

Regulatory Networks in Potato Tuber Development

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Abstract Potato (*Solanum tuberosum*) is one of the most important food crops in the world, and the formation and development of its tubers are key processes regulated by complex genetic, hormonal, and environmental factors. This study systematically analyzed the network regulating potato tuber development, focusing on genetic regulation, hormone control, environmental impact, and dormancy regulation. The study analyzed in detail the roles of key genetic factors such as transcription factors and epigenetic modifications in tuber initiation and growth, and explored the interactions between auxin, gibberellin, cytokinin, and abscisic acid on tuber maturation and dormancy. In addition, this article also discusses the latest advances in omics technology and CRISPR gene editing, which provide new possibilities for improving tuber yield and stress resistance. The review also pointed out the knowledge gaps in the current regulatory network and the future research directions, especially the opportunities in developing stress resistant potato varieties through targeted breeding and biotechnology methods. This study emphasizes the combination of genetic, hormonal, and environmental factors to promote sustainable potato cultivation in the context of global climate change.

Keywords Potato tuber development; Genetic regulation; Hormonal signaling; CRISPR gene editing; Stress resistance

1 Introduction

When it comes to potatoes (*Solanum tuberosum*), it feeds a lot of people, and hundreds of millions of people around the world rely on it to fill their stomachs. But you may not know that its tubers buried in the soil are not simple. In addition to starch, they also contain a lot of protein and vitamins. In fact, the growth of tubers depends on luck—genes are certainly important, but external factors such as light and temperature also tend to interfere. When it comes to tuber formation, how did the creeping stems that were originally crawling underground suddenly swell into tubers? Here, hormones such as gibberellin and cytokinin are playing tricks (Kondhare et al., 2020), but scientists are still figuring out how they actually work. Sometimes, even though the conditions are the same, some plants refuse to grow tubers properly. Do you think it's frustrating? These hormone signals are like conductors, controlling when the tubers grow, when they stop, and even when they go to sleep, the whole process is like a roller coaster going up and down.

Studying how potato tubers grow is actually quite a hassle. Scientists have discovered that when the temperature changes or the duration of light is altered, this thing starts to throw tantrums—sometimes it grows wildly, and sometimes it just won't move. Hormones are randomly mixed in, such as growth hormone, transcription factors like StSP6A, all mixed in. Especially during short-day periods, StSP6A acts like a switch, activated at will (Deng et al., 2021). However, to be honest, even if these molecular signals are clarified, the actual operation is still troublesome. After all, plants are not machines; how can they be adjusted at will? Nowadays, with technologies like transcriptomics and proteomics, it is possible to map out these chaotic regulatory networks. However, while mapping is one thing, if you really want the tubers to obediently grow longer and get sick less often, it still depends on luck.

The question of how potato tubers grow is actually quite complicated—genes, hormones, and weather are all mixed up in it. There are many people studying this now, but to be honest, many details are still unclear. For example, those plant hormones can cause the tubers to grow wildly at times, then let them rest, and with transcriptional regulation mixed in, the entire signaling pathway becomes chaotic like a ball of yarn. However, recently CRISPR gene editing technology has been quite popular, maybe it can be used to make potatoes produce more tubers or

make them less afraid of drought and insects. But the problem is, climate change is becoming increasingly sinister. Today is hot and sunny, but who knows if these technologies are reliable? So, current research not only focuses on molecular mechanisms, but also on how to make potatoes survive well in extreme weather conditions. There are still many unanswered questions in this regard, such as how certain hormones work or why tubers suddenly collapse when the temperature changes-all of which need to be further explored.

2 Genetic Regulation in Tuber Initiation

2.1 Transcription factors governing tuber formation

It's not that simple to say how potato tubers start to grow. Do you think gene is the the final say? Actually, it depends on whether the environment gives face or not-external factors such as lighting and temperature often come in handy. The key is that some specific transcription factors are pounding there, transmitting signals to the cells, allowing the creeping stem to slowly expand into a tuber. But it's interesting that sometimes even when the conditions are right, some plants just don't grow tubers. Do you think it's strange? This also involves how genes are activated, how cells divide and differentiate, and even how starch accumulates. What's more, these processes are also affected by epigenetic regulation, which means that although the gene is there, whether it can work depends on the mood (post transcriptional regulation also plays a role). So, don't think it's just a matter of growing tubers, it's actually a bunch of signals fighting and finally reaching a consensus to start developing.

If we talk about what controls potatoes to start growing tubers, there are actually several transcription factors working on it. For example, StBEL5 is quite interesting because it doesn't just stay in one place-it can run from leaves to creeping stems and become active especially when the days get shorter (Hannapel and Banerjee, 2017). However, it alone is not enough. We need to work together with the StCDF1 gene to raise the level of StSP6A, so that the tubers will emerge. But things are not that simple, there is also someone called StbHLH93 involved, specializing in the conversion of starch bodies. If we knock it out, the trouble would be big-the number of tubers is not only pitifully small, but their size will also shrink significantly (Yang et al., 2023). It's not surprising that they are all regulatory factors, some are responsible for initiating, while others specialize in starch accumulation. Their cooperation is quite seamless.

It is interesting that the StCDF1 factor is particularly active during short daylight hours, but its way of working is quite convoluted-it needs to be held down first so that StSP6A can work freely (Kondhare et al., 2019). When it comes to StSP6A, it is the "switch" that directly generates tubers. However, the matter of tubers is not over yet. Whether to sleep soundly or continue growing after they grow depends on StTCP15's expression. This transcription factor is particularly adept at balancing and regulating the hormones abscisic acid and gibberellin in a harmonious manner (Wang et al., 2022). You see, from the beginning of growth to dormancy and then to germination, there are different regulatory factors competing at each stage. No wonder the development of potato tubers is always unpredictable.

2.2 Epigenetic modifications

When it comes to how tubers start to grow, just looking at genes is not enough. Those invisible epigenetic modifications are actually playing a lot of tricks behind the scenes. DNA methylation, histone modification, these fancy modification methods can all cause gene expression to change constantly. Interestingly, there is a histone modification protein called StMSI1 that is particularly meddlesome. It moves around with the Polycomb inhibitory complex, controlling the key genes for the development of above-ground and underground tubers tightly (Kondhare et al., 2021). However, this matter is rather mysterious. The same gene may behave completely differently in different plants. It's probably these epigenetic modifications at play.

When it comes to tuber development, there is an interesting discovery-small things called phasiRNAs are also secretly manipulating the entire process. Don't be fooled by their small size, they have great abilities and are specifically responsible for silencing certain genes, especially those related to hormone signaling and stress response. For example, there is a phasiRNA called siRD29 (-) that specifically targets the GIBBERELLIN 3-OXIDASE 3 gene and tightly controls the synthesis of gibberellin (Malankar et al., 2023). This explains why sometimes even though genes are there, they just don't work. So, whether the tubers can grow smoothly depends

not only on the genes themselves, but also on the expression of these small RNAs. They are like the "tuner" of gene expression, silently adjusting every step behind the scenes.

It's not easy to make potato tubers grow well. It depends on whether transcriptional regulation and epigenetics can work together well. They are like a pair of bickering lovers who can only reach an agreement under suitable environmental conditions-when the temperature is right and the light is sufficient, the tubers can develop normally. However, this incident has served as a reminder to scientists: since these regulatory mechanisms are so important, could they be manipulated and artificially intervened through gene editing or other biotechnologies? Perhaps a new way to increase production can really be found. Of course, in practice, it might not be that simple. After all, the balance within a plant is not something that can be changed at will.

3 Hormonal Control in Tuber Growth and Maturation

3.1 Auxins and gibberellins

When it comes to the initial growth of tubers, auxin and gibberellin have caused a lot of trouble. Especially the auxin called IAA, which is always busy promoting cell elongation and division, is just like a contractor keeping an eye on the expansion of the tubers. Some people tried stuffing a few more auxin synthesis genes like *tms1* into genetically modified potatoes, and as a result, the yield actually increased (Kolachevskaya et al., 2017). However, this matter is not that simple-although gibberellin usually works separately from growth hormone, sometimes it can also get involved and cause trouble. What's more troublesome is that as soon as you move a finger with auxin, hormones like cytokinin and gibberellin immediately follow suit, causing the entire hormone network to become a complete mess. So, if you want the tubers to grow well, just focusing on one hormone won't do. You have to take good care of the whole family.

Gibberellin always tends to sing the opposite tune during tuber formation-the more active it is, the more vigorous the creeping stem grows, but it actually delays the tuber. Interestingly, as long as the activity of gibberellin is suppressed, the tuber yield immediately increases. For example, the enzyme *StGA3ox3* is specifically responsible for gibberellin synthesis. Inhibiting it can actually make the tubers grow more vigorously (Malankar et al., 2023). But the matter is not over yet. When the tubers start to grow, auxin and gibberellin still have to deal with other hormones, maintaining a delicate balance between them. If any hormone suddenly gets angry, the tubers will either not grow well or the yield will drop directly. At the end of the day, these hormones are like an orchestra, each one needs to work together well for the tubers to grow bigger and more.

3.2 Cross-talk between cytokinins and ABA

3.2.1 Cytokinin-driven cell proliferation

Cytokinin is quite an interesting thing. It acts like a midwife and is particularly active when the tubers just start to grow. Its main task is to make the meristem cells in the stolons divide vigorously and expand the tubers. However, there should be a limit to this matter. If there is too much cytokinin, the tubers will not grow well and the maturity period will be delayed (Zhang et al., 2023). From the perspective of transcriptome data, when tubers first start to grow and develop, the synthesis of cytokinin is indeed particularly active, and those genes responsible for cell division are also all busy. So, if you want the tubers to grow well, the amount of these hormones must be just right. Too much or too little won't do.

When it comes to how tubers grow, cytokinin and auxin are inseparable partners. Interestingly, the two of them work together in perfect harmony-cytokinins act like couriers, specifically responsible for transporting auxin back and forth, while auxin is responsible for making decisions on when to let cells divide (Kolachevskaya et al., 2021). However, this partner also has a strange temper. If one of them suddenly becomes too active or too negative, the tubers will grow crooked. For example, if cytokinins are too active, auxin may not keep up with the rhythm, resulting in tubers growing in strange shapes. So, these two hormones need to maintain a delicate balance, just like dancing, if one step is too fast or too slow, the whole dance cannot be performed.

3.2.2 ABA's function in maintaining dormancy

When it comes to the dormancy of potato tubers, ABA and cytokinins are like playing on a seesaw-when ABA dominates, the tubers obediently sleep; When cytokinins become dominant, the tubers begin to stir (Jiang and Xu,

2024). It's interesting that ABA is particularly cautious. As soon as the tubers mature, they frantically brush their presence and turn off all the genes that may cause the tubers to sprout. But when the environmental conditions are suitable, ABA will tactfully withdraw, and then cytokinins dare to emerge, urging the tubers to sprout and grow quickly. These two hormones work together seamlessly, as if discussed: ABA is responsible for 'don't move now', and cytokinin is responsible for 'move now'. If it weren't for them singing like this, the tubers would either oversleep or wake up too early, and it would be a mess.

3.3 Ethylene and maturation processes

3.3.1 Ethylene's role in tuber dormancy

Ethylene and ABA, this pair of enemies who manage the tubers while sleeping, are quite interesting. ABA is like a strict gatekeeper, guarding against the early awakening of tubers; Ethylene is like a troublemaker, always wanting to secretly wake up the tubers (although it depends on the weather). When the temperature and humidity change, ethylene's temper also changes-sometimes it helps ABA make the tubers sleep longer, and sometimes it urgently shakes the tubers awake. The most amazing thing is that these two are clearly competing with each other, yet they have to work together. Ethylene is like a fickle judge, its words are much more effective than ABA when it comes to whether tubers should sleep or wake up, but the specific judgment depends entirely on the environmental conditions at that time. So, ABA really doesn't decide when the tuber will sprout. It depends on which side of the "wall grass" ethylene will fall.

3.3.2 Regulation of tuber maturation

Speaking of the final sprint stage of tuber maturity, ethylene, the "versatile", has once again begun to work hard. It not only cares about sprouting, but also has to worry about how starch is stored, how tissues develop, and other miscellaneous tasks. Interestingly, just before the tubers enter dormancy, the ethylene content suddenly increases, acting as a supervisor to urge various storage proteins and starch metabolism enzymes to work quickly (Saidi and Hajibarat, 2021). However, it is not fighting alone-ABA is responsible for controlling the timing of dormancy, cytokinins monitor growth progress, and ethylene mainly manages logistics reserves. These three people gathered together like a construction team: ethylene was busy stocking up in the "warehouse", ABA was holding a watch to see when "work" would end, and cytokinins were always ready for the next "start". The most amazing thing is their coordinated rhythm. It doesn't matter whether it's a little more or less, they have to hold on a bit to make the tubers grow full and durable.

4 Environmental and Nutritional Influences on Tuberization

4.1 Environmental factors affecting tuber development

If the weather is too hot or too cold, the potato tubers will suffer. Especially in hot weather, the good substances in the tubers-such as carotenoids and anthocyanins-will decrease, and instead more potentially harmful steroidal glycoalkaloids will emerge (Fogelman et al., 2019). This is quite infuriating. The high temperature is like an unruly butler, messing up the nutrient synthesis route of the tubers. Too strong or too weak light is also a problem, which can disrupt the normal development rhythm of the tubers. The most fatal thing is that once these environmental factors cause trouble, the key biosynthetic pathways in the tubers will also go on strike, and the nutritional value of the tubers that eventually grow out will be greatly reduced. So, when it comes to growing potatoes, the most dreaded thing is encountering extreme weather. If the temperature is just a little off, the quality of the tubers will be affected.

The potato is extremely sensitive to light, just like a living light timer. When the days get shorter, it quickly initiates the tuber formation program as if receiving an alarm clock reminder (Kondhare et al., 2021). But if the day is too long, it will pretend not to hear and refuse to grow tubers no matter what. Interestingly, exposure to UV-B radiation is quite effective-it doesn't have to be too strong. With just a moderate amount of exposure, the starch and protein in the tubers will increase, and even the good stuff like anthocyanins will rise (Qi et al., 2020). However, this matter requires proper moderation. A large dose of UV-B can actually be counterproductive. So, growing potatoes is quite particular. The duration of light exposure should be short and the amount of ultraviolet rays should be moderate. Only in this way can the tubers that grow be both nutritious and healthy.

Planting potatoes, soil moisture is a technical task. Drip irrigation, a sophisticated watering method, is particularly effective-it can keep the soil at the right moisture level and prevent nutrient loss (Wichrowska et al., 2021). It's interesting that this not only increases the yield of tubers, but also improves their quality. Starch is fuller, protein is richer, and even antioxidants, which are good things, have increased. However, on the other hand, soil that is too dry or too wet is not acceptable. We need to balance it like taking care of a baby. So, to grow good potatoes, having good varieties alone is not enough. We also need to put effort into soil moisture management, creating a comfortable environment that is neither dry nor wet, so that the tubers can grow big and well.

4.2 Nutritional transport and metabolism

Nitrogen and phosphorus fertilizers are like side dishes to potatoes-too little is not good, but too much is bad. Especially nitrogen fertilizer, when used correctly, can increase the yield of tubers rapidly (Nurmanov et al., 2019). But if you apply too much by hand, trouble will come: the plants will focus on growing taller, while the tubers will be delayed. This is like feeding a child. The nutrition must be balanced-the nitrate nitrogen in the soil should be kept at just the right level, neither starving the plant nor overeating it. Interestingly, although phosphorus fertilizer is not as eye-catching as nitrogen fertilizer, the tubers still won't grow well without it. So when it comes to fertilizing, one really needs to be meticulous. A little more leads to fertilizer, and a little less leads to lean. Only by finding that golden ratio can one succeed.

Phosphorus is an "energy manager" in tuber development-once it is active, the metabolism within the plant is like being injected with adrenaline, and the number of tubers rises sharply (Darvishi et al., 2015). Interestingly, not only does it do the work by itself, but it also brings in hormone subordinates like ABA and IAA to work together. But the most amazing thing is the "nutritional balance" of the carbon-nitrogen ratio: raising the carbon level (just get more sun exposure), or pushing the nitrogen fertilizer down, the tubers are more active and start to expand earlier (Zheng et al., 2018). This is like playing the game of balance-when there is too much carbon, the plant focuses on growing tubers; when there is too much nitrogen, it is preoccupied with growing leaves. So the veteran farmers have to be able to read this "nutrition scale" to keep the carbon-nitrogen ratio at the most suitable position, so as to prevent the plants from growing wildly and also ensure that the tubers produce more and earlier.

5 Regulatory Pathways Governing Dormancy and Sprouting

5.1 Dormancy-related gene expression

5.1.1 Function of StSP6A in dormancy initiation

This StSP6A gene is quite interesting. It acts like a "switch controller" for the growth of tubers and is related to the FT gene for plant flowering. Under normal short-day conditions, it becomes active to prepare for the formation of tubers (Park et al., 2020). But when the weather gets hot, this creature wilts-high temperatures will make it be held back by various regulatory mechanisms from working, resulting in the tubers not growing when they should and not sleeping when they should. The most infuriating thing is that even if scientists force StSP6A to express more, although the tubers can barely grow under high temperatures, the sugar transport just can't keep up, and the yield still can't increase. This is like a butler with a strange temper: when it's cool, he arranges the tubers clearly, but when it gets hot, he just gives up. No matter how you try to persuade him, it won't work.

5.1.2 Expression patterns of StABI3

The StABI3 gene is like a "sleep switch" for tubers, working in the same pants as ABA. As soon as the ABA content increases, it becomes active and turns off all buttons for cell growth and division (Wang et al., 2020). It's interesting that these two work together very well-StABI3 exerts great force when the tubers are sleeping, and when they are about to sprout, it tactfully reduces its presence. But the most amazing thing about them is their "shift system": when BAs are on night shifts, they call StABI3 to stand guard, and when it's dawn (the end of hibernation), they let it go of work, so that the tubers can wake up on time and continue to grow. This operation is even more accurate than an alarm clock, ensuring that the tubers can sleep when they should and wake up when they should.

5.2 Sprouting regulation networks

5.2.1 Hormonal signals affecting sprouting

StABI3 and ABA work together seamlessly to manage the sleeping of tubers. As soon as ABA increases, StABI3 immediately enters a working state, like a strict conduit, tightly closing the gate of cell growth (Wang et al., 2020). But don't be fooled by its current dominance, when the tubers should wake up, it will slip faster than anyone else. The cooperation between these two is simply amazing-ABA is like a duty manager, calling StABI3, the 'night shift security guard', to work at the right time; Wait for the sleep period to end and let the security guard off work on time. The most wonderful thing is that this mechanism is particularly intelligent, neither making the tuber oversleep nor waking it up early, more reliable than any smart alarm clock. If it weren't for their precise regulation, the tubers would either not wake up or wake up too early, which would make storage very troublesome.

5.2.2 Role of StPIN proteins in hormone transport

StPIN4, the 'transport team leader', is really a key role, as it is specifically responsible for moving auxin around the tubers. Interestingly, its performance also depends on the expression of protein kinases such as StCDPK1- only when they are phosphorylated and activated can they function properly (Santin et al., 2017). This is like a sophisticated logistics system: where and how much growth hormone should be sent depends on StPIN4 scheduling. If this transportation system goes wrong, the trouble will be big-the tubers will either be stuck in bed or grow crooked. Most importantly, this transportation network is also subject to various post transcriptional regulation to ensure that auxin can appear in the correct position at the critical moment of dormancy and germination. So, if you want the tubers to sleep well and wake up cleverly, StPIN4, the 'delivery guy', must not fall off guard.

5.3 Research case: effect of temperature on potato dormancy duration

5.3.1 The impact of environmental variables on dormancy maintenance

In a low-temperature environment (2-4°C), the 'Favorita' potato tubers seem to have been hit by the pause button-the ABA content increases sharply, freezing the cell activities (Di et al., 2019). This is particularly interesting at this time. All the growth-promoting hormones have collectively gone on hold: the DWF1 and BRI1 genes of the BR hormone have wilted, and the synthesis of GA has also been blocked, just like a hibernating little animal. But when the temperature rises above 25°C, the situation is completely reversed: the ABA content drops sharply, and the "alarm hormones" like GA and ethylene start to output like crazy. Even StABI3, the hibernation manager, leaves work early. However, the sprouts produced by high temperatures often lack stamina because the nutrient reserves in the tubers are consumed too quickly, and the new plants that eventually grow are always wilted and droopy. This is just like forcibly pulling a sleeping person up to work. How could the efficiency be high?

5.3.2 Experimental results for the 'favorita' variety

It's quite interesting to conduct experiments with the variety 'Favorita'-the tubers were stored at different temperatures of 2°C, 12°C and 25°C respectively, and the results varied greatly. The coldest group (2°C) was just like being frozen. It didn't sprout for over 120 days. The test found that the ABA hormone was outrageously high, while the GA hormone was pitifully low. However, when the temperature is adjusted to 12°C, it's completely different. The dormancy period is directly cut by one third, and buds start to sprout around 90 days later, with the GA level also rising accordingly. The most exaggerated one was the group at 25°C, where the GA hormone seemed to have been injected with adrenaline. Unfortunately, I didn't remember all the data. These results do confirm the influence of temperature on the sleeping duration of tubers. However, strangely enough, in the same batch of experiments, there were always a few tubers that did not follow the usual pattern, not waking up when they should and just joining in the fun when they shouldn't.

5.3.3 Research case: the influence of temperature on the duration of potato dormancy

As soon as the temperature reaches 25 °C, the 'Favorita' tubers can no longer hold on and quickly sprout after about 30 days (Di et al., 2019). At this moment, ABA seemed to have let out its breath and fell down, while GA

and ethylene came to the rescue, urging the tubers to wake up quickly. However, the buds stimulated by high temperatures always have some innate shortcomings-the tubers are light and floating, and the seedlings grown are also wilted and droopy. In contrast, tubers stored at low temperatures may sleep longer, but when they wake up, they are more energetic. This experiment is quite interesting. The temperature is like an adjustment knob. Turning left will prolong the sleep period and improve the quality, while turning right will result in faster germination but poorer quality. Unfortunately, there is no middle gear that can achieve the best of both worlds.

6 Advances in Omics and Biotechnology Approaches

6.1 Omics-based discoveries in tuber development

6.1.1 Insights from transcriptomics

When it comes to how potatoes cope with drought, transcriptomics can be a great help. Drought resistant experts like Saturna and Alegria quickly activate water regulatory genes when water is scarce (Figure 1) (Sprenger et al., 2016). Sequencing revealed that they are particularly capable of activating "drought resistance specialists" such as PIP and HSPs-PIP is responsible for managing the water in cells, while HSPs act like emergency responders to deal with various stress injuries. However, Milva, a delicate variety, is not good anymore. When encountering drought, all key genes are wilted. Interestingly, the *PYL4* gene is particularly active in the ABA signaling pathway, making it a 'secret weapon' for drought resistance. By comparing these genetic data with field performance, we can understand why some varieties do not survive drought, while others wilt after two droughts. These findings not only explain the differences in drought resistance, but also point out a clear path for breeding experts-specifically targeting these drought resistant genes to improve varieties is definitely correct.

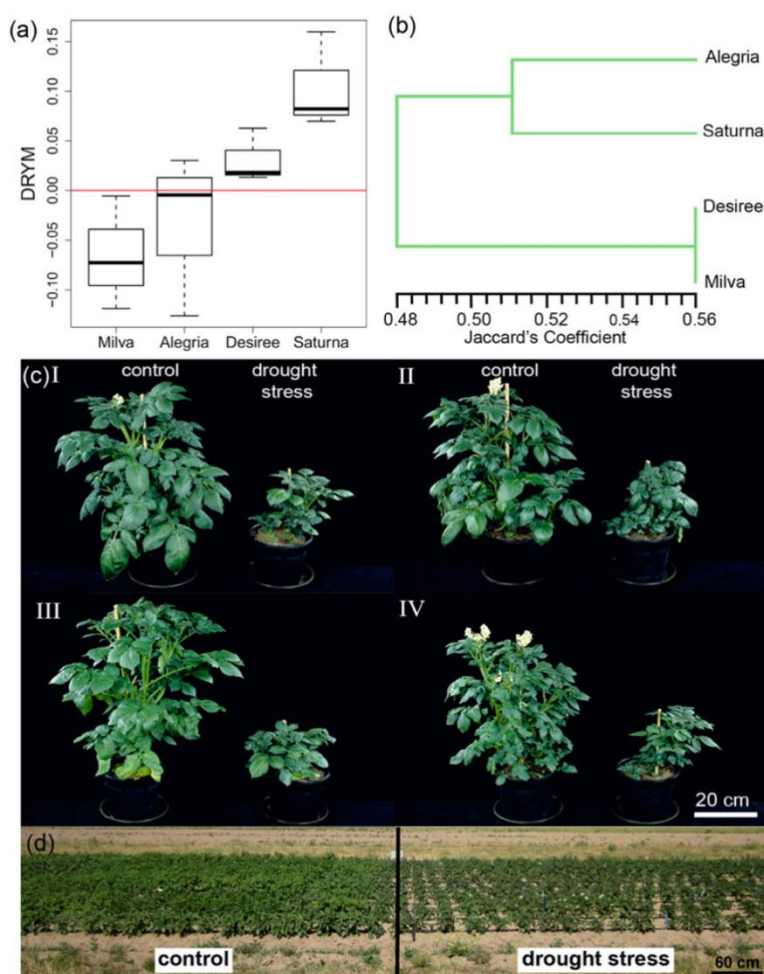


Figure 1 Characterization of the European reference potato cultivars, Milva, Alegria, Desiree and Saturna (*Solanum tuberosum* L.) (Adapted from Sprenger et al., 2016)

6.1.2 Contributions of proteomics

Proteomics is an interesting technique that provides a clear understanding of tuber development. Take starch synthesis as an example, the enzyme called GBSS is particularly critical-it works tirelessly during tuber enlargement, and the more work it does, the more starch it accumulates (Wellpott et al., 2024). However, the most practical thing is to discover those stress resistant proteins, such as antioxidant enzymes and heat shock proteins that work overtime together like a group of firefighters to maintain cell balance when encountering drought. It is interesting that the expression of proteins at different developmental stages is like a magic trick, sometimes involved in starch synthesis and sometimes busy with cell wall construction, with clear division of labor. These findings not only explain how tubers grow, but also provide new ideas for drought resistant breeding-if these stress resistant proteins can be expressed more, perhaps more robust potatoes can be grown.

6.1.3 Metabolomics and nutrient transport

Metabolomics is a very interesting technique that has shaken off the "family background" of tuber development. For example, discovering the two treasures of carbohydrates and amino acids, jumping up and down in the tubers all day long, directly determines whether the tubers that grow in the end are delicious or nutritious (Yang et al., 2019). The most practical thing is to identify the drought resistant "little masters"-proline and soluble sugars, and these two brothers desperately brush their presence during drought. However, what's even more remarkable is that those secondary metabolites, such as flavonoids and phenolic substances, which are not usually noticeable, can help tubers resist bacterial invasion at critical moments. These findings are like a comprehensive examination of the tuber, not only knowing how it grows, but also understanding its "survival strategy" to cope with harsh environments, which is of great help in cultivating better potato varieties.

6.2 Genome editing and CRISPR applications

6.2.1 CRISPR-Cas9 targeting of tuber-related genes

CRISPR, this "gene scissors", has recently done quite a few brilliant jobs on potatoes. Take the fight against late blight as an example. Scientists just cut the StSR4 gene, and the potatoes immediately became much more resilient-in fields prone to diseases, the treated plants managed to withstand the attack of late blight (Han, 2024). Interestingly, this technology can not only treat diseases but also improve quality: By altering the GBSS gene, the quality of starch can be enhanced accordingly (Moon et al., 2022). However, the most surprising thing is that these edited plants perform quite stably in the field, unlike traditional breeding methods which are prone to problems. Of course, there are still many genes whose functions have not been fully understood at present. But judging from the current achievements, CRISPR has indeed opened up a new path for potato breeding.

6.2.2 Gene editing for yield improvement

CRISPR technology has made another big splash recently-by altering the trehalose enzyme gene, potatoes can suddenly "save water". This is quite interesting. The originally ordinary potato, after gene editing, has produced many more tubers than the common variety in arid land (Razzaq et al., 2021). The key point is that these "water-saving" potatoes are particularly good at budgeting. Their water utilization efficiency is ridiculously high, just like installing a smart water meter on the plants. However, the most surprising thing is that not only did they not reduce production under water shortage conditions, but their output also rose sharply. Although the current promotion area is still not large, this technology has indeed brought new hope for growing potatoes in arid regions.

6.3 Research case: CRISPR-enhanced drought-resistant potato varieties

6.3.1 Genetic targets for water efficiency

The trehalose enzyme gene is truly a "treasure target" in potato drought resistance-scientists have developed a new variety that is not afraid of drought by tinkering with CRISPR (Lola et al., 2023). These 'water-saving experts' are particularly meticulous in their calculations, able to lock in water even in dry weather. The most amazing thing is that they can not only carry the load, but also maintain their yield, and even grow half a beat faster than ordinary varieties. However, it is interesting that there are always a few strains in the same batch of

experiments that do not follow the routine, indicating that there may be regulatory mechanisms hidden behind this gene that we have not fully understood. But in any case, the ability to stabilize tuber development and yield under extreme drought conditions is already impressive enough.

6.3.2 Performance in field trials under drought conditions

The drought-resistant potatoes treated with CRISPR in the field experiments were indeed quite remarkable-by modifying the trehalose enzyme gene, they immediately became "water-saving pioneers" (Yang et al., 2019). The data in Figure 2 is particularly interesting. Just as the drought began, "emergency teams" such as Aquaporin PIP and heat shock proteins were working overtime collectively within 1-2 hours, busy maintaining the water balance of cells like rescue teams. When the drought lasted for two hours, the "logistics forces" like glycine-rich proteins took over again. The most amazing thing is that the changes in gene expression are exactly in line with the actual performance: the moisture is locked in, the yield is stable, and even the growth rate does not slow down. However, if you look closely at Figure 2, you will find that the response time differences among different genes are quite interesting. Some are impatient and act as soon as the drought emerges, while others are slow and wait until the drought becomes severe before taking action. These findings not only explain the molecular tricks of drought resistance, but also reveal the potential of CRISPR technology in combating climate change-after all, precisely regulating these "drought-resistant genes" is equivalent to equipping crops with an intelligent water-saving system.

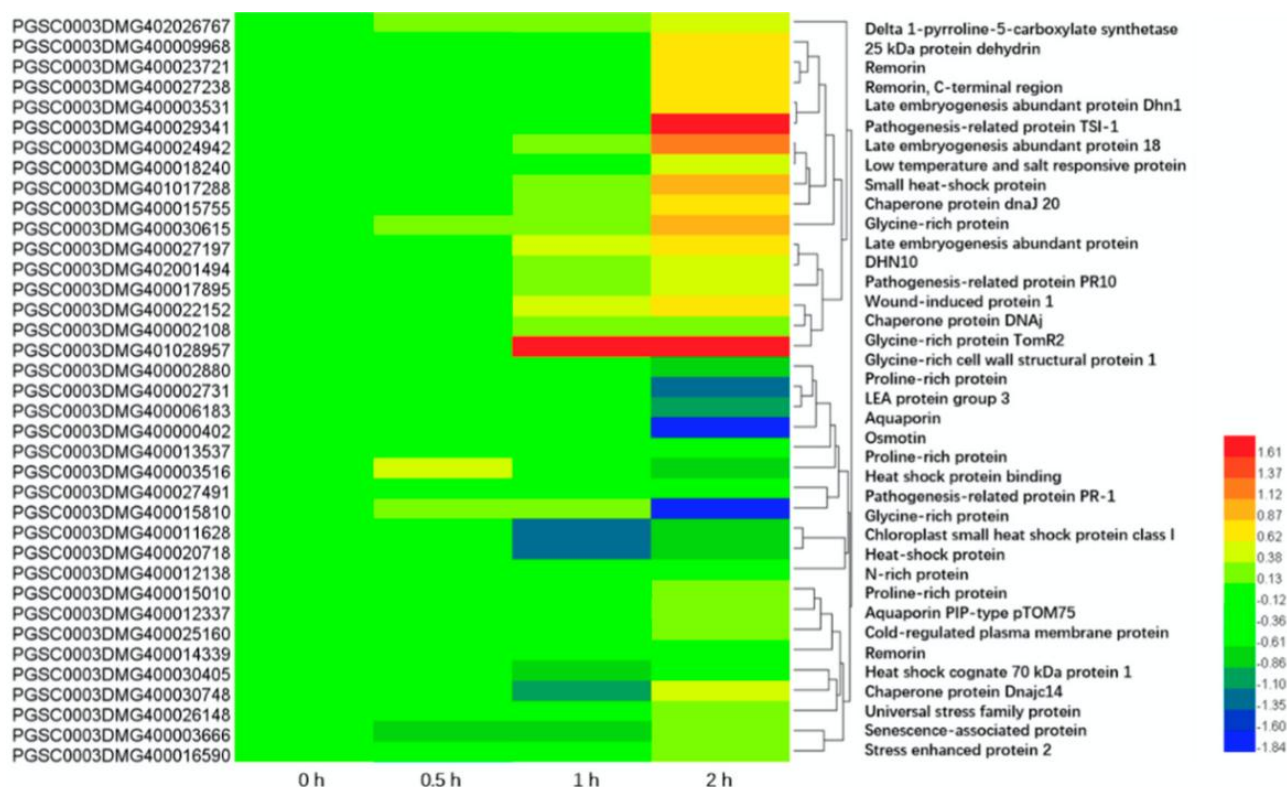


Figure 2 Genes coding for osmotic adjustment proteins differentially expressed under drought stress (Adapted from Yang et al., 2019)

Image caption: Figure 2 presents a heatmap showing the differential expression of genes coding for osmotic adjustment proteins at different time points under drought stress. The heatmap uses a color gradient to represent gene expression levels, with green indicating low expression, yellow indicating moderate expression, red indicating high expression, and blue indicating downregulation. The clustering on the right groups the genes based on the similarity of their expression patterns across the different time points (Adapted from Yang et al., 2019)

7 Challenges and Future Directions

Potato research is currently facing a rather interesting bottleneck-although transcription factors like WRKY and ARF have been identified, how they "cooperate" with other genes remains a mystery. This is just like knowing a

few star players in a team but not understanding the tactical coordination of the entire team (Yang et al., 2019). What is particularly headache-inducing are those "off-site guidance" such as lncRNA and miRNA. Despite their frequent fluctuations in adverse conditions like drought and diseases, it remains unclear exactly how they operate. New technologies such as single-cell RNA sequencing might be of help, just like installing a surveillance camera on each cell to capture real-time images of how genes respond to stress. However, to be fair, the biggest problem now is that these regulatory networks are too troublesome-the same gene can do completely opposite things under different circumstances. No wonder researchers always complain that it's like untangle a tangled mess. If one truly wants to understand the ins and outs, it would probably be necessary to record all the performances of these "acting genius genes" in different adversities.

Climate change has made potato cultivation increasingly difficult to manage, but gene editing, this "molecular scissors", has brought new hope. Take CRISPR for example. Now scientists have been able to precisely prune genes such as WRKY and NAC, enabling potatoes to be both disease-resistant and drought-resistant (Yang et al., 2019). Interestingly, it has recently been discovered that "small" molecules such as miRNA and lncRNA are particularly adept at handling situations-although they do not encode proteins, they interfere in plants' responses to harsh environments. However, in actual operation, it is still troublesome. For instance, the same WRKY gene is responsible for both drought resistance and disease resistance. If it is adjusted too vigorously, it may affect the yield; if it is adjusted insufficiently, it will have no effect. But in any case, these findings at least point to a direction: future breeding should not only focus on protein-coding genes, but also take these regulatory molecules into account. Perhaps one day we will be able to cultivate "super potatoes" that are both water-saving and disease-resistant, and still have high yields even in high temperatures. That would solve a big problem.

Breeding has now come up with a new approach-combining the breeding methods passed down from our ancestors with high-tech technologies such as gene editing, we can actually create "hard core" potatoes that are both drought resistant and salt resistant. However, to be honest, the biggest problem now is that many of the relationships between regulatory genes have not been clarified, just like a puzzle is missing a few key pieces (Yang et al., 2019). It is interesting to note that some inconspicuous small RNAs have recently been found to be particularly problematic during stress resistance, which has reminded breeding experts that focusing solely on large genes is not enough, and these "behind the scenes" must also be taken into account. Although there is still a long way to go before cultivating super varieties that can perfectly adapt to climate change, at least the direction is clear now-as long as the loopholes in these regulatory networks are filled in, allowing crops to achieve high and stable yields even in harsh environments, global food security will be more guaranteed. Ultimately, it requires both technological breakthroughs and respect for the survival wisdom of plants. Only by working hard on both ends can we see the truth.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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