horticulturae

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Review

Mechanism of Tolerance to Head-Splitting of Cabbage (*Brassica oleracea* L. var. *capitata* L.): A Review of Current Knowledge and Future Directions

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Abstract: Cabbage (*Brassica oleracea* L. var. *capitata* L.) is an important cruciferous vegetable, which is rich in dietary fiber, vitamins, beta-carotene and even good for cancer prevention. So, it is widely planted around the world. However, in the production of cabbage, the property of head-splitting not only reduces the appearance quality and commercial value of cabbage but also easily infects the area with head-splitting by germs, resulting in yield reduction, even no yield, and economic losses. For the head-splitting of cabbage, this paper introduced the causes, evaluation methods and indexes, and anatomic properties and reviewed some QTLs that have been obtained. But the cabbage molecular research of head-splitting is still in its infancy compared with other vegetable plants. Head-splitting is greatly affected by water. Although the cultivation and management methods can reduce the head-splitting rate, genetic improvement of head-splitting is still the most economic and efficient way in the long run. Therefore, the changes in the substances regulating cell water potential, the development of cell wall, ductility and toughness, calcium ion-regulated pectinase and cellulase activities, expansin genes, and even the ETH and ABA pathways related to maturation and abscission can provide ideas and directions for future gene mining and mechanism analysis for head-splitting tolerance, and thus accelerate the molecular breeding process.

Keywords: evaluation methods; related factors; QTL mapping; molecular mechanism; research progress

Citation: Wang, Y.; Li, Q.; Zhang, G.; Gu, L.; Zhao, Y.; Zhou, L.; Dong, Y.; Dong, H.; Song, X. Mechanism of Tolerance to Head-Splitting of Cabbage (*Brassica oleracea* L. var. *capitata* L.): A Review of Current Knowledge and Future Directions. *Horticulturae* **2023**, *9*, 251. https://doi.org/10.3390/horticulturae9020251

Academic Editor: Giovanni Battista Tornielli

Received: 7 January 2023
Revised: 6 February 2023
Accepted: 10 February 2023
Published: 12 February 2023

1. Background

Common head cabbage (*Brassica oleracea* var. *capitata* L.), also known as cabbage, is one of the important cruciferous vegetables, which is characterized by outstanding adaptability and stress tolerance [1], high in nutritional value, rich in dietary fiber, vitamins, VB1, VB2, calcium, and iron, lutein, β-carotene and even cancer-preventing substances [2–5]. So, it was recommended by the World Health Organization as one of the best vegetables. Now it is extensively planted in all parts of the world [6,7]. The planting area and yield of cabbage in China are on the rise year by year, taking first place in the world [8,9]. Although there have been many studies on cabbage yield and quality, head-splitting is still a crucial problem in the later growth period of cabbage [10]. The head-splitting of cabbage is a physiopathy that decreases the appearance quality and commodity value, thus decreasing farmers' income to a substantial extent; furthermore, a more significant problem is the fact that it is also the door to bacteria, fungi and pests, and increases the cost of storage and transportation, and even cause serious economic losses [11].

In the case of sufficient moisture, the head-splitting of cabbage is mainly determined by the genetic property of the variety [10]. Screening germplasm and breeding tolerance varieties are the fundamental ways to solve the problem [12]. It is necessary to clarify the current screening and identification methods, anatomic properties, and the molecular progress of research related to them. But because the molecular mechanism of cabbage head-splitting is less studied, it is also closely related to the moisture condition [13]. Therefore, this paper will also involve the discussion of external factors that induce the expression of related genes to provide ideas for the study of molecular mechanisms and breeding of head-splitting tolerance.

2. Introduction to and Evaluation of the Head-Splitting Properties of Cabbage

The head-splitting property of cabbage is the phenomenon of splitting of cabbage leaf head. In cultivation, it occurs mostly in the late stage of cabbage growth. When cabbages reach the heading stage, if they are not picked after the number, and weight of the heading leaves that make up the head reaches a certain level but continue to grow, it will cause the outermost heading leaves of cabbage leaf heads to split, which is called the head-splitting [14]. The top of the head is the common splitting part of the cabbage, and there are also lateral or 'crossed' dehiscences, which are mostly linear. At last, the inner tissues were exposed. The properties of its splits are transverse split, longitudinal split and mixed split [3,15]. The degree of splitting also gradually deepens, starting from the outermost leaves of the leaf head and gradually extending to the inner side. In severe cases, it can be split to the dwarf stem. The degree of splitting can be expressed by the length, width and depth of the split in the cabbage leaf head [10].

Although the physiological basis of splitting/cracking is not fully understood [16], there are main causes of head-splitting of cabbage, as follows. On the one hand, the cabbage head is prone to split when too much water is provided from outside during the late growth stage. It is easy to occur split in the waterlogged field after heavy rain or heavy irrigation. Especially when there is a sudden heavy rain or water flooding during drought, it is more likely to cause head-splitting. The main reason is due to the brittle tissue and poor cell flexibility; excessive water absorption leads to cell swelling and splitting.

On the other hand, When the cabbage harvest is delayed, the number of cabbage with head-splitting will increase. Sale experience has demonstrated that cabbage varieties in the same maturity stage are often put on the market in a concentrated way, resulting in a drop in the price of cabbage. In an attempt to coordinate the market demand and increase farmers' income, the measure often taken is to delay picking, which will raise the risk of head-splitting of cabbage during the storage period in the field [17]. Although the cabbage has reached harvest and marketing conditions, it still continues to grow in the soil until head-splitting occurs, and this period is called the storage period in the field (called the 'Cunpu' period in China) [18]. The storage period in the field reflects the tolerance to head-splitting of the cabbage variety, and the stronger the tolerance to head-splitting, the longer the storage period in the field [19]. During large-scale production of cabbage, if the storage period in the field is too long, the cabbage put on the market will split in the field because it cannot be sold in due course, resulting in the loss of its commercial value [20]. Planting cabbage varieties with head-splitting tolerance can directly prolong the harvesting time of cabbage so that farmers can selectively harvest cabbage within a suitable range of selling price, increase the output value of cabbage and reap higher economic benefits.

These reasons above are closely related to the genetic characteristics of cabbage, in which different cabbage varieties showed different performances in head-splitting properties. Although the genetic base and molecular mechanism of cabbage are still poorly understood compared with other vegetable crops [21], collecting, evaluating and acquiring the germplasm resources of cabbage with head-splitting tolerance serves as the basis for cultivating varieties of cabbage with head-splitting tolerance. At present there is currently no uniform standard for evaluating the head-splitting property of cabbage. A few days after the cabbage reaches the appropriate harvest stage, the head-splitting rate of cabbage will be investigated to measure the head-splitting property of cabbage. At first, the splitting time of the mature leaf heads is taken as the identification index [22]. Subsequently, the head-splitting rate of cabbage or head-splitting rate is used in combination with the head-splitting time. However, owing to the different research materials, there also exist differences in the time consumed for different scholars to determine the head-splitting rate. After identifying the head-splitting tolerance of 35 common head cabbage varieties in the alpine environment of northwest Hebei province in China, it was found the best time to identify the head-splitting tolerance was to harvest the leaves 15 days late after maturity in this area [23]. The head-splitting of nine cultivated varieties in spring (cabbage in spring) was studied, and it was found that the investigation time of splitting tolerance thereof was 10 days after the maturity of leaf heads [24]. Since there are differences in the location, degree (split size and depth), split speed and split properties of cabbage leaf heads, some scholars, with a view to better judge and measure, have introduced the number of split layers, split size [25] and others have used comprehensive indexes. For instance, Ma M. et al. [2] used the ratio of split arc length to the maximum circumference in the middle of leaf head + ratio of split width to head height + ratio of split depth to 1/2 head width as an index to comprehensively evaluate the degree of head-splitting of cabbage. Su Y.B. et al. [26] established the evaluation method and grading standard of splitting tolerance of cabbage in combination with the maximum number of split layers and split area.

3. Study on Anatomic Properties of Head-Splitting Properties of Cabbage and Other Internal Factors

If cabbage is not harvested in a timely manner after maturity, it is a kind of adversity to prolong the nursery stage. Thus, cabbage varieties (lines) with head-splitting tolerance will mobilize all forces to adapt to unfavorable factors, including anatomic properties, hormone level and quality-related properties, in a bid to guarantee that they can successfully overcome adversity. The microstructure of cabbage cells is closely associated with its head-splitting tolerance. As far as the number of cells is concerned, whether for head-splitting-tolerant varieties or head-splitting-prone varieties, the number of cells in the heading stage is more than that in previous stages, but there is no significant difference between the head-splitting-tolerant varieties and the head-splitting-prone varieties (Figure 1A) [27]. The comparison of single cells reveals that, in general cases, the cells of head-splitting-tolerant cabbage are comparatively regular, with thick cell walls, a high degree of lignification, a compact arrangement between cells, relatively small cell gaps, and thickened periclinal walls and anticlinal walls (Figure 1B) [28]. The lower epidermal cells of head-splitting-prone cabbage varieties are large in size and low in density, particularly the Expansin [29] of cell walls makes the microfibrils of cell wall cellulose arranged loosely and in a separated state, which promotes the relaxation and thinning of cell walls, and besides, all the above properties can be passed on to offspring(Figure 1C) [27]. In terms of the whole tissue, there are numerous vascular bundles and secondary xylem vessels, which increase the supporting force, making it able to resist the head-splitting phenomenon resulting from water absorption. The cuticle of the head-splitting-prone cabbage is relatively thick, particularly the cuticle around guard cells, which helps to resist the poor environment [28]. The head-splitting tolerance of cabbage is also associated with the wax content. When the wax content is increased, the accumulation will become tight, making it not easy for water to penetrate, which can avoid the head-splitting phenomenon resulting from water absorption and swelling of cabbage leaf cells [30]. Some studies also suggest that [27] wax thickness is more closely relevant to insect resistance, which is not the primary factor affecting head-splitting tolerance. Throughout the heading stage, the change value of ABA in head-splitting-tolerant and head-splitting-prone materials is obvious, which shows that ABA content plays a vital part in the head-splitting of cabbage. In the late growth stage of leaf heads, the higher the ratio of the sum of auxin, gibberellin and zeatin nucleoside to ABA, the greater the growth rate than the apoptosis rate and the more tolerant to head-splitting [31]. In comparison with head-splitting-prone cabbage varieties, the activities of cellulase and pectinase are lower in head-splitting-tolerant cabbage varieties, resulting in higher contents of cellulose and protopectin [32]. In the meanwhile, there is a certain relationship with the shape of the leaf head as well. Cabbage leaf head properties can be classified into different categories, but at present, the focus is chiefly on the research of oblate and round leaf heads. The research indicates that round cabbage is more susceptible to splitting than oblate cabbage [11,12]. Moreover, some quality properties of common head cabbage are also in connection with head-splitting. For example, the bigger the ratio of leaf head to side leaves and the ratio of the length of the central column of cabbage in spring delayed for 5 days, the stronger the head-splitting tolerance, although the higher the texture density of cabbage leaf head, the better the compactness of leaf head, the worse its splitting tolerance. For the content of dry matter and crude fiber of the heading leaves of cabbage, it is inversely proportional to head-splitting [33].

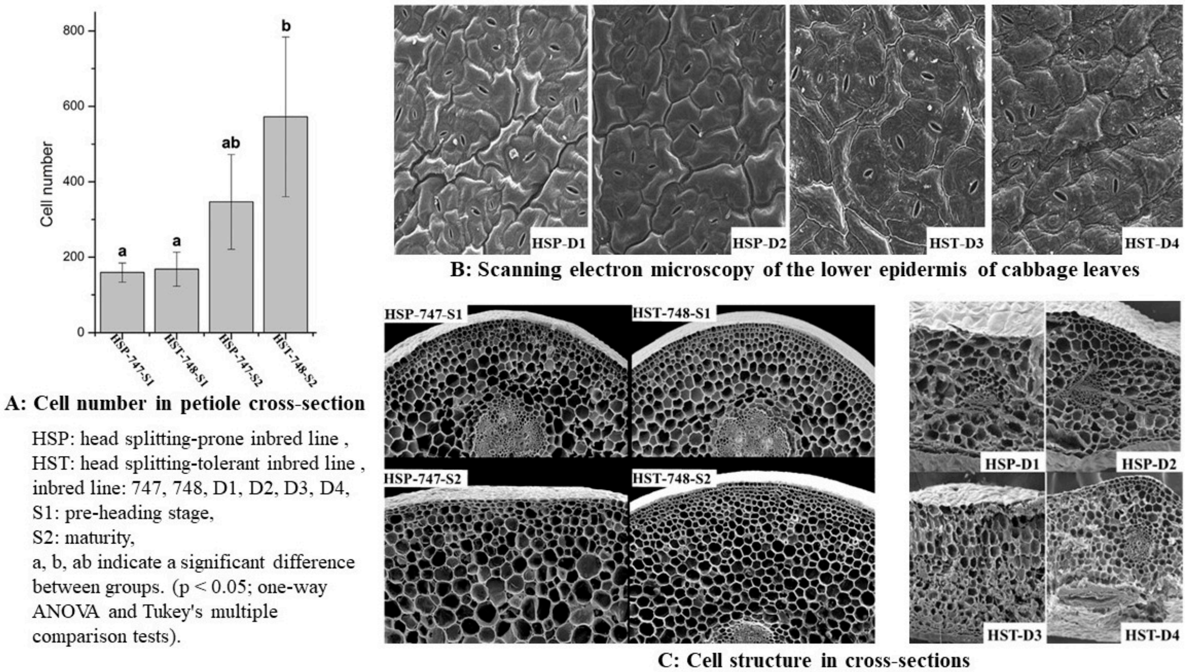

Figure 1. Effects of head-splitting on the cell number and anatomical parts of cabbage leaf (Source: References [27,28]).

4. QTL Location of Head-Splitting Properties of Cabbage

The genetic basis and molecular mechanism of head-splitting tolerance of common head cabbage is also a research direction, but so far, its research is still in the primary stage. In QTL mapping of the head-splitting property of cabbage, the construction of mapping population is associated with the performance and identification of head-splitting tolerance, and the selection of evaluation indexes of head-splitting tolerance can not be ignored as well, e.g., head-splitting rate, head-splitting index, head-splitting grade, etc. It is directly concerned with the number and existence of QTL mapping, and the evaluation indexes of different mapping populations are not entirely the same. The mapping populations used in the research on the head-splitting property of cabbage are $F_{2/3}$ temporary population and DH population. The study explores the relevant loci with a genetic map and then develops relevant molecular markers, laying a molecular foundation for cultivating splitting-tolerant cabbage varieties.

The early research on the head-splitting property of cabbage revealed that it is a quantitative trait that is controlled by multiple genes (Tables 1 and 2). Chiang M.S. [22] studied that the head-splitting property of cabbage is controlled by three pairs of genes. Zhuang M. et al. [34] analyzed 15 cross combinations of six common head cabbage configurations and learned that the non-additive effect also plays a role in head-splitting tolerance, but it is still dominated by the additive effect of genes, and moreover, the additive effect is more important over the growth time of cabbage in the field. Su Y.B. et al. [25] analyzed the property of head-splitting tolerance in six combined generations with the mixed genetic model of major genes + polygenes and figured out that this property is controlled by two pairs of major genes, and the additive effect is dominant, and there is also the effect of gene interaction. Some scholars constructed F_2 mapping population with head-splitting tolerant cabbage lines and head-splitting-prone lines chosen as parents and drew the genetic map of nine linkage groups with 270 markers. The total length of the map was 830.9 cm, and the average distance between adjacent markers was 3.6 cm. Six QTLs associated with the head-splitting property of cabbage were detected in total, among which two QTLs, *SPL-2-1* and *SPL-4-1*, located on chromosome 2 and chromosome 4, were stable sites repeatedly detected in 2 years, and four QTLs were detected as well, all of which were the results of the 1-year experiment, suggesting that it is tremendously influenced by the environment [21]. DH population was constructed by anti-infective strains, constructed genetic map, and detected major QTLs (*Hsr4.2, Hsr7.2, Hrs9.3* and/or *Hsr9.1*) [35] and QTLs (*Hsr3.2*, *Hsr4.2* and *Hrs9.2*) [36] associated with head-splitting in 2 years by means of two mapping methods. The analysis of two DH populations revealed that the splitting tolerance property of cabbage is jointly controlled by three pairs of major genes + multiple genes. The heritability of head-splitting tolerance genes is comparatively high, and it is dominated by the additive effect of major genes. In the meanwhile, the genes controlling head-splitting are tremendously influenced by the environment [25,37]. The QTL locus (*qHST1.1*) associated with the head-splitting time of cabbage by QTL-seq technique was detected, and analyzed the candidate genes in this locus, and discovered they have homology with two genes involved in the synthesis and metabolism of main components of the cell wall in Arabidopsis thaliana [38]. Conventional breeding usually takes 7–8 years. To save the time consumed, the DH line can be established by virtue of isolated microspore culture technology, and phenotype and molecular marker-assisted selection can be combined to speed up the breeding process [39]. By taking this method, not only the head-splitting-tolerant cabbage lines were created, but the head-splitting-tolerant properties and Fusarium wilt-resistant properties were polymerized [10].

Table 1. Genetic analysis of head-splitting tolerance in cabbage.

Generations	Method	Results	Reference
15 cross combinations involving 6 backbone parents	Analyzing the combining ability and heritability of head-splitting tolerance	1. Head-splitting tolerance was controlled by additive effect and non-additive effect, but mainly by additive effect. 2. GCA variance accounted for a large proportion of the total genetic variance; early generation selection should be emphasized.	Zhuang M. [34]
P_1, P_2, Two parental lines, their F_1, F_2, and two backcross progenies	Analyzing the combining ability and heritability of head-splitting tolerance	1. It was concluded that there were at least three gene pairs for controlling head-splitting. 2. Gene action was mostly additive, but partial dominance for early splitting was detected. 3. Narrow sense heritability was estimated at 47%.	Chiang, M.S. [22]
P_1, P_2, F_1, B_1, B_2, F_2	Mixed major gene plus polygene inheritance model	1. The efficient selection should be in the early generation of F_2 and B_1 2. Head-splitting tolerance was controlled by two additive-dominant-epitasis major genes plus additive-dominant-epitasis polygenes 3. The additive effect for the two major genes was foremost, while there was some interaction effect between them 4. Head-splitting tolerance was dominated by major genes	Su Y.B. [25]
P_1, P_2, F_1, F_2, DH	Mixed major gene plus polygene inheritance model	1. Head-splitting tolerance was controlled by three additive-epitasis major plus additive-epitasis polygenes 2. Head-splitting tolerance had higher heritability 3. Head-splitting tolerance was dominated by major genes, although the environmental factors had a great effect on it	Su Y.B. [36]

Table 2. Details of QTLs of head-splitting tolerance in different references.

Pop	Year/Method	Chr	QTL	Position (cM)	LOD	Marker Interval	R^2 (%)	A	Primer/Reference
DH	2011 (MQM)	4	*Hsr 4.2*	100.0	3.01	Scaffold12597a-Scaffold55516	9.1	9.19	2170 SSR markers, 1013 expressed sequence tag (EST)-SSR markers [35]
		7	*Hsr 7.1*	7.3	4.03	Scaffold195-BOE569	9.7	–9.80	
		7	*Hsr 7.2*	43.5	4.30	Scaffold195-Scaffold46873	10.5	–10.81	
		9	*Hsr 9.2*	51.1	3.38	Scaffold47852-Scaffold21727	9.1	10.84	
	2012 (MQM)	4	*Hsr 4.1*	51.8	3.05	Scaffod61158-Scaffod38160	8.6	8.75	
		4	*Hsr 4.2*	95.0	3.61	Scaffold12597a-Scaffold55516	10.2	8.81	
		7	*Hsr 7.2*	41.4	2.48	Scafford728-Scaffold46873	7.1	–7.62	
		9	*Hsr 9.3*	126.4	3.06	BOE344-B0E975	12.1	–12.93	
	2011 (ICIM)	4	*Hsr 4.2*	95.0	2.55	Scaffold12597a-Scaffold55516	5.6	6.87	
		6	*Hsr 6.1*	68.0	2.73	Scaffold37061-Scaffold1044	7.1	8.08	
		9	*Hsr 9.1*	34.0	2.80	Scaffold36132-Scaffold146827	9.2	–9.08	
		9	*Hsr 9.2*	58.0	2.54	Scaffold21727-Scaffold13994	5.6	7.18	
		9	*Hsr 9.3*	128.0	3.60	BoE344-BoE975	10.1	–9.38	
	2012 (ICIM)	4	*Hsr4.2*	95.0	5.41	Scaffold12597a-Scaffold55516	11.1	9.15	
		6	*Hsr 6.1*	66.0	2.67	Scaffold37061-Scaffold1044	5.7	6.86	
		9	*Hsr 9.1*	34.0	3.54	Scaffold36132-Scaffold146827	10.6	–9.14	
		9	*Hsr 9.2*	58.0	2.79	Scaffold21727-Scaffold13994	5.5	6.76	
		9	*Hsr 9.3*	128.0	5.84	BoE344-BoE975	13.9	–10.40	
DH	2011 (MQM)	4	*Hsr 4.2*	80	5.46	SF12597a-SF11933	11.80	9.46	149 pairs of InDel primers, a set of 2170 SSR markers and 1013 expressed sequence tag (EST)-SSR markers [36]
		7	*Hsr 7.1*	37.2	3.42	SF46873-SF6178	7.70	−6.78	
		7	*Hsr 7.2*	68	3.74	Indel112-Indel113	8.50	−7.84	
		9	*Hsr 9.2*	63.2	5.62	SF13994-Indel146	13.60	10.94	
	2012 (MQM)	4	*Hsr 4.1*	23	3.86	SF13319-Indel58	8.60	25.00	
		4	*Hsr4.2*	81.4	5.61	SF12597a-SF11933	12.80	10.78	
		7	*Hsr 9.2*	63.2	5.48	SF13994-Indel146	11.10	−10.02	
		9	*Hsr 9.3*	112.8	3.66	BoE344-BoE975	7.44	−6.92	
	2011 (ICIM)	3	*Hsr 3.1*	112	3.36	Indel117-SF31711	5.50	−6.78	
		3	*Hsr 3.2*	143	7.31	Indel42-SF10471	16.93	11.76	
		4	*Hsr 4.1*	23	6.16	SF13319-Indel58	12.56	10.18	
		4	*Hsr 4.2*	80	6.96	SF12597a-SF11933	12.86	10.37	
		9	*Hsr 9.2*	63	5.74	SF13994-Indel146	11.26	9.76	
	2012 (ICIM)	3	*Hsr 3.2*	143	7.86	Indel42-SF10471	15.36	11.76	
		4	*Hsr 4.2*	80	6.93	SF12597a-SF11933	11.10	9.15	
		9	*Hsr 9.1*	34	4.62	SF36132-SF146827	9.20	−9.08	
		9	*Hsr 9.2*	63	5.93	SF13994-Indel146	11.82	10.38	
		9	*Hsr 9.3*	111	3.44	BoE344-BoE975	8.67	−8.20	
$F_{2:3}$	2012	2	*SPL-2-1*	47.51	6.16	BRPGM0606-MR104	10.47	0.45	SSR markers, 272 IP markers and BAC-derived simple sequence repeats (SSRs) [21]
	2014	2		37.71	6.05	BRPGM0606-BRPGAW0693	14.95	0.37	
	2014	2	*SPL-2-2*	30.41	4.56	ACMF00872-BRPGAW606	2.18	0.29	
	2012	4	*SPL-4-1*	49.21	5.46	BRPGM0704-BRPG0433	7.84	0.58	
	2014	4		49.21	4.93	ACNP0072-cnum246a	8.93	0.30	
	2012	6	*SPL-6-1*	32.71	4.71	FTO036-BRPGN107	18.54	0.40	
	2012	6	*SPL-6-2*	40.31	4.18	FTO203-FTTO204	14.05	0.31	
	2014	6	*SPL-6-3*	90.41	4.327	BRPGM0639-ACMP00359	14.84	0.33	

Pop: Population, Chr: Chromosome, A: Additive effect.

5. Conclusions and Prospect

Although the head-splitting-tolerant properties are directly associated with the appearance quality, yield, storage and transportation of cabbage, and are closely bound up with farmers' income. However, compared with other horticultural crops, there is poor research on genetic base and molecular mechanism, particularly during the 13th 5-Year Plan phase of China, and research on the head-splitting properties of cabbage is relatively rare [8]. The head-splitting property of cabbage is not only influenced by internal factors but by environmental (external) factors (Figure 2) [40,41]. Therefore, we hoped to analyze the effect of external factors on cabbage head-splitting and then tried to explain in depth its inner response to the external factors of the plant, reaching the goal of modifying the plant itself, adapting it to external disadvantages, and passing excellent genes on to future generations.

5.1. The Role of Substances That Regulate Cell Water Potential, the Development, Ductility and Toughness of the Cell Walls

As the leaves of cabbage are relatively more and the amount of water transpiration is larger, cabbage needs more water in the stage of vegetative growth. So cabbage is more sensitive to soil water stress. If the water is not enough in the early stage, the heading will not only be small but also not tight. However, in the later stage of vegetative growth, once the cabbage is heading, the water supply should be appropriately decreased; otherwise, the head-splitting phenomenon will occur because the cells absorb too much water, which is also the fundamental cause of the head-splitting of cabbage. Thus, the usual way in production is to reduce the number of irrigation times or the time of each irrigation, and particularly after the rain in the later stage, attention should be paid to drainage, and reasonable water management is the key. Meanwhile, organic fertilizer can increase the content of soil organic matter and improves the soil's ability to retain water and fertilizer [42,43], especially in the late stage of cabbage growth, to reduce the adverse effects on plants due to the sudden increase in soil moisture [44].

Water absorption of crops is also related to the water potential of the cells. The study topic is how the plant regulates the water potential of the cell by the substances, especially sugar [40]. For plant growth, excessive soil water content belongs to water stress. In order to better adapt to the external adversity environment, various organic and inorganic substances in plant cells are constantly adjusting, which responsively changes the water potential of cells. And these substances include inorganic ions, proline, betaine, and soluble sugars [45–47].

There is also a correlation between the amount of fertilizer applied and the head-splitting property of cabbage. Compared with other mineral elements, nitrogen absorbed contributes to cabbage-head formation at any of the different growth stages [17,48]. But, if the nitrogen from the roots is not supplied in the proper proportion to the growth of the head leaves, problems can occur [49]. Studies demonstrate that [30], the higher the amount of nitrogen applied beyond a certain range, the higher the head-splitting rate of cabbage because excess nitrogen may cause loosehead formation. The reason may lie in that the nitrogen fertilizer applied will influence the structure of cells and tissues as well as the waxy layer and then influence the head-splitting tolerance of cabbage. The splitting/cracking incidence was significantly correlated with the cell wall and wax thickness and the content of cell wall protopectin and cellulose [40]. Under the condition of sufficient water, the head-splitting property of cabbage varieties is subject to the genetic factors of the varieties themselves, while the amount of fertilizer and harvest time exert no significant effect on it [50].

So, regarding water and fertilizer absorption of the crop, it is also considered the structure and development of cell walls, as well as the ductility and toughness of the cell walls in the presence of excessive soil moisture [51].

5.2. The Role of Calcium Ions, Expansin Gene and Plant Hormones

However, spraying calcium fertilizer can lower the role of head-splitting of cabbage. Studies reveal that [33] spraying 0.11 $g \cdot L^{-1}$ CaO can significantly enhance the head-splitting tolerance of cabbage. Spraying $CaCl_2$ and GA_3 many times during the heading stage can alleviate the head-splitting of medium-tolerant materials, but it exerts no effect on head-splitting-prone cabbage varieties [32]. In the meanwhile, the potassium content of splitting-tolerant cabbage leaf heads is higher than that of non-splitting-tolerant cabbage leaf heads, and the calcium content of the former is lower than the latter [52]. Calcium ions act as important intracellular second messengers in response to environmental signals in plants under adverse stress [53]. It indicated that cabbage varieties with tolerant head-splitting are more sensitive to calcium ions. Calcium ions significantly reduced pectinase and cellulase activities and significantly increased original pectin and cellulose contents [54]; pectinase and cellulase activities were positively correlated with cracking/splitting rate. So, calcium ions play a more important role in splitting/cracking tolerance.

In the research on plant shedding, the higher the content of pectinase and cellulase, the easier it is for cell walls to separate, resulting in shedding. In the meanwhile, Expansins loosen the cell wall through the disruption of non-covalent bonds between matrix glycans and cellulose microfibrils [55]. And relevant molecular evidence has been collected that it is effective to silence the expansin gene in other plants [56]. Thus, in future research, it is advisable to attach special importance to the aforementioned genes in connection with the expansin proteins of cell walls or development genes of cell walls. Also, plant hormones play a role in resistance to stress, and the expression of genes related to the relevant hormones are aspects considered. In particular, ABA and ETH [57].

5.3. The Importance of Breeding Cabbage Varieties with Head-Splitting Tolerance

To prevent the occurrence of head-splitting, farmers take some other measures in addition to water and fertilizer management. The head-splitting rate in the later stage will also gradually increase along with the extension of the growth time of cabbage seedlings in the plug. So, the splitting time of leaf heads with a seedling age of 30d is the latest [18]. Among the cultivation and management measures, the plantation density has little relationship with the head-splitting rate of cabbage leaf head [17], while the installation cultivation conditions determine whether it is necessary to choose the head-splitting-tolerant cabbage varieties. Due to the lack of protection measures for cultivation conditions in the open field, cabbage is easily affected by rain and harvesting conditions, particularly in the late maturity stage. Compared with installation cultivation, varieties that are extremely resistant to cracking should be chosen for open-field cultivation [58]. However, the ways to control external factors are labor-intensive, expensive and not easy to operate in actual production. In comparison, genetic improvement of head-splitting is the most fundamental and efficient way. Furthermore, It is imperative to breed and plant cabbage varieties with head-splitting tolerance [27].

Although related studies have been carried out on evaluation indexes, structural anatomy, physiological characteristics, cultivation and management measures, QTL mapping, etc., there is no unified standard has been worked out in the evaluation of the head-splitting property of cabbage. The related studies, especially molecular research of head-splitting in cabbage, are still in their infancy compared with other vegetable plants (tomato) with cloned cracking genes [59]. From the existing information, we can analyze that head-splitting tolerance in cabbage was dominated by major genes and showed an additive effect, although the environmental factors had a great effect on it, and QTLs information is useful to MAS, especially the QTL *SPL-2-1* related to cell structures. For breeders, early generation selection was efficient.

Exploring head-splitting tolerance-related QTL lays a foundation for molecular marker-assisted selection and cloning of related genes. Meanwhile, it is hoped that through the collection and identification of germplasm resources, the phenotypes and genotypes of cabbage susceptibility or tolerance to head-splitting can be analyzed at different levels so as to provide a basis for breeding, improving varieties and enriching germplasm resources (Figure 3). Relatively speaking, the microspore culture technology in cabbage breeding is relatively mature, and the DH line acquired can accelerate the breeding process and lay a foundation for the cultivation of cabbage varieties [10]. Finally, for the head-splitting tolerance of cabbage, we look forward to accelerating the research process and using molecular breeding methods to cultivate cabbage varieties with head-splitting tolerance rather than relying on cultivation measures.

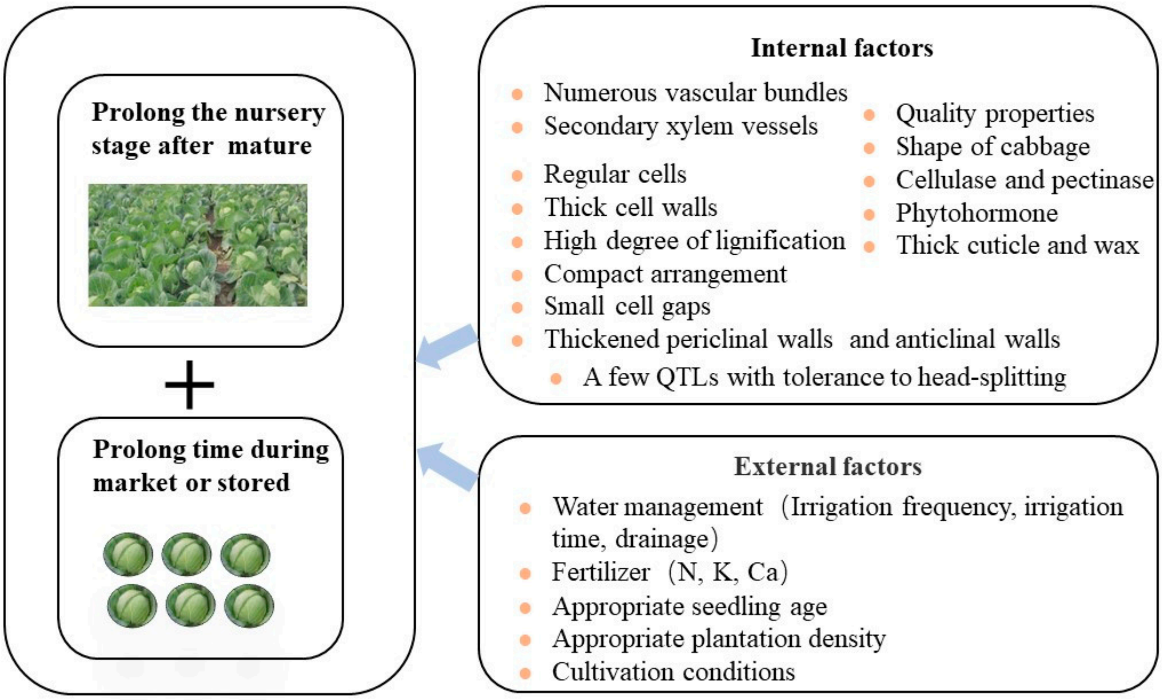

Figure 2. Factors improving tolerance to head-splitting of cabbage.

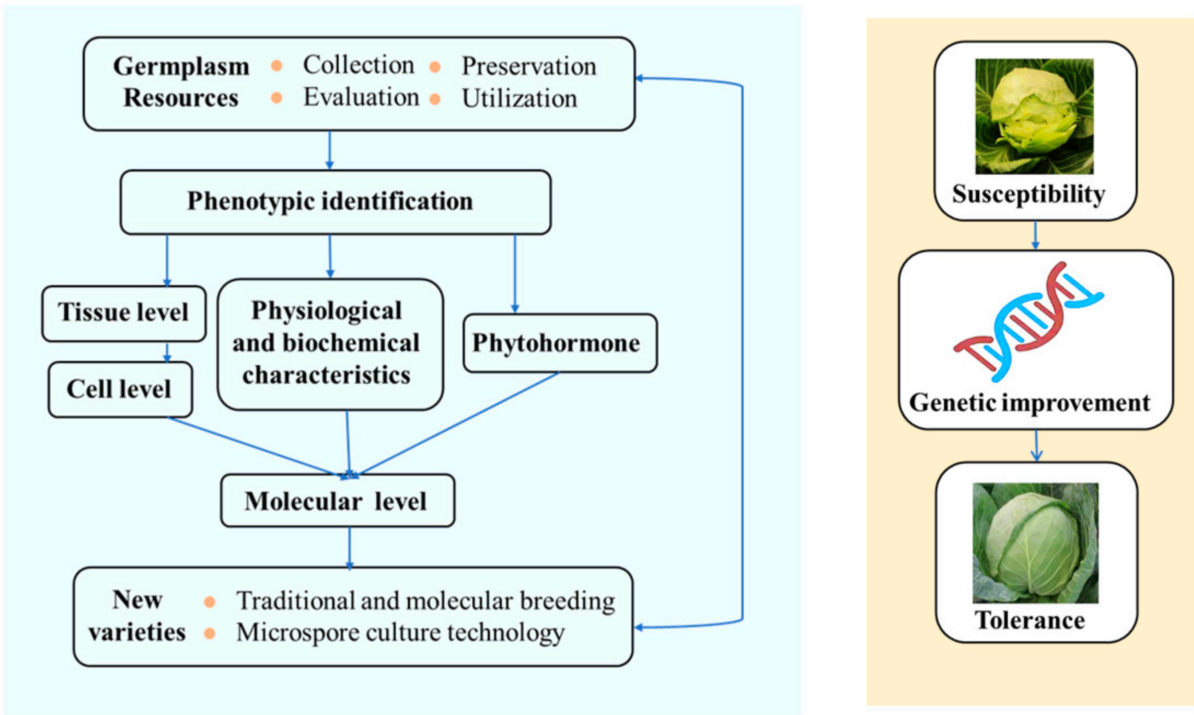

Figure 3. Breeding idea of improving tolerance to head-splitting of cabbage.

Author Contributions: Conceptualization, Y.W., Q.L. and X.S.; formal analysis, G.Z., L.G. and Y.Z.; resources, G.Z., L.Z., Y.D. and H.D.; data curation, writing—original draft preparation, Y.W. and Q.L.; writing—review and editing, Y.W., G.Z. and X.S.; funding acquisition, Q.L. and Y.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the S&T Program of Hebei (21326341D), the Natural Science Foundation of Hebei (C2020105002), the S&T Program of Tangshan (22150212A), the Colleges and Universities in Hebei Province Science and Technology Research Project (QN2020514) and the Foundation of Tangshan Normal University (2023B18).

Data Availability Statement: All relevant data are within the paper. And more information can be found in the references.

Conflicts of Interest: The authors declare no conflict of interest.

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