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A model to simulate tiller dynamics of perennial forage grasses under severe Mediterranean drought

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SUMMARY – The STICS crop model is used to simulate growth and forage production of grass pastures in cool temperate conditions (INRA France, www.avignon.inra.fr/stics/). To extend it to Mediterranean areas and to use it to anticipate future effects of the global warming, its forecasting performances during hot dry summers need to be improved, especially by taking into account variations of plant and tiller densities. The adapted formalism dealt with four successive phases: (a,b) cessation of leaf growth and plant development, followed by progressive lamina senescence, computed as a function of soil water deficit; (c) progressive tiller mortality, as a function of the actual/potential evapotranspiration ratio at individual tiller level; and (d) sward growth and tillering rates after autumn rainfalls, as a function of surviving tiller density, remaining leaf area index, and plant reserves at the end of the drought period. The model will be parameterized and tested for different species and types of cultivars. Future developments will aim to simulate the evolutions of plant densities of bi- or tri-specific mixtures.

Keywords: Modelling, perennial grasses, drought resistance, tiller dynamics, forage yield, STICS.

***RESUME –** "Modèle pour simuler la dynamique de tallage des graminées fourragères pérennes sous forte sécheresse méditerranéenne". Un modèle d'estimation de la croissance des prairies, incluant la variation de peuplement de talles, est un outil important pour anticiper et gérer les situations de crises ou l'effet du changement climatique. Pour disposer d'un tel modèle dans le cas des prairies monospécifiques en conditions méditerranéennes, nous avons ajouté un module de dynamique de talles au modèle de culture STICS, déjà validé pour les prairies de graminées en climat tempéré (INRA France,* www.avignon.inra.fr/stics/*). Les formalismes modifiés décrivent quatre étapes successives : (a, b) arrêt de l'allongement foliaire et du développement, puis sénescence foliaire, en fonction du déficit hydrique ; (c) mortalité progressive des talles, en fonction du ratio "évapotranspiration réelle / évapotranspiration potentielle" ; et (d) reprise et retallage après les pluies d'automne, en tenant compte d'un potentiel de reconstitution. Le modèle sera paramétré pour différentes espèces et types variétaux. Les travaux futurs viseront à simuler le fonctionnement pluriannuel de prairies plurispécifiques en conditions méditerranéennes.*

***Mots-clés :** Modélisation, prairie permanente, résistance à la sécheresse, dynamique de talles, STICS.*

Introduction

For perennial forage plants like cocksfoot, tall fescue or alfalfa, drought resistance has a different meaning according to climatic areas. In temperate areas, it is the ability of plants to maintain growth during short periods of moderate water stress and moderately high temperatures, which depends mainly on root depth. In very dry (arid and lower semi-arid) Mediterranean climates with climatic deficits higher than 700 mm, leaf growth ceases completely during five or six months and summer yield is not expected. Drought resistance criteria are survival rates and regrowth quality after autumn rainfalls. The most resistant plants are summer dormant Mediterranean cultivars with low growth potential in summer and/or high dehydration tolerance of meristems (Volaire *et al*., 2006). In intermediate areas (sub-humid and semi-arid Mediterranean with dry period of 3 to 6 months with cumulated climatic deficits of 300 to 700 mm), cultivars must be able to follow both strategies depending on summer drought duration and cumulated water deficits.

Climate experts forecast a global increase in temperature from 1.8 to 4°C and modifications in rainfall distribution until 2100 (IPCC, 2007). Severe droughts have been unusually frequent recently in South-East France (2003, 2005 and 2006), with dramatic impacts on livestock farms. To model pluriannual production in Mediterranean conditions, and to anticipate the effect of climate evolutions, forage production models are necessary, and they must integrate the possible effects of drought on growth and the evolutions of plant densities in a wide range of conditions. The STICS model (Brisson *et al.*, 2002) was chosen to carry out this work. It is validated for monospecific pasture in cool temperate conditions (Ruget *et al.*, 2006; Ruget and Brisson, 2007). In this study, we aimed to extend the validity of this model to Mediterranean conditions. To reach this objective, a tiller density module had to be integrated into the pre-existing STICS model, to simulate tiller mortality imposed by summer conditions, and partial or total recovery by tillering in next autumn and winter. The final objective is to model pluri-annual production (cumulative effects of droughted/humid seasons alternation) and to take into account types of plants exhibiting contrasting drought resistance strategies (cocksfoot/tall fescue, temperate/Mediterranean, deep or shallow root systems, summer dormant or not).

Methods: modelled mechanisms and formalisms

In Mediterranean areas, after the hay cut of grasses at heading (between 1 April and 15 May), growth is generally stopped by drought onset in May or June. After cessation of leaf growth, pasture response and modelling questions relative to summer drought effect could be synthesized in three successive periods (Fig. 1): (a) reserves accumulation, (b) progressive lamina senescence, (c) progressive apex and tiller mortality, followed by (d) regrowth after autumn rainfall including both production of new tillers and growth of surviving ones (Volaire *et al.*, 1998; Volaire and Lelièvre, 2001).

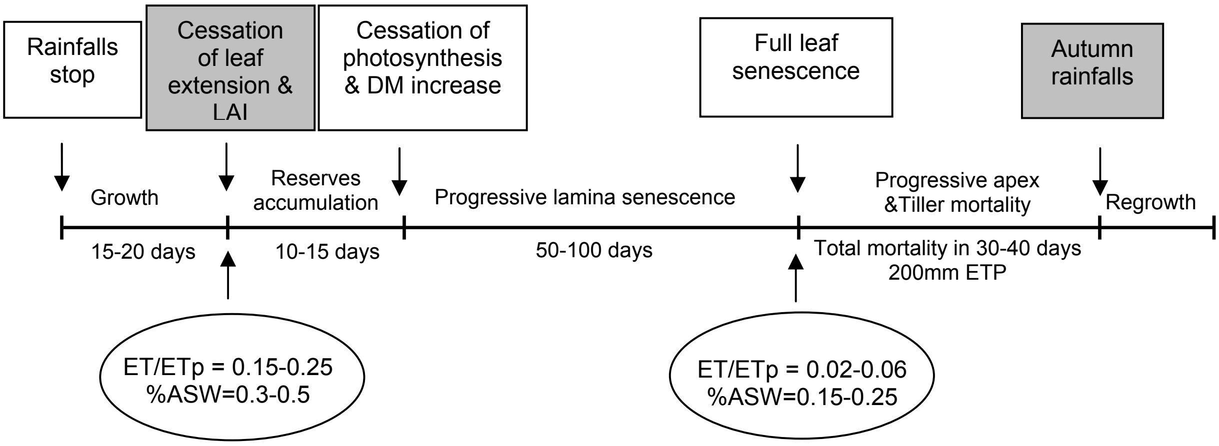

Fig. 1. Schematic representation of grass pastures physiology during and after long and intense summer drought. Data of ET (actual evapotranspiration), ET_p (potential evapotranspiration), ASW (available soil water) and duration (days), correspond to grasses in deep soils at 38-43°N.

(a)- Beginning of the dry period (cessation of leaf growth and plant development under the control of increasing water deficit; reserves accumulation): following autumn optimal sowing, plant density at the end of winter will be optimal (N_0 about 3000 tiller/m² for dactylis). When drought progresses at the end of spring, leaf growth, appearance of new leaves, and differentiation of leaf primordia, stop progressively and simultaneously. The decrease of leaf elongation being more rapid than the decrease of photosynthesis activity, water soluble carbohydrates accumulate in sheaths and enclosed meristems. At this period, concentrations of plant reserves are at highest levels, the quantity R_0 being generally between 30 and 60 g/m², mainly in the 5 basal cm of vegetation. It comes in addition with residual structural dry matter after cut (SDM_0 = 60 to 120 g/m²). SDM_0 and R_0 are divided between N_0 tillers.

(b)- Lamina senescence and progressive LAI reduction as water deficit increases: the STICS model applied in cool temperate conditions (extended to humid periods in the Mediterranean) generates leaf area senescence, considering that a given element of LAI has a lifespan. It is the direct consequence of self-umbrage effect in optimal or sub-optimal growth conditions: on a tiller, the leaf n-4 becomes senescent when the leaf n appears. Under drought, self-umbrage effect does not occur because leaf appearance is totally stopped. A young leaf starting its elongation just before the onset of drought in early June can resume its elongation in next autumn, 3 or 4 months later. Its lifespan can be higher than 2000 degree-days versus 400 d-d in optimal growth conditions. This is taken into account through conditioning degree-days of life duration by a stress function.

Moreover, when LAI is close to zero, transpiration is maintained to a minimum because of cuticular transpiration through surviving sheaths and apices. The model has been adapted by including a virtual non photosynthetic leaf area (LAI_{apex}). This LAI_{apex} appears when the LAI is lower than a threshold (parameter) and the addition of LAI and LAI_{apex} cannot be higher than this threshold.

(c) Tiller density decrease in late severe drought: when plants have lost most leaf area, tillers begin to die progressively. Susceptibility of cultivars is a function of root depth, capacity to uptake water at low potential, level of summer dormancy, etc. (Volaire and Lelièvre, 2001). We introduced a mortality module in STICS. For a given day j, daily mortality m_j is calculated as indicated below, and the new tiller density for day j+1 is: $N_{j+1} = N_j - m_j$. The residual structural dry matter, reserves quantity, and root density are affected by the evolution of N_j. Tiller mortality along time is modelled by using a stochastic approach representing the variability of water flux through tillers having variable access to the soil water reserve. Variability is represented by a distribution law of individual ratios ET/ET_p. Individual tiller mortality occurs at a given "mortality ET/ET_p threshold" for a given species and cultivar. A constraint is to choose a mathematical law which does not give negative values for this ratio. In fact, a negative ET is not acceptable. The gamma law was chosen because of its ability to have different patterns and its simplicity (two parameters). Its characteristic functions and properties are:

Probability density function:

$$f(x) = x^{k-1}\frac{\exp(-x/\theta)}{\Gamma(k)\,\theta^k}$$

$E(x) = k\,\theta$ k : shape parameter

$V(x) = k\,\theta^2$ θ : scale parameter

Cumulative distribution function:

$$F(x) = \frac{\gamma(k, x/\theta)}{\Gamma(k)}$$

(d) Growth and development recovery of surviving tillers, tillering dynamics after autumn rehydratation: a rapid regrowth is generally observed, which cannot be explained by direct photosynthetic activity restarting from very low residual LAI at the end of the drought. Rapid regrowth is permitted by mobilisation of reserves in sheaths and apices (Volaire *et al.*, 1998). In the model, the remaining reserves at the end of drought (Rf, depending on surviving density Nf) are remobilised and converted into LAI and roots during a short period (around 120 degree-days, 6 to 8 days) following first autumn rainfalls. After this, daily growth depends only on photosynthetic activity splitted into lamina, new tillers, and new roots. Further tiller density Nj will have maximum values which are a function of surviving density Nf. The limit of Nj will impose maximum values to daily LAI and DM increase, which affects future yield potential when Nf is under a threshold (around 500 surviving tillers/m² in cocksfoot).

Results

All these formalisms were integrated into the STICS-grass model in a collaborative work between grass-pasture agronomists (INRA Montpellier) and STICS modellers (INRA Avignon). A version of the model is now parameterized for grass pasture (Mediterranean non dormant cocksfoot and tall fescue). It allows simulating the effect of different levels of plant drought resistance characterised by root depth and different mortality ET/ET_p thresholds. Fig. 2 shows results for several mortality thresholds in a deep soil (1.5 to 2 m deep) with high water reserve. The climate data are those of 2003 (a hot dry year in South-East of France) in Montpellier-France, except rainfall regime which is modified (rainout shelter with last water supply on 30 April, and no rainfall until rehydratation on 5 September), simulating a drought period of 153 days with 910 mm of climatic deficit.

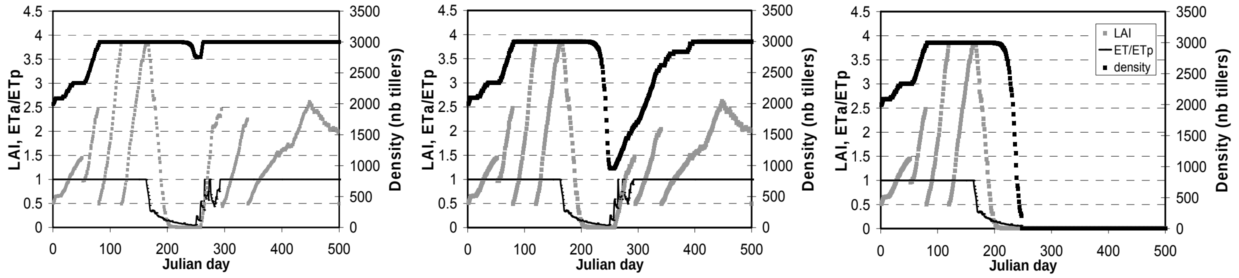

Fig. 2. Simulations of tiller mortality under intense summer drought and recovery after autumn rainfall of sward grasses, for three mortality thresholds: (a) 0.02; (b) 0.03; (c) 0.04 from left to right.

In the first case (a), with a mortality threshold ET/ET_p = 0.02 corresponding to a drought resistant cultivar, the LAI senescence is complete but no significant mortality appears. At rehydratation the regrowth is rapid. In the second case (b), resistance is lower (mortality threshold 0.03), there is a significant mortality (Nf around 900 tillers/m²). The first regrowth after rehydratation is significantly lower than in the first case, but the potential is not affected; the third regrowth recovers totally compared to (a). In the last case (c), the cultivar is not enough resistant and all tillers disappear. These examples give a realistic representation of grass cultivars reactions at long intense Mediterranean summer droughts. We obtain similar variations when root depth is depending on species and cultivars (Volaire *et al*., 1998)

Discussion: parameterization, validation and future adaptation

The proposed formalisms result from a limited number of experiments conducted at INRA Montpellier-Mauguio in France. Other experiments are running in Montpellier to complete a first set of parameterization relative to different types of cocksfoot and tall fescue (no summer dormant, Mediterranean *vs* temperate types). It includes cultivars of *Festuca* (Flecha, Australia; Soni, France) and *Dactylis* (Porto, Australia; Medly, France). Measurements concern production (LAI and dry matter), tiller density and reserves quantity (water soluble carbohydrates). At autumn rehydratation we will measure tiller survival rates, LAI recovery rate and progressive population reconstruction (tillering). We aim to obtain different parameterizations for identified group of cultivars regarding to drought resistance. The most important parameters are root depth and mortality threshold.

After parameterization for different cultivars, the model validation will be carried out with data already collected in a network of trials developed in a European project (PERMED) with sites in Montpellier (France), North Sardinia, Algeria, and Elvas (Portugal). This ultimate validation with data coming from semi-arid Mediterranean areas will also give validation for correct simulation of climate change in actual sub-humid Mediterranean areas.

Some new improvements are already considered for the future. In fact, a good simulation of grass pasture under severe drought conditions needs to take into account: (i) the dehydration tolerance (Volaire *et al*., 1998), and (ii) the capacity of some genotypes to exhibit summer dormancy (Volaire and Norton, 2006). Another important future objective will aim to simulate pluri-annual evolutions of plant densities, growth, and yield, of mixed pastures with two or three components over Mediterranean summer droughts.

Acknowledgements

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