Field Crops Research xxx (2014) xxx–xxx

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Shoot biomass in wheat is the driver for nitrogen uptake under low nitrogen supply, but not under high nitrogen supply

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ARTICLE INFO

Article history:
Received 29 January 2014
Received in revised form 7 April 2014
Accepted 9 April 2014
Available online xxx

Keywords:
Biomass
Nitrogen uptake
Root growth
Vigorous growth
Wheat

ABSTRACT

This study was aimed to determine whether the accumulation of shoot biomass is the driver of greater nitrogen (N) uptake in genotypes with higher vigorous growth, or whether greater N uptake leads to the greater growth. Two glasshouse experiments were conducted to answer this question. In experiment 1 (Expt 1), N uptake was manipulated by growing wheat plants in vertically divided pots which allowed 100, 50 and 30% of the root system to be supplied with N. Two cultivars were included that contrasted in vigorous growth (rate of shoot biomass accumulation). In experiment 2 (Expt 2), shoot biomass accumulation was manipulated by removing tiller primordial. Two commercial cultivars were grown which differed in their tillering capacity. For each cultivar, one treatment had biomass accumulation constrained by the surgical removal of young tillers as they were exserted. Exposure of 100, 50 and 30% of the root system to N supply generated differences in N uptake at stem elongation and N uptake was positively correlated to accumulation of shoot biomass ($R^2 = 0.97$). N uptake per unit of root biomass with access to N increased to meet shoot requirements. Removal of young tillers generated differences in accumulation of shoot biomass at flag leaf stage. In the high N treatment in Expt 2, the root:shoot ratio increased in both genotypes in response to tiller removal; the reduction in N uptake in the cultivar Janz was proportional to the reduction in shoot biomass whereas in the cultivar Wyalkatchem, the reduction in N uptake was less than the reduction in biomass. Under low N supply, differences in shoot biomass appeared to be the driver for the differences in the N-uptake rather than the differences in N-uptake generating differences in biomass, while in Expt 2 a poor correlation between shoot N uptake and shoot biomass was found under high N supply. This has implications for selection of genotypes for great N-uptake efficiency.

1. Introduction

Nitrogen (N) is one of the most expensive nutrients to supply to wheat crops and commercial fertilisers represent a major input-cost in wheat production (Fillery and McInnes, 1992; Garnett et al., 2009). However, wheat crops are inefficient users of the N that is available in the soil profile at planting as well as of the N applied as fertiliser (Fillery and McInnes, 1992). The agronomic N-use efficiency of wheat comprises both the uptake efficiency and the utilisation efficiency and the process of uptake is the foundation on which the total agronomic efficiency is built (Dhugga and Waines, 1989; Tong et al., 1999). An average of 30% to 50% of the N applied as fertiliser is actually taken up by wheat (Garnett et al., 2009), although in some cases N uptake efficiency in wheat could be much higher (e.g. Le Gouis et al., 2000). The remainder of applied N are lost to surface run-off, leaching of nitrates, ammonia (NH_3) volatilisation or bacterial competition (Garnett et al., 2009). Not only does this represent a major cost to the producer, the N lost can have significant off-site environmental consequences. The ability of wheat to capture N from the soil depends on soil type, climate and genotype (Halvorson and Wienhold, 2001). Efficient capture of N depends on the synchronisation of the availability of NO_3^- in the soil profile and the NO_3^- demand by the wheat crop; this is a particular issue in coarse textured soils and where rainfall early in the growth cycle is intense (Anderson et al., 1998; Liao et al., 2004).

Previous studies showed a curvilinear relationship between grain yield and plant N accumulation ranging from 50 to 300 kg N ha^{-1} in maize (Wortmann et al., 2011), between biomass yield and the N supply with the optimum at 30 kg N ha^{-1} in water

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http://dx.doi.org/10.1016/j.fcr.2014.04.009
0378-4290/

spinach (Luyen and Preston, 2004), annual dry matter production and the amount of N fertiliser applied in paspalum-white clover pasture (Roufail, 1978). In those studies, biomass/yield increased linearly with increasing N availability then after a certain level of N availability, there is no further increase when more N is available. Wheat N uptake has been found strongly correlated to shoot biomass (Rodgers and Barneix, 1988; An et al., 2006). Thus, increased early vigour of wheat genotypes has been postulated as a method to increase uptake efficiency in wheat (Liao et al., 2004). The faster above-ground growth is often associated with a faster accumulation of root biomass, root length and surface area; traits which could be expected to enhance the capacity of wheat to capture soil NO_3^- before it is leached, whether through a capacity to explore deeper soil layers or greater root length density (Anderson et al., 1998; Liao et al., 2004). The close coordination between shoot growth, root growth and N-uptake across genotypes makes it difficult to distinguish the underlying cause of the variation that drives the correlation. This will be important for identifying appropriate selection strategies for ongoing efforts to develop more N-efficient wheat genotypes. In this study we use manipulative treatments to investigate whether the shoot requirement or the ability to capture nitrogen by the root system is the more important factor in driving the level of N uptake by wheat genotypes that differ in vigorous growth rate.

Two glasshouse experiments were conducted using three wheat genotypes differing in vigour and N uptake, and in tillering and shoot biomass (Liao et al., 2004; Liao et al., 2006). In Expt 1, access by the root system to the available N was manipulated by growing the plants in split pots in which the root system was divided in the vertical plane (Brouder and Cassman, 1994; de Jong van Lier et al., 2009). In Expt 2, plants were grown in non-split pots and the accumulation of biomass was manipulated by surgically removing the primordia of tillers.

2. Materials and methods

2.1. Experiment 1

Wheat (*Triticum aestivum* L.) cv. Janz, a commercial cultivar widely adapted to Western Australia, and the vigorous growth wheat line, Vigor18 selected by Drs R. Richards and G. Rebetzke at CSIRO Plant Industry for greater vigour and plant height (Rebetzke and Richards, 1999; Richards and Lukacs, 2002) were grown in split pots designed to allow the root system of an individual plant to be partitioned between two equally sized compartments. One compartment was supplied with high nitrogen (+N) and the other had low nitrogen (−N). The pots were constructed from polyvinyl chloride (PVC) and were 0.40 m high and 0.15 m in diameter. The pots were divided with a vertical PVC partition (0.02 mm width) down the centre. The joins were sealed with water proof tape and silicone sealant so that the compartments were hydraulically isolated (Fig. 1a). Each compartment had drainage holes. The pots were filled to 0.35 m with sand that had been washed and passed through a 2-mm sieve. The pots were packed to a bulk density of approximately 1.53 g cm^{-3}.

Seeds of the two wheat genotypes were germinated in the dark on wet filter paper in Petri dishes for 4 days. Germinated seeds were then transplanted on 5 May 2012. One seed of the appropriate genotype with seminal roots of 0.03 m long was placed in a 0.02 m-long flexible plastic gutter fixed in a furrow on the top of the central partition (Fig. 1b). The seminal roots were then carefully diverted into the two compartments and the seeds covered with aluminium foil to prevent dehydration. The foil was removed once the plumule was exserted and the roots established in the soil. The number of new roots exserted was checked every second day. New roots were carefully diverted to the appropriate compartment and covered with wet soil until no new roots were being produced. The number of roots partition to each compartment reflected the treatment as explained below. Compartment 1 was the root section which was always supplied with nitrogen, while Compartment 2 was the root section either supplied or not supplied with nitrogen.

Immediately after transplanting, the pots of each genotype were randomly allocated to one of three treatments. In the first treatment, the root system of the plant was partitioned equally between Compartments 1 and 2, targeting 50% of the roots in each compartment. A nutrient solution with the equivalent of 50 kg N ha^{-1} was equally applied to each compartment (Control; 100% N). In the second treatment, the root system of each plant was again partitioned equally between Compartments 1 and 2 but nutrient solution with the equivalent of 50 kg N ha^{-1} was applied to one compartment only. The other compartment received nutrient solution without N (50% N). In the third treatment, the root system was partitioned in such a way as to target 30% of the roots in Compartment 1 and 70% into Compartment 2. The nutrient solution with the equivalent of 50 kg N ha^{-1} was applied to the compartment with 30% of the roots while the compartment with 70% of the roots received a nutrient solution without N (30% N). No addition of extra N in Compartment 2 in 50% N and 30% N treatments caused very low N availability in Compartment 2, which was for the purpose of studying enhanced nitrate uptake capacity per unit root in Compartment 1.

Each compartment of each pot received 100 ml of the appropriate nutrient solution (+N or −N) twice a week. The +N and −N solutions were modified from Liao et al. (2004). The −N solution contained 2 mM KH_2PO_4, 2 mM $MgSO_4$, 3.5 mM K_2SO_4, 3.5 mM $CaCl_2$, 3 mM KCl, 0.35 mM FeNa-EDTA, 3.5 mM MES and micronutrients. The +N solution in addition contained 3 mM Ca $(NO_3)_2$ and 3 mM KNO_3. Each compartment was watered every other day by hand to maintain the sand close to field capacity and to avoid drainage of excess water and nutrients. No drainage of water at the bottom of pots was observed. The plants were grown in a naturally lit, temperature-controlled glasshouse in Perth, WA, with day/night temperatures of 20/10 °C, and natural photoperiod (about 12 h).

The experiment was a two factorial (genotype × root partitioning treatment) with five replicates per treatment, giving a total of 30 pots. The pots were arranged in a completely randomised design.

Shoot and root biomass were measured 35 days after transplanting when plants were at stem elongation (Z31; Zadoks growth scale for cereals) (Zadoks et al., 1974). The plants were harvested by cutting the shoots from the roots at the crown and the leaf area was measured using a LI 3100 area meter (Licor, Inc., Lincoln NE, USA) before being dried at 70 °C for 48 h and weighed. Immediately after the shoots were harvested, the roots in each compartment were recovered from the soil by washing and sieving at 1.4 mm to produce a clean sample. Cleaned root samples were dried and weighed.

Total N in the above-ground plant material was determined using a VG-Micromass Sira 10 (V-G Isogas Ltd., Middlewich, England) connected to a Europa Roboprep C-N Analyzer (Europa Scientific Ltd., Crewe, England) after plant tissue was ground to a fine powder using a ball mill.

Statistical analyses were performed using Genstat version 15.2 (Lawes Agricultural Trust, Rothamsted Experimental Station, UK, 2012). Data for growth and other parameters were analysed using general analysis of variance (ANOVA). Significant differences between the treatments were accepted at $P = 0.05$.

2.2. Experiment 2

In Expt 2, the influence of shoot biomass accumulation on N uptake was explored using two commercial cultivars and artificial manipulating of tiller number. The cultivar Janz, is widely

Please cite this article in press as: Kamiji, Y., et al., Shoot biomass in wheat is the driver for nitrogen uptake under low nitrogen supply, but not under high nitrogen supply. Field Crops Res. (2014), http://dx.doi.org/10.1016/j.fcr.2014.04.009