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The effect of duration of the vegetative phase in irrigated semi-dwarf spring wheat on phenology, growth and potential yield across sowing dates at low latitude

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ABSTRACT

In order to study the effect of duration of the vegetative period (sowing to floral initiation) on potential yield, sister spring wheat semi-dwarf cultivars, Yecora and Cajeme, the latter having an extra vernalization sensitive allele (Vrn-A1v) and a photoperiod sensitive one (Ppd-D1b), were grown at 4–5 sowing dates over 5 years under irrigation and high fertility in northwest Mexico (latitude 27°N). In the earliest sowings (late Oct-early Nov) Cajeme had a 20 day longer vegetative period; this delay decreased steadily to 8 days in the latest sowings (mid-late January); anthesis date for Cajeme was, respectively, 17 and 6 days later. Relationships to minimum temperature levels in the vegetative phase strongly suggest that this sowing date by cultivar interaction arises largely because of the difference in vernalization alleles in an environment where there is limited vernalizing cold. Cajeme produced a greater maximum number of shoots, more spikelet nodes per spike, greater green area index, and greater above ground dry matter at anthesis and at physiological maturity. However Cajeme yielded no more than Yecora, even when yield was plotted against anthesis date, tending to have fewer grains/m^2. A similar conclusion was reached when grains/m^2 were related to preanthesis photothermal quotient, and grain weight to grain filling mean temperature: both cultivars responded similarly although Cajeme had slightly fewer grains/m^2 and heavier kernels, thus weather around flowering dominated determination of these yield components. Some other yield components were also slightly, but significantly, affected by cultivar in a manner independent of flowering date and weather. Thus Cajeme had a significantly higher spike dry matter at anthesis and a significantly lower fruiting efficiency of Cajeme (73.8 *versus* 84.2 grains/g spike dry matter). It is suggested that the latter was a consequence of the longer vegetative period leading to greater tillering, poorer tiller survival and a more competitive preanthesis canopy, causing poorer floret survival in grain-bearing spikes. The excessive tillering may have been exaggerated by supplying all nitrogen fertilizer at sowing.

1. Introduction

Potential yield is defined as the yield of crop product in the absence of biotic stresses and lack of water, but with an optimal level of other manageable inputs, and with levels of unmanaged inputs (e.g. solar radiation, temperature, soil type) representative of the region of interest (Fischer 2015). The farm yield of crops has increased over the last 50 years or so largely due to the adoption of technologies that increased potential yield, achieved through breeding, agronomy, and positive interactions between the two (Fischer et al., 2014). A major challenge for crop scientists is to continue raising potential yields. This contribution reports on one aspect of the challenge as it related to the potential yield of wheat.

The duration of a crop is obviously one determinant of potential yield because it limits solar radiation capture of the crop, and hence the potential production of biomass (hereafter termed above-ground dry matter, DM). However the successive phenological phases within the total duration may be of greater or lesser importance for yield. Development in a determinate crop like wheat can be divided into three major phases or periods, namely a vegetative period up to floral initiation,[1] a reproductive period from

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[1] Some consider that the vegetative period ends at terminal spikelet formation, some 7–14 days after floral initiation, for this is closely linked but a few days after the onset of stem elongation, a readily observable event (Borras-Gelonch et al., 2012).

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Table 1
Allelic composition of spring wheat cultivars Yecora and Cajeme (H. Eagles and B. Trevaskis, pers. comm.), and response of days to anthesis to seed vernalization (vern, 4 weeks at 1–2 °C) and to photoperiod extension (ppd, from 10 to 14 h) when grown in a growth cabinet at constant 20 °C (Midmore et al., 1982).

Cultivar	Vernalization alleles			Photoperiod alleles		Days to anthesis at 20 °C in growth cabinet				Response in days to vrn		Response in days to ppd	
	Chromosome			Chromosome		10 h ppd		14 h ppd		10 h ppd	14 h ppd	No vern	Vern
	A1	B1	D1	B1	D1	No vern	Vern	No vern	Vern				
Yecora	a	v	a	b	a	68.5	56.5	47	47	−12	0	−21.5	−9.5
Cajeme	v	v	a	b	b	105	61	76	47	−44	−29	−29	−14

a = insensitive allele.

floral initiation to anthesis, and a final grain-filling period. Genetic variation in overall duration is largely related to variation in the vegetative period, with significant but generally less genetic variation in the reproductive period, and even less in the grain-filling one. In a prescient paper Bunting (1971), from experience with sorghum, rice and winter wheat, argued that the duration of the vegetative period, usually quite long in traditional varieties, may be unnecessarily long for modern agricultural situations.

For wheat, the genetic determination of phasic development is summarized by Slafer et al. (2009) and Fischer (2011). The duration of the vegetative period is governed by alleles controlling the response to photoperiod and to vernalizing cold, as well as ones affecting "intrinsic earliness", defined as the period's duration in degree days when the former environmental responses are fully satisfied. There is also genetic variation in the reproductive period under the control of photoperiod sensitivity mechanisms, probably the same alleles as operate in the vegetative period, but possibly supplemented by others; however there is little or no direct response to vernalizing cold, and limited evidence of variation in "intrinsic earliness" in this period. The net result is that duration of the reproductive period can show considerable independent genetic variation relative to that of the vegetative period, even within a given fixed overall duration sowing to anthesis (Slafer et al., 2009; Borras-Gelonch et al., 2012).

Single vernalization alleles can cause delayed floral initiation in autumn-sown spring wheats, especially in environments with mild winters, as can photoperiod sensitivity alleles (Eagles et al., 2010). Of interest here is the effect of the presence of two such alleles, a vernalization one and a photoperiod one, leading to one to several weeks delay in floral initiation and in anthesis, when compared to a near isoline without the alleles in a low latitude environment with mild winter temperatures. Does the longer growth period before anthesis lead to more DM production at anthesis (DM_a), and to greater grains/m^2 (GN) and grain yield (GDM), as commonly assumed in some simulation models (e.g. APSIM relates GN to stem weight at anthesis which is actually DM_a less leaf lamina weigh, a minor component of crop DM by then (APSIM, 2014))? Other models give more emphasis to crop DM accumulation only in the latter part of the reproductive period (e.g., STICS, Brisson et al., 2002), being based on the strong relationship of GN to spike dry weight (g/m^2) at anthesis, the latter accumulating during this period (Fischer 1985, 2011; Slafer et al., 2009).

The inclusion in a largely unpublished time of sowing experiment conducted some 40 years ago of a pair of high yielding semi-dwarf spring sister lines, recently found by molecular marker analysis to differ in one vernalization and one photoperiod allele, permits a retrospective examination of the above questions. The 5 year experiment under optimal agronomy comprised four or five sowing dates each year, in order to have anthesis occurring across a range of calendar dates, so that the sister lines can be compared at the same anthesis as well as sowing dates.

2. Methods

2.1. Genotypes

The near isogenic pair comprised two cultivars from the same cross in the CIMMYT breeding program and released in early 1970s for growth under irrigation in northwest Mexico. They were:

Yecora 70 = CIANO67′S′/3/SONORA64/KleinRendidor//Siete-Cerros66 II-23584-26Y-2M-1Y-0M

Cajeme 71 = CIANO67′S′/3/SONORA64/KleinRendidor//Siete-Cerros66 II-23584-26Y-2M-3Y-2M-0Y

Thus the cultivars were derived from different selected plants in F4 generation, coming from the same plant selected in F2 and in F3, from the same 4-way cross in which two parents (CIANO67 and SONORA64) shared a coefficient of parentage of 0.50. The coefficient of parentage between Yecora70 and Cajeme71 is therefore at least 0.953. At the time of release these two cultivars of spring habit were amongst the highest yielding, each having both major Norin-10 dwarfing genes, namely Rht-B1b and Rht-D1b; also they were both awned and of non-erect leaf habit. No other cultivars named Yecora 70 or Cajeme 71 have been released (apart from Yecora Rojo in California which is Yecora 70), so that hereafter the cultivars are known as Yecora and Cajeme.

Recent molecular marker analysis has revealed the major development alleles in Yecora and Cajeme (Table 1). The later variety, Cajeme, has an additional vernalization allele on chromosome A1 (abbreviated Vrn-A1v, Eagles et al., 2010), only the lack of a vernalization allele on chromosome D1 preventing it being a true winter wheat, as is its parent Klein Rendidor. Growth cabinet studies (Midmore et al., 1982) confirmed that Cajeme had a modest response to vernalization whereas Yecora showed little response and only under short days (Table 1). This is in agreement with other measures of the Vrn-A1v (Zheng et al., 2013), the strongest of the three vernalization alleles and including the interaction effect showing a stronger response to vernalization in shorter days. There is also a difference between the cultivars in the photoperiod sensitivity allele on Chromosome D1, Yecora having the insensitive allele (Ppd-D1a) and Cajeme the sensitive one (Ppd-D1b, B. Trevaskis pers. comm.), leading to a larger response to photoperiod extension in Cajeme, especially when unvernalized (Table 1). Table 1 also suggests there is no difference in intrinsic earliness between Yecora and Cajeme, both reaching anthesis at 47 days after vernalization and under long days.

2.2. Location, weather, sowing date treatments and cultural management

The experiments were conducted at CIANO (Centro de Investigaciones Agricolas del Noroeste)[2] in north west Mexico (27° 20′ N, 109° 54′ W, and 40 m above sea level, masl) between 1970 and 1975. This irrigated research station has for many years been the loca-

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[2] Now renamed CENEB(Centro de Investigaciones Norman E Borlaug).