

MODELIZATION IN NATURAL FORESTS : STAND STABILITY

MODELIZATION OF NATURAL FORESTS

The modelization of forests is a very busy area of research. It is in great demand from managers, but the models available for describing the dynamics are still unsatisfactory. Compartmental models seem to hold some promise. BRUMER & MOSER (1973), LOWELL & MITCHELL (1987), BUONGIORNO & LU (1990), and MICHIE & BUONGIORNO (1984) have obtained findings which can be directly applied to natural forest studies. Nevertheless, the theory is still not sufficiently developed to guarantee that the forecasts obtained will be reliable. As a result, authentication of findings over the medium and long term is a tricky problem, and a burdensome one, too, because it calls for the gathering of measurement data over long periods, with large sample sizes.

Another problem involves the concept of stand stability and the modelization thereof. Several authors have dealt with the study of this set of problems. Thus, for a given transition matrix, USHER (1969) worked out the stable stand structure, and BUONGIORNO & MICHIE (1980) add a regulation to the model by considering recruitment as a function of the basal area, obtaining a more or less long-term stand stability based on a fixed transition matrix. We give a solution to the inverse problem by calculating the transition matrix guaranteeing the stability of the numbers of trees in each diameter class, when these numbers are known.

COMPARTMENTAL MODELS

Compartmental models for describing growth have been used by LESLIE (1945) and adapted to the problem of the growth of trees in forests by USHER (1969). With these models it is possible to describe stand evolution by diameter class, using MARKOV processes. Let the stand distribution be defined as the numbers of trees in each diameter class, it is then possible to obtain the stand dis-

tribution at time $t + T$, by knowing the stand distribution at time t (in practice, the unit of time is the year).

NOTATIONS

For a given stand, the trees are grouped in k diameter classes defined by bounds a_i :

$$0 \leq a_0 < a_1 < \dots < a_k = \infty$$

Let n_{it} denote the number of trees in the class $[a_{i-1}, a_i]$ subsequently called class i , in year t , i equal 1 to k . The stand distribution is characterized by the column vector N_t ,

$$N'_t = (n_{1t}, \dots, n_{kt})$$

The dynamic of the system is described by :

- the matrix P_t of dimensions (k, k) containing the probabilities $p_{ij}(t)$ that a tree in class i in year t ends up in class j in year $t + 1$, knowing *a priori* that it has remained alive over this period. Under this condition, we clearly have :

$$\sum_j p_{ij} = 1$$

- the diagonal matrix S_t containing the survival probabilities, in other words the probabilities s_{ii} that a tree in class i in year t is still alive in year $t + 1$;
- lastly, the column matrix R_{t+1} of recruitments containing the numbers of trees r_{it+1} which are added to the stand in class i between years t and $t + 1$.

The general model is described by the formula :

$$N_{t+1} = P_t S_t N_t + R_{t+1} \quad (1)$$

ADDITIONAL OBSERVATIONS AND HYPOTHESES

The choice of the bounds a_i conditions the structure of the matrices P_t and R_t . To simplify the presentation of our study, we shall assume that the bounds a_i are such that :

$$\begin{aligned} \forall ij, p_{ij}(t) &= 0 & \text{si } j - i \neq 0 \text{ ou } 1 \\ \forall i, r_{it} &= 0 & \text{si } i \neq 1 \end{aligned}$$

In this article reference is made to experiments for which the growth rate of the stands being studied is such that these conditions are verified. Model (1) can then be expressed in the form of a k equations system :

$$\begin{aligned} n_{1t+1} &= p_{11}(t) s_1 n_{1t} + r_{1t+1} \\ n_{2t+1} &= (1 - p_{11}(t)) s_1 n_{1t} + p_{22}(t) s_2 n_{2t} \\ &\vdots \\ n_{kt+1} &= (1 - p_{k-1,k-1}(t)) s_{k-1} n_{k-1t} + p_{kk}(t) s_k n_{kt} \end{aligned} \quad (2)$$

It is evident that $p_{kk}(t)$ equals one, because it is not possible to leave the last class $[a_{k-1}, \infty[$ except in the event of mortality ($s_{kt} < 1$).

Insofar as one studies more specifically the conditions attaching to a situation of stability, in other words a situation which is developing either not at all or only slightly with time, it is acceptable to assume that the matrices \mathbf{P}_t and \mathbf{S}_t are independent of time. This is what we shall subsequently do, and these matrices should be noted \mathbf{P} and \mathbf{S} .

This model is generally used to forecast forest behaviour in a more or less long-term deterministic way. The transition matrix \mathbf{P} can be estimated by the maximum likelihood estimators given by ANDERSON & GOODMAN (1957), if the measurement of each tree in times t and $t + 1$ is known, and by LEE *et al.* (1968), if only the frequency distributions \mathbf{N}_t and \mathbf{N}_{t+1} are available. In the case where the measurements on each tree are known, the maximum likelihood estimator of p_{ij} is $n_{ij}(t)/n_i(t)$, where $n_{ij}(t)$ is the number of trees moving from diameter class i to diameter class j in time t and $n_i(t)$ is the number of trees in diameter class i surviving the period t .

The model described in (1) differs from that used by USHER (1969) by the fact that the recruitment is independent of the stand distribution.

STUDY OF THE MODEL

There may be different attitudes towards the equations (2), depending on the nature of the observations made. For example :

□ \mathbf{N}_{t+1} , \mathbf{N}_t and \mathbf{R}_{t+1} are given and one tries to evaluate the p_{ij} and the s_i , that is, the probabilities which describe the dynamics of the system. We are in the presence of a non-linear system with $2k - 1$ unknowns and k equations, and there is no chance of obtaining interesting solutions except by introducing additional constraints.

□ \mathbf{N}_{t+1} , \mathbf{N}_t , \mathbf{R}_{t+1} and \mathbf{S} are given and one tries to evaluate the p_{ij} . This latter case presupposes that one knows the probabilities $(1 - s_i)$ of mortality. This type of situation is not unrealistic for a forester who relies on a sound observation of recent blowdowns and the standing mortality of trees in the stand. One obtains a linear system with $k-1$ unknowns and k equations ($p_{kk} = 1$), which only admits a single solution insofar as the equations are not independent, which implies a certain coherence in the data \mathbf{N}_{t+1} , \mathbf{N}_t , \mathbf{R}_{t+1} and \mathbf{S} expressed by the equation :

$$r_1 = \sum_{i=1}^k n_i(1 - s_i)$$

which in turn implies that the recruitment is equal to the overall mortality.

STABILITY

The concept of stability is of immediate concern in undisturbed forests, whose floristic and diametric structures only develop very slightly with regard to the time scale, which is that of the observer. In using the previous model, the stability may be expressed in different ways, depending on the degree of restriction that is deemed pertinent to introduce. In this study, we talk in terms of complete stability if the stand distribution is retained between years t and $t + 1$, $\mathbf{N}_{t+1} = \mathbf{N}_t$, and if recruitment is constant. In reference to the model, the stability is expressed by the constraint,

$$\mathbf{N} = \mathbf{P}'\mathbf{S}\mathbf{N} + \mathbf{R} \quad (3)$$

Let us consider the case where the stand distribution and the mortality rate are known. There is a single solution in \mathbf{P} and r_1 to the system of equations (3) :

$$\begin{aligned} r_1 &= \sum_{i=1}^k n_i(1 - s_i) \\ p_{ii} &= \frac{\sum_{i=1}^i n_i - r_1 - \sum_{i=1}^{i-1} s_i n_i}{s_i n_i} \end{aligned} \quad (4)$$

This solution is obtained by direct substitution in the system of equations (2) and is only valid if $s_i n_i > 0$ for each i .

OBSERVATIONS

□ The solution given in (4) always exists and it is the only one for strictly positive numbers of trees.

□ The elements of matrix **P** may be negative but never greater than 1. For an element p_{ii} to be negative, a necessary condition is :

$$n_i < \sum_{j=i}^k n_j (1 - s_j),$$

which means that there are fewer survivors in class i than dead trees in the classes above. In the case of a constant mortality rate, $s = s_i$, for i equal 1 to k , we thus have a constraint on s :

$$\forall i, \quad s > \frac{\sum_{j=i+1}^k n_j}{\sum_{j=i}^k n_j}$$

and thus on r :

$$\forall i, \quad r < \frac{n_i}{\sum_{j=i}^k n_j}$$

(in particular, $r < n_0$, where $n_0 = \sum_i n_i$).

□ The transition matrix is interpreted as the growth by diameter classes necessary to guarantee the stability of the system. Solution (1) is first and foremost a function of growth calculated to guarantee the stability of a forest system. Growth by diameter classes may be described as the number of stems which progress from class i to class $i + 1$ between times t and $t + 1$, i.e. $s_i(1 - p_{ii})$, or as the average growth in diameters of trees in class i , i.e. ΔD_i . An approximation of this average growth is obtained by considering a uniform distribution of the n_i trees in class i : $\Delta D_i = s_i(1 - p_{ii}) (a_i - a_{i-1})$. This approximation, which is rough but simple to calculate, may be refined by using a spline function to smooth the stand distribution. The calculations are more complicated but a more realistic approximation is obtained.

□ Solution (4) is deterministic. It is associated with a frequency vector **N** and with a mortality rate **S**. Each pair (**N**, **S**) is associated with a transition matrix **P** and a recruitment r_1 . From this standpoint, the aim is not to determine a stable state, but rather the growth function to preserve the state (**N**, **S**). The more accurate the stand distribution and mortality rate, the more reliable the matrix of transition probabilities.

THE EFFECT OF ERROR ON THE MORTALITY RATE

The mortality rate is generally only available in the form of a more or less sound estimation. Let us suppose that the mortality rate that we observe $\varepsilon = 1 - s$ is constant. In practice, a value of around 1 % is usually observed in tropical moist forest. The recruitment is directly proportionate to ε , because $r_1 = n_0 \varepsilon$. Where transition probabilities are concerned, the following approximation is obtained :

$$p_{ii} = \frac{n_i + (1 - s) \sum_{j=1}^{i-1} n_j - r}{s n_i} = \frac{-\varepsilon \sum_{j=i}^k n_j + n_i}{n_i(1 - \varepsilon)}$$

$$= \left(1 - \varepsilon \frac{\sum_{j=i}^k n_j}{n_i} \right) (1 + \varepsilon + \varepsilon^2 + \dots) \approx 1 - \varepsilon \frac{\sum_{j=i+1}^k n_j}{n_i}$$

giving a linear equation between the p_{ii} and the mortality rate. This almost linear equation recurs in the growth rate, because :

$$\Delta D_i = s(1 - p_{ii}) (a_i - a_{i-1}) \approx (a_i - a_{i-1}) \frac{\sum_{j=i+1}^k n_j}{n_i} \varepsilon.$$

EXAMPLE

The Paracou arrangement in French Guiana is used as an example of the procedure. A stand which has not been logged, and which has been measured over 8 years between 1985 and 1992, is used. The table p. 31 gives the frequencies n_i for a division of the stand into 9 diameter classes, the p_{ii} values being estimated by formula (4) for $s = 0.99$ and 0.98 , and the values of p_{ij} being estimated by the method of maximum likelihood (MML), taking the evolution of **N** over 8 years into account. We should add that the mortality rate observed over these 8 years and for all the diameter classes is around 0.015. The figure p. 31 shows the graph of probabilities, making it easier to make a comparison with the transition probabilities.

We note that the transition probabilities calculated to guarantee stability are very close to the probabilities calculated by the MML. The most significant differences are obtained in the last two diameter classes, which is explained by the low frequencies of the extreme classes which lead to rough estimations by the MML (standard error of around 0.004), but this may also be the sign of a greater instability in associated stands (large tree

blowdowns). Furthermore, the choice of the mortality rate does not affect, or hardly affects, the general shape of the curves illustrating the evolution of the transition probabilities from one class to the next. This, incidentally, is what is expressed by the approximations given in « *The effect of error on the mortality rate* », p. 30. There is accordingly a correct identification of the inter-class dynamics.

DISCUSSION

We have just shown that, with a stable forest, it is possible to assess the growth dynamics either directly by means of the diametric structure, or in a classical manner by observing growth rates over a given period. It is noteworthy that the first approach may give suitable findings. This is not surprising, if one bears in mind that the

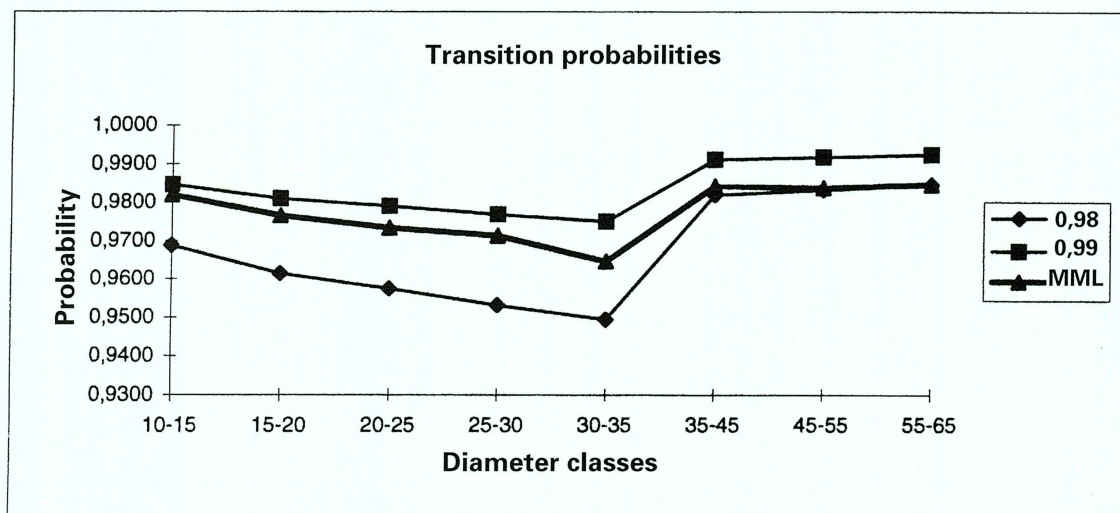
stand distribution, at any given moment, contain information about the past as a whole, and hence about the growth rate of the forest. *A posteriori*, this approach is possibly more relevant than a measurement of growth rates over a too small period of time, and one thus subject to random upheavals associated with particular circumstances (unusual annual climatic conditions, spasmotic pollution...).

The probabilistic context has not been made mention of, because the aim here has been to make the link between the stand distribution and the survival rate, on the one hand, and the transition matrix and recruitment on the other. A study of the random variations of a system in a state of equilibrium, and of the effects of these upheavals on the transition matrix is possible. Such a study has been undertaken, but is outside the scope of this study.

For bibliography, see the French version.

Frequencies over 8 years of measurement and on 18.75 ha. Transition probabilities for death rates of 0.98, p_{ii} (1) and 0.99, p_{ii} (2). Transition probabilities by the MML, p_{ii} (3).

Diameter classes	10-15	15-20	20-25	25-30	30-35	35-45	45-55	55	65+
Frequencies	4,602	2,432	1,489	942	622	816	396	186	143
p_{ii} (1)	0.9688	0.9614	0.9574	0.9531	0.9494	0.9819	0.9831	0.9844	1.0000
p_{ii} (2)	0.9846	0.9809	0.9789	0.9768	0.9750	0.9910	0.9916	0.9923	1.0000
p_{ii} (3)	0.9819	0.9765	0.9733	0.9713	0.9646	0.9841	0.9837	0.9845	1.0000



Graph of transition probabilities.