Field Crops Research 125 (2012) 98–108

Contents lists available at SciVerse ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Inter-plant variation of grain yield components and kernel composition of maize crops grown under contrasting nitrogen supply

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ARTICLE INFO

Article history:
Received 25 April 2011
Received in revised form 6 September 2011
Accepted 7 September 2011

Keywords:
Maize
Zea mays
Nitrogen
Inter-plant variation
Kernel number
Kernel weight
Kernel composition

ABSTRACT

High intra-specific competition pressure, which is common at most maize (*Zea mays* L.) cropping conditions, promotes inter-plant variation and the appearance of extreme plant hierarchies with different ability to capture scarce resources (i.e., dominant and dominated plants) within a stand. The objectives of the current work were to analyze (i) inter-plant variation of grain yield per plant (GYP), GYP components (KNP: kernel number per plant; KW: kernel weight), and kernel composition, together with those of their physiological determinants, i.e., plant growth (PG) rate around silking (PGR_S), PGR_S per kernel (PGR_S KNP^{-1}) and PG during the effective grain-filling period per kernel (PG_{GF} KNP^{-1}), under contrasting N supply and (ii) the contribution of dominant and dominated plants to changes in inter-plant variation and mean values of the studied traits. For these purposes two maize hybrids previously characterized by their contrasting inter-plant variation under N stress (low: AX820 and high: AX877) were cultivated at high stand densities (9 and 12 pl m^{-2}) at two N supplies (N_0: control and N_{200}: 200 kg N ha^{-1}) without water restrictions. For AX820, PGR_S data set at both N levels explored a similar range (1–7.4 and 1.2–7.4 g pl^{-1} d^{-1} for N_0 and N_{200}, respectively) with a positive skewness in N_0, and an almost normal distribution of data in N_{200}. In contrast, for AX877, inter-plant variation of PGR_S exhibited a normal distribution in both N levels, and N fertilization only produced a displacement of data to higher PGR_S values (0–4.3 and 0.7–5.7 g pl^{-1} d^{-1} for N_0 and N_{200}, respectively). The effect of inter-plant variation of PGR_S on the coefficient of variation (CV) of KNP was of a greater magnitude in AX877 than in AX820 due to the more linear KNP response to PGR_S of the former. For both hybrids, mean values of KW increased and the CVs decreased in response to high N supply. Differences among plants and N levels in KW were related to the duration of the effective grain-filling period. Inter-plant variation of protein and starch concentrations was higher in N_0 than in N_{200}, but that of oil concentration was not affected by N supply. The analysis of plant hierarchies resulted useful to understand changes in mean values and frequency distributions of several agronomic traits.

1. Introduction

Maize (*Zea mays* L.) production in Argentina is mainly concentrated within the most productive areas of the Pampas grassland (Soriano, 1991). Under these environments, maize hybrids are commonly cultivated under rainfed conditions, with fertilizer applications (N and P) and stand densities close to 80–90,000 plants ha^{-1}. Water and nutrient deficits, however, often occur (Hall et al., 1992), enhancing the natural inter-plant variation of maize crops (Edmeades and Daynard, 1979; Vega and Sadras, 2003; Boomsma et al., 2009), which may be reflected on grain yield losses, especially at high stand densities (Tollenaar and Wu, 1999; Caviglia and Melchiori, 2011).

The effect of crowding stress on inter-plant variation of grain yield components and kernel composition of four maize hybrids has been quantified without water restriction under nutrient sufficiency (Maddonni and Otegui, 2006). At supra-optimum stand densities (i.e., ≥12 plants m^{-2}), grain yield per plant (GYP) and kernel number per plant (KNP) presented a larger inter-plant variation (quantified by the coefficient of variation; CV) than kernel weight (KW) and kernel composition (starch, protein and oil concentrations). A more detailed analysis considered the onset of contrasting plant hierarchies in terms of ability to capture resources (i.e., dominant and dominated individuals) within the same stand and revealed that dominant and dominated plants yielded different KNP, slightly different KW, but similar kernel composition (Maddonni and Otegui, 2006). In a recent work, where the response

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doi:10.1016/j.fcr.2011.09.004

to N stress was analyzed, the increase in GYP of dominated plants after N fertilization was applied reduced the CV of GYP of the stand (Caviglia and Melchiori, 2011). Interestingly, the response of each plant hierarchy to N supply was differentially associated with GYP components. Dominated plants had a higher KNP response to N than dominant plants. Mentioned works have only evaluated inter-plant variation of GYP components and kernel composition, but not that of the physiological determinants of these traits.

At the plant-level analysis, KNP is determined by plant growth rate (PGR) around silking (PGR_S) (Tollenaar et al., 1992; Vega et al., 2001). At contrasting stand densities (sub-optimum, optimum and supra-optimum), the lowest CV values of PGR_S were registered at optimum stand density (~9 plants m^{-2}) and the lowest CVs of KNP corresponded to crops grown at sub-optimum (~6 plants m^{-2}) and optimum stand densities (Maddonni and Otegui, 2004). The response of KNP to PGR_S of each genotype determined a particular relationship between the CVs of both variables. Most maize hybrids exhibit a curvilinear response of KNP to PGR_S, but other hybrids have linear relationships or at least a linearity of response over a certain range of PGR_S (Gambín et al., 2008; D'Andrea et al., 2008). Therefore, the less curvilinear the response of KNP to PGR_S is, the more linear the relationship between the CVs of both traits (Andrade and Abbate, 2005). In a recent work (Rossini et al., 2011) the CVs of PGR_S and KNP augmented at supra-optimum stand density (~12 plants m^{-2}), and the effect of N fertilization on inter-plant variation of these traits depended on the genotype. Inter-plant variation of both KNP and PGR_S were analyzed but plant hierarchies were not distinguished and no information of KW and kernel composition was given.

In a recent review (Borrás and Gambín, 2010), changes of KW were analyzed as an integrated system, modulated by processes linking diverse levels of organization (the different kernel tissues, the whole kernel, the plant and the canopy). Thus, at the plant-organization level, mean KW depends on the potential kernel size established by the flux of available assimilates per kernel at the end of the critical period for kernel set (ca. 15 days after silking), and the plant capacity to provide assimilates needed to fulfill this potential during the grain-filling period. Gambín et al. (2006) proposed using the ratio between PGR_S and KNP (i.e., $PGR_S\,KNP^{-1}$) for estimating resource availability per established kernel during the first stages of grain filling (i.e., the lag phase) and the ratio between PGR during the effective grain-filling period (PGR_{GF}) and KNP (i.e., $PGR_{GF}\,KNP^{-1}$) for estimating plant capacity to provide assimilates for kernel growth. Mean KW was more related to $PGR_S\,KNP^{-1}$ than to $PGR_{GF}\,KNP^{-1}$ (Gambín et al., 2008) but KW reductions were observed whenever growth conditions reduced PGR_{GF}, like defoliations (Egharevba et al., 1976; Sala et al., 2007a,b), drought stress (Westgate, 1994) or episodes of shadings (Andrade and Ferreiro, 1996; Tanaka and Maddonni, 2009). From Gambín et al. (2008) data, a lower inter-plant variation of KW and $PGR_S\,KNP^{-1}$ is inferred for a hybrid showing a linear response of KNP to PGR_S and a higher inter-plant variation for two hybrids with a curvilinear response of KNP to PGR_S. In the mentioned study, crops were cultivated under irrigated conditions without nutrient restrictions, and inter-plant variation was obtained pooling together control plants with those of other treatments without any identification of plant categories.

Finally, considering kernel composition, a decrease in $PG_{GF}\,KNP^{-1}$ beyond a given threshold, promoted a reduction in protein concentration and an increase in starch concentration, but had no effect on oil concentration (Borrás et al., 2002). Hence, for the wide range of $PG_{GF}\,KNP^{-1}$ promoted by contrasting stand densities (sub-optimum and optimum stand densities) and pollination treatments (i.e., altering KNP), protein and starch concentrations exhibited a larger inter-plant variation than oil concentration.

Collectively all quoted studies have described inter-plant variation of several traits under variable growing conditions, promoted by different stand densities, thinning, shading, and pollination treatments. However, no information exists of the impact of N supply on inter-plant variation of GYP components, and kernel composition together with those of their physiological determinants, i.e., PGR_S, $PGR_S\,KNP^{-1}$ and $PG_{GF}\,KNP^{-1}$. Additionally, some of these studies have only quantified inter-plant variation using the CV, without providing other statistical descriptors (kurtosis, skewness, median) of the frequency distribution of a trait (Vega and Sadras, 2003). The objectives of the present research were to (i) asses exhaustively changes in inter-plant variation of GYP components and kernel composition due to contrasting N supplies identifying dominant and dominated plants of the stand, (ii) to determine genotypic differences in the response patterns, and (iii) to analyze the physiological determinants underlying these responses. Therefore, a thorough statistical description of N effect on inter-plant variation of GYP, KNP, KW, kernel composition and their physiological determinants was performed from data set of two maize hybrids previously characterized by their contrasting inter-plant variation under N stress (low: AX820 and high: AX877). N effect on inter-plant variation of kernel growth dynamic (i.e., lag phase duration, grain-filling rate and the duration of the effective grain-filling period) was also analyzed.

2. Materials and methods

2.1. Crop husbandry and experimental design

Field experiments were conducted during 2006–2007 (Exp. 1) and 2007–2008 (Exp. 2) in the Experimental Station of the National Institute of Agricultural Technology (INTA) located at Pergamino (33°56′S, 60°34′W), on a silty clay loam soil. The top soil (0–40 cm layer) had an organic matter content of ca. 23 g kg^{-1}, mean mineral P content of ca. 115 mg kg^{-1}, and inorganic N at sowing of ca. 14 g kg^{-1}. Two maize hybrids previously characterized (Rossini et al., 2011) by their contrasting inter-plant variation under N stress were used: Nidera AX877 CL-MG (hereafter AX877) with high variation and Nidera AX820 CL-MG (hereafter AX820) with low variation. Each hybrid was grown at two (Exp. 1) or three (Exp. 2) stand densities (D_n) and two nitrogen (N_n) levels. Tested stand densities were 6 (D_6; only in Exp. 2), 9 (D_9) and 12 (D_{12}) plants m^{-2}. In this work, only D_9 and D_{12} were analyzed. N rates were a control with no added N (N_0) and 200 kg of N ha^{-1} (N_{200}) added as urea at the six-ligulated leaf stage (V_6; Ritchie and Hanway, 1982). Urea (46% of N) was manually applied along the rows and then incorporated into the soil. Treatments were distributed in a split-plot design with three replicates ($n = 3$). N levels were in the main plot and all hybrid × stand density combinations in the sub-plots (herein termed plots). Plots had six rows with an E–W orientation, 0.7 m between rows and 18 m length.

Manual sowing took place on 20-October (Exp. 1) or 22-October (Exp. 2) at a rate of 3–4 seeds per hill. Plots were thinned to one plant per hill at the end of the heterotrophic phase (ca. V_3; Pommel, 1990). All experiments were kept free of weeds by means of chemical (4 L of atrazine 0.5 a.i. per ha plus 2 L of acetochlor 0.9 a.i. per ha at sowing) and manual controls. Water stress was prevented by means of sprinkler irrigation, with the uppermost soil profile (1 m) near field capacity throughout the crop cycle.

Daily values of incident global solar radiation, and mean air temperature were obtained from a LI 1200 (LI-COR, Inc., Lincoln, NE) weather station installed at the experimental field. Accumulated thermal time (TT; degree day units with a base temperature 8 °C; Ritchie and NeSmith, 1991) was computed from mean daily air temperatures from sowing onward. Mean air temperature around

silking (ca. 22.5 °C) and during the grain-filling period (21.5 °C) resulted similar among experiments. Similarly, mean solar radiation around silking (ca. 25 MJ m^{-2} d^{-1}) and during the grain-filling period (ca. 23 MJ m^{-2} d^{-1}) of both growing seasons were similar.

2.2. Measurements

A total of 10 (Exp. 1) or 12 (Exp. 2) consecutive plants of similar size (visual assessment) were tagged at V_3 in each plot. Ontogenic stages were registered weekly (V_n stages) or daily (silking, R_1) on all tagged plants. Plant biomass was also estimated weekly between V_3 and R_1 + 15d for these plants, by means of allometric models based on non-destructive morphometric measurements. Details of the non-destructive technique and the obtained allometric models were presented in the previous paper (Rossini et al., 2011).

All tagged plants were harvested at physiological maturity (R_6). This ontogenic stage was established when kernels from mid position of the ear attained the half-milk line stage (Afuakwa and Crookston, 1984). Plants were oven dried at 70 °C until constant weight to determine final plant biomass, and GYP. The KNP was counted and KW was calculated as the quotient between GYP and KNP. Kernels were analyzed for oil, protein, and starch concentrations by near-infrared transmittance (Infratec 1227, Tecator, Sweden). All intact kernels of each plant constituted each sample which was rehydrated to 14.5% of moisture content. Samples with less than 30 kernels were not analyzed. Calibration of near-infrared transmittance instrument was performed by Monsanto Argentina, with the most representative maize hybrids cultivated in the world.

The PGR_S was estimated from the slope of the linear regression fitted to the response of plant biomass to time. This function was fitted to data obtained at R_1 − 12d, R_1 and R_1 + 15d. Assimilate availability per kernel around silking (PGR_S KNP^{-1}) was estimated as the ratio between PGR_S and KNP. The PG_{GF} KNP^{-1} was quantified by the ratio between plant shoot biomass produced during the effective grain-filling period (plant biomass at R_6 − plant biomass at R_1 + 15d) and KNP.

All traits were computed on a plant basis and on the mean plant basis by averaging trait values of all tagged plants of the plots.

2.3. Method for plant classification

Final plant biomass at physiological maturity was taken as indicator of plant competitive capacity for resource capture within the stand (Maddonni and Otegui, 2004). According to this criterion, all tagged plants (10–12 plants per replicate) of each plot were classified into three groups based on the ranking of final plant biomass. For this purpose, final plant biomass of all tagged plants were ranked in ascending order. Three categories were established: (i) plants with final plant biomass ranked within the uppermost 33% of the data set (i.e., dominant plants), (ii) plants with final plant biomass ranked within the lowermost 33% of the data set (i.e., dominated plants), and (iii) plants with final plant biomass values ranked between 33% and 66% of the data set (i.e., the mean plants). Other measured traits (GYP, KNP, KW, oil concentration, protein concentration and starch concentration, PGR_S, PGR_S KNP^{-1}, PG_{GF} KNP^{-1}) were linked to this classification, except for parameters of kernel growth dynamic. For these traits, plants were classified based on the ranking of PGR_S (for more details see Section 2.4).

2.4. Kernel growth dynamic

To analyze inter-plant variation of kernel growth dynamic (only in Exp. 2), six areas per plot were randomly selected and 12 successive plants per area were tagged at the four central rows. Phenological stages and morphometric variables were recorded on all tagged plants to quantify PGR_S.

Kernels were collected weekly from R_1 + 15d to R_6 + 15d. At each sampling date, one area per plot was used to obtain twelve individual samples of kernels from tagged plants. From each plant, 10–20 kernels were sampled from similar spikelet positions (10 to 20 from the bottom of the ear) to avoid variations of KW along the ear (Tollenaar and Daynard, 1978; Borrás and Otegui, 2001; Tanaka and Maddonni, 2009). Each sample was dried at 70 °C until constant weight and its KW value was assigned to a plant category based on PGR_S and then, averaged within each plant group.

A bilinear model with plateau was fitted to mean KW of each plant category and TT after silking (Eqs. (1) and (2)):

$$KW = a + b\,TT, \quad \text{for } TT \le c \tag{1}$$

$$KW = a + bc, \quad \text{for } TT > c \tag{2}$$

where b and c parameters estimated the grain-filling rate and the duration of the grain-filling period, respectively.

Hence, parameters of kernel growth dynamic were estimated for each plant category. The duration of the lag phase was calculated as $-a/b$ and the duration of the effective grain-filling period was calculated as the difference between c and lag phase duration (Borrás and Otegui, 2001; Tanaka and Maddonni, 2009).

2.5. Data analysis

The effect of treatments (i.e., N level and stand density) and their interactions were evaluated across years for all described traits by ANOVA. Correlation analyses among traits of each hybrid were performed.

For each hybrid, a data set of each N level (N_0 and N_{200}) was built comprising all tagged plants (10–12 plants per replicate) of each replicate, at two plant population densities (D_9 and D_{12}) in both experiments. Descriptive statistics (mean, CV, minimum, median, maximum, skewness and kurtosis) were used to analyze inter-plant variation of the traits under study. Briefly, the skewness allows us to identify if data is evenly distributed around the arithmetic mean. Kurtosis determines the degree of concentration that values present in the central region of the distribution (i.e., the arithmetic mean). When the data distribution has a coefficient of skewness = 0 ± 0.5 and a coefficient of kurtosis = 0 ± 0.5, is called a normal curve. A Shapiro–Wilk test was also applied to examine whether data conforms to a normal distribution. We rejected the null hypothesis that the data were normally distributed when the P-value was smaller than 0.05.

For each data set (i.e., hybrid × N level) frequency distribution functions of the analyzed traits were depicted and the dominant and dominated plants were identified. For GYP, KNP and PGR_S frequencies were calculated over the total number of individuals of each data set. For KW, PGR_S KNP^{-1} and PG_{GF} KNP^{-1} frequencies were calculated over the total number of non-sterile individuals (i.e., KNP < 10; Tollenaar et al., 1992). For oil, protein and starch concentrations frequencies were computed over the total number of individuals with KNP > 30.

For each hybrid, N effect on the mean value of all traits was tested with the two-sample T test (i.e., the difference between mean values = 0). A test for equality of variance was previously performed to analyze the assumption of equal or different group of variances. N effect on KW, lag phase duration, the duration of effective grain-filling period and grain-filling rate was also tested with the two-sample T test. Data set of each hybrid × N combination comprised three plant types (dominant plants, mean plants, and dominated plants), two plant population densities and three replicates.

For the data set of each hybrid (two N levels and three stand densities), KNP was related to PGR_S by means of a hyperbolic function (Vega et al., 2001) of the type described in Eq. (3).

$$KNP = \frac{d(PGR_S - PGR_{ST})}{1 + e(PGR_S - PGR_{ST})}, \quad \text{for } PGR_S > PGR_{ST} \tag{3}$$

where d is the initial slope, PGR_{ST} is the threshold plant growth rate for KNP = 0 and e is the degree of curvilinearity at high PGR_S.

Correlation analyses, descriptive statistics, Shapiro–Wilk test and two-sample T test were performed with Statistix 7.0 (Statistix, 2000). The fitting of (1) + (2) and (3) models were performed by the user-defined functions routine of TableCurve 2D (Jandel TBLCURVE, 1992).

3. Results

3.1. Treatment effects on the mean values of grain yield components, kernel composition and their physiological determinants

In both experiments, low N supply and increased stand density reduced GYP (ca. 70.2 and 129.4 g pl^{-1} for N_0 and N_{200}, respectively; ca. 111.8 and 87.8 g pl^{-1} for D_9 and D_{12}; respectively), KNP (ca. 320 and 474 pl^{-1} for N_0 and N_{200}, respectively; ca. 432 and 362 pl^{-1} for D_9 and D_{12}; respectively) and KW (ca. 218.3 and 269.6 mg k^{-1} for N_0 and N_{200}, respectively; ca. 249.8 and 238.1 mg k^{-1} for D_9 and D_{12}; respectively) (Table 1). Hybrid AX877 exhibited a lower KW (ca. 239 mg k^{-1}) and a higher oil concentration (ca. 59.1 g kg^{-1}) than AX820 (ca. 249 mg k^{-1} and 57.7 g kg^{-1} for KW and oil concentration, respectively). A significant ($P < 0.05$) experiment × hybrid × stand density interaction on oil concentration was detected. Oil concentration of AX877 increased in response to high stand density (ca. 59.5 and 62.3 g kg^{-1} for D_9 and D_{12}, respectively) only in Exp. 2. A higher protein concentration value was recorded in Exp. 2 (ca. 90.6 g kg^{-1}) than in Exp. 1 (ca. 71.6 g kg^{-1}), but low N supply reduced protein concentration (ca. 66.7 and 95.5 g kg^{-1} for N_0 and N_{200}, respectively) during both growing seasons. A significant ($P < 0.05$) experiment × N × hybrid interaction on starch concentration was detected. In Exp. 2 kernels of both hybrids exhibited a higher starch concentration in N_0 (ca. 718 g kg^{-1}) than in N_{200} (ca. 686 g kg^{-1}).

Considering the physiological determinants of GYP components and kernel composition, N supply and stand density affected PGR_S (ca. 2.3 and 3.6 g pl^{-1} d^{-1} for N_0 and N_{200}, respectively; ca. 3.3 and 2.6 g pl^{-1} d^{-1} for D_9 and D_{12}, respectively) in both experiments (Table 1). Only PGR_S of AX820 differed between years (ca. 3.57 and 2.37 g pl^{-1} d^{-1} in Exp. 1 and Exp. 2, respectively). N supply affected PGR_S KNP^{-1} at D_9 (ca. 7 and 7.9 mg k^{-1} d^{-1} for N_0 and N_{200}, respectively) and differences between hybrids in this trait were only detected in Exp. 1 (ca. 7.91 and 6.78 mg k^{-1} d^{-1} for AX820 and AX877, respectively). Similarly, N effect on PGR_S KNP^{-1} was more pronounced in Exp. 1 (ca. 6.78 and 7.91 mg k^{-1} d^{-1} for N_0 and N_{200}, respectively) than in Exp. 2 (ca. 7.7 and 7.1 mg k^{-1} d^{-1} for N_0 and N_{200}, respectively). Only N supply affected PG_{GF} KNP^{-1} (ca. 100.2 and 144.4 mg k^{-1} for N_0 and N_{200}, respectively).

3.2. Inter-plant variation of grain yield components, kernel composition and their physiological determinants at contrasting N supply

For AX820 data sets, GYP and KNP exhibited higher CV values than those of KW and kernel chemical compounds (Table 2). Protein concentration yielded CVs higher than KW, oil and starch concentrations. Starch concentration exhibited the lowest CVs. The CVs of GYP, KNP, KW, oil, protein and starch concentrations in N_{200} were lower than those in N_0. In N_0, data of GYP and KNP were not evenly distributed around the mean (i.e., skewness >0.5) and data of KW were uniformly distributed around the mean (i.e., skewness ~0). Acute peaks around the mean and fat tails (i.e., positive kurtosis; leptokurtic distribution) were observed for GYP and KW. On the contrary, KNP exhibited a kurtosis ~0 (i.e., mesokurtic distribution) (Table 2 and Fig. 1a–c). In N_{200} GYP, KNP and KW exhibited a negative skewed distribution, with longer left tails, most data concentrated at high values and few data at low values (i.e., left-skewed distribution). GYP and GYP components exhibited leptokurtic distributions (Table 2 and Fig. 1a–c). In both N levels, data sets of oil, protein and starch concentrations (Table 2 and Fig. 2a–c) exhibited leptokurtic distributions skewed to the right (i.e., the right tail is longer with few high values; most data is concentrated on the left of the figure). Therefore, in any N level GYP components and kernel composition of the AX820 did not exhibit a normal distribution ($P < 0.01$) (Table 2). Two-sample T tests revealed that mean values of mentioned traits differed ($P < 0.01$) between N levels, with the exception of oil concentration (Table 2). Among the physiological determinants of GYP components and kernel composition, PG_{GF} KNP^{-1} exhibited the highest CVs at both N levels (Table 2). N fertilization increased the mean values of PGR_S and PG_{GF} KNP^{-1}, but only reduced CV of PGR_S. Data of mentioned traits did not exhibit a normal distribution in any N level (Table 2). The frequency distribution of PGR_S in N_{200} had shorter right tail and wider peak around the mean than in N_0 (Fig. 3a). In both N levels, data of PGR_S KNP^{-1} and PGR_{GF} KNP^{-1} exhibited leptokurtic distributions, skewed to the right for the former (Fig. 3b), and to the left for the latter (Fig. 3c).

For AX877 data set, CV values of GYP, KNP, KW and kernel composition followed a similar pattern than those of AX820 (Table 3). In N_0, the CVs of GYP, KNP, oil, protein and starch concentrations of AX877 were higher than those of AX820, whereas in N_{200}, only the CVs of GYP, KNP and starch concentration of AX877 resulted higher than those of AX820. Data of GYP and KNP of AX877 in both N levels exhibited non-normal distributions, but evenly distributed around the mean (i.e., skewness ~0 ± 0.5) with negative kurtosis in N_0 and skewed to the left with positive kurtosis in N_{200} (Table 3 and Fig. 1d, e). Contrarily, data of KW (Fig. 1f) and protein concentration (Fig. 2e) changed from a leptokurtic distribution skewed to the right in N_0 to a normal distribution in N_{200} (Table 3). Oil concentration exhibited positive kurtosis in both N levels skewed to the right in N_0 and to the left in N_{200} (Fig. 2d). Contrarily, starch concentration showed a leptokurtic distribution skewed to the right in N_0 and a negative kurtosis with data distributed around the mean (i.e., skewness ~0 ± 0.5) in N_{200} (Fig. 2f). Two-sample T test revealed that mean values of mentioned traits differed ($P < 0.001$) between N levels, with the exception of oil and starch concentrations (Table 3). Considering the inter-plant variation of the physiological determinants, CVs of PGR_S were lower than that of PGR_S KNP^{-1} and PG_{GF} KNP^{-1} (Table 3). N fertilization increased the mean value of PGR_S, but did not affect those of PGR_S KNP^{-1} and PG_{GF} KNP^{-1}. In N_{200} CVs of PGR_S and PG_{GF} KNP^{-1} were lower than those in N_0, but the opposite trend was observed for PGR_S KNP^{-1}. Data of PGR_S had a normal distribution at any N level (Table 3 and Fig. 3d). In both N level, data of PGR_S KNP^{-1} exhibited leptokurtic distribution skewed to the right (Fig. 3e), and PG_{GF} KNP^{-1} had also leptokurtic distributions but skewed to the left in N_0 and to the right in N_{200} (Fig. 3f).

3.3. Nitrogen effect on inter-plant variation of kernel growth dynamic

For AX820 and AX877 data sets, plants in N_0 yielded a lower KW than those in N_{200} by a shorter effective grain-filling period (Table 4). Contrarily, lag phase duration and grain-filling rate were not affected by N supply. Differences in KW between hybrids (~294 and 274 mg k^{-1}, for AX820 and AX877,

Table 1
Mean values and ANOVA of grain yield per plant (GYP); grain yield components (KNP: kernel number per plant; KW: kernel weight); kernel composition; plant growth rate (PGR_S) and plant growth rate per kernel around silking ($PGR_S\ KNP^{-1}$) and during the effective grain filling period ($PGR_{GF}\ KNP^{-1}$) of two hybrids (H) cultivated at two plant population densities (D) and two nitrogen (N) levels (N_0: unfertilized; N_{200}: fertilized). Values are the mean of two experiments (Exp. 1 and Exp. 2; E).

Hybrid	Density ($pl\ m^{-2}$)	Nitrogen	GYP ($g\ pl^{-1}$)	GYP components		Kernel composition ($g\ kg^{-1}$)			PGR_S ($g\ pl^{-1}\ d^{-1}$)	$PGR_S\ KNP^{-1}$ ($mg\ k^{-1}\ d^{-1}$)	$PGR_{GF}\ KNP^{-1}$ ($mg\ k^{-1}$)
				KNP	KW ($mg\ k^{-1}$)	Oil	Protein	Starch			
AX820	9	N_0	78.51	335	224.39	59.1	67.5	721.6	2.56	7.37	109.5
		N_{200}	143.58	499	284.42	58.0	91.8	700.5	4.05	8.02	158.9
	12	N_0	69.73	310	222.10	58.1	66.7	723.7	2.21	7.13	109.4
		N_{200}	110.59	418	263.64	55.7	93.5	708.3	3.08	7.30	136.3
AX877	9	N_0	76.39	359	215.25	58.6	62.2	721.0	2.40	6.72	104.9
		N_{200}	148.79	534	275.12	59.8	98.7	703.6	4.20	7.87	147.2
	12	N_0	56.15	276	211.43	60.2	70.4	727.0	2.03	7.78	77.2
		N_{200}	114.73	446	255.28	57.9	98.0	704.5	3.07	6.91	135.4
Significance level of main and interactions effects											
	E		ns	ns	ns	ns	**	ns	ns	ns	ns
	N		**	**	***	ns	***	**	**	ns	**
	H		ns	ns	*	*	ns	ns	ns	ns	ns
	D		***	**	*	ns	ns	ns	***	ns	ns
	E × N		ns	ns	ns	ns	ns	*	ns	*	ns
	E × H		ns	ns	ns	ns	ns	**	**	**	ns
	N × H		ns	ns	ns	ns	ns	ns	ns	ns	ns
	H × D		ns	ns	ns	**	ns	ns	ns	ns	ns
	E × D		ns	ns	ns	*	ns	ns	ns	ns	ns
	N × D		ns	ns	ns	ns	ns	ns	ns	*	ns
	E × N × H		ns	ns	ns	ns	ns	*	ns	ns	ns
	E × N × D		ns	ns	ns	ns	ns	ns	ns	ns	ns
	E × H × D		ns	ns	ns	*	ns	ns	ns	ns	ns
	E × H × D		ns	ns	ns	ns	ns	ns	ns	ns	ns
	E × N × H × D		ns	ns	ns	ns	ns	ns	ns	ns	ns

ns: not significant.
* Significance level: $P < 0.05$.
** Significance level: $P < 0.01$.
*** Significance level: $P < 0.001$.

Table 2
Descriptive statistics and normality test for grain yield per plant (GYP); GYP components (KNP: kernel number per plant; KW: kernel weight); kernel composition; plant growth rate (PGR_S) and plant growth rate per kernel around silking ($PGR_S\ KNP^{-1}$) and during the effective grain filling period ($PGR_{GF}\ KNP^{-1}$) of maize hybrid AX820 at two N levels (N_0: unfertilized; N_{200}: fertilized). The two-sample *T* tests (N_0 vs N_{200}) were also included. Data set of each N level comprises all plants (10–12 plants per replicate) of each replicate ($n = 3$), at two plant population densities (9 and 12 plants m^{-2}) during two growing seasons.

Hybrid	Nitrogen	Descriptive statistics	GYP ($g\ pl^{-1}$)	GYP components		Kernel composition ($g\ kg^{-1}$)			PGR_S ($g\ pl^{-1}\ d^{-1}$)	$PGR_S\ KNP^{-1}$ ($mg\ k^{-1}\ d^{-1}$)	$PGR_{GF}\ KNP^{-1}$ ($mg\ k^{-1}$)
				KNP	KW ($mg\ k^{-1}$)	Oil	Protein	Starch			
AX820	N_0	*n*	132	132	132	130	130	130	132	132	132
		Mean	72.61	317.26	222.63	58.83	67.72	722.11	2.34	7.45	101.55
		CV (%)	51.06	37.94	19.36	10.97	26.36	3.49	48.60	23.25	59.00
		Minimum	10.20	98.00	46.10	47.04	37.12	676.39	1.04	3.70	−137.00
		Median	59.95	292.25	219.20	58.27	65.11	716.00	1.99	7.15	101.20
		Maximum	192.90	663.80	355.60	91.37	147.75	827.10	7.38	13.70	261.10
		Skew	1.27	0.72	0.01	2.12	1.69	1.43	2.26	1.43	−0.78
		Kurtosis	1.40	−0.22	2.66	7.94	4.75	3.37	5.68	3.01	2.44
		Normality test (*P*)	***	***	***	***	***	***	***	***	***
	N_{200}	*n*	132	132	131	130	130	130	132	131	131
		Mean	125.09	451.48	276.07	56.97	93.54	703.48	3.50	7.83	144.95
		CV (%)	27.92	23.76	14.20	9.26	16.67	3.11	33.51	30.67	53.05
		Minimum	0	0	61.30	45.19	63.56	650.00	1.21	3.30	−351.80
		Median	132.35	458.25	275.80	57.23	91.44	701.91	3.37	7.50	150.50
		Maximum	200.90	639.00	356.50	89.29	147.14	805.45	7.43	25.80	334.00
		Skew	−0.88	−1.13	−1.15	1.54	0.98	1.34	0.74	3.28	−2.03
		Kurtosis	1.24	2.62	5.47	9.37	1.15	3.99	0.46	22.38	12.16
		Normality test (*P*)	***	***	***	***	***	***	**	***	***
	N_0 vs N_{200}	Sig.	***	***	***	ns	***	**	*	ns	**

ns: not significant.
* Significance level: $P < 0.05$.
** Significance level: $P < 0.01$.
*** Significance level: $P < 0.001$.

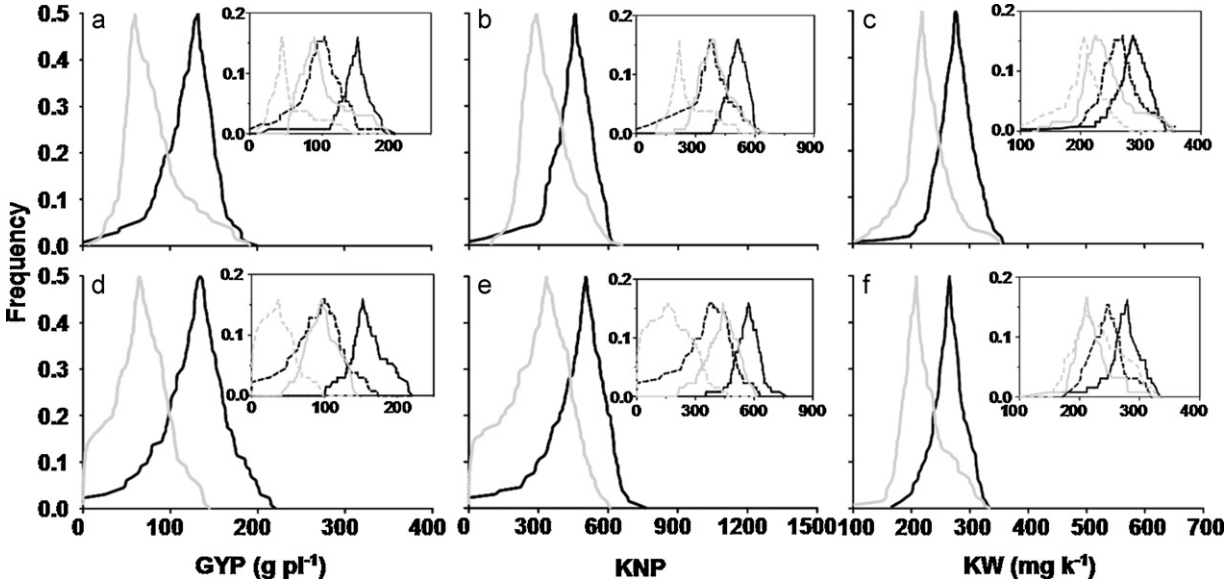

Fig. 1. Frequency distribution of grain yield per plant (a, d), kernel number per plant (b, e) and kernel weight (c, f) of AX820 (a, b, c) and AX877 (d, e, f) data sets in two N levels (N_0: grey line, N_{200}: black line). Data set of each N level comprises all plants (10–12 plants per replicate) of each replicate ($n = 3$), at two plant population densities (9 and 12 plants m^{-2}) during two growing seasons. The insets show the frequency distribution for dominant (solid line) and dominated (dotted line) plants from the same data set.

respectively) were only related to the distinct grain-filling rates (~0.51 and 0.47 mg °C d^{-1} k^{-1} for AX820 and AX877, respectively). For both hybrids, KW of dominant plants (~256 mg k^{-1}) was higher ($P < 0.01$) than those of dominated plants (~246 mg k^{-1}) due to a longer effective grain-filling period (data not shown). Consequently, KW variation of each hybrid data set was positively ($r^2 = 0.78$–0.89, $P < 0.001$) related to the duration of the effective grain-filling period (Fig. 4).

4. Discussion

Most traits of both hybrids exhibited high mean values and low CVs under high N supply. The positive effect of N fertilization on mean GYP, KNP and KW is well documented (e.g., Uhart and Andrade, 1995; Andrade et al., 2002; Melchiori and Caviglia, 2008; Boomsma et al., 2009). Less information exists of N effect on inter-plant variation of these traits. In recent works (Boomsma et al., 2009; Caviglia and Melchiori, 2011), CV of GYP decreased after N fertilizer application, but no information of the CVs of KNP and KW was reported. In our experiments, GYP data set of both hybrids was positively and linearly related to KNP data set ($r > 0.90$). Therefore, equivalent effects of N supply on the CVs of GYP and of KNP are expected results. An equal response of the CVs of GYP and KNP to light stress (i.e., contrasting stand densities) was described for other maize genotypes (Edmeades and Daynard, 1979; Echarte et al., 2000; Vega and Sadras, 2003; Maddonni and Otegui, 2006). Frequency distributions of both traits were also reported by Edmeades and Daynard (1979), Echarte et al. (2000)

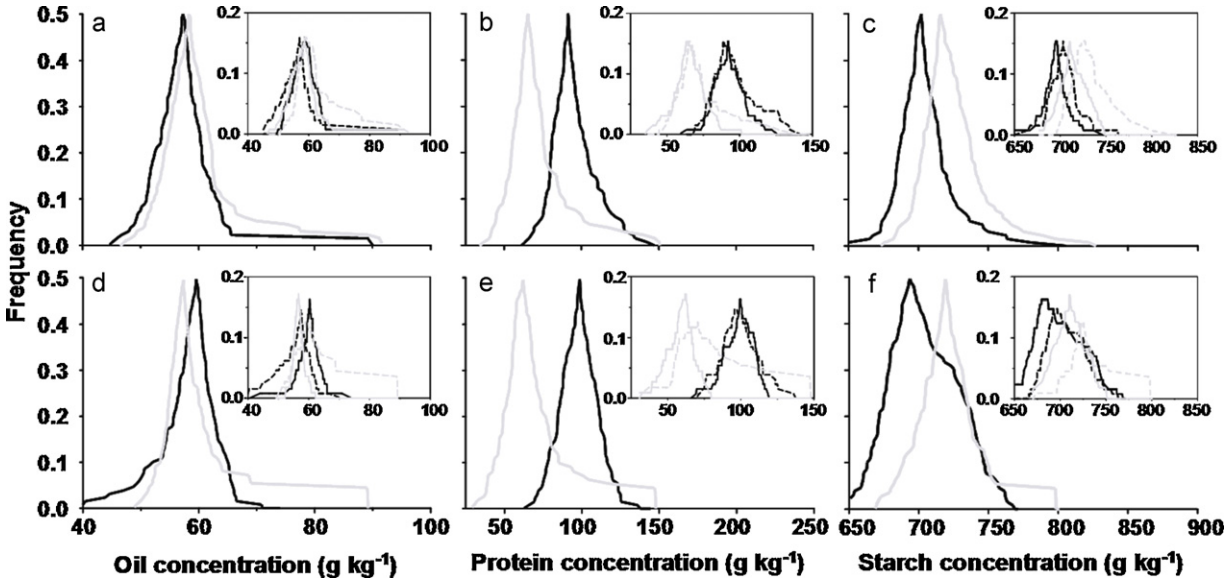

Fig. 2. Frequency distribution of oil (a, d), protein (b, e) and starch concentrations (c, f) of AX820 (a, b, c) and AX877 (d, e, f) data sets in two N levels (N_0: grey line, N_{200}: black line). Data set of each N level comprises all plants (10–12 plants per replicate) of each replicate ($n = 3$), at two plant population densities (9 and 12 plants m^{-2}) during two growing seasons. The insets show the frequency distribution for dominant (solid line) and dominated (dotted line) plants from the same data set.

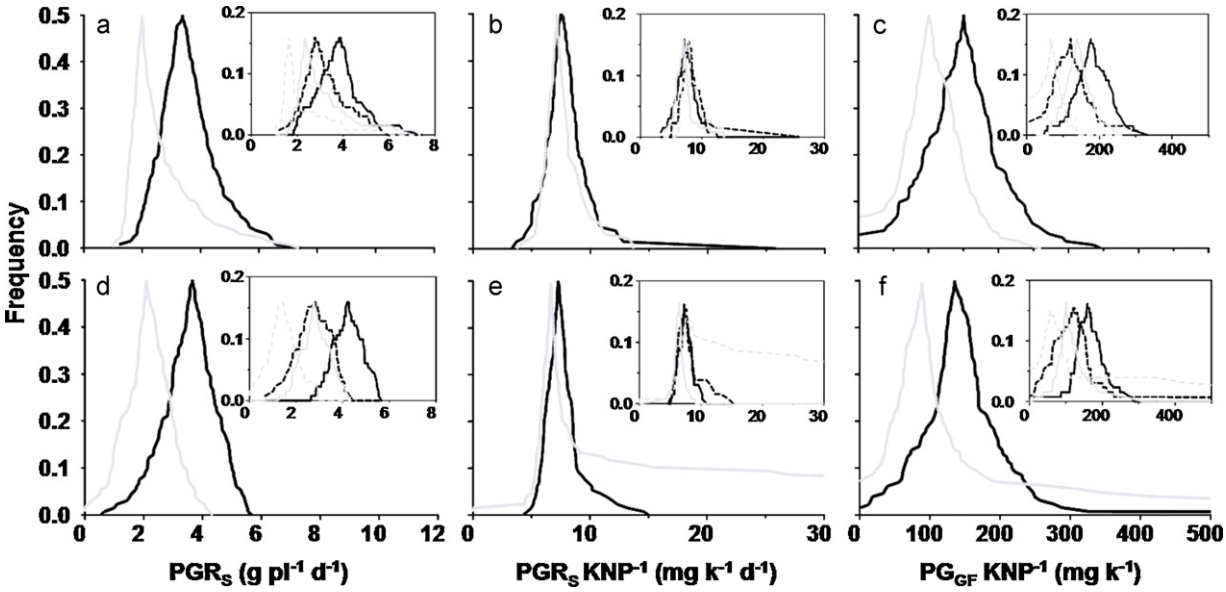

Fig. 3. Frequency distribution of plant growth rate around silking (PGR_S) (a, d), plant growth rate around silking per kernel ($PGR_S\ KNP^{-1}$) (b, e) and plant growth per kernel during the effective grain-filling period ($PG_{GF}\ KNP^{-1}$) (c, f) of AX820 (a, b, c) and AX877 (d, e, f) data sets in two N levels (N_0: grey line, N_{200}: black line). Data set of each N level comprises all plants (10–12 plants per replicate) of each replicate ($n = 3$), at two plant population densities (9 and 12 plants m^{-2}) during two growing seasons. For each variable, a single *x* scale was used to allow comparisons between hybrids. Values out of *x* scale were not presented. The insets show the frequency distribution for dominant (solid line) and dominated (dotted line) plants from the same data set.

and Vega and Sadras (2003). In mentioned studies, at very low plant population densities, data of GYP and KNP followed normal distributions. By contrast, at high population densities, negative kurtosis and left-skewed distribution revealed bimodality of KNP data and authors suggested the existence of individuals with different ability to set kernels: dominant plants at the right of the distribution and the most suppressed plants, with very low KNP or also barrenness, at the left of the distribution. In our experiments, the frequency distribution of GYP and KNP in both N levels did not follow an equivalent pattern. Moreover, hybrids did not exhibit a similar distribution of KNP data especially in low N supply. For the AX820, barrenness (i.e., KNP < 10; Tollenaar et al., 1992) almost did not occur and very few plants (frequency < 0.01) set less than 100 kernels. Nitrogen fertilization did not change the range of KNP (~70–700 kernels pl^{-1}), but enhanced kernel setting of both plant categories, reduced inter-plant variation of the dominant plants

Table 3
Descriptive statistics and normality test for grain yield per plant (GYP); GYP components (KNP: kernel number per plant; KW: kernel weight); kernel composition; plant growth rate (PGR_S) and plant growth rate per kernel around silking ($PGR_S\ KNP^{-1}$) and during the effective grain filling period ($PGR_{GF}\ KNP^{-1}$) of maize hybrid AX877 at two N levels (N_0: unfertilized; N_{200}: fertilized). The two-sample *T* tests (N_0 vs N_{200}) were also included. Data set of each N level comprises all plants (10–12 plants per replicate) of each replicate ($n = 3$), at two plant population densities (9 and 12 plants m^{-2}) during two growing seasons.

Hybrid	Nitrogen	Descriptive statistics	GYP (g pl^{-1})	GYP components		Kernel composition (g kg^{-1})			PGR_S (g pl^{-1} d^{-1})	$PGR_S\ KNP^{-1}$ (mg k^{-1} d^{-1})	$PGR_{GF}\ KNP^{-1}$ (mg k^{-1})
				KNP	KW (mg k^{-1})	Oil	Protein	Starch			
AX877	N_0	*n*	132	132	126	111	111	111	132	126	126
		Mean	65.50	312.51	214.01	59.30	67.26	722.07	2.17	22.01	11.55
		CV (%)	59.57	55.61	19.02	14.43	38.19	3.82	44.10	298.18	6951.9
		Minimum	0	0	99.99	49.33	30.72	669.34	0	0	−6654.30
		Median	65.02	336.00	208.13	57.33	62.18	719.83	2.10	6.70	89.33
		Maximum	146.02	612.00	335.00	89.22	147.84	800.98	4.35	512.76	2540.40
		Skew	−0.09	−0.48	0.86	2.64	1.88	1.00	−0.04	5.57	−5.46
		Kurtosis	−0.74	−0.80	0.94	6.67	3.59	1.62	−0.44	32.97	40.98
		Normality test (*P*)	**	***	***	***	***	***	ns	***	***
	N_{200}	*n*	132	132	130	129	129	129	132	130	130
		Mean	130.49	486.70	264.63	59.97	98.73	702.38	3.62	15.17	151.64
		CV (%)	34.04	29.00	12.34	9.15	15.60	4.69	30.27	577.23	91.58
		Minimum	0	0	171.37	40.00	65.80	640.83	0.66	4.67	−8.40
		Median	135.44	505.75	264.81	59.5	98.91	694.33	3.67	7.31	135.53
		Maximum	220.60	765.00	334.75	74.03	144.39	771.08	5.67	1006.10	1574.00
		Skew	−0.57	−1.17	−0.23	−0.79	0.23	0.36	−0.30	11.27	8.33
		Kurtosis	0.59	1.96	−0.01	2.04	−0.18	−1.02	−0.42	124.92	83.10
		Normality test (*P*)	*	***	ns	***	ns	***	ns	***	***
	N_0 vs N_{200}	Sig.	***	***	***	ns	***	ns	***	ns	ns

ns: not significant.
* Significance level: $P < 0.05$.
** Significance level: $P < 0.01$.
*** Significance level: $P < 0.001$.

Table 4
Two-sample *T* tests (N_0 vs N_{200}) for kernel weight (KW), lag phase duration, the duration of the effective-grain filling period and grain filling rate of maize hybrids AX820 and AX877 at two N levels (N_0: unfertilized; N_{200}:fertilized) during Exp. 2. Data set of each hybrid × N combination comprises three plant types (dominant plants, mean plants, and dominated plants), two plant population densities and three replicates.

Hybrid	Nitrogen	KW (mg k^{-1})	Lag phase	Effective grain-filling period (°C d)	Grain-filling rate (mg °C d k^{-1})	*n*
AX820	N_0	257.19	200.41	516.29	0.50	18
	N_{200}	303.34	200.77	588.48	0.52	18
	N_0 vs N_{200} (Sig.)	***	ns	***	ns	
AX877	N_0	252.55	196.23	531.70	0.48	18
	N_{200}	289.10	190.29	625.25	0.46	18
	N_0 vs N_{200} (Sig.)	***	ns	***	ns	

ns: not significant.
*** Significance level: $P < 0.001$.

and increased inter-plant variation of the most suppressed plants (Fig. 1b inset). By contrast, in N_0 dominated plants of AX877 exhibited both a higher inter-plant variation of KNP and barrenness (~8% of the population) than those of AX820 (Fig. 1b, e insets). N fertilization reduced the number of barren plants (<2%), increased the range of KNP of the dominated plants and displaced the range of this trait to higher values in the dominant plants (Fig. 1e inset). Hence, as was previously documented, N fertilization smoothed inter-plant variation of GYP (Caviglia and Melchiori, 2011), but the extent of this benefit was genotype dependent (Rossini et al., 2011).

Differences between hybrids in KNP variation (i.e., CVs of AX877 higher than AX820) were determined by the response of KNP to PGR_S and the effect of N supply on the latter. For both hybrids, inter-plant variation of KNP, promoted by plant densities and N levels, was related to PGR_S by a single function (Fig. 5a, b), indicating that the only effect of treatments on KNP was through changes in PGR_S (Andrade et al., 2002). Hence, a negative effect of N (D'Andrea et al., 2008) and light stress (Echarte et al., 2004; Luque et al., 2006; Pagano and Maddonni, 2007) on biomass partitioning to the ear was not recorded. In comparison with AX820, hybrid AX877 presented (i) a higher proportion of plants with $PGR_S < 1$ g pl^{-1} d^{-1} especially in N_0 (frequency = 0.14) where bareness occurred (Fig. 3a, d) and (ii) a more linear response of KNP to PGR_S at high PGR_S values (Fig. 5a, b). Therefore, for AX877, high CVs of KNP were recorded in both N levels (i.e., at low and high PGR_S values), and the impact of inter-plant variation of PGR_S on the CV of KNP was of a greater magnitude than for the AX820 (Andrade and Abbate, 2005). For AX877, inter-plant variation of PGR_S exhibited a normal distribution in both N supplies because N fertilization produced a similar displacement of both plant categories' data to higher values (Fig. 3d inset). By contrast, the ranges of PGR_S for AX820 in N_0 and in N_{200} were similar and inter-plant variations exhibited frequency distributions skewed to the right at both N level, but with a fatter right tail in N_{200} (Fig. 3a). A detailed analysis of the frequency distribution of the dominant and dominated plants, revealed that N fertilization smoothed the differences of PGR_S among individuals within each category and between plant categories (Fig. 3a inset).

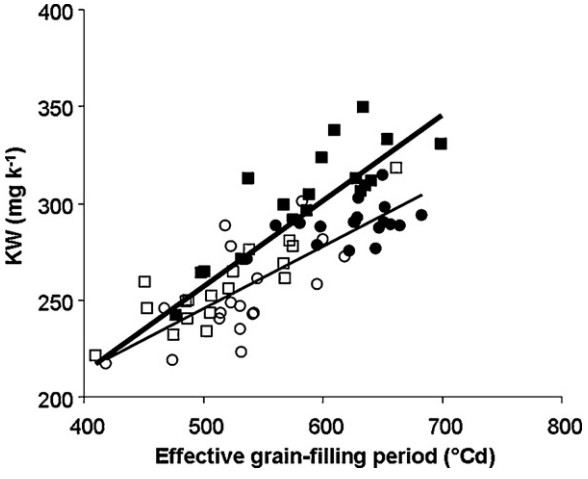

Fig. 4. Kernel weight of AX820 (square symbols) and AX877 (circle symbols) as a function of the duration of the effective grain-filling period. Each point corresponds to KW of each plant category (dominant plants, dominated plants and mean plants) of each replicate in two contrasting N levels (N_0: empty symbols and N_{200}; solid symbols). Lines represent linear models fitted to the whole data set of each hybrid (thick line: AX820; thin line: AX877). For AX820, KW = 0.45 duration + 35.04 ($r^2 = 0.80$, $P < 0.001$). For AX877, KW = 0.32 duration + 84.85 ($r^2 = 0.64$, $P < 0.001$).

Consequently, a symmetric competition for N among plants of the stand seemed to take place for hybrid AX877 (Casper and Jackson, 1997; Berntson and Wayne, 2000), because an increase in the availability of N allowed a similar growth recovery of both plant categories. On the other hand, for AX820, high N supply had a higher impact on PGR_S of the most suppressed individuals, suggesting an asymmetric-competition for N. An asymmetric competition for N and a differential recovery of dominant and dominated individuals after N fertilization has been recently reported in maize crops (Caviglia and Melchiori, 2011). In a previous work, maize hybrids differed in the capacity of dominant and dominated plants to increase their growth after light stress was reduced (Pagano and Maddonni, 2007). Genotypic differences of several photo-morphogenic responses (changes of assimilates allocation to roots, stem elongation, leaf re-orientation) triggered by the early detection of neighbors (Maddonni et al., 2002), may alter the competitive capacity of plants within the stand for capturing scarce resources (Rajcan and Swanton, 2001).

As was previously documented (Edmeades and Daynard, 1979; Echarte et al., 2000; Maddonni and Otegui, 2006), inter-plant variation of KW was lower than CVs of KNP and GYP. For both hybrids, mean values of KW increased and the CVs of this trait decreased in response to high N supply. In N_0 low KWs were attained by a high frequency of dominated plants of AX820 and high frequencies of both plant types of AX877 (Fig. 1c, f insets). In N_{200} dominant plants of both hybrids attained higher KWs than dominated plants. Despite of mentioned patterns of KW, both plant types exhibited similar ranges of PGR_S KNP^{-1} and frequency distributions of this trait almost overlapped (Fig. 3b, e insets). Only in N_0, ~10% of the dominated plants of AX877 with very low KNP exhibited high PGR_S KNP^{-1} (Fig. 3e inset). By contrast, the frequency distributions of PG_{GF} KNP^{-1} of both plant categories at each N level (Fig. 3c, f insets), seems to be in accordance with inter-plant variation of KW (Fig. 1c, f insets). Our analysis of inter-plant variation of kernel growth dynamic revealed that differences in KW between dominant and dominated plants in both N levels were related to the duration of the effective grain-filling period. The reduced PG_{GF} KNP^{-1} of the dominated plants probably determined the premature cessation of the grain-filling period, which was reflected on a KW different from the potential one, previously established

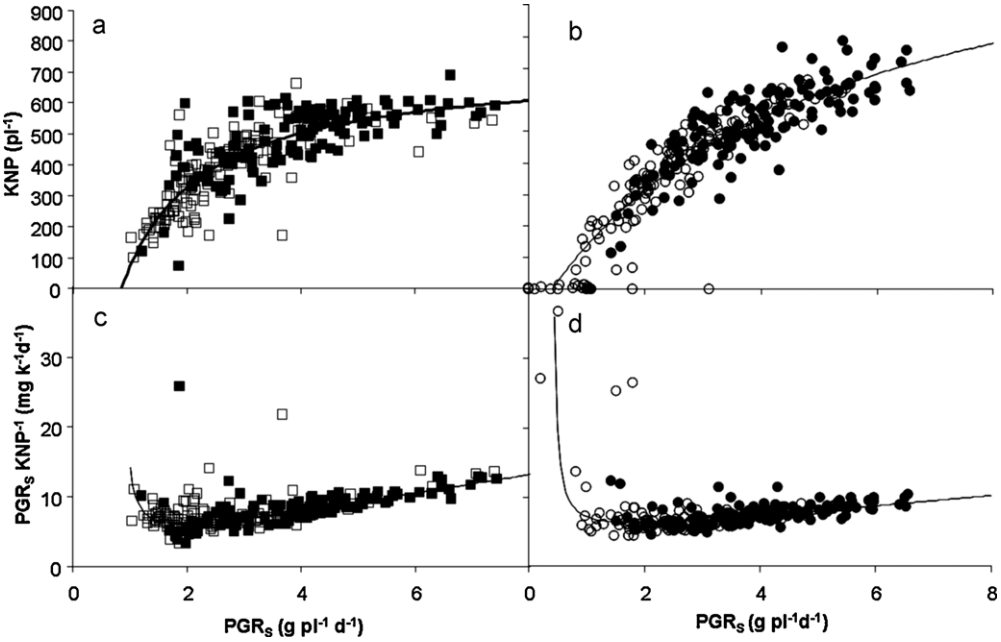

Fig. 5. Relationship between kernel number per plant (KNP) to plant growth rate around silking (PGR_S) (a, b) and PGR_S KNP^{-1} as a function of PGR_S (c, d) of AX820 (a, c) and AX877 (b, d) at two contrasting N levels. Symbols as in Fig. 4. For AX820 (a): $KNP = 454(PGR_S - 0.85)/(1 + 0.58(PGR_S - 0.85))$ for $PGR_S > 0.85$ ($r^2 = 0.74$, $n = 334$). For AX877 (b): $KNP = 384(PGR_S - 0.40)/(1 + 0.82(PGR_S - 0.40))$ for $PGR_S > 0.40$ ($r^2 = 0.84$, $n = 332$). In c, d the line depicts the calculated inverse from the models fitted in a, b. Note that for AX820, PGR_S KNP^{-1} was <40 mg k^{-1} d^{-1} (c). By contrast for AX877 some plants attained PGR_S KNP^{-1} >40 mg k^{-1} d^{-1} but these data were not included (d).

around silking (i.e., PGR_S KNP^{-1}). These results agree with those reported at the canopy levels for water stress (NeSmith and Ritchie, 1992), defoliations (Echarte et al., 2006; Sala et al., 2007a), shadings (Tanaka and Maddonni, 2009) and N stress × sowing date interaction (Melchiori and Caviglia, 2008).

Among kernel chemical compounds, only mean oil concentration was not affected by N supply. Moreover, for any hybrid, frequency distributions of oil concentration data of N_0 and N_{200} were almost overlapped and only few dominated plants in N_0 (frequency < 5%) attained higher oil concentrations (Fig. 2a, d insets). Hence, our results extend previous evidences of the high homeostasis of maize oil concentration (Thomison et al., 2003; Tanaka and Maddonni, 2008) to crops grown under N restrictive environments and reveal the similar kernel oil concentration of the contrasting plant categories. By contrast, N fertilization increased protein concentration, and reduce inter-plant variation of this trait, suggesting that kernels in N_0 were growing under source-limited conditions to maximize protein concentration (Fig. 2b, e). Thus, few dominated plants of both hybrids (~5–10%) in N_0 attained protein concentrations (>65 g kg^{-1}) similar to N_{200} (Fig. 2b, e insets) in accordance with their high PG_{GF} KNP^{-1} (Fig. 3c, f insets). Finally, at post-flowering conditions that enhance and reduce protein and starch concentrations respectively, inter-plant variation of the latter is generally lower than that of the former (Borrás et al., 2002). Thus, in our experiments CV of starch concentration was lower than that of protein concentration and N fertilization reduced mean value of the former. In N_0, inter-plant variation of starch concentration of the dominated plants of AX877 was larger than that of AX820 (Fig. 2c, f insets). Moreover, this pattern was also observed for the other kernel chemical compounds, suggesting that under N stress AX877 exhibited the highest inter-plant competition pressure.

5. Conclusions

In a previous work, we have reported that after N fertilization was applied, hybrid AX820 exhibited a lower inter-plant variation of plant growth than hybrid AX877. In this work we have focused on N effect on inter-plant variation of GYP components, kernel composition and their physiological determinants of both hybrids. We have found that the higher inter-plant variation of PGR_S of AX877 at both N levels was similarly reflected on KNP and GYP variation. The factors behind this response were (i) barrenness at low PGR_S, (ii) the linear response of KNP to PGR_S at high PGR_S and (iii) the low KW variation due to an almost stable PGR_S KNP^{-1}. N stress did not affect PGR_S KNP^{-1} (the determinant trait of potential KW), but reduced the duration of the effective grain-filling period of both hybrids, due to a lower post-flowering source–sink ratio (i.e., PGR_{GF} KNP^{-1}), and this fact was reflected on KW and kernel composition. Under N stress, hybrid AX877 exhibited the highest inter-plant variation of GYP components and kernel composition.

Acknowledgments

This work was supported by the Universidad de Buenos Aires (UBACyT G061 and G070) and the Agencia Nacional de Promoción Científica y Tecnológica (PICT483). L.I. Mayer had an undergraduate scholarship of the Universidad de Buenos Aires and has a graduate scholarship of the National Council for Research (CONICET). M.A. Rossini has a graduate scholarship of and G.A. Maddonni is member of CONICET.

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