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in

Porqueddu C. (ed.), Tavares de Sousa M.M. (ed.).
Sustainable Mediterranean grasslands and their multi-functions

Zaragoza : CIHEAM / FAO / ENMP / SPPF
Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 79

2008
pages 275-278

Modelling growth responses of annual legumes to water shortage

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SUMMARY – Knowing growth changes of plants as a response to environmental constraints is essential in management. The acquisition of this knowledge can be greatly facilitated by testing several growth models and chosing the best in terms of fitting. The present research models growth responses of three annual legumes [*Trifolium angustifolium* L., *Medicago disciformis* DC., and *Onobrychis caput-galli* (L.) Lam.] to water shortage. The plants were left to grow as monocultures (nine plants) in pots. Two irrigation treatments were applied: (i) full irrigation (at field capacity); and (ii) low irrigation (40% of the field capacity). There were three replications for each treatment. After seedling emergence, plant height was recorded approximately every four days. Twelve growth models were tested to find out the best in terms of fitting. Model diagnosis was based on the residual sum of squares, the Akaike information criterion, and the Schwarz criterion. The four-parameter Janoschek's model simulates best the growth pattern of *T. angustifolium* and *M. disciformis* and the four-parameter Morgan-Mercer-Flodin's model is appropriate for simulating the growth of *O. caput-galli*. There was not any differentiation between treatments regarding the best model selection. The suitability of models in terms of prediction is further discussed.

Keywords: *Trifolium angustifolium*, *Medicago disciformis*, *Onobrychis caput-galli*, growth models, Mediterranean.

***RESUME** – "Modélisation des réponses de croissance des légumineuses annuelles au déficit hydrique". Les connaissances concernant les modifications du modèle de croissance des plantes à cause des contraintes du milieu ont été considérées prépondérantes afin d'adopter un aménagement des territoires pâturés bien raisonné. Dans le cadre de cet article on a eu comme but de modéliser la croissance chez trois plantes légumineuses annuelles [*Trifolium angustifolium *L.,* Medicago disciformis *DC., et* Onobrychis caput-galli *(L.) Lam]. sous la contrainte hydrique. Les plantes ont été cultivées en pots (9 plantes/pot) sous deux régimes hydriques: (i) plantes bien irriguées ; et (ii) plantes irriguées au niveau de 40% des premières bien irriguées. Il y avait trois répétitions pour chaque traitement. La hauteur des plantes était mesurée tous les quatre jours à partir de leur émergence. On a utilisé douze modèles de croissance afin de tester le meilleur ajustement aux tendances de croissance des plantes. Comme critères on a adopté : la somme résiduelle au carré, le critère d'information d'Akaike, et le critère de Schwarz. Les résultats obtenus suggèrent que le modèle de Janoschek et de Morgan-Mercer-Flodin (modèles à quatre paramètres) étaient ceux qui présentaient le meilleur ajustement chez *T. angustifolium, *M. disciformis* et *O. caput-galli* respectivement. Il n'y avait pas de différenciation entre traitements concernant le choix du meilleur modèle. L'aptitude des modèles et leur convenance en termes de prédiction ont été analysées.*

Mots-clés : Trifolium angustifolium*,* Medicago disciformis*,* Onobrychis caput-galli*, modèles de croissance, Méditerranée.*

Introduction

The temporal behaviour of plant growth pattern is an important informative tool for conservation and management purposes. Generally, there are two approaches in codifying growth, the classical, analogue approach (e.g. calculation of relative growth rate) and the functional one (Hunt, 1982). The latter exploits the advantages of (linear/non linear) regression analysis and it is widely used, particularly after the development of computer-demanded modelling tools. Benefits gained from functional growth analysis are the simplicity in describing a rather obscure procedure like plant growth, the comprehensive parameterisation of growth drivers, the ability to screen growth information obtained from different treatments/environments, and that growth models are structured by using all the temporal sequence of the values of the examined growth parameter. In addition, most of the assumptions used in calculating growth indices through the classical analysis are not considered; the only basic assumption in the functional analysis is the selected model to fit the data. Finally, functional analysis uses rather short time data, thus avoiding plant losses.

The incorporation of environmental impact on plant growth is one of the most important issues in the domain of plant modelling (Prusinkiewicz, 1998). This impact is often depicted in changes of growth pattern and it is represented either in changes in the adoption of the best growth model that fits the data or in changes of model parameters. It is important, especially for prediction purposes, to explore both alternatives and to point out new growth patterns. The purpose of this study was to explore the growth responses of three annual, self-reseeding legumes to the irrigation regime and reveal growth patterns by using functional growth analysis.

Materials and methods

The research was conducted in spring 2006. Three annual self-reseeding legumes (*Trifolium angustifolium* L., *Medicago disciformis* DC., and *Onobrychis caput-galli* (L.) Lam.) were selected, commonly found in northern Greece. Seeds of the three species were let grown in pots under greenhouse conditions. When seedlings were approximately 10 cm height above soil surface they were thinned to nine plants per each pot. That time a differentiation in irrigation regime was started. For each species half of the pots was regularly irrigated (until 100% of the field capacity) while the rest half was less irrigated (40% of the field capacity). There were three pots per species and irrigation regime. Plant size (height/length) records were taken approximately every four days and expressed in mm. In summary the size of a total of 27 plants (3 pots x 9 plant/pot) per species and treatment was recorded every time.

The course in time of plant size changes was simulated with the means of twelve growth models. The mathematical expressions of these models are found in Seaby and Henderson (2006). Initially, best model selection was based on growth data obtained from controlled conditions (irrigation until 100% of the field capacity). In a second step, the same procedure was applied in the growth data obtained under the "less-irrigation" regime, as to infer about the first alternative, i.e. if a different type of growth model is more appropriate to describe changes of growth pattern in time. If the first alternative was not true and the same type of growth model fitted the data obtained from both treatments, then basic model parameters, especially those of biological meaning, were further compared. Statistical comparisons (two-tailed *t*-tests for independent samples with level of significance α=0.050) were made for: (i) the parameter that expresses the growth rate, and (ii) the parameter determining inflection point.

Model selection, in terms of best fitting, was based on three basic diagnostic tools, i.e. the Weighted Sum of Squares of Residuals (WSS), the Akaike Information Criterion (AIC) and the Schwarz Criterion (SC) (Seaby and Henderson, 2006). The sum of squared residuals gives a measure of the deviation of the observed size values from that predicted by the selected model. If standard deviations (*SD*) have been given for the mean size at age, then *WSS* is calculated as:

$$WSS = \sum_{i=1}^{i=n} \frac{1}{SD_i^2} (Y_{observed,i} - Y_{calculated,i})^2$$

where *n*: number of observations. The AIC and SC criteria take into account both the closeness of fit of the points to the model, and the number of parameters used by the model. They are calculated as:

$$AIC = N \log(WSS) + 2M \text{ , and } SC = N \ln(WSS) + \ln(N) M$$

where *N*: number of data points, and *M* is the number of model parameters.

Model parameters, their statistics and model diagnostics were calculated using the *Growth II* modelling package (ver. 2.1.0.48) of © 2006 PISCES Conservation Ltd, designed by R.M.H. Seaby and P.A. Henderson.

Results and discussion

The four-parameter Janoschek's model simulates best the growth pattern of *T. angustifolium* and *M. disciformis* and the four-parameter Morgan-Mercer-Flodin's model is appropriate to simulate the growth of *O. caput-galli* (selected examples of the curves' shape are illustrated in Figs 1 and 2). Model diagnostics indicated that there was not differentiation in best model's selection due to the applied treatment; the same model fitted to the growth data obtained either from full irrigation or limited irrigation (Table 1).

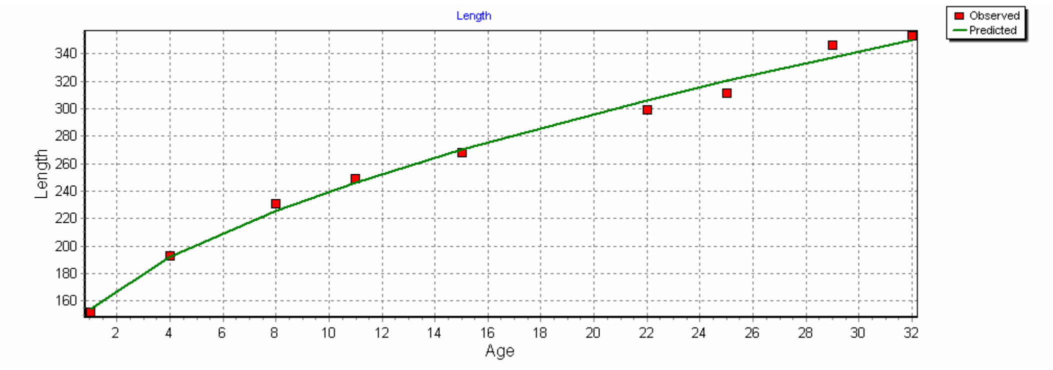

Fig. 1. Fitting of the Janoschek's growth curve in the *Trifolium angustifolium* size data when it was 100% irrigated.

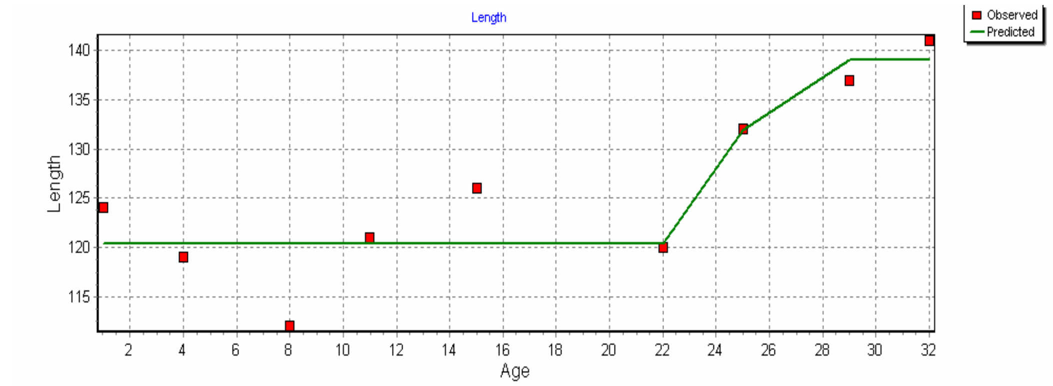

Fig. 2. Fitting of the Morgan-Mercer-Flodin's growth curve in the *Onobrychis caput-galli* size data when it was 100% irrigated.

Table 1. Diagnostics for the selected best model fit

Treatment	Species	Best model fitted	WSS	AIC	SC
100% irrigated	*Trifolium angustifolium*	Janoschek	265.04	58.22	59.01
	Medicago disciformis	Janoschek	339.24	60.44	61.23
	Onobrychis caput-galli	Morgan Mercer Flodin	125.37	51.48	52.27
40% irrigated	*Trifolium angustifolium*	Janoschek	375.93	61.36	62.15
	Medicago disciformis	Janoschek	1125.92	71.24	72.03
	Onobrychis caput-galli	Morgan Mercer Flodin	337.43	60.39	61.18

Irrigation regime significantly affects the *K*-parameter determining the growth rate for *T. angustifolium* (Data not shown). Under full irrigation the *K*-parameter (K_{100}=0.0072) was significantly higher than under less irrigation (K_{40}=0.0042) ($t_{(0.05,\ df=16)}$=5.953***, P=0.0000203, for equal variances assumed since F_{Levene}=1.647NS, P=0.218). On the contrary, irrigation regime has not any significant effect on δ-parameter (δ_{100}=0.583, δ_{40}=0.667) that determines the inflection point of growth curve ($t_{(0.05,\ df=16)}$=-1.547NS, P=0.142, for equal variances assumed since F_{Levene}=0.543NS, P=0.472). For *M. disciformis* the *K*-parameter was not significantly affected by the irrigation regime (K_{100}=0.0023, K_{40}=0.0033) ($t_{(0.05,\ df=16)}$=-1.416NS, P=0.176, for equal variances assumed since F_{Levene}=1.552NS, P=0.231), while the δ-parameter was significantly higher under full irrigation (δ_{100}=1.291) than less irrigation (δ_{40}=0.491) ($t_{(0.05,\ df=16)}$=9.156***, P=0.0000000923, for equal variances assumed since F_{Levene}=0.045NS, P=0.834). Similarly, for *O. caput-galli* the *K*-parameter was not significantly affected by the irrigation regime (K_{100}=0.0403, K_{40}=0.0344) ($t_{(0.05,\ df=14.29)}$=0.731NS, P=0.476, equal variances not assumed since F_{Levene}=4.589*, P=0.048), while the δ-parameter was significantly higher under less irrigation (δ_{40}=108.20) than full irrigation (δ_{100}=51.33) ($t_{(0.05,\ df=16)}$=-9.650***, P=0.0000000450, for equal variances assumed since F_{Levene}=0.0014NS, P=0.971).

Plant growth models play a broad role in management. Used to advantage and in conjunction with other resource and environmental data, growth models may serve to formulate management prescriptions, and make predictions (Vanclay, 1995). Functional growth models are important informative tools to these purposes, especially when their parameters are of biological importance. It was shown that the *K*- and δ-parameters highlight the intrisic rate of growth (the former) and the passing from the vegetative to reproductive stage (the latter) (Vrahnakis, 2000). As *K* increases in magnitude, the curve becomes steeper and rises faster towards the asymptotic value, and as δ decreases in magnitude, the point of inflection moves to the right and the curve becomes less steep. The results here showed that the growth of the three species may be described by the same functional model, either their plants are full or less irrigated, and that under less irrigation (i) the growth rate of *T. angustifolium* is decelerated, but the flowering process remains unaffected, (ii) the growth rate of *M. disciformis* remains unaffected, but the flowering process is decelerated, and (iii) the growth rate of *O. caput-galli* remains unaffected and the flowering process is accelerated. Further flowering experiments may help us to predict the exact flowering time, so provide us with an important management information.

Conclusions

The four-parameter Janoschek's model simulates best the growth pattern of *T. angustifolium* and *M. disciformis* and the four-parameter Morgan-Mercer-Flodin's model is appropriate to simulate the growth of *O. caput-galli*.

There was not differentiation between treatments in respect to the best model selection.

Under less irrigation (i) the growth rate of *T. angustifolium* is decelerated, but the flowering process remains unaffected, (ii) the growth rate of *M. disciformis* remains unaffected, but the flowering process is decelerated, and (iii) the growth rate of *O. caput-galli* remains unaffected and the flowering process is accelerated.

Acknowledgements

This paper is a part of the researching project "Impact of Climate on the Ecophysiology, Seed Dormancy, and Viability of Self-Reseeding Legumes". The Project is co-funded by the European Social Fund and National Resources - (EPEAEK-II) ARCHIMIDIS.

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