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Nitrogen (N) metabolism related enzyme activities, cell ultrastructure and nutrient contents as affected by N level and barley genotype (

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Abstract

Development of the new crop cultivars with high yield under low nitrogen (N) input is a fundamental approach to enhance agricultural sustainability, which is dependent on the exploitation of the elite germplasm. In the present study, four barley genotypes (two Tibetan wild and two cultivated), differing in N use efficiency (NUE), were characterized for their physiological and biochemical responses to different N levels. Higher N levels significantly increased the contents of other essential nutrients (P, K, Ca, Fe, Cu and Mn), and the increase was more obvious for the N-efficient genotypes (ZD9 and XZ149). The observation of ultrastructure showed that chloroplast structure was severely damaged under low nitrogen, and the two high N efficient genotypes were relatively less affected. The activities of the five N metabolism related enzymes, i.e., nitrate reductase (NR), glutamine synthetase (GS), nitrite reductase (NiR), glutamate synthase (GOGAT) and glutamate dehydrogenase (GDH) all showed the substantial increase with the increased N level in the culture medium. However the increased extent differed among the four genotypes, with the two N efficient genotypes showing more increase in comparison with the other two genotypes with relative N inefficiency (HXRL and XZ56). The current findings showed that a huge difference exists in low N tolerance among barley genotypes, and improvement of some physiological traits (such as enzymes) could be helpful for increasing N utilization efficiency.

Keywords: barley, enzyme, genotype, nitrogen, ultrastructure

1. Introduction

The application of chemical nitrogen (N) fertilizers has

resulted in a great increase of global food production in the past a few decades. In China, a 3-fold increase in amount of N fertilizer application has contributed up to 70% increase in grain production since 1980 (Guo *et al.* 2010). However, plants consume less than 50% of the N applied to soil (Good *et al.* 2004), the remaining part leads to environmental pollution, enhancing emission of greenhouse gases, soil acidification or water eutrophication (Guo *et al.* 2010; Liu *et al.* 2013). Furthermore, the extensive usage of commercial N fertilizers considerably increases the cost of crop production. It has been well documented that the development of N-efficient varieties (genotypes), with better N utilization efficiency (NUE), would reduce N fertilizer application without compromising the yield, ultimately reducing

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the cost of production and environmental pressure. So it would be of great interest to identify the genotypes with significant difference in NUE to elucidate the physiological and molecular mechanisms of high N use efficiency.

The major form of inorganic N fertilizers is nitrate in aerobic soils, and ammonium in flooded wetland or acidic soils. The utilization of both nitrate and ammonium by plants passes through various steps, including uptake, assimilation, translocation, recycling and remobilization (Xu et al. 2012). Prior to its incorporation into organic form, all higher plants reduce inorganic nitrogen to ammonia (Lea et al. 1993). Nitrate is reduced through the two distinct reactions catalyzed by different enzymes. The first reaction, reducing nitrate to nitrite, occurs in cytosol, which is catalyzed by nitrate reductase (Crawford and Arts 1993). Nitrite, produced in cytosol, is transported into chloroplasts in leaves, where it is further reduced to ammonium ions by nitrite reductase (Lea et al. 1993). Ammonia is further assimilated into organic form as glutamine and glutamate, which serve as the nitrogen donors in the biosynthesis of all essential amino acids. The individual isoenzymes of glutamine synthetase (GS, E.C.6.3.1.2), glutamate synthase (NADH-GOGAT-E.C.1.4.1.14. FD-GOGAT-E.C.1.4.7.1), and glutamate dehydrogenase (NADH-GDH: EC.1.4.1.2; NADPH-GDH: E.C.1.4.1.4) play the crucial role in three important ammonium assimilation processes: primary nitrogen assimilation, re-assimilation of photo-respiratory ammonia and re-assimilation of "recycled" nitrogen (Lea et al. 1993). Glutamine (Gln) and glutamate (Glu) are used to form aspartate (Asp) and asparagines (Asn), and these four amino acids are then utilized to translocate organic nitrogen from sources to sinks (Peoples and Gifford 1993). The primary assimilation of ammonium into the four N-transport amino acids Glu/Gln and Asp/Asn is accomplished by glutamine synthetase (GS), glutamate synthase (GOGAT), aspartate amino transferase (AAT), and asparagines synthetase (AS) enzymes. However, the function of glutamate dehydrogenase (GDH) in N metabolism of higher plants is still debatable, as there is no clear evidence for proving that the enzyme plays a significant role either in ammonia assimilation or carbon recycling in plants (Dubois et al. 2003; Laforgue et al. 2004).

In plants, the interaction between nutrients occurs when the supply of one nutrient affects the absorption and utilization of other nutrients. Nutrient interactions in plants may be synergistic or antagonistic (Sumner and Farina 1986), and is also influenced by both environmental factors, such as nutrient concentration, temperature, light intensity, soil aeration, pH and moisture, and biological factors, such as root architecture, transpiration rate, respiration, plant age, growth rate, as well as plant species and genotype. As interaction occurs, changes are initiated at the subcellular level which may alter many physiological processes such as rates of respiration, photosynthesis, cell division and expansion, utilization, and translocation of carbohydrates and organic acids, ultimately affecting the overall performance of the plants (Fageria 2001). Understanding interactions of N and other essential nutrients is fundamentally important in improving plant growth and development. Generally, more supply of N enhances plant growth, and consequently, increases the demand for other essential nutrients (Wilkinson et al. 1999). Numerous researchers have reported synergistic interaction between N and other nutrients. However the relevant mechanisms are not well understood. Wilkinson et al. (1999) reported that N could increase P uptake in plants by promoting root growth, ultimately increasing the ability of roots to absorb and translocate P, and by increasing the solubility of fertilizer P as a result of reduced pH due to absorption of ammonium. According to Kemp et al. (1983), the increase of N concentration in growth medium would result in increase or decrease of K concentration in the plant tissues depending on K level. N also interacts with micronutrients mainly due to the change of rhizospheric pH. Application of NH,⁺ and NO,- fertilizers would cause decrease and increase of soil pH, respectively. However on the whole, the interaction between N and other nutrients is still controversy among the reports available.

Barley (Hordeum vulgare L.) is the fourth major cereal crop worldwide, only after wheat, maize and rice. The NUE of several spring-barley genotypes, grown under different environments showed the dramatically genotypic and environmental variability, with low-N soil having greater NUE while yield decrease by 10% (Anbessa et al. 2009). With the improvement of modern breeding methods and intensive farming, the genetic uniformity of barley cultivars is increasingly enhanced, losing many valuable alleles. Actually, cultivated barley shows more and more susceptibility to various abiotic and biotic stresses, including low soil fertility. In contrast, wild barley is rich in genetic diversity, containing the important genes or alleles for barley breeding to break through the bottleneck in genetic improvement. The modern barley originates from the wild barley of the Qinghai-Tibet Plateau of China and the Middle East "Fertile Bay" (Fertile Crescent) (Dai et al. 2012). The earlier studies showed the wide genetic diversity of the wild barley in the Middle East, in particular for the tolerance to disease and abiotic stresses, such as drought, nitrogen starvation (Ellis et al. 2000) and salinity (Nevo et al. 2005; Yan et al. 2008). The recent researches showed that wild barley of the Qinghai-Tibet Plateau had the wider genetic diversity as compared to that of the Middle East (Feng et al. 2006; Wang et al. 2009), and some accessions performed well in the poor soil or under limited N supply, indicating the chance of identifying the distinctive genotypes with high NUE or low

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