Comparative Physiology of a Central Hardwood Old-Growth Forest Canopy and Forest Gap

A.R. Gillespie, J. Waterman, and K. Saylors[1]

Abstract: Concerns of poor oak regeneration, changing climate, biodiversity patterns, and carbon cycling in the Central Hardwoods have prompted ecological and physiological studies of old-growth forests and their role in maintaining the landscape. To examine the effects of old-growth canopy structure on the physiological productivity of overstory and understory species, we measured physiological parameters of canopy trees in an old-growth oak-maple forest in east-central Indiana. Mid-day measurements of photosynthesis, transpiration, stomatal conductance, photosynthetically-active radiation, humidity, vapor pressure deficit, air temperature, and ambient carbon dioxide levels were taken during the peak of the growing season along the profile of a canopy gap within the forest, and along a height transect within the continuous canopy. Productivity, physiological, and micro-environmental profiles are presented for this old-growth forest and their relationship to current and future tree species composition and forest structure is discussed.

As we move toward the 21st century, our forests of the Central Hardwood Region are moving as well. With the establishment of many of our current forests near the beginning of this century, these mostly even-aged stands are aging, experiencing mortality, and becoming uneven-aged in structure. The growing restrictions on even-aged management will accelerate this metamorphosis. Thus, in many parts of the Central Hardwood Region, foresters must adapt to a changing management regime, recognizing changes in forest structure and composition of species. In the Central Hardwood Region, there is already experience with uneven-aged management, though favored species such as oaks (*Quercus* spp.) are discriminated against due to shade in uneven-aged cuts. And there are ecological studies of individual tree mortality and gap dynamics in these forests (e.g. Runkle, 1991; Parker et al., 1985). What can these studies and management experiences tell the land manager? What information can the silviculturist derive for vegetation management? What the practicing forester finds is a sugar maple (*Acer saccharum* Marsh.) forest replacing oak, usually one to several trees at a time on tracts receiving only partial cutting. The pattern is evident, but we may learn from the casual mechanisms.

If we examine forest dynamics in the eastern U.S., we find that forests can regenerate following major natural disturbances or through replacement of canopy trees, either singly or in small groups, from natural gap formation. The Central Region is mostly characterized by the latter type of disturbance regime and resulting canopy dynamics (Runkle, 1990). The resulting canopy structures and stand age class distributions also influence habitat for regional or migratory wildlife.

When studying the silvics of gap formation and resulting tree regeneration, old-growth forests of the Central Hardwood Region can provide important information for management. These are the forests we might expect to be relatively stable as surrounding forest changes through repeated

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[1]Dept. of Forestry and Natural Resources, Purdue University, 1159 Forestry Building, West Lafayette, IN 47907-1159.

disturbance and natural succession. These forests are important because of their role in maintaining diversity and habitat for late-successional species in the Midwest landscape. But also because gap formation, characteristic of old-growth forest dynamics, is a natural phenomenon increasingly being mimicked through silvicultural operations in this region. Unfortunately, many of these forests are also undergoing change (e.g. Parker et al. 1985; Botkin, 1990). The pattern again is evident, old-growth oak (usually mesic-site oaks) being replaced by sugar maple. The operative physiological and ecological mechanisms, and their implications for uneven-aged silviculture, are the subject of this research.

METHODS

A study has been initiated to examine in detail the physiological processes of different canopy layers in an old-growth forest in east-central Indiana and how they scale up to the ecological processes of succession through gap dynamics. This report is of a preliminary comparison of environmental and physiological parameters between intact old-growth canopy structure and a gap within the canopy.

Study Location and Stand Description

The present study is being conducted in a 20.6 ha old-growth forest remnant on the Davis-Purdue Agricultural Center in Randolph County, IN (Section 23, T21N, R12E). This wet-site oak forest, managed as a research natural area since 1917 by Purdue's Department of Forestry and Natural Resources, is located within the Tipton Till Plain physiographic province (Homoya et al., 1985). Overstory old-growth oaks consist of red oak (*Quercus rubra* L.), white oak (*Q. alba* L.), bur oak (*Q. macrocarpa* Michx.), swamp white oak (*Q. bicolor* Willd.), chinkapin oak (*Q. muehlenbergii* Engelm.), shumard oak (*Q. shumardii* Buckl.), and pin oak (*Q. palustris* Muenchh.). Long-term forest dynamics of this forest have been monitored by the tagging and monitoring of each stem ($\geq$ 10.0 cm dbh) since 1926 (Prentice, 1927; Parker et al., 1985). The last reported structural analysis of this stand (Parker et al., 1985) showed increasing numbers of tree species and increasing stem density and stand basal area (to 320 trees ha^{-1} and 31 m^2 ha^{-1}, respectively). Though basal area growth was mostly associated with residual old-growth oak stems, increasing density was a function of new individuals of sugar maple, Ohio buckeye (*Aesculus glabra* (Willd.), shagbark hickory (*Carya ovata* (Mill.) K. Koch), American elm (*Ulmus americana* L.), and American hornbeam (*Carpinus caroliniana* L.). Additionally, new stems of sugar maple and American elm also contributed significantly to increased basal area. The diameter distribution of the stand is well-represented by the negative exponential model or "inverse J-shaped" curve typical of uneven-aged stands.

Canopy Measurements

During 1991, two 30 m towers were erected into the canopy of the old-growth forest. The first was located in continuous canopy (Figure 1) where multiple stems surrounded the tower, and their crowns and others intersected the tower at multiple levels within the canopy. The second tower was located at the western edge of a roughly circular canopy gap, approximately 10-15 m in diameter. Old-growth shumard oak and shagbark hickory intersected the tower at upper levels. Sugar maple and American elm were found near the base of the tower at the edge of the gap. Previously, elms would have intersected this tower at approximately 5 and 7 m, but recent mortality due to dutch elm disease left standing snags adjacent to the tower (Figure 2).

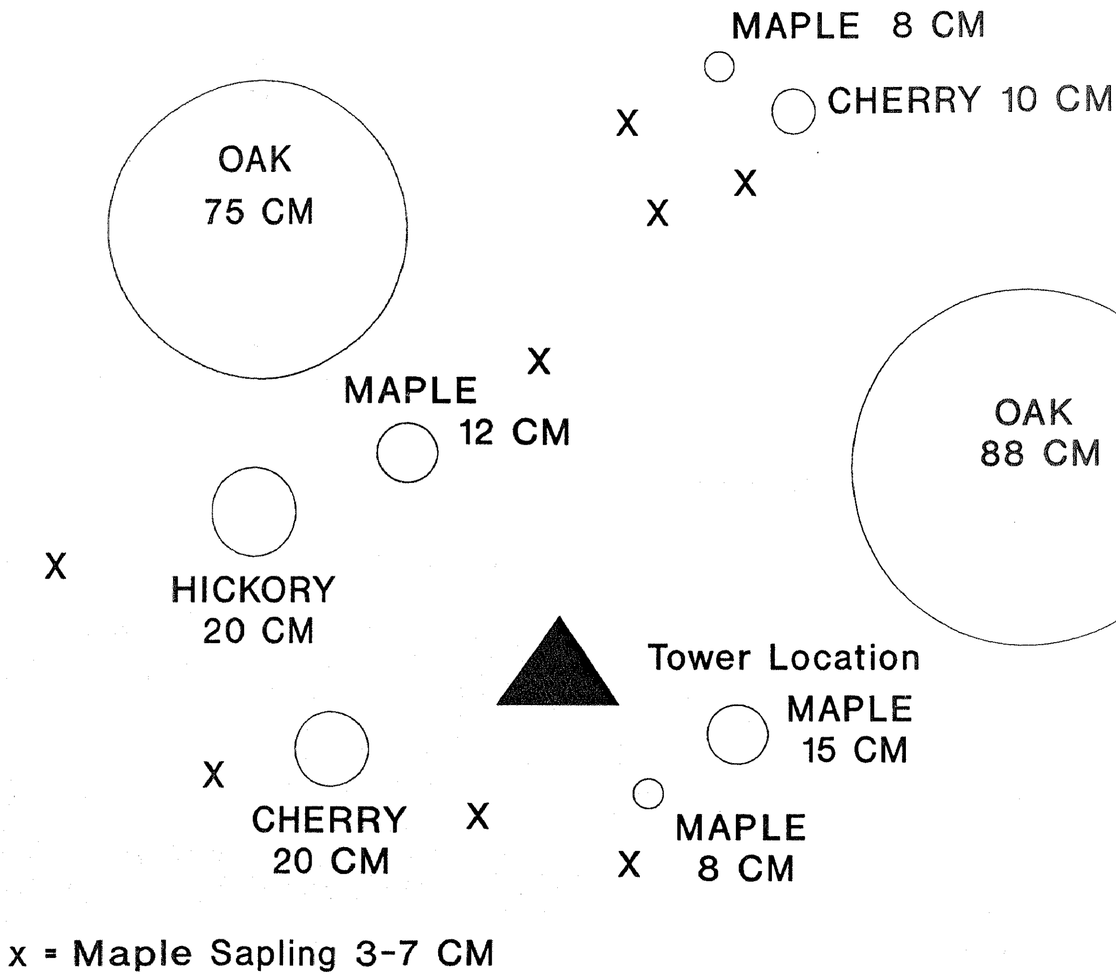

Figure 1.—Stem locations adjacent to a tower in continuous forest canopy in an old-growth forest in east-central Indiana.

As a preliminary comparison to guide future research, mid-growing season, mid-day measures of photosynthesis, transpiration, stomatal conductance, photosynthetically-active radiation, humidity, vapor pressure deficit, air temperature, and ambient carbon dioxide levels were taken for each crown intersection on each tower. Measurements were taken on one day, representative of a typical mid-growing season week in this part of the region. Additionally, ambient environmental measurements were taken at an open area on the gap tower (10 m) and at both locations at the forest floor (sunflecks). For each species-height measurement, three sample leaves were selected and physiological and environmental parameters noted above were measured simultaneously with an ADC LCA-3 portable infra-red gas analyzer (IRGA).

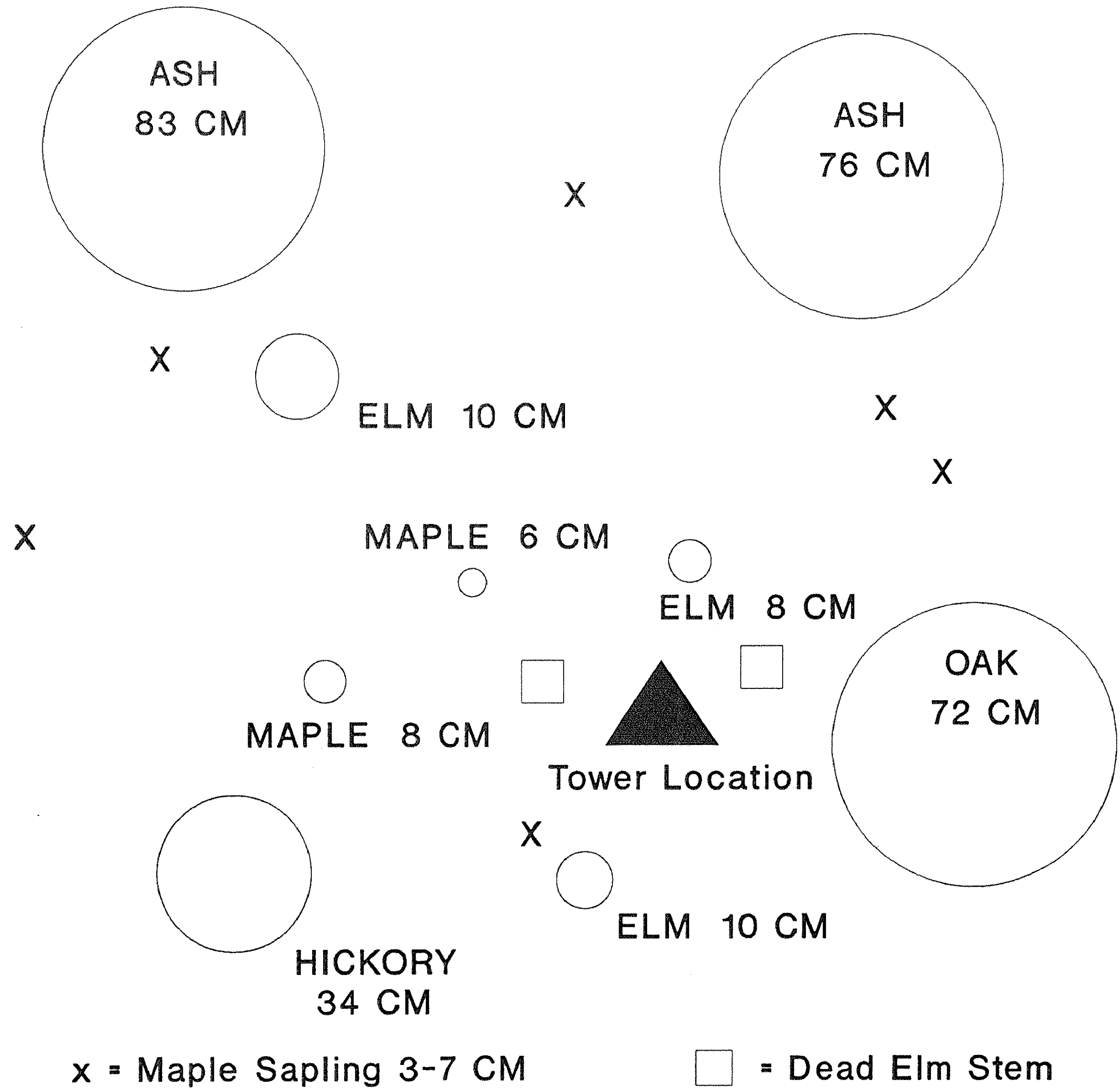

Figure 2.—Stem locations adjacent to a tower in a canopy gap in an old-growth forest in east-central Indiana.

RESULTS AND DISCUSSION

The microenvironmental gradient within the forest canopy is shown in Table 1. Though air temperature and vapor pressure deficit (VPD) were relatively constant from the forest floor to the top of the canopy at 30 m, this was not the case for humidity, ambient CO_2 concentrations, or light flux. As would be expected, light levels dropped very quickly with increasing depth within the canopy. Values near full sunlight dropped to near zero underneath the main canopy composed of old-growth shumard oak and shagbark hickory stems, approximately 10 m from the top of the canopy (20 m from the forest floor). Both humidity and CO_2 concentration increased with depth, being greatest near the forest floor. The humidity and VPD gradients represented only a few percent or kPa, respectively. The CO_2 gradient was substantial, with large concentrations at the top and at the bottom of the canopy. Concentrations at the forest floor were 20% greater than ambient concentrations in the main crown. Similar microenvironmental gradients have been shown for other mixed hardwood forest canopies (oak-hornbeam: Elias et al., 1989; oak-maple: Reich et al., 1990).

The physiological parameters are closely coupled with light flux (incident radiation) in this canopy (Table 1). Rates of photosynthesis, transpiration, and stomatal conductance are greatest at the top of the canopy where incident radiation is greatest. All parameters decrease below the main canopy, where light intensity is much reduced. In this environment, sunflecks become important for carbon assimilation during different periods of the day and growing season. Measured sunfleck values greatly exceed ambient light conditions at the forest floor (Table 1). At such low levels of light, there is very little herbaceous understory and few seedlings. The understory of saplings is composed only of sugar maple, a species able to photosynthesize at these low light levels. These physiological parameter gradients are also characteristic of mature, mixed-hardwood forests where oak overstories are found above more shade-tolerant species (Reich et al., 1990; Marek et al., 1989).

Thus, the microenvironment and physiology of old-growth oak-hickory-maple stands is similar to that of mature, second-growth stands. However, unlike these even-aged second-growth stands, old-growth canopies are not uniform (Parker, 1989), and mortality causes gaps in the overstory canopy. These gaps change the canopy structure and subsequent microenvironment found in old-growth forests. Microenvironmental parameters for the gap in the old-growth canopy are given in Table 2. Again, the air temperature and VPD are fairly stable from the top of the canopy at 30 m to the forest floor. In contrast to the situation in a closed canopy, humidity and CO_2 concentrations show only small gradients, again being greatest near the forest floor. Without tree cover in the gap (except near the forest floor), the flux of water vapor and CO_2 are relatively unaffected. Light, however, shows significant change as one would expect. Significant levels of light reach to the canopy of the sugar maple regeneration at the bottom of the gap, approximately 26 m from the top of the surrounding old-growth (4 m from the forest floor). And light below this height is equivalent to light levels below the main old-growth canopy of the closed-canopy tower location (Table 1). The result of this is significant rates of physiological activity low in the forest relative to the same height under closed canopy (Table 2). Photosynthesis of sugar maple and elm regeneration allows steady growth toward the main canopy (at least until disease removes the elms as has happened at about 7 m). Though oak seed is plentiful in this forest, oak is a very minor constituent of gap regeneration (Parker and Sherwood, 1986). The ability of maple and elm to photosynthesize at the low light levels of the forest floor probably allows establishment before gaps occur, providing an advantage over oak seedlings. As gaps do occur, these tolerant species would pre-empt the space that oak seedlings would need to respond to the significant addition of light near the forest floor. Of more importance is the effect of introduced light on photosynthesis of crowns at intermediate levels in the canopy that constitute the edges of the gap. Appreciable rates of photosynthesis (about 7 umol $m^{-2}s^{-1}$) are occurring in this gap from 4 m to 20 m for edge trees (Table 2). There is also the question of enhanced light effects on the productivity and dynamics of species adjacent to, but not immediately bordering, the canopy gap. Again, sunflecks can play an important role. This

Table 1.—Microenvironmental and physiological parameters measured along a canopy height profile in closed canopy in an east-central Indiana old-growth forest. Values are means (standard deviations) of three measurements.

Species	Height	Ambient CO_2 concentration	Humidity	Vapor pressure deficit	Light flux density	Air temperature	Net Photo-synthesis	Leaf transpiration & conductance	
	(m)	(ppm)	(%)	(kPa)	(umol/m²/s)	(°C)	(umol/m²/s)	(mmol/m²/s)	
Shumard oak	30	361 (4.7)	51.9 (0.6)	2.1 (0.0)	958 (651)	30.6 (0.1)	12.3 (5.0)	3.5 (0.8)	369.1 (158.0)
Black cherry	24	333 (0.6)	50.1 (0.0)	2.4 (0.0)	718 (521)	31.8 (0.0)	6.8 (3.4)	2.0 (1.0)	126.6 (76.0)
Shagbark hickory	20	331 (0.6)	50.4 (0.0)	2.3 (0.0)	207 (168)	31.7 (0.1)	3.7 (1.2)	1.5 (0.2)	80.5 (15.2)
Sugar maple	20	330 (0.0)	50.1 (0.6)	2.4 (0.0)	475 (222)	31.8 (0.1)	6.8 (2.5)	2.3 (0.6)	148.5 (55.7)
Sugar maple	18	329 (0.5)	51.0 (0.6)	2.3 (0.0)	54 (19)	31.5 (0.1)	1.5 (0.8)	1.1 (0.1)	59.5 (8.1)
Sugar maple	18	328 (0.0)	51.0 (0.0)	2.2 (0.0)	40 (19)	31.2 (0.1)	1.2 (0.5)	1.1 (0.2)	57.3 (13.4)
Sugar maple	15	327 (0.0)	51.0 (0.0)	2.2 (0.0)	27 (6)	31.1 (0.1)	0.9 (0.3)	0.9 (0.1)	45.7 (4.8)
Sugar maple	12	329 (0.6)	51.7 (0.0)	2.2 (0.0)	16 (4)	30.9 (0.1)	0.7 (0.5)	0.7 (0.1)	37.6 (4.6)
Sugar maple	10	329 (0.7)	51.3 (0.0)	2.2 (0.0)	22 (3)	30.9 (0.1)	1.2 (0.4)	0.8 (0.1)	38.9 (5.6)
Sugar maple	5	345 (4.7)	52.3 (0.0)	2.1 (0.0)	9 (1)	30.4 (0.1)	0.8 (0.3)	0.6 (0.1)	30.6 (4.5)
Sugar maple	4	348 (0.6)	52.6 (0.0)	2.1 (0.0)	13 (2)	30.3 (0.0)	0.6 (0.3)	1.0 (0.1)	55.6 (5.2)
Sugar maple	2	376 (3.5)	54.8 (0.0)	1.9 (0.0)	10 (0)	29.7 (0.0)	0.2 (0.2)	0.9 (0.0)	56.9 (0.0)
Ambient	0	404	54.0	2.0	5*	30.0			

*Sunfleck = 896 umol/m²/s

Table 2.—Microenvironmental and physiological parameters measured along a canopy height profile in a canopy gap in an east-central Indiana old-growth forest. Values are means (standard deviations) of three measurements.

Species	Height	Ambient CO_2 concentration	Humidity	Vapor pressure deficit	Light flux density	Air temperature	Net Photo-synthesis	Leaf transpiration & conductance	
	(m)	(ppm)	(%)	(kPa)	(umol/m²/s)	(°C)	(umol/m²/s)	(mmol/m²/s)	
Shumard oak	30	338 (2.3)	51.0 (1.8)	2.2 (0.1)	649 (306)	30.6 (0.6)	5.4 (2.4	1.5 (0.6)	96.1 (55.6)
Shagbark hickory	20	337 (0.6)	46.4 (0.6)	2.7 (0.1)	270 (17)	32.9 (0.3)	7.6 (1.6)	2.5 (0.4)	132.6 (22.3)
Ambient	10	336	50.0	2.3	226	31.6			
Sugar maple	4	346 (4.0)	51.4 (0.0)	2.2 (0.0)	406 (94)	30.8 (0.1)	7.1 (0.5)	1.8 (0.1)	115.3 (6.9)
Sugar maple	2	361 (4.0)	51.7 (0.0)	2.1 (0.0)	45 (15)	30.5 (0.1)	1.7 (0.3)	1.1 (0.1)	63.1 (5.3)
American elm	2	363 (1.7)	52.2 (0.6)	2.1 (0.0)	54 (12)*	30.0 (0.1)	2.1 (0.2)	1.3 (0.2)	77.2 (10.5)

*Sunfleck = 401 umol/m²/s

is currently a point of controversy in the ecological literature (see e.g. Lieberman et al., 1989; Publicover and Vogt, 1991; Brokaw 1982). The effects of the canopy gaps in old-growth probably reach beyond the immediate opening. Light, in particular, probably impacts nearby seedlings and samplings (as measured by sunflecks, Table 1 & 2). Though not part of the current study these effects will be measured in future research. We speculate, however, that these gaps hasten the change to shade tolerant species, providing just enough light to accelerate growth of these species within the understories of the adjacent closed canopy areas.

The differences in architecture between closed-canopy forest and canopy gaps are evident. In old-growth forests, these differences are part of the process of mortality and tree replacement, unlike many even-aged, second-growth Central Hardwood stands. The effect of the different architectures is spatial variation (horizontal and vertical) in microenvironment and resulting physiology, ultimately affecting productivity and species dynamics. But these are the parameters we will change as we apply silvicultural techniques for uneven-aged management or management to mimic old-growth structure. From the present data we can see a change in the rate of important physiological processes at different canopy levels. Their implications for changing rates of ecological processes must be evaluated, and this is the focus of continuing research.

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