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DARWIN REVIEW

Gibberellins: extending the Green Revolution

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Abstract

The Green Revolution more than doubled crop yields and food production in crop species such as wheat and rice. This was primarily accomplished by altering the gibberellin (GA) signaling pathway to reduce plant height and prevent plants from falling over when growth was promoted with fertilizer application. Similar approaches have not been successfully accomplished in other grass crop species, such as maize, due to pleiotropic deleterious traits that arise from altering the GA pathway. This review highlights new findings in GA research across grass crop species. We have primarily focused on the developmental role of GAs in plant architecture and growth. We discuss how alteration of GA effects could be used to alter plant morphology and development of ideal plant ideotypes for grass crop species. To further extend the Green Revolution and improve food production from cereal crop species, targeted and tissue-specific regulation of the GA pathway will have to be undertaken.

Keywords: Development, gibberellins, maize, plant architecture, rice, wheat.

Introduction

Gibberellins (GAs) are a group of plant hormones that control almost all facets of plant growth and development. These growth-promoting metabolites were first identified in the 1930s from a fungus, *Gibberella fujikuroi*, that caused elongation of rice stems (Takahashi *et al.*, 1991). Since then, regulation of GA has been modulated to improve agricultural outputs across crop species. The Green Revolution utilized GA-insensitive short plants of *Triticum aestivum* (wheat) that were resistant to lodging (falling over) and stem rust (Li *et al.*, 2022). A similar approach was used in *Oryza sativa* (rice) throughout Asia in the 1960s where a semi-dwarfing gene involved in GA biosynthesis was utilized to reduce plant height and increase yields (Spielmeyer *et al.*, 2002). Historically, modulation of plant architecture in *Zea mays* (maize) using the GA pathway has been difficult due to deleterious effects on reproductive development. However, recent efforts to marginally knock down the GA biosynthetic pathway in maize have successfully reduced plant height without having negative effects on yield (Paciorek *et al.*, 2022), indicating that modification of the GA pathway can be harnessed to increase yield in any cereal crop.

The GA biosynthetic pathway in land plants begins in the proplastids with the production of *ent*-kaurene from the

precursor geranylgeranyl diphosphate by two different diterpene cyclases (Hernandez-Garcia *et al.*, 2021). The *ent*-kaurene metabolite is then converted into GA_{12} by two different cytochrome P450 monooxygenases at the membrane of the endoplasmic reticulum. To convert GA_{12} into bio-active GAs, the final reactions occur in the cytoplasm where several GA 20-oxidase and GA 3-oxidase enzymes synthesize more highly bio-active C_{19}-GAs which include GA_1 and GA_4 (Sakamoto *et al.*, 2004). GA levels are also regulated through catabolic enzymes, GA 2-oxidases, to inactivate the bio-active GAs by 2β-hydroxylation (Sun, 2008) (Fig. 1A–C). Many genes involved in the biosynthetic pathway of GAs have also been molecularly characterized in crop species (Bensen *et al.*, 1995; Sakamoto *et al.*, 2004; Huang *et al.*, 2012; Wang *et al.*, 2013).

GAs have been shown to be transported between tissues to regulate growth in parts of the plant other than where they were synthesized (Sun, 2010). GA transport has been hypothesized to contribute to the formation of a GA concentration gradient, critical in rapidly growing organs (Rizza and Jones, 2019). Long-distance transport of GAs in phloem and xylem has been shown to be important for shoot and root development (Binenbaum *et al.*, 2018, 2023; Camut *et al.*, 2019). The NRT1/PTR family (NPF) of proteins can transport GAs, among other hormones and substrates (Corratgé-Faillie and Lacombe, 2017). Uptake of GA was also shown to be dependent on the Sugars Will Eventually be Exported Transporters (SWEET) family proteins in Arabidopsis and rice (Kanno *et al.*, 2016; Morii *et al.*, 2020). NPFs and SWEETs have expanded in grasses (Binenbaum *et al.*, 2018), warranting further investigation into their specific roles in GA transport.

Bio-active GAs are perceived by the GA receptor, GIBBERELLIN INSENSITIVE DWARF1 (GID1), to activate the GA signaling pathway (Ueguchi-Tanaka *et al.*, 2005, 2007). GID1 functions in GA signaling by promoting the degradation of the GA repressor DELLA domain protein (DELLA) (Sun, 2010). GID1 recruits an F-box protein as part of the Skp/Cullin/F-box complex (SCF) which polyubiquitinates DELLAs and targets them to the 26S proteasome for degradation (Dill *et al.*, 2004). This degradation of the DELLAs allows for GA signaling to occur (Fig. 1D). DELLAs do not directly regulate gene expression, as they do not contain a DNA-binding motif (P. Wang *et al.*, 2020). When GA is not present, the DELLAs act to repress GA signaling by interacting with other transcription factors that contain a DNA-binding motif (Davière *et al.*, 2008; Phokas and Coates, 2021; Shani *et al.*, 2024). DELLAs have also been identified in cereal grasses and include rice SLR1, wheat Rht1, and maize D8/D9 (Hedden, 2003; Lawit *et al.*, 2010; Tang *et al.*, 2021).

There have been reports of DELLA-independent transcriptional responses in some eudicots, many of which are unrelated to GA action (Fuentes *et al.*, 2012; Livne *et al.*, 2015). However, a recent transcriptomic study in maize showed that exogenous application of GA resulted in no DELLA-independent responses to GA (Best and Dilkes, 2022), raising questions about the fundamental difference in DELLA regulation of transcriptional responses between eudicots and monocots. Further research is needed to clarify the roles of both DELLA-independent and DELLA-dependent responses, especially in grass crop species.

In this review, we present new research findings on GA-regulated developmental outcomes in grass crop species, with a focus on maize, rice, and wheat. We describe phenotypes of GA-deficient or -dominant mutants that include significant effects on plant height, leaf size, tillering, inflorescence branching, and nutrient-use efficiency (NUE) (Wu *et al.*, 2020; Best and Dilkes, 2022). Therefore, this review is broken down into subsections on specific developmental effects of GA on plant architecture. Engineering future grass crops to have an optimal balance in GA regulation of growth and stress tolerance will be essential for improving crop yields and to combat deficits caused by a changing environment. Finally, we explore the potential of targeted GA pathway regulation to develop plant ideotypes for the next phase of the Green Revolution.

Stem elongation and role of GA

Stem structure in plants is defined during vegetative development when phytomers, repeated structures consisting of a node, internode, leaf, and axillary bud, are formed. Later in grasses, the stem elongates due to the activity of the intercalary meristem (IcM) at the base of each internode in the stem (Awale and McSteen, 2023). IcMs originate from the apical meristem by transverse division in the rib meristem and become separated from the apical meristem due to internode differentiation (McKim, 2019). Rapid cell division in the IcM at the base and subsequent cell elongation in the region just above the IcM drive internode elongation (Sachs, 1965; McKim, 2020; Z. Liu *et al.*, 2021). The molecular mechanism of internode elongation in deep-water rice has been recently reviewed in detail by Nagai and Ashikari (2023). This section of the review will focus more on the elongation of internodes that occurs after the reproductive transition in rice and maize, which is essential for elevating the inflorescence or panicle out of the whorl of leaves and for resistance to lodging.

GA is required for internode elongation in grasses. Reduced GA levels and signaling cause semi-dwarfism to extreme dwarfism in plants due to shorter internodes, as seen in multiple GA biosynthesis, metabolism, and signaling mutants (Zhou *et al.*, 2023) (Table 1). In these mutants, reduced cell numbers (Fang *et al.*, 2021) or cell size (Chu *et al.*, 2019; Duan *et al.*, 2020; Fang *et al.*, 2024) result in shorter internodes. Treatment with the phytotoxin coronatine, which affects the GA pathway via CORONATINE INSENSITIVE (COI) receptor-mediated degradation of DELLA (Feiz *et al.*, 2024), produces a similar negative effect on internode growth. Transcriptomic analysis of maize internodes treated with coronatine showed down-regulation of multiple GA biosynthesis and cell cycle-related

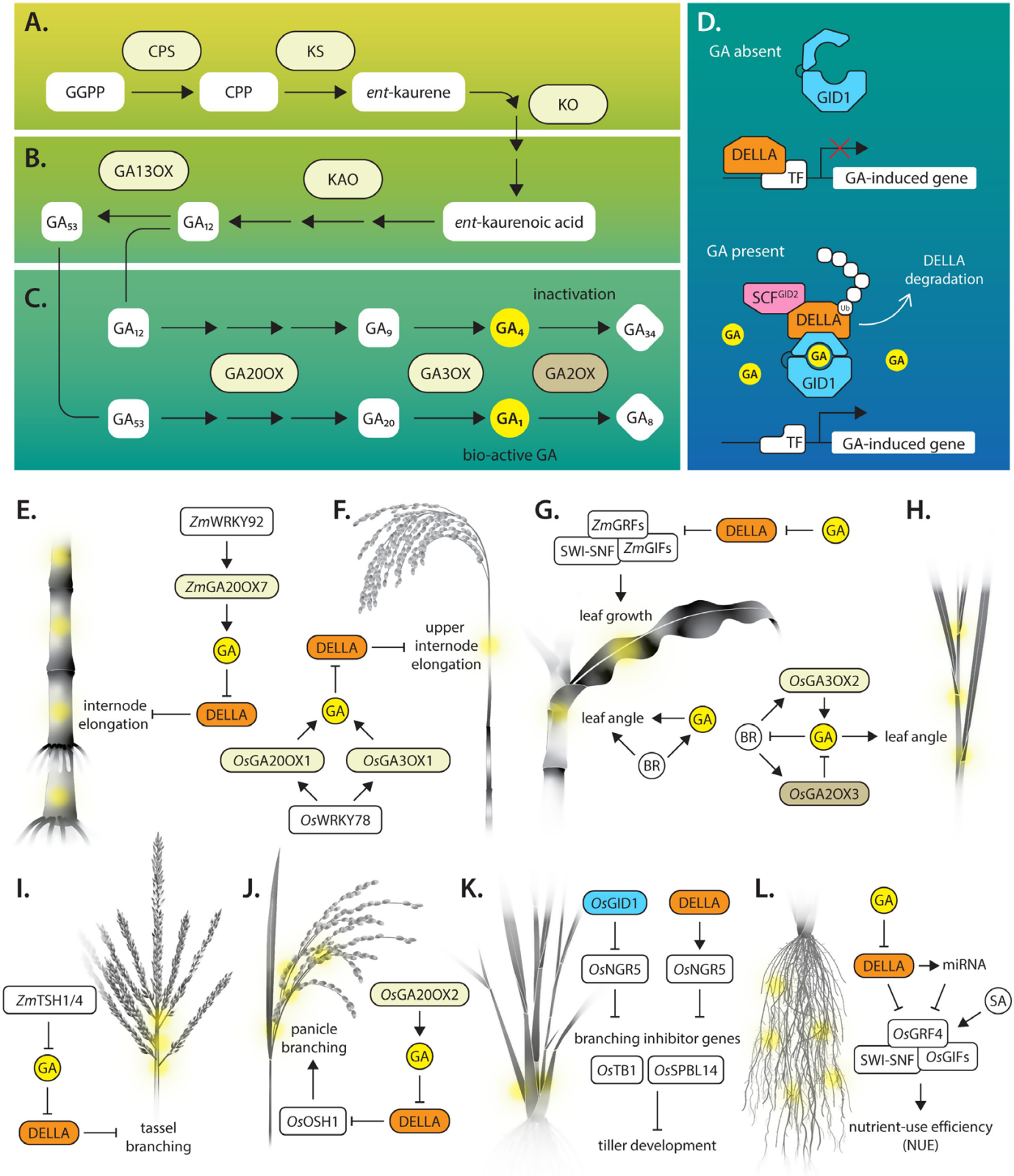

Fig. 1. GA-mediated regulation of grass crop architecture. (A–D) Generalized GA metabolism and signaling pathways in plants. (E–L) Examples of GA-mediated mechanisms regulating grass crop architecture: (E, F) internode length (Fang *et al.*, 2024; Mei *et al.*, 2024); (G, H) leaf growth (Nelissen *et al.*, 2015; Zhang *et al.*, 2018) and leaf angle (Tong *et al.*, 2014; Best *et al.*, 2016; Kong *et al.*, 2017); (I, J) tassel and panicle branching (Ashikari *et al.*,

2002; Su *et al.*, 2021; Best and Dilkes, 2022; Wang *et al.*, 2022; Xiao *et al.*, 2022); (K) tiller development in rice (Wu *et al.*, 2020; Huang *et al.*, 2021); and (L) nutrient-use efficiency in rice (Gao *et al.*, 2020; Li *et al.*, 2018; Lu *et al.*, 2021; Sun *et al.*, 2023; Zhang *et al.*, 2020c). Abbreviations: GGPP, *trans*-geranylgeranyl diphosphate; CPP, *ent*-copalyl diphosphate; CPS, *ent*-copalyl diphosphate synthase; KS, *ent*-kaurene synthase; KO, *ent*-kaurene oxidase; KAO, *ent*-kaurenoic acid oxidase; GA, gibberellin; GA13OX, GA 13-oxidase; GA20OX, GA 20-oxidase; GA3OX, GA 3-oxidase; GA2OX, GA 2-oxidase; DELLA, DELLA domain protein; GID1, GA-insensitive1 receptor; TF, transcription factor; SCF^{GID2}, Skp, Cullin, $F\text{-box}^{GID2}$; Ub, ubiquitin.

genes, indicating that GA plays a role in transcriptional activation of cell proliferation in the internode (Ren *et al.*, 2023).

Several transcription factors affect internode length by regulating GA levels during internode elongation in grasses. In rice, *Os*APETALA2/*Os*ETHYLENE RESPONSE FACTOR (*Os*AP2/OsERF), *Os*Cys2His2 ZINC FINGER (*Os*C2H2), and *Os*WRKY transcription factors have been shown to negatively regulate internode length by reducing bioactive GA levels. The role of these transcription factors and others are reviewed in detail by Zhou *et al.* (2023). Recently, two grass WRKY transcription factors that positively regulate the GA pathway have been identified. In maize, *Zm*WRKY92 promotes internode elongation by directly binding the promoters and activating the expression of the GA biosynthesis gene *ZmGA20OX7* and the GA signaling gene *ZmGID1L2* (Fang *et al.*, 2024). *Zmwrky92* mutants exhibit reduced plant height due to shorter internodes caused by smaller cell size, while stem strength is significantly higher (Fang *et al.*, 2024). Since *Zm*WRKY92 is expressed in stems and leaves, but not in reproductive organs, targeted mutation of this gene could be useful for developing lodging-resistant maize cultivars. In rice, *Os*WRKY78 is required for proper panicle exertion, driven by internode elongation. A loss-of-function mutation in *OsWRKY78* leads to failed panicle exertion due to reduced growth in the top two internodes of the mutants. *Os*WRKY78 directly binds the promoters of GA biosynthetic genes, *OsGA20OX1* and *OsGA3OX1*, and activates their expression, and overexpression of *OsGA20OX1* rescues the internode defect (Mei *et al.*, 2024). These studies show that targeting specific WRKY genes to modulate GA levels in particular stem internodes can potentially fine-tune plant architecture in maize, rice, and other grass species.

In addition, two repressors of the rice Green Revolution gene (*OsSD1*/*OsGA20OX2*) have recently been identified: *Os*ZFP207 (a C2H2 zinc finger protein) (Duan *et al.*, 2020) and *Os*BASIC REGION/LEUCINE ZIPPER MOTIF01 (bZIP01) (Xinli *et al.*, 2024). These proteins bind directly to the *OsSD1* promoter. Therefore, overexpression of these genes leads to a significant reduction in *OsSD1* mRNA levels and causes semi-dwarfism due to shortened internodes, an effect that can be rescued by exogenous GA application (Xinli *et al.*, 2024). *OsbZIP01* is predominantly expressed in the vegetative tissues, with lower expression in reproductive structures. Overexpression lines show slower germination, while knockout mutants germinate faster due to the pleiotropic effect of GA on germination. Partial knockdown of this gene could modulate GA biosynthesis to improve germination rates and seedling establishment, and reduce plant height to prevent lodging. Therefore, this study demonstrates how targeting genes upstream of the GA biosynthetic pathway can improve plant architecture while minimizing pleiotropic effects.

To achieve optimal plant height to adapt to changing climates, tweaking GA and associated pathways could be effective. Targeted mutations in specific tissues offer a promising approach. For example, increased expression of GA 2-oxidase paralogs with tissue-specific expression profiles results in semi-dwarf phenotypes in wheat (Ford *et al.*, 2018; Sun *et al.*, 2019; Buss *et al.*, 2020). Recently, maize dwarf plants were developed by repressing two GA biosynthesis genes, *ZmGA20OX3* and *ZmGA20OX5* (Paciorek *et al.*, 2022). The mutants exhibit reduced internode length and significantly increased stem diameters, making them more resistant to lodging. Importantly, there was no significant effect on yield. Thus, semi-dwarf maize plants can adapt better to increasingly more frequent and severe storms (Stokstad, 2023). Rising water levels also pose a significant challenge, especially in rice-growing regions. Deep-water rice can elongate their stems in response to flooding in a GA-dependent manner, allowing them to survive in high water conditions. By introducing internode elongation genes/alleles from deep-water rice to normal paddy-rice, it may be possible to enhance internode elongation to adapt to high water levels (Nagai and Ashikari, 2023).

GA regulation of leaf growth and development

The role of GA in regulating leaf growth in grasses was recognized long before its biosynthesis and actions were fully understood. GA-treated wild-type plants exhibit longer leaves, while GA-deficient and some GA-insensitive mutants produce shorter, wider leaves (Table 1) (Brian, 1958). How then does GA control leaf growth? This section examines the cellular and molecular mechanisms underlying this control and explores how they can be targeted to optimize leaf traits crucial for grass crop productivity.

The grass leaf consists of a strap-like blade and a sheath that wraps around the tubular stem. During steady-state growth, after the blade–sheath boundary is established, cells in the blade's basal region proliferate to form the division zone (DZ). Distal to this region, cells stop dividing and grow expansively in the elongation zone (EZ), then cease growing and differentiate in the maturation zone (MZ) (Strable and Nelissen, 2021). This linear organization in the grass leaf establishes a

basipetal gradient, enabling spatial–temporal correlations between cell growth rates and molecular processes (Avramova *et al.*, 2015). Nelissen *et al.* (2012) analyzed hormone and gene expression dynamics across the growth zones of maize leaves to understand how hormones regulate organ growth. They found that while auxin and cytokinin peak at the proximal DZ, bioactive GAs peak in a narrow distal region between the DZ and EZ. This GA concentration peak, which is maintained by GA metabolism, may be crucial for the transition of dividing cells to the expansion phase. Both experimental data and computational models reveal that altering GA biosynthesis or signaling leads to changes in the size of the DZ (Nelissen *et al.*, 2012; De Vos *et al.*, 2020). This regulation of proliferative growth could explain why longer leaves with higher GA concentrations, such as those in wild rice varieties (Jathar *et al.*, 2022), exhibit expanded expression of

Table 1. GA biosynthesis and signaling genes

Protein type	Role in GA pathway	Organism	Mutant, transgenic line	Reported developmental effect	Reference
ent-Copalyl diphosphate (CPP) synthase	Early step in GA biosynthesis	Maize	*Zmcpp synthase1/Zmanther ear1* (*Zmcps1/Zman1*)[a] and *Zmcps2/Zman2*[a]	Dwarf plant; short internodes; short and broad leaves; conversion of female imperfect flower to perfect flower	Bensen *et al.* (1995); Murphy *et al.* (2018); Zhang *et al.* (2020b)
		Maize	*Gossypium hirsutum GhCPS1*[c] in *Zmcps1/Zman1* knockout mutant[a]	Normal-height plant; partially sensitive to growth retardant, mepiquat chloride	Zhang *et al.* (2020b)
		Rice	*Oscpp synthase1* (*Oscps1*)[a]	Severely dwarf; reduced inflorescence development	Sakamoto *et al.* (2004)
ent-Kaurene synthase	Early step in GA biosynthesis	Maize	*Zment-kaurene synthase-like3/Zmdwarf plant5* (*Zmksl3/Zmd5*)[a]	Dwarf plant; short internodes; short and broad leaves	Fu *et al.* (2016); Katsumi *et al.* (1964); Li *et al.* (2023)
		Rice	*Osent-kaurene synthase1* (*Osks1*)[a]	Severely dwarf plant; does not develop flowers	Sakamoto *et al.* (2004)
ent-Kaurene oxidase	Early step in GA biosynthesis	Rice	*Osent-kaurene oxidase2/Osdwarf35* (*Osko2/Osd35*)[a]	Dwarf plant	Itoh *et al.* (2004); Sakamoto *et al.* (2004)
		Rice	*Osent-kaurene oxidase1* (*Osko1*)[a]	Semi-dwarf plant; delayed germination	H. Zhang *et al.* (2020)
		Rice	*Osent-kaurene oxidase1* (*Osko1*)[a], *Osko3*[a], *Osko4*[a], and *Osko5*[a]	Semi-dwarf to severely dwarf plants; sterile	Chen *et al.* (2019)
ent-Kaurenoic acid oxidase	Intermediate step in GA biosynthesis	Maize	*Zment-kaurenoic acid oxidase1/Zmdwarf plant3* (*Zmkao1/Zmd3*)[a]	Dwarf plant; short internodes; short and broad leaves	Helliwell *et al.* (2001); Winkler and Helentjaris (1995)
		Rice	*Osent-kaurenoic acid oxidase* (*Oskao*)[a]	Severely dwarf plant; sterile	Chen *et al.* (2019); Sakamoto *et al.* (2004)
GA 20oxidase	Intermediate step in GA biosynthesis	Maize	*Zmga 20oxidase3* (*Zmga20ox3*)[a]	Semi-dwarf plant	Liu *et al.* (2023a); Zhang *et al.* (2020a)
		Maize	miRNA-based suppression[c] of *ZmGA20OX3* and *ZmGA20OX5*	Semi-dwarf plant due to shorter internodes; normal reproductive development	Paciorek *et al.* (2022)
		Maize	*UBI::AtGA20OX-1*[c] in maize and UBI::*ZmGA20X-1*[c]	Tall plant; long stem; longer leaf due to faster leaf elongation rate	Nelissen *et al.* (2012); Voorend *et al.* (2016)
		Rice	*Osga 20oxidase2/Ossemi-dwarf1* (*Osga20ox2/Ossd1*)[a], *Osga-20ox3*[a], and *Osga20ox4*[a]	Semi-dwarf plant	Ashikari *et al.* (2002); Chen *et al.* (2019); Qin *et al.* (2012); Sakamoto *et al.* (2004); Sasaki *et al.* (2002); Spielmeyer *et al.* (2002)
		Rice	*Osga 20oxidase2/Ossemi-dwarf1* (*Osga20ox2/Ossd1*)[a] mutation in rice landraces	Semi-dwarf plants with better resistance to lodging	Hu *et al.* (2019)
		Rice	*35S::OsGA20OX1*[c]	Tall plant; long internodes	Oikawa *et al.* (2004)
		Rice	*OsGA20OX1 RNAi*[a]	Semi-dwarf plant	Oikawa *et al.* (2004)
		Wheat	*Taga 20oxidase1* (*Taga20ox1*) and *Taga20ox2* triple mutants	Plants with slight height reduction (*Taga20ox1*); semi-dwarf plants (*Taga20ox2*)	Ndreca *et al.* (2024)
		Wheat	*Taga 20oxidase2* (*Taga20ox2*)/*Tasemi-dwarf1* (*Tasd-A1*, *Tasd-B1*, and *Tasd-D1*) triple knockout[a]	Semi-dwarf plant	Kumagai *et al.* (2022)
GA 3oxidase	Late step in GA biosynthesis	Maize	*Zmga 3oxidase2/Zmdwarf plant1* (*Zmga3ox2/Zmd1*)[a]	Dwarf plant; short internodes; short and broad leaves	Chen *et al.* (2014)
		Rice	*Osga 3oxidase2/Osdwarf18* (*Osga3ox2/Osd18*)[a]	Dwarf plant; broad leaves	Sakamoto *et al.* (2004)

Table 1. Continued

Protein type	Role in GA pathway	Organism	Mutant, transgenic line	Reported developmental effect	Reference
GA 2oxidase	GA inactivation	Wheat	*TaReduced height12* (*TaRht12*)[b] and *TaRht18*[b]	Semi-dwarf plant	Buss *et al.* (2020); Ford *et al.* (2018); Sun *et al.* (2019)
		Rice	*Osga2ox3*[a], *Osga2ox5*[a], *Osga2ox6*[a], and *Osga2ox9*[a]	Semi-dwarf or severely dwarf plant with pleiotropic effects	Chen *et al.* (2019)
		Rice	T-DNA activation-tagged *Osga2ox6* (*H032*)[b]	Dwarf plant; with normal flowering and seed set	Huang *et al.* (2010)
		Rice	T-DNA activation-tagged *Osga2ox3*[b], *Osga2ox5*[b], *Osga2ox6*[b], and *Osga2ox9*[b]	Severely dwarf plant	Lo *et al.* (2008)
		Rice	*35S::Os*GA2OX5[c] and *35S*::*Os*GA2OX6[c]	Severely dwarf plant	Huang *et al.* (2010); Shan *et al.* (2014)
		Rice	*UBI::OsGA2OX5*[c] and *UBI::OsGA2OX6*[c]	Severely dwarf plants	Lo *et al.* (2008)
		Rice	*ACT*::*OsGA2OX1*[c]	Dwarf or severely dwarf plant with effects on flower production	Sakamoto *et al.* (2003)
		Rice	*OsD18::OsGA2OX1*[c]	Semi-dwarf plant without effects on flower production	Sakamoto *et al.* (2003)
		Rice	Overexpression of *TaGA 2oxidase1* (*UBI*:*TaGA 2OX1*)[c] genes in rice	Normal-height, semi-dwarf, to severely dwarf plants	Tang *et al.* (2019)
		Wheat	UBI::*Phaseolus coccineus PaGA2OX1* in wheat	Semi-dwarf to severely dwarf plants; increased tillering	Appleford *et al.* (2007)
GA 13oxidase	GA inactivation	Rice	*Os*cyp714d1/*Oselongated uppermost internode1* (*Oseui1*)[a]	Tall plant due to longer upper internodes	Zhu *et al.* (2006)
		Rice	*35S::OsEUI*[c] in rice	Severely dwarf plant	Zhu *et al.* (2006)
		Rice	*35S*::*AtEUI-LIKE1*(*OsELA1*)[c] and *35S*::*AtELA2*[c] in rice	Severely dwarf plant (*35S*::*AtELA1*); semi-dwarf with an increased tiller efficiency (*35S*::*AtELA2*)	Zhang *et al.* (2011)
		Rice	*Oscyp714b1; Oscyp714b2* double mutant[a]	Tall plant due to longer upper internodes	Magome *et al.* (2013)
GID1 GA-binding lipase	GA perception	Rice	*Osgibberellin insensitive dwarf1* (*Osgid1*)[a]	Severely dwarf plant	Shimada *et al.* (2008); Ueguchi-Tanaka *et al.* (2005, 2007)
DELLA	GA response repression	Maize	*ZmDwarf plant8* (*ZmD8*)[b] and *ZmD9*[b]	Dwarf plant; broad leaves	Lawit *et al.* (2010); Peng *et al.* (1999)
		Wheat	*TaReduced height1* (*TaRhtB1* and *TaRhtD1*)[b]	Semi-dwarf plant	Peng *et al.* (1999)
		Rice	*Osslender rice1* (*Osslr1*)[a]	Tall plant	Ikeda *et al.* (2001)
		Rice	Overexpression of *OsSLENDER RICE1-LIKE1* which lack the DELLA domain (*ACT::OsSLRL1*)[c]	Semi-dwarf or dwarf plant	Itoh *et al.* (2005)
GID2 F-box protein	GA response activation	Rice	*Osgibberellin insensitive dwarf2* (*Osgid2*)[a]	Severely dwarf plant; broad leaves	Sasaki *et al.* (2003)

[a] Loss-of-function.
[b] Gain-of-function.
[c] Overexpression or misexpression.

cell cycle-promoting genes. Therefore, spatial regulation of GA action can be an effective strategy for modulating cell division and leaf size in grasses.

GA controls the cell division rate in the leaf via DELLA proteins (Achard *et al.*, 2009). Since the discovery of the GA-inducible GROWTH-REGULATING FACTOR1 (*Os*GRF1) in rice (van der Knaap *et al.*, 2000), the GRF gene family has emerged as a potential DELLA-dependent target for leaf growth regulation (Gonzalez *et al.*, 2012; Nelissen *et al.*, 2016; Lu *et al.*, 2021; Jathar *et al.*, 2022). GRFs form a module with GRF-INTERACTING FACTORs (GIFs) and the SWI/SNF chromatin-remodeling complex to control gene expression (Kim, 2019). Over the past decade, genes within the GRF–GIF–SWI/SNF module have been shown to affect leaf growth (as well as other aspects of development) in maize and rice, producing phenotypes comparable with those of plants with altered GA levels (Wu *et al.*, 2014; Nelissen *et al.*, 2015; Li *et al.*, 2018; Shimano *et al.*, 2018; Zhang *et al.*, 2018; Lu *et al.*, 2020). In maize, various GRFs form complexes with *Zm*GIF1/*Zm*ANGUSTIFOLIA3 across leaf growth zones,

demonstrating context-specific interactions that may regulate growth transitions (Nelissen *et al.*, 2015). Interestingly, DELLA proteins in rice physically interact with GRFs and may play a role in regulating their expression (Lu *et al.*, 2021). However, given the extensive diversification of GRFs in grasses (Schneider *et al.*, 2024) and the involvement of DELLA proteins in various regulatory networks that target the cell cycle (Vercruysse *et al.*, 2020), GA probably acts through multiple pathways to influence cell division under diverse genetic and environmental conditions. Thus, further research is needed to determine whether the GRF–GIF–SWI/SNF module constitutes a fundamental, tunable DELLA-dependent pathway for controlling leaf growth in grasses.

During steady-state growth, exponential cell expansion in the DZ and EZ drives rapid leaf elongation, with dominant axial growth producing the characteristically elongated leaves of grasses (Skinner and Nelson, 1995; Muller *et al.*, 2001). Thus, anisotropic cell growth is essential for grass leaf elongation. GA enhances cell growth anisotropy by promoting longitudinal growth rates in the leaf (Sprangers *et al.*, 2020). As observed in a wild-type maize leaf, anisotropic longitudinal cell growth is highest in the DZ and continues throughout the EZ until the cells reach their maximum volume at the MZ. Conversely, in a GA-deficient mutant, leaf cells lose anisotropy and become wider and shorter, while in a GA-overproducing line, they grow longer and narrower. However, a compensatory effect on the time spent by the cells in the EZ was observed, indicating that GA influences the rate and direction of cell expansion, but other factors might be involved in the control of the duration of cell expansion during leaf growth (Sprangers *et al.*, 2020).

To control cell expansion, GA alters cell wall biomechanical properties. In excised wheat leaves, GA treatment increases cell wall extensibility in the wild type but not in *TaRht* mutants, suggesting DELLA-dependent regulation (Keyes *et al.*, 1990). Expanding cells adapt to turgor stress by loosening and extending the cell wall. Xyloglucan endotransglucosylases (XETs) and expansins are key to these processes by altering polymer organization and adhesion, respectively (Cosgrove, 2022). GA induces the expression of XETs and expansins in rice and other grass species, but how it does so remains unknown (Cho and Kende, 1997; Uozu *et al.*, 2000; Lee and Kende, 2001; Xu *et al.*, 2016). Additionally, GA promotes cell growth anisotropy by orienting cortical microtubule alignment (Baluška *et al.*, 1993). In the EZ, cells usually have microtubules aligned perpendicular to the long axis. In GA-deficient barley mutants, this alignment becomes more randomized, suggesting GA's role in maintaining transverse microtubule orientation during cell elongation (Wenzel *et al.*, 2000). Consistently, DELLA proteins negatively regulate tubulin folding required for proper microtubule orientation (Locascio *et al.*, 2013). As a result, the role of DELLA proteins in controlling both cell wall extensibility and microtubule orientation leads to a binary outcome when GA levels or DELLA protein stability are altered: a shorter, wider leaf or a longer, narrower one, as seen in GA biosynthesis and signaling mutants (Table 1).

Targeting cell-specific downstream pathways may therefore provide a refined approach to altering leaf shape and size in grasses. One such pathway involves GA-regulated cell expansion through light-responsive transcription factors, PHYTOCHROME INTERACTING FACTORs (PIFs) (Feng *et al.*, 2008). In dark-grown Arabidopsis seedlings, elevated GA levels promote hypocotyl elongation by enabling PIFs to activate expansin expression. In contrast, light inhibits GA accumulation, allowing DELLA proteins to sequester and degrade PIFs, thereby suppressing organ growth (de Lucas *et al.*, 2008; Li *et al.*, 2016). A similar dark/light-dependent mechanism may operate in a growing grass leaf, where the EZ remains hidden within the shoot. Alternatively, cell growth duration in grasses may also be regulated via the cytochrome P450 protein, PLASTOCHRON1 (PLA1), which has been functionally characterized in both maize and rice (Miyoshi *et al.*, 2004; Sun *et al.*, 2017). Exploring how DELLA proteins interact with such pathways could thus offer new ways to fine-tune leaf growth for optimal adaptation and light capture.

GA does not appear to have a direct role in leaf patterning and architecture, as leaf morphology and anatomy are not affected in plants with perturbed GA biosynthesis and signaling (Strable and Nelissen, 2021; Robil and McSteen, 2023). However, known regulators of leaf morphogenesis interact with the GA pathway. For example, in maize, the *Zm*KNOTTED1 (*Zm*KN1) KNOX (KNOTTED1-RELATED HOMEOBOX) transcription factor defines the blade–sheath boundary by controlling cell differentiation through GA metabolism, while auxin modulates lateral proliferative growth through GA biosynthesis (Bolduc and Hake, 2009; Robil and McSteen, 2023). In rice, *Os*WUSCHEL-RELATED HOMEOBOX3A/*Os*NARROW LEAF2/3 (*Os*WOX3A/*Os*NAL2/3) is involved in the negative feedback regulation of GA biosynthesis to control lateral leaf expansion (Cho *et al.*, 2016). Similarly, brassinosteroid (BR) interacts with GA to regulate leaf angle, a key trait for high-density planting. Genetic and pharmacological experiments show that BR acts upstream of GA to control leaf angle in maize and rice (Tong *et al.*, 2014; Best *et al.*, 2016, 2017; San *et al.*, 2020; Cao *et al.*, 2022). This interaction suggests that GA plays a crucial role in modulating leaf angle by influencing the size of the auricle, a pair of wedge-shaped tissues at the blade–sheath boundary (Kong *et al.*, 2017). Collectively, these studies show that the GA pathway can be exploited to modify leaf morphology, especially leaf angle, in grass crops.

GA and the regulation of meristem size

GA plays several important roles in meristems, the growing points of the plant. Above-ground meristems contain stem cells which are found in the central zone (CZ), overlying the organizing center (OC), while the peripheral zone (PZ) gives

rise to the lateral organs and the rib zone (RZ) gives rise to the stem and internodes. Defects in the coordination of CZ and PZ activities leads to a smaller meristem and termination of growth or a larger meristem and overgrowth or fasciation (Kitagawa and Jackson, 2019). Meristem size is agriculturally important as it directly affects grain number (McSteen and Kellogg, 2022).

In the vegetative shoot apical meristem (SAM), GA levels are predicted to be low, as KNOX transcription factors, which are required for meristem maintenance, promote GA degradation and inhibit GA biosynthesis (Shi and Vernoux, 2022). Similarly in maize, *Zm*KN1 directly binds to the promoter of the GA catabolism gene *Zm*GA2OX1 and, furthermore, *Zm*KN1 and *Zm*GA2OX1 expression overlaps at the base of the SAM, indicating that *Zm*KN1 keeps GA out of the SAM (Bolduc *et al.*, 2012), which has recently been confirmed at the single-cell level (Satterlee *et al.*, 2020). However, even though there are predicted to be low levels of GA in the SAM, the GA biosynthesis mutant *dwarf plant3* (*Zmd3*) in maize has a larger, wider vegetative SAM that is auxin dependent (Robil and McSteen, 2023). This counterintuitive result could be the result of a threshold effect of GA levels or a non-autonomous effect of GA in vegetative SAMs which warrants further investigation.

In Arabidopsis, GA is required for flowering time regulation (Li *et al.*, 2024). In addition, during the transition from SAM to inflorescence meristem (IM), flowering time genes induce expression of genes required for GA biosynthesis and decrease expression of GA degradation genes, resulting in a presumably higher level of GA in the IM (Kinoshita *et al.*, 2020). This increase in GA is required for the increase in meristem size that occurs during this transition as mutants in GA biosynthesis genes such as *AtGA20OX2* have smaller meristems (Kinoshita *et al.*, 2020). The increase in meristem size is caused by an increase in cell number and cell size in the PZ. Although GA plays a role in inducing flowering under long days in wheat, barley, and rye grass (Fjellheim *et al.*, 2014), DELLA- or GA-deficient mutants in maize, rice, and wheat do not have effects on flowering time (Tang *et al.*, 2021; Paciorek *et al.*, 2022). There are flowering time quantitative trait loci (QTLs) that are associated with DELLAs in maize (Thornsberry *et al.*, 2001), but further population structure analysis showed that DELLAs were not the causative loci of these QTLs (Larsson *et al.*, 2013). Therefore, it is not known if GA mediates the increase in meristem size that also occurs during the SAM to IM transition in cereals (McSteen *et al.*, 2000).

During inflorescence development, DELLAs were shown to regulate IM size (independently of plant height) in Arabidopsis and barley (Serrano-Mislata *et al.*, 2017). In Arabidopsis, GA-deficient mutants have decreased IM size while quintuple *della* loss-of-function mutants have enlarged meristem size, indicating that GA promotes IM size. One of the mechanisms by which GA promotes IM size is that DELLA directly regulates the expression of cell cycle kinase inhibitors in the RZ and internode. Together with a previous study (Davière *et al.*, 2014) which showed that DELLAs negatively regulate TCP transcription factors that regulate the cell cycle, this indicates that GA increases the cell cycle activity, leading to increased IM size. In barley, the *slender* DELLA gain-of-function mutant was also shown to have decreased IM size and fewer spikelets, indicating that GA also promotes IM size in barley (Serrano-Mislata *et al.*, 2017). As will be seen in the next section on inflorescence branching, GA-deficient mutants in cereals have decreased branching and spikelet number in the inflorescence, indicating that GA does appear to function in IM size in cereals too, although the effect on IM size is not always examined directly. It should be possible to manipulate the GA pathway to further increase GA and increase IM size, leading to increased branch, spikelet, and seed number, and also increased yield in cereals, in an alternative approach to how the CLV–WUS pathway has been manipulated in maize (Kitagawa and Jackson, 2019).

Below-ground meristems have a different structure from those above ground, with the root tip consisting of a DZ with a QC, followed by the EZ and MZ, where lateral root primordia originate from pericycle cells embedded in the root. Despite these differences, GA also regulates meristem size in the root apical meristem (RAM) (reviewed by Shtin *et al.*, 2022). In Arabidopsis, GA promotes cell proliferation in the DZ (Achard *et al.*, 2009) and cell expansion in the EZ (Ubeda-Tomas *et al.*, 2008). The recent development of a GA biosensor has enabled visualization of a GA gradient in the root, and modeling indicates that GA biosynthesis and transport are important in establishing and maintaining the gradient (Rizza *et al.*, 2021). The tissue-specific expression of GA biosynthetic genes is likely to contribute to the gradient (Barker *et al.*, 2021).

GA (together with auxin) also plays a role in root architecture in cereals, which have fibrous rather than tap root architecture and hence have additional root types: adventitious seminal, crown, and brace roots, in addition to primary and lateral roots (Hochholdinger *et al.*, 2018). GA-deficient mutants in maize and rice have additional brace roots due to an extended juvenile phase (Hostetler *et al.*, 2021). In rice, external GA application suppresses primary root growth (Li *et al.*, 2020), increases seminal root length (Vlaminck *et al.*, 2020), and inhibits crown root number (Nguyen *et al.*, 2024). Importantly, GA (as well as auxin and cytokinin) plays a role in nutritropism—the movement of root tips towards nutrients (Yamazaki *et al.*, 2024), and therefore plays a role in foraging of roots for nutrients, as further discussed in the section on GA and NUE. Therefore, accurate modifications of the GA pathway could be used to adjust root architecture to optimize water and nutrient uptake as well as lodging resistance through the formation of additional brace roots (Sparks, 2023).

The role of GA in reproductive development

GA has been shown to activate the florigen gene *FLOWERING TIME* (*FT*) in Arabidopsis under long-day conditions, but was

not shown to have influence under short days (Conti, 2017). This effect on florigen genes has not been studied in maize, rice, or wheat. As stated previously, inhibiting GA biosynthesis or altering GA signaling in maize and wheat does not affect flowering time (Tang *et al.*, 2021; Paciorek *et al.*, 2022). This again is surprising since GA has been shown to promote the juvenile to adult phase change in Arabidopsis (Manuela and Xu, 2020) and maize (Evans and Poethig, 1995). Altering GA to improve traits in breeding lines should not have deleterious effects on flowering time.

GA regulates branching and inflorescence architecture in grasses. Exogenous application of GA to developing maize tassels affected tassel branch number in a background-dependent manner. Most commonly, it would increase tassel branch number (Best and Dilkes, 2022). In rice, the GA20OX2 mutant *Ossemi dwarf1* (*sd1*) has fewer primary and secondary panicle branches and reduced panicle length, which resulted in fewer grains per panicle (Ashikari *et al.*, 2002). The reduction in GA levels in *Ossd1* results in higher levels of the GA repressor DELLA domain protein *Os*SLENDER1 (*Os*SLR1). It was shown that *Os*SLR1 physically interacts with the meristem maintenance KNOX protein, *Os*OSH1, to reduce its activation of downstream genes controlling panicle architecture (Su *et al.*, 2021; Wang *et al.*, 2022). Therefore, increasing GA in rice or wheat panicles should increase inflorescence branching and increase yields. In maize, *Zm*TASSELSHEATH1 (*Zm*TSH1) and *Zm*TSH4 proteins act to suppress inflorescence leaf growth, or bracts, and promote branching. Knockout mutants of *Zmtsh1* and *Zmtsh4* had lower transcript levels of GA catabolic genes and GA response inhibitors, indicating that they may inhibit GA signaling to suppress bract growth and promote branching in maize (Xiao *et al.*, 2022).

GA inhibits vegetative branching in almost all species. GA has been shown to repress vegetative branching in Arabidopsis via the DELLA–SQUAMOSA-PROMOTER BINDING PROTEIN LIKE 9 (SPL9) complex (Q.-Q. Zhang *et al.*, 2020). Mutants with lower GA levels or dominant DELLA mutants make more tillers (vegetative branches) than their wild-type siblings (Lawit *et al.*, 2010; Best *et al.*, 2016; Kaur *et al.*, 2024), which could add to yield gains. In rice, a mechanism has been described for a nitrogen-induced branching by *OsNITROGEN-MEDIATED TILLER GROWTH RESPONSE5* (*OsNGR5*). *Os*NGR5 physically interacts with GA-activated *Os*GID1 to be degraded by the 26S proteasome. This allows for expression of branching inhibitor genes, such as *Os*TEOSINTE BRANCHED1 and *Os*SQUAMOSA PROMOTER BINDING PROTEIN-LIKE-14. When GA is absent, the DELLA domain proteins competitively inhibit the interaction of *Os*NGR5 with *Os*GID1 to promote expression of branching inhibitor genes and reduce tiller formation (Wu *et al.*, 2020; Huang *et al.*, 2021). In maize, the mechanism by which GA inhibits tiller development has not been extensively studied but has been shown to depend on BR function (Best *et al.*, 2016).

GA regulates reproductive organ development in grasses. This has been mostly studied in maize. Maize is monoecious as it has a staminate tassel at the apex of the plant and a separate pistillate ear on an axillary branch of the main stalk (Guerrero-Méndez and Abraham-Juárez, 2024). Therefore, GA regulation of reproductive development could have broad implications in hybrid seed reproduction. Exogenous application of GA to developing maize tassels results in retention of pistils and reduction of stamen development (Best and Dilkes, 2022). This regulation is highly dependent on the genetic background, with some inbred lines not producing pistils even under application of high concentrations of GA, indicating that there may be presence/absence variation in GA regulation throughout maize diversity. Furthermore, the retention of pistils in the maize tassel is not correlated with the effect on plant height (Best and Dilkes, 2022). This indicates that GA regulation of reproductive development and plant height is likely to be controlled by different molecular mechanisms, and GA's control of these two developmental traits can by uncoupled. Using tassel-specific promoters to increase GA concentrations in the male tassel, it could be possible to suppress anther development and create a new type of male-sterile line. This approach could also be leveraged into other species, such as rice and wheat, to improve production of hybrid varieties.

GA has also been shown to regulate stamen development. A loss of GA biosynthesis or constitutive repression of GA signaling by the DELLA domain proteins results in retention of stamens in the normally pistillate maize ear, therefore producing perfect flowers on the ear, but has no effect on reproductive development in the tassel (Bensen *et al.*, 1995; Winkler and Helentjaris, 1995; Best and Dilkes, 2022). This ear trait is deleterious for maize breeders as retention of stamens in the husk leaves results in higher moisture content and can lead to more severe disease. In rice, the DELLA domain protein *Os*SLR1 is also required for proper anther development. The *Os*SLR1 protein was shown to interact with *Os*MALE STERILE188 (*Os*MS188) to activate expression of essential transcripts for the development of the tapetum, a layer of nutritive cells in the anther required for development of pollen grains. The knockout mutant *Osslr1-5* shows premature programmed cell death of the tapetum and therefore does not produce mature pollen (Jin *et al.*, 2022). The rice *Oswrky53* mutant was cold tolerant at the booting stage because of increased GA biosynthesis in the developing anthers. It was shown that *Os*WRKY53 can bind to the promoters of GA biosynthetic genes to repress their transcription. Thus, the knockout mutants relieved this repression, increased GA levels in the anther, and allowed proper development of the tapetum (Tang *et al.*, 2022). The *Os*SWOLLEN ANTHER WALL1 (*Os*SAW1) protein was also shown to activate expression of *Os*GA20OX3 required for proper development of the rice anther (B. Wang *et al.*, 2020). Taken together, a repression of GA biosynthesis or signaling is required for normal production of stamens in monocots. Therefore, utilizing tissue-specific promoters to modulate GA effects on plant

height will be necessary to lower the pleiotropic effects of GA on reproductive development.

GA has also been shown to influence grain filling in monocots. Knockout of the maize *ZmKAURENE SYNTHASE3* (*ZmKS3*) gene resulted in shorter and skinnier ears and seeds. This resulted in lower grain yields as compared with wild-type siblings (Wu *et al.*, 2023). In rice, a QTL was identified for grain size and was found to encode a GA-regulated GAST family member, *Os*GW6. The knockout mutant of *Osgw6* resulted in reduced grain size and weight. A natural variant was found in the promoter of *Os*GW6 and its expression is correlated with rice grain width and weight (Shi *et al.*, 2020). Therefore, upregulated GA responses during grain filling can promote grain size and increase yields. This would be especially important in rice and wheat tillers and the tips of maize ears where yield potential is not reached due to insufficient grain fill.

GA and nutrients

GA has been shown to play an important role in the response of plants to nutrient deficiency such as of nitrate, phosphorus, potassium, and iron (Jia *et al.*, 2022). The original Green Revolution semi-dwarf plants had the unfortunate side effect of having low NUE, requiring increased levels of fertilizer to maximize yield (Liu *et al.*, 2022). Determination of the molecular basis for low NUE enabled the development of semi-dwarf varieties of rice and wheat without reduced NUE (Li *et al.*, 2018). In rice, DELLA represses activation of the transcription factor gene *OsGRF4* which regulates nitrogen uptake and utilization genes (Li *et al.*, 2018). Naturally occurring gain-of-function variants of *OsGRF4* were shown to have increased yield and NUE while maintaining the semi-dwarf growth habit. Furthermore, transgenic overexpression of *OsGRF4* also increased NUE in wheat (Li *et al.*, 2018). Recent work has identified additional regulators of the pathway providing additional mechanisms to modify NUE. *GRF* genes are GA induced and regulated by miRNA (Lu *et al.*, 2021). CRISPR (clustered regularly interspaced palindromic repeats) knockout of *miR396ef* (which degrades *Os*GRF4) can also increase grain yield under low nitrogen (Zhang *et al.*, 2020c). *OsMYB61* which regulates cellulose biosynthesis was shown to be directly targeted by *Os*GRF4, and a natural variant allele with increased expression of *OsMYB61* had higher NUE and had been selected during domestication of rice (Gao *et al.*, 2020). It was previously shown that a natural variant, *Os*DWARF717 (*Os*D17), an enzyme in the strigolactone (SL) biosynthetic pathway causing partial loss of function, was co-selected along with *sd1* in rice and conferred increased yield (Gao *et al.*, 2020). Recently, it was shown that the SL signaling pathway directly regulates *Os*GRF4 in parallel to GA under low nitrogen which increases SL levels (Sun *et al.*, 2023). As previously discussed, the basis of nitrogen-responsive tillering was shown to be due to chromatin regulation of *OsNGR5* (Wu *et al.*, 2020), and gain-of-function variants of *OsNGR5* had increased tillering and NUE. Therefore, there are multiple means by which GA-mediated NUE could be modified which could be applied to other cereals.

GA is also required for nitrate uptake in maize. Under nitrogen deficiency, GA levels decrease in roots, stem, and leaves (Peyami, 2004). Y. Wang *et al.* (2020) used CRISPR to knock out a GA biosynthesis enzyme, *Zm*GA3OX, and showed that GA-deficient mutants were more sensitive to low nitrogen stress, and had reduced nitrate uptake in roots and allocation to shoots, and reduced expression of nitrate transporters. Although orthologs of the GRF pathway (Lu *et al.*, 2021) have been identified in maize, whether the pathway can be used to increase NUE in maize should be further investigated.

In Arabidopsis, GA also plays a role in nitrate, phosphate, potassium, and iron deficiency. For example, Camut *et al.* (2021) demonstrated that nitrate signaling promotes GA biosynthesis and destabilization of DELLA, indicating conservation with maize and rice. Jiang *et al.* (2007) showed that dominant DELLA mutants are also more sensitive to phosphate deficiency. DELLA accumulates in the primary root meristem to suppress growth in response to both phosphate (Jiang *et al.*, 2007) and iron deficiency (Wild *et al.*, 2016). Furthermore, DELLA accumulates in lateral root primordia, inhibiting growth in response to potassium deficiency (Hetherington *et al.*, 2021). As it has already been shown that rice plants can be engineered to mitigate the effects of reduced NUE, it may also be possible to engineer cereal crops to withstand phosphate, potassium, and iron deficiency, although less is known of the molecular mechanisms of GA in nutrient deficiency in grasses (Jia *et al.*, 2022). In support of this idea, GA levels are reduced under phosphate, potassium, and sulfur deficiency in maize (Peyami, 2004). Furthermore, GA promotes growth of maize roots under phosphate deficiency (Zhang *et al.*, 2019). In rice, GA also regulates iron uptake (B. Wang *et al.*, 2017), but it is not known if the mechanism of action is the same, as grasses use a different strategy for iron uptake compared with eudicots.

Conclusion

GA has pleiotropic effects on plants, with GA-deficient mutants in cereal grasses being dwarf and tillered along with additional phenotypes described in this review. These pleiotropic effects are mediated by the fact that DELLAs interact with hundreds of transcription factors and cause a myriad of responses, either activating or repressing transcription in the presence or absence of GA (Shani *et al.*, 2024). Furthermore, the GA signaling pathway intersects with many environmental and endogenous factors such as light, temperature, and nutrients (Bouré and Arnaud, 2023). Separation of these pleiotropic effects is required to enable manipulation of GA to be utilized in crop improvement to produce the ideal crop morphology or ideotype.

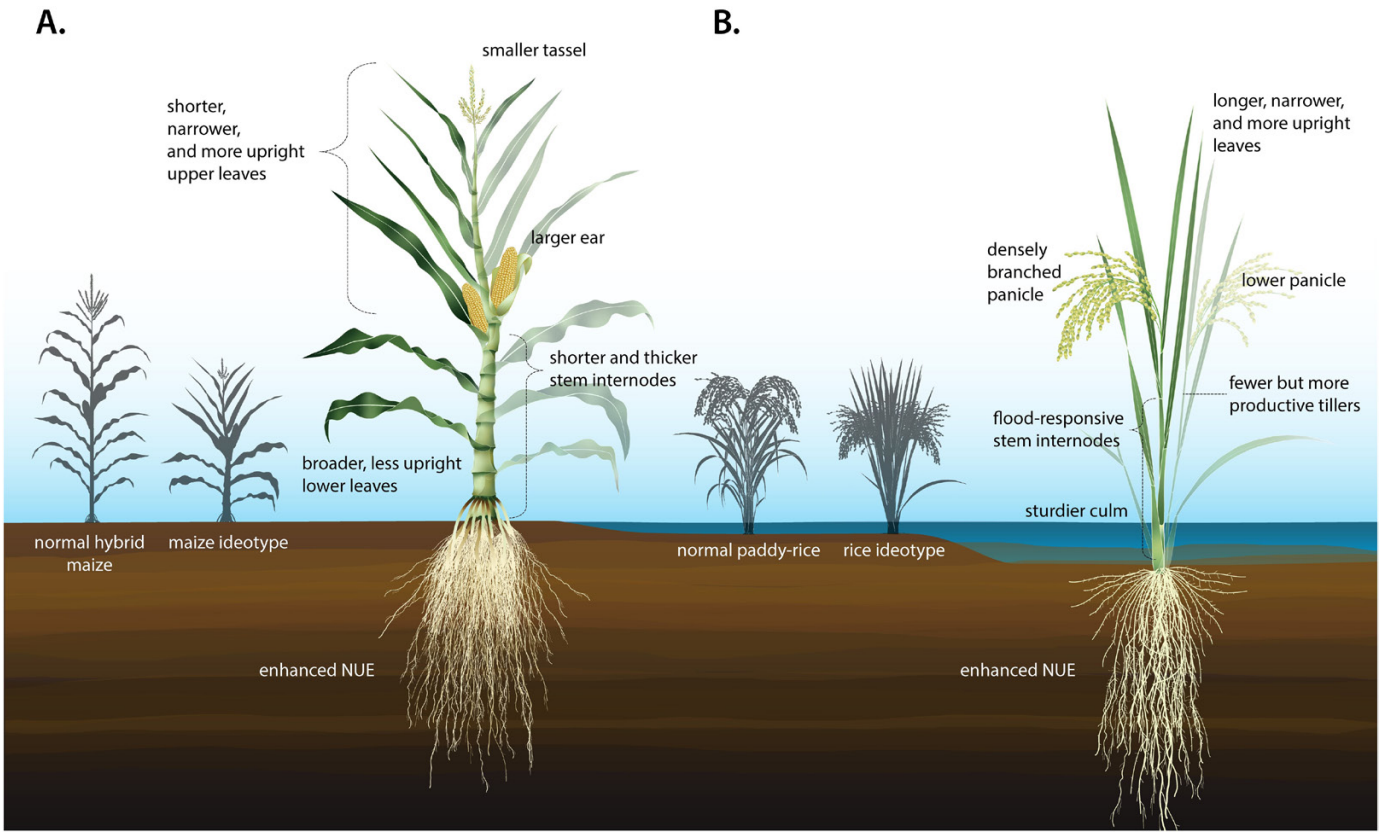

Fig. 2. Maize and rice ideotypes based on targeted regulation of the GA pathway. Each ideotype silhouette is compared with a typical breeding line. (A) The maize ideotype exhibits short stature with thicker shorter internodes and distinctive leaf traits, including broad lower leaves and shorter, narrower upper leaves. Reproductive traits are characterized by a smaller tassel and a larger ear. (B) The rice ideotype exhibits a lower, densely branched panicle with larger grains. It features a sturdier culm with flood-responsive stem internodes and longer, narrower, and more upright leaves. It produces fewer but more productive tillers promoting efficient nutrient allocation. Both maize and rice ideotypes possess root systems optimized for enhanced nutrient-use efficiency.

The maize ideotype would have short internodes and thick stems to resist lodging and stem rust, leaf morphology that maximizes canopy architecture and photosynthesis, reduced tassel size to reduce water use, increased ear size to optimize grain number, and root architecture to maximize water uptake and mineral use efficiency (Fig. 2A). Early in development, the ideal canopy architecture would be large wide right-angled leaves to cover the soil surface and reduce weed growth. As the plant matures, at around phase change, the optimal leaf architecture would be short, narrow, and upright to allow higher penetrance of light to the lower canopy and maximal light capture and photosynthesis. Shorter and narrower adult leaves provide thermal and hydraulic benefits, helping to minimize overheating damage and improve water-use efficiency (Baird *et al.*, 2021). Optimal root architecture would be deep (long roots) for uptake of water and nitrogen but also shallow (either by changing angle or increasing the number or length of lateral roots) for uptake of phosphorus (Kirschner *et al.*, 2024). Ideal wheat and rice ideotypes would be similar and would both need to increase panicle branch and seed number to increase yield (Fig. 2B). Increasing branch or spikelet number can be achieved through regulation of branching or meristem size (as described in McSteen and Kellogg, 2022). A strong culm to resist lodging and a lower panicle to allow greater light interception by upright leaves would be beneficial (Murchie and Burgess, 2022). Increasing tiller number would increase panicle number but with the trade-off of reduced seed set so increases in grain number would only increase yield if there were no negative impacts on grain quality and size. Therefore, maximizing photosynthesis by modifying canopy architecture as well as increasing grain fill will be critical. Below we describe some approaches that have been and could be undertaken to improve grass crop species architecture.

Broadly targeting GA metabolism genes to modify plant architecture has mostly failed to produce ideal phenotypes due to pleiotropic effects (Table 1). Natural variant alleles that have modified regulatory elements have been used to separate out these pleiotropic effects (Liu et al., 2023b). Examples in rice include natural variants that increased expression of *OsGRF4* (Li *et al.*, 2018), *OsMYB61* (Gao *et al.*, 2020), and *OsNGR5* (Wu *et al.*, 2020) or decreased expression of *OsD17* (Y. Wang et al., 2020) which resulted in higher yields and NUE as

discussed previously. Furthermore, stacking alleles of *OsGRF4* with *OsNGR5* (Wu *et al.*, 2020) or *OsMYB61* (Gao *et al.*, 2020) further increased yield. Natural variants in coding regions that affect the interaction with downstream components have also enabled separation of GA effects. For example, alleles of *TaRht-1* have been identified in wheat that maintained the semi-dwarf trait but had increased NUE (Liu *et al.*, 2022). Furthermore, a naturally occurring miRNA-resistant allele of *OsGRF4* increased NUE beyond increasing expression alone (Li *et al.*, 2018). Therefore, natural variation has been and will continue to be a rich source of alleles, for both gene identification and agricultural uses, in rice and could also be used in wheat and maize to separate out the pleiotropic effects of GA.

A more efficient mechanism to utilize the GA pathway without negative effects is to use tissue-specific promoters or tissue-specific gene family members. This method was effectively used by Paciorek *et al.* (2022) in the development of short maize varieties without impacts on reproductive development, by utilizing stem-specific promoters. Short maize varieties which withstand storms and high winds will be on the market soon, illustrating the utility of this approach (Stokstad, 2023). Other approaches include using synthetic promoters, for example a promoter–TALE system was used for tunable and tissue-specific expression of multiple genes in rice (Danila *et al.*, 2022), or a more targeted approach, such as the hormone-activated Cas9-based repressors (HACRs) demonstrated in Arabidopsis, could be used to fine-tune GA responses in different tissues and developmental stages (Khakhar *et al.*, 2018). Regulatory elements can be accurately modified by CRISPR editing to generate weak alleles with increased utility for agriculture. For example, in maize, CRISPR modification of the promoter of *Zm*CLE7 (a ligand for the CLV–WUS stem cell maintenance pathway) enabled a small increase in IM size in the ear, leading to higher kernel row number, without negative impacts on ear length (L. Liu *et al.*, 2021). Alternatively, regulators of the GA pathway could be modified to enable separation of GA effects. For example, CRISPR knockout of Os*MIR396E* and Os*MIR396F* (which negatively regulate *OsGRF4*) increased rice yield under nitrogen-deficient conditions (Zhang *et al.*, 2020c). Multiplex Cas9-based gene editing techniques can significantly accelerate the heritable modification of multiple regulators (Ellison *et al.*, 2020; M. Wang *et al.*, 2017).

Many of the context-specific responses of GA are mediated by the hundreds of transcription factors that interact with DELLA (Shani *et al.*, 2024). Identification of these transcription factors enables separation of GA pleiotropic effects. For example, overexpression of *OsGRF4* with the rice actin promoter led to increased NUE and yield without sacrificing the semi-dwarf phenotype in rice (Li *et al.*, 2018). Additional examples from Arabidopsis which could be investigated in grass species include DELLA and PIF interaction to coordinate light and GA response (Li *et al.*, 2016), as well as BZR and DELLA interactions to coordinate BR and GA interactions (Li *et al.*, 2012). In the future, using single-cell RNA-seq technologies to identify cell-specific gene expression patterns will allow for development of promoters to be utilized with CRISPR techniques to enable tissue-specific knockouts of GA regulators or downstream GA-responsive genes. While integrating the ideotype into mainstream breeding programs poses challenges, optimizing plant development through GA offers a promising roadmap for creating resilient grass crops.

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Conflict of interest

The authors declare no conflicts of interest.

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