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Impact of Crop Husbandry Practices and Environmental Conditions on Wheat Composition and Quality: A Review

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ABSTRACT: The increasing interest in the production of bread wheat (*Triticum aestivum* L.) with specific quality traits requires a shift from the current breeding goal, being yield, to improved compositional and, consequently, functional traits. Since wheat is a key food crop, this must be attained while maintaining or even further increasing yield. Furthermore, as compositional requirements for specific applications are not well-defined, both protein and gluten content as well as the enzymatic activity remain most important. Given that these traits are majorly impacted by both genotype and environment, it is very complex to predict and ultimately control them. Different strategies, such as applying optimized agronomic practices, can temper these uncontrollable determinants which are equally important to steer wheat quality. As current research on their contribution to specific traits is highly fragmented, this report provides a comprehensive review of the influence of crop husbandry and environmental conditions on wheat yield and composition.

KEYWORDS: *Triticum aestivum L., crop husbandry practices, environmental conditions, gluten composition, yield*

INTRODUCTION

With a global annual production of 751 million tons, bread wheat (*Triticum aestivum* L.), together with maize and rice, forms the main staple food crop for 35% of the world's population.[1] It contains essential amino acids, minerals, and vitamins, along with nutritionally beneficial secondary metabolites and dietary fibers.[2,3] Last decade, breeders mainly focused on yield increases, with grain quality being a secondary breeding objective.[4,5] In 2014, average yields for Northern and Western European countries ranged from 6.8 to 7.8 ton ha^{-1} with Ireland, Belgium, and The Netherlands as the countries with the highest yields (10.0, 9.4, and 9.1 ton ha^{-1}, respectively). These are generally higher in comparison with central America, which tends to have an average lower yield (up to 5.2 ton ha^{-1}), mainly due to the use of spring wheat. Globally, average wheat yield (winter and spring wheat under intensive and nonagricultural practices in suited or inadequate growing conditions) reaches only 3.3 ton ha^{-1}.[1] Although yields globally tend to increase, in many countries a yield stagnation is experienced. On one hand, this can be attributed to climate change, especially global warming,[6] and the therefrom resulting higher occurrence of extreme weather conditions. On the other hand, intensive genetic selection, which has led to genetic erosion in modern breeding pools, partially contributes to this phenomenon. According to Reif et al.,[7] wheat's genetic diversity was narrowed from 1950 to 1989 but was again enhanced from 1990 to 1997. This occurred through the introgression of new genes or alleles provided by landraces which are a valuable source of genetic diversity. These races can be used to breed varieties adapted to local environmental conditions according to the origin of the landraces.[8] Using a SNP-based diversity map, Cavanagh et al.[9] characterized the impact of breeding on genomic and geographic patterns of genetic diversity. It was concluded that most of the diversity present in the modern varieties was also present in landraces, with a 6% reduction in the population size. On the basis of microsatellites, Huang et al.[10] observed a dip in the genetic diversity of European winter wheat varieties in the 1960s in comparison to the genetic diversity in the earlier 1940s. On the other hand, in the later decades, a quantitative increase of genetic diversity was found. So, according to these authors, modern plant breeding has resulted in changes of alleles present in the wheat germplasm which rather led to an improvement of the genetic diversity.

Additionally, the results of several studies corroborate the evidence that a considerable breeding progress, especially with respect to yield, was achieved during the last decades. Brisson et al.[11] and Oury et al.[12] demonstrated that the stagnation of bread wheat yield in France did not correspond to a slowing down in the genetic progress. It appeared that since the end of

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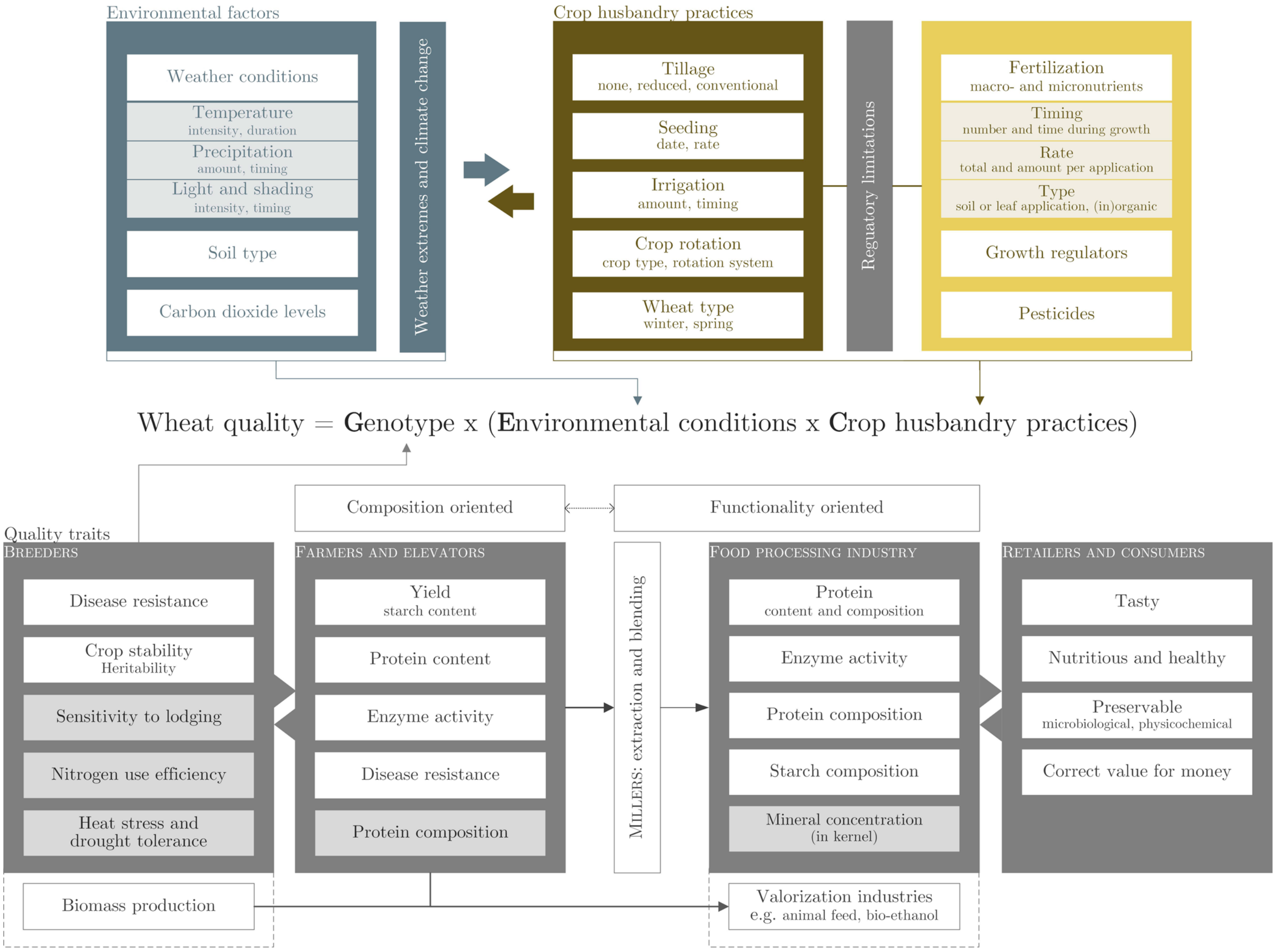

Figure 1. Schematic overview of the quality traits for wheat per stakeholder in a general supply chain and how these are influenced by environmental and cultivation practices.

the 1980s the genetic progress has been partly or totally counterbalanced by the adverse effects of climate change. Also Laidig et al.[13] concluded that, based on analysis of German wheat trials, winter wheat breeding progress remains to be very successful with a large gain in grain yield (24%). On the contrary, location specific environmental policies mainly focus on the restriction of the use of fertilizers. For example, in the European Union, nitrogen and phosphorus fertilization became strictly regulated which could also contribute to the stagnation of wheat yield.[14]

Last years the wheat demand is rising, partly as a result of population growth, but also because of an increasing consumption per capita. Many people consume wheat based foods on a daily basis as this substantiates the dietary guideline for carbohydrate intake. In China, wheat consumption increased more than 6-fold from just over 19 mt in 1962 to 123 mt in 2012. In the EU wheat consumption has been fairly flat in recent years. The figure of 121.5 mt in 2012 represents an increase of only 7% over the figure in 1999. Wheat consumption in the USA increased from 16 mt in 1962 to 38 mt in 2012, which is less than one-third that of the EU.[15] However, for these figures, no distinction between wheat used for human or animal consumption and (second generation) bioethanol production is made. Nevertheless, in the USA and Europe (mostly in France and the U.K.), wheat straw is used instead of the wheat kernel as this results in a higher ethanol yield.[16] Therewith, Semenov et al.[17] stated that, considering the limitations on expanding crop-growing areas, a significant increase in crop productivity will be required to achieve the projected need to raise the world food supply by 70% by 2050. Nevertheless, to meet the more specific demands of the food industry, to prevent food losses and to optimally utilize the available resources, the production of high-quality wheat with distinct properties is equally important.

Besides yield gain, there is a continuously growing interest in the cultivation of high-quality and nutritious wheat. Since wheat derivatives (whole meal, white flour, extracted starch, and gluten) are applied in a wide range of industrially produced foods, differing compositional characteristics are desired. This is further augmented by the diversified processing techniques (e.g., extrusion or working with preferment in bread making) related to these novel or conventional areas of application. Moreover, quality is also a multidisciplinary concept due to the various stakeholders involved in the wheat breeding, cultivation, and processing chain (gray boxes in Figure 1). While farmers generally look at yield and production costs, millers and industry are mainly interested in processing quality and the resulting functional properties.[18] Consumers on the other hand want a tasty end-product,[19] and their increased awareness of food related health issues, authenticity, and sustainability has led to an enlarged food diversity.[20] Furthermore, the ethical and economic importance of food losses, manifesting on both the industry and household level, calls for a more detailed understanding of the various spoilage mechanisms. Physicochemical degradation (staling), which is most commonly observed in bakery products, is still far from being fully elucidated. The review of Fadda et al.[21] points out the central role of starch and starch−gluten interactions in the staling mechanism and highlights the effect of different ingredients such as hydrocolloids, waxy wheat flours, and enzymes, which are able to retard staling.

For food producing companies and the related stakeholders, the market value of wheat grain is mainly determined by its protein concentration.[22] In addition, the Zeleny sedimentation value, which is often used as an overall quality indicator, and the α-amylase activity (indirectly determined by the Hagberg falling number [HFN]) are measures to differentiate between wheat suitable for bread making purposes or for less demanding bakery applications. In addition, protein composition, mainly the gluten protein fraction, is found important in determining the baking quality. Xue et al.[23] concluded that a variety's suitability for bread making purposes conceivably improved when gliadins and glutenins are present in the correct quantity and ratio, thereby giving wheat based dough its unique rheological behavior. Besides gluten proteins, nongluten protein fractions, albumin, and globulin (comprising 15−20% of the total wheat flour proteins) account partially for the variation found in baking quality.[24] Furthermore, kernel hardness, (dough) rheological properties, water absorption, presence of essential amino acids, dietary fibers, and quality-impairing substances (e.g., mycotoxins) are important characteristics influencing the functional, technological, and nutritional properties of wheat both directly or indirectly.[25−28]

Both yield and quality traits of wheat depend on its genotype but is also clearly influenced by the environment and the mutual interaction between both factors.[27,29,30] Various studies have reported the significantly stronger effect of environmental conditions on wheat yield and composition in comparison with the effect of the genotype. It is estimated that the improvement of the genetic stock contributes for 30−50%, while agricultural techniques contribute for 50−70% to increasing yields.[31] More recent studies approve that the environment is the predominant source of yield variation.[29,32] This implies that when the same wheat variety is grown in environments with differing meteorological conditions and/or varying crop husbandry practices, a heterogeneous group of products, all with different compositional properties and consequently a specific quality, can be obtained. Therefore, a thorough understanding of the driving factors governing environmental variations in grain quality is a prerequisite to cultivate wheat with specific properties in a sustainable and repeatable way. Especially in a industrial baking process, a stable wheat quality is desired since continuously adjusting ingredients and dough handling is highly demanding. In that evidence, industry is majorly interested in how specific characteristics can be controlled during growth or which varieties are less susceptible to environmental fluctuations. Extensive research has been performed in order to estimate the effect of a wide range of environmental factors on the composition of the harvested wheat grain. In this review, we tried to summarize the key environmental factors influencing wheat yield and quality traits such as protein content and composition (Figure 1).

■ CROP HUSBANDRY PRACTICES

Crop Rotation. Using crop rotation is generally preferred above monoculture since the yield of crops grown in a continuous monoculture declines as a result of an accumulation of soil or stubble-borne diseases specific to the monoculture crop (e.g., *Fusarium*). Moreover, the use of crop rotation can improve soil structure, water and nutrient use efficiency, and mycorrhizal associations and can provide better weed control.[33−35] These effects can enhance both grain yield and quality traits such as the grain protein content.[33] The advantages of crop rotation and the use of catch crops, either sown every year in a rotation system or during wheat growth (under-sowing or relay intercropping), depend on the type of crop and the post-treatment (mulching, ploughing, and residue return). Legume crops will decrease volatilization and leaching of N due to their ability to fix a substantial amount of nitrogen from the air (96−376 kg N ha^{-1}[36]) in symbiosis with rhizobia and their humification and thus N mineralization potential. This results in an improved soil mineral status with an increased N-availability for the subsequent crop. Additionally, as some legumes are deeper rooting than other agricultural plants, leached nutrients can be pumped up and will consequently become partially available for the preceding crop roots. For example, roots of *Lupinus angustifolius* and *L. consentinii* can reach a depth up to 2.2 m compared with 1.3 m for wheat.[37] Furthermore, some legumes (e.g., *Lupinus albus*) also enhance the mobilization of fixed phosphorus in the soil through the formation of cluster roots. Supplementary, thanks to the decomposed network of in-depth root hairs, the water capillarity of the soil is enhanced resulting in less drought stress for the following crop.[38]

Rahimizadeh et al.[34] illustrated the beneficial effects of crop rotation using potato, silage corn, clover, or sugar beet as the preceding crop. A yield increase from 2.1 ton ha^{-1} to 3.9 ton ha^{-1} was obtained for the potato-wheat rotation in comparison to the continuous wheat system (wheat−wheat). Concerning the grain protein content, clover as a preceding crop was most effective as it resulted in an absolute increase of 1.11% in the grain protein content (from 13.01% to 14.12%), independent from the applied N fertilizer rate. These findings are in accordance with research from Doltra et al.[39] who noticed that specifically including legumes in the catch crop mixture had a positive effect on winter wheat yield. Nevertheless, as environmental conditions such as high degrees of precipitation or elevated temperatures can induce leaching of mineralized N from the cover crop's biomass, the time between the incorporation of the residues and the sowing of the subsequent crop is determining. It was shown that, depending on the development rate of the cover and main crop and the N availability (intrinsic or through fertilization), under-sowing or intercropping can lead to a competition for N.[40,41] Bergkvist et al.[42] investigated if the yield of winter wheat was affected by white clover while applying multiple N fertilization rates. No effect of under-sowing on the yield was noted which was also confirmed by Amossé et al.[35] and Conrad and Fohrer.[43] In their research, wheat grain yield was not significantly disturbed by intercropping whatever the above-ground development of legumes (black medic, alfalfa, red and white clover). In general, the use of crop rotation systems has been found to have beneficial effects on both the soil conditions and crop yield. Nevertheless, its magnitude is highly dependent on the type of system used, the meteorological conditions (mainly precipitation), and the fertilization regime. In case the cover crop biomass is incorporated before sowing the wheat, it can form an additional source of N. When relay intercropping, undersowing, or crop rotation without ploughing is used, the cover crop aids in fixating the N in the soil, reducing losses due to leaching or volatilization.

Tillage. Tillage is an important agricultural practice, influencing the physical, chemical, and biological characteristics of the soil by mechanical agitation such as digging, stirring, and overturning. To prepare the seedbed, a continuum of tillage methods can be amended, ranging from zero tillage (ZT), minimum, or reduced tillage (RT) to conventional tillage (CT).[44] In Coventry et al.,[45] the effect of ZT on grain yield and protein concentration of wheat cultivated in NW India was studied. It was concluded that grain yields were lower with ZT than with CT, whereas the grain from the ZT treatments had a higher protein (1−3%) concentration and grain hardness (3−10%) compared to CT. Šíp et al.[46] evaluated the effect of two tillage systems (CT (22 cm depth) and RT (8−10 cm depth)) and two fertilization input levels (low input level, 70−100 kg N ha^{-1}, split into three applications and without fungicides or growth regulators; high input level, 120−150 kg N ha^{-1}, split into three applications and sprayed with fungicides) on grain yield and protein concentration and other grain quality traits (gluten concentration and index, Zeleny sedimentation value, falling number, and test weight). The effect of tillage on the examined traits was generally lower than the effects of environment (trails were conducted at two locations in the Czech Republic), variety, and input level. It was found that RT in combination with high inputs leads to the highest grain yields (9.4 ton ha^{-1} compared to 8.55 ton ha^{-1} for CT with a low input level). Under conditions of drought stress, as was the case in this experiment, RT can be preferred above CT. RT systems are more able to cope with a water deficit and thereby can prolong the uptake of, e.g., N during short-term drought episodes. However, under CT combined with a high input level, protein concentration, wet gluten content, and Zeleny sedimentation volume were increased (respectively, by 4.1%, 5.0%, and 6.2% compared to the means obtained under the high input RT), while gluten index, falling number, and test weight were not significantly affected. Brennan et al.[47] studied the effect of CT and RT on the yield of winter wheat at field trials in Carlow (Ireland) under five levels of N fertilizer (0, 140, 180, 220, and 260 kg N ha^{-1}). These authors reported a significantly higher grain yield in case CT was adopted. However, the effect of tillage varied between years. In years with excessive rainfall during crop establishment, RT led to significantly lower yields. This can be explained by the fact that RT results in poor infiltration, resulting in a lower plant density and, subsequently, lower yields. From the study of Woźniak and Gos,[48] it was concluded that the grain yield of spring wheat sown in the CT and RT systems was higher by 13.5% (4.65 ton ha^{-1}) and 8.4% (4.39 ton ha^{-1}), respectively, than in the ZT system (4.02 ton ha^{-1}). Protein and wet gluten content were not influenced by the tillage method. Grahmann et al.[49] concluded that there were no significant differences in wheat yield between RT and CT for wheat grown in the arid climate of Northwestern Mexico. In addition to these ambiguous findings, Šíp et al.[46] sometimes noted an inconsistent effect of tillage on yield under the low and high input levels. Although this indicates tillage × input level interaction, various other researchers did not observe such an effect.[50−52] When applying crop rotation (e.g., maize-wheat) and residue management, the highest yields were observed under ZT circumstances in comparison to CT or ZT without leaving crop residues in the field.[53] It is clear that the results on the effect of tillage on wheat yield and quality traits are diversified and dependent from both the cultivation location and other crop husbandry practices. In general, it can be concluded that in areas with a low precipitation, higher yields are noted for wheat cultivated in the RT than the CT system.

Seeding. As winter wheat requires cold (5−10 °C) for vernalization, it should be sown, depending on the region and prevailing climate, between September and November. The optimal moment during this time span is mainly determined by the timing of precipitation.[54] Moreover, when the wheat is sown beyond the optimum period, the average yield decreases, resulting in a relatively increased protein content.[54,55] In addition, Ehdaie and Waines[56] observed that early sowing (days to anthesis, 129−151) resulted in a longer vegetative growth period. This, however, did not lead to a higher grain yield in comparison to later sown wheat (119−146 days to anthesis). Only straw length, and thus total biomass, increased. In contrary, Baloch et al.[57] found that earlier planting and a prolonged growth period, results in an enhanced ear development and thus in an increased yield. For spring wheat varieties, comparable effects were obtained by Subedi et al.[58] A 15−45% yield reduction was observed for the delayed sowing times (10 or 20 days after the first sowing). Besides differences in the optimal timing due to environmental variation, this is also greatly influenced by the genotype.

Gooding et al.[59] conducted experiments to evaluate the effect of seed rate on wheat yield and quality. It was shown that a lower number of seeds per area unit (≤200 seeds m^{-1}) was associated with delayed, and more variable, crop maturation. This asynchronous grain development, which is common for wheat, will be more pronounced in case low seeding rates are used.[60] In one experiment, grain yield followed a parabolic response to seed rate with apparent reductions in yield at very high seed rates (tested at 50, 100, 200, 350, and 600 seeds m^{-1}). Plants compensated for low plot densities by increased production and survival of tillers and, to a lesser extent, increased grain numbers per ear. Effects of seed rate on grain specific weight and thousand kernel weight were small and inconsistent, possibly due to varying compensation effects. HFN increased (thus, α-amylase activity decreased) linearly with seed rate which was associated with a quicker maturation of the crop. Grain protein concentration was reduced by increasing seed rate from 50 to 100 seeds per square meter, due to competition for nitrogen.

Compensation effects, resulting in more tillers (with a higher number of spiklets per ear) at lower seeding rates, can be indirectly used to gain a maximized yield or an altered protein composition. Li et al.[61] found that wheat yield can be increased by decreasing the number of basal and top sterile spiklets and by enhancing (through breeding) the grain weight at the center grain positions. Moreover, a parabolic effect was noted for the number of grains per spiklet in function of its position in the ear. In addition, Jie et al.[60] also found a parabolic response within the spiklet for grain weight and protein content. Individual grain protein content also decreased with increasing grain position (base of the ear to top). A variety effect became more pronounced under low nitrogen input levels.

Fertilization. Although fertilization rate and splitting is studied most often, the number of applications and their timing as well as the used form of fertilizer is also important.

Moreover, as wheat can be cultivated in various regions throughout the world, the soil type and composition (initial fertilizer content, availability, etc.) and the prevailing meteorological conditions affect these concentration effects. Besides these environmental variables, genotype influences this as well by the efficiency to translocate and remobilize the components during the different growth stages. As this review tries to summarize the various effects, each of the aforementioned influencing factors is discussed separately.

Nitrogen. Nitrogen (N) is a major element essential for plant growth and a fundamental component of amino acids and therefore proteins. Moreover, since N is also part of the enzymes associated with chlorophyll synthesis, its availability impacts all phases throughout crop development, affecting seedling establishment, tillering, canopy development, and grain filling. In general, an increased N supply drives the plant toward a higher productivity and a higher grain protein content.[62] To optimize fertilization, insight into the availability of N in the soil is detrimental. Factors affecting this availability are both soil type and watering conditions (irrigation or rainfed) as well as information on the depletion should be obtained. Furthermore, the form in which N is administered as well as the times and the distribution across the different fractions (splitting) must be considered. In addition, excessive use of N can also have negative effects, e.g., delayed maturity and increased risk of lodging. Moreover, it adversely affects the environment by creating favorable conditions for weeds or algae when N comes into waterways, rivers, and oceans.[63] To achieve a certain protein concentration and composition, while ensuring a sustainable production, optimized N fertilization practices are essential.

Fertilization Rate and Timing. The effect of N fertilization and irrigation on yield and protein content of winter wheat grown on the sandy loam soil in Cambridge (U.K.) was investigated by Pushman and Bingham.[64] Grain yield increased by both irrigation and N fertilization, whereas protein content increased by applying additional N but decreased by 18% in the irrigated plots compared to the nonirrigated plots. Applying an additional dose of 90 kg N ha^{-1} in Zadoks G.S. 32 resulted in a yield increase of 21.1% and 4.8%, while the grain protein content grew by 14.1% and 33.7%, with and without irrigation, respectively. An additional dose of 45 kg N ha^{-1} (applied as an aqueous foliar spray of urea) at anthesis (Zadoks G.S. 60), resulted in additional yield increase of 5.5% for the irrigated plots and a further increased protein content by 12.4% for the irrigated plots and by 7.5% for the nonirrigated plots. Martin[65] studied the effect of N fertilization on both winter and spring wheat by applying three fertilizer regimes: (1) 50 kg N ha^{-1} at late tillering (Zadoks G.S. 30), (2) 100 kg N ha^{-1} at late tillering, and (3) 50 kg N ha^{-1} at late tillering combined with 50 kg N ha^{-1} at booting (Zadoks G.S. 45). For winter wheat, it was seen that the 50 + 50 kg N ha^{-1} and 100 kg N ha^{-1} treatments gave similar yields (7.9 ton ha^{-1} and 8 ton ha^{-1}), which were about 1 ton ha^{-1} higher than the 50 kg N ha^{-1} treatment. Furthermore, significant differences in grain N content were noticeable between the treatments for winter wheat. The wheat fertilized with 50 + 50 kg N ha^{-1} had a significantly higher N content than in the case when 100 kg N ha^{-1} was applied (1.82% N versus 1.70% N), which in turn was significantly higher than in the 50 kg N ha^{-1} treatment (1.58% N). In spring wheat, applying extra N had no significant effect on yield or grain N percentage. In Garrido-Lestache et al.,[66] the effect of N rate and splitting on yield of spring wheat grown in Mediterranean conditions was investigated. For the N rate experiment, 0, 100, 150, or 200 kg N ha^{-1} was applied in equal amounts (1/3rd) at sowing, tillering (Zadoks G.S. 20-25), and stem elongation (Zadoks G.S. 30-35). Yield increased from 3 to 4 ton ha^{-1} when applying 100 kg N ha^{-1} compared to the control without N fertilization (0 kg N ha^{-1}). However, no significant yield increase was recorded for the higher N rates. For grain protein concentration, a highly significant response to N fertilizer rate was noted. The grain harvested from the unfertilized control treatment contained 11.2% protein, whereas 100, 150, and 200 kg N ha^{-1} resulted in grain with a protein concentration of 13.5%, 14.6%, and 14.8%, respectively. Only for the two highest concentrations no significant differences were found. Furthermore, the influence of timing was studied by applying 150 kg N ha^{-1} split in various proportions between sowing, tillering, and stem elongation (0 + 0 + 0, 150 + 0 + 0, 100 + 50 + 0, 100 + 0 + 50, 75 + 75 + 0, 75 + 0 + 75, 50 + 100 + 0, 50 + 50 + 50, 0 + 150 + 0, and 0 + 75 + 75 kg N ha^{-1}). The best grain yield response was obtained when half or one-third of the total N fertilizer rate was applied at stem elongation (100 + 0 + 50, 75 + 0 + 75, 0 + 75 + 75). Also the grain protein content was highest for these treatments, or in some cases when N was applied only at tillering. Splitting of the total N rate between sowing and tillering prompted a lower yield, and the lowest yields were observed when the total rate of 150 kg N ha^{-1} was applied at sowing. Analogously to the yield reduction, the latter treatment lead to a significant decline in grain protein content. Szentpétery et al.[67] conducted a series of fertilization experiments on winter wheat grown in Hungary, with the following doses: 40, 80, 120, 40 + 80, and 80 + 40 kg N ha^{-1} applied at tillering (Zadoks G.S. 25) and after anthesis (Zadoks G.S. 60). Increasing amounts of fertilizer resulted in a considerably higher baking quality, particularly in case it was applied in two rounds (40 + 80 kg N ha^{-1} or 80 + 40 kg N ha^{-1}). The latter was found to be the most effective treatment since the large first dose provided the wheat with the nutrient boost required for the first phase of its growth. The 40 kg N ha^{-1} applied after anthesis, enabled the genetic potential (given the season) resulting in a maximized baking quality. Abedi et al.[68] studied the effect of nitrogen rate (0, 120, 240, and 360 kg N ha^{-1}), each applied in three equal fractions (1) at sowing, tillering, and stem elongation, (2) at tillering, stem elongation, and grain filling, (3) at sowing, stem elongation, and grain filling, or (4) at sowing, tillering, and grain filling (Zadoks G.S. 70), on winter wheat yield and grain quality grown in Iran. The results indicated that the highest grain yields were obtained at a rate of 240 kg N ha^{-1} when it was applied through the vegetative growth stages (sowing, tillering, and stem elongation). Additionally, application of 240 kg N ha^{-1} resulted in the maximum protein concentration, irrespective of the timing. Although only insignificant effects of N rate on gluten content were noticed, N timing however altered this significantly. Highest gluten contents were obtained in case fertilization was applied at tillering, stem elongation, and grain filling (treatment 2). Finally, this study showed that over-application of N (360 kg N ha^{-1}) decreased the protein content. A similar effect for yield was reported by Noureldin et al.[69] who studied the effect of six nitrogen levels ranging from 0 to 125 kg N ha^{-1}, applied as urea in two equal portions. Adding 75 kg N ha^{-1} resulted in the highest yield (53% higher compared to the unfertilized control). Both lower and higher N rates adversely affected grain yield. On the basis of experiments with winter wheat under Mediterranean conditions, Erekul et al.[70] concluded that grain yield increases up to 210 kg ha^{-1} N without substantial losses in the grain quality. In contrast, Mandic et al.[71] already noticed a stagnation in winter wheat yield at a N level up to 75 kg N ha^{-1}.

Uptake Efficiency. From the results obtained by independent researchers, it is clear that the N fertilization rate is important, but the timing and splitting of the application is critical as well. The application rate influences the grain yield and protein content quantitatively, whereas the timing mainly impacts the protein composition. The appropriate amount of N fertilizer depends on how much N the soil can supply, the growth rate of the crop, and the nitrogen use efficiency (NUE). The latter, which has been the subject of a wealth of literature, is defined as the ratio between the amount of N removed from the field by the crop and the amount of N applied as fertilizer. A higher NUE is the result of a better N translocation (portion of N absorbed after anthesis and allocated to the grain) and/or a better N remobilization (N which is recycled from other plant tissues[72]). Accumulation and redistribution of N are important processes determining grain yield and grain quality. In wheat, around 60−95% of the demand for N during grain filling comes from remobilized N which was stored in vegetative organs (roots, shoots, leaves, and stems) before anthesis. If these sources would be depleted, the photosynthetic capacity of the leaves is reduced, resulting in a natural leaf senescence. Through this process, N is recycled following from protein hydrolysis and is subsequently exported in the form of amino acids to grains. Increasing their senescence, and consequently shortening grain filling duration, will also substantially impact yield.[17] A remaining fraction (5−40%) of grain N comes from the postflowering N uptake and translocation to the grain. However, this will only occur if the assimilated N in the leaves is insufficient.[73,74] Furthermore, the potential contribution of an organ as a supplier of N depends on the growing conditions. For example: the role of the flag leaf, in comparison to other upper parts of the plant, as a potential supplier of N to grains increases under improved growing conditions. In contrast, the relative importance of the ear and peduncle increases under water stress conditions.[75] The NUE is determined both by the wheat genotype (e.g., root size and morphology) and by the environment. Indeed, N uptake depends upon the N availability and soil moisture along with root related traits. In many climates, the dry conditions associated with the period of crop maturation may limit postanthesis N uptake.[62] Furthermore, split- and late season-applications of mineral N fertilizers are common approaches to improve NUE.[66] In Brennan et al.,[47] the NUE at 0, 140, 180, 220, and 260 kg N ha^{-1} of winter wheat grown in a cool Atlantic climate (Ireland) was studied. It was concluded that the NUE efficiency ranged from 14.6 kg grain per kg N in the case where 260 kg N ha^{-1} was applied to 62.4 kg grain per kg N in the case where no additional fertilization was applied. The fact that the NUE declines at high N rates was approved by Mandic et al.[71] At 75 and 150 kg N ha^{-1}, a NUE of 58.62 and 29.96 kg grain kg^{-1} N was observed for winter wheat grown in Serbia.

Beyond the effect of N rate and timing, the used N form may also influence soil pH and thus the availability of other nutrients, particularly micronutrients.[76] Urea (UR) is the most produced and used N source in agriculture. However, depending on soil and weather conditions, volatilization can lead to considerable NH_3−N losses when applied on the soil surface. Because of high costs of N fertilizers, the use of N sources which promote lower NH_3−N losses by volatilization, such as calcium nitrate (CN) or ammonium sulfate (AS), would be a way to increase fertilizer efficiency and maximize wheat yield.[77] To gain insight into the effect of different N fertilizers, three N rates (40, 80, and 120 kg N ha^{-1}) in the form of UR, CN, or AS were applied in top dressing at tillering. For the three N sources, wheat grain yield was highest when 80 kg N ha^{-1} was applied. The N sources only provided significant differences in wheat grain yield when the higher N rates were applied (80 and 120 kg N ha^{-1}). Grain yield was significantly higher with the use of CN and AS than with UR at 80 kg N ha^{-1}. At 120 kg N ha^{-1}, grain yield was higher with the application of CN compared to the use of AS and UR. Garrido-Lestache et al.[66] also conducted experiments with different N types using 150 kg N ha^{-1}, equally divided over an application at sowing, tillering, and stem elongation. N was applied either in the form of UR at sowing and ammonium nitrate (AN) as top-dressing or as UR at sowing and AS as top-dressing. In addition to the 150 kg N ha^{-1}, one leaf fertilization at ear emergence (control, 25 kg S ha^{-1}, 25 kg N ha^{-1}, 25 kg S ha^{-1} + 25 kg N ha^{-1}, and 50 kg N ha^{-1}) was applied. It was concluded that use of different types of fertilizer to the soil and of N and/or S fertilizer to the leaf had no significant effect on the grain yield. However, grain protein content increased when the maximum leaf N rate was applied at ear emergence (50 kg N ha^{-1}).

Method of Application. Grahmann et al.[49] studied the effect of fertilizer application method (broadcast, applied in furrows or disk-banded on top of beds) and timing (applied before planting or split between preplanting and first node (Zadoks G.S. 31)) of 120 kg N ha^{-1} as urea in northwestern Mexico (a hot and arid climate, where spring wheat is cultivated during winter). A preplanting application of 120 kg N ha^{-1} resulted in lower wheat yields compared to a split application. Furthermore, the results showed a clear advantage of furrow and bed application over broadcast application to increase wheat yield and quality. Highest test weights were obtained with 40 kg N ha^{-1} bed, 80 kg N ha^{-1} furrow, or 80 kg N ha^{-1} bed−40 kg N ha^{-1} furrow. Basal broadcast application resulted in significantly lower protein content than the other fertilized treatments.

As mentioned above, the optimal N fertilization is highly dependent on the initial soil properties, the wheat variety, and type (winter or spring). So, no general conclusions concerning the N rate that has to be applied can be drawn. Applying additional N, up to a certain limit, improves grain yield and protein content. However, over N fertilization has an adverse effect on yield and favors plant logging. Concerning the timing, it can be concluded that N application before sowing has an effective role on seed germination and plant settlement, whereas the influence on yield and quality is rather limited. According to Abedi et al.,[68] N fertilization before wheat planting is unnecessary due to two reasons. First of all, soil N is in most cases sufficient for seed germination and early growth and, moreover, in most cases the N applied presowing moves beyond the root zone, especially in irrigated fields or fields with a high amount of precipitation around sowing. Early N, applied at tillering, will be used mainly by the plant for yield attainment, while for increasing grain protein N applications should be made between booting and ear emergence. By applying N at anthesis, the grain-filling period can be prolonged, given appropriate weather conditions this can result in the preference for protein build-up over starch synthesis. Furthermore, additional N fertilization at heading (Zadoks G.S. 50-59)

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improves loaf volume of wheat flour based breads by increasing the grain protein concentration and altering its composition. N splitting in four fractions enhances the percentages of gliadins and glutenins as well as certain high molecular weight glutenin subunits (HMW-GS), which leads to an overall improved baking quality.[23] Therefore, it is argued that N splitting is more effective in improving wheat quality than the increase in N rate. This offers the potential to cut down N fertilization rates in wheat production systems. Furthermore, from the literature review above, it is clear that late season N application improves wheat quality. Nonetheless, late applications (postanthesis) do not guarantee an increase in bread-making quality.[64] However, in an in-depth study of Li et al.[78] in which labeled N was used to differentiate between the amounts absorbed pre- and postanthesis, contradictory observations were made. It was shown that N stored after anthesis mainly contributed to the concentration of the storage proteins (globulin and glutenin) in the kernel. Moreover, the authors proposed that optimizing N application during the growth stages postanthesis could be a feasible approach to regulate the distribution of the protein fractions in the grain for specific end-use.

Currently, the timing of N fertilization is mostly studied in relation to the growth stage. However, modern nondestructive imaging techniques give the opportunity to assess crop N status and thus more accurately estimate crop N fertilization requirements. By using spectroradiometers, reflectometers, imagery from satellite sensors and digital cameras, optical properties, such as crop canopy reflectance, leaf transmittance, chlorophyll and polyphenol content, can be measured to estimate N in the plant. These technologies allow for highly sensitive plant N status information and may thus contribute to better N management.[79,80] In practice, these techniques can be applied for precision agriculture allowing farmers to apply the right input, in the right amount, to the right place, at the right time and in the right manner improving agronomic, economic, and environmental efficiency.[63]

Sulfur. Besides N, sulfur (S) is an element essential for plant growth as it is a key element in the formation of chlorophyll. Moreover, it forms a building block of various proteins, including the gluten proteins as they contain more S-rich amino acids such as cysteine and methionine. The S requirement for optimal wheat growth is about 15−20 kg S ha^{-1}.[81] Although findings with regard to the yield gain achieved by applying additional S vary greatly between studies, it is indisputably demonstrated that S deficiency results in a reduced yield. According to Järvan et al.,[82] for winter wheat grown in a nitrogen background of 75 and 100 kg N ha^{-1}, additional S (10 kg S ha^{-1} divided over two applications) can lead to a yield increase from, respectively, 7.7% to 43%, depending on the prevailing weather conditions and the time point at which the fertilizer is applied. For spring wheat Klikocka et al.[83] reported a yield increase of 3.58% with respect to the control without S fertilization, by applying 50 kg S ha^{-1} (40 kg S ha^{-1} before sowing and 10 kg S ha^{-1} at heading) in combination with 80 kg N ha^{-1} (40 kg N ha^{-1} before sowing and 40 kg N ha^{-1} at stem elongation). Stroud et al.[84] even reported a yield decrease from 1 to 15%, depending on the year, when no S fertilization was applied.

Fertilization Rate. Besides affecting yield, S affects both total grain protein concentration and the accumulation of different protein groups during grain development.[70,82,83,85,86] However, the effect of S on total protein concentration in the wheat kernel is, in most cases, rather limited.[87] Additionally, according to Järvan et al.,[82] protein content can even decrease when crop yield responds to S due to a dilution of nitrogen in the grain. Therefore, the main benefit associated with S fertilization is considered to be the effect on protein composition rather than on the protein content. Wheat designated for application in bakery products such as bread, requires a correct balance both between the gluten proteins, gliadin and glutenin, as well as within their respective subgroups (α-, β-, ω-, and γ-gliadin and LMW- and HMW-GS). The latter group mainly contributes to the elastic character of bread dough in contrast to gliadin which provides the extensibility. Therefore, an optimal composition aids in the formation of a strong but flexible gluten network with a high gas retention capacity. Sulfur deficiency leads to the accumulation of S-poor storage proteins such as ω-gliadin and HMW-glutenin subunits at the expense of S-rich proteins (α-, β-, and γ-gliadins and LMW-GS). Therefore, S-deficient wheat is characterized by lower concentrations of S containing compounds (cysteine and methionine). These changes in protein composition are associated with alterations of dough rheology and thus breadmaking quality.[88] Dough made from S-deficient flour is more stiff, has increased mixing requirements, reduced extensibility, and smaller loaf volumes.[82,85] From the experiments with spring wheat of Klikocka et al.,[83] it was concluded that S application significantly increased the gluten content (3.2%), and the concentration of cysteine (6.0%) and methionine (16.5%). The most beneficial effect on the total protein and gluten content was observed with an application rate of 80 kg N ha^{-1} (40 kg N ha^{-1} before sowing and 40 kg N ha^{-1} at stem elongation) and 50 kg S ha^{-1} (40 kg S ha^{-1} before sowing and 10 kg S ha^{-1} at heading). Erekul et al.[70] confirmed these findings for winter wheat by demonstrating a significant increase in the gluten-index (ratio strong gluten over total gluten) and especially the sedimentation value as a result of S fertilization.

Furthermore, studies have shown that bread making quality parameters were correlated with the grain S concentration, more than with the N concentration.[85,89−91] In addition, a synergistic effect between the applied N and S fertilizers appears to occur, increasing N and S assimilation in wheat grain, consequently improving bread making quality. Podlesna and Cacak-Pietrzak[92] noted that the magnitude of response to S varies with the rate of N added. Although all levels of N fertilization (30, 60, 90, 120, 150 kg N ha^{-1}) resulted in an increased grain yield, the applied S only showed an effect on yield in the middle range of N doses (60 and 90 kg N ha^{-1}). Besides protein properties, Li et al.[93] demonstrated that combined N and S fertilization influenced starch properties, such as total starch concentration, amylose and amylopectin concentrations and ratio, and thus pasting properties, when a critical concentration (230 kg N ha^{-1} and 46 or 76 kg S ha^{-1}) is exceeded.

Timing. In analogy of the findings for N application, the timing of S fertilization is equally important. Wheat appears to be more sensitive to S deficiency during the generative growth stages resulting in reduced yields.[85] To enhance baking quality on the other hand, Zörb et al.[94] found that a late S fertilization around flag leaf sheet opening (Zadoks G.S. 47) is most suitable. S accumulation itself occurs mainly after flowering (Zadoks G.S. > 69), as is noted by an increased expression of high affinity S transporters in the flag leaves. The latter functions as a sink organ to the kernels. In S-starved plants, their expression increases only after anthesis.[95] During this developmental stage, large amounts of S are remobilized from

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the flag leaf to supply the developing kernels.[87] Presumably, S only gets remobilized due to senescence when S fertilization is applied in high dosages and late during the growth.[96] Also the results from Monaghan et al.[97] highlight the importance of S uptake (translocation) after anthesis to the accumulation of S in grain.

Potassium and Phosphorus. The influence of potassium (K) and phosphorus (P) is mainly an aggregate of the functions played by nutrients in mitigating negative effects of biotic and abiotic stresses. Plants provided with sufficient amounts of K and P are less vulnerable to water deficiency, low temperatures, and pathogen attacks. Potassium aids in maintaining the crop structure and firmness, reducing the risk of lodging, preventing comprised quality as a result of increased enzymatic activity and a lower specific weight. Furthermore, K is an indispensable component during the main stages of protein biosynthesis. Its deficiency can lead to a decrease in the protein concentration. Since this occurs regardless of the N uptake, a possible accumulation of nonprotein nitrogen will occur which fosters fungal infections.[98] Furthermore, K deficiency impedes nitrogen uptake which results in the decreased leaf assimilation surface thereby reducing the uptake and transport of nitrates in the plant.[99] This can also result in less photosynthesis and therefore a general slower plant development.

Although phosphorus (P) is the second most important nutrient for wheat,[100] many agricultural soils in Europe have large P reserves.[101] In The Netherlands, France, and Germany, recent national P surpluses are on average as high as 25−30 kg ha^{-1},[102,103] while in Sweden, Norway, and the U.K. the P surpluses of intensive livestock farms are about 8−20 kg ha^{-1}.[104] In contrast, agricultural lands in tropical and subtropical areas are suffering from P deficiency which is partially a result of high rainfall.[105] Furthermore, it has to be noted that P is often slowly available to plants within the soil environment. This is mainly due to soil P being adsorbed to the soil reactive clay surfaces, Al and Fe oxides, carbonates, and organic matter[106] as well by the high P fixation. The use of rhizosphere bacteria to solubilize fixated P is a majorly studied subject as this forms a sustainable approach to be able to conform with the increasingly stricter regulation on P fertilization.[107] This ecofriendly microbial mediated P management could be a cost-effective alternative for regions where soil P reserves are large.[108]

Cereal crops require about 20 kg P ha^{-1} for normal growth. Adequate P availability enhances many aspects of plant physiology like photosynthesis, flowering, seed maturity, and seed development.[109] It is generally applied preplant or at seeding since deficiency during the early growth stages has a much larger impact on yield than P limitations later in the season. Application of P fertilizers positively influences both grain yield and the number of tillers.[110] According to Haileselasse et al.,[100] a combined 1:1 to 1:3 P/N fertilizer is required. The response of spring wheat yield to various levels of P_2O_5 (0, 72, 108, 144, and 180 kg ha^{-1}) in combination with 180 kg N ha^{-1} (applied in three factions) under Chinese conditions was studied by Zhu et al.[111] The response of wheat grain yield to P fertilizer showed a quadratic response. When P was applied at a moderate level, grain yield dramatically increased with an optimum at 108 kg ha^{-1} P_2O_5. When P was overapplied, however, the grain yield did not further increase, it even decreased. Concerning the wheat quality, the results of the study of Gaj et al.[112] showed that increasing P rates had no direct effect on the protein and gluten content in grain which confirms the results of Cambell et al.[113] who state that P only slightly affects grain protein composition in winter wheat.

Micronutrients. Apart from the main macronutrients (N, P, K, S), micronutrients (Cu, Mg, Zn, Fe, Mn, etc.) have an impact on the nutritional value and wheat quality. An insufficient amount of these elements in the soil leads to yield losses, which makes the application of trace elements necessary. The requirement of micronutrients occurs mainly at the stem elongation stage (Zadoks G.S. 30-37) when the plant goes through an intense cell division process.[114]

Furthermore, by the application of fertilizers combined with micronutrients, nutritionally enhanced cereals can be obtained. Besides artificial fortification of wheat-based products with minerals, biofortification forms a cost-effective and more sustainable approach to enhance micronutrient concentration of cereal-based foods.[115] This strategy can reduce deficiencies in societies that depend on wheat consumption. Zinc and iron are currently the two most important biofortificants in wheat.[116,117] This can be explained by the fact that due to the introduction of high-yielding varieties, a possible dilution effect of Zn, and to a lesser degree of Fe, has emerged.[118] Moreover, since most micronutrients are concentrated in the outer layers of the wheat grain, a significant proportion is lost during the milling process. However, these concentration losses significantly differ among elements depending on their location in the grain kernel. The elements Fe, Zn, Cu, Mn, and Mo are mainly localized in the aleurone layer and germ of the wheat grain, so the wholemeal is an important source of these minerals. Szira et al.[119] showed that, respectively, 73%, 71%, 44%, and 88% of the Fe, Zn, Cu, and Mn content is lost during the milling process. Since Mo is more highly concentrated in the fine and coarse bran fractions than in flour fractions, milling substantially reduces its concentration in white flour.[84] In contrast, Se is mostly found in a protein-bound form in the wheat grain; therefore, it is more evenly distributed in the kernel and a higher proportion is stored in the endosperm.[120] The challenge is thus to modify the milling process to increase the micronutrient recovery or to incorporate these micronutrient rich fractions in the end product.

As copper (Cu) is essential for chlorophyll synthesis, protein synthesis, and plant respiration,[121] its application, as a foliar spray at late tillering and/or booting stage ($CuSO_4 \cdot 5H_2O$, 0.2 kg Cu ha^{-1}), leads to an increased grain yield. Moreover, Flynn et al.[122] briefly illustrated a significant improvement of the baking quality due to a Cu treatment applied at the booting stage. It was found that both dough rheology and loaf volume was enhanced. More recent studies on the other hand show no significant or even an adverse effect of Cu application.[123,124] Another important trace element is zinc (Zn). Zinc is a component in many plant enzymes and plays an important role in the formation of proteins and N assimilation process in grains of winter wheat.[125] According to Bharti et al.,[126] the application of 20 kg $ZnSO_4$ ha^{-1} in combination with a foliar spray of 0.5% solution of $ZnSO_4$ (1 week after flowering) led to an 80% increase in grain Zn concentration, 61.3% in methionine concentration, and a decrease of 23.2% in phytic acid. The study of Liu et al.[127] showed that Zn fertilization, up to 10 mg Zn kg^{-1} soil, increased activity of nitrate reductase and glutamine synthase in flag leaves after flowering. Furthermore, an increase in Zn fertilization (up to 20 mg Zn kg^{-1} soil) was associated with a genotype-dependent increase in both the total and group specific (gliadins, glutenins, albumins, and globulins) protein concentration in the grain and the flour, respectively. This effect was followed by a decrease of all three protein types at 40 mg Zn kg^{-1} soil demonstrating the occurrence of an optimal fertilization rate for Zn. Moreover, these results demonstrate that Zn nutrition can alter flour protein concentration and composition and thus flour quality. Despite these positive findings, an enhanced uptake of Zn (gained, for example, by breeding) could also result in an increased cadmium (Cd) uptake as both ions are transported via a common carrier.[128] Cd accumulation in the plant, from soil uptake or indirectly as a contaminant in phosphate fertilizer,[129] could result in phytotoxic effects such as a decreased shoot and root biomass, root length and leaf area, thus in a decreased crop yield.[130] Moreover, as it gets translocated to the edible parts, it may represent a threat to food safety.[129] Selenium (Se) and molybdenum (Mo) are both essential plant micronutrients which have been repeatedly shown to enhance crop growth and crop tolerance to abiotic stresses when applied in trace amounts. For example, Wang et al.[131] and Yu et al.[132] related Mo deficiency to a decreased cold tolerance and an increase in the nitrate reductase activity. Both resulted in a increased grain yield after Mo application. Se is also known to influence the S metabolism in wheat. From Boldrin et al.,[133] it was concluded that Se treatment mimics S deficiency by activating specific sulfate transporter expression to stimulate S uptake, resulting in the selenate-induced S accumulation. An over 3-fold increase of S levels following selenate treatment (up to 10 μM Na_2SeO_4) was observed in shoots of all wheat lines as a result of the increased transcription of proteins responsible for S uptake and redistribution.[84,134]

Organic Fertilization Treatments. Both organic and inorganic fertilizers provide plants with the nutrients needed to grow and to be, to a certain degree, stress tolerant. However, they each contain and supply these nutrients in different ways. Organic fertilizers (OF) work over time to create a healthy growing environment, while inorganic fertilizers (IF) provide rapid nutrition. Černý et al.[135] evaluated the influence of inorganic and organic fertilization on winter wheat yield. Lowest grain yields (4.00 t ha^{-1}) were obtained in nonfertilized plots. The manure-fertilized plots and the application of sewage sludge resulted in a yield increase of, respectively, 30% and 41% compared to the control. The highest yield was obtained after application of inorganic fertilizers under which an average yield increase of 59% was observed. With respect to wheat yield and quality, Buráňová et al.[136] evaluated the effect of fertilizers on winter wheat grown after potatoes; six treatments were compared: (1) control, (2) sewage sludge (SS) (320 kg N ha^{-1}−207 kg P ha^{-1}−44 kg K ha^{-1}), (3) farmyard manure (FYM) (330 kg N ha^{-1}−102 kg P ha^{-1}−307 kg K ha^{-1}), (4) N in inorganic fertilizers (N) (140 kg N ha^{-1}), (5) NPK (140 kg N ha^{-1}−30 kg P ha^{-1}−100 kg K ha^{-1}), and (6) N in inorganic fertilizers + spring barley straw (N + ST). Remark that the organic fertilizers (SS and FYM) were applied only to the potatoes in the crop rotation. For inorganic N fertilization, calcium ammonium nitrate was used. For winter wheat, the dose of N was divided into two fractions which were administered during vegetative growth (regeneration fertilization) and at grain filling (production fertilization). The highest grain yields were obtained after the application of inorganic fertilizer compared to sewage sludge or farmyard manures. The grain protein concentration was highest in case N or N + ST was applied, whereas the organic fertilizers resulted in the lowest protein concentrations.

Humic and fulvic acids, which both act as biocatalyst and biostimulant, form key components of soil fertility since they control chemical and biological properties of the rhizosphere by combining minerals into organic compounds (chelator) that are more available to plants. Tufail et al.[137] studied the effect of humic acid (0, 5, 7.5, 10, 12.5 kg ha^{-1} applied 60 days after sowing) combined with NPK (128−114−62 kg ha^{-1}) on the development of roots and shoots and yield of winter wheat grown in Pakistan. It was observed that by increasing the humic acid concentration, the root, shoot, and yield production was increased. A similar experiment was set up by Asal et al.[138] who investigated the effect of different combinations of inorganic NPK fertilizer and humic acid (the recommended dose of NPK, 75% NPK + 2.38 kg ha^{-1} humic acid, 50% NPK + 4.76 kg ha^{-1} humic acid, 25% NPK + 7.14 kg ha^{-1} humic acid, 7.14 kg ha^{-1} humic acid) on the yield and protein content of two winter wheat varieties. The highest grain yield was observed in the case of when 75% of the recommended dose NPK was applied in combination with 2.38 kg ha^{-1} humic acid whereas humic acid alone resulted in the lowest yield (6.3 ton ha^{-1} and 3.60 ton ha^{-1}, respectively). The protein concentration was highest in case the recommended doses of NPK was applied (9.96%). However, the combination of 75% NPK + 2.38 kg ha^{-1}, resulted, thanks to the highest yield, in the highest protein yield (614 kg protein ha^{-1}). It can thus be concluded that 25% of the NPK fertilizer can be replaced with humic acid.

It can be concluded that the application of OF alone is not beneficial to obtain competitive yields. However, many researchers advocate that an integrated use of IF and OF has synergistic effects and plays an important role to sustain soil fertility and crop productivity. Indeed, according to Gopinath et al.,[139] the application of organic fertilizers improves soil properties in terms of lower bulk density, increased pH, oxidizable organic C, total N, and total and available P and K in the soil. Also Cheraghi et al.[140] observed that the highest grain yield was obtained in case 20 ton ha^{-1} OF was combined with inorganic phosphate fertilization. This synergistic effect on yield and yield properties (e.g., 1000-kernel weight, ear morphology, and the number of grains per ear) can be attributed to a positive interaction between microorganisms present in the rhizosphere and the plant roots. An increased availability of P and other nutrients can be obtained in case both OF and IF are applied.[62] Furthermore, from the study of Wang et al.[141] it was concluded that compost application increased available K, Fe, Zn, and Mn concentrations. Various studies have indeed shown that combination of OF and an inorganic N source can be preferred to achieve sustainable yield.[141−143] According to Shah et al.,[144] highest wheat yields and best NUE can be achieved when OF and IF are applied in the ratio of 1:3. Nevertheless, a dependency from the field conditions (density, initial concentration, etc.) can be expected. Furthermore, according to Lu et al.[145] there is a markedly different gene expression in wheat grown with OF or IF. Such genes, if shown to be causally related to utilization of organically originating N, might represent useful starting points for the targeted breeding of varieties that perform better under organic growing conditions.

Growth Regulators. One strategy to increase wheat productivity is by optimizing plant architecture (defined by e.g. tillering, stature, and leaf and ear morphology) by using plant growth regulators.[146] Culm shortening changes the distribution between vegetative and generative mass. Reducing culm length in wheat prevents lodging and reduces intrashoot (ear vs culm) competition for assimilates. Both impacts are beneficial for increasing grain yield.[147] Miziniak and Matysiak[148] evaluated the effect of growth retardants trinexapac-ethyl, chlormequat, and prohexadione calcium, applied in mixtures with paraffin oil adjuvant or organosilicone surfactant. When applied on winter wheat at Zadoks G.S. 31 (first node), a varying impact on the protein, starch, and gluten content of grains and on the Zeleny sedimentation value was noted. Depending on the year of study and weather conditions, an increased or decreased wheat quality was observed. The objective of study of Ramburan and Greenfield[149] was to assess the effects of chlormequat chloride and ethephon, applied either individually or in combination with each other at the tillering, stem elongation, or the flag leaf stages on agronomic and quality parameters of three winter wheat varieties. This study indicated that the combination of both plant growth regulators was most effective in controlling lodging with applications at the flag leaf stage. In case lodging was successfully controlled, the plant growth regulators improved grain yields. Furthermore, an improved hectoliter weight and grain protein content was obtained after the application of both plant growth regulators at the flag leaf stage. Additionally, preharvest sprouting tolerance was generally improved. Okon et al.[150] investigated the effect of the growth regulator furolan on the starch and protein composition of three different winter wheat varieties. Furolan undoubtedly influenced the protein and starch contents as well as an increased amylose content (0.8−1.2%) was noted in all furolan treated varieties. Furthermore, the combined application of ethephon and chlormequat offers a degree of protection against O_3 related yield losses.[151]

Disease Control. Wheat is prone to the several diseases leading to yield and quality losses. Among the economically most important diseases affecting winter wheat yield and quality are obligate parasites (*Blumeria graminis f. sp. Tritici*, *Puccinia graminis f. sp. Tritici*, *Puccinia triticina*, *Puccina striiformis f. sp. Tritici*) and crop residue-borne necrotrophic pathogens (*Pyrenophora tritici-repentis*, *Zymoseptoria tritici*, *Parastagonospora nodorum*, *Cochliobolus sativus*, *Fusarium* species).[152] Globally, potential grain yield losses due to diseases (pathogens and virusses) have been estimated at 18.1% in the period between 2001 and 2003. Despite the current disease control measures, still 12.6% of the global acreage actually gets lost.[153]

Septoria tritici Blotch (STB), caused by *Zymoseptoria tritici*, poses a serious and persistent challenge to wheat grown in temperate climates throughout the world. This pathogen secrets enzymes that destroy the plant cell wall to enable them to feed on the glucose within the cell, reducing the plant's grain-filling potential, thus reducing the thousand-grain weight.[154] On the basis of artificially inoculated field trials in Argentina, Castro and Simón[155] investigated the potential yield and quality losses due to STB. The results revealed that yield reduction fluctuated between 18% and 49.6% depending on the variety. Regarding the effect of STB on protein concentration, the results of this work evidenced an increment with the inoculum concentration. This is in accordance with the results of Watson et al.,[156] who observed a relative increase in grain protein concentration of 0.04% for every 1% increase in STB severity. Nevertheless, this seemingly positive ability results from a reduced carbohydrate accumulation and thus, a lower kernel yield. Protein yield will in fact be lower when STB is present during growth.

Powdery mildew, caused by *Blumeria graminis*, can affect all above ground plant parts. Yield losses in Canadian winter wheat of up to 20% were observed by Conner et al.[157] The protein content of the grain of the moderately resistant varieties was unaffected, but it decreased by 0.7% in the susceptible varieties. Significant negative correlations between yield and protein content on the one hand and the powdery mildew disease index on the other hand were noted by Cao et al.[158] The regression coefficients of the models relating disease index at Zadoks G.S. 59 (ear emergence) to protein content indicated a variable protein decrease from 0.06 to 0.12% for every percent increase in disease index. The fact that powdery mildew reduces grain protein content can be caused by the fact that mildew retains nitrogen in the leaves. Furthermore, mildewed leaves appear to lose both nitrogen as well as ammonia gas. As a result, additional N loss from the plant may be in the production and dispersal of conidia.[159]

Additionally, leaf rust (caused by *Puccinia triticina* Eriks) and stripe rust (caused by *P. striiformis f. sp. Tritici*) affect both grain yield and quality. In the field trial of Sharma et al.[160] in China, severe stripe rust infections resulted in a yield reduction up to 36%. Also grain protein content is often reduced with infection by rust as was confirmed by the findings of Devadas et al.[161] They observed a reduction in grain protein from 11.7% to 11.2% by the presence of stripe rust due to the loss of N from the plant tissue by the pathogen, principally as spores. Furthermore, infections can lead to a reduced uptake of N and a reduced remobilization from vegetative tissue into the grain after anthesis.

Yield reductions caused by the above-described leaf pathogens are mainly due to a loss of photosynthetic capacity,[162] whereas ear pathogens, e.g., *Fusarium* species, kill or damage spikelets before grain filling. Additionally, kernels in infected heads are shriveled and shrunken resulting in a lower thousand kernel weight. Concerning the effect of Fusarium head blight on quality, it has been reported that proteases from *Fusarium* spp. in infected grains have the ability to degrade gluten proteins.[163,164] Mosleth et al.[165] reported severe gluten protein degradation in winter wheat from Norwegian fields in 2011 having extremely low R_{max} (resistance to extension as measured by an extensigraph) values. Furthermore, *Fusarium* infection can lead to the accumulation of mycotoxins, low molecular secondary fungal metabolites which can induce acute and chronic toxic effects. Capouchová et al.[166] discovered significant negative correlation coefficients between the content of mycotoxins and many technological grain characteristics, for example, between DON content (as an indicator for DON-producing Fusarium species) and Zeleny sedimentation value ($r = -0.60$) and also between DON content and volume weight ($r = 0.63$). Furthermore, *Fusarium* infection worsened rheological quality and had a negative effect on the protein as well as starch part of the Mixolab curves. Detrimental effects on gluten, dough, and bread characteristics were found by Schmidt et al.[167] as a result of strongly increased enzyme concentrations (proteases, amylases, xylanases, and lipases) after artificially infecting the grains with *Fusarium culmorum*. In addition, as the deterioration of the bread quality after storage was independent of the level of initial infection, the importance of optimal storage conditions can be emphasized. In general, a reduction for various quality traits was found in previous research as summarized by Ács et al.[168] The varying results, nevertheless, can be assigned to the variety resistance and the environmental conditions related to *Fusarium* infestation. Furthermore, the presence of fungal and thermostable alpha-amylases result in an increased enzymatic degradation of starch at, respectively,

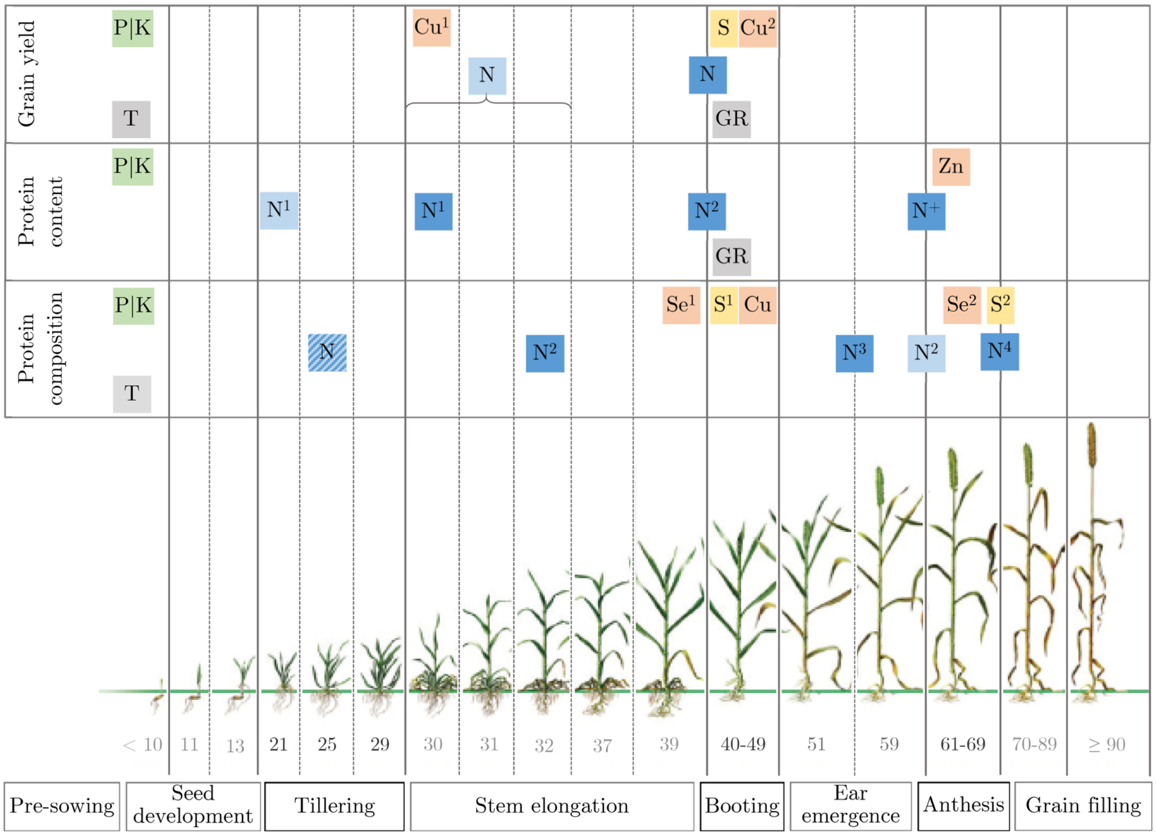

Figure 2. Influence of nitrogen (N), sulfur (S), phosphorus (P), potassium (K), and micronutrient (Cu, Zn, Se) fertilization timing and splitting (numbers in superscript), tillage (T), and the application of growth regulators (GR) on yield, protein content, and composition.

relatively low (30 °C) or high (100 °C) temperatures which is detrimental for both the dough handling and the end product quality. Gooding et al.[169] and Kettlewell[170] suggested that fungicides can also lower HFN by retarding the grain drying process. In addition, prematurity alpha-amylase activity is stimulated by delayed leaf senescence.

Figure 2 shows a comparison between the various agricultural treatments that can be applied to gain an increased grain yield or protein concentration as well as how an enhanced protein composition in winter wheat can be achieved. Nevertheless, besides the proposed practices, meteorological conditions, mutual interactions, and the genotype effect must be kept in mind. Moreover, as is marked by the light and dark blue color, various options for N-fertilization are possible.

■ ENVIRONMENTAL CONDITIONS

Soil Type. Although a loam soil is found to be the best for wheat cultivation, this versatile crop can be grown in various types of soils ranging from sandy to heavy clay. However, most conclusive in the plant's ability to extract water and nutrients is the water holding capacity of the soil and, therefore, its response to rainfall. Limited water availability for the plant and an unfavorable moisture distribution in the soil during the vegetative wheat growth period can, especially on sandy soils, lead to a high variability in yield and protein concentration with substantial effects on the bread-making quality.[171] The results of the experiment from Erekul and Köhn[172] showed that the influence of soil type on the yield of winter cereals gains its significance if weather conditions become more unfavorable. Low grain yields, mainly as a result of a reduced ear density, and high crude protein concentrations were more pronounced on the poor silty sand soil than on the loamy sand soil in a dry year. Furthermore, principally higher values were found for Zeleny sedimentation value, wet gluten content, gluten index, and HFN in a dry year on the loamy sand soil in comparison to the wet year on the silty sand soil. The relation between soil type and wet gluten content was, on the other hand, not coherent.

Weather Conditions. Despite improved varieties and advances in cultivation techniques such as irrigation systems, precision agriculture, etc., crop production is highly vulnerable to unfavorable weather conditions. Seasonal and interannual weather variations are important issues for farmers. Moreover, it has been shown that climate change is of increased concern to them. From this point of view, there have been numerous attempts to uncover the correlation between quality traits and meteorological variables. Similar to crop husbandry practices, weather conditions influence yield and protein both quantitatively and qualitatively. Furthermore, these adverse effects can occur in a direct or in an indirect way since imposing stress alters the gene expression patterns which on its turn influences, for example, fertilizer efficiency.

Irrigation and Precipitation. Drought in the phase of germination and at early tillering can result in a sparse set of plants and a lower intensity of tillering, both leading to a reduction the number of ears per square meter. Moreover, a shortened growth period resulting from an expedite heading and early maturity (7−10 days prematurely) shortens the growth period. These factors contribute to substantial yield losses. In general, drought stress can form an obstacle during early vegetative growth stages, but it is most sensitive during shooting and booting. Similar detrimental consequences are observed when drought stress arises at the time of head (inflorescence) emergence and at flowering and leads to a shorter ear length. High temperatures and water deficit during the grain filling period shorten the grain filling process and accelerate ripening which, on its turn, reduces the weight of the grain ears and hence the yield.[71,173]

In contrast to drought stress effects, precipitation prior to grain filling is negatively related to protein concentration. It is thought that the dilution of early N reserves by vegetative proliferation forms the basis of this effect. Although N losses increase due to leaching and other forms of soil nitrogen loss, precipitation augments soil moisture reserves. The latter extends leaf life during grain growth, thus favoring carbohydrate assimilation and translocation exceeding that of nitrogen. The results from literature concerning the effect of rainfall during, instead of prior to, the grain filling period on the protein concentration are less consistent.[174] According to Garrido-Lestache et al.[66] and Lpez-Bellido et al.,[175] rainfall or irrigation during grain filling is often positively associated with grain protein concentration. Others, however, report that grain protein concentration increases under conditions of drought or low rainfall.[176] This is in accordance with the results from Ozturk and Aydin[177] who found that continuous water stress increased grain protein concentration by 18.1%, Zeleny sedimentation value by 16.5%, wet gluten content by 21.9%, and decreased 1000-kernel weight by 7.5 g compared to fully irrigated conditions. Generally, smaller effects could be noticed when water stress was induced later in the growing season (8.3%, 8.7%, 10.8% increase in protein content, Zeleny sedimentation value, and wet gluten content and a reduction of 3.8 g in 1000-kernel weight, respectively). Early water stress and rainfed conditions showed similar effects, encompassing an increased Zeleny sedimentation value and wet gluten content as well as a decreased 1000-kernel weight. However, the effect of late water stress on grain quality was more pronounced than that of early water stress. These results can be explained by the fact that grain protein concentrations are the result of interactions between N and water availability, yield, and temperature, whose complexity in many cases hinders their examination.[66]

To study the effect of drought stress on protein composition, Zörb et al.[178] created drought stress by withholding rainfall during the whole vegetation period and the plants were entirely grown on the stocked soil water reserves. Control plants were grown next to the shelter with optimal water supply (approximately 800 mm). By analyzing the grain protein fractions, an increase in HMW and some LMW glutenin subfractions was detected. Under the different environmental scenarios, the glutenin fraction in general seemed to be most variable in their gene expression patterns. The drought stress applied in the experiment also led to a significantly decreased yield, ranging between 20 and 55%. Furthermore, it was demonstrated that the protein concentration increased with drought although this effect was only significant for some varieties.

Temperature. Summer temperatures (up to 30 °C) during the grain filling period, negatively correlate with yield, thus positively influencing protein concentration.[179] Under conditions of heat and drought, the grain-filling period is shorter and grain yield lower, resulting in wheat with a relatively higher protein concentration.[176,180,181] Dupont and Altenbach[18] report that maximum yields are achieved when temperatures are between 15 and 20 °C as temperatures in this range give the longest duration for the grain filling period. Furthermore, Johansson and Svensson[182] found that mean day temperature at the end of the growing season was negatively correlated with protein concentration. According to this Swedish research, high temperatures in July (grain filling, sown mid-September) and a low temperature in August (ripening, harvested between August 15−25) will lead to the highest protein concentration.

On the basis of the forecasts of global climate change models, heath stress during the reproductive phase (anthesis and grain filling) will be more common due to the predicted increase of 1.8 to 5.8 °C in mean ambient temperatures. As is stated by Farooq et al.,[183] this increase can cause pollen sterility, tissue dehydratation, and lower CO_2 assimilation. Moreover, elevated photorespiration can be expected resulting in an overall decline of plant health. Photorespiration is, in contrary to photosynthesis, a seemingly wastefull process, consuming O_2 for the assimilation of nitrate from soil. It is activated at low plant CO_2 levels. Despite the expected increase of CO_2, the elevated ambient temperature will force the plant to close its stomata to prevent moisture loss, thus lowering the leaf CO_2 concentrations.[184] In addition, RuBisCo, which is the key enzyme in photorespiration, is less able to discriminate between CO_2 and O_2 at higher temperatures.

Some work has already shown that a certain threshold (∼30 °C) exists before the positive correlation between grain protein percentage and dough strength is lost. For heat-sensitive varieties, the aforementioned threshold is even lower. The correlation may even become negative as the accumulation of gliadin is less reduced by elevated temperatures than that of glutenin, resulting in an increased gliadin/glutenin ratio.[185,186] For spring wheat, the influence of weather conditions on the protein quality seems to be even more pronounced than on its concentration due to the shorter growth period. Protein quality, represented by the mixogram index, showed a correlation with the mean day temperature during May ($r = -2.65$, $p < 0.05$), June ($r = 2.83$, $p < 0.01$) and July (head emergence until late milk stage) ($r = 3.63$, $p < 0.005$). This is a longer period compared to the most important period determining protein concentration (July and August, early dough stage until harvest).[182] Also lower resistance to stretching of the gluten dough (R_{max}), possibly due to higher gliadin concentrations, was reported when the mean daily temperature dropped below 17−18 °C. Moldestad et al.[187] found that temperature during grain filling was the most determinative weather parameter since its powerful association with gluten quality.

Alpha-amylase activities are often higher when the weather is relatively cool and wet during grain filling or when a heat shock occurs during this growth stage. A lower HFN arises when harvest is delayed due to unfavorable weather conditions.[188] According to García et al.[189] postanthesis warm nights reduced thousand grain weight and yield by ∼3 and 4%, respectively, per degree Celsius the night temperature increased. In the experiment, the night air temperature was artificially increased by ∼4.1 °C which resulted in an accelerated development, in turn leading to a shorter effective grain filling period and consequently reducing the final grain weight. A similar conclusion was drawn by Alvarez Prado et al.[190] who observed reductions in mean grain weight due to increases in both the number of hours above 30 °C and mean night temperature.

DuPont et al.[191] studied the effect of temperature on wheat flour proteins during grain development. It was seen that high temperatures during grain filling increased protein content and altered the relative proportion of S-containing proteins by the increased accumulation of S-poor proteins in comparison to S-rich proteins.

Light Intensity and Shading. Besides temperature and rainfall, also light intensity is an important factor influencing wheat growth and development since it affects both the photosynthesis and respiration rate of crops.[192] Li et al.[193] studied the effects of various levels of shading (92%, 85%, 77% of full radiation) on wheat yield. The results indicated that the effect on grain yield was dependent on the level of shading. Under heavy shading (77%), the yield loss ranged between 5.9% and 6.7%, depending on the variety. Under less shaded conditions (85%), the yield loss was limited to 2.3%. Thus, it was concluded that yield losses were much lower than the reduction in radiation, indicating that there must be physiological and morphological compensation effects at both leaf and canopy level to mitigate the adverse effect on grain yield under shading. Additionally, a slight increase in grain yield was observed in case 92% of full radiation was applied. These results are in line with the results obtained by Xu et al.[194] wherein mid and severe shading (67% and 35% of full radiation) led to substantial yield losses. Reductions up to 23% for mid shading and up to 82% for severe shading were observed. However, under slight shading (88% of full radiation), leaf senescence was delayed and photosynthesis rate was stimulated resulting in an increase in grain yield up to 8.5% compared to full radiation. According to results of Hernández-Barrera and Rodríguez-Puebla,[195] the increase of solar radiation over Spain, due to climate change, could force an overall yield decrease. This can be attributed to the fact that higher solar radiation increases transpiration demand, thus supporting water stress and consequently lowering yields. In addition, more solar radiation implies less cloudiness, less precipitation, lower minimum temperatures, and higher maximum temperatures. On the basis of the findings of Maydup et al.,[196] selection of varieties with higher ear photosynthesis (e.g., ears with longer awns) could counteract this possibly unfavorable evolution as grain yield is substantially affected by ear photosynthesis capacity. Results showed that this could contribute for 13−33% under nonstress conditions and for 22−45% when the plant was defoliated or when a water deficit was applied.

Carbon Dioxide Levels. Following the start of the industrial revolution in the 19th century, the atmospheric levels of carbon dioxide (CO_2) have been steadily rising. In 2013, CO_2 levels surpassed 400 ppm. Though different climate change scenarios predict a wide range of trends, all predict a further increase in CO_2 levels over this century, with some of the scenarios predicting a doubling or even trebling of today's levels.[197] These elevated levels have a profound effect on the growth, physiology, and chemistry of plants.[198] Especially in C3 plants, such as wheat, elevated CO_2 levels enhance photosynthesis rate and water use efficiency (due to a reduction in stomatal conductance) which, as a consequence, boost yields. According to Bannayan et al.,[199] yield increase per unit change of CO_2 (1 ppm^{-1}) was considered 0.05%. The review of Amthor[200] summarizes results from 50 papers evaluating the effects of elevated CO_2 levels on wheat yield. It was seen that in experiments with superambient CO_2 levels, combined with ample water and nutrients and favorable temperatures, CO_2 levels up to 2000 ppm increased yield, with a maximum yield increase (37%) at about 890 ppm of CO_2. On average, doubling CO_2 levels from 350 to 700 ppm increased yield by approximately 31%. From the meta-analysis based on 59 papers conducted by Wang et al.,[201] it was also concluded that elevated CO_2 levels (450−800 ppm) significantly increased yield (24%). Furthermore, it was seen that the foliar chlorophyll and soluble protein content declined significantly with 7.5% and 11%, respectively, and that the N concentration in the whole-shoot was reduced by 23%. These changes, along with remarkably increased aboveground biomass (28%), demonstrate that the increased growth rates accompanying elevated CO_2 levels were not matched by increased N acquisition or assimilation, leading to a dilution of shoot N. In contrast to increasing yields, evidence is mounting that ramping CO_2 levels reduce grain quality by decreasing protein content, changing the balance of amino acids and the stoichiometry of several trace elements.[202] The average decrease in grain protein content, estimated in a meta-analysis by Taub et al.,[203] was 10−15% in the case of CO_2 levels elevated from the ambient 400 ppm to 540−958 ppm. Another meta-analysis by Broberg et al.[204] revealed that the response function for the relationship between N concentration and CO_2 showed a quadratic behavior (change in $N = 49.9 - 0.2x + 0.0017x^2$, with x = CO_2 levels). This equation shows an initial reduction in N concentration with increasing CO_2 levels, reaching a minimum at 600 ppm. Myers et al.[205] stated that the decrease in protein content, which was found to be 6.3% lower at CO_2 levels of 546 ppm in comparison to the ambient concentration of 382 ppm, was not solely as a result of a dilution effect. Therefore, according to Wang et al.,[201] key targets for future wheat breeding are to select new genotypes which have higher sink capacity for photosynthetic products and are capable of increasing N uptake under elevated CO_2. Because of the higher stimulation of net photosynthesis by the ear compared to the flag leaf under high CO_2 atmospheric conditions, selecting varieties with higher ear photosynthesis could increase assimilated availability to fill the grains, thus supporting yield increases.[196]

Additionally, the effects of elevated CO_2 levels on Fe, S, and Zn are very comparable with the effects on protein content. A reduction of the Zn and Fe content by 9.3% and 5.1%, respectively, was reported for C3 crops based on meta-analysis data.[205] Both mineral elements are most strongly negatively affected by the rising CO_2 levels. In contrast, minimal (B, Cu, Mn) or even nonsignificant (K) effects were observed for other mineral elements.[204]

From the literature overview above, it is clear that various crop husbandry practices can be adopted to reach a certain production goal. Currently, protein concentration and composition are the benchmark indicators of wheat quality and arguably the most informative measures determining its suitability for baking purposes. Protein concentration can considerably vary in response to weather conditions and crop management.[206] This gives the farmers the opportunity to steer grain quality by implementing certain crop husbandry practices. The negative relationship between yield and grain protein concentration is a reality in wheat production. Nevertheless, this does not imply that higher grain protein concentration cannot be obtained at high-yield levels. Both yield and protein can be increased simultaneously, up to a certain level, given an adequate fertilization. Wheat protein concentration and composition are mainly influenced by fertilization since fertilizers provide the main building blocks for proteins. Generally, a higher fertilizer rate leads to a higher yield and an altered protein composition and concentration. However, various agricultural regulations (e.g., Dir. 91/676/EEC; Dir.

2009/128/EC, etc.) introduced thresholds in the use of fertilizers and pesticides to come to a more sustainable agriculture. These strict measures have an impact on productivity and protein quality. Therefore, in some countries, e.g., Belgium, the cultivation of wheat for baking purposes decreases.[207] There is no doubt that the extensive use of chemicals and fertilizers negatively impacts the environment. Therefore, gaining insight into the specific needs, both in time and space of a certain crop is extremely important. Moreover, an appropriate combination of fertilizers or fertilizer type (e.g., organic vs inorganic) is equally important. The quality of wheat is radically increased by the application of a harmonized combination of nitrogen, phosphorus, and potassium. It was shown that, apart from fertilization, also tillage and crop protection methods have both a direct and indirect effect on wheat yield and quality. Besides crop husbandry practices, also weather conditions and additional environmental conditions affect wheat properties, both directly and indirectly.

Withal, no directly applicable recommendations with regard to crop husbandry practices can be made based on the analyzed studies. At the basis of this hiatus lies the insurmountable variability in the experimental setups (e.g., combined or sole treatments, implementation of control, considered genotypes, etc.) and the prevailing environmental conditions (e.g., initial soil mineral status, climate and weather extremes, field or greenhouse, etc.) in which they are conducted. Mainly for fertilization treatments or the application of growth regulators, of which the effects are highly dependent on the timing, rate, and application type as well as on the interaction with tillage, crop rotation practices, temperature and precipitation, no absolute conclusions can be drawn. Furthermore, an incalculable diversity in wheat varieties is grown throughout the world under very distinct conditions and is applicable in various fields in both food and feed industries. Therefore, this review paper summarizes the main factors influencing compositional parameters and quality traits and can form a solid basis for further research topics.

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