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▶ To cite this version:

Christophe Bailly, Maria Victoria Gomez Roldan. Impact of climate perturbations on seeds and seed quality for global agriculture. Biochemical Journal, 2023, 480, pp.177 - 196. 10.1042/bcj20220246 . hal-04092695

Biochemical Journal (2023) **480** 177–196
https://doi.org/10.1042/BCJ20220246

Review Article

Impact of climate perturbations on seeds and seed quality for global agriculture

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In agriculture, seeds are the most basic and vital input on which croplands productivity depends. These implies a good starting material, good production lines and good storage options. High-quality seed lots must be free of pests and pathogens and contain a required degree of genetic purity. Seeds need also to be stored in good condition between harvest and later sowing, to insure later on the field a good plant density and higher crop yield. In general, these parameters are already widely accepted and considered in many countries where advanced technologies evaluate them. However, the more and more frequently devastating climate changes observed around the world has put seed quality under threat, and current seeds may not be adapted to hazardous and unpredictable conditions. Climate-related factors such as temperature and water availability directly affect seed development and later germination. For these reasons, investigating seed quality in response to climate changes is a step to propose new crop varieties and practices that will bring solutions for our future.

Introduction

For many centuries, humans have domesticated plants to improve several traits that are adapted to specific agroecological environments. Many of these traits are related to seeds, such as productivity and uniformity, but also loss of dormancy, reduction in seed coat thickness, increased seed size, pericarp density, and nutritional composition, as examples [1]. These substantial morphological and physiological changes of domesticated crops, allowed the sedentary lifestyle of humans and the establishment of modern societies. In the last decades, crop production under altered environmental conditions has open new question about how to adapt the genetic material so far used, to increase tolerance against climatic perturbations affecting agronomic traits such as seed development, dormancy and germination.

Seed germination is a key phenological step in plant life, because it permits the survival of plant species in natural environments and influences crop yield in agriculture. Shifts in germination phenology and early seedling growth resulting from climate changes, in particular drought and high temperature episodes, will strongly influence all agrosystems' productivity. Seed germinative properties are acquired during their development on the mother plant [2]. Climate change will modify the intrinsic physiological seed properties through an effect on the seed developmental pattern. The seed ability to germinate in a large range of environmental conditions, usually referred to vigor [3], will be modified by higher temperature and/or drought stress that are expected to prevail during seed development. Similarly, dormancy, an endogenous blockage of seed germination, is also likely to be altered by a changing maternal environment [4]. These two traits acquired on the plant, i.e. vigor and dormancy, are major regulators of seed germination and they act in concert with the environmental conditions at the time of sowing for regulating germination [4–6]. In particular sub- or supra-optimal conditions of temperature, water and oxygen availability during seed imbibition can dramatically inhibit this

Received: 13 October 2022
Revised: 5 January 2023
Accepted: 16 January 2023

Version of Record published:
7 February 2023

process. Indeed, the germination process by itself, which lead to radicle protrusion though the seed covering structures is strictly regulated by environmental factors as water, light, oxygen and temperature [4].

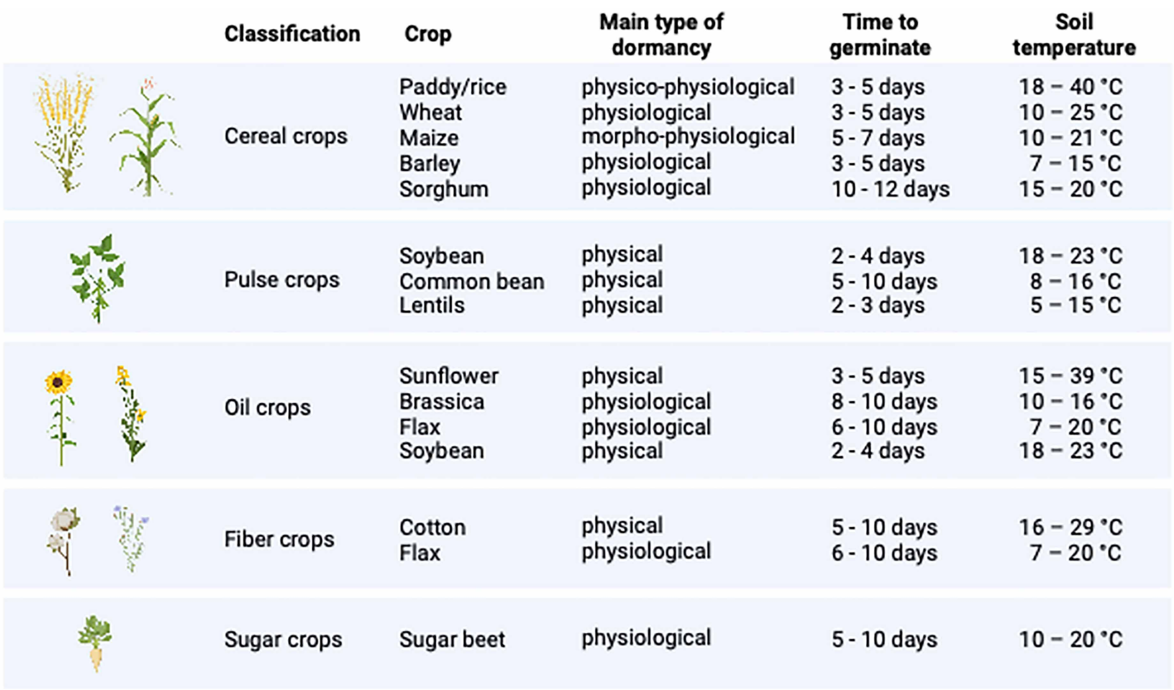
From the list of crops prone to be the more susceptible to climate changes, field crops are those on the top of the list, because they are sown directly as a seed in the open field (compared with horticultural crops that usually growth in controlled and irrigated conditions). This group of crops can be divided into cereals (wheat, barley, rice and maize) and other crops (pulses, sunflower, rapeseed, etc). Field crops account among the most extensive cultivated plants that provide the food, feed grain, oil, and fiber for domestic consumption. Field crops are plants that grown on a vast scale, mostly seasonal and mainly relies on rainfall for water supply [7]. For this reason, they are particularly at risk from the adverse effects of climate change, such as drought, high or cold temperatures, flooding, etc. Environmental changes can have a significant impact on field crop development and yield. Farmers adapt to these disturbances, in part, by changing sowing time or farming practices to maintain their production. Nevertheless, breeding of new climate-adapted genotypes need to be implemented to ensure the availability of food for the world population.

In this review, we detail the physiological, morphological and genetic characteristics of seeds, the starting material to cultivate field crops. We focus mainly on 13 of the most important field crops growing worldwide (Figure 1). We describe each step, from seed maturation to seed germination and the effects of climate changes on the physiology of the seeds. We explore the genetic factors helping to ideotype new crops varieties and finally we provide a number of practical options (management, production, selection and breeding) that could alleviate the impact of climate change on the crop seed sector.

Features of seed maturation, dormancy and germination in field crops

Seed development and maturation

The seed development process in angiosperms is initiated by the double fertilization of the ovule, where one sperm nucleus fertilizes the egg cell (to form the diploid embryo) and the other fertilizes the central cell (to form the triploid endosperm) [8]. The embryo represents the genetic content of the future plant, whereas the



Classification	Crop	Main type of dormancy	Time to germinate	Soil temperature
Cereal crops	Paddy/rice Wheat Maize Barley Sorghum	physico-physiological physiological morpho-physiological physiological physiological	3 - 5 days 3 - 5 days 5 - 7 days 3 - 5 days 10 - 12 days	18 – 40 °C 10 – 25 °C 10 – 21 °C 7 – 15 °C 15 – 20 °C
Pulse crops	Soybean Common bean Lentils	physical physical physical	2 - 4 days 5 - 10 days 2 - 3 days	18 – 23 °C 8 – 16 °C 5 – 15 °C
Oil crops	Sunflower Brassica Flax Soybean	physical physiological physiological physical	3 - 5 days 8 - 10 days 6 - 10 days 2 - 4 days	15 – 39 °C 10 – 16 °C 7 – 20 °C 18 – 23 °C
Fiber crops	Cotton Flax	physical physiological	5 - 10 days 6 - 10 days	16 – 29 °C 7 – 20 °C
Sugar crops	Sugar beet	physiological	5 - 10 days	10 – 20 °C

Figure 1. Classification of the most cultivated field crops.

Field crops are here classified based on its economic use. For each class, the most representative crops are listed as well as its type of dormancy and its optimal growing condition. Created with BioRender.com.

endosperm and the seed coat (maternal tissues) contribute as a physical and nutritional heritage, that can significantly affect quality and storability of the seed.

Mature seeds in monocots and dicots plant species share and differ in several aspects. One of the main differences between cereal (monocots) and other field crops (dicots) occurs during seed maturation, which leads to different volume ratios between the endosperm and the embryo [8]. The development of a characteristic prominent endosperm in monocot seeds, while most of it is consumed during dicot seed development. The envelop, called pericarp (in cereals) and seed coat (in dicots), plays also a strategic role in coordinating endosperm and embryo growth during seed development, as well as in dormancy and germination, depending of the species. The last two phases of seed development are characterized by the accumulation of reserves, leading to an increase in seed dry mass, and a concomitant loss of moisture content. From the time of fertilization till the mature seeds, the moisture content in ovules differs between field crops, going from 80 to 30% (loss of fresh weight in immature and mature seeds) in cereals and from 80 to 50% in dicots [9]. The seed filling is a critical process which involves the mobilization and transport of various constituents in mature seeds, such as proteins, carbohydrates and lipids. This process is highly sensitive to environmental changes, causing over or under accumulation of nutrients and also affect the final seed weight, both being primary components of the qualitative and quantitative traits of total seed yield.

Seed dormancy

Seed dormancy is a current condition of most seeds, that consist in an incapacity to germinate even in a favorable environment [10]. Seed dormancy is induced by desiccation and accumulation of the plant hormone abscisic acid (ABA) during the process of seed maturation. In nature, dormancy enables seeds to prevent germination during unfavorable periods. Several dormancy classes have been defined: morphological dormancy, which refers to seeds that have an underdeveloped embryo and require longer time to grow and germinate; physiological dormancy, that involves ABA and gibberellins (GAs) metabolism, morphophysiological or combinational dormancies; and physical dormancy, which involves the development of a water-impermeable seed coat [11]

In field crops, seed dormancy before harvest (primary dormancy) can be very low or highly dependent of species (Figure 1). During domestication a reduced seed dormancy was genetically selected in many crops to ensure rapid and uniform germination in the field, it was the case in many cereals and cultivated legumes [12–14]. However, some degree of seed dormancy is a favorable trait for some crops, and more intermediate levels of seed dormancy are now been incorporated in elite varieties of wheat and soybean to prevent premature sprouting prior to harvest [15, 16]. Instead, strong seed dormancy in sunflower is considered to be a serious constraint in seed production [17]. The dormancy of sunflower seeds is partly due to an inhibitory action of the envelopes (pericarp and seed coat), but exposing seeds to different treatments can reduced it, and improve germination [18]. Thus, primary dormancy is caused by the physiological, morphological and/or physical characteristics of the seeds, which are genetically determined. However, the maintenance of seed dormancy can also be modulated by the maternal environment during seed maturation. Environmental conditions such as temperature, day length, water and nutrient availability during seed development generally change seed dormancy capacities of field crops [13, 17]. Thus, understanding the genetics × environment (G × E) interactions for each crop is important to select the adequate dormancy requirements under particular environments.

Another undesirable trait observed in some field crops is the capacity of some seeds to enter in a so-called secondary dormancy. In crops, this type of dormancy is mainly caused by post-harvest treatments and bad storage conditions, and refers to the reversion of a non-dormant seed to a state of dormancy in unfavorable environmental conditions. Applied stresses such as anoxia, temperature or light induce secondary dormancy in barley and other cereals [19].

Seed germination

Seed germination begins with water uptake (imbibition, Phase I), continues an increase in metabolic activities and repairing processes (Phase II), and ends with initiation of growing and the elongation of the radicle through the seed coat (Phase III). Seed germination is a complex trait determined by the genetic background, by internal (hormones and metabolic content) and external (environmental) components of the seed. Endogenous ABA and GA levels negatively and positively control seed germination, respectively [10]. In addition to the phytohormones, polyphenolic compounds, such as anthocyanidins and pro-anthocyanidins (PAs), have an indirect role during seed imbibition by hampering radicle protrusion, and are therefore important determinants of seed coat-regulated germination in some pulses and oil seed crops [20].

In terms of crop diversity, field crops include several domesticated cereals (mainly *Poaceae*), pulses (*Fabaceae*), oil (*Asteraceae*, *Brassicaceae*), fiber (*Linaceae*, *Malvaceae*) and sugar (*Chenopodiaceae*) plants, each of them displaying specificities in terms of seed development, dormancy and germination (Figure 1). Therefore, the capacity of adaptive responses of seeds of different plant families to unpredictable climate changes has to be considered individually.

One of the most critical limiting external factors during seed germination is water availability. Seed germination is a sensitive stage in plants and moderate soil temperature and moisture following rainfall events are necessary after planting a field. Seed imbibition drives the reactivation of several metabolic, physiological, and biochemical processes necessary for the seed-to-seedling transition [21]. This transition from heterotrophic to autotrophic nutrition, requires the resumption of respiratory activity, acquisition of energy, activation of DNA repair mechanisms, protein biosynthesis from stored and newly synthesized mRNA, and reserve mobilization. In many crops, seed germination also declines rapidly in excess water. As during domestication many crops were selected for rapid imbibition that accelerate germination, they became particularly susceptible to flooding, which limits the availability of oxygen. This is a major issue, especially in pulses which are often grown during rainy seasons and in soils with poor drainage [22].

Temperature and light are also important environmental determinants of seed germination. Each type of seed germinates only within a particular temperature range. The temperature at which maximum germination takes place in the shortest time is called the most suitable temperature. All these parameters have a big impact on the successful establishment of seedlings in the field, and account as the first step to obtain good yield and quality.

The effects of the maternal environment

The environmental conditions on which the seed develops have not only an impact on seed yield but also on the phenotypic plasticity of the next generation. Thus, some of the environmental factors experienced in parental generations can alter how seeds respond to their own environments. The exact molecular mechanisms explaining this process are still not well understood but recent studies shown that epigenetic changes occurring in the maternal heritance [21].

Epigenetic alterations commonly involve DNA methylation, post-translational histone modifications, ATP-dependent alterations to chromatin and non-coding RNA transcripts. These heritable changes do not affect the DNA/RNA sequence, but are usually associated with differing expressions of the epialleles and are potentially reversible [23]. Several key players have been identified in the model plant *Arabidopsis thaliana,* being one of them the *DELAY OF GERMINATION1* (*DOG1*) gene, involved in coordination of seed maturation and acts in concert with ABA to inhibit seed germination. DOG1encodes an heme-binding protein that promotes seed dormancy by enhancing ABA signaling through its binding to PP2C ABA HYPERSENSITIVE GERMINATION (AHG1/AHG3) [24]. Several epigenetic regulators and histone modifiers have been shown to dynamically regulate *DOG1* expression to control seed dormancy [24]. In addition, enhanced *DOG1* expression under low-temperature conditions during seed development, has been associated with increased seed dormancy [25, 26]. Therefore, DOG1 is likely to exhibit environmental sensitivity. Interestingly, a high number of *AtDOG1* homologs have been found in other species of *Brassicaceae* and in cereals [27]. However, the amino acid sequences of cereal DOG1-like proteins do not have much similarity with those of dicot plants. Still, *DOG1* homologous and other epigenetic players would be good candidates to try to manipulate seed dormancy in environment challenged conditions.

Physiological mechanisms affecting seed dormancy and germination under stress

Temperature stress

Among the environmental factors that are likely to be affected by global change, temperature is a major factor [28]. Temperature has a dramatic effect on seed germination and is generally considered as the most determinant environmental factor of this process. Temperature is regulating each step of seed life from development on the plant to the germination process by itself including removal and induction of dormancy and seed ageing during storage.

Effect of temperature on seed development

The maternal environment that prevails during seed set on the plant is known for long as being crucial for the germinative properties of the progeny (Figure 2). In many species temperature has been shown to alter the depth of dormancy during seed maturation [2, 29, 30]. For example, in annual ryegrass, *Arabidopsis thaliana or Lolium perenne* high temperatures reduce dormancy and negatively affect the final seed yield [31–33]. In *Brassica napus* heat stress during seed filling also decreased seed dormancy [34], whereas in rice high temperature during the grain filling induced slower germination of the progeny without inducing primary dormancy [35]. The effect of warm temperature on depth of dormancy has been attributed to a low expression of *DOG1* [29, 36], and to an ABA breakdown [37]. However, in contrast, higher temperatures during seed development were also shown to promote dormancy for some species [38], suggesting that the seed response to maternal temperature is species specific [39]. In addition, temperature stress can also alter seed vigor [33]. This is the case for soybean [40], pepper [41], *Vicia sativa* [42] or field pea [43], for example. Warm temperatures during seed development can also have a negative effect on seed longevity after harvest [44, 45].

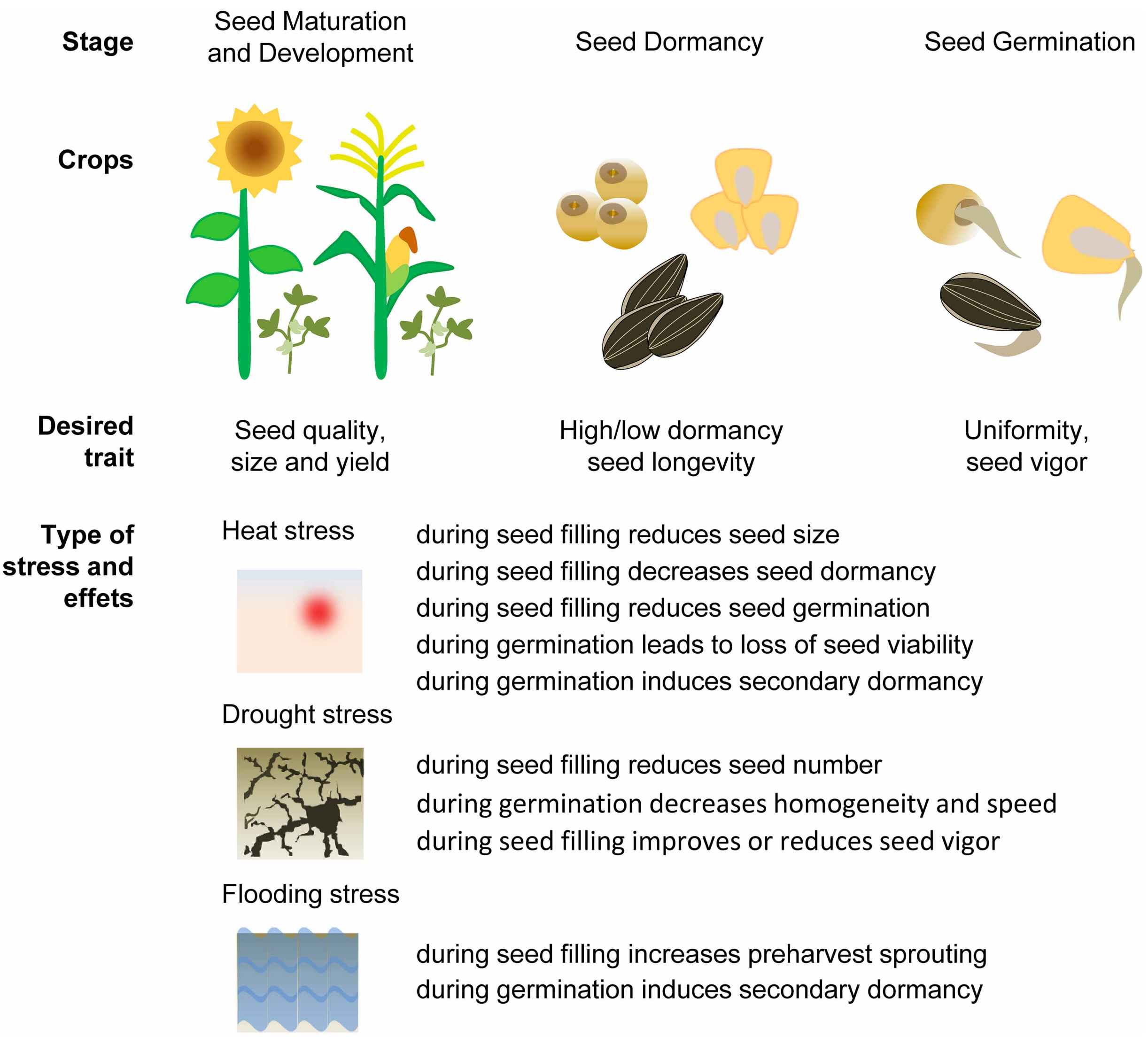


Figure 2. Environmental factors influencing seed development, dormancy and germination.
For each stage of development different agronomic and seed quality traits are evaluated to insure later a high crop yield. The physiological effects on the seed will depend on the type of stress (heat, drought or flooding) encountered as well as the intensity and timing during development.

Effect of temperature on seed germination

Temperature plays a determinant role in seedling emergence and its range during seed imbibition directly determine the ability to germinate (Figure 2). Thus, seeds of each species germinate in defined range of temperatures enclosed between 2 cardinal temperature, Tb and Tm, which respectively correspond to the minimal and maximal temperature allowing germination [46]. These temperatures are also dramatically altered by the origin of the seed (i.e. the maternal environment, as discussed previously), the presence of dormancy or the age of the seed. When imbibed at supra-optimal temperatures, seeds are considered to be thermoinhibited which results in an inhibition, or a dramatic decrease, of germination that can ultimately lead to loss of seed viability. However, thermoinhibited seeds can rapidly germinate when they return to a permissive temperature for germination [47]. Excessive temperatures during seed imbibition can alternatively induce secondary dormancy, which corresponds to a loss of ability of the seed to germinate at lower temperatures [47]. Secondary dormancy is distinguished from primary dormancy because this former is established during seed development and in contrast secondary dormancy is acquired in dispersed seeds after primary dormancy lost [2]. When secondary dormancy is released then seeds become again able to germinate at their optimal temperature. Distinction between thermoinhibition and secondary thermodormancy is not always easy to detect and the mechanisms involved in both processes often overlap [48]. For example, ABA synthesis and signaling has been demonstrated as playing a role in thermoinhibition [49], but has been shown to be involved in the induction of secondary dormancy [50]. Reactive Oxygen Species (ROS) are generally over-produced when seeds are germinated in supra-optimal conditions of temperature [51] and they are also involved in the regulation of primary dormancy, but their role in the induction of secondary dormancy has not been clearly established yet.

Drought stress

Occurrence of severe drought episodes is a dramatic side effect of global warming. It is expected that drought, similarly to heat, will significantly reduce crop productivity and yields in a near future [52]. All steps of plant life are sensitive to drought and, at the seed level, the major consequences are an alteration of intrinsic properties of seeds that develop on the mother plant and poor stand establishment.

Effect of drought stress on seed development

Similarly to heat stress drought during the plant reproductive phase is likely to deeply modify seed germinative properties of the progeny. One the one hand, drought stress during seed development can decrease seed vigor [53–55]. On the other hand, it has also been shown to improve seed vigor of the progeny [18, 56, 57] (Figure 2). This detrimental/beneficial effect on seed germination probably relies on the level and duration of drought stress but also on the time window at which drought stress is applied on the mother plant, as evidenced by Vancostenoble et al. [18]. Interestingly, Vancostenoble et al. [18] also demonstrated that drought stress during sunflower seed development provided tolerance to water, hypoxic, cold and salt stresses during seed germination, but that it also induced lower dormancy. Some other studies have also shown that water stress on the mother plant reduced seed dormancy, as for example in Sorghum [58], *Avena fatua* [59] or *Amaranthus retroflexus* [60]. ABA is largely acknowledged as the plant hormone associated with response to drought [61]. In sunflower it has been demonstrated that plants grown under drought conditions accumulated more ABA in seeds than plants grown under well irrigated conditions [62] but without any link with performance of germination. In contrast, Vancostenoble et al. [18] showed that sunflower seeds that developed under drought stress and that were less dormant accumulated less ABA. In barley, under drought stress, developing seeds accumulated not only ABA but diphaseic acid (DPA), a product of ABA catabolism [63] and it has been proposed that the imported ABA in excess in seeds is cleaved to inactive catabolites phaseic acid (PA) and DPA [61]. The relationship between ABA metabolism in developing seeds and drought stress during the reproductive stage is therefore not so clear and will require further investigations.

Effect of drought stress on seed germination

Water is a critical component of the germination process and the presence of water is an absolute prerequisite for seed germination. Water is absorbed by the dry seed during the imbibition phase, which is then followed by a plateau phase (so-called the *sensu stricto* germination phase or phase II) that occurs at a constant moisture content. Finally, a novel uptake of water is associated with radicle elongation and the emergence of the radicle characterizes the completion of germination [46]. Any disturbance in water availability within the soil at the time of sowing can decrease seed germination and subsequent seedling growth thus leading to poor stand establishment for crop species. The relationship between germination and water availability have been integrated through the hydrotime concept that allows the quantification of the germination speed (θ_H), water stress tolerance (base water potential, Ψ_b) and the germination uniformity ($\sigma_{\Psi b}$) [64]. Typical effects of drought stress on sunflower seed germination were for example shown using a range of polyethylene glycol (PEG) solutions giving a range of decreasing water potential solutions [65, 66]. Decrease in water availability first induced a decrease in homogeneity and speed of germination and lower water potential totally prevented seed germination, but this depended on initial seed vigor of the seed batches highlighting genetic and maternal components in the ability of seeds to germinate under drought stress [65] (Figure 2). As for whole plants the mechanisms associated with water stress tolerance at the germination stage often relies on ROS detoxifying mechanism, synthesis of osmolytes (e.g. proline or polyamines), chaperon proteins (e.g. HSPs) and ABA metabolism [66]

Flooding stress

Beside the thermal-related stresses of global warming, such as heat and drought, an unexpected consequence of climate change on crop productivity relies on flooding events. Flooding actually affects ca 16% of agricultural production worldwide [67], but is likely to increase dramatically in the forthcoming years due to more frequent heavy and erratic rainfalls [68]. Seed germination can be dramatically altered by flooding events mostly because flooding directly limits oxygen availability within the soil and causes hypoxia [69]. However, oxygen is a critical factor of seed germination since it allows the resumption of respiration and metabolism that are essentials for the completion of this process [70]. Therefore, germination of seeds of most species is dramatically inhibited under restricted oxygen availability (Figure 2). In addition, seed oxygen sensitivity also depends on environmental factors including temperature, osmotic pressure of the medium and light and on intrinsic factors such as depth of dormancy [70]. In addition, prolonged exposure of imbibed seeds to hypoxic conditions can induce secondary dormancy. For example, in barley it has shown that 3 d treatment of caryopses in O_2 tensions lower than 10% at 15°C induced secondary dormancy [19]. Mechanisms of oxygen sensing and response in seeds involve transcription factors of the group VII ethylene response factors (ERF-VIIs) [71], ethylene signaling pathway [72] and ROS homeostasis and metabolism [70, 73].

Genetic and molecular mechanisms involved in tolerance to climate changes in field crops

To elucidated key genetic loci and genes controlling agronomical and adaptive traits in crops, several approaches have been implemented. The accessibility to genetic resources and the rapid development of high-throughput technologies have allowed to apply functional and comparative genomics studies on each type of crop. Thus, quantitative trait loci (QTL) and genome-wide association studies (GWAS) analysis are two methods widely used to identify significant regions associated with complex traits, such as heat stress or drought tolerance [74]. Although, several single genes with significant positive effects have been identified, only few of them have been introgressed in elite crop varieties. Here, we summarize recent advances in research on several field crop that helped to identify the responsible genetic factors or underlying genes associated to seed dormancy and germination under constrain environmental conditions (Table 1).

Cereal crops

According to the FAO, world cereal production in 2021 reached 2793 million tones [100]. Cereal production is strictly linked to weather, and susceptibility to specific environmental changes can affects their economic yield. One serious problem in cereal crops such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) is a phenomenon called preharvest sprouting (PHS), which causes severe yield loss and poor quality of the grain [15]. PHS is the germination of grains in the mother plant before harvest [15]. Changes in climate (heavy rainfall occurring at or near seed maturity) are increasing the occurrence of this phenomenon in cereal crops. A key way to prevent PHS is to select genotypes with the ideal pattern of seed dormancy, means remaining dormant before harvest but losing dormancy after to allow fast and homogenous germination at sowing.

Wheat is a hexaploid crop ($2n = 6x = 42$, AABBDD) and is known that *Aegilops tauschii*, the D subgenome donor, has strong seed dormancy, but the genetics of seed dormancy in *Ae. tauschii* are still not well understood [101]. Only a few causal genes for dormancy QTL have been identified, two of them associated to chromosomes 3 and 4 on the A subgenome (*Triticum urartu*). Using wheat cultivars and breeding lines, a mapping

Table 1 List of genes and molecular markers associated with abiotic stress identified in field crops Part 1 of 3

Field crop	Desired trait	Associated gene/QTL	Gene description	Conditions/ Comments	Reference
Wheat	Tolerance to drought	*TraesCS5A02G022100, TraesCS5B02G014200* and *TraesCS5D02G563900*	GATA transcription factor (TF), RING/ U-box superfamily protein and Glutathione S-transferase (GST)	Putative candidate genes associated to QTL involved in the drought tolerance at the germination stage	[75]
	Preharvest sprouting	*MKK3*	MAP kinase activity protein	Putative gene of seed dormancy in QTL *Phy1*	[76]
		Ta-*MFT*	Phosphatidylethanolamine-binding protein	Gene resides in the seed dormancy QTL *QPhs.ocs-3A.1*	[77]
Barley	Preharvest sprouting	*AlaAT*	Alanine aminotransferase protein	Causal gene of seed dormancy in QTLs *Qsd1*	[78]
		MKK3	MAP kinase activity protein	Causal gene of seed dormancy in QTLs *Qsd2-AK*	
	Tolerance to drought	*HORVU6Hr1G008640, HORVU6Hr1G008730, HORVU6Hr1G008880 and HORVU6Hr1G008880*	Catalase 1, Catalase 3, heat shock 70 kDa protein C and AP2-like ethylene-responsive TF	QTL at chromosome 6H associated with germination percentage related traits	[79]
Maize	Tolerance to cold stress	*Zm00001d039219* and *Zm00001d034319*	MAPK signalling and fatty acid metabolic processes.	Significantly up-regulated expression in low-temperature resistant line	[80]
		Zm00001d010458, Zm00001d050021, Zm00001d010454, and *Zm00001d010459*	mannosyl-oligosaccharide 1, 2-alpha-mannosidase, CBL-interacting protein kinase and abscisic acid 8′-hydroxylase3	Contrasting gene expression profiles between the chilling-sensitive line (SCL127) and tolerant line (SCL326) under cold stress	[81]
	Tolerance to drought	*ZmbZIP72*	Zinc-finger domain protein	Induced by ABA	[82]
		ZmCPK4	Calcium-dependent protein	Enhanced ABA sensitivity in seed germination	[83]
		ZmWRKY58	WRKY transcription factor	Positive regulator in drought and salt stress	[84]
Sorghum	Tolerance to cold	*Sb06g022095*	NAC transcription factor	Improve field emergence percentage	[85]
		Sobic.007G037000, Sobic.007G00540 and *Sobic.007G005500.*	Alpha/beta hydrolase domain protein, DnaJ/Hsp40 motif-containing protein, YTH domain RNA-binding protein	*qRB7* and *qTB7* loci involved in lipid homeostasis, chaperone, and signalling activities are highly expressed under chilling stress	[86]
Paddy/ Rice	Tolerance to anaerobic germination	*OsTPP7*	Trehalose-6-phosphate phosphatase protein	*AG1* loci enhances starch mobilization during embryo growth	[87]

Continued

Table 1 List of genes and molecular markers associated with abiotic stress identified in field crops Part 2 of 3

Field crop	Desired trait	Associated gene/QTL	Gene description	Conditions/ Comments	Reference
		LOC_Os07g11020	Basic helix-loop-helix protein	Part of *AG2* loci involved in red pericarp development	[88]
		OsCLSY1	RNA-directed DNA methylation protein	Control of 24-nt siRNA production, methylation, and gene expression	[89]
	Tolerance to cold	*OsSAP16*	Zinc-finger domain protein	Expression enhances germination at low temperature	[90]
		Os07g0585700	*Seed dormancy 4* (*Sdr4*)	Promising candidate in loci 95 is involves in seed dormancy	[91]
Soybean	Tolerance to drought	*Glyma.12g174000, Glyma.12g174100, Glyma.13g202200* and *Glyma.06g188400*	Serine/threonine-protein kinase, Auxin response factors, Carotenoid cleavage dioxygenase and MYB transcription factor	QTL linked to drought tolerance at the germination stage	[92]
		GmSMXLs	Eight genes coding for Suppressor of MAX2.1-Like proteins	Elements of the karrikin (KAR) and strigolactone (SL) signalling pathways, significantly down-regulated during seed germination under drought treatment	[93]
	Seed storability	*qSG-A2, qSV-C2.1, qSV-C2.2, qSV-C2.3qSV-D1b*	QTL associated to seed viability and seed vigor	Detected QTL for seed storability at 25 and 35 for six months	[16]
	Tolerance to anaerobic germination	*GmERFVII1, GmERFVII2 & GmERFVII3 and MAPK1*	Ethylene Response Factors, and MAP kinase activity protein	Genes up-regulated in a seed-flooding tolerant wild soybean variety	[94]
Common bean	Tolerance to anaerobic germination	Phvul.006G054700, Phvul.008G039400	Cytochrome P450, SNF1-related protein kinase 1	Andean-specific QTL associated with germination under flooding conditions	[22]
Sunflower	Seed dormancy	*Sger.6.1, Sger.10.1*	QTL detected for speed of germination	Using a recombinant inbred line population, QTL involved in seedling vigour and development were identified	[95]
		Sd3.1 3, sd11.1 11, sd15.1 15	QTL effects were in the predicted direction (wild alleles decreased self-pollination and seed germination)	QTL for seed dormancy in a backcross population between a wild self-incompatibility (SI, dormant) and an elite (SP, nondormant) parent	[96]
Brassica	Tolerance to drought	*BnaC01g35030D, BnaC01g32600D and BnaC01g30750D*	Abscisic acid stimulus, oxidative stress, and ABA signalling and cold stress associated genes	Genes associated with drought tolerance detected within the QTLs on chromosome C01	[97]

Continued

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https://doi.org/10.1042/BCJ20220246

Table 1 List of genes and molecular markers associated with abiotic stress identified in field crops Part 3 of 3

Field crop	Desired trait	Associated gene/QTL	Gene description	Conditions/ Comments	Reference
		BnaGA1, BnaKO1, BnaGID1a and BnaEXPA8	GA biosynthetic pathway, GA receptors, and GA responsive genes	Genes identified using a transcriptomic, metabolic, and hormonal data at different stages upon seed imbibition	[98]
Cotton	Tolerance to drought	*GhMFT1* and *GhMFT2*	Phosphatidylethanolamine-binding protein	involved in seed germination	[99]

analysis showed that *MOTHER OF FT AND TFL1* (*MFT*) on chromosome 3A colocalized with the seed dormancy QTL *QPhs.ocs-3A.1* [77]. Interestingly, *MFT* seems to be one of the key temperature regulator factors of seed germination in wheat. In wheat, cold temperatures during seed development produce high levels of seed dormancy, whereas, low temperatures at germination stimulate seed germination [13]. In mature seeds of two wheat varieties, the expression level of *MFT* from plants that were grown at 13°C (after anthesis) was four times higher than that at 25°C, and its expression in the embryo was positively correlated with the level of seed dormancy [77].

More recently, the *mitogen-activated protein kinase kinase 3* (*MKK3*) gene on chromosome 4A, was identified as the causal gene for the second seed dormancy QTL in wheat, *Phs1* [76]. In this study, complementation with the *MKK3-A* allele from a nondormant cultivar into a dormant wheat cultivar showed a clear decrease in seed dormancy. Interestingly, the same gene was also identified as the genetic cause for the grain dormancy QTL *Qsd2-AK* (SD2) in barley, but the mutant allele in barley (N260) display strong dormancy in contrast with the mutant allele in wheat (N220K) which is non-dormant [76, 78]. These results clearly illustrate the importance of finding particular alleles on each crop and how this information can be useful to develop new varieties with higher levels of dormancy and improve PHS tolerance.

Besides wheat and barley, tropical crops such as maize (*Zea mays* L.), sorghum (*Sorghum bicolor* L.) and rice (*Oryza sativa* L.) encounter other type of problem related with low tolerance to early-stage chilling temperatures, which limit its cultivation in cooler regions of the world [81, 86, 90, 91]. A northern shift of tropical crops production area would allow them not to suffer from water deficit during their growth and land re-allocation of such crops can a long-term adaptation to global warming [102, 103]. However, seed field emergence and later seedling vigor, are negatively affected by cold [104]. Maize is now cultivated in a wide range of latitudes and several genetic and agricultural methods have been implemented to maintain competitive yields. Several genetic loci on cold resistance during germination have been identified using QTL and GWAS [105], however, only few candidate genes and the associated regulatory network have been validated on the field. Among these genes, two genes were identified using GWAS and RNA-seq analysis coding for a Mitogen activated protein kinase (MAPK) and a fatty acid hydroxylase; and appeared to be related to low-temperature signal transduction and cell membrane fluidity in maize [80]. Moreover, using a maize association panel composed of 300 inbred lines, four additional candidate genes involved in maize chilling-germination were revealed [81], but the genetic validation is still missing.

Less world-wide distributed than maize, sorghum is a multipurpose food crop commonly cultivated in non-irrigated lands of Africa. Sorghum is well adapted to high temperature and dry conditions, but its sensitivity to cold stress during germination clearly limits its adoption in higher latitudes [106]. Unfortunately, in the 20th century a strong selection for alleles that reduce seed tannins and plant height were inadvertently introduced in grain sorghum varieties resulting in the loss of early-season chilling tolerance. Marla et al. [79] proposed several breeding models to obtain chilling tolerance while bypassing undesirable characteristics, in particular by the introgression of new QTL identified in Chinese sorghum varieties. Furthermore, a GWAS analysis was performed on a sorghum association panel grown under control (30/20°C; day/night) and chilling (20/10°C) conditions. This analysis helped identify a relevant genomic region on chromosome 07 that controls the early-season chilling tolerance in sorghum and did not co-localize with tannin content [86]. The expression of several candidate genes involved in key physiological functions including lipid homeostasis, chaperone and signaling activities, were significantly higher under chilling stress [86]. Moreover, a collection of 194 sorghum lines was scored using a GWAS analysis and identified a region in chromosome 06 associated to a transcript encoding for a NO APICAL MERISTEM protein (NAM), as putatively improving field emergence percentage under low-temperature conditions [85]. Functional validation of these genes will help to improve early growth events in sorghum (increased emergence index and seedling vigor), and potentially induce higher tolerance to chilling conditions.

Drought is among the most detrimental stress conditions for cereals crops, causing serious problems for seed germination, development, and productivity [75, 107]. Maize is more sensitive to drought than other cereals [108]. The molecular regulation of maize seed germination under water-deficit conditions have then been extensively studied but only few genes have been identified. One particular reason is the difficulty of studying drought stress tolerance in crop under lab conditions. This problem has been circumvented by inducing osmotic stress induced by either mannitol or PEG. Both approaches decrease water uptake and thus germination, and had allowed rapid screening of tolerant or sensitive maize germplasm in a short time compared with field conditions. In that way, a bZIP transcription-factor gene, *ZmbZIP72*, which expression was induced by ABA, was identified as a gene influencing seed germination under drought stress [82]. Also, a calcium-dependent protein kinase gene, *ZmCPK4*, was identified as enhancing ABA sensitivity in seed germination and increasing drought stress tolerance [83]. The calcium signaling associated to seed germination also involves the expression of a WRKY transcription factor, ZmWRKY58, and a calmodine protein (ZmCaM2); which together may act as positive regulators in drought and salt stress response in cereals [84]. More recently, one study using a multi-parent advanced generation inter-cross (MAGIC) population and the other a gene bank collection, allowed identifying several QTL and maize accessions associated to drought stress at germination [109, 110]. Additional studies are needed to validate these results under field conditions and identify potential genes and genotypes for breeding commercial strategies.

Tolerance of anaerobic germination (AG) is a unique and sought trait for the development of new rice varieties. Due to a combination of economic, environmental and ecological constrains, rice cultivation is shifting from transplanting seedlings to direct sowing of seeds. Extensive research is ongoing to find new rice cultivars with high tolerance for AG adapted to direct seeded. However, AG tolerance is a rare trait among most high-yielding modern cultivated varieties. A major QTL on chromosome 9, (referred as *AG1*), has been fine mapped and characterized at the gene level. The gene underlying *AG1,* which enhances AG tolerance, codes for a trehalose-6-phosphate phosphatase protein (OsTPP7) [87]. In an attempt to discover new AG tolerant loci, an enriched-GWAS combined with a transcriptome analysis between AG tolerant donors and susceptible accessions, revealed the *AG2* peak region (containing 27 genes), includes the *Rc* gene, responsible for red pericarp development in pigmented rice [88]. Furthermore, 3000 rice genome germplasm from the International Rice Research Institute (IRRI) were used to quantify the percentage of germination in anaerobic conditions. This study determined AG as a polygenic trait associated with several transcription factors linked to ethylene responses, small RNA and methylation pathways. A gene involved in the RNA-directed DNA methylation (RdDm) pathway, *CLASSY 1* (*OsCLSY1*), was shown to highly contributes to the capacity of rice to germinate under submerged conditions [89].

Pulse crops

Pulse crops are the edible seeds of plants from the legume family. Legume seeds are the second most important plant protein source, after cereals. The particularity of legumes resides in their ability to fix atmospheric nitrogen allowing them to be adaptable to poor soils.

Soybean (*Glycine max*) is the most widely grown seed legume in the world and it provides high protein contents compared with any other crop [111]. *G. max* bears seeds with little to no dormancy because uniform and rapid germination are important for soybean cultivation and food processing. However, some commercial cultivars possess a water-impermeable seed coat, called hardseedness, which causes physical dormancy. This dormancy is release in response to temperature changes in the habitat, resulting in testa permeability to water and germination. Using recombinant inbred lines (RILs), five QTLs were detected, indicating that the impermeability of soybean seed is genetically related to the surface roughness (SR) of the seed coat [112]. Seed hardseedness is also an important trait because has been associated with a high degree of seed storability in climates with high temperature and humidity. Seed storability is a complex trait easily influenced by the environment that controls seed viability and seed vigor. Recent studies identified five QTLs associated to seed viability after storage at 25 or 35°C for 6 months [16]. Seed hardseedness due to genetic and environmental factors has also been reveled in the cultivated legume lentil (*Lens culinaris* or *L. esculenta*). Crosses between cultivated and wild

Biochemical Journal (2023) **480** 177–196
https://doi.org/10.1042/BCJ20220246

lentil species (*L. orientalis* and *L. ervoides*) seemed to suggest that the trait was controlled be a single locus [113]. However, unusual dominance relationships between the alleles of the three taxa introduced during lentils domestication need to be clarify to better understand the relation between hard seed coat and seed dormancy.

Soybeans are also relatively sensitive to drought, and face significantly reduced yield in low-rainfall regions. Genes belonging to the *Suppressor of MAX2 1-Like* (*SMXL*) family are downstream elements of the karrikin and strigolactone signaling pathways. A recent study has found that soybean SMXLs participate in the regulation of seed germination in response to drought stress [93]. These findings also indicated that down-regulation of *GmSMXLs* may be regulated by phytohormones (ABA and GA) and stress, but functional analysis of those genes need still to be further explored. In addition, using a GWAS with a large germplasm diversity panel of Chinese soybean cultivars, Liu et al. [92] proposed a genetic mechanism underlying drought tolerance at the seed germination stage. Although, none of the SNPs significantly associated to germination rate under drought stress was located in coding regions, functional annotations of closed genes identified a putative MYB transcription factor, a protein kinases and an auxin response factor [92]. In addition, a putative carotenoid cleavage dioxygenase was also listed on this analysis, suggesting a potential variation of ABA biosynthesis genes in drought-tolerant varieties of soybean.

The germination and emergence of soybean can also be hindered by the presence of excessive water due to rainfall just after field sowing of soybean. To evaluate seed-flooding tolerance in soybean, transcriptomic and QTLs analysis have been employed. Three genes coding for the Ethylene Response Factors group VII and a MAP-Kinase were predicted as the possible candidate genes for seed-flooding tolerance [94]. Excess water has also been reported as the main production issue in common bean (*Phaseolus vulgaris* L.). Two genomic regions (*P06/16.0* and *Pv08/3.2*) associated with flooding tolerance at germination stage were identified using a collection of 277 genotypes from the Andean Diversity Panel [22].

Oilseed crops

Oilseed rape (*Brassica napus L., AACC,* $2n = 4x = 38$) is one of the world's most important sources of high-quality vegetable oils for human and vegetable protein diets for livestock. *B. napus* productivity is being challenged by variable environmental conditions that affect the reliability of seed germination in the field. *B. napus* is very sensitive to drought stress, making important the development of varieties with high tolerance to drought. Using a number of germination-related traits and a QTL mapping in *B. napus*, 128 drought tolerant-related candidate genes were identified [97]. Several QTL were detected on the chromosome C1; including genes involved in ABA stimulus and oxidative stress. Moreover, one QTL for germination percentage under drought stress was detected in the chromosome A10 [97]. Also, a complete analysis using six winter *B. napus* accessions at different stages upon seed imbibition had identified a combination of metabolites, hormones, and genes (aspartate, malate, IAA/IAA-asp, GA/ABA, *BnaGA1*, *BnaKO1*, *BnaGID1a*, *BnaEXPA8*) that correlate with germination performance and could be putative targets for crop improvement of *B. napus* [98].

Sunflower (*Helianthus annuus* L.) is one of the most lucrative oilseeds in the world. Origin and domestication of sunflower is located in North America but it has been adapted to many habitats. Reduced sunflower seed dormancy at harvest, fast and uniform seed germination, resistance to lethal temperatures and increase tolerance to lower water potentials during seed germination, are traits that have been introgressed from compatible wild sunflower relatives. Still, several sunflower varieties may have become non-adapted to future climate conditions. In sunflower, no major genes of large effect have been identified for seed dormancy but many small-effect QTL [12, 95, 96].

Among other sources of vegetable oil, flaxseed or linseed (*Linum usitatissimum L.*) is emerging as an important crop with high content of essential fatty acids. Seed color in flax had been associated with germination efficiency in the field, thus yellow seeds had a lower germination frequency than brown seeds. Interactions between genotype (yellow vs. brown) and chilling conditions (0°C during 96 h) significantly increased germination percentages of flax seeds [114]. However, regarding the identification of the genetic factors associated with important seed traits are still missing in flax which is a multipurpose crop, used on both oil and fiber production.

Fiber crops

Upland cotton (*Gossypium hirsutism* L.) is a leading natural fiber crop, and it is grown for the textile industry due to its high yield and wide adaptability. Drought is one of the most devasting abiotic stress problems in cotton production in arid and semi-arid regions. Drought stress can decrease cotton yield by up to 50–67%.

Cotton is a tetraploid crop (2n = 4x = 52) with 26 chromosome pairs. In addition, a large number of accessions that showed high levels of genotypic and genetic variation have been identified as an ideal resource for association mapping. However, only few QTL analyses of stress tolerance have been reported in cotton, and almost none on stress tolerance at the seed-germination stage. Instead, some examples of the functional characterization of candidate genes through overexpression and/or knockdown experiments revealed a significant role of a protein in enhancing drought stress tolerance in cotton. Arabidopsis seeds overexpressing the *Acyl coenzyme A oxidase 3* (*GhACX3*) gene exhibited high tolerance to drought stress by having higher root germination rate relative to WT. GnACX3 is an enzyme involved in the β-oxidation pathway of fatty acids, and its overexpression seems to increase the concentration of antioxidants [115].

As cotton is native of warm places, which makes it relatively susceptible to injury when exposed to low temperatures. Interestingly, two MFT homolog genes, *GhMFT1-A/D* and *GhMFT2-A/D*, were identified by genome-wide. *Arabidopsis* overexpressing plants indicated that GhMFT1 and GhMFT2 may act redundantly to inhibit seed germination at the early stage in cotton [99]. As MFT has been shown to be an important regulator of germination at low temperature in other crops, these results may contribute to increase our knowledge in cotton agronomic traits.

Sugar crops

A relatively new crop with economic importance for sugar and bioethanol production is the temperate crop sugar beet (*Beta vulgaris ssp. vulgaris* L.). The dispersal unit of sugar beet is a woody fruit, called seedball, on which the true seeds are wrapped by an extra layer of maternal tissue, the pericarp (seed coat). Industrial processing (polishing and washing) of sugar beet fruits restricts that physical dormancy [116]. However, a phenomenon of cold-induced secondary dormancy has also been observed due to early season frost and chilling temperatures. Transcriptomics analysis using several seed lots identified several genes with temperature-specific expression pattern, including *BvABI5*, *BvABF2* and *BvMFT* which were up-regulated at 5°C in the secondary dormancy sugar beet lot [117].

Effective solutions to control seed dormancy and enhance germination under stress conditions

Identifying new resources and strategies to minimize the damages caused by climate changes on agricultural productivity is one of the most important challenges for the next years. Some practices (e.g. seed priming, new areas for seed production) are currently implemented for several crops and shown convincing results, whereas others (e.g. crop migration, crop diversification) imply important collective and economic decisions. More innovative and original formulations (e.g. parental shading, nanoparticles) are now emerging in the agricultural sector, and can contribute to the sustainability of agriculture [118, 119].

Inducing stress memory by priming

Priming techniques can empower faster and uniform germination of seeds under stressful conditions. Two approaches have been used: the priming of the parent plant (inter/transgenerational priming), or directly of the seeds to be sown (seed priming).

Stress priming is based on the phenomena of stress memory, on which pre-exposing crops to stress conditions lead to enhanced adaptation to subsequent stress responses in the current or future generation(s). Primed material may increase the tolerance to a wider range of stresses, such as drought, heat, and frost; and significantly enhance crop productivity [120]. Several reports have well documented the biochemical and molecular changes induced by stress priming in crop plants [121, 122]. Further studies are still required to determine the stages (pre- or post-anthesis) and the intensity of the priming applied to each crop to precisely elicit the desired stress memory [122].

Seed priming consists in a pre-sowing treatment during which a controlled hydration of seeds allows the first stages of germination (till end of phase II which is reversible) but prevent radicle emergence (irreversible stage) [123]. Primed seeds, that can be dried back and stored till sowing, are much less sensitive to environmental factors and germinate rapidly in a wide range of agroclimatic conditions. A variety of seed priming techniques including hydropriming, osmopriming, chemical priming, biopriming, hormonal priming, thermopriming, nutrient priming, or redox priming, are used to enhance abiotic stress tolerance in plants [121]. Still, each seed priming technique and duration need to be adapted to each crop. By example, a recent study about the effects of two hydro- and osmo-priming durations (8 and 16 h) on sunflower seeds under water stress, showed that only in the case of hydropriming the priming duration can influence the dormancy-breaking and germination indices [124]. Seed priming was found to improve germination and seedling vigor by regulating cell cycle, improving antioxidant defense system, repairing of cell damage, increasing energy metabolism and mobilizing reserves from the endosperm to the embryo. During priming, accumulation of osmoprotectants such as proline, soluble sugar and soluble proteins, help to enhance water uptake. Also, activation of protective enzymes, such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), can reduce ROS-induced oxidative damages [125].

Interestingly, several type of priming methods can be combined to increase tolerance to additional stresses. On bread wheat, seeds from parent plants exposed to drought stress on the field at reproductive stage, were then collected and subjected to hydropriming and osmopriming (with 1.5% $CaCl_2$). The changed seed composition from drought compared with well-watered plants significantly improved the salt tolerance in wheat by modulating the water relations, osmolytes accumulation and lipid peroxidation [126].

Furthermore, a new technology-based agricultural revolution is now emerging, the seed nano-priming. Instead of employing water or other solutions (hormones, nutriments) as in conventional seed priming, nanoseed priming uses a media that contains nanoparticules [119]. Different nanomaterials, including metallic, biogenic metallic, and polymeric nanoparticles can be used either to actively cause a biological effect (active nanoparticules) or designed to respond to different environmental stimuli (sustained release nanocarrier systems). Several studies have already shown promising results in maize, wheat, soybean and rice [127–130].

New seed-production areas and farming practices

Each crop requires different climate and environmental conditions to grow (see Figure 1). Increased temperatures and little precipitations are expected to be more frequently and unpredictable. These environmental behaviors have imposed that management actions have been rapidly adopted by farmers to compensate with their agricultural production. Changes in agronomic practices include shifting the sowing time to alleviate effects of heat waves and drought episodes in summer. A study that recorded the dates of sowing, flowering, and maturity of wheat, oats and maize in Northern and Central Europe conducted during the period 1985–2009, predicted an advancement of sowing date of spring cereals by 1–3 weeks depending on climate models and regions for 2040 [131]. Similar studies in other regions (southern and western regions of Australia) have shown the effect of temperature changes on productivity of mustard, chickpea and barley, and have recommended shifting the sowing time as an adaptation strategy [132].

Moreover, seed production for several crops is also shifting towards more suitable growing locations [7]. Using spatially explicit climate and crop area data from 1973 to 2012 of maize, wheat, rice, and soybeans, Sloat et al. [7] have measured an increase in 0.9, 1.1, 0.7, and 0.7°C, respectively, in growing season temperatures. Because Northern areas are exposed to warmer temperatures, new growing areas are now adapted to grow crops more exigent on warmer temperature to germinate such as maize and soybean. In that sense, rainfed maize areas increased by 24%, and new rainfed soybean areas increased by 158% in the last 40 years [7].

Although, the expansion of the areas available for crop production and changes in cultivation period can be seen as positive alternatives to alleviate seed productivity and quality, it is imperative to explore other strategies. The effect of parental shading growing conditions in subsequent seed development and dormancy/germination is a new research field [118]. Recent studies have compared germination rate of seeds generated by two soybean (*Glycine max*) seed production systems, monocropping (MC) and maize–soybean intercropping (IC). The shade signal is characterized by a decrease in the blue light intensity and the red (R): far-red (FR) ratio, caused by neighboring plants. In this condition, a faster seed germination was observed in IC seeds compared with MC seeds. This effect was attributed to an increase in the biosynthesis of pro-anthocyanidins, fatty acids, and phytohormones ABA and GA [133].

Diversification of crops and varieties

Today, nearly 50% of our daily calorie consumption come from rice, maize, and wheat alone. On the same way, most of the agronomic research efforts to identify or develop more drought- and heat-tolerant cultivars is currently made on conventional crops. However, several genetic resources and alternative crops are now emerging as favorable crops for production in marginal soils and in highly variable climates. Biodiversification seems to be the most advantageous solution. The renewal of indigenous crops such as quinoa (*Chenopodium quinoa*), native of South America; and the traditional grains, sorghum and millet (*Panicum miliaceum*), in

Africa, are very promising. These plants are extremely salt, drought and heat tolerant, are more resistant to pest and are less dependent on fertilizers [134].

Nonetheless, more research and breeding programs need to be organized on the future to cope with essential traits that need to be improved on unconventional crops. By example, the mechanisms that regulate quinoa seed dormancy and seed viability is still poorly understood. The variability of the seed dormancy trait in quinoa varieties (including wild relatives) is very diverse, going from a combination of primary and physiological dormancy to no dormancy [135]. It has been suggested that both embryo and seed coat-imposed dormancy play a role in quinoa germination programs.

Cowpea (*Vigna unguiculata*) is an annual legume considered more tolerant to drought and better adapted to sandy soils than soybeans. Originated from Southern Africa, it now an important economic crop in many developing regions, due to is high protein content and adaptability. During domestication, one of the most important changes in cowpea's agronomic traits were the selection of increase seed size, reduced seed dormancy and increased seed germination [136]. Phenotypic evaluation of a RILs population (cross between a cultivated cowpea and a wild variety) have allowed to identify four QTLs for thickness of the seed testa and one QTL for water absorption by the seeds [137]. Nonetheless, more research efforts are still needed in cowpea to improve other agronomical and yield traits.

Conclusions

Climate change will dramatically affect phenological events of crop plants including seed development and seed germination. Shifts in germination phenology will directly influence productivity of agrosystems inducing serious threat to global and local food security. In addition, global warming will also disturb the phenology of weeds, pests and pathogens, thereby enhancing their negative environmental and economic impact. This makes research on seed biology critical since seed quality underpins agriculture and food security. Addressing fundamental questions in seed biology, such as a better understanding of the molecular responses to environmental cues, will help to address the concerns of agronomic stakeholders and actors of seed industry regarding the effect of stressful conditions on seed physiology. The identification of genes and functional markers that are strongly associated to dormancy and germination traits using genomics and genetics approaches will be important tools to develop new varieties that ensure global food security under climate change.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

CRediT Author Contribution

Christophe Bailly: Writing — original draft, Writing — review and editing. **Maria Victoria Gomez Roldan:** Writing — original draft, Writing — review and editing.

Abbreviations

ABA, abscisic acid; AG, anaerobic germination; *DOG1*, *DELAY OF GERMINATION1*; DPA, diphaseic acid; GWAS, genome-wide association studies; IC, intercropping; MAPK, mitogen activated protein kinase; MC, monocropping; *MFT*, *MOTHER OF FT AND TFL1*; *MKK3*, *mitogen-activated protein kinase kinase 3*; PEG, polyethylene glycol; PHS, preharvest sprouting; QTL, quantitative trait loci; RILs, recombinant inbred lines; ROS, reactive oxygen species.

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