gate bias depletes the channel of holes, turning the device off. At low $V_{DS}$, the TFT shows typical transistor behavior as $I_D$ increases linearly with $V_{DS}$. Current saturation, with only a small ohmic component, is observed at high $V_{DS}$ as the accumulation of holes in the channel is pinched off near the drain electrode.

Device operation is adequately modeled by the standard field-effect transistor equations that apply to both organic and inorganic TFTs. From the plot of $I_D$ and $I_{D1/2}$ versus $V_G$ (Fig. 3B) used to calculate current modulation ($I_{ON}/I_{OFF}$) and field-effect mobility, $\mu$, in the saturation regime, the field-effect mobility for this device is $0.55 \text{cm}^2/\text{V} \cdot \text{s}$ for a $\pm 50$-V sweep of $V_G$ at $V_{DS} \approx 60 \text{ V}$. This mobility is typical for $\left(\text{C}_6\text{H}_{5}\text{C}_2\text{H}_4\text{NH}_2\right)_2\text{SnI}_4$ as it has been calculated for many devices on the same wafer, on different wafers, and from different preparations of the hybrid. These same device characteristics scale to smaller voltages as the gate oxide thickness is reduced. The highest mobility measured for this material, on a $1500 \text{ A}$ gate oxide at $V_{DS} = -30 \text{ V}$, is $0.62 \text{cm}^2/\text{V} \cdot \text{s}$, which is six times higher than that of any other spin-coated material (2) and comparable to a-Si and the best organic semiconductors deposited in high vacuum.

The field-effect mobility of these organic-inorganic TFTs depends on $V_G$ (Fig. 3C) as reported for organic TFTs (12) and a-Si (21). Increasing $V_G$ decreases the number of accumulated charges available in the channel to fill localized traps in the material. At higher $V_G$, the trap states are filled, enabling additional charges to move with carrier mobilities defined by the delocalized bands of the hybrid semiconductor. Filling of trap states is likely responsible for the discontinuities shown in Fig. 3B, which suggests that higher mobilities may be achieved at lower $V_G$ in TFTs with high dielectric gate insulators, which may be deposited on plastic substrates (12).

Materials that can be solution processed and exhibit a high $I_{ON}/I_{OFF}$ are required for TFTs in low-cost large-area applications. The $\left(\text{C}_6\text{H}_{5}\text{C}_2\text{H}_4\text{NH}_2\right)_2\text{SnI}_4$ TFT (Fig. 3B) has an $I_{ON}/I_{OFF}$ of $10^4$. There is an increase in leakage as $V_{GS}$ increases for large positive voltages as the gate oxide thickness is reduced. The highest mobility measured for $\left(\text{C}_6\text{H}_{5}\text{C}_2\text{H}_4\text{NH}_2\right)_2\text{SnI}_4$ has shown the best device characteristics, organic-inorganic perovskites with a tin(II) iodide framework and a variety of aliphatic (for example, alkyl-) and aromatic, ammonium, and diammonium cations have been incorporated in TFT devices and exhibit similar characteristics to those shown here. Increasing the dimensionality of the hybrid by increasing the number of repeated inorganic layers per organic layer may further increase film mobility. Improvements in materials processing and tailoring of the organic component are expected to increase mobilities in organic-inorganic TFTs with a SnI$_4$ framework up to at least $50 \text{ cm}^2/\text{V} \cdot \text{s}$. The flexibility in the chemistry of organic-inorganic hybrid materials may provide a path to preparation of both n-type and p-type transporting materials, which are necessary for complementary logic and normally “on” or “off” organic-inorganic TFTs.

The cheap, low-temperature processing techniques suggest that organic-inorganic TFTs may be suitable for applications that require low cost, a large area, and the mechanical flexibility of plastic substrates. Semiconducting organic-inorganic hybrid materials may be designed with a wide range of organic and inorganic components for use in TFTs. Although $\left(\text{C}_6\text{H}_{5}\text{C}_2\text{H}_4\text{NH}_2\right)_2\text{SnI}_4$ has shown the best device characteristics, organic-inorganic perovskites with a tin(II) iodide framework and a variety of aliphatic (for example, alkyl-) and aromatic, ammonium, and diammonium cations have been incorporated in TFT devices and exhibit similar characteristics to those shown here. Increasing the dimensionality of the hybrid by increasing the number of repeated inorganic layers per organic layer may further increase film mobility. Improvements in materials processing and tailoring of the organic component are expected to increase mobilities in organic-inorganic TFTs with a SnI$_4$ framework up to at least $50 \text{ cm}^2/\text{V} \cdot \text{s}$. The flexibility in the chemistry of organic-inorganic hybrid materials may provide a path to preparation of both n-type and p-type transporting materials, which are necessary for complementary logic and normally “on” or “off” organic-inorganic TFTs.

References and Notes

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The Root of Angiosperm Phylogeny Inferred from Duplicate Phytochrome Genes

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An analysis of duplicate phytochrome genes (PHYA and PHYC) is used to root the angiosperms, thereby avoiding the inclusion of highly diverged outgroup sequences. The results unambiguously place the root near Amborella (one species, New Caledonia) and resolve water lilies (Nymphaeales, ~70 species, cosmopolitan), followed by Austrobaileya (one species, Australia), as early branches. These findings bear directly on the interpretation of morphological evolution and diversification within angiosperms.

The evolution of flowering plants fundamentally altered the biosphere. Deciphering the causes and consequences of their origin and radiation requires knowledge of phylogeny, especially the order in which branches diverged near the root of the tree (1). However, the root of angiosperms has remained unresolved, as different lines of evidence have suggested many disparate alternatives (2). This ambiguity stems in part from uncertainty surrounding the identity of their closest relatives (3–5), and from the great differences between angiosperms and all other living lines of seed plants. Such differences render homology assessments exceptionally difficult in morphological analyses, and may lead to “long branch attraction” in molecular analyses, which occurs when convergent nucleotide substitutions cause the spurious connection of highly diverged sequences (6). In analyses of angiosperms, distant outgroup sequences might connect (perhaps with confidence) to the most divergent angiosperm sequence or sequences. For this reason it has been suggested that the angiosperm root may never be resolved using nucleotide sequence
We used analysis of duplicate genes to root the angiosperm phylogeny without outgroups. This approach has been used to root the entire tree of life, for which outgroups are unknown (8). It seldom has been used elsewhere (9) but might be of general use, especially for rooting clades that are highly diverged from all known relatives. We reasoned that simultaneous analysis of members of a gene pair that duplicated along the line leading to extant angiosperms should yield an unrooted network of two identical (or very similar) gene subtrees connected by a single branch. If the subtrees are congruent, rooting the network along the connecting branch allows the network to fit into a rooted species tree without requiring additional hypotheses of gene duplication, sorting, or horizontal transfer events (2).

Phylogenetic analyses of phytochrome genes in green plants suggest that the phytochrome gene pair, PHYA and PHYC, diverged along the branch leading to angiosperms (2, 10). PHYA and PHYC are found in most angiosperms examined, whereas only one gene lineage related to this pair is known from other seed plants (10, 11). We obtained and analyzed PHYA and PHYC sequences from 26 angiosperms (12) representing most taxa previously suggested to be early-diverging lineages. Parsimony analysis yielded six shortest unrooted networks. The strict consensus of these networks best fits a rooted tree with rooting along the branch leading to angiosperms from 26 angiosperms (1104 nucleotide sites, of which 634 are parsimony-informative). Heuristic parsimony analysis (100 random taxon addition replicates with tree bisection and reconnection swapping in PAUP* 4.0 (33)) yielded trees of 6423 steps [retention index (RI) = 0.50; consistency index (CI) = 0.24, excluding autapomorphies], identical components in the PHYA and PHYC subtrees are labeled A through Q. Bootstrap percentages (from 500 replicates with the same search parameters, but using 10 random addition replicates) are above branches. Arrows indicate branches that collapse in the strict consensus.

Variation (7).

Fig. 1. One of the six most parsimonious networks of PHYA and PHYC from 26 angiosperms (1104 nucleotide sites, of which 634 are parsimony-informative). Heuristic parsimony analysis (100 random taxon addition replicates with tree bisection and reconnection swapping in PAUP* 4.0 (33)) yielded trees of 6423 steps [retention index (RI) = 0.50; consistency index (CI) = 0.24, excluding autapomorphies], identical components in the PHYA and PHYC subtrees are labeled A through Q. Bootstrap percentages (from 500 replicates with the same search parameters, but using 10 random addition replicates) are above branches. Arrows indicate branches that collapse in the strict consensus.

The conclusion that Amborella, water lilies, and Austrobaileyia [which occurs in a clade with Illiciaceae and Schisandraceae (14–18) and Trimenia (17, 20)] form a grade at the base of the angiosperms has major implications for early evolution in flowering plants. Factors that may have contributed to their diversification include carpel closure (21), self-incompatibility (22), and the evolution of vessels (23). Our results imply that the carpels of the first angiosperms were sealed by secretions, and that postgenital fusion of epidermal layers evolved later (24). In our trees, Chloranthus and Nelumbo could represent reversions to closure by secretion; however, the placement of Chloranthus is only weakly supported. The conclusion that the first angiosperms were self-compatible plants (25) should be reexamined. Self-incompatibility has been noted in Austrobaileya and Illicium, implying either that it originated in the clade including these plants (probably early in angiosperm evolution) or

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that it was retained from the first angiosperms. Self-incompatibility may occur within in water lilies, but the data are ambiguous (25). The condition in Amborella, with mostly unisexual flowers, is unknown, but possibly could be determined if functional stamens were found in otherwise carpellate flowers (26, 27). Our results suggest that xylem vessels evolved after the origin of the branch containing Amborella, which is vesseless. Vessels with small pores in the pit membranes are reported from most, but not all, water lilies (28), implying either that vessels originated (28) or were lost several times within water lilies. If the first water lilies had such vessels, they may have been transitional to typical vessels that lack pit membranes at maturity, perhaps through intermediates that retain remnants of pit membrane, as seen in Illiciaceae and Chloranthaceae (29). The absence of vessels in Winteraceae and the Trochodendronales may represent losses (30).

Our finding that the earliest branches within angiosperms are not species-rich could imply massive undetected extinction within these lineages. More likely it supports the conclusion that a shift in diversification rate did not coincide directly with the origin of flowering plants, but occurred later (31). Our results suggest that the first angiosperms probably were woody plants, in which case one or more shifts to the herbaceous habit may have fueled the major radiation of angiosperms.

References and Notes
8. N. Inabe, K.-I. Kuma, M. Hasegawa, S. Osawa, T. Houtteynia, which is vesselless. Vessels with small pores in the pit membranes are reported from most, but not all, water lilies (28), implying either that vessels originated (28) or were lost several times within water lilies. If the first water lilies had such vessels, they may have been transitional to typical vessels that lack pit membranes at maturity, perhaps through intermediates that retain remnants of pit membrane, as seen in Illiciaceae and Chloranthaceae (29). The absence of vessels in Winteraceae and the Trochodendronales may represent losses (30).

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A Species of Small Antisense RNA in Posttranscriptional Gene Silencing in Plants

Andrew J. Hamilton and David C. Baulcombe*

Posttranscriptional gene silencing (PTGS) is a nucleotide sequence–specific defense mechanism that can target both cellular and viral mRNAs. Here, three types of transgene-induced PTGS and one example of virus-induced PTGS were analyzed in plants. In each case, antisense RNA complementary to the targeted mRNA was detected. These RNA molecules were of a uniform length, estimated at 25 nucleotides, and their accumulation required either transgene sense transcription or RNA virus replication. Thus, the 25-nucleotide antisense RNA is likely synthesized from an RNA template and may represent the specificity determinant of PTGS.

Posttranscriptional gene silencing occurs in plants and fungi transformed with foreign or endogenous DNA and results in the reduced accumulation of RNA molecules with sequence similarity to the introduced nucleic acid (1, 2). Double-stranded RNA induces a similar effect in nematodes (3), insects (4), and protozoa (5). PTGS can be suppressed by several virus-encoded proteins (6) and is closely related to RNA-mediated virus resistance and cross-protection in plants (7, 8). Therefore, PTGS may represent a natural antiviral defense mechanism and transgenes might be targeted because they, or their RNA, are perceived as viruses. PTGS could also represent a defense system against transposable elements and may function in plant development (9–11).

To account for the sequence specificity and posttranscriptional nature of PTGS, it has been proposed that antisense RNA forms a duplex with the target RNA, thereby promoting its degradation or interfering with its translation (12). If these hypothetical antisense RNA molecules are of a similar size to typical mRNAs, they would have been readily detected by routine RNA analyses. However, there have been no reports of such antisense RNA that is detected exclusively in plants or animals exhibiting PTGS. Nevertheless, PTGS-specific antisense RNA may exist, but may be too short for easy detection. We carried out analyses specifically to detect low molecular weight antisense RNA in four classes of PTGS in plants (13). The first class tested was transgene-induced PTGS of an endogenous gene ("cosuppression"). We used five tomato lines (T1.1, T1.2, T5.1, T5.2, and T5.3), each transformed with a tomato 1-aminocyclopropane-1-carboxylate oxidase (ACO) cDNA sequence downstream of the cauliflower mosaic virus 35S promoter (35S). Two lines (T5.2 and T5.3) exhibited PTGS of the endogenous ACO mRNA (Fig. 1A). Low molecular weight nucleic acids purified from the five lines were separated by denaturing polyacrylamide gel electrophoresis, blotted, and hybridized to an ACO sense (antisense-specific) RNA probe (Fig. 1B). A discrete, ACO antisense RNA (14) of 25 nucleotides (nt) was present in both PTGS lines but absent from the nonsilencing lines. Twenty-five–nucleotide ACO RNA of sense polarity and at the same abundance as the 25-nt ACO antisense RNA was also present only in the PTGS lines (Fig. 1C).

PTGS induced by transgenes can also occur when a transgene does not have homology to an endogenous gene (1). Therefore, we tested whether this type of PTGS was also associated with small antisense RNA. We analyzed three tobacco lines carrying 35S-β-glucuronidase (GUS) transgenes. Two of these lines, T4 (15) and 6b5 (16), exhibited PTGS of GUS. The third line (6b5×271) tested was produced by crossing 6b5 with line 271 (17), in which there is a transgene suppressor of the 35S promoter in 6b5. There was no PTGS of GUS in 6b5×271 because of the transcriptional suppression of the 35S GUS transgene (18). Hybridization with a GUS-specific probe revealed that low molecular weight GUS antisense RNA was present in T4 and 6b5 (Fig. 2, lanes 1 and 2) but absent from line 6b5×271 (Fig. 2, lane 3). The amount of antisense RNA correlated with the extent of PTGS: Line 6b5 has stronger PTGS of GUS than line T4 (18) and had more GUS antisense RNA (Fig. 2).

27. L. B. Thein, unpublished data.