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MERIS GPP/NPP product for Estonia: II. Complex meteorological limiting factor and optimum leaf area index

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Abstract. The merits and possible problems of the light use efficiency-concept based GPP/NPP models applied together with satellite images and meteorological data to quantitatively understand the role of different meteorological factors in forest productivity are analysed. A concept of the complex meteorological limiting factor for plant productivity is introduced. The factor includes the effects of incoming photosynthetically active radiation as well as the temperature and water limiting factors. Climatologically averaged seasonal courses of the complex meteorological limiting factor derived from the records of two contrasting meteorological stations in Estonia – inland Tartu/Tõravere and coastal Sõrve – are shown. Leaf phenology, here described via the seasonal course of leaf area index (LAI), is interpreted as a possible means to maximise the carbon gain under particular meteorological conditions. The equations for the optimum seasonal course of LAI as derived from the NPP model are presented. As the daily adjustment of plant LAI to sudden changes in meteorological conditions is not possible, several approximate strategies for LAI seasonal course to maximise the yearly NPP of vegetation are analysed. Typical optimal courses of LAI show some seasonal asymmetry resulting in lower values of LAI in the second half of the vegetation period due to higher air temperatures and respiration costs. Knowledge about optimum LAI courses has a cognitive value, but can also be used as the simulated LAI courses in several models when the measured LAI values are not available. As the considered GPP/NPP models fail to adequately describe the local trends in forest and agricultural productivity in Estonia, the ways to improve the model's performance are shown.

Key words: forest productivity, optimum LAI, fAPAR, satellite images, MODIS, MERIS.

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Introduction

The present paper is the second part of the series. In the first part (Nilson *et al.*, 2012), a light use efficiency (LUE) concept-based (Monteith, 1972, 1977) model EST_PP was described and applied to predict yearly gross (GPP) and net primary production (NPP) over Estonia. The main ideas of the EST_PP model are basically the same as in the MODIS GPP/NPP model (Zhao *et al.*, 2011; Heinsch *et al.*, 2003), however, a different temperature limiting factor was applied. To run the model, two main vege-

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tation-related variables driving the model, fAPAR and LAI, were determined from the respective MERIS land surface products (Gobron *et al.*, 2004). Presently, no gradient tower info is available in Estonia to test the model-predicted NPP. The stem wood volume increment from forest inventory and crop yield statistical data are the only practical data to compare with the simulation results. One of the problematic issues found in the MODIS GPP/NPP and EST_PP model simulation results was that the local spatial trends of forest and agricultural crop productivity in Estonia were not adequately represented (Eenmäe *et al.*, 2011; Nilson *et al.*, 2012). To improve the model performance, we need to know how the model is functioning and how sensitive are the simulated NPP values to model inputs. Three main factors responsible for the spatial distribution of GPP/NPP could be pointed out: the distribution of biome classes, the meteorological factors and vegetation state variables (LAI and fAPAR). In this study the main emphasis is on the role of meteorological variables.

The two considered LUE-type models (MODIS GPP/NPP and EST_PP) are rather simple in their basic structure. However, the present formulation of the models still allows a further simplification to better analyze selected general properties of the models. In particular, it is possible to aggregate all the meteorological factors into one. The primary limit for vegetation NPP in Estonia is the seasonal course of incident PAR, i.e. the energy available for photosynthesis. According to the LUE-type NPP models under consideration, additional two important meteorological limits are the air temperature and the water availability, the latter described by the water vapour pressure deficit (VPD) in the air. These three factors may be combined together to form a complex meteorological limiting factor, thus describing the meteorological constraint for GPP in a given geographical location.

Another simplification of the models is related to the respiration formulas in the NPP calculation. Namely, in the present formulation (Zhao *et al.*, 2011) leaf and fine-root maintenance respiration terms appear to be proportional to the daily leaf area index (LAI) and live wood maintenance respiration to the seasonal maximum of LAI (LAI_{max}). This fact enables us to consider the respiration terms in a more compact form where the negative feedback effect of LAI on NPP is apparent.

Vegetation phenology is closely related to the meteorological constraint (De Beurs & Henebry, 2010). Leaf phenology is often viewed as a kind of way to optimise the carbon gain under the available meteorological conditions (e.g. Caldararu *et al.*, 2013). It appears to be important to study how well vegetation phenology and the complex meteorological limiting factor match each other to reach maximum NPP. Suppose that the vegetation GPP and NPP behave just like our LUE-type model prescribes. As a possible application of LUE-type NPP models, a problem of optimum seasonal course of green LAI to get a maximum yearly NPP in given meteorological conditions is set up and the respective formulas for the optimum LAI are derived. The optimum conditions for GPP and NPP are different. GPP has no negative feedback from respiration, so the maximum GPP is achieved when LAI has a maximum possible value. However, for NPP extremely high values of LAI are not reasonable, since these cause elevated respiration. The respiration feedback leads to existing an optimum daily LAI for NPP in the given meteorological conditions. For maximum carbon gain, LAI of the biome should be close to the optimum value. Knowledge of optimum LAI has certainly some theoretical significance. It is also possible to speculate that long evolution has lead to plant species which use the resources in optimal way. Optimum LAI can also be interpreted as a kind of model-predicted LAI. By comparing the measured seasonal courses of

LAI to the optimum LAI course, it appears to be possible to estimate how far are the biomes from the optimum.

Typically, reanalysis datasets of meteorological factors are used to simulate GPP/NPP over large territories. Although the methods of reanalysis have improved, there is still a considerable uncertainty in the data. However, for analyses of model performance and to show some general tendencies, data from meteorological stations can be used. These data are reliable and the climatological average values of driving meteorological parameters can easily be calculated. Estonia is small, nevertheless trends in meteorological variables exist. According to the meteorological records, Estonia can roughly be divided into distinct coastal and inland regions (Tarand *et al.*, 2013; Climate Normals, 2015). As the Estonian land cover is rather variable, there is practically no possibility to find meteorological stations clearly representing homogeneous patches of relevant land cover classes (coniferous, deciduous or mixed forests, cropland, grassland). The same biomes are found in the coastal and inland regions of Estonia. As a first step to estimate the typical range of meteorology-caused variability of NPP, it is reasonable to compare NPP simulations with the data from an inland and coastal station from Estonia.

Several types of global and regional vegetation NPP models have been derived. In spite of some success in modelling, so far no model has been capable to adequately describe the temporal and spatial variability of GPP/NPP (e.g. Schwalm *et al.*, 2010; Keenan *et al.*, 2012). Nevertheless, the models help us to understand the key factors in plant productivity and carbon sequestration. The main aim of the present paper is to show the merits and problems of the LUE-concept based GPP/NPP models applied together with satellite images and meteorological data to better and quantitatively understand the role of different meteorological factors in forest productivity. In addition, we will show some ways to improve the model's performance.

Erratum

The authors would like to refer to an error in the first part of the paper (Nilson et al., 2012). Namely, when analysing the NPP estimates of forests, in the regression equations for ANPP from (Turner et al., 2004) (Eqs. 22) MAI was wrongly interpreted as the yearly increment of carbon in trunks while in the original paper it was defined as the total aboveground mass (in C units) divided by stand age. So, the estimates of NPP in (Nilson et al., 2012) derived from the volume increment data cannot be trusted.

Materials and methods

MODIS GPP/NPP and EST_PP models

The main methods and data used are the same as in the first part of the paper series (Nilson *et al.*, 2012). Following the principles of LUE models (Zhao *et al.*, 2011; see also Nilson *et al.*, 2012), the yearly GPP for a 1x1km^2 vegetated pixel, GPP_{year}, was calculated as

$$\begin{aligned} GPP_{year} &= \sum_{i=1}^{365} GPP_i = \\ &= \varepsilon \sum_{i=1}^{365} PAR_i\, fAPAR_i\, g(T_i)\, h(W_i) = \\ &= \varepsilon \sum_{i=1}^{365} fAPAR_i\, M_i, \end{aligned} \quad (1)$$

where GPP_i (gC/m^2) is the daily gross primary production, ε (gC /MJ) is the biome specific maximum light use efficiency, $fAPAR_i$ is the fraction of absorbed PAR, $PAR(t_i)$ – the daily sum of incident PAR (MJ/m^2), $g(T_i)$ and $h(W_i)$ are the daily reduction factors (dimensionless) due to limiting air temperature (T_i) and humidity (W_i – daily average water vapour pressure deficit (VPD) in the air), respectively. The quantity $M(t_i) = PAR(t_i)\cdot g(T_i)\cdot h(W_i)$, called here as the complex meteorological limiting factor, integrates the effects of all meteorological factors on GPP. As the temperature and water constraints are biome specific, the complex meteorological limiting factor is biome specific, too.

Following the MODIS NPP algorithm (Zhao *et al.*, 2011) the expression for yearly NPP (kgC/m2) may be written in the form where the respiration terms are proportional to the daily LAI ($LAI(t_i)$) or to the seasonal maximum LAI ($LAI_{\max}$), respectively:

$$NPP = \sum_{i=1}^{365} \{0.8[\varepsilon\, fAPAR(t_i) M(t_i) - LAI(t_i) N(T(t_i))] - LAI_{\max} O(T(t_i))\} \quad (2)$$

where $N(t)$ – the maintenance respiration (kgC/m2/day) of leaves and fine roots and $O(t)$ – the maintenance respiration of live wood per unit LAI, both depending on daily average air temperature, LAI_{max} – the seasonal maximum of LAI. Factor 0.8 takes into account losses due to growth respiration. The expressions for $N(t)$ and $O(t)$ are:

$$N(t) = \frac{1}{SLA}\left[Leaf\_mr\_base \cdot Q10\_mr\_leaf^{(\mathrm{Tavg}-20)/10} + Froot\_leaf\_ratio \cdot froot\_mr\_base \cdot Q10\_mr^{(\mathrm{Tavg}-20)/10}\right] \quad (3a)$$

$$O(t) = \frac{livewood\_leaf\_ratio \cdot livewood\_mr\_base \cdot Q10\_mr^{(\mathrm{Tavg}-20)/10}}{SLA} \quad (3b)$$

where *Leaf_mr_base*, *Froot_leaf_ratio*, *froot_mr_base*, *livewood_leaf_ratio*, *livewood_mr_base*, *Q10_mr*, *SLA* are biome-specific constants given in the lookup table, *Q10_mr_leaf* = 3.22 - 0.0466T_{avg}, T_{avg} being the daily average air temperature. The set of biome-specific input parameters used in this study is described in Table 1.

Table 1. Lookup table for biome properties from (Zhao & Running, 2010) used in the paper. The values for the three additional parameters for the EST_PP temperature limiting factor are also given (Tmin, Tmax, Topt). Land cover types used: Evergreen Needleleaf Forest (ENF), Deciduous Broadleaf Forest (DBF), Mixed Forests (MF), Grassland (GRASS) and Cropland (CROP).

Tabel 1. Töös kasutatud bioomi-parameetrite otsingutabel (Zhao & Running, 2010). Lisatud on kolm parameetrit (Tmin, Tmax, Topt), mis on vajalikud EST_PP mudelis kasutatava temperatuuri piirangufunktsiooni jaoks. Kasutatud maakatteklassid: Igihaljas okasmets (ENF), heitleheline laialeheline mets (DBF), segamets (MF), rohumaa (GRASS) ja põllumaa (CROP).

UMD_VEG_LC quantity, unit	ENF	DBF	MF	GRASS	CROP
LUEmax, kgC/MJ	0.000962	0.001165	0.001051	0.000860	0.001044
TMINmin, °C	−8.00	−6.00	−7.00	−8.00	−8.00
TMINmax, °C	8.31	9.94	9.50	12.02	12.02
VPDmin, Pa	650	650	650	650	650
VPDmax, Pa	4600	1650	2400	5300	4300
SLA, m^2/kgC	14.1	21.8	21.5	37.5	30.4
Q10_mr*	2.0	2.0	2.0	2.0	2.0
Froot_leaf_ratio	1.2	1.1	1.1	2.6	2.0
Livewood_leaf_ratio	0.182	0.203	0.203	0	0
Leaf_mr_base	0.00604	0.00778	0.00778	0.0098	0.0098
Froot_mr_base	0.00519	0.00519	0.00519	0.00819	0.00819
Livewood_mr_base	0.00397	0.00371	0.00371	0	0
Tmin, °C	0	2	1	2	4
Tmax, °C	37	39	38	39	41
Topt, °C	24	26	25	26	28

* For leaves Q10_mr is given by a temperature-dependent relation (Zhao *et al.*, 2011)

Meteorological data

Meteorological data (daily air temperature, humidity and total cloudiness) from Estonian meteorological stations as provided by Estonian Meteorological and Hydrological Institute (now named Estonian Environment Agency) are used. In addition to the period of years (2000–2011) covered by the GPP/NPP model simulation, climatological data from the period of years from 1981–2010 (Climate Normals, 2015) are used in the analysis. Data records from Tartu-Tõravere station (58°15′53″N, 26°27′42″E) representing a typical inland site are used. This station is well-known for its high-quality actinometric records and belongs to the world set of baseline surface radiation network (BSRN). Daily sums of incident solar radiation from Tõravere form the basis of GPP/NPP model calculations. The meteorological field is surrounded by a park around Tartu Observatory (mainly grass and sparse trees) in Tõravere.

As a representative of coastal sites meteorological data from the Sõrve station (57°54′45″N, 22°03′45″E) are used. The station is located just at the seaside and adjacent to a natural grassland with sparse trees. As routine radiation measurements are not carried out at Estonian coastal stations, daily sums of incident PAR in Sõrve were calculated by the method suggested in (Nilson *et al*., 2012). The daily sums of measured total radiation from Tõravere were corrected by the non-linear cloud cover factor, based on daily cloudiness records in both locations.

Satellite data

The same set of satellite data was used as in the first part of the study (Nilson *et al*., 2012). Estonian land cover map at 1km² resolution was produced making use of the DMCII high resolution images. In this study the following land cover classes were considered: deciduous broadleaf forest, mixed forest, evergreen needleleaf forest, cropland, grassland.

Daily green LAI and fAPAR maps (years 2003–2011) over Estonia were created from the MERIS TOA products using the ESA BEAM software (Gobron *et al*., 2004). Both maps were resampled into 1km² pixel. The time series of LAI and fAPAR were smoothed and interpolated between the cloud free days using the Timesat algorithm (Jönsson & Eklundh, 2002).

Determination of PAR extinction coefficient

To simplify the further analysis, we assume that there is an exponential relationship between fAPAR and LAI:

$$fAPAR(t_i) = 1 - \exp[-(\mathrm{G}\Omega/\mu)\mathrm{LAI}] = \qquad (4)$$
$$= 1 - \exp[-K(t_i)\,LAI(t_i)],$$

$K(t_i)$ being the PAR extinction coefficient (can vary with DOY). In Eq. (4) G(θ) (G-function, (Ross, 1981)) is the projection of unit foliage area onto a plane perpendicular to direction of sunrays θ, where θ is the daily effective solar zenith angle, Ω(θ) is the clumping factor responsible for leaf clumping at all spatial scales (Chen, 1996) and μ = cos θ. In Eq. (4) the parameter $K = \Omega G/\mu$ could be interpreted as a single structural and optical parameter, that includes the effects of leaf angle distribution, clumping factor and 'effective' sun angle. According to Baret *et al*. (2006), the effective sun angle may be approximated as the sun elevation at 10 o'clock of local time. Here, the value of *K* should consider changes in leaf optical parameters (leaf colour), too. For each land cover class, the *K* values were estimated from the MERIS fAPAR and LAI images by applying Eq. (4). The fAPAR and LAI values were averaged over all pixels of the same land cover class and years 2003–2010 to get smoother seasonal courses of *K*. This way, the *K* values derived were biome-specific. The values of *K* are determined by the MERIS LAI and fAPAR algorithms and rely on them. The seasonal courses of effective *K* values for the main biome classes as determined from Eq. (4) are shown in Figure 1.

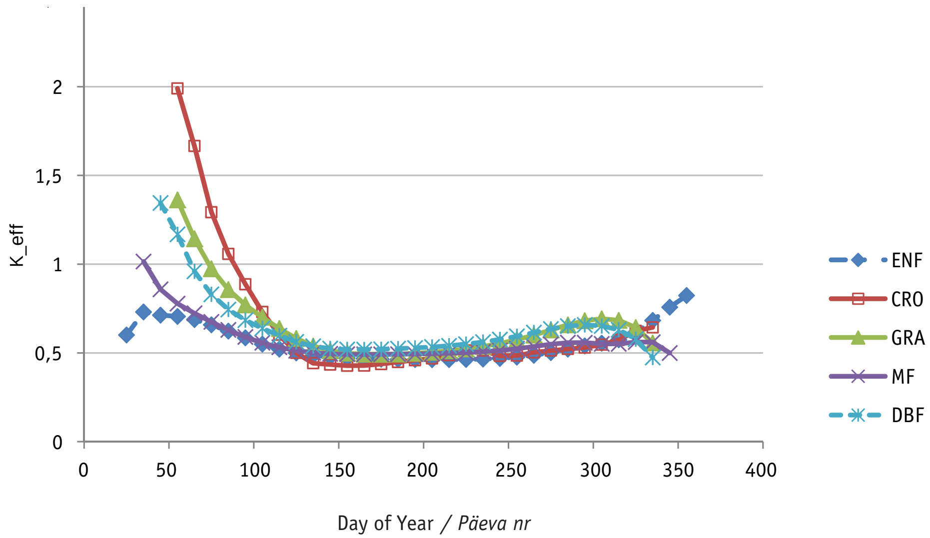


Figure 1. The seasonal course of effective value of PAR extinction coefficient *K* derived from MERIS LAI and fAPAR products over Estonia and averaged over all pixels of the respective land cover class and years 2003–2010. ENF – evergreen needleleaf forest, CRO – cropland, GRA – grassland, MF – mixed forest, DBF – deciduous broadleaf forest.

Joonis 1. Fotosünteetiliselt aktiivse kiirguse nõrgenemise koefitsient K tuletatuna MERIS LAI ja fAPAR tulemitest keskmistena üle kõigi vastava maakatteklassi pikslite Eestis ja aastate 2003–2010. ENF – igihaljas okasmets, CRO – põllumaa, GRA – rohumaa, MF – segamets, DBF – heitleheline lehtmets.

Optimum conditions for GPP

According to Eq. (1), the yearly GPP is determined by the time course of the complex meteorological limiting factor $M_i = PAR_i\, g(T_i)\, h(W_i)$ and by the time course of the fAPAR for the vegetation under study. The product gives us a maximum possible GPP under the meteorological conditions considered, provided all incident PAR has been used by the vegetation ($fAPAR(t_i) = 1$). With a given complex meteorological limiting factor $M(t_i)$, GPP has its maximum, if fAPAR has the maximum possible value all the time when $M(t_i) > 0$. Thus, the larger the LAI the larger fAPAR and GPP. A simple seasonal strategy follows from this: To get a maximum value of the yearly GPP, fAPAR of the pixel should be as large as possible, at least for the time of year when the complex limiting factor *M* has a positive value (growing season). We know that fAPAR is at its maximum when the green LAI is sufficiently large. Typically there are limited resources for plants (trees) to develop and maintain green foliage. In case it is not possible to keep a constantly high fAPAR throughout the vegetation period, the time course of fAPAR should fit with the time course of the meteorological limiting factor. First of all, the start and end of the vegetation period as defined by the meteorological limiting factor should be synchronized by the onset of green leaf development and leaf fall and senescence, respectively.

Derivation of optimal LAI for NPP

Having a quantitative relation in Eq. (4) between the fAPAR and LAI, it is possible to formulate the problem of optimum daily LAI and of its seasonal course to get maximum daily and seasonal total NPP under particular meteorological conditions. The fAPAR term in Eq. (2) is an increasing function of LAI while the respiration terms are negative. As a result, there should exist an optimum LAI to obtain the highest NPP for each day of the season. Typically, in Estonian climatic conditions the complex meteorological limiting factor is close to zero during the winter period due to temperature constraint when air temperatures are systematically below zero. It is obvious that during the period of $M(t) = 0$, it is not reasonable to keep positive green LAI values, because of respiration costs (although those could be small due to low temperatures).

The daily NPP has its maximum value, if the derivative of NPP with respect to $LAI(t_i)$ is zero. Taking the derivative from the daily NPP formula in Eq. (2) and considering the fAPAR-LAI relation in Eq. (4), after some simple arrangements the optimum LAI value for the DOY = t_i can be calculated as follows:

(5)

$$LAI_{opt} = 0, \text{if } \varepsilon KM(t_i) \le N(t_i) \quad (5a)$$

$$LAI_{opt} = \frac{1}{K}\ln\left(\frac{\varepsilon KM(t_i)}{N(t_i)}\right), \quad (5b)$$

$$\text{if } LAI_{opt} \le LAI_{max,opt}$$

$$LAI_{opt} = LAI_{max,opt} = \frac{1}{K} ln\left(\frac{0.8\,\varepsilon\, K M(t_{max})}{0.8\, N(t_{max}) + O(t_{max})}\right), \quad (5c)$$

$$if\ LAI_{opt} > LAI_{max,opt}$$

where t_{max} corresponds to the DOY when the LAI_{opt} in Eq. (5b) or the quantity $K\,M(t)/N(t)$ takes its seasonal maximum value. This way, it is possible to calculate LAI_{opt}, if

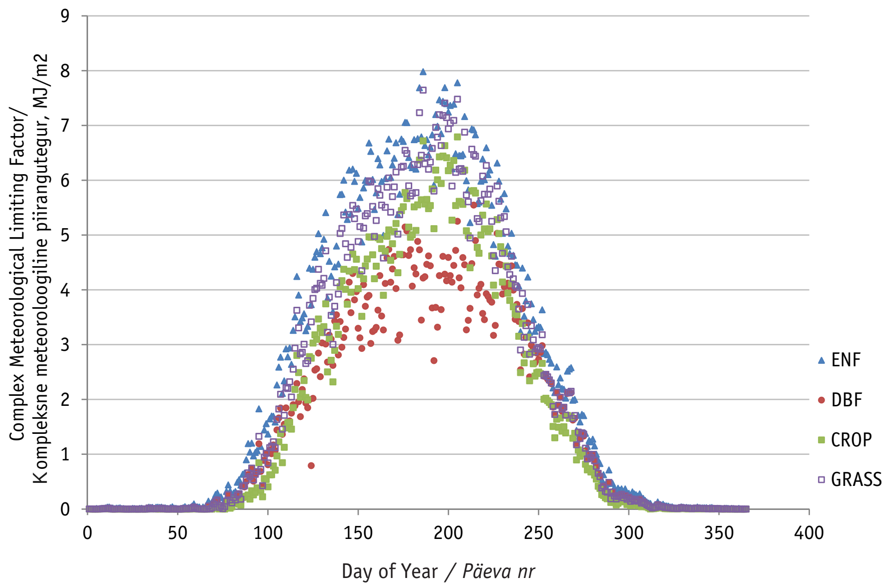


Figure 2. Averaged over 2000–2010 seasonal course of the daily sums of complex meteorological limiting factor *M* (MJ/m^2), based on the meteorological records of Tartu-Tõravere station for different biomes and temperature and water limiting factors according to EST_PP model. ENF – evergreen needle leaf forest, DBF – deciduous broadleaf forest, CROP – cropland, GRASS – grassland. Note the considerable scatter of points even on the averaged data set.

Joonis 2. Kompleksse meteoroloogilise piirangutegeuri M keskmine päevasumma (MJ/m^2) üle aastate 2000–2010, arvutatuna Tartu-Tõravere meteoroloogiajaama andmete alusel erinevatele bioomidele EST_PP mudeli temperatuuri ja niiskuse mõju teguri järgi. ENF – igihaljas okasmets, DBF – heitleheline lehtmets, CROP – põllumaa, GRASS – rohumaa. Paneme tähele, et punktide hajuvus on suur isegi keskmistatud andmetel.

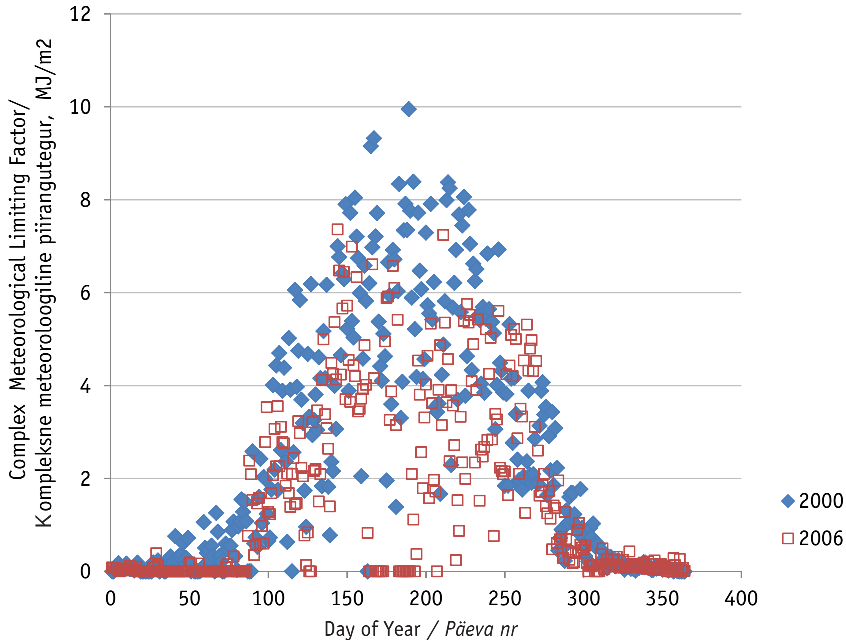


Figure 3. Seasonal course of the complex meteorological limiting factor for the deciduous broadleaf forest (DBF) biome for two different years: a "normal" (2000) and drought year (2006). Note that in case of severe drought the daily values of the factor M could be zero even in midsummer.

Joonis 3. Komplekse meteoroloogilise piirangutegurі sesoonne käik heitlehelise lehtmetsa (DBF) jaoks kahel erineval aastal: "tavaline" (2000) ja põuane (2006) aasta. Paneme tähele, et tugeva põua korral võib tegur M olla null isegi keskusuvel.

the values of daily complex meteorological limiting factor M, of extinction coefficient K, of respiration functions N and O, as well as the other necessary biome specific parameter values are known. The maximum LAI_{opt} value is given by Eq. (5c) due to the way how the maintenance respiration of live wood is calculated in the model (proportional to the seasonal maximum of LAI for forests). Condition in Eq. (5c) sets an upper limit value ($LAI_{max,opt}$) for LAI_{opt} and as a result, the seasonal LAI_{opt} curves become truncated from above.

The optimal LAI is related to the most important meteorological/ecological variable $Q(t) = M(t)/N(t)$ via a non-linear logarithmic relation. If Eq. (5) is applied for a period of several days (e.g. week or 10 days) with a considerable variation in meteorological conditions, Eq. (5) may be treated as a non-linear function of random argument Q. Hence, when calculating the mean value of optimum LAI for an extended period of days, the problem of non-linearity correction arises – the mean LAI_{opt} is not equal to LAI_{opt} at mean Q. By approximating the logarithmic function with the second order Taylor expansion, instead of Eq. (5b), the optimum LAI could be approximately calculated as follows (Sveshnikov, 1968):

$$LAI_{opt} \approx \frac{1}{avg(K)} ln[\varepsilon\, avg(K) avg(Q)] - \quad (6)$$

$$- \frac{var(Q)}{2avg(K)avg^2(Q)},$$

where $avg(K)$ and $avg(Q)$ denote average values of K and Q, respectively, and $var(Q)$ variance of Q for the time period considered. The second term in Eq. 6 is determined by the second derivative of Q and takes into account the non-linearity correction. As the correction term is always negative, LAI_{opt} is always less under variable conditions than its value when the average meteorological conditions are considered. The correction term in Eq. (6) is proportional to the variance of Q.

Results and Discussion

Complex meteorological limiting factor

The climatological average seasonal course of *M* for different biomes and an example of the variability of the seasonal course of *M* between different growing seasons are presented in Figure 2 and Figure 3, respectively. Since the shape of the temperature limiting factor is different in the EST_PP and MODIS GPP models, the complex meteorological limiting factors are somewhat different, too. The examples in Figures 2 and 3 have been calculated by the EST_PP model. As the temperature and water constraint functions of the biomes are different, the seasonal courses of *M* are different, too.

The seasonal course of *M* resembles that of incident PAR while the temperature limiting factor does not much modify the shape of *M*, since the incident PAR and air temperature are positively correlated. The correlation coefficient between the daily values of air temperature and PAR was R = 0.659 in Tõravere, when all data from 2000 to 2010 were pooled (winter days with typically negative correlation included). However, the water limiting factor may considerably reduce the midsummer maximum value of *M*, especially during dry summers (Figure 3) and just that factor causes considerable midsummer differences between biomes.

Which of the three meteorological factors is mostly responsible for the variation in yearly GPP? According to actinometric records from Tartu-Tõravere station for the period 1955–2000, the mean value and standard deviation of the yearly sum of global radiation are 3491 and 172 MJ/m^2, respectively (Russak & Kallis, 2003). When these numbers are transferred into the PAR region with an average coefficient of 0.45, we obtain 1471 and 77.4 MJ/m^2, respectively. For the period from 2000 to 2011 considered here, the mean yearly sum was 1535 MJ/m^2, standard deviation 89.2 MJ/m^2 and coefficient of variation 5.8%.The yearly sums of incident PAR in Tõravere vary then approximately 5–6%. The estimated yearly sum of incident PAR in Sõrve varies for the same period about 9%. However, the yearly sums of the complex meteorological limiting factor *M* vary more – 8–13% in Tõravere and 11–13% in Sõrve depending on the biome and applied algorithm for the temperature limiting factor (Table 2). This increase in the coefficient of variation is mainly caused by the positive correlation between the daily sum of PAR and air temperature. Comparing the complex meteorological limiting factors from a coastal Sõrve and inland Tõravere stations, the coastal region is more favourable for GPP (see also Figure 4). The yearly sums of PAR in Sõrve exceed those in Tõravere due to less cloudiness. Also, the air temperature in coastal region is more favourable for plant growth compared with inland during most of the growing season (except for early period in spring). Even the VPD tends to be more favourable at the coast – the average yearly values of partial pressure of water vapour are 8.3 hPa in Tõravere and 9.2 hPa in Sõrve (Climate Normals, 2015).

The active vegetation period tends to be longer in the coastal areas, too. For the period of years from 1965 to 2013, the permanent transfer of the daily average temperature over 5 °C in spring occurred on average on 26 April (DOY = 116) in Sõrve and 17 April (107) in Tõravere, while below 5 °C in autumn on 10 November (314) and 23 October (296), respectively (Kadaja & Keppart, 2014). Thus the average length of the vegetation period in Sõrve (198 days) exceeds that in Tõravere (189 days). The difference is still larger, if the temperature level 0 °C is considered as the beginning and end of the vegetation period.

The value of complex meteorological factor is the main reason why the MODIS GPP/NPP and EST_PP models predict higher productivity of forests and crops in coastal regions compared to those inland. As the statistical data of Estonia demonstrate just the opposite tendency (e.g. Eenmäe *et al.*, 2011; Nilson *et al.*, 2012; Lang *et al.*, 2013), the considered LUE-type models in their present form are not able to adequately describe the spatial NPP differences in Estonia. We did not find reliable differences in MERIS LAI and fAPAR values in coastal and inland regions to explain the higher simulated GPP/NPP at the coast. The most problematic seems to be the way how the water limiting factor has been considered in the models. The water vapour deficit in the air might not be a suitable index to describe water deficit in the soil, at least in the coastal regions. It seems that the amount of water vapour in the air is too much influenced by the transport of humidity from the sea. This way, the effect of water stress is underestimated in the coastal regions. In fact, the amount of precipitation is larger in inland: during the period from April to September the average amount of precipitation was ~30% higher in Tõravere compared with Sõrve (Climate Normals, 2015).

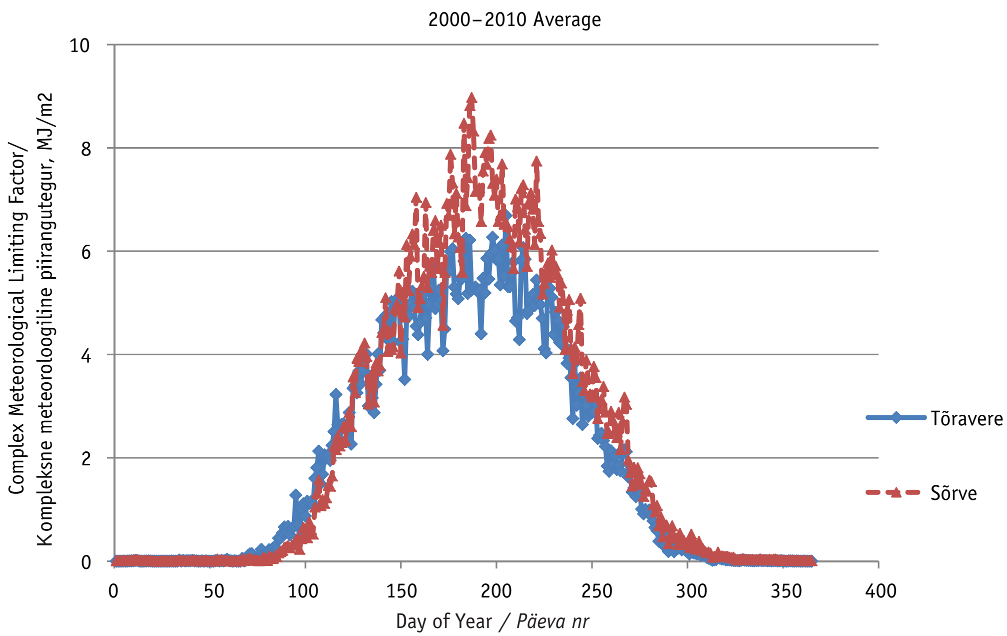


Figure 4. Averaged over 2000–2010 daily sums of the complex meteorological limiting factor *M* for deciduous broadleaf forest as calculated from the meteorological records of Tõravere and Sõrve meteostations. The temperature limiting factor corresponds to that of the EST_PP model.

Joonis 4. Komplekse meteoroloogilise piirangutegur üle aastate 2000–2010 keskmistatud päevasummade sesoonsed käigud arvutatuna heitlehelisele lehtmetsale Tõravere ja Sõrve meteojaamade andmetel. Temperatuuri piirangutegur vastab EST_PP mudeli omale.

Table 2. Average values (Avg) over years 2000–2010, standard deviations (Stdev) and coefficients of variation (Coef var) of yearly sums of the complex meteorological limiting factor *M* (MJ/ m^2) using the records from inland (Tõravere) and coastal (Sõrve) meteorological stations. Different temperature limiting factors from the MODIS and EST_PP models were applied. ENF – evergreen needleleaf forest, DBF – deciduous broadleaf forest, CROP – cropland, GRASS – grassland.

Tabel 2. Komplekse meteoroloogilise piiranguteguri M aastasumma keskväärtused (MJ/m^2) üle aastate 2000–2010, kasutades meteoroloogiajaama andmeid sisemaalt (Tõravere) ja rannikult (Sõrve). Kasutatud on MODISe ja EST_PP mudelite erinevaid temperatuuri mõjutegureid. ENF – igihaljas okasmets, DBF – heitleheline lehtmets, CROP – põllumaa, GRASS – rohumaa.

Quantity / Biome	ENF	DBF	CROP	GRASS
Tõravere, using MODIS temperature reduction function				
Avg	1128.2	827.9	1015.6	1033.8
Stdev	103.1	110.0	116.8	120.0
Coef var, %	9.14	13.3	11.5	11.6
Sõrve, using MODIS temperature reduction function				
Avg	1370.2	1263.7	1264.8	1267.3
Stdev	128.4	118.0	118.9	119.4
Coef var, %	9.37	9.33	9.40	9.42
Tõravere, using EST_PP temperature reduction function				
Avg	897.7	591.9	671.8	801.5
Stdev	58.0	72.5	57.9	60.6
Coef var, %	6.46	12.25	8.62	7.56
Sõrve, using EST_PP temperature reduction function				
Avg	917.8	824.4	719.2	853.2
Stdev	102.8	89.0	90.2	97.1
Coef var, %	11.13	10.80	12.54	11.48

In agricultural meteorology, the concept of growing degree-days (GDD) or temperature time is often used to describe the speed of time from the point-of-view of plant development and phenology (e.g. McMaster & Wilhelm, 1997). As an alternative, the cumulative value of the complex meteorological limiting factor *M* as a certain "meteorology" time could be used. Instead of only temperature considered in the GDD concept, the meteorology time takes into account the three meteorological limiting factors together. However, since the parameters defining the temperature and water limiting factors are biome-dependent, the meteorology time depends on biome, too. Similarly to the temperature time, the start of the season corresponds to the date when the factor *M* permanently exceeds the zero value after winter-time.

Optimum leaf area index

The formulas for calculating the optimum LAI are given by Eq. (5). The optimum LAI value appears to be the larger, the larger the complex meteorological limiting factor, the larger the light use efficiency parameter ε and the less the temperature-dependent respiration losses per unit LAI. Note that the value of LAI_{opt} is logarithmically related with the ratio M/N, so twofold changes in the ratio would reflect in LAI_{opt} change by approximately 0.7 only. Also, the values of ε and PAR extinction coefficient *K* have an essential role in LAI_{opt}. The optimum LAI is somewhat sensitive with respect to the form of relation between the fAPAR and LAI. However, if more sophisticated relations between fAPAR and LAI were to be applied instead of the simple relation Eq. (3), the main qualitative conclusions should remain the same.

One of the main problems with such of optimum condition is that the complex meteorological limiting factor *M* could be extremely variable from one day to another (see Figure 3 as an example). Consequently, the optimum LAI should vary from one day to another as well. If the plants (trees) try to get maximum NPP, their LAI should be close to the optimum LAI. From the point of view of a tree growth, several possible theoretical leaf display strategies can be viewed, such as:

1. The optimal conditions are fulfilled every day. In typical Estonian weather conditions the resulting optimum LAI time course is extremely variable in time. Such rapid changes in LAI would be extremely costly. Within the framework of the LUE models under consideration, no such costs for rapid changes in LAI are foreseen, so there is no possibility to evaluate the strategies to rapidly change LAI. The strategy is practically impossible, since it requires daily sudden increase or decrease of LAI depending on the random changes in cloudiness, air temperature and humidity of the day.
2. Plants follow the LAI course derived from Eq. (5), where some smoothed values are used in the role of $M(t)$, ($N(t)$ and $O(t)$). In an example below, seasonal courses of $M(t)$, $N(t)$ and $O(t)$ for the growing season of a particular

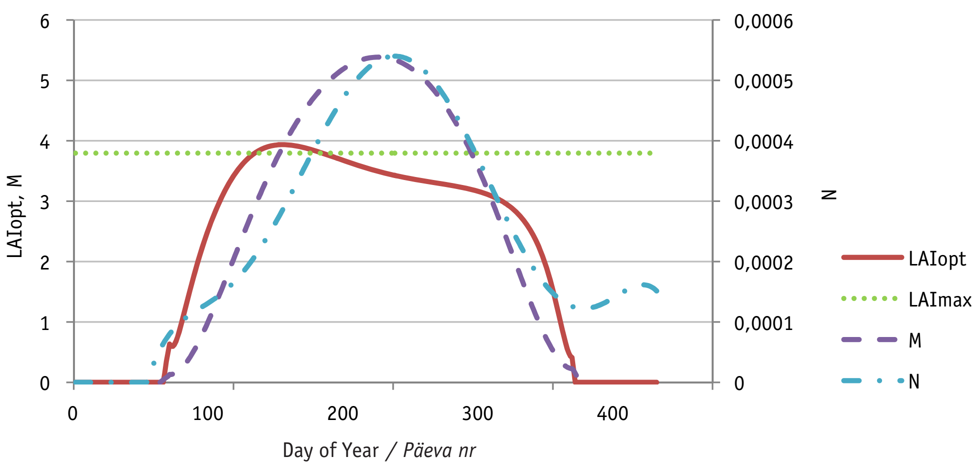


Figure 5. An example of the seasonal course of LAI_{opt} and of important functions *M* and *N*. The complex limiting meteorological factor *M* and maintenance respiration of leaves and fine roots per unit LAI, *N*, correspond to the averaged (over 2000–2011) and smoothed seasonal courses of these factors from Tartu-Tõravere meteorological data. LAI_{max} determines the upper limit of LAI_{opt} (Eq. (5c)). The biome parameters used are those of MODIS NPP model and deciduous broadleaf forest (DBF). Note that the secondary y-axis has been used for function *N*.

Joonis 5. LAIopt ja kahe olulise teda kujundava funktsiooni M and N sesoonne käik. Kompleksne meteoroloogiline piirangutegur M ja lehtede ning peenjuurte säilitushingamine ühikulise LAI kohta, N, vastavad Tartu-Tõravere meteojaama keskmistatud (üle 2000–2011) ja silutud andmetele. LAI_{max} *määrab LAIopt ülemise piiri (Valem (5c)). Kasutatud bioomi parameetrid vastavad MODISe NPP mudelile ja heitlehelisele lehtmetsale (DBF). Funktsiooni N jaoks on kasutusel parempoolne y-telg.*

year were approximated by 6th order polynomials. Alternatively, smoothed average values over a certain period could be used. Rather similarly, in their phenology model to predict leaf gain Caldararu *et al*. (2013) use averaging of the available solar radiation over several days.

3. Plants adapt themselves to the climatological optimal LAI seasonal course and try to develop an average optimal LAI over an extended period of years.

Climatological optimum LAI

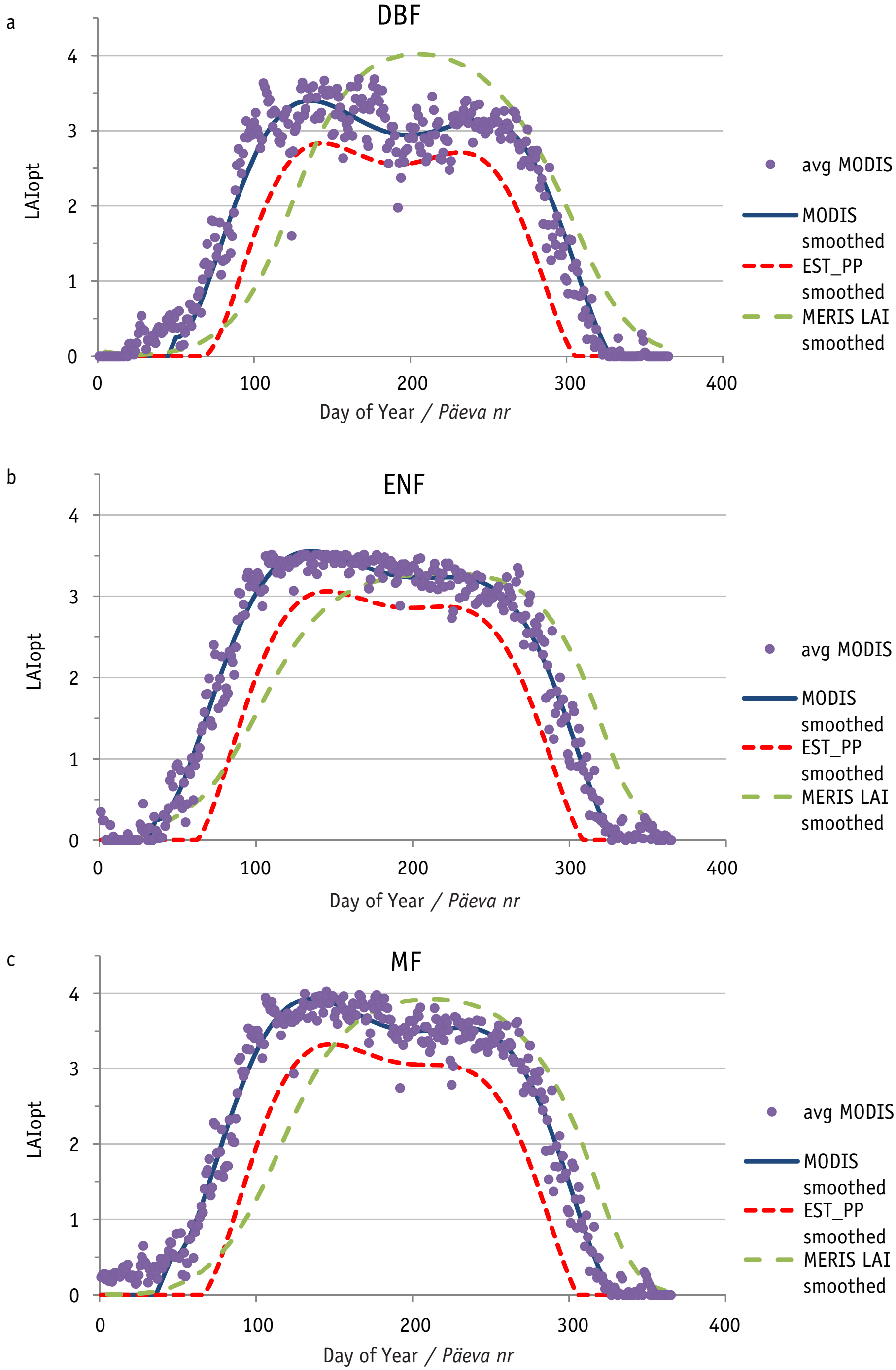
By applying Eqs. (5) or (6), optimum values of LAI can be easily calculated. A typical 'climatological' seasonal course of the optimum LAI is presented in Figure 5. The course of LAI_{opt} is mostly determined by the logarithm of the ratio M/N while its seasonal maximum value is limited from above by relation in Eq. (5c). The optimal seasonal LAI profiles (Figures 5–6) show a rather rapid increase of LAI at the beginning of the season and rapid decrease at the end of the season, relatively high values during the most of the vegetation period and display some asymmetry with respect to the peak of season. Optimum LAI values in the second half of the season appear to be systematically lower than in the first half. This is due to typically higher air temperatures causing larger respiration losses (function N) during the second half of the season. There are some differences in the climatological optimum LAI courses between the biome classes as determined by the values of input parameters in the lookup table. The seasonal maximum values of optimum LAI for the MODIS NPP version vary between 3.5 for grassland and 4.0 (mixed forest).

Among forests the seasonal profiles of optimum LAI are partly influenced by Eq. (5c) determining the seasonal maximum LAI value and setting an upper limit to large midsummer LAI_{opt} values. As a result of the limit set by Eq. (5c), the average climatological LAI_{opt} for coniferous forests has an almost constant value for a considerable time period at the peak of season. Remember that in the model the yearly live wood maintenance respiration is assumed to be proportional to the yearly maximum LAI. Since this respiration term is zero for non-forest classes, Eq. (5c) has no effect on LAI_{opt} seasonal course of non-forest biomes (crop, grassland).

Comparison of optimum LAI with MERIS LAI

The seasonal maximum LAI_{opt} values as calculated by means of Eqs. (5) appear to be surprisingly realistic. This means that the parameter sets (at least for the MODIS NPP model) have been carefully tuned. However, the simulated optimal LAI courses differ in timing from the typical LAI profiles for evergreen needleleaf, deciduous broadleaf, mixed forest, grassland and crop profiles as determined from a series of MERIS images in Estonia (Figures 6a–6e). The MERIS LAI seasonal curves are systematically late relative to LAI_{opt} curves predicted by the MODIS or EST_PP models. If the MERIS seasonal LAI curves are correct, it would mean that some amount of potential production is inevitably lost by forests in our present meteorological conditions. The dates of onset of green development as estimated by the MERIS LAI agree much better with the start of season as estimated from the simulated LAI_{opt} by the EST_PP model compared with that of the MODIS NPP model. However, the situation is vice versa at the end of the growing season where MODIS LAI agrees better with the course of LAI determined from the MERIS images. The optimum LAI values as estimated with the MODIS NPP algorithm, exceed those of the EST_PP algorithm. The main reason for this is the systematically lower values of the temperature reduction factor in the ESP_PP model compared with the MODIS NPP model.

In the GPP/NPP model the dates of the onset of green development in spring are determined by the T_{min} (EST_PP model) or


a
DBF
LAIopt
0
1
2
3
4
0
100
200
300
400
Day of Year / *Päeva nr*
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MODIS smoothed
EST_PP smoothed
MERIS LAI smoothed
b
ENF
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Day of Year / *Päeva nr*
avg MODIS
MODIS smoothed
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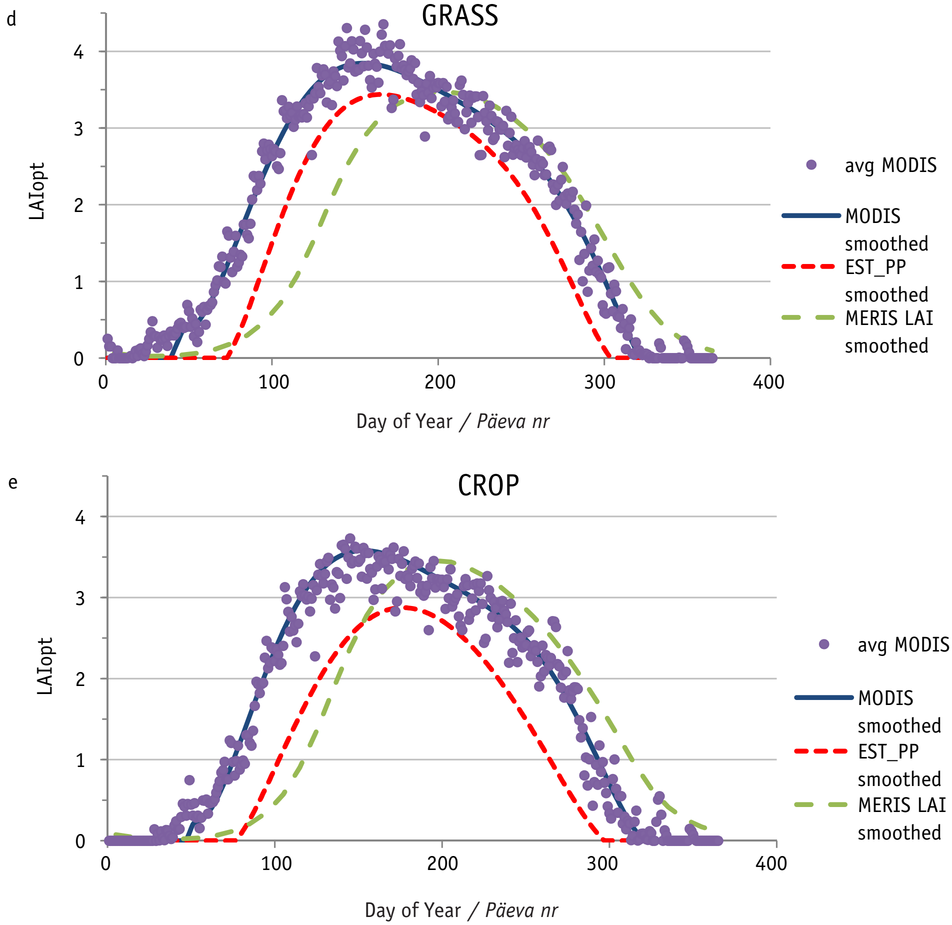

Figure 6. Averaged over years 2000–2010 (points) and smoothed (full line) seasonal courses of LAI_{opt} as calculated with the parameter set of the MODIS NPP model (avg MODIS, MODIS smoothed) and of the EST_PP model (EST_PP smoothed) compared with the smoothed average over 2003–2010 MERIS LAI (MERIS LAI). a – deciduous broadleaf forest (DBF), b – evergreen needleleaf forest (ENF), c – mixed forest (MF), d – grassland (GRASS), e – cropland (CROP).

Joonis 6. Aastate 2000–2010 keskmine (punktid) ja silutud optimaalse LAI (pidev joon) sesoonne käik, arvutatuna MODIS NPP mudeli parameetrite abil (avg MODIS, MODIS smoothed) võrrelduna EST_PP mudeli abil arvutatud LAI_{opt} *(EST_PP smoothed) ning MERIS LAI keskmise sesoonse käiguga üle aastate 2003–2010 (MERIS LAI). a – heiteleheline lehtmets (DBF), b – igihaljas okasmets (ENF), c – segamets (MF), d – rohumaa (GRASS), e – põllumaa (CROP).*

$TMIN_{min}$ (MODIS NPP algorithm) value given in the biome lookup table. The set of MODIS NPP model parameters (Zhao & Running, 2010) for different biomes has been chosen mainly based on the results of measurements on eddy covariance towers. It seems that the value $TMIN_{min}$ in the MODIS NPP algorithm which is the responsible parameter in the biome parameter list for the start of season, has been chosen too low for typical Estonian conditions. $TMIN_{min}$ values close to 0 °C should be chosen instead of –8 °C and –6 °C, used in Zhao & Running (2010). Then the simulated start of season would begin approximately at the same time (DOY ≈ 107) as the average start of season in Tartu according to the 5 °C level definition of temperature time (Kadaja & Keppart, 2014).

However, for the end of the growing season in autumn, these low values create the LAI courses closer to those estimated from the MERIS images, if compared with the EST_PP model temperature limiting factor. We have to keep in mind that the MERIS LAI seasonal courses for different land cover classes are also problematic at the applied 1 km^2 resolution, since practically all pixels in Estonia are mixed. The methods used in the Timesat algorithm (Jönsson & Eklundh, 2002) to approximate the seasonal MERIS LAI and fAPAR courses and typical lack of cloud free images at the end of growing season have their effect on the behaviour of LAI at the start and end of the season, too.

Comments on model performance

The mid-summer maximum values of LAI_{opt} on Figures 6 as calculated by Eqs. (5) agreed with the maximum LAI values from the MERIS dataset somewhat better when the MODIS NPP version of the model is used compared with those obtained with the EST_PP model. In the EST_PP model higher values of ε should be applied to compensate for systematically lower values of the temperature limiting factor $g(T)$ to get the maximum LAI_{opt} values comparable to maximum LAI values from the MERIS data. The mid-summer depression in the simulated LAI_{opt} seasonal courses appeared for the DBF and MF class and is hardly notable for coniferous forests, but it is not present for non-forest classes. In the lookup table for biomes, the deciduous forests have given the lowest *WPDmax* value (1650 Pa compared with 4600 Pa for the conifers) among all the land cover classes. For that reason the DBF class is the most susceptible to drought conditions among the land cover classes considered. However, MERIS LAI does not show midsummer depression for any of the classes considered. Further research is needed to establish whether such mid-summer depression could be found in our deciduous forests, especially during summers with considerable drought.

For the coniferous forests (ENF), the simulated LAI_{opt} stays almost constant for a long period in summer, mostly because of considerable restriction for the LAI_{max} and the truncating effect caused by Eq. (5c). If the seasonal courses of LAI_{opt} are compared for forest classes as estimated by the MODIS and EST_PP algorithms, we see that the midsummer LAI_{opt} values are not in a logical order (deciduous < mixed < conifer) as expected, LAI_{opt} for mixed forests being the largest. It seems that the choice of the input parameter set for mixed forests is responsible for that. Anyway, the careful tuning of the whole set of parameters is still to be done. We should also emphasize the important roles of $M(t)$ and of the PAR extinction coefficient $K(t)$ in determining the seasonal course of optimum LAI.

Table 3 indicates that daily adjustment of LAI to the meteorological conditions of the particular day would be the most productive, if the cost to create new leaves due to sudden changes in LAI is ignored. Here we may consider the adjustment to daily optimum LAI as an ideal that is never achieved. Compared with the ideal case, adjustment to the course of the smoothed meteorological limiting factor of the year would result in a loss of 2.5% for GRASS and 6.4% for DBF biomes in the yearly sum of NPP. At the same time applying an average climatological seasonal course of LAI would cause a decrease in NPP by 5.0% for GRASS and 6.9% for DBF. On individual years, such as 2006 with considerable midsummer drought, the losses in NPP from non-optimal courses of LAI are essentially higher. In general, the gain from following the optimal LAI seasonal course is not extremely large and thus optimal LAI is probably not a factor of the highest priority for plant survival and competition.

Table 3. Averaged over 2000–2010 yearly sums of NPP (kgC/m^2) calculated by using different strategies of seasonal LAI development: Daily LAIopt - daily optimum values; Smoothed LAIopt – daily optimum LAI values calculated using the smoothed by 6^{th} order polynomials for $M(t)$, $N(t)$ and $O(t)$ values of the particular year; MERIS LAI – smoothed MERIS LAI values of the respective land cover class and year; Climatological LAIopt – averaged over the considered time period (2000–2010) optimal LAI values, the same values applied every year. Land cover classes grassland (GRA) and deciduous broadleaf forest (DBF), respectively. MODIS NPP model.

Tabel 3. Aastate 2000–2010 keskmised NPP aastasummad (kgC/m^2) arvutatuna kasutades erinevaid LAI sesoonse muutumise strateegiaid: Daily LAIopt – päevane optimaalne LAI; Smoothed LAIopt – päevased optimaalse LAI väärtused kui kasutada vastava aasta kohta 6. astme polünoomi abil silutud M(t), N(t) ja O(t) väärtusi; MERIS LAI – silutud MERIS LAI väärtused vastavale maakatteklassile ja aastale; Climatological LAIopt – keskmistatud üle kogu vaadeldava perioodi (2000–2010) optimaalsed LAI väärtused, samad igal aastal. Maakatteklassid vastavalt rohumaa (GRASS) ja heitleheline lehtmets (DBF). MODIS NPP mudel.

Biome	Quantity	Daily LAIopt	Smoothed Daily LAIopt	MERIS LAI	Climatological avg LAIopt
Grassland, GRASS	Yearly NPP sum	0.239	0.233	0.216	0.227
	Relative	1	0.975	0.904	0.950
Deciduous broadleaf forest, DBF	Yearly NPP sum	0.389	0.364	0.324	0.362
	Relative	1	0.936	0.833	0.931

Table 4. Some statistics of the seasonal maximum value of LAI_{opt} ($LAI_{max,opt}$) as simulated with the meteorological records from Tartu-Tõravere station from years 2000–2010 and biome parameter sets by the MODIS NPP and EST_PP models. Statistics: Avg – average, Stdev – standard deviation, Min – minimum and Max – maximum value, Coef var – coefficient of variation.

Tabel 4. LAI_{opt} sesoonse maksimumväärtuse ($LAI_{max,opt}$) statistika arvutatuna Tartu-Tõravere meteoroloogiajaama andmetest aastatest 2000–2010 ja kasutades MODIS NPP ja EST_PP mudeli sisendparameetreid erinevatele bioomidele. Avg – keskväärtus, Stdev – standardhälve, Min – minimaalne ja Max – maksimaalne väärtus, Coef var – variatsioonikoefitsient.

	Seasonal maximum value of LAI_{opt}				
Biome, model	Avg	Stdev	Min	Max	Coef var
DBF, MODIS	3.74	0.40	3.03	4.47	0.107
DBF, EST_PP	3.19	0.27	2.67	3.46	0.085
ENF, MODIS	3.51	0.23	3.11	4.07	0.066
ENF, EST_PP	3.05	0.22	2.57	3.37	0.071
MF, MODIS	4.04	0.46	3.05	4.89	0.115
MF, EST_PP	3.48	0.19	3.15	3.79	0.053
CROP, MODIS	3.67	0.32	3.15	4.43	0.086
CROP, EST_PP	2.87	0.18	2.67	3.20	0.063
GRASS, MODIS	3.61	0.38	3.12	4.46	0.107
GRASS, EST_PP	3.21	0.34	2.69	3.75	0.104

The seasonal course of LAI_{opt} depends on the meteorological conditions of the particular year. In Table 4 the mean values and standard deviations of simulated seasonal maximum LAI_{max} values of LAI_{opt} are given, as calculated with the smoothed by 6-th order polynomials of functions $M(t)$, $N(t)$, $O(t)$. We see that the typical expected coefficients of variation of LAI_{max} are of the order of magnitude 10% which is just about the same as the typical uncertainty of LAI determination by modern ground based methods. Anyway, further systematic LAI measurements should be undertaken to establish the magnitude of variation of LAI from year to year and during the season. Model simulations show also that the dates when the maximum LAI is achieved vary considerably between years.

Possible improvements of the NPP model

One of the main conclusions from this study is that if the LUE concept holds, we may expect positive correlations between the yearly sums of the product of the complex meteorological limiting factor and fAPAR and yearly yield of agricultural crops and/ or yearly wood or carbon increment in forests. In the present versions of the models considered, the site quality can effect on the simulated NPP through the values of fAPAR and/or LAI, only. A previous study (Nilson *et al.*, 2008) demonstrated that using the Landsat image-based NDVI estimates of fAPAR over a selection of birch-dominated forests in Järvselja, Estonia had a fairly good relationship between the yearly stemwood volume increment and fAPAR. Among the infertile and medium fertile sites the relation was linear. However, very fertile sites could not be discriminated from fertile sites by fAPAR, nevertheless, their yearly increments of trunk volume and mass (carbon) are reliably different. Thus, LUE-concept based simulated NPP estimates cannot make difference between NPPs on these very fertile sites, too. To obtain distinct NPP estimates from the MODIS NPP or EST_PP models, we have to assume that some of the biome-specific constants in the lookup table depend on site fertility. There has been evidence that on fertile sites trees need not to grow as much fine roots as on infertile sites (e.g. Vanninen & Mäkelä, 1999). A possibility to consider this effect could be an assumption that the fine root/leaf ratio (*Froot_leaf_ratio*, see Table 1) should depend on site fertility. For the practical application of this assumption in the NPP model, site fertility information is required, that could be obtained from a digital soil map. However, different values of *Froot_leaf_ratio* lead to differences in the respiration function N and, based on Eq. (5), differences in the optimum LAI values, too. For instance, by changing the parameter *Froot_leaf_ratio* for the DBF class from the present value 1.1 to 0.9, the respective LAI_{opt} value would change from 3.57 to 3.73. This way, the site fertility effect should result in somewhat higher values of LAI and fAPAR through the different allocation pattern.

A likely cause of problems with coastal-inland contrasts of NPP could be in the water limiting factor in the model. Currently, it is defined via VPD in the atmosphere and not by the water content in the soil. In addition to higher precipitation in inland compared with the coastal areas, the average water holding capacity tends to be better for inland soils. Although some authors support the idea of using VPD as an index of water stress (Mu *et al.*, 2007), it seems that in coastal transitional regions this index does not work properly. So, a likely improvement of the model performance could be achieved by introducing a different water limiting factor, more closely related to water stress in the soil.

Several dynamic global vegetation models (e.g. Friend *et al.*, 1995; Kucharik *et al.*, 2000; Sitch *et al.*, 2003) allow to estimate prognostic LAI values. The optimum LAI courses derived here could also be viewed as a kind of prognostic LAI, based on intrinsic properties of LUE-type NPP models. Knowledge of the optimal seasonal course of LAI in particular meteorological conditions has certainly some cognitive value. One can imagine some practical use, too. For instance, LAI is needed as an input in many vegetation-related models, such as GPP/NPP models, evapo-transpiration models, etc. In cases no other sources of information are available, LAI can be calculated as the optimal LAI course where the necessary functions $M(t)$, $N(t)$ and $O(t)$ correspond to smoothed values of these functions. Anyway, the quantitative relations like Eq. (5) to estimate the optimum LAI support the idea that the LAI and its seasonal course are mostly determined by local meteorological conditions and somewhat modified by biome.

Conclusions

The concept of complex meteorological factor in the LUE-type GPP/NPP models was introduced. It helps to understand the role of meteorological factors in GPP and separate the effects of meteorological factors from the biome variables. People who try to establish correlations of forest growth or agricultural yield with some meteorological factors should use the complex meteorological factor as the predictor, instead of any single meteorological factor. Based on comparison of the values of complex meteorological factor from a coastal and inland station, we may conclude that the present LUE-type models predict higher productivity in the coastal areas. As the measured forest and crop growth data show just the opposite, the GPP/NPP models need to be modified. The main problem related to the failure of the considered GPP/NPP models to describe local NPP trends in Estonia seems to be in the way how the water limiting factor is defined.

Formulas for the optimum LAI to obtain maximum daily NPP under given meteorological conditions were derived. The optimum LAI is logarithmically related to the ratio of the complex meteorological factor to the maintenance respiration per unit LAI. Possible strategies to achieve the optimum LAI in variable meteorological conditions were discussed. Typical optimal courses of LAI show some seasonal asymmetry resulting in lower values of LAI in the second half of the vegetation period due to higher air temperatures and respiration costs as compared with the first half. Even mid-summer depression of LAI could be present for some biomes (e.g. deciduous broadleaf forest) in Estonia. Average seasonal courses of MERIS LAI are systematically late relative to optimal LAI, while the seasonal maxima agree relatively well. Knowledge on optimum LAI courses has a cognitive value, but can also be used as the prognostic LAI in several models when the measured LAI values are not available.

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MERIS'e GPP/NPP tulem Eesti jaoks: II. Kompleksne meteoroloogiline piirangutegur ja optimaalne lehepinnaindeks

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Kokkuvõte

Analüüsitakse artikli esimeses osas kirjeldatud kiirguse kasutamise efektiivsusetüüpi taimkatte produktiivsuse (GPP/NPP) mudeleid, mida rakendatakse koos satelliidipiltide ja meteoroloogilise infoga, et kvantitatiivselt kirjeldada erinevate faktorite mõju metsade produktiivsusele. Tuuakse sisse komplekse meteoroloogilise piiranguteguri mõiste. See faktor võtab kokku kolm olulist taimkatte produktiivsust kujundavat meteoroloogilist tegurit: pealelangev fotosünteetiliselt aktiivne kiirgus ning õhutemperatuuri ja vee piirangutegurid. Tuletatakse klimatoloogilised keskmised komplekse meteoroloogilise piiranguteguri sesoonsed käigud Eesti kahe kontrastse meteojaama andmete alusel – sisemaad iseloomustav Tartu/Tõravere ja rannikupiirkonda iseloomustav Sõrve meteojaam. Tuuakse näiteid komplekse meteoroloogilise piiranguteguri sesoonsetest käikudest vastavalt Tõravere ja Sõrve meteojaamade andmetele ning arvutatuna erinevatele bioomidele/maakattetüüpidele vastavate mudeli sisendparameetrite alusel aastatest 2000-2011. Komplekse meteoroloogilise piiranguteguri arvutused näitavad, et rannikualadel on meteoroloogilised tingimused taimede kasvuks keskmiselt paremad kui seda on sisemaal. Et aga meie metsade juurdekasvu ja põldude produktiivsuse andmed näitavad just vastupidist, siis järeldatakse töös, et peamiseks selle vastuolu põhjuseks on veerežiimi arvestamine vaadeldavates NPP mudelites. Nimelt arvestatakse praegustes mudeli versioonides veedefitsiidi mõju taimedele veeaururõhu defitsiidi kaudu atmosfääris. Viimane on aga rannikualadel oluliselt mõjustatud veeauru horisontaalsest transpordist merelt ja ei pruugi hästi iseloomustada tegelikku veedefitsiiti mullas. Sademete analüüs näitab, et keskmiselt on läänerannikul ja saartel sademeid veidi vähem kui sisemaal ja pealegi on läänerannikumuldade veehoiuvõime väiksem kui sisemaal. Seega tuleks üle vaadata mudeli veedefitsiidi mõju arvestamise skeem ja asendada see enam tegelikku veedefitsiiti mullas kirjeldava versiooniga.

Taimede fenoloogilise arengu iseloomustamiseks kasutatakse töös lehepinnaindeksi (LAI) sesoonset käiku. Fenoloogilist arengut vaadeldakse kui taimede võimalust maksimaalselt ära kasutada antud koha meteoroloogilisi tingimusi. Näidatakse, et kiirguse kasutamise efektiivsuse kontseptsioonil baseeruvad taimkatte produktiivsuse (NPP) mudelid võimaldavad suhteliselt lihtsalt tuletada analüütilised valemid päevase optimaalse LAI ja selle sesoonse käigu arvutamiseks. Optimaalne LAI annab antud meteoroloogilistes tingimustes maksimaalse produktsiooni. Töös tuletatud valemite kohaselt on optimaalne LAI võrdeline naturaal-logaritmiga komplekse meteoroloogilise piiranguteguri ja ühikulisele lehepindalale

vastava hingamise intensiivsuse suhtest (valemid (5)). Optimaalse LAI väärtused ja sesoonne käik olenevad lisaks meteoroloogilistele tingimustele ka bioomist, kuna NPP mudeli sisendparameetrid on bioomispetsiifilised.

Kuna meteoroloogilised tingimused muutuvad Eestis päevast päeva väga kiiresti (peamiselt päikesepaisteliste ja pilves ilmade vahelduмise tulemusena), siis konkreetsel aastal muutub ka optimaalne LAI päevast päeva ja kaunis suurtes piirides. Seetõttu ei ole taimedel otstarbekas täpselt järgida komplekse meteoroloogilise piiranguteguri poolt kujundatud juhuslikku ja sageli suure dispersiooniga ajalist käiku. Töös vaadeldakse mõningaid ligikaudseid strateegiaid, kuidas taimed (puud) peaksid oma lehepinnaindeksit sesooni jooksul muutma, et kindlustada suuremat aastast produktsiooni. Töös leitud valemite alusel tehtud arvutused näitavad, et optimaalse LAI klimatoloogiline keskmine sesoonne käik on maksimumiga kesksuvel. Samas optimaalne LAI ei ole sümmeetriline kesksuve suhtes, vaid suve teisel poolel on optimaalse LAI väärtused reeglina madalamad kui esimesel poolel. See on tingitud suve teise poole kõrgematest õhutemperatuuridest, (mis tingib suuremaid kulutusi hingamisele) ja ka sagedasemast veedefitsiidist. Mõnedel põuastel suvedel on võimalik isegi optimaalse LAI kesksuvine depressioon.

Optimaalse LAI sesoonseid käike erinevatele bioomidele võrreldi töös MERIS'e satelliidipiltidelt (2003–2011) samade bioomide Eesti keskmiste LAI käikudega. Selgus, et kevadine lehtede puhkemine ja seega ka vegetatsiooniperioodi algus on MERIS'e piltidelt määratuna märksa hilisem kui seda võimaldaks komplekse meteoroloogilise piiranguteguri poolt määratud optimaalne LAI. Ajaliselt hilinenud lehtede puhkemise tõttu kaotavad meie lehtpuud ja põlluviljad osa võimalikust produktsioonist. Sesooni maksimaalse optimaalse LAI väärtused kesksuvel on enam-vähem samasugused nagu MERISe piltidelt leitud väärtused, milline asjaolu kinnitab optimaalse LAI valemite tõepärasust.

Optimaalse LAI teadmine omab eelkõige tunnetuslikku tähtsust ja ei ole oluline ainult Eesti kontekstis, vaid üldiselt. Samas saab toodud valemite abil arvutatud optimaalse LAI väärtusi kasutada erinevates taimkatte produktiivsuse, transpiratsiooni jms mudelites kui antud geograafilise paiga prognostilisi LAI väärtusi. See on eriti oluline neil juhtudel kui tegelikke LAI väärtusi ei õnnestu mõõta.

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