nature portfolio

https://doi.org/10.1038/s41586-021-04247-y

Supplementary information

Monocotyledonous plants graft at the embryonic root–shoot interface

In the format provided by the authors and unedited

Supplementary information for

Monocotyledonous plants graft at the embryonic root-shoot interface

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Keywords: grafting, grasses, cereals, monocot, mesocotyl, vascular connection, wheat, rice, rootstock, scion, transcriptome

One sentence summary: Embryogenic tissues allow grafting within and between different species of monocotyledons.

Contents

1 Supplementary Notes

1.1 Graft compatibility within monocotyledons

Note 1 Grafting, the horticultural practice of fusing two plants so that they grow as one, has been used over thousands of years for crop improvement[1]. Across all plant taxa, most species within a genus are able to graft to each other, and in some cases species within a family can be grafted. Although rare, it is sometimes possible to graft species from different families. Examples of this exist in the Solanaceae, Cactaceae, and other families[16,24].

Some graft combinations (even self-grafts), however, are considered to be significantly challenging. Most notably are grafts within the monocotyledons, which comprise the second largest group of plants—representing approximately 20 % of all land plants (approximately 70,000 species)[44,45].

All seed plant (spermatophyte) clades (*e.g.*, eudicotyledons, magnoliids, basal angiosperms, and gymnosperms) apart from the monocotyledons are capable of grafting[46,47]. Successful grafting of monocotyledons is thought to be precluded because they lack vascular cambium tissue in their stems. The most common rationalization of this apparent loss is that the vascular anatomy of monocots became incompatible to grafting[48].

The vascular bundles of most spermatophytes feature vascular cambium, a meristematic tissue that provides cells for secondary xylem and phloem. Contact between the cambia of rootstock and scion is hypothesized to allow tissue fusion and vascular reconnection. Alignment of cambia is facilitated in dicotyledons (non-monocot angiosperms, a paraphyletic assemblage) by the arrangement of the vascular bundles in a ring at the periphery of the stem. Monocot vascular bundles do not contain cambium and are dispersed randomly across the stem, precluding both regenerative capacity and alignment[49].

Many recent research articles and university textbooks state grafting monocotyledons is not feasible, with some reports actually stating categorically that it is impossible. Some examples of these are listed below:

> *"**Monocots cannot be grafted**, moreover grafting of a monocot plant onto a dicotyledonous plant is also not possible. This is because vascular bundles in monocots are scattered and they lack cambium, which is a basic requirement for graft union formation. The parallel venation in the leaves of monocots indicates that the veins do not interconnect to each other like they do in dicots. Thus, it is the lack of vein connection in stem and leaves of monocot plants **which makes grafting in monocots an impossible task.**"*
>
> RASOOL *et al.*, 2020[50]

> *A key remaining technical problem is the **failure of grafting for monocotyledonous species** (the other class of flowering plants besides eudicots). Wheat, rice, and maize provide two-thirds of global human calories. The vasculature of these and other monocots differs from those of all other flowering plants, and grafts between monocots and eudicots may fail because of anatomical incompatibilities in reconnecting phloem and xylem vasculature... However, **monocot scions also fail to graft successfully to monocot rootstocks**. Understanding and overcoming this limitation is important to protect future global food security.*
>
> MCCANN, 2020[7]

> *"The ability to be grafted is not ubiquitous across taxa; dicotyledonous plants graft together easily, whereas **grafting is not possible in monocots** as they lack a vascular cambium."*
>
> GAUTIER *et al.*, 2019[51]

> *"Eudicots and gymnosperms, a group of nonflowering plants that includes pine trees, tend to form compatible grafts to themselves (i.e., autografts), but **monocots such as maize (Zea mays) or rice (Oryza sativa) typically cannot**."*
>
> GAUT *et al.*, 2019[52]

*"… in **monocots where regular grafting is impossible**."*

SIDOROV *et al.*, 2018[53]

*"Of the 25 most-produced fruit and nut crops, 20 may be grafted onto rootstocks, including grape and walnut (Juglans regia). The five crops not grafted are all **monocots where grafting is not possible**."*

MIGICOVSKY AND MYLES, 2017[54]

*"**The majority of homografts are compatible, with the exception of monocots**. Since the wound required for grafting disrupts the plant vascular system, reconnection of the vasculature is necessary to maintain normal water and nutrient transportation. Most monocots do not have vascular cambia, which may be a reason why grafting fails. This further suggests that vascular differentiation during wound healing is a prerequisite for successful grafting."*

WANG *et al.*, 2017[49]

*"Because monocots have vascular bundles and not continuous vascular cambia like dicots, **grafting is generally not possible in monocots** due to the impossibility of aligning the vascular bundles of monocots."*

HYDE *et al.*, 2015[55]

*"The significance of axillary bud outgrowth on the yield of major crops has been recognised for a long time, but this process is harder to study **in monocots because these plants are not amenable to grafting**… "*

KEBROM *et al.*, 2013[56]

*"**Plants lacking cambium (example: monocots such as corn) cannot be grafted**."*
*"Plants belonging to **monocots** (e.g., the grass family) lack cambium and **cannot be grafted**."*

KUMAR, 2011[57]

*"**Some taxonomic groups are extremely recalcitrant to grafting. The most significant of these are the monocots**, which include all grasses and cereals, and therefore many major crop and research model species. The fundamental problem in monocots appears to be their vascular anatomy which is unsuited to regeneration of successful vascular connections."*

TURNBULL, 2010[48]

*"But grafting has been limited by incompatibility between unrelated species and by the fact that **monocots are not amenable to grafting**."*

ZEEVAART, 2008[58]

*"**Successful grafting of monocots has generally been considered unlikely** due to the scattered nature of their vascular bundles and their lack of cambial tissue."*

WONGKAEW & FLETCHER, 2004[59]

"Grafting is usually restricted to dicotyledonous plants, since their vascular bundle arrangement and presence of a continuous cambium offer a greater degree of potential grafting success than with monocotyledonous species."

ANDREWS & MARQUEZ, 1993[60]

*"Tissue culture may make it possible to synthesize chimeras between graft incompatible plants and between **monocots, which with few exceptions, cannot be successfully grafted**."*

MARCOTRIGIANO & GOUIN, 1984[61]

*"This failure of cell division in response to wounding is probably the explanation for why most **monocots are difficult to graft**, since tissues of many monocots do not readily dedifferentiate to form callus."*

MOORE & WALKER, 1981[62]

1.2 Historical reports of monocotyledon grafting

Note 2 Compared with the numerous reports of dicotyledonous grafting that span many millennia, there are a small number of articles that claim monocotyledon grafting[4–6,63,64]. We were unaware any of these reports existed when we serendipitously discovered monocotyledons could be grafted at embryonic tissues (see Extended Data Fig. 1). A summary of these reports is provided next.

The botanist, Isidoro Calderini, reported attempts to graft monocotyledons in 1843 in Milan, Italy[4]. To our knowledge, this is the oldest report of monocotyledon grafting. Without disclosure of the underlying methods, Calderini claimed that attempts to graft rice (*Oryza sativa*) to *Panicum crus-galli* (now known as *Echinochloa crus-galli*) were successful. He also claimed the grafted plants had an increase in yield and even disease resistance. With our current knowledge, and at face value, this statement is consistent with the behavior of grafted dicotyledonous plants. However, he continues to say that these traits caused by the rootstock were transferred to the offspring of the scion when grown in 1845. This concept termed "graft transformation" was popular at the time. For example, graft chimera in *Citrus* sp. were common in Italy then which were falsely considered hybrids[65,66]. The study does not report the number of plants grafted, the percent fusion rate, nor provides any evidence of vascular connections.

Muzik and La Rue, 1952; 1954[5,63] reported grafting of large grasses: bamboo, sugarcane, guinea grass, and Merker grass. In this case, they provided some insight into the methods used, and termed the approach "intercalary meristem grafting". They reported an average of 3 % success, and therefore stated, "*It is doubtful that these techniques will soon find practical application, unless a greater percentage of success can be achieved*". Furthering this work, they grafted a few more species at internodes and provide microscopic evidence that monocotyledon grafts form vascular reconnections. They concluded that probably other species of monocotyledons will ultimately be grafted, though their process seemed to offer no economic use. This is most likely because their technique has some disadvantages: Adult plants are used that have moved from vegetative to reproductive growth and so only the central stem associated with this transition, late in the life-cycle, was suitable for grafting. As a consequence, the effect of the rootstock on the grafted plant may be insignificant. Moreover, intercalary meristems occur primarily in grasses, and are not a common feature among all monocotyledons.

Obolensky, 1960[6] described a seed dissection method for grafting the endosperm of winter wheat to spring wheat, and of wheat to maize. These involved endosperm transplantation which did not lead to true grafts, as the endosperm and embryo axis are not symplastically linked in monocotyledons. However, adding another step to this endosperm transplantation, Obolensky, 1960 applied dissection of the part of the embryo axis to graft these plants together. Although, the methods described by Obolensky seemingly appear similar to our approach, careful reading demonstrates that the outcomes differ substantially. The outcomes of this second method described by Obolensky (1960) likely lead to true grafts, however the resulting plants were comprised of the same scion source as rootstock, which were connected by tissue of a different accession. Thus, these plants had the shoot and root system of the same individual. This was acknowledged in the report as well, *"The grafted seedling represents herewith a complicated formation, the root and stalk being from one variety and the connecting meristematic tissue of another one."* Later this is mentioned again, "*Such grafts differ somewhat from an usual one, thus the terms stock and scion can hardly be applied to it.*" Moreover, Obolensky then goes onto claim that

“vegetative hybrids”, which had inherited characteristics from the interstock, were produced from the seeds of the shoot. This result may have been biased by the controversial concept of non-genetic based environmentally acquired inheritance (*i.e.*, "Lysenkoistic inheritance"), as it was officially illegal to disagree with Lysenkoistic inheritance in the former USSR, where Obolensky conducted this research, from 1948 until 1964[67,68].

Taken as a whole, previous reports of grafting within monocotyledons either lack convincing evidence or report very low grafting efficiencies. Interestingly, none of the methods above have become routine (or used at all, to our knowledge) in either agriculture or basic research. As such, none of these reports provide a method for practical application of grafting monocotyledons.

2 Description of Supplementary Information Items

2.1 Description of Supplementary Tables

Supplementary Table 1. Spreadsheet containing total numbers and rates for grafting all monocotyledons in this study. Individual sheets are labeled according to the source data used in each figure of this article.

Supplementary Table 2. Spreadsheet of FPKM values for all genes expressed in across the replicates of grafted, non-grafted, or wounded rice at one, three, five and seven days after grafting. Plots for any gene of interest can be displayed. Up to four plots can be displayed side-by-side for visual comparisons.

Supplementary Table 3. Spreadsheet of all differentially expressed genes between grafted and non-grafted rice, or grafted and wounded rice. Each sheet is separated according to each timepoint and up- or down-regulated genes.

Supplementary Table 4. Spreadsheet of all statistically significant gene ontology (GO) terms between grafted and non-grafted rice, or grafted and wounded rice. Each sheet is separated according to each timepoint and up- or down-regulated GO terms.

Supplementary Table 5. Spreadsheet of all statistically significant gene ontology (GO) terms between grafted rice at adjacent timepoints during graft union formation partly shown in the bar plots of Extended Data Figure 5a. Each sheet is separated according to each timepoint and up- or down-regulated GO terms.

Supplementary Table 6. Spreadsheet with gene ID information for the transcript abundance of cell expansion, cell elongation, cell cycle, and cell growth regulators in grafted rice shown in the heatmap plots of Extended Data Figure 5b.

Supplementary Table 7. Spreadsheet with gene ID information for the transcript abundance of differentially expressed genes within the AP2/ERF, NAC, MYB, DOF, and ARF transcription factor families between grafted and non-grafted rice shown in the heatmap plots of Extended Data Figure 6a.

Supplementary Table 8. Germination and growth protocols for monocotyledonous species grafted in Fig. 3b.

2.2 Description of Supplementary Videos

Supplementary Video 1. Attempted mechanical separation and dissection of a grafted wheat seedling. Realtime footage shows two pairs of forceps attempting to pull apart a grafted intra-specific wheat seedling on wet filter paper one week after grafting. No adhesive or physical attachment were used to aid grafting. The junction did not separate when force was applied in opposing directions from the rootstock and scion. The junction was then bisected laterally with a razor blade to show the fused tissue. This procedure was used to evaluate grafts throughout this study. The video footage was captured at 10X magnification with an iPhone SE mounted to a Zeiss Stemi 508 stereomicroscope and was edited using Blender (version 2.80).

Supplementary Video 2. Intra-specific cereal grafting. A Demonstration of embryonic shoot (plumule) and embryonic root (radicle) microdissection used to graft different individuals within five cereal species. Following this procedure, seeds are germinated into grafted plants. The video footage was captured on a Leica S8 APO stereomicroscope (Milton Keynes, UK) with a GT Vision GXCAM HICHROME-MET High Resolution Camera (Sudbury, UK) at 10X magnification, sped up 2.5 times, and was edited in Blender (version 2.80).

Supplementary Video 3. Inter-specific cereal grafting. A Demonstration of embryonic shoot (plumule) and embryonic root (radicle) microdissection used to graft different individuals among five cereal species. Following this procedure, seeds are germinated into grafted plants. The video footage was captured on a Leica S8 APO stereomicroscope (Milton Keynes, UK) with a GT Vision GXCAM HICHROME-MET High Resolution Camera (Sudbury, UK) at 10X magnification, sped up 2.5 times, and was edited in Blender (version 2.80).

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