

EVALUATION OF THE INTERCOM MODEL FOR PREDICTING GROWTH OF FOREST HERBS

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Abstract – The ecophysiological model INTERCOM was evaluated for its suitability in predicting the growth of perennial forest herbs. A field experiment was conducted to obtain data on photosynthesis and growth parameters of two spring flowering understorey geophytes. Results were used to parameterize the model and its performance was evaluated using the average normalized difference (AE) between predicted and observed biomass and the leaf area index. The model was assumed to provide accurate simulations if the AE was smaller than 0.4. Adjusting the photosynthetic intensity parameters in the model to reflect observed changes in photosynthesis throughout the growing period resulted in the accurate prediction of *Scilla bifolia* and *Arum maculatum* biomass (AE=0.13 and AE=0.021, respectively) and LAI (AE=-0.16 and AE=-0.08, respectively). Ecophysiological models may be useful tools for predicting the biomass accumulation of forest understorey species in response to varying environmental conditions, which could be useful for monitoring forest ecosystem health.

Key words: Forest herbs, *Scilla bifolia*, *Arum maculatum*, photosynthesis, leaf area index, biomass production, ecophysiological model

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INTRODUCTION

Understorey vegetation cover has a great indicative value in studying the effects of environmental changes in forest ecosystems. In temperate forests, understorey vegetation plays an important role in annual biomass production and in the nutrient and carbon cycles (Yarie, 1980; Whigham, 2004; Pavliainen et al., 2005a; Popović et al., 2005a) due to the rapid turnover of biomass and the large proportion of easily decomposable litter (Zavitkovski, 1976; Janković et al., 1982; Chapin, 1983; Popović and Karadžić, 1992). Also, understorey plants account for a considerable part of the total biodiversity of temperate forests, since much plant and animal biodiversity in temperate forest ecosystems is comprised within, or depends upon, this layer (Gerit et al., 2007). Floristic composition and development of forest understorey provides information about soil fertility, water availability and climatic conditions in forest ecosystems. The biomass of the herbaceous layer mostly depends on stand density

and the stage of stand development, and is usually affected by various disturbances that occur periodically or as incidental events (Roberts, 2004). Characterization of the current state of forest vegetation on the basis of floristic composition of the forest floor, and detecting the changes in vegetation productivity in relation to natural and anthropological environmental factors has been utilized for monitoring forest ecosystem health (Alaback, 1982; Kubiček and Brechtel, 1970; Kubiček et al., 1994; Reader, 1987; Tappeiner, 1989; Meier et al., 1995; Skov and Svenning, 2003; Pavliainen et al., 2005b).

Although most forest succession models developed have focused on the dynamics of tree species (e.g. Baker, 1989; Acevedo et al., 1996), some authors have recognized the importance of the dynamics of ground vegetation, since it has a large impact on the initial stages of tree growth and survival (Elemans, 2005; Ramming et al., 2006). There were also some studies that provided predictive information on the response of field layer species to

environmental variables (Corney et al., 2004), where analyses were mostly dealing with the floristic composition of the field layer communities over time (presence or absence of species at the site). Muukkonen and Mäkipää (2006) emphasized the need for understorey biomass quantification, and recommended a new method for estimating this value according to site and stand attributes. The model developed by these authors considers only above-ground biomass, which makes up approx. 30% of the estimated biomass of field layer vegetation (Abrahamson, 1979; Kubiček and Simonovič, 1982; Havas and Kubin, 1983; Kubiček et al., 1994).

In addition to site and stand characteristics, disturbance, and environmental factors, biomass production of the forest understorey will be influenced by interspecific interactions with other understorey species as well as those making up the forest canopy. Ecophysiological models are strongly suited for predicting the productivity of the forest herb layer (Bazzaz, 1979; Grime, 1979). The advantage of using an ecophysiological approach in modeling forest herb growth has been shown by applying the RGRP software for simulating the growth of *Scilla bifolia* L. (Liliaceae) (Karadžić et al., 1999). This integrated software for computing the relative growth rate of plants (RGR) is based on the calculation of leaf area, being more flexible in comparison with previously developed specialized programs for RGR, since it combines the classical approach and the regression approach (Karadžić et al., 1999, and references therein). Incorporating the calculation of leaf area, i.e. morphometric analysis, RGRP allowed more realistic predictions of growth dynamics of species based on their ecophysiological adjustments to environment.

The INTERCOM model simulates plant growth and interplant competition for light and soil water based on the response of eco-physiological processes to the environment, providing a tool to analyze the complex interactions between co-existing plants (Kropff and van Laar, 1993). The objectives of this research were to parameterize INTERCOM and evaluate its performance in

predicting the biomass and leaf area index (LAI) of two spring flowering understorey geophytes: *Scilla bifolia* and *Arum maculatum*.

MODEL DESCRIPTION

INTERCOM was developed to account for the effects of temperature, radiation, rainfall and soil hydrological characteristics on plant growth in natural or agricultural ecosystems, where between-plant competition for resources is present. Accordingly, the model simulates the following aspects of growth and competition: phenological development, morphological development, dry matter accumulation, allocation of dry matter over the plant organs, soil water balance, evaporation, and transpiration, and competition for capture of light and water. Input requirements of the model are: geographical latitude, standard daily weather data (incident solar radiation, minimum and maximum temperature, rainfall, average wind speed, and vapor pressure), soil physical properties (field capacity) and numerous parameter values that describe the morphological and physiological characteristics of the species. Under conditions of adequate soil water supply, the water balance component of the model can be removed. The time step of integration is one day. It can be applied for modeling the performance of one species or for modeling the growth of two co-existing, competing species. In this work, we apply it for modeling the biomass and LAI of two understorey species growing in monoculture.

Under favorable growth conditions, light is the main factor determining plant growth rate. From the leaf area index (LAI) of the species and the vertical distribution of that leaf area, the light profile within the canopy is calculated. The following equation quantifies relative LAI over relative plant height within INTERCOM (Lindquist and Mortensen, 1999):

$$LAI_r = 1 - \exp\left(-\left(\frac{1-KI_r}{LDA}\right)^{LDB}\right)$$

where LAI_r is the leaf area index within a layer divided by total LAI, HTr is the height of layer h divided by total height, LDa is the relative height at which maximum leaf area density (m² leaf m⁻³ leaf canopy) occurs, and LD_b defines the slope of the curve through the inflection point. Based on the light profile within the canopy, the quantity of leaf area within a layer, and the photosynthetic characteristics of leaves, the photosynthetic profile of each species in the mixed canopy is obtained. The following equation was incorporated in INTERCOM, based on the approach of Sinclair and Horie (1989), to account for the effect of leaf nitrogen content on light-saturated CO₂ assimilation rate (*A_i*):

$$A_i = A_{max} \left(\frac{2}{1 + \exp(-a(Nl - b))} - 1 \right),$$

where *A_{max}* is the absolute maximum possible CO₂ assimilation rate, *Nl* is the nitrogen content of leaves (g N m⁻² leaf), *a* and *b* are shape coefficients. Integration of instantaneous photosynthetic rate over height of the canopy and over the day gives the daily CO₂ assimilation rate for each species. This is converted to glucose production by multiplying by 30/34 (molecular weights of CH₂O/CO₂). After subtraction of respiration requirements for maintenance and growth of the species, the net daily growth rate in kg dry matter per ha per day is obtained. The dry matter produced is partitioned among the various plant organs using partitioning coefficients that are introduced as a function of the phenological development stage of the species. The plant developmental stage is represented as a dimensionless scale, where 0 is assigned at plant emergence, 1 at flowering and 2 at seed maturity, and tracked in the model as a function of daily average temperature. Integration of daily growth rates of the organs and specific leaf area results in the time course of LAI and dry biomass throughout the growing season.

This model was used for predicting the growth and interplant competition of several annual species in agro-ecosystems (Kropff and van Laar, 1993; Kropff et al., 1994; Lindquist and Mortensen, 1999;

Lindquist, 2001; Wang et al., 2007). We evaluated INTERCOM for predicting the growth and LAI dynamics of two perennial species with known starting biomass (biomass of below-ground organs before emergence), and propose an appropriate application of the model.

MATERIAL AND METHODS

A field experiment was conducted in a *Quercus-Carpinetum serbicum* community (Borisavljević et al., 1955) at 300-400 m a.s.l. on Avala Mountain, near Belgrade. Two spring flowering geophytes, *Scilla bifolia* L. (Liliaceae) and *Arum maculatum* L. (Araceae) were investigated for their ecophysiological performance and biomass productivity during the whole growing period (from the beginning of March till the end of May).

The photosynthetic rate was measured on single leaves of each species using a LI-6200 closed photosynthesis system (Li-Cor, Lincoln, NE, USA). After routine calibration of the instrument at the start of each sampling date, all measurements were conducted with a leaf chamber CO₂ concentration of 350 μL/L, a chamber temperature of 20°C and relative humidity of 55%. Photosynthetic photon flux density was measured with a selenium cell mounted on the leaf chamber. Sampling was usually conducted between 09:00 and 12:00 h, and only the data on CO₂ uptake above the light saturation level were considered (*A_{max}* at PPFD > 550 μmol m⁻² s⁻¹). Photosynthetic measurements were performed over 3 months, at approximately 7-day intervals (15 measurements 4 times monthly, *n* = 60). As the data from four monthly measurements of photosynthesis were not significantly different, these were summarized as mean monthly photosynthesis.

For each species, the plant material of 25 individuals from five randomly selected plots (each 0.25 m x 0.25 m) (*n* = 75) was sampled simultaneously with measurements on photosynthesis. Each plant was collected using a shovel, keeping most of its root system intact. Plants were gently

washed to remove all soil from roots, separated into above- and below-ground organs, and oven-dried at 75°C to a constant weight. For each harvested plant, total plant dry mass (Wt) was determined, as well as dry mass of above-ground (Wa) and below-ground (Wb) organs. To estimate the total leaf area index (LAI), six plots (each 0.25 m x 0.25 m) were randomly selected, and all leaves from these plots were scanned in order to determine the total leaf area of each species (m² of leaf per m² of ground area) (Karadžić et al., 1999). Plant sampling for dry biomass and leaf area measurement were performed with the same frequency as photosynthetic measurements, at approximately 7-day intervals.

Results were used to parameterize the model for these species and to evaluate INTERCOM performance in predicting their biomass accumulation and LAI. Data inputs required for INTERCOM simulations included: daily weather data (obtained from Avala meteorological observation station, approximately 1.5 km from study site); initial conditions (leaf area index, leaf dry biomass, stem dry weight, root dry biomass and plant height at emergence); developmental rate parameters (base temperature for plant development; base temperature for leaf development; development rate); dry matter partitioning parameters (FAG - fraction of total dry matter increase allocated to above-ground plant parts; FBG - fraction of total dry matter increase allocated to below-ground plant parts; fraction of FAG allocated to leaves and stems, respectively; fraction of FBG allocated to storage organs); photosynthetic efficiency parameters (photosynthetic intensity); maintenance respiration parameters (maintenance respiration coefficient of plant organs); death rate and redistribution parameters (death rate of leaves, stems, roots); LAI data (leaf area index at different developmental stages); specific leaf weight (leaf biomass to leaf area ratio at different developmental stages); growth rate parameters (relative growth rate of leaf area calculated from temperature sum and time passed in subsequent development stages). Plant density was assumed to be 50 plants per m². Maintenance respiration parameters for roots, storage organs and stems were assumed to be very low, i.e. 0.005 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Outputs of simulation were Wa (dry biomass of above-

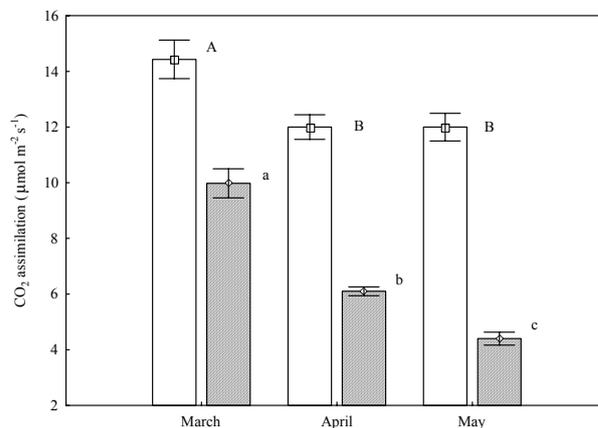


Figure 1. Assimilation of CO₂ in *S. bifolia* (empty bars) and *A. maculatum* (filled bars) over the growing season. Mean values \pm S.E. Statistically significant differences between the monthly data sets are indicated with different upper cases (*S. bifolia*) and lower cases (*A. maculatum*), respectively.

ground organs), Wb (dry biomass of storage below-ground organs and roots), Wt (total plant dry biomass) and LAI (leaf area index).

Differences among average monthly values of Amax (CO₂ assimilation above the light compensation point) and LAI were taken as significant if $p < 0.05$, tested by one-way break down ANOVA test. INTERCOM performance was evaluated by calculating the normalized deviation $((P_i - O_i)/O_i)$ where P_i and O_i are predicted and observed values, respectively) for each sampling date and averaging them to obtain an average error (AE; Lindquist, 2001). The AE is similar to the coefficient of variation. We assume that an average error less than 0.4 indicates the model accurately simulates plant biomass or LAI. Data were processed using the statistical package Statistica 6.0 for Windows.

RESULTS

Observed photosynthetic rates of both species decreased over the growing period. *S. bifolia* photosynthesis was $14.43 \pm 1.55 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the beginning of March and decreased to $12.6 \pm 0.97 \mu\text{mol m}^{-2} \text{s}^{-1}$ in April and to $12.0 \pm 1.11 \mu\text{mol m}^{-2} \text{s}^{-1}$ in May, whereas *A. maculatum* photosynthesis started lower ($9.98 \pm 1.17 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the beginning of March) and declined to 6.1 ± 0.35

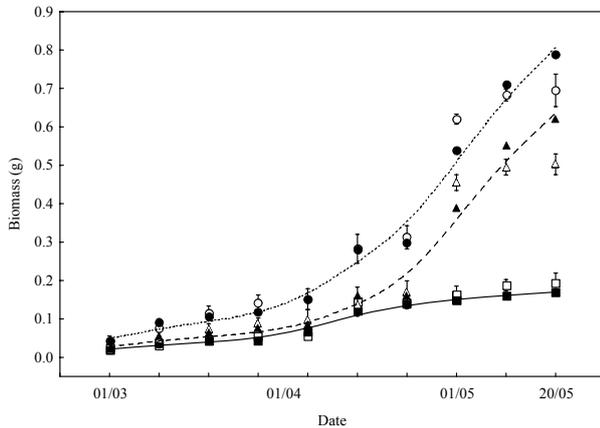


Figure 2. Observed and simulated biomass dynamics of *S. bifolia*. Mean values \pm S.D. of observed above-ground biomass W_a (empty square), below-ground biomass W_b (empty triangle) and total biomass W_t (empty circle). Filled symbols are simulated data fitted with best fitting curves for above-ground, below-ground and total biomass (filled line, broken line and dotted line, respectively).

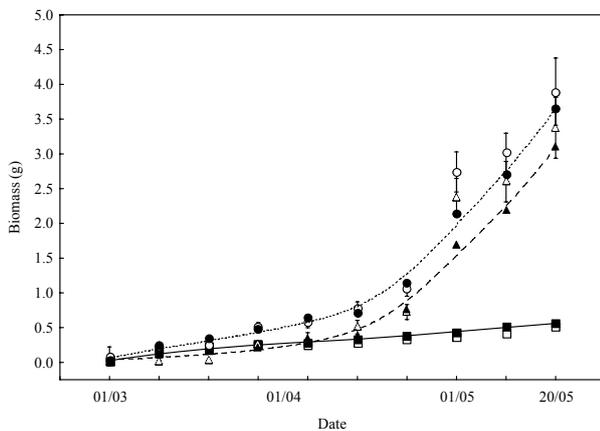


Figure 3. Observed and simulated biomass dynamics of *A. maculatum*. Mean values \pm S.D. of observed above-ground biomass W_a (empty square), below-ground biomass W_b (empty triangle) and total biomass W_t (empty circle). Filled symbols are simulated data fitted with best fitting curves for above-ground, below-ground and total biomass (filled line, broken line and dotted line, respectively).

$\mu\text{mol m}^{-2} \text{s}^{-1}$ in April and to $4.41 \pm 0.52 \mu\text{mol m}^{-2} \text{s}^{-1}$ in May (Figure 1). The total decrease in light-saturated photosynthesis was 27 % in *S. bifolia* and 56 % in *A. maculatum*. In contrast, the LAI of both species increased throughout most of the growing season, and then declined after April 20th as leaves senesced (Figure 4).

The dynamic of biomass accumulation was similar in both species (Figures 2, 3). Above-ground biomass increased slowly throughout the growing season until leaf senescence began at about May 20th. The below-ground biomass was significantly greater than the above-ground biomass in both species (2.5 and 7.5 times greater in *S. bifolia* and *A. maculatum*, respectively), most of that mass occurring in the *S. bifolia* bulb and the *A. maculatum* tuber. The maximal increase in below-ground biomass occurred after the flowering period in both species as carbohydrates were partitioned to below-ground reserves for next year's growth. The above-ground biomasses of the two species were similar throughout the growing season, but *A. maculatum* had more than four times greater total biomass than *S. bifolia*, most of it occurring in its tuber.

The first simulation was run using the seasonal average photosynthetic rate as model input. Simulated biomass from this run substantially over-estimated above-ground biomass and LAI, resulting in poor model performance. Therefore, subsequent simulations were sub-divided into smaller steps according to observed changes in the measured photosynthetic intensity in both species. For *S. bifolia* A_{max} was changed from $14.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $12.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ on the 18th day after emergence. For *A. maculatum* this adjustment was applied twice, changing A_{max} from $10.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $6.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 18 d after emergence and to $4.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ on the 30 day after emergence. After these adjustments, simulated biomass and LAI was quite accurate, with average errors smaller than 0.4 (for W_t of *S. bifolia* 0.13; for W_t of *A. maculatum* 0.012; for LAI of *S. bifolia* -0.16; for LAI of *A. maculatum* -0.08). Figure 4 shows both simulated and observed biomass and LAI of *S. bifolia* and *A. maculatum*.

DISCUSSION

Vernal forest ephemerals complete their above-ground growth during a short spring period characterized by dynamic environmental changes as the forest canopy changes from nearly open to

full canopy closure. Forest floor herbs prior to and during the period of tree foliation are exposed to very different light conditions, and so their photosynthetic apparatus is acclimated to seasonally changing quantities and qualities of available light (Shultze, 1982).

Both physiology and morphology of plant assimilative organs are affected by environmental changes, contributing to the effectiveness of plant adaptive responses in the natural stand (Poorter, 1989). Seasonal decline in photosynthesis that occurs in forest vernal ephemeroïds - as an adaptation to changed light level or as a natural consequence of plant developmental stage and leaf aging - can be effectively compensated with alternated dry matter partitioning (Hirose et al., 1997, Popović et al., 2006, Popović, 2007). An important trait of geophytes is their investment in storage organs during the whole vegetation season, but predominantly after leaf senescence when dry matter partitioned in leaves is being distributed into below-ground plant parts (Popović et al., 2005b). Therefore, an integral model which can predict both above-ground and below-ground biomass dynamics would provide the best insight into dry matter partitioning for this plant life form.

Our results show that modifying photosynthetic parameters within INTERCOM to accurately reflect natural changes in photosynthesis throughout the growing period will result in accurate simulation of *S. bifolia* and *A. maculatum* growth dynamics. Accurate data on the timing of the changes in photosynthesis were essential for effectively modifying these parameters within the model. Besides the need to recognize crucial periods when changes in photosynthetic intensity occur, further knowledge of the initial (pre-emergence) biomass of plant organs was required.

Along with an understanding of the dynamics of forest canopy vegetation, which is the subject of most silvicultural studies, research is needed to quantify the composition and growth of herbs, shrubs and trees in the understorey. Predicting the potential growth of understorey vegetation may provide information on

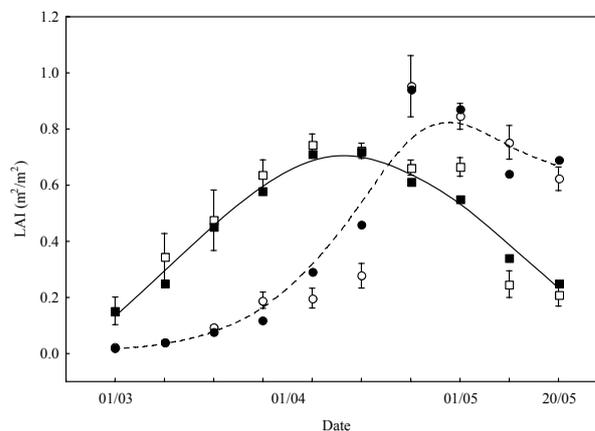


Figure 4. Observed and simulated seasonal dynamics of LAI of *S. bifolia* and *A. maculatum*. Mean values \pm S.D. of observed LAI of *S. bifolia* (empty square) and *A. maculatum* (empty circle). Filled symbols are simulated data fitted with best fitting curves for LAI of *S. bifolia* and *A. maculatum* (filled line and broken line, respectively).

changes in overstorey density and have some management implications in order to preserve natural ecosystems. Models may help in understanding plant response to further ecosystem disturbance such as clearcutting, which results in completely opening the canopy, loss of litter, and potentially a subsequent destruction of understorey vegetation owing to exposure to high light and desiccation. Forest floor species may be eliminated by competition from taller herbs and shrubs for light and nutrients (Rogers, 1982; Whigham, 2004). Further, some vernal species may occupy very specific types of microhabitats on the forest floor, and once displaced may not be able to survive on other, less suitable sites (Whigham, 2004; Elemans, 2005). Moreover, the potential growth of same species on another site can be predicted by changing the weather conditions in the model data.

The maintenance of populations of understorey herbs depends on a number of biotic and abiotic factors, including competition for light, pollinators and nutrients, species' microhabitat preferences, canopy species, and stand history (Whigham, 2004, and references therein). Forest herbs usually have limited dispersion and slow dispersal, so their distribution over the habitat is also an indication of system stability. It was shown that the species with evenly distributed populations in a primary forest are

patchy in distribution in a restored forest system (Honnay et al., 2002). Newly established populations of forest herbs with their growth potential have a significant role in the case of forest restoration.

Further, logging may allow more disturbance-tolerant genera to increase in frequency and cover, displacing populations of less disturbance-tolerant forest floor herbs. Predictive growth dynamics based on species' ecophysiology may indicate their degree of disturbance-tolerance.

Observed variation between simulated and field data on plant biometric parameters showed the importance of knowledge of light utilization and photosynthetic performance of particular species within the plant community. Our results confirm the advantage and benefit of using ecophysiological models in predicting the growth of plants that inhabit seasonally varying environments and possess highly variable physiological and morphological parameters over their growing season. The possibility to adjust photosynthesis, the crucial parameter that indicates whole plant productivity, makes the INTERCOM mostly acceptable for predicting growth in perennial herbs. While we only used the model to simulate mono-species growth of these two species, the model could be effectively used to assess the performance of these species in the presence of different canopy species or in mixture with more early successional herbaceous plants following disturbance.

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ОЦЕНА ЕФИКАСНОСТИ МОДЕЛА INTERCOM У СИМУЛАЦИЈИ РАСТА ШУМСКИХ ЗЕЉАСТИХ БИЉАКА

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У раду је испитивана ефикасност примене екофизиолошког модела INTERCOM за процену раста вишегодишњих шумских зељастих биљака. Мерења фотосинтезе и параметара раста двеју пролећних раноцветајућих шумских геопита су обављена на природном станишту. Резултати мерења су коришћени за параметризацију модела и његова ефикасност је процењена употребом просечне нормализоване разлике (АЕ) између симулираних и измерених вредности за биомасу и индекс лисне површине. Претпостављено је да модел даје поуздану симулацију уколико је вредност АЕ мања од 0.4.

На основу измерених вредности интензитета фотосинтезе извршено је прилагођавање овог параметра у моделу, што је омогућило поуздано предвиђање динамике биомасе *Scilla bifolia* и *Arum maculatum* (АЕ=0.13 и АЕ=0.021), као и индекса лисне површине ових двеју врста (АЕ=-0.16 и АЕ=-0.08). Екофизиолошки модели могу бити веома корисни у процени акумулирања биомасе од стране шумских биљака приземног спрата, што је нарочито значајно у односу на промене услова спољашње средине као начин мониторинга стања шумског екосистема.

