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Indirect assessment of flooding duration as a driving factor of plant diversity in wet grasslands

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Abstract Flooding duration in wet grasslands represents a crucial indicator for agricultural and biodiversity targets. However, flooding duration in wet grasslands is not an easy variable to observe by itself, all the more so because it is really heterogeneous in space, due to subtle topographic relief. Moreover, actual plant diversity, composition and community structure are the synthetic results of the hydro-meteorological history in the past. Wet grasslands are thus truly ungauged with respect to flooding duration, which has to be simulated in a robust manner both over the spatial territory and back over the past many years. A water-balance modelling with a daily time step, based on available meteorological data and on a precise topographic characterization, was proposed to assess the flooding duration at any location of a studied area situated along the west coast of France and over a period of six years. The simulated (calculated) flooding durations were used in the plant species distribution modelling based on 350 sampled vegetation quadrats. From field-based milestone observations of water level, the hydrological modelling was shown to predict well the annual cumulative flooding duration at any spot. A strong and consistent effect of flooding duration was evident for 29 species. Plant diversity appeared to reach a maximum at an intermediate flooding duration. The hydrology-vegetation modelling approach could thus lead to a robust and versatile tool to predict the consequences of changes in flooding regime on vegetation patterns.

Key words flood-meadows; modelling; PUB; response curve; species richness; water balance

INTRODUCTION

The distribution of plants in wetland ecosystems is primarily controlled by hydrology (e.g. van der Valk *et al.*, 1994). Indeed, the location of a plant along a flooding gradient has larger influence than biotic factors such as interspecific competition (Brose & Tielbörger, 2005) or the composition of the seed-banks (Keddy & Reznicek, 1982; Schneider & Sharitz, 1986; Weiher & Keddy, 1995; Lenssen *et al.*, 1999). Flooding regime has two major components which influence vegetation distribution: water depth and flooding duration. Effects of flooding duration on vegetation arrangement has received little attention as most studies have dealt with water level data only (e.g. Spence, 1982; Keddy & Reznicek, 1986; van der Valk, 1994; Seabloom *et al.*, 1998, 2001). However, flooding duration in wet grasslands represents a crucial indicator for agricultural and biodiversity targets as it could largely determine primary production, its quality and time-pattern together with species diversity, and guidelines for water management decisions appear now much in demand. In many marshlands situated along the west coast of France, flooding duration could be controlled by locks since field depressions are connected to canals. In some wetlands, land use managers have proposed to increase flood duration in order to ameliorate the carrying capacity for birds. Only few studies have directly dealt with flooding duration (e.g. Bouzillé *et al.*, 2001; Hölzel & Otte, 2001; Warwick & Brock, 2003) as this parameter is very time-consuming to collect in the field, and cannot be easily assessed at fine temporal and spatial scales. The lack of gauging is a major problem as regards this parameter and a robust indirect assessment is therefore needed.

In this study, a simple hydrological model with a daily time step was used to assess the flooding duration at any location of a studied depression, over a period of six years, which is considered to be influential on the actual diversity. Such a model allows us to propose data collection on flooding duration at a very fine spatial scale. The consequences of variations in space of the flooding duration on the realized niche of a species were investigated through coupling hydrological and vegetation modelling. Basically, the approach consisted in: (a) modelling the flooding duration at any location of the studied area through a simple water balance model; and then (b) linking these data to vegetation composition with a generalized linear model in order to predict the realized niche of each species. The results of the niche model were then used to predict the most likely plant composition (assemblage of species) and the expected species richness for any flooding duration.

MATERIALS AND METHODS

Study area

Data were collected in an experimental site in the Marais Poitevin (46°28′N and 1°13′W), situated on the Atlantic coast of France (Loucougaray *et al.*, 2004). It is located on a 250-ha commonly-owned meadow that was formed during the tenth century. This land was traditionally used for extensive grazing from April to December, mainly by mixed herds of cattle and horses. Topography is irregular with many low-lying seasonally flooded depressions and high level flats with intermediate gentle slopes with up to 50 cm elevation difference. The plant community is a continuum of mesophilous, meso-hygrophilous and hygrophilous vegetation (Amiaud *et al.*, 1998). In this area, we studied one isolated depression which is not connected to the surrounding canal. This depression is the highest of the neighbourhood.

Hydrological modelling

To assess the flooding duration (in days) at any location of the studied area a simple hydrological model has been implemented. The general time-discretized water balance equation is:

$$\Delta V(t) = V(t+\Delta t) - V(t) = I(t) - O(t) \tag{1}$$

where $\Delta V(t)$ is the change of water storage (in m^3) during the time interval $[t,t+\Delta t]$; $V(t)$ is the volume of water (in m^3) in the depression at time t; $I(t)$ and $O(t)$ are respectively the total inputs and outputs of water (in m^3) during the time interval $[t,t+\Delta t]$.

The studied depression cannot receive water from overflow of other depressions. Thus, the inputs during the time interval $[t,t+\Delta t]$, $I(t)$, are only the accumulated precipitation, $P(t)$ (in m), that falls over the total area of the depression basin, S_{tot} (in m^2):

$$I(t) = P(t) \cdot S_{tot} \tag{2}$$

Percolation is firstly assumed to be negligible in the studied system as the soils are rich in clay (Amiaud *et al.*, 1998). Then the outputs during the time interval $[t,t+\Delta t]$, $O(t)$ are only caused by evapotranspiration, $ETP(t)$ (in m), which depends on $S(t)$, the surface area covered by water at time t (in m^2). In addition, when the water content exceeds the total volume (V_{max}) of the depression, the excess water, $V_{overflow}(t)$ (in m^3), is lost by overflow:

$$O(t) = ETP(t) \cdot S(t) + V_{overflow}(t) \tag{3}$$

A precise topographic mapping of the studied area has been carried out using a theodolite (Wild T1000) providing a precision of one centimetre on the Z-axis and based on a sampling of 3000 topographic points. Then a digital elevation model (DEM) was built using the program AUTOMAP 14© of the AUTOCAD© package. The resulting DEM was used to identify the set of (Z, S, V) values and furthermore the surface-volume and level-volume curves. These allowed us to express equation (1) in terms of $Z(t)$, the temporal evolution of the water level. At any point A, characterized by its 3-D Cartesian coordinates (X_a, Y_a, Z_a), and any time step t, the comparison of $Z(t)$ and Z_a indicate whether the point is flooded or not. Iterating this comparison for each day allowed us to assess the annual flooding duration at any point of the depression during one hydrological year (from 1 August to 31 July). The model was initialized on the 1 August 1996 by considering that each depression was empty as it is always the case in summer. The model was further re-initialized ($V(0) = 0$) each year on the 1 August in order to correct for the infiltration, which may not be negligible in summer. The studied explicative vegetation variable is the mean annual flooding duration, d_a (mean annual flooding duration at the point A) (flooding duration, hereafter), which represents the average of annual flooding durations during six hydrological years (from 1996 to 2002). The choice of using the time-integrated variable d_a is driven by two hypotheses: (a) the topographic changes are negligible on a six-year period; (b) the variable integrates the temporal climatic variability and its resulting consequences on vegetation.

Meteorological data from 1 August 1996 to 31 July 2002 were obtained from the Météo France weather station of St-Gemme-La-Plaine located 10 km from the studied site, with no difference of climatic context due to orographic or oceanic effects. The station provided the daily cumulated precipitation and the daily cumulated evapotranspiration (Penman-Monteith's ETP) for this six-year period.

The broad model performance was assessed during spring of 2002: the water level was measured for six dates (between April and June) and compared to simulated values.

Vegetation modelling

A random sampling of 350 quadrats (25 × 25 cm) was carried out in the studied depression, and all the observed species and the precise location of the quadrats were recorded. The logit distribution of the probability of occurrence of the *i*th species was assumed to be a quadratic function of the flooding duration:

$$\ln(p_i(d_a) / (1 - p_i(d_a)) = b_{i0} + b_{i1}.d_a + b_{i2}.d_a^2 \qquad (6)$$

where $p_i(d_a)$ is the conditional probability of species i being present at the point A where the flooding duration is d_a, and b_{ij} is the jth regression coefficient for the species i.

Values of b_{ij} were estimated by maximizing the likelihood of the observations with the GENMOD procedure of SAS© Software. Chi-square tests (asymptotical approximation of likelihood ratio tests, McCullagh & Nelder, 1989) were sequentially used to assess the significance of the terms (d_a and d_a^2) included in the model. The significance threshold was set to 0.01. As the analysis was simultaneously performed on 40 plant species, a Bonferonni correction was applied to account for multiple tests.

For the sake of simplicity, the probability of occurrence of any species in the assembly was assumed to depend only on the flooding duration and not on the plant community composition and other abiotic factors. With that simplifying assumption, the expectancy of the total number of species $R(d_a)$, that is species diversity, in a quadrat situated at a location characterized by a flooding duration d_a is easy to compute:

$$R_i(d_a) = \Sigma_i\, p_i(d_a) \qquad (7)$$

RESULTS

Hydrological modelling

Observed and simulated water levels during the period April to June 2002 are reported in Fig. 1. During this period, the error of the hydrological model was on average of 1.3 cm corresponding to an error of one week of flooding duration in a year.

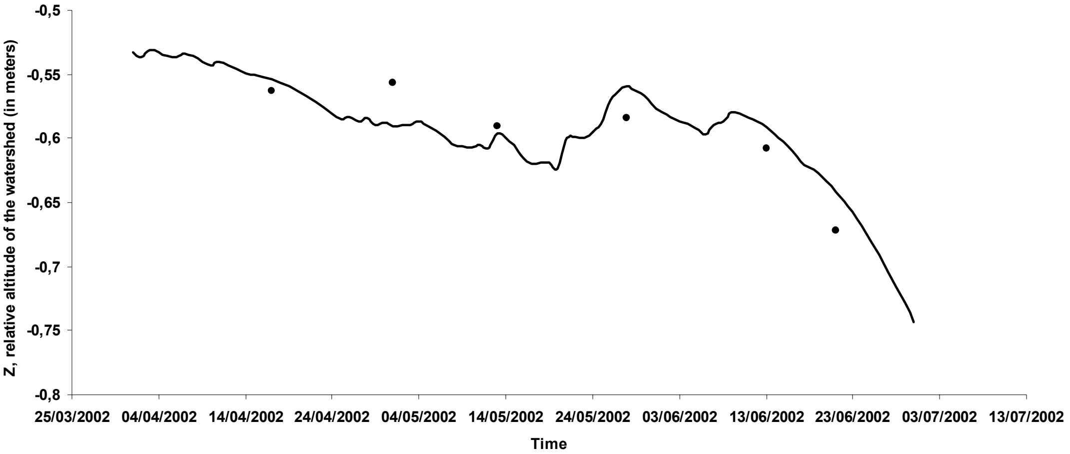


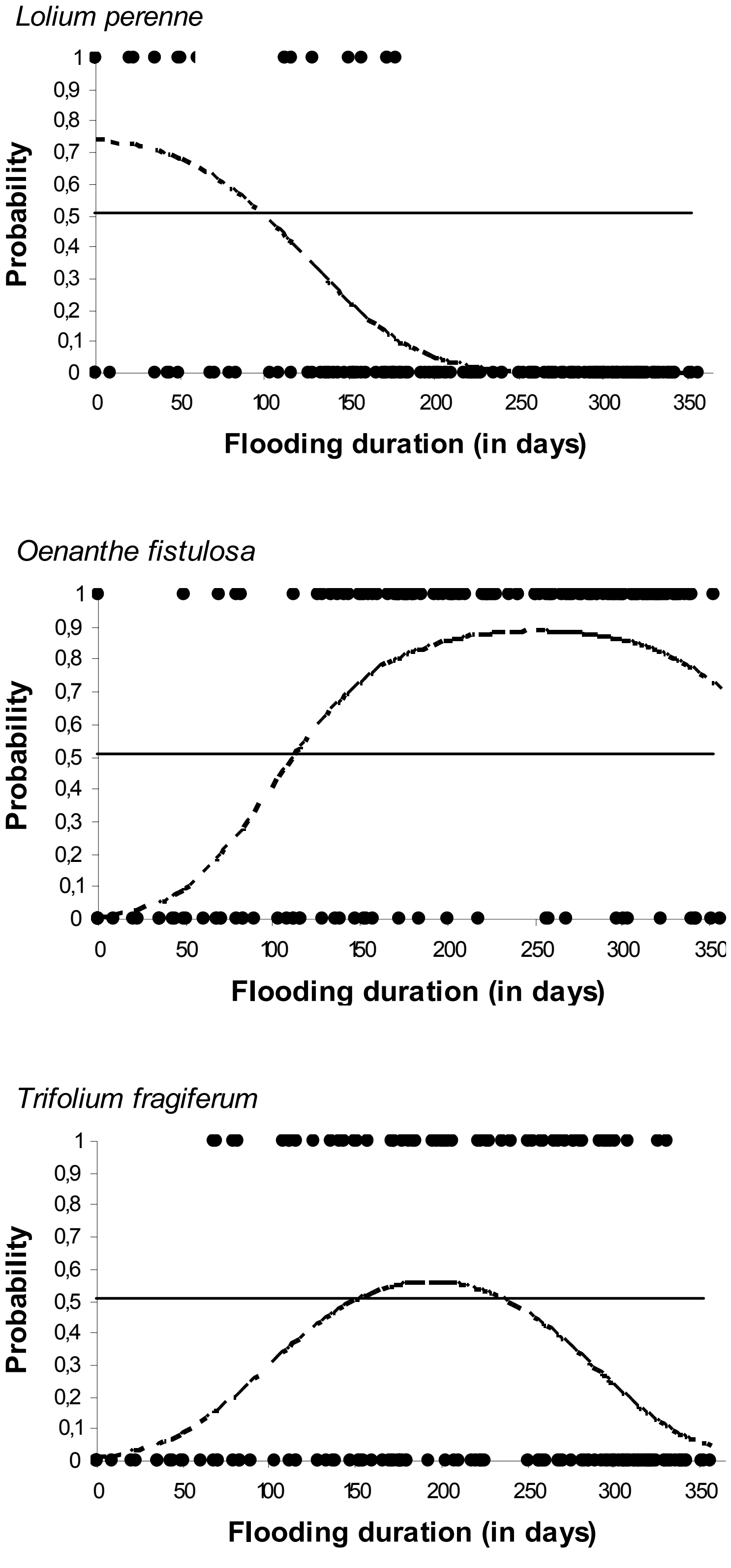
Fig. 1 Observed (points) and simulated (line) water levels during spring of 2002.

Species response curves and species richness

Forty species have been observed (Table 1). The effect of the flooding duration on the probability of occurrence was significant for 29 species. Figure 2 presents an example of the types of response curve obtained. Modelled species richness showed a rapid increase with flooding duration up to about 90 days of flooding, followed by a slow decrease for flooding durations exceeding 90 days (Fig. 3).

Table 1 List of observed species and the results of logistic regressions for each species (S: significant; NS: non-significant).

Species	P	Effect
Agrostis stolonifera	2.13E-06	S
Alopecurus bubosus	1.06E-07	S
Alopecurus geniculatus	5.60E-03	NS
Baldellia ranunculoides	1.19E-09	S
Bellis perennis	9.15E-07	S
Bromus commutatus	1.22E-12	S
Carex divisa	6.96E-20	S
Cerastium glomeratum	0.118	NS
Cynosurus cristatus	1.26E-07	S
Eleocharis palustris	1.65E-27	S
Elymus repens	4.60E-08	S
Galium debile	3.13E-08	S
Gaudinia fragilis	0.126	NS
Geranium dissectum	3.26E-06	S
Glyceria fluitans	6.67E-14	S
Hordeum marinum	3.11E-09	S
Hordeum secalinum	6.49E-11	S
Juncus articulatus	1.09E-15	S
Juncus gerardi	3.68E-09	S
Leontodon autumnalis	2.69E-04	NS
Leontodon taraxacoides	1.55E-04	S
Lolium perenne	6.39E-20	S
Lotus tenuis	0.062	NS
Mentha pulegium	5.69E-08	S
Myosotis laxa	3.71E-03	NS
Oenanthe fistulosa	1.78E-22	S
Parapholis strigosa	8.69E-10	S
Plantago coronopus	6.55E-08	S
Poa annua	1.44E-06	S
Ranunculus ophioglossifolius	1.03E-06	S
Ranunculus repens	1.88E-07	S
Ranunculus sardous	0.200	NS
Ranunculus trichophyllus	0.184	NS
Rumex conglomeratus	0.198	NS
Spergularia marina	2.41E-04	S
Taraxacum officinale	1.46E-02	NS
Trifolium fragiferum	4.95E-10	S
Trifolium michelianum	3.56E-06	S
Trifolium resupinatum	2.58E-03	NS
Trifolium squamosum	1.14E-05	S


Lolium perenne

Oenanthe fistulosa

Trifolium fragiferum

Fig. 2 Probability of occurrence of *Lolium perenne, Oenanthe fistulosa, Trifolium fragiferum* as a function of mean annual flooding duration as predicted by logistic regression models (dotted lines). The dots are the observations (in presence/absence) used to fit the models.

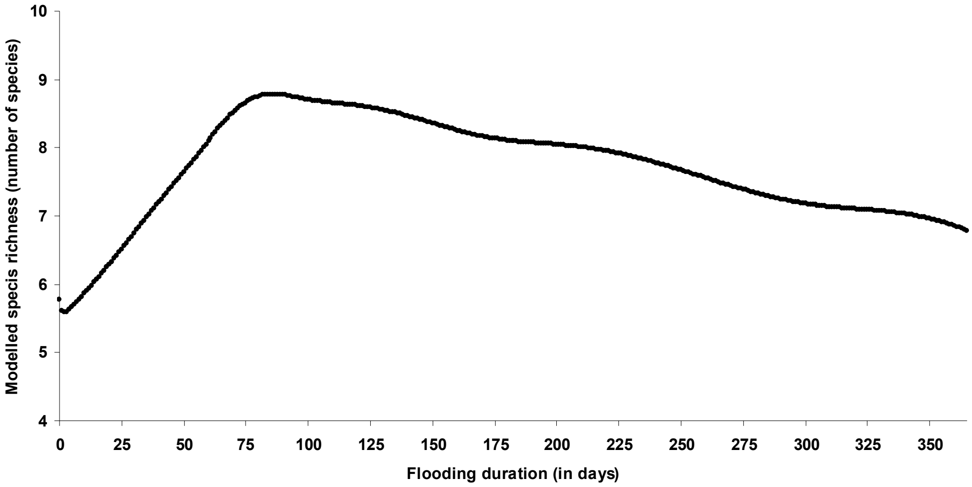


Fig. 3 Modelled species richness (number of species) as a function of mean annual flooding duration.

DISCUSSION

Model validation performed during the spring of 2002 showed a high reliability of the hydrological model in spite of its simple assumptions. The accuracy could, however, be lower in summer when the model seems to overestimate the flooding duration. This could be due to a non-negligible infiltration in summer because clay-rich soils can develop surface cracks during the dry season that can complicate the relationship between rainfall and runoff (Novak *et al.*, 2000). However, the annual resetting of the model on 1 August is probably sufficient to correct most of this bias.

Modelled flooding duration appeared to be a driving factor of the distribution of 73% of the plant species. Moreover, the relationship between species diversity and flooding duration was not monotonic. Indeed species diversity reached its maximum at an intermediate level of flooding duration (about 90 days). This result could have some important implications for flooding management. Indeed land-use managers have proposed to extend flooding duration to increase the carrying capacity for birds. Findings of this study suggest that such a manipulation could result in a loss of plant richness. The flooding duration associated to the highest level of biodiversity (90 days) is inferior to the threshold duration required for both *Ranunculus ophioglossifolius* and *Trifolium michelianum*, the two species of regional interest that can be encountered in the studied area (136 and 117 days of flooding, respectively). In these multifunctional wetlands, land use managers will then have to select the best trade-off between achieving the highest biodiversity, increasing the probability of occurrence of rare species or enhancing the carrying capacity for birds. Finally, it is necessary to evaluate the potential reduction in agricultural value of meadows subjected to prolonged flooding duration.

CONCLUSION

Coupling hydrological and vegetation modelling is generally poorly used in the context of land use management (Wassen & Grootjans, 1996; Porporato & Rodriguez-

Iturbe, 2002). However, in this study, hydrological modelling has been shown to be an efficient tool to describe vegetation distribution along a flooding gradient. This kind of simple modelling could also be used to predict consequences of changes in the flooding regime on vegetation. The work presented in this paper focused on a single isolated depression, but the hydrological model can be extended to describe the hydrological dynamics of an entire population of depressions as Pyke (2004) has done for vernal pools in California. In the studied region, wetland managers can easily act on flooding duration and on water depth in field depressions through managing water depth in the surrounding canals and determining whether or not to allow water to "run off" the depressions in the spring period. Coupling hydrology and vegetation models could then allow the prediction of the consequences of any management decision on vegetation patterns in the field. The proposed mixed model could consequently provide the core of a decision support system for wetland managers.

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