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Garlic Sprouts Grown Indoors at Kitchen Sites

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ABSTRACT

Recently, garlic shoots have been used as vegetable and functional food in additional to the bulbs. In the present research, garlic sprouts were produced from garlic cloves with different sizes. The cloves were grown onto paper towels sprayed with tap water every two days at kitchen sites under room temperature (fluctuated from 6°C in the night to 16°C around midday) or in a growth chamber (25±1/20±1°C, day/night). The final fresh and dry biomass indicated that the tiny cloves could also produce edible sprouts though they were not as strong as those produced by large and medium cloves. Fresh biomass was measured each day until harvest and the data were used for analysis of the dynamic growth of these garlic sprouts by a sigmoid model, $g_G = g_T\{1+(1-\beta t)e^{[-\alpha(t-\tau)]}\}^{(-1)}+g_0(1-\beta t)$. One incidence named as "Biomass Downcast Phenomenon" occurred as shoot fresh biomass sharply declined when the nutrients in the clove were used up at the later growth stages of garlic sprouts. The curve phase of the sharp declining was analyzed using an exponential model, $g_D = g'_T+(g_{max}-g'_T)e^{[-\gamma(t-14)]}$, and the biomass downcast was quantified using definite integral formula, $g_{(\delta)}$ = *1. Leaf photosynthesis was low due to the weak light in kitchen site conditions. It quickly reached light saturation point (LSP) as the photosynthetic phonon flux (PPF) increased to 250 μmol m^{-2} s^{-1}. Photoinhibition occurred once PPF suddenly increased above LSP and it was quantified by definite integral formula, $P_{(i)}$= *2. In conclusion, garlic cloves, even in small size of no marketing value, can be used to produce fresh sprouts with high edible value at kitchen sites. The sprouts should be harvested before the nutrition in the cloves is used up when the so-called "Biomass Downcast Phenomenon" occurs. The mathematical approach adopted in this research for garlic sprout growth is of high reference value to plant scientists.

*1 $\frac{\int_a^b (g_{G(t)} - g_{D(t)})dt}{b-a}$ *2 $\frac{\int_{a'}^{b'} (P_N(i) - P_I(i))di}{b'-a'}$

Keywords: *Allium sativum*, biomass downcast, growth, mathematical approach, modeling, photoinhibition, photosynthesis

INTRODUCTION

Sprouts from seeds of many species are used as vegetables because many valuable functional and nutritive components are developed during germination and sprouting (Park *et al*. 1998; Takaya *et al*. 2003; Mizuno and Yamada 2006). Originally, these sprouts were produced indoors with a home sprouting kit at kitchen sites for family vegetable supplies. Sooner or later, mass production systems were developed in response to the market demand. Recently, concerns on health and food safety increase and lead to admirations to sprout vegetables as functional food (Berry *et al*. 2002). As a consequence, species used in producing sprout vegetables have increased from soybean (Park *et al*. 1998; Kylen *et al*. 2007), mungbean (Funaki *et al*. 1972; Kylen *et al*. 2007; Kavas and Sedef 2008), green onion (Kauwya and Wahab 1984), watercress (Moriyama and Oba 2004) and radish (Takaya *et al*. 2003) to alfalfa (Bhathena and Velasquez 2002; Kylen *et al*. 2007), sunflower (Cho *et al*. 2007), lentil (Urbana *et al*. 1995; Kylen *et al*. 2007; Kavas and Sedef 2008), pea (Urbana *et al*. 2005), buckwheat (Kim *et al*. 2004) and garlic (Park *et al*. 1998). The merits and advantages in indoors production of sprouting vegetables include the opportunity to try several varieties that would enrich dinner tables without being limited to seasonal vegetables, efficient use of the seeds that have lost their economic value on the market, development of a model for a business, organic methods easily performed, and the simple equipment of only a couple of trays or kits instead of a garden. Using sprouts is another way of making vegetables available in the off-season and expected vegetables can be produced to compensate the seasonality and fluctuations in supplies of the same species. As the added advantages, the processing is home based, and the seeds can be stored and sprouted easily during periods when vegetables are scarce. As a functional food, garlic has the highest antioxidant activity among the common vegetables and sprouts based on the fresh weight (Cao *et al*. 1996). Garlic has been used as both food and medicine in many cultures since the old ages. Garlic is claimed to offer protection from cancers (Galeone *et al*. 2006) and prevention of heart disease (Ackermann *et al*. 2001) including atherosclerosis (Berthold and Sudhop 1998), high cholesterol (Berthold *et al*. 1998) and high blood pressure (Pedraza-Chaverrí *et al*. 1998). In addition to the medicinal and functional benefits, the tender sprouts from garlic cloves serve as a fresh culinary and salad, especially the fresh ones made indoors at the kitchen sites. In most cases, germination and sprouting need an appropriate warm temperature to be maintained. However, with the exception, garlic adapts to a broad range of temperature especially at lower temperatures since it is a winter crop in most areas. Nevertheless, because of the larger size, cloves of garlic contain a larger amount of nutrition and are easier to generate strong sprouts compared to species with small seeds. Garlic is one of kitchen gardener's dream crops, as it is planted after other crops are cleared out in winter. Cold weather stimulates garlic cloves to root and sprout (Nei *et al*. 2007). It will quickly develop strong-tasting sprouts, and

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cloves can supply enough nutrients for the young sprouts to grow (Mateljan 2006). The tiny cloves among the normal ones are usually not used for planting and often thrown away as they will not amount to much other than "green garlic". However, tiny cloves might be preferred in kitchen site gardening. If the really miniscule cloves cannot be planted in the field, they can be planted in a moist container in a row fairly close together, and tender fresh sprouts can be harvested for use as spice and salad culinary or for stir-fries. Nevertheless, one problem is that cloves grown in kitchen site conditions without soil and enough light often produce weak and yellow green sprouts or seedlings, which affects the edible values. Considering the above problem, in the present experiment, garlic cloves with different sizes were chosen as seeds for sprouting to make sure whether the miniscule cloves can produce normal sprouting greens in comparison with large and medium cloves under kitchen site conditions. Mathematical models were adopted to analyze the growth dynamics and photosynthetic activities of garlic sprouts.

MATERIALS AND METHODS

Grades of garlic cloves

Individual garlic cloves (*Allium sativum* L. 'Jinxiang No. 1') were separated from bulbs and sorted into seven grades by size indicated as fresh biomass per clove. The seven grades were as follows: Grade 1, 8.27 g; Grade 2, 7.04 g; Grade 3, 5.59 g; Grade 4, 4.28 g; Grade 5, 3.79 g; Grade 6, 2.70 g; and Grade 7, 1.57 g. Cloves in seven grades were further defined into large (Grades 1 and 2), medium (Grades 3 and 4) and small (Grades 5, 6 and 7) cloves on the size basis.

Treatments and planting

Polystyrene plates used in this experiment were 44 cm long, 32.5 cm wide and 7.5 cm high. A layer of white towel, seven layers of gauze and 70 pieces of tissue papers were paved at the bottom of each plate as they could quickly absorb water and maintain moisture for garlic sprouting. Each plate was divided into two parts that were served as treatment repeats, and three plates repeated for each treatment. Cloves with the same grade were placed closely in one row (**Fig. 1**) and the plates were left open. The number of cloves in each row was different because of the different sizes in each grade. In Grade 1, 10 cloves were grown per row; Grade 2, 11 cloves per row; Grade 3, 12 cloves per row; Grade 4, 13 cloves per row; Grade 5, 14 cloves per row; Grade 6, 17 cloves per row; and Grade 7, 20 cloves per row. Tap water of 500 ml was sprayed every two days to each plate to ensure the water supply to garlic sprouts. Two temperature regimes were adopted in room (fluctuated from 6°C in the night to 16°C around midday) and chamber (25±1/20±1°C, day/night) conditions, respectively. There was no additive illumination supplement. The lighting condition in both room and chamber was 0-15 μmol m^{-2} s^{-1} as the natural light changed during day and night.

Fig. 1 Garlic cloves grown in plates at kitchen sites (taken on planting day).

Analyses of sprout growth and biomass dynamics

Five garlic sprouts of each grade were sampled everyday until Day 28 for measurements of the fresh biomass. The final fresh and dry masses of seven grades were recorded on harvest day (Day 18 in chamber conditions and Day 28 in room conditions). As the whole fresh garlic sprout can be used edible, data of the total fresh biomass were used for the analysis of growth. A mathematical approach was adopted to the analysis of biomass accumulation of during sprouting and growing of the garlic sprouts.

Measurement and analysis of photosynthesis

Photosynthesis was measured for and compared between sprouts from the large and small cloves. Photosynthesis in the fully expanded leaves of the garlic sprouts was measured using Li-6400 Portable Photosynthesis System (LI-COR Inc. Lincoln, Nebraska, USA) on harvest day. Mathematic approaches were adopted to analyses of the photosynthesis and photoinhibition in response to increasing light intensity.

RESULTS AND DISCUSSION

Sprout growth and biomass dynamics

The final increment in fresh and dry biomass of garlic sprouts indicated that nutrients stored in garlic cloves could support the growth of cloves into edible sprouts when there was only water supplied and no other substrate or nutrient solution added. Although the final increment in fresh and dry masses in the same grade showed no significant difference between the room and the chamber conditions (**Table 1**), high temperature advanced garlic sprouts to reach edible state at maximum biomass 10 days earlier. In the present study, low temperature in room conditions delayed the growth and it cost 28 days to reach the maximum biomass in edible status. The final biomass was significant different among seven grades. It was far less in small cloves than in larger ones (**Table 1**). However, most importantly, even the tiny cloves of Grade 7 could also produce sprouts in good shape though they were not as strong as those produced by large and medium cloves.

Table 1 The final fresh and dry biomass (g $sprout^{-1}$) of garlic sprouts under room and chamber conditions.

Grade	Room (Day 28)			Chamber (Day 18)		
		Final increment			Final increment	
	Final FM	Fresh	Dry	Final FM	Fresh	Dry
1	11.23 aA	4.05 aA	0.76 aA	11.73 aA	4.06 aA	0.76 aA
2	8.73 bB	3.02 aAB	0.48 bB	9.82 bB	3.77 aAB	0.60 bB
3	9.10 bB	3.69 bB	0.56 bB	8.54 cC	3.23 bB	0.49 cC
4	6.60 cC	1.91 cC	0.33 cC	6.46 dD	2.39 cC	0.41 dCD
5	5.25 dD	1.97 cC	0.33 cC	5.56 eE	2.39 cC	0.39 dD
6	3.77 eE	1.52 cCD	0.25 cCD	3.42 fF	1.15 dD	0.19 eE
7	2.32 fF	0.87 dD	0.14 dD	2.14 gG	0.68 eD	0.11 fE
Condition	ns	ns	ns	ns	ns	ns
Grade	**	**	**	**	**	**
Condition×Grade	*	*	*	*	*	*

*, P≤0.05; **, P≤0.01; and ns, no significant difference according to ANVOA.
Different letters show significant differences at P≤0.05 and P≤0.01 according to LSD test.

Table 2 Parameters of the sigmoid growth curves of garlic sprouts from cloves in different sizes under cold room and warm chamber conditions.

Condition	Grade	g_T (g)	β ($\times 10^{-3}$ day^{-1})	α (day^{-1})	τ (day)	g_0 (g)
Room	1	4.76 ± 0.26	-10.22 ± 1.27	0.44 ± 0.06	8.88 ± 0.24	7.43 ± 0.05
	2	3.67 ± 0.23	-8.81 ± 1.87	0.57 ± 0.09	8.76 ± 0.24	5.81 ± 0.06
	3	3.04 ± 0.24	-1.84 ± 1.76	0.47 ± 0.04	8.48 ± 0.17	5.10 ± 0.06
	4	2.70 ± 0.32	1.77 ± 2.74	0.36 ± 0.04	8.62 ± 0.25	3.82 ± 0.08
	5	2.31 ± 0.26	-0.03 ± 2.64	0.38 ± 0.05	7.65 ± 0.26	3.18 ± 0.08
	6	1.39 ± 0.55	38.65 ± 16.78	0.13 ± 0.05	10.36 ± 0.79	1.43 ± 0.02
	7	0.58 ± 0.09	-5.08 ± 2.28	0.14 ± 0.08	8.73 ± 0.31	1.13 ± 0.31
Chamber	1	5.01 ± 0.75	0.67 ± 4.06	0.45 ± 0.07	9.96 ± 0.24	7.63 ± 0.10
	2	4.26 ± 0.81	2.84 ± 4.99	0.34 ± 0.07	9.82 ± 0.32	6.27 ± 0.11
	3	3.62 ± 0.60	1.37 ± 4.41	0.43 ± 0.07	9.70 ± 0.28	5.51 ± 0.08
	4	3.27 ± 0.81	4.29 ± 7.07	0.33 ± 0.08	8.22 ± 0.50	3.88 ± 0.21
	5	3.83 ± 1.44	11.47 ± 79.63	0.23 ± 0.08	8.42 ± 0.84	2.98 ± 0.45
	6	2.40 ± 1.24	3.84 ± 19.59	0.26 ± 0.13	7.48 ± 1.02	1.82 ± 0.41
	7	1.30 ± 0.66	3.31 ± 13.09	0.21 ± 0.09	5.83 ± 1.05	1.76 ± 0.48

Dynamic of sprout growth and biomass downcast

The dynamic changes of the fresh biomass during the sprout growth were analyzed using a sigmoid model as follows:

$$g_G = g_T\{1+(1-\beta t)e^{[-\alpha(t-\tau)]}\}^{(-1)}+g_0(1-\beta t).$$

Here, g_T is the total increment in fresh biomass by growth; g_0 is the original fresh biomass of the clove; β is constant associated with other factors than the growth; α is constant associated with the fast growth; τ is the time point for the biomass increase to reach the half maximum; and t is the growth time (day) (Xu *et al*. 2000).

The fresh biomass of sprouts declined sharply at later growth stage as the nutrients stored in cloves were used up. This incidence was named as "Biomass Downcast Phenomenon". The curve phase of the sharp declining was analyzed by an exponential model as follows:

$$g_D = g'_T+(g_{max}-g'_T)e^{[-\gamma(t-14)]}.$$

Here, g'_T is the total fresh biomass decrement in the biomass downcast; g_{max} is the maximum fresh biomass before it begins to decline; γ is the time constant; and t is the growth time (day).

The biomass downcast was quantified using definite integral formula:

$$g_{(\delta)} = \frac{\int_a^b (g_G(t) - g_D(t))dt}{b-a},$$

where $g_{(\delta)}$ is the average fresh biomass decrement due to biomass downcast; integral interval from a to b is from 14 to 26; g_G (t) is the sigmoid growth curve and g_D (t) is the exponential decline curve; and the right side of the equation is the difference (Δ-integral area) between g_G (t) and g_D (t).

Although the growth curves showed some distinction among the seven grades, garlic spouts of each grade grew in a manner of exponential dynamic (**Fig. 2**). The rapid growth started mainly on Day 8 or Day 9 (shown by the parameter τ). α is proportional to the fast growth of the sprouts. The bigger the α value, the faster the growth. The value of α in small cloves was much lower than that in large and medium cloves (**Table 2**), which indicated the slower growth in smaller cloves.

Fresh biomass accumulation of garlic sprouts under room conditions declined and even sharply decreased at the later growth stages. This sharp decrease in fresh biomass was more obvious under chamber condition with the higher temperature regime (25±1/20±1°C, day/night) (**Fig. 3**). The sudden decrease in fresh biomass, the phenomenon called "biomass downcast", began on day 14 when the fresh biomass reached the maximum, and before that time the growth followed the sigmoid model.

Although higher temperature promoted the growth of garlic sprouts and shortened the time for sprouts to reach harvestable status, nutrients stored in cloves were depleted quickly as the growth of garlic sprouts progressed. Furthermore, photosynthate at the low light conditions was hard to supplement the depletion by respiration and it was the high respiration that resulted in an amazingly fast growth at the middle stage (**Fig. 4**). High temperature accelerated respira-

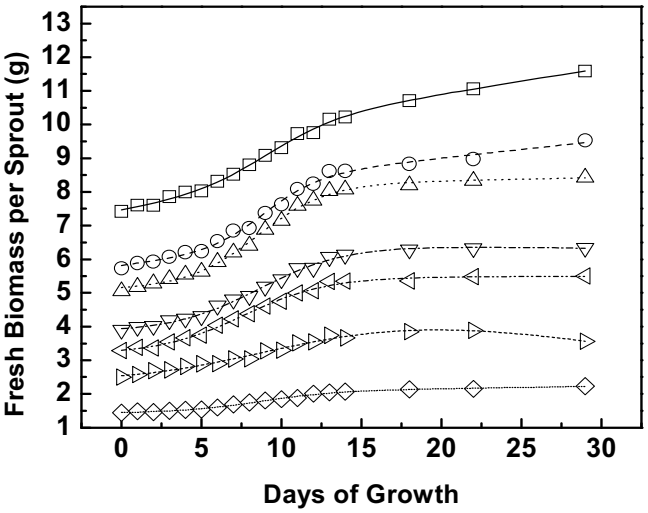

Fig. 2 Sigmoid growth curves for garlic sprouts from cloves in seven different sizes under cold room condition. From the top down: Grades 1, 2, 3, 4, 5, 6 and 7.

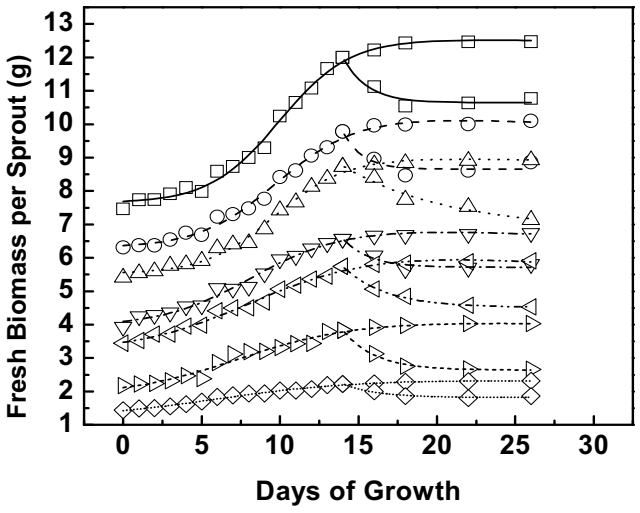

Fig. 3 Sigmoid growth curves for garlic sprouts from cloves in seven different sizes under warm chamber conditions. From the top down: Grades 1, 2, 3, 4, 5, 6 and 7. The last four data (on day 16, 18, 22 and 26) in the upper part of each curve were analog data according to the sigmoid growth curves from day 0 to day 14, and the four data in the lower part of each curve were the real data that followed exponential declining curves.

Table 3 Parameters of the growth declining curves of garlic sprouts under chamber condition from day 14 to day 26.

Grade	g'_T (g)	g_{max} (g)	γ (day^{-1})	Biomass downcast*	$g_{(\delta)}$ (g)
1	10.64 ± 0.13	12.01 ± 0.18	0.65 ± 0.29	18.99	1.58
2	8.66 ± 0.15	9.79 ± 0.23	0.84 ± 0.65	14.92	1.24
3	6.85 ± 0.50	8.75 ± 0.15	0.15 ± 0.08	13.75	1.15
4	5.72 ± 0.10	0.58 ± 0.14	0.60 ± 0.30	10.52	0.88
5	4.52 ± 0.03	5.74 ± 0.04	0.37 ± 0.04	12.90	1.07
6	2.64 ± 0.04	3.83 ± 0.05	0.49 ± 0.06	13.60	1.34
7	1.82 ± 0.03	2.22 ± 0.04	0.47 ± 0.15	4.70	0.39

Table 4 Photosynthetic capacity (P_C), quantum yield (Y_Q) and dark respiration rate (R_D) of garlic sprouts under different environment conditions.

Condition	Size	P_C (μmol m^{-2} s^{-1})	R_D (μmol m^{-2} s^{-1})	Y_Q (mol mol^{-1})
Room	Large	6.39	0.62	0.025
	Small	5.76	2.13	0.030
Chamber	Large	5.20 ± 0.43	3.92 ± 0.36	0.013 ± 0.000
	Small	5.13 ± 0.66	4.55 ± 0.56	0.017 ± 0.001

Fig. 4 garlic sprouts grown under cold room (left) and chamber (right) conditions at later growth stage (taken on day 26).

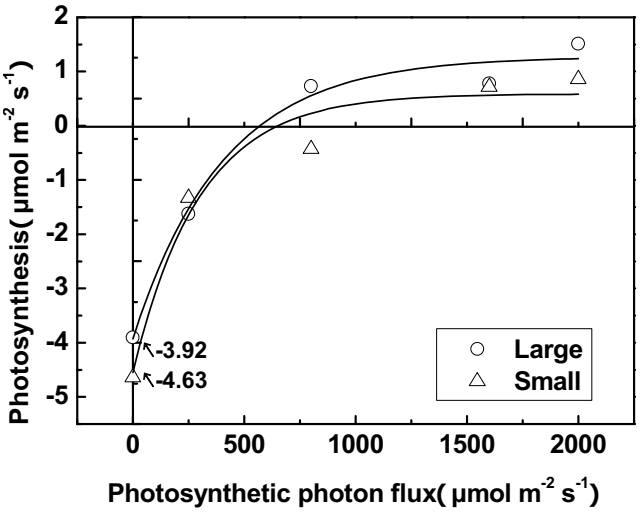

Fig. 5 The response curves of photosynthetic rate to the increasing *PPF* for garlic sprouts grown under warm chamber conditions. The intersection points that the curves crossed with Y-axis were respiration rate (R_D).

tory depletion during the later growth periods (**Fig. 5**). That was why the biomass downcast occurred to a larger extent in the chamber conditions. Larger cloves produced thicker and stronger sprouts in which the respiration (respiration rate × leaf area) was higher than that in thinner and weaker sprouts. The values of biomass downcast* and the average fresh biomass decrement ($g_{(\delta)}$) were high in large and medium garlic sprouts, and only 4.70 in biomass downcast and 0.39 in $g_{(\delta)}$ in the sprouts produced by miniscule cloves (Grade 7) (**Table 3**). Biomass downcast was the main reason for nutrition loss of garlic sprouts. Therefore, growing garlic sprouts in kitchen site conditions should avoid the occurrence of biomass downcast and garlic sprouts that have reached edible status should be harvested in time before the biomass downcast occurs.

* $\int_a^b (g_G(t) - g_D(t))dt$

Photosynthesis and photoinhibition

The response curves of photosynthetic rate to the increasing photosynthetic photon flux (*PPF*) were analyzed using an exponential equation:

$$P_N = P_C (1\text{-}e^{-Ki})\text{-}R_D.$$

Here, P_N is the net photosynthetic rate; P_C is the maximum gross photosynthetic capacity; R_D is dark respiration rate; K is a constant, equivalent to the reciprocal of the *PPF* at which P_N reaches 63% of P_C; and i is the *PPF* and the maximum quantum yield was shown as $Y_Q = KP_C$ (Togari 1973; Steven 1998; Xu 2000).

Photosynthetic rate in leaves of garlic sprouts was low as a result of the weak light in room conditions (**Figs. 5, 6; Table 4**). Another photosynthetic phenomenon called photoinhibition was observed in garlic sprouts grown under room conditions in the present study. The curve phase of the fast declining by photoinhibition was analyzed using an exponential formula:

$$P_I = P_0 + P_D\, e^{\alpha'(i\text{-}250)}.$$

Here, in large cloves P_0 is the maximum photosynthetic rate before photosynthesis begins to decline, and in small cloves P_0 is the minimum photosynthetic rate after photoinhibition; P_D is the decreased photosynthesis and α' is a constant (Xu *et al*. 2000).

The photoinhibition was quantified using a definite integral formula:

$$P_{(i)} = \frac{\int_{a'}^{b'} (P_N(i) - P_I(i))di}{b' - a'},$$

where P_N (i) is the photosynthetic light response curve that would be without photoinhibition and P_I (i) is the curve of photoinhibition; integral interval from a' to b' was from 250 to 2000 μmol m^{-2} s^{-1};

$$\int_{a'}^{b'} (P_N(i) - P_I(i))di$$

is the difference (Δ-integral area) between P_N (i) and P_I (i).

Photosynthetic capacities of garlic sprouts were low because there was lack of enough light in both the room and chamber conditions. Photosynthesis in the sprouts grown under room conditions quickly reached the light saturation point as the phonon flux increased to 250 μmol m^{-2} s^{-1} (**Fig. 6**). Photoinhibition, the reduction in a plant's capacity for photosynthesis, is often caused by exposure to strong light that is above the saturation point (Noam *et al.* 2003). In the present study, low lighting, deficiency of nutrients and the low temperature under room conditions together resulted in the serious photoinhibition phenomenon once the *PPF* suddenly increased to a level above 250 μmol m^{-2} s^{-1}. In addition, photoinhibition in small cloves was greater than that

Table 5 Parameters and definite integral showing the characteristics of photosynthetic declining caused by photoinhibition in garlic sprouts under cold room conditions.

Size	P_0	P_D	$P_{(i)}$	$\int_{a'}^{b'}(P_N(i)-P_l(i))di$	α' (μmol^{-1} m^2 s)
	μmol m^{-2} s^{-1}				
Large	3.37	-0.029	1.91	3349.76	0.0023
Small	0.53	1.48	2.20	3847.99	-0.0035

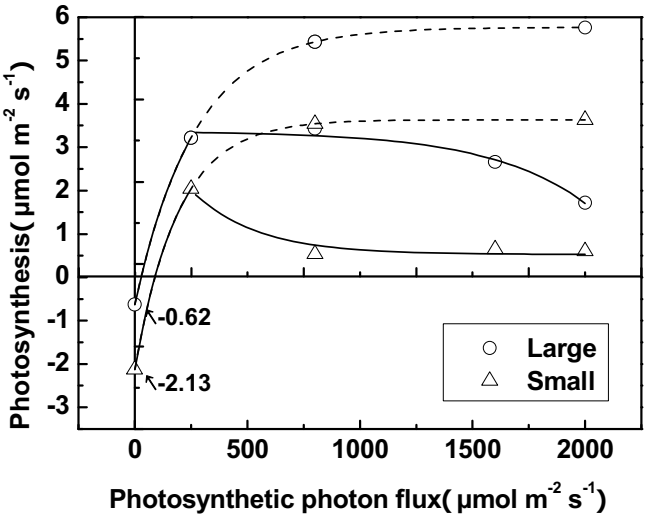

Fig. 6 The response curves of photosynthetic rate to the increasing *PPF* for garlic sprouts grown in cold room conditions. The dash parts of the curves were modeling curves without photoinhibition. The solid lines show the real photosynthetic declining caused by photoinhibition as *PPF* increased. The intersection points that the curves crossed with Y-axis were respiration rate (R_D).

in large cloves (data of $P_{(i)}$, **Table 5**). The possible reasons might be the high respiration rate (2.13 μmol m^{-2} s^{-1}) and low clove nutrition supply in thin sprouts produced by small cloves. Although the photosynthetic capacity was low in garlic sprouts grown under chamber conditions, photoinhibition did not exist because the sprouts adapted to the high temperature that might be associated with high light (**Fig. 5**).

CONCLUSIONS

The experiment confirmed that tiny cloves of garlic without seed and marketable values could be used to produce garlic sprouts in good shape. Warm temperatures by heating systems and supplemental lighting were not necessary for garlic production and the sprouting could be performed even under the cold room conditions. Sprouts should be harvested before the stored nutrition in the cloves was used up when the so-called "biomass downcast" might occur. In the present study, mathematical methods were used to model and analyze the dynamics of growth and biomass accumulation in the garlic sprouts. The equations and the analytical methodology are valuable in reference to plant scientific research.

One who grows garlic sprouts in the kitchen site conditions should be advised as follows: 1) garlic sprouts need light even in weak status in the room conditions; 2) temperature should be not high in avoidance of excessive growth; and 3) harvest at optimum edible stage. In this experiment, Day 26-28 was the best harvest time for garlic sprouts grown under cold room conditions, and Day 14 for sprouts grown in the chamber under 25±1/20±1°C (day/night) because of the biomass downcast. Although the illumination was low in room conditions and consequently resulted in a weak photosynthetic activity, the sprouts developed leaves in good shape and normal green in the cold room conditions. At least, light was needed for the cholorophyll formation in the sprout leaves, no matter how much the photosynthate contributed to the biomass in addition to the contribution from the nutrition supplied by cloves as the main sources. In case of large cloves are not available or at high cost, tiny cloves can also produce sprouts in good shape and the thinner and shorter size do not affect the edible value.

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List of symbols and abbreviations used in this study

Symbol	Unit	Definition
LSP		Light saturation point
PPF	μmol m^{-2} s^{-1}	Photosynthetic photon flux
g_G	g	Fresh biomass at a given growth time
g_T	g	Total increment in fresh biomass
g_0	g	Original fresh biomass of the clove
α	day^{-1}	Constant associated with the fast growth
β		Constant associated with other factors than growth
τ	day	Time point for the biomass increment to reach the half maximum
t	day	Variable of growth time
g_D	g	Biomass at a given time during the biomass downcast
g'_T	g	Total fresh biomass decrement in the biomass downcast
g_{max}	g	Maximum fresh biomass before the biomass downcast
γ		Constant associated with biomass declining in biomass downcast
$g_{(\delta)}$	g	Quantity of the average biomass decrement due to biomass downcast
$g_G(t)$	g	Sigmoid growth curve
$g_D(t)$	g	Exponential biomass declining curve
P_N	μmol m^{-2} s^{-1}	Net photosynthetic rate
P_C	μmol m^{-2} s^{-1}	Maximum gross photosynthetic capacity
R_D	μmol m^{-2} s^{-1}	Dark respiration rate
K	m^2 s μmol^{-1}	Constant for photosynthetic light response curve, equivalent to the reciprocal of the *PPF* at which P_N reaches 63% of P_C
i	μmol m^{-2} s^{-1}	Variable of photosynthetic photon flux
Y_Q	mol mol^{-1}	Maximum quantum yield shown as $Y_Q = KP_C$
P_I	μmol m^{-2} s^{-1}	Photosynthetic rate at a given *PPF* during photoinhibition
P_0	μmol m^{-2} s^{-1}	Photosynthetic rate before or after photosynthesis begins to decline due to photoinhibition
P_D	μmol m^{-2} s^{-1}	Maximum decrement in photosynthesis due to photoinhibition
α'	μmol^{-1} m^2 s	Constant associated with photoinhibition
$P_{(i)}$	μmol m^{-2} s^{-1}	Quantity of the average photosynthesis decrement due to photoinhibition
$P_N(i)$		Photosynthetic light response curve that would be without photoinhibition
$P_I(i)$		Curve of photoinhibition