

Effect of Seed Vigor on Intraspecific Competition and Grain Yield in Maize

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ABSTRACT

High-vigor seeds result in faster emergence of seedlings and crop establishment than low-vigor seeds. These characteristics could enhance plant competitive ability and could have direct effects on maize (*Zea mays* L.) grain yield. This study examined the hypothesis that seed vigor heterogeneity in maize seed lots could increase intraspecific competition and negatively affect crop grain yield. A 2-yr experiment was executed combining two hybrid maize seed lots, possessing high-vigor and low-vigor seeds, in seven different distributions in the sowing row. The distributions of the plants originating from high- and low-vigor seeds were evaluated at harvest for dry mass accumulation, prolificacy, number of grains per row, number of rows per ear, 1000-grain mass, and grain yield. A replacement series design for data analysis of two homogeneous populations and five seed mixture populations was applied. We concluded that, in plant populations originating from heterogeneous seed lots, intraspecific competition was intensified, resulting in losses of dry mass accumulation and grain yield. Plants originating from low-vigor seeds had less competitive ability and reduced plant dry mass accumulation and grain yield than those originating from high-vigor seeds and were responsible for crop yield losses. Plants originating from high-vigor seeds had a dominant effect on those originating from low-vigor seeds and had no compensatory effects. The major production component affected by intraspecific competition was the number of grains per row.

IN THE CROP environment, competition may be defined as plant-to-plant interference with equal use of density-limited environmental resources by genetically identical plants of a cultivar (Fasoula and Fasoula, 1997). In maize, plant-to-plant variability occurs naturally and is measurable by several phenotypic traits that are magnified as intraspecific competition is increased (Pagano et al., 2007). As the sharing of environmental resources becomes unequal, the competition among genetically identical plants increases, and it occurs mainly because of acquired dissimilarity in growth and development (Fasoula and Fasoula, 1997).

In the last decade, several studies have analyzed the impact of plant-to-plant variability on maize grain yield at the canopy level (Liu et al., 2004a, 2004b; Andrade and Abbate, 2005; Tollenaar et al., 2006). These researchers concluded that a nonuniform spatial distribution of plants along the sowing row and uneven seedling emergence result in plant-to-plant variability in biomass among adult plants and reduced canopy grain yield.

A number of factors, including seed vigor, could affect the uniformity of seedling emergence and be a factor leading to

yield loss in the field. Glenn and Daynard (1974) suggested that crop management designed to encourage uniform plant establishment, such as a uniform seed bed and constant planting depth, should maximize the yield of maize grown for grain. According to Liu et al. (2004b), variation in maize seedling emergence affects subsequent plant growth and reduces grain yield. For example, late-emerging plants must compete for incident solar radiation, water, and nutrients with earlier emerging neighboring plants that are often taller and have a more developed root system. They also concluded that the early-emerging plants were unable to compensate for lower yield of the late-emerging plants in the field. In addition, Merotto et al. (1999) reported that plants with delayed emergence showed less shoot and root growth, resulting in less capacity for competition for natural resources, which reduced plant yield at the end of the cultivation cycle.

Seed vigor comprises those seed characteristics that determine the potential for emergence as well as rapid and uniform development of normal seedlings under a wide range of environmental conditions (Association of Official Seed Analysts, 1983). Thus, low-vigor seeds require more time from sowing to emergence and have a lower final percentage of emerged seedlings, initial size, leaf area, plant growth rate, and dry matter accumulation (Schuch et al., 1999, 2000; Höfs et al., 2004). According to Hampton (2002), seed vigor has an important influence on the establishment of the initial plant population and development, which affect crop yield.

When plants develop from seeds with different vigor levels, the plants with the higher growth capacity might create greater intraspecific competition, which reduces both the intensity and composition of incident light on plants with less growth capacity in the plant population. Kolchinski et al. (2005) evaluated the development of individual plants in soybean [*Glycine max* (L.) Merr.] populations and found that plants from high-vigor seeds

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had greater seed yields even though those plants did not show dominance over adjacent plants from low-vigor seeds in the same sowing row. Similar results were reported by Melo et al. (2006) and Mielezrski et al. (2008) in studies conducted with rice (*Oryza sativa* L.) seeds, showing that plants from high-vigor seeds had greater yield than plants from low-vigor seeds.

Competition among plants also occurs in plant populations when plants are dominated by earlier emerging neighboring plants (Merotto et al., 1999) due, for example, to differences in seed vigor. In this situation, differences in the emergence rate affect the development of the crop canopy, and the seedlings that emerge first shade those that emerge later (Pommel et al., 2002). This effect may occur when seed lots that are heterogeneous in terms of seed vigor are used.

Differences in emergence rate should be minimized because they increase the possibility of yield loss (Merotto et al., 1999), especially in maize, which is particularly sensitive to intraspecific competition (Maddonni and Otegui, 2006). Large interplant differences in growth and development reduce the yield per unit area because the reduced average yield of poorly performing plants is not compensated by the higher yields of other plants (Fasoula and Fasoula, 1997). Thus, this work tested the hypothesis that seed vigor heterogeneity in maize seed lots could intensify intraspecific competition and negatively affect crop grain yield.

MATERIAL AND METHODS

The research was conducted at Piracicaba, SP, Brazil (22°42'30" S, 47°38'0" W, 546 m asl). The soil, a Rhodic Kandiudalf with 24 kg m⁻³ of organic matter and a pH of 4.9, was prepared conventionally for the experiments. On the day before planting, the area was mechanically furrowed, and N, P, and K were applied at rates of 32, 112, and 64 kg ha⁻¹, respectively. The maize hybrid Dow 8480 was planted in plots on 8 Oct. 2006 and 15 Jan. 2008 in the prepared sowing rows. Plots received 90 kg ha⁻¹ of N at the five-leaf stage and were kept free of weeds, pests, and diseases throughout the crop cycle. During the first year, the experiment was irrigated, guaranteeing unstressed crop development; in the second year, irrigation was performed only to allow normal seedling emergence and to obtain the desired plant stand. Total rainfall and average temperature during the experiments were 1014.9 mm and 24.7°C for 2006–2007 and 865.0 mm and 22.3°C for 2008. Plots with three rows measuring 11 m and spaced at 0.7 m were used, and the evaluation area was 10 m in the central row, excluding 0.5 m from each end.

For each year, one seed lot was used. Before the experiment, the seed lots were divided in two parts, and stored for 3 mo (July–October of each year) under different conditions. One part was stored under uncontrolled conditions and the other at a controlled temperature (25°C) and relative humidity (40%). Those differences in storage were responsible for seed vigor differences between samples. Samples were characterized as high (H) and low (L) vigor seed lots based on their performance in a number of physiological tests: germination, accelerated aging, seedling emergence, seedling emergence index, and electrical conductivity (Table 1).

Germination was tested in rolled paper towels using four replicates of 50 seeds each per seed lot. The seeds were placed on two germination paper towels moistened with water to 2.5 times the mass of the dry paper and covered with another moistened paper towel. The rolled paper towels were oriented vertically and placed in a dark germination chamber at 25°C. The number of normal seedlings was recorded on the fourth and seventh days (Ministry of Agriculture, Livestock and Food Supply, Brasil, 2009).

Accelerated aging was tested using four replicates of 50 seeds each per seed lot. The seeds were placed on a screen inside a transparent plastic box (11.5 by 11.5 by 3.5 cm) and suspended over 40 mL of water. The boxes were placed in a germination chamber maintained at 41 ± 1°C for 96 h. After the aging period, the seeds were tested for germination as described above and evaluated on the fourth day after planting (Mondo and Cicero, 2005).

Electrical conductivity was determined using four replicates of 50 seeds each per seed lot. The samples had been previously weighed (0.1-g accuracy) and were placed in plastic containers (200 mL) with 75 mL of deionized water and kept at 25°C for 24 h in a germination chamber. The electrical conductivity of the solution was determined using a Digimed DM-20 conductivity meter (μS cm⁻¹ g⁻¹) (Mondo and Cicero, 2005).

Seedling emergence (Fessel et al., 2000) and the seedling emergence index (SEI) (Maguire, 1962) were evaluated in an experimental field area using eight replicates of 50 seeds each per seed lot. The seeds were uniformly planted 5 cm deep in rows 2.5 m long and 0.5 m apart. The soil was watered to provide sufficient moisture for seedling emergence. Emerged seedlings were counted daily for 14 d after planting. The results were expressed as percentage of emerged seedlings, and the seedling emergence index (Maguire, 1962) calculated as: $SEI = \sum (E_t/D_t)$, where E_t is the number of newly emerged seedlings on the t th day and D_t is number of days after sowing.

Table 1. Physiological potential characterization of maize seed lots used in each experimental year: germination (G), accelerated aging (AA), seedling emergence (SE), seedling emergence index (SEI), and electrical conductivity (EC).

Test	First year			Second year		
	Lot 1	Lot 2	CV %	Lot 1	Lot 2	CV %
G, %	98 ns†	95	1.93	100 ns	98	2.45
AA, %	95 ns	88	6.74	98 a‡	91 b	0.61
SE, %	96 a	92 b	1.55	98 ns	96	2.39
SEI	13.85 a	12.73 b	3.50	15.96 a	14.77 b	2.85
EC, μmhos m ⁻¹ g ⁻¹	2.095 ns	2.135	4.13	1.782 a	2.377 b	5.97

† ns, not significant by *F* test ($P < 0.05$).

‡ For each year, means followed by the same letter within a row are not significantly different by Scott–Knott test ($P < 0.05$).

The plots comprised different distributions of high- and low-vigor seeds in the sowing row to simulate the use of homogeneous (uniform) and heterogeneous (nonuniform) seed lots in terms of seed vigor. The distributions were as follows: (i) all high-vigor seeds (1H:1H [100% H]); (ii) three high-vigor seeds followed by one low-vigor seed (3H:1L [75% H]); (iii) two high-vigor seeds followed by one low-vigor seed (2H:1L [67% H]); (iv) one high-vigor seed followed by one low-vigor seed (1H:1L [50% H]); (v) one high-vigor seed followed by two low-vigor seeds (1H:2L [33% H]); (vi) one high-vigor seed followed by three low-vigor seeds (1H:3L [25% H]); and (vii) all low-vigor seeds (1L:1L [100% L]).

The seeds were manually sown at 5-cm depth according to the seed proportions previously described. Due to possible variability in vigor among seeds from the same lot and to obtain more representative seedlings from lots of high- and low-vigor seeds, three seeds were sown per hole for the high-vigor locations and four seeds were sown per hole for the low-vigor locations. The plots were later thinned to leave the earliest emerging seedling for the high-vigor seed locations and the latest emerging seedling for the low-vigor seed positions, obtaining a total population of 71,429 plants ha⁻¹. This procedure was required to obtain homogenous H plants and L plants in the sowing row, considering that in a seed lot each seed is physiologically different and the results for seed vigor analysis characterize the entire seed lot. During sowing, all plant locations were labeled, enabling subsequent measurements.

The following variables were determined at the time of harvest: dry matter accumulation, prolificacy (ears plant⁻¹), number of rows per ear and grains per row, 1000-grain mass, and grain yield. Four plants of each vigor level and sowing location were harvested for individual evaluations in each plot in addition to grain yield, which was assessed by harvesting all plants of each vigor level and sowing position in each plot. Means of populations were calculated as the weighted average based on the percentage of each plant type in each distribution. Ears were collected, sun dried, and manually shelled. All grains of each maize ear were counted, weighed, and values corrected to 13% moisture content. The 1000-grain mass was determined by taking a subsample of 1000 grains from the harvested plants and weighing. These procedures were performed according to the Rules for Seed Analysis (Ministry of Agriculture, Livestock and Food Supply, Brasil, 2009). The grain moisture content was measured by the incubation method at 105 ± 3°C for 24 h (Ministry of Agriculture, Livestock and Food Supply, Brasil, 2009). To determine dry matter accumulation, whole plants were collected, chopped, placed into paper bags, and then dried in a convection oven at 65°C until a constant weight was achieved, at which time the weight was recorded. The total dry weight of the maize ear and grain from each plant were added to the dry matter accumulation value. All weights were measured on an analytical balance accurate to 0.01 g.

For crop performance and intraspecific competition experiments, a randomized block design with four replicates was applied and the data subjected to conventional analysis for replacement series experiments (de Wit, 1960), which is performed visually with the aid of graphs of the relative responses of plants for each variable (Radosevich, 1987; de Carvalho and Christoffoleti, 2008) depending on the proportion

of seeds. This method consists in keeping the total density of the plant population constant and varying the ratio between two species or biotypes (Harper, 1977). Thus, using a modified method, combinations of plants from high- and low-vigor seeds (heterogeneous distribution) were compared with populations composed of plants from one seed type (homogeneous distributions). The relative results for all ratios were calculated by dividing the results for each ratio by the average results obtained for homogeneous seed vigor distributions (de Wit and van den Berg, 1965; McGilchrist and Trenbath, 1971; Harper, 1977; Christoffoleti, 1992). The expected, i.e., linear relationship between the increase in the percentage of each type of plant and its performance for each variable, and the observed results were compared using the standard mean.

Seed lot characterization was conducted in a completely randomized design with four replicates. Data were analyzed by ANOVA (*F* test) and, in case of significance of the *F* test, means were grouped by Scott–Knott test (5%) (Scott and Knott, 1974).

RESULTS AND DISCUSSION

Among the existing methodologies for studying plant competitive interactions, replacement series experiments (de Wit, 1960) can be an option for better understanding competition among plants, especially for studies examining the effects of density and proportion of plants in a weed community (Christoffoleti and Victoria-Filho, 1996). Such experiments have been used to find which of two competing species or biotypes is the best competitor for resources and to understand how this interaction occurs (Cousens, 1991). This type of experiment allows the analysis of the performance of plant populations from types of seed lots that are heterogeneous in terms of seed vigor.

In the first year (Fig. 1A), for dry mass accumulation evaluation, differences were slight and did not show a pattern of seed vigor influence on crop performance. In the second year (Fig. 1B), when the experiment was conducted under unirrigated conditions, the limited water supply may have been responsible for the observed increase in intraspecific competition and may have been a factor in the performance of high- and low-vigor plants. In this situation, the use of heterogeneous seed vigor lots resulted in reduced crop dry matter accumulation in mixed populations, except for the 75H:25L treatment. High-vigor plants performed similarly as expected and low-vigor plants performed less than expected, causing crop losses due to increased intraspecific competition.

The same effect was observed for grain yield (Fig. 2). Low-vigor plants in the first year performed as expected, but in the second year, when competition was maximized, low-vigor plants showed higher grain yield reductions when the variability among plants was greater, for example in the 50H:50L treatment. Also, in both evaluations, high-vigor plants could not compensate for the losses from low-vigor plants, which was expected because maize has low plasticity. It is interesting to note that Liu et al. (2004b) showed that maize plants were able to compensate in terms of dry mass accumulation when positioned close to gaps in the sowing row. The same researchers, as well as Andrade and Abbate (2005), however, found that grain yield reductions in late-emerging plants were not compensated by early emerging plants. The results obtained in this study agree with those reported by Maddonni and Otegui (2004), who found that the

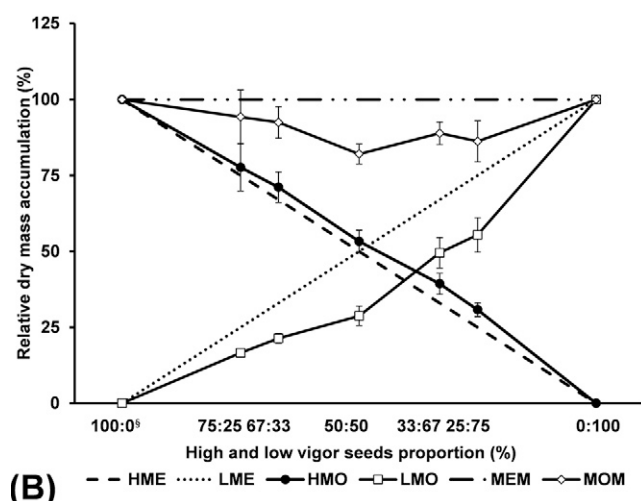
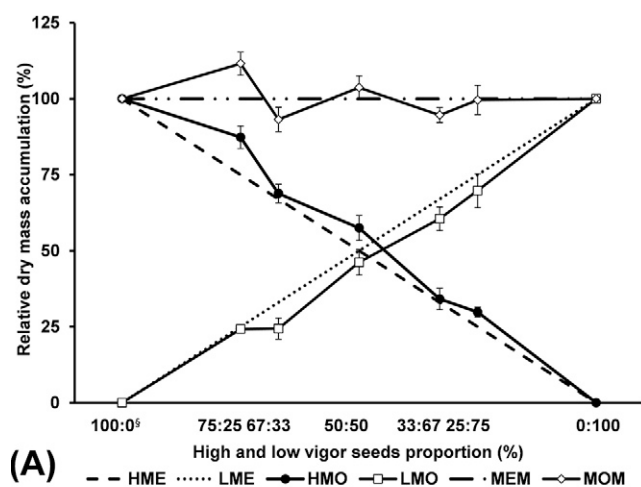


Fig. 1. Relative dry mass accumulation of plant populations consisting of different proportions of plants originating from high- (H) and low-vigor (L) seeds for the (A) first and (B) second experimental years. §Percentages of plants originating from H and L seeds in plant population (HME, expected relative contribution from H plants on dry mass accumulation; LME, expected relative contribution from L plants on dry mass accumulation; HMO, observed relative contribution from H plants on dry mass accumulation; LMO, observed relative contribution from L plants on dry mass accumulation; MEM, expected relative mean dry mass accumulation; MOM, observed relative mean dry mass accumulation).

accumulation of dry matter per plant decreased with increasing intraspecific competition in maize.

Fasoula and Fasoula (1997), in a comprehensive review about competition, reported that the unequal sharing of resources in a crop environment brings about uneven suppression of yield per plant. They stated that yield gains from competition of some plants fail to counterbalance yield losses of other plants, which results in undercompensation and reduction of yield per unit area. This conclusion supports the results found for dry mass accumulation in this study.

Ford and Hicks (1992) also observed reductions in maize grain yield in a study on the effects of uneven seedling emergence. They found reductions of 5.0 and 12.8% in the final maize grain yield when the emergence of half of the plants was delayed by 7 and 14 d, respectively, which resulted in greater intraspecific competition. Höfs et al. (2004) also confirmed that a reduction of final grain yield is most likely associated with greater

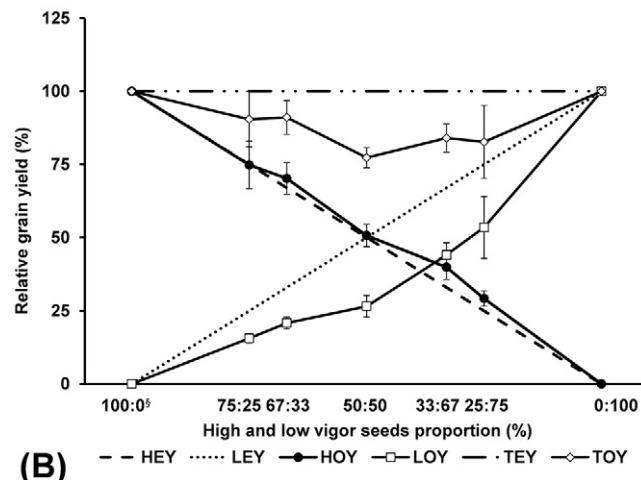
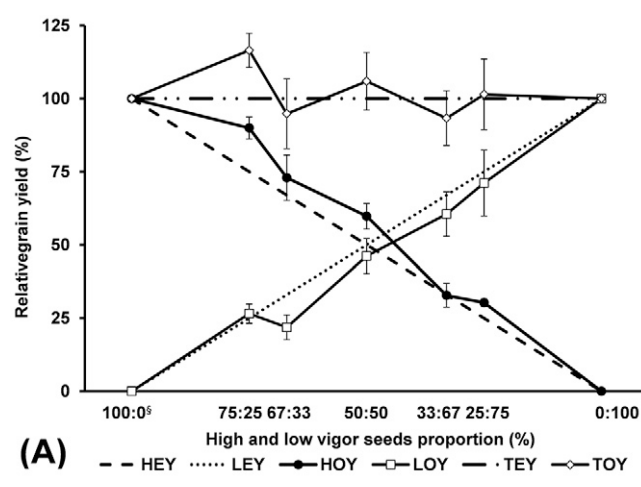


Fig. 2. Relative grain yield of plant populations consisting of different proportions of plants originating from high- (H) and low-vigor (L) seeds for the (A) first and (B) second experimental years. §Percentages of plants originating from H and L seeds in plant population (HEY, expected relative yield from H plants; LEY, expected relative yield from L plants; HOY, observed relative yield from H plants; LOY, observed relative yield from L plants; TEY, total expected relative yield; TOY, total observed relative yield).

unevenness of emergence, and consequently, late-emerging seedlings would be subjected to a higher degree of intraspecific competition, which would be reflected in reduced components of production.

In addition, Fig. 2B shows that the 50:50 ratio (50% each of high- and low-vigor seed) is the point of equal density of plants from each seed type. At this point, we clearly observe which plants have greater competitive ability, i.e., which plants more efficiently capture natural resources that is translated into greater plant growth under conditions of equal density. Thus, in terms of grain yield, high-vigor plants performed as expected, while low-vigor plants suffered more from competition, yielding less than expected, which indicates that the high-vigor plants were better competitors. Due to the low intrinsic plasticity of maize, however, the high-vigor plants were not able to convert the greater availability of natural resources into higher grain productivity and were not able to compensate for losses resulting from the low-vigor plant production, as noted by the reductions in grain yield. According to Tollenaar and Wu (1999), losses from less competitive plants are usually greater than the gains from dominant plants, which supports the results of this study.

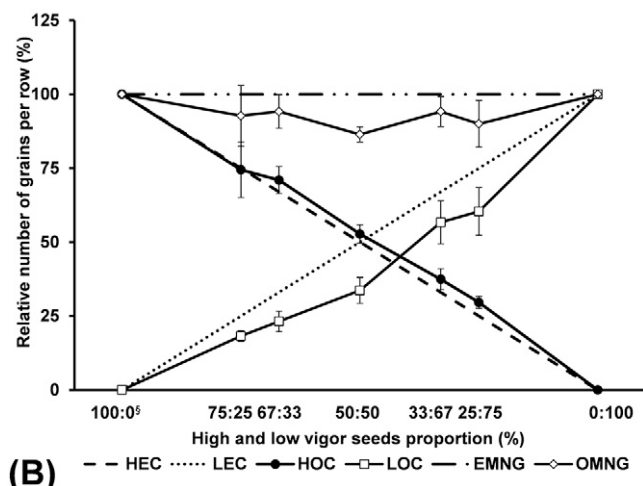
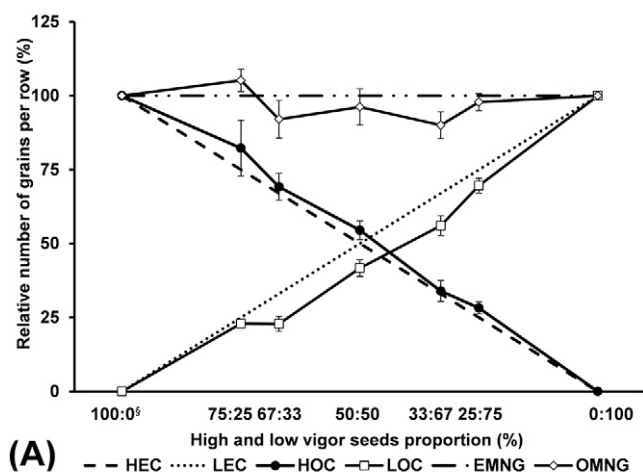


Fig. 3. Relative number of grains per row in plant populations consisting of different proportions of plants originating from high- (H) and low-vigor (L) seeds for the (A) first and (B) second experimental years. §Percentages of plants originating from H and L seeds in plant population (HEC, expected relative contribution from H plants to number of grains per row; LEC, expected relative contribution from L plants to number of grains per row; HOC, observed relative contribution from H plants to number of grains per row; LOC, observed relative contribution from L plants to number of grains per row; EMNG, expected mean number of grains per row; OMNG, observed mean number of grains per row).

Thus, high seed vigor is responsible for faster maize seedling emergence, which enables better solar energy capture and favors the growth of high-vigor plants, as previously observed by de Almeida et al. (1998) and Walker et al. (1988). Those plants represent individuals with greater competitive ability during the crop cycle, which can be identified by dominant plants in the plant population, in contrast with the dominated plants, which were smaller and showed less ability to capture resources (Maddonni and Otegui, 2006).

According to Pagano and Maddonni (2007), the variability in maize seedling emergence reduces grain yield per area due to the low fertility of seedlings with delayed emergence. Low plant fertility could be identified by analysis of the number of rows per ear, number of grains per row, and prolificacy.

Overall, the relative number of rows (data not shown) per ear for the plant population remained similar in both years, indicating that this variable was not altered by increased intraspecific competition among plants resulting from seed vigor

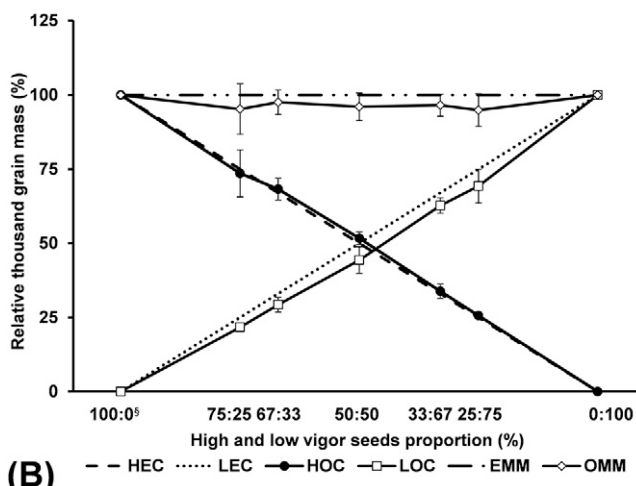
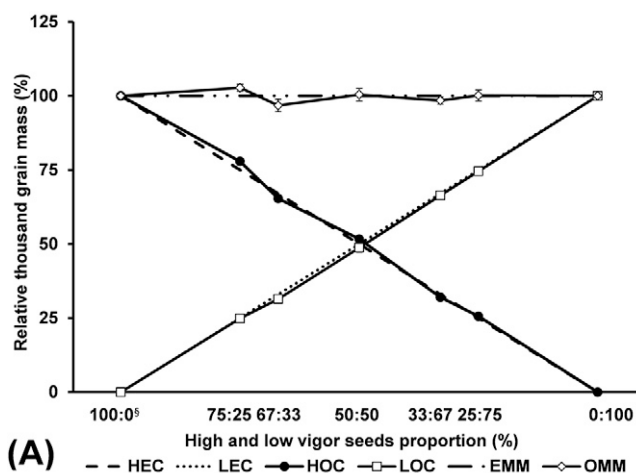


Fig. 4. Relative 1000-grain mass of plant populations consisting of different proportions of plants originating from high- (H) and low-vigor (L) seeds for the (A) first and (B) second experimental years. §Percentages of plants originating from H and L seeds in plant population (HEC, expected relative contribution from H plants to 1000-grain mass; LEC, expected relative contribution from L plants to 1000-grain mass; HOC, observed relative contribution from H plants to 1000-grain mass; LOC, observed relative contribution from L plants to 1000-grain mass; EMM, expected mean 1000-grain mass; OMM, observed mean 1000-grain mass).

heterogeneity. This pattern occurred for plants from both high- and low-vigor seeds. Thus, it is possible that the intraspecific competition among plants became more pronounced after the phenological stage of eight leaves, which is the point at which the number of rows per ear is established (Magalhães et al., 2002). Also, prolificacy results did not vary, and all individuals produced one ear (data not shown), showing that this parameter was not affected by intraspecific competition and did not contribute to the resultant grain yield losses.

The relative number of grains per row (Fig. 3) was lower than expected for the plants from low-vigor seeds in the plant populations from heterogeneous seed lots in both years, suggesting that the effects of competition among plants influences the number of ovules (potential number of grains) or affects pollination. In contrast, the plants from high-vigor seeds in the same populations obtained the expected results, showing that the differences in relative mean values among these populations and the populations from homogeneous lots were also caused by reductions obtained from low-vigor plants,

especially in the second year (Fig. 3B), when there was less water availability. According to Maddonni and Otegui (2004), who studied intraspecific competition in maize populations, dominant plants had more grains per maize ear than less dominant plants at various sowing densities and row spacings.

The 1000-grain mass in the first year (Fig. 4A) did not differ for any seed distribution; i.e., there was no interaction between the proportion of high- and low-vigor seeds and this variable. Under unirrigated conditions (Fig. 4B), reductions in the 1000-grain mass were obtained for the low-vigor plants in populations from heterogeneous lots. These results were not enough to influence the 1000-grain masses of those plant populations, which remained similar to the 1000-grain masses of populations of plants from homogeneous lots.

Thus, there was a clear effect of the competitive ability of the high-vigor plants on the low-vigor plants, which was more apparent in the second year of the study, resulting in lower dry matter accumulation and grain yield. Moreover, the number of grains per row and the 1000-grain mass were the components of grain yield that influenced yield losses from low-vigor plants in mixed populations. The influence of 1000-grain mass was not as pronounced as the number of grains per row, however, and did not affect crop performance. The influence of this component on grain yield has been reported in several studies showing that the number of grains per ear is the main factor that determines the final grain yield (Bolaños and Edmeades, 1993, 1996; Cirilo and Andrade, 1994). Maddonni and Otegui (2004) also found that early intraspecific competition among plants in maize crops led to different capacities for competition between individuals, and if the development of a plant hierarchy (dominant and dominated plants) began before the critical period for determining the number of grains per ear, decreases in the final mean number of grains would be observed.

The use of seed lots that are heterogeneous in terms of vigor, whether resulting from factors that occurred during the production process in the field, improper harvesting practices, the transport or processing of seeds, or even from mixing lots produced in different years, will result in fields with uneven seedling emergence, differential plant growth, and elevated intraspecific competition in maize crops. In these situations, a plant hierarchy is established, and plants from low-vigor seeds will have less capability to compete for resources, such as water, light, and nutrients, resulting in dominated plants, whereas plants from high-vigor seeds have a greater competitive capability and do not suffer the effects of elevated intraspecific competition.

Thereby, this study has shown that the use of seed lots that are heterogeneous in terms of seed vigor negatively impact the development of maize crops. To increase grain yield, control of seed quality is crucial. According to Fasoula and Tollenaar (2005), competition among plants can be reduced by genetic and agronomic measures, i.e., the use of fields with ample and evenly distributed growth resources, the even distribution of plants, and the synchronous germination, growth, and development of plants, which can be obtained using high-quality seeds. It should be stressed, however, that the use of high-vigor seeds is intended to ensure the establishment of adequate plant populations under different environmental conditions during emergence, where low-vigor seeds would have more difficulty withstanding unfavorable environmental conditions.

Tolerance of environmental stresses has been recognized as the physiological characteristic most strongly linked to breeding maize hybrids for better grain yield (Tollenaar and Wu, 1999). In modern genotypes, the tolerance of maize to intraspecific competition for resources available at high plant densities has advanced more than any other environmental stress tolerance in the last 40 or 50 yr (Tollenaar and Lee, 2002; Tokatlidis and Koutroubas, 2004). It is important to recognize that our experiments were conducted with a plant population close to 70,000 plants ha⁻¹ (a population commonly used in Brazilian agriculture) and that seed vigor effects on intraspecific competition should therefore be even more evident at higher plant populations.

CONCLUSIONS

For the maize plants evaluated (71,429 plants ha⁻¹) in plant populations originating from seed lots consisting of high- and low-vigor seeds (seed lots heterogeneous in terms of seed vigor): (i) seed vigor heterogeneity affected intraspecific competition in the maize plant populations, resulting in losses of dry matter accumulation and grain yield per area; (ii) plants from low-vigor seeds had lower competitive ability than plants from high-vigor seeds; (iii) plants from low-vigor seeds had reduced dry matter accumulation and grain yield and were responsible for crop yield reductions; (iv) plants from high-vigor seeds had a dominant effect on plants from low-vigor seeds but had no compensatory effect; (v) the major production component affected by intraspecific competition was number of grains per row; and (iv) the effect of seed vigor on intraspecific competition of maize plants in the field was intensified under unirrigated conditions, which is typical for Brazilian agriculture.

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