

Insights into Seasonal Dormancy of Perennial Herbaceous Forages

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Abstract

Seasonal dormancy is an adaptive mechanism where plants suspend growth and become physiologically inactive to avoid extreme environmental conditions. Environmental factors like temperature, photoperiod, nutrients, and soil moisture control plant growth and development through various complex molecular mechanisms. Crown and seed dormancy of plants are mostly influenced by day length and temperature. Genes and physiological pathways triggered by these two factors along with genotype variability are some targets to manipulate seasonal dormancy. There is genetic variation in the depth and duration of seasonal dormancy. Therefore, their genetic manipulation is possible. Manipulations of summer and fall dormancy are relatively easier compared to winter dormancy because plants require protection of their apical meristem from freezing temperatures and limited water supply. Genetic factors that regulate seed dormancy may also have regulatory role for seasonal dormancy of the maternal plants. Limited genetic and genomic information are available for seasonal dormancy in herbaceous perennial species. Knowledge of genes controlling seasonal dormancy of eudicots, forest trees, and horticultural crops could be interpolated to explore possible dormancy mechanisms in perennial forages. This study reviews current knowledge of seasonal dormancy of herbaceous forages emphasizing the genetic and physiological context that would be valuable to breeders and plant biologists to expand the production season of perennial species by developing non-dormant and semi-dormant cultivars.

Keywords

Herbaceous Perennials, Seasonal Dormancy, Genes, Endodormancy, Forages, Hormones

1. Introduction

Herbaceous forage grasses and legumes are the cornerstone of feed resources for livestock and food security globally [1]. In the USA, forage ecosystems include more than 1500 grass species and 4000 legume species [2]. Forages are also valuable for their roles in wildlife habitat, watersheds, land conservation, soil reclamation, bioenergy, and sustainable agricultural systems [3]. Forage crops are either grazed directly on pasture or transported as hay, silage, green-chop, and pellets [4]. Forage species include both annual and perennial species and are categorized into cool season and warm season based on their primary growth period and availability [5]. Cool-season species, also known as temperate forages perform best at temperature ranges from 20°C to 25°C. Both high (>30°C) and low (<10°C) temperatures affect plant growth and development causing a major yield reduction [6]. Many of these temperate crops exhibit C3 carbon fixation pathway (<http://forages.oregonstate.edu>).

Warm-season grasses evolved mostly in subtropical climates and perform optimally at temperature of 30°C - 35°C. Plant growth begins when soil temperature reaches 15°C - 20°C (<http://forages.oregonstate.edu>). Warm-season crops exhibit C4 carbon fixation pathway and are efficient in fixing atmospheric carbon dioxide. These grasses are excellent alternative forage sources in summer when cool season grasses are not abundant [7]. An ideal seasonal distribution of forages can be obtained by a combination of cool and warm-season species which helps avoiding fodder gaps (Table 1). To meet the increasing demand in feed, manipulation of seasonal dormancy is a potential target to improve the annual forage production and seasonal distribution of perennial species.

Seasonal dormancy is the state where a plant becomes physiologically inactive and its growth is reduced or suspended for a certain time period [8]. Seasonal dormancy was suggested as an essential feature for perenniality. It enables plants to avoid and survive unfavorable environmental conditions such as summer heat and drought or winter freeze [9]. Forage species *Festuca arundinacea*, *Poa scabrella*, *P. bulbosa*, *P. secunda*, *Hordeum bulbosum* L., *Dactylis glomerata* ssp. and *Hispanica* “Kasbah” exhibit summer dormancy [10] [11], and alfalfa (*Medicago sativa* L.) [12], pensacola bahia grass (*Paspalum notatum*) and bermudagrass (*Cynodon dactylon* L.) [13] [14] [15] exhibit fall/winter dormancy. Winter dormancy is prevalent in several perennial herbaceous species and deciduous trees [16]. Seed and bud dormancy also exist in several plant species leading to delay in germination and flowering time [17]. The underlying mechanisms of the different forms of dormancy may have some similarities because all of them are more or less controlled by photoperiod, temperature, and endogenous factors. Meristems and crowns are the major plant organs perceiving signals for seasonal dormancy [18]. Shifting from the active growth to dormancy involves complex developmental, genetic and metabolic processes. Nutrient remobilization from shoots to crowns inhibits meristematic activity in buds and plants cease growth [19]. Therefore, understating the ecological and endogenous processes controlling

Table 1. Thirty common forages and their availability in Georgia and southeast leading to complete to partial forage deficiency.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Cool-season forages												
Alfalfa	-	-	-	+/-	+	+	+	+	+	+	+/-	-
Tall Fescue	-	-	+/-	+/-	+/-	+/-	+/-	+/-	+	+	+	+/-
Red clover	-	-	-	-	-	+	+	+	+	+/-	-	-
Orchardgrass	-	-	-	+/-	+	+	+	+	+	+	+	+/-
White clover	-	-	+	+	+/-	-	-	+	+	+	+	+/-
Perennial ryegrass	-	-	-	+/-	+	+	+	+	+	+/-	-	-
Bluegrass	-	+/-	+	+	+	-	-	-	-	-	-	-
Annual ryegrass	+	+	+	+	+	+/-	-	-	-	-	-	+/-
Barley	+	+	+	+	+	+/-	-	-	-	-	-	+/-
Oat	+	+	+	+	+	+/-	-	-	-	-	-	+/-
Cereal Rye	+	+	+	+	+	+/-	-	-	-	-	-	+/-
Wheat	+/-	+	+	+	+	+/-	-	-	-	-	-	+/-
Arrowleaf clover	+	+	+	+	+	+	-	-	-	-	-	+/-
Ball clover	-	-	+	+	+	-	-	-	-	-	-	-
Triticale	+/-	+	+	+	+/-	-	-	-	-	-	-	-
Warm-season forages												
Corn	-	-	-	-	+/-	+	+	+	+	-	-	-
Foxtail millet	-	-	-	-	-	+	+	+	+/-	-	-	-
Sorghum	-	-	-	-	+/-	+	+	+	+	-	-	-
Crabgrass	-	-	-	-	+	+	+	+	+	+/-	-	-
Forage soybean	-	-	-	-	-	+/-	+	+	+	-	-	-
Pearl millet	-	-	-	-	-	+	+	+	+/-	-	-	-
Teff	-	-	-	-	-	+	+	+	+/-	-	-	-
Browntop millet	-	-	-	-	+/-	+	+	+	+	+/-	-	-
Bahiagrass	-	-	-	-	+/-	+	+	+	+	+/-	-	-
Bermudagrass	-	-	-	-	+/-	+	+	+	+	+	+/-	-
Dallisgrass	-	-	-	-	-	+	+	+	+/-	-	-	-
Johnsongrass	-	-	-	-	-	+	+	+	+/-	-	-	-
Big bluestem	-	-	-	-	-	+	+	+	+	+	-	-
Indiangrass	-	-	-	-	-	+	+	+	+	+/-	-	-
Switchgrass	-	-	-	-	+	+	+	+	+/-	+/-	-	-

Source: <http://www.caes.uga.edu/> and <http://plants.usda.gov/>; Note: + availability; - non-availability; +/- limited availability.

seasonal dormancy is valuable for the manipulation of this trait through breeding and genetic technologies to improve crop yields and persistence.

In this review, we discuss the types of seasonal dormancy in herbaceous forage species and the potential for manipulating these traits to improve forage production and seasonal distribution. We provide insights into the possible genetic and genomic factors controlling seasonal dormancy of vegetative buds and seeds of common herbaceous species with focus on the roles of photoperiod and temperature in controlling such traits. We also compile published information on genes and genomic features of some eudicots that could be extrapolated to infer the underlying molecular basis of grass seasonal dormancy.

2. Forage Gaps Resulting from Seasonal Dormancy

Overcoming the forage deficit during the dormancy season of perennial forage species (**Table 1**) presents a major challenge to livestock producers. Farmers often resort to growing annual species such as wheat (*Triticum aestivum*), triticale (*x Triticosecale* spp.), *Elytricum* spp., *Brassicarapa*, *B. oleracea*, grasspea (*Lathyrus sativus* L.) etc. to fill the gap resulting from growth suspension of dormant species [20] [21] [22]. However, most farmers have limited land areas, and perennial crops may not be compatible with growing other annuals to reduce the herbage deficit. The best strategy to mitigate forage shortage is by reducing the span of seasonal dormancy of perennials species and develop semi or non-dormant germplasm. Growing cool season forages could partially help filling the seasonal forage gaps that occur in late fall, winter and early spring as a result of dormancy of warm season species. It is worth noting though that some of the most valuable cool-season perennial forages such as alfalfa exhibit fall/winter dormancy in temperate environments. Although no precise data is available on the economic loss due to seasonal forage dormancy, there is substantial evidence from hay feeding and supplementation that there is an economic effect on the farm economy due to the seasonal gaps in herbage availability.

3. Types of Seasonal Dormancy

3.1. Summer Dormancy

Summer dormancy (SD) refers to the temporary growth cessation of some plant species in the summer season even under favorable soil moisture conditions [23]. It is an evolutionary response that some grasses adopted as an avoidance strategy to escape summer drought and heat [24] [25] [26] [27]. Numerous ecotypes of cool-season perennial grasses originating from the Mediterranean Basin of southern Europe and northern Africa, and the Mediterranean environments of California exhibit summer-dormancy, primarily in response to increasing day length and probably high temperatures [9] [24] [28]. Summer dormant grasses resume their growth once moisture is adequate [29]. For example, temperate grasses in semi-arid and arid Mediterranean regions such as Cocksfoot (*Dactylis* spp.), tall fescue and canary-grass exhibit SD to escape drought stress [30]. The

specific characteristics of the summer dormant plants include no or low leaf development, increased senescence of mature leaves, and generation of quiescent organs [11]. Several reports highlighted the relationship between summer dormancy and drought stress, concluding that SD provides superior survival under drought stress [31] [32]. Under extreme dry summers, SD is considered as an indicator of drought tolerance in cool-season grasses such as tall fescue, where survival and persistence of various cultivars of contrasting dormancy fluctuated with summer drought stress [33]. Therefore, growing summer-active fescue cultivars under conditions of limited moisture is not recommended [33]. Similar observations for the relationship of dehydration tolerance and SD were reported in other perennial grasses such as, orchardgrass (*Dactylis glomerata* L.), pine bluegrass (*Poa scabrella*) [24], bulbous bluegrass (*P. bulbosa*) [34] [35] and *Hordeum bulbosum* [36]. Because of the common manifestation of both trait such as leaf desiccation, defoliation, and reduced growth, characterizing SD and dehydration-tolerance is a confounding job under severe drought, although they are independent responses [31]. Thus, dormancy testing should be carried out only in plants growing under sufficient soil water condition [23].

3.1.1. Characteristics of Summer Dormancy

Based on the regulatory factors, summer dormancy has been classified into two types: eco-dormancy and endo-dormancy [37]. Eco-dormancy, also called enforced dormancy, is caused by the lack of suitable environmental conditions. The plant resumes growth once it regains the standard amount of water, temperature, and other factors which were previously limiting [10]. On the other hand, plants undergoing endo-dormancy, also referred to as physiological dormancy, will remain dormant even when environmental factors are favorable until the physiological pathways relaxes and releases dormancy [10] [11]. Eco-dormancy is regulated mostly by environmental factors through complex interaction of stress responses [11]. Summer-dormant cool-season perennial grasses produce dormant regenerating buds at tiller bases during spring, from which growth resumes in response to increased water availability and decreasing temperatures in autumn. Regulation of endo-dormancy involves complex physiological processes regulated by various genes, hormones, as well environmental responses like temperature and photoperiod [11]. Temperature and photoperiod affect endo-dormancy in plants through the regulation of timing of reproductive maturity, and meristem activities [33]. Effects of temperature and day length on summer dormancy in different species have been reported elsewhere. Endo-dormancy is induced independently from soil moisture, even though it can be accelerated by drought [33]. The process is most likely initiated under short photoperiods and relatively low temperatures during winter. Orchardgrass (*Dactylis glomerata* L.) and tall fescue [*Lolium arundinaceum* (Schreb.) S.J. Darbyshire] must be exposed to these conditions for the summer dormancy trait to be fully expressed under the subsequent long photoperiods and high temperatures of summer [33] [38]. Metabolic activity in the summer dormant *D. glomerata*

was found to be reduced when tested using biochemical and physiological experiments. Monosaccharides content decreased in the leaf blades of dormant plants even before summer [39]. Two levels of summer dormancy are defined; complete dormancy and incomplete dormancy [33]. A complete summer dormant plant suspends growth for at least four weeks in summer with dehydration of living parts and senescence of herbage as in cock's-foot grasses (*Dactylis* spp.) [38]. Incomplete summer dormancy occurs if the plant shows moderate dormancy symptoms such as some genotypes of tall fescue [11]. Differences between dormancy types may be gradual and depend on responsiveness to inductive and synergistic factors (*i.e.* day length, high temperature, soil moisture status), depth of dormancy induction and kinetics of dormancy relaxation during summer [10].

Summer dormant and semi-dormant cool-season grasses have been considered ideal to grow in regions with prolonged hot summers to avoid desiccation [11]. For instance, obligatory dormant tall fescue germplasm or the semi-dormant Harding grass (*Phalaris aquatica* L.) is thought to be ideal for the U.S. Southern Great Plains for better persistence [40] [41]. Along with improved persistence, summer dormant tall fescue and cocksfoot cultivars have faster fall regrowth in Mediterranean type climates [38] [40]. Hence, manipulation of the SD trait to improve the sustainability of forage production requires clear understanding of the genetic basis of dormancy, accurate phenotyping, as well as knowledge of the climatic and edaphic environments that control it.

Information regarding genomic features and associated genes controlling the summer dormancy trait is limited. Scientists believe that molecular mechanism of SD comprises several endogenously regulated pathways, which provide the plant genotypes better persistence in dry environment allowing the meristem to remain alive [29] [30] [37]. Molecular studies from three different morphotypes of tall fescue: Continental, Mediterranean, and rhizomatous show that the Mediterranean morphotype is evolutionarily distinct with both the Continental and rhizomatous types, and has different levels of summer dormancy [42] which lead us to believe that summer dormancy variability present in tall fescue germplasms has breeding value.

3.2. Fall/Winter Dormancy (FD)

3.2.1. Fall Dormancy and Winter Hardiness

Fall dormancy (FD) refers to the slow growth of certain plant species in autumn leading to low height and decumbent shoot growth. Under temperate or continental climates, low temperature is usually the major limitation for the growth of forage plants, and fall/winter dormancy are the main adaptive responses [43]. Unlike summer dormancy, complete senescence and zero growth are common in the fall dormant species. Even though fall dormancy is typical to most C4 warm season herbaceous species, several C3 perennial species like alfalfa (*Medicago sativa* L.) evolved fall dormancy as an escape mechanism to protect themselves from cold winter temperatures in the most northern latitudes.

FD is considered a critical trait that enables alfalfa to survive in climatic zones outside its natural range [44]. Fall dormancy in alfalfa is evaluated through fall regrowth pattern after cutting [45]. FD responses of plants generated from reciprocal cleft grafts between dormant and non-dormant showed that the canopy height is essentially shaped by shoot and crown's genotype [46]. Contrary to the common belief that dormant alfalfa is low yielder, annual average yield of some dormant cultivars showed higher biomass than non-dormant cultivars in their environment of adaptation [<http://oregonstate.edu/>]. Fairey *et al.* (1996) described the relationship between North American alfalfa cultivars in terms of their source of germplasm and FD performances [47], which led to the development of 11 FD classes as check cultivars [48]. A significant interaction between location and variety has been found among the 19 tested varieties with 7 FD classes (2 to 8) over five locations in China [49]. These extensive phenotypic studies carried in alfalfa make it a suitable model crop for FD studies in herbaceous perennial crops [50]. FD is also common in summer grasses like bermudagrass [51] and influences herbage yield and winter survival of the dormant species.

Winter hardiness (WH) is a complex trait referring to the ability of the plant to survive under sub-optimal winter conditions. Challenges to plants in winter include freezing temperature, diseases, moisture level, snow, and low light intensity [52] [53]. Similarly, cold tolerance simply indicates the plant's ability to survive freezing temperature stress [52]. Understanding the mechanism of WH is critical to grow alfalfa in northern climates (North Central US and Canada) since it influences yield, persistence, survival, and forage quality. WH is also influenced by physiological and morphological factors such as nutrient (C and N) and lipid metabolism, cold acclimation potential, plant health and disease, plant root and crown structure as well as the dormancy level of the genotypes [54].

Fall dormancy and winter survival in alfalfa have been considered to be positively correlated traits [55]. Realizing the relationship between fall dormancy and winter survival, several alfalfa-breeding programs use dormancy as a surrogate for winter hardiness and indirectly select for WH by selecting more dormant germplasm [56]. Winterkill in alfalfa stands depends on the extent of the cold that alfalfa roots can withstand as well as the overall hardiness of genotypes [57]. Alfalfa cold hardiness also relies on soil moisture, and the amount of insulation provided to the roots by the soil environments [57]. Recent findings based on genetic analysis suggested that dormancy and cold tolerance are inherited independently and could be analyzed as unlinked traits [44] [54] suggesting that the two traits were carried together through long-term selection.

Even though WH of alfalfa genotypes can be phenotypically predicted to some extent using FD levels, it is affected by other factors. Nitrogen metabolism was found to be associated with the development and maintenance of alfalfa hardiness [58]. Similarly, fertilization in fall affects the cold tolerance of Kentucky bluegrass [59], and autumn mowing also effects the winter survival of love grass

(*Eragrostis cilianensis*) [60]. In saltgrass (*Distichlis spicata* L.), the extent of variation in FD and plant growth is dictated by the environmental conditions in the location of origin of germplasm. Therefore, cold tolerance could be a challenge if the germplasm is moved to climatic regions more northern of their region of adaptation [61]. In the dicot species Flordaking peach tree (*Prunus persica*), the time and duration of fall defoliation and chilling accumulation correlate with vegetative bud out breaking in spring [62].

3.2.2. Fall Dormancy Characteristics

Classifying fall dormancy levels of germplasm and recommending specific niches is an important step for the selection and development of adapted cultivars. Alfalfa is the only herbaceous perennial species where fall dormancy has been characterized. Based on plant regrowth in autumn, there are 11 standard classes of fall dormancy and the classes are assigned based on regression with standard checks [48]. The 11 FD classes are divided into sub-categories: dormant, 1 - 4 FD; semi dormant, 5 - 7; and non-dormant, 8 - 11 [63]. However, defining fall dormancy (FD) classes in alfalfa is time-consuming due to its complexity and the influence of different environmental factors and their interactions. Furthermore, it is imperative to grow the germplasm in the field for at least two years at multiple locations in order to have an accurate estimate of fall dormancy classes [48]. Near infra-red reflectance spectroscopy was evaluated as a potential tool to estimate FD classes in alfalfa [64], but has never been applied in practice. Therefore, identifying associated genes and genomic locations underlying fall dormancy through genetic mapping and developing markers would be very beneficial. The manipulation of dormancy alleles using molecular markers will enable the development of cultivars with an extended growing season.

3.2.3. Growth Cessation in Winter

Winter in the temperate regions is usually associated with freezing temperature and low soil moisture. Perennial plant species grown in high latitudes rely on winter dormancy and growth suspension during the cold months for survival and persistence under cold temperatures [9] [65]. Plants have also undergone evolutionary changes in morphology and anatomy to cope with sub optimal growing conditions. Most of the higher trees senesce and undergo defoliation in winter as a mechanism of tolerance and to survive harsh winter conditions. In the United States, almost every state has a historical record of freezing temperature indicating low temperature as one of the major limitation for the growth of forage species in the cold season. Therefore, cold tolerance and winter survival in herbaceous crops are very important considerations for the manipulation of winter dormancy.

4. Temperature, Photoperiod and Dormancy

Photoperiod and temperature are major environmental components controlling growth responses in plants [9] [66] [67]. Several studies have indicated the role

of these two factors in inducing seasonal bud and seed dormancy of crops. Warm season grasses like big bluestem (*Andropogon gerardii*), indiagrass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum* L.) are photoperiod sensitive, which is under genetic control. Photoperiod requirements for flowering and fall senescence for these species differ depending on latitude of their origin, as in alfalfa [68]. For example, evolution of northern and southern switchgrass ecotypes was shaped by two major factors: length of the growing season and winterkill susceptibility [69]. Therefore, if southern ecotypes are moved to far north, they may not develop full vegetative growth because of insufficient photoperiod during the shorter growth season.

Exposing switchgrass plants to extended photoperiod resulted in increased number of tillers and biomass accumulation [70]. Increased yield was observed in three subtropical forage grasses: bahiagrass, bermudagrass, and star grass (*Cynodon nlemfuensis* Vanderyst) when exposed to 15 hrs. of light instead of natural day length [71]. Ofir and Koller [72] [73] reported induction of dormancy in a perennial grass *Hordeum bulbosum* L. during early stages of reproductive growth when exposed either to low temperature or short days followed by long days while long days and increased temperature collectively induce summer dormancy in *Poa bulbosa* L., *P. scabrella*, *Allium cepa* L., *A. sativum* L., *Ranunculus* spp., and *Anemone coronaria* L. [74]

Temperature is another factor controlling plant metabolic processes in warm-season grasses, whereby metabolic pathways such as photosynthesis, respiration, and growth processes are catalyzed by enzymes whose activities are affected by temperature. Blue grama (*Bouteloua gracilis*) flowered in both long and short days when temperature remained fairly high at 75°F but failed to flower at lower temperature of 60°F [75]. Big bluestem bloomed in short days (10 hours) at a fairly high temperature of 75°F during the day and cool temperature of 60°F during the night, but did not bloom in this short day when the temperature was kept at 75°F throughout. These results indicate that big bluestem is a short-day plant and day-night temperature determines whether it will flower [75]. Temperature used for acclimation in controlled environment fluctuates the level of cold tolerance in perennial ryegrass [43].

Photoperiod and temperature also play notable roles in regulating seed dormancy. Information is scarce regarding seed dormancy studies in forage grasses, however, several reports are available for other grass species like rice (*Oryza sativa* L.) and eudicots. Research has shown that photoperiod experienced by the seed parent as well as levels of stratification influence the extent and speed of seed germination in *Arabidopsis thaliana* [76]. Short-day photoperiod was found to be helpful for enhanced germination rates. It was hypothesized that the magnitude of seed germination under certain temperatures might indicate the response of its parent plant in the same environmental condition [76]. In addition, photoperiod used for seed maturation can be a determinant of the seasonal responses of new seeds [76]. Researchers have found that high-dormancy cultivars

of switchgrass showed low germination rate under a constant, warm temperature (30°C), however, low-dormancy cultivars show good germination percentage under the same temperature condition [77]. Additionally, germination for both low and high-dormancy cultivars showed similar germination in the dark condition.

5. Photoperiod, Temperature and Parental Genotype

Virtually almost all plant genes and genetic factors are photoperiod and temperature responsive. The circadian rhythm in plants responds to the effect of changing photoperiod and light [78]. Genes expressed in seed-parent plant, which is mostly under the control of light and temperature, influence seasonal dormancy of seeds. Maternal control of germination includes thickness of seed coat, endosperm, and hormonal composition in response to light signals [79]. Dormancy and other phenotypic characteristics of seeds are influenced in several ways by the seed-parent's environment [80]. Light and nutrients acquired by the maternal parent can result in bigger seeds with reduced germination percentage [81] and parental environment shapes the genetic variation in the seeds. In a bermudagrass (*Cynodon* spp. Rich.) cultivar "Tifton419" and Kentucky bluegrass (*Poa pratensis* L.) cultivar "Midnight II", the levels of sugar and Abscisic acid (ABA) increased and Gibberellic acid (GA) level decreased resulting in the induction of fall dormancy, as a consequence of decreased illumination duration [51]. In *Arabidopsis*, seeds obtained ABA from maternal tissues [82].

6. Molecular Mechanisms of Seasonal Dormancy

6.1. Genetic Control of Dormancy

Several plant genes control seasonal dormancy and relaxation (Table 2). Ding and Missaoui (2017) confirmed CONSTANS and TERMINAL FLOWER (TFL), dormancy-associated MADS-box (DAM), auxin response factors (ARFs) and heat shock proteins (HSPs) as potential candidate genes involved in the control of tall fescue summer dormancy (Table 2) [83]. Similarly, SD in a perennial ornamental plant *Narcissus tazetta* var. *Chinensis* might be regulated by a gene *Narcissus FT* gene homologue (NtFT) [84]. In a monocot *Lilium longiflorum*, SD is induced by higher temperature and accumulation of ABA, which is under the control of 9-cis-epoxycarotenoid dioxygenase (NCED) gene [85]. Similarly, in grapevine (*Vitis vinifera*), genes related to growth regulators ABA, auxin, ethylene, and salicylic acid metabolism are involved in regulating summer dormancy and relaxation [86].

Fall dormancy genomic information is expanding due to several studies performed on alfalfa. Some traits related to fall dormancy such as freezing tolerance and cold acclimation were believed to be controlled by C repeat binding factor (CBF) pathway. The binding of a transcription factor to the C motif triggers the expression of a cascade of cold-regulated (COR) genes. The expression of these genes helps the plant resist injury when exposed to freezing temperature.

Table 2. Vegetative and flower bud dormancy related genes in plant.

Species	Genes	Characteristics	Sources
Arabidopsis & Leafy spurge	DAM genes	Expressed in bud and shoot tips of leafy spurge, delays flowering, associated to AGAMOUS-LIKE 24 and SHORT VEGETATIVE PHASE transcription factors.	[95]
Sorghum	phyB	Photoreceptor, inhibit bud outgrowth	[166]
Tall fescue	CO, TFL	Meristem determinacy and summer dormancy genes	[83]
Tall fescue	ARFs and HSPs	Heat and temperature responsive genes	[83]
Peach	bZIP	Transcription factor	[167]
Pear	DAM: PpMADS13-1, PpMADS13-2	Trigger seasonal dormancy, downregulated with endodormancy	[168]
Peach	PpDAM5 and PpDAM6	DAM genes of peach	[169]
Tomato	<i>JOINTLESS</i>	Homologs of SVP of apple, pedicel abscission and bud dormancy	[170]
Maize	MADS-box genes	Encode transcription factor, controls flower and inflorescences	[171]
Populus	ABI1B and ABI3	Associated with the ABA	
Populus	PHYA	Photoperiod related gene	
Kiwifruit	SOC1	Control dormancy duration	[172]
Sorghum	TB1 and MAX2	Branching related genes, suppress bud outgrowth, TB1 is controlled by phytochrome B (phyB)	[173]
Pea	DRM1	Dormancy gene of axillary buds	[174]

In addition to CBF and COR genes, cold acclimation specific (CAS) genes *cas15* and *cas30*, along with C-repeat motif and likely CBF-regulated genes, were also reported to be expressed in relation to freezing tolerance [87]. Zhang and Wang (2014) performed transcriptome profiling using RNA-seq analysis and observed differential expression of some potential genes associated with FD in alfalfa [88]. A cold acclimation specific gene, *CAS18*, from *Medicago falcata* may have a potential role in alfalfa fall dormancy [89]. Moreover, an allele *al* from a cold related gene *MSAIC B* showed correlation with autumn plant regrowth height in the cultivar WISFAL-6 [90]. Recent progress in next generation sequencing enabled the understanding of the genetic basis of complex traits like dormancy. Recently a genotyping-by-sequencing (GBS) based linkage map for fall dormancy of tetraploid alfalfa was reported [91]. The linkage groups identified on auto-tetraploid *M. sativa* were mostly syntenous with *M. truncatula*.

Although grasses diverged from eudicots millions of years ago [92], they still include conserved homologous and paralogous genes. Thus, analyzing dormancy related genes from other species is valuable to study grass dormancy. Expression analysis based on Real-time PCR showed up-regulation of a carbohydrate metabolism and adventitious bud dormancy gene, beta-amylase gene (Ee-BAM1) in leafy spurge (*Euphorbia esula*) [93]. Similarly, Saito *et al.* (2013) examined winter bud dormancy-associated MADS-box (DAM) genes, MADS13, at expression and structural levels in Japanese pear (*Pyrus pyrifolia* Nakai) [94]. They observed a low expression of MADS13 genes during endodormancy phase

transition. The expression of dormancy-associated MADS-box genes (DAM2) has been correlated with endodormancy induction in leafy spurge (*Euphorbia esula*), and DAM1 overexpression in Arabidopsis delayed flowering (Table 2) [95]. DORMANCY ASSOCIATED MADS-box (DAM) genes, which are closely related to SVP, have been identified to play a role in endodormancy initiation, where expression of DAM genes may be required for down-regulating FT and CENL1 during the endodormancy in some perennial species [96] [97]. Several components of the circadian clock are known to interact with two floral-regulating MADS-box transcription factors in poplar, flowering locus c (FLC) and SHORT VEGETATIVE PHASE (SVP) [98] [99] [100]. These two factors also regulate FT and CENL1 in Arabidopsis [101] [102] [103]. Similarly, other circadian clock genes; late elongated hypocotyl1 (PttLHY1), PttLHY2 and time of cab expression (PtTOC1) are putatively involved in the control of seasonal growth cessation, bud regrowth, and freezing tolerance in *Populus* [104]. There are multiple pathways linking environmental input signals to dormancy regulation and flowering. In *Arabidopsis*, phytochromes and cryptochromes perceive photoperiod and temperature signals and are associated with circadian clock [105]. Circadian control involves feedback loop interactions among genes such as CIRCADIAN CLOCK ASSOCIATED1 (CCA1), EARLY FLOWERING 3 - 4 (ELF3 and ELF4), GIGANTIA (GI), LATE ELONGATED HYPOCOTYL (LHY), PHTOCHROME-INTERACTING FACTOR3 (PIF3), PSEUDO-RESPONSE REGULATORS (PRR9, PRR7 and PRR5), TIMING OF CAB1 (TOC1), LUX ARRHYTHMO (LUX) and ZEITLUPE (ZTL) [106] [107].

Cessation of meristem activity in determinate cultivars as result of floral induction might be regulated by a similar process as in the cessation of growth of meristematic cells in seasonal dormancy [108]. Different genes from various crops have been listed as control factors in determinacy of meristem. For instance, the maize ortholog of Arabidopsis terminal flower1 (*TFL1*) called ZEA CENTRORADIALIS (ZCN1) acts on maize plant meristem indeterminacy, flowering delay, as well as flower architecture [109]. Proteins regulating flowering in Arabidopsis, such as FLOWERING LOCUS T (FT), TERMINAL FLOWER 1 (TFL1), PHYTOCHROME A (PHYA), and CONSTANS (CO), have been associated with growth cessation and endodormancy in poplar [110] [111] [112] [113]. CENTRORADIALIS-LIKE 1 (CENL1), an orthologue of TFL-1 also regulates seasonal growth cessation and dormancy in poplar [110] [112]. The *CEN1/TFL1* gene family also controls flowering [114].

6.2. Molecular Mechanism of Seed Dormancy

Seed dormancy refers to the condition where viable seed does not germinate, even in favorable environment [115]. Seed dormancy of grasses has been rigorously researched in the last few decades and scientists hypothesized several evolutionary significances of seed dormancy in grasses. In herbaceous perennial plants, both seed and maternal plant dormancy exist and are probably controlled

by similar mechanisms [116] [117]. Seed dormancy has been classified into physiological dormancy, morphological dormancy, morpho-physiological dormancy, physical dormancy, and combinational dormancy [118]. For example, seed dormancy in switchgrass has been identified as non-deep physiological dormancy, with the pericarp layer as a major influential factor [119]. Seed germination for switchgrass can be increased by scarification, stratification, and after-ripening period, among others [120]. Burson *et al.* (2009) indicated that switchgrass seed dormancy controlled by multiple genes and the trait exhibits strong genotype x environment interaction [121].

Relationship between seed dormancy and seasonal bud dormancy is still a matter of debate. A recent study indicated that seed dormancy may have relationship correlation with seasonal plant dormancy of tall fescue, and seed dormancy could be used as a surrogate phenotype for summer dormancy of the parent genotype [37]. However, Adkins *et al.* (2002) suggested that seeds of warm season grasses have embryo cover and the embryo itself is the location and origin of dormancy [122]. Several plant genes involved in seed dormancy have been discovered (Table 3). Costa *et al.* (2015) identified several putative genes such as EARLY RESPONSIVE TO DEHYDRATION 7, LEA14, BXL2, JAZ1 etc. for desiccation tolerance and seed dormancy of *Arabidopsis thaliana* whose orthologs were also present in other plants such as, *M. truncatula* and *C. plantaginum* and *S. stapfianus* [123]. They highlighted that desiccation tolerance has co-evolved with seed dormancy sharing common processes that help the plant to adapt to stress environments. Similarly, QTL for rice seed dormancy have been mapped and rice homologues of Arabidopsis seed dormancy genes were also identified [124]. Wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) reduced seed dormancy causes pre-harvest sprouting resulting in significant yield loss [125]. Barley has two major quantitative traits (QTL) for seed dormancy, SD1 and SD2, on chromosome 5H [125]. Nakamura *et al.* also reported that mitogen-activated protein kinase cascade regulates seed dormancy in barley [125]. Similarly, Lin *et al.* (2009) reported seed dormancy QTL in barley [126].

Seed dormancy is a major player in plant population diversification, colonization of new environments, and extinction. Its regulation could evolve with the seed itself [127]. Enhanced seed dormancy was observed in transgenic lines with over-accumulated ABA [128] [129] [130] [131]. This implies that ABA inhibits seed germination and induces dormancy. The role of gibberellin (GA) in triggering germination via countering the effect of ABA is well documented [132]. Various genes involved in the ABA and GA pathways that are known to influence seed dormancy and germination are shown (Figure 1).

7. Hormonal Control of Seasonal Dormancy

The major plant hormones ABA, Auxin, GA, ethylene, and cytokinin are vital to almost all plant biological processes. These growth regulators are also necessary for the regulation of vegetative bud, seed, and flower bud initiation, sprouting,

Table 3. Genes involved in seed germination and seed dormancy of various plant species.

Species	Genes	Characteristics	Sources
<i>Bromussecalinus</i>	pBS128	Up-regulated when seed hydrated	[175]
<i>Brachypodium</i>	BdNCED1, BdNCED2, BdABA8cOH-1 and BdABA8cOH-2	ABA synthesis and catabolism	[176]
Barley	SD1, SD2	Mitogen-activated protein kinase cascade	[125]
Rice	GA20-oxidase	Gibberellic acid (GA) synthesis pathway	[177]
Rice	<i>Oryzasativa</i> Sdr4 (<i>OsSdr4</i>)	Seed dormancy and pre-harvest sprouting	[115]
Rice	qSD, qSD12	qSD12 promotes ABA accumulation	[178] [179]
36 different species	<i>Sdr4</i> like gene (<i>Sdr4L</i>)	Gene of Sdr4 gene families and found in <i>Ricinus communis</i> , <i>Carica papaya</i> , <i>Malus domestica</i> , rice, maize, brachypodium, setaria, switchgrass, cucumber, bean etc.	[115]
Hybrid <i>Leymus</i>	(DRG50)	Seed dormancy and shattering	[180]
Arabidopsis	DOG1, ABI3, FUSCA3 (FUS3), LEC1 and LEC2	DOG1 is quantitative trait locus; ABI3, FUS3, LEC1 and LEC2 are transcription factors, seed maturation regulators	[181]
Arabidopsis, Rice, and Maize	VP8/PLA3/GO/AMP1	Specific effect in seed dormancy	[182]
Arabidopsis	PYR, PYL/RCAR; ABI1, ABI2, HAB1, AHG3; KAI1/MAX2	Hormone regulators	[182]
Wheat and Arabidopsis	MOTHER OF FT AND TFL1 (MFT)	Regulation of germination	[183]
Arabidopsis	SPT, PIL5, AtrbohB, PRT6, ATE	Seed dormancy releasing genes	[182]
Arabidopsis	FLC	MADS-box TF	[182]
Arabidopsis	CBF	Cold response pathway	[182]
Arabidopsis	HUB1, HUB2; RDO2; VIP4, VIP5, ELF7, ELF8, ATXR7; EFS; FIE and KYP/SUVH4, SUVH5	Epigenetic regulators of seed dormancy	[182]
Arabidopsis	LHY, CCA1, GI, ZTL, and LUX	Circadian clock genes	[184]

and dormancy. ABA is involved in plant storage deposition, prevention of pre-harvest sprouting, dehydration tolerance, and dormancy induction at early stage. Transcription factors like ABI3/VP1, ABI4, ABI5, LEC1, LEC2, and FUS3 are involved in ABA signaling and production [133]. The genes from CYP707A gene family are also associated with ABA levels in Arabidopsis seeds [128]. ABA also induces summer dormancy in *Poa bulbosa* [134] and its level in the plant changes under dehydrated conditions [135]. ABA controls bud dormancy in grapes where its level increases in autumn and its metabolism is modified by the stimuli of dormancy release [136].

Hormonal activity is associated with plant dormancy in several ways. Summer dormancy in *Poa bulbosa* is induced by long day photoperiod or by water deficit, and both situations show increase in ABA levels [74]. ABA counteracts the role of Auxin for apical dominance when it is applied to decapitated shoots in

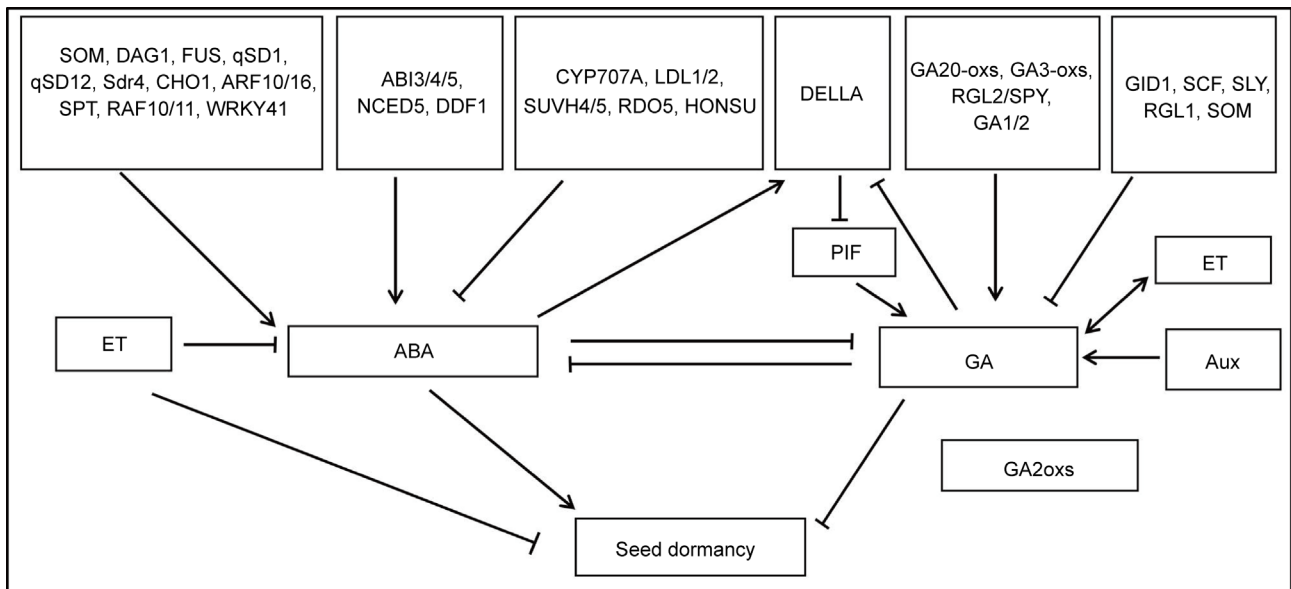


Figure 1. Schematic diagram showing the effect of major hormones and some important genes in seed dormancy of plants. The symbol “→” indicates the up regulation and “┐” indicates negative effect to the resulting components or processes [185] [186].

Ipomoea nil, *Solanum lycopersicum* and *Helianthus annuus* [137]. In the case of physiological dormancy, the level of ABA increases and that of gibberellin and cytokinin decreases [138] [139]. Mohapatra *et al.* (1988) studied the effect of ABA induction in freezing tolerance in alfalfa [140] and observed ABA regulation of some gene expression during cold acclimation. Most researchers believe that the physiological mechanisms that control the transition between dormancy and germination are hormonal in nature [141] [142]. The balance between ABA and gibberellic acid (GA) is also important in this process. GA promotes germination [120] [143] while ABA induces and maintains dormancy [144] [145]. The embryo produces ABA when the seed is developed in the mother plant, which can control dormancy and germination through the endogenous concentration and seed sensitivity [146] [147]. However, with exogenous ABA application, germination decreased. In hybrid aspen (*Populustremula* × *tremuloïdes*), proper distribution of GA in vascular tissue is essential to trigger auxin for flowering and bud outgrowth [148].

In the tree peony (*Paeonia suffruticosa*) the accumulation of ABA and sugars in winter might induce the dormancy [149]. Further, GA accumulation and degradation of ABA in spring releases bud dormancy, and temperature becomes the major controlling factor in hormonal regulation. Application of GA impacts positively the post-harvest longevity of grass like *Miscanthus sinensis* [150]. However, gibberellin inhibits growth in mild dehydration condition, similar to ethylene [135]. Alfalfa roots contain variable amounts of GA3, indole-3-acetic acid (IAA), and ABA depending on their fall dormancy levels [151] and these endogenous hormones play, at least, a partial role in spring regrowth variation in alfalfa.

Zhuang *et al.* (2015) described the transcriptomic and metabolic changes brought by GA treatment on the release of flower bud dormancy in Japanese Apricot (*Prunus mume*) [152]. Cytokinin was found to be essential for meristem activity in potato tubers [153]. Auxin plays a role in shoot branching, bud outgrowth, and dormancy [154]. Other auxin responsive genes control growth and are involved in most of the aspects of plant growth and development [155]. Changing levels of ARR5::GUS activity in *Populus × canescens* indicated that change in the concentration of cell and tissue specific cytokinin in winter and summer leads to variability in dormancy and sprouting [156].

8. Breeding for Seasonal Dormancy

Genetic variation in germplasm, accurate phenotyping, and genotyping are essential components for successful selection. There is a limited availability of germplasm of herbaceous perennial species that has been well characterized for summer, fall, and winter dormancy in order to manipulate the trait. An exception is alfalfa fall dormancy where several dormant, semi dormant and non-dormant checks and commercial cultivars are available. Since alfalfa fall dormancy may be associated with winter hardiness, we can use phenotypic data of cold hardiness to indirectly select for dormancy and vice-versa. Various reports showed a close connection between winter hardiness and accumulation of raffinose and stachyose in roots and crowns [157], which might be valuable information to the study of FD. Exploitation of indoor selection methods as a reliable phenotyping process to freezing tolerance of alfalfa are also described [158], and could be useful in the prediction of FD in alfalfa. Consecutive cycles of recurrent selection coupled with indoor screening have been suggested as a suitable approach to develop freezing tolerant alfalfa [159]. Although most of the grasses are allogamous, still some species show pseudo self-compatibility such as switchgrass [160], and the characteristic could be useful for breeding semi-dormant cultivars. Germplasm sources for bermudagrass fall dormancy and winter hardiness studies include all released cultivars and natural wild germplasms [15]. Similarly, other studies indicated that the continental type and Mediterranean type tall fescues could be valuable sources for summer dormancy breeding since most of them show variability in dormancy. Ding and Missaoui (2016) showed that seed dormancy and germination at low and high temperature of tall fescue could be used as a surrogate phenotype to determine summer dormancy of the plant itself [37].

9. Genomic Resources for Seasonal Dormancy

Clear understanding of the molecular pathways and genetic basis governing plant growth responses to seasonal changes in herbaceous perennial species is still lacking. However, various functional genomics, statistical, and bioinformatics tools available today are conducive to study genetic traits of interest in herbaceous perennial species. Phytozome genomics portal, for example, enables the

study of seasonal dormancy of herbaceous plants and their genetic and genomics values, using the structure of annotated genes, protein homologs, gene ancestry, and expression [161]. The orthologs of vegetative bud dormancy genes in *Brachypodium distachyon* found a leucine zipper (bZIP) transcription factor at locus *Bradi1g17210* as an associated gene (Figure 2). Blast search (BlastX) for the other related plant proteins in Jbrowse (Figure 3) which can be linked from the same portal page, returned related proteins in *Sorghum bicolor*, *Oropetium Zeamays* etc. (Figure 3). The transcription factor bZIP is one of the highly conserved plant genes controlling several biological processes such as seed and flower development [162]. Seed germination control by ABI5, a bZIP gene, supports the involvement of this transcription factor in dormancy. Therefore, comparative genomics approaches may enable the use of information from woody plants to find out homologous and paralogous genes associated with seasonal dormancy in herbaceous perennials.

Blast 2GO is another comprehensive suite for functional analysis of plant genomics and it provides a universal tool for annotation, visualization, and analysis. Based on gene ontology vocabulary, it optimizes function transfer from homologous sequences [163]. The comparative genomics platform CoGe (<http://www.genomeevolution.org>) which is available through iPlant Collaborative [164] can be used to analyze and compare various genomes. It is a web-based system that provides more than 30 interconnected applications to analyze, compare, and visualize nearly 20,000 genomes with tools like single gene, multiple gene, whole genome, multiple-genome as well as synteny analyses [165].

10. Conclusions

Seasonal dormancy in herbaceous perennial grasses and legumes is an adaptive

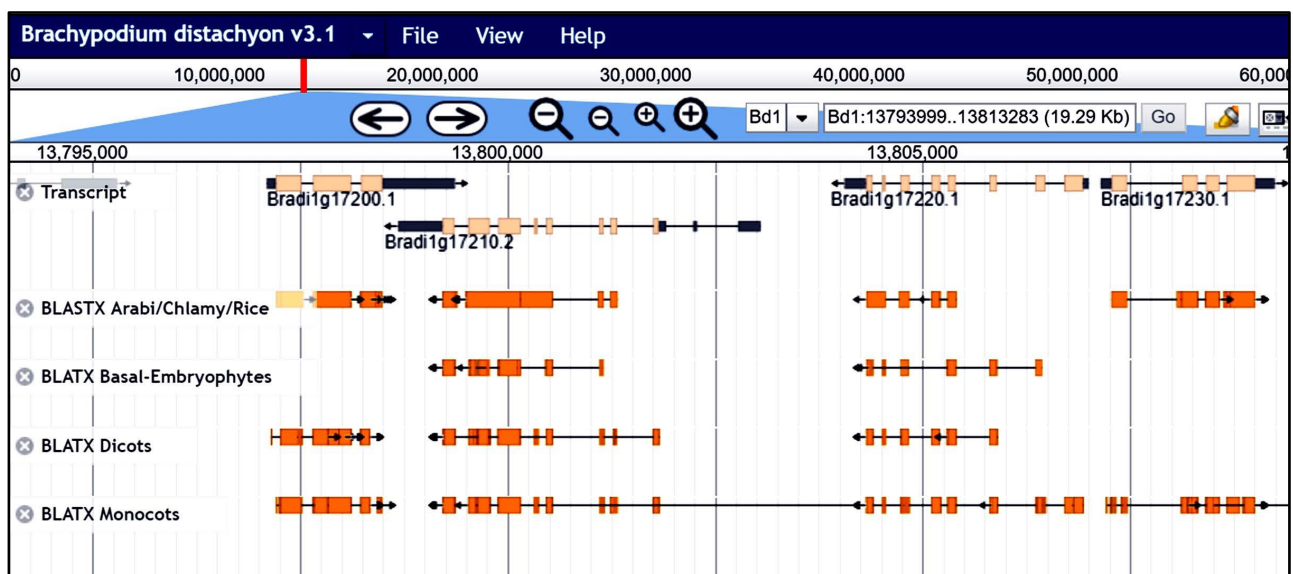


Figure 2. Structure of *Brachypodium distachyon* bud dormancy related gene, leucine zipper (bZIP), obtained using JBrowse of Phytozome 12.1 portal (<https://phytozome.jgi.doe.gov>).

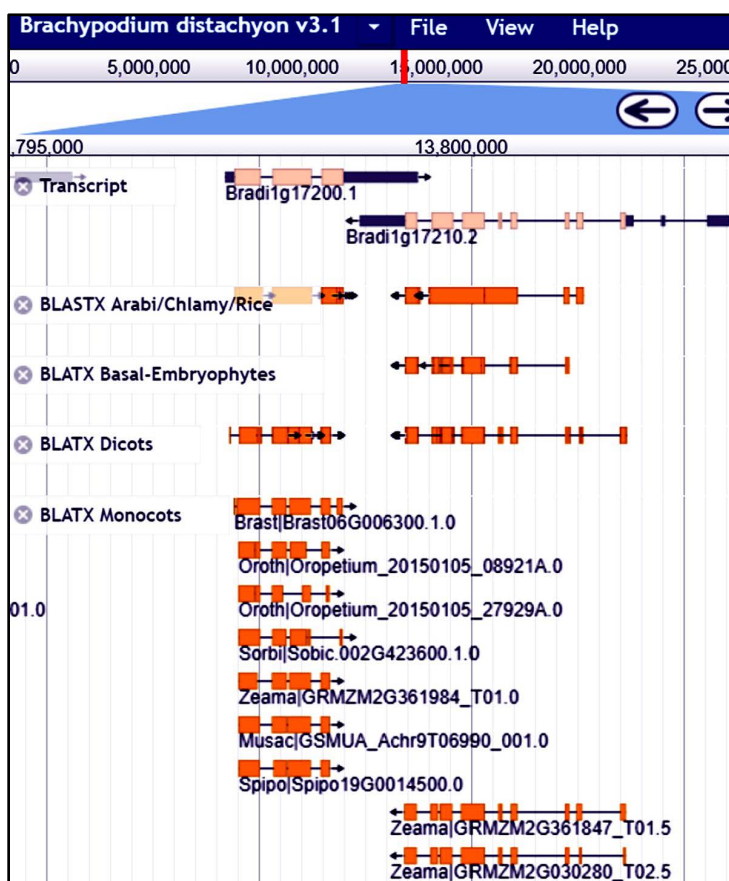


Figure 3. *Brachypodium distachyon* bZIP gene and related proteins in other organisms: *Oropetium*, *Zeamays*, *Sorghum bicolor* etc. viewed in JBrowse of Phytozome 12.1 portal (<https://phytozome.jgi.doe.gov/jbrowse>).

mechanism to survive in harsh environments. It can be manipulated through conventional selection and breeding, and using genomics to increase the growing season and crop yield. Weather extremes in summer and winter challenge herbage production. Improving forage production through dormancy manipulation to extend the growing season would be economically profitable. There is available germplasm for breeding species like alfalfa, bermudagrass, and tall fescue that can be exploited to develop non-dormant cultivars. Furthermore, knowledge of genes and genomic features controlling eudicots could be applicable to improve herbaceous forages, although they are evolutionarily divergent. Technological advances in genotyping, genomic selection, and high throughput phenotyping will play an important role in future dormancy related studies. This review summarizes important updates for plant dormancy related studies and the information could be useful to manipulate seasonal dormancy to develop non-dormant and semi-dormant cultivars that can overcome forage shortage in off seasons.

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Abbreviations

ABA: Abscisic Acid
 ABI: ABA-Insensitive
 ARF: Auxin Response Factors
 ATE: Arginyl-Trna: Protein Arginyltransferase
 AUX: Auxin
 BZIP: Leucine Zipper
 CAS: Cold Acclimation Specific Genes
 CBF: C Repeat Binding Factor
 CCA: Circadian Clock Associated
 CENL 1: Centroradialis-Like 1
 CHO1: Chotto1
 CO: Constans
 COR: Cold-Regulate Gene
 DAG1: Dof Affecting Germination 1
 DAM: Dormancy-Associated Mads-Box
 DDF : Dwarf And Delayed Flowering 1
 DOG: Delay Of Germination
 DRM: Dormancy-Associated Protein Gene
 ELF: Early Flowering

ET: Ethylene
FLC: Flowering Locus C
FT: Flowering Locus T
FUS: Fusca
GA: Gibberellic Acid
GA2OXS: Gibberellin 2- Oxidases
GI: Gigantia
GID1: Ga-Insensitive Dwarf1
HAB: Hypersensitive To Aba
HSP: Heat Shock Proteins
HUB1: Histone Monoubiquitination1
IAA: Indole-3-Acetic Acid
KYP: Kryptonite
LEC: Leafy Cotyledons
LHY: Late Elongated Hypocotyl
LUX: Lux Arrhythmo
MAX2: More Axillary Growth
NCED: 9-Cis-Epoxycarotenoid Dioxygenase
PHY: Phytochrome
PIF3: Phytocrome-Interacting Factor3
RDO: Reduced Dormancy
RGA: Repressor Of Ga1-3
RGL: Rga-Like
SCF: Skp1-Cullin-F-Box
SDR4: Seed Dormancy Gene 4
SLY: Sleepy
SOC1: Suppressor Of Overexpression Of Constans 1
SOM: Somnus
SPT: Spatula
SPY: Spindly
SVP: Short Vegetative Phase
TB: Teosinte Branched
TFL: Terminal Flower
TOC 1: Timing Of Cab 1
VP 1: Viviparous 1
ZCN1: Zea Centroradialis
ZTL: Zeitlupe