Structure and dynamics of a clonal plant population: Classical model results in a non-classic formulation

Dmitrii O. Logofet, Nina G. Ulanova, Iya N. Klochkova, Anna N. Demidova

Institute of Atmospheric Physics, Russian Academy of Sciences, 3 Pyzhevsky Lane, Moscow 119017, Russia
Department of Geobotany, Biological Faculty, Lomonosov Moscow State University, Moscow, Russia

Received 27 December 2004; received in revised form 17 June 2005; accepted 18 July 2005
Available online 20 October 2005

Abstract

The structure of a clonal plant population is studied in Calamagrostis canescens, a perennial grass colonizing forest areas which have become open due either to tree-felling or windthrow. A scale of ontogenetic stages is defined where the stages of individual plants (tussocks) are described in terms of their morphology. No strict correspondence has been revealed between the stage of the tussock and its chronological age. Therefore, the formal classification of individuals considers both the age and the stage in ontogenesis, which results in a life-cycle graph defined on a finite two-dimensional lattice. The origin of individuals (seed reproduction or vegetative propagation) has also appeared to predetermine different pathways within the life cycle. The traditional way to formally relate population dynamics to the population structure leads to a matrix model, while the special pattern of the life-cycle graph, together with that of the corresponding population vector, results in a non-traditional form of the projection matrix. This form differs from the classical Leslie and Lefkovitch ones with certain nonzero entries (vital rates), which complicates the routine mathematical analysis of the model. We demonstrate that the classical model outcomes, like the asymptotic rate of population growth (or decline), the equilibrium population structure and the reproductive values of the population groups can still be obtained from a given set of the age-stage-specific vital rates. The potential-growth indicator is also shown calculable from the vital rates and it appeared useful in a procedure of model calibration on a short series of empirical data. The model can thus serve as a research tool specialised for applied problems which may be associated with the double-structured population dynamics in a clonal plant species.

Keywords: Population structure; Calamagrostis canescens; Matrix models; Life-cycle graph; Projection matrix; Vital rates; Potential-growth indicator; Calibration

1. Introduction

Plant species possess a great deal of variability in individual ontogenetic behaviour. This is especially...
true in vegetation stands after large-scale disturbances like windthrow or forest felling. To understand the course and outcome of the early stage in the secondary succession, it is necessary to study the life history of species, especially the dominating ones. Studying the ontogeny in the dominant species gives a certain insight into the structure and functioning of the plant community.

The role a plant population plays in a vegetation stand is determined by its structure and abundance expressed in terms of: (i) the ontogenetic stages, and (ii) the chronological age of the individuals. The ontogenetic stages mark biological ages of plants. It is fairly difficult to determine the calendar age of many herbs and woody plants, whereas a classification by ontogenetic stages is quite feasible (Ulanova, 1995a, b). We use the Russian classification of ontogenetic stages according to Rabotnov (1978, 1985), Uranov (1975) and their co-workers (Zhukova and Ermakova, 1985).

The ontogeny of plants can be subdivided into the different stages based on the origin of individuals (either from seeds or vegetative reproduction) as well as on certain juvenile and adult characteristics. Pre-reproductive (juvenile), reproductive (adult), and post-reproductive (senile) stages can thus be distinguished.

The present study aims at developing a formalism to describe the population structure and dynamics of the woodreed [*Calamagrostis canescens* (Web.) Roth.], the major perennial grass species dominating on clearcut areas of coniferous forests. A traditional way would lead us to a formalism known as Lefkovitch model for stage-structured population dynamics (Lefkovitch, 1965; Caswell, 2001), where the chronological age of individuals is absent in explicit form. However, the techniques we used in the field and laboratory studies of *C. canescens* yields data both on the stage and chronological age of individual plants (hereafter called tussocks). Although a potential of matrix models in description of population structures with a double basis for classifying individuals was revealed and developed long ago (Law, 1983; Csetenyi and Logofet, 1989; Logofet, 1991; a recent survey is given in Caswell, 2001), models of plant populations where the two dimensions represent specifically the age and stage are quite rare (Ulanova et al., 2002; Logofet, 2002; Volis et al., 2004). Meanwhile, it is this type of classification which may be of importance in applications as the chronological age is apparently linked with time projections, while the stages are more important in intraspecific and interspecific relations. For example, it is the stage structure, rather than the age one, which may serve as indicator of the population fate in competition for shared resources or/and colonizing new habitats, e.g. in the course of secondary succession after tree felling.

The formalism we develop here uses the double classification (age and stage) and a certain list of possible age-stage groups which constitute the population structure. It leads to a pattern of the projection matrix which differs from the known classic ones, like Leslie or Lefkovitch matrices, and from its recent expansions (Klochkova, 2004). We demonstrate however that the notions and characteristics which are traditional for matrix models of population dynamics are still applicable in this non-traditional case.

2. Materials and methods

2.1. Key species

The population structure is considered as a set of individuals differing in their ontogenetic stage, chronological (calendar) age and origin (generative or vegetative reproduction).

*C. canescens* is taken as a key species for modelling. It is a perennial, clonal, long-rhizome, polycarpic grass with high seed production. *C. canescens* is a dominant species in the grass layer of clearcuts in boreal forests. In addition to seed reproduction, it has an ability to spread extensively by means of long horizontal rhizomes. Such clonal species can be very successful in colonizing large areas of clearcuts.

The studies were carried out in Southern Taiga forests (Tver Region, Russia), in the center of the Russian Plain. Climatically, it is a humid forest area with *Picea abies* (L.) Karst and *Pinus sylvestris* L. as dominant tree species. The spruce and pine forests are found here to vary in composition depending on geomorphology.

Investigation has been carried out on a two-year clearcut of a wet pine forest (*Piceetum sphagnosum*) in Tver Region, Russia (56°5–10' North, 32°0–10' East) in August, when the grass layer of vegetation has been completely formed. Ten sample plots (50 cm × 50 cm) were arranged in patches where *C. canescens* was dominating. All the tussocks (*N* = 762) were investigated...
2.2. Ontogeny of *C. canescens*

The total course of ontogeny in *C. canescens* has been described elsewhere (Ulanova and Demidova, 2001; Demidova and Ulanova, 2003). Here, we distinguish the following ontogenetic stages: seedlings (*p*), juvenile plants (*j*), immature plants (*im*), young virginal tussocks of seed origin (*sv*), mature virginal tussocks of seed origin (*sv*), old virginal tussocks of seed origin (*sv*), young virginal tussocks of vegetative propagation (*v*), mature virginal tussocks of vegetative propagation (*v*), old virginal tussocks of vegetative propagation (*v*), young reproductive tussocks of vegetative propagation (*g*), mature reproductive tussocks of vegetative propagation (*g*), old reproductive tussocks of vegetative propagation (*g*), subsenile tussocks of vegetative propagation (*ss*), senile tussocks of vegetative propagation (*s*), subsenile tussocks (*ss*), senile tussocks (*s*).
Seedlings (p) can only be found on disturbed microsites of clearcuts. A seedling usually consists of a primary shoot with one to three flat leaves and a primary root. Juvenile plants (j) have a small primary shoot bearing from three to six nodes but without branches of higher orders. The leaves display mature form and structure. The root system includes a primary root or its residuals, lateral roots of second and higher orders and adventitious roots. These tussocks grow rapidly and the most of them reach the virginal ontogenetic stage the same year (in July–August).

Virginal tussocks (v) look like mature plants but do not produce any seeds. A virginal plant has one–three (five) leader shoots (v₁, v₂, v₃, respectively) with branches of I–III (IV) orders. Its root system is completely developed. Virginal plants may be of seed origin (sv₁, sv₂, sv₃ depending on vitality). They are isolated in space. The majority of them usually die at the end of the first or second vegetative season. The strongest tussocks form one or two daughter rhizomes of 2–3 cm long. Such individuals start to reproduce in a vegetative mode.

Young reproductive tussocks (g₁) are similar to the adult tussocks. Their reproductive structures have mature features. These tussocks usually have one generative shoot and sometimes one–two vegetative shoots. The plant’s growth in height is fast. The branching order of the generative shoot increases relatively to that of the shoots of the pre-reproductive period. The inflorescence is a panicle. Sometimes generative plants of seed origin (sg) may be found. Their habitus resembles that of generative plants of vegetative propagation.

Mature reproductive tussocks (g₂) usually have two generative shoots and sometimes one to two (three) vegetative shoots. Old reproductive tussocks (g₃) usually have three generative shoots and sometimes one to two (three) vegetative shoots. This stage may be found in favourable conditions (sufficient light and soil moisture).

Subsenile tussocks (m) have one vegetative shoot of a juvenile type. The vegetative shoots of the second and third orders are usually absent. The root system consists mainly of adventitious roots. The generative shoots are absent. Seeds do not appear at all. This ontogenetic stage may be found on third–fifth year of the tussock development.

Senile tussocks (s) have alive shoots. The leaves may be of a juvenile type. Most of the root system is decayed. Senile tussocks can be found on the fourth to fifth (sixth) year of the life cycle. This ontogenetic stage is fairly rare.

The following characteristics were used to determine the chronological age of an individual tussock: the number of dry past-year shoots, the location of old past-year shoots, the presence and number of young rhizomes, the general habitus of communication rhizomes and shoots/tussocks bases, the integrity of roots and rhizomes, the colour and extent of decay in dry past-year shoots. Plants of seed origin grow typically apart and they do not have maternal communication rhizomes. Plants of different origin constitute two groups with markedly different pathways in the life cycle, yet an interplay between the groups is quite possible via the different ways to produce new tussocks.

2.3. Modelling approach

A finite number of specified stages and discrete moments of population census suggest a classical Lefkovitch-matrix-based approach (Lefkovitch, 1965; Caswell, 2001) to modelling population dynamics of C. canescens, yet the age dimension in data calls back to even “more” classical Leslie matrix (Leslie, 1945). The double (age and stage) classification of individuals implies the state variables of the model to be represented in respectively two dimensions:

\[
N(t) = \begin{bmatrix}
1 & 2 & 3 \\
sv₁ & sv₂ & sv \\
sg₁ & sg₂ & sg \\
v₁ & v₂ & v₃ \\
v₄ & v₅ & v₆ \\
sv₁ & sv₂ & ss \\
\end{bmatrix}
\]
where the letters within cells designate the size of the corresponding age-stage groups, and the superscript means chronological age of tussocks in years (empty cells mean the absence of the corresponding age-stage groups in the observations). Development of *C. canescens* individuals originating from seed is very rapid during the first year, and here we omit the stages lasting less than one year since the model equations have to relate the next-year state of the population to that at the current year. Thus, what is called "virginal" stage (sv) means here a combination of seedlings and juvenile to virginal plants. Tussocks of seed origin form groups called sv and sg, while those of vegetation propagation form v, g, ss. For the sake of simplicity, we have also combined v1, v2 and v3 into a single virginal stage v, while stages g1 and g2 into a single generative stage g. The senile stage is omitted as it was not yet observed in the study area.

General knowledge of *C. canescens* life history (Fig. 1) and particular observations on the study area result in what is shown in Fig. 2 as possible transitions among the specified age-stage groups of individual tussocks and what is normally called the life cycle graph (LCG, Caswell, 2001).

Nodes of the LCG represent the age-stage statuses of plants, differing also in the kind of origin (seed/vegetative), while the arrows mean possible changes in the status after one year. Each arrow corresponding to the development and aging has a horizontal constituent of length 1 and a vertical constituent of length 0, 1, or 2. A horizontal arrow corresponds to the delay at the given stage for one year more, an inclined arrow indicates an ontogenetic transition. These transitions usually take place into the next ontogenetic stage (vertical constituent of length 1). Ontogenetic transition v2 → ss3 (the superscript meaning age), with the vertical constituent of length 2, represents a tussock getting old without passing the generative stage. Arrow g2 → sv1 corresponds to seed reproduction. All the arrows of vegetative reproduction direct to the single state v1 (1-year-old virgin individuals of vegetative propagation). In particular, reproductive arrow g2 → v1 means that generative tussocks exhibit vegetative propagation along with seed reproduction (g2 → sv1). Arrow sv1 → v1 suggests that young virginals of seed origin give shoots which develop to the virgin stage within a year. Note that virginals of vegetative origin are unable to do so (no arrow sv1 → v1). This signifies the interplay of seed and vegetative reproduction.

The Latin letters a, b, ... , n, p denote the age-stage-specific vital rates, i.e. the rates of survival, reproduction, or ontogenetic transitions. Each arrow in the LCG generates a simple linear term in the dynamic equations represented in Table 1. These equations express the assumption of linearity in the population growth and explain respectively the meaning of the coefficients gathered in the fourth column of Table 1. For example, the survival rate a shows which portion of tussocks sv1 stays one year longer in the young virgin stage of seed origin, i.e. gets to state sv2 before the next year census. The reproduction rate k shows how many tussocks of state v1, on the average, appear a year later from one tussock of state v1. We assume that censuses are all conducted at phenologically the same moment within the growing season, when the most of tussocks in state v1 have formed. The ontogenetic rate n shows which
portion of tussocks \( v^1 \) transforms into the generative stage in one time step, i.e. gets to the state \( g^1 \) next year, and so on.

If the population were single-stage- or age-stage-structured and described by a (column) vector \( x(t) \), then fixing a LCG results immediately in a certain pattern structured and described by a (column) vector and so on.

projection by means of the well-known equation:

\[
x(t + 1) = Lx(t), \quad t = 0, 1, 2, \ldots
\]

in the traditional vector-matrix form. In case of the double-stage- and age-stage-structured population, however, tackling \( X(t) \) mathematically as a matrix (1) was shown to be incapable of producing model equations in any traditional form (Logofet, 2002).

But if we concatenate the eight real components of the population age-stage status \( X(t) \) into a column vector \( x(t) \) where the order of vector components is governed first by the origin, then by stage and eventually, within each stage, by the age (Logofet, 2002), i.e. with:

\[
x(t) = [x^1, x^2, v^1, v^2, v^3, v^4, s^1, s^2]^T,
\]

then all the equations of Table 1 can still be expressed in the vector-matrix form

\[
x(t + 1) = Ax(t), \quad t = 0, 1, 2, \ldots
\]

where \( A \) is the \( 8 \times 8 \) projection matrix:

\[
A = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & p & 0 \\
\vdots & & & & & \vdots & \\
0 & 0 & 0 & k & m & n & 0 \\
0 & 0 & d & 0 & e & 0 & 0 \\
0 & f & 0 & 0 & g & 0 & h \\
0 & g & 0 & h & 0 & 0 & 0 \\
\end{bmatrix}
\]  \hspace{1cm} (4)

(the empty spaces meaning zero entries). The pattern of matrix (4) is different from that of the classic Leslie matrix. It is also different from the Lefkovitch matrix, which would appear if we classified individuals only by stages of development and ignore their chronologically age (Lefkovitch, 1965; Caswell, 2001; Logofet and Klochkova, 2002). In particular, zero elements on the principal diagonal of matrix (4) symbolize the fact that the age of an individual does change in one time step, i.e. staying in the same group is impossible in one time step.

Matrix (4) is unfortunately different also from the more general Logofet-type projection matrix for age-stage structured population dynamics (Logofet

---

**Table 1**

Quantitative relations among the age-stage groups of *C. canescens*

| Components of the age-stage structure, \( x_{st} \) | Dynamic equations | Coefficients (vital rates) | Relative indices (%)
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Age-stage status</td>
<td>Designation</td>
<td>Estimation from data</td>
<td>Equilibrium structure</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>229</td>
<td>( x^2(t + 1) = px^2(t) )</td>
<td>( p )</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>12</td>
<td>( x^2(t + 1) = ax^2(t) )</td>
<td>( a )</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>1</td>
<td>( x^2(t + 1) = bx^2(t) )</td>
<td>( b )</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>302</td>
<td>( x^2(t + 1) = cx^2(t) + dx^2(t) + ex^2(t) )</td>
<td>( c, d, e )</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>171</td>
<td>( x^2(t + 1) = dx^2(t) )</td>
<td>( d )</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>5</td>
<td>( x^2(t + 1) = cx^2(t) )</td>
<td>( c )</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>31</td>
<td>( x^2(t + 1) = f x^2(t) )</td>
<td>( f )</td>
</tr>
<tr>
<td>( s^2 )</td>
<td>11</td>
<td>( x^2(t + 1) = gx^2(t) + hx^2(t) )</td>
<td>( g, h )</td>
</tr>
<tr>
<td>( x(t) )</td>
<td>762</td>
<td>( x(t + 1) = Ax(t) )</td>
<td>( A )</td>
</tr>
</tbody>
</table>
and Klochkova, 2002; Klochkova, 2004) as it contains both the first non-zero line corresponding to seminal reproduction and the fourth non-zero line corresponding to vegetative propagation. However, traditional questions to the mathematical analysis of matrix models for structured population dynamics, e.g. asymptotic properties of the solutions to Eq. (3) with matrix (4), get quite certain answers in this case, too. They produce, once the model is calibrated to fit the field data, such general quantitative characteristics of population dynamics as the maximal rate \( \lambda_1 \) of population growth/decline, the population structure \( \pi^* \) which provides for the dynamics at the maximal rate, and the vector \( y^* \) of relative contributions by the structural groups into the dynamics when the initial population structure is different from \( \pi^* \) (see, e.g. Caswell, 2001).

3. Results

3.1. Population structure of C. canescens

Flowering of *C. canescens* occurs annually in June and July. Seeds are disseminated during a period from the middle of August till late autumn. Seedlings emerge the next spring or summer from the soil seed bank on wet and disturbed microsites. This takes place during the first and second years after cutting. Two-year plants begin to flower when reaching the generative stage. Further years, *C. canescens* colonizes vegetation-free sites mainly by vegetative propagation from rhizomes. After colonizing a favourable site, an established population of *C. canescens* is able to maintain itself during later successional stages (Demidova and Ulanova, 2003).

The population structure in two-year-old clearings is of the invasive type with predominance of virginal tussocks (Fig. 3). There are only a few juvenile plants. The particular set of states shown in figure assumes the lack of individuals older than three years and the lack of senile-stage plants. Indeed, the three-year-old tussocks (virginal, generative, and subsenile) are rather rare and have all the vegetative origin. They remained apparently from the previous forest population.

When aggregated according to representation (1), the observation data from Fig. 3 yield the following age-stage structure:

\[
\begin{array}{ccc}
1 & 2 & 3 \\
229 & 12 & sv \\
1 & & sg \\
302 & 171 & 5 v \\
31 & & g \\
& 11 & ss \\
\end{array}
\]

The corresponding eight-dimensional vector \( x_{av} \) (2) serves as the basis for a special kind of model calibration (see Appendix A).

3.2. Basic properties of the model

Standard characteristics of the model population, such as the maximal growth rate (the dominant eigenvalue, \( \lambda_1 \), of the projection matrix), the equilibrium structure \( \pi^* \) (normalized dominant eigenvector) and the reproductive value of groups \( y^* \) (normalized dominant left (row) eigenvector) can still be found for model (3) with non-classical form of its projection matrix (4). If one considers the LCG in Fig. 2 as a directed...
graph (digraph) $G$ with eight nodes and 12 edges associated with matrix $A$ (Svirezhev and Logofet, 1978; Roberts, 1986; Logofet, 1993), it can be noticed that digraph $G$ is not strongly connected (one cannot get from any node to any other one by a directed route), but it decomposes into the following strongly connected components (strong subgraphs of $G$):

$$[sv^1, v^1, v^2, v^3, g^1], [sv^2], [sg^2], [sv^2]$$

(a trivial subgraph of a single node is a strong component by definition). Hence, the spectrum (i.e. the set of eigenvalues) of $A$ is the union of $A_1$ spectrum and those of the rest, trivial, submatrices:

$$A(A) = A(A_1) \cup \{0\} \cup \{0\} \cup \{0\}$$

where $A_1$ is the principal submatrix of $A$ corresponding to the five strongly connected nodes $sv^1, v^1, v^2, v^3, g^1$ in Fig. 2. These are only those age-stage groups which take part in seed reproduction and vegetative propagation.

Matrix $A_1$, after a pertinent permutation of its rows (which never affects the above-mentioned characteristics of a matrix), takes on the following form:

$$A_1 = \begin{bmatrix} 0 & k & m & n & c \\ d & 0 & 0 & 0 & 0 \\ 0 & e & 0 & 0 & 0 \\ f & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & p \end{bmatrix}$$

Thus, it is the spectrum of $A_1$, which determines entirely the asymptotic properties of any solution to Eq. (3). Note that, in the digraph $G$, associated with matrix $A_1$, there are simple cycles (loops) of lengths 2, 3, and 4, the greatest common divisor of the cycle lengths being equal to 1. It means that matrix $A_1$ is primitive (see, e.g., Vojevodin and Kuznetsov, 1984), i.e. its dominant eigenvalue $\lambda_1$ is the only one of the maximum absolute value. Hence, the asymptotic dynamics of the models (3) and (4) is described by the relation $x(t) \sim \lambda_1^t x^0$ valid for great enough $t$ and for any initial population structure $x(0)$ – the lack of memory in the linear model.

It follows that permanent oscillations are impossible in this linear model, while the population size either grows or declines geometrically, or remains steady, with the factor $\lambda_1$, which can be respectively greater than, less, or equal to 1.

The characteristic polynomial of matrix $A_1$ can be algebraically shown to take on the form

$$p(\lambda) = \lambda^5 - \lambda^3(dk + fn) - \lambda^2(df + cfp).$$

Given a set of parameter values (vital rates), numeric calculation of the polynomial roots might certainly determine $\lambda_1$, hence fix whether $\lambda_1$ greater than, less than, or equal to 1.

Another way to learn whether $\lambda_1$ greater than, less than, or equal to 1 leads to what is called the ‘potential-growth indicator’, a simple expression $R(A)$ calculable directly from the vital rates and indicating the above condition for $\lambda_1(A)$ by its own value. For the classical Leslie matrix, $R(L)$ is long known to equal the expression of $1 - p(1)$ and to be quite simple as so simple is the characteristic polynomial in the Leslie case (Svirezhev and Logofet, 1978). Recent results expand the same property of $R(L)$ to the Lefkovitch-type matrices and even to a wider set of matrix patterns called Logofet-type matrices (Logofet and Klochkova, 2002; Klochkova, 2004; see the footnote on page 6). It was noted above that matrix $A$ (4) is not of the Logofet type; but its submatrix $A_1$ (6) is apparently so. Therefore, the standard expression $1 - p(1)$ does possess the potential-growth indicator property, and, following (7), it takes on the form of

$$R(A_1) = 1 - p(1) = dk + fn + dem + cfp.$$
observation data to get an estimation of vital rates for a zero-growth case (see Appendix A).

So, the maximal growth rate and the corresponding limit distribution of the structural components are determined only by eight of the all 12 vital rates of the population. These eight parameters are associated logically with those five components of the population age-stage structure which constitute the reproductive core of the population or, in the formal terms, the major, non-trivial, strong subgraph of $G$ in its decomposition (5).

The other, non-reproductive, components of the population structure do logically not contribute into the rate of population growth, the mathematical reason for that being due to the spectrum decomposition ensuing from (5). They do contribute into the limit distribution $x^\infty$, the contributions being calculable from the eigenvalue equation $A x^\infty = \lambda_1 x^\infty$, once the dominant eigenvector $e_1$ is found for the submatrix $A_1$. A similar situation takes place in classical models where post-reproductive age or stage classes are present (Geramita and Pullman, 1984; Logofet, 1993; Caswell, 2001).

Should the model population grow or decline, its structure $x(t)$ is asymptotically proportional to $(\lambda_1 / \lambda_2) e_1$, the proportion rate being equal to a weighted sum of the components present in the initial structure $x(0)$. The corresponding weights, $y^\infty$, are called reproductive values of the age classes (Caswell, 2001), or of the age-stage groups in our case. Calculated as the left (i.e. row) dominant eigenvector of matrix $A$, vector $y^\infty$ is also presented in Table 1. The generative group $g^2$ of the vegetative propagation has the maximal reproductive value, yet a quite low percentage in the equilibrium structure.

4. Discussion

The scale of ontogenetic stages developed for C. canescens (Fig. 1) has enabled the study of species population structure in terms of both the stages and the chronological ages of individuals, the origin (from seed or rhizome) of individual plants being also distinguished. This diversification certainly makes representation (1) more complex than a simple vector of age or stage structure. A question arises whether those simpler structures can still represent the dynamics we get from greater detail. In other words, suppose we aggregate the dynamics we observe in terms of our double structure (2) into a representation by stages alone, while ignoring all the rest specificity, i.e. into a three-component vector:

$$z(t) = [x^1 + x^2 + v^1 + v^2 + g^1 + g^2 + s^1 + s^2]^T.$$

(9)

Can we then reproduce the ensuing dynamics $z(t + 1) = Lz(t)$ by means of any Lefkovitch matrix $L$? And if those dynamics be the same as we get from our model Eq. (3) with projection matrix $A$ (4) and then apply aggregation (9) to vector $x(t + 1)$?

In the mathematical terms, this kind of problem was studied in Logofet (2002) as an exact aggregation problem. In the present case, the problem has appeared to have no feasible solution (see Appendix B). It means that an aggregated model loses not only the age specificity in population structure, but also some important features in population dynamics. This justifies the complications caused by the double structure in a structured model population.

The rates of transitions between the age-stage groups (vital rates of the population) during the life cycle (Fig. 2) have been estimated from one-moment observation data and the equilibrium model assumption. If the observed population structure is assumed to equal the equilibrium one, then reproductive values of the groups can also be calculated (Table 1). Although these indices, together with the vital rates, may in general serve the ground to speculate on the comparative role of various age-stage groups in the population dynamics, we refrain from certain conclusions in our particular case since the one-moment calibrating assumption is fairly artificial. While the greatest reproductive value was quite expected at stage $g^2$, its production rate of seed-origin virginals ($p$) 13-time greater than that of vegetative virginals ($n$) should rather be considered as a model artefact. While the equilibrium assumption forces the model to deduce the great size of group $sv^1$ from the small one of $g^2$, the true interpretation attributes it rather to an abundant seed bank in the soil.

The matrix model constructed for C. canescens age-stage-structured population dynamics has the projection matrix (4) of size $8 \times 8$ with eight major and four minor vital rates, which are age-stage-specific.
Despite the matrix pattern does not belong to the known classic types of the projection matrix, the matrix (4) does possess certain properties of traditional matrix models for population dynamics. In particular, the dominant eigenvalue $\lambda_1$, which depends here on the eight major parameters, does define the rate of asymptotic growth (or decline), while the corresponding right and left eigenvectors (depending on the 12 parameters) define respectively the equilibrium population structure (absolute or relative), to which all the model trajectories converge, and the (relative) reproductive values of the structural groups in the population. Given the eight major vital rates, the potential-growth indicator (8) can be easily calculated to indicate population growth or decline as well as it does in the classic cases. It is useful, in general, to assess the growth potential of any given set of vital rates and it has appeared useful, in particular, to reduce the uncertainty level in the ‘equilibrium calibration’ procedure applied for one-moment observation data (see Appendix A).

Although not illustrated here, the standard sensitivity and elasticity analysis (Caswell, 2001) can also be applied to the projection matrix (4) once the dominant eigenvectors are found. This analysis reveals contributions of matrix entries into any small change in the value of $\lambda_1$. It may be crucial in further calibration procedure(s) where the equilibrium-based calculation be replaced with those based on a time series – even a short one – of data for the population age-stage structure. This would allow to get rid (or, at least, to reduce the number) of the hypotheses still substituting for the lack of data and to pose a number of applied problems in studying the early stage of the secondary (post-cut) forest succession, like, e.g. a problem to find a quantitative relationship between the model population growth rate $\lambda_1$ and an estimated speed of rhizome linear accretion in the field (Fiala, 2000). The model could thus serve as a research tool specialised for applied problems which may be associated with the double-structured population dynamics in a clonal plant species.

Note that the linear model of unlimited population growth has certainly a limited range of applications, confined to situations where the limiting, density-dependent factors can still be ignored in the population dynamics. However, it is of certain importance in methodology of modelling, providing for a reference framework to further, non-ignoring, modifications of the vital rates in response to the factors.

Acknowledgement

The research was supported by INT AS (01-0527), RFBR (04-04-48469), Grant of the President of Russia for Leading Scientific Schools (2125 2003.4). We are grateful to the anonymous reviewers whose corrections/suggestions markedly improved the original manuscript.

Appendix A. Equilibrium’ calibration: calculation of model parameters from one-moment data

For the lack of any time series of observations, the model parameters (i.e. the coefficients of model equations) can be calculated from the assumption that the model steady state coincides with vector $x_{av}$, the population age-stage structure averaged over all the sample plots available for similar environmental conditions (the second column of Table 1). Since the steady state is just the eigenvector of matrix $A$ corresponding to its dominant eigenvalue assumed to equal 1, we have $Ax_{av} = x_{av}$. This condition, together with the unit value of the potential growth indicator, engenders eight independent equations for the 12 model parameters, and one must still find complementary conditions to deduce the parameters in a certain way.

Calculation of six parameters $p, a, b, d, e, f$ is trivial since there is only one term in the right-hand side of the corresponding equations (see Table 1). The remaining six unknown parameters are bound up by two equations only, and we need additional hypotheses or assumptions to reduce the uncertainty to the acceptable level. For instance, while using the parameter values just found and solving sequentially the remaining equations, we accepted the hypothesis of proportionality: the contribution which a ‘recipient’ component gets from a particular ‘donor’ component is proportional to the population size of that component in the previous year. We also used the potential-growth indicator (8) equalling 1 to provide for exact (rational) values of the
vital rates, which do not lead the dynamic equations out of the integer population sizes. It has resulted in the following exact values:

\[
A = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & \frac{229}{31} & 0 \\
12/229 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1/229 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
21/229 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{229} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{21}{26} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{2}{7} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{205}{361} & 0 \\
\end{bmatrix}
\] (10)

This calibrated matrix may serve as a zero-growth reference for further efforts in model calibration on data for more than one time moments.

Appendix B. Exact aggregation problem for model (3)–(4)

Aggregation of the age-stage structure (2) into the stage structure (9) is achieved by the linear transformation \( z(t) = P x(t) \) with matrix:

\[
P = \begin{bmatrix}
1 & 1 & 0 & 1 & 1 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\end{bmatrix}
\] (11)

The stage-based model is well known to be defined by a Lefkovitch matrix, which takes on the form:

\[
L = \begin{bmatrix}
b_1 & b_2 & b_3 \\
0 & r_1 & r_2 \\
0 & 0 & r_3 \\
\end{bmatrix}
\] (12)

with non-negative parameters \( b_j, s_j, r_j \) \( (j = 1, 2, 3) \) meaning the stage-specific birth, survival, and remain rates, respectively (Caswell, 2001). The basic model equation \( z(t + 1) = L z(t) \) generates \( z \)-dynamics which may be generally not coincident with what can be aggregated directly from the \( x \)-dynamics generated by Eq. (3). Therefore, the exact aggregation problem has a solution if and only if a feasible solution exists there in the following system of equations:

\[
L P = PA
\] (13)

w.r.t. the model parameters.

System (13) with matrices (4), (11) and (12) can be treated by means of symbolic algebra software (e.g. Symbolic Math Toolbox in MATLAB® environment), and it reveals the following equality-type relationships among the (non-negative) model parameters:

\[ a + c = d = k + e = m = 0, \quad b = f = 0. \]

Zero values of these parameters result in a pattern of the LCG quite different from what is shown in Fig. 2, hence the problem has no feasible solution.

References


