John C. Almendinger
Ecological Land Classification Program
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Mesic Hardwood Forest System:
Ecological Facts & Concepts Pertinent to Management

Mesic hardwood forests in Minnesota

- Mesic hardwood forests are a geologically recent component of our state's vegetation. Suitable climate did not exist in Minnesota until about 4,000 years ago and the spread of mesic hardwoods since that time has been limited to sites that afford protection from fire.
  - The dominants of mesic hardwood forests, sugar maple and basswood, produce very much less pollen than trees dependent upon the wind for pollen dispersal. Thus, studies of pollen in lake sediments are hard to interpret with regard to mesic hardwood forests unless the studies have that intent.
  - Studies aimed at reconstructing the history of mesic hardwood forests suggest that these forests first appeared in north-central and east-central Minnesota about 4,000 years ago. It seems likely that such forests continued to develop westward from that time and were actively forming when the first settlers came to the state. Mesic hardwood forests in the EBF Province developed as recently as 300 years ago.
  - Component trees, especially basswood, elm, and red oak, have been in the state much longer than that, particularly in the Blufflands Subsection in the southeast. However, there are no good stratigraphic records from there that allow us to be certain that MH communities existed as these trees can occur in other ecological systems.
  - The antiquity of mesic hardwood forests in the North Shore Highlands Subsection is unknown.
- Mesic hardwood forests throughout much of the state are highly correlated with soils that have clayey subsoil horizons or hardpans (mostly Alfisols). It takes time for such soils to form in fresh glacial drift, and this may explain the delayed development of mesic hardwood forests.
  - Nation-wide these soils (mostly alfisols) are correlated with oak trees because the acid litter of oak trees decalcifies the upper solum which is a pre-requisite for moving clay particles down in the soil profile. Mesic hardwoods like elm, basswood, and sugar maple have the *opposite* effect by enriching the soil surface with calcium and other base elements.
  - It is highly significant that Minnesota's mesic hardwood forests occupy sites that were once oak forests. Thus, it seems that oak forests "pre-adapt" sites so that they can be invaded by mesic hardwood trees.

Site conditions favoring mesic hardwoods

- Minnesota's climate is suitable for mesic hardwood trees almost anywhere, but it is also sufficiently dry that fire can deter the development of mesic hardwood trees. Thus, site conditions that make fire unlikely determine more than climate where mesic hardwood forests can form.
  - Rough topography has the effect of slowing wildfires and provides patches of forest less likely to burn such as low swales, ravines, cool north-facing slopes, etc. Mesic hardwood forests are most correlated with rough topography in the Eastern Broadleaf Forest.
  - Lakes and rivers can serve as fire breaks that protect patches of mesic hardwood forest from wildfire. These water bodies provide this service most effectively in the Eastern Broadleaf Forest and Prairie and Aspen Parkland Provinces.
  - In bedrock-cored landscapes, soils must be greater than about 40" to provide habitat for mesic vegetation. Not all deep soils in the Northern Superior Uplands and the Blufflands support mesic hardwood forest because context, slope, and aspect can still provide situations where fire was likely.

- When slopes exceed about 15%, aspect and slope position are important, with northeastern slopes and lower slope positions favoring mesic hardwood forest.

- The link between fire-sensitive mesic hardwood forests and alfisols (and similar soils) seems to be the fact that these soils perch water, are saturated in the spring, have moist duff, and promote early green-up. This greatly reduces the likelihood of spring fires in these forests.

Organic matter and nutrients

- Plant life in mesic hardwood forests revolves around the production and maintenance of a thick humus layer that is enriched in nutrients.
  - The deciduous leaves of mesic hardwood trees are the primary component of the humus layer and species like sugar maple, basswood, and elm shed their leaves while they are full of nutrients. Thus, the trees act like a nutrient "pump" as they extract nutrients from deep in the soil and enrich the soil surface. Exotic earthworms perform much the same function as they bring un-weathered mineral particles to the surface in their casts.
  - It is broadly true that mesic hardwood forest plants enrich or "sweeten" the soil in contrast to fire-dependent forests and Sphagnum peatlands where that become acidic and evolve to nutrient poverty. In all cases, the plants are promoting a soil environment where they have competitive advantage.
  - Removing the humus layer by burning, logging, or by exotic earthworms changes dramatically the species composition of the understory.
- Organic matter, living and dead, is extremely important because it contains most of the nitrogen in a forest.
  - The growth of vegetation in Minnesota's forests is limited by nitrogen, with the possible exception of Floodplain Forests enriched by input of commercial fertilizers.
  - The rate at which nitrogen is cycled (mineralized) in our forests is a good predictor of wood production.
  - Mesic hardwood forests cycle nitrogen about 4 times faster than fire-dependent forest. Bacteria and invertebrates rather than fungi are the primary decomposers.
- Plants in mesic hardwood forests are adapted to an annual cycle of production and decomposition of organic matter.
  - Production occurs in the fall and is composed mostly of deciduous leaves.
  - Decomposition occurs mostly in the spring when moist leaves are subject to aerobic "composting."
  - Humus production and decomposition reach an equilibrium whereby about 3-6 inches of organic matter is in varying states of decay is a constant feature of mesic hardwood forests. It's presence and the timing of nutrient release (particularly nitrate) is far more predictable than in fire-dependent forests where fire episodically consumes organic matter and in wetter forests where the unpredictability of precipitation events controls soil saturation and release of nitrogen as nitrate when dry and ammonium when wet.

Plant adaptations

- Mesic hardwood forests have comparatively high amounts of nutrients and moisture, thus light is the commodity that is often in short supply and the plants have morphological features that help them compete for light and tolerate shade.
  - Understory plants in mesic hardwood forests produce "cheap, disposable" leaves that lack energetically expensive elements of canopy leaves or leaves of plants in harsher environments. Mostly, structural elements associated with water loss (cuticles) and gas exchange can be minimized because the multiple canopies of mesic hardwood forests provide some protection.
  - Understory plants in mesic hardwood forests maintain minimal amounts of enzymes involved in photosynthesis because exposure to sunlight is brief, if not momentary, as sun flecks coming through holes in the canopy pass over the plants.
  - Understory plants in mesic hardwood forests have accessory pigments in their leaves that help use wavelengths of light commonly reflected or transmitted by leaves in the canopy.

- Some species in mesic hardwood forests avoid competing for light by maturing before the overstory trees fully leaf-out.
  - A consequence of maturing early is that energy captured during the leaf-off period must be stored for metabolic maintenance and seed production beneath the full canopy. Thus, many mesic hardwood forest herbs have tubers, roots, and rhizomes capable of storing energetic compounds.
  - The ephemeral habit, whereby plants grow, reproduce, and then die when the canopy has developed is the extreme example of shade avoidance in our mesic hardwood forests. There are many more species of ephemeral plants in our southern mesic hardwood forests (MHs) in comparison to such forests in our central, northern, and northwestern floristic regions.
  - For many herbs in mesic hardwood forests, rapid and early development is facilitated by producing fully differentiated vegetative "buds" in the fall. Trilliums, for example, do this and dissection of the underground buds collected in the fall reveal a complete miniature plant with the stem, leaves, and floral parts differentiated to the point that the species can be identified.
- Because of shade competition, plants of mesic hardwood forests are capable of extensive lateral growth as they "search" for openings in the canopy.
  - Many mesic hardwood herbs are colonial and spread throughout the forest. In some cases individuals in sunnier spots can share resources with colony members that find themselves in dense shade. Alternatively, the shaded individuals die and colonies "migrate" across the forest floor directed by their recent success in finding openings.
  - Some mesic hardwood plants are plastic in their growth form, meaning that they have a creeping or spreading shade-form, and tend to exhibit a more vertical sun-form upon finding a canopy gap. Slippery elm and pagoda dogwoods, for example, creep when in the shade and produce the more familiar tree form when in sunnier habitats.
  - Ecologists suspect that lateral growth below ground is more extensive than is evident above. This may be an adaptation to "searching" for light in cases where aerial stems appear in response to increased light levels, but the plants may be searching for nutrients as much as light.
  - In very old mesic hardwood stands, where the current trees have grown up through individual tree gaps, the ability of trees to lean into gaps or produce large, nearly horizontal branches is evident. Trees in this condition are good indicators of old-growth mesic hardwoods.
- Trees in mesic hardwood forests tend to have seeds where dormancy is broken after a full winter of burial and germination coincident with the spring release of nutrients. Thus, unlike fire-dependent forests where there is a seed bank, mesic hardwoods have a seedling bank.
  - Silviculture around advance regeneration is most appropriate for mesic hardwood forests.
  - Seedlings in mesic hardwood forests may be subsidized through root grafts with parent trees.

Disturbance regimes

- The hallmark of mesic hardwood forests is the near lack of catastrophic disturbance. This is true statewide and disturbance does not explain compositional variation among the NPC classes.
  - Statewide, rotations of catastrophic windthrow or stand regenerating fire were estimated exceed 400 years, and rotations greater than 1000 years are common.
  - The rotation of disturbances that cause partial canopy loss approximate the longevity of the trees, roughly 50 to 150 years. This suggests that mesic hardwood stands were perpetuated by such disturbances and that there is age-dependent mortality of established trees.
- Fire suppression in Minnesota has allowed mesic hardwoods to double or triple their range and abundance since pre-settlement times. Site conditions that defined the "natural" niche of mesic hardwoods are now less confining because fire is not a major influence.