CHAPTER 16

Management and Breeding Strategies for the Improvement of Grain and Oil Quality

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1. INTRODUCTION

The quality of a harvested organ can most simply be defined as its suitability to the intended market or processing and product manufacture. The term quality may therefore encompass many criteria, as the compositional (chemical) and textural (biomechanical) requirements may vary from one product to another. For example, for oilseed sunflower it includes the potential industrial yield, the nutritional value of the oil and its stability (Box 1). For bread wheat, it includes the milling performance, the dough rheology, the baking quality, the nutritional value for humans or animals and its suitability for storage. Moreover, for a given end product, the relative importance of quality attributes changes along the market chain from grower to consumer. For example, elevated oil or protein concentration is of economic importance for farmers where a premium is paid for these attributes, whereas high baking quality in wheat or oxidative stability in oilseeds are of economic importance to food manufacturers. Also for a given crop species, quality criteria vary depending on the product end use (Box 1). For example, high-protein flours are required for leavened bread or pasta, while their low-protein counterparts are desirable for biscuits, crackers, cakes or oriental noodles. An efficient agro-industrial production system, therefore, needs to know the year-to-year variation in composition of raw materials that can be obtained in different regions or under different management practices.

The identification of novel genes or loci with major effects on quality traits has resulted in new cultivars with improved quality (Velasco and Fernandez-Martinez, 2002; DePauw et al., 2007, Chapter 14). Nonetheless, dealing with genotype-by-environment (G × E) interactions, and with pleiotropic effects (i.e. trait-by-trait interactions) remains a major difficulty in plant breeding, especially for grain quality (de la Vega and Chapman, 2001). A physiological perspective provides useful insights into G × E, as shown in this and other chapters of this book (Section 3.1 in Chapter 11; Sections 3 and 4 in Chapter 10). Further in this chapter, we argue that grain oil and protein concentration and composition are primarily determined at the crop level, and cannot be correctly understood or predicted by extrapolating from the individual plant to the population. We will show how physiological concepts and methods classically applied to yield analysis can be used to investigate and model the genetic and environmental determinants of grain oil and protein concentration and composition, for example, identification of critical periods (Section 5 in Chapter 12; Section 3.2.2 in Chapter 15), kinetics of biomass and nitrogen accumulation and partitioning (Chapters 7 and 8). Models can range from detailed mechanistic descriptions to simple response curves to environmental variables, which are 'meta-mechanisms' at the plant or crop level (Tardieu, 2003). If models are robust enough, one set of parameters represents one genotype (Hammer et al., 2006; Chapter 10), and thus they can be used to analyse complex traits with G × E and pleitropic effects.

BOX 1 Selected properties of vegetable oil and its components

Vegetable oils are composed mainly of triglycerides (or triacylglycerol, TAG), which are formed by the esterification of three fatty acids with a glycerol. Fatty acids are usually classified based on the length of their carbon chain and the number and position of double bonds. The fatty acid composition defines the nutritional, industrial and organoleptic quality of the oil. Fatty acids are expressed as a percentage of all the fatty acids in the oil.

Saturated fatty acids, with the exception of stearic acid, increase the levels of cholesterol in humans (Velasco and Fernandez-Martinez, 2002). Polyunsaturated acids, such as linoleic acid, are essential to mammals, have a potent hypocholesterolemic effect and reduce the risk of cardiovascular diseases (Kris-Etherton and Yu, 1997). They can also be used as feed to dairy cattle yielding milk with a high level of conjugated linoleic acid (Kelly et al., 1998). On the other hand, saturated fatty acids provide the oil a higher oxidative stability than unsaturated fatty acids. Therefore, for cooking and food industry, sunflower oils with oleic acid concentration near those of mid-oleic cultivars (oleic acid concentration between 60 and 79%) are often preferred (Binkoski et al., 2005). Oils with high concentration of oleic acid also allow for margarine with less proportion of undesirable *trans* fatty acids. For biodiesel, oils containing fatty acids with low degree of unsaturation are preferable, because they decrease the iodine index (inversely related to stability), and increase biodiesel cetane number (a measure of combustion quality) (Clements, 1996).

Tocopherols (α, β, γ and δ isomers) are natural antioxidants that inhibit lipid oxidation in biological systems by stabilising hydroperoxyl and other free radicals (Bramley et al., 2000). The antioxidant activity of tocopherols increases oil stability (Martínez de la Cuesta et al., 1995; Bramley et al., 2000). Tocopherols are essential for humans, and they have been associated with delayed cellular aging (White and Xing, 1997), reduced risk of cardiovascular diseases and regression of several cancers in cell culture. At high temperatures, β- and γ-tocopherols present a higher antioxidant activity than α-tocopherol and are thus preferred for cooking oil. On the other hand, α-tocopherol has the highest vitamin E activity compared to the other three isomers (Mullor, 1968).

In this chapter, quality is restricted to the biochemical composition of grains, and the focus is on sunflower as an oilseed model and bread wheat as a cereal model. Comparisons with other species are included to emphasise similarities and differences with these model crops. The rationale for the use of these model species is threefold. First, research on model species has proven useful in other areas of knowledge, for example, *Arabidopsis thaliana* and rice as models for dicotyledonous and monocotyledonous plants in genetics, respectively. Second, grain oil and protein, major storage compounds in sunflower and wheat, are important in human and animal diets and increasingly important for non-food uses. Third, our knowledge of quality aspects in these two species is sufficient to allow for meaningful quantitative models that capture major genetic, environmental and G $\times$ E effects.

This chapter comprises three main parts. First, we briefly review the effects of environmental, genetic and G $\times$ E factors on grain oil and protein concentration and composition. Second, we outline process-based crop models accounting for grain yield in both species, and for concentration and composition of oil (sunflower) and protein (wheat). Third, we use a combination of modelling and experiments to analyse the relationships between quality traits and yield, and management and breeding strategies for the improvement of grain quality.

2. ENVIRONMENTAL AND GENETIC EFFECTS ON GRAIN OIL AND PROTEIN CONCENTRATION AND COMPOSITION

2.1. Oil concentration

Grain oil accumulates mainly in the endosperm (e.g. castor bean and oat), embryo cotyledons and axis (e.g. rapeseed and sunflower), embryo scutellum and aleurone layer (e.g. maize) or mesocarp (e.g. olive and oil

palm), depending on the species (Murphy, 2001). Grain oil concentration (usually expressed in percent of grain dry mass) mainly determines the industrial yield of the grains. As a consequence, in some countries, sunflower grains with an oil concentration above a threshold are paid a premium over the regular price.

Grain oil concentration is genetically determined, and plant breeding has improved it in many crops. In sunflower, low-oil varieties and hybrids (38–47% oil) have been replaced by modern high-oil hybrids (47–53% oil; de la Vega et al., 2007; Izquierdo et al., 2008). In maize and oat, high-oil hybrids (up to 18%) have been developed, although most of currently grown hybrids have 3.9–5.8% oil (Frey and Holland, 1999). The improvement in oil concentration was mainly achieved by increasing the proportion of tissue in which oil is stored (e.g. Doehlert and Lambert, 1991, in maize; Tang et al., 2006, in sunflower) rather than by increasing the oil concentration in this tissue. In sunflower, the difference in oil concentration between low-oil and high-oil hybrids is caused by differences in the duration rather than the rate of oil accumulation (Mantese et al., 2006; Izquierdo et al., 2008).

High oil concentration is associated with a high sensitivity of oil concentration to environmental conditions, as opposed to the almost stable oil concentration of low-oil hybrids (Dosio et al., 2000; Izquierdo et al., 2008), even when genotypes differ only in a single genetic region (8.1 cM) conferring the high-oil trait (León et al., 1996). Environmentally induced variation of sunflower grain oil concentration has been largely related to variation in embryo oil concentration (Santalla et al., 2002; Izquierdo et al., 2008). Variation in grain oil concentration associated with changes in the embryo-to-pericarp ratio has been found in response to temperatures above 30 °C (Rondanini et al., 2003).

Grain oil is synthesised from carbohydrates either from current photosynthesis or from the remobilisation of storage carbohydrates (Hall et al., 1990). Therefore, grain oil accumulation greatly depends on the carbon economy of the crop during grain filling (Andrade and Ferreiro, 1996; Dosio et al., 2000). In sunflower, grain oil concentration is mainly determined by the amount of photosynthetically active radiation (PAR) intercepted per plant during the grain-filling period (Andrade and Ferreiro, 1996; Dosio et al., 2000; Izquierdo et al., 2008). Likewise, in rapeseed, Izquierdo (2007) found reductions in oil concentration from 50.3 to 36.3% when incident radiation was reduced by 80%. In contrast, Andrade and Ferreiro (1996) did not detect any effect of intercepted radiation on grain oil concentration in soybean and maize. Other authors have attempted to use the source–sink ratio as the explanatory variable, finding either no relationship (Ruiz and Maddonni, 2006) or a relationship worse than that of source alone (Izquierdo et al., 2008).

In sunflower, final grain dry mass and oil concentration are most sensitive to the amount of intercepted radiation between 250 and 450 °C day after flowering (base temperature 6 °C; Aguirrezábal et al., 2003). A linear–plateau relationship between final grain oil concentration and intercepted radiation during the mentioned period was found, with a maximum (OC_{max}) at approximately 26.3 MJ per plant for high-oil hybrids (Dosio et al., 2000; Izquierdo et al., 2008; Figure 1a). This critical period, however, has not been detected yet in other oil crops (Izquierdo, 2007).

The response of grain oil concentration to temperature during grain filling depends on the species. For flax, both the quantities of oil per grain and oil concentration decrease linearly with daily average temperature between 13 and 25 °C (Green, 1986). For soybean, grain oil concentration increases with daily average temperature up to approximately 28 °C and decreases with higher temperature (Piper and Boote, 1999; Thomas et al., 2003). In sunflower, the duration of the grain-filling stage is inversely related to temperature (Ploschuk and Hall, 1995; Villalobos et al., 1996), and thus higher temperature would shorten the time for radiation interception and therefore reduce grain oil concentration (Aguirrezábal et al., 2003). However, results from the field should be interpreted with caution, since variations in temperature and radiation are usually correlated. Under controlled conditions, where temperature and daily radiation were decoupled, oil concentration has been inversely related to temperature (Canvin, 1965; Geroudet and Aguirrezábal, unpublished results). With temperature above 30 °C, oil concentration can decrease markedly, depending on the stage of grain filling (Rondanini et al., 2003, 2006).

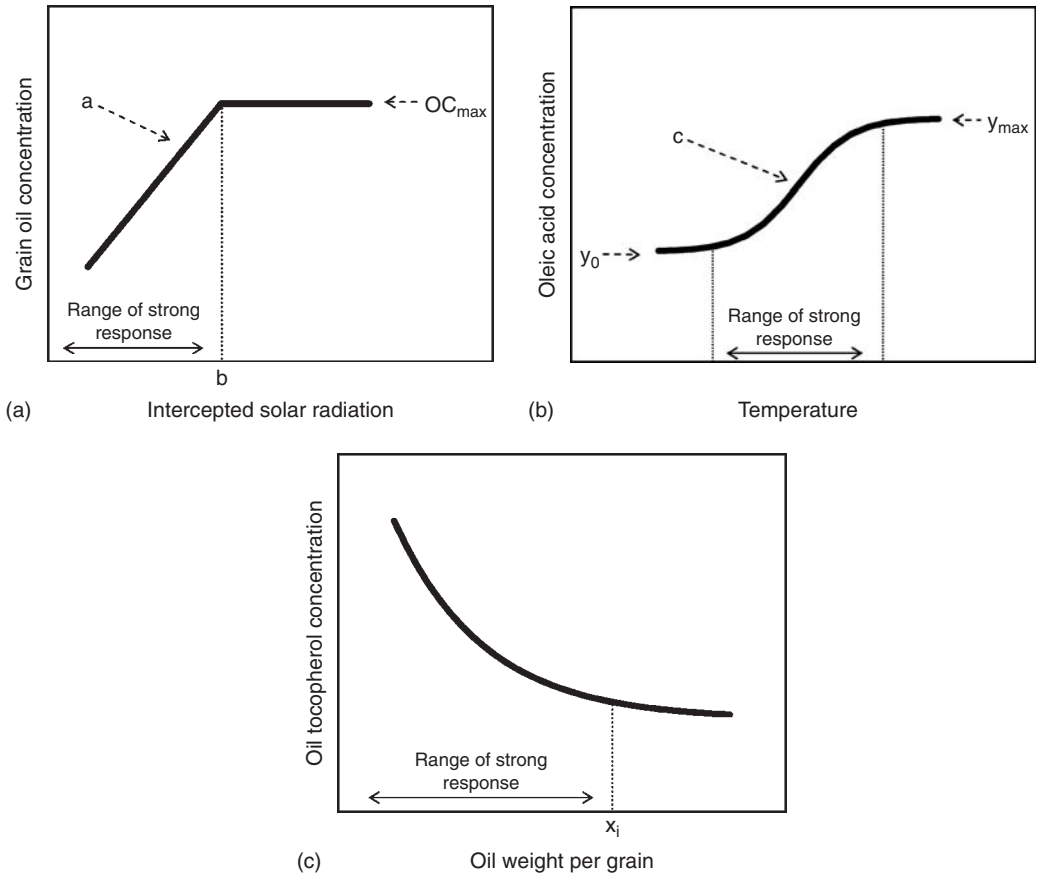

FIGURE 1

Modelling quality traits in sunflower, an oilseed model crop. (a) Linear-plateau response of grain oil concentration to intercepted solar radiation during the period 250–450°C day after flowering; parameters are the slope of the linear phase (a), the minimum intercepted radiation to obtain the maximum oil content (b), and the maximum oil concentration (OC_{max}). (b) Sigmoid function describing the relationship between oleic acid concentration and minimum night temperature during the period 100–300°C day after flowering; parameters are the maximum slope (c), the minimum oleic acid concentration (y_0) and the maximum oleic acid concentration (y_{max}). (c) Negative exponential relationship between oil tocopherol concentration and oil weight per grain; x_i is the oil weight per grain above which oil tocopherol concentration shows a stabilisation-like phase.

Water deficit during grain filling, even for a short period, can reduce grain oil concentration (Hall et al., 1985). The first effect of water shortage is the reduction of leaf expansion, which could have significant effect on radiation interception and thus on grain oil concentration. More severe water deficit can also affect leaf photosynthesis or accelerate leaf senescence, thereby reducing the availability of carbohydrate for oil synthesis. Excess nitrogen availability can also affect oil concentration, mainly through an increase in protein concentration (Steer et al., 1984, and references therein). While part of the effect of other environmental factors and management practices can be explained by their effect on intercepted radiation per plant, temperature or crop photosynthesis (e.g. foliar diseases, sowing date and sowing density), these factors can also have direct effects on grain oil concentration, as it has been shown for other oil yield components (Andrade et al., 2002). More research is needed to clarify this issue.

2.2. Oil composition

Fatty acid composition is the main determinant of oil quality, as outlined in Box 1. Fatty acid chains are built through a cycle of biochemical reactions involving the multi-enzyme fatty acid synthase FAS and the low-molecular-weight acyl carrier protein ACP. They are converted to acyl-CoA and then incorporated into TAG. The desaturation of fatty acids is mediated mainly by the enzymes stearoyl-ACP desaturase, oleoil-ACP desaturase and linoleoil-ACP desaturase. Although our knowledge of the enzymes involved in the synthesis and the desaturation of oil fatty acids, the genes that code for these enzymes and their environmental regulation has increased over the past years, our understanding of the regulation of oil synthesis and storage is still far from complete.

Oil fatty acid composition is genetically controlled. The fatty acid composition of oil varies largely among species, and also within species (Figure 2). The oil composition of traditional high-linoleic cultivars of sunflower has been modified, mostly by altering the function of major genes through mutagenesis (Lagravere et al., 1998; Fernández-Martínez et al., 1989; Lacombe and Bervillé, 2000). High-oleic cultivars have over 80% oleic acid resulting from a reduced activity of oleoil-ACP desaturase (Garcés and Mancha, 1991; Kabbaj et al., 1996). Mid-oleic sunflower oil (60–79% oleic acid) is usually produced by crossing a high oleic and a traditional line. Sunflower lines with increased concentrations of saturated fatty acids (high stearic or high palmitic) were also developed (Osorio et al., 1995; Fernández-Martínez et al., 1997). High-stearic sunflower cultivars are the result of low activity of the enzyme stearoyl-ACP desaturase or of high activity of the enzymes FATA and FATB, which increase the accumulation of stearic acid in the endoplasmic reticulum and thus reduce its desaturation.

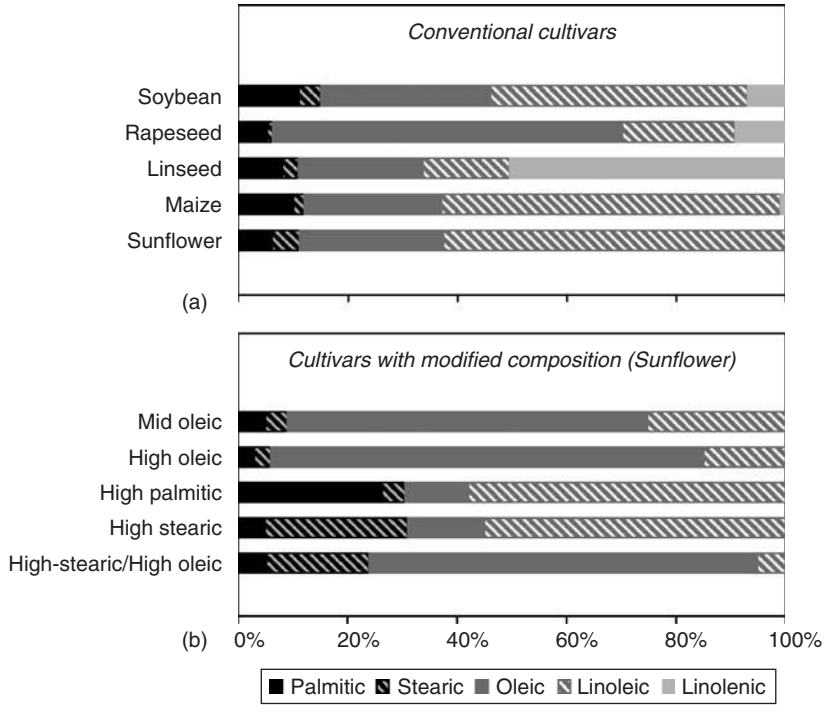

FIGURE 2

Typical oil fatty acid composition for (a) conventional cultivars of soybean, rapeseed, linseed, maize and sunflower and (b) sunflower cultivars with modified fatty acid composition: mid oleic, high oleic, high palmitic, high stearic and high stearic/high oleic. (Source: Data from Velasco and Fernandez-Martinez, 2002; Aguirrezábal and Pereyra, 1998; Izquierdo, unpublished.)

Inbred lines combining the high-stearic trait with the high-oleic trait (high stearic or high oleic) have also been obtained (Serrano-Vega et al., 2005). High-oleic, high-linoleic and high-stearic cultivars of soybean have been developed (Schnebly et al., 1996; Stojšin et al., 1998; Primomo et al., 2002; Serrano-Vega et al., 2005), but they have not been released to the seed market yet. In rape, a species with erucic acid in its oil, cultivars with low (for human consumption) or high (for industrial uses) concentrations of this fatty acid have also been developed (Velasco et al., 1999).

Oil fatty acid composition varies according to the environmental conditions (Strecker et al., 1997; Pritchard et al., 2000; Roche et al., 2006). It has long been known that an increase in temperature increases the oleic-to-linoleic acid ratio in the oil of several oilseed crops (Canvin, 1965) by affecting the total activity of the desaturase enzymes (e.g. oleoil-ACP desaturase in sunflower; Garcés et al., 1992; Kabbaj et al., 1996). The accumulation of saturated fatty acids is also affected by environmental factors (Roche et al., 2006; Izquierdo and Aguirrezábal, 2008).

Several authors observed that oleic acid concentration in sunflower oil was decreased by low temperatures (e.g. Harris et al., 1978; Rochester and Silver, 1983; Izquierdo et al., 2002). Oleic acid concentration was better related to night minimum temperature than to other temperature descriptors (Izquierdo et al., 2006). The circadian rhythm of the oleoil-ACP desaturase activity seems to be associated with this effect of temperature during the dark period (Pleite et al., 2008). In soybean and maize, however, a clear relationship between oleic acid concentration and night-time or minimum temperatures could not be detected. Rather, it has been related to daily average temperature, probably because of a lower effect of temperature on fatty acid composition in these species (Izquierdo, 2007). As found for oil concentration, very high daytime temperatures ($>30°C$) also affect fatty acid composition in sunflower (Rondanini et al., 2003), but probably through different (and possibly interacting) mechanisms than moderately high temperatures.

Environmental factors other than temperature, such as solar radiation (Santalla et al., 1995), rainfall (Pritchard et al., 2000), nitrogen availability (Steer and Seiler, 1990), soil salinity (Irving et al., 1988) and crop health (Zimmer and Zimmerman, 1972), can also affect fatty acid composition. However, these factors generally produce small variations in fatty acid composition than those driven by temperature (e.g. 10 vs. 40% oleic acid for sunflower). However, variations in oleic acid concentration through changes in intercepted radiation in soybean and maize (Izquierdo, 2007) were similar to those driven by latitude, extreme sowing dates and temperature (Muratorio et al., 2001; Izquierdo and Aguirrezábal, 2005; Izquierdo, 2007).

The total activity of the enzyme oleoil-ACP desaturase is maximum early during grain filling (Garcés et al., 1992; Kabbaj et al., 1996); therefore, the effect of temperature in this period could be stronger than during the rest of the grain-filling stage. Correspondingly, minimum night temperature between 100 and 300°C day after flowering (base temperature 6°C) accounted for most of the variability in the concentration of oleic and linoleic acids in two traditional hybrids and a high-oleic hybrid (Izquierdo et al., 2006; Izquierdo and Aguirrezábal, 2008). This supports the idea (usually assumed in crop simulation models; e.g. Villalobos et al., 1996; Stöckle et al., 2003) that the timing of a critical period is the same for different genotypes, provided that it is expressed in relation to developmental events and in thermal time. Such a critical period, however, could not be found in maize or soybean (Izquierdo, 2007).

The knowledge on the effects of the environment on fatty acids other than oleic and linoleic acids is more limited. Izquierdo and Aguirrezábal (2008) found a relationship to describe the response of other fatty acids to temperature in different sunflower hybrids. With increased temperature, the proportion of saturated fatty acids was reduced, mainly due to a reduction in the concentration of stearic acid (the concentration of palmitic acid remained fairly constant), indicating that there is also a temperature effect on stearoyl-ACP desaturase, as reported by Kabbaj et al. (1996). The synthesis of stearoyl-ACP desaturase peaks earlier during grain filling than that of the oleoil-ACP desaturase (12 vs. 20 days after flowering; Kabbaj et al., 1996), suggesting that the critical period for saturated fatty acids precedes the critical period for oleic-to-linoleic ratio (Izquierdo et al., 2006).

Izquierdo and Aguirrezábal (2008) investigated the response of oleic and linoleic acids to temperature in sunflower hybrids, using the empirically based relationship established by Izquierdo et al. (2006).

The concentration of oleic acid showed a sigmoidal response to minimum night temperature between 100 and 300°C day after flowering, increasing almost linearly within a given range of temperatures (Figure 1b). Outside this range, the concentration of this fatty acid remained almost constant. The same mathematical expression characterised the response of oleic acid concentration to temperature in both traditional and high-oleic hybrids; as it could be expected, relationships between linoleic acid concentration and temperature showed inverse trends. However, the parameters of the response curves showed significant genetic variability. Differences among traditional hybrids were observed for the minimum and maximum concentrations of oleic acid and also for the maximum slope and the range of the response; differences were particularly high for the minimum concentration of this fatty acid, which ranged between 15 and 32%. The low sensitivity to the environment of a high-oleic hybrid was evidenced by the small difference between the parameters for minimum and maximum oleic acid concentrations (6.9%), as compared to traditional hybrids (16.3–43.9%). Since the same function characterised the response of several hybrids, it is possible to easily incorporate the estimation of oil fatty acid composition in crop simulation models using hybrid-specific parameters. Finally, the analysis of the variability of these parameters gives important information on the nature of the observed G × E interactions and provides new traits (parameters) that are independent of the environment. This can be used to obtain new genotypes with specific responses to environmental variables, as proposed by Tardieu (2003) and discussed further in Section 4.4.

2.3. Oil tocopherol concentration

Tocopherols (Box 1) are synthesised from specific precursors, via the isoprenoid pathway or the homogentisic acid pathway (Bramley et al., 2000). Their synthesis is regulated by the availability of these precursors. In plants, four isomers of tocopherol have been identified (α-, β-, γ- and δ-tocopherols), which differ in the position of the methyl group in the molecule, and also in their in vitro and in vivo antioxidant activities (Kamal-Eldin and Appelqvist, 1996). The relative quantities of these isomers are controlled by the enzymes catalysing the methylations. In sunflower, α-tocopherol accounts for 91–97% of the total tocopherol, with little genetic variation (Nolasco et al., 2006).

The tocopherol concentration in sunflower grain is very responsive to environmental conditions (Kandil et al., 1990; Marquard, 1990; Velasco et al., 2002). The amount of intercepted radiation per plant during grain filling was negatively correlated to tocopherol concentration in the oil in sunflower (Nolasco et al., 2004), soybean, maize and rape (Izquierdo, 2007). The effect of temperature on tocopherol concentration, however, is unclear, with many contradictory reports (Dolde et al., 1999; Almonor et al., 1998; Izquierdo et al., 2007).

Tocopherols are present in the grain in a small quantity diluted in oil (typically 500–1200 $\mu g g^{-1}$; Marquard, 1990; Nolasco et al., 2004), and their concentration depends on the amount of both tocopherol and oil. Nolasco et al. (2004) found that the variation in oil weight per grain accounted for 73% of the variation in total tocopherol concentration in sunflower oil. The relationship between tocopherol concentration in oil and oil weight per grain showed a dilution-like shape (Figure 1c), independently of location, the hybrid and its maximum oil concentration, or the intercepted radiation during grain filling (Nolasco et al., 2004). Oil weight per grain also accounted for much of the variation in oil tocopherol concentration in traditional varieties of soybean and rape but not in maize, a species with a low grain oil concentration (Izquierdo, 2007). The simple relationship between tocopherol concentration in oil and oil weight per grain can be easily incorporated into crop simulation models and used to identify management practices useful to obtain grains with greater quantity of tocopherols. Also, these relationships could be useful for commercialisation and grain processing, to estimate the tocopherol concentration of a grain lot from weight per grain and oil concentration, which are simpler, faster and less expensive to measure than tocopherol concentration.

2.4. Protein concentration

Grain protein concentration, usually expressed in percent of grain dry mass, is the main determinant of the end-use value of most cereal and grain legume species. This is particularly true for wheat, which is mostly

consumed by humans after processing. Cereal grains contain a relatively small concentration of protein, typically between 8 and 18%, but the large dependence on maize, wheat and rice as main sources of carbohydrates and energy means these species account for 85% of dietary proteins for humans (Shewry, 2007).

In the field, variations in grain protein concentration induced by weather, water and nitrogen availability, especially during the grain-filling period, are much larger than variations due to genotype (Cooper et al., 2001). For wheat, variations in grain protein concentration in response to temperature, solar radiation, CO_2 or soil water availability are mainly related to variation in the quantity of carbon compounds (i.e. starch and oil) per grain, while the quantity of nitrogen compounds (i.e. proteins) per grain is relatively stable (Panozzo and Eagles, 1999; Triboi and Triboi-Blondel, 2002; Triboi et al., 2006). In oil crops, an increase in oil concentration is generally associated with a decrease in protein concentration (López Pereira et al., 2000; Morrison et al., 2000; Uribelarrea et al., 2004), as a result of a dilution effect (Connor and Sadras, 1992).

The interplay between carbon and nitrogen compounds leading to a final concentration of protein in grain can most simply be explained by the effects of environmental factors during the filling period on the rate and duration of accumulation of starch, oil and protein. Starch, oil and protein depositions in the grain are relatively independent from each other and are controlled differently (Jenner et al., 1991). The synthesis of grain starch and oil mostly relies on current photosynthesis. Therefore, the quantity of starch and oil per grain is mainly determined by the duration in days of the grain-filling period. The rate of accumulation of carbon compounds per day is little modified by post-anthesis environmental factors, while the duration of grain filling in thermal time shows little variation (Triboi et al., 2003; DuPont et al., 2006b). This explains why, usually, grain dry mass is closely correlated with the rate of accumulation of grain dry mass per degree-day or with the duration of grain filling in days. In contrast, under most conditions, the synthesis of grain protein relies mostly on nitrogen remobilisation from the vegetative organs. Chapter 8 (Section 3.1) discussed the relative contribution of current assimilation and reserves to the carbon and nitrogen economy of grains, and emphasised differences between wheat and rice, for which 60–95% of the harvested grain nitrogen derives from remobilisation of stored N, and maize where this proportion is only 45–65%.

The rate of grain nitrogen accumulation per degree-day is little modified by temperature or water supply (Triboi et al., 2003; DuPont et al., 2006b), which means that any temperature-driven decrease in the duration in days of the grain-filling period is compensated by an increase in the rate of accumulation of grain nitrogen per day. Under water deficit or high temperature, the higher rate per day of nitrogen remobilisation of pre-flowering nitrogen from the plant to the grain results in an acceleration of canopy senescence and a reduced remobilisation of pre-anthesis carbon (Palta et al., 1994; Triboi and Triboi-Blondel, 2002). Under very high temperature (maximum daily temperature higher than 30–35°C, depending on the species), this compensation phenomenon decreases and the quantity of nitrogen per grain may decrease. If environmental constraints are applied during the early phase of grain development (i.e. during the phase of endosperm or cotyledon cell division), then the rate of accumulation of carbon may be reduced, which accentuates the increases of grain protein concentration (Gooding et al., 2003). The effects of these environmental factors before anthesis on grain protein concentration depend mainly on their effect on the sink-to-source ratio, but the processes described above still drive grain protein concentration (Chapter 8).

In contrast with the effects of post-flowering temperature, radiation or water supply, the effects of nitrogen supply on grain protein concentration are mostly due to changes in the amount of nitrogen per grain, which for most crop species is regulated by nitrogen availability in the vegetative organs and in the soil during the grain-filling period (e.g. Lhuillier-Soundele et al., 1999; Martre et al., 2003). The number of grains set usually matches the growth capacity of the canopy during the grain-filling period (Sinclair and Jamieson, 2006), and as a consequence, average grain dry mass is little modified (or increases slightly) under pre- and/or post-flowering soil nitrogen shortage (Triboi et al., 2003; Uribelarrea et al., 2004).

To model the effects of the environment on protein concentration, it is necessary to take into account the dynamics of carbon and nitrogen accumulation in the grain. This has been successfully achieved in the

wheat model *SiriusQuality*1 (Martre et al., 2006), which is described in Section 3.2. In this model, the accumulation of structural proteins and carbon, which occurs during the stage of endosperm cell division and DNA endoreduplication, is assumed to be sink regulated and is driven by temperature. In contrast, the accumulation of storage proteins and starch, which occurs after the endosperm-cell-division period, is assumed to be source regulated (i.e. independent of the number of grains per unit ground area) and is set daily to be proportional to the current amount of vegetative non-structural nitrogen.

2.5. Protein composition

Storage proteins account for 70–80% of the total quantity of reduced nitrogen in mature grains of cereals and grain legumes, and their composition greatly influences their processing and nutritional quality (Wieser and Zimmermann, 2000; Gras et al., 2001; Khatkar et al., 2002). It is important to note that grain protein concentration in wheat has decreased linearly with the year of cultivar release, but flour functionality has increased significantly (Ortiz-Monasterio et al., 1997; Fufa et al., 2005). This trend is partly associated with the selection of favourable storage protein alleles after the mid-1980s (Branlard et al., 2001). Although the qualitative protein composition of grain depends on the genotype, its quantitative composition is largely determined by environmental factors, including nitrogen and sulphur availability (Graybosch et al., 1996; Huebner et al., 1997; Panozzo and Eagles, 2000; Zhu and Khan, 2001).

Wheat storage proteins are encoded by over 100 genes located at different loci (Shewry and Halford, 2003), coding for high-molecular-weight glutenin subunits (HMW-GS), low-molecular-weight glutenin subunits (LMW-GS), α/β-gliadins, γ-gliadins and ω-gliadins. Gliadins and glutenins are collectively referred to as prolamins. Glutenins are polymeric proteins that form very large macro-polymers with viscoelastic properties (responsible for the unique rheological properties of wheat flours; Don et al., 2003), while gliadins are important in conferring extensibility to dough (Branlard et al., 2001). Grain storage proteins accumulate mainly during the linear phase of grain filling. For wheat, during the desiccation phase after physiological maturity (Box 1 in Chapter 12), glutenin proteins form very large polymers (Carceller and Aussenac, 2001) whose size distribution plays a central role in determining wheat flour functionality (Don et al., 2003).

Environmentally induced changes in grain protein composition are associated with the altered expression of genes encoding storage proteins, in response to signals that indicate the relative availability of nitrogen and sulphur (Bevan et al., 1993; Peak et al., 1997; Chiaiese et al., 2004; Hernandez-Sebastia et al., 2005). These signals trigger transduction pathways in developing grains that, in general, balance the storage of nitrogen and sulphur to maintain homoeostasis of the total amount of protein per grain (Tabe et al., 2002; Islam et al., 2005). Emergent properties of these regulation networks, which are still poorly understood at the molecular level, are allometric relations between the amount of nitrogen per grain and the amount of the different storage protein fractions (Sexton et al., 1998b, for soybean; Landry, 2002, for maize; Triboi et al., 2003, for wheat). These relations are independent of the causes of variations of the quantity of nitrogen per grain and are similar for developing and mature grains (Figure 3a–c, compare main panels and insets; Daniel and Triboi, 2001; Triboi et al., 2003), meaning that environmental factors, including supply of water and nitrogen, do not directly influence grain protein accumulation, but only indirectly through their effect on grain nitrogen accumulation. It thus appears that the gene regulatory network involved in the control of the synthesis of storage proteins is coordinated in such a way that the grain reacts in a predictable manner to nitrogen availability, yielding a meta-mechanism at the grain level (Martre et al., 2003).

A consequence of this meta-mechanism is that grain protein composition is closely related to the total quantity of proteins per grain, independently of the cause of its variation. For wheat, the proportion of total glutenin in grain protein, as well as the proportion of each HMW-GS in the total HMW-GS (Wieser and Zimmermann, 2000; DuPont et al., 2007), appears to be independent of the quantity of nitrogen per grain; in contrast, the proportion of gliadin in grain protein shows significant environmental variation (Figure 3c). Changes in the proportion of gliadin are directly related to the variation in the quantity of nitrogen per grain and are compensated by a proportional decrease of non-prolamin protein. These variations in grain protein composition are accompanied by changes in amino acid composition with the total quantity of nitrogen per grain

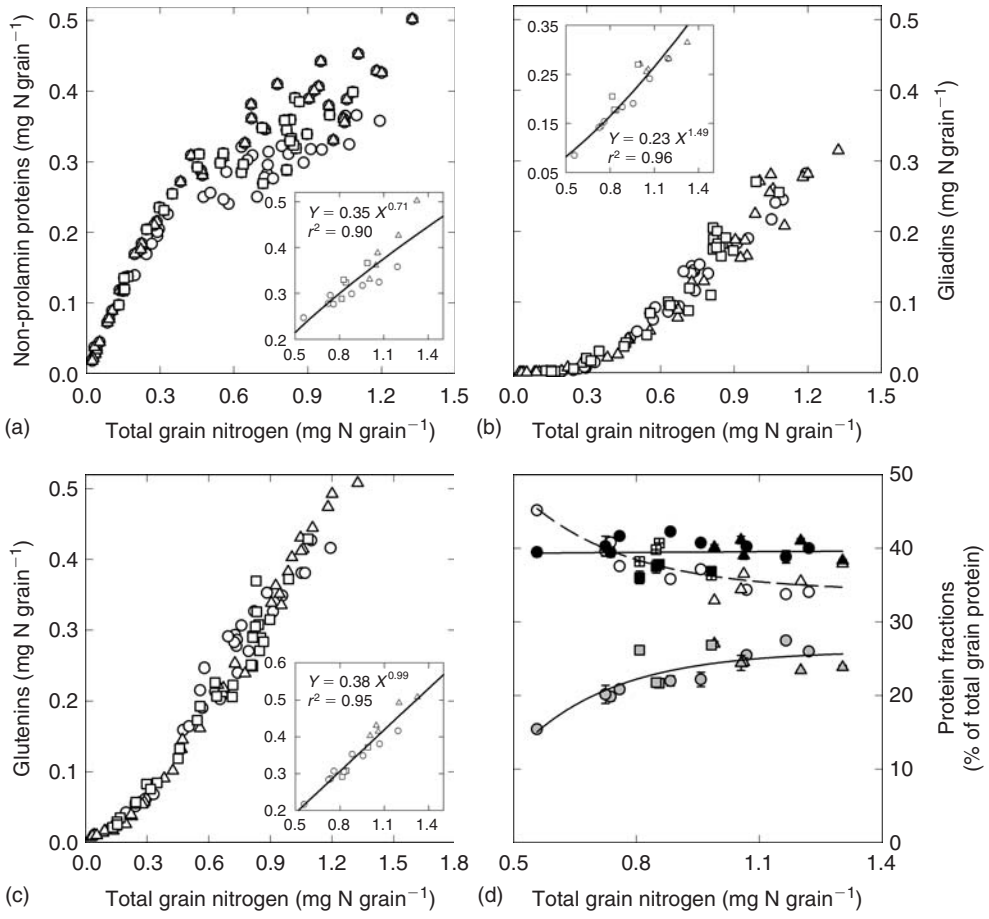

FIGURE 3

Quantities of (a) non-prolamin proteins, (b) gliadins, (c) and glutenins per grain versus the total quantity of nitrogen per grain for developing and mature grains of bread wheat. Insets show the allometric relations between the quantity of each protein fraction and the total quantity of nitrogen for mature grains only. (d) Percentages of non-prolamin proteins (open symbols), gliadins (grey symbols), and glutenins (closed symbols) versus the total quantity of nitrogen per grain for mature grains. Crops were grown in semi-controlled environments with different post-anthesis temperatures (triangles) and water supplies (rectangles), and in the field with different rates and times of nitrogen fertilisation (circles). (Source: Redrawn with permission from Triboi et al., 2003.)

(Eppendorfer, 1978; Mossé et al., 1985). A practical implication of these relations is that grain protein and amino acid composition can be calculated directly from the quantity of nitrogen per grain, independently of the growing conditions. Analysis of the genetic variations of the allocation coefficients of nitrogen in bread wheat showed that, even though there are some statistically significant variations among genotypes, genotypic differences in grain protein composition are primarily driven by variations in the total quantity of nitrogen per grain (Martre and Samoil, unpublished results).

Nitrogen supply determines the level of protein accumulation in the grain and its gross allocation between storage protein fractions, but, at a given level of nitrogen supply, sulphur supply fine-tunes the composition of the protein fractions by regulating the expression of individual storage protein genes (Hagan et al., 2003;

Chiaiese et al., 2004). Interestingly, DuPont et al. (2006a) noted that any factor that increases the amount of nitrogen per grain also increases the proportion of sulphur-poor (ω-gliadins and HMW-GS) storage protein at the expense of sulphur-rich (α/β-gliadins, γ-gliadins and LMW-GS) storage protein. These authors proposed a putative molecular mechanism by which nitrogen activates the synthesis of glutamine and proline, thus favouring the synthesis of sulphur-poor proteins rich in these amino acids. An alternative hypothesis is that the accumulation of sulphur-rich storage proteins, determined by sulphur availability, generates a signal of sulphur deficiency, which increases the expression of sulphur-poor storage proteins to the extent of nitrogen available to it. The latter hypothesis is substantiated by reported differences in temporal appearance and spatial distribution of sulphur-rich and sulphur-poor storage proteins in developing grains of maize (Lending and Larkins, 1989) and wheat (Panozzo et al., 2001).

Very high temperature, above a threshold of daily average temperature of about 30°C, can have marked effects on wheat dough strength, and these effects are largely independent of grain protein concentration (Randall and Moss, 1990; Blumenthal et al., 1991; Wardlaw et al., 2002). Relatively small variation in the proportions of the different types of gliadin and glutenin subunits have been reported in response to chronic or short periods of very high temperature, and it is difficult to convincingly relate such variations to changes in flour functionality. Weaker dough from grains that experience one or several days of very high temperature has been related to a marked decrease in the proportion of large-molecular-size glutenin polymers (Ciaffi et al., 1996; Corbellini et al., 1998; Wardlaw et al., 2002; Don et al., 2005). The aggregation of glutenin proteins, which occurs mainly during the phase of grain desiccation after physiological maturity (Carceller and Aussenac, 2001), is likely the major process responsible for heat-shock-related dough weakening.

Extended periods of high temperature are common in many cereal-growing areas of the world, and above-optimal temperature is one of the major environmental factors affecting small grain cereal yield and composition (Randall and Moss, 1990; Borghi et al., 1995; Graybosch et al., 1995). Some results suggest that very high temperature around mid-grain filling has positive effects on wheat dough strength (Stone et al., 1997; Panozzo and Eagles, 2000), whereas very high temperature around physiological maturity has a negative effect on dough strength (Randall and Moss, 1990; Blumenthal et al., 1991; Stone and Nicolas, 1996). This difference in the response of dough properties according to the timing of heat shock may be related to different effects on the gliadin-to-glutenin ratio and the size of glutenin polymers at each developmental stage. Further experiments to identify the relative sensitivity of different development stages in terms of gliadin and glutenin accumulation and glutenin polymer formation are clearly required. Important genetic variation in the relative response of grain protein composition and flour functionality to very high temperature has been reported (Blumenthal et al., 1995; Stone et al., 1997; Spiertz et al., 2006), but the genetic and physiological bases of these differences are still largely unknown.

3. INTEGRATION OF QUALITY TRAITS INTO CROP SIMULATION MODELS

Crop simulation models for grain yield have been developed for all the major crop species (Section 4 in Chapter 20). Some sunflower models also simulate oil yield (e.g. Villalobos et al., 1996), but only recently, aspects of oil quality have been included (Pereyra-Irujo and Aguirrezábal, 2007). Most wheat models simulate crop nitrogen accumulation and partitioning (primarily because crop nitrogen status greatly affects crop biomass and grain yield); however, few models have extended the simulation of nitrogen dynamics to account for grain nitrogen concentration (Sexton et al., 1998a; Asseng et al., 2002; Martre et al., 2006). In this section, we outline simulation models for sunflower and wheat, which have integrated grain oil or protein quality modules, based on the relationships described in Section 2. In Section 4, these models will be used to explore strategies to improve quality traits through crop management or breeding.

3.1. Modelling oil concentration and composition and tocopherol concentration in sunflower

The model of Pereyra-Irujo and Aguirrezábal (2007) integrates empirical relationships (Section 2) as shown in Figure 4a. The model includes a temperature-driven phenology module that allows for the critical periods of determination of yield and quality components to be estimated. Fatty acid composition is predicted through its relationship with temperature during its critical period (Figure 1b). Grain oil concentration (Figure 1a) and yield components are estimated taking into account intercepted radiation per plant, which is calculated at the population level. Leaf growth is predicted through its relationship with temperature and plant density. Radiation interception depends, on the one hand, on plant density and individual plant leaf area (which determines the leaf area index) and, on the other hand, on incident solar radiation at the top of the canopy. Then, oil tocopherol concentration is calculated from oil weight per grain (Figure 1c), which in turn depends on grain weight and grain oil concentration.

The original model (Pereyra-Irujo and Aguirrezábal, 2007) was expanded to simulate quality traits for biodiesel (i.e. density, kinematic viscosity, heating value, cetane number and iodine value), using validated empirical relationships with oil fatty acid composition (Pereyra-Irujo et al., 2009). The model provided estimations of potential grain yield similar to those of a more complex model, and good estimates of oil quality and intermediate variables (e.g. phenology, intercepted radiation during different critical periods) over a wide range of environmental conditions (Pereyra-Irujo and Aguirrezábal, 2007; Pereyra-Irujo et al., 2009).

3.2. Modelling grain protein concentration and composition in wheat

Simulation of grain nitrogen content requires first simulating the uptake of nitrogen into the vegetative tissues of the plant, followed by a step where nitrogen is transferred to the grains from vegetative tissues. A mechanistic approach to simulate crop nitrogen accumulation and partitioning has been implemented in the wheat simulation model Sirius (Jamieson and Semenov, 2000; Martre et al., 2006). Figure 4b summarises this model. Nitrogen is distributed to leaf and stem tissues separately, with simplifying assumptions that nitrogen per unit leaf area is constant at the canopy level (Grindlay, 1997), but that the stem could store nitrogen. The effect of nitrogen shortage is to reduce first stem nitrogen concentration and then leaf expansion to maintain specific leaf nitrogen concentration. One advantage of this approach is that it reduces the number of parameters and the need to define stress factors, compared with the demand-driven approaches based on nitrogen dilution (e.g. van Keulen and Seligman, 1987; Stöckle and Debaeke, 1997; Brisson et al., 1998). This approach also provides more plasticity in the response of the crop to nitrogen availability.

The latest version of Sirius (*SiriusQuality*1; Martre et al., 2006) models nitrogen transfer to the grain more mechanistically than previous models (Sinclair and Amir, 1992; Sinclair and Muchow, 1995; Gabrielle et al., 1998; Bouman and van Laar, 2006). Accumulations of structural proteins and carbon, during the stages of endosperm cell division and DNA endoreduplication, and of storage proteins and starch, after the period of endosperm cell division, are explicitly considered. The accumulation of structural proteins and carbon per grain is assumed to be sink regulated and is driven by temperature. On the other hand, the accumulation of storage proteins and starch is assumed to be source regulated (i.e. independent of the number of grains per unit ground area), and is set daily to be proportional to the current amount of vegetative nonstructural nitrogen. Sirius and *SiriusQuality*1 successfully simulated yield and protein concentration for contrasting pre- and post-flowering N supplies, post-anthesis temperature and water supply in France (Martre et al., 2006), under the dry climates of Arizona and Australia, across variations in air CO_2 concentration, water and nitrogen supplies and cultivars (Jamieson et al., 2000; Ewert et al., 2002; Jamieson et al., 2009), and under the cooler climate of New Zealand for a range of rates and patterns of water and nitrogen availabilities, locations and cultivars (Jamieson and Semenov, 2000; Armour et al., 2004).

The allometric relations between the total amount of nitrogen per grain and the amount of storage protein fractions presented in Section 2.5 have been used to model gliadin and glutenin accumulation in developing wheat grain (Martre et al., 2003). This model has been implemented in *SiriusQuality*1 and has been evaluated

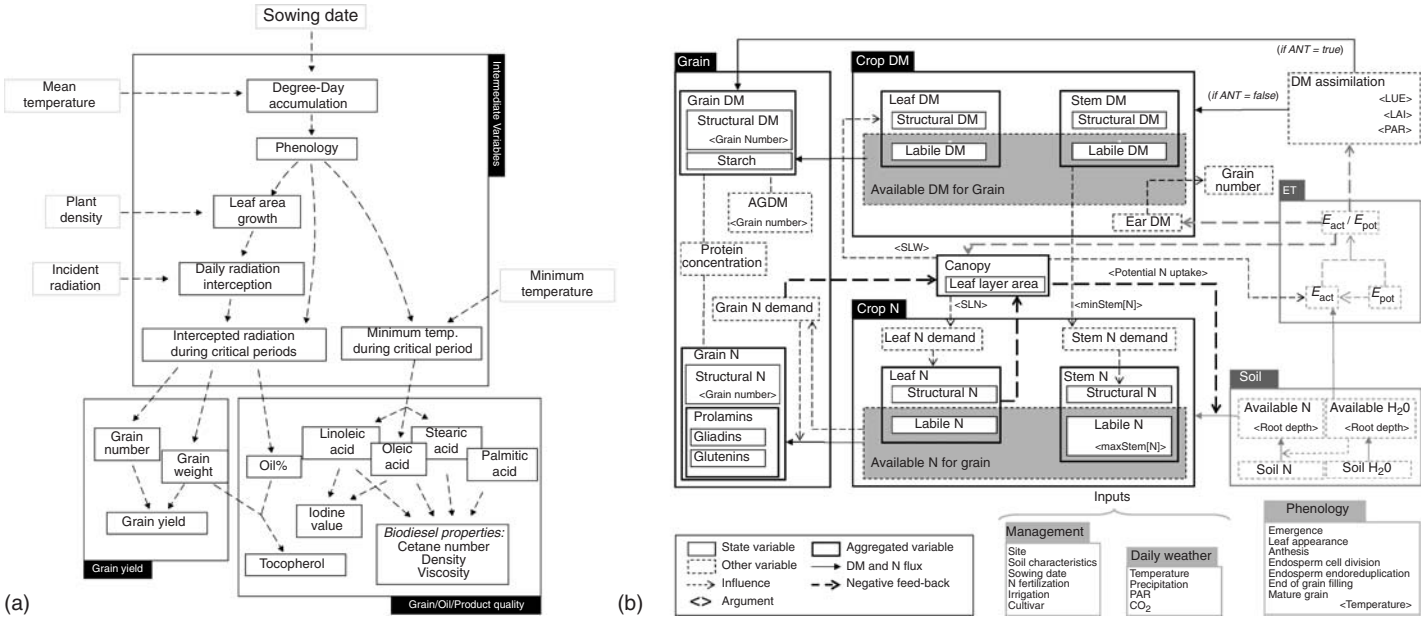

FIGURE 4

(a) Schematic representation of the sunflower simulation model from Pereyra-Irujo and Aguirrezábal (2007) and Pereyra-Irujo et al. (2009) showing the relationships between input variables (outside boxes), intermediate variables and output variables (yield and quality). (Adapted from Pereyra-Irujo and Aguirrezábal, 2007.)
(b) Schematic representation of the wheat simulation model SiriusQuality*1 (Martre et al., 2006) showing the main variables, influences and feedbacks. AGDM, average grain dry mass; ANT, anthesis; DM, dry matter; N, nitrogen;* E_{act}*, actual transpiration;* E_{pot}*, potential transpiration; LAI, leaf area index; LUE, light use efficiency; maxStem[N], maximum stem nitrogen concentration; minStem[N], minimum stem nitrogen concentration; PAR, photosynthetically active radiation; SLN, leaf nitrogen mass per unit of leaf surface area; SLW, leaf dry mass per unit of leaf surface area.*

against a wide range of nitrogen supply and post-anthesis temperature and water supply (Martre et al., 2006). The existence of environment-independent relations of nitrogen allocation for different cereals species (but with different parameter values) suggests that the model developed for wheat can be used to analyse and simulate the allocation of storage proteins for other cereals. The next step would be to model the effect of sulphur availability on the allocation of storage proteins and its interaction with nitrogen availability.

4. APPLYING CROP PHYSIOLOGY TO OBTAIN A SPECIFIC QUALITY AND HIGH YIELDS

In many agronomically relevant conditions, the trade-off between yield and quality is an obstacle to achieve the dual objective of high yield and high quality. This section thus presents a physiological viewpoint of the relationships between yield and oil attributes in sunflower and between yield and protein in wheat, and outlines the physiological concepts of potential value for management and breeding aimed at improving grain quality while obtaining high yields.

4.1. Sunflower yield and oil composition

The interactions between yield and quality in sunflower were analysed for a traditional and a high-oleic sunflower hybrid, using the model presented in Section 3.1 (Figure 4a). Quality attributes were estimated for a wide range of sowing dates and three plant densities, using 35 years of weather data from three locations in Argentina with contrasting radiation and temperature regimes. The same interactions were analysed experimentally in a trial network where five hybrids were sown in 11 locations between 26.7 and 38.6°S (Peper et al., 2007). Large variation in observed and simulated yield and grain and oil quality traits were obtained both among and within locations.

Positive or negative associations between yield and quality traits depend on the nature of the quality trait. For most of the situations, grain oil concentration and linoleic acid concentration were positively correlated with yield, while the concentration of oleic acid (Figure 5a) and oil tocopherol concentration were negatively correlated with yield. Results for the traditional hybrids in the trial network showed a similar pattern of negative correlation between oleic acid concentration and yield (Peper et al., 2007), which suggests that it might be possible to infer the physiological causes of these correlations from the mechanisms operating in the model.

Simulations showed that temperature differences among locations were the main cause of the negative correlations between yield and oleic acid. Oleic acid concentration increases with temperature between 100 and 300°C day after flowering, whereas grain yield decreases with temperature around flowering (Cantagallo et al., 1997) and during early grain filling (between 250 and 450°C day after flowering; Aguirrezábal et al., 2003), when the grain number and grain dry mass are determined, respectively. Because of this overlap of the critical periods for oleic acid concentration and yield, it is not easy to avoid this negative correlation when sowing a traditional sunflower hybrid. However, because this overlap was only partial, in a given year and location, temperature fluctuations over the reproductive period can reverse the general tendencies. So, despite the average negative correlation, it is possible to calculate, from model outputs, the probability of obtaining relatively high product quality (in this case oleic acid concentration) with a high yield at a given location. For instance, the probability of obtaining oil with more than 35% oleic acid in Paraná is 50% if yield potential is lower than $2.5\,t\,ha^{-1}$, and decreases to 27% for higher yields (Pereyra-Irujo and Aguirrezábal, unpublished results).

In some cases, genetic improvement can break negative correlations between quality traits and yield. This is easiest when quality traits depend on relatively few genes (as for high-oleic trait in sunflower, Section 2.2). For instance, simulated and experimental data showed that oleic acid concentration for sunflower cultivars with high-oleic genes was almost independent of yield (Figure 5b; Peper et al., 2007).

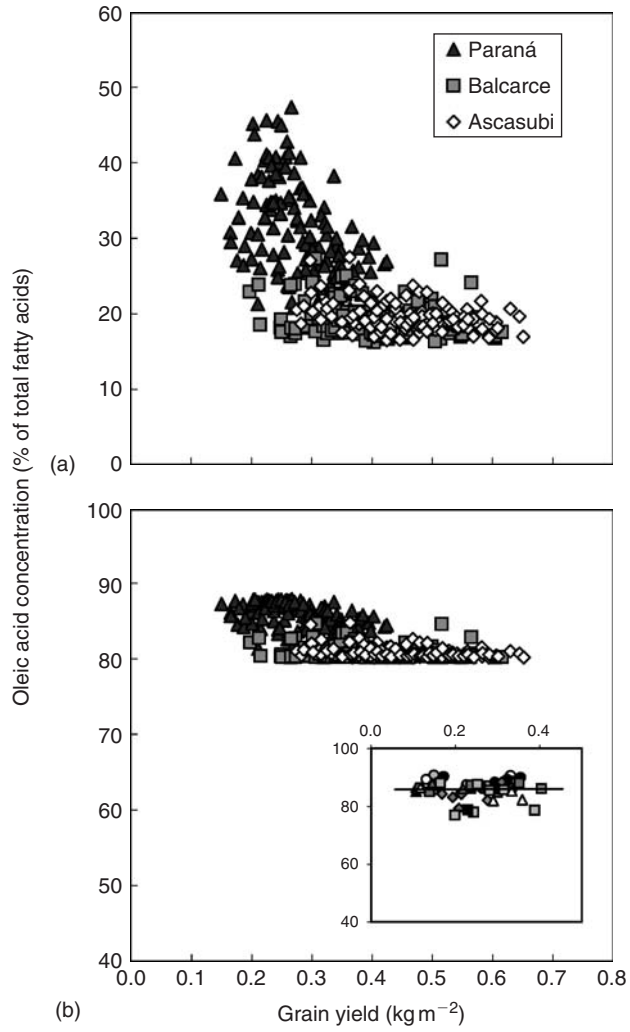

FIGURE 5

Relationship between simulated oleic acid concentration and crop grain yield for (a) a traditional hybrid and (b) a high-oleic hybrid, for three contrasting locations in Argentina. Inset: relationship between measured oleic acid concentration and grain yield for 15 high-oleic sunflower hybrids sown in different locations in Argentina (Source: Pereyra-Irujo and Aguirrezábal, unpublished).

In sunflower, oil tocopherol concentration was negatively correlated with yield (Pereyra-Irujo and Aguirrezábal, 2007). In this case, the response was the same at all locations, but depended strongly on the sowing density. This was because, at higher densities, the same yield can be obtained with a higher number of smaller grains, for which the response curve of tocopherol concentration to variations in oil concentration is steepest (Figure 1c). The negative correlation between oil tocopherol concentration and yield results from the relationship between oil tocopherol concentration and oil weight per grain. This relationship follows a dilution-like curve, with a steeper slope for grains with less than 15 μg oil (Figure 1c). Within this range, oil tocopherol is therefore inversely correlated with weight per grain, which is the main driving component of

oil weight per grain, and also one of the two components of yield. However, it is well known that yield is mainly driven by the number of grain per square metre and that the correlation between grain number and weight per grain is weak for sunflower (Cantagallo et al., 1997). Therefore, it could be expected that high oil tocopherol concentration could be obtained together with high yield, provided that this yield results mainly from a high grain number per square metre with small grains. This deduction, based on simulations and application of physiological principles was confirmed in a trial network (Peper et al., 2007), where oil tocopherol concentration was negatively related with oil weight per grain, but no clear correlation was found with yield. For hybrids genetically producing small grains, oil tocopherol concentration higher than $800\,\mu g\,g\,oil^{-1}$ and yield higher than $3100\,kg\,ha^{-1}$ were obtained when grain number was higher than $6700\,grains\,m^{-2}$ (A. Peper, personal communication), i.e. close to the maximum number of grains per square metre observed under normal field conditions (López Pereira et al., 1999).

4.2. Wheat yield and protein concentration

Negative relationships between yield and grain protein concentration in wheat have been known for more than 70 years (Waldron, 1933; Metzger, 1935; Neatby and McCalla, 1938; Grant and McCalla, 1949), and crop physiologists have analysed the effect of environmental factors on this relation for over 40 years (Terman et al., 1969). Since the pioneer works on wheat, this negative grain yield–protein concentration relation has been reported for all the major crops, including maize (Dubley et al., 1977), sunflower (López Pereira et al., 2000), soybean (Wilcox and Cavins, 1995) and cowpea (Olusola Bayo, 1997). This correlation is observed when comparing different genotypes and also for a given genotype in response to environmental conditions or management practices.

Several putative physiological causes of the relationship between yield and protein concentration have been proposed, but the picture is still incomplete (reviewed in Feil, 1997). It has been hypothesised that the energetic cost of protein synthesis limits crop nitrogen assimilation and protein synthesis in the grain (Bhatia and Rabson, 1976; Munier-Jolain and Salon, 2005). However, nitrogen uptake during the pre- and/or post-flowering periods and/or the efficiency of nitrogen translocation from vegetative organs to grains are more likely to explain this correlation (Kade et al., 2005). Consistently with this hypothesis, late (between heading and flowering) application of nitrogen fertiliser often increases grain protein concentration, without reducing yield (Triboi and Triboi-Blondel, 2002). It has also been suggested that the observed genetic correlation between grain yield and protein concentration is at least in part due to the increase in dry matter harvest index (i.e. grain-to-straw dry mass ratio), which has accompanied most of the genetic progresses in yield over the last 50 years, resulting in a reduction of the storage capacity of the crop for nitrogen (Kramer and Kozlowski, 1979). There is contradicting evidence concerning this issue (Cox et al., 1985; Slafer et al., 1990; Bänziger et al., 1992; Calderini et al., 1995; Uribelarrea et al., 2004; Abeledo et al., 2008), which possibly results from different patterns of spatial and temporal availability of soil nitrogen (taking into account soil moisture) throughout the growing season. Some authors (e.g. Feil, 1997) argued that the seemingly universal genetic negative correlation between grain yield and protein concentration is an artefact of inadequate availability of soil nitrogen in most experiments. However, several reports showed significant variations of crop nitrogen yield independently of yield, suggesting that a significant part of the negative relation is under genetic control (e.g. Monaghan et al., 2001; Laperche et al., 2007).

The effects of weather and specific environmental factors on the grain yield–protein concentration relation were studied using *SiriusQuality*1 (Martre et al., 2006). The model was run for a wide range of nitrogen availabilities, using 100 years of synthetic daily weather data representing typical conditions in France, as well as scenarios where conditions were modified by increasing or decreasing temperature or radiation.

At medium nitrogen supply, a unique relationship was observed, independently of the causes of yield and grain protein concentration variation (Figure 6a). The simulated effects of post-flowering temperature, radiation and water supply were very similar to those observed experimentally (Terman et al., 1969; Pushman and Bingham, 1976; Terman, 1979; Triboi et al., 2006). Interestingly, for a large range of simulated yield, the relationship with protein concentration was non-linear. The analysis of the few experimental results

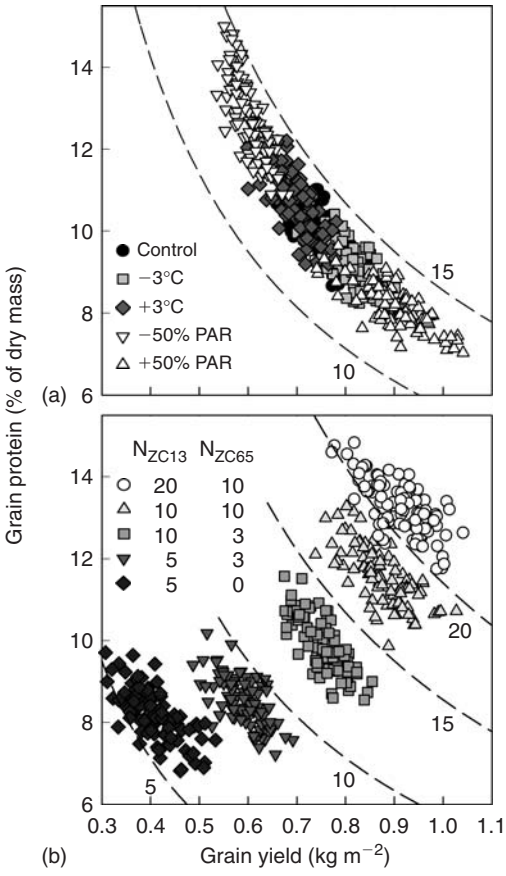

FIGURE 6

Simulated grain protein concentration versus grain yield for wheat crops in response to variations (a) of the post-flowering temperature (average daily temperature increased or decreased by 3°C) or solar radiation (daily cumulated radiation increased or decreased by 50%) and (b) of nitrogen fertilisation (indicated rates in g N m^{-2}) were applied when the crops had three leaves [N_{ZC13}] or at anthesis [N_{ZC65}]). In (a) the crops received 10 g N m^{-2} at three leaves and 10 g N m^{-2} at anthesis. Simulations were performed with the wheat simulation model SiriusQuality*1 (Martre et al., 2006) for 100 years of daily synthetic weather generated with the LARS-WG stochastic weather generator (Semenov and Brooks, 1999) for Clermont-Ferrand, France. Dashed lines are grain nitrogen yield isopleths (g N m^{-2}). Details of the soil and cultivar characteristics are given in Martre et al. (2007).*

with significant ranges of grain yield also clearly indicates that the relation deviates from linearity (Metzger, 1935; Simmonds, 1995; Rharrabti et al., 2001). The non-linearity is due to the dilution of a roughly constant amount of nitrogen in an increasing amount of carbon components. The negative relation also tends to deviate slightly from the grain nitrogen yield isopleths showing decreases of the simulated crop grain nitrogen yield for the higher yielding conditions. This was associated with a decrease in the total crop N yield rather than with a systematic effect on the nitrogen harvest index (data not shown). These high-yielding conditions were associated with long growth cycles (when simulation was performed considering that average daily temperature was increased by 3 °C), with late grain filling occurring under water-limited conditions, thus limiting crop nitrogen accumulation. This phenomenon probably reflected an interaction

between the simulated treatment and the climate structure of the study site rather than an absolute outcome of the model. More generally, it is interesting to note that, in *SiriusQuality*1, the dynamics of nitrogen and dry matter are mostly independent from each other. This relation is therefore an emergent property of the model. The model was thus able to simulate the observed effects of temperature, radiation and water and nitrogen supplies on the negative relation, although it was not part of the model assumptions. These results give confidence for using *SiriusQuality*1 to analyse environmentally induced variation of grain yield and protein concentration, and the interactions between carbon and nitrogen metabolisms at the crop level.

At low nitrogen availability, grain yield increases linearly with the amount of nitrogen available, and a constant grain protein concentration is expected. For higher availability of nitrogen, the rate of increase of grain yield with soil nitrogen availability decreases (nitrogen use efficiency decreases), grain protein concentration increases faster than grain yield and a positive correlation between grain yield and grain protein concentration is expected (Fowler et al., 1990); Section 4.3 in Chapter 8 further discusses the trade-offs between nitrogen use efficiency and protein content. Similarly, the simulated effect of nitrogen fertiliser on the grain yield–protein concentration relation (Figure 6b) is in agreement with the existing literature (Pushman and Bingham, 1976; Oury et al., 2003; Triboi et al., 2006). Some experimental data suggest possible weaker correlation with very high or low nitrogen supplies (Kramer, 1979; Fowler et al., 1990). Such effects were not observed in the present simulations, but extreme treatments would probably have more drastic effects on the grain yield–protein concentration relationship in an environment with a more marked inter-annual variability for water stress during the growth cycle.

Figure 7 summarises the effects of environmental variables on grain yield and protein concentration. At a given nitrogen supply and sink-to-source ratio, environmental factors modify grain yield and protein concentration symmetrically, and a close negative correlation between grain yield and protein concentration is observed (Terman et al., 1969; Terman, 1979; Triboi et al., 2006). If environmental conditions reduce the sink-to-source ratio, then a partial compensation may occur; the grain yield–protein concentration relation is then shifted. If the sink capacity (number of grains) is limited by early drought, by high temperature or genetically, then the duration of grain filling can be shortened. In this case, yield decreases despite

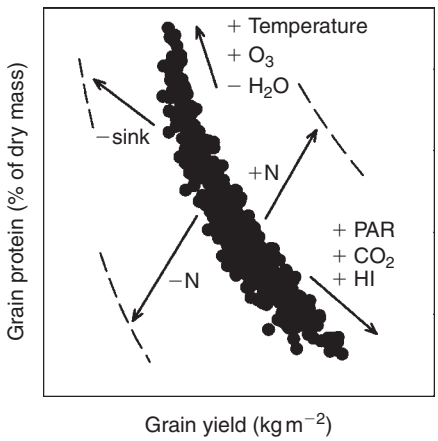

FIGURE 7

Summary of the effects of temperature, CO_2, O_3, radiation, supply of nitrogen and water, and ecophysiological traits (-sink: low sink-to-source ratio; +HI: increased dry mass harvest index) on the relationship between grain yield and protein concentration. Genetic progress has continuously increased grain yield while grain N concentration has decreased linearly with yield (closed symbols). The environmental factors have contrasting effects on this relation, depending if they modify or not the sink–source ratio, and on their effects on grain yield. HI, harvest index; PAR, photosynthetically active radiation. (Source: Triboi et al., 2006.)

an increase in single grain dry mass. At the grain level, the sink-to-source ratio increases more for nitrogen than for carbon, and grain protein concentration can be higher than under conditions of non-limiting sink. Under limiting-nitrogen conditions, the slope of the genetic yield–protein concentration relationship decreased (Triboi et al., 2006), and thus grain protein concentration became slightly more sensitive to yield variation than under non-limiting-nitrogen conditions (Figure 7).

The grain yield–protein concentration relationship is often hidden by environmental and management effects and, on average, can often be non-existent (Simmonds, 1995; Oury et al., 2003; Munier-Jolain and Salon, 2005). As shown here, this is explained by the different effects of environmental factors and management practices on crop dry mass and nitrogen dynamics, but these effects can be successfully analysed through simulation models.

4.3. Management strategies for obtaining a target grain and oil composition

4.3.1. Grain oil concentration

Grain oil concentration in sunflower depends on intercepted radiation per plant during a critical period (Figure 1a). High oil concentration would therefore require adjustment of management practices (e.g. sowing date, choice of cultivar, sowing density and fertilisation) to enhance intercepted radiation during such period. For instance, late sowing decreases not only grain yield but also grain oil concentration in high-oil sunflower hybrids. For three locations in Argentina, simulated grain oil concentration decreased when sowing date was delayed (Pereyra-Irujo and Aguirrezábal, 2007). This was due to the fact that, on average, radiation decreases more rapidly than temperature after the summer solstice, causing a steady decline in the amount of radiation intercepted per plant. Delaying sowing decreased grain oil concentration at 1–2% per month, but with a different magnitude, according to the location. When a low intercepted radiation during grain filling is expected (e.g. late sowing), the oil yield of low-oil hybrids is similar to that of high-oil hybrids (Izquierdo et al., 2008); therefore, cultivar choice can be based on other traits.

A fine-tuning of nitrogen supply and demand is necessary to obtain high oil concentration. Excessive fertilisation can reduce grain oil concentration and therefore decrease the commercial quality of the product in sunflower and rape (e.g. Steer et al., 1984; Jeuffroy et al., 2006). In sunflower, this situation can be frequent, since sunflower nitrogen requirements are relatively low, with respect to other crops (Andrade et al., 1996). Models and spatial technologies accounting for soil variation can assist in a more precise prevision of nitrogen requirements for specific yield and grain quality targets (Section 2.2 in Chapter 19; Jeuffroy et al., 2006).

4.3.2. Oil fatty acid composition

Hybrid selection, sowing date and location are the three main management practices that can be used to obtain oils with different properties (Box 1), as illustrated in Figure 8. To obtain oil with a high proportion of oleic acid using traditional hybrids, crops should be grown in warm regions, sowing date should be adjusted so that minimum temperatures are high during grain filling and hybrids with a high maximum concentration of oleic acid should be used (about 50%, close to a mid-oleic hybrid) (Figure 8). High-oleic hybrids, on the other hand, would yield oil with low unsaturation (80% oleic acid), independently of location or sowing date (Figure 8). To obtain oils with a high proportion of linoleic acid, hybrids with a low minimum oleic acid concentration (high maximum linoleic acid concentration) should be used, and they should be sown early at high latitudes (Figure 8).

Several quality parameters of biodiesel are highly dependent on fatty acid composition (Clements, 1996). Simulated density, kinematic viscosity and heating value produced from sunflower oil were very stable, whereas simulated iodine value and cetane number were highly variable between hybrids, regions and sowing

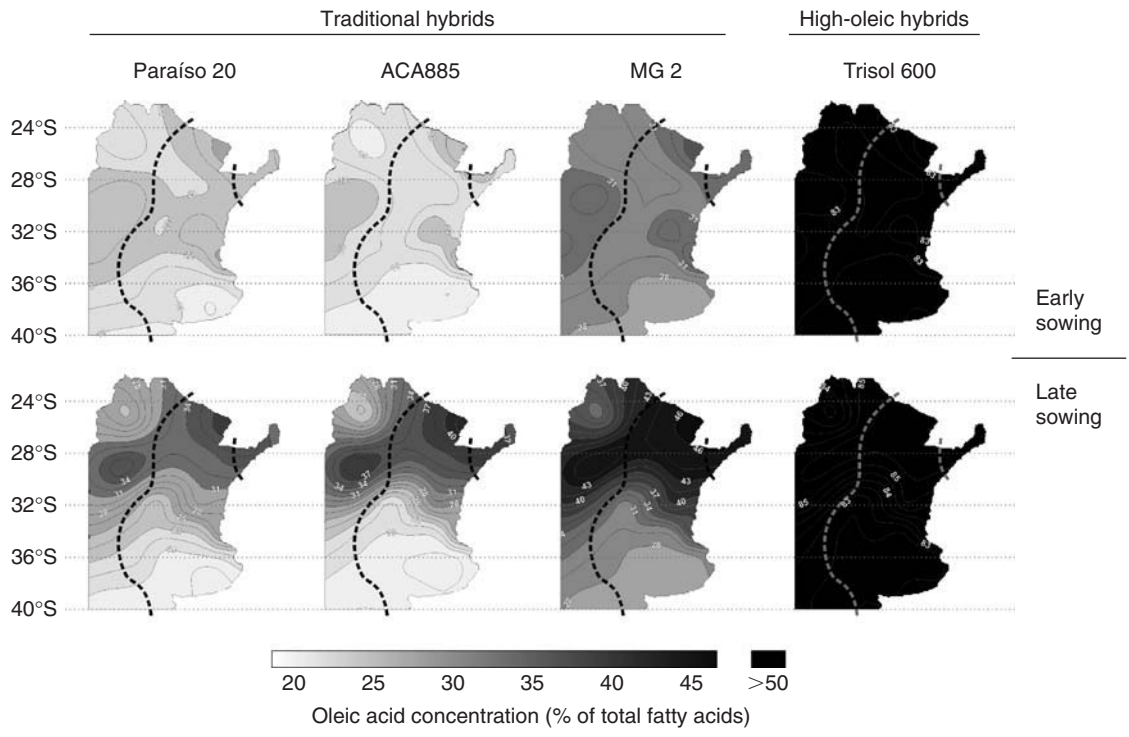

FIGURE 8

Simulated oleic acid concentration for traditional and high-oleic sunflower hybrids. Early (top maps) and late (bottom maps) sowings were used in simulations. Simulations using the optimum sowing date (not shown) yielded results intermediate between those of early and late sowings. The main sunflower growing region of Argentina is between the two dotted lines. Details of the simulations are given in Pereyra-Irujo et al. (2009).

dates. For the high-oleic sunflower cultivar, all the analysed parameters fell within the limits of the two main biodiesel standards (ASTM D6751 from the United States, and EN 14214 from Europe). For traditional cultivars, the US standard was met in almost all cases, whereas the European specifications were met only by the hybrid with the highest maximum oleic acid concentration. For a given cultivar, biodiesel quality tended to be higher at lower latitudes and in late sowings, following the degree of oil saturation (Figure 8).

4.3.3. Grain protein concentration

In most intensive cropping areas, management of nitrogen fertiliser is the main approach to obtain a targeted grain yield and protein concentration. This practice has an important economical cost for the farmer – for example, in France, it represents about 60% of the cost of growing a wheat crop – but also has a potentially deleterious environmental effect (Section 1 in Chapter 8). Until very recently, considerations of fertiliser needs have been mostly driven by yield rather than protein targets, except in crops such as barley where narrower bands of grain protein have a more marked influence on grain price. Management of nitrogen fertilisation is discussed in other parts of this book; Chapter 8 (Section 2.3) details physiological approaches for the diagnosis of nitrogen deficiency, and Chapter 19 (Section 2.2) combines physiological principles, modelling and spatial techniques to deal with the elusive nitrogen-by-water interaction driving fertiliser needs in dry land farming.

4.4. Strategies for genetic improvement of quality traits

4.4.1. Grain oil concentration

As mentioned earlier, genetic analyses of crosses between high-oil sunflower hybrids have identified alleles that could potentially increase grain oil concentration (Mestries et al., 1998; Mokrani et al., 2002; Bert et al., 2003). These studies, however, did not link the differences in oil concentration to anatomical or physiological characteristics. This information could be of importance to determine, for instance, whether future increases in grain oil concentration through decreased pericarp weight (and therefore decreased grain weight) could be negatively correlated to yield, if grain number is not able to compensate for a reduced grain weight (Mantese et al., 2006).

As genetic differences become smaller among modern, high-oil, sunflower hybrids, and given the relative environmental instability of their oil concentration (as compared to low-oil hybrids), the effect of the environment becomes increasingly important. However, the effect of environmental conditions and their interactions with genotype on oil concentration have received less attention than the effect of genotype. The well-known effect of radiation on grain oil concentration (Figure 1a) is probably one of the causes of the frequent co-localisation of QTLs for flowering date and grain oil concentration (Section 3.1.2 in Chapter 11; León et al., 2000). In sunflower, a critical period during grain filling has been identified (Aguirrezábal et al., 2003), during which grain oil concentration is closely associated with intercepted radiation and temperature, following a predictable response curve. Based on this relationship, two (possibly complementary) strategies for improving oil concentration can be proposed, which are represented in Figure 9a:

(i) Selecting for traits that result in increased radiation interception during this period (e.g. stay-green mutants, resistance to leaf diseases) should lead to increased oil concentration (Figure 9a). Also, care should be taken that increases in 'greenness' effectively result in increased photosynthesis, which is not always the case with stay-green mutants (Hall, 2001; see also Box 1 in Chapter 9). Likewise, visual disease symptoms are not always correlated to reductions in photosynthesis (e.g. Sadras et al., 2000).

(ii) Another strategy could be to select for higher maximum oil concentration (dotted line in Figure 9a). A simple way to measure this trait would be to thin, after flowering, crops sown at a normal density. This would result in high radiation interception per plant, without the confounding effects of high grain number per plant or high grain weight potential (Aguirrezábal et al., 2003).

4.4.2. Oil fatty acid composition

Crop breeding has achieved many modifications of the fatty acid profile of oil in many species, mainly through the incorporation of genes with large effects (for a review, see Velasco and Fernandez-Martinez, 2002). The effect of the environment on these genotypes with modified fatty acid composition is relatively small (e.g. up to 6.9% for high-oleic sunflower; Izquierdo and Aguirrezábal, 2008), but it can still be a concern, especially with strict market standards. The stability of improved fatty acid compositions and the achievement of a desired quality under specific environments are important breeding objectives.

The parameters of the model in Section 2.2 showed a wide variation between traditional high-linoleic sunflower hybrids (Izquierdo and Aguirrezábal, 2008). The stability of minimum and maximum oleic acid concentrations for temperatures outside the range of strong response (Figure 1b) provides a simple way to screen for high or low values of individual parameters (γ_0 and γ_{max}, dotted lines in Figure 9b), by sowing at locations or on dates of known temperature, or under semi-controlled conditions, for example, greenhouse. Of these two parameters, γ_0 showed the highest genetic variability. Such screening could be simpler and less expensive than direct screening for the trait (oleic acid percentage). Another approach could be to develop cultivars for specific environments. For instance, a genotype yielding very-high-linoleic oil under low temperature could be obtained by selecting for a low γ_0, irrespective of other parameters.

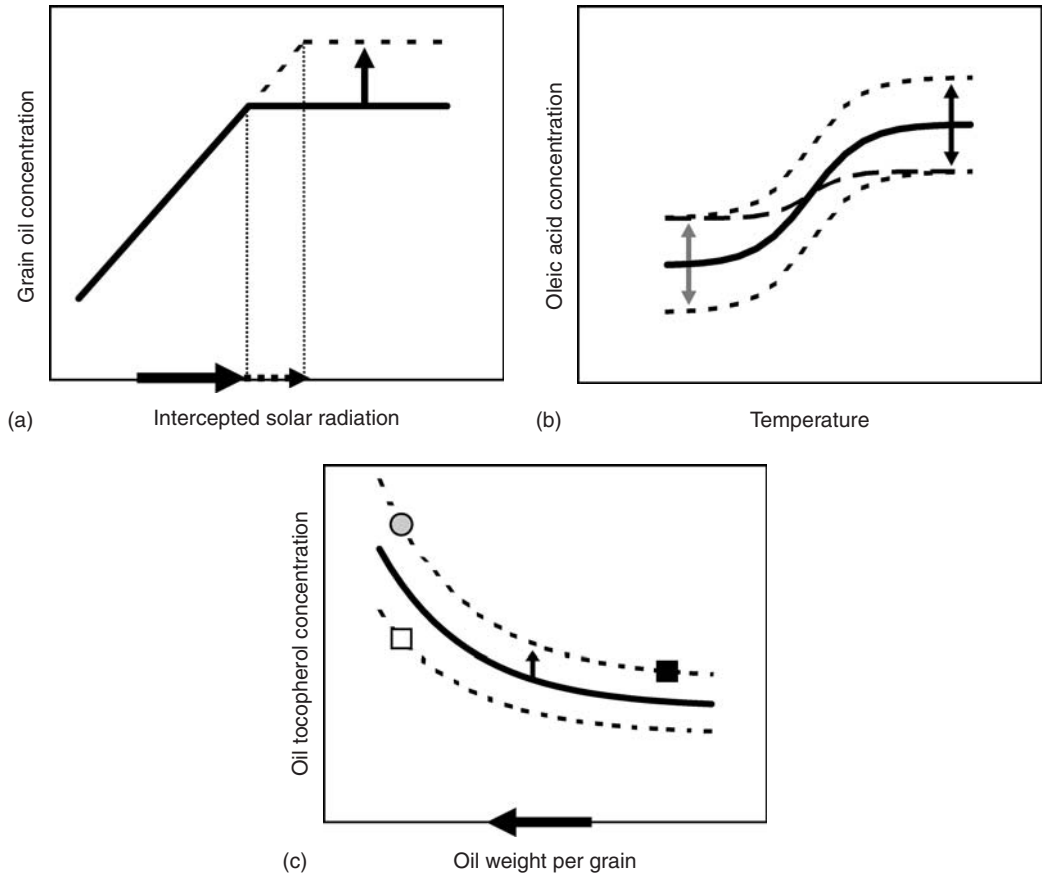

FIGURE 9

Main avenues proposed for the genetic modification of sunflower quality traits, based on relationships presented in Figure 1: (a) grain oil concentration: increased radiation interception during the critical period (arrows along the x-axis), and higher maximum oil concentration (dotted line); (b) oleic acid concentration: changes in the plateau values for minimum (grey arrows) and maximum (black arrows) oleic acid concentrations, to obtain either higher or lower average concentration (dotted lines) or increased stability (dashed line); and (c) oil tocopherol concentration: increased tocopherol concentration relative to that expected through the dilution curve (vertical arrow), and decreased oil weight per grain (arrow along the x-axis), combined to obtain high oil tocopherol concentration (grey circle); black and white squares: see text.

This model is also valid for a high-oleic hybrid. Breeders have improved high-oleic sunflower mostly by indirectly selecting for a high γ_0. There are, however, high-oleic genotypes that differ in their response to temperature, although this genetic variability has not been quantified using the approach described above. An interesting breeding goal for these genotypes would be to increase the stability of fatty acid composition by selecting for low $slope_{max}$, that is, a low difference between the minimum and maximum concentrations of oleic acid (dashed line in Figure 9b).

For other species, the lack of a robust model, and the need to take into account the effect of radiation (and possibly the interaction between temperature and radiation), could make these approaches more difficult.

4.4.3. Oil tocopherol concentration

In sunflower, an inverse relationship between tocopherol concentration and oil weight per grain (Figure 1c) accounts for most of the environmental effect; therefore, this relationship can theoretically be used to quantify the genetic variability of oil tocopherol concentration. Nolasco et al. (2006) analysed the genetic variability of tocopherol concentration among a group of sunflower hybrids, finding the effect of the environment to be larger than the genotypic effect. A re-analysis of data from Nolasco et al. (2004) through a two-way ANOVA, using the ratio between the measured and expected (according to the dilution-like curve) values (as opposed to the raw tocopherol concentration data), showed that environmental and G × E effects were reduced, the effect of the genotype was increased and differences between genotypes were detected.

Based on this relationship, two strategies for improving oil tocopherol concentration have been proposed:

(i) An ideotype for high-tocopherol concentration in the oil could be defined as a plant with a small amount of oil in each grain. Reducing oil weight per grain (solid arrow along the x-axis in Figure 9c) should preferably be achieved through smaller grains, and not through reduced grain oil concentration (which is an important quality trait per se). Therefore, to avoid negative consequences on grain yield, a smaller grain weight should be compensated by an increased grain number (see also section 4.1).

(ii) Using the relationship between tocopherol concentration and oil weight per grain, screen for genotypes with an improved tocopherol concentration, independently of genetic or environmental variations in oil concentration or grain weight. Such a genotype would be one with a positive deviation from the expected 'dilution' curve (e.g. black square in Figure 9c). A genotype with a higher absolute tocopherol concentration but with a negative value relative to the curve (e.g. white square in Figure 9c) would be expected to have a negative direct effect on tocopherol concentration. This latter genotype should, however, have a positive indirect effect through a decreased oil weight per grain, according to strategy (i). Provided the independence of these two effects, the two strategies presented here could hypothetically be applied simultaneously (grey circle in Figure 9c).

4.4.4. Grain protein concentration

The yield–protein concentration correlation and the large genotype-by-management and G × E interaction components of variance relative to the genotypic component (Cooper et al., 2001) have significantly restrained genetic improvements of grain protein concentration. Breaking this negative relationship remains a major challenge for cereal breeders (DePauw et al., 2007; Oury and Godin, 2007).

Both grain yield and protein concentration are genetically determined by a large number of independent loci. On this basis, some authors have concluded that genetic restrictions caused by linkage or pleiotropy are not sufficient to simultaneously hinder the improvement of both traits (Kibite and Evans, 1984; Monaghan et al., 2001); several breeding programmes have been successful in breaking or shifting this correlation, demonstrating that there is no physiological or genetic barriers to breeding high-yielding, high-protein genotypes. Cober and Voldeng (2000) developed high-protein soybean populations exhibiting a very low or no association between grain yield and protein concentration. Similarly, high-protein and low-protein maize strains resulting from long-term divergent recurrent selection allowed to shift the negative grain yield–protein concentration relation (Uribelarrea et al., 2004). More recently, the transfer of a chromosomic region from an accession of emmer wheat (*Triticum turgidum* L. var. *dicoccoides*) associated with high grain protein concentration into high-yielding bread wheat (DePauw et al., 2007) and durum wheat (Chee et al., 2001) cultivars also allowed to shift the correlation.

Crop simulation models can be used to assess the link between physiological traits (model parameter) and grain yield or protein concentration (Boote et al., 2001; Hammer et al., 2006). The wheat simulation models Sirius and *SiriusQuality*1 (Martre et al., 2007; Semenov et al., 2007) and APSIM-Nwheat (Asseng and Milroy, 2006) have been used to analyse the effect of single-plant or crop traits on both grain yield and protein concentration. These simulations showed that variations in weather and nitrogen treatments induced larger

variations in grain yield and protein concentration than most of the physiological traits considered, and revealed strong trait-by-nitrogen and trait-by-water interactions.

Monaghan et al. (2001) showed that under western European conditions, positive departures from the grain yield–protein concentration relation were associated with the amount of nitrogen accumulated by the crop after flowering. The sensitivity analysis of *SiriusQuality*1 was consistent with this finding: for high nitrogen supply, increasing the maximum rate of nitrogen uptake during grain filling allowed to shift the negative grain yield–protein concentration correlation (Figure 10b). To analyse the effect of the rate of nitrogen remobilisation from leaves and stems to grains on crop dry matter and nitrogen dynamics, a scaling parameter (β) changing proportionally the daily rate of accumulation of grain nitrogen was introduced in *SiriusQuality*1 (Martre et al., 2007). For both low and high nitrogen supply, simulated grain yield increased significantly when the rate of grain nitrogen accumulation was decreased, whereas grain nitrogen yield, post-flowering nitrogen uptake and nitrogen harvest index were very similar, even for high nitrogen supply (Figure 10c and d). Therefore, increasing in the model the daily rate of grain nitrogen accumulation leads to a dilution of grain nitrogen. Surprisingly, about 75% of the increase in grain yield was due to the increase in dry matter harvest index, which increased by about 6% when β was decreased from 1 to 0.7. In good agreement with this result, pot-grown stay-green mutants of durum wheat in a greenhouse had a higher grain yield per plant than the wild type, but the grain nitrogen yield was the same for the mutants and the wild type; therefore, the grain protein concentration was lower in the mutants than in the wild type (Spano et al., 2003). In contrast, Uauy et al. (2006a, b) reported that acceleration of canopy senescence in transgenic wheat plants under-expressing a NAC transcription factor located at a QTL for high grain protein concentration paralleled acceleration of nutrient remobilisation from leaves to grains, leading to higher grain protein concentration; however, grain yield was not reported in these studies.

A survey of UK winter wheat cultivars revealed a positive association between grain yield and stem nitrogen concentration at flowering (Shearman et al., 2005). In the sensitivity analysis of *SiriusQuality*1, the nitrogen storage capacity of both leaves and stems was considered. Under limiting nitrogen supply, increasing the storage capacity of the leaves or stems did not shift the negative correlation between grain yield and protein concentration (Figure 10e and g). The increase in leaf nitrogen mass per unit leaf surface area was associated with a reduction in grain yield because of reduced leaf expansion due to nitrogen shortage. In contrast, under high nitrogen supply, increasing maximum stem nitrogen concentration or leaf nitrogen mass per unit of leaf surface increased both grain yield and grain protein concentration (Figure 10f and h). Similar trends in grain yield and protein concentration were observed when the efficiency of nitrogen remobilisation was modified, but changes in grain yield and protein concentration were much more limited. This simulation analysis shows that, under high nitrogen inputs, increasing the nitrogen storage capacity of the leaves and stem and/or the efficiency of nitrogen remobilisation may significantly shift the negative grain yield–protein concentration correlation. Moreover, it may also reduce the risk of nitrogen losses by leaching and volatilisation.

5. CONCLUDING REMARKS

Diverse industries require grains with high and reliable quality for specific uses, and breeders have responded by tailoring new cultivars to these demands (DePauw et al., 2007; Velasco and Fernandez-Martinez, 2002). There is therefore an increasing need for knowledge of the physiology of quality traits, in support of both breeding and crop management aimed at the dual objective of high yield and high quality. While breeding for crop yield has been always performed at the population (crop) level, the improvement of quality traits has mostly focused on individual plants or plant parts (i.e. grain). Combining experiments and simulations, we demonstrated that most quality traits, and certainly quality–yield interactions, cannot be correctly understood or predicted by extrapolating from individual plants to the population. The determination of quality traits – such as that of yield components – should be analysed at the crop level, and crop physiology concepts and methods classically applied to yield analysis can be powerful tools.

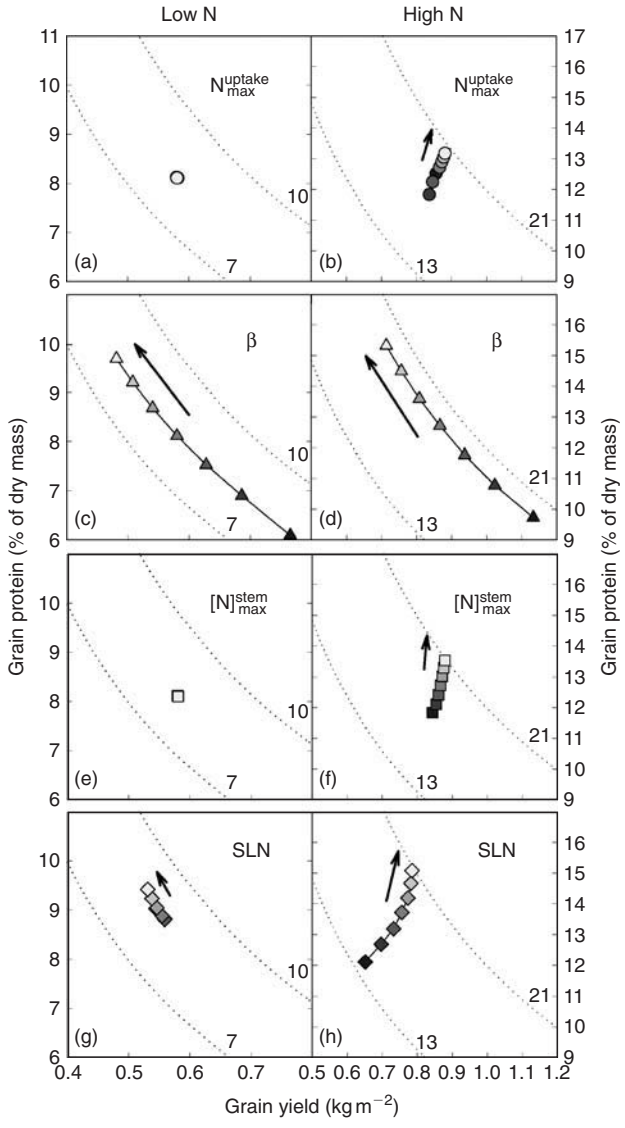

FIGURE 10

Simulated grain protein concentration versus grain yield for wheat crops in response to (a, b) variations of the maximum rate of nitrogen uptake at anthesis (N_{max}^{uptake}, default value 4 g N m^{-2} ground day^{-1}), (c, d) a scaling parameter modifying the daily rate of grain nitrogen accumulation (β, default value 1), (e, f) the nitrogen storage capacity of the stem ($[N]_{max}^{stem}$, default value 10 mg N g^{-1} DM) and (g, h) leaf nitrogen mass per unit of leaf surface area (SLN, default value 1.5 g N m^{-2} leaf). Simulations were performed with the wheat simulation model SiriusQuality*1 (Martre et al., 2006). Data are means for 32 years at Clermont-Ferrand at low (8 g N m^{-2} applied in two splits; a, c, d and g) and high (25 g N m^{-2} applied in four splits; b, d, f and h) nitrogen supplies. The grey intensity of the symbols decreases as the parameters increase by 10% increments from −30% to +30% of their default value. Arrows indicate the way of the increase of the parameter values. Dotted lines are grain nitrogen yield (g N m^{-2}) isopleths. Details of the soil and cultivar characteristics are given in Martre et al. (2007). (Source: Martre et al., 2007.)*

Much of our current knowledge about the physiology of grain quality in oilseed crops and cereals has been obtained in sunflower and bread wheat, and hence the value of these species as models for quality studies illustrated in this chapter. Examples were presented where relationships (and underlying processes) between a given quality trait and its predictor, first identified in model crops, were then found to be common to other crops. This research strategy seems promising for further insights into the physiology of quality traits in several crops.

Mathematical crop models have incorporated quality modules that allow for the simultaneous simulation of grain yield and quality (Section 3). Several cases were presented to illustrate how, by means of these models, crop physiology can be used for designing better management and breeding strategies for improving quality in oil crops and cereals. Interestingly, these models are more than a means to gather physiological knowledge; they also help creating new knowledge by highlighting emergent properties that arise from the combination of different processes. For example, crop models realistically reproduced relationships between yield and quality traits (Section 4), which are assumed to be independent processes in the models.

Dealing with G × E interactions is still one of the major challenges for plant breeders. As a complement to classical approaches, quantitative relationships between quality traits and environmental drivers in this chapter are a more robust means of quantifying G × E interactions, and of generating new 'traits' (model parameters) that are largely independent of the environment. These relationships represent meta-mechanisms at the plant or crop level and, therefore, could help to fill the current gap between genotype and phenotype, specially for complex traits (see also Chapter 10). Coupling physiological and genetic approaches to improve quality traits, we argue, represents one of the next challenges for crop physiology and breeding.

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