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Leaf emergence, tillering, plant growth, and yield in response to plant density in a high-yielding aerobic rice crop

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ABSTRACT

The traditional transplanted and flooded rice cropping system is threatened by water shortage and labor cost increase in many Asian countries and is currently evolving toward direct-seeded and water-saving systems. However, yield penalties generally accompany this evolution and ongoing research targets their mitigation. In a previous research, slower plant development rate was observed in aerobic crops, possibly caused by the increased plant density. This possible factor was tested in experiments conducted at IRRI's farm, Los Baños, Philippines, in 2012 and 2013. One elite variety was direct-seeded at three plant distances (6, 10, and 20 cm × 20 cm) and sprinkler-irrigated to keep the soil water potential above −10 kPa. Weekly measurements were made to dissect crop and plant physiological differences. Data from previous experiments on tillering in the greenhouse of four varieties and in fields in aerobic and flooded conditions were added to strengthen the results from the current experiment.

The last upper leaves of the main stem appeared faster at higher plant density, thus increase plant density was not the cause for the slower leaf appearance in aerobic than in flooded crops. Plants at higher plant density also had earlier panicle initiation, earlier earing, and 0.8 leaf less than plants at low density. The number of outgrowing tillers was linked to the number of leaves on the main stem by a variety-specific relationship that is independent from plant density and water management. Tiller density was regulated by the cessation of the outgrowth of tillers triggered by the onset of stem elongation at 20-cm plant distance and occurred earlier at shorter distances probably in response to the high root density. Grain yields were significantly higher at higher plant density (6-cm and 10-cm plant distances) and correlated with a higher tiller density. Thus for aerobic crops, seedling density higher than 50 plants m^{-2} remains the way to get high yields for the type of variety used in this study.

1. Introduction

The increasing human demand for water results in scarcer water supply. Sixty to 70 percent of worldwide water consumption is for agriculture. In Asia, rice alone uses up 50% of the water set aside for irrigation (Bouman et al., 2007). Aerobic rice culture, which consists of dry-seeded rice cultivation with frequent irrigations to always keep free water in soil porosities (or water content above field capacity), has been developed to enhance water-use efficiency.

Such crop management used, on average, 20% less water than the conventional flooded system with only a 6% yield penalty (Bouman et al., 2007). Earlier studies, however, showed that continuous cropping of aerobic rice generates a fast and continuous decrease in yield (George et al., 2002; Peng et al., 2006). Kato and Katsura (2014) reviewed recent experimental results and showed that, although high yield can be reached in aerobic culture (even higher than in flooded areas in Japan), yields are also more variable under aerobic conditions and so there should be better understanding of how to control this variability.

Yield reduction in aerobic crops was associated with reduced plant height, lower harvest index (Clerget et al., 2014; Lafitte and Bennett, 2002), less crop biomass, and lower leaf area index (Belder et al., 2005; Okami et al., 2011). Plant height and leaf elongation rate

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were found to be sensitive even to small reductions in the water available in the soil (Nguyen et al., 2009). Clerget et al. (2014) additionally reported slower leaf appearance rates and reduced number of leaves (one to two leaves) on the main tiller in direct-seeded aerobic crops when compared with transplanted flooded crops. However, many factors were changed between the two cropping systems. In a pot experiment, the rate of leaf appearance decreased only slightly in aerobic pots and the number of leaves declined by only 0.4 in comparison with flooded pots (Clerget and Bueno, 2013). Thus, watering was not the main factor responsible for the change in leaf appearance kinetics.

Planting density has been intensively studied in transplanted flooded crops in every country where rice is grown in paddy fields. Observations consistently showed that higher planting density induced fewer tillers per plant, higher tiller density in the crop, and a reduced number of grains per panicle, while grain weight remained unchanged. Within a range of 5 to about 100 plants m^{-2}, grain yield generally increased with planting density (Hayashi et al., 2006; Nakano et al., 2012; San-Oh et al., 2008). For more than 100 plants m^{-2}, there was no significant gain in yield but rather yield remained stable through a balance between tiller density and number of grains per panicle (Fukushima et al., 2011; Jones and Snyder, 1987; Ottis and Talbert, 2005). Few references on density experiments in aerobic conditions could be found. A positive relationship between plant density and yield was also generally observed as well as the same balance as in flooded conditions between tiller number and number of grains per panicle (Lampayan et al., 2010; Mishra and Salokhe, 2010; Sunyob et al., 2012).

Plant density was found to be one of the main factors influencing tillering in cereals, together with nitrogen availability (Evers et al., 2006). Under non-limiting conditions, the dynamics of tiller appearance by plants was stable and strictly related to the number of leaves already appeared on the main stem, fitting a Fibonacci series in wheat and barley, and the appearance of tillers ceased earlier as plant density increased (Dreccer et al., 2013; Evers et al., 2006; Kirby et al., 1985). Dreccer et al. (2013) summarized the three processes influencing the cessation of tiller appearance: (1) C balance and partitioning that changed when stems started to elongate (Kirby et al., 1985), (2) light attributes (Casal et al., 1986; Evers et al., 2006; Lafarge and Hammer, 2002), and (3) the hormone-related control (McSteen, 2009). The decrease in red:far red ratio and to a lesser extent the decreased amount of light at the basis of the canopy were mentioned as triggers of the cessation of tillering. Regarding hormone control, movement of cytokinin coming from the roots was reported to promote axillary bud outgrowth while another newly discovered hormone, strigolactone, also coming from the roots, inhibited this outgrowth.

Two studies carried out in Europe using temperate japonica varieties previously reported the effect of plant density on the rate of leaf appearance in rice (De Raïssac et al., 2004; Martínez-Eixarch et al., 2013). These authors used large ranges of planting densities, 20–400 and 50–500 plants m^{-2}, and came to similar conclusions. At higher plant densities, phyllochrons were longer, panicle initiation occurred earlier, and the total number of leaves on the main stem decreased by one to two leaves.

The aim of the study was to quantify in extenso, at plant and crop scales, the effects of plant density at sowing on the rate of leaf development, tiller outgrowth and cessation, plant growth, and yield in an aerobic crop irrigated with sprinklers to maintain soil humidity close to saturation and managed with high inputs. Data from previous experiments on tillering in the greenhouse of four varieties and in fields in aerobic and flooded conditions were added to strengthen the results from the main experiment. The study is part of an overall search for the main traits altered by the shift from flooded to aerobic environment and the extent of the consequent yield penalty to eventually recommend possible improvements through breeding and crop management.

2. Materials and methods

2.1. Site description

The experiment was conducted during the 2012 and 2013 dry seasons at the International Rice Research Institute (IRRI) farm in Los Baños, Laguna, Philippines (14°11′N, 121°15′E, 21 m elevation, plot UZ1). The soil was a Lithic Haplustept, with a topsoil of 33% clay, 38% silt, and 29% sand, 10.11 g organic C kg^{-1}, 1.35 g total N kg^{-1}, a mean pH of 6.5, and a cation exchange capacity (CEC) of 25.4 meq/100 g.

2.2. Experimental design and crop management

The experiment was laid out in a randomized complete block design with three replications and three plant distances within rows: 6, 10, and 20 cm. Rows were 20-cm apart. Individual plot area was 72 m^2. The variety used was NSIC Rc222, a high-yielding variety released in 2010 that was developed for flooded environments but has shown good adaptation for rainfed conditions. It was assumed to be photoperiod-insensitive before its reaction to daylength was observed and reported (Egle et al., 2015).

The plot had been under fallow before the first year of experimentation. Crop rotation with mungbean was done during the intercalary wet season before the second experiment. The soil was dry-tilled (disk plowing, rotavator passes, and land leveling) before the dry-seeding. On 6 January 2012, four seeds per hill were manually seeded at the targeted plant distances and thinned to one plant per hill 10–14 days after emergence (83, 50, and 25 kg ha^{-1} seeds). The distance of 6 cm was considered as the minimal distance manually manageable to obtain a uniform plant stand. The second-year experiment was sown on 11 December 2012 with a monoseeder for experimental plots (Wintersteiger AG monoseeder B, Ried/I., Austria) at 2-cm distance and thinned per plot 10–14 days after emergence to adjust the distances between plants (unique rate of 63 kg ha^{-1} seeds). In both years, phosphorus (40 kg P ha^{-1} as single superphosphate), potassium (40 kg K ha^{-1} as muriate of potash), and zinc (5 kg Zn ha^{-1} as zinc sulfate heptahydrate) were applied and incorporated before sowing. A total of 200 kg N ha^{-1} in the form of urea was applied in five equal splits every other week from the second week after sowing. Irrigation was supplied through a 9-m-distant 100% overlapping impact sprinkler system with a planned triggering at −10 kPa soil water potential at 15-cm depth. Plots were maintained weed-free through a pre-emergence application of oxadiazon (500 g ha^{-1}) and six manual weedings in 2012 and three weedings in 2013.

2.3. Measurements

Weather information was recorded from sensors installed at one field extremity. Incident global sun radiation (LI-200 Pyranometer, Li-Cor, Lincoln, NE, USA), air temperature at 2 m above ground level (HMP 45C, Vaisala, Helsinki, Finland), and soil temperature at 2-cm depth (T thermocouples, PyroControle, Vaulx en Velin, France) were measured at 1-min intervals, averaged on an hourly basis, and stored in a datalogger (CR10X, Campbell Scientific, Logan, UT, USA). Data on daily rainfall were acquired from the IRRI Climate Unit. Soil water tension at 15 and 40 cm was recorded daily from 16 and 10 tensiometers (Jet Fill 2725, Soil Moisture Equipment Corp., Goleta, CA, USA) in 2012 and 2013, respectively, installed in pairs at regular distances to cover the whole field. The amount of water applied was recorded immediately after each irrigation, using 6 and 30 (2012