Yield of summer maize hybrids with different growth duration determined by light and temperature resource use efficiency from silking to physiological maturity stage

Jiyu Zhao, Baizhao Ren, Bin Zhao, Peng Liu and Jiwang Zhang*

State Key Laboratory of Crop Biology and College of Agronomy, Shandong Agricultural University, Tai'an, China

In order to explore the physiological mechanism of different yield of summer maize (Zea mays L.) hybrids with different growth duration, a field experiment was conducted to study the growth stage, leaf photosynthetic characteristics, dry matter accumulation (DMA), transport and distribution characteristics and yield of the early maturity hybrid Denghai 518 (DH518) and the mid-late maturity hybrid Denghai 605 (DH605) from 2017 to 2021. The results showed that the yield of DH605 was significantly higher than that of DH518. The growth period of DH518 was 7-10 days shorter and the days of the growth stage of the sowing-silking stage (R1) were 5-6 days shorter compared to that of DH605. The contribution to grain dry matter by leaf and stalk dry matter remobilization (DMRC) of DH518 was significantly higher than that of DH605. There was a significant negative correlation between pre-silking growth days and harvest index (HI). The 13C distribution to grains of DH518 was significantly higher than that of DH605, and the HI and the corresponding contribution of HI to yield was also higher than that of DH605. The light and temperature resource use efficiency from silking to physiological maturity stage of DH605 was significantly higher than that of DH518. The yield per GDD of DH605 increased by 7.25% than that of DH518. At post-silking, the duration of higher leaf area index (DLAI) (>56 days) and active photosynthesis duration (APD) (>50 days) of DH605 were longer compared with that of DH518, and the average plant growth rate was 7.15% higher than that of DH518, which significantly increased the DMA of DH605. Therefore, the significant reduction of DH518 yield compared with DH605 was not due to the shortening of the growth stage of sowing-R1, but the lower light and temperature resource use efficiency from silking to physiological maturity stage.

KEYWORDS
maize, harvest index (HI), resource use efficiency (RUE), yield, dry matter
Introduction

Maize has become the largest cereal food crop in China since 2013, which was responsible for 22% of the global maize output (Liu et al., 2017; FAO, 2020). Increasing maize production is critical to ensuring global food and energy security in China (Liu et al., 2020). In a global crisis like COVID-19, food insecurity and disparity can become a serious problem not only in densely populated developing countries (Guha and Chandra, 2021; Odunitan-Wayas et al., 2021) but also in some developed countries (O’Hara and Toussaint, 2021; Oncini, 2021). Under the wheat-maize double-cropping model in the North China Plain, light and heat resources are not enough, so it is impossible to guarantee sufficient maize grain filling duration and late grain dehydration time (Sun et al., 2007; Wang et al., 2012). In order to increase yield, farmers are accustomed to plant mid-late maturity or late maturity hybrids for a long time (Edwards et al., 2005). However, with the wide application of the whole mechanized maize planting mode, the hybrids with a long growth period and slow dehydration in the later stage are increasingly unsuitable for production requirements. Due to the shortening of the growth period, the yield of early maturity hybrids is lower than that of middle-late maturity hybrids (Zhao et al., 2021). Therefore, how to improve the yield of early maturity hybrids becomes an urgent problem to be solved.

Aboveground dry matter accumulation (DMA) and harvest index (HI) are two simple and valuable characteristics for evaluating plant traits and improving yield (Donald and Hamblin, 1976). The characteristics of DMA, distribution, and transfer during the growth period are the important factors to determine the yield of maize (Saidou et al., 2003). The fundamental way to achieve a high yield is to increase DMA and distribution to grains (i.e. HI) as much as possible (Chen, 1994). With the upgrading of hybrids, the DMA per plant also increased, especially at post-silking (Hu et al., 1998). The post-silking DMA accounts for 50% of the total DMA at R6, which is mainly supplied to the grain (Rajcan and Tollenaar, 1999; Tollenaar et al., 2004; Lee and Tollenaar, 2007). In addition, the HI has improved (Echarte and Andrade, 2003; Hou et al., 2012; Ma et al., 2014). However, other studies have shown that the HI does not change continuously over time (Meghji et al., 1984; Tollenaar, 1989). Therefore, it is necessary to explore the differences between DMA and HI and their contribution to the yield of summer maize hybrids with different growth duration.

Leaves are the decisive organs for photosynthesis in terrestrial plants (Piazza et al., 2005). Higher LAI, longer active photosynthesis duration and slower leaf senescence play a positive role in the increase of DMA and yield after silking (Ma and Dwyer, 1998; Borrell et al., 2001; Duvick, 2005). Temperature plays an important role in the growth and development of crops (Lin et al., 2011). It affects the synthesis and distribution of photosynthetic matter in maize (Ptaszynska and Silesia, 2008) and the duration of growth period (Ileleji et al., 2007). In addition, the light and temperature resource use efficiency of high-yield maize hybrids are also higher (Slattery and Ort, 2021). DH605 is one of the most popular maize hybrids in China at present, and DH518 is a newly released hybrid that is being promoted. DH605 (mid-late hybrid) and DH518 (mid-early hybrid) have different growth duration, which are widely representative (Ma et al., 2022). Therefore, we analyzed the yield, accumulated temperature demand characteristics, leaf photosynthetic characteristics, and DMA and distribution characteristics of different summer maize hybrids to explore the effects of the changes in the growth duration on DMA and distribution and yield. We aimed to determine: a) whether the changes in growth period affect the contribution of dry matter and HI to yield, and b) what is the physiological mechanism of yield difference of summer maize hybrids with different growth duration. These results will provide an important reference for improving the yield of early maturity hybrids adapted to mechanical grain harvest.

Materials and methods

Plant materials and experimental design

Field experiments were conducted at an experimental farm of Shandong Agricultural University (36.09°N, 117.09°E) from 2017 to 2021. The weather conditions of the summer maize growing season in the planting area are shown in Figure 1. The early maturity hybrid Denghai 518 (DHS518) and the mid-late maturity hybrid Denghai 605 (DH605) were used as test materials with a row spacing of 60 cm and a planting density of 75,000 ha⁻¹. Both hybrids are widely planted in the province of Shandong, China. The hybrid maturity is classified as 113 d for DH605 and 103 d for DH518. The growing season duration (from sowing to harvest dates) for two hybrids in different years were shown in Table 2. Each treatment was repeated three times, in a completely randomized design, and the plot area was 54 m² (9 m × 6 m). The N, P, and K fertilizers were applied as base fertilizer: 84 kg ha⁻¹ N (urea, 46% N), 52.5 kg ha⁻¹ P₂O₅ (calcium superphosphate, 17% P₂O₅), and 67.5 kg ha⁻¹ K₂O (muriate of potash, 60% K₂O). At the ninth leaf stage (V9) 126 kg ha⁻¹ N fertilizer (urea, 46% N) was applied as supplementary fertilizer.

Investigation of growth stage and calculation of the growing degree days

After sowing, the date on which the plant reached the sixth leaf stage (V6), the 12th leaf stage (V12), silking stage (R1), milk
stage (R3), 45 days after silking (R5) and physiological maturity stage (R6) were observed and recorded. The R6 is defined as the date when the black layer forms at the base of the kernel and the milk line has disappeared. The weather conditions data were provided by the Agricultural Experimental Station of Shandong Agricultural University. GDD was calculated as follows (Gregory and Wilhelm, 1997):

\[
\frac{1}{2} (T_{\text{max}} + T_{\text{min}}) - T_{\text{base}}
\]

where \(T_{\text{max}}\) is the daily maximum temperature, \(T_{\text{min}}\) is the daily minimum temperature, \(T_{\text{base}}\) is the maize growth base temperature (10 °C).

**Leaf area index**

Six typical plants were signed from each plot at V6, V12, R1, R3, R5 and R6 stage to measure and calculate leaf area and LAI, according to the method of (Montgomery, 1911).

**Chlorophyll content**

Ten typical plants leaves SPAD value was measured as leaf chlorophyll content at V6, V12, VT, R3 and R6 stage. SPAD value of functional leaf was metered using a chlorophyll meter (SPAD-502, Minolta, Japan), and replicated at least eight times (Wu et al., 1998).

**Leaf gas exchange parameters**

The net photosynthetic rates (\(P_n\)), stomatal conductance (\(G_s\)) and intercellular \(CO_2\) concentration (\(C_i\)) were measured in the middle of five ear leaves representational in each treatment from 10:00 to 12:00 at R1, R3 and R5 stage by using a portable infrared gas analyzer (CIRAS-III, PP System, Hansatech, USA). The active photosynthesis duration (APD) and the duration of higher LAI (DLAI) was defined by (Zhang and Cheng, 1992) as the number of days when \(P_n\) and LA decrease from the maximum to 50%.

\[
\text{Canopy photosynthetic capacity} = P_n \times LAI
\]

**Accumulation, distribution and transport of dry matter**

5 randomly selected plants from each plot were sampled at each physiological stage. At R1 and R6 stage, plants were separated into leaf, stalk (at R1 and R6 stage), and reproductive parts (bract, cob, and grain at R6 stage) for analysis. Plant samples were killed at 105 °C for 30min, then dried at 80 °C to constant weight, and the dry matter weight was measured. Post-silking DMA in aboveground biomass (PoSDMA). Pre-silking and post-silking DMA ratio in aboveground biomass (PrSDMAR and PoSDMAR), dry matter remobilization efficiency (DMRE) of vegetative tissues, and contribution to grain dry matter by leaf and stalk dry matter remobilization (DMRC) were estimated according to the following formulas (Mi et al., 2003; Chen et al., 2014; Chen et al., 2015b):

\[
\text{PrSDMAR} = \frac{\text{Total DMA at R1}}{\text{Total DMA at R6}} \times 100
\]

\[
\text{PoSDMA} (g \text{ plant}^{-1}) = \frac{\text{Total DMA at R6} - \text{Total DMA at R1}}{\text{PoSDMA}} \times 100
\]

\[
\text{PoSDMAR} (g \text{ plant}^{-1}) = \frac{\text{PoSDMA}}{\text{Total DMA at R6}} \times 100
\]
DMR of leaf or stalk (g)
= leaf or stalk DMA at R1 – leaf or stalk DMA at R6

DMRE(%) of leaf or stalk
= (DMR of leaf or stalk/leaf or stalk DMA at R1) × 100

DMR of leaf or stalk to grain (g)
= DMR of leaf or stalk × 13C distribution to grains

DMRC(%) of leaf or stalk
= (DMR of leaf or stalk to grain/grain DMA at R6) × 100

Harvest index was calculated as per (Ciampitti et al., 2013):
HI = Grain DMA at R6/Total DMA at R6

13C Pulse labeling, sampling and analysis

At R1 stage, five plants were selected for 13CO2 labeling and five for reference from the different summer maize hybrids in 2017, 2018, 2020 and 2021. The ear leaf was placed in the labeling chamber (a transparent plastic oven bag sealed at both ends) and 60 mL of 13CO2 air was pumped into the labeling chamber. After one hour, the bags were removed from the plants. At R6 stage, three labeled 13CO2 plants and three reference plants without labeled 13CO2 were separated into stalk, leaf, grain and other. These samples were dried, weighed, and ball-milled for analysis (Schussler and Westgate, 1994).

Yield and yield components

Thirty ears from the middle three rows of each plot were sampled to measure yield and yield components. Maize kernels with 14% moisture content were determined.

\[
\text{Yield per GDD} = \frac{\text{Yield}}{\text{Total GDD}}
\]

\[
\text{Sink capacity} = \frac{\text{Number of ears per unit area at R6} \times \text{Grains per ear} \times \text{grain weight}}{	ext{Sink capacity/ LA at R1 stage}}
\]

\[
\text{Grain/leaf} = \frac{\text{Sink capacity/LA at R1 stage}}{\text{Sink capacity/ LA at R1 stage}}
\]

Data analysis

Microsoft Excel 2016 (Microsoft, Redmond, WA, USA) and SigmaPlot 12.5 (Systat Software, Inc., Richmond, CA, USA) were used for data processing and plotting, curve expert 1.4 for model fitting. Differences between years or hybrids were compared using ANOVA and Student’s t test with p < 0.05 (LSD 0.05). Correlation were carried out according to the method of Piepho (2018). Correlations and regression analyses were estimated as Pearson’s correlation coefficient. The main effects of year, hybrid, and their interactions were tested for the grain yield, dry matter remobilization, DMRC, Grain/leaf and HI using IBM SPSS Statistics 21 (IBM Corporation, Armonk, NY, USA).

Results

Yield

There was no significant year × hybrids interaction effects on the yield (Table 1). The yield of DH605 was significantly higher and was increased by 3.4-7.3%, compared with that of DH518. The increase in maize yield was mainly due to the significant increase in the 1,000-grain weight of DH605 (Table 1). There was no significant difference in the number of ears and grain number per ear (except in 2019) among summer maize hybrids with different growth duration (Table 1). The effective accumulated temperature of DH605 after silking was 53.1 °C lower than that of DH518 in 2019 because the sowing date is more than 6 days later than that of other years, resulting in a decrease in 1000-grain weight of DH605 (Table 2).

Growth process and demand characteristics of GDD

The growth period of DH518 was shorter than that of DH605, and different period was mainly from V6 to R1 stage. The growth period of DH518 was 7-10 days shorter than that of DH605 and the pre-silking GDD was significantly lower. The pre-silking days and GDD of DH605 were increased 5-6 days and 77.3-100.8°C than those of DH518. There was no significant difference in post-silking GDD among different hybrids (Table 2). At post-silking, the yield per GDD of DH605 (12.73 kg ha⁻¹ (°C d)⁻¹) was significantly higher than that of DH518 (11.87 kg ha⁻¹ (°C d)⁻¹).

Dry matter accumulation

The PrSDMA and PoSDMA of DH605 were significantly higher than DH518. Compared with DH518, the PrSDMA and
PoSDMA of DH605 increased by 9.7% and 10.2% respectively (Figure 2A). There was no significant difference between PrSDMAR and PoSDMAR of summer maize hybrids with different growth duration. The PoSDMA of the two hybrids was higher than the PrSDMA. Summer maize hybrids with different growth duration accumulated 40% of the total plant dry matter from sowing to R1 (Figure 2B), which indicated that hybrids with higher PrSDMA had greater PoSDMA production potential. The DMA of various organs of DH605 was significantly higher than that of DH518. The DMA of grain, leaf, stalk and other organs of DH605 at R6 increased by 5.3-9.7%, 12.1-22.4%, 21.6-33.0% and 9.4-13.5%, respectively, compared to DH518. (Figure 2C)

**DMRE and DMRC of leaf or stalk**

The DMR of leaf and DMRE of leaf and stalk of DH605 were significantly lower than those of DH518, but there was no significant difference in DMR of stalk between two hybrids. Compared with DH605, the DMRE of leaf and stalk of DH518 increased by 8.0-11.2% and 5.1-5.9%, respectively (Table 3). The DMRC of leaf or stalk of DH518 was significantly higher than that of DH605, and the contribution to grain dry matter by PoSDMA of different summer maize hybrids was 90.0-93.6%, which was significantly higher than DMRC. (Table 4).

Compared with DH605, the 13C distribution to grains of DH518 increased by 3.4-4.4%, while the 13C distribution in

### Table 1: Grain yield and yield components of summer maize hybrids with different growth duration from 2017 to 2021.

| Year | Hybrid | Grains per ear | 1000-grain weight(g) | Harvest ear number(10^4 ha^-1) | Yield(kg ha^-1) |
|------|--------|----------------|----------------------|-------------------------------|----------------|
| 2017 | DH518  | 497 ± 5.9a     | 355 ± 2.5b           | 6.91 ± 0.06a                  | 12245 ± 145.1b |
|      | DH605  | 487 ± 6.7a     | 378 ± 2.2a           | 6.94 ± 0.05a                  | 12796 ± 130.6a |
| 2018 | DH518  | 495 ± 14.5a    | 349 ± 1.8b           | 6.86 ± 0.07a                  | 11860 ± 237.7b |
|      | DH605  | 514 ± 10.7a    | 361 ± 1.0a           | 6.86 ± 0.08a                  | 12720 ± 107.1a |
| 2019 | DH518  | 521 ± 7.0b     | 359 ± 2.3a           | 6.57 ± 0.18a                  | 12286 ± 173.5b |
|      | DH605  | 570 ± 8.7a     | 334 ± 1.5b           | 6.67 ± 0.08a                  | 12701 ± 151.8a |
| 2020 | DH518  | 518 ± 12.6a    | 346 ± 3.4b           | 6.83 ± 0.09a                  | 12238 ± 214.3b |
|      | DH605  | 520 ± 10.1a    | 363 ± 2.0a           | 6.89 ± 0.17a                  | 13009 ± 289.0a |
| 2021 | DH518  | 543 ± 12.0a    | 299 ± 2.4b           | 7.32 ± 0.09a                  | 11889 ± 385.8b |
|      | DH605  | 561 ± 3.8a     | 308 ± 2.1a           | 7.39 ± 0.16a                  | 12754 ± 272.4a |

In the same year, means followed by a common letter are not significantly different by LSD test at the 5% level of significance. DH518, Denghai518; DH605, Denghai605. **p< 0.01.

### Table 2: Growth process and effective accumulated temperature of summer maize hybrids with different growth duration from 2017 to 2021.

| Year | Hybrid | Sowing (M/D) | V6 (M/D) | R1 (M/D) | R6 (M/D) | Days before silking (d) | Effective accumulated temperature before silking(°C d) | Days after silking (d) | Effective accumulated temperature after silking (°C d) | Total growth period (d) | Total effective accumulated temperature (°C d) |
|------|--------|--------------|----------|----------|----------|------------------------|------------------------------------------------------|-----------------------|-------------------------------------------------|--------------------------|---------------------------------------------|
| 2017 | DH518  | 6/10         | 7/1      | 7/25     | 9/20     | 45                     | 806.9                                                | 58                    | 933.3                                           | 104                      | 1740.2                                      |
|      | DH605  | 6/10         | 7/2      | 7/31     | 9/30     | 51                     | 904.6                                                | 62                    | 955.8                                           | 114                      | 1860.4                                      |
| 2018 | DH518  | 6/7          | 6/28     | 7/23     | 9/18     | 46                     | 826.5                                                | 58                    | 952.5                                           | 104                      | 1779.0                                      |
|      | DH605  | 6/7          | 6/30     | 7/29     | 9/26     | 52                     | 918.2                                                | 60                    | 940.3                                           | 111                      | 1858.4                                      |
| 2019 | DH518  | 6/16         | 7/7      | 8/1      | 10/3     | 46                     | 846.1                                                | 63                    | 860.3                                           | 109                      | 1647.1                                      |
|      | DH605  | 6/16         | 7/9      | 8/6      | 10/10    | 51                     | 931.5                                                | 65                    | 807.2                                           | 116                      | 1719.9                                      |
| 2020 | DH518  | 6/9          | 7/1      | 7/25     | 9/23     | 46                     | 708.3                                                | 60                    | 923.7                                           | 106                      | 1632.0                                      |
|      | DH605  | 6/9          | 7/3      | 7/30     | 9/30     | 51                     | 785.6                                                | 62                    | 915.9                                           | 113                      | 1701.5                                      |
| 2021 | DH518  | 6/8          | 6/30     | 7/24     | 9/21     | 46                     | 794.8                                                | 59                    | 864.9                                           | 105                      | 1659.7                                      |
|      | DH605  | 6/8          | 7/1      | 7/30     | 9/29     | 52                     | 895.6                                                | 61                    | 853.7                                           | 113                      | 1749.3                                      |

DH518, Denghai518; DH605, Denghai605.
TABLE 3 Dry matter remobilization of vegetative tissues of summer maize hybrids with different growth duration from 2017 to 2021.

| Year | Hybrid  | Dry matter remobilization of stalk (g) | Dry matter remobilization efficiency of stalk (%) | Dry matter remobilization of leaf (g) | Dry matter remobilization efficiency of leaf (%) |
|------|---------|---------------------------------------|--------------------------------------------------|--------------------------------------|--------------------------------------------------|
| 2017 | DHS518  | 17.81 ± 1.96a                         | 25.49 ± 1.76a                                    | 5.26 ± 0.96a                         | 15.38 ± 3.19a                                    |
|      | DH605   | 15.75 ± 1.32a                         | 19.99 ± 1.98b                                    | 1.98 ± 1.17b                         | 5.62 ± 3.35b                                     |
| 2018 | DHS518  | 19.36 ± 0.95a                         | 27.20 ± 1.91a                                    | 5.36 ± 1.30a                         | 14.21 ± 2.58a                                    |
|      | DH605   | 18.38 ± 2.00a                         | 21.98 ± 2.42b                                    | 2.55 ± 0.87b                         | 6.22 ± 2.18b                                     |
| 2019 | DHS518  | 19.68 ± 0.79a                         | 24.65 ± 1.32a                                    | 5.19 ± 1.51a                         | 14.07 ± 4.81a                                    |
|      | DH605   | 18.38 ± 0.49a                         | 22.03 ± 0.72b                                    | 2.09 ± 0.42b                         | 5.38 ± 0.94b                                     |
| 2020 | DHS518  | 19.16 ± 0.57a                         | 26.51 ± 1.11a                                    | 6.01 ± 1.43a                         | 16.13 ± 3.51a                                    |
|      | DH605   | 18.40 ± 0.67a                         | 21.40 ± 0.66b                                    | 1.95 ± 0.42b                         | 4.88 ± 1.12b                                     |
| 2021 | DHS518  | 18.82 ± 1.03a                         | 27.34 ± 1.72a                                    | 5.87 ± 1.43a                         | 15.82 ± 4.21a                                    |
|      | DH605   | 18.16 ± 0.46a                         | 21.45 ± 1.03b                                    | 1.73 ± 0.47b                         | 4.65 ± 1.13b                                     |

Year (Y) 0.989 0.570 0.131 0.062
Hybrid (H) 1.653 23.923** 68.011** 70.256**
Y × H 0.104 0.298 0.388 0.312

In the same year, means followed by a common letter are not significantly different by LSD test at the 5% level of significance. DHS518, Denghais518, DH605, Denghai605. ** indicated significantly different at the 0.01 and 0.05 probability levels, respectively.
stalks decreased by 2.6-11.2%. The distribution of $^{13}$C in different organs of different summer maize hybrids is as follows: grain > others > stalk > leaf. The proportion of $^{13}$C in ear is more than 60% (Figure 3).

**Photosynthetic characteristics**

The dynamic variation in the post-silking population leaf area was shown in Figure 4. The overall change trend of the LAI of DH518 and DH605 were the same, which gradually increased from V6-R1 stage, at R1 the LAI was the highest and gradually decreased after R1 (Figure 4). The LAI of DH605 at the R1 and post-silking was significantly higher than that of DH518. Compared with DH518, the LAI of DH605 in R1, R3 and R6 increased by 10.8-19.0%, 9.6-15.1% and 12.7-23.6%, respectively. The change of post-silking LAI conformed to the Gaussian model. The analysis showed that the LAI max of the two hybrids appeared 3-8 days after silking. The DLAI of DH605 was more than 56 days, while that of DH518 was less than 51 days, which significantly accelerated the rapid decay process of DH518. Canopy photosynthetic capacity is a comprehensive

![FIGURE 4](image)

**TABLE 4** Contribution to grain dry matter by leaf and stalk dry matter remobilization of summer maize hybrids with different growth duration (2017-2018; 2020-2021).

| Year | Hybrid | DMR of leaf and stalk to grain(g) | DMRC of leaf and stalk(%) | Yield per GDD(kg ha$^{-1}$C$^{-1}$ d$^{-1}$) |
|------|--------|----------------------------------|---------------------------|-------------------------------------------|
| 2017 | DH518  | 14.34 ± 2.02a                    | 9.50 ± 1.27a              | 11.83 ± 0.14b                             |
|      | DH605  | 10.53 ± 0.61b                    | 6.61 ± 0.37b              | 12.49 ± 0.13a                             |
| 2018 | DH518  | 14.75 ± 0.22a                    | 9.99 ± 0.02a              | 11.21 ± 0.22b                             |
|      | DH605  | 13.29 ± 0.75b                    | 8.20 ± 0.55b              | 12.42 ± 0.10a                             |
| 2020 | DH518  | 13.76 ± 0.10a                    | 9.04 ± 0.59a              | 12.05 ± 0.21b                             |
|      | DH605  | 10.32 ± 0.41b                    | 6.43 ± 0.15b              | 13.29 ± 0.30a                             |
| 2021 | DH518  | 14.75 ± 0.48a                    | 9.87 ± 0.05a              | 12.39 ± 0.46b                             |
|      | DH605  | 11.03 ± 0.08b                    | 6.95 ± 0.16b              | 13.90 ± 0.30a                             |

| Year (Y) | 3.830*                           | 4.147*                           | 34.123**                           |
| Hybrid (H) | 43.622**                      | 70.621**                      | 133.933**                         |
| Y × H   | 1.733                           | 0.975                           | 3.177                             |

DMR, dry matter remobilization; DMRC, contribution to grain dry matter by leaf and stalk dry matter remobilization. In the same year, means followed by a common letter are not significantly different by LSD test at the 5% level of significance. DH518, Denghai518; DH605, Denghai605. ** and * indicated significantly different at the 0.01 and 0.05 probability levels, respectively.
The post-silking canopy photosynthetic capacity of DH605 was significantly higher than that of DH518. Compared with DH518, the canopy photosynthetic capacity of DH605 in R1, R3 and R5 increased by 17.0-25.9%, 11.5-22.8% and 79.5-104.3%, respectively. The SPAD value of DH605 was significantly higher than that of DH518 at R6, and the SPAD value of DH605 increased by 21.9-59.7% compared with DH518 at R6. There was no significant difference between different hybrids before R3 (Figure 4).

The $P_n$, $G_s$, and $C_i$ of ear leaf of summer maize hybrids with different growth duration were not significantly different at R1 and R3 stages (Figure 5). The $P_n$ and $G_s$ of DH605 was significantly higher than those of DH518, and the $C_i$ of DH605 was significantly lower than that of DH518. Compared with DH605, the $P_n$ and $G_s$ of DH518 decreased by 28.2-33.3% and 22.7-35.1%, respectively, and the $C_i$ increased by 14.4-65.7%, indicating that the decrease of $P_n$ in the later stage of DH518 was limited by stomatal factors and the decline of mesophyll cell function. The linear fitting of $P_n$ after full expansion of ear leaf showed that the APD of DH605 was more than 10 days longer than that of DH518 (Table 5).

The correlation analysis

Correlation analyses showed different relationships between yield and DMA and HI of summer maize hybrids with different growth duration. The yield of DH518 was positively correlated with dry matter and harvest index. DH518 reached significant levels in 2017 and 2020, and DH605 reached significant levels in 2018, 2020 and 2021 (Table 6). The HI was negatively correlated with the days from sowing to R1 ($r=0.922$, $p<0.01$), but not with the days of R1-R6 ($p>0.05$) (Figure S1).
Discussion

The light and temperature resource use efficiency from silking to physiological maturity stage of different summer maize hybrids

In the past few decades, breeding programs in pursuit of higher yields have extended the fertility period of maize (Valentinuz and Tollenaar, 2004; Luque et al., 2006). Compared with early maturity hybrids, the senescence of mid-late maturity hybrids occurs slower (Valentinuz and Tollenaar, 2004), which shows that the post-silking chlorophyll activity steady phase (RSP) of mid-late maturity hybrids lasted longer (Ding et al., 2005). Our results showed that the decline rate of SPAD value of DH605 was lower than that of DH518 after silking, which greatly delayed the senescence of leaves (Figure 4). Late maturity hybrids have higher leaf area index, longer photosynthesis time, slower leaf senescence and higher DMA rate at filling stage (Ma and Dwyer, 1998; Borrell et al., 2001; Duvick, 2005), which has a positive effect on the increase of yield (Rajcan and Tollenaar, 1999; Valentinuz and Tollenaar, 2004; Ding et al., 2005). The photosynthetic characteristics of leaves are closely related to the yield (Motto, 1987; Ma and Dwyer, 1998). DH605 had larger leaf area than that of DH518. The time of DH605 entering the rapid decay stage was more than 15 days later than that of DH518 (Figure 4). The DLAI of DH605 was 5 days and the APD of DH605 was more than 10 days longer than that of DH518 (Table 7). There is no doubt that the yield of mid-late maturity hybrids is higher than that of early maturity hybrids (Scott and Hector, 1997; Morinaka et al., 2006; Table 1), not only because of the extension of growth period (Table 2), but also because DH605 has higher light and temperature resource use efficiency. When the GDD was increased by 1 °C, the yield of DH605 was higher than that of DH518 by 0.86kg ha⁻¹. Therefore, the light and temperature resource use efficiency from silking to physiological maturity stage is key to determine the yield of summer maize hybrids with different growth duration. In the future, in the research on the yield of summer maize hybrids with different growth duration,

| Year | Hybrid | Linear fitting equation | Correlation coefficient | Pi | APD |
|------|--------|------------------------|------------------------|----|-----|
| 2017 | DH518  | y=43.34-0.58x           | 0.994                  | 46.07 | 40.27 |
|      | DH605  | y=45.04-0.47x           | 0.989                  | 48.23 | 50.67 |
| 2018 | DH518  | y=43.97-0.52x           | 0.946                  | 46.33 | 44.34 |
|      | DH605  | y=45.40-0.41x           | 0.958                  | 48.13 | 57.02 |
| 2019 | DH518  | y=44.94-0.54x           | 0.952                  | 47.83 | 43.11 |
|      | DH605  | y=45.93-0.43x           | 0.973                  | 48.37 | 55.76 |
| 2020 | DH518  | y=45.07-0.55x           | 0.967                  | 48.57 | 41.79 |
|      | DH605  | y=46.04-0.42x           | 0.966                  | 49.27 | 55.57 |
| 2021 | DH518  | y=44.75-0.51x           | 0.952                  | 47.63 | 45.09 |
|      | DH605  | y=46.19-0.43x           | 0.983                  | 48.70 | 55.84 |

Pi, initial net photosynthetic rate; APD, active photosynthesis duration (the days from Pi to half of Pi).

Duvick, 2005), which has a positive effect on the increase of yield (Rajcan and Tollenaar, 1999; Valentinuz and Tollenaar, 2004; Ding et al., 2005). The photosynthetic characteristics of leaves are closely related to the yield (Motto, 1987; Ma and Dwyer, 1998). DH605 had larger leaf area than that of DH518. The time of DH605 entering the rapid decay stage was more than 15 days later than that of DH518 (Figure 4). The DLAI of DH605 was 5 days and the APD of DH605 was more than 10 days longer than that of DH518 (Table 7). There is no doubt that the yield of mid-late maturity hybrids is higher than that of early maturity hybrids (Scott and Hector, 1997; Morinaka et al., 2006; Table 1), not only because of the extension of growth period (Table 2), but also because DH605 has higher light and temperature resource use efficiency. When the GDD was increased by 1 °C, the yield of DH605 was higher than that of DH518 by 0.86kg ha⁻¹. Therefore, the light and temperature resource use efficiency from silking to physiological maturity stage is key to determine the yield of summer maize hybrids with different growth duration. In the future, in the research on the yield of summer maize hybrids with different growth duration,

| Year | Hybrid | Yield × DMA (y= a + bx) | Yield ×HI (y= a + bx) |
|------|--------|-------------------------|-----------------------|
|      |        | a           | b     | r   | a           | b     | r   |
| 2017 | DH518  | 43.544      | 0.018 | 0.999* | 0.554      | 2.27×10⁻⁶ | 0.633 |
|      | DH605  | -64.458     | 0.027 | 0.995  | -0.231     | 6.18×10⁻⁵ | 0.999* |
| 2018 | DH518  | -43.551     | 0.026 | 0.919   | 0.294      | 2.30×10⁻⁶ | 0.912 |
|      | DH605  | -90.840     | 0.031 | 0.999*  | 0.393      | 1.19×10⁻⁵ | 0.845 |
| 2019 | DH518  | -92.757     | 0.030 | 0.981   | 0.159      | 3.40×10⁻⁶ | 0.762 |
|      | DH605  | -50.962     | 0.027 | 0.994   | -0.361     | 7.20×10⁻⁵ | 0.947 |
| 2020 | DH518  | -57.909     | 0.026 | 1.000** | 0.426      | 1.20×10⁻⁵ | 0.893 |
|      | DH605  | 81.237      | 0.017 | 1.000*  | 0.339      | 1.52×10⁻⁵ | 0.938 |
| 2021 | DH518  | 64.431      | 0.016 | 0.937   | 0.465      | 9.55×10⁻⁶ | 0.996 |
|      | DH605  | -29.644     | 0.025 | 0.998*  | 0.157      | 3.04×10⁻⁶ | 0.943 |

r, correlation coefficient. ** and * indicated significantly different at the 0.01 and 0.05 probability levels, respectively. DH518, Denghai518; DH605, Denghai605.
we should pay attention not only to the changes of growth period of different hybrids, but also to the differences of light and temperature resource use efficiency from silking to physiological maturity stage. In addition, it is necessary to further explore the physiological and molecular mechanisms that cause this difference, such as changes in the expression of genes and metabolic enzymes related to plant senescence.

Accumulation, distribution and transport of dry matter in different summer maize hybrids

Grain filling of cereal crops depends on two sources of photosynthate, current photosynthate transferred directly to the grain and redistribution of photosynthate from reserve pools in vegetative tissues (Johnson and Tanner, 1972; Pheloung and Siddique, 1991; Kobata et al., 1992; Schnyder, 1993; Blum et al., 1994; Yang and Zhang, 2006). The characteristics of PrSDMR and PrSDMRC of different summer maize hybrids have been widely studied (Ning et al., 2013; Horacio et al., 2014; Chen et al., 2015a). However, the calculation of the proportion of DMRE and pre-silking and post-silking DMRC are not accurate. For example, about 40% of the PrSDMA was used to meet the development of other organs such as cob and bract (Figure 3), which was not taken into account in most articles. Therefore, $^{13}$C pulse labeling technique was used to investigate the dry matter distribution characteristics of summer maize hybrids with different growth duration in this experiment. The $^{13}$C distribution to grains of DH518 was significantly higher than that of DH605, and the contribution rate to yield of HI and the HI of DH518 was significantly higher than that of DH605 (Table 8; Figure S2). This may be related to the activities of related enzymes in the process of sucrose transport, and higher amylase and SPS activities can promote starch degradation and photosynthetic redistributed from stalk to grain (Wang and Zhang, 2020). The next step could

| Year | Hybrid | Grain/leaf (kg m$^{-2}$) | Harvest index |
|------|--------|---------------------------|---------------|
| 2017 | DH518  | 0.268 ± 0.003a             | 0.582a         |
|      | DH605  | 0.252 ± 0.003b             | 0.559b         |
| 2018 | DH518  | 0.269 ± 0.005a             | 0.567a         |
|      | DH605  | 0.247 ± 0.002b             | 0.544b         |
| 2019 | DH518  | 0.274 ± 0.004a             | 0.576a         |
|      | DH605  | 0.259 ± 0.003b             | 0.554a         |
| 2020 | DH518  | 0.253 ± 0.004a             | 0.572a         |
|      | DH605  | 0.241 ± 0.005b             | 0.537b         |
| 2021 | DH518  | 0.267 ± 0.009a             | 0.578a         |
|      | DH605  | 0.249 ± 0.003b             | 0.544b         |
| Year (Y) |        | 12.697**                  | 6.399**        |
| Hybrid (H) |       | 91.963**                  | 134.497**      |
| Y × H |        | 0.990                     | 1.491          |

In the same year, means followed by a common letter are not significantly different by LSD test at the 5% level of significance. DH518, Denghai518; DH605, Denghai605. ** indicated significantly different at the 0.01 and 0.05 probability levels, respectively.
be to focus on the changes in the activities of these related enzymes to explain the reasons for the higher HI of DH518. This indicates that DH518 distributes more photosynthate from stalks to grains to ensure grain development. Non-structural carbohydrates stored in vegetative tissues can be remobilized and exported to grains during grain filling (Yang et al., 2001), but their contribution is limited (Cliquet et al., 1990). In wheat, 7-36% of the yield comes from the PrSDMR, and most of the yield comes from current photosynthate transferred directly (Austin et al., 1977; Papakosta and Gagianas, 1991; Masoni et al., 2007). The duration of sowing-R1 were 5-6 days shorter than that of DH605 (Table 1). The results based on 13C pulse labeling showed that the DMRC of DH518 was significantly higher than that of DH605 (Table 4), which indicated that the shortening of sowing-R1 had no negative effect on yield. Most of the grain dry matter of maize comes from the photosynthetic products produced during grain filling (Tollenaar et al., 2004; Lee and Tollenaar, 2007), which is supported by the post-silking slight decrease of dry matter in vegetative tissues (Table 3). The PoSDMA of DH605 was significantly higher than that of DH518 (Figure 2). More PoSDMA may eventually make a significant contribution to higher yield. Our results showed that the contribution rate of PoSDMA to the yield of different summer maize hybrids was more than 90% (Table 4), which played a decisive role in the increase of yield.

**HI and DMA of summer maize hybrids with different growth duration**

The effects of HI and DMA on yield varied with crop species. The wheat yield was mainly attributed to the increase in HI (Nass, 1980; Brancourt-Hulmel et al., 2003; Xiao et al., 2012; Lo Valvo et al., 2017). In rice, the increase in yield before 1980 was related to the increase in HI, while after 1980 that was due to the increase in biomass production (Peng et al., 2000), which was similar to the succession of Chinese Japonica hybrids (Xiong et al., 2011). So far, hybrid rice and super rice have higher yields, which was mainly due to an increase in DMA rather than an increase in HI (Yang et al., 2006). However, maize as a C₄ plant is different from most small-grain crops. Our results showed that the increase in DH518 yield in different years was mainly due to the increase in DMA and HI, while the increase in the yield of DH605 in different years was mainly depended on the increase in DMA. The grain/leaf ratio and HI of the population could be a better way to reflect the source-sink relationship of the population (Rajcan and Tollenaar, 1999). According to the theoretical value of the target yield of 15,000kg ha⁻¹ and the LAI was 5-6 when intercepting 95% solar radiation, the grain-leaf ratio was 0.3–0.25 (Wang, 2008). The grain/leaf ratio of different summer maize hybrids was higher than 0.25 kg·m⁻² (Table 8). On the premise of increasing the grain-leaf ratio,
increasing the density and “expanding the pool and strengthening the source” can make the leaves per unit area to supply more grains and further increase the yield. With the increase of density, the DMA of maize per unit area increased significantly (Duvick, 2005; Li et al., 2015). Our results showed that the contribution rate of DMA to yield of different summer maize hybrids was higher than that of HI (Figure S2). Our previous studies have confirmed that the yield of DH518 was significantly lower than that of DH605 under 75,000 ha⁻¹ planting density. There was no significant difference between the yield of DH518 at 90,000 plants ha⁻¹ and that of DH605 at 75,000 plants ha⁻¹, both of the two treatment yields were significantly higher than that of DH518 under 75,000 ha⁻¹ planting density. (Wan et al., 2018; Figure 6 and S3). Therefore, the yield loss caused by the decrease of the light and temperature resource use efficiency from silking to physiological maturity stage could be made up by increasing the planting density of DH518 to increase the population DMA and light and temperature resource use efficiency.

**Conclusion**

The yield of DH605 was significantly higher than that of DH518. The difference in the growth period of different hybrids was mainly in the V6 to R1 stage. Compared to DH518, the higher light and temperature resource use efficiency from silking to physiological maturity stage of DH605 led to higher yield. The shortening of the growth stage of DH518 from sowing to R1 stage could make up for the yield loss by increasing the harvest index. The yield of DH518 could be increased by reasonably increasing planting density. Therefore, it is necessary to further study the carbon transport process of the plant to explain the association between the shortened growth period and the increased HI of early maturity hybrid. This study can provide a feasible research direction for the breeding and high yield and high efficiency cultivation of early maturity summer maize in the future.

**Data availability statement**

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

**Author contributions**

JyZ: Data curation, writing—original draft, visualization, and investigation. BR, BZ, and PL: Supervision. JwZ: Conceptualization, writing—review and editing, and funding acquisition. All authors contributed to the article and approved the submitted version.

**Funding**

This work was supported by Province Key Research and Development Program of Shandong (2021LZGC014-2), National Natural Science Foundation of China (32172115), the earmarked fund for CARS (CARS-02-21).

**Conflict of interest**

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Publisher’s note**

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

**Supplementary material**

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.992311/full#supplementary-material
Oncini, F. (2021). Food support provision in COVID-19 times: a mixed method study based in greater Manchester. Agric. Hum. Vol. 38, 1201–1213. doi: 10.1007/s10460-021-00122-2

Papakosta, D. K., and Gagianas, A. A. (1991). Nitrogen and dry matter accumulation, remobilization, and losses for Mediterranean wheat during grain filling. Agron. J. 83, 864–870. doi: 10.2134/agronj1991.00021962008300050010x

Peng, S. B., Laza, R. C., Visperas, R. M., Sansico, A. L., Cassman, K. G., and Khush, G. S. (2000). Grain yield of rice cultivars and lines developed in the Philippines since 1966. Crop Sci. 40, 307–314. doi: 10.2135/cropsci2000.402307x

Pheloung, P., and Siddique, K. (1991). Contribution of stem dry matter to grain yield in wheat cultivars. Funct. Plant Biol. 18, 53–64. doi: 10.1071/FP910005

Piazza, P., Jasinski, S., and Tsiantis, M. (2005). Evolution of leaf developmental mechanisms. New Phytol. 167, 693–710. doi: 10.1111/j.1469-8137.2005.01466.x

Ptaszyńska, G., and Silesia, H. (2008). Yield variation of maize hybrids with different growing period in climatic conditions of central wielkopolska region. Dulwich Centre Review. 7, 93. doi: 10.1063/1.1692755

Rajcan, I., and Tollenaar, M. (1999). Source: sink ratio and leaf senescence in maize. Dry matter accumulation and partitioning during grain filling. Field Crops Res. 60, 245–253. doi: 10.1016/s0378-4290(98)00142-7

Radda, A., Janssen, B. H., and Tenningh, E. J. M. (2003). Effects of soil properties, mulch and NPK fertilizer on maize yields and nutrient budgets on fertility soils in southern Benin. Agr. Ecosyst. Environ. 100, 265–273. doi: 10.1016/S0167-8809(03)00184-1

Schnyder, H. (1993). The role of carbohydrate storage and redistribution in the source-sink relations of wheat and barley during grain filling - a review. New Phytol. 123, 233–245. doi: 10.2307/2557991

Schussler, J. R., and Westgate, M. E. (1994). Increasing assimilate reserves does not prevent kernel abortion at low water potential in maize. Crop Sci. 34, 1569–1576. doi: 10.2135/cropsci1994.0011183X003400060002x

Scott, C. C., and Hector, J. B. (1997). Using a chlorophyll meter to estimate specific leaf nitrogen of tropical maize during vegetative growth. Agron. J. 89, 557–562. doi: 10.2134/agronj1997.00022196008900040004x

Slattery, R. A., and Ort, D. R. (2021). Perspectives on improving light distribution and light use efficiency in crop canopies. Plant Physiol. 185, 34–48. doi: 10.1093/plphys/kaa006

Sun, H. Y., Zhang, X. Y., Chen, S. Y., Pei, D., and Lu, C. M. (2007). Effects of harvest and sowing time on the performance of the rotation of winter wheat-summer maize in the north China plain. Ind. Crop Prod. 25, 239–247. doi: 10.1016/j.indcrop.2006.12.003

Tollenaar, M. (1989). Genetic improvement in grain yield of commercial maize hybrids grown in Ontario from 1959 to 1988. Crop Sci. 29, 1365–1371. doi: 10.2135/cropsci1989.0011183X002900040007x

Tollenaar, M., Ahammadzadeh, A., and Lee, E. A. (2004). Physiological basis of heterosis for grain yield in maize. Crop Sci. 44, 2086–2094. doi: 10.2135/cropsci2004.2086

Valentiniu, O. R., and Tollenaar, M. (2004). Vertical profile of leaf senescence during the grain-filling period in older and newer maize hybrids. Crop Sci. 44, 827–834. doi: 10.2135/cropsci2004.8270

Wang, Y. J. (2008). Study on population quality and individual physiology function of super high-yielding maize (Zea mays L.) (Taian Shandong Agric. Univ.). doi: 10.7666/d.y1374885

Wang, J., Wang, E., Yang, X., Zhang, F., and Hong, Y. (2012). Increased yield potential of wheat-maize cropping systalk in the north China plain by climate change adaptation. Climatic Change. 113, 825–840. doi: 10.1007/s10584-011-0385-1

Wang, G., and Zhang, J. (2020). Carbohydrate, hormone and enzyme regulations of rice grain filling under post-anthesis soil drying. Environ. Exp. Bot. 178, 104165. doi: 10.1016/j.envexpbot.2020.104165

Wan, Z. H., Ren, B. Z., Zhao, B., Liu, P., and Zhang, J. W. (2018). Grain filling and dehydroning characteristics of summer maize hybrids with different growth duration and effect of plant density. Acta Agron. Sin. 44, 1517–1526. doi: 10.3724/SP.J.1006.2018.01517

Wu, F. B., Wu, I. H., and Xi, F. H. (1998). Chlorophyll meter to predict nitrogen sidegrew requirements for short-season cotton (Gossypium rursaturn). Field Crops Res. 56, 309–314. doi: 10.1016/s0378-4290(97)00108-1

Xiao, Y. G., Qian, Z. G., Wu, K., Liu, J. J., Xia, X. C., Ji, W. Q., et al. (2012). Genetic gains in grain yield and physiological traits of winter wheat in Shandong province, China, from 1969 to 2006. Crop Sci. 52, 44–56. doi: 10.2135/cropsci2011.05.0246

Xiong, J., Chen, G. L., Wang, S. H., and Ding, Y. F. (2011). The difference in grain yield and plant type among typical japonica hybrids in different years in jiangsu province. J. Nanjing Agric. Univ. 34, 1–6. doi: 10.7685/jissn.1000-2030.2011.05.001

Yang, J. C., Wang, P., Liu, L. J., Wang, Z. Q., and Zhu, Q. S. (2006). Evolution characteristics of grain yield and plant type for mid-season indica rice cultivars. Acta Agron. Sin. 07, 949–955. doi: 10.3321/journals.cnki.xjns.0.2006.07.001

Yang, J., and Zhang, J. (2006). Grain filling of cereals under soil drying. New Phytol. 169, 223–236. doi: 10.1111/j.1469-8137.2005.01597.x

Yang, J. C., Zhang, J. H., Wang, Z. Q., Zhu, Q. S., and Wang, W. (2001). Remobilization of carbon reserves in response to water deficit during grain filling of rice. Field Crops Res. 71, 47–55. doi: 10.1016/S0378-4299(01)00147-2

Zhang, R. X., and Cheng, Z. Q. (1992). Preliminary study on the net photosynthetic active duration of leaf in wheat. J. Nanjing Normal Univ. (Natural Sci. Edition). 15, 76–86. doi: cnki:issn:1000-0000-0000-0000

Zhao, J. Y., Ren, B. Z., Zhao, B., Liu, P., and Zhang, J. W. (2021). Relationship between growth and development characteristics and yield formation of summer maize hybrids with different growth duration. Sci. Agric. Sin. 54, 46–57. doi: 10.3864/j.issn.0578-1752.2021.01.004