Agri Articles
(e-Magazine for Agricultural Articles)
Volume: 06, Issue: 01 (JAN-FEB, 2026)
Available online at http://www.agriarticles.com

Breeding for Photoperiod Insensitivity in Wheat

*Ipsa Rath
M.Sc. Research Scholar, Department of Plant Breeding and Genetics,
College of Agriculture, OUAT, Bhubaneswar, Odisha, India-751003
*Corresponding Author's email: ipsarath060@gmail.com

Breeding for photoperiod insensitivity (PI) is fundamental to the global adaptability and yield stability of wheat (*Triticum aestivum* L.), as it allows the crop to flower and mature regardless of day length across diverse latitudes and sowing dates. Historically a cornerstone of the Green Revolution, PI was introgressed into high-yielding varieties through Norman Borlaug's shuttle breeding approach, which selected for lines that could thrive in contrasting environments. The trait is primarily governed by the *Ppd-1* gene family (*Ppd−A*1, *Ppd−B*1, *Ppd−D*1), where mutant alleles accelerate flowering by triggering the floral activator FLOWERING LOCUS T1 (FT1) through molecular mechanisms like promoter deletions and copy number variations. While breeders employ various techniques—including traditional pedigree selection, marker-assisted selection (MAS), and modern CRISPR/Cas9 genome editing—to develop PI varieties, they must manage a critical trade-off: PI acts as a "genetic insurance policy" against terminal heat and drought, yet it can reduce intrinsic yield potential by shortening the developmental phase and decreasing the number of fertile florets. Ultimately, the strategic manipulation of these alleles remains essential for synchronising wheat's life cycle with favourable environmental conditions to maximise global productivity

Keywords: Photoperiodism, photoperiod insensitivity, Green Revolution, Ppd-1 genes (Ppd-A1, Ppd-B1, Ppd-D1), Wheat adaptation, Flowering time regulation, Climate resilience

Introduction

The global success of wheat (*Triticum aestivum* L.) as a staple food crop is fundamentally linked to its remarkable adaptability to a vast range of environments. Breeding wheat for photoperiod insensitivity has been a key strategy in adapting this crop to a wide range of environments and farming systems. Photoperiod insensitivity allows wheat plants to flower and mature regardless of day length, which is crucial for stable yields across diverse latitudes and sowing times. Photoperiodism is the physiological response of an organism to the length of the day or night. It is a fundamental mechanism by which plants synchronize their life cycles with predictable seasonal changes. Ancestrally, wheat is a facultative long-day (LD) plant, meaning its transition to flowering is accelerated by long days. The transition from vegetative to reproductive growth, culminating in flowering is the most crucial phase in the plant's life cycle. The timing of this event must be synchronized with the most favorable environmental conditions of a given location to maximize grain yield. Flowering too early exposes the developing floral organs to the risk of late-season frosts, while flowering too late can subject the sensitive grain-filling period to terminal heat and drought stress, both of which can severely affect the productivity. Photoperiod sensitivity means that plant development is tied to specific light durations. However, this sensitivity restricts geographical adaptability and causes yield instability if environmental conditions deviate. Breeding for photoperiod insensitivity allows wheat to be grown across a wider range of latitudes and planting dates.

History of Photoperiod Insensitivity and Green Revolution

Prior to the introduction of semi-dwarf wheats, India was cultivating tall, photosensitive and late maturing genotypes. Wheat production in India increased dramatically after introduction of semi-dwarf wheats, Lerma Rojo (*Rht1*) and Sonoro 64 (*Rht2*) in 1965. The dwarfing genes (*Rht1*, *Rht2*) provided lodging resistance by reducing the plant height genetically. A major innovation of Borlaug's wheat-breeding programme in Mexico became was 'shuttle breeding'. In this approach, one generation was grown at CIMMYT in or near Toluca, Mexico, at an elevation of 2090 m, and the next generation in Ciudad Obregon, Mexico, at 38 m elevation. Borlaug worked in the field from early morning until late evening, breeding thousands of lines of wheat. This shuttle-breeding approach resulted in wheat lines that were much less dependent on the length of the day. The deliberate breeding for photoperiod insensitivity was a cornerstone of the Green Revolution in the mid-20th century. Such 'daylength insensitivity' or 'photoperiod insensitivity' allowed the Borlaug wheats to be grown widely across the world, including India and Pakistan, where millions of people had been starving because of food shortages. Incidentally, during green revolution photoperiod insensitive genes (*Ppd1*, *Ppd2*) were also introgressed into CIMMYT breeding programme at the same time as the two dwarfing genes. Both photoperiod insensitive (*Ppd-D1*) and height reducing (*Rht1*, *Rht2*) genes got introduced into Indian cultivars from Mexico and now are widely distributed in indigenously developed cultivars.

Genetics of Photoperiod Insensitivity in Wheat

The primary genes controlling photoperiod sensitivity in wheat are *Ppd-1* genes, which exist in three homeologous forms: *Ppd-A1*, *Ppd-B1*, and *Ppd-D1* (located on chromosomes 2A, 2B, and 2D).

- **Sensitive Alleles (Wild-type):** This are the ancestral or wild-type alleles. (*Ppd-A1b*, *Ppd-B1b*, *Ppd-D1b*). These alleles confer a photoperiod-sensitive (PS) phenotype, where plants exhibit delayed flowering under Short Day conditions.
- **Insensitive Alleles (Mutant):** These are the Mutant alleles that confer photoperiod-insensitivity (*Ppd-A1a*, *Ppd-B1a*, *Ppd-D1a*). These alleles accelerate development and allow for earlier flowering, particularly under ShortDay conditions.
- **Allelic Hierarchy:** There is a well-established hierarchy in the potency of the insensitive alleles to promote earliness. *Ppd-D1a* exerts the strongest effect, followed by *Ppd-B1a*, with *Ppd-A1a* having the weakest effect.

  ***Ppd-D1a* (strongest) > *Ppd-B1a* (intermediate) > *Ppd-A1a* (weakest).**

Molecular Mechanisms of Insensitivity

The PI phenotype in wheat has arisen through several distinct molecular mechanisms-

- **Promoter Deletions:** The most common mechanism, particularly for the most potent alleles, involves large deletions in the promoter region upstream of the gene's coding sequence.

✓ ***Ppd-D1a*** is characterized by a deletion of approximately 2 kb in its promoter region. This leads to aberrant expression and FT activation.

✓ ***Ppd-A1a*** is associated with several independent deletion events in its promoter, including deletions of 1027 bp, 1117 bp, and 1085 bp, all of which result in misexpression and an early flowering phenotype

- **Copy Number Variation (CNV):** The *Ppd-B1a* allele represents a different evolutionary solution. Its PI phenotype is not caused by a sequence mutation but by an increase in the copy number of the entire gene. This gene duplication leads to higher overall transcript levels, which is sufficient to accelerate flowering. Genetic evidence suggests that alleles with increased copy number have arisen independently on at least two separate occasions during wheat's domestication and breeding history.

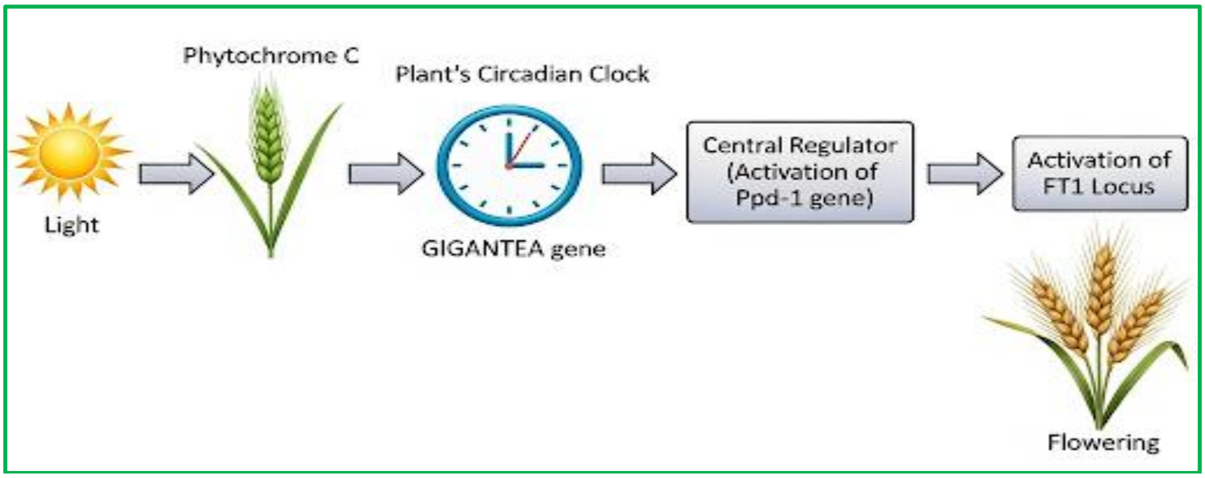
Locus	Allele Type	Allele Name	Molecular Basis	Relative Effect on flowering	Key Source/ Varieties
2D	Insensitive	*Ppd-D1a*	2089 bp promoter deletion leading to misexpression and FT activation	Strongest	Akakomugi, sonoro 64, Mazhamai,Youzimai
2B	Insensitive	*Ppd-B1a*	Gene copy number variation, elevated expression	Intermediate	Shiroboro 21, Chinese spring
2A	Insensitive	*Ppd-A1a*	1027, 1117 bp promoter deletion leading to misexpression and FT activation	Weakest	Purple straw
2D,2B,2A	Sensitive	*Ppd-D1b, Ppd-B1b, Ppd-A1a*	Intact promoter, single copy	wildtype	Local landraces, HD-2687, C-306

Molecular Pathway of Flowering

A sophisticated network translates day length into a flowering signal.

- **Light Perception:** Photoreceptors in the leaves, particularly PHYTOCHROME C (PHYC), sense changes in red light.
- **Internal Clock:** The plant's internal circadian clock integrates the light signal to measure day length. Key genes involved *GIGANTEA* (a promoter) and *ELF3* (a repressor).
- **Central Regulator:** The *Ppd-1* gene acts as the main switch, becoming activated under the right light and clock conditions.
- **The "Go" Signal:** Activated *Ppd-1* triggers the production of FLOWERING LOCUS T1 (FT1), a mobile protein signal (florigen) that travels to the shoot tip to initiate the switch to reproductive growth.

In wheat, the primary florigen gene is *FLOWERING LOCUS T1* (*FT1*). The elevated expression of *Ppd-1a* alleles leads to a strong and sustained upregulation of *FT1* transcription in the leaves. The FT1 protein is then transported through the phloem to the shoot apical meristem, where it acts as a floral activator, triggering the developmental switch from vegetative leaf production to reproductive spikelet formation.



Breeding Methods for Development of Photoperiod Insensitive Wheat Varieties

1. Introduction

It refers to the process of takin a genotype or a group of genotypes of plants into a new aera or region where they were not being grown before.

The semi-dwarf wheat varieties were developed by Dr. Norman E Borlaug and his associates at CIMMYT, Mexico by using a Japanese variety Norin 10 as the source of dwarfing gene.

In 1963, these varieties got introduced into India. In later studies it was found that these semi-dwarf varieties also possessed genes for photoperiod insensitivity.

Examples- Sonoro 64, Lerma Rojo 64A

2. Pureline Selection

It refers to a process where a large number of plants are selected from a self-pollinated crop and harvested individually and then the individual plant progenies are evaluated and the best progeny is released as pureline variety.

This method can be used to select the photoperiod insensitive plants from heterogeneous populations.

Examples- Kalyan Sona and Sonalika are selections from introductions from CIMMYT, Mexico.

3. Hybridization and selection

It refers to the process of crossing two genetically different organisms.

By using hybridization method, photoperiod insensitive donors can be crossed with locally adapted varieties and progenies and be selected for insensitivity. For performing selections in segregating populations, following three methods are used-

- **Pedigree Selection**- In this method, individual plants are selected from F_2 and subsequent generations, their progenies are grown and a record of all the parent offspring relationships is maintained. Individual plant selection is continued till the progenies become virtually homozygous.
- **Bulk Method**-In this method, F_2 and the subsequent generations are harvested in bulk to raise the next generation. At the end of the bulking period, individual plants are selected and evaluated in similar manner as in the pedigree method.
- **Backcross method**- A cross between a hybrid and one its parents is known as Backcross. In backcross method, the hybrid and the progenies in the subsequent generations are repeatedly backcrossed to one of the F_1.

Examples- PBW 373, WR 544, Raj 3765, Halna, HD 3117, Japanese NILs eg. H(A), H(B), H(C), H(D) from Haruhikari x Saitama 27, Paragon NILs (with alleles from Chinese Spring, GS-100).

4. Shuttle Breeding

It is a modified pedigree-bulk method. In this method breeding populations are grown and selected in two or more contrasting environments in alternating generations to accelerate breeding cycle and improve adaptation. By using shuttle breeding method, Dr. Norman E Borlaug developed several photoperiod wheat varieties which became the key component in Green Revolution

Examples- Sonoro 64, Lerma Rojo 64A, Siete Cerros 66, Tobari 66

5. Mutation Breeding

It is a method that uses induced mutations to create new plant varieties with desirable traits. This method can be used to induce mutations in Ppd genes to break photoperiod sensitivity.

Example- Sharbati sonoro -γ ray induced mutant of Sonoro 64.

6. Marker Assisted Selection (MAS)

It refers to the indirect selection for a gene or QTL based on molecular markers closely linked to the desired gene or QTL. DNA markers can be used to detect insensitive alleles for early selection.

Example- Gale (OR2180377) It is a variety adapted to the Willamette Valley in western Oregon. It was developed using molecular markers for photoperiod insensitivity and resistance to certain diseases.

7. Genome editing

It refers to the modification of genomic DNA at a specific target site in a wide variety of cell types and organism, including insertion, deletion and replacement of DNA, resulting in inactivation of target genes or acquisition of novel genetic traits. Genome Editing can be used to precisely modify the Ppd genes to remove sensitivity.

Example- CRISPER/Cas9 has been successfully employed to simultaneously modify the three homoelogs of the *Ppd-1* gene in wheat, leading to the generation of Tappd-1 mutant plants.

Advantages and challenges

- **The Advantages:**
- ✓ **Broad Adaptation:** Enabled wheat cultivation across a vast range of latitudes and sowing dates.
- ✓ **Stress Avoidance:** Early flowering helps the crop escape end-of-season heat and drought.
- **Challenges**

Yield Potential: Photoperiod insensitivity shortens the time to flowering. When plants flower early, they develop faster. This fast growth reduces the time for the plant to form and support florets. This leads to fewer fertile florets and, therefore, fewer grains per spike.

The strongest allele, *Ppd-D1a*, causes the greatest reduction in floret number, followed by *Ppd-A1a* and *Ppd-B1a*. Conversely, the fully sensitive genotype consistently produces the highest number of fertile florets, especially when grown under shorter days that naturally prolong its development. Hence, photoperiod sensitivity (*Ppd-1b*), allows for longer developmental phases and more fertile florets—also carries the highest risk of catastrophic failure if that long duration pushes flowering into a stressful period. Conversely, photoperiod insensitivity (*Ppd-1a*) acts as a genetic "insurance policy," shortening the lifecycle to escape end-of-season stress, but this security comes at the cost of a lower intrinsic yield potential.

Advancement

Recent research has begun to dissect the molecular pathway downstream of *Ppd-1* to identify new targets for manipulation.It is now known that *Ppd-1* influences the expression of a suite of transcription factors that control meristem identity and spikelet development.

A landmark discovery in this area is the identification of *ALOG1*, a transcription factor regulated by *Ppd-1*. In a remarkable finding, deleting the *ALOG1* gene was shown to induce branching in the normally unbranched wheat spike, indicating it is a major suppressor of this trait.

Conclusion

- The manipulation of photoperiod sensitivity has been one of the most impactful achievements in wheat breeding, enabling its global success.
- This trait involves a fundamental trade-off between environmental adaptation and intrinsic yield potential, which breeders manage using *Ppd-1* alleles.
- Breeding methods have advanced from slow field observation to rapid and precise molecular selection.

References

1. Tanio, M., & Kato, K. (2007). Development of near-isogenic lines for photoperiod-insensitive genes, Ppd-B1 and Ppd-D1, carried by the Japanese wheat cultivars and their effect on apical development. *Breeding Science*, 57(1), 65–72.
2. https://www.jstage.jst.go.jp/article/jsbbs/57/1/57_1_65/_article

3. Yang, F. P., Zhang, X. K., Xia, X. C., Laurie, D. A., Yang, W. X., & He, Z. H. (2009). Distribution of the photoperiod-insensitive *Ppd-D1a* allele in Chinese wheat cultivars. *Euphytica*, 165(2), 445–452.
4. https://doi.org/10.1007/s10681-008-9745-y
5. Seki, M., Chono, M., Matsunaka, H., Fujita, M., Oda, S., Kubo, K., Kiribuchi-Otobe, C., Kojima, H., Nishida, H., & Kato, K. (2011). Distribution of photoperiod-insensitive alleles *Ppd-B1a* and *Ppd-D1a* and their effect on heading time in Japanese wheat cultivars. *Breeding Science, 61*(4), 405–412. https://doi.org/10.1270/jsbbs.61.405
6. Vinod, Sharma, J. B., Tomar, R. S., Singh, B., & Tomar, S. M. S. (2012). Breeding for earliness and thermo-tolerance in wheat suited to early, late and very late sowing in northwestern India. *Indian Journal of Genetics and Plant Breeding*, 72(01), 15–24. https://www.isgpb.org/journal/index.php/IJGPB/article/view/783
7. Phillips, R. L. (2013). Norman Ernest Borlaug. 25 March 1914 – 12 September 2009. Biographical Memoirs of Fellows of the Royal Society, 59, 59–72. https://royalsocietypublishing.org/doi/pdf/10.1098/rsbm.2013.0012
8. Chen, L., Du, Y., Lu, Q., Chen, H., Meng, R., Cui, C., Lu, S., Yang, Y., Chai, Y., Li, J., Liu, L., Qi, X., Li, H., Mishina, K., & Hu, Y.-G. (2018). The photoperiod-insensitive allele Ppd-D1a promotes earlier flowering in Rht12 dwarf plants of bread wheat. *Frontiers in Plant Science, 9*, Article 1312. https://doi.org/10.3389/fpls.2018.01312
9. Pérez-Gianmarco, T. I., Slafer, G. A., & González, F. G. (2019). Photoperiod-sensitivity genes shape floret development in wheat. Journal of Experimental Botany, 70(4), 1339–1348
10. https://pmc.ncbi.nlm.nih.gov/articles/PMC6382326/
11. Singh, B. D. (2021). Plant breeding: Principles and methods (12th ed.).
12. Errum, A., Rehman, N., Uzair, M., Inam, S., Ali, G. M., & Khan, M. R. (2023). CRISPR/Cas9 editing of wheat Ppd-1 gene homoeologs alters spike architecture and grain morphometric traits. Functional & Integrative Genomics, 23(1), 66. https://pubmed.ncbi.nlm.nih.gov/36840774/