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Review

Potential for novel production of omega-3 long-chain fatty acids by genetically engineered oilseed plants to alter terrestrial ecosystem dynamics

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ABSTRACT

Two bioactive omega-3, long-chain, fatty acids (EPA and DHA), found in algal and fish oils, can now be produced in genetically engineered (GE) terrestrial oilseed crops. These fatty acids are involved in key physiological functions in invertebrates and vertebrates. They are known to be synthesized by primary producers in aquatic ecosystems, but not by terrestrial crop plants. Thus, the production of EPA and DHA by GE seed oil crops represents a fundamental shift in the accessibility of bioactive fatty acids to terrestrial consumers; one that may change their physiology and survival thereby altering ecological interactions among terrestrial organisms. Here we discuss the potential ecological and evolutionary consequences of the novel production of EPA and DHA by GE oilseed crops.

1. Introduction

Oilseed crops have recently been genetically engineered (GE) to produce two novel bioactive omega-3 (also called n-3) long-chain fatty acids (eicosapentaenoic acid [EPA, 20:5n-3] and docosahexaenoic acid [DHA, 22:6n-3]) which significantly enhance the seed's nutritional value. These GE oilseed plants represent a new type of crop because these fatty acids are not known to be naturally produced by terrestrial crop plants (Fig. 1). These two omega-3 long chain polyunsaturated fatty acids (LC-PUFA) are bioactive compounds known to be critically involved in key physiological functions in invertebrates and vertebrates (including humans), and, in particular, for their generally positive effects on vertebrate cardiovascular and neurological health (Mozaffarian and Wu, 2012; Bazinet and Laye, 2014; Calder, 2015). Therefore, minimum daily intakes of EPA and DHA, which depend on age, gender, health status, reproductive status, and medical history, are recommended by various public health institutions (e.g. World Health Organization, American Heart Association; Kris-Etherton et al., 2009).

Both EPA and DHA are naturally produced, primarily by algae, in aquatic environments (Brett and Müller-Navarra, 1997; Galloway and Winder, 2015; Colombo et al., 2017) and are generally selectively retained by higher trophic level organisms (e.g., fish; Fig. 1). We generally obtain the bulk of our EPA and DHA by eating seafood, or taking fish- or algal-oil pills (Arts et al., 2001; Calder, 2015). While aquaculture has increasingly become a major source of seafood, farmed fish also require a dietary source of EPA and DHA, typically from oil derived from wild fisheries (Tocher, 2015). However, many wild fish stocks are now at, or beyond, exploitable limits and cannot further support the growing demand for fish oil needed for aquaculture, and other industries, including pharmaceutical, livestock, and the food fishery (FAO, 2016).

A viable, terrestrial source of EPA and DHA would significantly reduce dependency on wild fisheries. Thus, the purpose of these GE oilseed crops is to provide an alternate source of EPA and DHA for aquaculture, livestock, and human consumption (Fig. 1). The functional genes incorporated into these new crops primarily came from marine algae, a marine fungus, and a moss (Petrie et al., 2014; Ruiz-Lopez et al., 2014; Walsh et al., 2016). Collectively, these genes, and the enzymatic activities they encode, represent a toolkit by which the metabolic engineer/synthetic biologist can attempt to reconstitute the capacity to synthesise EPA and DHA in a crop plant species (Napier et al., 2015). The resulting fatty acid profile of the seed oil, compared to the wild-type cultivar, is closer to that of fish oil, because it contains EPA and DHA at levels similar to fish oil (Fig. 2). To date, two oilseed crop species have been identified as potential hosts for the omega-3 LC-PUFA biosynthetic trait: canola (*Brassica napus* L.) and camelina (*Camelina*

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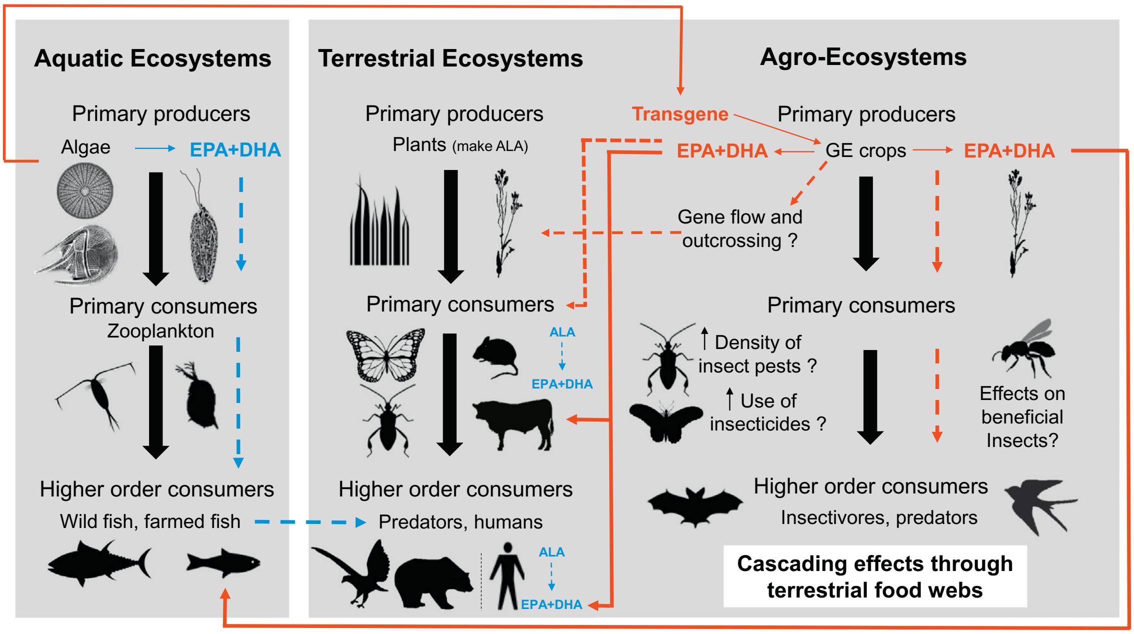

Fig. 1. The production and transfer of EPA + DHA in aquatic, terrestrial, and agro-ecosystems. These compounds are not naturally synthesized by primary producers in terrestrial or agro-ecosystems; however, genetically engineered oilseed crops have been designed to produce EPA + DHA at levels similar to that in fish oil. The transgenes originated mainly from marine algae, as well as a species of fungus and a moss. As the production of EPA + DHA by terrestrial plants is novel, transfer and retention of these compounds within agro- and terrestrial food webs may lead to potential downstream effects that are not yet fully understood. Blue lines (▬) and blue text indicate the natural production and transfers of EPA + DHA, while solid red lines (▬) and red text indicate the intended production, transfers and use of EPA + DHA via GE crops. Dashed red lines (▬ ▬) indicate unintended transfers of EPA + DHA as a result of production via GE crops. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

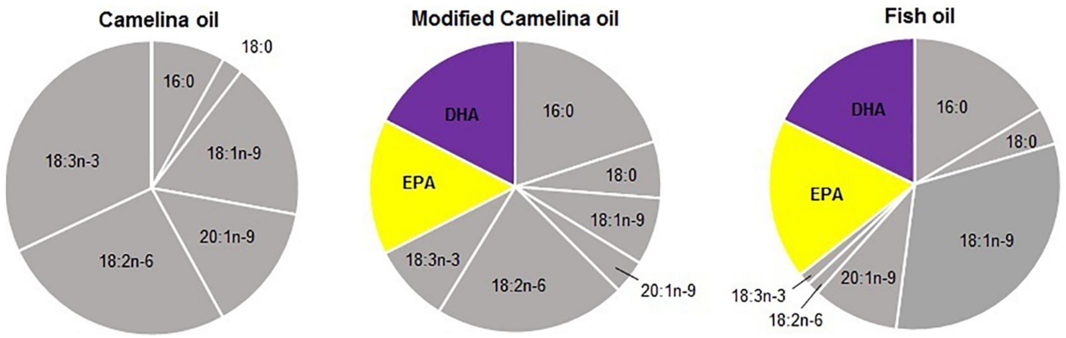

Fig. 2. Comparison of fatty acid composition in different sources of n-3 LC-PUFAs. The major fatty acids present in either camelina oil (Hixson, 2014), modified camelina oil (Ruiz-Lopez et al., 2014), and bulk fish oil (herring; Hixson, 2014) are presented. Note: The unmodified camelina oil is devoid of EPA and DHA.

sativa). Transgenic lines of both camelina and canola have been developed, and this has enabled the production of up to 30% EPA + DHA of total fatty acids (Napier et al., 2015), or 12% DHA only in camelina (Petrie et al., 2014), and 4% EPA + DHA in canola (Walsh et al., 2016). This research has been made publicly available by two groups, Rothamsted Research (United Kingdom) and The Commonwealth Scientific and Industrial Research Organisation (CSIRO in Australia). To our knowledge, only transgenic camelina has been tested in outdoor field trials in the UK (Usher et al., 2015, 2017). There has also been commercial development in transgenic canola by international agricultural corporations which have patents on the technology, such as Cargill and BASF (Einstin-Curtis, 2016), Dow Agrosciences and DSM Nutritional Products (Walsh et al., 2016), and Nuseed (Moore, 2014). However, information on field trial testing or updates on commercialization by these corporations has not been widely publicized (ISAAA, 2017).

While there are some examples of crops with nutritionally improved traits intended to provide health benefits for consumers and animals, for the most part, these enhancements are the result of conventional plant breeding and selection (Newell-McGloughlin, 2008). There are also examples of GE crops that feature enhanced nutrient profiles (e.g., golden rice). However, the majority of these crops have not yet reached full-scale commercialized production (Newell-McGloughlin, 2008). Importantly, such traits are not entirely novel as the same nutrients are found in other terrestrial crops. In contrast, EPA and DHA, which are common fatty acids in aquatic ecosystems, are not known to be produced by terrestrial crops (Hixson et al., 2015; Twining et al., 2016a). In fact, EPA and DHA are the main drivers of the difference in fatty acid content observed between aquatic and terrestrial primary producers (Fig. 3a), and all organisms (Fig. 3b).

The proposed introduction of greater levels of EPA and DHA to terrestrial ecosystems would be unique because these highly bioactive fatty acids could then be consumed and metabolized, for the first time, by animals in the agro-ecosystem. This warrants careful regulatory consideration of these new GE-oilseed crops as they are not equivalent to other GE crops. Here we discuss the potential consequences of wide-scale production of novel terrestrial crop-plant sources of EPA and DHA, which have the capacity to alter the natural production, distribution, and accessibility of n-3 LC-PUFA in regions where these crops