Mathematical study of the effects of temperature and humidity on the morphological development of Pleurotus eryngiiafruit body

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Abstract. The king oyster mushroom (*Pleurotus eryngii*) is one of the most popular mushrooms in Asia, Europe and North America. Its growth is influenced by environmental conditions, particularly air temperature and humidity. Using traditional methods of cultivation in plastic greenhouses, P. eryngii can be grown only in spring and autumn. However, mass cultivation using modern commercial methods is unrestricted by season, but precise environmental control is crucial, as the process is costly and a high energy consumption. Through experimentation and analysis of the effects of variations in air temperature and relative air humidity on morphological development, a mathematical model for these effects was developed. This model can be used to predict the optimal ranges of air temperature and humidity for various indices of morphological development of the fruiting body, and to guide commercial production. Using the model, standard values of morphological development, optimal environmental control ranges for each day of the fruiting body growth period were calculated. These values provide a reference suitable for application to actual production.

Key words: Fruit body; morphology; air temperature; relative humidity; mathematical model; Pleurotus eryngii.

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1 Introduction

Mushrooms are known for their nutritional and medicinal value, and the diversity of their bioactive components[1]. These organisms have long been valued as highly tasty and nutritious foods by many societies throughout the world. Among the edible mushrooms, the king oyster mushroom (*Pleurotus eryngii*) is one of the most popular in Asia, Europe and North America[2]. P. eryngii has several bioactive components, such as β-glucan[3] and ribonuclease[4] , which have been isolated from the fruiting bodies of edible mushrooms. However, the fresh fruiting bodies are mainly used as a food sources. In Japan, production increased from 60 t in 1995 to over 29,000 t in 2003[5]. Even greater increases in production have occurred in China, where commercial production began in the late 1990s. Chinese growers produced an estimated 7300 t in 2001, and 114,100 t in 2003[6-7]. In the US, commercial production began in 2000 and has reached 85 t by 2004[8].

As a commodity, the ideal morphology of the *P. eryngii* fruit body is generally columniform. The cap is smaller than that of the natural state, and can even be smaller than the stipe. Air environment seems to be very important for induction of fruiting body formation. The appropriate air environment is not only crucial for production, but also influences the ideal morphology. When air temperature and humidity are lower than optimal, the fruiting body does not growth, and can even wilt and die. Conversely, when air temperature and humidity are higher than optimal, the fruiting body grows quickly, but a higher proportion of anamorphic fruiting body.

Most studies focusing on the relationship between fungal growth and air environment have been qualitative, because of the large range of the environmental control variables in conditions of traditional cultivation in plastic greenhouses. In modern methods of mass commercial cultivation of *P. eryngii*, air environment is monitored through air temperature and relative humidity probes placed in the cultivation room. Air temperature and humidity are then adjusted in real time through air conditioning, humidifiers and fans controlled by a dedicated computer. Environmental control is thus very precise. Accurate environmental control can reduce the overall costs through increased yield.

The objective of this research, therefore, was to analyze the effect of different air temperatures and relative humidity on the morphological growth of the *P. eryngii* fruiting body, through experimental methods. A mathematical model for the effects of air temperature and humidity on growth was then established. Using the model, the

appropriate environmental ranges for morphological growth of *P. eryngii* in commercial production were obtained. Finally, the model could make useful predictions about air environment variables to guide environmental control in the commercial production of *P. eryngii*.

2 Materials and methods

2.1 Experiments

In this study, the air climate control in the growing rooms was designed and manufactured by Patron AEM; temperature, humidity and CO_2 concentrations in the growing rooms could be controlled very precisely and efficiently. There were two treatments. The first was with air temperatures of 14 ℃, 15 ℃, 16 ℃, 17 ℃ and 18 ℃. The second was with relative humidity of 89%, 91%, 93%, 95% and 97%. The intensity of illumination in the growing room was 500-1000Lx. The experiment was a 2 (supplement) × 5 (treatment) design with three replicates per treatment. Morphological growth indicators were measured daily (every 24 h), with 8 bottles for each experiment. Each value is the mean of 24 measured results (3 replicates × 8 bottles).

The morphological growth is characterized by three indicators: first, cap diameter, which reflects the size of the circular cap of fruiting body; second, stipe diameter, which is measured at the base and reflects the approximate size of the columniform stipe of the fruiting body; and third, stipe height, which is measured from the base of the stipe to the cap. Each day, two or three of the bigger fruit bodies in each cultivated bottle of eight examples were measured by vernier caliper.

2.2 Model validation

To validate the model the three morphological growth indicators described above were computed with the model and then compared with field data. The following three indices were computed under two situations to assess the closeness of the estimated data to the measured values: correlation coefficient (*R*), bias (*Bias*)[9], root mean square error (*RMSE*)[10], and the percent root mean square error (*%RMSE*)[11].

$$Bias = \frac{1}{n} \sum |OBS_i - SIM_i|$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(OBS_i - SIM_i)^2}{n}}$$

$$\%RMSE = RMSE \times 100/(\frac{1}{n}\sum OBS_i)$$

OBS_i and SIM_i are the measured and simulated value, respectively, for the ith data point of n observations.

3 Results

During the growth period of the fruiting body, the three morphological growth indices of *P. eryngii* showed significant changes over different days (Table 1). We found that the optimal air temperature and humidity facilitated cap expansion, stipe heightening and thickening. For any single growth indicator, the optimal air temperature and humidity was different on each day (Table 2). Multiple statistical comparisons (Table 2) showed that over five days of growth, the optimal air temperature was 16 ℃, 17 ℃ and 18 ℃ in the first three days, and 17 ℃ or 18 ℃, and 16 ℃ for the last two days. Variation in air relative humidity over a range of 89–97% did not significantly affect morphological growth of the fruiting body in these experiments (Table 2), but comparatively, the optimum relative humidity was 97%, followed by 95% and 93%.

Table 1. The values of morphological growth indices of *P. eryngii* on each day.

Time/d Indices	1	2	3	4	5
Cap diameter	0.729 [a]	1.164 [b]	1.890 [c]	2.922 [d]	4.041 [e]
Stipe height	1.540 [a]	2.415 [b]	3.608 [c]	4.774 [d]	5.825 [e]
Stipe diameter	1.170 [a]	1.433 [b]	1.881 [c]	2.347 [d]	2.639 [e]

*The value of each index was each day's mean growth for both treatments. Different letters indicate statistically different values (ANOVA/LSD) (P<0.05).

Table 2. The multiple comparisons result showing the influence of different air temperatures and relative humidity levels on morphological growth of the fruiting body of *P. eryngii* on each day.

	Time/d	Cap diameter	Stipe height	Stipe diameter
Air temperature treatment	1	18℃,17℃,16℃	16℃,17℃,18℃	16℃,18℃,17℃
	2	17℃,16℃,18℃	16℃,17℃,18℃	17℃,18℃,16℃
	3	17℃,18℃	18℃,16℃	16℃,18℃,17℃
	4	17℃	18℃	16℃,18℃
	5	17℃	18℃	16℃
Air relative humidity treatment	1	97%,95%,91%	93%,89%,95%	97%,95%,89%
	2	97%,95%,91%	93%,97%,91%	93%,91%,97%
	3	97%,89%,93%	93%,97%,89%	93%,89%,91%
	4	93%,97%,89%	97%,93%,89%	97%,93%,89%
	5	97%,91%	97%,93%,91%	97%,93%

*The relative humidity/temperature was not considered in the air temperature/relative humidity treatment, and the effect of air temperature/relative humidity was analyzed on morphological growth.

*The former three air temperature and relative humidity conditions that showed no differences between them were listed in the table.

There is complexity and uncertainty in biological growth and *P. eryngii* is no exception. The optimal air temperature is independent of optimal relative humidity. For example, the optimum air temperature for stipe heightening is 18℃, but at that temperature, 93% is not the only optimum relative humidity. Therefore, it is necessary to further analyze and confirm the optimal air environment.

The optimal air temperature for cap expansion is 17℃ (Table 3) under relative humidity conditions of 93–97% analyzed above. The optimal relative humidity for cap expansion is dependent on temperature (Table 3): 97% at 16℃ and 18℃, and 91–97% at 17℃. So the optimal air temperature and relative humidity conditions for cap expansion are 17℃ and 97% respectively.

Under better relative humidity conditions of 93–97%, the optimal air temperature for stipe heightening is 18℃ at 93% and 97% relative humidity, and is 17℃ and 18℃ at 95% relative humidity. The optimal relative humidity for stipe heightening is also dependent on temperature (Table 3): 97% at 16℃; 91%, 95% and 97% at 17℃; 93% and 97% at 18℃. So the optimal air temperature and relative humidity conditions for

stipe heightening is 18 ℃ and 97% relative humidity.

Under better relative humidity conditions of 93–97%, the optimal air temperature for stipe thickening are 16 ℃ and 17 ℃ at 95% and 97%, 16 ℃ and 18 ℃ at 93% relative humidity. The optimal relative humidity for stipe thickening is also dependent on temperature (Table 3): 93% and 97% at 16 ℃; 91%–95% at 17 ℃; 97% at 18 ℃. So the optimal air temperature and relative humidity conditions for stipe thickening is 16 ℃ and 93% relative humidity.

Table 3. The results of multiple comparisons of influence of different air relative humidity/temperature treatment on fruiting body growth under specific air temperature/relative humidity conditions.

	#1	16 ℃	17 ℃	18 ℃	#2	91%	93%	95%	97%
Cap diameter	93%		√		16 ℃				√
	95%		√		17 ℃	√	√	√	√
	97%		√		18 ℃				√
Stipe height	93%			√	16 ℃				√
	95%		√	√	17 ℃	√		√	√
	97%			√	18 ℃		√		√
Stipe diameter	93%	√		√	16 ℃		√		√
	95%	√	√		17 ℃	√	√	√	
	97%	√	√		18 ℃				√

#1 the optimum air temperature in temperature treatment under specific air relative humidity condition; #2 the optimum air relative humidity in humidity treatment under specific air temperature condition. The air relative humidity/air temperature conditions that no difference for the morphology growth were marked by the symbol " √ ".

Through comprehensive analysis of the data, we believe that the optimal air temperature and relative humidity conditions for morphological development of the fruiting body in the growing room is 16–18 ℃ at a relative humidity of 93% and above. On different days, the optimal air temperature and relative humidity conditions for morphological development of the fruiting body are slightly different. In the appropriate range, lower air temperature and relative humidity are better for stipe thickening, higher air temperature and relative humidity are better for stipe heightening.

4 Model description

4.1 The morphological development simulation model

4.1.1 Effects of air temperature on morphology development (ETMD) sub-model

From the experimental results, the relationships between air temperature and cap diameter, or stipe diameter were single-peak curves; the relationship between air temperature and height of the stipe was a single-peak curve on the first day, and linear on the other days. Mathematically, the effects of air temperature on morphological development of the fruiting body can be presented as follows:

$$D_{JG} = a_{11} \cdot T^2 + b_{11} \cdot T + c_{11} \tag{1}$$

$$L_{JB} = \begin{cases} a_{21} \cdot T^2 + b_{21} \cdot T + c_{21} & t = 1 \\ u_1 \cdot T + k_1 & t > 1 \end{cases} \tag{2}$$

$$D_{JB} = a_{31} \cdot T^2 + b_{31} \cdot T + c_{31} \tag{3}$$

where D_{JG} is cap diameter, L_{JB} is stipe height, D_{JB} is stipe diameter, T is air temperature (14 –18 ℃), a_{11}, b_{11}, c_{11}, a_{21}, b_{21}, c_{21}, a_{31}, b_{31}, c_{31}, u_1 and k_1 are parameters, t is time (1–5 days).

With values of T, D_{JG}, L_{JB} and D_{JB} measured experimentally, a_{11}, b_{11}, c_{11}, a_{21}, b_{21}, c_{21}, a_{31}, b_{31}, c_{31}, u_1 and k_1 were estimated through the nonlinear least squares method using *Statistica* 6.0. Because of the small effect of humidity observed experimentally on morphological development of the fruiting body, humidity was not considered in the parameters estimated. As there were substantial differences in the three growth indicators and temperature on different days of the fruiting body growth period, the parameters were estimated separately for each day (see Table 4) over five days.

Table 4. Estimated parameters in Eqs. (1) – (3)

Time/d	a_{11}	b_{11}	c_{11}	a_{21}	b_{21}/u_1	c_{21}/k_1	a_{31}	b_{31}	c_{31}
1	-0.02	0.76	-5.84	-0.03	0.87	-5.69	0.02	-0.56	4.69
2	-0.03	1.10	-8.74		0.27	-1.93	-0.02	0.80	-6.02
3	-0.03	1.25	-9.81		0.42	-3.02	0.02	-0.40	3.68
4	-0.04	1.49	-10.73		0.47	-2.64	0.02	-0.50	4.78
5	-0.22	7.11	-52.11		0.46	-1.57	0.06	-1.78	16.08

4.1.2 Effects of relative humidity on morphological development (EHMD) sub-model

Although there was not significant observed effect of varying relative humidity on morphological development, air humidity is almost certainly an important environmental factor for the production of *P. eryngii*. Therefore the mathematical relationship between air humidity and morphological development was also simulated. From the results, the optimal air temperature for *P. eryngii* is 16 ℃ and above. At temperatures of 16 ℃ and higher, the morphological development of the fruiting body has the following mathematical relationship with relative humidity:

$$D_{JG} = a_{12} \cdot H^2 + b_{12} \cdot H + c_{12} \qquad (4)$$

$$L_{JB} = u_2 \cdot H + k_2 \qquad (5)$$

$$D_{JB} = a_{32} \cdot H^2 + b_{32} \cdot H + c_{32} \qquad (6)$$

in which H is relative humidity (89–97%), a_{12}, b_{12}, c_{12}, a_{32}, b_{32}, c_{32}, u_2 and k_2 are parameters.

With the experimentally measured H, D_{JG}, L_{JB} and D_{JB}, a_{12}, b_{12}, c_{12}, a_{32}, b_{32}, c_{32}, u_2 and k_2 were estimated using the same method as for the parameters in Eqs. (1) – (3). As there were substantial differences of morphological development indices on different days of fruiting body growth period, the parameters were estimated separately for each day (see Table 5) over five days.

Table 5. Estimated parameters in Eqs. (4) – (6)

Time/d	a_{12}	b_{12}	c_{12}	a_{32}	b_{32}	c_{32}	u_2	k_2
1	-0.004	0.66	-29.74	-0.001	0.10	-3.26	0.01	0.44
2	-0.01	1.78	-81.63	-0.002	0.40	-17.12	0.09	-5.65
3	-0.0003	0.05	-0.69	-0.002	0.43	-17.81	0.10	-4.74
4	-0.005	0.94	-40.78	-0.001	0.10	-2.39	0.12	-6.23
5	-0.02	3.68	-166.35	0.004	-0.69	34.34	0.09	-2.41

4.2 Validation of the morphological development simulation model

The morphological development simulation model was validated by assessing the correlation coefficient (*R*), bias (*Bias*), root mean square error (*RMSE*) and the

percent root mean square error (*%RMSE*) for the measured and estimated values. The detailed results are shown in Table 6.

From the mathematical model, the effect of air temperature gave the following results: *R, Bias*, *RMSE* and *%RMSE* were 88.6%, 0.325 cm, 0.335 and 13.42%, respectively, for cap diameter (Eq.1); 93.7%, 0.226 cm, 0.305 and 8.40%, respectively, for stipe height (Eq.2); and 92.6%, 0.173 cm, 0.213 and 10.09%, respectively, for stipe diameter (Eq.3).

The effect of relative humidity resulted in the following:R, Bias, RMSE and %RMSE were 85.4%, 0.350 cm, 0.396 and 17.42%, respectively, for cap diameter (Eq.4); 91.7%, 0.297 cm, 0.392 and 9.84%, respectively, for stipe height (Eq.5); 93.4%, 0.237 cm, 0.276 and 19.97%, respectively, for stipe diameter (Eq.6).

The estimated morphological development indices are correlated well with the measured values. This is also shown from Figures 1-3.

Table 6. The values of validation indices for the morphological development simulation model

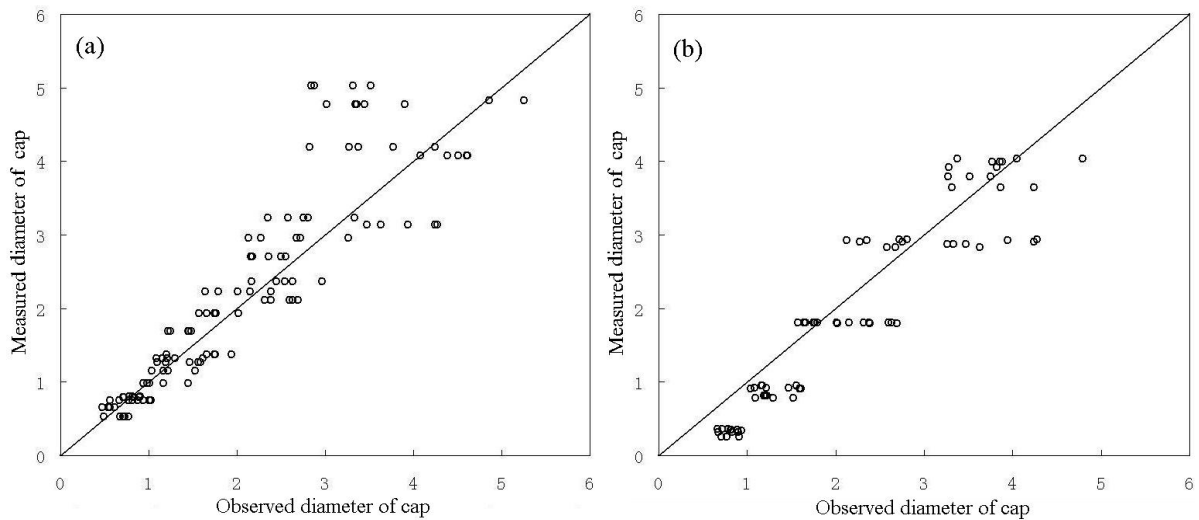| Model	Index	Model validation indexes			
		R^2	Bias /cm	RMSE	%RMSE
ETMD sub-model	Cap diameter	88.6%	0.325	0.335	13.42%
	Stipe height	93.7%	0.226	0.305	8.40%
	Stipe diameter	92.6%	0.173	0.213	10.09%
EHMD sub-model	Cap diameter	85.4%	0.350	0.396	17.42%
	Stipe height	91.7%	0.297	0.392	9.84%
	Stipe diameter	93.4%	0.237	0.276	19.97%

Fig. 1 Measured vs. simulated diameter of the cap

(a) Simulations using the effects of air temperature on the morphological development sub-model (Eq. 1); (b) simulations using the effects of relative air humidity on the morphological development sub-model (Eq. 4). The dashed line (——) is the 1:1 line.
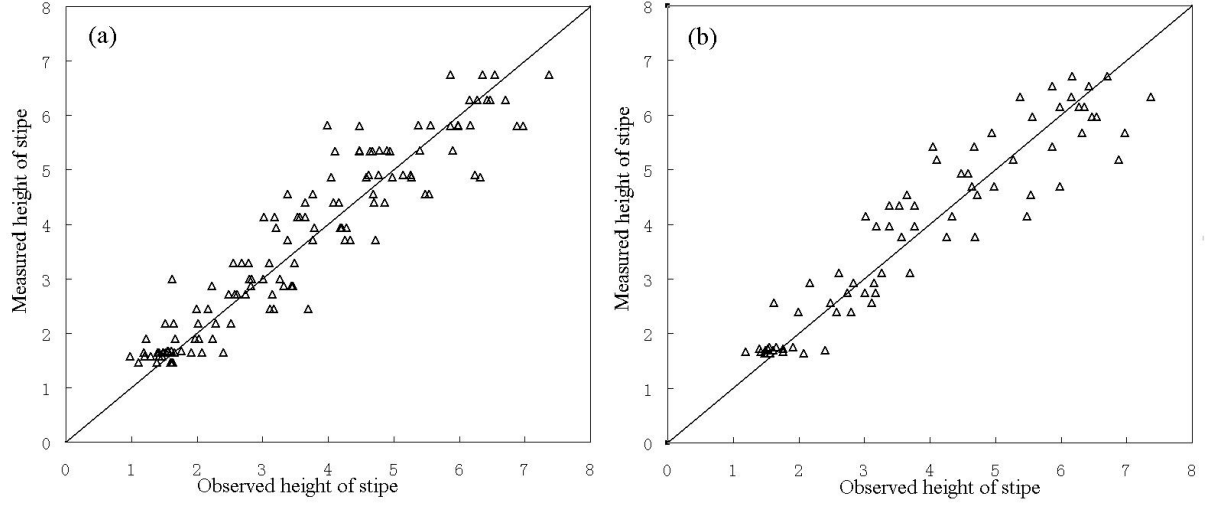

Fig. 2 Measured vs. simulated height of the stipe

(a) Simulations using the effects of air temperature on morphological development sub-model (Eq. 2); (b) simulations using the effects of relative air relative humidity on the morphological development sub-model (Eq. 5). The dashed line (——) is the 1:1 line.
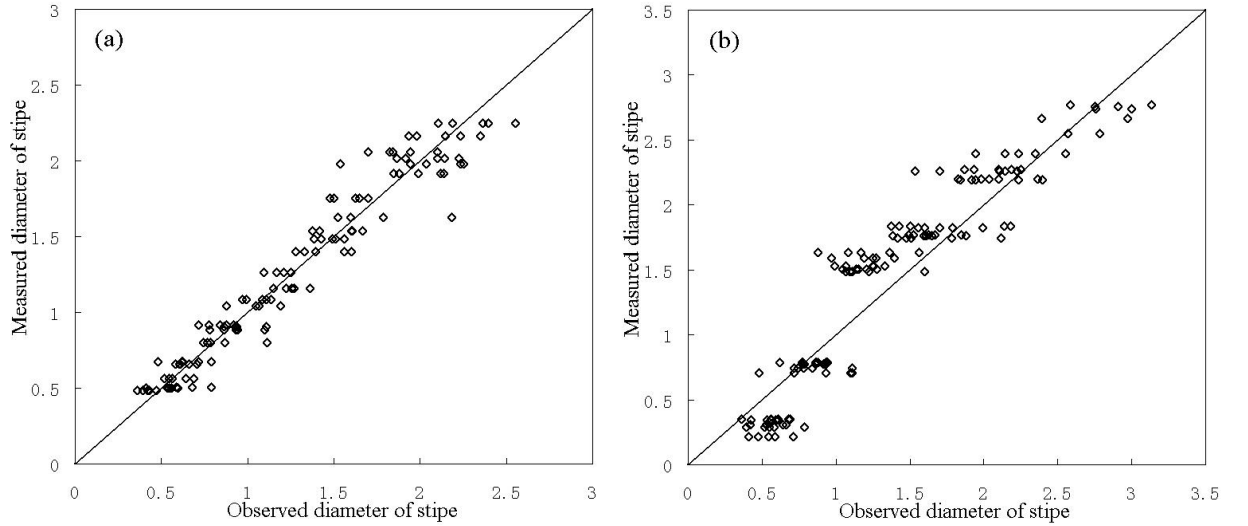
Fig. 3 Measured vs. simulated diameter of the stipe

(a) Simulations using the effects of air temperature on the morphological development sub-model (Eq. 3); (b) simulations using the effects of relative air humidity on the morphological development sub-model (Eq. 6). The dashed line (——) is the 1:1 line.

4.3 The appropriate environment range model for morphological development

4.3.1 The appropriate air temperature range sub-model for morphological development

From equations (1) – (3), we obtained the following formulas:

$$T_{opt-JG} = [\frac{-b_{11} - \sqrt{b_{11}^2 - 4a_{11}(c_{11} - SD_{JG})}}{2a_{11}}, \frac{-b_{11} + \sqrt{b_{11}^2 - 4a_{11}(c_{11} - SD_{JG})}}{2a_{11}}] \tag{7}$$

$$T_{opt-LJB} = \begin{cases} [\dfrac{-b_{21} - \sqrt{b_{21}^2 - 4a_{21}(c_{21} - SL_{JB})}}{2a_{21}}, \dfrac{-b_{21} + \sqrt{b_{21}^2 - 4a_{21}(c_{21} - SL_{JB})}}{2a_{21}}] & t = 1 \\ (SL_{JB} - k_1)\big/ u_1 & t > 1 \end{cases} \tag{8}$$

$$T_{opt-DJB} = [\frac{-b_{31} - \sqrt{b_{31}^2 - 4a_{31}(c_{31} - SD_{JB})}}{2a_{31}}, \frac{-b_{31} + \sqrt{b_{31}^2 - 4a_{31}(c_{31} - SD_{JB})}}{2a_{31}}] \tag{9}$$

$$T_{opt} = T_{opt-JG} \cap T_{opt-LJB} \cap T_{opt-DJB} \tag{10}$$

where $T_{opt-DJG}$ is the optimal air temperature for cap diameter, $T_{opt-LJB}$ is the optimal air temperature for stipe height, $T_{opt-DJB}$ is the optimal air temperature for stipe diameter. T_{opt} is the optimal air temperature for the fruiting body, which is the intersection of $T_{opt-DJG}$, $T_{opt-LJB}$ and $T_{opt-DJB}$. SD_{JG}, SL_{JB} and SD_{JB} are standard values of cap diameter, stipe height and stipe diameter on different days, and is taken from the average value of the indices in this study (see Table 7).

4.3.2 The appropriate relative humidity range sub-model for morphological development

From equations (4) – (6), we obtained the following formulas:

$$H_{opt-JG} = [\frac{-b_{12} - \sqrt{b_{12}^2 - 4a_{12}(c_{12} - SD_{JG})}}{2a_{12}}, \frac{-b_{12} + \sqrt{b_{12}^2 - 4a_{12}(c_{12} - SD_{JG})}}{2a_{12}}] \tag{11}$$

$$H_{opt-LJB} = \frac{(SL_{JB} - k_2)}{u_2} \tag{12}$$

$$H_{opt-DJB} = [\frac{-b_{32} - \sqrt{b_{32}^2 - 4a_{32}(c_{32} - SD_{JB})}}{2a_{32}}, \frac{-b_{32} + \sqrt{b_{32}^2 - 4a_{32}(c_{32} - SD_{JB})}}{2a_{32}}] \tag{13}$$

$$H_{opt} = H_{opt-JG} \cap H_{opt-LJB} \cap H_{opt-DJB} \tag{14}$$

where $H_{opt-DJG}$ is the optimal relative humidity for cap diameter, $H_{opt-LJB}$ is the optimal relative humidity for stipe height, $H_{opt-DJB}$ is the optimal relative humidity for stipe diameter. H_{opt} is the optimal relative humidity for the fruiting body, which is the intersection of $H_{opt-DJG}$, $H_{opt-LJB}$ and $H_{opt-DJB}$.

4.3.3 Simulated optimal environmental conditions for the fruiting body growth period

Using equations (7) – (14), the optimal environmental control standards can be computed for each day of the fruiting body growth period (Table 7).

Table 7. The standard values of morphological development and the simulated optimal environment conditions in the fruiting body growth period

Time /d	SD_{JG} /cm	SL_{JB} /cm	SD_{JB} /cm	Optimal temperature range / ℃	Optimal humidity range /%
1	0.729	1.540	1.170	[15.4,16.9]	[87,96]
2	1.164	2.415	1.433	[15.9,19.1]	[89,95.4]
3	1.890	3.608	1.881	[15.8,16.4]	[87,96]
4	2.922	4.774	2.347	[15.8,16.4]	[91,96]
5	4.041	5.825	2.639	[14.5,17.2]	[91,94]

5 Conclusion

When compared with traditional cultivation in plastic greenhouses, modern methods of commercial mass cultivation of fungi has the advantage of uniform growth, high efficiency and is unrestricted by season. However, production is costly and has high energy consumption. Therefore, optimal environmental control is crucial. Higher fungi are considered difficult to cultivate in the laboratory without complex

growth medium[12] because of the limited growing space in a laboratory. Environmental control needs to be very precise in modern commercial production of fungi, and the application of the optimal climate control parameters is crucial for ideal fruiting body development, and therefore these study results have great practical significance. Using the simulation models morphological development rate and optimal climate control values can be obtained to guide the actual environmental control settings in the commercial production of *P. eryngii*.

In general, fungi are very difficult to study through experimental means alone because of the complexity of their natural growth habitat (e.g., soils) and the microscopic scale of growth (e.g., tip vesicle translocation and hyphal tip extension)[13]. Some research focus on shape is on the cell[14].Mathematical modeling provides a complementary, powerful and efficient method of investigation. The aim of mathematical modeling is to reduce a complex (biological) system into a simpler (mathematical) system that can be analyzed in far more detail and from which key properties can be identified[13].

Temporal effects were considered in the model. The parameters in the model varied for each day. The relationship between the indices of morphological development and air environment in this paper was represented by a quadratic equation with one variable, reflecting the experimental results which showed that the estimated optimal air temperature and relative humidity are not the highest values of appropriate air temperature and relative humidity. The calculated optimal air temperature and relative humidity values predicted by the model are different for each day. For this reason, environmental parameters should be varied daily in the commercial production of *P. eryngii*, and not set at temperatures of 16–18 ℃ or 93% above relative humidity, as analyzed to be optimal by the experiments. This also illustrates the practical value of the model.

We conclude that our model described in this article provides a powerful tool to predict the morphological development rate according to air environment, and to guide real-time adjustment of air environment for commercial production of *P. eryngii*.

Acknowledgements

Carbohydr. Polym.

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