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Richards Plant Growth Model

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With 3 figures and 2 tables

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Abstract

In this paper, the Richards function in the form $y(t) = A(1 + be^{-kt})^{1/(1-m)}$ was used to precisely analyze plant growth. The first, second and third derivative formulae of the above function were given. A new parameter, $G_{1,2} = f(m)$ was derived, enabling the calculation of the coordinates of critical points which mark the principal growth phases. The coefficients of Richards model describing the dry matter accumulation in buckwheat plants were numerically calculated. The growth curve, growth rate curve and the growth acceleration curve were also drawn. A high usefulness of approximation of the growth process of buckwheat plants by means of Richards function was confirmed statistically.

Key words: Plant growth analysis — Richards function — critical points of growth — buckwheat — *Fagopyrum esculentum* Moench.

Comprehensive Richards function has been often applied in the quantitative analysis of plant growth (Richards 1959, Richards 1969, Żelawski and Lech 1980, Hunt 1982, Larsen 1990, Ramachandra Prasad et al. 1992, Aikman and Benjamin 1994).

Transforming Bertalanffy's equation (Bertalanffy 1957), Richards proposed the following growth model:

$$y = A(1 + be^{-kt})^{1/(1-m)} \quad \text{when} \quad m > 1, b > 1 \tag{1}$$

where y = growth size (e.g. dry matter), t = time, A = asymptotic value of growth size, m, b, k = constant coefficients ($k > 0$).

The Richards function is very flexible and has a horizontal asymptote, and its graph has a characteristic sigmoid shape. Eqn (1) can be transformed to a linear form:

$$\ln[(y/A)^{1-m} - 1] = \ln b - kt \tag{2}$$

The linear form of Richards function can not be useful for determining its constant parameters using analytical methods. This is because the considered growth model has up to four independent coefficients: A, b, k, m. The constant coefficients of Richards function may be calculated (after previously estimating their values) using numerical methods.

During plant growth, there are three characteristic critical moments that can be marked as P_1, P_i, P_2 on the graphs. At the point P_1, maximum acceleration of growth and the first inflection of the growth rate curve takes place. At the point P_i the growth rate attains its maximum point. At the point P_2, maximum deceleration takes place, i.e. maximum negative acceleration of growth, while at the same time there is a second inflection of the growth rate curve. The points P_1 and P_2 separate the entire growth period into three phases: the exponential phase, the linear phase (from P_1 to P_2) and the ageing phase. Because of the importance of these three critical points, it is important to know their coordinates on the appropriate graphs. To achieve this, to analyze the variation course of Richards function, it is necessary to calculate its first, second and third derivative with respect to time.

The first derivative of Richards function (1) is equal to:

$$y' = dy/dt = ky/(m-1)[1 - (y/A)^{m-1}] \tag{3}$$

or

$$y' = Abk/(m-1)e^{-kt}(1 + be^{-kt})^{m/(1-m)} \tag{4}$$

The second derivative is in the form:

$$d^2y/dt^2 = y'' = ky'/(m-1)[1 - m(y/A)^{m-1}] \tag{5}$$

or

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$$y'' = \frac{Abk^2 e^{-kt}}{(m-1)^2(b+e^{kt})}(1+be^{-kt})^{m/(1-m)} \times [b+(1-m)e^{kt}] \quad (6)$$

The third derivative can be presented in the following expressions:

$$\frac{d^3y}{dt^3} = y''' = \frac{ky'}{m-1}\left\{\frac{k}{m-1}\left[1-m\left(\frac{y}{A}\right)^{m-1}\right]^2 - y'm(m-1)\frac{1}{A}\left(\frac{y}{A}\right)^{m-2}\right\} \quad (7)$$

$$y''' = \frac{k^2y}{(m-1)^2}\left[1-\left(\frac{y}{A}\right)^{m-1}\right]\left\{\frac{k}{m-1}\left[1-m\left(\frac{y}{A}\right)^{m-1}\right]^2 - \frac{k}{m-1}m(m-1)\left[1-\left(\frac{y}{A}\right)^{m-1}\right]\left(\frac{y}{A}\right)^{m-1}\right\} \quad (8)$$

The first derivative is positive, so function (1) is always ascending; it also has horizontal asymptote $y = A$.

$$\lim_{t\to\infty} A(1+be^{-kt})^{1/(1-m)} = A \quad (9)$$

The relative growth rate RGR amounts to:

$$RGR = y'/y = k/(m-1)[1-(y/A)^{m-1}] \quad (10)$$

Equating the second derivative to zero we obtain coordinates of the inflection point $P_i(t_i, y_i)$ of Richards curve:

$$t_i = (1/k)\ln[b/(m-1)], \quad y_i = Am^{1/(1-m)} \quad (11)$$

The initial value of growth curve for $t = 0$ amounts to:

$$y(0) = A(1+b)^{1/(1-m)} \quad (12)$$

The coordinates of the inflection points of the growth rate curve are obtained after equating the third derivative to zero. After substitution in eqn (8):

$$(y/A)^{m-1} = x \quad (13)$$

a square equation is obtained:

$$(2m^2 - m)x^2 - (m^2 + m)x + 1 = 0 \quad (14)$$

Eqn (14) has two roots:

$$x_{1,2} = \frac{m(m+1) \mp (m-1)\sqrt{m(m+4)}}{2m(2m-1)} \quad (15)$$

It seems as if the intentional introduction of new dual coefficient $G_{1,2}$, facilitates calculations:

$$G_{1,2} = \left[\frac{m(m+1) \mp (m-1)\sqrt{m(m+4)}}{2m(2m-1)}\right]^{1/(m-1)} \quad (16)$$

Now, using eqn (13) we can give the ordinates of two remaining critical points of analyzed growth curve:

$$y_1 = AG_1, \quad y_2 = AG_2 \quad (17)$$

The nondimensional coefficients G_1 and G_2 are included in the interval (0,1) and are defined, respectively, as part of the final size attained by the plants in critical points P_1 and P_2. For example, at $m = 2$, when Richards function becomes a logistic function, we get $G_1 = 0.211$ and $G_2 = 0.789$.

Using the equations (2), (11) and (17), abscissas of the inflection points of the growth rate curve are obtained in the form:

$$t_1 = t_i + \frac{1}{k}\ln\left[\frac{(m-1)G_1^{m-1}}{1-G_1^{m-1}}\right] \quad (18)$$

$$t_2 = t_i + \frac{1}{k}\ln\left[\frac{(m-1)G_2^{m-1}}{1-G_2^{m-1}}\right] \quad (18a)$$

Now we can also calculate the ordinates of the critical points of the growth rate curve by Richards:

$$y_1' = AkG_1/(m-1)(1-G_1^{m-1}) \quad (19)$$

$$y_2' = AkG_2/(m-1)(1-G_2^{m-1}) \quad (19a)$$

and

$$y_i' = Akm^{m/(1-m)} \quad (20)$$

From the point of view of growth quantitative analysis, an interesting item, rarely seen in literature (Gregorczyk 1991), is the growth acceleration course $y'' = f(t)$, which is a curve describing growth rate changes with time of vegetation of plants $[y'(t)]$. It is known that $y''(t_i) = y_i'' = 0$; on the contrary, maximal ordinate (y_1'') and minimal ordinate (y_2'') of growth acceleration are given in the following formulae:

$$y_1'' = [Ak^2G_1/(m-1)^2](1-G_1^{m-1})(1-mG_1^{m-1}) \quad (21)$$

$$y_2'' = [Ak^2G_2/(m-1)^2](1-G_2^{m-1})(1-mG_2^{m-1}) \quad (21a)$$

With formulae (18) and (18a) we can calculate the time duration of the linear phase Δt, which is known

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Table 1: Experimental and theoretical values of dry matter accumulation in the buckwheat plants during vegetation

Measurement	Time (days)	Values (g) experimental	theoretical
1	10	0.024	0.149
2	20	0.274	0.478
3	30	1.54	1.50
4	40	4.70	4.34
5	50	9.78	10.32
6	60	18.06	17.50
7	70	21.65	21.94
8	80	23.52	23.66
9	90	23.96	24.19
10	100	24.75	24.35

from old times in botanical literature as 'grand period of growth' (Żelawski and Lech 1980):

$$\Delta t = t_2 - t_1 = \frac{1}{k} \ln \frac{G_2^{m-1}(1-G_1^{m-1})}{G_1^{m-1}(1-G_2^{m-1})} \qquad (22)$$

The above theory was used for the precise description of dry weight accumulation in buckwheat (*Fagopyrum esculentum* Moench). The adequate primary growth data was taken with the authors' permission from the work of Maciorowski et al. (1996). The buckwheat plants grew in optimal condition of fertility and soil humidity in Mitscherlichs pots. The dry matter of green parts was taken every 10 days after the planting. The experiment was conducted at the stage of full maturity. Table 1 presents the mean values obtained from the measurements of 15 plants (3 pots with 5 plants each).

The primary data contained in Table 1 helped in calculating the constant coefficients of Richards function (eqn 1). Coefficients A, b, k, m were numerically derived by using Rosenbrock's method (Machura and Mulawa 1973), available in package Statistica for Windows. The starting values of the desired parameters were given based on the results of the preliminary approximation (Gregorczyk 1994). After achieving precision in task calculation the theoretical model by Richards was obtained:

$$y(t) = 24.41(1 + 855.3\,e^{-0.1265t})^{1/(1-2.077)} \qquad (23)$$

Statistical analysis points to a high approximation efficacy in buckwheat growth using the Richards function. It is confirmed by the high value of the determination coefficient $R^2 = 99.89\%$. The χ-square goodness-of-fit test was also applied. The

Table 2: Coordinates of the critical points of the growth curves of the buckwheat plants

Point	Abscissa t (days)	y (g)	Ordinate y′ (g day^{-1})	y″ (g day^{-2})
P_1	42.2	5.37	0.507	0.0354
P_i	52.8	12.38	0.754	0
P_2	63.4	19.38	0.501	−0.0365

empirical value was $\chi^2 = 0.2825$ at critical value $\chi^2_{0.05} = 16.921$.

Knowing the value of the coefficient m in Richards function enables the calculation of parameters $G_1 = 0.220$ and $G_2 = 0.793$, and the next coordinates of the critical points in the growth of buckwheat. The values of the coordinates of these points are shown in Table 2.

Against a background of the experimental points, a course of the growth curve was drawn (Fig. 1). The estimated values of the dry matter of investigated plants are given in Table 1. The growth rate curve (Fig. 2) and the growth acceleration curve (Fig. 3) were also drawn. The critical points (P_1, P_i, P_2) which characterize the critical moments during the growth of buckwheat are marked in all the curves.

The dry weight of the green parts was initially small ($y_0 = 0.046$ g), and increased exponentially to the beginning of the flowering stage (point P_1) on the 42nd day of growth. At this moment, the acceleration of growth achieved its maximum value,

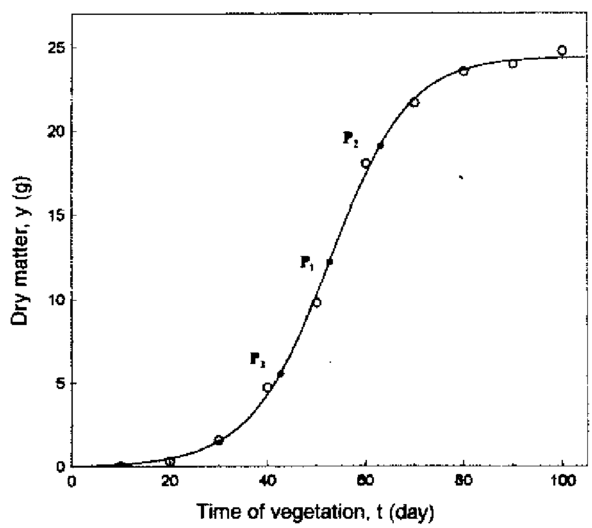

Fig. 1: Richards growth curve of the buckwheat plants as compared with experimental points

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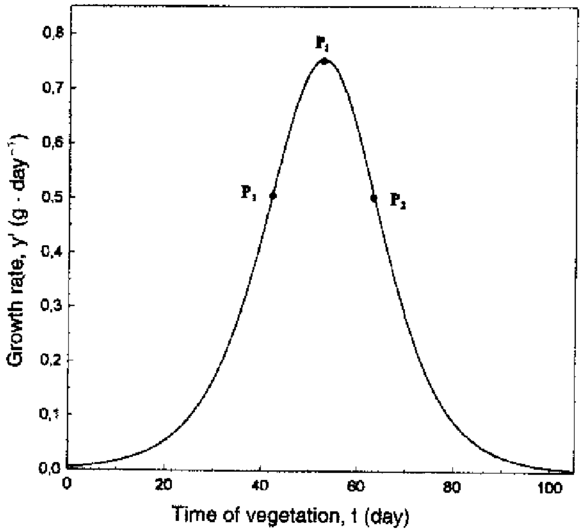

Fig. 2: Growth rate curve of the buckwheat plants

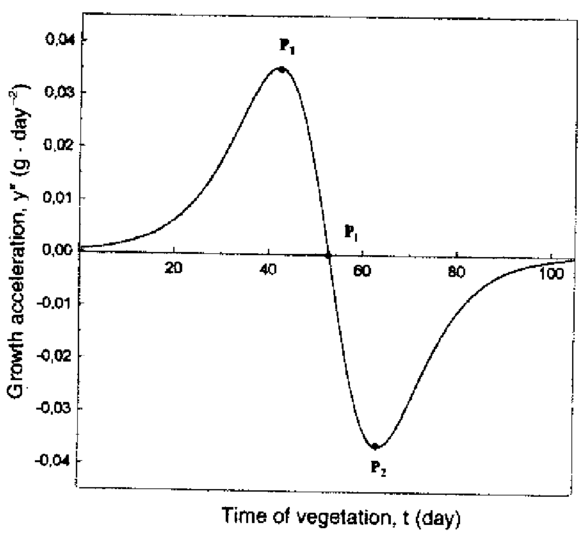

Fig. 3: Growth acceleration curve of the buckwheat plants

$y_1'' = 0.0354\,\mathrm{g\,day^{-2}}$ and the linear phase of growth starts, and lasted for about 21 days. At about the 53rd day of growth (in the middle of flowering) the inflection of the curve occured (point P_i) which simultaneously corresponded to maximum growth rate, $y_i' = 0.754\,\mathrm{g\,day^{-1}}$ and zero acceleration. The linear phase of growth ended at about the 63rd day of vegetation (point P_2). At this time the plants were at the early dough stage and growth acceleration had a minimum value of $y_2'' = -0.0365\,\mathrm{g\,day^{-2}}$. Later, there was an exponential fall in the growth rate of buckwheat with a relatively small increase in dry weight which lasted until the full maturity stage. Generally, it could be noticed that the accumulation curve of buckwheat dry matter had a typical sigmoid shape. In all the graphs, the three characteristic phases of growth, marked as critical points, could be precisely defined. The Richards function, containing as many as four independent coefficients, is very flexible. Because of this, it is possible to model even a relatively complicated growth process (Causton et al. 1978, Venus and Causton 1979a, Venus and Causton 1979b). The disadvantage of this method is the necessity of applying the nonlinear regression method, which is not easily accessible. However, this should not incline us to refrain from using these procedures.

Zusammenfassung

Pflanzenwachstums-Modell nach Richards

In der Arbeit wurde zur genauen Analyse des Pflanzenwachstums eine mathematische Funktion nach Richards angewendet in Form: $y(t) = A(1 + b\,e^{-kt})^{1/(1-m)}$. Es wurden die erste, die zweite und die dritte Ableitung dieser Funktion genannt. Außerdem wurde der neue Parameter $G_{1,2} = f(m)$ ausgerechnet, der bei der Berechnung der Koordinaten von kritischen Punkten behilflich ist. Die kritischen Punkte bestimmen die Hauptwachstumsphasen der Pflanzen. Die Koeffizienten des Richards-Modells, das die Akkumulation der Trockenmasse des Buchweizens beschreibt, wurden numerisch berechnet. Es wurden auch die Wachstumsverlaufs-, Wachstumsgeschwindigkeits- und Wachstumsbeschleunigungskurven graphisch dargestellt. Für die Approximation des Wachstumsverlaufs von Buchweizen stellte man eine sehr hohe statistische Absicherung fest.

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