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Sex and the single fern: Separation of the synthesis and sensing of a signaling molecule controls sex in ferns

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Unlike animals, plants have two alternating generations: a diploid sporophyte and a haploid gametophyte. Through meiosis, the sporophyte produces haploid spores, which then give rise to gametophytes, a multicellular haploid structure that produces gametes for sexual reproduction. All seed plants and some non–seed plants are heterosporous, producing spores of different sizes: large female spores and small male spores. Most ferns, on the other hand, are homosporous; they produce a single type of spore. After germination, each fern spore has the potential to develop into a male, female, or hermaphrodite gametophyte. The developmental decision that determines the sex of a particular gametophyte depends on an interplant communication system mediated by chemical signals, termed antheridiogens (1, 2). On page 469 of this issue, Tanaka *et al.* (3) show that an antheridiogen in the Japanese climbing fern (*Lygodium japonicum*) functions as more than a simple chemical signal. Covalent modification of the antheridiogen is required to trigger the fern's response to form male gametophytes. Temporal and spatial separation of the biosynthetic pathway between the early- and late-maturing gametophytes ensures the production of the antheridiogen, and the active male-inducing chemically modified form, at just the right time and place.

In a fern population, the early-maturing gametophytes (from spores that germinated first) produce and secrete into the aqueous environment antheridiogens, which promote differentiation of the neighboring younger gametophytes into males. These early-maturing antheridiogen-producing gametophytes will mainly develop the egg-forming female sex organ. This mechanism results in a small number of female gametophytes being surrounded by male gametophytes, promoting out-crossing and the maintenance of genetic diversity. Although this phenomenon was first discovered in 1950 (4), very little is known about how antheridiogen production is regulated and how this signal is perceived.

Tanaka *et al.* (3) show that an antheridiogen gibberellin (GA) A₉ methyl ester (GA₉-Me) is C3 hydroxylated and de-methylated to become an active GA (GA₄). This antheridiogen is produced via the conserved gibberellin biosynthetic pathway in plants (3, 5, 6), although the methyl transferase and methyl esterase for the conversion between GA₉ and GA₉-Me have not yet been identified. Importantly, Tanaka *et al.* find that genes encoding several enzymes for the production of GA₉ are more highly expressed in the early-maturing gametophyte than in the late-maturing young gametophytes. In contrast, the gene encoding the enzyme

(GA 3-oxidase) for the conversion of GA₉ to the active GA₄ is preferentially expressed in the late-maturing young gametophytes, which are known to be highly sensitive to antheridiogens. This gene expression partitioning explains why only the early-maturing gametophytes produce the antheridiogen GA₉-Me and only the late-maturing younger gametophytes can respond to this pheromone to become males (see the figure).

In seed plants, GA₄ is an active hormone that plays a key role in regulating both vegetative and reproductive development (5, 6). However, GA₉-Me is inactive. GA₄ turns on the GA signaling pathway by activating its nuclear receptor GIBBERELLIN INSENSITIVE DWARF1 (GID1) to interact with and induce degradation of the DELLA master growth repressors (7, 8). Tanaka *et al.* find that GA₄ in the Japanese climbing fern (a non-seed plant) activates the GA response pathway in a similar manner: GA₄, but not GA₉-Me, induces the GID1-DELLA interaction. Moreover, GID1 is preferentially expressed in the late-maturing young gametophyte, and treatment of such a gametophyte with a GID1 inhibitor blocks the male-inducing effect of GA₉-Me, supporting the idea that the GAGID1-DELLA signaling module controls sex organ differentiation in this fern.

An outstanding critical question is how the fern is able to respond to a signal made endogenously at low levels and which is then further diluted upon secretion into the environment. Tanaka *et al.* measured the biochemical properties of the key enzyme GA 3-oxidase and the GA receptor GID1 and found that these proteins have up to 24- and 100-fold higher affinity, respectively, for substrate and ligand than their seed plant counterparts, facilitating the necessarily highly sensitive response to the scarce antheridiogen. Another key question the authors addressed is why ferns do not simply produce GA₄ as an antheridiogen. Tanaka *et al.* show that GA₉-Me is more efficiently taken up than GA₄ by the young gametophytes, likely because the hydrophobic GA₉-Me can easily diffuse through the cell membrane. However, how GA₉-ME is transmitted through the aqueous environment is unknown; Tanaka *et al.* suggest that a protein transporter may facilitate this process.

Sex determination in plants can be controlled by genes located on the sex chromosomes or by chemical signals, such as hormones in seed plants, and pheromones (such as antheridiogens) in non-seed plants, such as ferns (2). However, the detailed molecular mechanisms of sex determination in plants are presently largely unknown. The identification of the conserved GA-GID1-DELLA signaling module as the central regulator in sex organ differentiation in the fern is important, especially because GA also controls sex determination in some seed plants, such as *Zea mays* (corn) and *Cucumis sativa* (cucumber). Future studies of the downstream signaling pathways from DELLA in different plant species will reveal whether the GA-regulated sex determining process is conserved more broadly across plants.

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References and Notes

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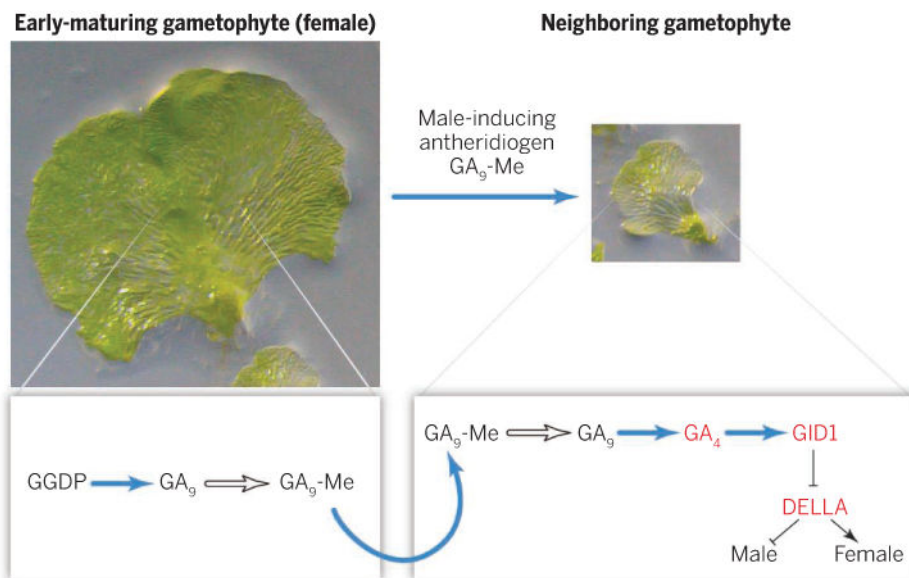


Figure. Sorting out sexual differentiation

Interplant communication via antheridiogen between early- and late-maturing gametophytes is achieved by physical separation of the GA biosynthetic pathway in these individuals. The antheridiogen (GA_9-Me) is produced and secreted by the early-maturing gametophyte (left). Once taken up by the neighboring late-maturing young gametophyte (right), GA_9-Me is converted to the active GA_4 . GA_4 activates its receptor $GID1$, which in turn promotes male sex organ formation by inhibiting the GA signaling repressor $DELLA$. The open arrows represent steps catalyzed by unidentified enzymes. GGDP, geranylgeranyl diphosphate.