Journal of Oil Palm Research Vol. 26 (1) March 2014 p. 1- 24

THE FUTURE OF OIL PALM AS A MAJOR GLOBAL CROP: OPPORTUNITIES AND CHALLENGES

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ABSTRACT

In recent years, the oil palm sector has witnessed a period of historically high prices with buoyant global demand and high levels of production driven largely by economic development in major Asian countries such as India and China. However, the oil palm sector is also confronted by many important challenges that require attention. Such challenges include fragmentation of the industry, stagnating yields, and an image problem that is largely due to the conversion of tropical rainforest and peatlands in a few regions in South-east Asia. The biological and managerial tools to surmount these challenges already exist but need more focussed application and political support. Potentially groundbreaking biological tools include the new molecular breeding technologies, such as those made possible by the recent publication of the oil palm genome sequence (Singh et al.*, 2013a, b). Two key R&D targets for the industry are:*

- *higher oil yield in fruits and trees; and*
- *higher mesocarp oleic acid composition – preferably over 65% w/w.*

The more focussed use of new and traditional technologies can also help to confront pest and disease problems, to redesign of crop architecture, and to facilitate yield and harvesting efficiency. In the medium-term future, we can look forward to a considerable geographical extension of oil palm cultivation in a broad zone across the tropics of Africa, Asia and the Americas. If these and other measures can be taken, increased palm oil output could more than meet the highest projections for future vegetable oil requirements while minimising adverse environmental consequences. Improved oil palm varieties could also considerably increase the global market share for this highly productive tropical crop at the expense of some of the less efficient temperate oilseed crops.

Keywords: oil yield, high oleic, genomics, breeding, management.

Date received: 19 August 2013; **Sent for revision:** 11 September 2013; **Received in final form:** 16 January 2014; **Accepted:** 16 January 2014.

INTRODUCTION

Oil palm is a uniquely productive tropical crop with a potential yield capacity well in excess of 10 t of oil per hectare (t ha^{-1}). However, current yields are well below this figure and are typically about 4-6 t ha^{-1} for the best commercial plantations and 3-4 t ha^{-1} for smallholders. Palm oil is mainly used as an edible product and is an increasingly important dietary component for well over one billion people worldwide. The oil palm also has many uses in the non-food sector, with examples ranging from high value oleochemicals to more basic biomass-derived materials such as paper and plywood (Suleiman *et al.*, 2012). In commercial terms, the major product

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of the crop is the oil that accumulates in the fleshy mesocarp of the fruits, which is often referred to as palm oil, crude palm oil or mesocarp oil. About 84% w/w of the mesocarp oil is made up of palmitic (C16:0) and oleic (C18:1) acids and this oil has been used as a traditional food source in parts of Africa for many thousands of years.

Palm fruits also contain a single hard seed, or kernel, which is enriched in a different type of oil, often referred to as palm kernel oil, that makes up about 11% of the total oil fraction of the crop. Palm kernel oil is enriched in the medium chain fatty acids, lauric (C12:0) and myristic (C14:0) acids, which together make up 74% w/w of this oil. These fatty acids make palm kernel oil a useful source of many industrial and cosmetic products such as soaps, detergents and cleaning agents. Lauric acid is also used in several edible applications including as a shortening agent for margarine and cream products and can even be applied as an anti-microbial agent.

Both types of palm fruit oil have been used historically as fuels, most commonly for lighting in traditional settings. Since 2000, increasing amounts of palm oil and other vegetable oils have been converted into their methyl ester derivatives in order to produce biodiesel fuel for vehicles (Rosillo-Calle *et al.*, 2007). This has led to concerns about the diversion of some palm oil from edible uses with possible increases in food prices and increased pressures to convert undeveloped forest and peat habitats to oil palm plantations (Bringezu *et al.*, 2009; Johnston *et al.*, 2009). However, to put this in context, in 2013 the biodiesel sector accounted for well under 10% of total palm oil production and the future growth of this sector is far from assured. For example, concerns about the environmental credentials of some biofuels have recently led the European Union (EU) to reduce targets for renewable fuels for transport. This reduction applies specifically to biofuels (such as palm oil biodiesel) from food crops where the 10% target of replacing fossil fuels has been halved to 5% (Van Noorden, 2013). The result of this policy shift will be a decreased demand for biodiesel in the EU, which is currently the largest global user of this product. Therefore, while biodiesel has been responsible for some of the increase in demand for palm oil, this is unlikely to be the case in the medium-term future. Instead, by far the major factor driving increased future demand for palm oil will continue to be the burgeoning global requirement for more edible oils, especially in Asia.

The two major species of oil palm, *Elaeis guineensis* and *Elaeis oleifera*, have their centres of origin respectively in West Africa and South America (Corley and Tinker, 2003). Due to its higher yield, the African oil palm, *E. guineensis*, is the species that is overwhelmingly used for commercial cultivation, even in South America. However, as discussed below, although it is not a particularly good crop plant, *E. oleifera* contains useful genetic variation that can be incorporated into breeding programmes for creation of improved commercial varieties of *E. guineensis*. Oil palm was first grown on a widespread scale when African trees were introduced into Sumatra and Peninsular Malaysia as plantation crops in the early 20th century. Commercial cultivation increased dramatically, first in Malaysia after independence in 1957 and subsequently in Indonesia early in 21st century. By 2012, Malaysia and Indonesia collectively produced about 57 million tonnes of oil, which made up over 85% of global palm production (*Table 1*) and almost 40% of the entire world output of all forms of vegetable oil (USDA, 2012).

For most of the period of its cultivation as a plantation crop, oil palm has been relatively uncontroversial. However, over the past decade various aspects of the introduction, management, and end use of oil palm have come under increasing scrutiny, and in some cases criticism. Many, but not all, of the most negative comments about oil palm have come from certain groups in Europe and to a lesser extent in North America. Often such comments have focussed on the environmental consequences (such as forest clearance) of increased oil palm cultivation and also its increasing use as a biofuel crop. Other concerns about the high level of saturated fatty acids in palm oil have been voiced but it is far from clear whether palm oil saturates like palmitate have the same negative health consequences as more typically animal-derived saturates such as stearate. On the other hand, there is an ever growing demand for palm oil products, especially for food use in developing countries. This demand needs to be satisfied somehow, which leads to the question: how can oil palm production be increased without adverse environmental consequences?

The conversion of land to agriculture has been a feature of human development for thousands of years. This process has already resulted in the mass clearance of forests for crop cultivation in much of Europe and the Americas. Since the late 20th century, the continued conversion of land in some parts of the world has come under increased scrutiny, particularly from environmental groups. Such attention has particularly been focussed on the conversion of land to oil palm in parts of South-east Asia and to soyabean crops in South America. There is a broad consensus that it is undesirable in principle to mass-convert some ecologically sensitive habitats, such as pristine rainforests or some deep peat regions, to oil palm plantations. Also, if new plantations are already being established, it is desirable to do this in a way that minimises the eco-environmental side effects of the land conversion. For example, in some areas the establishment of protected areas linked by wildlife corridors can enable plantations to coexist with traditional native

TABLE 1. MAJOR CENTRES OF OIL PALM CULTIVATION

Rank	Country	Production (million tonnes)
1	Indonesia	31.0
2	Malaysia	19.0
3	Thailand	2.1
4	Colombia	1.0
5	Nigeria	0.9
6	Papua New Guinea	0.6
7	Ecuador	0.6
8	Honduras	0.4
9	Ivory Coast	0.4
10	Brazil	0.3
	Others	0.7
	Total	57.0

Source: Data from the United States Department of Agriculture (2012).

fauna. In other cases, replanting existing plantations with higher yielding palms can reduce the need to establish new plantations.

In the remainder of this article, I will assess the current status of oil palm as a major global crop and describe how both biological and management approaches can contribute to addressing many of the current concerns about this valuable and frequently misunderstood plant.

OIL PALM IS BY FAR THE MOST EFFICIENT CROP-BASED HYDROCARBON PRODUCTION SYSTEM

Oil crops such as oil palm and the temperate oilseeds (*e.g.* soyabean, rapeseed, sunflower, peanut, and cotton) are renewable sources of oils that can used either as edible foodstuffs or as industrial feedstocks to replace products that are otherwise derived non-renewable mineral oils. Industrial uses include manufacture of a wide range of basic oleochemicals, chemical intermediates, and more highly processed finished products such as coatings, lubricants, and biopolymers, plus biofuels such as biodiesel. As we will now see, oil palm is by far the highest yielding biological source of oil-based hydrocarbons and is significantly more efficient than any of other commercial oil crop.

In 2012, the estimated global production of total palm oil was almost 65 million tonnes, of which 58 million tonnes was mesocarp oil and 6.8 million tonnes was kernel oil (USDA, 2012). Typical average yields of palm oil on a global basis are in the region of 4 t ha^{-1}. This figure far outstrips the yield of the major temperate annual oilseed crops where yields range from 0.3 to 1.2 t ha^{-1}. This high yield means that the current global output of 65 million tonnes palm oil requires cultivation of only 15 million hectares, which contrasts dramatically with the 194 million hectares needed to produce just 87 million tonnes oil from the temperate annual oilseed crops (Oil World, 2012). Therefore, in terms of total oil yield (kernel + mesocarp oil) per hectare, oil palm is already more than 6.5-fold more efficient than the average combined yields of the temperate oilseed crops. Given the realistic prospects of further increases in palm oil yield in the next decade, the future for oil palm as a global vegetable oil crop seems even more promising during the coming years.

In addition to its high oil yield, oil palm is also a much more efficient crop that its competitors in terms of the required intensity of land management, harvesting and processing. For example, the annual oilseed crops require replanting each year which involves regular disruption of the soil structure and rhizosphere by ploughing. These crops also require a brief but intensive annual period of harvesting and processing that often must be completed in a matter of days, whatever the weather. In contrast, an oil palm can be cultivated for 20-30 years without disturbing the soil. Also, within a given plantation, harvesting and processing can take place on a continual year-round basis within a relatively predictable climatic regime that has far less seasonal fluctuation than in temperate regions.

This means that the workforce, machinery and other assets can be employed on a continuous basis throughout the year on oil palm plantations, rather than for a single intensive period as is the case for annual oil crops. To make an analogy with microbial biotechnology, oil palm husbandry resembles an efficient continuous culture system rather than the much less efficient batch-processing system represented by annual crop husbandry. As well as having a competitive edge over the temperate oilseed crops, oil palm is also more productive than other oil-bearing tree crops such as olive or coconut, which respectively yield oil at about 2.0 t ha^{-1} and 0.3 t ha^{-1}.

Clearly, therefore, oil palm is far more efficient than all other oil crops in terms of oil yield, land usage and asset deployment. This efficiency is reflected in the pricing of palm oil, which is almost invariably considerably cheaper than its rivals. For example, in November 2013, the wholesale price for palm oil was about USD 826 per tonne while the average for soyabean, sunflower and rapeseed oils was more than USD 1020 per tonne, representing a discount for palm oil of almost 20% over its major competitors (MPOB website, www.mpob.gov.my). It should be noted, however, that one of the reasons for the higher prices of rapeseed and soyabean oils (compared to palm oil) is their higher oleate content. As discussed below, the development of high oleate palm oil would greatly increase the value of the oil and should therefore be a major R&D priority for the industry.

Given its higher productivity and lower price, it is not surprising that palm oil overtook soyabean oil as the major global vegetable oil in 2007 and that it is increasingly sought after as the edible oil of choice by developing countries throughout the world. As shown in *Table 2*, palm oil production in Indonesia and Malaysia has risen steadily in response to global demand in recent years and this process shows no sign of stopping in the short- to medium-term future. Before 2005, Malaysia was the major global palm oil producer but since then it has been overtaken by Indonesia. In the six years from 2005 to 2011, Indonesia increased oil palm production by 68%, largely due to land conversion to new plantations. In contrast, Malaysia had a more modest production increase of 17% that reflected much lower rates of land conversion.

In order to position the oil palm industry to meet the ever growing requirement for its major products, it is important to understand why these oils are such desirable commodities. This information will also enable the sector to ensure that its R&D programmes are designed to optimise the delivery of the highest possible quality of oil with the minimum environmental footprint. In achieving this goal, it will be essential to satisfy consumer demands for oil functionality and also to adequately address sustainability criteria for the overall crop production and processing systems used to generate palm oil.

FURTHER INCREASES IN DEMAND FOR PALM OIL ARE INEVITABLE

At present, the major drivers for continued increases in demand for palm oil include population growth and economic development in those countries

TABLE 2. INCREASE IN PALM OIL PRODUCTION IN INDONESIA AND MALAYSIA

Year	Oil production (million tonnes)	
	Indonesia	Malaysia
2000	8.3	11.9
2001	9.2	11.9
2002	10.3	13.2
2003	12.0	13.4
2004	13.6	15.2
2005*	15.6	15.5
2006	16.6	15.3
2007	18.0	17.6
2008	20.5	17.3
2009	22.0	17.8
2010	23.6	18.2
2011	26.2	18.2
2012	28.5	18.8
2013	31.0^{+}	19.4^{+}

Note: * The year Indonesia became the largest producer. $^{+}$ Estimated value.

Source: Data from FAO (2013).

importing oil for food and, to a much lesser extent, the demand for biofuels in other countries such as the EU. The major importers of palm oil for food are in the Indian subcontinent (India, Pakistan and Bangladesh), China, and West Asia (*Table 3*). Collectively these regions import over 22 million tonnes of palm oil, which is mainly used either directly in cooking or as an ingredient in a host of processed foods. These three regional blocs account for about 75% of current imports of palm oil, the vast majority of which (85% in 2013) was obtained from the two major producing countries, namely Malaysia and Indonesia. So, why is palm oil experiencing such sustained increases in demand from these particular importing countries? The answer is mostly related to economic and demographic factors.

In terms of demography, the Indian subcontinent, China, and West Asia have all experienced rapid increases in population over the past few decades. This will obviously result in higher demands for food products in general. However, demographics are only a small part of the reasons behind the current demand for palm oil. For example, population increases have now started levelling off, especially in China, but demand for palm oil has continued to rise. This brings us to the key role of economics as a driver for increasing demand for vegetable oils and is related to a well-known correlation between per capita income and the consumption of fats and oils in the human diet.

Higher Incomes Drive Increased Demand for Edible Oils

The reason for the correlation between household income and fat consumption is that dietary fats are particularly desirable to people who have historically subsisted mainly on starch- and vegetable-based diets made up of relatively dull and tasteless foodstuffs, such as boiled rice, manioc or potatoes. The addition of fats or oils to such a diet considerably enhances nutrient content (*i.e.* the lipophilic vitamins A, D and E), and increases the calorific value of the food. The use of fats in cooking also greatly enhances the taste and odour of foods because heated fats and oils produce a complex bouquet of attractive flavour compounds, many of them volatile. Fats also solubilise, and thereby enhance, otherwise cryptic flavours that may be present in non-fatty foodstuffs (Murphy, 2007). This explains the perennial human craving for lipidic foodstuffs such as vegetable oils.

TABLE 3. MAJOR PALM OIL IMPORTERS

Country/region	Imports in 2012 (million tonnes)
Indian subcontinent*	12.6
China	6.6
European Union	5.8
West Asia+	3.2
USA	1.0

Note: * India, Pakistan and Bangladesh.
+ Egypt, Iran, United Arab Emirates, Turkey, Saudi Arabia and Iraq.

Source: Data from www.indexmundi.com

In line with this phenomenon, it was found that, following rising income levels across much of the developing world in the 1990s, vegetable oil consumption increased much faster than general food intake. For example, during the 1990s, per capita vegetable oil consumption rose by 31% in Mexico, 35% in South Africa, 64% in China, 65% in Indonesia, and 94% in India (Murphy, 2007). As people became more affluent, they switched to a more satisfying diet containing much higher amounts of oil. Interestingly, the reverse is also true and, when times are particularly hard, people tend to cut back on 'luxuries' like fats and oils. Such an effect was seen during the economic collapse that followed the fall of the Soviet Union when, between 1990 and 1994, consumption of food oil in Russia fell by 35%. As predicted by the correlation between oil and income, food oil consumption in Russia rose once again during the 2000s as the economy recovered and average incomes increased.

According to a report from the United Nations Food and Agriculture Organisation (FAQ):

'… vegetable oils and oil products still have relatively high income elasticities in the developing countries ... In our earlier projections to 2010, the per capita food consumption of all vegetable oils, oilseeds and products (expressed in oil equivalent) was projected to rise from 8.2 kg in 1988/90 to 11 kg in 2010. By 1997/99, it had grown to 9.9 kg. In the current projections, the per capita food demand for the developing countries as a whole rises further to 12.6 kg in 2015 and to nearly 15 kg by 2030. We have already noted earlier that average per capita food consumption (all food products) in developing countries may rise from the 2680 kcal of 1997/99 to 2850 kcal in 2015 and to 2980 kcal by 2030. Vegetable oils and products would contribute some 45% of this increase. This is an acceleration of the historical trend for these commodities to account for an ever-increasing part of the growth in food consumption in the developing countries. They had contributed 18% of the total increment in the decade from the mid-1970s to the mid 1980s and 27% in the subsequent decade.' (FAO, 2003).

Meeting Increasing Demands for Food Oil Should be the Top R&D Priority

The bottom line from the FAO projections quoted above is that edible vegetable oils already account for almost half of the increased food demand in developing countries and that this trend will be maintained in the next few decades. On a global basis, the annual per capita consumption of vegetable oils increased by an impressive 40% from 11.3 kg to 15.9 kg between 1997 and 2010 (Gunstone, 2011). Despite the economic slump experienced across much of Europe and North America between 2007 and 2013, many parts of Asia have continued to experience modest to good growth rates and future prospects appear promising.

We can therefore predict with some confidence that, providing Asian economies continue their current steady growth, there should be a corresponding increase in demand for vegetable oils, and particularly for oil palm, from this region and perhaps in other developing regions. In most parts of the world, palm oil is consumed as a refined product with uses varying from vanaspati/ghee in India to margarine, cooking oils, and biscuits in Europe and the United States. In contrast, in its centre of origin in West Africa, virgin red palm oil (highly enriched in carotenoids and tocopherols) is widely used in soups and baked dishes. As the increasing demand is overwhelmingly for edible oils, the palm oil sector should focus on maximising production of oils that are optimised for global food markets.

In order to satisfy these major edible markets, which include well over one billion people per day consuming palm oil products, there are two obvious targets for breeders. The first priority should be to increase the oil yield both per fruit bunch and per tree. Increased palm oil yield is urgently required to address the ever-rising global demand for edible oils. The second priority should be to maximise the oleic acid content and reduce the amount of saturated palmitic and stearic acids. Although these saturated fatty acids have some advantages in terms of producing solid fats such as margarines, they are generally regarded as nutritionally less desirable than monounsaturated oleic acid. This is one of the main reasons why existing high oleic acid commodity vegetable oils, such as rapeseed, command a price premium over palm oil as edible feedstocks. High oleic oils have the additional advantage that they can also be used as highly versatile raw materials for production of a wide range of renewable and biodegradable oleochemicals and other industrial products (Murphy, 2010).

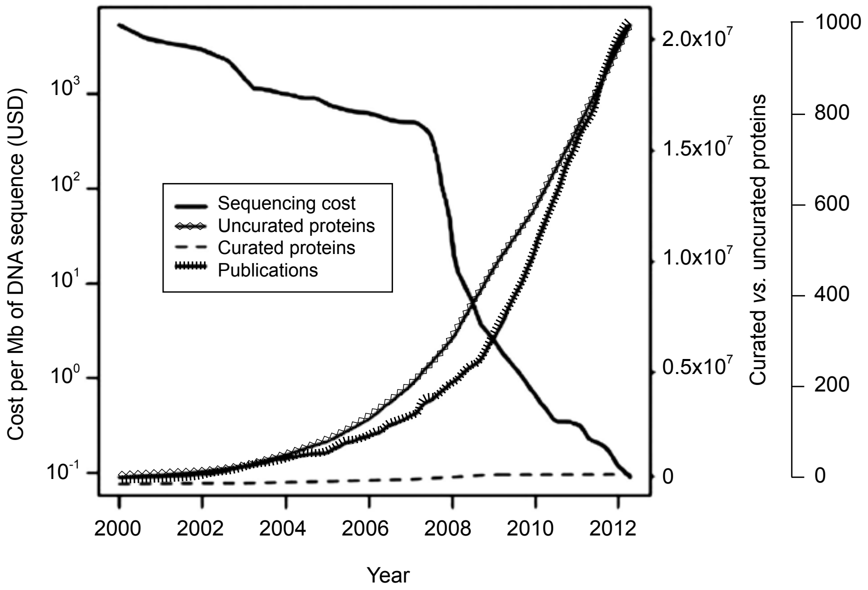
BIOLOGICAL TECHNOLOGIES FOR OIL PALM IMPROVEMENT

The last few decades have witnessed huge advances in our understanding of plant biology and in the development of new technologies for the manipulation of plants for human benefit. The application of relatively straightforward breeding and selection methods were behind the 'Green Revolution' of the 1960s and 1970s that effectively doubled or trebled food production in much of the world and averted mass famine in Asia. During the 1980s and 1990s, more complex methods such as hybrid creation, assisted crosses and introgression of wild germplasm were instrumental in enabling rice yield to increase five-fold in some regions. The so-called 'miracle rice' that yields as much as 10 t ha^{-1} has enabled China to become largely self sufficient in grain crops and also laid the foundations of its recent economic advancement. During the 2000s, much attention has been focussed on genomic approaches to plant breeding with the deployment of a new generation of technologies, such as marker-assisted selection, next-generation sequencing, transgenesis (genetic engineering or GM) and automatic mutagenesis/selection (TILLING, TargetIng Local Lesions IN Genomes) (Murphy, 2011; Soh, 2011; Xu, 2010). These methods have great potential for oil palm improvement, as we will now discuss.

Sequencing the Oil Palm Genomes

Probably the most dramatic example of technology improvement in the 21st century has been in DNA sequencing where the cost per base has decreased by an amazing 100 000-fold since 2000, as shown in *Figure 1* (Mardis, 2008; Shendure and Ji, 2008). The first plant genome to be fully sequenced was the model species, *Arabidopsis thaliana,* published in 2001, while the first crop genome was rice, where a high quality sequence was published in 2005. The sequencing of the much larger maize genome required a massive effort by company and public laboratories and the results were published in a series of papers in 2009. Other large-scale projects are currently underway for developing country crops such as sorghum and foxtail millet and sequence data are now being publicly released at an increasingly rapid pace. Advances in next generation sequencing technologies are enabling the genomes of even comparatively minor crops to be characterised (Edwards and Batley, 2010).

In some cases, a single sequencing method has been used but, more commonly, several technologies are used in combination for best results. For example, Roche 454 technology was used to sequence the 430 Mb genome of cocoa, *Theobroma cacao*, and the 1700 Mb genome of oil palm. In contrast, a combination of Sanger and Roche 454 sequencing was used for the apple and grape (500 Mb) genomes. A combination of Illumina Solexa and Roche 454 sequencing was used for the genomes of polyploid cotton. Roche 454 sequencing has been used for Miscanthus, while Sanger, Illumina Solexa, and Roche 454 sequencing are being used for banana. Illumina GAII sequencing has been used for the *Brassica rapa* genome, while Sanger and Illumina Solexa technologies were used for the cucumber genome. The cheapness and speed



Source: Data from Pubmed and NCBI.

Figure 1. Decreasing DNA sequencing costs over the past decade has been mirrored by a huge increase in the proportion of uncurated proteins in public databases. Since the early 2000s, the cost of sequencing genomes has plummeted by more than four orders of magnitude. This has created a glut of raw data, much of which has yet to be curated in terms of definite identification of functional genes and proteins. By 2012, for each curated protein sequence in public databases there were several million uncurated sequences.

of genome sequencing is now making it possible to sequence, not just a single reference genome for each species, but many individual genomes in a population. This approach will be used to uncover genome-wide variations that underlie some of the more complex developmental and agronomic traits in crops such as oil palm (Cook and Varshney, 2010; Murphy, 2011; Paterson *et al*., 2010).

Although sequencing costs have fallen dramatically in recent years, the initial sequencing and basic annotation of a relatively large genome such as that of oil palm still amounted to several million US dollars during the period 2007-2010 when much of the basic data were compiled. In the case of most large crop or animal genomes, sequencing has been carried out by public/private consortia that include technology providers and potential end-users. Unfortunately for researchers in general, in a few cases the same crop genomes have been sequenced multiple times by different commercial groups who have not released their data. The sequencing of the oil palm genome is an example of this latter phenomenon. While such a duplication of effort and an unwillingness to share the data publicly may be based on sound commercial factors in the short-term, it nevertheless arguably represents a failure in strategic vision for the industry as a whole. This is because DNA sequence data on their own have little value and even relatively basic tools for their assembly into a recognisable annotated genome are still under development. Therefore, it is normally most effective in terms of rapid exploitation to release sequence data as a public resource that can then be mined by large numbers of researchers across the world as a specialised form of 'crowd sourcing'.

In the case of oil palm genome, in May 2008, the Asiatic Centre for Genome Technology (ACGT – a subsidiary of Genting Berhad), in collaboration with Synthetic Genomics (whose CEO, Craig Ventor, led part of the human genome sequencing effort), announced completion of the first draft sequence. However, the data were not released and no details of the work were published in the scientific literature. A year later in May 2009, Sime Darby Plantation Sdn Bhd announced sequencing and annotation of about 94% of a different oil palm genome. Once again very few technical details were released and none of the data were made available in the public domain. The Sime Darby-led project also involved an international consortium that included a bioinformatics company, Synamatix Sdn Bhd and a US technology provider, 454 Life Sciences (a Roche company). The third oil palm sequence announcement came in November 2009 when a consortium led by the publicly funded Malaysian Palm Oil Board (MPOB) and the US private company, Orion Genomics, reported that three genomes had been sequenced from the two oil palm species, *E. guineensis* and *E. oleifera* (Meerow *et al*., 2012).

Happily for oil palm researchers, the MPOB/Orion-led consortium has now published an account of their genomic sequences in the journal *Nature* in July 2013 (Singh *et al.,* 2013a). These sequences are available for breeders and other scientists to study and use for the benefit of crop R&D (data are deposited at DDBJ/EMBL/GenBank under the accessions ASJS00000000 for *E. guineensis* and ASIR00000000 for *E. oleifera*). This landmark article was accompanied by another equally significant paper that described the identification of a single gene, called *Shell*, which was found to regulate the *tenera* trait of fruit shell thickness (Singh *et al.,* 2013b). The *tenera* trait is found in hybrids between naturally occurring *dura* (thick shelled) and *pisifera* (non-shelled) fruit forms of oil palm. The *dura* fruits have low oil yields and *pisifera* fruits are normally female-sterile but the *tenera* hybrids are fertile, high oil yielding plants that are now the basis for all commercial oil palm production in South-east Asia. Identification of the *Shell* gene will enable breeders to use molecular markers to select suitable breeding lines, instead of waiting three to four years or more for the young plants to produce fruits for selection via a visual phenotype.

Beyond the Genome: Other ´Omic Technologies

In order to move beyond gene composition through to gene expression, protein function and their ultimate manifestations as phenotypes in an organism, it is often necessary to analyse structural and functional molecules, such as proteins, membrane lipids, and carbohydrates in particular plant cells or tissues. At a more detailed level, there are many thousands of smaller metabolites whose composition differs greatly according to tissue, developmental stage, and in response to environmental conditions. The ability to simultaneously analyse large numbers of often complex molecules is the basis of the so-called ´omic technologies. Hence, transcriptomics is the analysis of transcribed genes in the form of mRNA; proteomics is the analysis of protein composition; lipidomics is the analysis of lipid composition; metabolomics is the analysis of small metabolites, and so on. Several automated analytical techniques have been developed to separate and identify each of these classes of biomolecules.

The transcriptome is a comprehensive list of the genes expressed in a particular tissue at a particular stage of development and/or in response to particular environmental stimuli. In many ways, transcriptome sequences can be much more useful than genome sequences because they only include the particular fraction of the tens of thousands of genes that are expressed under specific conditions. In the case of oil palm, the analysis of the fruit transcriptome during oil accumulation is already proving very useful in identifying key genes that may regulate this vital process (Bourgis *et al*., 2011; Dussert *et al*., 2013; Tranbarger *et al*., 2011). In two other studies, transcriptome data from normal and mantled oil palm fruits have been compiled to shed light on this abnormality which still plagues micropropagation of the crop (Shearman *et al*., 2013) while a similar approach has been used to study somatic embryogenesis (Lin *et al.,* 2009).

The metabolome is the complete list of metabolites found in a particular organelle, cell, or tissue under a specific set of conditions. The identification of important plant metabolites in a plant such as oil palm, which include carotenoids, phenols, and fatty acyl components, used to be a very slow process relying on bulky, expensive equipment that could only be operated by a few skilled specialists. However, new lightweight devices, supplemented by robotic and informatics approaches, now make it possible to automate the process and even to assign accurate identities to complex mixtures of such molecules.

Metabolome analysis can help uncover the details of oil palm fruit or leaf development at a molecular level (Neoh *et al*., 2013; Teh *et al*., 2013; Tahir *et al*., 2013). Metabolome studies can also indicate how plants are reacting at the molecular level to specific stimuli, *e.g*. by comparing stressed and unstressed plants we can gain important information about how some plants can tolerate certain stresses while others cannot. In other cases, metabolome analysis can give useful information about molecular changes caused by the addition of transgenes to plants. This kind of analysis is often used as part of the process of regulation of transgenic crops where it may be necessary to test whether a transgenic variety is 'substantially equivalent' to non-transformed varieties of the same crop (Beale *et al*., 2009).

The proteome is defined as the expressed protein complement of an organism, tissue, cell or subcellular region (such as an organelle) at a specified stage of development and/or under a particular set of environmental conditions. Perhaps the most important molecules in cells are the proteins, some of which are structural while many others act as enzymes responsible for the biosynthesis of most of the other molecules in a cell. Proteins are the direct products of gene expression and the timing and spatial distribution of their accumulation and function results in the phenotype of a particular organism. However, patterns of gene expression as measured by transcription, *i.e*. the formation of mRNA, are not always reflected by patterns of accumulation or activity of the corresponding proteins.

In some cases, the mRNA may not be efficiently translated to protein. In other cases, the protein might be synthesised but is then either broken down or remains inactive. A protein might be present in a cell but is inactive due to incomplete post-translational processing, *e.g.* failure to bind a ligand, or due to inhibition, *e.g.* by phosphorylation. There are many examples where proteins might be present in a cell but remain in an inactivated state until they are activated by a specific stimulus. In such cases, both transcriptome and proteome data would indicate that the gene was active and the protein was being synthesised but this would be misleading in terms of function if the protein was not active. Ideally, the information in the proteome should therefore include any post-translational processing undergone by each protein analysed. The 1st-generation proteomics was mainly concerned with identifying the gross protein composition of samples, but new-generation technologies are beginning to focus on questions such as post-translational processing and the biological activities of such proteins (Murphy, 2011). Despite these advances, it remains a significant challenge to identify which proteins within a given proteome are partially or completely functionally active.

It is only by addressing these latter questions that we can verify not only that a particular protein has been synthesised and is in the right location, but also that it has the appropriate biological function. Therefore, we can learn a lot about the actual function of a genome in a specific cell or tissue by examining its proteome. Like the metabolome, the proteome in a plant sample can vary greatly according to genotype, tissue location, developmental stage, and environmental conditions (Gómez-Vidal *et al.*, 2009; Zamri, 2013). The full proteome will comprise thousands of proteins, some of which may be present in high abundance while others are at very low levels. The analysis of low-abundance proteins poses considerable difficulties for proteomics that have yet to be resolved but given the rate of progress it is likely that automated or semi-automated methods will be developed for the near-complete description of the oil palm proteome in the not too distant future.

Bioinformatics

Bioinformatics is a relatively new discipline that brings together biologists, mathematicians and computer scientists to make sense of the avalanche of data generated by genome sequencing and profiling programmes; and from the other ´omic technologies described above (Kanehisa and Bork, 2003). The sheer volume of data generated by these methods often makes it virtually impossible to analyse raw results manually. For example, a next-generation DNA sequencer can generate thousands of sequence fragments making up millions of base pair readouts per day. These fragments need to be analysed for overlaps and then assembled into 'contigs', or continuous sequences of many fragments that will eventually be collated to make up an entire chromosome. This process is now done automatically using algorithms, or repetitive step-by-step mathematical procedures.

Other algorithms are used in genome annotation. This involves the identification of putative genes, including their promoters, regulatory elements, introns, exons, and mRNA/protein products. Other software can detect possible regions encoding small, non-coding RNA and specific repetitive elements in genome sequences. Such sequences are now known to play important roles in several aspects of genome function in complex eukaryotes such as higher plants and animals (López-Flores and Garrido-Ramos, 2012; van Wolfswinkel and Ketting, 2011). Software is also used to drive robotic and other automated systems used in tasks such as mass-profiling of large populations. Advances that enable non-specialists to use sophisticated software have been facilitated by improved computing technology and more powerful linked networks. This has been especially crucial in enabling massive amounts of data, often measured in many terabytes (10^{12} bytes), that are generated by some of the new technologies. For example, a single 2 hr run on an Illumina GAII DNA sequencer can generate 10 terabytes of data.

One potential problem here is that the vast amounts of raw data generated by DNA sequencers are beyond the ability of many laboratories, or even companies, to archive. Therefore, the raw data are often immediately processed by proprietorial software developed by instrument manufacturers and only the much-reduced processed data are saved. Even with the most advanced computing technology, the costs of storing the original raw data can be greater than the cost of repeating the entire sequencing run. Another challenge for future software development is to improve the assembly of processed sequence data for the increasingly diverse applications required by researchers. To address this, new forms of open-source bioinformatics software, such as SOLiD, are being developed where members of the community can adapt and improve software tools to fit their own applications.

One of the challenges with the automatic annotation and public release of genomic data can be the lack of quality control mechanisms that ideally require the intervention of human experts. There are now many hundreds of publicly accessible genomes that have already been annotated, sometimes by older methods that have now been greatly improved upon. In some cases, different laboratories use different algorithms for annotation, which can complicate cross-genome comparisons. Ideally more generic tools should be developed and some degree of editing or re-annotation made possible as improved methods are invented. For example, in a collaboration with Fujitsu, we have recently developed an improved tool called *cisExpress* for the detection of specific motifs in genome sequences (Tříska *et al.*, 2013). We have also publicly released the tool at www.cisexpress.org where it is available as a stand-alone open-source application or via a web interface.

In the future it will be desirable for bioinformatics researchers to work closely with biologists to develop a wider range of broadly applicable tools for the extraction of useful information from the various 'omics databases related to oil palm. As this is pre-competitive research, both the databases and analytical tools such as algorithms should ideally reside in the public domain as open-source products. The magnitude of this problem is demonstrated in *Figure 1*, which shows how the massive decrease in sequencing costs has resulted in an avalanche of gene and protein sequence data in public repositories. However, there are currently more than one million uncurated protein sequences for each curated sequence. Clearly, there is an urgent need to curate and validate many more genes and proteins in these databases.

A major aspect of the usefulness of public databases is the ability of the entire research community to access and curate their contents at a level of detail impossible in a non-public resource as shown in the following example. Many DNA sequencing projects are now performed in specialist commercial laboratories where tissues from several different sources may be being analysed at the same time, with the obvious potential for cross contamination. The result of such contamination might be the erroneous inclusion in a genomic database of a DNA sequence from a different organism. Unfortunately, this is not always easy to detect because, as we are increasingly recognising, naturally occurring horizontal gene transfer between unrelated organisms is much more common than previously suspected (Boto, 2010; Keeling and Palmer, 2008). There are now numerous examples of genes originating from animals, fungi and bacteria being found in some plant genomes (Bock, 2009). However, it can also be the case that an anomalous DNA sequence may be present in a genomic database due to human error or contamination rather than as a result of horizontal gene transfer.

For example, during an analysis of a public database, I was initially intrigued to discover a plant-like gene in the genome of a tick and the possible implication that the gene had been somehow transferred from a plant to an animal. However, further investigation showed that this gene was identical to that of a lipid peroxygenase gene in a plant genome that was being sequenced in the same laboratory as the tick genome. Therefore the 'tick' peroxygenase gene was not another example of horizontal gene transfer but rather was the result of contamination of the tick DNA by plant DNA followed by their mistaken inclusion in the same genomic database. Luckily, we were able to resolve this particular case of mis-annotation but it is likely that there are similar examples in genome databases. One study of protein sequences in public databases found surprisingly high levels of mis-annotation that averaged 5%-63% across the six superfamilies (Schones *et al.*, 2005). This is one of the many reasons why it is beneficial for genomic data to be made publicly available in such a way that the research community as a whole can help to improve the quality of the data and the accuracy of its annotation.

Marker-assisted Selection (MAS)

Several types of genetic marker can be used to assist the selection of favourable traits in plant breeding. Morphological and biochemical markers, such as fruit colour, fatty acid composition, or dwarfism, are relatively easy to observe or measure but many other key agronomic traits such as disease resistance are not so easily assessed in this way. By far the most useful class of genetic markers are those based on DNA sequences. Such markers are now being applied to almost every aspect of plant and animal breeding, and also in medicine, basic research and even in forensic science. The use of modern techniques like association genetics and quantitative trait loci (QTL) analysis are enabling chromosomal regions and individual genes involved in the regulation of important traits to be mapped and identified (Rafalski, 2010; Xu, 2010). These methods have recently been used to map the lipase gene involved in oil deterioration in ripe palm fruits (Morcillo *et al*., 2013) and QTL analysis of genes regulating the fatty acid composition of palm oil (Montoya *et al*., 2013).

DNA-based MAS can save time and money in crop breeding programmes as follows. In order to select most characters of interest, it is normally necessary to grow up and analyse each new generation of the crop before it is possible to perform phenotypic selection of appropriate plants. Many traits, such as disease resistance or salt-tolerance cannot be measured until plants have been grown, often to full maturity, and then tested in the field. A DNA-based molecular marker is used to identify a segment of genomic DNA within which allelic variation in sequence has allowed its location to be genetically mapped. In breeding programmes, such markers are chosen because of their close proximity to a gene of interest so that the marker and target gene are inherited together. This enables breeders to use the marker as a relatively straightforward way of screening very large populations for the presence of a target gene without needing to perform complex phenotypic tests. Hence, MAS can be used to track the presence of useful characters in large segregating populations in crop-breeding programmes. Using molecular markers, breeders can screen many more plants at a very early stage and save several years of laborious work in the development of a new crop variety.

This is especially useful for crops like oil palm where it can take three to four years or more for a fruit phenotype to become fully apparent. Molecular markers have now been developed for most of the major commercial crops, including several tree species. In addition to their increasingly prominent role in genetic improvement of crops, molecular markers are useful for many other applications such as characterising crop genetic resources, management of gene banks, and disease diagnosis. At present, MAS systems are being developed for oil palm by several international public-private partnerships (PPP) and comprehensive genetic and physical maps of the genome are now available. Genetic maps have recently been used to localise oil palm genes involved in the regulation of important traits such as fatty acid composition (Singh *et al*., 2009; Montoya *et al*., 2013), embryogenesis and callogenesis (2013), seed coat thickness (Singh, 2013b).

Several types of DNA-based marker have been developed for basic research and plant breeding and these are constantly being refined to increase their utility and decrease costs. Early markers included RFLP (restriction fragment length polymorphisms), AFLP (amplified fragment length polymorphisms), and RAPD (random amplified polymorphic DNA). More recently, MAS has used much cheaper and more informative PCR-generated markers, such as microsatellites and SNP (single nucleotide polymorphisms). Microsatellites are short sequences of repetitive DNA, such as poly(TG), that can be amplified using PCR: they are highly polymorphic with respect to the numbers of the repeat units between individuals in a population. Even in relatively inbred crop species, microsatellites are polymorphic, enabling individuals to be genotyped separately. Detailed genetic maps based on microsatellites are available for most major crop species. Some of the most useful markers are SNP. SNP occur very frequently in genomes, *e.g*. once every 60-120 bp in maize, and are used widely both for research and breeding.

The use of MAS in crop breeding was initially restricted to a few economically important temperate crops that are bred and marketed by major private sector firms, but the list of MAS-enabled crops is expanding. As well as annual crops such as cereals and legumes, MAS has been useful in perennial crops, including subsistence and cash crops in developing countries. Examples include oil palm, coconut, coffee, tea, cocoa, and tropical fruit trees such as bananas and mangoes. MAS technologies have also benefited from more efficient screening methods including PCR, DNA/DNA hybridisation, and DNA sequencing. Most MAS technologies in crops now use PCR-based methods, such as sequence-tagged microsatellites and SNP. By using DNA markers in conjunction with other new breeding technologies like clonal propagation, it should be possible to make rapid strides in the creation and cultivation of greatly improved varieties of crops like oil palm.

Transgenic Technologies

Numerous high-tech breeding tools have been successfully used for crop improvement over the past 50 years. Transgenic technologies have been available since the 1880s and enable breeders to manipulate genomes using recombinant DNA methods that are continually being improved and refined. It is important to realise that breeders never employ transgenesis on its own; instead it is used in combination with technologies such as tissue culture/regeneration, hybrid creation, mutagenesis, backcrossing, and MAS. This means that it can be misleading to speak of a new crop variety as 'transgenic' or 'GM' as if it had only been created using transgenic technologies. In reality, the transgenic or GM stage is just one part of the initial creation of new genetic diversity at the beginning of the breeding process. After this initial stage, there are many other non-GM stages required before the plants can be used in agriculture. Hence, in 2012 about 180 million hectares was reported as being planted with transgenic/GM crops around the world. It is estimated that the total global land area used for crop production is about 1500 million hectares (Thenkabail *et al*., 2010), which means that transgenic crops already occupy 12% of total arable area (*Table 4*). However, each of these crops has also benefited from one or more of the non-transgenic technologies listed above. For example, well over three-quarters of all crops grown, including almost all transgenic varieties, have resulted from some form of conventional hybridisation and backcrossing.

Despite the fact that transgenesis is simply one of several alternative strategies for variation enhancement in breeding programmes, the resultant plants are treated very differently from almost-identical non-transgenic varieties by government agencies and by sections of the general public. Transgenic varieties have a different legal status and are subject to much more complex regulatory systems in various regions of the world, which can hinder their development and uptake. Indeed transgenic crops are even banned or heavily restricted in some countries. For this reason, we need to look at the development of transgene technology in a different way to other technologies. As we will see below, some developments such as so-called 'clean gene' technologies are aimed more at satisfying generalised public concerns rather than addressing proven safety issues or wider aspects of crop improvement *per se*.

TABLE 4. MAJOR GLOBAL TRANSGENIC CROPS AND TRAITS IN 2012

Crop	Area (million hectares)	%
Soyabean	83	50
Maize	55	31
Cotton	21	14
Rapeseed/canola	8	5
Sugar beet	0.5	<1
Alfalfa	0.1	<1
Others	<0.1	<1
Total	170.3	100

Trait	Area (million tonnes)	%
Herbicide tolerance	100	60
Insect resistance (Bt)	28	18
Herbicide tolerance + Insect resistance	43.7	22 25
Others	<0.1	<1
Total	170.3	100

Source: Data from James (2012). Global status of commercialised biotech/GM crops: 2012. ISAAA Brief 44. http://www.isaaa.org/resources/publications/briefs/44/default.asp

There are several ways in which transgene technology can be improved to make it technically easier, more efficient, wider in its scope, and better able to address concerns expressed by certain sections of the public. Some technical issues and areas of public concern are listed below:

- in the future, it will be desirable to generate transgenic crops that do not contain selection markers, such as genes for antibiotic or herbicide tolerance;
- until now transgenic plants have been created using random insertion of transgenes, which can lead to variations in transgene behaviour and other unpredictable pleiotropic effects. In order to achieve stable and predictable transgene expression under a variety of field conditions, transgene introduction technologies need improvement;
- the spread of transgenes into wild populations via cross pollination can be prevented using genetic use restriction technologies (GURT); and
- biocontainment strategies should be incorporated into certain types of transgenic plants, *e.g.* expressing non-edible or pharmaceutical products to prevent risk of contamination of human or animal food/feed chains.

The development of transgenic oil palm is still in its infancy and is fraught with many technical challenges. For example, it is still unclear whether biolistics or *Agrobacterium*-mediated gene transfer will be the gene delivery method of choice (Izawati *et al*., 2012; Parveez and Bahariah, 2012). The choice of plant material is also crucial with some of the best options including various types of callus culture. Then there is the issue of which gene promoters to use. Unlike most existing commercial transgenic crops where constitutive viral promoters are used, the manipulation of palm oil composition will require deployment of strong mesocarp-specific or kernel-specific gene promoters, ideally sourced from the oil palm genome itself. Also, in order to achieve a high oleic oil, it will probably be necessary to down-regulate some genes while adding or up-regulating other genes. Even when the primary transgenic plantlets have been produced they will still need to be grown on for three to five years to obtain fruits that can be screened for oil content. Finally, these primary transformants will need to be taken through several sexual generations, backcrossed with existing elite lines, and then multiplied via micropropagation before any new commercial transgenic varieties can be released.

It is likely that this process of transforming oil palm will take several decades. However, it is still important that such programmes are continued for the long-term future of crop improvement. This is because there may be traits that are not possible to create using non-transgenic approaches. For example, although it may be possible to create a medium-high (55%-65%) oleic oil phenotype via conventional methods, a more desirable ultra-high (80%-90%) oleic trait might only be possible via transgenic technology. Another example where the use of transgenic methods is essential is the production of completely novel compounds, such as biopolymers like polyhydroxyalkanoates, in oil palm. In this case, it is necessary to transfer several bacterial genes to the crop. Meanwhile, newer technologies such as RNAi, trait stacking, chromosome engineering, pathway engineering and more efficient gene cassettes will play important roles in expanding the scope of transgenic crops in the future.

SOME KEY TARGETS FOR BIOLOGICAL IMPROVEMENT OF OIL PALM

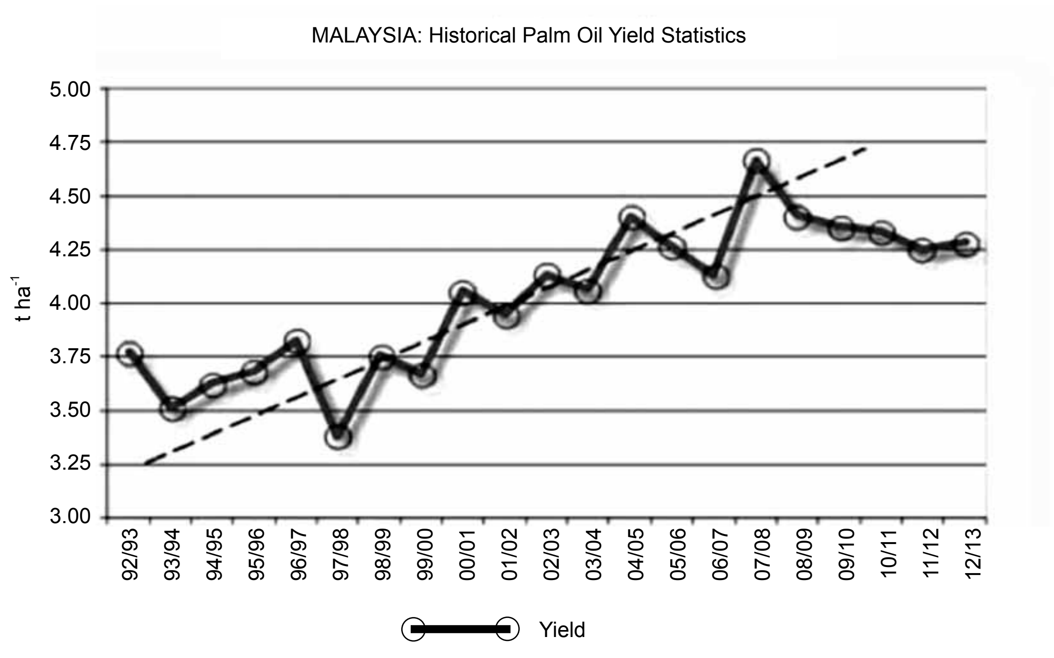
The biology of a long-lived crop such as oil palm is a complex topic with many fascinating aspects relating to its ecology, physiology and agronomy. The large size and long generation time of oil palm create many formidable challenges for researchers and breeders, especially in comparison with the much smaller annual oilseed crops like rapeseed or soyabean. It is therefore essential that biological approaches to oil palm improvement focus on a limited number of key target traits. As discussed below, by far the most important biological traits relate to overall oil yield and quality, together with tolerance to pests and diseases. The role of improved farming practices is discussed under crop management in the Role of Improved Management in Addressing Challenges for Oil Palm section.

Oil Yield

The relatively poor yield of palm oil in commercial and smallholder plantations compared to the proven potential yield of some existing varieties, coupled with the lack of progress in improving this situation over the past decade, has attracted much comment in the industry and more widely (USDA, 2012). In Malaysia, for example, oil palm yields actually declined between 2008 and 2012 to levels that were 9% below the 4.7 t ha^{-1} achieved in 2008 (*Figure 2*). In contrast, yields of most major commercial crops have experienced steady and sustained increases in the region of 1%-2% per year, over the past 20-30 years. To a considerable extent, this situation is the result of a failure to replant new or ageing plantations with the best available varieties. However, there is also immense and largely untapped scope for far greater increases in oil yield via modern breeding methods. If new oil palm varieties producing 10-20 t ha^{-1} oil become widely available this would be an enormous incentive for the industry to accelerate its sluggish replanting programme.

Palm oil yield in the plant is primarily determined by biological factors such as crop genetics and the incidence of pests and diseases. It is known from the study of other crops that the overall yield of a key crop product such as starch, oil or protein can be manipulated in several ways. The most direct route is to select plants where their biosynthetic pathways are more efficient at making the desired end product at the expense of other less desirable products. In the case of oil-bearing seeds or fruits this means a greater flux of carbon towards oil and reduced flux towards other less useful products such as starch or fibre (Rahman *et al*., 2013). Genetic loci that regulate much of the flux of carbon towards oil in soyabean have been described (Chung *et al*., 2003). Recent advances in genomics and biochemistry have identified regulatory genes such as WRI1 that are able to massively up-regulate oil accumulation, even in tissues such as leaves that do not normally accumulate high levels of storage lipids (Bourgis *et al*., 2011; Ma *et al*., 2013). The continued scope for dramatic increases in oil yield even in established oil crops has been highlighted by the recent discovery of rapeseed varieties that accumulate almost 65% w/w oil in their seeds compared to about 45% or less in most commercial varieties – a yield gain of about 44% (Hu *et al*., 2013).

Although palm fruits are considered as relatively enriched in oil, a freshly picked ripe fruit bunch only contains about 21%-23% w/w oil. In contrast, mature oilseeds typically contain 40%-46% w/w oil while some oil-rich nut crops contain as much as 75% w/w oil (Murphy, 2010). The other major oil-rich drupe



Source: Data from USDA (2012).

Figure 2. After a period of stagnation in the mid 1990s, palm oil yields gradually rose from 1998 until 2008 but then declined from 2008 until 2013. There are probably several causes for the recent decline, including failure to replant ageing plantations, conversion of new land in East Malaysia, and labour issues as discussed in the main text.

crop is olive, where the oil content of the whole fruit is generally in the range of 18%-28% w/w, although some varieties can accumulate as much as 34% w/w oil. Avocados can accumulate between 5% and 30% of fruit weight as oil. This indicates that it may be possible to create new varieties of oil palm that accumulate much higher levels of oil – possibly in the region of 30%-40%, which would be double the current oil yield per fruit. The recent publication of the annotated genomic sequences of several oil palms (Singh, 2013) and several biochemical, transcriptome and molecular mapping analyses of palm fruits (Bourgis *et al*., 2011; Dussert *et al*., 2013; Montoya *et al*., 2013; Morcillo *et al*., 2013; Ramli *et al*., 2009) have laid the foundations for identification and manipulation of the regulatory genes that may facilitate the creation of much higher levels of oil in palm fruit tissues in the foreseeable future.

One possible way of increasing palm oil yield is to channel more carbon towards lipid biosynthesis, and less towards other less valuable end products such as starch or lignin. At present, a typical mature oil palm of around 10-15 years of age is a relatively tall plant with the fruit bunches produced at the top of a trunk about 10 m above the ground. There are three major problems with this form of plant architecture. Firstly, the majority of the carbon assimilated via photosynthesis is used to produce a lignified trunk that has relatively little economic value. The much more valuable fruit oil therefore only represents a small fraction of the total crop biomass. Secondly, it is difficult and laborious to harvest the fruits from such a height and there can be much loss of yield due to spoilage when fruits fall onto the ground. Finally, the height of the fruit bunches makes it difficult to inspect them closely for signs of pest and diseases or to assess the degree of ripening.

In many other crops, ranging from annual cereals to perennial orchard fruits, the manipulation of plant architecture has already resulted in greatly increased yield. Probably the most dramatic example of this is the creation of semi-dwarf varieties of the major cereal crops such as wheat, rice and barley in the 20th century (Murphy, 2011). These dwarf varieties are typically only 20%-40% as tall as traditional varieties and much of the carbon saved in producing a shorter stem is used instead to form more grain. The genetic basis of the dwarf phenotype is now known to be associated with disruption of action of the hormone gibberellin, which normally causes stem elongation. Oil palms can also produce short phenotypes and the use of modern molecular breeding approaches may make it possible to select dwarf trees that have higher yields of oil-bearing fruits.

Similar modifications of tree crop architecture have already been achieved in the case of several hard-fruit species of which the most dramatic example is apples. Traditional apples were grown in orchard plantations as medium sized bushy trees that could reach 20 m in height. Fruit picking was difficult and most of the biomass of the crop was in the form of wood rather than fruits. A combination of genetic selection and careful pruning has now transformed these trees into much smaller, 1-3 m tall, vine-like plants that produce much higher fruit yields and much less wood. A further bonus is that in many cases these short plants can now be harvested mechanically which saves greatly in terms of labour costs and fruit spoilage. Mechanisation of fruit harvesting has also been successfully developed in citrus crops (Murphy, 2011) and several systems are under development for date palms. The development of high-yielding dwarf oil palm varieties could open the door to full scale mechanisation of harvesting in plantations. This would save costs and would greatly alleviate the increasingly problematic labour issues confronting the industry as discussed below in the Labour Issue section.

Oil Composition

Palm mesocarp oil typically contains about 35%-40% oleic acid plus 40%-50% palmitic and about 10% linoleic acids. By far the most important quality trait target for oil palm breeding is a much higher oleic acid composition in the mesocarp oil. This would open up new markets for edible palm oil and could eventually lead to the displacement of existing less efficient high oleic oilseeds such as soyabean, rapeseed and sunflower. There are several precedents for the creation of completely new market opportunities by breeding high oleic varieties of oil crops. Perhaps the most dramatic example is that of rapeseed, which like other brassica oilseeds, such as mustard and crambe, historically produced a seed oil that consisted of >50% erucic acid. While erucic acid can be used in some food applications, several studies claimed that its consumption by rats was associated with cancers and in the 1960s rapeseed oil was banned from use in the USA. This led Canadian breeders to develop new rapeseed varieties with 60%-65% oleic acid and very low levels of erucic acid. These new forms of high oleic rapeseed were called 'canola' and soon dominated the market, creating an entirely new multi-billion dollar export crop for Canada and a new relatively cheap and nutritious vegetable oil for consumers around the world (Murphy, 2007).

The new canola varieties were the result of naturally occurring mutations that inactivated the fatty acid elongase system responsible for converting C18:1 oleic acid to C22:1 erucic acid. In order to isolate and characterise these mutants, many thousands of seeds from diverse accessions were laboriously screened in a process that took almost a decade. A similar approach was used to screen seeds of sunflower, which normally contain high levels of the polyunsaturate, linoleic acid (C18:2). In a few cases, mutated sunflower seeds were found where inactivation of oleate desaturase genes resulted in a greatly reduced ability to form linoleic acid and the accumulation instead of an oil containing 60%-75% oleic acid. In other cases, induced mutagenesis has been used to create new genetic variation in seed oil content. For example, this mutagenesis approach was used to develop high oleic versions of linseed where the seed-specific desaturases responsible for converting C18:1 oleic acid to C18:3 linolenic acid were inactivated by several mutations (Murphy, 2007).

More recently, similar conventional (*i.e.* non-transgenic) breeding approaches have led to the development of very high oleic oils such as rapeseed/canola with 75%; soyabean with 83%; sunflower with 80%-90%; safflower with 75%; and olive with 75% oleate. The use of induced mutagenesis in crop breeding, including fatty acid manipulation, has recently been made much more effective by the automated mutagenesis/selection system termed TILLING (Murphy, 2011; Shu, 2009; Xu, 2010). In other cases, transgenic (GM) approaches have been used by commercial companies to produce very high oleate and low polyunsaturate varieties of some of the major annual oilseed crops. Examples include rapeseed/canola (89% oleate); Indian mustard (73% oleate); soyabean (90% oleate); and cottonseed (78% oleate). These transgenic lines are based on antisense or RNAi technologies and several other gene deletion technologies with potential use in oil palm are also under development (Murphy, 2011).

In principle, all of the above approaches can be used to create high oleic varieties of oil palm. Major challenges for palm breeders include the long generation time of this tree crop, a lack of genetic variation for oleate content, and developing the ability to use modern high-tech approaches such as TILLING and MAS. To some extent, the genetic variation issue is being addressed by extensive searches by MPOB and various plantation companies for new germplasm in the oil palm centres of origin in West Africa and South America. Already some accessions have been found with oil contents of 50%-60% oleic acid, which is very promising for introgression into current commercial varieties. Perhaps more interestingly, this medium to high oleic material can now be analysed by modern genomic, transcriptomic and proteomic methods to elucidate the genetic and biochemical basis behind the accumulation of higher levels of oleic acid in mesocarp oil. Such knowledge would provide targets for future attempts to engineer fatty acid and oil metabolism so that palmitate was more effectively elongated to stearate, desaturated to oleate, and then transferred to glycerol to form the triacylglycerol-rich mesocarp oil.

Pest and Disease Tolerance

Oil palm has numerous pests and diseases in the major centres of cultivation in South-east Asia but two of the most important are the fungal pathogen, *Ganoderma boninense*, and the rhinoceros beetle, *Oryctes rhinoceros*, which can cause yield losses well in excess of 50% in affected areas (Flood and Bridge, 2000; Panchal and Bridge, 2005; Flood *et al*., 2010). In terms of long-term management of these and other harmful organisms, it is generally more effective to enable the crop to tolerate small levels of infection/infestation rather than to aim at total eradication. The problem with selecting for complete resistance, rather than tolerance to pests and pathogens, is that it leads to high selection pressures for the emergence of new variants of the pest/pathogen that can overcome the resistance in the crop. Over recent decades we have seen the emergence of numerous new strains of pest/pathogen that have overcome crop resistance and therefore pose serious threats to major food crops such as wheat and rice.

G. boninense is a soil-borne fungus that causes basal stem rot and has become an increasingly serious problem especially in areas where palm plantations have been present for many decades. In the past, research on *Ganoderma* has been hampered by its genetic and morphological variability, but the use of biochemical and molecular genetic markers has now greatly improved the identification and localisation of the more virulent strains (Bridge *et al*., 2000). More recently a joint Malaysian/US programme has started to sequence the genomes of several virulent and non-virulent strains of *Ganoderma*. This should help greatly in the identification of genes related to virulence and help breeders to develop more tolerant varieties of oil palm and/or to investigate the feasibility of out-competing high virulence strains of *Ganoderma* with other lower virulence strains. The latter approach would greatly reduce the likelihood of the re-emergence of virulence in the future.

In terms of combating the immediate threat of *Ganoderma,* there have also been advances in using molecular genetic technologies to diagnose infections at earlier stages. Previously, by the time a *Ganoderma* infection was diagnosed, it was already too far advanced to save the tree in question, and it was possible that neighbouring trees had also become infected. It has been reported that within 15 years of getting into a plantation, *Ganoderma* can kill as many as 80% of oil palm trees (USDA, 2012). Early detection of *Ganoderma* infection is therefore an important prerequisite to its eventual control. Although there is still a long way to go, there are promising signs that improved diagnostic methods will eventually help in the identification and management of this serious pathogen (Bridge *et al*., 2000; Panchal and Bridge, 2005).

The rhinoceros beetle has emerged as the major pest of oil palm in South-east Asia since the 1980s. Chemical insecticides can be effective but such agents are expensive as they can sometimes also affect beneficial insects, and the target organisms may develop resistance as has been found with many other insecticides. Among the most promising biocontrol strategies for this pest are the deployment of two efficient pathogens of the beetle, namely the entomophagous fungus *Metarhizium anisopliae* and the *Oryctes* virus (Ramle *et al*., 2005). Both pathogens are specific to rhinoceros beetles and as such will not affect other insects. The *Oryctes* virus appears to be endemic in the beetle population, and deliberate augmentation can raise its infection levels to above 75%. The *Metarhizium* fungal spores can be applied to areas of infestation as a spray that is highly effective at controlling, but not totally eradicating, the beetles. The combined use of these and other natural pathogens of the rhinoceros beetle have the potential to reduce its harmful impact on the crop, while also minimising risks of resistance development.

With the projected increase in oil palm replanting over the next few years, it will be important to consider the wider release of such biocontrol agents into areas where the incidence of rhinoceros beetles is particularly high. These and other forms of integrated pest management are being investigated as primary options in plantations across South-east Asia (Caudwell and Orrell, 1997). The rapid expansion of high intensity commercial plantations in new regions such as West Africa and South/Central America will doubtless lead to the emergence of new pests and pathogens. Therefore, it will be important for the public sector and industry to work together in developing improved methods of surveillance and early detection of such threats.

Other Traits

The three trait groups discussed above (oil yield, oil quality, and pest/disease tolerance) are by far the most important priorities in terms of increasing the overall output of the oil palm industry and in expanding its market share into the lucrative high oleic sector that is currently dominated by the temperate oil crops. There are many other possible targets for trait modification but in terms of global income generation they must be regarded as of secondary importance to these three priority traits.

In terms of edible and health markets, virgin palm oil is already enriched in carotenoids, lycopenes, tocopherols and tocotrienols that are sources of the lipophilic vitamins A and E. For most edible applications, these useful compounds are removed during processing which presents two options for additional value creation. For the first option, vitamin-rich virgin palm oil, which is bright red in colour, could be more effectively marketed as a healthy vegetable oil similarly to virgin olive oil, which is green and cloudy. Such a campaign would be more effective if high oleic varieties of palm oil are developed. The second option would be to develop a more cost-effective process to recover these useful compounds during oil processing and then sell them as affordable dietary supplements or for other applications. Another possibility is to manipulate the oil composition to include desirable fatty acids such as DHA (docosahexaenoic acid) or EPA (eicosapentaenoic acid) that are currently found in some fish oils. This would involve transgenic methods and would take well over a decade to achieve. It is also uncertain whether there would be a sufficiently strong market demand for substitute fish oils to make such a breeding programme worthwhile.

In terms of non-food markets, palm oil composition could be modified to include high levels of various industrially useful fatty acids, although even in the case of more easily manipulated annual oilseeds progress in this area has been disappointingly slow over the past few decades, so this remains a very long-term option for oil palm (Murphy, 2009a). Another interesting possibility is to engineer the accumulation of biodegradable biopolymers in palm fruits (Sudesh, 2013). This technology is gradually being developed in some annual crops where the transfer of three bacterial genes can enable plants to convert acetyl-CoA into polyhydroxyalkanoate beads instead of triacylglycerol oils (Gumel *et al*., 2013). Providing these beads can be extracted from the plant tissue (which is currently proving rather challenging), they can be used to manufacture several types of thermoplastic materials that, unlike conventional petroleum-derived polymers, are both renewable and biodegradable (Murphy, 2010).

A major issue with all of these oil-modification schemes is that palm fruits that have been modified to produce new types of oil would need to strictly segregated after harvesting and in all of the downstream processing steps. This would add considerably to production costs and it is far from certain whether sufficiently reliable markets would be available to guarantee adequate returns on the high investment and operating costs on such niche products. In summary, most of these additional traits can certainly be considered as part of a long-term wish list for oil palm R&D but they cannot be justified to the same extent as the three major priority traits, namely oil yield, oil quality, and pest/disease tolerance.

THE ROLE OF IMPROVED MANAGEMENT IN ADDRESSING CHALLENGES FOR OIL PALM

The study and manipulation of oil palm biology and genetics will continue to make possible considerable advances in crop improvement as outlined above. However, the translation of these biological benefits into increased oil yields in a given plantation or during downstream processing is a separate challenge that has not always received sufficient attention in the past. The actual amount of palm oil produced at a national or regional level can be affected by many non-biological factors such as climate, soil type, and the effectiveness of crop management systems. Of these by far the most important set of factors is the overall management of the cropping and processing systems. To a great extent, deficiencies in these systems are responsible for the otherwise puzzling failure of oil palm producers to obtain yield increases comparable with other major crops, including their oilseed competitors. A recent study by the US Department of Agriculture (USDA, 2012) has highlighted several areas of concern which will now be discussed.

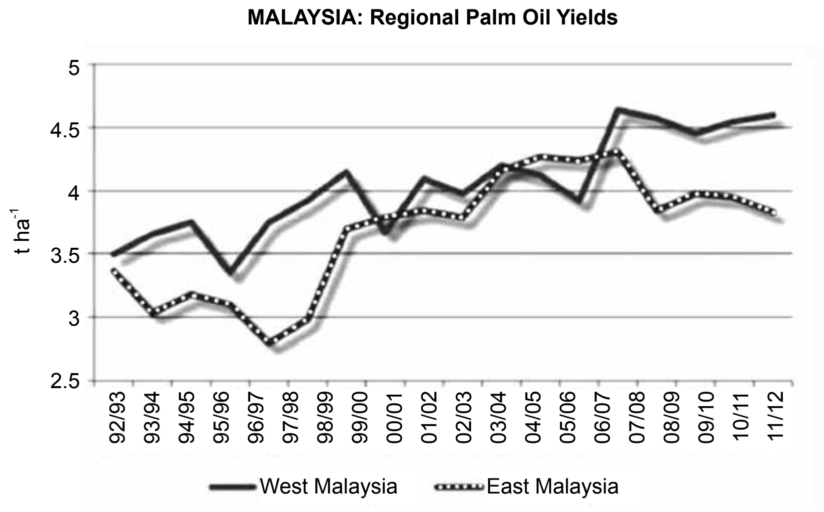
The Labour Issue

As shown in *Figure 2*, palm oil yields per hectare in Malaysia were relatively stagnant from 1992-1997, rose slowly over the next decade, but then actually decreased during the period from 2008-2013. This is of considerable concern because Malaysia is the longest established centre for large-scale commercial oil palm production and is also the world leader in R&D into the biology and management of the crop (Abrizah, 2012). Current average oil yields for Malaysia as a whole are only slightly above 4 t ha^{-1}. However, some plantations are able to routinely achieve yields over 6 t ha^{-1}, which points to a failure in other parts of the industry either to plant the best available varieties and/or to manage cropping and processing systems in a more efficient manner (Murphy, 2007).

As shown in *Figure 3*, there are also regional discrepancies of palm oil yield within Malaysia. Following a period of similar oil yields from 2001-2007, yields in the East fell from 2007-2013 while those in the West stagnated. To some extent, this may be due to the creation of new plantations on peat soils in East Malaysia and a consequent yield lag. However, it is likely that management factors have also played a considerable role in the relative underperformance in East Malaysia. One of the most important of these factors is the shortage of appropriate labour. The original labour force on oil palm plantations in the mid-late 20^{th} century was largely made up of Malaysian citizens. However, thanks to the considerable improvements in education and economic prospects over recent decades, very few young Malaysians now wish to do this type of heavy manual outdoor work. Instead, about 500 000 overseas workers, largely unskilled young males from Indonesia, now provide the basic labour force on commercial plantations. These labourers must harvest the palm fruits manually and also provide basic management services such as pruning and fertilising trees and applying pest/pathogen control measures.

There are several problems with this labour force that make it increasingly difficult to ensure that optimal yields of palm fruits are harvested and efficiently delivered to processing mills. Firstly, there is an overall shortage of manpower caused by government policy to restrict the numbers of migrant labourers granted visas. Secondly, better economic prospects in Indonesia itself, including the expansion of oil palm plantations in that country, have created more opportunities for employment and have reduced incentives to travel to Malaysia for such relatively low paid work. Thirdly, the migrant labourers are restricted to five-year visas, meaning that they have little opportunity to become highly experienced in plantation work, especially compared to the original Malaysian workers who often did such jobs for decades. A high level of experience is vital for tasks like recognising when a fruit bunch is ready to pick or to spot potential problems such as the initial symptoms of pest or disease outbreaks. If fruits are harvested too soon or too late the oil yield can be greatly reduced, and failure to pick up pest/disease problems can result in huge losses of productivity and increased mitigation costs in the future.

The labour issue is especially acute in East Malaysia where the Sarawak Oil Palm Plantation Association has reported a 20%-30% manpower shortfall that has resulted in 15% losses due to rotting fruits. Note that this region has also experienced the greatest recent decline in palm oil yield (*Figure 3*), which indicates that the yield problem is mainly associated with labour issues rather than other factors. There have been calls for the plantation sector to institute an across the board increase in wages combined with enhanced medical and educational benefits to the migrant labourers in order to retain their services. So far such appeals have been resisted by much of the industry despite relatively high palm oil prices and healthy gross margins that have been estimated at 60%-80% by MPOB. Meanwhile, the government is loath to increase the number of visas for a combination of security and political reasons. While there may be good reasons for this lack of action to confront the labour issue, it does mean that labour problems will continue to dog the industry and their



Source: Data from MPOB (2013).

Figure 3. West (peninsular) Malaysia has historically tended to have higher palm oil yields that East Malaysia but the yield gap between the two regions has widened since 2008.

possible knock on effects on oil yield seem destined to become more serious in the coming years.

One possible long-term solution to this seemingly intractable problem is to reduce labour requirements via a combination of radically increased mechanisation and the redesign of the architecture of the oil palm tree (Murphy, 2009b). Already there have been some advances in the redesign of cutting equipment for fruit harvesting. The development of lighter, powered and more ergonomically efficient fruit cutters can increase efficiency and improve health and safety of the workforce. Other devices are being developed to facilitate fruit transport and the collection of loose fruits that have fallen from trees. However, the uptake of many of these innovations has been limited by relatively high purchasing and running costs (Shuib *et al*., 2010). Additionally, the process of fruit harvesting is currently determined by the need to assess the ripeness and then to cut and lower a heavy fruit bunch that is at the top of a 10 to 20 m tree. As discussed above, the introduction of dwarf varieties in several other crops has facilitated mechanisation and led to reduction of the labour force to a much smaller and more highly skilled cadre of specialists. If this could be achieved with oil palm there would be little for unskilled foreign labour and instead workers would have a much less arduous and more skilled job that might even appeal to some local Malaysians.

Replanting with Elite Germplasm

An oil palm has a productive lifetime of 25-30 years with oil yields gradually rising to a peak from 9-18 years followed by a gradual but steady decline. As Indonesia is a relatively new centre of oil palm production, many of the oil palm in its plantations are still relatively young. In contrast, Malaysia is a more mature region where it is estimated that 26% of plantations are 20-28+ years old while 65% are 9-28+ years old (USDA, 2012). Therefore, the majority of the trees in Malaysia have already reached or will soon reach their peak productivity. Over the next decade, there will be inevitabled declines that will continue to exacerbate the poor national yield statistics. The obvious solution is to replace these older oil palm with some of the newer varieties that are already available. This replanting needs to be carried out on a continuous basis so that lower yielding older oil palm, that may also carry higher loads of pests and pathogens, do not accumulate in plantations. Such a scheme would also make it possible to continually refresh the genetic pool of the plantation trees with the best and most recent varieties available from modern breeding programmes.

In reality, however, the situation is more complex and economics, in particular, has played a role in inhibiting the desire to replant. One significant factor has been the high prices available for palm oil in international markets. This has meant that, in many cases, even an ageing plantation with old oil palm varieties can still produce sufficient palm oil to generate a healthy profit for the grower, who therefore has little incentive to replant. Moreover, the decision to replant is rather costly for the grower in the short-term. First, there is the expense of removing the old oil palm and planting new seedlings, and second there is a lengthy period of lost productivity. As the new seedlings will produce no fruits for the first three to four years so the plantation owner would have no income but still would need to manage the growing young oil palm. After three to four years, the oil yield will gradually rise to reach peak output by 8-10 years. This scenario makes it a costly decision even for a large commercial plantation to embark on replanting, but for a smallholder who may only have 5-10 ha of oil palm that are all at the same age the income loss from replanting can potentially be disastrous.

The Malaysian government is now addressing this problem and in 2013, it committed USD 135 million to facilitate a national replanting programme that is particularly targeted at smallholders (USDA, 2012). The government has estimated that 365 000 ha of mainly smallholder oil palms are 25-37 years old, which means that they are well beyond their normal productive lifetime. The aim is to replace 100 000 ha of ageing oil palm per year by providing grants to smallholders for the replanting costs plus an annual allowance of USD 1884 for the first two years of zero productivity. It is hoped that the larger commercial plantations will also replant a further 100 000 ha yr^{-1} so that by 2018 one million hectares will have been replanted. If this can be achieved, and with the conservative assumption that new oil palm capable of 5-6 t ha^{-1} replace the ageing stock producing 2-3 t ha^{-1}, this could result in an additional oil yield in the region of three million tonnes in Malaysia by 2020. This >10% increase in yield can be readily achieved without converting any new land to oil palm and only relies on currently available varieties. In reality, much higher yielding varieties will be available from breeding programmes so there is even greater potential to increase Malaysia palm oil yields in the coming years.

The replanting issue that is currently such an urgent problem in Malaysia will also eventually affect Indonesia, which is an even larger palm oil producer. Many plantations in Indonesia were installed during a comparatively brief period, meaning that they will also require replacement, and consequent loss of income for growers, at about the same time. The situation in Indonesia will be exacerbated by the far larger proportion of oil palm cultivated by smallholders compared to Malaysia. Smallholders account for about 40% of the oil palm area in Indonesia and over the next decade as much as 500 000 ha yr^{-1} will require replanting. It would therefore be prudent for the Indonesian government to use some of the considerable revenues it is now receiving thanks to a buoyant palm oil market to set aside funds for a large-scale national replanting programme in the early 2020s. Such a scheme, which would have a guaranteed bonus in generating higher oil yields, could also reduce future pressures to convert pristine habitats to oil palm plantations. Failure to implement oil palm replanting will mean declining yields in the coming decade and, given the likelihood of continuing international demand for palm oil, impoverished smallholders might well be encouraged to embark on a new round of ecologically undesirable land conversion.

Addressing Sustainability Criteria

It is beyond the scope of this article to address sustainability criteria in detail. However, the wider environmental impacts of all forms of agriculture, including oil palm cultivation, are rightly of considerable public concern and must be taken into account in future planning. Probably the major concern about oil palm is the ongoing expansion of the crop area, especially into environmentally sensitive regions such as pristine rainforest and deep peat soils. As outlined above, in the medium-term the need for such land expansion can be considerably reduced by the yield benefits that can be brought about by breeding and improved management. In the shorter-term, efforts should be made to avoid environmentally sensitive areas as much as possible. In addition, where land conversion does occur the impacts on wildlife should be mitigated by the inclusion of refuges and transit corridors.

The main areas of concern in this regard are in Indonesia and some parts of the Malaysian Borneo. As these two countries produce the vast majority of global exports of palm oil, it is in their joint interest to ensure that valid environmental concerns are addressed, for example by encouraging growers to join certification schemes such as RSPO (Roundtable on Sustainable Oil Palm, www.rspo.org). To a great extent, the larger commercial plantation companies that are already focussed on international trade have both the means and the incentive to improve their sustainability status. However, a major additional challenge in some regions will be to meet RSPO or similar criteria while still facilitating the economic development of the estimated three million oil palm smallholders worldwide who face real difficulties in complying with such schemes (ZSL, 2013).

It is in the interests of the oil palm industry as a whole to try to address these issues together, rather than on a piecemeal company-by-company or region-by-region basis. For example, the poor image of palm oil presented by some NGO has led to an increasing trend in some parts of Europe for boycotts of oil palm products by both retailers and consumers. Such blanket bans show that there tends to be no differentiation between 'good' and 'bad' sources of palm oil and the entire sector ends up being tarred by poor practice in a few areas. It is also both logistically difficult and expensive to begin segregating a globally traded commodity like palm oil on the basis of provenance unless the market is prepared to offer a significant premium, which is unlikely given the current economic circumstances. There has been some progress in addressing environmental issues over the past few years but, given the very real potential for further increases in palm oil production, it is highly desirable that this huge global industry, which is worth over USD 50 billion annually, should collectively redouble its efforts to address sustainability and public image issues as a matter of priority.

FUTURE PROSPECTS FOR OIL PALM

In this article, we have seen that there are powerful drivers for the continued expansion of demand for palm oil in the mediums to long-term future. In 2013, a global area of about 15 million hectares produced 65 million tonnes of palm mesocarp + kernel oils. Forecasting future levels of demand for any commodity is always challenging but estimates from reliable sources predict requirements of about 77 million tonnes palm oil by 2018 (FAO) and between 93 and 156 million tonnes by 2050 (Corley, 2009). Therefore, it can be confidently predicted that global demand will remain high and that there will be sustained pressure for yield improvements and additional land conversion for decades to come. Given these projections, it would be prudent for the sector to invest significantly right now in priority R&D areas like yield and oil quality and to address management-related issues such as environmental impact, product image, tree replanting, labour supply and mechanisation.

Some of these measures could have a significant impact on output within the next five years. For example, if the planned replanting programme in Malaysia is carried out, it could deliver an additional annual yield of 5 million tonnes palm oil without the need to use any more land. If some of the best existing experimental breeding material, which could theoretically yield 8-10 t ha^{-1}, can be developed for commercial planting throughout the sector then yield could be increased by 50% or more. This could deliver as much as 30 million tonnes more oil per year – again without requiring further land conversion. Further into the future, there is the prospect of additional yield gains by using modern breeding technologies to produce fruits with a higher oil content and dwarf oil palm that bear more fruit and are easier to harvest mechanically. At present, we cannot quantify the benefits of such biological innovations but they could potentially deliver tens of millions of tonnes of additional oil.

Although, it should be possible to produce a lot more palm oil by increasing the crop yield, we should also accept that some additional land conversion will be necessary, particularly in the short-term. Providing this is carried out in an environmentally responsible manner there are benefits from diversifying oil palm cultivation into other regions of the world. For example, a more dispersed cropping area will be more resilient to threats from climatic factors or locally adapted pests and pathogens. In this respect, the current concentration of >85% of global palm cultivation in one geographical area (Malaysia/Indonesia) is not ideal. The expansion of cultivation into suitable areas of West Africa and South/Central America that is now underway will create a more secure production system in the longer term.

Currently, the three major centres of oil palm cultivation in Central/South America are Colombia, Ecuador and Honduras with a collective annual output of 2 million tonnes oil. According to IIASA estimates, these three countries and Peru have some modest potential to expand cultivation but by far the largest new prospective area is in Brazil. Oil palm is more suitable as a crop in low elevation regions in the humid tropics and can even tolerate the highly acidic non-forest soils of Amazonia (Butler and Laurance, 2009). In Brazil, an estimated 32 million hectares (excluding rainforest) are suitable for oil palm production (EMBRAPA, 2010), which is more than double the entire global crop area at present. In contrast to South-east Asia and parts of West Africa, the vast majority of this possible expansion into oil palm in South America would be on grassland or planted pasture with very little forest conversion (Pacheco, 2012). Conversion of such land would therefore have a lower impact on biodiversity and other sensitive environmental indicators that the conversion of tropical forest.

West Africa is the historical home of the commercial oil palm plant and, prior to the 1960s, Nigeria in particular was a globally dominant producer of palm oil. Since then, civil conflict coupled with poor investment and management of the largely smallholder dominated industry meant that palm oil production declined until by 2000, it was unable even to met local demand and the country became a net importer of edible oils (Ugbah and Nwawe, 2008). However, the same buoyant international demand for palm oil that is driving land conversion in Central/South America is now fuelling increasing investment in replanting disused plantations or establishing new plantations in several parts of West and Central Africa. A great deal of this expansion will be required simply to meet local requirements for vegetable oil that is currently imported at considerable expense from abroad. For example, in 2010, Africa imported 2.4 million tonnes palm oil, mostly from Malaysia, despite its potential capacity to produce this amount of oil, and much more, locally. For example, it is estimated that a staggering 24 million hectares could be potentially used to grow oil palm in Nigeria alone (Business Day, 2013).

In terms of climate and agronomy, another promising region for new oil palm cultivation in Africa is in the Congo river basin (Persson and Azar, 2010). Plantation companies are also steadily acquiring land in other parts of Africa (Global Forecasting Service, 2011). Some idea of the scale of these acquisitions can be seen from the following figures of land purchases or leases by overseas companies – note that the list is only a sample of the total land being acquired: Congo DR – 1 080 000 ha; Liberia – 600 000 ha; Gabon – 205 000 ha; Nigeria – 110 000 ha; Congo, R – 110 000 ha; Sierra Leone – 100 000 ha; Cote d'Ivoire – 55 000 ha; Cameroon – 40 000 ha (Carrere, 2010). In 2013, it was estimated that at least 1 million hectares in the region was currently available for conversion to oil palm plantations. Investors include a variety of overseas oil palm businesses based in South-east Asia and Europe as well as USD-based investment companies. There are also ongoing multi-billion investments by overseas companies in new oil palm infrastructure, such as processing plants, port facilities and transport links. For example, in 2013 the French-based SIFCA Group announced plans to spend USD 417 million on plantations and processing plants in Ghana, Nigeria and Liberia.

Therefore, it is clear that over the next decade, West and Central Africa will emerge alongside Central/South America as a major producer of palm oil, initially for local consumption but eventually for export to global markets. Between them, West/Central Africa and Central/South America have the capacity to convert well over 30-40 million hectares to oil palm with a current yield potential of 130-170 million tonnes oil and much more than that if the expected increases in crop yields are realised. It is highly unlikely that such a vast area, which is more than double the present oil palm area, will be converted. However, even if only a quarter of this land is changed to oil palm plantations, these regions could be producing as much as 50-60 million tonnes oil by 2025. This is close to the present global total and demonstrates that a doubling of palm oil production in the next few decades is quite feasible.

CONCLUSION

The oil palm industry faces many challenges in the future. However, the tools to surmount these challenges already exist and have the potential to further transform this historic crop into a truly global source of nutritious food and valuable non-food products for the growing world population. We can look forward to an extension of oil palm cultivation right across the tropics of Africa, Asia and the Americas with higher yielding varieties that have improved oil compositions. A redesign of crop architecture and improved pest/disease tolerance could also facilitate its management and processing. If these and other measures can be undertaken, increased palm oil output could more than meet the highest projections for future vegetable oil requirements and might even displace some of the less efficient temperate oilseed crops.

ACKNOWLEDGEMENT

I wish to thank the two anonymous referees for their useful and constructive comments on this article.

REFERENCES

ABRIZAH, A (2012). A bibliometric study on the worldwide research productivity of scientists in *Elaeis guineensis* Jacq. and *Elaeis oleifera*. *J. Oil Palm Res. Vol. 24*: 1459-1472.

BEALE, M H; WARD, J L and BAKER, J M (2009). Establishing substantial equivalence: metabolomics. *Methods Mol Biol., 478*: 289-303.

BOCK, R (2009). The give-and-take of DNA: horizontal gene transfer in plants. *Trends Plant Sci., 15*: 11-22.

BOTO, L (2010). Horizontal gene transfer in evolution: facts and challenges. *Proc. of the Royal Soc B 277*: 819-827.

BOURGIS, F *et al.* (2011). Comparative transcriptome and metabolite analysis of oil palm and date palm mesocarp that differ dramatically in carbon partitioning. *Proc. Natl. Acad. Sci. USA, 108*: 12527-12532.

BRIDGE, P D; O'GRADY, E B; PILOTTI, C A and SANDERSON, F R (2000). Development of molecular diagnostics for the detection of *Ganoderma* isolates pathogenic to oil palm. Ganoderma *Diseases of Perennial Crops* (Flood, J and Bridge, P eds.). CABI Publishing, Wallingford. p. 225-235.

BRINGEZU, S *et al.* (2009). Assessing biofuels: towards sustainable production and use of resources. United Nations Environment Programme, Paris, France. Available online: www.unep.org

BUSINESS DAY (2013). Reactivating Nigeria's oil palm industry. http://businessdayonline.com/2013/08/reactivating-nigerias-oil-palm-industry-2/

CARRERE, R (2010). Oil palm in Africa: past present and future scenarios. World Rainforest Movement. http://wrm.org.uy/countries/Africa/Oil_Palm_in_Africa.pdf

CAUDWELL, R W and ORRELL, I (1997). Integrated pest management for oil palm in Papua New Guinea. *Integr Pest Manag Rev., 2*: 17-24.

CHUNG, J; BABKA, H L; GRAEF, G L; STASWICK, P E and LEE, D J (2003). The seed protein, oil, and yield QTL on soyabean linkage group I. *Crop Sci., 43*: 1053-1067.

COOK, D R and VARSHNEY, R K (2010). From genome studies to agricultural biotechnology: closing the gap between basic plant science and applied agriculture. *Current Opinion in Plant Biology, 13*: 115-118.

CORLEY, R H V and TINKER, P B (2003). *The Oil Palm*. Fourth edition, Blackwell, Oxford, United Kingdom.

DUSSERT, *et al.* (2013). Comparative transcriptome analysis of three oil palm fruit and seed tissues that differ in oil content and fatty acid composition. *Plant Physiol, 162*: 1337-1358.

EDWARDS, D and BATLEY, J (2010). Plant genome sequencing: applications for crop improvement. *Plant Biotechnology Journal, 8*: 2-9.

EMPRAPA (2010). Dendê. Ministério da Agricultura, Pecuária e Abastecimiento. Brasil.

FAO (2003). World agriculture trends: towards 2015-2013. An FAO perspective. http://www.fao.org/docrep/005/y4252e/y4252e05d.htm

FLOOD, J and BRIDGE, P (2000). Ganoderma *Diseases of Perennial Crops.* CABI Publishing, Wallingford.

FLOOD, J; COOPER, R; REES, R; POTTER, U and HASAN, Y (2010). Some latest R&D on *Ganoderma* diseases in oil palm. Presented at the IOPRI/MPOB Seminar: Advances in the Controlling of Devastating Disease of Oil Palm (*Ganoderma*) in South East Asia, Jogjakarta, May 2010, http://r4d.dfid.gov.uk/Output/185439/

GLOBAL FORECASTING SERVICE (2011). Commodities - Softs - Palm Oil, Economist Intelligence Unit, http://gfs.eiu.com/Article.aspx?articleType=cfs&articleId=1178124702

GÓMEZ-VIDAL, S; SALINAS, J; TENA, M and LOPEZ-LLORCA, L V (2009). Proteomic analysis of date palm (*Phoenix dactylifera* L.) responses to endophytic colonization by entomopathogenic fungi. *Electrophoresis*, 30: 2996-3005.

GUMEL, A M; ANNUAR, M S M and CHISTI, Y (2013). Recent advances in the production, recovery and applications of polyhydroxyalkanoates. *J. Polymers Environ, 21*: 580-605.

GUNSTONE, F D (2011). Supplies of vegetable oils for non-food purposes. *European Journal of Lipid Science and Technology, 113*: 3-7.

HU, Z-Y; HUA, W; ZHANG, L; DENG, L-B and WANG, X-F (2013). Seed structure characteristics to form ultrahigh oil content in rapeseed. *PLoS ONE, 8(4)*: e62099.

IZAWATI, *et al*. (2012). Transformation of oil palm using *Agrobacterium tumefaciens*. *Methods Mol Biol., 847*: 163-175.

JOHNSTON, M *et al.* (2009). Resetting global expectations from biofuels. *Environmental Research Letters, 4*: 014004.

KALIDAS, P (2013). Pest problems of oil palm and management strategies for sustainability. *Agrotechnology, S11*: 001.

KANEHISA, M and BORK, P (2003). Bioinformatics in the post-sequence era. *Nature Genetics Supplement, 33*: 305-310.

KEELING, P J and PALMER, J D (2008). Horizontal gene transfer in eukaryotic evolution. *Nature Reviews Genetics, 9*: 605-618.

LIN *et al*. (2009). Transcriptome analysis during somatic embryogenesis of the tropical monocot *Elaeis guineensis*: evidence for conserved gene functions in early development. *Plant Mol Biol, 70*: 173-192.

LÓPEZ-FLORES, I and GARRIDO-RAMOS, M A (2012). The repetitive DNA content of eukaryotic genomes. *Genome Dynamics, 7*: 1-28.

MA, W *et al*. (2013). *WRINKLED1*, a ubiquitous regulator in oil accumulating tissues from *Arabidopsis* embryos to oil palm mesocarp. *PLoS ONE, 8(7)*: e68887.

MARDIS, E (2008). The impact of next-generation sequencing technology on genetics. *Trends in Genetics, 24*: 133-141.

MEEROW, A W *et al*. (2012). Coconut, date and oil palm genomics. *Genomics of Tree Crops* (Schnell, R J and Priyadarsham, P M eds.). Springer, New York. p. 299-351.

MONTOYA, C *et al*. (2013). Quantitative trait loci (QTLs) analysis of palm oil fatty acid composition in an interspecific pseudo-backcross from *Elaeis oleifera* (H.B.K.) Cortés and oil palm (*Elaeis guineensis* Jacq.). *Tree Genetics & Genomes*. Published online 23 June 2013, DOI 10.1007/s11295-013-0629-5.

MORCILLO, F *et al*. (2013). Improving palm oil quality through identification and mapping of the lipase gene causing oil deterioration. *Nature Comm, 4*: 2160.

MURPHY, D J (2007). Future prospects for oil palm in the 21st century: biological and related challenges. *Eur. J. Lipid Sci. Technol.*, *109*: 296-306.

MURPHY, D J (2009a). Industrial oil crops, when will they finally deliver on their promise? *Inform, 20*: 749-754.

MURPHY, D J (2009b). Oil palm: future prospects for yield and quality improvements. *Lipid Technology, 21*: 257-260.

MURPHY, D J (2010). Manipulation of oil crops for industrial applications. *Industrial Crops and Uses* (Singh, B P ed.). CABI Press, UK. p. 183-206.

MURPHY, D J (2011). *Plants, Biotechnology and Agriculture.* CABI Press, UK.

NEOH *et al*. (2013). Differential metabolite profiling of metabolites in oil palm mesocarp at different stages of oil biosynthesis. *J Agric Food Chem.*

OIL WORLD (2012). http://www.oilworld.biz/app.php

PACHECO, P (2012). Soyabean and oil palm expansion in South America. A review of main trends and implications. CFOR working paper 90, Center for International Forestry Research www.cifor.org/publications/pdf_files/WPapers/WP90Pacheco.pdf

PANCHAL, G and BRIDGE, P D (2005). Following basal stem rot in young oil palm plantings. *Mycopathologia, 159*: 123-127.

PARVEEZ, G K and BAHARIAH, B (2012). Biolistic-mediated production of transgenic oil palm. *Methods Mol Biol, 847*: 163-175.

PATERSON, A H; FREELING, M; TANG, H and WANG, X (2010). Insights from the comparison of plant genome sequences. *Annual Review of Plant Biology*, *61*: 349-372.

PERSSON, U M and AZAR, C (2010). Preserving the world's tropical forests - a price on carbon may not do. *Environmental Science & Technology, 44*: 210-215.

RAFALSKI, J A (2010). Association genetics in crop improvement. *Current Opinion in Plant Biology, 13*: 174-180.

RAHMAN, H; HARWOOD, J L and WESLAKE, R (2013). Increasing seed oil content in Brassica species through breeding and biotechnology. *Lipid Technology, 25*: 182-185.

RAMLE, M; WAHID, B; NORMAN, K; GLARE, T R and JACKSON, T A (2005). The incidence and use of *Oryctes* virus for control of rhinoceros beetle in oil palm plantations. *Malays J. Invertebr Pathol., 89*: 85-90.

RAMLI, U S *et al.* (2009). Use of metabolic control analysis to give quantitative information on control of lipid biosynthesis in the important oil crop, *Elaeis guineensis*. *New Phytol*, *184*: 330-339.

ROSILLO-CALLE, F; PELKMANS, L and WALTER, A (2007). *A Global Overview of Vegetable Oils with Reference to Biodiesel*. A Report for the IEA Bioenergy Task 40, International Energy Agency, http://www.bioenergytrade.org/downloads/vegetableoilstudyfinaljune18.pdf

SCHNOES, A M; BROWN, S D; DODEVSKI, I and BABBITT, P C (2009). Annotation error in public databases: misannotation of molecular function in enzyme superfamilies. *PLoS Comput Biol., 5(12)*: e1000605.

SHEARMAN *et al.* (2013). Transcriptome assembly and expression data from normal and mantled oil palm fruit. *Dataset Papers in Biology*: 670 - 926.

SHENDURE, J and JI, H (2008). Next-generation DNA sequencing. *Nature Biotechnology, 26*: 1135-1145.

SHU, Q Y (2009). Induced plant mutations in the genomics era. FAO, Rome. http://www.fao.org/docrep/012/i0956e/i0956e00.htm

SHUIB, A R; KHALID, M R and DERAMAN, M S (2010). Enhancing field mechanization in oil palm management. *Oil Palm Bulletin No. 61*: 1-10.

SINGH, R *et al.* (2009). Mapping quantitative trait loci (QTLs) for fatty acid composition in an interspecific cross of oil palm. *BMC Plant Biology, 9*: 114.

SINGH, R *et al.* (2013a). Oil palm genome sequence reveals divergence of interfertile species in Old and New worlds. *Nature doi*:10.1038/nature12309.

SINGH, R *et al.* (2013b). The Shell gene of the oil palm (*Elaeis guineensis*) controls oil yield and encodes a homologue of SEEDSTICK. *Nature doi*:10.1038/nature12356.

SOH, A C (2010). Genomics and plant breeding. *J, Oil Palm Res. Vol. 23*: 1019-1028.

SUDESH, K (2013). *Polyhydroxyalkanoates from Palm Oil: Biodegradable Plastics.* Springer, Berlin.

SULAIMAN *et al.* (2012). The potential of oil palm trunk biomass as an alternative source for compressed wood. *BioResources, 7*: 2688-2706.

TAHIR, N I *et al*. (2013). Identification of oil palm (*Elaeis guineensis*) spear leaf metabolites using mass spectrometry and neutral loss analysis. *J. Oil Palm Res. Vol. No. 25*: 72-83.

TEH *et al.* (2013). Differential metabolite profiles during fruit development in high-yielding oil palm mesocarp. *PLoS ONE, 8(4)*: e61344.

THENKABAIL, P S; HANJRA, M A; DHEERAVATH, V and GUMMA, M (2010). A holistic view of global croplands and their water use for ensuring global food security in the 21st century through advanced remote sensing and non-remote sensing approaches. *Remote Sens., 2*: 211-261.

TING, N-C *et al*. (2013). Identification of QTLs associated with callogenesis and embryogenesis in oil palm using genetic linkage maps improved with SSR markers. *PLoS ONE, 8(1)*: e53076.

TRANBARGER, T J *et al*. (2011). Regulatory mechanisms underlying oil palm fruit mesocarp maturation, ripening, and functional specialisation in lipid and carotenoid metabolism. *Plant Physiol, 156*: 564-584.

TŘÍSKA, M; GROCUTT, D; SOUTHERN, J; MURPHY, D J and TATARINOVA, T (2013). *cisExpress*: Motif detection in DNA sequences. *Bioinformatics doi 10.1093/bioinformatics/btt366*

UGBAH, M M and NWAWE, C N (2008). Trends in oil palm production in Nigeria. *J. Food Agriculture & Environment, 6*: 119-122.

USDA (2012). Malaysia: stagnating palm oil yields impede growth. *Commodity Intelligence Report (December 2012)*. http://www.pecad.fas.usda.gov/highlights/2012/12/Malaysia/

VAN NOORDEN, R (2013). EU debates U-turn on biofuels policy. Key vote could signal withdrawal of support from biodiesel. *Nature, 499*: 13-14.

VAN WOLFSWINKEL, J C and KETTING, R F (2011). The role of small non-coding RNAs in genome stability and chromatin organization. *J. Cell Sci., 123*: 1825-1839.

XU, Y (2010). *Molecular Plant Breeding*. CABI, Oxford, United Kingdom.

ZAMRI, R (2010*). Differential Expressions of Proteomes of Oil Palm* (Elaeis guineensis *Jacq.*) *and* Arabidopsis thaliana *Tissues during Callogenesis*. M. Sc. thesis, Universiti Putra Malaysia.

ZSL (2013). New Britain oil palm: smallholder. Overcoming challenges in certifying smallholders. ZSL website: http://www.sustainablepalmoil.org/growers-millers/growers/case-studies/new-britain-palm-oil