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Origin and Dispersal of Durian Germplasm in Southeast Asia: Gene Flow Between Wild Populations and Cultivated Varieties

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Abstract Durian (*Durio zibethinus*) is a famous tropical fruit and an important economic crop in Southeast Asia. It also has a special place in local culture. Studying the origin and dissemination of durian germplasm is very helpful for its conservation and breeding improvement. This study sorted out the genetic diversity, evolutionary process and species relationship of durian. We focused on the distribution differences between wild durian and cultivated durian, as well as their respective contributions to genetic composition. The study used genomic technology to further illustrate how genes flow between wild durian and cultivated durian, and also evaluated the value of these gene exchanges for breeding. At the same time, it also analyzed how human activities, such as migration and cultivation, affect the spread of durian germplasm. We also used Malaysia, Indonesia and Thailand as examples to study the genetic characteristics of local durian varieties and their wild "relatives". These cases help us understand the genetic structure of durian more clearly. Finally, the study pointed out that it is now necessary to use biotechnology to protect durian germplasm. Combining genetic research and conservation measures will help durian develop longer both commercially and ecologically.

Keywords Durian germplasm; Genetic diversity; Gene flow; Conservation; Southeast Asia

1 Introduction

Durian (*Durio zibethinus* Murr.) is a very representative fruit in Southeast Asia, and its cultivation history is very long. Because of its rich nutrition and special taste, it is often called the "king of fruits". Now, durian is mainly grown in countries such as Thailand, Malaysia and Indonesia. Part of the economy of these countries also depends on the income brought by durian. Durian has a strong taste and tastes sweet and fragrant. Many people like it, so it sells well in the market (Nawae et al., 2023). There are many varieties of durian. Different countries have their own unique varieties, adding up to hundreds of varieties. These durians have many differences in appearance, taste and genes. For example, Mustikarini et al. (2024) found more than 14 different varieties of durian on Bangka Island, Indonesia. Because durian is exported a lot and is very important to the local economy, it has also attracted many agricultural researchers to study it (Siew et al., 2018; Aziz and Jalil, 2019).

Studying durian germplasm is a very important thing. First of all, we can protect some old varieties, especially those that are about to disappear. In addition, some durian varieties are more disease-resistant, which is also useful for planting (Chen, 2024; Zhang, 2024). Now that climate change is getting worse, we need to know what genes durian has so that we can pick out varieties that are more suitable for the current environment. For example, some durians are more drought-resistant, some are less susceptible to disease, some have very sweet flesh, and some are even seedless. These varieties are not only high-yielding, but also good for the environment. But the problem is that now in order to grow land, many places have cut down the original trees, and the original growth area of durian has also been destroyed. So we must first figure out what the differences are between various durians. Only by understanding their relationship clearly can we know which ones are particularly important and which ones should be protected first (Sihaloho et al., 2021; Muryidin et al., 2024). Durian breeding is also a key thing. If we understand the genes of durian, we can pick out better varieties to cultivate. For example, durian has tastier flesh, is less susceptible to disease, and even has no core (Huy et al., 2023). There are also some new technologies, such

as molecular markers and genome sequencing, which can help us find useful genes faster and make breeding faster and simpler (Mursyidin et al., 2023).

The main purpose of this study is to see where the durian in Southeast Asia came from first and how it spread to other places. We are particularly interested in whether there is any genetic exchange between wild durian and artificially cultivated durian. We have also compiled some new research results to see how durian spread step by step. Next, we will discuss whether these research results are helpful for the genetic protection and sustainable cultivation of durian. We also hope that these studies can be of some use in breeding, to see if we can cultivate better-tasting, more nutritious, and more profitable durian in the future. These research results should have some reference value for the future protection and breeding direction of durian, and can also help durian improve its nutritional and economic benefits.

2 Genetic Origin of Southeast Asian Durian

2.1 Evolutionary history and phylogenesis of durian

Durian is a very important fruit in Southeast Asia, with a very long history of cultivation. Its evolution has a lot to do with the geography and climate here. In some countries, people think that durian represents wealth, some think it symbolizes power, and of course many people just like its unique taste. Teh et al. (2017) found that durian and cotton have some similar genes. This may be because the geology and climate in Southeast Asia have undergone great changes in the past. However, these genetic changes did not make durian evolve very quickly, probably because durian itself grows relatively slowly. This study helps us understand more clearly how durian evolves. Mursyidin (2022) found that durian in South Kalimantan, Indonesia, varies greatly when studying durian. Some can resist floods, and some can resist insects. Local people basically do not use pesticides when planting trees, so durian gradually grows different characteristics. After analyzing with genetic technology, he found that these varieties are very closely related, which may be related to the local ecology and long-term planting methods. Later, Mursyidin et al. (2023) also studied some key genes in durian. They found that the genes of the two species, *D. zibethinus* and *D. lowianus*, are very similar, which they believe may be due to both natural and human influences on durian evolution.

2.2 Distribution of wild durian populations

Wild durian can be seen in many places in Southeast Asia. These durians look different and have different genes. For example, in Nias Island, Indonesia, some people specialize in studying durian there. Hannum et al. (2020) used a method called “RAPD” to analyze their genes. They found that there are many types of durian there, divided into 13 groups in total. The durian in each group comes from different places. This shows that the genes of these durians are very rich and are a valuable resource. Aziz et al. (2017) also studied wild durian. They found that these durians are usually scattered in small areas. But there is still gene exchange between these small groups. This is because animals such as bats and bees fly between durian trees to help pollinate, carrying pollen from one tree to another. In this way, durian can exchange genes with each other. Human activities can also affect the genetic exchange of these durians. Sometimes people go into the forest to pick durian or cut down trees for planting, which may give the durians that were originally separated the opportunity to come into contact with each other. Although this may bring new genetic combinations, it may also destroy the original growth environment of durian. Therefore, Mursyidin et al. (2024) believe that protecting wild durian is not only about protecting the tree itself, but also about protecting the forest where durian grows.

2.3 Early domestication and selection of cultivated varieties

People in Southeast Asia have been growing durian for a long time, perhaps as early as the late Neolithic period. At first, people chose to grow those durians with large fruits and sweet taste. Over time, different durian varieties appeared in different places. They look very different. Some have thick flesh, while others have very thorny skin. Some have small seeds, while others have large seeds. People in some places also look at the flowering of durian, such as how many flowers bloom and whether the pollen is good, which will affect whether the durian can produce good fruits (Aziz and Jalil, 2019). Now Thailand has several particularly famous durian varieties, such as “Golden Pillow” and “Green Nee”; Malaysia also has “Musang King”. These varieties are also very different in

genes (Nawae et al., 2023). Scientists used a method called "whole genome resequencing" to find out their genetic differences. In the past, people mainly relied on experience to grow durian. Whoever's durian had large fruits, good taste, and ripened quickly would be kept and continued to grow. After generations of selection, the appearance and taste of durian gradually became fixed (Hannum et al., 2020). Now, scientists also use a technology called "SSR" to study the genes of durian. They can draw a "family tree" of durian and know which varieties are relatives and which are far apart. In the past, planting durian also depended on the weather. For example, Malaysia has a lot of rain, so the locals choose those varieties that are not afraid of rain. Now scientists not only look at what durian looks like, but also analyze the genes to see which durian everyone likes most (Huy et al., 2023).

3 Gene Flow Between Wild Populations and Cultivated Varieties

3.1 Genetic exchange mechanism of durian

Wild durian and human-grown durian often exchange genes. There are two main ways to do this: one is to rely on animals to help spread pollen, and the other is for people to deliberately crossbreed them when planting. The most common animals for pollination are bats and bees. For example, flying bats (Pteropodidae) will fly to the durian tree to eat nectar. When they eat, they will accidentally take away the pollen and bring it to other trees, thus helping the durian to complete pollination (Figure 1) (Hannum et al., 2020). The role of bees is similar. When humans grow durian, they will also specially select some trees with large fruits and good taste to breed. This selective breeding method has led to more mixing between durian varieties. Gradually, gene exchange has increased. Siew et al. (2018) used two technologies, SSR and RAPD, to analyze the genes of durian. They found that there were traces of mixing between many durian populations. This shows that gene exchange between wild durian and artificially grown durian is common and long-standing.

Figure 1 (a) Island flying fox (*Pteropus hypomelanus*); (b) Close-up of durian flower showing *Apis dorsata* foraging on anthers; (c) Deployment of camera stations in durian (*Durio zibethinus*) trees; (d) Durian fruit set (Adopted from Aziz et al., 2017)

3.2 Genomic studies on genetic variation

In recent years, more and more scientists have begun to study the genes of durian. For example, Nawae et al. (2023) used the method of "genome resequencing" to compare durian from Thailand and Malaysia. They found that although these durians look similar, they have many differences in genes. This shows that they may have taken different paths in evolution. They also used another method called SSR. This method can look more carefully and find out the genetic differences between durian varieties. Sometimes, durians that look similar are actually very different in genes. This also tells us that it is impossible to tell whether they are relatives just by looking at their appearance. Teh et al. (2017) also found some particularly important genes. These genes affect durian's tolerance to water and salt, and also affect when the fruit matures. Some durians have a lot of these genes, probably because the environment where they grow is relatively special and they need to adapt to different

climates. These studies help us better understand how durian adapts to different environments. In the future, these useful genes can come in handy when breeding to help us pick out durian that is more suitable for certain areas.

3.3 Implications of gene flow for conservation and breeding

In fact, wild durian and the durian we grow now do exchange genes with each other. This "gene flow" is helpful for the protection and breeding of durian. To protect durian, we must first understand the relationship between each variety. For example, we should give priority to protecting the durian with a small number; some varieties are particularly good and can also be used as “parents” for breeding (Huy et al., 2023). Scientists have now found many “genetic markers” that can help us distinguish the genetic differences between different varieties more clearly. Through these markers, we can know which durian is suitable for breeding and select varieties that are more suitable for local weather (Lin et al., 2022). Protecting wild durian is also crucial. Although some wild durians don't taste very good and there are not many of them, they may have very useful genes, such as drought resistance and disease resistance. If we want to breed new durians that can withstand weather changes in the future, we may have to rely on these genes to help (Mursyidin et al., 2024). Therefore, protecting wild durian is not just about preserving a variety, but also for the future of durian. The more we protect it now, the more genes we can use in future breeding, and the greater the chance of producing new durian.

4 Dispersal Pathways of Durian Germplasm

4.1 Role of human migration and trade networks

In the past, when people moved, they often took durian seeds or saplings with them. In this way, durian followed people and spread from one place to another. Later, people started to do durian business, and it was no longer just for their own family. Durian became an agricultural product that can be bought and sold. More and more people did durian business, and durian was brought to more places. Gradually, durian began to be grown in many countries in Southeast Asia, and people became more and more familiar with it. Take Thailand as an example. There are now several famous durian varieties there, such as Kradumthong, Monthong and Puangmanee. The emergence of these varieties is not accidental, but people spent a lot of time and selected them bit by bit (Nawae et al., 2023). In recent years, China has also begun to grow durian. Since 2018, China has imported a lot of durian seedlings from Southeast Asia. Many durian orchards have been built in places like Hainan. This shows that as long as someone wants to grow and sell it, durian can quickly gain a foothold in a new place (Lin et al., 2022).

4.2 Ecological and environmental factors in germplasm dispersal

In addition to humans, the environment also plays a big role in the spread of durian. When durian blooms, animals are needed to help spread pollen. Flying bats are important pollinators. For example, black-tailed flying bats (*Pteropus melanotus*) fly to durian trees at night to eat nectar. They take away pollen while eating, and when they fly to other places, they pass the pollen over, and may also spread durian seeds (Aziz et al., 2017). Therefore, the presence or absence of these animals has a great impact on whether durian can reproduce smoothly. If there are fewer pollinating animals, durian seeds will not be easily spread. Durian also has requirements for the environment. The humid and hot climate of the tropical rainforest is particularly suitable for the growth of durian, the seeds are easy to germinate, and the saplings grow fast. But if the forest is cut down, or animals such as bats disappear, the spread range of durian will become smaller. Tan et al. (2020) also found that the genetic structure of durian is closely related to the environment in which it lives. In other words, in order for durian to continue to reproduce healthily, it is necessary to protect its growth environment and the animals that help it pollinate.

4.3 Modern approaches to germplasm conservation and utilization

Nowadays, people use many new technologies to protect and utilize durian germplasm resources. Simply put, it is to first find out what genes durian has, and then breed or preserve them based on this information. Whole genome sequencing and SSR technology are currently commonly used tools. Siew et al. (2018) used these methods to study the genes of durian and found out which varieties have more special genes and which are more suitable to be kept. These results can help scientists make more accurate judgments. There are still many new methods to preserve durian germplasm. For example, the Singapore Botanic Gardens has frozen and preserved the embryos of 34 wild durians at an ultra-low temperature of -196℃, so that they can be preserved for a long time without

spoiling. Scientists can also find some special genes from wild durian, such as those that are drought-resistant and disease-resistant. Then use genetic technology to transfer these good genes to common cultivated varieties. The durian grown in this way is more resistant to climate change and easier to grow. This kind of durian is sometimes called “climate-smart durian” and is a very popular research direction now.

5 Case Study: Gene Flow in Southeast Asia

5.1 Historical background of durian cultivation in Southeast Asia

Durian is not uncommon in Southeast Asia. In countries like Malaysia, Thailand, Indonesia, the Philippines, and Vietnam, you can find it everywhere, on the roadside, in markets, and in orchards (Van Hau et al., 2023). In fact, durian has been grown by local people for a long time, but it was not spread at that time. Later, it was slowly spread to other places and became a fruit that everyone eats. The durian in Malaysia is particularly diverse, with more than 100 officially registered varieties, specifically 126 (Siew et al., 2018). This is only the registered varieties, and there may be more varieties circulating among the people. For the people there, durian is not only eaten, but also a part of culture in many cases. Speaking of genes, durian is not simple either. It has an astonishing number of genes, about 46,000, which is twice that of humans. How did this number come from? In fact, it did not increase all at once, but was the result of the accumulation of climate, environment, human selection, and cultivation methods. However, if there is one reason for the big changes, it has to be “gene flow”. Simply put, wild durian and human-grown durian are genetically intermixed (Mursyidin et al., 2024). This interbreeding has resulted in more species and characteristics of durian, making it more adaptable to different places.

5.2 Genetic analysis of local durian varieties and wild relatives

Although they look similar, durian in different countries and regions actually has quite different genes. Take Thailand as an example. There are several common varieties - Kradumthong, Monthong, and Puangmanee. Researchers used “gene resequencing” to analyze them and found that the genes of these durians are very different from those of Malaysia’s “Musang King” (Nawae et al., 2023). Judging from the results, their ancestors probably did not come from the same place, and their development paths were also different. Similar studies have also been done in Indonesia. Prakoso and Retnoningsih (2021), and Mursyidin (2022), used the “molecular marker” method to analyze several local Indonesian varieties. The results showed that durians in places like Blongko, Semarang, and South Kalimantan may not be particularly exaggerated in appearance, but they are quite different at the genetic level (Figure 2). Basically, durians in every place have a bit of “their own bloodline”. So, don’t just think that durians look similar. If you check their genes, you can tell which ones are not very related to each other.

5.3 Implications for future conservation and breeding strategies

In the final analysis, for durian to continue to develop, it must rely on protection and breeding. Some of these durians in Southeast Asia are wild, and some are artificially grown. There will be gene exchange between them. You may not think that this kind of “give and take” is particularly useful for breeding. Different genes can bring different benefits. For example, some are insect-resistant, some are drought-resistant, some are afraid of water but can still grow well, and some taste particularly good or have a lot of flesh (Lin et al., 2022). Some genes don't seem to matter on the surface, but in years with extreme weather or many diseases, they are very useful. Although wild durian may not taste very good, they often have some “backup options” hidden in their genes. When the climate really changes, we may have to rely on them for help. So now protecting these wild resources is not just “saving seeds”, but more like leaving more ways for the future. Scientists now have a lot of tools, such as “molecular markers” and “genetic analysis”. Using these methods, we can find suitable varieties for breeding more quickly. There is also a method called “marker-assisted selection (MAS)”, which simply means using molecular information to help select seeds. The durian selected in this way not only tastes good, but also better meets market requirements and sells well (Khaksar et al., 2024).

6 Challenges and Future Directions

6.1 Threats to durian germplasm conservation

Protecting durian genetic resources is easy to say, but it is difficult to do. One of the most troublesome problems is called “genetic erosion” - in fact, there is no need to be too professional, that is, everyone only grows the

best-selling varieties, and no one cares about the old varieties, and they gradually disappear. For example, in Hainan, China, the durians in the plantations look like the same variety, but the fruit shape and taste are very different. This shows that their genes are not so uniform, and they may not be the same at all (Lin et al., 2022). In this way, protection and breeding will become more complicated. The environmental impact is also not small. Some old durian trees were originally planted in the suburbs of Bangkok. It is said that they were brought here by Burmese soldiers in the past. Some of these trees have lived for hundreds of years. But then there were two major floods - one in 1871 and the other in 1942, which almost washed away these old trees. It is almost impossible to find their genes now. The situation of wild durian is not optimistic either. Some are almost extinct. If they are not taken care of, they may be completely gone in a few years. Although no one grows them, the genes hidden in them may be useful in the future. After all, if you wait until something goes wrong before looking for those genes, it may be too late (Mursyidin et al., 2023). We should act now while we can still harvest and protect them.

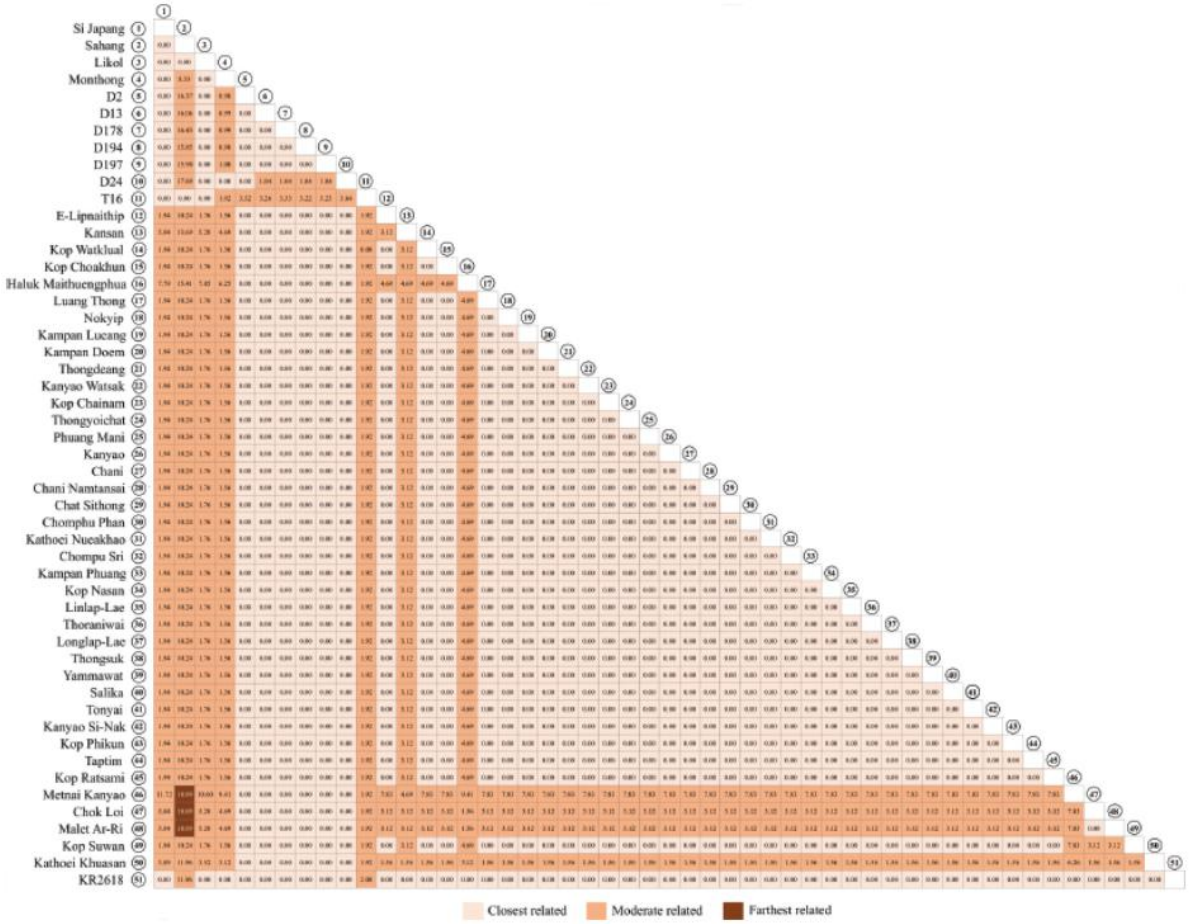

Figure 2 Genetic divergence among durian (*Durio zibethinus* Murr.) cultivars from South Kalimantan, Indonesia, and other cultivars (Adopted from Mursyidin, 2022)

6.2 Advances in biotechnology for germplasm improvement

Now breeding is indeed not as difficult as before. Because of some new tools, it is more convenient to operate. For example, SSR molecular markers are a common method used by everyone now. It can help us see the genetic structure of durian clearly and also help preserve those different varieties. What is the use of this thing? You can think of it as a sieve that can filter out durian with good genes. In this way, when breeding, we don't have to rely on guessing, but directly choose the "good" varieties. This process has a scientific name, called "marker-assisted selection" (MAS). In addition to SSR, there is also "QTL positioning", which is used to find genes related to fruit size, sweetness, and disease resistance (Khaksar et al., 2024). With them, we can know more accurately which durian is worth keeping. And now, the genome of durian has been figured out. Scientists have even found many key genes related to maturity time and disease resistance (Teh et al., 2017). These results are not only for research, but also can be used in breeding in the future.

6.3 Policy and collaborative efforts for germplasm preservation

No matter how many breeding tools there are and how accurate the genetic analysis is, if we really want to protect durian, technology is not enough. Policies and cooperation must also keep up. Some places have already taken action, such as building durian germplasm resource banks and using DNA fingerprints to register the "identity information" of durian. In this way, the origin and characteristics of each durian can be clearly checked, and it is also convenient for management and preservation (Siew et al., 2018). Don't forget that durian is not just a fruit in Southeast Asia, but also an important economic crop in many countries. Protecting it is not something that any country can do alone. Cooperation between multiple countries and sharing of genetic information are actually quite necessary (Nawae et al., 2023). There is also something that is easily overlooked-pollinators. If small creatures like bats and bees that help pollinate durian are really gone, durian itself will not bear fruit. Therefore, while protecting durian, we must also protect the habitats of these animals. In the final analysis, there must be supporting measures in policy. On the one hand, farmers must be motivated to plant, and on the other hand, the ecological environment cannot be destroyed. Only by taking care of both ends can we continue on the durian path.

7 Concluding Remarks

To be honest, the reason why there are so many types of durian cannot be explained by natural evolution alone. Part of it is due to its slow spread in the wild, and the other part is inseparable from people's continuous selection, planting and improvement. It's just that we didn't understand what the genes in it were before. Now that technology has advanced, many things can be seen more clearly. Tools like SSR and ITS, although they sound a bit professional, are actually helping scientists "look at genes". What are they looking at? For example, which two durians look alike but have very different genes, or which genes are particularly suitable for breeding. This technology is now not only used for classification, but also for picking out good varieties for special planting. However, wild durian cannot be ignored. Although it is not planted by humans, the genetic resources in it are not inferior at all, and some are even more important than artificial ones. In places like Malaysia, Indonesia, and Thailand, there are still many wild species. Although no one cares whether they bear fruit or not, they are definitely treasures in terms of genetic diversity. There is also a very interesting discovery. Scientists noticed during their research that there are actually overlaps in the genes of durian and some of its relatives. This shows that they actually "walked together" for a period of time on the road of evolution in the early years. There is actually no clear distinction between wild and artificial, and there has always been genetic exchange between them. This process was not arranged by anyone, but was promoted by nature, animals, and human activities. Now that there is more research, we are slowly figuring out how durian has become what it is today step by step. But understanding is not enough. If you want durian to flourish in the future, you can't just focus on a few mainstream varieties. Otherwise, it may end up like - the whole market has the same taste and the same appearance. It is better to do it early than to say it early about protecting diversity. When there is really only "one durian" left, it may be too late. It's not too late to start now.

Molecular biology and genetic technology are becoming more and more powerful. Whole genome sequencing, transcriptome analysis, and various molecular marker tools can help us find genes related to disease resistance, fruit quality, drought resistance, or flood resistance. In the future, if these research results are used in breeding, new durian varieties that are more delicious and more disease-resistant can be selected. However, technology alone is not enough. We also need to build seed storage and set up some wild protection areas to prevent the growth environment of durian from being destroyed. In particular, urban expansion should not be too fast, otherwise the living space of wild durian will become smaller and smaller. Southeast Asian countries should also strengthen cooperation. Everyone should communicate and share experiences more. Only in this way can the cultivation and protection of durian continue in a long-term and stable manner.

Whether durian can continue to grow is not up to one person alone. This is a complicated matter, and it is not something that can be achieved by just one person's efforts. Someone has to do the science, the policy has to keep up, the farmers have to have a solution, and the planting method cannot remain unchanged. Sometimes, when people talk about protecting durian, they first think of protecting the tree. But in fact, the most valuable thing is the genes hidden in the durian. They are like spare parts. They seem useless now, but they may come in handy in

the future. Especially in today's climate change, if these genes are lost, it will be difficult to cultivate a disease-resistant and drought-resistant durian. Of course, it doesn't mean that everything is too late now. There are still many things that can be done. For example, don't use pesticides blindly, and don't cut down trees at every turn. Bats, bees and other small animals that help durian pollinate, also need to be managed by someone. If the environment is gone, durian can't be grown no matter how good it is. Sometimes, farmers don't want to change, but there is no one to teach them. Therefore, policies should not just be put on paper. We need to provide practical training and tell everyone about new planting methods and effective technologies. Let them know how to save time and money while protecting the land and trees. The durian industry itself cannot always focus on immediate profits. Making money today does not mean you can continue tomorrow. Someone has to think about the long term and consider how to stabilize the industry step by step. In the final analysis, no one can be immune. Scientists, farmers, governments, and environmental organizations are all indispensable. When scientific research, ecological protection, and agricultural practice can really work together, durian may not only continue to be planted, but also grow better and better, and truly become a "family heirloom" in Southeast Asia.

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