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# Exploring Presence/Absence Variations in Barley for Agronomic Trait Improvement

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Received: 09 Mar., 2025

Accepted: 21 Apr., 2025

Published: 06 May, 2025

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**Preferred citation for this article:**

Yang W.Y., and Ma C.X., 2025, Exploring presence/absence variations in barley for agronomic trait improvement, Triticeae Genomics and Genetics, 16(3): 101-109 (doi: [10.5376/tgg.2025.16.0011](https://doi.org/10.5376/tgg.2025.16.0011))

**Abstract** Presence/absence variations (PAVs), a form of structural genomic variation, play a critical role in shaping phenotypic diversity in plants, including crop species like barley (*Hordeum vulgare*), which serves both as a globally important cereal crop and a model organism for genomic studies. In this review, we examined the molecular mechanisms underlying PAV formation, such as transposable element activity and large-scale deletions, and highlighted recent advances in technologies-including pangenome assemblies and high-throughput sequencing-that have enabled the comprehensive detection of PAVs. We further discussed the distribution patterns of PAVs among landraces, cultivars, and wild relatives of barley, emphasizing their evolutionary significance in domestication and adaptation. Functionally, PAVs were found to influence key agronomic traits such as disease resistance, abiotic stress tolerance, and yield-related characteristics. The integration of PAV knowledge into modern breeding programs was explored, with a focus on marker-assisted selection and pangenome-based strategies, including a case study on improving heat tolerance through PAV-informed breeding. Lastly, we considered the potential of combining PAV analysis with multi-omics data and phenotyping platforms, and the role of machine learning in modeling genotype-phenotype relationships. This study underscores the value of PAVs as a genomic resource for precision breeding and highlights future directions in expanding pangenomic datasets and developing breeder-friendly tools to facilitate their practical application.

**Keywords** Presence/absence variation (PAV); Barley (*Hordeum vulgare*); Structural genomic variation; Agronomic trait improvement; Pangenome-based breeding

## 1 Introduction

Sometimes, some important genetic information is not reflected in the familiar single nucleotide polymorphisms (SNPS). For instance, certain fragments in the genome appear in some barley individuals but cannot be found at all in others-this is what is called presence/absence variation (PAV). Although this variation sounds simple, it may directly affect a plant's stress resistance, yield, and even determine whether it can grow well under certain climatic conditions (Cai, 2024). Research also found that the number of PAVs in barley is not small. These variations not only change the number of genes but also affect the expression mode of genes (Jayakodi et al., 2020).

In fact, the significance of these structural variations is far more than just scientific exploration. Barley (*Hordeum vulgare*), as the fourth largest grain in the world, has a strong environmental adaptability by itself. This diversity of genetic background is precisely a resource that breeding research highly values (Desta et al., 2024). Especially in some regions with less favorable climatic conditions, barley can still be stably produced as feed, malt and human food. Behind this "tenacity" lies a genetic code at various structural levels. PAV happens to be one of the keys to unlocking these "codes".

Of course, SNPS remain important, but an increasing number of studies have shown that if PAV is ignored, recessive variations associated with important agronomic traits may be missed (Weisweiler et al., 2019). The emergence of the pan-genome has enabled us to no longer be confined to the "reference genome" version alone and has also made the mining of PAVs more feasible. This difference may be reflected in core indicators such as when the ears start to spike, how tall they grow, and whether they are resistant to diseases.

So, the purpose of in-depth research on PAV is actually quite straightforward-to find new clues that are useful for breeding. Combining PAV information with transcriptome and other genomic data is expected to make the prediction of complex traits more accurate and open up new paths for genomic selection and marker-assisted breeding. The ultimate goal is also very realistic, which is to screen out barley varieties that are more productive, more resilient and more nutritious. This is not only for the income of farmers, but also for food security and the sustainable development of future agriculture. Characterizing and utilizing PAV can accelerate the development of barley varieties with excellent agronomic performance and adaptability, supporting food security and sustainable agriculture.

## **2 Molecular Basis and Detection of Presence/Absence Variations in Barley**

### **2.1 Definition and genomic mechanisms leading to PAVs**

Not all genotypes contain exactly the same gene fragments. In barley, some DNA regions, such as an entire gene segment, may be "standard configuration" in one type of material but not present at all in another. This is known as PAV (Presence/Absence Variation). This kind of variation is not uncommon, and the mechanisms involved behind it are rather complex: factors such as transposition activity, fragment repetition or loss, and even some "accidental operations" during the DNA repair process may all create these differences. The factor of seat rotation is particularly worth mentioning. It can not only change the position of DNA, but sometimes it is also directly related to the increase or decrease of genes. Those genes that are not "essential", such as certain transcription factors, are prone to "get on board" when transposons are inserted. In addition, mechanisms such as single-chain annealing and template sliding are also involved (Munoz-Amatriain et al., 2013; Tong et al., 2024). In other words, the generation of PAV does not rely on a single method but is the result of the combined effect of multiple processes.

### **2.2 Technological advances enabling PAV discovery**

Finding these PAVs is not something that can be achieved simply by flipping through a genomic manual. Only when we have high-quality genetic assemblies of multiple barley varieties, wild types, and local strains can these hidden variations come to light (Figure 1). The establishment of the pan-genome is precisely based on the integration of this diversity, which helps us systematically classify PAVs across the entire species range. Of course, sequencing technology is also constantly advancing. High-throughput methods such as whole-genome resequencing and mRNA sequencing not only help us improve resolution but also enable us to identify genotypic and non-genotypic PAVs more quickly and accurately. Most importantly, they can also reveal whether these variations are related to traits such as disease resistance, plant height or flowering period (Jayakodi et al., 2020; Zhang et al., 2022).

### **2.3 Bioinformatics tools and pipelines for accurate identification and validation of PAVs**

Experimental methods alone are not enough. To a large extent, the identification of PAVs also depends on data processing. Some commonly used tools and methods nowadays, such as comparative genomic hybridization, k-mer whole-genome scanning, and even some new technologies that do not rely on reference genomes (like AgRenSeq), can already achieve highly accurate detection. Assembling multiple genomes for comparison not only enables the "targeted" positioning of PAV but also allows for the rapid comparison of differences among various haplotypes. If one wants to save costs and improve efficiency, the method based on mRNA sequencing is a good choice-it can not only capture structural variations but also directly obtain expression information, which is particularly suitable for large-scale screening in breeding materials (Weisweiler et al., 2019).

## **3 Distribution and Evolutionary Significance of PAVs in Barley**

### **3.1 Variation of PAVs across landraces, cultivars, and wild relatives**

Not all genes are present in every type of barley. In fact, whether it is local varieties, modern cultivated varieties or wild relatives, there are considerable differences in the number of genes among them. Researchers analyzed multiple inbred lines of spring barley using mRNA sequencing. The results showed that more than half of the genes had PAV phenomena-some genes only appeared in specific varieties, while others were not present at all. Strangely, these PAVs have little to do with the surrounding sequence variations, indicating that such variations

actually constitute a relatively independent layer of genetic diversity. What's more interesting is that local varieties and modern varieties each have their own PAV characteristics, which actually also indirectly confirms their different domestication paths and breeding histories. The close relatives of wild barley not only brought a lot of PAV that had disappeared in cultivated varieties, but sometimes also "contributed" some completely new alleles and gene quantities.

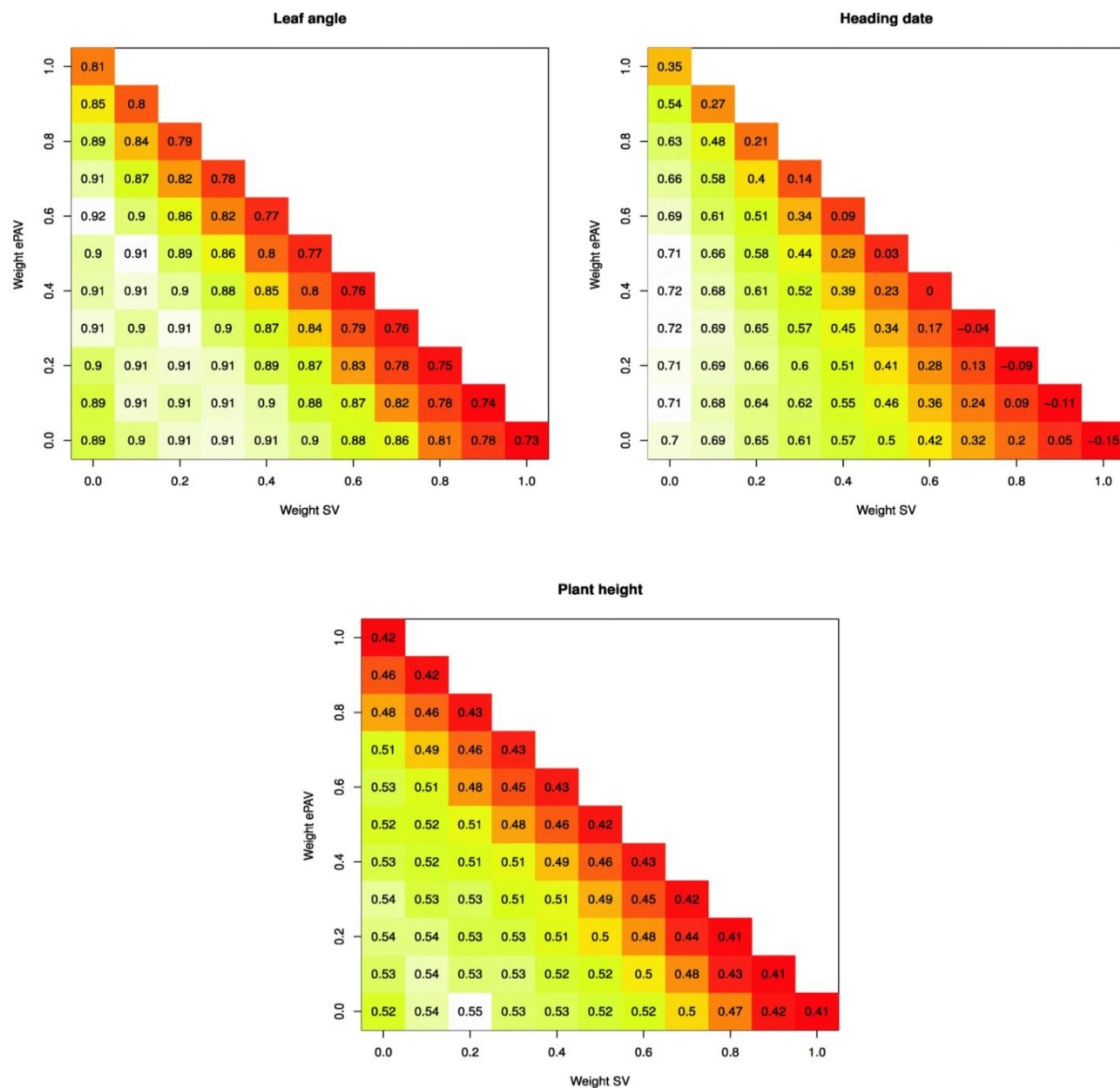


Figure 1 Prediction accuracy for three different traits. Prediction accuracy for the barley inbreds for leaf angle, heading date, and plant height, for 66 cases which differ in their weights for the predictors sequence variants (SV), expression presence/absence variation (ePAV), and gene expression in seedlings ( $T_s$ ). Their corresponding relationship matrices were joined with weights varying from 0 to 1 in increments of 0.1. Weights for SV and ePAV are shown at the respective scales; weights for gene expression are = 1-weight of SV-weight of ePAV. Plotted values represent medians of prediction accuracy across 1,000 cross-validation runs. Heat color schemes differ for the three traits ranging from white, indicating the respective highest value, to red for the respective lowest value (Adopted from Weisweiler et al., 2019)

### 3.2 Role of domestication and selection in shaping PAV distribution

Not all variations are the result of natural evolution. Human choices also play a very important role in it. As barley was domesticated and cultivated varieties were continuously selected and bred, some genes were retained while

others were discarded. Over time, the PAV models among different varieties have also become distinct. Large-scale genotyping techniques and whole-genome studies have demonstrated that modern cultivated barley often lacks PAV, which is only present in wild relatives. However, this does not mean that modern varieties are "lacking something", because through breeding and adaptive accumulation, they have gradually acquired a batch of new PAVs (Gao et al., 2020). These seemingly opposite processes actually jointly contributed to the formation of the genetic differences in barley among different groups that we see today.

### **3.3 Evolutionary consequences of PAVs for genome plasticity and adaptation**

With the change in climate and the increase in pests and diseases, how should crops respond? At this point, PAV might come in handy. They can enable crops to acquire or lose certain gene functions in a short period of time, thereby adjusting their own state to adapt to environmental changes. This "dynamic" response is actually a manifestation of the plasticity of the barley genome. Some PAVs are particularly focused on genes related to DNA integration, transposition activity and stress response, suggesting that they may have played an important role in species evolution and adaptation to new environments. More importantly, PAVs are not as easily screened out as other sequence variations. They are often "latent" genetic resources that can be rapidly "activated" once external pressure emerges. From this perspective, PAV does indeed make barley, as a crop, more resilient to wind and rain and have a brighter future.

## **4 Functional Impact of PAVs on Barley Agronomic Traits**

### **4.1 Influence on disease resistance genes and immune responses**

Not every barley plant can resist viral infection. The key lies in whether it has those "defensive" resistance genes. Genes like *Bdv2* and *RYd2* are present in some barley while in others they are completely absent. This is the difference brought about by PAV. Varieties with these genes, even if infected with pathogens like the barley yellow dwarf virus (BYDV-PAV), have less impact on the growth of their root systems and plants, and are less likely to experience a significant reduction in dry matter. Not only that, these resistance genes may also promote the synthesis of phenolic compounds and impede the transmission path of the virus in the phloem tissue, indicating that their roles in the defense system are not limited to one (Choudhury et al., 2018). But if these genes happen to be missing due to PAV, then the crops will be "completely defended" against the virus, and it is not surprising that this will eventually lead to more severe tissue damage and a decline in yield.

### **4.2 Associations with abiotic stress tolerance (e.g., drought, salinity)**

Some traits are not as conspicuous as diseases, such as the stress brought by drought or saline-alkali land. In such cases, whether barley can "withstand" may also be related to PAV. In the PAV region, some genes related to stress responses can often be found, such as functional genes involved in REDOX reactions, transmembrane transport, or DNA integration. Moreover, these expression variations of PAV usually do not have a direct correlation with the surrounding sequences, that is to say, they themselves can bring additional genetic diversity. This characteristic makes them particularly useful in predicting performance under abiotic stress. If PAV data is combined with other genomic information, the prediction of drought tolerance or salt stress will be more accurate and more conducive to breeding screening.

### **4.3 Contribution to yield-related traits (e.g., tiller number, grain size)**

A decline in output is not necessarily due to poor management; sometimes it is also closely related to genes. For instance, after some barley is infected with BYDV-PAV, both the grain count and the harvest index will drop significantly, and the overall yield can even be reduced by more than half (Nancy Arrow et al., 2021). This is actually directly related to the deletion of certain key genes, and these genes have precisely been "deleted" by PAV. Tillering number, grain size, biomass-these yield-related traits may all be affected by PAV. Sometimes, it is the existence of a certain type of PAV that enables certain varieties to maintain stable yields even in adverse conditions. In addition, if PAV is combined with other sequence variations, the prediction of yield performance will be more accurate, and it can even directly guide precision breeding work. Simply put, PAV itself is a very useful "trait marker library".

## 5 Application of PAV Knowledge in Barley Breeding

### 5.1 Use of PAV markers in marker-assisted and genomic selection

Often, traditional SNP markers are sufficient, but the genetic basis of some important traits cannot be fully explained by SNPs. At this point, the PAV marking becomes particularly crucial. Especially for expressive PAV, its linkage relationship with peripheral sequences is not strong; instead, it can independently reflect certain unique genetic differences. Some studies have attempted to combine PAV data with SNPs and gene expression levels, and the results show that the prediction effect for some key agronomic traits has become more accurate and stable. For breeding materials, low-coverage mRNA sequencing methods can quickly and cost-effectively extract these PAV information. In some scenarios, it may even replace SNP as the main characterization method. For instance, the genes *Ryd2* and *Ryd3* of barley that resist yellow dwarf virus were screened out by this PAV-based labeling method (Scheurer et al., 2001).

### 5.2 Incorporating PAVs into pangenome-informed breeding strategies

The traditional reference genome cannot encompass all variations of genes. It was only by constructing the pan-genome of barley that researchers identified millions of PAV tags, which gradually revealed the true genetic diversity. Sometimes, mining these rare PAVs from wild and local varieties is more direct and effective than looking for variations from modern varieties. Machine learning has also played a driving role in this-it enables us to screen out useful PAVs more quickly and use them for trait localization. Once PAV is anchored to a certain phenotype, it can be used for subsequent selection breeding, such as controlling traits like flowering time, plant height or grain size. This approach is also gradually changing the "blind selection" model of breeders in the past, making the improvement of target traits more controllable and efficient.

### 5.3 Examples of trait improvement through PAV-based introgression

Disease-resistant breeding is one of the typical application scenarios of PAV. For instance, barley varieties carrying *Ryd2* and *Ryd3* showed almost no significant decline in yield when infected by BYDV-PAV virus, while susceptible varieties often suffered a severe reduction in yield. The infiltration process of these genes is an example of combining traditional methods with genomic approaches (Wei, 2024). More notably, even in some "superior varieties" that were originally considered to have a very similar genetic background, the use of PAV markers can also uncover potential resistance differences (Ghanem et al., 2018; Alquicer et al., 2023). In addition, PAVs related to agronomic traits such as heading time and plant height have also begun to play a role in precise selection, enhancing the efficiency and pertinence of the entire breeding process.

## 6 Case Study

### 6.1 Identification of heat-responsive genes absent in susceptible genotypes

The hot weather has arrived. Some barley can withstand it, while others wilt quickly. This difference is often related to whether a group of key "heat response" genes are present, such as heat shock proteins, antioxidant enzymes, and those factors that maintain cell membrane stability and regulate hormone signals (Figure 2). These genes are common in heat-resistant varieties, but may not exist at all in some susceptible varieties. This is very likely the fault of PAV. In fact, similar situations have also been seen in other crops. In pearl millet, pan-genomic studies have identified some structural variations and PAVs, involving genes related to endoplasmic reticulum function, RWP-RK-type transcription factors, etc., which are either absent or underexpressed in heat-resistant materials (Yan et al., 2023). These findings suggest that barley may also have such a situation where "one or two key genes are missing". If the same PAV screening approach is applied, it might be possible to identify the core genes that determine its thermal adaptability.

### 6.2 Field validation of heat tolerance in pav-harboring lines under stress

Of course, merely looking at genes is not enough. What really works still needs to be tested in the fields. Especially when it comes to the property of heat resistance-its performance may vary in different years and on different plots. In some breeding projects, researchers plant materials carrying specific PAVs under high-temperature stress conditions to observe indicators such as grain filling speed, canopy temperature and yield stability (Driedonks et al., 2016). Although there are not many cases of barley in this regard, in other crops, it is



indeed observed that some genes related to PAV perform better and have more stable yields in field trials. This phenomenon also indicates from the side that such genes can be used as breeding markers. However, some genes seem to perform well in greenhouse experiments but lose their effectiveness in the field. Therefore, tests under different environments are necessary. Especially for structural variations like PAV that have a significant impact, conclusions cannot be drawn merely based on the data in the laboratory.

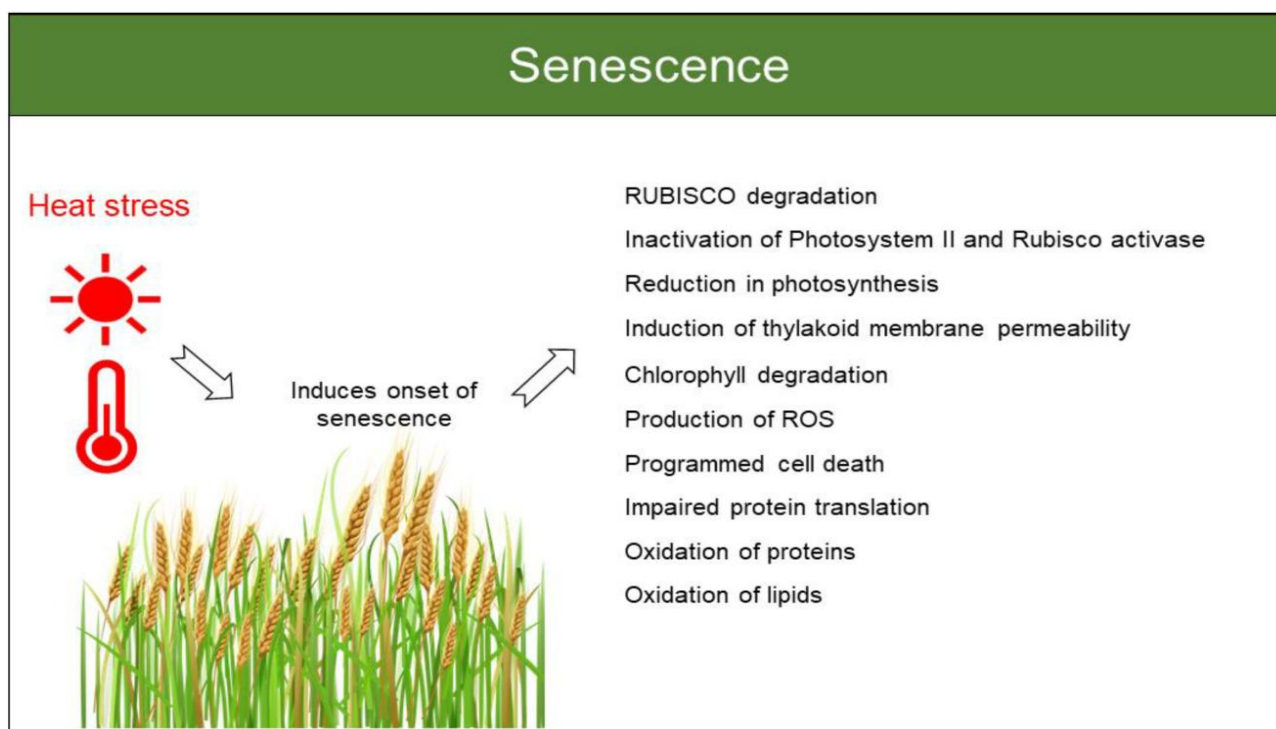


Figure 2 Adverse effects of induced senescence mediated by heat stress in plants (Adopted from Hill and Li, 2022)

### 6.3 Breeding implications: enhanced adaptation to climate change

Nowadays, high-temperature weather is becoming more and more frequent, and breeding work also needs to change its approach. Genetic information such as PAV may precisely fill the "blind spot" of traditional SNP markers and expression data. The introduction of materials carrying specific heat-responsive PAVs, such as some wild barley or local old varieties, has been proven to expand the gene pool on which breeding relies. Moreover, these rare variations often do not appear in the existing mainstream cultivated varieties. Introducing them can instead break through the bottleneck of genetic homogenization. Whether it is marker-assisted selection or whole-genome prediction, the addition of PAV can further enhance the efficiency of heat-tolerant breeding. More realistically, it also offers us a path to deal with climate change-production will not fluctuate greatly due to high temperatures, and food security will have an additional layer of protection.

## 7 Integration of PAVs with Multi-Omics and Phenotyping Platforms

### 7.1 Combining PAV data with transcriptomic and epigenomic insights

Looking at the PAV data alone sometimes seems "isolated". However, once combined with data such as transcriptome and epigenetics, many previously unclear issues can be clarified. Research has found that the presence or absence of a certain gene sometimes not only affects its own expression but may also alter the activity level of an entire regulatory pathway-which is actually crucial in the formation of plant traits. Some regulatory mechanisms, if studied separately by transcriptome or epigenome, are very likely to be invisible. But when you start from "whether PAV has this gene or not", and then continue to look at its expression and modification, the entire chain becomes much clearer. This layer-by-layer research approach, although it involves a large amount of data and complex logic, often can identify regulatory relationships that traditional research methods have overlooked and is more helpful for breeding decisions (Subramanian et al., 2020).

## 7.2 Leveraging high-throughput phenotyping for trait-PAV associations

Phenotypic data used to be difficult to quantify, but now it's different. With the help of a high-throughput phenotypic platform, the performance of different varieties in various environments can be quickly recorded, such as drought resistance, tillering number, grain size, etc., no longer relying solely on manual experience. These systems are highly automated and handle large sample volumes, which makes it easier for us to identify those "visible" connections between phenotypes and PAVs. Especially when phenomics data are analyzed together with multi-omics results, not only can key variations be identified, but also those candidate markers with true breeding value can be screened out more quickly (Cembrowska-Lech et al., 2023; Jiang et al., 2025).

## 7.3 Machine learning approaches to model genotype-phenotype links

Ultimately, multi-omics data is too complex for the human brain to sort out at once. At this point, machine learning comes in handy. It can automatically identify potential patterns among a bunch of seemingly unrelated variables, and is particularly suitable for studying cross-level associations such as those between PAV, transcriptome, and phenotypic data. Traditional statistical methods often only focus on the main effect, while ML models can capture more subtle genotype-phenotype interactions, and even nonlinear relationships. In this way, the accuracy of trait prediction has been significantly improved, which is of solid help in finding biomarkers and conducting precision breeding (Picard et al., 2021; Cao and Gao, 2022).

## 8 Future Perspectives and Concluding Remarks

The pan-genome of barley has accumulated a considerable amount of data, which is fine, but it is still far from being "complete". Many wild relatives, local old varieties, especially ecological types from different geographical regions, are still "absent" in the data at present. If these groups can be systematically included, many overlooked PAVs, new trait variations, and even rare alleles may come to light. These "supplementary data" are not just for fun; they may determine whether barley can adapt to more diverse climatic conditions in the future or whether it can withstand certain potential new stresses. Therefore, the further expansion of pan-genome resources is not an added bonus but one of the foundations for enhancing the long-term adaptability of barley.

But data alone is not enough. The next challenge lies in how to truly integrate these PAV studies into breeding practices. At present, there have been some technological advancements, such as low-cost mRNA sequencing or machine learning algorithms capable of handling complex data, which have enabled us to obtain a large number of datasets on the association between PAV and traits. However, these data are often difficult for breeders to handle. To solve this problem, the key lies in building a more user-friendly platform-one that can integrate PAV, SNP and multi-omics information and has a user-friendly interface. Only when these analysis results are useful to breeders can they be truly applied to assist in selection and decision-making, and PAV will not remain confined to scientific research papers.

From the perspective of breeding, PAV actually fills the "blind spot" that traditional SNP markers cannot see. It provides another independent source of variation for trait prediction, and many times, this information is precisely the key to improving the accuracy of prediction. Especially when we analyze PAV, phenotypic data and multi-omics information together, the breeding accuracy can also be improved accordingly. In the future, if the analysis process of integrating PAV becomes increasingly mature and the operational threshold is lowered, it is very likely to become one of the important tools for precision breeding, especially playing an increasingly core role in addressing climate change and maintaining yield stability.

## Acknowledgments

We are very grateful to Ms. Guo for critically reading the manuscript and her meticulous proofreading work improved the clarity of the text.

## Conflict of Interest Disclosure

The authors affirm 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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