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Multiple abiotic stresses on maize grain yield determination: Additive vs multiplicative effects

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ARTICLE INFO

ABSTRACT

Interactions between nitrogen (Ns) and water stress (Ws) effects on annual crops productivity have been widely investigated in Mediterranean-type regions, but not in the humid temperate ones as the central Pampas of Argentina, where early-sown maize crops are usually exposed to severe yield penalties due to the mentioned stresses. Additionally, the recommendation of increasing plant populations promoted by seed companies may push crops to high density stress (HDs), which has usually a multiplicative (i.e. less intensive) and not an additive (i.e. more intensive) effect when combined with other constraints. In current research we re-examined multiple stress effects (HDs, Ns, Ws and the interaction of HDs with either Ns or Ws) on the determinants of grain yield of two maize hybrids, and used relative plant biomass (SI = 1 − stress/reference) as an integrative seasonal index for describing their intensities. Field experiments included two maize hybrids of contrasting tolerance to stress (high for AX820 and low for AX877), grown under different combinations of stand densities (9 and 12 plants m^{-2}) and N offer (0 and 200 kg N ha^{-1}) or water regime (well-watered and water deficit). The SI of combined stresses was always larger than the SI of any individual stress. For the tolerant hybrid, effects of combined abiotic stresses on SI were always multiplicative, whereas for the intolerant one the response intensified (i.e., turned additive or even synergic) under Ws × HDs. For both hybrids, a single model described the sensitivity of certain traits (number of complete and total florets, number of exposed silks) to the wide range of evaluated SIs, whereas independent models were necessary to accommodate the variation observed in the anthesis-silking interval associated with Ws and Ns. The second pattern was also observed in the case of kernel number per plant and plant grain yield of the intolerant but not of the tolerant hybrid. The former was more sensitive to Ws than the latter. Our results confirm a different sensitivity of the analyzed traits according to the origin of stress and the genotypic variability in these responses.

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1. Introduction

Abiotic stress dominates the list of environmental constraints (e.g. drought, nutrient limitations) that reduce grain yield of annual crops worldwide (Mueller et al., 2012). These stresses can vary in duration and intensity, and can act simultaneously or sequentially (Loomis and Connor, 1996; Mooney et al., 1991; Sih et al., 1998). Loomis and Connor (1996) suggested that the law of minimum (von Liebig, 1855; de Wit, 1992) is adequate for capturing the effect of multiple stresses in a short time interval (e.g., hours), with growth affected by one stress at a time. In longer periods, however, the final effect of different factors that affect plant growth does not represent the effect of any individual factor but of their interaction. This interaction effect is frequently of multiplicative and not of additive nature when expressed in relative terms respect to potential conditions that maximize grain yield (Sadras, 2005). Moreover, multiplicative effects are usually the result of stresses that take place sequentially along the cycle (Sadras, 2005).

Interactions between N (Ns) and water stress (Ws) have been widely investigated in Mediterranean-type regions where annual crops are commonly exposed to terminal drought (Asseng et al., 2001; Cantero-Martinez et al., 1995; Pala et al., 1996; Palta et al., 1994; Sadras, 2002; van Herwaarden et al., 1998a,b,c). At the crop level, these interactions have often been interpreted within a framework that accounts for the effect of Ns on early growth and Ws on kernel set and grain filling (Fischer, 1979; Passioura, 1977). For these environments, several works have described the effect of Ns × Ws on grain yield penalties (i.e., the gap between potential and actual yields) of rainfed wheat and barley crops (Sadras, 2004, 2005; Cossani et al., 2010). The magnitude of Ns × Ws was quantified by using an integrative seasonal index (SI) described as 'co-limitation index', based on the theory of the equally limiting factors proposed by Bloom et al. (1985). This index was calculated as a function of N and water stress indices (e.g., Sadras, 2004) derived from crop simulation models (e.g., CropSyst model; Stöckle et al., 2003) or by the ratio between actual N uptake or water use and the amount required to achieve maximum yields (e.g., Cossani et al., 2010). However, implementation of this methodology could be limited by the several inputs required to run crop simulation models. It can be also limited by the use of a reference maximum N uptake or water use representative of a single potential grain yield, ignoring multisite and inter-annual variations due to factors not related to soil restrictions, as solar radiation and air temperature (Otegui et al., 1996). An alternative way to account for inter-annual variation in potential (unstressed) growth is by expressing actual (stressed) growth relative to the potential growth of each year (Sadras, 2005).

For humid temperate regions as the central Pampas of Argentina, information on the effect of multiple stresses on the productivity of annual crops is scarce. In this region, maize crops are usually exposed to a mid-summer (late December and January) water deficit of variable duration and intensity, which has a predominant negative effect on kernel set of early-sown crops (Hall et al., 1992; Maddonni, 2012). Additionally, maize crops generally do not receive large amounts of N fertilization due to the generally negative effect of this practice on the crop gross margin. This fact, together with intensive land use in the area caused a pronounced decrease in the organic sources of this nutrient as compared to decades ago (Maddonni et al., 1999), when periods under annual crops alternated with periods under regenerative ley pastures. Hence, the occurrence of Ns and/or Ws on maize crops could be expected and magnified by the current high stand densities recommended by seed companies, which may fall within the supra-optimum range (i.e., high density stress; HDs) when crops are exposed to Ns or Ws.

In current research we propose a re-examination of multiple stress effects (HDs combined with either Ns or Ws) on the determination of maize grain yield and its main component, kernel number per plant (KNP), of two modern hybrids a priori classified as contrasting in their grain yield stability across environments (Pagano and Maddonni, 2007; Rossini et al., 2011). For this purpose we included two stand densities within the optimum range recommended for potential growing conditions (Luque et al., 2006). We used relative plant biomass (quotient between stress condition and a reference growing condition) at different growth stages to obtain the SI (SI = 1 − stress/reference) of individual and combined stresses. We evaluated the response of the determinants of KNP (floret development, the number of exposed silks, and the anthesis-silking interval; Otegui and Andrade, 2000) to a range of SI produced by HDs, Ws, Ns and some of their two-way interactions. This index is also useful to analyze the penalty induced in mentioned traits by a similar intensity of different stresses. We hypothesize that (i) multiple stress factors will have a greater effect on plant biomass than individual stresses, (ii) their combined effect will be similar to the additive or multiplicative effect of individual stresses when stresses occur simultaneously or sequentially in time, respectively, (iii) a similar SI will cause a different response in the determinants of KNP depending on the limiting production factor or the interaction between limiting factors, and (iv) hybrids will differ in the magnitude of the established responses.

2. Materials and methods

2.1. Crop husbandry, treatments and experimental designs

Field experiments were conducted during 2006–2007 (Exp. 1), 2007–2008 (Exp. 2), 2008–2009 (Exp. 3) and 2009–2010 (Exp. 4). Experiments 1 and 2 were performed at the experimental station of the National Institute for Agricultural Technology (INTA) located in Pergamino (33° 56′S, 60° 34′W), Argentina, on a silty clay loam soil (Typic Argiudoll). Treatments included a factorial combination of two single-cross maize hybrids (AX820 and AX877) from Nidera Argentina, two stand densities (9 and 12 plants m^{-2}; D9 and D12, respectively) and two N levels (N0: control with no added N; N200: a fertilized condition with 200 kg of N ha^{-1} added to the soil). Hybrids were selected based on information provided by Nidera Argentina S.A., which classified them as similar in potential grain yield but of contrasting stability across environments. This information was supported by results obtained in a previous experiment (Rossini et al., 2011), where both hybrids reached a maximum grain yield of ca. 13.2 Mg ha^{-1}, but AX877 was more affected by N × HDs than AX820. Crops were conducted with supplemental sprinkler irrigation. Experiments 3 and 4 were carried out at the field of the Department of Vegetal Production FA-UBA, Buenos Aires (34° 35′ S, 58° 29′ W), Argentina, under a polyethylene shelter for avoiding rainfalls, on a deep silty clay loam soil (Vertic Argiudoll).Treatments included a factorial combination of the same single-cross maize hybrids (AX820 and AX877), two stand densities (D9 and D12) and two water regimes (WW: well-watered; WD: water deficit). Crops were conducted with supplemental drip irrigation up to the seven-ligulated leaf stage (V7; Ritchie and Hanway, 1982) in Exp. 3, or V5 in Exp. 4. Subsequent to those stages, WW plots were irrigated frequently (each 5-7 days), with the objective of maintaining plant available soil water content above 50% (Sadras and Milroy, 1996). By contrast, irrigation of WD plots was arrested at mentioned stages, which resulted in a sustained decrease of plant available soil water content along the cycle (Fig. 1) except for some WD plots of AX877 in Exp. 4., that received water from rainfalls at the end of the grain-filling period due to damage on one side of the shelter (Fig. 1d). Other evaluated factors (stand density and hybrid) did not produce changes in soil water contents. All plots were fertilized with 200 kg of N ha^{-1} in Exp. 3 and Exp. 4.

In Exps. 1 and 2, treatments were distributed in a split-plot design with three replicates. N levels were assigned to the main plots, and combinations of stand density (SD) and hybrids (H) to the sub-plots (hereafter termed plots). Plots had six rows, 0.7 m between rows and 18 m length. In Exps. 3 and 4, treatments were distributed in a split-plot design with two replicates. Plots had five rows, 0.5 m between rows and 8 m length. The WR was assigned to the main plots, SD to the sub-plots and H to the sub-subplots (hereafter termed plots).

Sowing was performed manually on 20-Oct 2007 (Exp. 1), 22-Oct 2008 (Exp. 2), 08-Dic 2009 (Exp. 3) and 25-Nov 2010 (Exp. 4), at a rate of 3–4 seeds per hill and thinned to one plant per site at the end of the heterotrophic phase (V3; Pommel, 1990). N was added as urea to all fertilized plots at V6, and incorporated into the soil. All experiments were kept free of weeds by means of chemical con-