

Ecophysiological Bases for Crop Management

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ABSTRACT

This review focuses on the effect of management practices on grain yield of maize, sunflower, soybean and wheat, the major extensive crops of the Argentine Pampas. We analyze and evaluate crop management practices in the light of the physiological determinants of growth and grain yield using basic information available for these crops. This approach also contributes to understand or explain the differential responses of crops to management practices observed among species or cultivars within species, or among different environmental conditions and production system. We center our discussion on the effects of sowing date, plant density, row spacing, plant distribution and emergence uniformity, and cultivar maturity group election on grain yield of maize, sunflower, soybean and wheat. The knowledge and quantification of the ecophysiological factors underlying crop growth and yield determination are critical for the design and selection of the most appropriate management practices for a specific genotype and environment combination. This approach constitutes a low cost technology that can contribute to (i) match crop demands to the particular environmental offer and (ii) an efficient use of environmental resources and inputs in a specific situation.

Keywords: crop ecophysiology, crop management, maize, soybean, sunflower, wheat

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INTRODUCTION

The knowledge and quantification of the ecophysiological (i.e. crop physiological) factors and mechanisms underlying crop growth and yield determination are critical for the design and selection of the most appropriate management practices (Andrade *et al.* 2005), aimed to an efficient use of environmental resources and inputs in a specific situation.

This review focuses on the effect of management practices on grain yield of maize (*Zea mays* L.), sunflower (*Helianthus annuus* L.), soybean [*Glycine max* (L.) Merr] and wheat (*Triticum aestivum* L.); the major extensive crops of the Argentine Pampas (Hall *et al.* 1992). Crops with axillary (maize) or apical (sunflower and wheat) reproductive sinks, or with sequentially developed fruits (soybean) are analyzed using a common comprehensive and simple conceptual framework. We analyze and evaluate crop management practices in the light of the physiological determinants of growth and grain yield using basic information available for these crops. The concepts of harvest-index stability, critical periods for grain yield determination (Fischer 1975), and vegetative and reproductive plasticity among others (Loomis and Connor 1992), constitute the basis for understanding crop grain yield as determined by management practices, cultivars, environmental conditions and the interactions among these factors. We emphasize the effect

of the environment on these relationships, by means of experimental results obtained from crops grown in the field at different sites of the Argentine Pampas, a region characterized by Hall *et al.* (1992).

Being the number of harvested kernels the component that mostly explain the variation in grain yield, the goal of crop management is to optimize the physiological condition of the crop during the most critical period for grain number determination, which is around flowering in maize and sunflower (Fischer and Palmer 1984; Cantagallo *et al.* 2004), before anthesis in wheat (Fischer 1975, 1985a), and from R3 to R6 in soybean (Shaw and Laing 1966). The physiological condition of the crop during a specific stage is characterized by crop growth (i.e. radiation capture and its conversion into crop dry matter) and dry matter partitioning to reproductive structures (Gambín and Borrás 2010).

We focus our discussion on the effects of sowing date, plant density, row spacing, plant distribution and emergence uniformity, and cultivar maturity group on grain yield of maize, sunflower, soybean and wheat. This work is an update of a review on the subject (Andrade *et al.* 2005), in which additional information on summer crops and another crop (wheat) were included.

SOWING DATE

In this section, we discuss the effects of sowing date on the physiological determinants of growth and yield of crops grown in a temperate region (the Argentina Pampas).

The selection of sowing date is critical because it may determine drastic changes in the photothermal environment (i.e. relationship between solar radiation and air temperature; Fischer 1985a) and water regime of the crop along the cycle (Abbate *et al.* 2004), and particularly during the critical period for grain yield determination. In general, grain yield of extensive grain crops is maximized when: (i) they take full advantage of the growing season, (ii) their critical periods avoid environmental constraints (e.g. water shortage, frost damage, heat stress), and (iii) these critical periods take place under optimal conditions for dry matter accumulation. Consequently, the main constraints to consider for sowing date selection in a specific region are the frost-free period, and the occurrence of heat stress (i.e. air temperature > 35°C in summer crops, > 28°C in winter crops) and water deficit periods. For the Pampas region of Argentina, the frost-free period increases from South to North and from West to East (Hall *et al.* 1992). Thus, sowings in the central maize region (i.e. Pergamino, 34° S) are frequently earlier than in the southern Pampa (e.g. Balcarce, 38° S). For deep soils with no permanent restrictions to root growth, summer water deficit increases from South to North and from East to West (Hall *et al.* 1992). In general, heat stress does not impose a serious limitation to crop growth during the frost-free period in most of the Pampas region.

Once the frost-free period for the crop cycle has been established, delays in sowing date result in substantial yield reductions in all the considered crops, when water deficit is avoided by means of irrigation (Fig. 1). Delayed sowing hastens plant development because of higher temperatures during the vegetative period in all these species (Major *et al.* 1975; Goynes *et al.* 1989; Cirilo and Andrade 1994a; Otegui *et al.* 1995; Ferrise *et al.* 2010), because of longer photoperiod during the vegetative period in wheat (Fischer 1985b; Abbate *et al.* 1990; Stapper and Fischer 1990) and because of shorter photoperiods during reproductive growth in soybean (Major *et al.* 1975; Kantolic and Slafer 2001). Long photoperiods in late sowings reduce developmental rate to flowering in maize and soybean (Major *et al.* 1975; Kiniry 1991) and have variable effects in sunflower (Goynes *et al.* 1989; León *et al.* 2001). Thermal effects, however, prevail over photoperiodic effects in determining the rate of development during the vegetative period of these crops (Major *et al.* 1975; Bonhomme *et al.* 1994). In wheat, long photoperiods and high temperatures in late sowings both lead to an increase in developmental rate (Stapper and Fischer 1990; Abbate and Bariffi 1998). In late sowings, for all four crops, vegetative growth rate is hastened and crops achieve maximal light interception in a shorter period from emergence (Cirilo and Andrade 1994a; Otegui *et al.* 1995; Hussain and Pooni 1997; Ferrise *et al.* 2010). However, shortening of the growing cycle decreases the total amount of radiation intercepted by crops and, thus, crop dry matter at harvest.

In these crops, delays in sowing date result in deterioration of the environmental conditions during the critical period for grain number determination and during the grain filling stage (Constable 1977; Miller *et al.* 1984; Cirilo and Andrade 1994b, 1996; Abbate *et al.* 1997; Calviño *et al.* 2003a, 2003b; Fischer and Edmeades 2010). Low incident radiation during the flowering stage in sunflower and maize, and during R3-R6 in soybean, results in reductions in grain set for the three crops. Late sowings in wheat result in shorter duration of the critical period for grain number determination and of the grain filling stage, as a consequence of an increase in temperature during these stages (Wiegand and Cuellar 1981; Abbate *et al.* 1990). Delayed sowing in maize, sunflower and wheat could place their critical stages for grain yield determination at periods with lower amount of incident radiation per unit of developmental time. Vari-

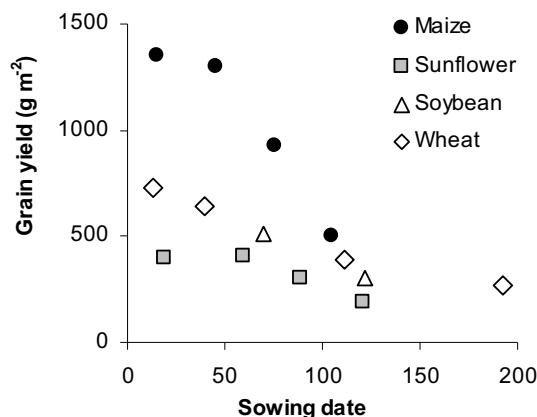


Fig. 1 Grain yield of maize (circles), sunflower (squares), soybean (triangles) and wheat (diamonds) as a function of sowing date expressed as days after 1 September for summer crops and after 1 August for wheat. Crops were grown under adequate levels of water and nutrient availability. Final plant densities were 8.5, 6.7 and 30.0 plant m⁻² for maize, sunflower and soybean, and from 225 to 430 plant m⁻² in wheat. SE are 24.6, 22.6, 19.0 and 23.3 g m⁻² to compare sowing dates within crops for maize, sunflower, soybean and wheat, respectively. Data from Andrade (1995) for summer crops and from Abbate (unpublished) for wheat.

ation in photothermal environment during the critical period through delays in sowing date would translate into decreases in grain set as was reported for maize (Cantarero *et al.* 1999), sunflower (Cantagallo *et al.* 1997) and wheat (Fischer 1985b; Abbate *et al.* 1990). In soybean, short photoperiods toward the end of the growing cycle in late sowings shorten the duration of the grain-filling period, prevailing over the opposite temperature effect (Major *et al.* 1975; Kantolic and Slafer 2001; Calviño *et al.* 2003b).

Reductions in incident radiation during the grain-filling period may reduce grain growth rate and/or grain-filling duration depending on the species (Andrade and Ferreiro 1996; Borrás *et al.* 2004; Borrás and Gambin 2010). On the other hand, low temperature toward the end of the season in late sowings reduces grain-filling rate in the three summer crop species (Egli and Wardlaw 1980; Connor and Hall 1997; Cirilo and Andrade 1996) and tends to extend grain-filling duration in maize and sunflower (Ploschuk and Hall 1995; Cirilo and Andrade 1996).

Using crop models for a series of 24 years of climatic records for the main maize region of Argentina (about 32 to 35°S and 58 to 62°W), Otegui *et al.* (1996) predicted a potential maize grain yield greater than 16 Mg ha⁻¹ in 50% of the years for September sowings, whereas with later sowings, median yields lower than 15 Mg ha⁻¹ (October sowings) and 14 Mg ha⁻¹ (November sowings) could be expected as a consequence of sowing date effect on the photothermal environment during the critical periods. Impact of delaying sowing date varies across latitudes. In fact, expected grain yield decreases for maize crops in response to delays in sowing date were largest at Balcarce (38° S, highest latitude), intermediate at Pergamino (34° S), and lowest at Las Lajitas (25° S, lowest latitude; Fig. 2).

Sowing date selection might also take into account the occurrence of environmental constraints for crop growth. Varying sowing date would become a recommended strategy to move a crop stage away from constraints like seasonal droughty periods, early or late frosts, biological adversities, rainy weather at harvest, etc. Moreover, extreme high temperature at pollination could affect seed set due to reduced pollen viability (Schoper *et al.* 1986) and biomass production (Cicchino *et al.* 2010), which is particularly usual in maize crops at northern latitudes in Argentina. In such regions, it could be convenient to delay the sowing date to avoid high temperature and atmospheric demand at flowering (Otegui and López Pereira 2003). Nevertheless, delays in sowings beyond the beginning of summer

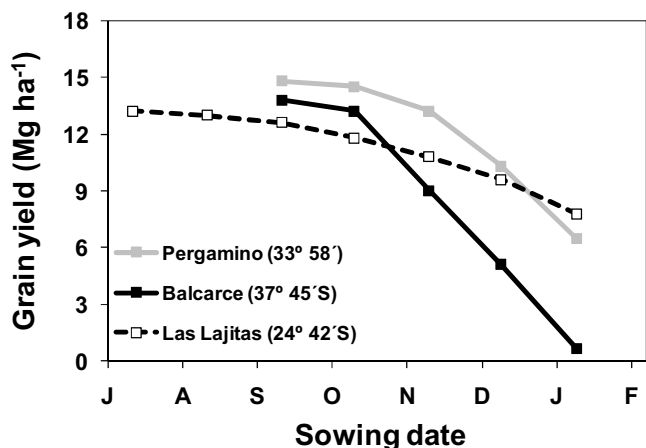


Fig. 2 Maize grain yield as a function of sowing date at Balcarce (black squares), Pergamino (grey squares), and Las Lajitas (open squares) for crops growing with no evident water or nutrient limitations and with full season cultivars. Latitudes for each location are included in the graph insert. Adapted from Cirilo (1994, 2001b) and Cirilo (pers. comm.).

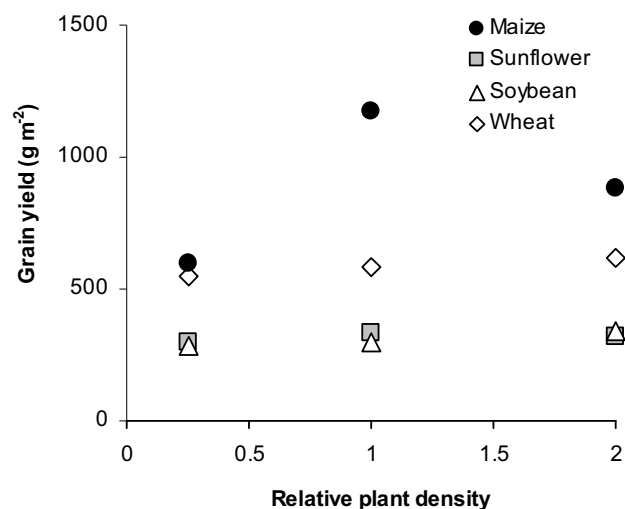


Fig. 3 Grain yield as a function of relative plant density in maize (circles), sunflower (squares), soybean (triangles) and wheat (diamonds). Crops were sown at optimal dates and were grown under adequate levels of water and nutrient availability. Yield at extreme densities were significantly different ($P < 0.05$) from yield at the reference densities (relative plant density 1) only in maize. Reference plant density was 8.5 plants m^{-2} for maize; 5.8 plants m^{-2} for sunflower, 29.8 plants m^{-2} for soybean and 336 plants m^{-2} for wheat. Data adapted from Valentinuz (1996) for summer crops; and from Abbate (unpublished) for wheat.

(December) were also associated with reductions in grain yield at those latitudes (Cirilo unpublished).

As was discussed above, high temperatures during the vegetative period due to delays in sowing date increase crop growth rate in all four crops. However, in soybean, sunflower and wheat, late sowings hasten vegetative development more than growth, so plants are generally smaller with less leaf area (Carter and Boerma 1979; Stapper and Fischer 1990; Weaver *et al.* 1991). The opposite is generally observed in maize (Knap and Reid 1981; Cirilo and Andrade 1994a). These physiological responses presented by late sown crops have relevance in the selection of other management practices, and are discussed in the next sections.

PLANT POPULATION DENSITY

Plant density should be adjusted for each genotype-environment combination to maximize grain yield and to minimize

the effects of adversities, such as lodging and diseases. In this section, however, we focus on the physiological aspects of the crop response to plant density.

Crops differ in their response to plant density (Fig. 3). The largest grain yield responses are observed in maize (Tetio-Kagho and Gardner 1988a, 1988b; Karlen and Camp 1985; Andrade *et al.* 1996; Otegui 1997; Hammer *et al.* 2009; Tollenaar and Lee 2010). The proportion of change in grain yield of soybean (Wells 1991; Carpenter and Board 1997; Walker *et al.* 2010), sunflower (Steer *et al.* 1986; Villalobos *et al.* 1994), or wheat (Holliday 1960; Puckridge and Donald 1967; Fischer *et al.* 1976; Darwinkel 1978; Willey and Holliday 1971; Whaley *et al.* 2000; Abbate unpublished) is much smaller. At one-fourth of the recommended plant density, yield is significantly reduced in maize but not in soybean, sunflower and wheat (Fig. 3). Two mechanisms explain these effects: the capacity of the crop to intercept solar radiation and the reproductive plasticity of the individuals.

Decreasing plant density results in greater reductions of intercepted photosynthetically active radiation at the critical period for grain number determination in maize than in soybean, sunflower (Valentinuz 1996) and wheat (Fischer *et al.* 1976; Whaley *et al.* 2000). The decrease in radiation interception in maize results in reduced crop growth rates at flowering, and in turn, in lower number of grains per unit surface area and lower grain yield (Andrade *et al.* 1999). Physiological mechanisms explain the differential stability in radiation interception among crops when plant density was reduced. Soybean, sunflower and wheat have greater capacity than maize to compensate a lower number of individuals per unit area with greater leaf area per plant and plant growth rate (i.e. vegetative plasticity). Accordingly, plant biomass of isolated plants is many times larger than that of plants at recommended densities in soybean, sunflower (Vega *et al.* 2000) and wheat (Holliday 1960; Puckridge and Donald 1967; Satorre 1999; Whaley *et al.* 2000) but not in maize (Vega *et al.* 2000; Boomsma *et al.* 2009; Hammer *et al.* 2009). This difference is mostly related to large variation in (i) individual leaf size in sunflower, (ii) ramification in soybean, and (iii) tillering in wheat.

Reproductive plasticity further helps to explain the differential responses of crops to reductions in plant density. As resources per plant and plant growth rate are increased as a result of reductions in plant density, soybean and wheat shows greater plasticity to increase grain number per plant than maize and sunflower (Whaley *et al.* 2000; Vega *et al.* 2001a). This is reflected in the relationship between seed number per plant and plant growth rate at the critical period for grain yield determination (PGR_c), which is linear in soybean and wheat, and curvilinear in maize and sunflower (Vega *et al.* 2001a; Fig. 4A, 4B). Only soybean and wheat adjust the number of reproductive sinks in balance with availability of assimilates in the plant (Fischer 1975; Jiang and Egli 1993; Board and Tan 1995; Fig. 4A, 4B). This indicates a ceiling in number of seeds per plant in maize and sunflower associated with morphogenetic restrictions in the production of additional reproductive sinks under high levels of resource availability per plant (Villalobos *et al.* 1994; Valentinuz *et al.* 1996; Andrade *et al.* 1999). The degree of restriction is highest in maize hybrids with low prolificacy or low uppermost ear plasticity (Otegui 1995; Sarquis 1998; Echarte and Andrade 2003). In sunflower, Villalobos *et al.* (1994) noted that the response of the number of flowers per head to plant density was greater in long-season cultivars than in short-season cultivars.

Increments in grain weight with decreasing plant density are largest in sunflower, intermediate in maize and lowest in soybean (Stivers and Swearingin 1980; Wade *et al.* 1988; Tetio Kagjo and Gardner 1988b; Capristo 2000) and wheat (Fischer *et al.* 1976; Whaley *et al.* 2000; Abbate unpublished).

Increases in plant density above the optimum cause significant yield reductions in maize but not in soybean, sunflower (Vega and Andrade 2002; Tollenaar and Lee 2010)

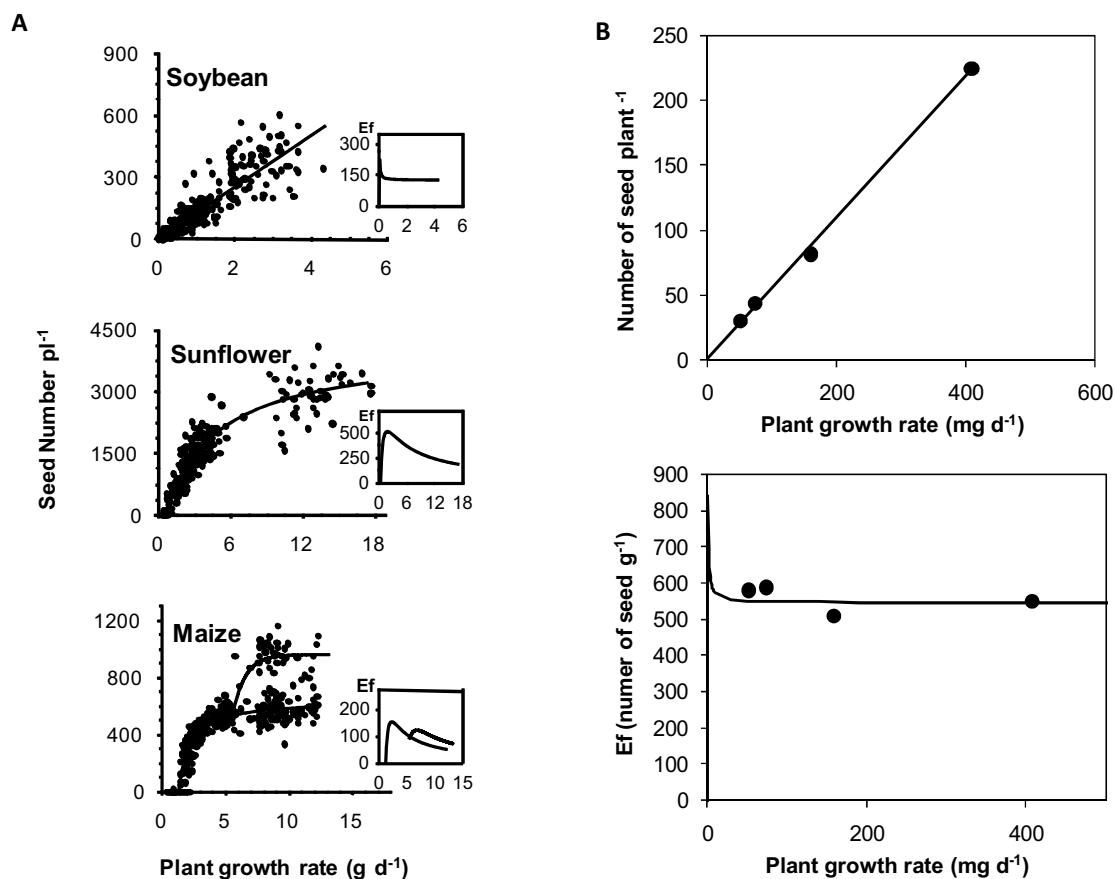


Fig. 4 Seed number per plant (SNP) as a function of plant growth rate during the critical period for seed set (PGR_c) in: (A) soybean, sunflower and maize, and (B) spring wheat. Fitted equations are $y = 4.5 + 124x$ ($r^2 = 0.77$) for soybean; $y = 864(x - 0.39) / (1 + 0.21(x - 0.39))$ ($r^2 = 0.84$) for sunflower; $y = 632(x - 1.02) / (1 + 0.96(x - 1.02))$ ($r^2 = 0.72$) for uppermost ears of non-prolific maize plants, and $y = 0.30 + 0.55x$ ($r^2 = 0.99$) for spring wheat. In maize, the second curve indicates total seeds in prolific plants. The inserts in A and the companion graph in B show the relationship between seed set efficiency ($Ef = SNP \cdot PGR_c^{-1}$) and PGR_c . Adapted from Vega *et al.* (2001) in A, and data from Abbate (unpublished) in B.

and wheat (Fischer *et al.* 1976; Darwinkel 1978) (**Fig. 3**). Grain yield reductions are mainly associated with reductions in grain number per unit surface area. A larger number of plants per unit area compensate for the lower production per plant in soybean, sunflower and wheat but not in maize.

The high yield-sensitivity of maize to high plant density is mainly explained by its low harvest-index stability in response to decreases in available resources per plant (Vega *et al.* 2000; Echarte and Andrade 2003; Maddonni and Otegui 2006). Accordingly, maize shows the largest plant-growth thresholds for seed set (**Fig. 4A**), reflecting significant reductions in dry matter partitioning to reproductive structures and developing kernels when plant growth rate at flowering decreases as a result of increasing plant density (Tollenaar *et al.* 1992; Hashemi-Dezfouli and Herbert 1992; Andrade *et al.* 1999; Vega *et al.* 2001a, 2001b; Pagano and Maddonni 2007; Pagano *et al.* 2007; Tollenaar and Lee, 2010). This response of maize is enhanced by the establishment of plant hierarchies (i.e. dominant and dominated individuals) when crowding stress increases (Edmeades and Daynard 1979), which takes place very early during the cycle (Maddonni and Otegui 2004). Dominated individuals exhibit delayed ear development (Pagano *et al.* 2007) and reduced biomass allocation to this organ (Borrás *et al.* 2007; Pagano and Maddonni 2007), which may finally determine the arrest of ear growth and plant barrenness.

Selection for high grain yield increased maize tolerance to high plant density (Tollenaar and Lee 2002; Lee and Tollenaar 2007; Tollenaar and Lee 2010). The improved performance under crowding stress of modern cultivars seems related to (i) their enhanced kernel set per unit PGR_c close to the threshold for seed set (Tollenaar *et al.* 1992; Echarte *et al.* 2001; Luque *et al.* 2006), and (ii) improved

biomass partitioning to reproductive structures at low PGR_c (Luque *et al.* 2006). These traits resulted from indirect selection under progressively higher plant densities in yield-testing programs, and from a wide testing area that includes low-yielding environments (Tollenaar and Wu 1999; Tollenaar and Lee 2002). In soybean, sunflower, and wheat low plant-growth thresholds for seed set (Vega *et al.* 2001a; Abbate unpublished; **Fig. 4A, 4B**) contribute to explain their tolerance to increases in plant density.

The response of a crop to plant density depends on the environment and other crop management practices. The high vegetative and reproductive plasticity of soybean and wheat in response to resource availability per plant is not expressed in late sowings (Carter and Boerma 1979; Weaver *et al.* 1991) or under poor growing conditions during the vegetative period (Magrín *et al.* 1983; Board and Hall 1984). Thus, these crops are highly responsive to increases in plant density in such situations (Boquet 1990; Calviño *et al.* 2003a).

An increase in plant density is a recommended management practice to compensate for low percent radiation interception during reproductive growth in late sown soybean and wheat (Spink *et al.* 2000; Calviño *et al.* 2003a, 2003b; Abbate 2004). Maize does not show reductions in percent radiation interception at flowering with delays in sowing date, but PGR_c decreases in response to the deterioration of the environmental conditions during this critical stage. Thus, the recommendation is to reduce plant density to avoid reductions in grain set and harvest index attributable to decreases in PGR_c .

Environments with low water and nutrient availability during vegetative growth would require higher plant density to compensate for reductions in leaf area per plant (Egli

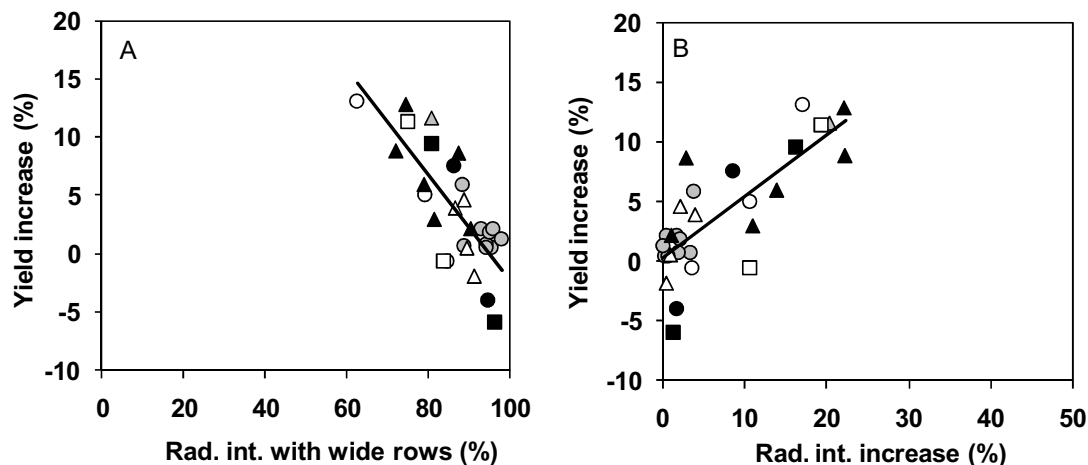


Fig. 5 Relationship between (A) percent grain yield increase in response to reductions in row spacing and radiation interception observed in wide rows (70 cm) and (B) percent grain yield increase in response to narrow rows and radiation interception increase at the critical periods in response to the same treatment, for maize (circles), sunflower (squares) and soybean (triangles). For A, $y = 42.9 - 0.5x$; $r^2 = 0.60$; $P < 0.001$. For B, $y = 0.17 + 0.52x$; $r^2 = 0.63$; $P < 0.001$. Radiation interception was measured at flowering in maize and sunflower and at R3 in soybean. Different symbols indicate different experiments. Adapted from Andrade *et al.* (2002).

1988; Moore 1991). This would be a recommended practice for soybean but not for maize (Boomsma *et al.* 2009). In soybean, increasing plant density does not imply risks relative to dry matter partitioning to reproductive organs (Vega *et al.* 2001a; **Fig. 4B, 4B**). In poor environments, maize plant density should be reduced (Gardner and Gardner 1983; Russell 1986) to avoid PGR_c close to threshold values that result in ear growth suppression (Andrade *et al.* 2002a; Echarte and Tollenaar 2006; D'Andrea *et al.* 2008). The low harvest-index stability of maize in response to available resources per plant indicates that there is a need for careful adjustment of plant density to environmental conditions and input levels. In environments in which all these crops rely largely on soil stored water, a reduction in plant density would result in a conservative use of water and higher water availability for reproductive growth (Debaeke and Abou-drare 2004).

ROW SPACING

Decreasing row spacing at equal plant densities generally produces a more equidistant plant distribution. This distribution decreases plant-to-plant competition for available water, nutrients and light, and increases intercepted radiation and biomass production (Shibles and Weber 1966; Bullock *et al.* 1988). It also reduces the leaf area index required to intercept 95% of the incident radiation because of an increase in the light extinction coefficient (Flenet *et al.* 1996). However, the benefits of a more equidistant plant distribution for crops growing without important water and nutrient deficiencies are variable. Some researchers reported grain yield increases (Scarsbrook and Doss 1973; Bullock *et al.* 1988; Board *et al.* 1992; Egli 1994; Walker *et al.* 2010) but others did not (Ottman and Welch 1989; Zaffaroni and Schneiter 1991; Blamey and Zollinger 1997; Westgate *et al.* 1997).

Higher crop growth rates during the critical stages for yield determination would allow more grains to be set, and thus higher grain yields (Andrade *et al.* 1999). Crop growth rate is directly related to the amount of radiation intercepted by the crop (Andrade *et al.* 2002b). Therefore, the response of grain yield to narrow rows can be analyzed through the effect on the amount of intercepted radiation at the critical periods for grain set.

Grain yield responses to decreased distance between rows are inversely proportional to percent radiation interception achieved with the wide row control treatment during the critical period for grain number determination (Andrade *et al.* 2002c; **Fig. 5A**). Moreover, when row spacing was

reduced, a common relationship for maize, sunflower and soybean was determined between increases in grain yield and in radiation interception during the critical periods (Andrade *et al.* 2002c; **Fig. 5B**). Thus, grain yield increase in response to narrow rows is closely related to the improvement in light interception during the critical period for grain set. Mean grain yield response to narrow rows was close to zero when percent light interception with wide rows was > 90 (**Fig. 5A**). Mean grain yield responses increased to 4.5 and 8.8% for percent interception values in wide rows of 80 to 90 and 70 to 80, respectively (**Fig. 5A**). On the other hand, when row distance was reduced, the relative increase in grain yield was approximately 50% of the relative increase in radiation interception (**Fig. 5B**).

Full light interception can probably not be achieved when (i) short-season and/or erect-leaf cultivars are grown (Anderson *et al.* 1998); (ii) plants are defoliated by frost, hail or insects; or (iii) plants are subjected to water or nutrient stress at vegetative stages (Alessi *et al.* 1977; Barbieri *et al.* 2000). Since drought or nutrient deficiencies during vegetative periods limit leaf area expansion (Trapani and Hall 1996; Salah and Tardieu 1997; Sadras and Trapani 1999), they would increase the probability of response to reduced row spacing. Early sowing in maize and late sowing in soybean could also increase the response to reductions in row spacing, as these practices lead to smaller plants with fewer leaves (Duncan *et al.* 1973; Weaver *et al.* 1991; Andrade *et al.* 1996). Reported increases in radiation interception in response to decreases in row spacing below typical values are often large in late sown soybean (Board *et al.* 1992; Egli 1994; Board and Harville 1996), generally low in maize (Scarsbrook and Doss 1973; Bullock *et al.* 1988; Ottman and Welch 1989; Westgate *et al.* 1997) and none to negligible in wheat (Yumusa *et al.* 1993) and sunflower (Robinson 1978; Zaffaroni and Schneiter 1991). Differences in plant architecture and vegetative plasticity among cultivars would modify the response of crops to row spacing.

Maize response to row spacing is low or nil at low plant densities (Fulton 1970) because of its low reproductive plasticity and because the decrease in transmitted photosynthetically active radiation between the rows is compensated for by an increase in transmitted radiation between the plants in the row. Greater responses to reduced row spacing are expected in crops when plants are closer together within the row. At high plant densities, where maize crops in wide rows attain percent light interception values larger than 95, row spacing reductions would not contribute to increase intercepted radiation around silking and thereafter. Under

these conditions, narrow rows could reduce post-silking radiation use efficiency (Maddonna *et al.* 2006) because photosynthetic source activity during grain filling would depend on the light environment within the maize canopy which is in turn related to plant spatial arrangement. In fact, the red/far-red radiation ratio was impoverished at the lowermost leaf stratum of crops in response to reductions in row spacing at high plant population densities (Borrás *et al.* 2003). Differences among cultivar in terms of canopy architecture and source-sink relationship during grain filling would modify these responses and their effect on grain weight and final grain yield.

Other advantages of reduced row spacing include a decrease in water evaporation from the soil surface (Yao and Shaw 1964; Nunez and Kamprath 1969; Karlen and Camp 1985), an inhibition of weed growth (Forcella *et al.* 1992; Teadsdale 1994) and an improved uptake of limiting nutrients from the soil (Stickler 1964; Rosolem *et al.* 1993; Barbieri *et al.* 2000, 2008). In some of these cases, responses to reductions in row spacing could be greater than predicted from intercepted radiation. Narrow rows usually increase the transpiration/evaporation ratio in a crop (Adam *et al.* 1976; Tompkins *et al.* 1991a, 1991b). Thus, when crops are subjected to progressive drought, depend mostly on stored water and soil evaporation is low, narrow rows would decrease yield since higher radiation interception would increase early water use by transpiration (Alessi and Power 1982; Zafaroni and Schneider 1989; Debaeke and Aboudrare 2004) resulting in a more severe water stress at the critical periods for grain yield determination.

STAND UNIFORMITY

Crop species and, to a lesser extent, cultivars differ in their response to stand uniformity. Understanding the response of crops to spatial and temporal heterogeneity involves consideration of plant traits, such as vegetative and reproductive plasticity, and population-level traits. Early signals allow plants to detect the presence of competitive neighbors and respond to them by, for instance, increasing the rate of internode elongation and changing the pattern of dry matter allocation (Ballaré *et al.* 1994; Aphalo and Ballaré 1995; Maddonna and Otegui. 2004; Pagano and Maddonna 2007). Small differences in plant size early during the growing cycle are usually amplified as the season progresses and competition for resources intensifies. This reinforcement of size hierarchies with time implies that small and random variation in initial plant size could also be a factor in crop heterogeneity (Goss *et al.* 1989). As a result of this highly dynamic process, crop yield can be affected (Crawley 1983).

Non-uniformity in plant size at constant plant density could be increased by variation in time of plant emergence and in plant spacing (Andrade and Abbate 2005). Variations in sowing depth, surface residue distribution in conservation tillage systems, seed-bed condition (soil moisture, seed-soil contact, upper-layer soil strength) and seed vigor are responsible for uneven time of seedling emergence in the field. On the other hand, planters with low precision in seed placement and careless sowing operation (not properly adjusted planters, high planting speed) are the main causes of variable gap size between plants within the row in stands of equivalent mean plant density.

Increasing variation in time of emergence and in plant spacing does not affect yield in soybean, sunflower and wheat. In soybean, for example, yield did not respond to increases in standard deviation for within-row plant spacing from 2.7 to 7.0 cm (Andrade and Abbate 2005). Uneven emergence increased variation in plant size and grain yield per plant but did not affect soybean yield per unit area (Andrade and Abbate 2005), which corroborated the findings of Egli (1993). Similar responses were determined for sunflower (Cardinali *et al.* 1985; Trápani *et al.* 2000). Results in maize, however, have been controversial. Some authors (Krall *et al.* 1977; Vanderlip *et al.* 1988) reported a decrease in maize grain yield in response to increased vari-

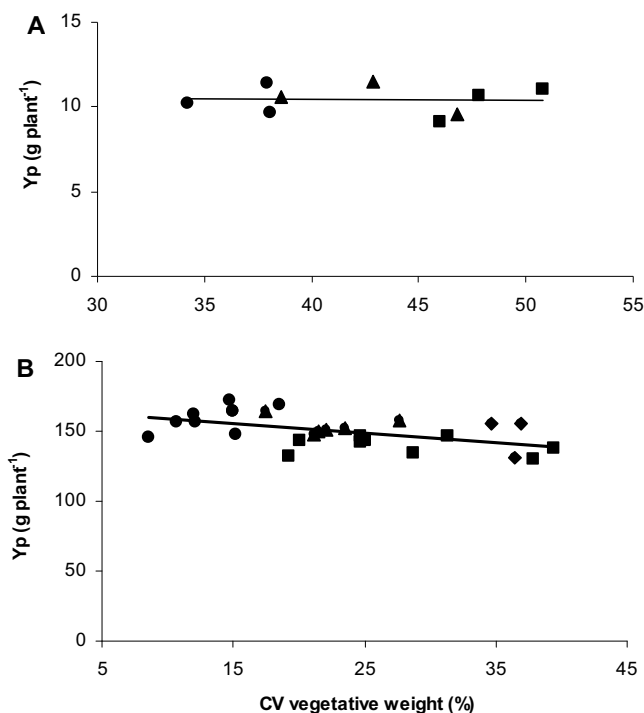


Fig. 6 Grain yield per plant (Y_p) of soybean (**A**) and maize (**B**) as a function of within-row plant vegetative biomass coefficient of variation (CV). Crops were sown at optimal dates and grown under adequate levels of water and nutrient availability. Data from the control (circles), and from the temporal (squares), spatial (triangles) and temporal-spatial (diamonds) non-uniformity treatments. The relationship between the two variables was significant for maize ($y = 165.9 - 0.68x$; $r^2 = 0.53$; $P < 0.01$) but not for soybean. Reprinted from Andrade F, Abbate P (2005). Response of maize and soybean to variability in stand uniformity. *Agronomy Journal* 97, 1263-1269 ©2005, with kind permission from The American Society of Agronomy, USA.

ation in plant distribution along the row, and a penalty of approximately 100 kg ha⁻¹ was computed for every centimeter increase in standard deviation for plant spacing (range between 1.5 and 12.6 cm). Contrarily, Erbach *et al.* (1972), Muldoon and Daynard (1981), Otegui *et al.* (1992) and Liu *et al.* (2004) found no difference in grain yield between uniform and non-uniform crops. Liu *et al.* (2004) determined that only temporal variability had a negative effect on maize grain yield for a moderate stand density of 6.7 plants m⁻². Similarly, Andrade and Abbate (2005) computed a decrease in grain yield of 4% or more per day increase in time of emergence standard deviation but found no significant response to spatial variability at a near optimum stand density (8 plants m⁻²). Spatial variability had little or no effects at this plant density but it should be considered at higher plant populations, when more plants may become barren due to extremely reduced plant growth rate around silking (Fig. 4A) promoted by enhanced crowding stress due to poor distribution (Pommel and Bonhomme 1998; Tollenaar *et al.* 2006). Combining the data from experiments with spatial and temporal variation, average maize yield per plant decreased 0.68 g for every unit increase in vegetative biomass percent coefficient of variation; contrarily, soybean grain yield per plant was not affected by increments in plant size variation (Fig. 6A, 6B).

Traits behind crop-specific responses to uniformity in seedling emergence and plant spacing are above-described differences in (i) vegetative plasticity (Andrade and Abbate 2005), and (ii) the response pattern of grain number per plant to plant growth rate during the critical period for grain set (Andrade *et al.* 1999; Vega *et al.* 2000, 2001a; Andrade and Abbate 2005). Briefly, within-row plant unevenness would not be detrimental to yield if it does not decrease average vegetative biomass per unit surface area and if there is no reproductive sink limitation. According to the

characteristics of the plants, this is more likely to occur in soybean, sunflower and wheat than in maize. Then, yield loss in late emerging plants is compensated for by increased yield of early emerging plants in soybean but not in maize. Moreover, grain yield loss of plants placed very close to their competitive neighbors would be compensated for by the additional yield of plants supplied with additional available resources (i.e. radiation, water and nutrients) in soybean but not in maize.

The effect of unevenness in plant sizes on maize grain yield would depend on the characteristics of the cultivar. Maize cultivars differ in the type of response of yield per plant to resources available per plant (Echarte and Andrade 2003) and in the response of seed number per plant to PGR_c (Echarte *et al.* 2004; Luque *et al.* 2006). Therefore, the response to uniform stands would be less pronounced among cultivars with (i) high prolificacy or uppermost-ear plasticity, low PGR_c thresholds for grain set and low curvature in the yield per plant to vegetative biomass per plant relationship, because yield gain of dominant plants would tend to balance yield losses of dominated plants, and with (ii) long cycle, because of their enhanced capacity to explore available resources.

Management or environmental conditions would also affect the response of crops to non-uniformity in plant distribution or emergence. Variation in the response is not surprising, as plant and population compensatory mechanisms are strongly influenced by environmental constraints (Oosterheld and McNaughton 1991; Sadras 1995).

These genetic and environmental effects would be the reasons for the contrasting response of maize grain yield to variability in intra-row spacing reported in the literature (Erbach 1972; Krall *et al.* 1977; Johnson and Mulvaney 1980; Muldoon and Daynard 1981; Doerge and Hall 2002). Differences in morphological and physiological traits among species, however, are consistent with the observed responses of maize, sunflower, soybean and wheat to stand heterogeneity, which are commonly negative or neutral in maize and neutral in the other crops.

Finally, there are other benefits from uniform stands since uniform plant size facilitates harvest machinery calibration and uniform grain drying in the field prevents harvest delays.

CULTIVARS

Crop breeding produced cultivars with improved yield and tolerance to biotic and abiotic stresses (Lopez Pereira *et al.* 2008; Cirilo *et al.* 2009; Fischer and Edmeades, 2010; Tollenaar and Lee 2010; Jin *et al.* 2010). Cultivars within a crop species not only differ in yield potential and stress tolerance but also in cycle length and plasticity, which in turn affect their responses to management practices.

Cultivars show a wide range of variation in duration of the growing cycle (Summerfield *et al.* 1991). Base temperature, thermal time requirement, vernalization requirement, photoperiod threshold and sensitivity for a specific stage of development vary among genotypes within species (Cregan and Hartwig 1984; Goyne and Schneider 1987; Slafer and Rawson 1994). Accordingly, broad variation within crop species in development during vegetative and reproductive stages has been reported (Stapper and Fischer 1990; Baigorri 1997a; Capristo *et al.* 2007; Tollenaar and Lee 2010). A lot of information is available in the literature regarding genomic studies for flowering time (Chardon *et al.* 2004; Cockran *et al.* 2007). Recently, QTL associated with vegetative and/or reproductive development were identified in maize (Sarlangue *et al.* 2007a). Moreover, Leon *et al.* (2001) identified QTL associated with phenology and photoperiodic response in sunflower. Finally, a good number of studies in wheat and related Triticeae species (reviewed in Landjeva *et al.* 2007) have led to the identification and cloning of genes and QTL responsible for vernalization response and photoperiod sensitivity.

The length of the growing cycle is critical in deter-

mining genotype adaptability to the environment. In conventional farming systems where the aim is to increase yield per crop (kg ha⁻¹), best cultivars for a specific location are those that fully explore and exploit the potential growing season fitting constraints of the local environment. High yields for a specific crop by environment combination can only be achieved if the cultivars used are phenologically adapted to the seasonal resource patterns of the target production region.

At low latitudes, temperature and radiation do not vary much along the year, and long season hybrids of maize and sunflower are generally the most suitable because they use the available resources more efficiently than shorter hybrids (Lafitte and Edmeades 1997; Bruns and Abbas 2006). Contrarily, at high latitudes, radiation and temperature decrease markedly during the grain filling stage of summer crops and grain yield usually decreases as hybrid maturity class increases (Neild and Newman 1985; Ruget 1993). At Balcarce (38° S), an area characterized by low average temperatures that limit early growth and a rapid decrease in radiation and temperature towards the end of the growing season, maize total above ground biomass increased with hybrid maturity class, and grain yields were lowest for short season hybrids and similar between mid and long season hybrids (Capristo *et al.* 2007; Fig. 7). Long season hybrids showed the highest cumulative radiation interception but the lowest radiation use efficiency during reproductive growth. Sink-source relationship and the apparent reserve remobilization increased with hybrid maturity class, indicating that grain yield of short season hybrids would be more limited by the capacity of the reproductive sinks during grain filling compared with their long season counterparts. At Pergamino (34° S), however, a region located at lower latitude and with an average temperature during the growing season 3°C higher than at Balcarce, grain yield increased linearly and continuously along a similar range of hybrid maturity classes (Cirilo unpublished data). At higher latitudes than Balcarce, grain yield decreased more sharply with hybrid cycle length (Ruget 1993). These contrasting results would be explained by the deterioration of the environmental conditions during the last part of the growing season, which is more pronounced as latitude increases.

In soybean, the wide variation in maturity groups determined by photoperiodic and thermal requirements provides crop adaptation to an ample range of latitudes (Baigorri 1997a). For a specific region, adapted short season soybean cultivars show high yield potential related to high crop growth rate during the critical period for grain yield determination whereas, adapted long season cultivars present high yield stability because of their long vegetative and reproductive periods (Baigorri 1997a). In general, the longer the growing season, the longer the maturity group of adapted cultivars. In more intensive farming systems where the goal is to maximize yield per unit time, full-season cultivars are not necessarily the best option. This is likely the case for systems based on wheat-soybean double cropping in the southern Pampas (Caviglia *et al.* 2004). Moreover, the cultivar maturity group in combination with sowing date can be used as a strategy to avoid stress during critical periods (Debaeke and Aboudrare 2004).

Cultivars within a species differ in vegetative plasticity and in the response of reproductive output to variation in the amount of resources available per plant which, in turn, modulates crop responses to plant population density, row spacing and stand uniformity (see previous sections). A short-season cultivar, with low leaf area per plant and low vegetative plasticity (Egli 1993; Villalobos *et al.* 1994) generally benefits more from increments in plant density and reductions in row spacing than a long-season cultivar (Fig. 8), because the former may not achieve full light interception at the critical stages (Ball *et al.* 2000a, 2000b, 2001; Sarlangue *et al.* 2007b). The effect of increasing plant density on radiation interception and biomass production were larger in short season maize hybrids than in their long season counterparts. A larger harvest index in response to in-

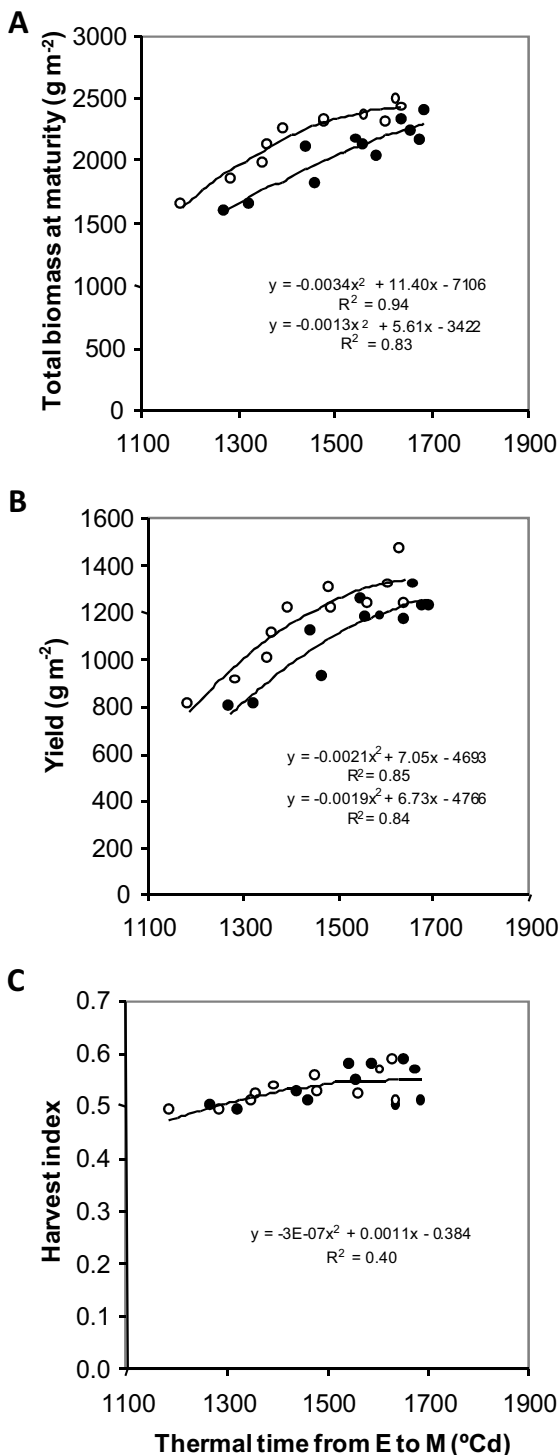


Fig. 7 Total biomass at maturity (A), yield (B) and harvest index (C) as a function of the hybrid maturity expressed as thermal time elapsed (cumulative growing degree days) from emergence (E) to physiological maturity (M). Data from 11 maize hybrids cultivated in 2000-2001 (closed symbols) and 2001-2002 (open symbols) growing seasons. Lines show the quadratic regression for each growing season (A and B) and for pooled data of both seasons (C). SE were 80 and 81 g m⁻² for cumulative dry matter, 33.8 and 20.3 g m⁻² for grain yield, 0.008 and 0.006 for harvest index, for the first and second growing seasons, respectively. E = emergence; and M = maturity. Reprinted from **Capristo P, Rizzalli R, Andrade F** (2007) Ecophysiological yield components of maize hybrids with contrasting maturity. *Agronomy Journal* 99, 1111-1118 ©2007, with kind permission from The American Society of Agronomy, USA.

crements in plant density was only observed in hybrids with low reproductive plasticity (Sarlangue *et al.* 2007b).

The detrimental effects of delays in sowing date in maize, sunflower and wheat are, in general, more pro-

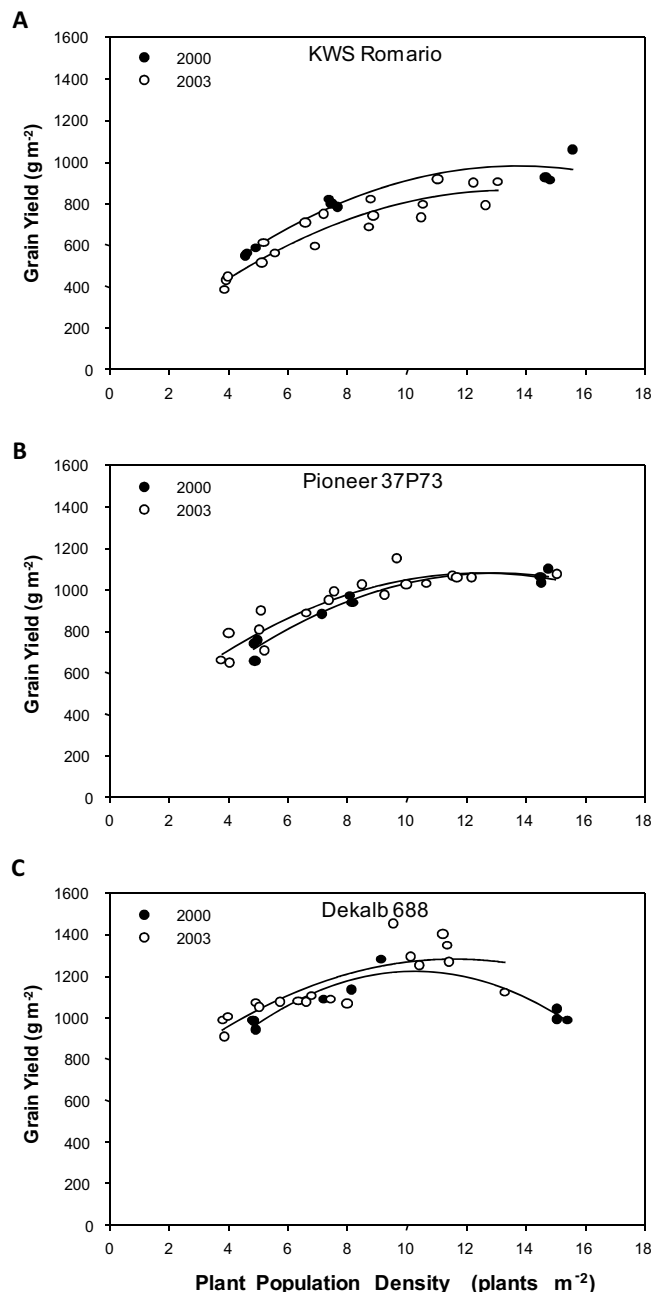


Fig. 8 Grain yield (g m⁻²) as a function of plant population density (plants m⁻²) for short season hybrids KWS Romario (A) and Pioneer 37P73 (B) and for the long season hybrid Dekalb 688 (C) in two years (2000 and 2003). Quadratic equations for year 2000 were: KWS Romario $y = -4.96x^2 + 136.2x + 45$, $R^2 = 0.93$; Pioneer 37P73 $y = -5.55x^2 + 144.2x + 144$, $R^2 = 0.96$; Dekalb 688 $y = -8.8x^2 + 180.5x + 292$, $R^2 = 0.86$. Reprinted from **Sarlangue T, Andrade F, Calviño P, Purcell L** (2007b) Why do maize hybrids respond differently to variations in plant density? *Agronomy Journal* 99, 984-991 ©2007, with kind permission from The American Society of Agronomy, USA.

nounced in long-season cultivars. These cultivars benefit most from early sowings and show the largest reductions in grain yield in response to delays in sowing date (Olson and Sander 1988; Blamey and Zollinger 1997). The benefit of planting early-maturity cultivars in late sowings depends on the magnitude of the delay and the potential length of the growing season (Lauer *et al.* 1999; Andrade and Cirilo 2002). When maize was sown late in mid-December, early-maturity hybrids outyielded the late-maturity ones at Balcarne (+24%), but not at Pergamino (-17%), when crops were grown without water or nutrient limitations (Cirilo and Andrade 1994a; Cirilo 2001). Nevertheless, when maize crops were sown later than mid-December at Pergamino, mid-season hybrids yielded more than their long-season

counterparts (Cirilo 2001). Similarly, when the growing season is short and the risk of diseases in sunflower crops is high, the use of short-season hybrids is recommended. In fact, greatest sunflower grain yield in late sowings were obtained with short-season hybrids at Balcarce and with long-season hybrids at a northern location close to Pergamino (unpublished data). For late planted soybean, the recommendation is to increase the maturity group in areas with long potential growing season to compensate for the shortening of the reproductive period under these conditions (see above). At higher latitude, however, the only option is to decrease maturity group to avoid climatic or biotic adversities towards the end of the growing season (Baigorri 1997b). In wheat, the recommendation for late sowings is to shorten the cultivar cycle length in order to avoid a delay in the flowering date that would expose the pre-anthesis and grain filling periods to high temperatures and low photo-thermal quotients (Abbate *et al.* 1990; Stapper and Fischer 1990).

CONCLUSIONS

The effects of crop management practices on crop performance were analyzed based on the physiological determinants of crop growth and yield.

The concepts of critical periods for grain yield determination, and vegetative and reproductive plasticity among others, constituted the basis for understanding crop yield as determined by management practices, environmental conditions, genotype and the interactions among these factors. They also contributed to understand or explain the differential responses of crops to management practices observed among species or cultivars within species, or among different environmental conditions and production systems.

The knowledge and quantification of the ecophysiological factors underlying crop growth and yield determination are critical for the design and selection of the most appropriate management practices for a specific genotype and environment combination.

The main focus of this work was placed on sowing date, plant density, row spacing, plant distribution and emergence uniformity, and cultivar maturity group election. This approach, however applies to other management practices as well. For example, the impact of fertilization and irrigation practices on grain yield can be inferred from the effects of water and nutrient availability on the light-capture system and the physiological condition of the crop at the critical periods for grain yield determination. Irrigation or fertilization strategies must ensure a good physiological condition of the crop at the critical periods for grain yield determination. This approach can contribute to (i) match crop demands to the particular environmental offer and (ii) an efficient use of environmental resources and inputs in a specific location.

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