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An Individual Based Model of Wound Closure in Plant Stems

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ABSTRACT Wound closure in plant stems (after either fire or mechanical damage) is a complex, multi-scale process that involves the formation of a callous tissue (callus lips) responsible for cell proliferation and overgrowth at the injury edges, resulting in coverage of the scarred tissue. Investigating such phenomena, it is difficult to discriminate between cell-specific growth responses, associated with physiological adaptations, and cell proliferation reactions emerging from specific cambium dynamics due to changes in mechanical constraints. In particular, the effects of cell–cell mechanical interactions on the wound closure process have never been investigated. To understand to what extent callus lip formation depends on the intra-tissue mechanical balance of forces, we built a simplified individual-based model (IBM) of cell division and differentiation in a generic woody tissue. Despite its simplified physiological assumptions, the model was capable to simulate callus hyperproliferation and wound healing as an emergent property of the mechanical interactions between individual cells. The model output suggests that the existence of a scar alone does constrain the growth trajectories of the remaining proliferating cells around the injury, thus resulting in the wound closure, ultimately engulfing the damaged tissue in the growing stem.

INDEX TERMS Cell mechanics, fire-scar, wound healing, wood anatomy, IBM, mathematical modelling.

I. INTRODUCTION

In plants, wounded regions deriving from either internal (e.g. leaves abscission) or external (e.g. mechanical damage or fire) processes (Fig. 1) may represent unprotected entry points for pathogens and insects, then it is not surprising that evolution favored wound isolation strategies [1]–[4]. In case of deep wounds sustained by the plant stem, the vascular cambium is often responsible for the production of a physicochemical barrier that will eventually isolate the wound [5]. The isolation process starts with a “first line” chemical defense at the site of the wound and then goes through the subsequent compartmentalization of the wounded area [6], [7]. One of the first events of compartmentalization is the almost immediate production of callus lips, i.e. chaotic callus tissue proliferating at the edges of the injury, in order to develop the so-called barrier zone [7]–[9]. Such tissue is

impervious to most pathogen species, because it is generally accompanied by lignification and suberization of cell walls, as well as the accumulation of occlusions of various chemical nature, thus slowing down the spread of microorganisms [6]–[10]. The cells produced by the vascular cambium around the wound will form a barrier of parenchymatous cells [5] which will restrict the development of decay and discoloring fungi in the newly formed tissues, making it a robust protective zone against the spread of microorganisms into the xylem formed after wounding [5], [6]. After its establishment, the barrier zone will act as a living boundary separating the infected wood from the new-formed healthy wood [8]. In fact, the callus lips will continue to proliferate until completely engulfing the wound and, in time, differentiating into vascular tissues [7].

When a tree trunk is wounded, the continuity of its vascular cambium is destroyed. As a consequence, tissue formation is disrupted in the injured segment of the tree, and high production of abnormal cells is expected the first year after

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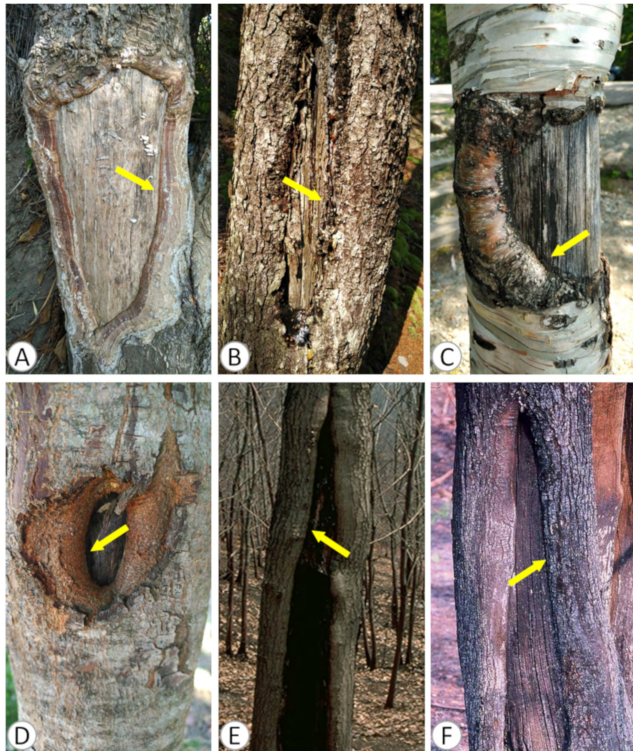


FIGURE 1. Examples of stem scars by mechanical damage and fire. Yellow arrows indicate the proliferating new woody tissues performing the wound closure. Mechanical damages in A: *Populus tremula*; B: *Pinus lambertiana*; C: *Betula pendula*; D: *Acer rubrum*. E and F: *Castanea sativa*, fire scars.

wounding since the wound hole must be sealed and the continuity of the vascular cambium re-established [5], [7]. As the vascular cambium is restored in the wounded area, standard xylem cell differentiation processes gradually resume, thus allowing for the eventual formation of normal xylem cells. The cells in the barrier zones differ from normal xylem cells in size, shape, relative proportion and orientation [6]. In particular, they present shortened cell length and constitute disoriented axial tissues [5]. Moreover, the formation of traumatic resin ducts is promoted in conifers, aiding chemical compartmentalization [11].

Scars in trees can remain evident for years before becoming fully embedded into the growing woody tissues; in case of fire-scars, their location within the trunk cross-section can be used for dating past wildfire occurrence using dendrochronological techniques (e.g. [12]). Forest fires contribute to shaping ecosystem biodiversity also because, at the individual level, fire-induced wounding affects the growth potential of trees through tissue reactions depending on several factors such as the relative distance from the scar, physiological and environmental constraints [9], [13].

Due to the complexity of the wound healing process, it is important to discriminate between the anatomical traits of the barrier determined by metabolic/molecular processes and those emerging from mechanical dynamics. On the one hand, it is well known that de-differentiation of vascular cells into

a callus is dependent on the balance between auxins and cytokinins and that many molecular pathways triggered by mechanical damage are also responsible for wood development [14]. On the other hand, to our knowledge, the role of cell-cell mechanical interactions over callus lips formation and wound closure has never been investigated.

Plant tissue growth behavior is known to be dependent on both cell-cell interactions and subcellular dynamics [15]. This dependence, together with the complexity of genetic networks underlying subcellular dynamics, makes difficult to design experimental tests on morphogenesis and stress response which are able to capture essential information related to the spatial dynamics (both molecular and mechanical) that result in the emergence of specific structural patterns.

Computer simulations developed in the last two decades have proven to be valuable additions to the biologist's toolbox, by helping disentangle the aforementioned multi-scale interactions and giving valuable insights over theoretical hypotheses [16], [17]. For example, mathematical modeling provided valuable insights into a wide degree of biological phenomena, like embryogenesis (e.g. [18]), microbial ecology (e.g. [19]), epidemiology (e.g. [20]) and vascular tissue differentiation in plants [21]–[23].

To understand to what extent “callus/wood lip” formation depends on the mechanical balance of forces, we simulated the process of wound closure in a tree using a cell-based modeling paradigm [16] which can describe processes at the inter- and intra-cellular scale, with specific emphasis on mechanical dynamics.

II. MODEL DESCRIPTION

We developed a simplified model of cell proliferation in a scarred trunk, adapting an existing tool named VirtualLeaf [24] to simulate wound closure. VirtualLeaf is a cell-based framework [16] for modeling plant tissue dynamics, describing cells as polygons delimited by walls, each considered as a separate entity shared among adjacent cells. Walls are assimilated to mechanical springs, and growth and mechanical interactions are computed by means of a Markovian relaxation algorithm, while cell division and differentiation processes are defined by individual-based logical rules [24].

The aim of the model is to simulate wound healing dynamics by taking into consideration only mechanical and geometrical rules. Indeed, we aimed to understand whether and to what extent the sole mechanical forces associated with cell proliferation does contribute to the formation of callus lips and to the determination of the engulfing behavior observed in cell proliferation around the wound. Molecular processes and possible interactions with physiological and biochemical processes associated with the chemical compartmentalization are not considered.

The presented model considers the process of differentiation among four cell types: vascular cambium, callus, xylem and cortex. For parsimony, all cell types that differentiate outside the vascular cambium (hereafter always referred to

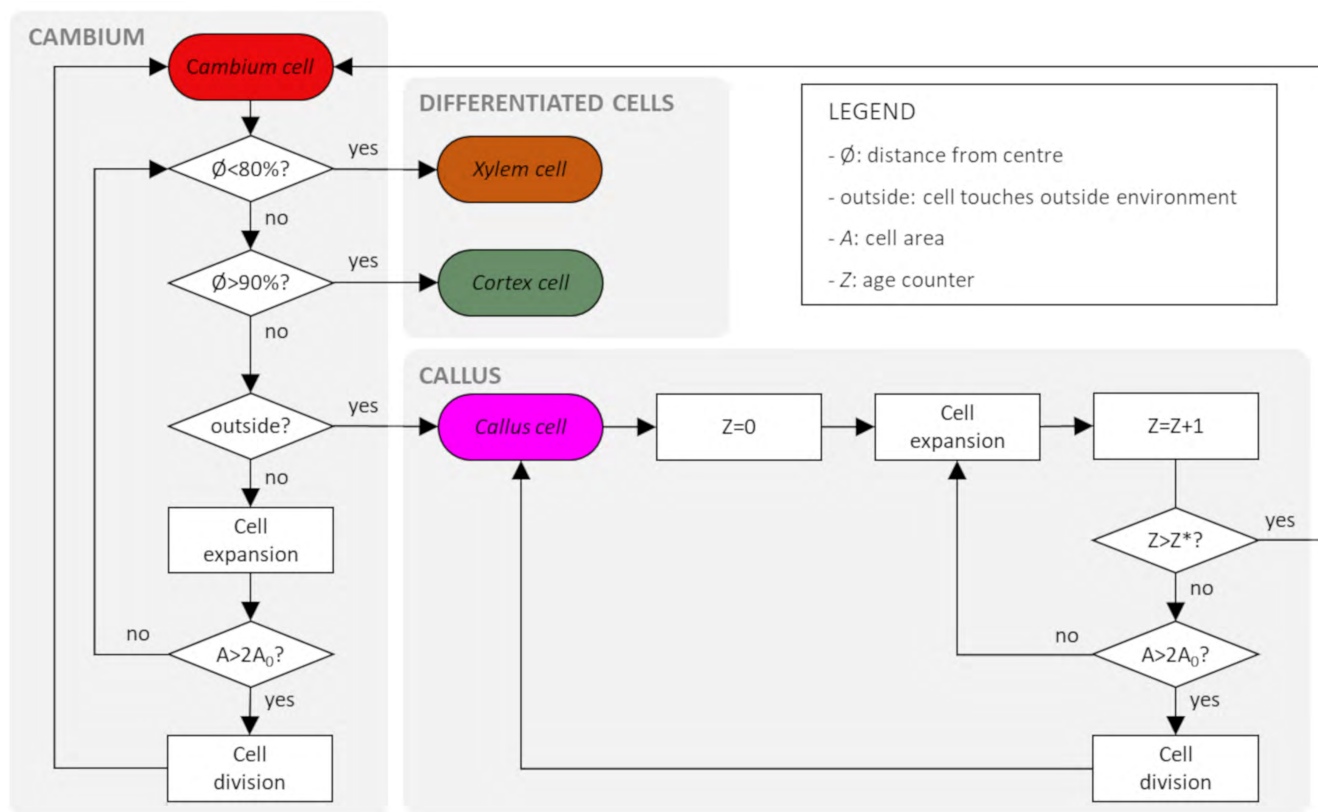


FIGURE 2. Flowchart of the model algorithm. The diagram shows the model working procedure for each individual cell where rectangles represent actions, rounded rectangles represent the different cell types while diamonds represent decisions based on logical rules.

as “cambium”), including phloem, cork cambium and phellem, are represented in the same group “cortex”. As well, we do not distinguish among different xylem cell-types.

We described cell enlargement in cambium and callus cells as the consequence of cell wall yielding due to water entering the cell at a constant rate. Cambium and callus cells can divide and will do so if their respective size (A) is double compared to the initial cell size (A_0).

In the model, after a division event, each cambium cell can differentiate into another cell type according to its spatial position. The model behavior is summarized as a flowchart in Figure 2. We assume that cambial cells dividing towards the inner part of the stem differentiate into xylem, while the ones that divide towards the outer part of the section become cortex cells. In modeling terms, this is simulated by checking the distance between the center of the cambium cell and the center of the cross-section of the stem. If the position (\emptyset) of the center of each cambial cell is below 80% of the total section radius, the cell differentiates into xylem, while if the distance is above 90% the cell expands and becomes cortex. If the position of the center is between 80 and 90% of the radius, the cell can encounter different destinies. More specifically, such a cambium cell becomes a callus cell if its cell wall is in contact with the outside environment, namely if it has at least one segment without contact with

neighboring cells. Alternatively, when such a cambium cell is completely surrounded by neighboring cells (i.e. no segments of its cell walls are in contact with the outside environment), it performs cell enlargement and eventually divides if its area A satisfies the condition $A > 2A_0$. Moreover, callus cells are assumed to re-differentiate into cambial cells if they can no longer divide due to mechanical constrains (i.e. wound closure is completed and the callus cells proliferating from the two edges of the wounded zone come in contact each other). Specifically, each callus cell has an internal counter (Z) that keeps track of the time passed since the last division; after each division, this counter is set to zero and increases by one unit at each simulation step. When Z is below the threshold value Z^* (arbitrarily set to 10 in the presented simulations), the cell either encounter expansion or division depending on its size. If the value of Z increases above the threshold value Z^* , i.e. if for mechanical constrains its area cannot reach the threshold value for division, the callus cells become cambium.

We applied our model to simulate the effect of wounding on a simplified version of a generic woody species. The presented simulation is set up with a stem cross-section, with distinct zones representing xylem, cambium, and cortex, scarred by the removal of a group of cells.

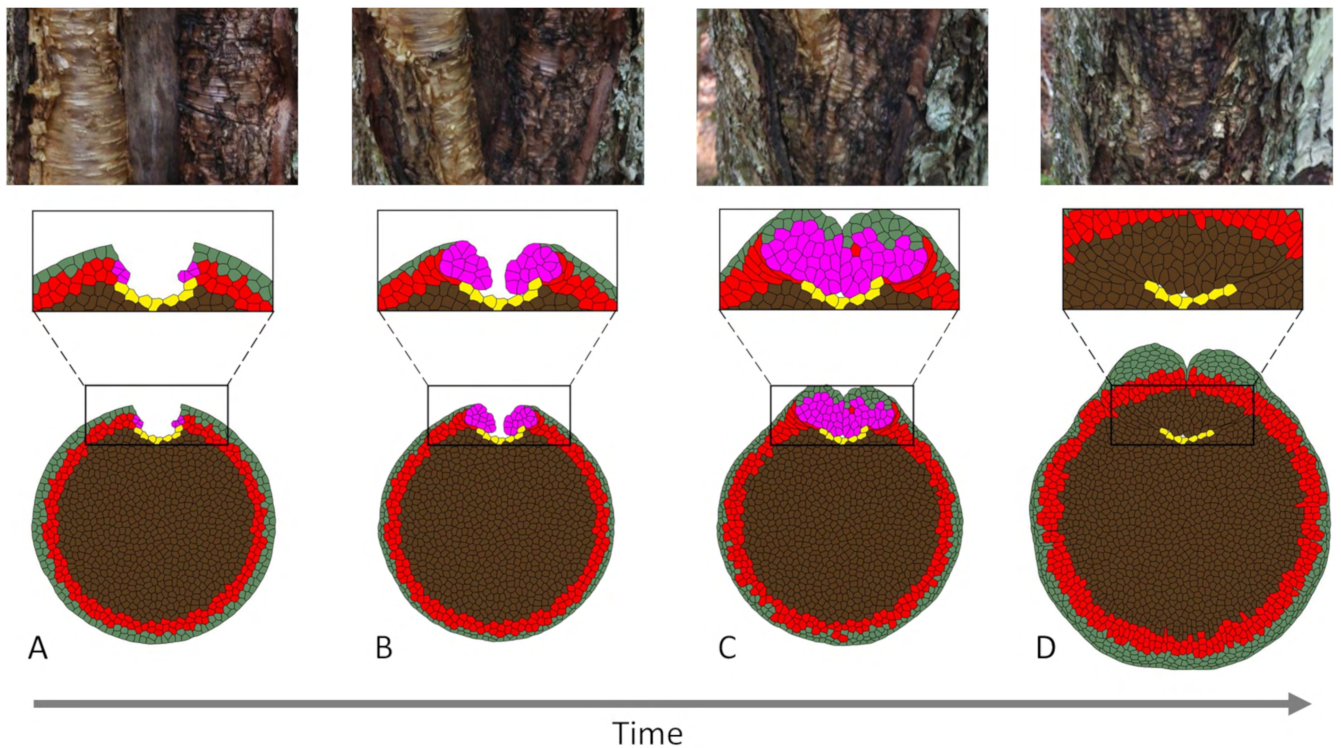


FIGURE 3. Model simulation of wound closure in a plant stem cross-section. A–D: From left to right, each column represents a snapshot in time of the simulation. The upper row presents pictures of a trunk wound to be compared with the evolution of the simulation. Yellow cells represent the wound; red cells are cambium; brown cells are xylem; green cells are cortex; magenta cells are callus.

III. RESULTS

Tissue wounding triggers the differentiation of cambial cells near the scar into hyper-proliferating callus cell (in magenta, Fig. 3A). Cells at the surface of wounded wood are marked in yellow to signal the zone as a potential entry point for pathogens.

In the first stages of wound healing, the callus lips proliferate towards the gap created by the dead/removed cells (Fig. 3B). As the simulation proceeds (Fig. 3B–C), the callus lips fill the wound, gradually engulfing the wounded wood and isolating it from the outside environment. After filling the gap, the callus cells start to have less volume to enlarge and divide with two main consequences: initially their proliferation becomes directed towards the outside forming a visible bulge and then, since some cells never reach the threshold area to divide, they de-differentiate into cambium and then to either xylem or cortex according to their spatial position (Fig. 3C–D). From this point on, the healthy portion of the tissue far from the wound continues to proliferate, increasing stem girth, while the zone surrounding the wound starts to bulge.

At the end of the simulation (Fig. 3D), the wound is completely surrounded by wood cells and isolated from the outside. The simulation results can be qualitatively compared to wood sections where a scar is visible (Fig. 4).

IV. DISCUSSION

Reaction to wounding in stems is a critical process in dendrochronology, wood technology, and wood ecology. Studying how wound healing emerges from cellular behavior is considered a daunting task, because of the multi-scale interactions involved and the underlying processes which are hard to study experimentally. Using computer models have been proved to be useful to elucidate complex multi-scale dynamics. Cell-based models have been successfully used to simulate tissues where mechanical properties were considered as key factors.

Here, we presented a simple mechanical model describing wound closure using a cell-based paradigm. It is fair to assume that the phase-mediated wound closure dynamics are the same regardless of the agent causing the wound [3]. In our simulated system, cell growth is a probabilistic process affected by the interplay between mechanical properties of the cell wall and internal pressure of the protoplast. The framework assumes that a cell enlarges until reaching a state where internal pressure (i.e. water potential) and wall tension balance each other, as per the turgor-driven hypothesis [25]. Such formulation is widely used in plant modeling because of its robustness and its simplicity. Of course, when multiple connected cells experience simultaneous growth, each one of them will also be affected by the mechanical pressure exerted by its neighbors. Therefore, the shape of a cell and its

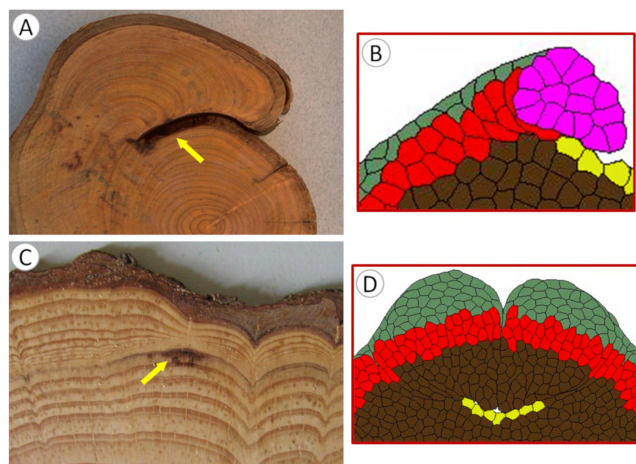


FIGURE 4. Comparisons between real scarred wood cross-sections with simulations. **A and B:** Single lobe of new wood growing over the scar on one side. **C and D:** completely covered wound. Yellow arrows indicate the fire scars.

growth rate will be influenced by the mechanical properties of both the cell itself and the cells surrounding it. Neighbors' influence means that cells will exhibit different emergent behaviors based on their relative position within the tissue.

The presented simulations allowed to build images of a wounded stem in successive phases of the wound-closure process that are not far from what can be truly observed in scarred plants. In the process of wood compartmentalization after stem wounding, a callus tissue is formed and cell overgrowth at the edges of the injured zone promptly occurs to reduce the exposed area up to the complete closure of the wound [8]. In our simulation, two distinct phases could be observed: a recovery phase (Fig. 3B-C) associated to the mechanical dynamics described above with progressive coverage of the wounded region by newly formed callus cells; and a stabilization phase (Fig. 3D), when the wounded zone is fully covered and the new cambium starts to contribute again to secondary growth in the same area.

During the recovery phase, the hyper-proliferating callus will slowly fill the void left by the scarring, because the simultaneous action of autonomous and non-autonomous cell interactions will constrain cell growth toward the now-free wound space (Fig. 3B-C). The proliferating callus exerts mechanical tension over the cambial cells that surround it, causing the cambium in that zone to stretch. In the Supplementary Video 1 (<http://wpage.unina.it/giannino/PlantWound/>), it is possible to appreciate how the proliferation direction of the lips change, with the callus starting to proliferate along the radius. Once the callus lips come in contact and start push against each other, the mechanical forces are redistributed thus modifying the constraint on the growth directions. Such change substantially modifies the tissue growth inverting the proliferation direction, as the callus starts to form a bulge toward the tissue boundary, and slows down their expansion, leading to the re-differentiation of the callus cells (as per model assumption). The stabilization phase then comes as an

emergent of the mechanical interactions between the dividing callus cells. At the end of the recovery phase (Fig. 3C), it is possible to observe a small gap remaining between the callus tissue and the xylem. This space will be filled neither by the xylem (that is static) nor by the callus (because of the limited degree of cell deformability associated with this model). In the real system, the high pressure between the lips, together with the production of occluding materials (e.g. gums, resin), is supposed to seal the wound.

The similarity between our simulation and a real scar (Fig. 4) shows how the chosen modeling approach is able to reproduce the selected biological phenomenon, despite the simplification of the model assumptions. In fact, the simulation shows how simple mechanical dynamics are sufficient to capture the main features of the wound closure process. Even in the presented simplified case, the time dynamics of the simulated tissue show that the existence of a scar causes an alteration of the growth trajectories of the cells proliferating around the injury, that is engulfed in the tissue as a consequence of this alteration.

The presented model simulations clearly show that mechanical interactions have a pivotal role in wound closure dynamics. Even though the presented model has no explicit time units and thus does not allow comparing simulated timings of wound closure with real data, it is possible to analyse the relative effect of parameters related to timing on the model behavior.

In particular, regarding the temporal dynamics of wound closure, the enlargement rate of cells and the division threshold are the two most relevant parameters.

First, model analysis shows that the enlargement rate obviously positively correlates with the velocity of wound closure (simulations not shown). This is consistent with a previous study by [26] reporting a clear correlation of speed of wound closure and growth of trunk diameter in several species. Beside the inter-specific differences, the author also pointed out the occurrence of high variability in the intra-specific observed rates. This suggests that the mechanical constrains driving callus formation might be more relevant than the specific growth rate of the cells. In fact, assuming that individuals of the same species growing in the same environment have the same growth potential, we can infer that the stochastic variability of the trunk shape and the specific position of the damage are what predominantly influences the wound closure rate.

On the other hand, changes of the cell division threshold parameter do not produce significant effect on the timing of wound closure when tested within a realistic range of variation, showing a robustness of the model dynamic behavior in respect to this parameter.

More studies, both with experimental and simulation approaches, are needed to better disentangle the complex cell-cell interactions that drive callus formation and wound closure. Once implemented in a hybrid system [17] adding a module of intracellular (metabolic and molecular) processes (e.g. [22]), it could become a powerful tool to study

and understand the complex dynamics behind different patterns of cambial activity, under both ordinary and traumatic conditions.

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