A Matrix Approach to the Management of Renewable Resources, with Special Reference to Selection Forests

A MATRIX APPROACH TO THE MANAGEMENT OF RENEWABLE RESOURCES, WITH SPECIAL REFERENCE TO SELECTION FORESTS

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The manager of a renewable resource is concerned with a set of organisms that are growing older or larger, and with the exploitation of some of these organisms. Conservation of the resource is required in order that a sustained production can be achieved, and this in turn implies that the exploited organisms are being replaced by younger ones. To achieve a maximum sustained production the proportions of the different size or age classes of the resource will have to be determined, and the amount of replacement by younger organisms calculated.

Black (1965) asks the question: 'if it were possible to remove all the factors acting to maintain yields at a low level, what would then determine yield and what might the yield then be?' It is proposed to answer a weaker form of this question: 'given the effect of the site factors on the growth of the resource, what then is the structure of the resource that will achieve the maximum sustained yield?'.

Selection forests have been chosen as an example of a renewable resource. Management of these forests on an experimental basis was conceived by Gurnaud in the nineteenth century. Biolley (1920, 1954) codified the ideas and from them a system of management known as the check method has evolved. Biolley concludes that the check method provides management with an experimental foundation. The system of management aims at producing as much timber as possible, consistent with the constraints of quality and conservation.

Methods of selection working are considered by Colette (1934, 1960). The exploitation of the stand is based on the results of periodic enumerations, recording all trees by species and circumference classes. Colette calculates an overall percentage recruitment from one circumference class to the class above, and this figure is used in calculating the exploitation. The stem-number curve forms a graphical check on the state of the stand. It is compared with a theoretical smooth curve in which the number of trees in each successive class is represented by a decreasing geometric progression. Successive terms in this progression are related by the 'coefficient of diminution', due to de Liocourt. The method of calculating this coefficient is described later in this paper.

A manager of the selection forests wants to know which forest structure will give him the greatest production, but yet will conserve his forest. The manager of any renewable resource wants to know similar facts about his resource. He is thus maximizing the volume of production, subject to conservation of the resource. Another possible approach, that is not developed in this paper, would be to maximize the economic yield, consistent with conservation. It is proposed to show that a theoretical structure can be determined from a knowledge of the individual recruitments in each class of the resource to the class or classes above, and that this structure can be defined for any set of management objectives. The importance of this theoretical structure is that it is unique, and that it will optimize the yield from the resource over a long period. Though greater production could be obtained over a shorter period by a different structure, for example, by having a large excess of trees that were exploitable, there could be no sustained production at this higher level. The best theoretical structure is thus characterized, and it should be the aim of the resource manager to approximate to this as closely as he can.

A MATHEMATICAL MODEL

The stable age structure in an animal population, or in populations measured by age classes, has been investigated by Leslie (1945, 1948) and Williamson (1959). Lefkovitch (1965) has considered insect populations grouped by stages of development. The data concerning the population are used to calculate the elements of a matrix that will link the numbers in the various age groups at successive times. The link is provided by the matrix equation

$$\begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_{n-1} & f_n \\ p_0 & \cdot & \cdot & & \cdot & \cdot \\ \cdot & p_1 & \cdot & & \cdot & \cdot \\ \cdot & \cdot & p_2 & & \cdot & \cdot \\ \vdots & & & & & \\ \cdot & \cdot & \cdot & & p_{n-1} & \cdot \end{bmatrix} \begin{bmatrix} n_{t,0} \\ n_{t,1} \\ n_{t,2} \\ n_{t,3} \\ \vdots \\ n_{t,n} \end{bmatrix} = \begin{bmatrix} n_{t+1,0} \\ n_{t+1,1} \\ n_{t+1,2} \\ n_{t+1,3} \\ \vdots \\ n_{t+1,n} \end{bmatrix}$$

In the matrix, f_i ($i = 0, 1, 2, \ldots, n$) refers to the fecundity of a female in the ith age group, and p_i ($i = 0, 1, 2, \ldots, n-1$) is the probability that a female in the ith age group will be alive in the $(i+1)$th age group. It is evident that $p_i \leqslant 1$, since a female must either die or become one age group older during the period over which the matrix operates. In the vectors, $n_{t,i}$ is the known number of animals in the ith age group at time t, and $n_{t+1,i}$ is the predicted number in the same age group at time $t+1$. The matrix equation means that the ith element in the vector on the right-hand side of the equation is equal to the inner product of the ith row of the matrix and the vector on the left-hand side of the equation. The matrix can be broken down into the sum of two matrices, one stochastic matrix which gives the probability that an individual will be in another class at the end of the period of time, and a second matrix that gives the reproductive data for all classes.

Renewable resources measured in terms of size attributes rather than age will be considered in developing a model for their management. Thus an organism which is in the ith class at the start of a period of time can be in the same class at the end of the period, or it can be in a class characterized by a larger size of that attribute, or it can have died. If the organism dies, it will be assumed to form part of the exploitation. A convention in forest enumeration is that trees that have died during the period since the previous enumeration are measured and counted as part of the current exploitation. Thus it is assumed that the probability of an organism disappearing during a period is zero. If organisms either move up one class, or remain in the same class, the recruitment data can be represented by a stochastic matrix:

$$\mathbf{P}' = \begin{bmatrix} a_0 & . & . & . & \cdots & . & . \\ b_0 & a_1 & . & . & & . & . \\ . & b_1 & a_2 & . & & . & . \\ . & . & b_2 & a_3 & . & . & . \\ \vdots & & & & & & \\ . & . & . & . & & a_{n-1} & . \\ . & . & . & . & & b_{n-1} & a_n \end{bmatrix}$$

a_i ($i = 0, 1, 2, \ldots, n$) is the probability that an organism in the ith class will remain in that class during the period, and b_i ($i = 0, 1, 2, \ldots, n-1$) is the probability that an organism in the ith class will recruit up to the $(i+1)$th class during the period. P' is thus a square matrix with $n+1$ rows and columns.

It is assumed that exploitation occurs at the end of one period of time, just prior to the start of the next period, and that exploitation from the largest class is enhanced since larger trees are not required. This latter assumption implies that $a_n < 1$. Since the loss of an organism during the period is assumed impossible.

$$a_i + b_i = 1 \quad (i = 0, 1, 2, \ldots, n-1) \tag{1}$$

Also, since all the $n+1$ classes represented by the matrix are attainable, a proportion of the organisms in each class, except the nth class, must move up a class. It is possible that all organisms in a class might move up. Thus the following bounds can be put on the probabilities

$$0 \leqslant a_i < 1 \tag{2}$$

and from equation (1) it follows that

$$0 < b_i \leqslant 1 \tag{3}$$

The matrix $\mathbf{P}'$ accounts for the processes of enlarging, but regeneration processes must also be considered by adding another square matrix with $n+1$ rows and columns. This second matrix contains zero elements except for some positive elements in the first row. These elements represent functions of the regeneration that will be discussed below. The resultant matrix is:

$$\mathbf{Q} = \begin{bmatrix} a_0 & k_1 & k_2 & k_3 & \cdots & k_{n-1} & k_n \\ b_0 & a_1 & . & . & & . & . \\ . & b_1 & a_2 & . & & . & . \\ . & . & b_2 & a_3 & & . & . \\ \vdots & & & & & & \\ . & . & . & . & & a_{n-1} & . \\ . & . & . & . & & b_{n-1} & a_n \end{bmatrix}$$

where k_i ($i = 1, 2, \ldots, n$) are functions of the regeneration from the ith class. Consider also the column vector

$$\mathbf{q}_t = \{q_{t,0}, q_{t,1}, q_{t,2}, \ldots, q_{t,n}\}$$

where the element $q_{t,i}$ ($i = 0, 1, 2, \ldots, n$) gives the number of organisms in the ith class at the time t. Since the matrix $\mathbf{Q}$ contains estimates of the regeneration and of the probabilities that organisms will change classes, the structure of the resource at time $t+1$ is given by

$$\mathbf{q}_{t+1} = \mathbf{Q}\,\mathbf{q}_t$$

The stability of the resource can be investigated by comparing the structures at times t and $t+1$. If the resource has reached a stable structure the proportions of organisms in each class will be the same at both times, even although the number of organisms in the resource has increased during the period. The increase will be harvested. Thus, if λ is a constant, then the equation

$$\mathbf{q}_t = \frac{1}{\lambda}\,\mathbf{q}_{t+1}$$

would characterize a stable resource. Assuming that stability has now been reached, and letting the stable structure by proportions be represented by the vector $\mathbf{q}$, then

$$\mathbf{Q}\,\mathbf{q} = \lambda\,\mathbf{q}$$

Clearly λ is a latent root of the matrix $\mathbf{Q}$. Since $\mathbf{Q}$ is a matrix with $n+1$ rows and columns there are $n+1$ possible values of λ, though some of these might be negative, repeated or imaginary.

If there is a value of λ that is greater than unity then the number of organisms can be seen to increase over the period of time, and the increase in the number of organisms is a measure of the potential exploitation. Hence, if there are N organisms at the start of a period and λN at the end, the potential exploitation by numbers is $(\lambda-1)N+q_n e_n$, where e_n is the proportional enhanced yield from the nth class. It can be seen that

$$a_n = 1 - e_n$$

It will be assumed that c_i ($i = 1, 2, \ldots, n$) organisms of class O can regenerate in a location previously occupied by an organism of class i that has been exploited. c_i is thus a function of the number of smaller organisms that can occupy the space of a larger organism that has been exploited as well as the amount of this space which is taken by expansion of neighbouring organisms. Thus,

$$c_i \geqslant 0 \tag{4a}$$

and when i is sufficiently large

$$c_i > 1 \tag{4b}$$

In particular, $c_n > 1$.

These regeneration expressions can now be substituted for the k_i in the matrix $\mathbf{Q}$. Thus k_i is replaced by $c_i(\lambda-1)$, since c_i represents the number of organisms that will fill a location, and the proportion of locations after exploitation is $(\lambda-1)$. With an enhanced yield from the nth class,

$$k_n = c_n(\lambda-1) + c_n(1-a_n) = c_n(\lambda - a_n)$$

Thus, the regeneration and recruitment data can be represented by the matrix $\mathbf{Q}$, where

$$\mathbf{Q} = \begin{bmatrix} a_0 & c_1(\lambda-1) & c_2(\lambda-1) & \dots & c_{n-1}(\lambda-1) & c_n(\lambda-a_n) \\ b_0 & a_1 & . & & . & . \\ . & b_1 & a_2 & & . & . \\ . & . & b_2 & & . & . \\ \vdots & & & & & \\ . & . & . & & a_{n-1} & . \\ . & . & . & & b_{n-1} & a_n \end{bmatrix}$$

From the matrix equation

$$\mathbf{Q}\,\mathbf{q} = \lambda\,\mathbf{q} \tag{5}$$

it is shown in the appendix that there exists at least one latent root of the matrix $\mathbf{Q}$ that is greater than unity. It is also shown that the latent vector associated with such a latent root has all its elements of the same sign. Since latent vectors are determined only up to a constant factor, the sign of the elements can be taken as positive.

In a model of a renewable resource no significance can be attached to negative or imaginary numbers of organisms. It follows from the appendix that λ_0, which is any one of the latent roots greater than unity, is associated with a latent vector having positive elements. This root is not less than the absolute value of any other latent root, and thus it is the largest real latent root of the matrix. Thus it is proved that there is a unique optimal structure for a renewable resource, classified by some size attribute, that is meaningful (having no negative or imaginary terms). This structure is associated with the greatest latent root of the matrix and therefore maximizes the yield from the resource.

AN APPLICATION OF THE MODEL TO A SCOTS PINE FOREST

The data given in the example are taken from the forest plantations at Corrour in Inverness-shire. Since 1952 the Department of Forestry and Natural Resources of Edinburgh University has applied the check method of management to a part of these plantations. The forest contains a large mixture of species, predominantly Norway and Sitka spruce and Scots pine. The stands of Sitka spruce and Scots pine are generally quality class III (Hummel & Christie 1953). The management of the area is divided into six roughly equal blocks, each one of which is enumerated every sixth year. The enumeration consists of recording all the trees in the block by species and by quarter girth classes. The enumeration data for Scots pine have been used in this example.

The pooled enumeration data for Scots pine are summarized in Table 1. The table also shows how the transition probabilities, a_i and b_i, are estimated. The data for the regeneration terms have not been measured in the field, and values for these terms have been estimated from yield tables for Scots pine given by Hummel & Christie (1953). They have been calculated as the ratio of the number of trees of size class 0 per acre to the number of trees of class i. The figures are interpolated from the quality class III table. It has been assumed that gaps caused by the felling of small trees are utilized by the crowns of surrounding trees, and that they do not form foci for regeneration.

The matrix $\mathbf{Q}$ is therefore

$$\mathbf{Q} = \begin{bmatrix} 0{\cdot}72 & 0 & 0 & 3{\cdot}6(\lambda-1) & 5{\cdot}1(\lambda-1) & 7{\cdot}5\lambda \\ 0{\cdot}28 & 0{\cdot}69 & 0 & 0 & 0 & 0 \\ 0 & 0{\cdot}31 & 0{\cdot}75 & 0 & 0 & 0 \\ 0 & 0 & 0{\cdot}25 & 0{\cdot}77 & 0 & 0 \\ 0 & 0 & 0 & 0{\cdot}23 & 0{\cdot}63 & 0 \\ 0 & 0 & 0 & 0 & 0{\cdot}37 & 0 \end{bmatrix}$$

It will be assumed that the objects of management are to have a sustained yield of Scots pine timber, and that class 5 trees are the largest that are required, and hence all trees in this class will be exploited. Hence the a_5 term in the matrix $\mathbf{Q}$ is zero.

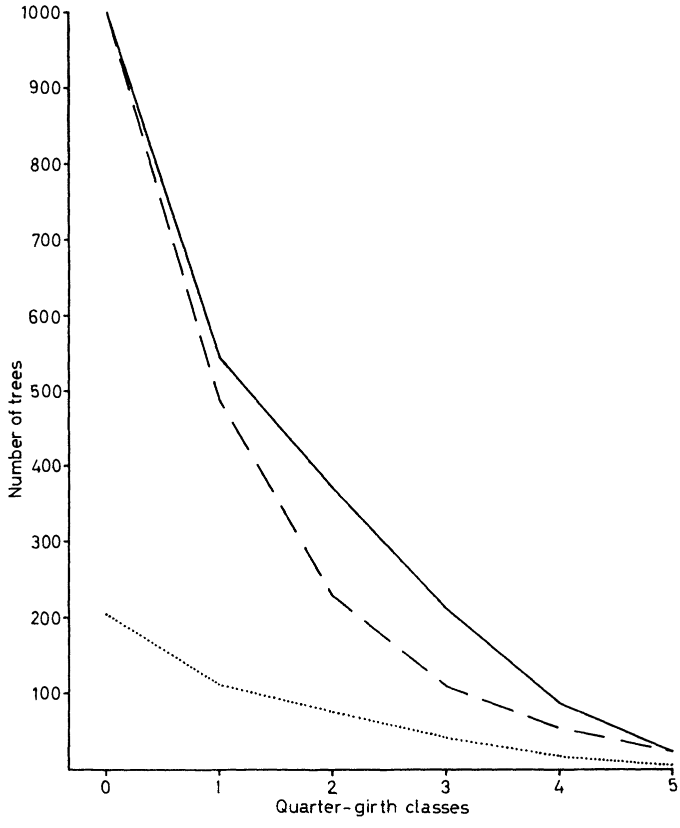

FIG. 1. The relation between number of trees and quarter girth classes. The solid line represents the stem-number curve using the matrix model developed in this paper. The dashed line represents a model based on a geometric progression. The exploitation expected under the matrix model is shown as a dotted line.

The coefficient of diminution can be calculated as the average of every d_i weighted by the number of trees in the ith class (see Table 1). This is found to be 2·08. Colette's (1934) 'courbe d'équilibre théoretique' is a geometric progression in which the number of trees in each class is 2·08 times the number in the following class. This forms the smooth stem-number curve that is illustrated in Fig. 1.

Table 1. *The basic enumeration data for a Scots pine forest at Corrour, Inverness-shire. The method of estimating the probabilities (a_i and b_i) used in the matrix model is shown. The coefficient of diminution is a weighted average of the ratios d_i*

Class i	Trees at first enumeration N	Ratio $d_i = \frac{N_{i-1}}{N_i}$	Trees felled in exploitation at time of first enumeration F	Trees remaining at start of period $S = N - F$	Trees measured at end of period E	No. of trees moving up one class during period $U_i = E_{i+1} - R_{i+1}$	Percentage of trees moving up $b_i = \frac{100U_i}{S_i}$	No. of trees remaining in class during period $R_i = S_i - R_i$	Percentage of trees remaining in class $a_i = \frac{100R_i}{S_i}$
Below 0	–	–	–	–	–	944	–	–	–
0	5877	–	1416	4461	4158	1247	28	3214	72
1	3761	1·56	835	2926	3276	897	31	2029	69
2	1331	2·83	245	1086	1710	273	25	813	75
3	280	4·75	58	222	444	51	23	171	77
4	33	8·49	6	27	68	10	37	17	63
5	2	16·50	2	0	10	–	–	–	–

The stable structure represented by the matrix **Q** can be found by a process of iteration. Matrix equation (5)

$$\mathbf{Q}\,\mathbf{q} = \lambda\,\mathbf{q}$$

yields a set of $n+1$ simultaneous linear equations in $n+2$ unknowns. These equations are

$$0{\cdot}72\,q_0+3{\cdot}6(\lambda-1)\,q_3+5{\cdot}1\,(\lambda-1)\,q_4+7{\cdot}5\,\lambda\,q_5 = \lambda\,q_0$$
$$0{\cdot}28\,q_0+0{\cdot}69\,q_1 = \lambda\,q_1$$
$$0{\cdot}31\,q_1+0{\cdot}75\,q_2 = \lambda\,q_2$$
$$0{\cdot}25\,q_2+0{\cdot}77\,q_3 = \lambda\,q_3$$
$$0{\cdot}23\,q_3+0{\cdot}63\,q_4 = \lambda\,q_4$$
$$0{\cdot}37\,q_4 = \lambda\,q_5$$

whence

$$\left.\begin{aligned} q_1 &= \frac{0{\cdot}28}{\lambda-0{\cdot}69}\,q_0 \qquad & q_2 &= \frac{0{\cdot}31}{\lambda-0{\cdot}75}\,q_1 \\ q_3 &= \frac{0{\cdot}25}{\lambda-0{\cdot}77}\,q_2 \qquad & q_4 &= \frac{0{\cdot}23}{\lambda-0{\cdot}63}\,q_3 \\ q_5 &= \frac{0{\cdot}37}{\lambda}\,q_4 & & \end{aligned}\right\} \tag{6}$$

and

$$z = (\lambda-0{\cdot}72)\,q_0-3{\cdot}6\,(\lambda-1)\,q_3-5{\cdot}1\,(\lambda-1)\,q_4-7{\cdot}5\,q_5 = 0 \tag{7}$$

If q_0 is chosen arbitrarily as 1000 (as was chosen for the stem-number curve using the coefficient of diminution) trial values of λ can be used to give the structure represented by the q terms in equations (6). When these q terms and the trial value of λ give a value of $z = 0$ in equation (7) then the actual value of λ has been found.

As an example, the trial value of λ, $\lambda_1 = 1{\cdot}2$, was used with $q_0 = 1000$. From equations (6) this gave the results $q_1 = 549{\cdot}020$, $q_2 = 378{\cdot}213$, $q_3 = 219{\cdot}891$, $q_4 = 88{\cdot}728$, $q_5 = 27{\cdot}358$. On putting these values in equation (7), $z_1 = 15{\cdot}045$. It is useful at this stage to work with three or four decimal places. These can be dropped after the final value of λ has been obtained.

If z is positive the trial value of λ is too small. Conversely, if z is negative, λ is too large. A second approximation to λ, $\lambda_2 = 1{\cdot}21$, was tried with $q_0 = 1000$. The results from equations (6) are $q_1 = 538{\cdot}462$, $q_2 = 362{\cdot}876$, $q_3 = 206{\cdot}180$, $q_4 = 81{\cdot}761$, $q_5 = 25{\cdot}001$ giving a value of z, $z_2 = -19{\cdot}679$. λ_2 is thus too large, and the actual value of λ lies between 1·20 and 1·21. A revised estimate, based on linear interpolation between λ_1 and λ_2, is given by

$$\lambda_3 = \lambda_1+(\lambda_1-\lambda_2)\left(\frac{z_1}{z_2-z_1}\right) = 1{\cdot}2043$$

Using λ_3 with $q_0 = 1000$ gives the results $q_1 = 544{\cdot}429$, $q_2 = 371{\cdot}501$, $q_3 = 213{\cdot}851$, $q_4 = 85{\cdot}644$, $q_5 = 26{\cdot}313$ giving $z_3 = -0{\cdot}119$. If $\lambda_4 = 1{\cdot}2042$ is tried the result $z_4 = 0{\cdot}230$ is obtained, and thus a value of λ correct to four places of decimals is 1·2043. The structure of the stable forest is represented by the vector

$$\{1000, 544, 372, 214, 86, 26\}$$

This stem-number curve is plotted in Fig. 1. Comparing it with the geometric curve shows that far more trees in the middle size classes are required for a stable forest structure. It will be noticed in this model that the concept of a smooth stem-number curve, as was obtained with a geometric model, is no longer valid.

After each enumeration period of 6 years there will be a harvest of $[(1\cdot204-1)/1\cdot204]\times 100\%$ or, approximately, 17% of the stand plus the extra taken from the largest class. The exploitation is shown in Fig. 1.

It is for the forest manager to decide what stocking is required, since neither the matrix model nor the geometric model can determine the actual number of trees per unit of area. Only the relationship between the actual numbers is given. Thus in the examples used the smallest class is assumed to have 1000 trees. It follows from this that the latent vector is determined except for an arbitrary constant by which each element in the vector can be multiplied. The forest manager can also revise the elements in the matrix **Q** as more accurate estimates of the probabilities become available by periodic enumeration or sampling. Replacement of the elements by functions involving the stand density would also be possible, but insufficient data are available from Corrour to estimate such functions. The manager will also have to ensure that regeneration is sufficient to meet the recruitment into class 0 required by the model.

Table 2. *The effect of small changes in the probabilities used in the matrix* **Q** *on the dominant latent root and latent vector of the matrix*

	Normal (matrix **Q**)	Recruitments increased 5%	Recruitments decreased 5%
Latent root	1·204	1·232	1·177
Vector class 0	1000	1000	1000
1	544	549	539
2	372	363	382
3	214	209	220
4	86	88	82
5	26	29	24

The concept of error in the assessment of the elements of the matrix is important. If the latent root and latent vector are to provide a firm foundation for management they should not be too sensitive to small inaccuracies in the estimation of the elements in the matrix. Table 2 gives some comparisons that suggest that the matrix is able to determine a stable structure that is not very sensitive to small errors in the enumeration data.

The approach to stability can also be predicted by the matrix model. If the value of $\lambda = 1\cdot2043$ is inserted in the matrix **Q**, then

$$\mathbf{Q} = \begin{bmatrix} 0\cdot72 & 0 & 0 & 0\cdot74 & 1\cdot04 & 9\cdot03 \\ 0\cdot28 & 0\cdot69 & 0 & 0 & 0 & 0 \\ 0 & 0\cdot31 & 0\cdot75 & 0 & 0 & 0 \\ 0 & 0 & 0\cdot25 & 0\cdot77 & 0 & 0 \\ 0 & 0 & 0 & 0\cdot23 & 0\cdot63 & 0 \\ 0 & 0 & 0 & 0 & 0\cdot37 & 0 \end{bmatrix}$$

and if the present structure of the forest after exploitation, $\mathbf{q}_0$, is known, then

$$\mathbf{r}_1 = \mathbf{q}_1 + \mathbf{e}_1 = \mathbf{Q}\,\mathbf{q}_0$$

where $\mathbf{r}_1$ is the forest structure before exploitation, $\mathbf{q}_1$ is the structure after exploitation that continues into the second period, and $\mathbf{e}_1$ is the exploitation. When k periods of time have elapsed the structure and exploitation at $k+1$ is estimated as

$$\mathbf{r}_{k+1} = \mathbf{q}_{k+1} + \mathbf{e}_{k+1} = \mathbf{Q}\,\mathbf{q}_k$$

e_{k+1} is thus an estimate of the exploitation after $k+1$ periods of time and hence management forecasts could be based on such information.

The structure at the present time, $\mathbf{q}_0$, is given in Table 1 as

$$\mathbf{q}_0 = \{4461, 2926, 1086, 222, 27, 2\}$$

though the two class 5 trees will be taken as enhanced yield. Pre-multiplying this vector by the matrix $\mathbf{Q}$ gives the forest structure after 6 years as

$$\mathbf{r}_1 = \{3422, 3268, 1722, 442, 68, 10\}$$

If a yield of 17% ($\lambda = 1{\cdot}2043$) is taken, then

$$\mathbf{e}_1 = \{581, 554, 292, 75, 11, 2\}$$

leaving a structure, $\mathbf{q}_1$, for the next period

$$\mathbf{q}_1 = \{2841, 2714, 1430, 367, 57, 8\}$$

where the eight class 5 trees will be taken as enhanced yield.

If $\mathbf{r}_1$ is compared with the trees measured at the end of the period, E, in Table 1 it

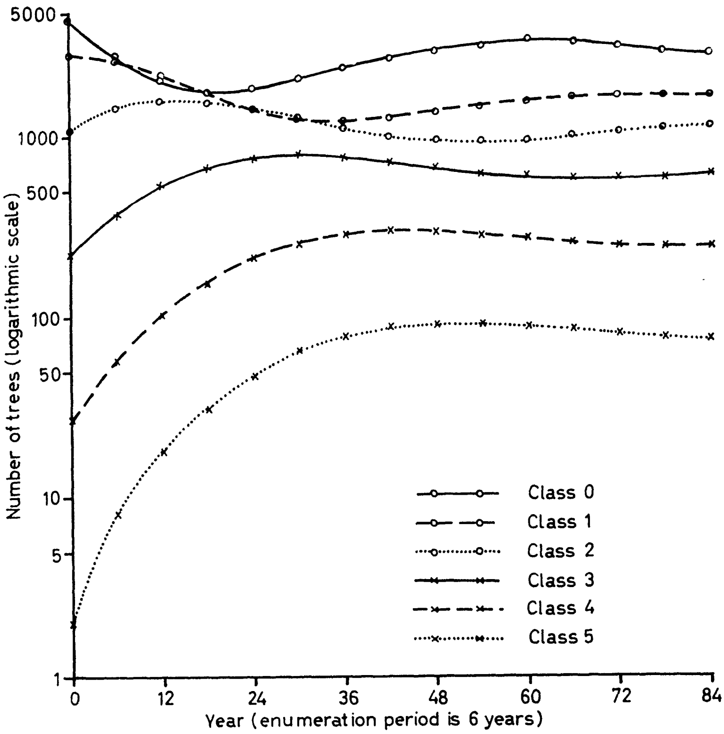

FIG. 2. The structure of a Scots pine forest estimated, after an exploitation of 17%, for the next fourteen 6-year enumeration periods. The forest has approximated to its stable structure after about twelve periods.

will be seen that the structures agree closely above class 0. Class 0 differs since there is an excess of young Scots pine trees at Corrour, and hence there has been excessive recruitment into class 0. The forest structures, $\mathbf{q}_i$, for values of i from 0 to 14 have been plotted in Fig. 2. The curves drawn in the figure connect the same class during the fourteen periods. Interpolation between points is not possible since the structures are plotted for the exploited stand just prior to the commencement of a 6-year period. It can be seen that the forest would be brought to approximately its stable structure, previously calculated as $\mathbf{q}$, after about twelve enumeration periods. This period would allow for the gradual build-up of the older growing stock, replacing the excessive young stock, that is shown by Fig. 2.

ACKNOWLEDGMENTS

I wish to thank Professor M. H. Williamson, University of York, who stimulated my interest in the application of matrix algebra to biological systems.

I also wish to thank many members of staff in the Departments of Mathematics and Forestry and Natural Resources in the University of Edinburgh who have discussed the problems with me. I am indebted to the Nuffield Foundation for financial assistance.

SUMMARY

The management of a renewable resource, classified by size classes, is considered. A mathematical model which predicts the stable structure of such a resource is developed. Data on the percentage recruitment of organisms from one class to the class above and data on the regeneration of young organisms are used as elements of a matrix. The largest real latent root of this matrix gives the maximum exploitation, and the latent vector associated with this root gives the stable structure.

The model is illustrated by reference to a Scots pine forest in Inverness-shire. An iterative process for finding the latent root and vector is described. This matrix method is compared with a geometric method.

APPENDIX

AN ALGEBRAIC PROOF OF THE EXISTENCE OF A LATENT ROOT OF Q GREATER THAN UNITY

Consider the matrix $\mathbf{Q}$ and the matrix equation (5) that have been previously defined. The equation (5) gives a set of $n+1$ simultaneous linear equations in $n+2$ unknowns, $\lambda, q_0, q_1, q_2, \ldots, q_n$. Expanding equation (5) gives

$$\begin{aligned} a_0 q_0 + c_1 q_1(\lambda-1) + c_2 q_2(\lambda-1) + \ldots + c_{n-1} q_{n-1}(\lambda-1) \\ + c_n q_n(\lambda - a_n) = \lambda q_o \end{aligned} \tag{8}$$

and

$$\left.\begin{aligned} b_0 q_0 + a_1 q_1 &= \lambda q_1 \\ b_1 q_1 + a_2 q_2 &= \lambda q_2 \\ &\vdots \\ b_{n-1} q_{n-1} + a_n q_n &= \lambda q_n \end{aligned}\right\} \tag{9}$$

From equations (9), in the general case,

$$q_i = q_0 \frac{b_0}{b_i} \prod_{j=1}^{i} \left(\frac{b_j}{\lambda - a_j}\right) \qquad (i = 1, 2, \ldots, n) \tag{10}$$

where $\prod_{j=x}^{y}$ represents the product over all values of j from x to y inclusive. Substitution of the values of q_i given by (10) in equation (8) gives

$$\begin{aligned} a_0 + b_0 c_1 \frac{(\lambda-1)}{(\lambda-a_1)} + \ldots + \frac{b_0 c_i}{b_i} (\lambda-1) \prod_{j=1}^{i} \left(\frac{b_j}{\lambda-a_j}\right) \\ + \ldots + \frac{b_0 c_n}{b_n} (\lambda - a_n) \prod_{j=1}^{n} \left(\frac{b_j}{\lambda-a_j}\right) - \lambda = 0 \end{aligned} \tag{11}$$

The factor q_0 has been cancelled since this can be arbitrarily chosen as non-zero, otherwise all qs are zero.

If λ is put equal to one in equation (11) then the left-hand side becomes

$$a_0 + \frac{b_0 c_n}{b_n} (1 - a_n) \prod_{j=1}^{n} \left(\frac{b_j}{1-a_j}\right) - 1 \tag{12}$$

where b_n is defined as $1 - a_n$.

Expression (12) becomes

$$\begin{aligned} & a_0 + b_0 c_n - 1 && \text{since } 1 - a_j = b_j \\ & = b_0 (c_n - 1) > 0 && \text{since } c_n > 1 \text{ and } b_0 > 0 \end{aligned}$$

Now, letting λ tend to infinity in equation (11), the left hand side becomes

$$a_0 - \infty + b_0 c_1 < 0 \qquad \text{since } a_0,\ b_0 \text{ and } c_1 \text{ are finite.}$$

Thus, when $\lambda = 1$, the left-hand side of equation (11) is positive, whereas as $\lambda \to \infty$ this expression is negative. Therefore there exists at least one value of λ greater than unity for which equation (11) is satisfied. Values of λ satisfying equation (11) are the required solutions of the matrix equation (5). In equation (10), if a value of $\lambda > 1$ is substituted, and if q_0 is chosen positive, then the terms q_i $(i = 1, 2, \ldots, n)$ are all positive. Thus associated with any latent root greater than unity there is a latent vector such that all its elements can be chosen as positive numbers.

The properties of latent roots and vectors of matrices with positive and non-negative elements have been studied by Frobenius (1912), Fan (1958) and Brauer (1957, 1961, 1962). They show that there exists a latent root λ_0 of any non-negative matrix $\mathbf{N}$ such that: (i) corresponding to the latent root λ_0 there exists a latent vector having all its elements positive. λ_0 is the only latent root of $\mathbf{N}$ for which a corresponding latent vector exists with all its elements non-negative; and (ii) λ_0 is not less than the absolute value of any other latent root of $\mathbf{N}$. Theorems 3 and 4 of Brauer (1962) show that the latent root λ_0 is greater than or equal to the smallest row sum of $\mathbf{N}$, and that λ_0 is greater than the greatest main diagonal element $\mathbf{N}$. The same inequalities are true of column sums as well as row sums.

If a value of λ greater than unity of the matrix $\mathbf{Q}$ is considered, then $\mathbf{Q}$ has only non-negative elements. If λ_i, which is a root greater than unity of the matrix $\mathbf{Q}$, is inserted in $\mathbf{Q}$ to give $\mathbf{Q}^{(\lambda_i)}$, then there are $n+1$ possible roots of this matrix. One of these is λ_i, and the other n would not normally be latent roots of $\mathbf{Q}$. It has been shown above that λ_i is associated with a latent vector with all its elements positive. It therefore follows from the theorems stated above that λ_i is the largest latent root of $\mathbf{Q}^{(\lambda_i)}$, and that it is the only root associated with a vector of positive elements. Thus, any latent root greater than unity of the matrix $\mathbf{Q}$ determines a unique structure that is biologically meaningful. It cannot yet be proved that there is only one latent root greater than unity which satisfies the matrix $\mathbf{Q}$. There is, however, an optimal solution corresponding to the largest latent root.

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(*Received* 24 *September* 1965; *revision received* 6 *March* 1966)