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REVIEW

Research Progress and Application of Plant Branching

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ABSTRACT

Plant branching development plays an important role in plant morphogenesis (aboveground plant type), the number and angle of branches are important agronomic characters that determine crop plant type. Effective branches determine the number of panicles or pods of crops and then control the yield of crops. With the rapid development of plant genomics and molecular genetics, great progress has been made in the study of branching development. In recent years, a series of important branching-related genes have been validated from *Arabidopsis thaliana*, rice, pea, tomato and maize mutants. It is reviewed that plant branching development is controlled by genetic elements and plant hormones, such as auxin, cytokinin and lactones (or lactone derivatives), as well as by environment and genetic elements. Meanwhile, shoot architecture in crop breeding was discussed in order to provide theoretical basis for the study of crop branching regulation.

KEYWORDS

Plant branching; branching development genes; hormone; environment; crop breeding

1 Introduction

Phenotypic plasticity in plants is dramatic. Their plasticity of growth enables plants to thrive in a myriad of environments and respond to biotic and abiotic stresses through changes in growth and development [1]. Shoot architecture is an excellent example of this and remains one of the most variable determinants of yield in many crops. Plant type refers to the morphological characteristics and spatial arrangement of plant objects, which is mainly determined by the morphological characteristics and spatial arrangement of roots, stems, leaves, branches, flowers and so on. For crops, plant type is an important factor that determines crop yield, and an ideal plant type can effectively improve plant yield [2].

In the 1950s, some research experts put forward the concept of ideal breeding but did not make a specific boundary. Chinese scholars believe that the ideal plant type mainly refers to the morphological characteristics and arrangement of plants in space. At the same time, it also believes that the physiological and ecological role of plants in the process of growth. Plant type mainly refers to the growth form of plant leaves or the posture of photosynthesis. The ideal plant type is mainly to analyze the shape of the whole plant growth environment to ensure that plants can use good growth posture to carry out photosynthesis in the process of growth and increase economic yield [3].

Plant branching is such an important factor that it determines its morphogenesis. It not only affects the distribution of leaf curtain, the number and yield of flowers and fruits, but also it affects the competition between plants and weeds or insects [4]. It is a common growth phenomenon of plants, axillary buds after formation, further grows to form lateral branches, and axillary buds on lateral branches can also develop into lateral branches, and then form strains.

It not only affects crop yield, but also affects crop cultivation density and nutrient distribution. More branches will lead to poor ventilation, which can easily lead to crop diseases and reduce yield. In addition, branching is also an important plant type character of ornamental plants, and the growth state of branches can affect the landscaping effect of ornamental plants. In recent years, the aboveground character gradually preferred by breeders is branching.

2 Branching Mode and Influencing Factors

2.1 Branching Mode

Because of the nature of plants which are differences in quality and species, by observing the branching morphology of plants, all branches can be divided into five categories: monopodial branching (such as *Arabidopsis* and *Cucumis sativus*, etc.), Sympodial branching, false dichotomous branching (*Solanum melongena*), dichotomous branching (*Capsicum* spp.) and tiller (Fig. 1).

Dichotomous branching
(*Capsicum* spp.)

Monopodial branching
(*Arabidopsis and Cucumis sativus*)

Sympodial branching
(*Solanum lycopersicum*)

False dichotomous branching
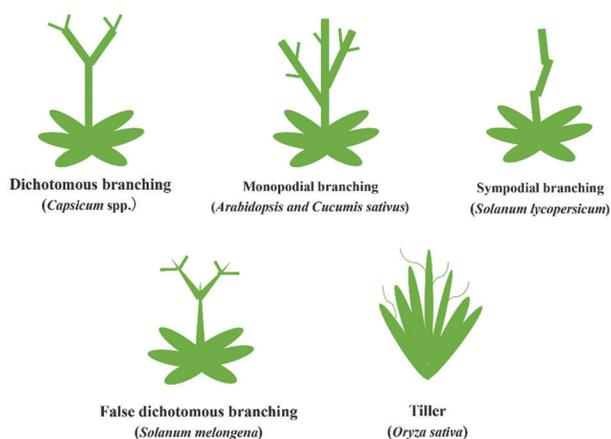(*Solanum melongena*)

Tiller
(*Oryza sativa*)

Figure 1: Plant branching type

2.2 Plant Branches and Plant Endogenous Hormones

Plant hormone is an essential factor to break the dormancy of lateral buds and the continuous growth of branches [5]. The change of external environment can make the plant hormone change accordingly, promote the dynamic balance of plant hormone, and then stimulate the expression of plant branching genes.

2.2.1 Plant Branches and Auxin

It was first found that the hormone acting on plant branches is indole-3-acetic acid (IAA). After increasing the level of IAA in bean plants, the number of lateral branches decreased significantly [6,7]. The number of lateral branches decreased significantly after increasing the level of IAA in plants. The results showed that IAA in cucumber shoot tips could not inhibit the growth of axillary buds independently, needed to act together with other substances that inhibited the growth of axillary buds [8]. After spraying IAA on rice with spikelets removed, the tiller elongation of rice was inhibited [9].

It is found that the lowest IAA content is the key to the initiation of axillary meristem (AM) [10]. The mutants of two important genes *YUCCA* (*YUC*) and *TRYPTOPHAN AMINOTRANSFERASE OF*

ARABIDOPSIS 1 (*TAA1*) in the IAA synthesis pathway do not have a strong ability to synthesize IAA, which results in the inhibition of apical dominance and the promotion of *Arabidopsis* branching [11]. *YUCCA* (*YUC*) gene in *Arabidopsis thaliana* is related to auxin biosynthesis and plays an important role in all aspects of development. In maize, *SPI1* is a specific member of YUC gene family in monocotyledons and is also important for maize inflorescence development. The functional loss of *SPI1*, a homologous gene of *YUC* in maize, will lead to defects in the initiation and lateral organ development of AM, thus reducing branching [12]. Mutations or deletions of key genes *IAA3, IAA5* and *IAA15* in IAA signal transduction promote tomato lateral branch growth by affecting IAA signal transduction [13].

2.2.2 Plant Branches and Cytokinin

Cytokinin (CTK) can activate lateral buds and promote plant branches by promoting cell division. Spraying CTK directly on plant lateral buds could inhibit apical dominance and make lateral buds grow. It was found that the content of CTK in *A. thaliana* mutants as *sho* and *hoc* was high, indicating that CTK was regulating plant branching [14]. Applying CTK to the base of *A. thaliana* could weaken the apical dominance and promote the growth of lateral buds [15]. CTK can also promote the initiation and lateral bud formation of AM. The increase of CTK level in *Arabidopsis* multibranched mutant *supershoot* (*sps*) leads to the formation of multiple AM in the leaf axils of rosette and cauline leaves, which increases the number of branches and promotes the elongation of lateral branches [16]. The high expression of *ISOPRENYLTRANSFERASE* (*IPT*), the key gene of CTK synthase, can promote the activation of CTK on lateral buds, and then promote the branching of *A. thaliana* [17].

2.2.3 Plant Branches and Strigolactone

Strigolactones (SLs) is a new type of plant hormone ubiquitous in plants, which can stimulate seed germination of parasitic plants and inhibit lateral bud germination directly or indirectly. SLs can be used as a long-distance signal substance to inhibit the growth and development of lateral buds, and as a graft transfer substance to regulate the branch inhibitory transcription factors BRC1, teosinte of TCP family. TEOSINTE BRANCHED 1 (TB1) and FINE CULM 1 (FC1), thereby inhibiting lateral bud elongation [18,19]. SLs can inhibit lateral bud growth by down regulating the level of CTK in axillary buds of pea [20].

There are three inhibitors in the SLs signal pathway, namely SMXL6, SMXL7 and SMXL8. It has been found that without SLs, SMXL6 and TPL protein can directly bind to the promoters of SMXL6, SMXL7 and SMXL8 and inhibit their expression to increase the content of SLs, thus inhibiting *Arabidopsis* branching.

At the same time, smxl6 can also form complexes with unknown transcription factors, which are expected to recognize and bind the promoters of BRC1, TCP1 or PAP1, thereby inhibiting their transcription and promoting *Arabidopsis* branching [21].

2.2.4 Plant Branches and Other Hormones

It has been found that gibberellin (GA), abscisic acid (ABA) and brassinolide (BR) can regulate plant branching. Rice *TILLER ENHANCER* (*TE*) gene can inhibit tillering, and high levels of GA can activate APC/CTE (E3 ubiquitin ligase complex) and promote MONOCULM 1 (MOC1) degradation of AM, thus inhibiting rice tillering [22]. High concentration of ABA could inhibit the germination of *Arabidopsis* lateral buds and thus inhibit the branching [23]. *BRASSINAZOLE RESISTANT* (*BZR1*) ncodes a positive regulator of the brassinosteroid (BR) signaling pathway that mediates both downstream BR responses and negative feedback regulation of BR biosynthesis. *BZR1* inhibits the expression of *CUP-SHAPED COTYLEDON* (*CUC*), the key gene of AM initiation in *A. thaliana*, thus inhibiting AM initiation and branching [24].

2.3 Plant Branches and Environmental Factors

As the growth position of the plant cannot be moved, the change of it surrounding environment will have a great impact on the plant [25]. Therefore, plants can adapt to the changing environment only by constantly changing their developmental state according to various signals. There is growing evidence that the environment can affect the branching of plants. Understanding the molecular mechanism of plant branching response to environmental changes will help us to cultivate excellent crop varieties with high and stable yield under special environmental conditions. The following mainly discusses the effects of light, temperature, water and nutrition on crop branching.

In general, high intensity light promotes the growth of lateral buds. Studies have shown that high intensity light can promote the growth of lateral buds of vaccinium and thus promote branching [26]. Low light quantum flux density reduces *A. thaliana* branching [27]. When the ratio of red light to far red light decreased, the expression of branch inhibitor *BRANCHED 1* (*BRC1*) increased, which led to the decrease of branching in *A. thaliana* [28,29]. The decrease of photosynthetic area could promote the expression of branch suppressor gene *TB1* and reduce the tillering of maize [30]. Beyond a certain range of light density, the content of monopodium lactone (SLs) and the expression of SLs synthesis gene *CAROTENOID CLEAVAGE DIOXYGENASE 7* (*CCD7*) in tomato increased, thus inhibiting tomato branching [31]. In addition, the increase of light/dark (7 h/7 h) transition frequency could inhibit the development of axillary buds in *A. thaliana* and reduce the branching [32].

Temperature is also one of the important factors affecting branching. Low temperature will induce the expression of SLs signal gene *MORE AXILLARY GROWTH 1* (*RwMAX1*) in rose, promote it to form a gradient in stem nodes, and then affect the germination rate of lateral branches [33]. Low temperature also promoted the transcription of SLs receptor gene *DWARF 14* (*D14*), which inhibited tillering in rice [34].

Water is also an important factor affecting the formation of branches. When rice is under drought in the early stage of development, the number of tillers can be reduced by SL and OsTB1 pathway to adapt to drought conditions [35].

Nutrition is also essential for plant branching. When the plant is undernourished, SL will be synthesized in the roots of the plant, and part of the SL will be transported upward to inhibit the production of lateral buds and branches, thus reducing the consumption of nutrients [36]. Nitrogen is the most important nutrient, and the main sources of nitrogen are nitrate and ammonium fertilizer. Studies have shown that nitrate signals can promote carbon and nitrogen metabolism and plant endogenous hormone synthesis [37], and then promote the growth of axillary buds. Nitrate transporter (nitrate and peptide transporter family, NPF) promotes nitrogen uptake and regulates plant growth and development. *OsNPFs* gene can promote nitrate absorption and increase the number of tillers in rice. Phosphate also helps to tiller rice [38]. When phosphorus was deficient in the plant, the content of SL and the growth of tiller buds were inhibited. When there was enough phosphorus in the plant, the content of SL decreased and promoted the growth of tiller buds.

These studies show that many genes can combine stress response with branching regulation to make plants better adapt to the dynamic environment. Generally, the branching of environmental impact is ultimately involved in the branching of plants by affecting the balance of endogenous hormones.

2.4 Hereditary Factors

Besides environmental factors and plant hormones, there are also genetic factors that affect plant branching. Genetic factors fundamentally determine the branching characteristics of plants. The branching of the plant is differentiated from the axillary meristem, and the formation of lateral buds is first the expression of genes for special traits in the axils of leaves; then, the axillary meristem grows; then it grows into lateral buds. In this process of life activities, the genes that control branching and plant

hormones coordinate to control the branching traits of plants. Many genes that affect plant branching have been reported one after another, and their mechanisms are different. Therefore, the internal regulatory genes are divided into three types: one is the lateral bud initiation development regulation gene; the second is the lateral bud elongation development regulation gene; the third is the lateral bud initiation and elongation development co-regulation gene.

2.4.1 Genes Regulating the Initiation of Lateral Bud Development

The initiation of plant lateral buds is mainly regulated by genes. *EXCES SIVE BRANCHES1* (*EXB1*) belongs to the WRKY transcription factor family, which can promote the initiation of AM and produce more lateral buds to promote the branching of *A. thaliana* [39]. *REGULATORS OF AXILLARY MERISTEMS1-3* (*RAX1-3*) belongs to the family of MYB transcription factors [40] and regulates *A. thaliana* branching. *EXB1* upstream in *RAXs*, is regulating the transcription of *RAXs* to promote AM initiation, thus promoting *Arabidopsis* branching. Blind gene in tomato is a homologous gene of *RAX* and participates in AM initiation.

NAC transcription factor CUC is activated with *Arabidopsis* AM. *CUC3* plays an important role in *Arabidopsis* AM formation. It was found that *CUC2* and *CUC3* directly bind to the promoter of DA1 (its peptidase substrate UBP15 can inhibit the initiation of AM) and activate its expression to form a *CUC2/CUC3*-DA1-UBP15 regulatory module to control the initiation of AM in *A. thaliana* [41]. *LATERAL SUPPRESOR* (*LAS*) belongs to the GRAS transcription factor family, which promotes AM formation and regulates *Arabidopsis* branching [42].

Studies have shown that during the initiation and establishment of AM, *LAS* and *MOC1* play a role in the upstream of *Arabidopsis SHOOTMERISTEMLESS* (*STM*). *REVOLUTA* (*REV*) belongs to the HDZIP transcription factor family and acts on *Arabidopsis* AM initiation [43]. *REV* can up-regulate the expression of *SAM* gene to start *Arabidopsis* AM [44]. *STM* belongs to the KNOX transcription factor family, which promotes AM formation in *A. thaliana* by regulating the differentiation of AM cells [45].

WUSCHEL (*WUS*) is a homeobox gene that controls the stem cell pool. Expressed in the center of the stem cell tissue of the meristem. Stem cells need to be kept in an undifferentiated state. The regulation of *WUS* transcription is the core checkpoint in stem cell control, which promotes axillary bud primordium formation by maintaining stem cell activity and regulating downstream genes. And reactive oxygen species (ROS) affects *WUS* gene, which in turn affects cell maintenance and differentiation. It is worth noting that the activities of stem tip meristem (SAM) and root tip meristem (RAM) have been proved to be affected by the interaction between ROS, redox components and plant hormones [46]. *BARREN STALK1* (*Ba1*) gene in maize and *REGULATOR OF AXILLARY MERISTEM FORMATION* (*ROX*) gene in *Arabidopsis* are homologous genes of *LAX1*, which regulate tillering or branching by coding proteins [47,48].

2.4.2 Genes Regulating the Development of Lateral Bud Elongation

BRC1, *TB1* and *FC1* are homologous genes in *Arabidopsis*, maize and rice, respectively, and they are all members of the TCP transcription factor family, which inhibit the growth of branches and tillers. Through QTL mapping, it was found that the *TB1* gene of Yumi caused the structural difference between maize and multi-tiller Teosinte maize. *TB1* is mainly expressed in AM to coordinate maize bud growth [49]. *FC1* is expressed at the base of AM and SAM, which inhibits rice tillering by promoting bud dormancy [50]. The *BRC1* gene of *A. thaliana* is expressed in axillary buds and inhibits axillary bud elongation and development. It is the downstream gene of multiple regulatory pathways. Cucumber branching inhibitor *CsBRC1* cooperates with auxin polar transport gene *CsPIN3* to regulate cucumber branching. *CYP831* gene belongs to the cytochrome P450 family, which promotes *Arabidopsis* branching by reducing IAA content and inhibiting apical dominance. In *A. thaliana*, *AXR1* gene is an IAA responsive gene that can inhibit the growth of axillary buds. *PINOID* (*PID*) gene negatively regulates IAA signal transduction,

which can promote *Arabidopsis* branching. *AtMYB2* gene negatively regulates CTK content, thus inhibiting *Arabidopsis* branching [51].

BUD1 gene belongs to member of plant mitogen-activated protein kinase group D. *Bud1* mutants have been reported, in which MAP kinase 7 (MKK7) is structurally activated, resulting in multiple phenotypic changes. It is known that mitogen-activated protein kinase (MAPK/MPK) plays an important role in a series of signals such as biotic and abiotic stress and hormone-mediated development in higher plants. Genetic analysis showed that MKK7-MPK6 cascade is specifically responsible for the regulation of shoot branching, hypocotyl gravitropism, filament elongation, and lateral root formation [52]. *D27* gene participates in SLs synthesis in rice to inhibit branching [53]. *MAX1* gene encodes cytochrome P450, which acts on the downstream of *MAX3* and *MAX4*. It is the key gene of SLs signal transduction and inhibits *Arabidopsis* branching. *D3* gene in rice is homologous to *MAX2* gene in *A. thaliana*, which is an important motif in SLs regulatory genes. It plays a role in the downstream of *MAX1*, *MAX3* and *MAX4* and can inhibit branching [54]. *HTD1* gene in rice is homologous to *MAX3* gene in *Arabidopsis* and allele to *D17*, which is the key gene encoding SLs synthetase and inhibits branching, while *D10* gene in rice is homologous to *MAX4* gene and participates in SLs biosynthesis and inhibits branch [55].

In rice, three alleles *D14*, *D88* and *HTD2* play a role in SLs signal transduction and are negative regulators of tillering [56]. *D53* is the suppressor of SLs signal transduction and is positively regulating rice branching [57].

2.4.3 Co-Regulatory Genes of Lateral Bud Initiation and Elongation Development

The genes that play a role in both AM initiation and lateral bud development are *SPS* and *BUSHY* (*BUS*). They are homologous genes. *SPS* gene is mainly strongly expressed in leaf axils and controls the synthesis of IAA to regulate *Arabidopsis* branching [58]. The *sps* mutant of *A. thaliana* is characterized by an increase in the number of meristems formed in leaf axils and the stagnant release of lateral buds, resulting in many lateral buds, thus forming repeatable branches. Some studies have also shown that *SPS* gene reduces the concentration of CTK in leaf axils by accelerating the oxidative degradation of CTK, which inhibits the initiation of AM and the development of axillary buds [59], resulting in reduced branching of *A. thaliana* (Fig. 2).

3 Summary and Prospect

Plant type is a comprehensive and important agronomic character. Through the optimization of individual plant type, we can construct the optimal population under specific environmental conditions, including adversity, and make effective use of light, heat, water, fertilizer and other resources to obtain the highest yield and best quality. It is the direction of agricultural breeding and cultivation in the future. Compared with conventional breeding methods, molecular breeding methods represented by molecular marker-assisted selection, transgenic and gene editing cannot only shorten the breeding cycle, but also achieve accurate improvement of crop specific traits with higher efficiency (*Oryza sativa* L., *Triticum aestivum*, *Zea mays*, etc.). In the aspect of crop plant type, we should further excavate the new key genes controlling crop plant type and the explanation of their regulatory mechanism, develop molecular markers closely linked to plant type, transfer several key genes controlling crop plant type to good parents by means of molecular breeding and molecular design, and cultivate new crop varieties with ideal plant type, which will be an important direction of crop genetic improvement in the future, which has important practical significance.
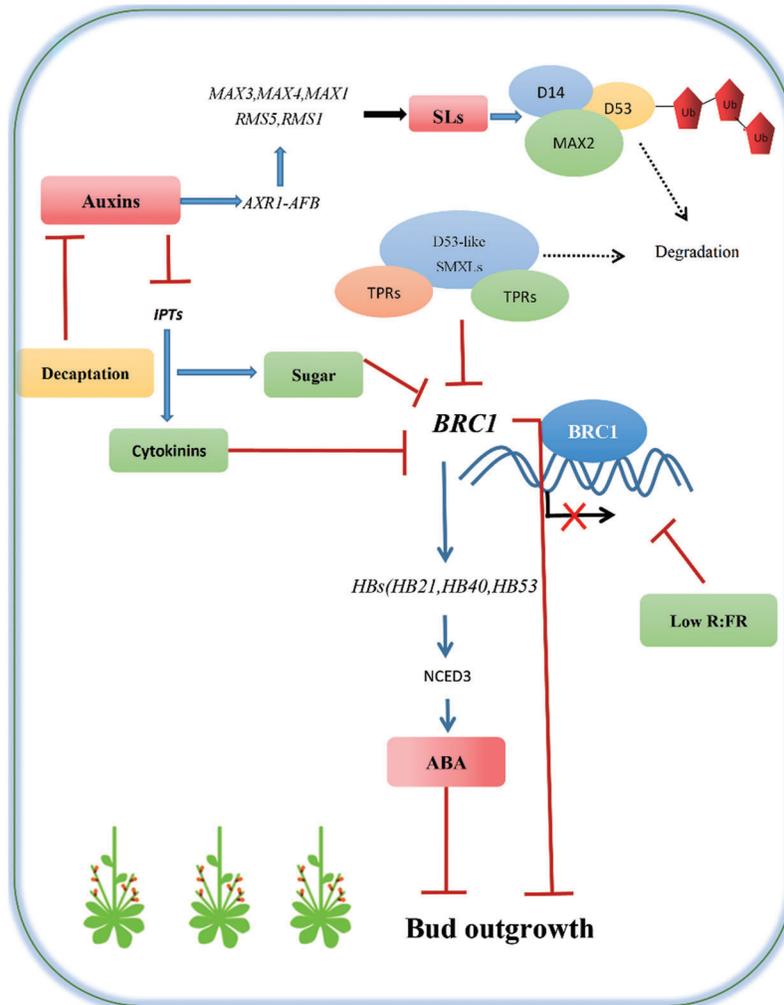
Figure 2: Plant hormones, environmental conditions and key regulatory genes control bud outgrowth

3.1 Make Great Efforts to Improve Plant Type

Plant type is a comprehensive and important agronomic character, which is an important character affecting the population structure and yield formation of plant. Plant type plays a common role at both individual and population levels. In a specific natural environment, plant ontogeny interacts with population structure to obtain reasonable individual plant type and population structure, which can not only increase biological yield, but also improve light transmission and ventilation conditions, reduce the occurrence of germs and insect pests, reduce the use of pesticides and so on. Plant type determines plant yield potential, harvest index, disease resistance and its adaptability to growth environment.

Through the optimization of individual plant type, we can construct the optimal population under specific environmental conditions, including adversity, and make effective use of light, heat, water, fertilizer and other resources to obtain the highest yield and best quality. it is the direction of agricultural breeding and cultivation in the future.

Identify the key genes controlling crop plant type, develop molecular markers closely linked to plant type, transfer several key genes controlling crop plant type to good parents by means of molecular

breeding and molecular design, and cultivate new crop varieties with ideal plant type will be an important direction of crop genetic improvement in the future.

The key genes controlling plant type through map-based cloning or homologous cloning and the development of molecular markers linked to plant type are the premise and basis for the molecular improvement of plant type of these crops.

3.2 Continue to Increase Crop Yields

The output value of vegetables in China is about 2.2 trillion yuan, which has surpassed that of food crops to become the largest industry in the planting industry. *Solanum lycopersicum* L. *Cucumis sativus* and *Solanum melongena* L. are the main vegetable crops under protected cultivation in China. Because of more branches, pruning, branching, hanging vines and other labor-consuming operations need to be carried out frequently in the production of eggplant fruits and melons, which increases the labor cost. Secondly, more branches are easy to cause uneven distribution of plant nutrients and diseases, thus reducing the yield and quality of vegetable crops [60]. With the gradual increase of labor cost, the cultivation of eggplant fruit and melon vegetable varieties with ideal plant type (few or weak lateral branches) and suitable for light and simplified cultivation is one of the urgent problems to be solved in China's vegetable industry. In the production process, in addition to selecting the ideal plant type varieties, the branching of eggplant fruits and melons can also be regulated according to the above research results.

First, plant branching can be regulated by changing the growth environment. For example, branching can be reduced by appropriately increasing far red light, lowering temperature or applying more nitrogen fertilizer in the cultivation environment, or by reducing potash and sugars.

Second, plant hormones can be used to regulate branching. The branching was reduced by spraying IAA, SLs, GA, ABA, BRs and so on, and the branching was also reduced by CTK inhibitor treatment.

Third, using the identified plant branching regulatory genes to develop molecular markers, through molecular marker-assisted breeding to cultivate new varieties of ideal plant type.

Fourth, using the cloned plant branching regulatory genes, new germplasm with different branching types can be obtained by gene editing technique. In cucumber, Professor Zhang Xiaolan of China Agricultural University cloned *CsBRC1*, a key gene regulating branching development of cucumber [61]. Because cucumber cultivars in China tend to select varieties with small number of lateral branches, short length and late germination, we can use *CsBRC1* gene information to develop molecular markers or identify and create cucumber germplasm resources with different branching types by gene editing techniques.

With the deepening of people's understanding of plant branching regulation, it will effectively solve the problem of more branches in the production of eggplant fruits and melons, innovate germplasm resources, and cultivate new varieties of high-quality and high-yield vegetables that meet the goal of breeding. Effectively solve the problems of difficult and expensive labor in the process of vegetable production, reduce the cost of vegetable production, improve vegetable production and simplify cultivation.

Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

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