PHILIPP AGRIC SCIENTIST
Vol. 100 No. 4, 337–346
December 2017
ISSN 0031-7454

Dry Matter Accumulation Characteristics of Maize Cultivars Released from the 1950s to the 2010s in China

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Dry matter accumulation (DMA) is the basis of maize (*Zea mays* L.) grain production. In order to investigate the traits related to DMA before and after flowering of maize, experiments were conducted on maize cultivars released from the 1950s to the 2010s, which were grown at densities of 37,500 and 82,500 plants ha^{-1}. In improved cultivars, the contribution of total DMA (54–88%) to grain yield gain was greater than the contribution of harvest index (HI) (12–46%). A significant increase in total DMA for maize cultivars resulted from increase in DMA during the reproductive stage (DMA$_R$) and DMA$_R$ rates. Leaf area index at anthesis or dent stage and the staygreen index significantly increased. Leaf area duration was greater for new cultivars than for old ones, both before and after anthesis. These traits could be selected for by maize breeders to improve DMA, and thus increase maize grain yield in China.

Key Words: dry matter accumulation, dry matter accumulation rate, dry matter accumulation traits, harvest index, leaf area duration, maize cultivars, staygreen index

Abbreviations: OPC – open-pollinated cultivar, DMA – dry matter accumulation, HI – harvest index, LD – low density (37 500 plants ha^{-1}), HD – high density (82 500 plants ha^{-1}), LAI – leaf area index, LAD – leaf area duration, NAR – net assimilation rate, DMA$_V$ – dry matter accumulation during the vegetative stage, DMA$_R$ – dry matter accumulation during the reproductive stage, DMSL – dry matter of stems and leaves, LAD$_V$ – leaf area duration at the vegetative stage, LAD$_R$ – leaf area duration at the reproductive stage, NAR$_V$ – net assimilation rate at the vegetative stage, NAR$_R$ – net assimilation rate at the reproductive stage

INTRODUCTION

The average yield of maize (*Zea mays* L.) has increased globally, from 1942 kg ha^{-1} in 1960 to 5616 kg ha^{-1} in 2014 (FAO 2017). In China, the average grain yield of maize has increased from 1185 to 5809 kg ha^{-1} over the past 50 yr, and similar trends have been reported in Canada, Argentina, and the US, according to FAO statistics (FAO 2017).

Genetic selection has substantially contributed to maize yield gains (Duvick et al. 2004; Niu et al. 2013; Ma et al. 2015). In Iowa, USA approximately 51% of the maize yield increases from 1930 to 2001 could be attributed to genetics (Duvick et al. 2004). Ma et al. (2015) reported an average yield increase of 7.97 t ha^{-1} in China from the 1950s to the 2010s, 50.5% of which was due to genetic improvement. Research on the morphological, physiological, and lodging-resistance traits of maize cultivars released in different years has identified significant genotypic variability in these traits (Duvick 2005; Ding et al. 2005; Ci et al. 2012; Ma et al. 2014a, b).

Dry matter accumulation (DMA) is regarded as one of the main factors influencing grain formation, and increasing the accumulation and distribution of dry matter in economically important plant parts (i.e., grains) can help improve grain yield (Chen 1994). The rate of DMA is regarded as the main factor limiting maize yield (Ottaviano and Camussi 1981). Previous studies have suggested that dry matter accumulates faster in more modern maize cultivars than in older cultivars, and thus significantly enhances the grain yield of newer cultivars (Tollenaar 1991; Tollenaar and Wu 1999; Echarte et al. 2008).

The majority of grain biomass is derived from photosynthates produced during grain filling, although some reserved photosynthates produced before flowering can be reallocated to grains during later stages of development (Simmons and Jones 1985; Cliquet et al. 1990; Masoni et al. 2007). Ding (2005) reported that grain mass reallocated from the shoots of maize cultivars from the 1990s was greater than that of cultivars from the 1970s. However, He et al. (2005) and Ning et al. (2013) reported that the grain yield of new maize cultivars results from the remobilization of pre-silking carbon reserves, which are less abundant than reserves of earlier-senescing cultivars, but the reason for this difference is uncertain.

Leaves are the major photosynthetic organs determining DMA in maize (Piazza et al. 2005). At low, moderate, or higher plant densities, DMA is highly related to green leaf area during the late grain filling period (Antonietta et al. 2014). Leaf area duration (LAD) is the product of green leaf area and green leaf duration, both of which indicate the potential photosynthetic productivity of leaves during a specific growth period or all growth stages (Hunt 1978). According to Ma and Dwyer (1998), maize genotypes with a long duration of active photosynthesis produce 24% more dry matter than genotypes that senesce early during grain filling.

Net assimilation rate (NAR) represents the relationship between DMA and green leaf area. During the vegetative stage, NAR is related to the establishment of reproductive structures (Westgate and Bassetti 1991; Tollenaar and Wu 1999). After anthesis, NAR is associated with DMA and ultimately affects grain yield (Zhang 2003).

Few studies have estimated the genotypic variation in DMA rates and other DMA-related traits before and after anthesis (Ding 2005; Ning et al. 2013; Zhang 2003). Thus, the objectives of this study were (1) to examine DMA characteristics including DMA rate, DM remobilization, leaf area index (LAI), staygreen index, LAD, and NAR of maize cultivars before and after flowering, and (2) to suggest traits that could be selected for by breeders to improve DMA and increase maize grain yield in China.

MATERIALS AND METHODS

Description of the Study Area

Field studies were performed at the Gongzhuling Experimental Station of the Institute of Crop Sciences, Chinese Academy of Agricultural Sciences (CAAS) in Gongzhuling, Jilin Province, China (43°30′N, 124°50′E). The study area is located in northeast China, where mean annual air temperature is 5.6 °C, mean annual precipitation is 594.8 mm, and mean annual frost-free period is approximately 144 d. Spring maize was grown from late April to late September of 2011 and 2012 under rainfed conditions and with ridge planting. The average precipitation during the maize growing period was 361.7 mm in 2011 and 482.3 mm in 2012; total sunshine time was 1180.8 h in 2011 and 1124.7 h in 2012; and cumulative temperature (⩾10 °C) was 3124.1 °C in 2011 and 3110.9 °C in 2012.

The soil was classified as loam (USDA 2016) with a mean pH of 6.2, organic matter content of 26.3 g kg^{-1}, total N content of 1.5 g kg^{-1}, available N content of 0.12 g kg^{-1}, available P content of 0.028 g kg^{-1}, and available K content of 0.18 g kg^{-1} in the 0–30 cm soil layer.

Plant Material

The experiments were conducted in 2011 and 2012. Six maize cultivars, including five single-cross cultivars and one open-pollinated cultivar (OPC), were grown during both years (Table 1). In 2012, we added the cultivars YLZ, DY13, JD180, and NH101, which are grown on more than 2.8 million ha in China (Ma et al. 2014a).

Experimental Design

A randomized complete block design (CRD) with three replications was implemented. Individual plots were 24 m^2, and each plot contained six rows (6 m long) spaced 0.65 m apart. Three seeds were sown per hole, and the plants were thinned at the five-leaf stage. Experiments were conducted on maize grown in the field under 37,500 plants ha^{-1} (low density, LD) and 82,500 plants ha^{-1} (high density, HD) to simulate optimal and stressful conditions, respectively. Nitrogen was applied at the rate of 150 kg ha^{-1} before sowing, with an additional 75 kg ha^{-1} applied at the V6 (24–30 d after emergence) and V12 (42–46 d after emergence) stages, respectively. Fertilizers (P_2O_5 and K_2O) were applied at the rate of 42.5 kg ha^{-1} before sowing. Weeds and pests were controlled with chemicals.

Trait Measurements

Five adjacent plants in the center row of each plot were selected during the anthesis and dent stages (R5). Green leaf area was measured according to the standards described by Subedi and Ma (2005). The staygreen index, also known as delayed leaf senescence (Crosbie 1982; Meghji et al. 1984), was calculated as:

$$\text{Staygreen (\%)} = 100 - (LAI1 - LAI2)/ LAI1 \times 100 \quad [1]$$

where $LAI1$ and $LAI2$ are the leaf area indices at the anthesis and dent stages, respectively.

Table 1. Maize cultivars used in this study.

Genotype Name	Pedigree	Year of Release	Institution Developing the Hybrid
BH[†]	Open-pollinated cultivar	1950s	Gongzhuling farm of Jilin Province, Gongzhuling, China
YLZ[§,†]	Open-pollinated cultivar	1950s	Introduced to Liaoning Province
JD101	Ji63 × M14	1967	Maize Institute of Jilin AAS[#], Gongzhuling, China
ZD2	Mo17 × Zi330	1972	Chinese AAS, Beijing, China
DY13[§]	Mo17 × E28	1981	Dandong AAS of Liaoning Province, Dandong, China
JD180[§]	J853 × Mo17	1986	Maize Institute of Jilin AAS, Gongzhuling, China
YD13	Ye478 × Dan340	1998	Laizhou AAS of Shandong Province, Laizhou, China
ZD958	Zheng58 × Chang7-2	2000	Luohe AAS of Henan Province, Luohe, China
XY335	PH6WC × PH4CV	2004	The Tieling Pioneer Limited Company, Tieling, China
NH101[§]	NH60 × S121	2010	Beijing Jin Se Nong Hua Seed S &T Co., Ltd.

[§]Not included in the field trials in 2011, but included in 2012
[#]AAS – Academy of Agricultural Sciences
[†]BH and YLZ were used widely in maize production during the 1950s.

LAD and NAR before and after anthesis were estimated according to the equations of Hunt (1978):

$$\text{LAD (d)} = [(LAI1 + LAI2) \times (t1 - t2)]/2 \qquad [2]$$

$$\text{NAR (kg ha}^{-1}\text{ d}^{-1}) = \text{DMA/LAD} \qquad [3]$$

where DMA is dry matter accumulation, *LAI*1 and *LAI*2 are the leaf area indices at time *t*1 and *t*2, respectively, and *t*1 and *t*2 represent the dates of the first and second harvests, respectively.

Plant dry matter was measured at anthesis and physiological maturity. Five plants from the center row of each plot were cut at ground level and divided into stems, leaves, and grains. Aboveground DMA was measured by oven-drying samples at 70 °C to a constant weight. The percentage of total DMA before and after anthesis was calculated and values during different stages for maize cultivars released in different years were compared.

Statistical Analyses

Analysis of variance (ANOVA) was conducted to compare the percentage of DMA during the vegetative stage (DMA_V) and the percentage of DMA during the reproductive stage (DMA_R) across cultivars. DMA_V and DMA_R for different genotypes over the growing year and for different plant densities were analyzed using General linear model univariate analysis (GLM-Univariate). Least significant differences (LSDs) were computed to identify significant differences in treatment means at the 0.05 probability level.

Simple linear models (Y = a + bX) were fitted to estimate the relationship between DMA characteristics and the year of cultivar release. The independent variables (X) included the years during which the six experimental cultivars were released (for the 2011 data) and the years during which the ten experimental cultivars were released (for the 2012 data).

The contributions of total DMA and harvest index (HI) to grain yield were calculated according to the proportion of partial regression square sum (V_i) of the independent variable DMA(X_1), HI(X_2) in the regression equation (Li and Wang 2008). V_i was estimated based on the equation:

$$V_i = b_i^2 / C_{ii}$$

where V_i is the partial regression square sum of a variable X_i, b_i is the coefficient of regression estimate, and C_{ii} is the i[th] element on the primary diagonal of inverse matrix of the dispersion matrix.

All data analyses were conducted using SPSS 16.0 software and Excel 2010.

RESULTS AND DISCUSSION

Contribution of Total DMA and HI to Yield

Maize grain yield, total DMA, and HI significantly and linearly increased from the 1950s to 2010 (Ma et al. 2014a, b). Total DMA contributed 81% and 88% of the grain yield in 2011 and 2012 under LD, respectively; HI contributed the remaining 19% and 12% in 2011 and 2012 under LD, respectively (Table 2). Under optimal density conditions (LD), the contribution of total DMA was far greater than that of HI. The contribution of HI increased with increasing plant density during both years. Under stressed conditions (HD), HI contributed 46% and 29% of the grain yield in 2011 and 2012, respectively (Table 2).

Previous reports have indicated that the total DMA of US maize cultivars did not change with increased yield (Duvick 1997, 2005; Wang et al. 2011), suggesting that maize yield increases in the US were due to improvements in HI. Thus, Chinese and US maize cultivars respond differently to selection for total DMA. In China, breeders typically select maize genotypes with high total DMA and HI to increase grain yield. Similarly, other studies have reported that Chinese maize yield increases with enhanced accumulation and distribution of dry matter to economically important plant organs (Wang et al. 2011; Li et al. 2011).

Table 2. Contributions of total dry matter accumulation (DMA) and harvest index (HI) to grain yield in 2011 and 2012 at low (LD) and high (HD) plant densities.

Source	Grain Yield (2011)		Grain Yield (2012)	
	LD	HD	LD	HD
Total DMA	81%	54%	88%	71%
HI	19%	46%	12%	29%

DMA and DMA Rates

The growth periods of maize examined in this study include the vegetative and reproductive stages with the start of the latter indicated by anthesis. Growing year, cultivar, and plant density significantly influenced the percentage of DMA, DMA_V and DMA_R, but their interactions (with the exception of density × cultivar) had no significant effects on these traits (Table 3). To fully reflect cultivar characteristics, trait means were analyzed under the same density treatment each year.

The percentage of DMA_V decreased and the percentage of DMA_R increased with increasing year of cultivar release (from the 1950s to 2010) under both densities in 2011 and 2012. The percentage of DMA_R under HD was 48.92%, 54.58%, 54.43%, 60.16%, 64.67%, and 60.75% in 2011 and 45.06%, 49.64%, 49.86%, 58.96%, 61.12%, and 60.90% in 2012 for the cultivars BH, JD101, ZD2, YD13, ZD958, and XY335, respectively. The percentage of DMA_R was lower than that of DMA_V for open-pollinated cultivar (OPC) in the high-density treatment (Fig. 1), suggesting limitation due to high-density planting (Table 4).

The amount of DMA_V was not associated with the year of cultivar release, but DMA_R significantly increased with increasing year of cultivar release under both densities. Overall, DMA_R increased by an average of 0.07–0.09 t ha^{-1} yr^{-1} (LD) and 0.15 t ha^{-1} yr^{-1} (HD) from the 1950s to the 2010s (Table 4). However, previous studies have shown that the DMA_V of summer maize significantly increased from the 1950s to the 1970s and 1990s (Ding 2005). These differences can be attributed to the growing conditions and tested cultivars. The higher DMA_R values for new hybrids compared with old ones under high density may be due to reasonable light distribution for new cultivars in the canopy (Ma et al. 2014a).

The rate of DMA_V was not associated with the year of cultivar release, whereas the rate of DMA_R increased from the 1950s to the 2010s. Overall, the DMA_R rate increased by an average of 1.17–1.32 kg ha^{-1} yr^{-1} (LD) and 2.08–2.81 kg ha^{-1} yr^{-1} (HD) from the 1950s to the 2010s (Table 5). This is consistent with the results of Ding (2005), who indicated higher DMA_R rates for cultivars from the 1990s relative to those released in the 1970s or 1950s. Differences in DMA_R rates between old and new cultivars were enhanced by increased plant density (Table 5). Thus, breeders should focus on increasing cultivars' tolerance to stress, especially from high density planting (Ci et al. 2012).

Dry matter of stems and leaves (DMSL) was higher at physiological maturity than at anthesis, indicating that DMSL produced before flowering was not reallocated to grain during the grain filling stage, and the difference was always greater in new than in old cultivars. For example, changes in DMSL increased by 0.016 t ha^{-1} yr^{-1} (LD) in 2012, 0.025 t ha^{-1} yr-1 (HD) in 2011, and 0.048 t ha^{-1} yr^{-1}

Table 3. Mean squares for the percentage of DMA_V or DMA_R, DMA_V, DMA_R from the analyses of variance.

Source of Variation	Percentage of DMA_V/ DMA_R	DMA_V	DMA_R
Year	155**	8.74**	7.05*
Plant density	996**	407**	149**
Cultivar	230**	1.24*	64.5**
Year × density	0.07	1.19	0.07
Year × cultivar	12.23	0.49	1.32
Density × cultivar	41.3**	1.40*	6.9**
Year × density × cultivar	4.26	0.59	0.3
Error	11.51	0.52	0.99

DMA_V: dry matter accumulation during the vegetative stage; DMA_R: dry matter accumulation during the reproductive stage
*, ** Significant at the 0.05 and 0.01 levels, respectively

Table 4. Dry matter accumulation (DMA) of maize cultivars released between the 1950s and 2010s before and after anthesis and with growth at low (LD) and high density (HD) in 2011 and 2012. Regressions of trait value for the year of cultivar introduction.

Cultivar (Release Year)	DMA_V (t ha^{-1}) LD-2011	LD-2012	HD-2011	HD-2012	DMA_R (t ha^{-1}) LD-2011	LD-2012	HD-2011	HD-2012
BH(1950)	7.2bc†	7.3abcd	11.1a	12.8bc	10.4a	9.4ab	10.7a	10.5ab
YLZ(1950)	--	7.4abcd	--	2.5abc	--	8.4a	--	9.3a
D101(1967)	6.9ab	7.9cde	10.4a	11.9abc	11.3b	10.1bc	12.6ab	11.8bc
D2(1972)	6.7ab	7.1abc	10.9a	12.3abc	11.9b	10.8cd	13.1b	12.3bc
Y13(1981)	--	6.8ab	--	13.4c	--	12.0d	--	13.6c
D180(1986)	--	8.5e	--	12.1abc	--	10.6bc	--	15.8d
YD13(1998)	6.6a	6.6a	10.6a	11.3ab	13.1c	14.2e	16.0c	16.3de
ZD958(2000)	7.1abc	7.6bcde	10.8a	11.7ab	14.5d	13.6e	19.8d	18.4ef
XY335(2004)	7.5c	8.2de	11.6a	11.2a	14.4d	13.3e	17.9cd	17.4def
NH101(2010)	--	8.2de	--	12.8bc	--	14.4e	--	18.7f
Slope‡ ($year^{-1}$)	0.002	0.01	0.002	-0.01	0.07	0.09	0.15	0.15
R^2	0.01ns	0.07ns	0.01ns	0.16ns	0.94**	0.90**	0.88**	0.96**

DMA_V: dry matter accumulation during the vegetative stage; DMA_R: dry matter accumulation during the reproductive stage
†Different letters in the same column indicate significant differences ($p < 0.05$).
‡Slope, linear regression coefficients of cultivar on year of release

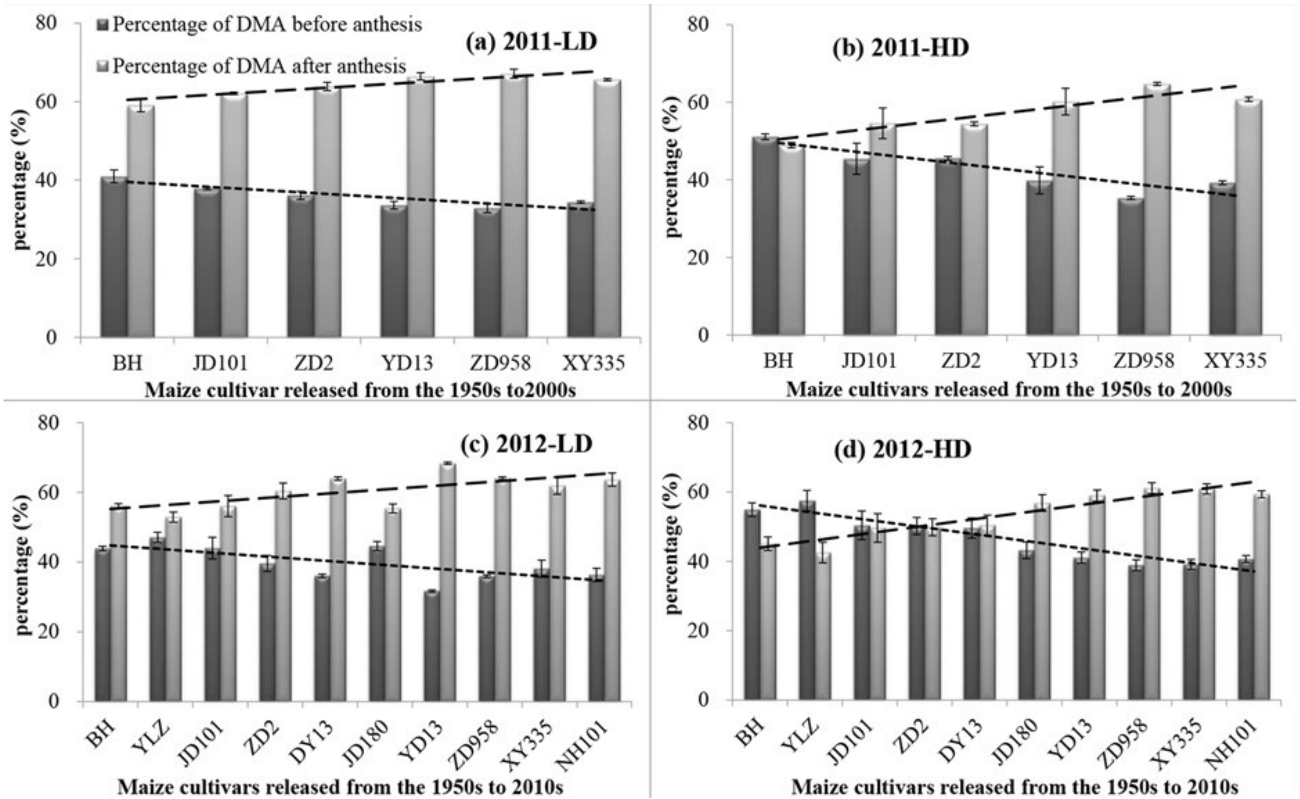

Fig. 1. Percentage of total dry matter accumulation (DMA) before and after anthesis in maize cultivars released in different years.

Table 5. Dry matter accumulation (DMA) rates of maize cultivars released between the 1950s and 2010s before and after anthesis and with growth at low (LD) and high density (HD) in 2011 and 2012. Regressions of trait value for the year of cultivar introduction.

Cultivar (Release Year)	DMA_V Rate (kg ha^{-1} d^{-1})				DMA_R Rate (kg ha^{-1} d^{-1})			
	LD-2011	LD-2012	HD-2011	HD-2012	LD-2011	LD-2012	HD-2011	HD-2012
BH(1950)	118.0bc†	111.3ab	168.8a	191.0bcd	180.0a	148.7ab	186.7a	169.2ab
YLZ(1950)	--	119.8bcd	--	201.6d	--	130.0a	--	145.4a
JD101(1967)	115.7abc	127.8d	160.0a	191.6cd	195.1b	158.80bc	224.5b	183.8bc
ZD2(1972)	110.6ab	104.3a	163.2a	176.0abc	205.4b	177.5cd	233.3b	207.9cd
DY13(1981)	--	100.0a	--	191.5cd	--	193.3d	--	227.3de
JD180(1986)	--	126.9cd	--	180.0abcd	--	155.5ab	--	232.8def
YD13(1998)	108.7a	98.0a	163.1a	161.8a	225.7c	228.3f	285.9c	276.3h
ZD958(2000)	112.2ab	113.8bc	163.6a	174.1abc	258.1d	194.1de	359.3d	262.7fh
XY335(2004)	123.4c	122.3bcd	170.0a	159.4a	247.5d	190.4d	325.3d	260.0efh
NH101(2010)	--	122.4bcd	--	191.7cd	--	211.4ef	--	275.4h
Slope‡ (year^{-1})	-0.013	0.006	-0.01	-0.40	1.32	1.17	2.81	2.08
R^2	0.003ns	0.0001ns	0.003ns	0.39*	0.90**	0.69**	0.88**	0.95**

†Different letters in the same column indicate significant differences ($p < 0.05$).
‡Slope, linear regression coefficients of cultivar on year of release

(HD) in 2012 (Table 6). Some studies have shown that reserved photosynthates in different maize cultivars produced before flowering can be reallocated to grain (Rajcan and Tollenaar 1999; Ding 2005; He et al. 2005; Ning et al. 2013). This discrepancy can be attributed to differences in environmental conditions, especially climatic factors such as temperature, sunshine duration, solar radiation, and precipitation, all of which have marked influences on maize growth and the accumulation and distribution of biomass (Stone et al. 1999; Yang et al. 2004; Tasneem et al. 2008; Liu et al. 2013; Ma et al. 2015). Almost no remobilization of dry matter occurs during maize growth in cool climates (Maddonni et al. 1998). Dai et al. (2011) reported remobilization of dry matter from vegetative organs of the cultivar in Changping during grain filling, but the phenomenon did not occur in Xunxian and Nong'an. Therefore, the effect of climatic factors on DMA remobilization before anthesis is greater than the effect of cultivar type.

Table 6. Change in DMSL values of maize cultivars released between the 1950s and 2010 before and after anthesis and with growth at low (LD) and high density (HD) in 2011 and 2012. Regressions of trait value for the year of cultivar introduction.

Cultivar	DMSL Change (t ha^{-1})			
(Release Year)	LD-2011	LD-2012	HD-2011	HD-2012
BH(1950)	2.55a[†]	2.15bc	1.98a	1.65a
YLZ(1950)	--	1.51a	--	1.17a
JD101(1967)	3.17b	2.00b	3.51c	2.38b
ZD2(1972)	3.31b	2.46cd	2.27ab	2.36b
DY13(1981)	--	2.98e	--	3.29c
JD180(1986)	--	2.54cd	--	4.11de
YD13(1998)	3.51b	3.63f	3.41bc	4.15de
ZD958(2000)	3.50b	2.42cd	3.56c	4.32e
XY335(2004)	3.06ab	2.43cd	3.55c	3.63cd
NH101(2010)	--	2.62de	--	3.91cde
Slope[‡] ($year^{-1}$)	0.011	0.016	0.025	0.048
R^2	0.49ns	0.39*	0.59*	0.85**

DMSL: dry matter of stems and leaves
[†]Different letters in the same column indicate significant differences ($p < 0.05$).
[‡]Slope, linear regression coefficients of cultivar on year of release

Leaf Area Index (LAI) and Staygreen Index

During the anthesis and dent stages, LAI significantly increased in cultivars introduced from the 1950s to the 2010s, and the rate of increase was higher in the HD treatment (Fig. 2). For example, LAI at anthesis increased by 0.08–0.011 yr^{-1} (LD) and 0.014–0.02 yr^{-1} (HD) with cultivar improvement. However, studies involving a set of Iowa cultivars showed no change in LAI over time (Crosbie 1982; Russell 1991; Duvick 1997); these differences can be attributed to the selected morphological traits of the investigated cultivars (Ma et al. 2014a). From the 1950s to the 1990s, breeders in China selected for high LAI to increase photosynthetic area.

The staygreen index also increased with increasing year of cultivar release. Staygreen increased at a rate of 0.59% yr^{-1} under LD and 0.65% yr^{-1} under HD in 2012 (Fig. 2). Many studies have compared the staygreen trait in old and modern cultivars and reported improvements over time under environmental stress (e.g., drought, N-deficiency, HD) (Valentinuz and Tollenaar 2004; Duvick et al. 2004; Antonietta et al. 2014) or under well-watered conditions (Barker et al. 2005). Thus, the staygreen index may be the most effective selection criterion for maize breeding programs in China or abroad.

LAD and NAR

Differences in vegetative LAD (LAD_V) and reproductive LAD (LAD_R) among the maize cultivars in 2011 and 2012 were highly significant (Table 7). LAD_V increased significantly by approximately 0.36–0.38 d yr^{-1}, and LAD_R increased at a rate of 1.09–1.32 d yr^{-1} under LD growth. The rates of increasing LAD_V and LAD_R were enhanced by HD growth. This result is consistent with several studies indicating higher LAD_R in newer maize cultivars relative to older ones (Tollenaar and Aguilera 1992; Ma and Dwyer 1998; Rajcan and Tollenaar 1999). Thus, LAD may be one of several morpho-physiological traits associated with the genetic improvement of maize yield.

Vegetative NAR (NAR_V) decreased with increasing year of cultivar release, but no clear trends in reproductive NAR (NAR_R) were observed (Table 8). These results are not consistent with those of Zhang (2003), who evaluated 20 maize inbred lines and four cultivars from the 1960s in China and reported that the NAR_R of the cultivars was greater than that of the inbred lines. High NAR was not necessarily associated with high yield due to the negative correlation between NAR and LAI (Chen 1994). Based on this study, increases in maize grain yield in China have resulted from selection for LAI.

In conclusion, increased maize grain yield has resulted from improvements in total DMA and HI in China since the 1950s. The contribution of total DMA to yield gains was greater than the contribution of HI. It is clear that selection of increased DMA is required to continue linear yield gains in China.

The mean rates of DMA_R and DMA_R significantly and linearly increased from the 1950s to the 2010s under both density treatments, suggesting that the total DMA of newer cultivars was higher relative to that of older ones due to improvements in DMA_R and DMA_R rates. Likewise, LAI, staygreen, and LAD significantly and linearly increased from the 1950s to the 2010s. Selected DMA traits respond similarly to increasing plant density, and differences between modern and old cultivars were enhanced as plant density increased. Newer hybrids showed increased tolerance to high density. Therefore, higher LAI, staygreen, and LAD may be the most effective selection criteria for maize breeding programs to increase DMA after anthesis and to increase maize grain yield in China.

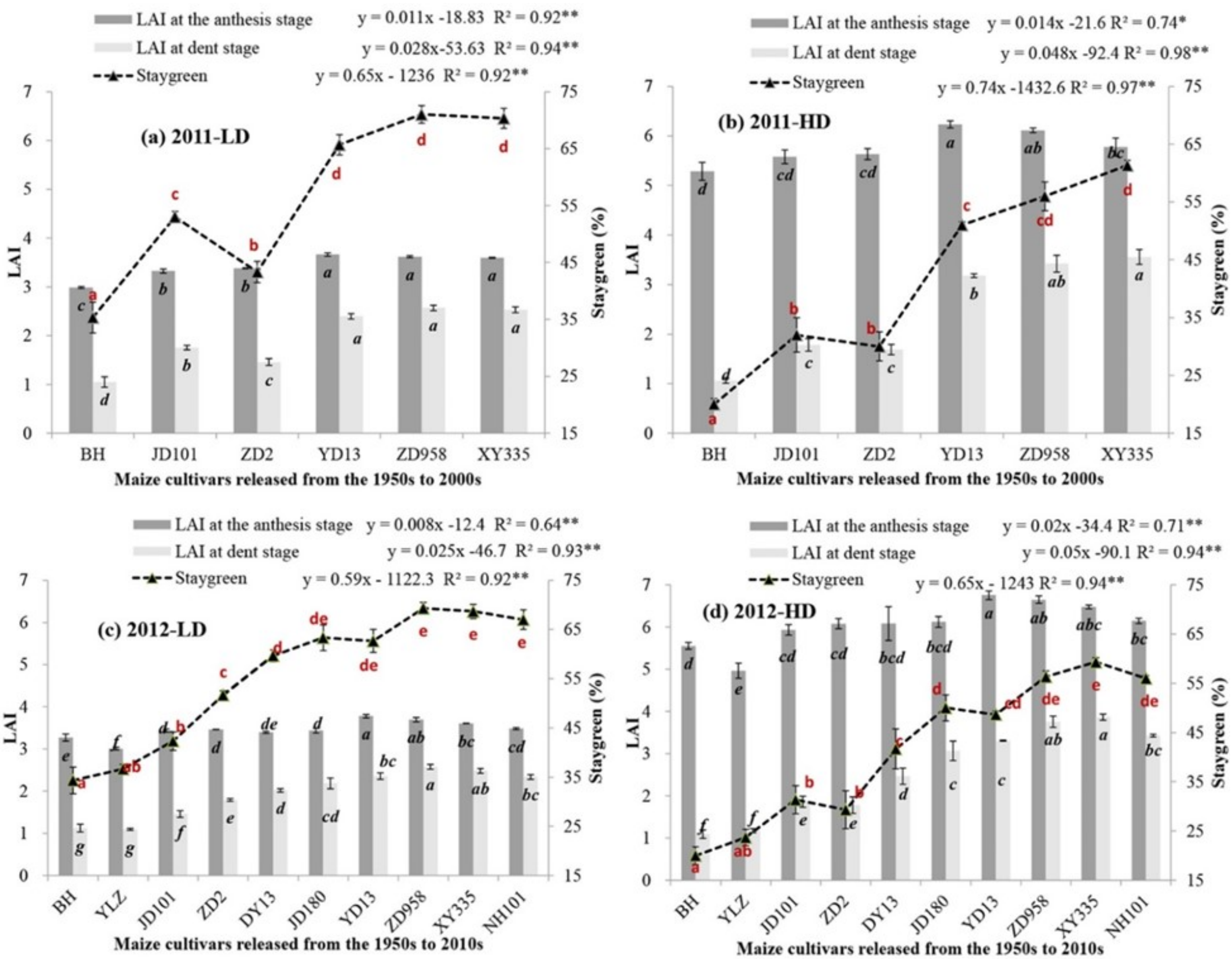

Fig. 2. Leaf area index (LAI) and staygreen index of maize cultivars grown at low density (LD) and high density (HD) in 2011 and 2012. Regression analysis for the year of introduction of cultivars. Within the same treatment, points with different letters were significantly different.

Table 7. Leaf area duration (LAD) of maize cultivars released between the 1950s and 2010s before and after anthesis and with growth at low (LD) and high density (HD) in 2011 and 2012. Regression analysis of trait values for the year of cultivar introduction.

Cultivar	LAD_V (d)				LAD_R (d)			
(Release Year)	LD-2011	LD-2012	HD-2011	HD-2012	LD-2011	LD-2012	HD-2011	HD-2012
BH(1950)	91.1a[†]	107.9b	174.4a	186.0bc	117.0a	138.4a	180.9a	206.1a
YLZ(1950)	--	93.3a	--	153.9a	--	131.4a	--	196.5a
JD101(1967)	99.6b	106.6b	181.3ab	184.0b	147.2c	156.7b	206.2b	249.5bc
ZD2(1972)	103.1c	117.6cd	188.7bc	212.7de	140.3b	160.2bc	204.9b	231.8b
DY13(1981)	--	115.4cd	--	212.8de	--	167.9c	--	256.4c
JD180(1986)	--	115.0c	--	205.1cd	--	191.1d	--	312.3de
YD13(1998)	111.8de	126.6f	202.6d	236.5f	175.7d	190.3d	263.5c	296.9d
ZD958(2000)	114.0e	123.8ef	201.7cd	222.7def	173.3d	219.4e	262.2c	364.2f
XY335(2004)	109.8d	120.8de	196.3cd	226.9ef	177.6d	213.0e	256.5c	346.8f
NH101(2010)	--	116.7cd	--	205.9d	--	197.9d	--	325.5e
Slope[‡] ($year^{-1}$)	0.38	0.36	0.50	0.90	1.09	1.32	1.61	2.51
R^2	0.93^{**}	0.66^{**}	0.91^{**}	0.64^{**}	0.96^{**}	0.89^{**}	0.96^{**}	0.86^{**}

LAD_V: leaf area duration at the vegetative stage; LAD_R: leaf area duration at the reproductive stage
[†]Different letters in the same column indicate significant differences (p < 0.05).
[‡]Slope, linear regression coefficients of cultivar on year of release
[**]Significant at the 0.01 level

Table 8. Net assimilation rate (NAR) of maize cultivars released between the 1950s and 2010 before and after the anthesis stage and with growth at low (LD) and high density (HD) in 2011 and 2012. Regression analysis of trait values for the year of cultivar introduction.

Cultivar (Release Year)	NAR_V (kg ha^{-1} d^{-1})				NAR_R (kg ha^{-1} d^{-1})			
	LD-2011	LD-2012	HD-2011	HD-2012	LD-2011	LD-2012	HD-2011	HD-2012
BH(1950)	79.3c[†]	68.1cde	64.0b	68.8e	85.9c	67.6bcd	59.0a	51.0ab
YLZ(1950)	--	79.6f	--	81.2f	--	63.7b	--	47.2a
JD101(1967)	69.2b	74.3ef	57.4ab	64.4de	76.8ab	64.7bc	60.9ab	47.1a
ZD2(1972)	65.4ab	60.3abc	58.0ab	57.9abcd	84.8bc	67.6bcd	63.8ab	52.9ab
DY13(1981)	--	58.5ab	--	63.0de	--	71.4cd	--	53.3ab
JD180(1986)	--	73.9ef	--	58.9bcde	--	55.3a	--	50.7ab
YD13(1998)	59.3a	51.9a	52.3a	47.9a	74.4a	74.4d	60.6ab	54.9ab
ZD958(2000)	62.0a	61.6bcd	53.5a	52.4abc	83.5abc	61.9ab	74.0c	50.6ab
XY335(2004)	68.5b	67.9cde	59.0ab	49.2ab	80.8abc	62.6b	69.7bc	50.2ab
NH101(2010)	--	70.3de	--	62.4cde	--	72.6d	--	57.5b
Slope[‡] (year^{-1})	-0.24	-0.16	-0.14	-0.36	-0.12	0.035	0.19	0.088
R^2	0.59[*]	0.16ns	0.53ns	0.61[**]	0.25ns	0.02ns	0.50ns	0.356ns

NAR_V: net assimilation rate at the vegetative stage; NAR_R: net assimilation rate at the reproductive stage
[†]Different letters in the same column indicate significant differences ($p < 0.05$).
[‡]Slope, linear regression coefficients of cultivar on year of release
[*], [**], ns Significant at the 0.05 level; significant at the 0.01 level; not significant

ACKNOWLEDGMENTS

Research was supported financially by the National Basic Research Program of China (973, Program: 2015CB150401), National Key Research and Development Program of China (Grant No. 2016YFD0300101). We are grateful to the anonymous reviewers for perceptive comments on the manuscript.

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