PLANT GENETICS

A cucurbit androecy gene reveals how unisexual flowers develop and dioecy emerges

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Understanding the evolution of sex determination in plants requires identifying the mechanisms underlying the transition from monoecious plants, where male and female flowers coexist, to unisexual individuals found in dioecious species. We show that in melon and cucumber, the *androecy* gene controls female flower development and encodes a limiting enzyme of ethylene biosynthesis, ACS11. *ACS11* is expressed in phloem cells connected to flowers programmed to become female, and *ACS11* loss-of-function mutants lead to male plants (androecy). *CmACS11* represses the expression of the male promoting gene *CmWIP1* to control the development and the coexistence of male and female flowers in monoecious species. Because monoecy can lead to dioecy, we show how a combination of alleles of *CmACS11* and *CmWIP1* can create artificial dioecy.

Most angiosperms are hermaphroditic, producing exclusively bisexual flowers. Sex determination is a developmental process that leads to unisexual flowers in ~10% of angiosperm species (*1*). About half of these are monoecious species, with male and female flowers on the same plant, and half are dioecious species, with separate male and female individuals (*1*). The evolutionary pathways from hermaphroditism have been modeled, but empirical evidence is scanty (*2*–*4*). Dioecy appears to have evolved most frequently via monoecy through a series of mutations that alter the ratio of male and female flowers. Dioecy may have also evolved through emergence of unisexual individuals that coexist with hermaphrodites, creating gynodioecy or androdioecy populations (*3*–*6*).

Cucurbitaceae is a large plant family of species that display mostly unisexual flowers. Out of some 800 species investigated, 460 are monoecious and 340 are dioecious, and there have been numerous shifts between monoecy and dioecy (*7*). Several *Cucurbitaceae* species, including cucumber and melon, show different sexual morphs (fig. S1). In monoecious melon (*Cucumis melo*), most of the flowers are male, and female flowers develop at the youngest lateral branches of the growing vines. Cloning of naturally occurring mutations leading to transition from monoecy to different sexual morphs has brought insight to the sex-determination pathway (*8*, *9*). The *andromonoecious* gene *CmACS-7* controls stamina development in female flowers (*9*). The *gynoecious* gene *CmWIP1* controls male flower development, and its loss of function leads to purely female plants (*8*). However, it is not known how male and female flowers coexist on the same plant, in monoecious species, and how purely male plants can emerge from monoecious or hermaphrodite populations.

Because solely male plants have not been described in melon, we investigated natural polymorphisms in the related species cucumber (*Cucumis sativus*) (*10*). Cucumber is also monoecious, and its sex determination system is conserved with melon (*11*). Cucumber plants homozygous for the *androecious* allele (*a*) bear only male flowers (*12*).

We cloned the *androecious* gene (*a*) in cucumber using a positional cloning strategy (fig. S2) that involves a cross between the monoecious line

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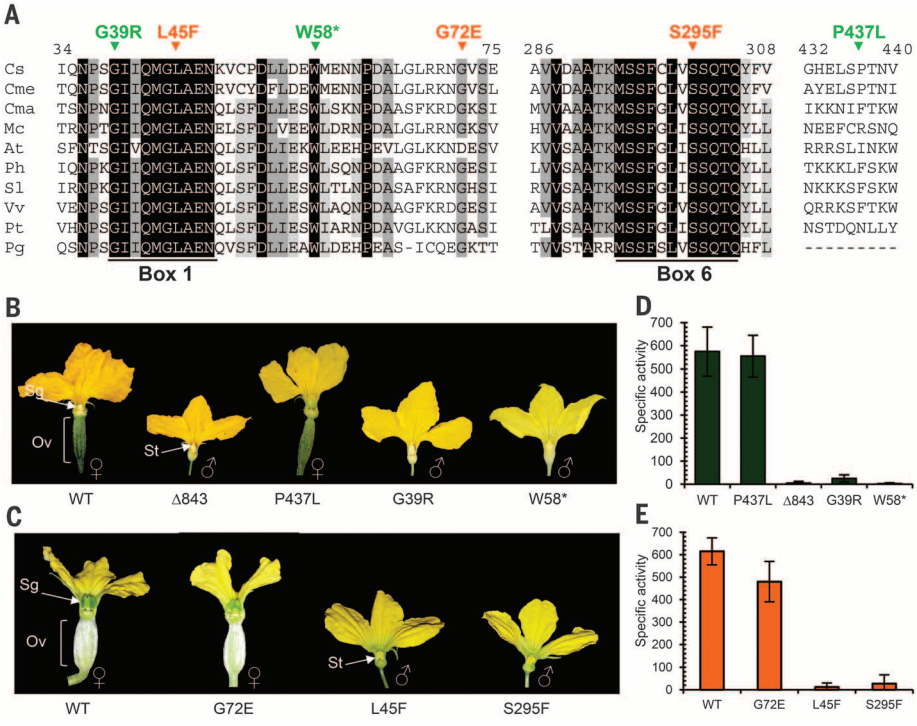


Fig. 1. Molecular characterization of alleles of ACS11. (**A**) Alignments of CsACS11 with homologous proteins from Cme (*Cucumis melo*), Cma (*Cucurbita maxima*), Mc (*Momordica charantia*), At (*Arabidopsis thaliana*), Ph (*Petunia hybrida*), Sl (*Solanum lycopersicum*), Vv (*Vitis vinifera*), Pt (*Populus trichocarpa*), and Pg (*Picea glauca*). Boxes 1 and 6 indicate conserved domains in ACS proteins. TILLING mutations in CsACS11 and CmACS11 are shown above the alignment in green and orange, respectively. (**B**) Cucumber flower types from monoecious plant (WT), androecious (Δ843), and mutants G39R, W58*, and P437L. (**C**) Melon flower types from monoecious plant (WT) and mutants G72E, L45F, and S295F. Ov, ovary; Sg, stigma; St, stamen. (**D** and **E**) ACS enzymatic activity of WT and mutants (D) CsACS11 and (E) CmACS11 isoforms.

Oman and the androecious line Erez. Sequence analysis of the (*a*) locus revealed a single nonsynonymous nucleotide deletion, Δ843, within exon 3 of *Csa2G353460*. This 1–base pair (bp) deletion leads to a premature stop codon, suggesting that Erez is null for *Csa2G353460* (fig. S2, C and D). *Csa2G353460* encodes a 1-aminocyclopropane-1-carboxylic acid synthase (ACS), hereafter CsACS11 (fig. S3). ACS catalyzes the rate-limiting step in ethylene biosynthesis, the production of 1-aminocyclopropane-1-carboxylic acid (ACC) from *S*-adenosylmethionine (SAM). Ethylene is then made from ACC by the ACC oxidase (*13*). To investigate whether this 1-bp deletion is associated with androecy, we resequenced *CsACS11* in a panel of 50 cucumber accessions of different sexual morphs. In contrast to the 1-bp deletion, none of the observed polymorphisms was associated with androecy, supporting that the 1-bp deletion underlies androecy in cucumber (figs. S4 and S5).

Because there is no efficient cucumber transformation protocol, we produced a TILLING (Targeting Induced Local Lesions in Genomes) collection from a monoecious cucumber line and screened for mutations in *CsACS11*. We identified 10 induced mutations with seven silent, one nonsense (W58*), and two missense mutations (G39R and P437L) (table S1) (*14*). G39R occurs in a highly conserved amino acid position and is predicted to affect the function of the protein, whereas the P437L modification affects a nonconserved amino acid (Fig. 1A and fig. S5). Crosses support that the P437L and silent mutations have no impact on the sex of the plant, whereas plants homozygous for the G39R or W58* mutations were androecious, with no female flowers (Fig. 1B and table S1). On the basis of these data, we concluded that *CsACS11* is the *androecious* gene (*A*).

To test whether the genetic determinant controlling female flower development is conserved in *Cucumis*, we screened for mutations in the melon ortholog of *CsACS11*, *MELO3C010779*, hereafter *CmACS11* (fig. S3). CmACS11 and CsACS11 share 92% amino acid sequence identity and are syntenic (figs. S5 and S6). We isolated 10 silent or intronic changes and three missense mutations—L45F, G72E, and S295F—in *CmACS11* (Fig. 1A and table S1). L45F and S295F mutations are in highly conserved amino acid positions and are predicted to affect the function of the protein, unlike the G72E mutation, which is in a nonconserved amino acid position (table S1 and fig. S5). We back-crossed *CmACS11* missense mutant lines to the wild type and observed no effect on the sex of the plant correlated with the G72E mutation, nor for silent and intronic mutations (Fig. 1C and table S1). In contrast, plants homozygous for L45F or S295F mutations were androecious (Fig. 1C). We therefore conclude that CmACS11 controls female flower development in melon and that *ACS11* function evolved before the divergence of *Cucumis melo* and *Cucumis sativus*, ~10 million years ago (*10*).

In the parental line Erez, the *androecy* allele encodes a truncated form of ACS11. In the TILLING screens, all induced mutations leading to androecy are predicted to be loss-of-function (Fig. 1 and figs. S5 and S7). We expressed the ACS11 mutant proteins and assayed their activity in vitro (*11*). As expected, the mutations that lead to androecy—W58*, Δ843, L45F, G39R, and S295F—all display low to undetectable ACS activities, whereas mutations not affecting the sex of the plant, G72E and P437L, have activities comparable with those of the wild type (Fig. 1, D and E). We conclude that *ACS11*-mediated ethylene production is necessary for the development of female flowers in monoecious *Cucumis* species, whereas loss of ACS activity leads to female-to-male transition. Consistent with this, *ACS11* loss-of-function mutants treated with the ethylene-releasing agent Ethephon developed female flowers (fig. S8).

ACS11 mRNA can only be detected in female flower buds from monoecious cucumber and melon plants at stage 4 (Fig. 2, A to C and G) (*15*), in which the bud sex is not morphologically distinguishable, with expression at later stages (Fig. 2, D and I). No *ACS11* expression was detected in vegetative tissues or male flowers (Fig. 2, E and H, and fig. S9). *ACS11* mRNA was strongly localized in vascular bundles of female flowers in both internal and external fascicular phloems (Fig. 2F and fig. S10) but not in the extrafascicular phloem (*16*). This strong signal corresponds to the companion cell sieve element complex in the phloem connected to flower buds with a developing carpel (fig. S10, C and E). In the andromonoecious plants—developing male and hermaphrodite flowers—*ACS11* is highly expressed in the phloem of hermaphrodite flower buds but not in male buds (fig. S11). This supports that *ACS11*-mediated ethylene production is required for the development of the carpel in monoecious and andromonoecious *Cucumis* species.

Expression of *CmWIP1* inhibits carpel development, and the nonexpression or loss-of-function of *CmWIP1* releases this inhibition (*8*). Hence, *CmACS11* function is antagonistic to *CmWIP1* function in flowers programmed to develop carpels. To test the hypothesis that *CmACS11* may be the repressor of *CmWIP1*, we analyzed

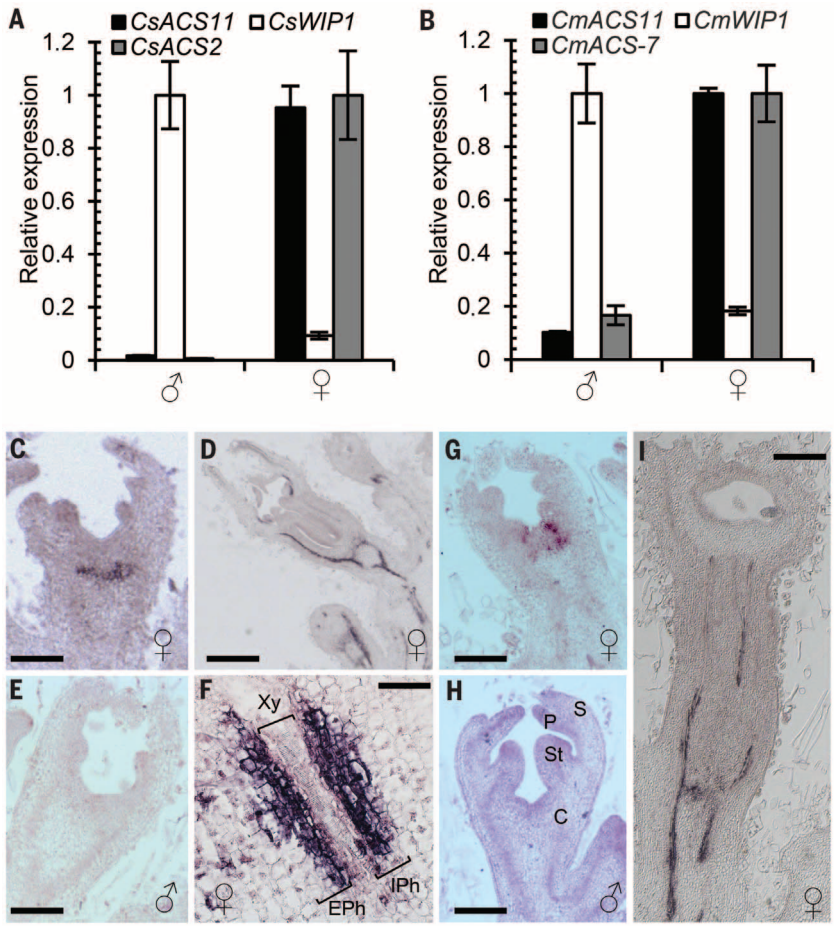
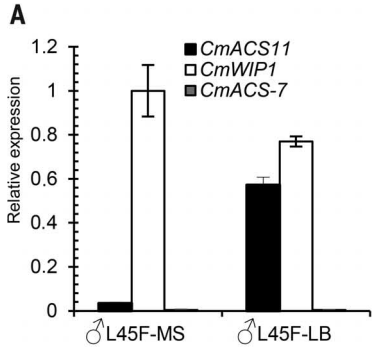


Fig. 2. Expression patterns of *ACS11* in unisexual melon and cucumber flowers. (**A** and **B**) Quantitative reverse transcription polymerase chain reaction (RT-PCR) of *ACS11*, *ACS7*, and *WIP1* in male or female flower buds, collected at stage 4, of (A) cucumber and (B) melon. Shown are the mean ± SD of three biological replicates. (**C** to **E** and **G** to **I**) *ACS11* in situ expression in flower buds at [(C), (E), (G), and (H)] stage 4 and [(D) and (I)] stage 8 of [(C) to (E)] cucumber and [(G) to (I)] melon. (**F**) Longitudinal section of a vascular bundle of a cucumber female flower. C, carpel; St, stamen; P, petal; S, sepal. Xy, xylem; EPh, external phloem; IPh, internal phloem. Scale bars, (F) 15 μm; (C) to (E), (G), and (H) 200 μm ; (I) 500 μm.

the expression of *CmWIP1* in flowers that do or do not express *CmACS11* and in flowers impaired in *CmACS11* function. *CmWIP1* and *CmACS11* expression was diametrically opposite, with *CmWIP1* highly expressed in male buds but not in female buds that express *CmACS11* (Fig. 2B). Expression of *CmWIP1* is reactivated in *CmACS11* loss-of-function mutants (Fig. 3A). We also generated and phenotyped *Cmwip1Cmacs11* double mutants, which were gynoecious like the *Cmwip1* single mutant (Fig. 3B), indicating that *CmWIP1* is epistatic to *CmACS11*. These data also imply that *CmACS11* acts upstream of *CmWIP1* in the sex-determination pathway. We thus generated and characterized double and triple *CmACS11*, *CmWIP1*, and *CmACS-7* mutants (Fig. 3B). The results support a model in which expression of the carpel inhibitor, *CmWIP1*, is dependent on nonexpression of *CmACS11*, and expression of the stamina inhibitor, *CmACS-7*, is dependent on nonexpression of *CmWIP1* (Figs. 2B and 3C). In monoecious and andromonoecious plants, male flowers result from nonexpression of *CmACS11*, which permits *CmWIP1* expression (Figs. 2H and 3C and fig. S11). Female flowers develop on the branches because of expression of *CmACS11* that represses the expression of *CmWIP1*. Consequently, the nonexpression of *CmWIP1* releases the expression of *CmACS-7* that inhibits the stamina development (Fig. 3C). If nonfunctional *CmACS-7* is expressed, hermaphroditic, instead of female, flowers develop (Fig. 3C). Androecious plants result from a loss of function of *CmACS11*, leading to expression of *CmWIP1* in all flowers on a plant. Gynoecious plants are obtained by inactivation of *CmWIP1* function, and hermaphrodite plants are obtained by inactivation of *CmWIP1* and *CmACS-7* (Fig. 3C).

In angiosperms, dioecy is believed to arise most frequently via monoecy and less frequently from other sexual systems, such as gynodioecy (*1*, *3*). Dioecy is theorized to arise from a minimum of two mutations, in which one results in female plants and the other in male individuals (*2*). *CmWIP1* and *CmACS11* fit a single sex-determination model and can explain the development of unisexual flowers (Fig. 3C). We produced a 1:1 sex ratio segregating dioecious population (*G* test) (*17*) by crossing female plants homozygous for the recessive alleles *Cmwip1* and *Cmacs11* and male plants of *Cmwip1*/*CmWIP1* and *Cmacs11*/*Cmacs11* genotype (Fig. 4A). Thus, a combination of alleles of genes controlling monoecy theoretically can result in dioecy (Fig. 4B).

The cloning of the androecy gene and its integration into a genetic model of sex determination indicate the molecular underpinnings of how unisexual flowers coexist and how their relative numbers could be modulated on the same plant in monoecious species, and provide a possible route toward dioecy. The expression of *CsACS11* in the phloem shows that ethylene is a likely signal to be controlling the sex of flowers on the branches. Nevertheless, it still unknown whether *ACS11* mRNA, protein, ACC, or ethylene is the signal. Ethylene signaling controls inhibition of stamina development, through expression



B

Sexual phenotype	Genotype		
	G locus	*M* locus	*A* locus
Gynoecious	*wip1/wip1*	*ACS7/-*	*-/-*
Androecious	*WIP1/-*	*-/-*	*acs11/acs11*
Hermaphrodite	*wip1/wip1*	*acs7/acs7*	*-/-*
Monoecious	*WIP1/-*	*ACS7/-*	*ACS11/-*
Andromonoecious	*WIP1/-*	*acs7/acs7*	*ACS11/-*

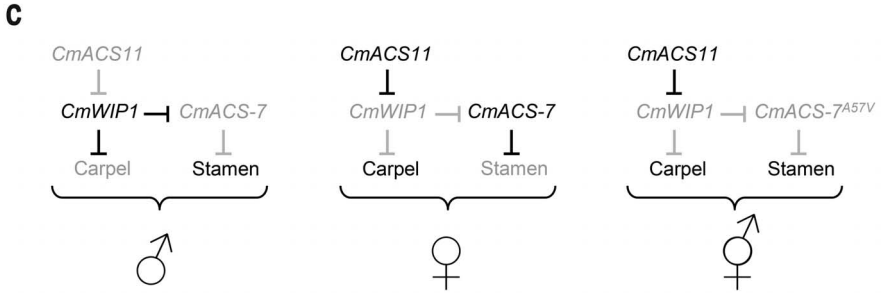


Fig. 3. Expression and function of *CmACS11*, *CmWIP1*, and *CmACS-7* correlates with sex. (**A**) Quantitative RT-PCR of *ACS11*, *ACS-7*, and *WIP1* in stage 4 male flower buds, collected from the main stem (M45F-MS) or the first three nodes of the lateral branches (L45F-LB), of an androecious (male) *Cmacs11*-L45F plant. Shown are the mean ± SD of three biological replicates. (**B**) Sexual morphs of melon plants across a combination of alleles at *G*, *M*, and *A* sex loci. Minus symbol indicates any allele at the locus. (**C**) Model of the sex-determination pathway in melon integrating *CmACS11*, *CmWIP1*, and *CmACS-7* genetic and functional information.

A

Segregation	Total siblings	Female plants	Male plants	Sex ratio	G test
Offspring 1	86	46	40	0.53	0.42 ns
Offspring 2	90	43	47	0.48	0.18 ns

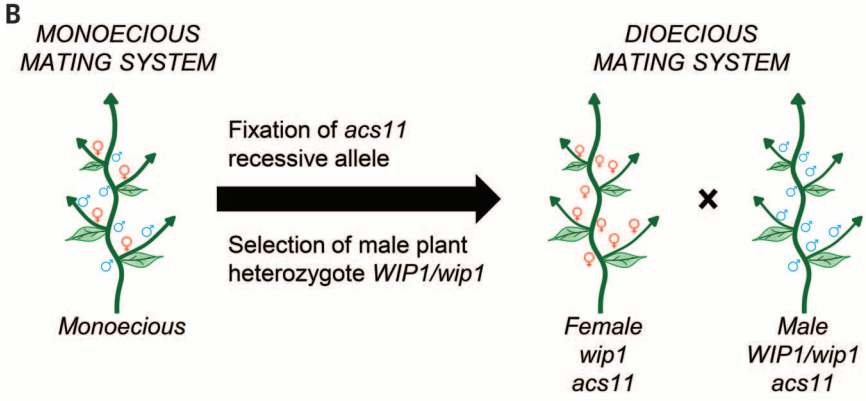


Fig. 4. Engineering dioecy from monoecious melon. (**A**) Fixation of *Cmacs11* loss-of-function alleles at the population level and the maintenance of the dominant allele of *CmWIP1* at the heterozygous level in male plants lead to a dioecious mating system. (**B**) Segregation analysis of two consecutive crosses between male plant of *WIP1/wip1 acs11/acs11* genotype and female plant of *wip1/wip1 acs11/acs11* genotype shows dioecy. Sex ratio was calculated as females/(females + males). *G* statistical test (*G*) is indicated with the level of significance [not significant (ns), $P > 0.05$].

of *CmACS-7* as well as the development of the carpel through expression of *CmACS11*. This is likely due to a tight control of the kinetics of the production of this hormone during sex determination. Because ethylene seems to be a major hormone in sex determination in angiosperms (*18*), it is likely that our model of sex determination in a monoecious plant can be used as a framework for investigations of sex determination in other plant families. Furthermore, this work may allow easier breeding and optimization of the synchronization of male and female flower development on the same plant so as to improve fruit yields in nonmodel, cultivated *Cucurbitaceae* species.

REFERENCES AND NOTES

1. S. S. Renner, *Am. J. Bot.* **101**, 1588–1596 (2014).
2. B. Charlesworth, D. Charlesworth, *Am. Nat.* **112**, 975 (1978).
3. S. S. Renner, R. E. Ricklefs, *Am. J. Bot.* **82**, 596 (1995).
4. S. C. Barrett, *Nat. Rev. Genet.* **3**, 274–284 (2002).
5. D. Lewis, *Biol. Rev. Camb. Philos. Soc.* **17**, 46–67 (1942).
6. D. Charlesworth, B. Charlesworth, *Heredity* **41**, 137–153 (1978).
7. A. Kocyan, L. B. Zhang, H. Schaefer, S. S. Renner, *Mol. Phylogenet. Evol.* **44**, 553–577 (2007).
8. A. Martin *et al*., *Nature* **461**, 1135–1138 (2009).
9. A. Boualem *et al*., *Science* **321**, 836–838 (2008).
10. P. Sebastian, H. Schaefer, I. R. Telford, S. S. Renner, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 14269–14273 (2010).
11. Supplementary text and materials and methods are available as supplementary materials on *Science* Online
12. B. Kubicki, *Genet. Pol.* **10**, 101–122 (1969).
13. P. W. Oeller, M. W. Lu, L. P. Taylor, D. A. Pike, A. Theologis, *Science* **254**, 437–439 (1991).
14. Single-letter abbreviations for the amino acid residues are as follows: A, Ala; C, Cys; D, Asp; E, Glu; F, Phe; G, Gly; H, His; I, Ile; K, Lys; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; R, Arg; S, Ser; T, Thr; V, Val; W, Trp; and Y, Tyr. In the mutants, other amino acids were substituted at certain locations; for example, G39R describes a mutant in which glycine at position 39 is replaced by arginine.
15. S. L. Bai *et al*., *Planta* **220**, 230–240 (2004).
16. R. Turgeon, K. Oparka, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 13201–13202 (2010).
17. M. L. Tang, Y. B. Pei, W. K. Wong, J. L. Li, *Stat. Methods Med. Res.* **21**, 331–345 (2012).
18. T. F. Law, S. Lebel-Hardenack, S. R. Grant, *Am. J. Bot.* **89**, 1014–1020 (2002).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/350/6261/688/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S13
Tables S1 to S3
References (*19*–*28*)

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NONHUMAN GENOMICS

The *Symbiodinium kawagutii* genome illuminates dinoflagellate gene expression and coral symbiosis

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Dinoflagellates are important components of marine ecosystems and essential coral symbionts, yet little is known about their genomes. We report here on the analysis of a high-quality assembly from the 1180-megabase genome of *Symbiodinium kawagutii*. We annotated protein-coding genes and identified *Symbiodinium*-specific gene families. No whole-genome duplication was observed, but instead we found active (retro) transposition and gene family expansion, especially in processes important for successful symbiosis with corals. We also documented genes potentially governing sexual reproduction and cyst formation, novel promoter elements, and a microRNA system potentially regulating gene expression in both symbiont and coral. We found biochemical complementarity between genomes of *S. kawagutii* and the anthozoan *Acropora,* indicative of host-symbiont coevolution, providing a resource for studying the molecular basis and evolution of coral symbiosis.

Dinoflagellates are alveolates, with the mostly parasitic apicomplexans as their closest relatives (fig. S1A). Members of the genus *Symbiodinium* are essential photosynthetic endosymbionts in coral reefs (*1*). Dinoflagellates show enigmatic genetic and cytological characteristics, including permanently condensed chromosomes and a high proportion of diverse methylated nucleotides, and often feature large nuclear genomes (up to 250 Gb) (*2*). We report a 0.935-Gbp assembly of the 1.18-Gbp genome of *Symbiodinium kawagutii* (figs. S1B and S2), a Clade F strain originally isolated from a Hawaiian reef ecosystem (*3*). A high-quality *S. kawagutii* genome assembly corresponding to ~80% of the genome was achieved from ~151-Gbp Illumina genome shotgun sequence (~130x genome coverage) (tables S1 to S4 and fig. S3). Genome annotation revealed 36,850 nuclear genes, with 68% occurring in families (1.69 genes per family) (table S5). Only ~9% (3280) of *S. kawagutii* genes were in tandem arrays (1279 clusters) (table S6), with 2 to 10 repeats (76% being ≤4 repeats) per array. The genome encodes the common metabolic pathways expected for typical photosynthetic eukaryotes (fig. S4 and table S7), and we found genes involved in sexual reproduction, cyst formation and germination, and telomere synthesis (table S8). The telomeric motif (TTTAGGG)n was identified at the ends of scaffolds and was also detected by fluorescence in situ hybridization (fig. S1B).

Globally, our analysis revealed extensive genomic innovation in dinoflagellates. A total of 25,112 gene families were clustered from the genomes of *S. kawagutii* and eight other species representing higher plants, chlorophytes, rhodophytes, diatoms, phaeophytes, alveolates, and cnidarians. *S. kawagutii* has 12,516 gene families, of which 7663 were gained in the ancestor of *Symbiodinium* (Fig. 1A and table S9). These genes were enriched in 62 metabolic gene ontologies (table S10). When the gene families were normalized to *z* scores to balance the effect of different total gene numbers, 96 gene families had shrunk (table S11) and 265 gene families had expanded in *Symbiodinium* (table S12). The LINE-1 reverse transcriptase (a retroelement) is the most highly expanded family.

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A cucurbit androecy gene reveals how unisexual flowers develop and dioecy emerges

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