Effects of dwarfing genes on water use efficiency of bread wheat

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Abstract Climate change has increased the risk of drought, which significantly limits plant productivity. Various ways of increasing water availability and sustaining growth of crop plants in drought-prone environments are available. Genetic advances in grain yields under rainfed conditions have been achieved with the introduction of dwarfing genes. A thorough understanding of the effects of different dwarfing genes on root growth, coleoptile length, grain yields and water using efficiency (WUE) will provide opportunities to select appropriate *Rht* genes for breeding high WUE and grain yield cultivars. This review focuses on the mechanism involved in *Rht* genes that reduce plant height and affect root and coleoptile length, their consequent effects on grain yields and WUE, and suggests that for rainfed and irrigation-limited environments, combining GAR and GAI dwarfing genes in breeding may help boost WUE and yields, and more materials from different parental sources should be collected to assess opportunities for potential comprehensive application of specific *Rht* genes.

Keywords coleoptile length, wheat, dwarfing genes, grain yield, root, water use efficiency

1 Introduction

The Green Revolution, which was outlined by Dr. Norman Borlaug at the third international wheat genetics symposium in 1968 and which occurred from the 1940s to the 1960s, led to the development of high-yielding, disease resistant wheat cultivars with dwarfing genes (reduced height, *Rht* genes) that are lodging resistant and highly responsive to inputs such as heavy fertilizer and pesticide application. The success of these cultivars likely constitutes the most important event in the history of modern agricultural research[1]. Spectacular increases in wheat yields achieved during the 'Green Revolution' were enabled with the introduction of dwarfing traits into wheat plants[2]. Such increases in crop yields have also proven instrumental in providing for growing global populations over the past 40 years[3,4]. However, climate change has increased the instability of crop grain production by increasing the unpredictability of the timing and amounts of rainfall and by causing extreme heat and cold spells that have affected grain yields worldwide and threatened food security. Sources of specific adaptation related to drought and heat and the breeding of genetic traits will help maintain grain yields in dry and warm years. The effects of drought are expected to increase with climate change and increasing water shortages[5]. The adverse effects of climate change-induced rainfall patterns on agroecosystems exceed the effects of remedial agricultural measures such as fertilization or the physiological and morphological responses of wheat plants[6]. Thus, securing wheat productivity under conditions of climate change is essential for human nutrition and for meeting increasing demands for wheat from a growing world population[7]. The use of limited water resources to produce more grain is an important objective that can be achieved by breeding high water use efficiency (WUE) crop cultivars. According to previous study with eight varieties released from the 1940s to the 2010s under two water conditions, with an increase in plant height, WUE values decrease (Fig. 1)[8]. It is thus possible to enhance wheat WUE through the introduction of dwarfing genes.

The most important effect of dwarfing genes in wheat
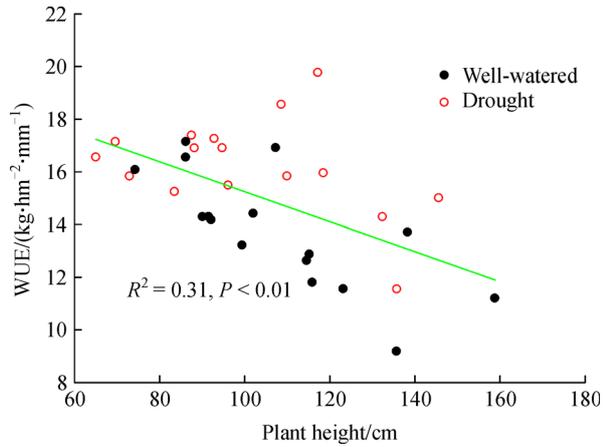
production was that it greatly strengthened the lodging resistance and improved the harvest index[9]. In recent decades, a number of studies conducted by breeders and agronomists have focused on dwarfing genes. More than 20 dwarfing genes have been identified (Table 1). According to their responses to exogenous gibberellic acid (GA), dwarfing genes are divided into two classes: GA-insensitive (GAI) and GA-responsive (GAR) genes. Up to 2000, more than 70% of commercial wheat cultivars world-wide contained the GAI dwarfing genes (*Rht-B1b* and *Rht-D1b*)[2,18]. In China, these two genes were also widely used in North China winter wheat region and Yellow and Huai Valley facultative wheat region, which had relatively high rainfall or irrigation and good climate conditions; while in the North-western spring wheat region and South-western China autumn-sown spring wheat region, in which agriculture was rainfed and rainfall was low, a large fraction of wheat cultivars contained the GAR dwarfing gene *Rht8* or were without dwarfing genes[19,20]. This showed that different dwarfing genes might have different effects on the drought tolerance and WUE of bread wheat. Nowadays, the problem we all face is how to use limited water resources to produce more grain to feed increasing population. So measuring the effect of *Rht* genes on wheat grain WUE in detail and selecting genes with higher WUE is urgently needed. Thus, in this review, first, we summarize the mechanism of plant height reduction induced by *Rht* genes, then the effects of these dwarfing genes on the root system, coleoptile length, the physiological performance and on wheat biomass and grain yield under drought stress conditions, to obtain a thorough understanding for proper utilization of those

Table 1 Dwarfing wheat genes

Gene	Principal donors	Chromosomal position	Sensitivity to GA$_3$	Inherited character	Variation type	Reference
Rht-B1b	Norin 10	4BS	I	P	N	[10]
Rht-D1b	Norin 10	4DS	I	P	N	[10]
Rht-B1c	Tom Thumb	4BS	I	S	N	[11]
Rht4	BurtM937	2BL	R	R	γ rays	[12]
Rht5	Marfed M1	3BS	R	S	EMS	[13]
Rht6	Burt	–	R	R	N	[14]
Rht7	Bersee Mult	2AS	R	R	EMS	[14]
Rht8	Mara, Sava	2DS	R	R	N	[15]
Rht9	Mara	7BS	R	R	N	[16,17]
Rht-D1c	Ai-Bian	4DS	I	S	N	[16,17]
Rht11	Karlik1	–	R	R	MNH	[14]
Rht12	Karcag522M7K	5AL	R	D	γ rays	[12]
Rht13	Magnifi41M1	7BL	R	P	MNH	[12]
Rht14	Castelporziano	–	R	S	thN	[16]
Rht15	Durox	–	R	P	EMS	[16,17]
Rht16	Edmore M1	–	R	S	EMS	[16]
Rht17	Chris M1	–	R	R	DES	[14]
Rht18	Icaro	–	R	S	fN	[16]
Rht19	Vic M1	–	R	S	EMS	[16]
Rht20	Burt M860	–	R	R	γ rays	[14]
Rht21	XN0004	2AS	I	P	–	[16,17]

Note: I and R in the sensitivity to GA$_3$ column denote insensitivity or responsiveness. P, S, D and R in the inherited character column denote partial dominance, semidominance, dominance and recessiveness, respectively.

dwarfing genes in wheat improvement for drought tolerance and water use efficiency.

2 Possible mechanisms involved in *Rht* gene-induced reduction in plant height

The mechanism of GAI gene-induced reduced plant height is associated with DELLA proteins[21]. Wild-type DELLA proteins repress plant growth and are degraded in the presence of GA, thereby removing this growth restriction. *Rht-B1b* and *Rht-D1b* each contain a single nucleotide polymorphism that encodes a premature stop codon, producing a truncated DELLA protein with reduced GA sensitivity and reduced plant height[10]. *Rht-B1c*, the allele of DELLA protein-encoding gene *Rht-B1a*, differs from *Rht-B1a* by one 2 kb Veju retrotransposon insertion, three coding region single nucleotide polymorphisms (SNPs), one 197 bp insertion, and four SNPs in the 1 kb upstream sequence, resulting in DELLA motif primary structure disruption[11].

The causes of GAR *Rht* gene-induced reduced plant height are less well understood. Gasperini et al.[22] examined the endogenous GA content of 6-week-old wild-type and semidwarf *Rht8* lines and found there was no significant difference between these test lines. Traditionally, *Rht8* has been classified as a GA-sensitive gene because plants respond to the exogenous application of GAs[12]. Thus, *Rht8* is not involved in gibberellin biosynthesis or signaling[22]. Finally, for exogenous brassinosteroid assays, it was found that the leaves of *Rht8* lines are less sensitive to brassinosteroids[22]. In studies on *Rht12*, results show that *Rht12* mutants may be deficient in GA biosynthesis rather than GA signal transduction[23] and that *Rht12* lines also exhibit a normal brassinosteroid response[16].

Relatively few studies have been conducted on the mechanism involved in Rht gene-induced reduction in wheat plant height. However, according to studies on rice and *Arabidopsis thaliana*, the dwarfing was associated with gibberellin biosynthesis or signaling/brassinosteroid signaling[24–26]. Moreover, deficiencies of brassinosteroid biosynthesis-induced plant height reduction have been found in tomato and *Arabidopsis*[27,28]. Therefore, we hypothesize that these two phytohormones have key roles in facilitating Rht gene-induced wheat plant height reduction.

A central role of the GA class of growth hormones in responses to abiotic stress is becoming increasingly evident. A reduction of GA levels and signaling has been shown to contribute to plant growth restriction with exposure to several stresses, including cold, salt and osmotic stress. Conversely, increased GA biosynthesis and signaling promotes growth in plant escape responses to shading and submergence. In several cases, GA signaling has also been linked to stress tolerance[29]. In the GA signaling process, the DELLA protein is a major repressor of GA-dependent processes, and GA promotes the proteasome-dependent degradation of DELLAs to promote growth[21]. Studies on the DELLA function have shown that DELLAs restrain growth and promote survival through adverse conditions by reducing levels of reactive oxygen species (ROS) and that DELLAs cause ROS levels to remain low following exposure to biotic or abiotic stress, thus delaying cell death and promoting tolerance[30]. Other studies have confirmed that under abiotic stress, GA$_3$ levels decline rapidly in maize leaves subjected to water stress[31], and for *Arabidopsis thaliana* seedlings, exposure to salinity triggers a reduction in endogenous bioactive GAs that coincides with DELLA accumulation[32]. Again, all of these results show that GA biosynthesis and DELLA functions contribute to stress tolerance.

Brassinosteroid (BR) has been found to provoke response to many abiotic stresses like cold, drought, salt and so on[33–35]. In the process of root water uptake, the symplastic and transcellular pathways are collectively referred to as the 'cell-to-cell' pathway and studies have confirmed that this pathway plays important roles in root water uptake under drought stress[36,37]. It had been reported that this pathway could be largely controlled by the activity of aquaporins, which respond relatively rapidly and reversibly, causing changes in root hydraulic conductance[38,39]. In *Arabidopsis thaliana*, BR was shown to be involved in modification of transmembrane transport of water by controlling aquaporin activities[40].

Taking all those into consideration, we can conclude that the *Rht* genes reduce plant height by controlling the signal or biosynthesis of GA or BR, which affects the stress response, so the introduction of *Rht* genes might affect the stress response and WUE of wheat.

3 Effects of dwarfing genes on drought resistance traits of wheat

The most important function of dwarfing genes is to reduce plant height to improve lodging resistance. Compared with lines without dwarfing genes (*rht*), *Rht* lines reduced height from 10% to 64% (Table 2). The *Rht-B1c* and *Rht-D1c* had the strongest effect on stem reduction (64%), while GAR *Rht8* gene was the weakest dwarfing gene (10% reduction).

Coleoptile length is believed to be the most important index for evaluating the drought tolerance of wheat seeds[41]. Coleoptile lengths are heavily influenced by the allelic constitution of *Rht* loci and by water statuses ($P < 0.001$). GAI dwarfing genes (e.g., *Rht-B1b* and *Rht-D1b*) reduce coleoptile length significantly compared to *rht* lines ($P < 0.001$, Table 2)[20,42,43] while GAR dwarfing genes Rht8 and *Rht12* have much less effects in terms of shortening coleoptile length[20,43,44]. According to Wang's experiment, *Rht13* genes also have no negative effects on coleoptile length[45]. Other GAR genes (e.g., *Rht4*, *Rht5*,

Table 2 Effect of dwarfing genes on stem reduction, coleoptile length and seedling vigour

Gene	Stem reduction	Coleoptile length	Seedling vigour
Rht-B1b	24%	R	R
Rht-D1b	24%	R	R
Rht-B1c	64%	R	R
Rht4	45%	N	N
Rht5	50%	N	N
Rht6	–	N	N
Rht7	24%	N	N
Rht8	10%	N	N
Rht9	–	N	N
Rht-D1c	> 64%	R	R
Rht11	–	R	R
Rht12	46%	N	N
Rht13	24%	N	N
Rht14	34%	N	N
Rht15	–	–	–
Rht16	–	R	R
Rht17	–	R	R
Rht18	–	R	R
Rht19	–	–	–
Rht20	–	–	–
Rht21	–	–	–

Note: N and R indicate that there was no significant difference and significant decrease between Rht line and rht lines, respectively.

Rht6, Rht7 and Rht14) have no negative effect, either[46], while other GAI genes (e.g., Rht-B1c, Rht11, Rht16, Rht17, Rht18 and Rht-D1c) reduce coleoptile length[46,47]. Short coleoptiles exhibit poor levels of emergence when cultivars are sown deep to access deep water reserves. Occasionally, plants with long coleoptiles also generate larger leaves and exhibit faster rates of emergence.

The other effect of dwarfing genes in wheat is to influence the seedling vigour. This result is similar to the result for coleoptile length i.e. the GAR dwarfing genes have no negative effect on seedling early vigour, while GAI genes reduce it (Table 2)[46–48].

Water from precipitation or irrigation can be lost in the form of crop respiration, soil evaporation and percolation into deeper soil layers. Plants can re-access water that has entered deep percolation only when they sustain long and vigorous root growth at early stages[49].

It is important to assess the effects of Rht genes on wheat root growth at the seedling stage as results vary depending on experimental media used (Table 3). Studies have shown that Rht genes have a direct effect on root growth during seedling establishment rather than a secondary partitioning effect[50]. However, this study also showed that dwarfing alleles did not alter either the total root length or the root architecture (average root diameter and lateral root/total root ratio). According to research conducted in a greenhouse, the effects of dwarfing genes (Rht1, Rht2 and Rht3) on root dry matter are relatively minor[55]. However, root dry matter was sampled at maturity in this study. In another study, under three different experiment conditions (gel, soil-filled columns and field grown), Rht8 was not found to have a negative effect on total root length compared to the control line (rht lines) while Rht-B1c and Rht-D1c were found to produce significantly shorter total root lengths under the latter two conditions[50,56]. Arabidopsis semi-dwarfs, independent of loss-of-function mutations at GA locus 5 (GA_5), which is an ortholog of green revolution dwarf alleles in rice and barley, showed decreased root length in comparison to related wild-type[57,58]. Another study on the Rht8 gene also found reduced root proliferation[59]. Thus it appears that the effects of Rht genes on root growth are influenced by genetic features and experimental conditions. If we wish to achieve an ideal root system using different Rht genes, it is necessary to breed lines using as many parental combinations as possible under a specific environment. In the future, more data on the different growth stages of Rht wheat roots must be generated.

4 Effects of Rht on wheat WUE under drought conditions or osmotic stress

Given the objective of using fewer water resources to produce higher grain yields, plant cultivars exhibiting higher WUE are urgently needed. WUE is defined as the ratio of grain yields (GY) to evapotranspiration (ET). ET includes water from plant transpiration (PT) and evapora-

Table 3 Effect of dwarfing genes on root traits

	Rht-B1b	Rht-D1b	Rht-B1c	Rht-D1c	Rht8	Rht12	Rht13
TRL	N[42,50]	N[42,50]	R[50], N[42]	R[50]	N[50]	R[50], N[16]	N[41,45,51,52]
RD	–	N[45]	–	–	–	–	N[41,45,51,52]
RV	–	R[45]	–	–	–	–	I[45], N[51]
RSA	–	R[45]	–	–	–	–	N[45,51]
RDW	N[53], R[54]	N[50]	N[50,53]	N[50]	N[50]	R[16], I[50]	–

Note: TRL, total root length; RD, root diameter; RV, root volume; RSA, root surface area; RDW, root dry weight. N, R and I indicate that there was no significantly difference/significant decrease and increase between Rht line and rht lines, respectively.

tion from the soil surface (ES). It can be expressed in the following terms:

$$\text{WUE} = \frac{GY}{PT + ES}$$

The above expression shows that crop WUE can be increased by either increasing GY or decreasing the magnitude of PT and ES[60]. As many studies have focused on yields only, water use specifications remain unknown. A secondary objective would be to breed high grain yielding wheat cultivars in rainfed or semiarid areas. Below, we discuss effects on grain yields and then on WUE. Effects of decreasing the magnitude of PT and ES have been reviewed by Richards[61].

One study focusing on the adaptation strategies of replacement cultivars subjected to short-term osmotic stress found that following the introduction of dwarfing genes, leaf transpiration rates decrease ($P < 0.05$)[62]. Field experiments on different wheat cultivars/lines containing different dwarfing genes showed that water consumption over whole growth periods showed no significant difference between these lines while the grain yield decreased with an increase in plant height (from 70 to 150 cm, $R^2 = 0.25$, $P < 0.05$, Fig. 2a and Fig. 2b) and the WUE decreased with an increase in plant height ($R^2 = 0.57$, $P < 0.01$, Fig. 2). Another study also found the grain yield was the highest at a plant height of 70 cm[64]. This shows that under drought conditions, the introduction of dwarfing genes may increase WUE by increasing grain yield.

Regarding the relationship between plant height and grain yields, one experiment has shown that higher yields can be achieved by using lines of between 70 and 100 cm in height[9]. That experiment also found no specific advantages associated with major dwarfing genes (*Rht1* and *Rht2*). It was also found that tall lines perform equally well or better ($P < 0.05$) than all other classes (*Rht-B1b* and *Rht-D1b*) for grain yields, test weight, and kernel weight in all environments under a range of soil moisture condi-

tions[65]. While another study showed that *Rht-B1b* and *Rht-D1b* lines generate higher yields than wildtype lines (*rht*) and *Rht8* lines in most environments and are superior to *Rht8* as a source of height reduction for spring wheat[66,67]. *Rht-D1b* was found to yield more than *Rht-B1b* lines while their yields were still higher than rht lines in spring wheat[68]. Other studies also confirmed that there was no significant difference in yield between these two genes[69–71]. Butler et al.[65] considered that *Rht-B1b* lines yield more than *Rht-D1b* lines only in the fully irrigated environment. Thus, the same dwarf gene showed different effects in different environments.

More recently, researchers have focused more on GAR genes. *Rht5* lines decrease grain yields more than wild-type lines in north-western China and Australia[13,72]. *Rht4* and *Rht12* lines increase grain yields ($P < 0.05$)[13]. The *Rht13* gene increases grain quantities and wheat yields in Australia[73] while in north-western China, the *Rht13* gene decreases grain yields[45]. As the only GAR gene that has been used in commercial breeding, *Rht8* has been studied more than all of the genes listed above[22,74,75]. However, results achieved from different areas and stock plants have varied.

Rht-B1b, *Rht-D1b* and *Rht-B1c* have been found to depress WUE by 15% as a result of specific genetic backgrounds, with the reduction in total water used being less than that of grain yields[55]. Another study found that *Rht1* and *Rht2* lines reduce WUE under certain environmental conditions[76]. However, higher levels of soil water depletion by standard height sunflower hybrids in agronomy trials are attributed to deeper rooting depths compared to those of dwarf hybrids[77]. Grain yields, however, were not given, and so the effects of dwarf genes on sunflower WUE remain unknown. Dwarf *Rht-B1c* (*Rht3*) seedling plants are characterized by a reduced decreased in photosynthesis, delayed non-stomatal limitations on photosynthesis, higher instantaneous WUE levels and better functional states of the photosynthetic apparatus under drought conditions compared to tall *Rht-B1a*
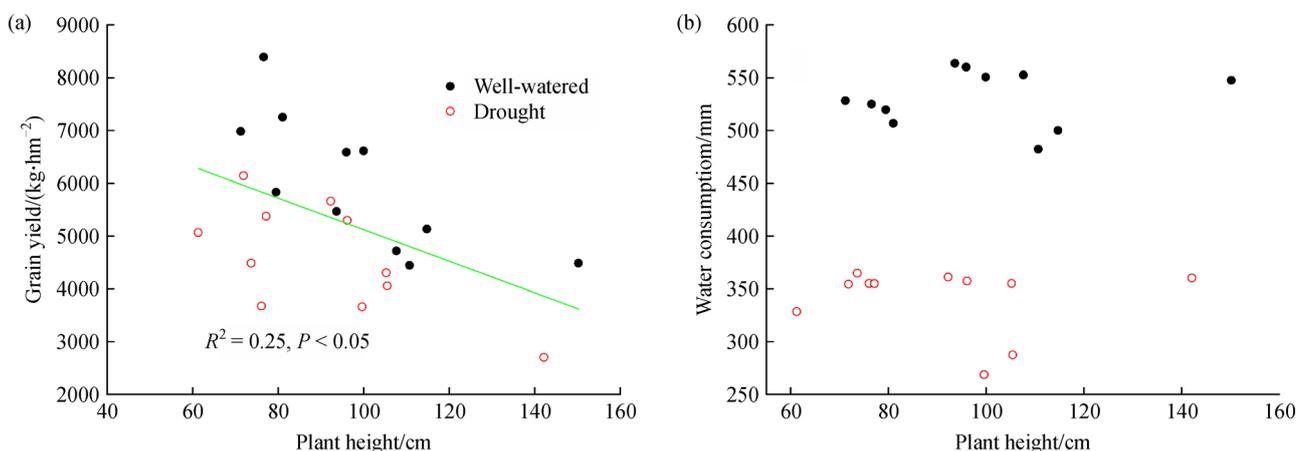

Fig. 2 The relationship between plant height and grain yields (a) and water consumption (b) (data from reference[63] and unpublished data)
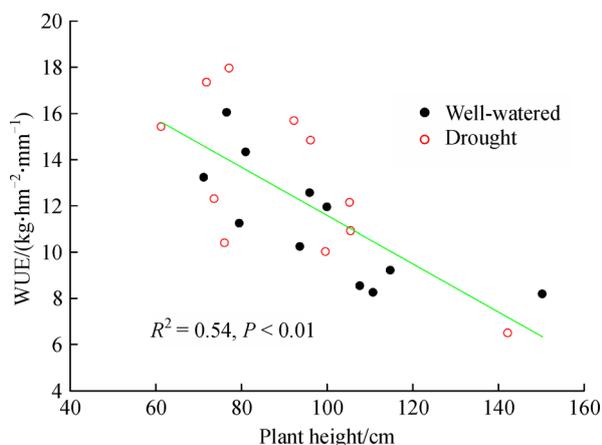
Fig. 3 The relationship between plant height and water use efficiency (WUE) under two water conditions (data from reference[63] and unpublished data)

plants[78]. However, *Rht-B1b* plants have an intermediate character between wild type and Rht-B1c lines that often does not significantly differ from that of the *Rht-B1a* plants examined in the study. *Rht-B1c* seedling plants maintain a lower injury index and less malondialdehyde content under osmotic stress[79,80]. These results suggest that *Rht-B1c* seedlings can better modulate antioxidant defense systems to sustain membrane integrity and higher levels of photosynthesis. However, in field experiments, lines with tall alleles (*Rht-B1a* and *Rht-D1a*) have been found to perform equally well or better than ($P < 0.05$) all other classes for grain yields, test weight, and kernel weight under drought stress[71]. In another study, *Rht-B1b* and *Rht-D1b* genes were not found to improve yields under marginal environmental and management conditions[67]. In previous studies on winter wheat cultivars released from the 1940s to the 2010s, it was found that under well-watered conditions, grain yields of cultivars released after 1980s were higher than those released before, but under drought stress, grain yield improvements vanished[8]. Taking these results into consideration, plants with GAI *Rht* genes may be able to adapt to short-term osmotic stress rather than to mitigate field water stress.

GAR *Rht* genes are expected to improve grain yields, reducing plant heights[73,81]. The semidwarfing *Rht8* was also found to exhibit greater drought tolerance in one of Alghabari's experiments[82]. However, specific studies on the effects of GAR genes on drought stress have been quite rare. Under natural conditions, the *Rht10* gene negatively affects the IWUE via higher levels of leaf transpiration[52]. Under two contrasting water conditions, *Rht13* and *Rht8* wheat lines were found to show increased WUE at grain yield levels. In this study, the authors found that *Rht13* and *Rht8* lines generate higher grain yields under two water conditions ($P < 0.05$), but water consumption over the growth period showed no significant difference ($P > 0.05$)[63]. All of these results show that higher grain yields contributes to higher WUE and that the introduction of *Rht13* and *Rht8* genes has no negative effects on root water uptake.

Although the water consumption over the growth period was not significantly different between different lines, there may be a change in the proportion of PT and ES. The reduced plant height reduces the distance between the leaves and the soil, which may increase the coverage rate and reduce the ES. And the increase in early seedling vigor can also reduce the evaporative loss from the soil surface[61].

5   Avenues for future research

The effects of *Rht* genes on wheat grain appear to vary for different trial materials and under different environments, and it seems that specific *Rht* genes exhibit low levels of eurytopicity. Therefore, in future studies on specific *Rht* genes in specific areas, more materials from different parental sources should be collected to assess opportunities for potential comprehensive application. GAR and GAI dwarfing genes may be combined during breeding to increase WUE and yields. Studies show that the simultaneous selection of Rht8 + Rht-B1b or Rht-D1b sesquidwarfs during early generation may facilitate the rapid development of high-yielding cultivars targeting both favorable and unfavorable environments[81]. Breeders may also collaborate with crop cultivation experts to develop better cultivation methods, as ES from well-managed wheat crops represents 40% of evapotranspiration, and this value is often substantially higher for poorly managed crops. In addition, selecting cooler canopies of wheat may prove useful for PT decline, and results confirm that newer wheat cultivars maintain cooler canopies under drought conditions[83].

Although researchers have done a lot of fruitful jobs, the effect of the most dwarfing genes on yield and other physiological and agronomy traits still remain unclear. In the future, we should give more focus to the effect of dwarfing genes on drought resistance and WUE of wheat to promote their application. In addition, exploring more dwarfing genes with higher drought resistance and WUE is needed.

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