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Agronomic Drivers of Harvest Index Variation in Winter Rapeseed Cultivars from Different Breeding Eras

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ABSTRACT

Understanding harvest index (HI) variation is essential for improving seed yield in rapeseed. This study evaluated 60 winter rapeseed cultivars differing in release year, plant height, and growth duration across two locations and two seasons in China. HI ranged from 0.031 to 0.30, with mean values 48.6% higher at Bijiang than at Sinan. A 0.1 increase in HI was associated with seed yield gains of 115-967 kg ha^{-1}. HI was positively correlated with main stem seed yield but negatively associated with stem and pod wall dry weight, particularly at Sinan. Cultivars released after 2015 exhibited 5.9%-13.3% higher HI than those released before-2010. In addition, dwarf and early-maturing cultivars consistently showed superior HI values. The results indicate that reducing structural dry matter allocation to stems and pod walls, while maintaining transport capacity, represents a promising strategy for further HI improvement in rapeseed breeding. These results demonstrate that modern rapeseed breeding has indirectly increased HI through reduced plant height and shorter growth duration. Further gains may be achieved by optimizing biomass partitioning without compromising transport capacity to reproductive organs.

Keywords: rapeseed, harvest index, seed yield, stem dry weight, plant height, growth duration.

INTRODUCTION

Rapeseed (*Brassica napus* L.) is one of the most important oil crops worldwide, with its seed oil widely used for edible purposes, bioenergy, and industrial materials (Wittkop et al., 2009). With increasing population pressure and limited arable land, further improvement of seed yield per unit area has become a major goal in rapeseed (Hu et al., 2022). However, the genetic gain in seed yield of rapeseed has slowed over the past decades, and breeding strategies solely based on increasing biomass production have encountered bottlenecks (Kirkegaard et al., 2016). Hence, harvest index (HI) has regained considerable attention as a key indicator of the efficiency of photosynthate allocation to seeds (Diepenbrock, 2000).

In major cereal crops, substantial progress has been made in the genetic improvement of HI. For instance, the green revolution in rice and wheat was largely attributed to the introduction of dwarfing genes, which significantly increased HI. In contrast, HI improvement in rapeseed has been relatively slow, with reported HI values varying widely from 0.15 to 0.35 (Habekotté, 1997; Diepenbrock, 2000). This reflects, on one hand, the high genetic diversity of HI in rapeseed (Lu et al., 2016; Chao et al., 2019), and on the other hand, the significant regulation of HI by environmental conditions (Takashima et al., 2013; Alizadeh et al., 2022). Studies have shown that HI in rapeseed exhibits moderately low heritability with pronounced genotype-by-environment interactions (Biabani et al., 2021; Alizadeh et al., 2022). Furthermore, the relationship between HI and seed yield varies depending on genetic background and environmental conditions (Youssefi et al., 2011), and the relative contribution of yield components to HI in rapeseed remains to be further clarified (Garcia et al., 2025). Regarding the effects of dry matter accumulation and partitioning in vegetative organs on HI, most existing studies have been conducted in single environments or with limited genotypes (Singh et al., 2002; Chugh and Sharma, 2022), having relatively less systematic evaluation for these bred varieties in recent

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years (Kuai et al., 2021). Meanwhile, the allocation patterns of mineral nutrients among different rapeseed organs and their indirect effects on HI have gradually attracted attention, although substantial uncertainties remain (Grzebisz et al., 2020; Guo et al., 2021).

The trend of HI change during varietal evolution in rapeseed and its relationship with the succession of important agronomic traits represent another important research direction (Wittkop et al., 2009; Hu et al., 2022). Compared with early varieties, modern rapeseed varieties have undergone significant changes in plant height, growth duration, lodging resistance, and other traits (Miersch et al., 2016; Shen et al., 2024). Some studies suggest that HI of modern varieties exhibits an increasing trend, but the underlying agronomic drivers remain controversial (Hu et al., 2022). Some researchers propose that reduction in plant height may be an important cause of HI improvement (Miersch et al., 2016), while others have pointed out that excessive morphological modification may lead to negative consequences such as reduced photosynthetic area (Manoj and O'Maoileidigh, 2026). Similarly, changes in growth duration may indirectly affect HI by modulating the utilization efficiency of temperature and light resources (Singh et al., 2002; Liu et al., 2019). However, systematic comparisons of HI among rapeseed varieties of different release years, plant height classes, and growth duration categories are still lacking (Chao et al., 2019; Biabani et al., 2021).

This study employed 60 rapeseed varieties with diverse genetic backgrounds and conducted field experiments over two consecutive growing seasons at two cropping areas. The objectives of this study were: (1) to reveal the genetic variation and regional adaptation characteristics of HI in rapeseed; (2) to clarify the effects of yield and yield components on HI; and (3) to evaluate the contributions of variety release year, plant height, and growth duration to HI.

MATERIAL AND METHODS

Experimental site and design

Field experiments were conducted over two consecutive growing seasons (2022-2023 and 2023-2024) at two sites in Tongren City, Guizhou Province, China: Bijiang District (E 109.19°, N 27.72°) and Sinan County (E 108.26°, N 27.94°). Bijiang (BJ) is characterized by a subtropical monsoon climate, with red loam soil, an annual precipitation of 1303 mm, a mean annual temperature of 16°C, and a frost-free period of 280 days. Sinan (SN) is characterized by a mid-subtropical humid monsoon climate, with yellow loam soil, an annual precipitation of 1142 mm, a mean annual temperature of 17.5°C, and a frost-free period of 294 days. The basic physical and chemical properties of the soil at each experimental site in both seasons are presented in Table 1.

Table 1. Basic physical and chemical properties of soil at each experimental site in both seasons

Year	Site	Organic matter ($g \cdot kg^{-1}$)	Total nitrogen ($g \cdot kg^{-1}$)	Available P ($g \cdot kg^{-1}$)	Available K ($g \cdot kg^{-1}$)
2022	Bijiang	31.63	1.37	12.55	83.72
2023	Bijiang	32.01	1.42	13.17	79.54
2022	Sinan	28.67	1.14	12.69	68.35
2023	Sinan	29.03	1.25	12.57	71.83

The experiments evaluated sixty winter rapeseed cultivars, which widely cultivated in China over recent decades and still in use. Seeds were sown on October 2, 2022, and October 3, 2023, for the respective growing seasons. The 60 cultivars were classified according to three criteria. By breeding year, they were divided into 15 old cultivars (OB) bred before 2010 (2000-2009), 31 modern cultivars (MB) bred between 2010 and 2015, and 14 recently bred cultivars (NB) after 2015. By plant height, they were grouped into 14 short-height (SH, <150 cm), 25 medium-height (MH, 151-170 cm), and 16 tall-height

(HH, >170 cm) cultivars. By growth duration, they were categorized as 17 late-maturing (LM, >220 days), 20 medium-maturing (MM, 215-220 days), and 13 early-maturing (EM, <215 days) cultivars.

Each plot measured 10 m² (2 m × 5 m) and was arranged in a randomized complete block design with three replications. The planting density was 45×10^4 plants ha^{-1} with a row spacing of 30 cm. Fertilizer was applied at the local recommended rates: urea (180 kg ha^{-1} N), superphosphate (90 kg ha^{-1} P_2O_5), potassium chloride (75 kg ha^{-1} K_2O), and borax (7.5 kg ha^{-1} boron). Phosphorus, potassium, and borax were applied entirely as basal fertilizer before sowing, while urea was split-applied, with 50% at sowing and 50% during the overwintering period. Seedlings were thinned to the designated density at the 5th leaf stage. All other field management practices followed local conventional methods.

Sampling and Measurements

Morphological traits were assessed at maturity using plant samples collected from the central rows of each plot. All morphological and physiological measurements were conducted under both field and laboratory conditions. Prior to manual harvesting in the field, all effective plants in each row were labeled and numbered. The four central rows of each plot were harvested separately and placed into labeled mesh bags. During harvest, the effective plants in each row were dissected into branches and main stems, which were then packed separately into correspondingly labeled mesh bags. After all plots were harvested, the samples were transported indoors, where pods were manually removed from the main stems and branches and placed into separate labeled mesh bags. Subsequently, all samples were air-dried indoors and oven-dried. The dried samples were then weighed, threshed, and the dry weight of each plant fraction was determined.

Data Analysis

Data were processed using Microsoft Excel 2010. Analysis of variance (ANOVA) and correlation analyses were performed with SPSS 22.0 to assess significance among experimental blocks. Figures were generated using SigmaPlot 10.0.

RESULTS AND DISCUSSION

Genetic variation in harvest index among rapeseed varieties

To characterize the genetic variability of harvest index (HI) across rapeseed varieties, we analyzed HI distribution patterns among 60 varieties under two field environments (Figure 1A). HI varied substantially among varieties, ranging from 0.031 to 0.30. At the Bijiang (BJ) site, the minimum HI was 36.3% (2022-2023) and 61.5% (2023-2024) lower than the maximum HI, while at the Sinan (SN) site, the differences were more pronounced, reaching 78.6% and 87.9%, respectively. The same variety also exhibited marked differences in HI between the two planting regions. Across both seasons, the mean HI of all varieties at SN was 48.6% lower than that at BJ. At BJ, HI values were mainly distributed between 0.189 and 0.282, accounting for over 86.4% of the varieties, with the most concentrated range of 0.207-0.268 comprising 40 varieties. At SN, the predominant HI range was 0.082-0.159, representing more than 54.5% of the varieties.

Across both seasons at BJ, the main distribution ranges for seed yield, pod wall dry weight per plant, stem dry weight, main stem seed yield, and branch seed yield were 2102-3333 $kg{\cdot}hm^{-2}$, 6.5-9.0 g, 13.9-19.2 g, 4.5-5.6 g, and 6.6-7.1 g, respectively . At SN, the corresponding values were 1066-1194 $kg{\cdot}hm^{-2}$, 12.8-19.9 g, 9.9-11.1 g, 1.8-3.1 g, and 0.9-1.8 g (Figure 1B-F). Seed yield, stem dry weight, main stem, and branch seed yields were significantly higher at BJ than at SN, whereas pod wall dry weight showed the opposite trend.

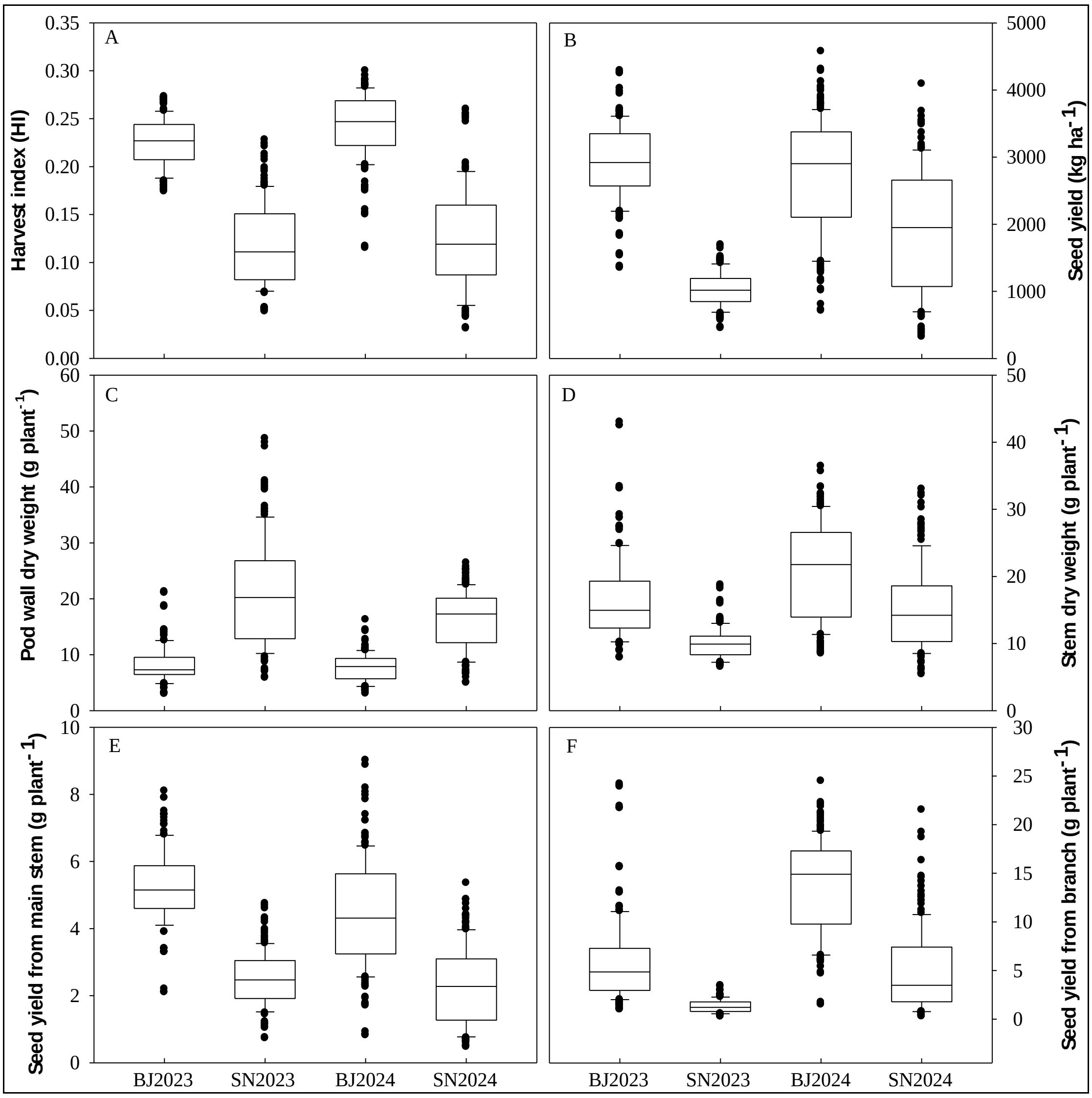

Figure 1. Overall variation of harvest index (HI) and its related traits for different varieties.
In the figure, the upper and lower parts of the box represent 25% and 75% of the loci, the upper and lower limits represent 1.5 times of the quartile, the horizontal line in the box represents the median, the square represents the average, and the dot represents the outlier. Different letters represent significant differences (LSD test, P<0.05).
HI (A), seed yield (B), pod wall dry weight (C), stem dry weight (D), seed yield from main raceme (E), seed yield from branches (F) for different rapeseed varieties. The abscissa BJ2023, SN2023, BJ2024 and SN2024 in the figure represent the field experiment I in Bijiang in 2022-2023, experiment II in Sinan in 2022-2023, experiment III in Bijiang in 2023-2024 and experiment IV in Sinan in 2023-2024 in Guizhou Province of China, respectively.

Effects of yield and yield components on harvest index

A linear positive relationship between HI and seed yield was observed across both seasons and sites, with seed yield increasing as HI increased (Figure 2). Regression analysis indicated that a 0.1 increase in HI corresponded to a seed yield increase of 419-967 kg·hm^{-2} at BJ and 115-381 kg·hm^{-2} at SN.

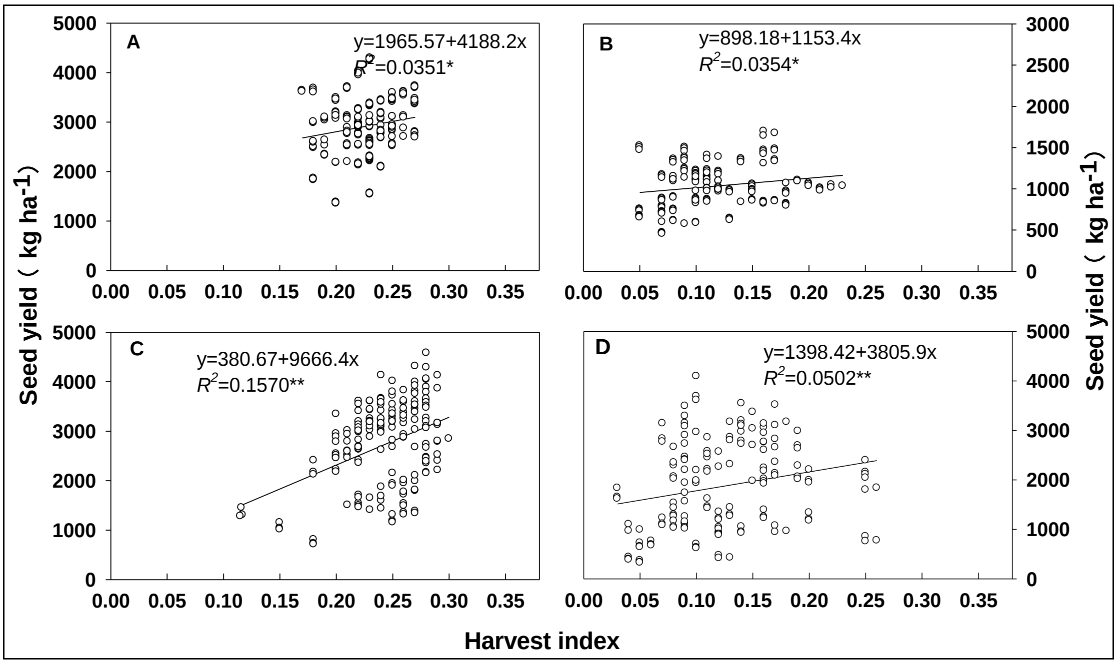

Figure 2. Relationship between harvest index (HI) and seed yield under different rapeseed varieties. The figure A, B, C and D represent the field experiment in Bijiang in 2022-2023 (BJ2023), experiment in Sinan in 2022-2023 (SN2023), experiment in Bijiang in 2023-2024 (BJ2024) and experiment in Sinan in 2023-2024 (SN2024) in Guizhou Province of China, respectively. *: significant difference (p<0.05); **: significant difference (p<0.01); ns: no significant difference (p>0.05). The same below.

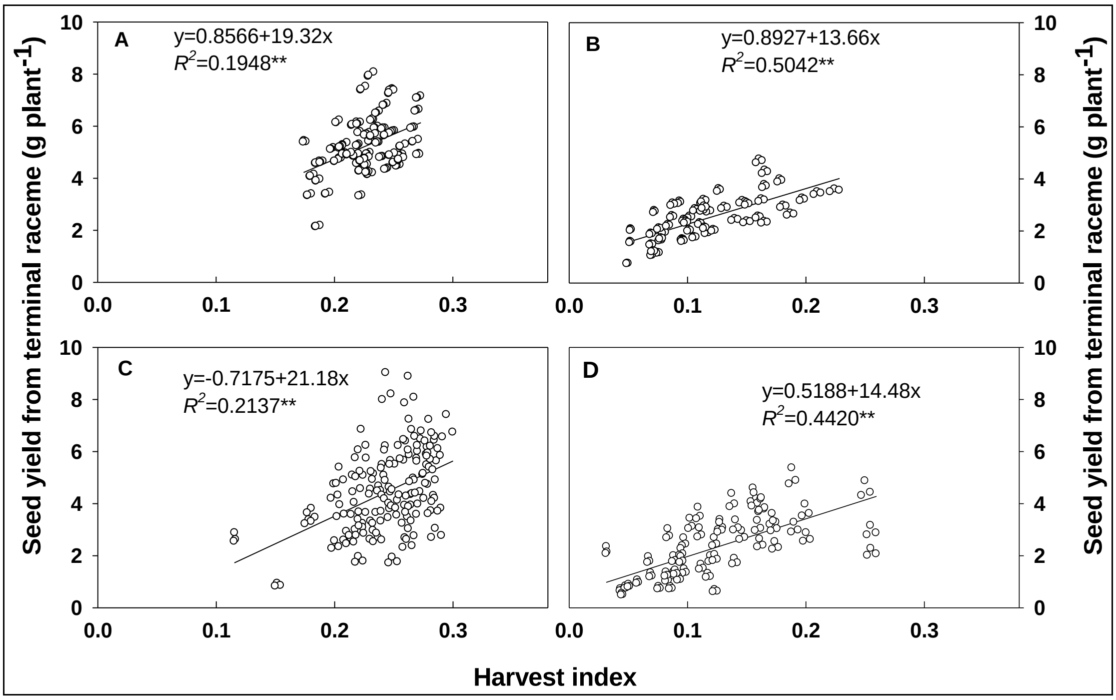

Figure 3. Relationship between harvest index (HI) and seed yield from terminal raceme per plant for different rapeseed varieties

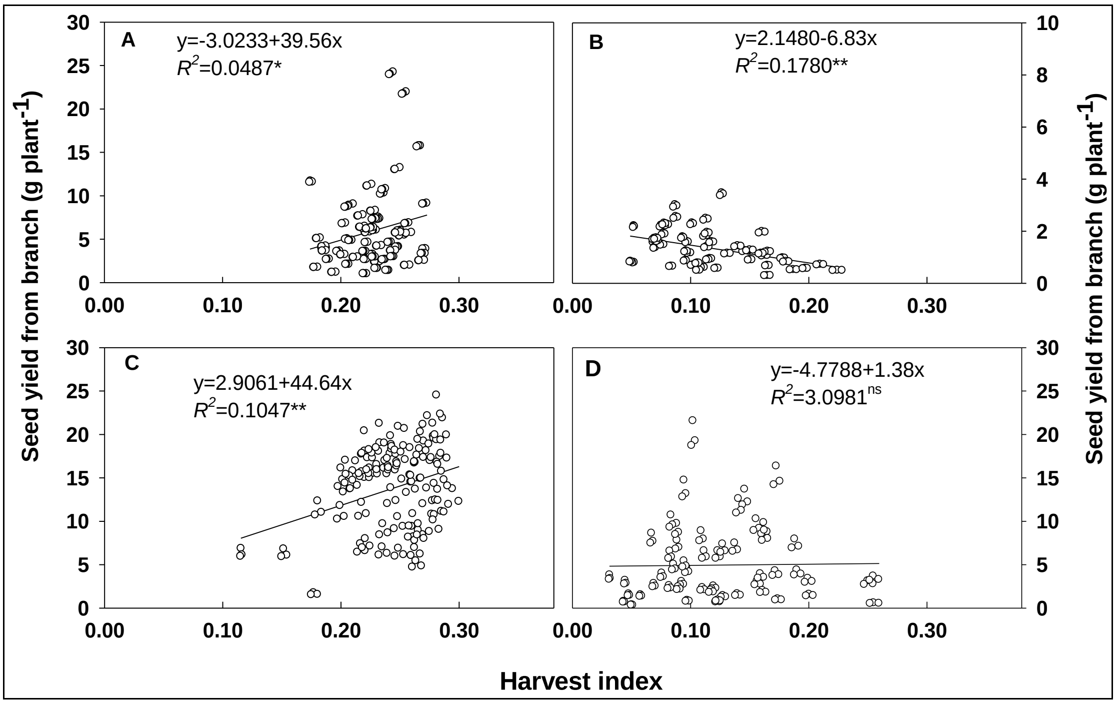

Figure 4. Relationship between harvest index (HI) and seed yield from branches per plant for different rapeseed varieties

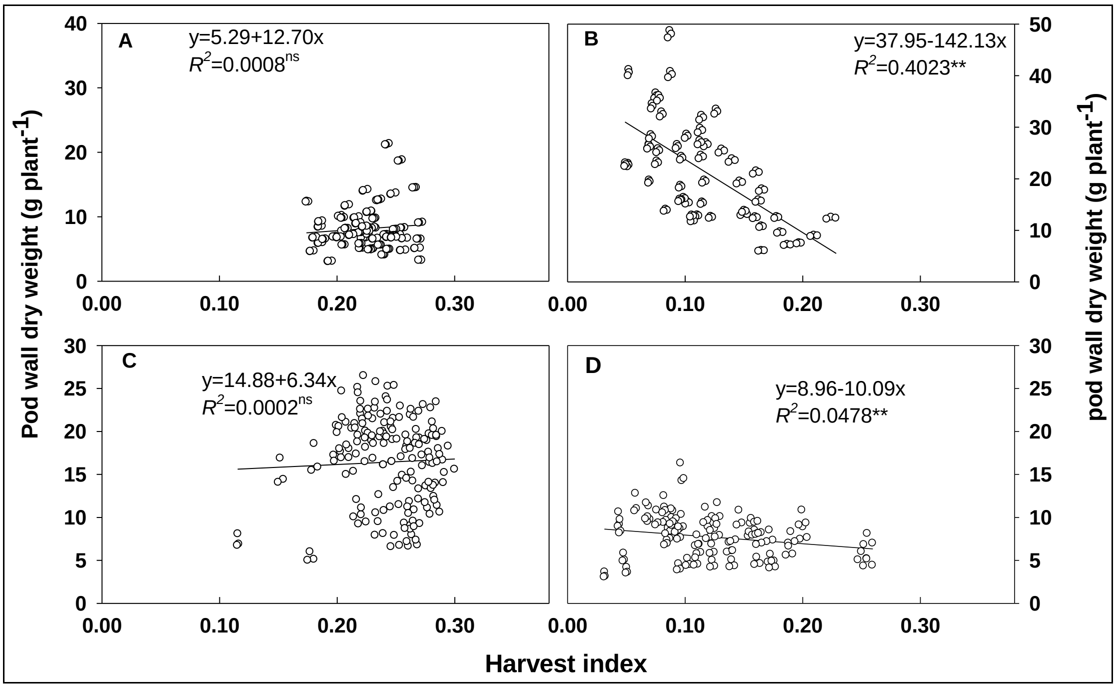

Figure 5. Relationship between harvest index (HI) and pod wall dry weight per plant for different rapeseed varieties

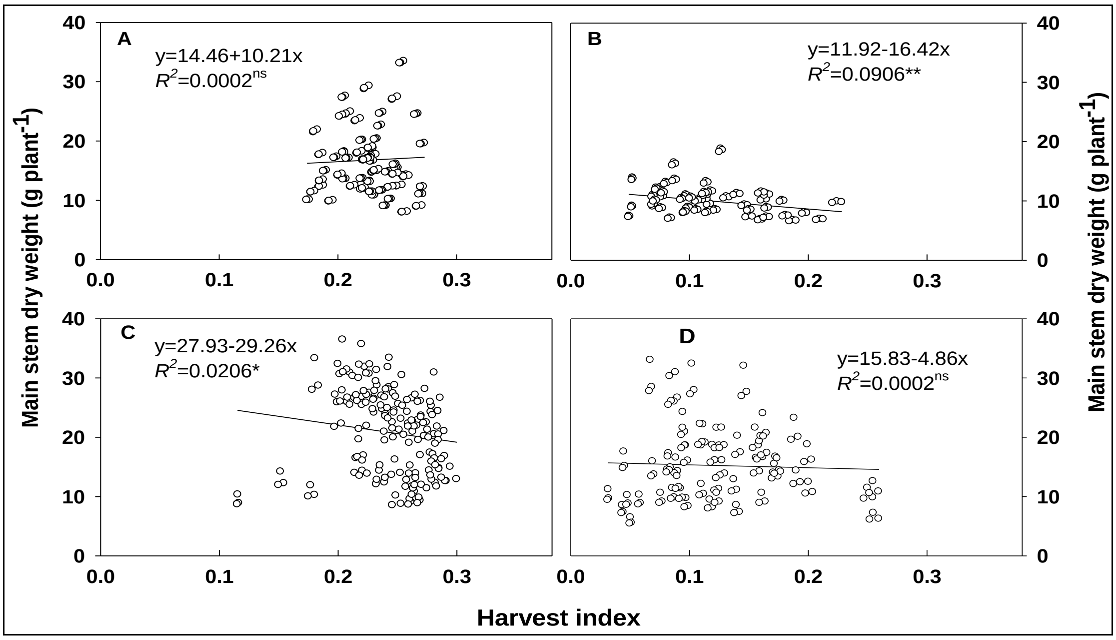

Figure 6. Relationship between harvest index (HI) and stem dry weight per plant for different rapeseed varieties

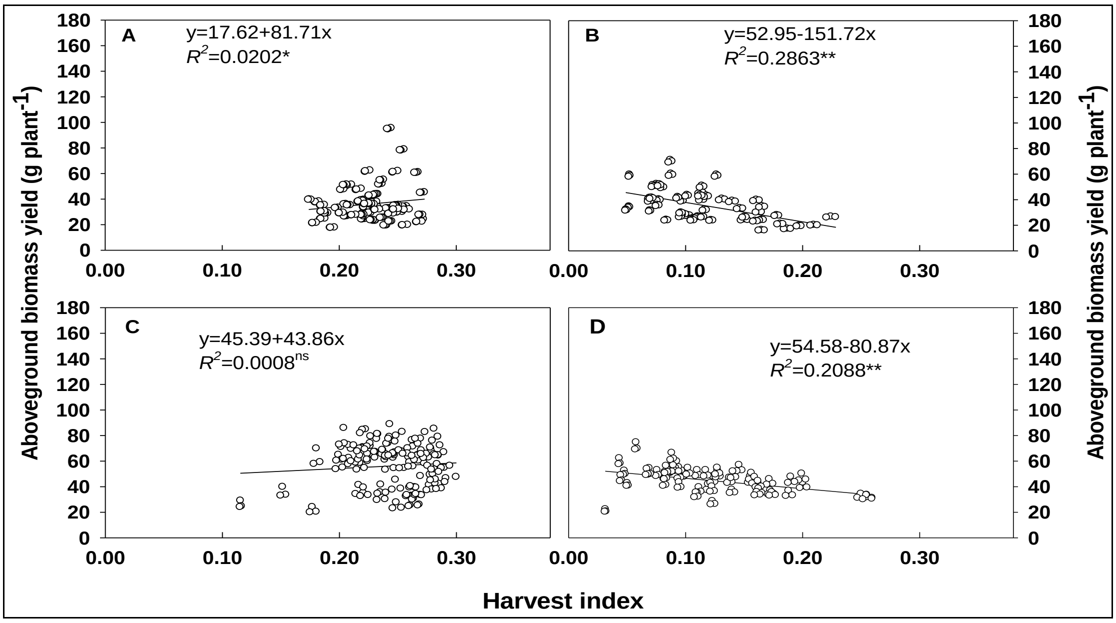

Figure 7. Relationship between harvest index (HI) and aboveground biomass yield per plant for different rapeseed varieties

HI was significantly and positively correlated with main stem seed yield per plant ($P<0.01$) (Figure 3). However, the relationship between HI and branch seed yield per plant varied by the experimental sites: a significant positive correlation was observed at BJ ($P<0.01$) (Figure 4), whereas a negative trend was found at SN. The correlation between HI and pod wall dry weight also differed by sites, showing a significant negative relationship at SN ($P<0.01$) (Figure 5) but a positive (non-significant) trend at BJ. Over the 2022-2024 seasons, HI tended to negatively correlate with stem dry weight per plant at SN (Figure 6); at BJ, a significant negative correlation was observed in the second season (2023-2024) but not in the first (2022-2023). Regression analysis of HI against aboveground biomass per plant revealed a significant positive relationship at BJ but a negative one at SN (Figure 7).

Effects of release year, plant height, and growth duration on harvest index

Across both continuous seasons, all varieties exhibited significantly higher HI at BJ than at SN, indicating strong site-specific effects (Figure 8). Varieties released in different years showed significant differences in HI at both sites, with more pronounced differences at BJ. Compared with varieties released after 2015, those released before 2010 had 13.3% (BJ) and 5.9% (SN) lower HI, suggesting an increasing trend of HI in modern varieties.

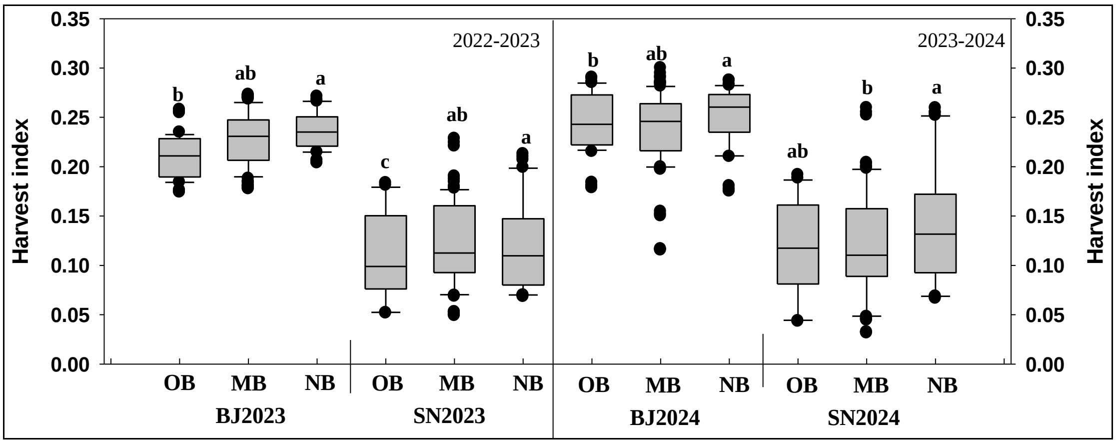

Figure 8. Changes of harvest index (HI) among rapeseed varieties in different breeding ages.
In the figure, OB: old varieties bred for more than ten years, MB: modern varieties bred for ten to twenty years, NB: new varieties bred for less than 10 years. The different letters indicate significant different. The same below.

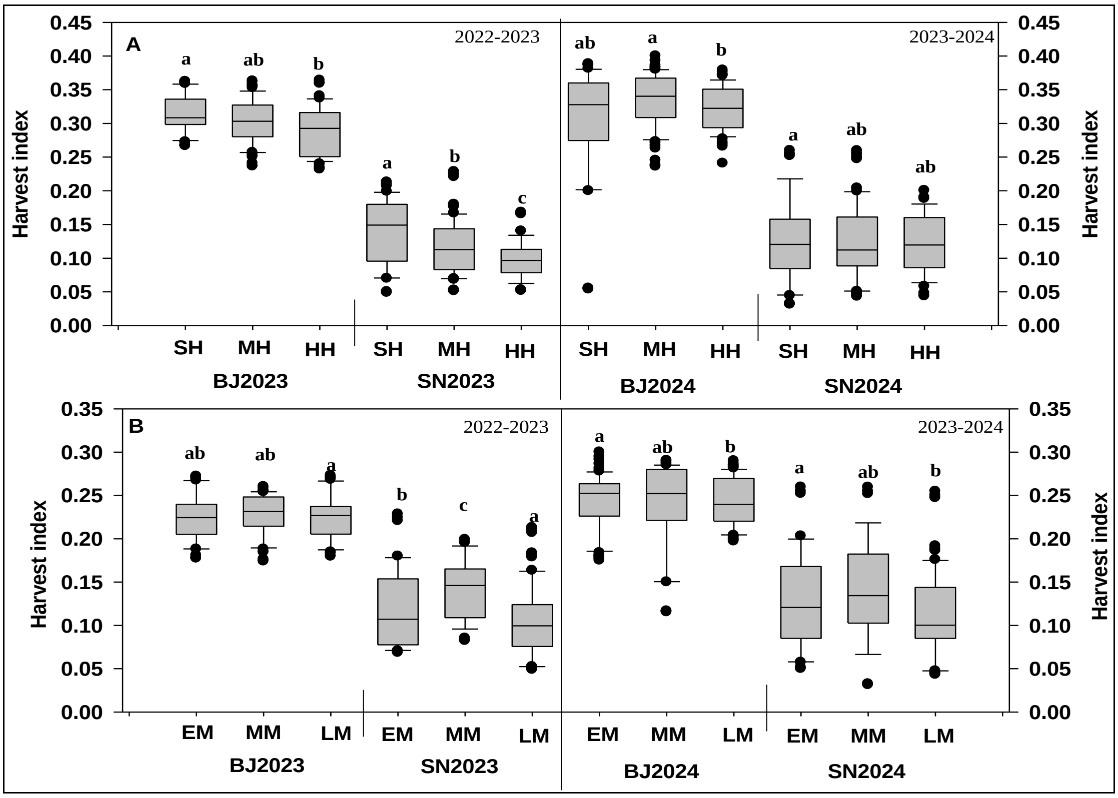

Figure 9. Changes of harvest index (HI) among rapeseed varieties with different plant height and HI among rapeseed varieties with different growth duration. In figure (A), SH: Short plant height variety, MH: Medium plant height variety, HH: High plant height variety. In figure (B), EM: early maturity varieties, MM: Medium early maturity varieties, LM: later maturity varieties. Varieties with mature plant height >170 cm (HH) had significantly lower HI than those with height ≤150 cm (SH) or between 150 and 170 cm (MH), with reductions of 3.3% (BJ) and 15.9% (SN). Dwarf varieties (S) consistently exhibited higher HI at both sites (Figure 9A). Varieties with growth duration >220 d (LM) had lower HI than those with duration <215 d (EM), while varieties with intermediate duration (215-220 d, MM) showed intermediate HI values (Figure 9B).

By evaluating 60 rapeseed varieties across two experimental sites over two consecutive growing seasons, this study clarified the genetic variation in HI and its relationships with yield, yield components, and agronomic traits. The research demonstrated the strong regional adaptation of HI in rapeseed (Takashima et al., 2013; Alizadeh et al., 2022), confirmed that reducing stem and pod wall dry weight could enhance HI (Kuai et al., 2021; Chugh and Sharma, 2022), and indicated that the increase in HI of modern varieties is primarily attributable to shorter growth duration and reduced plant height (Miersch et al., 2016; Hu et al., 2022).

Regional adaptation of harvest index and its physiological basis

We found that HI of the same variety differed more between planting regions than between years within the same region (Figures 1, 8), indicating that HI is strongly influenced by the environment and exhibits pronounced site specificity (Takashima et al., 2013). This result aligns with findings in the Yangtze River Basin rapeseed belt, which reported that HI stability is low and mainly regulated by temperature and light conditions from flowering to pod development (Biabani et al., 2021; Alizadeh et al., 2022). In our study, HI at BJ was significantly higher than at SN, and the ranking of HI across varieties was not consistent between the two sites, suggesting a genotype-by-environment interaction (Youssefi et al., 2011; Biabani et al., 2021). HI is not merely an indicator of seed filling efficiency but a comprehensive reflection of assimilate accumulation and partitioning under specific environmental conditions (Habekotté, 1997; Diepenbrock, 2000). Favorable temperature and light conditions help maintain post-anthesis photosynthetic capacity and source-sink coordination, thereby improving assimilate translocation to seeds (Garcia et al., 2025; Manoj and O'Maoileidigh, 2026). Therefore, HI should be considered an important criterion for regional adaptation when selecting varieties for different planting areas (Kirkegaard et al., 2016; Cong et al., 2023).

Reducing stem and pod wall dry weight to increase HI

Our regression and correlation analyses showed that at the SN site, HI was significantly negatively correlated with stem dry weight per plant (Figure 6) and pod wall dry weight (Figure 5); similar trends, though not always significant, were observed at BJ (Kuai et al., 2021; Chugh and Sharma, 2022). These results support the concept that increasing HI can be achieved by reducing dry matter retention in non-seed organs, particularly stems and pod walls (Habekotté, 1997; Diepenbrock, 2000). Recent studies have shown that stems and pod walls are major sites of "luxury uptake" of mineral nutrients (Grzebisz et al., 2020; Guo et al., 2021). When nutrient supply exceeds seed demand, the surplus is stored in these organs, which on one hand avoids metabolic burden on reproductive organs, and on the other hand induces structural thickening of stems and pod walls, consuming substantial amounts of photosynthates and ultimately lowering HI (Yang et al., 2009; Wang et al., 2025b). Moreover, as the primary photosynthetic organ during late growth stages and the final transit station for assimilate redistribution to seeds, the pod wall's efficiency in exporting photosynthates directly determines HI (Manoj and O'Maoileidigh, 2026). In this study, pod wall dry weight at SN was significantly higher than at BJ (Figure 1), whereas HI showed the opposite pattern, suggesting that greater dry matter retention in pod walls is detrimental to HI (Garcia et al., 2025). Therefore, breeding strategies aimed at moderately reducing the structural dry weight of pod walls while enhancing their physiological export efficiency represent a promising approach to improve HI (Lu et al., 2016; Chao et al., 2019).

Dwarfism and early maturation benefiting harvest index improvement in modern varieties

Our results showed that varieties bred after 2015 exhibited 13.3% (BJ) and 5.9% (SN) higher HI compared with those bred before 2010 (Figure 8), and that dwarf (plant height ≤150 cm) and short-duration (<215 d) varieties had significantly higher HI (Figure 9A, 9B). This confirms that the increase in HI of modern rapeseed varieties is closely associated with reduced plant height and shortened growth duration (Miersch et al., 2016; Hu et al., 2022). Similar trends have been extensively documented in rice and wheat. The underlying mechanisms are that dwarfism reduces dry matter investment in vegetative organs (especially stems), allowing more assimilates to be allocated to seeds (Miersch et al., 2016; Kuai et al., 2021), while early maturation shortens the pre-anthesis vegetative growth period, reducing unnecessary assimilate retention in vegetative tissues (Singh et al., 2002; Liu et al., 2019). Importantly, the stem not only serves as a supporting structure and transport conduit but also functions as a temporary storage site for assimilates (Kuai et al., 2021; Chugh and Sharma, 2022). The negative correlation between HI and stem dry weight observed in this study suggests that varieties may differ in assimilate transport efficiency: excessive stem thickness may reflect lower transport efficiency, leading to assimilate retention in the stem and further stimulating structural growth, which in turn consumes more photosynthates in a positive feedback loop (Kuai et al., 2021; Chen et al., 2024). Thus, an ideal rapeseed variety should achieve a source–sink–flow configuration characterized by "efficient transport and minimal storage", minimizing stem dry weight while maintaining adequate mechanical strength and transport capacity (Wang et al., 2025a; Khan et al., 2026).

Although we identified negative correlations between HI and stem and pod wall dry weights, we did not directly measure physiological parameters such as assimilate transport velocity in stems or photosynthetic export efficiency of pod walls, which limits mechanistic understanding (Chugh and Sharma, 2022; Manoj and O'Maoileidigh, 2026). Future research should employ stable isotope tracing and other approaches to dissect the regulatory networks underlying dry matter retention in stems and pod walls (Lasisi and Liu, 2023; Chen et al., 2024).

CONCLUSIONS

Harvest index in winter rapeseed exhibited substantial genetic variation and strong site specificity. Modern cultivars bred after 2015 showed 5.9%-13.3% higher HI than older ones, largely attributable to reduced plant height and shortened growth duration. Lower stem and pod wall dry weight were key drivers of HI improvement. Future rapeseed breeding should target reduced structural dry matter investment in stems and pod walls while maintaining adequate transport capacity to achieve further yield gains.

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