

The effect of kernel number on growth, yield and quality of forage maize*

Efecto del número de granos en el crecimiento, rendimiento y calidad del forraje de maíz

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Abstract

The number of reproductive sinks can affect dry matter production and forage quality. Trials were conducted during two years to study the effect of kernel number per ear upon production and distribution of dry matter and forage quality in maize. Treatments were four kernel reduction levels in the first year (0%, 33%, 66% and 100%) and three in the second year (0%, 50% and 100%). Kernel number reduction was obtained by covering the ear to prevent pollination at different times during silking. In the crop without or with very few kernels total dry matter yield was 23% lower and stem biomass was 55 to 60% higher than in the control. In the first period after silking (from R1 to R3), the plants with the least kernel number had the greatest rate of stem growth. This alternative sink supported unrestricted crop growth and photosynthetic rate only during the initial stages of grain filling. Reduction in biomass yield was directly proportional to the reduction in kernel number per plant. The increase in the number of grains per ear resulted in a significant reduction in neutral detergent fiber (NDF) of the fresh material and in stem dry matter digestibility. The treatments did not significantly affect dry matter percentage, dry matter digestibility, nor total protein percentage of the forage at harvest. The low proportion of grain in the forage in the treatments with low number of grains per ear was at least partially compensated for by an increase in stem dry matter digestibility. The fermentative parameters pH and total N did not differ among treatments. Contrarily, the buffer capacity and the NH₃/NT ratio were significantly higher for the treatment with no grains than for the control treatment. The similar pH values among treatments would indicate that the amount of substrate was adequate to achieve an appropriate fermentation. In treatments with no grain, and because of its high buffer capacity, a greater substrate consumption was needed to lower the pH to values similar to those obtained with the control treatment.

Key words: forage maize, silage, source/sink relations, silage quality.

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Resumen

El número de destinos reproductivos puede afectar la producción de materia seca y la calidad del forraje. Se condujeron ensayos durante dos años con el fin de estudiar el efecto del número de granos por espiga sobre la producción y distribución de la materia seca y la calidad del forraje de maíz. Los tratamientos fueron cuatro niveles de reducción de granos en el primer año (0%, 33%, 66% and 100%) y tres en el segundo (0%, 50% and 100%). La reducción en el número de granos por planta se obtuvo cubriendo la espiga en diferentes momentos durante la floración para prevenir la polinización. En el cultivo sin granos la materia seca total fue 23% menor y la biomasa de tallos fue 55 a 60% mayor que en el tratamiento sin reducción de granos (testigo). En el primer periodo después de floración (desde R1 a R3), las plantas con el menor número de granos tuvieron la mayor tasa de crecimiento y de fotosíntesis durante los estadios iniciales del llenado de granos. Reducciones en rendimiento de biomasa fueron directamente proporcionales a la reducción en número de granos por planta. El incremento en el número de granos por espiga resultó en una significativa reducción en fibra detergente neutra (NDF) del material fresco y en la digestibilidad de los tallos. Los tratamientos no afectaron significativamente el porcentaje de materia seca, la digestibilidad de la materia seca, ni el porcentaje de proteína del forraje en la cosecha. La baja proporción de grano en el forraje en los tratamientos con bajo número de granos por espiga fue al menos parcialmente compensada por un incremento en la digestibilidad de la materia seca de los tallos. Los parámetros fermentativos pH y N total no difirieron entre tratamientos. Contrariamente, la capacidad buffer y la relación NH_3/NT fueron significativamente más altas en los tratamientos sin granos que en los testigos. Los valores similares de pH entre tratamientos indicarían que la cantidad de sustrato fue adecuada para lograr una fermentación adecuada. Debido a la alta capacidad buffer de los tratamientos sin granos, un mayor consumo de sustrato fue necesario para bajar el pH a valores similares a aquellos obtenidos en el testigo.

Palabras clave: maíz para forraje, relación fuente-destino, calidad de silaje.

Introduction

The number of grains in the ear and the proportion of grain mass in the total biomass are determined by a number of management and climatic factors, among them: i) stress during silking (Andrade et al., 2002), ii) sowing density (Graybill et al., 1991; Sarlangue et al., 2007), iii) sowing date (Cirilo and Andrade, 1994) and iv) harvest date (Elizalde et al., 1993). Varying the number of kernels changes the reproductive source-sink relationship during the grain filling period (Borrás et al., 2004), which leads to an altered accumulation and distribution of non-structural carbohydrates (NSC) in the plant (Phipps et al., 1984; Uhart and Andrade, 1991; Uhart and Andrade, 1995). Reduction in sink demand usually leads to carbohydrate accumulation in the leaves

and stems and to depression in the rate of photosynthesis (Koch et al. 1982; Prioul, 1996; Paul et al 2001; Rolland et al; 2002; McCormick et al. 2006). In maize plants from which the ears had been removed, Moss (1962) and Graybill et al., (1991) found reduced total biomass production and reduced photosynthetic rate, which may have been caused by reduced sink demand and from the kernels and limited capacity of alternative sinks (stems and leaves) to compensate for reduced ear growth (Prioul and Schwebel-Dugué, 1992). It is not known, however, for how long during the grain filling period the alternative sinks can support unrestricted crop growth. Moreover, little is known about the relationship between biomass production and the degree of kernel number reduction.

Variations in the source-sink ratio can also modify the nutritive and fermentative quality of maize fresh material (forage) and silage. The nutritional quality of the plant is affected by dry matter digestibility, cell wall proportion and its digestibility, and kernel proportion (Fisher and Burns, 1987a; Burns, 1987b; Elizalde et al., 1993; Holland and Kezzar, 1995; Roth and Undersander, 1995). The relationship between kernel proportion in the plant and quality of the rest of the plant is fundamental to determine the energy concentration of the plant material (Wilkinson et al, 1978; Fahey, 1983; Elizalde et al, 1993). The quality of the fermentation process, in turn, depends upon factors such as soluble NSC concentration, dry matter (DM) percentage and buffer capacity (BC) (McDonald, 1981; McDonald et al., 1991).

The present study was designed to determine the effects of a gradient in kernel number in the ear upon the growth and dry matter partitioning of a maize crop and upon nutritional and fermentative quality of maize forage.

Materials and Methods

The data were obtained from two experiments conducted at the Instituto Nacional de Tecnología Agropecuaria Balcarce Experimental Station (37° 45' S, 58° 18' W, 130 m alt), during two growing seasons (1996-97 and 1997-98). The soil was a Typic Argiudoll with a minimum effective depth of 1.5 m, and with an organic matter content of approximately 5.6% in the first 25 cm of depth. The area is characterized by low average temperatures during the growing season (17.8 °C) and a frost-free period of about 150 days. More details about the climatic regime of the Balcarce region were presented in Andrade (1995).

The Cargill maize hybrid 7301 FQ was sown on 8 October (1st season) and 10 October (2nd season) with a final density of 85000 plants*ha⁻¹. The plots consisted of five rows of 14 m long and 0.70 m apart. The crop was kept free of pests and weeds: at presowing atrazine + acetochlor (Ultrapack) were applied at a rate of 4.2 l*ha⁻¹ and post emergent weed control was by hoeing. Plots were fertilized

with 150 kg*ha⁻¹ of diammonium phosphate (18-46-00) at presowing and 300 kg*ha⁻¹ of urea at the V6 stage (6 leaves visible). Soil water content was maintained non-limiting by irrigation. Total irrigation was 120 mm in the first and 170 mm in the second growing season.

The source-sink relationship during grain filling was altered artificially by varying the number of kernels per plant. The treatments were a control and 3 (33, 66 and 100%) or 2 (50 and 100%) levels of intended reduction in the number of kernels per plant or per ear in the first year and second year, respectively. The experiments were complete randomized block designs with three replications. Modification of the number of kernels was achieved by preventing pollination by covering the ears with bags at different dates after silking. The full number of grains per ear was estimated to be 600. In the first year, the ears were covered when 0, 200 and 400 silks were visible to obtain 100, 66 and 33% reductions in kernel number, respectively. In the second year, the ears were covered when 0 and 300 silks were visible to obtain 100 and 50% reductions in kernel number, respectively. The number of silks were counted daily during the flowering period in all ears of the three central rows of the plots corresponding to treatments with partial kernel reduction to determine the time of ear covering. Ears in the 100% kernel reduction treatment were covered before flowering and those in the control treatments were left uncovered. All secondary ears were covered with bags to prevent pollination.

Ten plants per plot were sampled at R1 (silking), R3 (milk stage) and R5 (dent stage) to determine leaf, stem, ear and total above ground biomass. The R3 and R5 stages occurred 20 and 42 days after silking in the first year and 27 and 55 days after silking in the second year (cooler season). The tassel and the husks were included with the stem material. Each component was weighed fresh, then dried to constant weight at 65°C in a forced air drying room. Intercepted photosynthetically active radiation was measured with a LICOR 188B radiometer connected to a line quantum

sensor LICOR 191SB. Readings were taken between 11.00 h and 13.00 h on clear days close to sampling dates. Photosynthetically active radiation (PAR) interception was calculated as $(1 - I/I_0)$, where I is the incident PAR just below the lowest layer of photosynthetically active leaves and I_0 is the incident PAR at the top of the canopy. Daily fraction interception values between determinations were estimated by linear interpolation. Daily total incident PAR was multiplied by the correspondent daily fraction of PAR interception, and accumulated to obtain PAR intercepted by the crop along the reproductive period. Radiation use efficiency (RUE) was calculated as the slope of the regression of cumulative dry matter on cumulative intercepted PAR. The photosynthetic rates of the ear leaves were measured with a portable photosynthesis system (LICOR LI-6200) at stages R3 and R5 (Ritchie and Hanway, 1982). Measurements were taken on 10 randomly selected plants per plot between 11.00 h and 13.00 h on clear days. Soluble NSC concentration in stems was measured using the reaction with anthrone method, described by Bailey (1958).

At the first growing season, plant material was harvested at R5, grounded to an approximated particle size of 3 cm and conserved as silage during 60 days in PVC buckets (5 l)

ensuring anaerobic conditions. DM percentage, Soluble NSC concentration (Morris, 1948), *in vitro* DM digestibility (Tilley and Terry, 1963), neutral detergent fiber (NDF) (Goering and Van Soest, 1970), crude protein (semi MicroKjeldhal method) and starch (Mac Rae y Armstrong, 1968) were determined in fresh material and silage samples. Buffer capacity was determined on fresh material (McDonald and Henderson, 1962), and pH and ammonium nitrogen were determined on silage samples (with a colorimetric autoanalyser Technicon, Model 2).

Data were processed by ANOVA tests and regression analyses. Means were compared using the least significant difference (LSD) test.

Results

Dry matter accumulation and photosynthesis

Treatments effectively reduced the number of kernels per plant (KNP) (Table 1). Control treatments yielded close to 1200g m⁻² of ear dry matter in both years. The effect of kernel number per plant upon ear dry matter at harvest (expressed in g m⁻²) was highly significant ($y = 2.053 \text{ KNP} + 143.6$; $R^2 = 0.96$; $n=21$; $p<0.001$ $n= 21$). Total above ground dry matter accumulation up to harvest expressed

Table 1: Effect of kernel number per ear on the relative rate of photosynthesis at R3 and R5 Mean of 10 leaves. Different letters in columns (in the same year) indicate significant differences ($p<0,05$).

Cuadro 1: Efecto del número de granos por espiga en la tasa relativa de fotosíntesis en R3 y R5. Media de 10 hojas. Letras diferentes en columnas (en el mismo año) indican diferencias significativas ($p<0,05$).

Year	Proposed grain number reduction (%)	Number of grains per ear	Photosynthetic rate (%)	
			R3	R5
1	0	534	100 a	100 a
1	33	340	88.7 a	82.5 a
1	66	202	83.5 a	79.5 a
1	100	9	81.2 a	32.2 b
2	0	495	100 a	100 a
2	50	251	90.9 ab	95.0 ab
2	100	15	76.0 b	71.0 b

in similar units was less in treatments with kernel number reduction than in control treatments ($y = -0.0008 \text{ KNP}^2 + 1.3514 \text{ KNP} + 2152$; $R^2 = 0.65$, $n=21$; $p<0.001$). The reduction in total biomass at harvest with respect to

the control ranged from 23% for the treatments with near zero kernels to around 11% for treatments with moderate reductions in kernel number (Figure 1). Only the extreme treatments showed significant differences in

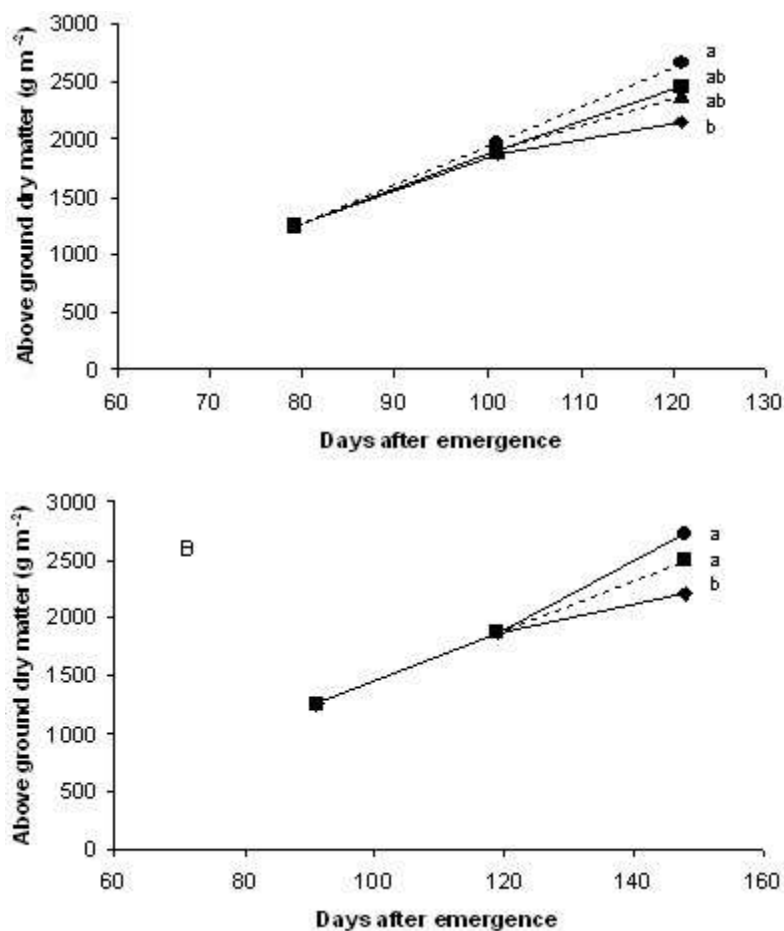


Figure 1: Above ground dry matter accumulation from silking to harvest for 100 (◆), 66 (▲), 33 (■) and 0% (● control) proposed reduction in the number of kernels per ear in the first year (upper); and for 100 (◆), 50 (■), and 0% (● control) proposed reduction in the number of kernels per plant in the second year (lower). Points with different letters show significant differences at R5 stage. No differences were found at R3 stage. SE at R5 were 200 and 120 g m⁻² for the first and second year, respectively.

Figura 1: Acumulación de materia seca aérea desde floración hasta cosecha para una reducción de 100 (◆), 66 (▲), 33 (■) and 0% (● control) en el número de granos por espiga en el primer año (arriba) y para una reducción de 100 (◆), 50 (■), and 0% (● control) en la misma variable en el segundo año (abajo). Puntos con diferentes letras indican diferencias significativas en el estadio R5. No se encontraron diferencias en el estadio R3. EE en R5 fueron 200 and 120 g m⁻² para el primer y segundo año, respectivamente.

total biomass production ($p < 0.05$). The weight of the leaf component was not different among treatments ($y = -0.0465 \text{ KNP} + 402.38$; $R^2 = 0.14$ $n=21$; $p > 0.05$) and was fairly constant from silking to silage harvest. Reductions in kernel number resulted in increased stem

biomass. The relationship between stem biomass at R5 (expressed in g m^{-2}) and KNP was $y = -1.105 \text{ KNP} + 1634$ ($R^2 = 0.88$; $n=21$; $p < 0.001$). In the treatment with near zero kernels, stem biomass was close to 60% larger than the untreated control (Figure 2).

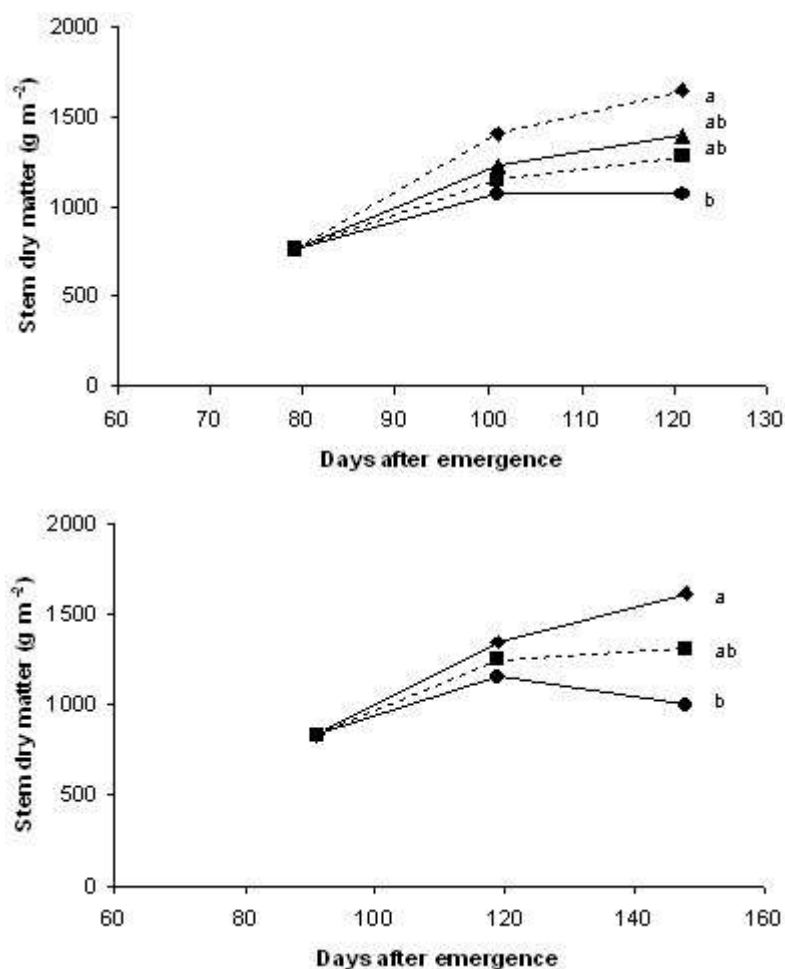


Figure 2: Stem dry matter accumulation from silking to harvest for 100 (◆), 66 (▲), 33 (■) and 0% (● control) proposed reduction in the number of kernels per ear in the first year (upper); and for 100 (◆), 50 (■), and 0% (● control) proposed reduction in the number of kernels per plant in the second year (lower). Points with different letters show significant differences at R5 stage. No differences were found at R3 stage. SE at R5 was were 150 g m^{-2} for both years.

Figura 2: Acumulación de materia seca en los tallos desde floración hasta cosecha para una reducción de 100 (◆), 66 (▲), 33 (■) and 0% (● control) en el número de granos por espiga en el primer año (arriba) y para una reducción de 100 (◆), 50 (■), and 0% (● control) en la misma variable en el segundo año (abajo). Puntos con diferentes letras indican diferencias significativas en el estadio R5. No se encontraron diferencias en el estadio R3. EE en R5 fue 150 g m^{-2} para ambos años.

In the R1-R3 period, crop growth rate did not significantly differ among treatments nor was it related to kernel number ($R^2=0.03$, ns). In contrast, in the R3-R5 period differences among treatments in crop growth were observed. Crop growth rate during this period was positively associated with kernel number per plant ($R^2=0.53$, $p<0.01$).

Nonstructural carbohydrate (NSC) concentration was highest in stems of plants with reduced kernel number (Figure 3). Differences were not significant at stage R3. At stage R5, however, there were significant differences in stem NSC concentration between the control and the other three treatments.

At R3 stage, photosynthetic rates were significantly affected by the treatments in the second year, but not in the first year (Table 1). At R5 stage, differences between 0% (control) and 100% reduction in kernel number were significant in both years. Accordingly, RUE from R1 to R3 did not differ among treatments, but RUE from R3 to R5 decreased in response to reductions in kernel number (data not shown).

Forage quality

The effect of the reduction in the number of grains per ear on the nutritive and fermentative quality of the plant material is presented on Table 2. The treatments did not affect dry matter percentage, dry matter digestibility, nor total protein percentage of the forage at harvest (Table 2; $p>0.05$). The decrease in the number of grains per ear resulted in a significant increase in NDF of the fresh material and in stem dry matter digestibility (Table 2). As expected, starch percentage in the forage at harvest was affected by the treatments, being highest for the plants with normal ears and lowest in those with no grains (data not shown). The buffer capacity of the forage at harvest was significantly higher for the treatment with no grains than for the control treatment (Table 2).

After the silage process, no significant differences were found in dry matter percentage even though this variable was lowest for the treatment with near zero grains (23.1%) and highest for the control with normal ears

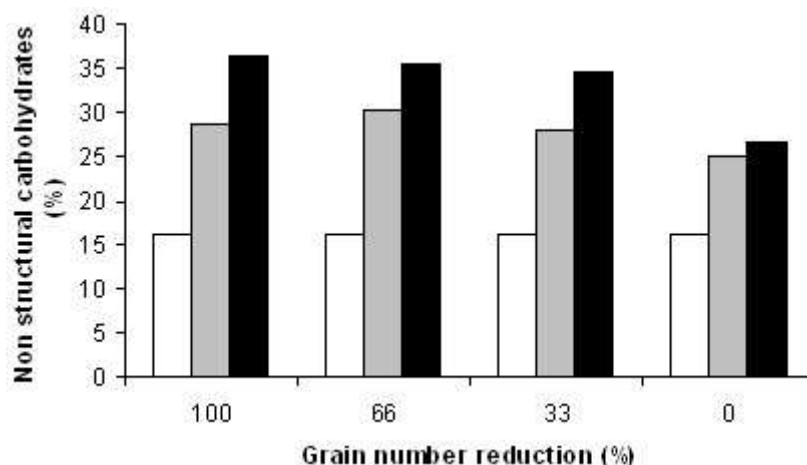


Figure 3: Effect of reduction in number of kernels per ear on non-structural carbohydrates concentration in the stem at flowering (white), R3 (grey) and R5 (black) stages. Data from first season; SE = 0.75

Figura 3: Efecto de la reducción en el número de granos por espiga sobre la concentración de carbohidratos no estructurales en los tallos en floración (blanco), R3 (gris) y R5 (negro). Datos del primer año; SE = 0,75

Table 2: Effect of kernel number reduction on forage quality and buffer capacity of the plant material at harvest and on pH and NH₃/TN of the silage. Different letters indicate significant differences ($p < 0.05$). NDF= Neutral detergent fiber; BC= Buffer capacity; TN= Total nitrogen. Data from first growing season.

Cuadro 2: Efecto de la reducción en número de granos por espiga sobre la calidad del forraje y la capacidad buffer del material vegetal en la cosecha y sobre el pH y la relación NH₃/TN del silaje. Letras diferentes indican diferencias significativas ($p < 0,05$). NDF= Fibra detergente neutra; BC= Buffer capacity; TN= Nitrógeno total. Datos del primer año.

	Proposed grain number reduction (%)				SE
	0	33	66	100	
Dry matter (%)	2750	2786	2857	2786	ns
Total digestibility	57.4	56.6	56.6	55.9	ns
Stem digestibility	54.5c	59.6b	61.4b	68.7a	1.1
NDF	53.9b	55.3b	58.4a	60a	0.59
Protein (%)	8.6	8.7	8.1	8.5	ns
BC (meq/100g)	16.6a	18.2ab	18.4ab	20.7b	0.89
pH	3.83	3.83	3.80	3.77	ns
NH ₃ /TN	7.46c	8.37bc	10.16ab	11.80a	0.76

(25.4%). No differences among treatments were found in dry matter digestibility nor in protein percentage (data not shown). Soluble NSC percentage were higher in the controls (plants with complete ears) than in treatments with no or few grains (6.9 vs 4.1%, $p < 0.06$). NDF tended to increase as number of grains decreased (from 50.9 to 55.3) but this effect was not significant.

The fermentative parameters pH and total N did not differ among treatments (Table 2). Contrarily, the NH₃/TN ratio was significantly higher for the treatment with no grains than for the control treatment (Table 2).

Discussion

Dry matter accumulation and photosynthesis

Reductions in kernel number resulted in reduced total biomass and increased stem biomass. At R5, shoot biomass was positively related to kernel number. The slope constants (2.05 vs -1.10) indicate that more than half of the effect of reduced kernel number on ear biomass was compensated for by an increase in

stem biomass. Similarly, Leshem and Werncke (1981) found that the reduction in ear yield was partly compensated for by the increased stem weight. Thus, reductions in reproductive sink strength strongly affected dry matter partitioning as it was shown by Koch et al. (1982) for maize mutants with starch deficient endosperm.

The lack of differences among treatments in shoot biomass at R3 (Figure 1) and in crop growth rate between R1 and R3 indicates that reduced ear growth in treatments with low kernel number was totally compensated for by increased stem dry matter accumulation (Figure 2). In contrast, the positive association between crop growth rate during R3-R5 and kernel number per plant indicates that stem growth did not compensate low ear growth during this period. In fact, the stems of plants with no or very few kernels accumulated biomass from R3 to R5 at a lower rate than during the R1-R3 period (Figure 2).

Extreme reductions in kernel number reduced leaf photosynthetic rates during grain filling. The photosynthetic response to grain number agrees with results presented in the

literature. Sadras et al. (2000) found a significant reduction in leaf photosynthetic rate at 30 and 38 days after flowering in maize plants with no kernels compared with control plants. Additionally, Moss (1962) informed a 45% reduction in photosynthetic rate in plants from which the ears had been removed.

The reduction in photosynthetic rate was more pronounced after R3 in agreement with the results observed for crop growth rate. Leaf photosynthetic rate at R5 was directly associated with crop growth rate from R3 to R5 and inversely related to NSC concentration in stems at R5 ($p < 0.05$). The apparent reduced capacity of this crop to accumulate assimilates in vegetative organs may have been responsible for the reduced levels of photosynthesis (Table 1) and radiation use efficiency (RUE) during the R3-R5 period observed in the treatment with no or with very few kernels. Low sink demand in maize leads to an increase in the levels of sugar and starch in the upper leaves which is associated with rapidly reduced levels of photosynthesis (Prioul 1996; Paul and Foyer, 2001; Rolland et al., 2002) and accelerated senescence (Thomas, 1992). As pointed out by Moss (1962) these effects appear in maize because it is a plant with determinant growth that has no other important alternative sink apart from the stem and the leaves; even so, the feed back effect on photosynthesis is delayed until these limited alternative sinks are replenished. The lack of differences in stem NSC levels among the treatments with reduced kernel number suggests that even a moderate reduction in this yield component causes a close to maximum NSC concentration in stems. These results agree with those presented by Deinum and Knoppers (1979). Maize does not have the capacity to allocate assimilates to stems as sugar cane does (Pammenter and Allison, 2002).

We showed that above ground biomass yield at the time of silage harvest was positively associated with the number of kernels per plant and that alternative sinks supported unrestricted crop growth and photosynthetic rates only during the initial stages of grain filling (approximately up to the R3 stage).

The decrease in total above ground biomass production in response to almost complete reductions in kernel number found in this work was lower than those found in regions where maize is commonly sink limited during grain filling (27 to 36%; Moss, 1962; Campbell, 1964), but higher than those observed in regions where source capacity is the major limitation during this stage (6 to 14%; Bunting, 1975, 1976; Deinum and Knoppers, 1979). Thus, the degree to which growth of vegetative organs can compensate for the loss of reproductive sinks may vary according to the source-sink relationship during the grain filling period of the control treatment.

Silage quality

The low proportion of grain in the forage of the treatments with low number of grains per ear was at least partially compensated for by an increase in stem dry matter digestibility (Table 2). Similarly, Leshem and Wermke (1981) concluded that the reduction of forage quality due to the absence of ears was partly compensated for by the increase in quality of stems. These results also agree with those presented by Bunting (1975) and McAllan and Phillip (1977).

Buffer capacity was negatively related to kernel number per ear. When grain proportion was modified by plant density or harvest time, a negative association between grain percentage and buffer capacity was also observed (Fisher y Burns, 1987b). Buffer capacity is associated with organic acid anions and amino groups of nitrogenous compounds (McDonald, 1981, McDonald et al., 1991). These last compounds are more exposed and reactive in vegetative organs than in grains.

After the fermentation, soluble NSC was lower for the treatment with no or few grains than for the control, even though the former treatments had started the fermentation with higher sucrose concentration in the stem (Figure 3). In treatments with no grain, and because of its high buffer capacity, a greater substrate consumption was needed to lower the pH to values similar to those obtained with the control treatment (McAllan y Phillips, 1977).

The negative association between ammonium concentration in the silage and the number of grains per plant (Table 2) resulted from the fact that most of the proteins in plants with a high number of grains are in the kernel endosperm which is less exposed to the fermentative processes (Oshima et al., 1979).

The harvested material presented, in all cases, values of soluble NSC and buffer capacity within the range considered adequate for a good fermentation process. (McDonald, 1981; McDonald et al., 1991; Fisher y Burns; 1987b, Woolford, 1984). The similar pH values among treatments would indicate that the amount of substrate was adequate to achieve an appropriate fermentation (Woolford, 1984).

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