Plant Archives
Journal home page: www.plantarchives.org
DOI Url: https://doi.org/10.51470/PLANTARCHIVES.2021.v21.no1.077

GENETIC VARIATION IN WEED SEED DORMANCY AND THEIR MANAGEMENT IN CROPS: A REVIEW

Bhagirath Singh Chauhan[1], Michael Thompson[1] and Romesh Kumar Salgotra[1,2*]

[1]Queensland Alliance for Agriculture and Food Innovation (QAAFI), the University of Queensland, Gatton, Queensland 4343, Australia
[2]School of Biotechnology, Sher-e-Kashmir University of Agricultural Sciences & Technology of Jammu, Chatha, Jammu-180009 (J & K), India
*E-mail: rks_2959@rediffmail.com

(Date of Receiving-09-11-2020; Date of Acceptance-04-02-2021)

ABSTRACT

Evolution in the seed dormancy depends on the presence of heritable variation in weed populations. This genetic variation in weeds arises because of abundant, grow rapidly, and produce large numbers of off springs. Compared with other plant species, populations of weed species frequently show limited genetic variation in seed dormancy due to colonization, extensive clonal propagation, inbreeding, and the relative environmental homogeneity. Nevertheless, populations of weed species contain substantial store of genetic variation and genetic differentiation for seed dormancy and other reproductive traits because of pervasive feature of widely distributed nature of weed species. As a result, high level of genetic diversity among the weeds is fostered by hybridization, habitat longevity, environmental heterogeneity, outcrossing and large population size. The objective of this review is to update the existing literature concerned with genetic variation in seed dormancy and reproductive traits in weeds.

Keywords: genetic variation, seed dormancy, reproductive traits, molecular, weeds management

INTRODUCTION

Seed dormancy is a complex trait regulated by various physiological, biochemical, genetic and environmental factors. This complex trait is controlled by polygenes and its expression is modified according to environmental factors. Genetically, seed dormancy is a quantitative trait controlled by a number of other traits (Li and Foley, 1997). Weed seed dormancy is a serious problem in agriculture, causing high grain yield losses. Genetic variation exists within and between weed populations and results in the expression of different phenotypes. Hybridization and mutation are the main factors responsible for creating and maintaining genetic variation (Slatkin, 1987). Variation in weed seed dormancy also occurs as a result of genetic differentiation due to different gene expression and the suppression and activation of sets of genes during seed developmental stages under varied environmental conditions. The extent of intraspecific variation differs widely among weed species.

Seed dormancy is an inherent trait in a variety of weed species (Foley and Fennimore, 1998), many of which are highly competitive (Table 1). The dormancy of weeds, such as the *Avena* species, is also affected by genetic variation, which enables the seeds to remain dormant and viable in the soil for several years (Naylor and Jana, 1976; Seeley, 1977; Simpson, 1978; Naylor, 1983). The genes responsible for variation in seed dormancy enable us to understand the mechanism underlying seed dormancy. Variation in seed dormancy is predominately present among populations as well as within a particular population. Some of the species such as *Arabidopsis thaliana* showed vast variation within and amongst populations for seed dormancy and other phenological characteristics (Brachi *et al*., 2013). The variation in seed dormancy is also due to the result of genotype x environment interaction and the degree of dormancy is influenced by the genetic background of the species. Seed dormancy is governed by many genes and these genes expressed differentially in different developmental stages of dormant seeds (Li and Foley, 1997). The genetic variation for seed dormancy has also been exhibited in numerous cross-pollinated and self-pollinated crops (Warwick, 1990; Bennett, 1997; Cocks, 1999; Nichols and Cocks, 2006). Characterization of variables that impact dormancy and germination of weeds are important for growers as farmers can adjust the planting of crops according to the timing of the germination of weed seeds. This helps farmers avoid the maximum competition between weed seeds and crop seeds for water, nutrients and light.

Seed dormancy other reproductive characteristics in weeds are controlled genetically with the influence of environmental factors. Biochemical factors such as isozymes and molecular techniques further accelerate the conventional methods of genetic variation (Salgotra *et al*., 2015). Moreover, molecular approaches applied to access the genetic variation in seed dormancy are cost-effective, time saving, quick and precise. In this review, the existing knowledge of the genetic variation of weed seed dormancy and other reproductive traits is reviewed and discussed through various genetic and molecular approaches.

Seed dormancy in weeds

Seed dormancy is a complex trait that allows for soil seed bank persistence which undermines weed management techniques and frequently drives environmentally

Table 1: Weed species with known hereditary components involved in seed dormancy

S. No.	Common name	Latin name	References
1.	Wild oats	Avena fatua	Adkins *et al.,* 1986
2.	Downy brome	Bromus tectorum	Meyer and Allen, 1999
3.	Blue-eyed Mary	Collinsia verna	Kalisz, 1986
4.	Milanje finger grass	Digitaria milanjiana	Hacker, 1984
5.	Lisianthus	Eustoma grandiflorum	Ecker *et al.,* 1994
6.	Ryegrass	Lolium perenne	Hayward and Breese, 1966
7.	Wild radish	Raphanus raphanistrum	Cheam, 1986
8.	Townsville stylo	Stylosanthes humilis	Cameron, 1965
9.	Cow vetch	Vicia cracca	Sain, 1948

Figure 1. Seed dormancy and germination stages of weeds.

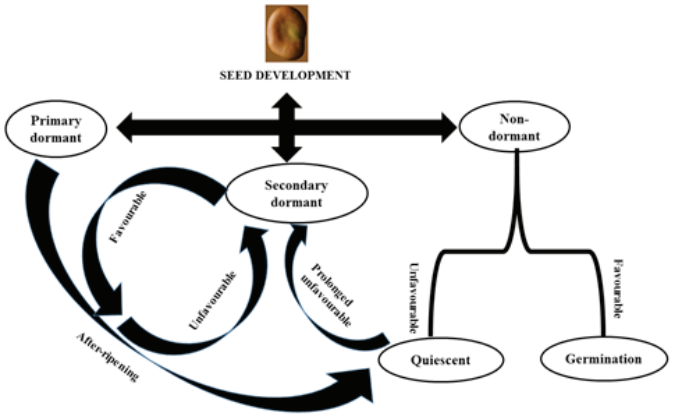
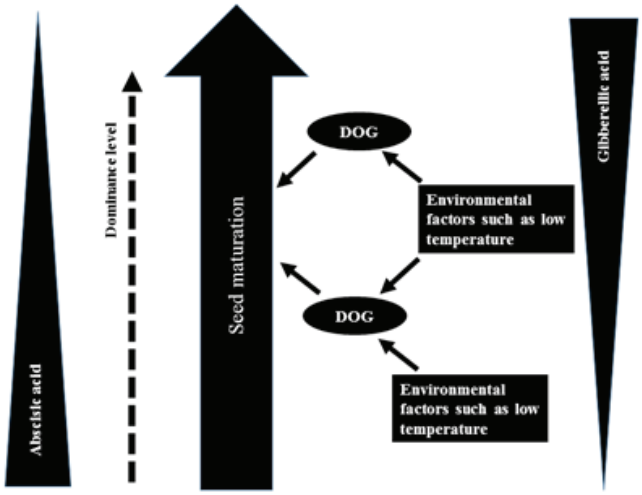


Figure 2. Roles of environmental and endogenous factors in seed dormancy. Dormancy and germination are regulated by the balance between ABA and GA. Factors controlling the induction of dormancy during seed maturation.



unfriendly conditions. (Simpson, 1990). In primary seed dormancy the seed is already in a dormant state when released from the plant whereas in secondary seed dormancy, the dormancy is due to environmental factors. Coat induced dormancy and embryo dormancy are two types of primary dormancy (Figure 1).

Seed quiescence, a non-dormant condition, is different from seed dormancy. Seed dormancy is due to some internal inhibition of seed germination under favourable conditions, whereas in quiescence, the normal seed germination is inhibited due to the non-availability of favourable conditions such as absence of favourable temperature, moisture etc. Generally, quiescent seeds begin germination under favourable conditions with the projection of the radicle from the seed (Bewley and Black, 1994). In nature, wild seed ranges from highly dormant to non-dormant (Naylor and Jana, 1976), and the genetic and environmental factors have a strong influence on the degree of seed dormancy (Bewley and Black, 1994).

Generally, seed dormancy is divided into seed coat imposed dormancy and embryo induced dormancy (Bewley and Black, 1994). The seed coat and embryo tissues are subject to modification and show variation due to fluctuations in temperature and light during the development of the seed. Thus, variation in environmental conditions during seed development provides another route for developing variation in seed dormancy. Different conditions such as cool-wet, warm-wet, cool-dry, or hot-dry lead to the progress of after-ripening which is genotypic or species specific. The quantification of seed dormancy characteristics is very difficult and the best way to measure seed dormancy is to estimate the post-mature requisite, which involves numerous analyses.

Seed dormancy is considered an undesirable characteristic in cultivated crops (Ringlund, 1993). Dormant seeds may remain in the soil for extended periods and germination can be impacted by seed burial depth. Weeds possess a wide range of genetic variation for dormancy in seeds (Gianinetti and Cohn, 2008). In addition to genetic variation, dormancy is also controlled by light, temperature, moisture and depth of seeds in the soil (Roberts, 1961; Gianinetti and Cohn, 2008). While genetic variation has been recorded in many species over the period of primary dormancy, there have been far fewer efforts to determine the genetic factors causing dormancy. In one experiment, inbred non-dormant and dormant genotypes were cross-pollinated to produce the segregating population to study the effect of cytoplasmic male sterility factors on seed dormancy (Li and Foley, 1997). The segregating population developed from non-dormant and dormant genotypes showed that seed dormancy is a polygenic trait and is controlled by a number of genes. Besides the various morphological and biochemical approaches used to study the genetics of

dormancy, recent molecular techniques seem to provide the best alternative to map the loci in weed seed dormancy.

Genetics of morphological traits in seed dormancy

In some cases, seed dormancy occurs when particular morphological traits such as the rudimentary and linear embryo are not fully developed at the time of maturity. The heritable components controlling morphological character have a genetic basis which correlates the changes in morphological traits with changes at the genetic level, i.e. allele or genotype level (van Eck, 2007). Particular weed populations often show variation in the degree of expression of morphological traits. Much of this morphological variability in seed dormancy is also a result of morphological trait plasticity. The morphological variation observed in weed populations differs from species to species, but may not reflect a high level of genetic diversity. Slender wild oat (*Avena barbata*) is genetically less variable than wild oat (*Avena fatua*) but shows greater overall phenotypic variation. It appears that slender wild oat depends more on phenotypical plasticity and less on genetic variation (Marshall and Jain, 1968; Jain and Marshall, 1967; Jain *et al*., 1969).

Gene mutation causes a sudden heritable change in DNA sequence, which may affect the traits controlled by that gene. Genetic variability in seed dormancy can be estimated when two species with different alleles in genes impacting dormancy are compared in similar environmental conditions that allow for the penetrance of phenotypic differences. Gene mutations also have a significant effect on seed dormancy in weeds. A study on seed shape mutation was conducted to know the significance of seed testa in seed dormancy. The study showed that the seed testa played an important role in determining the seed dormancy in *A. thaliana.* A decrease in seed dormancy was observed because testa in *A. thaliana* has three layers instead of five (Leon-Kloosterziel *et al*., 1994).

Heterostyly

Heterostyly is a form of polymorphism where the stamens and styles of flowers can be positioned at different heights in different plants of the same species. Darwin (1877) believed heterostyly was an adaptation to promote outbreeding. The different morphological structures of flowers such as long stamens, medium stamens, short stamens, big anthers, small anthers, long and short styles etc., play an important role in outbreeding and subsequent seed development. However, in the case of aquatic pickerel weed (*Pontederia cordata*) no significant difference was observed in seed germination from long, medium and short styles of flowers (Price and Barrett, 1982). Conversely, purple loosestrife (*Lythrum salicaria*), seeds showed a lesser percentage of seed germination from mid-style flowers than their short-style flowers (Anderson and Ascher, 2000).

Microgametophyte competition

The generation of the sporophyte trait is influenced by the selection of macrogametophyte because of an increase in the efficiency of the pollen tube and ovule interaction. Therefore, high loads of pollen result in better sporophytes than low pollen loads. This pollen tube and ovule interaction is also influenced by the harmful effect of gene mutations, where growth of the pollen tube in the ovule can slow down. This can be overcome by increasing the deposition of pollen load on the stigma for complete fertilization of all the stigmas in the flower, which would also increase the hybrid (F_1) vigour in subsequent generations. Moreover, the selection of macrogametophyte is also influenced by the heritable nature of pollen tube growth and gene expression overlaps. Similarly, pollen tube and ovule interaction efficiency is also influenced by the multiple paternity because of deposition of different types of pollen on the stigmas by different pollinators (Bernasconi, 2003).

Variation in weed seed dormancy

As dormancy in seeds is the absence of seed germination due to genetic factors even under favourable environmental conditions (Hilhorst, 1995). Several processes such as the polygenic nature of inheritance, epistatic and genotype x environment are involved in the stimulation of seed dormancy. In addition to these factors, different plant growth hormones (IBA, IAA) are involved in the induction of dormancy. All factors responsible for seed dormancy are controlled by genes. Variation in seed dormancy is also due to the interactive effects of genotype and environment. This results in incredible variation in dormancy resulting in the evolution of diverse dormancy periods in weeds. In nature, the genetic variation in seed dormancy originates due to crossing (hybridization), non-Mendelian inheritance and mutation.

Hybridization

The hybridization of domesticated crops to wild species has generated new races of weeds (Ellstrand *et al*., 1999). This process, as well as natural selection, may also lead to the evolution of new genotypes with varying degrees of seed dormancy in weeds. Hybridization is intentionally used for transferring useful traits in the development of hybrids, appropriate lineage diversity, and to produce unique phenotypes. The advancement of genomics and proteomic tools has further increased the interest in hybridization and outbreeding (Payseur and Rieseberg, 2016).

Hybridization and outbreeding have played major roles in the evolution of some weed species. Gene flow among different genera and taxa has been well studied with the use of modern biotechnological tools. Hybridization and outbreeding lead to the generation of divergent phenotypes and further speciation under varied environmental conditions. Moreover, immediate phenotypic expression of hybrids can be observed through hybridization. Hybrid speciation may occur either at the level of the homoploid or polyploid level, each with its attendant genetic and evolutionary consequences. While allopolyploidy has since been recognized as an essential mode of plant speciation,

in most weeds, the consequences of genome duplication have not typically been considered. Outbreeding leads to the adaptation of species through gene flow in weed genotypes, where allele introgression from dormant genotypes results in the evolution of new weed species after introduction and selection of allele that have varied levels of seed dormancy. Hybridization at the same ploidy levels or different ploidy levels of a species serves as the point of origin for the evolution of new species. Desired characteristics can also be transferred to species at different ploidy levels along with many other potential and demonstrated effects (Cronn and Wendel, 2004).

Non-mendelian (maternal) influence

Maternal influence has a direct impact on cytoplasmic or extranuclear inheritance (Kerdaffrec and Nordborg, 2017), environmental impacts seed growth and development, and indirectly impacts epigenetic modification of genes controlling propensity for germination/dormancy (Battle and Whittington, 1971). During fertilization, genes or genetic material are transmitted to the offspring in plastids and/or mitochondria. Most angiosperms have plastid maternal inheritance, but selected species have also shown non-Mendelian influence (Harel *et al*., 2015). It has been shown that the non-Mendelian effect on dormancy of seed is regulated by various inhibitors during germination, which is transferred to the seeds (Battle and Whittington, 1971). Some dormancy inducing chemicals were also generated in the embryo by the mother and deposited into weed seeds (Morley, 1958).

Mutation

Mutations are the main sources of variation in the seed dormancy and reproductive traits of weeds. The mutations cause variations in weed seed reproductive traits that may affect the pollination and fertilization processes. Variations in weed seed dormancy also originate through spontaneous or artificial mutations. Due to the spontaneous nature of mutation, the gene frequency is very low compared to induced mutations. The mutant of common wheat (*Triticum aestivum*) showed a significantly longer seed dormancy period than its wild relative, which may result in reduced pre-harvest sprouting of grains on spikes (Abe *et al*., 2019). Three independent events with multiple mutations in the mutant were observed compared with the wild type.

Genetic basis for seed dormancy

Seed dormancy is a polygenic trait which is regulated by a number of genes with minor and cumulative effects (Foley and Fennimore, 1998). In quantitative traits, the environment may strongly interact with genotypes to produce the resulting phenotype (Naylor, 1983). Genetic seed dormancy studies are complicated by the fact that various tissues within a seed have different parentage. Factors such as genetic makeup, maternal environment during maturation and the age of the plant play a significant role in the different levels of dormancy in weeds (Fenner, 1991). These factors are also influenced by genetic variation that regulates seed dormancy differences among species. In some species, such as wild oat, embryo genotype has been shown to be of overriding importance in determining seed dormancy except when it is masked by true embryo dormancy (Garbutt and Witcomb, 1986). Gu *et al*. (2003) suggested the presence of genetically complex networks in the regulation of variation for seed dormancy in natural populations of weedy rice. Multiple loci and epistasis control genetic variation for seed dormancy in the weed. Iso-chromosomes have been also mentioned to determine seed germination and dormancy. However, molecular studies on dormancy genetics are clearly rare, and there is a need for research in this aspect and genetic dormancy differences among and between weed species and their populations and the link of these with environmental conditions.

Dormancy is a genetically complex trait controlled by polygenes with effects modified by the genetic background and environmental factors. A major approach to determine the genetic architecture for seed dormancy is to dissect it into quantitative trait loci (QTL), such as in Arabidopsis, barley, sorghum, rice, and wheat (Alonso-Blanco *et al*., 2003). Quantitative trait loci analysis is also a prerequisite to clone and characterize genes that directly regulate seed dormancy and germination and to facilitate marker-assisted selection for resistance to PHS in breeding programmes. Genotype-by-environment (G x E) interactions have been reported for seed dormancy in several species (Gu *et al*., 2003). The growth environment greatly affects both the number and the influence of individual QTL in a mapping population. Epistasis, the interaction between or among alleles at two or more loci, is critical to advanced quantitative genetic models. Assembly of favorable epistatic combinations is considered as the single most important genetic basis underlying the evolution of adaptiveness in plants. On the basis of Mendelian approaches, two- and three-locus epistasis for the control of dormancy have been postulated for rice, wheat, and wild oat (Gu *et al*., 2003). Epistasis between two dormancy QTL was reported in an Arabidopsis, a barley, and a wheat mapping population (Alonso-Blanco *et al*., 2003). Rice is greatly divergent in the degree of seed dormancy. Some of the most highly dormant genotypes are found among the nondomesticated accessions from wild (*O. rufipogon*) and weedy rice (*O. sativa*). These nondomesticated genotypes likely harbor major genes or alleles for seed dormancy that might have been eliminated during domestication. As a first step toward cloning dormancy genes, we have characterized some weedy rice strains for the types and levels of seed dormancy and the genetic aspects of coat-imposed dormancy (Gu *et al*., 2003). Here we report construction of a weedy rice genetic map, identification of dormancy QTL, and characterization of the QTL for epistasis and QTL-by-environment (QTL x E) interaction. The higher-order epistasis strongly suggest the presence of

genetically complex networks in the regulation of variation for seed dormancy in natural populations and make it critical to select for a favorable combination of alleles at multiple loci in positional cloning of a target dormancy gene (Gu *et al*., 2003).

Seed dormancy has been an inherited element in both cultivated crop species as well as weeds. Genetic investigations have shown that the complex nature of dormancy is regulated by activities of a number of genes. For example, Gu *et al.,* (2008) identified the quantitative trait locus (QTL) *qSD12* which controls dormancy in weedy/red rice (*Oryza sativa*) Genes involved in dormancy behave quantitatively for controlling their various respective morphological traits. Mutation of these genes results in the occurrence of new variants of dormancy with particularly different dynamics of genetic inheritance. Genes controlling seed dormancy show interactions with each other, and their cumulative effects change the phenotypic expression of a trait. Moreover, with the advancement and availability of new genomics tools our understanding of seed dormancy in the field of genetics has improved significantly (Bentsink and Koornneef, 2008).

Mapping in seed dormancy

In QTL mapping, a region in the genome which is associated with a particular trait of interest is identified and mapped using molecular markers. In *A. thaliana,* seven QTLs have been identified that account for more than 60 per cent of phenotypic variation in after-ripening requirements (Alonso-Blanco *et al.,* 2003). The main factors responsible for the genetic variation in seed dormancy in *A. thaliana* are molecular pathways and cumulative genetic effects (Bentsinka *et al.,* 2010). In *A. Thaliana*, dry non-dormant seeds have less abscisic acid than the dormant seeds along with an expression of dormancy associated genes. A gene expression study using transcriptome analysis in *A. thaliana* compared non-dormant and dormant seeds and indicated that no significant correlation was observed with seed dormancy and genes, namely: *ABA-insensitive 3* (*AB13*)*, FUSCA 3* (*FUS3*) (Luerssen *et al*., 1998) and *LEAFY COTYLEDONS* (*LEC1*) (Lotan *et al.,* 1998). Similarly, the 1-cysPrx level showed no correlation with the time period required for seeds of *A. thaliana* to after-ripen. Moreover, the dormant seeds showed lower levels of abscisic acid than non-dormant (after-ripened) seeds in *A. thaliana* due to the presence of the *AtCYP707A2* gene (Alonso-Blanco *et al.,* 2003).

In QTL mapping, the identified genome region on the chromosome may accommodate a number of genes for a QTLS or candidate gene(s) In order to narrow down the candidate gene region, other molecular techniques such as genome-wide association study (GWAS) are used. In GWAS-like Association Mapping a naturally diverse population is used instead of a biparental population. GWAS is an effective approach to avoid the use of biparental populations and their phenotypic evaluations. Compared to the biparental population, having a diverse population in GWAS identifies a greater number of alleles linked with the candidate genes. The limitations of QTL analysis can be overcome using GWAS, which can narrow down the candidate regions using natural populations (Lu *et al.,* 2017). A combination of GWAS and haplotype analysis has suggested an involvement of independent genes and alleles that lead to seed dormancy control and natural variation in rice populations (Lu *et al*., 2017). The GWAS method has been employed in a number of crops to identify potential candidate genes. A GWAS study for dormancy was conducted in rice accessions in which nine significant single nucleotide polymorphisms (SNPs) were identified which contributed to 34.9% of the phenotypic variation (Lu *et al.,* 2017). Similarly, a GWAS investigation was carried out in a set of *A. thaliana* species to study the effect of temperature on variation in seed dormancy and reported that it is controlled by the interaction of maternal environmental factors and genotypes. They have also identified a number of candidate genes controlling this trait (Kerdaffrec and Nordborg, 2017). Further, the GWAS technique can potentially be used for the identification of candidate genes for complex traits in seed dormancy of weeds.

Molecular basis of seed dormancy

While genetic studies to explore the complex trait of seed dormancy have been carried out, literature on the molecular basis of seed dormancy is limited despite recent studies that have been possible due to the advancement of molecular techniques such as genomics, transcriptomics, proteomics etc. The model plant *A. thaliana* has been studied to some extent after the availability of its complete genome sequence and is considered an ideal plant for study of seed dormancy. A large number of mutations have been artificially generated for affecting seed dormancy and germination, and subsequent studies have been conducted using genetic, physiological and molecular approaches. For example, the mutant genotypes for *LEAFY COTYLEDONS* (*LEC1* and *LEC2*) (Lotan *et al*., 1998), *ABA-insensitive 3* (*ABI3*) and *FUSCA 3* (*FUS3*) (Luerssen *et al.,* 1998) have non-dormant seeds with some defects, suggesting that these genes play an integral role during the developmental stages of seed dormancy. It has also been observed that mutants have altered biosynthesis of phytohormones during the process of seed development. The biosynthesis of the phytohormone gibberellin is affected by the non-germinating mutants and abscisic acid (ABA) by non-dormant mutants and these two phytohormones demonstrated opposite roles in seed dormancy (Debeaujon and Koornneef, 2000). In phytochrome photoreceptor deficient mutants, light-induced stimulation is affected (Casal and Sanchez, 1998) which affect the seed dormancy in *A. thaliana* (McCullough and Shropshire, 1970). Seed germination is affected by DNA-binding with one finger (*DOF*) (Papi *et al*., 2000), *LEAFY COTYLEDON 1 (LEC1*) and *LEAFY COTYLEDON 1 (LEC2*) (Lotan *et al.*, 1998), *FUSCA3* (*FUS3*) (Luerssen *et al*., 1998) Similarly, other genes like *RDO1, RDO2, RDO3,* and *RDO4* also help

in establishing seed dormancy (Léon-Kloosterziel *et al.,* 1996; Peeters *et al.,* 2002).

Besides mutagenesis approaches, several molecular approaches have been carried out considering *A. thaliana* as a model plant for seed dormancy. Nonetheless, it has only recently become possible to analyse the multifactorial genetic variation into the individual loci by using the QTL mapping procedure. This method is used to study the genetic variation in seed dormancy in cultivated species such as rice, barley and wheat. In *A. thaliana*, a cross between two different accessions such as Landsberg *erecta* (L*er*) and Columbia (Col) results in differences in seed dormancy and thus allows mapping of genes controlling the concerned trait. Gu *et al*., (2004) identified QTLs in weedy/red rice (*Oryza sativa*) for ripening period, high level production of ABA and red pericarp colour with high phenotypic variations.

Numerous studies were conducted to identify QTLs linked with seed dormancy using naturally diverse populations and recombinant inbred lines (RILs) populations in *A. thaliana* (Lawrence, 1976; Ratcliffe, 1976; Bentsink *et al*., 2007; Meng *et al*., 2008). The *Delay of Germination 1* (*DOG1*) QTL showed association with seed developmental stages and was observed to be a novel QTL linked with seed dormancy (Bentsink *et al*., 2006). The microarray analysis in *A. thaliana* indicated an increased level of expression for more than 30 genes, however, a decreased level of expression was observed for *DOG1* in non-dormant seed. The *hub 1* mutant, characterized by a decreased seed dormancy along with a decrease in the expression of *DOG1* indicates the role of *DOG1* in controlling dormancy rates. For example, *ABA hypersensitive germination 1* (*AHG1*) interacts with *DOG1* to play a positive role *in vitro* as well as *in vivo* in the regulation of seed dormancy (Nishimura *et al*., 2018).

Strategies to manage the seed dormancy of weeds

Weeds are the main persistent problem present in all agriculture systems. They are one of the main factors responsible for crop yield losses everywhere in the world. These losses can exceed those inflicted by insect pests and diseases. Seed dormancy is generally imposed due to seed coat coverage and embryo induced dormancy. Both seed coat coverage and embryo induced dormancy are genetically controlled with the influence of environmental factors (Bewley and Black, 1982). Both seed coat and embryo induced dormancy are regulated during different developmental phases and are affected by micro- and macro-environments. Accordingly micro- and macro-environment factors affect seed germination and dormancy and these may either inhibit or encourage seed germination. Studying mutant weed genotypes which fail to establish dormancy can help to identify genes that enhance weed seed dormancy. For example, ABA inhibits germination of seeds and is responsible for establishing dormancy in weed seeds. The complex nature of seed dormancy is due to the significant interaction between the developmental stages of a seed and its environment (Figure 2).

Dormancy is normally overcome by after-ripening. After-ripening dormancy is a period when seeds do not germinate even under favourable environmental conditions. The requirements for weed seed germination are different to those of crop seed germination. The state of dormancy is induced when unfavourable environmental conditions occur in partially after-ripened seeds. Some seeds, such as naked seeds, require long term after-ripening treatments. The germination of these seeds occurs at any time in a year with a light-dark period. In addition, after-ripening of weed seeds can allow dormant seeds to germinate under suitable a condition which favours germination. These various traditional and modern physiological treatments can be used to manage weed seed dormancy and their alteration can help to break dormancy.

Increasing our knowledge of the seed dormancy mechanisms is very important for breaking seed dormancy. To address this, consideration should be given to genetics as well as the molecular and environmental factors responsible for germination. Different genes are expressed differently at different seed developmental stages in response to favourable environmental conditions in *A. thaliana*. Transcriptome analysis would help to understand gene expression at different levels (Yazdanpanah *et al.,* 2017). To provide in-depth knowledge about the mechanism of seed dormancy, more studies of differential gene expression should be conducted.

Concluding remarks and future perspectives

Seed dormancy in weeds is influenced by the interaction of genotypes and environmental factors which affect the various developmental stages of a seed including its reproductive traits. There is great potential for further study of this type of interaction which influences seed dormancy. More research should be conducted to in order to understand the genetic and environmental interaction in relation to seed germination and dormancy. Due to the polygenic nature of seed dormancy, variation exists even within weed species. As seed dormancy is also controlled genetically, studies should be conducted to determine the underlying mechanisms of seed dormancy. Although molecular approaches such as genomics, transcriptomics and proteomics have been used for the study of the mechanism of germination and seed dormancy in *A. thaliana* and some cultivated crop species, the information on the use of molecular techniques in weed seed dormancy is very limited. Advanced molecular approaches of genomics, transcriptomics and proteomics should also be applied for underlying the mechanism of seed dormancy in weed seeds. This will further help in the identification of QTLs and any candidate gene(s) responsible for seed dormancy. The mechanical, physiological, genetic, biochemical and molecular fields will assist researchers to better understand the mechanism of seed dormancy. This will give impetus to researchers as well as farmers who are facing acute problems in the management of weeds in crop

fields. Accordingly, these studies will inform policymakers for better management of weeds to enhance crop yields and reduce grower hardship. A comprehensive study of the genetics, genomics, transcriptome and proteomics are required to understand the mechanism of seed dormancy in weed species. This will help in determining the underlying genes responsible for dormancy in different weeds.

ACKNOWLEDGEMENTS

The author would like to gratefully acknowledge to Queensland Alliance for Agriculture and Food Innovation (QAAFI) to carry out the research under Endeavour Executive Fellowship Programme.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

REFERENCES

Abe, F.A., Haque, F., Hisano, H., Tanaka, T., Kamiya, Y., Mikami, M., Kawaura, K., Endo, M., Onishi, K., Hayashi, T. and Sato, K. (2019). "Genome-edited triple-recessive mutation alters seed dormancy in wheat". *Cell Reports,* 28, 1362-1369.

Adkins, S.W., Loewen, M. and Symons, S.J. (1986). "Variations within pure lines of wild oats (*Avena fatua*) in relation to degree of primary dormancy". *Weed Science,* 34, 859-864.

Alonso-Blanco, C., Bentsink, L., Hanhart, C.J., Blankenstijn-de Vries, H. and Koornneef, M. (2003). "Analysis of natural allelic variation at seed dormancy loci of *Arabidopsis thaliana. Genetics,* 164, 711-729.

Anderson, N.O. and Ascher, P. (2000). "Fecundity and fitness in cross-compatible pollination of tristilous North American *Lythrum salicaria* populations". *Theoretical Applied Genetics,* 101, 830-843.

Barrett, S.C.H. and Richardson, B.J. (1986). "*Ecology of biological invasions an Australian perspective".* In: Genetic Attributes of Invading Species, pp. 21–33. Groves, R.H. and J.J. Burdon (eds.) Australian Academy of Science, Canberra, Australia.

Battle, J.P. and Whittington, W.J. (1971). "Genetic variability in time to germination of sugar-beet clusters". *The Journal of Agricultural Science,* 76(01), 27-32.

Bennett, S.J. (1997). "Genetic variation between and within two populations of *Trifolium glomeratum* (cluster clover) in western Australia". *Australian Journal of Agriculture Research,* 48, 969-976.

Bentsink, L. and Koornneef, M. (2008) "Seed dormancy and germination". *Arabidopsis American Society of Plant Biologists,* doi: 10.1199/tab.0119.

Bentsink, L., Jowett, J., Hanhart, C.J. and Koornneef, M. (2006). "Cloning of *DOG1*, a quantitative trait locus controlling seed dormancy in *Arabidopsis". Proceeding of Natural Academy of Science USA,* 103, 17042–17047.

Bentsink, L., Soppe, W.J.J. and Koornneef, M. (2007). "*Genetic aspects of seed dormancy. Seed Development, dormancy and Germination."* eds Bradford KJ, Nonogaki H (Blackwell Publishing, Oxford), pp. 113-127.

Bentsinka, L., Hansona, J., Corrie, J.H., Blankestijn-de Vriesb, H., Coltraned, C., Keizerc, P., El-Lithyb, Alonso-Blancoe, C.M., Teresa de Andrése, Reymondf, M., Fred van Eeuwijkc, Sjef Smeekensa and Koornneef, M. (2010). "Natural variation for seed dormancy in *Arabidopsis* is regulated by additive genetic and molecular pathways". *PNAS,* 107 (9), 4264-4269.

Bernasconi, G. (2003). "Seed paternity in flowering plants: an evolutionary perspective". *Perspectives in Plant Ecology, Evolution and Systematics,* 6(3), 149-158.

Bewley, J.D. and Black, M. (1982). "*Physiology and Biochemistry of Seeds in Relation to Germination. 2. Viability, Dormancy and Environmental Control".* Berlin: Springer-Verlag.

Bewley, J.D. and Black, M. (1994). "*Seeds: physiology of development and germination"* Springer.

Bewley, J.D. (1997). "Seed germination and dormancy". *Plant Cell,* 9, 1055-1066.

Brachi, B., Villoutreix, R., Faure, N., Hautekeete, N., Piquot, Y., Pauwels, M., Roby, D., Cuguen, J., Bergelson, J., Roux, F. (2013). "Investigation of the geographical scale of adaptive phenological variation and its underlying genetics in *Arabidopsis thaliana". Molecular Ecology,* 22, 4222– 4240.

Brown, A.H.D. and Burdon, J.J. (1983). "Multilocus diversity in an outbreeding weed". *Echium plantagineum* L. *Australian Journal of Biological Science,* 36, 503-509.

Cameron, D.F. (1965). "Variation in flowering time and in some growth characteristics of Townsville Lucerne (*Stylosanthes humilis*)". *Australian Journal of Experimental Agriculture and Animal Husbandry,* 5, 49-51.

Casal, J.J. and Sanchez, R.A. (1998). "Phytochromes and seed germination". *Seed Science Research,* 8, 317-329.

Cheam, A.H. (1986). "Seed production and seed dormancy in wild radish (*Raphanus raphanistrum* L.) and some possibilities for improving control". *Weed Research,* 26, 405-413.

Cocks, P.S. (1999). "*Reproductive strategies and genetic structure of wild and naturalized legume populations"*. In: Genetic Resources of Mediterranean Pasture and Forage Legumes, pp. 20–31. Bennett, S.J. and P.S. Cocks (eds.) Kluwer Academic Publishers, Dordrecht, Netherlands.

Cronn, R. and Wendel, J.F. (2004). "Cryptic trysts, genomic mergers, and plant speciation". *New Phytology,* 161, 133-142.

Darwin, C. (1877). "*The different forms of flowers on plants of the same species".* John Murray, London.

Donaldson, T.W. (1986). Wild radish (*Raphanus raphanistrum* L.): a review of research on biology and control in Victoria 1976–1982". *Plant Protection and Quarantine,* 1, 160-162.

Dunbabin, M.T. (2001). "*Genetic variation in the outbreeding coloniser capeweed in South-Western Australia". pp: 51–62*. University of Western Australia, Perth, Australia.

Ecker, R., Barzilay, A. and Osherenko, E. (1994). Population means and correlation analysis of growth parameters in lisianthus (*Eustoma grandiflorum* Shinn.)". *Euphytica,* 78(3), 193-197.

Ellstrand, N.C., Prentice, H.C. and Hancock, J.F. (1999). "Gene flow and introgression from domesticated plants into their wild relatives". *Annual Review of Ecology System,* 30, 539-563.

Fenner, M. (1991). "The effects of the parent environment on seed germinability". *Seed Science Research,* 1, 75-84.

Foley, M.E. and Fennimore, S.A. (1998). "Genetic basis for seed dormancy". *Seed Science Research,* 8, 173-182.

Garbutt, L.K. and Witcomb, J.R. (1986). "The inheritance of seed dormancy in *Sinapis arvensis". Heredity,* 56, 25-31.

Gianinetti, A. and Cohn, M.A. (2008). "Seed dormancy in red rice. XIII. Interaction of dry after ripening and hydration temperature". *Seed Science Research,* 18, 151-159.

Gill, G. (1995). "Development of herbicide resistance in annual ryegrass populations (*Lolium rigidum* Gaud.) in the cropping belt of western Australia". *Australian Journal Experimental Agriculture,* 35, 67-72.

Gu, X.Y., Turnipseed, E.B. and Foley, M.E. (2008). "The *qSD12* locus controls offpring tissue-imposed seed dormancy in rice". *Genetics,* 179, 2263-2273.

Gu, X.Y., Kianian, S.F. and Foley, M.E. (2004). "Multiple loci and epistases control genetic variation for seed dormancy in weedy rice (*Oryza sativa*)". *Genetics,* 166, 1503-1516.

Hacker, J.B. (1984). "Genetic variation in seed dormancy in *Digitaria milanjiana* in relation to rainfall at the collection site". *Journal of Applied Ecology,* 21 (3), 947-959.

Harel, T., Pehlivan, D., Caskey, T. and Lupski, J.R. (2015). "*Mendelian, non-Mendelian, multigenic inheritance and epigenetics*". Rosenberg's Molecular and Genetic Basis of Neurological and Psychiatric Disease (Fifth Edition), pp. 3-17.

Hayward, H.D. and Breese, E.L. (1966). "The genetic organisation of natural populations of *Lolium perenne*. I. Seed and seedling characters". *Heredity,* 21, 287-304.

Hilhorst, H.W.M. (1995). "A critical update on seed dormancy. I. Primary dormancy". *Seed Science Research,* 5, 61-73.

Jain, S.K. and Marshall, D.R. (1967). "Population studies in predominantly self-pollinating species. X. Variation in natural populations of *Avena sativa* and *A. barbata. American". Nature,* 101, 19-33.

Jain, S.K. (1969). "Comparative ecogenetics of *Avena* species occurring in central California". *Evolution Biology,* 3, 73-118.

Kalisz, S. (1986). "Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae)". *Evolution,* 40(3), 479-491.

Kerdaffrec, E. and Nordborg, M. (2017). "The maternal environment interacts with genetic variation in regulating seed dormancy in Swedish *Arabidopsis thaliana". PLOS One,* https://doi.org/10.1371/journal.pone.0190242.

Lawrence, M.J. (1976). "*Variations in natural populations of Arabidopsis thaliana* (L.) Heynh." *pp. 167–190.* In The Biology and Chemistry of the Cruciferae, edited by J. G. Vaughan, A. J. Macleod and B. M. G. Jones. Academic Press, London/New York/San Francisco.

Leon-Kloosterziel, K.M., Keijzer, C.J. and Koornneef, M. (1994). "A seed shape mutant of *Arabidopsis* that is affected in integument development". *Plant Cell,* 6, 385-392.

Leon-Kloosterziel, K.M., van de Bunt, G.A., Zeevaart, J.A.D. and Koornneef, M. (1996). "*Arabidopsis* mutants with a reduced seed dormancy". *Plant Physiology,* 110, 233-240.

Li, B. and Foley, M.E. (1997). "Genetic and molecular control of seed dormancy". *Trends in Plant Science,* 2, 384-389.

Londo, J.P. and Schaal, B.A. (2007). "Origins and population genetics of weedy red rice in the USA". *Molecular Ecology,* 16, 4523-4535.

Lotan, T., Ohto, M., Yee, K.M., West, M.A., Lo, R., Kwong, R.W., Yamagishi, K., Fischer, R.L., Goldberg, R.B. and Harada, J.J. (1998). "*Arabidopsis* LEAFY COTYLEDON1 is sufficient to induce embryo development in vegetative cells". *Cell,* 93, 1195-1205.

Lu, Q., Niu, X., Zhang, M., Wang, C., Xu, Q., Feng, Y., Yang, Y., Wang, S., Yuan, X., Yu, X., Wang, Y., Chen, X., Liang, X. and Wei, X. (2017). "Genome wide association study of seed dormancy and the genomic consequences of improvement footprints in rice (*Oryza sativa* L.). *Frontier in Plant Science,* 8, doi: 10.3389/fpls.2017.02213.

Luerssen, H., Kirik, V., Herrmann, P. and Misera, S. (1998). "*FUSCA3* encodes a protein with a conserved VP1/AB13-like B3 domain which is of functional importance for the regulation of seed maturation in *Arabidopsis thaliana". Plant Journal,* 15, 755-764.

Marshall, D.R. and Jain, S.K. (1968). "Phenotypic plasticity of *Avena sativa* and *A. barbata". American Nature,* 102, 457-467.

McCullough, J.M. and Shropshire, W.J. (1970). "Physiological predetermination of germination response in *Arabidopsis thaliana* (L) Heynh". *Plant Cell Physiology,* 11, 139-148.

Meng, P.H., Macquet, A., Loudet, O., Marion-Poll, A. and North, H. (2008). "Analysis of natural allelic variation controlling *Arabidopsis thaliana* seed germinability in response to cold and dark: Identification of three major quantitative trait loci". *Molecular Plant,* 1, 145-154.

Meyer, S.E. and Allen, P.S. (1999). "Ecological genetics of seed germination regulation in *Bromus tectorum* L. Phenotypic variance among and within populations". *Oecologia,* 120, 27-34.

Morley, F.H.W. (1958). "The inheritance and ecological significance of seed dormancy in subterranean clover (*Trifolium subterraneum* L)". *Australian Journal Biological Science,* 11, 264-271.

Naylor, J.M. and Jana, S. (1976). "Genetic adaptation for seed dormancy in *Avena fatua*" *Canadian Journal of Botany,* 54, 306-312.

Naylor, J.M. (1983). "Genetic studies on the control of some physiological processes in seeds". *Canadian Journal of Botany,* 61, 3561-3576.

Nichols, P.G.H. and Cocks, P.S. (2006). "*Use of bulk hybrid populations to select for adaptation to contrasting environments in subterranean clover".* In: Breeding for success*: Diversity on Action*, Proceedings of the 13th Australasian Plant Breeding Conference, pp. 330–338. Mercer, C.F. (ed.) Christchurch, New Zealand.

Nishimura, N., Tsuchiya, W., Moresco, J.J., Hayashi, Y., Satoch, K., Kaiwa, N., Irisa, T., Kinoshita, T., Schroeder, J.I., Yates, J.R., Hirayama, T. and Yamazaki, T. (2018). Control of seed dormancy and germination by DOG1-AHG1 PP2C phosphatase complex via binding to heme". *Nature Communication,* 9(1), DOI: 10.1038/s41467-018-04437-9.

Owen, M.J. and Powles, S.B. (2010). "Glyphosate-resistant rigid ryegrass (*Lolium rigidum*) populations in the western Australian grain belt". *Weed Technology,* 24, 44-49.

Papi, M., Sabatini, S., Bouchez, D., Camilleri, C., Costantino, P. and Vittorioso, P. (2000). "Identification and disruption of an *Arabidopsis* zinc finger gene controlling seed germination". *Genes Development,* 14, 28-33.

Payseur, B.A. and Rieseberg, L.H. (2016). "A genomic perspective on hybridization and speciation". *Molecular Ecology,* 25, 2337-2360.

Price, S.D. and Barrett, S.C.H. (1982). "Tristyly in *Pontederia cordata* (Pontederiaceae)". *Canadian Journal of Botany,* 60, 897-905.

Ratcliffe, D. (1976). "Germination characteristics and their inter- and intra-population variability in *Arabidopsis". Arabidopsis Information Service,* 13, 34-45.

Ringlund, K. (1993). "*The importance of pre-harvest sprouting research".* In: Walkersimons MK and Ried JL (Ed.) pp. 3-7, Pre-Harvest Sprouting in Cereals. American Association of Cereal Chemists, St. Paul.

Roberts, E.H. (1961). "Dormancy of rice seed. I. The distribution of dormancy periods". *Journal of Experimental Botany,* 12, 319-329.

Sain, S.S. (1948). "Inheritance of hard seeds in perennial leguminous forage". *Herbarium,* 43, 206.

Salgotra, R.K., Gupta, B.B. and Sood, M. (2015). "Biotechnological interventions and their role in sustainable hill agriculture". *Journal Plant Science and Research,* 2(1), 118.

Seeley, C.I. (1977). "Seed dormancy in wild oats". *Proceeding of Western Society Weed Science,* 30, 33-35.

Shivrain, V.K., Burgos, N.R., Scott, R.C., Gbur, E.E., Estorninos, L.E. and Mcclelland, M.R. (2010). "Diversity of weedy red rice (*Oryza sativa* L.) in Arkansas, USA in relation to weed management". *Crop Protection,* 29, 1-8.

Simpson, G.M. (1978). "*Metabolic regulation of dormancy in seeds - a case history of the wild oat (Avena fatua*)". pp. 167-200 in E. Clutter, ed. Dormancy and Development Arrest. Academic Press, New York.

Simpson, G.M. (1990). "*Seed dormancy in grasses".* Cambridge, UK, Cambridge Univ. Press, 297.

Slatkin, M. (1987). "Gene flow and the geographic structure of natural populations". *Science,* 236, 787-792.

Smith, F.P., Cocks, P.S. and Ewing, M.A. (1995). "Variation in the morphology and flowering time of cluster clover (*Trifolium glomeratum* L.) and its relationship to distribution in southern Australia". *Australian Journal of Agriculture Research,* 46, 1027-1038.

van Eck, H.J. (2007). Genetics of morphological and tuber traits". *Potato Biology and Biotechnology,* 91, 115.

Warwick, S.I. (1990). "Allozyme and life history variation in five north wardly colonizing north American weed species". *Plant Systematic Evolution,* 16, 41-54.

Webb, S.R. and Hall, J.C. (1995). "Auxinic herbicide resistant and susceptible wild mustard (*Sinapis arvensis* L.) biotypes: Effect of auxinic herbicides on seedling growth and auxin binding activity". *Pest Biochemistry Physiology,* 52, 137-148.

Woodward, R.G. and Morley, F.H.W. (1974). "Variation in Australian and European collections of *Trifolium glomeratum* L. and the provisional distribution of the species in southern Australia". *Australian Journal of Agricultural Research,* 25, 73-88.

Yazdanpanah, F., Hanson, J., Hilhorst, H.W.M. and Bentsink, L. (2017). Differentially expressed genes during the imbibition of dormant and after-ripened seeds – a reverse genetics approach". *BMC Plant Biology,* 17, DOI 10.1186/s12870-017-1098-z.