



Research article

Effects of low sink demand on leaf photosynthesis under potassium deficiency

Yonghui Pan^{a, b}, Zhifeng Lu^{a, b}, Jianwei Lu^{a, b}, Xiaokun Li^{a, b}, Rihuan Cong^{a, b},
Tao Ren^{a, b, *}^a Key Laboratory of Arable Land Conservation (Middle and Lower Reaches of Yangtze River), Ministry of Agriculture, Wuhan 430070, China^b Microelement Research Center, Huazhong Agricultural University, Wuhan 430070, China

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ABSTRACT

The interaction between low sink demand and potassium (K) deficiency in leaf photosynthesis was not intensively investigated, therefore this interaction was investigated in winter oilseed rape (*Brassica napus* L.). Plants subjected to sufficient (+K) or insufficient (−K) K supply treatments were maintained or removed their flowers and pods; these conditions were defined as high sink demand (HS) or low sink demand (LS), respectively. The low sink demand induced a lower photosynthetic rate (P_n), especially in the −K treatment during the first week. A negative relationship between P_n and carbohydrate concentration was observed in the −K treatment but not in the +K treatment, suggesting that the decrease in P_n in the −K treatment was the result of sink feedback regulation under low sink demand. Longer sink removal duration increased carbohydrate concentration, but the enhanced assimilate did not influence P_n . On the contrary, low sink demand resulted in a high K concentration, slower chloroplast degradation rate and better PSII activity, inducing a higher P_n compared with HS. Consequently, low sink demand decreased leaf photosynthesis over the short term due to sink feedback regulation, and potassium deficiency enhanced the photosynthetic decrease through carbohydrate accumulation and a lower carbohydrate concentration threshold for initiating photosynthesis depression. A longer duration of limited sink demand and sufficient potassium supply resulted in a higher photosynthesis rate because of delayed chloroplast degradation. This finding indicates that the nutritional status plays a role in leaf photosynthesis variations due to sink-source manipulation.

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1. Introduction

Photosynthesis contributes to more than 90% of crop biomass (Makino, 2011). Consequently, exploring the mechanism underlying enhanced photosynthesis is pivotal in increasing crop yield

Abbreviations: B, boron; C_a , ambient CO_2 concentration; C_i , intercellular CO_2 concentration; DASR, days after sink removal; ETR, linear electron transport rate; F_m , maximum fluorescence; F_0 , light-adapted initial fluorescence; F_v/F_m , capture efficiency of the excitation energy by open PSII; g_s , stomatal conductance; HS, high sink demand; K, potassium; LS, low sink demand; N, nitrogen; P, phosphorus; P_n , net photosynthesis rate; PPF, photosynthetic photon flux density; PSI, photosystem I; PSII, photosystem II; qP, photochemical quenching coefficient; TNC, total non-structural carbohydrate concentration; T_r , transpiration rate; α , leaf absorbance; β , partitioning of absorbed PPF between PSI and PSII; Φ_{PSII} , effective quantum efficiency of PSII.

* Corresponding author. Key Laboratory of Arable Land Conservation (Middle and Lower Reaches of Yangtze River), Ministry of Agriculture, Wuhan 430070, China.

E-mail address: rentao@mail.hzau.edu.cn (T. Ren).

(Long et al., 2015). The manipulation of the sink-source relationship is one of the key regulators of leaf photosynthesis (Damatta et al., 2008; Quentin et al., 2013). Numerous previous studies have shown that low sink demand inhibits leaf photosynthesis, presumably as a result of a lower assimilate transport rate (Franck et al., 2006; Damatta et al., 2008). Based on the phenomenon, the end-product feedback inhibition hypothesis was proposed, which stated that sugar accumulation in leaves resulted in the down-regulation of the related metabolic enzymes and further decreased leaf photosynthesis (Neales and Incoll, 1968). Many techniques, such as de-fruited and girdling, have been used to prove this hypothesis (Duan et al., 2008; López et al., 2015). However, there have also been a number of contradictory results. Rom and Ferree (1986) revealed that sugars would not accumulate in apple leaves in which the photosynthetic rate decreased under low sink demand. It has also been documented that low sink demand indeed caused carbohydrate accumulation and a decrease in

photosynthesis, but the related metabolic enzymes did not change (Damatta et al., 2008). Moreover, Fan et al. (2010) found that leaf photosynthesis did not decrease or even increased under sink-limited conditions. Viewed from these perspectives, the sink effect on photosynthesis is still unclear. Zhang et al. (2013) explained that sink demand was not the only factor influencing leaf photosynthesis, and competition for nutrients exists between sink fruits and source leaves. Under high sink demand conditions, if nutrients are insufficient for the normal growth of every sink, leaf photosynthetic capacity would be restricted due to nutrient deficiency. Therefore, it is necessary to consider the nutritional status of the source and sink when explaining leaf photosynthesis alteration due to source-sink relationship manipulation.

It is well documented that potassium is necessary for assimilate translocation from leaves to fruits and other sinks (Patrick et al., 2001). And photosynthates will accumulate in source leaves when subjected to potassium deficiency, leading to an impaired sink activity, and then leaf photosynthesis declined (Kanai et al., 2007). If low sink demand impose a feedback inhibition on leaf photosynthesis due to assimilate accumulation, we assumed that low sink demand will have a more negative effect on leaf photosynthesis in potassium deficient plants because of its poor assimilate translocation ability. Winter oilseed rape requires large amounts of potassium to maintain growth and to produce high yield. Generally, maximum potassium uptake of oilseed rape occurs during the flowering stage (Liu et al., 2011). Moreover, the competition between the sink (pods and flowers) and source (leaves) for photosynthate and potassium is prominent during this period. If a decreased sink demand is induced by de-fruited or girdling, carbohydrates may accumulate, resulting in a decrease in leaf photosynthesis. However, this effect might be transient, in part owing to reduced carbohydrate accumulation associated with a lower photosynthetic rate, suggesting that low sink demand may not consistently repress photosynthesis. Long-term effects of low sink demand on photosynthesis may provide new insights into the sink demand effects on photosynthesis. Therefore, we examined the changes in leaf photosynthesis of rapeseed (*Brassica napus* L.) under low sink demand (removal of all flowers and pods during the full-bloom stage) and potassium deficiency for 3 weeks in a field experiment. The objectives of this study were to: (1) examine the long-term response of photosynthesis to sink removal; (2) determine the role of potassium in sink removal effects on leaf photosynthesis; and (3) reveal the underlying mechanism through which sink removal influences photosynthesis.

2. Materials and methods

2.1. Study site and growth conditions

A field experiment was conducted in Wuxue county (30°06'46"N, 115° 36'9"E), Hubei province, China, during the 2014–2015 oilseed rape growing season. The site is characterized with a subtropical monsoon climate and receives 670.0 mm of rainfall and has a mean temperature of 12.2 °C during the oilseed rape growing period. The soil is a sandy loam, and its chemical properties in the 0–20 cm layer are as follows: pH 5.7, organic matter 37.1 g kg⁻¹, total N 2.0 g kg⁻¹, Olsen-P 14.6 mg kg⁻¹, NH₄OAc-K 45.3 mg kg⁻¹; this is considered as a K-deficient soil (Lu et al., 2007).

2.2. Experimental design

A split-plot design was used in this experiment. The main plots were two K treatments: (1) K deficiency treatment (–K), no mineral K fertilizer was supplied; and (2) Sufficient K treatment (+K), a

recommended K fertilizer (120 kg K₂O ha⁻¹) was applied. It was proved that a reduction in rapeseed yield would occur if K fertilizer was not added on the basis of soil NH₄OAc-K in this study site, and 120 kg K₂O ha⁻¹ is sufficient for rapeseed growth and yield formation in this region (Ren et al., 2015). Different sink demands constituted the subplots: low sink demand (LS) and high sink demand (HS). The treatment where all flowers and pods were removed (pedicels were retained to diminish the mechanical injury) was considered as LS, whereas the plants whose flowers and pods were retained was considered as HS (Fig. 1). Treatments were conducted at the beginning of full bloom stage, and in the LS treatment new pods and flowers which initiated thereafter were also removed twice a week. Thus, four treatments with three replicates were established: (i) sufficient K under low sink demand (+K + LS); (ii) K deficiency under low sink demand (–K + LS); (iii) sufficient K under high sink demand (+K + HS); and (iv) K deficiency under high sink demand (–K + HS). The whole experiment area was 235 m², which was separated from adjacent field experiment by a 1-m-wide protecting belt. Individual plot size was 20 m² (10 m × 2 m), and around the plots was a 0.5-m-wide ditch.

The winter oilseed rape variety Zhongyouza 12 was used in this experiment. Seeds were sown in a seedbed on 22nd September and then on 26th October, uniform oilseed rape seedlings with four to five leaves were transplanted by hand at a spacing of 0.3 m × 0.25 m in each 20 m² (2 m × 10 m) plot, corresponding to a plant density of 112,500 plants ha⁻¹ which is a common plant density used in transported oilseed production (Wang et al., 2014; Geng et al., 2015). The plants were subjected to local agricultural practices used for oilseed rape production, including weed, pest and disease control. To ensure nutrients other than K would not limit plant growth, the application rates were the same for all

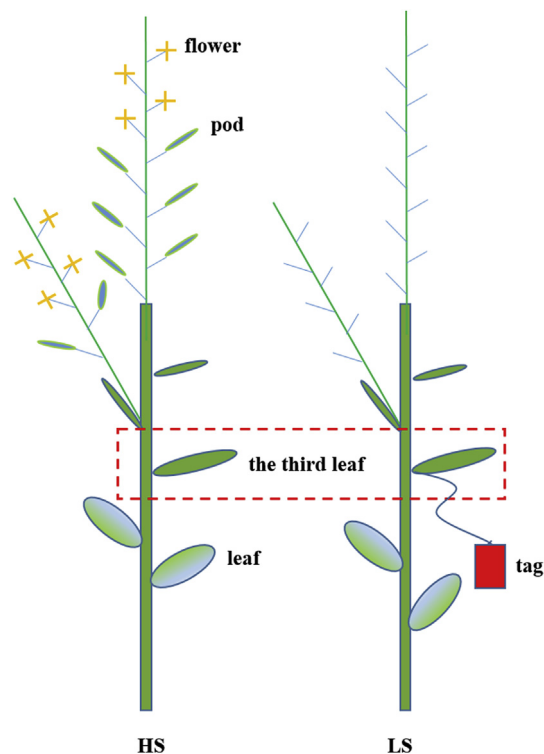


Fig. 1. A schema about leaf tagging and sink removal method. The third leaf (only on the main-stem) from the apex downwards were attached to a tag. In the LS treatment, pod and flowers were removed but the pedicel was retained in order to diminish the mechanical injury caused by sink removal; in the HS treatment, pods and flowers were retained.

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