LA PLANTE

V.1. Assimilation du carbone

Le palmier à huile présente une photosynthèse de type C3. Des taux élevés d'assimilation maximale de 23 μmoles_{CO2} m^{-2} s^{-1} ont été mesurés sur des palmiers à huile encore jeunes, âgés de 5 et 9 ans (Dufrêne and Saugier, 1993). Sur des palmiers plus âgés, un taux moyen de 17 µmoles CO_2 m^{-2} s^{-1} a été mentionné par différents auteurs (Bolle-Jones, 1968, Corley, 1983, Dufrêne, 1989, Lamade, 1993).

Il est établi que la photosynthèse du palmier à huile est sensible à certains paramètres environnementaux. L'intensité du rayonnement photosynthétiquement utilisable (RPU) est saturant à partir de 1100 $\mu\text{moles}_{\text{photons}}$ m^{-2} s^{-1} (Dufrêne, 1989). Un déficit de pression de vapeur de l'air supérieur à 1,7 kPa, provoque une fermeture des stomates (Michaux, 1961, Dufrêne, 1989, Cornaire *et al.*, 1994, Henson, 2006b) ce qui s'accompagne d'une diminution progressive de la photosynthèse. Comparé à d'autres espèces, le palmier à huile est donc une espèce très sensible au VPD. L'impact de températures élevées est sujet à controverse. Dufrêne et Saugier (1993) et Smith (1989) ne relèvent pas d'effet dépressif de températures élevées (jusqu'à 38°C) sur l'assimilation carbonée. Hong et Corley (1976) et Lamade et Setiyo (1996) observent, de leurs cotés, une réduction importante de celle-ci à partir de 34°C. Une fermeture précoce des stomates (et donc une diminution de l'assimilation carbonée) est observée lorsque le profil du sol s'assèche, cela bien avant qu'il n'atteigne le point de flétrissement (Dufrêne, 1989).

Afin d'équilibrer son bilan carboné, une plante peut ajuster son taux d'assimilation carbonée à sa demande globale à un instant *t*. Sur caféier, Frank (2006) montre, par la mesure, un ajustement de l'assimilation carbonée sur la demande reproductive (i.e. la charge en fruits). Une augmentation des teneurs en glucides dans les folioles pouvant entrainer la répression de certains gènes spécifiques (Paul and Pellny, 2003) ou encore une modification des concentrations en azote et en phosphate inorganique (Harmens *et al.*, 2000) pourraient être des signaux perçus par la plante, déclenchant un ajustement de l'offre sur la demande. Ce mécanisme de régulation s'observe également sur d'autre espèces telles que le manguier (Urban *et al.*, 2004), le cerisier (Roper *et al.*, 1988) ou encore le pêcher (Jordan and Habib, 1996, Quilot *et al.*, 2002). Sur cocotier, l'hypothèse d'une rétroaction de la demande reproductive sur les organes source a également été formulée par Mialet-Serra *et al.* (2008). A ce jour, aucun travail sur ce sujet n'a été recensé sur palmier à huile.

Certaines espèces montrent d'importantes variations intra-spécifiques de leur taux d'assimilation (Galmes *et al.*, 2007, Ullah *et al.*, 2008). Sur palmier à huile, Lamade (1996) a comparé la réponse photosynthétique de plusieurs clones en Indonésie. Les résultats obtenus indiquent des variations sensibles entre matériels utilisés. Ces observations confirment celles faites par Smith (1993) qui souligne une assimilation et une conductance stomatique différentes pour des génotypes ayant des productions contrastées. Cependant, les résultats de ces études sont à confirmer afin de s'assurer que les différences d'assimilation observées sont bien génotypiques et non liées à l'environnement.

Lors de sécheresses, les variations importantes de l'assimilation carbonée peuvent s'expliquer par une régulation stomatique très efficace chez le palmier à huile qui permet, par ailleurs, une économie d'eau par la plante. La transpiration d'une plantation adulte peut-être ainsi réduite de 10 à 20% de sa transpiration potentielle (Wormer and Ochs, 1959). Les stomates sont sensibles aux contraintes extérieures (VPD élevé, rayonnement intense…) mais également à l'état hydrique de la plante (état des réserves hydriques dans la plante, adaptation possible ou non des structures cellulaires à la déshydratation) (Cornaire *et al.*, 1994, Nouy *et al.*, 1999).

V.2. Allocation du carbone

L'accumulation de biomasse dans la plante dépend de la quantité de carbone photosynthétisée et de la fraction de carbone convertie en matière sèche (Lindquist *et al.*, 2005). L'estimation de la demande en carbone des différents organes d'une plante nécessite de quantifier leur croissance, de mesurer leur contenu en carbone mais également d'estimer leur demande en terme de respiration (Lescourret *et al.*, 1998). Classiquement, la respiration se décompose en deux composantes : la respiration de maintenance et la respiration de croissance (Johnson, 1990). La respiration de maintenance traduit les besoins métaboliques des organes (Penning de Vries, 1975). Quant à la respiration de croissance, elle considère le contenu en énergie des composés biochimiques (i.e. des carbohydrates, des lipides, de la lignine, des acides organiques, des minéraux et, enfin, des protéines) et le coût nécessaire à leur construction (Penning de Vries *et al.*, 1989).

La production de matière sèche du palmier adulte, en Indonésie, est estimé à environ 40 t_{MS} ha^{-1} an^{-1} (I Mialet-Serra, CIRAD, 'pers.comm'), production très élevée comparée à d'autres espèces tropicales ou tempérées. Un cocotier à l'âge adulte produit seulement 25 t_{MS} ha^{-1} an^{-1} environ (Mialet-Serra *et al.*, 2005). La croissance végétative d'un palmier à huile adulte, en pleine production, est supposée constante (Van Kraalingen, 1985, Corley and Tinker, 2003c). Elle est, par ailleurs, supposée prioritaire sur la croissance reproductive ce qui pourrait mettre en évidence un système limité par les sources (Van Kraalingen, 1985, Corley and Tinker, 2003c, Henson, 2007). Les assimilats dans le palmier se répartiront entre le stipe (48%), les feuilles (25%), les racines (10%), les bases pétiolaires (13%) et les inflorescences femelles principalement (3%) (les inflorescences mâles représentant un faible poids) (Corley and Tinker, 2003c, Legros *et al.*, 2006).

Afin de prendre en compte l'effet de l'environnement et, en particulier, du rayonnement solaire sur la croissance d'une plante, le calcul du ratio quantité de biomasse aérienne produite sur quantité de rayonnement absorbé par la plante (communément appelé « RUE » dans la littérature) à un pas de temps donné s'avère utile et pratique (Baille *et al.*, 2006). Ce paramètre est une variable intégrant les processus impliqués dans le développement, la morphologie, la physiologie et la biochimie de la plante (Tesfaye *et al.*, 2006). Il sera ainsi affecté par plusieurs facteurs abiotiques tels que la température, l'humidité relative, l'humidité du sol ou encore la nutrition de la plante (Lecoeur and Ney, 2003). Par ailleurs, le calcul de la RUE permet d'estimer la croissance et le rendement d'une même plante dans des environnements contrastés (Lindquist *et al.*, 2005) et de mettre en évidence des comportements distincts entre génotypes. La valeur maximale de RUE estimée pour le palmier à huile est d'environ 1,3 g_{DM} MJ^{-1} (Henson, 1991, Corley and Tinker, 2003c) ou de 1,6 g_{DM} MJ^{-1}, en tenant compte du contenu en huile des régimes. Ces valeurs sont inférieures à celles relevées chez les cultures tempérées (par exemple, la RUE du maïs est autour de 2 g_{DM} MJ^{-1} (Earl and Davis, 2003)) mais restent similaires à d'autres *Arecaceae* tel que le cocotier (Mialet-Serra *et al.*, 2008).

Un déséquilibre du bilan de carbone chez une plante entraîne inévitablement une limitation de la croissance avec, à terme, un arrêt de production de biomasse (Frank, 2005, Luquet *et al.*, 2006) ou/et une modification de la morphologie de différents organes (Balaguer *et al.*, 2001). Cependant, chaque espèce s'adapte différemment à son environnement et à ses variations. Cette plasticité phénotypique reflète la variabilité du phénotype que peut présenter un génotype placé dans des environnements différents (Barthod, 2006). Elle peut être de nature compensatrice en induisant un changement dans le nombre ou la taille des organes émis (Dingkuhn *et al.*, 2007) suite à une augmentation de la production de matière sèche ou de la vitesse de croissance végétative mais également en augmentant la mise en réserves des assimilats. Chez le palmier à huile, les variations phénotypiques dues à l'environnement dans lequel évolue la plante peuvent passer par des modifications biométriques et morphologiques de l'appareil végétatif (variation de la hauteur et du diamètre du stipe, augmentation ou diminution du nombre de feuilles produites et changement de rythme de croissance) et/ou de l'appareil reproducteur (variation du nombre et du poids moyen des régimes) (Ziller *et al.*, 1955). Chez le palmier à huile, les impacts de déséquilibres internes ou de conditions externes sur les changements de rythmes et sur les délais d'ajustement des croissances végétatives et reproductives ont rarement été quantifiés, seules des observations morphologiques et phénologiques ont été couramment réalisées.

V.3. Mise en réserves

Le stockage est une fonction majeure de chaque plante (Chapin *et al.*, 1990). Les réserves sont définies comme des ressources accumulées qui restent mobilisables afin de subvenir à la croissance et permettre un bon fonctionnement de la plante dans des conditions où la demande est supérieure à l'offre (Mialet-Serra, 2005). La nature des glucides non structuraux stockés varie en fonction des espèces et des génotypes (Kozlowski, 1992). Le saccharose, produit important de la photosynthèse, constitue des réserves durables pour beaucoup d'espèces telles que *Saccharum officinarum* (Komor, 2000), *Sorghum saccharatum* (Heller, 1969) ou encore *Cocos nucifera* (Mialet-Serra *et al.*, 2005). Cependant, l'amidon reste la forme de réserve la plus courante dans le monde végétal (Kozlowski, 1992). Il peut être stocké sous différentes forme selon la saison et l'espèce considérée.

Dans le cas du palmier à huile, le glucose est le glucide majoritaire dans la plupart des compartiments végétatifs (Legros *et al.*, 2006). Il représente plus de 50% des glucides totaux suivi du saccharose et de l'amidon qui représentent à eux deux 40% des glucides totaux. Le glucose est principalement localisé dans le stipe qui stocke à lui seul 65% des glucides totaux de l'arbre. Chez le palmier à huile, l'amidon, contrairement au cocotier (Mialet-Serra *et al.*, 2005), ne représente plus un glucide mineur. Le saccharose et l'amidon, se répartissent selon un gradient longitudinal ascendant, de la base vers le haut du stipe, contrairement au glucose présent à des teneurs plus élevées à la base du stipe. Au total, les glucides représentent 20% de la biomasse végétative totale de l'arbre (seulement 8% pour le cocotier, (Mialet-Serra *et al.*, 2005)).

Les variations saisonnières des pools de réserves et leur déterminisme sont des phénomènes complexes ; ils sont fonction de l'espèce mais également des conditions environnementales telles que l'alimentation hydrique, la température ou le rayonnement (Kozlowski, 1992). Des variations dans l'accumulation des réserves peuvent grandement influencer le métabolisme et la croissance des plantes. L'utilisation des réserves peut servir à la fois de tampon lors de déséquilibres saisonniers (Mialet-Serra, 2005) ou bien d'appoint pour redémarrer la croissance après les périodes de dormance ou de défoliation (Lacointe *et al.*, 1993). Les études qui se sont focalisées sur le rôle des réserves carbonées dans la régulation du métabolisme carboné (Hrubec *et al.*, 1985, Jordan and Habib, 1996, Silpi *et al.*, 2007), montrent que les changements de concentration en glucides solubles peuvent constituer un signal déclenchant des ajustements organogénétiques et morphogénétiques dans la plante (Luquet *et al.*, 2006, Dingkuhn *et al.*, 2007). Les variations saisonnières des glucides de réserve observées sur palmier à huile (Legros *et al.*, 2006, Mialet-Serra *et al.*, 2006) sont importantes. Leur rôle chez cette espèce reste à ce jour encore mal connu (Mialet-Serra *et al.*, 2006). Leur importance quantitative laisse penser qu'ils représentent potentiellement un réservoir tampon, qui, en l'absence complète d'assimilation carbonée, pourrait subvenir à la croissance de l'arbre pendant sept mois (Legros *et al.*, 2006) et donc tamponner les déséquilibres source-puits possibles en certaines périodes (Henson, 1999a). Des études sur palmier à huile, en cours sur ce sujet, devraient prochainement infirmer ou valider ces hypothèses notamment lors de déséquilibres saisonniers, en relation avec les variations de la demande des puits et de l'offre carbonée.

VI. PROBLEMATIQUE ET OBJECTIFS DE LA THESE

Les espèces fruitières tempérées se caractérisent par un fonctionnement rythmique marqué. Leur phénologie est ponctuée par trois événements périodiques majeurs qui sont (i) le débourrement (ou feuillaison), ponctuant la reprise de la croissance végétative après une période hivernale de quelques mois, (ii) la floraison, ponctuelle dans le temps, suivie par (iii) la fructification, phase de croissance reproductive intense. D'une année à l'autre, en fonction des aléas climatiques, ces évènements phénologiques peuvent apparaître de façon légèrement décalée dans le temps. Néanmoins, sous nos latitudes, ce calendrier s'étale sur une période courte, de quelques mois. Chez ces espèces, les croissances des compartiments végétatifs et fructifères sont généralement découplées dans le temps limitant les compétitions internes à un seul compartiment (i.e. le compartiment fructifère). Par ailleurs, en réponse à des changements environnementaux, les adaptations architecturales et fonctionnelles au sein d'une espèce sont très variées.

En conditions optimales de culture, le fonctionnement d'un palmier à huile à l'âge adulte apparaît continu. Chez cette espèce, le calendrier phénologique ne peut être facilement raisonné à l'échelle de la plante entière mais plutôt à l'échelle du phytomère (une feuille + un entre-nœud + une inflorescence mâle ou femelle). Rappelons que l'unique méristème apical produit continuellement et à intervalles supposés réguliers de nouveaux phytomères ; que chaque phytomère suit un calendrier phénologique long, quatre années s'écoulant de l'initiation de la feuille à la maturité du régime de fruits qu'elle axille et, en grande partie, caché au sein du méristème ce qui rend son suivi difficile. Au cours de ces quatre années, les principales composantes du rendement que sont le nombre et le poids des régimes à la récolte, sont dépendants chronologiquement du sex-ratio (proportion d'inflorescences femelles), d'un taux d'avortement dit précoce, d'un avortement possible du régime après nouaison (en conditions extrêmes), du ratio pulpe (ou mésocarpe) sur régime et, enfin, du ratio huile sur pulpe. Au cours de chacune de ces phases clés du développement d'un régime, un ajustement peut se produire, ajustement dont l'amplitude, l'intensité et le déterminisme (exogène et/ou endogène) sont actuellement mal connus et dont les effets ne seront visibles que plusieurs mois voire jusqu'à quatre années après. Enfin, contrairement à ce que l'on observe chez la plupart des espèces fruitières tempérées, la concomitance des croissances végétatives et reproductives suggère l'existence de compétitions plus ou moins fortes entre puits végétatifs et fructifères, mais également entre puits fructifères, qui, en fonction de leurs différents stades de maturité manifesteront des demandes énergétiques d'intensité variable. Ils semblent constituer autant de puits dont la présence et le niveau de développement à un instant donné rend ces compétitions difficiles à dissocier. Il est probable que tous ces effets conjugués soient la cause principale de variations de production intra- et interannuelles d'amplitudes fortes chez le palmier à huile.

En nous appuyant largement sur les travaux menés antérieurement sur une espèce proche du palmier à huile, le *cocotier*, nous poserons comme hypothèses de base (i) que, contrairement aux compartiments végétatifs (aériens), le compartiment fructifère d'un palmier à huile adulte est plastique et non prioritaire, probablement alimenté par un surplus d'assimilats carbonés non utilisés par la croissance végétative ; (ii) que la plasticité morphologique des compartiments en présence est supposée limitée ; et par ailleurs, (iii) que les déséquilibres que peut rencontrer un palmier adulte sont compensés, en grande partie, par une efficience d'utilisation de la lumière variable et, dans une moindre mesure, par les réserves carbonées. Par conséquent, afin d'équilibrer quotidiennement son bilan carboné, un palmier adulte mettrait en jeu trois mécanismes possibles d'ajustements (i) un ajustement de la demande reproductive (sexualisation et avortement des inflorescences, jouant sur leur nombre et leur dimension), ces ajustements sont connus, leurs déterminismes moins, (ii) un ajustement du taux d'assimilation carbonée à l'échelle foliaire, et enfin, (iii) dans une moindre mesure, le stockage et le déstockage de réserves carbonées.

Afin de suivre et décrire les demandes végétatives (aériennes) et reproductives au cours du temps (variations intra- et interannuelles), les croissances du stipe, des feuilles et des inflorescences en terme de production mensuelle de biomasse sont estimées sur 22 mois (de juillet 2006 à mai 2008), sur deux matériels végétaux (six palmiers par génotype suivi) qui diffèrent significativement par leurs performances, enregistrées sur plusieurs années depuis leur plantation en champ, et sur deux sites expérimentaux, tous deux, proches de l'équateur mais présentant des conditions agro-environnementales contrastées ; l'un présentant des conditions plutôt favorables à la culture du palmier à huile (périodes de sécheresse peu intenses), l'autre présentant des périodes de sécheresse intenses et aléatoires. La phénologie (épanouissement des nouvelles feuilles, floraisons et récolte des inflorescences femelles) est également suivie dans le temps. Parallèlement à la croissance des compartiments végétatifs et reproducteurs, des échantillons sur le principal compartiment de stockage (le stipe) sont prélevés tous les deux mois afin de suivre la variation saisonnière des réserves. Ponctuellement, sur ces mêmes palmiers, les échanges gazeux à l'échelle foliaire sont mesurés entre août et novembre 2006 et entre mai et septembre 2007.

Enfin, afin de modifier l'équilibre source-puits et, par là-même, jouer artificiellement sur les compétitions présumées fortes entre organes en croissance, une ablation systématique de toutes les inflorescences avant nouaison est réalisée en continu sur un génotype (six palmiers suivis) sur le site expérimental favorable à la culture du palmier à huile. Les paramètres de mesures précédemment décrits sont suivis dans le temps sur ces palmiers.

Nous décrirons dans le chapitre II les mécanismes d'ajustements phénologiques et de croissance des deux génotypes étudiés en relation avec les conditions environnementales variables et parfois contraignantes rencontrées lors de notre période d'observations. Compte tenu des phases longues de développement spécifiques au palmier, des séries antérieures de données climatiques et de production sont utilisées afin de parfaire cette analyse. Nous examinerons dans le chapitre III, pour une situation de rapport source : puits modifié, les mécanismes d'ajustements phénologiques, de croissance mais également physiologiques (ajustements de l'assimilation carbonée et des niveaux de réserves). Dans le chapitre IV, l'ensemble de ces résultats est repris au regard de la gestion des réserves carbonées, pool en quantité très importante à l'échelle de la plante mais aussi très variable en fonction du temps. Enfin, un modèle conceptuel cohérent décrit et explique les relations source-puits chez le palmier à huile notamment en conditions de contraintes hydriques. Ces trois derniers chapitres sont rédigés sous forme d'articles scientifiques; les deux premiers ont été soumis à *Annals of Botany*, le troisième a été soumis à *Tree Physiology*. Enfin, à partir des principaux résultats acquis, nous exposerons les perspectives ouvertes par ce travail.

CHAPITRE II:

PHENOLOGY AND GROWTH ADJUSTMENTS OF OIL PALM (ELAEIS GUINEENSIS JACQ.) TO CLIMATE VARIABILITY

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Running Title: Oil palm responses to climate

RESUME EN FRANÇAIS

AJUSTEMENTS DE LA PHENOLOGIE ET DE LA CROISSANCE DU PALMIER A HUILE (*ELAEIS GUINEENSIS* JACQ.) FACE A LA VARIABILITE DU CLIMAT

Introduction

La floraison et la production du palmier à huile montrent des variations saisonnières dont les causes sont mal connues. De plus, des périodes de sécheresse parfois intenses se rajoutent, ce qui rend difficile l'analyse de la rythmicité observée et à terme une prévision du rendement. Dans ce chapitre, phénologie, croissance, production du palmier à huile et variations climatiques intra et interannuelles sont mises en relation.

Matériels et Méthodes

A l'âge adulte, deux génotypes (63 et 83) qui diffèrent par leurs performances ont été observés pendant 22 mois consécutifs (juillet 2006 – mai 2008) sur deux sites indonésiens (Kandista (0°55'N) et Batu Mulia (3°12'S)), Batu Mulia se caractérisant par des périodes de sécheresse dont la sévérité peut être très variable d'une année sur l'autre. Afin d'évaluer l'intensité des périodes sèches rencontrées au cours de notre période expérimentale, deux variables intégratives sont simulées : (i) le « bilan hydrique climatique », différence entre la pluviométrie et l'évapotranspiration potentielle (CWB), caractérisant l'intensité du déficit hydrique sur une base climatique et (ii) la fraction d'eau du sol transpirable (FTSW), caractérisant la fraction d'eau du sol disponible pour la plante. Les productions de biomasses aériennes végétative et reproductive, la morphologie de ces différents compartiments ainsi que leur phénologie sont mesurées. Les teneurs en sucres solubles et en amidon dans les stipes sont, par ailleurs, déterminées tous les deux mois. L'efficience d'utilisation de la lumière (RUE), rapport entre la production de biomasse sèche totale aérienne et la lumière absorbée par le couvert est calculée chaque mois. Compte tenu des durées longues de différenciation et de développement des feuilles et des inflorescences, cinq années de données climatiques et de production, antérieures à 2006, sont, par ailleurs, utilisées afin de compléter et parfaire notre analyse. Celle-ci repose principalement sur de possibles effets de la photopériode (facteur pouvant imposer un rythme régulier de production) et d'autre part, sur des effets des périodes sèches (facteur pouvant perturber ce rythme).

Résultats majeurs

Pendant notre période expérimentale, les conditions climatiques sont, sur Kandista, optimales, similaires en moyenne à celles observées au cours des 12 années précédentes ; sur

Batu Mulia, 2006 et 2007 sont deux années exceptionnelles avec une saison sèche très intense en 2006 (août-octobre 2006) suivie d'une année 2007 très arrosée et d'une saison sèche peu marquée.

A Kandista, la production (qui est fonction du nombre d'inflorescences femelles différenciées) est négativement corrélée avec la photopériode. Les deux pics annuels de production semblent confirmer la théorie récente d'un contrôle circadien. Les phases sensibles à la photopériode ont été estimées à 3 (ou 3+12×n) mois avant l'anthèse pour un phytomère donné.

Une période sèche intense affecte différemment la croissance végétative et la croissance reproductive. La croissance végétative et la fréquence d'apparition des feuilles, en particulier, sont très sensibles à l'intensité des périodes sèches qui ont alors un impact en temps réel. En revanche, les impacts de périodes sèches sur la production du palmier à huile sont différés dans le temps ; ils surviendraient 29 mois avant la maturité du régime (ou récolte) ou encore 23 mois avant l'anthèse, phase pendant laquelle la différentiation sexuelle de l'inflorescence se produirait. Le nombre de régimes récoltés est alors affecté, leurs masses peu.

La grande variabilité de la RUE chez le palmier à huile, observée notamment à Batu Mulia, traduit bien les ajustements à des déséquilibres source-puits parfois marqués. Elle est, par ailleurs, corrélée négativement avec le PAR incident et positivement avec la demande reproductive. En effet, les différents décalages induits par les effets de l'environnement sur le développement des organes provoquent des déséquilibres source-puits qui sont alors tamponnés par une RUE variables et un compartiment « réserves » important et dynamique dans le stipe.

Conclusion

Les pics de floraison saisonniers du palmier à huile semblent contrôlés, même à proximité de l'équateur, par la réponse d'un phytomère à des variations même faibles de la photopériode. Ces fluctuations « naturelles » se confondent et sont parfois masquées par les effets de périodes sèches qui affectent la floraison (ou la production) avec un long décalage dans le temps. Les dynamiques qui en découlent sont complexes mais, après confirmation des ces résultats, une prévision des rendements à l'aide d'un modèle devient envisageable.

ABSTRACT

- *Background and Aims*: Oil palm flowering and fruit production show seasonal maxima whose causes are unknown. Drought periods confound these rhythms, making it difficult to analyze or predict dynamics of production. This study aimed at analyzing phenological and growth responses of adult oil palms to seasonal and inter-annual climatic variability.

- *Methods:* Two oil palm hybrids planted in a replicated design at two sites in Indonesia underwent monthly observations during 22 months in 2006-2008. Measurements included growth of vegetative and reproductive organs, morphology and phenology. Drought was estimated from climatic water balance (rainfall – potential evapotranspiration) and simulated fraction of transpirable soil water (FTSW). Radiation use efficiency was also estimated. Production history of same plants for 2001-2005 was used for inter-annual analyses.

- *Key Results:* Drought was absent at the equatorial Kandista site (0°55′N) but the Batu Mulia site (3°12′S) had a dry season with variable severity. Vegetative growth and leaf appearance rate fluctuated with drought level. Yield, a function of number of female inflorescences produced, was negatively correlated with photoperiod at Kandista. Dual annual maxima were observed, supporting a recent theory of circadian control. Photoperiod sensitive phases was estimated at 3 (or 3+12×n) months before anthesis for a given phytomer. Main sensitive phase for drought effects was estimated at 29 months before bunch maturity (23 months before anthesis), presumably associated with sex determination. Different time lags for environmental effects on organ development caused sink-source imbalances that were buffered by variable RUE and a large and dynamic carbohydrate reserve pool in the stem.

- *Conclusion:* It is assumed that seasonal peaks of flowering in oil palm are controlled, even near the equator, by photoperiod response within a phytomer. These patterns are confounded with drought effects that affect flowering (yield) with long lag. Resulting dynamics are complex but if present results are confirmed it will be possible to predict them with models.

Keywords: Photoperiodism, *Elaeis guineensis* Jacq., flowering, phyllochron, drought, radiation use efficiency, source-sink relationships, phenotypic plasticity.

INTRODUCTION

Among the major cultivated plants, oil palm (*Elaeis guineensis* Jacq.) has a unique organization that enables continuous flowering and fruiting through a linear succession of phytomers, each of them contributing to both carbon assimilation and reproduction. Oil palm is also one of the world's major sources of vegetable oil. Industrial cultivation began early in the 20th century and production has grown six-fold since 1981, expected to exceed soybean oil production in 2008 (41 vs. 39 M tons; Esteulle and Perennes, 2007). Area under oil palm is now over 13 M ha, with about 60% located in SE Asia (FAOSTATS, 2008). Increasing demand driven by global population growth and increasing per capita consumption, now at 19.8 kg vegetable oil year^{-1} capita^{-1}, is expected to be boosted further by demand for biodiesel.

Oil palm is by far the highest yielding oil crop, with fresh fruit yields exceeding 13 t ha^{-1} year^{-1}, or until 10 t ha^{-1} year^{-1} oil under favourable conditions. However, oil palm is sensitive to drought (Bredas and Scuvie, 1960, Maillard *et al.*, 1974, Nouy *et al.*, 1999). It is thus strongly affected by the increasing frequency climates anomalies such as El Niño, causing drought in SE Asia. Intra- and inter-annual yield variations are reportedly increasing (Henson, 1999a). This observation is difficult to analyze because even the physiological causes of general seasonal variation in yield are largely unknown (Henson, 2006b). Annual production is continuous but mostly (but not always) shows marked seasonal peaks which can neither be explained by carbon assimilation nor by phenology alone (Henson, 2006b).

Oil palm is a perennial, arborescent, monocotyledonous crop. Plants have a single woody stem without secondary growth. The stem has constant diameter and variable height. A single apical shoot meristem continuously produces new phytomers in regular succession consisting of a leaf, an internode and a male or female inflorescence. The development period of a phytomer, beginning with leaf initiation and ending with maturity of its axillary inflorescence, is about four years (Corley, 1977). This period, however, varies by several months (Henson, 2007) because flowering and maturity dates show a marked seasonal rhythm, whereas the corresponding phytomers are initiated at intervals supposed regular. The causes of this seasonal variation is poorly understood and does not seem to be directly related to climatic variables (Henson, 2006b).

The main yield components of oil palm are the number and weight of fruit-bearing (female) harvested bunches per month (Corley, 1977, Corley and Tinker, 2003c). They are, in chronological order, determined by sex-ratio, fraction of aborted inflorescences, fraction of bunch failure and the rates of pulp into the bunch and of oil into the pulp (determining the oil extraction rate) (Corley, 1977). These successive adjustment processes of yield components are affected by various external and internal factors (Corley and Tinker, 2003c).

In contrast to reproductive growth, vegetative growth and development are continuous and comparatively constant (Corley and Tinker, 2003c, Henson, 2007; for coconut: Mialet-Serra *et al.*, 2008). It was therefore suggested that vegetative growth and development of oil palm constitute priority sinks for assimilates, whereas reproductive growth is highly plastic and depends on excess assimilates not needed for vegetative growth (Henson, 2007).

Given the long development period of inflorescences, the different adjustment processes of yield components during this period, and the large number of inflorescences in different developmental stage present on a plant at any given time, it is difficult to study the effect of climatic variability on yield. For example, some effects of a drought period on yield components occur with long lag periods because drought-sensitive processes such as sexualization or early inflorescence abortion take place months or years before the maturity of a given bunch (Dufour *et al.*, 1988, Caliman and Southworth, 1998). The same stress period may thus cause different responses on different phytomers (Jones, 1997). These phytomers, in turn, are not independent from each other because they depend on shared resources within the plant, probably causing complex feedbacks at the scale of the plant.

In plants having limited morphological plasticity and long lags between organ initiation and expansion, such as oil palm and coconut (Mialet-Serra *et al.*, 2008), large fluctuations in whole-plant assimilate source-sink relationships can be expected due to season (periods of fruit load) or drought periods. For coconut, biologically and structurally similar to oil palm, it was observed that such transitory imbalances are in small part buffered by carbohydrate reserves, and to a greater extent by fluctuations in radiation use efficiency (RUE) (Legros *et al.*, 2006, Mialet-Serra *et al.*, 2008). Adjustments in phenology, organ growth rate and final organ size, however, have too long a lag period to compensate for sink-source discrepancies in the short term (Jones, 1997).

The recent findings on coconut may provide a model for the study of yield variability in oil palm. However, the specificities of oil palm, such as yield components (e.g. environment effects on bunch sexualisation), the seasonal rhythms of flowering and the extraordinary yield potential distinguish this crop from coconut. The present study attempted to relate seasonal and inter-annual variations in RUE, vegetative growth, phenology and yield components to climatic variables and rainfall. Adult populations of two genotypes reputed to differ in productivity were observed during two years at two sites in Indonesia, one of them prone do seasonal drought periods indeed severe drought periods. The results will serve to build a crop model for oil palm.

MATERIALS AND METHODS

Experimental site

The study was conducted on two experimental plantations of the SMART Research Institute (SMARTRI, SMART Tbk.) located in Kandista Estate (Riau province, Sumatra island, Indonesia, 0°55′0′′ N, 101°21′0′′ E, 100 m asl) and Batu Mulia Estate (South Kalimantan province, Borneo island, Indonesia, 3°12′15.4′′ S, 116°01′46.9′′ E, 15 m asl). Both sites have tropical humid climate. In Kandista, the rainy season occurs between November to January, in Batu Mulia between March to May with a monthly mean rainfall of 240 mm month^{-1} (averages for 1993 – 2005 in Kandista and 2001 - 2005 in Batu Mulia). A drier season usually occurs from June to August in Kandista and from August to October in Batu Mulia. Importantly for this study, the dry season in Batu Mulia (67 mm month^{-1}) is more pronounced than in Kandista. Mean daily global radiation (Rg) during the dry season (wet season) in Kandista and Batu Mulia is 18.9 MJ m^{-2} day^{-1} and 17.2 MJ m^{-2} day^{-1} (16.9 MJ m^{-2} day^{-1} and 16.1 MJ m^{-2} day^{-1}). Mean air temperature is 27.4°C and 27.6°C (27.0°C and 27.8°C), mean relative humidity is 79.0% and 75.8% (81.1% and 81.5%), mean vapour pressure deficit (VPD) is 0.98 kPa and 1.25 kPa (0.84 kPa and 0.93 kPa) and mean evapotranspiration (Penman-Monteith) is 4.5 mm and 4.1 mm (3.9 mm and 3.6 mm). Kandista is considered favourable (drought free) site for oil palm with regular water deficit periods being short and climatic water balance not falling below 150 mm month^{-1} (see climatic water balance in Fig. 1). Batu Mulia is characterized by longer and sometimes severe dry seasons.

Soil in Kandista is a sandy loam of homogeneous texture with more than 3 m depth (78.0% sand, 11.1% silt and 10.8% clay). Soil water content at field capacity (pF 2.5) and permanent wilting point (pF 4.2) is 0.17 and 0.06 m^3 m^{-3} respectively. Soil in Batu Mulia is a silty clay soil with 2 m depth (25.1% sand, 44.1% silt and 30.8% clay). Soil water content is 0.37 m^3 m^{-3} at pF 2.5 and 0.24 m^3 m^{-3} at pF 4.2.

Plant material

Two genotypes were studied (genotype 63 and 83). Both are *tenera* hybrids, commonly high-yielding for palm oil and results of crosses between *dura deli* origin (fruits with thin mesocarp and large kernel) and *pisifera avros* origin (fruits with thick mesocarp, no endocarp and small kernel) varieties. Genotype 63 is reputed to have higher productivity and supposed to have greater drought resistance than 83. Genotypes were also chosen because of different mean yields (higher for 63) at the two sites in 2000-2005 (Table 1) and, according to visual assessment, different crown characteristics (more profuse for 83).

TABLE 1. Mean annual yield and yield component of oil palm genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia for 2000-2005. Values are means ± s.e.m. of 64 plants. Significance level of effects (ANOVA): ns = not significant, ** = very significant ($0.01>P>0.001$), *** = highly significant ($P>0.001$). Different letters within a column indicate a significant difference at $P<0.05$ (Tukey's test).

Site	Effect	Number of mature bunches (plant^{-1} year^{-1})	Total bunch dry mass yield (kg plant^{-1} year^{-1})	Mean bunch dry mass (kg bunch^{-1})
	Genotype			
Kandista	Genotype 63	14.26 ± 0.25 a	122.2 ± 2.0 a	8.6 ± 0.1
	Genotype 83	12.97 ± 0.24 b	114.4 ± 1.8 b	8.9 ± 0.1
	P	***	**	ns
Batu Mulia	Genotype 63	12.65 ± 0.44 a	98.5 ± 3.5 a	7.9 ± 0.1 b
	Genotype 83	9.75 ± 0.28 b	81.7 ± 1.9 b	8.5 ± 0.2 a
	P	***	***	**
	Site			
	P (genotype 63)	**	***	***
	P (genotype 83)	***	***	ns
	Genotype×Site			
	P	ns	ns	ns

Experimental design

The experimental plots were part of two larger, long-term genetic trials covering 30 ha in Kandista and 9 ha in Batu Mulia. Planting density was 136 plants ha^{-1} in a 9.5 m equilateral, triangular pattern. Plants were 13 years old at the onset of the study (July 2006). The present experiment took advantage of the replicated block design already in place. Our study had six replicates at each site and for each genotype, based on one plant per replicate selected randomly from within plots, and located sufficiently far from the plot border to avoid border effects.

Calculation of photoperiod, climatic water balance and Fraction of Transpirable Soil Water

Photoperiod (PP) or day length was defined as the duration between sunrise and sunset including civil twilight. It was calculated according to Forsythe *et al.* (1995) and Almorox *et al.* (2005).

To evaluate drought extent, two integrative variables were calculated. Climatic water balance (CWB), calculated as rainfall minus potential evapotranspiration (PET), is the core indicator for the length of growing period in agro-ecological zoning for rainfed systems (FAO, 1996). PET (mm month^{-1}) was calculated according FAO guidelines (Allen *et al.*, 1998). The second indicator of drought used, the simulated fraction of transpirable soil water (FTSW), estimated the soil water available to the plant on the basis of daily rainfall, estimated runoff (considered zero in Kandista because of light-textured soil), soil surface evaporation (function of topsoil humidity, PET and the fraction of radiation penetrating the canopy), soil water extraction by the plant (function of PET, crop coefficient K_c and FTSW acting as brake on transpiration according to FAO guidelines (Allen *et al.*, 1998)), water holding capacity of the soil between wilting point (pF 2.5) and field capacity (pF 4.2), and deep drainage of the fraction of precipitation not consumed by these processes.

The model used here, '*EcoPalm 2008*' (http://ecotrop.cirad.fr) will not be presented here in full because only its water balance routine was used. Only essentials of this routine are described in the following because it is an adaptation of a generic FAO model (Allen *et al.*, 1998) and has been described elsewhere in detail (Sultan *et al.*, 2005, Mishra *et al.*, 2008).

Two soil layers were defined: a top (with a z_S depth or thickness) and a deep (with a z_D thickness) layers; the root front depth was defined as z_S+z_D. For each site, soil was considered homogeneous through the profile. FTSW, calculated at daily time step (t), was defined as the ratio between the available soil water and the maximum available soil water in the two previous layers:

$$FTSW(t)=\frac{AW_S(t)+AW_D(t)}{TAW_S+TAW_D}$$

where TAW_S and TAW_D are the maximum available soil water in the top (TAW_S) and deep (TAW_D) layers. $AW_S(t)$ is defined as the daily water storage in the top layer of soil, $AW_D(t)$ as the daily water storage in the deep layer of soil.

In the top layer, $AW_S(t)$ is calculated as:

$$AW_S(t)=AW_S(t-1)+R(t)-\left(R_f(t)+E_S(t)+Tr_P(t).\frac{z_S}{z_S+z_D}\right)$$

where $AW_S(t-1)$ is the water storage in the top layer of soil calculated during the previous day; $R(t)$, the daily rainfall (mm day^{-1}); $R_f(t)$, the run-off (mm day^{-1}); $E_S(t)$, the soil evaporation (mm day^{-1}) calculated as described by Allen *et al.* (1998); and Tr_P is plant transpiration (mm day^{-1}).

In the deep layer, $AW_D(t)$ is calculated as:

$$AW_D(t) = AW_D(t-1) + R(t) - \left(D_r(t) + Tr_P(t).\frac{z_D}{z_S + z_D} \right)$$

where $AW_D(t-1)$ is the water storage in the deep layer of soil calculated during the previous day; $D_r(t)$, the drainage (mm day^{-1}) after run-off, soil evaporation and plant transpiration and Tr_P is plant transpiration (mm day^{-1}).

The depth of the soil horizon in which the majority of oil palm roots (ca. 80%) are present was set to 3 m in Kandista and 2 m in Batu Mulia, based on observation made in several trenches dug on each plot (data not presented). Trenches were made sufficiently far from the plant individua studied to avoid effects on their water balance.

We are aware that FTSW simulated with this model corresponds to reality in absolute terms, which would require a more detailed and carefully calibrated model. For this study, simulated FTSW represents an index variable that has the advantage, as compared to CWB, to take into account soil water depletion during protracted periods of water deficit.

Measurement of stem growth rate

Stem height (from the rachis basis (the insertion point of the first leaflets on the rachis) of the leaf rank 17 (a fully and mature expanded leaf, counted from the youngest leaf rank 1 in the crown top) to the ground) was measured monthly since July 2006. Oil palm stem has no secondary growth and therefore has constant diameter. New biomass growth was assumed to occur at the top of the stem only. Stem growth rate (kg_{DM} month^{-1}) consisted of three fractions, (i) the dry mass production of new internodes associated with new phytomers and new leaf emission, (ii) the dry mass increment of the older stem parts due to lignification (Corley and Tinker, 2003c), assumed to be constant (equal to 0.00074 g cm^{-3} month^{-1}, I. Mialet-Serra, CIRAD, 'unpubl. res.') and (iii) non-structural carbohydrate reserve variations calculated from observed variations of concentrations at four different stem heights and dimensions. Due to reserves, overall vegetative growth was alternatingly positive and negative, depending on reserve mobilization and storage.

Measurement of leaf growth rate

The total number of fully expanded leaves, of newly appeared leaves and of pruned or broken leaves were recorded twice a month from July 2006 onwards. The morphology of each fully expanded leaf was described when leaves were pruned at the time of bunch harvest. Dry mass of the whole petiole, rachis and the leaflets, and the leaflet number were measured. To obtain the aggregate and monthly dry mass growth rates for all leaves on a plant, we plotted the time-course of monthly dry mass increment of each new leaf produced. We assumed that leaf growth followed a linear function over three months, the time of the rapid growth just before the date of the leaf appearance.

Reproductive growth rate and yield components

Time of anthesis (equal to spathe opening date, for female inflorescence only) and maturity (equal to harvest date for female inflorescence or bunch) were monitored. At maturity, the number of fertilized and unfertilized fruits was recorded, dry mass of the peduncule, the spikelets and the two major fruit compartments (pulp and kernel), and oil:pulp dry mass ratio were measured. Growth rate (kg_{DM} $month^{-1}$) of each developing female inflorescence was assumed to follow a linear function over ten months (time of rapid growth before and after anthesis) and plotted each month.

The proportion of female inflorescences was expressed as a fraction of the productive phytomers over the experimental period (ratio between the total number of harvested bunches and the number of newly appeared leaves).

Partitioning of aboveground dry matter production to fruits was assessed as harvest index (HI: entire fruit dry mass production divided by total aboveground dry mass production for a given month).

Radiation use efficiency (RUE)

Radiation use efficiency (RUE, g_{DM} MJ^{-1}) was determined at monthly integration as the ratio between monthly aboveground dry mass production and absorbed PAR. Dry matter production thereby included the incremental weight gain of leaf and inflorescence growth using interpolation, stem structural growth calculated from height and width, and stem carbohydrate reserve pool as measured on drill cores. PAR absorption was calculated from: (i) LAI determined monthly as mean of leaflet dry mass multiplied by the specific leaf area (SLA, measured on pruned leaves) and total fully expanded leaf number in the crown; and (ii) the monthly absorbed PAR by the canopy. The latter was calculated with a radiation transfer model coupled with a 3D architectural model (Dauzat and Eroy, 1997, Mialet-Serra *et al.*, 2001) of oil palm calibrated by the observed LAI and specific architectural parameters measured on separate sets of plants on the same plots (leaf length, insertion angle, curvature and geometry of the leaves). The 3D model was canopy based and thus took distance between plants into account. The same procedure for RUE estimation was reported for coconut by Mialet-Serra *et al.* (2008).

Non-structural carbohydrates in the stem

Sampling for sugar analyses used similar methods as those used in a previous study on coconut trees (Mialet-Serra *et al.*, 2008). Observations were made every two months for a period of 22 months (from July 2006 to May 2008). Samples were generally taken in the morning, a procedure that took several days and two hours per day. Radial core samples were taken using a Pressler drill (6.6 mm × 300 mm). On the stem, the samples (one or two cores) were collected at four levels (stem height divided by four from the point below the lowest leaf of the crown). Sampled cores were placed in an ice box until further processing in the laboratory. The biochemical method used in the laboratory for sugar analysis was based on High Performance Liquid Chromatography (HPLC) and was reported in detail by Mialet-Serra *et al.(2005)*.

Statistical analysis

Two-way analysis of variance (ANOVA, Statistix, version 8.1, Analytical Software, Tallahassee, USA) was performed to evaluate the effect of genotype (genotypes 63 and 83) and site (Kandista and Batu Mulia) on yield and growth parameters. Linear regression analyses (Statbox, version 6.5, Grimmersoft) were used to identify correlations between monthly number of harvested bunches (corresponding to flowering events six months earlier), photoperiod (PP) and fraction of transpirable soil water (FTSW). It was thereby assumed that factors affect bunch number with specific delays (lag periods) in the order of months to maximally four years, which is the estimated maximal development period for an individual phytomer (Corley, 1977, Adam *et al.*, 2005). Resulting regression slope variables (indicating magnitude of effect) were used to identify propably lag periods.

The same statistical package was used to perform stepwise multiple linear regressions to explain RUE variations using various climatic variables and plant parameters as predictors. Monthly incident PAR was thus retained as principal predictor.

RESULTS

Production and climatic history of the experimental plots

Mean annual production statistics are shown in Table 1. Dry fruit yield was significantly higher in genotype 63 than in 83, and higher in Kandista than in Batu Mulia. Differences in yield were mainly due to bunch number and not due to mean bunch weight which was similar for both genotypes.

Regular seasonal peaks of production, resulting from seasonal concentration of flowering events, are usually observed after the 10th year after planting (JP Caliman, SMARTRI, Indonesia, 'pers. comm.'), corresponding to about late 2003 in this study. The known production history of the genotype population in terms of number of harvested bunches per month and per hectare (Fig. 1) confirms the occurrence of synchronous production peaks for the two cultivars from about 2003 onwards at both sites, whereas a rather chaotic dynamics was observed earlier. In Kandista, production after 2003 showed a seasonal rhythm with peaks occurring early in the 2nd half of the year (August to October), corresponding to peak flowering dates six months earlier (February to April). This pattern was associated with the absence of a marked dry season, as shown by the climatic water balance (CWB) in Fig. 1: only rarely, the CWB was negative in two consecutive months, and whenever it happened, it was not during a consistent time of year. In Batu Mulia, seasonal peaks of production after 2003 were much more irregular than in Kandista although mostly simultaneous for the two cultivars, falling roughly on Nov. 2003, May 2004, May 2005, Jan. 2006, May 2006, May 2007 and Nov. 2007. Marked minima of production occurred for both cultivars around Aug. 2003, Mar. 2004, Mar. 2005 and Nov. 2006 (Fig. 1). These time courses were associated with the occurrence of a marked dry season early in the second half of the year (i.e. August to October), as indicated by clusters of months having negative CWB. This dry season, however, varied among years in intensity and duration, and was completely absent in 2003. Neither the peaks nor the minima of production coincided consistently with dry periods.

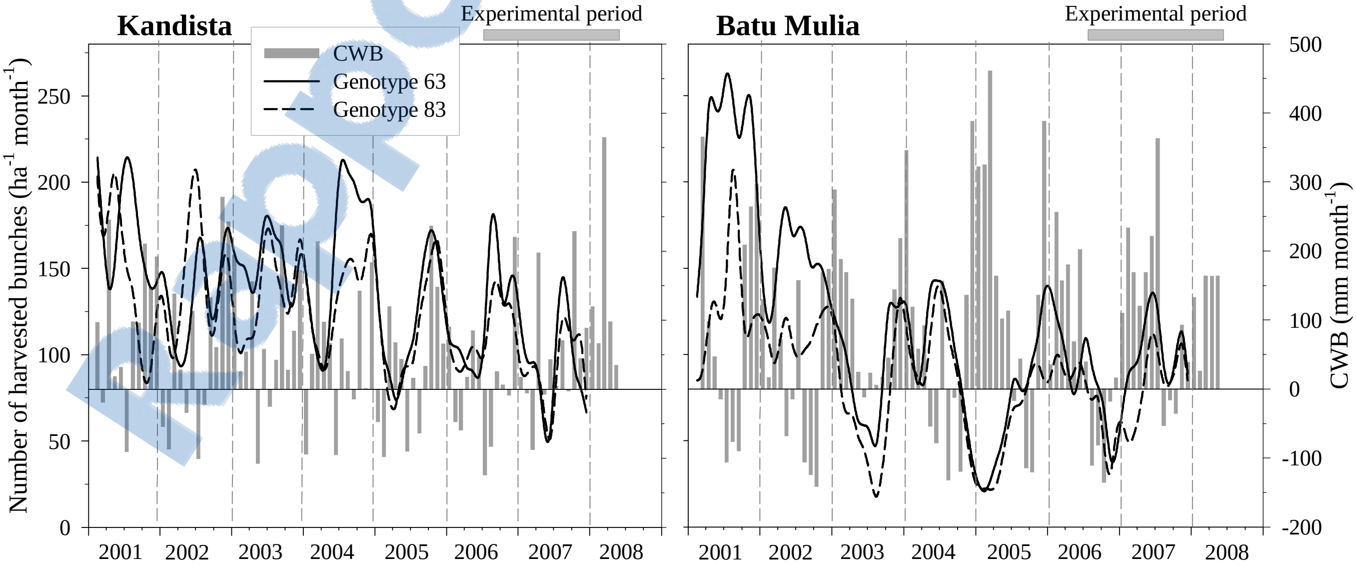

FIG. 1. Time courses of monthly number of mature bunches and climatic water balance (CWB = monthly rainfall – potential evapotranspiration) for oil palm genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia for January 2001 - April 2008. Data source: SMARTRI data base.

Production rhythms vs photoperiod and drought periods

Given the probability that environmental effects on production involve long lag periods in oil palm due to phenology of reproductive organs, the thus described plot production and climatic history will be used where appropriate to explain the experimental observations. In particular, we will consider possible effects of photoperiod (as a potential cause of underlying production rhythms) and drought periods (as a factor disturbing such rhythms).

Maxima of production related to photoperiodic control of flowering should be annually recurrent and inverted between Kandista and Batu Mulia because the former is located North and the latter is South of the equator (although both are nearly equatorial). Consistently recurring annual peaks of bunch number (corresponding to female inflorescences) fell roughly on September-October in Kandista and on May in Batu Mulia, although peaks were at times small at the latter site. Additional, sometimes dominant peaks were observed around November in Batu Mulia. This November peak was absent in 2004 and possibly masked by an 8-month long depression of production of unknown origin.

Climatic conditions during the period of detailed plant observations

In Kandista, climatic conditions during the experimental period (July 2006 to May 2008; Fig. 2) were similar to the average recorded for the previous 12 years. The beginning of this period was characterized by a 2-month drought spell (July and August 2006), followed by mostly abundant rainfall. In Batu Mulia, however, 2006 and 2007 were unusual years, 2006 having a severe dry season (only 51 mm) from August to October, and 2007 being a wet year with heavy rainfall in June and July (750 mm) followed by a mild dry season. Mean monthly Vapour Pressure Deficit (VPD), to which oil palm is known to be sensitive (Dufrêne and Saugier, 1993), fluctuated between 0.7 and 1.0 kPa in Kandista and 0.8 and 1.2 kPa in Batu Mulia, except during the severe dry season of 2006 when it attained 1.7 kPa. In Batu Mulia, maximum temperature was around 33.2 in 2006 i.e. 1°C higher than in 2007 whereas minimum temperature were similar among years (22.5°C).

In Batu Mulia, simulations suggested that during the 2006 dry season, mean monthly FTSW dropped to 0.25 and remained for three months below 0.5, whereas it barely dropped to 0.5 in the 2007 dry season. In Kandista, mean monthly FTSW dropped to 0.4 in August 2006, constituting a mild stress.

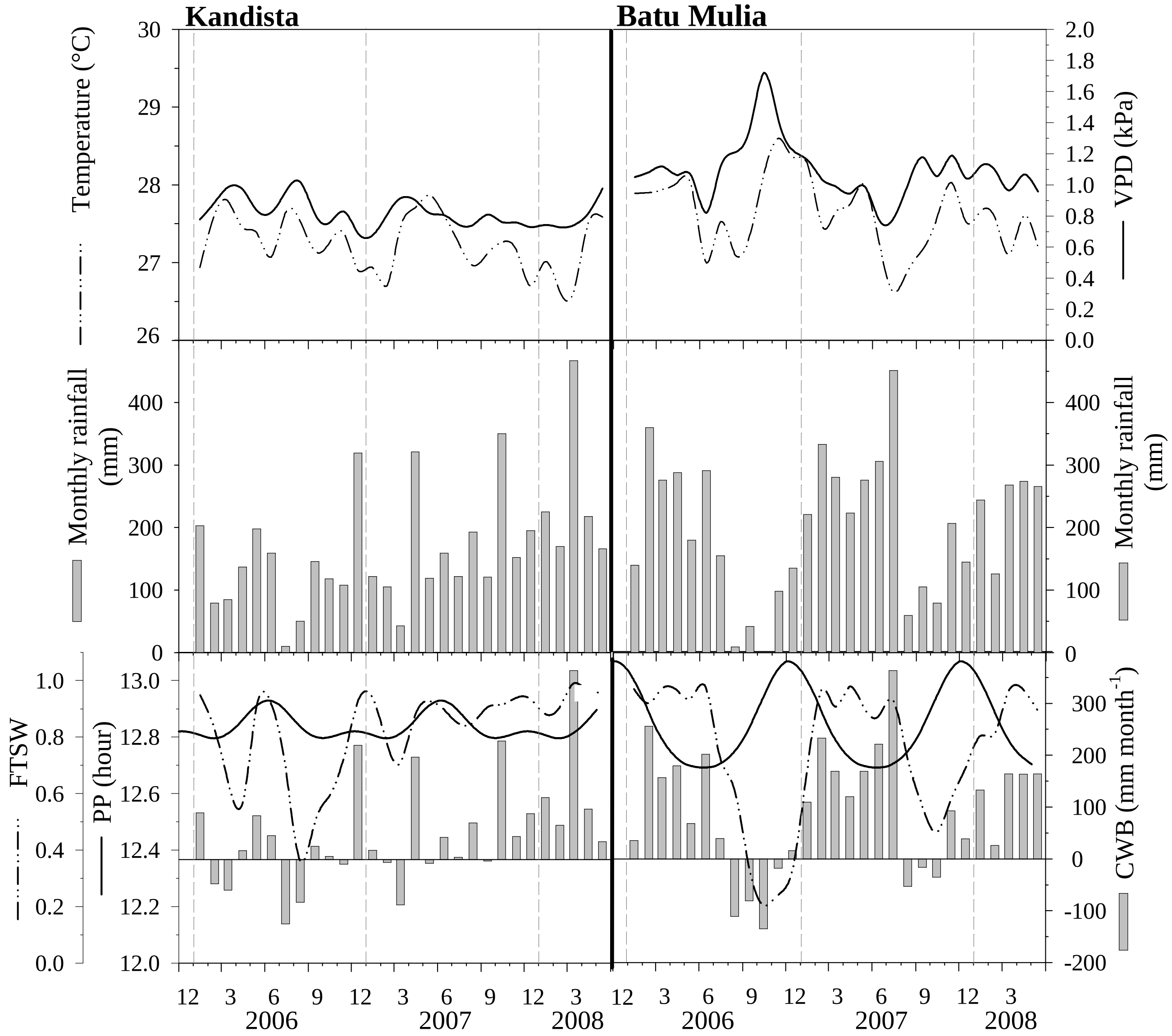

FIG. 2. Time courses of environmental parameters at Kandista and Batu Mulia sites in Indonesia for January 2006 – May 2008. Top: monthly averages of daily mean air temperature and vapour pressure deficit (VPD). Center: monthly cumulative rainfall. Bottom: Photoperiod (PP), simulated fraction of transpirable soil water (FTSW) and climatic water balance (CWB = monthly rainfall – potential evapotranspiration)

Plant and canopy structure

Vegetative plant development was generally inferior in Batu Mulia, the site affected by a marked dry season, than at the more favourable site Kandista (Table 2). The two genotypes had the same LAI at Kandista (5.1) but genotype 63 had slightly lower LAI than 83 in Batu Mulia (3.66 *vs* 3.93, $P<0.05$). The morphological components (leaf number, SLA) of LAI were different among the genotypes, genotype 63 having a smaller number of leaves in the crown and higher SLA, but larger and heavier leaves and leaflets than genotype 83. (Mean leaf and leaflet weights were not statistically different *per se* but the significant differences in SLA, LAI and leaf number indicate that leaf size must have been different.) Simulated light interception was similar among genotypes and sites (85% in Kandista and 82% in Batu Mulia).

TABLE 2. Mean canopy properties of oil palm genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia for the experimental period (July 2006 – April 2008). Values are means ± s.e.m. of six replicates. Significance level of effects (ANOVA): ns = not significant, * = significant ($0.05>P>0.01$), ** = very significant ($0.01>P>0.001$), *** = highly significant ($P>0.001$). Different letters within a column indicate a significant difference at $P<0.05$ (Tukey's test). LAI, Leaf Area Index; SLA, Specific Leaf Area; PAR, Photosynthetically Active Radiation.

Site	Effect	Mean fully expanded leaves	LAI	SLA	Dry mass		PAR interception
		(plant^{-1})		(m² kg^{-1})	(g leaf^{-1})	(g leaflet^{-1})	(%)
	Genotype						
Kandista	Genotype 63	29.5 ± 0.9	5.10 ± 0.11	7.88 ± 0.08 a	4050 ± 124	1554 ± 34	85.5 ± 0.3
	Genotype 83	33.4 ± 1.7	5.09 ± 0.24	7.02 ± 0.18 b	3684 ± 203	1460 ± 80	85.4 ± 0.6
	P	ns	ns	**	ns	ns	ns
Batu Mulia	Genotype 63	25.1 ± 1.5 b	3.66 ± 0.21 b	7.66 ± 0.17 a	3806 ± 107	1315 ± 51	81.7 ± 0.5
	Genotype 83	30.9 ± 1.1 a	3.93 ± 0.14 a	7.09 ± 0.09 b	3714 ± 123	1274 ± 63	82.4 ± 0.3
	P	*	***	*	ns	ns	ns
	Site						
	P (genotype 63)	*	***	ns	ns	**	***
	P (genotype 83)	ns	**	ns	ns	ns	**
	Genotype×Site						
	P	ns	ns	ns	ns	ns	ns

Vegetative growth and development rate

Phyllochron was not different between genotypes but significantly longer ($P<0.01$) in Batu Mulia (20 days) than in Kandista (17 days) (Table 3). Mean stem axial growth rate for the experimental period was identical for the genotypes and sites. Overall plant height was similar for the genotypes but slightly lower in Batu Mulia than in Kandista, particularly for genotype 63 (8.2 m in Batu Mulia *vs* 9.7 m in Kandista).

TABLE 3. Mean stem height at the beginning of observations period in July 2006, and mean stem height growth and phyllochron duration from that date until May 2008, for oil palm genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia. Values are means ± s.e.m. of six replicates. Significance level of effects (ANOVA): ns = not significant, ** = very significant ($0.01>P>0.001$), *** = highly significant ($P>0.001$).

Site	Effect	Initial stem height (cm)	Stem growth (mm day^{-1})	Phyllochron duration (days)
	Genotype			
Kandista	Genotype 63	973 ± 26	1.73 ± 0.11	17.1 ± 0.5
	Genotype 83	894 ± 47	1.69 ± 0.08	16.9 ± 0.5
	P	ns	ns	ns
Batu Mulia	Genotype 63	825 ± 19	1.62 ± 0.09	19.8 ± 0.5
	Genotype 83	778 ± 36	1.72 ± 0.24	20.4 ± 0.6
	P	ns	ns	ns
	Site			
	P (genotype 63)	***	ns	**
	P (genotype 83)	ns	ns	**
	Genotype×Site			
	P	ns	ns	ns

Monthly time courses of the structural growth rate (excluding non-structural carbohydrates in the stem) of bulk, aboveground, vegetative organs (stem+leaves) were near-identical for the two genotypes at each of the two sites (Fig. 3C-D). In Kandista, only minor fluctuations over time were observed, among them a significant ($P<0.05$) depression in September to October 2006 that coincided with a dry spell, as indicated by CWB and simulated FTSW (Fig. 3A). Another such dip, which fell into a wet period, was observed around December 2007. The magnitude of these fluctuations did not exceed ±10% of the mean, or 9 kg plant^{-1} month^{-1}, for both genotypes.

In Batu Mulia, time course variations of structural aboveground vegetative growth rate were much greater (Fig. 3D). In particular, rates dropped to 3 to 4 kg plant^{-1} month^{-1} for both genotypes in October and November 2006, associated with a particularly pronounced dry season as indicated by CWB and simulated FTSW (Fig. 3B). During the subsequent dry season in August to October 2007, which was much milder, a slight depression of growth rates was also observed.

The time courses of the leaf appearance rate (the reciprocal of phyllochron) were nearly identical to that of vegetative growth rate at both sites (Fig. 3G-H). Again, the genotypes showed near-identical behaviour, both in terms of absolute rates and their variability.

Overall, CWB seemed to explain vegetative growth rates better than FTSW because changes of the latter occurred with a 1-month delay, a result of the buffer effect of the soil water reservoir. It therefore seems that vegetative growth responses to drought were rapid, either related to the more rapid changes in the top soil layer or to atmospheric drought. The abrupt drop of growth rates in June 2007, however, was probably not related to drought (which set on only 2 months later) but to excess rainfall resulting in water logging (observed visually in the field, no data available).

Total aboveground vegetative growth rates, including structural growth and dynamics of the non-structural carbohydrate reserve pool in the stem (Fig. 3E-F), were markedly different from structural growth alone. Strong seasonal oscillations were observed indicating periods of storage and mobilization, and only some of them could be explained by the measured environmental variables. Among them, in Kandista, was a significant ($P<0.05$) depression in September to October 2006, observed for both genotypes, that coincided with a dry spell, as indicated by negative values of CWB and low simulated FTSW (Fig. 3A). The subsequent, complex dynamics of total aboveground vegetative growth rates (Fig. 3E) showed no similarity with dynamics of environmental variables and were probably in part related to variations in demand for reproductive growth, which also showed strong seasonal variations (Fig. 4), and in part related to large experimental errors caused by calculations of differentials between subsequent months.

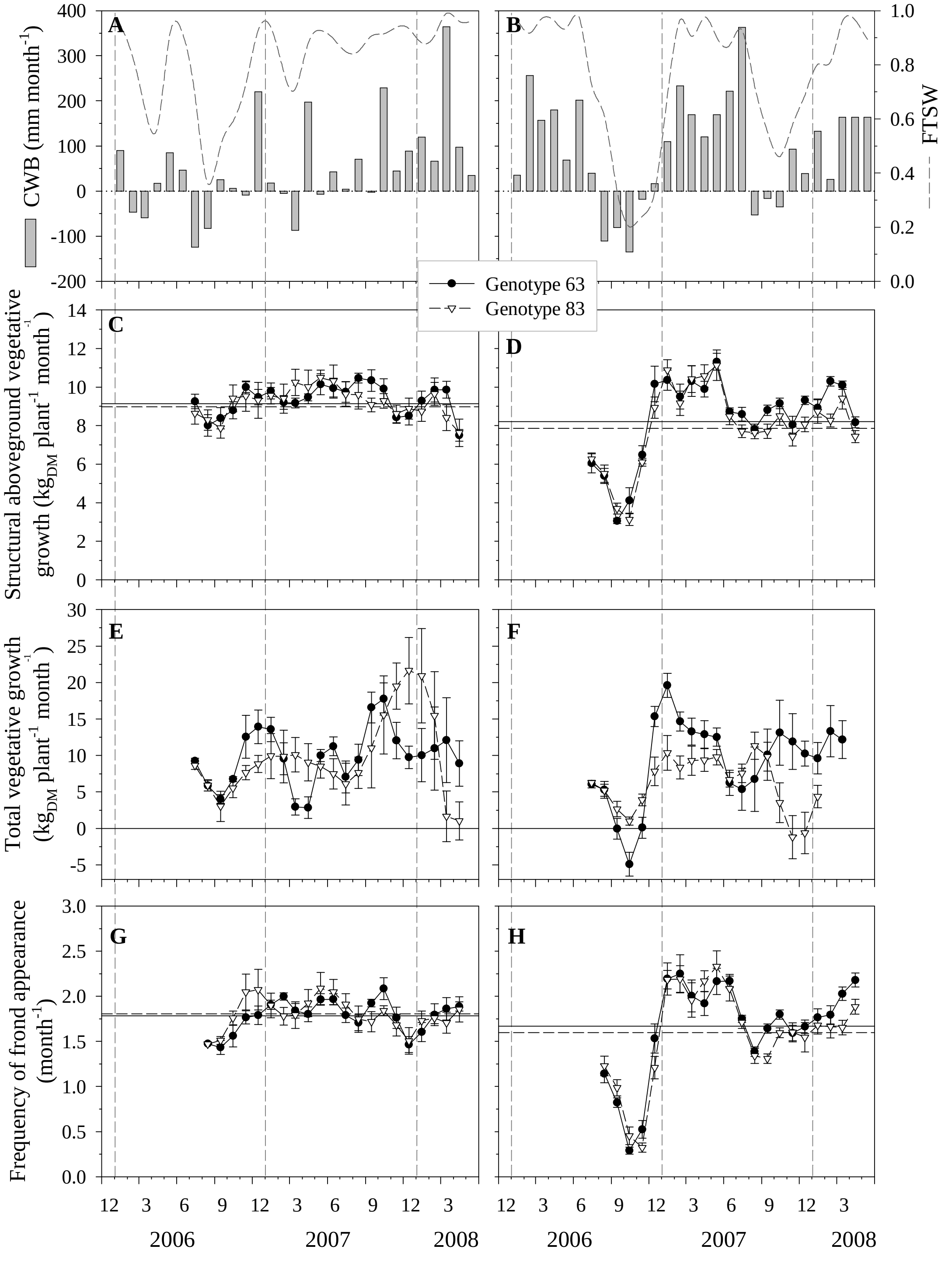

FIG. 3. (A-B) Time courses of drought indicators (FTSW and CWB as in Fig. 2) and (C-D) structural aboveground vegetative growth, (E-F) total aboveground vegetative growth and (G-H) development rates of aboveground vegetative organs for oil palm genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia for July 2006 - April 2008. Values are means of six replicates and bars indicate s.e.m. (______) and (_ _ _ _ _) lines indicated means for genotypes 63 and 83, respectively, over the observation period.

In Batu Mulia, time course variations of total aboveground vegetative growth rate (Fig. 3F) showed a depression for both genotypes centered in October 2006 which was associated with the particularly severe dry season (Fig. 3B). Growth rates dropped to -4.9 kg plant^{-1} month^{-1} for genotype 63 and 1.0 kg plant^{-1} month^{-1} for genotype 83 (Fig. 3F).During the subsequent dry season in August to October 2007, genotype 83 also showed a depression of growth but genotype 63 did not. Again, large experimental errors and possible interactions of demand for reproductive growth (Fig. 4) with reserve dynamics may have caused these complex patterns. Reserve dynamics (data not presented) constituted a dominant component of stem dry weight dynamics and were thus responsible for most of the strong seasonal fluctuations observed for vegetative aboveground growth.

Reproductive growth rate

Dry-matter based, monthly rates of growth of bulk reproductive organs (Fig. 4C-D) varied strongly at both sites and for both genotypes. In Kandista, growth rates varied between 3 and 15 kg plant^{-1} month^{-1} for genotype 63 (mean: 8.5 kg plant^{-1} month^{-1}) and between 4 and 13 kg plant^{-1} month^{-1} for genotype 83 (mean: 7.9 kg plant^{-1} month^{-1}) (Fig. 4C). Time courses of the two genotypes had some similarities, e.g. a maximum at the beginning of the observation period and a minimum in mid 2007. The number of bunches harvested per month (Fig. 4E) largely explained the dynamics of reproductive growth rate.

In Batu Mulia, reproductive growth (Fig. 4D) showed a similar magnitude of monthly variations but at a slightly lower level (means: 7.1 kg plant^{-1} month^{-1} for genotype 63 and 6.5 kg plant^{-1} month^{-1} for genotype 83). Again, time courses were similar for the two genotypes, with maxima in mid 2007 and late 2007, and pronounced minima in late 2006 and early 2008. The number of bunches harvested per month (Fig. 4F) followed these patterns closely, thus explaining most yield variation. Consequently, the number of female inflorescences was the main determinant of yield fluctuations at both sites and for both genotypes. In contrast to structural vegetative growth rates, peaks or depressions of reproductive growth rate did not coincide consistently with drought level (FTSW) or photoperiod (PP) minima (Fig. 4A-B).

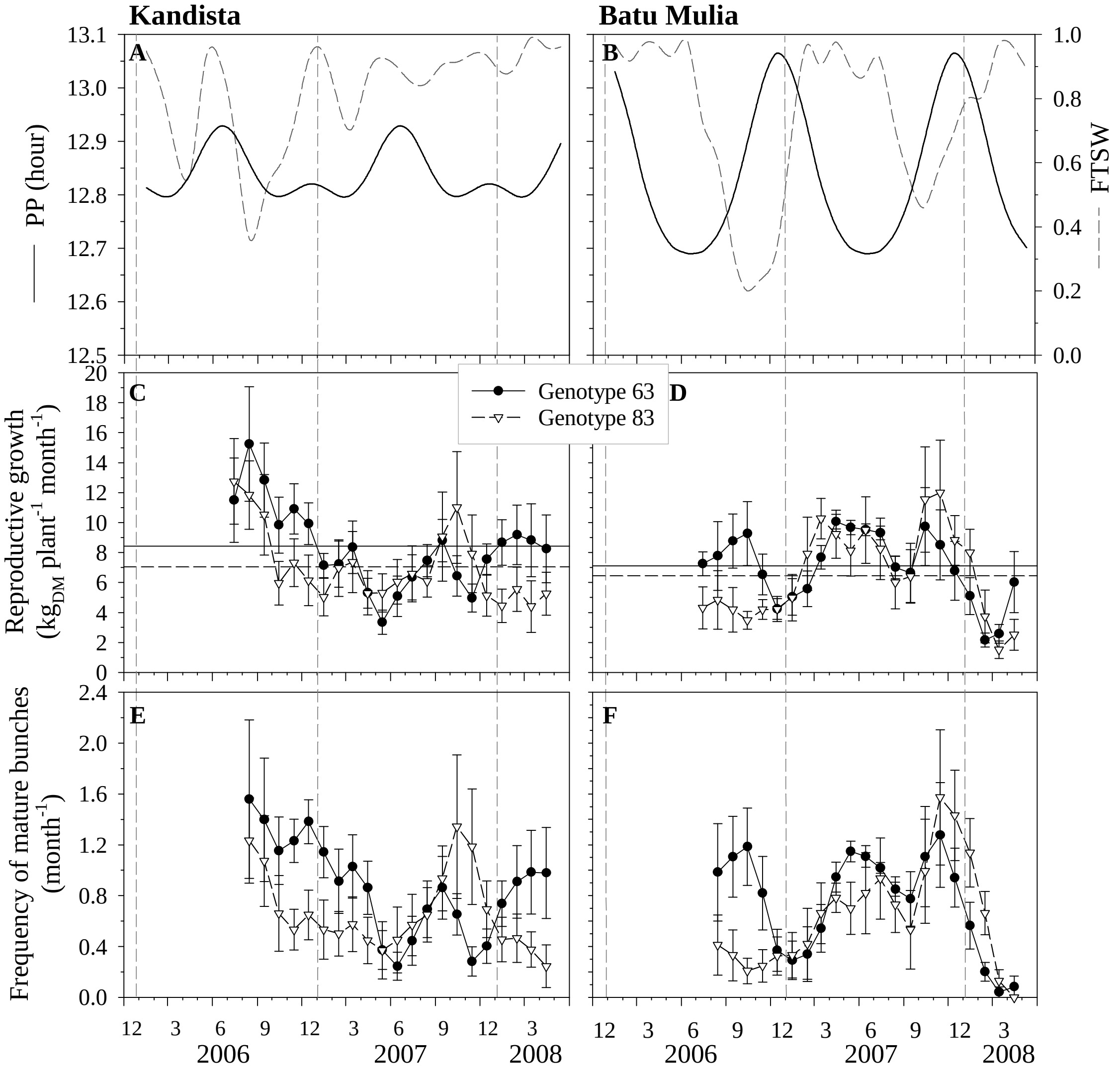

FIG. 4. Time courses of monthly, (C-D) bulk growth rate of reproductive organs and (E-F) frequency of mature fruit bunches for oil palm genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia for July 2006 - April 2008. (A-B) Dynamics of photoperiod (PP) and simulated fraction of transpirable soil water (FTSW) are provided as potential explanatory environmental variable. Values are means of six replicates and bars indicate s.e.m. (_____) and (_ _ _ _ _) lines indicated means for genotypes 63 and 83, respectively, over the observation period.

Yield components

During the experimental period of July 2006 to April 2008, detailed observations were made on yield components (Table 4). Yield components showed the same trends as observed for the 2000-2005 records (Table 1), with inferior yield and bunch number for genotype 83 and for Batu Mulia (differences were not statistically significant because of the smaller sample and shorter period observed). The fraction of productive phytomers was between 0.39 and 0.46, indicating that more than half of the inflorescences were either male or aborted, with no differences observed between the sites. Bunch yields translated into a harvest index were between 44% and 48%. In caloric terms, the harvest index was substantially higher because fruits contained a large fraction of lipids (data not presented).

Lower yields observed in Batu Mulia, the climatically less favourable site, were in part due to a higher rate of unfertilized fruits (parthenocarpic fruits that are smaller) but this did not translate into site differences in mean bunch dry weight. Mean mature, fertilized fruit dry weight was higher in Kandista for genotype 63 and higher in Batu Mulia for genotype 83, resulting in a strong ($P<0.01$) genotype × site interaction.

TABLE 4. Mean yield component parameters for oil palm genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia during the experimental period (July 2006 - April 2008). Values are means ± s.e.m. of six replicates. Significance level of effects (ANOVA): ns = not significant, * = significant ($0.05>P>0.01$), ** = very significant ($0.01>P>0.001$), *** = highly significant ($P>0.001$). Different letters within a column indicate a significant difference between genotypes in one site at $P<0.05$ (Tukey's test).

Site	Effect	Number of mature bunches (plant $month^{-1}$)	Total bunch dry mass yield (kg_{DW} $plant^{-1}$ $month^{-1}$)	Mean bunch dry mass (kg_{DW} $bunch^{-1}$)	Productive phytomers (%)	Harvest Index (%)	Unfertilized fruit rate (%)	Mean fertilized fruit dry mass (g $fruit^{-1}$)
	Genotype							
Kandista	Genotype 63	0.86 ± 0.02	8.5 ± 0.3	9.9 ± 0.5	46.0 ± 1.3	47.7 ± 1.6	27.3 ± 2.8 a	6.6 ± 0.2 a
	Genotype 83	0.73 ± 0.1	7.9 ± 1.1	10.8 ± 0.5	39.0 ± 5.8	45.2 ± 3.4	18.5 ± 1.2 b	5.8 ± 0.2 b
	P	ns	ns	ns	ns	ns	*	*
Batu Mulia	Genotype 63	0.75 ± 0.05	7.1 ± 0.7	9.5 ± 0.3 b	45.8 ± 4.1	45.2 ± 2.6	35.0 ± 3.0	5.6 ± 0.3 b
	Genotype 83	0.63 ± 0.07	6.5 ± 0.7	10.4 ± 0.2 a	40.0 ± 4.0	44.3 ± 2.7	36.8 ± 1.4	6.6 ± 0.3 a
	P	ns	ns	*	ns	ns	ns	*
	Site							
	P (genotype 63)	ns	ns	ns	ns	ns	ns	*
	P (genotype 83)	ns	ns	ns	ns	ns	***	*
	Genotype×Site							
	P	ns	ns	ns	ns	ns	*	**

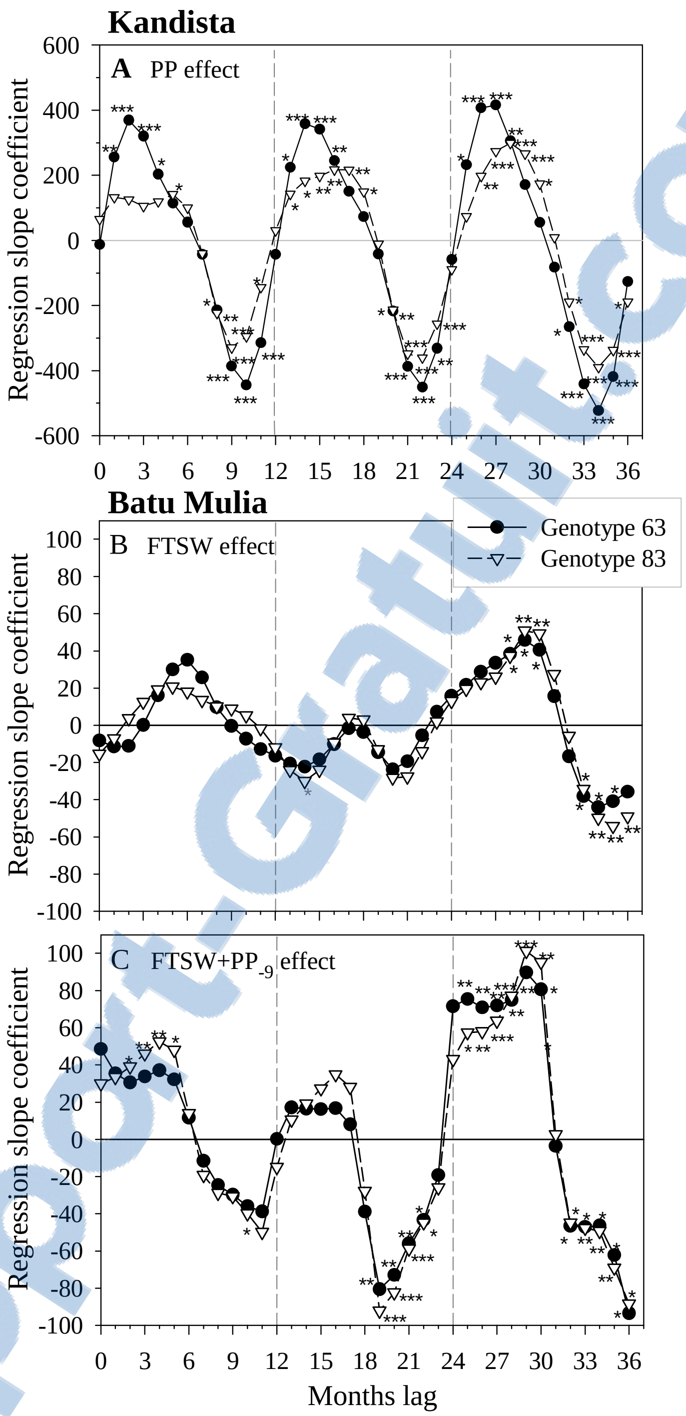

FIG. 5. Analysis of possible lag periods for photoperiod (PP) and FTSW effects on dynamics of fruit bunch production for oil palm genotypes 63 and 83. (A) Regression slope coefficient values of the linear correlation *mature bunch number vs PP* with a hypothetical n-month lag, using n = 1 to 36, for the Kandista site; (B) regression slope coefficient values of the linear correlation *mature bunch number vs FTSW* using the same range lag periods, for the Batu Mulia site; and (C) as in (B), but using PP at -9 months lag as co-variable for multiple, linear correlation. Significance level of correlations: * = significant (0.05>P>0.01), ** = very significant (0.01>P>0.001) or *** = highly significant (P<0.001).

Photoperiod (PP) and FTSW effects on production

Possible effects of photoperiod were analyzed for the Kandista site (years 2001 to 2005) where confounding effects of drought stress are unlikely, with simulated FTSW never decreasing below 0.5. Regression slope coefficient of PP from the linear regression between mature bunch number and PP, determined for hypothetical lags between 1 and 36 months, gave an oscillating pattern that was near identical for both genotypes (Fig. 5A). Best correlations ($r^2 = 0.28$ to 0.35, with $P<0.0001$) were observed for lags of 9 to 10, 21 to 22 and 33 to 34 months. In all cases, the best correlations were negative as can be expected for a tropical and therefore short-day plant (r^2 for the positive maxima of the slope coefficient varied between 0.15 and 0.20). The best correlations between mature bunch number and PP were thus associated with a lag of 9 to 10 months plus 0, 1 or 2 years (corresponding to a lag for flowering of 3 months plus 0, 1 or 2 years). In the following analyses, we assume for convenience that the photoperiodic lag for flowering is 3 months, without discarding the possibility that it is actually 15 or 27 months.

As it can be expected from the variable intensity of dry seasons and comparatively irregular seasonal peaks of production observed at Batu Mulia (Fig. 1), the same analysis conducted for that site produced much poorer correlations between bunch number and PP (data not presented). Regressing mature bunch number against FTSW (Fig. 5B), however, resulted in significant correlations for a lag of 29 months (positive, $r^2 = 0.07$ to 0.13, with $P<0.05$) and 35 months (negative, $r^2 = 0.05$ to 0.15, with $P<0.05$). It was assumed that only the positive correlations are physiologically meaningful, the negative ones being their mirror images at a shift of ±6 months, because drought is a yield reducing factor in oil palm (Hemptinne and Ferwerda, 1961, Caliman and Southworth, 1998).

The correlation of maturing bunch number with the FTSW observed 29 months earlier at Batu Mulia improved further when PP at -9-month lag (using the lag estimated for Kandista) was used as co-variable in a multiple linear regression analysis (Fig. 5C). The correlations combining a -9-month lag for PP and a -29-month lag for FTSW effects were highly significant ($P<0.01$ for genotype 63 and $P<0.0001$ for genotype 83), although they explained only a fraction of the observed variability (16% for genotype 63 and 35% for genotype 83).

This model was graphically applied to the available bunch production data from 2001 to 2008 (Fig. 6). For Kandista, where drought was considered to a negligible factor, it was observed that each of the two annual minima of photoperiod (a phenomenon that is specific to locations near the equator) was each associated with a peak of production. The peaks thus occurred in pairs, except for 2005 where a single peak was observed. Coincidentally or not, the missing second peak in 2005 was associated, at a lag of -29 months, with the most pronounced among the many short dry spells observed at the site.

At Batu Mulia, each of the dry seasons was associated with a depression of mature bunch number 29 months later. The greatest depression (early 2005) was associated, at a lag of -29 months, with the lowest FTSW simulated for the time series. Conversely, only a very small dip in bunch production was observed in early 2006, associated with an exceptionally mild dry season 29 months earlier. Several peaks of bunch production coincided, at a -9-month lag, with PP minima, but this association was less regular than in Kandista, probably because of the dominance of production minima presumably associated with drought.

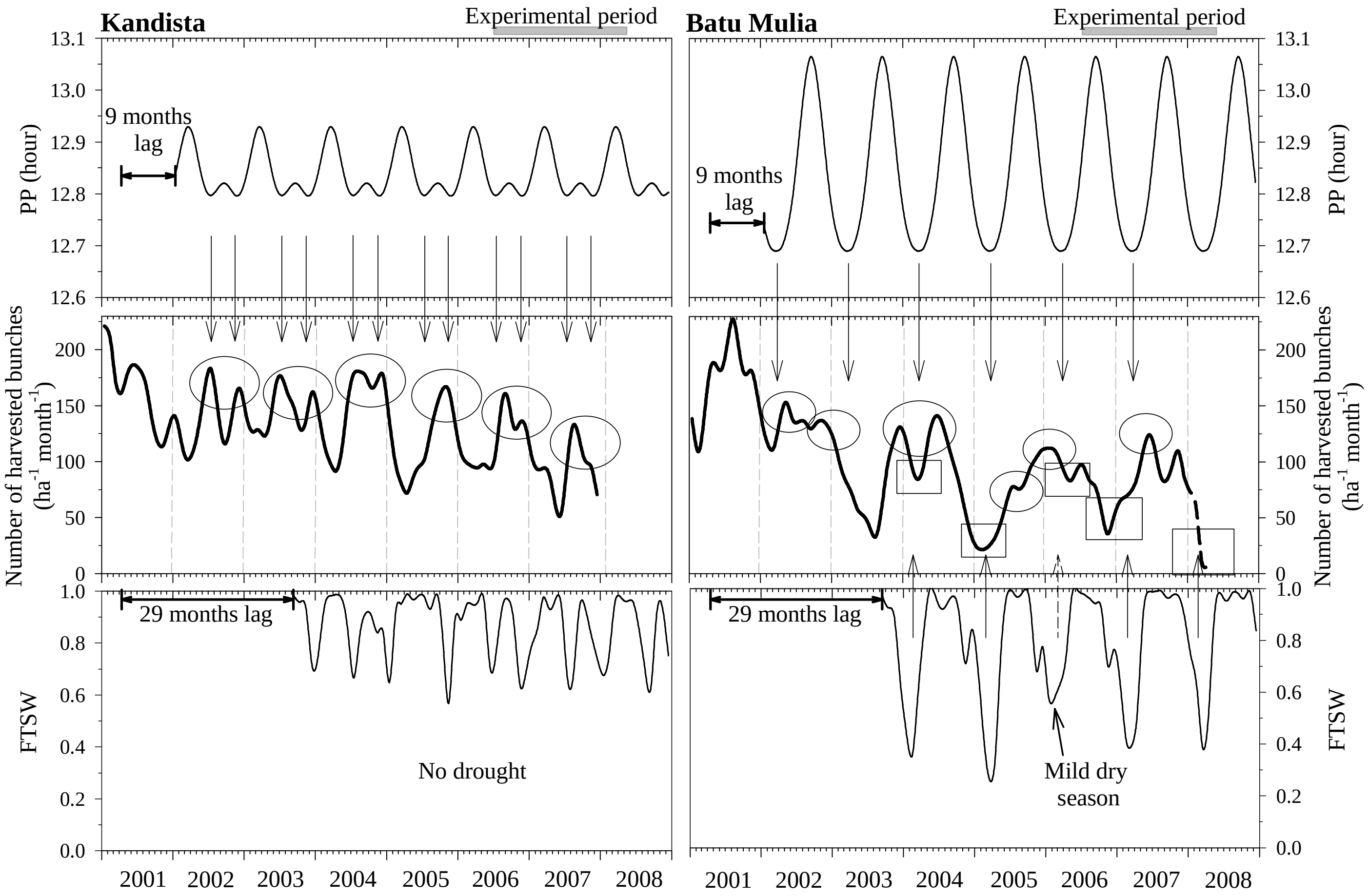

FIG. 6. Semi-schematic diagram of association of the dynamics of monthly harvested bunch number (center; means for genotypes 63 and 83) with photoperiod (PP) at -9 months lag (top) and with FTSW at -29 months lag (bottom); at Kandista (left) and Batu Mulia (right). Arrows indicate hypothetical environment effects on peaks (enhanced by circles) and minima (enhanced by squares) of harvested bunch number. Data source: SMARTRI data base.

RUE, source-sink relationships

Radiation use efficiency (RUE) was estimated because this parameter might convey whole-plant adjustments to sink-source imbalances, as previously observed in coconut (Mialet-Serra *et al.*, 2008). Such imbalances are likely to occur as a result of the present hypothetical model involving long lag periods between environmental constraints and plant responses to them.

Monthly means of RUE in Kandista varied between 0.7 and 2.3 g MJ^{-1} for genotype 63 (genotype 83: 0.4 to 2.4 g MJ^{-1}) and in Batu Mulia between 0.3 and 2.1 g MJ^{-1} for genotype 63 (genotype 83: 0.4 to 1.8 g MJ^{-1}) (Fig. 7A and B). Mean RUE over the 22-month period of genotype 63 was 1.44 g MJ^{-1} in Kandista and 1.43 g MJ^{-1} in Batu Mulia, and slightly lower for genotype 83 (1.33 g MJ^{-1} in Kandista and 1.12 g MJ^{-1} in Batu Mulia).

Time courses of RUE in Kandista and Batu Mulia (Fig. 7) showed strong fluctuations and large errors, particularly in late 2007 and in 2008, making interpretation difficult. In general, RUE was low in most situations of water deficit (low FTSW), and where drought was absent (FTSW near 1), RUE appeared to be positively associated with the frequency of mature fruit bunches (Fig. 4E-F). Following the approach of Mialet-Serra *et al.* (2008) for coconut, multiple linear stepwise regression analyses were done to identify explanatory variables for RUE variability, using monthly means of weather variables, FTSW, current plant fruit load and number of fruit bunches arriving at maturity.

The best single predictor of RUE was incident PAR, which generally had a negative effect as previously described by Mialet-Serra *et al.* (2008) and explained 43% of RUE variation for genotype 63, in Kandista ($P = 0.0006$) and 33% in Batu Mulia ($P = 0.004$). PAR *vs* RUE correlations were not significant for genotype 83. The best combination of predictors was generally incident PAR (negative), FTSW (positive) and maturing fruit bunch number (positive). These three variables together explained 54% ($P<0.001$) of variation of RUE for genotype 63 in Kandista and 28% ($P<0.05$) in Batu Mulia; and 38% ($P<0.05$) for genotype 83 in Kandista and 73% ($P<0.0001$) in Batu Mulia. Across sites and genotypes, the following model was obtained:

$$\text{RUE} = 2.48 - 0.0083\times\text{PAR} + 0.732\times\text{FTSW} + 0.322\times\text{Bunch number};$$

($n=84$; $r^2=0.36$; $P<0.00001$; Partial P values: 0.00005 (PAR), 0.0009 (FTSW), 0.004 (Bunch number))

Although this relationship explained only 36% of variation of RUE across genotypes and environments, probably owing to third factors and experimental noise, each of the predictors was highly significant. It can thus be ascertained that at monthly aggregation of data, incident PAR affected RUE negatively, FTSW affected it positively and mature-bunch number also positively. PAR and FTSW are environmental variables whereas mature-bunch number is a plant variable related to demand for assimilates, because the physiologically costly synthesis of oil happens mainly during the last 1-2 months before maturity.

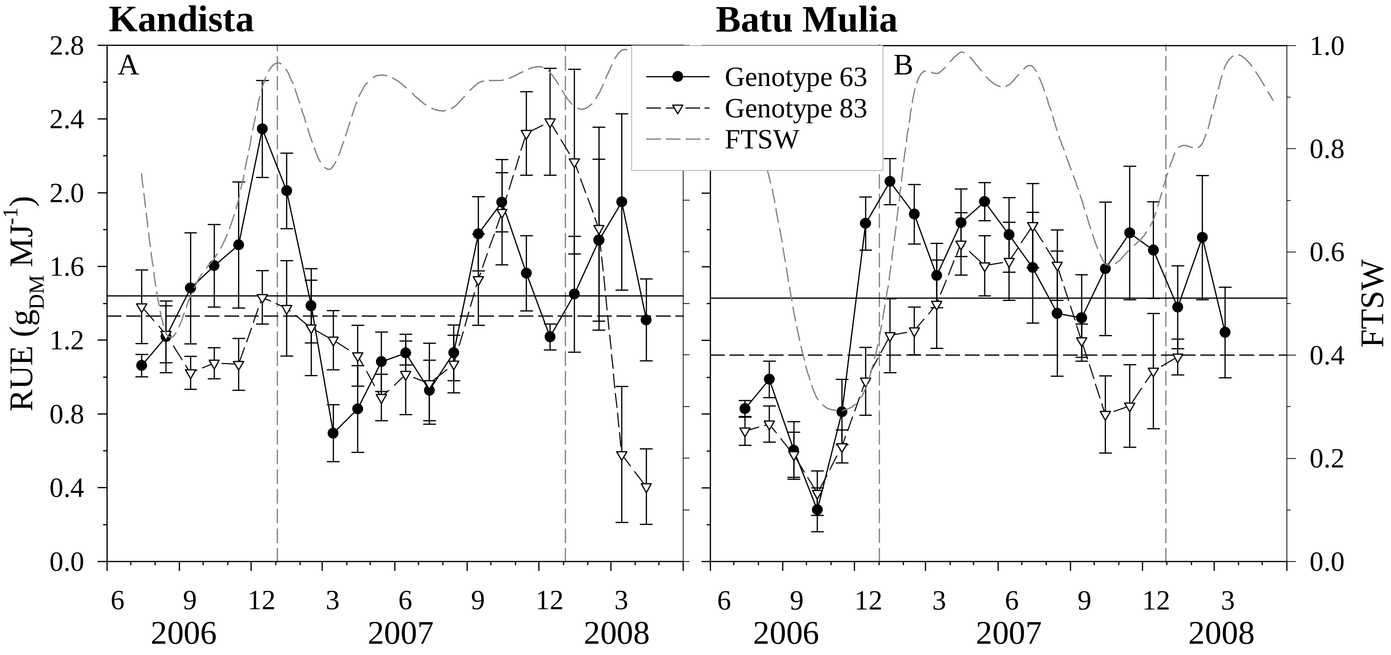

FIG. 7. Time courses of radiation-use efficiency (RUE) for genotypes 63 and 83 at Kandista and Batu Mulia sites in Indonesia during the experimental period (July 2006 - April 2008). Values are means of six replicates and bars indicate s.e.m. (______) and (_ _ _ _ _) lines indicated means for genotypes 63 and 83, respectively, over the observation period. Simulated fraction of transpirable soil water (FTSW; dashed line without symbols) is plotted as environmental reference variable.

DISCUSSION

Choice of environments and genotypes

This study used contrasting climatic environments, notably characterized different severity of dry seasons, to explain the variable patterns of phenology, growth and production of oil palm. The choice of observation periods (22 months, augmented with five years of historical records on the same populations) and sites provided sufficient natural variability to develop causal hypothesis derived from parameter correlations. The choice of the two genotypes, recommended by experts for their different productivity and assumed sensitivity to drought, was less meaningful because the genotypes, despite different absolute levels of productivity and some morphological differences, responded similarly to environment. Their similar growth and phenological dynamics therefore strengthen the results in terms of repeatability but provided little insight into genotypic differences.

Photoperiodism as a possible cause of baseline rhythms of flowering?

Observations confirmed numerous previous reports (Bredas and Scuvie, 1960, Corley, 1977, Henson and Mohd Tayeb, 2004) indicating pronouced, regular, seasonal baseline rhythms of production dynamics in the absence of environmental stresses, and the modification of these baseline rhythms when plants are affected by drought spells.

The seasonal rhythms of bunch production at the hydrologically favourable site Kandista became regular in 2003 when plants were 9-years old (Fig. 6). Oil palm usually shows such rhythms about 10 years after planting (Corley and Gray, 1976b). The observed rhythms were mainly due to the number of fruit bunches harvested per month, and thus a function of flowering events on female inflorescences. Such phenological, seasonal rhythms in tropical, perennial plants can either be related to recurrent climatic patterns or to photoperiodism. For tropical dicotyledon trees, Singh and Krushwaha (2006) distinguished among five flowering types: summer flowering (on foliated shoots), rainy-season flowering (on foliated shoots following significant rains), autumn flowering (on shoots with mature leaves), winter flowering (on shoots undergoing leaf fall) and dry-season flowering (on leafless shoots). Seasonal climatic patterns are sometimes responsible for these patterns, for example in rubber tree where flowering seems to be synchronized by periods of high solar radiation intensity observed near the equator (Yeang, 2007). This author argues that photoperiodism is unlikely to be involved in such cases because day length varies little or not at all, although Rivera and Borchert (2001) reported that several tropical trees are sensitive to annual variations in photoperiod of less than 30 min. More recently, Borchert *et* *al.* (2005) postulated that even at the equator, photoperiodism controls flowering of tropical trees on the basis of the same circadian oscillators that have been found to be involved photoperiod responses in *Arabidopsis thaliana*. Plants are thereby able to measure precisely the duration from sunset to sunset and from sunrise to sunrise. In fact, the total day length including day and night varies significantly at all latitudes including the equator.

Photoperiodic control of flowering at equatorial latitudes is thus physiologically possible and should, because of the peculiar biphasic pattern of day length prevailing there, result in two flowering peaks per year (Borchert *et al.*, 2005). This is what we observed at Kandista, the equatorial (0°55.0′ N) and hydrologically favourable site. The present analysis and resulting hypothesis on the photoperiodic nature of the dual, annual maxima of flowering in Kandista, however, are simplistic and require further confirmation. Namely, the linear regression based correlation of monthly bunch number with photoperiod, which indicated that the photoperiodic stimulus for flowering happens about 3 (or 15, or 27) months before anthesis (or 9, 21, or 33 months before bunch maturity), did not take into account the non-linear response commonly observed. We also assumed that oil palm is a short-day plant like most tropical plants (Rivera and Borchert, 2001, Kouressy *et al.*, 2007), but would have obtained nearly equally good correlations with the opposite assumption, which would resulte in a stimulus occurring 6 months earlier. Our model also assumes that the stimulus is effective at the phytomer scale and not transferable to other phytomers (that are necessarily *n* plastochrons earlier or later in development), which is an unproven hypothesis. Lastly, it is not necessarily the minima of day length that constitute the effective stimulus but any parameter of the day length dynamics that plant theoretically can perceive. Clerget *et al.* (2004) and Borchert *et al.* (2005) elaborated several alternative models that can be considered. The present results render photoperiodic explanations of flowering control in oil palm likely and should motivate further investigation into the question.

Different lag periods for drought effects on vegetative and reproductive growth?

The observations at the drought-prone site of Batu Mulia suggested the presence of flowering peaks associated with minima of photoperiod in accordance with the model developed for Kandista, but this pattern seemed to be confounded by other, more dominant sources of variation. Annual drought periods recurring with variable intensity were the most likely explanation.

Drought intensity was estimated by climatic water balance (CWB) and simulated FTSW. The former is an established agro-climatic term (Benoit, 1977, Kar and Verma, 2005) commonly used in agro-ecological zoning (FAO, 1996) but has the disadvantage of not taking into account cumulative effects of continuous drought, such as depletion of the soil water reserve. FTSW does consider this effect but on a hypothetical basis, because profiles of water infiltration, deep drainage and extraction by roots were not measured and the model thus not validated in this respect. Despite this uncertainty we preferred using simulated FTSW as reference for soil water resources because oil palm root systems are quite dense in the 0-1.5 m horizon (Jourdan and Rey, 1997a), resulting in water depletion in this horizon during drought. It is known, however, that not only soil water resources but also atmospheric drought affects gas exchange (Dufrêne, 1989, Cornaire *et al.*, 1994) and growth of oil palm. Within the soil profile having roots, the main activity of roots is located in the upper 80 cm of the soil, and particularly in the surface horizon (Jourdan and Rey, 1997b), water extraction occuring preferentially and rapidly in this zone (Nelson *et al.*, 2006). Consequently, we considered both the instantaneous parameter CWB and the cumulative parameter FTSW in the analysis.

Our results suggest that drought affected structural, vegetative growth and development very differently from that of the reproductive system. Leaf and stem structural mass gain, as well as leaf appearance rates, were affected in real time by drought (within the temporal resolution of sampling, which was monthly). Phyllochron of oil palm has been reported to be sensitive to water deficit, followed by rapid appearance and expansion of leaves as the stress subsides (Corley, 1977, Nouy *et al.*, 1999), a behaviour that has been termed developmental plasticity (Tesfaye *et al.*, 2006). These characteristics are largely masked in the dynamics of total aboveground vegetative, including stem carbohydrate reserves, because (1) the reserve pool is large and thus contributes much to overall growth dynamics, and (2) the reserve pool appears to interact with assimilate demand for fruit growth.

By contrast, reproductive mass growth and its main developmental component, the frequency of appearance of fertile, female inflorescences, was affected by drought with an estimated lag of -23 months (or -29 months until bunch fruit maturity). The seemingly irregular fluctuations of reproductive growth (Corley, 1977, Dufour *et al.*, 1988), have been attributed to several drought sensitive phase during the roughly four years of development from phytomer initiation to bunch maturity, each sensitive phase corresponding to a different yield component (Corley, 1977, Dufour *et al.*, 1988, Adam *et al.*, 2005). The main yield components of oil palm are bunch number per palm, bunch weight and oil content. Bunch number depends on sex differentiation (determined 30-32 months before bunch harvest) and rate of inflorescence abortion (9-11 months before harvest) (Corley, 1976, 1977, Dufour *et al.*, 1988). Bunch weight is determined by fruit number and finally by oil synthesis (3-4 months before harvest). Environment thus affects yield by modifying developmental events largely before the main reproductive growth processes take place.

The present conclusion that strong drought effects on bunch number happen 29 months before maturity are supported by Dufour *et al.* (1988) who reported one of several sensitive phases to occur 30 months before harvest. Dufour *et al.* (1988) and Caliman and Southworth (1998) found a sensitive period around ten months before harvest in Ivory Cost and Lampung province in Indonesia respectively. The two sensitive phases probably correspond to sexual differentiation (ca. 29 or 30 months before harvest) and abortion (ca. 10 months before harvest) (Corley, 1976, 1977, Dufour *et al.*, 1988). The latter drought-sensitive phase may coincide with the photoperiod-sensitive phase as estimated here, making their distinction difficult.

How does the plant cope with seasonal sink-source imbalances?

The long lag periods of drought stress effects on reproductive growth and development, combined with the apparent absence of such lag periods for vegetative growth, are bound to cause source-sink imbalances in the plant. Mialet-Serra *et al.* (2008) recently addressed this problem for coconut, hypothesizing that non-structural carbohydrate reserves may buffer such imbalances. They found, however, that the main adjustment at the whole-plant level was variable RUE.

Maximal values of RUE found in this study are similar to previous findings on oil palm (1.6 g_{DM} MJ^{-1}; Corley and Tinker, 2003). As reported by Mialet-Serra *et al.* (2008) for coconut, RUE is not constant across seasons, partly because it decreases under high radiation due to increasing saturation of photosynthesis, and partly because RUE appears to be dependent on plant demand for assimilates. The present results on oil palm, based on stepwise linear multiple regressions, confirmed that RUE is negatively affected by incident PAR ($P<0.0001$) and positively by simulated FTSW, a measure of soil water availability ($P<0.001$). Fruit load, in terms of mature bunch production per month, also had a positive effect but weaker than the two environmental factors ($P<0.01$). The latter, demand driven effect on RUE may have many potential causes, such as sugar-mediated feedback inhibition of photosynthesis (Iglesias *et al.*, 2002, Frank *et al.*, 2006, Haro *et al.*, 2007), luxury respiration (Musgrave *et al.*, 1986, Lecoeur and Ney, 2003, Whitehead *et al.*, 2004, Allen *et al.*, 2005) or variable root growth (Palacio *et al.*, 2007), a parameter that is not included in the conventional RUE term.

Perspectives for an integrative model of oil palm

The present results provide crucial elements for the development of a model for oil palm development and growth. No model currently exists that captures the specificities of this plant, shared in part with other members of the palm family such as coconut (Mialet-Serra, 2005, Mialet-Serra *et al.*, 2008): regular successions of phytomers on a single axis that each potentially produce an inflorescence; a range of phenological adjustment processes to environment, happening during specific sensitive stages of phytomer development along its multi-annual phenology; sink-source imbalances compensated by variable RUE and to some extent, stored reserves; and, to be confirmed by further studies, photoperiodic control of flowering resulting in latitude-specific, seasonal maxima of flowering and fruiting. Such a model would not only be of interest to oil palm agronomists and breeders, but encapsulate the physiological and developmental organization of a plant type that differs markedly from other cultivated plants such as cereals, legumes and dicotyledonous trees.

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CHAPITRE III:

PHENOLOGY, GROWTH AND PHYSIOLOGICAL ADJUSTMENTS OF OIL PALM (ELAEIS GUINEENSIS JACQ.) TO SINK LIMITATION INDUCED BY FRUIT PRUNING

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Running Title: Oil palm responses to fruit pruning

RESUME EN FRANÇAIS

AJUSTEMENTS DE LA PHENOLOGIE, DE LA CROISSANCE ET DE LA PHYSIOLOGIE DU PALMIER A HUILE (ELAEIS GUINEENSIS JACQ.) FACE A UNE REDUCTION DE LA DEMANDE REPRODUCTIVE

Introduction

Une architecture simple et une faible plasticité phénotypique caractérisent le palmier à huile à l'âge adulte ; la phénologie et les relations source-puits, chez cette espèce, sont complexes. Le développement d'un phytomère est long (jusqu'à quatre années) ; ainsi des conditions climatiques contraignantes à un instant *t* ont des effets visibles nettement décalés dans le temps. Les ajustements mis en jeu par la plante pour faire face à ces déséquilibres source-puits récurrents et peu prévisibles restent encore mal connus. Ce chapitre tente d'analyser et de décrire les ajustements mis en jeu dans de telles situations.

Matériels et Méthodes

A Kandista (0°55'N), deux traitements sont mis en place : un traitement témoin et un traitement « ablation totale des régimes » (FPT), sur un génotype donné (63). Cette expérience est conduite pendant 22 mois (juillet 2006 - mai 2008) sur six répétitions par traitement. Les productions de biomasses aériennes végétative et reproductive, la morphologie de ces différents compartiments ainsi que leur phénologie sont mesurées. Les teneurs en sucres solubles et en amidon dans le stipe sont, par ailleurs, déterminées tous les deux mois. L'assimilation carbonée (A_{max}) à l'échelle foliaire est régulièrement mesurée. L'efficience d'utilisation de la lumière (RUE), rapport entre la production de biomasse sèche totale aérienne et la lumière absorbée par le couvert est calculée chaque mois pour chacun des deux traitements.

Résultats majeurs

L'ablation totale de tous les puits reproducteurs induit une accélération du rythme de développement, avec la mise en place d'un plus grand nombre de phytomères et la diminution du phyllochrone. Ces observations se maintiennent dans le temps. La taille et la morphologie des feuilles restent, cependant, inchangées. Toujours sur ce traitement, le nombre d'inflorescences avortées chute 10 mois après l'application du traitement ; le nombre d'inflorescences femelles augmente 18 à 20 mois après son application. Au cours des neuf mois qui suivent le début du traitement, la RUE sur FPT diminue pour revenir ensuite à un niveau comparable à celui du témoin. L'intensité de l'assimilation carbonée (A_{max}), à l'échelle foliaire reste similaire à celle mesurée sur les témoins. En revanche, les teneurs en glucides non-structuraux augmentent significativement sur toute la hauteur du stipe, notamment celle en amidon (environ 50% du poids sec) dans la partie haute du stipe.

Conclusion

Une réduction importante de la demande permet une accélération de la mise en place de nouveaux phytomères. Le développement d'un palmier à huile n'est donc pas seulement piloté par le temps thermique mais également par la disponibilité en assimilats carbonés, le niveau élevé des réserves carbonées étant alors un bon indicateur. De plus, l'impact d'une période sèche sur le nombre d'inflorescences avortées peut être largement contrebalancé par cette même disponibilité en assimilats au même titre qu'elle entraine une féminisation significative des inflorescences. La faible plasticité de la taille des organes décrits et l'absence de ramifications chez cette espèce laissent penser qu'une partie du surplus en assimilats pourrait être détournée vers un puits existant, non observé dans notre cas i.e. le système racinaire ou encore un nouveau puits alternatif. Cela reste hypothétique mais il est clair que le compartiment réserves absorbe une grande partie du surplus en assimilats, expression d'un ajustement physiologique important du palmier à huile en réponse à un déséquilibre des relations source-puits.

ABSTRACT

- *Background and Aims*: Despite its simple architecture characterized by low phenotypic plasticity, oil palm has complex phenology and source-sink interactions. Development of a new phytomer takes years, involving long lag periods between environmental influences and their effects on sinks. Plant adjustments to resulting sink-source imbalances are poorly understood. This study investigated oil palm adjustments to imbalances caused by severe fruit pruning.

- *Methods*: An experiment with six replications and two treatments (control and complete fruit pruning (FPT) during 22 months in 2006-2008) was conducted in Indonesia. Phenology, growth of shoot vegetative and reproductive organs, leaf area, leaf morphology, inflorescence sex differentiation, dynamics of carbohydrate reserves and leaf light-saturated net assimilation (A_{max}) were monitored; radiation use efficiency (RUE) was estimated from these variables.

- *Key results*: Plant responses to artificial sink limitation included acceleration of development rate, resulting in higher phytomer, leaf and inflorescence numbers. Leaf size and morphology remained unchanged. FPT also suppressed the abortion of male inflorescences, estimated to be triggered at about 10 months before anthesis. Number of female inflorescences increased after an estimated lag of 18-20 months, corresponding to time from sex differentiation to anthesis. RUE was reduced by sink limitation during 9 months and then returned to control levels. Variation in RUE was not associated with A_{max}. The most important adjustment process was increased assimilate storage in stem, attaining nearly 50% of dry weight in stem top, mainly as starch. Glucose, the most abundant storage non-structural carbohydrate in oil palm, decreased.

- *Conclusion*: It was shown that development rate of oil palm is in part controlled by sink-source relationships. Although increased rate of development and proportion of female inflorescences constituted effective adjustments to sink limitation, the low plasticity of plant architecture (constant leaf size, absence of branching) limited compensatory growth. Reserve storage was thus the main adjustment process. The results will enable developing a simulation model for oil palm.

Keywords: carbon allocation, non-structural carbohydrates, source-sink relationships, radiation use efficiency, *Elaeis guineensis* Jacq., phenotypic plasticity, photosynthesis.

INTRODUCTION

Oil palm (*Elaeis guineensis* Jacq.) has a simple, mono-axial shoot architecture that produces phytomers in linear succession arranged in a continuous spiral. Each phytomer produces a single leaf and inflorescence. This simplicity stands in marked contrast to the species' complex phenology and the resulting seasonal and inter-annual dynamics of fruit production (Legros *et al.*, 2008a). These authors demonstrated that the long development period of the organs produced by a given phytomer, up 50 months for leaves (Henry, 1955b) and 40 months for inflorescences (Corley, 1977), involves long lag periods for the effects of environmental influences, such as photoperiod or drought (Legros *et al.*, 2008a). The long lags, in turn, frequently lead to discrepancies between available resources and demand, or sink-source imbalances. The present study attempts to characterize plant adjustment processes to such imbalances, namely sink limitation.

Assimilate partitioning among growing organs is a function of active sinks in the plant (Marcelis, 1996, Heuvelink, 1997), and yield can thus be limited by the capacity of reproductive sinks, either in absolute terms or relative to the strength of competing, vegetative sinks. For oil palm, Henson (2006b, 2007), reported that vegetative growth and development constitute priority sinks that are comparatively invariable due to low architectural plasticity, whereas fruit production is more plastic and able to adjust to available resources. This type of behaviour was confirmed for coconut (Mialet-Serra *et al.*, 2008), a plant that is biologically close to oil palm.

Although Legros *et al.* (2008a) reported highly variable production of inflorescences and fruit for oil palm in response to environment; it is improbable that this variability is a simple expression of resources available for reproductive growth, or of adjustments of reproductive sinks to current sink-source imbalances. In fact, adjustments of sexual differentiation (inflorescence of oil palm can be male or female) and probability of abortion of inflorescences on a given phytomer are determined between months and years before fruit filling, which is the main period of reproductive sink activity (Corley, 1977, Dufour *et al.*, 1988, Gerritsma, 1988, Corley and Tinker, 2003c, Legros *et al.*, 2008a). Among the environmental factors that have been related to these adjustment processes are photoperiod (Legros *et al.*, 2008a), drought (Ochs and Daniel, 1976, Dufour *et al.*, 1988, Caliman and Southworth, 1998, Nouy *et al.*, 1999, Legros *et al.*, 2008a), and unfavourable conditions for carbon assimilation in general such as leaf diseases (Ng, 1977, Corley and Tinker, 2003d) or artificial defoliation (Corley and Tinker, 2003c). Because of the long lag periods between a given environmental influence and its effect on the reproductive sink, however, the phenological adjustments of the reproductive apparatus do not necessarily prevent sink-source disequilibria and in fact, frequently contribute to them (Legros *et al.*, 2008a). Consequently, the concept of oil palm being a plant whose rigid architecture is compensated by highly plastic reproductive development is insufficient to explain how the plant maintains its physiological equilibrium.

For oil palm and coconut, where the problem is similar, three alternative mechanisms were suggested to buffer acute source-sink imbalances (Mialet-Serra *et al.*, 2008): (1) variable partitioning to roots, (2) variation radiation use efficiency (RUE) through regulated photosynthetic rates (Iglesias *et al.*, 2002, Dingkuhn *et al.*, 2007) or respiration (Hrubec *et al.*, 1985, Musgrave *et al.*, 1986, Whitehead *et al.*, 2004) or both, and (3) a large and dynamic reserve compartment for carbohydrates located in the stem (Mialet-Serra *et al.*, 2005, Silpi *et al.*, 2007, Mialet-Serra *et al.*, 2008).

The objective of this study was to analyze oil palm adjustments to an artificial sink limitation induced by continuous pruning of female inflorescences upon their appearance, thereby eliminating nearly the entire reproductive sink. Under non-pruned conditions, this sink absorbs about 45% of dry matter produced (representing the crop's harvest index; Legros *et al.*, 2008), or even more in energy terms because the fruits are rich in lipids. Specifically, we sought to evaluate responses of dry matter partitioning among organs (except roots, for technical reasons), radiation use efficiency, leaf photosynthesis, and carbohydrate storage in stem, in order to identify the pruned plant's mechanisms to restore its disturbed equilibrium.

MATERIALS AND METHODS

Experimental site

The study was carried out on an experimental plantation of the Smart Research Institute (SMARTRI, Smart Tbk.) located in Kandista Estate (Riau province, Sumatra Island, Indonesia, 0°55′0″ N, 101°21′0″ E, 100 m asl). A tropical humid climate characterized this area. The rainy season occurs between November to January, with a monthly rainfall average of 240 mm month^{-1} (averages for 1993 – 2005). A drier season usually occurs from June to August, with, in this case, a monthly mean of 140 mm month^{-1}. Mean daily global radiation (Rg) during the dry season (wet season) is 18.9 MJ m^{-2} day^{-1} (16.9 MJ m^{-2} day^{-1}). Mean air temperature is 27.4°C (27.0°C), mean relative humidity is 79.0% (81.1%), mean vapour pressure deficit (VPD) is 0.98 kPa (0.84 kPa) and mean evapotranspiration (Penman-Monteith) is 4.5 mm (3.9 mm). The beginning of the experimental period (July 2006 - May

2008), was characterized by a 2-month drought spell (July and August 2006), followed by mostly abundant rainfall (Fig. 1). The other climatic parameters (mean temperature, incident photosynthetically active radiation (PAR_i), Vapour Pressure Deficit (VPD)), during this period, were similar to the average recorded for the previous 12 years (Legros *et al.*, 2008a). To evaluate drought extent, climatic water balance (CWB) was calculated as rainfall minus potential evapotranspiration (PET). CWB is the core indicator for the length of growing period in agro-ecological zoning for rainfed systems (FAO, 1996). PET (mm $month^{-1}$) was calculated according FAO guidelines (Allen *et al.*, 1998).

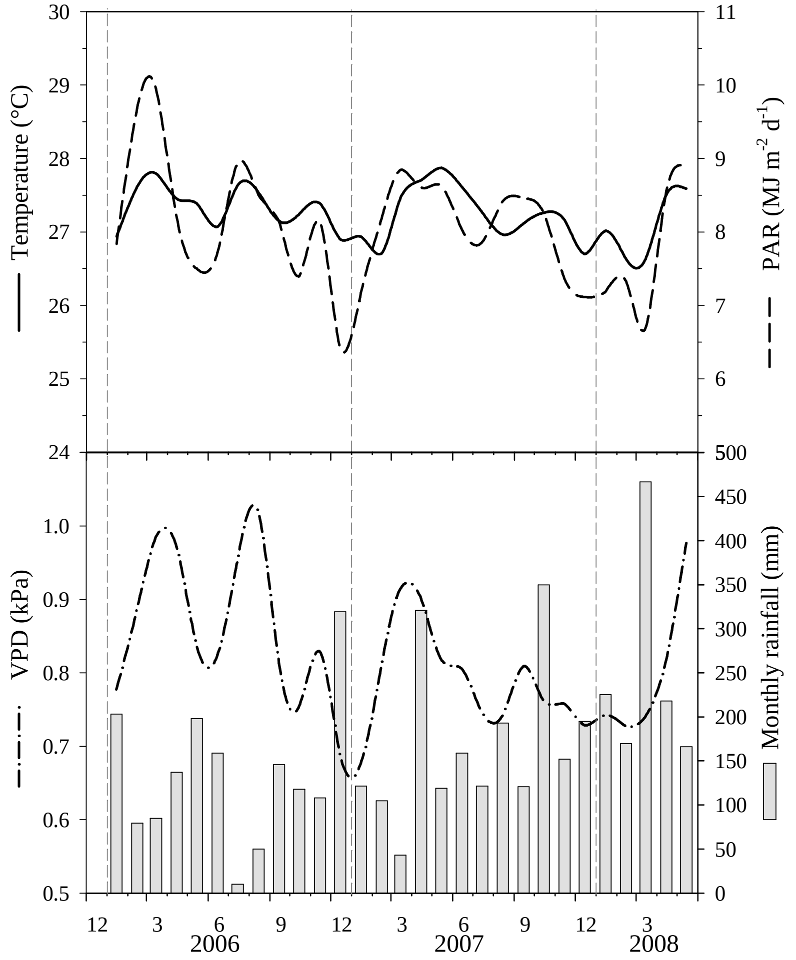

FIG. 1. Time courses of environmental parameters for January 2006 - May 2008. Top: mean monthly of air temperature and incident photosynthetically active radiation (PAR_i). Bottom: mean monthly vapour pressure deficit (VPD) and monthly rainfall at the SMART Research Institute.

The soil is a sandy loam of homogeneous texture and of more than 3 m depth (78.0% sand, 11.1% silt and 10.8% clay). Soil water content values at field capacity (pF 2.5) and wilting point (pF 4.2) were 0.17 and 0.06 m^3 m^{-3} respectively.

Planting material

The experiment follows genotype 63 which was a *tenera* hybrid, commonly high-yielding for palm oil and result of cross between a *dura deli* origin (fruits with thin mesocarp and large kernel) and a *pisifera avros* origin (fruits with thick mesocarp, no endocarp and small kernel) varieties.

Experimental design

The experimental plot is a part of a larger, long-term genetic experiment covering about 30 ha. Planting density was 136 plants ha^{-1} in a 9.5 m equilateral, triangular pattern. Plants were 13 years old at the onset of the study (July 2006). The present experiment took advantage of the replicated block design already in place. Our study had twelve plants selected randomly from within plots for the considered genotype, and located sufficiently far from the plot border to avoid border effects. A set of six plants (replicates) was selected randomly from the 12 plants to apply the treatment.

Treatment

The objective of the fruit pruning treatment (FPT) was to reduce the sink for assimilates that is to say to decrease the reproductive demand and then to follow physiological adjustments by the plant. All inflorescences (bunches) were systematically removed from the plant at time of anthesis, preventing fruit set during development. Treatment started in July 2006.

Measurement of stem growth rate

Stem height, from the rachis basis (insertion point of the first leaflet on the rachis) of the leaf rank 17 (a fully and mature expanded leaf, counted from the youngest leaf rank 1 in the top of the leaf crown) to the ground, was measured monthly since July 2006. Oil palm stem has no secondary growth and therefore has constant diameter; new biomass growth was assumed to occur at the top of the stem only. Stem growth (kg_{DM} $month^{-1}$) consisted of two fractions, (i) the production of new internodes associated with new phytomers and new leaf emission, and (ii) a gradual increase in wood density in older stem parts due to lignification (Corley and Tinker, 2003c), assumed to be constant (equal to 0.00074 g cm^{-3} $month^{-1}$, I Mialet-Serra, CIRAD, 'pers. comm.') and (iii) non-structural carbohydrate reserve variations calculated from observed variations of concentrations at four different stem heights and dimensions. Due to the latter, overall stem growth was alternatively positive and negative, depending on reserve mobilization and storage.

Measurement of leaf growth rate

The total numbers of fully expanded leaves, of newly appeared leaves and of pruned or broken leaves were recorded twice a month from July 2006 onwards. The morphology of each fully expanded leaf was described when leaves were pruned at the time of bunch harvest or monthly for FPT palm trees. Dry mass of the whole petiole, rachis and the leaflets, and the leaflets number were measured. To obtain the aggregate and monthly dry mass growth rates for all leaves on a plant, we plotted the time-course of monthly dry mass increment of each new leaf produced. We assumed that leaf growth followed a linear function over three months, the time of the rapid leaf growth just before the date of the leaf appearance.

Inflorescences appearance rate

Inflorescences belonged to one of three types: female, male and aborted. Upon their appearance (i.e. spathe opening date or anthesis), their type was recorded and, for FPT, the inflorescence was abscised. For control plants, bunch maturity (i.e. harvest date for female inflorescence only) was noted. At maturity, the number of fertilized and unfertilized fruits was recorded, dry mass of the peduncle, the spikelets and the two major fruit compartments (pulp and kernel), and oil:pulp dry mass ratio were measured. Growth rate (kg_{DM} $month^{-1}$) of each developing female inflorescence was supposed to followed a linear function over ten months (time of rapid growth before and after anthesis) and plotted each month.

Radiation use efficiency (RUE)

Radiation use efficiency (RUE, g_{DM} MJ^{-1}), was determined at monthly integration as the ratio between monthly aboveground dry mass production and absorbed PAR. Dry matter production thereby included the incremental weight gain of leaf and inflorescence growth using interpolation, stem structural growth calculated from height and width, and stem carbohydrate reserve pool as measured on drill cores. PAR absorption was calculated from: (i) LAI determined monthly as mean of leaflet dry mass multiplied by the specific leaf area (SLA, measured on pruned leaves) and total fully expanded leaf number in the crown; and (ii) the monthly absorbed PAR by the canopy. The latter was calculated with a radiation transfer model coupled with a 3D architectural model (Dauzat and Eroy, 1997, Mialet-Serra *et al.*, 2001) of oil palm calibrated by the observed LAI and specific architectural parameters measured on separate sets of plants on the same plots (leaf length, insertion angle, curvature and geometry of the leaves). The 3D model was canopy based and thus took distance between plants into account.

Photosynthesis measurements

The leaf gas exchange measurements were made regularly between July and November 2006 and between May and September 2007. In both cases, sampled leaves were full expanded and mature (leaves between rank 14 to 18, counted from the youngest leaf (rank 1) in the top of the leaf crown) and leaflets located at the three quarter of the rachis. One leaf per plant (six replicates) and one leaflet per leaf were daily sampled. Each set of plant replicates was followed during two consecutive days during two consecutive weeks each two months. During a day, two set of measurement were done, in the morning (0900 h – 1200 h) and in the afternoon (1400 h – 1600 h). Measurements of leaf gas exchanges were conducted with a portable IRGA (LCA-4, Analytical Development Company, Bio Scientific Ltd., Hoddesdon, Hertfordshire, England) to determine light-saturated net CO_2 assimilation (A_{max}). Measurements were made with a broadleaf chamber (6.25 cm^2) and an integrated light source (ADDA, DC Brushless). The curves were performed under controlled conditions, with saturating irradiance (1200 µmol photon m^{-2} s^{-1}, Dufrêne (1989)), at constant cuvette temperature (30°C), relative humidity (65-70%) and air CO_2 concentration (360 ppm). Leaf temperature (T_{leaf}) was measured with a thermocouple inside the cuvette of the LCA-4. The leaflet was placed in the cuvette one and half minute before the first recording. Three measurements (replicates) were recorded at one minute lag.

Non-structural carbohydrate and nitrogen analyses

Two different sampling procedures were used; the first was to follow seasonal variations of non-structural carbohydrate concentrations in the stem; the second was to follow non-structural carbohydrate and nitrogen concentrations in the leaflets linked to A_{max} variations. Sampling for non-structural carbohydrate analyses used similar methods as those used in a previous study on coconut trees (Mialet-Serra *et al.*, 2008). Observations were made every two months for a period of 22 months (July 2006 - May 2008). Samples were generally taken in the morning, a procedure that took several days and two hours per day. On the stem, radial core samples were taken using a Pressler drill (6.6 mm × 300 mm). The stem samples (one or two cores) were collected at four levels (at each quarter of the stem from the ground to the lowest leaf of the crown). Leaflets close to the leaflet used for photosynthesis measurement were harvested three times a day (morning, midday and afternoon) on each replicate plant, between July and November 2006 and between May and September 2007. In both procedures, sampled cores were placed in an ice box until further processing in the laboratory. The biochemical method used in the laboratory for sugar analysis was based on High Performance Liquid Chromatography (HPLC) and was reported in detail by Mialet-Serra *et al.* (2005). Total nitrogen concentration in the leaflets was determined after dry combustion following the Dumas method (Edeling, 1968).

Statistical analysis

One-way analysis of variance (ANOVA, Statistix, version 8.1, Analytical Software, Tallahassee, USA) was performed to evaluate the effect of the fruit pruning treatment (FPT) on growth, non-structural carbohydrate concentrations, assimilation and nitrogen concentration.

Statbox (version 6.5, Grimmersoft) was used to perform stepwise multiple linear regressions to explain RUE variations using various climatic variables and plant parameters as predictors. Monthly PARi, VPD, the number of Oil Synthetizing Bunches (OSB) and total non-structural carbohydrate concentrations in the stem were thus retained as best predictors.

RESULTS

Canopy structure, plant growth and dry matter partitioning

During the 22-month period of differential ablation treatment, stem height of pruned plants increased on average by 2.03 mm day^{-1} as compared to 1.73 for control plants resulting in mean total stem height of 1171 cm and 1094 cm for FPT and controls respectively at the end of the experiment (Table 1). Leaf Area Index (LAI), however, was significantly higher ($P<0.01$) due to shorter phyllochron ($P<0.01$) resulting in higher leaf number ($P<0.01$), whereas leaf rachis length and number of leaflets per leaf were unchanged. Leaflets had slightly but significantly ($P<0.01$) lower SLA and thus were probably thicker for FPT. Leaflet number and rachis length were extremely stable morphological parameters that did not vary by more than 6% (leaflet number) or 5% (rachis length) among the about 40 subsequent phytomers appeared during the 22 months. Means of leaflet numbers for all new leaves appeared after application of the treatment were 405 for control and 402 for FPT. Rachis length was similarly stable, indicating that oil palm has low phenotypic plasticity of leaf morphology.

TABLE 1. Mean stem height at the end of the observation period in May 2008, mean stem height growth, mean leaf and canopy properties and mean phyllochron duration for the experimental period (July 2006 – May 2008) of control and fruit pruning (FPT) palm trees. Values are means ± s.e.m of six replicates. Significance level of effects (ANOVA): ns = not significant; * = significant (0.5>P>0.01); ** = very significant (0.01>P>0.001). LAI, Leaf Area Index; SLA, Specific Leaf Area; PAR, Photosynthetically Active Radiation.

Treatment	Final stem height (cm)	Mean stem growth (mm day^{-1})	Mean fully expanded leaves ($plant^{-1}$)	Mean phyllochron duration (days)	Mean LAI unitless	Mean rachis length (cm)	Mean number of leaflets ($leaf^{-1}$)	Mean SLA (m^2 kg^{-1})	Mean extinction coefficient unitless	Mean PAR interception (%)
Control	1094 ± 26	1.73 ± 0.11	29.5 ± 0.85	17.1 ± 0.5	4.95 ± 0.11	665 ± 7	405 ± 2	7.88 ± 0.08	0.379 ± 0.005	85.5 ± 0.3
FPT	1171 ± 28	2.03 ± 0.12	35.9 ± 1.02	15.1 ± 0.3	6.02 ± 0.13	675 ± 7	402 ± 3	7.22 ± 0.13	0.357 ± 0.007	87.4 ± 0.7
P	ns	ns	**	**	**	ns	ns	**	*	*

Given the long lifespan of oil palm leaves in the crown (about two years if not pruned, according to Henry (1955b)), nearly half of the leaves observed during the 22-month experimental period were already present when differential treatments began, and the other leaves appeared during that period. Within the latter group, only a few leaves completed their development during the observation period. The natural life span of the leaves was not known because they were pruned at maturity of the fruit bunch they carried (or at the equivalent date in the case of male or aborted inflorescences), as generally done in oil palm plantations.

Greater LAI in FPT, resulting accelerated leaf appearance rate, translated only into a marginal increase of PAR interception (Table 1) because plant architecture, geometry and crown diameter remained unchanged, and the observed LAI (5 for controls and 6 for FPT) was sufficient to ensure near-complete interception of PAR (Gerritsma, 1992, Henson, 1995, Corley and Tinker, 2003c). The extinction coefficient k calculated for the plants using a 3D structural model was 0.38 for control and 0.36 for FPT, indicating that a large proportion of the leaf area had strong inclination. In fact, young leaves were erect, old leaves droopy and only mid-aged leaves had horizontal orientation (but with a curvature along their entire length).

Mean aboveground dry matter production (Fig. 2A) was 18.2 kg plant^{-1} month^{-1} or 2475 kg ha^{-1} month^{-1}, or 29.7 t ha^{-1} year^{-1} for controls, and only 14.6 kg plant^{-1} month^{-1} for FPT, corresponding to a reduction by 20%. The absence of reproductive sinks in FPT was partly compensated by significantly ($P<0.01$) increased growth of both leaves and stem, with stem growth rate nearly doubled. Partitioning of the incrementally produced aboveground dry matter to leaves, stem and fruits (Fig. 2B) was 0.45 for fruits, this being the mean harvest index observed during the 22-month observation period. Partitioning to leaves was 0.39 in controls and increased to 0.62 in FPT. Partitioning to stem was 0.16 in controls and increased to 0.38 in FPT. Partitioning coefficients for roots were not measured. Unpublished results (C Jourdan, CIRAD, France, ‘unpubl. res’) indicated that about 15% of the total incremental dry matter produced by mature oil palms is partitioned to roots.

Treatment effect on aboveground, vegetative dry matter gain (leaves and stems) became significant ($P<0.05$) during the second month after ablation treatment onset (Fig. 3A) and remained positive during most months thereafter. The mean monthly increase was 4.8 kg plant^{-1} or 48.3% of control mean. Time courses of vegetative growth of FPT plants closely followed those of controls, but at a higher level. A major peak in vegetative growth rate was observed for FPT in September-October 2007. In fact, all six replicates showed this peak, which was mainly due to a surge in carbohydrate storage in stem.

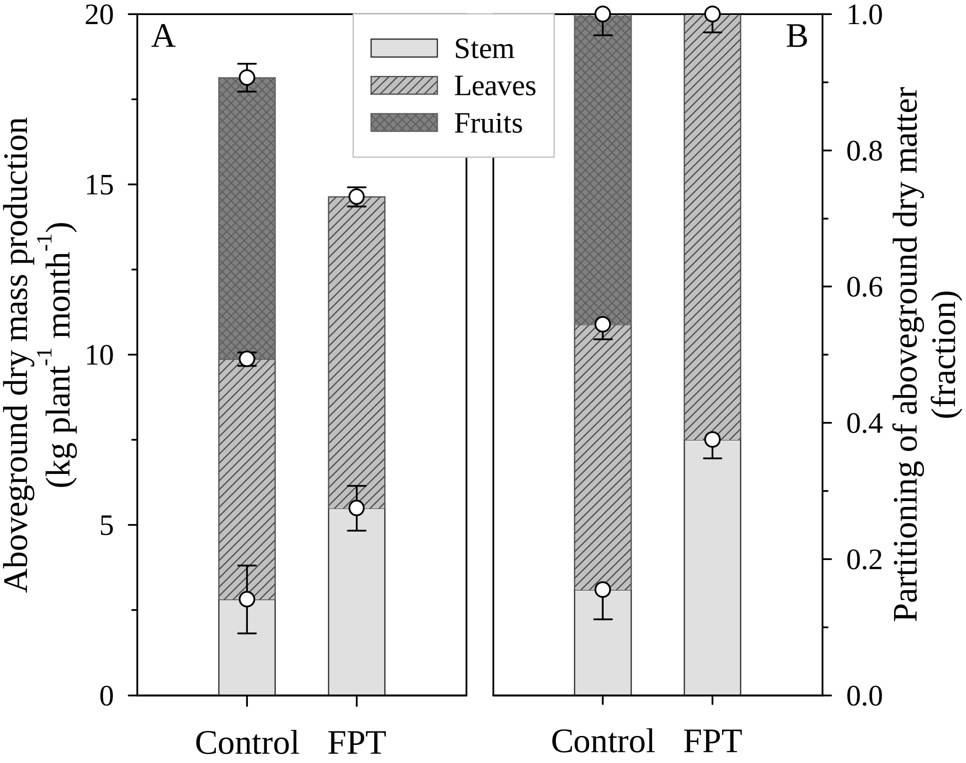

FIG. 2. (A) Mean monthly total aboveground dry matter production (absolute values) and (B) fraction of total dry matter production for each aboveground compartment for control and fruit pruning (FPT) palm trees for July 2006 - May 2008. Values are means of six replicates and bars indicate s.e.m.

Development rate

Development rate in terms of leaf appearance rate (phyllochron^{-1}) was significantly ($P<0.05$) increased in FPT in the second month after treatment onset (Fig. 3B). This difference between treatments remained nearly constant throughout the experiment. Time courses showed marked but irregular seasonal oscillations of unknown origin, the two treatments exhibiting strictly synchronous maxima and minima of development rate. Cumulative number of leaves appeared after treatment onset (Fig. 3C) was significantly ($P<0.05$) greater in FPT than in controls from the 8th month onwards. The difference was highly significant after 14 months. The rapidity of the accelerating effect of FPT on development rate (Fig. 3), and the fact that this effect was sustained thereafter, are surprising observations because leaves are initiated about two years before they appear (Henry, 1955b). There are thus about 40 to 50 leaves (Henry, 1955b, Corley and Tinker, 2003a) developing and "queuing up" to appear. The accelerated leaf appearance rate should thus deplete this "queue" and eventually diminish, unless leaf initiation and all processes happening between initiation and appearance are also sped up. The present results thus demonstrate indirectly that fruit pruning accelerated phytomer development in general, and not only leaf appearance.

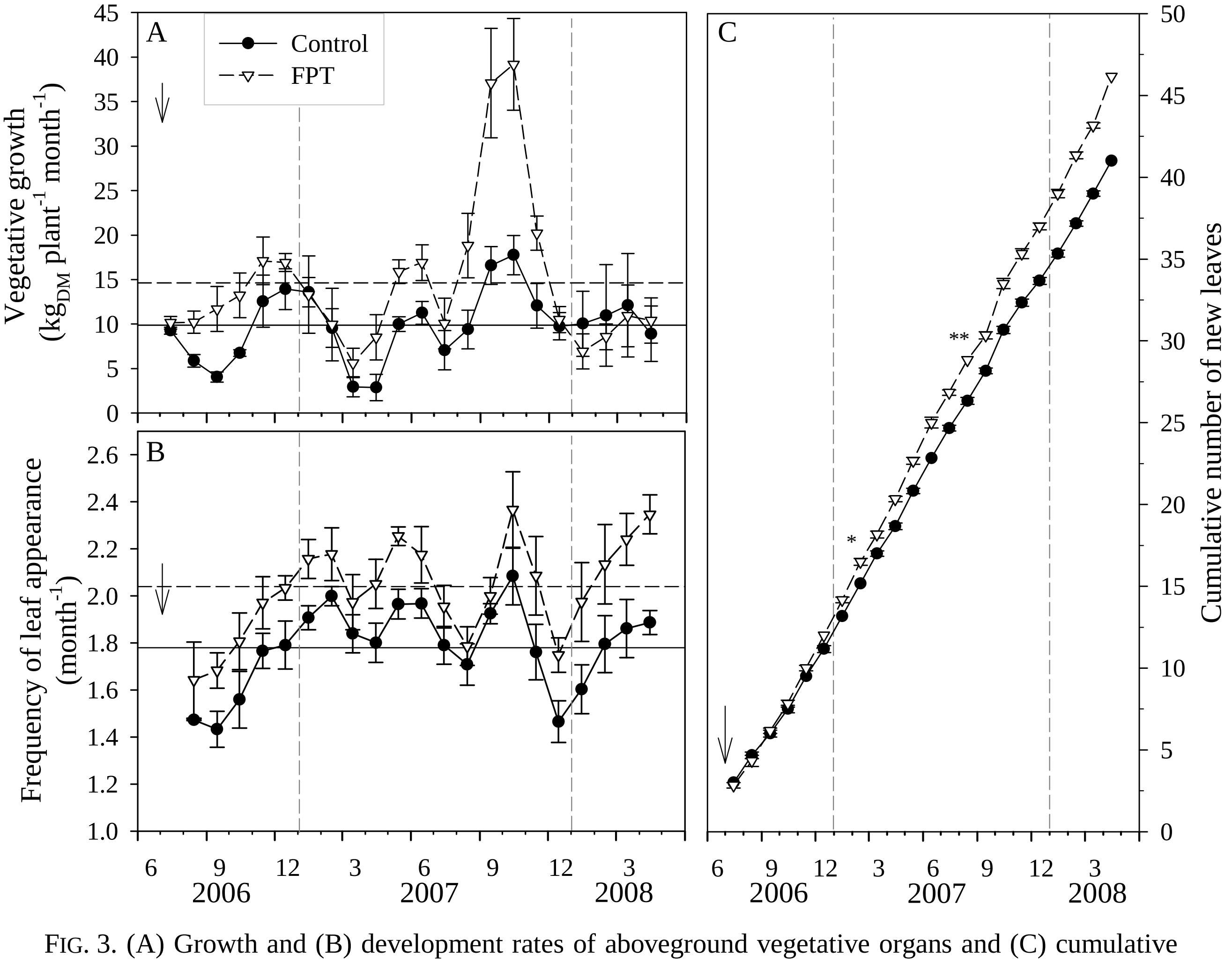

FIG. 3. (A) Growth and (B) development rates of aboveground vegetative organs and (C) cumulative number of new emitted leaves for control and fruit pruning (FPT) palm trees for July 2006 - April 2008. Values are means of six replicates. Significance level of effects (ANOVA): * = significant; ** = very significant (0.01>P>0.001). Arrows indicate the beginning of the treatment and bars indicate s.e.m. (______) and (_ _ _ _ _) lines indicated means for control and FPT, respectively, over the experimental period.

The appearance rate of new inflorescences (Fig. 4) (as indicated by the opening of the spathe or anthesis) was on average (for the entire 22-month period) accelerated to the same extent as that of the appearance rate of new leaves, but dynamics were not synchronized between FPT and controls. For controls, strong seasonal fluctuations of inflorescence appearance rates (between 1.0 and 2.5 month^{-1}) were observed with maxima occurring in March-April and July-August. These fluctuations were interpreted in a previous paper as the result of photoperiodic control (Legros *et al.*, 2008a). For FPT, strong but different variations occurred during the initial five months of treatment, followed by a comparatively stable plateau rate. Fruit pruning thus did not only increase inflorescence appearance rate on average, but also suppressed much of its seasonal variation.

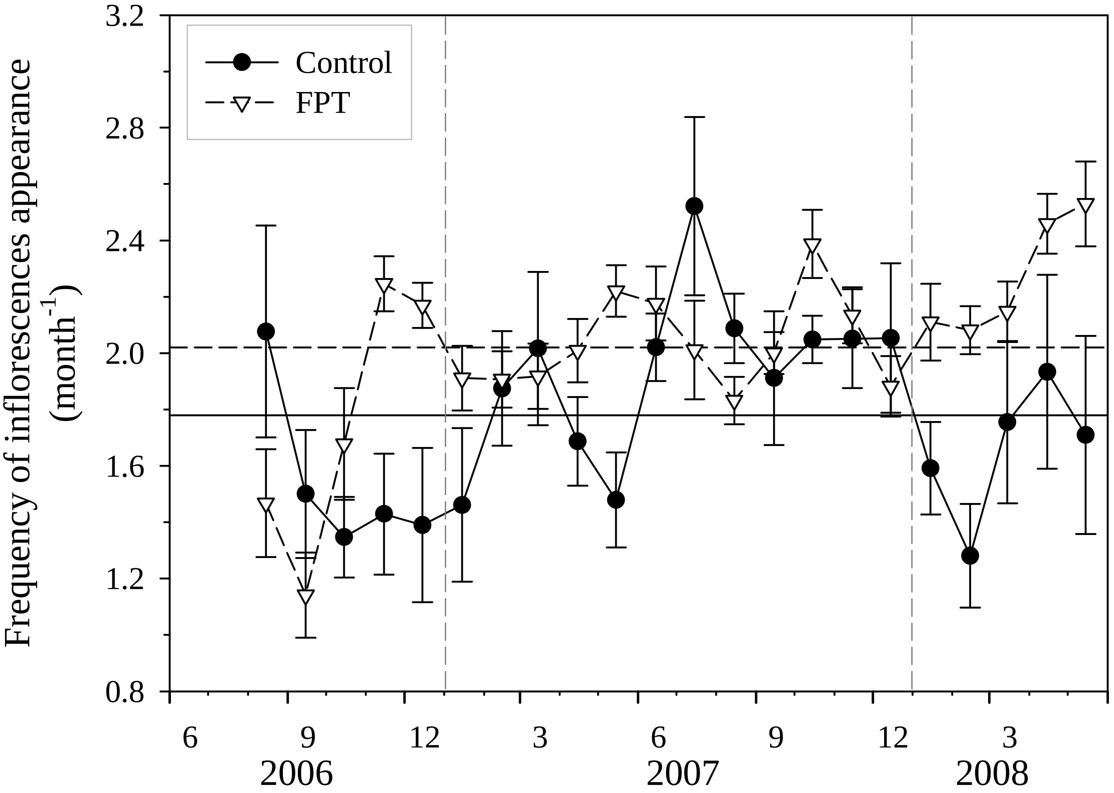

FIG. 4. Time courses of monthly frequency of inflorescence appearance (female + male + aborted) for control and fruit pruning (FPT) palm trees for July 2006 - May 2008. Values are means of six replicates and bars indicate s.e.m. (_____) and (_ _ _ _ _) lines indicated means for control and FPT, respectively, over the experimental period.

Sex differentiation and abortion rate of inflorescences

The monthly frequency of female, male and aborted inflorescences is presented in Fig. 5. Frequency of female inflorescences fluctuated strongly during the year preceding treatment onset, but was roughly synchronous between controls and FPT (Fig. 5A). Fruit pruning led to a marked acceleration and thus, de-synchronization of dynamics of appearance of female inflorescences, seasonal peaks and minima occurring earlier. From early 2008 (ca. 18-20 months after FPT onset), the frequency of female inflorescences became continuously higher in FPT than in controls. Frequency of male inflorescences (Fig. 5B) also fluctuated in both treatments and was on average higher for FPT than for controls. Frequency of aborted inflorescences (Fig. 5C) was mostly lower than for fertile inflorescences, but for controls it showed a marked peak in May to August 2007, followed by a smaller peak around November. These peaks were absent for FPT.

Partitioning ratios of inflorescences among female, male and aborted types are presented in Fig. 6B-C, along with dynamics of the climatic water balance (CWB) (Fig. 6A). The two abortion peaks observed for controls can hypothetically be associated with two dry spells that happened about 10 months earlier. The dry spell in July-August 2006 was particularly severe and exceptional for the site (Fig. 1) (Legros *et al.*, 2008a). Another observation that could be associated with the main abortion peak around June 2007 is major bushfires that caused a thick haze over Sumatra Island in August-October 2006. Whatever the cause of the abnormal abortion peak in controls, it occurred at or after the date of FPT treatment onset (because FPT inflorescences were not aborted), and FPT plants were not sensitive to it. Abortions affected mainly male inflorescences (Fig. 5 and Fig. 6).

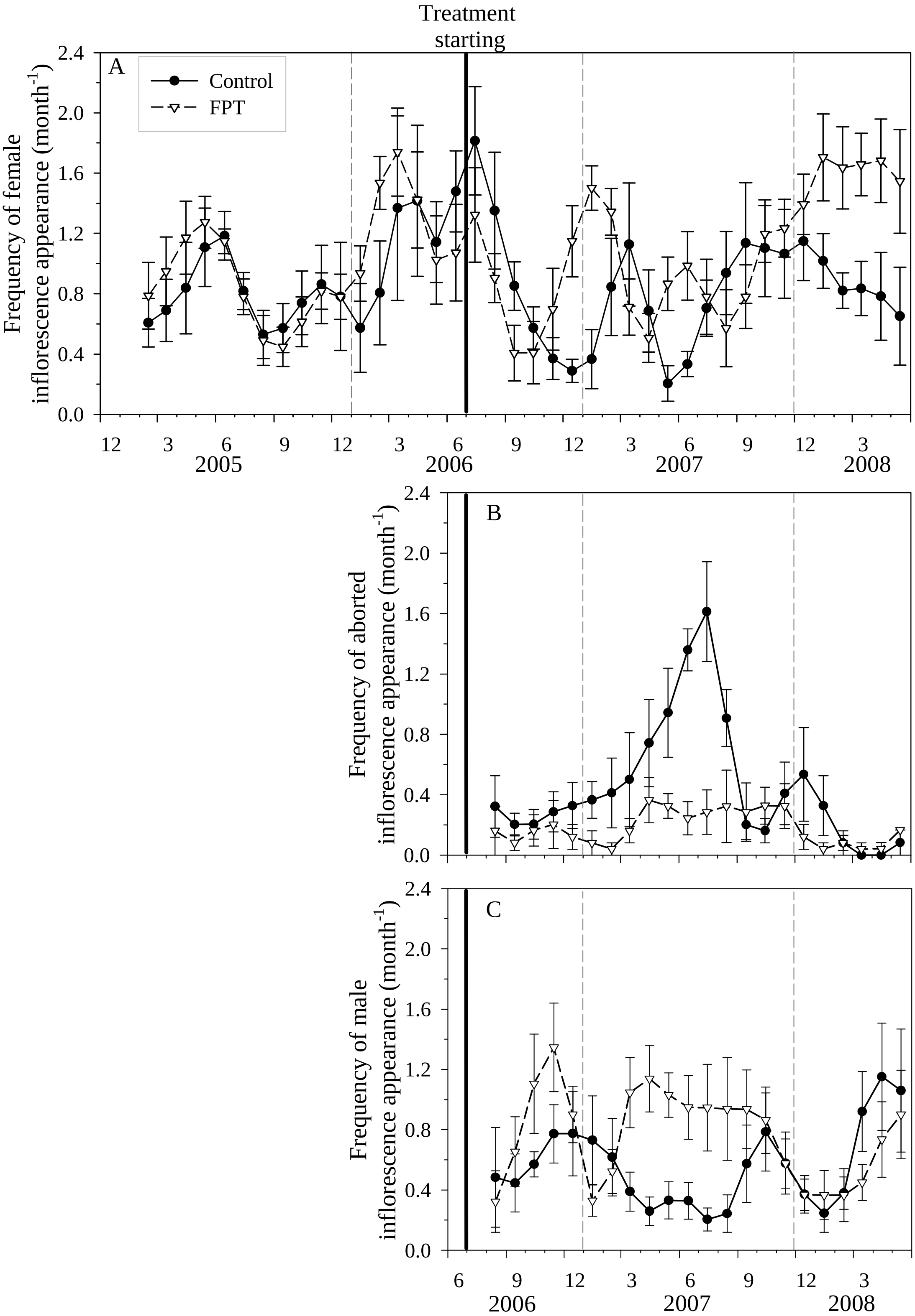

FIG. 5. Time courses of monthly frequency of (A) female inflorescences appearance from January 2005 to April 2008, (B) male inflorescences and (C) of aborted inflorescences appearance for August 2006 - May 2008 for control and fruit pruning (FPT) palm trees. Values are means of six replicates and bars indicate s.e.m.

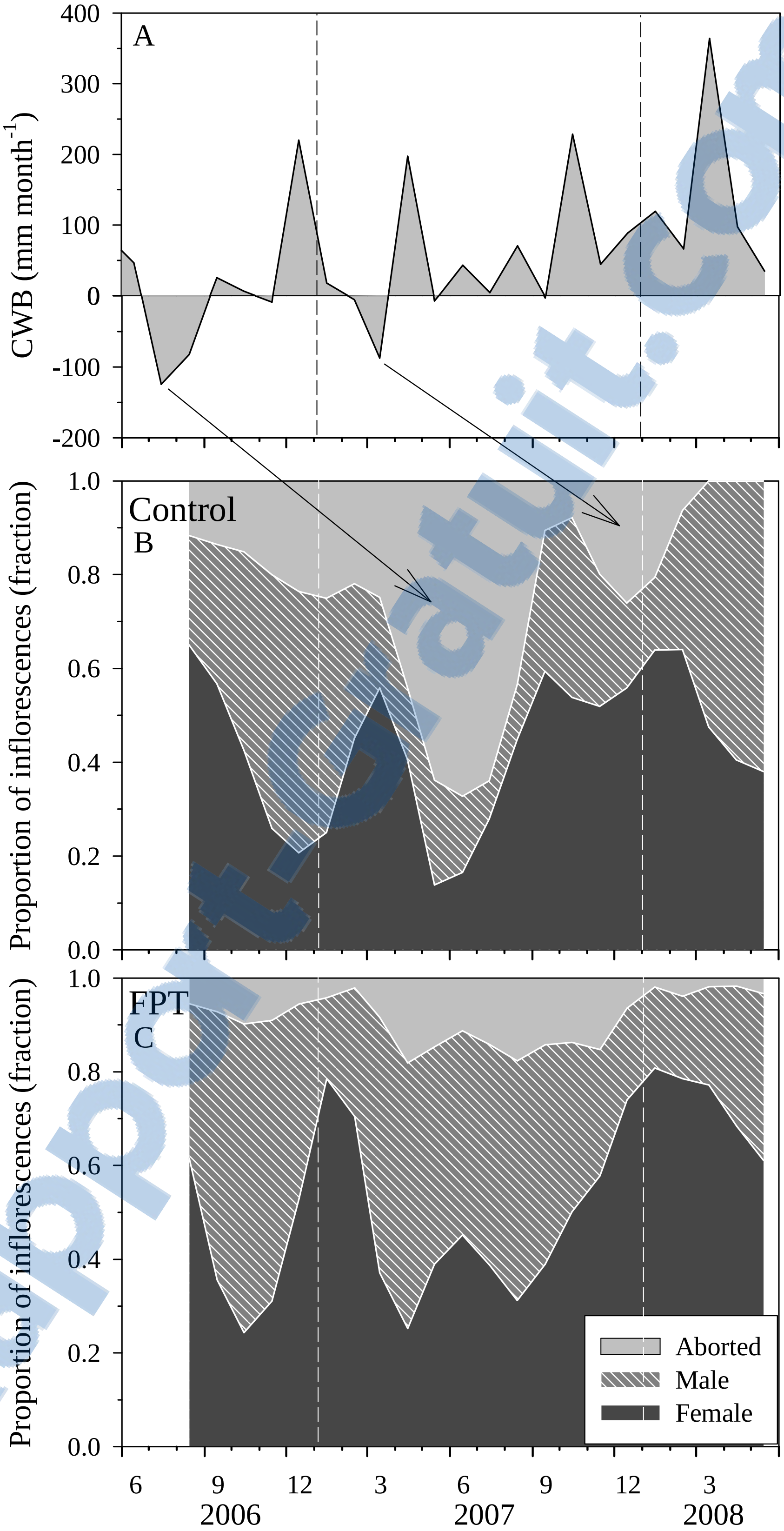

FIG. 6. Time courses of monthly (A) drought indicator (climatic water balance, CWB = monthly rainfall – potential evapotranspiration), (B-C) fraction of each inflorescence (female, male and aborted) for control and fruit pruning (FPT) palm trees for August 2006 - May 2008.

Non-structural carbohydrates

Fruit pruning treatment caused a gradual and highly significant ($P<0.01$) increase in total non-structural carbohydrate concentrations (starch and soluble carbohydrates) in the top part of the stem (Fig. 7A), a compartment that was previously shown to accumulate substantial carbohydrate reserves, notably starch (Legros *et al.*, 2006). This resulted in a 1.8-fold increase compared to control in the course of 22 months, attaining values up to nearly 500 mg g^{-1}. Not all non-structural carbohydrates participated in this increase: in FPT, glucose concentration consistently decreased in this compartment and starch strongly increased. The observed seasonal fluctuations in glucose in controls, as opposed to the smoother dynamics in FPT, were not correlated with any other variable observed on the plant.

Relative contribution of individual carbohydrate to total carbohydrate reserves in stem top fluctuated strongly in controls (Fig. 7B). Starch and glucose were the dominant fractions, on average 79.3 and 76.9 mg g^{-1}, followed by sucrose (45.7 mg g^{-1}) and fructose (21.0 mg g^{-1}). In FPT (Fig. 7C), the starch fraction increased and constituted more than two-third of carbohydrate reserves at the end of the experiment, whereas the glucose fraction declined, and sucrose and fructose fractions remained about constant.

A marked vertical gradient in non-structural carbohydrate concentration and composition was observed on the stem (Table 2). In controls, total non-structural carbohydrates showed decreasing concentration from the top to the bottom. This gradient was mainly due to starch whereas glucose did not show a clear gradient. In FPT, the gradient was further amplified and starch accounted almost entirely for the increases in total non-structural carbohydrates. Reserve accumulation in FPT thus resembled a gradual filling-up process of starch from top to bottom. The storage of soluble carbohydrates, namely glucose, thereby remained substantial fraction of total reserves, although they did not participate in the accumulation process under the sink-source imbalance caused by FPT.

Reserve dynamics constituted a dominant component of stem dry weight dynamics and were thus responsible for most of the strong seasonal fluctuations observed for vegetative aboveground growth (Fig. 3A). These fluctuations showed similar patterns between controls and FPT and also among replicates (as indicated by the small s.e.m. of monthly means for the aggregate growth rates, Fig. 3A), and were thus not due to experimental noise.

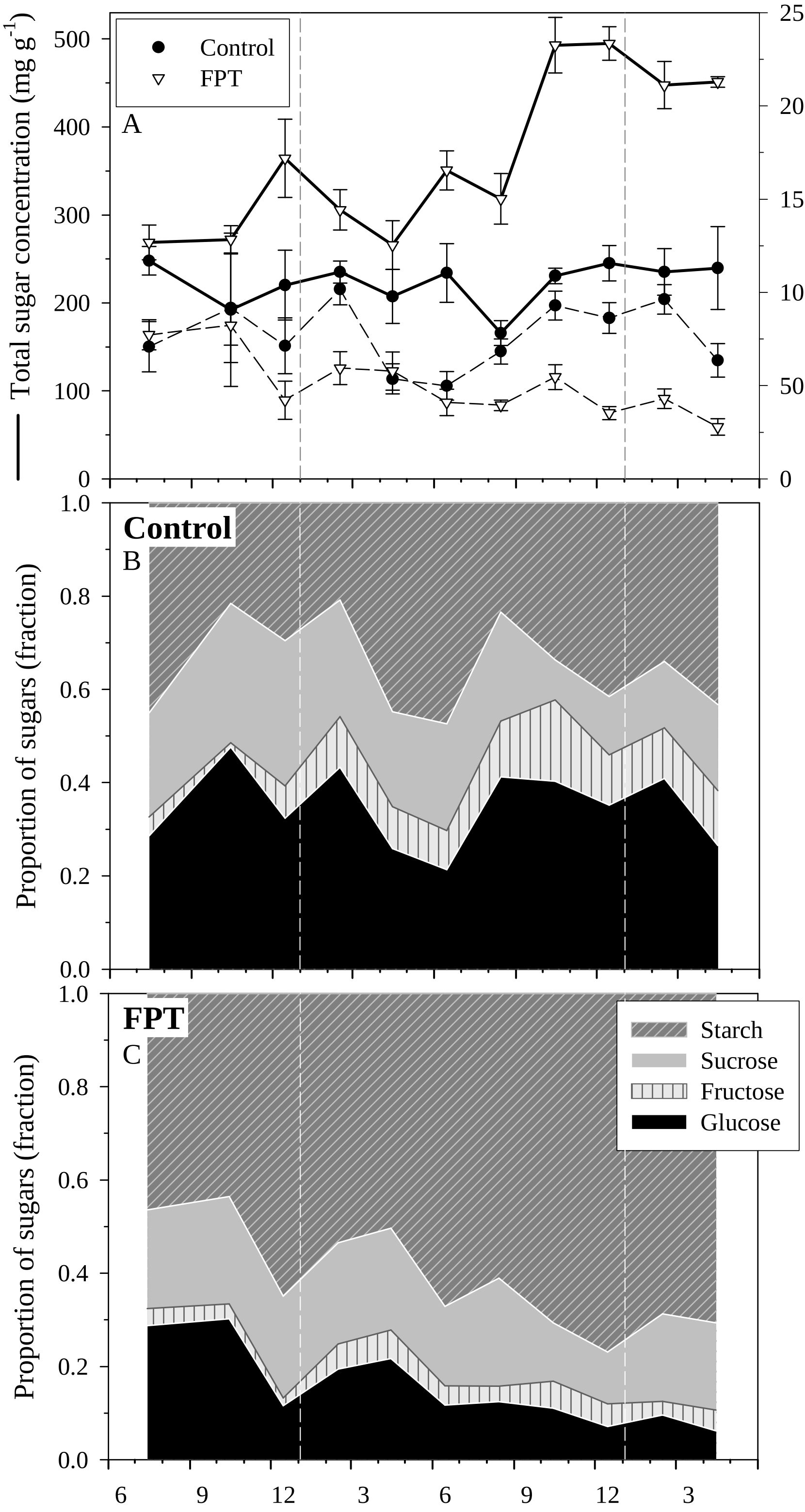

FIG. 7. (A) Time course of total non-structural carbohydrate (monosaccharides + sucrose + starch) and glucose concentrations in the top of the stem for control and fruit pruning (FPT) palm trees for July 2006 - April 2008. Values are means of six replicates and bars indicate s.e.m. (B-C) Fraction of each non-structural carbohydrate (glucose, fructose, sucrose, starch) in the top of the stem for control and fruit pruning (FPT) palm trees from July 2006 to April 2008.

TABLE 2. Mean glucose, starch and total non-structural carbohydrate (NSC) concentrations at four levels (at each quarter of the stem from the ground to the top stem, below the lowest leaf) on the stem of control and fruit pruning (FPT) palm trees 12 months after the beginning of the treatment (July 2007). Values are means ± s.e.m of six replicates. Significance level of effects (ANOVA): ns = not significant; * = significant (0.5>P>0.01); ** = very significant (0.01>P>0.001); *** = highly significant (P<0.001).

Treatment	Effect	Glucose mg g_{DM}^{-1}	Starch mg g_{DM}^{-1}	Total NSC mg g_{DM}^{-1}
Stem top	Control	38.4 ± 5.8	101.4 ± 17.5	208.1 ± 24.8
	FPT	29.4 ± 3.9	252.8 ± 11.5	354.0 ± 18.7
	P	ns	ns	ns
Stem ¾	Control	79.8 ± 4.9	48.3 ± 14.4	191.7 ± 12.9
	FPT	51.0 ± 9.5	177.0 ± 34.9	315.0 ± 28.7
	P	ns	**	*
Stem ½	Control	68.3 ± 7.1	11.5 ± 6.1	124.9 ± 13.5
	FPT	51.8 ± 4.2	48.8 ± 6.6	166.6 ± 3.6
	P	*	**	**
Stem ¼	Control	50.9 ± 7.0	7.5 ± 5.1	99.0 ± 13.5
	FPT	42.9 ± 6.3	55.8 ± 21.4	151.3 ± 29.2
	P	ns	***	***

Radiation use efficiency and leaf photosynthesis

Monthly mean RUE varied between 0.70 and 2.35 g MJ^{-1} (controls) and between 0.37 and 2.80 g MJ^{-1} (FPT) (Fig. 8). Mean RUE during the experimental period was 1.44 g MJ^{-1} for controls and 1.12 g MJ^{-1} for FPT. Marked seasonal fluctuations were observed for both treatments and where consistent between the treatments. The FPT treatment reduced RUE by about 30-40% during the initial nine months (July 2006 and March 2007). Thereafter, FPT showed a marked peak (September-October 2007) and then declined below control values about 18 months after treatment onset. This peak was associated with the surge in stem carbohydrate reserves already described, observed along the entire length of the stem and for all replicates (apical compartment: Fig. 7A).

Multiple linear stepwise regression analyses were used to identify explanatory variables for RUE variability, using weather variables, plant fruit load and plant reserve status as predictors. In controls, 43% of monthly variation in RUE (P = 0.0006) was explained by monthly incident PAR variation alone:

$$RUE_{(control)} = 4.52 - 0.0128 \times PAR_i \quad (\text{adjusted } r^2 = 0.43, P<0.001, n=21)$$

With RUE = radiation use efficiency (g_{DM} MJ^{-1}) and PAR_i = mean monthly incident photosynthetically active radiation (MJ m^{-2} $month^{-1}$).

A three-factorial model explained RUE variation slightly better (52%) but had lower overall probability ($P = 0.0009$) due to lesser degrees of freedom:

$RUE_{(control)} = 2.71 + 0.201 \times OSB + 0.00546 \times TNSC - 3.306 \times VPD$ (adjusted $r^2 = 0.52$, $P<0.001$, $n=21$)

With RUE = radiation use efficiency ($g_{DM}\ MJ^{-1}$); OSB = number of fruit bunches undergoing oil synthesis in the last two months before maturity; TNSC = concentration of total non-structural carbohydrates in stem (mg g_{DM}); VPD = mean monthly vapour pressure deficit (kPa).

The weather variables PAR (best predictor in single-factor model) and VPD (retained for multiple-factor model) were strongly auto-correlated (adjusted $r^2 = 0.54$). The conventional RUE term used here was based on dry matter and thus did not give differential weight to calorically different compounds. An RUE term using caloric weighting would result in higher values during fruit filling periods because of lipid accumulation (Corley and Tinker, 2003c). This would increase the (positive) contribution of OSB in the multiple linear regression model (data not presented).

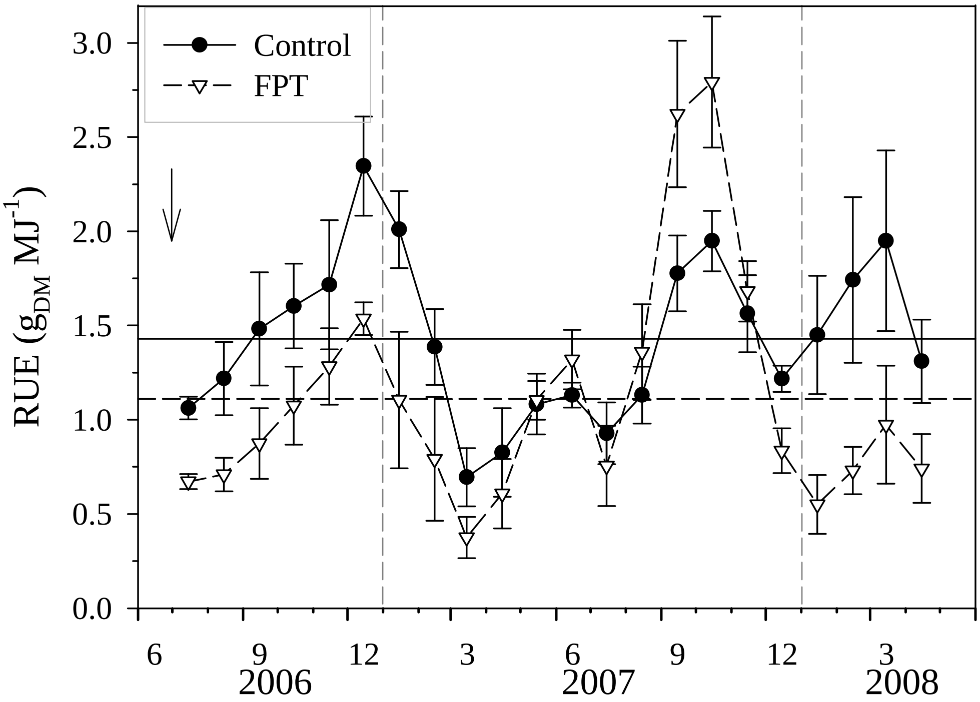

FIG. 8. Time courses of radiation use efficiency (RUE) for control and fruit pruning (FPT) palm trees for July 2006 - April 2008. Values are means of six replicates and bars indicate s.e.m. Arrow indicates the beginning of the treatment.

Light-saturated net CO_2 assimilation rate (A_{max}) of leaflets was observed in regular intervals in 2006 and 2007, along with sampling of leaflets for non-structural carbohydrate and nitrogen content analyses. Means for 2006 and 2007 observations are presented in Table 3. Despite the strongly reduced RUE calculated for FPT (Fig. 8), this treatment was not associated with reduced A_{max}. In fact, means of A_{max} were by 14% higher in 2006 and by 7% higher in 2007 for FPT, although not significantly. This trend was possibly due to differences in SLA (Table 1), whereas leaflet total non-structural carbohydrate (as for glucose, sucrose and starch) and nitrogen concentrations were unaffected by treatment (Table 3). Consequently, the reduction of RUE observed for FPT during the initial nine months of treatment was not due to A_{max}.

TABLE 3. Mean light-saturated net CO_2 assimilation (A_{max}), mean non-structural carbohydrate (glucose, sucrose, starch and total NSC) and mean nitrogen concentrations in leaflets for control and fruit pruning (FPT) palm trees between July and November 2006 and between May and September 2007. Values are means ± s.e.m of six replicates. Significance level of effects (ANOVA): ns = not significant.

Year	Treatment	A_{max} (µmol m^{-2} s^{-1})	Glucose (mg g_{DM}^{-1})	Sucrose (mg g_{DM}^{-1})	Starch (mg g_{DM}^{-1})	Total NSC (mg g_{DM}^{-1})	Nitrogen (%)
2006	Control	14.93 (0.80)	21.37 ± 1.18	12.08 ± 2.70	9.65 ± 0.79	62.65 ± 2.97	2.57 (0.05)
	FPT	16.99 (0.84)	22.17 ± 2.08	12.16 ± 3.22	12.43 ± 1.92	67.22 ± 3.95	2.54 (0.05)
	P	ns	ns	ns	ns	ns	ns
2007	Control	12.87 (0.43)	20.70 ± 1.70	17.70 ± 3.53	11.34 ± 0.99	67.35 ± 1.89	2.50 (0.04)
	FPT	13.80 (0.70)	21.15 ± 1.56	18.78 ± 3.42	12.02 ± 0.76	70.43 ± 1.31	2.59 (0.02)
	P	ns	ns	ns	ns	ns	ns
Year × Treatment							
	P	ns	ns	ns	ns	ns	ns

DISCUSSION AND CONCLUSION

This study followed up on two previous studies, one investigating the phenotypic plasticity of coconut growth and development under experimentally imposed sink-source imbalances (Mialet-Serra *et al.*, 2008) and the other investigating oil palm growth and development responses to naturally varying environments (Legros *et al.*, 2008a). The studies indicated that phenological and morphological adjustment processes in tropical palm family crops occur with substantial lags in the order of months to years, due to long development periods of individual phytomers and organs (Henry, 1955b, Corley and Gray, 1976a) and to the inherent architectural rigidity of these plants (Corley *et al.*, 1971, Henson, 1999b, Henson, 2006a), particularly their vegetative architecture. In both species, plants adjusted to the resulting, transitory, sink-source imbalances in the short term with variable, apparently demand-driven RUE, and in the long term through variable fruit load. The morphology and development rate of vegetative plant parts thereby remained remarkably unaffected in coconut (Mialet-Serra *et al.*, 2008), whereas phyllochron and bulk leaf growth were sensitive to environment in oil palm (Legros *et al.*, 2008a).

Phenotypic plasticity of oil palm induced by sink limitation

The present study applied an artificial fruit pruning treatment (FPT) to investigate oil palm adjustments to severe sink limitation. Some morphological plant characteristics, such as leaf size and leaflet number, were not at all affected by FPT, neither initially nor after 22 months. This characteristic of oil palm, previously observed by Siregar (2006), was also found for coconut (Mialet-Serra *et al.*, 2008), but is probably shared by few other species because leaf size is generally considered to be resource dependent (van Staalduinen and Anten, 2005, Luquet *et al.*, 2006, Gordon and Dejong, 2007). Older reports, however, observed variable frond length and weight on oil palm (Calvez, 1976, Corley and Hew, 1976b, a).

In contrast to leaf morphology, leaf appearance rate of oil palm was strongly modified (accelerated) by sink limitation in this study. This is not the case, or much less, for coconut (Mialet-Serra *et al.*, 2008). The precursor study to this article also reported leaf appearance rate of oil palm to be highly sensitive to water deficit (Legros *et al.*, 2008a). The acceleration of phyllochron by sink limitation (and thus, luxurious assimilate supply) was found to last at least as long as FPT continued (22 months). If the treatment had only accelerated leaf appearance through enhanced elongation of developing leaves, this effect would have soon exhausted itself, unless the initiation and development of new leaves would have been accelerated as well. It is therefore evident that sink limitation accelerated the entire developmental cascade of phytomer and leaf initiation, development and appearance. We thus conclude that oil palm development is not only driven by thermal time (Ong, 1982) and slowed by physiological stresses (Bredas and Scuvie, 1960, Nouy *et al.*, 1999), as observed in many monocotyledonous plants and particularly grasses (Wu *et al.*, 1997), but also driven by assimilate availability. Sink limitation accelerated the appearance of inflorescences (totals including female, male and aborted) on average to the same extent as it accelerated leaf appearance (Fig. 4 *vs* Fig. 3).

Sex differentiation and inflorescence abortion

The acceleration of inflorescence appearance by FPT was associated with a gradual loss of intra-annual (seasonal) variations (Fig. 4). This observation is difficult to interpret because it was associated with changes in proportion among female, male and aborted inflorescences, the fraction of aborted ones being much smaller in FPT.

The high but variable fraction of aborted inflorescences in controls appeared to be related to water deficit experienced about 10 months earlier. If this hypothesis is true, FPT, and thus luxurious assimilate availability, counteracted drought effects on abortion rate. Even if the evidence for drought effects on abortion does not amount to proof, it is certain that the trigger of the abortion peak observed in controls did not happen more than 10 months before anthesis because the peak disappeared in FPT, a treatment that began at around that time. This time lag for inflorescence abortion agrees with previous reports (Dufour *et al.*, 1988, Caliman and Southworth, 1998). Corley (1976) reported that aborted inflorescences are predominantly female. In the present study, the opposite was the case because prevention of the two abortion peaks by FPT mainly increased the male fraction of inflorescences.

Seasonal oscillations of the frequency of female inflorescences were conserved under FPT but were markedly accelerated, an observation that is in accordance with the general acceleration of development rate observed for that treatment. It took 18 to 20 months of treatment, however, to induce a significant change (increase) of female inflorescence number (Fig. 5). This increase can be interpreted as a treatment effect on sex differentiation. Corley (1977), Dufour *et al.* (1988) and Caliman and Southworth (1998) estimated that sex determination happens about 24 months before anthesis, probably followed by a period of several months during which sex determination is reversible (Corley and Tinker, 2003c). Sex determination, or the resulting sex ratio, is environment dependent in oil palm; unfavourable conditions increasing the frequency of male inflorescences (Corley, 1977). In the present study, FPT increased available resources through sink limitation, as indicated by the continuous and strong increase in carbohydrate reserves. This was probably the cause of the increased rate of phytomer and inflorescence development (both an immediate and continuous effect), of the suppression of environment-induced abortions (lag period of around ten months) and also of the greater numbers of female inflorescences (lag period of nearly 20 months).

Dry matter partitioning and sink-source imbalances

The FPT treatment effectively created a pronounced and continuous sink limitation in the plant system, as indicated by the accelerated organogenesis, increased aboveground vegetative growth and storage of reserves. Accelerated organogenesis, however, was insufficient to absorb the surplus of available assimilates, resulting in reduced overall growth (Fig. 2A).

It appears that the extraordinarily low plasticity of organ size (Table 1) and the absence of branching in the vegetative architecture of oil palm limited the scope for major adjustments in partitioning of assimilates to new or enhanced, alternative sinks. An unknown entity in this equation is the root system which inherently has greater plasticity than shoot architecture (Henson and Chai, 1997, Corley and Tinker, 2003c) and may have absorbed and used some of the extra assimilates made available by fruit pruning. If FPT enhanced root growth, this would probably be limited to structural growth because root systems of oil palm (Legros *et al.*, 2006) and coconut (Mialet-Serra *et al.*, 2005, Mialet-Serra *et al.*, 2008) store only small amounts of carbohydrate reserves.

A major reservoir absorbing excess assimilates under FPT was non-structural carbohydrate storage in the stem. Top part of the stem contained between 40 and 50% of reserves (soluble carbohydrates and starch confounded), associated with an increase of diameter of those parts of the trunk (data not presented). The nearly doubled stem mass growth observed for FPT (Fig. 2A) was to more than 80% due to reserves, thus constituting the main pathway for the utilization of excess assimilates.

Legros *et al.* (2006) reported that about 65% of plant carbohydrate reserves of oil palm are located in stem, their largest overall fraction being glucose. Glucose was accumulated along the entire stem, whereas starch was accumulated at stem top. Coconut shows a similar pattern, but the predominant soluble carbohydrate accumulated along the entire stem is sucrose (Mialet-Serra *et al.*, 2005).

Reserve carbohydrate pools are known to respond to source-sink imbalances (Jordan and Habib, 1996, Silpi *et al.*, 2007). Models simulating phenotypic plasticity, such as *EcoMeristem* (Luquet *et al.*, 2006), consider transitory reserves as a passive buffer of such imbalances, but Lacointe *et al.* (2004) and Silpi *et al.* (2007) reported that reserve formation in vegetative organs can constitute a sink in its own right, thus competing with other sinks.

Reserve accumulation induced by FPT consisted entirely of starch and followed an acropetal gradient, whereas glucose concentration declined, particularly in tissues where starch was accumulated. It thus seems that glucose and starch do not have the same function, and glucose may not serve a storage function at all despite concentrations attaining 100 mg g^{-1} in stem top of controls (Fig. 7).

Radiation use efficiency and leaf CO_2 exchange rate

Mialet-Serra *et al.* (2008) reported that in coconut undergoing fruit ablation treatment, carbohydrate storage in stem constituted only a minor adjustment process to the sink limitation, whereas reduced RUE explained a much larger part of plant response in quantitative terms. The physiological cause of decreased RUE was not known, but the authors speculated that leaf photosynthetic rates might have been smaller. In fact, many reports describe end product inhibition of leaf photosynthesis, mediated by soluble carbohydrates, as a major adjustment mechanism to sink or transport limitation (Iglesias *et al.*, 2002, Frank *et al.*, 2006, Susiluoto *et al.*, 2007).

The present results on oil palm differ markedly from those reported for coconut. FPT consistently reduced RUE during the initial 9 months but to a lesser extent than previously observed on coconut (25-40% *vs* 60-80%). RUE then caught up with controls and even exceeded it (Fig. 8), and finally significantly dropped below control values about 18 months after treatment onset. These results suggest that RUE did initially participate in adjustment processes to sink limitation, but then returned to normal (control) values. We suggest that this regain of control levels was due to other sinks absorbing the excess assimilates, namely stem parenchyma and leaves appearing in accelerated succession. The decrease in RUE at the end of the treatment period, however, might be due to saturation of the storage compartment in the stem, but this hypothesis is difficult to prove experimentally.

Variation of RUE over time in control plants was very strong. About 40% of this variation was explained by mean monthly incident PAR, which had a negative effect. This is in agreement with previous findings on coconut (Mialet-Serra *et al.*, 2008) and can probably be explained with PAR dependent saturation levels of leaf photosynthesis because palm family plants are generally of the C3 type (Haynes, 1998). In coconut, however, RUE was also negatively correlated with leaflet soluble carbohydrate concentration which was not the case for oil palm (data not presented). Instead, we observed a positive contribution of fruit load and stem reserve concentrations on RUE, although their explanatory power was much smaller than that of incident PAR. Fruit load is a determinant of plant demand for assimilates (Heuvelink, 1997, Valantin *et al.*, 1998) and an indicator of the ability of the plant to use photosynthates (Lecoeur and Ney, 2003). But such effects on RUE, if they played a significant role in the plants studied, were not due to variation in leaf light-saturated net CO_2 assimilation rate (A_{max}). Variation in A_{max}, in turn, was not related to leaflet non-structural carbohydrate or nitrogen concentration, which did not vary between treatments. Consequently, feedbacks of plant demand for assimilates or an accumulation of non-structural carbohydrates in leaflets were not factors affecting RUE in this study.

Conclusion

This study sought to identify the adjustment processes to sink-source imbalances, and particularly sink limitation, enabling oil palm to maintain a state of equilibrium between assimilate production and utilization. The plant was found to rapidly adjust the rate of developmental processes to sink limitation, accelerating substantially the number of phytomers produced, including leaves and inflorescences. This response contributed demand for assimilates and thus, represented an effective adjustment. No plasticity was observed, however, with regards to leaf size and leaflet number per leaf.

Sink limitation also suppressed the abortion of male inflorescences, estimated to be triggered at about 10 months before anthesis. It also increased the number of female inflorescences produced, but only after an estimated lag of 20 months, approximately corresponding to the period of sex differentiation. This effect can also be considered as a positive adjustment to sink limitation because it increases assimilate demand for fruit filling, albeit with a delay that may render this adjustment ineffective in most situations, such as biophysical or biotic stresses of limited duration.

In contrast to previous findings on coconut, RUE was only temporarily affected by sink limitation and returned to control levels after 9 months of treatment. No treatment effect on A_{max} was observed, indicating that end product inhibition of photosynthesis was not among the adjustment processes at work.

In quantitative terms by far the most important adjustment process was increased assimilate storage in stem, mainly as starch. This reservoir thus constitutes an important buffer for sink-source imbalances in oil palm. It remains unclear, however, why the fruit ablation treatment specifically increased starch storage and reduced glucose storage, whereas glucose is quantitatively the most abundant non-structural carbohydrate reserve in oil palm under normal (non-fruit pruned) growth conditions.

These results, in combination with those presented in the precursor study on the effects of natural environment variability on oil palm sink-source relationships and phenology (Legros *et al.*, 2008a), will enable the development of a phenological and growth model for the palm species.

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CHAPITRE IV:

ROLE OF TRANSITORY CARBON RESERVES DURING ADJUSTMENTS TO CLIMATE VARIABILITY AND SINK-SOURCE IMBALANCES IN OIL PALM (*ELAEIS GUINEENSIS* JACQ.)

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Running Title: Carbon reserves in oil palm

RESUME EN FRANÇAIS

ROLE DES RESERVES CARBONEES DANS LES AJUSTEMENTS FACE A LA VARIABILITE DU CLIMAT ET AUX DESEQUILIBRES SOURCE-PUITS CHEZ LE PALMIER A HUILE (*ELAEIS GUINEENSIS* JACQ.)

Introduction

Le palmier à huile (*Elaeis guineensis* Jacq.) est une monocotylédone, pérenne, tropicale qui se caractérise par une architecture simple, une faible plasticité phénotypique et un cycle de développement long des phytomères (jusqu'à quatre années). Les variations environnementales affectent les puits végétatifs et reproducteurs de façon décalée dans le temps, provoquant des déséquilibres source-puits fréquents. Ce chapitre tente de décrire et d'analyser le rôle des deux principales sources de carbone, l'assimilation carbonée et la mobilisation des carbohydrates non-structuraux dans les ajustements observés lors de tels déséquilibres.

Matériels et Méthodes

En Indonésie, un génotype donné (63) est suivi dans trois situations contrastées : (i) un site favorable à la culture (Kandista, 0°55'N) ; (ii) un traitement « ablation totale des régimes » (FPT) sur ce même site, est appliqué afin de limiter la demande fructifère ; (iii) un site se caractérisant par des périodes de sécheresse dont la sévérité est variable d'une année sur l'autre (Batu Mulia, 3°12'S). L'assimilation carbonée (A_{max}) à l'échelle foliaire est régulièrement mesurée. Les teneurs en sucres solubles et en amidon dans le stipe sont, par ailleurs, déterminées tous les deux mois. Les productions de biomasses aériennes végétative et reproductive sont estimées tous les mois. L'intensité des périodes sèches est estimée par simulation de la fraction d'eau du sol transpirable (FTSW).

Résultats majeurs

Les déséquilibres source-puits sont principalement dus à (i) une réduction rapide du taux d'assimilation carbonée pendant les périodes de sécheresse, et ce principalement à Batu Mulia ; (ii) une réponse rapide de la croissance végétative structurale à la sécheresse ; (iii) des effets différés (16 à 29 mois après) de l'environnement sur le développement des puits reproducteurs. Ces déséquilibres sont alors tamponnés par des variations importantes du pool de carbohydrates non-structuraux localisés dans le stipe, majoritairement composé de glucose et d'amidon. Le pool d'amidon qui varie significativement, tamponne les fortes variations de la demande de la plante. Le rôle spécifique du glucose reste, lui, inexpliqué. Même en conditions de déséquilibre interne important (lié à l'ablation des régimes), aucune régulation de l'assimilation carbonée (A_{max}) par rétroaction n'est détectée chez le palmier à huile.

Conclusion

Les effets plus ou moins décalés dans le temps des variations de l'environnement sur les sources et les puits du palmier à huile sont principalement tamponnés par une accumulation de carbohydrates non-structuraux dans le stipe ; dans le haut du stipe, ce pool peut représenter plus de 50% de la biomasse. Le rôle de l'amidon est de tamponner les déséquilibres source-puits observés alors que les variations de glucose seraient davantage liées à des conditions environnementales sèches. Les dynamiques de croissance et de production du palmier à huile montrent une rythmicité complexe liée à l'émission de cohortes de phytomères d'âges différents puisant, à tout moment, dans un pool commun de réserves carbonées.

ABSTRACT

- *Background and Aims:* Oil palm (*Elaeis guineensis* Jacq.) is a perennial, tropical, monocotyledonous plant characterized by simple architecture and low phenotypic plasticity, but long development cycles of individual phytomers. Environmental effects on vegetative or reproductive sinks occur with various time lags depending on the process affected, causing sink-source imbalances. This study investigated how the two instantaneous sources of carbon assimilates, CO_2 assimilation and mobilization of transitory, non-structural carbohydrate reserves, may buffer such imbalances.

- *Methods:* An experiment was conducted in Indonesia during a 22-month period (from July 2006 to May 2008) in two contrasting locations (Kandista and Batu Mulia) and in two treatments (control and complete fruit pruning (FPT)) in Kandista. Measurements included leaf gas exchange, dynamics of non-structural carbohydrate (NSC) reserves and dynamics of structural aboveground vegetative and reproductive growths. Drought was estimated from simulated fraction of transpirable soil water (FTSW).

- *Key results:* Main sources of variation of sink-source relationships were (i) short-term reductions in light-saturated leaf CO_2 assimilation rate (A_{max}) during seasonal drought periods, particularly in Batu Mulia; (ii) rapid responses of structural aboveground vegetative growth rate to drought; (iii) marked lag periods between 16 and 29 months of environmental effects on the development of reproductive sinks. The resulting sink-source imbalances were buffered by fluctuations in non-structural carbohydrate reserves (NSC) in stem which consisted mainly of glucose and starch. Starch was the main buffer for sink variations, whereas glucose dynamics remained unexplained. Even under strong sink limitation, no negative feedback on A_{max} was observed.

- *Conclusion:* The different lag periods for environment effects on assimilate sources and sinks in oil palm are chiefly buffered by NSC accumulation in stem which can attain 50% in stem top. Starch thereby is a buffer for sink-source imbalances whereas glucose dynamics may appear to be linked to drought. Resulting dynamics of growth and production are complex because several dozen phytomers of different phenological age develop at any given time, but interact with a common pool of reserves.

Keywords: carbon assimilation, glucose, growth, non-structural carbohydrates, phenotypic plasticity, source-sink relationships, starch.

INTRODUCTION

For higher plants, two carbon sources involved feed organ growth, (i) photosynthesis and (ii) transitory carbon reserve pools located in vegetative organs. Oil palm is a C3 species exhibiting high leaf photosynthetic rates up to 23 $\mu mol_{CO2}\ m^{-2}\ s^{-1}$ on adult trees under favourable conditions (Dufrêne and Saugier, 1993), but stomata are extremely sensitive to climate variability, particularly high vapour pressure deficit (VPD) (Michaux, 1961, Dufrêne, 1989, Cornaire *et al.*, 1994, Henson, 2006b) and top soil humidity (Dufrêne, 1989). Unlike several other tropical tree crops (Iglesias *et al.*, 2002, Frank, 2005, Susiluoto *et al.*, 2007, Mialet-Serra *et al.*, 2008), leaf photosynthesis of oil palm seems insensitive to demand associated with fruit load, or sink-source relationships, in general (Legros *et al.*, 2008b).

Transitory storage is a major physiological function in plant metabolism (Chapin *et al.*, 1990). In adult oil palm trees, under favourable conditions, non-structural carbohydrates (NSC) representing about 20% of total vegetative plant dry matter including roots, with 65% located in the stem (Legros *et al.*, 2006). The chemical nature of NSC reserves varies among species (Kozlowski, 1992). Dicotyledonous trees mainly store reserves in insoluble form (mainly starch), whereas soluble sugars such as sucrose are abundant in large grass species such as sugarcane (Komor, 2000), sorghum (Heller, 1969) or millet (Asthir and Singh, 1995). This is also the case for some palm species such as coconut (Mialet-Serra *et al.*, 2005). In adult oil palm trees, however, glucose constitutes the major form of reserve pool (50% of total NSC), followed by starch and sucrose (20% each) (Legros *et al.*, 2006).

The physiological role of transitory NSC storage has received much attention in the case of annual (Hoffmann-Thoma *et al.*, 1996, Blum, 1998) and perennial (Hrubec *et al.*, 1985, Jordan and Habib, 1996, Silpi *et al.*, 2007) plants. It serves to buffer fluctuations in assimilation rate during periods of high internal demand such as fruit filling (Blum, 1998, Willenbrink *et al.*, 1998) or periods of insufficient supply due to environmental stress (e.g. drought; Karsten and MacAdam, 2001).

Variations of soluble sugar concentrations in plant tissue are also believed to constitute a feedback signal permitting adjustments in organogenetic and morphogenetic processes to current resource availability (Dingkuhn *et al.*, 2005, Luquet *et al.*, 2006, Dingkuhn *et al.*, 2007, Luquet *et al.*, 2007). This mechanism is thought to be a major determinant of plant phenotypic plasticity (Wingler *et al.*, 2006).

In oil palm, resource- or stress-induced phenotypic plasticity has little effect on plant architecture or morphology, such as leaf size, but strongly affects development processes such as phytomer production rate and reproductive processes such as sex differentiation of inflorescences (Legros *et al.*, 2008b). These adjustment processes to environment modulate demand for assimilates with considerable lags in the order of months to years (Corley and Gray, 1976b, Dufour *et al.*, 1988, Cornaire *et al.*, 1994, Caliman and Southworth, 1998), whereas environment effects on carbon assimilation rate are mostly instantaneous or short-term. In coconut, a species similar to oil palm, sink-source imbalances were found to be compensated mainly by variable radiation use efficiency (RUE) and to a lesser extent by NSC reserve dynamics (Mialet-Serra *et al.*, 2008). Recent results reported by Legros *et al.* (2008a, 2008b) suggest the opposite for oil palm.

The present study sought to compare variations in A_{max}, growths and NSC composition and time-courses in the plant for a genotype exposed to three environments affecting source-sink relationships differently, during a period sufficiently long to study phenological adjustment processes (22 months). The three environments were (i) a climatically favourable site in Indonesia, Kandista; (ii) a continuous and complete fruit pruning treatment at the same site; and (iii) a seasonally drought prone site in Indonesia, Batu Mulia. Furthermore, the study sought to shed light on the variation of the large glucose and starch pools observed in oil palm stem.

MATERIALS AND METHODS

Study sites

The study was conducted on two experimental plantations of the SMART Research Institute (SMARTRI, SMART Tbk.) located in Kandista Estate (Riau province, Sumatra island, Indonesia, 0°55′0′′ N, 101°21′0′′ E, 100 m asl) and in Batu Mulia Estate (South Kalimantan province, Borneo island, Indonesia, 3°12′15.4′′ S, 116°01′46.9′′ E, 15 m asl). Both sites have tropical humid climate. In Kandista, the rainy season occurs between November to January, in Batu Mulia between March to May with a monthly mean rainfall of 240 mm month^{-1} (averages for 1993 – 2005 in Kandista and 2001 - 2005 in Batu Mulia). A drier season usually occurs from June to August in Kandista and from August to October in Batu Mulia. Mean daily global radiation (Rg) during the dry season (wet season) in Kandista and Batu Mulia is 18.9 MJ m^{-2} day^{-1} and 17.2 MJ m^{-2} day^{-1} (16.9 MJ m^{-2} day^{-1} and 16.1 MJ m^{-2} day^{-1}). Mean air temperature is 27.4°C and 27.6°C (27.0°C and 27.8°C), mean relative humidity is 79.0% and 75.8% (81.1% and 81.5%), mean vapour pressure deficit (VPD) is 0.98 kPa and 1.25 kPa (0.84 kPa and 0.93 kPa) and mean evapotranspiration (Penman-Monteith) is 4.5 mm and 4.1 mm (3.9 mm and 3.6 mm). Kandista is considered favourable (drought free) site for oil palm with regular but short water deficit periods (Legros *et al.*, 2008a). Batu Mulia is characterized by irregular, longer and sometimes severe dry seasons.

During the experimental period, climatological conditions (Fig. 1) were largely described in Legros *et al.* (2008a) (see chapter II). In Kandista, they were similar to the average recorded for the previous last 12 years. The beginning of the experimental period was characterized by a 2-month drought spell, followed by mostly abundant rainfall. In Batu Mulia, 2006 and 2007 were unsusual years, 2006 having a severe dry season (only 51 mm) from August to November, and 2007 being wet with heavy rainfall in June and July (750 mm) followed by a mild dry season.

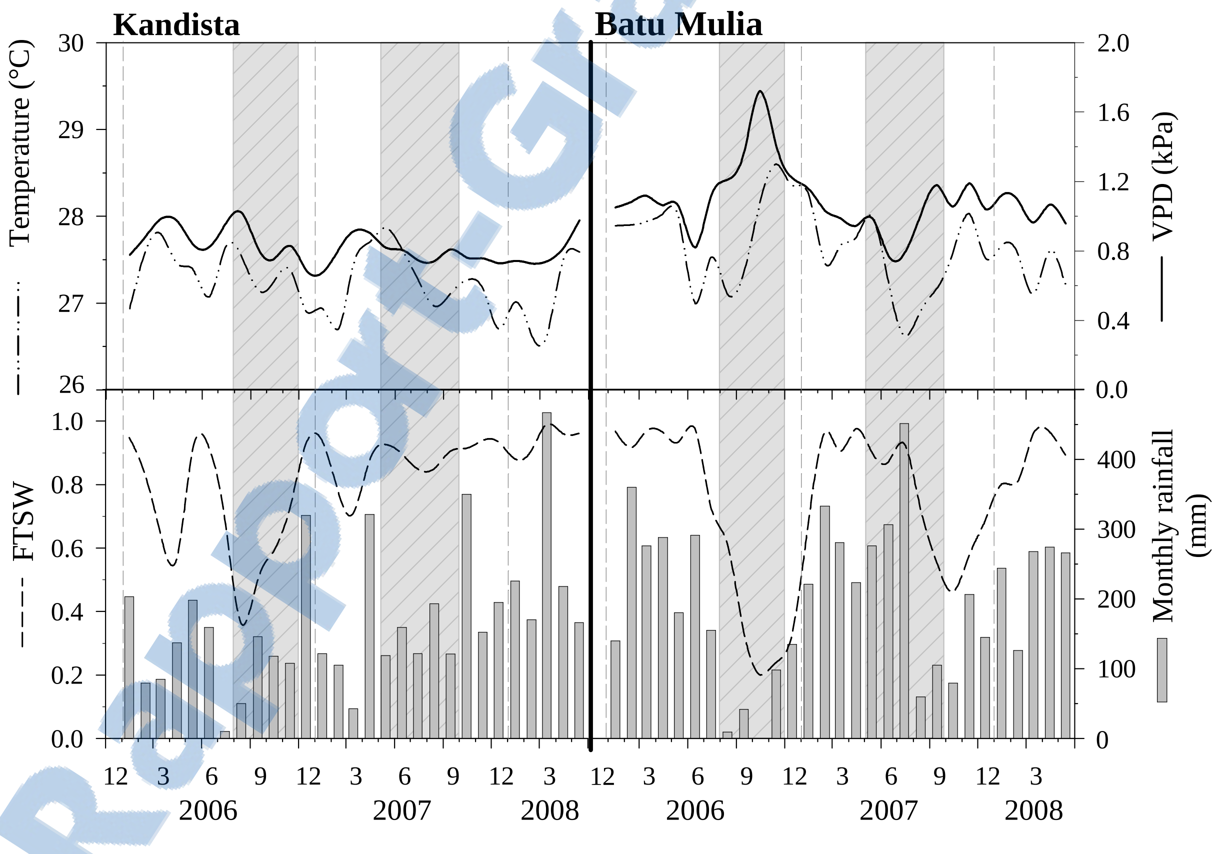

FIG. 1. Mean monthly air temperature (°C), vapour pressure deficit (VPD), monthly rainfall and monthly fraction of transpirable soil water (FTSW) from January 2006 to May 2008 in Kandista and Batu Mulia sites. The coarse and grey boxes indicate the two periods of leaf gas exchange measurement (from August to November 2006 and from May to September 2007).

Soil in Kandista is a sandy loam of homogeneous texture with more than 3 m depth (78.0% sand, 11.1% silt and 10.8% clay). Soil water content at field capacity (pF 2.5) and permanent wilting point (pF 4.2) is 0.17 and 0.06 $m^3 m^{-3}$ respectively. Soil in Batu Mulia is a silty clay soil with 2 m depth (25.1% sand, 44.1% silt and 30.8% clay). Soil water content is 0.37 $m^3 m^{-3}$ at pF 2.5 and 0.24 $m^3 m^{-3}$ at pF 4.2.

Plant material and experimental design

The experiment follows progeny 63 which is a *tenera* hybrid, commonly high-yielding for palm oil and result of cross between a *dura deli* origin (fruits with thin mesocarp and large kernel) and *pisifera avros* origin (fruits with thick mesocarp, no endocarp and small kernel) varieties.

The experimental plots were part of two larger, long-term genetic trials covering 30 ha in Kandista and 9 ha in Batu Mulia. Planting density was 136 plants ha^{-1} in a 9.5 m equilateral, triangular pattern. Plants were 13 years old at the onset of the study (July 2006). The present experiment took advantage of the replicated block design already in place. Our study had six replicates at each site and for each treatment, based on one plant per replicate selected randomly from within plots, and located sufficiently far from the plot border to avoid border effects.

Treatment

A fruit pruning treatment (FPT) was applied in Kandista in order to reduce the sink for assimilates i.e. to decrease the reproductive demand. All inflorescences were systematically removed from the plant at time of anthesis, preventing fruit set during development. Treatment started in July 2006.

Calculation of fraction of transpirable soil water

To evaluate drought extent, fraction of transpirable soil water (FTSW), an integrated parameter, was simulated as described by Legros *et al.* (2008a). The FTSW estimated the soil water available to the plant on the basis of daily rainfall, estimated runoff (considered zero in Kandista because of light-textured soil), soil surface evaporation (function of topsoil humidity, potential evapotranspiration (PET) and the fraction of radiation penetrating the canopy), soil water extraction by the plant (function of PET, crop coefficient (K_c) and FTSW acting as brake on transpiration according to FAO guidelines (Allen *et al.*, 1998)), water holding capacity of the soil between wilting point (pF 2.5) and field capacity (pF 4.2), and deep drainage of the fraction of precipitation not consumed by these processes.

The water balance routine of the model, '*EcoPalm 2008*' (http://ecotrop.cirad.fr) was used here. It was largely described in Legros *et al.* (2008a) (see chapter II). For this study, simulated FTSW represented an index variable that has the advantage to take into account soil water depletion during protracted periods of water deficit.

Leaf gas exchange measurements

The leaf gas exchange measurements were made regularly between July and November 2006 and between May and September 2007. In both cases, sampled leaves were full expanded and mature (leaves between rank 14 to 18, counted from the youngest leaf (rank 1) in the top of the leaf crown) and leaflets located at the three quarter of the rachis. One leaf per plant (six replicates) and one leaflet per leaf were daily sampled. Each set of plant replicates was followed during two consecutive days during two consecutive weeks each two months. During a day, two set of measurement were done, in the morning (0900 h – 1200 h) and in the afternoon (1400 h – 1600 h). Measurements of leaf gas exchanges were conducted with a portable IRGA (LCA-4, Analytical Development Company, Bio Scientific Ltd., Hoddesdon, Hertfordshire, England) to determine light-saturated net CO_2 assimilation (A_{max}, $\mu mol_{CO2}\ m^{-2}\ s^{-1}$), stomatal conductance (gs, $mol_{H2O}\ m^{-2}\ s^{-1}$) and transpiration (E, $mmol_{H2O}\ m^{-2}\ s^{-1}$). Measurements were made with a broadleaf chamber (6.25 cm^2) and an integrated light source (ADDA, DC Brushless). The curves were performed under controlled conditions, with saturating irradiance (1200 µmol photon $m^{-2}\ s^{-1}$, Dufrêne (1989)), at constant cuvette temperature (30°C), relative humidity (65-70%) and air CO_2 concentration (360 ppm). Leaf temperature (T_{leaf}) was measured with a thermocouple inside the cuvette of the LCA-4. The leaflet was placed in the cuvette one and half minute before the first recording. Three measurements (replicates) were recorded at one minute lag.

Transpiration efficiency (TE, $\mu mol_{CO2}\ mmol_{H2O}^{-1}$) was calculated as the ratio between light-saturated net CO_2 assimilation (A_{max}) and transpiration (E) (Yang *et al.*, 2008).

Non-structural carbohydrates in the stem

Sampling for non-structural carbohydrate (NSC) analyses used similar methods as those used in a previous study on coconut trees (Mialet-Serra *et al.*, 2008). Observations were made every two months for a period of 22 months (July 2006 - May 2008). Samples were generally taken in the morning, a procedure that took several days and two hours per day. Radial core samples were taken using a Pressler drill (6.6 mm × 300 mm). The stem samples (one or two cores) were collected at four levels (at each quarter of the stem from the ground to the lowest leaf of the crown). Sampled cores were placed in an ice box until further processing in the laboratory. The biochemical method used in the laboratory for NSC analysis was reported in detail by Mialet-Serra *et al.* (2005). Samples were ground with liquid nitrogen to 100 µm particle size with a ball grinder. Soluble sugars were extracted with 80% EtOH at 80°C and filtered on activated carbon. After evaporation of ethanol, soluble sugars were quantified by high performance ionic chromatography (HPLC) with pulsated amperometric detection (Dionex system). Starch was solubilized with 0.02 N sodium hydroxide at 90°C, and hydrolyzed with α-amyloglucosidase. Glucose was quatified spectrophotometrically using hexokinase, glucose-6-phosphate-dehydrogenase and NADP.

Structural vegetative, reproductive and total growth rates

The calculations of monthly leaf and reproductive growth rates were described in details in Legros *et al.* (2008a, 2008b) (see chapters II and III). Stem growth (kg_{DM} $month^{-1}$) consisted of three fractions, (i) the dry mass production of new internodes associated with new phytomers and new leaf emission, (ii) the dry mass increment of the older stem parts due to lignification (Corley and Tinker, 2003c), assumed to be constant (equal to 0.00074 g cm^{-3} $month^{-1}$, I. Mialet-Serra, CIRAD, 'unpubl. res.') and (iii) non-structural carbohydrate reserve variations calculated from observed variations of concentrations at four different stem heights and dimensions. The sum of the two first fractions described previously is assumed to be the structural stem growth rate. To obtain the aggregate and monthly total dry mass growth rates, we plotted the time-course of dry mass increment of stem, leaves and inflorescences for each month at the whole plant scale. Daily vegetative and reproductive growth rates were calculated by dividing monthly vegetative or reproductive growth increment by the total day number per month.

To compare NSC content (in glucose equivalents) variations with growth variations at the whole plant scale, the energy (in glucose equivalents) required to build total structural dry mass was estimated. The method used was defined and described by Penning de Vries *et al.* (1989). Synthesis costs of leaves, stem, non-oil synthesizing bunches and palm oil compartments were, respectively, equal for oil palm tree to 1.45, 1.40, 1.45 and 3.19 $g_{glucose}$ g_{DM}^{-1} (I. Mialet-Serra, CIRAD, 'unpubl. res.').

Statistical analysis

Two-way analysis of variance (ANOVA) was performed to evaluate the effects of treatment (control and FPT) and season on daily vegetative et reproductive growth and leaf gas exchange parameters. Multiple mean comparisons were made by the tukey test and considered significant at $P<0.05$.

A bilinear regression analysis as described by Clerget *et al.* (2008) was used to characterize A_{max} and gs responses to FTSW using Excel software solver:

$$y = a + b * \min(c; x) + d * \max((1-c); x))$$

With *a*, Y-axis intercept of the linear relation 1, b and d, the slopes of linear relations 1 and 2 respectively, and c, the threshold to pass from linear relation 1 (values below *d*) to 2.

Simple and multiple linear regressions were performed to explain NSC concentrations and NSC content variations using various climatological variables and internal plant parameters as predictors. FTSW, VPD, monthly structural aboveground vegetative and reproductive growths were thus retained as the best predictors.

RESULTS

Leaf photosynthetic rates and plant aboveground growth rates

Leaf gas exchange measurements were conducted daily during blocks of periods measuring one or several months in Kandista (control and FPT treatments) and in Batu Mulia. These periods differed in drought level as expressed by simulated FTSW (Table 1). A_{max} on control plants was 14.3 µmol m^{-2} s^{-1} under drought-free conditions (FTSW>0.80) in Kandista but was only 7.8 µmol m^{-2} s^{-1} (45% lower; $P<0.05$) during a two-month, moderate dry spell (August to September 2006, mean FTSW = 0.55). The reduction in A_{max} was associated with a decrease in stomatal conductance (gs) (0.19 *vs* 0.39 mol m^{-2} s^{-1}; $P<0.05$) and a slight decrease in transpiration efficiency (TE) ($P<0.01$). The aboveground, vegetative growth rate during the same periods was also reduced under drought by 46% (203.8 *vs* 375.3 g day^{-1}; $P<0.0001$), whereas the reproductive growth rate was by 58% ($P>0.05$, ns) higher in the drought-free than in the drought period.

In Kandista, leaf gas exchange parameters were similar on control and FPT plants. Vegetative growth rates, however, were much greater in FPT plants than in control plants, by 60% in the drought-prone period in 2006 and by 79% in the favourable period in 2007 ($P<0.0001$).

TABLE 1. Effects of fruit pruning treatment (FPT) and seasons (based on the fraction of transpirable soil water (FTSW)) on light-saturated net CO2 assimilation (A_{max}), stomatal conductance (gs), transpiration efficiency (TE, A_{max} : transpiration ratio) and daily vegetative and reproductive growth rates for oil palm (*Elaeis guineensis*) trees in Kandista and in Batu Mulia sites between August 2006 and September 2007. Values are means (± s.e.m.) of six replicates. Significance of treatment and season effects (ANOVA): ns = not significant, * = significant (0.05>P>0.01), ** = very significant (0.01>P>0.001), *** = highly significant (P>0.001). Different letters within a column indicate a significant difference among treatments or seasons at P<0.05 (Tukey's test).

Site	Effect	FTSW	A_{max}	gs	TE	Vegetative growth	Reproductive growth
			$\mu mol_{CO2}\ m^{-2}\ s^{-1}$	$mol_{H2O}\ m^{-2}\ s^{-1}$	$\mu mol_{CO2}\ mmol_{H20}^{-1}$	$g_{DM}\ day^{-1}$	$g_{DM}\ day^{-1}$
Kandista	August - September 2006						
	Control	0.55 ± 0.03	7.78 ± 2.53	0.19 ± 0.07	3.61 ± 0.16	203.8 ± 17.0 b	390.3 ± 98.6
	FPT	0.53 ± 0.03	11.34 ± 3.88	0.32 ± 0.11	3.09 ± 0.70	335.5 ± 36.5 a	0
	P treatment		ns	ns	ns	**	
	May - September 2007						
	Control	0.85 ± 0.01	14.27 ± 0.46	0.39 ± 0.03	4.16 ± 0.06 b	375.3 ± 18.5 b	247.4 ± 26.0
	FPT	0.83 ± 0.01	15.31 ± 0.35	0.43 ± 0.02	4.38 ± 0.06 a	672.9 ± 46.1 a	0
	P treatment		ns	ns	*	***	
	P season		*	*	**	***	ns
Batu Mulia	September 2006						
		0.53 ± 0.01	13.43 ± 1.52 a	0.33 ± 0.07 a	4.73 ± 0.09 a	14.8 ± 3.7 c	288.7 ± 86.0
	November 2006						
		0.26 ± 0.00	3.41 ± 0.93 b	0.06 ± 0.02 b	3.22 ± 0.37 b	12.1 ± 20.0 c	280.5 ± 80.1
	May 2007						
		0.80 ± 0.00	12.13 ± 0.74 a	0.31 ± 0.03 a	3.98 ± 0.10 ab	381.3 ± 8.5 a	262.2 ± 26.2
	July - September 2007						
		0.97 ± 0.01	13.14 ± 1.03 a	0.39 ± 0.05 a	4.40 ± 0.19 a	211.5 ± 13.7 b	280.1 ± 11.2
	P season		***	***	**	***	ns

In Batu Mulia, A_{max} averaged 13.4 µmol m^{-2} s^{-1} in September 2006, the beginning of the severe dry spell (FTSW = 0.53). Despite these high gas exchange rates, vegetative growth rate was extremely low during that period (15 g day^{-1}). In November 2006, when drought was maximal (FTSW = 0.26), A_{max} averaged only 3.4 µmol m^{-2} s^{-1}. This was associated with low gs (0.06 mol m^{-2} s^{-1}) and TE (3.22 µmol mol^{-1}), and vegetative growth rate was extremely low at 12 g day^{-1}. Reproductive growth rate, however, remained at the same level during all gas exchange measurement periods in Batu Mulia. During the last two measurement periods (May and July-September 2007) in Batu Mulia, no drought was observed and gas exchange and vegetative growth rate were comparatively high.

Plots relating A_{max} and gs directly with FTSW and VPD across environments (Fig. 2) confirmed the sensitivity of oil palm to climatic parameters. At FTSW below 0.45, A_{max} and gs decreased strongly (Fig. 2A). The same variation in gas exchange parameters can also be explained by atmospheric drought as expressed by VPD: A_{max} and gs dropped strongly when VPD exceeded 1.0 kPa (Fig. 2B).

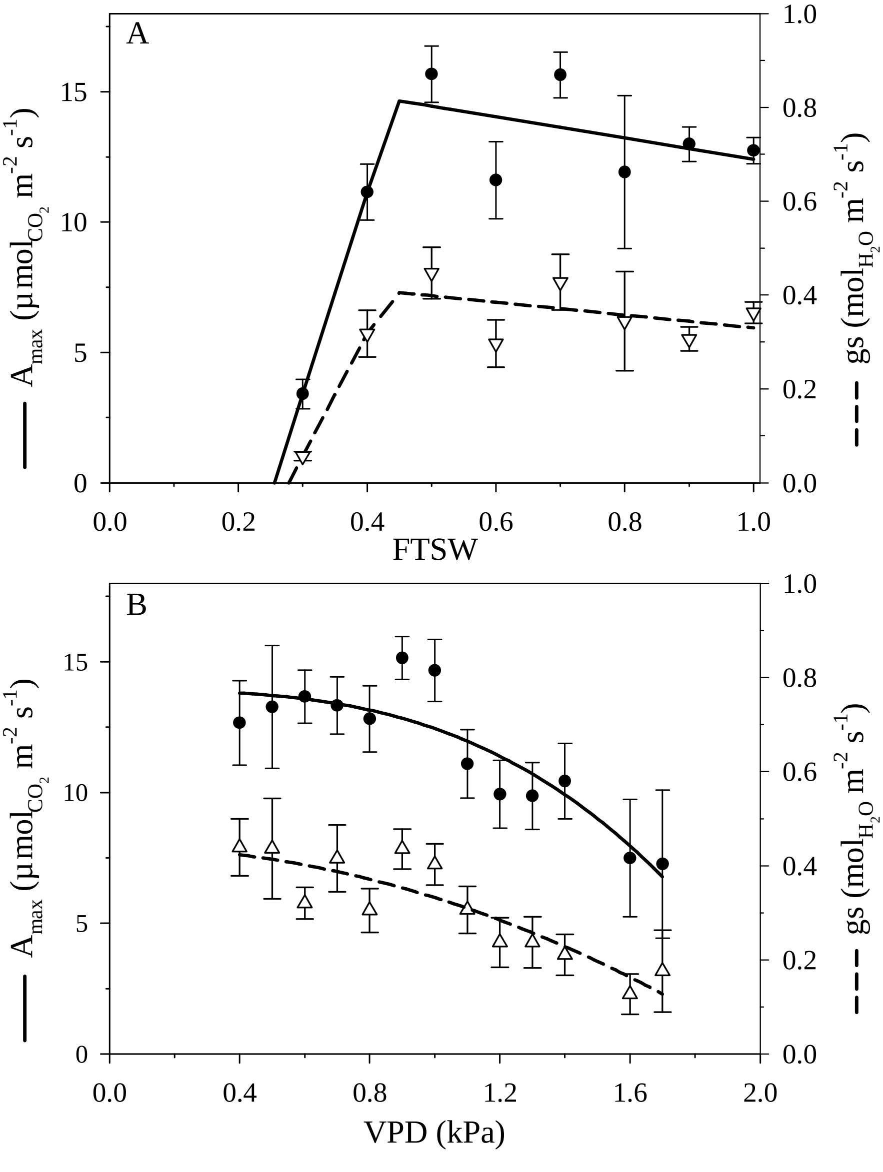

FIG. 2. Effects of FTSW (A) and VPD (B) on light-saturated net CO_2 assimilation (A_{max}) and stomatal conductance (gs) for oil palm (*Elaeis guineensis*) trees in Kandista and in Batu Mulia sites between July and November 2006 and between May and September 2007. Values are means (± s.e.m.) of six replicates. $A_{max} = -19.8 + 77.45 \times \min(FTSW;0.45) - 4.07 \times \max(FTSW-0.45;0)$; $gs = -0.73 + 2.61 \times \min(FTSW;0.44) - 0.14 \times \max(FTSW-0.44;0)$; $A_{max} = 13.89 - 0.00145 \times VPD^3$; $gs = 0.440 - 0.00108 \times VPD^2$.

Time courses of carbon reserves

It was previously reported that NSC reserves are distributed in an acropetal gradient along the stem, with starch mostly present at the top and glucose showing an opposite, but less marked gradient (Legros *et al.*, 2008b). In Fig. 3, the dynamics of starch and glucose in the top compartment of the stem are presented. In Kandista, NSC concentrations varied between 180 and 260 mg g^{-1} in control plants. They showed much greater variability in Batu Mulia (130 to 280 mg g^{-1}). This was mainly caused by a strong depression in NSC levels during the drought period in September to November 2006. In Kandista, the FPT treatment caused a 1.8-fold increase in NSC concentration as compared to control, maximal values in September 2007 attaining nearly 500 mg g^{-1}.

Starch and glucose showed contrasting dynamics in the three environments. Starch concentrations were more variable and their dynamics thus reflected those of total NSC. Glucose frequently showed opposite peaks, for example in October 2006 and in June 2007 in Kandista, or May 2007 and January 2008 in Batu Mulia. The total NSC accumulation caused by the FPT treatment in Kandista was exclusively due to starch while glucose concentration declined. Consequently, starch was clearly a “spill-over” pool fed by excess assimilates, in the case of FPT induced by sink ablation. Glucose, although also a highly dynamic pool, didn’t exhibit the same function.

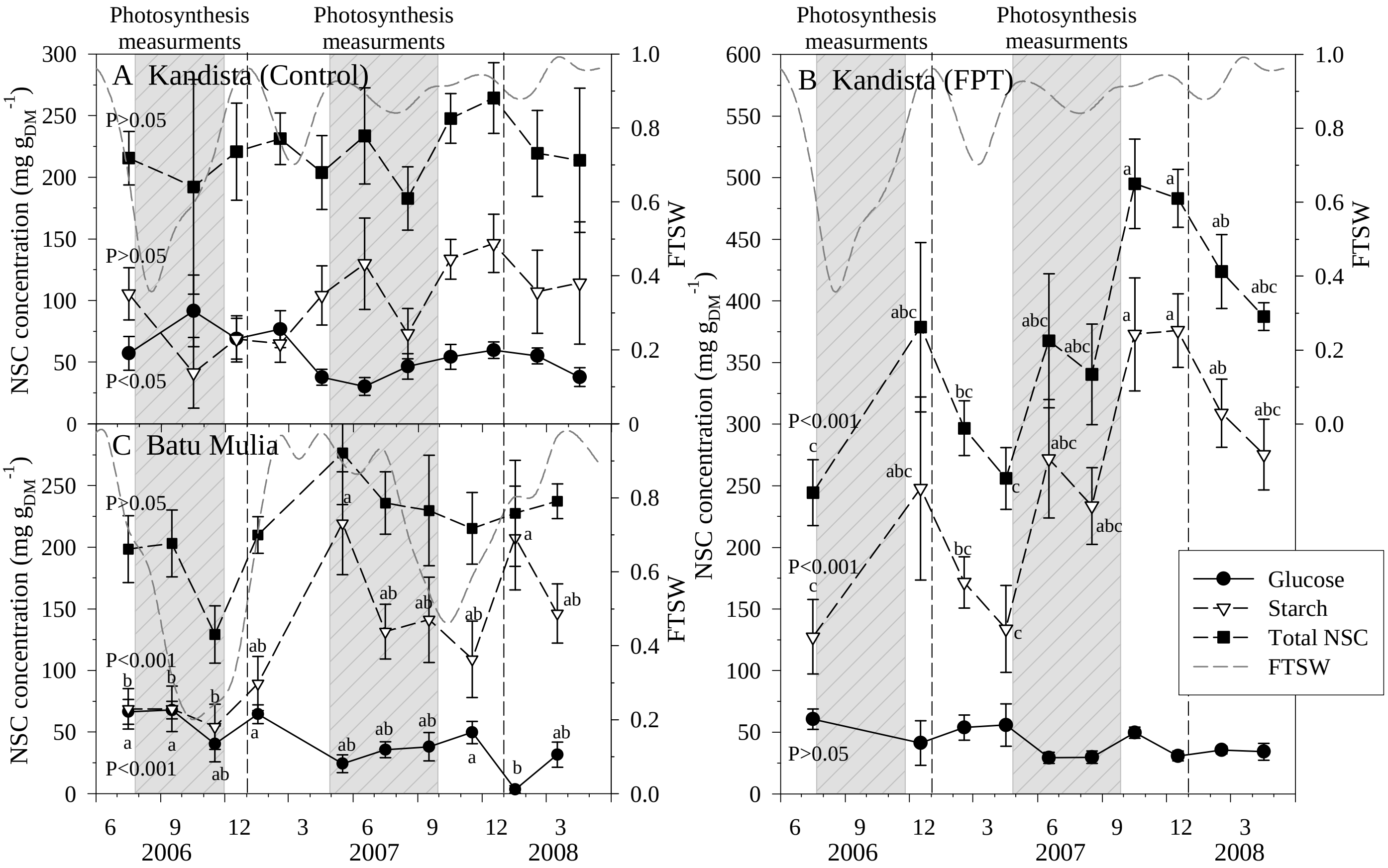

FIG. 3. Time courses of glucose, starch and total non-structural carbohydrates (NSC) concentrations in the stem top of oil palm (*Elaeis guineensis*) trees (A) in controls and (B) in fruit pruning (FPT) plants in Kandista and (C) in Batu Mulia. Values are means (± s.e.m.) of six replicates. The coarse and grey boxes indicate the two periods of leaf gas exchange measurement (from August to November 2006 and from May to September 2007).

Total, vegetative and reproductive growth time courses

In Kandista, mean total aboveground dry matter production (Fig. 4A) was 18.1 kg plant^{-1} month^{-1} for controls, and only 14.6 kg plant^{-1} month^{-1} for FPT, corresponding to a reduction by 20%. In terms of energy (glucose equivalents) required to build this dry matter (but not taking into account transport and maintenance respiration), growth of controls in Kandista was 32.7 kg$_{glucose}$ month^{-1} and only, 18.7 kg$_{glucose}$ month^{-1} for FPT. This amplified difference between treatments was due to the oil content of fruit produced by controls. Time courses of total aboveground dry matter production showed marked but irregular seasonal oscillations of unknown origin, the two treatments exhibiting synchronous maxima and minima of growth rate. Maxima occurred in December 2006, May-June 2007, October-November 2007 and April 2008; minima in March 2007, July 2007 and January-February 2008.

Mean structural, aboveground, vegetative growth rate (Fig. 4C) was defined here as the growths of all vegetative organs but without including stem NSC reserves. It was significantly ($P<0.05$ on most months) increased by FPT, on average by 2.5 kg plant^{-1} or 26%. Time courses for the two treatments were similar, FPT plants closely following those of controls but at a higher level. The increase of structural growth by FPT was a consequence of increases of leaf appearance rate (data not presented).

Monthly growth rates of bulk reproductive organs (Fig. 4E) varied strongly between 3 and 15 kg plant^{-1} month^{-1} for controls (mean: 8.5 kg plant^{-1} month^{-1}). Time courses showed four maxima in August 2006, March and September 2007 and in February 2008, and two pronounced minima in May and November 2007.

A third component of aboveground growth were NSC reserves in stem (Fig. 4G). Its dynamics showed alternating storage and mobilization patterns, with controls and FPT in Kandista showing converging minima and maxima. Overall, FPT showed more storage and less mobilization than controls.

In Batu Mulia, mean total aboveground dry matter production (Fig. 4B) shown a marked depression during the drought period in September to November 2006, followed by rapid recovery as stress (as indicated by simulated FTSW) subsided. Structural, aboveground, vegetative growth (Fig. 4D) and NSC reserve time-courses (Fig. 4H) showed a similar depression, followed by a rebounding behaviour that can be interpreted as catch-up growth. Reproductive growth (Fig. 4F), however, showed oscillations that seemed not to be related to observed stress periods. Two pronounced minima were observed in December 2006 and February 2008, explained previously by dry spells that had occurred 29 months before (Legros *et al.*, 2008a). Moreover, the very low growth rates during the second minimum can also be associated with an abortion peak of inflorescences that occurred during the severe dry spell of November 2006, 16 months before harvest (or 10 months before anthesis) of the inflorescences concerned (Legros *et al.*, 2008b).

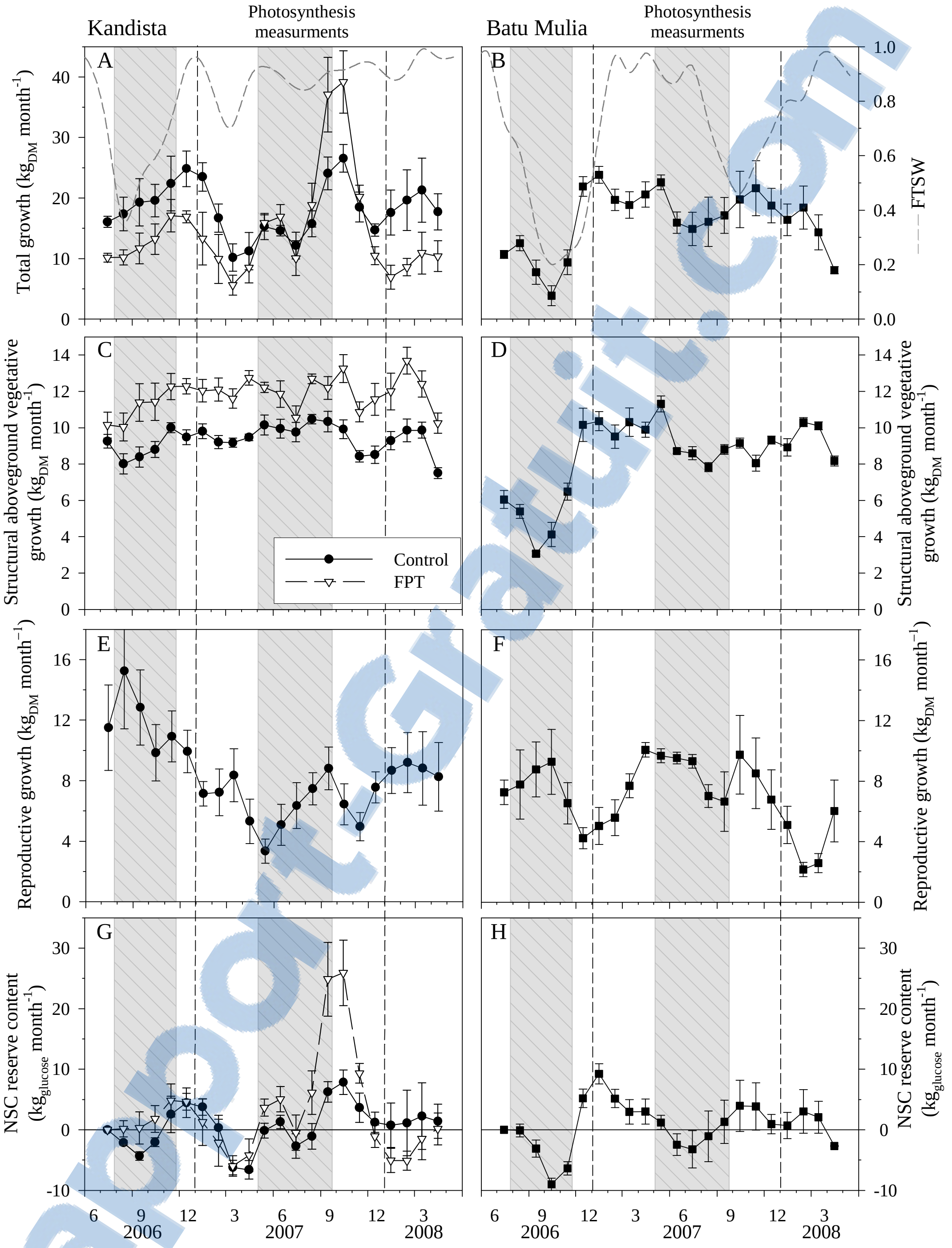

FIG. 4. Mean monthly (A) total (structural + non-structural) growth in control and in fruit-pruned (FPT) oil palm (*Elaeis guineensis*) trees in Kandista and (B) in Batu Mulia; (C) structural aboveground vegetative growth in control and in fruit-pruned (FPT) oil palm (*Elaeis guineensis*) trees in Kandista and (D) in Batu Mulia; (E) reproductive growth in control oil palm (*Elaeis guineensis*) trees in Kandista and (F) in Batu Mulia; (G) NSC reserve content variations in control and in fruit-pruned (FPT) oil palm (*Elaeis guineensis*) trees in Kandista and (H) in Batu Mulia. Values are means (± s.e.m.) of six replicates. The coarse and grey boxes indicate the two periods of leaf gas exchange measurement (from August to November 2006 and from May to September 2007).

At both sites, Kandista and Batu Mulia, total aboveground growth was mainly an expression of NSC reserve time-courses. For Batu Mulia, a multiple linear regression model was constructed, explaining variations in NSC reserve content of plants (NSCvar) (Fig. 4H) with monthly structural aboveground vegetative growth (SVG, in Fig. 4D) and reproductive growth (RG, in Fig. 4F):

$$\text{NSCvar} = -3.318 - 0.735\times\text{RG} + 1.123\times\text{SVG} \quad (\text{adjusted } r^2=0.58;\ P<0.0001;\ n=20)$$

This correlation indicates a positive effect of structural aboveground vegetative growth (SVG) and a negative effect of reproductive growth (RG) on NSCvar. Consequently, NSC reserves behaved like vegetative growth (high growth rates coinciding with storage) and behaved reciprocally to reproductive demand (high fruit production coinciding with mobilization).

Behaviour of starch and glucose reserves

When plotting stem glucose reserves against total NSC (Fig. 5A; all stem segments, treatments, replications and sites confounded), a linear, upper envelope curve emerged that was close to the 1:1 function, representing situations where NSC is exclusively composed of glucose. Such situations were not rare but occurred most frequently in lower stem segments. The scatter plot also indicated that a maximal glucose concentration exists and is located between 150 and 200 mg g^{-1}. Total NSC concentrations beyond that level were generally associated with increasing concentrations of other carbohydrates, namely starch (up to 500 mg g^{-1}) and decreasing glucose concentration.

The same analysis, conducted for the apical segment of the stem only and representing means of the six replicates (Fig. 5B), identified two populations of means that were either characterized by variable glucose or by variable total NSC concentration.

Starch concentration in the apical segment of the stem (Fig. 5C), however, was linearly correlated with total NSC concentration, indicating that NSC accumulation was driven by starch, whereas the variation of soluble sugars was not directly related to total NSC accumulation. Similar relationships were observed for other stem segments (data not presented). The linear regression model observed for stem top was as follows:

$$\text{Starch} = -86.8 + 0.91\times\text{NSC} \quad (r^2 = 0.86,\ P<0.0001,\ n=180)$$

In stem top, starch was negatively correlated with glucose concentration (Fig. 5D; $\text{Starch} = 199.5 - 1.797\times\text{Glucose}$; $r^2 = 0.60$, $P<0.0001$, $n=20$). This relationship, based on means of replications, confounded Kandista and Batu Mulia sites but excluded the FPT treatment.

The latter differed significantly from the baseline starch *vs* glucose relationship due to much higher concentrations of starch.

Multiple, linear, stepwise regression analyses were used to identify factors responsible for the variability of glucose concentration at constant total NSC concentration (cluster in Fig. 5B forming a vertical ellipse) and of total NSC concentration at constant glucose concentration (cluster forming horizontal ellipse). Two regression models were constructed using the available climatic variables, FTSW and plant variables such as structural vegetative growth, reproductive growth or fruit load as potential determinants:

Horizontal cluster

$$\text{NSC} = 73.3 - 11.2\times\text{RG} + 25.6\times\text{SVG} \quad (\text{adjusted } r^2=0.70;\ P<0.0001;\ n=18)$$

Vertical cluster

$$\text{Glucose} = 240.4 - 126.9\times\text{FTSW} - 96.5\times\text{VPD} \quad (\text{adjusted } r^2=0.51;\ P<0.0001;\ n=21)$$

Variation of total NSC was thus negatively correlated with demand for reproductive growth, resulting in mobilization, and positively with structural vegetative growth, resulting in storage. These two explanatory variables are plant state variables that are directly related to source-sink relationships. Variation of glucose, on the other hand, was negatively correlated with VPD and FTSW, two environmental variables related to atmospheric drought (VPD) and soil water deficit (FTSW). This latter regression model, however, is difficult to interprete because VPD and FTSW are necessarily negatively auto-correlated, and because the regression coefficient ($r^2=0.51$) explained only half of the variation. We thus retain from these models only the conclusion that total NSC dynamics (mainly determined by starch dynamics) were mainly driven by transitory source-sink imbalances, whereas glucose dynamics may appeared to be driven by environmental variables related to water deficit.

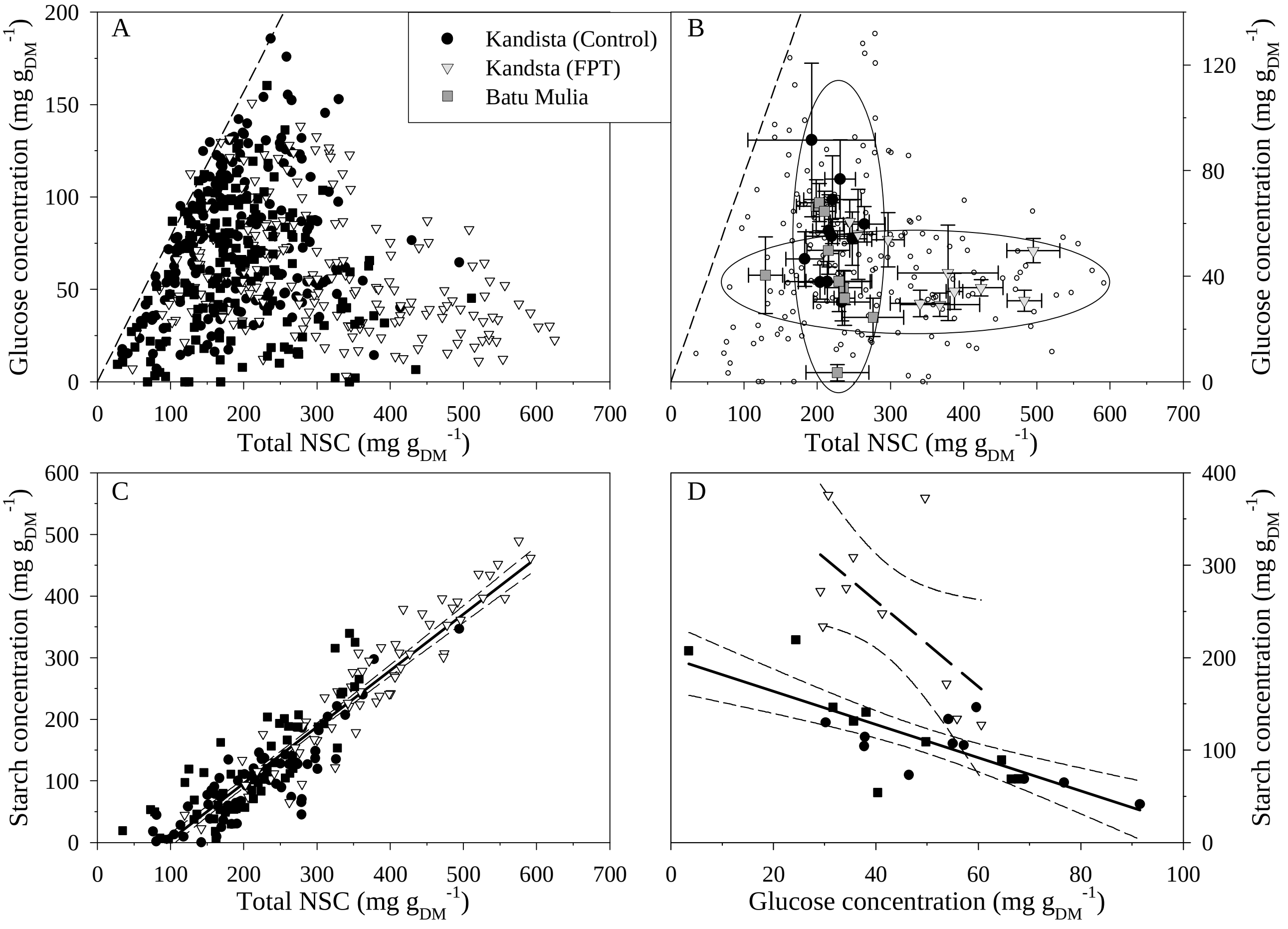

FIG. 5. (A) Relationship between glucose and total non-structural carbohydrate (NSC) concentrations along the whole stem; (B) Relationship between mean glucose and total non-structural carbohydrate (NSC) concentrations in the top part of the stem in control and fruit-pruned (FPT) oil palm (*Elaeis guineensis*) trees in Kandista and in Batu Mulia sites during the 22-month experimental period (between July 2006 and April 2008). Values are means (± s.e.m.) of six replicates. Empty circles represented all individual points (gross data); (C) relationship between starch and total non-structural carbohydrate (NSC) concentrations in the top part of the stem; (D) relationship between mean starch and glucose concentrations in the top part of the stem (values are means of six replicates) of oil palm (*Elaeis guineensis*) trees in Kandista on control and fruit pruning (FPT) treatments and in Batu Mulia sites during the 22-month experimental period (between July 2006 and April 2008).

DISCUSSION AND CONCLUSION

Oil palm does not adjust to sink-source imbalances by regulating photosynthesis

Mialet-Serra *et al.* (2008) observed that severe sink and source limitation in coconut, induced experimentally by fruit and leaf pruning, strongly affected RUE but only to a small extent NSC reserve dynamics. They concluded that CO_2 assimilation rates of coconut are probably in part driven by physiological demand, as observed on coffee (Frank *et al.*, 2006) and other tree crops (Iglesias *et al.*, 2002, Paul and Pellny, 2003). The present study rejects this hypothesis for oil palm because leaf A_{max} was not negatively affected by fruit pruning and the resulting over-supply of assimilates, as indicated by the accumulation of NSC caused by the treatment. We found that RUE strongly fluctuates seasonally in oil palm, but these dynamics were not only related to fruit charge (Legros *et al.*, 2008a, 2008b). Although much of the variation of RUE remained unexplained and was probably in part due to experimental error, some of its variation could be explained with incident PAR (negative effect, in accordance with Mialet-Serra *et al.* (2008)) and drought.

Leaf A_{max} observed here was similar with A_{max} reported previously for oil palm (14 to 20 µmol m^{-2} s^{-1}; (Dufrêne, 1989, Haniff, 2006)) and was comparable with A_{max} measured on other C3 perennial plants (e.g., 10 to 20 µmol m^{-2} s^{-1} for coconut (Braconnier, 1998, Gomez *et al.*, 2008); 10 to 20 µmol m^{-2} s^{-1} for oak (Galle *et al.*, 2007)).

The present results also confirm the high sensitivity of oil palm to climatic variations, namely atmospheric drought and soil water deficit (Corley and Tinker, 2003c). The experimental results did not permit distinguishing between atmospheric (VPD) and soil-borne (FTSW) effects on A_{max} and other gas exchange variables because they were correlated with both. A_{max}, stomatal conductance and transpiration efficiency decreased when simulated FTSW dropped below 0.45. This value should be viewed with appropriate caution because the exact depth of the root system was not known, a variable that affects the calculation of FTSW. Furthermore, there is evidence that oil palm responds to water deficit in the top soil even if deeper roots have good access to water. FTSW thresholds for leaf gas exchange have been reported to be different among crop species (Lecoeur and Sinclair, 1996, Liu *et al.*, 2005, Pellegrino *et al.*, 2006). The comparatively high sensitivity of oil palm to VPD was reported to stabilize leaf water potential on dry days (Bacelar *et al.*, 2007). This behaviour can be classified as isohydric (Diaz-Espejo *et al.*, 2007), a response pattern associated with high sensitivity of growth to atmospheric drought. In fact, the reductions of growth of vegetative organs during the 2006 dry season in Batu Mulia were extreme, given the comparatively mild drought conditions occurring at this equatorial site.

Transitory carbon reserves, the main buffer for sink-source imbalances

The main physiological function of transitory NSC storage is to balance sink and source fluctuations, at different temporal scales from within a day to seasons (Haddad *et al.*, 1995, Jordan and Habib, 1996, Silpi *et al.*, 2007). The recent, detailed study on seasonal NSC reserve dynamics in coconut (Mialet-Serra *et al.*, 2008) confirmed that the storage and mobilization of such reserves does have a short-term compensatory function for periods of sink or source limitation, but that its contribution is quite small. The present findings on oil palm, however, identify NSC reserves as being the main such buffer mechanism. This function is vital because (i) assimilate demand for fruit filling is high because of the physiologically costly process of oil synthesis (Van Kraalingen, 1985, Dufrêne, 1989, Penning de Vries *et al.*, 1989) and the high annual harvest index achieved by the crop (Legros *et al.*, 2008a), (ii) strong seasonal fluctuations of fruit production that are largely independent of current environmental conditions because fruit load is determined early during phytomer development (Corley, 1977, Dufour *et al.*, 1988, Corley and Tinker, 2003c, Legros *et al.*, 2008a, Legros *et al.*, 2008b), and (iii) carbon assimilation rates are insensitive to current demand, as demonstrated in this article. Since roots of palm family plants, unlike dicotyledonous trees, store only very little NSC (coconut: Mialet-Serra *et al.,* 2005, 2008; oil palm: Legros *et al.*, 2006), vegetative aboveground organs have to assume this function.

We demonstrated that NSC reserve dynamics in the stem of oil palm constitute a major component of plant growth. In Kandista, the more favourable site, stem NSC reserves varied between 11 and 16% of total aboveground plant dry matter, at the drought-prone site Batu Mulia between 10 and 17%, and for fruit-pruned plants at Kandista between 17 and 29%. In stem tops, NSC constituted up to 50% of dry matter under sink limitation. These observations show that the NSC reserve pool was not only large, but was also extremely dynamic, indicating intense storage and mobilization activity.

Legros *et al.* (2006) reported that NSC reserves in oil palm, mainly located in the stem in the forms of glucose and starch, are a resource that can theoretically sustain overall tree growth for seven months. The present results confirm that this reserve pool is indeed used by the plant on a regular (seasonal) basis and not only under conditions of protracted stress periods. The entire stem thereby serves as storage organ, but the highest starch concentrations and greatest fluctuations occur at its top, topologically close to the main sinks (fruits and expanding leaves) and the single, apical meristem. The present analysis did not take into account NSC storage in the leaf rachis, also topologically close to the main sinks. This compartment is also known to serve NSC storage but is quantitatively less important than the stem (coconut: Mialet-Serra *et al.*, 2005, 2008; oil palm: Legros *et al.*, 2006).

Function of different chemical components of transitory stem reserves

Across sites and treatments, multiple linear regression analysis showed that 59% of the variation of NSC reserves in the stem was explained by two variables of plant growth, structural aboveground vegetative growth and growth of reproductive organs, the former having a positive and the latter a negative effect. These results suggest that periods of strong structural, vegetative growth are associated with increased allocation of fresh assimilates to the reserve pool, whereas periods of high assimilate demand for fruit filling lead to reserve mobilization.

As reported by Legros *et al.* (2006) and confirmed here, reserves consisted of starch, glucose and sucrose, but very little fructose. The two main components of stem NSC, glucose and starch, however, differed markedly in topological distribution and temporal dynamics, suggesting different physiological function. The concentrations of the two substances were negatively correlated in the top segment of the stem (Fig. 5D), but this relationship, observed at both study sites, was not robust because fruit pruning treatment broke it. Some evidence on the function of glucose and starch reserves is provided by Fig. 5B, which identified two clusters of situations, one characterized by variable glucose (with little variation in NSC) and the other by variable NSC (with little variation in glucose, NSC variation thus mainly being due to starch). Seventy percent of variation within the latter cluster was explained by source-sink relationships (demand for structural-vegetative and reproductive growth), indicating that stem starch reserves are indeed a buffer enabling the plant to cope with seasonal sink-source imbalances. This function of transitory starch reserves has been observed in many species but appears to be particularly vital in oil palm because of its inherent tendency to develop sink-source imbalances (Legros *et al.*, 2008a, 2008b).

The cluster of situations characterized by variations in glucose concentration (Fig. 5B) could not be explained with plant growth or demand parameters. The best predictors were environment variables related to water (FTSW and VPD; $r^2 = 0.51$). Interpreting glucose dynamics as being a function of drought, however, would be speculation, for several reasons. First, the effect of both FTSW and VPD on glucose concentration was negative, but it should be negative for VPD if high VPD is considered a stress condition (which, for oil palm, it is the case (see Fig. 2; (Dufrêne and Saugier, 1993)). Second, different environment variables are generally auto-correlated and thus not conductive to causal physiological analyses when fluctuating naturally. The role of transitory glucose reserves in oil palm stems, a unique phenomenon to our knowledge, thus needs more study.

A conceptual model of oil palm organization and interactions with environment

This study followed up on two previous studies (Legros *et al.*, 2008a, 2008b), the first investigating growth and development responses of oil palm to naturally varying environments and the second investigating the phenotypic plasticity of oil palm growth and development under experimentally imposed sink-source imbalances, analogous to a similar precursor study on coconut (Mialet-Serra *et al.*, 2008). The present study adds crucial results to this body of information, namely regarding the behaviour and nature of the transitory reserve pool and the absence of feedbacks on photosynthetic rates, contrary to previous hypotheses (Mialet-Serra *et al.*, 2008). A conceptual model, and eventually as quantitative whole-plant model, can now be constructed.

The key to understanding the whole-plant physiological organization of oil palm is the fact that the plant produces in rapid, continuous succession phytomers comprising a leaf, nodal tissue that adds to stem growth, and an inflorescence that can either be female, male or aborted, depending on environment. These phytomers each develop over 3 to 4 years (Henry, 1955b, Corley and Gray, 1976a), and the time and the nature of anthesis of the inflorescence is determined by environmental factors (photoperiod: Legros *et al.*, 2008a); stresses and sink-source relationships: Legros *et al.*, 2008a, 2008b) involving substantial lag periods in the order of months and several years (Corley, 1977, Dufour *et al.*, 1988, Caliman and Southworth, 1998). Environment effects on the assimilate source (photosynthesis) and leaf appearance rates (Legros *et al.*, 2008a, 2008b), however, are much more rapid and thus not synchronized with those on reproductive sinks. Furthermore oil palm has low architectural and morphological plasticity (example: constant leaf size and morphology across resource situations; Legros *et al.*, 2008b). The resulting sink-source imbalances are buffered by a very large and dynamic NSC reservoir in the trunk. This reserve pool seems to play a generic buffer, probably serving all demand and supply functions in the plant system, regardless of phytomer and organ type.

Probably because oil palm originates from equatorial, humid forest environments (Corley and Tinker, 2003e), plant growth and leaf gas exchange are extremely sensitive to drought, including VPD (Dufrêne and Saugier, 1993, Cornaire *et al.*, 1994, Jourdan and Rey, 1997a, Corley and Tinker, 2003c, Nelson *et al.*, 2006). These stresses also have rapid effects on leaf initiation and appearance rates (Nouy *et al.*, 1999, Corley and Tinker, 2003c, Legros *et al.*, 2008a). They also affect NSC reserves, as demonstrated here, either through the resulting sink-source imbalances (apparent role of starch) or more directly (possibly the case of glucose). Transitory reserves, and possibly in particular glucose, may play a role in accelerated leaf appearance and expansion upon recovery from a drought period, a phenomenon that can be interpreted as catch-up growth setting on with the first rains (Nouy *et al.*, 1999, Corley and Tinker, 2003c).

A quantitative model, *EcoPalm* (JC Combres, CIRAD, 'unpubl. res.'), integrating these processes and responses of oil palm to environment is being developed, based on concepts derived from an existing model of phenotypic plasticity, *EcoMeristem* (Dingkuhn *et al.*, 2005, Luquet *et al.*, 2006). It will not only permit the simulation of oil palm as an agricultural crop, but also permit the quantitative systems analysis of a plant organization that differs markedly from that of annual plants and dicotyledonous trees.

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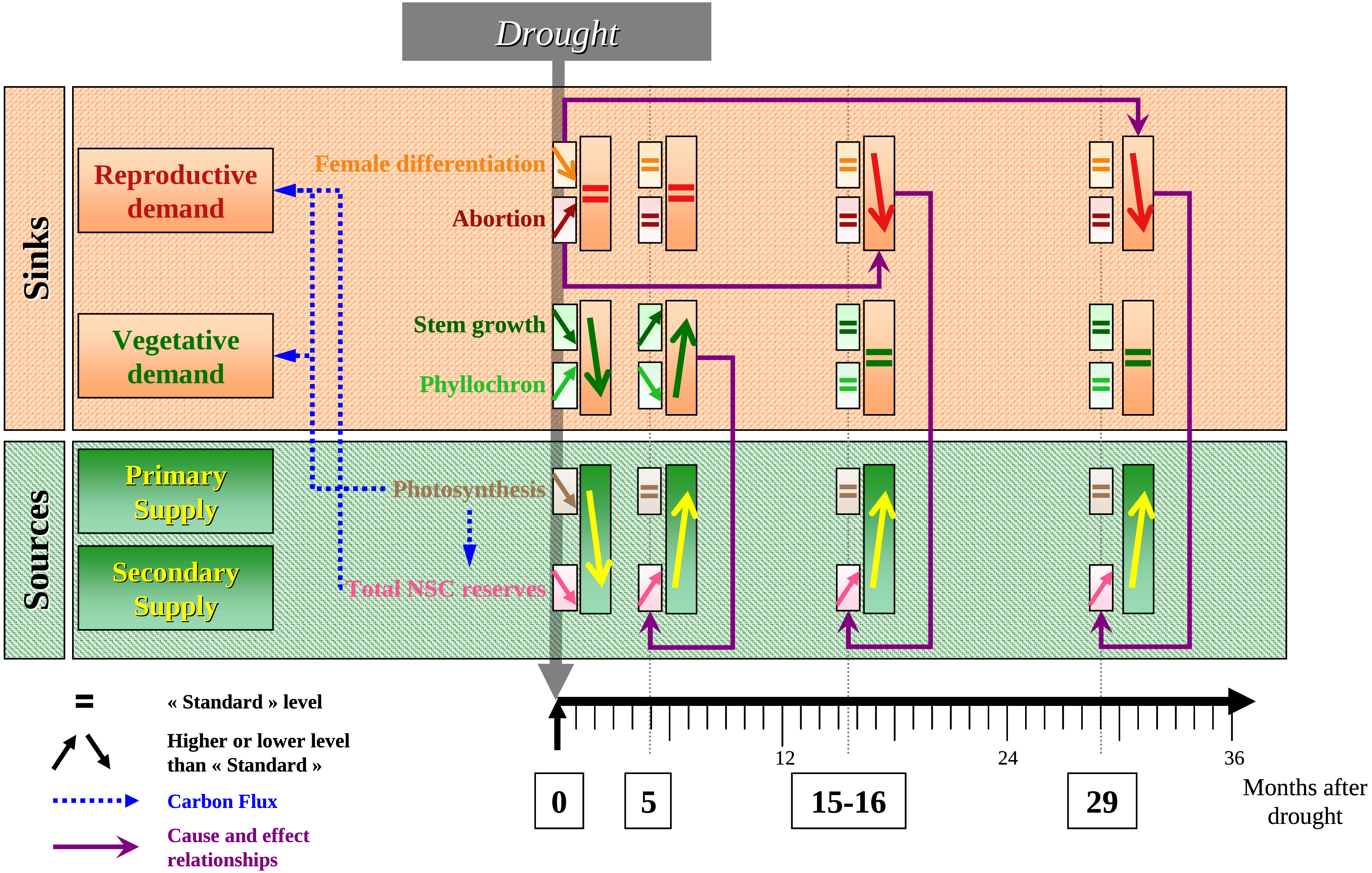
CONCLUSION ET PERSPECTIVES

Le palmier à huile se caractérise par une architecture simple et immuable : un axe ou stipe unique avec une croissance exclusivement en hauteur, surmonté d'une couronne de plusieurs dizaines de feuilles. En conditions favorables de culture, croissances végétatives et reproductives sont continues ; le nombre d'inflorescences femelles est déterminé plusieurs mois à plusieurs années avant leur développement et leur récolte. Les incidences des aléas rencontrés sont fortement décalées dans le temps, rendant difficile l'analyse du rôle des différents facteurs impliqués dans la croissance et la production de cette espèce.

Nos sites d'étude présentent des situations contrastées. Le premier (Kandista) est considéré comme favorable et proche de l'optimum de végétation. Le second (Batu Mulia) représente une zone de culture à saison sèche de périodicité et d'intensité irrégulières avec un déficit annuel qui peut être fort, entrainant, à terme, une chute significative du rendement annuel. Les années 2006 et 2007 sur ce site sont opposées ; 2006 est une année très sèche, 2007 très humide. Par ailleurs, une situation de déséquilibre source-puits est provoquée artificiellement par l'ablation systématique à la floraison de toutes les inflorescences.

Les objectifs de cette étude étaient de décrire et d'analyser, en fonction de situations de déséquilibres source-puits naturels ou provoqués, les ajustements rencontrés et les mécanismes mis en jeu par un palmier à huile adulte et de tenter de caractériser la nature (exogène et/ou endogène) de leurs déterminismes. Pour ce faire, la phénologie, les croissances des différents compartiments aériens de la plante, la gestion du carbone par la plante à travers son assimilation et son stockage temporaire ont été suivis dans le temps et mis en relation.

SCHEMA 1. Modèle conceptuel expliquant les relations source-puits et les ajustements mis en place en situations de déséquilibre source-puits chez le palmier à huile.



SYNTHESE DES RESULTATS OBTENUS

L'intensité et la périodicité de la production du palmier à huile sont décrites ; des hypothèses sur leur déterminisme proposées ; un modèle conceptuel expliquant les ajustements mis en place lors de déséquilibres source-puits a, alors, pu être élaboré (Schéma 1). Dans des conditions optimales de culture, la périodicité des pics de production est positivement corrélée à une photopériode courte, décalée de 9+12×n mois avant la récolte. Le contrôle de ce rythme serait circadien. En conditions contraignantes (humidité du sol limité, dessèchement de l'air ambiant…), l'amplitude des pics de production intra et interannuelle apparait comme très variable. Cela pourrait être la résultante de contraintes hydriques apparues environ 29 et 16 mois avant la récolte (Schéma 1) ; les premières provoquant une masculinisation des inflorescences en cours de différenciation et les secondes provoquant un taux important d'avortement des inflorescences différenciées. Le nombre d'inflorescences femelles différenciées, composante principale de l'élaboration du rendement, est donc un paramètre très plastique chez le palmier à huile. En revanche, la masse d'un régime et le nombre de fruits sur régime ne sont jamais, dans nos conditions, affectés.

Autant les incidences des aléas sur la croissance reproductive sont différées dans le temps, autant les ajustements observés sur la croissance végétative et le développement sont, eux, rapides et donc peu décalés dans le temps (Schéma 1). La fréquence d'apparition des feuilles est significativement ralentie en particulier lors d'un stress hydrique et accélérée dès la reprise des premières pluies (épanouissement de feuilles en attente dans la couronne) pour revenir ensuite à une période normale. Par ailleurs, en conditions prouvées de surplus en assimilats carbonés, la fréquence d'apparition des feuilles s'accélèrent également, sans phénomène de file d'attente (à l'épanouissement) dans la couronne comme observé précédemment. Cette accélération perdure dans le temps, s'intensifie même, laissant penser que le plastochrone, à terme, est également modifié. En revanche, comme pour les régimes de fruits, la masse des feuilles et leur surface restent inchangées au cours du temps et en dépit des aléas subis.

Parallèlement, deux paramètres physiologiques sont suivis : l'assimilation du carbone à l'échelle foliaire et son stockage dans le stipe. L'assimilation carbonée apparaît très sensible aux conditions environnementales et chute de façon drastique lors de périodes de sécheresse intense. Ce processus chez le palmier à huile n'est, en aucun cas, piloté par la demande interne de la plante. Elle reste, en effet, à un niveau stable et élevé aussi bien en conditions de demande forte qu'en conditions de demande faible ou limitée (ablation systématique des régimes). Dans de telles conditions, aucune accumulation de glucides dans les folioles, signe d'un engorgement, ne se produit. L'hypothèse d'une rétroaction, imaginée chez cette espèce en situations de demande limitée à l'échelle de la plante, semble être écartée. Les assimilats produits et non utilisés sont alors absorbés par le compartiment « réserves » qui enfle. Le pool de carbohydrates non-structuraux augmente significativement, notamment celui en amidon dans l'extrémité haute du stipe, à proximité de l'unique méristème, des organes source et des puits nombreux que représentent les régimes en cours de différenciation et de maturation. Un palmier à huile adulte accumule des réserves notables en glucose et en amidon. Ces réserves se constituent lorsque la photosynthèse excède la demande, dans la mesure où le réservoir principal (dans notre cas, le stipe) a cru suffisamment pour les accumuler. En condition d'assimilation limitée, l'intensité de la mobilisation sur le stipe est plus élevée, révélant le rôle supplétif du compartiment « réserves ». Le rôle tampon de ce pool nous paraît établi. Cependant, à l'issue de ce travail, le rôle physiologique du glucose, présent en très grande quantité chez cette espèce, reste encore mal compris.

En résumé, les mécanismes d'ajustements mis en place par un palmier à huile adulte face à la variabilité du climat et aux déséquilibres source-puits quotidiens sont principalement phénologiques, affectant développement et croissances des différents compartiments aériens, mais aussi fonctionnels, les réserves carbonées tamponnant, en fonction de la demande, excès et déficit d'offre primaire. Dans nos conditions d'étude et sur la durée de nos observations aucune plasticité morphologique des compartiments suivis n'est visible.

PASSAGE A UNE ANALYSE PLANTE ENTIERE, INCLUANT LE COMPARTIMENT RACINAIRE

Seuls les ajustements au niveau des compartiments aériens ont été étudiés. Il serait pertinent de rajouter à notre analyse le compartiment racinaire. En effet la définition conventionnelle de l'efficience d'utilisation de la lumière (RUE) intègre seulement la production en biomasse des compartiments aériens, sans tenir compte des variations liées à celle du système racinaire (Mialet-Serra *et al.*, 2008). Or, en conditions de demande limitée, il est difficile d'affirmer si tous les assimilats non utilisés (le surplus en assimilats) par la plante sont absorbés par le compartiment « réserves ». Comme observé sur le cocotier (C. Jourdan, CIRAD, 'comm. pers.'), il est probable que le compartiment racinaire, en général connu pour être plastique, voit sa production de biomasse augmenter significativement dans cette situation chez le palmier à huile. Des données en cours d'acquisition sur ce compartiment sur nos deux sites d'étude devraient nous permettre prochainement de lever ces interrogations.

VALIDATION PARTIELLE DU MODELE *ECOPALM*

Un modèle physiologique de simulation de la production mensuelle du palmier à huile à l'âge adulte, *EcoPalm* (version 3, J-C. Combres, CIRAD, 'comm. pers.'), a été développé. Cet outil a pour objectif appliqué la prévision saisonnière des récoltes en fonction du climat. Les informations acquises au cours de ce travail, devraient permettre de valider ou d'invalider une partie des concepts développés dans cette version afin de décrire la phénologie du palmier à huile et la gestion du carbone dans la plante.

Comme décrit brièvement dans Mialet-Serra (2005), *EcoPalm* s'applique à des plantations adultes, à partir de 9 à 10 ans après plantation et dont le LAI est supposé constant au cours du temps. Les processus de photosynthèse et de transpiration sont calculés à l'échelle du couvert, au pas de temps journalier. L'allocation de carbone se fait par 'grands' compartiments végétatifs et reproducteurs ; les compartiments végétatifs et la respiration (assimilée à un seul grand compartiment) étant prioritaires. La production annuelle de biomasse végétative, modulée par des variations saisonnières, est considérée comme constante d'une année sur l'autre. Le taux de respiration de maintenance, également constant, est calculé à 25°C. Le modèle suppose une production de régimes (absorbant les assimilats non utilisés par les parties végétatives) plastique en nombre et en poids.

Le cœur du modèle repose sur plusieurs hypothèses simplificatrices, concernant la phénologie. Certaines d'entre elles seront en partie validées par notre étude.

(i) L'inflorescence au cours de son développement serait sensible à la photopériode qui agirait à l'échelle du phytomère et non à l'échelle de la plante entière.

Notre analyse montre bien une sensibilité à la photopériode notamment pour expliquer la rythmicité des pics et des creux de production observés à proximité de l'équateur, sur le site dépourvu de stress hydrique significatif. Par ailleurs, cette phase de sensibilité à la photopériode serait située 3+12×n mois avant l'anthèse ou encore 9+12×n mois avant la récolte.

Dans le cas du palmier à huile, la vitesse de développement (dite PhotoPériode efficace, *PPeff*) est simulée comme étant le rapport entre la durée du jour et la durée de la nuit (J-C. Combres, CIRAD, 'comm. pers.'). La phase sensible à la photopériode (*PSP*) se termine lorsque la somme des vitesses de développement atteint un seuil (*SeuilPP*) caractéristique de la plante.

(ii) Le modèle suppose que l'état trophique de la plante détermine la sexualisation et les avortements des inflorescences en cours de développement. L'état trophique de la plante est caractérisé par un indice de compétition interne (Ic), rapport entre l'offre (production d'assimilats par photosynthèse) et la somme des demandes (croissance végétative+croissance reproductive+respiration de maintenance) des différents puits en présence. Cet indice de compétition interne influence féminisation et avortement à différents stades critiques du développement de l'inflorescence. En conditions favorables, l'Ic prend des valeurs supérieures à 1. L'excès de carbone (non utilisé pour la croissance et la respiration) est alors alloué aux réserves. Le compartiment « réserves » dans *EcoPalm* est un compartiment unique et de taille illimitée. Le processus de mise en réserves est, par ailleurs, considéré comme un processus passif, comme c'est le cas dans beaucoup d'autres modèles. En conditions limitantes, l'Ic devient inférieur à 1. La plante mobilise alors une partie de son pool de réserves pour répondre à la demande. Cette mobilisation a un coût et ne couvrira qu'une partie de la demande potentielle qui sera alors probablement réduite.

Notre analyse montre bien que l'intensité des pics de récolte est bien corrélée à des périodes défavorables survenues environ 29 et 16 mois avant. Bien que ces relations aient été établies dans des contextes certes différents, un défaut de production à un instant *t* peut être clairement mis en relation (x mois avant) avec une photosynthèse insuffisante pour couvrir les demandes courantes et nécessite, pour combler ce déficit d'offre primaire, la mobilisation d'une partie des carbohydrates non-structuraux. Dans ces cas, le rôle tampon des réserves carbonées chez un palmier à huile est donc clairement démontré. De plus, nos données montrent que les teneurs en carbohydrates non-structuraux ne dépassent jamais 60% de la masse sèche du stipe ; le compartiment « réserves » pourrait être dorénavant limité à ce seuil dans le modèle.

(iii) Par ailleurs, le développement des inflorescences, dans le modèle, est considéré comme indépendant de celui des feuilles. Dans cette version, en d'autres termes, le retard à l'épanouissement des feuilles, observé en cas de période sèche est supposé ne pas avoir d'influence sur la vitesse de développement de l'inflorescence.

Notre analyse montre que sur le traitement ablation des fruits, le rythme d'apparition du phytomère entier (feuille+inflorescence+entre-nœud) est modifié. En toute logique, le rythme d'apparition de l'inflorescence ne peut être en aucun cas indépendant de celui de la feuille. Le rythme d'épanouissement des feuilles est notamment rapidement accéléré lors de pluies même faibles qui suivent une période sèche.

RELATIONS GENOTYPE × ENVIRONNEMENT

La comparaison des deux génotypes choisis car présentant des productivités significativement différentes est restée, dans le cadre de notre étude, limitée. Néanmoins notre étude a mis le doigt sur quelques paramètres physiologiques clés et plastiques qui jouent significativement sur l'équilibre source-puits chez l'espèce *Elaeis guineensis*. Une étape maintenant prévue est l'exploitation de la diversité génétique du palmier à huile et l'étude de son comportement dans des environnements variables dans le cadre d'expériences génotype × environnement. Dans un premier temps, il s'agit d'évaluer la diversité des caractères d'adaptation aux contraintes hydriques et minérales de l'espèce *Elaeis guineensis* Jacq. sur des provenances d'origines variées. Pour ce faire, une large gamme de paramètres phénologiques, morphologiques et physiologiques sera étudiée. Ces investigations systématiques supposent, au préalable, la mise au point et la maîtrise d'approches méthodologiques simplifiées car développées à grande échelle, sur un nombre conséquent de répétitions. Bien que, dans un premier temps, une approche de phénotypage au champ sera privilégiée, elle pourrait être suivie et enrichie, à terme, d'une approche assistée par modélisation, utilisant *EcoPalm*. Ce modèle intégrera les observations faites et pourrait permettre, par méthode heuristique, la simulation et l'analyse comparée de paramètres phénologiques cachés tels que le positionnement des phases sensibles.

Nos résultats ont montré que le système était complexe ; découpler les mécanismes en jeu n'a pas été chose simple et n'a été dans certains cas que partiellement réalisé. Cependant, de nouvelles perspectives de recherches s'ouvrent à nous avec la comparaison de situations géographiques contrastées couplée à celle de différents génotypes, qui devraient permettre, à terme, (i) l'identification de caractères d'intérêts pour la sélection et l'amélioration génétique du palmier à huile et (ii) le développement d'outils de diagnostic basés sur la physiologie de la plante ainsi que d'outils de prévision saisonnière des rendements du jeune âge à l'âge adulte intégrant les effets du changement climatique.

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ANNEXES

↳ COMMUNICATION ORALE

International Oil Palm Conference – IOPC 2006

OPTIMUM USE OF RESOURCES:

CHALLENGES AND OPPORTUNITIES FOR SUSTAINABLE OIL PALM DEVELOPMENT

19-23 June 2006
Bali International Convention Center
Nusa Dua – Bali, Indonesia

Carbohydrates Reserves in 9 Years Old Oil Palm: Nature, Distribution and Seasonal Changes

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ABSTRACT

Transitory carbohydrate storage plays a vital physiological role in functioning of woody plants and may serve as indicator of source/sink relationship. Contrary to temperate trees, little work has been done on this subject for tropical, perennial trees. The objectives were to describe the nature, the distribution and the quantity of carbohydrate reserves and to study their seasonal variations in relation with vegetative growth, fruit production and climate. The study was carried out on Riau Estate (Sumatra Island, Indonesia) on thirty-two, 9 years old oil palm trees, representative of a large population and felled on 4 sampling dates between October 2002 and February 2004. The experimental design comprised two treatments (control and 'leaf-pruning' i.e. removing leaves except the 17 youngest), replicated four times. Accumulation zones were identified by sampling and measurement of dry mass and sugars concentrations for all vegetative organs: stem, fronds, roots, persistent leaves bases, and meristem.

Non-structural carbohydrates represented 20% of total dry vegetative biomass. Plants contained large quantities of glucose (53% of total carbohydrates), sucrose and starch (20% each) and little fructose. Reserves were predominantly located in the stem. Glucose concentration decreased from bottom to top and from centre to periphery of the stem, whereas sucrose showed reverse gradients. Starch was nearly absent in the lower parts of the stem but attained a concentration of 150 mg g^{-1} at the top. Monosaccharides concentration was high, and sucrose and starch concentration low, at the end of the dry period (October, when fruit production was high). At the end of the rainy season (February), fruit production and glucose concentration were low. Leaf pruning decreased sugar concentrations at the beginning of the experiment in most plant parts and then this difference disappeared (October 2003 and February 2004). No significant effects of pruning treatment were observed on fruit production.

The results indicated that oil palm is one of the rare species using glucose as transitory reserve sugar. Further studies on the agro-ecological and physiological function of these reserves are in progress.

Keywords: non-structural carbohydrates – productivity – oil palm – growth – seasonal variation – leaf pruning

INTRODUCTION

Assimilate reserves are defined as resources accumulated in mobilizable form sustain growth and other functions of the plant that may temporarily demand more assimilates than are being produced (Mialet-Serra *et al.*, 2005). Perennials plants accumulate non-structural carbohydrates during periods of excess production of photoassimilates and use them when demand exceeds production, resulting in a high utilisation ratio (Kozlowski, 1992). Contrary to temperate trees, little work has been done on this subject for tropical, perennial trees. On this subject, Oil palm has been studied by Scheideker *et al.* (1958) and more recently by Henson *et al.* (1999).

Like the majority of the agricultural produces, the world levels of the palm oil record important fluctuations which tend to tighten the producers' margins (Anonymous, 2001). This economic context is worsened by an irregular production from one season or one year to another even under optimum crop conditions and by the appearance of extreme weather events in South-East Asia, with long dry periods. These natural fluctuations remained to be explained. Many authors showed, in particular on temperate fruit-bearing species that the production variation can be closely related to carbohydrates levels in the plant, directly assimilated by the leaves, but also stored in time in the various vegetative compartments. They privileged a "trophic" approach to explain yield variations. Like basic hypothesis, the carbohydrates reserves of an adult oil palm, can represent a buffer, likely to compensate an insufficient photosynthesis to support plant demands.

The objectives of this study were (i) to describe the nature, the distribution and the quantity of carbohydrate reserves, (ii) to study their seasonal variation in relation with vegetative growth, fruit production and climate and (iii) to describe the effects of carbon supply limitation (by leaf pruning) on storage function.

MATERIALS AND METHODS

Experimental site and plant material

The study was carried out on Riau Estate (Sumatra Island, Indonesia) on the oil palm plantation of PT Smart Corporation. The climate is tropical oceanic and favourable for the growth of oil palm. Mean annual rainfall is 2020 mm year^{-1} (*figure 1*). A relative dry season generally occurs from July to September. The soil is slimy and sandy, well drained, and is about 150 cm depth.

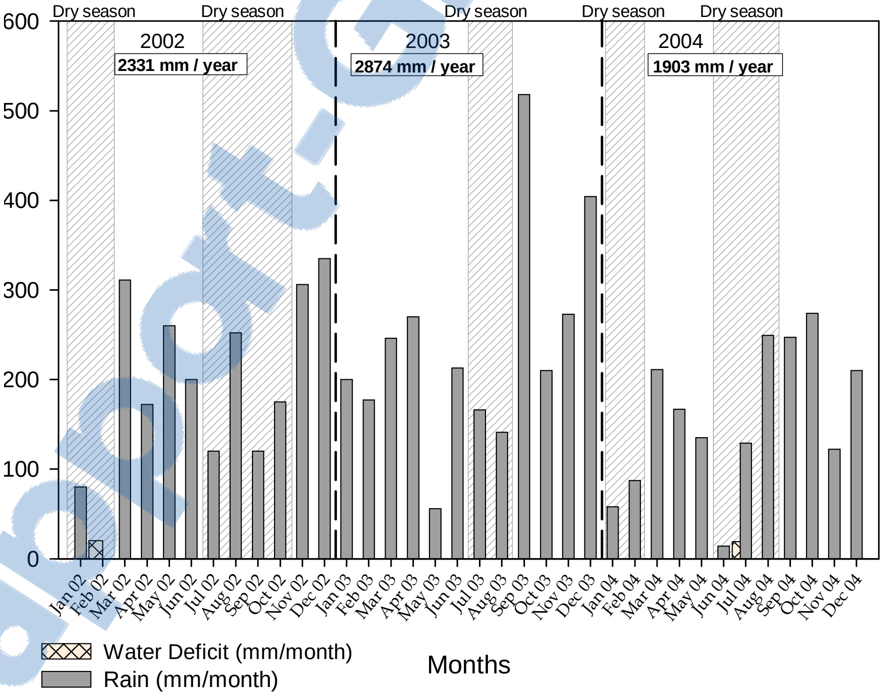

Figure 1: Rain distribution during experience duration between 2002 and 2004

The cultivar studied was a *Tenera* hybrid. Plants were 9 years old at the beginning of our study. Population density was 143 plants ha^{-1}. Thirty-two oil palms representative of a large population were selected. These 32 plants measured 5.9 ± 0.11 m (*s.e.*) stem height and had produced 14.4 ± 0.5 (*s.e.*) bunches year^{-1} and 230 ± 8 (*s.e.*) kg bunches fresh matter year^{-1} tree^{-1} between 2001 and 2002 (just before the beginning of our experience). The experimental design comprised two treatments (control and 'severe leaf-pruning'). Severe leaves pruning, which serve to limit assimilate supply, consisted of removing on a monthly basis all leaves except the 17 youngest on each crown on 16 palms from June 2002. Mean leaves number is 40 leaves per crown on control trees.

Sampling procedure

Oil palms were felled and roots dug up for sampling (four palms for each sampling date) during October 2002 and 2003 (end of 'dry' season) and February 2003 and 2004 (end of 'rainy' season).

On the stem, two radial samples (two radial sections with 10 cm length) were taken in the apical area, at the top (sub-apical area), at 1.2 m height, at the base (200 mm from ground), and in the stump (underground). Each section was divided into four sub samples ('bark', outside, middle and 'heart') representing the four radial zones that have a decreasing density of woody, vascular trends from periphery (i.e. 'bark') to centre (i.e. 'heart').

Leaves on one of the eight spirals were collected corresponding to rank 1, 9, 17, 25, 33, and (if present) 41 and 49. Sub samples were taken from the base, middle portion and end of the petiole; from middle and end portions of the rachis; and from leaflet situated at the middle portion of the rachis.

On the root system, large roots (R1), medium size roots (R2) and fine roots (R3) were distinguished; samples were taken from the white portion in the course of differentiation located close to the meristem (zone 1) and the mature, differentiated zone (zone 2).

Remaining petiole bases sample were taken at different levels of the stem (at the top, at 1.2 meter height and at the base).

Estimate of plant total dry matter by type of organ

Stem dry matter was calculated from stem dimensions (radius and height) and specific mass (dry weight volume^{-1}) of the stump, at the base, 1.2 m height and at the top. The dry matter content of the petioles, rachis and leaflets was estimated by weighing the entire organs after drying at 105°C, then multiplying by the total number of such organs present on the plants. Root sampling was performed for one-twelfth on the theoretical, hexagonal soil surface available to a plant. Roots were collected from three 80-cm deep excavation, sieved, sorted by type, dried at 105°C, weighed and their weight extrapolated to the full hexagon associated with the plant. The result was multiplied by 1.1 in order to take into account deep roots, based on previous observations made on the same plot (Kansou, 2003).

Biochemical analyses

The samples were lyophilized and ground. After extraction, glucose, sucrose, fructose and starch were quantified by indirect enzymatic method (Boehringer, 1988) and followed by spectrophotometry of NADPH at 340 nm. The results were expressed either as bulk organ or plant concentrations (mg g^{-1} Dry Matter) or the total content of each organ (g) on a single-plant basis.

Statistical analysis

The multiple comparisons of averages are carried out by using the test of Tukey to the threshold of 5%.

RESULTS AND DISCUSSION

Sugar natures

Glucose was the dominant temporary storage sugar (53% of total sugars) in all vegetative compartments of oil palms, followed by sucrose and starch (20 % each) and little fructose (only 7% of total carbohydrates) (*figure 2*). These results confirmed previous observations which showed that soluble sugars were the most important form of carbohydrate in oil palm (Scheideker *et al.*, 1958; Henson, 1999). In contrast to the majority of higher plants (Kozlowski, 1992), oil palm does not use starch as a major form of carbohydrate storage. Oil palm is one of the rare species using glucose as transitory reserve sugar, an energy supply directly usable in all biological processes.

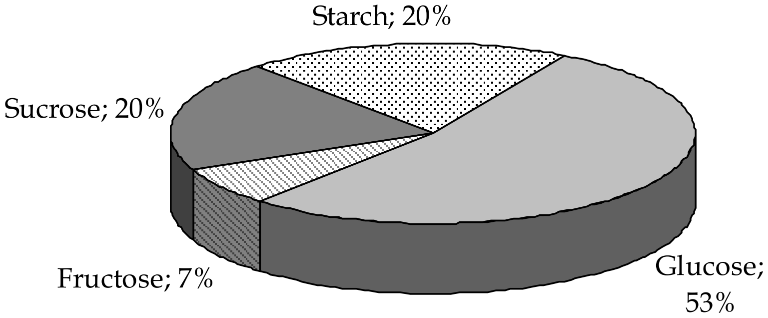

Figure 2: Proportion (%) of different sugars in Oil palm.

Distribution in the vegetative compartments

The carbohydrate were mainly located in the stem (65% of total sugars), followed by the leaves (17 % of total carbohydrate) and persistent leaves bases (*figure 3*). Roots were poor in reserves (only 2%).

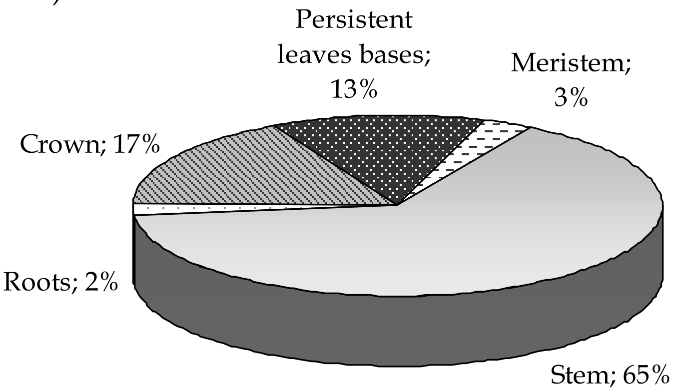

Figure 3: Distribution (%) of transitory reserves in the vegetative compartments.

The stem

The by far dominating reserve sugar in the stem was glucose, followed by starch and sucrose. Total sugar concentrations increased from bottom to the top. Monosaccharides (glucose + fructose) accounted for 77% or more of the total sugar concentrations except the fractions of the top, where starch accounted for up to 33% (170 mg g^{-1}) and except in the meristem, with higher sucrose concentrations (360 mg g^{-1}) (*figure 4*).

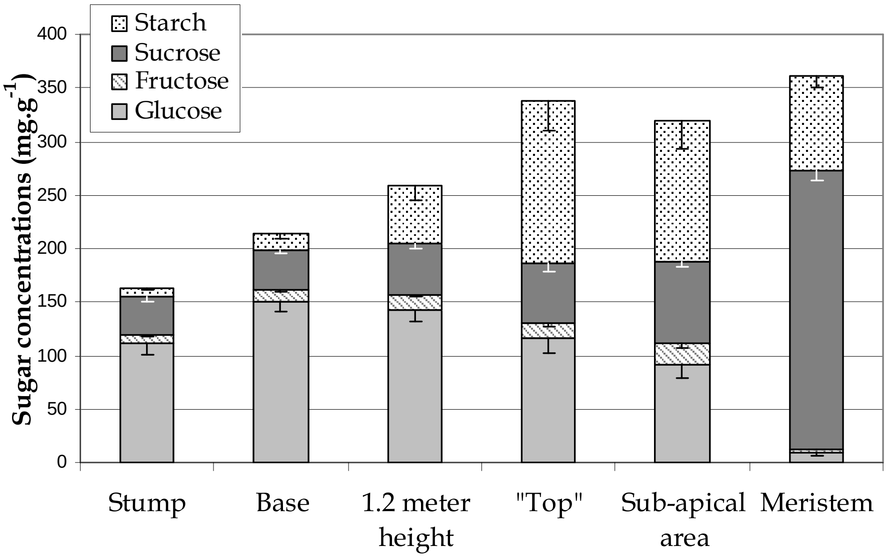

Figure 4: Sugars concentrations (mg g^{-1}) at different height on the stem. Vertical bars indicate standard error of mean (*s.e.*) of sixteen replications.

Total sugar concentrations increased from the periphery (i.e. outside) to the centre (i.e. “heart”). At the stem base, monosaccharide concentrations were more important in the heart of the stem whereas sucrose and starch were higher in the periphery (*figure 5*). At the top, sucrose showed a reverse radial gradient, higher in the heart than in the stem bark. The concentration gradients were not steep in either direction (radial or axial), suggesting that the stem in all of its parts serves as a storage organ.

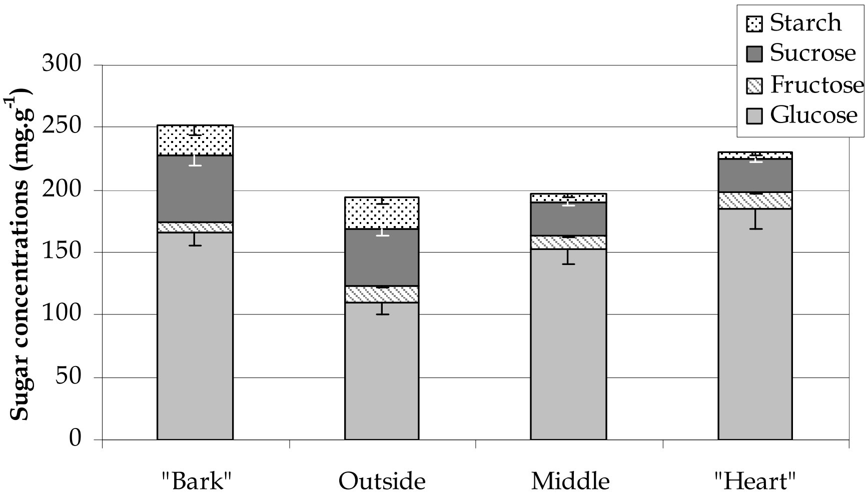

Figure 5: Sugars concentrations (mg g^{-1}) in different radial zones at the stem base. Vertical bars indicate standard error of mean (*s.e.*) of sixteen replications.

The persistent petiole bases

Like in the stem, the by far dominating reserve substance in the persistent petiole bases was glucose, followed by sucrose and starch. No consistent total sugar gradient was found along the stem. Longitudinal gradients were quite similar as on the stem, glucose decreased from the bottom to the top and starch increased from bottom to the top (*figure 6*). Persistent leaves bases served as storage organs like the stem and did not differ in their reserve status as a function of stem position.

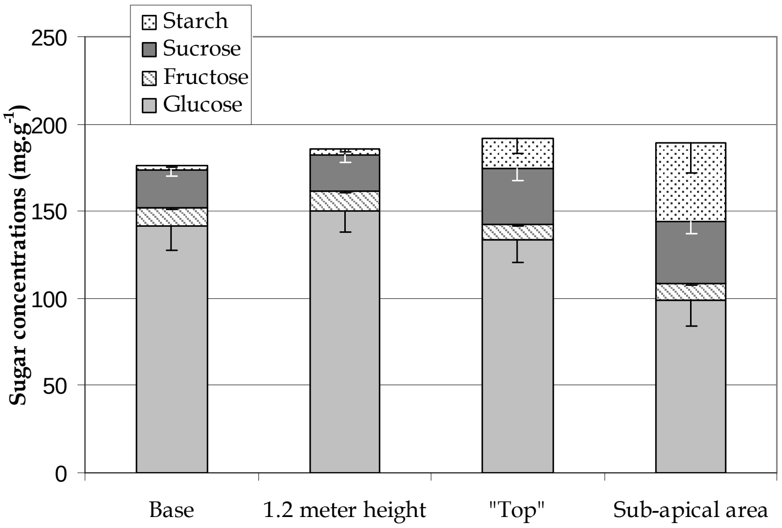

Figure 6: Sugars concentrations (mg g^{-1}) in the persistent leaves bases along the stem. Vertical bars indicate standard error of mean (*s.e.*) of sixteen replications.

The leaves

Glucose concentration was high in the leaves petiole and rachis than in the leaflets (21 mg g^{-1}). It varied little among the petiole (131 mg g^{-1}) and the rachis (113 mg g^{-1}). Starch concentrations were extremely low except at the petiole base (*figure 7*). According the rank of leaves, glucose did not show a marked pattern distribution (*figure 8*). Fruit growth and maturation did not seem to have an influence on the glucose concentrations in the different compartments of the leaves.

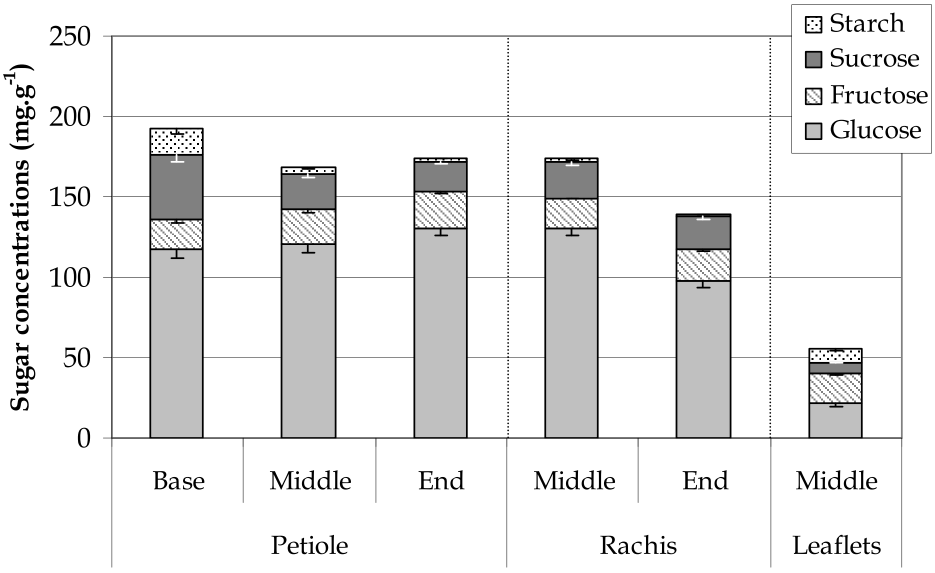

Figure 7: Sugars concentrations (mg g^{-1}) in various compartments of oil palm leaves. Vertical bars indicate standard error of mean (*s.e.*) of sixteen replications.

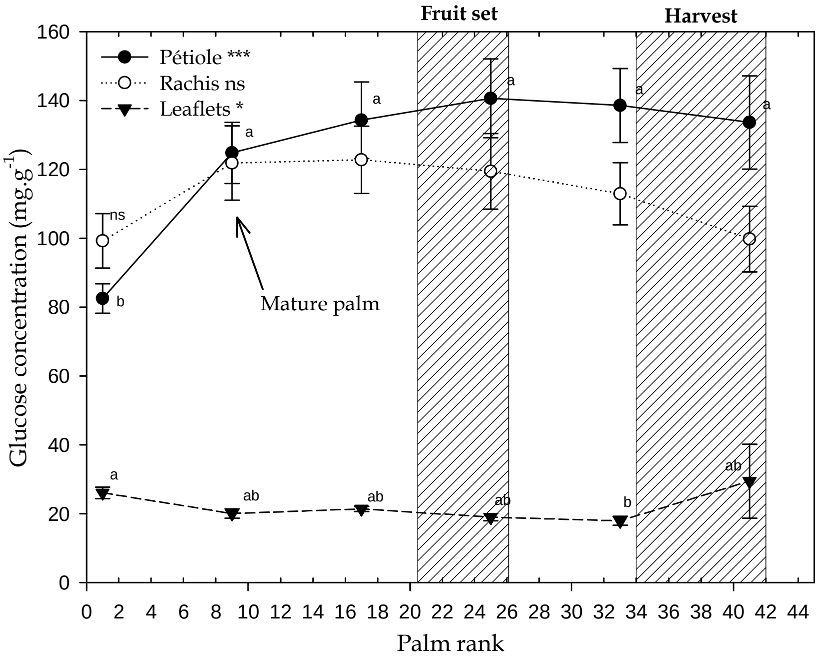

Figure 8: Glucose concentration in leaf petiole, rachis and leaflets of oil palm as a function of leaf position. Vertical bars indicate standard error of mean (*s.e.*) of sixteen replications.

The roots

Total sugar concentration exhibited a strong gradient from large (R1) to fine (R3) roots (*figure 9*). This gradient was apparent for glucose, whereas starch was present only in traces. Consistent gradient was found along "R1" (as indicated by the two zones sampled), suggesting that young (zone 1) and mature (zone 2) portions for this type of roots differed strongly in their reserve status. Overall, except in zone 1 of R1, roots had much lower sugar concentrations than the stem and leaf petiole and rachis.

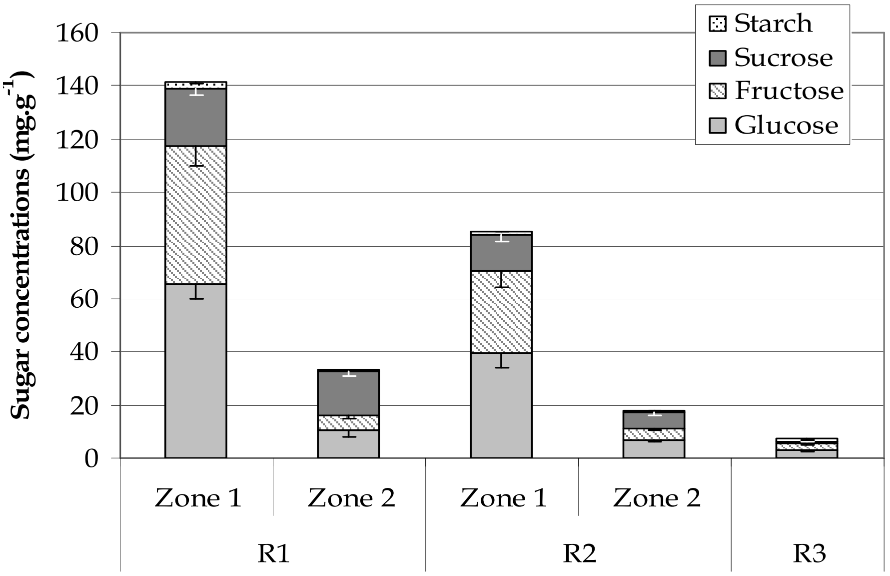

Figure 9: Sugars concentration (mg g^{-1}) in various compartments of coconut roots. Vertical bars indicate standard error of mean (*s.e.*) of sixteen replications.

Effect of applied treatment on reserves natures and distribution

Leaf pruning treatment did not modify significantly the nature of reserve sugars and gradients in all vegetative compartments.

Seasonal changes

Seasonal variations of the vegetative dry matter and sugar contents

Total vegetative dry matter including roots was 645 kg, corresponding to 92 t .ha^{-1} for the population. With 315 kg, the stem accounted for 49% of the total dry matter. The leaf crown contributed 26%, persistent leaves bases 14% and root system 11% to the total (*figure 10*). Dry matters of all of these did not varied significantly with season.

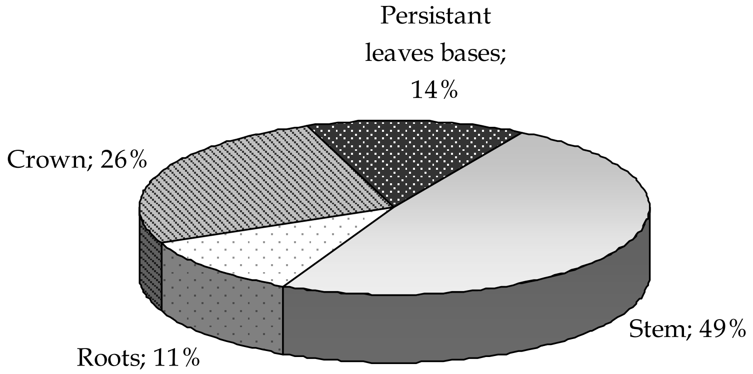

Figure 10: Standing vegetative Biomass distribution (%) of oil palm by type of organ

On a whole plant scale, the total quantity of non-structural carbohydrates (127 kg per plant) amounted to 20% of total dry biomass. Reserves were predominantly located in the stem (80 kg per plant or 11.4 t ha^{-1}). Reserves pool in coconut, considered as substantial quantitative importance, represented only 8% of total dry biomass (Mialet-Serra, 2005). The presence of large quantities of sugars in the stem was compatible with its anatomy (Henson, 1999; Fougerolles, 2004); the inner part was formed by living parenchymatous tissues in which there were vascular and fibrous bundles.

The leaf pruning treatment did not modify significantly dry matter and sugar contents of the stem and the roots during the experiment.

A way of evaluating the physiological significance of the sugar reserve pool is by estimating the period during which it can theoretically substitute for photosynthesis. Daily dry matter production (dMdplant) is calculated from the product of solar radiation (S), canopy light interception (f), radiation use efficiency (RUE) and the ratio of total dry biomass (Mdplant) and above-ground dry biomass (Mdag):

$$dM_{dplant} = 0.5 \times S \times f \times RUE \times (M_{dplant} / M_{dag})$$

(The coefficient of 0.5 represents the fraction of global radiation constituting photosynthetically active radiation PAR)

Assuming that mean daily S of the site is 16.6 MJ m^{-2}, f is 0.70, RUE is estimated at 1.3 g MJ^{-1} on PAR basis (Squire and Corley, 1987; Gerritsma and Wessel, 1997) and the total/above-ground dry weight is 1.1, the total daily dry matter production of an oil palm plantation would be 8.3 g m^{-2} d^{-1} or 83 kg ha^{-1} d^{-1}. On a yearly basis this results in 30300 kg dry matter produced per hectare. In order to compare plant sugar reserves with daily growth rates we return to the scale of the individual plant which occupies 69.9 m^{2} ground area (143 plants per hectare) and consequently grows at an average rate of 8.3 g m^{-2} d^{-1} × 69.9 m^{2} = 580 g d^{-1}. The observed reserves (127 000 g plant^{-1}) would theoretically sustain growth for 7.2 months, assuming that growth efficiency is 0.7 (g glycoside/g Dry Matter). Consequently, sugar reserves in oil palm can potentially serve as a very substantial buffer for periods of low assimilation or high demand for assimilates.

Seasonal variations in fruit number and dry matter

The studied genotype produced high fruit number and bunch dry mass per tree (*table 1*). Variability between individual trees was higher than between season or between treatments. So no significant effects on fruit production appeared with season (four sampling dates) and with applied treatment. Just a tendency would be observed with a decrease of fruits number, harvested bunch dry mass (35%) and an increase of 10% of parthenocarpic fruits number on the leaf-pruning treatment. Corley (1976b; 1977) showed that pruning effect could appear on yield more than 15 months after first pruning. The duration of our experience (18 months) would be probably too short and the treatment effect would depend of the plant material. Further studies on the leaf-pruning effect are in progress on a longest duration (36 months).

Table 1: Fruit production on control and leaf-pruning treatments

	Control		**Severe Leaf Pruning**		
	Mean	*sem*	***Mean***	*sem*	*treshold*
Tree scale					
Number of bunches	**4,9**	0,65	**4,7**	0,64	ns
Sex-ratio	**0,6**	0,06	**0,7**	0,07	ns
% parthenocarpics fruits	**32% (15% to 67%)**	0,05	**41% (16% to 80%)**	0,07	ns
Fruits number per trees	**6208**	911	**4602**	722	ns
Total Fruits dry matter (kg)	**12.6**	2.1	**8.2**	2.2	ns
Bunch scale					
Pulp biomass in ripe fruit (g)	**5**	0,7	**3**	1,2	ns

Seasonal variations of reserves pools

In the *stem*, glucose concentration was higher at the end of 'dry' season (October) than at the end of 'rainy' season (February) (*figure 11A*), the opposite observed for fruit production; lower at the end of 'dry' season. Starch and sucrose, on the opposite of glucose, was lower at the end of 'dry' season than at the end of 'rainy' season (as fruit production) (*figure 11B*). *Figure 11B* showed that severely pruned trees had lower starch concentration than control trees. This difference was significant between treatments at the beginning of our experiment (October 2002) and not at the end (February 2004). In this case, starch varied very clearly and could be a good indicator of a carbohydrate surplus or reserves reconstitution during a stress. Kozlowski (1992) found this phenomenon in numerous temperate woody species.

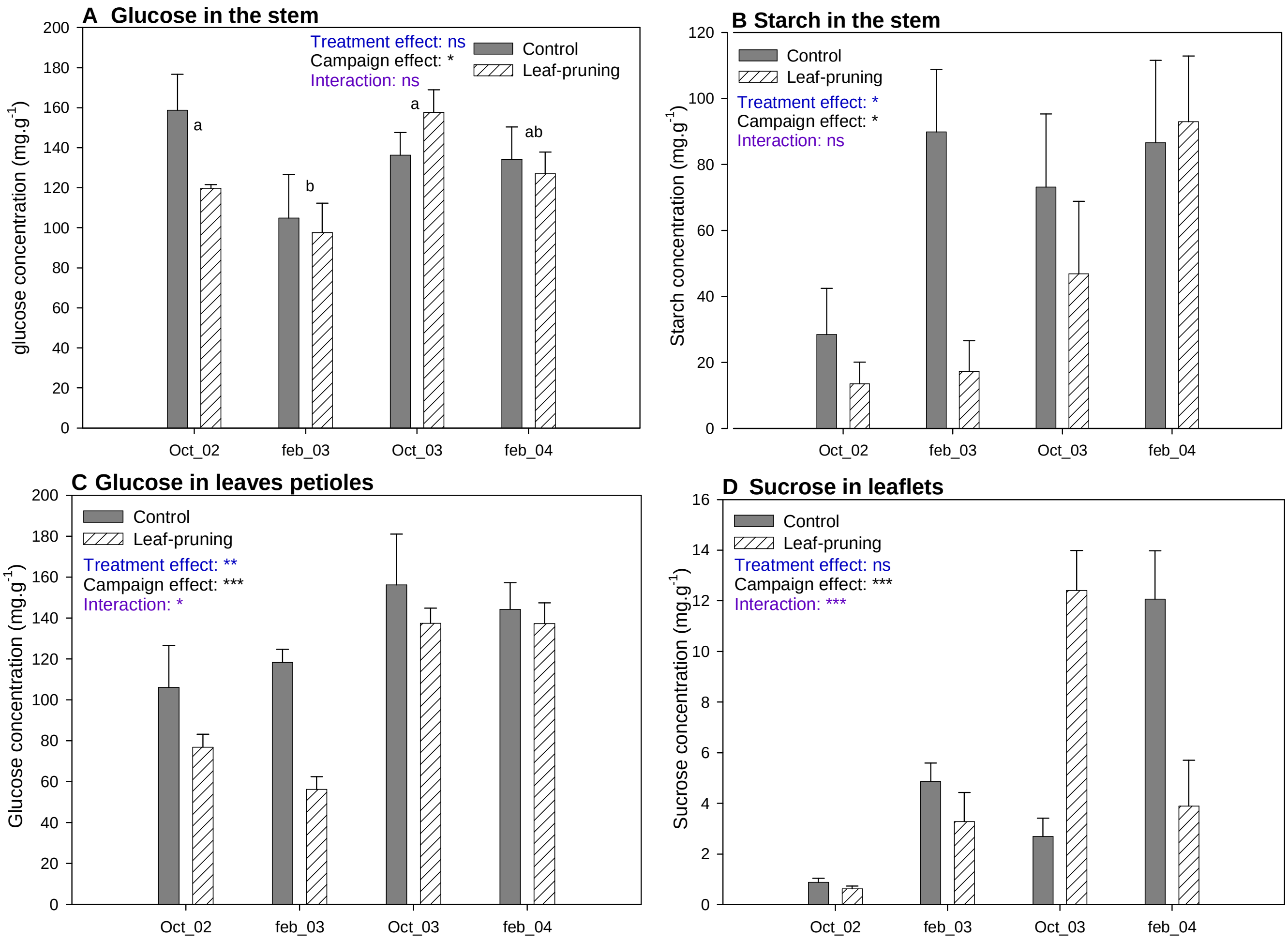

Figure 11: Seasonal variations of sugar concentrations (mg g^{-1}) on the control and leaf-pruning treatments (A) glucose concentrations in the stem (B) starch concentrations in the stem (C) glucose concentrations in leaves petioles and (D) sucrose concentrations in leaflets. Vertical bars indicate standard error of mean (*s.e.*) of four replications.

In the *petioles*, glucose concentration increased with sampling campaign (*figure 11C*). It was lower in severely pruned trees than in control trees, mainly at the beginning of the experiment. This significant difference disappeared at the end of the experiment. In the *leaflets*, "source" compartment, a sucrose accumulation was observed in February 2004 for control and 4 months before (October 2003) for leaf-pruning trees (*figure 11D*). This observation along with comparable sugar concentrations between treatments after 12 months (from first pruning) would tend to a boosted photosynthesis (hypothesis) on the severely leaf-pruning treatment and an adjustment to maintain productivity within physiological limits that it would be interesting to investigate on this Arecaceae.

CONCLUSIONS AND PROSPECTS

Like in coconut (Mialet-Serra *et al.*, 2005), this study is the first of a series investigating the role of carbohydrate reserves in oil palm. These results have established glucose to be the 'genus' main storage compound in vegetative organs, its distribution in the plant and its pool size. We conclude that the mobilizable sugars accumulated in a fertile oil palm plant of the type investigated here is theoretically sufficient to sustain growth rates for *seven months* in the absence of fresh assimilates. Consequently, the reserve pools are significant in size and are probably important in sustaining growth and production like for coconut palm (Mialet-Serra *et al.*, 2005).

Further studies on the agro-ecological and physiological roles of reserves in oil palm are in progress. The next steps will to characterize the annual and seasonal dynamics of the reserves pools in more details and to model their probable role as a physiological buffer. This hypothetical role of reserves pools will be tested and analyze by the experimental removal of sinks (fruits ablation) and sources (severe leaves pruning) and by the imposition of water stress by root pruning. This study lays the foundation for a larger study aiming at developing an oil palm growth model (EcoPalm, CIRAD) capable of simulating climate-driven production, crop phenology, sink-source relationships and in particular the effect of the carbon reserves status on the capacity of the plant to sustain production during period of low assimilation. A PhD is in progress aiming an analysis and modelling of the carbon balance of the plant at the infertile and mature ages under different water conditions in Indonesia.

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AJUSTEMENT DE LA PHENOLOGIE, DE LA CROISSANCE ET DE LA PRODUCTION DU PALMIER A HUILE (*ELAEIS GUINEENSIS* JACQ.) FACE A DES ENVIRONNEMENTS VARIABLES : MECANISMES DE LA PLASTICITE PHENOTYPIQUE

La floraison et la production du palmier à huile montrent des variations saisonnières parfois fortes dont les causes sont mal connues. Notre analyse montre d'une part que la périodicité observée semble être contrôlée par des variations même faibles de la photopériode, d'autre part, que les variations d'amplitudes intra et interannuelles observées résultent de conditions défavorables apparues 16 à 29 mois avant la récolte provoquant, respectivement, des avortements d'inflorescences déjà différenciées et une différenciation accrue d'inflorescences mâles. En conditions de déséquilibres source-puits, différents mécanismes d'ajustements phénologiques et physiologiques ont pu être mis en évidence. Au cours d'une sécheresse sévère, l'assimilation et la croissance des compartiments végétatifs aériens, très sensibles aux conditions hydriques de l'air et du sol, déclinent rapidement. Les réserves carbonées en quantité importante dans le stipe tamponnent une partie du déficit en assimilats et couvrent ainsi la demande reproductive. L'important pool d'amidon dans la partie haute du stipe enregistre alors des fluctuations importantes. En conditions de demande limitée, aucun ajustement de l'assimilation carbonée n'a été observé, l'hypothèse d'une rétroaction de la demande sur l'assimilation semble être écartée chez le palmier à huile. L'excès d'assimilats est en partie absorbé par un enflement du compartiment réserves pouvant atteindre dans le haut du stipe 50% de la masse sèche totale alors majoritairement constitué d'amidon. Le rôle physiologique du glucose, glucide majoritaire chez le palmier, reste encore obscur ; il semble plus sensible aux conditions hydriques que l'amidon, piloté par la demande interne. L'ensemble de ces observations a permis la construction d'un modèle conceptuel expliquant les relations source-puits pour le palmier à huile et apporte une base solide pour la validation partielle du modèle physiologique, *EcoPalm*, développé en parallèle sur cette espèce.

PHENOLOGY, GROWTH AND PRODUCTION ADJUSTMENTS OF OIL PALM (*ELAEIS GUINEENSIS* JACQ.) TO ENVIRONMENTAL VARIABILITY: MECHANISMS OF PHENOTYPIC PLASTICITY

Oil palm flowering and fruit production show seasonal variations whose causes are unknown. Our analysis shows, first, that the rythmicity of the production is probably controlled, even near the equator, by photoperiod; second, intra- and inter-annual variations result from unfavourable conditions that have occurred 16 to 29 months before harvest, causing, respectively, abortion of differentiated inflorescences and an increase of frequency of male inflorescences. Under source-sink imbalance conditions, several phenological and physiological adjustments were identified. During severe drought, assimilation and aboveground vegetative growth, both sensitive to air and soil humidity, decreased. Non-structural carbohydrate reserves, mainly located in the stem, partially buffered this lack of assimilates and hence cover demand for reproductive growth. Strong fluctuations are thus recorded for the large pool of starch located in the top part of the stem. Under low-demand conditions, no feed-back inhibition of CO_2 assimilation was observed, thus rejecting the hypothesis that regulation of photosynthesis is an important adjustment process to sink-source imbalances in oil palm. Excess assimilates are partly absorbed by reserve pool in stems which can reach, in the stem top, 50% of the total dry mass, mainly consisting of starch. The physiological role of glucose, the most abundant storage carbohydrate in oil palm, remains unexplained. It may be related to drought adjustment processes. These results permitted the development of a conceptual model of adjustments to source-sink relationships in oil palm and provide crucial information for the improvement and validation of the physiological model *EcoPalm*, currently being developed.

MOTS-CLES : allocation du carbone, efficience d'utilisation de la lumière, carbohydrates non structuraux, palmier à huile, photopériode, photosynthèse, plasticité phénotypique, relations source-puits, sécheresse.

KEYWORDS: carbon allocation, drought, non-structural carbohydrates, oil palm, phenotypic plasticity, photoperiodism, photosynthesis, radiation use efficiency, source-sink relationships.

DISCIPLINE : Ecophysiologie

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