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Response of five wheat cultivars to early drought in the Pampas

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Abstract – Wheat production in the Pampas of Argentina is frequently reduced because of early drought occurring during vegetative growth. The plant morphological and physiological traits required to resist such an early drought and to produce substantial grain yields is still controversial. In this study we have investigated the behaviour of five wheat cultivars in terms of their vegetative growth, water use, phenological development, biomass accumulation and grain yield, under irrigated and water-stressed treatments. When looking at the vegetative growth, we pointed out that some cultivars were favoured by high tillering capacities and apparent vigorous root system, even in irrigated treatments. Others developed adaptive capacities when submitted to drought, such as production of second generation of tillers after the water stress period or enhancement of the rooting front. Among yield components, it appeared that the two most favourable traits were a long grain filling period and/or a high harvest index. The investigated cultivars exhibited various strategies to achieve this. Some strategies correspond to a specific physiological functioning. This is the case of the durum wheat cultivar, which showed a high level of late growth rate. Some other strategies correspond to adaptation of plants to limited water supply, such as developmental plasticity. An important finding is that vegetative drought resistance did not infer the final grain yield. Moreover, luxuriant vegetative growth appeared to be a disadvantage for grain yield.

wheat / drought resistance / vegetative growth / grain filling / water uptake / genetic variability

Résumé – Réponse de cinq variétés de blé à la sécheresse précoce dans la Pampa. La production de blé dans la Pampa argentine est fréquemment pénalisée à la suite des sécheresses précoces qui se produisent pendant la croissance végétative. Les critères morphologiques et physiologiques utiles pour résister à une telle sécheresse précoce et produire des rendements substantiels sont encore controversés. Dans cette étude, nous avons analysé le comportement de cinq variétés de blé en termes de croissance végétative, consommation en eau, développement phénologique, accumulation de biomasse et rendement, avec et sans irrigation. L'analyse de la croissance végétative a permis de mettre en évidence que certaines variétés étaient favorisées par de fortes capacités de tallage et un système racinaire vigoureux, même en conditions irriguées. D'autres variétés ont développé des capacités d'adaptation à la sécheresse : seconde génération de talles après la période de stress hydrique ou augmentation du front racinaire. En ce qui concerne la mise en place des composantes du rendement, il est apparu que les deux caractéristiques les plus favorables étaient une période de remplissage des grains longue et/ou un indice de récolte élevé. Les variétés étudiées semblent avoir développé des stratégies variées pour tendre vers l'une ou l'autre de ces caractéristiques. Certaines de ces stratégies correspondent à un fonctionnement physiologique spécifique. C'est le cas pour la variété de blé dur qui a montré une croissance tardive particulièrement élevée, sans doute due à la photosynthèse de l'épi. D'autres stratégies relèvent de l'adaptation des plantes aux conditions d'alimentation en eau limitées ; c'est le cas de la plasticité du développement phénologique. Un résultat important de cette étude est que la résistance à la sécheresse développée par les organes végétatifs n'a pas toujours été favorable au rendement final.

blé / résistance à la sécheresse / croissance végétative / remplissage du grain / absorption d'eau / variabilité génétique

Communicated by Serge Rambal (Montpellier, France)

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INTRODUCTION

The Pampas is the main productive region for cereals in Argentina. In spite of a high level of annual rainfall, ranging from 600 to 1000 mm, winter crops mostly suffer from water shortage during vegetative growth because of the seasonal distribution of rain [12, 28]. To cope with such a drought pattern, it is important to combine proper management practices and genetic properties [14]. A considerable variation exists among wheat cultivars for drought resistance [9, 13]. For early drought conditions, controversy remains over the optimum plant type that would confer substantial and stable grain yields. Lazar et al. [23] analyse such a failure as the result of the complexity of drought resistance traits combined with the plasticity of crop response to stress.

Among the morphological traits required to resist early drought, a deep and dense rooting system is probably the most important one [17, 38] because the roots make soil water available for the crop, but also because they partly control the development of the leaf area by hormonal signals in the presence of water stress [36]. The reduction in above-ground growth can be considered as an advantage because it limits transpiration and conserves soil water [34]. On the other hand, it may also limit photosynthetic capacity and therefore yield. This may explain contrasting results in the literature about the role of tillering in drought resistance [4, 28]. For Arraudeau [3], high tillering is disadvantageous when drought occurs before anthesis, while other authors [25, 42] insist on the importance of tillers for early vigour and plasticity of the plant. Moreover, a limitation in early vegetative growth does not necessarily penalise yield. For example, Christen et al. [8] found that moderate stress during vegetative growth increased grain yield of the stressed treatment relative to the control.

Regarding grain yield, different keys have been proposed for understanding or analysing the relation between final yield and its components under conditions of water stress [26]. One classical agronomic approach is to analyse the components *spike number* \times *grains per spike* \times *grain weight*. Each yield component is known to be set during a specific phenological phase, and the impact of water shortage can be related to a specific yield component that is most vulnerable during the onset of stress. Another analysis is that of Passioura [35], who described yield as the product *water transpired* \times *water use efficiency* \times *harvest index*. It is also possible to rely on broad physiological traits using the framework of Levitt [24]. These traits include *drought escape*, *drought resistance* and *drought tolerance*. Breeders use the notions of *potential yield* and *yield stability* to characterise differential behaviours of varieties in the face of

drought [9]. The various ways of describing crop responses to drought underline how complex it is.

The effect of early drought is different from that of terminal drought [26]. One view is that water stress is less damaging to grain yield when occurring early in the crop cycle [6]. An example of this was reported by Simane et al. [43]. Adaptive features to drought or plasticity are mentioned by Subbarao et al. [45].

To understand such variability in the response of wheat to early drought, we compared the agrophysiological behaviour of five cultivars grown in the field under water deficit and under well-watered conditions. We chose five cultivars of wheat, which seemed to exhibit different responses to early drought. In an effort to make results relevant to conditions of the Pampas, we first focused on vegetative growth and water use. Second, we analysed the differential yield performances of the five cultivars to establish relations between vegetative growth and grain yield.

1. MATERIALS AND METHODS

1.1. Experimental design

The experiments were located at the INTA experimental center at Pergamino (33°55'S 60°33'W) in the north-west of Buenos Aires province, Argentina. Four bread wheat cultivars (*Triticum aestivum* L.): Nesser, La Paz, Queguay and LAJ3333 and one durum wheat cultivar (*Triticum durum* L.): Aconchi were sown on 17 July 1995 at 270 plants·m⁻² on 13 m² wide plots. The soil was a typical deep Argiudol with an estimated maximal available water of 300 mm in 2 m soil profile. The organic nitrogen content was 0.16% in the first 20 cm and 0.10% between 20 and 40 cm in the soil. The experimental field was divided into two parts, one of which was irrigated during vegetative growth and the other covered by a rainout shelter between 59 and 77 days after sowing (DAS) to exclude water during most of the stem-elongation phase. The two water treatments will be referred to hereafter as the I – for irrigated – and the S – for stressed – treatments. The differential water supply between the two treatments was 150 mm (Fig. 1). Each part was subdivided into five elementary plots, one per cultivar. A fertilisation of 80 kg N·ha⁻¹ was applied at sowing and pests, diseases and weeds were controlled. The initial available water in the soil at sowing was 260 mm (87% of the maximal) and the mineral nitrogen content was 68 kg·ha⁻¹.

1.2. Plant measurements

Above-ground biomass was harvested at 65, 85, 93, 105, 123 DAS and separated into leaves, stem and ears. Leaf area index (LAI) was measured with a LICOR 3100 lai-meter. Each sample corresponded to two adjacent lines of 0.50 m long each. On the same samples, all the tillers with at least one fully expanded leaf were counted. Biomass was weighted after drying at 70 °C for 48 hours. All plant measurements were made on 3 replicate samples. Phenological stages were noted from observation on 10 plant samples and translated into the decimal Zadoks' scale [47]. Phenological time was calculated in Growing Degree Days (GDD) above 0 °C.

1.3. Weather

Daily weather data were provided by the meteorological station of the experiment station. They included maximum and minimum temperature, global radiation, rainfall, wind velocity and air humidity, which allowed the calculation of reference evapotranspiration with the Penman formula [40].

1.4. Soil water and estimations of water use

Soil water content was measured nine times throughout the crop cycle at nine different levels in the soil. Gravimetric measurements were done in the superficial layers while neutron probe (TROXLER 2000) was used from 0.40 m down to 2.00 m. The calibration of the neutron probe was done, layer by layer, by regressing neutron counts with gravimetric water contents [48]. One access tube was installed in each of the ten plots.

Water use was calculated from the measured changes in soil water storage and rainfall, assuming neither drainage nor capillary rise at the bottom of the soil profile (2.0 m). The measurements from individual access tubes showed almost no change of water content during the growing season at 2.0 m depth so that the assumptions of no drainage and no capillary rise introduced very slight errors in the water balance. Runoff was also neglected.

Relying on the works by Gregory and Monteith [18, 30], we estimated the effective rooting depth for each treatment. It consisted of attributing the drying of each soil layer between two measurements to root water uptake. The calculated effective rooting depth was assumed valuable only when the change in volumetric water content was superior to the experimental error (estimated to 1% in volumetric content). Obviously, this

method could not be applied to the superficial layers submitted to the evaporation process, which is the reason why we considered calculations giving effective rooting depths deeper than 40 cm as valuable (Fig. 4). The method did not allow differentiation between actual root uptake and capillary rise under the influence of roots drying up the soil. Consequently the resulting information was used in a relative manner just to compare cultivars and treatments.

Rooting front velocities were estimated by regressing effective rooting front estimates against time, excluding the numerous points on the plateau of the maximum rooting depth.

2. RESULTS

2.1. Environment

The crops experienced a gradual increase in daily maximum and minimum temperatures, radiation and potential evapotranspiration (Fig. 1). Prior to 44 DAS, both treatments received nearly no water, but during this period the atmospheric demand was low. From 45 DAS to 77 DAS, i.e. during the early vegetative period, the I treatment received 200 mm while the S treatment just received 50 mm. From 78 DAS on, both the I and S treatments received 192 mm.

2.2. Leaf Area Index

In the I treatment, all cultivars reached a LAI of 4, which can be considered as a non-limiting value for radiation use (Fig. 2). Nesser, Queguay and LAJ3333 peaked at 6-7, while La Paz and Aconchi peaked around 4. Fast senescence occurred for LAJ3333 and Aconchi, while it was slower for the others. As a consequence, the leaf area duration (integration of LAI versus time) in the I treatment was the highest for Nesser and LAJ3333 (around 400 m²·m⁻² days) and the lowest for Aconchi (200 m²·m⁻² days), Queguay and La Paz being intermediate (around 300 m²·m⁻² days).

In the S treatment, all cultivars reduced their LAI dynamics (Fig. 2) as a result of reduced leaf growth and accelerated senescence. This reduction was particularly severe for Nesser and Aconchi. Yet Nesser maintained a maximum LAI around 2 while for Aconchi it did not exceed 1. In terms of leaf area duration the classification differed from the I treatment: for LAJ3333 and Queguay, it was about 200 m²·m⁻² days, for Nesser and La Paz, it was between 100 and 130 m²·m⁻² days and for Aconchi, it was about 70 m²·m⁻² days.

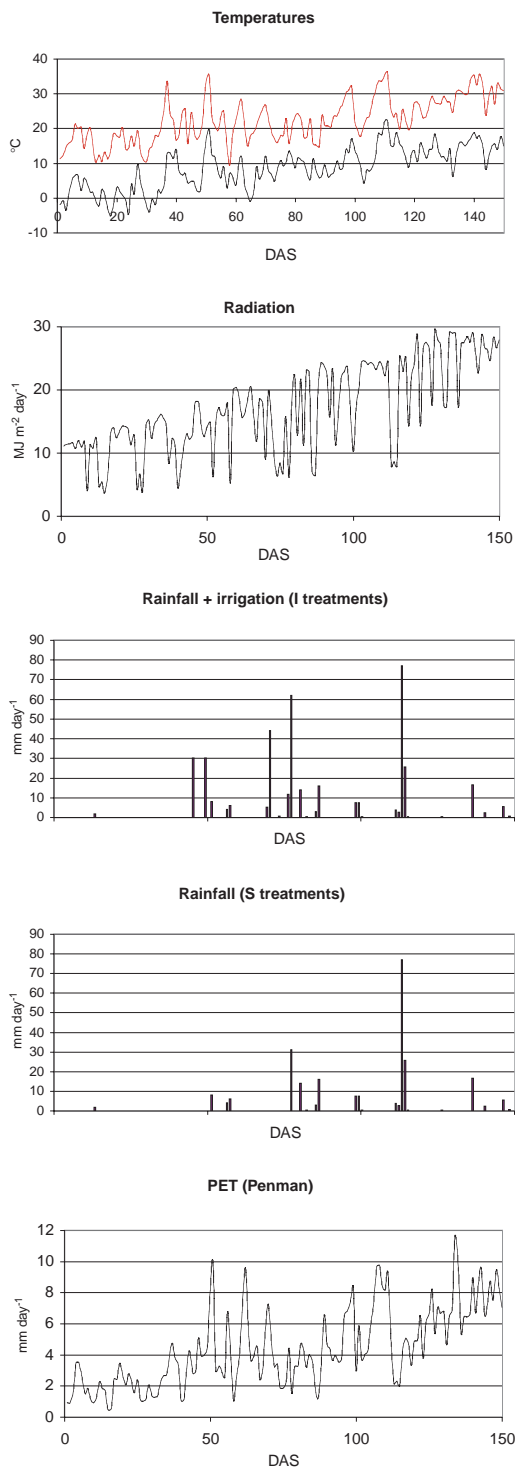


Figure 1. Evolution of the meteorological variables during the crop cycle: minimum and maximum temperatures, solar radiation, water supply in I and S treatments, potential evapotranspiration.

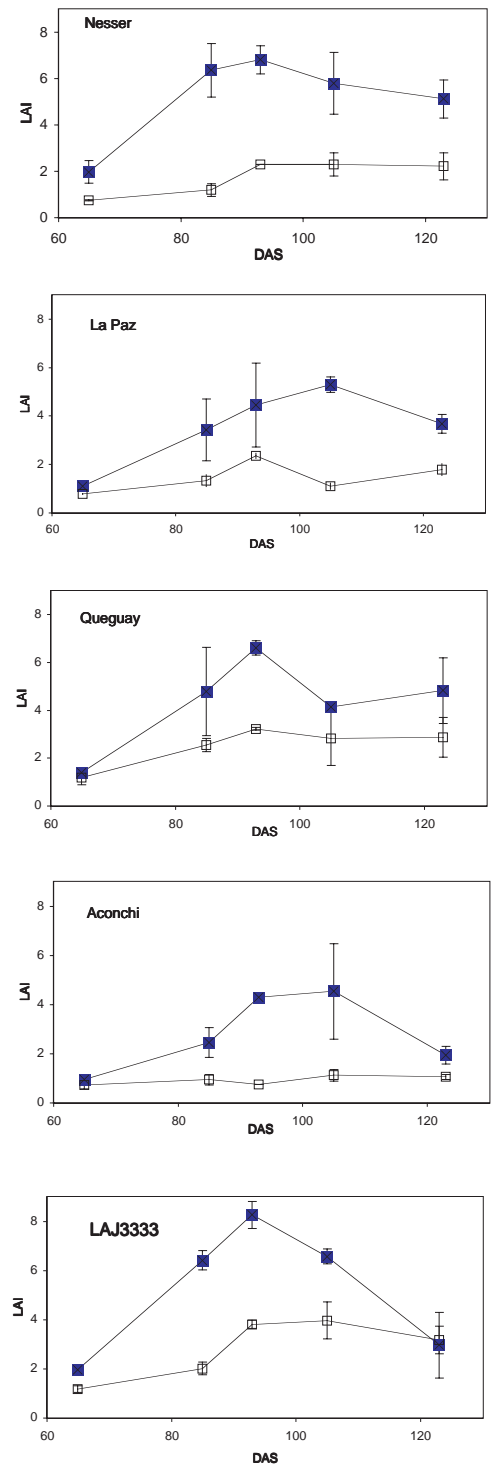


Figure 2. Evolution of the LAI for the five cultivars in I (full symbols) and S (open symbols) treatments. Error bars are \pm standard deviations.

2.3. Tillering

In the absence of water deficit, the cultivars demonstrated contrasting capacities of tillering (Fig. 3). Nesser and LAJ3333 produced up to 1200–1400 tillers·m⁻². On the other hand, in the same conditions, Aconchi only produced up to 800 tillers·m⁻² only. Yet tiller death was significant for Nesser and LAJ3333, so that the number of fertile tillers was about the same value as for La Paz, around 800 tillers·m⁻². In the case of drought, tiller dynamics displayed a very different pattern. During water deficit period, less tillers were produced. The difference between the I and S treatments regarding tiller production during this period was particularly significant for Nesser, LAJ3333 and La Paz. From 80 DAS, once the dry period had stopped (Fig. 1), the same cultivars set up a second generation of tillers, so that final tiller number was quite similar to that of the I treatment. This process did not occur for Queguay and Aconchi, whose final number of tillers per m² was around 400. The standard errors were great for the first two measurements after 80 DAS, giving an idea of the heterogeneity of the canopy during this period of transition between the dry and the wet period.

2.4. Water uptake

In the I treatment, there was about 30 mm difference between the least consuming cultivar, i.e. Queguay, and the most consuming one, i.e. LAJ3333 (Tab. I) which corresponds to 7% out of the total water uptake. The rooting front velocities were estimated to 1.3, 1.5, 1.0, 2.2 and 2.4 cm of soil per day for respectively Nesser, La Paz, Queguay, Aconchi and LAJ3333.

In the S treatment, differences between cultivars were increased: 70 mm between Queguay and LAJ3333, i.e. 30% out of the total. Nesser, La Paz and Aconchi used a similar amount of water. The effective rooting depth

Table I. Crop water uptake from sowing to harvest. Lines of data preceded by the same small letter are not significantly different at $P < 0.1$ according to t-Student test.

Cultivars	Significance in-between cultivars	Crop water uptake (mm)	
		Irrigated	Stressed
Nesser	a	456	296
La Paz	a	465	294
Queguay	b	440	241
Aconchi	a	453	285
LAJ3333	c	470	330

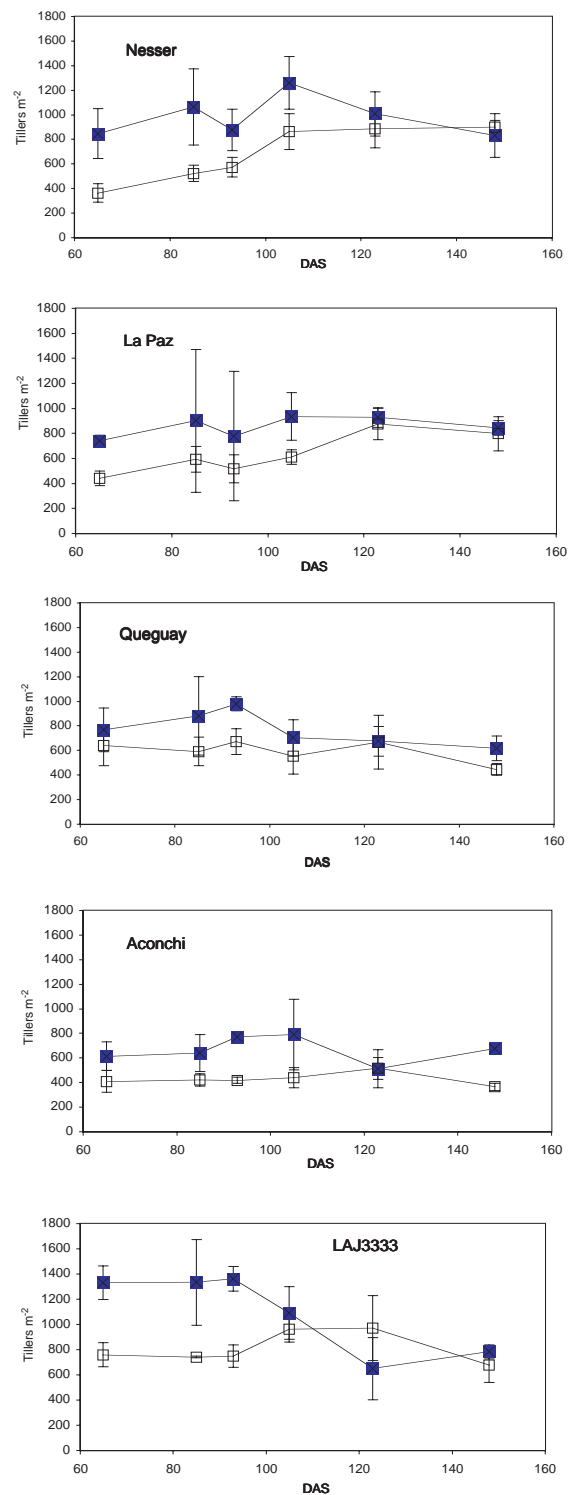


Figure 3. Evolution of the number of tillers per m² of the five cultivars in I (full symbols) and S (open symbols) treatments. Error bars are \pm standard deviations.

dynamics displayed in Figure 4 show a faster exploration of the soil volume for the S treatment for all cultivars except for LAJ3333 and Aconchi, which exhibited the most rapid root front velocities in the I treatment. In the S treatment, the rooting front velocities were estimated to 1.5, 2.1, 1.7, 2.1 and 1.9 cm of soil per day for respectively Nesser, La Paz, Queguay, Aconchi and LAJ3333. La Paz and Aconchi were the most rapid ones and Nesser was the slowest one. Another important criterion is the final depth achieved, which was deeper than 1.60 m for all cultivars except for Queguay.

2.5. Phenology

In the I treatment, differences in the phenological stages of the varieties were observed (Fig. 5). For example the “flag leaf” stage occurred at 900 GDD for Aconchi, 950 GDD for Nesser, 1075 for La Paz and Queguay and 1170 for LAJ3333. In most cases the earlier the anthesis, the longer the grain filling period (Tab. II). Hence in well-irrigated conditions the cultivars La Paz and Aconchi exhibited the longest grain filling periods while LAJ3333 had the shortest one, both in terms of absolute and relative durations.

In the case of drought, there was a general trend of acceleration of the phenological development from the beginning of stem elongation. LAJ3333 seemed the least sensitive to this effect and remained nearly as late in the S as in the I treatment. Except for LAJ3333 harvesting occurred 300 GDD earlier for the S than for I treatments. For Nesser, the shortening of the cycle affected preferentially the vegetative phase (Fig. 5) and preserved the grain filling period (Tab. II), which was not the case for La Paz and Queguay. For Aconchi it was the reverse: the vegetative phase was almost not shortened (Fig. 5) while the grain filling period was drastically reduced.

2.6. Biomass accumulation and grain yield

In the I treatments nearly all cultivars reached the same level of final biomass. La Paz was the only one slightly superior to the others (Tab. III). The growth rate globally decreased during the last phase of the cycle for all the bread wheat cultivars while it increased for the durum wheat cultivar Aconchi (Fig. 6).

Under water deficit, the final biomass reduction was low for LAJ3333 and Nesser (Tab. III) as a result of a high late growth rate (Fig. 6). On the contrary, La Paz and Queguay decreased their growth rate earlier. Though the final biomass of Aconchi was largely reduced in

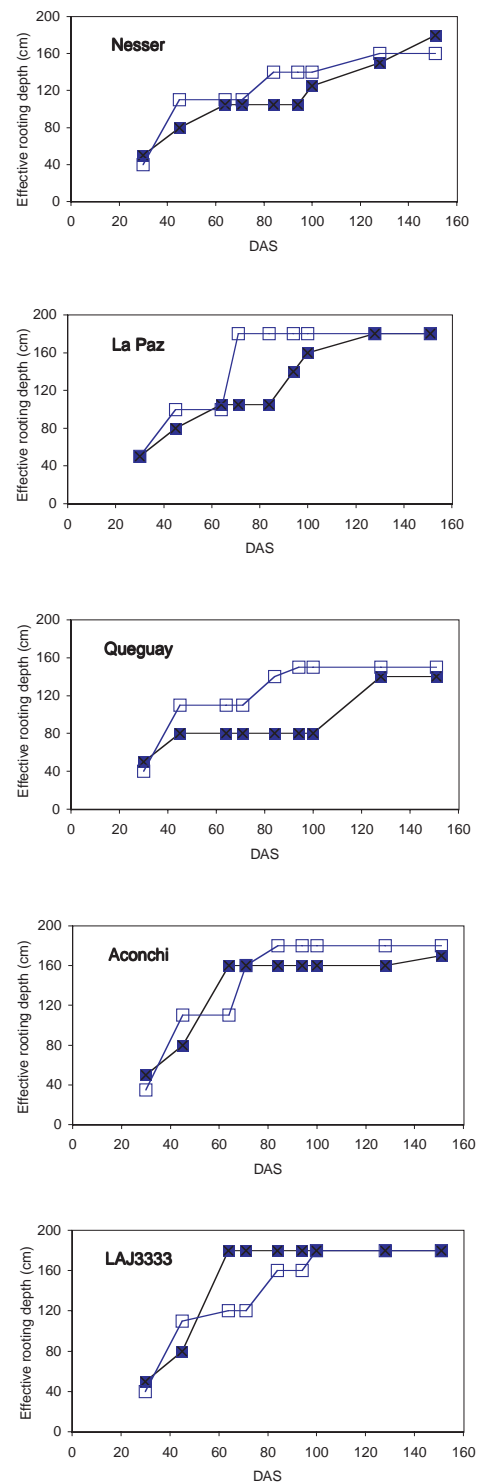


Figure 4. Effective rooting depth in cm for the five cultivars in I (full symbols) and S (open symbols) treatments.

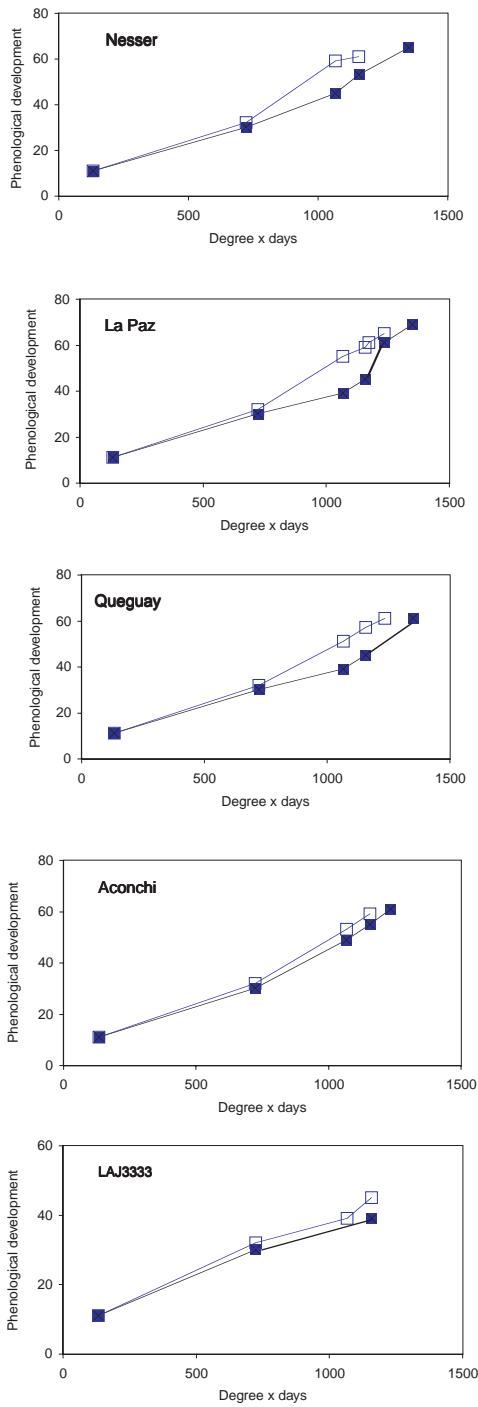


Figure 5. Phenological stages until anthesis expressed in the Zadoks' scale for the five cultivars in I (full symbols) and S (open symbols) treatments. In the Zadocks' scale, emergence is 10, beginning of stem elongation is 30, booting is 40, heading is 55 and anthesis is 65. X-axis has been graduated in cumulated growing degree \times days (GDD) since sowing (above 0 °C).

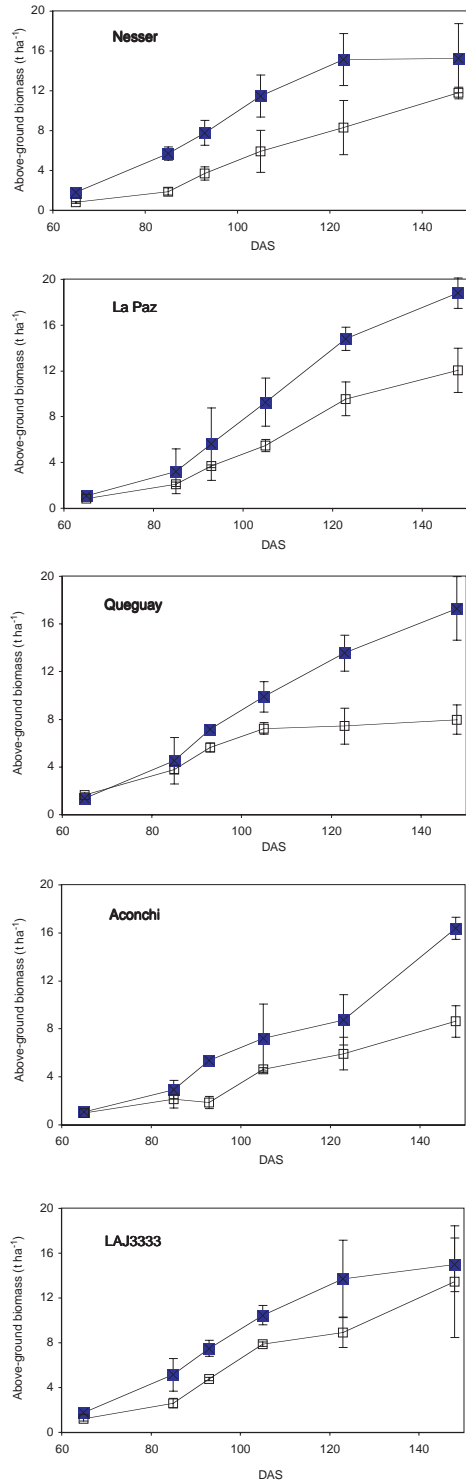


Figure 6. Above-ground biomass (t ha⁻¹) evolution for the five cultivars in I (full symbols) and S (open symbols) treatments. Error bars are \pm standard deviations.

Table II. Partitioning of the cycle duration in the vegetative and reproductive phases. GDD: Growing Degree Days above 0 °C.

Cultivars	Treatment	GDD from sowing to anthesis	GDD from anthesis to harvesting	Grain filling period as a proportion of the cycle duration
Nesser	Irrigated	1351	919	0.40
Nesser	Stressed	1158	812	0.41
La Paz	Irrigated	1236	1034	0.46
La Paz	Stressed	1175	795	0.40
Queguay	Irrigated	1351	919	0.40
Queguay	Stressed	1236	734	0.37
Aconchi	Irrigated	1200	1070	0.47
Aconchi	Stressed	1175	795	0.40
LAJ3333	Irrigated	1400	870	0.38
LAJ3333	Stressed	1351	919	0.40

Table III. Final above-ground biomass, yield and harvest index for both S and I treatments. Data followed by the same small or capital letter are not significantly different at $P < 0.1$ between cultivars or between treatments, respectively, according to t-Student test.

Cultivars	Final biomass (t/ha)		Yield (t/ha)		Harvest index (%)	
	Irrigated	Stressed	Irrigated	Stressed	Irrigated	Stressed
Nesser	13.34 aA	10.29 aB	7.63 aA	6.09 aB	57 aA	59 aB
La Paz	16.44 bA	9.53 aB	8.87 aA	5.75 bB	54 aA	60 aA
Queguay	15.12 aA	6.95 bB	8.09 aA	3.46 cB	53 aA	50 bA
Aconchi	13.87 aA	7.56 bB	8.55 aA	4.76 bB	62 bA	63 aA
LAJ3333	13.68 aA	11.76 aB	5.89 bA	5.10 bB	43 cA	43 cA

comparison with the I treatment, it also displayed some late growing capacity.

Even in irrigated conditions, there were significant differences between cultivars in the harvest index (Tab. III) with three levels: high and low levels for Aconchi and LAJ3333 respectively and medium levels for the three other cultivars. The dynamics displayed in Figure 7 show that for Nesser, Aconchi and La Paz the grain began to fill as soon as the crop reached 5 t·ha⁻¹ of biomass while for LA J3333 it started only at 10 t·ha⁻¹. In terms of yield, LAJ3333 clearly contrasted with the other four cultivars (Tab. III).

There was a significant difference in the final harvest index between the two water treatments only for Nesser (Tab. III). And Figure 7 shows a general trend of grains starting to fill at lower levels of above-ground biomass with dynamics more or less similar to the I treatments. Again those results show the importance of the grain filling duration (Tab. II) which defines the final level reached by the harvest index. Queguay was drastically disadvantaged regarding this point and to a lesser extent this was also the case for Aconchi and La Paz (Tab. III).

2.7. Correlation study

In order to understand the respective role of growth and phenological characteristics on drought tolerance, correlation coefficients between yield levels of S treatments and various parameters were calculated (Tab. IV). No high correlation coefficient appeared that could have pointed out one parameter explaining most of the variability between cultivars, as was the case in irrigated conditions (correlation between I yields and harvest index is 0.8). Another important finding was the independence of S and I yields. The vegetative growth (LAI and root front velocity) was negatively correlated to yield, while the reproductive growth (grain filling duration and harvest index) was positively correlated to yield.

3. INTERPRETATION AND DISCUSSION

The various cultivars demonstrated contrasting abilities in the face of early drought. They differed in their potential aptitude in growth and grain set. We propose to interpret the I treatments as allowing the exhibition of

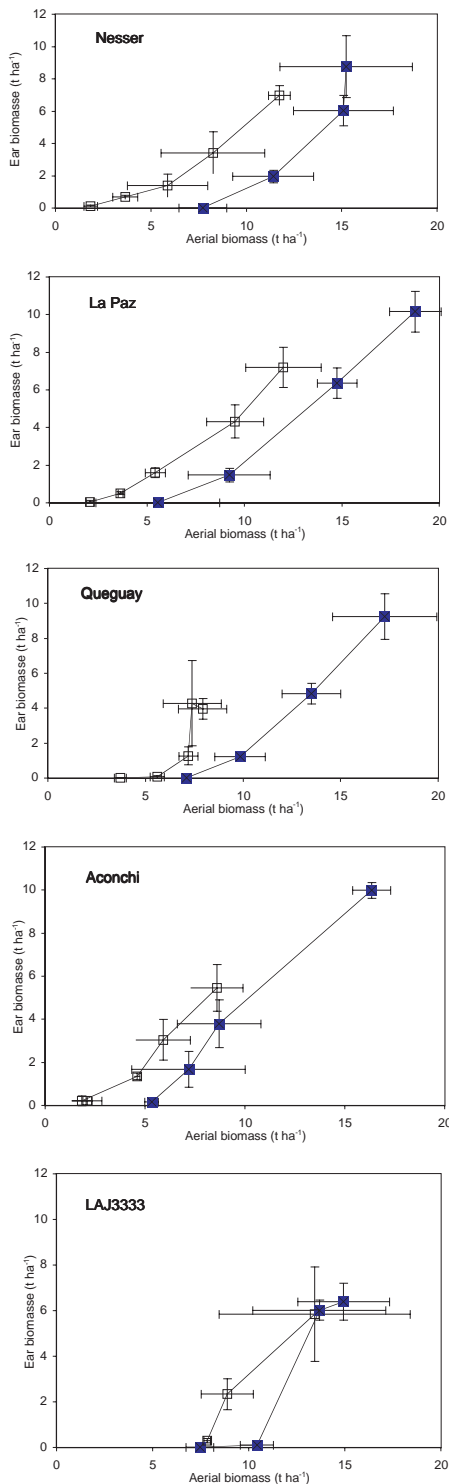


Figure 7. Ear biomass ($\text{t}\cdot\text{ha}^{-1}$) versus total biomass ($\text{t}\cdot\text{ha}^{-1}$) for the five cultivars in I (full symbols) and S (open symbols) treatments. Error bars are \pm standard deviations.

those potentialities. The cultivars also differed in their plasticity to drought, i.e. the ability to adapt their growth pattern to limited water supply. We propose to analyse this plasticity in front of drought by examining the differential behaviour between the I and S treatments. To help in the interpretation, we have elaborated a qualitative summary of the results in Table V: the potentialities of the cultivars were estimated from the results of the I treatment and the plasticity of the cultivars was estimated from ratios between results in the S and I treatments. Two synthetic columns were elaborated to globalise “vegetative” and “reproductive” characters.

3.1. Vegetative growth and water uptake

The cultivars we have chosen greatly differed in tillering capacities, known to be under genetic control [21]. Such differences caused variation in the LAI course of the I treatments (Tab. V). We observed that the more tillers the higher LAI (Nesser and LAJ3333) and the less tillers the lower LAI (Aconchi). Regarding effective rooting depth, the pattern exhibited by Aconchi and LAJ3333 in the I treatment is favourable to a fully exploration of soil volume, which is an advantage in the case of drought. On the contrary Queguay is disadvantaged by the apparent limited depth of its roots, even in the I treatments, so that the level of its evapotranspiration is the lowest in any case. For Nesser, the moderate rate of apparent root growth does not seem to limit its water uptake (Tab. V). To go further in the explanation of such behaviour, we would need more detailed measurements of roots to get an idea of differences in hydraulic conductances [15, 41]. The genetic variation in root systems of cereals is well documented [32, 46] and the number of seminal roots appears as the main source of variation [16].

In addition to this contrast among varieties exhibited in well watered conditions, we observed differential plasticity to drought such as the capacity for Nesser, La Paz and LAJ3333 to produce new tillers when water constraint was withdrawn. This process is often observed in plants of high tillering capacity, submitted to limited water supply during the first part of their cycle [28]. It did not occur for Aconchi and Queguay, which had a limited number of tillers, even in well watered conditions. Another form of plasticity concerns the enhancement of the effective rooting, particularly important for Queguay (Tab. V). This finding concurs with the results of various authors who have observed an increase in the allocation of assimilate to roots in the case of water stress [19, 27]. For Wahbi and Gregory [46] this trait is typical of plant plasticity. Yet for LAJ3333, this did not

Table IV. Correlation coefficients between “stressed” yields and maximal LAI, effective root front velocity, grain filling duration, harvest index and “irrigated” yield.

LAI -0.23	Root front velocity -0.45	Grain filling duration 0.44	Harvest index 0.37	Yield in I treatment -0.04
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occur. This example demonstrates a sort of compensatory effect between “potentialities” and “plasticity”.

An important criterion in drought resistance seemed to be the balance between water supply, i.e. root system, and demand, i.e. LAI. For example, Aconchi and LAJ3333 seemed to have adequate root systems for their leaf surfaces, which resulted in high levels of water uptake though levels of LAI were opposite. On the other hand, Queguay had an inefficient root system in relation to its leaf surface, so that its water uptake was reduced.

3.2. Phenology and reproductive growth

The global cycle duration was the same for all the cultivars but the partitioning between vegetative and reproductive periods varied (Tab. V). The most efficient drought-favouring trait concerning phasic development seemed to be a long grain filling period (Aconchi and La Paz) in relation to the earliness of anthesis. On the other hand, the cultivar LAJ3333 was clearly hampered by a long vegetative cycle and a short grain filling period, which led to a low harvest index. In well irrigated conditions, harvest index was closely related to grain filling duration and to grain yield (coefficient of correlation of 0.8). Aconchi was the only durum wheat cultivar and it was also the one that exhibited the highest harvest index. This result may be related to the major contribution of the ear of durum wheat in providing grains with neoformed assimilates [2]. This feature was probably not only due to the presence of awns on the ears [5] because all the cultivars tested in this study did have awns.

Differential phasic plasticity to drought such as the global reduction in the crop cycle course for all the cultivars except for LAJ3333 was also observed. The general trend of stress hastening phenological development has been observed for many annual crops [1, 7, 11, 37, 39, 43, 44]. Nevertheless when water stress occurs very early, it may also delay anthesis [6, 39, 43]. The developmental plasticity is considered as an adaptive feature to escape drought [24, 26]. In the case of Nesser, the shortening of the cycle preferentially affected the vegetative phase, preserving the grain filling period, while for La Paz, Queguay and Aconchi, the grain filling period was the most shortened phase. To explain this process, we should refer to the drought-induced increase in the

crop temperature [20, 22] since it is recognised that plant temperature is a better descriptor of the phenology than the air temperature [7, 11, 31, 33].

The literature gives us an indication to try to understand this phenological hastening. In the previous paragraph, it was pointed out that the crop water use was maximal for LAJ3333 and minimal for Queguay (Tab. I). Consequently the increase in crop temperature was probably higher for Queguay than for LAJ3333, which could explain that for LAJ3333 the phenological course in the S treatment nearly remained as in the I treatment, while it was drastically reduced for Queguay. A slow growth velocity of the effective rooting front for Nesser was also observed ($1.5 \text{ cm}\cdot\text{day}^{-1}$), contrasting with the other cultivars (from 1.7 to $2.1 \text{ cm}\cdot\text{day}^{-1}$). This feature probably allowed a saving use of soil water, which can explain why the partitioning of the cycle is more favourable to the grain filling phase for this cultivar, in the case of stress.

Another trait participating in the global plasticity of the crop facing drought was the enhancement of the harvest index, for La Paz and Nesser. This feature is typical of pre-anthesis stresses and Debaeke et al. [10] explain that it is due to an increase of the remobilisation of stored assimilates to grains in the case of drought.

3.3. Identification of various strategies

The cultivars might be classified according to the strategy they developed to produce significant grain yield under early water stress. There are genotypes with favorable “potential” features exhibited in the irrigated treatments. This is the case of Aconchi due to an important late growth rate but not LAJ3333 in which the luxuriant vegetative growth decreased the grain growth (Tab. V). This compensatory effect between vegetative and reproductive growths is underlined in Table IV. Similar observations were made by Entz and Fowler [13] and Christen et al. [8]. On the other hand, Nesser exhibited few favourable traits in irrigated treatment but compensated by its ability to adapt its growth and phenological development to the adverse conditions of drought. Such a strategy appears to be very efficient in the climatic conditions of the Pampas. The least productive genotype was Queguay with neither “potential” nor

“adaptive” traits that could prevent yield reduction. On the contrary, La Paz demonstrated both types of traits, allowing the higher yield in irrigated conditions and a good yield level in dry conditions thanks to its adaptive traits (Tab. V). The global efficiency of plasticity is attested by the absence of correlation between S and I yields (Tab. IV). The positive effect of the slow rooting front velocity (Nesser) is somewhat in contradiction with the traditional view of vigorous roots as a major feature of high yield in water-limited environment [26]. It results from the drought conditions imposed in this study, where the S crops were grown in stored soil water.

4. CONCLUSION

In this study we noticed differences in the cultivar strategies for resisting early drought. We gave keys to analyse differential behaviours by separating “potentialities”, considered as the drought-favouring traits exhibited under well irrigated conditions and “plasticity” considered as the adaptive traits exhibited by the crop when submitted to the adverse conditions of drought. This approach is quite similar to the breeders’ one [9].

In all cultivars, more or less, both type of properties exist. Yet the study of the vegetative growth was clearly insufficient to explain drought resistance in terms of economic grain yield since vegetative growth does not infer grain growth. Once more the concept of drought resistance was observed to be complex, resulting from the combination of various elementary favouring traits [6, 29]. The most important finding of this study is probably the efficiency of plasticity versus potentialities in the Pampas environment. The relationship between plasticity, rooting pattern and transpiration invoked in this study is worthwhile being analysed in depth as one of the potential explanations of plasticity. It would be interesting to use a simulation crop model to analyse those various adaptive strategies in a more general manner.

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