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FOREST SERVICE, U. S. DEPT. OF AGRICULTURE, 6816 MARKET STREET, UPPER DARBY, PA

BIRCH REGENERATION: A STOCHASTIC MODEL

Abstract. The regeneration of a clearcutting with paper or yellow birch is expressed as an elementary stochastic (probabalistic) model that is computationally similar to an absorbing Markov chain. In the general case, the model contains 29 states beginning with the development of a flower (ament) and terminating with the abortion of a flower or seed, or the development of an acceptable stem, unacceptable stem, dead seedling, or nongerminate (the six absorbing states). Expressions are given for the expected mean number of occurrences of each state, and the probability of arriving at any absorbing state after the occurrence of any transient state.

Many biological phenomena in forestry are the result of a long series of related events. For example, the regeneration of a clearcut area may be considered a chain of events that begins with the initiation of flower buds on potential seed trees, continues through flowering, fertilization, fruiting, seed development, seed dispersal, germination, and survival; and finally terminates with the occurrence of established seedlings in the reproduction. Stochastic-process theory provides the basis for constructing a hypothetical probabalistic model that simulates the essential behavior of such a biological process.

A stochastic model may be constructed by specifying the probabilities of moving from each individual state to each succeeding event in the process. Thus, the probability of ending up with a particular result can be predicted from a given set of original circumstances. In the case of a regeneration process, this enables us to predict the number of established seedlings that will be obtained under various circumstances if the assumptions of the model are met. Such information is useful in determining the chances of obtaining successful regeneration in a particular situation or in evaluating the need for special measures to improve the chances of success.

A description of a stochastic model for the regeneration of paper birch or yellow birch is presented in this paper.

The Regeneration Process

The regeneration of a clearcutting with paper or yellow birch can be described conveniently as a series of five steps:

- *Flower development.* Conceptually, a tree or stand contains a given total number of potential flower buds, which contain a given number of potential ovules. These potential buds actually develop into flower buds, leaf buds, or dormant or aborted buds with probabilities that no doubt depend upon environmental and physiological conditions. For our purpose, we may consider flowers to be developed when the female ament[1] is fully formed and ready to receive pollen. Flowers that do not reach this stage will be considered aborted.
- *Seed development.* A female ament contains ovules that may or may not develop into mature seeds, depending upon pollination and upon environmental and physiological conditions. Seed will be considered developed when it has matured and is ready for dispersal. Seed that does not reach this stage will be considered aborted.
- *Seed dispersal.* After mature seed is produced, it may be dispersed varying distances into a clearcutting. We shall recognize eight different dispersal distances. (Under fall, winter, or early spring logging, seed dispersed before logging is also available in addition to seed subsequently dispersed from border trees.)
- *Microenvironment.* After dispersal, the seed might alight on any of several microenvironments[2] that affect germination, growth, and survival. Shade might be provided by border trees or any vegetation remaining on the clearcut area. Rainfall pattern and soil type would influence the amount of available moisture, which is particularly important during the germination stage. The amount of disturbance to the forest floor would affect the type of seedbed material. We shall recognize 13 microenvironments made up of various seedbed conditions, exposures, and moisture conditions.
- *Seed response.* Once a seed has been dispersed to a particular environment, it may: (1) fail to germinate, (2) germinate and then die,

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[1] Birch aments generally are borne singly.

[2] See, for example: Marquis, David A., John C. Bjorkbom, and George Yelenosky. EFFECT OF SEEDBED CONDITION AND LIGHT EXPOSURE ON PAPER BIRCH REGENERATION. J. Forestry 62:876-881, illus. 1964.

(3) produce an unacceptable stem, or (4) produce an acceptable stem. The definition of acceptable may vary to suit the need.

With this arrangement, 29 possible states or conditions are represented in these five steps. The 29 states are:

1. Flower developed.
2. Seed developed.
3. Seed dispersed up to 1 tree height.
4. Seed dispersed to between 1-2 tree heights.
5. Seed dispersed to between 2-3 tree heights.
6. Seed dispersed to between 3-4 tree heights.
7. Seed dispersed to between 4-5 tree heights.
8. Seed dispersed to between 5-6 tree heights.
9. Seed dispersed to between 6-7 tree heights.
10. Seed dispersed to 7+ tree heights.
11. Microenvironment of damp, shaded, mineral soil.
12. Microenvironment of damp, sunny, mineral soil.
13. Microenvironment of dry, shaded, mineral soil.
14. Microenvironment of dry, sunny, mineral soil.
15. Microenvironment of damp, shaded, humus.
16. Microenvironment of damp, sunny, humus.
17. Microenvironment of dry, shaded, humus.
18. Microenvironment of dry, sunny, humus.
19. Microenvironment of damp, shaded, litter.
20. Microenvironment of damp, sunny, litter.
21. Microenvironment of dry, shaded, litter.
22. Microenvironment of dry, sunny, litter.
23. Micorenvironment of rock or other unproductive material.
24. Acceptable stem.
25. Unacceptable stem.
26. Dead seedling.
27. Nongerminate.
28. Flower aborted.
29. Seed aborted.

The Stochastic Model

The 29 events can be expressed as an elementary type of stochastic model that is computationally equivalent to an absorbing Markov chain[3]

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[3] Reviewers have pointed out that the process described here can be represented in other forms, e.g. as a branching "tree" of probabilities. Also, this process differs in some respects from certain classical examples of Markov chains. Thus we are describing the process as computationally equivalent to an absorbing Markov chain.

Table 1.—Symbolic initial vector and transition matrix for the 29-state birch regeneration process, showing positive (+) probabilities for the possible transitions from transient states and certainties ($p = 1$) for the "transitions" from absorbing states. The 4 computational submatrices—Q, R, O, and S—of the transition matrix are shown

States	States[1]																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Initial vector:	+																											+	
Transition matrix:																													
1. Flower developed		+																											+
2. Seed developed			+	+	+	+	+	+	+	+																			
3. Dispersal — 1 tree height											+	+	+	+	+	+	+	+	+	+	+	+	+						
4. 1-2 tree heights											+	+	+	+	+	+	+	+	+	+	+	+	+						
5. 2-3 tree heights											+	+	+	+	+	+	+	+	+	+	+	+	+						
6. 3-4 tree heights											+	+	+	+	+	+	+	+	+	+	+	+	+						
7. 4-5 tree heights											+	+	+	+	+	+	+	+	+	+	+	+	+						
8. 5-6 tree heights											+	+	+	+	+	+	+	+	+	+	+	+	+				R		
9. 6-7 tree heights											+	+	+	+	+	+	+	+	+	+	+	+	+						
10. 7+ tree heights											+	+	+	+	+	+	+	+	+	+	+	+	+						
11. Seedbed — shaded, damp, mineral																								+	+	+	+		
12. sunny, damp, mineral																								+	+	+	+		
13. shaded, dry, mineral																								+	+	+	+		
14. sunny, dry, mineral																								+	+	+	+		
15. shaded, damp, humus												Q												+	+	+	+		
16. sunny, damp, humus																								+	+	+	+		
17. shaded, dry, humus																								+	+	+	+		
18. sunny, dry, humus																								+	+	+	+		
19. shaded, damp, litter																								+	+	+	+		
20. sunny, damp, litter																								+	+	+	+		
21. shaded, dry, litter																								+	+	+	+		
22. sunny, dry, litter																								+	+	+	+		
23. unproductive																								+	+	+	+		
24. Acceptable stem																								1					
25. Unacceptable stem																									1				
26. Dead seedling																										1			
27. Nongerminate																											1		
28. Flower aborted																									S			1	
29. Seed aborted												O																	1

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[1] The states listed under *Transition matrix* represent the present states. The colum numbers across the top represent the future states. For example, reading across the row from state 1, "flowers developed", we find a + under states 2 and 29; this indicates that in one step, an ovule in a developed flower may either develop into a mature seed (state 2) or abort (state 29).

with stationary (constant) transition probabilities. In general, an absorbing Markov chain consists of an array of possible states that are occupied in a series of succeeding steps (a change of state). The outcome of each step in the process is dependent upon (conditional upon) the outcome of the one previous step. The possible outcomes at each step in the process have probabilities that sum to 1. The process consists of a series of transient states—states that are never permanently occupied. Finally, the process reaches an absorbing state—a state that is never left once it is occupied. This terminates the process. States 1 to 23 are transient states, while states 24 to 29 are absorbing states.

A Markov chain is completely defined by a matrix of transition probabilities P and an initial vector A (a (1), a (2) . . .), which gives the probability distribution for the states (1, 2 . . .) at time zero. The matrix P contains the conditional probabilities of moving in one step from each state in the process to each other state.

The locations of positive entries in the initial vector and transition matrix (table 1) illustrate the specific course followed by the process. It begins with the development (state 1) or abortion (state 28) of a female ament. After nondevelopment of the ament, the process remains (is absorbed) in this state. If the ament develops, the process moves to the development of any given ovule into a ripe seed (state 2) or the abortion of the seed (state 29). Seed abortion is considered an absorbing state, and thus the process never leaves this condition. If the seed develops, the process moves to the dispersal of the seed to various distances (states 3 to 10). For each dispersal distance, any of several seedbed conditions (states 11 to 23) might be encountered with given probabilities. For each seedbed condition, the process moves to the development of any of various classes of seedlings or a nongerminate (states 24 to 27). These last four states also are considered absorbing states, which terminate the process.

Properties and Applications[4]

It is convenient to divide the transition matrix P into four submatrices:

$$(1)\quad P = \begin{array}{ccc} \text{1-23} & \text{24-29} & \\ Q & R & \text{1-23} \\ O & S & \text{24-29} \end{array}$$

Submatrix S covers the behavior of the process after it enters one of the absorbing states. Submatrix O is all zeros. Submatrix Q concerns the

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[4] Kemeny, John G., and J. Laurie Snell. FINITE MARKOV CHAINS. 210 pp. D. Van Nostrand Co., Inc., New York. 1960.

process while it remains in transient states. Submatrix R covers the transition from transient to absorbing states.

Many of the properties of an absorbing chain are developed through use of the so-called fundamental matrix, which is defined as:

$$(2)\ N = (I - Q)^{-1}$$

where I is the 23 x 23 identity matrix (matrix with a diagonal of 1-values, and zeroes elsewhere).

Beginning with any present state i, the expected number of times that the process is in a given transient state equals:

$$M_i\ (n_j) = N$$

where $M_i\ (n_j)$ is a 23 x 23 matrix. For example, if we assume that a flower has developed, the ratio between the average number (number < 1 in this application) of seeds developed before the process reaches an absorbing state and the average number of seeds reaching shaded, damp, mineral soil would equal $M_1\ (n_2)\ /\ M_1\ (n_{11})$.

For any given initial probability vector A (excluding the absorbing states):

$$M_A\ (n_j) = AN$$

where $M_A\ (n_j)$ is a 1 x 23 vector.

Of particular interest is the probability of arriving at a given absorbing state if the process currently is in a given transient state. This matrix of probabilities is given by:

$$B = b_{ij} = N\ R$$

where B or b_{ij} is a 23 x 6 matrix, where i refers to the initial or current state and j refers to the six absorbing states.

For example, the probability that a developed seed will produce an acceptable stem is given by: $b_{2,1}$. For a given number of seeds = S, the expected number of acceptable stems would be $b_{2,1}$ x S. Furthermore, assuming that a given number of seeds or potential seeds are independently distributed into the absorbing classes with constant probabilities, we could estimate the probabilities of various numbers of occurrences of each absorbing state by using the ordinary multinominal distribution.

The probabilities provided by matrix B can also be developed by taking the original transition matrix P to successive powers. In the classical absorbing chain, $P^{n \rightarrow \infty}$ approaches a limit. In the present example, P^4 has reached a limit so that $P^4 \times P^n = P^4$.

For any given initial probability vector of transient states, the probability of arriving at any absorbing state would be:

$$B_A = A\ N\ R$$

where B_A is a 1 x 6 matrix.

Discussion

A number of silvicultural considerations can be incorporated into this theoretical model of the birch regeneration process. Silvicultural operations like scarification of the seedbed can be reflected simply by revising the estimated probabilities of encountering various seedbed conditions. Clearcutting in winter, which provides both a before-logging seed source during the first spring and an after-logging seed source in ensuing years, could be handled by a change in dispersal probabilities. Regeneration after small clearcuttings, patch cuttings, or strip cuttings requires the summation of expected numbers from more than one seed production source, as well as consideration of the effects of small cuttings on seedbed conditions. Finally, new biological information on the birch regeneration process would be reflected by greater accuracy in estimated probabilities and by new or refined definitions of the states in the process. As our knowledge of the process increases, we may find a need for incorporating additional states, recycling the process through certain states more than one time, and perhaps breaking the process into subprocesses.

The use of stochastic models appears to be a promising means not only for theoretically representing the birch regeneration process, but also for knitting together isolated available information into useful estimates of both regeneration probabilities and expected numbers. Based on the theory presented in this paper, further work is underway on the development and testing of numerical models and on the generation of practical estimates covering a range of natural and manmade regeneration conditions.

—WILLIAM B. LEAK
Principal Silviculturist
Northeastern Forest Experiment Station
Durham, New Hampshire

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