Competition between plants affects phenology in rice cultivars

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Abstract

Whole cycle and successive phases durations of crop are key traits for adaptation to local conditions. They are known as highly genetically controlled and rice breeders used to refer lines and genotypes to short, medium or late materials. However, even expressed in thermal time, these crop and phases durations are also influenced by environment conditions. To test effect of competition levels between plants on rice phenology, a density experiment was carried out in fields in Camargue region, France, with two genotypes on two consecutive years.
Results show that leaf appearance rate is affected by densities during the two observed phases of leaf appearance : the rapid one up to beginning of stem elongation and slower one after. They also show that, with increasing plant densities, rice cultivars reduce the number of leaves on the main stem, initiate panicle sooner, and delay flowering date. Analysis shows that relative growth rates during successive phases are highly correlated to observed variations.

Media summary

Increasing crop densities, that enhance level of competition between plants, affect components of rice development. Several of these variations were correlated with corresponding relative growth rates.

Key Words

Oryza sativa L., phyllochron, leaves number, vegetative and reproductive phases

Introduction

Crop duration is an important trait in rice and others cereals. First because, up to an “optimal duration”, it correlates positively with yield potential : Akita (1989) found in IRRI rice varieties an increasing yield when crop duration increased from 95 to 110 days and a maximum constant yield of 9 T/ha when crop duration was over 110 days. Secondly because timing of critical phases must fit to environmental conditions. In cases of drought, breeders used as first mechanism of adaptation the escape one, that allows plant not to undergo stress during critical phases (heading, flowering or grain filling stages). Whole crop and phases durations are genetically controlled and heritable. In rice, most of differences between short, medium and late terms varieties are mainly due to differences in vegetative phase duration (Vergara and al, 1969; Dingkuhn and Asch, 1999).

But variations in environmental factors have influence on phases duration, even expressed in thermal time : sensitivity to photoperiod is one classical example but water stress is also known to delay flowering time in rainfed rice. The question arises to understand mechanisms underlying the observed phenomenon : in the case of water stress, can the reduced growth explain a delay in development ? More, does the delay occur only on flowering time, or yet at panicle initiation ? In other words, is the plastochron affected as well ? Behind these questions, the challenge is to model, in a more accurate way, the successive phases of rice crop development, on the basis of leaf appearance rate and number of leaves expanded in the main stem. In this paper, we uses several plant densities to generate variations of competition levels between plants within a crop, and to test the hypothesis that theses variations can modify developmental stages components.

Methods

Two field experiments were carried out during 2002 and 2003 cropping season on two different sandy loam fluvial soils in Camargue region, France. Two improved temperate rice cultivars, Ari?te and Soulanet, were grown in irrigated conditions in a split plot experiment design with four replications. Density was used as sub-treatment. In year 2002, cultivars were grown at two densities?: D1 = 20 pl/m? and D2 = 200 pl/m?. In year 2003, treatments were D1, D2 and D3 = 400 pl/m?. Fields were fertilized with a basal application of 250 kg ha^{-1} N as urea. An additional topdressing of ?150?kg ha^{-1} N as urea was made at 30 days after sowing.

The leaf development stage on the main stem was quantified on 5 defined plants in each “cultivar x density x replication” plot using Haun index (Haun, 1973). Water temperature was monitored hourly using an immersed Tinytag device that gave estimation of meristem temperature before stem elongation. Afterwards, meristem temperature was estimated by air temperature monitored under canopy. Thermal time was calculated using the Oryza model equations (Kropff and al., 1994), with following critical temperatures : Tb = 12 ?C, Topt = 30?C, Tmax = 42 ?C. Estimation of panicle initiation dates was obtained retrospectively with the date of last leaf appearance on the main stem, according to relationships given by Nemoto and al (1995). The panicle initiation is synchronised with the appearance of the fourth leaf before the last one on the main stem.

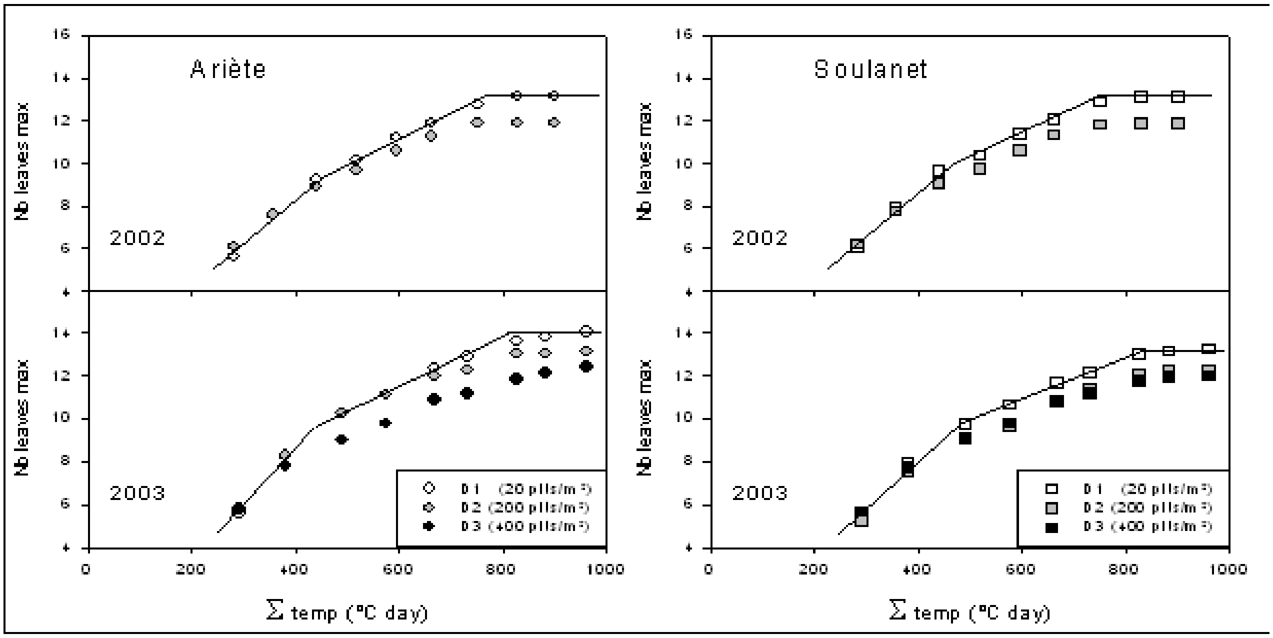
Total shoot growth was measured at 42, 70 and 90 days after sowing. Consequently, relative growth rate (RGR) was calculated for two periods, 42-70 and 70-90, that fit respectively with the tillering phase (from beginning of tillering to panicle initiation) and the reproductive one (from panicle initiation to heading stage).

Results and discussion

Leaf appearance rate

The number of leaves on the main stem fits with a bi-linear model, as already observed by Baker and al (1990) on wheat and Tivet (2000) on rice. Linear regressions are drawn in figure 1 for low density treatment (D1) : a first phase is characterized by a rapid emergence of leaves, followed by a second phase of slower appearance for both cultivars. Same patterns are observed for higher densities treatments, with displaced break points. The main observation is the density effect on leaf appearance rate : higher is the density, slower is the rate for both years.

Figure 1?: Leaf appearance rate and thermal time at different densities. Camargue, France. 2002-2003



Variance analysis on phyllochron values confirms a main density effect where as differences between cultivars and interactions are not significant (Table I). It is worthwhile to notice that phyllochron increases between 2002 and 2003 for all treatments.

Leaf appearance rate highly correlates with relative growth rate (RGR) during phase 1 (Fig. 2) : with increasing densities, RGR lowers and leaf appearance slows down. This can be due to higher level of competition between plants in the high densities treatments, in accordance with measurements in Leaf Area Index (data not shown) at these stages. In opposition, no correlation is found in phase 2 (Fig. 2), probably because of little variation of RGR for closed canopy and the existence of other sinks for assimilates (not only leaves, but also panicles and stems growth) : leaf appearance rate remains low and constant while assimilate availability for growth controls stem and panicle elongation rates.

Table I: Variance analysis on phyllochrone. Camargue, France, 2002-2003.

	2002				2003			
	Phyl 1 (?C day)		Phyl 2 (?C day)		Phyl 1 (?C day)		Phyl 2 (?C day)	
	Ari?te	Soulanet	Ari?te	Soulanet	Ari?te	Soulanet	Ari?te	Soulanet
D1	51.7	54.7	82.9	85.8	57.23	63.58	87.34	93.79
D2	66.8	67.3	94.6	96.6	65.09	70.76	97.84	81.82
D3					75.90	78.02	107.06	86.45
Density effect	***		***		***		ns (0.92)	
Varietal effect	ns (0.45)		*		ns (0.22)		ns (0.51)	

Density * Variety	ns (0.59)	ns (0.70)	ns (0.88)	ns (0.74)

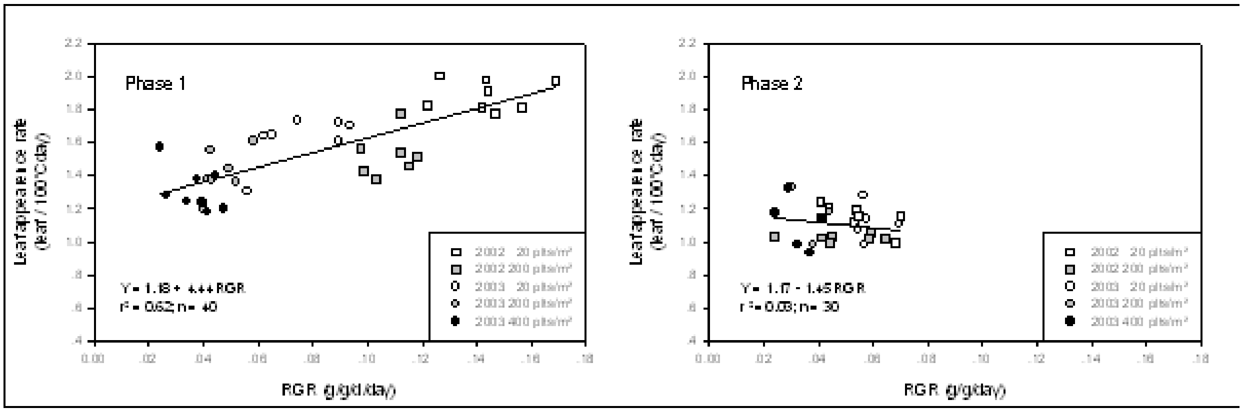


Figure 2?: Relationship between leaf appearance rate and relative growth rate. Camargue, France. 2002-2003.

Number of leaves on the main stem

As shown in figure 1 and 3, increasing densities reduce the number of leaves on the main stem. Similar process have already been observed in rice (Tivet, 2000) and sorghum (Lafarge, Clerget personal communications). The reasons why are unknown and further investigations are needed on relationships between apical meristem activity and number of initiated organs. Year 2003 has systematically more leaves at the same densities than year 2002 for both varieties, which can be relied to better initial growth for all treatments in year 2003.

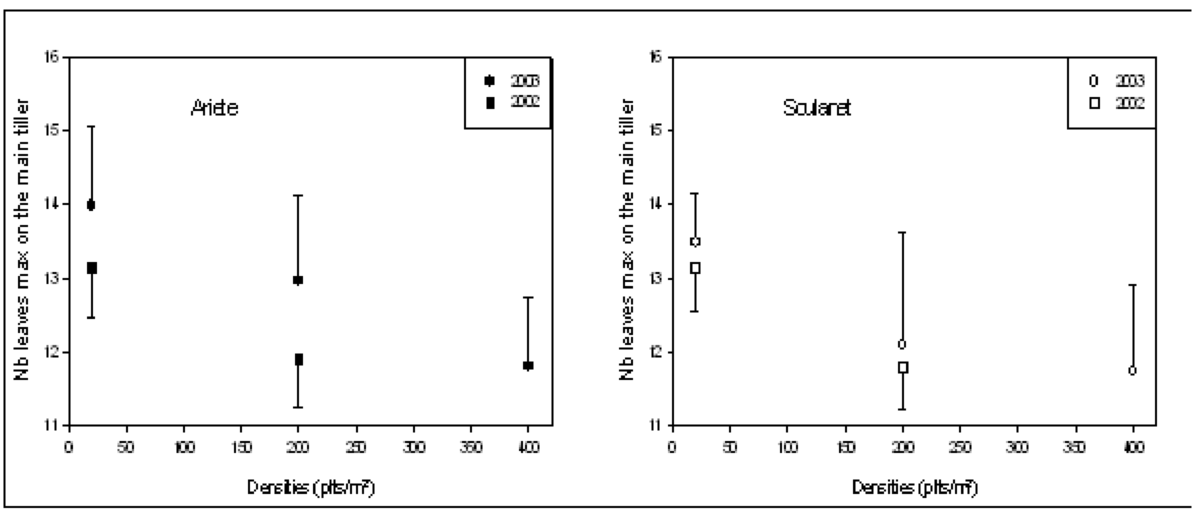


Figure 3?: Density effect on number of leaves in main stem. Camargue, France. 2002-2003

Incidences on phases durations

With increasing crop densities, plants simultaneously reduce the rate of leaves appearance and number of leaves, in such a way we cannot predict hypothetical variations in phases durations. Variance analysis (Table II) shows an highly significant effect of density on phases 1 and 2 durations : increasing densities shorten tillering phase and lengthen reproductive phase. This results in a delay in heading date in Ariete but not in Soulanet (interaction on total duration).

Table II : Variance analysis on phases durations. Camargue, France, 2002-2003. Ari?te V1 and Soulanet V2

	2002						2003					
	Phase 1 (?C day)		Phase 2 (?C day)		Total (?C day)		Phase 1 (?C day)		Phase 2 (?C day)		Total (?C day)	
	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
D1	434	413	425	411	858	825	496	442	457	443	953	885
D2	377	369	438	440	815	809	424	422	482	463	906	885
D3							406	389	510	495	916	884
Density effect	***		***		*		**		***		ns (0.45)	
Varietal effect	ns (0.10)		ns (0.23)		ns (0.24)		ns (0.11)		***		**	
Density * Variety	ns (0.45)		ns (0.10)		ns		ns (0.36)		ns (0.79)		ns (0.45)	

Conclusion

This study aimed at analyzing development patterns of two rice cultivars in relation with crop densities. Variations in densities were used to fix different dynamics of competition between plants?: higher is the density, earlier competition starts and more intensive it is. The results show how increasing competition between plants, traduced by a decreasing relative growth rate, modifies developmental patterns : number of leaves decreases as well as their rate of appearance, inducing an earlier panicle initiation and having contrasting incidence on heading time. This means that phenological module in ecophysiological models have to take into account these variations in order to predict with more accuracy critical stages of development. The present study points out the use of relative growth rate as complementary driving variable.

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