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Keywords

maize, seed set, molecular mechanism

Disciplines

Agricultural Science | Agronomy and Crop Sciences | Molecular Genetics | Plant Breeding and Genetics

Comments

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Molecular mechanisms controlling seed set in cereal crop species under stress and non-stress conditions

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Abstract Maximizing seed yield is the ultimate breeding goal in important cereal crop species. Seed set is a key developmental stage in the process of seed formation, which determines grain number, seed mass, and realized yield potential, and can be severely affected by abiotic and biotic stress. However, seed set can also be substantially reduced by genetic factors even under optimal fertilization conditions. The underlying molecular genetic mechanisms are still obscure. In this review, we elucidate the process of seed set of cereal crop species in detail, including development of floral structures, formation of viable gametes, double fertilization, seed development and abortion. We discuss how genetic and non-genetic factors affect seed set in different development stages. Finally, we will propose novel strategies to study genetic mechanisms controlling seed set and exploit genetic resources to improve seed set in cereal crop species.¹

Keywords: maize, seed set, molecular mechanism

1. Introduction

Food security is of global concern, especially in developing countries (Rosegrant *et al.* 2003). The six most widely grown crops in the world are maize, rice, wheat, soybean, barley, and sorghum. These crops are grown for seed on more than 40% of global cropland area, and account for 55% of non-meat calories and over 70% of animal feed. Among all seed crop species, cereal crops are most important for humans, which provide over 70% of the food consumed by humans. Though the seed yield per land area has increased during the last decades, 20-40% of the world's potential crop production still is lost because of weeds, pests, diseases, and abiotic stress factors according to the Food and Agriculture Organization of the United Nations (FAO) (FAO Statistical Databases Available from: <http://faostat.fao.org>). Even in major cereal crops producing countries, rice, wheat, and maize still have a 10-15% yield gap between actual and potential seed yield (Tollenaar and Lee 2002; Cassman *et al.* 2003; Grassini *et al.* 2011). However, there can be about 50% yield gap in specific crop planting areas. For example, the average maize yields in the US is 10,7 Mg ha⁻¹, but maximum yields exceed 18,8 Mg ha⁻¹. Maize yield in China has the potential to increase dramatically due to the introduction of hybrids that are better adapted to denser planting conditions, mechanization, and improvements in seed technology (Li *et al.* 2011). Yield potential is defined as the yield of a cultivar grown under non-limiting abiotic and biotic conditions in an environment to which it is adapted. Causes for the yield gap are unfavorable abiotic or biotic growth conditions, limited water and nutrient supply, or exposure of plants to abiotic and/or biotic stress. Increased seed yield of cereal crops is predominantly the result of improved stress tolerance (Duvick 1997; Fasoula and Fasoula 2002).

In cereal crops, the process of seed formation can be divided into three stages: seed set, seed growth, and seed

maturation (Ruan *et al.* 2012). Seed set is established during and soon after fertilization with two genetically identical male sperm cells. One male sperm cell fuses with the haploid egg cell, resulting in a diploid embryo. The other sperm cell fuses with two (female) haploid central cells, resulting in a triploid endosperm. This double fertilization event initiates seed development. Embryo and endosperm are surrounded by a maternally derived seed coat, which provides a shield for the developing seed (Köhler *et al.* 2006). The newly formed seed then undergoes cell expansion and accumulation of storage products, mainly proteins, starch and oils, which are typical features of growth and maturation stages (Weber *et al.* 2005).

During the process of seed formation in cereal crops, seed set features a transition from fertilized ovules to seed, which has a profound impact on later seed developmental stages, and determines seed number by determining cell numbers, and seed yield potential (Fig. 1). Seed set is more sensitive to internal or external stresses compared to later stages of seed development or vegetative growth (Boyer *et al.* 2007; Suwa *et al.* 2010; Zinn *et al.* 2010). Stresses include insufficient supply of nutrients, drought, heat, cold, high plant density, presence of weeds, plant diseases, and insect pests, which often induce floral or seed abortion and irreversible seed yield losses.

Maize and rice are the two most important cereal crops in the world, which have different floral architectures (monoecious vs hermaphrodite species, respectively) and photosynthetic pathways (C_4 vs. C_3 , respectively). Here, we focus on discussing genetic mechanisms controlling seed set in maize and rice at four developmental stages: (1) development of floral structure; (2) formation of viable gametes; (3) double fertilization; and (4) seed development and abortion.

2. Development of male and female floral architectures

Seed set is influenced by the floral architecture in cereal crops, which depends on the number and arrangement of floral branches (Vollbrecht *et al.* 2005). Variation in branching patterns lead to diversity in inflorescences and seed number (Satoh-Nagasawa *et al.* 2006). Maize possesses two types of inflorescences: the tassel and the ear. The tassel is a terminal, staminate inflorescence. The ear is a pistillate inflorescence produced on a lateral branch, which is a major yield trait controlled by the developmental fate of axillary shoot meristems (Satoh-Nagasawa *et al.* 2006). The units of rice floral structure are spikelets and florets. Spike (an unbranched inflorescence in which stalkless spikelets are arranged on an elongated axis) initiation and spikelet (contains one or more florets enclosed by two glumes) formation is the first phase of reproductive growth. This process provides the developmental basis for spike differentiation, which contributes to altering final seed number and yield potential (Sreenivasulu *et al.* 2012). In the past decades, various major genes or QTL affecting the development of floral architecture have been cloned. In maize, inflorescence branching is regulated by three RAMOSA genes. RAMOSA1 (*RA1*) is a plant specific Epidermal Patterning Factor-like protein (EPF-like protein), regulating the branching architecture of maize inflorescence. In *RA1* mutants, both the tassel and ear become more branched. RAMOSA2 (*RA2*) encodes a Lateral Organ Boundaries-domain protein (LOB-domain protein) whose RNA is expressed at the edge of the bract and meristem early in inflorescence development. RAMOSA3 (*RA3*) encodes a trehalose 6-phosphate phosphatase and is expressed in discrete domains subtending axillary inflorescence meristems. *RA2* and *RA3* act upstream of *RA1*, and *RA3* may act in parallel with *RA2* (Vollbrecht *et al.* 2005; Satoh-Nagasawa *et al.* 2006). In rice, grain number 1a (*Gn1a*), encoding a cytokinin oxidase in rice (*OsCKX2*), Wealthy Farmers Panicle 1 (*WFP1*), encoding *OsSPL14*, and Dense and Erect Panicle1 (*OsDEP1*), encoding a truncated phosphatidylethanolamine-binding protein are three important genes controlling the development of floral organs. Reduced expression of *OsCKX2* causes cytokinin accumulation in inflorescence meristems and increases the number of reproductive organs, resulting in enhanced grain yield (Ashikari *et al.* 2005). In contrast, increased expression of *OsDEP1* enhances meristematic activity, resulting in a reduced length of inflorescence internodes,

an increased grain number per panicle and consequently, increased grain yield. Increased expression of *OsDEP1* reduces the level of *OsCKX2* expression, suggesting that *OsDEP1* acts upstream of *OsCKX2* to control cytokinin homeostasis in panicle meristems (Huang *et al.* 2009). Increased expression of *OsSPL14* in the reproductive stage promotes panicle branching and grain yield, and also controls shoot branching at the vegetative stage (Miura *et al.* 2010). Although those genes are involved in different pathways to control the development of floral architecture, they play important roles in regulating seed number and arrangement.

Flowering time is also an important selection criterion in cereal breeding, which not only influences plant demand for resources and a plant's ability to capture resource for growth (Dong *et al.* 2012), but also influences floral development and seed set. Among cereal crops, winter wheat relies on vernalization for flowering. Rice is a short day plant, and flowering time is day length sensitive. Maize undergoes the transition to flowering after a fixed number of leaves has been produced (Itoh *et al.* 2010; Bortiri *et al.* 2007). Tropical maize is an exception, which is photoperiod sensitive for flowering time, and unadapted to temperate latitudes. However, the basic genetic mechanisms controlling flowering time are largely conserved among cereals (Lagercrantz 2009; Song *et al.* 2010). For example, the FRUITFUL1 (*FUL1*)/VERNALIZATION1 (*VRN1*) protein is associated with specifying competence to flower initiation and transition after a cold treatment (vernalization) in wheat (Danyluk *et al.* 2003; Murai *et al.* 2003; Loukoianov *et al.* 2005). In maize, *ZMM4* is a MADS-box gene in the *FUL1* family that regulates floral transition and inflorescence development, which can be activated after floral transition in early developing inflorescences. Over-expression of *ZMM4* leads to early flowering in transgenic maize (Danilevskaya *et al.* 2008). In rice, overexpression of *OsMADS18* can induce early flowering, accelerate the formation of axillary shoot meristem (Fornara *et al.* 2004). Although evidence from various studies supports a complex gene network responsible for floral transition and floral development in cereals (Yano *et al.* 2001; Izawa *et al.* 2003; Boss *et al.* 2004; Bernier and Perilleux 2005), the function of *VRN1* in wheat, *ZMM4* in maize, *OsMADS18* in rice is similar to that *APETALA1* (*API*) in *Arabidopsis*. *API* plays a central role in the transition from floral induction to flower formation (Wellmer *et al.* 2010).

In addition, water stress during flower induction and inflorescence development leads to a delay in flowering (anthesis), or even to complete inhibition (Mahalakshmi 1985; Wopereis 1996; Winkel 1997). High temperatures during floret formation cause complete or partial abortion (Sanini and Aspinall 1982), in which the main effect of heat stress is reduction of kernel number (Fischer 1985).

3. Formation of viable (male, female) gametes

In cereal crops, pollen and ovary development greatly depend on an adequate import or utilization of photoassimilates, mainly in the form of sucrose and starch. For pollen to be viable, it is necessary to synthesize sufficient starch, cellulose and callose, which are main components for building internal pollen wall tubes. Starch, cellulose, and callose are all polymerized from glucose in α -1,4, β -1,4, and β -1,3 linkages respectively (Kudlicka *et al.* 1997, Cai *et al.* 2011). Glucose can be derived from sucrose hydrolysis and starch degradation by cell wall invertase (CWIN) and α -amylase, respectively (Fig. 2). The CWIN mediated metabolic pathway is the main route to produce glucose. Reduction in CWIN expression or sucrose content leads to male sterility and seed abortion in wheat under drought stress (Koonjul *et al.* 2005) and in rice under cold stress (Oliver *et al.* 2007). Sucrose-rich pollen survives for a longer time than sucrose-poor pollen in maize and other crops (Hoekstra *et al.* 1989; Buitinik *et al.* 1996; Pacini 1996). Thus, sucrose supply and CWIN activity are key to male fertility and seed set.

Many studies also showed that viability of pollen is related to its water content and the humidity of atmosphere. Pollen needs strong protection (anther) against desiccation in time. Low water content of pollen can

affect pollen growth speed and survival. However, anthers will not open at high air humidity, which can lead to premature loss of viability (Aylor 2003).

Ovary abortion has similar molecular mechanisms as pollen sterility (Ruan *et al.* 2010). In maize ovaries, phloem-imported sucrose supplies carbon for starch accumulation in ovary walls and to generate high glucose concentrations by CWIN in pedicels (McLaughlin *et al.* 2004). Upon imposing a water deficit five days before anthesis, sucrose import is blocked due to inhibited leaf photosynthesis and remobilized ovary wall starch reserves. However, these become rapidly depleted, if drought persists for several days. Concomitantly, CWIN activities and glucose concentrations decrease, leading to ovary abortion and yield loss. A CWIN glucose signaling pathway is the primary genetic mechanism controlling maize ovary abortion (McLaughlin *et al.* 2004). Glucose can repress the programmed cell death (PCD) pathway and promotes cell division of filial cells (Ruan *et al.* 2012). Under stress conditions, photosynthetic activity is reduced (Schussler *et al.* 1991; Chaves *et al.* 2003), which results in decrease of glucose levels, followed by pollen sterility in anthers and activation of a PCD pathway leading to seed abortion in ovaries (Fig. 2). In summary, glucose is a key factor for pollen fertility and ovary development and, therefore, seed set in cereal crop species (Fig. 2).

4. Double fertilization

For successful seed set, pollen and ovaries in cereal crops must remain viable, pollen tubes must grow properly and release two sperm cells into the ovular embryo sac for double fertilization to produce embryo and endosperm. In maize, heat stress (>38°C) can lead to reduced pollen germination ability and pollen tube elongation, resulting in reduced seed set and seed production (Fischer 1985; Schoper *et al.* 1987). Increased temperature during the mid-anthesis period decreased the grain number per ear in spring wheat (Ferris *et al.* 1998), demonstrating heat sensitivity of fertilization and seed set. High-temperature stress at flowering reduces spikelet fertility in rice. Sterility is caused by poor anther dehiscence and low pollen grain production, and hence a low number of germinating pollen grains on the stigma (Matsui *et al.* 2002; Prasad *et al.* 2006).

During flower induction and inflorescence development, drought stress leads to failure of panicle exertion and anther dehiscence in rice and sorghum (Ekanayake *et al.* 1990; Craufurd *et al.* 1993; Wopereis *et al.* 1996), which leads to a substantial reduction in seed set. In maize, seed abortion is highly dependent on the timing of water stress. Low water availability before pollination results in seed abortion even if sufficient water was available at the time of pollination. Drought stress inhibits maize pistillate flower development, pistil integrity, ovule functions, and grain weight (Westgate 1994), while timing of male inflorescence development and pollen shed is less affected, resulting in increased anthesis-silking intervals (ASI). An extended ASI reduces the chance that female spikelets will be self-pollinated and contribute to incomplete pollination (Fuad-Hassan *et al.* 2008), and thus increases the risk of yield reduction (Monneveux *et al.* 2006; Brekke *et al.* 2011).

In summary, pollen development is more prone to heat stress than that of ovaries. However, fertility of ovaries has a greater influence on seed set than that of pollen under drought stress in cereals (Boyer *et al.* 2007; Barnabás *et al.* 2008). Cereal breeding must develop cultivars tolerating multiple types of stresses impacting seed production (Tester *et al.* 2005). Low ASI under abiotic stress conditions is, therefore, an important breeding goal.

In nature, self-incompatibility (SI) is a genetic mechanism to prevent self-fertilization by inhibiting the germination of pollen on stigmas, or the elongation of pollen tubes. Several grass species share a common incompatibility mechanism controlled by two unlinked loci, S and Z (Li *et al.* 1997). SI promotes cross-fertilization to produce heterozygous and vigorous plants. SI can be inactivated by high temperatures leading to pseudocompatibility in perennial ryegrass and *Ipomoea fistulosa* (Prabha *et al.* 1982; Wilkins *et al.*

1992). Pseudocompatibility will lead to self-pollination, and inbred offspring and thus directly and indirectly reduces seed set and seed yield. Although SI has not been reported in cereal crops including maize, rice, wheat and barley, breeders have tried to utilize SI in F₁ hybrid breeding systems (Do Canto *et al.* 2016). Self-incompatibility (SI) is also widespread in grasses and other plant families.

5. Seed development and abortion

Seed development is regulated by the interplay of phytohormones. Gibberellic acid (GA₃) increases source strength by improving photosynthetic efficiency by influencing photosynthesis related enzymes (i.e., Rubisco, fructose-1,6-biphosphatase, and sucrose phosphate synthase), leaf area, light interception, and phloem loading (Iqbal *et al.* 2011). GA₃ also increases sink strength by promoting cell division, general growth, and carbohydrate import by inducing sucrolytic activities, namely CWIN, a key enzyme in the regulation of phloem unloading (Roitsch *et al.* 2004). GA₃ signaling is involved in metabolic adjustment for maintaining source-sink relations, increasing the efficiency of assimilate production and transport under limiting environmental conditions (Achard *et al.* 2006). However, most studies indicate that GA₃ signaling in response to stress reduces growth to allow plant adaptation and survival. Cytokinin (CK) levels play a key regulatory role for plant growth and survival. Optimal CK levels are necessary to increase leaf longevity and photosynthetic capacity (source strength) but also growth of sink organs (sink strength) under abiotic stress (Ha *et al.* 2012; Zalabák *et al.* 2013). Constitutive over-expression of the CK-degrading enzyme cytokinin oxidase (CKX) or inhibition of the CK-biosynthetic IPT1, IPT3, IPT5, and IPT7 genes resulted in CK deficiency and enhanced drought and salt stress-tolerant phenotypes in *Arabidopsis thaliana* (Nishiyama *et al.* 2011). However, in rice, reduced expression of *OsCKX2* causes cytokinin accumulation in inflorescence meristems and increases the number of reproductive organs, resulting in enhanced grain yield (Ashikari *et al.* 2005). Auxins influence carbon partitioning and stimulate mobilization of carbohydrates in leaves and the upper stem and increase translocation of assimilates towards sink organs (Smith *et al.* 2013). Auxins regulate the activity of CWIN and thus sucrose allocation in sink organs (Albacete *et al.* 2008). ABA has been implicated in male sterility of tomato, rice, and wheat (Morgan 1980; Morgan *et al.* 1984; Westgate *et al.* 1996). Exogenous ABA application inhibits the activity of invertases and monosaccharide transporters to reduce sucrose content, leading to pollen sterility and PCD in barley (Parish *et al.* 2012). However, some studies in cereals reported positive correlations between grain ABA content and efficient seed filling by optimizing faster remobilization events from stem reserves (nonstructural carbohydrates), a critical factor in sustaining grain filling and grain yield under drought stress (Yang *et al.* 2004). Ethylene is often regarded as a growth inhibitor (Pierik *et al.* 2007). Male gametophyte development is susceptible to ethylene at the stage of pollen mitosis. Ethylene has been used to manipulate the development of pollen grains by application of an ethylene inhibitor, to promote dry mass accumulation and concentrations of starch and reducing sugars in anthers of basal spikelets leading to improved seed set in rice (Naik *et al.* 1999). In summary, seed set is controlled by a phytohormone interplay, controlling the balance between source and sink strength under both optimal and stress conditions.

Seed development greatly depends on adequate supply of photosynthetic products and nutrient use efficiency. Water deficiency results in inhibition of photosynthesis, and reduces nutrient supply to generative organs. At the same time, water shortage limits N uptake from soil and decreases the nitrate concentration in xylem, affecting ABA accumulation in leaves, which leads to altered ear structure and yield reduction (Carcova *et al.* 2000). In addition, high planting density decreases light penetration into the canopy, reducing photosynthetic capacity (Hammer *et al.* 2009), which then affects the final kernel number and characteristics (Borras *et al.* 2003). Many studies reported that grain number and weight both decreased in maize as plant density increased, suggesting a complex interaction between the sink and assimilate supply (Sangoi *et al.* 2002; Hashemi *et al.* 2005; Lashkari *et al.* 2011). Under full sunlight, plants are exposed to relatively equal fluxes of light with

wavelengths of 600-700 nm (red light) and 700-800 nm (far-red light) (Holmes *et al.* 1977). When plant density increases, red light is intercepted, while far-red light is largely reflected, creating a far-red light enriched environment. Under this condition, a series of morphological changes take place, including increased plant height, decreased leaf blade area (Smith 1995), decreased stem diameter (Lashkari *et al.* 2011), and delayed pollen shed and silking (Tokatlidis *et al.* 2004). Plant growth rate is reduced during reproductive stages (Rossini *et al.* 2011), resulting in partitioning of more assimilates towards vegetative instead of reproductive growth (Kebrom *et al.* 2007). In addition, the axillary position of ears in maize is subject to apical dominance, assimilates are partitioned to the shoot rather than the ear under high planting density (Sangoi *et al.* 2002), which increases the risk that ears will have poor or not seed set.

Biotic stress occurs as a result of damage to plants by bacteria, viruses, fungi, parasites, insects, and weeds. Plants are under constant assault by pathogens and competitors during their development (Pimentel 1991), and evolved a myriad of defenses to meet requirements for cellular maintenance, growth and reproduction (Tian *et al.* 2003, Berger *et al.* 2007). Although defense response to different biotic stressors is highly variable, the transcriptional response to biotic stress is highly coordinated, which means that biotic stress globally down-regulates photosynthesis genes (Zou *et al.* 2005; Berger *et al.* 2007; Bilgin *et al.* 2010). In order to trigger defenses to dissuade biotic stresses, plants will newly allocate resources from growth to defense by a reduction of photosynthetic capacity in leaf tissues (Nabity *et al.* 2009), which leads to reduced carbon assimilation, resulting in poor seed set. Abiotic and biotic stress factors are most likely to occur simultaneously under field conditions, which has a devastating impact on crop productivity. Combined effects of these stresses are greater than the effects of single stress factors alone (Suzuki *et al.* 2014). Moreover, studies still found that abiotic stresses can reduce the resistance of plants to biotic stresses (Szittyá *et al.* 2003). Groszmann *et al.* (2015) suggests that a suppression of defense response gene activities are important for generating the hybrid vigor phenotype. So over-expression of defense and stress response genes will reduce seed production or hybrid vigor in cereal crops.

In contrast to sexual seed formation, apomixis is an evolutionary mechanism of seed formation without fertilization, which can occur by various genetic regulators reported for more than 300 species in 30 out of 460 angiosperm families (Kandemir *et al.* 2015). Although these different mechanisms have not yet been fully elucidated, it is now generally agreed that apomixis is a qualitative trait controlled by a few genes (Hanna *et al.* 1998; Barcaccia and Albertini 2013). *Fertilization-independent seed (FIS)* mutants in *Arabidopsis thaliana* have the ability to form seed-like structures without fertilization (Chaudhury *et al.* 1997), which give significant clues about the genetic mechanism of apomixis. Three important genes have been identified and cloned in *Arabidopsis thaliana*, which includes the *FIE* gene (Fertilization Independent Endosperm, encoding a WD type POLYCOMB protein) (Ohad *et al.* 1996), the *MEDEA* gene (encoding a SET domain type POLYCOMB protein) (Grossniklaus *et al.* 1998), and the *FIS2* gene (Fertilization Independent Seed 2, encoding a zinc finger protein) (Chaudhury *et al.* 1997). In recent years, apomixis has been seen as a way of multiplying superior genotypes clonally by seed. However, apomixis has not been found in cereals (Bashaw 1980; van-Dijk *et al.* 2016). Recently, a apomixis gene, *ASGR-BABY BOOM*-like in *Pennisetum* (PsASGR-BBML) has been cloned and introduced into rice and the resulting plants developed embryos from egg cell without fertilization. But the negative feature is low seed set in artificially induced apomictic plant (Ozias-Akins 2015). Although transfer of apomixis to crop species through wide crosses has many additional hurdles so far (Kandemir *et al.* 2015), understanding the function of natural apomixis genes and the introduction of apomixis into cereal crop species would significantly alter breeding strategies of agricultural crop species.

6. Future prospects for studying seed set in cereal crop species

Seed set is a complex quantitative trait, which is affected by various environmental factors. However, it is critically important for cereal crop yield. Substantial progress has been made in understanding the biology of seed set. Several genetic pathways have been identified to control seed set in cereal crops. Moreover, the benefits of whole-genome sequence information generated in rice, maize and *Arabidopsis* can be extended using synteny and collinearity relationships among cereal crop species. For example, rice chromosome 1 shows regions of sequence similarity with chromosomes 3, 6, and 8 in maize (Salse *et al.* 2004) and group 3 chromosomes in bread wheat (Moore *et al.* 1995), where some QTL for grain yield and other agronomic traits have been mapped (Dilbirligi *et al.* 2006). Gn1a (*OsCKX2*) in rice might correspond to these maize and wheat QTL, and orthologous CKX genes might regulate yield in other cereal crops (Ashikari *et al.* 2005). Once identified through synteny, these genes for seed set can be manipulated to improve grain yield. However, it is still unclear how genetic and non-genetic factors coordinate control of seed set in cereal crops. As we know, seed yield improvement in cereal crops may have been the result of an improved genetic×agronomic management interactions, rather than the result of either genetic and/or agronomic improvement per se (Tollenaar and Lee 2002). For example, grain yield of U.S. maize hybrids from the 1930s to 1990s did not differ when plants were grown under low-density conditions, where competition among plants for soil moisture, soil nutrients and incident solar radiation was negligible (Duvick 1997). Thus, yield improvement in cereal crops has been associated with increased stress tolerance. Under environmental stress, plants reallocate resources to defense of biotic and abiotic stress. Today, the main challenge is to decrease the yield gap between the potential seed yield and realized seed yield. Future research is required on tradeoffs between growth processes and defense response to stress. More generally, there is a need to establish a genetic framework for seed set and to better define and prioritize the molecular mechanisms and factors controlling seed set.

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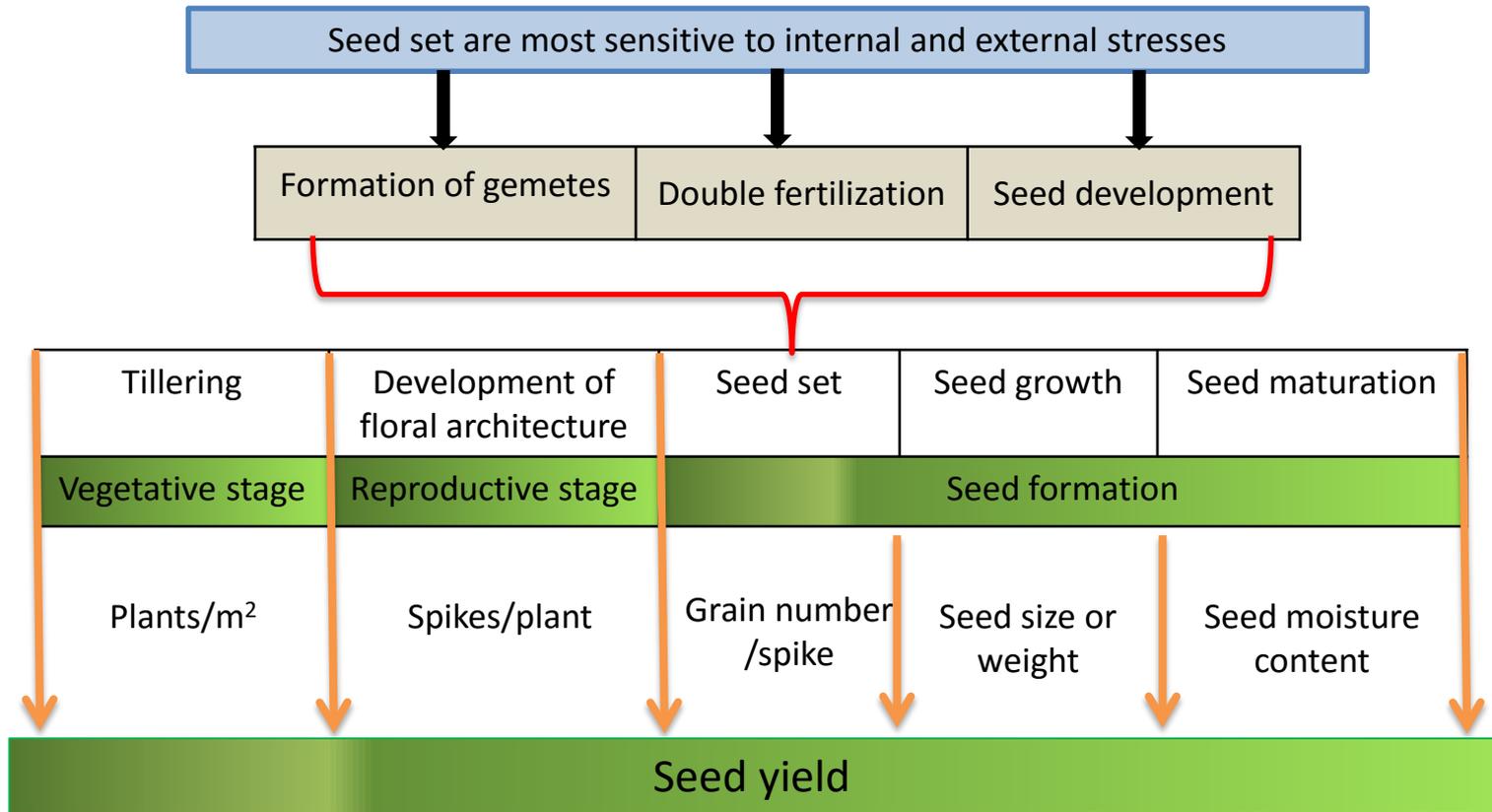


Figure 1. The major development stage and seed yield component in cereals.

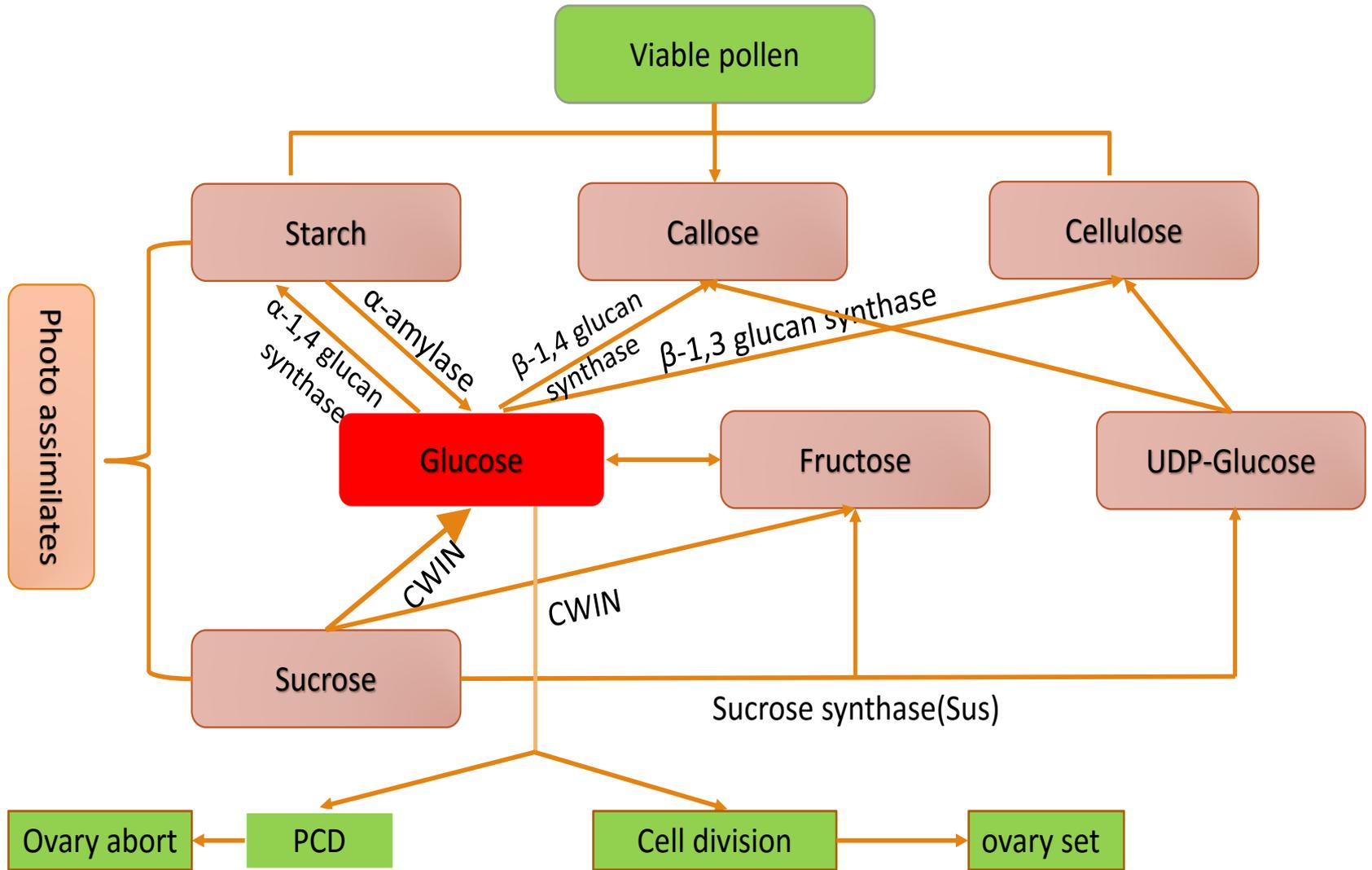


Figure 2. The sugar regulated mechanism for pollen and ovary fertilization