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Soil water availability and plant competition affect the yield of spring wheat

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ABSTRACT

This study was conducted to determine the effect of both inter-cultivar and intra-cultivar competition on the growth of three spring wheat (*Triticum aestivum* L.) cultivars released in different periods that had different root:shoot ratios, differed in water extraction from dry soil, and differed in height. Two water regimes were imposed to compare competitive effects under irrigated and rainfed conditions. Our main hypotheses were that the different distribution of biomass between shoot and root in old and new wheat cultivars will alter their competitive ability, that differences in root size will alter their competitive ability through different water uptake patterns, and differences in the gradient for water uptake will alter their competitive ability in different environments by enabling water extraction from drier soil.

In monoculture, the recent cultivars had significantly more grain yield and higher water use efficiency for grain (WUE_G) than the old cultivar. Under the two water regimes the old cultivar had more root biomass, and extracted water in deeper soil layers, whereas the modern cultivars extracted more water in dry soil layers. The old cultivar benefited from inter-cultivar competition in terms of both grain yield and above-ground biomass accumulation at the expense of the modern cultivars, which showed significantly reduced growth in mixtures compared to in monoculture. Our study suggested that the below-ground competitive ability of cultivars may have a negative relationship with the grain yield and WUE_G in monoculture. The yield superiority of modern and recent cultivars was mostly due to increased above-ground biomass, kernel number and WUE_G and a smaller proportion of root biomass. Our results demonstrate that inter-plant competition is an important factor affecting spring wheat productivity in contrasting environments, but the extent and intensity of these effects depend on the adaptation of root traits to available soil water. Reducing root growth redundancy and enhancing the ability to deplete more soil water are clearly adaptive features for wheat for water-limited conditions.

1. Introduction

Rainfed crops grown in semiarid regions experience unpredictable water deficits during their life cycle. Lack of available water is the main factor limiting wheat yields in the semiarid regions of China (Deng et al., 2006). In water-limited environments, the most competitive individuals are likely to gain a disproportionate share of the water in the soil, but partitioning of limited assimilates to the roots to improve water capture requires a reduction in reproductive partitioning to grain. This competitive asymmetry may lead to excessive growth of some resource-foraging organs to such an extent that not only grain production but also total crop production may be lowered (Zhang et al., 1999). Annual plants competing for nutrients can produce an excess of roots and engage in a 'tragedy of the commons' (Hardin, 1968; Gersani et al., 2001). In wheat grown primarily for its grain yield, the competition for water in a water-limited environment needs to be balanced by apportioning assimilates to the grain. According to Donald (1968), an important way to increase yield potential in annual grain crops would be to develop a 'communal' ideotype that minimizes growth redundancy. Known as the game-theory model of root allocation (Gersani et al., 2001; Maina et al., 2002; Laird and Aarssen, 2005), plants competing for a common pool of soil-based resources produce an excess of roots at the expense of above-ground biomass. While growth redundancy is adaptive in a competitive situation, it is detrimental to the performance of a crop population.

The ability of a plant to change its root distribution to exploit deeper stores of soil water may be an important mechanism to avoid drought stress and enhance competitive ability (Lucas et al., 2000; King et al., 2003). However, a large root:shoot ratio might be more

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appropriate for a wild plant than a cultivated one and drought resistance might be improved by decreasing the size of the root system (Passioura, 1983). The root:shoot ratio can potentially be reduced in a cultivated plant because the role of a large root system in taking up water might be counterbalanced by a decreased reproductive allocation (harvest index). The role of root size and its influence on competitive ability may be tested by comparing cultivars having different root traits under adequately watered and water-limited conditions.

Previous studies in pots have shown that an old landrace grown in China in the 1940s–1970s, Heshangtou, had a lower water use efficiency and a lower root efficiency (total biomass per root biomass) than a recent cultivar, Gaoyuan 602, grown in the 1970s–1990s, and a modern cultivar, Longchun 8275, popular in China since the late 1990s (Fan et al., 2008). Moreover, the modern cultivars were able to extract more water from dry soil than the old landrace, presumably because of greater osmotic adjustment (Xiong et al., 2006; Fan et al., 2008). We therefore used these three cultivars of wheat to determine the role of root traits on the competitive ability in the field under water-adequate and water-limited conditions, recognizing that the root traits required for high yield in the field may be different from those observed in pot studies. Height is also considered an important characteristic in inter-plant competition so the two modern cultivars were chosen as they differed in height. In the present study, field trails were conducted in consecutive years under rainfed and irrigated conditions. The three cultivars were grown in monocultures and in binary and ternary mixtures to determine the performance on the cultivars with inter-cultivar and intra-cultivar competition. The hypotheses we tested were that (i) the different distribution of biomass between shoot and root in old and new wheat cultivars will alter their competitive ability, (ii) differences in root size will alter their competitive ability through different water uptake patterns, and (iii) differences in the gradient for water uptake will alter their competitive ability in different environments by enabling water extraction from drier soil. Root and shoot biomass and water extraction were measured to monitor cultivar interactions and analyze the competitive mechanisms determining the growth and yield over time.

2. Materials and methods

2.1. Site description

Field experiments were conducted in two consecutive years: 27 March–21 July 2005 (Year 1) and 19 March–13 July 2006 (Year 2) at the Yuzhong Experimental Station of Lanzhou University (104°09′E, 35°57′N, 1749 m altitude) on the Loess Plateau of north-west China. Representative of the rainfed farming in the region, spring wheat is grown from March to July with tillering to heading occurring from the end of April to May. The area to be planted was cultivated before sowing to produce a fine seedbed and 128 kg N, 120 kg P and 15 kg K ha^{-1} was applied before planting. The soil at the site is an orthic entisol of yellow earth (Gong, 1999) with a bulk density of 1.27 g cm^{-3}, a field capacity of 26.7% (by weight), and permanent wilting percentage of 9.3%. Meteorological data were obtained from a standard weather station located about 200 m from the experimental site.

2.2. Plant materials

Competitive interactions were studied using three hexaploid spring wheat (*Triticum aestivum* L.) cultivars developed for the semiarid dryland agricultural area of the Loess Plateau: seeds of cvs. Heshangtou (HST), Gaoyuan 602 (GY602) and Longchun 8275 (LC8275) were obtained from the Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Science, Beijing, China. HST is an “old” landrace popular in the 1940s–1970s, Gaoyuan 602 is a “recent” cultivar grown from 1970s–2000, and Longchun 8275 is a “modern” cultivar grown from the late 1990s onwards. All the cultivars were among the most successful releases of their respective eras, based on the area cropped and length of the period of cultivation in the region. HST is a typical long-stemmed and awnless cultivar. GY602 was produced by crossing the semi-dwarf cv. Gaoyuan 182 with the long-stemmed genotype 3987-88(3); GY602 plants were 15–20 cm shorter than the other two long-stemmed cultivars. LC8275 is a long-stemmed cultivar similar to HST except that it has awns. These three cultivars have similar phenologies and are easy to distinguish from each other.

2.3. Experimental design

The field experiment was a split-plot randomized complete block design. Main plots were the different water regimes, and there were three subplots: (i) each cultivar grown in a pure stand, (ii) binary cultivar-mixtures in the ratio 1:1, and (iii) ternary cultivar-mixtures in the ratio 1:1:1. The competition treatment was the simplest form of replacement series design (de Wit, 1960). The planting arrangements are shown in Fig. 1. Seeds were sown individually by hand to a depth of approximately 5 cm in rows 4 cm apart and 2 m long. The space between the rows was 16 cm in plots with 2 rows of seeds and 22 cm in plots where all three cultivars were planted in each row, and 4 cm between plants within rows, giving a density of 267 seeds m^{-2} in both pure stands and mixtures. To distinguish the cultivars in the mixtures, nylon strings were laid on the ground between the cultivars in each row at sowing time. Each treatment was replicated three times giving a total of 42 plots. The plots were 4 m long and 2 m wide, with 21 rows per plot. Half of each plot was used for measuring the yield at maturity and the rest for destructive plant samples at five times during growth. The water regimes were: (1) irrigation (IR) with 35 mm irrigation applied at early tillering, heading, flowering and during grain filling (see Fig. 2) by flood irrigation using a flow meter to measure the irrigation applied; (2) rainfed (RF) where no water other than rainfall was added. Fungicides and insecticides were sprayed as required to prevent disease and insect damage, and weeds were removed by hand.

2.4. Plant sampling

Ten adjacent plants of each species were cut off at ground level from each plot at 11, 34, 49, 70 and 89 days after sowing (DAS), starting from a randomly selected end of each plot. Within each plot, the two outside rows were left intact and two rows were left between sampling dates. All sampled material from each plot was weighed after drying in an oven at 70 °C to constant weight. At full maturity all the plant material was sampled from 1 m^2 per plot and each cultivar separated from the mixture. Height, fertile tillers and number of grains per head were measured on 25 plants of each cultivar for each plot. Biomass and grain weight at maturity was determined after air drying the samples in the sun for 1 month and thousand kernel weight (TKW) and harvest index (HI) were determined for each species. HI is the ratio of harvested grain yield to total above-ground biomass.

Root distribution for each treatment was measured at 20-cm depth intervals to a depth of 140 cm at maturity. A tube 9 cm in diameter and 1.6 m long was used to take cores from within and between the crop rows at two locations within each replicate plot and the samples in each 20-cm layer combined. Roots were washed free of soil using a 0.4-mm screen. Soil debris was separated from roots using tweezers, and the weight of the roots after oven drying at 70 °C to constant weight was recorded.