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Evidences for the association between carbon isotope discrimination and grain yield—Ash content and stem carbohydrate in spring wheat grown in Ningxia (Northwest China)

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ABSTRACT

Carbon isotope discrimination (Δ) has been repeatedly reported to positively correlate with grain yield in wheat grown under post-anthesis stress environments. Several hypotheses have been put forward to explain this association. However, there is few reported direct evidence clarified the relationship between Δ and grain yield, which is the objective of the present work. The relationships between Δ and grain yield (GY), harvest index (HI), ash content (m_a), specific stem dry weight (SSDW) and carbohydrate in stem, were studied in a collection of 20 bread wheat cultivars (landraces, released cultivars and advanced lines) in Yinchuan of the Ningxia region (Northwest of China) in three successive years (2006, 2007 and 2008). Relationships between GY, HI, stem specific dry weight, accumulation and mobilization of stem reserved carbohydrate and Δ were analyzed. The effects of year, sampling time and genotypes on measured traits were significant. Positive correlations between grain yield and Δ were noted in 2007 and 2008 when stress occurred after anthesis, but not in 2006 when soil water condition was nearly optimal. Significant and positive correlations among m_aL_m, grain Δ and harvest index were found. Stem water-soluble carbohydrate content (SWSCC) and specific dry weight 7 days after anthesis was positively associated with Δ. Remobilization efficiency of stem water-soluble carbohydrate and total carbohydrate (the sum of water-soluble carbohydrate and starch) was also found to be significantly and positively correlated to Δ. There were negative relationships between ΔG_m, ΔS_m, and SSDW at maturity. In conclusion, Δ may predict yield when irrigation does not meet crop's water requirement and wheat experiences a slight water stress after anthesis in central region of Ningxia. Δ or m_aL_m is related to the efficiency of carbon partitioning to the grain. Basal mature stem Δ seems to be an integrated character reflecting both early carbohydrate assimilation and dry matter remobilization to grain during grain-filling.

1. Introduction

Ningxia Hui autonomous region is located on the loess Plateau of Northwest China, between 104.17°E and 107.38°E and 35.14°N and 39.23°N and its total area is 60,400 km^2. In the northern part of the Province, spring wheat is cultivated from March to July and is irrigated with Yellow River water, through well established irrigation systems [1]. Because of the recent decrease in Yellow river water flow [2], irrigation is restricted and inadequate during the late growth cycle. In addition, the temperature dramatically goes up during the grain-filling period imposing a post-anthesis stress on spring wheat [3].

Carbon isotope discrimination (Δ) has been proposed by several authors as an indirect selection criterion for wheat grain yield under drought [4–6]. Although reported correlations under drought conditions vary, the relationship between Δ and grain yield is significantly positive and stable under terminal (post-anthesis) drought stress environments [3,5,7–9] and high-Δ genotypes, maintaining higher stomatal conductance, perform better than low-Δ genotypes [5,10,11]. Under other drought stress scenarios, however, the relationship between grain Δ and yield

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Abbreviations: Δ, carbon isotope discrimination; C_i/C_a, ration of internal leaf CO_2 concentration; *gs*, stomatal conductance; ΔL_a, carbon isotope discrimination of flag leaf at anthesis stage; ΔG_m, carbon isotope discrimination of grain at maturity stage; m_aL_m, ash content of flag leaf at maturity stage; m_aG_m, ash content of grain at maturity stage; WSC, water-soluble carbohydrate; SSDW, stem specific dry weight.

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highly varies with rainfall amount and distribution and with the quantity of water stored in the soil at sowing. A wide variation of this relationship was found across years under early (pre-anthesis) water stress [3,9] and residual soil moisture conditions [12].

Because of the high cost for Δ analysis, the identification of surrogates remains an important objective. Ash mineral content (m_a) has been proposed as a promising alternative selection criterion for Δ [13]. Association was reported between Δ and ash content of leaf and grain of different C_3 species. Positive associations between leaf Δ and leaf m_a, and negative associations between grain Δ and grain m_a were found in cereals [8,13–15].

A positive correlation between harvest index (HI) and Δ has been reported by many authors [16], enhancing the value of Δ in breeding program. These authors hypothesized that lower transpiration efficiency (TE), the ratio of dry matter produced to water transpired, may result in higher dry matter partitioning to grain. However, this was based just on the observation of field trial and speculation. There is scarce of reported concrete evidence underlying the association between HI and Δ. It is relevant to explore the relationship between stem carbohydrate, including starch and water-soluble carbohydrate (WSC), measured at different phases after anthesis, and carbon isotope discrimination of different organs on a set of genotypes with contrasting genetic background.

Since the carbon isotope discrimination occurs not only in the carbon assimilation but also in other metabolic events following assimilation [17], the isotopic signal has been used as "natural tracer" for studying the refixation of CO_2, while Gebbing and Schnyder used tank CO_2 for labeling the photo-assimilates and thus the substrates and respired CO_2 [18]. Badeck et al. showed using a huge number of published data that the leaves are in general ^{13}C depleted compared with other organs, indicating post-photosynthetic fractionation that further modifies the isotopic signatures of individual plant organs and consequently leads to consistent differences in $\delta^{13}C$ between plant organs [17]. The main causes of this ^{13}C depletion in leaves have been deeply discussed in many documents, e.g. (i) discrimination during assimilate exportation well studied by some authors who show that a fractionation could occur during assimilate export, or the products exported could themselves be ^{13}C-enriched compared with the source organic matter during phloem loading implying a spatial or biochemical compartmentalization occurred prior to the export, which contributes to the relative ^{13}C depletion of autotrophic organs compared with other plant parts [19–22], and (ii) respiratory metabolism (thus respiratory discrimination) differing between organs which could lead to isotopic difference between autotrophic and heterotrophic organs. Recent work done on dark respiration of C_3 leaves has demonstrated that the CO_2 released is significantly ^{13}C-enriched (between 2‰ and 6‰) compared with sucrose, the putative substrate [17,19,23,24]. To the contrary, the released root-respired CO_2 is ^{13}C depleted compared with total soluble sugars. Thus, the well-known – yet poorly explained – relative ^{13}C depletion of autotrophic organs compared with heterotrophic organs may be explained by the strong negative respiratory fractionation in the former and slightly positive respiratory fractionation in the latter where ^{13}C-depleted carbon relative to organic matter is lost through respiration [19], (iii) different fractions of plant tissue were reported to have different isotopic signature and the whole plant tissue was reported to be depleted in ^{13}C relative to starch, sucrose pools or water-soluble carbohydrate [25–27].

Stem stored water-soluble carbohydrates may act as a buffer to maintain a steady rate of grain-filling. Under stress condition, photosynthetic activity is depressed by drought or after anthesis, the stem plays a major role in partitioning assimilates to compensate for sink demand and mobilized stem reserves may represent 22–60% of the dry matter that accumulates in the grain [28–30]. The contribution of stem mobilized dry matter in upper and lower internodes to grain-filling was reported to be different. Ehdaie et al. reported that the maximum amount of WSC was accumulated in the lower internodes where stored WSC was mobilized faster than those in the upper internodes [31], highlighting the key role of lower internodes in carbohydrate store and the grain-filling.

Considering phloem loading or assimilate transport affecting the isotopic signal in involved organs, a hypothesis can be deduced as that the varieties with high efficiency in partitioning C stored in stem to grain would load more ^{13}C-enriched water-soluble carbohydrate to phleom and resulting in negative isotopic fractionation in the stem, namely, the stem $\Delta^{13}C$ would turn to be higher (reversely, lower $\delta^{13}C$, reciprocal of $\Delta^{13}C$). Besides, difference in carbon assimilation efficiency at early stage when stress is not serious and varied contribution of pre-anthesis photosynthate to grain-filling would also exert influence on grain and stem carbon isotope composition. In post-anthesis water stress conditions, the higher Δ values characterize genotypes high dependence on the remobilization of pre-anthesis reserves for grain-filling [4], with pre-anthesis assimilate being accumulated during periods of reduced stress and having consequently higher Δ values [5]. Based on the analysis and speculation above, we hypothesized that the genotypic variation in the carbohydrate translocation and accumulation efficiencies would lead to the variation in the stem carbon isotope composition ($\delta^{13}C$), with high stem Δ genotypes being more efficient in assimilating carbohydrate at early stage and partitioning carbon from stem to grain at later growth cycle. This may be the physiological basis underlying the positive association between Δ and yield in post-anthesis stress conditions.

The objective of the present study was (i) to analyze the relationship between Δ, harvest index and yield; (ii) to confirm the association between Δ and ash content; and (iii) to determine the change in specific stem dry weight (SSDW) and the content of water-soluble carbohydrate, starch and total carbohydrate in stem at different stages, accumulation and remobilization efficiencies of the three kinds of carbohydrates and their correlations with yield and Δ of different organs in spring wheat grown in Ningxia limited irrigation region, Northwest China.

2. Materials and methods

2.1. Plant material

Twenty bread wheat (*Triticum aestivum* L.) genotypes including landraces, elite improved varieties and advanced lines were used in the experiments (Table 1). They were selected for their contrasting adaptation to different water regimes, based on multi-location and multi-year evaluations carried out by the Ningxia Academy of Agricultural and Forestry Sciences (Yinchuan, Ningxia) and the Guyuan Institute of Agricultural Science (Guyuan, Ningxia). For example, Ningchun 4 developed from crosses involving the CIMMYT variety Sonora has a broad adaptation and was the leading cultivar in the Northern (Zone VII) and Northwestern part (Zone VIII) of the country from 1983 to present. Its annual sowing acreage reached 330,000 ha mostly in Ningxia, Gansu, and Inner Mongolia. The cultivars Yong 3119 and Ningchun 32 are very productive under well-watered conditions, while Ningchun 27 performs well under rain-fed condition. Hongmangmai and Maohuomai are old local varieties which have early vigor and yield well under rain-fed condition. 98H30, bred by anther culture, is a salt tolerant advanced line. The twenty genotypes did not highly differ in phenology (a mean range of 9.7 and 8.3 days for heading and maturity date, respectively), but differed for morphological traits such as plant height and harvest index.