Changes of Photosynthesis Efficiency during the Process of Modern Maize Breeding

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Abstract: Crop yield has always been an important problem in solving the demand of the global population increase and food supply. In addition to increasing planting density, improving crop photosynthetic efficiency is the most effective measurement to increase crop yield. Maize is the world's largest crop with a typically high photosynthetic efficiency, however, how to further increase its photosynthetic efficiency is still largely unknown, especially since its photosynthetic efficiency change during the process of modern maize breeding has not yet been reported. In this study, several typical important photosynthetic efficiency indexes, including chlorophyll content, maximum photochemical efficiency () and actual photochemical efficiency (ΦPSII), were compared between representative inbred lines of different ages. The results showed that the chlorophyll content, Fv/Fm and ΦPSII were significantly increased with age during the modern maize breeding process, which guided the breeding and improvement of new varieties of maize with high photosynthetic efficiency.

1. Introduction

The world's population is growing at 1.2% per year and is expected to exceed 10 billion people by around 2050. Combined with unpredictable natural disasters, such as floods, high temperatures, drought and freezing damage, crop yields will be severely reduced. For example, the global climate is showing a continuous warming trend, and the average annual surface temperature has significantly increased. It was reported that the average annual temperature in the areas where wheat, barley, maize, rice and soybeans are grown has increased by 0.6 °C between 1990 and 2000, and it is expected to increase by 2.5-4.3 °C by 2080 due to the influence of greenhouse gases (Tebaldi et al. 2006). The warming of the climate will directly affect crop yields. A one-degree increase in average temperature will result in a 4-6% decrease in wheat, a 7.4% decrease in maize, a 3.2% decrease in rice and a 3.1% decrease in soybean (Asseng et al., 2015; Khan et al., 2023). Yields of crops such as cassava, oats and potatoes are also significantly reduced due to higher average temperatures (Agnolucci et al., 2020). In addition, the frequency of extremely high temperatures has increased in recent years, which increasing crop mortality and thus having a more adverse impact on crop yields (Xu et al., 2021). As a result of extremely high temperatures, a 39% and 38% decrease in the production of camelflower and rapeseed was recorded, respectively (Ahmad et al., 2021). Thus, considering the population increase and natural disasters, enough food supply is currently the most essential challenge for the growing population. It is estimated that global food production needs to increase by at least 2.4% per year on average to meet the demand for global food. However, the production of the four major crops (maize, wheat, rice and soybean) has been growing at a rate of only 0.9% to 1.6% per year in recent years, and the growth rate is increasingly slow and has reached a plateau (Ray et al., 2013). Therefore, to meet the needs of food growth, it is urgent to seek new ways and strategies.

Long-term breeding practice has shown that high-density planting is an effective way to increase crop yield per unit area with limited arable land. The essence of a plant with density tolerance is that it can reasonably distribute light and nutrients under a high-density environment to ensure excellent stress resistance, so as to achieve good adaptability to the population environment, high photosynthetic efficiency, reasonable and efficient operation of the source, flow and reservoir of photosynthetic products, and finally obtain higher population yield. The compact plant architecture plays an important role in light interception, improvement of photosynthetic efficiency and reasonable distribution of assimilates (source enhancement and flow thinning) (Zhu et al. 2010). Take maize as an example, the increase of yield per plant and heterosis is not obvious in the process of modern maize breeding, and the increase of yield per plant is more dependent on the continuous growth of variety density tolerance and planting density. It was found that transforming compact maize varieties into flat plantings was not conducive to dense planting, and the

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yield reduction could reach 13.79% under dense planting conditions, whereas transforming flat plantings into compact maize varieties could significantly improve the density tolerance and increase the yield by 16.9% under dense planting conditions (Ren et al., 2010). In the United States, maize planting density rose from the ~35,000 plants/ha in 1930s to ~80,000 plants/ha in 2010s, and the corresponding yield also increased from 1287 kg/ha to 9595 kg/ha (2010s). The 7-folder yield increase between 1930s to 2010s mainly depends on the increase in planting density while the increase of yield per plant and heterosis was not obvious. Studies on maize varieties of different ages in China also showed that, compared with earlier varieties, current varieties showed better adaptability to high-density cultivation conditions in terms of yield, photosynthetic efficiency, lodging resistance and empty stalk ratio (Luo et al., 2023). It showed that the increase of planting density contributed much more to total production growth than the increase in yield per plant.

In addition to increasing crop planting density, in recent years, theoretical model analysis and a large number of crop genetic improvement studies have shown that improving crop photosynthetic efficiency can not only meet the needs of grain yield but also save arable land, which is the most effective way to increase the yield for almost all crops. Improve the photosynthetic efficiency of crops and cultivating the crop varieties with high photosynthetic efficiency is different from reforming the morphological structure of plants and improving the absorption efficiency of light energy, instead, it focuses on the physiological and biochemical functions of plants and selects and cultivates crop varieties with low carbon dioxide compensation point, high net photosynthetic rate and high light-energy utilization efficiency. Compared with other energy use efficiency in nature, plants are more sensitive to light. The energy utilization efficiency of plants is rather low with only about 1% of light energy from the sun used for material production, and the rest of the light energy is lost in the environment as heat. Under natural conditions, the theoretical light energy utilization rate of crops is 6% ~ 8%, however, considering the differences in varieties, environment and nutritional status, the actual light energy utilization rate of crops is rather lower than the theoretical effect with only 0.5% ~ 1.0%. Therefore, breeders believe that high light efficiency breeding can effectively improve the photosynthetic efficiency of crops in several ways, including improving the population canopy light interception capacity, optimizing the efficiency of light energy absorption, transfer and conversion, improving the efficiency of carbon assimilation, reforming and assembling C4 photosynthetic pathway and CO_2 concentrating mechanism, and synergistically improving high photosynthetic efficiency and resource efficiency. So far, several studies have been conducted to increase photosynthetic efficiency by increasing the content of chlorophyll or the size of the light-trapping antenna. For example, the biomass of the tobacco yellow mutant increased by 25% compared with the wild type (Kirst et al., 2017). By heterologically expressing the coding genes of violaxanthin deepoxide, zeaxanthin epoxide and photosystem II subunit S protein involved in the lutein cycle in Arabidopsis thaliana into tobacco and soybean, the light energy use efficiency of the transgenic plants could be improved by reducing non-photochemical quenching and thereby increasing tobacco biomass by 14%-20% and soybean yield by up to 33% (Taylor et al., 2017; Wang et al., 2020; Kromdijk et al., 2016; De Souza et al., 2022).

Maize (*Zea mays ssp.mays L.*) is one of the most important crops in the world, which can be used to prepare feed, food additives, chemical raw materials and bioenergy. Maize is one of the earliest domesticated crops and is now widely cultivated around the world. Zea mays ssp. Parviglum is from southern Mexico and North America is the ancestor of modern maize, and whereafter different varieties of maize are widely cultivated in temperate and subtropical regions of the globe (Yang et al., 2017). The archaeological findings and botanical evidence from different regions show that maize spreads north and south from the southern Mexico region where it originated, and gradually adapted to different climatic and environmental conditions. After Columbus discovered the New World, maize was first introduced to Spain, and gradually spread from the Mediterranean to the European continent. Recent studies have shown that early cultivated maize was independently domesticated from the subspecies of teosinte 9,000 years ago and then introduced into the central plateau of Mexico around 6,000 years ago, and a cross occurred with the Mexican plateau subspecies, introducing about 18% of the Mexican plateau subspecies genome, achieving the second domestication of maize (Yang et al., 2023). Thus modern maize breeding originated in the Americas and has a long breeding history. After that people have made many improvements to maize varieties resulting from the foundation for the later development of maize breeding. In the early 20th century, with the rise of agricultural mechanization and the application of modern molecular biology techniques, maize breeding made great progress. Different growing environments facilitated the selection of new and superior genes, which also facilitated the adaptation of maize varieties to a wider range of regions and environments. In the past few centuries, with the continuous improvement and perfection of maize breeding methods, maize varieties have been optimized and improved to adapt to diverse ecological environments and people's requirements for food quality and yield, such as cold-tolerant varieties, drought-tolerant varieties, disease-resistant varieties, insect-resistant varieties and so on.

Maize is ones of the typical C4 crops with relatively high photosynthesis efficiency compared with C3 crops such as rice, wheat and cotton. However, there are few studies on the changes in photosynthetic efficiency in the process of modern maize breeding, which limits the further genetic improvement of maize with higher photosynthetic efficiency for more grain yields per arable land to meet the great demand of global food. In this study, representative inbred lines widely used in modern maize breeding in China and the United States, the main maize planting country was collected, and the important parameters related to photosynthetic efficiency, including the chlorophyll content, actual photochemical efficiency and maximum photochemical efficiency, were individually investigated and analyzed to reveal their change with maize breeding process. This study aims to provide some information and guidance for the breeding and improvement of maize varieties with high photosynthetic efficiency.

2. Materials and methods

2.1 Material Planting

The experiment was conducted from May 2023 to August 2023 at the Maize Comprehensive Test Base of the Agricultural University of Hebei (37.88°N, 115.16°E). The maize lines included 150 representative inbred lines from different breeding ages in China and the United States. The maize was sown in the field in May 2023, and the indexes were investigated at the V7-stage leaves in July 2023.

2.2 Chlorophyll content determination

The Chlorophyll content was determined with the hand-held SPAD chlorophyll analyzer SPAD-502 Plus (Konica Minolta, Japan). To determine the chlorophyll content, the third mature maize leaf (from top to bottom) was used and the flat parts and non-vein areas were selected for detection, and the measurement was repeated three times for each leaf, and more than 8 plants were determined for each inbred line.

2.3 Determination of the actual photochemical efficiency

The actual photochemical efficiency determination was conducted between 9:00 am and 11:00 am on a sunny day, the chlorophyll fluorescence analyzer PAM-2500 Waltz (Germany) was used to determine the fully developed leaf parts of the third mature leaf (from top to bottom) of maize, and the actual photochemical efficiency was determined in the non-vein area. Each leaf was measured for three times, and more than 8 plants were determined for each inbreeding line.

2.4 Determination of maximum photochemical efficiency

To detect the maximum photochemical efficiency of each inbred line, the middle and upper part of the third mature leaf (from top to bottom) of every plant was detached and put in the darkroom for 30 minutes. Then, the chlorophyll fluorescence analyzer above is used to determine the flat and non-vein area of each leaf. Each leaf is measured for three times to calculate the maximum photochemical efficiency, and more than 8 representative plants of each inbred line are determined. The average value of was representative plants of each inbred line taken as the maximum photochemical efficiency of the inbred line.

2.5 Data processing and graphing

The data were sorted by Excel 2010 software, and the mean and standard deviation were calculated by SPSS 26.0 software. Statistical bar charts were generated by inputting the raw values with the statistical software GraphPad Prism (version 8.3.0).

3. Results

3.1 Change of chlorophyll content

To analyze the changing trend of photosynthetic efficiency in the process of modern maize breeding, the 150 representative inbred lines widely used in different breeding periods in China and the United States were collected. Among them, the Chinese maize inbred lines were selected from the 1960s, 1980s and 2010s, with 30 representative inbred lines in each decade. For the United States inbred lines, 30 the early public inbred lines (Public-US) and 30 the expired proprietary inbred lines (Ex-PVP) were selected. Thus a total of 150 inbred lines were investigated for comparative analysis in this study (Figure 1A). These inbred lines were planted in the field and measured during the V7 stage with the seventh leaf fully spread out. The leaves of these maize inbred lines present different types in terms of leaf color, leaf shape and vein striation (Figure 1B).

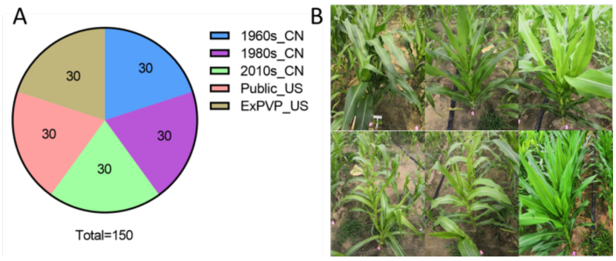

Figure 1. The 150 modern maize inbred lines of different years for China and the US were used in this study. The lines show obvious differences in leaf color (chlorophyll content) and leaf veins.

Photosynthesis in plants is the process of converting light energy from the sun into chemical energy through chloroplasts, which are stored in organic matter and released with oxygen. The first step in photosynthesis is for the light energy to be absorbed and ionized by the chlorophyll. The resulting chemical energy is temporarily stored in adenosine triphosphate (ATP) and eventually converts carbon dioxide and water into carbohydrates and oxygen. The chlorophyll of plants can be divided into chlorophyll a and chlorophyll b, depending on their molecular structure. Chlorophyll absorbs most red and violet light but reflects green light, so the chlorophyll appears green and can be seen as embedded between the protein layer and a carotenoid lipid with a chain of chlorophyll phytols. Chlorophyll plays a central role in light absorption in photosynthesis. The higher the chlorophyll content, the stronger the plant's ability to absorb light energy, and the higher the rate of photosynthesis, suggesting there is a positive correlation between the chlorophyll content of plants and photosynthesis (Šesták et al., 1965).

The investigation shows that the total chlorophyll content of maize inbred lines from different ages in China is significantly different and it shows a trend with the increase of chlorophyll content of maize leaves with modern maize breeding process. The chlorophyll content in the inbred lines from the 1960s, 1980s and 2010s were 40.63 ± 5.06, 43.33 ± 3.95 and 45.95 ± 4.46, respectively (Figure 2A). Similarly, the comparison of chlorophyll content of inbred lines from different breeding periods in the United States also showed that the chlorophyll content of inbred lines in the early breeding period (Public-US) was significantly lower than that of recent expired proprietary inbred lines (Ex-PVP), with 38.59 ± 4.36 and 44.91 ± 3.72 for Public-US and Ex-PVP, respectively (Figure 2B).

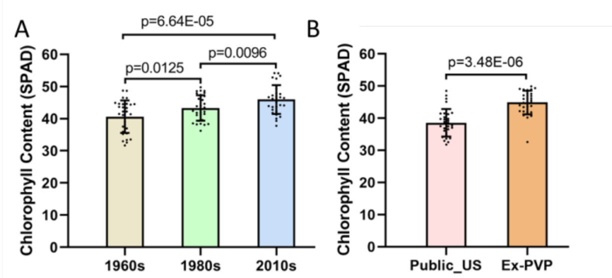

Figure 2. The chlorophyll content rises with the modern maize breeding process between eras in China and the US. Values are means ± SD (n=30 lines).

3.2 Changes in actual photochemical efficiency

Chlorophyll fluorescence in vivo is an effective probe to investigate living photosynthesis, which not only reflects the primary reaction processes of photosynthesis in vivo such as light energy absorption, excitation energy transfer and photochemical reaction, but also relates to electron transport, the establishment of proton gradient, ATP synthesis and CO_2 fixation. Chlorophyll fluorescence reflects the photosynthetic physiological state of plants quickly, easily and without damage, and its parameters include maximum photochemical efficiency (Fv/Fm), actual photochemical efficiency (APE), non-photochemical quenching amount (NPQ) and so on. The actual photochemical efficiency refers to the efficiency of light energy used by plants in actual photosynthesis, indicating the efficiency of photochemical reaction in the process of photosynthetic electron transfer and the ability of effective light energy of photosynthesis to be converted into chemical energy. In photosynthesis, plants convert carbon dioxide and water into organic matter and oxygen by absorbing light energy. Actual photochemical efficiency is a quantitative measure of a plant's ability to use light energy under specific environmental conditions. In this study, the actual photochemical efficiency was detected on a sunny day from 9:00-11:00 am and the fully developed leaves of representative maize inbred lines of different ages in China and the United States were measured. The results showed that the actual photochemical efficiency of Chinese maize inbred lines gradually increased with the increase of breeding age, and their difference between ages is significant, with 0.641±0.131, 0.676±0.134 and 0.708±0.136 for the 1960s, 1980s and 2010s, respectively. (Figure 3A). Similarly, the actual photochemical efficiency of late maize inbred lines in the United States (Ex-PVP) was significantly higher than that of early maize inbred lines (Public_US), with 0.649±0.133 and 0.701±0.134, respectively (Figure 3B).

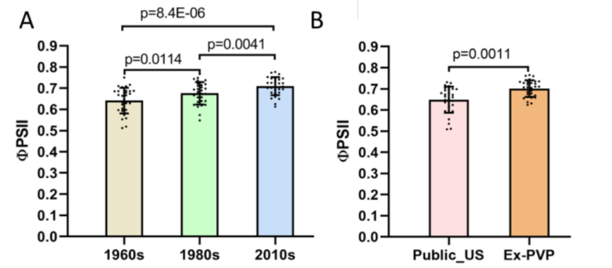

Figure 3. The actual photochemical efficiency rises with the modern maize breeding process between eras in China and US. Values are means ± SD (n=30 lines).

3.3 Maximum photochemical efficiency change

The maximum photochemical efficiency reflects the quantum yield when all reaction centres of PSII are open and all non-photochemical processes are at the minimum in the dark adaptation state, which is the potential maximum quantum yield and indicates the maximum potential of plant photochemical reaction. In this study, all the fully developed leaves of representative maize inbred lines of different ages were collected at 9:00-11:00 am on a sunny day and put in the dark room for 30 minutes and then the maximum photochemical efficiency was detected for each leaf. The results showed that the maximum photochemical efficiency of Chinese maize inbred lines gradually increased with the increase of breeding age with 0.705±0.141, 0.743±0.146 and 0.776±0.144 in the 1960s, 1980s and 2010s, respectively (Figure 4a), suggesting there are significant differences between ages. Similarly, the maximum photochemical efficiency of late maize inbred lines (Ex-PVP) in the United States was significantly higher than that of early maize inbred lines (Public_US), with 0.750±0.139 and 0.779±0.144, respectively, for early and late maize inbred lines (Figure 4b).

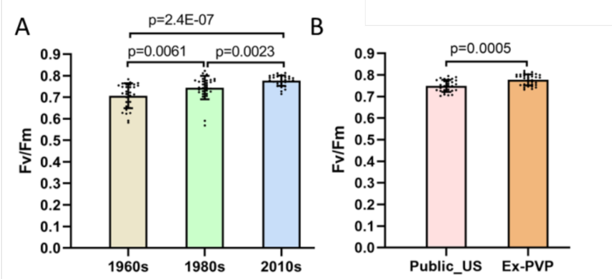

Figure 4. The maximum photochemical efficiency rises with the modern maize breeding process between eras in China and US. Values are means ± SD (n=30 lines).

4. Conclusion and discussion

In the face of global population growth, the decreasing of available arable land and the increasing occurrence of natural disasters, the global food supply is becoming increasingly severe. A reasonable increase in planting density to a certain extent can significantly increase the yield of some crops such as maize and sorghum per unit area while increasing the photosynthetic efficiency of plants is the fundamental measure to increase the yield of all crops. Maize is the largest crop in the world, and its yield is of great importance in addressing food supply. In the past few decades, with the improvement of maize varieties and cultivation methods, the yield per unit area of maize has greatly increased. Maize has the typical Kranz structure of C4 plants and special vascular sheath cells in leaves and has the characteristics of high light intensity saturation point, extremely low light respiration, and relatively low carbon dioxide compensation point, so its genetic improvement progress of high light efficiency is rather slower compared with rice and wheat.

In this study, 150 representative inbred lines from different ages of modern maize breeding process in China and the United States were selected to conduct field experiments and compared the important photosynthetic efficiency, including chlorophyll content, maximum photochemical efficiency and actual photochemical efficiency, with an attempt to reveal the changes of photosynthetic efficiency during the process of modern maize breeding. The results showed that the chlorophyll content, maximum photochemical efficiency and actual photochemical efficiency of maize in different ages in China and the United States all showed a significant increase trend with the maize breeding process in China and the United States, indicating that germplasm with high photosynthetic efficiency potential was selected and retained in the modern breeding process (2010s and Ev-PVP for China and the United States, respectively). Thus, the key genes involved in photosynthetic efficiency will be further identified from the current representative maize inbred lines and their useful and functional natural variations and excellent haplotypes in genetic structure will be compared with those of earlier varieties. The natural variations and excellent haplotypes will be introduced into the current varieties with excellent agronomic traits but low photosynthetic efficiency. At the same time, usable molecular markers will be developed from the current maize inbred lines with high photosynthesis efficiency and applied to identify the common maize inbred lines.

Additionally, only 30 inbred lines in each decade and a total of 150 inbred lines from China and the United States were selected for field experiments, and only three indexes for each inbred line, including the chlorophyll content, maximum photochemical efficiency and actual photochemical efficiency, were investigated in this study, thus its results preliminarily revealed the changing trend of photosynthetic efficiency in the modern breeding process. In the future, we will collect more inbred lines in each era, and comprehensively investigate and measure more parameters related to maize photosynthetic efficiency, including net photosynthetic rate, intercellular carbon dioxide concentration, leaf stomatal conductance, and other chlorophyll fluorescence parameters, to accurately reflect the changes of photosynthetic efficiency in modern maize breeding. In addition, considering the natural disasters often encountered in actual agricultural production such as high temperature, drought and waterlogging, we will simulate these natural disaster conditions to detect the changes in the photosynthetic efficiency of these inbred lines during modern maize breeding.

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