

Reports and Reviews

The Flowering of Botany at the Harvard Forest

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The Harvard Forest is less than 100 miles (less than a 2-hour drive) from Providence, RI. The Fisher Museum, featuring twenty-three internationally acclaimed dioramas portraying the history, conservation and management of central New England forests, is open Monday - Friday 9am - 4pm and Saturday - Sunday 12pm - 4pm from May – October. Self-guided trails are always open.

Introduction to the Harvard Forest

Located within the New England Upland physiographic region, the Harvard Forest's rolling hills and valleys range from 220m to 410m above sea level. The bedrock underlying the terrain is a mixture of metamorphic rocks formed during continental collisions during the middle Devonian. Local site conditions are driven by the stony glacial tills deposited during the Wisconsin ice age. These are interspersed with local glacial outwash deposits and wetland peats. Soils are stony and acidic, with a wide range of depth and moisture. The very few calcareous or shoreline sites contain a disproportionate amount of the floral diversity of the Forest.

Since its establishment in 1907 the Harvard Forest has served as Harvard University's outdoor laboratory and classroom for research and education in forest biology, ecology, and conservation. Located 65 miles west of Cambridge in the rural town of Petersham, Massachusetts, the land base includes diverse forests, wetlands and streams, as well as the 70-acre Harvard Pond (**Figure 1**). From a center comprising 3500 acres of land, research facilities, classrooms, residences and the Fisher Museum (Foster and O'Keefe 2000),

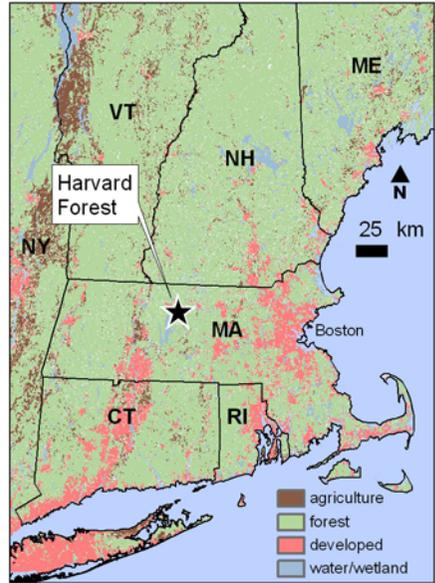


Figure 1. Harvard Forest's location in New England (Map: B.R. Hall).

the scientists, students, and collaborators at the Forest explore topics ranging from forest and biodiversity conservation and environmental change to land-use history and the ways in which physical, biological and human systems interact to change our earth.

The climate is cool, moist temperate: July mean temperature is 68°F and the January mean temperature is 21°F. Throughout the region, winter temperatures have warmed nearly 5°F over the last 40 years, a remarkably rapid change. The average annual precipitation is 110cm and is distributed fairly evenly throughout the year as rain and snow. Forest cover dominates the current landscape. While there are some quite old trees, the land was largely cleared for agriculture during the 18th and 19th centuries (**Figure 2**). Remaining primary forests were used as woodlots during the agricultural period, and remnant old-growth forests were blown down in the Great 1938 Hurricane. Historical land-use determines the basic patterns of vegetation distribution even after more than 100 years (Motzkin et al. 1999).

The Harvard Forest Long Term Ecological Research Program (NSF) has served as a foundation for integrated, long-term studies of forest dynamics since 1988. Beginning this



Figure 2. Second-growth forest with stonewall legacies of the agricultural past (photo: D.R. Foster)

year, the National Ecological Observatory Network (NEON) is initiating research at Harvard Forest as part of its continental-scale network of ecological observatory sites. The Harvard Forest is a department within the Faculty of Arts and Sciences of Harvard University and administers the Graduate Program in Forestry and a Summer Research Program in Ecology. The Forest has extensive field research infrastructure including three eddy flux towers, two walk-up towers, a mobile canopy lift, a meteorological station, two gauged low-order watersheds, numerous long-term experimental plots, and paleoecological, historical and permanent plot studies. Twelve buildings (70,000 ft²) provide laboratories, an archive, library, museum, lecture hall for 125, two classrooms and numerous discussion rooms, dormitories and single-family housing, commercial kitchen and a dining room for 100. The on-site staff of 35, together with >100 collaborating scientists, engage in research spanning a wide range of the biological, physical, social, and computer sciences. An integrated administrative and facilities staff supports all aspects of research, education and outreach.

Despite the geographic distance, faculty at the



Figure 3. The 2010 Harvard Forest Freshman Seminar class. The course title this year is "Global Change Ecology – Forests, Ecosystem Function, and the Future" (photo: D.R. Foster)

Forest fulfilled their teaching obligations mainly in Cambridge so that interaction between them and both graduate and undergraduate students was always a priority. Forest staff were early adopters of Harvard's innovative Freshman Seminar program, which has been conducted for nearly 30 years (**Figure 3**). The course runs over four weekends at Harvard Forest, introducing basic concepts of forest biology to generations of first-year students. The success of this seminar and recognition of the unique facilities for field research prompted the formation of a summer research program in ecology, instigated by current director David Foster and now superbly led for more than 25 students annually by Senior Ecologist Aaron Ellison. The program involves Forest staff and mentors from collaborating institutions, and makes full use of the Forest's accommodations, laboratories and field facilities.

Botanical Research at the Forest

Through the years, researchers have focused on forest management, soils and the development of forest-site concepts, the biology

of temperate and tropical trees, plant ecology, forest economics, landscape history, conservation biology, and ecosystem dynamics. Historically, we may recognize three periods, each with a different emphasis: first, the establishment of an understanding of the nature of the forests themselves as exemplars of forest dynamics in New England, which coincided with a lengthy period of active forest management and research in silviculture; second, a period when research was funded extensively by the Maria Moors Cabot Foundation during which a diversity of botanical projects were supported; and third, the current period when the Harvard Forest returned to its strong integration of field, laboratory and theoretical studies and became part of the Long-Term Ecological Research program funded by the National Science Foundation with the main focus on the ecological dynamics of the vegetation and land-use at the Forest and throughout New England. Throughout the

many studies of silvics and soils. Most publications from this era focused on the growth and site relations of commercial timber species, with some work conducted on wood anatomy by Irving Bailey, who earned the Master of Forestry at Harvard in 1909 and then served on the Harvard faculty (e.g., Bailey 1910).

The first records of the woody plants at Harvard Forest were collected by John George Jack and his students in 1908. Jack was an assistant professor of dendrology at the Arnold Arboretum, and published his findings in the 1911 *Bulletin of the Harvard Forestry Club*.

The Blossoming of Botanical Research, 1937-1987

As a consequence of efforts by Fisher's successor, Ward Shepard and botanical administrator Edwin D. Merrill, the Maria Moors Cabot Foundation for Botanical Research was established at Harvard University in 1937 with funding from Godfrey L. Cabot, a Boston industrialist. For fifty years, this foundation would provide steady support for a wide range of research at Harvard's botanical institutes, including the Harvard Forest. Dr. Cabot, the benefactor, was particularly interested in enhancing the productivity of trees, with a



Figure 4. Fisher Museum diorama depicting the first thinning of a mixed-hardwood forest, ca. 1930.

various programs researchers at the Forest and beyond have maintained a strongly collaborative approach, which is a hallmark of the scientific community in Petersham.

Establishment of the Forest, 1907-1937

The early years saw the establishment of extensive experimental forest plantations and the development of mixed-species silviculture (**Figure 4**), notably by R.T. Fisher, who served as the Harvard Forest's first director from 1907-1934, and his student and third director Albert C. Cline. Demonstration of sustained yield forestry was a primary focus, supported by



Figure 5. This 1910s photo of the old-growth Pisgah tract appeared in Merrill's announcement of the Cabot Foundation in *Scientific Monthly*. The forest was destroyed one year later by the Great Hurricane of 1938 (photo: Harvard Forest Archives)

rationale that sounds quite modern: to better utilize the energy embodied in living plants so that we might be less dependent on fossilized plant remains (fossil fuels). Professor Merrill's announcement of the foundation in *The Scientific Monthly* (Merrill 1937) featured several photos of forest types and experiments at the Harvard Forest (**Figure 5**).

The botanist Hugh M. Raup came to the Harvard Forest in 1937 and served as director from 1946-1967. He made many fine botanical collections that were complemented by his wife Lucy's collections of lichens and bryophytes and produced a *Checklist of the Vascular Plants of Petersham*, but much of his botanical work was in the Arctic. His broad-minded



Figure 6. Hugh Raup holds court next to a birch growing on top of a treefall mound (photo: Harvard Forest Archives).

understanding of the ecology, geography, botany and history of the Arctic and New England led to his challenge to stable-state successional theory with his counter-message of change, unpredictability of natural and human systems, and ecosystem resilience (**Figure 6**).

Later, in association with the newly established Department of Organismic and Evolutionary Biology at Harvard, academic horizons were

broadened when as many as five faculty made Harvard Forest their home. Notably they laid emphasis on the purpose of the Cabot Foundation, which was to support research on trees and communicate this knowledge widely. The scholarly presence always focused on interactions among different researchers, a well-sustained tradition with all Forest visitors.

Martin Zimmerman, who was brought to the Forest in 1954 by Professor Raup and became Harvard Forest Director in 1969, had an insightful ability to combine structure with function that led to a better understanding of long distance transport in woody plants (Zimmerman 1971, 1983). His reach extended well beyond the Forest itself. For example, he made fundamental discoveries about the anatomy of palm trees that could be translated back to more conventional trees.

John G. Torrey chose to move his research from Cambridge to Petersham in order to build state-of-the-art laboratories and greenhouse facilities that made possible the study of plants outside their natural habitat in order to explore the development and physiology of roots (Torrey and Clarkson 1975). His work on the symbiotic relations between trees and microbial organisms bridged the interface between physiology and ecology (Torrey 1978). Peter DelTredici, now Lecturer in the Department of Landscape Architecture and Senior Research Scientist at the Arnold Arboretum, assisted this research during the 1970s.

On his appointment at Harvard in 1971, Barry Tomlinson chose to be located in Petersham so as to continue a long-established research association with Martin Zimmerman. He brought an international perspective to the study



Figure 7. The palm *Rhaps excelsa* L.S. crown (photo: P.B. Tomlinson)

of trees and other plants relating to prior experience in the tropics and subtropics. In retirement he still uses Forest facilities and has recently updated an early study of palm anatomy in collaboration with Jack B. Fisher and J.W. Horn (**Figure 7**).

Botanical Research in an Ecological Context, 1988-Present

As the Cabot funding era came to a close, John Torrey was instrumental in positioning Harvard Forest to become an NSF-funded Long-Term Ecological Research Site. Since then, botany has been explicitly tied to conservation (Foster et al. 2005) and ecology and engages many faculty including Richard Forman from the Graduate School of Design, Steve Wofsy from Earth and Planetary Sciences, Paul Moorcroft, Andrew Richardson and Anne Pringle from Biology. Plant population dynamics, scaling leaf-level physiology to whole-forest function, studying how plants become invasives, and documenting physiological response to climate change are all examples of botanical research in an ecological context (Foster and Aber 2004). The students of Fakhri Bazzaz conducted work in many sites including the Harvard Forest, linking plant allocation, competition, and genetic strategies, with the field of global change biology. A former post-doc, Kristina Stinson is a now plant population ecologist at the Forest, and her current studies include population-to-landscape studies of invasive plants and the mechanisms of increased ragweed pollen production in response to climate change.

Research on long-distance transport of water in trees by Missy Holbrook at the Harvard Forest informs long-term monitoring of carbon and water exchange between the forest and the atmosphere and extends the research legacy of Zimmerman. Twenty years of phenology monitoring of tree leaf-out by Dr. John O’Keefe complements a new phenology web-cam at the Forest that is part of a regional phenology network.

This year, the Harvard Forest is installing a 35-hectare Forest Dynamics Plot in which all woody stems >1cm will be censused every five years, allowing detailed understating of tree demographics in this temperate forest and

comparisons to the Center for Tropical Forest Science network of tropical and temperate plots throughout the world. In addition, David Orwig



Figure 8. Coring a 400-500 year-old black gum (*Nyssa sylvatica*) near the Harvard Forest (photo: D.R. Foster)

conducts detailed dendroecology research on problems including tree response to invasive pests such as the Asian Long-horned beetle and developing a better understanding of the dynamics of the pockets of old-growth forest that remain in Massachusetts (**Figure 8**).

Aaron Ellison uses the northern pitcher plant, *Sarracenia purpurea*, to study the dynamics of food webs. The inquiline foodwebs within the water-filled pitchers of *Sarracenia* are a model system for community ecology work. At the other end of the temporal spectrum, current Forest director David Foster maintains a paleoecology laboratory in which he and others investigate the assembly of vegetation communities over hundreds to thousands of years.

A Centennial Flora

A complete update and analysis of the vascular flora of Harvard Forest was conducted by Jerry

Jenkins, Glenn Motzkin and Kirsten Ward from 2004-2007. This is an elegant, thoughtful work that includes comparisons to previous floras and an analysis of change over the past 100 years. The work is explicitly embedded in an ecological context:

“Harvard Forest is an ecological research station, and our goal in the centennial flora project was to provide an ecological description of the flora. To us this meant that we had to both enumerate the species that were present and describe what they were doing. . . our guiding principle was that plant populations are ecologically interesting entities in a way that individual plants are not. A few stems of a rare species, seen once in one place, are an interesting botanical detail but provide little ecological information. A group of occurrence of the same species starts to have an ecological shape; a group of occurrences with a habitat and a history have a story to tell.” (Jenkins et al. 2008, p.21)

In addition to lively species accounts and an extensive discussion of the taxonomy of “badly behaved species,” the *Flora* provides an analysis of how site, land-use change, climate change and natural disturbance influenced changes over four surveys since 1911. Despite a dynamic century, the native flora has been remarkably stable. The number of alien species has increased, but they have not (yet) made many inroads into the intact second-growth forests.

Conclusion

Investigating the lives of plants will continue as the Harvard Forest settles into its second century, and we look forward to the surprises that await discovery. Here is but one small example. The first author (a forester by training, so no crack botanist) observed purple fringed orchid in 2008, a species never-before recorded at the Harvard Forest. Glenn Motzkin identified the species as *Platanthera grandiflora*, the greater purple fringed orchid (**Figure 9**). While its congener, the lesser purple fringed orchid (*Platanthera psycodes*) was observed elsewhere on the Forest in 1933 and 1947, this species is a new addition to the flora. After even the most careful botanical survey and a century



Figure 9. Large purple-fringed orchid (photo: A. Barker Plotkin)

of intensive research, the woods reveal new and lovely surprises.

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