HOKKAIDO UNIVERSITY

Title	Qualitative analysis of dynamic states of the Larix-permafrost ecosystem under climate warming
Author(s)	Antonovsky, Mikhail Ya.; Korzukhin, Mikhail D.; Shugart, Herman Henry
Citation	Eurasian Journal of Forest Research, 20, 21-25
Issue Date	2017-12
Doc URL	https://hdl.handle.net/2115/67943
Type	departmental bulletin paper
File Information	03EJFR20_Antonovsky.pdf

Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

Qualitative analysis of dynamic states of the *Larix*-permafrost ecosystem under climate warming

ANTONOVSKY Mikhail Ya.[1], KORZUKHIN Mikhail D.[2], SHUGART Herman Henry[3]*

[1]Institute of Global Climate and Ecology of Rosgydromet and Russian Academy of Science, Moscow, Russia (107258, Moscow, Glebovskaya, 20Б)
[2]Institute of Global Climate and Ecology of Rosgydromet and Russian Academy of Science, Moscow, Russia (107258, Moscow, Glebovskaya, 20Б)
[3]Herman H. Shugart (Corresponding Author), Department of Environmental Sciences, 291 McCormick Drive, University of Virginia, Charlottesville, Virginia, 22904-4123, USA

Abstract

Dahurian Larch, *Larix gmelinii,* grows as a tree in the continuous permafrost region of eastern Siberia. Along with other allied Larch species and/or subspecies (notably *L. cajanderi*), it can grow on continuous permafrost. The expected warming of the climate in Siberia from global warming will reduce the permanent permafrost area, and will have an effect on the reduction in distribution of the larch. We investigate the possible forest succession effects in the interactive system among larch, dark conifers and climate using a simple conceptual model. The basic variables are the larch biomass, B_L, the dark conifer biomass, B_D, and the water content in the active soil layer, W. External parameters include precipitation, P, and air temperature, T_a. We track three processes: biomass growth as a function of T_a and W; carbon losses on respiration and decay; competition within a species as well as between species that limit biomass growth. Analysis of evolution the equilibria of the model under current growing-season temperatures has a stable condition of larch forest that can became unstable, so that larch can be replaced by dark conifers. More increased temperatures produce a new non-trivial equilibrium with a coexistence of Larch with "dark conifers" (*Pinus sibirica*, *Picea obovata* and *Abies sibirica*). Further temperature increase leads to a stable state in which the Larch is fully displaced by the dark conifers.

Key words: global warming, *Larix gmelinii*, continuous permafrost, tree succession.

Introduction

Larch-dominated forests (genus *Larix* Mill.) cover over 37% of Russian forested territory, and are located primarily in permafrost zone in eastern Siberia. They are a subject of special interest because of ecological importance of continuous permafrost in this region (Osawa *et al.* 2010). *Larix gmelinii* can grow under conditions of continuous permafrost as can *L. cajanderi* in regions east of the Lena River. The taxonomy of *L. gmelinii* and related taxa is complex (Polezhaeva *et al.* 2010) and *L. cajanderi* is considered a subspecies of *L. gmelinii* by some. Other (dark) conifer species (*Pinus sibirica*, *Picea obovata* and *Abies sibirica*) survive under the conditions in warm river valleys or on hills with a permafrost layer so deep that it does not affect the trees above (Osawa *et al.*, 2010). Expected warming of climate in Siberia (as a result of global warming) will lead to the reduction of permafrost and can be expected to produce change in the *L. gmelinii* distribution.

Theoretical calculations of stationary state or dynamics of *Larix* forests have been developed mostly for regional investigations. The models differ in the kind of description of ecological mechanisms involved: semi-phenomenological biogeographical models (Tchebakova *et al.*, 2010); intermediate complexity stationary-biome models (Kaplan and New, 2006); detailed dynamical individual based models or IBMs (Shuman *et al.*, 2011; Zhang *et al.*, 2011). Some of these studies do not include permafrost as an explicit ecological factor.

Of special interest is the phenomenon of bifurcation or "tipping-point" in modern terms, which feature an abrupt reaction to slow changes of system parameters. During the past two decades, examples of expected bifurcation in natural ecosystems have accumulated. Usually, these examples often are the product of examination of two types of models, either detailed mechanical models or low-dimensional dynamical analytical models. Ecosystem examples involve vegetation dynamics that can potentially exhibit tipping-point behavior, including a diversity of examples:

- The existence of two stable climate and vegetation states in northern Africa (Patricola and Cook, 2008 using mechanistic model; Brovkin *et al.*, 1998; Moorcroft, 2003 for low-dimensional model);
- Three distinct modes for tree cover dynamics in the tropics (Nes *et al.*, 2014 from a low-dimensional model), or two modes (Oyama and Nobre, 2003 from a mechanistic model);
- Desert-forest transition with two or more stable states

(Received; June. 8, 2017: Accepted; Sep. 5, 2017)
* Corresponding author: hhs@virginia.edu

(Zeng et al, 2002 - low-dimensional model);
- *Larix* to dark conifer species change (Zhang *et al.*, 2011 – mechanical model).
- Low-dimensional models are used in analysis of possible instabilities in feedbacks with the global or regional climate system induced by global warming. Physical mechanisms of such instability are based on positive feedbacks between variables. Physical systems interactions (e.g., the significant feedback among sea ice, albedo, and climate) allow more precise numerical calculation than systems of interactions that include vegetation cover. However, for the vegetation-involved feedbacks, the problem is usually approached using reasonable estimates of expected responses.

Model Development

This paper will explore a simple and familiar model, which is basic in ecological modelling and sufficient to our purposes, namely a version of Lotka-Volterra (Volterra and Berlot 1931, Lotka 1932) system for competing species rewritten into biomass terms. The model can be analyzed graphically and qualitatively. Despite its conceptual nature, it allows examination of some of the important features of the system, namely: its possible climax states, their stability, variants of stability changes under parameter changes, and whether the loss of stability takes place gradually or abruptly. Our intention is to explore the expected dynamics of the ecosystem to indicate the classes of dynamics that might proceed from numerical solutions of more specifically parametrized models. This is a standard procedure for theoretical investigations. The reliability of our conclusions principally depends mainly on the degree of mechanistic realism implemented in representing the system-parameter dependence on ecological factors. In our formalization, we intentionally deal with a minimum number of such dependencies represented in a physically realistic form that mimics the observed system features. Our investigation uses equilibrium state(s) analysis, and not the systems dynamics proper. The method involves the graphical analysis of the phase portraits and their change with parameter variation for the system under consideration. In its complete form, this method was proposed by H. Poincaré (see: Oeuvers de Henri Poincaré 1916-1954). It has since been successfully used in numerous works (e.g., Antonovsky *et al.*, 1990; Antonovsky and Korzukhin, 2012). Many introductory ecology textbooks present a simple graphical analysis from this method using the Lotka-Volterra equations as examples.

Adequate description of any system requires knowledge about the principal controlling factors, which in this case is derived from an extensive literature (e.g., Euskirchen *et al.*, 2006; Osawa *et al.*, 2010; Zhang *et al.*, 2011). Factors that are usually mentioned as controlling factors are permafrost, forest fires and soil moisture. Evapotranspiration and soil temperature regime depend on forest and subcanopy cover. All these factors are governed by air temperature and precipitation. The exact mechanisms of interactions and the quantitative interdependencies among these variables are often not clear (see Osawa *et al.* (2010) for more details).

Field observations indicate that system [*Larix* - permafrost] is self-sustainable. There are indications that after air temperature exceeds a certain threshold, rapid change is probable including altered species composition. This result was obtained numerically in an individual-based model (Shuman *et al.*, 2011; Zhang *et al.*, 2011) with critical temperature increment δT around 2-4ºC.

In our model, variables are total *Larix* biomass (BL), total dark conifer biomass (BD) and water content in active soil layer (W). External parameters are precipitation, P, and air temperature, Ta. The processes under consideration are biomass growth, carbon losses to respiration and decay, and interspecies competition. As it was mentioned above, the Volterra model (Volterra and Brelot, 1931) is appropriate for our aim, but it has to be extended by equation for W, so the whole system will be

$$\begin{aligned} dBL/dt &= a_L \times BL - r_L \times BL^2 - c_L \times BL \times BD; \\ dBD/dt &= a_D \times BD - r_D \times BD^2 - c_D \times BL \times BD; \\ dW/dt &= P - fW \times W, \end{aligned} \qquad (1)$$

where: a_L, a_D are specific rates of biomass growth (net growth that includes all carbon losses), rL, rD describe growth limitation due to intraspecies competition, while c_L, c_D are growth limitations due to responsible for interspecies competition. Function fW has complex structure and describes the processes of soil-water loss, namely evapotranspiration and percolation, which depend on permafrost depth, soil temperature, and forest biomass. The governing external factor is Ta (for climate change, precipitation P is less important than Ta). The dependencies on Ta and W are given below.

Results and Discussion

Following sequence of physical relations responsible for stability of [*Larix* – permafrost] system are: increase of Ta $\rightarrow$ lowering of permafrost layer $\rightarrow$ increase of water percolation from root zone $\rightarrow$ decrease of water available $\rightarrow$ worsening of mineral supply of trees. Instead of giving functions that describe each of these processes, which is a considerable challenge one can exclude these intermediate steps and postulate fW as some increasing monotonic function of Ta that corresponds to direct field observations (e.g., Lopez *et al.*, 2007; Osawa *et al.*, 2010).

Note that permafrost depth and accompanying processes adjust quickly to current temperature value, so that these processes are much faster than forest dynamics proper. This fact allows one to change the last equation in system (1) for its quasistationary analogue that arises from dW/dt = 0, and to get soil water content as its solution:

$$W(Ta) = P/fW(Ta). \qquad (2)$$

Specific rates of biomass growth, a_L and a_D, are

increasing functions of W up to very high values when a shortage of oxygen in soil starts. In the system under consideration, the main growth limiting factor is W, so in the first approximation a_L and a_D, are taken as independent of Ta. Also, *Larix* is more sensitive to W decrease than dark conifer species because of its shallower root location. After these simplifications, system (1) reduces to:

$$dBL/dt = a_L(W(Ta))\times BL - r_L\times BL^2 - c_L\times BL\times BD;$$
$$dBD/dt = a_D(W(Ta))\times BD - r_D\times BD^2 - c_D\times BL\times BD; \quad (3)$$

This system is completely examined in Lotka (1932) and the results are presented below.

Consider is the system [*Larix* – evergreen dark conifer species - permafrost] under a temperature increase. Ecological mechanism of the dynamic change consists in soil moisture decrease leading to decrease of growth rates $a_L(W)$ and $a_D(W)$, with $a_L(W)$ (or $a_L(Ta)$) falling more rapidly than $a_D(W)$. For the sake of simplicity, one can suppose that only $a_L(Ta)$ decreases.

System (3) has two on-axis equilibria: $[BL_0, 0]$ where:

$$BL_0 = a_L/r_L,$$

and [0, BD0] where

$$BD_0 = a_D/r_D,$$

and one nontrivial equilibrium $[BL_{00}, BD_{00}]$, where

$$BL_{00} = (a_Lr_D-a_Dc_D)/(r_Lr_D-c_Lc_D);\ BD_{00} = (a_Dr_L-a_Lc_L)/(r_Lr_D-c_Lc_D). \quad (4)$$

Equilibrium $[BL_{00}, BD_{00}]$ do not necessary lay in the positive quadrant.

Stability/instability of these equilibria are governed by signs of corresponding eigenvalues:

$[BL_0, 0]$: $\lambda L_1 = - a_L$; $\lambda L_2 = (a_Dr_L-a_Lc_L)/r_L$;
$[0, BD_0]$: $\lambda D_1 = - a_D$; $\lambda D_2 = (a_Lr_D-a_Dc_D)/r_D$;
$[BL_{00}, BD_{00}]$: $\lambda LD_1, \lambda LD_2$

are the roots of quadratic equation

$$\lambda^2+(r_LBL_0+r_DBD_0)\lambda+BL_0BD_0(r_Lr_D-c_Lc_D)= 0$$

which roots are always real. Under $(r_Lr_D-c_Lc_D) > 0$, $\lambda LD_1, \lambda LD_2 < 0$ while under $(r_Lr_D-c_Lc_D) < 0$ $\lambda LD_1 > 0$, $\lambda LD_2 < 0$. Consider now an idealized scenario when $a_L(Ta)$ is a single parameter depending on Ta while all others are constant, and $a_L(Ta)$ decreases with Ta.

First, consider the case of weak interspecies competition $(r_Lr_D-c_Lc_D > 0)$. Let Ta0 be the current value of temperature. When $a_L(Ta)$ is big enough, λL_1, $\lambda L_2 < 0$; it is easy to show that $\lambda D_2 > 0$ so equilibrium $[0, BD_0]$ is unstable and that $[BL_{00}, BD_{00}]$ is out of positive quadrant. So, the system is in the stable equilibrium $[BL_0, 0]$ and the phase plane has the structure depicted in Fig. 1a. This case can be identified with current situation when the *Larix* ecosystem is stable.

The first bifurcation takes place when $a_L(Ta)$ decreases to the value such that λL_2 becomes positive, and that equilibrium $[BL_0, 0]$ becomes unstable. This happens when:

$$a_L(Ta_1) = a_Dr_L/c_L \text{ under some } Ta_1 > Ta_0.$$

This event coincides with the origin of nontrivial stable positive equilibrium $[BL_{00}, BD_{00}]$, which can be shown from (4). The phase plane takes the structure depicted on Fig. 1b. This case can be identified with a situation when *Larix* and dark conifer species coexist.

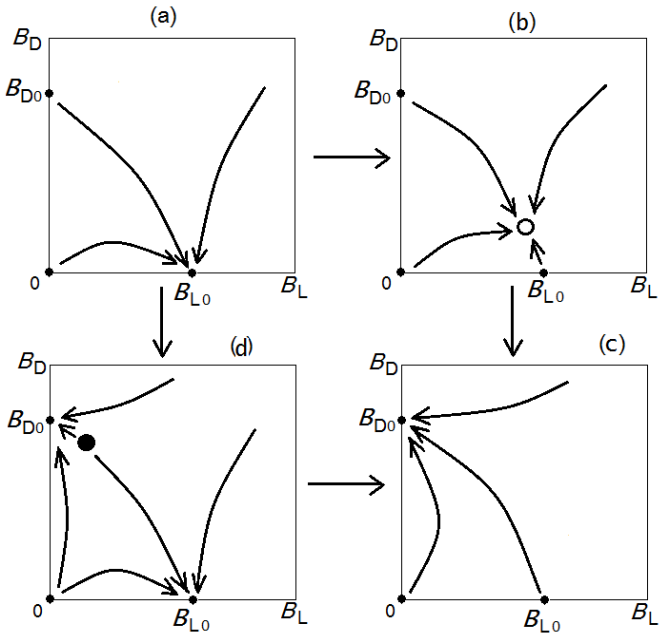


Figure 1. Phase plane structure shows two conceivable ways of evolution of the [larix (BL) – evergreen dark conifer (BD) species] system under temperature rise. Depending on parameter values, the system can move from originally stable equilibrium $[BL_0, 0]$, (a) which is the nontrivial stable equilibrium $[BL_{00}, BD_{00}]$ (○) to (b). Further temperature rise leads to its fusion with stable equilibrium $[0, BD_0]$ – (c). A second type of evolution goes through the origin of nontrivial unstable equilibrium $[BL_{00}, BD_{00}]$ (•) from $[0, BD_0]$ - (d); further temperature rise leads to its fusion with stable equilibrium $[BL_0, 0]$ – (c); the last loses its stability, and the system goes over to the stable equilibrium $[0, BD_0]$.

Further growth in temperature (decrease of $a_L(Ta)$) leads to the second bifurcation when λD_2 becomes negative, so that equilibrium [0, BD_0] becomes stable; that happens when $a_L(Ta_2) = a_D c_D / r_D$ under some $Ta_2 > Ta_1$. This event coincides with the extinction of nontrivial positive equilibrium [BL_{00}, BD_{00}] which fuses with [0, BD_0] (which again can be shown from (4)). The phase plane takes the structure depicted on Fig. 1c. This case can be identified with a situation when *Larix* disappears and only dark conifer species remain.

The case of strong interspecies competition ($r_L r_D - c_L c_D < 0$) is analyzed in the same manner. Briefly, under growing temperature evolution from the original state (Fig. 1a) to the (Fig. 1c) final state goes through the origin of nontrivial unstable positive equilibrium [BL_{00}, BD_{00}] (Fig. 1d). The loss of stability of equilibrium [B_{L0}, 0] takes place sharply by means of extinction of its local zone of stability ("tipping-point" effect) when equilibrium [BL_{00}, BD_{00}] fuses with [BL_0, 0]. If one depicts current and forecasted borders of permafrost, a territory between them can be treated as the potential zone where substitution of *Larix* by dark conifer species could happen (Fig. 2).

Both of two ways of evolution of forest pattern correspond well to the empirical-model scheme of behavior of [*Larix* – evergreen dark conifer species] system. In this case, the result was achieved by means of introduction of only one monotonic function of temperature, $a_L(Ta)$, in right parts of basic system (3).

This work examines potential changes in species composition in ecological system of Larch forests, Evergreen dark conifer species, and permafrost situated in eastern Siberia and within the zone of the continuous permafrost with an application of a conceptual, low-dimensional model. One-species models of this kind do exist but their generalization to multi-species case still awaits implementation. For example, the Sheffield Dynamic Global Vegetation Model (Woodward and Lomas, 2004) operates by formalization of one tree species growth in the form of two-variable model (B – stand biomass, and LAI – leaf area index). Inter-species competition is accounted for indirectly (implicitly) by means of comparison of species' NPP values. This is true for other Dynamic Global Vegetation models (DGVMs and for equilibrium models like BIOME3 (Haxeltine and Prentice, 1996).

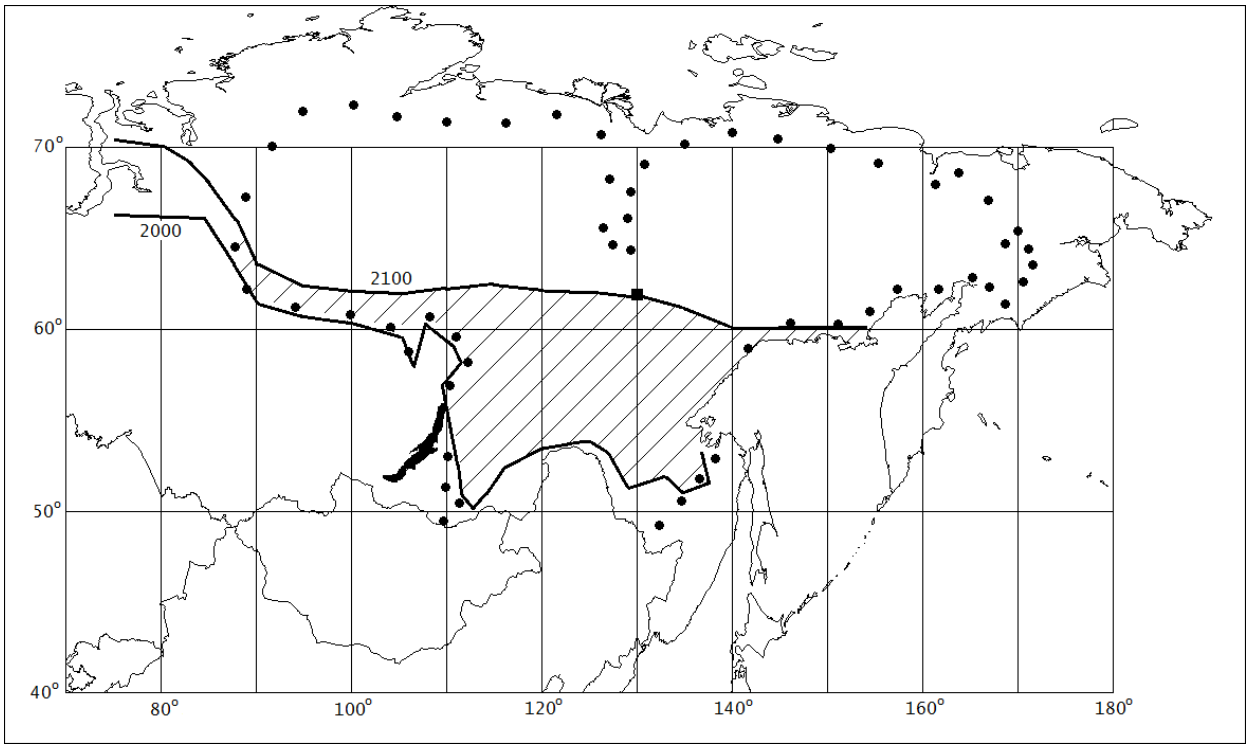


Figure 2. Current range of *L. gmelinii* (•), and two southern limits of permafrost distribution in Siberia: lower is the currently observed one (Osawa *et al.*, 2010) while the upper is its forecast to the end of this century under global temperature rise $\delta T \sim 4^{o}C$ (Romanovsky *et al.*, 2008). Hatched area depicts a territory where *L. gmelinii* can be displaced by dark conifer species. ■ – location of Yakutsk.

References

Antonovsky M.Ya., Fleming R.A., Kuznetsov Yu.A., *et al.* (1990) Forest-pest interaction dynamics: the simplest mathematical models. *Theoretical Population Biology* 37:343-367.

Antonovsky M.Ya. and Korzukhin, M.D. (2012) A Dynamic Model of the Immune Response to the Onset of a Tumor. *Doklady Biochemistry and Biophysics* 451:176–179.

Brovkin V., Claussen, M. Petouknov, V. and Ganopolski, A. (1998). On the stability of the atmosphere–vegetation system in the Sahara Sahel region. *Journal of Geophysical Research* 103:613–624.

Euskirchen E.S., McGuire, A.D., Kicklighter, D.W., Zhuang, Q., Clrin, J.S, Dargaville, R.J., Dye, D.G., Kimball, J.S., McDonald, K.C., Melillo, J.M., Romanovsky, V.E., and Smith, N.V. (2006) Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Global Change Biology* 12:731–750.

Haxeltine A. and Prentice, I.C. (1996) BIOME3: An equilibrium terrestial biosphere model based on ecological constrains, resource availability, and competition among plant functional types. *Global Biochemical Cycles* 10: 693–709.

Kaplan J.O. and New, M. (2006) Arctic climate change with a 2 °C global warming: Timing, climate patterns and vegetation change. *Climatic Change* 79:213-241.

Lopez M.L., Saito, H., Kobayashi, Y., Shirota, T., Iwahana, G., Maximov, T.C., and Fukuda M. (2007) Interannual environmental-soil thawing rate variation and its control on transpiration from *Larix cajanderi*, Central Yakutia, Eastern Siberia. *Journal of Hydrology* 338:251–260.

Lotka A.J. (1932) The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences* 22:461-469.

Moorcroft P.R. (2003) Recent advances in ecosystem–atmosphere interactions: an ecological perspective. *Proceedings of Royal Society of London, B, Biological Sciences* 270: 1215–1227.

van Nes E.H., Hirota, M., Holmgren, M., and Scheffer, M. (2014) Tipping points in tropical tree cover: linking theory to data. *Global Change Biology* 20:1016–1021.

Oeuvers de Henri Poincaré, 11 vols. (Paris, 1916-1954); Les méthodes nouvelles de la mécanique céleste, 3 vols. Paris, 1892-1899.

Osawa A., Matsuura Y., Kajimoto T. (2010). Characteristics of permafrost forests in Siberia and potential responses to warming climate, Chap. 24 in: Permafrost Ecosystems: Siberian Larch Forests. Osawa *et al.* (eds.). Springer, Berlin, Ecological studies, vol. 209, pp. 459–481.

Oyama M.D. and Nobre, C.A. (2003) A new climate - vegetation equilibrium state for tropical South America. *Geophysical Research Letters* 30:2199.

Patricola C.M. and Cook, K.H. (2008) Atmosphere/vegetation feedbacks: A mechanism for abrupt climate change over northern Africa. *Journal of Geophysical Research: Atmospheres*, vol. 113, D18102.

Permafrost Ecosystems, Siberian Larch Forests. 2010. Osawa *et al.* (eds.). Springer, Berlin. Ecological studies, vol. 209.

Polezhaeva MA, Lascoux, M and Semerikov. 2010. Cytoplasmic DNA variation and biogeography of *Larix* Mill. in Northeast Asia. *Molecular Ecology* 19:1239-1252. DOI:10.1111/j.1365-294X.2010.04552.x

Romanovsky V.E., Kholodov, A.L., Marchenko, S.S., Oberman, N.G., Drozdov, D.S., Malkova, G.V., Moskalenko, N.G., Vasiliev, A.A., Sergeev, D.O. and Zheleznyak, M.N., (2008) Thermal state and fate of permafrost in Russia: First Results of IPY. *Proc. of the 9th Intern. Conf. on Permafrost. U. of Alaska, Fairbanks, June 29–July 3*. Ed. by Douglas L. Kane and Kenneth M. Hinkel, vol. 2, pp. 1511-1518.

Shuman J.K., Shugart, H.H. and O'Halloran, T.L. (2011) Sensitivity of Siberian larch forests to climate change. *Global Change Biology* 17:2370–2384.

Tchebakova N.M., Rehfeldt G.E., and Parfenova E.I. (2010) Chap. 22 in: *Permafrost Ecosystems: Siberian Larch Forests*. Osawa *et al.* (eds.). Springer, Berlin, Ecological studies, vol. 209, pp. 427-446.

Volterra V. and Brelot, M. (1931) Lecons sur la Theorie Matematique de la Lutte pour la Vie. Gauthier-Villars. Paris. 214 pp.

Woodward, F.I., and Lomas M.R. (2004) Vegetation-dynamics – simulating responses to climate change. *Biological Reviews* 79: 643–670.

Zeng N., Hales, K. and Neelin, J.D.. 2002. Nonlinear Dynamics in a Coupled Vegetation–Atmosphere System and Implications for Desert–Forest Gradient. *Journal of Climate* 15:374-387.

Zhang N., Yasunari T., and Ohta T., 2011. Dynamics of the larch taiga–permafrost coupled system in Siberia under climate change, *Environmental Research Letters*, vol. 6, 024003.