Jour. Korean For. Soc. 89(4) : 502 - 512. 2000
韓國林學會誌 89(4) : 502 - 512. 2000

Prediction of Old-Growth Development in Second-Growth Hardwood Forests using Computer Simulation[1]

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Computer Simulation을 利用한 二次闊葉樹林의 老熟林 發達豫測[1]

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ABSTRACT

Old-growth development for two different second-growth northern hardwood stands in the North America was evaluated with a computer simulation. The two sites compared were a representative 77 year old even-aged stand (Phelps) with heavy dominance by pole size classes, and an older uneven-aged stand with some existing old-growth structural features (Wildcat Creek). Each stand was evaluated in its natural progress toward old-growth structural conditions with stand structure, size distribution of live and dead trees, percent stand area in canopy gaps, and visual canopy profile and overhead view.

The Phelps stand reached the minimum structural threshold for the old-growth stage after 74 years. Only 13 years was required for Wildcat Creek stand to reach the old-growth threshold. During the 45 years of simulation, the diameter distributions of both stands became broader and flatter. DBH distribution of dead trees had a general descending trend over the simulation in each stand. Gaps at Phelps were typically small after 45 years. Gap area at Wildcat Creek was somewhat more constant over the 45 years of simulation but a big gap was formed because of the death of several adjacent large trees.

Keywords : computer simulation, old-growth, hardwood forests, size distribution, canopy gaps

要 約

컴퓨터 시뮬레이션을 통하여 미국 북부 이차 활엽수림지역의 2개 임분을 대상으로 노숙림 발달과정을 평가하였다. 한 임분 (Phelps)은 77년생 임목들이 대부분 차지하고 있는 동령임분이고, 다른 임분 (Wildcat Creek)은 노숙림의 구조적 특징을 다소 갖고 있는 연령이 많은 임목들이 있는 이령임분이다. 각 임분은 노숙림 자연발달 과정을 평가하기 위하여 임분구조, 직경분포, 고사목의 크기분포, 임분의 숨틈 (Gap)크기, 3차원 임분공간도 및 수관투영도와 같은 구조적 특징을 이용하여 실시하였다.

본 시뮬레이션에 의하면, Phelps 임분은 현재를 기준으로 74년 후 에, Wildcat Creek 임분은 13년 후 에 노숙림 초기단계에 각각 도달하였다. 45년 시뮬레이션 동안 두 임분의 흉고직경분포는 직경크기가 커짐에 따라 모두 넓고, 평평한 형태를 나타냈으며, 고사목 크기분포에서는 두 임분 모두 직경크기가 커짐에 따라 고사목 수가 감소하는 경향을 나타냈다. Phelps의 숲틈 크기는 시뮬레이션 초기 연도보다 45년 후에 작게 나타난 반면, Wildcat Creek의 숲틈은 시뮬레이션 동안 일정한 패턴을 보였고, 큰 나무들의 고사로 인하여 큰 숲틈이 형성되었다.

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INTRODUCTION

In recent years, interest in old-growth forest has increased because old-growth not only provides humans with aesthetic and recreational values, but also provides important habitat for a number of animal and plant species. Important old-growth structural features include cavity trees and dead snags of various sizes, large fallen logs, tip-up mounds, canopy gaps in various stages of recovery, and a forest canopy with multiple layers of foliage. These structural features appear to be correlated with population levels of certain animal and plant species. For instance, coarse woody debris enhances habitat suitability for certain vertebrates, such as salamanders, pine marten, and cavity nesting birds (Maser and Trappe, 1984; Raphael and White, 1984; Swallow et al., 1986; Aubry et al., 1988; Conner et al., 1994). Similarly, canopy gaps have a significant effect on species composition as well as on the structural attributes of individual stands (Woods and Whittaker, 1981; Hibbs, 1982; Runkle, 1982; Yetter and Runkle, 1986; Mladenoff, 1990; Runkle, 1990; Cole, 1991; McClure and Lee, 1993).

Old-growth stands are, however, currently rare in northern Wisconsin because of extensive logging at the turn of the century. The present second- growth northern hardwood stands are predominantly young even-aged (60-80 yr), and typically have a uniformly dense canopy with few trees >40 cm dbh (Lorimer and Krug, 1983; Guldin and Lorimer, 1985). These young even-aged stands also have few canopy gaps, limited vertical stratification of foliage, and low amounts of coarse woody debris (Goodburn, 1996). In recent years, there has been an increasing desire to manage some second-growth forests for old-growth characteristics, including aesthetic diversity. For example, all the major public land agencies in the Lake States (e.g., U.S. Forest Service, Wisconsin and Minnesota Departments of Natural Resources, National Park Service) have expressed a public commitment to fostering the development or restoration of more forests with old-growth characteristics (Rominske and Busch, 1991). The Wisconsin DNR and the U.S. Forest Service have already established modified silvicultural prescriptions designed to enhance the development of old-growth features in existing second-growth stands.

To investigate old-growth development over a long-term period, a computer simulation approach is clearly necessary. Forest growth models have been used in many studies to simulate forest development and long-term forest succession (Botkin et al., 1972; Shugart, 1984).

In the present paper, we use an individual-tree based model of stand development to investigate changes in the size distribution, gap structure, and coarse woody debris. The specific objectives of the study are to simulate the natural progress of second-growth stands and to predict effects of the development of old-growth structural features, especially in the size distribution of live and dead trees and canopy gap structure.

METHODS

1. Study areas

The model used in this paper was specifically designed for simulating long-term dynamics of northern hardwood stands on mesic sites in the upper Great Lakes region in the North America. The original field data used in calibrating the growth model development had been collected from 1987-1991 in fifteen northern hardwood stands in north-eastern Wisconsin and western Upper Michigan (Cole and Lorimer, 1994; Dahir, 1994; Singer and Lorimer, 1997; Cole and Lorimer, unpublished).

The study sites lie within sub-subsections IX.3.1, IX.3.2, and IX.3.3 of the ecological landscape classification of Albert (1995). Mean monthly temperature ranges from -12.3℃ in January to about 19.5℃ in July. Annual precipitation average is 820 mm and is fairly well distributed throughout the year. Elevations range from 500-550 m. Soils are classified as well or moderately well drained loamy Spodosols, originating from eolian deposits on glacial till or glacial outwash.

The data set included 382 trees from a wide range of ages (17-311 years) in second-growth even-aged stands, managed uneven-aged stands, and uneven-aged old-growth stands. Of the 382 subject trees, 91 were >100 years old, 53 were >150 years, and 28 of the sample trees were >200 years. Residual basal area ranged from 14.4 m^2/ha to 37 m^2/ha. Intensity of treatments in the managed stands ranged from >20 to 65% basal area removal in thinnings, selection harvests, and shelterwood harvests.

2. Field methods

1) Plot design and general measurement

In 1996, further data were collected in two (Phelps and Wildcat Creek) of the original 15 stands in order to have spatially explicit stem and crown information for trees on a large, contiguous plot for the purpose of simulating long-term response to restoration treatments. The Phelps stand had been mostly clearcut about 1919, with one or two thinnings made since that time. It was therefore selected as a representative even-aged stand about 77 years old in 1996. The Wildcat Creek stand had not been cut as heavily in the early 20th century. Although it likewise has a cohort of trees about 75 years old, it is broadly uneven-aged, with many trees ranging from 135 to 250 years of age. At least two selection harvests have been made in the stand, resulting in some sizable canopy gaps and layering of vegetation. The Wildcat Creek stand was selected to be representative of second-growth stands that already have some old-growth structural features. The expectation was that the Wildcat Creek stand would require a shorter time for restoration of old-growth character than the Phelps stand (Table 1).

A single large 50×50 m plot was established in each stand in order to reduce plot edge effect as well as be able to have enough trees to constitute a small stand, even after mortality and harvests reduce the number of trees as the stand progresses toward an old-growth condition. The plot was divided into 10×10 m subplots to facilitate measurement of Cartesian coordinates for each tree.

Table 1. Site and initial stand structural characteristics for each study area.

Stand	Phelps	Wildcat Creek
Soil texture	Loam	Loam
Habit type	*Acer-Viloa -Osmorhiza*	*Acer-Viloa -Osmorhiza*
Total tree*(No/ha)	612	676
Suger maple	556	340
Ironwood	0	288
Basswood	44	28
White ash	0	12
Black cherry	8	8
yellow birch	4	0
DBH range	4.0 - 46.0 cm	4.0 - 54.5 cm
Stand basal area	29.0 m^2/ha	27.7 m^2/ha
%Basal area of stand		
Tree ≥26cm dbh	75.9%	80.5%
Tree ≥46cm dbh	2.3%	46.5%
Suger maple	85.6%	89.4%

* ≥4cm DBH

Locations of all stems (≥4 cm dbh) within the entire plot were mapped using Cartesian coordinates along the east-west (x) and north-south (y) axes of the plot. Species, dbh, and crown class were recorded for all trees on the plot, using the following set of crown classes for live trees : dominant, codominant, intermediate, overtopped, understory sapling, and gap sapling (similar to Smith, 1986). Height measurements were taken to the base, widest point, and top of each tree crown using a clinometer or height pole. Total crown radii were measured along four cardinal compass directions by extending a tape measure horizontally from the front of bole to the crown edge. Exposed crown radii were measured as the portion of the total radii free from direct overlap by branches of taller trees. The point perpendicular to the crown margin was sighted using a clinometer.

3. Simulation design and structure

1) General rationale

The simulation runs utilized the model framework of the Visual Forest Management Simulator (VFMS) (Vanderwerker and Martin, unpublished). An empirical species-specific individual-tree growth model was used. The model uses standard mensurational variables such as dbh, crown class, and stocking level. The individual tree data are spatially explicit in the simulation. The model describes basal area growth, total height, total crown radius, and mortality (Table 2). There are, however, no ingrowth equations, so the simulation deals only with the growth and annual mortality of trees in the initial cohorts. The simulation iteration is 1-year-basis.

2) Model Components

The dependent variables of the growth model are basal area increment ($\triangle$BA, cm^2/yr), height (H, m), total crown radius (CR, m) and annual mortality rate.

Independent variables for prediction of basal area increment are diameter, relative diameter, and percent stocking. Dbh is also used as independent variable for allometric equations to predict height and crown radius. For the mortality equation, diameter, competition index, canopy status, and a categorical stand stage variable are used as independent variables (See mortality equation in Table 2).

Relative diameter ($D/\bar{D}$) was calculated by dividing bole diameter of the subject tree by the arithmetic mean diameter for all codominant and dominant trees on the plot.

Percent stocking level (%STOCKING) was based on the Lake States northern hardwood stocking chart from Tubbs (1977). For the present study, numerical stocking values were calculated by dividing the plot basal area by the basal area of stands shown on the chart to be at the level of "average stocking" of managed stands with 20-49% basswood basal area.

A diameter-based competition index(CI) was calculated using the following formula :

$$(\sum_{i=1}^{n} D_j) / D_i$$

where D_j is the diameter of competitor tree j and D_i is the subject tree diameter.

A competitor must be of equal or higher crown class than the subject tree to be included in the formula.

Species-specific linear equations were used to predict basal area increment of individual trees. The model used equations previously defined as providing the best fit to the data (Choi, 1999). Because ironwood is a small-statured understory tree that rarely exceed 15cm dbh, growth of individual ironwood stems were not simulated. (Table 2)

Cumulative height growth for individual trees was based on an allometric relationship with dbh, using the height and diameter data of Cole (1991). The height equation is an asymptotic nonlinear model (Table 2).

Cumulative crown radius was predicted for each species based on an allometric relationship with dbh, using the data of Cole (1991). Crown growth was therefore assumed to be symmetric about the stem. For the minor species, the sugar maple equations were used for basal area increment, height, and crown radius. (Table 2)

The sugar maple mortality equation developed by Dahir (1994) was used for this study. The sugar maple equation was applied to all species because sugar maple is heavily dominant (>70% of stand basal area) and site-specific equations are not available for the other species. Dbh, competition index, and two categorical variables indicating canopy status and stand developmental stage were used as independent variables. The stand developmental stage variable changes from 0 to 1 when the forest passes the minimum threshold for old-growth conditions. The forest reaches the minimum threshold for old-growth conditions when trees ≥26 cm dbh make up ≥85% of total stand basal area and %basal area in trees ≥46 cm dbh exceeds 50%. Crown status variable consists of canopy (code = 1) or subcanopy (code=0). As the mortality equations were developed from 11 year permanent plot data, annual mortality was recalculated for this study using the equation of

Table 2. Simulation models used in VFMS.

Model	Equation	*n*	R^2	MSE
Basal area increment equations				
Suger maple	$\ln \triangle BA=6.47+0.77\ln DBH+0.53\ln RD-1.37\ln \%STOCKING$	204	0.76	0.33
Basswood	$\ln \triangle BA=-0.10+1.34\ln DBH-0.43\ln \%STOCKING$	66	0.70	0.21
White ash	$\ln \triangle BA=-2.45+1.55\ln DBH$	33	0.69	0.45
Allometric height equations				
Suger maple	$H=27.55(1-\exp(-0.061DBH))$	246	0.94	3.87
Basswood	$H=28.21(1-\exp(-0.058DBH))$	71	0.94	3.12
White ash	$H=27.92(1-\exp(-0.078DBH))$	53	0.97	3.36
Allometric crown equations				
Suger maple	$CR=0.94+0.09DBH$	195	0.76	0.47
Basswood	$CR=0.35+0.08DBH$	54	0.76	0.40
White ash	$CR=0.89+0.09DBH$	33	0.77	0.44
Mortaliy equations				
Suger maple	$P(\text{mortality for 11 yr})= [e^x/(1+e^x)]$			
	$x = -4.1577+0.000595DBH^2 \cdot StandStage-0.8828StandStage+0.8601\ln CI-0.8639CS$			

$\triangle BA$=annual basal area increment, ㎠/yr, H=height, m, CR=crown radius, m, RD=relative diameter ($D/\bar{D}$), %STOCKING=percent stocking based on chart of Tubbs (1997)

StandStage variable is 1 if (basal area for trees ≥ 26cm dbh is ≥ 85% of stand basal area) and (basal area for trees ≥ 46cm dbh is ≥ 50% of stand basal area), otherwise 0

CI=competition index ($\sum D_j/D_i$) where D_i is dbh of subject tree and D_j is dbh of competitor j

CS=canopy status (0=understory, 1=overstory)

Hamilton and Edwards (1976) : P(Annual mortality) = 1 - [P(11-year survival)$^{(1/11)}$].

The mortality component of the model was expressed by comparing the probability of tree mortality with a computer-generated uniform random number on the open interval 0 to 1. If the random number is less than the mortality rate, the tree is considered to have died in that year.

In the simulation, when a tree reaches a dbh greater than 95 cm, it is killed within ten years regardless of calculated probability of mortality because northern hardwood trees >95 cm dbh are extremely rare in the Lake States, even in old-growth forests.

3) Model operation

In this section, a sequence of steps in a flowchart is explained for model operation (Fig. 1). In order to simulate the effects of local competition on the growth of individual trees, the main plot (50×50 m) was divided into square subplots with an area equal to 3.5 times the mean crown radius of canopy trees (intermediate, codominant, dominant trees) in the main plot (Lorimer, 1983; Ganzlin and Lorimer, 1983). The width of the square subplot was calculated using the square root of the circular subplot size. The plot width was used to subdivide the entire

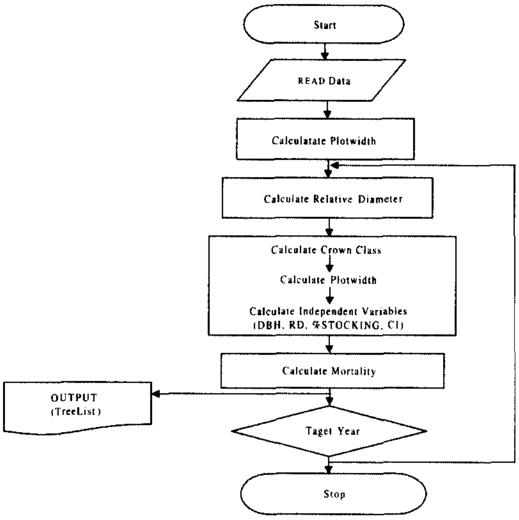

Fig. 1. Flow diagram of the computer simulation model in VFMS.

sample area into square subplots starting at the south-west boundary of the stand and measuring east and north. In order for the subplots along the eastern and northern edge of the stand to have the same length and width as the others, it is necessary to measure the plot width back from the eastern and northern boundaries, resulting in some overlap of subplots along these edges. The subplot width was updated each year, reflecting changes in the changed crown radius of canopy trees. (Fig. 2)

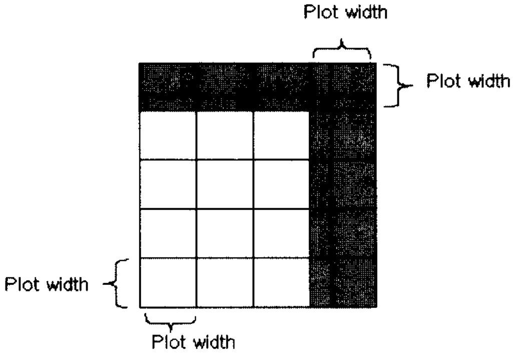

Fig. 2. Flow diagram of main plot (50m×50m) at Phleps and Wildcat Creek study sites, divided into subplots. Subplot size in any iteration is a function of mean overstory crown radius. Shaded subplots show how fractional subplots are adjusted in size to maintain a constant area.

When the simulation was initiated, the initial subplot width was calculated using the crown class observed in the field before simulation proceeded to the main loop. A new crown class was assigned based on relative diameter criteria for the given subplot size. With the new crown class, plot width was recalculated. The simulation then proceeded to the main loop for annual iterations. The general procedure overview of VFMS simulation with subroutines is shown in the flowchart in Fig. 1.

Crown class is correlated with relative diameter, and so changes in relative diameter during the simulation were used to update crown class. The following thresholds were used to define crown class : dominant : >0.95 relative diameter, codominant : 0.70-0.95 relative dbh, and intermediate : 0.40-0.70 relative dbh. Sapling and suppressed trees are those with a relative diameter <0.40.

In the updated subplot, independent variables indicating relative size and competition (relative diameter, percent stocking and competition index) were calculated before entering the main loop for growth. The relative diameter, percent stocking, and competition index variables were calculated using the first subplot on which it occurs. Relative diameter was restricted to a maximum of 2.5 based on the observed range of values in the data of Cole (1994). In case there was only one tree on the subplot, the relative diameter was set to 1.8. The mean dbh for relative size and percent stocking were calculated using both dominant and codominant trees in the subplot, because of the possibility that a subplot may have no codominant trees.

4. Old-growth evaluations

At each iteration, each stand was evaluated in its natural progress toward old-growth condition over 200 years. After 45 year simulation, the old-growth structural conditions such as stand structure, size distribution of live and dead trees, percent stand area in canopy gaps, and visual canopy profile and overhead view were evaluated in each stand. The minimum threshold for old-growth condition was set when trees $\geq 85\%$ of total stand basal area and %basal area in trees $\geq$26cm dbh exceeds 50% (used as the stand developmental variable in mortality equation).

For the calculation of percent gap size, a dot grid transparency was used to calculate the ratio of dots in gaps to the dots of the area of the overhead map generated by VFMS. A 3 m wide border zone was excluded around the plot perimeter when calculating percent gap area. Trees were no longer considered to be in a gap, but part of main canopy, when tree height was $>67\%$ of the height of the main canopy. For this model we used threshold diameter, rather than height, because this model uses diameter-based variables. To update the gap sapling/canopy threshold diameter, we used an allometric equation based on the data of Cole (1991). The equation was DBH = $-0.62 + 0.066H^2$ where H is equal to the threshold height.

RESULTS AND DISCUSSIONS

1. Time to reach old-growth threshold

In a 200 year simulation with natural development, the Phelps stand reached the minimum structural threshold for the old-growth stage after 74 years (total stand age 151 years). Only 13 years was required for the Wildcat Creek stand to reach the old-growth threshold. Threshold for old-growth conditions was when the percentage of stand basal area in trees ≥26 cm dbh exceeds 85% and percent basal area in trees ≥46 cm dbh exceeds 50%. As expected, old-growth development was also accelerated by most treatments in an older uneven-aged stand, Wildcat Creek.

The maximum basal area of Phelps and Wildcat Creek approached 39 m^2/ha and 35 m^2/ha respectively after 60-70 years (Fig. 3). This is similar to observed stand basal area in old-growth hardwoods in the Sylvania Wilderness (Goodburn, 1996). The two stands show a similar stand basal area trend over time. The Phelps' stand basal area remained higher than Wildcat Creek during the simulation. Stand basal area of both sites declined after 100 years of simulation because the model does not include in growth of younger trees (Fig. 3). For this study, a forest reaches the minimum threshold for old-growth conditions when the percentage of stand basal area in trees ≥26 cm dbh exceeds 85% and percent basal area in trees ≥46 cm dbh exceeds 50%. This criterion only applies to the early stage of old-growth development (i.e., late aggradation stage of Bormann and Likens, 1979), and does not indicate the time needed to reach later stages such as the transition and steady state. So an important question is whether stands after 45 year simulations just barely meet the minimum structural criteria of old-growth forest (late aggradation stage) or whether they have progressed to a level of structural development more similar to the later stages.

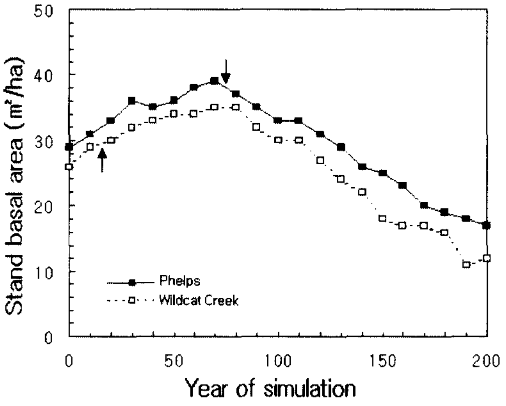

Fig. 3. Projection of stand basal area for the two study sites for 200 years with computer simulation model. Note that ingrowth is not included, which accounts for much of the decline after year 100. The arrows indicate the starting point of the old-growth minimum threshold.

2. Mean tree size and diameter distribution

The mean dbh of the dominant-codominant cohort at the Phelps stand was initially 32.4 cm dbh and

Table 4. Characteristics of all canopy trees after 45 years of simulation in each stand.

Stand		Mean DBH* (cm)	Mean Height† (m)	Stems/ha >45cm DBH	%BA >45cm DBH	%Gap area
Phelps	0 yr	32.4	20.0	4 (0)	2.3 (0.0)	15.3
	45 yr	40.1	23.8	72 (0)	39.1 (0.0)	9.4
Wildcat Creek	0 yr	42.4	21.0	56 (0)	41.8 (0.0)	11.4
	45 yr	46.8	24.5	68(24)	54.1(23.4)	10.9

* mean diameter of codominant and dominat tree only.

† mean height of intermediate, codominant and dominant tree only.

The values in parentheses are for tree >60cm dbh.

reached 40.1 cm after 45 years. Large trees (>45 cm dbh), which initially occupied only 2% of the stand basal area (4 trees/ha), increased to 72 trees/ha and occupied 39% of the stand basal area after 45 years. This is, however, still less than 50% of stand basal area required for minimum old-growth status. In contrast, the Wildcat Creek stand closely approached the minimum old-growth criteria even in the initial year (Table 1). The mean dbh of the dominant-codominant cohort at Wildcat Creek was initially 42.4 cm and reached 46.8 cm dbh after 45 years with 68 large trees per hectare and 24 trees/ha greater than 60 cm dbh. The large trees occupied 54.1% of the stand basal area, exceeding by far the minimum old-growth criteria.

The Phelps diameter distribution was classified as a concave descending curve at the beginning of the simulation. The pole-size trees (20-32 cm dbh) are relatively dense (35% of the stand) (Fig. 4). The diameter distribution of Wildcat creek was classified as somewhat unimodal but broader and flatter than Phelps as would be expected for an older stand (Fig. 4). During the 45 year simulation, the diameter distributions of both stands became increasingly broader and flatter toward to typical old-growth stand. (Tyrrell and Crow, 1994; Goodburn, 1996)

3. Natural mortality and CWD

Although there were large dead trees in Wildcat Creek during simulation, the mean dbh (12.1 cm) of dead trees was lower than 18 cm of the mean dbh at Phelps stand (Table 5). The reason is that

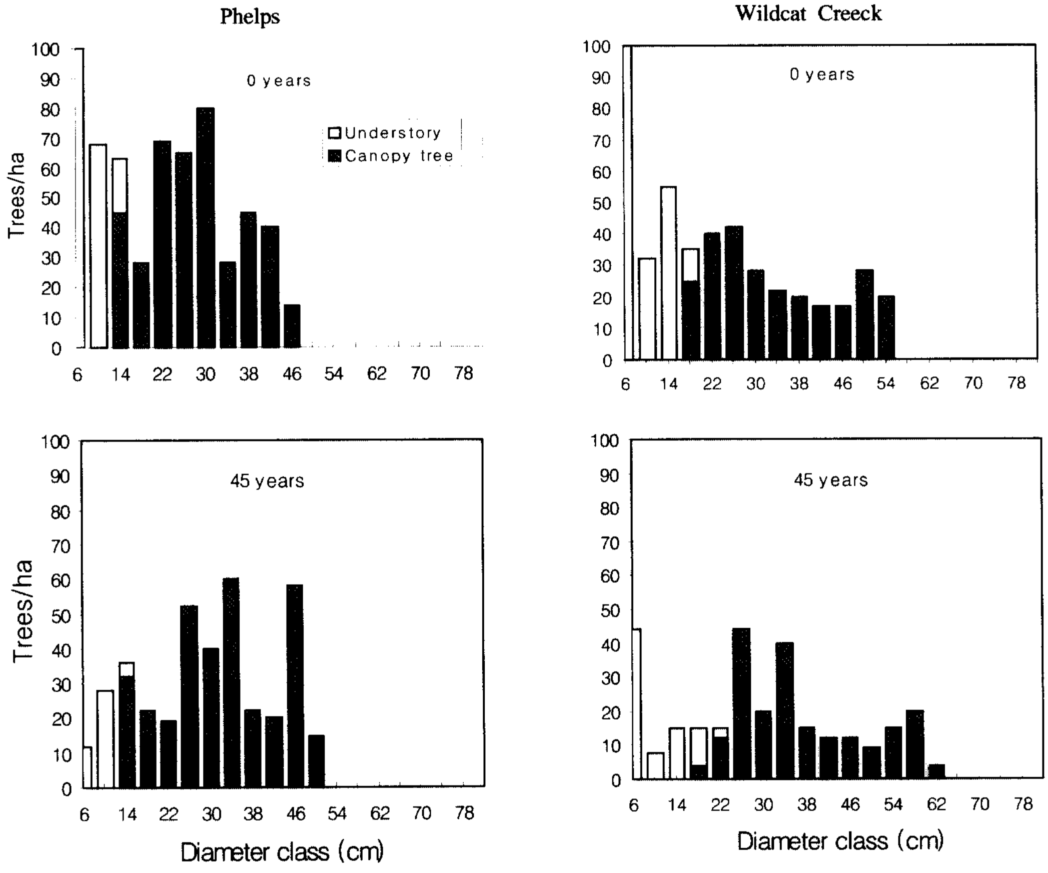

Fig. 4. Simulated diameter distributions of the two stands after 45 years. Only the initial cohorts were simulated (regeneration and ingrowth not included).

Table 5. Characteristics of coarse woody debris for 45 years of simulation in each stand.

Stand	Mean DBH (cm)	Total dead trees (ha)	%mortality of total trees	Basal area (m^2/ha) (≥4cm DBH)
Phelps	18.0	232(8)	37.9	8.4
Wildcat Creek	12.1	368(28)	54.4	10.3

The values in parentheses and for tree >45cm DBH

more saplings of Wildcat Creek had died for 45 years (especially ironwood). The mortality rate of large trees(>45cm dbh) was substantially higher in Wildcat Creek because mortality had increased in larger trees since 13 year simulation when a threshold old-growth stand stage started. 28 trees larger 45 cm dbh in Wildcat Creek were more than 17 trees/ha at Slyvania Wilderness in old-growth stand (Goodburn, 1996) because there was relatively high mortality of large trees during simulation.

Size distribution of standing dead trees had a general descending trend over the simulation period in both stands, reflecting in part the higher risk of mortality for small and overtopped trees (Fig. 5). Saplings less than 10 cm dbh had very high mortality in both stands (especially Wildcat Creek). However, mortality occurred in all diameter classes over the 45 year period. A higher proportion of pole-mature trees died during the simulation, compared with a previous study in northern hardwoods (Dahir, 1994). The size distribution of mortality in Wildcat Creek during 45 year simulation is presumably a process toward a asymmetric U-shape, which typically appears in the old-growth stand in northern hardwoods (Dahir, 1994).

4. Canopy gaps and canopy profile

To investigate trends in gap and canopy development, crown map and canopy profiles of the two stands for the 45 year simulations are shown in Fig. 6. Percent gap area at Phelps decreased from an initial value of 15.3% of stand area to 9.4% at year 45. Gap area at Wildcat Creek was somewhat more constant from 11.4 % in the initial year to 10.9% at year 45 (Table 4). Gaps at Phelps were typically small. At Wildcat Creek, a big gap formed after 45 years because of the death of several adjacent large trees. The characteristics of young stand were clearly evident at Phelps based on visual criteria of dbh, height, and total crown area in the stand overhead view and canopy profile (Fig. 6). Mean height of canopy trees in each stand was fairly constant for 45 years. The mean canopy tree height, based on dominant, codominant, and intermediate crown class trees, is similar in both stands (23.8 m for Phelps, 24.5 m for Wildcat Creek). After 45 years, the canopy profile and crown map shows that the Phelps stand still had the characteristics of a mature stand. In contrast, the Wildcat Creek stand had an old-

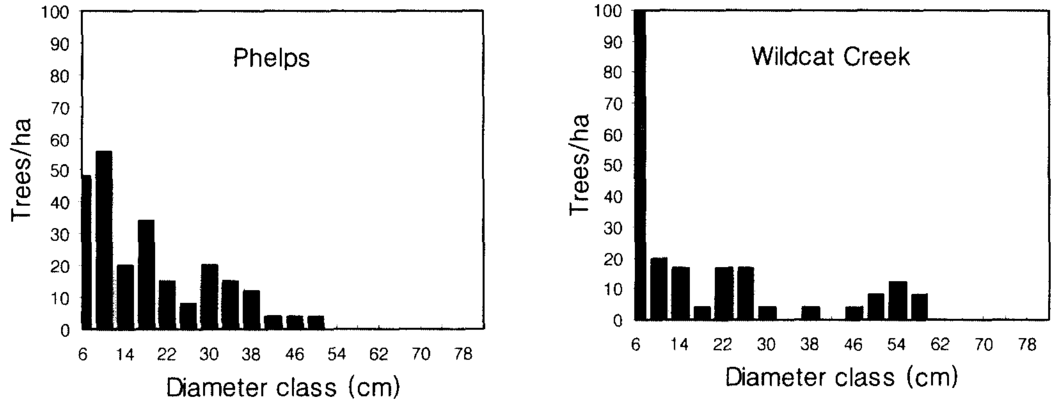

Fig. 5. Cumulative size distributions of trees killed by natural processes over 45 years of simulation.

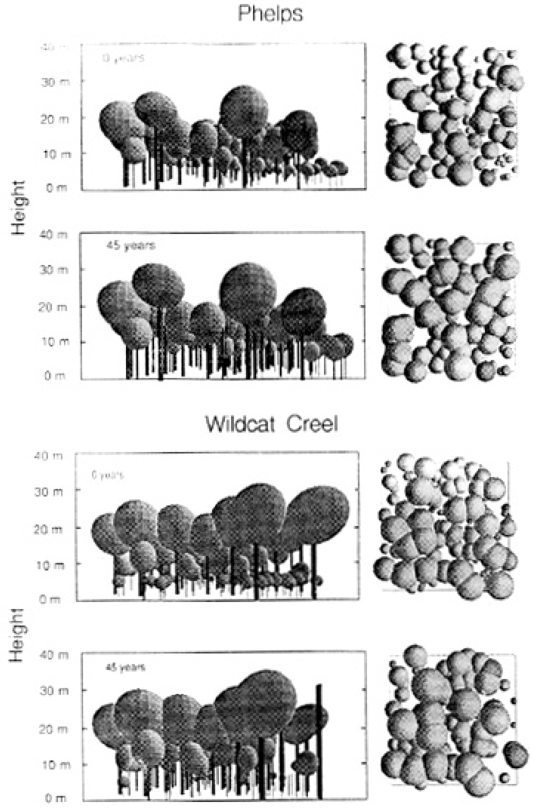

Fig. 6. Simulated canopy profiles and overhead view after 45 years in each stand.

growth appearance with large trees and large standing dead snags (Fig. 6).

For this study, it was possible to evaluate two different hardwood stand conditions which are most likely to result in old growth either by quantitative simulation or qualitative analyses. However, the present simulations were only restricted to natural progress without various thinning methods. Therefore, it was not possible to predict effects of alternative restoration methods in hastening the development of old-growth structural features. Also, the lack of provision for asymmetric crown growth, seedling establishment, and sapling growth in the simulation results in a limited understanding of canopy gap dynamics. Such features are necessary for understanding issues such as lateral gap closure by border trees and gap capture by saplings, and would also result in more accurate estimates of the fraction of the stand occupied by canopy gaps. Further development of the updated simulation model may help resolve some of these questions. The simulation model used in the present study, however, does provide a simple but useful framework for analyzing some of the principal features of long-term natural forest development.

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