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Genetic variability of nitrogen use efficiency in rainfed upland rice

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ABSTRACT

In sub-Saharan Africa and in Madagascar, upland rice is mostly grown for subsistence by resource-poor farmers in low-input production systems with low yields. In this context, soil nitrogen availability is a major limiting factor. To determine the appropriate breeding strategy to improve nitrogen use efficiency (NUE), the genetic variability and the level of G × N interaction of NUE need to be evaluated. NUE and its components are complex quantitative traits and the study of their relationship with other simpler traits should help understand the mechanisms involved in NUE and identify ways to improve it. A study was conducted at mid-altitude in Madagascar using 13 adapted tropical japonica rice varieties over three cropping seasons with two contrasted levels of applied N (high N with 90–120 kg N ha^{-1} as urea and low N without mineral fertilizer) in rainfed upland conditions. Year × N and Year × G interactions were significant due to contrasted rainfall distributions across the three cropping seasons. Agronomic efficiencies of N fertilization were low (11.5 kg grain kg^{-1} N in the best year) because of N loss through leaching or volatilization. Our results also suggest gaseous loss of N by plants between flowering and harvest, particularly under the high N treatment. The experiment revealed significant genetic variability for NUE, nitrogen uptake efficiency (NUPE) and nitrogen utilization efficiency (NUTE) in both high N and low N treatments but a low level of G × N interaction. The variation in NUPE accounted for more of the variation in NUE than the variation in NUTE. There was no correlation between NUPE and NUTE, either under high N or under low N. We found no negative relationship between grain yield and grain N concentration under low N. The relationship between NUE and agronomic and N-related traits differed from one year to the next, illustrating the plasticity of the contribution of the different agronomic traits to NUE as a function of the contrasted climatic conditions (particularly the rainfall distribution pattern). However, two traits, the number of panicles per m^2 and the harvest index were consistently positively correlated with NUE. The difference between total N uptake at flowering and at harvest was positively correlated with NUE, particularly under the low N treatment.

1. Introduction

Demand for rice is increasing in sub-Saharan Africa (SSA) where rainfed upland rice accounts for 38% of rice cultivated areas. However, yields of upland rice are very low, ranging from 1 to 2 t ha^{-1} (Balasubramanian et al., 2007). In SSA, upland rice is mostly grown for subsistence by resource-poor farmers in low-input production systems on poor soils (Saito and Futakuchi, 2009). In Madagascar, where upland rice cultivation is expanding in the highlands (Raboin et al., 2014), the situation is similar. Use of mineral fertilizer is uniformly very low because of its high cost (Minten et al., 2007) and animal manure is the only source of fertilizer (Alvarez et al., 2014). In such economic and environmental contexts that have been left aside by the "green revolution", adapting crops to low inputs may be possible through breeding programs that specifically target low-input environments (Atlin and Frey, 1989; Ceccarelli, 1996). Soil nitrogen availability is a major limiting factor in low-input farming systems with limited access to mineral N and hence greater reliance on sources of organic inputs and their mineralization (Dawson et al., 2008). Nitrogen is the most important mineral nutrient for plant development and nitrogen use

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efficiency (NUE) may play a central role in low-input systems. For a given fertilization level, improving NUE should positively impact rice production both qualitatively and quantitatively. The genetic variability available for nitrogen use efficiency in breeders' germplasm, the level of genotype × N input interaction as well as the accuracy of selection with different levels of N inputs need to be evaluated to identify appropriate breeding strategies (Garnett et al., 2015).

Nitrogen use efficiency (NUE) is usually defined as grain yield per unit of N supplied by the soil and by fertilizer (Moll et al., 1982). NUE is the product of N uptake efficiency (NUPE; crop N uptake per unit of N supply) and N utilization efficiency (NUTE; grain yield per unit of N uptake). NUE and its components are complex quantitative traits and the study of their relationship with other simpler morphological or physiological traits could help understand the mechanisms involved in NUE and identify ways to improve selection efficiency. Genetic variability of both N uptake efficiency and N utilization efficiency has been demonstrated in a large number of crops (Hirel et al., 2007). Interactions between genotype and N may exist (Le Gouis et al., 2000; Gallais and Coque, 2005; Ju et al., 2015). The genetic variability of traits related to NUE and its components (NUPE and NUTE) thus needs to be investigated under both low and high nitrogen levels.

Many studies on rice have revealed a significant genetic variability for NUE mostly in irrigated rice or rainfed lowland rice (De Datta and Broadbent 1988, 1990, 1993; Tirol-padre et al., 1996; Singh et al., 1998; Inthapanya et al., 2000; Koutroubas and Ntanos, 2003; Haefele et al., 2008; Wu et al., 2016). A negative correlation between NUTE and grain and straw N concentrations has been reported (Tirol-padre et al., 1996; Inthapanya et al., 2000; Koutroubas and Ntanos, 2003; Wu et al., 2016). Indica varieties were shown to have higher NUTE than japonica varieties due to both a higher harvest index and a higher nitrogen harvest index (Koutroubas and Ntanos, 2003). Grain yields of rice under high and low nitrogen supplies have been shown to be significantly correlated (De Datta and Broadbent, 1990; Singh et al., 1998; Haefele et al., 2008) although the correlation was looser in rainfed lowland than in irrigated conditions (Haefele et al., 2008). In contrast, Ju et al. (2015) reported a significant genotype x nitrogen supply level interaction for grain yield and N uptake in irrigated conditions. They linked the high NUE of two lowland japonica varieties with greater root biomass, deeper root distribution, longer root length, greater root oxidation activity. Pan et al. (2016) also found significant positive correlations between total nitrogen accumulation and total root length, root superficial area, and root volume. Nitrogen remobilization has been shown to play a central role in NUE in rice, as it accounts for 70–90% of the total panicle N (Mae, 1997; Tabuchi et al., 2007). De Datta and Broadbent (1993) found that remobilization, measured as changes in the ratio of leaf weight to total biomass or the percentage loss of leaf N between the maximum accumulation of leaf N and harvest, was linked to NUE. Wu et al. (2016) dissociated concentration of N in the straw between leaf N concentration and stem N concentration, thereby revealing distinct relationships with NUTE: improvements in NUTE were associated with lower leaf N concentration when NUTE was < 50 kg kg^{-1}, while further improvements in NUTE were associated with a decrease in stem N concentration. As a way to improve NUTE, these authors thus proposed to increase N translocation from the stems instead of leaves, to delay leaf senescence during the grain filling period.

Upland rice is often cultivated with no supply of inorganic N despite low soil fertility, but little is known about rice NUE in this ecosystem. So far, only data from greenhouse experiments are available (Zaharah and Hanafi, 2009, 2014; Fageria et al., 2010) which showed significant differences in total N uptake between upland rice varieties. The total N uptake at maturity of six upland rice landraces was correlated with their root length 14 days after sowing (Zaharah and Hanafi, 2009). The purpose of the present study was thus to analyze (i) the extent of genotypic variability of NUE in the tropical japonica germplasm used in rainfed upland conditions; (ii) the relationships between NUE components and some other agronomic traits in order to identify proxy target traits for NUE improvement with a particular focus on low N conditions. The study was conducted at mid-altitude in Madagascar using 13 upland rice varieties over three cropping seasons. As the focus was on genetic diversity for NUE, the experiments were conducted with the recommended doses of P and K in order to minimize risks of interaction with other nutritional stresses.

2. Materials and methods

The experiments were conducted in three consecutive rice growing seasons, 2012–2013, 2013–2014 and 2014–2015 (hereafter referred to as 2013, 2014 and 2015), each extending from November to April of the following year.

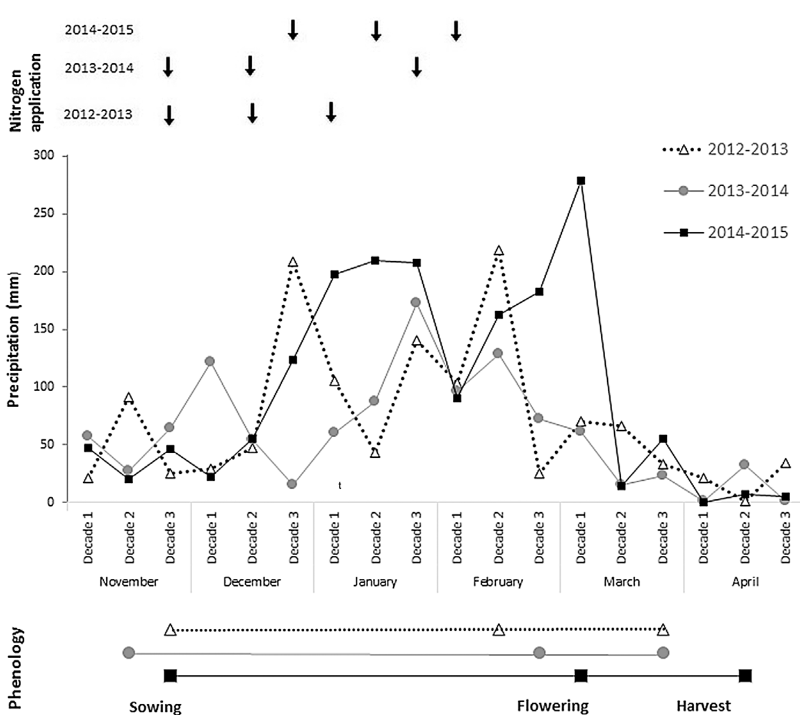

Fig. 1. Cumulated decadal rainfall distribution, sowing date, mean of flowering and harvesting date, nitrogen application date in the three cropping seasons (2013–2015) at the Ivory experimental station in Madagascar.