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Maize plants and the brace roots that support them

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Summary

Brace roots are a unique but poorly understood set of organs found in some large cereal crops such as maize. These roots develop from aerial stem nodes and can remain aerial or grow into the ground. Despite their name, the function of these roots to brace the plant was only recently shown. In this article, I discuss the current understanding of brace root function and development, as well as the multitude of open questions that remain about these fascinating organs.

I. Introduction

Whether preventing a tree from falling onto your house or keeping a crop standing in the field, plant biomechanics is at the heart of plant health. In agriculture, plant mechanical failure is called lodging, and causes widespread losses in both crop quantity and quality (Flint-Garcia *et al.*, 2003; Rajkumara, 2008; Mizuno *et al.*, 2018; Tirado *et al.*, 2021; Hostetler *et al.*, 2022). Despite the negative economic impacts of crop lodging, lodging is a complex problem and simple solutions have been elusive. The Green Revolution provided one solution to lodging by decreasing the height of crop plants (e.g. rice and wheat), thus placing their center of gravity closer to the ground and increasing their mechanical resilience (Hedden, 2003). However, as the demand for high crop yields continues, mechanical constraints once again have lodging incidence on the rise (Fig. 1; Hirano *et al.*, 2017).

The plant height reduction of the Green Revolution primarily targeted small cereal crops, with larger cereal crops, such as maize, having continued to suffer significant losses from lodging (Tirado *et al.*, 2021; Hostetler *et al.*, 2022). Interestingly, the relationship between maize height and lodging is not straightforward, being shown to: have no correlation (Sharma & Carena, 2016), have a low positive correlation (Hostetler *et al.*, 2022) or function only as a secondary factor in models of lodging (Brune *et al.*, 2018). This weak and inconsistent relationship between plant height and lodging, as compared to other grains, is probably due to the difference in plant architecture of maize (side weight of an ear) as compared to other cereal crops (top weight of a panicle; Fig. 2a). However, other architectural traits that confound the relationship between plant height and lodging in maize are the presence of aboveground stem-borne roots, called brace roots (Fig. 2b; Hostetler *et al.*, 2022). When I first heard of these structural roots, I expected that their function was well defined – why else would

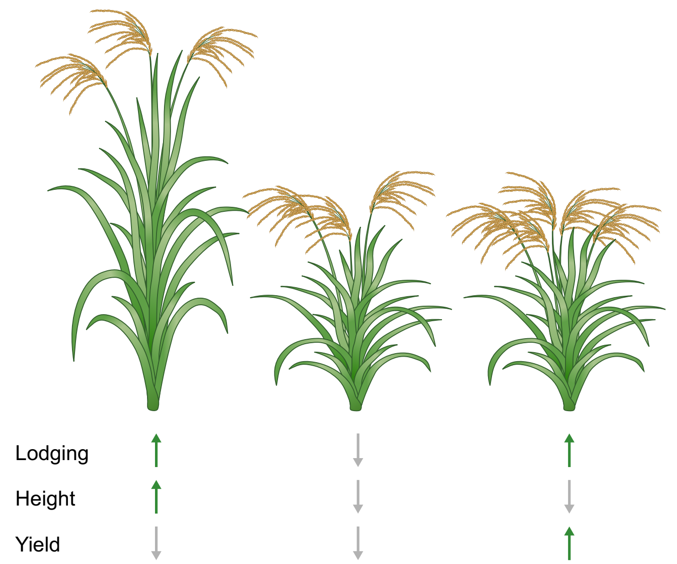

Fig. 1 Before the Green Revolution, the incidence of lodging was high for grain plants such as rice, due to their tall stature (left panel). The Green Revolution reduced plant height, which correspondingly reduced the incidence of lodging (middle panel). However, as yields continue to increase, lodging is again becoming a problem (right panel).

they be named 'brace' roots? Yet, after digging through the scientific literature I found scant evidence of their function, and the only data in support of their function were limited to correlations (Liu *et al*., 2012; Sharma & Carena, 2016; Shi *et al*., 2019). This led to the basis of my research – what is the function of brace roots?

II. What is a brace root? The importance of naming precision in root biology

Before we can get to the question of brace root function, we must first address the issue of naming since the terminology for brace roots can be confusing (Blizard & Sparks, 2020). I am often asked – What is the difference between a brace root, a prop root and a stilt root? Isn't a brace root just an adventitious root? Why are these roots named after their function instead of their developmental origin? I will briefly address these questions to provide context for the later discussion of brace root function.

Brace roots fall under the umbrella of adventitious roots, which refers to any root that develops from a nonroot origin. However, this term is all-encompassing and loses the nuances of different types of adventitious roots, for example whether the roots are part of endogenous development or caused by wounding, or whether the roots are forming in a eudicot or monocot plant (Steffens & Rasmussen, 2016). Brace roots are also known as nodal roots, based on their developmental origin from stem nodes. However, nodal roots can come from stem nodes below the soil (termed crown roots in cereals) or from above the soil. Adding to the complexity, some aboveground nodal roots stay aerial while others penetrate the soil. Historically, the term brace root was used only for those nodal roots that stayed aerial as these roots were anticipated to brace the plant if it fell over, but the term has shifted over time to encompass all aboveground nodal roots. The terms brace, prop and stilt root may have subtle nuances in their definition, but in practice these terms are used interchangeably. Unsurprisingly, this mixed terminology has led to a wealth of literature that is difficult to interpret due to a lack of precision in naming. For example, a paper describing results on nodal roots could refer to belowground nodal roots, aboveground nodal roots that enter the soil, aboveground nodal roots that remain aerial or any combination of the above. Roots are unique organs based on their development, function and environment, yet we fail to recognize these nuances when data are aggregated or root types are poorly named. I am not the first to highlight these issues, and I refer the reader to these excellent other papers for additional information on root nomenclature (Zobel & Waisel, 2010; Dubrovsky, 2022).

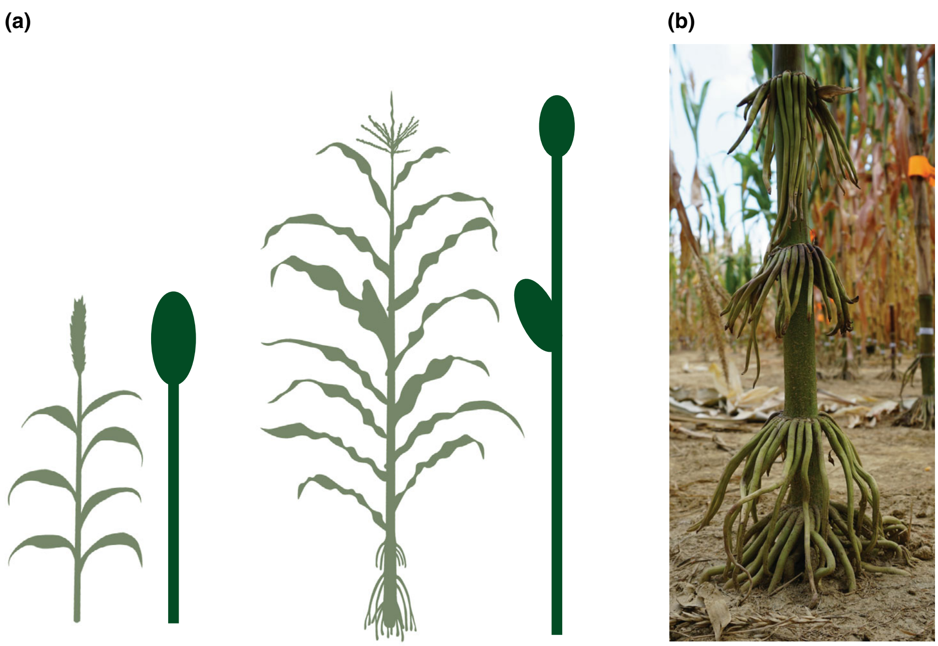

Fig. 2 (a) The mechanics of cereal crops varies due to the weight distribution of the grain. Most cereal crop mechanics are driven by the top weight of a panicle, which is illustrated here by a silhouette of wheat and the simplified weight distribution accompanying the illustration. By contrast, maize has a differential weight distribution with a smaller weight at the top from the tassel and a larger weight at the side from the ear, again illustrated with a silhouette alongside a simplified weight distribution. (b) Perhaps as a consequence of this larger and uneven distribution of weight, maize plants also have brace roots that originate from the stem above the soil.

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III. The function of brace roots

Throughout this article I use the term brace root to refer collectively to the aboveground nodal roots of maize. I will differentiate the brace roots that do not enter the soil by the designation of aerial brace roots (Fig. 2b). Now back to the main question – what is the function of brace roots? We recently showed that the brace roots that enter the soil directly support maize stalks (Fig. 3; Reneau *et al*., 2020; Hostetler *et al*., 2022; Obayes *et al*., 2022). We first showed this by flexing the maize stalk and measuring the bending resistance with brace roots intact. We then repeated this measurement after manually excising the brace roots that entered the soil (Reneau *et al*., 2020). With this approach we showed that the removal of brace roots reduced the bending resistance (i.e. made the stalks more flimsy), although the amount of reduction was variable by genotype (Hostetler *et al*., 2022). Thus, brace roots are acting to anchor (brace) the stalk and limit horizontal deflection. We further showed with this approach that brace root phenotypes (e.g. root angle, root width, number of roots) are important in predicting the contribution of brace roots to anchorage (Hostetler *et al*., 2022), which opens the door for the future optimization of brace root function in anchorage. To complement this initial study, we took a second approach of applying wind to plants and using digital image correlation to measure the fine-scale movement of these plants. We again measured movement with brace roots intact and excised (Obayes *et al*., 2022). This approach supported the finding that brace roots are anchoring the stalk to limit horizontal deflection. However, what we were surprised to find is that brace roots were also limiting the vertical deflection to prevent uplift (Obayes *et al*., 2022). This suggests that brace roots are functioning similar to a guy-line on a tent to provide anchorage and stability to the maize plants. This foundational work has established that brace roots do function to brace plants against external forces.

The naming of a brace root based on its mechanical function has led to the assumption that this is the only function of these roots. However, brace roots also probably play important roles in water and nutrient acquisition (Fig. 3). It has long been suggested that brace roots must play a key role in the uptake of water and nutrients based on the large size and number of the xylem elements (Hoppe *et al*., 1986; Wang *et al*., 1994; Yu *et al*., 2015). Indeed, brace roots alter their growth in response to nutrient availability (Trachsel *et al*., 2013), which further supports their probable role in resource acquisition. Direct measurements of brace root water or nutrient uptake have not been reported in the literature, and are a critical next step to understanding brace root function. Interestingly, one study recently showed that the aerial brace roots of local maize varieties from Mexico can associate with nitrogen-fixing bacteria, which is an unpredicted function of these roots (Fig. 3; Van Deynze *et al*., 2018).

The number of stem nodes that produce brace roots is linked to the phase of the shoot meristem (Hostetler *et al*., 2021). In other words, when the shoot is actively growing, brace roots continue to be produced from higher nodes, and brace roots from lower nodes continue to grow and enter the soil. This continued growth and development is probably associated with the need to meet the physiological demand of the growing plant. The positive

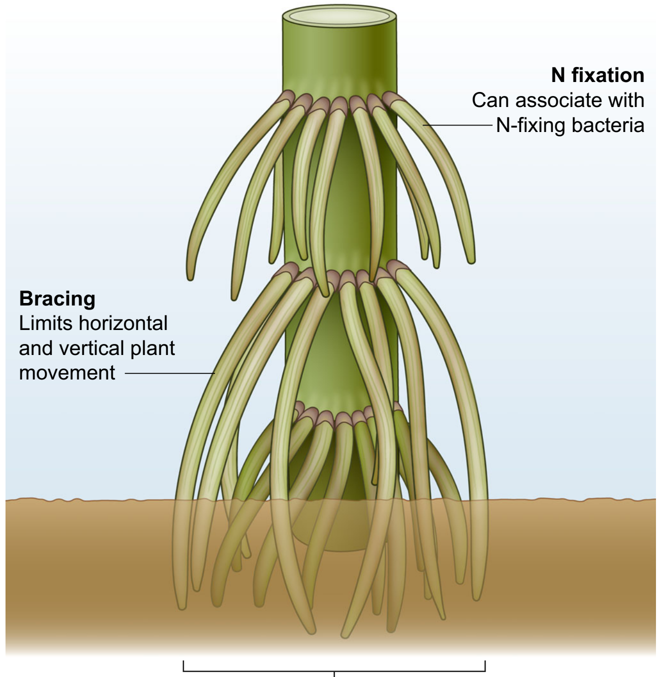

Fig. 3 The many functions of maize brace roots are just starting to be uncovered. The roots that are aerial–subterranean play a role in bracing the plant from perturbations. The roots that are aerial can associate with nitrogen (N)-fixing bacteria. The subterranean portion of brace roots probably also plays a key role in soil resource acquisition.

relationship between the production of stem-borne roots and plant growth may be conserved in other large monocot plants. Specifically, *Pandanus* is a monocot species that shows a strong correlation between plant height and the number of aerial stilt roots, although in this case it was hypothesized that the relationship is due to the increasing demand for structural support in taller plants rather than physiology (Rasmussen *et al*., 2018). Overall, there is unexplored potential for understanding brace root functions other than structural stability. As these brace root functions continue to be defined, a careful integration of different functions will be required to understand how these roots may be optimized for future crop production.

IV. The development of brace roots

Due to their physiological importance, untangling the mechanism of brace root development has proven more challenging than one might think. In a recent review, we mined the literature for genes that are known to affect brace root development and found that 14 of the 20 loci associated with brace root changes also had effects on the phase of the shoot meristem (Hostetler *et al*., 2021). Conversely, we collated published nodal root trait quantitative trait loci (QTL) data and identified an overlap with flowering time and phase change genes (Hostetler *et al*., 2021). The current challenge is to

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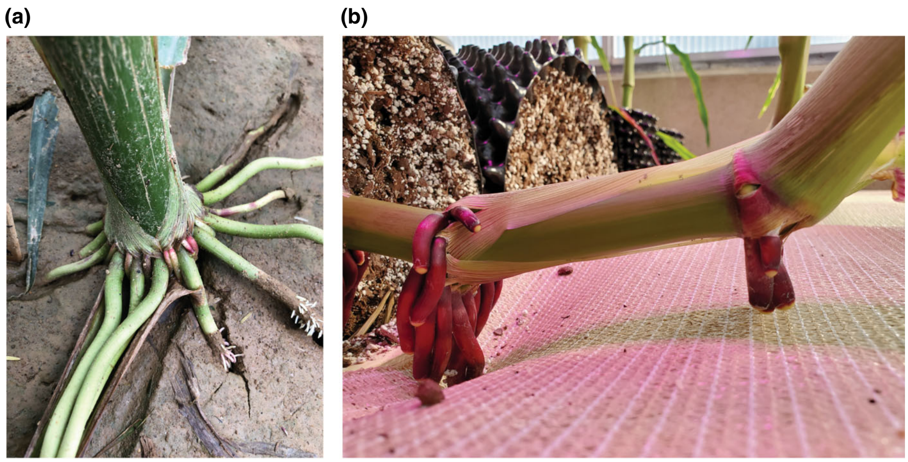

Fig. 4 (a) Variation in the regularity of brace root development has been observed with small-diameter roots developing at the upper junction of larger brace roots. (b) In response to being tipped over, brace roots emerge from the lower side of stem nodes.

separate brace root developmental defects that arise due to changes in whole plant physiology from changes in brace root development due to a direct regulation of root development. Of the maize mutants that impact brace root development independent of the shoot meristem phase, the most well defined is a LATERAL ORGAN BOUNDARIES DOMAIN (LBD) transcription factor mutant called *rootless concerning crown and seminal roots* (*rtcs*), which is defective in the initiation of seminal (seed-borne roots), crown (belowground nodal roots) and brace (aboveground nodal roots) roots (Hetz *et al.*, 1996). Interestingly, a recent article has shown that RTCS is part of a subclade of LBD proteins that play a conserved function in angiosperm shoot-borne root development (Omary *et al.*, 2022). Despite this seminal paper, there is still very little known about the mechanisms of brace root development.

The developmental program for the induction and initiation of brace roots is probably the same as crown roots and even other shoot-borne roots (Blizard & Sparks, 2020; Hostetler *et al.*, 2021). However, after initiation, brace roots begin to emerge and grow through the air. The developmental programs probably differ between crown roots, brace roots and other adventitious roots due to their different environments (e.g. soil vs air). The aerial growth environment affects brace root anatomy, with the outermost cell layer of the epidermis dying in the aerial portion of the root (Hoppe *et al.*, 1986). It remains unknown if the epidermis of all aerial brace roots dies, if there is an advantage to the epidermis dying and if something triggers the death (e.g. the presence or absence of a cue). Perhaps we can learn from other aerial roots. For example, the aerial feeder roots of the monocot *Rhodospatha oblongata* exhibit cell death of the exterior cell layers, but also death of the epidermis, exodermis and outer cortex layers (Filartiga *et al.*, 2021). These outermost layers are replaced by a lignified cork, which is a rare occurrence in monocots, and the acquisition of a green color (Filartiga *et al.*, 2021). In their study, the authors propose that these changes are adaptations to the aerial growth environment and improve water retention and provide small photosynthetic capacities (Filartiga *et al.*, 2021). By contrast, orchid aerial roots have a specialized outer layer called the velamen radicum, which consists of layers of dead cells that act to absorb water from the air (Hauber *et al.*, 2020). Perhaps these aerial root anatomical differences are due to the aerial–subterranean (*R. oblongata*) vs aerial-only (orchid) nature of the different types of aerial roots. To my knowledge there has been no comprehensive analysis of aerial root anatomy or function that would allow us to form hypotheses about the commonalities and differences among aerial root types.

Brace roots are also an interesting system to investigate general principles of organ development such as mechanical constraints and gravitropism. In terms of mechanical constraints, brace roots generally form side-by-side, completely filling the stalk circumference (Fig. 2b). By this definition, when comparing plants with the same stalk circumference, there are half as many brace roots when the diameter is $2x$ compared to brace roots with a diameter of $1x$. There are always exceptions, of course, and we have observed smaller brace roots forming at the upper junction of larger brace roots (Fig. 4a). It remains unclear if this is a genetic or environmental process, and whether this is related to the mechanical constraints of organ formation at the node.

Additionally, after root lodging brace roots will emerge from the side of the node closest to the soil up the length of the plant (Fig. 4b). The process that triggers this development is poorly defined – whether gravitropism, hydrotropism or thigmotropism. Interestingly, a recent article on *Brachypodium distachyon* suggests that the formation of roots from stem nodes after lodging is due to the physical interaction with the soil – thus suggesting a potential role for thigmotropisms in this process. As shown in Fig. 4(b), maize brace roots form in the absence of a physical interaction and the absence of water, thus suggesting a role of gravitropism. This further suggests divergence in the mechanism of lodging-induced root development in the grasses that has yet to be explored.

V. Conclusions

Brace roots, adventitious roots, aerial roots – each of these classifications is filled with scientific unknowns. While we have shown that brace roots function to anchor stalks, we still do not know if they are essential – in other words, could we reallocate resources to the belowground root system to achieve the same end? My inclination is no, that brace roots provide a unique function that cannot be achieved through the underground root system alone. Building computational models in which structural iterations of roots can be tested quickly should help address this question, which would be difficult through empirical studies alone. Looking to learn from other adventitious or aerial root systems, we find there is scattered research, which makes generalizations nearly impossible. Indeed, adventitious roots are often ignored completely in discussions of the importance of roots (Freschet *et al*., 2021).

In a changing climate, there is a pressing need for crops that can withstand external forces (e.g. wind) and remain productive. Achieving this goal is difficult, but understanding how brace roots contribute to mechanical resilience is the first step. Ultimately, there is a need to move beyond looking at single organs (e.g. roots or shoots) and establish more holistic approaches to understand whole plant mechanics and whole plant physiology.

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