Vegetative tillering plasticity modulates agronomical optimum plant density in winter wheat

by

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B.S., University of Sao Paulo, 2019

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Department of Agronomy
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2024

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Abstract

Agronomic optimum plant density (AOPD) is the minimum number of plants per area required to maximize grain yield. In winter wheat (*Triticum aestivum L.*), this concept becomes complex due to the tillering trait and its phenotypic variance due to the interaction between genotype and environment (G × E). In this scenario, phenotypic plasticity is an insightful crop ecology perspective to understand G × E. Our objectives were to explore the relations of winter wheat AOPD as a function of environmental and genotypic characteristics in dryland environments from the perspective of phenotypic plasticity. We hypothesize that vegetative tillering phenotypic plasticity is positively correlated with vegetative tiller production and that genotypes with greater vegetative tillering phenotypic plasticity have lower AOPD since greater tiller production may buffer for sub-optimal environmental conditions. A complete factorial experiment evaluated twenty-four wheat varieties seeded at two plant densities (100 and 300 seeds m^{-2}) during two seasons in twelve environments. We analyzed the interaction of traits and plant density in a phenotypic plasticity framework. Bayesian hierarchical model was used to estimate grain yield response to plant density and vegetative tillering phenotypic plasticity interaction in a quadratic plateau regression. The effect of vegetative tillering plasticity on the AOPD was evaluated and associated with statistically significant weather variables. Our results demonstrated that beyond the positive effects of the plant density in the traits' phenological response per area, at an individual plant level, traits are affected by plant density in an exponential decay relation, not only for tiller production $plant^{-1}$, but also for productive tillers per $plant^{-1}$, spikes $plant^{-1}$, and grain yield g $plant^{-1}$. This effect limits the potential of the plant to convert vegetative tillers at high plant densities, not only at individual levels but also at crop levels (productive tillers per area). Vegetative tillering plasticity was positively correlated to

vegetative tillering production across plant densities at environments with higher tillering potential, and neutral in lower tillering potential environments. Also, vegetative tillering plasticity was positively related to multiple wheat traits in high-potential environments and was not related to most of the traits' phenotypic expression at lower-potential environments. Overall, winter wheat tillering traits (vegetative and productive) are associated with crop season fall and winter temperature and precipitation. Grain yield with the temperature precipitation and solar radiation experienced during the critical period. On the other hand, the weather variables that lead responsive environments to the vegetative tillering plasticity effect on AOPD (plants m^{-2} unit. $plasticity^{-1}$) are cumulative growing degree days (°C d^{-1}) during winter and grain filling, cumulative precipitation rates (mm) at spring and grain filling, maximum temperatures at winter and grain filling and minimum temperature at spring. Our findings have the following modeling implications, agronomic, and breeding: (i) Seeding rate models and tools, could be improved by accounting for the phenotypic tillering response for a more assertive seeding rate, reducing costs, increasing attainable grain yields, or both. (ii) Under growers' environmental conditions, individual vegetative tillering plasticity may be a tool in the reduction of seed costs, preserving similar yield rates. (iii) Dissecting and stating the genetic basis of winter wheat tillering phenotypic plasticity remains a challenge, as well as their interactions with other management practices.

Keywords: Winter wheat, vegetative tillering, agronomical optimum plant density, phenotypic plasticity.

Table of Contents

List of Figures

List of Tables

Acknowledgements

I would like to express my sincere gratitude to my advisor, Dr. Romulo P. Lollato, for providing me the opportunity to pursue my Master's in Agronomy in his research programs. I appreciate his guidance, the constructive way he challenged me in my learning experience, his mentorship, and his personal life tips. Who not only taught me “no free lunch”, but also, that a good lunch exists for those who work hard. I want to express my gratitude for letting me be responsible for coordinating his team, lab, and fields, where true learning about agriculture, research, leadership, and people management came to fruition. I am the kind of person who really respects someone's work, and I am aware of the extra effort he puts in to support the program, which includes my salary, classes, and the resources I need to develop my research.

I also want to thank my advisory committee, Dr. Mary J. Guttieri, Dr. P.V. Vara Prasad, Dr. Rachel L. Veenstra Cott, for dedicating their time serving on my committee, for their support and constructive criticism, and for encouraging me to keep learning.

I need to thank the amazing people at the K-State Wheat and Forage program. Dr. Luana Simao, thank you for teaching me consistent literature review and writing with multiple tools. Nicolas Giordano, I am grateful for your consistent guidance in programming and new statistical approaches. Jorge Romero, your teachings on crop modeling and countless parametric adjustments. Luke Ryan, thank you for showing me how to solve issues with machines and implements. Aastha Gautam, I appreciate you teaching me storytelling and its vocabulary. Dr. Carlos Pires and Dr. Peng Chen, your personal and professional advisement meant a lot to me. To all of you, thank you for sharing your knowledge and for teaching me how to do so many things; your support was crucial to my master's. A special shout-out to the undergrads and hourly students who put a lot of effort into helping me get everything done.

I want to leave a special thank you to all those who helped me be here today. This story does not start three years ago when I was admitted to Dr. Lollato's program as a research scholar, but more than ten years ago when I was still a teenager dreaming of obtaining a university diploma in agricultural engineering. I leave my deepest thanks to the families: Tanuri, Donadom, Almeida, Morselli, Saladini, Dario, Del Valle, Salles, Masnello, Brodignon, Ferro, Kraus, Oliveira, de Oliveira, Vieira Santos, Ridder, and Leuthold.

To the Kansas community, Kansas farmers, Kansas Wheat Commission, and Kansas State University, I cannot thank you enough for your hospitality, opportunities, and support. To Dr. Amanda de Oliveira Silva, Mr. Robert Calhoun, and Oklahoma State University who received me so sweetly and friendly.

To my fraternity, República Gato Preto (ESALQ-USP), which supported me through a life change, those were years lived with my friends, and here I must highlight Dr. Borgato, Barbosa, Couto, Pacheco, Antunes, Franquilino, and Rossitti. Also, Luiz Vicente de Souza Queiroz and Ermelinda Ottoni de Souza Queiroz, a couple that changed Brazilian agriculture.

To Mariana de Oliveira Mota, who made my life light by always being there for me. I'm so grateful to have you in my life.

Lastly, but foremost, to my family. I cannot find words to express how grateful I am. To my mother, Fabiana Sant`Anna Branco Pradella, and my father, Euclydes Pradella Junior, thank you for your unwavering love and support.

Dedication

This work is dedicated to my parents, Fabiana Sant`Anna Branco Pradella and Euclydes Pradella Junior, who have always believed in me and supported my dreams, and to my partner, Mariana de Oliveira Mota, whose love and patience have been my strength throughout this journey.

In memoriam of Antonio Carlos Ferreira da Cruz Souza, my cousin and brother; Luiz Antonio Saladini, my uncle; Renan Izildo Antonio, a true friend; and Luiz Carlos Junqueira de Oliveira, my life master teacher.

Chapter 1 - Review of Literature

Wheat (*Triticum aestivum L.*) has been consumed in various ways throughout human history. Bread, flour, porridge (semolina), pasta, cookies, cakes, and whole grains are just a few examples among many others. The success of this crop at historical time scales is undoubtedly related to its high nutritional values in contrast with other grain crops. Wheat grains have ~12% protein, ~2% lipids, ~2% reducing sugars, ~2% ash, ~2.2% crude fibers, ~1.8% minerals, ~6.7% pentose, and ~59.2% starch, totaling about 70% carbohydrates and acting as a source of both energy and protein, providing approximately 4,000 kcal kg^{-1} (Awika, 2011; Bolarinwa & Adeola, 2012; Rosenfelder et al., 2013; Verma et al., 2019; Zijlstra et al., 1999). In addition to its nutritional characteristics, many physiological and adaptation traits allowed for the crop's domestication and were essential for the success of wheat as a cultivated crop. All these characteristics have contributed to wheat being among the most widely grown, consumed, and commercialized crops in the world at historical timescales (Erenstein et al., 2022). Consequently today, wheat ranks among the three most widely cultivated cereals in the world (Awika, 2011; Shiferaw et al., 2013).

1.1 Global Wheat Crop Production Overview

During the period from 2012 to 2022, wheat was the crop with the largest harvested area in the world with a total of 219 M ha in 2022 (2012-2022 mean of 218 M ha)(Food and Agriculture Organization of the United Nations, 2024). This compares to total harvested areas of 203 M ha for maize (*Zea mays L.*) in 2022 (average in 2012-22: 194 mi), 165 M ha for rice (*Oryza sativa L.*) in 2022 (average in 2012-22: 163mi), 26 M ha for sugar cane (*Saccharum officinarum L.*) in 2022 (average in 2012-22: 26 mi), and 134 M ha for soybean (*Glycine max*

[L.] Merr.) in 2022 average in 2012-22: 122 mi) (Food and Agriculture Organization of the United Nations, 2024). During these ten years, the average total wheat production in the world was approximately 746 million metric tons, ranking fourth among production crops behind sugar cane (1.8 billion metric tons), maize (one billion metric tons), and rice (753 million metric tons) (Food and Agriculture Organization of the United Nations, 2024). China is the largest producer of wheat, with an average of 138 million metric tons (i.e. 14.5% of global production), followed by India with 108 million metric tons (11.3%), Russia with 104 million metric tons (11%), and the United States (U.S.) with 44 million metric tons, which corresponded to 4.7% of global wheat production (Food and Agriculture Organization of the United Nations, 2024).

Wheat demand is forecasted to increase at a rate of ~12 million metric tons per year by 2050, based on the current consumption per capita (Erenstein et al., 2022; Giraldo et al., 2019) and the projected global population increase by 25% in 2050 (Gerland et al., 2022). Increasing crop yield per unit area is one of the best ways to attend to this increasing demand without advancing agriculture into new uncultivated lands (Tilman et al., 2011). These increments in grain yield can be achieved in a short or moderate term by reducing the yield gap with more accurate and efficient agronomic management at a local scale (Erenstein et al., 2022; Hatfield & Beres, 2019; Kucharik et al., 2020; Neumann et al., 2010).

1.2 U.S. Wheat Crop and Production Overview

In the season 2023-24, the U.S. wheat production was 49.3 million metric tons from a harvested area of 15 million hectares and an average yield of 3.2 Mg ha^{-1} (USDA-NASS, 2024a). Different wheat classes are produced in the U.S., including hard red winter, hard red spring, soft red winter, white (soft and hard), and durum (*Triticum durum* Desf.). These classes correspond approximately to 33%, 25%, 24%, 12%, and 3% in the total U.S. production (USDA-NASS,

2024a). In 2023, the states that contributed to the largest share of wheat production in the U.S. were North Dakota (ND), Kansas (KS), Montana (MT), Washington (WA), Idaho (ID), and Minnesota (MN) respectively (USDA-NASS, 2024c). Many of these states are part of the " U.S. Wheat Belt", except for Idaho and Washington. The wheat belt is a region in North America (U.S. and Canada) where wheat is the dominant crop, and predominantly corresponds to the Great Plains region of North America.

The U.S. Great Plains is the largest contiguous dryland winter wheat growing area in the world (Fischer et al., 2014), with 27.7 MMt produced from 6.32 M ha (USDA-NASS, 2024). This region has large intra- and interannual climate variability (Lollato et al., 2017; Lollato, Bavia, et al., 2020) and consequently producers exhibit conservative behavior as it relates to crop management. This conservative behavior leads to large yield gaps in winter wheat grown in this region (Jaenisch et al., 2021; Kucharik et al., 2020; Lollato et al., 2017; Lollato, Ruiz Diaz, et al., 2019). Yield gap is the difference between the attainable (i.e., maximum yield obtained with optimum management, only limited by climatic and edaphic conditions) and actual yield, and is a benchmark of potential increase in crop production from a given region (Van Ittersum et al., 2013). Yield gaps for wheat in this region are large and some evidence suggests that they may have increased in the last few decades due to the lower slope in the actual grain yield increment as compared to gains in yield potential (Kucharik et al., 2020; Patrignani et al., 2014).

1.3 Kansas Wheat Crop and Production Overview

During consecutive years, Kansas, which is situated in the U.S. Great Plains, has been the largest wheat producing state in the U.S. with a production of 5.4 million metric tons in 2023 (USDA-NASS, 2024b), although this rank varies year-to-year with North Dakota (USDA-NASS,

2024b). This alternation is mainly attributable to the environmental conditions of the season in question.

Kansas's average planted area ranges from 3.2 to 3.8 million hectares and average production ranges from 5.4 to 10.4 MMT during the 2012-2023 period (USDA-NASS, 2016, 2023). Kansas' average wheat yield was 2.35 Mg ha^{-1} during 2022-23 (USDA-NASS, 2023). During the 2015-2016 growing season, the state of Kansas experienced the highest average wheat yield on record (i.e., 3.8 Mg ha^{-1}; (USDA-NASS, 2016). This fact may indicate that 3.0 Mg ha^{-1} is close to 75% of the farmer`s yield potential (water-limited wheat grain yield, a yield potential nest to the local farm reality) of the local area or state region (Van Ittersum et al., 2013). Lollato et al. (2017) suggested a water-limited wheat grain yield of approximately 5.2 Mg ha^{-1}, suggesting that current yields are about 57% of their water-limited potential. Since average farm yields tend to plateau when they reach 75 - 80% of the yield potential under rainfed conditions (Van Ittersum et al., 2013) current yields could economically increase up to ~3.9 - 4.2 Mg ha^{-1} (Lollato et al., 2017; Lollato, Ruiz Diaz, et al., 2019; Patrignani et al., 2014; Van Ittersum et al., 2013).

Kansas winter wheat production regions can be divided into west, central, and east sub-regions, according to the yearly precipitation totals. Annual precipitation in Kansas ranges from less than 450 mm in the west to more than 1150 mm in the east (Frankson & Kunkel, 2022). This steep rainfall gradient causes corresponding differences in cropping systems and growing conditions. For instance, wheat grain yield in these regions during 2022-23 were 2.5 Mg ha^{-1} in the west and 3.5 Mg ha^{-1} in the east (USDA-NASS, 2024c).

A number of management practices have enhanced grain yield of winter wheat in this region (Cruppe et al., 2017, 2021; Giordano et al., 2024; Jaenisch et al., 2021, 2022; Munaro et

al., 2020; Raj et al., 2023). Among these, adjustments to seeding rates and consequent plant densities have arisen as a unique opportunity to optimize wheat grain yield and perhaps reduce the large yield gap (Bastos et al., 2020; Hochman & Horan, 2018; Lollato, Ruiz Diaz, et al., 2019). Some pieces of evidence suggest that it can interact with other crop management practices such as fertilization (Jaenisch et al., 2022) and genotype traits (Bastos et al., 2020).

1.4 Plant Density, Tillering Production, and Wheat Grain Yield

Yield components directly or indirectly modulate crop yield (Güler et al., 2001; Slafer et al., 2014). Grains m^{-2} and above-ground biomass normally have positive correlations to yield (Al-Tabbal & Al-Fraihat, 2012; Sadras & Rebetzke, 2013). Other yield components (e.g., grain weight and harvest index) may not be related, or even show negative correlations with grain yield (Reynolds et al., 1996; Slafer et al., 2014). This results from compensation mechanisms among yield components and highlights their interdependency. Yield components are indeed related to complex pathways (Miralles & Slafer, 2007; Slafer et al., 2023) and may not be assumed in isolation as a direct relation with the yield (Slafer et al., 2014). Primary winter wheat yield components are individual grain weight and grains per unit area, which result from interplay among spikes per unit area and grains per spike (Slafer et al., 2014). Secondary yield components (i.e., crop components that are related to crop yield but do not constitute it) include biomass accumulation and harvest index (i.e., the ratio of grain yield over above-ground biomass), grain filling duration, spike morphology (spike length, density, spikelets number, etc.), plant height, tillering, and root system architecture.

Plant density modulates the crop's ability to capture environmental resources, such as nutrients, water, and solar radiation (Bastos et al., 2020; Fischer et al., 2019; Lollato, Ruiz Diaz,

et al., 2019; Sadras & Denison, 2009; Salazar et al., 1996). Optimal plant populations maximize yield by adjusting spikes per area, either through high seeding rates resulting in predominantly primary tillers (Destro et al., 2001; Elhani et al., 2007; Slafer et al., 1996; Spink et al., 2000) or through lower plant populations resulting in a greater production and survival of tillers. Within this context, the agronomic optimal plant density (AOPD) is the minimum number of plants per area that can maximize grain yield (Bastos et al., 2020) by reducing intraspecific competition of resources among neighboring plants (Bastos et al., 2020; Satorre & Slafer, 1999). The AOPD may differ among environments according to the predominant resource limitation. For instance, in dry environments where wheat yield is usually water-limited, lower populations reduce evapotranspiration during vegetative growth stages, saving water for reproductive stages, thus optimizing grain yield (Satorre & Slafer, 1999). In this case, increasing plant density (thus, intra and interspecific competition) can reduce wheat grain yield, above-ground biomass, grains per plant, and tiller survival (Fang et al., 2019; Holliday, 1960; Sadras & Rebetzke, 2013). Alternatively, sub-humid environments may warrant crop traits or management practices that maximize radiation interception early in the season (Sciarresi et al., 2019); thus, higher seeding rates may be warranted (Destro et al., 2001). At higher plant densities, tillering production is reduced exponentially (Joseph et al., 1985; Pradella & Lollato, 2023). Otherwise, a large space between plants can result in lower grains per unit area, which can explain the typical parabolic response of grain yield to plant density (Holliday, 1960). Therefore, the seeding rate can affect the main and secondary grain yield components (Bastos et al., 2020; Guitard et al., 1961; Jaenisch et al., 2022; Lollato, Ruiz Diaz, et al., 2019). The differences in plant density management as function of predominant environmental stressors indicate that AOPD may be

associated with wheat grain yield environment (Bastos et al., 2020; Lollato, Ruiz Diaz, et al., 2019; Sadras & Rebetzke, 2013; Shanahan et al., 1985).

Wheat grain yield response to plant density is inconsistent across studies. Increasing plants per area can increase the number of spikes per area until a threshold where the curve becomes asymptotic negative (Bastos et al., 2020; Guitard et al., 1961; Joseph et al., 1985). Grain yield shows consequent linear or quadratic increments until such thresholds, which depend on genotype, environment, and their interaction (Bastos et al., 2020; Blue et al., 1990; Lloveras et al., 2004). However, the increment of spikes per area may reduce spike size (i.e., kernels spike^{-1}) as well as individual kernel weight, not always increasing yield (Blue et al., 1990; Lloveras et al., 2004). The literature exploring the relationships among wheat grain yield and yield components overarchingly suggests that wheat yield is sink-limited (i.e., the canopy usually has more capacity to produce carbohydrates than the kernels' sink capacity reducing the crops' carbohydrate partitioning) (Aggarwal et al., 1990; Fischer, 2007). Since wheat yield is usually sink-limited and each tiller is a sink during its initial development (Sadras & Denison, 2009), the interactions among plant density, tiller production and survival, and grain yield, are complex and require further exploration and understanding.

Lollato et al. (2019) suggested AOPD for winter wheat grown in commercial winter wheat fields in Kansas, U.S., ranged from 93 to 121 plants per m^{-2} with a yield penalty at plant densities greater than ~305 plants per m^{-2} (-2.7 Mg ha^{-1} for each increment of 100 plants per m^{-2}). This data was anecdotal. More recent work using experimental data from replicated trials suggested quadratic relations where wheat yield was maximized between 120 and 159 plants m^{-2} under similar intensively managed conditions (Lloveras et al., 2004; Lollato et al., 2024). Currently, the seeding rate recommendations in the state of Kansas are between 200 to 300 seeds

m^{-2} (Shroyer et al., 1997). On the other hand, Bastos et al. (2020) suggested an AOPD ranging from 58 to 397 plants m^{-2} for this region, with lower seeding rates for genotypes with high tillering potential in higher yield environments. These divergent results indicate a considerable environmental and genotype-specific tillering production potential on AOPD, and consequently on the grain yield, leading to the hypothesis that winter wheat phenotypic plasticity of tillering can impact AOPD and grain yield (Jaenisch et al., 2022).

Comparing different studies investigating AOPD requires a detailed, thorough, and hairsplitting analysis due to structural and statistical differences (e.g., plant density versus seeding rate, different criteria for model fitting, etc.). The target population is usually not equivalent to the actual plant density. Genetic traits; physical, biotic, and abiotic environmental factors can affect the germination of the seeds and consequently plant establishment and the final plant density; therefore, it is important to understand whether studies evaluated the target plant population (seeding rate) or the actual plant density. Additionally, the target seeding rates can be reported in different ways such as number of seeds per area (Bastos et al., 2020; Lollato, Ruiz Diaz, et al., 2019) or weight of seeds per area (Darwinkel et al., 1977; Geleta et al., 2002; Guitard et al., 1961). Knowledge about the seed size (i.e., seeds per unit weight) would be necessary to convert the latter into the number of planted seeds (Darwinkel et al., 1977). In most cases, seed size can vary from more than 44,000 seeds Kg^{-1} to less than 22,000 seeds Kg^{-1} (conventionally, commercial genotypes are around 26,000 to 40,000 seeds Kg^{-1}) (Klein et al., 2005).

Row spacing is another crucial factor to be considered when contextualizing yield response to seeding rate studies. Geleta et. al. (2002) placed 0.3 m between rows in their studies in Nebraska. Basto et al. (2020) used 0.19 and 0.25 m row spacing in fields across the state of

Kansas. Josephe et al. (1985), demonstrated that among similar seeding rates, the plants m^{-2} and tillers $plant^{-1}$ did not differ statistically at row spacings of 0.1 and 0.2 m in Virginia (with associated seeding rates between 186 to 558 seeds m^{-2}). Also in this study, narrower row spacing resulted in greater grain yield due to the higher levels of soil fertility by higher fertilizer rates provided in the management, which probably reduced the penalty from competition for resources. Conventionally, the space between rows in Kansas winter wheat fields ranges from 0.19 to 0.25 m (Bastos et al., 2020; Jaenisch et al., 2022), with some fields in western Kansas adopting row spacing as wide as 0.31 m.

Another management practice that interacts with plant density is sowing date (Darwinkel et al., 1977; Spink et al., 2000; Staggenborg et al., 2003). The date of sowing impacts wheat canopy development due to the accumulation of temperature in the fall and consequent tiller production (Blue et al., 1990). Consequently, modulate water uptake and interception of solar radiation by the wheat crop (Baloch et al., 2010; Musick & Dusek, 1980; Thiry et al., 2002). Blue et. al 1990 demonstrated the effect of the temperature accumulation due to different sowing dates on the relative grain yield of wheat through a quadratic regression of a negative coefficient, suggesting that while the management of sowing dates can increase solar radiation interception and consequently yield, sowing too early can reduce grain yield. Similar quadratic responses of wheat grain yield to sowing dates were reported for Kansas (Jaenisch et al., 2021) and the wider U.S. southern Great Plains (Munaro et al., 2020).

1.5 Winter Wheat Tillering

In most crops, seeding rate does not necessarily match the final plant population due to various adversities that can occur during the crop season, from suboptimal seed germination

properties to climate adversities (Bastos et al., 2020; Destro et al., 2001; Jaenisch et al., 2022; Tilley et al., 2019a, 2019b). Wheat belongs to the Poaceae family (Gramineae family), and as a grass, it is resilient and robust in obtaining resources from a wide range of environments largely due to its profuse tiller production (Jewiss, 1972). Tiller production and mortality are affected by environmental conditions such as fall weather (e.g., precipitation, evapotranspiration, temperature accumulation), agronomic management (e.g. sowing date, seeding rate, fertilization, and variety selection) (Bastos et al., 2020; Jaenisch et al., 2022; Lollato, Ruiz Diaz, et al., 2019; Pradella & Lollato, 2023; Thiry et al., 2002).

Tillers are additional stems that develop from the main stem (or coleoptile stem). Primary tillers are formed from the axils of the first true leaves (after about three or more), and under favorable conditions, secondary tillers will grow from the leaf axils of primary tillers. Mortality of these tillers might occur at any time but more commonly from the jointing until anthesis stages of development (GS31 – GS69) when competing sinks result in plant prioritization of resource usage (Klepper et al., 1982; Tilley et al., 2019a). Additionally, not all surviving tillers will produce a spike depending on plant carbohydrate partitioning. Thus, more efforts to understand the sterility and mortality of vegetative tillers to understand better the partitioning of the carbohydrates into the plant and how they affect the crop grain yield are warranted (Jewiss, 1972; Rawson, 1971).

Tillers can be enumerated as they arise in the shoot as well as T_0 for main stem, for primary tillers T_1, T_2, T_3, etc., and secondary tiller should be correlated with their primary tiller, for instance, $T_{n.1}$, $T_{n.2}$, $T_{n.3}$, etc. where *n* is the corresponding primary tiller. Third-order tillers should follow the same methodology (e.g. $T_{n.m.x}$) (Klepper et al., 1982). Rawson (1971) demonstrated that oldest tillers contribute more than younger ones for the wheat grain yield, with

the four primary tillers and the main stem being responsible for ~30% of the plant grain yield. An interesting fact in his work is that T_1 and T_2 (and in a few cases T_3) were more productive than the main stem at a density of 192 plants m^{-2}, likely because the coleoptile node is not the first node present on the axis, it may be the second node or third node (Avery, 1930; Klepper et al., 1982) depending on the production of abscisic acid that affects different levels of tiller shoot growth and is regulated by gene expression (Dong et al., 2023). At 350 plants m^{-2}, secondary tillers represented ~ 32% of the grain yield in irrigated areas (Elhani et al., 2007). Destro et al. (2001) demonstrated that even though secondary tillers represented ~ 10% of the total stems m^{-2} at seeding rates of 400 plants m^{-2}, they only contributed ~ 5% of the grain yield when compared with the main stem. The authors also demonstrated that the tiller harvest index can be similar to the main stems under well-watered conditions, depending on the genotype.

While the contribution of the tillers to grain yield may oscillate in percentage depending on the factors above, it is clear that the total number of stems in the area is positively correlated with the grain yield (Bastos et al., 2020; Blue et al., 1990; Finnan et al., 2018; Guitard et al., 1961; Lloveras et al., 2004), with an incremental positive effect from secondary tillers in yield and/or grain yield components (Elhani et al., 2007; Gautam et al., 2012). While this compensatory effect when the crop has access to more resources from the environment results in greater spikes m^{-2}, its effects on kernels per spike and thousand kernel weight (TKW) during partitioning is only partially understood (Lloveras et al., 2004; Sadras & Rebetzke, 2013; Salazar et al., 1996). On the other hand, a lower contribution from secondary tillers to the total grain yield, which is dependent on the interaction of genotype tiller production nested in the environment, can indicate that the carbohydrate partitioning will follow the sink strength (Destro et al., 2001). Many divergences from the different studies come from the vastly different

genotypes, environmental conditions, and management of these trials. Within the management piece the different seeding rates used across different trials can likely explain differences in results regarding drivers of tiller production and survival (Lloveras et al., 2004) since plant density has a large effect on secondary tillers per steam, affecting the shoot and crop iteration with the environment. Along the same line, genotypes with a lower tillering potential (see subsequent section for definition) are more dependent on the seeding rate to express their grain yield potential (Jaenisch et al., 2022; Valério et al., 2008, 2009). Since the number of tillers is a strong lead to spike number, the tiller production trait can be studied to maximize wheat yield by reducing sowing rates in genotypes with greater trait expression (Bastos et al., 2020; Tilley et al., 2019a). Therefore, a better understanding and quantification of the interaction G×E×M (genotype, environment, and management) is necessary to direct the growers to better management of tillering stages focusing on maximizing yield and/or profitability (Beres et al., 2020a).

Two important definitions within the context of this thesis are tillering potential and phenotypic plasticity of tillering. The definition of tillering potential is based on the definition of yield potential by Evans and Fischer (1999). Here, tillering potential is the tillering production of an adapted genotype growing without stressors such as diseases, lodging, nutrient deficiencies, pests, weeds, and any other biotic or abiotic stress factors. Tillering potential would be different for irrigated versus dryland systems but otherwise defined based on available environmental resources (solar radiation, temperature, moisture availability) and genetic propensity throughout for tillering of the genotype being grown. Alternatively, phenotypic plasticity of tillering is the environmentally-induced tillering of a given genotype (DeWitt and Scheiner, 2004). In other words, phenotypic plasticity is the inverse of stability (i.e., the genotype's ability to produce a

predetermined phenotype that is invariant under particular environmental conditions) (Palmer & Strobeck, 1997). While stability refers to genotypes whose phenotype is more dependent on its genetic characteristics than on the environment and/or gene-environment interaction (Møller & Shykoff, 1999; Palmer & Strobeck, 1997), plasticity would be the opposite since they are inversely proportional (higher plasticity results in lower stability). Phenotypic plasticity of a given trait can be positive (i.e., neutral in environments with low trait expression and associated with increased expression in conducive environments); neutral (i.e., not associated with the trait across environments); negative (i.e., neutral in environments with high trait expression and negatively related with trait expression in environments of low trait expression); and asymmetric (i.e., differential responses in environments of high and low trait expression) (Sadras, Lake, et al., 2016; Sadras et al., 2019; Sadras & Rebetzke, 2013).

Winter wheat genotypes have different phenotypic plasticity of tillering and different tillering potentials, resulting in differential compensation for environmental variations led by plant density and potentially achieving a similar number of different yield components (e.g., spikes per square meter, kernels per spike, grain weight, etc.) across different plant densities (Lloveras et al., 2004). Bastos, et al. (2020) suggested that genotypes with high tillering potential compensated for low plant densities by achieving similar number of spikes and kernels per area, indicating the relevance of productive tillers in wheat. Similarly, Lloveras et al. (2004) demonstrated that an increment in plant density via higher seeding rates linearly increased the number of spikes per square meter (i.e., from 487, 391, and 384 spikes per square meter at the target plant densities of 500, 175, and 150 plants per square). However, higher seeding rates decreased the number of spikes per plant.

Lollato et al. (2019) demonstrated the potential management of winter wheat genotypes in the U.S. Great Plains by focusing on individual genotypes' tillering potential. Without grain yield losses, estimating the optimal seeding rate for each genotype would require trials established in a large number of environments per year (Eberhart & Russell, 1966). Eberhart and Russell (1966) suggested that the minimum number of environments required for stability analyses is two. However, they advised that a larger number of environments will be necessary to develop reliable estimates, especially if environments cover the range of expected responses. In general, within Kansas wheat production, sowing at seeding rates of 93 to 121 seeds m^{-2} may produce optimum yields (Lollato, Ruiz Diaz, et al., 2019; Lollato et al., 2024). Moreover, unpredictable environments present barriers to achieving high productivity and profitability in agriculture. These barriers can be overcome with several approaches in the target environments using indirect, trait- or genomic-based methodologies (Cattivelli et al., 2008; Ceccarelli et al., 2007; Fleury et al., 2010; Sadras & Richards, 2014). A better understanding of individual genotype's tillering plasticity within the target environment is essential to derive optimal seeding rates (Bastos et al., 2020; Lollato, Molssato, et al., 2019; Tilley et al., 2019a). However, to date, tiller production has only been classified as high versus low, which is insufficiently accurate to adjust seeding rates (Bastos et al., 2020).

1.6 Principles of the Phenotypic Plasticity

Phenotypic plasticity is the ability of an organism to produce different phenotypes (morphology, physiological state, and/or behavior) in relation/response to the distinct environmental conditions in which it is grown (Schlichting & Pigliucci, 1998; West-Eberhard, 1989). Thus, it can be interpreted as how the environmental conditions affect gene expression

(West-Eberhard, 1989). DeWitt and Scheiner (2004) defined phenotypic plasticity as "environment-dependent phenotype expression". This concept explains traits beyond the conventional approach of G × E × M (DeWitt & Scheiner, 2004; Scheiner & Goodnight, 1984). In this approach, the interaction “G[E]” (genotype nested within environment) leads the individuals to a response (trait expression) that may be different than expected for its population (race or species).

It is important to clearly differentiate phenotypic plasticity from acclimatization and acclimation. Acclimatization and acclimation are important concepts that represent physiological phenotypic plasticity. Acclimatization refers to an organism's physiological changes in natural conditions and acclimation refers to the phenotypical physiological response under controlled laboratory conditions and is limited to one or two well-defined environmental parameters (light incidence, temperature, pressure, etc.) (Whitman & Ananthakrishnan, 2009). Normally they are correlated to the ability of the individual to adjust itself to short-term changes. On the other hand, phenotypic plasticity evolved through natural/artificial selection and is connected to short and long-term changes (Garland & Kelly, 2008; Whitman & Ananthakrishnan, 2009; Willmer et al., 2006). In other words, phenotypic plasticity is not only connected to the variation in the weather but also the climate. Phenotypic plasticity for any particular trait may be an evolutionary adaptation whose details vary among organisms and may not be reversible depending on the time that the individual is exposed to the environment, or the time its several generations would be under natural selection (Garland & Kelly, 2008). These irreversible traits, associated with multiple stressors, can explain as well the reduction of phenotypic plasticity, since under selection/adaption for a specific environment the individual/population would be unable to

“readjust” itself to another environment, this fact can be related to the trade-offs of phenotypic plasticity (Garland & Kelly, 2008, 2008).

Phenotypic plasticity is part of the evolutionary theory and relates to the organism’s adaptation ability, thus it is a complex concept in the adaptation under selection (natural/artificial). During the primordial evolution theory approaches, phenotypic plasticity was associated with noise, error, outliers, or “unfortunate defects” (Schlichting & Pigliucci, 1998; West-Eberhard, 1989). However, it is important to state that in modern approaches, the developmental noise is still being considered and estimated, normally as the error in the phenotypic plasticity estimation (DeWitt & Scheiner, 2004). In the most recent approaches studying the role of plasticity, phenotypic plasticity is also analyzed affecting population and splitting populations across environments, which can lead or contribute to the migration or isolation of individuals (which will crossbreed amongst themselves) and resulting the emergence of new races and/or species (DeWitt & Scheiner, 2004; Schlichting & Pigliucci, 1998; Schmid & Guillaume, 2017; Willmer et al., 2006). Phenotypic plasticity can allow individuals of a population to survive new conditions imposed on the population, so the offspring of these select individuals will result in a new branch of the species' evolutionary tree (Sommer, 2020).

This concept can connect phenotypic plasticity with the individual’s adaptation, resulting in an individual’s competitive advantage. Here, the greater the organism's ability to vary its characteristics (higher plasticity), the greater its ability to succeed in different environmental conditions and under strong competition (West-Eberhard, 1989). This concept led to the proposition that individuals with higher variance in these response variables tend to have a higher rate/incidence/production of this variable across environments when compared with individuals with lower variances. Furthermore, individuals with higher phenotypic plasticity will

present a higher phenotypic expression in favorable environments, since it may allow individuals to express phenotypes closer to the "environmental optimum" (Schmid & Guillaume, 2017). However, this proposal may not be true in all cases, since negative relationships between phenotypic plasticity and phenotype expression have been reported (DeWitt & Scheiner, 2004; Sadras, Lake, et al., 2016). For instance, Sadras et al. (2016) found a linear negative response in HI phenology as a function of harvest index phenotypic plasticity in chickpea (*Cicer arietinum L.*). Schlichting and Pigliucci (1998) state that we can observe linear, non-linear, and non-plastic (flat slope) regressions in the relation between phenotype expression and phenotypic plasticity. However, they state that the limitation of the data set (especially the number of environments) can be a limitation of the methodology and induce a misinterpretation. Therefore, it is important to state that the values obtained in the phenotypic plasticity analyses are limited to the data set present in the study, the set of environments, and the genotypes' group.

Most of the classic approaches for measuring phenotypic plasticity of a given trait require genotypic variation (e.g., different individuals in genetic terms, species, genotype), environmental variation (e.g. different conditions in altitude, pressure, temperature, light incidence, nutrients, etc.), and a response variable (traits such as yield, biomass production, carbohydrate partitioning, etc.) (Sadras et al., 2013). DeWitt and Scheiner (2004) suggest the following model to understand the phenotypic variance: "$V_P = V_G + V_E + V_{G\times E} + V_{errror}$" (Where: V_P is the phenotypic variance, V_G is the genetic effects, V_E is the environmental effects (plasticity), $V_{G\times E}$ is the genotype-environment interaction, and V_{errror} is the developmental noise).

Since measures of genetic variation and plasticity are derived from a single analysis, Scheiner and Goodnight (1983) listed the advantage of using vegetative clones in the phenotypic plasticity measurements, this practice can reduce the noise of the genetic variability practically to

zero. Here, zero can be a strong affirmation since it is common knowledge that sporadic, spontaneous, or new mutations may occur throughout the individual's life (e.g. cancerous cells) (Ames et al., 1993). In plants however, a few groups of physiologic pathways (e.g. hormone pathways) reduce undesirable mutations, making them less frequent and not lethal as they are in animals (Doonan & Sablowski, 2010). Thus, considering probabilistic concepts, for practical and/or empirical purposes the proximity to zero is such that it allows us to accept zero as a fair approximation to genetic variability as a noise in the phenotypic plasticity analyses with vegetative clones. In crop science, considering the pure lines, inbreeding practices, and genetic similarities in the breeding process of genotypes, we accept the same genetic variability noise close to zero in individuals of the same cultivar (Labroo et al., 2021).

1.7 Phenotypic Plasticity in Crop Science

Phenotypic plasticity has proven to be an interesting tool for agronomy and crop sciences (Sadras et al., 2013), being either the essential objective of research or a tool that provides a deeper understanding of the results obtained. Since phenotypic plasticity can be a piece of information useful to understand significant G × E × M interactions, supporting breeders in selecting pertinent variations in the cultivars, and understanding how a particular genotype’s variation in phenotypic plasticity affects the main response variables of interest. Another important consideration is that with climatic changes, the expected new environments would be different than the environments where the natural/artificial selection happened; thus, exploring phenotypic plasticity variations may be a strong tool to overcome "maladapted" (an organism that is poorly suited or poorly adapted to its current environment) (R. J. Fox et al., 2019; Guo et al., 2024). In practical approaches, the phenotypic plasticity framework can allow for an

understanding of the environmental effect on the genetic pool (crop), individual (genotype), and the "environmental optimum" rate of this specific local (DeWitt & Scheiner, 2004; Schmid & Guillaume, 2017). As it pertains to management, information about a genotypes' phenotypic plasticity can support decision-makers as to what crop or genotype to choose, and what management at what level can or cannot affect the desired phenology in the environment (e.g. irrigation) (Bastos et al., 2020; Sadras et al., 2013).

Greater phenotypic plasticity can confer an evolutionary advantage to individuals since it can correlate with resilience (although plants' resilience may be plastic or not, and the plant can be well adapted or not) (Brooker et al., 2022; Napier et al., 2023). Moreover, the success of individual plants frequently relies on, or is associated with, their reproductive ability. Traditionally, humans harvest plants' reproductive structures, such as grains or fruits, making it plausible to conclude that plants' phenotypic plasticity results in higher production (quantitative and/or qualitative). However, the phenotypic plasticity of different traits can be associated or not, and can affect or not, other traits (Giordano et al., 2024; Sadras et al., 2013; Sadras & Rebetzke, 2013; Sadras & Richards, 2014; Veenstra et al., 2021). Consequently, plants' phenotypic plasticity embodies various characteristics and complexities worthy of further exploration.

Phenotypic plasticity is also an interesting tool in crop modeling and crop ecology, allowing researchers to correlate variables in terms of variance (Sadras et al., 2013), making trait variance a fundamental key to understanding the importance of this trait (phenotypic plasticity), which requires a practical approach to estimate phenotypic plasticity. Among the various ways proposed to calculate the phenotypic plasticity, two stand out compared to the others, due to their ease of implementation and interpretation in the face of complex and imprecise models. These methods are the Reymond's slope model (trait in relation to environment) and the variance ratios

(Sadras et al., 2013). Reymond et al. (2003) proposed to analyze the plasticity through the slope of the treatment as a function of the environmental characteristics (e.g. pressure, temperature, moisture, etc.) (Reymond et al., 2003). Also, for ordering the complex environment variability, others proposed the use of the environmental index, which can be calculated as a function of an environmental variable (Eberhart & Russell, 1966; Guo et al., 2024; X. Li et al., 2018) or as a function of the population phenotypic rate (trait), where the environment is ordered in function of its potential to let the population express its phenotype (Nascimento et al., 2021; Raj et al., 2023). Meanwhile, the variance ratio is a way to assess the phenotypic plasticity of the individual from the quotient of this individual variance divided by the population variance (Dingemanse et al., 2010; Giordano et al., 2024; Sadras et al., 2013; Sadras & Richards, 2014; Veenstra et al., 2021).

1.8 Hypothesis and Objectives

Evidence suggests that winter wheat AOPD is considerably lower than current plant population recommendations and that wheat genotypes may differ in their response to seeding rate. To our knowledge, there have been no attempts to quantify the importance of exploring this opportunity to reduce current seeding rates from a phenotypic plasticity framework. Our hypothesis is that vegetative tillering plasticity increases tillering production in higher potential environments, and the tiller buffer effect on grain yield will allow a reduction in plant density to achieve the attainable yield in these environments, which result in a reduction of the AOPD for genotypes with higher vegetative tillering plasticity. Thus, our objective in this thesis was to explore genotype × environment interactions using the plasticity framework to test whether

tillering plasticity can reduce AOPD in winter wheat, and weather factors that affect the effect of vegetative tillering plasticity on AOPD.

Chapter 2 - Vegetative Tillering Plasticity Modulates Agronomical Optimum Plant Density in Winter Wheat

2.1 Introduction

Agronomic optimum plant density (AOPD) is the minimum number of plants per area that maximizes grain yield (Bastos et al., 2020). Evidence suggests that wheat *(Triticum aestivum* L.) can maximize yield at populations in the vicinity of 100 plants m^{-2} in different parts of the world, including intensively managed winter wheat fields in Kansas, U.S. (Bastos et al., 2020; Lollato et al., 2024; Lollato, Ruiz Diaz, et al., 2019), and in high-yielding regions of the United Kingdom (Thorne & Wood, 1987) and the Netherlands (Darwinkel, 1978), as well as spring wheat under irrigation in Mexico (Hasan et al., 2022; Rodríguez-Casas et al., 2005) and in high-yielding rainfed environments of southern Chile (Bustos et al., 2013; Hasan et al., 2022). Meanwhile, the recommended seeding rates for wheat are usually in the 250 – 450 seeds m^{-2} range (Beres et al., 2020b; Frederick & Marshall, 1985; Lloveras et al., 2004; Staggenborg et al., 2003). This mismatch between wheat's potential AOPD and current recommendations warrants further investigation within the context of genotype × environment × management (G × E × M) interactions (Beres et al., 2020b).

The AOPD in wheat appears to be influenced by the availability of environmental resources and by genotype-specific traits (Bastos et al., 2020; Fischer et al., 2019; Lollato, Ruiz Diaz, et al., 2019; Sadras & Denison, 2009; Salazar et al., 1996; Veenstra et al., 2021), and is tightly linked to the crops' ability to produce tillers (Mehring et al., 2020; Rodríguez-Casas et al., 2005). Tillers are additional stems that develop from the main stem until approximately the jointing stage of development (GS13-GS31) (Zadoks et al., 1974). The primary tillers form from

the first true leaves' axils (around three or more), and under favorable conditions, secondary tillers will also develop. Usually, more tillers are developed than what the plant can sustain; thus, mortality might be observed especially from jointing until anthesis (GS31 – GS69) (Klepper et al., 1982; Tilley et al., 2019a) when there is a large source-sink competition for assimilates to the developing spike. Additionally, some tillers that survive through this phase may not produce a spike. Tiller production, sterility, and survival are impacted by plant carbohydrate dynamics that also influence grain yield (Jewiss, 1972; Rawson, 1971).

Tiller production is affected by environmental conditions such as the weather experienced around the sowing date and until the first frost day (in winter wheat), and from the spring beginning to jointing, and is positively affected by accumulated growing degree days and solar radiation (Zhou et al., 2020). The total time to full vernalization increases the maximum number of tillers per shoot and the final leaf number in the main stem (Spink et al., 2000), suggesting that the period from sowing until jointing (GS 31) (Zadoks et al., 1974) can affect vegetative tiller production (Zhou et al., 2020). Environmental conditions that promote tiller production, such as soil moisture, soil nitrate, and soil phosphorus rates, and weather variables such as total available water and its distribution, temperature, and solar radiation (Ritchie, 1983; Veenstra et al., 2023) are likely to reduce AOPD. This was demonstrated by Bastos et al. (2020), who identified a lack of yield response to plant density in high-yielding environments, with progressively greater AOPD as environmental yield potential decreased.

Cereals, including winter wheat, have genotype-specific tillering potential (Anderson & Barclay, 1991; Baker, 1982; Briggs & Ayten-Fisu, 1979; Faris & de Pauw, 1981; Mehring et al., 2020; Pendleton & Dungan, 1960; Wiersma, 2002) which allows for differential compensation for variations in population through compensatory mechanisms among yield components

(Lloveras et al., 2004). Usually, semi-dwarf varieties with the *Rht* height reducing allele, and with the insensitive allele for photoperiodism (*Ppd*), have lower tillering potential than their counterparts (Mehring et al., 2020). Li et al. (2002) quantified many tillering-related quantitative trait loci (QTL), suggesting that stems per plant are largely function of a region on the short arm of chromosome 6A and, to lower extents, a region on the short arm of chromosome 1D and the region of *Ppd*-D1. Genotypes with a lower tillering ability are more dependent on higher seeding rate (i.e., greater AOPD) to express their yield potential (Jaenisch et al., 2022; Valério et al., 2008, 2009) since the number of tillers per area influence spike number. Since tiller production of a given genotype can lower AOPD (Bastos et al., 2020; Tilley et al., 2019a), we argue that a better understanding and quantification of the interaction between genotype, environment, and management (G × E × M) in tiller production can improve recommendations to wheat producers aiming at maximizing grain yield and/or profitability.

Phenotypic plasticity of a trait reflects a genotype's ability to express a determined phenotype as function of environmental conditions (Palmer & Strobeck, 1997). This method is a tool to explore genotype × environment interactions since it allows for quantification of whether the trait is positive or negative in environments with differing trait expression levels (Giordano et al., 2024; Lollato, Roozeboom, et al., 2020; Sadras et al., 2013; Sadras & Rebetzke, 2013). Thus, it potentially allows for the selection of genotypes with more or less dependable phenotypes depending on the direction of the interaction of plasticity and trait expression and grain yield (Møller & Shykoff, 1999; Palmer & Strobeck, 1997).

This paper explores the relations of wheat AOPD as function of environmental and genotypic characteristics in dryland environments from the perspective of phenotypic plasticity.

We hypothesize that genotypes with greater vegetative tillering phenotypic plasticity have lower AOPD since greater tiller production may buffer below-optimal environmental conditions.

2.2 Conceptual framework

2.2.1 Phenotypic plasticity

The phenotypic plasticity framework described by Sadras & Richards (2014) can help disentangle G × M × E interactions. The coefficient of relative phenotypic plasticity for each trait *x* and each variety *i* can be calculated as the unitless variance ratio (VR*xi*). The variance of a particular trait within a given genotype (V*xi*) over the variance of the trait within a population of genotypes (V*xp*) (Dingemanse et al., 2010):

$$VR_{xi} = V_{xi}/V_{xp} \quad (1)$$

Regression analysis on the percentile-plasticity plots relating the 10^{th} and 90^{th} percentiles of the desirable trait data, against the variance ratio of each trait, then underpins the genotype × environment interaction (Sadras, Lake, et al., 2016). The 10^{th} percentile is associated with environments of low trait expression and the 90^{th} percentile is associated with environments of high trait expression.

2.2.2 Physiological basis of agronomic optimum plant density in wheat

The presence of an AOPD in a yield-density curve assumes three phases, (i) the first in which yields increase in response to increased plant density, (ii) a second region surrounding the AOPD where yields reach an asymptote, and (iii) a third region where yield plateaus (or decreases) in response to density. While we acknowledge that literature on wheat yield response to plant density is inconsistent, with reports of linear, quadratic-plateau, plateau-negative linear,

and quadratic responses, to inexistent (Bastos et al., 2020; Fischer et al., 2019; Holliday, 1960; Holman et al., 2021; Jaenisch et al., 2019, 2022; Lloveras et al., 2004; Lollato, Ruiz Diaz, et al., 2019; Mehring et al., 2020; Whaley et al., 2000), we adopt this three-phase model in this study because there are many reports of similar asymptotic association (Dai et al., 2013; Fischer et al., 2019; Frederick & Marshall, 1985; Lloveras et al., 2004; Valério et al., 2009) and more importantly, because it can be explained through different compensatory mechanisms among yield components (Bastos et al., 2020; Guitard et al., 1961; Jaenisch et al., 2022; Lollato, Ruiz Diaz, et al., 2019).

In phase (i), plant density is suboptimal, reducing intraspecific competition for resources. Consequently, auxin production also is reduced allowing for a numerical development of tiller buds (De Wit et al., 2016; Liu et al., 2011). While this maximizes tiller production and survival, and grain production per plant (Mehring et al., 2020; Rodríguez-Casas et al., 2005), the large space between plants results in a lower grain number per area and therefore yield per area is below the asymptote.

At the AOPD [phase (ii)], wheat capitalizes on the increased number of tillers and yield per plant, maximizing individual plants' use efficiency of resources while reducing the penalties associated with intraspecific competition for resources between neighboring plants (Bastos et al., 2020; Satorre & Slafer, 1999). The reduced shading from neighboring plants on the leaves of individual plants may increase radiation use efficiency (Fischer et al., 2019; Tao et al., 2018) since shading reduces the ratio red light / far-red light (Chelle et al., 2007) which also reduces tillering production (Casal, 1988; Evers et al., 2007) and grain yield (Ugarte et al., 2010). Also, increases in radiation use efficiency due to shading reduction may increase harvest index (Sadras, Villalobos, et al., 2016). Furthermore, an important factor for dryland systems is that a

smaller canopy during early stages reduces evapotranspiration, potentially saving water for reproductive stages and increasing water use efficiency (Ritchie, 1983). Thus, at AOPD, tiller survival is increased (Guitard et al., 1961; Joseph et al., 1985) and wheat can produce a higher quantity of spikes both per plant and per area, sustaining more grains per area (Bastos et al., 2020; Lollato, Ruiz Diaz, et al., 2019).

Finally, in phase (iii), tillers per plant are reduced exponentially due to high plant densities (Joseph et al., 1985) as function of reduced tiller survival under higher competition (Fang et al., 2019; Holliday, 1960; Sadras & Rebetzke, 2013). Thus, grain yield relies more on the main spike and potentially first tiller, and can be sustained due to compensatory mechanisms among yield components (e.g., fewer though larger spikes). However, very high densities can reduce crop yield due to a number of factors (e.g., increased disease and insect pressure, lodging, insufficient resources such as fertility, or excessive early season crop growth and water use) (Fischer & Kohn, 1966; Lloveras et al., 2004; Salgado et al., 2017; Van Herwaarden et al., 1998). The possibility of reducing plant population and maintaining yields offers an opportunity to better understand the genotype-specific tillering potential to provide optimal seeding rates without loss of production (Bastos et al., 2020; Lollato, Molssato, et al., 2019; Tilley et al., 2019a).

2.2.3 Hypothesis

Figure 2.1 illustrates examples where phenotypic plasticity of tiller production is depicted as a positive and as a negative trait, and our hypothesis as it relates to this trait's impact on AOPD in winter wheat. In **Figure 2.1A**, plasticity is related to greater tiller production under high tillering environments with no tradeoff in low tillering environments. In this example, a

highly plastic genotype would produce more tillers when conditions are favorable for tillering (e.g., low plant densities, ample environmental resources) while expressing the same number of tillers as a stable genotype under greater competition. **Figure 2.1B** portrays the yield-density response of the two hypothetical genotypes shown in **Figure 2.1A**, where plasticity was a positive trait. Here, the more plastic genotype produces more tillers in high tillering environments, being less dependent on plant density. Therefore, increases in phenotypic plasticity of tillering hypothetically reduces AOPD **(Figure 2.1C)**. In **Figure 2.1D**, plasticity is depicted as a negative trait, where stable and plastic genotypes do not differ in tiller production under high tillering environments, but stressful conditions for tillering (e.g., high plant densities, late sowing) reduces tiller production in the more plastic genotype. If phenotypic plasticity of tillering is a negative trait, expectedly tiller production in low tillering environments is reduced and consequently, AOPD of the more plastic genotype is greater than that of the more stable genotype **(Figure 2.1E)**. In this scenario, AOPD increases with increases in phenotypic plasticity of tillering **(Figure 2.1F)**. We note that these scenarios are not mutually exclusive: If phenotypic plasticity of tillering shows an asymmetric response (i.e., positive in high tillering environments and negative in low tillering environments), the responses of AOPD to phenotypic plasticity of tillering shown on both **Figure 2.1C and 1F** can exist in different environments.

This paper focuses on contrasting winter wheat genotypes cultivated under a large range of plant densities exposed to different seeding rates at a number of environments to test the following hypothesis:

1. Phenotypic plasticity of tillering is a positive trait for crop adaptation in dryland environments, reducing AOPD in winter wheat.

2. The impact of phenotypic plasticity of tillering on AOPD is dependent on environmental conditions experienced during the season; thus tradeoffs due to higher phenotypic plasticity of tillering may occur under harsh environmental conditions.

3. The presence of dwarfing- and/or photoperiod-related genes reduces tillering plasticity thus impacting crop's response to plant density.

2.3 Materials and Methods

2.3.1 Experimental Locations and Agronomic Management

Field experiments were conducted in twelve Kansas (U.S.) environments resulting from the combination of six locations and two growing seasons **(Table 2.1)**. The environments were purposefully selected to represent gradients in temperature and moisture availability during the fall, consequently impacting tillering potential of winter wheat. Thus, experiments were conducted under a range of management conditions, from fields conducted after a fallow period with timely sowing and conventional tillage (i.e., allowing for more soil moisture and fall temperature accumulation) to fields where wheat was sown late immediately after the harvest of a previous summer crop under no tillage practices (i.e., reducing soil moisture in the profile and fall temperature accumulation) **(Table 2.1)**. In Hutchinson during 2021-22, two nearby areas were sown at different sowing dates and contrasting cropping systems to further create a range in tillering potentials. All conditions evaluated were representative of commercial crop rotations typical for winter wheat in Kansas (Jaenisch et al., 2021).

Experiments were sown using a Great Plains NT606 drill. Experimental units were ~10 m long by seven rows wide using at ~0.19 m spacing. Management factors such as seed treatment, fertilizer rates, disease, weed, and insect control were carried out so that they were non-limiting

to grain yield. Seeds were treated with sedaxane, difenoconazole, mefenoxam, and thiamethoxam so that early-season biotic factors were not limiting at rates of 0.23, 1.04, 0.27, 3.1 kg ai/100 kg of seed. Di-ammonium phosphate (DAP 18-46-0) was applied in-furrow at sowing at a rate of 56 kg ha^{-1}. Nitrogen fertilizer was applied during early spring greenup (GS 30) (Zadoks et al., 1974) as urea (46-0-0) at rates sufficient to meet a yield goal of 6 Mg ha^{-1} considering the initial soil NO_3-N levels (Leikam et al., 2003). This yield goal was selected so that N was not limiting, since it closely reflects the long-term dryland yield potential in the region (Lollato et al., 2017). Weeds were controlled both prior to sowing and during early spring using commercially available herbicides. Foliar fungicide (i.e., 28 g ha^{-1} fluxapyroxad-group7, 118.8 g ha^{-1} Propiconazole-Group3, and 190.5 g ha^{-1} Pyraclostrobin-Group 11) and a non-ionic surfactant (292 g a.i. ha^{-1} as Phosphatidylcholine, methylacetic acid and alkyl polyoxyethylene ether) were sprayed at heading (GS 55) (Zadoks et al., 1974) using a backpack sprayer with a pressurized CO_2 tank and a hand boom to avoid potentially confounding effects from cultivar-specific genetic tolerance to different fungal diseases.

2.3.2 Treatments and Experimental Design

Experiments were conducted using a complete factorial treatment structure of winter wheat cultivars (n = 24) and seeding rates (n = 2) established in a randomized complete block design (RCBD) with three or four replications, depending on environment **(Table 2.1).** The twenty-four winter wheat cultivars were selected to reflect differences in breeding programs and based on anecdotal evidence for their tillering potential **(Table 2.2).** The two target seeding rates (100 and 300 seeds m^{-2}) were selected to represent current recommendations (300 seeds m^{-2}) and the minimum number of plants reported to achieve maximum yields in this region under highly

managed conditions (Lollato et al., 2024; Lollato, Ruiz Diaz, et al., 2019), allowing genotypes to express their respective tillering potential (Lollato et al., 2024).

2.3.3 Measurements and calculations

Composite soil samples consisting of 15 individual soil cores were collected prior to sowing from 0 to 15, and from either 15 to 45 or 15 to 60 cm soil depths to characterize initial soil fertility and soil texture of each experimental field **(Table 2.3)**.

A random area representing one linear meter of a center row was marked in each experimental unit for subsequent measures. Here, stand count was measured ~21-28 days after sowing (GS 20) (Zadoks et al., 1974). Stand count was later considered to be the number of main stems. Total number of vegetative tillers was measured after the winter dormancy and just prior to jointing (GS 31) (Zadoks et al., 1974). and the variable "vegetative tillers" was calculated by subtracting the number of main stems from the total number of stems per area. The number of tillers per plant was calculated by dividing the total tiller number by the stand count. At harvest maturity, above-ground biomass was sampled using an electric grass shear immediately above the soil surface. Samples were dried at 60 to 65°C by airflow dryer for approximately 48 hours until constant weight. Above-ground dry biomass weight was recorded, the spikes were counted and separated from the stover manually, and spikes and stover weights were recorded. Afterwards, spikes were threshed to separate the kernels from the chaff. Total sample grain weight was measured and the ratio between grain weight and total aboveground biomass weight (including stover, chaff, and grain) determined the harvest index (HI). The number of productive tillers per plant was calculated as the difference between spikes m^{-2} and main stems m^{-2} divided by plants m^{-2}. Plots were trimmed prior to harvest to avoid edge effects, and wheat was harvested

from ~11.5 m^2. Harvest occurred with a self-propelled small-plot combine (Massey Ferguson 8XP) that measured grain weight, test weight, and moisture. Yield was calculated based on the experimental unit area and corrected to 130 g kg^{-1} moisture content. Outliers were identified and removed based on three standard deviations for each measured trait in each environment (Dixon, 1953).

Daily weather data for precipitation, maximum and minimum daily temperatures, incident solar radiation, and reference evapotranspiration (ETo) were retrieved from nearby meteorological stations from the Kansas Mesonet system (Patrignani et al., 2020) for the twelve studied environments, and for the last 30-yr period. Missing daily solar radiation (<1% of the observations across all site-year data) was estimated as function of maximum and minimum daily temperatures (Hargreaves & Samani, 1982) based on FAO 56 (Allan et al., 1998). The categorical variables "site" and "year" were then translated into numerical variables to explore their impact during important phases of crop development. The critical period for yield determination was estimated for each environment to start 300 °Cd^{-1} before and last until 100 °Cd^{-1} after anthesis (measured at the site-year level) with a base temperature of 4.5°C (Fischer, 1985; Sadras et al., 2022; Slafer et al., 2021), and grain filling was estimated from 100 °Cd^{-1} to 600 °Cd^{-1} after anthesis with a base temperature of 0 °C for wheat (Dupont et al., 2006; Giordano et al., 2023; Raj et al., 2023). Dates of, and summarized weather variables for, anthesis, critical period, and grain filling are shown on **Table 2.4**. Daily weather variables were summarized (summed or averaged) for the fall (sowing date through 22 December), winter (23 December through 21 March), and Spring (22 March through harvest date) **(Table 2.5)**. At the crop season level, weather variables were summarized as Crop Fall Season (sowing date through December

31), Crop Winter Season (January 1 through critical period beginning), Critical Period, Grain Filling, and Total Season **(Table 2.6)**.

We calculated environmental variables that could impact tiller production including (i) departure from the optimum sowing date, representing the number of days from the actual to the optimum sowing date for each respective location (Munaro et al., 2020); (ii) temperature accumulation in the fall ($°Cd^{-1}$ at a base temperature of 0 °C); and (iii) fall precipitation **(Table 2.1)**. For weather variables potentially impacting grain yield, we calculated total growing season water supply as the sum of the total seasonal accumulated precipitation plus the soil available water at sowing, the latter calculated based on non-growing season precipitation and soil available water holding capacity at 1500 mm depth (Lollato et al., 2016). Plant available water holding capacity was calculated based on Ratliff`s methodology (Ratliff et al., 1983) using values for field capacity and wilting point (extractable water at 0.33 and 15 bars of pressure) considering field soil texture derived from USDA Soil Survey Data (USDA-NRCS, 2024a) **(Table 2.1)**. USDA Soil Survey (USDA-NRCS, 2024b) was used to identify the predominant agricultural soil type in each site **(Table 2.1)**, which was validated by soil analysis results **(Table 2.3)**, considering the USDA soil texture triangle (USDA, 2017), and respecting an adjacent variance (i.e., if the survey system showed a soil type within 10% of the one classified in the soil texture triangle, the survey system soil type and data was used; McBratney et al., 2000; Moreno-Maroto & Alonso-Azcárate, 2022; USDA, 2017).

2.3.4 Marker analysis

Marker analysis was performed by planting ten seeds of each variety in individual pots, and collecting leaf tissue at approximately 15-20 days after planting. DNA was extracted and

analyzed for known informative markers using the Agriplex Wheat 216 genotyping platform, which is an amplicon sequencing method (AgriPlex Genomics | Home, Agriplex Genomics, Cleveland, OH) (Kriaridou et al., 2020, 2023). Informative markers of interest for this study included Ppd-D1, Vrn-A1, Vrn-B1, vrn-D3, $2N^vS$ translocation, and *Rht*. Marker Ppd-D1 is located on wheat genome chromosome 2D and is associated with photoperiod sensitivity, which may affect traits such as flag leave area (Beales et al., 2007; Hussain et al., 2017; Korzun et al., 1998; Ma et al., 2007; Tadesse et al., 2015; Zhai et al., 2016). Vrn-A1 is located on wheat genome chromosome 5A and is correlated with vernalization, vrn-A1a allele presence is associated with earlier flowering (Galiba et al., 1995; Halloran & Boydell, 1967; G. Li et al., 2013; Yan et al., 2015). Vrn-B1 (located at chromosome 5B) is associated with a short vernalization requirement (Kumar et al., 2020; Y. Li et al., 2020; Mizuno et al., 2023). The vrn-D3 (located at chromosome 7D) is associated to physiological maturity but does not advance the stem elongation period (Bonnin et al., 2008; Chen et al., 2010; Katz et al., 2022; Wang et al., 2009). Both alleles Vrn-A1, Vrn-B1, and vrn-D3 are associated with vernalization. The $2N^vS$ translocation represents the Lr37/Yr17/Sr38 genes cluster, which are associated with rust resistance (Helguera et al., 2003; Skolotneva et al., 2021; Xue et al., 2018). *Rht* is associated with plant height (Grogan et al., 2016; Li et al., 2013; Wilhelm et al., 2013).

2.3.5 Crop modeling

Weather and soil data were used to run a mechanistic crop simulation model SSM-Wheat (Simple Simulation Model) (Soltani & Sinclair, 2012) for each environment to further characterize each environment and to compare with long-term crop season weather data. The model estimates daily wheat growth and development based on soil characteristics and observed

daily weather. Crop transpiration is estimated based on a transpiration efficiency coefficient, effective daily vapor pressure deficit, and crop daily dry matter production (Tanner & Sinclair, 2015) and evaporation from the soil is calculated based on a two stage soil evaporation model (Amir and Sinclair, 1991) based on potential evaporation rate calculated using a modified Priestly and Taylor model (Priestly and Taylor, 1972; Ritchie, 1998). Crop evapotranspiration (ETc) was then calculated as the sum of transpiration and evaporation. Crop parameters were derived from field collected data of seven drylands and four irrigated U.S. Southern Great Plains environments, free of biotic or abiotic limitations and using intensive management (Lollato and Edwards, 2015), broadly used and validated in this region (Lollato et al., 2024; Lollato & Edwards, 2015; Sadras & Angus, 2006). The crop model was run for the twelve environments of the study and for the 30-yr historical records from the nearest weather station.

2.3.6 Statistical analyses

All statistical analyses were performed using R software version 4.2.2 (R Core Team, 2022). First, Pearson's correlation analysis was used to evaluate the degree of linear association between crop establishment and weather conditions during the fall, as well as that between the environmental mean of the measured variables and weather variables during important phases of crop development. This analysis used the R package "*Hmisc*" (Harrell Jr & Harrell Jr, 2019).

2.3.6.1 ANOVA and ANCOVA models

Plant density (plants m^{-2}) data were analyzed using linear mixed effect model analysis of variance (ANOVA) in a 3-way factorial design where genotype, environment, seeding rate, and their interactions were considered fixed effects, and blocks as random effects (Dixon, 2016).

Since the treatment “seeding rate” resulted in vastly different emerged plant densities across experimental units, blocks, and environments, the treatment effects on the remaining measured traits were performed using a two-way analysis of covariance (ANCOVA) considering genotype, environment, and their interaction as fixed effects, plant density (continuous variable) as a covariate, and blocks nested within environment as a random effect (Dixon, 2016). Both ANOVA and ANCOVA models were fitted using the R packages "*lme4*" (Bates et al., 2015) and “*car*” (Fox & Weisberg, 2018), adjusting each for Type-III error rate (Fox, 2016). Effects were considered significant when $p \leq 0.05$, and main effects were not explored when a significant interaction occurred.

To identify the influence of markers and the measured variables, before conduce an ANOVA, data was summarized and the best linear unbiased estimator (BLUE) was accessed using the estimated marginal means (EMMs) for each environment using a linear mixed effect model which defined genotype as fixed effect, plant density as covariable, and blocks as random effect (Dixon, 2016). EMMs are adjusted for covariable and random effects simultaneously, which makes them equivalent to BLUEs in the context of estimating fixed effects (genotypes effect) allowing a better adjusted entry means in the next analyses (Covarrubias-Pazaran, 2023). This adjustment helps in comparing levels of the genotype factor while accounting for variability due to block random effects, counting the plant density as a covariable. Models were fitted using the R packages “nlme” (Pinheiro et al., 1999) and estimated marginal means were extracted via "*emmeans*" R packages (Lenth, 2017). ANOVA was conducted considering markers (i.e., Rht, Ppd-D1, Vrn-A1, Vrn-B1, vrn-D3, and $2N^{y}S$) as fixed effects and genotypes as random effects in a linear mixed model using the same packages and assumptions as above. For the cases of Individual and Crop Vegetative Tillering Plasticity, environmental effects were not included.

The analysis was carried out using the R packages "*lme4*" (Bates et al., 2015) and "*car*" (Fox & Weisberg, 2018), adjusting each for Type-III error rate (Fox, 2016). Effects were considered significant when $p \leq 0.05$. Both analyses were performed using R software version 4.2.2 (R Core Team, 2022). We note, however, that most of the alleles of interest were not present in a balanced ratio in our genotype population. With the exception of the vrn-D3 marker (which was close to balanced) and Rht and Ppd-D1 (which have 3 alleles), the other markers exhibited a ratio of ~2:1 between their alleles.

2.3.6.2 Relationships among measured variables

We evaluated impact of plant density on each measured individual trait (e.g., vegetative tillering plant^{-1}, spikes plant^{-1}, and grain yield plant^{-1}) using nonlinear least squares regression via the "*nls*" function in the R package "*ggplot2*" (Wickham et al., 2016); and its impact in each trait per area (e.g., vegetative tillers m^{-2}, etc.) using linear regression through the "*lm*" function in the R package "*stats*". Regression analyses of per plant and per area traits were performed within environment. A similar linear regression methodology was used to model the grain yield (g plant^{-1} and kg m^{-2}) as a function of vegetative and reproductive tiller density. To quantify the conversion efficiency from vegetative to reproductive tiller all sources of variation, we evaluated the relationships between vegetative tillers and productive tillers across environments at an individual (plant) level using linear regression analysis via the "lm" function in the R package "stats"; and per area using linear-plateau regression fitted using "*nlsLM*" from the "*minpack.lm*" package in R (Elzhov et al., 2016). Since regression coefficients of the data per area differed for high and low seeding rates, conversion efficiencies were calculated separately.

2.3.6.3 Phenotypic Plasticity

Phenotypic plasticity was quantified as the variance ratio for each trait according to Eq. 1. Briefly, variance ratio is the quotient of the variance of the trait for a given genotype to the overall phenotypic variance of the population of genotypes across environments and seeding rates at an individual plant level and at the crop level (Dingemanse et al., 2010; Giordano et al., 2024; Sadras & Rebetzke, 2013). Afterwards, we plotted all observed trait production versus plasticity relationships. Since plant density was a significant covariate in all analyses (see Results section), we plotted these relationships separately for both low and high seeding rates. Then, we fitted linear and quadratic regressions against the 10^{th} and 90^{th} percentiles, portraying low and high trait phenotype expression, to quantify whether traits conferred adaptation depending on environment. Percentile analyses were selected as a way to return an objective measure, focusing on the upper and lower limits of each trait expression, reducing the noise of extremes (Cade & Noon, 2003; Giordano et al., 2024; Sadras, Lake, et al., 2016; Sadras & Richards, 2014). The 10^{th} and 90^{th} quantiles were defined using "*quantile*" function, linear regressions were fitted using "*lm*" function, and quadratic regressions using "*poly*" function from "*stats*" package present in R. Linear regressions were preferred unless the quadratic regression was statically significant and increased model fit in 20% or more. These analyses were performed at the crop and individual plant levels. The relationship between the coefficients of phenotypic plasticity of vegetative tillers and of reproductive tillers at the crop and individual plant levels was assessed using linear regression using the "*lm*" function from the R package "*stats*".

2.3.6.4 Agronomic optimum plant density

We modeled grain yield as function of plant density for each cultivar in each environment using a Bayesian approach to capitalize on a flexible framework to capture complex relationships between predictors and response variables while incorporating prior knowledge and uncertainty (Hooten & Hefley, 2019). Bayesian models offer the possibility of including a probabilistic protection that takes care of multiple uncertainties in the model, which is ideal given the stochastic nature of grain yield due to its multiple predictor variables (Gelman et al., 1995; Hooten & Hefley, 2019). In crop science, Bayesian approaches have been used to predict maize hybrid performance (Alves et al., 2019; Lacasa et al., 2023), wheat grain yield response to nitrogen fertilization (Correndo et al., 2021; Giordano et al., 2024; Ouedraogo & Brorsen, 2018), and associations between phenotypic plasticity and protein concentration (Giordano et al., 2024).

We implemented a Bayesian hierarchical framework to model the yield-plant density relationship as affected by environment and, instead of using the categorical variable 'genotype name', we used each genotype's tillering plasticity at the plant level. Many studies on wheat response to plant density suggest the presence of asymptotic relation (Bastos et al., 2020; Lollato, Ruiz Diaz, et al., 2019; Tokatlidis, 2017). Thus, the model was written as follows:

$$y_{ij} \sim \mathrm{N}\left(\mu_{ij}, \sigma_{ij}^2\right), \tag{2}$$

$$\mu_{ij} = \begin{cases} \beta_{1ij} s_{ij} + \beta_{2ij} s_{ij} & if\ s_{ij} \leq AOPD_{ij} \\ \beta_{1ij} AOPD_{ij} + \beta_{2ij} AOPD_{ij} & otherwise, \end{cases} \tag{3}$$

$$\beta_{1ij} = \alpha_{0j} + \alpha_{1j} p_i\ , \tag{4}$$

$$AOPD_{ij} = \alpha_{2j} + \alpha_{3j} p_i\ . \tag{5}$$

In Equation 1, y_{ij} represents an observation of the response variable grain yield at the *i*th plot (*i*=1, 2,…,n) in the *j*th environment (*j*:1, 2,…,12) and follows a normal distribution with an

expected value μ_{ij} and variance σ_{ij}^2. Here, μ_{ij} follows a quadratic-plateau function with parameters terms β_{1ij}, β_{2ij} and $AOPD_{ij}$. Parameter β_{2ij} can be expressed as a function of β_{1ij} and $AOPD_{ij}$ using algebra:

$$\beta_{2ij} = \frac{-\beta_{1ij}}{2\ AOPD_{ij}}. \tag{6}$$

The proposed model novelty relies on the assumption that β_{1ij} and $AOPD_{ij}$ depend on the tillering plasticity (p_i) of the *k*th cultivar (*k*:1, 2,…,24). Thus, α_{0j} represents the intercept for linear term β_{1ij} and α_{1j} the linear effect of p_i on β_{1ij}. Similarly, as proposed in our objective we modeled how $AOPD_{ij}$ changed with p_i in Eq. 4 where α_{2j} represents the intercept for linear term $AOPD_{ij}$ and α_{3j} the linear effect of p_i on $AOPD_{ij}$.

Also, we defined the uninformative priors (based on previously published and unpublished literature) as follows:

$$\sigma_{ij} \sim \Gamma(1,1) \tag{7}$$

$$\beta_{1ij} \sim \mathrm{N}(0.085,0.24), \tag{8}$$

$$AOPD_{ij} \sim \mathrm{N}(105.76,50), \tag{9}$$

$$\alpha_{0j}, \sim \mathrm{N}(0.085,0.24), \tag{10}$$

$$\alpha_{1j} \sim \mathrm{N}(0.085,0.24), \tag{11}$$

$$\alpha_{2j} \sim \mathrm{N}(0,50), \tag{12}$$

$$\alpha_{3j} \sim \mathrm{N}(0,50). \tag{13}$$

In our analyses, uninformative priors derived from previously published literature and unpublished data. Published data included two studies in Kansas: (i) Lollato, Ruiz Diaz, et al.

(2019) who demonstrated a general AOPD in an interval from 93 to 121 seeds m^{-2} in commercial Kansas wheat fields, and (ii) Bastos et al. (2020) who demonstrated an AOPD interval from 58 to 284 seeds m^{-2} depending on yield environment, using data from small plot replicated trials. We also used unpublished data from other plant density and seeding rate response studies conducted by our research group in Kansas (data not shown) resulting in a general AOPD ~105 seeds m^{-2}.

The Bayesian model was fitted using Stan (Team, 2016) on the back-end using "*brms*" package (Bürkner, 2017) in R interface 4.2.0 (R Core Team, 2022). The model ran in 4 Monte Carlo-Markov Chains (Hooten & Hefley, 2019; Johansen et al., 2010) for 20,000 iterations, the first 10,000 posterior draws were discarded and we kept only 10,000 draws used for later inference. Later, summarizing simulations to obtain the mean and the 2.5th and 97.5th percentiles for each combination of phenotype, environment, and plant density and create a data frame for the next analyses. We plotted these relations using the "*geom_raster*" function in the R package "*ggplot2*" (Wickham et al., 2016).

Finally, to better understand the environmental drivers of the impact of vegetative tillering plasticity on AOPD (i.e., to answer to the question "in which environments can AOPD be reduced in more plastic cultivars?"), we used linear regression analyses to relate different weather variables experienced during important phases of the growing season on the parameter α_{3j} (i.e., representing the linear effect of plasticity on AOPD) using the "*lm*" function.

2.4 Results

2.4.1 Weather conditions and associations with crop components

Across the 12 environments, growing season precipitation ranged from 141 to 409 mm and plant available water at sowing ranged from 17 to 170 mm, resulting in seasonal water supply of 252 to 463 mm **(Figure 2.2)**. Meanwhile, seasonal ETc ranged from 214 to 356 mm

with large mismatches between water supply and crop water demand in HAY22, LEO22, HOI23, and LEO23. Overall, the fall, winter, and early spring were colder and drier, and late spring and summer were hotter and drier in 2021-22 when compared with 2022-23 season **(Figure 2.2)**. These conditions delayed the initiation of, and hastened the rate of, reproductive crop development **(Figure 2.2)**. The contrasting environments resulted in growing season length ranging from 253 to 285 days. We note in passing that, when compared to the 30-yr averages for each location, the 12 studied environments had 49 to 88% of the total seasonal water supply (mean: 72%), and 99 to 114% of the mean grain fill temperature (mean: 105%) **(Appendix Figure 2.A.1)**.

Vegetative tillers (both per plant and per area) related positively with crop fall minimum and maximum temperature, as well as with crop fall and related negatively with winter precipitation increment **(Table 2.7)**. Productive tillers (per plant and per area) related positively with cumulative growing degree days in the crop fall and during the critical period, and with crop fall maximum temperature; while relating negatively with crop winter precipitation. Productive tillers per area related negatively with minimum temperature during the crop winter. Grain yield related negatively to critical period, and incident solar radiation; while relating positively to critical period cumulative growing degree days and precipitation.

2.4.2 Associations of plant density, tiller production, and grain yield

Across all sources of variation, the different combinations of seeding rates, genotypes, and environments resulted in plant densities ranging from 16 to 451 plants m^{-2} **(Figure 2.3)**. Expectedly, seeding rates impacted plant density significantly at all environments, and increasing

seed rates from 100 to 300 seeds m^{-2} resulted in just over two-fold increment in plants m^{-2} (from 102 ± 5 to 227 ± 14 plants m^{-2}) **(Figure 2.3).**

As a covariate, plant density had a statistically significant impact on most measured variables **(Table 2.8)**. The effects of plant density on vegetative and reproductive tillers, as well as on grain yield, were more evident on a per plant basis versus on a per area basis **(Figure 2.4)**. Vegetative tillers per plant ranged from null to 30 and decreased exponentially as function of plant density within environment, with steeper slopes in environments with greater vegetative tillers per plant production (**Figure 2.4A).** Likewise, reproductive tillers per plant (range: null to 16) and grain yield per plant (range: null to ~14.3 g $plant^{-1}$) also followed exponential decay functions with increases in plant density **(Figure 2.4C, E)**. Meanwhile, across all sources of variation, data of vegetative tillers per m^{-2} (range: null to 2021), reproductive tillers m^{-2} (range: null to 1192), and grain yield (range: null to 0.731 Kg m^{-2}) were scattered as function of plant density, though showing some environment-specific significant relationships (six, eight, and three out of 12 environments, respectively) **(Figure 2.4B, D, F)**. Regression coefficients for the relationships shown on **Figure 2.4** are provided on **Tables 2.9 and 2.10**.

Grain yield per plant increased linearly with increases in vegetative tillers per plant (r^2 from 0.23 to 0.76), with slopes ranging from 0.27 to 0.97 g per vegetative tiller **(Figure 2.5A)**. These relationships tightened when yield per plant was plotted against reproductive tillers (r^2 from 0.68 to 0.87), slopes from 0.58 to 0.96 g per reproductive tillers **(Figure 2.5C)**. While grain yield was positively related to vegetative tillers m^{-2} (r^2 = from <0.01 to 0.25) (except for PHB23, which presented a very low negative slope), this relationship, in most of the environments, was considerably stronger with reproductive tillers m^{-2} (r^2 = from <0.01 to 0.18). Regression coefficients for the relationships shown on **Figure 2.5** are provided on **Tables 2.11 and 2.12**.

2.4.3 Conversion efficiency of vegetative tillers into productive tillers

Productive tillers per plant related linearly and positively with vegetative tillers per plant **(Figure 2.6A)**. Across environments, plant densities, and genotypes, vegetative tiller per plant produced 0.57 ± 0.01 productive tillers per plant. Meanwhile, when the data was analyzed as tillers per area, there were two important differences: (i) the best fit model was a linear-plateau (rather than linear), and (ii) there was an important effect of plant density, resulting in separate regressions for the higher versus lower seeding rates **(Figure 2.6B, C)**. Here, under high seeding rates, the linear plateau model predicted that each vegetative tiller m^{-2} produced 0.66 ± 0.01 productive tillers m^{-2} when less than 868 ± 22 vegetative tillers m^{-2} were present, while beyond this point, 573 productive tillers m^{-2} resulted independent of the number of vegetative tillers m^{-2}. Under low seeding rates, the conversion of vegetative to reproductive tillers m^{-2} was more efficient (0.77 ± 0.01) and a similar plateau (615 reproductive tillers m^{-2}) occurred with fewer vegetative tillers m^{-2} (798 ± 17). Regression coefficients for the relationship shown on **Figure 2.6** are provided on **Table 2.13.**

2.4.4 Vegetative tillering plasticity as a positive trait for wheat adaptation

Significant genotype × environment interactions impacted most measured variables, including tillering traits and yield **(Table 2.8)**. These interactions were further explored using the phenotypic plasticity framework. Vegetative tillering plasticity at the individual plant level ranged from 0.55 to 1.60 **(Table 2.2)** and related positively to high tillering environments (portrayed by the 90^{th} percentile) for vegetative tillers per area and plant **(Figure 2.7A, B)** and productive tillers per area and plant **(Figure 2.7C, D)**, grain yield per plant **(Figure 2.7F),** likely increasing yield through greater harvest index **(Figure 2.7G)**, and through greater biomass per

plant **(Figure 2.7H)** at both high and low plant densities, except for harvest index. Vegetative tillering plasticity at the low tillering environments (portrayed by the 10^{th} percentile) related positively with productive tillers m^{-2} **(Figure 2.7C)** and productive tillers $plant^{-1}$ **(Figure 2.7D)** at higher plant densities.

The range in vegetative tillering plasticity was narrower at the crop level than at the individual level (i.e., from 0.58 to 1.37**, Table 2.2**)**.** Relationships between crop tillering plasticity and individual and crop traits followed similar patterns to those for individual tillering plasticity **(Figure 2.8).** Vegetative tillering plasticity was a positive trait for vegetative and reproductive tillers per area in both plant densities at high tillering environments and low tillering environments under high plant density **(Figure 2.8A, C)**. Similar responses occurred for vegetative and reproductive tillers per plant except for a relative null impact of the trait on productive tillers per plant under low plant densities **(Figure 2.8B, D).** Vegetative tillering plasticity showing a penalty associated with biomass per area in low biomass environments under low plant densities **(Figure 2.8E)** at the crop level, and associated positively with biomass and grain yield per plant under high yielding environments and high plant densities **(Figure 2.8F, G)**. Crop vegetative plasticity associated with reduced mortality at high plant densities in environments with high tiller mortality but increased modestly in low mortality environments under low plant densities **(Figure 2.8H)**.

The coefficient of vegetative tillering plasticity was highly associated with the coefficient of productive tillering plasticity both at the crop and at the individual levels **(Figure 2.9)**.

2.4.5 Impact of allele presence on measured traits

The only two markers that demonstrated a statistically significant difference in measured variables were Vrn-A1, where vrn-A1b (late) increased grain yield per plant from 2.61 to 2.8 g

plant^{-1}, and Vrn-B1 where vrn-B1-early increased grain yield per plant from 2.64 to 2.81 g plant^{-1} and grain yield from 0.305 to 0.322 kg m^{-2} **(Table 2.14)**.

2.4.6 Agronomic optimum plant density as function of environment and tillering plasticity

Responding to our hypothesis proposed on **Figure 2.1**, the grain yield response of the two genotypes with the most contrasting phenotypic plasticity of tillering at the individual level (i.e., KS Dallas, plasticity = 0.55; WB4595, plasticity = 1.60) to increases in plant density is shown for three contrasting environments in **Figure 2.10.** In the high yielding environment of BEL22 (~5.3 Mg ha^{-1} mean yield), AOPD averaged 118 plants m^{-2} and tillering plasticity reduced AOPD by 12.2 plants m^{-2} unit.plasticity^{-1} **(Figure 2.10A)**. In the same location but subsequent year (BEL23), when yield potential was lower (~1.3 Mg ha^{-1} yield plateau), mean AOPD was 210 plants m^{-2} and tillering plasticity increased AOPD by 5.2 plants m^{-2} unit.plasticity^{-1} **(Figure 2.10B)**. In a contrasting environment also of low yield potential (HOI23, ~1.6 Mg ha^{-1} yield plateau), mean AOPD was 62 plants m^{-2} and plasticity reduced AOPD **(Figure 2.10C)**.

The environment-specific impact on the interaction between vegetative tillering plasticity and plant density in determining winter wheat AOPD is depicted for all environments in **Figure 2.11**. First, this analysis showed that AOPD ranged from as low as ~19 to 115 plants m^{-2} in 11 out of 12 environments, and only BEL23 required over 210 plants m^{-2} to attain AOPD. Within this range, in six out of 12 environments (i.e., GRB22, HTL22, HTO22, HAY23, HUT23, and LEO23), the highest grain yield was obtained by varieties with intermediate vegetative tillering plasticity sown at average to high plant densities. In three environments (BEL22, HAY22, and HOI23), the highest grain yield occurred in varieties with high vegetative tiller plasticity and

under high plant densities. In two environments (i.e., LEO22 and BEL23), there was no impact of plant density within the tested range, with greater grain yields attained by cultivars with greater vegetative tillering plasticity. Finally, in one environment (PHB23), the highest yields were attained by varieties with low vegetative tiller plasticity and under high plant densities.

To further understand the environmental drivers of individual vegetative tiller plasticity effect on AOPD, the slope of AOPD in response to vegetative tiller plasticity (plants m^{-2} unit.plasticity $^{-1}$) was plotted as function of different weather variables experienced during important phases of the growing season **(Figure 2.12, Table 2.15)**. Vegetative tiller plasticity had a greater reduction in AOPD in seasons characterized by greater spring and grain filling precipitation, greater growing degree day accumulation in the winter and during grain filling, and greater minimum temperature during the spring and maximum temperature during the winter **(Figure 2.11).** Grain filling maximum temperature was the only seasonal characteristic that led AOPD to increase with increases in vegetative tillering plasticity.

2.5 Discussion

The potential of wheat to produce tillers provides the crop with a buffer capacity on grain yield at plant density reduction (Bastos et al., 2020; Mitchell et al., 2013; Tokatlidis, 2014, 2017). We exposed a set of 24 commercial winter wheat genotypes to two contrasting seeding rates at 12 environments to create a range of plant densities and environmental conditions impacting tillering expression and grain yield to test hypotheses related to phenotypic plasticity of tillering reducing agronomic optimum plant density. Here, we quantified that, within the genotypes and environments evaluated, most of the reduction in AOPD increases in tillering plasticity were attributed to weather drivers allowing the vegetative tillers to become productive

(i.e., a higher allocation of carbohydrates to the grains). This study advances our understanding of the physiological mechanisms for winter wheat response to plant density at both the individual and crop levels. To our knowledge, this is the first report of environmental-specific phenotypic plasticity of vegetative tillering plasticity modulating AOPD in wheat.

2.5.1 Environment

The studied environments were warmer and drier than the historical weather averages for each respective location (except for three environments where grain fill temperatures were around average; **Appendix Figure 2.A.1**). The individual weather patterns indicated four environments with season-long drought, four environments with drought immediate pre-anthesis and followed by grain filling, and four environments where ETc and precipitation dynamics were similar **(Figure 2.2)**. These drought patterns are common in the study region (Couëdel et al., 2021; Sciarresi et al., 2019). Water deficit stress impacts the plant's metabolic regulation mechanisms and yield components differently depending on when they occur in reference to crop phenology (Sarto et al., 2017). Season-long drought impacts crop establishment, tillering, biomass production, and yield, pre-anthesis drought reduces kernel number. In contrast, grain filling drought reduces kernel weight. As it relates to our objectives, drought between jointing and anthesis (GS31– GS60) increased tiller mortality (Zhou et al., 2020) since there is enhanced competition for available resources for the increasing sink strength during this period; when developing leaves, stems, and spikes compete for the carbohydrate produced from solar radiation interception (Miralles & Slafer, 2007; Rosati & Benincasa, 2023; Slafer et al., 2023). Expectedly, the increase in tiller mortality correlated with higher ETo during the critical period **(Table 2.7)** and genotypes with higher phenotypic plasticity of vegetative tillering at the

individual level reduced AOPD in environments with high precipitation during spring and grain filling **(Figure 2.13)**.

2.5.2 Plant density and associated crop components

Seeding rate did not match the final plant density in our study, and differences were larger for high- versus low-seeding rate, which is common in seeding rate studies (Bastos et al., 2020; Destro et al., 2001; Jaenisch et al., 2022; Lollato et al., 2024; Tilley et al., 2019b). While it was beyond our objectives to understand the factors leading to this discrepancy, we note that it can be function of environmental factors such as adverse weather conditions around sowing (Lollato et al., 2024; Mehring et al., 2020), agronomic factors such as poor seedbed (Hanson & Lukach, 1992), or greater intraspecific competition in high seeding rates (Masle, 1985; Puckridge & Donald, 1967).

Plant density showed much clearer effects on response variables (i.e., vegetative and reproductive tillers, as well as grain yield) on a per plant versus per area basis **(Figure 2.4)**. The exponential decay of individual traits as function of plant density was observed previously (e.g., Mehring et al., 2020; Rodríguez-Casas et al., 2005). Rodríguez-Casas et al. (2005) reported an incidence of 135 to 4 tillers plant^{-1} at plant densities of 20 to 800 plants m^{-2} in irrigated spring wheat in northwest Mexico. We believe that the large tiller expression and steeper decay in their results as compared to ours are in part explained by the lack of water deficit in their irrigated trials, suggesting that plant density modifies the behavior of the individual plant response while the environment modulates the interval in which this modulation will occur.

At higher plant densities, there are less resources available per plant, which potentially limits the expression of tillers per plant. Beyond the competition for resources, more stressful

source-sink relations affect the plant's metabolic pathways. Under stress, the overexpression of auxin not only reduces the formation of new tillers (Beveridge, 2006; Dong et al., 2023; Hall & Mcwha, 1981; Ishikawa et al., 2005; Yao et al., 2021), but also increases main steam dominance, which increases the mortality of younger tillers (Zhang et al., 2009). Beyond auxin, other phytohormones (i.e., abscisic acid (ABA) and gibberellic acid (GA)) can be partially modulate plant's responses to water and competition stress (Hall & Mcwha, 1981; Lin et al., 2020).

The reduction in the number of dead tillers m^{-2} at lower plant densities in most of the environments (except for HAY23, LEO23, and PHB23 where it was statistically similar, data not shown), suggests that lower plant densities allowed each plant to be more efficient with regard to energy expenditure and resources obtained and used for grain production. In addition, the number of productive tillers was higher at lower seeding rates in four environments and similar in the remaining environments. In other words, lower plant densities were able to sustain a similar number of productive tillers per area resulting from more tillers per plant. These highlight the complex mechanisms driving the interactions between plant design and environment, both strong drivers of winter wheat trait expression.

2.5.3 Vegetative to reproductive tiller conversion

While the quantitative analysis of conversion efficiency from vegetative to reproductive tillers was ancillary to our objectives, it is a novel aspect of the current work advancing towards our understanding of wheat tillering physiology. The conversion of vegetative tillers into productive tillers was more efficient in lower than in higher plant densities, as indicated by greater slope and plateau, and lower breakpoint, of the linear-plateau regression of reproductive tillers as function of vegetative tillers per area **(Figure 2.6B, C)**. This suggests that the

partitioning of resources into the same plant is affected by the intraspecific competition for environmental resources, since each plant under lower seeding rates was more efficient in converting resources into yield components (spikes m^{-2}). This suggests that reduction in plant density and consequent alleviation of intraspecific competition can reduce the mortality rates and sustain a larger number of productive tillers and spikes per area.

These findings can be explained based on previous literature in tiller formation and survival. For instance, Rawson (1971) demonstrated that primary tillers contribute more than the younger tillers to wheat grain yield, with the four primary tillers and main stem accounting for ~68% to 95% of the plant's grain yield, depending on plant density and corresponding intraspecific competition (Destro et al., 2001; Rawson, 1971). This relation can be affected by other types of biotic inferences, such as disease incidence (Gautam et al., 2012). An interesting result in Rawson's work is that, in most of the cases, first and second tillers (T_1 and T_2), and in a few genotypes the third tiller (T_3), were more productive than the main stem at a density of 192 plants m^{-2}. This is perhaps explained by the fact that the coleoptile node is not the first node present on the axis as its growth and development are reduced by the physical resistance from the higher lignified coleoptile tissue (Avery, 1930; Klepper et al., 1982). Further literature in this subject suggests that the physical resistance from this more lignified coleoptile tissue depends on environmental, genetics, and their interactions determining its physiological drivers, such as auxin and abscisic acid production rates at initial growth stages (Beveridge, 2006; Dong et al., 2023; Hall & Mcwha, 1981; Ishikawa et al., 2005; Yao et al., 2021).

2.5.4 Vegetative tillering plasticity as an adaptive trait for winter wheat

Both at the individual and crop levels, tillering plasticity was agronomically adaptive since it associated with increased tiller production in high tillering environments and was neutral in low tillering environments **(Figure 2.7 and 8)**. We also note that there was greater tiller expression at low versus at high plant densities, evidenced by greater intercepts and slopes of the relationship of tillering plasticity versus vegetative tillers plant $^{-1}$, productive tillers plant^{-1}, grain yield plant^{-1}, and biomass plant^{-1} in environments with high trait expression. This suggests that high plant densities can limit the expression of the effect of vegetative tillering plasticity on these traits. Furthermore, the quadratic regression found at higher plant densities in the responsive environment for vegetative tillers m^{-2} **(Figure 2.7A)** suggests that high densities limit the production potential of vegetative tillers m^{-2} more in highly plastic varieties. These findings may indicate that phenotypic plasticity of tillering at the crop level maintains tolerance for competition in environments of higher intraspecific competition, but not at lower competition. While previous literature provided evidence for higher plant densities decreasing tiller production (e.g., Mehring et al., 2020; Rodríguez-Casas et al., 2005), to our knowledge this is the first report of higher densities reducing the expression of tillering plasticity.

The coefficient of vegetative tillering plasticity was highly correlated with the coefficient of productive tillering plasticity both at the crop and at the individual levels **(Figure 2.9).** This suggests an opportunity for crop breeders to phenotype and select for either trait, either at the population or individual levels, and still attain gains in the other traits at other biological levels of organization. However, because the genetic modulation of plasticity of a trait is partially independent of the trait per se (Alvarez Prado et al., 2014; Bradshaw, 1965; Diouf et al., 2020; Kusmec et al., 2018; Laitinen & Nikoloski, 2019; Reymond et al., 2003; Sadras, Lake, et al.,

2016), the quantification of whether phenotypic plasticity of tillering is a positive trait for other environments should be context-specific since our findings are constrained to the genetic pool of the 24 modern agronomically adapted winter wheat genotypes in the 12 environments evaluated.

2.5.5 Agronomic optimum plant density as function of environment and tillering plasticity

The Bayesian hierarchical model portrayed grain yield well, as a function of plant density and environment **(Figure 2.10)**, and of the interaction between plant density and phenotypic plasticity of vegetative tillering at the individual level within environment **(Figure 2.11)**. While there is extensive literature on G×E×M suggesting a genetic effect of wheat determining optimum plant density (Anderson & Barclay, 1991; Baker, 1982; Briggs & Ayten-Fisu, 1979; Khan et al., 2020; Lollato et al., 2024; Pendleton & Dungan, 1960), we believe this to be the first report of such analysis using Bayesian statistics coupled with the phenotypic plasticity framework. This approach and findings expand on previous work suggesting that a genotype's tillering potential and environmental variables were critical to define AOPD in wheat with broader implications by avoiding considering genotypes simply as a categorical variable and instead, as a quantifiable phenotypic plasticity coefficient.

Vegetative Tillering Phenotypic plasticity required specific environmental characteristics in order to be advantageous in reducing AOPD: The reduction in AOPD as function of phenotypic plasticity of tillering at the individual level was greater in seasons that had weather conditions more conducive to tiller formation and survival (e.g., greater precipitation during spring and grain filling, greater maximum temperature and GDD during the winter); on the other hand, greater maximum temperature during grain fill associated with increased AOPD of more

plastic varieties **(Figure 2.12)**. This aligns with the findings that phenotypic plasticity of tillering was an adaptive trait in high tillering environments **(Figures 2.7 and 2.8)**.

Spring precipitation matches the period when winter wheat is going through the jointing and anthesis stages of development (GS31 – GS69), a crucial period for tiller survival since water stress at jointing increases mortality and reduces biomass accumulation (Klepper et al., 1982; Musick & Dusek, 1980; Tilley et al., 2019a). Mortality of these tillers might occur at any time but more commonly from the jointing until anthesis stages of development when competing sinks result in plant prioritization of resource usage (Day & Intalap, 1970; Klepper et al., 1982; Musick & Dusek, 1980; Tilley et al., 2019a). Probably, environments with higher spring precipitation allowed genotypes to express their vegetative tillering production potential, justifying the reduction on AOPD for more plastic genotypes. Precipitation during grain filling may also have allowed greater expression of phenotypic plasticity, reducing AOPD through survival of later emerged tillers, allowing vegetative tillers not only to convert into productive tillers but also to allocate more carbohydrates in their spikes. The importance of precipitation and soil water available to wheat during grain fill is widely known (Gooding et al., 2003).

Warmer winters (i.e., accumulated GDD and maximum temperatures) increase tillers m^{-2}, above-ground biomass, and kernel weight in winter wheat (Hou et al., 2012), likely justifying the effect of winter temperatures allowing vegetative tillering phenotypic plasticity reduces winter wheat AOPD. Evidence suggests that higher temperatures during winter and early spring increase winter wheat grain yield by advancing phenology and mitigating leaf senescence (Du et al., 2022; He et al., 2020; Lollato, Roozeboom, et al., 2020; Paulsen & Heyne, 1983). These observations suggest a positive impact of warm winters and springs on the carbohydrate

ratio allocated to vegetative tillers during partitioning, again reducing the AOPD in function of individual vegetative tillering plasticity.

Brdar et al. (2008) demonstrated a quadratic plateau regression, with a positive slope in the relation between GDD at grain filling and grain dry weight, which may be associated with an early anthesis date that provides a gradual grain fill, avoiding the extremes of temperature and drought stress. The most interesting fact in this quadratic plateau regression is that the positive slope demonstrates that at grain filling the increment in the GDD probably allows an increment in the vegetative tillers' grain yield production reducing AOPD **(Figure 2.12C)**. The plateau demonstrates a limit in the response of this increment in higher levels of the accumulative temperature, which led us to the last regression.

Finally, maximum temperature at grain filling was the only weather driver identified in our analysis which increased AOPD in more plastic genotypes for vegetative tillering **(Figure 2.12E)**. Heat stress during grain filling is a critical limiting factor to wheat productivity (Cossani & Sadras, 2021; Jacott & Boden, 2020; Sadras et al., 2022) that interacts with water availability and is maximized during drought (Cossani and Sadras, 2021; Gooding et al., 2003; Tewolde et al., 2006). According to Cossani and Sadras (2021), elevated temperatures can be classified as (i) “non stressful”, where temperatures reduce yield mostly due to faster development; (ii) “stressful”, when temperatures disrupt reproduction; and (iii) elevated temperature increasing vapor pressure deficit and consequently reducing photosynthesis (Bonada and Sadras, 2015; Sadras and Dreccer, 2015). In the current work, ETo during grain filling reduced harvest index; allowing us to postulate that higher Tmax likely elevated vapor pressure deficit and impacted carbohydrate allocation in later tillers (more predominant in lower seeding rates and more plastic varieties).

2.6 Conclusion

This work proposes a phenotypic plasticity framework to analyze the effect of the phenotypic plasticity on AOPD. The weather drivers of this interaction exploit the effects of vegetative tillering plasticity at an individual plant and the crop level. Our findings have agronomic, breeding, and modeling implications: (i) Seeding rate models and tools, could be improved by accounting for the phenotypic tillering response for a more assertive or accurate seeding rate, reducing costs, increasing attainable grain yields, or both. (ii) Releasing that under growers' environmental conditions, individual vegetative tillering plasticity can be a tool in the reduction of seed costs, preserving similar yield rates. (iii) Dissecting and stating the genetic basis of winter wheat tillering phenotypic plasticity remains a challenge, as well as their interactions with other management practices. However, breeding programs may benefit from the fact that under unresponsive weather conditions, the selection of varieties may focus on other traits than vegetative tiller plasticity. On the other hand, in regions where the weather provides conditions to maximize yield at lower plant densities, this phenotype cannot be left aside. Also, the correlation between vegetative tillering phenotypic plasticity and the other winter wheat traits can be used to correlate varieties under different environments or small datasets for an empirical first approach of this trait for testing or developing varieties.

Table 2.1 Description of the twelve environments where field experiments were conducted, including year, location, site-year, longitude, latitude, elevation, soil type, previous crop, tillage, sowing date, number of blocks, departure from the optimum sowing date (OSD), cumulative fall temperature, cumulative fall precipitation, and total growing season water supply (WS).

Year	Location	Site Year	Lat.	Long.	Elev. (m)	Soil type	Previous crop	Tillage	Sowing date	Mean anthesis date	Harvest date	Blocks	Departure from OSD	Cumulative Fall Temp.	Cumulative Fall Prec.	Total growing season WS
2021 - 22	Belleville	BEL22	39.81	-97.67	466	Silty Clay Loam	Soybeans	No-till	10/7/2021	5/18/2022	7/11/2022	3	-3	619	61	492
2021 - 22	Great Bend	GRB22	38.36	-98.87	575	Silty Clay Loam	Soybeans	No-till	10/20/2021	5/10/2022	6/20/2022	3	-11	509	13	351
2021 - 22	Hays	HAY22	38.85	-99.34	616	Clay Loam	Fallow	Conv. till	9/28/2021	5/16/2022	6/23/2022	4	6	860	45	367
2021 - 22	Hutchinson (late)	HTL22	37.96	-98.12	498	Clay Loam	Soybeans	No-till	10/21/2021	5/7/2022	6/14/2022	3	-12	535	29	478
2021 - 22	Hutchinson	HTO22	37.92	-98.03	468	Loam	Terminated wheat	Conv. till	10/8/2021	5/6/2022	6/15/2022	4	1	756	78	415
2021 - 22	Leoti	LEO22	38.28	-101.23	981	Clay Loam	Fallow	No-till	9/25/2021	5/16/2022	7/5/2022	3	9	886	37	252
2022 - 23	Belleville	BEL23	39.81	-97.67	470	Silty Clay Loam	Soybeans	No-till	10/6/2022	5/17/2023	7/10/2023	3	-2	496	59	327
2022 - 23	Hays	HAY23	38.86	-99.34	612	Silty Clay Loam	Sorghum-fallow	Conv. till	9/29/2022	5/15/2023	6/27/2023	4	5	681	26	317
2022 - 23	Hoisington	HOI23	38.63	-98.87	598	Silty Clay Loam	Sorghum-fallow	No-till	9/28/2022	5/15/2023	6/28/2023	4	6	732	32	464
2022 - 23	Hutchinson	HUT23	37.93	-98.02	471	Loam	Terminated wheat	Conv. till	10/19/2022	5/10/2023	6/30/2023	4	-10	424	69	392
2022 - 23	Leoti	LEO23	38.27	-101.22	974	Clay Loam	Sorghum-fallow	No-till	9/27/2022	5/23/2023	7/12/2023	4	7	713	1	340
2022 - 23	Phillipsburg	PHB23	39.8	-99.33	617	Silty Clay Loam	Soybeans	No-till	9/29/2022	5/24/2023	7/22/2023	3	5	621	22	285

Table 2.2 Year of release (YOR), breeding program, alleles (Rht, Ppd-D1, Vrn-A1, Vrn-B1, vrn-D3, $2N^vS$), and phenotypic plasticity (unitless) of agronomic traits in 24 winter wheat commercial genotypes. Traits include vegetative tillers per m^2 (VTM), productive tillers per m^2 (PTM), grain yield per m^2 (GYM), and the same traits measured per plant (VTP, PTP, GYP) as well as harvest index (HI). Abbreviations: OGI, Oklahoma Genetics Inc.; AGP, Agripro, Syngenta; KSU-H, Kansas State University Hays; KSU-M, Kansas State University Manhattan; WB: Bayer Crop Science; DP, dual-purpose (graze plus grain); GO, grain-only.

Genotype	YOR	Breed. Prog.	Rht	Ppd-D1	Vrn-A1	Vrn-B1	vrn-D3	$2N^vS$	Phenotypic Plasticity (dimensionless)						
									VTM	PTM	GYM	VTP	PTP	GYP	HI
Bakers Ann	2018	OGI	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-late	vrnD3b-late	Neg.	0.65	0.94	1.09	1.06	1.30	1.38	1.05
Bob Dole	2017	AGP	rht-B1/rht-D1	Ppd-D1a_C67	vrn-A1a (early)	vrn-B1-late	vrnD3b-late	Pos.	1.00	0.77	0.91	0.63	0.51	0.55	0.71
DoubleStop CL Plus	2013	OGI	Rht-B1	Ppd-D1b_N	vrn-A1b (late)	vrn-B1-late	vrnD3a-early	Neg.	0.84	0.85	0.69	0.60	0.50	0.37	0.50
Duster	2006	OGI	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-late	vrnD3b-late	Neg.	0.99	1.15	1.05	0.90	0.99	1.10	1.07
Joe	2015	KSU-H	Rht-B1	Ppd-D1b_N	vrn-A1a (early)	vrn-B1-early	vrnD3a-early	Pos.	1.36	1.18	0.98	1.07	0.94	0.83	1.34
KS Ahearn	2021	KSU-M	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3a-early	Pos.	0.99	0.94	1.08	1.35	1.20	1.00	1.00
KS Dallas	2019	KSU-H	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3a-early	Pos.	0.79	0.77	1.08	0.55	0.63	0.95	0.9
KS Hamilton	2020	KSU-H	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3a-early	Pos.	1.08	1.08	0.93	1.53	1.22	1.00	0.81
KS Hatchett	2020	KSU-M	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3b-late	Pos.	1.14	1.08	0.99	1.22	1.48	1.10	1.05
KS Providence	2022	KSU-M	Rht-B1	Ppd-D1a_C67	vrn-A1a (early)	vrn-B1-early	vrnD3a-early	Neg.	0.88	0.75	1.05	0.64	0.71	0.81	1.14
KS Western Star	2019	KSU-H	Rht-B1	Ppd-D1b_N	vrn-A1b (late)	vrn-B1-late	vrnD3a-early	-	0.76	0.82	1.26	0.73	0.88	1.01	1.01

Larry	2016	KSU-M	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-late	vrnD3b-late	Pos.	1.30	1.13	1.11	1.31	1.23	1.01	0.80
OK Corral	2020	OGI	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3a-early	Neg.	0.9	0.61	0.87	1.44	0.92	1.26	1.07
Showdown	2018	OGI	Rht-B1	Ppd-D1b	vrn-A1b (late)	vrn-B1-late	vrnD3a-early	-	0.97	0.8	0.86	1.00	0.82	1.05	0.63
Smiths Gold	2017	OGI	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3b-late	Pos.	0.59	0.78	0.89	0.57	0.97	0.94	0.95
SY Monument	2014	AGP	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3b-late	Pos.	0.78	0.88	1.03	0.90	1.16	0.84	0.99
SY Wolverine	2019	AGP	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3a-early	Pos.	1.14	1.27	1.14	0.82	1.10	1.33	0.72
WB4269	2017	WB	Rht-B1	Ppd-D1a_C67	vrn-A1a (early)	vrn-B1-early	vrnD3a-early	Pos.	1.19	1.51	0.65	0.87	0.84	0.47	0.99
WB4303	2015	WB	Rht-B1	Ppd-D1a_C67	vrn-A1a (early)	vrn-B1-late	vrnD3a-early	Pos.	1.06	0.67	0.99	1.09	0.88	1.19	1.54
WB4401	2020	WB	Rht-D1	Ppd-D1a_C67	vrn-A1a (early)	vrn-B1-early	vrnD3b-late	Neg. / Pos.	0.80	0.81	0.94	0.65	0.82	0.97	0.93
WB4595	2018	WB	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3b-late	Neg.	1.37	1.10	1.06	1.60	1.12	1.23	0.67
WB4699	2018	WB	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3a-early	Pos.	1.10	0.91	1.05	1.45	1.42	1.35	0.69
WB4792	2018	WB	Rht-B1	Ppd-D1a_C67	vrn-A1b (late)	vrn-B1-early	vrnD3b-late	Pos.	1.00	0.88	1.23	1.17	0.98	1.25	0.75
Zenda	2016	KSU-M	Rht-D1	Ppd-D1a_C67	vrn-A1a (early)	vrn-B1-late	vrnD3b-late	Pos.	0.70	0.73	0.87	0.79	0.92	0.78	0.75

Table 2.3 Soil fertility measured at sowing in the 0-15 and 15-45 or 15-60 cm depths in each environment including organic matter (O.M.), pH, nitrate nitrogen (NO3–N), Mehlich-3 extractable phosphorus (P) and potassium (K), cation exchange capacity (CEC), soil texture (percent sand, silt and clay), and N rate applied to ensure 6 Mg ha^{-1} yield goal (N rate). For site-year abbreviation, please refer to Table 2.1.

Environment Site-year	Depth	OM	pH	NO_3-N	P	K	CEC	Sand	Silt	Clay	N rate
	cm	%		----------ppm----------			meq/100g		---------%---------		kg/ha
BEL22	0 to 15	2.7	5.1	17.5	76	572	25.3	20	56	24	137
BEL22	15 to 45	2.8	6.0	8.6	57	730	28.1	10	54	36	
GRB22	0 to 15	1.9	5.7	21.9	164	619	23.8	20	54	26	111
GRB22	15 to 45	1.3	7.2	12.9	57	558	27.7	20	40	40	
HAY22	0 to 15	1.8	6.0	26.4	76	709	25.1	18	52	30	68
HAY22	15 to 45	2	6.4	18.7	46	614	28.0	22	42	36	
HTL22	0 to 15	3.3	5.6	34.5	85	435	25.1	34	38	28	20
HTL22	15 to 45	2.3	5.9	21.2	52	386	26.7	26	44	30	
HTO22	0 to 15	1.6	6.7	37.7	47	214	15.2	38	42	20	0
HTO22	15 to 45	1.7	7.5	34.4	24	217	26.0	36	40	24	
LEO22	0 to 15	1.7	6.8	28.8	75	692	19.0	26	46	28	51
LEO22	15 to 45	1.8	7.4	20.9	33	677	26.3	26	43	31	
BEL23	0 to 15	2.7	5.1	4.8	35	398	22.9	11	63	26	201
BEL23	15 to 60	2.4	6.6	2.3	11	358	28.3	9	53	38	
HAY23	0 to 15	2.1	6.1	20.2	48	649	24.3	18	50	32	137
HAY23	15 to 60	1.8	7.4	5	23	505	27.6	14	49	37	
HOI23	0 to 15	2.7	5.2	34.6	29	499	22.4	19	57	24	139
HOI23	15 to 60	1.8	7.7	2.5	7	350	27.6	14	48	38	
HUT23	0 to 15	1.9	5.3	9.6	42	217	17.1	39	42	19	171
HUT23	15 to 60	1.9	7.3	3.3	11	200	25.3	34	40	26	
LEO23	0 to 15	2.0	6.6	10.9	45	776	23.0	24	48	28	161
LEO23	15 to 60	1.8	8.0	8.1	20	623	34.7	24	46	30	
PHB23	0 to 15	2.3	6.2	8.3	20	420	189.0	22	55	23	203
PHB23	15 to 60	1.8	7.5	1.4	7	459	25.5	15	51	34	

Table 2.4 Thermal Unit Crop Season Summary: Crop Phenological Dates (MM/DD/YY), anthesis date, critical period first day date, grain filling first day date, cumulated thermal unit °C d^{-1}, crop fall season, crop winter season, critical period, grain filling, and total season in each site-year at different locations in Kansas, U.S.A. Abbreviations: BEL, Belleville; GRB, Great Bend; HAY, Hays; MHT, Manhattan; HTL, Hutchinson Late sowing date; HTO, Hutchinson Optimum sowing date; HUT, Hutchinson; PHB, Phillipsburg; LEO, Leoti. Site-year abbreviation is followed by harvest year.

Environment Site-year	Critical Period First day	Grain Filling First day	Thermal Unit °C d^{-1}				
			Crop Fall Season	Crop Winter Season	Critical Period	Grain Filling	Total Season
BEL22	04/25/2022	05/28/2022	649	524	389	625	2186
GRB22	04/13/2022	05/15/2022	559	544	378	635	2116
HAY22	04/23/2022	05/24/2022	900	595	391	615	2501
HTL22	04/06/2022	05/12/2022	585	465	382	654	2085
HTO22	04/05/2022	05/12/2022	806	451	388	626	2271
LEO22	04/21/2022	05/26/2022	928	483	391	609	2411
BEL23	04/21/2023	05/25/2023	504	483	377	616	1982
HAY23	04/19/2023	05/23/2023	694	515	386	647	2241
HOI23	04/21/2023	05/24/2023	744	592	378	615	2329
HUT23	04/14/2023	05/17/2023	438	599	389	643	2070
LEO23	04/29/2023	05/30/2023	732	521	382	631	2266
PHB23	05/03/2023	05/31/2023	632	568	391	627	2218

Table 2.5 Meteorological Weather Season Summary: Mean Minimal Temperature (°C), Mean Maximal Temperature (°C), Cumulative precipitation (mm), Cumulative Grass evapotranspiration (Cumulative Eto, mm), incident solar radiation (Cumulative Solar Radiation, MJ m^{-2}), and Cumulative Growing degree days (°C D^{-1}) in each site-year at different locations in Kansas, U.S.A. Abbreviations: BEL, Belleville; GRB, Great Bend; HAY, Hays; MHT, Manhattan; HTL, Hutchinson Late sowing date; HTO, Hutchinson Optimum sowing date; HUT, Hutchinson; PHB, Phillipsburg; LEO, Leoti. Site-year abbreviation is followed by harvest year.

Env. Site-year	Season	Mean Minimum	Mean Maximum	Cumulative Precip.	Cumulative Eto	Cumulative Solar	Cumulative Growth
		----------°C ----------		---------- mm ----------		-- MJ m^{-2} --	--°C Day^{-1}--
BEL22	Fall	0.6	15.1	61	135	710	619
	Winter	-8.9	7.8	21	142	1010	236
	Spring	7.8	22.1	227	404	1840	1375
GRB22	Fall	0.6	16.2	13	136	664	540
	Winter	-6.8	10.4	24	185	1132	353
	Spring	9.5	23.8	216	503	2026	1531
HAY22	Fall	1.5	18.5	45	207	949	860
	Winter	-8.0	9.6	14	176	1094	297
	Spring	7.8	23.6	153	481	1955	1446
HTL22	Fall	0.9	16.0	29	121	606	535
	Winter	-6.7	10.7	16	169	1062	358
	Spring	9.2	22.8	288	386	1709	1373
HTO22	Fall	2.4	17.5	78	163	798	756
	Winter	-6.7	10.7	16	169	1062	358
	Spring	9.3	22.9	288	394	1735	1403
LEO22	Fall	1.2	18.7	37	247	901	886
	Winter	-7.8	8.6	9	162	906	271
	Spring	5.8	23.8	94	394	1850	1363
BEL23	Fall	-2.4	13.0	59	139	764	496
	Winter	-7.3	5.8	39	101	905	181
	Spring	7.1	23.1	71	410	1893	1391
HAY23	Fall	-1.3	16.0	26	211	947	681
	Winter	-7.2	7.9	30	129	973	218
	Spring	7.5	23.6	150	433	1879	1427
HOI23	Fall	0.3	15.7	32	207	1029	732
	Winter	-6.3	8.0	32	141	1036	249
	Spring	8.2	23.6	187	435	1940	1461
HUT23	Fall	-0.7	13.1	69	116	596	424
	Winter	-4.6	9.1	51	139	939	324
	Spring	9.2	24.0	243	406	1883	1523
LEO23	Fall	-1.4	16.5	1	227	774	713
	Winter	-7.8	7.6	10	125	746	203
	Spring	6.1	22.2	154	360	1507	1300
PHB23	Fall	-2.4	15.2	22	187	944	621
	Winter	-7.8	6.0	46	105	973	164
	Spring	6.9	23.0	127	415	1966	1375

Table 2.6 Meteorological Weather Crop Season Summary: Mean Minimal Temperature (°C), Mean Maximal Temperature (°C), Cumulative precipitation (mm), Cumulative Grass Evapotranspiration (Cumulative Eto, mm), incident solar radiation (Cumulative Solar Radiation, MJ m^{-2}), and Cumulative Growing degree days (°C d^{-1}) in each site-year at different locations in Kansas, U.S.A. Abbreviations: BEL, Belleville; GRB, Great Bend; HAY, Hays; MHT, Manhattan; HTL, Hutchinson Late sowing date; HTO, Hutchinson Optimum sowing date; HUT, Hutchinson; PHB, Phillipsburg; LEO, Leoti. Site-year abbreviation is followed by harvest year.

Env. Site-year	Meteorological Weather Season	Mean Minimal Temp.	Mean Maximal Temp.	Cumulative Precip.	Cumulative Eto	Cumulative Solar Radiation	Cumulative Growth Degree Days
		----------°C ----------		---------- mm ----------		-- MJ m^{-2} --	-°C Day^{-1}-
BEL22	Crop Fall	-0.2	14.6	61	146	784	649
	Crop Winter	-6.0	10.3	44	270	1584	524
	Critical Period	9.6	22.1	168	132	620	523
	Grain Filling	16.0	30.3	36	158	667	625
GRB22	Crop Fall	-0.2	16.0	13	154	744	590
	Crop Winter	-4.9	11.8	55	274	1512	544
	Critical Period	8.6	23.0	52	171	701	506
	Grain Filling	13.8	27.2	133	182	721	635
HAY22	Crop Fall	0.7	17.9	45	225	1030	900
	Crop Winter	-5.3	11.9	36	312	1699	595
	Critical Period	8.9	24.5	60	162	674	518
	Grain Filling	14.7	29.3	72	173	619	615
HTL22	Crop Fall	0.1	15.8	29	136	679	585
	Crop Winter	-5.3	11.3	44	209	1259	465
	Critical Period	7.1	21.6	64	163	706	515
	Grain Filling	14.2	26.7	196	155	695	654
HTO22	Crop Fall	1.5	17.1	78	178	870	806
	Crop Winter	-5.4	11.2	44	205	1244	451
	Critical Period	7.0	21.5	64	166	722	526
	Grain Filling	14.0	26.4	196	148	668	626
LEO22	Crop Fall	0.4	18.1	37	269	970	928
	Crop Winter	-5.9	10.8	11	262	1423	496
	Critical Period	6.5	23.8	73	150	689	531
	Grain Filling	13.7	31.4	20	139	620	609
BEL23	Crop Fall	-3.7	11.4	59	145	835	504
	Crop Winter	-4.3	10.0	49	225	1426	483
	Critical Period	7.1	22.3	32	144	708	499
	Grain Filling	14.3	29.7	32	148	643	616
HAY23	Crop Fall	-2.6	14.6	27	219	1021	694
	Crop Winter	-4.3	11.5	41	257	1477	515

	Critical Period	7.0	23.3	62	159	690	514
	Grain Filling	14.4	28.7	77	152	647	647
HOI23	Crop Fall	-1.0	14.2	34	216	1114	744
	Crop Winter	-3.4	12.1	45	281	1608	592
	Critical Period	7.9	22.6	67	148	687	503
	Grain Filling	15.1	28.8	110	143	619	615
HUT23	Crop Fall	-2.0	11.6	71	125	677	438
	Crop Winter	-2.2	12.4	50	236	1349	599
	Critical Period	8.3	23.0	71	149	654	516
	Grain Filling	14.1	27.4	157	135	657	643
LEO23	Crop Fall	-2.5	15.4	1	239	827	732
	Crop Winter	-4.9	11.2	34	271	1332	534
	Critical Period	9.2	24.1	57	119	514	516
	Grain Filling	14.2	27.8	86	125	512	631
PHB23	Crop Fall	-3.6	13.8	25	194	1016	632
	Crop Winter	-4.3	10.7	52	288	1826	568
	Critical Period	10.8	25.7	47	126	583	512
	Grain Filling	15.1	29.7	76	148	657	627

Table 2.7 Correlations between mean environmental winter wheat traits averaged across twenty-four varieties, and average or cumulative values of environmental factors during specific crop development periods for the 12 studied Kansas environments. All correlations have d.f. = 11. Abbreviations: GDD, growing degree days (°C d^{-1}); Tmax, maximum temperature (°C); Tmin, minimum temperature (°C); Precip., precipitation (mm); Rad., incident solar radiation (MJ m^{-2}); ETo, reference evapotranspiration (mm).

Crop Variable	Developmental window	Environmental Factor	Correlation	p-value
Grain Yield Kg m^{-2}	Critical Period	GDD	0.62	0.030
	Critical Period	Precipitation	0.55	0.070
	Critical Period	Radiation	-0.55	0.060
Spikes Kg m^{-2}	Crop Fall	Tmax	0.54	0.070
	Critical Period	GDD	0.79	<0.001
	Critical Period	Precipitation	0.56	0.060
	Crop Winter	Precipitation	-0.54	0.070
	Crop Winter	Tmin	-0.57	0.050
Productive Tillers m^{-2}	Crop Fall	GDD	0.53	0.080
	Crop Fall	Tmax	0.58	0.050
	Crop Winter	Precipitation	-0.59	0.040
	Crop Winter	Tmin	-0.55	0.060
Vegetative Tillers m^{-2}	Crop Fall	GDD	0.70	0.010
	Crop Fall	Tmax	0.89	<0.001
	Crop Fall	Tmin	0.83	<0.001
	Crop Winter	Precipitation	-0.58	0.050
	Crop Winter	Tmin	-0.63	0.030
Spikes $plant^{-1}$	Crop Fall	GDD	0.62	0.030
	Crop Fall	Tmax	0.65	0.020
	Crop Fall	Tmin	0.59	0.050
	Critical Period	GDD	0.85	<0.001
	Crop Winter	Precipitation	-0.57	0.050
Productive Tillers $plant^{-1}$	Crop Fall	GDD	0.62	0.030
	Crop Fall	Tmax	0.64	0.030
	Crop Fall	Tmin	0.58	0.050
	Crop Winter	Precipitation	-0.58	0.050
Vegetative Tillers $plant^{-1}$	Crop Fall	GDD	0.70	0.010
	Crop Fall	Tmax	0.80	<0.001
	Crop Fall	Tmin	0.82	<0.001
	Crop Winter	Precipitation	-0.51	0.090
Mortality Rate	Critical Period	ETo	0.72	0.010
	Critical Period	Radiation	0.79	<0.001
	Critical Period	Tmin	-0.51	0.090

Harvest Index	Crop Fall	Tmax	-0.51	0.090
	Crop Fall	Tmin	-0.60	0.040
	Critical Period	ETo	-0.71	0.010
	Critical Period	Radiation	-0.66	0.020
	Grain Filling	ETo	-0.60	0.040
	Grain Filling	Radiation	-0.52	0.080

Table 2.8 Two-way ANCOVA winter wheat traits in the function of the fixed and random effects.

	Vegetative Tillers m^{-2}	**Productive Tillers m^{-2}**	**Biomass m^{-2}**	**Grain Yield Kg m^{-2}**	**Vegetative Tillers $plant^{-1}$**	**Productive Tillers $plant^{-1}$**	**Biomass $plant^{-1}$**	**Grain Yield g $plant^{-1}$**	**Effective Tiller Rate**
Fixed Effects	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value
(Intercept)	0.002	<0.001	<0.001	<0.001	0.002	<0.001	<0.001	<0.001	<0.001
Plant density (PD)	<0.001	<0.001	0.827	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Genotype (G)	0.016	0.058	<0.001	<0.001	0.246	0.625	0.333	0.439	0.523
Environment (E)	0.001	<0.001	<0.001	<0.001	0.965	0.033	0.889	0.707	0.940
G × E	<0.001	<0.001	0.120	<0.001	<0.001	0.694	0.895	0.628	<0.001

Table 2.9 Estimated parameter and significance levels in multiple exponential decay regression analyses between plant density (plants m^{-2}) and individual traits (responsible variables) in each environment.

Resp. Variable (trait plant^{-1})	Environm.	Mean Plant Density (plant m^{-2})	Mean y	$y = a/(1+x^b)$		r^2
				a	b	
Vegetative Tillers plant^{-1}	BEL22	217.8	3.9	9.5	0.1	0.70
	GRB22	191.9	5.6	12.7	0.1	0.50
	HAY22	144.1	7.4	15.4	0.1	0.60
	HTL22	166.5	4.3	9.8	0.1	0.54
	HTO22	109.3	12.5	30.4	0.1	0.74
	LEO22	146.9	9.8	20.7	0.1	0.63
	BEL23	161.0	1.4	4.3	0.1	0.13
	HAY23	205.8	3.3	16.3	0.1	0.57
	HOI23	153.4	3.9	13.3	0.1	0.74
	HUT23	141.2	3.8	8.9	0.1	0.54
	LEO23	180.0	5.0	12.6	0.1	0.69
	PHB23	199.1	2.1	6.7	0.1	0.51
Productive Tillers plant^{-1}	BEL22	217.9	3.7	9.5	0.1	0.76
	GRB22	191.1	2.5	6.9	0.1	0.64
	HAY22	144.2	3.9	10.5	0.1	0.57
	HTL22	164.8	2.1	5.3	0.1	0.66
	HTO22	109.2	6.3	16.1	0.1	0.72
	LEO22	146.3	5.3	10.9	0.1	0.71
	BEL23	156.0	1.2	4.8	0.1	0.30
	HAY23	203.8	2.6	12.1	0.1	0.57
	HOI23	148.9	1.8	6.5	0.1	0.53
	HUT23	141.2	3.3	7.5	0.1	0.65
	LEO23	180.2	5.0	14.2	0.1	0.75
	PHB23	200.2	2.1	5.9	0.1	0.79
Grain Yield g plant^{-1}	BEL22	217.0	3.4	7.4	0.1	0.83
	GRB22	192.9	1.8	4.4	0.1	0.65
	HAY22	145.1	3.1	8.3	0.1	0.66
	HTL22	165.7	2.0	4.7	0.1	0.74
	HTO22	109.2	4.6	12.0	0.1	0.78
	LEO22	146.8	3.5	7.6	0.1	0.81
	BEL23	159.9	1.4	4.3	0.1	0.36
	HAY23	208.9	2.2	6.7	0.1	0.47
	HOI23	153.2	1.3	4.1	0.1	0.48
	HUT23	140.2	3.0	7.2	0.1	0.71
	LEO23	178.5	5.1	14.3	0.1	0.78

	PHB23	202.5	1.5	4.6	0.1	0.65
Spikes plant^{-1}	BEL22	217.9	4.7	10.5	0.1	0.76
	GRB22	191.1	3.5	7.9	0.1	0.65
	HAY22	144.2	4.9	11.5	0.1	0.57
	HTL22	165.8	3.1	6.3	0.1	0.67
	HTO22	109.2	7.3	17.1	0.1	0.72
	LEO22	146.3	6.3	11.9	0.1	0.71
	BEL23	160.0	2.0	5.8	0.1	0.29
	HAY23	205.0	3.5	13.1	0.1	0.56
	HOI23	153.3	2.7	7.5	0.1	0.56
	HUT23	141.7	4.3	8.5	0.1	0.65
	LEO23	180.2	6.0	15.2	0.1	0.76
	PHB23	201.6	3.0	6.9	0.1	0.82

Table 2.10 Linear regression between winter wheat traits m^{-2} (response variable), Vegetative Tillers m^{-2}, Productive Tillers m^{-2}, Spikes m^{-2}, Grain Yield Kg m^{-2} as a function of plant density (plants m^{-2}) in each environment.

Resp. Variable	Environm.	Mean y	y = a + bx		p-value	r^2
			a	b		
Vegetative Tillers m^{-2}	BEL22	693.6	636.7	0.26277	0.120	0.020
	GRB22	945.1	670.2	1.44423	<0.01	0.200
	HAY22	917.1	726.0	1.34683	<0.01	0.120
	HTL22	614.2	516.4	0.59330	<0.01	0.050
	HTO22	1177.7	1149.3	0.26287	0.550	<0.01
	LEO22	1249.5	1078.9	1.16726	<0.01	0.060
	BEL23	195.3	90.3	0.67207	<0.01	0.220
	HAY23	552.5	534.8	0.08692	0.620	<0.01
	HOI23	447.5	424.5	0.15843	0.220	<0.01
	HUT23	468.2	379.9	0.63124	<0.01	0.080
	LEO23	706.3	644.1	0.35650	0.030	0.030
	PHB23	334.9	359.9	-0.12659	0.360	<0.01
Productive Tillers m^{-2}	BEL22	646.6	647.2	-0.00292	0.980	<0.01
	GRB22	387.9	450.9	-0.33063	0.010	0.040
	HAY22	457.3	492.3	-0.24678	0.150	0.010
	HTL22	283.6	339.7	-0.34061	<0.01	0.070
	HTO22	588.4	601.2	-0.11906	0.610	<0.01
	LEO22	661.4	629.0	0.22166	0.340	<0.01
	BEL23	144.5	146.9	-0.01491	0.890	<0.01
	HAY23	419.0	393.9	0.12388	0.390	<0.01
	HOI23	195.3	232.9	-0.25907	<0.01	0.040
	HUT23	397.8	408.1	-0.07409	0.590	<0.01
	LEO23	681.2	709.1	-0.16010	0.280	<0.01
	PHB23	298.2	398.1	-0.50643	<0.01	0.250
Spikes m^{-2}	BEL22	863.2	647.2	0.99708	<0.01	0.309
	GRB22	578.3	450.9	0.66937	<0.01	0.153
	HAY22	599.2	492.3	0.75322	<0.01	0.094
	HTL22	448.5	339.7	0.65939	<0.01	0.219
	HTO22	696.6	601.2	0.88094	<0.01	0.068
	LEO22	803.4	643.7	1.10004	<0.01	0.142
	BEL23	300.7	146.9	0.98509	<0.01	0.411
	HAY23	614.1	412.0	1.00672	<0.01	0.220
	HOI23	338.2	234.7	0.71568	<0.01	0.242
	HUT23	535.2	414.9	0.86495	<0.01	0.178
	LEO23	855.6	709.1	0.83990	<0.01	0.161
	PHB23	492.6	403.2	0.45569	<0.01	0.228

Grain Yield Kg m^{-2}	BEL22	0.5	0.5	0.00022	<0.01	0.220
	GRB22	0.2	0.2	0.00005	0.140	0.020
	HAY22	0.3	0.3	0.00008	0.150	0.010
	HTL22	0.3	0.2	0.00011	0.030	0.030
	HTO22	0.4	0.4	0.00019	<0.01	0.050
	LEO22	0.3	0.3	0.00016	<0.01	0.050
	BEL23	0.1	0.1	0.00034	<0.01	0.390
	HAY23	0.4	0.3	0.00023	<0.01	0.090
	HOI23	0.2	0.1	0.00008	0.050	0.020
	HUT23	0.3	0.3	0.00008	0.170	0.010
	LEO23	0.6	0.6	-0.00017	<0.01	0.070
	PHB23	0.2	0.2	-0.00006	0.060	0.030

Table 2.11 Estimated parameter and significance levels in multiple linear regression analysis between winter wheat traits m^{-2} (response variable) as a function of vegetative tiller $plant^{-1}$ and productive tiller $plant^{-1}$ in each environment.

Predict Variable	Environmental	Resp. Variable	Mean y	y = a + bx		p-value	r^2
				a	b		
Vegetative Tillers $plant^{-1}$	BEL22	Grain Yield g $plant^{-1}$	3.3	0.4	0.73641	<0.001	0.76
	GRB22		1.8	0.2	0.28914	<0.001	0.41
	HAY22		3.1	-0.2	0.44331	<0.001	0.59
	HTL22		2	0.2	0.40796	<0.001	0.59
	HTO22		4.6	0.2	0.35078	<0.001	0.67
	LEO22		3.5	0.3	0.32382	<0.001	0.64
	BEL23		1.4	0.7	0.51366	<0.001	0.24
	HAY23		2.2	0.6	0.53556	<0.001	0.61
	HOI23		1.3	0.2	0.27444	<0.001	0.53
	HUT23		3	0.7	0.61118	<0.001	0.54
	LEO23		5.2	0.3	0.97243	<0.001	0.69
	PHB23		1.5	0.5	0.50634	<0.001	0.45
	BEL22	Grain Yield Kg m^{-2}	0.5	0.5	-0.00564	0.005	0.06
	GRB22		0.2	0.2	-0.00101	0.421	<0.01
	HAY22		0.3	0.3	0.00086	0.430	<0.01
	HTL22		0.3	0.2	0.00382	0.057	0.03
	HTO22		0.4	0.4	-0.00044	0.392	<0.01
	LEO22		0.3	0.4	-0.00178	0.049	0.03
	BEL23		0.1	0.1	-0.00333	0.430	<0.01
	HAY23		0.4	0.4	-0.00426	0.120	0.01
	HOI23		0.2	0.2	-0.00202	0.101	0.01
	HUT23		0.3	0.3	-0.00014	0.955	<0.01
	LEO23		0.6	0.6	0.00627	<0.001	0.08
	PHB23		0.2	0.2	0.00225	0.297	<0.01
Productive Tillers $plant^{-1}$	BEL22	Grain Yield g $plant^{-1}$	3.3	0.4	0.80161	<0.001	0.88
	GRB22		1.8	0.1	0.66578	<0.001	0.77
	HAY22		3.1	0.4	0.71614	<0.001	0.8
	HTL22		2	0.5	0.72710	<0.001	0.69
	HTO22		4.6	0.2	0.69542	<0.001	0.82
	LEO22		3.5	0.2	0.62232	<0.001	0.78
	BEL23		1.5	0.5	0.82746	<0.001	0.83
	HAY23		2.3	0.5	0.74370	<0.001	0.79
	HOI23		1.3	0.3	0.58275	<0.001	0.79
	HUT23		3.1	0.5	0.76453	<0.001	0.82
	LEO23		5.2	0.3	0.95690	<0.001	0.85
	PHB23		1.5	0.2	0.63831	<0.001	0.74
	BEL22	Grain Yield	0.5	0.6	-0.00719	<0.001	0.09

GRB22	Kg m^{-2}	0.2	0.2	0.00055	0.787	<0.01
HAY22		0.3	0.3	0.00373	0.012	0.03
HTL22		0.3	0.3	-0.00015	0.966	<0.01
HTO22		0.4	0.4	-0.00118	0.197	<0.01
LEO22		0.3	0.4	-0.0018	0.244	<0.01
BEL23		0.1	0.1	-0.01022	0.006	0.06
HAY23		0.4	0.4	-0.00451	0.190	<0.01
HOI23		0.2	0.2	-0.00004	0.985	<0.01
HUT23		0.3	0.3	0.00316	0.202	0.01
LEO23		0.6	0.6	0.00403	0.007	0.04
PHB23		0.2	0.2	0.00434	0.037	0.03

Table 2.12 Estimated parameter and significance levels in multiple linear regression analysis between winter wheat traits m^{-2} (response variable) as a function of vegetative tiller m^{-2} and productive tiller m^{-2} in each environment.

Predict Variable	Environmental	Resp. Variable	Mean y	y = a + bx		p-value	r^2
				a	b		
Vegetative Tillers m^{-2}	BEL22	Grain Yield g $plant^{-1}$	3.4	3.1	0.00037	0.600	<0.01
	GRB22		1.8	3.0	-0.00128	<0.01	0.110
	HAY22		3.1	4.2	-0.00116	0.030	0.030
	HTL22		2.0	2.1	-0.00022	0.620	<0.01
	HTO22		4.6	4.0	0.00052	0.440	<0.01
	LEO22		3.5	4.3	-0.00061	0.200	0.010
	BEL23		1.4	1.7	-0.00110	0.130	0.020
	HAY23		2.2	1.3	0.00170	<0.01	0.090
	HOI23		1.3	0.8	0.00108	0.030	0.030
	HUT23		3.0	3.5	-0.00100	0.220	<0.01
	LEO23		5.2	6.2	-0.00133	0.280	<0.01
	PHB23		1.5	1.4	0.00034	0.530	<0.01
	BEL22	Grain Yield Kg m^{-2}	0.5	0.5	0.00008	<0.01	0.110
	GRB22		0.2	0.2	0.00000	0.730	<0.01
	HAY22		0.3	0.2	0.00004	<0.01	0.050
	HTL22		0.3	0.2	0.00012	<0.01	0.250
	HTO22		0.4	0.3	0.00005	<0.01	0.100
	LEO22		0.3	0.3	0.00003	0.030	0.030
	BEL23		0.1	0.1	0.00013	<0.01	0.120
	HAY23		0.4	0.3	0.00007	<0.01	0.050
	HOI23		0.2	0.1	0.00004	0.070	0.020
	HUT23		0.3	0.3	0.00005	0.070	0.020
	LEO23		0.6	0.6	0.00001	0.550	<0.01
	PHB23		0.2	0.2	-0.00003	0.090	0.020
Productive Tillers m^{-2}	BEL22	Grain Yield g $plant^{-1}$	3.4	1.7	0.00264	<0.01	0.050
	GRB22		1.8	0.5	0.00334	<0.01	0.190
	HAY22		3.1	1.0	0.00463	<0.01	0.160
	HTL22		2.0	0.9	0.00404	<0.01	0.150
	HTO22		4.6	1.8	0.00491	<0.01	0.080
	LEO22		3.5	2.8	0.00113	0.170	0.010
	BEL23		1.5	0.7	0.00605	<0.01	0.330
	HAY23		2.3	1.0	0.00307	<0.01	0.180
	HOI23		1.3	0.5	0.00454	<0.01	0.260
	HUT23		3.1	1.2	0.00485	<0.01	0.140
	LEO23		5.2	1.6	0.00541	<0.01	0.090
	PHB23		1.5	-0.2	0.00566	<0.01	0.300
	BEL22	Grain Yield	0.5	0.5	0.00005	0.070	0.020

GRB22	Kg m^{-2}	0.2	0.2	0.00005	0.020	0.040
HAY22		0.3	0.2	0.00012	<0.01	0.150
HTL22		0.3	0.2	0.00008	0.030	0.030
HTO22		0.4	0.4	0.00006	<0.01	0.060
LEO22		0.3	0.3	0.00008	<0.01	0.100
BEL23		0.1	0.1	0.00006	0.150	0.020
HAY23		0.4	0.3	0.00010	<0.01	0.060
HOI23		0.2	0.1	0.00008	<0.01	0.040
HUT23		0.3	0.2	0.00020	<0.01	0.180
LEO23		0.6	0.6	0.00001	0.630	<0.01
PHB23		0.2	0.2	0.00006	0.030	0.040

Table 2.13 Estimated parameter and significance levels in regression analysis between productive tiller as a function of vegetative tiller in each environment. Linear regression at the individual level (tillers plant^{-1}) and linear plateau at crop level (tillers m^{-2}) at higher and lower plant density.

Predict Variable	Resp. Variable	Mean y	y = a + bx, when y < xs			r^2	SE b	SE xs	p-value b	p-value xs
			a	b	xs (Breakpoint)					
Vegetative Tiller plant^{-1}	Productive Tiller plant^{-1}	5.4	0	1.5	-	0.87	0.013	-	<0.001	-
Vegetative Tiller m^{-2} at higher plant density	Productive Tiller m^{-2}	427.6	0	0.7	869	0.34	0.013	22.5	<0.001	<0.001
Vegetative Tiller m^{-2} at lower plant density	Productive Tiller m^{-2}	445.0	0	0.8	793	0.47	0.012	17.3	<0.001	<0.001

Table 2.14 ANOVA Winter wheat traits average in the function of markers as fixed effects and as genotypes as random effects. Traits' data as Grain Yield Kg m-2; Veg. Tillers m-2, Vegetative tillering m-2; Produc. Tillers m-2, Productive Tillers m-2; Grain Yield g plant-1; Veg. Tillers plant-1, Vegetative tillering plant-1; and Produc. Tillers plant-1, Productive Tillers plant-1, is from estimated marginal means. Traits' data as Mean CVTPP, Mean Crop Vegetative Tillering Phenotypic Plasticity; and Mean IVTPP, Mean Individual Vegetative Tillering Phenotypic Plasticity are from the variance ratio calculus (one value per genotype), are dimensionless, and do not have an environmental or random effect in ANOVA. Agronomical Optimum Plant Density, AOPD (plants m-2); values were estimated based on the Bayesian approach (one value per genotype-environment interaction).

Trait	Alleles	Population Incidence (%)	Grain Yield Kg m^{-2}	Veg. Tillers m^{-2}	Produc. Tillers m^{-2}	Mean CVTPP	Grain Yield g $plant^{-1}$	Veg. Tillers $plant^{-1}$	Produc. Tillers $plant^{-1}$	Mean IVTPP	AOPD (plants m^{-2})
Rht	Rht-B1	87.5	0.317a	700a	435a	0.995a	2.76a	5.32a	3.35a	1.040a	78a
	Rht-D1	8.3	0.304a	630a	404a	0.749a	2.64a	4.86a	3.19a	0.721a	82a
	rht-B1/rht-D1	4.2	0.303a	641a	391a	1.001a	2.61a	4.86a	3.01a	0.633a	83a
Ppd-D1	Ppd-D1a_C67 (Ciano67)	83.3	0.315a	688a	431a	0.973a	2.75a	5.24a	3.33a	1.026a	78a
	Ppd-D1b	4.2	0.327a	639a	353a	0.967a	2.79a	4.82a	2.67a	0.998a	79a
	Ppd-D1b_N (Norstar)	12.5	0.319a	734a	452a	0.988a	2.69a	5.52a	3.44a	0.797a	81a
Vrn-	vrn-A1a (early)	29.2	0.308a	678a	409a	0.998a	2.61b	5.09a	3.12a	0.821a	81a
	vrn-A1b (late)	70.8	0.319a	697a	439a	0.965a	2.80a	5.33a	3.4a	1.069a	78a
Vrn-	vrn-B1-early	62.5	0.322a	704a	445a	1.008a	2.81a	5.36a	3.43a	1.054a	78a
	vrn-B1-late	37.5	0.305b	670a	407a	0.919a	2.64b	5.09a	3.13a	0.900a	80a
vrn-	vrnD3a-early	54.2	0.319a	706a	432a	1.005a	2.77a	5.36a	3.31a	1.010a	78a
	vrnD3b-late	45.8	0.312a	674a	429a	0.939a	2.72a	5.15a	3.32a	0.981a	79a
$2N^vS$	Negative	28.0	0.309a	673a	421a	0.920a	2.78a	5.14a	3.26a	0.985a	79a
	Positive	64.0	0.317a	699a	437a	1.001a	2.73a	5.31a	3.37a	0.997a	79a

Table 2.15 Linear correlation between weather drivers to individual vegetative tillering plasticity modulating agronomic optimal plant density.

Period	Measurement	Slope	p-value	r^2
Spring	Precipitation	-0.07748	0.002036	0.63
Grain Filling	Precipitation	-0.08129	0.009409	0.51
Spring	Tmin	-3.84248	0.012843	0.48
Winter	Tmax	-2.83667	0.015267	0.46
Grain Filling	GDD	-0.32454	0.020911	0.43
Winter	GDD	-0.06379	0.023434	0.42
Grain Filling	Tmax	2.785012	0.030257	0.39

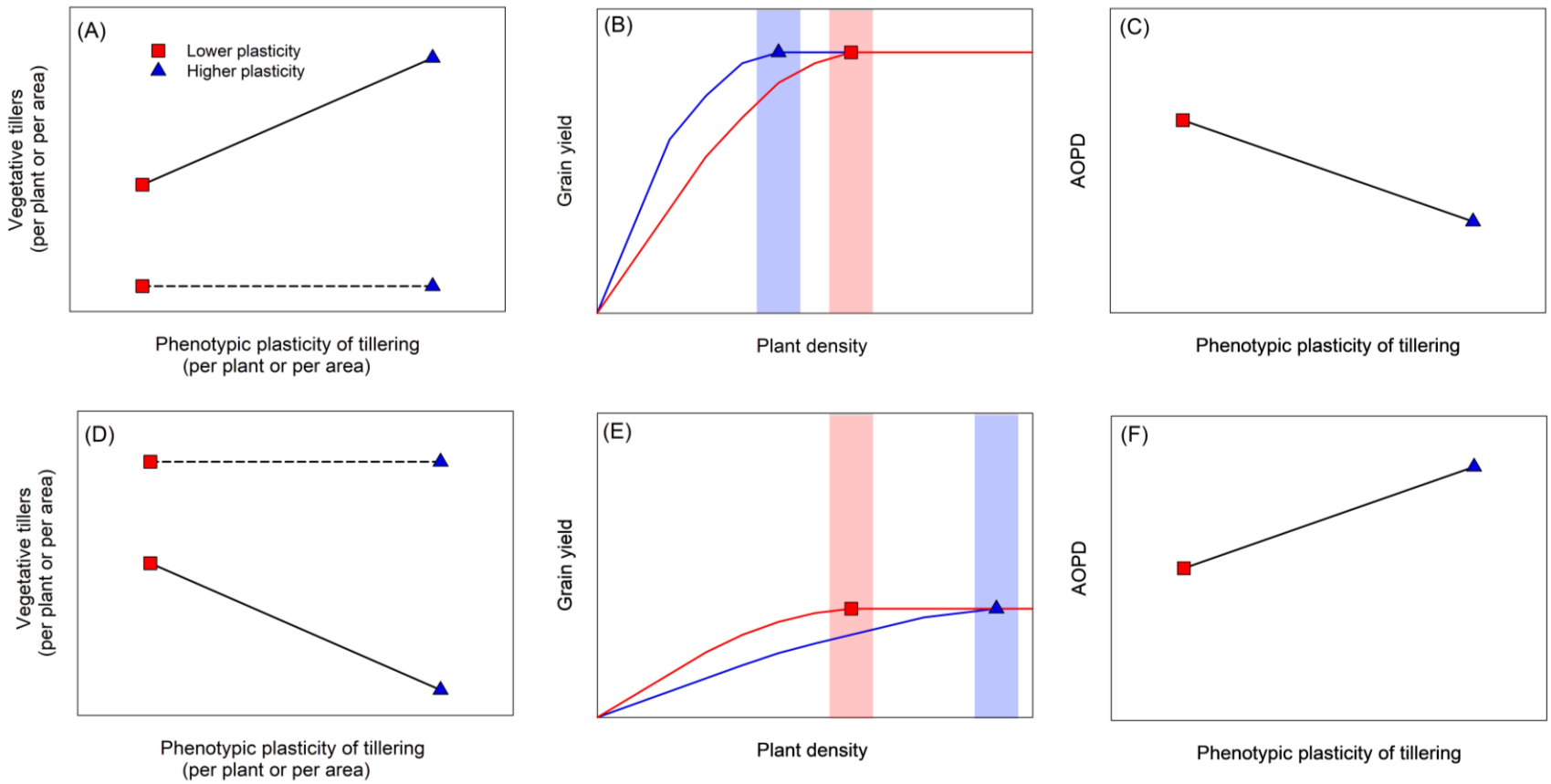

Figure 2.1 | Hypothesized interaction between vegetative tillering phenotypic plasticity and agronomic optimum plant density (AOPD). Panels A-C depict tillering plasticity as a positive trait, correlating positively with tiller production in high tillering environments (solid line in Panel A) and showing no tradeoff in low tillering environments (dashed line in Panel A). Stability is conferred by lower tillering potential in high tillering environments (red marker). As a positive trait, AOPD (hachured area in Panel B) is lower for the more plastic cultivar (blue marker) than for the stable cultivar and, when plotted across cultivars (Panel C), AOPD reduces with increases in phenotypic plasticity of tillering. Panels D-F depict phenotypic plasticity as a negative trait, where tillering expression in high tiller environments is similar for plastic and stable cultivars (dashed line in Panel D) but the more plastic cultivar has tiller expression reduced in low tiller environments (solid line in Panel D). Therefore, AOPD for the more plastic cultivar is greater than for the more stable cultivar (Panels E and F).

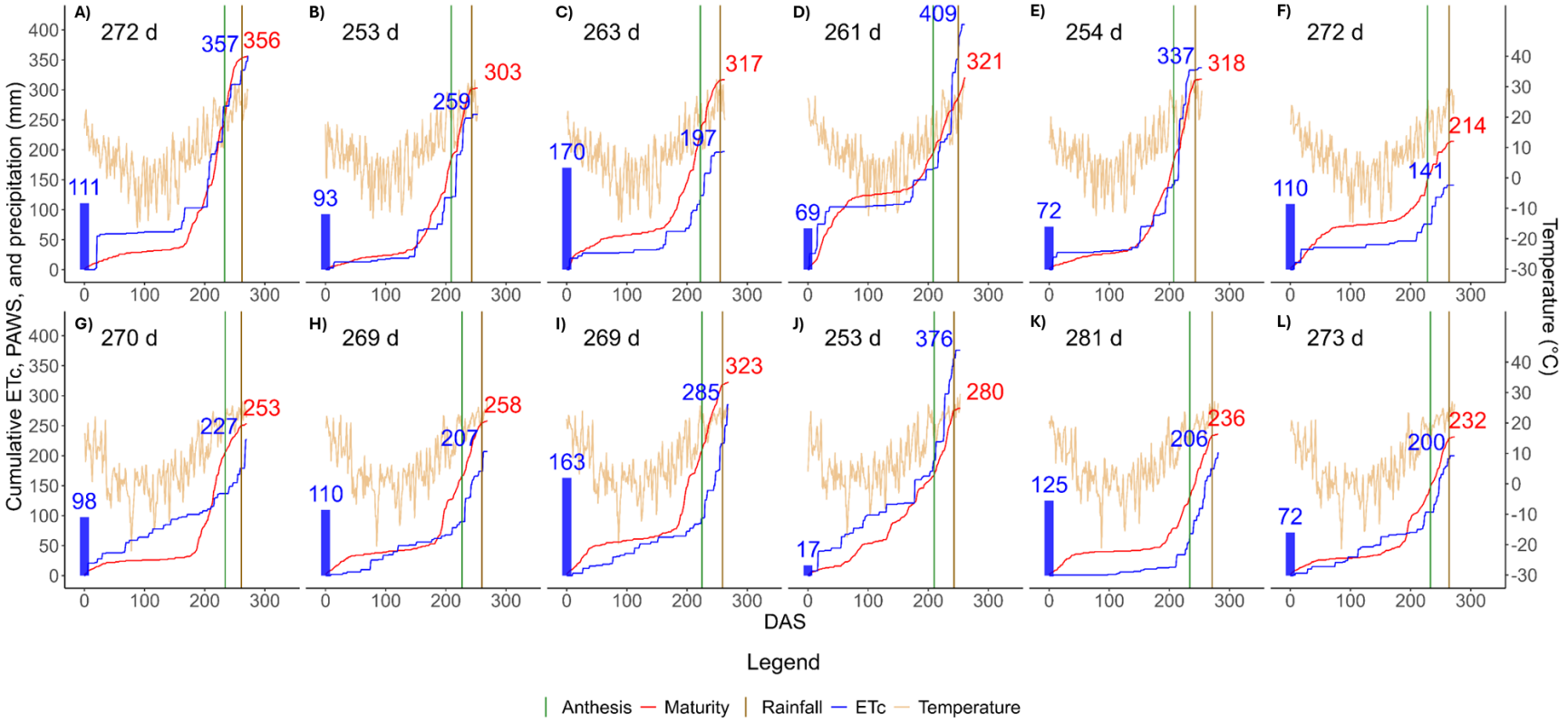

Figure 2.2 | Weather conditions experienced during the winter wheat-growing season at the twelve Kansas environments including BEL22 (A), GRB22 (B), HTL22 (C), HTO22 (D), HAY22 (E), LEO22 (F), BEL23 (G), HAY23 (H), HOI23 (I), HUT23 (J), LEO23 (K), and PHB23 (L). Plant available water at sowing (PAWS, blue bars and associated numbers), precipitation (blue lines and numbers), cumulative simulated crop evapotranspiration (ETc, red lines and numbers), crop season length (black numbers), and mean temperature (yellow lines) are shown. The green vertical lines denote anthesis date (Zadoks 60), and the brown vertical lines denote the end of grain filling (Zadoks 90).

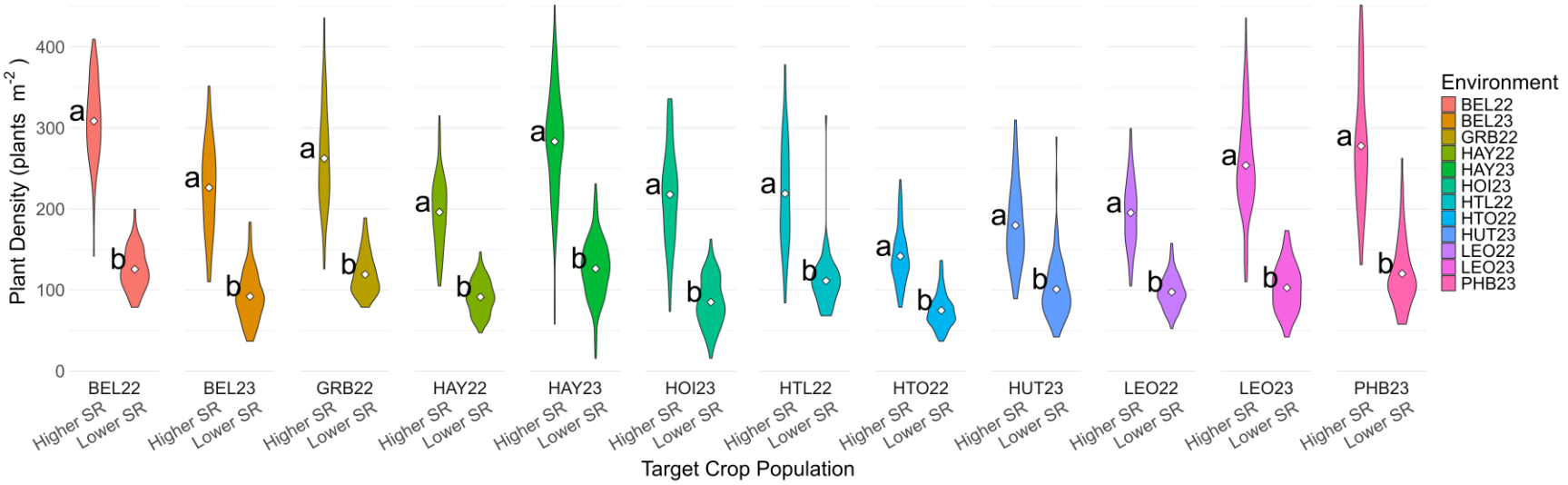

Figure 2.3 | Plant density distribution as function of environment and seeding rate. Data distribution is shown as a violin plot and means are denoted with white markers. Violin plots followed by the same letters indicate no statistically significant differences between seeding rates within environment using Tukey's Honestly Significant Difference (HSD) test.

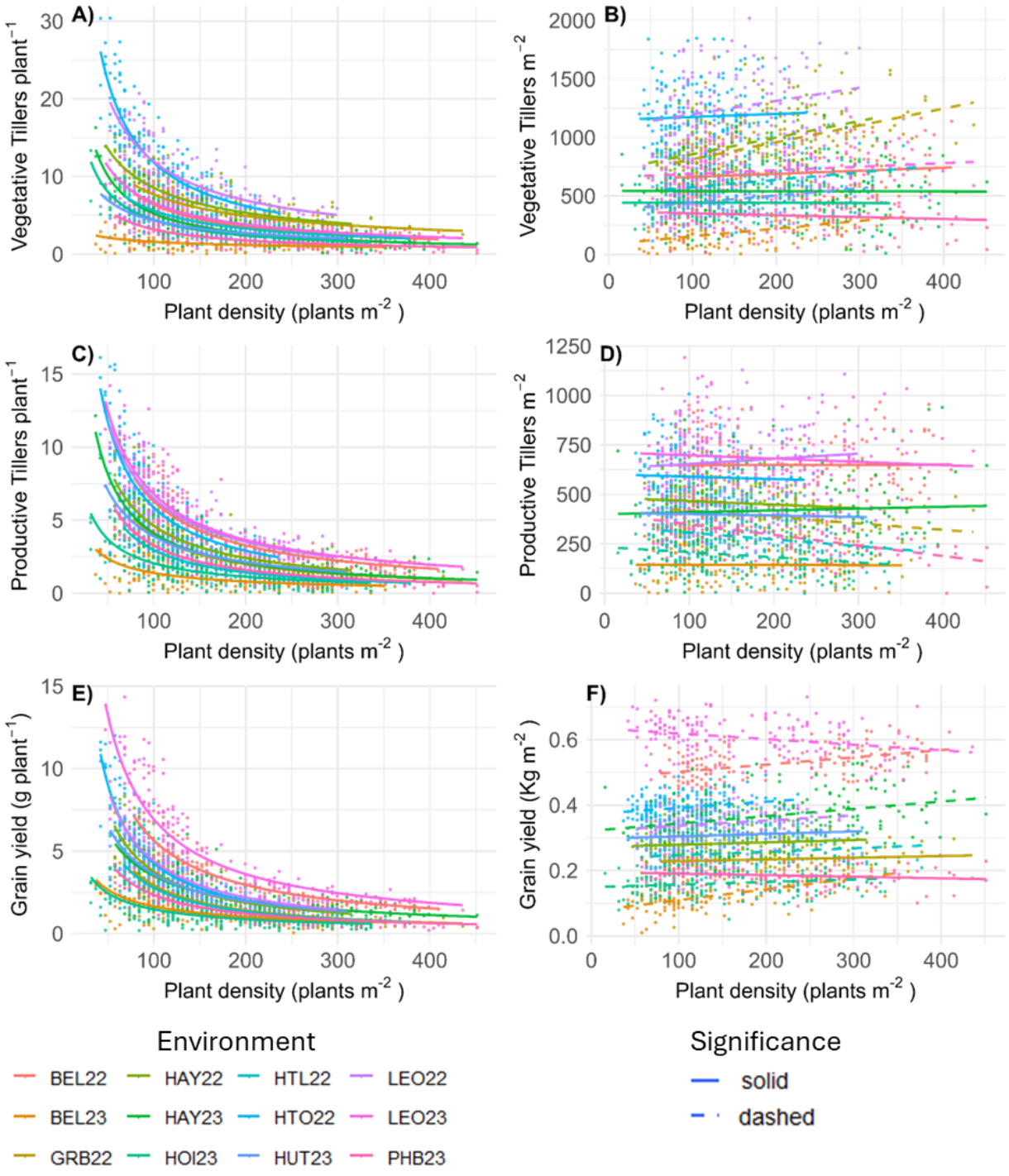

Figure 2.4 | Relationships between plant density and A) vegetative tillers Exponential decay model at an individual level to explain trait expression plant^{-1} (first column, A, C, E), and linear model explaining at crop levels trait production m^{-2} (second column, B, D, F) responses as a function of plant density for each environment. Vegetative tillers (A, B), Productive tillers (C, D), Grain yield (E, F). Solid lines indicate statistically significant regression ($p \leq 0.05$) dashed lines indicate not statistically significant regression ($p \leq 0.05$).

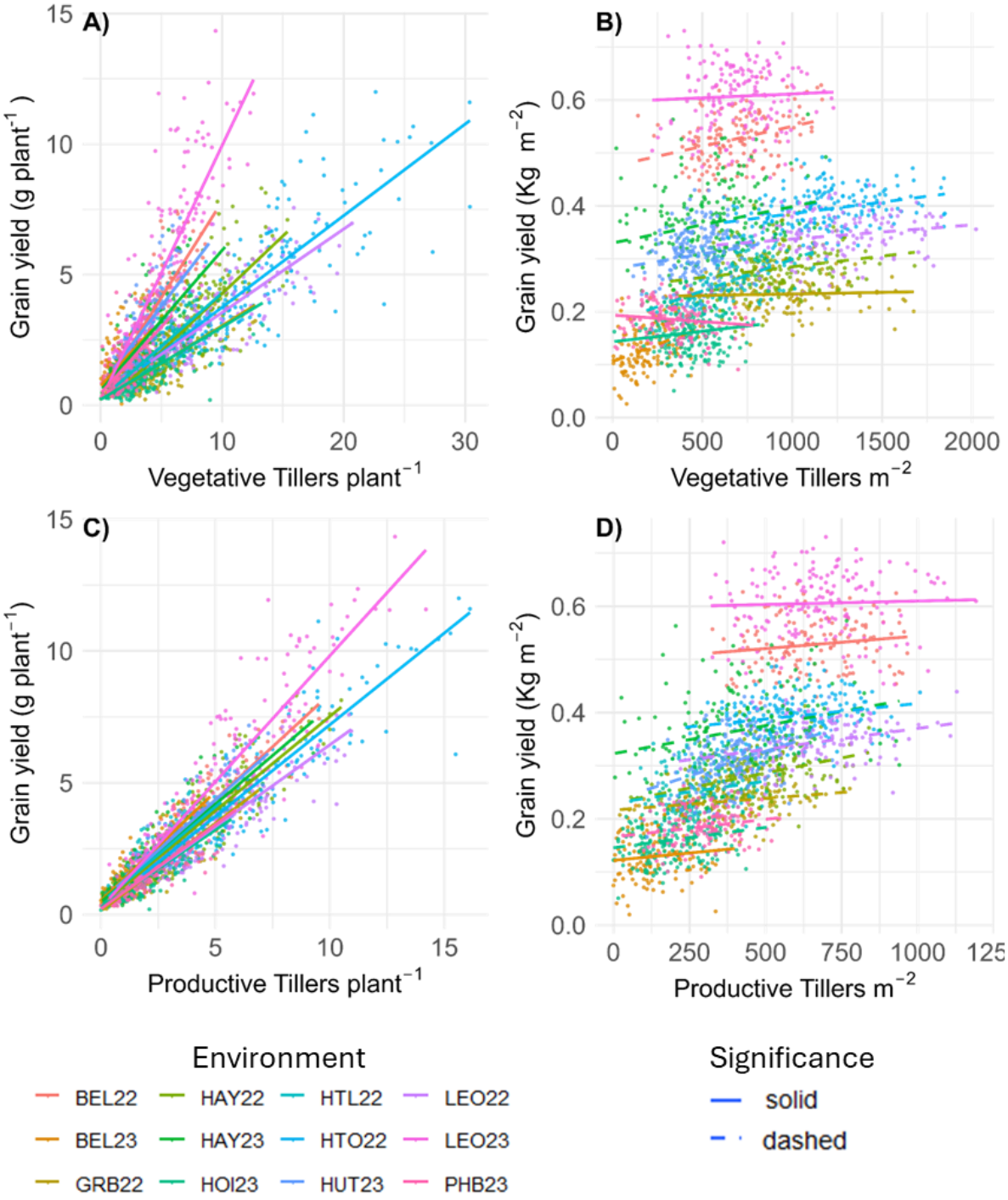

Figure 2.5 | Linear model at an individual level to explain grain yield g plant^{-1} (first column, A, C), and at crop levels grain yield Kg m^{-2} (second column, B, D) responses as a function of vegetative tillers density (A, B), and Productive tillers (C, D) for each environment. Solid lines indicate statistically significant regression ($p \leq 0.05$) dashed lines indicate not statistically significant regression ($p \leq 0.05$).

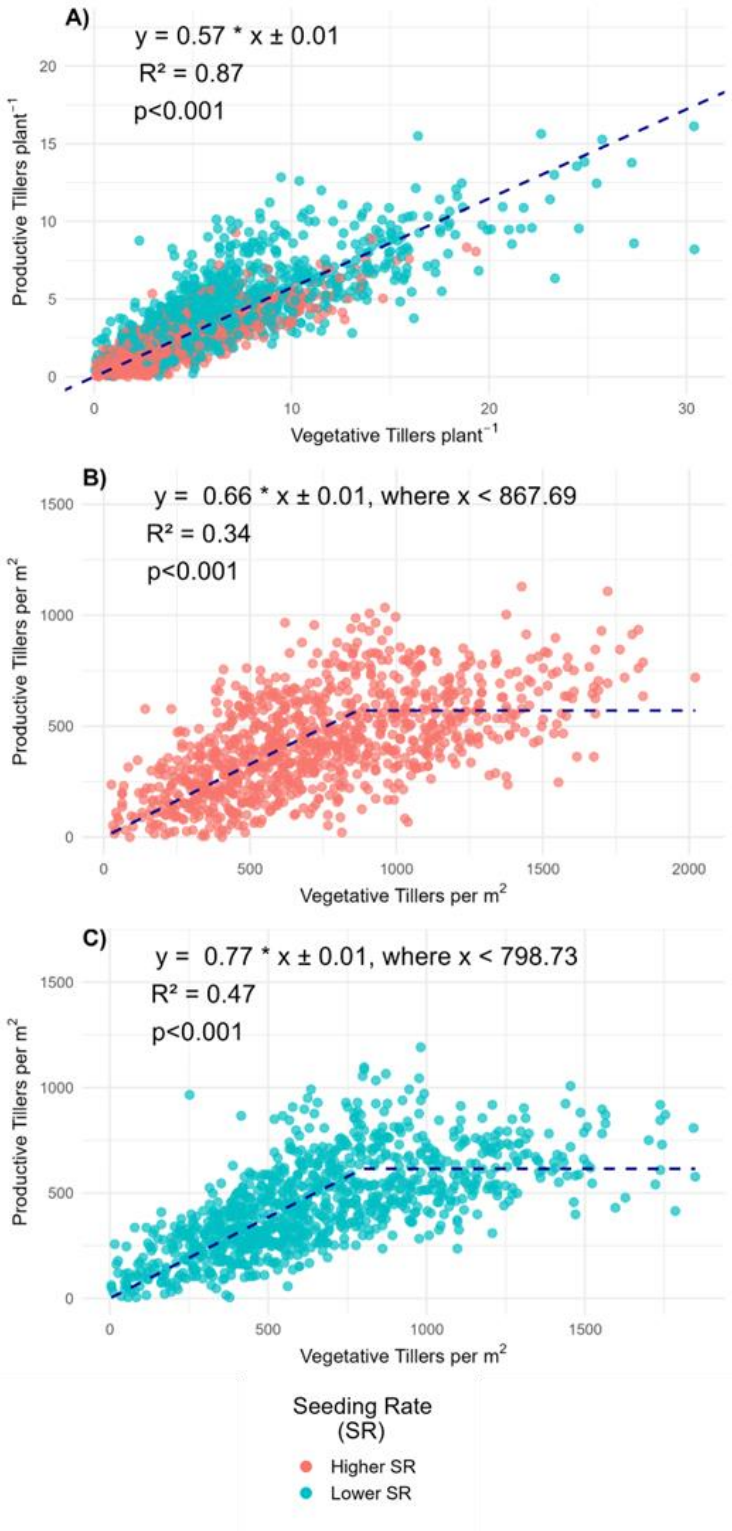

Figure 2.6 | Linear model describing the relation between vegetative tillers and productive tillers plant^{-1} across plant densities and environments (A). Linear-plateau models to describe the relationship between vegetative tillers and productive tillers across environments under different crop plant densities at high (B) and low (C) seeding rates.

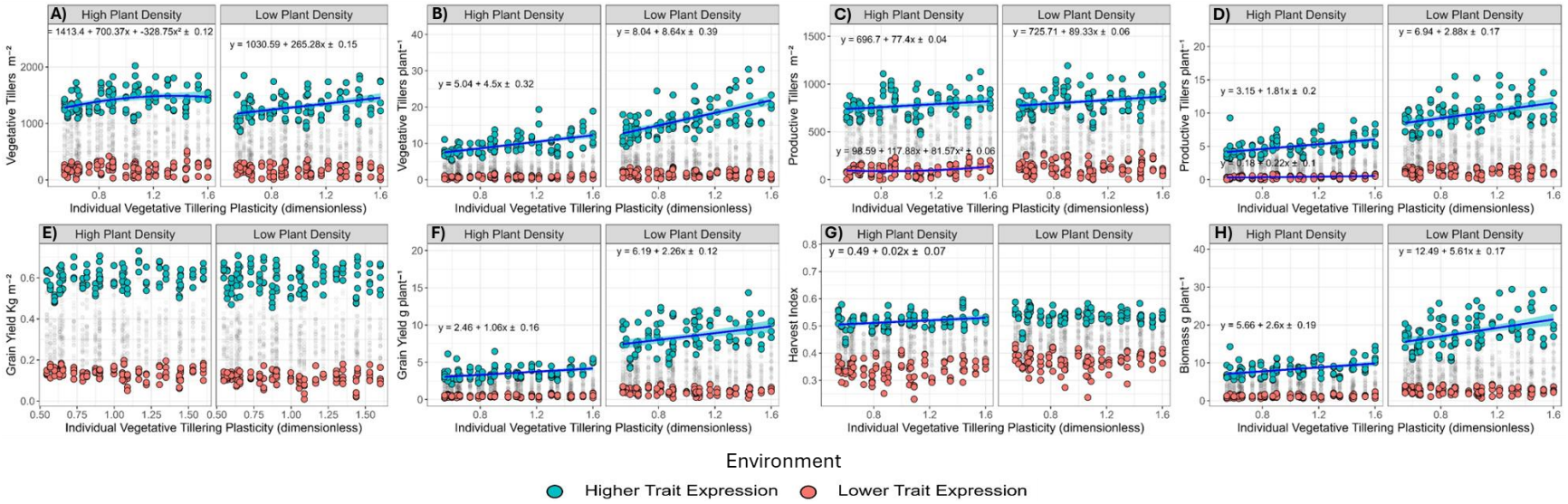

Figure 2.7 | Relationships between individual vegetative tillering plasticity and multiple traits, such as vegetative tillers m^{-2} (A), vegetative tillers $plant^{-1}$ (B), productive tillers m^{-2} (C), productive tillers $plant^{-1}$ (D), grain yield Kg m^{-2} (E), grain yield g $plant^{-1}$ (F), Harvest Index (%) (G), aboveground biomass g $plant^{-1}$ (H). Points are colored by quantiles (Turquoise – 90th quantile, and Salmon–10th quantile), representing environments of high and low variety trait potential respectively. Fitted linear regressions, when applicable $p \leq 0.05$. Fitted quadratic regression when $p \leq 0.05$ and $r^2 \geq (1.2 * \text{linear } r^2)$.

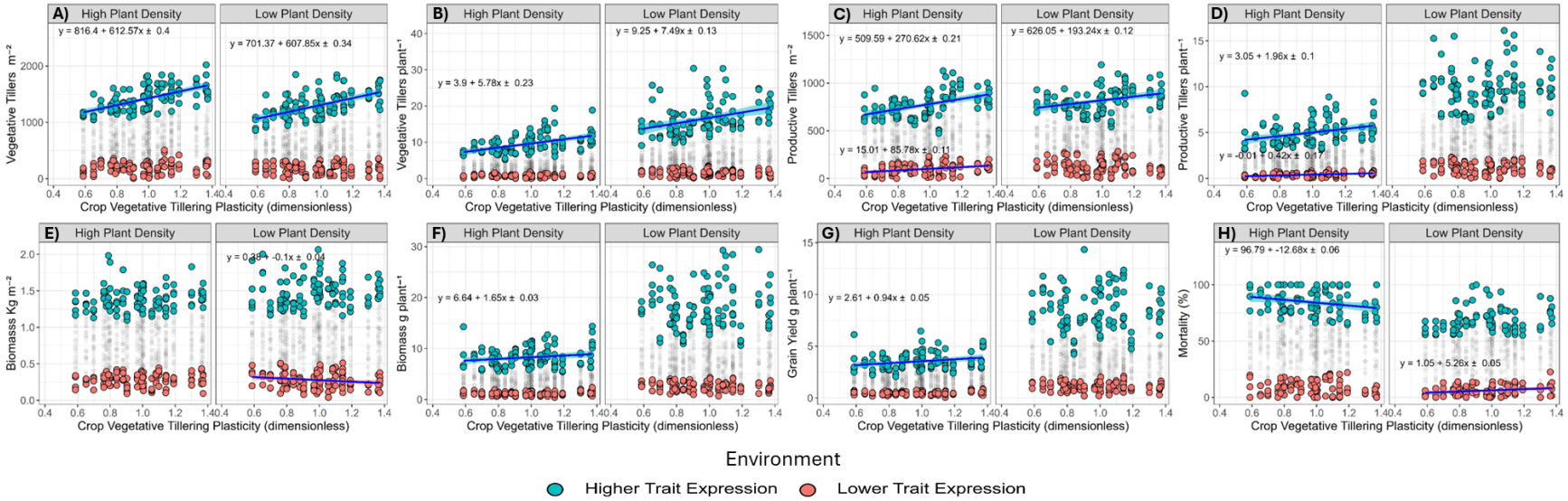

Figure 2.8 | Relationships between crop vegetative tillering plasticity and multiples traits, such as vegetative tillers m^{-2} (A), vegetative tillers $plant^{-1}$ (B), productive tillers m^{-2} (C), productive tillers $plant^{-1}$ (D), aboveground biomass Kg m^{-2} (E), aboveground biomass g $plant^{-1}$ (F), grain yield g $plant^{-1}$ (G), and Mortality (%) (H). Points are colored by quantiles (Turquoise – 90th quantile, and Salmon–10th quantile), representing environments of high and low variety trait potential respectively. Fitted linear regressions, when applicable $p \leq 0.05$. Fitted quadratic regression when $p \leq 0.05$ and $r^2 \geq (1.2 * \text{linear } r^2)$.

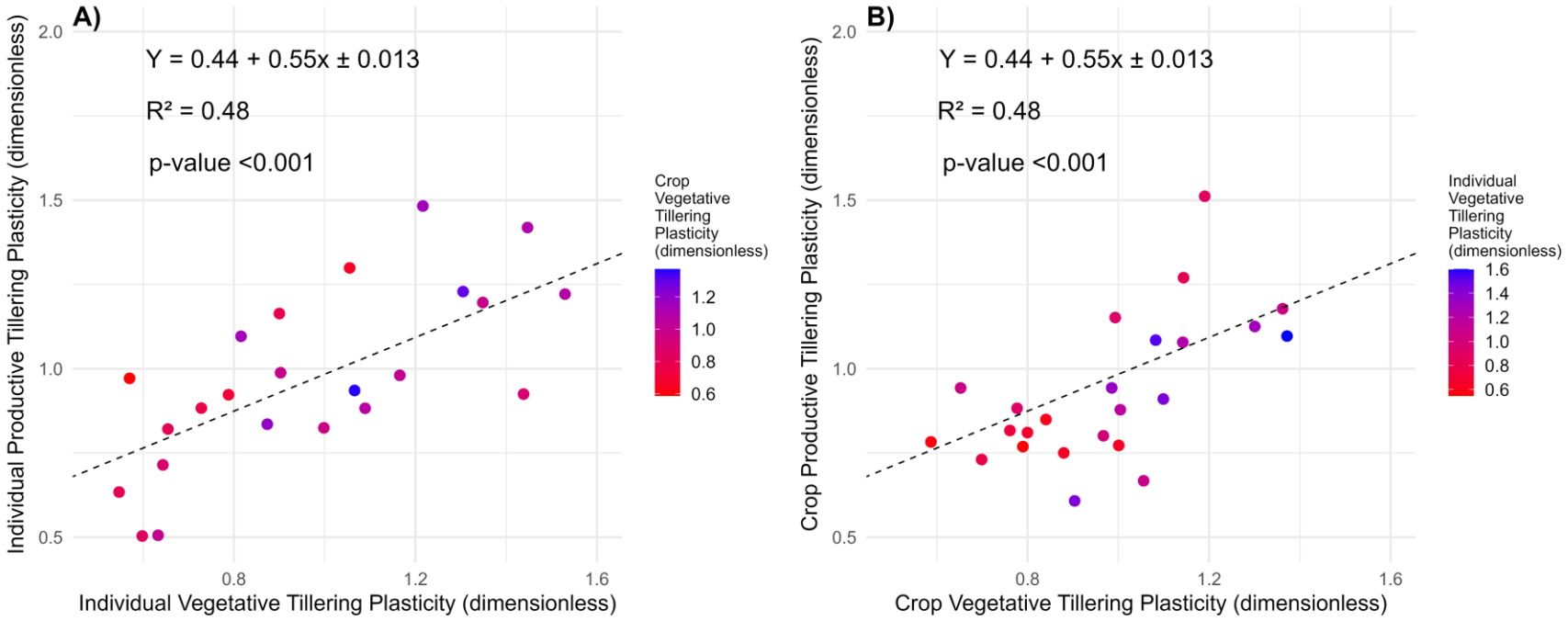

Figure 2.9 | Relationship between vegetative tillering plasticity and productive tillering plasticity at the individual (A) and crop (B) levels, colored by the vegetative tillering plasticity level.

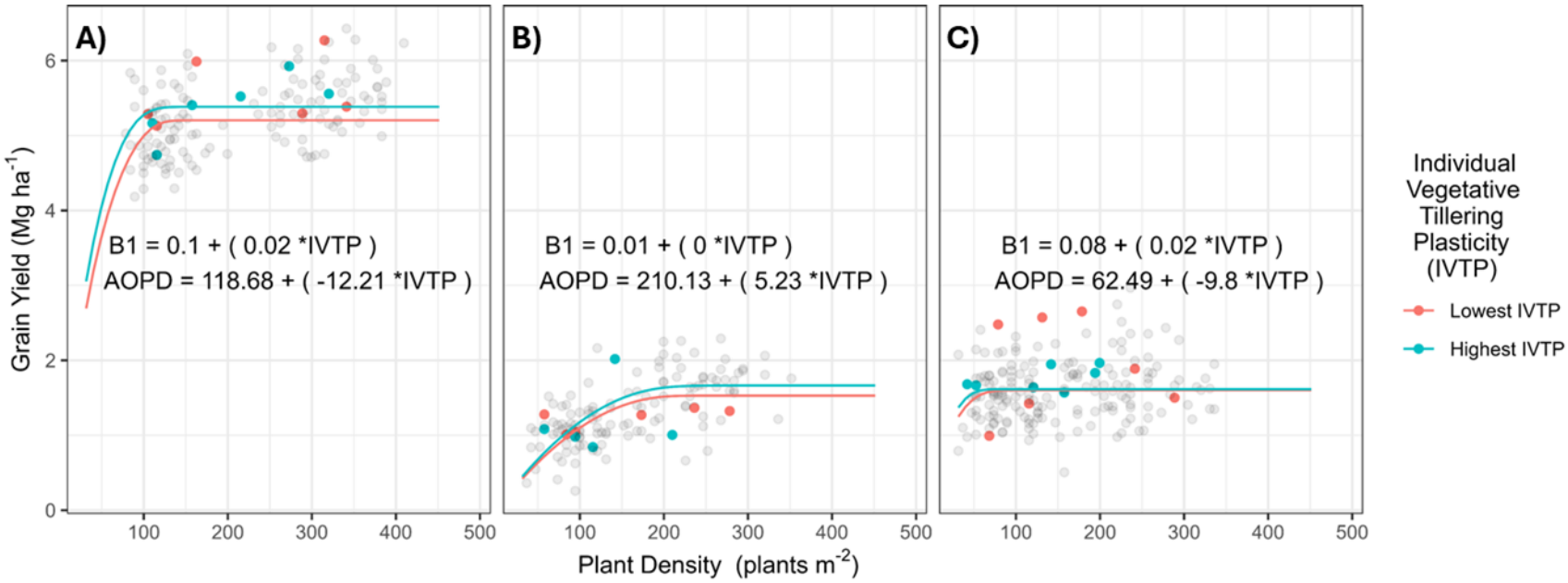

Figure 2.10 | Bayesian model of the relation between grain yield and plant density (plants m^{-2}) for WB4594 and KS Dalla, which are respectively the genotypes with highest (Turquoise) and lowest (Salmon) individual vegetative tillering plasticity phenotypes at three contrasting environments of BEL22 (A), BEL23 (B), and HOI23 (C).

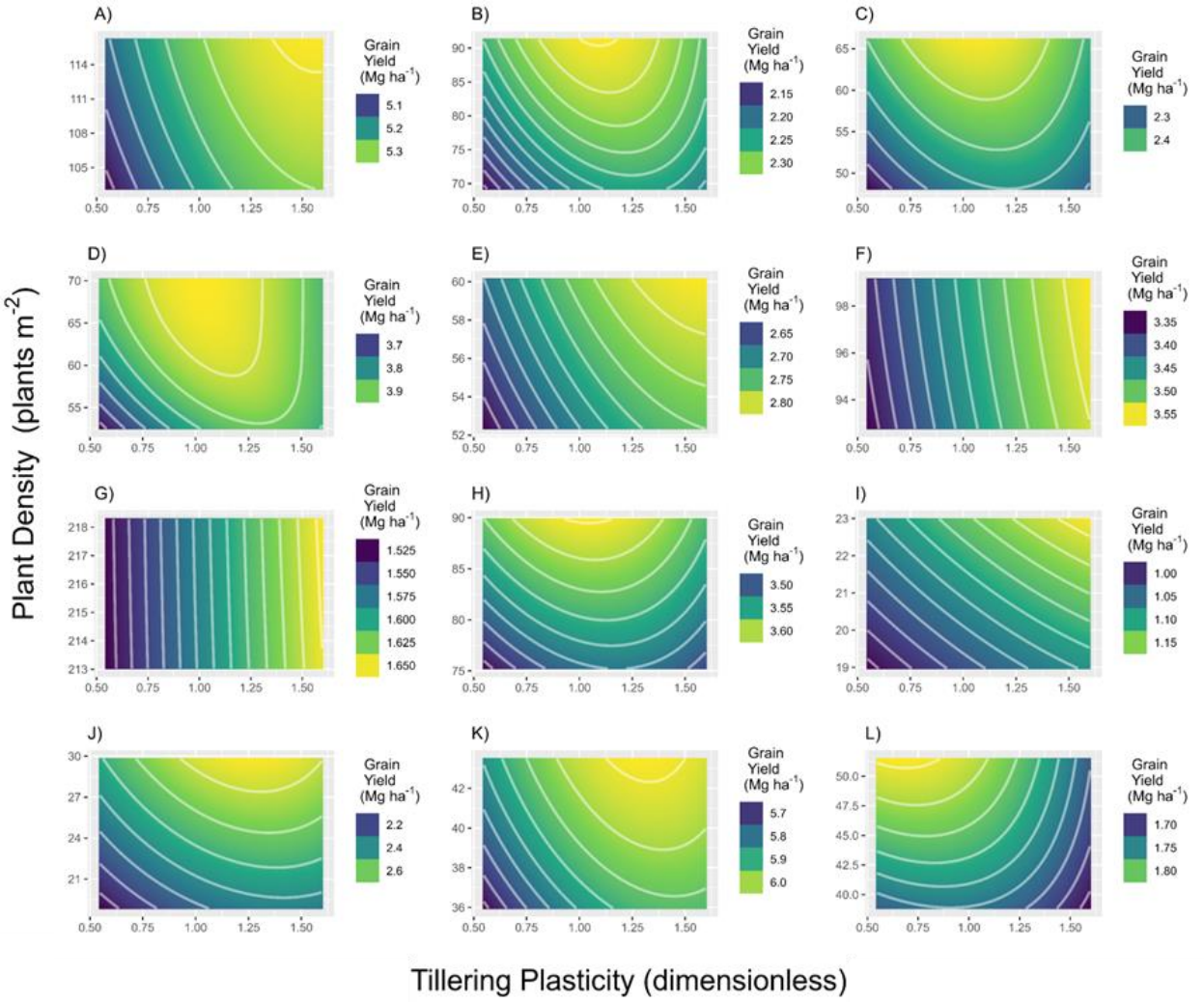

Figure 2.11 | Bayesian model predictions of grain yield as function of plant density in relation to individual vegetative tillering plasticity for the 12 studied Kansas environments. White lines are grain yield isolines. The maximum and minimum mean agronomical optimum plant density predicted by the model for each environment was used to limit the y-axis intervals. Environments are ordered as BEL22 (A), GRB22 (B), HTL22 (C), HTO22 (D), HAY22 (E), LEO22 (F), BEL23 (G), HAY23 (H), HOI23 (I), HUT23 (J), LEO23 (K), and PHB23 (L).

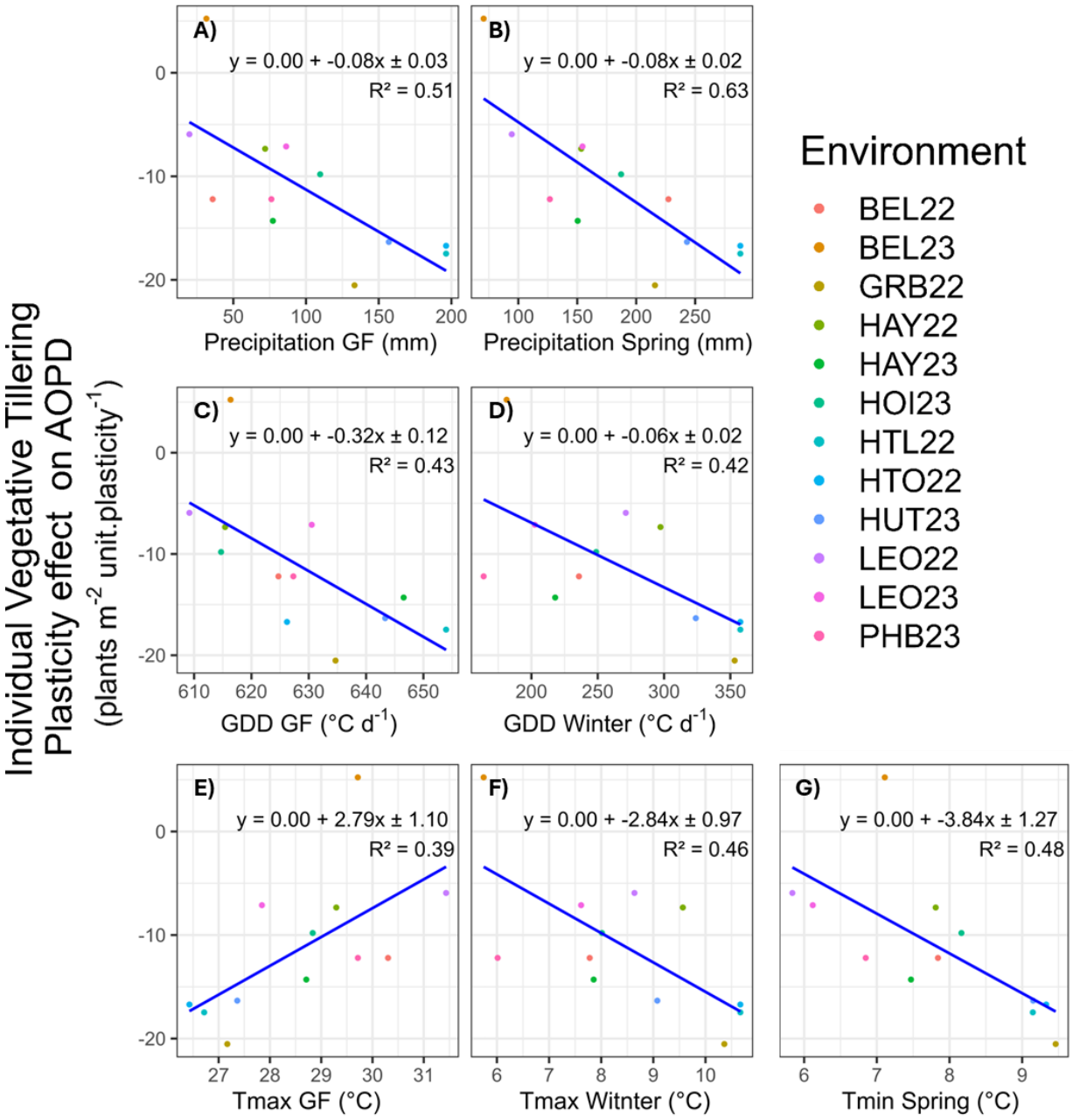

Figure 2.12 | Linear regression model showing the association between weather variables and the impact of the individual tillering plasticity on agronomic optimum plant density (AOPD) for Cumulative Precipitation (mm) at Grain Filling (A) and Spring (B); Growing degree days (°C Day $^{-1}$) at Grain Filling (C) and Winter (D); Maximum Temperature (°C) at Grain Filling (E) and Winter (F); and Minimum Temperature. Abbreviations: Grain Filling, GF; Cumulative Precipitation, Precipitation; Growing degree days, GDD; Maximum Temperature, Tmax; Minimum Temperature, Tmin.

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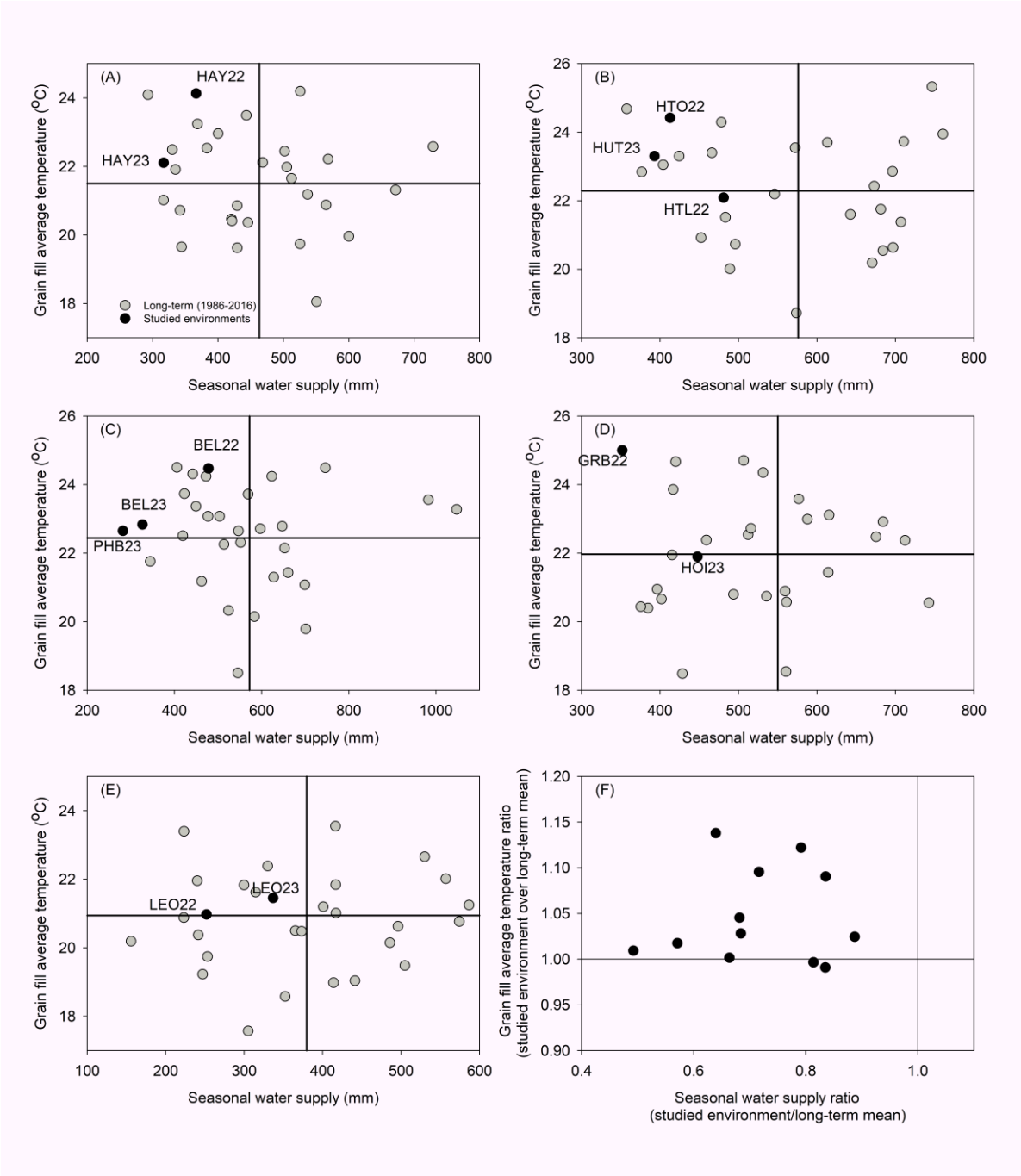
Appendix A - Chapter 2 Supplementary material



Appendix Figure A.1 | Grain filling average temperature and seasonal water supply comparison for the last 30 years in the respective regions near the environments, HAY22, HAY23 (A); HTL22, HTO22, HUT23 (B); BEL22, BEL23, PHB23 (C); GRB22, HOI23 (D); and LEO22, LEO23 (E). Inset values show cumulative rainfall, and Tave between grain filling (Zadok 70) and physiological maturity (Zadok 90). Panel (f) shows the comparison of total water supply and mean temperature at grain filling period for the twelve environments present in this study with the previous 30 growing seasons.