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Planting density effects on assimilation and partitioning of photosynthates during grain filling in the late-sown wheat

WANG Zhenlin, FU Jinmin, HE Mingrong, YIN Yanping and CAO Hongming

Department of Agronomy, Shandong Agricultural University, Taian,
Shandong Province 271018, P.R. China

Abstract

Leaf blades of the late-sown winter wheat produced the major portion, *i.e.*, more than 60 %, of the total ^{14}C-photosynthates at grain filling, but ear (rachis and glumes) only about 15 %, sheaths about 11 %, and stem internodes about 11 %. The change of plant density in this experiment had little influence on the $^{14}CO_2$-photoassimilation of the ear (rachis and glumes), flag leaf lamina, sheaths and stem internodes, but markedly affected photosynthesis of the second, the third and lower leaves. The photosynthetic rate [expressed as specific radioactivity, s^{-1} kg^{-1}(d.m.)] and the amount of $^{14}CO_2$ photosynthates decreased significantly in the second, the third and other lower leaves at a high plant density. Upon grain-filling of the late-sown wheat, the grain was the major importer of photosynthates. Yet partitioning to the stem internodes depended on the plant density. Stem was the importer of photosynthates at a low plant density, but the exporter at a high plant density. In plants at a low plant density a fairly large proportion of photosynthates was distributed into the roots. The middle and lower above-ground parts of the late-sown wheat at a high plant density decreased or lost their function early. As a result, the plant senesced earlier. However, the grain setting, filling and yielding were restricted. An appropriately low plant density was suitable for prolonging the function of the middle and lower organs, delaying the senescence of plant, increasing the source supply for grain filling, and improving the grain yield.

Additional key words: photosynthates; $^{14}CO_2$; ear; leaf insertion; photosynthesis; *Triticum aestivum* L.

Introduction

Because the photosynthates construct most of the wheat grain at grain-filling (Yu *et al.* 1964, 1983, 1990, Evans *et al.* 1969, Wang *et al.* 1995), a close relationship exists between the grain yield and the amount of photosynthates at grain-forming.

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Evans *et al.* (1969) showed that a linear relationship existed between post-anthesis leaf area duration and the yield of wheat grown in a range of evironments. Spiertz *et al.* (1971) found that 61-83 % of the variation in wheat grain yield could be statistically predicted from the green area duration values of flag leaf and peduncle. Krenzer (1975) and Fischer and Aguilar (1976) found that increasing photosynthate amount after anthesis was favourable for improvement of grain yield. Yet Austin and Bingham (1980), Gent and Kiyomoto (1985) and Gifford and Evans (1981) state that for this purpose it is most important to increase partitioning of the photosynthates in grain. An improvement in the photosynthates partitioning and enhancement of harvestable index are basic conditions for high yielding wheat (Yu *et al.* 1983).

Late-sown wheat is an important producer (Yun *et al.* 1990, Wang 1991). Proper genotype and timing of grain sowing, optimum ecological conditions, growth and development, and grain forming progress are necessary conditions (Yu *et al.* 1990, Wang 1991, Wang *et al.* 1995). However, there is little knowledge of the photosynthetic activity and partitioning of photosynthates at grain filling in the late-sown wheat. That is why we studied these problems. The goal was to understand the contribution of photosynthates in each organ to grain yield and their respones to given plant density, and thus to provide a theoretical basis for high yields in the late-sown wheat.

Materials and methods

Two identical treatment experiments with *Triticum aestivum* L. cv. Lumai 15, a late-sown, early ripe and semi-winter cultivar, were performed in three replicates in a randomized block design on the experimental farm of the Shandong Agricultural University in 1989 (preparatory experiment) and 1990 (main experiment). 4.5 kg of organic manure and 75 g of calcium superphosphate per m^2 were applied as basic fertilization, and 32.5 g of urea per m^2 was added at jointing. Plants were sown on 27 October using three sowing densities: 325, 488 or 650 plants per m^2. Selected plants of all treatments were labelled with ^{14}C synchronously at grain filling according to Yu *et al.* (1983). Samples harvested 0 h and 3 d after labelling were killed at 105 °C, then oven-dried at 80 °C and ground into powder. 50 mg subsamples were used for determining the radioactivity.

Results and discussion

C-assimilation of plant organs: The relative photosynthetic rate (*P*) declined in the series leaf, ear (glume), sheath, stem at all three densities (Fig. 1). Leaves accounted for more than 60 % of all ^{14}C-photosynthates in the plant, ear for about 15 %, and both the sheaths and stem for about 11 %. Flag leaf had the highest *P* and the second leaf from the top took the second place, but both leaves differed little (51.5 to 57.1 % of total ^{14}C), especially at a low sowing density (Fig. 2). The *P* of the 3rd leaf was about half of that of the flag and the 2nd leaves, but photosynthetic activity of other leaves was extremely low. The *P* and the amount of ^{14}C-photosynthates of the sheaths at different insertions were similar to those of the respective leaves (Fig. 2). Except for assimilating a certain amount of ^{14}C in peduncle, photosynthetic activities of other internodes were very weak.

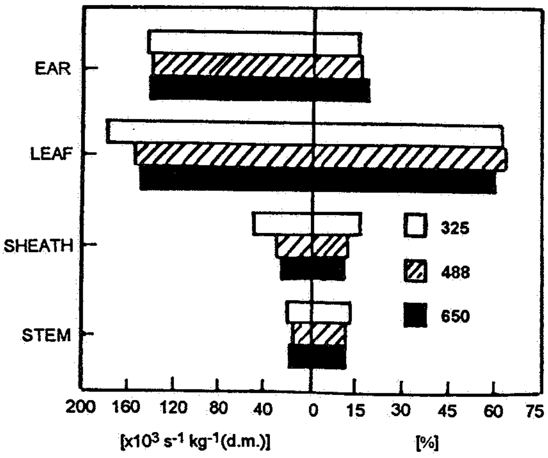

Fig. 1. Specific radioactivity (*left*) and mean % of assimilated $^{14}CO_2$ (*right*) in each part of the late-sown winter wheat. Figures in the graph give amount of plants per m^2.

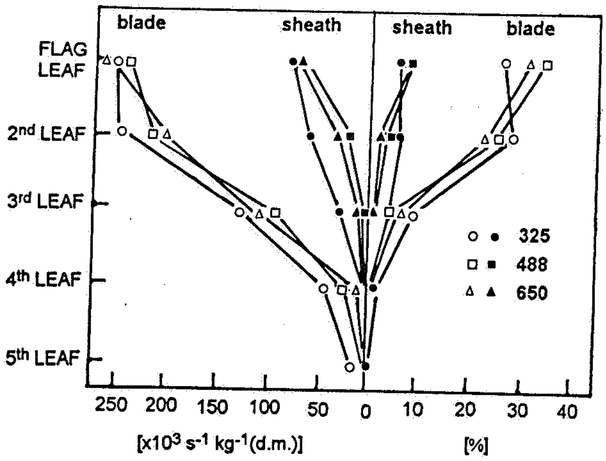

Fig. 2. Changes of specific radioactivity (*left*) and % of assimilated $^{14}CO_2$ in leaves and sheaths at different insertions. Figures in the graph give amount of plants per m^2.

Plant density effects: The *P* of the ear was about 140 000 s^{-1} kg^{-1}(d.m.) at all three densities, but ears of plants grown at different densities accounted for various % of the total ^{14}C; significantly larger was the proportion at a high density (Fig. 1). An enhanced plant density decreased the *P* of leaves, but did not significantly affect the % of total ^{14}C-photosynthates. Both the *P* and the proportion of total ^{14}C-photosynthates in leaf sheaths decreased with higher plant density (Fig. 1).

However, there was not a striking effect of plant density on ^{14}C-assimilation of the stem internodes (Fig. 1).

The *P* of the flag leaf at three densities did not differ, but varied greatly in other leaves. The *P* of the 2nd leaf declined from the low density through the middle density to the high one. The 2nd leaf had *P* similar to that of the flag leaf at a low density, but their *P* differed much at a high density. The *P* of the 3rd, 4th and 5th leaves at a low density were markedly higher than those at middle and high densities. The 4th and 5th leaves at middle and high densities showed much lower ^{14}C-assimilating activity and eventually lost it because of their dying (Fig. 2). A similar variance of the % of total ^{14}C-photosynthates existed among the leaves of different insertions. The flag leaf produced less ^{14}C-photosynthates at a low density than at the middle and high ones, but the 2nd and other leaves were more active at the middle and high densities.

There was not a significant difference of *P* and the proportion of total ^{14}C-photosynthates in flag leaf sheaths at different densities. The 2nd and 3rd leaf sheaths had a significantly higher *P* at low planting density than at the other two treatments. The 4th leaf sheath did not photosynthesize any more.

The above effects of plant density on ^{14}C-assimilation of the late-sown wheat at grain-filling made it clear that plant density did not affect much the CO_2-assimilation of the top parts of plant (ear, flag leaf and its sheath), but controlled the CO_2-assimilation of the middle and low parts of the plant (starting with the 2nd leaf). The suitable decline of planting density clearly improved *P* and the proportion of ^{14}C-photosynthates in the middle and low canopy parts.

Partitioning of ^{14}C-photosynthates into organs 3 d after the labelling: In late-sown wheat, grain was the major importer of ^{14}C-photosynthates at grain-filling. However, the major exporter were the leaves, second ear glumes, and third leaf sheaths. Stem, accounting for low proportion of exporting or importing ^{14}C-photosynthates, was an importer at a low plant density and an exporter at middle and high densities. There was a higher proportion of photosynthates translocated into grain and a lower one translocated into root at middle and high densities than at a low density. Leaves at different densities exported similar amount of ^{14}C-photosynthates, but slightly more at a high density. Ear was similar to leaf as concerns the effect of density on exporting proportion of total ^{14}C-photosynthates, but it exported much lesser amounts at a low density than at middle and high densities.

Increase in plant density changed the proportion of total ^{14}C-photosynthates and their export 3 d after labelling (compare Figs. 1 and 3). There was a similar % of total ^{14}C-photosynthates in leaves at different densities, but a higher export at the high density. The different % of total ^{14}C-photosynthates in leaf sheaths among densities was not reflected in export of ^{14}C-photosynthates. The stem at different densities assimilated a similar amount of ^{14}C, but 3 d after labelling there was an increase in ^{14}C in the stem at a low density and in its export at middle and high densities.

The above results showed that export of photosynthates from each plant part and their translocation to grain increased with the enhancement of density, but their amounts left in root and stem decreased with planting density.

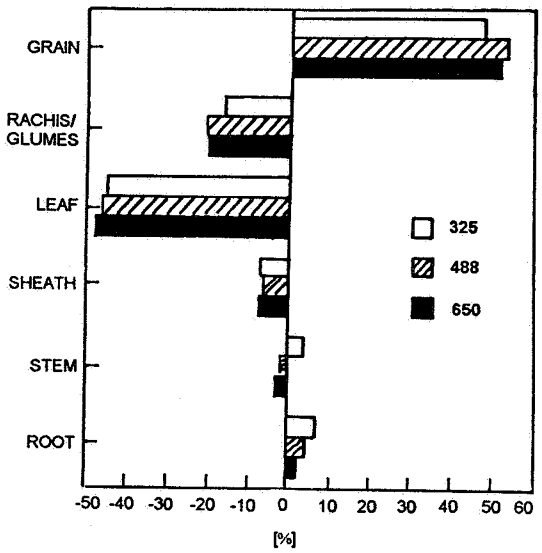

Fig. 3. Changes of % of assimilated $^{14}CO_2$ in each part of the plant between the 0 h (*left*) and 3 d after pulse labelling (*right*). Figures in the graph give amount of plants per m^2.

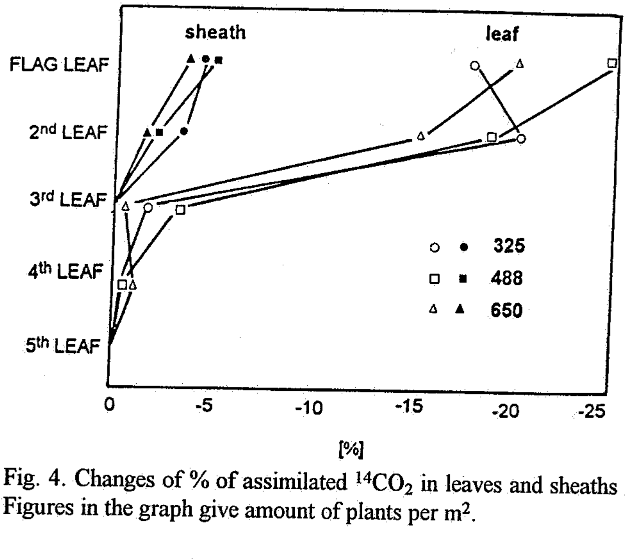

Fig. 4. Changes of % of assimilated $^{14}CO_2$ in leaves and sheaths during the 3 d after pulse-labelling. Figures in the graph give amount of plants per m^2.

Partitioning of ^{14}C-photosynthates in leaves of different insertion: At grain-filling in the late-sown wheat, the flag leaf and the 2nd leaf exported most ^{14}C-photosynthates, but the export from the 3rd and 4th leaves was much lower. At a low density, the most active exporter was the 2nd leaf. At middle and high densities, the flag leaf exported most (Fig. 4).

The flag leaf sheath exported more ^{14}C-photosynthates than the 2nd leaf sheath. The 3rd leaf sheath did not export ^{14}C-photosynthates. There was not a significant difference among planting densities in export of ^{14}C-photosynthates in the flag leaf sheath.

Table 1. The effect of plant density [plant m^{-2}] on the yield [g m^{-2}] and its components of late-sown wheat in years 1988 and 1990.

Plant density	Ear per m^2		Grain per ear		Grain mass		Grain mass/ear		Grain yield	
	1988	1990	1988	1990	1988	1990	1988	1990	1988	1990
325	453	462	31.4	30.2	42.3	40.4	1.33	1.22	611	555
488	513	508	28.2	27.2	41.4	38.6	1.17	1.05	548	509
650	547	543	26.3	27.1	41.6	39.2	1.09	1.06	534	484

Hence, selecting a proper planting density is important for maintaining normal functions of stem and root, preventing senescence, increasing photosynthate accumulation, prolonging filling duration of grain, and improving the grain yield (Table 1).

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