Dynamic growth models for continuous cover multi-species forestry in Iranian Caspian forests

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Abstract

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This study concerns some of the relevant topics of the Iranian Caspian forestry planning problem, in particular the first central components in this modelling process, such as forest modelling, forest statistics and growth function estimations. The required data was collected from Iranian Caspian forests. To do so, 201 sample plots were determined and the parameters such as number of trees, tree diameter at breast height and tree height were measured at each sample plot. Three sample plots at different 3 elevations were chosen to measure the tree increment. Data has been used to estimate a modified logistic growth model and a model that describes the growth of the basal area of individual trees as a function of basal area. General function analysis has been applied in combination with regression analysis. The results are interpreted from ecological perspectives. Furthermore, a dynamic multi-species growth model theory is developed and analysed with respect to dynamic behaviour, equilibria, convergence and stability. Logistic growth models have been found applicable for continuous cover forest management optimization. Optimization of management decisions in a changing and not perfectly predictable world should always be based on adaptive optimization.

Keywords: forest statistics; forest modelling; growth function; forest management

Forestry in Iranian Caspian forests is based on continuous cover forestry (CCF) management principles. Many different species of trees grow together in large parts of these forests. CCF often leads to higher expected present values than rotation forestry with clear cuts (Haight 1987; Pukkala et al. 2010; Tahvonen et al. 2010). Furthermore, CCF has environmental advantages of several kinds. Mixed species forests give advantages compared to monocultures, such as options to adapt harvesting of different species to changes in market prices, climate, species specific damage etc. Lohmander (2000, 2007) presented these perspectives and general results. Forest industries in Iran produce sawnwood and wood-based panels as well as pulp and paper from hardwood species. Moderate volumes of forest products, mainly paper, are imported. Modest quantities of wood are burned as fuel (Mohammadi Limaei 2010).

Forests are dynamic biological systems that continuously change over time. It is required to project these changes in order to obtain rel-

evant information for managing and decision making. Forest management decisions are made based on information about both current and future resource conditions. Inventories taken at one instant in time provide information on current wood volumes and related statistics. Growth and yield models describe forest dynamics (i.e., growth, mortality, reproduction, and associated changes in the stand) over time and hence have been widely used in forest management because of their ability to update inventories, predict future yield, and to explore management alternatives and silvicultural options, thus providing information for decision-making (Burkhart, Brooks 1990; Vanclay 1994). Growth modelling has a long history in forestry. In the early 1850s, central European foresters used graphical methods to model the growth and production of forests. Yield tables, based on complete observations of yield throughout entire rotations, were constructed for important tree species in Europe (Vuokila 1965).

Models provide an efficient way to prepare resource forecasts, but a more important role may be their ability to explore management options and silvicultural alternatives. For example, foresters may wish to know the long-term effect on both the forest and on future harvests, of a particular silvicultural decision, such as changing the cutting limits for harvesting. With a growth model, they can examine the likely outcomes, both with the intended and alternative cutting limits, and can make their decision objectively. The process of developing a growth model may also offer interesting new insights into stand dynamics (Vanclay 1994). Growth models provide a reliable way to examine silvicultural and harvesting options as well as to determine the sustainable timber yield for different areas and management strategies (Vanclay 1994). A growth model also has a broader role in regional forest management and in the formulation of forest policy. A forest growth model predicts future values of certain outputs such as timber volume, given inputs (control variables) such as silvicultural treatments. Both inputs and outputs are functions of time. This fact, and the dependence of the outputs on the entire past history of the stand, have caused considerable difficulties and confusion in growth modelling. The way out is well-known in other fields dealing with dynamic systems, and may be called the state-space approach (Bailey, Clutter 1974). A growth model that was initially proposed by Verhultst (1845) is called the logistic growth model or the Verhulst model. The biological growth function is built on a model of population dynamics which was first presented by Schaefer (1954). Schaefer's model rests upon the so-called Pearl-Verhultst, or logistic, equation of population dynamics.

Many papers have been written about growth functions in uneven-aged forests. It is not our aim to review all of them, but we mention some of them here.

The number of options to model the dynamics of forests is almost unlimited. You may use stand models, models of individual trees, diameter class models, models that describe altitude, slope and directions, models in continuous time, in discrete time etc. The international demand for forest sector products has started to change. Demand for some paper qualities has sharply decreased, mainly depending on lowered demand in the new internet based society. There exists much evidence about this fact, e.g. Kennan et al. (2014) describing the problems in Canada. This transformation affects the whole forestry supply chain, which has to be considered as an integrated dynamical system with a lot of disturbances. Hence, when to manage the forest using multi-species CCF, in our case in Iran, the main question for the forest industry is how much better this management regime is if the whole supply chain is considered and not only the management of the forest. However, we have to start in the forest and that part is described in this paper. The Iranian Caspian forests are mixed uneven-aged stands consisting of broadleaf species exploited for timber production according to the forest management plans for over 40 years. Forestry in Caspian forests is based on CCF management principles. Many different species of trees grow together in large parts of these forests. Studying the growth of natural uneven-aged forests for forest management practice requires to reflect the growth of stand in the relationship of both the growth and competition factors. Therefore, there is an urgent need to develop growth models for uneven-aged forests that are suitable to the actual situation of forest production, and satisfy the requirements of sustainable forest management (Nguyen 2009). The stock, size of individual tree in each sample plot, kind of species, slope, aspect, elevation are the most effective factors that influence the forest growth.

There are some studies that dealt with measuring forest growths in Iranian Caspian forests. Bonyad (2005) estimated the volume growth at 3 different elevations using a multivariate statical method in Caspian forests. Heshmatol Vaezin et al. (2008) provided a pilot increment model for

major species in the Caspian forests including hornbeam (*Carpinus betulus* Linnaeus), oriental beech (*Fagus orientalis* Lipsky) and alder (*Alnus cordata* C.A. Mey) by routinely measured variables in forest inventories. ZAHEDI AMIRI (1991) determined the annual growth rate of an uneven-aged forest in Caspian forests and the average annual increment of the forest was 8 m^3·ha^{-1}. LOHMANDER et al. (2016) estimated basal area growth and volume functions for beech in Iranian Caspian forests. HATAMI et al. (2017) investigated a basal area increment model for individual trees in mixed continuous cover forests in Iranian Caspian forests.

In all of the previous researches, the studies focused on relations between growth and some parameters like diameter, volume, etc. Hence, there was not any research in Iranian Caspian forests aimed at development of a dynamic multi-species growth model. There are some studies in the other countries related to a dynamic growth model such as PACALA et al. (1996), who simulated the long-term dynamics (species composition and basal area) of temperate mixed forest using a distance-dependent tree model.

Therefore, the aim of this study is to estimate a dynamic multi-species growth model with respect to dynamic behaviour, equilibria, convergence and stability.

MATERIAL AND METHODS

In order to collect volume and growth data, district No. 2 of Losara forests was chosen that is located in the Ploroad watershed (watershed No. 28), east of Guilan province in the north of Iran. Its latitude ranges from 36°57'38"N to 36°59'40"N and its longitude ranges from 50°12'10"E to 50°16'40"E (Fig. 1). These forests are located in the Caspian mountainous area and its altitude ranges from 400 to 1,200 m a.s.l. These are uneven-aged forests and the main species are: hornbeam (*Carpinus* sp.), beech (*F. orientalis*), oak (*Quercus* sp.), alder (*Alnus* sp.) etc.

The inventory area was 576 ha. An inventory was performed at the study area in 2009. The locations of sampling points were found by Global Positioning System in 2014. A systematic random sampling method with a network of 150 × 200 m was used for the inventory (Fig. 2). The shape of sample plot was circular with the radius of 17.84 m and area of 1,000 m^2. Therefore, 201 sample plots were determined and some parameters such as number of trees, tree DBH and tree height were measured at each sample plot.

In CCF, the forest growth is influenced by stand density, the size of individual trees in each sample plot, kind of species, slope, aspect, elevation, precipitation and temperature. Therefore, 3 sam-
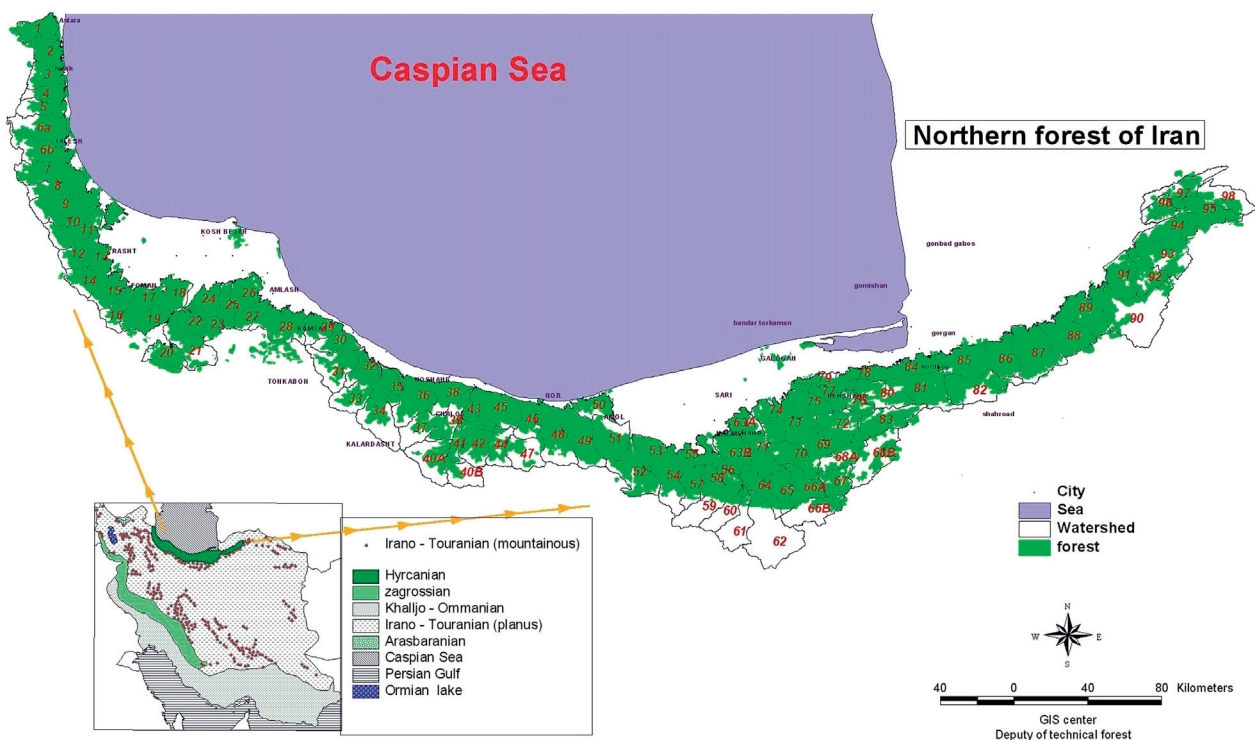

Fig 1. Iranian forests, Iranian Caspian forests and the study area (watershed No. 28)
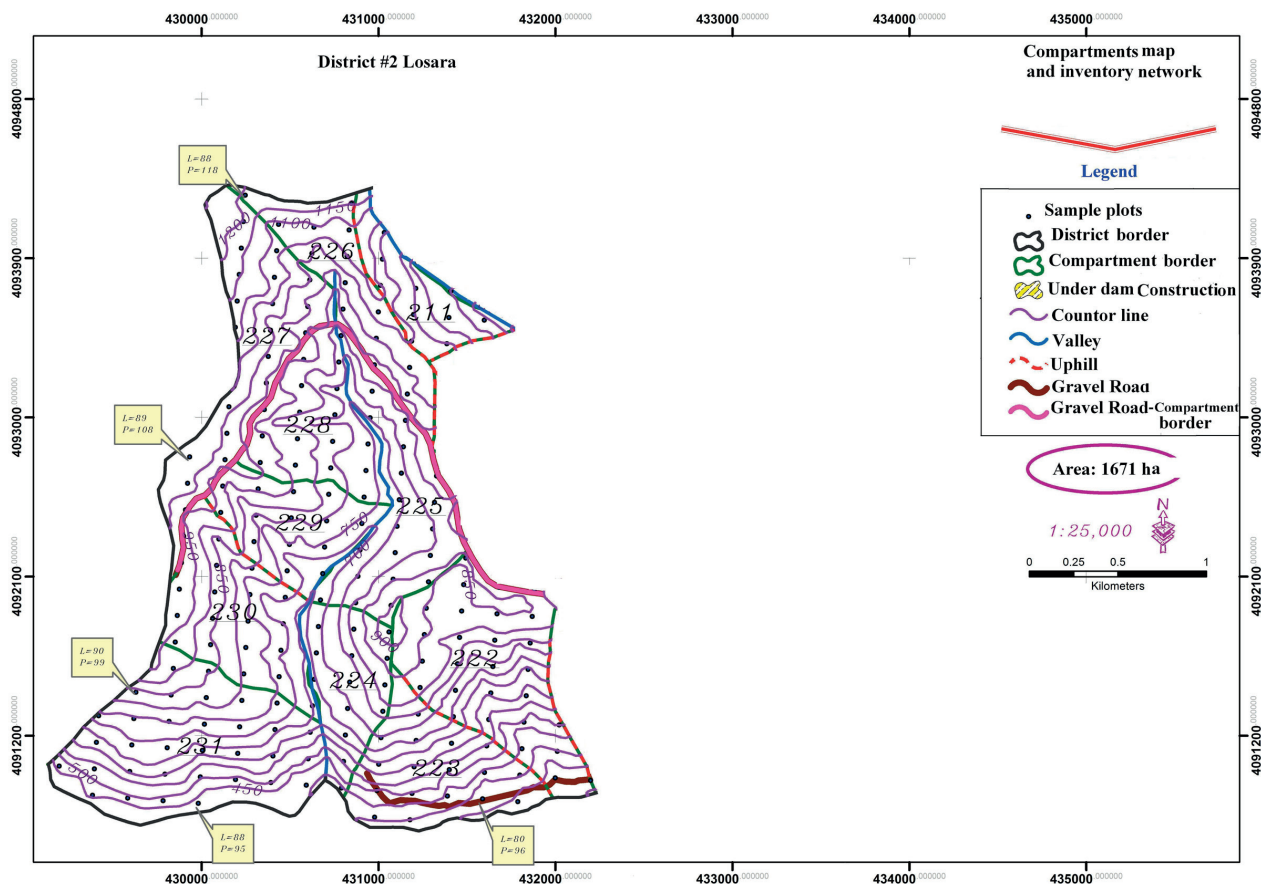
Fig 2. Location of sample plots
L – line of inventory, *P* – plot

ple plots at 3 different elevations were chosen to measure the tree increment (Schütz 2006). Forest growth may decrease with increasing altitude due to a decrease of temperatures and rainfall and shorter growing seasons.

Table 1 shows compartment areas and forest types in the study area. Hornbeam is a dominant species in the study area. Beech is the second spe-

cies in the study area based on frequencies and area coverage.

Summary of the inventories in 2009 and 2014 is shown in Table 2.

Three sample plots were chosen to measure the forest growth using an increment borer. The sample plots were situated at different altitudes (400, 700 and 1,000 m a.s.l.). The aspects of 3 sample plots along altitude variations were east, west and north, respectively.

Data analysis. The available empirical data was used to estimate a modified logistic growth model where stand density, altitude and species mixture were considered as explanatory variables. Logistic growth models have been found useful in continuous cover forest management optimization and examples of such studies are found in Lohmander (2007) and Lohmander and Mohammadi Limaei (2008).

For these reasons, it was necessary to remove some possible explanatory variables from the growth function and to adjust the functional form. The parameters of a function of the following type were estimated via ordinary least squares (OLS) regression analysis (Eq. 1):

Table 1. Areas and forest types of compartments (Losara district), Iranian Caspian forests

Compartment	Area (ha)	Forest type
222	82	hornbeam-date-plum, alder
223	57	hornbeam-Persian ironwood
224	37.5	hornbeam-alder, date-plum
225	57.5	
226	44	
227	66	hornbeam-beech-alder
228	47.5	
229	43.5	
230	58	hornbeam-alder, date-plum
231	102	hornbeam-Persian ironwood
211	28.5	Caspian locust-Persian ironwood
Total	576	

Table 2. Summary of the inventories in 2009 and 2014

Compartment	No. of sample plots	Volume (m³·ha⁻¹)			No. of trees per hectare	
		2009	2014	difference	2009	2014
222	25	292.83	308.5	15.67	292	301
223	17	206.5	219	12.5	437	439
224	14	304.1	300	−4.1	197	207
225	19	248.4	259	10.6	144	151
226	14	197.3	204.6	7.3	164	167
227	20	250.5	253.5	3	182	190
228	16	192.2	206	13.8	127	132
229	14	206.5	209.1	2.6	127	125
230	20	256	263	7	124	138
231	33	283.8	297	13.2	180	187
211	9	178	188	10	234	230
Total	201					

$$\overset{\bullet}{x} = \frac{dx}{dt} = sx\left(1 - \frac{x}{K}\right) + kA \tag{1}$$

where:
$\overset{\bullet}{x}$ – growth of species X (m³·ha⁻¹·year⁻¹),
x – stock level of species X (m³·ha⁻¹),
t – time (year),
s – intrinsic growth rate, it shows how much a species can grow between successive time periods,
K – carrying capacity (m³·ha⁻¹), it indicates the maximum population of a species in an environment over a period without destroying the resource base,
k – altitude parameter,
A – altitude (m a.s.l.).

We may express the growth function as in Eq. 2:

$$\overset{\bullet}{x} = \frac{dx}{dt} = sx - \frac{s}{K}x^2 + kA \tag{2}$$

We can define the parameter of the squared stock as Eq. 3:

$$b = -\frac{s}{K} \tag{3}$$

where:
b – parameter of the squared stock.

Then we get this function, suitable for OLS regression analysis, as Eq. 4:

$$\overset{\bullet}{x} = \frac{dx}{dt} = sx + bx^2 + kA + \varepsilon \tag{4}$$

where:
ε – series of random errors with normal distribution error,
$E(\varepsilon)$ – expected ε, $E(\varepsilon) = 0$, $E(\varepsilon^2) = \sigma^2$,
σ – standard deviation of the error term.

In some cases, it is possible to determine dynamic multi-species model parameters via steady-state observations of unmanaged forests. If we can observe x and y in several equilibria, in some cases we can estimate relations between the parameters. We can include altitude and slope exposure as parameters and evaluate the equilibria at different altitudes and directions of slope. A dynamic multi-species model describes how trees of different species develop in a mixed stand over time.

A system of two extended logistic models is explained below, as Eq. 5:

$$\begin{cases} \overset{\bullet}{x} = \dfrac{dx}{dy} = x\left(\alpha_x - \beta_{xx}x - \gamma_{xy}y\right) \\ \overset{\bullet}{y} = \dfrac{dy}{dt} = y\left(\alpha_y - \beta_{yx}x - \gamma_{yy}y\right) \end{cases} \tag{5}$$

where:
α_x, β_{xx}, γ_{xy}, α_y, β_{yx}, γ_{yy} – set of parameters,
y – stock level of species Y,
$\overset{\bullet}{y}$ – growth of species Y (m³·ha⁻¹·year⁻¹).

RESULTS

The result of OLS regression analysis is shown in Table 3. The F-value and the R^2 value indicate that model fits the data extremely well.

The intrinsic growth rate and the parameter of the squared stock have significant P-values on a 95% significance level. These parameters also have the expected signs and they jointly give a reasonable result in the carrying capacity calculation, which is found below (Eqs 6 and 7). We note that the intrinsic growth rate is very close to 2%:

$$K = -\frac{s}{b} \tag{6}$$

Table 3. Results of regression statistics

Parameter	Value	Standard error	t-Value	P-value
s	0.019970746	0.004215938	4.736963898	0.001469688
b	−2.60227E-05	1.11457E-05	−2.334774567	0.047804052
k	−0.000646858	0.000452609	−1.429175526	0.190816399

s – intrinsic growth rate, it shows how much a species can grow between successive time periods, b – parameter of the squared stock, k – altitude parameter, multiple R = 0.998, R^2 = 0.996, adjusted R^2 = 0.870, standard error = 0.2044, F = 699.3457225, P-value for F = 4.93053E-09, observations = 11

$$K = -\frac{0.0199707}{-0.0000260227} \approx 767.45 \qquad (7)$$

As a result, the carrying capacity can be estimated to be approximately 767 m³·ha⁻¹.

However, the P-value cannot be considered significant on a 95% significance level. However, since we expect the parameter to be relevant and since we cannot statistically reject the presence of a strictly negative parameter, we keep the estimated parameter in the growth equation (Eqs 8 and 9):

$$\overset{\bullet}{x} = \frac{dx}{dt} = sx\left(1 - \frac{x}{K}\right) + kA \qquad (8)$$

$$\overset{\bullet}{x} = \frac{dx}{dt} = 0.0200x\left(1 - \frac{x}{767}\right) - 0.000647A \qquad (9)$$

Growth according to the estimated function is shown in Fig. 3. In Fig. 4, we find the growth as a function of the stock (at sea level).

It is not usually sufficient to know the total growth per hectare. In order to optimize the management of forests with trees of different dimensions, it is also important to determine how trees of different sizes compete with each other.

Then we estimated the following function (Eq. 10), diameter growth of the individual tree per time unit (mm·yr⁻¹):

$$\frac{\Delta D}{\Delta t} = 1.506969 + 0.94225\ln(D) - 0.000183455B^3 \quad (10)$$

where:
D – diameter of the individual tree (mm),
B – basal area of bigger trees (trees with large diameter) per area unit (m²·ha⁻¹).

The development of individual trees affected by competition is shown in Fig. 5.

The following function (Eq. 11) for the growth of individual trees was estimated from the empirical data, using OLS regression:

$$z = 0.1586038\Phi^2\ln(\Phi) + 0.07038919999\Phi \qquad (11)$$

where:
Φ – basal area of individual tree – before growth (m²),
z – basal area growth of individual tree, as the area growth during the next ten years divided by 10 (m²·year⁻¹).
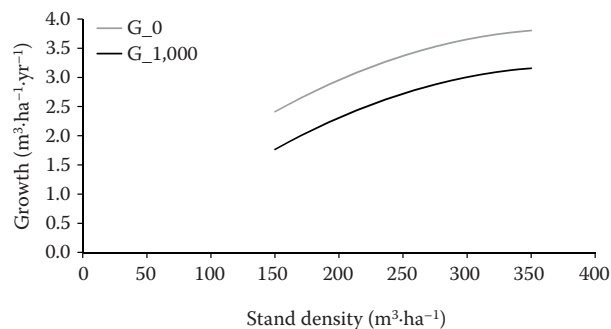

Fig. 3. Growth according to the estimated function as a function of stock and altitude. Note that the elevation levels in the empirical material are found in the interval from 580 to 1,080 m a.s.l. The stand densities vary between 188 and 320 m³·ha⁻¹ in the raw data

G_0 – altitude level 0 m a.s.l., G_1,000 – altitude level 1,000 m a.s.l.
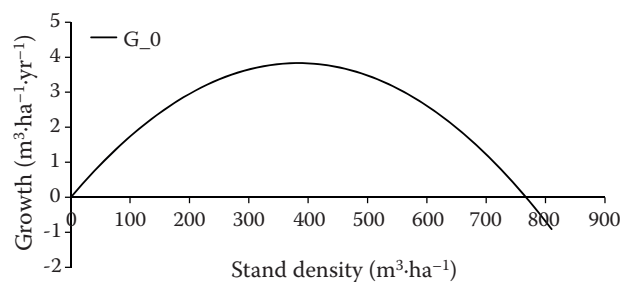

Fig. 4. Growth according to the estimated function as a function of the stock (if the forest is located at sea level). The function has been extrapolated far outside the empirical material. Note that there are two dynamic equilibria, at the stand densities 0 and 767 m³·ha⁻¹ (= the carrying capacity). The stock 0 is an unstable equilibrium and the carrying capacity represents a stable equilibrium

We may regard this as an approximation of continuous growth (Eq. 12):

$$z = \frac{\Delta\Phi}{\Delta t} \approx \frac{d\Phi}{dt} \tag{12}$$

In slowly growing forests, the approximation is rather good: (*i*) general regression statistics: $F = 211.8$, $R^2 = 0.872$, (*ii*) *t*-values of the estimated parameters: $t(\Phi) = 13.09$, $t(\Phi^2 \ln(\Phi)) = 9.56$.

Since the parameters are not determined with infinite precision (compare the *t*-values), we reduce the precision of the parameters in the following manner (Eq. 13):

$$z = 0.1586\Phi^2 \ln(\Phi) + 0.07039\Phi \tag{13}$$

Of course, the function could also be expressed in this way (Eq. 14):

$$z = \Phi(0.1586\Phi \ln(\Phi) + 0.07039) \tag{14}$$

Basal area growth of individual tree according to Eq. 11 is shown in Fig. 6.

Dynamic two species model with competition

Dynamic multi-species model parameters were determined via steady-state observations of unmanaged forests according to Eq. 5.

If we can observe *x* and *y* in several equilibria, at different altitudes and directions in Eq. 5, in some cases we can estimate relations between the parameters and simultaneously determine the species specific sensitivities to altitude and direction according to the following cases (Figs 7–10).

DISCUSSION

The aim of this study is to estimate a dynamic multi-species growth model with respect to dynamic behaviour, equilibria, convergence and stability in Iranian Caspian forests at 3 different elevations.

The general dynamics of forests based on logistic growth models was analysed and dynamic equilibrium conditions (stand densities and species mixes) for different altitudes were determined. The result of this research is in line with studies such as Lohmander (2007) and Lohmander and Mohammadi Limaei (2008).

In some cases, dynamic multi-species model parameters can be determined via steady-state ob-
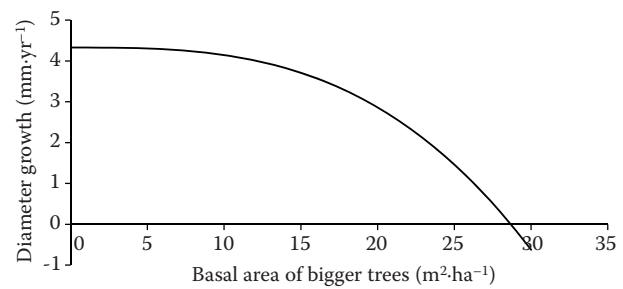

Fig. 5. The development of individual trees is affected by competition. This is one example of such a case. The diameter of the individual tree is assumed to be 200 mm before growth
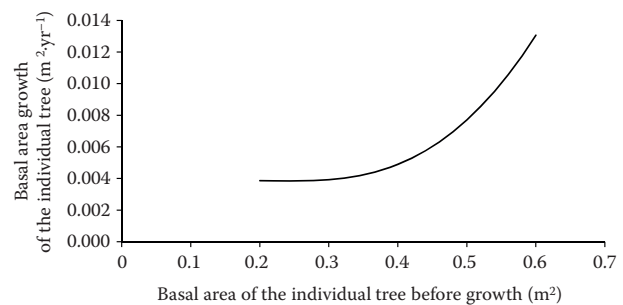

Fig. 6. Basal area growth of the individual tree as a function of the basal area of the individual tree before growth according to the estimated function
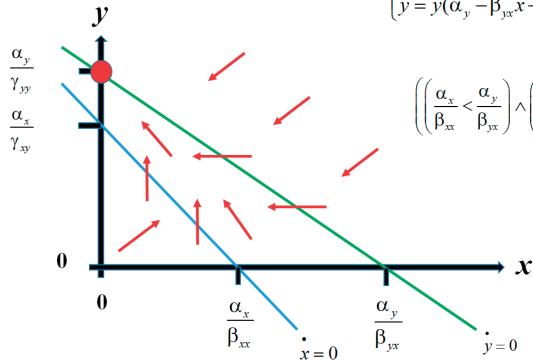
servations of unmanaged forests. Optimization of management decisions in a changing and not perfectly predictable world should always be based on adaptive optimization. Lohmander (2000) described these principles and typical implications for optimal forestry decisions. Adaptable logistic growth functions work well in such cases.

It would have been valuable to have more variation in the raw data. Now, the degrees of competition and the stand densities have low degrees of variation. In the presently analysed raw data, there are correlations different from zero between the possibly explaining variables direction of slope and altitude. There are also correlations different from zero between species and altitude. For instance, beech is almost only found at the highest elevations. In the future, datasets without such correlations should be developed.

The parameter of altitude in Eq. 5 is in general expected to be negative for the following reasons. Usually, the growth conditions get worse at higher altitudes. The temperature is usually lower, the amount of continuously available water is usually reduced and the growing seasons are shorter. On

(a) **CASE 1.**

$$\begin{cases} \dot{x} = x(\alpha_x - \beta_{xx}x - \gamma_{xy}y) & \alpha_x > 0; \beta_{xx} > 0; \gamma_{xy} > 0 \\ \dot{y} = y(\alpha_y - \beta_{yx}x - \gamma_{yy}y) & \alpha_y > 0; \beta_{yx} > 0; \gamma_{yy} > 0 \end{cases}$$

$$\left(\left(\frac{\alpha_x}{\beta_{xx}} < \frac{\alpha_y}{\beta_{yx}}\right) \wedge \left(\frac{\alpha_x}{\gamma_{xy}} < \frac{\alpha_y}{\gamma_{yy}}\right)\right) \Rightarrow (x_e, y_e) = \left(0, \frac{\alpha_y}{\gamma_{yy}}\right)$$

Unique and Stable

(b) **CASE 2.**

$$\begin{cases} \dot{x} = x(\alpha_x - \beta_{xx}x - \gamma_{xy}y) & \alpha_x > 0; \beta_{xx} > 0; \gamma_{xy} > 0 \\ \dot{y} = y(\alpha_y - \beta_{yx}x - \gamma_{yy}y) & \alpha_y > 0; \beta_{yx} > 0; \gamma_{yy} > 0 \end{cases}$$
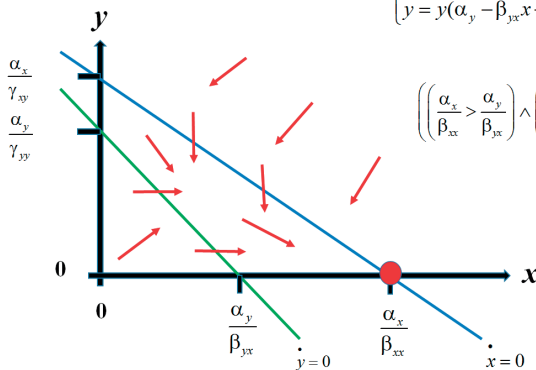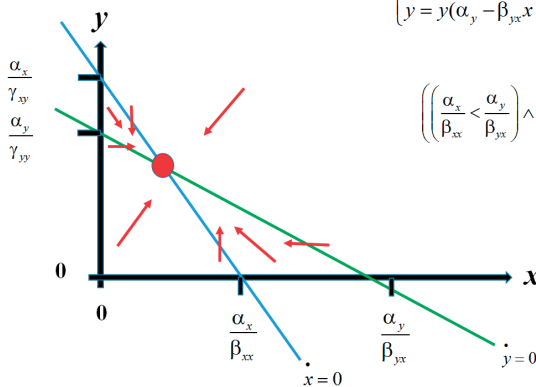

$$\left(\left(\frac{\alpha_x}{\beta_{xx}} > \frac{\alpha_y}{\beta_{yx}}\right) \wedge \left(\frac{\alpha_x}{\gamma_{xy}} > \frac{\alpha_y}{\gamma_{yy}}\right)\right) \Rightarrow (x_e, y_e) = \left(\frac{\alpha_x}{\beta_{xx}}, 0\right)$$

Unique and Stable

(c) **CASE 3.**

$$\begin{cases} \dot{x} = x(\alpha_x - \beta_{xx}x - \gamma_{xy}y) & \alpha_x > 0; \beta_{xx} > 0; \gamma_{xy} > 0 \\ \dot{y} = y(\alpha_y - \beta_{yx}x - \gamma_{yy}y) & \alpha_y > 0; \beta_{yx} > 0; \gamma_{yy} > 0 \end{cases}$$

$$\left(\left(\frac{\alpha_x}{\beta_{xx}} < \frac{\alpha_y}{\beta_{yx}}\right) \wedge \left(\frac{\alpha_x}{\gamma_{xy}} > \frac{\alpha_y}{\gamma_{yy}}\right)\right) \Rightarrow (x_e, y_e) = \left(x_e^0, y_e^0\right)$$

Unique and Stable

Fig. 7. In these cases, the system converges to a unique and stable equilibrium, where we have only species y (a), only species x (b), both species x and y (c)

$\dot{x}$ – growth of species X (m³·ha⁻¹·year⁻¹), x – stock level of species X (m³·ha⁻¹), α_x, β_{xx}, γ_{xy}, α_y, β_{yx}, γ_{yy} – set of parameters, $\dot{y}$ – growth of species Y (m³·ha⁻¹·year⁻¹), y – stock level of species Y, x_e – equilibrium value of x, y_e – equilibrium value of y, x_e^0 equilibrium value of x calculated by Cramer's rule applied to the differential equation system, y_e^0 – equilibrium value of y calculated by Cramer's rule applied to the differential equation system

the other hand, in this particular case, the tree species frequencies and the directions of the slopes are correlated with the altitude. For these reasons, the interpretation of the parameter k becomes less unambiguous. In any case, the regression analysis shows that the estimated parameter obtained the expected negative sign.

According to the results of Eq. 9, the diameter growth is a strictly increasing, strictly concave function of the diameter of the individual tree, which is similar to the results of Lнотка and Loewenstein (2011). Furthermore, note that the

diameter growth is a strictly decreasing concave function of the basal area of bigger trees. In the article, the exact functional form of the growth function was not motivated and the asymptotic properties of the function were not investigated. Hence, we may and should question if the influence of the diameter on diameter growth follows a logarithmic function. We should also question if the influence of competition can be described by the cube of the basal area of bigger trees. For instance, it is very hard to imagine negative diameter growth, which we may sometimes obtain with this function. It is

CASE 3 and 4: Interior equilibrium equations

$$\begin{cases} \dot{x} = x(\alpha_x - \beta_{xx}x - \gamma_{xy}y) & \alpha_x > 0; \beta_{xx} > 0; \gamma_{xy} > 0 \\ \dot{y} = y(\alpha_y - \beta_{yx}x - \gamma_{yy}y) & \alpha_y > 0; \beta_{yx} > 0; \gamma_{yy} > 0 \end{cases}$$

$$\left(\left(\frac{\alpha_x}{\beta_{xx}} < \frac{\alpha_y}{\beta_{yx}} \right) \wedge \left(\frac{\alpha_x}{\gamma_{xy}} > \frac{\alpha_y}{\gamma_{yy}} \right) \right) \Rightarrow (x_e, y_e) = \left(x_e^0, y_e^0 \right)$$
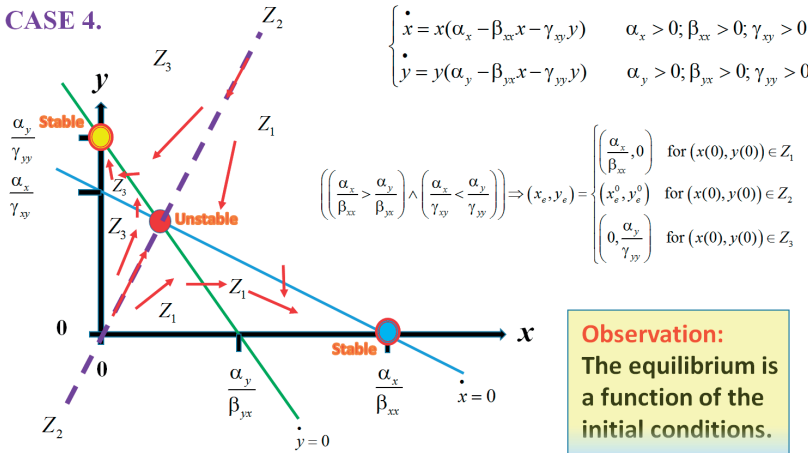
$$\begin{cases} \alpha_x - \beta_{xx}x - \gamma_{xy}y = 0 \\ \alpha_y - \beta_{yx}x - \gamma_{yy}y = 0 \end{cases}$$

$$\begin{bmatrix} \beta_{xx} & \gamma_{xy} \\ \beta_{yx} & \gamma_{yy} \end{bmatrix} \begin{bmatrix} x_e^0 \\ y_e^0 \end{bmatrix} = \begin{bmatrix} \alpha_x \\ \alpha_y \end{bmatrix}$$

$$x_e^0 = \frac{\begin{vmatrix} \alpha_x & \gamma_{xy} \\ \alpha_y & \gamma_{yy} \end{vmatrix}}{\begin{vmatrix} \beta_{xx} & \gamma_{xy} \\ \beta_{yx} & \gamma_{yy} \end{vmatrix}} = \frac{\alpha_x\gamma_{yy} - \alpha_y\gamma_{xy}}{\beta_{xx}\gamma_{yy} - \beta_{yx}\gamma_{xy}}$$
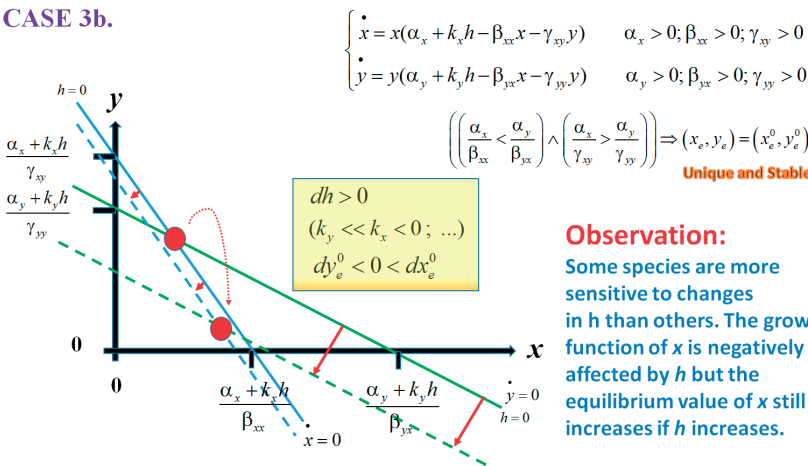
$$y_e^0 = \frac{\begin{vmatrix} \beta_{xx} & \alpha_x \\ \beta_{yx} & \alpha_y \end{vmatrix}}{\begin{vmatrix} \beta_{xx} & \gamma_{xy} \\ \beta_{yx} & \gamma_{yy} \end{vmatrix}} = \frac{\beta_{xx}\alpha_y - \beta_{yx}\alpha_x}{\beta_{xx}\gamma_{yy} - \beta_{yx}\gamma_{xy}}$$

Fig. 8. Derivation of the multi-species equilibrium solutions found in Figs 7c and 9

$\dot{x}$ – growth of species X (m³·ha⁻¹·year⁻¹), x – stock level of species X (m³·ha⁻¹), α_x, β_{xx}, γ_{xy}, α_y, β_{yx}, γ_{yy} – set of parameters, $\dot{y}$ – growth of species Y (m³·ha⁻¹·year⁻¹), y – stock level of species Y, x_e – equilibrium value of x, y_e – equilibrium value of y, x_e^0 – equilibrium value of x calculated by Cramer's rule applied to the differential equation system, y_e^0 – equilibrium value of y calculated by Cramer's rule applied to the differential equation system

CASE 4.

$$\begin{cases} \dot{x} = x(\alpha_x - \beta_{xx}x - \gamma_{xy}y) & \alpha_x > 0; \beta_{xx} > 0; \gamma_{xy} > 0 \\ \dot{y} = y(\alpha_y - \beta_{yx}x - \gamma_{yy}y) & \alpha_y > 0; \beta_{yx} > 0; \gamma_{yy} > 0 \end{cases}$$

$$\left(\left(\frac{\alpha_x}{\beta_{xx}} > \frac{\alpha_y}{\beta_{yx}} \right) \wedge \left(\frac{\alpha_x}{\gamma_{xy}} < \frac{\alpha_y}{\gamma_{yy}} \right) \right) \Rightarrow (x_e, y_e) = \begin{cases} \left(\frac{\alpha_x}{\beta_{xx}}, 0 \right) & \text{for } (x(0), y(0)) \in Z_1 \\ \left(x_e^0, y_e^0 \right) & \text{for } (x(0), y(0)) \in Z_2 \\ \left(0, \frac{\alpha_y}{\gamma_{yy}} \right) & \text{for } (x(0), y(0)) \in Z_3 \end{cases}$$

Observation: The equilibrium is a function of the initial conditions.

Fig. 9. In this case, the system has one unstable multi-species equilibrium and two stable single species equilibria

$\dot{x}$ – growth of species X (m³·ha⁻¹·year⁻¹), x – stock level of species X (m³·ha⁻¹), α_x, β_{xx}, γ_{xy}, α_y, β_{yx}, γ_{yy} – set of parameters, $\dot{y}$ – growth of species Y (m³·ha⁻¹·year⁻¹), y – stock level of species Y, x_e – equilibrium value of x, y_e – equilibrium value of y, x_e^0 – equilibrium value of x calculated by Cramer's rule applied to the differential equation system, y_e^0 – equilibrium value of y calculated by Cramer's rule applied to the differential equation system

CASE 3b.

$$\begin{cases} \dot{x} = x(\alpha_x + k_x h - \beta_{xx}x - \gamma_{xy}y) & \alpha_x > 0; \beta_{xx} > 0; \gamma_{xy} > 0 \\ \dot{y} = y(\alpha_y + k_y h - \beta_{yx}x - \gamma_{yy}y) & \alpha_y > 0; \beta_{yx} > 0; \gamma_{yy} > 0 \end{cases}$$

$$\left(\left(\frac{\alpha_x}{\beta_{xx}} < \frac{\alpha_y}{\beta_{yx}} \right) \wedge \left(\frac{\alpha_x}{\gamma_{xy}} > \frac{\alpha_y}{\gamma_{yy}} \right) \right) \Rightarrow (x_e, y_e) = \left(x_e^0, y_e^0 \right)$$

Unique and Stable

$dh > 0$
$(k_y \ll k_x < 0 ; \dots)$
$dy_e^0 < 0 < dx_e^0$

Observation:

Some species are more sensitive to changes in h than others. The growth function of x is negatively affected by h but the equilibrium value of x still increases if h increases.

Fig. 10. In this case, the system converges to a unique and stable equilibrium, where we have both species x and y. The graph shows how the stable equilibrium changes under the influence of parameter changes

$\dot{x}$ – growth of species X (m³·ha⁻¹·year⁻¹), x – stock level of species X (m³·ha⁻¹), α_x, β_{xx}, γ_{xy}, α_y, β_{yx}, γ_{yy} – set of parameters, $\dot{y}$ – growth of species Y (m³·ha⁻¹·year⁻¹), y – stock level of species Y, k_x, k_y – set of parameters, x_e – equilibrium value of x, y_e – equilibrium value of y, x_e^0 – equilibrium value of x calculated by Cramer's rule applied to the differential equation system, y_e^0 – equilibrium value of y calculated by Cramer's rule applied to the differential equation system, h – parameter that influences the growth of the two species (for instance, h may denote the altitude of the site), dh – change of h (for instance, if $dh > 0$, this may mean that the altitude increases, this influences the growth of the two species in different ways)

however very likely that the general properties of the function are close to reality, at least within the investigated parameter ranges.

It would be interesting to know how the individual trees grow in the forests of Iran. The estimated function (Eq. 9) shows that the growth of the individual tree strongly increases with size, which is supported by functions presented by Schütz (2006). When the tree is much bigger than the neighbour trees, the competition for light is almost eliminated. When the tree lives in the shade of the others, the struggle for existence is difficult.

Fig. 6 shows that the basal area growth appears to be a strictly convex function of the basal area before growth, at least in the range illustrated in Fig. 6. This is understandable from the following perspectives.

As the size (in different dimensions) of the individual tree increases, it gets access to more light, which is essential to the photosynthesis. Furthermore, it is likely that the area of the root system increases and that the available supplies of water and nutrients also increase. Hence, we should expect the total growth of the tree to increase with size. However, the trees live in a world of competition. The distribution of resources within the trees should be assumed to be optimized, since trees that do not optimize the use of resources, do not usually survive in the competition. Hence, it is very likely that it is optimal for the individual tree to use the available resources in this way:

(*i*) If the tree is small (and usually also has a low basal area) in relation to competing trees, it lives in the shadow and has limited access to light. Furthermore, the wind is not very strong because of protection from taller trees. Hence, it is rational to use most of the resources to become taller and get more access to light in the future. Growth of the basal area, which may stabilize the tree, is not very important. So, the basal area growth is low (and stable) when the basal area is low (compare Fig. 6);

(*ii*) If the tree is tall (and usually also has a large basal area) in relation to competing trees, it has good access to light. Hence it is not very important to become taller. Furthermore, if it becomes even taller, the winds may be too strong and the tree may fall down in a future storm. Hence, the growth resources should be used to stabilize the tree. The basal area increases and the area of the root system increases, giving even more access to water and nutrients. So, the basal area growth is a rapidly increasing function of basal area when the basal area is high (compare Fig. 6).

Results indicated that if the size of the individual tree increases, the number of bigger trees is reduced (Fig. 5). Hence, we should expect the growth of the individual tree to increase, in a strictly convex fashion, as the size of the individual tree increases (Fig. 6). These results are in line with Schütz (2006). According to the function presented by Schütz (2006), the growth of the individual tree is strongly reduced (via the cubic competition effect) by the competition from bigger trees.

Of course, it is not possible to determine the precise functional form without information about the tree size frequency distribution and other related conditions.

The results of this study could be used as inputs to an integrated optimization model of the forest supply chain, from forest production, via logistics, to the forest industry mills. A growth model can help the forest managers to have deep understandings of forest and to better explain data, forecast the future of forest dynamics with greater reliability, and to see the potential ramifications of decisions.

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