Additive model of *Larix sp.* forest stand biomass sensitive to temperature and precipitation variables in Eurasia

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**Abstract.** The first attempt of modeling changes in additive component composition of biomass of *Larix* sp. communities on the Trans-European hydrothermal gradients based on regional peculiarities of age and morphology of the forests is attempted. The increase of all biomass components of the tree layer with increasing temperature at the constant precipitation and its decrease with increasing precipitation at the constant temperature is established. The positive relationship of the understory biomass with the temperature in the areas of insufficient moisture as the transition to moisture-rich areas is replaced by the opposite one. The development of such models for basic forest-forming species in Eurasia will give possibility to predict any changes in the biological productivity of forest cover of Eurasia in relation to climate change.

1. Introduction
Since 1850 to the present, the amount of greenhouse gases in the atmosphere has doubled, threatening the planet with catastrophic climate change [1]. Today, much attention has been paid to the study of the adaptive capacity of the planet’s biological species in the context of climate change. One intriguing feature of forest trees from an evolutionary point of view is noted: they tend to have a high level of genetic diversity and, at the same time, have a low rate of evolution. The rapid rate of current climate change places serious constraints on the ability of trees to adapt to new conditions [2].

Modelling the response of vegetation to climate change due to an increase in atmospheric CO2 concentration shows that the greatest changes in the composition and spatial distribution of vegetation will occur in the high latitudes of the Northern hemisphere [3]. According to predict by K Kobak and N Kondrashova [3], devoted to change of natural zones areas in connection with evaporation and index of dryness by M Budyko [4], when the temperature will increase by 1.4°C to the year 2000, significant changes of borders of natural zones were supposed to occur, in particular, the area of the tundra must be covered by coniferous forests, which today is not observed.

Available in the literature, the biomass equations of forest stands are developed mainly for local conditions, and separately for the total biomass and its components (stems, foliage, branches, roots). As a result, they are not additive, i.e. the sum of the predicted biomasses of the all components is not equal to the value of the predicted total biomass of the forest stand. Apart from the lack of logical
consistency of the equations, they are statistically correct not enough, since the estimation of the parameters was not taken into account the internal correlation between the biomass components [5]. Unlike many developed additive models of biomass at a tree level (see overview: [6]), only single modeling results are published at a forest stand level [7], mainly at a regional level and without taking into account the influence of climatic factors.

In 2013, the prominent foreign ecologists formulated 100 main questions, which should be answered by the ecology of the XXI century. At the end of the list under number 97 is the question: “How atmospheric changes will affect the primary production of terrestrial ecosystems?” [8]. In the proposed article we try to partially answer this question, namely, we undertake, in essence, the first attempt to model changes in the additive component composition of biomass of forest phytocenoses on Trans-Eurasian gradients of mean temperatures and precipitation on the example of the genus *Larix* sp. In the development of additive systems of equations, preference is given to the principle “from general to particular”, in which the equation for the total biomass is “splitted” into additive equations for each of the constituent components by proportional weighing [9, 10].

2. Methods and Materials

From the database on the biomass of Eurasia’s forests [11] materials in the amount of 540 sample plots having definitions of biomass (t/ha) of phytocenoses of the genus *Larix* sp. are taken, within its areal from the *L. decidua* Mill. in Central Europe, the *L. leptolepis* Gord. in Japan, and *L. Principis-ruprechtii* Mayr in China. One means biomass of phytocenosis, not forest stand, because we analyze not only the stand, but also the understory layer. Naturally, both are considered in connection with the taxation indices of stands, but not phytocenoses.

Each sample plot on which phytocenosis biomass was determined is positioned relative to the isolines of the mean January temperature and relative to the isolines of the mean annual precipitation [12], and the matrix of initial data was compiled, in which the values of the biomass components and forest stand mass-forming indices are associated with the corresponding values of the mean January temperature and mean annual precipitation, and then included in the regression analysis procedure. A schematic map of the mean January temperature isolines rather than of the mean annual temperature is used, since warming is most pronounced in the cold half of the year [13].

The common view of the adopted model for biomass (1):

\[
\ln P_i = f \left\{ \ln A, (\ln A)^2, \ln M, \ln N, \ln A \cdot \ln N, \ln (Tm + 50), \ln PRm, \ln (Tm + 50) \right\},
\]

(1)

where \(P_i\) is the biomass of the \(i\)-th component, t/ha; \(A\) is the age of the stand, years; \(M\) is the stem volume, m³/ha; \(N\) is tree number, 1000/ha; \(i\) is the index of the biomass component: total phytocenosis, including the tree floor and understory (\(e\)), the understory, including undergrowth and living grass cover (\(u\)), total wood storey (\(t\)), aboveground wood storey (\(a\)), roots of a stand (\(r\)), tree crowns (\(c\)), stems above bark (\(s\)), foliage (\(f\)), branches (\(b\)), stem wood (\(w\)) and stem bark (\(bk\)); \(PRm\) is mean annual precipitation, mm; \(Tm\) is mean January temperature, °C. Since in the North of Eurasia the mean annual temperature in January has negative values, the corresponding independent variable is modified to the form \((Tm + 50)\).

In contrast to the two-step disaggregation additive model for above-ground biomass [10] and to the three-step disaggregation additive model for above-ground and under-ground biomass [9], in our study, the total biomass of forest phytocenosis (tree stand and understory), estimated by the initial equation, is divided into components according to the four-step scheme of proportional weighing presented in Figure 1.

3. Results and Discussion

The recursive system of the initial regression equations (1) is calculated by their approximation according to the harvest data using the common regression analysis software. After correcting on logarithmic transformation by G. L. Baskerville [14] and subsequent anti-log procedure, characteristics of equations is given in Table 1 and Table 2. Despite the relatively low determination
coefficients for the understory, all listed in Table 2 regression coefficients are statistically significant at the probability level 0.95 and above, and the equations are adequate to harvest data. Low values of the determination coefficient for the understory in comparison with those for the wood story are quite natural. If variability of the wood story biomass is explained by the structure of its mass-forming indicts mainly, variability of the understory biomass is explained by it significantly less.

![Figure 1](image)

Figure 1. The pattern of disaggregating four-step proportional weighting additive model. Designation: $P_c$, $P_u$, $P_r$, $P_a$, $P_s$, $P_w$, and $P_{bk}$ are phytocenosis biomass respectively: total phytocenosis, understory, total wood storey, underground (roots), aboveground wood storey, tree crown (needles and branches), stems above bark (wood and bark), foliage, branches, stem wood and stem bark correspondingly, t/ha.

The equations obtained are modified to additive form according to the above mentioned algorithm [9] in the sequence shown in the scheme (see Figure 1), and the final form of the transcontinental additive model of component composition of biomass of larch phytocenoses is shown in Table 3.

When tabulating additive model (1), a problem arises, which consists in the fact that we can specify the indices of only the forest stand age, temperature and precipitation, but the values of the stem volume and tree density can be entered into the resulting table in the form of calculated values obtained by a system of auxiliary recursive equations. Such equations have the common form:

$$N = f \left[ A, (Tm + 50), PRm \right]. \quad (2)$$

$$M = f \left[ A, N, (Tm + 50), PRm \right]. \quad (3)$$

The results of calculation of equations (2) and (3) are given in Table 4. The results of tabulating the equations in the sequence (2), (3), and (1) present a rather cumbersome table. We took from it the values of the component composition of biomass of larch forests for the age of 100 years and built graphs of their dependence upon temperature and precipitation (Figure 2).

Looking at the Table 3, all the components of biomass changes are of roughly the same common pattern, but in different proportions. Regularity unified to all the biomass components of wood story is following: increase with raising temperature in the range from -40 °C to 0 °C at the invariable precipitation and decrease with raising precipitation in the range from 200 to 900 mm at the constant temperature. The biomass of the understory changes differently: at $PRm = 200$ mm it increases with temperature growth in the range from -40 °C to 0 °C with constant precipitation, and at precipitation at the level of 900 mm under the same conditions it decreases. In other words, the positive relationship of the understory biomass to temperature in dry areas ($PRm = 200$ mm) as the transition to wet areas ($PRm = 900$ mm) is replaced by the opposite one.
Table 1. Characteristics of initial equations (1).

| Biomass components | Regression coefficients of the model | \(\text{adjR}^2\) | SE \(\text{b}\) |
|--------------------|-------------------------------------|------------------|--------|
| \(P_e\)           | 6.19E+09 \(A\) \(0.1398\) \(M\) \(0.5831\) \(N\) \(0.0922\) \(A\) \(0.0251\)ln\(N\) | 0.801            | 1.37   |
| \(P_u\)           | 4.89E-23 \(A\) \(0.3856\) \(M\) \(-0.4582\) \(N\) \(-1.0170\) \(A\) \(0.2240\)ln\(N\) | 0.232            | 3.05   |
| \(P_t\)           | 67.9543 \(A\) \(0.0497\) \(M\) \(0.8133\) \(N\) \(0.2032\) \(A\) \(0.0440\)ln\(N\) | 0.917            | 1.27   |
| \(P_a\)           | 0.0699 \(A\) \(-0.0118\) \(M\) \(-0.1988\) \(N\) \(0.1317\) \(A\) \(-0.0309\)ln\(N\) | 0.970            | 1.20   |
| \(P_r\)           | 15.3558 \(A\) \(0.2665\) \(M\) \(0.5891\) \(N\) \(0.1596\) \(A\) \(-0.0014\)ln\(N\) | 0.673            | 1.59   |
| \(P_c\)           | 0.00381 \(A\) \(-0.0226\) \(M\) \(0.6196\) \(N\) \(0.5232\) \(A\) \(-0.1014\)ln\(N\) | 0.9011           | 0.0118 |
| \(P_s\)           | 0.0309 \(A\) \(-0.0120\) \(M\) \(0.9941\) \(N\) \(0.0049\) \(A\) \(-0.0085\)ln\(N\) | 0.0285           | 0.0512 |
| \(P_f\)           | 1.35E-05 \(A\) \(-0.1671\) \(M\) \(0.5821\) \(N\) \(0.5450\) \(A\) \(-0.0777\)ln\(N\) | 0.9011           | 0.0118 |
| \(P_b\)           | 0.0102 \(A\) \(0.0166\) \(M\) \(0.6353\) \(N\) \(0.4595\) \(A\) \(-0.0956\)ln\(N\) | 0.0285           | 0.0512 |
| \(P_w\)           | 3.9306 \(A\) \(-0.0313\) \(M\) \(1.0235\) \(N\) \(-0.2805\) \(A\) \(0.0512\)ln\(N\) | 0.9011           | 0.0118 |
| \(P_{hk}\)        | 4.61E-05 \(A\) \(-0.0431\) \(M\) \(0.9011\) \(N\) \(-0.0118\) \(A\) \(0.0011\)ln\(N\) | 0.0285           | 0.0512 |

* \(\text{adjR}^2\) – determination coefficient adjusted for the number of variables;  
\(\text{SE}\) – standard error of the equation in the original dimension \(Pi\) (t/ha).

Table 2. Characteristics of initial equations (continued)(1).

| Biomass components | Regression coefficients of the model | \(\text{adjR}^2\) | SE \(\text{b}\) |
|--------------------|-------------------------------------|------------------|--------|
| \(P_e\)           | \((T+50)\) \(-3.5510\) \(PRm\) \(-2.6313\) \((T+50)\) \(-1.0086\)ln\(PRm\) | 0.801            | 1.37   |
| \(P_u\)           | \((T+50)\) \(16.1936\) \(PRm\) \(8.6572\) \((T+50)\) \(-2.6011\)ln\(PRm\) | 0.232            | 3.05   |
| \(P_t\)           | \((T+50)\) \(-0.7769\) \(PRm\) \(0.5969\) \((T+50)\) \(-0.1223\)ln\(PRm\) | 0.917            | 1.27   |
| \(P_a\)           | \((T+50)\) \(0.8427\) \(PRm\) \(0.4542\) \((T+50)\) \(-0.1408\)ln\(PRm\) | 0.970            | 1.20   |
| \(P_r\)           | \((T+50)\) \(-0.8437\) \(PRm\) \(-0.5449\) \((T+50)\) \(-0.1294\)ln\(PRm\) | 0.673            | 1.59   |
| \(P_c\)           | \((T+50)\) \(1.5820\) \(PRm\) \(0.6331\) \((T+50)\) \(-0.1966\)ln\(PRm\) | 0.784            | 1.52   |
| \(P_s\)           | \((T+50)\) \(0.8486\) \(PRm\) \(0.5527\) \((T+50)\) \(-0.1629\)ln\(PRm\) | 0.982            | 1.17   |
| \(P_f\)           | \((T+50)\) \(3.1743\) \(PRm\) \(1.5334\) \((T+50)\) \(-0.4829\)ln\(PRm\) | 0.711            | 1.64   |
| \(P_b\)           | \((T+50)\) \(1.1342\) \(PRm\) \(0.3531\) \((T+50)\) \(-0.1124\)ln\(PRm\) | 0.772            | 1.56   |
| \(P_w\)           | \((T+50)\) \(-1.0175\) \(PRm\) \(-0.3157\) \((T+50)\) \(-0.1562\)ln\(PRm\) | 0.963            | 1.20   |
| \(P_{hk}\)        | \((T+50)\) \(2.5172\) \(PRm\) \(1.5536\) \((T+50)\) \(-0.4782\)ln\(PRm\) | 0.887            | 1.32   |
Table 3. Four-step additive model of biomass component composition of larch forest stands designed according to scheme of proportional weighting

| Step 1 | \[ P_r = 6.19E+09 \times A^{0.1398} M^{0.3801} N^{0.0192} (T+50)^{6.8510} PRm^{7.6311} \] |
|--------|------------------------------------------------------------------------------|
| Step 2 | \[ P_r = P_r \{ 1 + 4.89E-23 A^{0.0352} M^{0.4585} N^{0.0170} (T+50)^{0.8572} PRm^{2.6011} \}^{-1} \] |
| Step 3 | \[ P_r = P_r \{ 1 + 6.7954 A^{0.0352} M^{0.8133} N^{0.1024} (T+50)^{0.3607} PRm^{0.1228} \}^{-1} \] |
| Step 4a| \[ P_r = P_r \{ 1 + 0.0699 A^{0.0725} M^{0.8985} N^{0.1311} (T+50)^{0.8447} PRm^{1.5542} \}^{-1} \] |
| Step 4b| \[ P_r = P_r \{ 1 + 15.36 A^{0.0662} M^{0.0014} N^{0.0309} (T+50)^{0.1468} PRm^{0.1394} \}^{-1} \] |

Table 4. Characteristics of the recursive system of auxiliary equations for mass-forming indices.

| Mass-forming indices | Regression coefficients of the model | \( \text{adj}R^2 \) | SE |
|----------------------|--------------------------------------|----------------|-----|
| \( N \)              | \( 26.3664 \)                        | \( 0.19006 \)  | 0.501 | 2.21 |
| \( M \)              | \( 9.10E-07 \)                       | \( 0.9987 \)   | 0.5372| 0.489| 2.34 |
| \( N \)              | \( (T+50)^{5.2930} \) PRm^{0.0615}   | \( (T+50)^{-0.3136} \) PRm | 0.4694 | 4.784 |
| \( M \)              | \( (T+50)^{5.2930} \) PRm^{1.1312}   | \( (T+50)^{-0.3136} \) PRm | 0.4694 | 4.784 |
Figure 2. Dependence of larch phytocenoses biomass of Eurasia upon the mean January temperature ($Tm$) and mean annual precipitation ($PRm$). Designations: $P_r$, $P_w$, $P_u$, $P_s$, $P_f$, $P_b$ are respectively biomass of: total wood storey, understorey, underground storey (roots), stems (wood and bark), foliage, branches, t/ha.
The obtained regularity on the tree layer is consistent with the results obtained in boreal forests of Canada, only partially, because in Canada’s conditions the relative radial increment, depersonalized by the species composition, increases with the growth of both mean annual temperature and annual precipitation [15]. The obtained regularities are also partially consistent with the results revealed for the biomass of spruce (genus of *Picea* sp.) in the hydrothermal gradients of Eurasia [16]: the positive trends of the biomass with an increase in the mean temperature are characteristic of both larch and spruce, but, in contrast to the larch, the decrease in the biomass of spruce forests with rising precipitation, observed in warm climatic zones, as we approach the circumpolar regions, this trend is leveled and at $T_m = -40$ °C does not depend on the level of precipitation.

A different, specific pattern was observed earlier at the local level in the marsh forests of the Siberia, where at the maximum amounts of temperature sums above 10 °C (2200 °C) there is an increase in the radial growth of stems by 30-50% with an increase in precipitation from 400 to 600 mm, and at the minimum amounts of temperature sums (1600 °C) the radial growth is reduced by 4-9 % with an increase in precipitation in the same range. Correspondingly, at the level of precipitation of 400 mm the radial growth is reduced by 14-20 % with an increase in the sum of temperatures from 1600 to 2200 °C, and it increases by 14-33 % in the same temperature range at the level of precipitation of 600 mm [17]. According to the results obtained by A A Molchanov [18], the temperature of the air has the greatest influence on the growth of the annual ring in the North of Eurasia, and precipitation plays the dominant role in the conditions of the southern forest-steppe.

Thus, for different tree species in different climatic and edaphic conditions, changes in production indices in hydrothermal gradients can be very different, up to opposite trends. This means that the development of transcontinental models of biomass, sensitive to climate change, should not be carried out at the level depersonalized by species composition and morphological structure of stands, as it was previously practiced [19], but it is necessary to create such models for each tree species separately and to find out the biological and ecological reasons for the differences in the results.

In our examples with biomass models of the transcontinental level, the change of biomass in the named gradient is analyzed under the assumption that the temperature and precipitation change with the same rate regardless of the regional features of the observed shifts in both temperature and precipitation. In fact, the effect of global warming in different parts of the world is uneven [20]. Therefore, when knowing the area of territories with different rates of warming, we can use the proposed models to calculate the biomass changes that will be not averaged, but weighted by the size of these areas.

4. Conclusion

Thus, the first attempt of modeling changes in additive component composition of biomass of larch communities on the Trans-Eurasian hydrothermal gradients based on regional peculiarities of age and morphology of the forests is fulfilled. It is showed the common for all the components of wood story regularity: increase with raising temperature at invariable precipitation and decrease with raising precipitation at the constant temperature. The biomass of the understory changes differently: the positive relationship of the understory biomass to temperature in dry areas is replaced by the opposite one as the transition to wet areas.

It should be noted that these patterns have a hypothetical character: they reflect long-term adaptive responses of stands to regional climatic features and do not take into account the rapid rates of current environmental changes, which impose serious restrictions on the ability of forests to adapt to new climatic conditions. So the question: "What determines the rate at which species distributions respond to climate change?", that one can read at the number 83 in the list of 100 main questions to which the ecology of the XXI century should give answers [8], remains open.
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