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EDITORIAL

Oil production in the extreme

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Vegetable oils are obtained from the seeds and fruits of crop plants such as Oilseed rape (*Brassica napus*), Sunflower (*Helianthus annuus*), Soybean (*Glycine max*) and Palm (*Elaeis guineensis* Jacq.). They are a major commodity and contribute significantly to the global economy with production surpassing 150 million tonnes per year and, led by developing countries, expected to increase over 30% by 2020. Oil palm is by far the highest yielding oil crop (4–10.5 t ha⁻¹), but future improvements in global production appear to derive from expansion of cultivation into drier environments where oil yields are lower. Although the impact of drought on oil palm physiology has been measured, a causal link has been difficult to establish because of the long interval between flower initiation and harvesting of the mature fruit (ca. 3 years). Currently oil palm is genetically vulnerable to future challenges and improvements in performance will likely come from the introduction of fresh breeding stocks. As such, new methods to evaluate the potential of novel genotypes to augment existing stocks are essential (see Wening *et al.*, 2012).

Vegetable oils consist principally of triacylglycerols (TAGs); which are composed of three fatty acids bound to a glycerol backbone. These molecules are an important source of calories in human and animal diets, and are also used in the preparation of margarines, salad oils and fried foods. They are also increasingly used as a source of biofuels, converted using transesterification or hydrogenation processes, into biodiesel and blended into fuel (Durrett *et al.* 2008). Consequently vegetable oils are a highly desired commodity whose world-wide consumption has increased by >50% during the past decade. However, annual yield improvement is expected to slow down, compared to the last decade, and the productivity gap between developing and developed countries will diminish only marginally. The growth in oilseed plantings is also projected to slow down markedly in both developed and developing countries due to

high marginal costs of area expansion, environmental constraints and sustained profitability of competing crops (OECD-FAO, Agricultural Outlook 2011–2012).

The influence of environmental perturbation on vegetable oil production and quality is significant. The impact of low temperatures on flowering and senescence is well established in the plant model of oil biosynthesis, *Arabidopsis thaliana* (Wingler, 2011). It is generally accepted that damage to cellular membranes is the major cause of stress injury in plants. In particular, detailed lipid analyses have shown that complex changes in lipid composition take place during stress, for example, an increase in the relative amounts of unsaturated phosphatidylcholine in the plasma membrane. However the role of lipids in plant stress is not just restricted to membranes. Recent work examining cold tolerance in *A. thaliana* (Degenkolbe *et al.*, 2012) demonstrated not only that total TAG content increased, but that there was also a change in composition with highly unsaturated fatty acids (specifically with four to eight double bonds in their three fatty acyl chains) up-regulated. In addition, fatty acid desaturase-6 (FAD6), which is responsible for the production of 18:2 (acyl carbons:double bonds) in the chloroplast, has been demonstrated as an absolute requirement for salt tolerance in *A. thaliana* (Zhang *et al.*, 2009).

The implications of a change in the plant lipidome as a result of abiotic stress are extensive and can incorporate a potential for a change in the responses of oil crops to pathogen attack. It has been demonstrated that a change in oleic acid content can affect constitutive defence signalling and enhanced resistance to multiple pathogens in soybean (Kachroo *et al.*, 2008). Furthermore, changes in lipid metabolism may affect surface lipid (fatty acid) composition, which have been shown to be relevant in wider interactions with pathogens (see Kachroo & Kachroo, 2009). It has been well established that lipids are involved in the response of plants to stress and pathogen attack, notably in signalling cascades. For

example, oxylipins are a diverse group of signalling molecules derived from the oxidation of polyunsaturated fatty acids. They are able to mediate responses to plant wounding and pathogen attack (Howe & Schilmiller, 2002). In addition the generation of phosphatidic acid and Phosphatidylinositol 4,5-diphosphate (PI(4,5)P₂) are involved in pathogen resistance pathways (Laxalt & Munnik, 2002). As yet, it is unclear what the effect of an extreme environment is on the ability of a plant to mobilise lipid signals and to resist pathogen attack.

Associated with stress tolerance, sphingolipids and their phosphorylated derivatives are ubiquitous bio-active components of cells involved in regulating cellular processes. They are important structurally in membranes and as dynamic regulators of cellular membranes. Although sphingolipids have a better defined role in animal systems they have been implicated in apoptosis in plants and have been demonstrated to play a role in drought-induced signal transduction and in the response to abiotic stress. It has also been proposed that sphingolipids (and sterols) accumulate in microdomains of the plasma membrane, with these so called lipid rafts playing important roles in sorting and trafficking of specific plasma membrane proteins (Michaelson, 2011). Significantly, recent work has demonstrated that different sphingolipid profiles are associated with the ability to tolerate different levels of abiotic stress. The $\Delta 8$ long chain base desaturase from the drought-tolerant legume *Stylosanthes hamata* shows a preference for producing the 8(Z)-isomer, which is the minority species in *A. thaliana*. When this gene was overexpressed in transgenic *A. thaliana* it conferred greater aluminium tolerance (Ryan *et al.*, 2007). In addition to this work it has recently been shown that sphingolipid $\Delta 8$ unsaturation is important for glucosylceramide biosynthesis and low-temperature performance in *A. thaliana* (Chen *et al.*, 2012).

Extreme weather events can cause stress resulting in damage to plants and subsequent yield loss. For example, unusual cold winter temperatures as recently experienced in Europe (Cattiaux *et al.*, 2010) affected many countries with winter-grown canola (*B. napus*) limiting production by frost and winter-kill. This has been particularly noticeable over recent winters in the European Union. In *B. napus* the effects of abiotic stress such as drought or salinity results in a depreciation of all yield components and a change in lipid composition (Albert *et al.*, 2012). In the UK at least, although the 2012 harvest yields were around average at 3.4 tonnes per hectare, low sunlight levels during pod fill resulted in the oil content being low and variable at 40–43% (Agriculture in the UK 2012; www.gov.uk). If crops do not have the capacity to tolerate cold winter temperatures damage from cold spells will be more severe, whereas in

the Mediterranean climates of Southern Europe, oil crops such as Sunflower, suffer repeated yield loss as a result of drought and increasingly salinity. Di Caterina *et al.* (2007) described not only the growth of Sunflowers in saline conditions resulting in worsening of leaf water status and an accumulation of toxic ions, leading to yield loss, but also a change in the composition of the harvested oil. The other oil crop associated with marginal Mediterranean-type agroecosystems is the Olive tree (*Olea europaea* L.). Although traditionally non-irrigated, the capacity to withstand severe and long drought periods is negatively correlated with growth and productivity, hence there is an increasing use of irrigation to improve yield. However, there is little understanding of the impact deficit irrigation has on the qualitative parameters of olive oil. It is likely that these irrigation regimes alter the intrinsic oxidative stability of the oils. The use of saline irrigation in regions where water availability is a major limitation has implications for oil production. For example, Yuldasheva *et al.* (2011) described the changes in the composition of TAG species (oil quality) in Olive fruits and Soybean under saline irrigation. However, they went on to describe in detail how Safflower (*Carthamus tinctorius*) a moderately salt-tolerant crop was able to maintain its oil and lipid composition when irrigated with moderate concentrations of saline water. This raises the possibility that vegetable oil production could not only continue in extreme environments, but also be expanded to more marginal land, like the Aral Sea basin.

Prospects for vegetable oil production in extreme environments

Camelina sativa (L.) Crantz (Brassicaceae), described by Martinelli & Galasso (2011), is an emerging alternative oilseed crop with rising interest in its use for both food and non-food purposes. *C. sativa* is adaptable to marginal land and has been shown to surpass yields of oilseed crops, such as Flax (*Linum usitatissimum*), under drought-like conditions. Furthermore, *C. sativa* has a number of agronomic attributes that make it attractive; namely a moderate-to-low requirement for nutrients, a low seeding rate, rapid growth cycle (reaching maturity in only 110 days enabling use in double-cropping systems with winter wheat) and a higher resistance of siliques to dehiscence. With respect to research and development, *C. sativa* is amenable to *Agrobacterium*-mediated transformation by simple floral dip infiltration under vacuum. This method permits the generation of transgenic *C. sativa* lines in 6–8 weeks allowing high through-put testing of improved seed

quality and agronomic traits with minimal technical expertise (Nguyen *et al.*, 2013).

Although crops such as *C. sativa* offer the possibility of a stress-tolerant oil production platform, if vegetable oil production is to be achieved in extreme environments it is essential to understand how seed oil metabolism operates in plants tolerating environmental perturbation. Therefore our attention must focus on those species that have the traits of oil synthesis and stress tolerance. Higher plants have adapted to virtually all terrestrial environments. In particular, extremophiles are those operating in the most challenging environments at the far end of the stress tolerance continuum. Biodiversity based prospecting as suggested by Rech & Arber (2013), for oil and stress tolerance traits in extremophile plants has the potential to provide viable options for oil supply. One such model for oil synthesis in extreme conditions are *Thellungiella salsuginea* and *Thellungiella parvula*, close relatives of the recognised oil seed model *A. thaliana*. The *Thellungiella* spp. have recently been utilised as models for identifying processes, pathways and genes of importance in plant abiotic stress tolerance; however, to date there has been no exploration of lipid metabolism or the role of their lipids in stress tolerance (Amtmann, 2009). The *Thellungiella* spp. have been studied for extreme salt, cold and drought tolerance and for efficient mobilisation of resources in poor or degraded soils. Due to the close phylogenetic relationship of *Thellungiella* spp. to *A. thaliana* and because many transcripts have nucleotide sequence identities with the better known model in the 90% range, focusing on *Thellungiella* spp. in order to derive a molecular-level understanding of oil production in challenging environments is particularly appropriate (Dittami & Tonon, 2012). The ability of an oilseed like *Thellungiella salsuginea* to tolerate a range of abiotic stresses is likely intimately connected with its lipid profile.

Exploring how oil seed production can be expanded into more marginal land and maintained in extreme environments is essential. To do this requires a step change in assessing abiotic stress tolerance, namely how to measure success. Much of the work in this area is from a physiological perspective; survival or recovery is the major trait representing plant-stress tolerance, whereas from an agronomic point of view, crop yield and quality are the key determinants of a successful stress-tolerant crop. If maintaining oil yield and quality traits are at the centre of any research strategy then it becomes obvious that a greater knowledge of how lipids (and ultimately storage oil) are linked to environmental perturbation is essential. It is clear that the different aspects of the lipidome or total lipid pool are independent; from *de novo* synthesis to maintenance of the fluidity of the membranes and the storage pools of TAG, remodelling of the lipids

can occur in response to the changing environment. This is a very useful trait and one that can be exploited to extend the range of environments in which an oil seed crop will flourish. Any increase in production will be based equally on continued area expansion and yield improvements. In terms of available land, relatively little new land has been brought into agriculture in recent decades. Indeed, areas like the US Great Plains and the Canadian Prairie are being compromised with increasing salinity in combination with short growing seasons and extremely cold winters. So recalling Mark Twain's famous quote to 'Buy land, they're not making it any more', then the development of oil seed crops that are able to contend with such environmental challenges is a key factor in increasing production. Research must apply new technologies to reveal mechanisms and signalling pathways that regulate not just the plant lipid response to abiotic stress, but also seed oil quality.

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