

CHAPTER 3

Seed composition in oil crops: Its impact on seed germination performance

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3.1 Introduction

The amount and composition of lipids stored in seeds of oil crops are the main determinants of their industrial yield and quality. Breeders have attempted to increase seed oil concentration to obtain higher industrial yields, and to modify seed oil fatty acid composition according to industrial demands. Nevertheless, both traits can also be modified by environmental conditions prevailing during seed filling in the mother plant. Several environmental factors have been found to affect the final seed oil concentration and the fatty acid composition as well. Moreover, predictions related to the effect of climate change on oil quality have been reported considering those environmental factors on seed reserves synthesis.

However, seeds are not only the harvest organ for industrial use but also are the perpetuation organ of the species. It is known that germination performance is affected by external factors (i.e., the environment) but also by intrinsic seed factors. Therefore, it is necessary to understand how variations in seed oil concentration and fatty acid composition may in turn affect germination. There is scarce information regarding these effects, but nevertheless its impact can be significant for the crop establishment.

In this chapter we describe the variability in seed oil concentration and lipid fatty acid composition among species and within species. The effects of both genetics and the environmental conditions prevailing during the seed filling in the mother plants are considered. Then, available information concerned the effects of seed oil concentration and lipid composition on germination performance is reviewed.

3.2 Sources of variation in seed lipid quantity and quality

3.2.1 Variation in seed lipid concentration

Lipids, carbohydrates, and proteins are the main components of all seeds and their relative proportions largely vary among species. Lipids are the main reserve energy product for the embryo in oil crops. This compound is most efficient in terms of energy because it provides 9 Kcal/g vs 4 Kcal/g of carbohydrates or proteins. Some species with high seed oil concentrations, such as sunflower, rapeseed, etc., are sown to obtain the lipids as the main product stored in the seed. In other species, oil is a co-product of industry, as, for example, in maize, which is mainly sown to obtain starch and proteins. In other species, however, lipids are seed components with no commercial use.

3.2.1.1 Inter- and intra-specific variations in seed lipid concentration

The amount of oil stored in seeds or fruits is very variable among species and among genotypes within species and it can range from <5% (e.g., maize) up to >60% (e.g., coconut fruit). An illustration of this wide variation in oil concentration is presented in Figure 3.1. This variation in seed or fruit oil concentration is associated with variations in protein and/or carbohydrate concentration, depending on the species.

In oil fruits such as, for example, palm or olive, there are differences in the concentration of lipids between the seed and the fruit. For example, the mesocarp of the olive fruit presents a lipid concentration of about 57% while olive seeds only have about 27% lipid concentration (Conde *et al.*, 2008). Although the major interest in these species is the oil stored in fruits, which can represent >95% of total lipids, the seed oil concentration can influence its germination performance.

Seed oil concentration is mostly genetically determined and breeders have attempted to increase its value in oil crops. In many species (e.g., maize, oat, and sunflower) seed oil concentration was improved mainly by increasing the proportion of the tissue which stores oil in the seed (e.g., Doehlert & Lambert, 1991; Frey & Holland, 1999; Tang *et al.*, 2006). For example, in sunflower

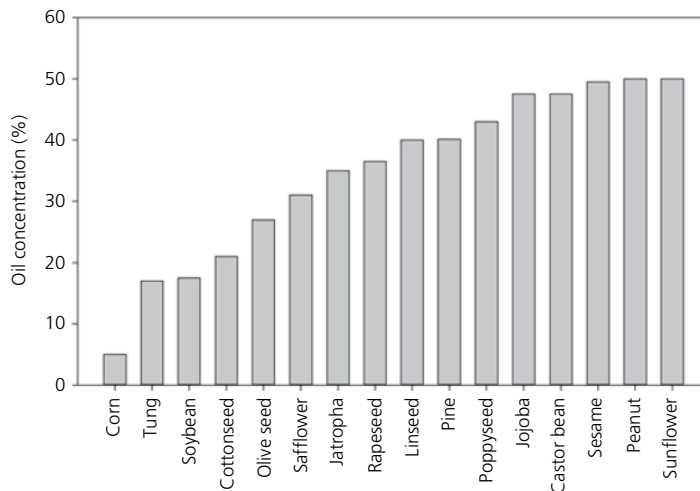


Figure 3.1 Mean seed or fruit oil concentration of several crop species. Data from Mason & D'Croz-Mason, (2002) for corn, Chempro (2015) for tung, soybean, safflower, jatropha, rapeseed, poppyseed, jojoba, castor bean, sesame, peanut and coconut, Conde *et al.* (2008) for olive seed, Bagci & Karaagacli (2004) for pine, and Wrigley *et al.* (2004) for cottonseed and linseed.

(which stores oil in the embryo), seed oil concentration was mainly increased by increasing the embryo/seed ratio and in a minor proportion by increasing the embryo oil concentration. In this species, genetic progress in oil concentration has been of about 0.19%/year in 20 years of plant breeding (de la Vega *et al.*, 2007).

3.2.1.2 Effect of the environment during seed filling on seed oil concentration

Although oil concentration is mostly genetically determined, the environment during seed filling in the mother plant may also affect the final seed oil concentration to a certain extent. In oil crops, the oil stored in the seeds is synthesized from end-products of contemporary photosynthesis, but in cases in which photosynthesis is limited, stored reserves can provide a substrate for this synthesis. Many environmental factors have been reported to affect the seed oil concentration, including the temperature, CO₂ concentration, water stress, and mineral nutrient absorption (Canvin, 1965; Thomas *et al.*, 2003; Edwards & Hertel, 2011; Hertel & Edwards, 2011). However, the magnitude of such effects is generally low, and they seem to be the consequence of effects on photosynthesis. For this reason, intercepted solar radiation during seed filling and/or the duration and activity of leaves for photosynthesis have been considered to be good predictors of final seed oil concentration in some species (for sunflower, Aguirrezábal *et al.*, 2003; Ruiz & Maddonni, 2006; Izquierdo *et al.*, 2008; Alberio *et al.*, 2015; for olive, Connor *et al.*, 2009; Cherbiy-Hoffmann *et al.*, 2013).

3.2.2 Variation in oil fatty acid composition

Lipids are mainly composed of triacylglycerol (95%), while minor components include antioxidants, vitamins, sterols, etc. Fatty acids esterified to the glycerol backbone vary in chain length (between C10 and C24) and saturation degree (saturated, mono or polyunsaturated). The most frequent saturated fatty acids in oil crops are palmitic (C16:0) and stearic acids (C18:0) and the most frequent unsaturated fatty acids are oleic (C18:1), linoleic (C18:2) and linolenic acids (C18:3), with one, two and three unsaturations, respectively. Lipid fluidity largely depends on the fatty acid concentration, since saturated fatty acids are more solid at low temperatures than unsaturated ones, and increasing the number of unsaturations increases the fluidity in parallel.

Characteristics of fatty acids may be important for industry as well as seed germination. In the former, different oil characteristics are desired by industry according to its final use. For example, oils used for direct consumption in salads need to be fluid at room temperature and stable to ensure a long shelf-life. For this use, oleic acid is preferred, although lower quantities of linoleic acid are also necessary since it is an essential fatty acid for human nutrition. In oils used for frying, fluidity is not so important and other properties become more important, such as its oxidative stability and smoke point (i.e., the temperature at which toxic compounds are formed and the oil smokes). In this case, saturated fatty acids are preferred because they are more stable than other oils. High concentrations of saturated fatty acids are also desired when the oil is developed to replace hydrogenated oils, in order to avoid the consumption of *trans* fatty acids. The concentration of *trans* fatty acids increases during industrial hydrogenation, and its consumption is associated with several pathologies, including cardiovascular disease and allergies (Hu *et al.*, 1997; Eckel *et al.*, 2007).

There is abundant evidence indicating that the fatty acid composition of the cell membranes affects the seed germination response to temperature, and this effect is associated with membrane functionality (Shahandashti *et al.*, 2013; Liu *et al.*, 2015). At low temperature, a high proportion of polyunsaturated fatty acids helps maintain membrane fluidity, thus allowing the sustained activity of membrane-bound enzymes. However, possible effects of fatty acid composition of the reserve

lipids on seed germination at different temperatures have been almost unexplored. In this sense, recent evidence suggests that reserve lipid composition may also affect seed germination performance. This issue is discussed in Section 3.3.2.

3.2.2.1 Inter- and intra-specific variations in lipids fatty acid composition

Fatty acid composition in oils is mostly genetically determined and varies widely among species. For example, there are species that produce oil with high concentrations of saturated fatty acids, such as palmitic or stearic (e.g. palm and coco), while in other species polyunsaturated fatty acids (e.g. sunflower, soybean, linseed) are prevalent. Examples of fatty acid composition and iodine value of oilseed from several species are presented in Table 3.1.

There is also genetic variability in oil fatty acid composition within a species. For example, Izquierdo and Aguirrezábal (2008) reported variability in the oleic acid concentration of seed oil among traditional sunflower genotypes. However, in most cases, mutations that affect a pathway in the lipids biosynthesis were used to develop genotypes with modified fatty acid composition. The best developed of these modified genotypes are those with mutations that increase the oleic acid concentration. An example of these mutations is the *Perventes* in sunflower (Velasco & Fernández-Martínez, 2002), which decreases the oleoyl-PC desaturase enzyme activity and thus increases the oleic acid concentration, compared to traditional genotypes (Lacombe *et al.*, 2009; Aguirrezábal *et al.*, 2015). High oleic genotypes were also developed in soybean (Takagi & Rahman, 1996; Oliva *et al.*, 2006), rape (Schierholt & Becker, 2001; Spasibionek, 2006), and other species.

Genotypes with increased saturated fatty acids have also been developed: they include high stearic or high palmitic soybean (Rahman *et al.*, 2003; Boersma *et al.*, 2012), high stearic and high stearic-high oleic sunflower or high palmitic-low palmitoleic sunflower (Fernández-Moya *et al.*, 2005; Serrano-Vega *et al.*, 2005; Garcés *et al.*, 2012; Salas *et al.*, 2014) and high stearic cottonseed (Liu *et al.*, 2002). Although saturated fatty acids are generally not desired because their consumption is associated with several cardiovascular diseases, stearic acid was reported to present neutral effects on cholesterol metabolism in humans (Crupkin & Zambelli, 2008), so genotypes with increased stearic acid concentration are preferred over those with other saturated fatty acids.

Other modifications in seed fatty acid composition have also been reported, among them, reduced linolenic acid concentration in soybean, rapeseed, and mustard (Velasco *et al.*, 2002; Spasibionek, 2006; Baux *et al.*, 2008). Examples of genotypes with modified seed oil fatty acid composition in cotton, soybean, safflower, and sunflower are presented in Figure 3.2. The potential use of transgenic plants with unusual fatty acids, such as lauric, petroselinic, ricinoleic, vernolic, crepenynic, and eleostearic has been discussed by Jaworski and Cahoon (2003).

Finally, as described for oil concentration, there are also variations in oil fatty acid composition among fruit parts. For example, the oleic acid concentration of lipids from the mesocarp and the seed of olive were >75% and <65%, respectively (García Inza, 2015).

3.2.2.2 Effect of the environment during seed formation on lipids' fatty acid composition

Although oil fatty acid composition is mostly determined by genotype, the environment during the seed filling in the mother plant can also exert some pressure. Variations in fatty acid compositions in seed oil among different environments in several species were reported, for example, in soybean (Muratorio *et al.*, 2003; McNaughton *et al.*, 2015) and olive (Rondanini *et al.*, 2011; Trentacoste *et al.*, 2012).

Several environmental factors have been reported as the likely cause of such variation in oil fatty acid composition. They include temperature (Izquierdo *et al.*, 2002; Rondanini *et al.*, 2003), solar radiation (Izquierdo *et al.*, 2009; Echarte *et al.*, 2012; Zuil *et al.*, 2012), nitrogen (Rahim *et al.*, 2015),

Table 3.1 Fatty acid composition and iodine value of stored lipids in seeds or fruits of different species.

Species	Reference	Fatty acid composition (%)					Iodine value* (g iodine/100 g lipids)
		<C16:0	C16:0	C18:0	C18:1	C18:2	C18:3
Pine (<i>Pinus radiata</i>)	(Bagci & Karaagacil, 2004)	–	4.0	2.0	16.9	45.2	17.3
Sunflower (<i>Helianthus annuus</i>)	(Harwood, 1997)	–	6.0	5.0	19.0	68.0	Trace
Soybean (<i>Glycine max</i>)	(Harwood, 1997)	–	11.0	4.0	22.0	53.0	8.0
Peanut (<i>Arachis hypogaea</i>)	(Chempro, 2015)	–	7.5	4.5	56.0	20.0	Trace
Linseed (<i>Linum usitatissimum</i>)	(Harwood, 1997)	–	6.0	3.0	17.0	14.0	60.0
Wheatgerm (<i>Triticum aestivum</i>)	(Chempro, 2015)	–	13.5	3.5	19.0	54.5	7.0
Olive fruit (<i>Olea europaea</i> L)	(COI, 2013)	–	13.8	<5.0	69.0	12.3	<1.0
Rapeseed (<i>Brassica napus</i>)	(Spasibonek, 2006)	–	5.0	1.2	65.0	18.4	8.7
Palm kernel (<i>Elaeis guineensis</i>)	(Chempro, 2015)	70.0	8.9	2.0	15.0	1.2	Trace
Coffee (<i>Coffea arabica</i>)	(Villarreal et al., 2009)	–	33.0	7.0	10.1	43.4	1.5
Corn (<i>Zea mays</i>)	(Chempro, 2015)	–	10.0	3.5	34.0	48.0	Trace
Jatropha (<i>Jatropha curcas</i>)	(Chempro, 2015)	0.9	14.4	7.0	49.0	29.0	Trace
Castor bean (<i>Ricinus communis</i>)	(Chempro, 2015)	–	2.0	1.0	7.0	5.0†	–
Safflower (<i>Carthamus tinctorius</i>)	(Chempro, 2015)	–	4.9	2.5	17.0	76.0	–
Mustard (<i>Sinapis alba</i>)	(Chempro, 2015)	–	1.5	0.4	22.0	14.2	6.8
Sesame (<i>Sesamum indicum</i>)	(Chempro, 2015)	–	8.0	4.5	45.0	40.0	110
Coconut (<i>Cocos nucifera</i>)	(Chempro, 2015)	79.0	9.5	2.0	6.5	Trace	Trace
Rice (<i>Oryza sativa</i>)	(Wrigley et al., 2004)	–	15.0	<3.0	45.0	35.5	<1
Cottonseed (<i>Gossypium hirsutum</i>)	(Wrigley et al., 2004)	2.0	21.5	1.5	27.5	50.0	–

*Iodine value was calculated as = (%C 18:1 x 0.860) + (%C 18:2 x 1.732) + (%C 18:3 x 2.616).

† In castor bean almost 90% of fatty acids correspond to ricinoleico (12-hidroxi-9-*cis*-octadecenoico).

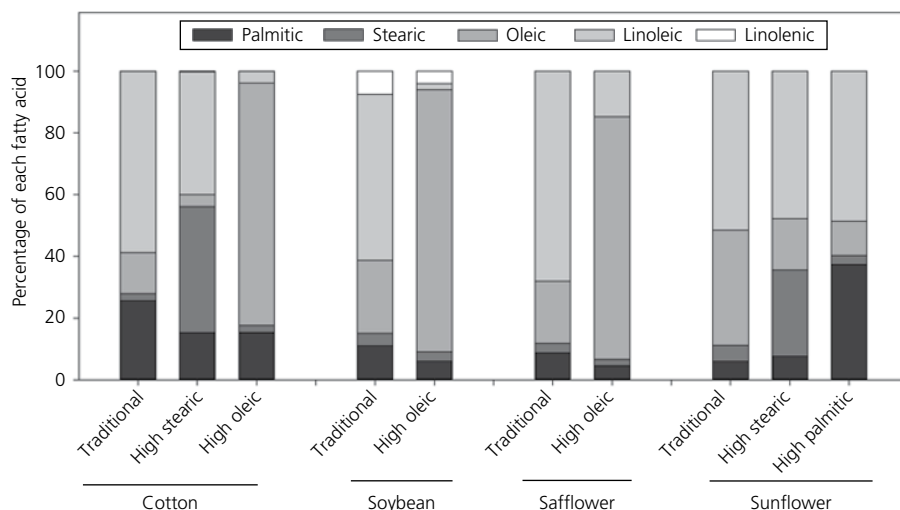


Figure 3.2 Oilseed fatty acid composition, for traditional and genetically modified genotypes within a species. Data were obtained from Liu *et al.* (2002) for cotton, Serrano-Vega *et al.* (2005) for sunflower, and Wrigley *et al.* (2004) for soybean and safflower.

soil salinity (Flagella *et al.*, 2004; Di Caterina *et al.*, 2007) and water availability (Pritchard *et al.*, 2000; Baldini *et al.*, 2002; Roche *et al.*, 2006), among others. The variations in fatty acid composition occur via effects on the enzyme activities of the lipid biosynthesis systems and/or via effects on the substrates for that synthesis. For example, in sunflower, it has been shown that increasing the temperature during seed filling reduces the activity of the oleate desaturase enzyme, increasing the concentration of oleic acid at the expense of linoleic acid. This increase in monounsaturated/polyunsaturated fatty acids when temperature increases was also reported for other species, for example, soybean and maize (Izquierdo *et al.*, 2009) and safflower (Esteban *et al.*, 2004). In olive, although the first report showed an inverse trend, (i.e. increasing temperature reduced oleic acid concentration), it was recently found that this inverse trend occurs only in lipids of the fruit, while the composition of seed lipids presents the same trend as that reported for seeds of other oil crops (García Inza, 2015).

The effect of the environment on oil fatty acid composition varies among species. For example, increasing temperature from 13 to 25°C increased the oleic acid concentration from 17 to 59% in sunflower but only from 24 to 34% in soybean (Izquierdo *et al.*, 2009). There is also variability among genotypes within a species regarding the response of fatty acid composition to environmental conditions. For example, high oleic genotypes in sunflower present a more stable fatty acid composition than traditional genotypes in a wide range of temperatures during grain filling (Tribou-Blondel *et al.*, 2000; Izquierdo & Aguirrezábal, 2008).

3.3 How quantity and composition of oil reserves may affect germination

Because of its role in stand establishment, germination is one of the most important events in crop production. Many physiological aspects relevant to seed germination, including seed longevity, dormancy, and water absorption, may be affected by seed composition. Furthermore, models have

been developed to characterize germination under different temperature and water availability conditions. Parameter values resulting from fitting these models to germination data of seeds from different genotypes may be used to evaluate the impact of oilseed composition on germination.

3.3.1 Models describing seed germination performance

In the field, temperature and water availability are the major environmental factors controlling seed germination under non-limiting oxygen conditions (Bewley *et al.*, 2013). To describe and quantify the germination response of seed lots to prevailing temperature and water potential Garcia-Huidobro *et al.* (1982) and Gummerson (1986) developed the thermal-time and hydro-time models, respectively.

The thermal-time model is based on the accumulation of thermal-time units (i.e., degree-days) above a minimum or base temperature (T_b) for the process to proceed. The model assumes that T_b is unique for the seed population, while thermal-time required for germination (θ_T) is different for each seed fraction ($\theta_{T(g)}$), thus accounting for the spread in germination times in the seed population. This model characterizes the germination time-course curves for a seed population through the following equation:

$$\theta_{T(g)} = (T - T_b) t_g \quad (3.1)$$

or,

$$GR_g = 1 / t_g = (T - T_b) / \theta_{T(g)} \quad (3.2)$$

where GR_g is the germination rate of fraction g of the seed population and T is the germination temperature. This means that each seed fraction requires a certain amount of $\theta_{T(g)}$ to germinate that will be accumulated above T_b , depending on prevailing temperature; thus, as the difference between $T - T_b$ increases, t_g decreases proportionately (i.e., the seeds germinate faster). The model is applied in the suboptimal temperature range, between T_b and T_o (T_o is the temperature where the germination rate is maximum), where the germination rate linearly increases with the temperature.

The appliance of this thermal-time approach has been a useful tool in modeling and analyzing germination responses of different species to sub-optimal temperatures (Garcia-Huidobro *et al.*, 1982; Dahal & Bradford, 1994; Wang *et al.*, 2004; Hardegree, 2006). This thermal-time analysis has been extended to account for the effect of temperature on germination in the supra-optimal thermal range, between T_o and T_m (the maximum temperature for seed germination (Covell *et al.*, 1986; Ellis *et al.*, 1986; Hardegree, 2006). However, under most usual cropping conditions in temperate climates, the seed bed soil temperature is within the sub-optimal thermal range, thus the application of the model to the supra-optimal thermal range will not be discussed further in the present chapter.

The hydro-time model is conceptually similar to the thermal-time model but takes into account the effect of water availability on seed germination. In this model, seeds require to accumulate a certain quantity of hydro-time (MPa-hours or MPa-days) to germinate. Hydro-time units are accumulated above a minimum or base water potential (Ψ_b) for the process to proceed, a similar concept to that of T_b for the effect of temperature on seed germination. However, in the hydro-time model, it is assumed that all seeds in the population need to accumulate an equal quantity of hydro-time for germination, while seed fractions vary in their Ψ_b thresholds above which hydro-time units are accumulated; below this $\Psi_b(g)$ value, radicle protrusion is prevented for each seed fraction. In this case, the spread in germination times among individual seeds is accounted for by the variation in Ψ_b

for different seed fractions, $\Psi_b(g)$. This distribution of the values of $\Psi_b(g)$ in the seed population can be characterized by their mean and standard deviation assuming that $\Psi_b(g)$ values are normally distributed among seeds in the population (Gummerson, 1986; Bradford, 1990; 1995). Based on the above considerations, the hydro-time model can be defined as stated by (Gummerson, 1986):

$$\theta_H = [\Psi - \Psi_{b(g)}] t_g \quad (3.3)$$

or,

$$GR_g = 1/t_g = [\Psi - \Psi_{b(g)}] / \theta_H \quad (3.4)$$

By analogy with the thermal-time concept, the time to germination for a given seed fraction (g) is inversely related to the magnitude of the difference between the current environmental Ψ and the Ψ_b for that fraction ($\Psi_b(g)$). This means that all seeds in the population require the same amount of θ_H to germinate, but it will be accumulated for each seed fraction according to the distribution of Ψ_b in the seed population and the current Ψ of the germination medium. The hydro-time model has been successfully used for modeling and analyzing seed responses to water potential in many cultivated and wild species (Alvarado & Bradford, 2002; Batlla & Benech-Arnold, 2004; Finch-Savage *et al.*, 2005; Boddy *et al.*, 2012; Schellenberg *et al.*, 2013).

The thermal-time and the hydro-time models can be combined into a single model that accounts for the combined effect of sub-optimal temperature and water availability on seed germination, the hydro-thermal-time model. This approach has been shown to successfully describe the germination curves of various species over a wide range of temperatures and water potentials. Although in this chapter we are not going to examine further the hydro-thermal-time model approach, there are outstanding examples in the literature covering this issue (Bradford, 2002; Alvarado & Bradford, 2005; Finch-Savage *et al.*, 2005; Allen *et al.*, 2007; Bloomberg *et al.*, 2009a, 2009b; Bewley *et al.*, 2013).

3.3.2 Does the concentration and composition of oil reserves affect seed germination?

Not much has been written about the effect of the quantity and/or composition of lipids reserves on seed germination. This is particularly relevant for oil crops' seed which display lipid concentrations as high as 38–53% (de la Vega *et al.*, 2007; Izquierdo *et al.*, 2008). It is necessary to know these effects, considering the wide variability in those traits among and within species. In particular, it is important for breeders to understand how the variations in seed oil quantity and fatty acid composition could affect the seed germination performance.

3.3.2.1 Effect of seed lipid concentration on water absorption

Considering that lipids are hydrophobic it could be expected that their concentration in the seed might at least affect the water absorption in the beginning of seed germination. However, there is almost no information regarding this possible effect in the literature. In sunflower, González Belo *et al.* (2014a) analyzed the dynamics of water absorption by seeds when they were incubated in either distilled water or in a solution with a water potential of -0.9 MPa. It was observed that the rate of water absorption was inversely associated with the seed lipid concentration (Figure 3.3) independent of the water potential of the medium. However, germination was not delayed because of the higher oil concentration. In fact, seeds with high oil concentration germinated with a lower content of water in the seed (Figure 3.4), because they reached the equilibrium moisture content

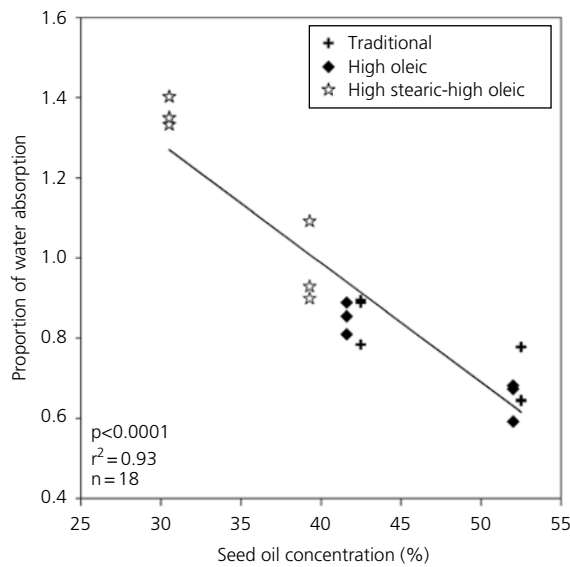


Figure 3.3 Water absorption (given as proportion of initial seed weight) at the moment of radicle protrusion, plotted against seed oil concentration in three sunflower genotypes (a traditional, a high oleic and a high stearic-high oleic). Seeds were incubated at 5°C and embedded with distilled water (0MPa) with or without seed coats.

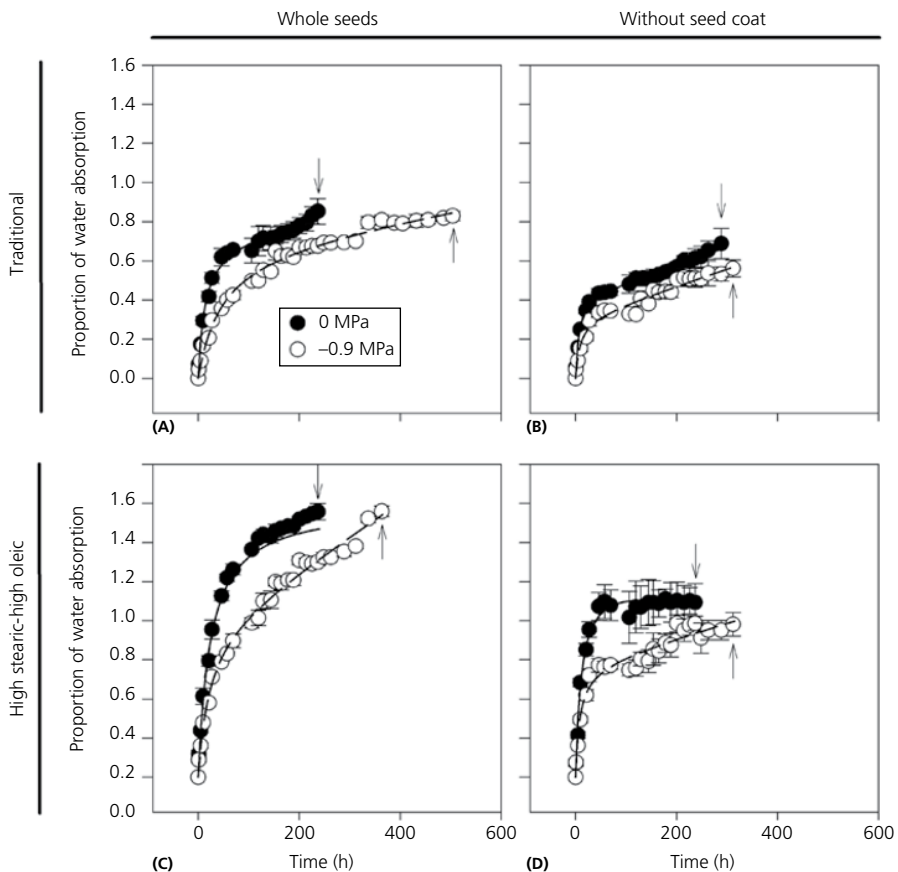


Figure 3.4 Dynamics of water absorption (given as proportion of initial seed weight) of two sunflower genotypes with contrasting seed oil concentration (30.5 vs. 42.5%). Seeds were incubated at 0 MPa (distilled water) or -0.9 MPa (polyethylene glycol solution) at 5°C with or without seed coats. Arrows indicate protrusion of the first radicle in each seed lot.

with lower water absorption. The results were similar even when seeds were incubated without their seed coat, which is the first barrier for water uptake (Dahal & Bradford, 1994) (Figure 3.4). González Belo *et al.* (2014a) also compared genotypes with different oil fatty acid composition (traditional, high oleic and high stearic-high oleic; with iodine values ranging from 65 to 141 g iodine/100g oil), and the differences in water absorption were attributable to variations in seed oil concentration. On the other hand, changes in fatty acid composition seem not to affect the rate of water absorption.

3.3.2.2 Effect of seed oil composition on germination performance

The available studies about the effect of oil fatty acid composition on germination ability are scarce and sometimes contradictory. For example, a negative linear relationship between time to germination and linoleic acid concentration was observed in sunflower seeds incubated at 4°C (Downes, 1985); however, Murcia *et al.* (2006) did not find any relationship between oleic and linoleic acid concentrations and mean germination time in this species. Recent work done by González Belo *et al.* (2014b) reported significant differences among sunflower genotypes' germination responses to temperature. Based on a thermal-time analysis of sunflower seed germination at different temperatures, these authors found that the variability observed in T_b among different tested genotypes could be partially accounted for by the differences in fatty acid composition, showing an increase in T_b values with an increment in oleic acid concentration and a decrease with an increase in linoleic acid (see Figure 6 in González Belo *et al.*, 2014b). In line with these results, Hernandez and Paoloni (1998) tested germination and the field emergence of four sunflower genotypes differing in their fatty acid composition, and found that the germination rate under sub-optimal temperatures (15–20°C) and the days taken from sowing to first emergence in early sowing dates were inversely related to the genotype linoleic to oleic acid content ratio. Differences in time to first emergence in the field were scored for three different sowing dates in order to expose seeds to different thermal environments during the sowing-emergence phase. These authors observed that early sowing dates (and also low soil temperature, 8.2°C) result in longer sowing-emergence periods. Similarly, and as mentioned above, Downes (1985) observed that stand establishment in the field in a winter sowing increased significantly with an increment in seed linoleic acid content.

A relationship between fatty acid composition and germination was also reported for species other than sunflower. Bartkowski *et al.* (1977) also reported that cotton seedling emergence under field conditions with a low soil temperature exhibits a strong positive correlation ($r > 95\%$) with unsaturated to saturated fatty acid ratios of total seed and polar lipids. Duhalde *et al.* (1991) found that maize inbred lines, which achieved higher germination percentage at low temperatures (7°C), presented a higher linoletae to oleate ratio than those of cold-sensitive lines. Such differences were greater in the phospholipids than in the triacylglycerols, which is consistent with the hypothesis that germination cold sensitivity can be ascribed to cell membrane-related events. Additionally, through reciprocal crossing of cold-tolerant and sensitive lines, Duhalde *et al.* (1991) showed that the linoletae to oleate ratio is an inheritable trait mainly affected by the maternal genotype. Finally, Miquel and Browse (1994) observed that seeds of *fad2* mutant *Arabidopsis thaliana* with reduced lipid contents had a slower germination at 10°C and 6°C than wild type seeds, suggesting that for some oilseed species at least, molecular genetic manipulation of oleate levels in the oil may result in plant lines with an unacceptable performance in the field.

The relationship between germination performance and lipid unsaturation among oil crops was further investigated through a meta-analysis of the existing literature. In this analysis, T_b was

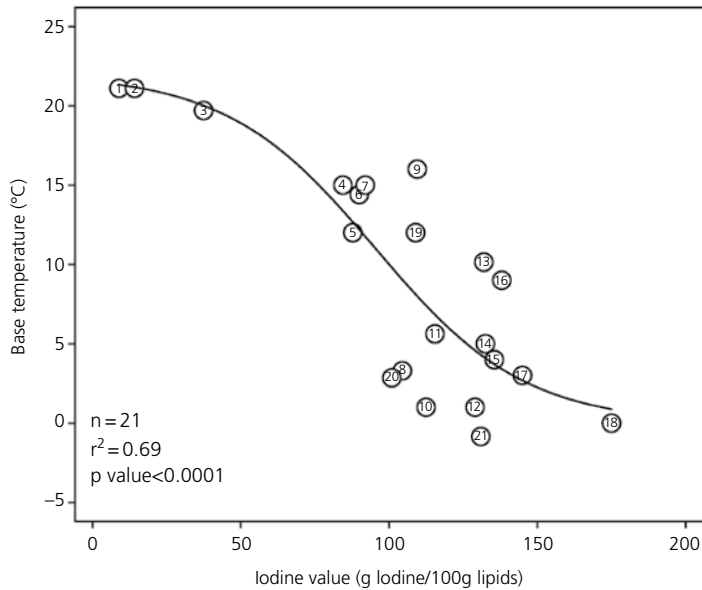


Figure 3.5 Base temperature for seed germination (°C) as a function of iodine value of seed lipids. Data of iodine value correspond to those of Table 3.1. Base temperature data for the different species (indicated by a number within each symbol) are from (1) Coconut (Meerow & Broschat, 1996); (2) Palm kernel (Meerow & Broschat, 1996); (3) Cacao (Daymond & Hadley, 2004); (4) Castor bean (Amorim Neto *et al.*, 2001); (5) Coffee (Lima & da Silva, 2008); (6) Jatropha (Windauer *et al.*, 2012); (7) Peanut (Ketring *et al.*, 1982); (8) Mustard (Dorsainvil *et al.*, 2005); (9) Sesame (Bennett, 2011); (10) Canola (Edwards & Hertel, 2011); (11) Corn (Finch-Savage *et al.*, 2005); (12) Wheat germ (Seefeldt *et al.*, 2002); (13) Grapefruit (Orrù *et al.*, 2012); (14) Sunflower (Khalifa *et al.*, 2000); (15) Soybean (Covell *et al.*, 1986); (16) Pine (Bloomberg *et al.*, 2009a); (17) Safflower (Balashahri *et al.*, 2013); (18) Linseed (Kurt, 2012); (19) Cottonseed (Ludwig, 1932); (20) Rice (Adam *et al.*, 2010); (21) Quinoa (Bois *et al.*, 2006).

plotted against the iodine value of seed lipids (Figure 3.5). An inverse sigmoidal relationship was found, indicating that the lower the iodine value (i.e., the degree of oil unsaturation), the higher the base temperature. This relationship includes saturated species, such as coconut or palm, with iodine values close to 10 g iodine/100 g lipid and very unsaturated species, such as safflower and linseed with iodine values >140 g iodine/100 g lipid. The sigmoidal aspect of the relationship found suggests the existence of upper and lower T_b values, which in turn may correspond to the biological temperature range under which germination occurs.

Taken together, the evidence supports the notion that increasing the level of polyunsaturated fatty acid can ameliorate seed performance in the field at low temperatures, through a reduction of T_b . Although González Belo *et al.* (2014b) also reported changes in thermal-time required for 50% germination ($\theta T_{(50)}$) in association with the variation in genotypes' fatty acid composition, $\theta T_{(50)}$ decrease with increasing oleic acid concentrations and increase with an increase in linoleic acid, showing an inverse relationship to that described before for T_b . This could be possibly just an artifact of the compensation for changes in T_b in the thermal-time analysis and may play a minor role in the germination behavior of seeds in the field. Furthermore, a meta-analysis to relate thermal-time and the seed oil iodine value of different oil crops is still not possible, as the literature regarding germination model parameters other than T_b is still very scarce.

3.3.2.3 Biochemical aspects of the oil composition effects on germination performance

The fatty acid composition of the cell membranes may affect their functionality, and ultimately the seed germination. At low temperatures, a high proportion of the polyunsaturated fatty acids maintains membrane fluidity, thus allowing sustained activity of membrane-bound enzymes (Li *et al.*, 2015). However, while the effects of membrane composition on seed germination are well known (e.g., Steim *et al.*, 1969; Nishida & Murata, 1996; Gomès *et al.*, 2000), the possible effects of fatty acid composition of the reserve lipids on seed germination at different temperatures remain almost completely unexplored. The possible mechanisms involved in these responses include variations in membrane functionality and reserve lipids' breakdown during germination. First, it is well known that a phase transition of membrane lipids, from crystalline-liquid to solid gel, takes place when the temperature decreases (Steim *et al.*, 1969; Nishida & Murata, 1996), and this process affects the membrane permeability and the enzyme functionality (Gomès *et al.*, 2000). The temperature at which this change occurs depends on the lipid composition, being lower with higher lipids' unsaturation. Sunflower genotypes with modified fatty acid composition have been shown to present variations in both reserve and membrane lipids (Fernandez-Moya *et al.*, 2000). Therefore, a better membrane functionality at low temperatures in genotypes bearing a high percentage of polyunsaturated fatty acids might be expected and this might explain the fact that T_b was inversely related to the linoleic acid concentration.

The second possibility concerns the oil reserve breakdown in germinating seeds. During the early phases, reserves located near the embryo are the most important ones to provide energy to the germinating seed (Nonogaki *et al.*, 2010; Sanchez-Linares *et al.*, 2012; Bewley *et al.*, 2013). These reserves become accessible via a hydrolization catalyzed by a triacylglycerol lipase, and then oxidation of the free fatty acids occurs. For triacylglycerol with linoleic acid, there is a specific linoleate 13-lipoxygenase enzyme that is capable of oxygenating linoleate still sterified to the triacylglycerol, without the preceding action of a lipid-hydrolyzing enzyme (Feussner *et al.*, 1997). The oxygenated fatty acid fraction is preferentially released from the lipid bodies to undergo oxidation (Feussner *et al.*, 2001). Therefore, genotypes with a high concentration of linoleic acid would have an advantage during germination by presenting this preferential pathway of lipid breakdown.

3.3.2.4 Other germination aspects modified by seed oil quantity and composition

Fatty acid composition was also found to modify base water potential (Ψ_b); indeed, a high oleic genotype showed a much lower (i.e., more negative) base water potential (Ψ_b) than other genotypes when incubated at low temperatures (i.e., 5°C) and a slightly lower one when incubated at higher temperatures (González Belo *et al.*, 2014b). These results suggest that improving germination at low temperatures might work against the possibility of ameliorating seed performance at low soil water content. On the other hand, at low water potentials and high temperatures, an induction of thermo-dormancy took place, resulting in greatly reduced final seed germination in all the genotypes studied (González Belo *et al.*, 2014b).

Two other aspects of seed performance might be considered in relation to oil and oil-type concentration: dormancy and longevity. Dormancy is a complex trait and it would not be surprising that modifications in oil or oil-type concentration would lead to changes in dormancy. Unfortunately no research has been carried out in that respect to the best of our knowledge. Similarly, seed longevity might be modified through oil concentration. It is well known that seeds rich in lipids have limited longevity due to their specific chemical composition; for example, sunflower seed storage demands special attention due to its high oil content (Balešević-Tubić *et al.*, 2010). But, on the other hand, seed protection against the deteriorative effect of reactive species is mediated by means of

different protective molecules that scavenge free radicals; among them, tocopherols (Vitamin E) can be mentioned, which are poorly soluble in water but are lipid-soluble. From this, it could be argued that, contrary to the generally accepted short longevity of oilseeds, a high oil content might favor the antioxidant protection from tocopherols. Certainly, research is required to clarify this relationship between seed oil composition and longevity.

3.4 Conclusion and future prospects

Based on the still limited available literature, in this chapter we have reviewed evidence suggesting that seed composition may affect its germination performance. Seed lipid concentration appears to affect the dynamics of water absorption, without an impact on the parameter values of thermal-time or hydro-thermal-time models. On the other hand, the lipid fatty acid composition of oil reserves appears to exert an important effect on germination.

The unsaturation of seed oil reserves appears to be associated with the minimum temperature for germination. The mechanisms underlying this relationship are still unknown and require more investigation. However, this result is important not only to understand the variability in T_b among species (e.g., temperate vs tropical species) but also to predict the germination performances of new designed genotypes with modified fatty acid composition.

As a consequence of global change, mean temperatures are rising, but also the likelihood of extreme temperature events (Christensen *et al.*, 2007). Rising temperatures during the maturation of seeds may affect not only their oil fatty acid composition by decreasing the unsaturation of oil reserves, but also their ability to germinate at low temperatures, because of rising T_b . This could be further aggravated by the occurrence of late freezing events (that would keep soil temperatures very low) in species that are sown in Spring. There is wide evidence that the frequency of such events is rising as a consequence of global change. These considerations may be relevant when breeding species with modified composition of lipid reserves.

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