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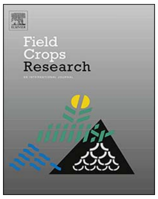

Water use efficiency for grain yield in an old and two more recent maize hybrids

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ABSTRACT

Increasing water use efficiency for grain production, WUEg (i.e. the quotient between grain yield and seasonal evapotranspiration, ET) is of relevance in rainfed crops. A greater WUEg is expected in more recent than in old maize (*Zea mays* L.) hybrids, based on different reports indicating higher grain yield, higher stress tolerance or similar seasonal ET in more recent than in old maize hybrids. However, there are no reports quantifying WUEg in maize hybrids released in different decades. In this study we quantify WUEg and its components (i.e. grain yield and seasonal ET) and we examine physiological traits during the critical period for kernel set (i.e. plant growth rate, PGRcp; ear growth rate, EGRcp; ET, ETcp and stomatal conductance), in an old and in two more recent maize hybrids grown under contrasting soil water availability. Three maize hybrids, DK2F10 (old hybrid released in 1980) and DK682RR and DK690MG (more recent hybrids, released in 2004), were grown in 5 experiments during 4 seasons; and irrigation and rainfed treatments were used to promote contrasting soil water availabilities. Soil water content was measured every 7–10 days with a neutron probe. Maximum WUEg tended to be higher for more recent (25.1 kg ha^{-1} mm^{-1}) than for the older hybrid (23.1 kg ha^{-1} mm^{-1}); and advantages of WUEg were larger and significantly higher in the more recent than in the older hybrid, at lower water availability. The greater WUEg of more recent hybrids was associated with greater grain yield at all water supplies; which was the result of a greater KNP. At low water availability, the greater KNP in more recent hybrids was related to greater PGRcp, ETcp and stomatal conductance than in the old maize hybrid.

1. Introduction

Water use efficiency for grain yield (WUEg) involves grain yield production and seasonal crop evapotranspiration (i.e. Grain yield/ET; Passioura, 1996). Understanding the associated physiological mechanisms contributing to its determination is required to better orientate breeding efforts, modeling and agronomic management towards greater yields stability under increasing climate variability (IPCC, 2014). It is known that the grain yield component of the WUEg has increased during the last decades for maize (*Zea mays* L.) hybrids (e.g. Echarte et al., 2000; Tollenaar and Lee, 2011). In Argentina, grain yield potential (i.e. when hybrids were grown in environments to which they are adapted and with no resource availability limitations) increased at a rate of 107 kg ha^{-1} yr^{-1} between 1965 and 2010 (Di Matteo et al., 2016). That increment was mainly attributed to a sharp rise in harvest index between 1982 and 1993 and to consistent increments in shoot biomass production (Echarte and Andrade, 2003; Luque et al., 2006; Echarte et al., 2013; Di Matteo et al., 2016). Higher grain yields under resource limited environments were also demonstrated in more recent than in older hybrids (e.g. Tollenaar and Wu, 1999). For example, more recent hybrids are more tolerant to low soil nitrogen availability (Rajcan and Tollenaar, 1999; Echarte et al., 2008), weed interference (Tollenaar et al., 1997) and high plant population density (Duvick and Cassman, 1999; Echarte et al., 2000; Tollenaar and Lee, 2002; Duvick et al., 2004). Moreover, tolerance to high plant density and stability across environments were closely associated in hybrids released in different decades (Di Matteo et al., 2016). Thus, the comparison between more recent and older maize hybrids has the potential to identify underlying processes influencing a greater grain yield under low water availability. Nevertheless, grain yield response to water deficiencies in particular, has been less studied in more recent than older hybrids. Retrospective studies focusing on water deficiency effects, have associated greater grain yield under low water availability with lower anthesis-silking interval and bareness reduction (e.g. Bolaños et al., 1993; Edmeades, 2013; Campos et al., 2006); however, in these studies, WUEg was not quantified.

The seasonal crop ET component of WUEg has remained similar among temperate maize hybrids released in different decades, under

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Table 1

Mean photosynthetically active radiation (PAR), mean air temperature, accumulated reference evapotranspiration (ET_0), and accumulated rainfall per month, in Experiments 1–5 and for a series of 30 years (H) at Balcarce, Argentina. Accumulated irrigation per month is depicted for the treatments: irrigated (I), rainfed from silking (Rs), rainfed during critical period for kernel set (Rc) and rainfed during grain filling (Rf), in Exp. 1–5.

	PAR (MJ m^{-2} d^{-1})					Mean air temperature (°C)					ET_0 (mm)					Rainfall (mm)					Irrigation (mm)									
Exp.	1	2	3	4-5	*H*	1	2	3	4-5	*H*	1	2	3	4-5	*H*	1	2	3	4-5	*H*	1		2			3	4		5
																					I	Rs	I	Rf	Rc	I	I	R	I
Oct	8,8	9,0	7,7	8,3	*8,0*	13,9	13,9	13,5	14,9	*13,6*	92	109	92	96	*88*	29	30	45	51	*86*									
Nov	10,7	10,2	10,1	10,8	*10,0*	19,8	17,2	16,3	17,8	*16,5*	136	132	120	137	*116*	53	70	116	64	*85*							51	16	27
Dic	11,6	10,9	12,5	11,2	*11,2*	20,7	19,2	20,9	20,2	*19,2*	162	151	175	165	*145*	31	121	33	239	*86*	121	121	21	21		153	134	11	53
Ene	12,3	11,1	11,4	10,3	*11,0*	22,5	22,9	22,3	21,1	*21,1*	188	170	159	143	*148*	25	84	185	152	*119*	72		140	36		51	53		22
Feb	10,2	9,7	10,2	10,6	*9,7*	22,2	20,4	20,1	21,1	*20,2*	138	114	116	133	*115*	64	108	33	33	*66*	24		159		159	58	144		133
Mar	7,2	6,8	8,2	7,7	*7,5*	20,5	18,5	19,9	16,4	*18,3*	105	86	111	90	*93*	66	203	22	114	*78*			64		64	19	17		8

low and under high water availability (Nagore et al., 2014; Reyes et al., 2015). In agreement, soil water content throughout the season was not different among tropical maize cultivars differing in cycle of selection (Bolaños et al., 1993). These results together, suggest greater WUEg in more recent than in older maize hybrids; and there is a lack of information regarding WUEg under contrasting soil water availability in hybrids released in different decades.

A greater WUEg of more recent maize hybrids is likely mediated by a greater kernel number set (e.g. Di Matteo et al., 2016). However, it is noteworthy that there are no previous studies focusing on the understanding of the mechanisms underlying kernel set determination together with crop ET, and under contrasting soil water availability in older and in more recent maize hybrids. Kernel number per plant (KNP) is associated with plant growth rate during the critical period for kernel set (PGRcp; Tollenaar and Daynard, 1978; Fischer and Palmer, 1984; Kiniry and Ritchie, 1985; Aluko and Fischer, 1988; Andrade et al., 1999). In maize, the KNP–PGRcp relationship has been described by two successive curves to account for the first and second ear in prolific plants, or a single curve in nonprolific plants (Tollenaar et al., 1992; Andrade et al., 1999; Vega et al., 2001; Echarte et al., 2004). The KNP-PGRcp relationship indicates a PGRcp threshold for kernel set at low PGRcp and a value of the asymptote at high PGRcp that represents the potential KNP (Tollenaar and Aguilera, 1992; Andrade et al., 1999; Vega et al., 2001; Echarte et al., 2004; Echarte and Tollenaar, 2006). A greater KNP at low and at high soil water availability could be associated with greater PGRcp and/or with greater KNP per unit PGRcp (KNP/PGRcp; Echarte and Tollenaar, 2006). Although seasonal ET was similar between older and more recent maize hybrids, daily ET during the critical period for kernel set (ETcp) was greater in more recent than older hybrids under low water availability (Nagore et al., 2014). Therefore, a greater PGRcp might contribute to a greater KNP in more recent than in older hybrids under low water availability. A greater KNP/PGRcp, by means of greater dry matter partitioning to the ear during the critical period for kernel set (i.e. greater ear growth rate, EGRcp), might also contribute to a greater KNP as suggested by Bolaños et al. (1993) and Reyes et al. (2015). In addition, a greater KNP/EGRcp might also influence a greater KNP/PGRcp in more recent than in the old hybrids.

We tested the hypothesis that WUEg is greater in more recent than in an old maize hybrid. The objectives of this study were to quantify WUEg and to examine physiological traits (i.e. PGRcp, EGRcp, stomatal conductance) and their association with ETcp and KNP, in an old and two more recent maize hybrids, under contrasting soil water availability. Results of this study will contribute to elucidate ecophysiological mechanisms associated with a greater WUEg in maize hybrids.

2. Materials and methods

2.1. Site and crop management

Maize crops were grown at Balcarce, Argentina (37°45′S;58°18′W; elevation 130 m) during four seasons: 2008–2009 (Season 1, Exp. 1); 2009–2010 (Season 2, Exp. 2); 2010–2011 (Season 3, Exp. 3) and 2012–2013 (Season 4, Exps. 4 and 5). Soil was a silty clay loam soil (Typic Argiudoll; USDA Taxonomy) with a petrocalcic horizon between 140 cm and 160 cm depth, a clayey layer (Bt) between 40 cm and 90 cm depth, and with 5.4% top soil organic matter. Experiments were conducted under conventional tillage and crops were fertilized with 45 kg N ha^{-1} at sowing and with 150 kg N ha^{-1} at the V6 stage (Ritchie and Hanway, 1982). Sowing dates were October 23, 21, 20 and 25 during Seasons 1–4, respectively. The plots were over sown and thinned during V3 stage, to 7.5 pl m^{-2}, which is the recommended plant density for current hybrids in this area and it doesn‘t promote grain yield reductions in older hybrids (Echarte et al., 2000; Di Matteo et al., 2016). Weeds and insects were adequately controlled with mechanical and chemical methods. This area is characterized with

Table 2
Year of release, cross type, endosperm type, relative maturity and thermal time from sowing to R1 and from R1 to Maturity, for three maize hybrids.

Hybrid	Years of release	Cross type	Endosperm type	Relative maturity	Thermal time (°C día-1)	
					Sowing- R1	R1-Maturity
DK2F10	1980	Single	Flint	117	893	672
DK682RR	2004	Single	Semident	118	872	685
DK690MG	2004	Single	Semident	119	902	727

temperate mean temperatures during the growing season and a frost free period of around 150 days. Monthly weather data during Seasons 1–4 and historic data corresponding to a series of 30 years (1983–2013) are presented in Table 1. Seasonal rainfall differed among seasons; it was lower than historic data during Seasons 1 and 3 (i.e. 47 and 14% lower than historic data, respectively) and it was higher than historic data during Seasons 2 and 4 (i.e. 19 and 26% higher than historic data, respectively). In addition, rainfall during January, which is the most critical month for kernel set in the South East of Buenos Aires, Argentina (Andrade et al., 1996), was 20 and 70% lower than the historic value in season 1 and 2, respectively, and rainfall was higher 55 and 28% in season 3 and 4, respectively.

2.2. Plant material, treatments and experimental design

Treatments combined (i) three maize hybrids differing in their year of release, and (ii) contrasting water regimes. Maize hybrids included, the old hybrid DK2F10 released in 1980 and two more recent hybrids released in 2004, DK682RR (characterized with high adaptability to poor environments) and DK690MG (characterized with low adaptability to poor environments; De Santa Eduviges, 2010; Table 2). These single cross maize hybrids were selected because of their commercial importance in the area under study; since they were among the eight most cultivated hybrids in the Argentinean Pampas for at least 5 years after their release. Water treatments comprised: i) drip irrigation (I) during the whole season in all experiments; ii) rainfed (R) condition during whole season, in Exps. 1, 3, 4 and 5; and iii) rainfed during specific development period: from silking to physiological maturity (Rs) in Exp. 1 and rainfed during critical period for kernel set (Rcp) or during grain filling period (Rf) in Exp. 2. In Exp. 2, the entrance of water from rain was avoided adding soil plastic covers, which were also added to irrigate treatments. An additional experiment was conducted during Season 4 (Exp. 4) under a rain out shelter without laterals walls, with irrigation and rainfed treatments during the whole season. Hybrids and water treatments performed in each experiment are depicted in Table 3.

The experimental design was a split plot randomized complete-block design with three replications with water regimes as main plots and hybrids as subplot. Subplots comprised 7 rows, 0.7 m apart and 14 m long, in Exps. 1, 2, 3 and 5. Subplots in Exp. 4 comprised 6 rows, 0.7 m apart and 6 m long according to the shelter measurements, and included only two repetitions.

Table 3
Experiments (1–5) and their corresponding season (1–4), water treatments (irrigated, I; rainfed, R; rainfed from silking, Rs; rainfed during the critical period for kernel set, Rcp; rainfed during the filling period, Rf; no irrigation, NI) and maize hybrids (DK2F10, DK682RR, DK690MG).

Experiment	Season	Water treatments	Hybrids
Exp.1	1	I, R, Rs	DK2F10, DK682RR
Exp.2	2	I, Rcp, Rf	DK2F10, DK682RR, DK690MG
Exp.3	3	I, R	DK2F10, DK682RR, DK690MG
Exp.4 (shelter)	4	I, NI	DK2F10, DK682RR
Exp.5	4	I, R	DK2F10, DK682RR

2.3. Measurements

Silking dates (R1; Ritchie and Hanway, 1982) were recorded for each plot as the dates when 50% of the plants presented at least one emerged silk from the husk, in 20 plants in the central row. The critical period for kernel number determination was estimated as R1 ± 15 days.

Soil water content was measured weekly with a neutron probe (Troxler 103 A, Troxler Electronic Lab, NC) in each experimental unit. The method combined gravimetric measurements between 0 and 10 cm depth and the use of the neutron probe in 10 cm increments between 10 and 40 cm depth and in 20 cm increments from 40 to 140 cm depth in each experimental unit. Time per measurement was set to 15 s. One access tube per experimental unit was placed midway between the two central harvest rows, and the neutron probe quantified water status in an area with a diameter of 50 cm. Probe data were expressed in water content according to Suero and Travasso (1988).

Shoot biomass was determined at around 15 days before and at 15 days after silking, in samples of 10 plants; leaving borders of at least 1 m between successive harvests. In all cases, samples were taken from the central rows of each subplot; plants were separated into stem, leaves, ears and husks and were oven-dried (forced air at 60 °C) to constant weight and weighed. Morphometric variables (i.e. basal stem diameter and diameter at the widest position of the ear and ear length) were recorded in 10 tagged plants per treatment that remained in the field and in 5 harvested plants, in Exp. 4.

Grain yield was determined at physiological maturity by collecting consecutive ears in 5 m from each of the two central rows. Ears were dried to constant weight and shelled. Kernel weight was obtained by counting and weighing two samples of 500 kernels each.

Leaf carbon exchange rate (leaf CER) and stomatal conductance were measured during the critical period for kernel set, once a week in clear-sky days at midday on light-adapted leaves. Measurements were taken on the ear leaf or on the first leaf above the topmost ear of 3 plants per plot, in all experiments. Leaf CER and stomatal conductance were measured with a portable, open-flow gas exchange system LI-6400 (LI-COR, Lincoln, NE) at 2000 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) at the leaf surface using the 6400–02 LED light source (LI-COR). The flow rate of air through the sample chamber was set at 350 μmol s^{-1}. The sample chamber CO_2 concentration was adjusted to 400 μmol CO_2/mol air using the system's CO2 injector (model 6400-01, LI-COR).

2.4. Estimations and data analysis

Soil water content in each experimental unit was expressed either in mm or as a percentage of soil available water (AW), which was calculated as:

$$AW\ (\%) = (SW - PWP)/SAW \times 100$$

where SW is soil water content (i.e. the sum of the water content in all layers for each date of measurement expressed in millimeters), PWP (mm) is permanent wilting point, and SAW is soil available water (i.e. the difference between maximum water holding capacity and permanent wilting point expressed in millimeters). Maximum water holding capacity was determined according to Cassel and Nielsen (1986). Briefly, a plot of soil free of crops or weeds was covered with polyethylene and soil water content was measured after wetting the soil profile; the soil moisture was monitored from 2 days after wetting and until the water content rate of change was null (i.e. negligible drainage). The permanent wilting point was determined according to Richards and Weaver (1943).

Crop evapotranspiration (ET) was calculated as rainfall plus irrigation minus change in soil water storage between two observation dates, minus runoff. Water drainage was estimated as the difference between maximum water holding capacity and measured soil water content. Crop ET calculations assumed precipitation was effective, the application efficiency of supplemental irrigations was 100%, and runoff was zero. These assumptions were based on the fact that the experimental area was flat and well drained. Evapotranspiration during the critical period for kernel set (ETcp) was calculated accumulating daily ET for the period of R1 ± 15 days. Crop ET was not calculated in Exp. 2 since it was not possible to accurately determine the entrance of water from rainfall; because plastic covers did not fully avoid the entrance of rainfall to the soil.

Shoot and ear biomass of tagged plants were estimated with allometric relationships between morphometric variables and shoot biomass in Exp. 4 (Table 4), according to Echarte et al. (2004).

Plant growth rate during the critical period for kernel set (PGRcp) was estimated as the quotient of accumulated biomass in shoots and the duration of the period in growing degree-days (GDDs). Growing degree-days were calculated from daily average temperatures above 8 °C (Ritchie and NeSmith, 1991; Cirilo and Andrade, 1996) and accumulated during the critical period for kernel number determination. Ear growth rate (EGR) was estimated as the quotient between accumulated ear biomass to 15 days after silking.

Kernel number per unit area was calculated as the quotient between grain yield and individual grain weight. Kernel number per unit area was then divided by plant density to obtain kernel number per plant (KNP).

Water use efficiency for grain yield (WUEg) was calculated as the quotient between grain yield and seasonal crop ET.

Grain yield and KNP reductions were calculated for each hybrid under rainfed treatments in relation to irrigated treatment, in all experiments.

Analysis of variance, using the statistical software R 3.1.0 (2014-04-10), was used to test the effect of water regimes, hybrids and their interactions on grain yield, crop ET, ETcp, WUEg, KNP, PGRcp, EGRcp, grain yield reduction and KNP reduction in each experiment. Regression analyses including all experiments were used to test differences between an old and two more recent hybrids, across ET/ET_0, PGRcp or stomatal conductance. Regression analysis was done by the least-squares method and regression coefficients were analyzed by *t*-test (Steel and Torrie, 1980), with a significant level of 0.05.

The least significant difference test (LSD) was used to determine significant differences among means ($p < 0.05$).

Table 4
Relationships between morphometric variables (sd = stem diameter, mm; ed = ear diameter, mm) and (i) shoot biomass at the beginning (S0) and at the end (S1) of the critical period for kernel set, or (ii) ear dry matter of the uppermost ear (E) for two hybrids in Exp. 4. All models were significant at $p < 0.05$.

Hybrid	Shoot biomass	Ear dry matter
DK2F10	S0 = 8.828 * sd − 108.08 S1 = 11.28 * sd − 67.33	E = 0.01588 * ed − 7.38
DK682RR	S0 = 7.095 * sd − 79.24 S1 = 13.43 * sd − 110.69	E = 1.1437 * ed − 21.98

3. Results

3.1. Soil water availability and grain yield

Water regimes resulting from rainfall and irrigation, provided an ample range of soil water availability in the 5 experiments (Fig. 1). Characteristics of soil water availability in Experiments 1 and 3 were already published in Nagore et al., 2014, as season 1 and 2 respectively. Briefly, soil water deficiencies (i.e. soil available water < 50%; AW; Doorenbos and Kassman, 1979) occurred during the critical period for kernel set and during the grain filling in Exp. 1 and 3 in rainfed treatments; and water deficiency was greater in Exp. 1 than Exp. 3 (Fig. 1a, b, c and g, h, respectively). Water deficiencies were moderated and occurred during the grain filling period only, in Exp. 4 and 5 (Fig. 1i–l). In Exp. 2 water deficiencies were moderated and occurred during the grain filling or during the critical period (Fig. 1d–f). In general, irrigation treatments were able to maintain water availability above 50% during the critical period for kernel set; but in Exps. 1 and 2, mean AW among hybrids was as low as 50 and 52%, respectively; while in Exps. 3, 4 and 5, mean AW among hybrids was between 74 and 76% during the same period (Fig. 1).

More recent hybrids out yielded the older one in the 5 experiments ($p < 0.05$; Table 5). Hybrid x water regime was not significant for grain yield ($p > 0.05$). Grain yield reductions due to water supply treatments were in accordance with the degree of water deficiencies obtained in each experiment. Thus, greater grain yield reduction due to water availability occurred in Exps. 1 and 3 and were 52% and 22%, respectively in I vs. R treatments ($p < 0.05$; Table 5). Grain yield reductions were moderated in Exp. 2 (12%, when water supply was interrupted during the critical period; $p < 0.05$), and in Exp. 4 and 5 grain yield reductions ranged from null to 15% and were not significant, respectively ($p > 0.05$). In Exp. 1 that presented the largest grain yield reduction due to water deficiency, grain yield reduction in rainfed compared with irrigated treatments, was higher in the old hybrid (59%) than in the more recent hybrid (45%; $p < 0.05$). Grain yield reductions due to water deficiencies were associated with reductions in both grain yield components, KN and KW ($p < 0.05$). However, grain yield reductions due to water deficiencies were attributed mainly to KN reductions in the older hybrid and they were attributed to both components in more recent hybrid. For example, drastic grain yield reductions in Exp. 1 (59%) were associated with great kernel number reductions (56%) and low reductions in KW (5%) in the old hybrid; whereas, grain yield reduction (45%) was associated with 31% reduction in KN and 21% reduction in KW, in rainfed with respect to irrigated treatment in the more recent hybrid.

3.2. Shoot biomass and grain yield response to evapotranspiration

Seasonal crop evapotranspiration (ET) ranged from 282 to 662 mm among water regimes (rainfall and irrigation), hybrids and experiments (values of ET of Exp. 1 and 3 were published in Nagore et al., 2014). Reference ET_0 differed among experiments. It was 672 (Exp. 1), 636 (Exp. 3) and 609 mm (Exp. 4 and 5); thus, seasonal crop ET was relativized to ET_0 in order to compare crop ET among seasons (i.e. ET/ET_0; Fig. 2).

Increments in shoot biomass and in grain yield were associated with increments in seasonal ET/ET_0 among experiments ($p > 0.05$; Fig. 2a, b). Shoot biomass response to ET/ET_0 was linear and similar among hybrids ($p > 0.05$; Fig. 2a). Grain yield response to seasonal ET/ET_0 was curvilinear and grain yield was higher in the more recent hybrids than in the old one at any given value of seasonal ET/ET_0 ($p < 0.05$; Fig. 2b).

3.3. Water use efficiency for grain yield

Water use efficiency for grain yield (WUEg) ranged from 11 to

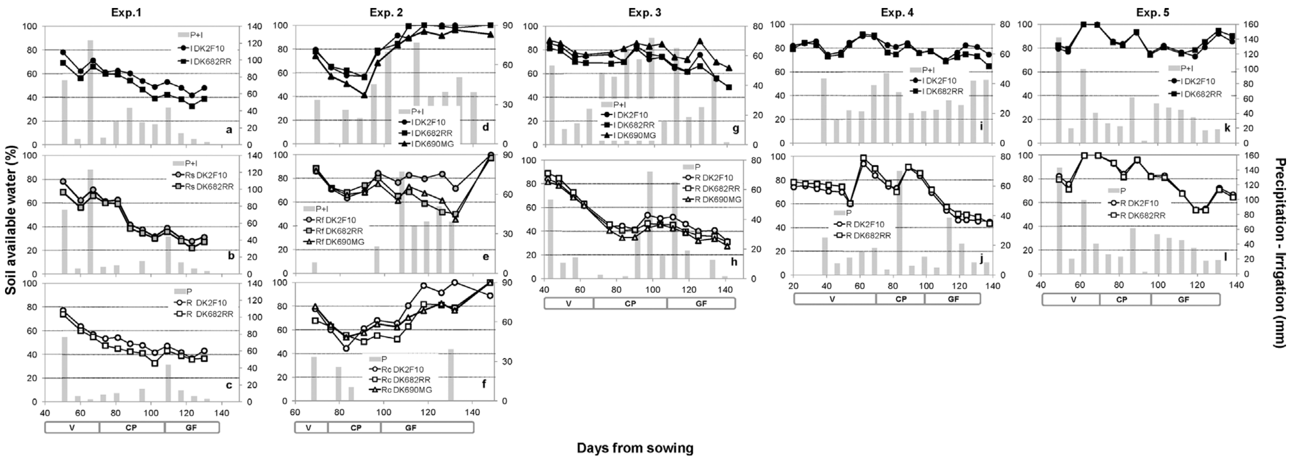

Fig. 1. Soil available water and precipitation plus irrigation as a function of days from sowing, in Exps. 1–5 for one old (DK2F10) and two more recent (DK682RR and DK690MG) maize hybrids, under different water regimes: irrigated (I: a, d, g, I and k), rainfed from silking (Rs: b), rainfed during the critical period for kernel set (Rc: f), rainfed during grain filling (Rf: e) and rainfed (R: c, h, j and l). Phenological stages were identified as vegetative period (V), critical period for kernel set (CP) and grain filling (GF).

27 kg ha^{-1} mm^{-1} among hybrids, water regimes and experiments (Table 5). Hybrid x water regime interaction for WUEg was not significant ($p > 0.05$). Water use efficiency for grain yield was greater in the more recent hybrids than in the old one for the whole range of seasonal ET/ET$_0$ explored ($p < 0.05$; Fig. 3). Maximum WUEg from adjusted quadratic curves tended to be higher in more recent hybrids (25.1 kg ha^{-1} mm) than in the older hybrid (23.1 kg ha^{-1}; $p > 0.05$); and occurred at similar seasonal ET/ET$_0$ (i.e. ET/ET$_0$ for maximum WUEg was 0.80 for the old hybrid and 0.79 for more recent hybrids; Fig. 3) which corresponded to around 400 mm of crop ET. With the treatments applied it was possible to explore environments with seasonal ET/ET$_0$ < 0.80 with the older hybrid and one more recent hybrid (i.e. DK682RR); and reductions in ET/ET$_0$ below 0.8 decreased WUEg to a greater extent in the older hybrid than in the more recent one. Thus, WUEg decreased 49% in the old hybrid and 31% in the more recent hybrid (at ET/ET$_0$ = 0.43). Values of ET/ET0 larger than 0.8 reduced WUEg by 18% in the old hybrid and by 13% in the more recent ones (i.e. at ET/ET$_0$ = 1.03).

3.4. KNP-PGRcp relationship, EGRcp and ETcp

Water regimes and experiments provided a wide range of PGRcp and KNP (Table 6). Hybrid × water regime interaction for both, KNP and PGRcp were not significant ($p > 0.05$). Mean reductions in KNP, in rainfed with respect to irrigated treatments among experiments, were 18% and 10% for the old and the two more recent hybrids, respectively. Severe water deficiencies during the critical period for kernel set (i.e. rainfed treatments in Exp. 1) reduced KNP by 56–33% in the old hybrid and 31–15% in the more recent hybrid in R and Rs water treatments, respectively. Consistent trends of greater PGRcp in the more recent hybrids than in the old one were evident in all the experiments (significant in two out of 5 experiments; $p < 0.05$, Table 6); PGRcp consistently tended to decrease in response to water supply reductions (significant in one out of 5 experiments, Table 6). Kernel number per plant per unit of PGRcp (KNP/PGRcp) did not present a clear trend among hybrids (not shown). Crop ETcp and standardized ETcp (i.e. ET/ET$_0$ during cp) were consistently greater in the more recent than in the older hybrid at each water regime in all the experiments (significant in

Table 5

Grain yield (kg ha^{-1}) and water use efficiency for grain yield (WUEg, kg ha^{-1} mm^{-1}) in an old hybrid (DK2F10) and two more recent hybrids (DK682RR and DK690MG) at different water regimes: irrigated (I), rainfed (R), rainfed from silking (Rs), rainfed during critical period for kernel set (Rc), rainfed during grain filling (Rf) and no irrigated (NI), in Experiments 1–5.

Exp.	Water regime	Grain Yield (kg ha^{-1})				WUEg (kg ha^{-1} mm^{-1})			
		DK2F10	DK682RR	DK690MG		DK2F10	DK682RR	DK690MG	
1	I	7891	9266		*A*	19	21		*A*
	Rs	5223	6665		*B*	16	20		*AB*
	R	3227	5093		*C*	11	18		*B*
		b	*a*			*b*	*a*		
2	I	9989	10899	11844	*A*				
	Rf	8900	10940	10648	*AB*				
	Rc	8514	9725	10568	*B*				
		b	*a*	*a*					
3	I	11897	13738	13385	*A*	18	21	22	*A*
	R	9354	10953	10215	*B*	22	25	23	*A*
		b	*a*	*a*		*b*	*a*	*a*	
4	I	12434	14195		*A*	21	24		*B*
	R	10704	11902		*A*	25	27		*A*
		b	*a*			*a*	*a*		
5	I	12135	13559		*A*	20	21		*A*
	R	12105	13609		*A*	24	27		*A*
		b	*a*			*b*	*a*		

Lower case letters and capital letters indicate differences among hybrids or among water regimes, respectively ($p < 0.05$; LSD).

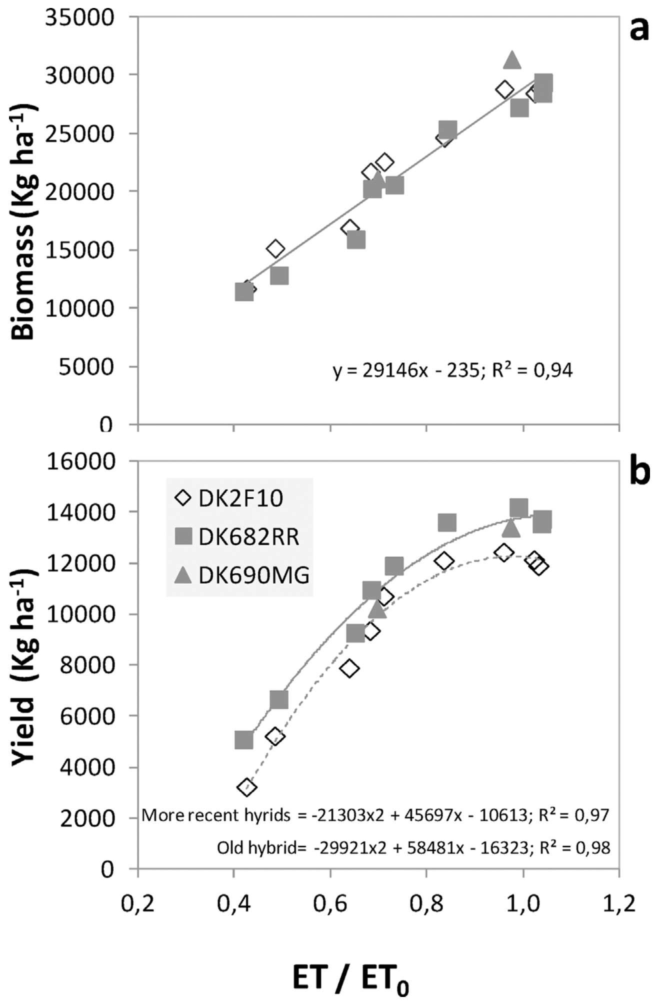

Fig. 2. Final shoot biomass (a) and grain yield (b), as a function of standardized seasonal ET (i.e. ET/ET_0); for one old (DK2F10) and two more recent (DK682RR and DK690MG) maize hybrids in 5 experiments including contrasting water regimes. One lineal function for all hybrids was fitted to the shoot biomass-seasonal ET/ET_0 relationship ($p < 0.05$). One quadratic curve for the old hybrid and one quadratic curve for the two more recent hybrids were fitted to the grain yield-seasonal ET/ET_0 relationship ($p < 0.05$).

2 out of 4 experiments; ETcp absolute values of Exps. 1 and 3 were reported in Nagore et al., 2014). These differences were greater at low water supply (i.e. rainfed in Exp. 1 and 3, Nagore et al., 2014).

One equation fitted the relationship between KNP and PGRcp for more recent and older maize hybrids (Fig. 4a). Also, variation in EGRcp was positively associated with variation in PGRcp among experiments and hybrids (Fig. 4b). The PGRcp was expressed in growing degree days in order to include all the experiments in the same relationship; similar results were obtained when PGRcp was relativized to ET_0 during the critical period for kernel set (not shown). However, KNP response to standardized ETcp (i.e. ET/ET_0 during cp) differed between hybrids (Fig. 5); thus, newer hybrids set more KNP at low and at high ET/ET_0cp than the older hybrid (Fig. 5).

The PGRcp and ET/ET_0cp were linearly and positively related across experiments (Fig. 6); and, in general, PGRcp of the more recent hybrids were greater than that of the old hybrid for the whole range of ET/ET_0cp ($p < 0.05$; Fig. 6). In addition, the relationship between leaf carbon exchange rate (CER) and stomatal conductance during the critical period for kernel set was curvilinear and one equation fitted the relationship for more recent and older hybrids (Fig. 7). Mean stomatal conductance was 0.14 mol H_2O m^{-2} s^{-1} for the old hybrid and it was 0.20 mol H_2O m^{-2} s^{-1} for the more recent hybrid, in the rainfed from silking (Rs) and irrigated (I) treatments of Exp. 1; which presented the lowest water availability during the critical period (i.e. mean WA was 51 and 47% for the old and the more recent hybrid, respectively).

4. Discussion

Water use efficiency for grain yield ranged from 11 to 27 kg ha^{-1} mm^{-1} among hybrids, water regimes and experiments (Table 5). Similar measured values of WUEg were reported in previous works for maize grown under variable conditions of water and/or nitrogen supply (e.g. Howell et al., 1998; Ogola et al., 2002; Barbieri et al., 2012; Hernandez et al., 2015; Tolk et al., 2016). Maximum WUEg tended to be higher in the more recent hybrids (25.1 kg ha^{-1} mm^{-1}) than in the old one (23.1 kg ha^{-1} mm^{-1}; Fig. 3); and maximum WUEg values of this study fit below the maximum limit (37 kg ha^{-1} mm^{-1}) estimated by Grassini et al. (2009) by means of crop models. Lower values of WUEg than the maximum limit might be related to large water losses and due to high evaporation and/or drainage; along with lower ceiling for potential productivity (radiation and temperature), and/or genotypic differences. In addition, WUEg of the more recent hybrids was larger than that of the older hybrid across an ample range of environments varying in water availability (Fig. 3). Moreover, WUEg advantage of more recent hybrids over the old hybrid was higher at lower water availability (Fig. 3). Advantages in WUEg of more recent compared with the old hybrid were mainly related with greater grain yield (Fig. 2b); since seasonal crop ET and shoot biomass production were similar among hybrids (Fig. 2a). Results of this work about similar seasonal crop ET among hybrids released in different decades, confirm our previous findings (Nagore et al., 2014) and others (Reyes et al., 2015). In addition, the greater grain yield of the more recent hybrids compared with the old one at all water availabilities (Fig. 2), are in agreement with previous findings from retrospective studies (Edmeades et al., 2003, cited by Campos et al., 2004; Reyes et al., 2015) and supports the greater general stress tolerance of more recent than old hybrids (e.g. Tollenaar and Wu, 1999; Di Matteo et al., 2016). The similar shoot biomass production but greater grain yield of more recent hybrids than the old one under contrasting water availabilities (Fig. 2), indicate that a greater WUEg of more recent hybrids (Fig. 3) is mainly related with a greater dry matter partitioning to the harvestable organs (i.e. harvest index). Although the number of hybrids used in this study was small to infer general trends with time in water relationships and coping mechanisms; results of this manuscript demonstrated detailed mechanisms contributing to explain the greater WUEg in two more recent hybrids and in an old one. These hybrids, however, were widely used by the time of their released and they follow the same trend across years than the mean grain yield of Argentinean maize production (Mastronardi, 2008).

Greater grain yields in more recent hybrids were associated with higher KNP at each water regime (Table 6). It is noteworthy that KNP was the grain yield component contributing to a greater extent to the grain yield reductions due to water deficiencies in the old hybrid. The reduction in both yield components contributed to explain the grain yield reductions in more recent hybrids. This is in agreement with previous work suggesting greater source limitations in more recent maize hybrids (Echarte et al., 2006; Di Matteo et al., 2016).

The relationship between KNP and PGRcp was curvilinear, when PGRcp varied due to water regimes (Fig. 4a); and there was a unique relationship for more recent and older hybrids. Previous studies (e.g. Echarte et al., 2004) demonstrated differences in PGRcp threshold for kernel set and on maximum KNP among hybrids released in different decades. However, the methodology used in this work was less exhaustive (i.e. mean plant per plot) than that in Echarte et al. (2004, along with lower reductions in resource availability due to water deficiencies, which did not allow the display of differences in the PGRcp threshold parameter. Nevertheless, in this study it was evident that at a similar water supply (i) PGRcp tended to be higher in more recent than in the older hybrid (significant in two Exps; Table 6), and (ii) there were

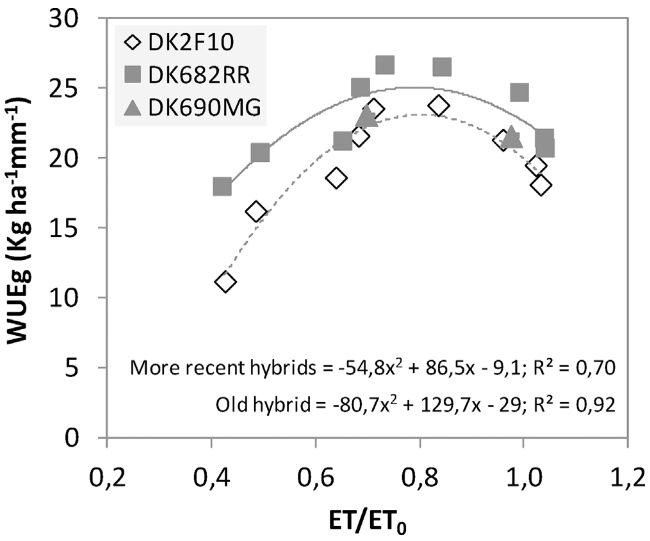

Fig. 3. Water use efficiency for grain yield (WUEg) as a function of standardize seasonal ET (i.e. seasonal ET/ET_0), for one old (DK2F10) and two more recent (DK682RR and DK690MG) maize hybrids grown in five experiments under contrasting water availability. One quadratic curve for the old hybrid and one quadratic curve for the two more recent hybrids were fitted to the WUEg-seasonal ET/ET_0 relationship ($p < 0.05$).

not evident trends among hybrids released in different decades in KNP/PGRcp (not shown), nor in EGRcp (Fig. 4).

In this study we showed a close association between ETcp and PGRcp (Fig. 6) and we also showed two distinctive features of the more recent hybrids that might explain their greater kernel set at low water availability. First, PGRcp of more recent hybrids was greater than that of the old hybrid at a similar ETcp; and second ETcp of more recent hybrids was greater than that of the old hybrid at a similar water supply. The greater ETcp of more recent hybrids compared with the old one confirm our previous finding (Nagore et al., 2014). In addition, during silking, leaf conductance of more recent hybrids was higher than that of the old hybrid (Fig. 7). At low values of stomatal conductance, little increments in stomatal conductance could result in large increment in CER due to the curvilinearity of the CER-conductance relationship (Fig. 7); supporting a significantly larger ETcp and a much larger PGRcp at a similar low water availability, in more recent than in

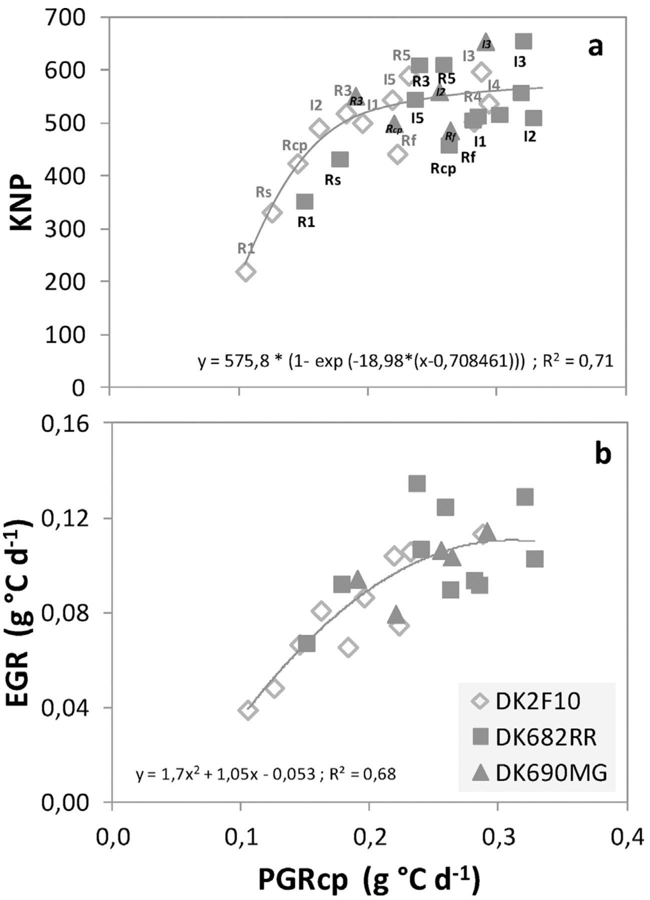

Fig. 4. Kernel number per plant (KNP) and ear growth rate during the critical period for kernel set (EGRcp, g °C d^{-1}) as a function of plant growth rate during the critical period (PGRcp, g °C d^{-1}) in one old (DK2F10) and two more recent (DK682RR, and DK690MG) maize hybrids in experiments 1, 2, 3 and 5; under contrasting water regimes: irrigated (I), rainfed from silking (Rs), rainfed during the critical period (Rc), rainfed during grain filling (Rf) and rainfed (R). Numbers in each data point indicate the experiment. One curve was fitted to all the hybrids ($p < 0.05$). Data from Exp. 4 was not included since PGR and EGR were obtained with a different methodology.

Table 6
Kernel number per plant (KNP) and plant growth rate during the critical period for kernel set (PGRcp; gr d^{-1}) in three maize hybrids (DK2F10, DK682, DK690MG) under different water regimes: irrigated (I), rainfed (R), rainfed from silking (Rs), rainfed during critical period for kernel set (Rc), rainfed during grain filling (Rf) and no irrigated (NI), in Experiments 1–5.

Exp.	Water	KNP				PGRcp (gr d^{-1})			
	regime	DK2F10	DK682RR	DK690MG		DK2F10	DK682RR	DK690MG	
1	I	500	514		*A*	3,1	4,5		*A*
	Rs	331	433		*B*	2,0	2,8		*B*
	R	219	353		*C*	1,7	2,4		*B*
		b	*a*			*b*	*a*		
2	I	490	511	560	*A*	2,6	5,3	4,1	*A*
	Rf	441	507	487	*AB*	3,6	4,5	4,2	*A*
	Rc	423	459	500	*B*	2,3	4,2	3,5	*A*
		b	*a*	*a*		*b*	*a*	*a*	
3	I	597	656	655	*A*	4,3	4,8	4,4	*A*
	R	518	610	552	*A*	2,8	3,6	2,9	*A*
		b	*a*	*ab*		*a*	*a*	*a*	
4	I	537	558		*A*	5,1	5,5		*A*
	R	502	517		*B*	4,9	5,2		*A*
		a	*a*			*a*	*a*		
5	I	543	546		*A*	3,8	4,1		*A*
	R	589	611		*A*	4,0	4,5		*A*
		a	*a*			*a*	*a*		

Lower case letters and capital letters indicate differences among hybrids or among water regimes, respectively ($p < 0.05$; LSD).

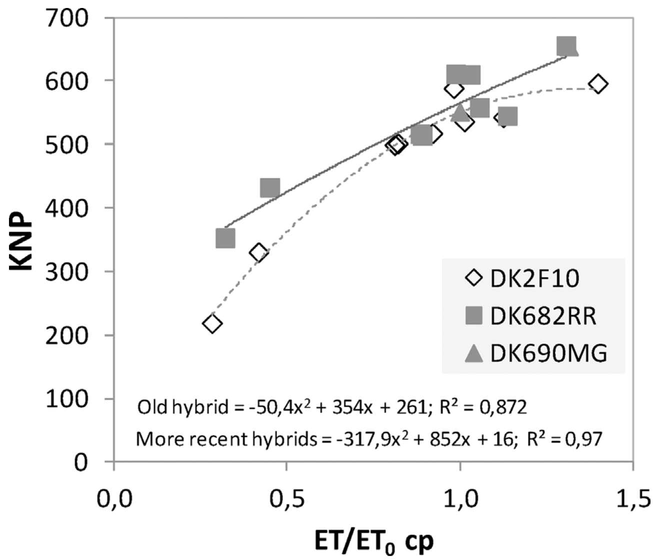

Fig. 5. Kernel number per plant (KNP) as a function of standardized ET during the critical period for kernel set (ET/ET$_0$cp), for an old (DK2F10) and two more recent maize hybrids (DK682RR and DK690MG) under different water regimens, in Experiments 1, 3, 4 and 5. One quadratic curve for the old hybrid and one quadratic curve for the two more recent hybrids were fitted to the KNP-ET/ET$_0$cp relationship ($p < 0.05$).

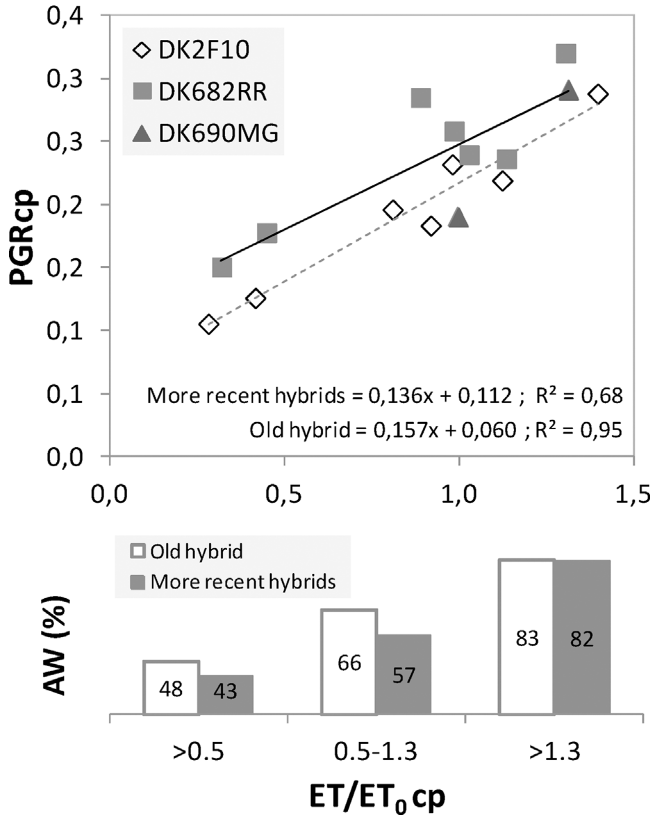

Fig. 6. Plant growth rate during the critical period for kernel set (PGRcp, g °C d^{-1}) as a function of standardized ETcp (ET/ET$_0$cp) in one old (DK2F10) and two more recent maize hybrids (DK682RR and DK690MG), in Experiments 1, 3 and 5. Significant fitted linear equations differed in the intercept between the old (continuos line) and the more recent (dashed line) maize hybrids ($p < 0.05$). Inset below, indicate the corresponding mean soil available water (AW%) for the old (white bar) and the two more recent hybrids (grey bar), at ET/ET$_0$cp ranges 0–0.5; 0.5–1.3 and > 1.3.

the old hybrid. Similarly, other studies at the leaf level that compared new and old hybrids concluded that more recent hybrids were able to have a higher photosynthetic rate and conductance around silking, when they were exposed to short water stress periods under greenhouse conditions (Nissanka et al., 1997). In our study, the maintenance of a greater stomatal conductance in more recent than in the old hybrid, under similar condition of water stress, might be associated with their greater leaf rolling (field visual observations in Exp. 3). Other factors, like osmotic adjustment under low soil water availability might also be involved in this response (Chimenti et al., 2006; Zinselmeier et al., 1999).

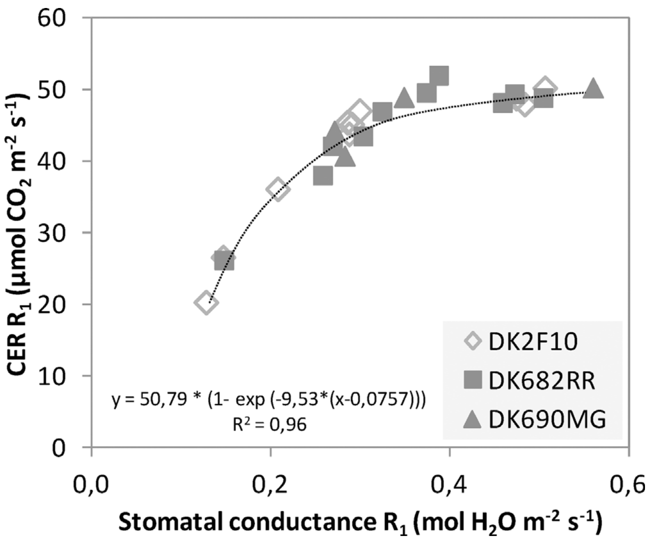

Fig. 7. Leaf carbon exchange rate (CER, µmol CO2 m^{-2} s^{-1}) as a function of stomatal conductance (mol H_2O m^{-2} s^{-1}), at silking (R1), for an old (DK2F10,) and two more recent maize hybrids (DK682RRand DK690MG) under different water regimens in Exp.1 to 5. One curve fitted all hybrids ($p > 0.05$).

5. Conclusion

In this study we quantified a significantly higher WUEg advantage in two more recent hybrids compared with an old one, under low water availability. Results of this study elucidated that the greater WUEg of more recent hybrids than that of the old hybrid is associated with greater grain yield and with similar seasonal ET. Greater grain yield at all water supplies in more recent than in older maize hybrids was the result of a greater KNP; and greater KNP under low water availability was related to greater PGRcp and greater ETcp, associated with greater stomatal conductance.

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