When families in the math group used the app the least (Bin 0), children with high-math-anxious parents grew significantly less in math achievement by the end of the school year relative to children with low-math-anxious parents ($\beta_{20} = -7.94, t = -2.42, P = 0.02$) (Fig. 2 and Model SS). Strikingly, using the math app mitigated this negative relation between parents’ math anxiety and children’s math achievement. When families used the app on average once a week or more, children with high-math-anxious parents made gains in math achievement by the end of the school year that did not significantly differ from those made by children with low-math-anxious parents (Bin 1: $\beta_{20} = 3.44, t = 1.53, P = 0.13$; Bin 2+: $\beta_{20} = -3.60, t = -1.21, P = 0.23$) (Model SS).

Thus, when parents and children interact about math story problems—even as little as once a week—children show increased math achievement by the end of the school year. The benefits of occasional math-related interactions are especially apparent for children whose parents are anxious about math. By providing an engaging way for math-anxious parents to share math with their children, the math app may help cut the link between parents’ high math anxiety and children’s low math achievement (6).

The current findings are of particular relevance in view of the multimillion-dollar educational app market (19). Scant research exists on the effectiveness of apps marketed as educational (20), and the research that has been done does not always find benefits for children’s learning. Use of enhanced e-books that target literacy can actually be detrimental to children’s basic reading comprehension when they contain distracting sounds and animations (21). The math app used here has several specific features that may have contributed to its effectiveness. First, it was basic in nature (very few sounds, animations, or videos) to avoid distracting elements. Second, it was designed to align with the goals of the Common Core Standards at varying grade levels. Third, it was designed to be used by parents and children together, based on the known importance of early parental input, and specifically parent math talk, for children’s achievement. The app may give parents—especially high-math-anxious parents or even parents with less skill or interest in engaging in math—more and better ways to talk to their children about math not only during app usage but also in other everyday interactions. We have shown that using this math app enhances the likelihood that children will succeed in math, which is essential for academic success and for the robustness of the science, technology, engineering, and math pipeline.

REFERENCES AND NOTES

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PLANT SCIENCE
Visualization of cellulose synthases in Arabidopsis secondary cell walls
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Cellulose biosynthesis in plant secondary cell walls forms the basis of vascular development in land plants, with xylem tissues constituting the vast majority of terrestrial biomass. We used plant lines that contained an inducible master transcription factor controlling xylem cell fate to quantitatively image fluorescently tagged cellulose synthase enzymes during cellulose deposition in living protoxylem cells. The formation of secondary cell wall thickenings was associated with a redistribution and enrichment of CESAs-containing cellulose synthase complexes (CSCs) into narrow membrane domains. The velocities of secondary cell wall–specific CSCs were faster than those of primary cell wall CSCs during abundant cellulose production. Dynamic intracellular trafficking of endomembranes in combination with increased velocity and high density of CSCs, enables cellulose to be synthesized rapidly in secondary cell walls.

Cellulose, the most abundant biopolymer on Earth, is a key biomechanical component of land plants and a valuable natural resource. Cellulose in the primary cell wall, which is laid down during plant growth, determines plant shape (1). However, the bulk of terrestrial biomass is composed of the cellulose in secondary cell walls, which are laid down after the cell has stopped growing to strengthen plant vasculature and structure (2). The strength of these walls is derived from the organization of cellulose microfibrils, which, relative to primary cell walls, possess cellulose with a higher degree of polymerization, increased microfibril crystalinity, and a higher degree of microfibril organization (2, 3).

Cellulose is synthesized at the plasma membrane by cellulose synthase (CESA) enzymes that are organized in multiprotein cellulose synthase complexes (CSCs) (4). In Arabidopsis thaliana, 10 CESA isoforms exist, with CESAl, CESAl3, and CESAl6 involved in primary cell wall synthesis...
(5, 6), and CESA4, CESA7, and CESA8 required for secondary cell wall production (7). At least three distinct isoforms are required for normal cellulose production (5–7). Live-cell imaging of primary cell wall CSCs clearly shows CESA velocity and distribution at the plasma membrane as well as intracellular trafficking (8–10). Secondary cell walls are produced in vasculature and fibers deep within plant tissues, limiting the resolution of live-cell imaging (11, 12). Here, we visualized cellulose synthesis in secondary cell walls using fluorescently tagged CESA7 in a unique system where live epidermal cells are induced to form secondary cell walls ectopically (13).

Arabidopsis plants were engineered to constitutively express a transcription factor controlling xylem tracheary element cell fate, VASCULAR NAC-DOMAIN7, fused to a glucocorticoid receptor (VND7::GR). When these plants are exposed to a glucocorticoid hormone such as dexamethasone (13), after induction, the secondary cell wall cellulose synthase genes were transcriptionally up-regulated by a factor of 1.5 to 3.0, whereas primary cell wall-related cellulose synthase genes were transcriptionally unaffected (table S1). Although it is not possible to know whether the VND7::GR levels in these plants are comparable to endogenous VND7 in protoxylem tracheary elements, the induced cells have features typical of developing protoxylem, such as secondary cell wall thickenings alternating with primary cell wall domains, in spiral or annular patterns. To investigate cellulose deposition, we crossed plants carrying the VND7::GR induction system with cesa7/irx3-4 null mutants complemented with a functional fluorescently tagged CESA7 (YFP::CESA7) driven by its native promoter (fig. S1). Fluorescent signal from CSCs was detectable in induced epidermal cells, although identification of individual plasma membrane–localized CSCs was possible only with the use of an optimized spinning disk confocal imaging system (optimization parameters are described in fig. S2).

Use of this optimized system permitted the visualization of discrete YFP::CESA7 particles in the plasma membrane of induced protoxylem tracheary elements (Fig. 1). Their linear movement at slow and steady velocities meets the criterion of actively synthesizing CSCs (movie S1) (8–10, 14). CSCs moved in a bidirectional fashion along plasma membrane domains underlying secondary cell wall thickenings. Relative to labeled primary cell wall CSCs (8–10), secondary cell wall CSCs showed a higher density at the plasma membrane, with overlapping signals from individual particles largely indistinguishable over extended areas (Fig. 1, B and C, and fig. S3). Moreover, CSC distribution changed over the course of secondary cell wall development. Early in development, the edges of forming secondary cell walls are revealed as uniform signal in subcortical optical sections. YFP::CESA7–labeled Golgi (arrowhead) are visible because of the increased depth of imaging through secondary cell wall thickenings. (D) TEM micrographs highlight plasma membrane (PM) curvature over secondary cell walls (2CW), lined by cortical microtubule (MT) bundles. Scale bars, 10 µm [(A) to (C)], 500 nm (D).
CESA7 signal was observed across the plane of the plasma membrane on tracks defined by bands of microtubules forming in the cell cortex (Fig. 1A, merged image, and table S2). As secondary cell wall synthesis progressed (Fig. 1B), CESA7 signal was enriched in regions of the plasma membrane associated with tight bundles of microtubules (Fig. 1B and table S2) (15). In late secondary cell wall development (Fig. 1C), the YFP::CESA7 signal was apparent as U-shaped plasma membrane furrows curving around the secondary cell wall thickenings. The majority of the CESA7 signal was evenly distributed and restricted to these curved domains (Fig. 1C, inset). When VND7::GR-induced cells were cryofixed and examined by transmission electron microscopy (TEM), tangential sections along the cell surface revealed the curved domain of plasma membrane around secondary cell walls, as well as their associated microtubules in the cell cortex (Fig. 1D).

The rate of cell wall deposition is the consequence of both the concentration of CSCs and the rate at which each CSC produces cellulose. The importance of the restriction of the CSCs to the curved membrane domains is that cellulose deposition is concentrated in a discrete area of intense production. Such concentration may help to explain why secondary cell walls are synthesized more quickly than primary cell walls (16).

With live-cell imaging, we measured deposition rates of individual CSCs. We assumed that CSC movement through the plasma membrane is a function of glucan chain biosynthesis and its subsequent crystallization into cellulose microfibrils, such that faster CSC velocities would reflect faster rates of synthesis (3, 17). To facilitate this comparison, we quantified the velocities of YFP::CESA7–labeled CSCs at the cell membrane and primary cell wall CSCs (GFP::CESA3) (9, 10) under identical growth and imaging conditions, alternating data collection between plant lines in an imaging session to control for possible environmental effects (Fig. 2). Time projections over a 5-min data collection period showed CSC tracks across the plasma membrane (Fig. 2, A and B). These tracks defined lines for kymograph analysis of particle velocity. In primary cell wall CSC kymographs, the tracks of each GFP::CESA3 were distinct (Fig. 2A). The tracks of CESA7 were more difficult to discern because of their higher density (Fig. 2B and fig. S3). The slope of the lines in the kymograph (Fig. 2, A and B, arrows) represents the CSC velocities, with steeper slopes indicating faster CSC movement (more displacement on the spatial axis). The average velocity of CESA7-containing CSCs producing secondary cell walls was 265 ± 75 nm/min [mean ± SD, n = 36 cells (40 CSCs per cell) from 12 plants] (Fig. 2D). Velocity changed over the course of protoxylem differentiation, which was divided into stages according to microtubule banding and secondary cell wall features. Average CESA7 velocity was 280 ± 29 nm/min during early development, 327 ± 37 nm/min during mid-development, and 187 ± 36 nm/min during late development (Fig. 2E). In contrast, primary cell wall CESA3-containing CSCs displayed an average velocity of 231 ± 34 nm/min (n = 12; 4 cells from 4 plants; Fig. 2C). Analysis of variance (ANOVA) identified significant variation among conditions (F3,44 = 38.7, P < 2.133 × 10^{-12}). Post hoc Tukey’s pairwise comparison tests indicated that primary cell wall CSC velocity was significantly different from all stages of secondary cell wall development. Secondary cell wall CSC velocity did not differ significantly between early and mid-development, but both were significantly different from late development (P < 0.01; Fig. 2E). This illustrates that

**Fig. 2.** Secondary cell wall CSCs have a higher velocity than primary cell wall CSCs during peak cellulose deposition. (A and B) CSC tracks in single frames and time projections for primary cell wall (A) and secondary cell wall (B) visualized using GFP::CESA3 and YFP::CESA7, respectively. Kymographs sampled along the yellow lines show CSC trajectories over time, from which CSC velocity was calculated. Scale bars, 10 μm. (C and D) Histograms of GFP::CESA3 (C) and YFP::CESA7 (D) velocities calculated from kymograph analysis. (E) Box plot of CSC velocities across stages of xylem cell development. Means with different letters represent statistically significant differences (Tukey’s pairwise comparison, P < 0.01). For each developmental stage, 480 CSC velocities were measured from 12 cells in four plants. In (D), 1440 velocities were pooled from all developmental stages. In (E), velocities were averaged for each cell before analysis.
secondary cell wall CSCs move more rapidly in the plane of the membrane during peak secondary cell wall synthesis, then slow as the cell nears maturity, prior to programmed cell death. Thus, both the high density and high velocity of synthesis by individual CSCs contribute to rapid cell wall synthesis during secondary cell wall formation.

Previous studies examining fluorescently tagged secondary cell wall CESAs, visualized through layers of tissue to the center of the root, could not resolve CSCs at the plasma membrane, although these authors made contributions to understanding the trafficking of CSCs in intracellular endomembranes (11, 12). The authors described “CESA7-containing organelles” actively streaming through the cytoplasm and pausing at domains of secondary cell wall deposition (12). However, because of technical limitations, the nature of the organelles was not clear. In the induced protostele xylem element system of the VND7::GR lines, we found that the CESA7-containing organelles were both small CESA-containing compartments (SmaCCs) (10) and Golgi (Fig. 3; red arrows in movie S2). SmaCCs were both Golgi-independent SmaCCs (blue arrows in movie S3) and Golgi-associated SmaCCs (yellow arrows), and their behaviors were most easily identified using fluorescence recovery after photobleaching (FRAP) (Fig. 3, A and B, and movies S3 and S4). After bleaching the bright plasma membrane–localized CSC signal, both SmaCCs and Golgi repopulated the underlying cytoplasm (Fig. 3A). Golgi and SmaCCs often moved in a coordinated fashion (movie S3; 40 ± 15% of SmaCCs were associated with Golgi, n = 3 cells), and frequently Golgi and associated SmaCCs would pause (ranging from 15 s to 3 min) at secondary cell wall domains, consistent with previous observations (12). When the Golgi moved on, a CSC signal would persist and split within 70 ± 20 s (n = 8 events; Fig. 3B and movie S4). This stationary signal followed by slow steady movement (280 ± 30 nm/min, n = 16 particles) fits the criterion for an insertion event of multiple CSCs into the plasma membrane, as defined for primary cell wall CSCs (10). We were unable to quantify the number of insertion events at secondary cell wall domains. However, it was

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**Fig. 3. Golgi and SmaCCs densely populate and rapidly deliver CSCs to domains of secondary cell wall formation.** (A) Fluorescence recovery after photobleaching (FRAP) of YFP::CESA7 in the boxed area, overlying a secondary cell wall thickening. Abundant Golgi-independent SmaCCs (red and blue arrows) rapidly repopulate bleached regions. Additionally, Golgi (arrowhead) and closely associated SmaCCs (yellow arrows) can be seen moving from one secondary cell wall band and pausing at another. (B) FRAP and kymograph analyses demonstrating insertion at the plasma membrane of at least two YFP::CESA7-labeled CSCs from a SmaCC (yellow arrow). After the Golgi (arrowhead) moves away, the signal from the SmaCC splits into two distinct punctae with steady velocities (red and orange arrows). (C) TEM micrographs of cytoplasm around secondary cell walls showing a diversity of closely associated vesicles. Trans-Golgi networks (arrows), secretory vesicle clusters (arrowheads), and electron-lucent vesicles (asterisks) are indicated. Scale bars, 5 μm (A), 2.5 μm (B), 500 nm (C).
apparent that CSC insertion events were restricted to thickenings (in 12 photobleached regions of $10 \mu m^2$ in six cells, no CSC inserted in plasma membrane regions between thickenings), hence the targeting of these events is tightly limited to secondary cell wall domains. TEM of induced developing protoxylem cells revealed several vesicle populations associated with Golgi that may carry CSCs, including trans-Golgi networks, secretory vesicle clusters, and larger vesicles lacking internal content (Fig. 3C). High-resolution live-cell imaging of CESA7-containing organelles demonstrates the dynamic exchange of CSCs among the Golgi, SmaCCs, and the plasma membrane associated with microtubule bands.

Previous studies of primary cell wall CSCs showed that disruption of cortical microtubules did not affect the rate of insertion of CSCs into the plasma membrane (10), although CSC distribution over the membrane was transiently disorganized (9, 10). To test the effect of loss of microtubule bundles on secondary cell wall CSC insertion events, we measured the velocities and trajectories of CESA7-containing CSCs in the VND7::GR induction system after oryzalin treatment. In contrast to the dimethyl sulfoxide (DMSO) control (Fig. 4A), where the tracks of CSCs were restricted to the secondary cell wall bands, the plasma membrane–localized CSCs in oryzalin-treated cells were disorganized (Fig. 4A and movie S5). These CSC clusters were similar to the “swarms” of primary cell wall CSCs described after treatment with an intermediate (8) but not higher (18) concentration of oryzalin. In the absence of microtubule bands, the velocity of secondary cell wall CSCs at the plasma membrane was unaffected (313 ± 41 nm/min for control, 324 ± 33 nm/min for oryzalin-treated; n = 12 cells from 4 plants for each; Fig. 4B) while CSC insertion events continued (Fig. 4C and movie S6). Oryzalin treatment also did not affect the total cellulose content produced by the differentiating cells (fig. S4). In contrast, inhibiting cellulose biosynthesis with 2,6-dichlorobenzonitrile (DCB) treatment influenced only cellulose deposition, while microtubule formation was unaffected (fig. S5). Therefore, the banded microtubule pattern is independent from secondary cell wall formation, and although microtubules are important for the overall secondary cell wall banding pattern, they are not necessary for CSC delivery from endomembranes to the plasma membrane, nor for reaching peak CSC velocity.

We attribute the rapid formation of the secondary cell wall to both increased concentration and velocity of CSCs at the plasma membrane. Secondary cell wall CSCs are delivered to these domains by populations of Golgi-associated and independent SmaCCs. These insertion events are associated with, but do not require, microtubule bundles underlying secondary cell wall domains. These secondary cell walls provide structural support and the water-conducting functions necessary for plants to inhabit land. These data provide important insights into how land plants produce secondary cell walls with the ultrastructural features required for upright growth.

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**Fig. 4.** Secondary cell wall CSC distribution at the plasma membrane is disorganized by the loss of microtubules after oryzalin treatment while CSC delivery and motility are unaffected. (A) VND7::GR-induced cells expressing YFP::CESA7 and RFP::TUB6 after oryzalin treatment. Plasma membrane–localized secondary cell wall CSCs follow aberrant tracks in the absence of microtubules. (B) CSC velocities were not significantly different between oryzalin- and DMSO-treated cells (Student’s t test, $P = 0.49$). For each condition, 40 CSC velocities were averaged for each of 12 cells in four plants. (C) FRAP of YFP::CESA7 signal revealed insertion of CSCs at the plasma membrane after microtubule loss (arrows). Scale bars, 10 μm [(A) and (B)].
Structure-function analysis identifies highly sensitive strigolactone receptors in Striga

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Strigolactones are small molecules that act as endogenous plant hormones to influence plant growth and development (1, 2). Unlike other plant hormones, multiple forms of bioactive strigolactones exist and vary in moieties attached to the A and B rings as well as the orientation of the D ring (fig. S1), making it difficult to determine which receptor binds which strigolactone with the highest affinity. Here, we show that the expression of strigolactone receptors in Arabidopsis thaliana is highly sensitive to picomolar concentrations of strigolactones. A crystal structure determined at atomic resolution for a strigolactone receptor reveals that the ligand binding pocket is large and flexible, allowing for a range of strigolactones to be bound with high affinity. This finding provides insights into the mechanism of strigolactone perception and offers a new perspective for the development of herbicides that target this pathway.
Visualization of cellulose synthases in *Arabidopsis* secondary cell walls


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**Secondary cell walls built with speed**

Plant cell walls provide the cellulose that is integral for wood, cotton fiber, and many biofuels. Cellulose is synthesized outside the cell membrane by cellulose synthase enzymes. Much of the secondary cell wall, responsible for the sturdiness of wood, is formed by xylem cells embedded in the core of the plant. Watanabe et al. leveraged ectopic expression to bring xylem-style cellulose synthase activity to the epidermal surface of the plant (see the Perspective by Schneider and Persson). Combining this improved accessibility with fluorescent tagging showed that secondary cell walls are built faster than primary cell walls, perhaps due to increased velocity and density of cellulose synthase complexes. *Science*, this issue p. 198, see also p. 156