Research progress on the bulb expansion and starch enrichment in taro *(Colocasia esculenta (L). Schott)*

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Background. Taro is an important crop in the world, and it can be used as food, feed, and industrial raw material. The yield and product of taro are mainly determined by the expansion degree and the state of starch enrichment. The expansion of taro bulb is a complex biological process, which involves the increase in the number and volume of bulb cells and the starch enrichment in the cells.

Results. This article introduces the formation and development of taro bulb through the process of amyloplast formation at the cytological level and the changes in bulb expansion and starch enrichment at physiological levels, which involve endogenous hormones and key enzyme genes for starch synthesis. The effects of environment and cultivation methods on taro bulb expansion were also reviewed. Finally, the future research directions and research focus about the development of taro bulb were prospected.

Conclusions. The development of taro bulbs is a complex biochemical process, including the accumulation of morphogenesis and assimilation products, involving gene expression, material metabolism, nutrient input, and the effect of external environmental conditions. At present, the research on the development of taro mainly focuses on evolutionary classification, genotype and isozyme analysis, cultivation, production, processing, and utilization. Limited research has been conducted on the physiological mechanism and hormone regulation pathway of taro growth and development, taro bulb expansion, key gene expression, and starch enrichment. There-fore, the following research will become the key research direction in the future.

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Abstract

Background. Taro is an important crop in the world, and it can be used as food, feed, and industrial raw material. The yield and product of taro are mainly determined by the expansion degree and the state of starch enrichment. The expansion of taro bulb is a complex biological process, which involves the increase in the number and volume of bulb cells and the starch enrichment in the cells.

Methodology. PubMed ,Web of Science and China National Knowledge Infrastructure databases were searched for relevant articles. After removing duplicate articles and the articles with little relevance, 73 articles were selected for the review.

Results. This article introduces the formation and development of taro bulb for the workers engaged in taro research. The content includes the process of amyloplast formation at the cytological level and the changes in bulb expansion and starch enrichment at physiological levels, which involve endogenous hormones and key enzyme genes for starch synthesis. The effects of environment and cultivation methods on taro bulb expansion were also reviewed. Finally, the future research directions and research focus about the development of taro bulb were prospected.

Conclusions. The development of taro bulbs is a complex biochemical process, including the accumulation of morphogenesis and assimilation products, involving gene expression, material metabolism, nutrient input, and the effect of external environmental conditions. At present, the research on the development of taro mainly focuses on evolutionary classification, genotype and isozyme analysis, cultivation, production, processing, and utilization. Limited research has been conducted on the physiological mechanism and hormone regulation pathway of taro growth and development, taro bulb expansion, key gene expression, and starch enrichment. There-fore, the following research will become the key research direction in the future.

Introduction

Taro is an underground bulbous crop planted in the tropical and subtropical regions (Figure 1). It originated in China, India, Malaysia, and other regions, and is widely cultivated in Asia, Africa, and other regions. It has a cultivation history of more than 2,000 years. At present, taro can be classified using three methods. According to the ecological type, it can be divided into aquatic taro and dry taro, and it can be classified into petiole, flower, and bulb taro according to the eating part, and it can be classified into Kui taro, multi-cormels taro, and multi-head taro according to bulb tillering habit (Wu et al., 2021). The three classifications of taros in agricultural production of China exhibit various characteristics (Figure 2). Kui taro has few sub taro and single mother-taro which is the main edible part. In multi-cormels taro, the sub taros are numerous and grow in groups which have strong tillering ability. In multi-head taro, there are few sub taros and the tillers of the mother taros grow in groups. The fundamental difference of taro bulb tiller is the difference of expansion between mother and sub taro. This phenomenon is caused by the difference in the number of chromosome and differential expression of genes (Zhu et al., 2018). Studies on taro chromosomes has proved that Kui taro is diploid (2n=2x=28), while the multi-head is triploid (2n=3x=42) (Huang et al., 2014). The chromosome multiples are related to the geographical distribution. Diploid is more common in hot and humid areas with low altitudes, and triploid is more common in dry and cold areas with high altitudes [4]. Taro is essential for the body, and it can be used as food, vegetable, feed, and health product. The taro bulb, which is rich in starch, carbohydrates, and energy, is one of the staple food in Asia, Africa, and India (Njintang et al., 2008). In comparison with potato, sweet potato, and cassava, taro starch granules are small and has a diameter of approximately 1.5 μm, making it easy to digest and providing therapeutic and health care functions. It has been used for the preparation of infant food in Haweii and some other islands in the pacific. Taro starch particles are small and uniform and have good cold and hot stability, good whiteness, and good adhesion. Therefore, it can be used as a brightener in cosmetics (Qi et al., 2015). Taro bulbs are rich in many nutrients, such as starch, and the starch content of different varieties of taro could reach 10%–36% (Falade et al., 2013). Taro contains a large amount of dietary fiber and various essential amino acids, but its fat content is low (Sefa-Dedeh et al., 2002). It is also rich in vitamins and amino acid, making it is a food for people of all ages (Han et al., 2018). Taro is a food and medicine homologous crop, which is often used for the treatment of diarrhea, internal bleeding, asthma, and skin diseases (Prajapati et al., 2011). It could also lower blood sugar and cholesterol (Sebnem et al., 2012). Therefore, taro has good prospects for medicinal development. Taro starch can be used as an industrial raw material. It could improve the stability of Pickering emulsion (Zhang et al., 2020), and it could be used for the treatment of wastewater generated in the printing and dyeing process (Zhou et al., 2018) and as an enhancer of starch film (Dai et al., 2015).

According to the statistics of the Food and Agriculture Organization of United Nations, taro is the 14th largest vegetable crop, with a global planting area of 1.6 million hectares and an annual output of 11.7 million tons. The cultivation area in China ranks first in the world and has a large number of wild resources and local varieties, which are mainly distributed in southern regions such as Yunnan, Taiwan, and the Yangtze River Basin. In recent years, taro has become an important input and export trade industry. The total export trade volume and total value were higher than the imports (Chang et al., 2019). With the rapid development of the taro industry, the demand for taro has increased. It has also introduced new and high requirements for taro production and basic theoretical research.

Survey methodology

PubMed ,Web of Science and China National Knowledge Infrastructure databases were searched for relevant articles. A total of 2525 articles appeared Pubmed database using ‘‘taro’’ as the search term and the date of publication from 1975/1/1 to 2022/5/1. After narrowing the search with keywords including ‘‘bulb of taro’’, ‘‘bulb expansion in taro’’, ‘‘bulb starch enrichment in taro’’, ‘‘amyloplast enrichment process of taro bulbs’’, ‘‘development of taro bulbs’’, ‘‘regulation of hormones on bulb development’’, ‘‘genes in starch synthesis’’, and ‘‘regulation of hormones on bulb swelling’’, 1532 studies were obtained. With ‘‘taro’’ as the search term, 2525 articles published between 1975–2022 appeared in the Web of Science database, of which 914 articles were selected as above. After removing duplicate articles and the articles with little relevance, 73 articles were selected for the review.

Taro expansion and development process

Taro is a perennial herbaceous plant, which belongs to the Araceae family, but it is generally cultivated as an annual crop in agricultural production. According to the growth and development characteristic of taro, its life circle is divided into five periods, namely, the germination, seedling, growth, taro expansion, and bulb dormancy period (Sun et al., 2014). Taro bulbs undergo metamorphosis during evolution. Take multi-cormels taro and multi-head taro for example. The bulb of taro is composed of mother and sub taro, and some varieties include grandson and great grandson taro (Figure 3). The mother taro of taro bulb is developed by the top bud of the sub taro. The sub taro is developed from the lateral bud on the mother taro, and the grandson taro is developed from the lateral bud of the sub taro. An axillary bud is present on each node of mother taro, and it can develop into sub taro. The axillary bud grown in the leaf axil and the leaf have a co-growth relationship. The growth site grows clockwise, and the angle between adjacent axillary buds is 144°. The positions of each axillary bud are roughly in a straight line, showing typical 2/5 phyllodes features (Xu et al., 2020). The sub taro of Kui taro grows first and then thickens, and the top swells to form a smaller sub-taro; the sub taro of taro with multi-cormels elongates and thickens, and the whole bulb also swells to form a conical shape; three small-molecular-weight proteins, namely, CSP2, CSP3 and CSP4, are present in the sub taro, which have spatiotemporal specificity and are related to the occurrence and expansion of the sub taro. the relative differences in the contents of CSP1, CSP2, and CSP4 in the mother taro are related to the apical dominance of the terminal buds of the mother taro. The greater the difference is, the more obvious the apical dominance and the lower the developmental degree of the sub taro is (Zhu et al., 2018). However, Luiz found that the expression of TC1 gene during bulb development is spatiotemporal and acts by encoding globulin Gd1, but TC1 gene is not a regulator gene of bulb expansion (Castro et al., 1992). The gene that determines bulb expansion is present at the beginning of bulb differentiation. The role of TC1 gene in the process of bulb expansion remains to be further studied. The proportion of fresh weight of taro first increases and then decreases in the growth process. Similarly, the water content of the bulbs first in-creases and then decreases, while the dry matter content gradually increases, showing an S-shaped growth trend. The dry matter accumulation of the sub taro in the later stage is greater than that of mother taro (Xu et al., 2020).

Figure 3. **The taro bulb's mother taro, sub taro and grandson taro**. (A) Multi-head taro; (B) Multi-cormels taro.

During the growth and development process of mother taro, the weight gradually increased, the water content gradually decreased, the total starch content gradually increased, and the soluble sugar content first increased and then decreased. The volume of parenchyma cells continued to increase, and the internal starch content gradually increased. The number and diameter of starch bodies showed an upward trend, and the number of starch granules in a single starch body also increases (Zhu et al., 2017). During taro bulb expansion, the number of links on the surface of the bulb gradually increased, the fresh and dry weight of a single bulb continued to increase; the volume of the parenchyma cells in the bulb continued to increase, the number and size of amyloplasts gradually increased, and the entire cell was enriched; with the expansion of the bulb, the vascular tissue gradually developed and perfected, and the area of the sieve tube increased in number and became irregularly arranged; the taro bulb was densely covered with mucous cavities, which spread out from the center of the bulb, but no mu-cus cavity was observed in the epidermal cells (Sheng et al., 2021).

Amyloplast enrichment process of taro bulbs

At present, the research on the development and proliferation of amyloplasts mainly focuses on the endosperm cells of grains. In the development of endosperm amyloplasts, the number of plastids continued to divide, and the number increased; then the number and volume of starch granules increased in the plastid; individual starch granules increased in size and then began to form small amyloplasts. As the development progressed, the envelope of the small amyloplasts was further extended and expanded. Finally, the newly expanded envelope is filled with starch granules, thereby forming the large amyloplasts. The amyloplasts of the large starch granules in the wheat endosperm formed small starch granules by budding, while the amyloplasts of the small starch granules proliferated by constriction or budding (Wei et al., 2002; Wei et al., 2008).

A few reports have focused on the proliferation mode of amyloplasts in under-ground rhizome crops. The starch bodies of the complex starch contained in sweet potato tubers exist in the form of “diplex”, “triad”, and “multiple”; for the growth mode of the amylosome, single grain starch directly expands and grows; the amyloplasts of multigranular starch first split into monomers, and then grow in the form of mono-mers; the amyloplasts of complex starch do not divide during the growth process and form large complex amyloplasts (Jing et al., 2013). According to the morphology of amyloids observed by scanning electron microscope, the cassava root amyloid membrane is either "constricted", "wrinkled", or "sprouted", forming multiple differentiation centers of amyloplasts; with the continuous expansion of the starch body, the membrane structure was degraded and disappeared, and the irregular starch granules were released (Min et al., 2010).

Zhu et al. (2018) divided the accumulation process of taro bulb starch into three stages, namely, starch formation, rapid starch accumulation, and starch body enrichment (Zhu et al., 2017). The specific performance is the formation of amyloplasts and the continuous increase in diameter, followed by the continuous increase in the number of starch-es, and finally the increase in the number of starch granules in the amyloplasts. The surface of taro starch body is mostly round and oval, belonging to complex starch, containing multiple polyhedral starch granules. Take Kui taro for example. in the early stage of development, amyloid was mostly distributed at the edge of the cell, and then gathered at the center of the cell. Later in development, the number and size of amyloplasts continued to increase (Figure 4). Transmission electron microscopy showed that the amyloplasts of taro bulbs were large, and the large amyloplasts split into several small starch granules. Some small starch granules (Figure 5A) were observed close to the free state at the edge of amyloplasts, and these granules were loosely arranged and smaller in size. With the development of the bulb, the starch granules with large diameters in the amyloplasts were mostly concentrated in one area, and their arrangement was relatively compact. The small starch granules were mostly distributed on the other side or around, and their arrangement was loose (Figure 5B).

Taro bulb starch originates from the precursor plastid, and starch granules are formed in the plastid and free in the cytoplasm of the membrane (Sheng, 2021). As the starch granules increase, the volume of the plastids increases, and the starch granules develop from the original irregular shape to a round shape. In the later stage, they gradually extruded each other into polygons. The starch bodies of taro bulbs were mostly com-plex starches. Amyloid proliferation is divided into two stages. In the first stage, the number of starch granules in the starch body changes; the starch granules gradually increase, fill up, squeeze, and deform each other. The large starch granules split into many small starch granules. The second stage involves the proliferation of amyloplasts. Taro amyloplasts can be split via membrane constriction proliferation and capsular vesicle proliferation. Capsule constriction and proliferation squeeze the starch gran-ules in the starch body to both sides through the inward depression of the amylosome envelope. Further, it is constricted into multiple amyloplasts, and the encapsulated vesicles proliferate in which the original amyloplasts spit out vesicles from the envelope, and new amyloplasts are generated and proliferated in the vesicles.

Effects of environment and cultivation methods on the development of taro bulbs

Taro adapts to high-temperature and -humidity environment and is not resistant to low temperature and frost. The optimum temperature for germination is 12–15 °C. The optimum temperature for growth is generally 25–30 °C. If the temperature is very low, the growth of taro will slow down or stop. If the temperature is very high, the condition will not be conducive to the development and expansion of taro bulb. Different varieties of taro have different requirements for temperature. Taro with Multi-cormels can be planted at low temperatures, making it widely distributed in temperate zones. Kui taro has strict requirements for high temperature. Therefore, Kui taro is mostly produced in tropical and subtropical regions with high temperature and humidity (Chang et al., 2019). Taro requires sunlight, and the light saturation point is approximately 50,000 lux. Taro is shade-tolerant and can grow under scattered light. The light intensity, composition, and light time remarkably affect the growth of taro, but strong light is conducive to the growth of taro and improves yield and quality. Under blue-violet light, the leaves of taro are large and thick, and the petioles are thick and short, and this condition is conducive to the growth and development of bulbs. In red and yellow light, the leaves are small, and the petioles are slender, and this condition is not conducive to the growth and development of bulbs. In the early stage of taro development, a longer light time is required to promote the increase of leaf area and the accumulation of photosynthetic products. The later stage of taro development requires a shorter light time to facilitate the formation and expansion of bulbs (Chang et al., 2019). Taro requires dampness. Calla taro is grown in paddy fields, but dry taro cannot be flooded for a long time. Taro has different requirements for humidity before different growth stages. The field should be kept moist during the germination stage to induce the germination of taro. During the taro-forming stage, the water demand is large, and the water supply needs to be guaranteed; the soil should be kept dry before harvesting to maintain good condition for the harvesting and storage of bulbs (Huang et al., 2016). Taro does not require very strict soil texture. Loose and fertile soil with deep soil layer and convenient irrigation and drainage is conducive to the growth of taro and the expansion of bulbs. Taro can grow normally in soil with pH of 4.1–9.1, but the optimum pH is 5.5–7.0. A highly acidic or highly alkaline soil is not conducive to the growth and development of taro (Huang et al., 2016).

Different cultivation methods remarkably affect the yield of taro. Film mulching can provide soil temperature in the early stage of taro growth, which is beneficial to the growth of taro and the expansion of bulbs. The growth and yield of taro bulbs in perforated film-covering cultivation was better than that in ridge film-covering cultivation. However, considering the inconvenience of cultivating a large amount of soil during the growth period of taro, ridge and perforation film-covering cultivation easily form green taro, thus affecting the quality of bulbs and the taste of eating (Wang et al., 2001). If no freezing damage is observed after emergence, early sowing is conducive to the devel-opment of taro root. The plant height of taro increases, the number of taro and taro in-creases, and the yield increases, but these changes only slightly affect the number of taro and the shape index of taro. If the planting is late, the life cycle of the taro will be shortened, which is not conducive to the growth and development of the bulb. This condition will lead to insufficient bulb expansion, thereby reducing the yield (Zheng, 2008). Nitrogen and potassium fertilizers have obvious effects on the yield and quality of taro, and potassium fertilizer has a greater effect than nitrogen fertilizer. A significant interaction effect was observed among nitrogen, potassium, and phosphorus fertilizer. Within the reasonable range of potassium and nitrogen fertilizer application, the yield gradually increases with the increase of the amount of fertilizer. Excessive fertilizer application will reduce the yield. Phosphate fertilizer alone only slightly affects the development of taro bulbs, and no obvious rule has been established. Reasonable fertilization is beneficial to the growth, development, and yield increase of taro bulbs (Song et al., 2004).

Regulation of hormones on bulb development

Regulation of endogenous hormones on bulb expansion and starch enrichment

Hormones is an important endogenous substance that regulates plant growth and is a key factor in bulb formation (Durbak et al., 2012). Some genes and proteins related to bulb formation are also closely related to plant hormone signaling pathways (Aksenova et al., 2012). Different plant hormones have different functions in bulb expansion, and gibberellin (GA) can inhibit or delay tuber formation (Vreugdenhil et al., 1989). Abscisic acid (ABA) does not participate in the induced metamorphosis process of tubers, but it counteracts the antagonism of other hormones (Shu et al., 2017). Auxin (IAA) can promote the metamorphic development of tubers and promote plant root development, and its concentration affects tuberous root thickening (Wang et al., 2006). Although GA and ABA are not directly related to tuber formation, they are related to the ratio of GA3/ABA. The balance of "inducing substances" and "inhibiting substances" is a key factor for tuber formation (Liu, 2001). Cytokinins (CTK) are mainly in-volved in the formation of tubers. Matsuo and Mitsuzono (1988) reported that the content of zeatin riboside (ZR) is significantly positively correlated with the formation and thickening of sweet potato tubers (Matsuo et al., 1988). The overexpression of CTK synthesis gene ipt in potato could form more tubers (Tao et al., 2010). IAA-related genes such as ARFs and Aux/IAAs are specifically expressed in early tuber development (Kloosterman et al., 2008). IAA and GA3 are necessary for potato stolon elongation. ABA and jasmonic acid (JA) are positive regulators for inducing tuber formation. GA3 is a negative regulator (Liu et al., 2019). JA and methyl jasmonate (MeJA), as classes of plant growth regulators, play an important role in tuber and bulb formation (Sarkar et al., 2006).

Plant endogenous hormone regulation is closely related to starch anabolism (Kim et al., 2005). The enlargement of plant bulbs mainly depends on starch accumulation and cell divi-sion enlargement, and starch accumulation mainly depends on sucrose synthesis and transportation. Plant hormone signal transduction affects starch accumulation. ABA can induce the expression of starch synthesis genes and enhance the transduction of sugar signals to promote starch accumulation (Akihiro et al., 2005). The level of GA at the grain filling stage of wheat is positively correlated with the final grain yield and starch yield. GA plays an important role in starch accumulation in wheat grains. Changes in endogenous hormone levels may indirectly affect starch accumulation in grains by affecting regulatory enzymes and regulatory processes (Xie et al., 2003). Scientists added IAA to MS medium, and the potato tuber starch content and starch granule size increased by 15%–30% (Gukasyan et al., 2005). In the study of tulip bulbs, IAA and ZR indirectly promoted starch accumulation by increasing the activity of ADP-glucose pyrophosphorylase (AGPase), thus catalyzing the production of a large number of products. Endogenous hormones may promote starch accumulation by participating in the starch synthesis pathway (Miao et al., 2016). Hormones have multiple roles and interact to form a regulatory network, thereby regulating tuber development (Jung et al., 2013). In the early stage of development, the content of endogenous hormones ABA, Z, and ZR showed an upward trend, while the content of IAA, GA3, and JA showed a downward trend. In the later stage of development, the content of endogenous hormones ABA, IAA, Z, and GA3 showed an upward trend. The content of ZR and JA showed a downward trend, but the contents of IAA, GA3, and JA hormones were generally high during the whole development process (Sheng, 2021). Other related studies on endogenous hormones on the growth and development of taro bulbs and starch enrichment have not been conducted.

Regulation of growth, development, and starch enrichment of bulbs by exogenous hormones

The effect of exogenous hormones on the rhizome expansion of potato, sweet potato, and other potato crops has been studied. Yang (2005) used four auxins to spray potatoes (Yang, 2005). The results showed that the four auxins increased plant height and stem diameter and prolonged the photosynthetic accumulation in the later stage. This condition allowed the tubers to accumulate more organic matter during the expansion stage, thereby substantially increasing the yield. The exogenous application of IAA can promote the formation of potato stolons and the development of tubers. It is achieved by accelerating starch accumulation and starch granule enlargement, which are beneficial to the formation and development of tubers (Gukasyan et al., 2005; Roumeliotis et al., 2012). GA also promotes the oc-currence of stolons. In the present experiment, stolons appeared on the second day after the medium containing GA3 and IAA was added, and the occurrence continued throughout the tuber setting period (Lian et al., 2002). However, the addition of GA alone could in-hibit or delay the formation of potato tubers, and inactivation of the active GA gene could promote potato tuber formation (Xu et al., 1998; Roumeliotis et al., 2012). Treatment with exogenous GAs inhibited SS and SSS activity, thus decreasing the sucrose and starch contents in tubers (Vreugdenhil et al., 1999). ABA is a promoting factor for the formation of potato tubers, and timely spraying is beneficial to potato formation (Krauss et al., 1982; Garcia et al., 2014). Varying results have been obtained about the role of ABA in the development of tuber plants. GA3 inhibits the formation of potatoes in vitro, while ABA promotes its tuber formation (Hu et al., 2017). Exogenously applied ABA can promote tuber expansion (Xu et al., 2022). However, in vitro, ABA cannot make stolons metamorphose into tubers smoothly (Yang, 2005). ABA does not participate in the induced metamorphosis process of tubers, but its presence counteracts the respective physiological ac-tivities of other hormones (Xu et al., 2022). CTK can promote potato tuber development, regulate the balance between source and sink, and participate in the transport of nutrients to storage organs (Roitsch et al., 2000). When a certain concentration of CTK is applied exogenously, the biomass of tubers remarkably increases, and the transformation of stolons to tubers is accelerated (Romanov, 2009). In vitro, CTK inhibits sucrose invertase activity but activates phosphorylase and AGPase, thereby promoting starch accumulation (Zhu et al., 2016). Therefore, CTK is an important factor in inducing tuber formation (Quan et al., 2002). The exogenous application of JA and its derivatives can induce the swelling of the stolon top, and the content of endogenous JA increases during this process (Abdala et al., 2002). After exogenous JA treatment, the in-tracellular sucrose accumulates, thus increasing the osmotic pressure of the cell wall, changing the structure of the cell wall, and increasing the cell ductility. More polysaccharides such as cellulose, hemicellulose, and pectin accumulate, indicating that JA controls the expansion of the cell by regulating the synthesis of intracellular sugar (Takahashi et al., 1995). This phenomenon induces the formation of the apical meristem of potato stolon and promotes tuber development (Cenzano et al., 2003).

The development of taro bulbs is remarkably affected by exogenous hormones. The diameter of taro bulbs that were irrigated with auxin increased significantly, the weight increased, and the filling degree of amyloplasts in parenchyma cells increased. Low concentration of 6-BA can promote the development of bulbs, but it is not conducive to the enrichment of amyloplasts, and high concentrations of 6-BA have a certain inhibitory effect on the development of bulbs. GA3 promotes the elongation of the petioles of taro plants, but it does not promote the expansion of the bulbs. High concentrations of GA3 (100–200 mg/L) have an inhibitory effect on the development of taro bulbs, but it promotes the development of taro and increases the number of taro (Sheng, 2021). Limited studies have focused on the effects of exogenous hormones on the development of taro bulbs and their enrichment of amyloplasts, and further research is need-ed.

Role of key enzyme genes in starch synthesis in starch enrich-ment

In crops mainly harvesting underground storage organs, the synthesis and accumulation of starch is a complex physiological and biochemical process, which is the result of the synergistic interaction of multiple enzymes. The key enzymes of starch synthesis in root crops, such as potato and lotus root, have been widely studied. The changes in AGPase and soluble starch synthase (SSS) activities have important effects on starch synthesis in potato tubers (Tang, 2015). However, SS and AGPase can remarkably promote the synthesis of starch in the process of lotus root rhizome expansion, and their activities affect the starch content of lotus root rhizomes at the mature stage (Li et al., 2006). Based on the study of substance accumulation and changes in related enzyme activities during the development of yam, sucrose phosphate synthase activity plays a key regulatory role in the development of yam tubers and is closely related to the main functional substances (Liang et al., 2011). Based on the study of taro bulbs, AGPase activity is positively correlated with total starch content (Zang et al., 2016). With the gradual deepening of the re-search on starch metabolism pathways, people have new understanding of the key enzyme gene sequences and related expression regulators in the pathway.

In sweet potato, the key enzyme genes of starch synthesis such as AGPase and SS have been cloned into the gene sequence. The expression and regulation of these genes have been studied, and these key enzyme genes play a key role in the sweet potato starch metabolism pathway (Tang et al., 2011). The genes controlling sweet potato starch synthesis include granule bound starch synthase (GBSS) gene I, SSS genes I and II, starch branching enzyme (SBE) genes I and II, starch de-branching enzyme (DBE) gene, AGPase gene A/B/C, sucrose synthase (SS) genes I and II, and isoamylase (ISA) gene (Kim et al., 2009).

GBSS I is a key enzyme that controls starch synthesis, and it catalyzes the synthe-sis of amylose. Otani et al. (2007) interfered with the expression of GBSS I by RNAi technology to make sweet potato taste more glutinous. SSSII can affect the structure of amylopectin and reduce the gelatinization temperature of starch (Otani et al., 2007). The reduction of starch gelatinization temperature is conducive to simplifying the starch hydrolysis process and reducing the production cost of starch fermentation (Takahata et al., 2010). AGPase im-proves the starch content of potato tubers (Song et al., 2005). However, the synergistic expression of starch synthesis-related genes under exogenous sucrose treatment promotes the con-version of sucrose to starch (Ahn et al., 2010). Peak synthase has been widely studied, but no direct research has been conducted on taro starch synthase.

Conclusions and future direction

The development of taro bulbs is a complex biochemical process, including the accumulation of morphogenesis and assimilation products, involving gene expression, material metabolism, nutrient input, and the effect of external environmental conditions (Figure 6). Limited studies have been conducted locally and abroad. Under-standing the development process, expansion mechanism, and regulation mechanism of taro bulbs has a guiding role in the production of taro and is important to ensuring food security and responding to food crises. At present, the research on the development of taro mainly focuses on evolutionary classification, genotype and isozyme analysis, cultivation, production, processing, and utilization. Limited research has been conducted on the physiological mechanism and hormone regulation pathway of taro growth and development, taro bulb expansion, key gene expression, and starch enrichment. Therefore, the following research will become the key research direction in the future.

Expansion of taro bulbs and the regularity of the development and spatial distribution of starch bodies

Starch is the main storage material of taro bulbs, and amyloplasts are the orga-nelles that synthesize and accumulate starch. The development of amyloplasts deter-mines the yield and quality of taro. Limited studies locally and abroad have focused on the development of taro corm and amyloplast, and they remain in the preliminary stage. The fine structure observation of amyloplast development, its proliferation mode, and the spatial distribution characteristics of taro corm amyloplast are not clear. In the future, the occurrence, division, proliferation, and enrichment of amyloplasts in parenchyma cells of different types of taro bulbs, the differences of physical and chemical properties of taro starch at different development stages, and the develop-ment and enrichment characteristics of amyloplasts in different spatial parts should be focused on.

Role of key enzyme genes in starch synthesis in starch enrichment

Starch is the main storage material of taro bulbs. The expansion process of taro is closely related to the synthesis of starch, and the genes related to starch synthesis are closely related to starch synthesis, which directly determine the starch content of taro. The research on starch synthase gene has remarkably progressed in wheat, rice, potato and other crops, but limited research has been conducted on taro starch synthase gene. Therefore, the differences in the expression of key enzyme genes (e.g., AGPase, GBSS, SSS, and SBE) for taro starch synthesis, the roles of these genes in regulating the starch enrichment process, and the exploration of individual gene functions will become the focus of research.

Regulation of hormones on bulb swelling and starch enrichment

The expansion of taro bulbs mainly depends on the increase in the number and volume of parenchyma cells, and this process results from the synergistic action of various hormones, especially IAA, GA, CTK, and other hormones The changes of hormones during bulb development, the relationship between hormones and bulb expansion, and the relationship between the expression of hormone synthesis genes and signal transduction-related genes and taro starch enrichment need to be investigated.

Hormone-regulated pathways promoting bulb expansion and starch enrichment

Exogenous hormones and plant growth regulators have important regulatory effects on taro bulb swelling, starch enrichment, and yield increase. The effects of exogenous substances such as 6-BA, 2,4-D, GA3, PP333, and 5-aminolevulinic acid (5-ALA) on the development, yield, and quality of taro corn, as well as the type and concentration of the best exogenous hormone to promote corm expansion and starch enrichment need to be studied, and plant growth regulators for increased yield and improved quality of taro should be developed to provide an important theoretical basis for taro production.

In a word, the development of taro bulbs still requires a lot of research. With the deepening of research and the solution of key problems, the production of taro will continue to improve, and the development and utilization of taro will be more efficient.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

E.J.Z., F.X. and W.Y.S. conceived the outline of the manuscript.
E.J.Z. and F.X. wrote the manuscript.
W.Y.S., W.J.J., W.L.L., X.R.Y., X.P.W. provided revisions.
All authors read and approved the final manuscript.

Data Avail

The following information was supplied regarding data availability:
There is no raw data or code in this literature review.

Ability Statement

All data were collected from the published research papers.

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Figure 1

Macrostructure and microstructure of taro

(A) plant; (B) leaf; (C) Leaf microstructure; (D) bulb; (E) Amyloid microstructure; (F) Amyloid ultrastructure; (AC) air cavity; (CT) spongy tissue; (PT) palisade cell; (VB) vascular bundle

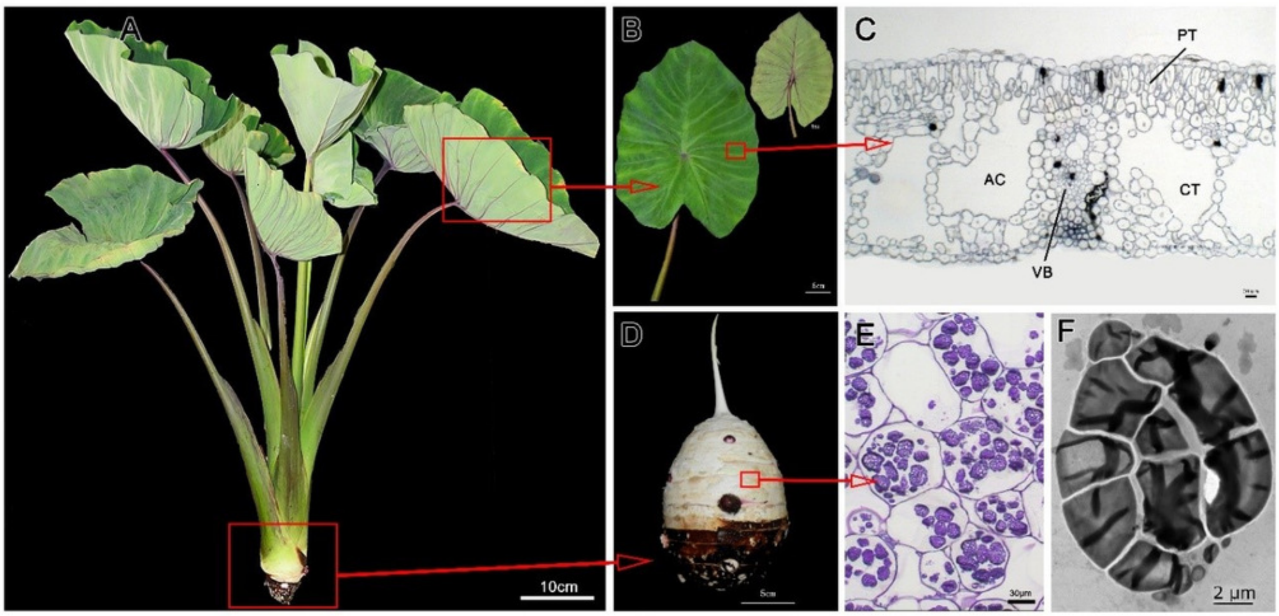

Figure 2

Three classifications of taros in agricultural production of China

(A) Kui taro; (B) Multi-cormels taro; (C) Multi-head taro.

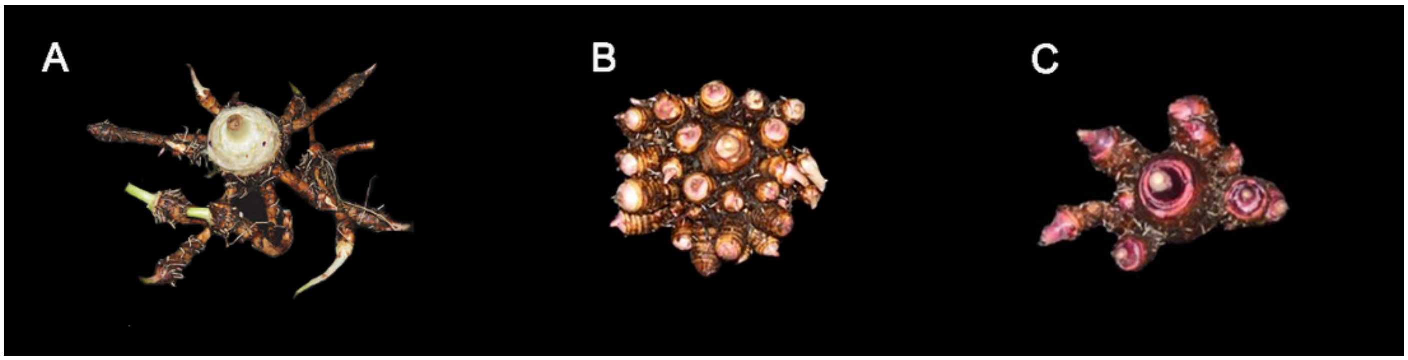

Figure 3

The taro bulb’s mother taro, sub taro and grandson taro.

(A) Multi-head taro; (B) Multi-cormels taro.

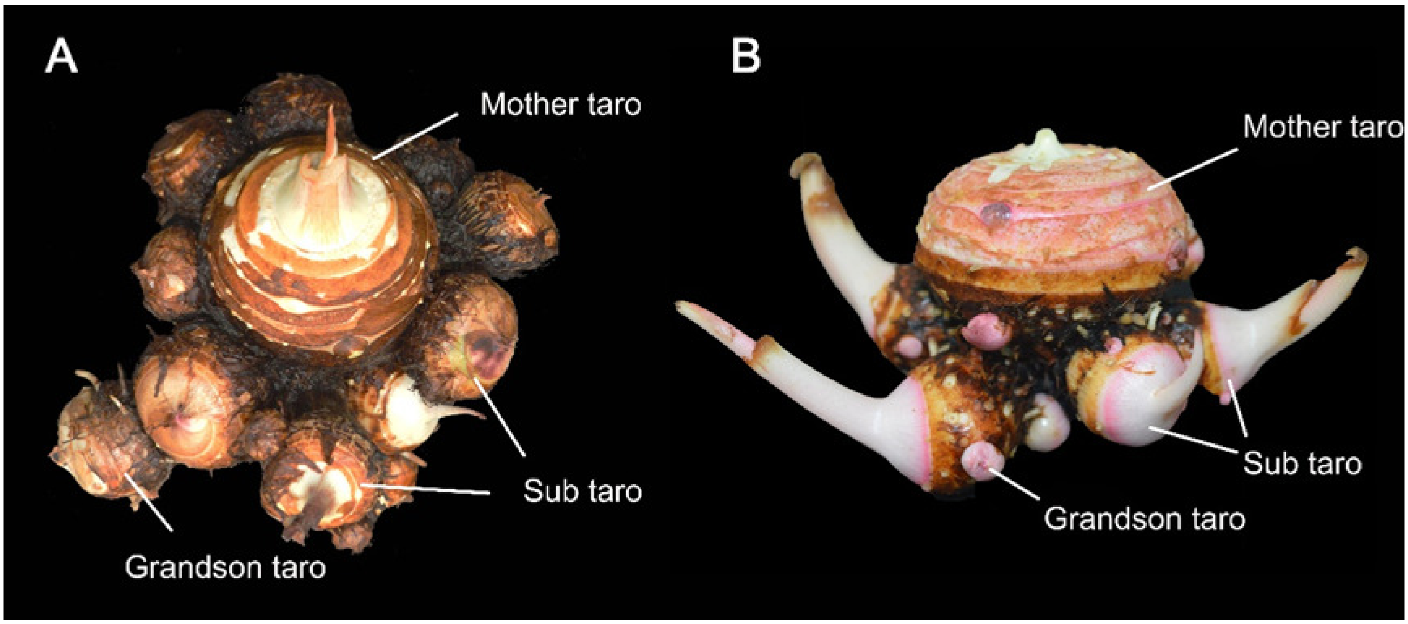

Figure 4

The development process of amyloplasts in the parenchyma cells of Kui taro bulbs

(A,E) Bulb diameter 1 cm; (B,F) Bulb diameter 5 cm; (C,G) Bulb diameter 9 cm; (D,H) Bulb diameter 13 cm; (Am) amyloid; (Cy) cytoplasm.

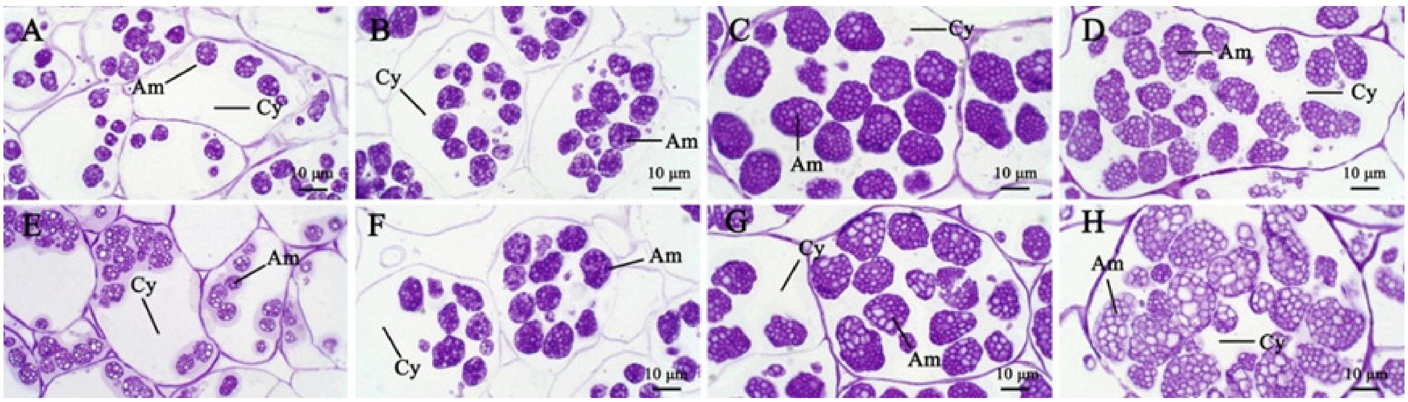

Figure 5

Transmission electron microscope pictures of starch grains of Kui taro bulbs

(A) Bulb diameter 1 cm; The proliferation of amyloplasts, the red box shows the small starch granules after the overflow and shrinkage, and the shape has changed from irregular to spherical. (B) Bulb di-ameter 5 cm; The arrangement of small starch granules in large starch bodies, red asterisks represent large starch granules, blue asterisks represent small starch granules, two types of starch granules are distributed on both sides of starch bodies.

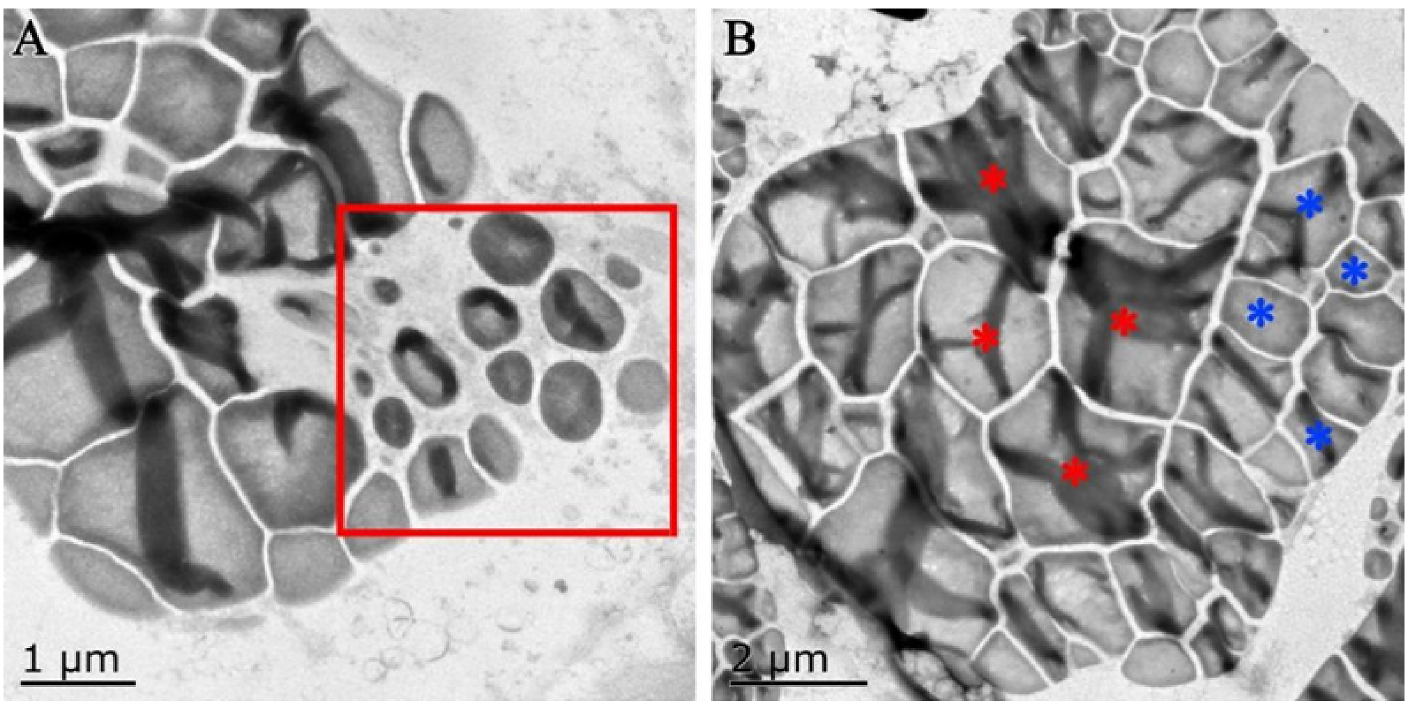

Figure 6

Effects of external environmental factors and internal factors on taro bulb swelling and starch enrichment.