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ANALYSIS OF A CLASS OF INTEGRO-DIFFERENTIAL EQUATIONS DESCRIBING AGE DYNAMICS OF A NATURAL FOREST

by

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Analysis of a Class of Integro-differential Equations Describing Age Dynamics of a Natural Forest

Director: Leonid V. Kalachev

In this thesis the age dynamics of a natural forest is modeled by the von-Foerster partial differential equation for the age density, while the seedlings density is obtained as a solution of an integro-differential equation. This seedlings density equation contains a small parameter, the ratio of seedlings re-establishment time and the life span of an average tree in the forest.

Several models are introduced that take into account various mortality curves and growth functions of trees, the dependence of seedlings carrying capacity on forest volume, and different types of seedlings re-establishment. Asymptotic, analytic and numerical methods are used to solve example problems. Existence and uniqueness of solutions and the convergence of numerical and asymptotic methods is proven for a class of models.

For a particular model the stability is examined, and a bifurcation point for the occurrence of oscillations is determined.

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Part I

Description of classes of models

1 Introduction

In the literature many descriptive models related to forest growth are now available. Usually, they establish static relationships between "macroscopic" variables, e.g., the number of trees per unit area, the age of the trees, the mean tree volume and other parameters. Although these types of models are very important in practical calculations of harvesting yields, they are not designed to describe any dynamics associated with forest regeneration and evolution, they cannot predict (even qualitatively) the consequences of disturbances. Other models take a "microscopic" approach in the sense that simulate forest evolution based on given initial conditions and characteristic parameters for each individual tree. These models allow in many cases useful predictions of forest growth including the effects of regeneration, but lack the simplicity of capturing forest dynamics with a small number of variables and parameters.

In this thesis a class of simple models is introduced, with only a few easily identifiable parameters, that allow us to qualitatively and quantitatively describe the long-term consequences of disturbances in a natural forest.

Perhaps the most common way to describe the structure of a forest is to tabulate the number of trees in different age classes on a unit area basis. Age structure models are useful in a variety of capacities. They can provide insight into tree growth responses from minor disturbance (e.g., low intensity fire, root rot pockets) or major disturbance (e.g., catastrophic fire, disease and/or insect epidemics). They can describe how seedlings and small trees become established on a site after catastrophic disturbance or within canopy gaps of established old-growth forests. They can also be linked to biomass/volume models to estimate the amount of fiber available for timber harvest. They also provide information about habitat quality for forest wildlife.

In the absence of catastrophic disturbance, age structure models can describe an "ideal" condition not usually found in natural forests where disturbance is the norm. This ideal condition can be thought of as a potential or stable condition. Even though no ideal state usually exists, these models can be used to examine how the structure of natural forests affects the response of the forest to disturbance events.

In this study, simple population growth models are developed that describe the age structure in a forest under conditions that the forest contains a single tree species, tree density is uniform across the landscape, no catastrophic disturbances (i.e., fire, disease, insects, logging, etc., that wiped out the majority of the trees) occurred in the forest for a long time (this condition must not necessarily be satisfied for a particular forest under consideration, it is assumed that such an *ideal* forest consisting of trees of the same type and on a land plot of comparable quality exists somewhere; this might be needed for obtaining the numerical values of some parameters in the models). Some other conditions will be formulated below.

Although no major disturbances are assumed to happen in the near past, the initial instant of time in the model below will correspond to occurrence of some (non-catastrophic) disturbance in the age structure of the forest (due to a small fire, disease that affected only a portion of trees, etc.). Our main goal will be to describe the response of the forest age structure to such (non-catastrophic) disturbance.

In this thesis a forest is called a *natural forest* if it regenerates itself after (catastrophic or non-catastrophic) disturbances and contains trees of different age groups. Unlike a natural forest, the *artificial* forest is planted, it usually contains trees of only one age, and the seedlings that might become trees are removed during a, so-called, thinning process.

2 Age structure model formulation

Stand density and forest growth

Initially, tree seedlings become established on a site following a non-catastrophic disturbance that eliminates the tree canopy. They will grow freely until the onset of competition for growing space with neighboring trees. Growing space can be thought of as the intangible measure of a plant's capacity to grow until one of the factors necessary for growth (i.e., a site resource) becomes limiting ([7]). Growing space can be defined in an abstract context when a particular factor is limiting to a tree (e.g., water, light), or in a dimensional context when the physical space for growth is limiting to a tree (e.g., hardpans). At this point, the growing space is fully occupied, and the trees begin to die as they compete for more growing space. Eventually, gaps form in the overstory canopy and growing space becomes available to newly established seedlings that begin to grow in these openings. Their survival, however, depends on the amount of larger overstory trees, where more overstory biomass results in higher seedling mortality. Larger, established trees are better able to capture the water, light, and nutrient resources on the site than smaller trees in the understory. Rarely, if ever, do seedlings detrimentally affect overstory trees.

An important factor in any population growth model is the reproductive rate of the organism. But, what is the reproductive rate of trees? Sexually mature trees can produce thousands of viable seeds, but only a fraction of these seeds will grow into seedlings. Surviving seedlings, rather than viable seeds, are used as the starting point of the analysis. We will assume that enough seedlings are always available. The question then becomes: how many will grow to adult trees?

Unlike seedlings which are generally abundant and easily killed by competition, mature trees that are established on the site are less likely to die from competition on such a large scale. Yet, many other factors can still cause a tree to die. The number of trees in a forest where competition between trees actively occurs is usually modeled as a *decreasing exponential function* (also known as *monotonically decreasing function*, *negative exponential curve*, *reverse J-shaped curve*) of age. This decline in the number of trees with age is a well recognized characteristic in forests ([5]).

Model assumptions

Let me list the assumptions underlying the model (some of the assumptions are related to empirical observations and others are used to simplify model formulation; note that some of the assumptions were already mentioned earlier). Assume:

(1) that the forest contains only a single tree species with tree density uniform across the landscape.

(2) *abundance of seeds* and seedlings in a *natural forest* (that is, in the self regenerating forest where no catastrophic disturbances occurred for some time).

(3) *exponential decline* in the number of trees with age (due to competition, weather, various other causes).

(4) that the number of seedlings that survive to become trees is defined by *available resources* (that is, by the biomass/volume/basal area of mature trees).

(5) that competition 'works' only in one direction: mature trees determine the survivorship of seedlings, but seedlings cannot influence the growth of mature trees (which is usually the case in a natural forest).

3 Model with logistic seedling re-establishment

Mathematical formulation

The age distribution of a tree population in a certain region is represented in this mathematical model as a differentiable function $N(t,a)$ of time t and chronological age a. If these are measured in years, the unit of N is trees per year, which means that at a fixed time t the number of trees between ages r and s is given by $\int_r^s N(t,a)\,da$. Since the age a is also measured chronologically, the increase of age in a time period Δt is given by $\Delta a = \Delta t$. Hence,

$$\frac{da}{dt} = 1 \tag{1}$$

for each tree at each instant of time. The total derivative of the age density with respect to time is therefore

$$\frac{d}{dt}N(t,a) = \frac{\partial N}{\partial t} + \frac{\partial N}{\partial a}\frac{da}{dt} = \frac{\partial N}{\partial t} + \frac{\partial N}{\partial a.} \tag{2}$$

Assuming a constant and age-independent death rate μ of the tree population in this model, we obtain that the satisfies the differential equation:

$$\frac{d}{dt}N(t,a) = -\mu N(t,a). \tag{3}$$

From (2) and (3) follows the von-Foerster partial differential equation

$$\frac{\partial N}{\partial t} + \frac{\partial N}{\partial a} = -\mu N(t,a). \tag{4}$$

Consider the initial value problem in the rectangle $0 \le t \le T$, $0 \le a \le a_{\max}$. The initial age distribution,

$$N(0,a) = \Phi(a), \tag{5}$$

is given for $0 \leq a \leq a_{\max}$ as a continous function of age a. Assume that the unknown *seedling function*,

$$N(t,0) = S(t), \tag{6}$$

satisfies a *seedling equation* of the logistic form

$$\frac{dS}{dt} = \beta S(t)\left(1 - \frac{S(t)}{K(V(t))}\right) \tag{7}$$

with initial condition

$$S(0) = N(0,0) = \Phi(0). \tag{8}$$

Here β is a positive constant (*re-establishment rate*), $K(V)$ is a nonnegative continous function (*seedling carrying capacity*) of the *forest size*

$$V(t) = \int_0^{a_{\max}} N(t,a)\, B(a)\, da, \tag{9}$$

and $B(a)$ is a monotone increasing, positive, continuous function representing the average *tree size* of a tree of age a, e.g. its height, or its basal area, or its volume.

The initial condition (8) follows from continuity of the age density $N(t,a)$ at the corner point $t = 0$, $a = 0$ of the domain of interest.

Equation (7) is a logistic type equation with growth rate β and carrying capacity K. However this carrying capacity is not a constant as in classical logistic growth, but is a decreasing function of tree volume in a forest: as the forest grows, the resources available for seedlings decrease. The *variable carrying capacity* $K(V)$ depends on the species of trees under consideration. Various functional representations can be used to model it. For example, one of the following functions can be used:

$$\text{linear:} \quad K(V) = S_{max} - \lambda V, \qquad \text{for } 0 \leq V \leq S_{max}/\lambda,$$

$$K(V) = 0 \qquad \text{for } V \geq S_{max}/\lambda, \tag{10}$$

$$\text{exponential:} \quad K(V) = S_{max} e^{-\lambda V},$$

$$\text{treshold:} \quad K(V) = S_{max}\left(1 - \frac{V}{\lambda + V}\right).$$

where λ and S_{max} are positive constants. Fig.1 illustrates qualitative shapes of these functions.

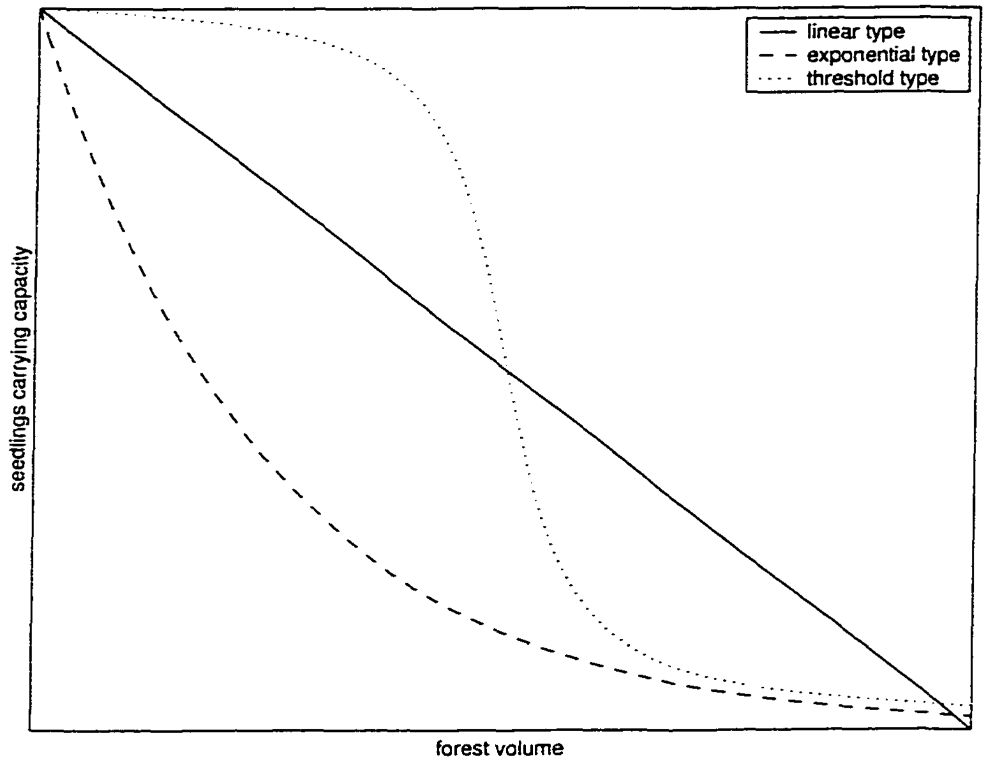

Fig.1: Qualitative dependence of seedling carrying capacity on forest volume: linear, exponential and threshold type.

In each case the number of seedlings is bounded from above by

$$S_{max} = K(V = 0), \tag{11}$$

the seedling carrying capacity of the empty forest.

In the linear case a forest that surpasses a critical size

$$V_{crit} = \frac{S_{max}}{\lambda} \tag{12}$$

can no longer support any seedlings, whereas in the exponential and the threshold case the carrying capacity remains positive at all times as it asymptotically approaches zero with increasing forest size.

In the threshold case the seedling density remains near its maximum value while the tree volume is small, but quickly drops to small values beyond a certain critical threshold volume of trees.

In this thesis only models with linear seedling carrying capacity $K(V) = S_{max} - \lambda V$. are investigated. Studies of models with other possible types of $K(V)$ will be published elsewhere.

Note that the model (4) - (9) is a particular case of a more general model formulation:

$$\begin{aligned} \frac{\partial N}{\partial t} + \frac{\partial N}{\partial a} &= -g(N, t, a) N, \\ \frac{dS}{dt} &= h(S, V, t), \end{aligned} \tag{13}$$

with V and additional conditions (specified at $t = 0$ and $a = 0$) given by (9), (5), (6) and (8). Here h describes the mortality rate of mature trees (that, in general, might be a function of time and age), and f describes the effect produced by the presence of mature trees on seedling dynamics.

Reduction to one integro-differential equation

The solution of partial differential equation (1-4) can be expressed explicitly in terms of the initial age distribution $\Phi(a)$ and the seedling function $S(t)$:

$$\begin{aligned} N(t,a) &= e^{-\mu a} \quad S(t-a) \quad \text{for } 0 \le a \le t \le T, \\ N(t,a) &= e^{-\mu t} \quad \Phi(a-t) \quad \text{for } 0 \le t \le a \le a_{\max}. \end{aligned} \tag{14}$$

Therefore function $N(t,a)$ can be eliminated from the equation for forest size (9):

$$V(t) = \int_0^t e^{-\mu a} S(t-a)\, B(a)\, da + e^{-\mu t} \int_t^{a_{\max}} \Phi(a-t)\, B(a)\, da. \tag{15}$$

So, the seedling equation becomes an integro-differential equation for the seedling function $S(t)$:

$$\begin{aligned} \frac{dS}{dt} &= \beta S(t) \left(1 - \frac{S(t)}{K\left(\int_0^t e^{-\mu a} S(t-a)\, B(a)\, da + L(t)\right)}\right), \\ S(0) &= \Phi(0), \end{aligned} \tag{16}$$

where

$$L(t) = e^{-\mu t} \int_t^{a_{\max}} \Phi(a-t)\, B(a)\, da \tag{17}$$

is the contribution of the *old* trees (already alive at the initial instant of time $t = 0$) to the forest size at time t. The convolution expression

$$\int_0^t e^{-\mu a} S(t-a)\, B(a)\, da \tag{18}$$

describes contribution of the *new* trees (that came into being after the initial instant of time) to the forest size.

Similar reduction to dimensionless variables can, in principle, be applied to the general model formulation (13). However, it will not always lead to explicit expressions of type (14) for $N(t,a)$. Thus, not every choice of g in (13) will produce an explicit integro-differential equation of type (16) for $S(t)$.

Rescaling

Define

$$S_{max} = \max_{0\le t\le T} S(t), \tag{19}$$

$$B_{max} = \max_{0\le a\le a_{max}} B(a). \tag{20}$$

The model with linear carrying capacity

$$\begin{aligned} K(V) &= S_{max} - \lambda V, && \text{for } 0 \le V \le S_{max}/\lambda, \\ K(V) &= 0 && \text{for } V \ge S_{max}/\lambda, \end{aligned} \tag{21}$$

can be re-formulated in terms of the following dimensionless quantities:

$$\begin{aligned} \alpha &= \mu a && \text{(tree age)}, \\ \alpha_{max} &= \mu a_{max} && \text{(maximum tree age)}, \\ \theta &= \mu t && \text{(time)}, \\ n(\theta,\alpha) &= N\left(\tfrac{\theta}{\mu}, \tfrac{\alpha}{\mu}\right)/S_{max} && \text{(age density)}, \\ s(\theta) &= S\left(\tfrac{\theta}{\mu}\right)/S_{\max} && \text{(seedling count)}, \\ b(\alpha) &= B\left(\tfrac{\alpha}{\mu}\right)/B_{max} && \text{(average tree size)}, \end{aligned} \tag{22}$$

$$\varphi(\alpha) = \Phi\left(\frac{\alpha}{\mu}\right)/S_{max} \qquad \text{(initial age density)},$$

$$v(\theta) = \frac{\mu V(\theta/\mu)}{S_{max}B_{max}} \qquad \text{(forest volume)},$$

$$k(v) = K\left(V\left(\frac{\theta}{\mu}\right)\right)/S_{max} = 1 - \frac{\lambda B_{max}}{\mu}v \qquad \text{(seedling carrying capacity)},$$

$$v_{crit} = \frac{\mu}{\lambda} \qquad \text{(critical forest volume)}.$$

Substituting equation (9) into the definition for the rescaled forest volume yields

$$v(\theta) = \int_0^{\alpha_{max}} n(\theta, \alpha)\, b(\alpha)\, d\alpha. \tag{24}$$

The rescaled seedling carrying capacity of an empty forest (volume zero) is

$$k^0 = k(0) = \frac{1}{S_{max}}K\left(\frac{S_{max}B_{max}}{\mu}0\right) = \frac{1}{S_{max}}K(0) = \frac{1}{S_{max}}S_{max} = 1. \tag{25}$$

After rescaling, equation (4) and corresponding additional conditions (5) and (6) will have the form

$$\frac{\partial n}{\partial \theta} + \frac{\partial n}{\partial \alpha} = -n(\theta, \alpha), \tag{26}$$

$$n(0, \alpha) = \varphi(\alpha), \tag{27}$$

$$n(\theta, 0) = s(\theta). \tag{28}$$

Representations (14) become

$$\begin{aligned} n(\theta, \alpha) &= e^{-\alpha} \quad s(\theta - \alpha) \quad \text{for } 0 \le \alpha \le \theta \le \mu T, \\ n(\theta, \alpha) &= e^{-\theta} \quad \varphi(\alpha - \theta) \quad \text{for } 0 \le \theta \le \alpha \le \mu a_{\max}. \end{aligned} \tag{29}$$

Substituting (29) into (24) we obtain the non-dimensionalized forest volume in terms of dimensionless seedling count:

$$v(\theta) = \int_0^\theta s(\theta-\alpha)\, e^{-\alpha} b(\alpha)\, d\alpha + e^{-\theta} \int_\theta^{\mu a_{\max}} \varphi(\alpha-\theta)\, b(\alpha)\, d\alpha. \tag{30}$$

This is a rescaled version of formula (15). Hence the integro-differential equation (16) for seedlings will now have the form

$$\begin{aligned} \frac{\mu}{\beta}\frac{ds}{d\theta} &= s(\theta)\left(1-\frac{s(\theta)}{k(v(\theta))}\right) \qquad (31)\\ &= s(\theta)\left(1-\frac{s(\theta)}{k\left(\int_0^\theta s(\theta-\alpha)\, e^{-\alpha} b(\alpha)\, d\alpha + l(\theta)\right)}\right), \\ s(0) &= \varphi(0) = \varphi^0, \end{aligned}$$

where

$$l(\theta) = e^{-\theta} \int_\theta^{\mu a_{\max}} \varphi(\alpha-\theta)\, b(\alpha)\, d\alpha. \tag{32}$$

Note that by the substitution $\alpha \to \theta - \alpha$ the integral in (31) can be written as

$$\begin{aligned} \int_0^\theta s(\theta-\alpha)\, e^{-\alpha} b(\alpha)\, d\alpha &= -\int_\theta^0 s(\alpha)\, e^{-(\theta-\alpha)} b(\theta-\alpha)\, d\alpha \qquad (33)\\ &= \int_0^\theta s(\alpha)\, e^{-(\theta-\alpha)} b(\theta-\alpha)\, d\alpha. \end{aligned}$$

Setting $b(\alpha) = 1$ in (30) we obtain the total number of trees in the forest as a function of dimensionless time θ :

$$\begin{aligned} p(\theta) &= \int_0^\theta n(\theta,\alpha)\, d\alpha \qquad (34)\\ &= \int_0^\theta s(\theta-\alpha)\, e^{-\alpha} d\alpha + e^{-\theta} \int_\theta^{\mu a_{\max}} \varphi(\alpha-\theta)\, d\alpha. \end{aligned}$$

Similarly, the rescaling can be performed in the general case (13).

Zero order asymptotic solution

The seedling equation (31) is of the form

$$\begin{aligned} \varepsilon\frac{ds}{d\theta} &= f\left(s(\theta), \int_0^\theta s(\alpha)\, g(\theta-\alpha)\, d\alpha, \theta\right) \\ s(0) &= \varphi^0, \end{aligned} \tag{35}$$

where the small parameter

$$\varepsilon = \frac{\mu}{\beta} \quad (0 \ll \varepsilon < 1) \tag{36}$$

is the ratio of the per capita tree death rate and the seedling re-establishment rate. This ratio is small, because the seedling re-establishment time (typically 1-5 years) is much smaller than the average life span of a tree (100 years or more). Let us perform perturbation analysis for the more general statement (35), and then apply the results to (31). Using the boundary function method (see [9], [10]) for singularly perturbed problems, represent the uniform asymptotic approximation of the solution of (35) in the form

$$s(\theta) = \overline{s}(\theta) + \Pi s\left(\frac{\theta}{\varepsilon}\right), \tag{37}$$

where $\overline{s}(\theta)$ is the regular part, and $\Pi s(\theta/\varepsilon)$ is the boundary layer part of the approximation. The boundary layer part is necessary to correctly describe the pulse of seedlings in the first few years of forest growth; it decays exponentially to zero as time increases. In what follows, the rescaled time variable of the boundary layer part is

$$\tau = \theta/\varepsilon. \tag{38}$$

Substitution of representation (37), with (38), into problem (35) yields

$$\begin{aligned}
\varepsilon\frac{d\overline{s}}{d\theta}+\frac{d\Pi s}{d\tau} &= f\left(\overline{s}(\theta)+\Pi s(\tau),\int_0^\theta\left(\overline{s}(\alpha)+\Pi s\left(\frac{\alpha}{\varepsilon}\right)\right)g(\theta-\alpha)\,d\alpha,\theta\right) \quad (39)\\
&= f\left(\overline{s}(\theta),\int_0^\theta \overline{s}(\alpha)\,g(\theta-\alpha)\,d\alpha,\theta\right)+\\
&\quad f\left(\overline{s}(\varepsilon\tau)+\Pi s(\tau),\int_0^{\varepsilon\tau}\left(\overline{s}(\alpha)+\Pi s\left(\frac{\alpha}{\varepsilon}\right)\right)g(\varepsilon\tau-\alpha)\,d\alpha,\varepsilon\tau\right)-\\
&\quad f\left(\overline{s}(\varepsilon\tau),\int_0^{\varepsilon\tau}\overline{s}(\alpha)\,g(\varepsilon\tau-\alpha)\,d\alpha,\varepsilon\tau\right),\\
\overline{s}(0)+\Pi s(0) &= \varphi^0.
\end{aligned}$$

Equation (39), can be split into two equations in variables θ and τ, respectively:

$$\begin{aligned}
\varepsilon\frac{d\overline{s}}{d\theta} &= f\left(\overline{s}(\theta),\int_0^\theta \overline{s}(\alpha)\,g(\theta-\alpha)\,d\alpha,\theta\right), \quad (40)\\
\frac{d\Pi s}{d\tau} &= f\left(\overline{s}(\varepsilon\tau)+\Pi s(\tau),\int_0^{\varepsilon\tau}\left(\overline{s}(\alpha)+\Pi s\left(\frac{\alpha}{\varepsilon}\right)\right)g(\varepsilon\tau-\alpha)\,d\alpha,\varepsilon\tau\right)-\\
&\quad f\left(\overline{s}(\varepsilon\tau),\int_0^{\varepsilon\tau}\overline{s}(\alpha)\,g(\varepsilon\tau-\alpha)\,d\alpha,\varepsilon\tau\right)\\
&= f\left(\overline{s}(\varepsilon\tau)+\Pi s(\tau),\varepsilon\int_0^{\tau}\left(\overline{s}(\varepsilon\tilde{\alpha})+\Pi s(\tilde{\alpha})\right)g(\varepsilon\tau-\varepsilon\tilde{\alpha})\,d\tilde{\alpha},\varepsilon\tau\right)-\\
&\quad f\left(\overline{s}(\varepsilon\tau),\varepsilon\int_0^{\tau}\overline{s}(\varepsilon\tilde{\alpha})\,g(\varepsilon\tau-\varepsilon\tilde{\alpha})\,d\tilde{\alpha},\varepsilon\tau\right),\\
\Pi s(0) &= \varphi^0-\overline{s}(0).
\end{aligned}$$

To obtain the zero order approximation of the solution, set

$$\begin{aligned}
\overline{s}(\theta) &= \overline{s_0}(\theta)+O(\varepsilon), \quad (41)\\
\Pi s(\tau) &= \Pi_0 s(\tau)+O(\varepsilon).
\end{aligned}$$

Here and below the notation $\beta(\varepsilon)=O(\varepsilon^\gamma)$ means that for some constants $C>0$, $\gamma>0$, $\varepsilon_0>0$,

$$|\beta(\varepsilon)|\le C\varepsilon^\gamma \text{ for } 0<\varepsilon<\varepsilon_0. \quad (42)$$

Substitution of (41) into (40), with omission of terms of order ε and higher, yields:

$$0 = f\left(\overline{s_0}(\theta), \int_0^\theta \overline{s_0}(\alpha)\, g(\theta-\alpha)\, d\alpha, \theta\right) \tag{43}$$

for the regular part, and

$$\begin{aligned} \frac{d\Pi_0 s}{d\tau} &= f\left(\overline{s_0}(0) + \Pi_0 s(\tau), 0, 0\right) - f\left(\overline{s_0}(0), 0, 0\right) \\ &= f\left(\overline{s_0}(0) + \Pi_0 s(\tau), 0, 0\right), \\ \Pi_0 s(0) &= \varphi^0 - \overline{s_0}(0) \end{aligned} \tag{44}$$

for the boundary layer part of the leading order asymptotic solution.

Taking into account the explicit form of function f for logistic seedling re-establishment (compare equations (31) and (35)), we obtain the nonlinear integral equation

$$\overline{s_0}(\theta) = k\left(\int_0^\theta \overline{s_0}(\theta-\alpha)\, e^{-\alpha} b(\alpha)\, d\alpha + l(\theta)\right) \tag{45}$$

for the regular part $\overline{s_0}(\theta)$. From (45) the initial value is calculated to be

$$\overline{s_0}(0) = k^0 = k(l(0)), \tag{46}$$

which is the initial seedling carrying capacity. Equation (45) can be solved numerically or by the method of successive approximations.

The leading order approximation $\Pi_0 s$ of the boundary layer part is found as the solution of the initial value problem

$$\begin{aligned} \frac{d\Pi_0 s}{d\tau} &= \left(k^0 + \Pi_0 s(\tau)\right)\left(1 - \frac{k^0 + \Pi_0 s(\tau)}{k^0}\right), \\ \Pi_0 s(0) &= \varphi^0 - \overline{s_0}(0) = \varphi^0 - k^0. \end{aligned} \tag{47}$$

Using the transformation

$$u(\tau) = k^0 + \Pi_0 s(\tau), \tag{48}$$

we obtain the problem with logistic differential equation

$$\begin{aligned} \frac{du}{d\tau} &= u(\tau)\left(1 - \frac{u(\tau)}{k^0}\right), \\ u(0) &= \varphi^0, \end{aligned} \tag{49}$$

with explicit solution

$$u(\tau) = \frac{k^0}{1 + e^{-\tau}\left(\frac{k^0}{\varphi^0} - 1\right)}. \tag{50}$$

Therefore,

$$\begin{aligned} \Pi_0 s(\tau) &= u(\tau) - k^0 \\ &= \frac{k^0}{1 + e^{-\tau}\left(\frac{k^0}{\varphi^0} - 1\right)} - k^0 \\ &= -\frac{k^0\left(\frac{k^0}{\varphi^0} - 1\right)}{e^{\tau} + \frac{k^0}{\varphi^0} - 1}. \end{aligned} \tag{51}$$

The leading order approximation of the solution of (31) is given by

$$s(\theta) = \overline{s_0}(\theta) + \Pi_0 s\left(\frac{\theta}{\varepsilon}\right) + O(\varepsilon). \tag{52}$$

Example 1: Logistic model with linear seedling carrying capacity function and linear tree size growth function

Consider a forest with logistic seedling re-establishment and

$$
\begin{aligned}
k(v) &= 1-\lambda v \quad \text{for } 0 \le v \le 1/\lambda, && \text{(linear seedling carrying capacity)},\\
k(v) &= 0 \quad \text{for } v > 1/\lambda, && \text{(seedlings vanish, if volume } > 1/\lambda),\\
b(\alpha) &= \alpha && \text{(linear tree growth)},\\
\varphi(\alpha) &= \varphi^0 e^{-\alpha} && \text{(exponential initial age distribution)}.
\end{aligned}
\tag{53}
$$

Assume here that $\alpha_{\max} = \infty$, $\lambda = 2$ and $\varphi^0 = 0.1$. Then

$$
\begin{aligned}
v(0) &= v^0 = \textstyle\int_0^\infty \varphi(\alpha)\, b(\alpha)\, d\alpha = 0.1 && \text{(initial volume)},\\
k(v(0)) &= k^0 = 1-\lambda v(0) = 0.8 && \text{(initial carrying capacity)},\\
\varphi(0) &= \varphi^0 = 0.1 && \text{(initial seedling density)}.
\end{aligned}
\tag{54}
$$

By virtue of (31), (32) and (36), the seedling density $s(\theta)$ satisfies the integro-differential equation

$$
\begin{aligned}
\varepsilon \frac{ds}{d\theta} &= s(\theta)\left(1-\frac{s(\theta)}{K(V(\theta))}\right), \qquad (55)\\
K(V(\theta)) &= 1-\lambda\left(\int_0^\theta s(\theta-\alpha)\, e^{-\alpha}\alpha\, d\alpha + e^{-\theta}\int_\theta^\infty \varphi^0 e^{-(\alpha-\theta)}\alpha\, d\alpha\right)\\
&= 1-\lambda\int_0^\theta s(\theta-\alpha)\, e^{-\alpha}\alpha\, d\alpha - \lambda\varphi^0(1+\theta)\, e^{-\theta},
\end{aligned}
$$

$s(0) = \varphi^0.$

To obtain the leading order approximation of the solution using the boundary function method, combine equations (37) and (41) and write

$$s(\theta) = \overline{s_0}(\theta) + \Pi_0 s(\theta/\varepsilon) + O(\varepsilon) \tag{56}$$

By (45) and (51) the regular part $\overline{s_0}(\theta)$ and the boundary layer part $\Pi_0 s(\theta/\varepsilon)$ are given by

$$\begin{aligned} \overline{s_0}(\theta) &= 1 - \lambda \int_0^\theta \overline{s_0}(\theta - \alpha) e^{-\alpha} \alpha d\alpha \\ &\quad -\lambda e^{-\theta} \int_\theta^\infty \varphi^0 e^{-(\alpha-\theta)} \alpha d\alpha \\ &= 1 - 2\int_0^\theta \overline{s_0}(\theta-\alpha) e^{-\alpha}\alpha d\alpha - 0.2(1+\theta) e^{-\theta}, \end{aligned} \tag{57}$$

$$\Pi_0 s(\theta/\varepsilon) = -\frac{k^0\left(\frac{k^0}{\varphi^0} - 1\right)}{e^\tau + \frac{k^0}{\varphi^0} - 1} = -\frac{5.6}{e^{\theta/\varepsilon} + 7}. \tag{58}$$

By Theorem 18 in the Appendix, the explicit solution of Volterra integral equation (57) is

$$\overline{s_0}(\theta) = \frac{1}{3} + e^{-\theta}\left(\frac{7}{15}\cos\sqrt{2}\theta + \frac{7\sqrt{2}}{30}\sin\sqrt{2}\theta\right). \tag{59}$$

Instead of using an asymptotic method, the seedling equation (55) can be solved numerically with a difference scheme (e.g. forward Euler method). Fig. 2a shows numerical approximations of seedling density and forest volume obtained with both methods. The steady states for seedling density and forest volume can be calculated from the seedling equation (55) by taking the limit $\theta \to \infty$, so that $s(\theta) \to s^*$ and $ds/d\theta \to 0$:

$$s^* = 1 - \lambda \int_0^\infty s^* e^{-\alpha} \alpha d\alpha = 1 - \lambda s^*, \tag{60}$$

that is

$$s^* = \frac{1}{1+\lambda} = \frac{1}{3}. \tag{61}$$

The steady state forest volume is given by

$$v^* = \int_0^\infty s^* e^{-\alpha} \alpha d\alpha = s^* = \frac{1}{1+\lambda} = \frac{1}{3}. \tag{62}$$

Fig. 2b shows the characteristic S shape of the logistic growth of the seedling density graph in the phase where it increases from its initial to its maximum value. The influence of parameter ε on the solution is demonstrated in Fig.2c: for larger re-establishment time ε the maximum of the seedling density is smaller and it is reached at a later time.

A larger value of the parameter λ, on the other hand, leads to a smaller equilibrium value $1/(1+\lambda)$ for both seedling density and forest volume expressed by (61) and (62) (see Fig. 2d).

The influence of initial forest size on the behavior of seedling count $s(\theta)$ is shown in Fig. 2e.

Finally, to derive the equilibrium age distribution of the forest, set

$$\frac{\partial n}{\partial \theta} = 0 \tag{63}$$

in the von-Foerster equation (26), thereby obtaining the ordinary differential equation

$$\frac{dn^*}{d\alpha} = -n^*(\alpha) \tag{64}$$

for the equilibrium age distribution

$$n^*(\alpha) = \lim_{\theta \to \infty} n(\theta, \alpha). \tag{65}$$

Differential equation (64) with the additional condition

$$n^{*}(0) = \lim_{\theta \to \infty} n(\theta, 0) = \lim_{\theta \to \infty} s(\theta) = s^{*}$$

has the solution

$$n^{*}(\alpha) = n^{*}(0)\, e^{-\alpha} = s^{*} e^{-\alpha}. \qquad (66)$$

This solution is shown in Fig. 2f for different values of parameter λ. The three-dimensional graph in Fig. 2g illustrates the convergence of tree age distribution to an equilibrium distribution.

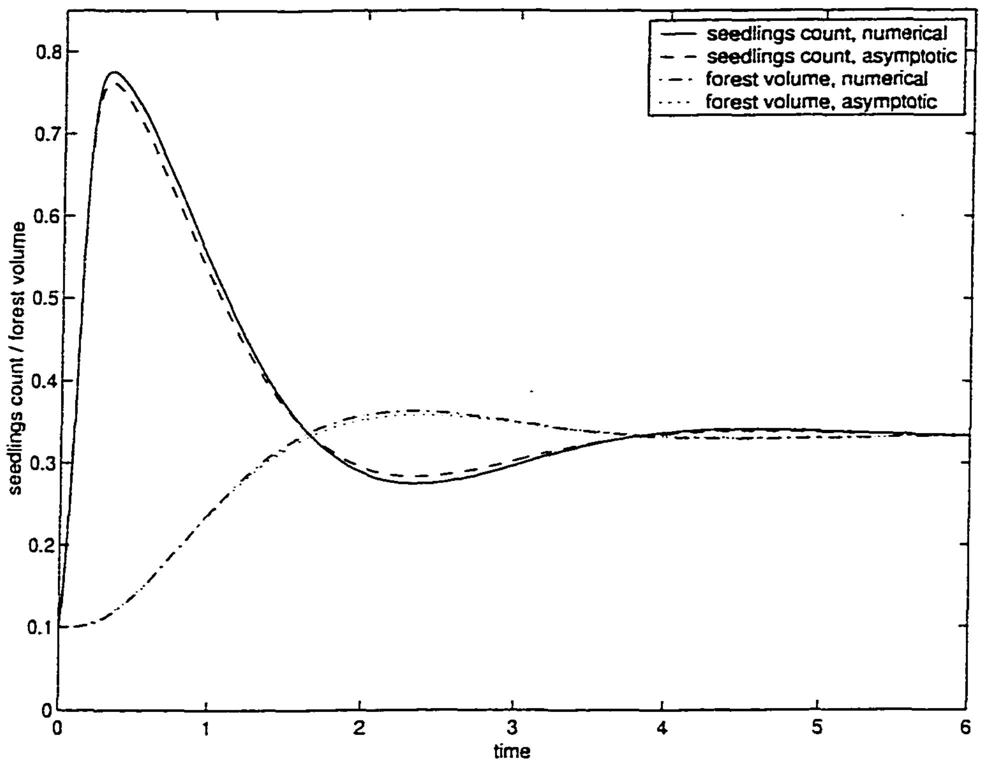

Fig.2a: Example 1. seedling count s and forest volume v as functions of time θ are shown. They are obtained by solving tree age density equation $\partial n/\partial\theta + \partial n/\partial\alpha = -n$ with $n(\theta,0) = s(\theta)$ and initial age distribution $n(0,\alpha) = 0.1e^{-\alpha}$, and seedling density equation $\varepsilon\frac{ds}{d\theta} = s(\theta)\left(1 - \frac{s(\theta)}{1-\lambda v(\theta)}\right)$ with parameters $\varepsilon = .05$, $\lambda = 2$. Forest volume is $v(\theta) = \int_0^\infty n(\theta,\alpha)\, b(\alpha)\, d\alpha$, and tree size growth function is $b(\alpha) = \alpha$. All quantities are rescaled as explained in the text. seedling count and forest volume approach their respective steady states, $1/(1+\lambda) = 1/3$, in an oscillatory fashion. Results obtained via numerical integration of the original statement of the problem using Euler difference scheme with time stepsize 0.01 and results obtained from the zero order approximation show good agreement.

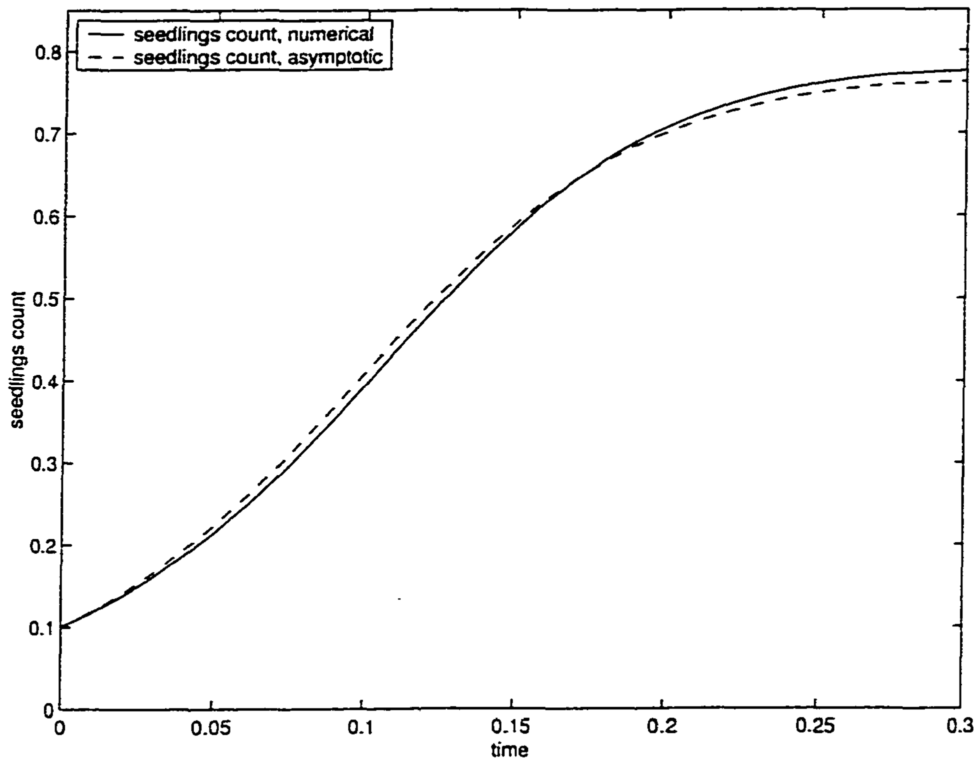

Fig. 2b: Example 1. Initial phase of the seedling count dynamics shown in Fig. 2a, during which $s(\theta)$ increases from its initial value to its maximum value.

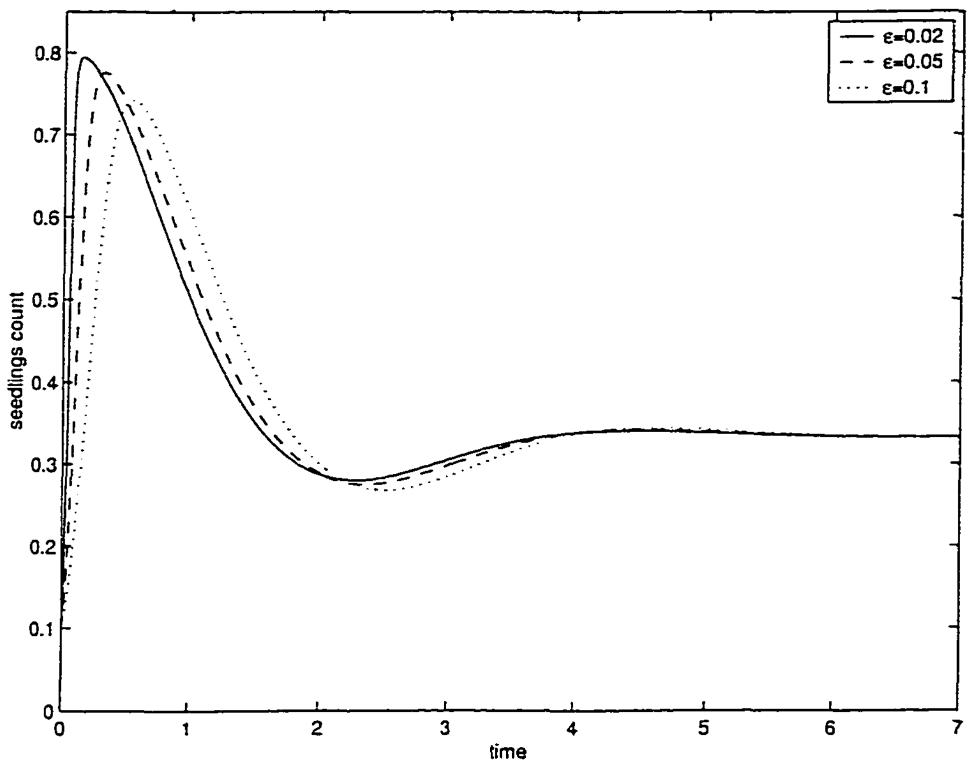

Fig.2c: Example 1. Influence of the magnitude of small parameter ε on the behavior of seedling count $s(\theta)$. All other parameters are the same as in Fig.2a.

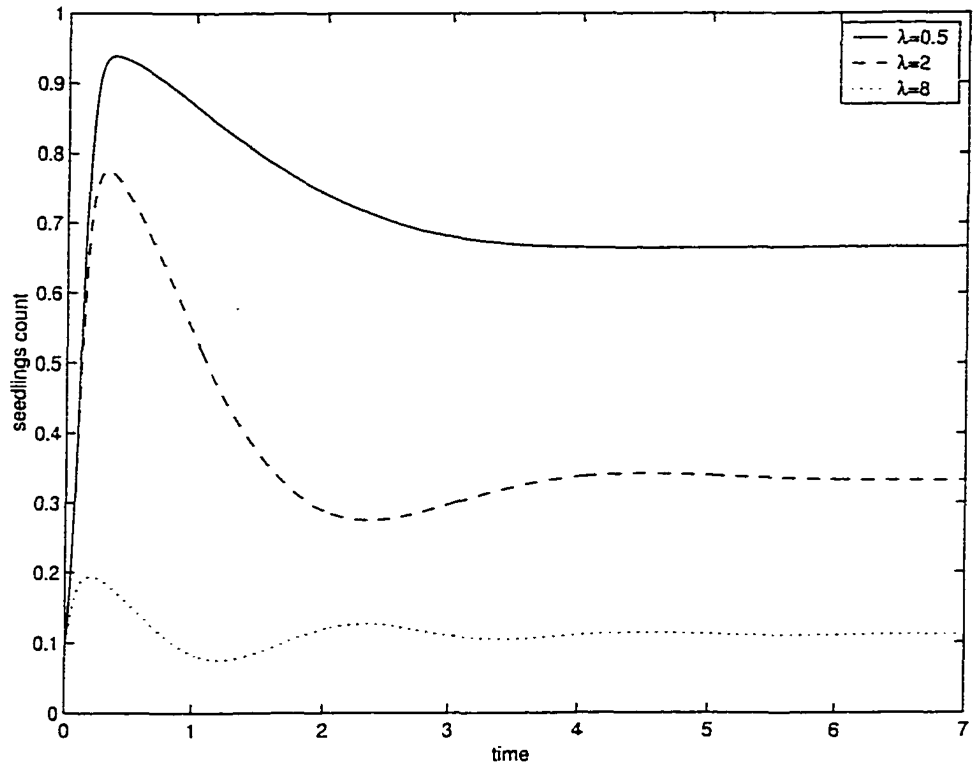

Fig.2d: Example 1. Same parameter values as in Fig. 2a, but different values of λ (which measures the inhibition of seedling count by forest volume).

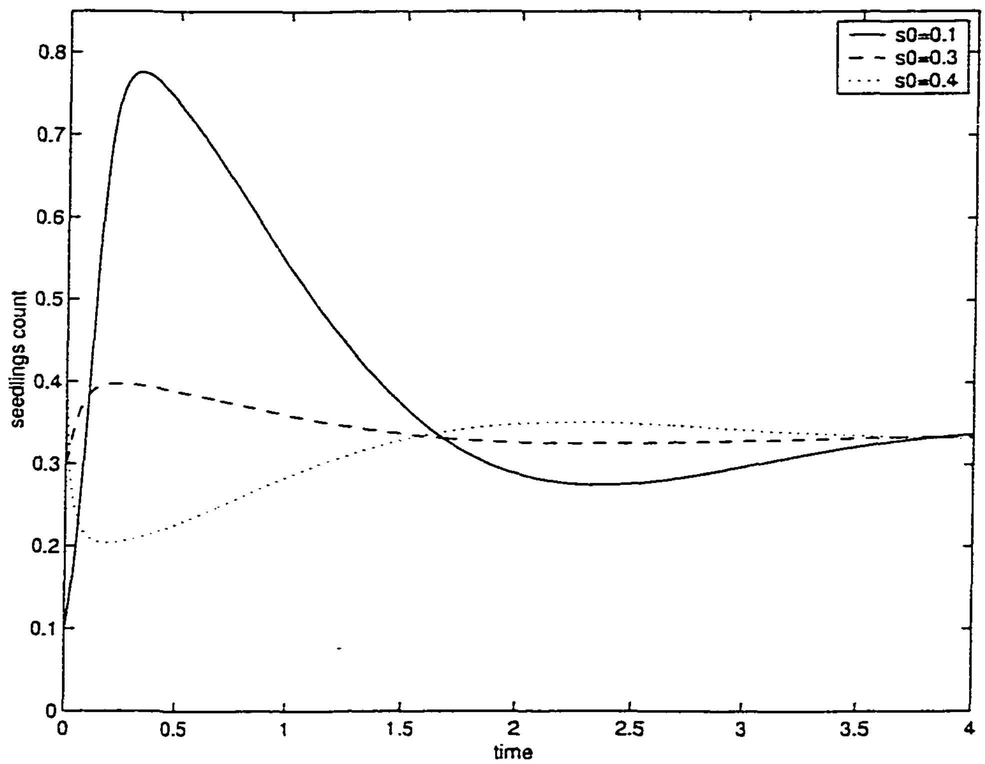

Fig. 2e: Example 1. Same parameter values as in Fig. 2a, but different initial forest sizes.

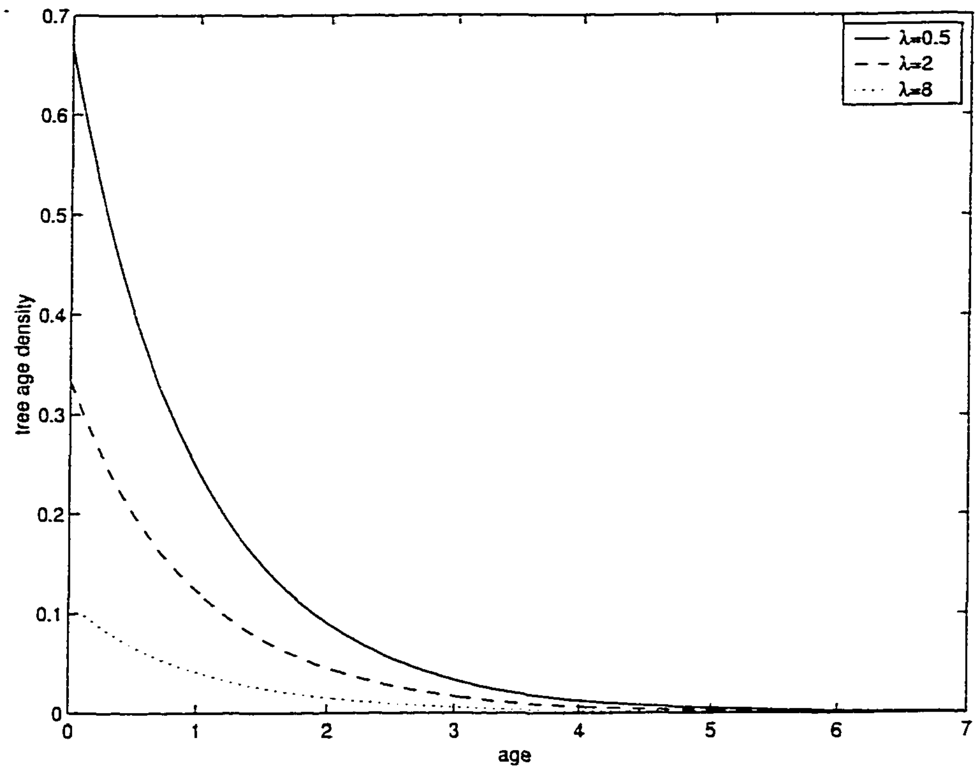

Fig. 2f: Example 1. Graphs of equilibrium tree age distributions obtained as time $\theta \to \infty$ for different values of λ. All other parameter values are the same as in Fig. 2a.

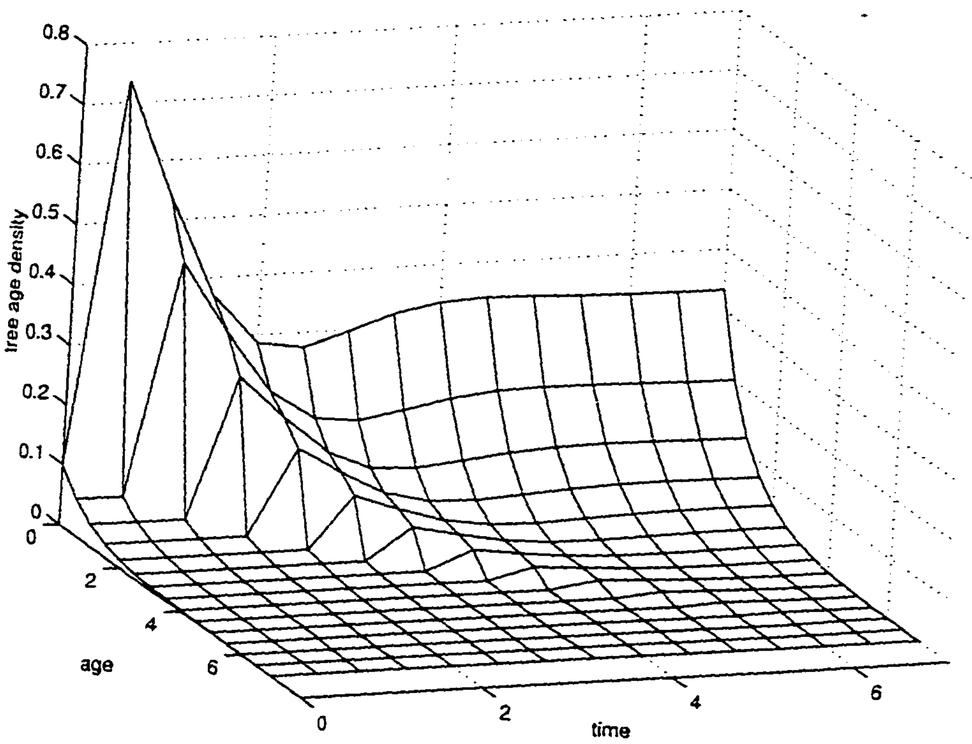

Fig. 2g: Example 1. Three-dimensional graph of tree age density as a function of time and age. Same parameter values as in Fig. 2a.

4 Linear model with exponential seedling re-establishment

Here is another particular statement of the general problem (13) (that can be reduced to (35)) for which all results can be obtained explicitly:

Model description and leading order approximation

In some models for particular tree species instead of the logistic-type equation for seedling growth we can use a linear equation describing exponential re-establishment of seedlings to the level defined by available resources. In this class of models the rate of seedling increase at any time θ is proportional to the difference of seedling carrying capacity $k(v)$, which depends on forest volume $v(\theta)$, and the seedling count $s(\theta)$, leading to the seedling differential equation

$$\varepsilon \frac{ds}{d\theta} = k(v) - s, \tag{67}$$

$$s(0) = \phi^0. \tag{68}$$

Note that when the seedling carrying capacity $k(v)$ is zero, this equation simplifies to

$$\varepsilon \frac{ds}{d\theta} = -s \tag{69}$$

with the explicit solution

$$s(\theta) = \varphi^0 e^{-\theta/\varepsilon}. \tag{70}$$

Equation (67) describing exponential seedling re-establishment is a special case of the general form of a singularly perturbed integro-differential equation given in (35). In the leading order approximation, the regular part is identical to that in the logistic model case. The boundary layer part, however, is different. It satisfies the problem

$$\begin{aligned} \frac{d\Pi_0 s}{d\tau} &= -\Pi_0 s(\tau), \\ \Pi_0 s(0) &= -\left(k^0 - s^0\right), \end{aligned} \tag{71}$$

with the explicit solution

$$\Pi_0 s(\tau) = -\left(k^0 - s^0\right) e^{-\tau}. \tag{72}$$

Example 2 : Exponential tree growth

As an example, let us consider a particular model where the individual tree size changes exponentially with age, and the seedling carrying capacity is a linear function of forest volume

$$\begin{aligned} b(\alpha) &= e^{\kappa_1 \alpha} && \text{for } \alpha \geq 0, && \text{size of tree of age } \alpha, \text{ where } 0 < \kappa_1 < 1, \\ k(v) &= 1 - \lambda v && \text{for } 0 \leq v \leq 1/\lambda, && \text{seedling carrying capacity for forest volume } v, \\ k(v) &= 0 && \text{for } v > 1/\lambda, && \text{seedlings vanish for } v > 1/\lambda. \end{aligned} \tag{73}$$

Same as in Example 1, take initial age distribution

$$\varphi(\alpha) = \varphi^0 e^{-\alpha}.$$

From (24) and (30), the forest volume is given by

$$
\begin{aligned}
v(\theta) &= \int_0^\infty n(\theta,\alpha)\, b(\alpha)\, d\alpha && (74)\\
&= \int_0^\theta s(\theta-\alpha)\, e^{-\alpha} e^{\kappa_1 \alpha} d\alpha + e^{-\theta} \int_\theta^\infty \varphi(\alpha-\theta)\, e^{\kappa_1\alpha} d\alpha \\
&= \int_0^\theta s(\alpha)\, e^{-(1-\kappa_1)(\theta-\alpha)} d\alpha + \frac{\varphi^0}{1-\kappa_1} e^{-(1-\kappa_1)\theta} && (75)
\end{aligned}
$$

Taking the derivative and using integration by parts yields the differential equation for the forest volume

$$
\begin{aligned}
v'(\theta) &= s(\theta) - (1-\kappa_1) \int_0^\theta s(\alpha)\, e^{-(1-\kappa_1)(\theta-\alpha)} d\alpha - \varphi^0 e^{-(1-\kappa_1)\theta} && (76)\\
&= s(\theta) - (1-\kappa_1)\, v(\theta).
\end{aligned}
$$

The same differential equation (76) is obtained for arbitrary initial age density $\varphi(\alpha)$. Setting $\kappa = 1-\kappa_1$, we obtain the autonomous system

$$
\begin{aligned}
\varepsilon s' &= 1 - \lambda v - s \quad \text{for } 0 \le v \le 1/\lambda, \\
\varepsilon s' &= -s \quad \text{for } v > 1/\lambda, && (77)\\
v' &= s - \kappa v,
\end{aligned}
$$

with initial conditions

$$
\begin{aligned}
s(0) &= s^0 = \varphi(0), && (78)\\
v(0) &= v^0 = \frac{\varphi^0}{\kappa}.
\end{aligned}
$$

This system has exactly one steady state

$$
s^* = \frac{\kappa}{\kappa+\lambda}, \quad (79)
$$

$$
v^* = \frac{1}{\kappa+\lambda}. \quad (80)
$$

Note that the steady state satisfies $0 \leq v^* \leq 1/\lambda$. Thus in the vicinity of the steady state, autonomous system (77) can be written in matrix form:

$$\begin{pmatrix} s' \\ v' \end{pmatrix} = \begin{pmatrix} -1/\varepsilon & -\lambda/\varepsilon \\ 1 & -\kappa \end{pmatrix} \begin{pmatrix} s \\ v \end{pmatrix} + \begin{pmatrix} 1/\varepsilon \\ 0 \end{pmatrix}. \tag{81}$$

Since the coefficient matrix

$$A = \begin{pmatrix} -1/\varepsilon & -\lambda/\varepsilon \\ 1 & -\kappa \end{pmatrix}$$

has negative trace $tr\ A = (-1/\varepsilon - \kappa)$ and positive determinant $\det A = (\kappa + \lambda)/\varepsilon$, both eigenvalues σ_1 and σ_2 have negative real parts. So, the steady state is stable. The solutions satisfying $0 < v < 1/\lambda$ are of the form

$$\begin{aligned} s(\theta) &= c_1 e^{\sigma_1 \theta} + c_2 e^{\sigma_2 \theta} + \frac{\kappa}{\lambda + \kappa}, \\ v(\theta) &= d_1 e^{\sigma_1 \theta} + d_2 e^{\sigma_2 \theta} + \frac{1}{\lambda + \kappa}, \end{aligned} \tag{82}$$

where the constants c_1, c_2, d_1, d_2 are determined by initial conditions (78) and by the eigenvectors of matrix A.

In general, the eigenvalues are complex numbers with negative real part, so that the seedling density approaches the steady state by damped oscillations. In the following, we will explore the age dynamics of the forest for the case that the eigenvalues are real:

$$\begin{aligned} \sigma_1 &= \frac{1}{2\varepsilon}\left(-1 - \varepsilon\kappa - \sqrt{(1-\varepsilon\kappa)^2 - 4\varepsilon\lambda}\right) < 0, \\ \sigma_2 &= \frac{1}{2\varepsilon}\left(-1 - \varepsilon\kappa + \sqrt{(1-\varepsilon\kappa)^2 - 4\varepsilon\lambda}\right) < 0. \end{aligned} \tag{83}$$

A sufficient condition for the eigenvalues to be real is

$$(1-\varepsilon\kappa)^2 - 4\varepsilon\lambda \geq 0, \tag{84}$$

which is equivalent to

$$\varepsilon \leq \frac{1}{4\lambda + 2}. \tag{85}$$

Let us classify possible initial conditions into five cases:

CASE (A): FOREST WITHOUT SEEDLINGS ($s^0 = 0$) AND WITH INITIAL VOLUME $v^0 \geq 1/\lambda$. According to (77) the forest volume decreases exponentially as

$$v(\theta) = v^0 e^{-\kappa\theta} \tag{86}$$

until $v(\theta_1) = 1/\lambda$ with $\theta_1 = \ln(\lambda v^0)/\kappa$. Since $v'(\theta_1) = -\kappa/\lambda$ for $\theta > \theta_1$, the solution $v(\theta)$ will enter the interval $0 \leq v \leq 1/\lambda$, and converge to the steady state v^* either decreasing monotonically or, after passing through a local minimum of volume, increasing monotonically. The seedling count $s(\theta)$ stays zero for $0 \leq \theta \leq \theta_1$ since $s = 0$ is a steady state of the seedling equation for $v \geq 1/\lambda$. For $\theta > \theta_1$, function $s(\theta)$ will increase monotonically and will reach eventually the steady state s^* (see Fig. 3a).

CASE (B): FOREST WITH SEEDLINGS ($s^0 > 0$) AND WITH INITIAL VOLUME $v^0 \geq 1/\lambda$.

The seedlings decrease as

$$s(\theta) = s^0 e^{-\theta/\varepsilon} \tag{87}$$

in the time interval $0 \leq \theta \leq \theta_2$, where θ_2 is specified below. Thence, the volume in this time interval satisfies

$$v' = -\kappa v + s^0 e^{-\theta/\varepsilon}, \quad (88)$$
$$v(0) = v^0,$$

with the explicit solution

$$v(\theta) = \left(v^0 + \frac{s^0}{\frac{1}{\varepsilon} - \kappa}\right) e^{-\kappa\theta} - \frac{s^0}{\frac{1}{\varepsilon} - \kappa} e^{-\theta/\varepsilon}. \quad (89)$$

This solution decreases monotonically and reaches at $\theta = \theta_2$ the value $1/\lambda$ (possibly after passing through a local maximum value). Since $v(\theta_2) = 1/\lambda$ and $v'(\theta_2) < 0$, we have $0 \leq v < 1/\lambda$ for $\theta > \theta_2$. As in case (A), the volume then converges to a steady state v^*, possibly after going through a local minimum first (see Fig. 3b).

CASE (C): FOREST WITHOUT SEEDLINGS ($s^0 = 0$) AND WITH INITIAL VOLUME $0 < v^0 < 1/\lambda$.

Now

$$s'(0) = \frac{1}{\varepsilon}\left(1 - \lambda v^0\right) > 0, \quad (90)$$
$$v'(0) = -\kappa v^0 < 0,$$

so seedling count and forest volume converge to their respective steady state values s^* and v^*, as shown in Fig. 3c.

CASE (D): FOREST WITHOUT SEEDLINGS ($s^0 = 0$) AND WITHOUT TREES ($v^0 = 0$).

Then

$$\begin{aligned} s'(0) &= \frac{1}{\varepsilon} > 0, \\ v'(0) &= 0, \\ v''(0) &= s'(0) - \kappa v'(0) = \frac{1}{\varepsilon} > 0, \end{aligned} \tag{91}$$

so the forest volume converges, monotonically increasing, to its steady state value, while the seedling count reaches the steady state value possibly after going through a local maximum (see Fig. 3d).

CASE (E): FOREST WITH SEEDLINGS ($s^0 > 0$) AND WITH INITIAL VOLUME $0 < v^0 < 1/\lambda$.

If the solution for the forest volume remains in the region $0 \leq v^0 < 1/\lambda$ for all times, then seedling count and forest volume converge to their respective steady state values. If at some instant of time θ_3, we have $v(\theta_3) = 1/\lambda$, and $v'(\theta_3) > 0$, then for $\theta > \theta_3$, immediately following θ, the function $v(\theta) > 1/\lambda$, and we arrive at case (B); see Fig. 3e.

A forest with seedlings ($s^0 > 0$) and zero volume ($v^0 = 0$) is impossible, because in the model under consideration, the seedlings have a nonzero volume. Therefore these five cases exhaust all possible initial conditions. The conclusions are:

1. The steady state is globally stable (the forest converges to it for every possible initial state).

2. If the seedling count is initially positive, it remains positive for all times;

so the seedlings cannot vanish in a natural forest that is described by this model, and neither can the forest volume vanish.

3. seedling count and forest volume are completely determined by the initial values of these two quantities, and do not depend on the initial age distribution of the forest.

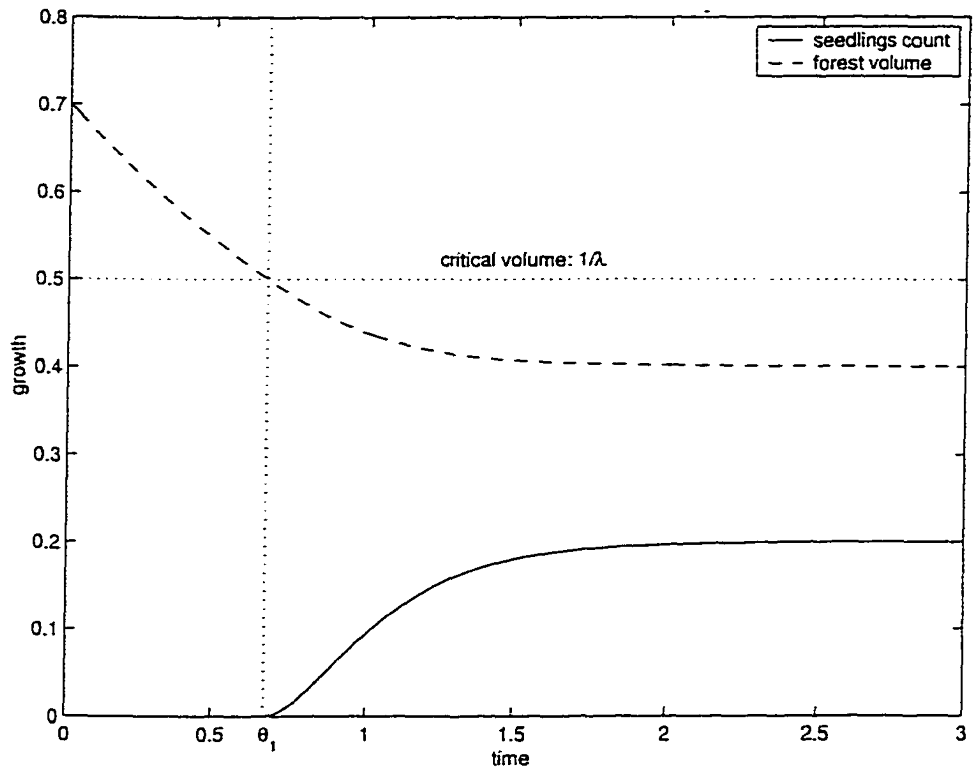

Fig.3a: Example 2, Case (A). seedling count s and forest volume v are shown as function of time θ. The exact solution is obtained by solving system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, $\kappa = 0.5$ and initial conditions $s^0 = 0$, $v^0 = 0.7 > 1/\lambda$. seedling count and forest volume converge to their respective equilibrium values $\kappa/(\kappa + \lambda) = 0.2$ and $1/(\kappa + \lambda) = 0.4$.

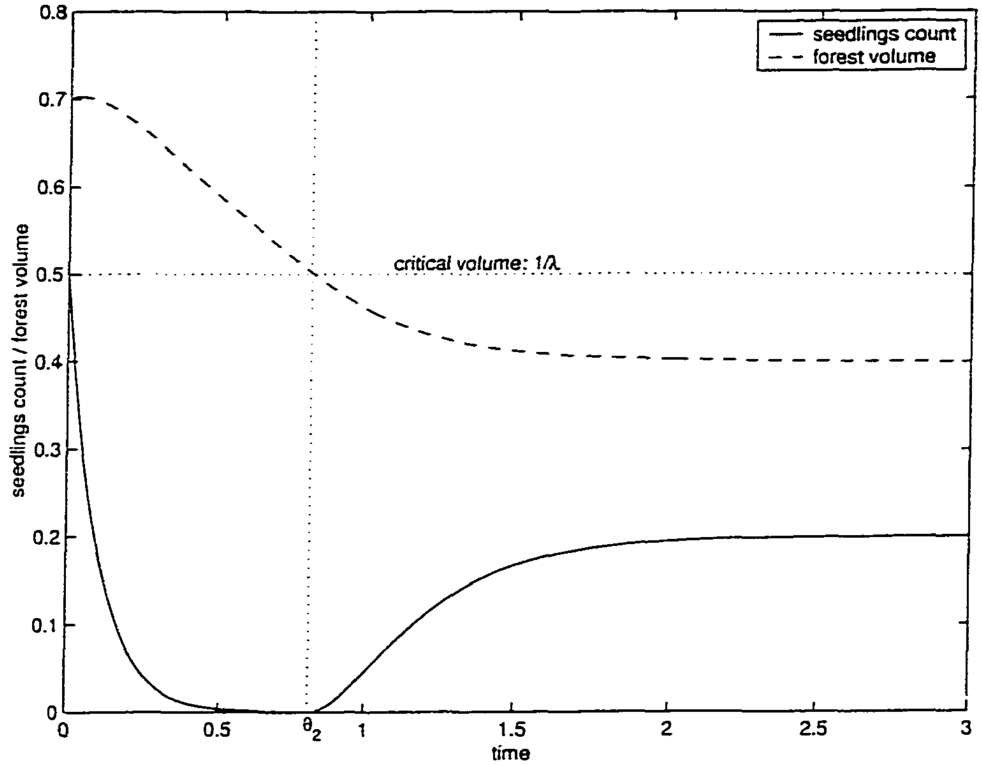

Fig.3b: Example 2, Case (B). seedling count s and forest volume v as functions of time θ obtained as the solution of the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, $\kappa = 0.5$ and initial conditions $s^0 = 0.5$, $v^0 = 0.7 > 1/\lambda$.

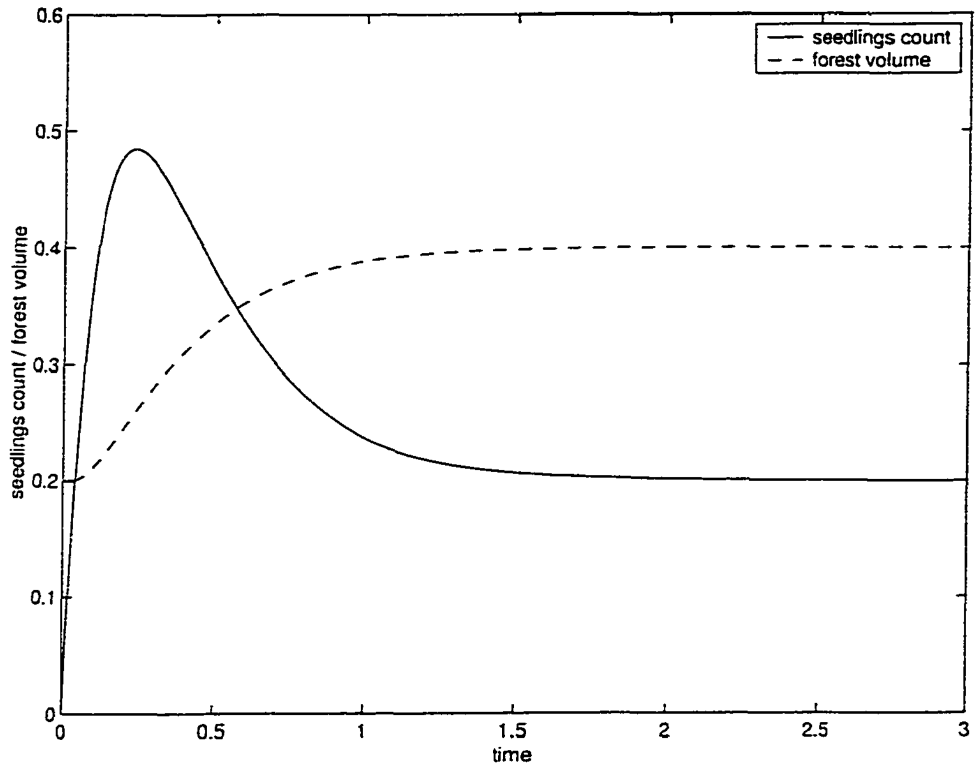

Fig.3c: Example 2, Case (C). seedling count s and forest volume v as functions of time θ obtained as solutions of the system $\varepsilon s' = \max(1-\lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, $\kappa = 0.5$ and initial conditions $s^0 = 0$, $v^0 = 0.2 < 1/\lambda$.

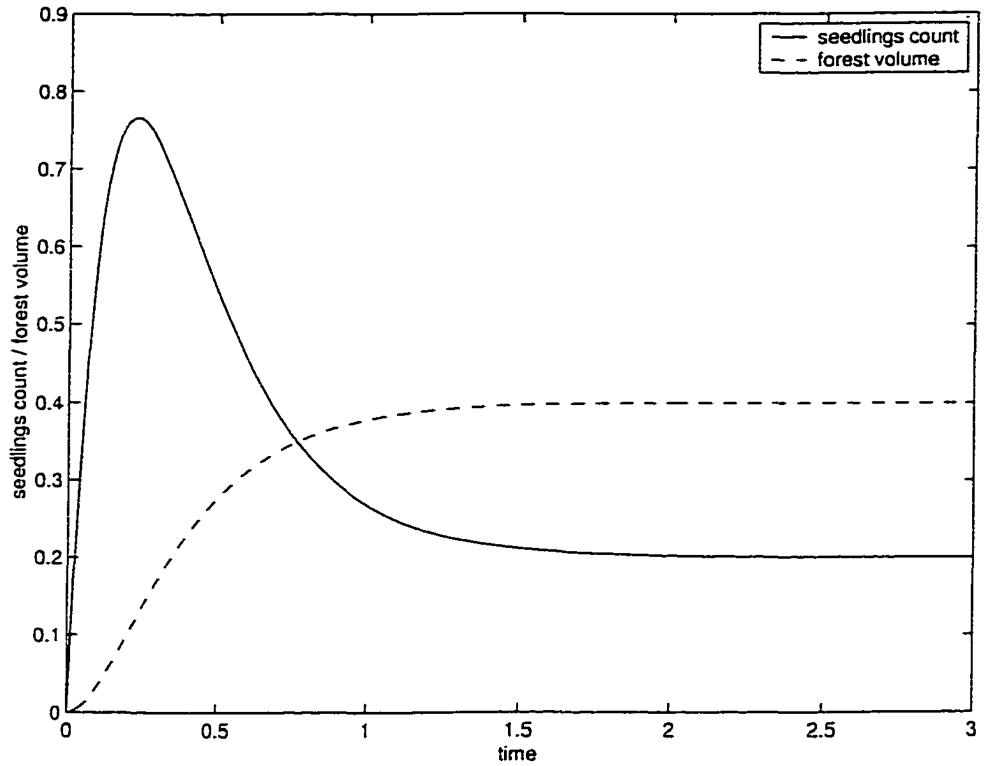

Fig.3d: Example 2, Case (D). seedling count s and forest volume v as functions of time θ obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, $\kappa = 0.5$ and initial conditions $s^0 = 0$, $v^0 = 0$, that is an empty forest.

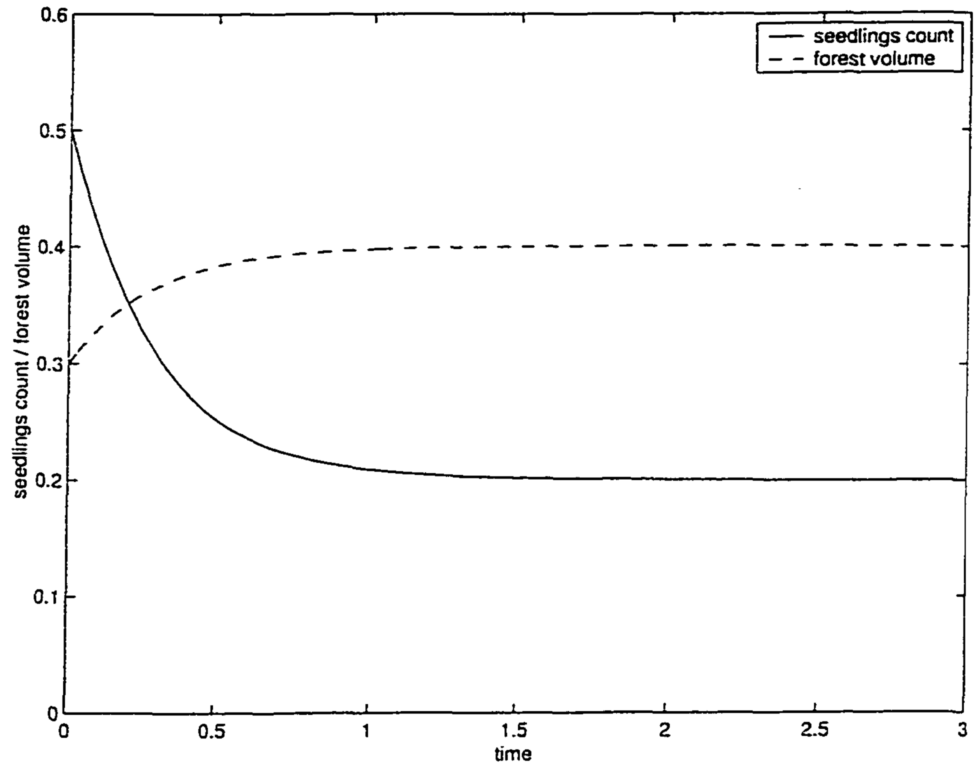

Fig.3e: Example 2, Case (E). seedling count s and forest volume v as functions of time θ obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, $\kappa = 0.5$ and initial conditions $s^0 = 0.5$, $v^0 = 0.3 < 1/\lambda$.

Example 3: Exponential tree growth compensating for forest decay

If the exponential growth rate of an individual tree is the same as the decay rate of the forest, set $\kappa_1 = 1$ (that is, $\kappa = 0$) in Example 2. Then we obtain from (77) and (78) the autonomous system :

$$\begin{aligned} \varepsilon s' &= 1 - \lambda v - s \quad \text{for } 0 \le v \le 1/\lambda, \\ \varepsilon s' &= -s \qquad\qquad \text{for } v > 1/\lambda, \\ v' &= s, \end{aligned} \tag{92}$$

with initial conditions

$$\begin{aligned} s(0) &= s^0, \\ v(0) &= v^0. \end{aligned} \tag{93}$$

The steady state is

$$s^* = 0, \tag{94}$$

$$v^* = \frac{1}{\lambda}. \tag{95}$$

The solutions in the region $0 \le v \le 1/\lambda$ are of the form

$$\begin{aligned} s(\theta) &= c_1 e^{\sigma_1 \theta} + c_2 e^{\sigma_2 \theta}, \\ v(\theta) &= d_1 e^{\sigma_1 \theta} + d_2 e^{\sigma_2 \theta} + \frac{1}{\lambda}, \end{aligned}$$

with suitable constants c_1, c_2, d_1, d_2, which are determined by initial conditions (93), and by the eigenvectors of system (92).

The corresponding eigenvalues of the system are

$$\sigma_1 = \frac{1}{2\varepsilon}\left(-1-\sqrt{1-4\varepsilon\lambda}\right), \tag{96}$$
$$\sigma_2 = \frac{1}{2\varepsilon}\left(-1+\sqrt{1-4\varepsilon\lambda}\right).$$

Since both eigenvalues have negative real part, the equilibrium is stable. Note that for

$$\varepsilon < \frac{1}{4\lambda} \tag{97}$$

both eigenvalues σ_1 and σ_2 are real and negative.

As in Example 2, we classify possible initial conditions into five cases.

Case (A): Forest without seedlings ($s^0 = 0$) and initial volume $v^0 \geq 1/\lambda$.

The forest volume remains constant, while the seedling count remains zero for all times.

Case (B): Forest with seedlings ($s^0 > 0$) and initial volume $v^0 \geq 1/\lambda$.

The seedling function is

$$s(\theta) = s^0 e^{-\theta/\varepsilon}. \tag{98}$$

Evidently, $s(\theta) \to 0$ as $\theta \to \infty$. Thus the volume satisfies the problem

$$v' = s^0 e^{-\theta/\varepsilon}, \tag{99}$$
$$v(0) = v^0,$$

with explicit solution (see Fig. 4a):

$$v(\theta) = v^0 + \varepsilon s^0 \left(1 - e^{-\frac{\theta}{\varepsilon}}\right) \to v^0 + \varepsilon s^0 > v^0 \geq \frac{1}{\lambda} \text{ as } \theta \to \infty. \tag{100}$$

CASE (C): FOREST WITHOUT SEEDLINGS ($s^0 = 0$) AND INITIAL VOLUME $0 < v^0 < 1/\lambda$.

Then

$$\begin{aligned} s'(0) &= \frac{1}{\varepsilon}\left(1 - \lambda v^0\right) > 0, \\ v'(0) &= 0, \\ v''(0) &= s'(0) = \frac{1}{\varepsilon}\left(1 - \lambda v^0\right) > 0. \end{aligned} \tag{101}$$

While the seedling count increases to a local maximum and then converges, monotonously decreasing, to zero, the forest volume converges, monotonically increasing, to its steady state $1/\lambda$ (see Fig. 4b).

CASE (D): FOREST WITHOUT SEEDLINGS ($s^0 = 0$) AND WITHOUT TREES ($v^0 = 0$).

Now

$$\begin{aligned} s'(0) &= \frac{1}{\varepsilon} > 0, \\ v'(0) &= 0, \\ v''(0) &= s'(0) = \frac{1}{\varepsilon} > 0, \end{aligned} \tag{102}$$

so the forest volume converges, monotonically increasing, to its steady state $1/\lambda$, while the seedling count approaches zero after going through a local maximum. (see Fig. 4c).

Case (E): Forest with seedlings ($s^0 > 0$) and initial volume $0 < v^0 < 1/\lambda$.

If the solution for the forest volume remains in the region $0 \leq v^0 < 1/\lambda$ for all times, then seedling count and forest volume converge to their respective steady state $s(\theta) \to 0$, $v(\theta) \to 1/\lambda$ (see Fig. 4d). If the forest volume increases beyond $1/\lambda$, we arrive at case (B) (see Fig. 4e).

Thus, the following conclusions are valid for all five cases:

1. The seedling count converges to zero for every possible initial state of the forest.

2. The forest volume converges to $1/\lambda$ in some cases and to a value greater than $1/\lambda$ in others.

3. As in Example 2, seedling count and forest volume are completely determined by the initial values of these two quantities, and do not depend on the initial age distribution of the forest.

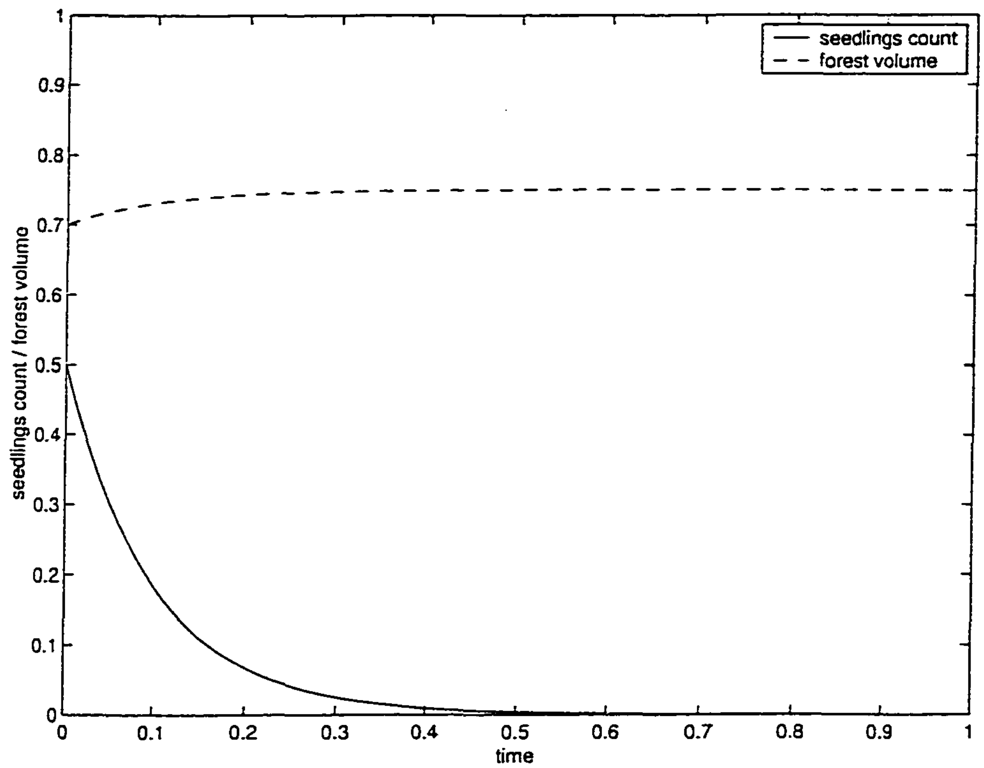

Fig.4a: Example 3, Case (B). seedling count s and forest volume v are shown as functions of time θ. These functions are obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, and initial conditions $s^0 = 0.5$, $v^0 = 0.7 > 1/\lambda$. seedling count converges to zero, while the forest volume converges to $v^0 + \varepsilon s^0 = 0.75$.

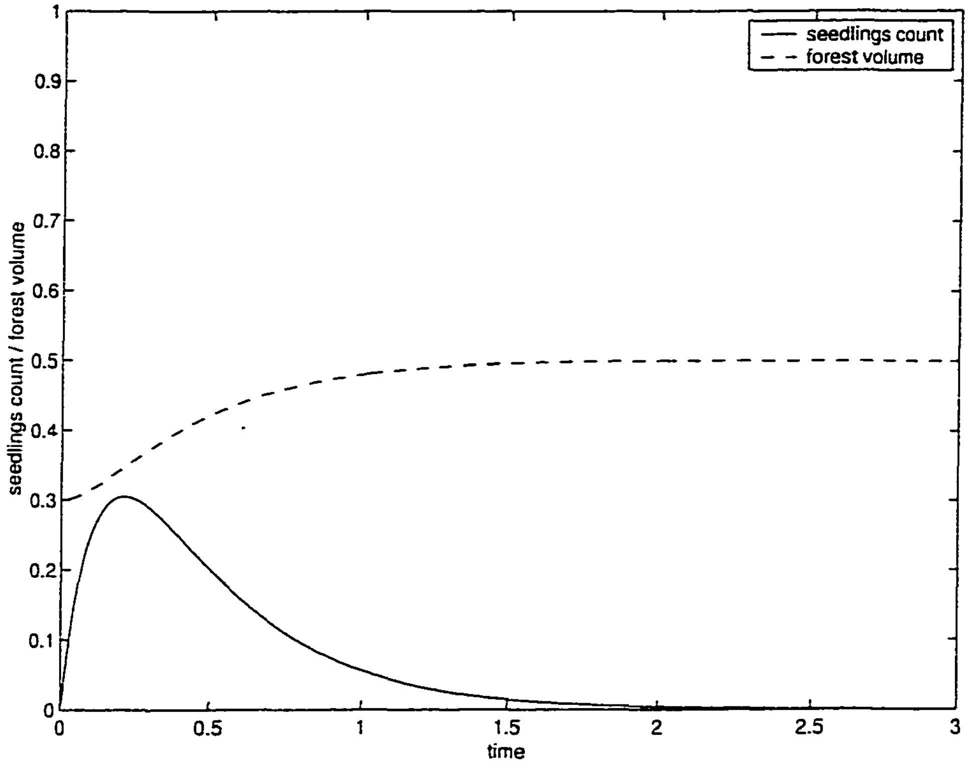

Fig.4b: Example 3, Case (C). seedling count s and forest volume v as functions of time θ, obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, and initial conditions $s^0 = 0$, $v^0 = 0.3 < 1/\lambda$. seedling count converges to zero, while the forest volume converges to $1/\lambda = 0.5$.

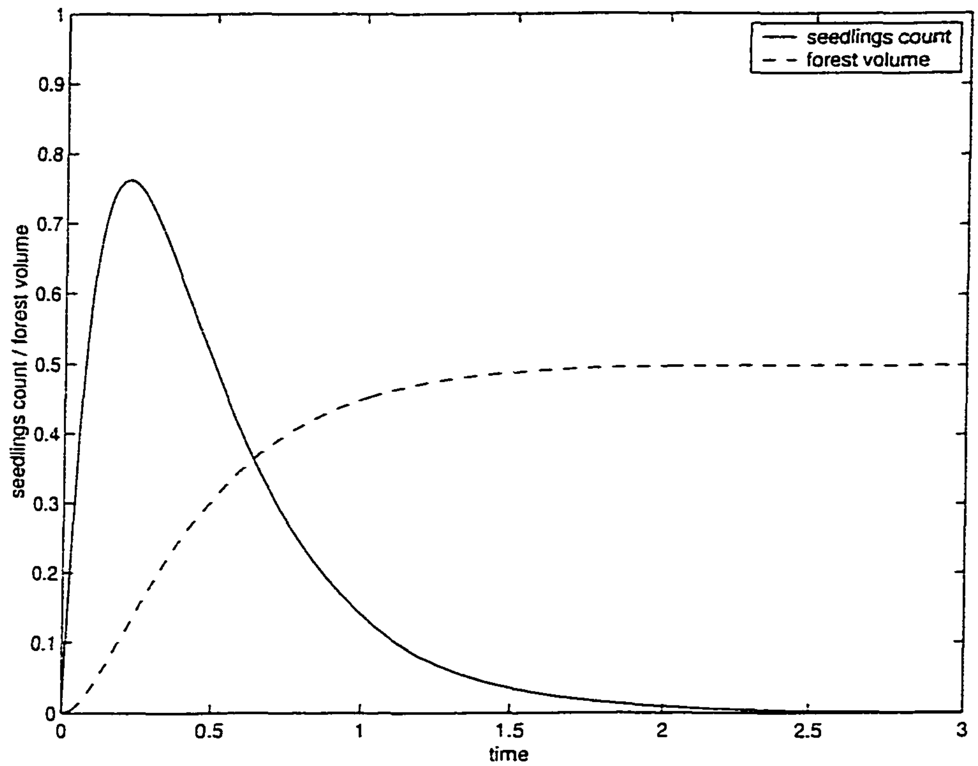

Fig.4c: Example 3, Case (D). seedling count s and forest volume v as functions of time θ, obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, $\kappa = 0.5$, and initial conditions $s^0 = 0$, $v^0 = 0$, that is an initially empty forest. The seedling count converges to zero, while the forest volume converges to $1/\lambda = 0.5$.

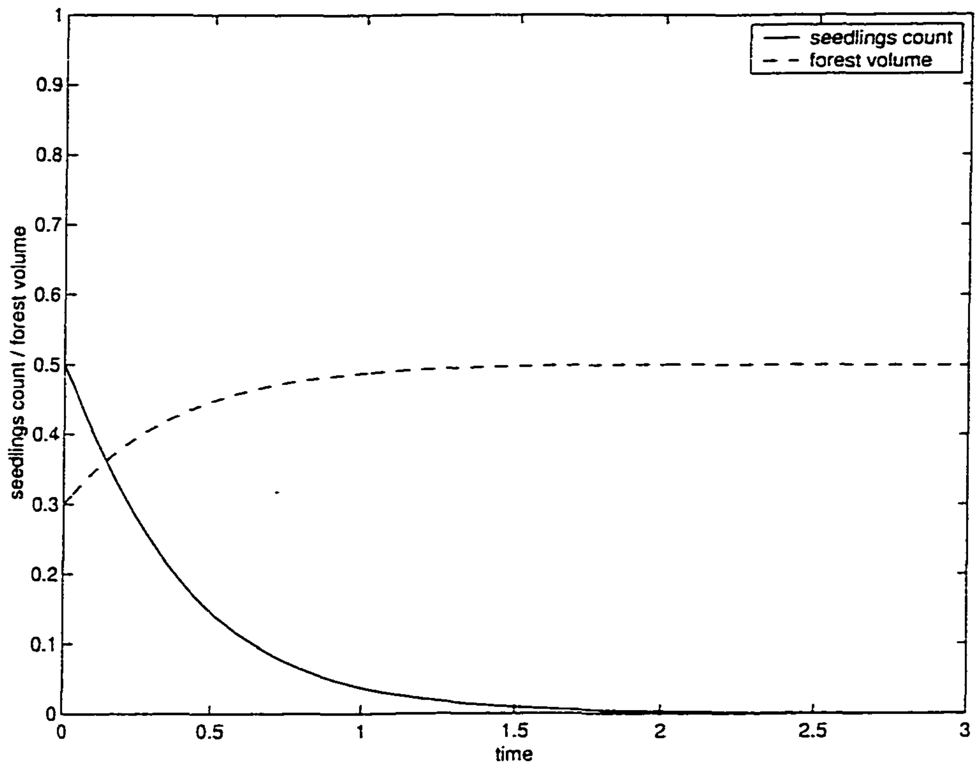

Fig.4d: Example 3, Case (E). seedling count s and forest volume v as functions of time θ, solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, and initial conditions $s^0 = 0.5$, $v^0 = 0.3 < 1/\lambda$. seedling count converges to zero, while forest volume converges to its equilibrium value $1/\lambda$ from below.

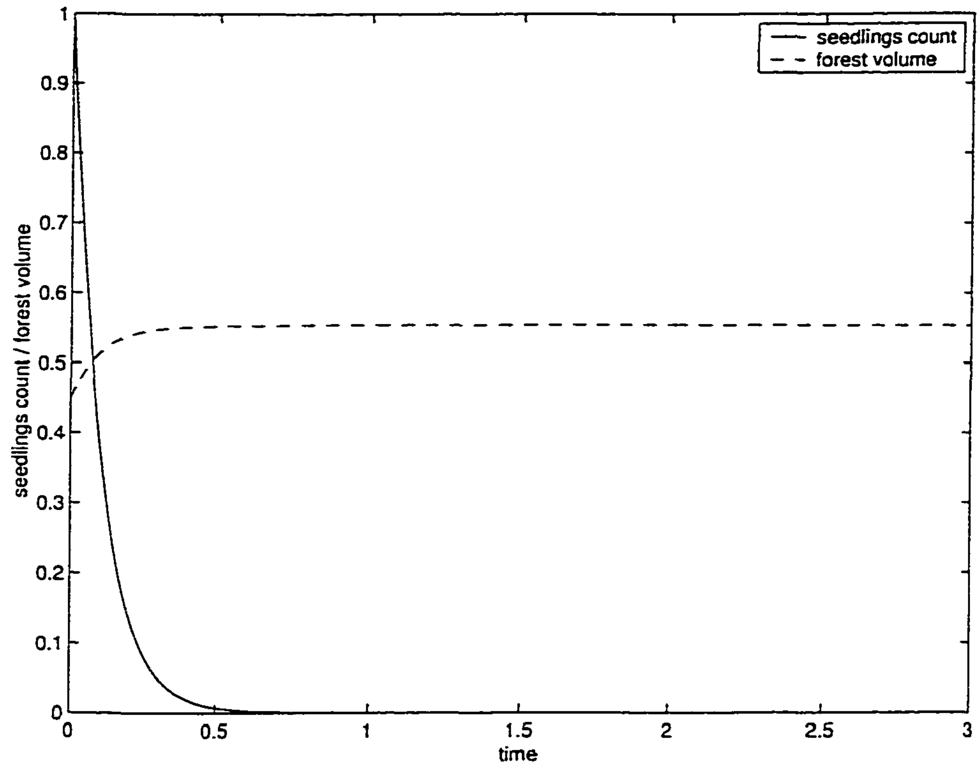

Fig.4e: Example 3, Case (E). seedling count s and forest volume v as functions of time θ, solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = s - \kappa v$ with parameters $\varepsilon = 0.1$, $\lambda = 2$, $\kappa = 0.5$, and initial conditions $s^0 = 1.0$, $v^0 = 0.45$. When the forest volume increases beyond $1/\lambda = 0.5$, the seedling count is positive. So, we arrive at Case (B) (compare with Fig. 4b). The forest volume approaches a limit value greater than $1/\lambda$.

Example 4: Linear tree growth

If individual trees grow linearly with age, and the seedling carrying capacity varies linearly with forest volume, we have

$$
\begin{aligned}
b(\alpha) &= \alpha + c \quad \text{for } \alpha \geq 0 \quad && \text{(size of tree of age } \alpha\text{,} \\
& && \text{where } c \text{ is a positive constant),} \\
k(v) &= 1 - \lambda v \quad \text{for } 0 \leq v \leq 1/\lambda \quad && \text{(seedling carrying capacity),} \\
k(v) &= 0 \quad \text{for } v > 1/\lambda \quad && \text{(seedlings vanish for } v > 1/\lambda\text{).}
\end{aligned}
\tag{103}
$$

Note that $k = 0$ means that the carrying capacity for seedlings is zero if the forest volume surpasses the critical value $1/\lambda$. However, because of the non-zero re-establishment time, seedlings can still exist even when $k = 0$.

From (30) and (34) it follows that $v(\theta)$ and the total number of trees $p(\theta)$ are given by

$$
\begin{aligned}
v(\theta) &= \int_0^\theta s(\alpha)\, e^{-(\theta-\alpha)}\,(\theta - \alpha + c)\, d\alpha \\
&\quad + e^{-\theta} \int_\theta^\infty \varphi(\alpha - \theta)\,(\alpha + c)\, d\alpha,
\end{aligned}
\tag{104}
$$

$$
\begin{aligned}
p(\theta) &= \int_0^\theta s(\alpha)\, e^{-(\theta-\alpha)} d\alpha + e^{-\theta} \int_\theta^\infty \varphi(\alpha - \theta)\, d\alpha \\
&= \int_0^\theta s(\alpha)\, e^{-(\theta-\alpha)} d\alpha + e^{-\theta} \int_0^\infty \varphi(\alpha)\, d\alpha.
\end{aligned}
\tag{105}
$$

Taking the derivative and using integration by parts, we obtain the differential equations

$$\begin{aligned}
v'(\theta) &= s(\theta)\,c - \int_0^\theta s(\alpha)\,e^{-(\theta-\alpha)}(\theta-\alpha+c)\,d\alpha \\
&\quad + \int_0^\theta s(\alpha)\,e^{-(\theta-\alpha)}d\alpha \\
&\quad - e^{-\theta}\left(\int_\theta^\infty \varphi(\alpha-\theta)(\alpha+c)\,d\alpha + \varphi(0)(\theta+c)\right) \\
&\quad - e^{-\theta}\int_\theta^\infty \varphi'(\alpha-\theta)(\alpha+c)\,d\alpha \\
&= s(\theta)\,c - \int_0^\theta s(\alpha)\,e^{-(\theta-\alpha)}(\theta-\alpha+c)\,d\alpha + \int_0^\theta s(\alpha)\,e^{-(\theta-\alpha)}d\alpha \\
&\quad + e^{-\theta}\left(-\int_\theta^\infty \varphi(\alpha-\theta)(\alpha+c)\,d\alpha + \int_0^\infty \varphi(\alpha)\,d\alpha\right) \\
&= cs(\theta) - v(\theta) + p(\theta), \qquad (106) \\
p'(\theta) &= s(\theta) - \int_0^\theta s(\alpha)\,e^{-(\theta-\alpha)}d\alpha - e^{-\theta}\int_0^\infty \varphi(\alpha)\,d\alpha \\
&= s(\theta) - p(\theta). \qquad (107)
\end{aligned}$$

In the integration by parts for (106) we used

$$\lim_{\alpha\to\infty}(\alpha+c)\,\varphi(\alpha-\theta) = 0, \qquad (108)$$

which requires the additional assumption that $\varphi(\alpha)$ satisfies an exponential estimate of the form

$$\varphi(\alpha) \le ce^{-\kappa\alpha}$$

for some positive constants c, $\kappa > 0$, or - alternatively - that $\varphi(\alpha)$ is eventually decreasing, that is decreasing for $\alpha \ge \alpha_0$ for a suitable $\alpha_0 > 0$.

We obtain the autonomous system of first order differential equations

$$\begin{aligned}
\varepsilon s' &= 1 - \lambda v - s \quad \text{for } 0 \le v \le 1/\lambda, \\
\varepsilon s' &= -s \qquad\qquad \text{for } v > 1/\lambda, \\
v' &= cs - v + p, \\
p' &= s - p,
\end{aligned} \tag{109}$$

with initial conditions

$$\begin{aligned}
s(0) &= s^0 = \varphi(0), \\
v(0) &= v^0 = \int_0^\infty \varphi(\alpha)(\alpha + c)\, d\alpha, \\
p(0) &= p^0 = \int_0^\infty \varphi(\alpha)\, d\alpha.
\end{aligned} \tag{110}$$

The initial conditions for v and p are obtained by setting $\theta = 0$ in (104). System (109) has exactly one steady state

$$s^* = \frac{1}{1 + \lambda(c+1)}, \tag{111}$$

$$v^* = \frac{c+1}{1 + \lambda(c+1)} = \frac{1}{\lambda + \frac{1}{c+1}} < \frac{1}{\lambda}, \tag{112}$$

$$p^* = \frac{1}{1 + \lambda(c+1)}. \tag{113}$$

The steady state is located in the interior of the region $0 \le v \le 1/\lambda$. Using matrix notation, system (109) can be written in this region as follows:

$$\begin{pmatrix} s' \\ v' \\ p' \end{pmatrix} = \begin{pmatrix} -1/\varepsilon & -\lambda/\varepsilon & 0 \\ c & -1 & 1 \\ 1 & 0 & -1 \end{pmatrix} \begin{pmatrix} s \\ v \\ p \end{pmatrix} + \begin{pmatrix} 1/\varepsilon \\ 0 \\ 0 \end{pmatrix}. \tag{114}$$

The eigenvalues of the matrix in (114) are solutions of the characteristic equation

$$X^3 + \left(2 + \frac{1}{\varepsilon}\right) X^2 + \left(1 + \frac{2 + c\lambda}{\varepsilon}\right) X + \frac{1 + \lambda + c\lambda}{\varepsilon} = 0. \qquad (115)$$

The Routh-Hurwitz conditions for all roots of any cubic polynomial

$$p(x) = x^3 + a_1 x^2 + a_2 x + a_3 \qquad (116)$$

to have negative real part are the following:

$$\begin{aligned} a_1 &> 0, \qquad (117) \\ a_3 &> 0, \\ a_1 a_2 - a_3 &> 0. \end{aligned}$$

In our case, since

$$\begin{aligned} a_1 &= 2 + \frac{1}{\varepsilon}, \qquad (118) \\ a_2 &= 1 + \frac{2 + c\lambda}{\varepsilon}, \\ a_3 &= \frac{1 + \lambda (c+1)}{\varepsilon}, \end{aligned}$$

the real parts of all eigenvalues are negative if and only if

$$\left(2 + \frac{1}{\varepsilon}\right)\left(1 + \frac{2 + c\lambda}{\varepsilon}\right) - \frac{1 + \lambda (c+1)}{\varepsilon} > 0, \qquad (119)$$

or, equivalently,

$$\lambda (c(\varepsilon + 1) - \varepsilon) > -2(\varepsilon + 1)^2. \qquad (120)$$

For $c \geq \varepsilon / (1 + \varepsilon)$ the real parts of the eigenvalues are negative for all values of the positive parameter λ. For $c < \varepsilon / (1 + \varepsilon)$, the real parts of the eigenvalues are negative for

$$\lambda < \frac{2(1+\varepsilon)}{\frac{\varepsilon}{1+\varepsilon} - c}. \qquad (121)$$

To find asymptotic approximations of the eigenvalues as $\varepsilon \to 0$, insert the representation

$$X = A_{-1}\varepsilon^{-1} + A_0 + A_1\varepsilon + A_2\varepsilon^2 + \ldots \tag{122}$$

into the characteristic equation (115). This method results in the approximations

$$\begin{aligned} X_1 &= -1/\varepsilon + O(1), \\ X_2 &= -1 - \left(c\lambda + \sqrt{c^2\lambda^2 - 4\lambda}\right)/2 + O(\varepsilon), \\ X_2 &= -1 - \left(c\lambda - \sqrt{c^2\lambda^2 - 4\lambda}\right)/2 + O(\varepsilon). \end{aligned} \tag{123}$$

In the region $v > 1/\lambda$ (where the seedling carrying capacity is zero), solve the system

$$\begin{aligned} \varepsilon s' &= -s, \\ v' &= -v + p, \\ p' &= s - p, \end{aligned} \tag{124}$$

with initial conditions (110). The explicit solution for $s^0 > 0$ is

$$\begin{aligned} s(\theta) &= s^0 e^{-\theta/\varepsilon}, \\ v(\theta) &= \alpha_1 e^{-\theta} + \alpha_2 e^{-\frac{\theta}{\varepsilon}}, \\ p(\theta) &= \beta_1 e^{-\theta} + \beta_2 e^{-\frac{\theta}{\varepsilon}}, \end{aligned} \tag{125}$$

with constants

$$\begin{aligned}
\alpha_1 &= v^0 + \frac{\varepsilon}{1-\varepsilon} p^0, \\
\alpha_2 &= -\frac{\varepsilon}{1-\varepsilon} p^0, \\
\beta_1 &= p^0 + \frac{\varepsilon}{1-\varepsilon} s^0, \\
\beta_1 &= -\frac{\varepsilon}{1-\varepsilon} s^0.
\end{aligned} \tag{126}$$

For $s^0 = 0$, however, the solution of (124) is given by

$$\begin{aligned}
v(\theta) &= \left(\theta p^0 + v^0\right) e^{-\theta}, \\
p(\theta) &= p^0 e^{-\theta}.
\end{aligned} \tag{127}$$

Fig. 5a - 5f show how the model behaves for some particular choices of parameter values and initial conditions.

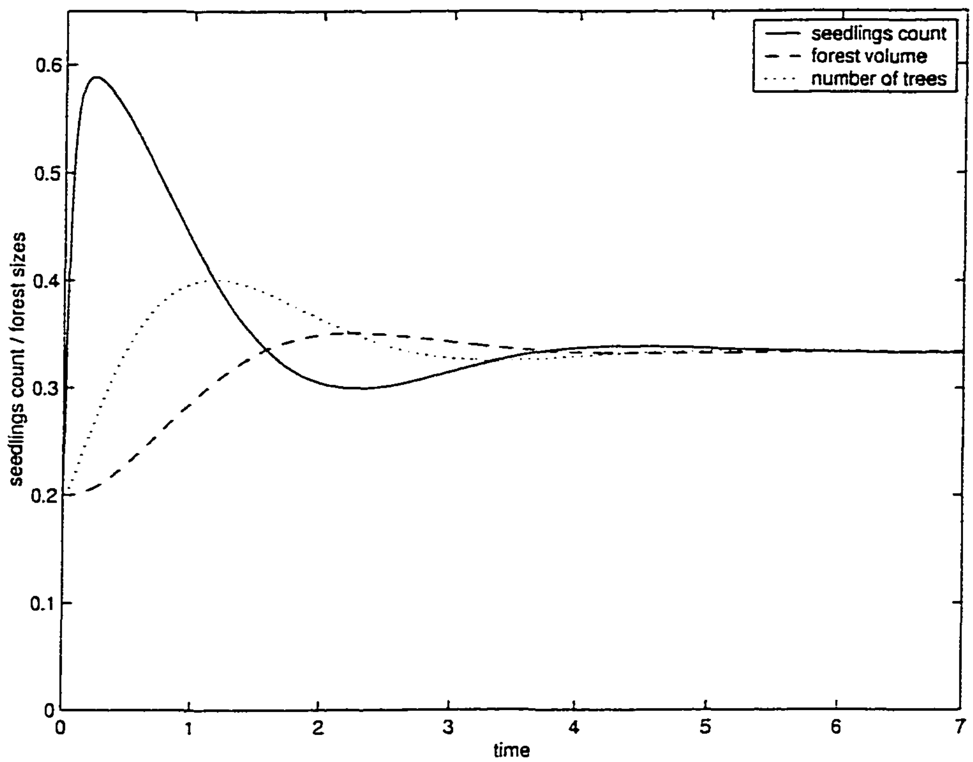

Fig.5a: Example 4. seedling count s, forest volume v and number of trees p as functions of time θ, obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = -v + p$, $p' = s - p$ with parameters $\varepsilon = 0.05$, $\lambda = 2$, and initial conditions $s^0 = v^0 = p^0 = 0.2$.

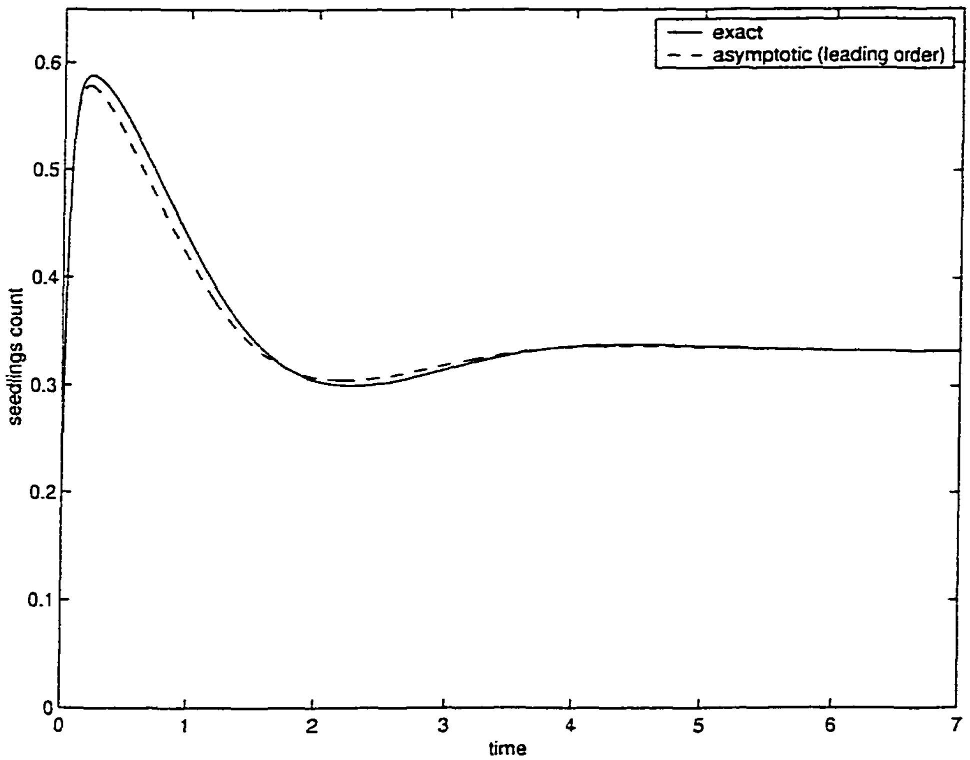

Fig. 5b: Example 4. seedling count as a function of time obtained for the same parameters as in Fig. 5a. One graph corresponds to exact solution, the other graph is obtained by leading order approximation of the eigenvalues of the system.

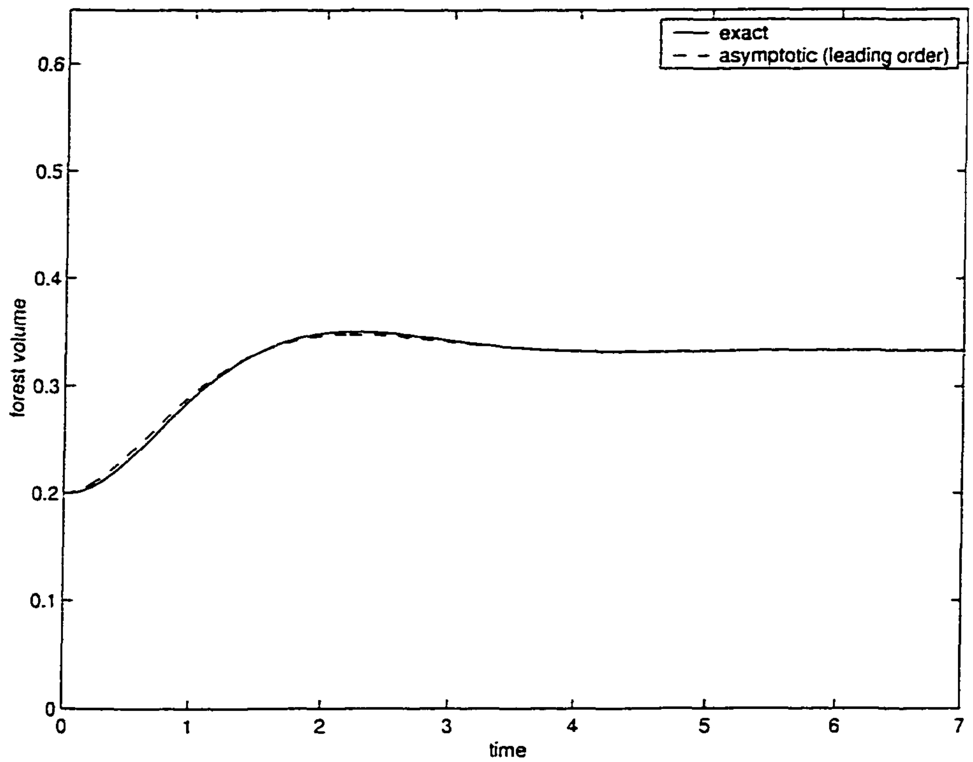

Fig. 5c: Example 4. Forest volume as a function of time, obtained by using the same parameters as in Fig. 5a. One graph represents exact solution, the other graph is obtained by leading order approximation of the eigenvalues of the system.

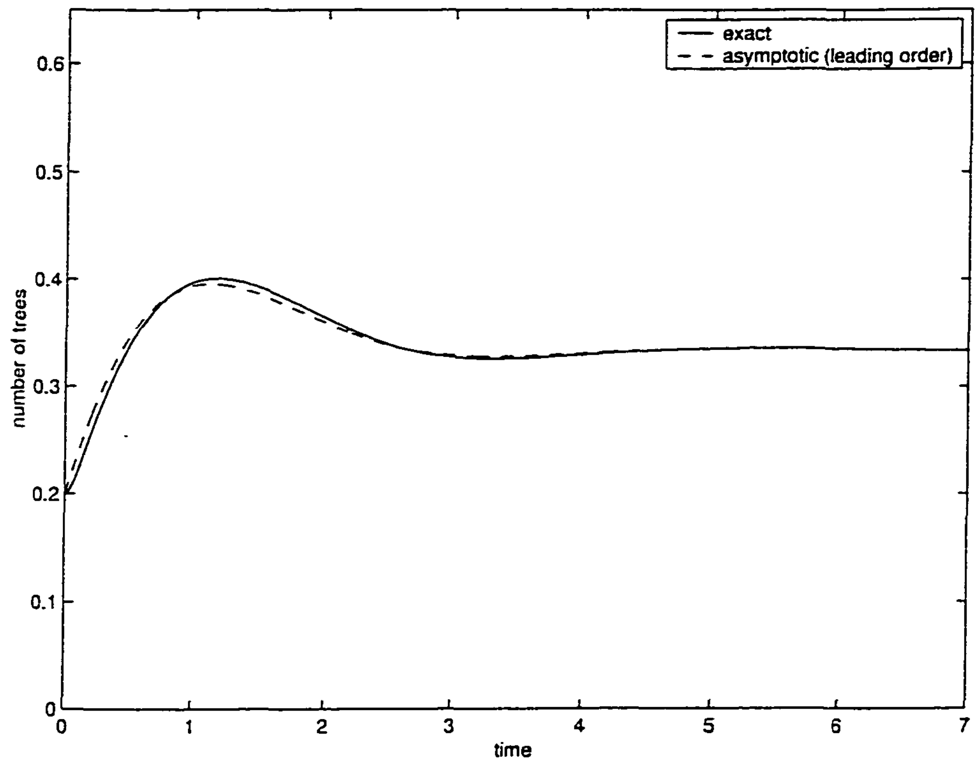

Fig. 5d: Example 4. Number of trees as a function of time, obtained using the same parameters as in Fig. 5a. One graph is exact solution, the other represents solution obtained by leading order approximation of the eigenvalues of the system.

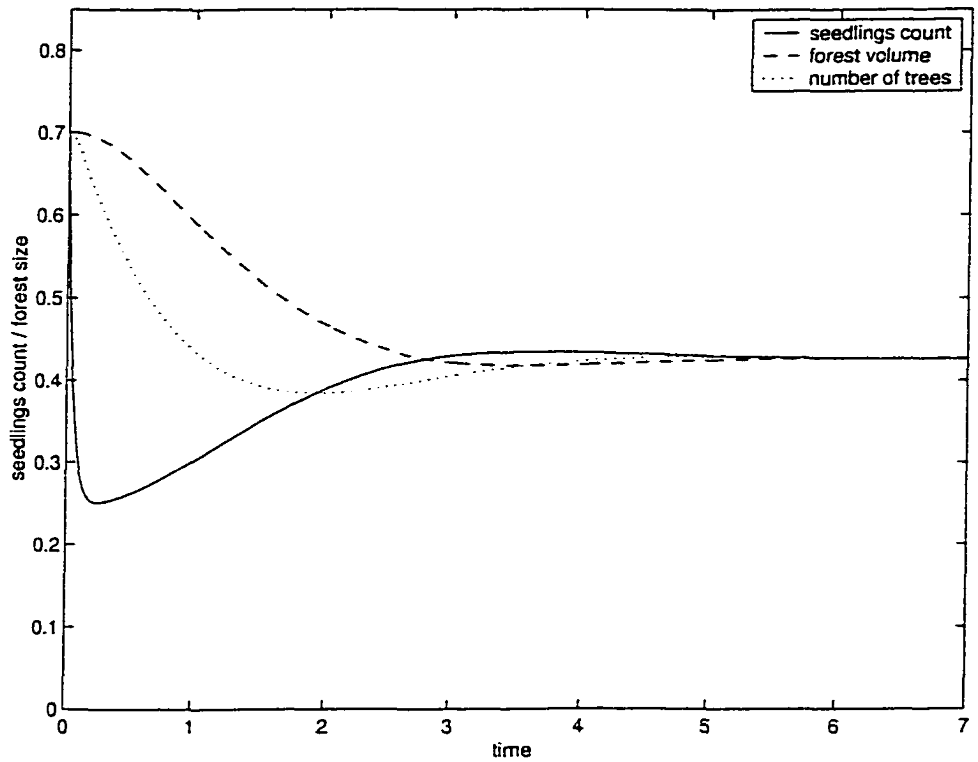

Fig.5e: Example 4. seedling count s, forest volume v and number of trees p as functions of time θ are shown. These functions are obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = -v + p$, $p' = s - p$ with parameters $\varepsilon = 0.05$, $\lambda = 2$ and initial conditions $s^0 = v^0 = p^0 = 0.7$.

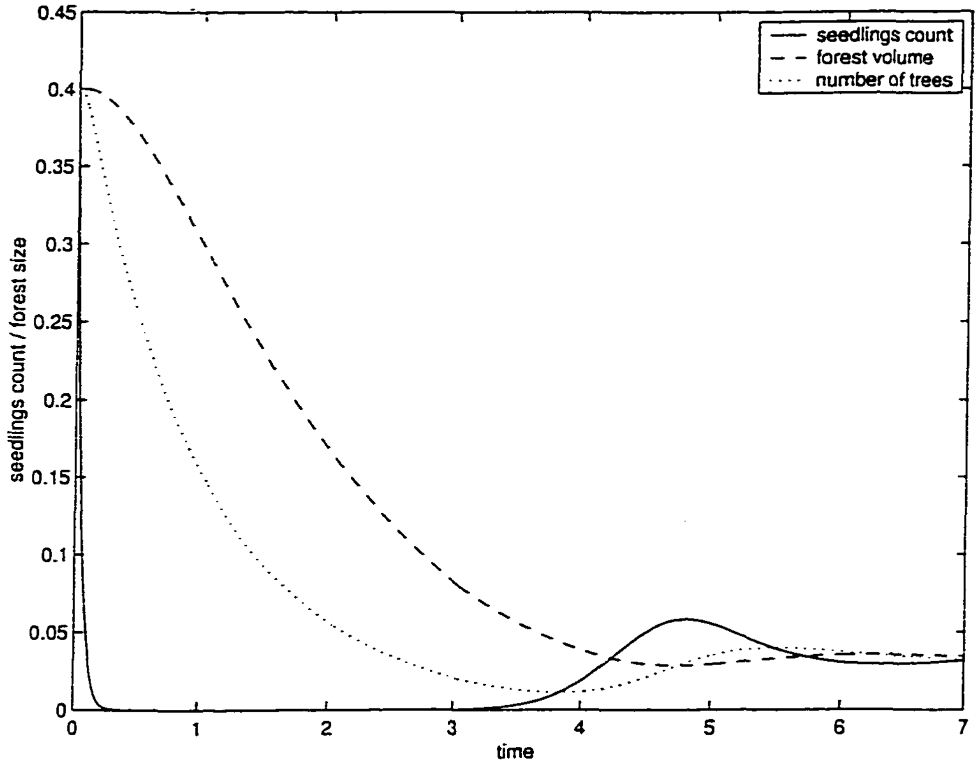

Fig.5f: Example 4. seedling count s, forest volume v and number of trees p as functions of time θ are shown. They are obtained by solving the system $\varepsilon s' = \max(1 - \lambda v, 0) - s$, $v' = -v + p$, $p' = s - p$ with parameters $\varepsilon = 0.05$, $\lambda = 100$, and initial conditions $s^0 = v^0 = p^0 = 0.4$.

5 Models with decreasing mortality rate of trees

For many tree species observations have shown that older trees in a forest of low density are less vulnerable to competition for resources and to diseases than younger trees in a high-density forest. This phenomenon can be modeled by a tree density equation which in rescaled form can be written as

$$\frac{\partial n}{\partial \theta} + \frac{\partial n}{\partial \alpha} = -n^p(\theta, \alpha), \tag{128}$$

with a constant $p > 1$. The initial and boundary conditions are of the form:

$$\begin{aligned} n(0,\alpha) &= \phi(\alpha), \\ n(\theta,0) &= s(\theta). \end{aligned} \tag{129}$$

As in the case of the tree density equation with constant death rate, the method of characteristics can be used to represent the solution in terms of the initial age distribution and seedling function:

$$\begin{aligned} n(\theta,\alpha) &= \left(\frac{\varphi^{p-1}(\alpha-\theta)}{1+\theta(p-1)\varphi^{p-1}(\alpha-\theta)}\right)^{1/(p-1)} \quad \text{for } 0 \le \theta \le \alpha, \\ n(\theta,\alpha) &= \left(\frac{s^{p-1}(\theta-\alpha)}{1+\alpha(p-1)s^{p-1}(\theta-\alpha)}\right)^{1/(p-1)} \quad \text{for } 0 \le \alpha \le \theta. \end{aligned} \tag{130}$$

Let us assume that the seedling function fulfills an initial value problem of type (67):

$$\begin{aligned} \varepsilon\frac{ds}{d\theta} &= k(v(\theta)) - s(\theta), \\ s(0) &= s^0. \end{aligned} \tag{131}$$

It can be easily seen that the problem (128), (129), (131) is also a particular case of the general statement (13). By substitution of (130) into (131), we obtain an integro-differential equation for the seedling function. This equation can be solved by the boundary function method or numerically. The procedure is similar to that performed for the case of constant mortality rate of trees. For linear seedling carrying capacity

$$\begin{aligned} k(v) &= 1-\lambda v = 1-\lambda \int_0^\infty n(\theta,\alpha)\, b(\alpha)\, d\alpha \quad \text{for } 0 \le v \le 1/\lambda, \\ k(v) &= 0 \qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{for } v \ge 1/\lambda, \end{aligned} \tag{132}$$

we obtain the seedling problem

$$\begin{aligned} \varepsilon\frac{ds}{d\theta} &= 1-s(\theta) \\ &\quad -\lambda\int_0^\theta \left(\frac{s^{p-1}(\theta-\alpha)}{1+\alpha(p-1)\,s^{p-1}(\theta-\alpha)}\right)^{1/(p-1)} b(\alpha)\, d\alpha \\ &\quad -\lambda\int_\theta^\infty \left(\frac{\varphi^{p-1}(\alpha-\theta)}{1+\theta(p-1)\,\varphi^{p-1}(\alpha-\theta)}\right)^{1/(p-1)} b(\alpha)\, d\alpha, \end{aligned} \tag{133}$$

for $0 \le v \le 1/\lambda$, and

$$\varepsilon\frac{ds}{d\theta} = -s(\theta), \tag{134}$$

for $v \ge 1/\lambda$,with initial condition

$$s(0) = s^0. \tag{135}$$

Example 5:

For linear tree growth $b(\alpha) = \alpha$, linear seedling carrying capacity and parameter $p = 1.5$, (133) becomes

$$\varepsilon\frac{ds}{d\theta} = 1-\lambda\int_0^\theta \frac{\alpha s(\theta-\alpha)}{\left(1+\frac{\alpha}{2}\sqrt{s(\theta-\alpha)}\right)^2} d\alpha - \lambda v_{old}(\theta) - s(\theta), \tag{136}$$

$$s(0) = s^0. \tag{137}$$

The volume of the old forest is -

$$
\begin{aligned}
v_{old}(\theta) &= \int_\theta^\infty n(\theta,\alpha)\, b(\alpha)\, d\alpha \\
&= \int_\theta^\infty \frac{\alpha\varphi(\alpha-\theta)}{\left(1+\frac{\theta}{2}\sqrt{\varphi(\alpha-\theta)}\right)^2} d\alpha \\
&= \int_0^\infty \frac{(u+\theta)\,\varphi(u)}{\left(1+\frac{\theta}{2}\sqrt{\varphi(u)}\right)^2} du,
\end{aligned}
\tag{138}
$$

and the number of trees in the old forest is

$$
\begin{aligned}
p_{old}(\theta) &= \int_\theta^\infty n(\theta,\alpha)\, d\alpha \\
&= \int_\theta^\infty \frac{\varphi(\alpha-\theta)}{\left(1+\frac{\theta}{2}\sqrt{\varphi(\alpha-\theta)}\right)^2} d\alpha \\
&= \int_0^\infty \frac{\varphi(u)}{\left(1+\frac{\theta}{2}\sqrt{\varphi(u)}\right)^2} du.
\end{aligned}
\tag{139}
$$

In Theorem 14 of the Appendix it is shown that both volume and number of trees of the old forest converge to zero as $\theta \to \infty$ if the initial age distribution has an exponential estimate of the form

$$
\varphi(\alpha) \le ce^{-\kappa\alpha} \text{ for } 0 \le \alpha < \infty, \tag{140}
$$

with some positive constants c and κ. In this case we can show by an indirect proof that there is no steady state s^* of (136):

$$
\begin{aligned}
0 &= 1-\lambda\int_0^\infty \frac{\alpha s^*}{\left(1+\frac{\alpha}{2}\sqrt{s^*}\right)^2} d\alpha - \lambda \lim_{\theta\to\infty} v_{old}(\theta) - s^* \\
&= 1-\lambda\int_0^\infty \frac{\alpha s^*}{\left(1+\frac{\alpha}{2}\sqrt{s^*}\right)^2} d\alpha - s^*.
\end{aligned}
\tag{141}
$$

Indeed, for $s^* = 0$ the integrand in this equation is zero, which yields the contradiction $0 = 1$. For $s^* > 0$ calculate the integral by substitution

$$
u = 1 + \frac{\alpha}{2}\sqrt{s^*} \tag{142}
$$

and obtain a contradiction:

$$\begin{aligned} 0 &= 1-\lambda\int_1^\infty \frac{2\,(u-1)\,/\sqrt{s^*}}{u^2}s^*\frac{2du}{\sqrt{s^*}}-s^* \\ &= 1-4\lambda\left(\int_1^\infty\frac{du}{u}-\int_1^\infty\frac{du}{u^2}\right)-s^* \\ &= 1-4\lambda\left(\int_1^\infty\frac{du}{u}+1\right)-s^* \\ &= -\infty, \end{aligned} \tag{143}$$

since the last integral diverges. Fig. 6a and 6b show the disappearance of seedlings after a finite time period for the initial age distribution

$$\varphi(\alpha)=\frac{1}{4}e^{-\alpha}. \tag{144}$$

In this example the old forest volume for $\theta > 0$ is given by

$$\begin{aligned} v_{old}(\theta) &= \int_\theta^\infty \frac{\alpha\frac{1}{4}e^{-(\alpha-\theta)}}{\left(1+\frac{\theta}{4}e^{-\frac{\alpha-\theta}{2}}\right)^2}d\alpha \\ &= \frac{1}{4}\int_0^\infty \frac{(u+\theta)\,e^{-u}}{\left(1+\frac{\theta}{4}e^{-\frac{u}{2}}\right)^2}du \\ &= \frac{1}{4}\int_0^\infty \frac{ue^{-u}}{\left(1+\frac{\theta}{4}e^{-\frac{u}{2}}\right)^2}du+\frac{1}{4}\theta\int_0^\infty\frac{e^{-u}}{\left(1+\frac{\theta}{4}e^{-\frac{u}{2}}\right)^2}du \\ &= \int_0^1\frac{(-\ln y)\,y}{\left(1+\frac{\theta}{4}y\right)^2}dy+\frac{\theta}{2}\int_0^1\frac{y}{\left(1+\frac{\theta}{4}y\right)^2}dy \\ &= \int_0^1\frac{\left(\frac{\theta}{2}-\ln y\right)y}{\left(1+\frac{\theta}{4}y\right)^2}dy\,, \end{aligned} \tag{145}$$

and

$$v_{old}(0)=\int_0^\infty\frac{\alpha\frac{1}{4}e^{-\alpha}}{1^2}d\alpha=\frac{1}{4}. \tag{146}$$

Here we used substitutions

$$\begin{aligned} u &= \alpha-\theta, \\ y &= e^{-u/2} \end{aligned} \tag{147}$$

in order to obtain a proper integral that can be approximated numerically, e.g. with Simpson's method. Note that the integrand is bounded on the interval $[0,1]$ with limit 0 as $y \to 0$ from the right.

With the same substitutions, the number of trees in old forest is given by

$$\begin{aligned} p_{old}(\theta) &= \int_\theta^\infty \frac{\frac{1}{4}e^{-(\alpha-\theta)}}{\left(1+\frac{\theta}{4}e^{-\frac{\theta-\alpha}{2}}\right)^2}d\alpha \\ &= \frac{1}{4}\int_0^\infty \frac{e^{-u}}{\left(1+\frac{\theta}{4}e^{-\frac{u}{2}}\right)^2}du \\ &= \frac{1}{2}\int_0^1 \frac{y}{\left(1+\frac{\theta}{4}y\right)^2}dy \\ &= \frac{8}{\theta^2}\ln\left(1+\frac{\theta}{4}\right) - \frac{2}{\theta\left(1+\frac{\theta}{4}\right)} \text{ for } \theta > 0, \end{aligned} \tag{148}$$

and

$$p_{old}(0) = \int_0^\infty \frac{1}{4}e^{-\alpha}d\alpha = \frac{1}{4}. \tag{149}$$

With L'Hôpital's rule it can be shown that the functions $v_{old}(\theta)$ and $p_{old}(\theta)$ are continuous at $\theta = 0$.

To solve (136), using the boundary function method, insert the representation

$$s(\theta) = \overline{s_0}(\theta) + \Pi_0 s(\theta/\varepsilon) + O(\varepsilon) \tag{150}$$

into (136), and obtain the system

$$0 = 1 - \lambda\int_0^\theta \frac{\alpha\overline{s_0}(\theta-\alpha)}{\left(1+\frac{\alpha}{2}\sqrt{\overline{s_0}(\theta-\alpha)}\right)^2}d\alpha - \lambda v_{old}(\theta) - \overline{s_0}(\theta), \tag{151}$$

$$\frac{d\Pi_0 s}{d\tau} = -\Pi_0 s(\tau), \tag{152}$$

with conditions

$$\overline{s_0}(0) + \Pi_0 s(0) = s^0, \tag{153}$$

$$\lim_{\tau\to\infty} \Pi_0 s(\tau) = 0.$$

Integral equation (151) can be solved numerically, discretizing the integral by means of the trapezoid method. The solution of (152) is explicitly given as

$$\Pi_0 s(\tau) = \left(s^0 - \overline{s_0}(0)\right) e^{-\tau}.$$

Fig. 6a - 6d show graphs for seedling count, forest volume, and number of trees.

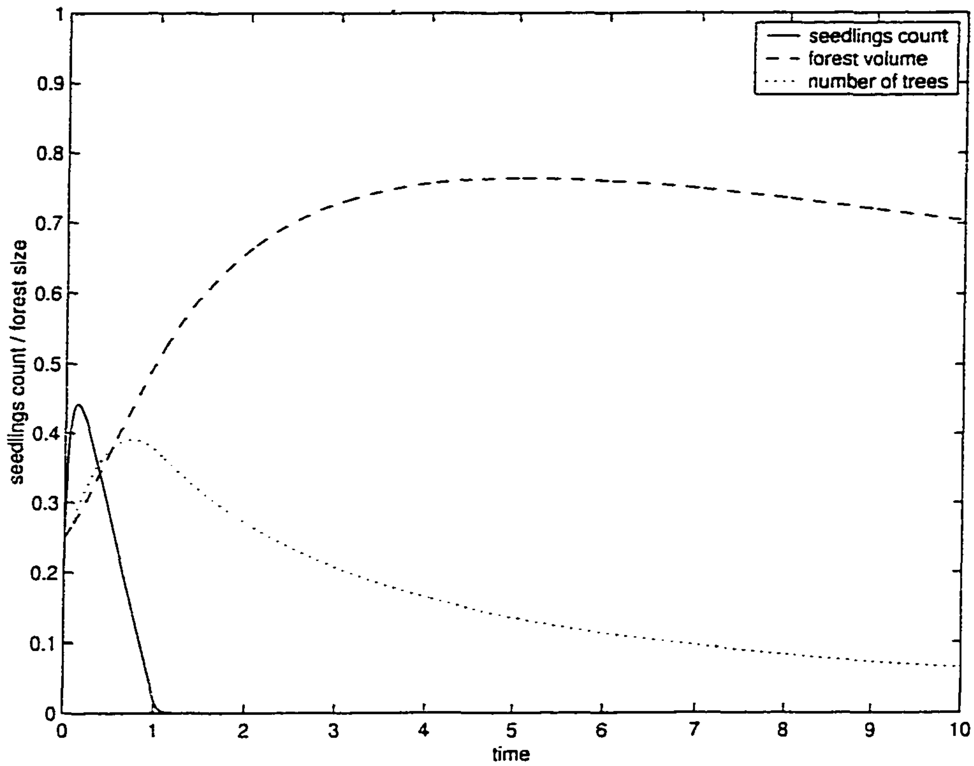

Fig. 6a: Example 5. seedling count, forest volume and number of trees as functions of time are shown. These functions are obtained by solving age density equation $\partial n/\partial\theta + \partial n/\partial\alpha = n^p$ and seedling equation $\varepsilon\frac{ds}{d\theta} = \max\left(1-\lambda\int_0^\infty n(\theta,\alpha)\,b(\alpha)\,d\alpha, 0\right) - s$ with parameters $p = 1.5$, $\varepsilon = .05$, $\lambda = 2$, tree growth function $b(\alpha) = \alpha$, and initial age distribution $n(0,\alpha) = 0.25e^{-\alpha}$.

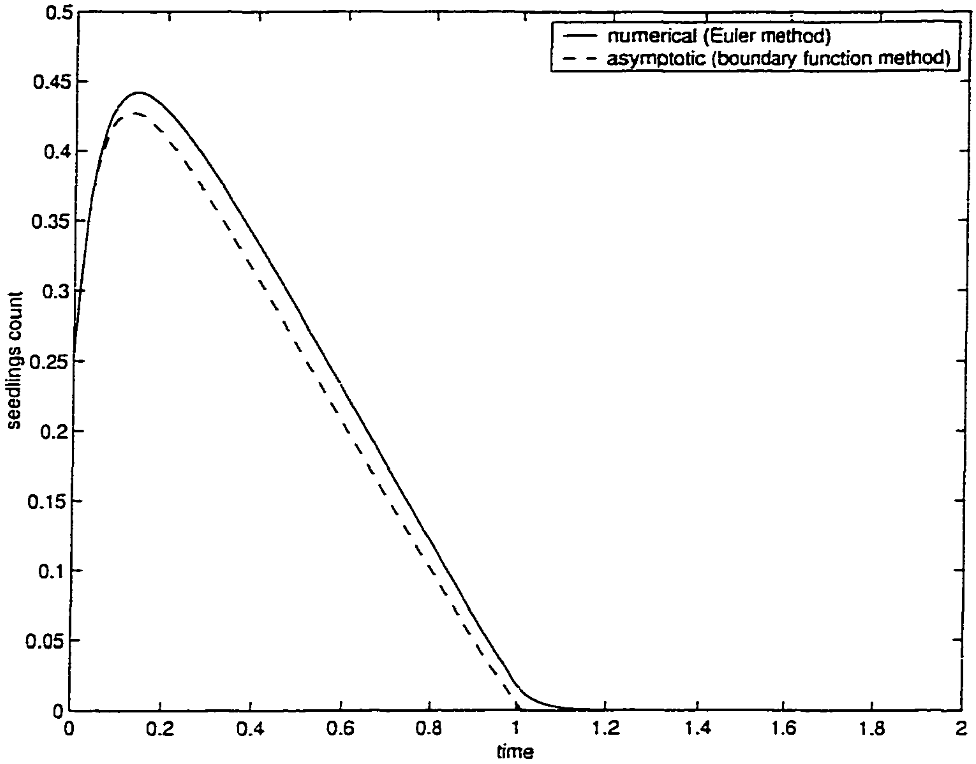

Fig. 6b: Example 5. seedling count as a function of time obtained for the same parameter values as in Fig. 6a. One graph is obtained by numerical approximation with Euler difference method (time stepsize 0.01), while the other graph represents the leading order boundary function approximation calculated numerically using the 0.01-stepsize trapezoid method.

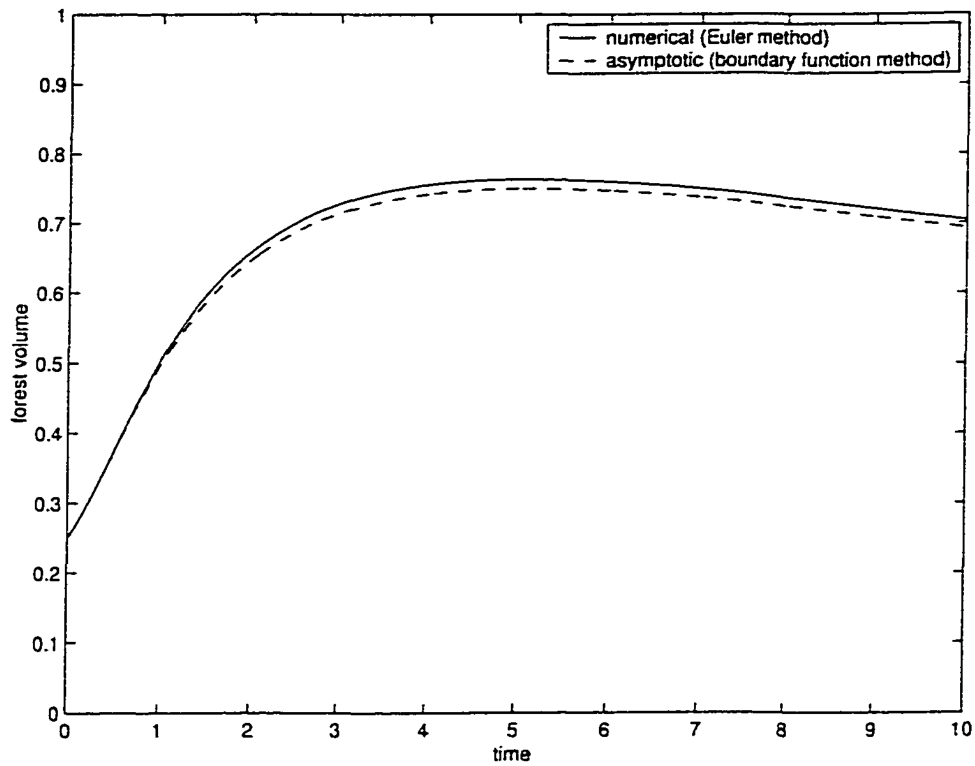

Fig. 6c: Example 5. Forest volume as a function of time obtained for the same parameter values as in Fig. 6a. The graphs represent a solution computed by Euler difference method and an approximation of the solution constructed by the boundary function method, respectively.

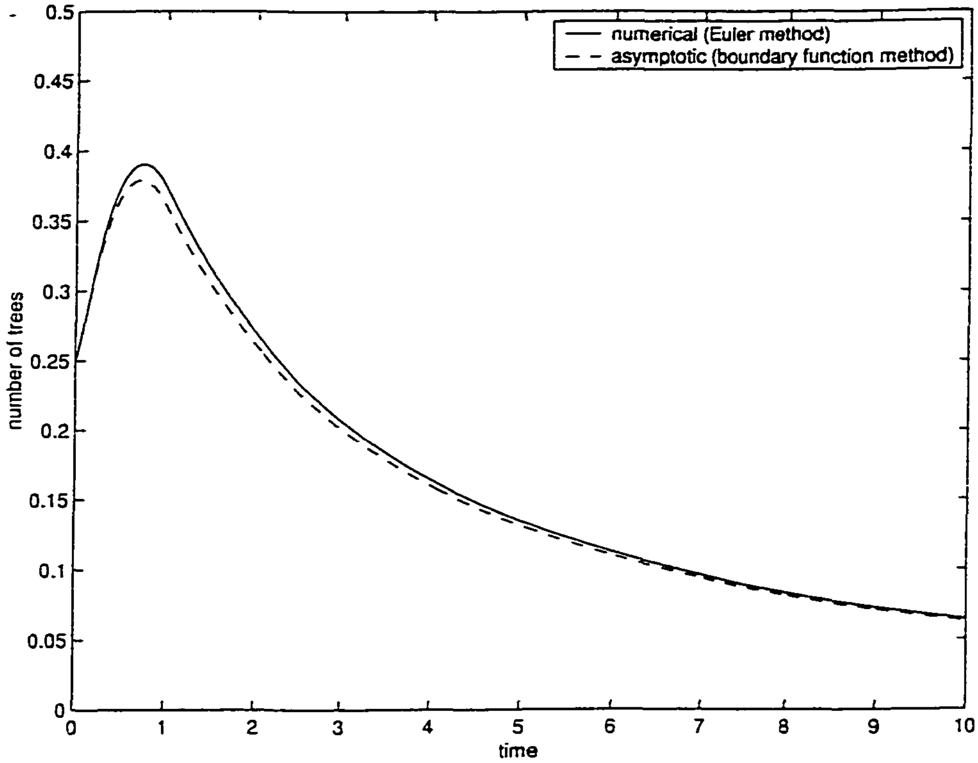

Fig. 6d: Example 5. Number of trees as a function of time obtained for the same parameter values as in Fig. 6a. One graph is obtained by numerical integration using Euler difference scheme, the other represents an approximation constructed using the boundary function method.

Part II

Existence, uniqueness, and error analysis of a particular model

In this part we use a unifying approach, Banach's fixed point theorem, to establish existence and uniqueness of the solution of the problem, convergence of a numerical scheme for solving the problem, and for proving the theorem on estimation of the remainder term for asymptotic approximation of the solution of the problem. These results provide the mathematical basis for the next steps of the analysis of age structure models related to explicit determination of functions and parameters entering the models by fitting the solutions to data from real field measurements using nonlinear least squares methods. Results of such nonlinear least squares fitting procedures applied to particular age structure models will be published elsewhere.

This part is organized as follows: Section 6 formulates the initial value problem for the seedling density, and presents the integral equation for the quasi-equilibrium solution. Section 7 proves existence and uniqueness of the solution of both above mentioned problems and derive some of their properties. Linear convergence of the numerical solution is shown in section 8. Section 9 contains the description of the algorithm for construction of an asymptotic solution using the boundary function method and the estimation of the remainder, which is the proof that the norm of the difference of asymptotic solution and exact solution is of order $O(\varepsilon)$. Some auxiliary results can be found in the Appendix.

6 Mathematical model

For a particular class of models introduced in [4], the integro-differential equation for seedling density $s(t)$ as a function of time, has the (rescaled) form

$$\varepsilon s'(t) = -s(t) + \max(0, 1 - \lambda v(t)), \tag{154}$$

$$v(t) = v_{old}(t) + \int_0^t b(a) e^{-a} s(t-a)\, da, \tag{155}$$

$$s(0) = s^0. \tag{156}$$

In (154), $0 < \varepsilon \ll 1$ is a small parameter, which represents the ratio of seedling re-establishment time and the average life span of a tree. The *competition factor* λ measures how competition from other seedlings and older trees inhibits the number of seedlings. Function $v(t)$ represents the total volume of the forest as a function of time. The *old forest volume* $v_{old}(t)$ describes the total volume of the trees already existing at the initial time, whereas the integral $\int_0^t b(a) e^{-a} s(t-a)\, da$ is the total volume of the trees that grew from seedlings after initial time. The *size function* $b(a)$ describes the average size of individual trees of age a. Depending on the particular model used, the size function represents either height, basal area, stem volume or crown area. The model assumes a constant relative death rate of trees, which has been rescaled to 1 and is reflected in the factor e^{-a} in the integral in (155). The term $\max(0, 1 - \lambda v(t))$ corresponds to the seedling quasi-equilibrium at time t, which is approached exponentially as expressed in equation (154). When the forest volume $v(t)$ increases above the *critical volume*

$$v_{crit} = 1/\lambda, \tag{157}$$

the seedling quasi-equilibrium becomes zero, and seedling density $s(t)$ decreases exponentially at per-capita rate $1/\varepsilon$. At the transition point where $v = v_{crit}$ a discontinuity of the second derivative of the seedling density occurs.

Let us consider problem (154) - (156) in a finite time interval $0 \leq t \leq T$. With notations

$$\begin{aligned} f(a) &= b(a)\, e^{-a}, & (158) \\ g(t) &= 1 - \lambda v_{old}(t), & (159) \\ Ks(t) &= g(t) - \lambda \int_0^t f(a)\, s(t-a)\, da, & (160) \\ K^+ s(t) &= \max(0, Ks(t)), & (161) \end{aligned}$$

the initial value problem can be written as

$$\begin{aligned} \varepsilon s'(t) &= -s(t) + K^+ s(t) \quad \text{for } 0 \leq t \leq T, & (162) \\ s(0) &= s^0. & (163) \end{aligned}$$

We also analyse the *quasi-equilibrium problem* associated with (162), (163) which is obtained by replacing the derivative in (162) by zero and omitting condition (163):

$$0 = -s(t) + K^+ s(t) \quad \text{for } 0 \leq t \leq T. \tag{164}$$

Assuming that the old forest volume function $v(t)$ and the size function $b(t)$ are continuously differentiable, the functions $f(t)$ and $g(t)$ defined in (158) and

(159) are also continuously differentiable, and the operators K and K^{+} map the space of continuous functions on the interval $[0,T]$ into itself. This space, which we denoted by $C([0,T])$, is a Banach space with the maximum norm

$$\|s\| = \max_{0 \leq t \leq T} |s(t)|. \tag{165}$$

Note that the solutions of the quasi-equilibrium problem (164) are the fixed points of the operator K^{+} in the Banach space $C([0,T])$. In what follows we often utilize the identity

$$\int_0^t f(t-a)\, s(a)\, da = \int_0^t f(a)\, s(t-a)\, da, \tag{166}$$

which results from the substitution $a \to t-a$ in the integral.

7 Existence, uniqueness, and properties of solutions

Theorem 1 *The quasi-equilibrium problem (164) has exactly one solution* $s_{qe}^{*}(t)$ *in* $C([0,T])$. *This solution is non-negative, bounded from above by* 1, *and satisfies a Lipschitz condition of order* 1 *with Lipschitz constant*

$$C_{qe} = \|g'\| + \lambda \|s\| (T \|f'\| + \|f\|). \tag{167}$$

Proof: To show that operator $K^{+} : C([0,T]) \to C([0,T])$ has a unique fixed point, consider any two functions $s_1, s_2 \in C([0,T])$ and any $t \in [0,T]$. By virtue of (160), (161), and Corollary 1 (see Appendix), we have the estimate

$$\begin{aligned}\left|K^{+}s_1(t)-K^{+}s_2(t)\right| &= \left|\max(0,Ks_1(t))-\max(0,Ks_2(t))\right| \qquad (168)\\ &\le \left|Ks_1(t)-Ks_2(t)\right|\\ &\le \lambda\int_0^t f(t-a)\left|s_1(a)-s_2(a)\right|da\\ &\le \|s_1-s_2\|\,\lambda\,\|f\|\,t.\end{aligned}$$

Using the same estimate (168) for $K^{+}s_1$ and $K^{+}s_2$ in the place of s_1 and s_2, respectively, yields

$$\begin{aligned}\left|K^{+}s_1(t)-K^{+}s_2(t)\right| &\le \lambda\int_0^t f(t-a)\left|K^{+}s_1(a)-K^{+}s_2(a)\right|da \qquad (169)\\ &\le \lambda\int_0^t f(t-a)\,\|s_1-s_2\|\;\lambda\;\|f\|\;a\,da\\ &\le \|s_1-s_2\|\,\frac{(\lambda\|f\|)^2t^2}{2},\end{aligned}$$

and similarly, by induction over n,

$$\left|(K^{+})^n s_1(t)-(K^{+})^n s_2(t)\right| \le \|s_1-s_2\|\,\frac{(\lambda\|f\|)^n t^n}{n!} \qquad (170)$$

for $n=0,1,2,\ldots$. Since the infinite series

$$\sum_{n=0}^{\infty}\frac{(\lambda\|f\|)^n T^n}{n!}=\exp(\lambda\|f\|T) \qquad (171)$$

converges, we conclude that

$$\lim_{n\to\infty}\frac{(\lambda\|f\|)^n T^n}{n!}=0. \qquad (172)$$

Therefore there exists N such that

$$\frac{(\lambda\|f\|)^N T^N}{N!}<\frac{1}{2}. \qquad (173)$$

From (170) it follows that

$$\left\| \left(K^{+}\right)^{N} s_1 - \left(K^{+}\right)^{N} s_2 \right\| \leq \frac{1}{2} \left\| s_1 - s_2 \right\|. \tag{174}$$

Hence $K\left(^{+}\right)^{N} : C\left([0,T]\right) \to C\left([0,T]\right)$ is a contraction mapping. By a corollary to Banach's fixed point theorem, the mapping K^{+} has exactly one fixed point $s_{qe}^{*}(t)$ in $C\left([0,T]\right)$. This fixed point is the unique solution of the quasi-equilibrium problem (164).

The function $s_{qe}^{*}(t)$ is non-negative, since

$$s_{qe}^{*}(t) = \max\left(0, K\left(s_{qe}^{*}(t)\right)\right) \geq 0. \tag{175}$$

It is bounded from above by 1, since by virtue of (159) and (160),

$$\begin{aligned} s_{qe}^{*}(t) &= \max\left(0, K\left(s_{qe}^{*}(t)\right)\right) \\ &\leq K\left(s_{qe}^{*}(t)\right) \\ &= 1 - \lambda\left(v_{old}(t) + \int_0^t f(a)\, s(t-a)\, da\right) \\ &\leq 1. \end{aligned} \tag{176}$$

The fact that $s_{qe}^{*}(t)$ satisfies a Lipschitz condition of order 1, follows from (164) and Corollary 1 (see Appendix). Indeed, for any $t_1, t_2 \in [0,T]$, we have

$$\begin{aligned}
\left|s_{qe}^*(t_1) - s_{qe}^*(t_2)\right| &= \left|\max\left(0, Ks_{qe}^*(t_1)\right) - \max\left(0, Ks_{qe}^*(t_2)\right)\right| \qquad (177)\\
&\leq \left|Ks_{qe}^*(t_1) - Ks_{qe}^*(t_2)\right| \\
&\leq |g(t_1) - g(t_2)| \\
&\quad +\lambda\left|\int_0^{t_1} f(t_1 - a)\, s(a)\, da - \int_0^{t_2} f(t_2 - a)\, s(a)\, da\right| \\
&\leq \|g'\|\,|t_1 - t_2| \\
&\quad +\lambda\left|\int_0^{t_2} \left(f(t_1 - a) - f(t_2 - a)\right) s(a)\, da - \int_{t_1}^{t_2} f(t_1 - a)\, s(a)\, da\right| \\
&\leq \|g'\|\,|t_1 - t_2| \\
&\quad +\lambda T\,\|f'\|\,\|s\|\,|t_1 - t_2| + \lambda\,\|f\|\,\|s\|\,|t_1 - t_2| \\
&= \left(\|g'\| + \lambda\,\|s\|\,(T\,\|f'\| + \|f\|)\right)|t_1 - t_2|. \qquad \blacksquare
\end{aligned}$$

Theorem 2 *The initial-value problem (162), (163) has exactly one solution* $s^*(t)$ *in* $C^1([0,T])$*. This solution is non-negative and bounded from above by* 1*. Its derivative is bounded in absolute value by* $1/\varepsilon$*, and it satisfies a Lipschitz condition of order* 1 *with Lipschitz constant*

$$C = \frac{\|(s^*)'\| + \|g'\| + \lambda\,\|s\|\,(T\,\|f'\| + \|f\|)}{\varepsilon}. \tag{178}$$

This means that

$$\left|(s^*)'(t_1) - (s^*)'(t_2)\right| \leq C\,|t_1 - t_2| \qquad \text{for } t_1, t_2 \in [0,T]. \tag{179}$$

Proof: Integrating both sides of (162) from 0 to t, we obtain:

$$\varepsilon\left(s(t) - s^0\right) = \int_0^t \left(-s(u) + K^+ s(u)\right) du, \tag{180}$$

or equivalently,

$$s(t) = s^0 + \frac{1}{\varepsilon}\int_0^t \left(-s(u) + K^+ s(u)\right) du =: L^+ s(t). \qquad (181)$$

If a function $s \in C([0,T])$ solves equation (181), then it is differentiable, it solves the integro-differential equation (162), and $s(0) = s^0$. Therefore it is sufficient to show that operator L^+ defined in (181) has a unique fixed point.

By virtue of estimate (168), it follows from (181) that for any two functions $s_1, s_2 \in C([0,T])$,

$$\begin{aligned} \left|L^+ s_1(t) - L^+ s_2(t)\right| &\le \frac{1}{\varepsilon}\int_0^t |s_1(u) - s_2(u)|\, du \\ &\quad + \frac{1}{\varepsilon}\int_0^t \left|K^+ s_1(u) - K^+ s_2(u)\right| du \qquad (182) \\ &\le \frac{1}{\varepsilon}\int_0^t \|s_1 - s_2\| \lambda \|f\|\, u du + \frac{1}{\varepsilon}\int_0^t \|s_1 - s_2\|\, du \\ &= \frac{1}{\varepsilon}\|s_1 - s_2\| \left(\lambda \|f\| \frac{t^2}{2} + t\right) \\ &\le \|s_1 - s_2\| \frac{\frac{\lambda}{2}\|f\| T + 1}{\varepsilon} t \end{aligned}$$

for $0 \le t \le T$. Using the same technique as in the proof of Theorem 1 it can be shown that, for a certain N, operator L^N is a contraction in the Banach space $C([0,T])$. Therefore operator L^+ has exactly one fixed point $s^*(t)$, the unique solution of (162), (163) in $C^1([0,T])$.

Since $K^+ s^*(t) \ge 0$, this solution $s^*(t)$ is greater than or equal to the solution of initial value problem

$$\begin{aligned} \varepsilon s'_{comp}(t) &= -s_{comp}(t), \qquad (183) \\ s_{comp}(0) &= s^0, \end{aligned}$$

for which we evidently have

$$s_{comp}(t) = s^0 e^{-\frac{1}{\varepsilon}t} \geq 0. \tag{184}$$

Hence, $s^*(t)$ is also non-negative in $[0,T]$.

The fact that the solution $s^*(t)$ is bounded from above by 1 can be verified by indirect proof. If there is any $t_2 \in (0,T]$ for which

$$s^*(t_2) > 1, \tag{185}$$

then due to continuity of the function $s^*(t)$ there exists a $t_1 \in (0, t_2)$ such that

$$s^*(t_1) = 1, \tag{186}$$

$$s^*(t) > 1 \quad \text{for all } t_1 < t \leq t_2. \tag{187}$$

By the mean value theorem, there exists some intermediate point $t_3 \in (t_1, t_2)$, where

$$(s^*)'(t_3) > 0. \tag{188}$$

By virtue of (162) and (159),

$$\varepsilon (s^*)'(t_3) = -s^*(t_3) + 1 - \lambda v_{old}(t_3) \leq -s^*(t_3) + 1 < -1 + 1 = 0, \tag{189}$$

which contradicts (188).

The bound $1/\varepsilon$ for the derivative is easily obtained from integro-differential equation (162), using (159), (160) and the upper bound for $s(t)$:

$$\varepsilon s'(t) = -s(t) + \max(0, Ks(t)) \leq -s(t) + 1 \leq 1, \tag{190}$$

$$\varepsilon s'(t) \geq -s(t) \geq -1. \tag{191}$$

To show that solution $s^*(t)$ satisfies Lipschitz condition of order 1, we proceed as follows. Let $t_1, t_2 \in [0,T]$. Then by virtue of (162) and Corollary 1,

$$\begin{aligned}
\left|s^{*\prime}(t_1) - s^{*\prime}(t_2)\right| &\le \frac{1}{\varepsilon}\left|-s^*(t_1) + s^*(t_2)\right| + \frac{1}{\varepsilon}\left|K^+s^*(t_1) - K^+s^*(t_2)\right| \qquad (192)\\
&\le \frac{1}{\varepsilon}\left|s^*(t_1) - s^*(t_2)\right| + \frac{1}{\varepsilon}\left|Ks^*(t_1) - Ks^*(t_2)\right|\\
&\le \frac{1}{\varepsilon}\left|s^*(t_1) - s^*(t_2)\right| + \frac{1}{\varepsilon}\left|g(t_1) - g(t_2)\right|\\
&\quad + \frac{\lambda}{\varepsilon}\left|\int_0^{t_1} f(a)\,s(t_1-a)\,da - \int_0^{t_2} f(a)\,s(t_2-a)\,da\right|\\
&\le \frac{1}{\varepsilon}\left(\left\|(s^*)'\right\| + \|g'\|\right)|t_1 - t_2|\\
&\quad + \frac{\lambda}{\varepsilon}\left|\int_0^{t_2} \left(f(t_1-a) - f(t_2-a)\right)s(a)\,da - \int_{t_1}^{t_2} f(t_1-a)\,s(a)\,da\right|\\
&\le \frac{1}{\varepsilon}\left(\left\|(s^*)'\right\| + \|g'\|\right)|t_1 - t_2|\\
&\quad + \frac{\lambda}{\varepsilon}T\,\|f'\|\,\|s\|\,|t_1 - t_2| + \frac{\lambda}{\varepsilon}\|f\|\,\|s\|\,|t_1 - t_2|\\
&= \frac{\left\|(s^*)'\right\| + \|g'\| + \lambda\|s\|\left(T\|f'\| + \|f\|\right)}{\varepsilon}\,|t_1 - t_2|. \qquad \blacksquare
\end{aligned}$$

8 Numerical approximation

Difference method for the initial value problem

To discretize the problem

$$\varepsilon s'(t) = -s(t) + \max(0, Ks(t)), \qquad 0 \le t \le T, \tag{193}$$

$$Ks(t) = g(t) - \lambda \int_0^t f(a)\,s(t-a)\,da, \tag{194}$$

$$s(0) = s^0. \tag{195}$$

using N equal time steps, we set

$$t_n = n\frac{T}{N} = nh \qquad \text{for } n = 0, 1, 2, ..., N. \tag{196}$$

Let us replace the derivative by a forward difference quotient, and approximate the integral in (194) by the trapezoid rule. Then for $n = 0, 1, 2, ..., N-1$,

$$s'(t_n) = \frac{s(t_{n+1}) - s(t_n)}{h} + \Delta_n \tag{197}$$

$$\int_0^{t_n} f(a)\, s(t_n - a)\, da = h \sum_{j=0}^{n} a_j s(t_j) f(t_{n-j}) + \overline{\Delta}_n, \tag{198}$$

where $a_0 = a_n = 1/2$ and $a_1 = a_2 = ... = a_{n-1} = 1$.

By Theorem 16 in the Appendix, the error terms Δ_n and $\overline{\Delta}_n$ have the estimates

$$|\Delta_n| \leq Ch, \tag{199}$$

$$|\overline{\Delta}_n| \leq \frac{5}{6} CTh^2, \tag{200}$$

where C is the Lipschitz constant given in (178). Substituting (197) and (198) into integro-differential equation (193), we obtain

$$\varepsilon \left(\frac{s(t_{n+1}) - s(t_n)}{h} + \Delta_n \right) \tag{201}$$

$$= -s(t_n) + \max\left(0, g(t_n) - \lambda \left(h \sum_{j=0}^{n} a_j f(t_{n-j})\, s(t_j) + \overline{\Delta}_n \right)\right),$$

$$s(0) = s^0. \tag{202}$$

The corresponding difference scheme is

$$\varepsilon \frac{s_{n+1} - s_n}{h} = -s_n + \max\left(0, g(t_n) - \lambda h \sum_{j=0}^{n} a_j f(t_{n-j})\, s_j\right), \tag{203}$$

$$s_0 = s^0. \tag{204}$$

Theorem 3 *The error of difference method (203), (204) for solving initial value problem (193)-(195) is of the order $O(h)$.*

Proof: A linear system for the error sequence

$$e_n = s(t_n) - s_n \tag{205}$$

is obtained by subtracting (203) from (201), and (204) from (202):

$$\begin{aligned} & \varepsilon\left(\frac{e_{n+1}-e_n}{h}+\Delta_n\right) \qquad (206)\\ = & -e_n + \max\left(0, g(t_n) - \lambda\left(h\sum_{j=0}^{n} a_j f(t_{n-j}) s(t_j) + \overline{\Delta}_n\right)\right) \\ & - \max\left(0, g(t_n) - \lambda h \sum_{j=0}^{n} a_j f(t_{n-j}) s_j\right), \\ e_0 = & \ 0. \qquad (207)\end{aligned}$$

Solving (206) for e_{n+1}, we get

$$\begin{aligned} e_{n+1} = & -h\Delta_n + \left(1-\frac{h}{\varepsilon}\right)e_n \qquad (208)\\ & + \frac{h}{\varepsilon}\max\left(0, g(t_n) - \lambda\left(h\sum_{j=0}^{n} a_j f(t_{n-j}) s(t_j) + \overline{\Delta}_n\right)\right) \\ & - \frac{h}{\varepsilon}\max\left(0, g(t_n) - \lambda h \sum_{j=0}^{n} a_j f(t_{n-j}) s_j\right). \end{aligned}$$

From (208), the triangle inequality, and Corollary 1 from the Appendix it follows that

$$\begin{aligned} |e_{n+1}| < & \left|1-\frac{h}{\varepsilon}\right||e_n| + \frac{\lambda h^2}{\varepsilon}\left|\sum_{j=0}^{n} a_j f(t_{n-j}) e_j\right| - h\Delta_n + \frac{\lambda h}{\varepsilon}\overline{\Delta}_n \qquad (209)\\ \leq & \left(\left|1-\frac{h}{\varepsilon}\right| + \frac{\lambda h^2}{2\varepsilon}|f(0)|\right)|e_n| + \frac{\lambda h^2}{\varepsilon}\sum_{j=0}^{n-1} a_j f(t_{n-j})|e_j| - h\Delta_n + \frac{\lambda h}{\varepsilon}\overline{\Delta}_n. \end{aligned}$$

If we make h small enough, that is if

$$\begin{aligned} h \leq 2\varepsilon \quad & \text{for} \quad f(0) = 0, \qquad (210)\\ h \leq \min\left(\frac{2}{\lambda f(0)}, 2\varepsilon\right) \quad & \text{for} \quad f(0) > 0, \end{aligned}$$

then (209) implies that

$$
\begin{aligned}
|e_{n+1}| &\leq |e_n| + \frac{\lambda h^2}{\varepsilon} \|f\| \sum_{j=0}^{n-1} |e_j| + h\Delta_n + \frac{\lambda h}{\varepsilon}\overline{\Delta}_n \\
&\leq |e_n| + \frac{\lambda h^2}{\varepsilon} \|f\| \sum_{j=0}^{n-1} |e_j| + Ch^2 + \frac{5\lambda T}{6\varepsilon} Ch^3 \\
&\leq |e_n| + \frac{\lambda \|f\|}{\varepsilon} h^2 \sum_{j=0}^{n-1} |e_j| + \left(1 + \frac{5\lambda T}{3}\right) Ch^2
\end{aligned}
\tag{211}
$$

By virtue of Lemma 7 from the Appendix and (196) it follows from (211) that

$$
\begin{aligned}
|e_n| &\leq n\left(1 + \frac{5\lambda T}{3}\right) Ch^2 \left(1 + \sqrt{\frac{\lambda \|f\|}{\varepsilon}} h\right)^n \\
&\leq \left(1 + \frac{5\lambda T}{3}\right) CTh \exp\sqrt{\frac{\lambda \|f\|}{\varepsilon}} \\
&= \left(\|(s^*)'\| + \|g'\| + \lambda \|s\| \left(T \|f'\| + \|f\|\right)\right) T \frac{h}{\varepsilon} \exp\sqrt{\frac{\lambda \|f\|}{\varepsilon}} \\
&= O(h).
\end{aligned}
\tag{212}
$$

Thus, the difference method for the initial value problem converges linearly in stepsize h. ■

Difference method for the quasi-equilibrium problem

Discretization of the quasi-equilibrium problem,

$$
0 = -s(t) + \max(0, Ks(t)), \tag{213}
$$

$$
Ks(t) = g(t) - \lambda \int_0^t f(a)\, s(t-a)\, da, \tag{214}
$$

with N equal time steps

$$
t_n = n\frac{T}{N} = nh \qquad \text{for } n = 0, 1, 2, ..., N, \tag{215}
$$

yields (here we approximate the integral with the trapezoid rule):

$$
s(t_n) = \max\left(0, g(t_n) - \lambda\left(h\sum_{j=0}^{n} a_j f(t_{n-j})\, s(t_j) + \bar{\Delta}_n\right)\right), \tag{216}
$$

where $a_0 = a_n = 1/2$ and $a_1 = a_2 = ... = a_{n-1} = 1$. In (216), $\tilde{\Delta}_n$ is an error term, for which Theorem 15 in the Appendix provides the estimate:

$$\left|\tilde{\Delta}_n\right| \leq \frac{1}{2} C_{qe} T h, \tag{217}$$

with constant C_{qe} explicitly given in (167).

Theorem 4 *The error of difference method*

$$\begin{aligned} s_0 &= \max(0, g(0)) = s(0), & (218) \\ s_{n+1} &= \max\left(0, g(t_{n+1}) - \lambda h \sum_{j=0}^{n} a_j f(t_{n-j}) s_j\right) & (219) \\ \textit{for } n &= 0, 1, 2, ..., & (220) \end{aligned}$$

for solving quasi-equilibrium problem (213) is of the order $O(h)$.

Proof: A system for the error sequence

$$e_n = s(t_n) - s_n \tag{221}$$

is obtained by subtracting (219) from (216):

$$\begin{aligned} e_0 &= 0, & (222) \\ e_{n+1} &= \max\left(0, g(t_n) - \lambda\left(h \sum_{j=0}^{n} a_j f(t_{n-j}) s(t_j) + \tilde{\Delta}_n\right)\right) \\ &\quad - \max\left(0, g(t_n) - \lambda h \sum_{j=0}^{n} a_j f(t_{n-j}) s_j\right). & (223) \end{aligned}$$

From the triangle inequality and Corollary 1 it follows that

$$\begin{aligned} |e_{n+1}| &\leq \lambda h \sum_{j=0}^{n} |f(t_{n-j})| |e_j| + \lambda \tilde{\Delta}_n & (224) \\ &\leq \lambda h \|f\| \sum_{j=0}^{n} |e_j| + \frac{1}{2} \lambda C_{eq} T h. \end{aligned}$$

By Lemma 8 from the Appendix, we obtain the estimate

$$|e_n| \leq \frac{1}{2}\lambda C_{eq} T h \left(1 + \lambda h \|f\|\right)^n. \tag{225}$$

The sequence $(1 + \lambda h \|f\|)^n$ is bounded uniformly in h since

$$(1 + \lambda h \|f\|)^n = \left(1 + \frac{\lambda \|f\| T}{n}\right)^n \uparrow e^{\lambda \|f\| T} \quad \text{as } n \uparrow \infty. \tag{226}$$

It follows from (225), (226) that

$$|e_n| \leq \frac{1}{2}\lambda C T e^{\lambda \|f\| T} h = O(h). \quad \blacksquare \tag{227}$$

Fig. 7 shows graphs of numerical solutions for a typical initial-value problem and the associated quasi-equilibrium problem. In Fig. 8 the solutions of the initial value problem are compared for different values of the time step h. It is not recommended to choose the $h > \varepsilon$, because then instabilities occur.

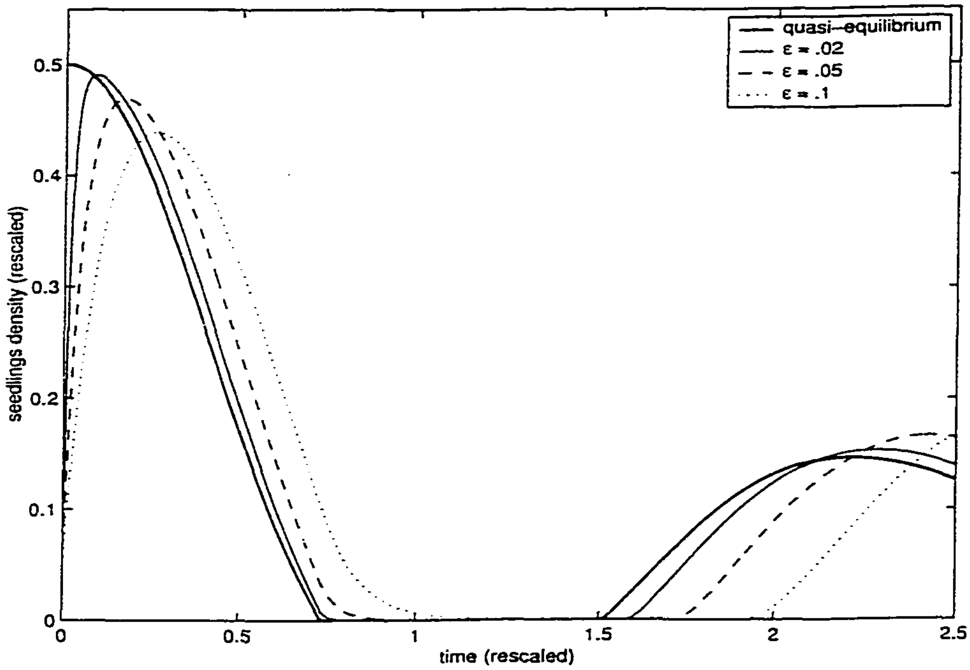

Fig. 7: Numerical solution (stepsize $h = 0.005$) of initial value problem

$\varepsilon s\prime(t) = -s(t) + max(0, 1 - \lambda v_{old}(t) - \lambda \int_0^t s(t-a)\, ae^{-a} da),$

$s(0) = 0.05$, for $\lambda = 10, v_{old}(t) = 0.05te^{-t}$, and three different values of ε. The quasi-equilibrium solution is shown as thick line.

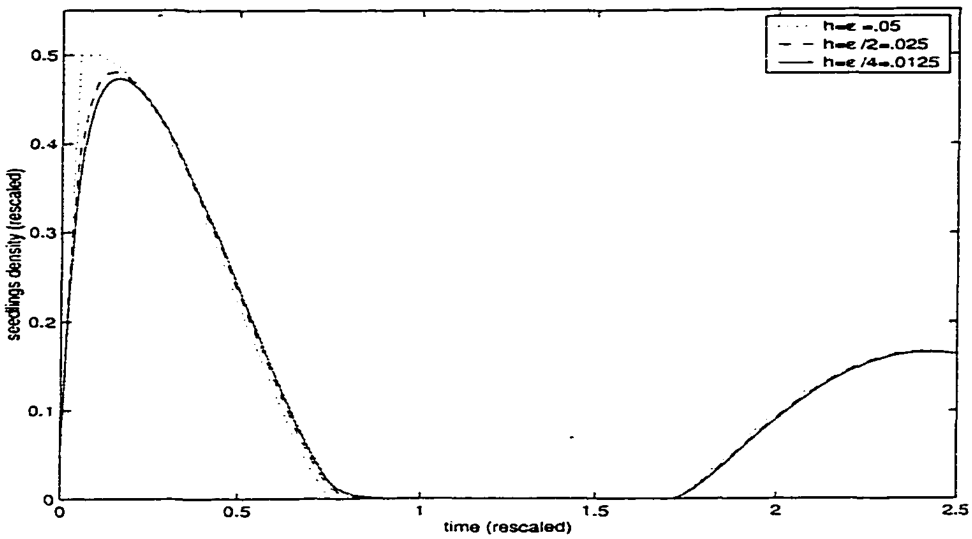

Fig. 8: Numerical solution with different stepsizes for initial value problem

$\varepsilon s\prime(t) = -s(t) + max(0, 1 - \lambda v_{old}(t) - \lambda \int_0^t s(t-a)\, ae^{-a} da)$,

$s(0) = 0.05$, for $\lambda = 10, v_{old}(t) = 0.05te^{-t}$, and $\varepsilon = .05$.

9 Asymptotic approximation

Leading order approximation: construction using the boundary function method

Using the boundary function method (see [2], [9], [10]) for singularly perturbed problems, represent the uniform asymptotic approximation of the solution of the singularly perturbed initial value problem

$$\varepsilon s'(t) = -s(t) + \max(0, Ks(t)), \quad 0 \le t \le T, \tag{228}$$

$$Ks(t) = g(t) - \lambda \int_0^t f(a)\, s(t-a)\, da, \tag{229}$$

$$s(0) = s^0 \tag{230}$$

in the form

$$s(t) = \overline{s}(t) + \Pi s\left(\frac{t}{\varepsilon}\right), \tag{231}$$

where $\overline{s}(t)$ is the regular part, and $\Pi s(t/\varepsilon)$ is the boundary layer part of the approximation. The boundary layer part is necessary to correctly describe the pulse of seedlings in the first few years of forest growth; it decays exponentially to zero as time increases. In what follows, the rescaled time variable of the boundary layer part is denoted by

$$\tau = t/\varepsilon. \tag{232}$$

Substitution of representation (231), with (232), into problem (228)-(230) yields

$$\begin{aligned}
\varepsilon\frac{d\overline{s}}{dt}+\frac{d\Pi s}{d\tau} &= -\overline{s}(t)-\Pi s(\tau) \qquad (233)\\
&\quad +\max\left(0, g(t)-\lambda\int_0^t f(t-a)\left(\overline{s}(a)+\Pi s\left(\frac{a}{\varepsilon}\right)\right)da\right),\\
&= -\overline{s}(t)+\max\left(0, g(t)-\lambda\int_0^t f(t-a)\,\overline{s}(a)\,da\right)\\
&\quad -\Pi s(\tau)\\
&\quad +\max\left(0, g(\varepsilon\tau)-\lambda\int_0^{\varepsilon\tau} f(\varepsilon\tau-a)\left(\overline{s}(a)+\Pi s\left(\frac{a}{\varepsilon}\right)\right)da\right)\\
&\quad -\max\left(0, g(\varepsilon\tau)-\lambda\int_0^{\varepsilon\tau} f(\varepsilon\tau-a)\,\overline{s}(a)\,da\right),\\
\overline{s}(0)+\Pi s(0) &= s^0. \qquad (234)
\end{aligned}$$

Equation (233) can be split into two equations in variables t and τ, respectively:

$$\begin{aligned}
\varepsilon\frac{d\overline{s}}{dt} &= -\overline{s}(t)+\max\left(0, g(t)-\lambda\int_0^t f(t-a)\,\overline{s}(a)\,da\right), \qquad (235)\\
\frac{d\Pi s}{d\tau} &= -\Pi s(\tau) \qquad (236)\\
&\quad +\max\left(0, g(\varepsilon\tau)-\lambda\int_0^{\varepsilon\tau} f(\varepsilon\tau-a)\left(\overline{s}(a)+\Pi s\left(\frac{a}{\varepsilon}\right)\right)da\right)\\
&\quad -\max\left(0, g(\varepsilon\tau)-\lambda\int_0^{\varepsilon\tau} f(\varepsilon\tau-a)\,\overline{s}(a)\,da\right).
\end{aligned}$$

To obtain the leading order approximation, substitute

$$\begin{aligned}
\overline{s}(t) &= \overline{s_0}(t)+O(\varepsilon), \qquad (237)\\
\Pi s(\tau) &= \Pi_0 s(\tau)+O(\varepsilon), \qquad (238)
\end{aligned}$$

into equations (235), (236) and into initial condition (234), and omit terms of order ε and higher. we obtain the integral equation

$$0=-\overline{s_0}(t)+\max\left(0, g(t)-\lambda\int_0^t f(t-a)\,\overline{s_0}(a)\,da\right) \qquad (239)$$

for the regular part, and the initial value problem

$$\frac{d\Pi_0 s}{d\tau} = -\Pi_0 s(\tau) + \max(0, g(0)) - \max(0, g(0)) \tag{240}$$

$$= -\Pi_0 s(\tau),$$

$$\Pi_0 s(0) = s^0 - \overline{s_0}(0) \tag{241}$$

for the boundary layer part of the leading order asymptotic solution. Integral equation (239) for the regular part is exactly the quasi-equilibrium problem (164). An approximate solution of (239) can be found numerically with difference method (218), (219).

The problem (240), (241) for the boundary layer part has solution

$$\Pi_0 s(\tau) = \left(s^0 - \overline{s_0}(0)\right) e^{-\tau}. \tag{242}$$

Fig. 9 illustrates how the asymptotic solution is obtained as a sum of regular and boundary layer parts. Fig. 10 displays asymptotic solution and numerical solution for the same initial value problem ($\varepsilon = .05, h = .005$).

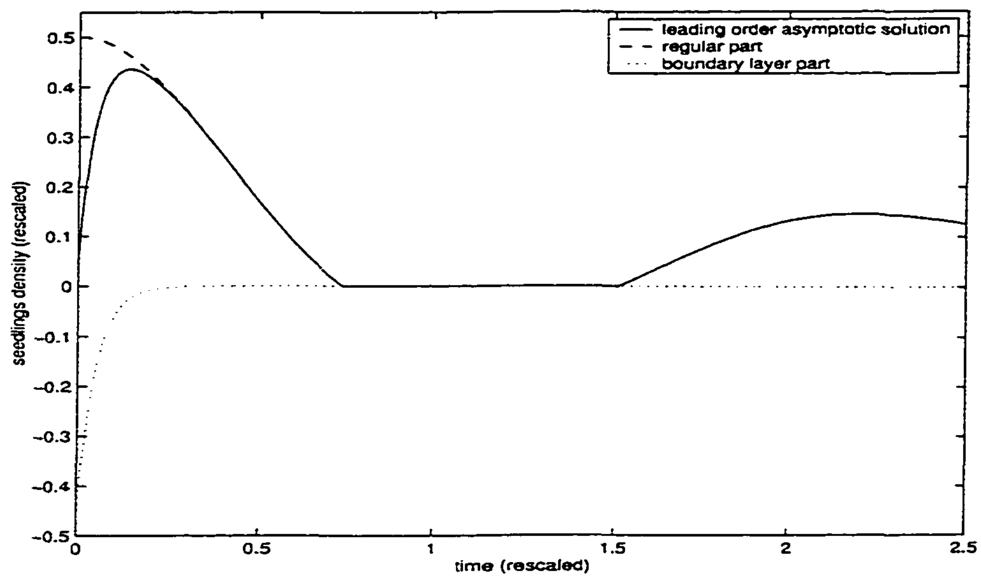

Fig. 9: Leading order asymptotic solution of initial value problem

$\varepsilon s\prime(t) = -s(t) + max(0, 1 - \lambda v_{old}(t) - \lambda \int_0^t s(t-a)\, ae^{-a}da)$,

$s(0) = 0.05$, for $\lambda = 10, v_{old}(t) = .05te^{-t}$, and $\varepsilon = .05$. The asymptotic solution (solid line) is the sum of regular part (quasi-equilibrium solution) and boundary layer part (exponentially decaying to zero).

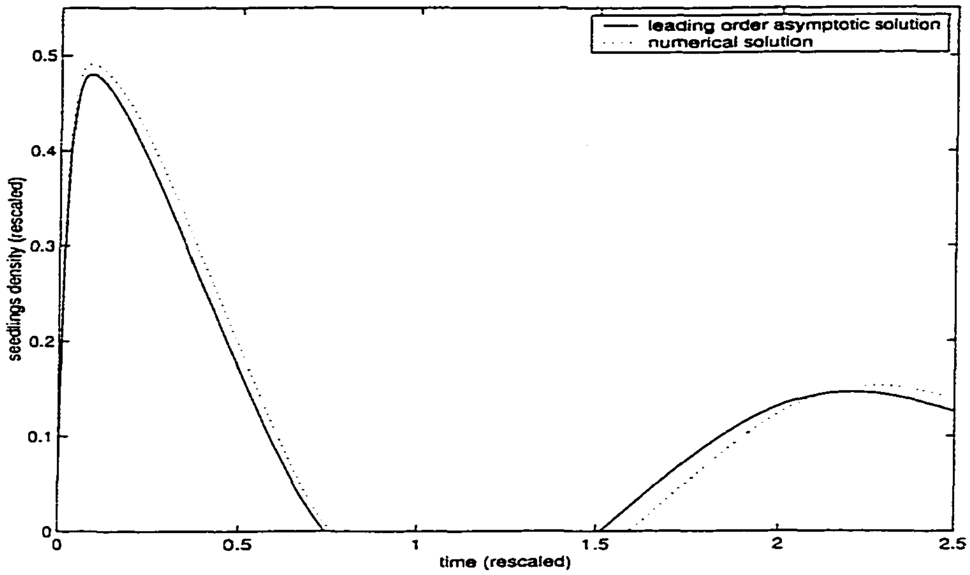

Fig. 10: Comparison of leading order asymptotic solution from Fig. 9 with numerical solution from Fig. 7 ($\varepsilon = .02, h = .005$).

textbfEstimation of the remainder

Let us represent the exact solution $s(t)$ of (228)-(230) in the form

$$s(t) = \overline{s_0}(t) + \Pi_0 s(\tau) + u(t), \tag{243}$$

where $\overline{s_0}(t)$ and $\Pi_0 s(\tau)$ are the regular and boundary layer parts, respectively, of the leading order approximation constructed in previous section, and $u(t)$ is the error or, so-called, *remainder* term. Substituting (243) into the initial value problem (228), (230) we obtainan integro-differential equation for the remainder $u(t)$:

$$\begin{aligned} &\varepsilon\frac{d\overline{s_0}}{dt} + \frac{d\Pi_0 s}{d\tau} + \varepsilon\frac{du}{dt} = -\overline{s_0}(t) - \Pi_0 s(\tau) - u(t) + \\ &\max\left(0, g(t) - \lambda\int_0^t f(t-a)\left(\overline{s_0}(a) + \Pi_0 s\left(\frac{a}{\varepsilon}\right) + u(a)\right) da\right), \end{aligned} \tag{244}$$

with initial condition

$$\overline{s_0}(0) + \Pi_0 s(0) + u(0) = 0. \tag{245}$$

By virtue of (239), (240) and (241), the initial value problem (244), (245) simplifies to

$$\varepsilon\frac{du}{dt} = -u(t) + R(u;t), \tag{246}$$

$$\begin{aligned} R(u;t) = &-\varepsilon\frac{d\overline{s_0}}{dt} \\ &+ \max\left(0, g(t) - \lambda\int_0^t f(t-a)\left(\overline{s_0}(a) + \Pi_0 s\left(\frac{a}{\varepsilon}\right) + u(a)\right) da\right) \\ &- \max\left(0, g(t) - \lambda\int_0^t f(t-a)\,\overline{s_0}(a)\, da\right), \end{aligned} \tag{247}$$

$$u(0) = 0. \tag{248}$$

Theorem 5 *The solution of initial value problem (246)-(248) is of order $O(\varepsilon)$.*

Proof: Instead of (246), (247) let us consider an equivalent integral equation

$$u(t) = \frac{1}{\varepsilon} \int_0^t e^{-\frac{t-a}{\varepsilon}} R(u;a)\, da, \tag{249}$$

and let us define the operator $J : C([0,T]) \to C([0,T])$ by

$$Jv(t) = \frac{1}{\varepsilon} \int_0^t e^{-\frac{t-a}{\varepsilon}} R(v;a)\, da. \tag{250}$$

Using Corollary 1 in the Appendix , we get that for all $v_1, v_2 \in C([0,T])$ and all $t \in [0,T]$,

$$\begin{aligned}
& |R(v_1;t) - R(v_2;t)| \qquad (251)\\
= \ & \left| \max\left(0, g(t) - \lambda \int_0^t f(t-a)\left(\overline{s_0}(a) + \Pi_0 s\left(\frac{a}{\varepsilon}\right) + v_1(a)\right) da\right) - \right. \\
& \left. \max\left(0, g(t) - \lambda \int_0^t f(t-a)\left(\overline{s_0}(a) + \Pi_0 s\left(\frac{a}{\varepsilon}\right) + v_2(a)\right) da\right) \right| \\
\leq \ & \left| -\lambda \int_0^t f(t-a)\, v_1(a)\, da + \lambda \int_0^t f(t-a)\, v_2(a)\, da \right| \\
= \ & \lambda \left| \int_0^t f(t-a)\left(v_1(a) - v_2(a)\right) da \right| \\
\leq \ & \lambda \|f\|\, t\, \|v_1 - v_2\| .
\end{aligned}$$

Using this estimate we conclude from (249) that

$$\begin{aligned}
|Jv_1(t) - Jv_2(t)| &\leq \frac{1}{\varepsilon} \int_0^t e^{-\frac{t-a}{\varepsilon}} |R(v_1;a) - R(v_2;a)|\, da \\
&\leq \frac{\lambda \|f\|}{\varepsilon} \|v_1 - v_2\| \int_0^t e^{-\frac{t-a}{\varepsilon}} a\, da \\
&= \frac{\lambda \|f\|}{\varepsilon} \|v_1 - v_2\| \left(\varepsilon t - \varepsilon^2 \left(1 - e^{-\frac{t}{\varepsilon}}\right)\right) \\
&\leq \frac{\lambda \|f\|}{\varepsilon} \|v_1 - v_2\|\, \varepsilon t.
\end{aligned}$$

Using the same technique as in the proof of Theorem 1, it can be shown that operator J^N for a certain positive integer N is a contraction with a Lipschitz constant $0 < q < 1$. It, therefore, has a unique fixed point u, which satisfies the estimate

$$\|u\| \leq \frac{1}{1-q} \left\| J^N v_0 \right\|, \tag{252}$$

where $v_0 \in C([0,T])$ is some starting function for the sequence of successive approximations $v_0, Jv_0, J^2v_0, \ldots$ To show that $\left\| J^N v_0 \right\|$ is of order $O(\varepsilon)$, we use an upper estimate for $R(v;t)$, where $v \in C([0,T])$. From the definition of R in (247) it follows (by virtue of Corollary 1 and the triangle inequality) that

$$\begin{aligned} |R(v;t)| &\leq \varepsilon \left| \frac{d\overline{s_0}}{dt} \right| + \lambda \left| \int_0^t f(t-a) \left(\Pi_0 s \left(\frac{a}{\varepsilon} \right) + v(a) \right) da \right| & (253) \\ &\leq O(\varepsilon) + \lambda \|f\| \left| \int_0^t \Pi_0 s \left(\frac{a}{\varepsilon} \right) da \right| + \lambda \|f\| \|v\| t & (254) \end{aligned}$$

In this estimate we utilized the fact that the derivative of $\overline{s_0}$ is piecewise continuous and therefore bounded. The integral of the boundary layer part $\Pi_0 s$ is of order $O(\varepsilon)$ because by virtue of (242),

$$\begin{aligned} \int_0^t \Pi_0 s \left(\frac{a}{\varepsilon} \right) da &= \left(s^0 - \overline{s_0}(0) \right) \int_0^t e^{-\frac{a}{\varepsilon}} da \\ &= \left(s^0 - \overline{s_0}(0) \right) \varepsilon \left(1 - e^{-\frac{t}{\varepsilon}} \right) \\ &\leq \left(s^0 - \overline{s_0}(0) \right) \varepsilon. \end{aligned}$$

From (250) and (252) it follows that

$$\begin{aligned} |Jv(t)| &\leq \frac{1}{\varepsilon} \sup_{0 \leq a \leq t} |R(v;a)| \int_0^t e^{-\frac{t-a}{\varepsilon}} da & (255) \\ &= \sup_{0 \leq a \leq t} |R(v;a)| \left(1 - e^{-\frac{t}{\varepsilon}} \right) \\ &\leq O(\varepsilon) + \lambda \|f\| \int_0^t |u(a)| \, da. \end{aligned}$$

Now consider the successive approximations

$$v_0 = 0, \tag{256}$$

$$v_{n+1} = Jv_n \quad \text{for } n = 0, 1, 2, 3, ... \tag{257}$$

Using (255), we obtain the recursion

$$|v_0(t)| = 0, \tag{258}$$

$$|v_{n+1}(t)| \leq C\varepsilon + \lambda \|f\| \int_0^t |v_n(a)|\, da \quad \text{for } n = 0, 1, 2, 3, ..., \tag{259}$$

where C is a suitable positive constant independent of ε. By induction we can prove the inequality

$$|v_n| \leq C\varepsilon \sum_{j=0}^{n-1} \frac{(\lambda \|f\| t)^j}{j!} \quad \text{for } n = 1, 2, 3, ... \tag{260}$$

Indeed, (260) is true for $n = 1$ since from (258), we have

$$|v_1(t)| \leq C\varepsilon. \tag{261}$$

Assume that (260) is satisfied for $j = 1, 2, ..., n$. Then, by recursion (259),

$$\begin{aligned} |v_{n+1}(t)| &\leq C\varepsilon + \lambda \|f\| \int_0^t C\varepsilon \sum_{j=0}^{n-1} \frac{(\lambda \|f\| a)^j}{j!} da \\ &= C\varepsilon + C\varepsilon\lambda \|f\| \sum_{j=0}^{n-1} \frac{(\lambda \|f\|)^j}{j!} \int_0^t a^j da \\ &= C\varepsilon + C\varepsilon\lambda \|f\| \sum_{j=0}^{n-1} \frac{(\lambda \|f\|)^j}{j!} \frac{t^{j+1}}{j+1} \\ &= C\varepsilon \sum_{j=0}^{n} \frac{(\lambda \|f\| t)^j}{j!}. \end{aligned} \tag{262}$$

Thus, (260) is true for $n + 1$, and the induction over n is completed. A consequence of (260) is that

$$
\begin{aligned}
|v_n(t)| &\leq C\varepsilon \sum_{j=0}^{\infty} \frac{(\lambda \|f\| t)^j}{j!} \\
&= C\varepsilon e^{\lambda \|f\| t} \\
&\leq C\varepsilon e^{\lambda \|f\| T}.
\end{aligned} \tag{263}
$$

Thence,

$$\|v_n\| \leq C\varepsilon e^{\lambda\|f\|T} = O(\varepsilon). \tag{264}$$

so, in particular,

$$\left\|J^N v_0\right\| = \|v_N\| = O(\varepsilon). \tag{265}$$

From (252) it then follows that

$$\|u\| = O(\varepsilon). \qquad \blacksquare \tag{266}$$

Part III

Asymptotic solution of the problem with a nonlinear seedling equation

10 Statement of the problem

Governing equations Let $N(t,a)$ be the age density of a tree population, depending on time t and chronological age a. This means that the number of individuals in an age interval $[r,s]$ at any time $t>0$ is given as $\int_r^s N(t,a)\,da$. Since

$$\frac{da}{dt}=1, \tag{267}$$

the rate of change of the age density $N(t,a)$ is

$$\frac{d}{dt}N(t,a)=\frac{\partial N}{\partial t}+\frac{\partial N}{\partial a}\frac{da}{dt}=\frac{\partial N}{\partial t}+\frac{\partial N}{\partial a}. \tag{268}$$

If the death rate constant μ of the population is constant over time and is age-independent, then the number of deaths in a given age interval and a given infinitesimal time period is proportional to the number of individuals in this class, so that

$$\frac{\partial N}{\partial t}+\frac{\partial N}{\partial a}=-\mu N, \tag{269}$$

In the experimental study of tree populations often a nonlinear dependence of the death rate in an age interval on the number of individuals in this age interval is observed, so that in generalization of (269) we assume the population follows the partial differential equation

$$\frac{\partial N}{\partial t} + \frac{\partial N}{\partial a} = -f(N), \tag{270}$$

where the function $f(N) : [0, \infty) \to [0, \infty)$ is zero at $N = 0$, positive for $N > 0$ and continously differentiable.

We consider the boundary value problem on the rectangle $0 \leq t \leq T$ and $0 \leq a \leq T_1$, where T and T_1 are positive time constants. Boundary conditions are the initial age distribution

$$N(0, a) = \Phi(a) \text{ for } 0 \leq a \leq T_1, \tag{271}$$

and the seedling function

$$N(t, 0) = S(t) \text{ for } 0 \leq t \leq T. \tag{272}$$

The initial age distribution $\Phi(a)$ is explicitly given as a differentiable function, whereas the seedling function $S(t)$ satisfies an ordinary differential equation of the form

$$\varepsilon \frac{dS}{dt} = F\left(S(t), \int_0^{T_1} N(t, a) B(a) \, da\right), \quad \text{if } S(t) > 0 \tag{273}$$

$$0, \quad \text{if } S(t) = 0, \tag{274}$$

Conditions on the function F will be imposed later in this paper to ensure existence, stability and uniqueness of the solution.

The initial value for the seedling function $S(t)$ is given by the compatibility condition

$$S(0) = \Phi(0) > 0, \tag{275}$$

which ensures that the age density function $N(t,a)$ is continuous in the rectangle $(t,a) \in [0,T] \times [0,T_1]$.

Reduction to one integro-differential equation

By using the method of characteristics, the solution $N(t,a)$ of the partial differential equation can be expressed in terms of the nonlinear term $f(N)$ and the boundary value functions $\Phi(a)$ and $S(t)$ as follows:

$$\frac{da}{1} = \frac{dt}{1} = \frac{dN}{f(N)}, \tag{276}$$

and thence by integrating N along the characteristics $a - t$ =constant,

$$t = \int_{\Phi(a-t)}^{N(a,t)} \frac{dn}{f(n)} \quad \text{for } 0 < t \leq a, \tag{277}$$

$$a = \int_{S(t-a)}^{N(a,t)} \frac{dn}{f(n)} \quad \text{for } 0 < a \leq t. \tag{278}$$

By the assumptions made in the previous section, the function

$$G(N) := \int_1^N \frac{dn}{f(n)} \tag{279}$$

is a strictly increasing differentiable function for $N > 0$, therefore its inverse G^{-1} exists, and we have for $0 < t \leq a$:

$$t = G(N(t,a)) - G(\Phi(a-t)), \tag{280}$$

and solving for $N(t,a)$ yields:

$$N^{-}(t,a) = G^{-1}\left(t + G\left(\Phi(a-t)\right)\right). \tag{281}$$

Similarly for $0 < a \leq t$,

$$a = G\left(N\left(t,a\right)\right) - G\left(S(a-t)\right), \tag{282}$$

and thence

$$N^{+}(t,a) = G^{-1}\left(a + G\left(S(t-a)\right)\right). \tag{283}$$

Note that because of the compatibility condition (275), the representations (281) and (283) yield the same solution for $a = t$:

$$\begin{aligned} N^{-}(t,t) &= G^{-1}\left(t + G\left(\Phi(0)\right)\right) \\ &= G^{-1}\left(t + G\left(S(0)\right)\right) \\ &= N^{+}(t,t). \end{aligned} \tag{284}$$

Using (281) and (283) to eliminate $N(t,a)$ in (273) we obtain a nonlinear integro-differential equation for the seedling function $S(t)$:

$$\varepsilon\frac{dS}{dt} = F\left(S(t), \int_0^t K\left(a, S\left(t-a\right)\right)da + L\left(t\right)\right) \text{ for } 0 \leq t \leq T. \tag{285}$$

where

$$K\left(a,s\right) = G^{-1}\left(a + G\left(s\right)\right)B\left(a\right) \tag{286}$$

$$L\left(t\right) = \int_t^{T_1} G^{-1}\left(t + G\left(\Phi\left(a-t\right)\right)\right)B\left(a\right)da \tag{287}$$

Since Φ and G are differentiable, so is $L(t)$, and substituting

$$L\left(t\right) = L\left(0\right) + \int_0^t L'\left(a\right)da \tag{288}$$

in (285), we obtain

$$\begin{aligned}
\varepsilon \frac{dS}{dt} &= F\left(S(t), L(0) + \int_0^t \left(K(a, S(t-a)) + L'(a)\right) da\right) \\
&= \widetilde{F}\left(S(t), \int_0^t \widetilde{K}(a, S(t-a))\, da\right),
\end{aligned} \tag{289}$$

where

$$\widetilde{F}(x, y) = F(x, L(0) + y) \tag{290}$$

$$\widetilde{K}(a, s) = K(a, s) + L'(a) \tag{291}$$

Writing F instead of $\widetilde{F}$ and K instead of $\widetilde{K}$, we obtain the integro-differential initial value problem for the seedling function $S(t)$ in the form

$$\varepsilon \frac{dS}{dt} = F\left(S(t), \textstyle\int_0^t K(a, S(t-a))\, da\right), \tag{292}$$

$$S(0) = \Phi(0). \tag{293}$$

When $S(t)$ is found, the solution for $N(t,a)$ is given by (281) and (283) as

$$N(t, a) = G^{-1}(t + G(\Phi(a-t))) \quad \text{for } 0 \leq t \leq a, \tag{294}$$

$$N(t, a) = G^{-1}(a + G(S(t-a))) \quad \text{for } 0 \leq a \leq t. \tag{295}$$

11 Asymptotic approximation of the solution

In order to find the leading order approximation using, e.g., the boundary function method, we assume that $F \in C^2([0,\infty) \times [0,\infty))$ and that there is a function $S^* : [0,T] \to [0,\infty)$ which satisfies the following three conditions:

(S1) $S^*(t)$ is a continuous solution of the auxiliary problem

$$F\left(S(t), \int_0^t K(a, S(t-a))\, da\right) = 0. \tag{296}$$

(S2)

$$F_x\left(S^*(t), \int_0^t K(a, S^*(t-a))\, da\right) < 0 \tag{297}$$

in the interval $0 \le t \le T$. Since this interval is closed and the functions F_x, S^*, and K are continuous, this implies the existence of a constant $m < 0$ such that

$$F_x\left(S^*(t), \int_0^t K(a, S^*(t-a))\, da\right) \le m \tag{298}$$

for all $0 \le t \le T$.

(S3) If $\Phi(0) > S^*(0)$, then $F(S,0) < 0$ for all $S^*(0) < S < \Phi(0)$; and if $\Phi(0) < S^*(0)$, then $F(S,0) > 0$ for all $\Phi(0) < S < S^*(0)$. We do not consider the case $\Phi(0) = S^*(0)$ here, because then $S^*(t)$ solves the initial value problem (1.21), and there is no need for an approximation.

Note that conditions **(S1)**, **(S2)** and **(S3)** imply that $S^*(0)$ is a stable equilibrium of the autonomous differential equation

$$\frac{dS}{dt} = F(S,0), \tag{299}$$

such that the initial value Φ^0 is in the domain of attraction of $S^*(0)$. To solve the initial value problem (293) using the boundary function method for singularly perturbed problems, the solution $S(t)$ is presented as a sum of the regular part $\overline{S}(t)$ and the boundary layer part $\Pi S(t/\varepsilon)$:

$$S(t) = \overline{S}(t) + \Pi S(\tau), \tag{300}$$

where $\tau = t/\varepsilon$ is a stretched time variable. In addition, we require that the boundary function decays to zero as $\tau \to \infty$.

Substituting (300) into equation (293) and representing its right-hand side in a form similar to (3-27), yields:

$$\varepsilon \frac{d\overline{S}}{dt} + \frac{d\Pi S}{d\tau} = F\left(\overline{S}(t), \int_0^t K\left(a, \overline{S}(t-a)\right) da\right) + \Pi F(\tau), \tag{301}$$

where

$$\begin{aligned} \Pi F(\tau) &= F\left(\overline{S}(\varepsilon\tau) + \Pi S(\tau), \varepsilon \int_0^\tau K\left(\varepsilon(\tau-\alpha), \overline{S}(\varepsilon\alpha) + \Pi S(\alpha)\right) d\alpha\right) \\ &\quad - F\left(\overline{S}(\varepsilon\tau), \varepsilon \int_0^\tau K\left(\varepsilon(\tau-\alpha), \overline{S}(\varepsilon\alpha)\right) d\alpha\right) \end{aligned} \tag{302}$$

The initial condition becomes

$$\overline{S}(0) + \Pi S(0) = \Phi^0. \tag{303}$$

In this equation and for the remainder of this paper, the notation of a function with upper index 0 denotes the value of the function at 0, e.g. Φ^0 means $\Phi(0)$, $\overline{S}_0'^{\,0}$ means $\overline{S}_0'(0)$ etc. Substituting asymptotic expansions

$$\overline{S}(t) = \overline{S}_0(t) + \varepsilon \overline{S}_1(\tau) + \ldots, \tag{304}$$

for the regular part and

$$\Pi S(t) = \Pi_0 S(t) + \varepsilon \Pi_1 S(\tau) + \ldots \tag{305}$$

for the boundary layer part into integro-differential equation (301) we obtain:

$$\begin{aligned}
&\varepsilon\frac{d\overline{S}_0}{dt}+\frac{d\Pi_0 S}{d\tau}+\varepsilon\frac{d\Pi_1 S}{d\tau}+\ldots \qquad (306)\\
=\ & F\left(\overline{S}_0(t)+\varepsilon\overline{S}_1(t)+\ldots,\int_0^t K\left(t-a,\overline{S}_0(a)+\varepsilon\overline{S}_1(a)+\ldots\right)da\right)\\
&+F\left(\overline{S_0}^0+\varepsilon\overline{S_1}^0+\varepsilon\tau\overline{S_0}'^0+\Pi_0S(\tau)+\ldots,\varepsilon\int_0^\tau K\left(0,\overline{S_0}^0+\Pi_0S(\alpha)\right)d\alpha+\ldots\right)\\
&-F\left(\overline{S_0}^0+\varepsilon\overline{S_1}^0+\varepsilon\tau\overline{S_0'}^0+\ldots,\varepsilon\int_0^\tau K\left(0,\overline{S_0}^0\right)d\alpha+\ldots\right)\\
=\ & \widetilde{F}+\varepsilon\overline{S_1}(t)\widetilde{F}_x+\varepsilon\int_0^t\overline{S_1}(a)K_y\left(t-a,\overline{S_0}(a)\right)da\widetilde{F}_y+\ldots\\
&+F\left(\overline{S_0}^0+\Pi_0S(\tau),0\right)+\varepsilon\left(\overline{S_1}^0+\tau\overline{S_0'}^0+\Pi_1S(\tau)\right)F_x\left(\overline{S_0}^0+\Pi_0S(\tau),0\right)\\
&+\varepsilon\left(\int_0^\tau K\left(0,\overline{S_0}^0+\Pi_0S(\alpha)\right)d\alpha\right)F_y\left(\overline{S_0}^0+\Pi_0S(\tau),0\right)\\
&-F\left(\overline{S_0}^0,0\right)-\varepsilon\left(\overline{S_1}^0+\tau\overline{S_0'}^0\right)F_x\left(\overline{S_0}^0,0\right)\\
&-\varepsilon\left(\int_0^\tau K\left(0,\overline{S_0}^0\right)d\alpha\right)F_y\left(\overline{S_0}^0,0\right)+\ldots
\end{aligned}$$

where we used the notation

$$\widetilde{F} = F\left(\overline{S_0}(t),\textstyle\int_0^t K\left(t-a,\overline{S_0}(a)\right)da\right) \qquad (307)$$

$$\widetilde{F}_x = F_x\left(\overline{S_0}(t),\textstyle\int_0^t K\left(t-a,\overline{S_0}(a)\right)da\right) \qquad (308)$$

$$\widetilde{F}_y = F_y\left(\overline{S_0}(t),\textstyle\int_0^t K\left(t-a,\overline{S_0}(a)\right)da\right) \qquad (309)$$

By equating terms of the zeroth order in ε depending on t, we obtain from (306) a nonlinear integral equation for $\overline{S_0}(t)$:

$$0 = F\left(\overline{S_0}(t),\int_0^t K\left(a,\overline{S_0}(t-a)\right)da\right). \qquad (310)$$

Assume that F and K are such that (310) has a unique solution $\overline{S_0}(t)$ for $t\geq 0$, with

$$\overline{S_0}^0 = S^* . \qquad (311)$$

By-equating terms of the zeroth order in ε depending on τ, we obtain from (306) a nonlinear differential equation for $\Pi_0 S(\tau)$:

$$\begin{aligned} \frac{d\Pi_0 S}{d\tau} &= F(S^* + \Pi_0 S(\tau), 0) - F(S^*, 0) \\ &= F(S^* + \Pi_0 S(\tau), 0). \end{aligned} \tag{312}$$

Here we used the fact that $F\left(\overline{S_0}(0), 0\right) = 0$ when $t = 0$ in (310). Taking into account (303), we get that $\Pi_0 S(\tau)$ must satisfy the initial condition

$$\Pi_0 S(0) = \Phi^0 - S^*. \tag{313}$$

Theorem 17 in the appendix deduces from the stability conditions (S1), (S2) and (S3) above that (312) has a unique solution for all $\tau \geq 0$ which satisfies an exponential estimate of the form

$$|\Pi_0 S(\tau)| \leq ce^{-\kappa\tau} \tag{314}$$

where c and κ are positive constants that do not depend on τ.

Equating terms of the order ε depending on t in (306), we arrive at the Volterra integral equation of the second kind for $\overline{S_1}(t)$:

$$\frac{d\overline{S_0}}{dt} = \overline{S_1}(t)\widetilde{F_x} + \int_0^t \overline{S_1}(a) K_y\left(t-a, \overline{S_0}(a)\right) da\widetilde{F_y}, \tag{315}$$

which can be written as:

$$\overline{S_1}(t) = -\int_0^t \overline{S_1}(a) K_y\left(t-a, \overline{S_0}(a)\right) da\frac{\widetilde{F_y}}{\widetilde{F_x}} + \frac{\frac{d\overline{S_0}}{dt}}{\widetilde{F_x}} \tag{316}$$

Finally, by comparing the terms of order ε depending on τ in (306) we obtain the linear ordinary differential equation for $\Pi_1 S(\tau)$:

$$\frac{d\Pi_1 S}{d\tau} = F_x(S^* + \Pi_0 S(\tau), 0)\Pi_1 S(\tau) + G(\tau), \tag{317}$$

with the inhomogeneity

$$\begin{aligned} G(\tau) &= \left(\overline{S_1}^0 + \tau\overline{S_0'}^0\right)\left(F_x\left(S^* + \Pi_0 S(\tau), 0\right) - F_x\left(S^*, 0\right)\right) \\ &+ \left(\int_0^\tau K\left(0, S^* + \Pi_0 S(\alpha)\right) d\alpha\right) F_y\left(S^* + \Pi_0 S(\tau), 0\right) \\ &- \left(\int_0^\tau K\left(0, S^*\right) d\alpha\right) F_y\left(S^*, 0\right) \\ &= \left(\overline{S_1}^0 + \tau\overline{S_0'}^0\right)\left(F_x\left(S^* + \Pi_0 S(\tau), 0\right) - F_x\left(S^*, 0\right)\right) \\ &+ \left(\int_0^\tau \left(K\left(0, S^* + \Pi_0 S(\alpha)\right) - K\left(0, S^*\right)\right) d\alpha\right) F_y\left(S^* + \Pi_0 S(\tau), 0\right) \\ &+ \left(\int_0^\tau K\left(0, S^*\right) d\alpha\right)\left(F_y\left(S^* + \Pi_0 S(\tau), 0\right) - F_y\left(S^*, 0\right)\right) \end{aligned} \tag{318}$$

and the initial condition

$$\Pi_1 S(0) = -\overline{S_1}^0. \tag{319}$$

The solution of this problem can be easily written out:

$$\Pi_1 S(\tau) = -\overline{S_1}^0 e^{-\int_0^\tau b(\sigma)d\sigma} + \int_0^\tau e^{-\int_\alpha^\tau b(\sigma)d\sigma} G(\alpha)\, d\alpha \tag{320}$$

where for all $\sigma \geq 0$,

$$b(\sigma) = -F_x\left(S^* + \Pi_0 S(\sigma), 0\right). \tag{321}$$

Since F_x is continuous, there is a $\delta > 0$ such that

$$F_x\left(S^* + x, 0\right) < 0 \tag{322}$$

for all $-\delta \leq x \leq \delta$. Moreover since $|\Pi_0 S(\tau)| \to 0$ exponentially as $\tau \to \infty$ there is $\tau_0 > 0$ such that

$$|\Pi_0 S(\tau)| \leq \delta \text{ for } \tau \geq \tau_0 \tag{323}$$

and thence

$$b_{\inf} = \inf_{\tau \geq \tau_0} b(\sigma) = -\sup_{\tau \geq \tau_0} F_x\left(S^* + \Pi_0 S(\sigma), 0\right) > 0. \tag{324}$$

Taking τ_0 as initial point of time, the solution of (317) can also be presented in the form

$$\Pi_1 S(\tau_0+\rho) = -\Pi_1 S(\tau_0)\, e^{-\int_{\tau_0}^{\tau_0+\rho} b(\sigma)d\sigma} + \int_{\tau_0}^{\tau_0+\rho} e^{-\int_{\alpha}^{\tau_0+\rho} b(\sigma)d\sigma} G(\alpha)\, d\alpha \quad (325)$$

From (318) we obtain an exponential estimate for the inhomogeneity $G(\tau)$:

$$\begin{aligned} |G(\tau)| &\le \left(\left|\overline{S_1}^{\,0}\right| + \tau\left|\overline{S_0}'^{\,0}\right|\right) \max_{|x|\le\delta} |F_{xx}(S^*+x,0)|\,|\Pi_0 S(\tau)| \\ &\quad + \left(\int_0^\tau \Pi_0 S(\alpha)\,d\alpha\right) \max_{|x|\le\delta}|K(0,S^*+x)| \max_{|x|\le\delta}|F_y(S^*+x,0)| \\ &\quad +\tau K(0,S^*) \max_{|x|\le\delta}|F_{xy}(S^*+x,0)|\,|\Pi_0 S(\tau)| \\ &\le (c_1+c_2\tau)\,e^{-\kappa\tau} \\ &\le c_3 e^{-\kappa\tau} \end{aligned} \quad (326)$$

for all $\tau \ge 0$, where c_1, c_2 and c_3 are some positive constants. In the last inequality we used the estimate

$$\tau e^{-\kappa\tau} = \left(\tau e^{-\frac{\kappa}{2}\tau}\right) e^{-\frac{\kappa}{2}\tau} \le \left(\max_{\tau\ge 0}\left(\tau e^{-\frac{\kappa}{2}\tau}\right)\right) e^{-\frac{\kappa}{2}\tau} = \frac{2}{e\kappa} e^{-\frac{\kappa}{2}\tau} \quad (327)$$

for $\tau \ge 0$. The exponential estimate for $\Pi_1 S(\tau)$ where $\tau \ge \tau_0$ now follows from (325) and (326):

$$\begin{aligned} |\Pi_1 S(\tau)| &= |\Pi_1 S(\tau_0 + (\tau-\tau_0))| \\ &\le |\Pi_1 S(\tau_0)|\, e^{-b_{\inf}(\tau-\tau_0)} + \int_{\tau_0}^{\tau_0+\rho} \left(c_3 e^{-\kappa\alpha}\right) d\alpha e^{-b_{\inf}(\tau-\tau_0)} \\ &= \left[\left(|\Pi_1 S(\tau_0)| + \frac{c_3}{\kappa} e^{-\kappa\tau_0}\right) e^{-b_{\inf}\tau_0}\right] e^{-b_{\inf}\tau} \end{aligned} \quad (328)$$

Higher order terms in the asymptotic expansion of the solution can be obtained in a similar way, and all terms of the boundary layer part can be shown to have exponential estimates.

12 Estimation of the remainder for leading order approximation

The exact solution of differential equation (293) can be represented as

$$S(t) = \overline{S_0}(t) + \Pi_0 S(\tau) + u(t), \tag{329}$$

where $\overline{S_0}(t)$ and $\Pi_0 S(\tau)$ denote the regular and boundary layer part of the zero order approximation respectively, and $u(t)$ is the error for the zero order approximation (or, so-called, remainder term).

Substituting (329) into equation (293) yields a nonlinear ordinary differential equation for the error function $u(t)$:

$$\begin{aligned} & \varepsilon \frac{d\overline{S_0}}{dt} + \frac{d\Pi_0 S}{d\tau} + \varepsilon \frac{du}{dt} \qquad (330) \\ = \; & F\left(\overline{S_0}(t) + \Pi_0 S(\tau) + u(t), \int_0^t K\left(t-a, \overline{S_0}(a) + \Pi_0 S\left(\frac{a}{\varepsilon}\right) + u(a)\right) da\right), \end{aligned}$$

$$\overline{S_0}(0) + \Pi_0 S(0) + u(0) = \Phi(0). \tag{331}$$

Because of (303), the initial condition for $u(t)$ simplifies to

$$u(0) = 0. \tag{332}$$

For the purpose of error analysis, equation (331) can be written as

$$\begin{aligned} \varepsilon \frac{du}{dt} = \; & -A(t)u(t) \\ & +B(t) \int_0^t \left[K(t-a, X_0(a) + u(a)) - K(t-a, X_0(a))\right] da \\ & +g(u,t) \qquad (333) \end{aligned}$$

where

$$X_0(t) = \overline{S_0}(t) + \Pi_0 S\left(\frac{t}{\varepsilon}\right), \tag{334}$$

is the zero order approximation, and $A(t)$, $B(t)$ and $g(u,t)$ are given by

$$\begin{aligned} A(t) &= -F_x\left(X_0(t), \int_0^t K\left(t-a, X_0(a)\right) da\right) && (335) \\ B(t) &= F_y\left(X_0(t) \int_0^t K\left(t-a, X_0(a)\right) da\right) && (336) \end{aligned}$$

$$\begin{aligned} g(u,t) = {} & F\left(X_0(t) + u(t), \int_0^t K\left(t-a, X_0(a) + u(a)\right) da\right) \\ & + A(t)u(t) \\ & - B(t) \int_0^t \left[K\left(t-a, X_0(a) + u(a)\right) - K\left(t-a, X_0(a)\right)\right] da \\ & - \varepsilon \frac{dX_0}{dt} \end{aligned} \tag{337}$$

The corresponding homogeneous equation

$$\frac{dU}{dt} = -\frac{A(t)}{\varepsilon} U \tag{338}$$

has the explicit solution

$$U(t) = c \exp\left(-\frac{1}{\varepsilon} \int_0^t A(\sigma) d\sigma\right) \tag{339}$$

with constant of integration c.

Using variation of constants, the nonlinear differential equation (333) for $u(t)$ can be rewritten as a nonlinear integral equation:

$$\begin{aligned} u(t) = {} & \int_0^t \exp\left(-\frac{1}{\varepsilon} \int_s^t A(\sigma) d\sigma\right) \\ & \left[\frac{B(s)}{\varepsilon} \int_0^s \left[K\left(t-a, X_0(a) + u(a)\right) - K\left(t-a, X_0(a)\right)\right] da - \frac{g(u,s)}{\varepsilon}\right] ds \\ =: {} & \Psi\left[u(t)\right]. \end{aligned} \tag{340}$$

Lemma 1

$$g(0,t) = O(\varepsilon) \tag{341}$$

uniformly in t.

Proof: By setting $u = 0$ in (337), we obtain

$$\begin{aligned} g(0,t) &= F\left(X_0(t), \int_0^t K(t-a, X_0(a))\,da\right) - \varepsilon\frac{dX_0}{dt} \\ &= F\left(X_0(t), \int_0^t K(t-a, X_0(a))\,da\right) - \varepsilon\frac{d\overline{S_0}}{dt} - F\left(\overline{S_0}(0) + \Pi_0 S(\frac{t}{\varepsilon}), 0\right). \\ &= F\left(X_0(t), \int_0^t K(t-a, X_0(a))\,da\right) - F\left(\overline{S_0}(t), \int_0^t K\left(t-a, \overline{S_0}(a)\right)da\right) \\ &- F\left(\overline{S_0}(0) + \Pi_0 S(\frac{t}{\varepsilon}), 0\right) + F\left(\overline{S_0}(0), 0\right) \\ &- \varepsilon\frac{d\overline{S_0}}{dt} \end{aligned} \tag{342}$$

It follows that

$$\begin{aligned} & g(0,t) + \varepsilon\frac{d\overline{S_0}}{dt} \\ = & \int_0^1 \frac{d}{d\sigma}\left[F\left(\overline{S_0} + \sigma\Pi_0 S, \int_0^t K\left(t-a, \overline{S_0} + \sigma\Pi_0 S\right)da\right) - F\left(S^* + \sigma\Pi_0 S, 0\right)\right]d\sigma \end{aligned} \tag{343}$$

Carrying out the differentiation in the integrand, we obtain:

$$\begin{aligned} & g(0,t) + \varepsilon\frac{d\overline{S_0}}{dt} \\ = & \int_0^1 \Pi_0 S F_x\left(\overline{S_0} + \sigma\Pi_0 S, \int_0^t K\left(t-a, \overline{S_0} + \sigma\Pi_0 S\right)da\right)d\sigma \\ & + \int_0^1 \int_0^t K_y\left(t-a, \overline{S_0} + \sigma\Pi_0 S\right)\Pi_0 S\,da F_y\left(\gamma_\sigma, \delta_\sigma\right)d\sigma \\ & - \int_0^1 \Pi_0 S F_x\left(S^* + \sigma\Pi_0 S, 0\right)d\sigma \\ & \int_0^1 \Pi_0 S\left(\overline{S_0} - S^*\right)F_{xx}\left(\gamma_1, \delta_1\right) + \int_0^t K\left(t-a, \overline{S_0} + \sigma\Pi_0 S\right)da F_{xy}\left(\tilde{\gamma}, \tilde{\delta}\right)d\sigma \\ & + \int_0^1 K_y\left(t-\tilde{a}, \overline{S_0}(\tilde{a}) + \sigma\Pi_0 S(\frac{\tilde{a}}{\varepsilon})\right)\int_0^t \Pi_0 S\,da F_y\left(\gamma_\sigma, \delta_\sigma\right)d\sigma, \end{aligned} \tag{344}$$

where

$$(\gamma_\sigma, \delta_\sigma) = \left(\overline{S_0} + \sigma\Pi_0 S, \int_0^t K\left(t-a, \overline{S_0} + \sigma\Pi_0 S\right) da\right) \tag{345}$$

and $\left(\widetilde{\gamma}, \widetilde{\delta}\right)$ is a suitable convex combinaton of the two points

$\left(\overline{S_0}(t) + \sigma\Pi_0 S(\frac{t}{\varepsilon}), \int_0^t K\left(t-a, \overline{S_0}(a) + \sigma\Pi_0 S(\frac{a}{\varepsilon})\right) da\right)$ and $\left(\overline{S_0}(0) + \sigma\Pi_0 S(\frac{t}{\varepsilon}), 0\right)$,

and where $\widetilde{a}$ is some point in the interval $(0,t)$. Now an upper bound can be established for $g(0,t)$ uniformly in $t \in [0,T]$, using the exponential estimate (314) for $\Pi_0 S(\tau)$:

$$\begin{aligned}
|g(0,t)| &\le ce^{-\kappa\frac{t}{\varepsilon}}\left(\left|\overline{S_0}(t) - \overline{S_0}(0)\right| \|F_{xx}\| + t\|K\|\|F_{xy}\|\right) \\
&\quad + \|K_y\| \int_0^t ce^{-\kappa\frac{a}{\varepsilon}} da \|F_y\| + \varepsilon \left\|\overline{S_0}'\right\| \\
&\le ce^{-\kappa\frac{t}{\varepsilon}}\left(t\left\|\overline{S_0}'\right\| \|F_{xx}\| + t\|K\|\|F_{xy}\|\right) \\
&\quad + \|K_y\| \left(\varepsilon\frac{c}{\kappa}\left(1 - e^{-\kappa\frac{t}{\varepsilon}}\right)\right)\|F_y\| + \varepsilon\left\|\overline{S_0}'\right\| \\
&\le \varepsilon c\left(e^{-\kappa\frac{t}{\varepsilon}}\frac{t}{\varepsilon}\right)\left(\left\|\overline{S_0}'\right\| \|F_{xx}\| + \|K\|\|F_{xy}\|\right) \\
&\quad + \varepsilon\frac{c}{\kappa}\|K_y\|\|F_y\|\left(1 - e^{-\kappa\frac{t}{\varepsilon}}\right) + \varepsilon\left\|\overline{S_0}'\right\| \qquad (346) \\
&\le \varepsilon\frac{c}{\kappa}\left[\frac{1}{e}\left(\left\|\overline{S_0}'\right\| \|F_{xx}\| + \|K\|\|F_{xy}\|\right) + \|K_y\|\|F_y\| + \left\|\overline{S_0}'\right\|\right] \\
&= O(\varepsilon), \qquad (347)
\end{aligned}$$

and hence (341).

The norms used in this estimate are the following:

$$\begin{aligned}
\|K\| &= \max\left\{\left|K\left(t-a,\overline{S_0}(a)+\sigma\Pi_0 S(\frac{a}{\varepsilon})\right)\right| : 0\le t\le T\ ,\ 0\le a\le t\ ,\ 0\le\sigma\le 1\right\}\\
\|K_y\| &= \max\left\{\left|K_y\left(t-a,\overline{S_0}(a)+\sigma\Pi_0 S(\frac{a}{\varepsilon})\right)\right| : 0\le t\le T\ ,\ 0\le a\le t\ ,\ 0\le\sigma\le 1\right\}\\
\|F_y\| &= \max\left\{\left|F_y\left(\overline{S_0}+\sigma\Pi_0 S,\int_0^t K\left(t-a,\overline{S_0}+\sigma\Pi_0 S\right)da\right)\right| : 0\le t\le T\ ,\ 0\le\sigma\le 1\right\}\\
\|F_{xx}\| &= \max\left\{\begin{array}{c} |\theta F_{xx}\left(\overline{S_0}+\sigma\Pi_0 S,\int_0^t K\left(t-a,\overline{S_0}+\sigma\Pi_0 S\right)da\right)\\ +(1-\theta)\,F_{xx}\left(S^{*\,0}+\sigma\Pi_0 S,0\right)| :\\ 0\le t\le T\ ,\ 0\le\sigma\le 1\ ,\ 0\le\theta\le 1\end{array}\right\}\\
\|F_{xy}\| &= \max\left\{\begin{array}{c} |\theta F_{xx}\left(\overline{S_0}+\sigma\Pi_0 S,\int_0^t K\left(t-a,\overline{S_0}+\sigma\Pi_0 S\right)da\right)\\ +(1-\theta)\,F_{xx}\left(S^{*\,0}+\sigma\Pi_0 S,0\right)| :\\ 0\le t\le T\ ,\ 0\le\sigma\le 1\ ,\ 0\le\theta\le 1\end{array}\right\}\\
\left\|\overline{S_0'}\right\| &= \max\left\{\left|\overline{S_0'}(t) : 0\le t\le T\right|\right\}
\end{aligned} \tag{348}$$

In deriving (347) we used the following:

$$\max\left\{e^{-\kappa\frac{t}{\varepsilon}}\frac{t}{\varepsilon}\mid 0\le t\le T \text{ and } \varepsilon>0\right\}=\max\left\{e^{-\kappa x}x\mid x\ge 0\right\}=\frac{1}{\kappa e}. \tag{349}$$

This immediately follows from the fact that $\frac{d}{dx}\left(e^{-\kappa x}x\right)=(1-\kappa x)\,e^{-\kappa x}$ has the root $x=1/\kappa$, and changes sign from positive to negative at this root. Hence the function $e^{-\kappa x}x$ has a local maximum at $x=1/\kappa$. Since the function $e^{-\kappa x}x$ vanishes at zero as well as for $x\to\infty$, this maximum is the global maximum in the interval $0\le x<\infty$., and its value is $e^{-\kappa\frac{1}{\kappa}}(1/\kappa)=1/(\kappa e)$. ■

Lemma 2

$$\|\Psi[0]\|=O(\varepsilon). \tag{350}$$

Proof: By Lemma 1, there is a positive constant c such that

$$|g(0,t)| \leq c\varepsilon \tag{351}$$

for all $0 \leq t \leq T$. By (298),

$$F_x\left(\overline{S}_0(t), \int_0^t K\left(t-a, \overline{S}_0(a)\right) da\right) \leq m < 0 \tag{352}$$

for $0 \leq t \leq T$ and some constant m. Because of the exponential estimate for the boundary function term $\Pi_0 S(\tau)$ there is a $\tau_0 > 0$ such that for $0 \leq t \leq T$,

$$A(t) = F_x\left(\overline{S}_0(t) + \Pi_0 S(\tau), \int_0^t K\left(t-a, \overline{S}_0(a) + \Pi_0 S\left(\frac{a}{\varepsilon}\right)\right) da\right) \leq \frac{m}{2} < 0. \tag{353}$$

It follows that

$$\begin{aligned} |\Psi[0](t)| &= \left|\int_0^t \exp\left(-\frac{1}{\varepsilon}\int_s^t A(\sigma)d\sigma\right)\left(-\frac{g(0,s)}{\varepsilon}\right) ds\right| \\ &\leq \int_0^t \exp\left(-\frac{1}{\varepsilon}\frac{m}{2}(t-s)\right)\frac{c\varepsilon}{\varepsilon} ds \\ &= c\frac{2\varepsilon}{m}\left(1-e^{-\frac{m}{\varepsilon}t}\right) \\ &\leq \frac{2c}{m}\varepsilon \end{aligned} \tag{354}$$

(350) has been shown. ■

Lemma 3 *Given positive constants c_1 and ε_0, there is a positive constant c_2 such that for all $0 < \varepsilon \leq \varepsilon_0$ and all u_1, $u_2 \in C^1([0,T])$ with $||u_1|| \leq c_1\varepsilon$ and $||u_2|| \leq c_1\varepsilon$, it follows that*

$$\max_{0\leq t\leq T} |g(u_1,t) - g(u_2,t)| \leq c_2\varepsilon \max_{0\leq t\leq T} |u_1(t) - u_2(t)|. \tag{355}$$

Proof: For all $0 \le t \le T$,

$$
\begin{aligned}
& g(u_1,t) - g(u_2,t) \qquad (356)\\
= \; & F\left(X_0(t) + u_1(t), \int_0^t K(t-a, X_0(a) + u_1(a)da\right) \\
& -F\left(X_0(t) + u_2(t), \int_0^t K(t-a, X_0(a) + u_2(a)da\right) \\
& -F_x\left(X_0(t), \int_0^t K(a, X_0(t-a)\right) u_1(t) \\
& +F_x\left(X_0(t), \int_0^t K(a, X_0(t-a)\right) u_2(t) \\
& -F_y\left(X_0(t), \int_0^t K(a, X_0(t-a)\right) \int_0^t K(t-a, X_0(a) + u_1(a))\, da \\
& +F_y\left(X_0(t), \int_0^t K(a, X_0(t-a)\right) \int_0^t K(t-a, X_0(a) + u_2(a))\, da \\
= \; & (u_1(t) - u_2(t)) \\
& \times F_x\left(X_0(t) + \theta_1 u_1(t) + \theta_1' u_2(t), \int_0^t K(t-a, X_0(a) + \theta_2 u_1(a) + \theta_2' u_2(a))\, da\right) \\
& + \int_0^t \left[K(t-a, X_0(a) + u_1(a)) - K(t-a, X_0(a) + u_2(a))\right] da \\
& \times F_y\left(X_0(t) + \theta_1 u_1(t) + \theta_1' u_2(t), \int_0^t K(t-a, X_0(a) + \theta_2 u_1(a) + \theta_2' u_2(a))\, da\right) \\
& - (u_1(t) - u_2(t)) \\
& \times F_x\left(X_0(t), \int_0^t K(t-a, X_0(a))\, da\right) \\
& - \int_0^t \left[K(t-a, X_0(a) + u_1(a)) - K(t-a, X_0(a) + u_2(a))\right] da \\
& \times F_y\left(X_0(t), \int_0^t K(a, X_0(t-a)\right)
\end{aligned}
$$

$$\begin{aligned}
= \quad & (u_1(t) - u_2(t))\,(\theta_1 u_1(t) + \theta_1' u_2(t))\, F_{xx}(\gamma_1(t), \vartheta_1(t)) \\
& + (u_1(t) - u_2(t)) \int_0^t \left[K(t-a, X_0(a) + \theta_2 u_1(a) + \theta_2' u_2(a)) - K(t-a, X_0(a))\right] \\
& \times F_{xy}(\gamma_1(t), \vartheta_1(t)) \\
& + \int_0^t \left[K(t-a, X_0(a) + u_1(a)) - K(t-a, X_0(a) + u_2(a))\right] da \\
& \times (\theta_1 u_1(t) + \theta_1' u_2(t))\, F_{yx}(\gamma_2(t), \vartheta_2(t)) \\
& + \int_0^t \left[K(t-a, X_0(a) + u_1(a)) - K(t-a, X_0(a) + u_2(a))\right] da \\
& \times \int_0^t \left[K(t-a, X_0(a) + \theta_2 u_1(a) + \theta_2' u_2(a)) - K(t-a, X_0(a))\right] da \\
& \times F_{yy}(\gamma_2(t), \vartheta_2(t))
\end{aligned}$$

for some $\theta_1 \in (0,1)$, $\theta_1' := 1 - \theta_1$, $\theta_2 \in (0,1)$, $\theta_2' := 1 - \theta_2$, and suitable intermediate points $\gamma_1(t)$, $\vartheta_1(t)$, $\gamma_2(t)$, $\vartheta_2(t)$. Now using the estimates

$$\begin{aligned}
|\theta_1 u_1(t) + \theta_1' u_2(t)| &\le \theta_1 |u_1(t)| + \theta_1' |u_2(t)| \\
&\le \theta_1 c_1 \varepsilon + \theta_1' c_1 \varepsilon \\
&= c_1 \varepsilon, \qquad (357)
\end{aligned}$$

we obtain:

$$\begin{aligned}
& \left| \int_0^t \left[K(t-a, X_0(a) + \theta_2 u_1(a) + \theta_2' u_2(a)) - K(t-a, X_0(a))\right] da \right| \\
\le \quad & \int_0^t \left|K(t-a, X_0(a) + \theta_2 u_1(a) + \theta_2' u_2(a)) - K(t-a, X_0(a))\right| da \\
= \quad & t \left|K(t-\widetilde{a}, X_0(\widetilde{a}) + \theta_2 u_1(\widetilde{a}) + \theta_2' u_2(\widetilde{a})) - K(t-\widetilde{a}, X_0(\widetilde{a}))\right| \\
= \quad & t \left|(\theta_2 u_1(\widetilde{a}) + \theta_2' u_2(\widetilde{a}))\, K_y(t-\widetilde{a}, \delta_3)\right| \\
\le \quad & T c_1 \varepsilon \, \|K_y\|, \qquad (358)
\end{aligned}$$

$$\left|\int_0^t \left[K(t-a, X_0(a)+u_1(a)) - K(t-a, X_0(a)+u_2(a))\right] da\right|$$

$$= \quad t\left|K(t-\overline{a}, X_0(\overline{a})+u_1(\overline{a})) - K(t-\overline{a}, X_0(\overline{a})+u_2(\overline{a}))\right|$$

$$= \quad t\left|(u_1(\overline{a})-u_2(\overline{a}))\, K_y(t-\overline{a}, \delta_4)\right|$$

$$\leq \quad T\left\|K_y\right\|\left\|u_1-u_2\right\| \qquad (359)$$

with suitable intermediate points $\widetilde{a}$, $\overline{a}$, δ_3, δ_4. Finally, we have:

$$\begin{aligned} |g(u_1,t)-g(u_2,t)| \leq\ & \|u_1-u_2\|\, c_1\varepsilon \|F_{xx}\| \\ & + \|u_1-u_2\|\, Tc_1\varepsilon \|K_y\| \|F_{xy}\| \\ & + T\|K_y\| \|u_1-u_2\|\, c_1\varepsilon \|F_{yx}\| \\ & + (T\|K_y\| \|u_1-u_2\|\, c_1\varepsilon \|F_{yx}\|)(Tc_1\varepsilon\|K_y\|)\|F_{yy}\|, \\ \leq\ & c_2\varepsilon \|u_1-u_2\| \end{aligned} \qquad (360)$$

where all norms are maximum norms as in the proof of Lemma 2, and

$$c_2 := 4c_1 \max\left(\|F_{xx}\|, T\|K_y\|\|F_{xy}\|, T^2\|K_y\|^2\|F_{xy}\|\|F_{yy}\|\right), \qquad (361)$$

The correctness of statement (355) follows by taking the maximum over $0 \leq t \leq T$ on the left-hand side of (360). ■

Lemma 4 *Given positive constants* c_1 *and* ε_0, *there exists a positive constant* c_3 *such that for all* $0 < \varepsilon \leq \varepsilon_0$ *and all* u_1, $u_2 \in C^1([0,T])$ *with* $\|u_1\| \leq c_1\varepsilon$ *and* $\|u_2\| \leq c_1\varepsilon$, *the following inequality holds:*

$$\max_{0\leq t\leq T} |\Psi[u_1](t) - \Psi[u_2](t)| \leq c_3\varepsilon \max_{0\leq t\leq T} |u_1(t)-u_2(t)|. \qquad (362)$$

Proof: By Lemma 3, there is a positive constant c_2 such that for every $0 < \varepsilon \leq \varepsilon_0$ and every u_1, $u_2 \in C^1([0,T])$ with $\|u_1\| \leq c_1\varepsilon$ and $\|u_2\| \leq c_1\varepsilon$, we have

$$\sup_{0\leq t\leq T} |g(u_1,t) - g(u_2,t)| \leq c_2\varepsilon \sup_{0\leq t\leq T} |u_1(t) - u_2(t)|. \tag{363}$$

Then for all $t \in [0,T]$, we have the estimates

$$\begin{aligned}
&|\Psi[u_1](t) - \Psi[u_2](t)| \\
\leq\ & \int_0^t \exp\left(-\frac{1}{\varepsilon}\int_s^t A(\sigma)d\sigma\right) \\
&\times \frac{B(s)}{\varepsilon}\int_0^s |K(t-a, X_0(a)+u_1(a)) - K(t-a, X_0(a)+u_2(a))|\, dads \\
&+ \int_0^t \exp\left(-\frac{1}{\varepsilon}\int_s^t A(\sigma)d\sigma\right)\frac{|g(u_1,s)-g(u_2,s)|}{\varepsilon}ds \\
\leq\ & \int_0^t \exp\left(-\frac{1}{\varepsilon}(t-s)\, m_A\right) \\
&\frac{B(s)}{\varepsilon}\int_0^s |K(t-a, X_0(a)+u_1(a)) - K(t-a, X_0(a)+u_2(a))|\, dads \\
&+ \int_0^t \exp\left(-\frac{1}{\varepsilon}(t-s)\, m_A\right) c_2\, \|u_1 - u_2\|\, ds
\end{aligned} \tag{364}$$

Changing the order of integration, we obtain:

$$\begin{aligned}
|\Psi u_1(t) - \Psi u_2(t)| &\leq \int_{a=0}^{t} \int_{s=0}^{t-a} \exp\left(-\frac{1}{\varepsilon}(t-s)\, m_A\right) \\
&\quad \frac{B(s)}{\varepsilon} \left| K\left(t-a, X_0(a)+u_1(a)\right) - K\left(t-a, X_0(a)+u_2(a)\right)\right| ds da \\
&\quad + \int_{s=0}^{t} \exp\left(-\frac{1}{\varepsilon}(t-s)\, m_A\right) c_2 \|u_1 - u_2\|\, ds \\
&= \int_{s=0}^{t} \left| K\left(t-s, X_0(s)+u_1(s)\right) - K\left(t-s, X_0(s)+u_2(s)\right)\right| \\
&\quad \left(\int_{a=0}^{t-s} \exp\left(-\frac{1}{\varepsilon}(t-a)\, m_A\right) \frac{B(a)}{\varepsilon} da \right) ds \\
&\quad + c_2 \|u_1 - u_2\| \int_0^t \exp\left(-\frac{1}{\varepsilon}(t-s)\, m_A\right) ds \\
&= \int_{s=0}^{t} \left| K\left(t-s, X_0(s)+u_1(s)\right) - K\left(t-s, X_0(s)+u_2(s)\right)\right| \\
&\quad \left(\int_{b=s}^{t} \exp\left(-\frac{1}{\varepsilon} b m_A\right) \frac{B(t-b)}{\varepsilon} db \right) ds \\
&\quad + c_2 \|u_1 - u_2\| \frac{\varepsilon}{m_A} \left(1 - \exp\left(-\frac{m_A}{\varepsilon} t\right)\right) \\
&\leq \int_{s=0}^{t} \|K_y\| \, |u_1(s) - u_2(s)| \\
&\quad \frac{\|B\|}{m_A} \left[\exp\left(-\frac{m_A}{\varepsilon} s\right) - \exp\left(-\frac{m_A}{\varepsilon} t\right)\right] ds \\
&\quad + c_2 \|u_1 - u_2\| \frac{\varepsilon}{m_A} \left(1 - \exp\left(-\frac{m_A}{\varepsilon} t\right)\right) \\
&\leq \frac{\|K_y\| \, \|B\|}{m_A} \int_{s=0}^{t} |u_1(s) - u_2(s)| \left[\exp\left(-\frac{m_A}{\varepsilon} s\right) - \exp\left(-\frac{m_A}{\varepsilon} t\right)\right] ds \\
&\quad + \frac{c_2}{m_A} \varepsilon \|u_1 - u_2\| \\
&\leq \frac{\|K_y\| \, \|B\|}{m_A} \|u_1 - u_2\| \int_s^t \left[\exp\left(-\frac{m_A}{\varepsilon} s\right) - \exp\left(-\frac{m_A}{\varepsilon} t\right)\right] ds \\
&\quad + \frac{c_2}{m_A} \varepsilon \|u_1 - u_2\|
\end{aligned} \tag{365}$$

Since

$$\begin{aligned}
\int_0^t \left(\exp\left(-\frac{m_A}{\varepsilon} s\right) - \exp\left(-\frac{m_A}{\varepsilon} t\right)\right) ds &= \left(1 - e^{-\frac{m_A}{\varepsilon} t}\right) \frac{\varepsilon}{m_A} - e^{-\frac{m_A}{\varepsilon} t} t \\
&\leq \frac{\varepsilon}{m_A},
\end{aligned} \tag{366}$$

it follows that

$$\|\Psi[u_1]-\Psi[u_2]\| \leq \left(\frac{\|K_y\|\,\|B\|}{m_A^2}+\frac{c_2}{m_A}\right)\varepsilon\,\|u_1-u_2\| \tag{367}$$

So the inequality (362) is satisfied with

$$c_3=\frac{\|K_y\|\,\|B\|}{m_A^2}+\frac{c_2}{m_A}. \qquad \blacksquare \tag{368}$$

Theorem 6 *Initial value problem (331), (332) for the remainder term $u(t)$ has a solution that is unique and fulfills the estimate*

$$u(t)=O(\varepsilon). \tag{369}$$

Proof: By virtue of Lemma 4, there are positive constants ε_1, c_1 and c_3 such that for all ε with $0<\varepsilon\leq\varepsilon_1$, we have a)

$$\|\Psi[0]\|\leq\frac{1}{2}c_1\varepsilon, \tag{370}$$

b)

$$\|\Psi[u_1]-\Psi[u_2]\|\leq c_3\varepsilon\,\|u_1-u_2\|. \tag{371}$$

for all u_1, $u_2\in C^1([0,T])$ with $\|u_1\|\leq c_1\varepsilon$ and $\|u_2\|\leq c_1\varepsilon$. Then for all $\varepsilon\in\left(0,\min\left(\frac{1}{2c_3},\varepsilon_1\right)\right)$, and all u_1, $u_2\in C^1([0,T])$ with $\|u_1\|\leq c_1\varepsilon$ and $\|u_2\|\leq c_1\varepsilon$, we have

$$\|\Psi[u_1]-\Psi[u_2]\|\leq\frac{1}{2}\|u_1-u_2\|. \tag{372}$$

Furthermore, by the triangle equality it follows that

$$\begin{aligned}\|\Psi[v]\| &\leq \|\Psi[v]-\Psi[0]\|+\|\Psi[0]\| \\ &\leq \frac{1}{2}\|v-0\|+\frac{1}{2}c_1\varepsilon \\ &\leq c_1\varepsilon\end{aligned} \tag{373}$$

for all $v \in C^1([0,T])$ with $||v|| \leq c_1\varepsilon$.

This means that Ψ is a contraction operator and maps the set of all $v \in C^1([0,T])$ with $||v|| \leq c_1\varepsilon$ into itself. Therefore by Banach's fixed point theorem, there is a unique fixed point $u \in C^1([0,T])$ with $||u|| \leq c_1\varepsilon$ such that $\Psi[u] = u$. This fixed point is the unique solution of the nonlinear integral equation (340). Thus we have shown that $u = O(\varepsilon)$. ■

Part IV

Periodic solutions

13 Seedling equation in the infinite time domain

Let us consider a particular seedling equation, not as an initial value problem as in parts I and II of the thesis, but in the infinite time domain:

$$\varepsilon \frac{ds}{dt} = -s(t) + \max\left(0, 1 - \lambda \int_{-\infty}^{t} (t-a)\, e^{-(t-a)} s(a)\, da\right) \text{ for } -\infty < t < \infty. \tag{374}$$

The goal in this part of the thesis is to find periodic solutions of (374) and of the quasi-equilibrium problem associated with it:

$$s(t) = \max\left(0, 1 - \lambda \int_{-\infty}^{t} (t-a)\, e^{-(t-a)} s(a)\, da\right) \text{ for } -\infty < t < \infty. \tag{375}$$

Existence and stability of such periodic solutions will be shown to depend on the parameter λ. First let us see if there are any constant solutions (steady states) and examine their stability.

14 Quasi-equilibrium problem: stability analysis of the steady state

Theorem 7 *Integral equation (375) has exactly one steady state, given by*

$$s^* = \frac{1}{1+\lambda}. \tag{376}$$

The steady state is stable for all $\lambda > 0$.

Proof: If $s^* > 0$ is a steady state of (375), its satisfies

$$\begin{aligned} s^* &= 1 - \lambda \int_{-\infty}^{t} (t-a)\, e^{-(t-a)} s^* da \\ &= 1 - \lambda s^* \int_{-\infty}^{t} (t-a)\, e^{-(t-a)} da \\ &= 1 - \lambda s^* \int_{0}^{\infty} u e^{-u} du \\ &= 1 - \lambda s^*, \end{aligned} \tag{377}$$

that is

$$s^* = \frac{1}{1+\lambda}. \tag{378}$$

Stability analysis of the steady state is performed by substituting a periodic perturbation

$$s(t) = s^* + Ze^{\omega t}, \tag{379}$$

into (375) and solving the resulting equation for the complex frequency ω. The steady state is stable if and only if the real part of ω turns out to be negative. The amplitude $|Z|$ of the perturbation may be chosen smaller than a suitable upper bound:

$$0 < |Z| \leq Z_0. \tag{380}$$

In our case, let us choose

$$0 < Z_0 < s^* \tag{381}$$

to ensure that the perturbed solution (379) is positive for $t = 0$. Substitution of (379) into (375) yields:

$$\begin{aligned} s^* + Ze^{\omega t} &= 1 - \lambda \int_{-\infty}^{t} \left(s^* + Ze^{\omega a}\right)(t-a)\, e^{-(t-a)} da \\ &= 1 - \lambda \int_{-\infty}^{t} s^* (t-a)\, e^{-(t-a)} da - \lambda \int_{-\infty}^{t} Ze^{\omega a} (t-a)\, e^{-(t-a)} da \\ &= s^* - \lambda \int_{-\infty}^{t} Ze^{\omega a} (t-a)\, e^{-(t-a)} da. \end{aligned}$$

Subtract s^* and divide by Z on both sides to get

$$e^{\omega t} = -\lambda \int_{-\infty}^{t} e^{\omega a} (t-a)\, e^{-(t-a)} da. \tag{382}$$

Let us differentiate (382) with respect to time:

$$\begin{aligned} \omega e^{\omega t} &= -\lambda \int_{-\infty}^{t} e^{\omega a} (1 - t + a)\, e^{-(t-a)} da \\ &= -\lambda \int_{-\infty}^{t} e^{\omega a} e^{-(t-a)} da + \lambda \int_{-\infty}^{t} e^{\omega a} (t-a)\, e^{-(t-a)} da \\ &= -\lambda \int_{-\infty}^{t} e^{\omega a} e^{-(t-a)} da - e^{\omega t} \end{aligned}$$

Differentiating again yields:

$$\begin{aligned} \omega^2 e^{\omega t} &= -\lambda e^{\omega t} + \lambda \int_{-\infty}^{t} e^{\omega a} e^{-(t-a)} da - \omega e^{\omega t} \\ &= -\lambda e^{\omega t} + \left(-\omega e^{\omega t} - e^{\omega t}\right) - \omega e^{\omega t} \\ &= (-\lambda - 2\omega - 1)\, e^{\omega t}. \end{aligned}$$

We thus obtain a quadratic equation for ω :

$$(\omega + 1)^2 = -\lambda. \tag{383}$$

The solutions are

$$\omega = -1 \pm i\sqrt{\lambda}. \tag{384}$$

The real part of ω is -1, therefore the steady state $s^* = 1/(\lambda+1)$ is stable for all $\lambda > 0$. ■

Note that the complex frequency (384) does not correspond to a meaningful solution of (375) in the infinite time domain, because the integral on the right side diverges. Theorem 18 in the Appendix contains a proof of asymptotic stability for the quasi-equilibrium problem in the positive time domain,

$$\begin{aligned} s(t) &= 1-\lambda\int_0^t s(a)(t-a)e^{-(t-a)}da-\lambda e^{-t}\int_t^\infty \varphi(a-t)\,da \qquad (385)\\ &= 1-\lambda\int_0^t s(a)(t-a)e^{-(t-a)}da-\lambda e^{-t}\int_0^\infty \varphi(u)(t+u)\,du, \end{aligned}$$

when the initial age density function $\varphi(a)$ is in a suitable neighborhood of the steady state age density s^*e^{-a}.

15 Nonexistence of positive periodic solutions besides the constant solution

For positive solutions $s(t)$, (375) simplifies to

$$s(t) = 1-\lambda\int_{-\infty}^t (t-a)e^{-(t-a)}s(a)\,da \text{ for } -\infty < t < \infty. \qquad (386)$$

Let us assume the existence of a positive periodic solution $s(t)$ with a certain period $T > 0$. Then we have

$$\begin{aligned}
\int_{-\infty}^{0} (t-a)\, e^{-(t-a)} s(a)\, da &= \sum_{k=1}^{\infty} \int_{-kT}^{-(k-1)T} (t-a)\, e^{-(t-a)} s(a)\, da \qquad (387) \\
&= \sum_{k=1}^{\infty} \int_{0}^{T} (t-u+kT)\, e^{-(t-u+kT)} s(u-kT)\, du \\
&= \int_{0}^{T} s(u) \sum_{k=1}^{\infty} (t-u+kT)\, e^{-(t-u+kT)} du \\
&= \int_{0}^{T} s(u)\, e^{-(t-u)} \left((t-u) \sum_{k=1}^{\infty} e^{-kT} + T \sum_{k=1}^{\infty} k e^{-kT} \right) du \\
&= \int_{0}^{T} s(u)\, e^{-(t-u)} \left((t-u) \frac{e^{-T}}{1-e^{-T}} + T \frac{e^{-T}}{(1-e^{-T})^2} \right) du \\
&= \frac{e^{-T}}{1-e^{-T}} \int_{0}^{T} s(u)\, e^{-(t-u)} (t-u)\, du \\
&\quad + \frac{Te^{-T}}{(1-e^{-T})^2} \int_{0}^{T} s(u)\, e^{-(t-u)} du \\
&= \left(\frac{e^{-T}}{1-e^{-T}} te^{-t} + \frac{Te^{-T}}{(1-e^{-T})^2} e^{-t} \right) \int_{0}^{T} s(u)\, e^{u} du \\
&\quad - \frac{e^{-T}}{1-e^{-T}} e^{-t} \int_{0}^{T} s(u)\, ue^{u} du
\end{aligned}$$

Substitution into (386) yields:

$$\begin{aligned}
s(t) &= 1 - \lambda \left(\frac{e^{-T}}{1-e^{-T}} te^{-t} + \frac{Te^{-T}}{(1-e^{-T})^2} e^{-t} \right) \int_{0}^{T} s(u)\, e^{u} du \qquad (388) \\
&\quad + \lambda \frac{e^{-T}}{1-e^{-T}} e^{-t} \int_{0}^{T} s(u)\, ue^{u} du - \lambda \int_{0}^{t} (t-a)\, e^{-(t-a)} s(a)\, da \\
&= 1 - \lambda (At+B)\, e^{-t} I_1(T) + \lambda A e^{-t} I_2(T) - \lambda t e^{-t} I_1(t) + \lambda e^{-t} I_2(t),
\end{aligned}$$

where we used the notations

$$A = \frac{e^{-T}}{1-e^{-T}}, \tag{389}$$

$$B = \frac{Te^{-T}}{\left(1-e^{-T}\right)^2}, \tag{390}$$

$$I_1(t) = \int_0^t s(u)\, e^u du, \tag{391}$$

$$I_2(t) = \int_0^t s(u)\, ue^u du. \tag{392}$$

By differentiating (388) twice with respect to t, we get

$$\begin{aligned} s'(t) &= -\lambda(-At + A - B)\, e^{-t} I_1(T) - \lambda A e^{-t} I_2(T) \qquad (393) \\ &\quad -\lambda(1-t)\, e^{-t} I_1(t) - \lambda e^{-t} I_2(t), \\ s''(t) &= -\lambda(At - 2A + B)\, e^{-t} I_1(T) + \lambda A e^{-t} I_2(T) \qquad (394) \\ &\quad -\lambda s(t) - \lambda(t-2)\, e^{-t} I_1(t) + \lambda e^{-t} I_2(t). \end{aligned}$$

Adding (393), (394) yields

$$s'(t) + s''(t) = \lambda A e^{-t} I_1(T) - \lambda s(t) + \lambda e^{-t} I_1(t), \tag{395}$$

which can be solved for $I_1(t)$:

$$I_1(t) = e^t \left(s(t) + \frac{s'(t) + s''(t)}{\lambda} \right) - A I_1(T). \tag{396}$$

Substitution of (391) into (396) yields

$$\int_0^t s(u)\, e^u du = e^t \left(s(t) + \frac{s'(t) + s''(t)}{\lambda} \right) - A I_1(T). \tag{397}$$

By taking the derivative with respect to t, we get

$$e^t s(t) = e^t \left(s(t) + \left(1 + \frac{1}{\lambda}\right) s'(t) + \frac{2}{\lambda} s''(t) + \frac{1}{\lambda} s'''(t) \right), \tag{398}$$

or, equivalently,

$$s''' + 2s'' + (\lambda + 1)\, s' = 0. \tag{399}$$

Integrating once in t, we get

$$s'' + 2s' + (\lambda + 1)\, s = c \tag{400}$$

for some constant of integration c. (400) is the differential equation of a damped harmonic oscillator, and has no periodic solutions except constant ones.

This result can be stated as

Theorem 8 *The only positive periodic solution of (375) is the constant solution* $s(t) = \frac{1}{1+\lambda}$.

16 Non-existence of periodic solutions for the quasi-equilibrium problem

Let us find a solution $s(t)$ of (375) with period $T > 0$ that satisfies the conditions

$$s(0) = 0, \tag{401}$$

$$s(t) > 0 \text{ for } 0 < t < T_1, \tag{402}$$

$$s(t) = 0 \text{ for } T_1 \le t \le T, \tag{403}$$

for certain $0 < T_1 < T$. Then, similar to (387), but employing the fact that $s(t)$ vanishes on the intervals $[-kT, -kT + T_1]$ for $k = 1, 2, 3, \ldots$, we have

$$\begin{aligned}\int_{-\infty}^{0} (t-a)\, e^{-(t-a)} s(a)\, da &= \sum_{k=1}^{\infty} \int_{-kT}^{-(k-1)T} (t-a)\, e^{-(t-a)} s(a)\, da \qquad (404)\\ &= \sum_{k=1}^{\infty} \int_{-kT}^{-kT+T_1} (t-a)\, e^{-(t-a)} s(a)\, da\\ &= \sum_{k=1}^{\infty} \int_{0}^{T_1} (t-u+kT)\, e^{-(t-u+kT)} s(u-kT)\, du = \ldots\\ &= \left(\frac{e^{-T}}{1-e^{-T}} te^{-t} + \frac{Te^{-T}}{(1-e^{-T})^2} e^{-t}\right) \int_{0}^{T_1} s(u)\, e^{u} du\\ &\quad - \frac{e^{-T}}{1-e^{-T}} e^{-t} \int_{0}^{T_1} s(u)\, ue^{u} du \text{ for } -\infty < t < \infty.\end{aligned}$$

In complete analogy to (388), and using the same notations (389) - (392), we obtain the equation

$$\begin{aligned}s(t) &= 1 - \lambda \left(\frac{e^{-T}}{1-e^{-T}} te^{-t} + \frac{Te^{-T}}{(1-e^{-T})^2} e^{-t}\right) \int_{0}^{T_1} s(u)\, e^{u} du \qquad (405)\\ &\quad + \lambda \frac{e^{-T}}{1-e^{-T}} e^{-t} \int_{0}^{T_1} s(u)\, ue^{u} du - \lambda \int_0^t (t-a)\, e^{-(t-a)} s(a)\, da\\ &= 1 - \lambda (At + B)\, e^{-t} I_1(T_1) + \lambda A e^{-t} I_2(T_1) - \lambda t e^{-t} I_1(t) + \lambda e^{-t} I_2(t)\end{aligned}$$

in the interval $0 \leq t \leq T_1$, which leads to the differential equation

$$s''' + 2s'' + (\lambda + 1)\, s' = 0. \qquad (406)$$

(406) is identical to equation (399). The difference is that instead of looking for a periodic positive solution in the infinite domain $-\infty < t < \infty$, we are now considering a solution in the bounded interval $0 \leq t \leq T_1$, with boundary

conditions

$$s(0) = 0, \tag{407}$$

$$s(T_1) = 0. \tag{408}$$

Theorem 9 *Problem (406) - (408) has infinitely many solutions.*

a) If

$$\sin\sqrt{\lambda}T_1 = 0, \tag{409}$$

the solutions are

$$s_\alpha(t) = \alpha e^{-t}\sin\sqrt{\lambda}t \text{ for } 0 \le t \le T, \tag{410}$$

where $-\infty < \alpha < \infty$ can be arbitrarily chosen.

b) If

$$\sin\sqrt{\lambda}T_1 \neq 0, \tag{411}$$

the solutions are

$$s_\alpha(t) = \alpha\left(1 - e^{-t}\cos\sqrt{\lambda}t + \beta e^{-t}\sin\sqrt{\lambda}t\right), \tag{412}$$

where $-\infty < \alpha < \infty$ can be arbitrarily chosen, and

$$\beta = \frac{e^{T_1} - \cos\sqrt{\lambda}T_1}{-\sin\sqrt{\lambda}T_1}. \tag{413}$$

Proof: Integrating (406) leads to the second order differential equation

$$s'' + 2s' + (\lambda + 1)s = c_1, \tag{414}$$

with constant of integration $-\infty < c_1 < \infty$. Its general solution is found to be

$$s(t) = \frac{c_1}{\lambda + 1} + e^{-t}\left(c_2\cos\sqrt{\lambda}t + c_3\sin\sqrt{\lambda}t\right) \tag{415}$$

with arbitrary constants $-\infty < c_2, c_3 < \infty$. The claims of the theorem are easily verified by inserting boundary conditions (407), (408) into (415). ■

In the following we derive a periodic solution of (375) with conditions (401) - (403). This solution is of the form given in Theorem 9, and the period T as well as the parameter λ will be expressed in terms of T_1. Let us first show the nonexistence of solutions for

Case 1:

$$\sin\sqrt{\lambda}T_1 = 0. \tag{416}$$

By Theorem 9, part (a), the solution is of the form

$$s(t) = \alpha e^{-t}\sin\sqrt{\lambda}t \text{ for } 0 \le t \le T, \tag{417}$$

with some constant α. Then

$$\begin{aligned} I_1(t) &= \int_0^t s(u)\, e^u du \qquad (418) \\ &= \alpha\int_0^t \sin\sqrt{\lambda}u du \\ &= \frac{\alpha}{\sqrt{\lambda}}\cos\sqrt{\lambda}t, \\ I_2(t) &= \int_0^t s(u)\, ue^u du \qquad (419) \\ &= \alpha\int_0^t u\sin\sqrt{\lambda}u du \\ &= \alpha\frac{\sin\sqrt{\lambda}t - \sqrt{\lambda}t\cos\sqrt{\lambda}t}{\lambda} \end{aligned}$$

in the interval $0 \le t \le T_1$. Thus, the only constant term in t on the right side of equation (405) is the term 1. Since there is *no* constant term in t on the left side of this equation, we have a contradiction. Therefore there are no solutions in Case 1.

Case 2:

$$\sin \sqrt{\lambda} T_1 \neq 0. \tag{420}$$

By Theorem 9, part (b), the solution is of the form

$$s(t) = \alpha \left(1 - e^{-t} \cos \sqrt{\lambda} t + \beta e^{-t} \sin \sqrt{\lambda} t\right), \tag{421}$$

for a certain α, and β being given in (413). Then

$$\begin{aligned} I_1(t) &= \int_0^t s(u) e^u du \qquad (422) \\ &= \alpha \int_0^t \left(e^u - \cos \sqrt{\lambda} u + \beta \sin \sqrt{\lambda} u\right) du \\ &= \alpha \left(e^t - 1 - \frac{1}{\sqrt{\lambda}} \sin \sqrt{\lambda} t + \frac{\beta}{\sqrt{\lambda}} \left(1 - \cos \sqrt{\lambda} t\right)\right), \\ I_2(t) &= \int_0^t s(u) u e^u du \qquad (423) \\ &= \alpha \int_0^t u \left(e^u - \cos \sqrt{\lambda} u + \beta \sin \sqrt{\lambda} u\right) du \\ &= \alpha \left((t-1) e^t + 1\right) \\ &\quad + \alpha \left(-\frac{1}{\sqrt{\lambda}} t \sin \sqrt{\lambda} t + \frac{1}{\lambda} \left(1 - \cos \sqrt{\lambda} t\right)\right) \\ &\quad + \alpha \left(-\frac{\beta}{\sqrt{\lambda}} t \cos \sqrt{\lambda} t + \frac{\beta}{\lambda} \sin \sqrt{\lambda} t\right), \end{aligned}$$

in the interval $0 \leq t \leq T_1$. Comparing the constant terms on both sides of equation (405) yields

$$\alpha = 1 + \lambda(-\alpha), \tag{424}$$

that is

$$\alpha = \frac{1}{1+\lambda} = s^*. \tag{425}$$

From the infinite set of solutions (421), only one remained:

$$s(t) = \frac{1}{1+\lambda}\left(1 - e^{-t}\cos\sqrt{\lambda}t + \beta e^{-t}\sin\sqrt{\lambda}t\right). \tag{426}$$

Theorem 10 *For any solution of (375) with conditions (401) - (403), we have*

$$\frac{\pi}{\sqrt{\lambda}} < T_1 < \frac{2\pi}{\sqrt{\lambda}}, \tag{427}$$

$$\beta > e^{\frac{\pi}{\sqrt{\lambda}}} - 1. \tag{428}$$

Proof: Using elementary calculus it is easily seen that the function

$$f(t) = \frac{e^t - \cos\sqrt{\lambda}t}{\sin\sqrt{\lambda}t} \tag{429}$$

is strictly increasing in the interval $0 < t < \frac{\pi}{\sqrt{\lambda}}$. By L'Hôpital's rule, we find the limit for $t \to 0$ to be

$$\lim_{t\to 0} f(t) = \lim_{t\to 0}\frac{e^t - \cos\sqrt{\lambda}t}{\sin\sqrt{\lambda}t} = \lim_{t\to 0}\frac{e^t + \sqrt{\lambda}\sin\sqrt{\lambda}t}{\sqrt{\lambda}\cos\sqrt{\lambda}t} = \frac{1}{\sqrt{\lambda}}. \tag{430}$$

Since on account of (413) we have

$$\beta = -f(T_1), \tag{431}$$

it follows that

$$\beta < -\frac{1}{\sqrt{\lambda}} \tag{432}$$

for $0 < T_1 < \frac{\pi}{\sqrt{\lambda}}$. But by virtue of (426), this implies

$$s'(0) = \frac{1}{1+\lambda}\left(1 + \beta\sqrt{\lambda}\right) < \frac{1}{1+\lambda}(1 + (-1)) = 0, \tag{433}$$

in contradiction to conditions (401), (402). Above, nonexistence of solutions was shown for $\sin\left(\sqrt{\lambda}T_1\right) = 0$, that is in particular for $T_1 = \frac{\pi}{\sqrt{\lambda}}$. Therefore, the first zero T_1 of the damped oscillation (426) must ocur in the second half-period, which implies (427). As a consequence, by equation (413) we obtain a lower bound for β :

$$\beta = \frac{e^{T_1} - \cos\sqrt{\lambda}T_1}{-\sin\sqrt{\lambda}T_1} > \frac{e^{\frac{\pi}{\sqrt{\lambda}}} - 1}{-(-1)} = e^{\frac{\pi}{\sqrt{\lambda}}} - 1. \quad \blacksquare \tag{434}$$

Still T and T_1 are undetermined. Comparing terms in te^{-t} on both sides of (405) yields

$$0 = -\lambda A I_1(T_1) - \frac{\lambda}{1+\lambda}\left(-1 - \frac{\beta}{\sqrt{\lambda}}\right), \tag{435}$$

or, solved for A,

$$\begin{aligned} A &= \frac{1 - \frac{\beta}{\sqrt{\lambda}}}{(1+\lambda) I_1(T_1)} \qquad (436) \\ &= \frac{1 - \frac{\beta}{\sqrt{\lambda}}}{e^{T_1} - 1 - \frac{1}{\sqrt{\lambda}}\sin\sqrt{\lambda}T_1 + \frac{\beta}{\sqrt{\lambda}}\left(1 - \cos\sqrt{\lambda}T_1\right)} \\ &= \frac{\sqrt{\lambda} - \frac{e^{T_1} - \cos\sqrt{\lambda}T_1}{-\sin\sqrt{\lambda}T_1}}{\sqrt{\lambda}(e^{T_1} - 1) - \sin\sqrt{\lambda}T_1 + \frac{e^{T_1} - \cos\sqrt{\lambda}T_1}{-\sin\sqrt{\lambda}T_1}\left(1 - \cos\sqrt{\lambda}T_1\right)} \\ &= \frac{\sqrt{\lambda}\sin\sqrt{\lambda}T_1 + e^{T_1} - \cos\sqrt{\lambda}T_1}{\sqrt{\lambda}(e^{T_1} - 1)\sin\sqrt{\lambda}T_1 - \sin^2\sqrt{\lambda}T_1 - \left(e^{T_1} - \cos\sqrt{\lambda}T_1\right)\left(1 - \cos\sqrt{\lambda}T_1\right)} \\ &= \frac{\sqrt{\lambda}\sin\sqrt{\lambda}T_1 + e^{T_1} - \cos\sqrt{\lambda}T_1}{\sqrt{\lambda}(e^{T_1} - 1)\sin\sqrt{\lambda}T_1 - (1 + e^{T_1})\left(1 - \cos\sqrt{\lambda}T_1\right)}. \end{aligned}$$

On account of (389), this implies that

$$
\begin{aligned}
T &= \ln\left(1+\frac{1}{A}\right) &(437)\\
&= \ln\left(1+\frac{\sqrt{\lambda}\left(e^{T_1}-1\right)\sin\sqrt{\lambda}T_1-\left(1+e^{T_1}\right)\left(1-\cos\sqrt{\lambda}T_1\right)}{\sqrt{\lambda}\sin\sqrt{\lambda}T_1+e^{T_1}-\cos\sqrt{\lambda}T_1}\right)\\
&= \ln\left(\frac{e^{T_1}\left(\sqrt{\lambda}\sin\sqrt{\lambda}T_1+\cos\sqrt{\lambda}T_1\right)-1}{e^{T_1}+\sqrt{\lambda}\sin\sqrt{\lambda}T_1-\cos\sqrt{\lambda}T_1}\right).
\end{aligned}
$$

Finally, comparing terms in e^{-t} on both sides in (405), we obtain

$$0=-\lambda BI_1(T_1)+\lambda AI_2(T_1)+1, \tag{438}$$

that is

$$\frac{1}{\lambda}=BI_1(T_1)-AI_2(T_1). \tag{439}$$

Since A and B are functions of T, which is expressed in terms of λ and T_1 in equation (437), equation (439) is a nonlinear relationship between the parameter λ and the time span T_1. It can be solved numerically. After some computer calculations, I suggest

Conjecture 1 *System (437), (439) for T and T_1 has no solution for any $\lambda \geq 0$. That means the quasi-equilibrium problem has no periodic solutions besides constant ones.*

Analytically a lower bound on λ can be given below which there cannot occur periodic solutions:

Theorem 11 *For the existence of an intermittent periodic solution of (375) it is necessary that*

$$\lambda > \lambda_1, \tag{440}$$

where λ_1 is the unique solution of the nonlinear equation

$$\lambda_1^{\lambda_1} = \exp\left(\frac{3\pi}{2}\right). \tag{441}$$

(A numerical approximation is $\lambda_1 \approx 3.6442$.)

Proof: The requirement $T_1 < T$ is, on account of (437), equivalent to

$$T_1 < \ln\left(\frac{e^{T_1}\left(\sqrt{\lambda}\sin\sqrt{\lambda}T_1 + \cos\sqrt{\lambda}T_1\right) - 1}{e^{T_1} + \sqrt{\lambda}\sin\sqrt{\lambda}T_1 - \cos\sqrt{\lambda}T_1}\right). \tag{442}$$

Exponentiation of both sides of this inequality yields

$$e^{T_1} < \frac{e^{T_1}\left(\sqrt{\lambda}\sin\sqrt{\lambda}T_1 + \cos\sqrt{\lambda}T_1\right) - 1}{e^{T_1} + \sqrt{\lambda}\sin\sqrt{\lambda}T_1 - \cos\sqrt{\lambda}T_1}, \tag{443}$$

If the denominator on the right side is positive, (443) is equivalent to

$$\left(e^{T_1} - 1\right)^2 + 2\left(1 - \cos\sqrt{\lambda}T_1\right) < 0, \tag{444}$$

which is impossible. By contraposition, the denominator must be negative, that is

$$e^{T_1} + \sqrt{\lambda}\sin\sqrt{\lambda}T_1 - \cos\sqrt{\lambda}T_1 < 0. \tag{445}$$

Clearly, the left side of (445) is positive for $\lambda = 0$ and, since it depends continuously on λ, is also positive in a certain neighborhood of $\lambda = 0$. Let us find the smallest positive λ that allows the function

$$f(\lambda, t) = e^t + \lambda\sin\lambda t - \cos\lambda t \tag{446}$$

to be zero for a certain $t \in \left(\frac{\pi}{\lambda}, \frac{2\pi}{\lambda}\right)$. To this end, we solve the nonlinear system

$$f(\lambda_1, t_1) = 0, \tag{447}$$

$$\frac{\partial f}{\partial t}(\lambda_1, t_1) = 0. \tag{448}$$

for λ_1 and t_1 :

$$e^{t_1} + \lambda_1 \sin \lambda_1 t_1 - \cos \lambda_1 t_1 = 0, \quad (449)$$

$$e^{t_1} + \lambda_1^2 \cos \lambda_1 t + \lambda_1 \sin \lambda 1_1 t_1 = 0. \quad (450)$$

Subtracting (450) from (449) yields

$$\left(\lambda_1^2 + 1\right) \cos \lambda_1 t_1 = 0, \quad (451)$$

therefore

$$t_1 = \frac{3\pi}{2\lambda_1}. \quad (452)$$

Substitution into (449) results in equation (441). ■

17 Re-establishment problem: stability analysis of the steady state

Theorem 12 *The re-establishment problem in the infinite time domain,*

$$\varepsilon s'(t) = -s(t) + 1 - \lambda \int_{-\infty}^{t} (t-u)\, e^{-(t-u)} s\,(u)\, du, \quad -\infty < t < \infty, \quad (453)$$

has exactly one steady state:

$$s^* = \frac{1}{1+\lambda}. \quad (454)$$

The steady state is stable if and only if

$$\lambda < \frac{2\,(\varepsilon+1)^2}{\varepsilon}. \quad (455)$$

Proof: It is easily verified that (454) constitutes the only constant solution of (453). Substituting the perturbed steady state

$$s(t) = \frac{1}{1+\lambda} + \alpha e^{\omega t} \tag{456}$$

with complex frequency ω into (453) yields:

$$\varepsilon \alpha \omega e^{\omega t} = -\frac{1}{1+\lambda} - \alpha e^{\omega t} + 1 - \lambda \int_{-\infty}^{t} (t-u)\, e^{-(t-u)} \left(\frac{1}{1+\lambda} + \alpha e^{\omega u} \right) du, \tag{457}$$

that is

$$\varepsilon \omega e^{\omega t} = -e^{\omega t} - \lambda \int_{-\infty}^{t} (t-u)\, e^{-(t-u)} e^{\omega u} du \tag{458}$$

Let us differentiate (458) twice with respect to t :

$$\begin{aligned} \varepsilon \omega^2 e^{\omega t} &= -\omega e^{\omega t} - \lambda \int_{-\infty}^{t} e^{-(t-u)} e^{\omega u} du + \lambda \int_{-\infty}^{t} (t-u)\, e^{-(t-u)} e^{\omega u} du \quad (459) \\ &= -\omega e^{\omega t} - \lambda \int_{-\infty}^{t} e^{-(t-u)} e^{\omega u} du - (1+\varepsilon\omega)\, e^{\omega t}, \\ \varepsilon \omega^3 e^{\omega t} &= -\omega^2 e^{\omega t} - \lambda e^{\omega t} + \lambda \int_{-\infty}^{t} e^{-(t-u)} e^{\omega u} du - (1+\varepsilon\omega)\, \omega e^{\omega t} \quad (460) \\ &= -\omega^2 e^{\omega t} - \lambda e^{\omega t} - \varepsilon \omega^2 e^{\omega t} - \omega e^{\omega t} - (1+\varepsilon\omega)\, e^{\omega t} - (1+\varepsilon\omega)\, \omega e^{\omega t} \end{aligned}$$

Division by the quantity $e^{\omega t}$ yields a cubic equation for ω :

$$\varepsilon \omega^3 + (1+2\varepsilon)\, \omega^2 + (2+\varepsilon)\, \omega + \lambda + 1 = 0, \tag{461}$$

or equivalently,

$$\omega^3 + \left(\frac{1}{\varepsilon} + 2 \right) \omega^2 + \left(\frac{2}{\varepsilon} + 1 \right) \omega + \frac{\lambda + 1}{\varepsilon} = 0. \tag{462}$$

The Routh-Hurwitz conditions, necessary and sufficient for all roots of this equation to have negative real part, are

$$\frac{1}{\varepsilon} + 2 > 0, \tag{463}$$

$$\frac{\lambda + 1}{\varepsilon} > 0, \tag{464}$$

$$\left(\frac{1}{\varepsilon} + 2\right)\left(\frac{2}{\varepsilon} + 1\right) - \frac{\lambda + 1}{\varepsilon} > 0. \tag{465}$$

(463) and (464) are fulfilled, because $\lambda > 0$ and $\varepsilon > 0$. The third condition (465) is equivalent to

$$\lambda < \frac{2\left(1+\varepsilon\right)^2}{\varepsilon}. \tag{466}$$

Hence the stability of the steady state is equivalent to (455). ■

11 shows the stable and unstable parameter regions in the $\epsilon - \lambda$ plane.

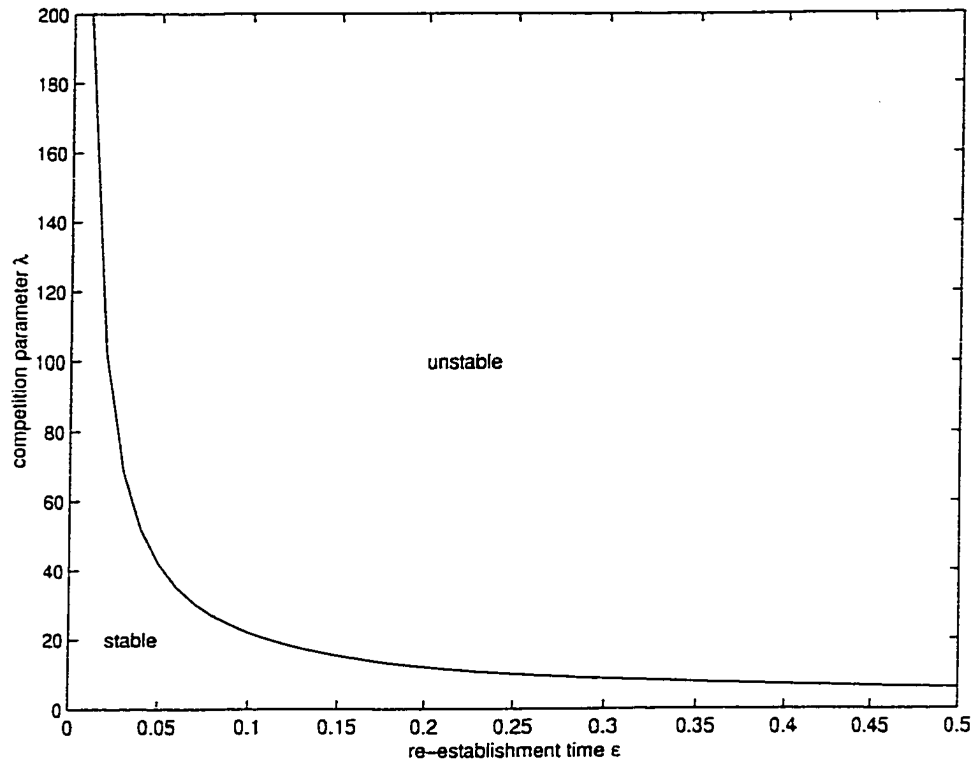

Fig. 11: Stability and instability regions of steady state $1/(1+\lambda)$ in the $\varepsilon - \lambda$ plane. The boundary is given by the bifurcation curve $\lambda = 2(1+\varepsilon)/\varepsilon$.

18 Positive periodic solutions of re-establishment problem

Theorem 13 *The re-establishment problem in the infinite time domain,*

$$\varepsilon s'(t) = -s(t) + 1 - \lambda \int_{-\infty}^{t} (t-u)\, e^{-(t-u)} s(u)\, du, \quad -\infty < t < \infty. \tag{467}$$

has a positive periodic solution if and only if

$$\lambda = \frac{2(\varepsilon+1)^2}{\varepsilon}. \tag{468}$$

Proof: Let me differentiate (467) twice with respect to time:

$$\begin{aligned} \varepsilon s'' &= -s' - \lambda \int_{-\infty}^{t} (1-t+u)\, e^{-(t-u)} s(u)\, du & (469) \\ &= -s' - (s - 1 + \varepsilon s') - \lambda \int_{-\infty}^{t} e^{-(t-u)} s(u)\, du \\ &= -(1+\varepsilon)\, s' - s + 1 - \lambda \int_{-\infty}^{t} e^{-(t-u)} s(u)\, du, \\ \varepsilon s''' &= -(1+\varepsilon)\, s'' - s' - \lambda s + \lambda \int_{-\infty}^{t} e^{-(t-u)} s(u)\, du & (470) \\ &= -(1+\varepsilon)\, s'' - s' - \lambda s - \varepsilon s'' - (1+\varepsilon)\, s' - s + 1 \\ &= -(1+2\varepsilon)\, s'' - (2+\varepsilon)\, s' - (\lambda+1)\, s + 1 \end{aligned}$$

This is an ordinary differential equation of third degree with constant coefficients. Its eigenvalues are the complex solutions of the cubic equation

$$z^3 + \left(\frac{1}{\varepsilon} + 2\right) z^2 + \left(\frac{2}{\varepsilon} + 1\right) z + \frac{\lambda+1}{\varepsilon} = 0. \tag{471}$$

Inserting the ansatz

$$z = iy \tag{472}$$

into (471) yields the condition

$$\frac{\frac{\lambda+1}{\varepsilon}}{\frac{1}{\varepsilon}+2} = \frac{2}{\varepsilon}+1, \tag{473}$$

which is equivalent to (468).

If this relationship between λ and ε is given, then the periodic solutions are harmonic oscillations with period

$$y = \sqrt{\frac{2}{\varepsilon}+1} \tag{474}$$

and constant amplitude

$$A \leq \frac{1}{1+\lambda}. \tag{475}$$

They can be written in the form

$$s(t) = \frac{1}{1+\lambda} + A\cos(yt+\varphi), \tag{476}$$

where $0 \leq \varphi < 2\pi$ is an arbitrary phase shift. ■

19 Pulsating periodic solutions of the re-establishment problem

If the competition parameter λ is increased beyond the critical value $\lambda_\varepsilon = 2(1+\varepsilon)^2/\varepsilon$, then oscillations are observed in which the function $s(t)$ appears in pulses, and is zero between the pulses. (see Fig. 12 and Fig. 13).

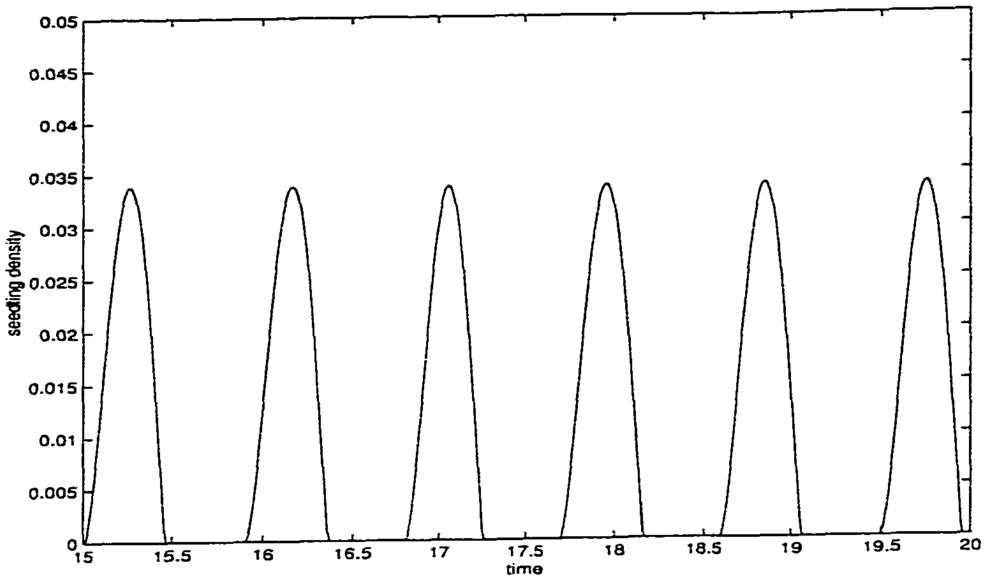

Fig.12: Periodic pulsating solution of $\varepsilon s'(t) = -s(t) + 1 - \lambda \int_{-\infty}^{t} (t-u)\, e^{-(t-u)} s(u)\, du$, $-\infty < t < \infty$, where $\varepsilon = .02$ and $\lambda = 100$.

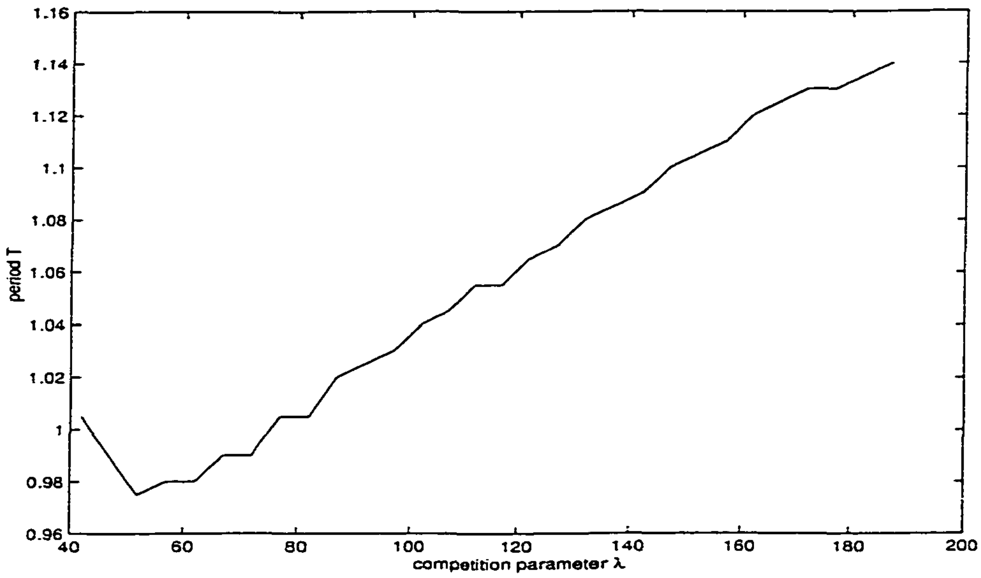

Fig.13: Dependence of period of pulsating oscillation on the competition parameter λ for fixed $\varepsilon = .05$. The integro-differential equation is of the same type as in Fig. 12: $\varepsilon s'(t) = -s(t) + 1 - \lambda \int_{-\infty}^{t} (t-u)\, e^{-(t-u)} s(u)\, du, -\infty < t < \infty$.

Part V

A two species model

20 Mathematical formulation

Consider two tree populations with age densities $N_1(t,a)$ and $N_2(t,a)$, which satisfy the partial differential equation

$$\frac{\partial N_i}{\partial t} + \frac{\partial N_i}{\partial a} = -f(N_i) \tag{477}$$

with initial age distribution

$$N_i(0,a) = \Phi(a) \text{ for } 0 \le a \le T_1, \tag{478}$$

and the "*seedling function*"

$$N_i(t,0) = S_i(t) \text{ for } 0 \le t \le T, \tag{479}$$

for i = 1 and 2, respectively. The seedling functions $S_1(t)$ and $S_2(t)$ obey ordinary differential equations of the form

$$\varepsilon\frac{dS_1}{dt} = \gamma_1 F\left(S_1(t) + S_2(t), \int_0^{T_1} (N_1(t,a) + N_2(t,a))\, B(a)\, da\right), \quad \text{for } 0 \le t \le T,$$
$$\varepsilon\frac{dS_2}{dt} = \gamma_2 F\left(S_1(t) + S_2(t), \int_0^{T_1} (N_1(t,a) + N_2(t,a))\, B(a)\, da\right), \quad \text{for } 0 \le t \le T. \tag{480}$$

with initial values

$$S_i(0) = \Phi(0) > 0 \tag{481}$$

for $i = 1, 2$. The assumptions made for the functions f, F, B and Φ are the same as those in chapter 1. α, β, γ_1, γ_2 are positive constants of order $O(\varepsilon^0)$. Using the notation $G(N) := \int_0^N \frac{dn}{f(n)}$ as in chapter 1, the solution of the partial differential equation (477) can be represented asiand solving for $N(t,a)$ yields:

$$N_i(t,a) = G^{-1}(t + G(\Phi(a-t))) \quad \text{for } 0 < t \leq a,$$
$$N_i(t,a) = G^{-1}(a + G(S_i(t-a))) \quad \text{for } 0 < a \leq t, \text{ i} = 1, 2. \tag{482}$$

where i = 1, 2. Using (482) to eliminate $N(t,a)$ in (480) we obtain a system of two nonlinear integro-differential equations for the seedling function $S_1(t)$ and $S_2(t)$.

$$\varepsilon \frac{dS_i}{dt} = \gamma_i F\left(S_1(t) + S_2(t), \int_0^t K(a, S_1(t-a), S_2(t-a))\, da + L(t)\right) \tag{483}$$

for $0 \leq T$, $I = 1, 2$, where

$$\begin{aligned} K(a, s_1, s_2) &= \left(G^{-1}(a + G(s_1)) + \beta G^{-1}(a + G(s_2))\right) B(a) \\ L(t) &= \int_t^{T_1} (1+\beta) G^{-1}(t + G(\Phi(a-t))) B(a)\, da \end{aligned} \tag{484}$$

Since Φ and G are differentiable, so is $L(t)$, and substituting

$$L(t) = L(0) + \int_0^t L'(a)\, da \tag{485}$$

in (483), we obtain

$$\begin{aligned} \varepsilon \frac{dS_i}{dt} &= \gamma_i F\left(S_1(t) + S_2(t), L(0) + \int_0^t (K(a, S_1(t-a), S_2(t-a)) + L'(a))\, da\right) \\ &= \gamma_i \widetilde{F}\left(S_1(t) + S_2(t), \int_0^t \widetilde{K}(a, S_1(t-a), S_2(t-a))\, da\right), i = 1, 2, \end{aligned} \tag{486}$$

where

$$\widetilde{F}(x,y) = F(x, L(0) + y)$$
$$\widetilde{K}(a, s_1, s_2) = K(a, s_1, s_2) + L'(a) \tag{487}$$

Writing F instead of $\widetilde{F}$ and K instead of $\widetilde{K}$, we obtain the integro-differential initial value problem for the seedling function $S(t)$ in the form

$$\varepsilon \frac{dS_i}{dt} = \gamma_i F\left(S_1(t) + S_2(t), \int_0^t K(a, S_1(t-a), S_2(t-a))\, da\right),$$
$$S_i(0) = \Phi(0), i = 1, 2. \tag{488}$$

When $S_1(t)$ and $S_2(t)$ are found, the solutions for $N_1(t,a)$ and $N_2(t,a)$ are given as

$$N_i(t,a) = G^{-1}(t + G(\Phi(a-t))) \quad \text{for } 0 \le t \le a,$$
$$N_i(t,a) = G^{-1}(a + G(S_i(t-a))) \quad \text{for } 0 \le a \le t, i = 1, 2. \tag{489}$$

21 Asymptotic approximation

To solve the initial value problem (488) using the boundary function method for singularly perturbed problems, the solution $S(t)$ is presented as a sum of the regular part $\overline{S}(t)$ and the boundary layer part $\Pi S(t/\varepsilon)$:

$$S_i(t) = \overline{S}_i(t) + \Pi S_i(\tau), \tag{490}$$

where $\tau = t/\varepsilon$ is a stretched time variable. In addition, we require that the boundary function decays to zero as $\tau \to \infty$. In the following we use the notation

$$
\begin{aligned}
\overline{R}(t) &= \overline{S}_1(t) + \overline{S}_2(t) \\
\Pi R(\tau) &= \Pi S_1(\tau) + \Pi S_2(\tau)
\end{aligned}
\tag{491}
$$

Substituting (491) into equation (488) and representing its right-hand side in a form similar to (490), yields:

$$
\varepsilon \frac{d\overline{S}_i}{dt} + \frac{d\Pi S_i}{d\tau} = \gamma_i \left[F\left(R(t), \int_0^t K\left(t-a, \overline{S}_i(a)\right) da \right) + \Pi F(\tau) \right], \tag{492}
$$

where

$$
\begin{aligned}
\Pi F(\tau) = \quad & F\left(\overline{R}(\varepsilon\tau) + \Pi R(\tau), \varepsilon \int_0^\tau K\left(\varepsilon(\tau-\sigma), \overline{S}_i(\varepsilon\sigma) + \Pi S_i(\sigma)\right) d\sigma\right) \\
- \; & F\left(\overline{R}(\varepsilon\tau), \varepsilon \int_0^\tau K\left(\varepsilon(\tau-\sigma), \overline{S}_i(\varepsilon\sigma)\right) d\sigma\right)
\end{aligned}
\tag{493}
$$

The initial condition becomes

$$
\overline{S}_i(0) + \Pi S_i(0) = \Phi(0). \tag{494}
$$

In this equation and for the remainder of this paper, the notation of a function with upper index 0 denotes the value of the function at 0, e.g. Φ^0 means $\Phi(0)$, $\overline{S}_0'^{\,0}$ means $\overline{S}_0'(0)$ etc. Substituting asymptotic expansions

$$
\overline{S}_i(t) = \overline{S}_i^0(t) + \varepsilon \overline{S}_i^1(\tau) + \ldots, \tag{495}
$$

for the regular part and

$$\Pi S_i(t) = \Pi_0 S_i(t) + \varepsilon \Pi_1 S_i(\tau) + \ldots \tag{496}$$

for the boundary layer part into integro-differential equation (492) we obtain:

$$\begin{aligned}
& \frac{1}{\gamma_i}\left(\varepsilon \frac{d\overline{S}_{0i}}{dt} + \frac{d\Pi_0 S_i}{d\tau} + \varepsilon \frac{d\Pi_1 S_i}{d\tau} + \ldots\right) \qquad (497) \\
= \; & F\left(\overline{R}_0 + \varepsilon \overline{R}_1 + \ldots, \int_0^t K\left(t-a, \overline{S}_{0i} + \varepsilon \overline{S}_{1i} + \ldots\right) da\right) \\
+ \; & F(\overline{R}_0(0) + \varepsilon \overline{R}_1(0) + \varepsilon \tau \overline{R}_0'(0) + \Pi_0 R(\tau) + \varepsilon \Pi_1 R(\tau) + \ldots, \\
& \varepsilon \int_0^\tau K\left(0, \overline{S}_{0i}(0) + \Pi_0 S_i(\alpha)\right) d\alpha + \ldots) \\
- \; & F\left(\overline{R}_0(0) + \varepsilon \overline{R}_1(0) + \varepsilon \tau \overline{R}_0'(0) + \ldots, \varepsilon \int_0^\tau K\left(0, \overline{S}_{0i}(0)\right) d\alpha + \ldots\right) \\
= \; & \widetilde{F} + \varepsilon \overline{R}_1(t) \widetilde{F}_x + \varepsilon \int_0^t \left(\overline{S}_{11}(a) K_y\left(t-a, \overline{S}_{0i}(a)\right) + \overline{S}_{12}(a) K_y\left(t-a, \overline{S}_{0i}(a)\right)\right) da \\
& \widetilde{F}_y + \ldots \\
+ \; & F\left(\overline{R}_0(0) + \Pi_0 R(\tau), 0\right) + \varepsilon\left(\overline{R}_1(0) + \tau \overline{R}_0'(0) + \Pi_1 R(\tau)\right) F_x\left(\overline{R}_0(0) + \Pi_0 R(\tau), 0\right) \\
+ \; & \varepsilon\left(\int_0^\tau K\left(0, \overline{S}_i(0) + \Pi_0 S_i(\alpha)\right) d\alpha\right) F_y\left(\overline{R}_0(0) + \Pi_0 R(\tau), 0\right) \\
- \; & F\left(\overline{R}_0(0), 0\right) - \varepsilon\left(\overline{R}_1(0) + \tau \overline{R}_0'(0)\right) F_x\left(\overline{R}_0(0), 0\right) \\
- \; & \varepsilon\left(\int_0^\tau K\left(0, \overline{S}_{0i}(0)\right) d\alpha\right) F_y\left(\overline{R}_0(0), 0\right) + \ldots
\end{aligned}$$

where we used the notations

$$\begin{aligned}
\widetilde{F} &= F\left(\overline{R}_0(t), \textstyle\int_0^t K\left(t-a, \overline{S}_i(a)\right) da\right) \\
\widetilde{F}_x &= F_x\left(\overline{R}_0(t), \textstyle\int_0^t K\left(t-a, \overline{S}_i(a)\right) da\right) \qquad (498) \\
\widetilde{F}_y &= F_y\left(\overline{R}_0(t), \textstyle\int_0^t K\left(t-a, \overline{S}_i(a)\right) da\right)
\end{aligned}$$

By equating terms of the zeroth order in ε depending on t, we obtain from (497) a nonlinear integral equation relating $\overline{S}_{01}(t)$ and $\overline{S}_{02}(t)$:

$$0 = F\left(\overline{S}_{01}(t) + \overline{S}_{02}(t), \int_0^t K\left(t-a, \overline{S}_{0i}(a)\right) da\right). \tag{499}$$

Setting $t = 0$, we obtain an equation for the initial values $\overline{S}_{01}(0)$ and $\overline{S}_{02}(0)$:

$$0 = F\left(\overline{S}_0(0) + \overline{S}_1(0), 0\right). \tag{500}$$

By equating terms of the zeroth order in ε depending on τ, we obtain from (497) a system of two nonlinear differential equations for $\Pi_0 S_1(\tau)$ and $\Pi_0 S_2(\tau)$:

$$\begin{aligned}\frac{d\Pi_0 S_i}{d\tau} &= \gamma_i F\left(\overline{S}_{01}(0) + \overline{S}_{02}(0) + \Pi_0 S_1(\tau) + \Pi_0 S_2(\tau), 0\right) - \gamma_i F\left(\overline{S}_{01}(0) + \overline{S}_{02}(0), 0\right) \\ &= \gamma_i F\left(\overline{S}_{01}(0) + \overline{S}_{02}(0) + \Pi_0 S_1(\tau) + \Pi_0 S_2(\tau), 0\right) \text{ for } i = 1, 2.\end{aligned} \tag{501}$$

Dividing $\frac{d\Pi_0 S_1}{d\tau}$ by $\frac{d\Pi_0 S_2}{d\tau}$ we obtain a differential equation for $\Pi_0 S_1$ as a function of $\Pi_0 S_2$:

$$\frac{d\left(\Pi_0 S_1\right)}{d\left(\Pi_0 S_2\right)} = \frac{\gamma_1}{\gamma_2}. \tag{502}$$

The solution of this differential equation provides a relation between $\Pi_0 S_1$ and $\Pi_0 S_2$:

$$\Pi_0 S_1(\tau) = \frac{\gamma_1}{\gamma_2} \Pi_0 S_2(\tau) + c. \tag{503}$$

The constant of integration c is zero, because both $\Pi_0 S_1$ and $\Pi_0 S_2$ approach 0 as $\tau \to \infty$. Then for $\tau = 0$,

$$\Pi_0 S_1(0) = \frac{\gamma_1}{\gamma_2}\Pi_0 S_2(0). \tag{504}$$

Taking into account (494), we get that $\Pi_0 S_i(\tau)$ must satisfy the initial condition

$$\Pi_0 S_i(0) = \Phi(0) - S_{0i}(0) \text{ for } i = 1, 2. \tag{505}$$

Equating terms of the order ε depending on t in (497), we arrive at a system of Volterra integral equations of the second kind:

$$\frac{1}{\gamma_i}\frac{d\overline{S}_{0i}}{dt} = \left(\overline{S}_{11}(t) + \overline{S}_{12}(t)\right)\widetilde{F}_x + \int_0^t \left(\overline{S}_{11}(a) + \overline{S}_{12}(a)\right) K_y\left(t-a, \overline{S}_{0i}(a)\right) da\widetilde{F}_y \tag{506}$$

for $i = 1, 2$, which can be written as:

$$\overline{S}_{11}(t) + \overline{S}_{12}(t) = -\int_0^t \left(\overline{S}_{11}(a) + \overline{S}_{12}(a)\right) K_y\left(t-a, \overline{S}_{0i}(a)\right) da\frac{\widetilde{F}_y}{\widetilde{F}_x} + \frac{\frac{d\overline{S}_{0i}}{dt}}{\gamma_i\widetilde{F}_x}. \tag{507}$$

Subtracting the equations for $i = 1, 2$ yields a solvability condition:

$$\frac{\frac{d\overline{S}_{01}}{dt}}{\gamma_1\widetilde{F}_x} = \frac{\frac{d\overline{S}_{02}}{dt}}{\gamma_2\widetilde{F}_x}, \tag{508}$$

which implies:

$$\frac{d\overline{S}_{01}}{d\overline{S}_{02}} = \frac{\gamma_1}{\gamma_2}, \tag{509}$$

with the solution

$$\overline{S}_{01}(t) = \frac{\gamma_1}{\gamma_2}\overline{S}_{02}(t) + c. \tag{510}$$

The constant of integration c is determined by the initial values of $\overline{S}_{01}(t)$ and $\overline{S}_{02}(t)$:

$$c = \overline{S}_{01}(0) - \frac{\gamma_1}{\gamma_2}\overline{S}_{02}(0). \tag{511}$$

Thus the system consisting of the linear equation

$$\overline{S}_{01}(t) - \overline{S}_{01}(0) = \frac{\gamma_1}{\gamma_2}\left(\overline{S}_{02}(t) - \overline{S}_{02}(0)\right) \tag{512}$$

and the nonlinear integral equation (499) allows to solve for the zero order approximations $\overline{S}_{01}(t)$ and $\overline{S}_{02}(t)$ of the regular part.

22 Conclusions

In this thesis simple models have been introduced that allow us to predict dynamic changes in the age structure of the forest after disturbances (fire, disease/insect epidemics, harvesting, etc.). The analysis of age structure dynamics can be used when making environmental policy decisions, harvesting/planting policy decisions, and for better understanding of overall process of forest regeneration. Let it be emphasized that this is only one of many possible approaches to formulation of age structure models. More comparison with real data is needed to decide which characteristic, the basal area or the tree volume, can be used to better define the carrying capacity of a site. The applications of the above models are limited to the cases when the characteristic parameters for an undisturbed forest of a given site index (where all the age groups are somehow presented) are known. However, most of the infomation available has been collected for even aged stand forests (i.e., forests with trees of the same age) since such forests are of most interest for the forest industry, and since they are more common.

Other possible model formulations and related problems are going to be addressed in the nearest future and asymptotics will be one of important methods of analysis. Note that the boundary function method approach was used in this thesis. More details on this asymptotic algorithm can be found in [10] and in [2]. Other asymptotic methods can also be used for analyzing this and related problems (see [6], [3], [8], and references therein).

23 Appendix

Lemma 5 *For any positive constant* κ,

$$xe^{-\kappa x} < \frac{2}{\kappa} e^{-\frac{\kappa}{2}x} \text{ for all } x > 0. \tag{513}$$

Proof: The graph of the natural logarithm $y = \ln x$ is located strictly below the graph of the linear function $y = x$ for all positive x. Therefore

$$\ln\left(\frac{\kappa}{2}x\right) < \frac{\kappa}{2}x \qquad \text{for all } x > 0. \tag{514}$$

By exponentiating both sides of (514) we get

$$\frac{\kappa}{2}x < e^{\frac{\kappa}{2}x}, \tag{515}$$

which is equivalent to (513). ■

Theorem 14 *If the initial age distribution* $\varphi(\alpha)$ *has an exponential estimate of the form*

$$0 \leq \varphi(\alpha) < ce^{-\kappa\alpha}, \tag{516}$$

then the volume of the old forest

$$v_{old}(\theta) = \int_{\theta}^{\infty} \frac{\alpha\varphi(\alpha-\theta)}{\left(1+\frac{\theta}{2}\sqrt{\varphi(\alpha-\theta)}\right)^2} d\alpha, \tag{517}$$

and the number of trees in the old forest

$$p_{old}(\theta) = \int_{\theta}^{\infty} \frac{\varphi(\alpha-\theta)}{\left(1+\frac{\theta}{2}\sqrt{\varphi(\alpha-\theta)}\right)^2} d\alpha \tag{518}$$

both converge to zero as $\theta \to \infty$.

Proof: For any fixed $\alpha \geq 0$, the integrands in (517) and (518) are monotonically increasing functions of $u = \sqrt{\varphi(\alpha - \theta)}$ since

$$\frac{d}{du}\left(\frac{u^2}{\left(1+\frac{\theta}{2}u\right)^2}\right) = \frac{d}{du}\left(\frac{u}{1+\frac{\theta}{2}u}\right)^2 = 2\left(\frac{u}{1+\frac{\theta}{2}u}\right)\frac{4}{(2+\theta u)^2} \geq 0 \tag{519}$$

for all $u \geq 0$. Therefore we obtain an upper estimate for v_{old} if we insert for the initial age distribution $\varphi(\alpha)$ its exponential estimate, and make a substitution $u = \alpha - \theta$ in the integral:

$$\begin{aligned} v_{old}(\theta) &\leq \int_\theta^\infty \frac{\alpha e^{-\kappa(\alpha-\theta)}}{\left(1+\frac{\theta}{2}e^{-\kappa(\alpha-\theta)/2}\right)^2}d\alpha \\ &= \int_0^\infty \frac{(u+\theta)\, e^{-\kappa u}}{\left(1+\frac{\theta}{2}e^{-\kappa u/2}\right)^2}du \\ &= \int_0^\infty \frac{u e^{-\kappa u}}{\left(1+\frac{\theta}{2}e^{-\kappa u/2}\right)^2}du + \int_0^\infty \frac{\theta e^{-\kappa u}}{\left(1+\frac{\theta}{2}e^{-\kappa u/2}\right)^2}du \end{aligned} \tag{520}$$

Now, using Lemma 5 and another substitution $w = e^{-\kappa u/2}$, we obtain the following estimate for the first integral:

$$\begin{aligned} \int_0^\infty \frac{u e^{-\kappa u}}{\left(1+\frac{\theta}{2}e^{-\kappa u/2}\right)^2}du &< \int_0^\infty \frac{\frac{2}{\kappa}e^{-\kappa u/2}}{\left(1+\frac{\theta}{2}e^{-\kappa u/2}\right)^2}du \\ &= \left(\frac{2}{\kappa}\right)^2 \int_0^1 \frac{1}{\left(1+\frac{\theta}{2}w\right)^2}dw \\ &= \left(\frac{2}{\kappa}\right)^2 \frac{2}{2+\theta} \to 0 \text{ as } \theta \to \infty. \end{aligned} \tag{521}$$

With the same substitution, we have for the second integral in (520) and for

$p_{old}(\theta)$ that

$$\int_0^\infty \frac{\theta e^{-\kappa u}}{\left(1+\frac{\theta}{2}e^{-\kappa u/2}\right)^2}du = \frac{2}{\kappa}\int_0^1 \frac{\theta w}{\left(1+\frac{\theta}{2}w\right)^2}dw \tag{522}$$
$$= \frac{2}{\kappa}4\left(\frac{\ln\left(1+\frac{\theta}{2}\right)}{\theta} - \frac{1}{2+\theta}\right)$$
$$\to 0 \text{ as } \theta \to \infty.$$

Therefore $v_{old}(\theta) \to 0$ and $p_{old}(\theta) \to 0$ as $\theta \to \infty$. ■

Lemma 6 *For all real numbers x, y, the following inequality holds:*

$$\max(0,x) - \max(0,y) \leq \max(0, x-y) \tag{523}$$

Proof:

If $x > 0$ and $y > 0$, then

$$\max(0,x) - \max(0,y) = x - y \leq \max(0, x-y).$$

If $x \leq 0$ and $y \leq 0$, then

$$\max(0,x) - \max(0,y) = 0 - 0 = 0 \leq \max(0, x-y).$$

If $x > 0$ and $y \leq 0$, then

$$\max(0,x) - \max(0,y) = x - 0 = x \leq x - y \leq \max(0, x-y).$$

If $x \leq 0$ and $y > 0$, then

$$\max(0,x) - \max(0,y) = -y < 0 \leq \max(0, x-y).$$

In all four cases, the claim (523) was verified. ■

Corollary 1 *For all real numbers x, y, the following inequality holds:*

$$|\max(0,x) - \max(0,y)| \leq |x-y|. \tag{528}$$

Proof: By Lemma 6,

$$\max(0,x) - \max(0,y) \leq \max(0,x-y) \leq |x-y| \tag{529}$$

and hence - by interchanging x and y -

$$\max(0,y) - \max(0,x) \leq |y-x| = |x-y|. \tag{530}$$

From (529) and (530) the claim in (528) follows. ∎

Lemma 7 *If a sequence of real numbers $(y_0, y_1, y_2, y_3, ...)$ satisfies*

$$y_0 = 0, \tag{531}$$

$$|y_1| \leq C, \tag{532}$$

$$|y_2| \leq 2C, \tag{533}$$

$$|y_{n+1}| \leq |y_n| + B\sum_{k=1}^{n-1}|y_k| + C \quad \text{for } n = 2,3,... \tag{534}$$

with positive constants B and C, then the following estimate holds:

$$|y_n| \leq nC\left(1+\sqrt{B}\right)^n. \quad \text{for } n = 0,1,2,... \tag{535}$$

Proof by induction: From the assumptions it is evident that the inequality in (535) holds for $n = 0,1,2$. Suppose that (535) holds for $n = 0,1,2,...,N$, where N is greater than or equal to 2. By substitution of these inequalities into recursion (534), we obtain an estimate for y_{N+1}:

$$\begin{aligned} |y_{N+1}| &\leq |y_N| + B\sum_{k=1}^{N-1}|y_k| + C \\ &\leq NC\left(1+\sqrt{B}\right)^N + B\sum_{k=1}^{N-1}kC\left(1+\sqrt{B}\right)^k + C. \end{aligned} \tag{536}$$

To complete the induction step it is sufficient to show that

$$|y_{N+1}| \leq NC\left(1+\sqrt{B}\right)^N + B\sum_{k=1}^{N-1}kC\left(1+\sqrt{B}\right)^k + C \leq (N+1)\,C\left(1+\sqrt{B}\right)^{N+1}. \tag{537}$$

Let us divide this inequality by C, and use the notation

$$x = 1+\sqrt{B} > 1 \tag{538}$$

to obtain an equivalent inequality.

$$Nx^N + (x-1)^2\sum_{k=1}^{N-1}kx^k + 1 \leq (N+1)\,x^{N+1}. \tag{539}$$

To prove (539), we start with the true inequality

$$0 \leq 2x^N + 2\sum_{k=0}^{N-1}x^k, \tag{540}$$

which is equivalent to

$$(N-1)\,x^N - \sum_{k=1}^{N-1}x^k \leq (N+1)\,x^N + \sum_{k=0}^{N-1}x^k. \tag{541}$$

On account of the identities

$$(x-1)\sum_{k=1}^{N-1}kx^k = (N-1)\,x^N - \sum_{k=1}^{N-1}x^k, \tag{542}$$

$$\frac{(N+1)\,x^{N+1} - Nx^N - 1}{x-1} = (N+1)\,x^N + \sum_{k=0}^{N-1}x^k, \tag{543}$$

(541) can be written as

$$(x-1)\sum_{k=1}^{N-1} kx^k \leq \frac{(N+1)\,x^{N+1} - Nx^N - 1}{x-1}. \tag{544}$$

By multiplication with $x-1$ and rearrangement of terms, (539) follows, and the induction proof is completed. ■

Lemma 8 *If a sequence of real numbers* $(y_0, y_1, y_2, y_3, \ldots)$ *satisfies*

$$\begin{aligned} |y_0| &\leq C, & (545)\\ |y_{n+1}| &\leq B\sum_{k=0}^{n} |y_k| + C \quad \text{for } n = 1, 2, \ldots & (546) \end{aligned}$$

with positive constants B*,* C*, then the following estimate holds:*

$$|y_n| \leq C\,(B+1)^n \quad \text{for } n = 0, 1, 2, \ldots \tag{547}$$

Proof by induction:

For $n = 0$ the claim (547) is true because of assumption (545). Assume now that it is also true for every $j = 0, 1, 2, \ldots, n$. Then, by recursion (546), it follows for $n+1$ that

$$\begin{aligned} |y_{n+1}| &\leq B\sum_{k=0}^{n} |y_k| + C & (548)\\ &\leq B\sum_{k=0}^{n} C\,(B+1)^k + C \\ &= C\left(B\sum_{k=0}^{n} (B+1)^k + 1\right) \\ &= C\left(B\frac{1-(B+1)^{n+1}}{1-(B+1)} + 1\right) \\ &= C\,(B+1)^{n+1}. \quad ■ \end{aligned}$$

Theorem 15 *Let $p(x)$ be a real-valued function, satisfying a Lipschitz condition of order* 1 *with Lipschitz constant $C > 0$ on the interval $[a,b]$, that is*

$$|p(y) - p(x)| \le C\,|y - x| \quad \textit{for all } x, y \in [a,b]. \tag{549}$$

Then

$$\begin{array}{lll} (a) & \left|\int_a^b p(t)\,dt - \frac{b-a}{2}(p(a)+p(b))\right| & < \frac{C}{2}(b-a)^2 \\ (b) & \left|\int_a^b p(t)\,dt - \frac{b-a}{n}\left(\frac{p(a)+p(b)}{2} + \sum\limits_{k=1}^{n-1} p\left(a + k\frac{b-a}{n}\right)\right)\right| & < \frac{C}{2}\frac{(b-a)^2}{n} \end{array}$$

for $n = 2, 3, 4, \ldots$

Proof of (a):

$$\begin{aligned} & \left|\int_a^b p(t)\,dt - \frac{b-a}{2}(p(a)+p(b))\right| \qquad (551) \\ = & \left|\frac{1}{2}\int_a^b (p(t)-p(a))\,dt + \frac{1}{2}\int_a^b (p(t)-p(b))\,dt\right| \\ \le & \frac{1}{2}\int_a^b |p(t)-p(a)|\,dt + \frac{1}{2}\int_a^b |p(t)-p(b)|\,dt \\ \le & \frac{1}{2}\int_a^b C(t-a)\,dt + \frac{1}{2}\int_a^b C(b-t)\,dt \\ = & \frac{C}{2}(b-a)^2. \end{aligned}$$

Proof of (b): Apply (a) to the integrals on the subintervals $\left(a + k\frac{b-a}{N}, a + (k+1)\frac{b-a}{N}\right)$ for $k = 0, 1, 2, \ldots, N-1$. Then sum over k. ■

Theorem 16 *Let $p(x)$ be a real-valued function, continuously differentiable on the interval $[a,b]$, and let the derivative $p'(x)$ satisfy Lipschitz condition of order* 1 *with Lipschitz constant $C > 0$, that is*

$$|p'(y) - p'(x)| \le C\,|y - x| \quad \text{for all } x, y \in [a,b]. \tag{552}$$

Then

$$\text{(a)}\quad \left|\tfrac{p(y)-p(x)}{y-x} - p'(x)\right| < C(y-x) \qquad \textit{for } a \le x < y \le b,$$

$$\text{(b)}\quad \left|\int_a^b p(t)\,dt - \tfrac{b-a}{2}\left(p(a)+p(b)\right)\right| < \tfrac{5C}{6}(b-a)^3, \tag{553}$$

$$\text{(c)}\quad \left|\int_a^b p(t)\,dt - \tfrac{b-a}{n}\left(\tfrac{p(a)+p(b)}{2} + \sum_{k=1}^{n-1} p\left(a + k\tfrac{b-a}{n}\right)\right)\right| < \tfrac{5C}{6}\tfrac{(b-a)^3}{n^2}$$

for $n = 2, 3, 4, \ldots,$

Proof of (a): For any $0 \le x < y \le T$, we know by the mean value theorem that there exists some $\xi \in (x, y)$ such that

$$\frac{p(y) - p(x)}{y - x} = p'(\xi) \tag{554}$$

By (552), we have the estimate

$$|p'(\xi) - p'(x)| \le C(\xi - x). \tag{555}$$

Substitution of (554) into (555) yields the result:

$$\left|\frac{p(y) - p(x)}{y - x} - p'(x)\right| = |p'(\xi) - p'(x)| \le C(\xi - x) < C(y - x). \tag{556}$$

Proof of (b): Let $t \in (a, b]$. Application of part (a) with $x = a$ and $y = t$ yields:

$$\left|\frac{p(t) - p(a)}{t - a} - p'(a)\right| < C(t - a). \tag{557}$$

Multiply (557) by $t - a$ and use the triangle inequality to get that

$$p(t) = p(a) + (t - a)p'(a) + \theta_t C(t - a)^2. \tag{558}$$

for some $\theta_t \in [-1, 1]$, which depends on t. In particular, for $t = b$,

$$p(b) = p(a) + (b - a)p'(a) + \theta_b C(b - a)^2. \tag{559}$$

Solving (559) for $p'(a)$ and substituting into (558), we obtain:

$$p(t) = \left(1 - \frac{t-a}{b-a}\right) p(a) + \frac{t-a}{b-a} p(b) + C\left(\theta_t (t-a)^2 - \theta_b (b-a)(t-a)\right). \tag{560}$$

Integrating with respect to t from a to b, we get

$$\int_a^b p(t)\,dt = \frac{b-a}{2}\left(p(a) + p(b)\right) + C\int_a^b \left(\theta_t (t-a)^2 - \theta_b (b-a)(t-a)\right) dt. \tag{561}$$

Thus

$$\begin{aligned} & \left| \int_a^b p(t)\,du - \frac{b-a}{2}\left(p(a)+p(b)\right)\right| \qquad (562) \\ = C\ & \left|\int_a^b \left(\theta_t (t-a)^2 - \theta_b (b-a)(t-a)\right) dt\right| \\ \leq C\ & \left(\int_a^b (t-a)^2\,dt + (b-a)\int_a^b (t-a)\,dt\right) \\ = \tfrac{5}{6}C\ & (b-a)^3. \end{aligned}$$

Proof of (c): Apply (b) to the integrals on the subintervals $\left(a + k\frac{b-a}{N}, a + (k+1)\frac{b-a}{N}\right)$ for $k = 0, 1, 2, ..., N-1$. Then sum over k. ■

Theorem 17 *Let $f \in C^2([a,b])$ with $f'(x) < 0$ in $[a,b]$, and $f(x^*) = 0$ for a certain $x^* \in [a,b]$. Then the solution of the ordinary differential equation*

$$\begin{aligned} \frac{dx}{dt} &= f(x),\ t > 0, \qquad (563) \\ x(0) &= x_0 \in [a,b], \end{aligned}$$

exists for all $t \geq 0$, is unique, and satisfies an exponential estimate

$$|x(t) - x^*| \leq |x_0 - x^*| e^{-\kappa t} \text{ for } t \geq 0 \tag{564}$$

for some positive constant κ that is independent of t.

Proof:

Let us assume without loss of generality that

$$a \le x^* < x_0 \le b. \tag{565}$$

Then the solution $x(t)$ of initial value problem (563) exists for all $t \ge 0$, is unique and is decreasing with

$$x^* \le x(t) \le x_0 \tag{566}$$

for all $t \ge 0$. Since $f(x)$ is continuously differentiable on the closed interval $[a, b]$, $f'(x)$ assumes its maximum value $-\kappa < 0$ in this interval.

By Taylor expansion of $f(x)$ about $x = x^*$, (563) implies that

$$\frac{dx}{dt} = f(x^*) + (x(t) - x^*) f'(\xi_t) = (x(t) - x^*) f'(\xi_t) \le (x(t) - x^*)(-\kappa), \tag{567}$$

where $\xi_t \in (x^*, x^0)$ is a suitable intermediate point. Dividing inequality (567) by $x(t) - x^* > 0$, we get

$$\frac{\frac{dx}{dt}}{x(t) - x^*} \le -\kappa. \tag{568}$$

Taking the definite integral from 0 to t on both sides of (568) yields

$$\ln \frac{x(t) - x^*}{x_0 - x^*} \le e^{-\kappa t}, \tag{569}$$

that is

$$x(t) - x^* \le (x_0 - x^*) e^{-\kappa t}. \tag{570}$$

Because of (566), this is equivalent to the claim (564). ■

Theorem 18 *The solution of quasi-equilibrium problem*

$$\begin{aligned} s(t) &= 1-\lambda\int_0^t s(a)(t-a)e^{-(t-a)}da - \lambda e^{-t}\int_t^\infty \varphi(a-t)\,a\,da \quad (571)\\ &= 1-\lambda\int_0^t s(a)(t-a)e^{-(t-a)}da - \lambda e^{-t}\int_0^\infty \varphi(u)(t+u)\,du \end{aligned}$$

converges to the steady state

$$s^* = \frac{1}{1+\lambda} \quad (572)$$

with exponential estimate

$$|s(t)-s^*| \le ce^{-t} \text{ for } t>0 \quad (573)$$

for some constant $c > 0$, *if the initial age density functions* $\varphi(a)$ *are non-negative, continuous on the interval* $[0,\infty)$, *and satisfy the exponential estimate*

$$\left|\varphi(a) - s^* e^{-a}\right| \le \delta e^{-a} \text{ for } a \ge 0, \quad (574)$$

where

$$\delta = \frac{1}{(3+\lambda)^2}. \quad (575)$$

Proof:

With the transformation

$$\psi(a) = \varphi(a) - s^* e^{-a} \quad (576)$$

(571) becomes

$$s(t) = 1-\lambda\int_0^t s(a)(t-a)e^{-(t-a)}da - \lambda e^{-t}\int_0^\infty \psi(u)(t+u)\,du - \lambda s^*(1+t)e^{-t}. \quad (577)$$

Differentiating (577) twice with respect to t yields

$$\begin{aligned} s'(t) &= -\lambda \int_0^t s(a)(1-t+a)e^{-(t-a)}da \\ &\quad -\lambda e^{-t}\int_0^\infty \psi(u)(1-t-u)\,du + \lambda s^* t e^{-t} \\ &= -\lambda \int_0^t s(a)e^{-(t-a)}da + 1 - s(t) \\ &\quad -\lambda e^{-t}\int_0^\infty \psi(u)\,du - \lambda s^* e^{-t}, \end{aligned} \tag{578}$$

$$\begin{aligned} s''(t) &= -\lambda s(t) + \lambda \int_0^t s(a)e^{-(t-a)}da - s'(t) \\ &\quad +\lambda e^{-t}\int_0^\infty \psi(u)\,du + \lambda s^* e^{-t} \\ &= -\lambda s(t) - s'(t) + 1 - s(t) - s'(t). \end{aligned} \tag{579}$$

We obtained the ordinary differential equation

$$s'' + 2s' + (1+\lambda)s = 1 \tag{580}$$

with initial conditions

$$\begin{aligned} s(0) &= s^* - \lambda \int_0^\infty \psi(u)\,u\,du, \\ s'(0) &= s^* - s(0) + \lambda \int_0^\infty \psi(u)(u-1)\,du. \end{aligned} \tag{581}$$

The solution is

$$s(t) = s^* + e^{-t}\left((s(0)-s^*)\cos\left(\sqrt{\lambda}t\right) + \frac{s'(0)+s(0)-s^*}{\sqrt{\lambda}}\sin\left(\sqrt{\lambda}t\right)\right). \tag{582}$$

Since

$$
\begin{aligned}
|s(0)-s^*| &\le \lambda \int_0^\infty \psi(u)\, u du \le \lambda \int_0^\infty \delta e^{-u} u du \le \lambda\delta, && (583)\\
|s'(0)| &\le |s(0)-s^*| + \lambda \int_0^\infty \psi(u)(u-1)\, du && (584)\\
&\le |s(0)-s^*| + \lambda\delta \left(\int_0^1 e^{-u}(1-u)\, du + \int_1^\infty e^{-u}(u-1)\, du \right)\\
&= |s(0)-s^*| + \lambda\delta \left(\frac{1}{e} + \frac{1}{e} \right)\\
&\le \lambda\delta \left(1 + \frac{2}{e} \right),
\end{aligned}
$$

we have the estimate

$$
\begin{aligned}
(s(0)-s^*)^2 + \left(\frac{s'(0)+s(0)-s^*}{\sqrt{\lambda}} \right)^2 &\le \lambda^2\delta^2 + \lambda\delta^2 \left(1 + \frac{2}{e} + 1 \right) && (585)\\
&\le (\lambda+3)^2 \delta^2\\
&= \frac{1}{(\lambda+3)^2} < \frac{1}{(\lambda+1)^2} = (s^*)^2 .
\end{aligned}
$$

(585) implies that (573) is fulfilled for the choice

$$
c = \frac{1}{(\lambda+3)^2}, \qquad (586)
$$

and guarantees that the solution (582) is positive. ■.

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