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How does increasing planting density regulate biomass production, allocation, and remobilization of maize temporally and spatially: A global meta-analysis

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A R T I C L E I N F O

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A B S T R A C T

Context: Increasing maize planting density is a major agronomic practice to enhance population grain yield, however, canopy shadowing at high density limits plant growth and per-plant grain yield. Dry mass (DM) accumulation, allocation, and remobilization are crucial factors determining grain yield. However, there is limited understanding regarding these processes in response to increasing planting density.

Objectives: This study aimed to evaluate how planting density affects DM accumulation, allocation, and remobilization, as affected by plant architecture, nitrogen (N) rates, N fertilization frequency, and water management.

Methods: A meta-analysis was conducted, involving 2363 observations from 253 peer-reviewed studies.

Results: Globally, population grain yield increased by 11.2 %, which was attributable to increases in a population pre-silking DM (PrS-DM) accumulation of 22.9 % and remobilization efficiency of 12.6 %. Temporally, under a high planting density, per plant DM production showed a decrease (8.3–16.0 %) during the pre-silking stage, but a greater reduction (24.0–25.4 %) during the post-silking stage. DM allocation to roots was greatly reduced, with a decline of 22.1–25.1 % in the root-to-shoot ratio (R/S), and a dropping rate of 5.2 % in harvest index (HI). Compact plant architecture showed a 12.2 % increase in grain yield and a reduction of 3.4 % in HI. Appropriate N rates coupled with splitting-N applications showed an increase in grain yield (up to 13.9 %) and PrS-DM (up to 27.1 %), but a decline in post-silking DM (PoS-DM) (up to 9.7 %) and HI (up to 9.0 %). Efficient water management, i.e., fertigation increased the grain yield (up to 16.9 %).

Conclusion: Increasing planting density increases grain yield mainly by efficiently utilizing light resources during the vegetative stage to increase population PrS-DM production and its remobilization to grain. In addition, less biomass is allocated to the root so that more assimilation is used for shoot growth.

Implications: Field management practices and breeding efforts should focus on facilitating early plant growth to increase population PrS-DM accumulation and developing sound root systems to increase efficiency and canopy-lodging resistance.

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1. Introduction

Maize (*Zea mays* L.) is one of the most important crops in the world, and it is essential to ensure food security (FAO, 2022). Optimizing planting density is a crucial management choice for maize production, as modern cultivars typically produce only one productive ear per plant and few tillers, even under favorable resource conditions (Sangoi, 2001; Stein et al., 2016). In North America, there has been a consistent rise in the agronomic optimum planting density at a rate of 700 plants per hectare per year from 1987 to 2016. This increase in planting density contributes to maize yield gain ranging from 8.5 % to 17 % (Assefa et al., 2018). In France, maize yield experienced a fourfold increase from the 1950s to the 1980s, owing to the adoption of density-tolerant modern cultivars (FAO, 2022). In Brazil, planting density witnessed an increase from 7.1×10^4 plants ha^{-1} in the 1970s to 8.5×10^4 plants ha^{-1} in the 1990s (Sangoi et al., 2002). In China, the mean planting density increased from 3.0×10^4 plants ha^{-1} in the 1950s to 6.0×10^4 plants ha^{-1} in the 2010s, paralleled by a concurrent increase in average maize yield from 1.3 to 5.9 Mg ha^{-1} over the same period (Luo et al., 2020; National Bureau of Statistics, 2022). Nevertheless, increasing planting density decreases the resources available for each plant, consequently resulting in a serious reduction in per-plant grain yield (Gonzalez et al., 2018; He et al., 2022). A conflict arises between individual plant growth and population yield, highlighting the advantage of dense planting in enhancing population yield while mitigating the individual plant impact. A compromise between these two results in an agronomic optimal planting density. Determining an agronomic optimal planting density and promoting per-plant yield are crucial factors contributing to overall yield gains (Assefa et al., 2018).

Dry mass (DM) production, allocation, and remobilization are important factors determining grain yield (Hou et al., 2020; Liu et al., 2020). Regarding DM accumulation, numerous studies have concentrated on investigating the contribution of pre-silking DM (PrS-DM) and post-silking DM (PoS-DM) to grain yield formation. One viewpoint suggests that grain yield formation predominantly arises from PrS-DM accumulation and DM remobilization from vegetative organs, with the remobilization efficiency reaching nearly 50 % (Egli, 2015; Meng et al., 2018; Qi et al., 2020; Ren et al., 2022; Yang et al., 2021). Conversely, another viewpoint suggests that PoS-DM plays a more substantial role in yield formation, and a high remobilization efficiency might not be necessary (Liu et al., 2019; Qingfeng et al., 2016; Zhou et al., 2016). There remains a gap in understanding the contributions of DM production, allocation, and remobilization to grain yield in response to planting density throughout both the vegetative and reproductive stages.

Based on the DM allocation perspective, the harvest index (HI) reflects the proportion of shoot DM (SDM) allocated to kernels. Previous findings suggest HI decreases as planting density increases (Tollenaar et al., 2006). However, alternative viewpoints contend that maize HI remains stable across a range of planting densities (Li et al., 2015; Liu et al., 2020). Due to the limited cultivars, density levels, and growing seasons, it is imperative to conduct a comprehensive investigation on a larger scale to elucidate the HI response to planting density. The root-to-shoot ratio (R/S) represents the allocation of photosynthates from aboveground to belowground (Hebert et al., 2001). In maize, insufficient photosynthate distribution to the roots results in a decrease in root growth, as evidenced by reduced root biomass. This may ultimately impede the plant's ability to acquire soil nutrients, hinder plant growth, and negatively affect crop performance (Shao et al., 2019, 2018). Owing to the difficulties in root sampling, there remains a scarcity of studies investigating the effects of planting density on root growth (Hochholdinger, 2016; Lynch, 2022).

The influence of planting density on maize production is determined by genotype, environment, and management factors (Incognito et al., 2020; Li et al., 2019; Ning et al., 2014; Perez et al., 2019). An ideotype plant architecture is proposed for achieving high yield under intensive production conditions via assessing changes in plant characteristics related to the high yield of maize cultivars cultivated in China and the US over the past 40 decades (Chen et al., 2021). Compact and ideotype cultivars regulate the middle and upper leaves to be more upright under dense planting. This improves light distribution in the canopy, maintains a larger green leaf area, delays canopy leaf senescence, increases DM accumulation and grain-filling rate, and produces a higher grain yield compared with flat cultivars (Liu et al., 2017, 2019). There is a lack of consensus regarding how plant architecture impacts DM production and remobilization before and after silking. One perspective suggests that compact cultivars accumulate more DM during the post-silking stage than flat ones, with no significant difference observed in HI and DM production before silking (Lauer et al., 2012). Another viewpoint argues that compact cultivars produce a higher grain yield by increasing Pre- and PoS-DM production, as well as DM translocation to kernels, resulting in a higher HI (Bai et al., 2019; Ren et al., 2017; Xu et al., 2017). The majority of current studies are conducted at a local, small scale with limited cultivars, which might restrict our understanding of how plant architecture affects grain yield through regulating dynamic DM accumulation, allocation, and re-translocation.

Nitrogen (N) is a major limiting factor for maximizing maize growth (Tilman et al., 2011). A high planting density aggravates plant competition for N, resulting in reduced N per plant, early senescence in the middle and lower canopy, decreased plant growth rates, and reduced DM accumulation (Li et al., 2019; Shi et al., 2016). However, disproportionately excessive N input exacerbates canopy shading, reduces solar utilization efficiency, and causes a series of environmental issues (Amanullah and Shah, 2010; Ju et al., 2009; Linquist et al., 2012). Striving for an optimal N rate to match high-density populations has long been a critical concern. In addition to the N rate, subdividing the total amount of N fertilizer into several applications throughout the growing season, based on maize demand for N is an effective strategy for increasing grain yield (Ciampitti and Vyn, 2011). The key to determining grain formation by optimizing N management is through regulating DM production, and balancing DM allocation and remobilization (Zhai et al., 2022). However, there is currently a limited understanding of how the N application amount and N fertilization frequency affect the characteristics of DM accumulation across the pre-silking and post-silking stages in response to planting density.

Water is another limiting factor for grain production (Deng et al., 2006; Sui et al., 2018). The response of maize yield to planting density is highly dependent on water availability throughout the growth season (Friedman, 2016; Hammer et al., 2009). To address this constraint, low planting densities are commonly adopted to ensure a greater amount of water per plant (Cooper et al., 2008; Turner, 2004). Fertigation, an integrated practice involving split N application and drip irrigation, proves to be an effective strategy for optimizing N utilization and enhancing maize grain yield (Guo et al., 2021; Lai et al., 2022; Li et al., 2023; Wang et al., 2021, 2022; Zhang et al., 2017; Zhou et al., 2017). In this study, we use maize production under fertigation and rainfed systems as a case study to investigate differences in DM production, allocation, and remobilization between farmers' practice and high-density practice. The objective is to discuss the feasibility of achieving high-density and high-yield maize production.

In this study, we conduct a global meta-analysis including 2363 observations from 253 studies. The objective is to elucidate the impacts of DM production, allocation, and remobilization on maize yields under high planting density. The findings are crucial for understanding the physiological mechanisms of grain production in response to planting density and providing guidelines for maize breeding in the future.

2. Materials and methods

2.1. Data collection and criteria

Literature search. We comprehensively searched the Web of

Science (http://www. www.webofscience.com), Google Scholar (The first 1051 records, http://scholar.google.com), and China National Knowledge Infrastructure (CNKI; https://www.cnki.net) for studies that examined maize biomass production and allocation with increasing planting density before December 2022. The keywords used were as follows: "plant*density*" OR "plant*population*" OR "population*density*" OR "seeding rate*" OR "sowing rate*" AND "maize*" OR "corn*" AND "grain yield*". The literature search was based on the procedures of Preferred Reporting Items for Systematic Reviews and Meta-Analyses (Fig. 1) (Moher et al., 2009).

Study selection. Publications were screened based on the following criteria:

(1) studies must be conducted in cropland, excluding indoor experiments using artificially potting soil (i.e., a mixture of sand, clay, and vermiculite, etc.) to grow plants;
(2) studies must be conducted in monoculture or rotation systems, excluding inter-cropping;
(3) studies must be conducted using common commercial maize cultivars, excluding inbred lines, silage corn and sweet corn;
(4) studies must be conducted with ample N supply; any study using zero-N addition or a low N supply was excluded;
(5) the mean, sample size, and standard deviation (SD) or standard error (SE) for studies could be derived from tables, digitized from figures (Getdata Graph Digitizer http://getdata-graph-digitizer.com/), or estimated using the *metagear* R package;
(6) the full text was written in English, or an English abstract was available.

2.2. Treatments for the meta-analysis

For each study, the planting density that was most similar to local farmers' practice (FP) was identified as the control, and higher plant densities (HD) were regarded as treatments. Plant densities less than the control were excluded. The final analysis was based on 2264 grain yields, 1660 HIs, 1652 shoot straws, 188 SDM-V6, 156 SDM-V9, 215 SDM-V12, 838 SDM-R1, 1701 SDM-R6, 838 PrS-DM, 1068 PoS-DM, 197 Root dry mass-R1 (RDM-R1), 62 RDM-R3, 19 RDM-R6, 86 R/S-R1, 21 R/S-R3, 28 R/S-R6, 233 DMRC (contribution of DM remobilization to grain yield), 230 DMRE (remobilization efficiency of DM within vegetative tissues), 230 DMRA (DM remobilization amount), 92 leaf area index-V6 (LAI-V6), 188 LAI-V9, 182 LAI-V12, 698 LAI-R1, 403 LAI-R3, 156 LAI-R5, and 298 LAI-R6, across 253 references. Variables abbreviations are listed in Table 1. The studies used in the meta-analysis are distributed as follows: East Asia (68.0 %), North America (17.2 %), South America (4.6 %), Africa (3.3 %), South Asia (2.6 %), Europe (2.3 %), and West Asia (1.9 %). Among them, China and the USA

Table 1
List of the parameters and their abbreviations examined in the study.

Variable	Abbreviation
FP	Plant density under farmers' practice
HD	High-density practice
DM	Dry mass
SDM-V6	Shoot dry mass at the V6 stage
SDM-V9	Shoot dry mass at the V9 stage
SDM-V12	Shoot dry mass at the V12 stage
SDM-R1	Shoot dry mass at the silking stage
SDM-R6	Shoot dry mass at the maturity stage
PrS-DM	Population DM accumulation during the pre-silking stage
PoS-DM	Population DM accumulation during the post-silking stage
DMRA	Population dry mass remobilization amount
DMRE	Remobilization efficiency of dry mass within vegetative tissues
DMRC	Contribution of dry mass remobilization to grain yield
RDM-R1	Root dry mass at the silking stage
RDM-R3	Root dry mass at milk stage
RDM-R6	Root dry mass at maturity stage
HI	Harvest index
LAI	Green leaf area index
R/S-R1	The root-to-shoot ratio at the silking stage
R/S-R3	The root-to-shoot ratio at the milk stage
R/S-R6	The root-to-shoot ratio at the physiological maturity stage

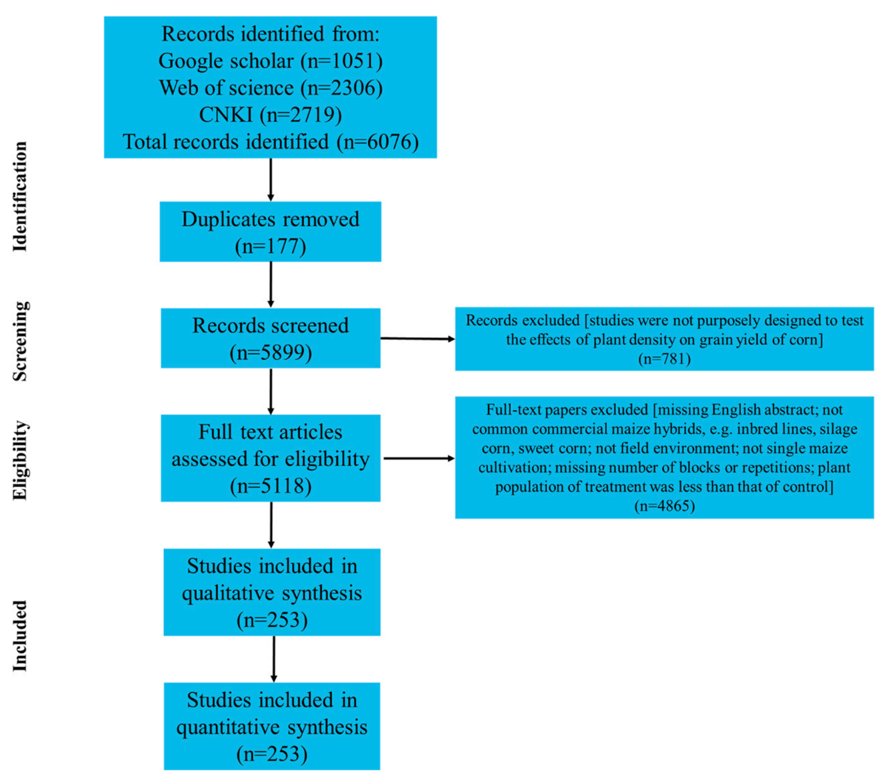

Fig. 1. PRISMA diagram showing the process of locating publications included in the present meta-analysis.

account for 66.7 % and 14.9 %, respectively (Fig. 2). These studies were published between 1966 and 2020. The number of experimental years per study included one (28.7 %), two (43.8 %), and three years or more (26.2 %). Planting densities ranged from 10,000 plants per hectare to 180,000 plants per hectare.

2.3. Data extraction

Indicators were extracted from individual and population levels using the planting density conversion factor. All root samples were collected using the Monolith method (Böhm, 2012) at a depth of 60 cm to 100 cm. After washing, root tissues were oven-dried at 60℃ to 80℃ to a constant weight to determine the root DM (RDM) per plant. The leaf length and maximum leaf width were measured. Leaf area per plant = Σ Leaf length × maximum leaf width × 0.75 (Gallais et al., 2006). The grain yields from all studies were adjusted to a standard moisture basis of 144 g kg^{-1}. The equations used are as follows:

SDM or RDM per hectare = SDM or RDM per plant × Plant populations per hectare (1)

SDM or RDM per plant = SDM or RDM per hectare / Plant populations per hectare (2)

Shoot straw production per hectare = Grain yield per hectare / HI ×(1-HI) (3)

R/S = RDM / SDM (4)

DMRE (%) = (DM of vegetative tissues at R1 - DM of vegetative tissues at R6) / DM of vegetative tissues at R1 × 100 (5)

DMRC = (DM of vegetative tissues at R1 - DM of vegetative tissues at R6) / Grain yield at R6 × 100 (6)

LAI = (Leaf area per plant × Plant populations) / Plot area (7)

In addition to the above variables, we also extracted N fertilizer rates, N fertilization frequency, cropland water management, and plant architecture (Table 2). Groups for N fertilizer input were divided (Cui et al., 2018; Hu et al., 2021). Due to limited information, our study exclusively conducted plant architecture analysis on maize cultivars bred in China. The categorization criterion for plant architecture was derived from descriptions on the official website of China Seed Association, 2022 (https://www.seedchina.com/).

2.4. Data analysis and publication bias

The effects of increasing planting density on the response variable X

Table 2
The levels of response variables are included in this meta-analysis.

Variable	Levels
N fertilizer rates (kg/ha)	Low: ≤50 (Africa), ≤150 (Asia), ≤180 (Other regions)
	Optimal: 50–120 (Africa), 150–250 (Asia), 180–250 (Other regions)
	High: >120 (Africa), >250 (Asia), >250 (Other regions)
N fertilization frequency	1
	2
	≥3
Water management	Rainfed
	Fertigation
Plant architecture	Flat
	Semi-compact
	Compact

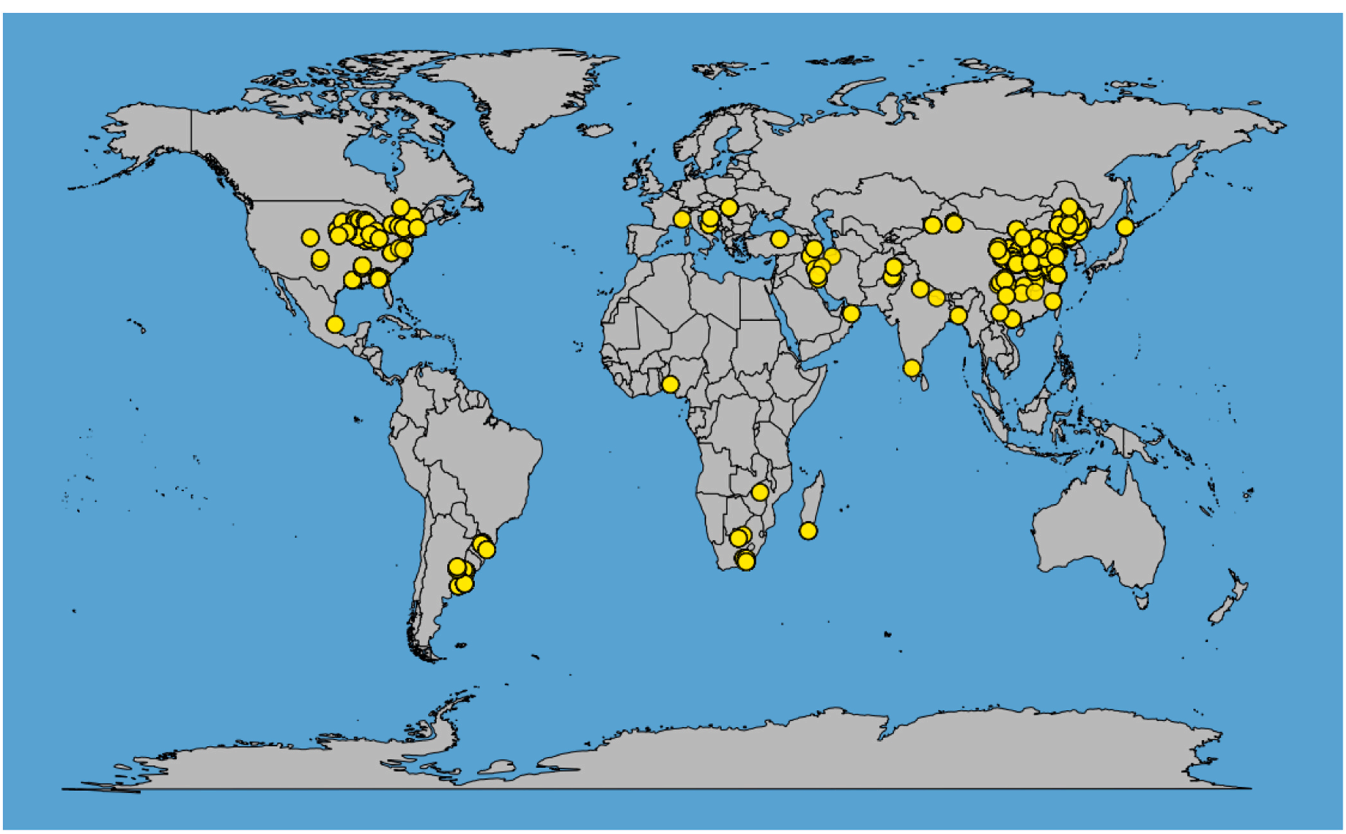

Fig. 2. Global distribution of field experiments included in this meta-analysis. The data set covers 2,363 paired observations from 253 field experiments across 21 countries from 1966 to 2020. The map was created with QGIS version 3.20 (Open Source Geospatial Foundation Project, http://qgis.osgeo.org). The global map was down-loaded from Natural Earth (http://www.naturalearthdata.com/).

(e.g., shoot or root biomass) were quantified by effect size, defined as the natural log of the response ratio (lnRR) with the following:

$$\mathrm{LnRR} = \mathrm{Ln}\left(\frac{X_T}{X_c}\right) \tag{8}$$

where X_T and X_C represent the mean value of treated and controlled planting densities for the response variable X. Natural log conversion of the response ratio was used to stabilize the variance (Hedges et al., 1999). The results were exponentially back-transformed and presented as the percentage of changes (RR-1) × 100 % in the variables under increased planting density. Positive or negative percentage changes denoted an increase or decrease in the corresponding variable.

Effect sizes were weighted by the inverse of the pooled variance (Wei et al., 2021). For studies that did not report a standard deviation (SD) or standard error (SE), the approach of (Sinclair and Bracken, 1992) was used to estimate SD in the *metagear* R package (version 3.6.1). A random-effects model was used according to the significance of the residual heterogeneity in the observations in the *metafor* R package (version 3.6.1). A mixed-effects model was used to assess the variations in effect size according to several categorical and continuous factors. The mean effect sizes and the 95 % confidence intervals (CIs) were presented in forest plots. Differences between treatments (FP) and controls (HD) were considered to be significant when the CIs did not overlap zero.

Path analysis and linear stepwise regression were conducted using a structural equation model (SEM) with the *piecewiseSEM* R package (version 3.6.1) to determine the effects of plant architecture, N fertilizer rates, N fertilization frequency, and fertigation adoption on PrS-DM, PoS-DM, DMRE, HI, and grain yield (Fig. 10). We used the *randomForest* package to determine key factors affecting grain yield in response to increased planting densities (Fig. S2).

Funnel plots were adopted to evaluate the publication bias (Makowski et al., 2018; Wei et al., 2021). We carried out a trim and fill analysis for funnel plots in the *metafor* R package (version 3.6.1). The results (effects) were considered acceptable if there was no significant difference before and after trim and fill (Makowski et al., 2018). In cases where the funnel plot test indicated publication bias, the bias-corrected effect size value was adopted, which was estimated using the trim and fill method (Fig. S4-S17).

3. Results

3.1. Overall effects of increasing planting density on DM accumulation, allocation, and remobilization

Increasing planting density exerted a great impact on DM production, allocation, and remobilization (Figs. 3, 4, 5). The transition from farmers' practice (FP) to high-density practice (HD) resulted in a decrease in shoot dry mass (SDM) per plant, ranging from 8.3 % to 25.4 % across the V6, V9, V12, R1, R3, and R6 stages (Fig. 3a). The root dry mass (RDM) per plant exhibited greater declines of 28.9–32.3 % across the R1, R3, and R6 stages (Fig. 3a). Concurrently, the SDM per population demonstrated increases of 18.9–33.1 %, with a gradually narrowing range (Fig. 3b). The RDM per population exhibited increases of 4.8–11.3 % across the R1 and R3 stages, while no significant difference was observed at R6 (Fig. 3b).

Globally, changing from FP to HD increased grain yield and shoot straw production by 11.2 % and 12.2 %, respectively. However, HI experienced a decrease of 5.2 % (Fig. 4a), and the R/S decreased by 22.1–25.1 % (Fig. 4b). The shift from FP to HD led to an increase of 22.9 % in population PrS-DM, but a decrease of 0.3 % in population PoS-DM (Fig. 5a). The DM remobilization amount (DMRA) increased by 35.7 %. The DM remobilization efficiency (DMRE) and contribution of DM remobilization to grain yield (DMRC) showed increases of 12.6 % and 23.2 % (Fig. 5b).

3.2. Effects of plant architecture

Before V12, the transition from FP to HD in flat cultivars showed a smaller reduction in per plant SDM, along with a relatively higher rate of increase in per population SDM compared with compact cultivars. As growth progressed, the improved plant compactness served to mitigate the effects of increasing planting density. Upon comparing FP to HD, the SDM per plant fell by 22.6–31.3 %, 13.4–18.7 %, and 15.8–22.5 % from the R1 to R6 stages for flat, semi-compact, and compact cultivars, respectively. The RDM per hectare showed an increase of 19.6 % in flat cultivars, exceeding the increase that was observed in compact cultivars (Fig. 6a, b).

As the planting density increased, adopting compact cultivars significantly increased grain yield and shoot straw production while minimizing the reduction in HI. From FP to HD, compact cultivars showed an increase of 12.2 % in grain yield and a rise of 12.9 % in shoot

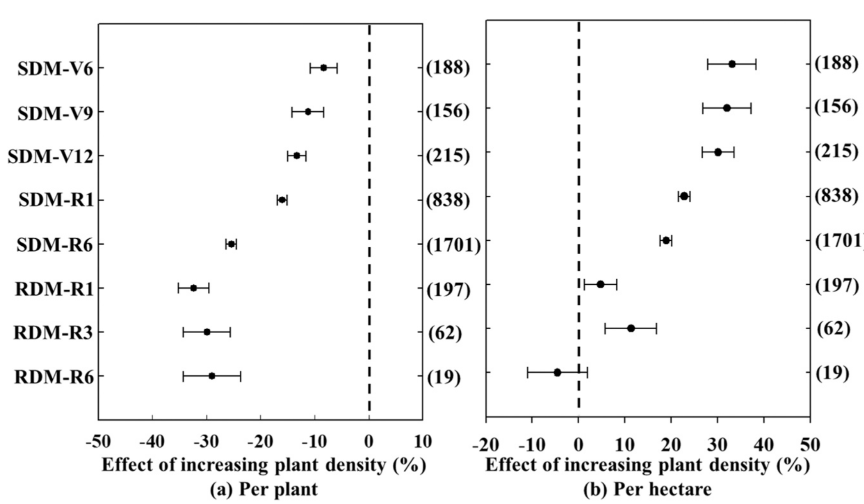

Fig. 3. Effects of increasing planting density on shoot and root dry mass per plant (a) and per hectare (b). SDM-V6 means shoot dry mass at V6 stage; SDM-V9 means shoot dry mass at V9 stage; SDM-V12 means shoot dry mass at V12 stage; SDM-R1 indicates shoot dry mass at silking stage; SDM-R6 indicates shoot dry mass at maturity stage, including shoot straw and grain; RDM-R1 is root dry mass at silking stage; RDM-R3 is root dry mass at grain-filling stage; RDM-R6 is root dry mass at physiological maturity stage. Error bars represent 95 % confidence intervals. Numbers in parentheses indicate the number of observations.

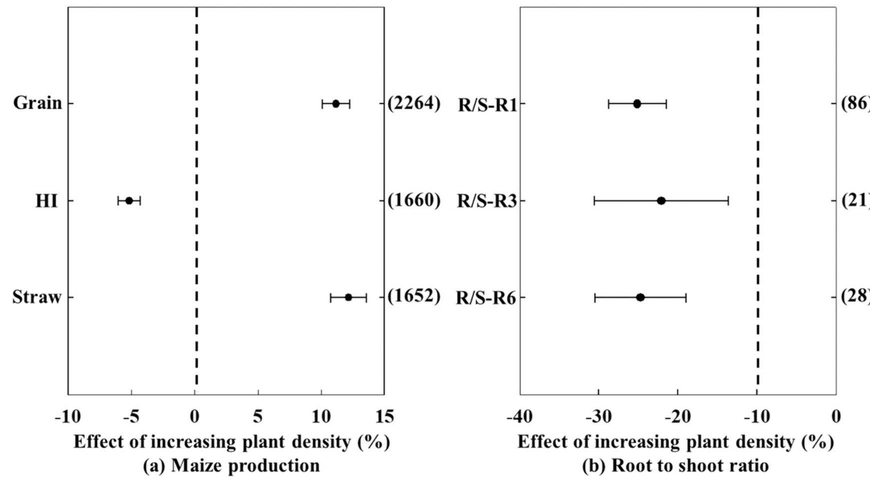

Fig. 4. Effects of increasing plant density on maize grain yield, HI and shoot straw (a); root to shoot ratio (b). HI means harvest index; R/S-R1, R/S-R3, and R/S-R6 indicate root-to-shoot ratio at silking, grain-filling, and maturity stage, respectively.

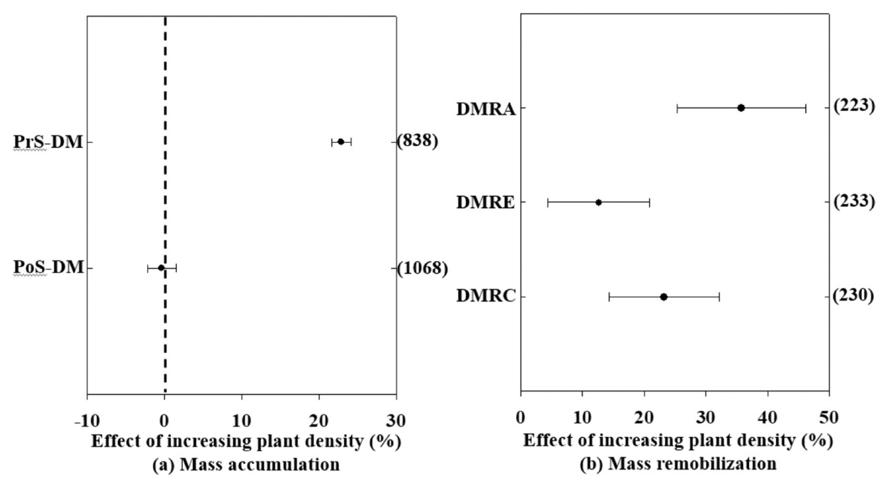

Fig. 5. Effects of increasing plant density on dry mass accumulation (a); dry mass remobilization (b). PrS-DM means population dry mass accumulation during the pre-silking stage. PoS-DM means population dry mass accumulation during the post-silking stage. DMRA means population dry mass remobilization amount. DMRE means remobilization efficiency of dry mass within vegetative tissues. DMRC means the contribution of dry mass remobilization to grain yield. Error bars represent 95 % confidence intervals. Numbers in parentheses indicate the number of observations.

straw production. The HI showed reductions of 13.1 % and 3.4 % for flat and compact cultivars (Fig. 6c). When the planting density shifted from FP to HD, there were no significant differences observed in population PrS-DM among cultivars. Population PoS-DM increased by 14.5 % for compact cultivars, whereas a decrease of 5.8 % was observed for flat cultivars (Fig. 6d). The improvement in plant compactness significantly increased DM remobilization to grain under a high planting density, with DMRE and DMRC increasing by 49.4 % and 50.7 % for compact cultivars (Fig. 6e).

3.3. *Effects of cropland N management*

3.3.1. *N fertilizer rates*

Increasing the N rate demonstrated a positive effect on DM accumulation. Throughout all growth stages, shifting from FP to HD increased SDM per population under the High, Optimal, and Low N groups. The increases ranged from 23.2 % to 35.3 %, 17.5–41.4 %, and 12.7–24.0 %, respectively. There was no significant difference in SDM per plant across N rates (Fig. 7a, b). The grain yields increased by 13.9 %, 9.7 %, and 9.8 % in the High, Optimal, and Low N groups. Shoot straw production increased by 14.9 %, 9.2 %, and 10.5 %. HI did not significantly differ among the N rate groups (Fig. 7c). The N rates had a pronounced impact on PrS-DM compared with PoS-DM. The PrS-DM increased by 25.5 %, 25.2 %, and 19.3 % for the High, Optimal, and Low N groups, when transitioning from FP to HD (Fig. 7d). There were no significant differences in DMRA, DMRE, and DMRC across N rates (Fig. 7e).

3.3.2. *N fertilization frequency*

Before V12, when the density changed from FP to HD, the Once and Twice groups exhibited a more rapidly increasing rate of SDM per population compared with the Thrice or more group. By implementing splitting-N throughout the growing season, the impact on per-plant SDM production caused by increasing planting density was reduced (Fig. 8a, b). The grain yield increased by 10.3 %, 10.4 %, and 12.8 % when shifting from FP to HD across the Once, Twice, and Thrice or more groups, respectively. Shoot straw production increased by 9.3 %, 11.1 %, and 15.8 %. The HI showed declines of 9.0 %, 5.1 %, and 2.4 % (Fig. 8c). In addition, the application of splitting-N fertilizer had a greater rate of increase in DMRE and RDM per population (R1) compared with the Once N group (Fig. 8a, b, d, e).

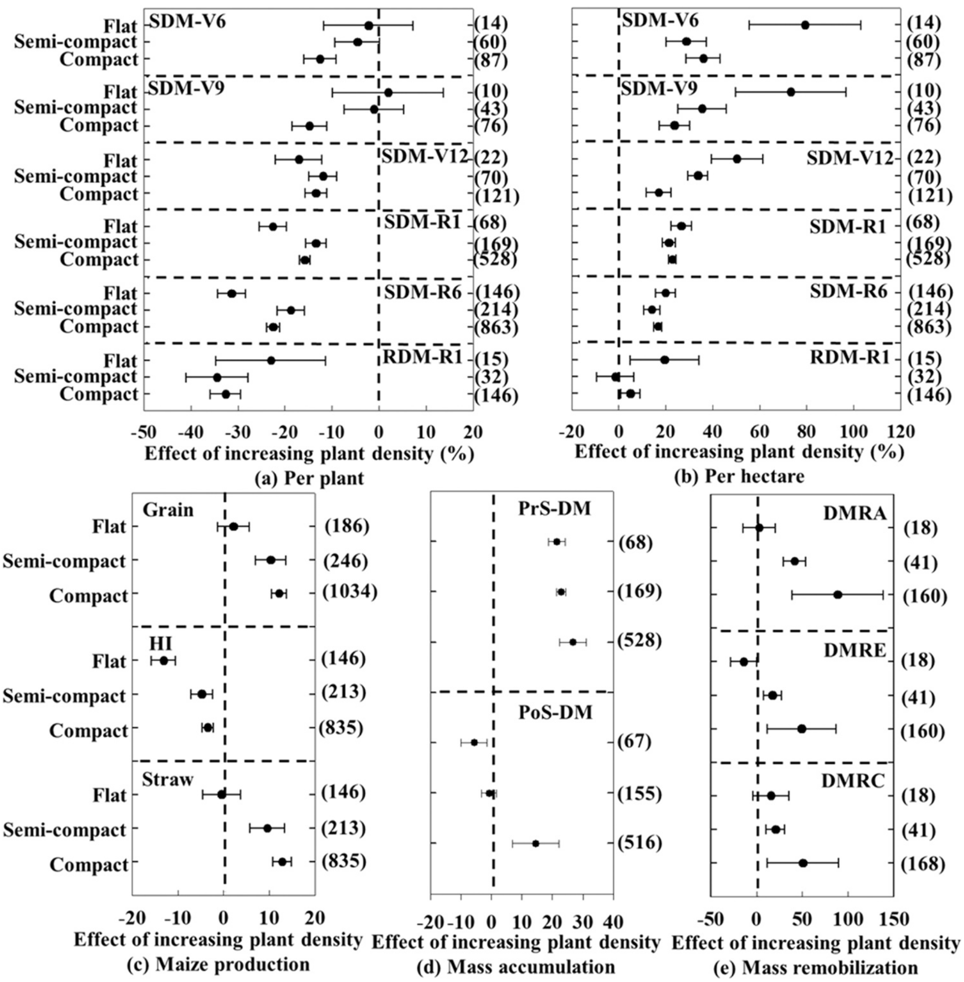

Fig. 6. The interaction effect of plant architecture and increasing plant density on shoot and root dry mass per plant (a); per hectare (b); grain yield, HI and shoot straw (c); dry mass accumulation (d); dry mass remobilization (e). SDM-V6 means shoot dry mass at V6 stage; SDM-V9 means shoot dry mass at V9 stage; SDM-V12 means shoot dry mass at V12 stage; SDM-R1 indicates shoot dry mass at silking stage; SDM-R6 indicates shoot dry mass at maturity stage, including shoot straw and grain; RDM-R1 is root dry mass at silking stage. HI means harvest index. PrS-DM means population dry mass accumulation during the pre-silking stage. PoS-DM means population dry mass accumulation during the post-silking stage. DMRA means population dry mass remobilization amount. DMRE means remobilization efficiency of dry mass within vegetative tissues. DMRC means the contribution of dry mass remobilization to grain yield. Error bars represent 95 % confidence intervals. Numbers in parentheses indicate the number of observations.

3.4. Effects of cropland water management

Fertigation considerably raised shoot and root DM accumulation per hectare compared with rainfed conditions. Throughout all growth stages, as the density changed from FP to HD, the SDM per population of the Rainfed and Fertigation groups showed increases ranging from 18.3 % to 39.8 % and 22.8–42.5 %, respectively. The RDM per population in the Rainfed and Fertigation groups increased by 1.3 % and 12.9 %, respectively (Fig. 9a, b). The grain yields of the Rainfed and Fertigation groups increased by 9.0 % and 16.9 %, respectively (Fig. 9c). No significant differences were observed in PoS-DM, PrS-DM, DMRA, DMRE and DMRC (Fig. 9d, 9e).

3.5. Relationships between DM accumulation, allocation, plant architecture, N fertilizer, and water management factors

The SEM explained 83 % of the variation in grain yields. Plant architecture had significant positive effects on PoS-DM. The N fertilization frequency had significant positive effects on PoS-DM and DMRE. The N fertilizer rates had significant positive effects on PrS-DM. Fertigation exerted significant positive effects on DM allocation to grain (Fig. 10).

4. Discussion

4.1. Mechanisms underpinning the enhanced maize yield with increasing planting density

Increasing planting density is one of the most effective strategies for improving maize grain yield (Assefa et al., 2016; Haarhoff and Swanepoel, 2018; Milander et al., 2016). Globally, we estimated an 11.2 % increase in grain yield owing to enhanced plant populations (Fig. 4a). According to Luo et al. (2023), dense planting and improved soil fertility could increase maize grain yield in China even by up to 52 % by the 2030 s. This increase in grain yield is predominantly attributable to improved DM accumulation and enhanced DMRE (Figs. 5, 10). Despite a great LAI, this does not guarantee a higher grain yield; its substantial increase may be advantageous for canopy closure, minimizing light leakage, and subsequently enhancing photosynthetic production (Fig. S1). This, in turn, may potentially contribute to grain production (Liu et al., 2022a, 2021a). The majority of studies consider that PoS-DM is the primary factor contributing to yield formation, and high remobilization efficiency might not be essential (Ciampitti et al., 2013; Liu et al., 2017, 2023; Cao et al., 2021; Rizzo et al., 2022). Recent findings suggest an increasing percentage of PoS-DM accumulation with

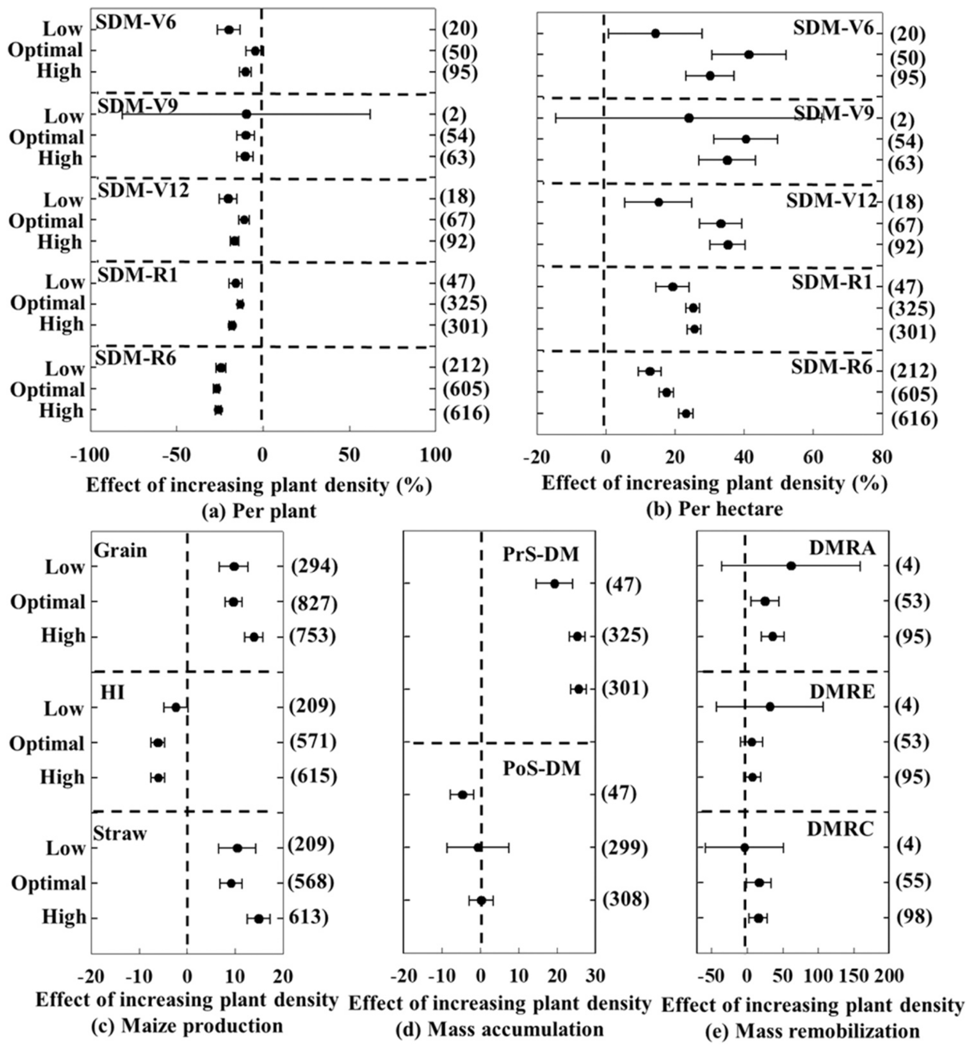

Fig. 7. The interaction effect of N fertilizer rates and increasing plant density on shoot dry mass per plant (a); per hectare (b); grain yield, HI, and shoot straw (c); dry mass accumulation (d); and dry mass remobilization (e). SDM-V6 means shoot dry mass at V6 stage; SDM-V9 means shoot dry mass at V9 stage; SDM-V12 means shoot dry mass at V12 stage; SDM-R1 indicates shoot dry mass at silking stage; SDM-R6 indicates shoot dry mass at maturity stage, including shoot straw and grain. HI means harvest index. PrS-DM means population dry mass accumulation during the pre-silking stage. PoS-DM means population dry mass accumulation during the post-silking stage. DMRA means population dry mass remobilization amount. DMRE means remobilization efficiency of dry mass within vegetative tissues. DMRC means the contribution of dry mass remobilization to grain yield. Error bars represent 95 % confidence intervals. Numbers in parentheses indicate the number of observations.

enhanced grain production, particularly when maize yield exceeds 25.0 Mg ha^{-1}, reaching up to 70 % (Liu et al., 2023, 2020; Meng et al., 2018). In this meta-database, about 85 % of grain yields were less than 15 Mg ha^{-1}. Nonetheless, there is an urgent need to improve PoS-DM accumulation and HI to further increase maize production under higher planting densities in the future.

Enhanced HI has been the main driver of maize yield during the "green revolution" (Duvick and Cassman, 1999; Evenson and Gollin, 2003; Ciampitti and Vyn, 2012). A higher HI indicates a greater DM allocation to the kernels, increasing the grain yield without extra DM production. Our study revealed that a high planting density marginally reduced HI by 5.2 %, suggesting a decreased photosynthate allocation to the kernels. Previous studies have documented similar results (DeLougherty and Crookston, 1979; Echarte and Andrade, 2003; Li et al., 2018, 2015; Liu et al., 2020). Carbon assimilation is essential for grain production during the process of kernel setting and grain filling (Cliquet et al., 1990; Schussler and Westgate, 1994). Increasing planting density results in the reduced availability of light interception and other resources for each plant, as well as limited assimilate delivery to the cob. This might lead to kernel abortion and a great reduction in grain weight (Hütsch and Schubert, 2017).

Root growth and maintenance require considerable quantities of photosynthates (Lynch, 2007; Poorter et al., 2012). Field-grown maize allocates 20–40 % of its photosynthates to below ground, with roughly half being employed for root construction (Hirte et al., 2018; Holz et al., 2018). Therefore, decreasing root photosynthate consumption allows more photosynthates to be used for shoot growth and grain yield (Freschet et al., 2015; Roumet et al., 2016). Here, we discover that the R/S ratio and root biomass decreased with increasing planting density. The root biomass per plant decreased from 28.9 % to 32.3 %, and the R/S ratio reduced by 22.1–25.1 % (Figs. 3a, 4b). These findings suggest a decreased photosynthate allocation to the roots under high planting density. The reduction in root biomass and the R/S ratio under high planting density aligns with previous observations (Gao et al., 2017; Shao et al., 2019, 2018). The concept of "root growth redundancy" is introduced, meaning that when a portion of the root satisfies plant growth requirements, other roots may contribute minimally but consume photosynthates (Zhang et al., 1999). Studies have demonstrated that reducing root growth redundancy can reduce energy consumption and improve economic yield (Yang et al., 2019; Zhang et al.,

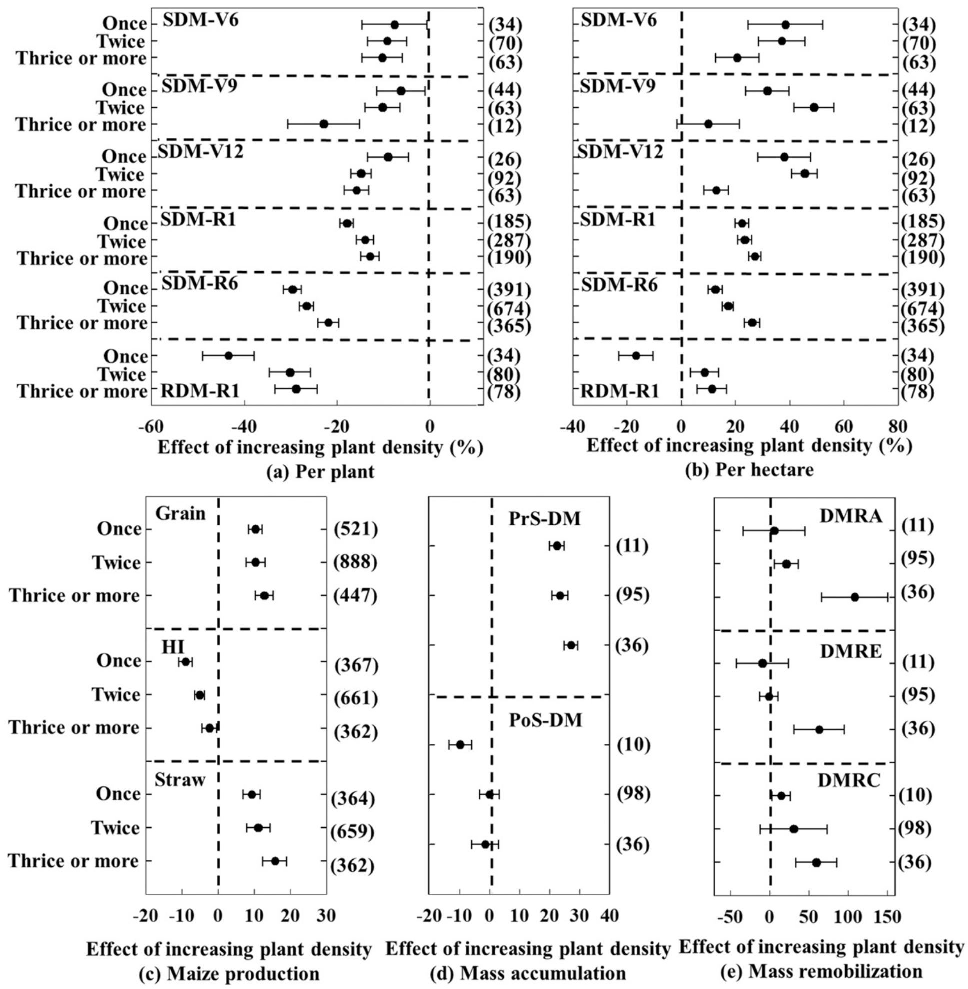

Fig. 8. The interaction effect of N fertilization frequency and increasing plant density on the shoot and root dry mass per plant (a); per hectare (b); grain yield, HI and shoot straw (c); dry mass accumulation (d); dry mass remobilization (e). SDM-V6 means shoot dry mass at V6 stage; SDM-V9 means shoot dry mass at V9 stage; SDM-V12 means shoot dry mass at V12 stage; SDM-R1 indicates shoot dry mass at silking stage; SDM-R6 indicates shoot dry mass at maturity stage, including shoot straw and grain; RDM-R1 is root dry mass at silking stage. HI means harvest index. PrS-DM means population dry mass accumulation during the pre-silking stage. PoS-DM means population dry mass accumulation during the post-silking stage. DMRA means population dry mass remobilization amount. DMRE means remobilization efficiency of dry mass within vegetative tissues. DMRC means the contribution of dry mass remobilization to grain yield. Error bars represent 95 % confidence intervals. Numbers in parentheses indicate the number of observations.

2022). The reduced R/S ratio reflects the allocation strategy of maize DM. Nevertheless, inhibited root growth under high planting density limits nutrient absorption and weakens root lodging resistance (Shao et al., 2021a, 2021b). To address this, a combined approach involving breeding efforts and optimized field management practices is recommended, aiming to regulate root growth, improve per unit root absorption efficiency and strength, and balance shoot and root growth.

4.2. Insights for future breeding and field management

Multiple factors, including plant architecture, N fertilizer rates, N fertilization frequency, and cropland water management practices, collectively affect the response of grain yield to planting density by determining DM accumulation and allocation (Incognito et al., 2020; Li et al., 2019; Ning et al., 2014; Perez et al., 2019). The random-forest analysis reveals that plant architecture and N fertilization frequency are the primary factors driving grain production, followed by N fertilizer rates and fertilization adoption (Fig. S2).

Plant architecture is an important factor in determining grain production, as establishing an appropriate plant canopy structure is crucial for distributing light evenly throughout the canopy, improving radiation use efficiency per plant, and maximizing crop yield (Boomsma et al., 2009; Ma et al., 2014; Van Roekel and Coulter, 2012). Compact cultivars showed an increase of 14.5 % in PoS-DM and a rise of 12.2 % in grain yield (Fig. 6). The possible reasons are as follows: First, compact cultivars possess more upright leaves and boosted leaf orientation, enabling efficient space utilization and contributing to an increased LAI. This facilitates intercepting more solar radiation (He et al., 2022; Woli et al., 2017; Xue et al., 2015). In addition, compact cultivars have a lower canopy attenuation coefficient, lessening the poor light environment induced by high planting density, reducing leaf senescence during grain filling, and promoting DM production (Ma et al., 2014; Lacasa et al., 2022). Second, compact cultivars typically have a smaller root system and a lower R/S ratio compared with flat cultivars (Fig. 6a, b). This helps to mitigate plant-to-plant competition and reduce energy loss, facilitating more photosynthate allocation to the shoot and increasing grain yield under high-density conditions (Lynch, 2007; Thomas and Ougham, 2014). Nevertheless, a small root system may be unfavorable for water and nutrient resources acquisition, as well as root-lodging resistance, which poses a great threat to maize production (Liu et al., 2012, 2021b; Mi et al., 2016). Future breeding and management efforts should prioritize enhancing root absorption efficiency and improving root system architecture (Chen et al., 2014; Zhang et al., 2023).

In addition to plant architecture, splitting-N is also beneficial for

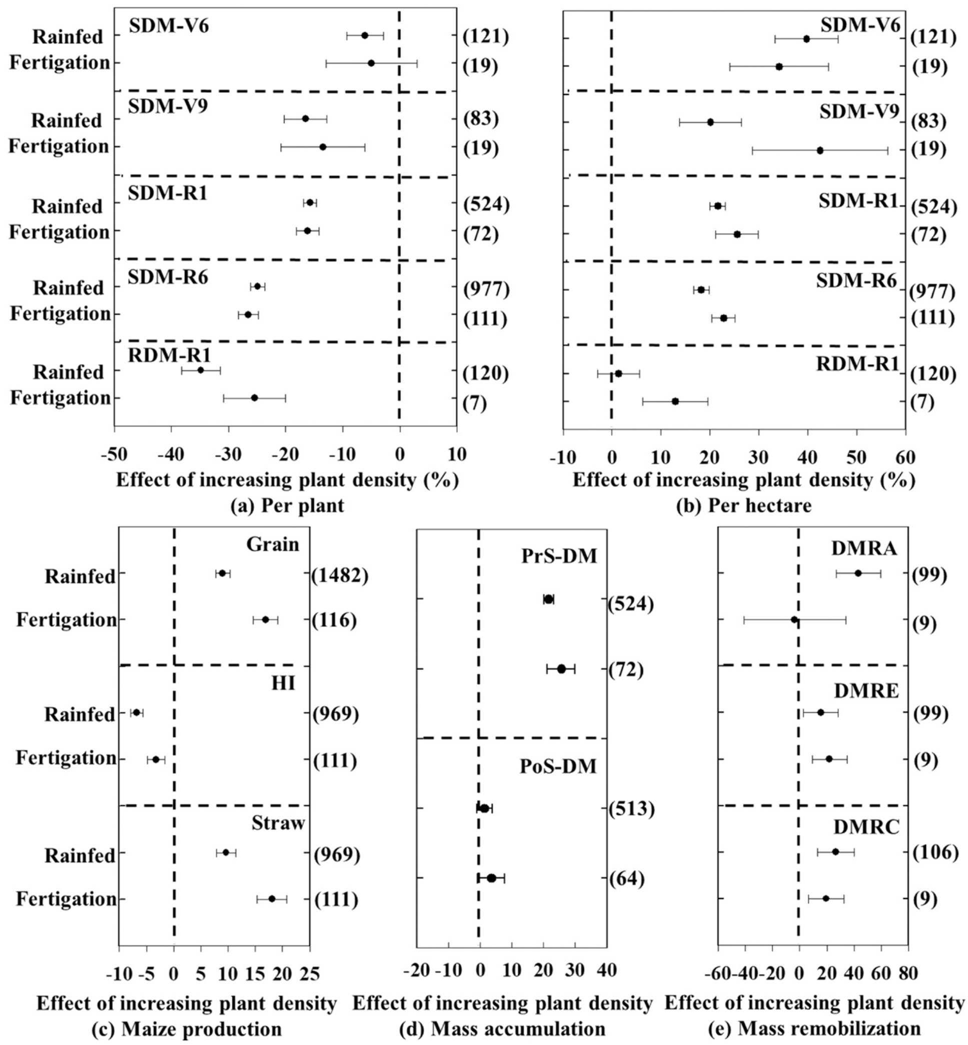

Fig. 9. The interaction effect of water management and increasing plant density on shoot and root dry mass per plant (a); per hectare (b); grain yield, HI, and shoot straw (c); dry mass accumulation (d); and dry mass remobilization (e). SDM-V6 means shoot dry mass at the V6 stage; SDM-V9 means shoot dry mass at the V9 stage; SDM-R1 indicates shoot dry mass at the silking stage; SDM-R6 indicates shoot dry mass at the maturity stage, including shoot straw and grain; RDM-R1 is root dry mass at silking stage. HI means harvest index. PrS-DM means population dry mass accumulation during the pre-silking stage. PoS-DM means population dry mass accumulation during the post-silking stage. DMRA means population dry mass remobilization amount. DMRE means remobilization efficiency of dry mass within vegetative tissues. DMRC means the contribution of dry mass remobilization to grain yield. Error bars represent 95 % confidence intervals. Numbers in parentheses indicate the number of observations.

enhancing grain yield (Nasielski et al., 2020). The Thrice or more group demonstrates an increase in grain yield up to 12.8 %, primarily attributable to the higher DM at maturity (Fig. 8). The increase in DM at maturity is predominantly attributable to the great remobilization of PrS-DM to the grain. For the Thrice or more groups, there were remarkable increases of 27.1 %, 63.3 %, and 59.8 % in PrS-DM, DMRE, and DMRC, respectively (Fig. 8c, d). The maize root system maintains a balance between old roots senescence and the new roots growth (Gao et al., 1998; Li et al., 2010). Large amounts of carbohydrates are utilized to facilitate new root growth and maintain respiration in old roots (Niu et al., 2010). However, during the grain-filling stage, grains serve as a stronger carbohydrate sink than the roots. Under this circumstance, insufficient C supply may impede root growth (Yan et al., 2011). Optimizing N application frequency helps to improve root growth and LAI (Fig. 8b and Fig. S1d). Chen et al. (2015) concluded that high root N uptake activity, rather than delayed root senescence, resulted in large N accumulation in the shoot. A critical aspect of splitting N is synchronizing N supply with the demand for high-yielding maize. Particularly, N application during the middle-late stage alters the source-to-sink ratio, contributing to greater DM accumulation (Qingfeng et al., 2012; Cheng et al., 2015; Yan et al., 2016; Li et al., 2020; Wang et al., 2020).

Optimizing the N fertilizer rates is another factor contributing to maize production. For instance, a high N rate increased grain yield by up to 13.9 %, indicating more N fertilizer is required at higher plant densities (Fig. 7c). Yan et al. (2016) demonstrated that for 60,000, 75,000, and 90,000 plants per hectare, respectively, the maximum maize grain yield could be obtained using the 70 %, 100 %, and 130 % optimal N rate treatments. Increased N fertilizer application has been shown in similar trials to be a substantial factor in increasing maize yields, particularly at high planting densities (Zhai et al., 2018; Ma et al., 2020). The effect of N application on grain yield is primarily through increasing total DM rather than influencing DM allocation, as indicated by the unaffected HI across N rates (Fig. 7c). Previous studies also suggest that the N rate has a greater influence on DM production than DM partitioning of to the grain under high plant density (Ciampitti and Vyn, 2011). Efforts should be directed toward promoting PoS-DM accumulation to produce higher grain yields in the future. However, the limited root growth and accelerated leaf senescence during the grain-filling stage could lead to relatively low N uptake efficiency at high planting densities (Du et al., 2021; Han et al., 2020; Shao et al., 2018; Yan et al.,

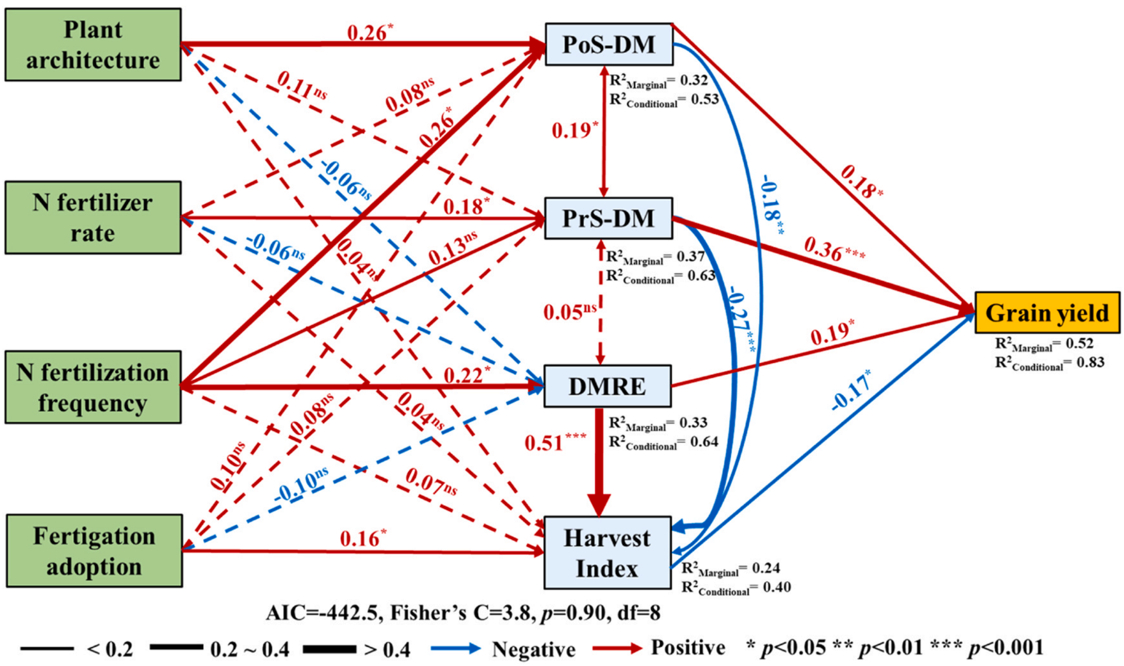

Fig. 10. Effects of plant architecture, N fertilizer rates, N fertilization frequency, and fertigation adoption on dry mass accumulation, dry mass remobilization, harvest index, and grain yield based on structural equation model (SEM). Numbers adjacent to arrows are standardized path coefficients, analogous to relative regression weights, and indicative of the effect size of the relationship. Continuous and dashed arrows indicate significant and non-significant relationships, respectively. The arrow width is proportional to the strength of the relationship. The proportion of variance explained (R^2) appears alongside every response variable in the model. Goodness-of-fit statistics for each model are shown in the lower right corner (df, degrees of freedom; AIC, Akaike information criterion). PrS-DM means population dry mass accumulation during the pre-silking stage. PoS-DM means population dry mass accumulation during the post-silking stage. DMRE means remobilization efficiency of dry mass within vegetative tissues.

2017; Zhang et al., 2020, 2019a).

Fertigation provides an effective method for coupling water and N, which combines the advantage of drip irrigation and splitting-N application (Zhang et al., 2019b). Fertigation promotes grain yield (up to 16.9 %) by enhancing DM accumulation and its allocation to grain (Fig. 9). Compared with rainfed maize, synchronous water, and nutrient optimization via drip fertigation improved root biomass (Fig. 9a, b). Vigorous root growth may help delay leaf senescence and promote water and nutrients absorption, which collectively contributes to DM production and maize grain yield (Kang et al., 2000; Li et al., 2009; Nacry et al., 2013; Hou et al., 2019; Wu et al., 2019). Moreover, a higher LAI during the grain-filling stage contributes to PoS-DM (Fig. S1e). For instance, adopting fertigation techniques with a compact cultivar (MC670) at a planting density of 13.5 plants m^{-2} established a national high-yield maize record with a yield of 24.95 Mg ha^{-1} in Xinjiang Province (Cheng et al., 2021). This may serve as a valuable reference for maize practitioners in high-density field management.

4.3. Limitations and implications for the future study

Our study still has some limitations that need to be addressed. First, a few of the studies did not provide SD or SE values. Despite the approach (Sinclair and Bracken, 1992) used to estimate SD in the "metagear" R package, this may affect the effect size estimation accuracy. Second, our analysis is mainly focused on plant architecture, N, and water management, and does not consider interactions with other factors such as climate, soil fertility, tillage, and cultivation practices. Due to data limitations, our study exclusively conducted plant architecture analysis on maize cultivars bred in China. There is a lack of detailed information regarding the categorization, which might introduce some uncertainties. Third, more than 65 % of these observations were distributed in Asia, particularly in China. Studies from North America, South America, Europe, and other major maize planting regions are lacking (Fig. 2). The results of meta-analyses might be influenced by the geographical distribution of these studies, potentially limiting the applicability to specific experimental sites.

An increase in planting density may increase maize shoot straw at maturity, as indicated by the reduced HI. On the one hand, maize shoots straw in the field may impede planting for the subsequent season if it cannot be effectively utilized. On the other hand, straw is growing ever more important in clean energy production and conservation tillage owing to its high energy content, nutrient richness, and soil carbon input (Liu et al., 2022b). Based on this viewpoint, a higher density combined with the facilitated utilization of maize straw is of great significance to the sustainable development of agricultural production.

5. Conclusions

Our meta-analysis is the first to demonstrate that increasing planting density increases maize yield by 11.2 % globally. This is attributable to the increased population PrS-DM production and DM remobilization into grain. In addition, less photosynthate is allocated to the root to ensure more DM for shoot growth. Our meta-analysis is also the first to explore the potential to increase grain yield by optimizing plant architecture, cropland N, and water management practices under high planting densities. The ideotype plant architecture mostly gains grain yield by enhancing PoS-DM. Splitting-N application promotes grain yield by enhancing PoS-DM and DM remobilization. A reasonable increase in the N rates enhances grain yield by promoting PoS-DM. Fertigation increases grain yield by increasing DM allocation to grain through coordinating water and N fertilizer supply. Our results provide a theoretical basis for future breeding and field management, aiming to improve population DM production and allocation to grain, to construct a favorable root system with high nutrient and water use efficiency, and canopy-lodging resistance.

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CRediT authorship contribution statement

Fengbo Zhu: Visualization, Investigation. **Haihang Chi:** Visualization, Investigation. **Xuebing Wu:** Visualization, Investigation. **Hui Shao:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Data curation, Conceptualization. **Guohua Mi:** Writing – review & editing, Supervision, Conceptualization. **Zhibiao Wei:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Yi Xu:** Writing – review & editing. **Wenjun Shi:** Writing – review & editing. **Jiahui Duan:** Visualization, Investigation. **Junhui Liu:** Visualization, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2024.109430.

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