7.346 Plants at War: How Conflicts Shape Plant Genetics, Molecular Biology, and Development

Thursdays, 1 p.m. – 3 p.m.

Instructors: Satyaki Rajavasireddy and Rebecca Povilus
(laboratory of Mary Gehring)

Course Description:

Plants might appear to be passive fixtures in the environment. However, these often over-looked organisms are constantly engaged in battles against a wide variety of assailants on scales small and large – from genomic to ecological. This course will take a plant's-eye-view of three main types of conflicts, and in doing so will explore core concepts across genetics and molecular and developmental biology.

- First, we will examine how plants deal with other organisms in the race for resources. We will discuss how parasitic plants hijack resources and genes of their hosts, how the plant immune system uses RNA-silencing to confront pathogens, how mutually-beneficial partnerships with bacteria are negotiated, and how plants use molecular signals to manipulate their environments to defend precious resources.
- Second, we will focus on conflicts during reproduction. We will explore the race between male gametes as they search for egg cells, as well as the struggle between parental genomes as each tries to maximize its own fitness while fighting over how maternal resources are invested into seeds. We will start with classic interploidy-cross experiments that uncovered this interparental conflict by altering parental genome dosage in the offspring, then look at more recent discoveries about how gene dosage, genetic imprinting, and epigenetic modifications are involved, and finally explore how this tug-of-war between mothers and fathers can lead to the creation of new species.
- Third, we will examine conflicts that occur within an individual plant, both during development and within the genome. We will discuss the molecular signals plants use while deciding to allocate resources to vegetative (leaves, branches) or reproductive (flowers, fruits) growth, and the resulting consequences for plant architecture and reproductive fitness. On a genomic scale, we will learn how selfish, self-replicating genetic elements known as transposons try to take over a plant's genome, and how some genes use a process called "meiotic drive" to manipulate the machinery behind chromosome segregation during meiosis to break the rules of Mendelian inheritance.

We will focus on the primary research literature so that students will learn the principles of experimental design and the practice of how to critically read a scientific paper. Students will analyze and prepare a written report about a paper of their own choosing, and then present and critique another paper to the class during an oral presentation. The course will include a field trip (in-person or virtual) to the Weld Hill plant biology research facility at Boston's Arnold Arboretum. Overall, this course will use plant biology not only as a context for learning about emerging topics in biology but also as an introduction to the dynamic, surprising, and often beautiful nature of plants.

Objectives:

This course will introduce students to primary scientific literature focused on plant biology and the conflicts plants face throughout their lives. As we discuss such conflicts at ecological, organismal, molecular and cellular scales, we will examine the wide variety of techniques and experimental approaches that are used during research in molecular biology, genetics, development, and evolutionary biology. Students will learn how to critically assess the design, results, and impact of key experiments, including how to distinguish between correlative and mechanistic studies.

Format: The class will meet weekly for two hours. Each week, students will critically read two papers from the primary research literature and will evaluate these papers, focusing on experimental design, control experiments, methods and interpretation of the data.

For each paper, students should be able to discuss major points from each figure, as well as how presented experiments relate to broader conclusions of the paper. While reading papers, the following questions should be considered:

- What are the key experiments (including controls) of the paper?
- Are the data presented sufficiently convincing to support the final conclusion? If not, what other experiments would be needed to support the conclusion?
- Is there a particular experiment missing that would have strengthened the findings?
- Are there additional controls that would have increased the robustness of the data?
- Is the interpretation of the experimental data clear and rational?
- Are there any questionable figures or data (e.g. bad western blots, statistical flaws, no quantifications etc.)?
- What related questions remain unanswered by this study? What new questions have arisen?
- Is there anything that you could not understand (methodology, etc.)?

At the end of each class, the instructors will give a short introduction to the papers for the following week.

Grading:

The course will be graded as "pass "or "fail." A passing grade will be given to students who attend the class, participate in discussions, and complete both assignments in a satisfactory manner.

Prerequisites:

Previous course-work in molecular biology, genetics, or plant biology is recommended; please consult the instructors (via email) if you are unsure about your background.

Attendance:

Students are expected to attend all sessions and take part in discussions. If a student needs to miss a class, they must contact the instructor as soon as possible, prior to the class through email. The student must submit a one-page report about one of the papers discussed in class before the next class session after the missed class. The report should include a brief statement of the goal of the research, identify the single most important experiment and control(s), and explain why the interpretation is or is not validated by that experiment.

Field trip to Arnold Arboretum of Harvard University *(virtual or in-person, pending current COVID situation)*:

The Arnold Arboretum is a 281-acre preserve in the heart of Boston and stewards one of the world's most comprehensive and best documented collections of temperate woody plants, with particular focus on the floras of eastern North America and eastern Asia. You may have enjoyed the Arnold Arboretum as the jewel of Boston's Emerald Necklace park system, but did you know that the living collections, herbarium, and library/archives support research at on-site laboratories and by scholars around the world? With this field-trip, we will talk to researchers at the Arboretum's Weld Hill Research Laboratory, as well as take a look at all the work that goes into maintaining a world-class plant germplasm collection. The field trip will be scheduled for April 1st.

Assignments:

1. Write an abstract: The written assignment, due Week 8 (Apr 8th) will discuss a peer-reviewed primary research paper (not included as one of the assigned weekly readings in the course) that relates to the course material. Early in the course we will discuss strategies for searching for high-quality research papers, so that students can select papers for assignments; selected papers should be sent to the instructors at least two weeks (Week 6, March 25th, 2021) in advance of the due date for instructor approval. Within two double-spaced pages, the student should briefly describe the paper's main questions and hypothesis and critically discuss the key experimental and control data and interpretation of the results.

2. Present a primary research paper: Final oral presentations will occur during the last class meeting (Week 14, May 20th). Students will give a 15-minute PowerPoint presentation discussing a chosen primary research paper which should relate to a broad, conflict-related topic to be chosen by the class (topic will be chosen during the class of Week 10, April 22nd). The paper needs to be approved by course instructors; the selected papers should be sent to the instructors at least two weeks in advance, by Week 12, May 6th, and should be different from the paper chosen for the first assignment. As with the written assignments, the oral presentation should outline the paper's main question(s) (2-3 slides), describe the key experimental and control data (up to 7 slides), and critically analyze the author's interpretation and conclusions (4-5 slides).

Sessions and papers:

1. Intro to course (*Feb. 18th, 2021*): (introductions, course mechanics, explanation of student projects, walk-thru of how to read a paper, walk-thru of how to find and access papers, "crash-course" intro to plant biology, including brief introduction to plant interactions via hormones and other signaling molecules)

Conflicts between individuals/species:

2. Conflict at an ecological scale (*Feb. 25th, 2021*): This section will cover how plants interact with, and influence, their environment as they compete for resources. *Venturelli et al. (2015)* focus on how plants can discourage competitors by secreting molecular signals into the soil. This paper follows the course of an investigation that begins with modeling molecular interactions, then demonstrates effects on plant growth, and finally uncovers the mechanism by which effects on growth are enacted. *Bastias et al. (2018)* approach the issue from an ecological perspective, dealing with how complex interactions among plants, symbiotic fungi, and herbivores are mediated by plant hormone signals. Notably, this paper demonstrates how complex phenomena can be broken down to identify key factors within a system.

    - Plants release precursors of histone deacetylase inhibitors to suppress growth of competitors. S. Venturelli, R. G. Belz, A. Kämper,A. Berger, K. von Horn, A. Wegner, A Böcker, G. Zabulon, T. Langenecker, O. Kohlbacher, F. Barneche, D. Weigel, U. M. Lauer, M.Bitzer, and C. Beckerf, Plant Cell (2015), 27(11): 3175–3189., https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4682303/

    - Jasmonic acid regulation of the anti-herbivory mechanism conferred by fungal endophytes in grasses. D. A. Bastías, M. A. Martínez-Ghersa, J. A. Newman, S. D. Card, W. J. Mace, P. E. Gundel, Journal of Ecology (2018), https://doi.org/10.1111/1365-2745.12990, https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2745.12990

    - 10-min introduction to plant immune response and small RNA pathways.

3. Plants vs. pathogens (*Mar. 4th, 2021*): Plants produce small RNAs that target pathogen mRNAs for degradation. In a fascinating arms race, some pathogens have also acquired the ability to repress the plant small RNA pathway. *Shamandi et al. (2015)* use genetic, biochemical and genomic means to show that faced with a viral infection, plants prioritize small RNA pathways essential for defense against viruses at the expense of other processes that use small RNAs. They also show that the virus, however, can respond by shutting down these host defense systems. *Cai et al. (2018)* use genetic and biochemical means to show that plants send anti-fungal small RNAs packaged in vesicles to invading fungi.

    - Plants encode a general siRNA suppressor that is induced and suppressed by viruses. N. Shamandi, M. Zytnicki, C. Charbonnel, E. Elvira-Matelot, A. Bochnakian, P. Comella, A. C. Mallory, G. Lepère, J. Sáez-Vásquez, H. Vaucheret, PLOS (2015), https://doi.org/10.1371/journal.pbio.1002326

    - Plants send small RNAs in extracellular vesicles to fungal pathogen to silence virulence genes. Q. Cai, L. Qiao, M. Wang, B. He, F. Lin, J. Palmquist, S. Huang, H. Jin, Science

(2018), 360(6393): 1126-1129, DOI: 10.1126/science.aar4142, https://science.sciencemag.org/content/360/6393/1126

- 10-min introduction to bacterial symbiosis

4. Bacteria - friend or foe? (*Mar. 11th, 2021*): Bacteria can represent pathogenic threats to a plant, or they can be beneficial symbionts that fix nitrogen in exchange for other nutrients. This section will explore how symbiotic relationships must operate in the context of the plant immune system. *Miyata et al. (2014)* address the topic by asking what role a known immune-response gene plays in regulating interactions between the plant and beneficial bacteria. *Van velzen et al. (2018)* take a different approach to understand how plant-bacteria symbiosis occur - by examining independent evolutionary acquisitions of that symbiosis to look for common components. Together, these papers explore how to study gene function in species with and without well-developed genetic resources/tools.

    - The bifunctional plant receptor, OsCERK1, regulates both chitin-triggered immunity and arbuscular mycorrhizal symbiosis in rice. K. Miyata, T. Kozaki, Y. Kouzai, K. Ozawa, K. Ishii, E. Asamizu, Y. Okabe, Y. Umehara, A. Miyamoto, Y. Kobae, K. Akiyama, H. Kaku, Y. Nishizawa, N. Shibuya, T. Nakagawa, Plant & Cell Physiology (2014), 55(11): 1864-1872 doi:10.1093/pcp/pcu129, https://academic.oup.com/pcp/article/55/11/1864/2756060?login=true

    - Comparative genomics of the nonlegume *Parasponia* reveals insights into evolution of nitrogen-fixing rhizobium symbioses. R. van Velzen, R. Holmer, F. Bu, L. Rutten, A. van Zeijl, W. Liu, L. Santuari, Q. Cao, T. Sharma, D. Shen, Y. Roswanjaya, T. A. K. Wardhani, M. S. Kalhor, J. Jansen, J. van den Hoogen, B. Güngör, M. Hartog, J. Hontelez, J. Verver, W. Yang, E. Schijlen, R. Repin, M. Schilthuizen, M. E. Schranz, R. Heidstra, K. Miyata, E. Fedorova, W. Kohlen, T. Bisseling, S. Smit, R. Geurts, PNAS (2018), 115(20): E4700-E4709; https://doi.org/10.1073/pnas.1721395115

    - 10-min introduction to parasitic plant biology

5. Host-parasitic plant interactions (*Mar. 18th, 2021*): Parasitism has evolved several times across plants and involves a wide array of morphological and physiological adaptations. However, all parasitic plants must establish a connection with their hosts. This section will address how parasitic plants tap into their hosts, and how host plants can defend themselves against parasitic plants. *Ogawa et al. (2020)* use tissue-specific RNA sampling to explore gene expression in the structure that forms the interface between a parasite and its host, and goes on to identify promoter regions and genes that are essential for parasite success. This paper is available as a preprint on bioRxiv; we will discuss the evolving role of preprint servers in academic publishing. *Alakonya et al. (2012)* uncover cross-species RNA interference as a mechanism by which the host can control parasite development. Together, these papers address the broader question of how cell-cell (and organism-organism) communication can occur across cell walls and protective epidermal layers.

    - Subtilase activity in the intrusive cells mediates haustorium maturation in parasitic plants. S. Ogawa, T. Wakatake, T. Spallek, J. K. Ishida, R. Sano, T. Kurata, T. Demura, S. Yoshida, Y. Ichihashi, A. Schaller, K. Shirasu, bioRxiv (2020),

https://doi.org/10.1101/2020.03.30.015149,
https://www.biorxiv.org/content/10.1101/2020.03.30.015149v1

- Interspecific RNA interference of SHOOT MERISTEMLESS-Like disrupts *Cuscuta pentagona* plant parasitism. A. Alakonya, R. Kumar, D. Koenig, S. Kimura, B. Townsley, S. Runo, H. M. Garces, J. Kang, A. Yanez, R. David-Schwartz, J. Machuka, N. Sinha, The Plant Cell (2012), 24 (7) 3153-3166, DOI: https://doi.org/10.1105/tpc.112.099994, http://www.plantcell.org/content/24/7/3153.short

- 10-min introduction to flowering plant life cycle and sexual reproduction (pre fertilization)

Conflicts during reproduction:

6. Competition between males (pollen tubes) (*March 25th, 2021*)**:** What happens after pollen lands on a flower? Hidden within the female tissues there is a race between sperm-bearing pollen tubes, to see which males get to father the next generation. Competition between male gametes (or here, gametophytes) has been an important force in plant evolution, shaping everything from floral forms to plant-pollinator interactions. *Swanson et al. (2016)* present foundational experiments in the study of pollen tube competition - which were performed more recently than you may expect. We will discuss why basic questions in the field of pollen tube competition had gone unanswered for so long. *Okudaa et al. (2013)* take advantage of the unique biology of the plant species *Tourinia fournieri* to determine how pollen tubes use molecular signals to find egg cells.

    - Pollen performance traits reveal prezygotic nonrandom mating and interference competition in *Arabidopsis thaliana*. R. J. Swanson , A. T. Hammond , A. L. Carlson , H. Gong , T. K. Donovan, American Journal of Botany (2016), https://pubmed.ncbi.nlm.nih.gov/26928008/

    - Acquisition of LURE-binding activity at the pollen tube tip of *Torenia fournieri*. S. Okudaa, T. Suzukiab, M. M. Kanaokaa, H. Moric, N. Sasakia, T. Higashiyama, Molecular Plant (2013), 6(4):1074-1090, https://doi.org/10.1093/mp/sst050, https://www.sciencedirect.com/science/article/pii/S1674205214609035

    - 10-min introduction to flowering plant sexual reproduction (post-fertilization)

    - DUE: propose paper for assignment #1

7. **Field Trip:** Visit to Arnold Arboretum (*Apr. 1st, 2021*). The field trip, whether virtual or in-person, will feature a seasonal highlight of the collections and meetings with researchers and collection managers to discuss the role of institutions like botanical gardens. *Meeting time may change in the case of an on-site visit (pending current COVID situation).*

8. Inter-parental conflict during seed development: developmental evidence (*Apr. 8th, 2021*): This session is about the interactions that occur with the complex, multi-generational system that is the flowering plant seed. We will start with a classic interploidy cross experiment in *Scott et al. (1998)* that alters parental genome dosage in offspring tissues to understand parental control of maternal resource distribution and offspring growth after fertilization. Experiments like these provided the foundation for inter-parental conflict theory. Applying to plants and animals alike,

inter-parental conflict predicts that, under certain conditions, mothers and fathers maximize their own fitness by enacting opposing strategies when it comes to offspring care. However, conflicts occur among siblings as well; *Wu et al. (2013)* make use of colorful genetic markers and the rare phenomenon of heterospermy in maize to test whether having different fathers impacts sibling cooperation.

- Parent-of-origin effects on seed development in *Arabidopsis thaliana*. R. J. Scott, M. Spielman, J. Bailey, H. G. Dickinson, Development (1998), 125: 3329-3341; https://dev.biologists.org/content/125/17/3329.short

- Kin recognition within a seed and the effect of genetic relatedness of an endosperm to its compatriot embryo on maize seed development. C. Wu, P. Diggle, W. H. Friedman, PNAS (2013), 110 (6) 2217-2222; https://doi.org/10.1073/pnas.1220885110, https://www.pnas.org/content/110/6/2217

- 10-min introduction to imprinting, DNA and histone methylation.

- DUE: Assignment #1

9. Inter-parental conflict during seed development: molecular mechanisms (*Apr. 15th, 2021)*: At the heart of the inter-parental conflict is the ability of parents to control gene expression in progeny after fertilization. When making gametes, parents can lay down epigenetic marks in the form of changes to DNA or histone methylation. Therefore, alleles from different parents, even if identical in DNA sequence, can be still be perceived differently by transcription factors and transcriptional machinery. In plants, these epigenetic marks are known to regulate expression in one of the offspring tissues: the endosperm. *Choi et al. (2002)* describe genetic approaches to identify a DNA demethylase that acts in the gamete to regulate gene expression in the endosperm. *Moreno-Romero* et al. *(2019)* use a genomics approach to interrogate epigenetic marks on maternally and paternally inherited chromosomes within the endosperm.

    - DEMETER, a DNA glycosylase domain protein, is required for endosperm gene imprinting and seed viability in *Arabidopsis*. Y. Choi, M. Gehring, L. Johnson, M. Hannon, J. J.Harada, R. B.Goldberg, S. E. Jacobsen, R. L. Fischer, Cell (2002), Volume 110(1), https://www.sciencedirect.com/science/article/pii/S0092867402008073#FIG2

    - Epigenetic signatures associated with imprinted paternally expressed genes in the *Arabidopsis* endosperm. J. Moreno-Romero, G. Del Toro-De León, V. Kumar Yadav, J. Santos-González, C. Köhler, Genome Biology (2019), vol. 20, https://genomebiology.biomedcentral.com/articles/10.1186/s13059-019-1652-0

    - 10-min introduction to hybrid incompatibility and reproductive isolation.

10. Evolutionary consequences of inter-parental conflict - speciation via hybrid incompatibility (*Apr. 22nd, 2021*): Conflicts lead to arms races and rapid evolution of molecular machinery. These rapid changes can in turn lead to evolution of incompatibilities and reproductive isolation. In previous classes, we discussed how imprinting might have evolved as the result of parental conflict. In this section, we discuss how parental conflict can drive the evolution of reproductive isolation. *Bushell et al. (2003)* provide evidence that the reproductive isolation barrier between *Arabidopsis thaliana* and *Arabidopsis arenosa* is sensitive to parental genome dosage and to DNA

methylation. *Lafon-Placette et al. (2018)* address the prediction that parental conflict should be higher in outcrossing species compared to inbreeding species. By crossing sister species that outcross or inbreed, they demonstrate how differences in imprinting associate with different reproductive strategies and how these differences might contribute to reproductive isolation.

- The basis of natural and artificial postzygotic hybridization barriers in *Arabidopsis* species. C. Bushell, M. Spielman, R. J. Scott, The Plant Cell (2003), DOI: https://doi.org/10.1105/tpc.010496, http://www.plantcell.org/content/15/6/1430

- Paternally expressed imprinted genes associate with hybridization barriers in *Capsella*. C. Lafon-Placette, M. R. Hatorangan, K. A. Steige, A. Cornille, M. Lascoux, T. Slotte, C. Köhler, Nature Plants (2018), 4: 352–357, https://www.nature.com/articles/s41477-018-0161-6

- 10-min introduction to meristems and modularity in development of plant body plan

- Choose broad topic for Student Presentations *(during class)*

Conflicts within an individual

11. Resource allocation between vegetative and reproductive organs *(Apr. 29th, 2021)*: Unlike animals, plants are perpetually embryonic and add new modules (which can include leaves, stems, roots, and reproductive structures) throughout their lives. This means that plants have to make decisions about how to deploy modules based on environmental inputs; for example, when should resources be allocated to vegetative growth or to reproduction? The first paper provides examples of how to analyze complex traits like "plant growth" throughout development to understand how developmental processes relate to each other. We will discuss how the information presented in this paper impacts experimental design for research using the 'lab rat' of plants, *Arabidopsis thaliana.* The second paper addresses the question of how plants regulate their own growth by controlling the behavior of meristems (plant 'stem cell' populations). Can a plant use information like "How many fruits have I already made?" to decide whether to keep making flowers? This paper uses experimental manipulation of plants and genes to build a model of genetic regulation of meristem activity.

    - Allometry and plasticity of meristem allocation throughout development in *Arabidopsis thaliana*. S. P. Bonser & L. W. Aarssen, Journal of Ecology (2001), 89(1): 72-79. https://www.jstor.org/stable/3072119?seq=1#metadata_info_tab_contents

    - Inflorescence meristem fate Is dependent on seed development and FRUITFULL in *Arabidopsis thaliana*. V. Balanzà1 I. Martínez-Fernández, S. Sato, M. F. Yanofsky, and C. Ferrándiz1, Front. Plant Sci. (2019), https://www.frontiersin.org/articles/10.3389/fpls.2019.01622/full

    - 10-min introduction to transposons in plants

12. Genomic conflicts with transposons *(May 6th, 2021)*: Transposons are extremely successful selfish genetic elements found across all organisms. Transposons treat the host genome as an ecosystem within which they can proliferate. Transposon proliferation can happen during some developmental stages, during S phase or in response to heat stress. This proliferation phase often

requires cross-talk between transposon encoded components and host machinery. This topic is the subject of the first paper. *Cavrak et al. (2014)* use genetic and molecular biological approaches to show how a heat responsive transposon, *ONSEN,* proliferates in responses to heat stress and use heat shock factor binding sites to hack into the plant heat stress response pathway. However, the proliferation of transposons can lead to their insertion into new sites in the genome. These insertions can disrupt host genes, increase ectopic recombination and confer DNA damage. The host therefore must be able to repress transposon activity. *Mari-Ordonez et al.* (2013) use genetic, genomic and molecular biological approaches to describe how a naive *Arabidopsis thaliana* strain defends against the invasion of the transposon *EVADE* via both transcriptional and post-transcriptional gene silencing mechanisms.

- Reconstructing de novo silencing of an active plant retrotransposon. A. Marí-Ordóñez, A. Marchais, M. Etcheverry, A. Martin, V. Colot, O. Voinnet, Nature Genetics (2013) 45: 1029–1039, https://www.nature.com/articles/ng.2703

- How a retrotransposon exploits the plant's heat stress response for its activation. V. V. Cavrak, N. Lettner, S. Jamge, A. Kosarewicz, L. M. Bayer, O. M. Scheid, PLOS (2014), https://doi.org/10.1371/journal.pgen.1004115

- 10-min introduction to centromeres, meiosis and segregation distortion

- DUE: Propose paper for assignment #2

13. Genomic conflicts -meiotic drive and its impacts on gametogenesis *(May 13th, 2021)*: During meiosis in diploids, the chance that either allele gets transmitted is 50% for most loci. However, in some cases, Mendelian segregation is violated when meiotic mechanisms preferentially transmit one of the two alleles to the offspring at a higher rate. This "meiotic drive" can make this preferred allele the predominant allele in the population. These drive systems can lead to disease phenotypes and to reproductive isolation. Several mechanisms have been proposed for how changes at the centromere power "meiotic drive." In this session, we will examine tests of two mechanistic models of meiotic drive. *Dawe et al. (2018)* describe a long-running effort to understand meiotic drive of Abnormal chromosome 10 (Ab10) in maize. This paper uses genetic, genomic and cell biological approaches to show that kinesin paralogs encoded on Ab10 bind and convert heterochromatic "knobs" found on Ab10 and other chromosomes into neocentromeres and preferentially drag knob containing chromosomes into egg cells. *Maheshwari et al. (2017)* test a very popular model that tries to explain why centromeric DNA and centromeric histones exhibit rapid changes in DNA sequence. Under this model, centromeric DNA rapidly changes in sequence composition because of meiotic drive, and centromeric histones change in sequence to be able to recognize the rapidly changing centromeric DNA. Work in this paper uses genetics, genomics and molecular evolutionary studies to show that this model is not applicable in *Arabidopsis* and that centromeric histones that do not co-evolve with a centromere can still bind it and support normal meiosis.

    - A kinesin-14 motor activates neocentromeres to promote meiotic drive in maize. R. Kelly R. K. Dawe, E. G.Lowry, J. I.Gent, M C. Stitzer, K. W. Swentowsky, D. M. Higgins, J. Ross-Ibarra, J. G. Wallace, L. B.Kanizay, M. Alabady, W. Qiu, Kuo-Fu Tseng, N. Wang, Z. Gao, J. A. Birchler, A. E. Harkess, A. L.Hodges, E. N. Hiatt, Cell, Volume 173, Issue 4, 3

May 2018, Pages 839-850.e18,
https://www.sciencedirect.com/science/article/pii/S0092867418302897?via%3Dihub

- Centromere location in *Arabidopsis* is unaltered by extreme divergence in CENH3 protein sequence, S. Maheshwari, T. Ishii, C. T. Brown, A. Houben, L. Comai, Genome Res. 2017. 27: 471-478, doi: 10.1101/gr.214619.116, https://genome.cshlp.org/content/27/3/471.full

14. Student Presentations *(May 20th, 2021).* See details above. Final discussion and course reviews.