Nitrogen Vertical Distribution Differed in Foliar and Nonfoliar Organs of Dryland Wheat during Grain Filling

Wei Chen, Linlin Wang, Kadambot H.M. Siddique, Xiping Deng,* and Yinglong Chen*

ABSTRACT

The role of N remobilization in nonfoliar and foliar organs influences the N vertical distribution and accumulation of N in grain. We hypothesized that the N concentrations in foliar and nonfoliar organs affect the remobilization, vertical distribution, and accumulation on N in grain. A 2-yr field experiment was conducted to evaluate the effects of N input and mulching practice on N remobilization and N vertical distribution in the canopy of winter wheat (Triticum aestivum L.). The results showed that foliar organs had higher N concentration than nonfoliar organs in all treatments. Among the nonfoliar organs, the flag leaf sheath had the highest N concentration, followed by glumes and rachillae combination, while the stem had the lowest N concentration at anthesis and maturity. In the different internode segments of the stem, N concentrations decreased with grain filling, except for the exposed part of the peduncle. There was a top-to-down decline in N concentration within the canopy. Foliar organs contributed the most N to grain followed by the stem and the glumes and rachillae combination. The N286 treatment significantly improved N accumulation, remobilization, and vertical distribution in the canopy and N content in grain. Nitrogen concentration in the grain was positively correlated with the difference in N concentrations between apical and basal vegetative modules.

Core Ideas
• There was a positive correlation between nitrogen concentration in grain and between Layer 1 and Layer 4 (Gtotal).
• The nonfoliar organs were involved in to determine the nitrogen vertical distribution in winter wheat canopy.
• The nitrogen contributions of various organs to grain nitrogen were determined.
as spikes, stem, and flag leaf sheath, play a vital role during grain filling in N accumulation and remobilization (Sanchez-Bragado et al., 2014). Nitrogen remobilization is often accompanied by senescence, which is associated with reduced protein and chlorophyll contents, and leaf yellowing (Schiltz et al., 2004). High nutrient mobilization efficiency is an intrinsic feature of plant senescence (Gregersen et al., 2008). Early senescence can remobilize more N from leaves to grain, but this remobilization impairs photosynthesis. Late senescence can prolong photosynthesis, which reduces N remobilization such that more N remains in leaves (Yang et al., 2001). Similar to the foliar organs senescence, the senescence of nonfoliar organs (leaf yellowing) also accompanies the remobilization of N (Sanchez-Bragado et al., 2014). However, the process of senescence in nonfoliar organs occurs later than that of foliar organs, which ensures the transport of a large amount of N compounds to grains during the later stage of grain filling (Lopes et al., 2006). Nonfoliar organs play important roles in photosynthesis and N remobilization (Kichey et al., 2007) and in determining final grain yield and grain N content (Aschan and Pfanz, 2003). Furthermore, nonfoliar organs may have photosynthetic advantages, particularly when plants encounter edaphic stress (Hu et al., 2012). A substantial amount of N from the soil and fertilizer by root acquisition is allocated to nonfoliar organs (e.g., stem, spike and sheath), which contributes to crop photosynthesis, particularly during the reproductive period (Bertheloot et al., 2012).

The second possibility is to improve the vertical distribution of N among leaves to increase crop productivity (Bertheloot et al., 2008). Leaf N vertical distribution in the plant canopy is non-uniform, with the lower shaded leaves generally having less N content than the upper illuminated leaves (Li et al., 2013a). The non-uniformity of N distribution in canopy is considered as an important adaptive response for efficient use of N (Bertheloot et al., 2012). When compared with uniform N vertical distribution, non-uniform N vertical distribution significantly improves canopy photosynthesis (Hirose, 2005; Li et al., 2013a) and increases daily carbon assimilation (Gastal and Lemaire, 2002).

Many agronomic practices, such as fertilization (Zhang et al., 2017), mulching (Liang et al., 2014), and irrigation (Hao et al., 2011) influence N metabolism (Diekmann and Fischbeck, 2005) and vertical distribution within a leaf canopy (Wang et al., 2005). Nitrogen vertical distribution determines the carbon gain of the canopy by influencing photosynthesis (Hikosaka, 2014). Many researchers have focused on the vertical distribution of N in leaves (Hao et al., 2011; Hikosaka, 2014; Muryono et al., 2017; Wang et al., 2005); however, there is relatively little knowledge of vertical distribution of N in nonfoliar organs. It is important to illustrate the contribution of nonfoliar organs to N deposition and calculate the vertical distribution of N involving nonfoliar organs in the wheat canopy. This study examined the influence of different N inputs and mulching practices on the dynamic change of N concentration in the winter wheat canopy during grain filling on the Loess Plateau. The aim of the study was to determine (i) the contribution of various vegetative organs to grain N; (ii) the vertical distribution of N in the wheat canopy involving foliar (three upper fully-expanded leaves) and nonfoliar organs such as the flag leaf sheath (FLS), glumes combined with rachiallae (G+R), and different internode segments; (iii) the correlation between N concentration in grain and that in different canopy organs; and (iv) the yield of winter wheat under different N inputs and mulching practices.

**MATERIAL AND METHODS**

**Site Description**

The field research was conducted at the Changwu Research Station of Agriculture and Ecology on the Loess Plateau of China (35.28° N, 107.88° E; ~1200 m elevation) during the 2011–2012 and 2012–2013 growing seasons. The site is located in a warm temperate zone with a continental monsoon climate and long-term average rainfall of 570 mm (1984–2010), with more than half falling from July to September. In the first season (2011–2012), total precipitation was 667 mm, of which 190 mm occurred during the summer fallow, and 477 mm occurred during the wheat growing period. In the second season (2012–2013), total precipitation was 422 mm, of which 188 mm occurred during the summer fallow, and 234 mm occurred during the wheat growing period (Fig. 1).

The soils at the site are Cumuli-Ustic Isohumosols (Gong et al., 2007) with a bulk density of 1.36 g cm$^{-3}$ and field capacity of 26% (determined gravimetrically). The top 20 cm of the soil contained 11.8 g kg$^{-1}$ organic matter, 0.87 g kg$^{-1}$ total N, 14.4 mg kg$^{-1}$ available P, 144.6 mg kg$^{-1}$ available K, and 3.15 mg kg$^{-1}$ inorganic N. Soil samples were collected pre-sowing in the 2011–2012 growing season.

**Experimental Design**

A widely planted winter wheat cultivar Changhan58 (released in 2004) was grown under different N inputs and mulching practices (N applied as urea unless otherwise stated):  
1. N195: 120 kg ha$^{-1}$ as basal fertilizer with an additional 75 kg ha$^{-1}$ top-dressed at jointing; no mulching applied;  
2. N286: 120 kg ha$^{-1}$ and 4.5 t ha$^{-1}$ ox manure (equivalent to 91 kg ha$^{-1}$ N) as basal fertilizer with additional 75 kg ha$^{-1}$ top-dressed at jointing; wheat straw mulching applied during the summer fallow and removed at sowing; and  
3. N150: 150 kg ha$^{-1}$ as basal fertilizer; plastic film mulching applied during the summer fallow and removed at sowing.
All treatments received 120 kg ha\(^{-1}\) P\(_2\)O\(_5\) (single superphosphate) as basal fertilizer. The inorganic fertilizer and ox manure were mixed into the topsoil before sowing. The ox manure contained 362.1, 20.3, 8.5, and 18.2 g kg\(^{-1}\) of total C, N, K, and P, respectively. Both the wheat straw and plastic film mulch were removed at sowing. The application of pre-sowing mulching can increase soil water content, owing to the uneven precipitation distribution in this region, and ox manure can help to increase soil nutrients. We used split N fertilizations to improve grain yield in this region.

Each treatment had four replicate plots arranged in a randomized complete block design. The plot size was 24 × 6 m, with row spacing of 20 cm. Winter wheat (Changhan58) was manually sown on 26 Sept. 2011 and harvested on 2 July 2012 in the first season and sown on 19 Sept. 2012 and harvested on 26 June 2013 in the second season. Hand weeding was done throughout the growing period; no incidences of diseases or pests were found during the experiment.

In the Loess Plateau region of China, an annual crop rotation of winter wheat and spring maize (one crop per year) is standard practice in rainfed agriculture. Local winter wheat practices were followed: sowing in autumn (September) and harvesting in summer (June). The average N rate applied in this region fluctuates between 120 and 200 kg ha\(^{-1}\). Many management practices affect winter wheat yields and N mechanisms as well as environmental stresses in the field. In this study we combined different N inputs and mulching practices to develop an appropriate practice for winter wheat production in the area.

**Measurements**

To determine the N concentration in different organs of winter wheat during grain filling, plants were sampled from anthesis (Zadoks 60) to physiological maturity (Zadoks 90) (Zadoks et al., 1974). Plants flowering on the same day were tagged for sampling at 5-d intervals from anthesis to maturity. For each sampling, 20 culms from each plot were collected to determine N concentration. The culms were divided into foliar and nonfoliar organs. Foliar organs were divided into three types based on their position: FL, penultimate leaf (PL), and lower internode leaf (ERL). Nonfoliar organs were divided into stem, spike, and flag leaf sheath (FLS). Stems were divided into five segments from the apical to basal (Fig. 2); exposed part of the peduncle (EXP), enclosed part (by flag leaf sheath) of the peduncle (ENP), penultimate internode (PI), lower internode (ERI), and lowest internode (ESTI). All internode segments excluded the node. The spike was separated into grain, and the glume combined with rachillae (G+R). The N concentration was analyzed in each sample, except for FLS and G+R, which were only measured at anthesis and maturity. The dry weight of each segment was determined after drying in an air-forced oven at 75°C for 48 h to constant weight.

For yield and yield component determination, a selected area of 1 m\(^2\) was harvested in three replications per plot, avoiding edge rows to prevent edge effects. Spike number and grain number were counted manually. Grain weight and yield were determined.

**Determination of Nitrogen Concentrations in Plant Organs**

Dried samples were ground in a Wiley Mill through a 1-mm opening screen, and N concentrations were determined using the standard macro-Kjeldahl. (Nitrogen Analysis System, Foss, Kjeltec-2300, Höganäs, Switzerland). Briefly, the standard macro-Kjeldahl process involves digestion, distillation, and titration. The plant sample was dried in an air-forced oven to constant weight then passed a sieve. Acid digestion used concentrated sulfuric acid and catalyst mixture (potassium sulfate + copper sulfate + selenium) at 380°C for 45 min followed by alkali distillation and a final titration with 0.1M sulfuric acid.

**Determination of Nitrogen Remobilization**

The following parameters were calculated to evaluate N remobilization (Xu et al., 2005):

1. Nitrogen accumulation amount (NAA) = N concentration of specific organ × dry weight of specific organ;
2. Nitrogen remobilization amount (NRA) = N accumulation amount of specific vegetative organ at anthesis– N accumulation amount of specific vegetative organ at maturity;
Table 1. Grain yield and yield components of winter wheat under different N inputs and mulching practices in two continuous growing seasons (2011–2012 and 2012–2013).

<table>
<thead>
<tr>
<th>Growing season</th>
<th>Treatment†</th>
<th>Grain yield mg seed−1</th>
<th>Grain weight mg seed−1</th>
<th>Grain no. per spike</th>
<th>Spike no. m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011–2012</td>
<td>N195</td>
<td>10.17b‡</td>
<td>11.2a</td>
<td>8.7b</td>
<td>101b</td>
</tr>
<tr>
<td></td>
<td>N286</td>
<td>10.31a</td>
<td>13.1b</td>
<td>10a</td>
<td>154a</td>
</tr>
<tr>
<td></td>
<td>N150</td>
<td>10.23c</td>
<td>14.1c</td>
<td>12c</td>
<td>190b</td>
</tr>
<tr>
<td>2012–2013</td>
<td>N195</td>
<td>11.31d</td>
<td>14.9c</td>
<td>12b</td>
<td>143c</td>
</tr>
<tr>
<td></td>
<td>N286</td>
<td>11.41d</td>
<td>16.1b</td>
<td>12b</td>
<td>107b</td>
</tr>
<tr>
<td></td>
<td>N150</td>
<td>11.67c</td>
<td>17.6c</td>
<td>12b</td>
<td>101b</td>
</tr>
</tbody>
</table>

† N195, N286, and N150 denote the different N input in summer fallow with plastic mulching and straw mulching applied for N195 and N286, respectively. ‡ For each parameter, mean data with the same letter are not significantly different (P < 0.05).

3. Nitrogen remobilization efficiency (NRE) = (N remobilization amount of specific vegetative organ/N amount of specific vegetative organ at anthesis) × 100%; and

4. Nitrogen contribution to final grain N (NC) = (N remobilization amount of specific vegetative organ/N amount in grain at maturity) × 100%.

Definition of Nitrogen Concentration in Different Layers

The nonfoliar organs were used to calculate the N vertical gradient in the plant canopy, according to the method described by Wang et al. (2005) with some modifications. Different internode segments, leaves, and the FLS were combined to determine the vertical gradient of N in the whole plant, which was divided into four layers from apical to basal: Layer 1 comprised FL and EXP; Layer 2 comprised FLS and ENP; Layer 3 comprised PL and PI; and Layer 4 comprised ERL and ER1 (Fig. 2).

Determination of Vertical Gradients of Nitrogen

The N concentration in Gradient 1 (G1) was defined as the difference in N concentration between Layer 1 and Layer 2, Gradient 2 (G2) was the difference in N concentration between Layer 2 and Layer 3, Gradient 3 (G3) was the difference in N concentration between Layer 3 and Layer 4, and Gradient total (Gtotal) was the difference in N concentration between Layer 1 and Layer 4.

Data Analysis

The experimental data were analyzed using one-way analysis of variance (ANOVA) with significant differences between treatments determined using Duncan’s multiple range test using SPSS statistical software (SPSS 20.0; SPSS Inc., Chicago, IL). Pearson’s correlation was used to assess correlations between N concentration in the wheat canopy layers was observed, except for Layer 2. At anthesis, the N concentration in different layers was greater than that at maturity (Table 3).

RESULTS

Grain Yield and Yield Components

The 2011–2012 growing season produced an average grain yield of 8.21 t ha−1, which was 45% more than that in 2012–2013 (Table 1). Grain yield increased with increasing N supply in all treatments in both growing seasons. The N286 treatment had the highest grain yield and spike number in both growing seasons. The N195 treatment had the lowest grain weight in the first season, and the N150 treatment had the lowest in the second season.

Nitrogen Concentration in Foliar Organs and Internode Segments

There were clear leaf positional differences in N concentration of the three upper leaves between treatments (Fig. 3). Flag leaf had the highest N concentration, followed by PL and ERL (Fig. 3). Nitrogen concentrations in foliar organs (FL, PL, and ERL) varied between treatments, and decreased from anthesis to maturity (Fig. 3). Nitrogen concentration declined rapidly in PL and ERL from 20 to 25 d after anthesis (DAA), which may be due to remobilization of N from PL and ERL to FL (Fig. 3). Nitrogen concentrations in foliar and nonfoliar organs increased with increasing N input; N286 had the highest N concentrations, followed by N195 and N150. Nitrogen concentrations were higher in the 2012–2013 growing season than the 2011–2012 growing season for all samples (Fig. 3). Different internode segments had marked spatial differences in N concentration (Fig. 4 and 5). Different treatments resulted in different N concentrations in canopies during grain filling (Figs. 3–5). The N concentration in the internode decreased from the apical to basal segment. From anthesis to maturity, N concentrations in all internode segments decreased, except for EXP (Fig. 4). In the EXP segment, the N concentration peaked 10 DAA and then decreased with the development of grain filling.

Nitrogen Vertical Distribution in Wheat Canopy

Table 2 shows the effect of the treatments on N concentration in different canopy layers. The apical layer (Layer 1) had the highest N concentrations among four different layers, on the contrast, Layer 2 had the lowest N concentrations. There was no foliar organ in Layer 2 because this layer had the lowest N concentration. A top-down gradient tendency in N concentration in the wheat canopy layers was observed, except for Layer 2. At anthesis, the N concentration in different layers was greater than that at maturity (Table 3).

Differences in the N concentration in the various gradients revealed treatment differences in N remobilization during grain filling (Table 3). The average N gradient at anthesis was greater than that at maturity in all treatments (Table 3). At anthesis, G1 had the highest N concentration followed by Gtotal and G3 in all treatment. G2 had the lowest N concentration in both growing seasons. There was no clear trend between the gradients and N concentration at maturity. The N286 treatment produced the highest N concentration in G1, and Gtotal at anthesis and maturity in both growing seasons (Table 3). There was a significant correlation between Gtotal at anthesis and grain N ($R^2 = 0.682^*$) and Gtotal at maturity ($R^2 = 0.968^{**}$) (Fig. 6).
Nitrogen Contribution to Grain Nitrogen

On average, foliar organs contributed relatively more N to final grain N (33.4%) than the whole stem (24.9%) or G+R (23.0%) (Fig. 7A). In foliar organs, FL and PL contributed relatively more N to grains than ERL (Fig. 7B). Among the internode segments, PI contributed relatively more N to grains followed by ENP, and ESTI contributed the least (Fig. 7C). Among the foliar organs, PL contributed relatively more N to grain, followed by FL and ERL (Fig. 7). Different treatments affected the N metabolism in different organs (Table 4). In the N286 treatment, more N was remobilized from vegetative organs to grain, which contributed to the high N content in grain (Fig. 8). On average, ERL had the highest NRE, followed by FL and PL in the different foliar organs. In the internode segments, PI and ERI had the highest NRA, and ESTI and EXP had the lowest (Table 4).

Grain N content differed significantly between the two growing seasons (Fig. 8). On average, the 2011–2012 growing season produced more N in grain than the 2012–2013 growing season. The N286 treatment had the highest grain N content in both growing seasons while there were no significant differences between N195 and N150.

DISCUSSION

Nitrogen Concentration in Different Organs

Nitrogen concentrations differed between the various organs during grain filling (Fig. 3, 4, and 5). On average, foliar organs had higher N concentrations than nonfoliar organs. The flag leaf had the highest N concentration, followed by FLS and the stem, which agrees with an earlier study by Wang et al. (2005). Among different organs, which had the different position in the wheat plant, the apical organs had the highest N concentrations, such as FL and EXP, which indicated more N distributed in the apical organs than the basal ones. As the grains started to fill, the N concentration in foliar and nonfoliar organs decreased as N was remobilized to the grain, except for EXP, which peaked at 10 DAA. These results indicated that EXP has a specific role in N metabolism, such as the higher PEPCase activity and chlorophyll content (Kong et al., 2010) and being an autotrophic part (Gebbing, 2003), it is likely that the other organs transferred N to EXP to maintain photosynthetic function. The exposed part of the peduncle had the highest N concentration in the apical internode, in response to the local light environment and that N is contained predominantly in the assimilatory enzyme Rubisco. During grain filling, other internode segments
may have remobilized N to EXP, such that more N accumulated in the apical vegetative organs (Fig. 4). Plant N moves easily from aging (basal) to younger organs (apical). To use radiation more efficiently, N concentrations are usually higher in the upper than lower leaves (Dreccer et al., 2000).

**Vertical Gradients of Nitrogen Distribution in Winter Wheat Canopy**

Vertical gradients of leaf N concentration are a common feature in crop canopies (Connor et al., 1995) and can significantly influence crop growth and production (Dreccer et al., 2000). In this study, a non-uniform vertical N distribution in the plant canopy occurred for foliar organs, with lower N contents in the lower shaded leaves and higher N contents in the upper illuminated leaves (Fig. 3). This finding agrees with those of Li et al. (2013b). In this study, vertical gradients of N distribution in winter wheat canopy were found, when the N concentration in nonfoliar were consideration. Also, apical internode segment (EXP and ENP) had higher N concentrations than basal internode segments (PI and ERI) (Fig. 4 and 5); this is likely to make full use of higher CO2 concentrations and light radiation in apical organs (Zhang et al., 2011).

Higher N concentrations in apical foliar and nonfoliar organs than basal foliar and nonfoliar organs are needed to maximize total canopy photosynthesis (Hirose and Werger, 1987) and to accumulate more photosynthate (Adam et al., 2000; Briggs

![Graphs showing nitrogen concentration over time](image)

**Table 2. Effect of different N inputs and mulching practices on N concentration (g kg⁻¹) in canopy layers in dryland wheat in two continuous growing seasons (2011–2012 and 2012–2013);†**

<table>
<thead>
<tr>
<th>Canopy layer†‡</th>
<th>Layer 1</th>
<th>Layer 2</th>
<th>Layer 3</th>
<th>Layer 4</th>
<th>Layer 1</th>
<th>Layer 2</th>
<th>Layer 3</th>
<th>Layer 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>N195</td>
<td>6.67Bb</td>
<td>4.18Ca</td>
<td>5.65Bb</td>
<td>4.91Cb</td>
<td></td>
<td></td>
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<tr>
<td>N286</td>
<td>7.12Aa</td>
<td>3.78Db</td>
<td>5.86Ba</td>
<td>5.14Ba</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>N150</td>
<td>6.42Bc</td>
<td>4.32Ba</td>
<td>5.45Cc</td>
<td>4.62Dc</td>
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<tr>
<td>2011/2012</td>
<td>6.79Cb</td>
<td>4.56Aa</td>
<td>6.00Aa</td>
<td>5.12Cb</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>2012/2013</td>
<td>7.35Ac</td>
<td>4.18Cb</td>
<td>6.18Aa</td>
<td>5.33Aa</td>
<td></td>
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<td>2011/2012</td>
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<td>2.71Db</td>
<td>6.00Aa</td>
<td>5.12Cb</td>
<td></td>
<td></td>
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<tr>
<td>2012/2013</td>
<td>6.64Bb</td>
<td>2.97Da</td>
<td>6.18Aa</td>
<td>5.33Aa</td>
<td></td>
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</tbody>
</table>

† N195, N286 and N150 denote the different N input in summer fallow with plastic mulching and straw mulching applied for N195 and N286, respectively.
‡ Layer 1 comprised of FL and EXP; Layer 2 comprised of FLS and ENP; Layer 3 comprised of PL and PI; and Layer 4 comprised of ERL and ERI. FL, flag leaf; FLS, flag leaf sheath; PI, penultimate internode; ERL, lower internode leaf; EXP, exposed part of peduncle; ENP, enclosed part (by flag leaf sheath) of peduncle; PL, penultimate internode; ERI, lower internode; ESTI, lowest internode.
§ For each layer across growing seasons and growth periods, data followed by the same capital letter are not significantly different (P < 0.05). For each treatment (column), data followed by the same lowercase letter are not significantly different (P < 0.05).
and Aytenfisu, 1980). The internode segments are one of the nonfoliar organs, which also contribute N to final yield since they can photosynthesize (Kong et al., 2010). Similar to the FL with higher N concentrations than the lower leaf, the apical internode segments had higher N concentrations than lower internode segments. The distribution of N in leaf layers has been discussed elsewhere (Wang et al., 2005; 2006). However, the role of nonfoliar organs in determining N vertical distribution was unclear. This study has demonstrated the role of nonfoliar organs in determining the vertical distribution of N under different N inputs and mulching practices. With the increase of N input, N concentrations increased in both foliar organs (Fig. 3) and nonfoliar organs (Fig. 4 and 5). Among the three treatments, N286 treatment had the largest difference in N concentrations between Layer 1 and Layer 4 and, therefore, the highest N concentration in Gtotal (N concentration in Gtotal is the differences between N concentration in Layer 1 and Layer 4 in this study). This result may explain the highest grain yield and grain N content achieved in this treatment (Table 1, Fig. 8). The non-uniform N distribution in the plant canopy increased canopy photosynthesis (Hirose, 2005), and thus contributed to the grain yield. Nonfoliar organs play a major role in N accumulation and redistribution (Kichey et al., 2007), photosynthesis (Aschan and Pfanz, 2003), and in determining the vertical gradients of N distribution. The positional differences in N concentration in internode segments in the three treatments may be a useful indicator of plant N status in wheat.

### Nitrogen Contribution of Different Organs to Grains Nitrogen

The remobilization of N during grain filling contributes to the final grain N content in wheat (Van Sanford and MacKown, 1987). Foliar organs contributed more N to grain than G+R, stem or FLS in this study (Table 4 and Fig. 7A), which is consistent with the findings of Xu et al. (2005). Among the foliar organs, FL contributed the most N to final grain N content, and PI contributed the most N to final grain N content of the internode segments (Figs. 7B and 7C). Nitrogen remobilization is dependent on NRE and the amount of available N (Barbottin et al., 2005). The superior N accumulation and remobilization in the N286 treatment may be due to adequate N release from manure to match crop demand (Kato and Yamagishi, 2011), improved soil physical characteristics (Shirani et al., 2002), and nitrogen contribution of different organs to final yield since they can photosynthesize (Kong et al., 2010). Similar to the FL with higher N concentrations than the lower leaf, the apical internode segments had higher N concentrations than lower internode segments. The distribution of N in leaf layers has been discussed elsewhere (Wang et al., 2005; 2006). However, the role of nonfoliar organs in determining N vertical distribution was unclear. This study has demonstrated the role of nonfoliar organs in determining the vertical distribution of N under different N inputs and mulching practices. With the increase of N input, N concentrations increased in both foliar organs (Fig. 3) and nonfoliar organs (Fig. 4 and 5). Among the three treatments, N286 treatment had the largest difference in N concentrations between Layer 1 and Layer 4 and, therefore, the highest N concentration in Gtotal (N concentration in Gtotal is the differences between N concentration in Layer 1 and Layer 4 in this study). This result may explain the highest grain yield and grain N content achieved in this treatment (Table 1, Fig. 8). The non-uniform N distribution in the plant canopy increased canopy photosynthesis (Hirose, 2005), and thus contributed to the grain yield. Nonfoliar organs play a major role in N accumulation and redistribution (Kichey et al., 2007), photosynthesis (Aschan and Pfanz, 2003), and in determining the vertical gradients of N distribution. The positional differences in N concentration in internode segments in the three treatments may be a useful indicator of plant N status in wheat.

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Fig. 7. The nitrogen contribution of different organs to final grain N content. (A) Organs, (B) foliar organs, and (C) internode segments. The data are the average of two growing seasons. Abbreviations: FL, flag leaf; EXP, exposed part of the peduncle; ENP, enclosed part (by flag leaf sheath) of the peduncle; ERL, lower internode leaf; ERI, lower internode; ESTI, lowest internode.

Table 4. Nitrogen remobilization and contribution in shoot organs to grain N in dryland wheat at grain filling under different N inputs and mulching practices.

<table>
<thead>
<tr>
<th>Treatment†</th>
<th>Leaf organs‡</th>
<th>Other organs‡</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FL</td>
<td>Other organs</td>
</tr>
<tr>
<td></td>
<td>EXP</td>
<td>ENP</td>
</tr>
<tr>
<td></td>
<td>NRA mg clum⁻¹</td>
<td>NRE %</td>
</tr>
<tr>
<td>N195</td>
<td>0.35b±</td>
<td>70.71a</td>
</tr>
<tr>
<td>N286</td>
<td>0.47a</td>
<td>73.52a</td>
</tr>
<tr>
<td>N150</td>
<td>0.37b</td>
<td>73.02a</td>
</tr>
<tr>
<td>Avg</td>
<td>0.40</td>
<td>72.42</td>
</tr>
</tbody>
</table>

† N195, N286, and N150 denote the different N input in summer fallow with plastic mulching and straw mulching applied for N195 and N286, respectively.
‡ NRA (mg clum⁻¹) is nitrogen remobilization amount; NRE (%) is nitrogen remobilization efficiency; and NC (%) is nitrogen contribution to final grain N. FL, flag leaf; FLS, flag leaf sheath; PL, penultimate leaf; ERL, lower internode leaf; EXP, exposed part of peduncle; ENP, enclosed part (by flag leaf sheath) of peduncle; PI, penultimate internode; ERI, lower internode; ESTI, lowest internode. Data are the means of two growing season (2011–2012 and 2012–2013).
§ For each organ (column), data followed by the same letter are not significantly different (P<0.05).
CO2 concentrations and light radiation can guarantee that photosynthetic capacity, and high al., 2004; Yang et al., 2001). Increased N concentrations in apical leaves. Early senescence shortens the grain-filling period, which 2000). However, the above two roles have competitive use of N in photosynthesis are two main functions of leaves (Masclaux et al., 2018). Nonfoliar organs have an important role in influencing N remobilization and determining the vertical distribution of N in the plant canopy. Investigations involving a wide range of N rates and combination with other practices under different environments are required in the follow-up studies.

The Role of Nonfoliar Organs in Moderating Nitrogen Use

Remobilization of N to grain and carbohydrate assimilation by photosynthesis are two main functions of leaves (Masclaux et al., 2000). However, the above two roles have competitive use of N in leaves. Early senescence shortens the grain-filling period, which impairs photosynthesis, leading to lower grain weights (Inoue et al., 2004; Yang et al., 2001). Increased N concentrations in apical nonfoliar organs can increase photosynthetic capacity, and high CO2 concentrations and light radiation can guarantee that photosynthesis will offset the loss of leaf photosynthesis, owing to early senescence (Zhang et al., 2011, 2013). Late senescence can prolong the photosynthesis, resulting in more carbohydrates and N left in straw leading to reduced harvest index (Zhang et al., 2008). Increasing N remobilization in nonfoliar organs and improving the vertical distribution of N among leaves enhances plant leaf photosynthetic capacity (Bertheloot et al., 2008). Under N deficiency, increased stem N remobilization may delay senescence by buffering leaf N remobilization to grain (Gaju et al., 2014). High N concentrations in those organs can remobilize more N to leaf organs (and inhibit early leaf senescence) and produce more photosynthetic capacity for grain filling.

CONCLUSIONS

Adequate soil N with the appropriate agronomic practices is essential to ensure high yields in winter wheat. Increasing the N input increased the N concentration not only in foliar organs but also in nonfoliar organs. Foliar organs contributed relatively more N to final grain N followed by whole stem and G+R. Nonfoliar organs have an important role in influencing N remobilization and determining the vertical distribution of N in the plant canopy. Investigations involving a wide range of N rates and combination with other practices under different environments are required in the follow-up studies.

ACKNOWLEDGMENTS

This research was financially supported by the Natural Science Foundation of State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau (A314021402-1610), Key Research Foundation of Baoji College of Arts and Science (ZK16066), National Basic Research Program of China (2015CB150402), National Natural Science Foundation of China (51479189 and 31471946), and Chinese Academy of Sciences ("Hundred Talent" Program, A31502144).

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