



Review

Controlling lipid accumulation in cereal grains

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ABSTRACT

Plant oils have so far been mostly directed toward food and feed production. Nowadays however, these oils are more and more used as competitive alternatives to mineral hydrocarbon-based products. This increasing demand for vegetable oils has led to a renewed interest in elucidating the metabolism of storage lipids and its regulation in various plant systems. Cereal grains store carbon in the form of starch in a large endosperm and as oil in an embryo of limited size. Complementary studies on kernel development and metabolism have paved the way for breeding or engineering new varieties with higher grain oil content. This could be achieved either by increasing the relative proportion of the oil-rich embryo within the grain, or by enhancing oil synthesis and accumulation in embryonic structures. For instance, diacylglycerol acyltransferase (DGAT) that catalyses the ultimate reaction in the biosynthesis of triacylglycerol appears to be a promising target for increasing oil content in maize embryos. Similarly, over-expression of the maize transcriptional regulators *ZmLEAFY COTYLEDON1* and *ZmWRINKLED1* efficiently stimulates oil accumulation in the kernels of transgenic lines. Redirecting carbon from starch to oil in the endosperm, though not yet realized, is discussed.

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1. Introduction

Vegetable oils constitute a key component of both human and livestock diets. As a direct consequence of a marked modification of diets of 2–3 billion people in the developing world and of the sharp increase of the world population, plant oil consumption is steeply increasing worldwide. Vegetable oil production has thus been multiplied by six over the last 50 years (<http://faostat.fao.org>).

Abbreviations: ATP, adenosine-5'-triphosphate; CoA, coenzyme A; EST, expressed sequence tag; LEC1, LEAFY COTYLEDON1; NADH, nicotinamide adenine dinucleotide; NADPH, nicotinamide adenine dinucleotide phosphate; QTL, quantitative trait locus; TAG, triacylglycerol; WRI1, WRINKLED1.

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Since fatty acids stored in seeds have a structure similar to aliphatic hydrocarbons found in petroleum, they also represent an alternative to hydrocarbon-based products for biofuel production [1] and synthons for green chemistry (e.g. detergents, paints, inks, plastics and lubricants) [2]. Fossil carbon is a limited resource, and in the light of rising environmental concerns, plant oils derived from oilseed crops are increasingly demanded for the provision of renewable industrial raw materials. Over the last decade, the relative proportion of rapeseed oil used for non-food purposes has thus increased from 5 to 30% [3].

To ensure that these new industrial uses of plant oil will not affect food supply at a time when the world population is estimated to be 9 billion people by 2050, the production of vegetable oil has to be dramatically increased [4]. This could be achieved by improving oil yields in oil crop species already widely cultivated – today, more than 80% of vegetable oil production relies upon palm oil (*Elaeis guineensis*), soybean (*Glycine max*), rapeseed (*Brassica napus*) and

sunflower (*Helianthus annuus*). Alternatively, new oil production systems are being considered. For instance, use of oilseed species capable of growing on non-arable land (e.g. *Jatropha curcas*) as well as production of oil by algae (either in tanks or in open ponds) have been proposed [5–7]. Furthermore, research is currently being carried out to trigger oil accumulation in vegetative organs of oilseed species [8]. Another way to generate new oil crop systems may consist in selecting or engineering cereals with increased grain oil content. Since cultivation of cereals is already widespread and agronomically optimized, this solution could become economically viable.

2. Triacylglycerols in cereal grains

2.1. Distribution within the grain

Cereal grains are composed of two zygotic tissues, namely the embryo (germ) and the endosperm, that are embedded in the maternal testa (or seed coat) and pericarp (or fruit wall), which fuse into a thin protective envelope (Fig. 1A). The aleurone layer that represents the outer cell layer(s) of the endosperm plays a key role during germination in the mobilization of reserve compounds stored in the endosperm [9]. The outer layer of the scutellum, a modified cotyledon (or seed leaf) of the embryo, also participates in this mobilization and absorbs nutrients coming from the endosperm during the germination process [10]. In most cereal grains, the large endosperm constitutes the major site of starch and seed storage protein deposition. Oil is mostly stored in the form of triacylglycerols (TAGs, esters of fatty acids and glycerol) within the embryo, which constitutes a rather limited part of the grain structure. Oil thus accounts for 2–3% of seed dry weight in wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) grains. The main fatty acid species accumulated are linoleate (C18:2), palmitate (C16:0), and oleate (C18:1) [11]. Oil content and lipid distribution within seeds have been precisely analyzed either by microdissection of the grain followed by GC analyses [12] or by non-destructive quantitative imaging of living seeds using nuclear magnetic resonance (NMR) [13]. In developing grains of barley for instance, the scutellum and nodular region of the embryo appear to be important sites of oil deposition, whereas the coleorhizae and coleoptile do not accumulate lipids [13]. Within the endosperm, steep gradients can be detected, with high lipid levels within the aleurone layer and very low lipid levels in the basal endosperm.

The kernel of maize is slightly richer in oil than the above mentioned cereal species. In traditional varieties, the kernel contains 4% oil by weight, this oil being accumulated in the embryo (preferentially in the scutellum) and in the aleurone layer [14,15]. The main fatty acid species found in maize oil are linoleate (60 mol%), oleate (25 mol%), and palmitate (12 mol%). Even though the oil content of traditional maize varieties is low, maize production is so widespread (one of the world's top three grains) that the total amount of oil available in maize kernels is sizeable (<http://faostat.fao.org>). The major portion of the maize kernel production and consequently of maize oil is used as feedstock for animal production (ruminant, pig and poultry). Oil contributes to feed efficiency due to its high caloric value. Maize oil is also a valuable by-product of the wet and dry milling to make maize meal, and is mainly used as edible vegetable oil. Over 2.2 Mt are produced every year, rivaling with olive oil (2.9 Mt) but lagging far behind palm oil (41.3 Mt). The desirable flavor and good oxidative stability (linolenate, C18:3, is present at less than 1 mol%) of maize oil contribute to its positive image and to its market acceptance [16]. Some maize varieties have been selected for high oil content (up to 20%) [17]. In the kernel of these high-oil maize lines, both the embryo oil

concentration and the relative proportion of this embryo, specifically the oil-rich scutellum, are increased [18]. Nevertheless, the yield and other agronomic characteristics of these lines are rather poor. For instance, a significant reduction of kernel size was measured. Although this genetic material has very little economic value, high-oil maize is used for certain poultry and livestock feed. Lower yield is balanced by higher calories.

Oat (*Avena sativa*) accumulates important amounts of oil in its grains as compared to other cereals apart from maize [19] and has been selected to feed horses because of this higher energy density. Oil concentration in oat groat can vary from 3 to 11% in different cultivars, and selection has led to the isolation of lines with oil contents as high as 18% [20]. The highest oil concentrations are in the embryo, scutellum, and aleurone layer (just as in other cereal grains). The inner endosperm also contains substantial amounts of oil. Given the relative proportion of these tissues within the groat, oat appears unique among cereals with a major proportion (almost 90%) of oil stored in the endosperm [21]. The agronomic characteristics and genetic diversity available have led to the current exploration of oat as a potential new oil crop for Europe (<http://epobio.net/>).

2.2. Cellular localization, remobilization

In most oil storing tissues, TAGs accumulate in subcellular oil bodies, comprising a matrix of TAGs surrounded by a phospholipid monolayer. A specific set of proteins is usually embedded in this monolayer. This proteome, first depicted in Brassicaceae (*Arabidopsis thaliana*, *B. napus*), has recently been described in germinating embryos of maize [22]. Among those proteins, oleosins are important actors that would prevent coalescence of the oil bodies and might play a key role in both storage and remobilization of TAGs [23,24]. The elimination of some isoforms of these oleosins by RNA interference (RNAi) in transgenic rice (*Oryza sativa*) strongly impacts on the structure of oil bodies. They appear as large, irregular oil clusters as a consequence of a lack of embedding oleosins. This has a clear negative impact on the amount of oil stored [25]. Nevertheless, the apparent lack of specificity of the RNAi constructs used prevents from attributing a precise function to each of the rice oleosin isoform investigated. Interestingly, in oat, while oil bodies occur as intact individual entities in the aleurone layer, scutellum, and embryo, they have diffuse boundaries and tend to fuse with each other in the starchy endosperm; they form a continuous smear between starch granules and protein bodies [26]. This fusion of oil bodies correlates with a reduction of the amount of available oleosins in this tissue and raises the question of the stability/quality of this oil and of the remobilization of these TAGs after germination. Time-course analyses of lipid and carbohydrate contents in dissected tissues of germinating oat groats suggest that TAGs stored in the endosperm are not a dead-end product and might be remobilized [27]. Similar observations were carried out in germinating seeds of oil palm (a non-cereal monocot) [28]. However, the exact mechanism responsible for the remobilization of TAGs in this tissue is still poorly understood and the nature of the metabolites transferred from the endosperm to the germinating embryo remains to be firmly established. These physiological aspects ought to be considered with care when selecting or engineering varieties with endosperm metabolism diverted from starch to oil. For instance, sufficient amounts of oleosins may be crucial for the elevated accumulation of TAGs within this tissue during seed filling. In the same line, a strong activation of the actors involved in the remobilization of TAGs (e.g. lipases or transporters) during germination may play a key role in maintaining both the germinative capacity of modified seeds and the successful establishment of corresponding siblings.

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