

Short communication

A simple equation for describing the temperature dependent growth of free-floating macrophytes

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Abstract

Temperature is one of the most important factors determining growth rates of free-floating macrophytes in the field. To analyse and predict temperature dependent growth rates of these pleustophytes, modelling may play an important role. Several equations have been published for describing temperature responses of macrophytes and algae. But they are often complex or are only applicable in a limited range of temperatures. In this paper, we present a simple three-parameter equation for describing the temperature dependent growth rates of pleustophytes. The equation that we developed is tested using results from laboratory growth experiments conducted with three different species of pleustophytes (*Lemna minor*, *Salvinia molesta* and *Azolla filiculoides*). The equation is simple and demonstrates reliable fits (adjusted R^2 reaching from 0.89 to 0.95). Additionally, our equation primarily uses parameters of biological significance, resulting in estimates of useful cardinal temperatures (minimum and maximum).

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1. Introduction

Free-floating macrophytes often have a large impact on freshwater ecosystems. In temperate and subtropical regions species like *Azolla filiculoides* and *Lemna minor* form dense mats covering the entire surface of a water body, especially when nutrient loading in the system is high (Portielje and Roijackers, 1995). Biodiversity in these systems is often low (Jansen and Van Puijenbroek, 1998) since the mats obstruct oxygen supply to the water column (Pokorný and Rejmánková, 1983) and cause light limitation of algae and submerged macrophytes (Wolek, 1974). In tropical regions, species like *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia molesta* are also known to cause serious problems, congesting waterways, drowning livestock and damaging fish habitats (Mehra et al., 1999; Hill, 2003).

Apart from nutrient supply, temperature is the most important factor determining growth rates of pleustophytes in the field (Rejmánková, 1973; Janes, 1998). The effect of temperature on the growth of macrophytes and algae has been

successfully described by several equations (Carr et al., 1997). However, these relations are only applicable in a limited range of temperatures (Carr et al., 1997) or the parameters lack any biological significance (Room, 1986; Carr et al., 1997).

In this paper, our objective is to predict the relative growth rate of floating macrophytes at different temperature values. For this purpose, we develop a simple three-parameter equation between temperature and the relative growth rates of free-floating macrophytes, covering a wide range of temperatures. Based on results obtained in laboratory growth experiments conducted with three species of floating macrophytes (*L. minor* Linné, *S. molesta* Mitchel and *A. filiculoides* Lamarck), we evaluate this equation with reference to two other established models used for predicting growth rates of terrestrial crops (Yan and Hunt, 1999) and growth rates of *S. molesta* (Room, 1986). See, for other equations, the review of Santamaría and Van Vierssen (1997).

2. Materials and methods

2.1. Experiments

For cultivation in the laboratory, *L. minor* and *A. filiculoides* were collected in the field and *S. molesta* was obtained from a

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gardening centre, all in the vicinity of Wageningen (The Netherlands).

The species were individually grown in 20-l aquaria under controlled conditions (temperature at ca. 25 °C, a 14-h photoperiod and a light intensity of 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR). The plants were kept on a medium based on Smart and Barko (1985), with additional elements (Szabo et al., 2003) and modified concentrations of phosphorus. As the optimal phosphorus concentration for *A. filiculoides* differs strongly from the two other species, the amount of phosphorus in the medium was 20 mg P l⁻¹ for *A. filiculoides* (Cary and Weerts, 1992) and 2 mg P l⁻¹ for *L. minor* and *S. molesta* (Lüönd, 1980, 1983; Cary and Weerts, 1983).

To determine the temperature dependent growth rates of the plants, laboratory experiments were conducted in climate rooms at seven different temperatures (water temperatures were 11, 15, 19, 25, 29, 33 and 38 °C). During the experiments, a 14-h photoperiod and a light-intensity of 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR was maintained in the climate rooms.

Plants of each species were randomly selected from the cultures, and placed under the different temperature regimes in 5-l aquaria. From the cultures of *A. filiculoides* and *L. minor*, at least 100 plants were taken for each temperature. For *S. molesta*, at least 20 ramets were selected per temperature regime.

After an incubation period of 3 days, a growth experiment was carried out in six-fold for each temperature and species. For each experimental unit of *A. filiculoides* and *L. minor*, 10 plants were randomly selected, weighed and moved to a 2-l aquarium with acclimatised medium. Units of *S. molesta* consisted of two 6-leaf ramets which were also weighed and placed in 2-l aquaria. After 4 days, the medium inside the aquaria was replaced with fresh acclimatised medium in order to prevent nutrient limitation and competition with algae. During the experiments, evaporation of water was compensated for by adding demineralised water accordingly, on a daily basis. After 7 days, the experiment was terminated and all samples were weighed again.

2.2. Calculations and modelling

The relative growth rates (R , day⁻¹) at the different temperatures of all three species were calculated assuming exponential growth:

$$R = \frac{\ln(B_1) - \ln(B_0)}{\Delta t} \quad (1)$$

Here B_1 and B_0 are the wet weights (g), measured, respectively, after and before the experiments, Δt is the time span (days) over which the experiment was conducted (7 days).

For describing the temperature dependent growth rates of the three species of macrophytes, three different equations were fitted by non-linear regression.

The first is a four-parameter equation based on two logistic equations. The equation was used by Room (1986) to describe temperature dependent growth rates of *S. molesta*:

$$R = R_{\max} e^{a(T_{\text{opt}}-T)^2}, \quad \text{for } T < T_{\text{opt}}$$

$$R = R_{\max} e^{b(T_{\text{opt}}-T)^2}, \quad \text{for } T > T_{\text{opt}} \quad (2)$$

In which R is the relative growth rate, R_{\max} the maximum relative growth rate (day⁻¹), T_{opt} the optimum temperature, T the ruling temperature (°C) and a and b are empirical constants.

Secondly, we fitted a three-parameter equation as proposed by Yan and Hunt (1999) intended for modelling temperature response of (terrestrial) crops:

$$R(T) = R_{\max} \left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \right) \left(\frac{T}{T_{\text{opt}}} \right)^{T_{\text{opt}}/(T_{\max} - T_{\text{opt}})} \quad (3)$$

T_{\max} is the maximum growth temperature threshold (°C). The equation assumes the minimum growth temperature to be zero (Yan and Hunt, 1999).

Finally, we developed a simple third-order polynome with one optimum and zero growth at T_{\min} and T_{\max} , based on a more complex equation for temperature dependent insect emergence (Brière et al., 1999):

$$R(T) = cT(T - T_{\min})(T_{\max} - T), \quad \text{with } T_{\min} \geq 0 \text{ and } T_{\max} > T_{\min} \quad (4)$$

In which T_{\min} is the minimum temperature threshold (°C) which is assumed to be positive and c is an empirical scaling constant.

This equation has an optimum at the temperature T_{opt} for all positive T_{\min} and T_{\max} :

$$T_{\text{opt}} = \frac{1}{3}(T_{\max} + T_{\min} + \sqrt{T_{\max}^2 - T_{\min}T_{\max} + T_{\min}^2}) \quad (5)$$

Rearranging this equation, we can also use an experimentally found optimal temperature to estimate either the minimum temperature or the maximum temperature:

$$T_{\min} = \frac{T_{\text{opt}}(3T_{\max} - 2T_{\text{opt}})}{-T_{\max} + 2T_{\text{opt}}} \quad \text{or} \quad T_{\max} = \frac{T_{\text{opt}}(3T_{\text{opt}} - 2T_{\min})}{-T_{\min} + 2T_{\text{opt}}} \quad (6)$$

After calculation of the optimum temperature T_{opt} (Eq. (5)) it is also possible to calculate the growth rate at the optimal temperature (R_{\max} , day⁻¹) by substitution of $T = T_{\text{opt}}$ in Eq. (4).

For comparison of the three functions we used adjusted R^2 , F -test of residual variances (Lederman and Tett, 1981), parsimony and the small sample unbiased Akaike Information Criterion (AIC_c) which takes both fit and complexity of the functions (i.e. number of parameters) into account (Johnson and Omland, 2004). According to this last criterion, the equation with the lowest AIC_c value is most appropriate.

We tried to apply the four-parameter equation of Johnson et al. (1974), which is a unimodal variant of the commonly used Arrhenius equation of reaction kinetics. A disadvantage of this equation is that its parameters lack any ecological interpretation. We do not present the results, as our iterative regression

procedure could not find reliable parameter values in most of our datasets.

3. Results

The highest temperature used in our experiments (38 °C) was lethal for both *L. minor* and *A. filiculoides* before the end of the experiments (Fig. 1a and b). Therefore, these results were not included for regression analysis.

The fit of all three equations was not significantly different (*F*-test) for all species. Regression results from the Yan and

Hunt equation and our equation (“simplified Brière”) on the *A. filiculoides* data showed an almost exact match on the parameters (Table 1) and curves (Fig. 1a) of both equations. Although the adjusted R^2 was almost equal for all functions (0.88–0.89), the AIC_c was slightly higher for the Room equation, and thus less favourable. Also, this equation still predicted a growth rate of 0.07 at 38 °C, while our experiments demonstrated that this temperature is lethal to the species.

For the data of *L. minor* our simplified Brière equation proved to be the most appropriate function by showing the lowest AIC_c . Compared to the Room equation and the Yan and Hunt equation, our function shows a better fit on the lower temperature ranges (Fig. 1b). Additionally, the Room equation failed to show an accurate estimation in the higher temperature ranges (beyond 33 °C). The minimum temperature of the simplified Brière equation was fitted at 6.2 °C (Table 1).

For *S. molesta* both the Room equation and the Yan/Hunt equation showed a slightly lower adjusted R^2 (0.90 for both), a higher AIC_c and a worse fit at the lower temperature ranges compared to our simplified Brière equation (R^2 : 0.91) (Fig. 1c). The optimum temperature estimated by the three equations varied slightly (Table 1). Similarly, the maximum growth rates found, differed somewhat. The minimum temperature of the simplified Brière equation for *S. molesta* was estimated at 10.7 °C.

4. Discussion

This study shows that our simple three-parameter equation is highly predictive with respect to temperature dependent growth of free-floating macrophytes. Compared to the Room and the Yan/Hunt equations, our equation demonstrates an equal or better fit, particularly in the lower and higher temperature ranges as the Yan/Hunt equation assumes that the minimum temperature is always 0 °C. Furthermore, our equation is mathematically simpler, which is also preferable (Lederman and Tett, 1981). In contrast to the Yan/Hunt equation and the Room equation, our three-parameter equation is able to estimate both the minimum and the maximum growth temperature.

The minimum growth temperature of *A. filiculoides* was estimated to be 0.1 °C. This may seem unrealistic since it is known that most species have a minimum temperature well above 0 °C (Yan and Hunt, 1999). However, Janes (1998) showed that *A. filiculoides* still continues to grow at 5 °C and is able to survive sub-zero temperatures below –5 °C, indicating that our estimate is reliable.

Among the genus *Azolla*, *A. filiculoides* has a poor tolerance for higher temperatures (Watanabe and Berja, 1983; Uheda et al., 1999). Short-term experiments (0.5–2 h) demonstrated that temperatures around 42–44 °C were lethal to most *Azolla* strains (Uheda et al., 1999). Our experiments showed that on a longer term even temperatures below 40 °C are lethal to *A. filiculoides* (1.5 weeks).

Landolt and Kandeler (1987) reported a long-term maximum temperature for *L. minor* around 33 °C. In the present study, however, we found that the species is able to grow at

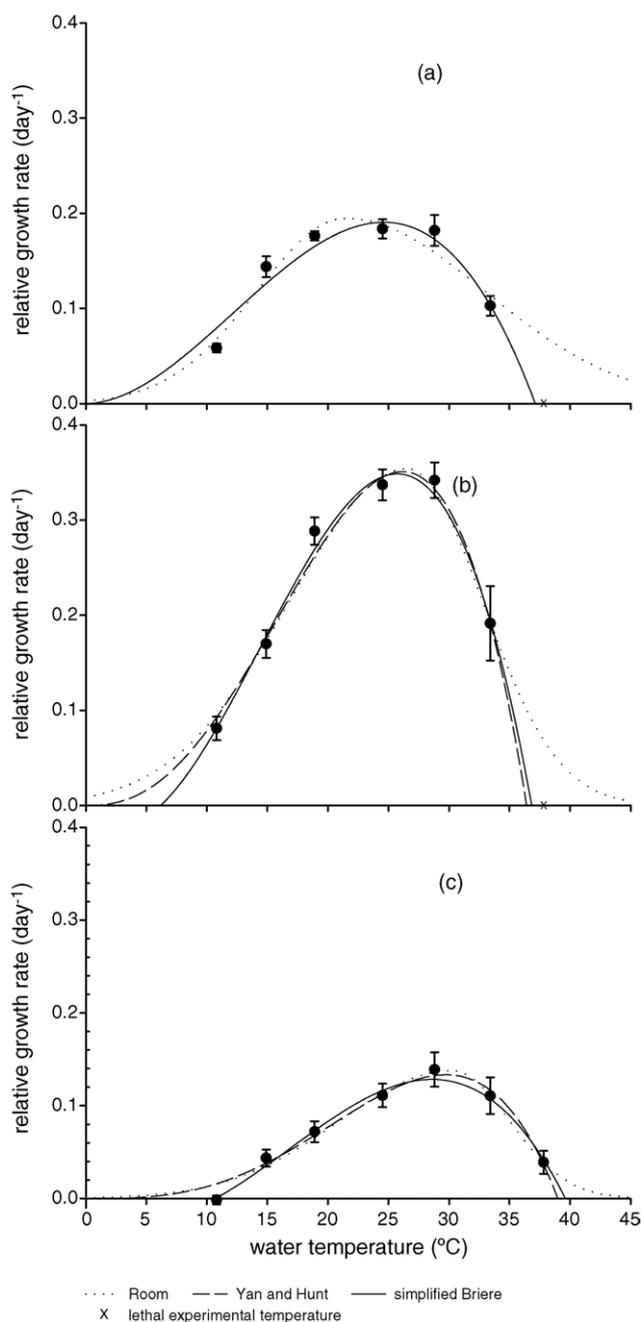


Fig. 1. The effect of temperature on the growth rates of *A. filiculoides* (a), *L. minor* (b) and *S. molesta* (c). In (a) the curves of the Yan and Hunt equation and the simplified Brière equation match each other. Error bars, ± 1 S.D.

Table 1
Overview of the fit (as adjusted R^2 and Akaike Information Criterion, AIC_c) calculated values (*) and estimated parameters for the Room (R), Yan and Hunt (Y/H) and our simplified Brière (sB) equations (\pm S.E.). The minimum temperature of the Yan and Hunt equation is zero by definition. The logistic Room equations never reach zero growth

	Adjusted R^2	AIC_c	R_{max} (day^{-1})	T_{min} ($^{\circ}C$)	T_{opt} ($^{\circ}C$)	T_{max} ($^{\circ}C$)	a ($^{\circ}C^{-2}$)	b ($^{\circ}C^{-2}$)	c ($^{\circ}C^{-2} day^{-1}$)
<i>A. filiculoides</i>									
R	0.89	-256.9	0.19	-	21.5	-	-9.32×10^{-3}	-3.77×10^{-3}	-
	-	-	$\pm 3.5 \times 10^{-3}$	-	± 0.6	-	$\pm 1.6 \times 10^{-3}$	$\pm 0.6 \times 10^{-3}$	-
Y/H	0.89	-257.1	0.19	-	24.6	37.1	-	-	-
	-	-	$\pm 3.2 \times 10^{-3}$	-	± 0.3	± 0.4	-	-	-
sB	0.89	-257.1	0.19*	0.1	24.7*	37.0	-	-	2.56×10^{-5}
	-	-	-	± 1.4	-	± 0.4	-	-	$\pm 0.23 \times 10^{-5}$
<i>L. minor</i>									
R	0.94	-210.1	0.35	-	26.6	-	-5.27×10^{-3}	-1.30×10^{-2}	-
	-	-	$\pm 5.5 \times 10^{-3}$	-	± 0.5	-	$\pm 0.5 \times 10^{-3}$	$\pm 2.6 \times 10^{-3}$	-
Y/H	0.95	-215.5	0.35	-	26.1	36.4	-	-	-
	-	-	$\pm 5.1 \times 10^{-3}$	-	± 0.2	± 0.3	-	-	-
sB	0.95	-218.4	0.35*	6.2	25.7*	36.8	-	-	6.24×10^{-5}
	-	-	-	± 0.6	-	± 0.2	-	-	$\pm 0.32 \times 10^{-5}$
<i>S. molesta</i>									
R	0.90	-294.9	0.14	-	30.3	-	-5.78×10^{-3}	-2.22×10^{-2}	-
	-	-	$\pm 4.0 \times 10^{-3}$	-	± 0.6	-	$\pm 0.7 \times 10^{-3}$	$\pm 5.2 \times 10^{-3}$	-
Y/H	0.90	-296.9	0.13	-	29.7	39.0	-	-	-
	-	-	$\pm 3.7 \times 10^{-3}$	-	± 0.3	± 0.4	-	-	-
sB	0.91	-301.5	0.13*	10.7	28.6*	39.6	-	-	2.27×10^{-5}
	-	-	-	± 0.6	-	± 0.3	-	-	$\pm 0.13 \times 10^{-5}$

higher temperatures. Differences between Landolt and Kandeler (1987) and our findings with respect to both optimum and minimum temperatures were small. Landolt and Kandeler (1987) reported 26 °C for the optimum temperature, which is almost equal to our estimates. Also, the minimum temperature estimated by our equation (6.2 °C) is within the range reported previously (4–9 °C) (Landolt, 1986; Landolt and Kandeler, 1987).

Whiteman and Room (1991) determined the lethal temperatures for *S. molesta* to be -3 and 43 °C in short exposure experiments (2–16 h). Although the lethal temperature does not necessarily coincide with the maximum temperature for growth, our results suggest a lower long-term lethal temperature (around 39–40 °C). The previously reported optimum temperature (30 °C) (Room, 1986) did not differ significantly from our results.

The minimum growth temperature can be an important parameter with respect to predicting climate related invasions of new habitats by pleustophytes. Recent studies have shown that rising temperatures due to global warming are causing dramatic shifts in plant communities, pushing warm-weather species towards higher latitudes (Walther et al., 2002). Minimum temperatures of these invasive species may become a deciding factor for colonization of new areas (Alward et al., 1999; Stachowicz et al., 2002). Because our equation is able to make estimations of these minimum growth temperatures, it can be implemented in predictive models (e.g., Driever et al., 2005), exploring temperature-induced shifts in plants communities.

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