

**Photosynthesis of phytoplankton  
studied with three different incubation methods**

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**Abstract**

In natural environments, algal cells that constitute the phytoplankton continuously experience light variations because of the vertical displacement within the water column due to hydrodynamics. The common method for determination of phytoplankton primary production is the static incubation, when photosynthesizing cells are exposed to constant light conditions. The *in situ* and laboratory measurement of planktonic primary production in Lake Balaton has been made so far only by static incubation. Therefore we compared the static and the dynamic incubation methods of the measurement of primary production in Siófok-basin of Lake Balaton in August 2007. The dynamic incubation was performed by an elevator operated with a stepper-motor. In sunny weather the natural UV radiance inhibited the photosynthesis of phytoplankton, therefore the laboratory incubation without UV radiation overestimated the primary production. In cloudy weather, however, the lower natural UV radiance stimulated photosynthesis. Significant differences have not been found between the results of the *in situ* dynamic and *in situ* static incubation. According to our results, the laboratory incubation method is suitable to estimate the algal primary production, however the *in situ* dynamic method is the best way to measure it, if the determination of photosynthesis-irradiance curve is not required.

**Keywords:** light conditions, photosynthetron, phytoplankton, primary production, UV radiation.

## Introduction

Various methods are applied for the measurement of primary biomass production of the phytoplankton. Some of these methods are based on field incubations, while others on laboratory incubation, in photosynthetrons with controlled environmental conditions.

The field incubation may happen with a static method, when the fixed water samples are incubated at different depths of the water column, or with a dynamic method, when the incubation vessels are moved up and down in the water column. Due to a very high photon flux density the algal photosynthesis is impaired in a process called photoinhibition. For a short period of time (for about ten minutes), planktonic algae are able to photosynthesize under strong light without any major damage (Gocke and Lenz 2004). Under natural conditions the freely moving algae (and during dynamic incubation) can make use of the higher light intensities when they arrive in the surface layers. In the course of the static incubation, the photosynthesis of algae fixed in stable points of the surface layers becomes inhibited by the permanent high light (Herodek and Tamás 1976, Pálffy and Vörös 2003, Gocke and Lenz 2004). These higher light intensities drive to a considerable underestimation of primary production in static systems (Nixdorf *et al.* 1990, MacIntyre 1993). Another important factor is UV radiation, by which photosynthesis of the algae is hampered likewise. During laboratory incubation in photosynthetrons the UV radiation is absent, and this fact may also lead to an overestimation of primary production in natural habitats. In the past primary production of the phytoplankton was determined with a static field method. At present, the primary production of phytoplankton is measured under laboratory conditions, with the help of photosynthetrons, because in many cases this approach is faster and more economic. This happened also in the case of Lake Balaton, where the field incubation method was used in the 1970's (Herodek and Tamás 1976), while laboratory incubation was applied in the last decade (Vörös *et al.* 2003).

Even if many studies compare the above mentioned two different methods, there are no previous investigations to simultaneously compare the static field and laboratory approaches and the dynamic field incubation method. Geravis and his colleagues (1997) measured higher primary production values with dynamic incubation than with static incubation. Their measurements were comparable with results obtained by Mara (1978), Nix-

dorf *et al.* (1990, 1992) and Nixdorf and Behrend (1991), according to which the dynamic *in situ* incubation gives higher primary production values than the static *in situ* method. Only very few studies exist that measured smaller integrated productivity in case of dynamic, than in case of static incubation. Ferris and Christian (1991) and Randall and Day (1984) observed this phenomenon in a turbid estuary. Several factors influence the answer of phytoplankton to the changing light regimes: species composition, depth and mixing, turbidity, the light intensity of light and UV radiation, as well as the method of incubation and measurement (Geravis *et al.* 1999). From among these factors we compared the static incubation with the dynamic one, and the field incubation with the laboratory one for determining phytoplankton production in an extensive shallow lake: the Balaton Lake.

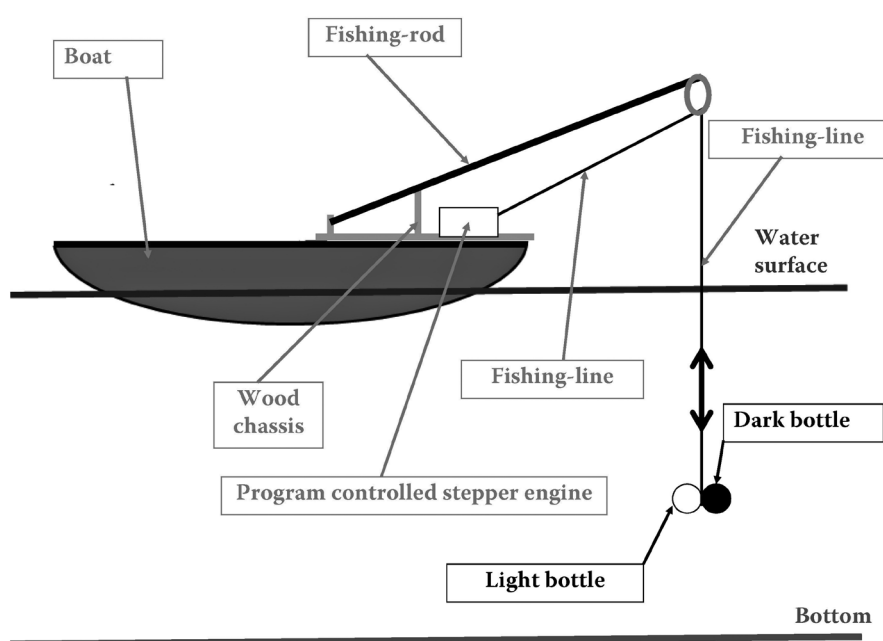
### Materials and methods

Our comparative measurements we made in three occasions in August 2007 (02.08.2007, 09.08.2007 and 16.08.2007) at the Siófoki-basin (Tihany sampling point). The same water samples were incubated in the field, with a static and a dynamic method, as well as in the laboratory, with a static method using the photosynthetron. The primary production of the phytoplankton was determined with the method based on the incorporation of the radioactively labeled  $^{14}\text{C}$  isotope in the algal biomass. The water samples were incubated with 0.4 MBq  $\text{NaH}^{14}\text{CO}_3$  solution, applying a dark control sample, during two hours, at the current temperature of the lake water. The water samples we filtered through a nitrocellulose filter (Millipore) with 0.45  $\mu\text{m}$  pore diameter. The radioactivity of algae collected on the filter was measured with a liquid scintillation counter, after 24 hours of exposure. The total inorganic carbon (TIC) concentration was measured with an Elemental High TOC analyzer. The underwater light intensity (photosynthetically active radiation) was measured with a LI-COR radiometer ( $2\pi$  sensor). The laboratory incubation was performed in 20 ml glass vessels at eight different light intensities (7, 12, 30, 80, 150, 290, 510 and 1000  $\mu\text{M m}^{-2}\text{s}^{-1}$ ) for two hours. In the case of the field static incubation, we incubated the water samples in seven different depths with different light intensities (at 10 cm, 25 cm, 50 cm, 100 cm, 150 cm, 200 cm and 300 cm under the water surface), in three parallels, in quartz test tubes (a total of 21 test tubes). For the dynamic field

incubation we designed an original, new equipment, the schematic drawing of this being shown in figure 1. In the case of dynamic incubation the water samples were put in quartz test tubes, and in UV-sheltered quartz test tubes (with filtering foil), each in three repeats (2x3 test tubes).

With the data collected in the course of the static field incubation and the static laboratory one, we estimated the main parameters of the photosynthetic primary production, applying the Eilers and Peeters model (1988). We also calculated the light inhibition parameter ( $I_{inh25\%}$ , i.e. the light intensity which causes 25% inhibition of the maximal photosynthetic production). If the value of the light inhibition parameter is high, it means that the light inhibition is small (Somogyi *et al.* 2007).

From the parameters of photosynthesis – light intensity curves (the vertical extinction coefficient, the light intensity measured on the field, and in the knowledge of the water depth) we calculated the phytoplankton pri-



**Fig. 1.** Schematic drawing of the equipment designed by us for the dynamic incubation of phytoplankton samples (original).

**1. ábra:** A fitoplankton minták dinamikus inkubálására tervezett berendezés vázlatos rajza (eredeti).

mary production on a surface base ( $\mu\text{g C m}^{-2} \text{ h}^{-1}$ ). In case of the field dynamic incubation, results were expressed considering the whole water column (in  $\mu\text{g C l}^{-1} \text{ h}^{-1}$ ). The values of primary photosynthetic production obtained with the different incubation methods were compared with the ANOVA significance test, using the Origin<sup>®</sup>7.5 software.

## Results and discussion

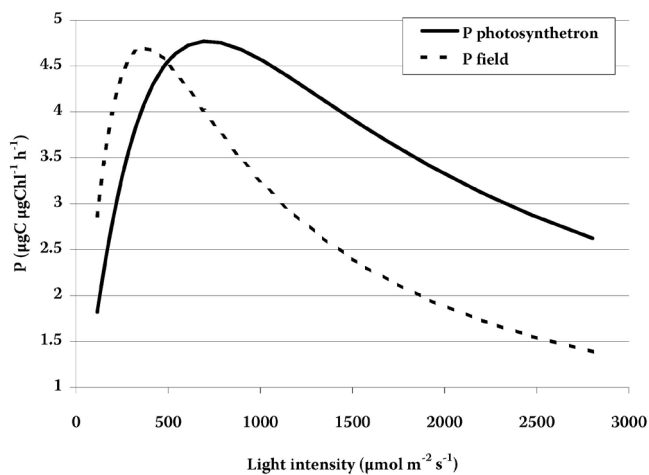
### *Dependence of photosynthesis of phytoplankton on light intensity*

Regarding the dependence of photosynthetic production on light intensity, determinations revealed that the main parameters of photosynthesis-light curves and the running down of these curves were different in the static field measurements and in the photosynthetrons (fig. 2).

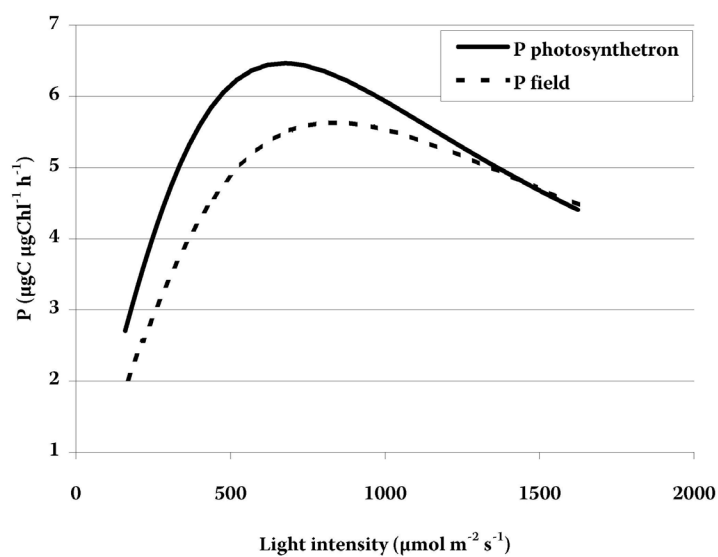
During the first set of measurements made in sunny weather (on 2<sup>nd</sup> of August 2007), the light intensity in the upper layer of the water reached  $3000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . In the course of the static field incubation the maximum photosynthetic production value ( $P_{\text{max}}$ :  $5.02 \mu\text{g C } \mu\text{g}^{-1} \text{ Chl h}^{-1}$ ) was higher than in the course of the laboratory incubation ( $P_{\text{max}}$ :  $4.76 \mu\text{g C } \mu\text{g}^{-1} \text{ Chl h}^{-1}$ ). At the same time, the light inhibition parameter obtained in the static field incubation of phytoplankton samples ( $I_{\text{inh}25\%}$ :  $447 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was much lower, than the one recorded in the course of the laboratory incubation ( $I_{\text{inh}25\%}$ :  $1062 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). This indicates that photoinhibition of photosynthesis was much lower in the course of the laboratory incubation, as compared with the static field conditions.

The second set of measurements was performed in cloudy weather (on 9<sup>th</sup> of August 2007), when the light intensity in the upper layer of the water was around  $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Under these conditions, in the course of the static field incubation a lower maximum production value was registered ( $P_{\text{max}}$ :  $5.63 \mu\text{g C } \mu\text{g}^{-1} \text{ Chl h}^{-1}$ ) than in the course of the laboratory incubation ( $P_{\text{max}}$ :  $6.52 \mu\text{g C } \mu\text{g}^{-1} \text{ Chl h}^{-1}$ ). In this case photoinhibition of photosynthesis was higher in the laboratory incubation system (field incubation:  $I_{\text{inh}25\%} = 934 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , laboratory incubation:  $I_{\text{inh}25\%} = 745 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ).

The third set of measurements was made in unclouded, sunny weather (on 16<sup>th</sup> of August 2007). In the course of the field static incubation, simi-



a



b

**Fig. 2.** Photosynthesis (P) – light intensity curve of the phytoplankton in cloudy (a) and sunny weather (b), established on the basis of static field and laboratory incubation, expressed as incorporated carbon per unit chlorophyll (Chl.) content and hour.

**2. ábra:** A fitoplankton statikus terepi és laboratóriumi inkubáció segítségével felvett fotoszintézis – fényintenzitás (P–I) görbéje napos (a) és felhős időben (b), klorofiltartalomra (Chl.) és időegységre vonatkoztatott szénasszimilációban kifejezve.

larly to the first set of measurements, a higher maximum production value was obtained ( $P_{\max}$ :  $4.04 \mu\text{g C } \mu\text{g}^{-1}\text{Chl h}^{-1}$ ) than in the case of the laboratory incubation ( $P_{\max}$ :  $3.83 \mu\text{g C } \mu\text{g}^{-1}\text{Chl h}^{-1}$ ). The value of the light inhibition parameter was lower during the static field incubation ( $I_{\text{inh}25\%}$ :  $445 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) than the value received in the course of the laboratory incubation ( $I_{\text{inh}25\%}$ :  $678 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), indicating that the extent of photoinhibition was lower in the phytoplankton samples grown in the photosynthetron.

In sunny weather, when the photon flux density is high, the photosynthesis of the phytoplankton showed a stronger photoinhibition (the light inhibition parameter was lower) in the natural aquatic environment than under laboratory conditions with the same light intensity. This suggests that at high light intensities the primary production measured in the photosynthetron is overestimated in relation with the primary production of the algae in their natural habitat. The most reasonable explanation for this difference is the presence of a high amount of UV radiation which penetrates into the upper water layers, while this high-energy radiation is excluded from the laboratory setups. In cloudy weather there is no harmful amount of UV radiation reaching the phytoplankton, but a low UV intensity rather exerts a photodynamic effect on algae. This may be the reason why in cloudy weather a stronger photoinhibition was registered in the photosynthetron than in the course of the field incubation. In the nature the low UV radiation which accompanies the low light intensity may stimulate the photosynthesis, while the strong UV radiation associated with high light intensities inhibits the photosynthetic biomass production of planktonic algae.

#### *Primary production of phytoplankton on water surface unit*

At high light intensities the phytoplankton primary production determined with the static field incubation method (PAR+UV) was  $57 \text{ mg C m}^{-2} \text{ h}^{-1}$ , with the dynamic incubation method its value was  $59 \text{ mg C m}^{-2} \text{ h}^{-1}$  when UV was not excluded (PAR+UV) and it reached  $72 \text{ mg C m}^{-2} \text{ h}^{-1}$  when samples were shielded from UV radiation (PAR only). With the static laboratory method (PAR without UV) the primary production showed an average value of  $63 \text{ mg C m}^{-2} \text{ h}^{-1}$  (tables 1, 2 and 3). There were no significant differences between the primary production values measured with the static field incubation and the static laboratory method. Furthermore, no significant difference could be found between the photosynthetic production of phytoplankton in the

static field experiments and in the full spectrum dynamic (PAR+UV) incubation experiments where a high intensity of UV radiation was present together with the high photon flux density, even if algae were exposed to high irradiation only temporarily during their vertical movement in the water. But the primary production measured with the UV-sheltered dynamic field incubation method (PAR only) significantly differed from the production of phytoplankton kept in static field incubation ( $P=0.026$ ), and it also exhibited a statistically significant difference from the values registered with the dynamic full spectrum incubation ( $P=0.017$ ), and with the

**Table 1.** Primary production referred to surface unit in the Siófoki-basin in August 2007 measured with the field static and with the laboratory static incubation (photosynthetron).  
**1. táblázat:** A terepi statikus és a laboratóriumi statikus inkubációval (fotoszintetron) meghatározott felületegységre vonatkoztatott elsődleges termelés a Siófoki-medencében 2007 augusztusában.

Date	Incubation method	P (mg C m <sup>-2</sup> h <sup>-1</sup> )	±SD
02.08.2007	static field PAR+UV	57	7,59
02.08.2007	static fotoszintetron PAR	63	3,9
09.08.2007	static field PAR+UV	23	3,32
09.08.2007	static photosynthetron PAR	30	1,01
16.08.2007	static field PAR+UV	31	3,93
16.08.2007	static photosynthetron PAR	36	4,02

**Table 2.** Primary production (P) of phytoplankton referred to surface unit in the Siófoki-basin in August 2007, determined with the static field incubation and with the dynamic field incubation system.

**2. táblázat:** A terepi statikus és a terepi dinamikus inkubációval meghatározott, felületegységre vonatkoztatott elsődleges termelés (P) a Siófoki-medencében 2007 augusztusában.

Date	Incubation method	P (mg C m <sup>-2</sup> h <sup>-1</sup> )	±SD
02.08.2007	static field PAR+UV	57	7,59
02.08.2007	dynamic field PAR+UV	59	5,7
09.08.2007	static field PAR+UV	22	3,32
09.08.2007	dynamic field PAR+UV	23	2,36
16.08.2007	static field PAR+UV	31	3,93
16.08.2007	dynamic field PAR+UV	24	4,01



static laboratory incubation ( $P=0.018$ ). This reflects that the exclusion of UV radiation increased the photosynthetic performance of phytoplankton in sunny weather, at high light intensities.

In the course of the second set of measurements (in cloudy weather) the primary production of phytoplankton was  $22 \text{ mg C m}^{-2} \text{ h}^{-1}$  in the case of static field incubation (PAR+UV),  $23 \text{ mg C m}^{-2} \text{ h}^{-1}$  were determined with the dynamic incubation method with UV (PAR+UV) and  $20 \text{ mg C m}^{-2} \text{ h}^{-1}$  with the same dynamic method but with exclusion of UV radiation (PAR only), while in the photosynthetron (PAR only) a primary production of  $30 \text{ mg C m}^{-2} \text{ h}^{-1}$  was registered (tables 1, 2 and 3). These results show that a significantly higher primary production was measured in the photosynthetron, as compared to both types of field experiments ( $P=0.023$  with the static field method and  $P=0.009$  for the dynamic field measurement). In contrast, at lower light intensities no significant difference could be detected between the values of primary production measured with the static and the dynamic field incubation methods.

In the course of the third set of measurements (in high light intensity) the primary production of phytoplankton, referred to surface unit, exhibited the following values:  $31 \text{ mg C m}^{-2} \text{ h}^{-1}$  with the static field incubation (PAR+UV),  $24 \text{ mg C m}^{-2} \text{ h}^{-1}$  with the dynamic incubation method with UV (PAR+UV),  $29 \text{ mg C m}^{-2} \text{ h}^{-1}$  in the dynamic system without UV (with PAR only), and  $36 \text{ mg C m}^{-2} \text{ h}^{-1}$  with the static laboratory method (PAR only)

**Table 3.** Primary production (P) of phytoplankton referred to surface unit in the Siófoki-basin in August 2007, determined with the full spectrum dynamic field incubation system and with UV protected dynamic field incubation.

**3. táblázat:** Terepi dinamikus inkubációval, UV sugárzással, illetve UV sugárzás kizárásával meghatározott, felületegységre vonatkoztatott elsődleges termelés (P) a Siófoki-medencében 2007 augusztusában.

Date	Incubation method	P (mg C m <sup>-2</sup> h <sup>-1</sup> )	±SD
02.08.2007	dynamic field PAR+UV	57	5,7
02.08.2007	dynamic field PAR	72	0,45
09.08.2007	dynamic field PAR+UV	23	2,36
09.08.2007	dynamic field PAR	20	5,53
16.08.2007	dynamic field PAR+UV	24	4,01
16.08.2007	dynamic field PAR	29	0,48

(tables 1, 2 and 3). No significant differences were found neither between the static and the dynamic field incubation, nor between the field and laboratory incubation methods.

Based on the above presented data, one may conclude that the static laboratory incubation system overestimates the primary production of phytoplankton with 10–36% as compared to the static field incubation method, but only when light intensity is high. The laboratory incubation is significantly cheaper and faster than the field incubation, and according to our results it is suitable for the rough estimation of photosynthetic performance of the phytoplankton when no high UV radiation exerts photoinhibition under natural conditions. On the other hand, field incubation is more beneficial for understanding the behavior of the natural algal assemblages in their environment. Static full spectrum dynamic field methods offer similar results concerning the amount of primary production under both high and low light intensities (table 2).

The results of experiments carried out with the exclusion of UV radiation in sunny weather show that the inhibitory effect of UV radiation is present in the case of both static and dynamic field incubation, while in cloudy weather the moderate UV radiation can stimulate the photosynthesis of phytoplankton.

In conclusion, our measurements suggest that there are no significant differences between the results of the field static incubation and of the field dynamic incubation methods applied in determining biomass production of phytoplankton. The dynamic method is cheaper, because it requires less equipment and  $^{14}\text{C}$  isotope. The field dynamic incubation method is the best method for the determination of primary production of phytoplankton, if the purpose of investigations is not the establishment of photosynthesis-light intensity curves. The dynamic incubation equipment developed by us is cheap, reliable, and equally applicable on small and large lakes.

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## **A fitoplankton fotoszintézise három különböző inkubációs technikával vizsgálva**

### **Összefoglalás**

A fitoplankton elsődleges biomassza-termelésének mérésére több különféle módszert alkalmaznak. A módszerek egy része terepi, más részük laboratóriumi inkubációt foglal magába (fotoszintetronban). A terepi inkubáció történhet statikus módszerrel, amikor a vízmintákat rögzítetten, több különböző vízmélységben inkubálják, illetve dinamikus módszerrel, amikor az inkubáló edényeket le-fel mozgatják a vízoszlopban. A terepi és laboratóriumi statikus módszerek legfőbb hátránya, hogy az algák folyamatosan állandó fényintenzitásnak vannak kitéve, míg egy tóban a szél általi vertikális keveredés következtében az algasejtek változó fényviszonyok között folyamatosan mozognak a vízoszlopban (MacIntyre 1993, Maestrini és mtsai. 1993). A tartósan túl erős fény hatására az algák fotoszintézise gátolódik, ezt fotoinhibíciónak nevezzük. Gocke és Lenz (2004) szerint a fitoplanktont alkotó algák rövid ideig (mintegy tíz percig) különösebb károsodás nélkül

képesek hasznosítani az erős fénysugárzást. Természetes körülmények között így a vízoszlopban (vagy a dinamikus inkubáció során az inkubáló edényekben) mozgó algák fel tudják használni fotoszintézisükhöz a felszíni vízrétegekben őket rövidebb ideig érő magas fényintenzitást. Ezzel szemben a statikus inkubáció során a helyhez rögzített algák fotoszintézise gátolódik (Herodek és Tamás 1976, Pálffy és Vörös 2003, Gocke és Lenz 2004), ami magasabb fényintenzitáson az elsődleges termelés jelentős alulbecsléséhez vezet ezekben a rendszerekben (Nixdorf és mtsai. 1990, MacIntyre 1993). Ugyanakkor egy másik fontos tényező az UV sugárzás, mely szintén gátolhatja az algák fotoszintézisét. A laboratóriumi inkubáció során a fotoszintetronban az algákat nem éri a természetben jelenlévő UV sugárzás, ez pedig ugyancsak a primer produkció túlbecsléséhez vezethet laboratóriumi körülmények között. Vizsgálatunk fő célja a fitoplankton fotoszintetikus primer produkciójának meghatározására használt három fő módszer eredményeinek összehasonlítása és kiértékelése, az egyes módszerek fő alkalmazási előnyeinek és hátrányainak alátámasztása. A primer biomassa-produkciót az időegység alatt asszimilált radioaktív szénizotóp mennyisége alapján határoztuk meg,  $\text{NaH}^{14}\text{CO}_3$ -ot alkalmazva szervesetlen szénforrásként. A statikus változatokban meghatároztuk a fotoszintézis fényintenzitás-függését is.

Vizsgálataink során a fotoszintetronban végzett statikus laboratóriumi inkubáció 10–36%-kal felülbecsülte a felületegységre vonatkoztatott elsődleges termelést a terepi statikus inkubációhoz képest, viszont a különbség csak magas fénybesugárzáson volt szignifikáns, amikor a természetben az UV sugárzás is erős. Tekintve, hogy a laboratóriumi inkubáció lényegesen olcsóbb és gyorsabb a helyszíni inkubációnál, eredményeink alapján alkalmas a fitoplankton fotoszintézisének becslésére olyan körülmények között, amikor az erős napsütés nem gátolja a természetes vizek fitoplanktonjának fotoszintézisét. Ellenben a természetes algaegyüttesek viselkedésének megértéséhez a terepi inkubáció előnyösebbnek bizonyult. A terepi statikus és a terepi (az UV sugárzás kizárása nélküli) dinamikus inkubációs módszerek között találtunk szignifikáns különbséget a felületegységre vonatkoztatott elsődleges termelés tekintetében. Az UV sugárzás kizárásával napos időben végzett kísérletek eredményei arra engednek következtetni, hogy sekély tavakban az UV sugárzás gátló hatása nem csak a statikus, hanem a dinamikus inkubáció esetén is érvényesül, ugyanakkor felhős időben a gyenge UV sugárzás serkentőleg hathat az algák fotoszintézisére.

Összefoglalásként elmondhatjuk, hogy nincs statisztikailag szignifikáns különbség a terepi statikus és a terepi dinamikus inkubációs módszerek között. Ezért a terepi dinamikus inkubációs módszer kisebb eszköz- és szénizotóp igénye miatt a legjobb módszer a fitoplankton elsődleges termelésének meghatározására abban az esetben, ha nem célunk a fitoplankton fotoszintézis-fényintenzitás görbéjének felvétele. Az általunk kifejlesztett dinamikus inkubáló berendezés olcsó, megbízható, kis és nagy tavakban egyaránt alkalmazható.