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Fatty acids composition of oilseed rape genotypes as affected by solar radiation and temperature

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ABSTRACT

Environmental parameters are known to affect the fatty acid profiles of oilseed crops. Whereas the role of temperature in fatty acid desaturation is well documented, the impact of solar radiation, and therefore photosynthetic activity, is less known. Moreover, the interaction between temperature and solar radiation has rarely been documented. This study is based on field data and an experiment under semi-controlled conditions. The first experiment in growth chambers was designed to assess independently the impact of light intensity and temperature; the analysis of the data from field experiments with natural variation in solar radiation and temperature showed their relation to the alpha-linolenic acid concentration (C18:3) at different growth stages. Temperature affected the fatty acid composition, by increasing the oleic acid concentration (C18:1) and decreasing the C18:3. The results validated with more years and genotypes that the period from 680 to 930°-days after onset of flowering (DDAF) was sensitive to the minimum temperatures. Solar radiation during seed filling was also found to be negatively correlated with C18:3. However, during an earlier sensitive period, from 100 to 300 DDAF, solar radiation had a positive impact on C18:3 concentration. These seemingly contradictory effects could be the consequence of the impact of solar radiation on the source-sink ratio, with a higher source-sink ratio leading to lower C18:3 concentration. Moreover, our data showed that the response of the C18:3 concentration to solar radiation and temperature depended on the genotype with a tendency to less intense effects on high-oleic low-linolenic (HOLL) genotypes. As a result of these findings, an empirical model with solar radiation from 100 to 300 DDAF and the minimum temperature from 680 to 930 DDAF, with genotype-dependent sensitivity, was proposed to predict C18:3.

1. Introduction

The use of oils depends on their fatty acid composition. Conventional oilseed rape (OSR) has about 60% C18:1 and 10% C18:3. Its nutritional quality is excellent, due to its high polyunsaturated fatty acids concentration, and low saturated fatty acids concentration, but the same reasons make it unstable at high temperatures (Mollers, 2002). In contrast, high-oleic low-linolenic (HOLL) OSR varieties are characterized by high oleic acid concentration (C18:1 > 75%) and low linolenic acid concentration (C18:3 < 3.5%), and therefore a better oxidative stability at high temperature (Carré et al., 2007). HOLL oilseed rape can therefore be used for deep frying without hydrogenation (Matthäus, 2007). This post-harvest treatment tends to produce *trans* fatty acids which raise concerns from consumers about the health effects (Ascherio and Willett, 1997; Koletzko and Decsi, 1997). It has been restricted in Switzerland since 2008 (Federal Office of Public Health, 2008). Consequently, the Swiss oil industry had a special interest on HOLL OSR oil and insisted on the very low C18:3 concentration, in order to secure oxidative stability.

Fatty acid composition is the balance between saturated, monounsaturated and polyunsaturated fatty acids, composing the triacylglycerol, storage form in oil crops. Photo-assimilates are imported into the plastids where fatty acids are elongated by the fatty acid synthase enzyme complex. Most of the stearic acid (C18:0) is then desaturated into C18:1 which is in a large part exported to the cytosol. A fraction of C18:1 is then desaturated into C18:2, and C18:2 into C18:3 through the action of the fatty acid desaturases (FAD) 2 and 3 respectively (Singer et al., 2016). A minor part of C18:1 is also desaturated in

Abbreviations: OSR, oilseed rape; HOLL, high-oleic low-linolenic; C18:3, alpha-linolenic acid concentration; C18:2, linoleic acid concentration; C18:1, oleic acid concentration; Tmin, minimum temperature; Rad, solar radiation; PTQ, photothermal quotient; DDAF, degree-days after the onset of flowering; FAD, fatty acid desaturase

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the plastids into C18:2 with FAD6, and then C18:2 can be desaturated by either FAD7 or FAD8 into C18:3 (Ohlrogge and Browse, 1995). Mollers (2002) reported that the activity of the desaturase enzymes mediating this reaction is affected during the breeding of HOLL OSR lines, in particular with a modification of the amino acid sequence of FAD2. In HOLL cultivars, the lower concentration of C18:2 and C18:3, compared to conventional genotypes, is due to lower activity of both oleate and linoleate desaturases (Baux et al., 2013).

Beside the genotypic variability, environmental factors such as temperature, solar radiation, water deficit, salinity, oxygen and soil nutriments, also influence the oil composition of oilseed crops (Singer et al., 2016). The impact of temperature on C18:3 concentration in OSR has been demonstrated by many studies (Canvin, 1965; Trémolières et al., 1982; Champolivier and Merrien, 1996; Deng and Scarth, 1998; Pritchard et al., 2000; Baux et al., 2008; Baux et al., 2013). In addition, a sensitive period has been identified, as well as interactions between temperature and genotype, for several species. Baux et al. (2013) showed that minimum temperatures from 680 to 930°-days (base 0 °C) after the onset of flowering (DDAF) had a negative impact on C18:3, and this effect was less intense for HOLL genotypes than for conventional genotypes, partly because the desaturation of C18:2 into C18:3 was no longer temperature dependent in mutated genotypes. The effect of the night temperature on C18:1 has also been reported for other oilseed crops, such as sunflower (Izquierdo et al., 2002), maize, and soybean (Zuil et al., 2012). For the sunflower, Izquierdo and Aguirrezábal (2008) found that the relation between the minimum night temperature and C18:1 was genotype-dependent. The impact of the temperature was explained by thermal regulation of the enzymes involved in the fatty acid biosynthesis (Wilmer et al., 1998; Garcia-Diaz et al., 2002).

Intercepted solar radiation also affected the fatty acid profile in OSR, soybean, maize, and sunflower, when modified by shading and thinning (Izquierdo et al., 2009). These authors showed that during grain filling, it impacted C18:1 positively and C18:3 negatively in OSR. However, Wang et al. (2016) found that C18:3 decreased when the pods were shaded during seed development. The interaction between solar radiation and temperature was also studied for other species. In controlled conditions, Echarte et al. (2010) found that the night temperature and the intercepted solar radiation had an additive effect on C18:1 in sunflower. C18:1 was sensitive to these environmental factors during distinct critical periods (Echarte et al., 2013). The intercepted solar radiation and the minimum temperature during grain filling were used to predict the C18:1 of the high oleic genotypes of maize and soybean (Zuil et al., 2012).

Variations in solar radiation and temperature affect the source-sink balance and explain the differences in seed yield (Diepenbrock, 2000; Jullien et al., 2011; Weymann et al., 2015) and oil content (Canvin, 1965; Willms et al., 1999). Impact on oil composition have also been studied on sunflower. Echarte et al. (2012) proposed a conceptual model that explains changes in the fatty acid composition by the impact of the intercepted solar radiation on assimilate availability. It was suggested that for high assimilate levels, the oleic acid desaturase was saturated, leading to an accumulation of C18:1. Conversely, at low assimilate levels, the enzymatic activity would no longer be the limiting factor, and thus, the percentage of C18:2 would increase. The intercepted solar radiation would regulate this equilibrium by determining the assimilate availability. In addition, Durruty et al. (2016) built a kinetic model for the sunflower to simulate grain filling and fatty acid biosynthesis. This model describes the enzymatic phases of the steps leading to the biosynthesis of oleic acid and its desaturation into linoleic acid.

The influence of environmental factors on fatty acid composition is better characterized for the sunflower than for OSR, and the potential impact of genotypic variability in OSR is unknown. Moreover, in OSR, the source of photo-assimilates changes between pod formation and seed filling, as the pods become autotrophic after about 300 ° days after mid-flowering (Leterme, 1985), which could results in difference among species.

The goals of this study are to determine whether solar radiation affects C18:3 concentration in OSR, to assess the role of the genotype in the response of C18:3 concentration to solar radiation and temperature, and to determine whether solar radiation can be used to improve the prediction of C18:3 based on the temperature.

2. Materials and methods

This study consists of two distinct parts with complementary objectives. First, because weather variables are strongly correlated (Bristow and Campbell, 1984; Prieto et al., 2009), an experiment in semi-controlled conditions was set up to test independently the effect of solar radiation and temperature on fatty acid composition. Second, a large dataset with multiple years and sites exposed to natural variations in solar radiation and temperature was analyzed to investigate the impact of the minimum temperature and solar radiation on fatty acid composition at the actual field scale.

2.1. Experiment in semi-controlled conditions

This experiment took place in Changins, Switzerland, and was conducted twice during the 2012/13 and 2013/14 crop seasons. A factorial design was used to evaluate independently the impact of the temperature and photosynthetically active radiation (PAR) on the fatty acid composition of three winter OSR varieties, two HOLL varieties (V141OL, V316OL), and one very low linolenic variety (without the high oleic mutation: MSP21), bred by Monsanto (St. Louis, USA) and DSV (Lippstadt, Germany).

The plants were sown on September 5, 2012, and September 13, 2013, in a mix of 18% sterile topsoil, 24% coco peat, 26% blond peat, and 32% black peat in 5 L pots. The seeds were sown to reach a density of three seedlings per pot. During the growth, nitrogen was supplied in a quantity corresponding to 120 kg/ha in the spring (1.12 g MgS-Ammonsalpeter 25% (Lonza, Basel, Switzerland) and 1 g ammonium nitrate 27% (Landor, Muttenz, Switzerland) per pot). Fungicide was applied in March 2013 (Horizon EW®, Bayer, 1 L/ha) at the phenological stage 32 of the BBCH scale (Lancashire et al., 1991). Insecticides was used against pollen beetles, *Meligethes aeneus,* in April 2013 (BBCH stage 59, Karatezeon®, Syngenta, 75 mL/ha) and in March 2014 (BBCH stage 55, Blocker®, Oyma AGRO, 0.3 L/ha) and against aphids (*Myzus persicae*; Pirimor®, Syngenta, 0.5 kg/ha) three times in May and June 2013 and 2014 (at the end of the flowering period).

From sowing until the beginning of the flowering period in April, the pots were kept outside but were protected from frost with a cold frame since the beginning of December. Inside the frame, the temperature was regulated with an isolating cloth and a small heater when needed to avoid frost damage. From flowering to maturity in July, the pots were moved into growth chambers and submitted to four treatments varying in temperature and solar radiation (Table 1). Two phytotrons (CMP3244, Conviron, Isleham, UK) were used, at a plant density of 48 plants per square meter, which was consistent with local field conditions. They were illuminated with 160W cool white fluorescent lamps (model F72T12-CW-VHO, Osram Sylvania, Mississauga, Canada). The photoperiod was fixed at 14 h inside the phytotrons. Each level of the temperature treatment was allocated to one phytotron. To apply two radiation levels, each phytotron was split into two parts of equal size with an opaque pane. In half of the phytotrons, light was partly shaded using aluminum strips. PAR in the 400–700 nm waveband was measured at the top of the canopy in $\mu mol\ m^{-2}\ s^{-1}$ with a ceptometer (AccuPAR LP-80, Decagon Devices, Pullman, USA). Measured PAR was converted into $W\ m^{-2}$ (from photon to energy units) using a factor of 0.22, which is suitable for this light source (Barta et al., 1992). In addition to the build-it sensor, the temperature was recorded every hour in each half-phytotron with a data logger (LogTag, Oceasoft,