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BOXCARTRAIN METHODS FOR MODELLING OF AGEING, DEVELOPMENT, DELAYS AND DISPERSION

J.Goudriaan
Department of Theoretical Production Ecology
Agricultural University
Bornsesteeg 65
6708 PD Wageningen
The Netherlands

1. Introduction

1.1. Development

Development means a coherent and irreversible change of a number of properties of a being (usually living) when it gets older. Basically the pattern of change is repeated in individuals of the same species, so that it is possible to establish a series of stages that every individual goes through.
Usually a reproductive phase of life succeeds a juvenile phase, without reproductive activity. In the last phase of life, when senescence occurs, the probability to die will strongly increase. For interaction with other species it is important to know how predation activity or also vulnerability for predation develop with age.
In population dynamics not just one individual is studied, and a means to describe the age or development composition of a whole population is needed. When the average composition is always the same, an average population characteristic may suffice. But seasonal changes often trigger the onset of population growth, so that the age distribution is changing all the time. Then, also population characteristics as relative reproductive rate change with the season.

1.2. Ageing and a development scale

Age dependent characteristics, such as reproductive activity or relative death rate, are in fact not a function of age but of internal development. Still age is often used as an indicator of the development because development and age are highly correlated. Especially in warm-blooded animals the internal environment is well stabilised so that external conditions have little influence on the rate of ageing. In cold-blooded animals and in plants, development is poorly related with age, because the rate of development is all but constant. Under influence of the environmental conditions the rate of development may be altered. The way in which environmental conditions influence the rate of development, is an important subject of experimental research. Ideally one would hope for this research to lead to the construction of a scale of development which is uniquely and linearly related to the integral of the developmental effect of the environmental conditions. Important developmental transitions, such as onset of flowering, are then not necessarily equally spaced on the developmental scale.

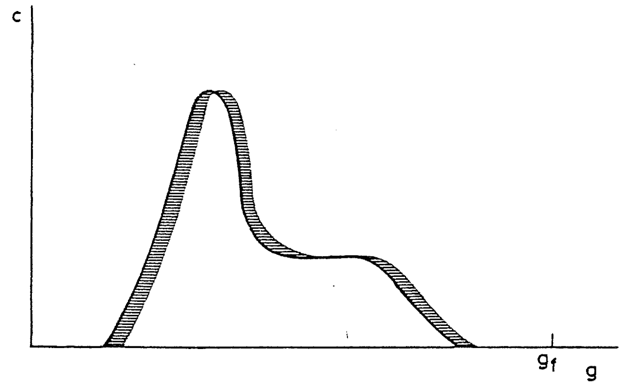

Fig. 1 A distribution of population density c with stage of development g

For most plant species the basis for the development scale is the temperature sum, defined as the integral of the excess of the daily mean temperature above a threshold temperature. In this simple situation the rate of development is proportional to temperature, but the different stages may well be separated by different increments in the temperature sum.

1.3. A mathematical formulation of development.

On a linear scale of development, the rate of development $\underline{v}$ is constant for constant environmental conditions. Rate of ageing is essentially dimensionless, because age is expressed in time, but rate of development has the unit development (g) per time (t).

To describe the age (or development) distribution of the population a density function c (Fig. 1) is needed. This density will also be called concentration because it is a measure of the degree of concentration of individuals at a certain age. Its unit is number of individuals per development unit (g^{-1}). It is clear that the numerical value of the concentration depends on the arbitrary choice of this unit. The size of the total developing population is given by

$$H = \int_{0}^{g_f} c\ (g)\ dg \qquad (1)$$

where g_f is the upper limit of the particular development bracket, e.g. the moment of molting, the onset of fruiting etc. Development means that the value of g of each individual increases with a rate v. Therefore development can be visualised as a shift to right in Fig. 1. Mathematically this can be expressed as

$$\frac{\partial c}{\partial t} = - \frac{\partial vc}{\partial g} = - v \frac{\partial c}{\partial g} \qquad (2)$$

where the latter equality is based on the assumption that v is independent of g. This assumption can always be realized by a linearization of the developmental scale versus some accumulated external factor, and if necessary by a breaking up of this scale in pieces that are internally homogeneous in environmental response.

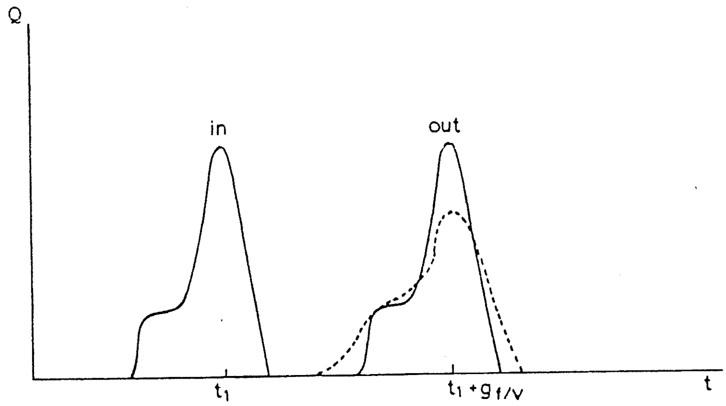

Fig. 2 Outflow shows a delay , and may be dispersed (dashed line)

1.4. Delay and dispersion

In the simplest situation there is no death, and only when an individual has reached the final development stage g_f a transition to another phase occurs. This will happen some time after the entrance of this individual into the development process. When the development rate is constant, there is a constant delay and the shape of the outflow curve is exactly equal to the shape of the inflow curve. In this simple situation the total delay period is by definition equal to the final development state g_f divided by the development rate v so that:

$$Q_{out}(t) = Q_{in}(t - g_f / v) \qquad (3)$$

where Q_{out} is outflow and Q_{in} is inflow.

When the inflow Q_{in} shows a peak at time t_1, the outflow Q_{out} should show exactly the same peak at time $t_1 + g_f / v$. (Fig. 2). Of course, in reality some dispersion may occur during development up to stage g_f.
Then a time course of Q_o may be observed as given by the dashed line in Fig 2. In this situation, Eqn 2 is not adequate and must be extended to allow for dispersion, as described in the next pages.

At this point the concept of dispersion deserves some attention. Dispersion is vaguely described as moving away from a densely populated centre to underpopulated areas. This means that dispersion tends to level out peaks and dips in the distribution of the population. Usually the process of dispersion occurs in true space, but here it occurs in the degree of development. The quantitative description of dispersion is often based on the analogy with physical diffusion processes, because diffusion also causes a levelling out of peaks and dips. Because of its simplicity of formulation we shall also use this analogy, but still a warning is necessary. In physical diffusion the driving force for the levelling process is formed by a gradient in concentration. In dispersion of development the driving force is the inherent variability of the rate of development. An important consequence of this difference is that backward movement is impossible, whereas in a physical diffusion process a strong concentration gradient may drive the net flow opposite to the general mass flow.

First the situation must be considered when there is no dispersion at all. The problem we face in numerical modelling is that it is very hard to avoid an artificial dispersion, that is caused by the model structure itself. The reasons for such an artificial dispersion will be discussed in the next pages.

2. Some numerical methods

2.1. Discretization in time

To solve numerically the differential equations for the rate of change of development and of concentration a discretization of time is necessary.
Errors introduced by this discretization depend on the time resolution of the integration interval, and also on the chosen integration method (Goudriaan 2.3. In: Penning de Vries and Van Laar, 1982). Simulation languages such as CSMP provide convenient software for the organization of the time axis. Ideally the time axis should be discretized to such a high degree of resolution that further refinement does not improve the results. With CSMP or a similar simulation language this ideal situation can be very closely approximated, except in extremely large or complicated simulation models.
Given these software tools, also the representation of the inflow curve (Fig. 2) does not present particular problems. When its shape must be externally provided, that means as an independent function of time, sufficient accuracy can be obtained by reading a table of points on the input curve and using an appropriate interpolation method. When on the other hand the inflow must be generated in the model itself, it is the time resolution of the integration method that determines the accuracy, and in this respect there is no difference with the simulation of any other flow or state variable in the model.

2.2. Fixed boxcar train, the escalator boxcar train, and the fractional boxcar train

Next, the development axis of the population is discretized into a number of classes, equal in width. It is clear that the resolution increases with the number of classes that we choose, but so does the computational effort.
After the discretization into N classes we can rewrite the integral expression (Eqn 1) into a summation:

$$H = \sum_{i=1}^{N} c_i \gamma \qquad (4)$$

where γ is the width of the developmental classes expressed in developmental units, and c_i is the average concentration in each class i.
The distribution of the population with respect to development is assumed to be known at time zero. For further handling of the classes a crucial choice must be

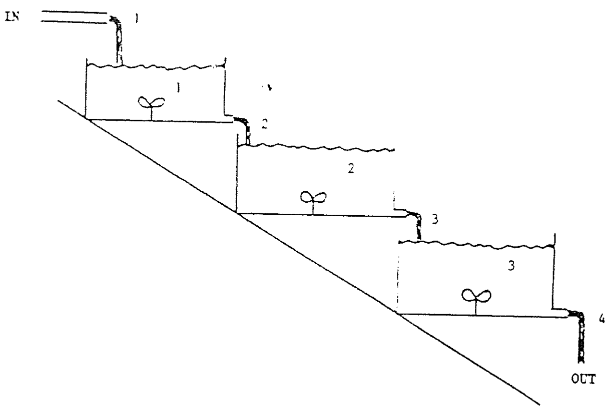

Fig. 3 A cascade of water tanks as a physical model of the fixed boxcartrain

made. It is possible to fix the class boundaries with respect to development, but it is also possible to follow the population classes in their development and let the class boundaries move with the same development rate. The two methods will be termed the fixed boxcar train and the escalator boxcar train, respectively. Which one we choose is largely determined by the amount of dispersion that we want to simulate.

In the escalator boxcar train the boundaries move with the same development rate as the individuals. Therefore there is no exchange of individuals across the boundaries and dispersion does not occur.

In the fixed boxcar train a continuous through flow of individuals occurs across the fixed boundaries. This flow does not only mean development, but also implies dispersion, because it establishes forward exchange between boxes.

In mathematical terms the fixed boxcar train describes the population distribution in Eulerian coordinates, and the escalator boxcar train in Lagrangian coordinates. The fractional boxcar train is a hybridization of these two methods. It offers the possibility to modify the dispersion during simulation relative to the delay.

3. Fixed boxcartrain

3.1. Its delay

A cascade of water tanks (Fig.3) is a model of the fixed boxcar train. The flow out of a box is assumed to be proportional to its contents H and inversely proportional to a time constant τ :

$$Q_{i+1} = H_i / \tau \tag{5}$$

where i denotes the number of the box, and Q_i the flow from box i-1 to box i. The average residence time $\bar{\tau}$ in box i can be found as the difference between the average time of outflow t_{i+1} and the average time of inflow t_i:

$$\bar{\tau} = \frac{\int_o^{t_f} t\, Q_{i+1}\, dt}{\int_o^{t_f} Q_{i+1}\, dt} - \frac{\int_o^{t_f} t\, Q_i dt}{\int_o^{t_f} Q_i\, dt} \tag{6}$$

To evaluate this expression it is necessary to assume that the box starts empty, and is practically empty again at time t_f. This means that the inflow shows a flush, and that t_f is chosen sufficiently long after the inflow has returned to zero, so that the outflow has become zero as well (Fig. 1). Under this condition the integrals of inflow and outflow are the same so that Eqn. (6) can be written as

$$\bar{\tau} = \frac{\int_o^{t_f} t\, (Q_{i+1} - Q_i) dt}{\int_o^{t_f} Q_{i+1}\, dt} \tag{7}$$

Because $Q_{i+1} - Q_i$ is equal to $-\frac{dH_i}{dt}$, this expression becomes

$$\bar{\tau} = \frac{-\int_o^{t_f} t\, dH_i}{\int_o^{t_f} Q_{i+1}\, dt} \tag{8}$$

Integration by parts of $\int_0^{t_f} t \, dH_i$, and using that $t H_i$ equals zero at both time zero and time t_i gives

$$\bar{\tau} = \frac{\int_0^{t_f} H_i \, dt}{\int_0^{t_f} Q_{i+1} \, dt} \qquad (9)$$

Now the relationship between outflow and contents (Eqn 5) must be used, which says that H_i is always τ times as large as Q_{i+1}. This relation also holds for their integrals so that indeed $\bar{\tau}$ is equal to τ.
It should be noted that in this derivation about the average residence time no assumption was made about the shape of the inflow. Therefore it is valid for each box in the cascade, even though the shape of the inflow curve may be altered on its way through the cascade. Because the boxes are connected in series, and all material must pass through all boxes the important conclusion can be drawn that:

- The total mean delay in the boxcar train is the sum of the delays in the individual boxes.

3.2. Its dispersion

The variance of the time of outflow from a box will usually be larger than that of the time of inflow. The difference is the dispersion added by the residence in the box. The definition of the dispersion σ_t^2 is

$$\sigma_t^2 = \frac{\int_0^{t_f} (t - t_{i+1})^2 \, Q_{i+1} \, dt}{\int_0^{t_f} Q_{i+1} \, dt} - \frac{\int_0^{t_f} (t - t_i)^2 \, Q_i \, dt}{\int_0^{t_f} Q_i \, dt} \qquad (10)$$

Using the same technique as in the previous paragraph it can be shown that

$$\sigma^2_t = \tau^2 \qquad (11)$$

Because each box in the cascade will add this amount of dispersion, whatever its position in the cascade, the conclusion can be drawn that:

- The total dispersion by a boxcar train is the sum of the dispersions by the individual boxes.

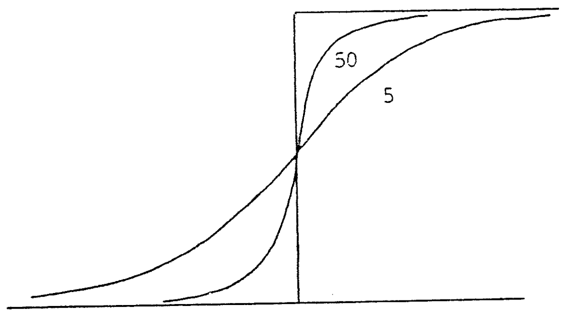

Fig 4. Higher order delays show less dispersion

3.3. The overall behaviour

It follows from the preceding paragraphs that the total delay time T_N and the total variance of the time of outflow σ^2_N are given by:

$$T_N = N\tau \tag{12}$$

$$\sigma^2_N = N\,\tau^2 \tag{13}$$

Consequently, the coefficient of variation of the outflow is equal to:

$$\frac{\sigma_N}{T_N} = \frac{1}{\sqrt{N}} \tag{14}$$

These simple relationships show that the relative dispersion, caused by the fixed boxcar train, decreases as the number of boxes in the boxcar train increases. This type of chained exponential delays is also often termed an N^{th}- order delay, where N indicates the number of boxes. The dynamic response of the outflow to a step wise change in the inflow is given in Fig. 4, for different values of N (Ferrari, 1978). An analytical expression for the contents of each box in the cascade was given by Goudriaan (1973).

3.4 Variable rate of development

When the rate of development v is variable with time, Eqn 5 must be replaced by the following equation:

$$Q_{i+1} = v\, c_i \tag{15}$$

To obtain the differential equation for H_i the concentration c_i must be expressed in H_i and in the developmental width γ of box i (see also Eqn 4):

$$c_i = H_i/\gamma \tag{16}$$

These two equations can be combined to

$$\frac{Q_{i+1}}{v} = \frac{H_i}{\gamma} \tag{17}$$

The rate of increase of the physiological time g is equal to the rate of development v:

$$dg = v\, dt \tag{18}$$

Using Eqn 17 and 18, the derivation of the average residence time and of the dispersion in paragraph 3.1 and 3.2 can be entirely written in terms of development instead of time. The coefficient γ replaces the time constant τ, and so the duration of residence in a box expressed in physiological time units is also γ. The physiological time g itself is replaced by $\int_0^t v\, dt'$. The physiological age of the individuals in the boxcartrain is given by the index number of the box, multiplied with γ.

4. The escalator boxcar train

4.1. Its functioning

The discretization of the population into N boxes of width γ is not different from the fixed boxcar train. But because the boundaries between the boxes now also "age", they move together with the population and the flow across the boundaries is zero. The following example can clarify the principle of the escalator boxcar train. In an imaginary school children are admitted on their 6^{th} birthday and they leave the school on their 12^{th} birthday. The school year starts on September 1. At that moment the school has 6 grades (or classes or boxes). In the first class are only children that were born between August 31 6 years ago and September 1 7 years ago, in the second class born between August 31 7 years ago and September 1 8 years ago etc. No children repeat a class. At the beginning of the school year all children in the first class are six years old, and all children in the six^{th} class are eleven years old. During the school year all children celebrate their birthday, but only those of the last class must leave the school when they become 12 years old. The children in the other classes stay in their class. The six^{th} class will gradually loose all its pupils, but for the school as a whole this loss is compensated by admission of children who become six years old. To accommodate these children a $zero^{th}$ class is established. At September 1 it is still empty, but it will gradually receive newcomers and by the next first of September this class will be termed the first class. Then also the number of the other classes is increased by unity. From then on these children will stay together, untill they leave the six^{th} class due to their age.

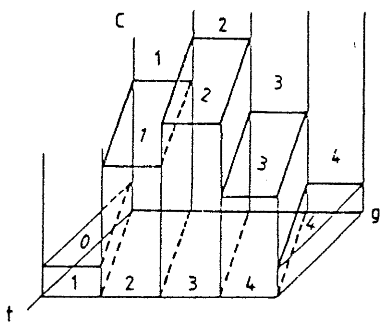

Fig. 5 Shift of the classes over the development scale with time in the escalator boxcartrain

4.2. The mathematical formulation

The only two boundaries that are fixed are the beginning and the end of the development scale. Therefore the inflow of the boxcar train is not zero, and neither is the outflow. The inflow is collected in an additional $zero^{th}$ box:

$$\frac{dH_o}{dt} = Q_{in} \tag{19}$$

The outflow is calculated with Eqn 15 and removed from the last box:

$$Q_{out} = v\ c_N \tag{20}$$

To illustrate the computation of c_N reference is made to Fig. 5. Because the boundaries between the boxes "age" themselves, the development width covered by the last box continuously decreases with increasing physiological age, until it completely vanishes. Before this moment the concentration can be simply calculated as

$$c_N = H_N \ / \ (\gamma - g') \tag{21}$$

where g' stands for the physiological age elapsed since the present last reached its position of "last box".
The ratio c_N is constant.
This can be seen by combining Eqns 20 and 21 to

$$\frac{dH_N}{dt} = - \frac{v\ H_N}{\gamma - g'} \tag{22}$$

or

$$\frac{dH_N}{H_N} = \frac{-v\ dt}{\gamma - g'} \tag{23}$$

Because vdt is the same as dg' also:

$$\frac{dH_N}{H_N} = \frac{d(\gamma - g')}{\gamma - g'} \tag{24}$$

so that H_N and γ-g' have the same relative rate of change. Therefore their ratio, which is c_N, is constant, until g' reaches the value of γ. At that moment the last box vanishes entirely, and the preceding box takes its function. Physically nothing happens to the intermediate boxes and they can smoothly move along. However, we must close the zeroth box and create a new box of newcomers in the population. To prevent an unwieldy growth of the number of boxes it is convenient to perform an act of renumbering right at this moment (Fig.5). The last box H_N will receive the contents of the preceding box and by working backwards to the zeroth box which will start with zero, the whole boxcar train has undergone a complete shift. Also the value of g', the development elapsed since the last shift, must be reset and be decreased with a quantity γ.

4.3. Delay in the escalator boxcar train

The total delay is the sum of the delays in the individual boxes.
The delay in the zeroth box, and also in the last box (with number N) is different from the delays in those numbered between 1 through N-1. In all these boxes the residence time τ is the same and equal to γ/v when v is constant. Their combined delay is equal to $(N-1)\tau$. The total delay in the fixed boxcartrain is $N\tau$, so that the delay of the zeroth and the last box together must be equal to τ, to obtain the same total delay.
For the last box the inflow is pulsed, but the outflow is continuous, and constant during the period τ between two shifts. Therefore the mean residence time in the last box is the arithmetic mean of 0 and τ, and equal to $\frac{1}{2}\tau$.
In the zeroth box the situation is the opposite; the inflow is continuous and the outflow is pulsed with intervals τ. Only for a constant rate of inflow is the mean residence time in the zeroth box now also equal to $\frac{1}{2}\tau$. For a growing rate of inflow there will be a bias towards a shorter mean residence time, and vice versa. The first approximation of the bias can be found by assuming a linear increase of inflow and neglecting the higher order terms. When the inflow Q at time zero is denoted by Q(o), and its rate of increase by Q'(o) the mean residence time in the box is equal to

$$\tfrac{1}{2}\tau\ (1 - \frac{\tau}{6}\ (Q'(o)/Q(o))$$

This expression can be found by evaluation of

$$\tau - \int_o^t t\ Q\ dt / \int_o^t Q\ dt$$

When τ is small enough this bias can be neglected. Then both the zeroth and the last box each cause a mean delay of $\frac{1}{2}\tau$, making up for the difference that remained between the total delay in the fixed boxcartrain and in the central boxes in the escalator boxcartrain. The methods therefore only differ in their influence on the dispersion.

4.4. Dispersion in the escalator boxcartrain

No dispersion occurs during the movement from box 1 to box N-1, because their exchange is zero. Within a box, however, the exchange is perfect. During a development cycle γ the inflow is collected in box zero, and whatever its variation, it is levelled out. How much dispersion is added by this process? The answer is, unfortunately, that it depends on the shape of the inflow. The stronger the variation of inflow within the time period of one development cycle, the higher the apparent dispersion. The strongest possible concentration of inflow is in the form of a single pulse. The outflow from the last box will occur some time later, and cover a time span τ, equal to γ/v. The dispersion around the average time of outflow t_d can be derived by

$$\sigma_t^2 = \frac{1}{H_o} \int_{t_d-0.5}^{t_d+0.5} (t-t_d)^2 \; Q_{out} \; dt \qquad (25)$$

Because during the time span τ an amount H_o must flow out, Q_{out} will be equal to H_o/τ and H_o cancels.
Substitution, and solving the integral gives $\sigma_t^2 = (1/12)\tau^2$. But in this equation the outflow is centred symmetrically around t_d. Dependent on when the pulse arrived in the cyclic development stage, the lower and upper boundaries may vary between $t_d - \tau$, t_d and t_d, $t_d + \tau$ resp.
Under the assumption of random arrival the dispersion is doubled so that:

$$\sigma_t^2 = \tau^2/6 \qquad (26)$$

and the coefficient of variation (c.v.)

$$\frac{\sigma_t}{N\,\tau} = \sqrt{6/N} \qquad (27)$$

This equation permits to choose the right number of boxes when the observed c.v. is small. For instance, when it is 5%, 8 boxes are required. An entirely dispersion free boxcar train does not exist.

5. The fractional boxcartrain

5.1. Its functioning

With the method of the fixed boxes it is possible to influence the dispersion by the choice of the number of boxes.

This number determines the coefficient of variation, and fixes it at $1/\sqrt{N}$. Once it is chosen, it cannot be changed during the simulation. But in several experimental data sets there is evidence that the delay and the dispersion are not equally influenced by for instance temperature, so that the coefficient of variation also varies. To allow for this change during the simulation a more flexible method than that of the fixed boxcar train is needed. Such a flexible method can be obtained by a hybridization of the methods of the fixed and of the escalator boxcar train. This method will be termed the fractional boxcar train, because it is based on a fractional repeated shift.

In the escalator boxcar train a cyclic renumbering occurs, but this can also be considered as a complete shift to the next box. In the fractional boxcar train not the complete contents is shifted, but only a fraction F of it. To compensate for the smaller amount, it must occur more frequently. Whereas in the escalator boxcar train the renumbering (or shift) occurs upon completion of the development cycle γ, in this method the fractional shift occurs upon completing a fraction F only of the development cycle γ.

The fraction F ranges between 0 and 1. The imaginary escalator school in the preceding chapter may be turned into a fractional shift school by a quarterly promotion system. Each quarter of the year one quarter of the box is moved to the next one (F = 0.25). The choice of the children is not based on age, but determined by lottery. If this system is always maintained, once can imagine that the children in the sixth grade show a wide variety of ages. This variety is an expression of dispersion. By choosing F equal to unity the escalator boxcar train can be retained with annual promotion of the whole box. On the other hand, F can also be chosen very small. If F is chosen at 1/365, every day a fraction 1/365 of each box (selected by lottery) is transferred to the next one. Now effectively the fixed boxcar train is obtained with a time step of integration of one day.

5.2. Its mathematical function

Because the movement through the boxes is pulsewise, the differential equations must be replaced by difference equations. In paragraph 4.2. the cyclic development g', elapsed since the last shift, was introduced. In the escalator boxcar train g' triggers the renumbering when it exceeds γ. Here, in the fractional boxcar train, the trigger level is set at $F\gamma$. When this level is exceeded the fractional shift occurs and g' is decreased with the quantity $F\gamma$. Also the contents of box i is decreased:

$$H_{i,j} = H_{i,j-1} - F\,H_{i,j-1} \qquad (28)$$

where j counts the number of shifts since the start. Here, just like for Equation 6, it is assumed that the preceding box is kept zero. Then $H_{i,j}$ will be given by

$$H_{i,j} = H_{i,o}\ (1-F)^{j} \tag{29}$$

A special situation occurs in the zeroth box. The contents of this box are entirely transferred to the first one, so that upon the shift $H_{o,j} = 0$.
The last box will receive the pulsewise transfer from the previous one, but it will not loose pulsewise. It will only release its contents gradually according to Eqn 20.

5.3. Its delay

The first fractional shift does not occur at time zero, but only when g' equals $F\gamma$. When the development speed v is constant, this happens at time $F\gamma/v$, or at time $F\tau$. The expression for the average residence time $\bar{\tau}$ is:

$$\bar{\tau} = \frac{1}{H_o} \sum_{j=1}^{\infty} \underbrace{j\ F\tau}_{\text{time}} \quad \underbrace{H_o(1-F)^{j-1}\ F}_{\text{quantity transferred}} \tag{30}$$

Evaluation of this expression gives

$$\bar{\tau} = \tau \tag{31}$$

This result shows that the delay per box is independent of the value of F. Also the total delay of the boxcar train is independent of F, and equal to $N\tau$.

5.4. Its dispersion

The dispersion can be evaluated by

$$\sigma_t^2 = \frac{1}{H_o} \sum_{j=1}^{\infty} \underbrace{(j\ F\tau - \tau)^2}_{\text{deviation}} \quad \underbrace{H_o(1-F)^{j-1}F}_{\text{quantity transferred}} \tag{32}$$

which gives

$$\sigma_t^2 = \tau^2 (1-F) \qquad (33)$$

This result shows that the dispersion is linearly related to the value of the fraction F. This dispersion occurs in each box so that the total dispersion of the whole boxcar train is

$$\sigma_t^2 = N \tau^2 (1-F) \qquad (34)$$

A complication is offered by the dispersion upon inflow, precisely as in the escalator boxcar train (Chapter 4.4). The width of the zeroth box is $F\tau$ at most. Using the same proportionality as in Chapter 4.4, we must add $F^2 \tau^2/6$ to the result of Eqn 34

$$\sigma_t^2 = \tau^2 (N(1-F) + F^2/6) \qquad (35)$$

6. The escalator boxcar train, applied to a demographic problem

For demography the best method is the escalator boxcar train, because age which is used as a characteristic, does not disperse. To illustrate its use, the same example will be given for the growth of the Dutch population as by De Wit and Goudriaan (1978). For clarity only the female part of the population is simulated, the male part being taken for granted.

The age dependence of relative death rate and of relative birth rate is given in Fig. 6. The corresponding fraction of survival FS is found by simulating a single cohort from birth onwards. Mathematically the relative death rate RDR and the fraction survival FS are related by:

$$RDR = -\frac{d(FS)}{dA}/(FS)$$

where A stands for age.

The listing of the CSMP-program used is given below. First data are supplied about the initial age distribution of the population . This is done by a TABLE specifying the contents of the 20 5-year classes of the population array W. Then two FUNCTIONS with a list of coordinate points of the relationship between relative death and

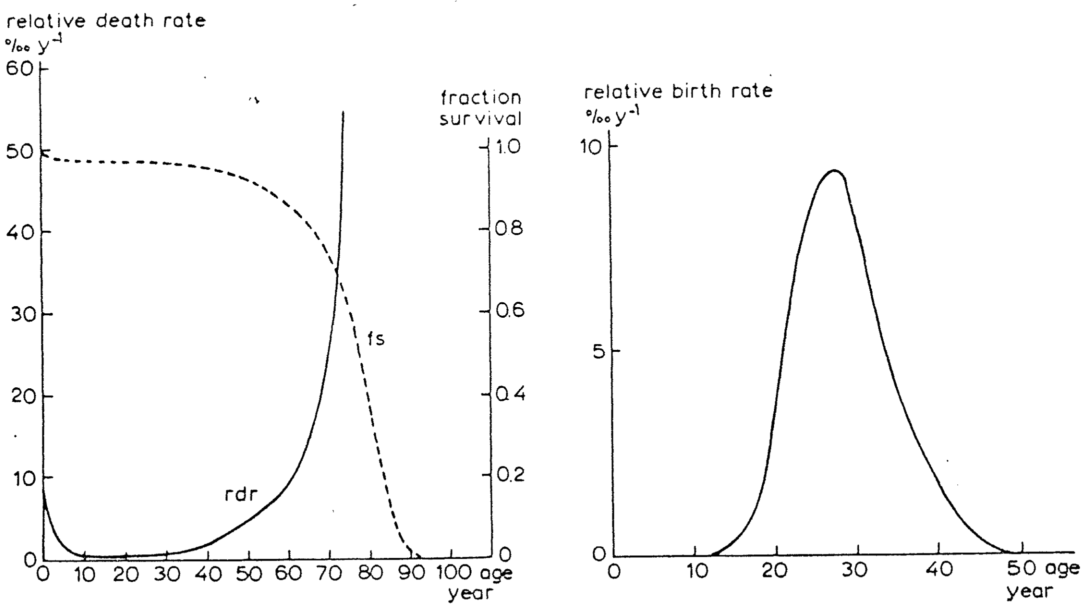

Fig. 6 The age dependence of relative death rate rdr and relative birth rate. The fraction survival fs (dashed line) is a function of rdr.

birth rates and age are supplied. In the INITIAL segment some computations are done for the discretization of age and development scale, necessary before the actual simulation in the DYNAMIC segment. The simulation itself requires computation of the rates of change, and of course the integration of these rates, which is done by the INTGRL statement. Also whole population totals are computed by summation over all age classes in a regular FORTRAN DO-loop. The data supplied for the FUNCTIONs are read by an AFGEN statement.

The shift as explained by the end of chapter 4.2 is performed in subroutine, called from the main program upon g' reaching γ.

This method results in a smooth time course of total population size and of birth rate, even on a time scale of one year, which is much smaller than the width of the boxes. In the method of De Wit and Goudriaan (1978) there was always the danger of a sawtooth behaviour of total population size, if one wanted a finer time resolution than the class width. Another disadvantage was that the age boundaries were defined in a much more complicated way, especially for the so-called pre-class. Here the role of this pre-class has been taken over by the zero class. This class has a clear meaning with well defined age boundaries.

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TITLE   GROWTH OF A HUMAN POPULATION
FIXED N,I
*  INITIAL CONTENTS OF AGECLASSES OF 5 YEARS WIDE, IN THOUSANDS
TABLE WI(1-20)=582.,587.,553.,543.,554.,420.,380.,381.,378.,376., ...
      330.,323.,298.,226.,150., 70., 25., 13.,  0.
*  AGE DEPENDENCE OF RELATIVE DEATH RATE, IN PROMILLE PER YEAR (FIG 6A):
FUNCTION WRDRT=0.,10.,2.5,4.,5.,1.8,7.5,0.8,10.,0.5,15.,0.3,20.,0.3,...
      30.,0.6,40.,1.6,50.,4.9,60.,8.5,65.,14.,70.,25.,75.,55., ...
      82.5,180.,87.5,380.,92.5,760.,97.5,900.,105.,900.
*  AGE DEPENDENCE OF RELATIVE BIRTH RATE; PER YEAR (FIG 6B):
FUNCTION RBRT=0.,0.,12.5,0.,17.5,0.02,22.5,.137,25.,.166,27.5,.188,...
      30.,.166,32.5,.113,37.5,.055,42.5,.016,47.5,.002,50.,0.,100.,0.
*  RATIO OF YOUNG BORN BOYS TO GIRLS
PARAM SEXR=1.048

INITIAL
*  100 YEARS OF AGE IS COVERED IN 20 CLASSES:
PARAM N=20,AGETOT=100.
*  RESIDENCE TIME IN ONE AGE CLASS:
      TC=AGETOT/N
*  DEVELOPMENT RATE; AND DEVELOPMENT WIDTH:
      DEVR=1.0/AGETOT
      GAMMA=TC*DEVR
*  THE FRACTION OF GIRLS IN THE YOUNG BORNS:
      FRGIRL=1.0/(1.0+SEXR)
NOSORT
*  CONVERSION OF THE INITIAL THOUSANDS TO INDIVIDUALS:
      DO 20 I=1,N
20    WI(I)=WI(I)*1000.

DYNAMIC
NOSORT

*  INTEGRAL OF THE DEVELOPMENT RATE
   GACC=INTGRL(0.,DEVR)
*  WHEN GACC EXCEEDS GAMMA, THE SHIFT IS APPLIED:
      IF(GACC.GE.GAMMA) CALL SHIFT(N,GAMMA,GACC,W,W0)
```

```
*  SUMMATION OF TOTAL BIRTH RATE AND OF TOTAL FEMALE POPULATION:
      TBR=0.
      TW=0.
      DO 100 I=1,N
      FLI=I
*  THE AGE AT THE CENTRE OF EACH CLASS:
      AGE=TC*(FLI-0.5) + GACC*AGETOT
      TBR=TBR + W(I)*AFGEN(RBRT,AGE)
*  THE DEATH RATE OF EACH CLASS:
      WR(I)= -W(I)*0.001*AFGEN(WRDRT,AGE)
100   CONTINUE

*  THE RATE OF BIRTH OF GIRLS:
      WBR=TBR*FRGIRL

*  THE ZERO CLASS RECEIVES THE BIRTH RATE, BUT ALSO DEATH
*  OCCURS AT AN AGE OF HALF ITS CURRENT WIDTH:
      WRO=WBR - WO*0.001*AFGEN(WRDRT,0.5*GACC*AGETOT)

*  INTEGRATIONS
      WO = INTGRL(0.,WRO)
      W  = INTGRL(WI,WR,20)

*     TIME IS EXPRESSED IN YEARS
TIMER FINTIM=50.,DELT=0.5,PRDEL=5.
*  TOTAL FEMALE POPULATION TW AND TOTAL BIRTH RATE TBR ARE PRINTED:
PRINT TW,TBR
METHOD RECT
END
STOP
      SUBROUTINE SHIFT(N,GAMMA,GACC,H,HO)
      DIMENSION H(N)
      DO 300 I=N,2,-1
300   H(I)=H(I-1)
      H(1)=HO
      HO  =0.
      GACC=GACC - GAMMA
      RETURN
      END
ENDJOB
```

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