

Modern maize hybrids in Northeast China exhibit increased yield potential and resource use efficiency despite adverse climate change

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Abstract

The impact of global changes on food security is of serious concern. Breeding novel crop cultivars adaptable to climate change is one potential solution, but this approach requires an understanding of complex adaptive traits for climate-change conditions. In this study, plant growth, nitrogen (N) uptake, and yield in relation to climatic resource use efficiency of nine representative maize cultivars released between 1973 and 2000 in China were investigated in a 2-year field experiment under three N applications. The Hybrid-Maize model was used to simulate maize yield potential in the period from 1973 to 2011. During the past four decades, the total thermal time (growing degree days) increased whereas the total precipitation and sunshine hours decreased. This climate change led to a reduction of maize potential yield by an average of 12.9% across different hybrids. However, the potential yield of individual hybrids increased by 118.5 kg ha⁻¹ yr⁻¹ with increasing year of release. From 1973 to 2000, the use efficiency of sunshine hours, thermal time, and precipitation resources increased by 37%, 40%, and 41%, respectively. The late developed hybrids showed less reduction in yield potential in current climate conditions than old cultivars, indicating some adaptation to new conditions. Since the mid-1990s, however, the yield impact of climate change exhibited little change, and even a slight worsening for new cultivars. Modern breeding increased ear fertility and grain-filling rate, and delayed leaf senescence without modification in net photosynthetic rate. The trade-off associated with delayed leaf senescence was decreased grain N concentration rather than increased plant N uptake, therefore N agronomic efficiency increased simultaneously. It is concluded that modern maize hybrids tolerate the climatic changes mainly by constitutively optimizing plant productivity. Maize breeding programs in the future should pay more attention to cope with the limiting climate factors specifically.

Keywords: climate change, dry matter accumulation, grain nitrogen concentration, maize, post-silking, stay-green, yield potential

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Introduction

Climate change has a crucial influence on crops because growth and development are affected by sunlight, temperature, and water. The impact of global changes in food security is of increasingly serious concern (e.g., Schmidhuber & Tubiello, 2007). Maize (*Zea mays* L.) is an important food crop worldwide. During the period 2000–2050 the global cereal demand is predicted to increase by more than 1000 million tons (56%); 45% of this increase is expected to constitute increased demand for maize (Hubert *et al.*, 2010). In China, the total maize yield in 2007 was 152.3 million tons (Li & Wang 2009). The Northeast China Plain, located from about 39–53°N,

is one of the most important areas in China for spring maize production. The maize yield is 50 million tons yr⁻¹ in this area, which is 35% of the total production in China (Yang *et al.*, 2007).

The effect of climate change on crop production depends on the interaction of various climatic factors and agricultural management parameters, such as nitrogen (N) input (Pan *et al.*, 2011). In Northeast China, climate change is manifested as an increase in temperature, but as a decrease in sunshine hours and precipitation (Pan *et al.*, 2011). Total grain production in the region increased rapidly because the increase in accumulated temperature led to northward expansion of the agricultural climate zone (Yang *et al.*, 2007). However, per unit maize production potential is predicted to decrease with climate change, mainly because of water shortage and extreme weather events (Pan *et al.*, 2011; Tao & Zhang, 2011).

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Crop growth may be manipulated to adapt to global climate change through adjustment of the cropping system and/or breeding of novel cultivars (Mendelsohn *et al.*, 1994). Plant breeding is a convenient technological response to environmental challenges, but the challenge is to determine which traits will have the greatest impact (Chapman *et al.*, 2012). Plant breeding has contributed to 40–50% of the increased maize yield in the USA (Tollenaar & Lee, 2002), and 35.5% in China (Wu *et al.*, 1998). However, it is not clear how genetic improvement has interacted with climate change to affect maize yield in recent decades (Duvick & Cassman, 1999). In this study, nine maize hybrids released between 1973 and 2000 in China were grown in Siping, Jilin province, Northeast China Plain, for 2 years under low and high N application levels. Grain yield, dry matter accumulation and re-translocation, N accumulation and remobilization, and photosynthesis-related traits were investigated. **Maize yield potential in the past four decades was simulated using the Hybrid-Maize model (Yang *et al.*, 2004).** The aims of the study were to investigate the effect of interaction between climate change and maize breeding on the change in potential yield, and to elucidate the adaptation mechanism of modern maize hybrids to climate change.

Materials and methods

Soil and climate of the study site

The field experiment was conducted at Siping (43°17'N, 124°26'E), Jilin province, Northeast China, in 2010 and 2011. This area is typical of those areas in which rain-fed spring maize is grown. The soil type was black soil. The soil chemical properties at the onset of the experiment were as follows: organic matter 17.5 g kg⁻¹, total N 1.2 g kg⁻¹, alkali-hydrolyzable N 176 mg kg⁻¹, available phosphorus (Olsen -P) 28.4 mg kg⁻¹, ammonium acetate extractable potassium (K) 110 mg kg⁻¹, and pH 5.4 (1 : 2.5 g/v). Meteorological data from 1973 to 2011 for Siping were obtained from the China Meteorological Administration (<http://www.cma.gov.cn>). The data set included daily sunshine hours, maximum temperature, minimum temperature, precipitation, relative humidity of the air, and wind speed. Detailed climatic data for 2010 and 2011 are shown in Figure S1.

Experimental design

The experimental design was a split-plot with four replicates, with N fertilizer treatments in the main plots and the maize hybrids in the subplots. Nine maize (*Zea mays* L.) hybrids released from 1973 to 2000 were used (Table 1). These hybrids were the dominant hybrids grown in Northeast China at the time of their release (Zhao *et al.*, 2011).

The plots were 5 m long and contained five rows spaced 60 cm apart. Plots were provided with 85 kg ha⁻¹ P₂O₅ and

90 kg ha⁻¹ K₂O before sowing. Three N fertilization treatments were employed: (1) no N application (N0); (2) 120 kg N ha⁻¹ (as N120), 60 kg ha⁻¹ N applied before sowing and 60 kg ha⁻¹ N at the V8 stage; and (3) 240 kg N ha⁻¹ (as N240), 120 kg ha⁻¹ N applied before sowing and 120 kg ha⁻¹ N at the V8 stage. For some analyses, N120 and N240 were combined as high N (HN) treatment and N0 was designated as low N (LN) treatment.

Maize seeds were hand-sown on 9 May 2010 and 4 May 2011, and harvested on 18 September 2010 and 6 October 2011. At V3 stage, seedlings were thinned to make a density of 60 000 plants ha⁻¹. Plots were kept free of weeds, insects, and diseases and no irrigation was applied in the 2 years.

Dry matter, and N accumulation and remobilization, and yield measurement

At silking and physiological maturity, the aboveground parts of three plants from each plot were cut at the soil surface and separated into leaves, stems (comprising the leaf sheath, tassels, and ear shoots), and grains. The samples were weighed and dried in an oven at 70 °C. Dry samples were ground to a powder and the N concentration was determined by the semi-micro Kjeldahl method. Silking date was determined when 50% of the ears in a plot attained silking. Physiological maturity date was determined when the black layer was visible at the grain base in 50% of the ears.

At 14 and 28 days after silking (DAS), 100 grains from the central position of five cobs from N240-treatment plots were sampled, dried, and weighed. The potential grain-filling rate (mg grain⁻¹ day⁻¹) for each hybrid was calculated as: (per grain dry weight at 28 DAS – per grain dry weight at 14 DAS)/(28–14).

At maturity, two rows were harvested for yield measurement. The numbers of fertile ears and infertile (barren) ears were recorded. Grains were oven-dried at 70 °C to determine the percentage grain moisture. Grain yield was standardized to 14% moisture. Hundred-grain weight was measured and the grain number per ear was calculated.

Based on the above measurements, the following parameters were calculated:

Dry weight (DW) per unit area (kg ha⁻¹) = whole-plant dry matter × ear density per unit area

N accumulation per unit area (kg ha⁻¹) = whole-plant N content × ear density per unit area

Harvest index (HI; %) = whole-plant grain yield/whole-plant DW × 100

N harvest index (NHI; %) = whole-plant grain N content/whole-plant N content × 100

DW translocation efficiency (%) = (whole-plant DW at silking – whole-plant DW in the stove at maturity)/whole-plant DW at silking × 100

N remobilization efficiency (NRE; %) = (whole-plant N content at silking – whole-plant N content in the stove at maturity)/whole-plant N content at silking × 100

N agronomic efficiency (kg kg⁻¹) = (grain yield per unit area under N-fertilized treatment – grain yield per unit area under non-fertilized treatment)/N application amount.

Table 1 Details of the maize hybrids used (source: Zhao *et al.*, 2011)

Cultivars	Parental combination	Breeding institution	Year of hybrid release
ZD2	Mo17 × Zi330	Chinese Academy of Agricultural Sciences, Beijing	1973
H417	Huangzao4 × Mo17	Beijing Academy of Agricultural and Forestry Sciences, Beijing	1978
DY13	Mo17 × E28	Academy of Agricultural Sciences in Dandong, Liaoning province	1979
ND60	5003 × Zong31	China Agricultural University, Beijing	1985
YD13	Ye478 × Dan340	Academy of Agricultural Sciences in Laizhou, Shandong province	1989
ND108	178 × Huang C	China Agricultural University, Beijing	1991
ZD958	Zheng58 × Chang7-2	Henan Academy of Agricultural Science, Henan province	1996
XD20	9058 × Xun92-8	Xunxian Institute of Agricultural Science, Henan province	1998
XY335	PH6WC × PH4CV	Tieling Seed-Pioneer Co., Ltd. Jilin province	2000

Climatic resource use efficiency was calculated as follows:

Climatic resource use efficiency during whole growth period = yield/climatic variables during whole growth period [sunshine hours, growing degree days (GDD), and precipitation]

Pre-silking climatic resource use efficiency = pre-silking DW accumulation/accumulated pre-silking climatic variables (sunshine hours, GDD, and precipitation)

Post-silking climatic resource use efficiency = post-silking DW accumulation/accumulated post-silking climatic variables (sunshine hours, GDD, and precipitation)

Physiological parameters

Green leaf area was quantified every 10 days from the silking stage until physiological maturity. Three plants with the same silking date were tagged in each plot and used for determination of green leaf area using the formula: green leaf area = leaf length × leaf width × 0.75 (Gallais *et al.*, 2006). Leaf area index (LAI) was calculated as the total green leaf area per unit of soil area.

To describe the leaf senescence process from silking to maturity, relative green leaf area (RGLA) was simulated using the curvilinear equation $y = ae^{b-cx}/(1 + e^{b-cx})$ (Liu *et al.*, 2009), where y is RGLA, x is days after silking, a is the initial value of RGLA at silking (RGLAs, set to 1 in the present study), b is relative to the onset of leaf senescence and c is relative to the rate of leaf senescence (Van Oosterom *et al.*, 1996). Using RGLA and the duration from silking to maturity (T), the following parameters were calculated (Liu *et al.*, 2009):

Relative green leaf area at maturity (RGLAm) = green leaf area at maturity / green leaf area at silking;

Mean rate of decrease in RGLA (V_m) = (RGLAs - RGLAm) / T ;

Date of onset of leaf senescence (t_s) = date when RGLA is 95% of initial value;

Maximum rate of decrease in RGLA (V_{max}) = $c/4$

Date of V_{max} (t_{max}) = b/c ;

Leaf area duration (LAD) = (GLAs + GLAm) × $T/2$

At the grain-filling stage, the light-net photosynthetic rate (P_n) curve of the ear leaf was measured in six maize hybrids (ZD2, DY13, YD13, ND108, ZD958, and XY335) using a portable photosynthesis system (Li6400; LI-COR, Lincoln, NE, USA). The light intensity was set to 0, 20, 50, 100, 200, 500,

1000, 1300, 1600, or 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. P_n was measured in two plants per plot from 09:00 to 15:00 hours.

Hybrid-Maize model

The Hybrid-Maize model integrates photosynthesis and respiration from SUCROS, WoFOST and INTERCOM, and the maize growth model from CERES-Maize (Jones & Kiniry, 1986; Kiniry *et al.*, 1997), and also incorporates some novel features (Yang *et al.*, 2004, 2006). In the Hybrid-Maize model, the maize yield potential is simulated based on not only light and temperature parameters but also the optimal crop management (Yang *et al.*, 2004, 2006). The model requires inputs consisting of daily weather data, soil properties, and crop parameters. Soil parameters were input as the defaults in the model. Weather parameters consist of daily maximum and minimum temperatures, relative humidity of the air, precipitation, solar radiation, and reference evapotranspiration. Solar radiation was calculated from sunshine hours and the reference evapotranspiration was calculated from daily maximum and minimum temperature, relative humidity of the air, solar radiation, and average wind speed. To stimulate the cultivar-specific yield potential, the following crop parameters were adjusted in accordance with measurements in the field experiment in 2011: potential kernel number, potential grain-filling rate, dry matter translocation efficiency, relative leaf area index at maturity, and total and pre-silking GDDs (Table 2). Planting date was set to 4 May, seeding depth was 4 cm, and planting density was 60 000 plants ha^{-1} .

Statistical analysis

The experimental data were analyzed by analysis of variance using SPSS Statistics 17.0 (SPSS, Inc., Chicago, IL, USA; Zhang & Dong, 2004). The differences were compared using the least significant difference (LSD) test. Pearson correlation coefficients were calculated using SPSS too.

Results

Climate change from 1973 to 2011

In the past four decades, the total sunshine hours and precipitation per year decreased at a rate of 6.0 h yr^{-1} and 4.1 mm yr^{-1} , respectively (Fig. 1A,C). In contrast,

Table 2 Crop parameters for the maize hybrids used as inputs for the Hybrid-Maize model

Cultivars	Potential grain number	Potential grain-filling rate	Dry matter translocation efficiency	Relative leaf area index at maturity	Total growing degree days	Pre-silking growing degree days	Phenology (days of the year, day)		
	(plant ⁻¹)	(mg grain ⁻¹ d ⁻¹)	(g g ⁻¹)	(m ² m ⁻²)	°C	°C	Sowing	Silking	Maturity
ZD2	545	6.62	0.37	0.21	1578	975	124	212	279
H417	619	8.32	0.27	0.09	1568	989	124	213	272
DY13	720	6.09	0.21	0.11	1586	1016	124	215	283
ND60	669	5.22	0.35	0.14	1586	975	124	212	283
YD13	747	6.52	0.37	0.33	1590	1004	124	214	285
ND108	718	7.01	0.18	0.71	1590	1004	124	214	285
ZD958	695	8.01	0.14	0.76	1590	975	124	212	285
XD20	740	6.84	0.26	0.60	1586	1004	124	214	284
XY335	675	8.70	0.17	0.70	1578	947	124	210	279

GDD = (maximum temperature + minimum temperature)/2 - T = 10 °C. GDD was set to be 0 °C when it was less than 0 °C.

the total thermal period, as indicated by GDDs for maize, increased gradually at a rate of 6.2 °C yr⁻¹ (Fig. 1B). The annual variation in GDD and sunshine hours was low and the respective coefficients of variation (CV) were 7.3% and 7.7%. However, precipitation varied hugely among years and the CV was as high as 19.2%. The maximum precipitation was 838 mm in 2010 and the minimum precipitation was only 369 mm in 2002.

The Hybrid-Maize model was used to simulate the silking date of each hybrid in the corresponding period that the hybrid was cultivated, and then the changes in climatic variables pre- and post-silking were calculated. During the maize growing season, both the pre- and post-silking sunshine hours decreased (Fig. 2). Pre-silking GDD decreased whereas post-silking GDD increased. Pre-silking precipitation showed a decreasing trend with high variation. Post-silking precipitation also showed marked but irregular variation.

Influence of climate change and genotype on yield potential of maize

The Hybrid-Maize model was used to simulate the potential maize yield from 1973 to 2011. The simulated maize yield in 2011 was highly correlated to the actual yield (Fig. 3), which indicated that the model was suitable for simulation of maize yield under the present experimental conditions.

When each of the tested hybrids was used to simulate the potential maize yield over the past four decades, all results indicated a trend for decreased potential yield with changing climatic conditions (Fig. 4), which suggested that the overall climatic change during the past four decades was unfavorable for maize growth. To compare the yield potential of different maize genotypes, the average yield potential of each hybrid during the period from 1973 to 2011 was calculated. The average yield potential of individual hybrids increased with increasing year of release (Fig. 5A), which indicated that modern genotypes generally showed higher yield potential regardless of climate change. The yield potential of the newest cultivar was 45% more than that of the oldest one. The increment was 118.5 kg ha⁻¹ yr⁻¹. If yield potential was simulated by matching each maize hybrid to the climatic conditions of the year(s) in which it was grown, for example ZD2 was used to simulate the yield potential from 1973 to 1977 and H417 was used to simulate the yield potential for 1978 (Table 1), the potential yield of maize hybrids still showed an increasing trend from 1973 to 2011 (Figure S2).

To test specifically whether or not the increase of yield potential is indeed an adaptive response of maize breeding to climate change, the reduction rate of yield

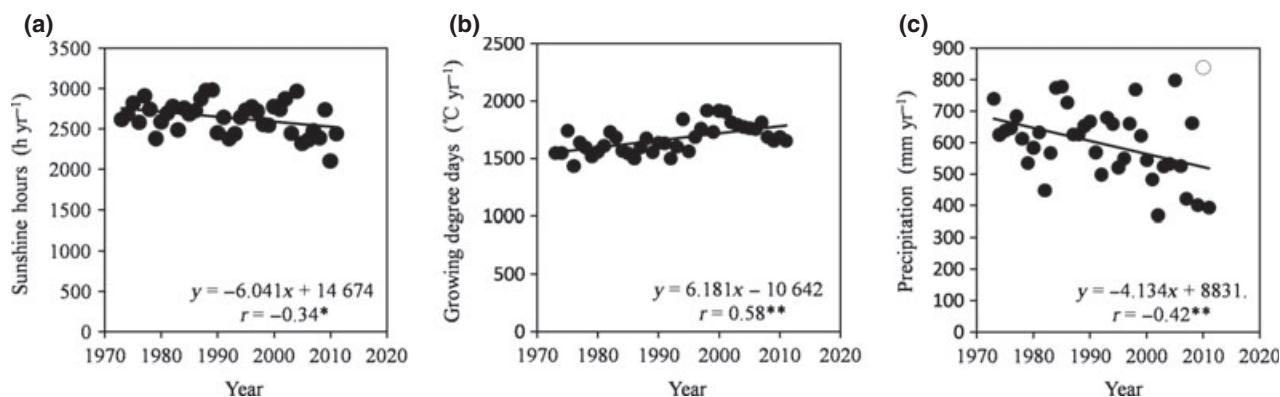


Fig. 1 Change of sunshine hours (A), GDD (B), and precipitation (C) per year from 1973 to 2011 in the experimental location. *, ** denotes significant at the 0.05 and 0.01 probability, respectively. Empty circles were excluded in the linear regression.

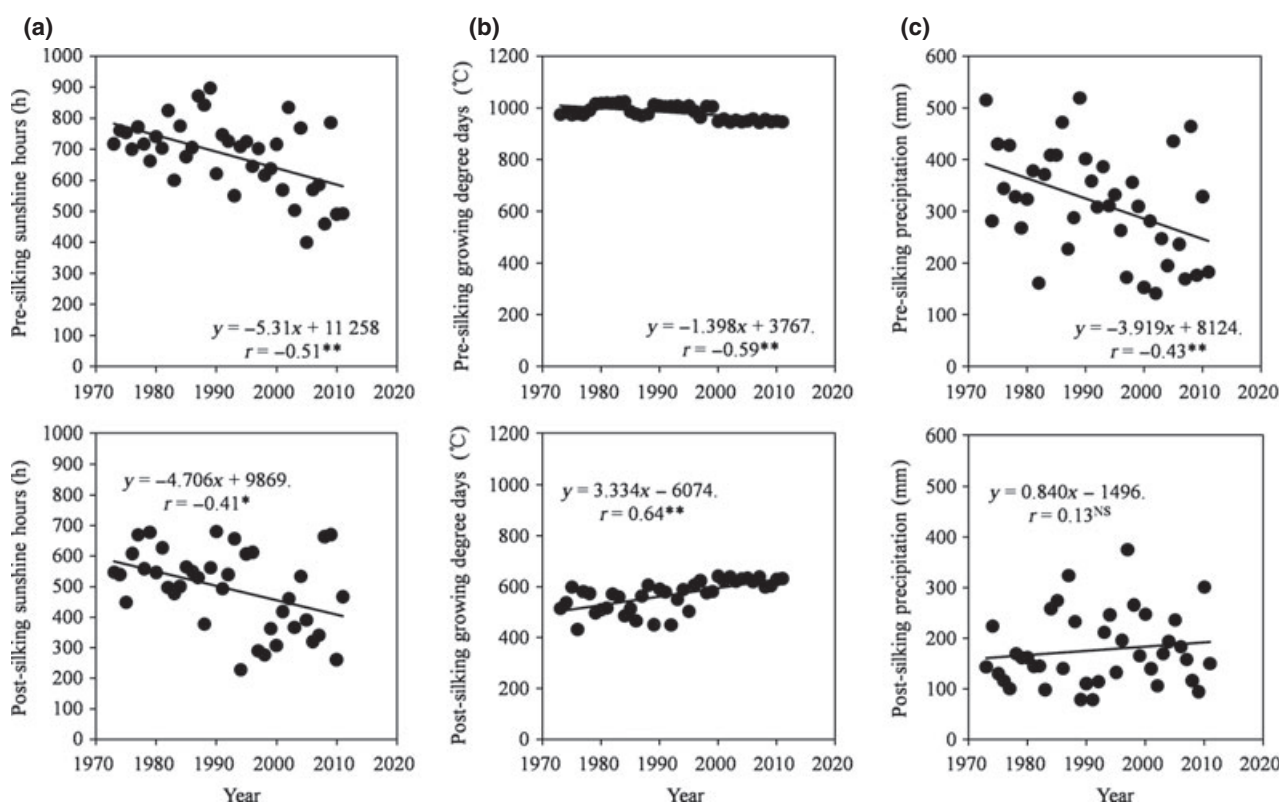


Fig. 2 Change of pre- and post-silking sunshine hours (A), GDD (B), and precipitation (C) during maize growing season from 1973 to 2011 in the experimental location. Maize planting date was set to May 4. The date of silking and maturity was determined by simulation using Maize-Hybrids model. * and ** denote significant at the 0.05 and 0.01 probability respectively. NS denotes not significant.

potential of maize grown in the climate condition of 2000s compared to that in 1970s was calculated for each hybrid (Fig. 5B). This climate change led to a reduction of maize potential yield by an average of 12.9% across different hybrids. For the two oldest hybrids, ZD2 and H417, the yield potential decreased by 14.6% and 17.4%, respectively. Thereafter, the reduction rate of yield potential significantly decreased to an average of 12.0% for the late released hybrids ($P = 0.02$). This

result suggested that modern maize hybrids were overall more adaptive to the current climate conditions. However, this adaptation happened mainly in the hybrids released from 1979 to 1991 which reduction rate of yield potential was 10.5% on the average. In comparison, the reduction rate of yield potential increased significantly to an average of 14.1% in the cultivars released after mid-1990s ($P = 0.04$). Therefore, maize cultivars released recently had mainly increased

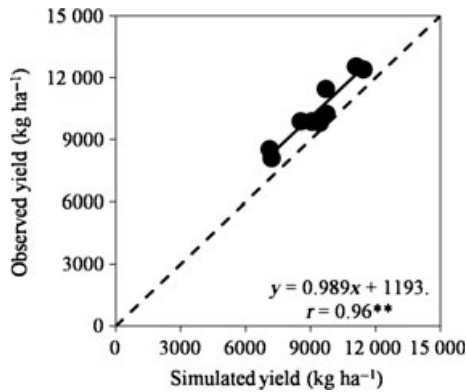


Fig. 3 Observed and simulated maize yield of 9 maize hybrids. **, significant at $P < 0.01$.

plant productivity without further improvement in the specific adaptation to climate change.

Climatic resource use efficiency in maize hybrids released in different years

To investigate how modern maize hybrids have increased yield despite the adverse climate change, the yields of the tested maize hybrids were recorded in 2010 and 2011 under three N application levels. Compared with the N0 treatment, grain yield increased significantly under the N120 and N240 treatments (Table 3). The difference in yield between the N120 and N240 treatments was not significant. Hence the grain yield and its component for these two N treatments were averaged and treated as high N treatment (HN) for further analysis. There was a positive linear relationship between grain yield and year of maize hybrid release under both low and high N treatment (Fig. 6A). Grain yield increased by 1.4% and 1.5% per year under low and high N treatment, respectively. Both dry matter accumulation (DM) and harvest index contributed to the higher yield in the new cultivars (Fig. 6B, Figure S3A). Besides, modern maize hybrids exhibited a higher ear density at harvest (Figure S3B). The increase in DM accumulation was more contributed by the increased in post-silking DM accumulation (73%) than that in pre-silking DM accumulation (22%) (Fig. 6C,D).

Climatic resource use efficiency was investigated further using two approaches: (1) using the simulated yield potential and climate data from 1973 to 2011 (Figure S4), and (2) actual yield and climate data recorded in 2010 and 2011 (Fig. 7). Both methods showed that, during the overall study period, the efficiency of sunshine hours, thermal time, and precipitation utilization showed a significantly increasing trend with increasing year of hybrid release. Overall, the use efficiency of sunshine hours, thermal time, and precipitation over

the study period increased by 37%, 40%, and 41%, respectively, in maize cultivars released between 1973 and 2000 (Fig. 7A1–A3). Interestingly, the gradient of the sunshine hours and thermal time use efficiency in the post-silking stage was higher than that in the pre-silking stage (Fig. 7B,C). The efficiency of pre- and post-silking precipitation utilization also showed an increasing trend with increasing year of hybrid release. Nonsignificance of the change in post-silking precipitation use efficiency was caused by the irregular data for XY335, which had an earlier silking date (on 18 July, 70 DAS) and therefore much higher post-silking precipitation in 2010 (Figure S1).

Mechanism for the higher plant productivity of modern maize hybrids

To investigate why DM accumulation in modern hybrids was higher at the post-silking stage, photosynthesis-related parameters were analyzed. Using parameters related to leaf senescence (Table 4), the hybrids were clustered into two groups, namely early-senescent and late-senescent cultivars (Figure S5). The early-senescent cultivars consisted of the five hybrids released before 1990 and the late-senescent cultivars comprised the four hybrids released after 1990 (Table 1). Compared with the early-senescent cultivars, the late-senescent cultivars had higher $RGLA_m$, LAD, T_s , and T_{max} , but lower V_m and V_{max} (Table 4). No significant difference in the maximum LAI was observed between the two groups of hybrids. The two groups differed in the leaf senescence rate at 30 DAS under low N and at 40 DAS under high N (Fig. 8). In the early-senescent cultivars, the average LAI at maturity was 0.8 under low N and 0.9 under high N. In the late-senescent cultivars, the average LAI at maturity was 1.4 under low N and 2.7 under high N. Hence, the leaf senescence rate in the late-senescent cultivars was more responsive to N supply than that in the early-senescent cultivars.

Genotypic difference existed in P_n and the light saturation point (Fig. 9). However, these differences were not significantly associated with the year of hybrid release. Among the hybrids, the maximum P_n and light saturation point of DY13 and XY335 were higher than those of the other four genotypes.

Leaf senescence is closely related to N nutrition in the leaf. Nitrogen accumulation per area increased with increasing year of hybrid release (Table 5). Across the N treatments, N accumulation at maturity increased by 28% during the past four decades, which was lower than the increase in dry matter accumulation at maturity (45%, Fig. 6B). In addition, in contrast to HI, NRE and NHI did not show an increasing trend (Table S2).

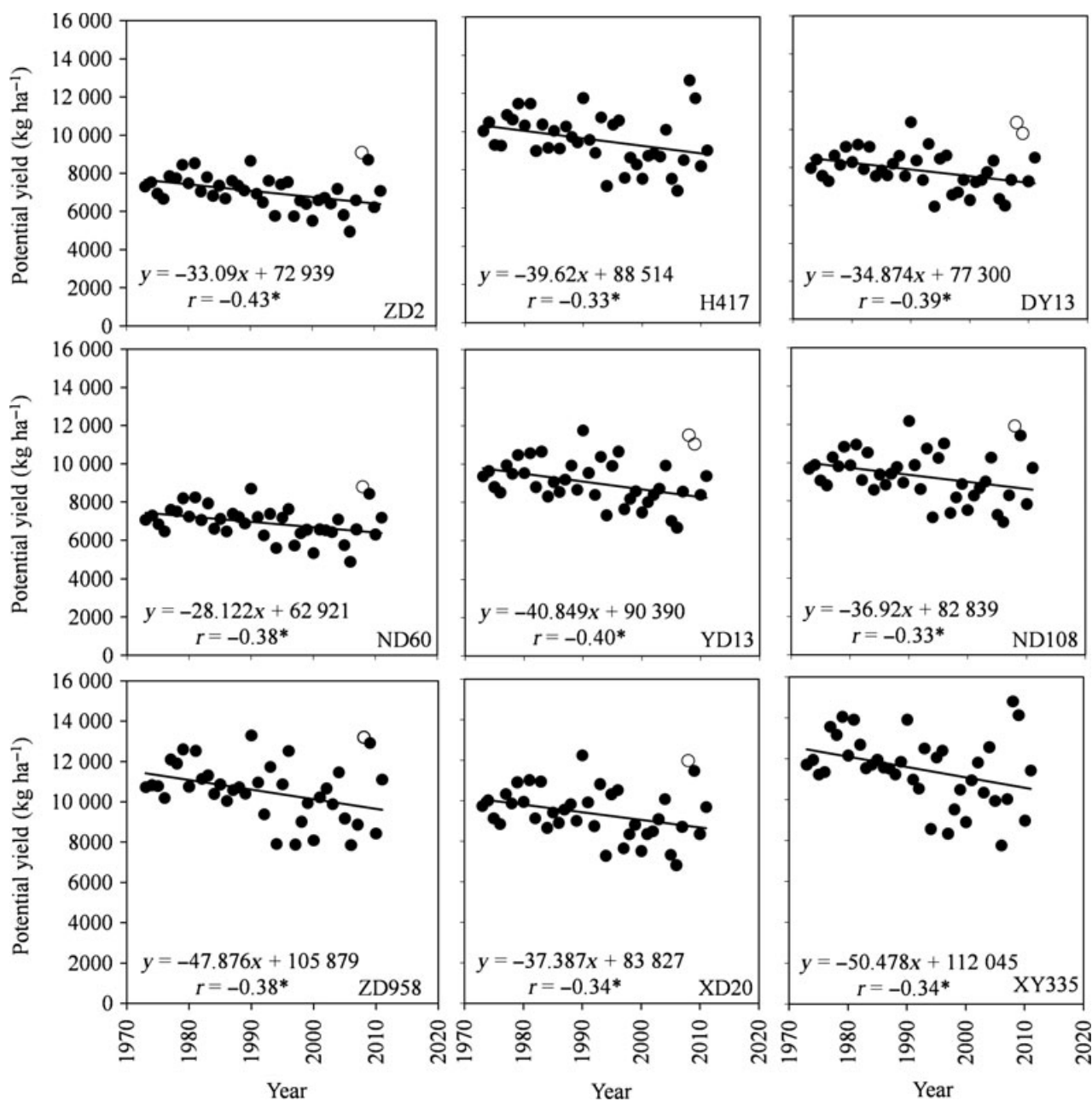


Fig. 4 Simulated yield potential of 9 maize hybrids under the climate conditions from 1973 to 2011. *, **Significant at the 0.05 and 0.01 probability level, respectively. Empty circles are excluded in the linear regression analysis.

Consequently, grain N concentration (GPC) decreased significantly with increasing year of hybrid release (Fig. 10).

Discussion

The study site, Siping, is centrally located in the North-east China Plain. During the past four decades, sunshine hours and precipitation decreased significantly and GDD increased to a small extent (Figs 1 and 2),

which resulted in a reduction in maize yield potential (Fig. 4). This finding is consistent with that predicted by Pan *et al.* (2011), Tao & Zhang (2011), and Liu *et al.* (2012). Nevertheless, the simulated yield potential of recently released maize hybrids was higher than that of old hybrids (Fig. 5A). The late developed hybrids showed less reduction in yield potential in current climate conditions than old cultivars (Fig. 5B), indicating some adaptation to new conditions. Since the mid-1990s, however, the yield impact of climate change

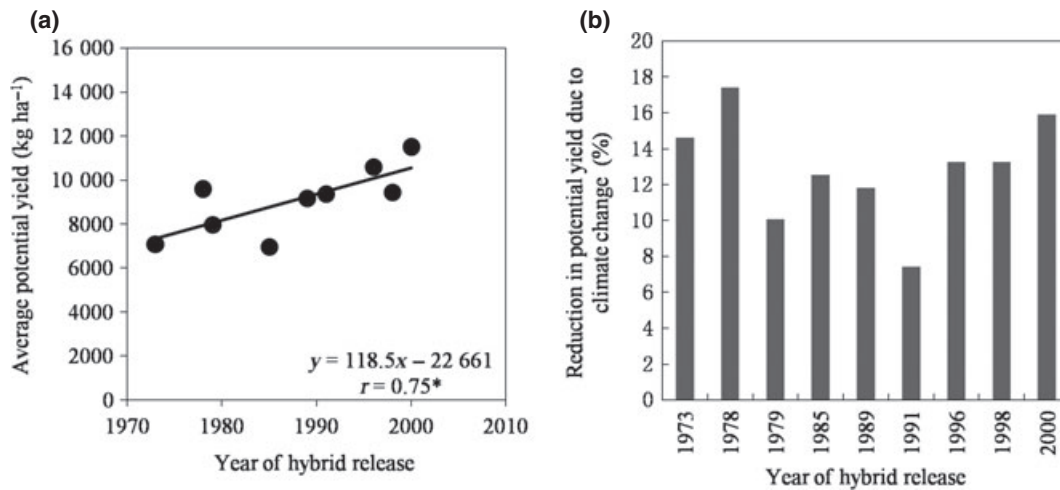


Fig. 5 Relationship between year of hybrid release and maize yield potential. A, average yield potential of each hybrid across the climate from 1973 to 2011; B, reduction in potential yield of each maize hybrid grown in the climate condition of 2000s in comparison to that in 1970s. *, ** Significant at the 0.05 and 0.01 probability level, respectively.

Table 3 Effect of N applications on grain yield, agronomic efficiency of applied N and yield components

Treatments	Grain yield (kg ha ⁻¹)	N agronomic Efficiency (kg kg ⁻¹)	Ear density at harvest (ha ⁻¹)	100-kernel weight (g)	Kernel number (ear ⁻¹)
N treatments					
N0	5508b	–	50700b	22.4c	427b
N120	9279a	44.8a	52708a	27.8b	641a
N240	9430a	24.7b	52510a	28.3a	640a
Cultivars					
ZD2	6607f	20.7d	43518d	27.7b	537c
H417	7748d	20.9d	54753ab	25.8cd	548c
DY13	7184e	24.6cd	51728bc	21.8f	610ab
ND60	7317de	13.5e	46235d	25.1d	626a
YD13	7507de	27.0bc	51482c	23.8e	588b
ND108	8512e	25.7c	53889abc	26.0c	598ab
ZD958	9661a	30.6ab	54680ab	28.1b	611ab
XD20	9109b	27.5abc	56173a	25.8c	619a
XY335	9375ab	31.9a	55370a	31.1a	540c

Data of 2010 and 2011 were pooled for variance analysis and significance test. Different letters in the same column denote significant difference at 0.05 level between N treatments or hybrids.

exhibited little change, and even a slight worsening for new cultivars. Modern maize breeding programs have mainly optimized plant productivity constitutively despite the adverse climate change. When grown in the same climatic conditions in 2010 and 2011, a positive linear relationship was observed between grain yield and year of hybrid release under both low and high N treatment (Fig. 6). The reason for this result is that, compared with old hybrids, modern cultivars better utilize climatic resources such as sunshine hours, thermal time, and precipitation (Fig. 7). Overall, the yield potential increment breeding is 118.5 kg ha⁻¹ yr⁻¹ during the past decades (Fig. 5A). The result is compatible

to that found by Duvick (2005a), who concluded that the contribution of genetic improvement to maize productivity is 115 kg ha⁻¹ yr⁻¹. Wang & Zhao (1998) found that the rate of DM accumulation was the dominant factor that determined the change in maize yield from 1986 to 1996. In a recent review by Ciampitti & Vyn (2012), higher total plant biomass accumulation during the post-silking period was observed in recently released cultivars (1991–2011) compared with older genotypes (1949–1990). Given that the growth period is not delayed in modern maize hybrids (Duvick, 2005b), the climatic resource use efficiency must be increased in modern hybrids in the United States of America. In

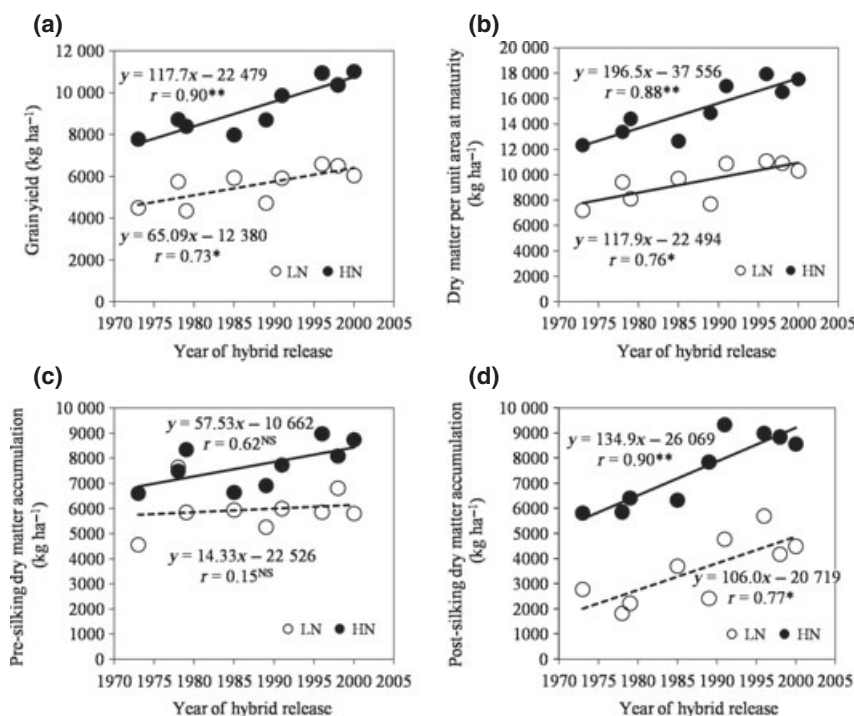


Fig. 6 Relationship between the year of hybrid release and grain yield (A), dry matter per unit area at maturity (B), pre-silking dry matter accumulation (C), and post-silking dry matter accumulation (D). LN indicates N0 treatment. Data of N120 and N240 was pooled as HN treatment. *, ** Significant at the 0.05 and 0.01 probability level respectively; NS Not significant at the 0.05 probability level.

the Northern China Plain, where summer maize is grown, Zhang *et al.* (1997) and Hu *et al.* (1998) reported that modern maize cultivars developed since the 1980s have both longer duration of post-silking DM accumulation and a higher DM/grain growth rate. Therefore, it appears that the rate of DM accumulation during reproductive growth has been generally enhanced during modern maize breeding worldwide.

Decreased sunshine hours and precipitation are two major limiting factors for maize growth (Fig. 2). The efficient use of light resources in modern cultivars may be associated with their better plant architecture (Table S1; Duvick, 2005b; Li & Wang, 2009; Zhao *et al.*, 2011) and green characteristic of the leaves (Fig. 8). The erect leaf of modern cultivars allows better light distribution in the canopy and increases their tolerance of a high planting density (Liu *et al.*, 2009). Genetic improvement of maize yield is largely dependent on improved tolerance of a high planting density in the United States of America (Duvick & Cassman, 1999; Tollenaar & Lee, 2002; Ciampitti & Vyn, 2012). In China, Wang *et al.* (2011) did not find a significant effect of planting density on genetic gain, whereas Ci *et al.* (2011) found that improved slightly in tolerance to high density during the release of hybrids from the 1970s to the 2000s. In addition, Xie *et al.* (2007) reported that modern maize genotypes released in China from the 1970s to the 2000s

showed a significantly decreased percentage of barren ears. In this study, we obtained similar results to those of Xie *et al.* (2007) and Ci *et al.* (2011). Although the planting density was identical (60 000 plants ha⁻¹), recently released hybrids produced more ears per unit area than older genotypes (Table 3, Fig. 5D). These data suggest that modern cultivars are better adapted to the decrease in sunshine hours experienced in recent decades (Fig. 1).

At the post-silking stage, the efficient use of climatic resources by modern hybrids was manifested as increased total DM accumulation and grain-filling rate (Fig. 6B, Table 2). Photosynthetic production is determined by leaf P_n and LAD (LAI \times photosynthetic period). The maximum P_n at the single-leaf level was unchanged among the hybrids (Fig. 9), which indicated that P_n potential may not play an essential role in the increased post-silking DW accumulation in modern cultivars. However, the higher grain-filling rate in modern hybrids may alter sink-source relationships to favor a higher average P_n in modern cultivars (Table 2; Long *et al.*, 2006). The leaves of cultivars released since the late 1980s are more erect, which allows better light distribution in the canopy and, therefore, may result in a higher average leaf P_n (Long *et al.*, 2006). Conversely, the high DM accumulation in modern cultivars during the post-silking stage may be explained largely by the

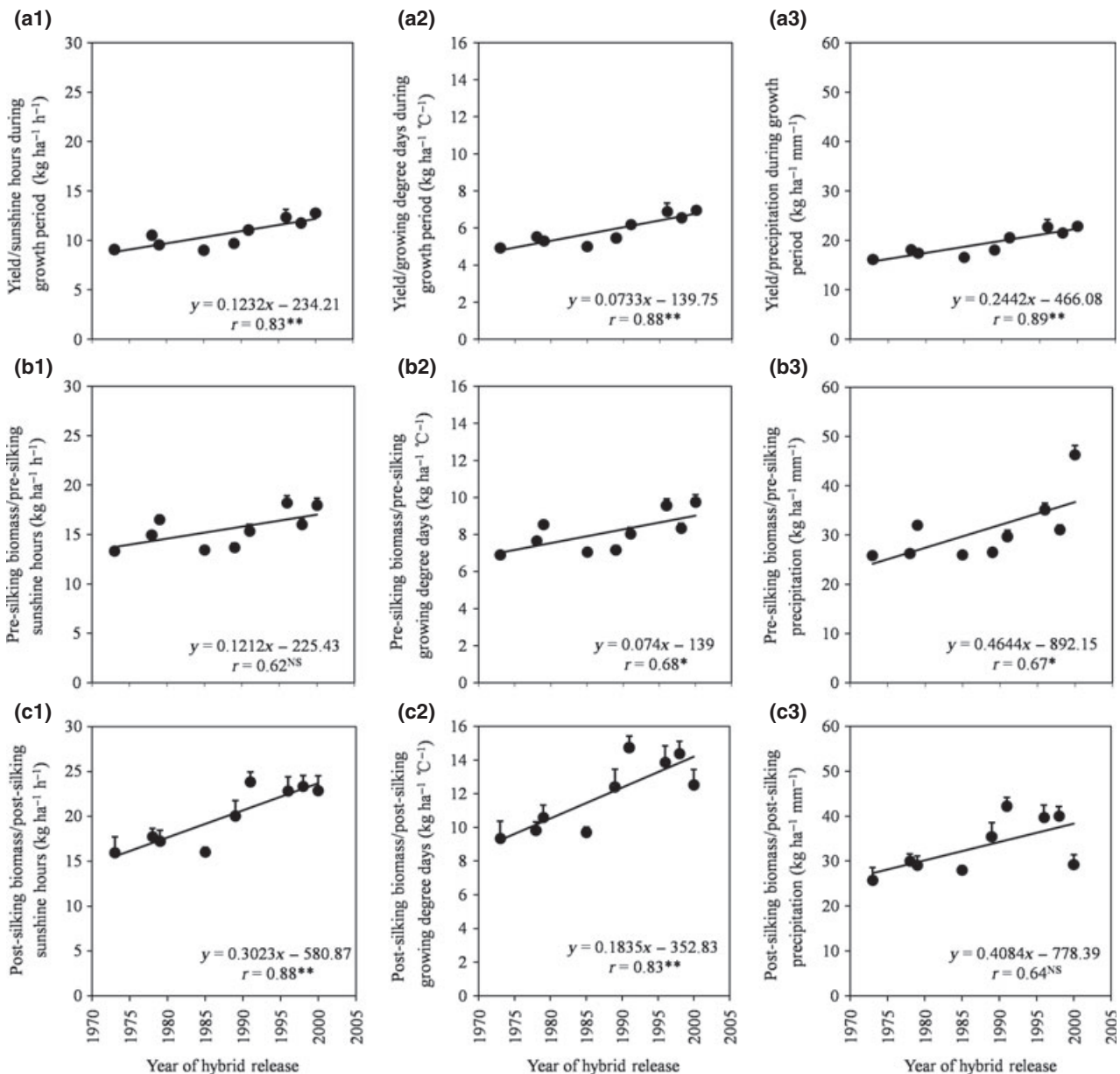


Fig. 7 Sunshine hours, thermal time, and precipitation use efficiency in maize hybrids released in different eras. A1–A3, climate resource use efficiency during the whole maize growth stage; B1–B3, climate resource use efficiency from sowing to silking stage; C1–C3, climate resource use efficiency from silking to maturity. Data of yield, pre- and post-silking dry matter accumulation in N120 and N240 treatments in 2010 and 2011 were pooled for the calculation. Each data denote the mean \pm SE.

delayed leaf senescence from silking to maturity (Fig. 8; Tollenaar *et al.*, 2004). Stay-green leaves at maturity are considered to be a major contributor to the genetic improvement in maize yield in the United States of America (Duvick, 2005b). Ahmadzadeh *et al.* (2004) suggested that maintenance of the leaf CO_2 exchange rate (CER) throughout a plant's life cycle, rather than potential leaf CER, is positively associated with DW accumulation during the grain-filling period and with grain yield. In China, stay-green leaves and late matu-

rity have become the main focuses in maize breeding to increase yield potential (Ding *et al.*, 2005; Li & Wang, 2009). Stay-green leaves may also contribute to higher water use efficiency in modern cultivars (Fig. 7). There is a close positive correlation between stay-green leaves and drought tolerance in maize and sorghum (Thomas & Smart, 1993; Borrell *et al.*, 2000; Zhang *et al.*, 2009), because stay-green genotypes have stronger photosynthetic ability and allocate a higher proportion of assimilates to the roots (Li *et al.*, 2004). Genetic analyses of

Table 4 Leaf traits of nine maize hybrids released in different eras

Cultivars	Year of release	RGLA _m (%)	V _m (%)	t _s (days)	V _{max} (%)	t _{max} (days)	LAD (m ² .days)
ZD2	1973	21.7	1.6	18	3.2	40	17.5
H417	1978	17.5	1.6	18	3.4	39	18.8
DY13	1979	11.0	1.8	7	3.1	33	21.7
ND60	1985	0.0	2.0	14	2.6	43	19.7
YD13	1989	30.3	1.4	18	3.1	43	20.7
ND108	1991	73.7	0.5	17	1.5	67	26.8
ZD958	1996	72.2	0.6	20	1.7	64	22.0
XD20	1998	41.3	1.3	19	2.5	47	22.1
XY335	2000	53.6	0.9	20	2.2	52	19.9

The curvilinear equation $y = ae^{b-cx} / (1 + e^{b-cx})$ was used to describe characteristic of relative green leaf area (Liu *et al.*, 2009), where y is RGLA, x is days after silking, a is the initial value of RGLA at silking (RGLAs, set to 1 in the present study), b is relative to the onset of leaf senescence and c is relative to the rate of leaf senescence (Van Oosterom *et al.*, 1996). RGLA_m, relative green leaf area at maturity; V_m, the mean decreasing rate of RGLA; t_s, the day of senescence starting (RGLA is 95%); V_{max}, the maximum reduction rate of RGLA; t_{max}, the day of V_{max}; LAD, leaf area duration. Data are from the N120 treatment.

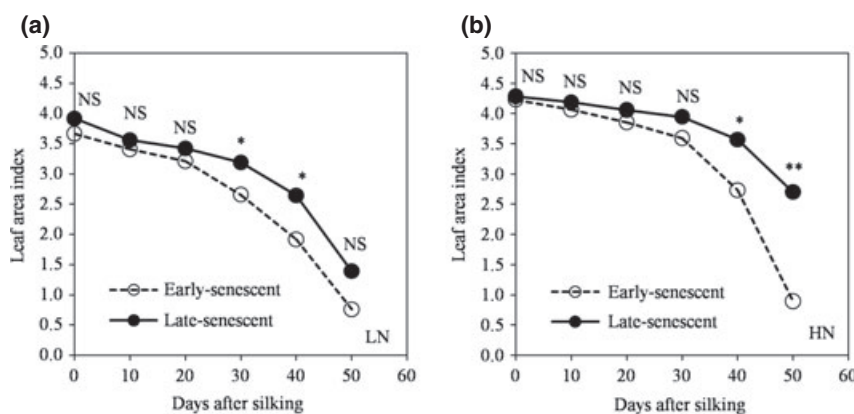


Fig. 8 Dynamics of leaf area index from silking to maturity of early-senescent and late-senescent maize hybrids under low N (A) and high N (B) supply. *, **Significant at the 0.05, 0.001 probability level, respectively. NS, Not significant.

quantitative trait loci that control stay-green traits have resulted in identification of several genomic regions associated with post-silking stress resistance (Sanchez *et al.*, 2002).

Leaf senescence is largely regulated by post-silking N uptake and remobilization of N accumulated in the pre-silking stage. However, these two N sources are also required for kernel development and protein deposition (Ta & Weiland, 1992; Masclaux-Daubresse *et al.*, 2008). Previously, it was reported that, compared with old early-senescent hybrids, the new stay-green maize cultivars show lower NRE and slightly higher post-silking N uptake (Rajcan & Tollenaar, 1999; Mi *et al.*, 2003). In the present growth conditions, although NRE was not consistently different among the hybrids, the increase in total N accumulation by modern cultivars (28%) was much lower than the increase in DM accumulation (45%) (Fig. 6B, Table 5). HI increased gradually with increasing year of hybrid release, whereas NHI did not change significantly. Consequently, grain

N concentration was significantly reduced with increasing year of hybrid release. A similar trend is also reported in the USA (Duvick & Cassman, 1999). A recent review by Ciampitti & Vyn (2012) showed that the increase in N utilization efficiency (ratio of grain yield to plant N uptake) in modern maize genotypes was primarily associated with reduced percentage grain N content. Uribelarrea *et al.* (2007) demonstrated that maize genotypes with high grain protein concentration exhibited higher NRE. Both the stay-green characteristic and low NRE in recently released cultivars may have contributed to the higher tolerance to N deficiency (higher grain yield in the absence of N-fertilizer application) and higher N agronomy efficiency (higher grain yield response per unit of N applied) (Table 3; Ciampitti & Vyn, 2012). However, grain protein concentration is an important trait for grain nutritional quality. A major challenge for maize breeding in the future is to increase post-silking dry matter production and NRE simultaneously (Masclaux-Daubresse *et al.*,

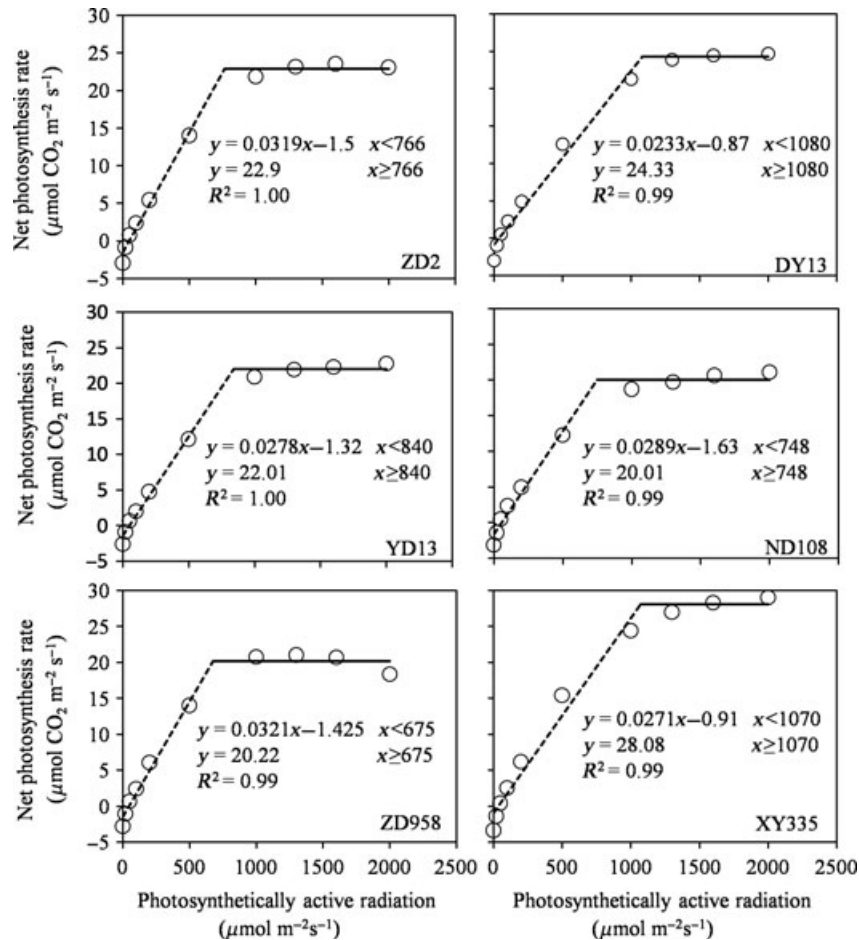


Fig. 9 Relationship between photosynthetically active radiation and net photosynthesis rate (Pn) of the ear leaf in six maize hybrids. Pn was measured at grain-filling stage in plants grown under N240 treatment. Data are simulated using linear + plateau model with SAS software.

2008). Otherwise, post-silking N uptake must be increased to meet the requirement of protein synthesis in grains.

Nevertheless, it should be noticed that, since 1990s, the increase in yield potential of maize hybrids has mainly been contributed by constitutively optimizing plant productivity and to a less extent by specifically adapting to the adverse climate factors (Fig. 5B). Therefore, maize breeding programs in the future should pay more attention to cope with the climate change specifically. For example, although the total GDD for maize growth per year increased in Northeast China Plain, the GDD of modern cultivars are little changed compared with those of old cultivars (Table 2). In the future, breeding for late-maturing maize hybrids may increase grain yield potential further. However, frost-resistance should also be improved because the frequent occurrence of frost in late autumn may limit the use of late-maturing hybrids (Duvick, 2005b). Long *et al.* (2006) suggested that actual yields may be

increased by increasing the environmental tolerance of radiation use efficiency. Under optimum conditions, the maximum radiation use efficiency may be increased by modifying the canopy architecture and functioning of the photosynthetic apparatus.

The effect of atmospheric CO_2 elevation may on the change of yield potential was not studied because the data are not available. Also CO_2 is not an input parameter in the Hybrid-Maize model. It is estimated that the average increment of atmospheric CO_2 is 1.4 ppmv per year from 1960 to 2005 (IPCC, 2007). So theoretically CO_2 concentration might increase by about 60 ppmv during the past four decades. It is difficult to estimate if or to what extent maize yield will be increased by such a small increase in CO_2 concentration in field conditions where the interactions between CO_2 concentration and reduced sunshine hour and precipitation, and increased temperature are complex. Most of the experiments in this area have been done with doubled CO_2 concentration, and the results are not consistent. For

Table 5 Nitrogen accumulation of maize cultivars released in different eras and grown under different N supplies

Treatments	Total N accumulation (kg ha ⁻¹)	Pre-silking N accumulation (kg ha ⁻¹)	Post-silking N accumulation (kg ha ⁻¹)
N treatments			
N0	75.4c	63.8c	18.3c
N120	180b	134b	52.3b
N240	212a	152a	60.0a
Cultivars			
ZD2	127c	84.1e	50.1a
H417	149b	109d	45.8ab
DY13	155b	125ab	38.3b
ND60	129c	113cd	25.8c
YD13	152b	111cd	54.6a
ND108	168a	130a	43.8ab
ZD958	179a	129a	54.1a
XD20	153b	119bc	47.4ab
XY335	172a	133a	54.7a
Types			
Early-senescent	143b	108b	42.7b
Late-senescent	168a	128a	49.7a

Different letters within N or cultivar treatment or types indicate significant difference at $P < 0.05$ probability level.

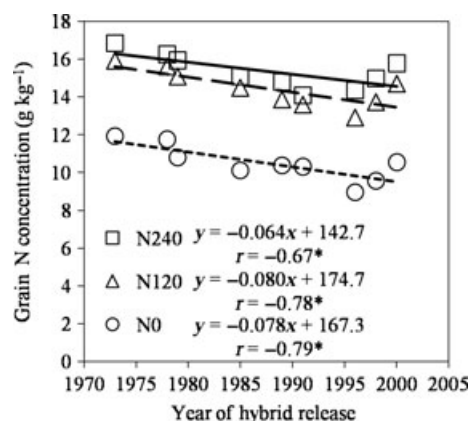


Fig. 10 Relationship between the year of hybrid release and grain N concentration under different N supplies. *Significant at the 0.05 probability level.

example, Kimball (1983) reported that a doubling CO₂ concentration, holding other factors constant, could lead to a 14% increase in agricultural yields of C4 plants. Whereas, Paruelo & Sala (1993) indicated a decrease of maize yield between 20% and 25% even under the scenario of doubled CO₂ concentration, because the direct effect of CO₂ enhancement did not compensate for the reduction in yield associated with the change of other climate factors. Erda *et al.* (2005) predicted that the yield of rain-fed maize in China will only increase by 1.1% if CO₂ concentration is elevated to 429 ppmv at 2020s. In this study, the atmospheric CO₂ concentration above the canopy is 380 ppmv. Modern breeding has led to an increase in maize yield

potential by 62%, which is much higher than the possible contribution of elevated CO₂ on yield increase (Kimball, 1983; Erda *et al.*, 2005). Therefore, the finding in this study is still true no matter whether the change of CO₂ concentration is considered.

In conclusion, during the past four decades, the total thermal time increased whereas the total precipitation and sunshine hours decreased in the Northeast China Plain. These climatic changes had a significant negative impact on maize yield potential. Nevertheless, maize breeding has increased yield potential significantly by increasing the climatic resource use efficiency of modern cultivars. Through delayed leaf senescence, increased grain-filling rate, and improved plant architecture, modern cultivars develop more ears per unit area and show increased DM accumulation, especially during the post-silking stage. Total N accumulation and NHI are little changed and therefore N agronomic efficiency has increased as well. The trade-off of delayed leaf senescence in modern cultivars is reduction in grain N concentration. The increase in yield potential of maize hybrids has mainly been contributed by constitutively optimizing plant productivity and to a less extent by specifically adapting to the adverse climate factors. Maize breeding programs in the future should pay more attention to cope with the limiting climate factors specifically.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Plant type of the tested maize hybrids.

Table S2. Nitrogen remobilization efficiency and N harvest index of nine maize hybrids under different N supplies.

Figure S1. Weather data in the experimental location Siping in 2010 and 2011.

Figure S2. Potential yield of each year × hybrid combination from 1973 to 2011.

Figure S3. Relationship between the year of hybrid release and harvest index (A), and ear numbers per unit area (B).

Figure S4. Sunshine hours, Thermal time, and Water use efficiency in maize hybrids released since 1973.

Figure S5. Cluster analysis of nine maize hybrids based on leaf senescence traits.