



Tillering and yield formation of a temperate *Japonica* rice cultivar in a Mediterranean rice agrosystem

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Abstract

Rice tillering is a crucial stage for yield formation. Deep understanding of the relationship between tillering dynamics and yield formation in a particular agrosystem is crucial to boost rice productivity. Research on rice tillering is mainly focused on tropical agrosystems whereas less is done in the Mediterranean, with direct water-seeding and *Japonica* cultivars. This study aims at characterizing tillering dynamics and identifying the main explanatory tillering traits of yield in a Mediterranean rice agrosystem, Ebro Delta (Northern Spain). A temperate *Japonica* cultivar grown in Spain, Gleva, was utilized. Plants and tillers were tagged to assess emergence and fertility ratios and grain yield; while changes in tillering number over time, yield and yield components for unit area were measured. Plant and tillering dynamics in the Ebro Delta rice fields can be accurately predicted through equations herein provided, which are based either on thermal time or leaf development. Plants grown under regional standard agricultural practices produced up to eight primary tillers of which two or three become productive. Maximum tiller number was the main explanatory variable of yield while high-yielding tillers within a plant are located on nodes with the highest emergence ratios and, after the main stem, they are the major contributors to yield. The decisive role of tiller development on yield along with the predictability of tiller dynamics raises options to optimize grain yield through tillering modulation. In this sense, results from this study suggests the promotion of early tillering followed by inhibition of late tillering as a strategy of tillering regulation.

Additional key words: *Oryza sativa* L.; tillering dynamics; tiller order; yield formation; emergence; fertility; curve fitting; synchrony

Abbreviations used: GDD (growing degree days); LN (leaf number); MS (main stem); Tb (base temperature); TiN (tiller number); TiNM2 (tiller number/m²); Tmax (maximum temperature); Tmin (minimum temperature); TT (thermal time)

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Introduction

Rice (*Oryza sativa* L.) is the staple food of more than half of the world's population. The rice growing area in Europe and in Mediterranean areas is about 1,300,000 ha, notably located in environmentally protected wetland ecosystems playing an important role in the maintenance of ecological equilibrium and biodiversity. In Spain, rice fields in the Mediterranean coast, such as the Ebro Delta and Valencia, are highly relevant not only environmentally but also socioeconomically being the main economic driver in these wetland agrosystems.

Tillering is a crucial phenological phase in rice, as it greatly influences grain yield (Gendua *et al.*, 2009)

through the determination of panicle density (Wu *et al.*, 1998), and formation of the crop canopy, and therefore it is the main source and sink of carbohydrates (Hammer *et al.*, 1987) and dry matter accumulation (Wu *et al.*, 1998).

Tillers are developed from axillary buds of leaves so that those arising from leaves on main stem are called primary tillers; secondary arises from primary tillers and so on for each category. Tiller hierarchy is defined by category and order, the last being the topological position of the node along the stem axis (Counce *et al.*, 1996).

Tillering dynamics is defined as the changes of tiller number per plant or per unit area over the growth

cycle: stem number increases up to maximum tiller stage from which tiller abortion processes are launched until the achievement of the eventual number of productive tillers. Tillering pattern at a plant level determines plant structure and it is assessed by ratios of emerged and productive tillers across nodal positions (Jaffuel & Dauzat, 2005).

Regulation of tiller dynamics, considering both timing of emergence and number of tillers, has implications on yield formation, hence it provides an opportunity to optimize grain yield. Temporal pattern is also relevant for grain yield (Miller *et al.*, 1991) as earlier tiller emergence is advantageous for resource capture (Lafarge *et al.*, 2002) whereas late tillers may cause significant waste of assimilates and thus limit overall yield plant potential (Mohapatra & Kariali, 2008). On the other hand, excessive tillering induces tiller abortion, low seed set and small panicle size, leading to reduced grain yield (Peng *et al.*, 1998) as opposed to low tillering which may lead to suboptimal tiller and panicle densities and eventually, reduced grain yield. At a plant scale, yield is distributed across panicle-bearing culms whose final number results from tillering dynamics and subsequent trade-offs between tiller emergence and senescence. Plant tillering ability (Otterson *et al.*, 2008), as well as topological position of tillers (Jaffuel & Dauzat, 2005), affect plant yield potential and tiller contribution to plant yield. Thus, knowledge of plant structure and dynamics is critical in understanding yield formation in rice.

Several studies on tiller dynamics have been carried out in cereals, such as barley (Lafarge, 2000), wheat (Otterson *et al.*, 2008), sorghum (Lafarge & Hammer, 2002b) and rice (Jaffuel & Dauzat, 2005). In rice, environmental (De Datta, 1981; Yoshida, 1981), genotypic (Kim & Vergara, 1990; Alam *et al.*, 2009; Gendua *et al.*, 2009) and agronomic variables such as nutrient supply (Otterson *et al.*, 2008), water management (Elhani *et al.*, 2007; Ohe *et al.*, 2010), plant density (Wu *et al.*, 1998; Ottis & Talbert, 2005) and planting method (Kariali *et al.*, 2008; Thakur *et al.*, 2009) influence the development of emergent tillers and the subsequent plant yield distribution among panicles. Such plasticity provides a promising tool to maximize grain yield through regulation of crop growth although it needs to be based on predictability of tiller dynamics. However, the influence of such a wide range of environmental and agronomic factors on rice tillering limits the applicability of this knowledge in a particular agri-environment. Most of studies on tillering dynamics and yield components are based on transplanted rice in tropical areas, where *Indica* type varieties are predominant. Nevertheless, in the European rice producing countries (Aldo, 2007; Agrama *et al.*, 2010) and the

north Pacific (Agrama *et al.*, 2010), temperate *Japonica* cultivars are the most cultivated. In most of the European countries rice is grown in Mediterranean climate, with a dry and warm summer and mild temperatures during spring and late summer and autumn, coinciding with crop emergence and maturity, respectively (Takaya *et al.*, 1974).

In general, *Japonica* cultivars have lower optimum temperature whereas *Indica* subspecies are better adapted to higher temperatures and submerged conditions (Yoshida, 1981). As a consequence, agronomic performance differs from both rice types, having *Japonica* varieties shorter cycle and lower tillering capacity than *Indica* type. To the best of our knowledge, little has been done in tillering pattern in direct-seeded rice in European rice systems, particularly in the Mediterranean climate. The objectives of the present study were to characterize the tillering dynamics of a temperate *Japonica* rice cultivar, Gleva, widely grown in Ebro Delta and Valencia, which is representative of the varietal profile grown in Eastern coast rice fields in Spain, and to relate it with yield formation in a typical Mediterranean rice crop system. Such knowledge will provide a better understanding of yield formation in this particular agro-environment and it will represent a first step towards the definition of strategies to optimize tillering dynamics in order to enhance crop productivity.

Material and methods

Three field experiments were carried out from 2007 to 2009 in Amposta (Ebro Delta region, North-eastern Spain; 40.7°N 0.6°E). Experiments were arranged according to a randomized block design with three replications and plots of 50 m². Cultivar Gleva, a *Japonica*-type rice cultivar representative of the varietal profile grown in Eastern coast rice fields in Spain, with medium grain size and a growth cycle of about 120 days from sowing to maturity, widely grown in the Ebro Delta area and Valencia, was used in the experiments. Meteorological data were obtained from a station located close to field experiments.

Plots were dry-land prepared by harrowing and laser-levelling. A total of 120 kg N/ha (according to the current environmental legislation at that moment) was applied in three applications of 40 kg N/ha each: one at pre-sowing (urea), the second at mid-tillering and the third at panicle initiation (ammonium sulphate). P-K fertilization was made to avoid deficiencies of these elements: 45 kg/ha of K₂O and of P₂O₅ was applied as at pre-sowing. Pre-emergence herbicide (Oxadiazon, 25%) was used for grasses (*Echinochloa* sp.) and red rice (*Oryza sativa* sp.) control and hand-weeding was conducted when

necessary during the crop growth. Other crop protection chemicals were used to minimize pest and diseases according to pest infestation in field and to European Union laws for phytosanitary substances regulation.

Pre-germinated seeds were sown at rates of 450 viable seeds/m² the 16th, 18th and 9th of May in 2007, 2008 and 2009, respectively. Plots were continuously flooded, with increasing depth of water layer from 2 to 10 cm according to increase in plant height. Plots were harvested during the last week of September.

Plant measurement and data collection

Tiller dynamics, yield and yield-related traits were determined at both plant and unit area levels. Accordingly, two subplots were delimited in each plot which provided two data sets.

Plant tiller dynamics and plant yield were recorded in a 0.20 m² subarea delimited during seedling establishment in which ten plants were tagged. Tiller emergence and leaf stage from each plant were monitored every three days during active tillering stage and weekly from the maximum tillering stage until heading time. Tillers from main stem (primary tillers) were identified according to tiller position which is defined by the leaf number from which it is developed. Leaf stage was determined using the Haun scale (Haun, 1973). At maturity, the ten tagged-plants were hand-harvested, oven-dried at 80°C until constant weight and then each panicle gently threshed by hand. Yield-related traits were measured at a tiller-position scale: grain weight, total and filled grain number per panicle was recorded while panicle fertility was calculated as the ratio of filled grain number over total grain number. Tiller pattern per plant was assessed by ratios of tiller emergence and tiller fertility which were calculated as the number of total emerged tillers and fertile tillers, respectively, in each tiller position over total number of plants. Tiller dynamics per unit area was recorded in a 0.13 m² subarea, in which number of tillers was counted every three days during active tillering stage, weekly from maximum tillering stage to heading and at maturity. Tiller efficiency was calculated as number of productive tillers divided by the maximum tiller number.

Grain yield and yield components per unit area were determined. Plant and panicle density per m² in each plot were determined by counting plant and panicle number in a 1-m² subarea at 4th leaf stage and at heading, respectively. A 6-m² area in each plot was hand harvested at maturity and threshed. Separate grains in each plot were weighted and put in individual bags. A 100-g sample of each plot was oven dried to determine humidity at harvest time and then yield was corrected to 14% humidity. Unfilled grains were separated by

using a blower (Oregon Seed Blower) and then, spikelet fertility (seed-set) was calculated by dividing weight of filled grains by weight of total (filled and empty grains). Thousand-grain weight was calculated from the mean weight of 200-grain samples whereas grain number per panicle was calculated by dividing average of panicle grain weight (calculated from 30 panicles randomly sampled) by thousand-grain weight.

Crop phenology was monitored. Seedling emergence and establishment was defined when tagged plants were at 1.5 and 4.0 Haun leaf stage, respectively; heading, when 50% of panicles were at least partially exerted from the boot; and maturity, when more than 80% of grains were yellow. To determine panicle initiation, 5 main stems were randomly sampled every two days from 50 days after sowing (based on previous data on the cultivar) and dissected in the laboratory. Panicle initiation stage was defined when panicle length was 1 to 2 mm.

Statistical analyses

Tillering dynamics was studied at different unit and time scales: tiller dynamics per plant was plotted against both thermal time and leaf development whereas tiller dynamics per unit area was plotted only against thermal time. Thermal time, expressed as accumulated growing degree days (°Cd) from seedling emergence, was calculated by summing daily degree days, according to McMaster *et al.* (2003):

$$\text{GDD} = \sum [(T_{\text{max}} + T_{\text{min}}) / 2] - T_b \quad [1]$$

where GDD is the growing degree days and T_{max} and T_{min} are maximum and minimum daily temperatures, respectively, and T_b is base temperature. Base temperature used was 8 °C (Yin & Kropff, 1996).

Observed data of each year and replication was curve fitted using Software Table Curve 2D v5. The goodness of fit of the function to observed data was evaluated using the coefficient of determination (*R*²). Tiller dynamics per plant was plotted against both thermal time (TT) and leaf development: the former was fitted by a linear regression (Eq. [2]) whereas the latest to a logarithmic equation (Eq. [3]).

$$TiN = a + b * TT \quad [2]$$

$$\text{Ln}(TiN) = a + b * \text{LN} + c * \text{LN}^2 \quad [3]$$

where TiN is tiller number/plant; TT is thermal time; and LN, leaf number on main stem.

Tiller dynamics per m² was plotted against thermal time and fitted by non-linear regression to the following rational equation (Eq. [4]):

$$\text{TiNM2} = (a + c \cdot \text{TT}^{0.5} + e \cdot \text{TT}) / (1 + b \cdot \text{TT}^{0.5}) \quad [4]$$

where TiNM2 is tiller number/m².

Variables with biological meaning were calculated from each equation and then used for tillering characterization: y_{\max} as maximum tiller number; x_{\max} as timing of maximum tillering stage; maximum and minimum first derivative of the function as maximum rate of tiller emergence and tiller mortality, respectively; x value for maximum and minimum first derivative as leaf stage when maximum rate of tiller emergence or tiller mortality occurs, respectively.

Adjustment of emergence time of primary tillers at a plant scale was done by regressing emergence of each primary tiller against emergence time. The slope of the linear function was used to estimate the rate of emergence of primary tillers.

Analyses of variance (ANOVA) were conducted to test the effect of year on tillering traits derived from curve fitting, yield and yield components.

Pearson correlation coefficients were determined for the mean values of the replications using yield, yield components and tillering traits variables. Stepwise regression analyses were carried out with grain yield as dependent variable and plant density, yield components (panicle density, grain number per panicle, panicle fertility and one thousand grain weight) and maximum tiller number as independent variables.

Panicle yield across tillers within a plant are not independent of each other and consequently it was analysed as repeated measurements (in space) using a mixed model (Piepho *et al.*, 2004) and the restricted

maximum likelihood (REML) for the estimation of variance components and the residual variances. Tiller order was used as the repeated factor. The effect of years as a fixed factor was analysed for each variable and tested using the Type III estimable functions. The least squared means were computed with the LSMeans statement and the Tukey test was used for the multiple comparison adjustment. When the fixed effect of the interaction Year \times Treatment was significant, the data were treated separated by year.

The statistical program used for ANOVA, analyses of repeated measures with mixed model, correlation analyses and stepwise regression was SAS 9.2 (SAS Institute Inc., 2008).

Results

Reproductive and maturity phenological stages occurred at following timings in 2007, 2008 and 2009, respectively: panicle initiation at 809, 746 and 726 GDD from seedling emergence (1.5 Haun leaf stage); heading at 976, 1076 and 1059 GDD; and maturity at 1595, 1684 and 1637 GDD.

Tillering dynamics per plant and its synchrony with leaf emergence

Rice plants were mainly composed by primary tillers, *i.e.* tillers emerging from axillary buds on main stem (MS), and few secondary tillers were developed

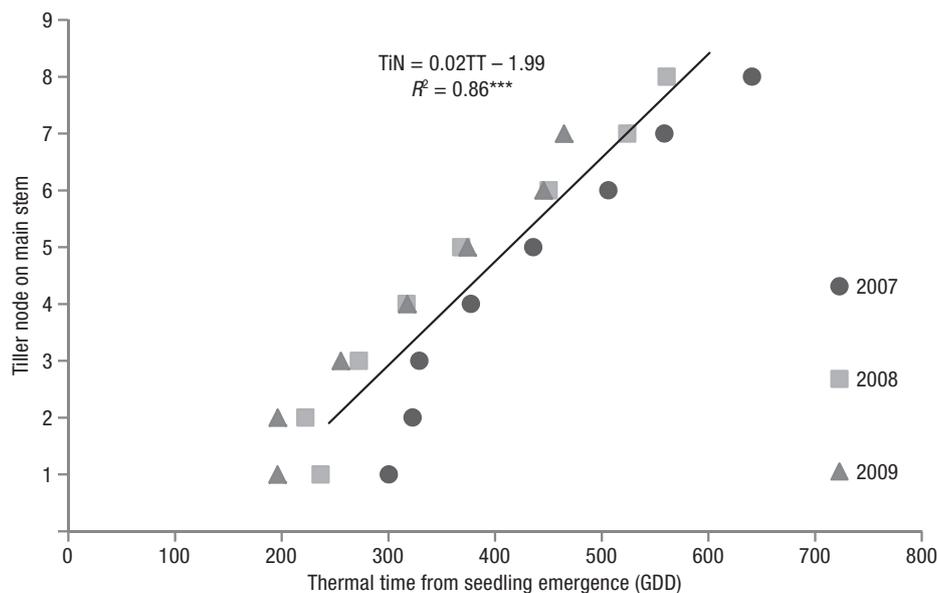


Figure 1. Linear regression model describing the pattern of primary tiller appearance on main stem for each tiller node on rice cv. Gleva. Data points are the average thermal time when tillers in each node were developed, regardless the total amount of tillers developed in each node over the experiment. TiN, tiller no.; TT, thermal time; GDD, growing degree days.

(14%). Development of primary tillers (Fig. 1) occurred from 200-300 GDD from seedling emergence (1.5 Haun leaf stage) to 425-600 GDD and thus, with some inter-annual variability: earlier and shorter tillering in 2009 (from 200 to 425 GDD) as opposed to later and longer tillering in 2007 (from 300 to 600 GDD). In calendar time, tillering duration in 2009 lasted 40 days whereas in 2007, 48 days (Fig. 1).

The relationship between thermal time and emergence of primary tillers on MS was lineal (Eq. [2]: $R^2=0.86$, $p<0.001$) with a constant time gap between subsequent primary tillers of 52.9 ± 2.1 GDD.

Rice plants produced up to 8 primary tillers (Fig. 1), from the first (T1) to the eight node position (T8). Emergence of tillers (Table 1) from middle nodes, those from nodes 4 and 5 (T4 and T5), was stable over the years with emergence rates superior to 74%. In contrast, development of lowermost (T1, T2) and uppermost (T6, T7 and T8) nodes on MS showed some interannual variability ($p<0.001$). Emergence of T1 and T2 overlapped, and T1 emergence was the lowest over the years (with a maximum emergence ratio of 16% in 2009). T7 did not emerge in 2009 and neither did T8 in 2008 and 2009.

Tiller emergence was synchronized with leaf emergence on MS (Eq. [3], Fig. 2); tiller emergence started at 3.5th-4th leaf stage and continued up to the maxi-

mum tiller stage (4.3 tillers/plant) at 9.6 leaf stage. Maximum rate of tiller emergence occurred at 6.3 leaf stage with a ratio of 0.8 tillers/leaf. From maximum tillering stage, tillering number decreased at the same maximum rate as emergence which happened at 12.6 leaf stage (Fig. 2).

Emergence of primary tillers was also linearly related to leaf emergence ($R^2=0.85$, $p<0.001$). Emergence of subsequent tillers occurred every 1.6 leaf emergence on main stem (at a rate of 0.64 ± 0.06 tillers/leaf).

Tiller dynamics per unit area

Changes in tiller number per unit area against thermal time fitted to a rational function (Eq. [4], Fig. 3) through which tillering parameters were estimated (Table 2). The ANOVA for the estimated parameters indicated that tiller dynamics pattern was stable over years, since no significant differences across years ($p<0.05$) were found for any of the parameters save for the rate of tiller mortality, which was higher in 2009 (1.2 ± 0.07 tillers/GDD) than in 2007 (0.80 ± 0.28 tillers/GDD). Tillering started at 145 ± 24 GDD which was around 10 days after seedling establishment. Tiller number increased with the maximum tillering stage occurring at 609 ± 28 GDD (40 days after seedling es-

Table 1. Mean values of emergence and fertility ratios (%), grain number and yield per panicle in each tiller node.

Tiller node ¹	Emergence ratio (%)			Tiller fertility (%)			Total grain n°/panicle	Grain weight/panicle (g)
	2007	2008	2009	2007	2008	2009		
MS	100	100	100	100	100	100	$84.1\pm 3.01a$	$2.33\pm 0.070a$
T1 ²	0	4	16	-	0	8	63.0 ± 38.0	1.6 ± 1.0
T2	7c	41b	77a	20b	26	54a	43.8 ± 6.0 c	$1.2\pm 0.2c$
T3	19b	48a	77a	13b	37a	36a	58.9 ± 4.3 ab	$1.7\pm 0.1b$
T4	74a	89a	85a	48a	63a	4	54.8 ± 6.3 b	$1.5\pm 0.2b$
T5	90a	96a	73a	67a	44ab	8	53.2 ± 3.7 b	$1.5\pm 0.1b$
T6 ²	73a	67a	15b	57a	15b	0	59.6 ± 2.7	1.8 ± 0.1
T7 ²	15	52	0	23	0	-	33.6 ± 14.7	1.0 ± 0.4
T8 ²	25	0	0	5	-	-	29.0 ± 0.8	0.8

Type III test of factors (REML)

Source of variation	Emergence ratio	Tiller fertility	Grain number	Grain weight/panicle
Year	ns	ns	ns	ns
Tiller node	*	ns	*	*
Year * Tiller node	*	*	ns	ns

¹ T1 to T8 denote the tiller position according to the leaf number from which the tiller was developed. MS, main stem. Emergence and tiller fertility ratios data presented are means in each tiller position within each year since the interaction effect was significant ($p<0.05$) while values presented for total grain number and grain weight per panicles are means across years for each tiller node as no year effect was observed. ² Not considered in yield traits mean separation as they were absent (<5%) in some year: T1 in 2007, T6 in 2009 and T7 and T8 in 2008 and 2009. *Significant differences ($p<0.05$); ns: non-significant differences ($p<0.05$); Dash (-) have been inserted in tiller fertility when fertility could not be calculated because of absence of tiller emergence as opposed to 0 values, which means that none of the emerged tillers became productive.

establishment) with 688 ± 40 tillers/m². Maximum rate of tiller emergence occurred half way between tillering onset and maximum tiller stage. Interannual non-significant variability was observed around maximum tillering stage in both timing and tiller density: in 2007, 50 tillers/m² less were produced than the following years and maximum tillering stage occurred 126 GDD later. Such a delay in phenology tended to vanish over the cycle: panicle initiation and heading took place on average 90 and 22 GDD later, respectively, whereas maturity it occurred 53 GDD earlier than in 2009. The interannual differences in tiller number were compensated by lower rates of tiller mortality in 2007, which was 80% lower than in 2008 and 2009, leading to

eventually same panicle density (250 ± 31 panicles/m²) over the three years. More than 60% of emerged tillers became fertile.

Yield and yield components

The comparison of the mean values for grain yield and yield components (Table 3) showed that grain yield was stable across years with a mean of 933 ± 42 g/m² of rough rice. However, yield in 2007 declined non-significantly by a 21% compared to the 2008-2009 average, as a consequence of the lower seedling establishment and subsequent low plant density ($p < 0.05$).

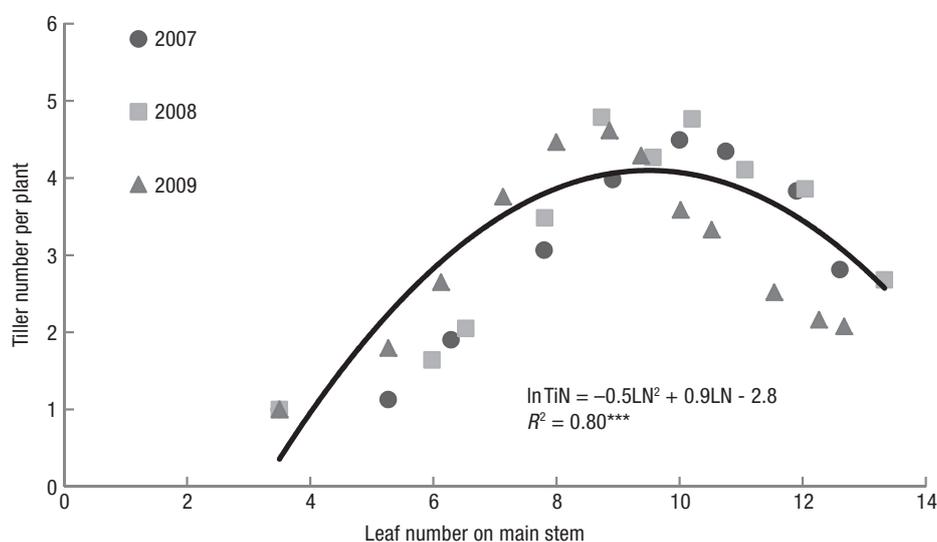


Figure 2. Relationships between the number of tillers per plant and the number of leaves on the main stem of rice cv. Gleva. Points represent the average of tiller number per plant over leaf development within each year. TiN, tiller no.; LN, leaf number.

Table 2. Mean values across experiments of the traits describing the tillering dynamics of rice cv. Gleva and ANOVA statistics for the effect of year.

Trait	Mean±SE	Mean square	F value
Thermal-time from seedling establishment to the onset of tillering (GDD)	145 ± 24.1	9722	2.58
Thermal-time from seedling establishment to maximum tiller number (GDD)	609 ± 27.9	16546	4.35
Rate of tiller appearance (no. of stems/GDD)	3.40 ± 0.30	0.93	1.14
Maximum no. of stems/m ²	688 ± 40.3	3354	0.18
Thermal-time to the maximum rate of tiller appearance (GDD)	456 ± 17.7	4715	4.58
Rate of tiller mortality (no. of stems/GDD)	-1.20 ± 0.15	0.53	6.26*
Thermal-time from seedling establishment to the maximum rate of tiller mortality (GDD)	737 ± 44.1	37349	3.43
No. of panicles/m ²	250 ± 30.8	8320	0.97
Fertile tillering (%)	63.5 ± 4.6	329	2.28

*Significant differences across years ($p < 0.05$). Data are means of field experiments conducted during three years. Significant differences between years were statistically significant ($p < 0.05$) only for the rate of tiller mortality.

Table 3. Mean values for growth traits, yield and yield components of rice cv. Gleva and ANOVA statistics for the effect of year as source of variation.

Trait	2007	2008	2009	Mean square	F value
Seedling establishment (%)	40.0±2.43 ^b	55.6±2.16 ^a	65.2±2.78 ^a	527	28.7
Density (plants/m ²)	180 ± 10.7 ^b	232 ± 9.5 ^a	254 ± 0.01 ^a	4302	21.0
Grain yield (g/m ²)	819 ± 34.9 ^a	987 ± 81.9 ^a	993 ± 57.2 ^a	29254	2.61
Grain yield (g/plant)	5.9 ± 1.9 ^a	4.7 ± 0.6 ^{ab}	3.8 ± 0.9 ^b	2.21	3.57
Panicle no./plant	3.1 ± 1.0 ^a	2.7 ± 0.2 ^a	2.1 ± 0.5 ^a	1.07	2.65
Panicle no./m ²	491 ± 20.2 ^a	491 ± 42.6 ^a	468 ± 36.6 ^a	508	0.14
Grain no./panicle	68.6 ± 2.3 ^a	62.3 ± 2.1 ^{ab}	57.8 ± 1.6 ^b	87.7	6.85
Panicle fertility (%)	98.0 ± 0.2 ^a	84.6 ± 2.3 ^b	97.5 ± 0.2 ^a	173	31.2
Thousand grain weight (g)	34.3 ± 0.9 ^a	35.2 ± 0.2 ^a	35.3 ± 0.3 ^a	0.99	2.50
Grain number/m ²	33638 ± 453 ^a	30453 ± 2635 ^a	26959 ± 1402 ^a	33470314	3.04

Means within rows with the same letter are not significantly different at $p < 0.05$.

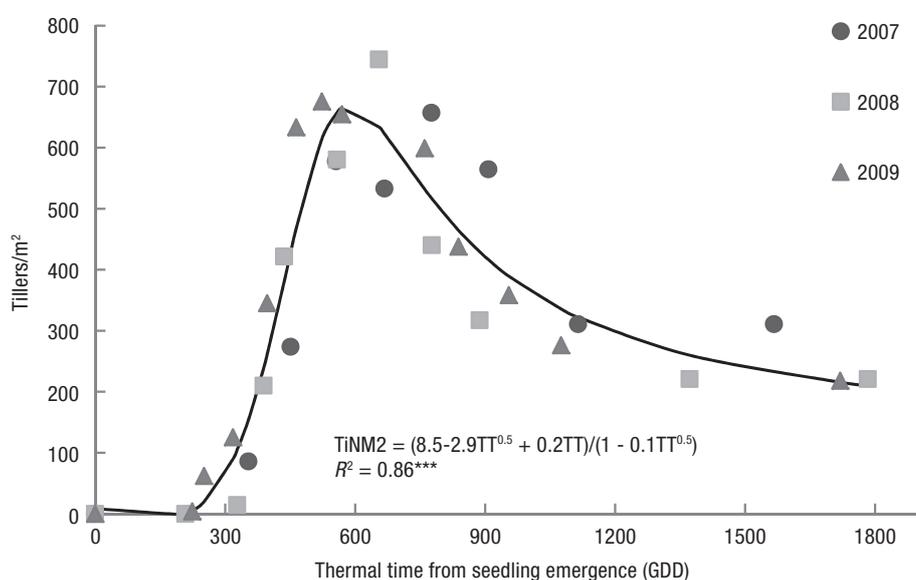


Figure 3. Pattern of changes in the number of living tillers per unit area during the development of rice cv. Gleva. TiNM2, tiller no./m²; TT, thermal time; GDD, growing degree days.

No significant differences in either panicle density or 1000-grain weight were found whereas grain number per panicle and panicle fertility significantly ($p < 0.05$) differed between years. Panicles in 2009 had less number of grains (57.8±1.7) than in 2008 (62.3±2.1) and 2007 (68.6±2.4) whereas percentage of filled grains per panicle in 2008 was 16% lower than in 2007 and 2009.

Grain yield per plant was more variable over the years following a decreasing trend that lead to significant differences between 2007 (5.9±1.9 g) and 2009 (3.8±0.9 g). The same pattern was observed for number of panicles per plant. Panicle number per plant also declined over the years, besides differing nodal position of fertile tillers along the MS; plants at maturity in 2007 and 2008 were mainly formed by T3 to T6 tillers whereas in 2009 they were formed by T2 and T3. However, same pattern of yield traits distribution along main stem over the years was observed. Panicles from main stem were larger (84.1±3.01 grains/panicle) and heav-

ier (2.33±0.07 g) than primary tillers (52.2±2.1 grains/panicle, 1.46±0.063 g/panicle) and thus contributed more (52.3%) to plant yield than primary tillers. Among primary tillers, higher panicle yield in terms of grain number and grain weight was located in tillers from T3 to T5 whereas remaining tillers showed either lower productivity and/or occasional presence in plant.

Effect of tiller dynamics on yield formation

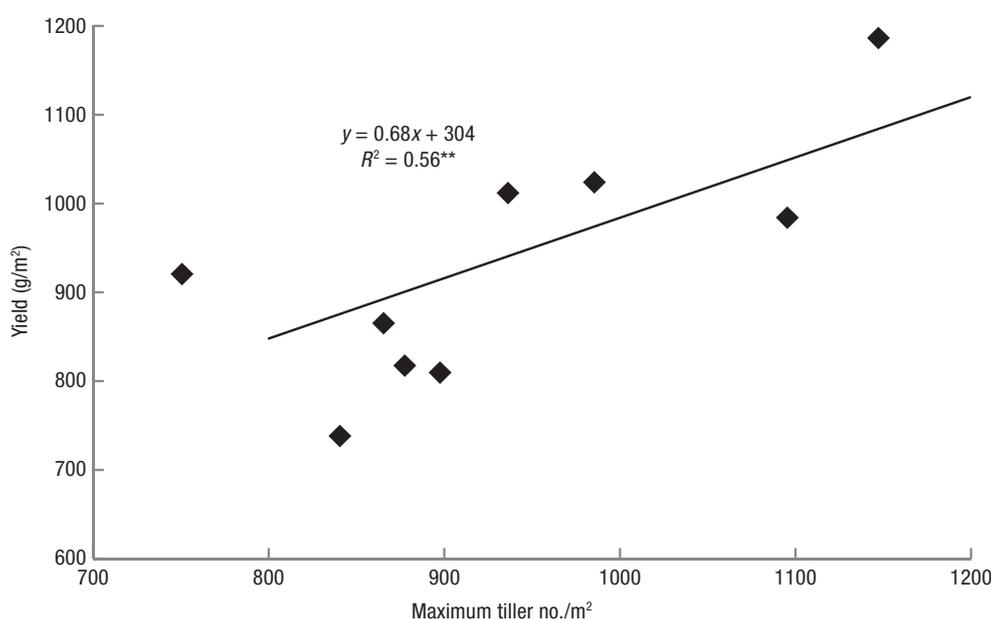
The stepwise regression analysis revealed that among all yield and tillering traits, *i.e.* plant density, yield components and maximum tiller number, the last was the most important trait explaining 56% of grain yield variation, as shown by the linear regression (Fig. 4).

Correlation analysis among yield, yield components and tillering dynamics (Table 4) revealed that grain yield was positively correlated with maximum tiller

Table 4. Matrix of Pearson correlation coefficients between yield, yield components and traits describing the tillering dynamics.

	Plant density	Grain yield	Panicle no./m ²	Grain no./panicle	Thousand grain weight	Grain no./m ²	Maximum tiller no.	Tiller mortality	Tiller efficiency
Density (plants/m ²)	1.00								
Grain yield (g/m ²)	0.21	1.00							
Panicle no./m ²	0.24	0.91*	1.00						
Grain no./panicle	0.80*	-0.19	-0.28	1.00					
Thousand grain weight (g)	-0.22	-0.10	-0.21	-0.12	1.00				
Grain number/m ²	-0.11	0.08*	0.88*	0.19	-0.12	1.00			
Maximum tiller no. (tillers/m ²)	0.44	0.83*	0.90*	0.69	-0.11	0.28	1.00		
Tiller mortality (tillers/GDD)	-0.56	0.22	0.45	0.44	-0.13	0.68	0.55	1.00	
Tiller efficiency (%)	-0.69	-0.64	-0.81*	0.70	-0.31	-0.48	-0.80*	-0.11	1.00

* $p < 0.05$. Data were averaged across years and replications.

**Figure 4.** Relationship between maximum tiller number and grain yield of rice cv. Gleva.

number, panicle density and grain number/m² ($p < 0.05$). Among yield components, negative correlations were found between panicle size (grain number per panicle) and maximum tiller number and tiller efficiency. Maximum tiller number and panicle density (panicle number/m²) were positively correlated with each other and with number of grains/m².

Discussion

Primary tillers are developed from axillary buds in each leaf on the main stem (Matsuo & Hoshikawa, 1993). Rice cultivar Gleva grown under standard agricultural practices in the Mediterranean agrosystem of the Ebro Delta develops on average 13 leaves on the main stem (Martínez-Eixarch *et al.*, 2013). Total leaf number on the main stem indicates the potential num-

ber of primary tillers, as they develop from the bud in the axil of the leaf (Nemoto *et al.*, 1995). The present study demonstrates that Gleva cultivar (representative of rice plant type in Mediterranean rice fields) grown under the standard crop practices in Ebro Delta develops up to eight primary tillers out of the thirteen potential ones, remaining the five uppermost axillary tiller buds latent. Tillering composition consists in a main middle tillering area (T4 -T5) on the main stem with low or nil emergences in the lowermost and uppermost nodes. Despite the emergence of tillers can occur until the 8th node (as happened in 2007) plants reach on average a maximum of 4.3 tillers which is far from the 8 primary tillers observed. The difference results from low and variable emergences ratios in lowermost and uppermost nodes along with tiller senescence taking place even before reaching maximum tillering stage.

Interannual variability in T2-T3 versus T6 positions defines two distinct types of rice plants: mid-late tillering (2007 and 2008) and early-tillering (2009) plants. Years 2007 and 2009 exhibited the most contrasting growing conditions despite the same agronomic management was used. Main differences were given by crop establishment which was lower and poorer in 2007 because of attack of midges (*Chironomus* sp. and *Cricotopus* sp.), which ate seeds embryo and radicles, causing lower plant density and impaired development of early tillers. Such scarce and weak development in early nodes was compensated by later tiller development (from T6 to T8) resulting in slight delays in the crop phenology that were eventually vanished after heading stage. In contrast, profuse vegetative growth in 2009, shown by high emergence ratios from T2 to T5, prevented from later tiller emergence in higher nodes. Previous studies reported that tillering cessation is induced by the achievement of critical values for leaf area index (Lafarge & Hammer, 2002a; Zhong *et al.*, 2002), foliar nitrogen concentration (Kim & Vergara, 1990; Sasaki & Toriyama, 2006), red:red-far light ratio or PAR (photosynthetically active radiation) value of the canopy (Evers *et al.*, 2007). Hence, earlier vegetative plant development in 2009 may have hastened the attainment of these critical values thus explaining the inhibition of further tiller emergence beyond T5. In addition, excess of stems was corrected by senescence of last emerged tillers (Mohapatra *et al.*, 2011).

Plant yield was modulated by tillering dynamics: lower internal plant competition in 2007 resulted in more panicles/plant and more grain number/panicle leading to higher plant yield. However, pattern of plant yield distribution was uniform over years exhibiting dominance of main stem over primary tillers which is in line with previous studies on rice (Awan *et al.*, 2007; Mohapatra & Kariali, 2008), barley (Cannell, 1969) and wheat (Metho *et al.*, 1998). Among primary tillers, location of highest-yield panicles occurred in nodes with the highest tiller emergence ratios whereas contribution of lowermost and uppermost tillers to plant yield was low and variable. Less time availability for vegetative growth in later tillers (T7 was developed 150 GDD later than T4; Fig. 1) and impaired bud development in lowermost nodes caused by flooding conditions (Yoshida, 1981; Sasaki *et al.*, 2002a, 2004) may have limited yield potential of these tillers. Therefore, the paddy cultivation causes a difference in the distribution of yield within the plant compared to other agrosystems in other crops such as barley and wheat, in which tillers on lower node positions, along with main stem, are the major contributors to plant yield (Cannell, 1969; Kirby *et al.*, 1985; Otteson *et al.*, 2008). The overall balance of tillering dynamics per

unit area resulted in more than 60% of tillers becoming productive (panicle bearing), which is in line with other studies in lowland and transplanted paddy rice in which tillering efficiency ranged from 53 to 73% (Yan *et al.*, 2009) and from 48 to 58% (Bueno & Lafarge, 2009; Bueno *et al.*, 2010) respectively. Similar interannual panicle density, which has been reported to be the main yield component in direct seeded rice (Miller *et al.*, 1991), resulted from higher tillering production per plant in 2007 that compensated lower seedling establishment. Maximum tiller number per unit area explained more than 50% of grain yield. In addition, grain yield was positively correlated with maximum tiller number, panicle density and grain number/m², which also correlated among them. Altogether, points out the relevance of tillering in yield formation in Ebro Delta rice agrosystem. Such contribution could be explained by the positive association existing between higher tiller production, sink strength and storage capacity of carbohydrates (Samonte *et al.*, 2006; Elhani *et al.*, 2007). The high percentage of filled grains/panicle observed in our study (>85%) suggests that grain filling was not limited (Lafarge & Bueno, 2009), hence sink size (*i.e.* spikelet number per unit area) rather than source strength (source availability during grain filling) is the limiting factor to grain yield. Accordingly, one might consider the use of strategies to promote sink strength through rice tillering to increase grain yield. However, compensatory relationships established over yield formation should be taken into account: early and luxuriant vegetative growth in 2009 did not result in higher grain yield because it was eventually offset by higher tiller abortion, which led to slight non-significant lower panicle density, and fewer spikelets per panicle. The higher tiller mortality rates (located on last developed tillers) along with the negative correlation between maximum tiller number and tiller efficiency despite similar maximum tiller density, suggests that more intense within-plant competition was set likely because of the longer and eventual excessive vegetative development. Since last developed tillers show higher mortality ratios and less yield potential, which is in line with Jaffuel & Dauzat (2005) and Mohapatra & Kariali (2008) for rice and with Lafarge *et al.* (2002) for sorghum, we hypothesize that early start of vegetative development along with inhibition of late tiller emergence might decrease internal competition so that superiority of early vegetative growth could be maintained until reproductive and grain filling stages resulting in higher grain yield. Then, our study indicates that the regulation of rice tillering through promotion of early tillering followed by inhibition of late tillering might optimize rice crop productivity. Studies to provide strategies to induce such tillering pattern in

a particular rice agro-system should be carried out. In this sense, total amount and timing of nitrogen fertilization should be considered given its influence not only on tillering capacity (Yoshida, 1981) but also on the temporal pattern by either promoting early tillering (Sasaki *et al.*, 2002b; Pham Quang *et al.*, 2004), limiting their emergence (Kim & Vergara, 1990; Zhong *et al.*, 2002; Sasaki & Toriyama, 2006) or even inducing tiller senescence (Zhong *et al.*, 2002; Pham Quang *et al.*, 2004).

Modulation of tiller dynamics through agronomic practices has important agronomic implications in terms of precise-farming, which consists on agricultural management based on crop phenology and needs of the crop at different growth stages. Regulation of tiller dynamics needs to be based on predictability of tillering pattern (Zhong *et al.*, 1999).

Our study provides a function to describe tiller dynamics per unit area based on GDD with high applicability at both technical and farm level. When water and fertilizer are not limiting factors, as usually happens in Ebro Delta rice system, tillering pattern at similar plant densities is mainly determined by solar radiation and temperature (Mi *et al.*, 2005). The strong relationship between these two meteorological variables allows tillering modelling to be based on the relationship between tillering dynamics and growing-degree-days (Caton *et al.*, 1998). At plant level, our study reveals, firstly that emergence of primary tillers in cv. Gleva is predictable and defined by constant interval time between subsequent tillers and secondly, that it is highly synchronized with leaf emergence. Tillering production in irrigated rice crop has been modelled (Zhong *et al.*, 1999) providing several models such as TILL (Penning de Vries *et al.*, 1989), RGR (Dingkuhn *et al.*, 1992) and SINK (Drenth *et al.*, 1994). However, these models are based on data from contrasting rice cultivation systems to Ebro Delta's, with different cultivars, climatic conditions and planting techniques that may influence on tillering pattern. Moreover, they require destructive sampling that increases their complexity and limits their applicability at a technical or farm level. The cultivar utilised for this study belongs to temperate *Japonica* subspecies, which are mostly grown in Europe (Aldo, 2007) and North Pacific (Agrama *et al.*, 2010). It has been reported that temperate *Japonica* rice germplasm has lower genetic diversity than *Indica* rice type (Shu *et al.*, 2009; Agrama *et al.*, 2010). Although environmental and genotypic specific calibrations are needed, the genetic similarity among *Japonica* varieties lead us to suggest that tiller dynamics equations herein provided may be considered as a basis for validation in further studies on rice tillering modelling in systems as those in the Mediterranean rice

agrosystems. In addition, calibration and validation to Mediterranean environment of alternative models as well as the comparison of their capacity to predict tiller dynamics with the equation we provide could also be considered in these studies.

In summary, plant and crop tillering dynamics in the Ebro Delta rice agrosystem can be accurately predicted through equations herein provided, which are based either on thermal time or leaf development. Plants of Gleva cv. grown under the standard agricultural practices develop up to 8 primary tillers and they are mainly composed by the main stem plus two primary tillers located on the low or middle tillering area with some variability explained by growing conditions. Our study demonstrates the crucial role of rice tillering on yield formation at two scales: at a plant level, as the main tillering zone in terms of emergence frequency becomes the most productive; and at crop level, since the maximum tiller number is the main explanatory variable of crop grain yield in this particular agrosystem. Therefore, we suggest more studies should be conducted to analyse options of tillering modulation to optimize rice grain yield.

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