The surprising structure of a shrub willow sex chromosome

April 20 2020, by Alison F. Takemura

Female S. purpurea flowers. Credit: Larry Smart, Cornell University

Sex in plants can be befuddling. Most species are hermaphrodites, expressing both male and female gametes in one individual. But some, including shrub willow Salix purpurea, employ the evolutionary strategy we are far more familiar with: differentiating into male and female sexes. For the first time, the sex chromosomes of shrub willow have been sequenced with sufficient resolution to analyze their structure. Scientists found both a gene likely important for sex determination and a shared genetic architecture with Y chromosomes in mammals: a structure that helps correct deleterious mutations.

Shrub willow and its close relative Populus trichocarpa, or the poplar tree, are potential biofuel feedstocks of interest to the U.S. Department of Energy (DOE). (Poplar is a Flagship Plant.) To engineer them, researchers need to select and breed cultivars for the next generation. Understanding the mechanisms by which they reproduce can help guide breeding efforts. For example, discovering genetic markers of sex enables scientists to develop molecular assays that can distinguish males and females even when plants with multi-year generation times are young and haven't physically differentiated. Understanding mechanisms of sex determination could also lead to new approaches to accelerate flowering, which can speed the pace of breeding. Once plant cultivars are optimized, the knowledge could also help prevent flowering, which would enhance the biosafety of genetically engineered trees.

The shrub willow differentiates into males and females, a development conferred by its sex chromosomes. In humans, males are "heterogametic": they have different sex chromosomes, i.e., XY instead

of XX. But, like some plant and songbird species, the system in shrub willow is flipped: females are heterogametic. To avoid confusion with the mammalian system, the sex chromosomes are called Z and W instead of X and Y, and ZW rather than ZZ encodes for females.

Male S. purpurea flowers. Credit: Larry Smart, Cornell University

To better understand how sex determination works in shrub willow, researchers investigated the structures of the sex chromosomes of one male and one female specimen. Stephen DiFazio, plant biologist at West Virginia University (WVU), led the study's international team, which included scientists from Oak Ridge National Laboratory and the U.S. Department of Energy (DOE) Joint Genome Institute (JGI), a DOE

Office of Science User Facility located at Lawrence Berkeley National Laboratory. The JGI sequenced the shrub willows through the Community Science Program, using long-read sequencing to assemble the repetitive areas of the complete sex chromosomes. The results were published in *Genome Biology*.

The team found that the shrub willow's W chromosome has palindromic structures, the first time seen in a plant sex chromosome. Palindromes are large inverted repeats with highly similar sequences so that their sequences read the same (or nearly) backward and forward, like the name "Hannah." Palindromes are thought to be important structures in the human Y chromosome because, like W chromosomes, they lack a partner with which to homologously recombine. Palindromes provide an alternative; because of their internal sequence similarity, they enable gene copies to fold back on each other and thus be used as templates to correct mutations. This process, called gene conversion, helps maintain the integrity of the sequences. The variety of palindromes observed in nature—for example, in humans Y chromosomes and some songbird W chromosomes—suggest that they are advantageous enough to have evolved multiple times independently.


XXII. 10.
39. Salicaceae.
A
C
D
B
2
1
110. Salix purpurea L. Bachweide.

An illustration of shrub willow (Salix purpurea) from Flora von Deutschland, Österreich und der Schweiz by Otto Wilhelm Thomé. Credit: Wikimedia Commons, user Kurt Stueber

The researchers also found a gene likely responsible for sex determination. Many genes differentiate the shrub willow's sex chromosomes, so the researchers investigated poplar for which genes might be shared in common between poplar's Y—poplar has an XY system—and shrub willow's W chromosomes. One shared gene stood out in particular: a cytokinin response regulator that was expanded in a palindrome and shown to be undergoing gene conversion in willow. This gene regulates the expression of other genes in response to cytokinin, a key plant hormone, making it a plausible mechanism for sex determination in these two species and, perhaps, more generally.

More information: Ran Zhou et al. A willow sex chromosome reveals convergent evolution of complex palindromic repeats, *Genome Biology* (2020). DOI: 10.1186/s13059-020-1952-4

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