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How do shoot clipping and tuber harvesting combine to affect *Bolboschoenus maritimus* recovery capacities?

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Abstract: In French Mediterranean wetlands, the combined effects of predation of tubers by wildlife and grazing of aboveground tissue by livestock on the recovery capacities of *Bolboschoenus maritimus* (L.) Palla are not well known. A container study was conducted that applied tuber harvests at varying levels (20%–90%) and shoot clipping (with or without). Response to harvesting and clipping was recorded as changes in total biomass, number, and mean mass of tubers (calculation of variation indexes). *Bolboschoenus maritimus* failed to recover from even the lowest tuber harvesting level of 20% and the total number of tubers and biomass decreased. A significant decrease in mean tuber mass over time and approximately no production of new tubers accounted for this absence of compensatory response. The harvesting level had a linear effect on the variation indices of total number of tubers and mean tuber mass. By separating the relative effect of shoot clipping from that of tuber harvesting alone, the results showed that clipping had an additive effect on mean tuber mass, reducing it by about 20%, without any effect on tuber number. The absence of compensatory response under our experimental conditions suggests that clonal plant regrowth partially depends on post-disturbance environmental conditions in the growing season, in our case, dry conditions.

Key words: additive/multiplicative effect, clonal plants, compensatory response, container experiment, tuber size.

Résumé : Dans les zones humides méditerranéennes, les effets combinés de la prédation des tubercules par la faune sauvage et du pâturage des parties aériennes par le bétail sur les capacités de régénération de *Bolboschoenus maritimus* (L.) Palla demeurent peu connus. Nous avons conduit une étude en containers consistant en des niveaux croissants de prélèvement de tubercules (20–90 %), avec ou sans coupe des parties aériennes. La réponse des clones au prélèvement des tubercules ou à la coupe a été estimée selon le changement de biomasse totale, le nombre et la masse moyenne des tubercules (calcul d'indices de variation). Nous n'avons constaté aucune régénération même pour le niveau de prélèvement le plus faible (20 %). Le nombre ainsi que la biomasse totale de tubercules ont diminué. Une baisse significative de la masse moyenne des tubercules et pratiquement aucune production de nouveaux tubercules sont à l'origine de cette absence de réponse. Le niveau de prélèvement a montré un effet linéaire sur les indices de variations du nombre total de tubercules et de la masse moyenne des tubercules. En séparant l'effet de la coupe du prélèvement seul, les résultats montrent que celle-ci a un effet additif sur la masse moyenne des tubercules, la diminuant d'environ 20 %, sans affecter le nombre de tubercules. L'absence de réponse compensatoire dans nos conditions expérimentales suggère que la régénération des plantes clonales dépend, au moins en partie, des conditions environnementales après perturbation, dans notre cas, le niveau d'humidité des containers.

Received 27 September 2008. Published on the NRC Research Press Web site at botany.nrc.ca on 14 September 2009.

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Mots-clés : effets additifs/multiplicatifs, plantes clonales, réaction compensatoire, expérience en récipient, dimension des tubercules.

Introduction

Apart from their ability to spread by sexual reproduction, clonal plants grow by developing stems horizontally, i.e., stolons and rhizomes, producing vegetative offspring called ramets. These plants can store resources in belowground organs, e.g., tubers, and by using them, replace tissues and organs after disturbance such as fire, herbivory, or trampling. It is well known that the mechanism underlying this phenomenon involves physiological integration, i.e., the transport of resources (e.g., water, carbohydrates, and minerals) between ramets (Marshall 1990; de Kroon et al. 1996). However, there is relatively few studies quantifying the regeneration abilities of clonal plants after disturbance. Theoretically, a compensatory continuum can be envisaged as the growth after damage may be (*i*) greater than (overcompensation), (*ii*) equal to (exact compensation), or (*iii*) less than (undercompensation) the initial plant biomass. Some papers reported assumptions underlying the theory that herbivory can benefit plants (Belsky et al. 1993; Agrawal 2000) as plants eaten respond by overcompensating, which can increase plant fitness (Paige and Whitham 1987; Agrawal 1998). Evidence of compensation or overcompensation has been found in clonal plants (Tolvanen et al. 1995; Wegener and Odasz 1997). These regeneration capacities seem intrinsic to plant species (Barrat-Segretain et al. 1998), but are also likely to depend on the severity level of the disturbance (e.g., proportion of disconnected rhizomes), as well as its nature (Miller et al. 1997).

Bolboschoenus maritimus (L.) Palla (Cyperaceae) is a long-lived rhizomatous species that dominates large areas in shallow wetlands in Europe and North America (Podlejski 1981; Kantrud 1996). In the Mediterranean marshes of the Camargue (Rhône delta, France), this plant has a role in the local economy through cattle grazing (Duncan 1992). In addition, the plant has a key role in the ecosystem as a food source for wintering Greylag Geese (*Anser anser*, Desnouhes and Lepley 2004) and wild boars (*Sus scrofa*, Dardaillon 1987). It is, therefore, important to determine the carrying capacity of wetlands and, in this perspective, the recovery abilities of stands of *B. maritimus* after damage to the tubers. Recovery is defined here as the ability to regain or exceed pre-disturbance tuber biomass. A good understanding of the effects of tuber predation by animals has come from laboratory experiments. For instance, Charpentier et al. (1998) showed that rhizome severing (i.e., what animals actually do by removing tubers from the soil) stimulates the emergence of a new ramet generation through the release of axillary buds from dormancy. Severed clones form more numerous tubers, but these are smaller compared with intact ones (Charpentier et al. 1998). Currently it is not clear how *B. maritimus* recovers from the combination of grubbing and grazing. In the case of herbivory, there is an intraclonal support of ramets experiencing a lower accumulation of photosynthates resulting from leaf surface reduction. If grazing puts additional strain on *B. maritimus* recovery, i.e., constraining clones in their reserve storages, then we would expect that grazing does not affect the total number of tubers produced, but does lead to their size being smaller. Thus this hypothesis was tested here through a laboratory experiment exploring the recovery capacities (defined in terms of total tuber biomass attained) of *B. maritimus* submitted to increasing levels of tuber harvesting, with or without shoot clipping. *B. maritimus* has been reported as having both high regenerative capacities (Kantrud 1996) and experiencing great reductions through grubbing by Greylag Geese (Esselink et al. 1997). These contrasting results suggest a plasticity of *B. maritimus* in its response to disturbance, which is likely to be due partly to different environmental conditions between studies. Hydrologic conditions are among factors that limit the distribution of *B. maritimus* (Stuefer et al. 1994; Kantrud 1996). This study was thus conducted in the context of French Mediterranean wetlands that are subject to severe summer droughts.

By applying increasing levels of tuber harvesting, our aim was also to investigate the mode of interaction between clipping and tuber harvesting. Indeed, in case of simultaneous occurrence of these two factors, an interaction may occur whereby the overall effect on tuber size would consist in a multiplicative (i.e., the product of the effects of each factor acting independently), rather than an additive (i.e., the simple sum of these factors) effect. In this study, we test for a possible shoot clipping × harvesting level interaction.

Materials and methods

Experimental design

The experiment was carried out outdoors at la Tour du Valat (43′30°N, 04′30°E; Camargue). The climate is classified as Mediterranean with a cold winter (Daget 1977) characterized by strong winds associated with a high number of sunshine hours (>2500 h/year) and high summer temperatures. This results in a mean deficit annual rainfall to evapotranspiration of 700 mm (Heurteaux 1970). Because a field study would involve the confounding effect of external factors, e.g., variations in soil environment, the study was conducted in containers and simulated summer drought conditions in the Mediterranean region.

Treatments

In March 2002, a single tuber of *B. maritimus* was planted in the centre of each of 125 plastic containers (48 cm long × 34 cm wide × 27 cm deep) containing a mixture of 70% sand – 30% compost. Water-saturated conditions were applied throughout spring (maintaining water level at the sediment surface). In July and August, the amount of water in the containers was reduced to mimic summer drought (only fortnightly, until water-saturation). Each of the 120 remaining containers was randomly assigned to 6 experimental treatments. The first three treatments were limited to tuber removal, and served as baseline references to assess the additional effect of clipping. We varied tuber removal to test for possible difference in sensitivity to clipping. The tuber removal treatments were characterized as follows: (*i*) tuber removal in two successive winters, with final harvest in the third winter; (*ii*) tuber removal during the first winter only, with final harvest in the third winter (i.e., with no disturbance the second winter); and (*iii*) tuber removal in the first winter, with final harvest in the second winter. The last three treatments were identical, but shoot clipping was added in the spring following tuber harvesting. For each type of treatment, eight levels of tuber harvesting were applied ranging in 10% intervals from 20% to 90%. Two replicates (i.e., two containers) were assigned to each harvest level with 4 of the 20 containers in each treatment serving as controls with no tuber harvesting and no clipping.

Shoot clipping consisted in cutting all aboveground shoots within a container to 2 cm above the sediment surface twice in the spring at one-month intervals in May and June. This high defoliation level mimics that commonly observed in the Saint-Seren marsh (nature reserve of la Tour du Valat), where large areas of *B. maritimus* stands are heavily grazed by cattle in spring and summer (F. Mesléard, personal communication).

Calculation of the index of variation

Tubers were harvested by imposing a grid divided into 20 cells of 9.6 cm × 8.5 cm over the surface of the container and removing the sediment and tubers from the randomly designed cells. The total number of tubers in a container at each tuber harvesting event was estimated as follows: (the number of tubers harvested from the container × 20) / the number of cells sampled (according to the harvesting level applied, e.g., six cells corresponded to a 30% harvesting level). The cells were subsequently refilled with a new sand–compost mixture. Because it might be too time consuming to separate all tubers from rhizomes, rootlets, and shoots, and count all of them, each container was subsampled at the end of the experiment (winter 2003 or 2004 according to treatments) to obtain an estimation of the total number of tubers as described above. All harvested tubers were then oven-dried at 70 °C for 48 h, and sorted by weight (dry mass) according to 5 classes of tuber mass: (*i*) 0.01–0.5 g; (*ii*) 0.51–1.0 g; (*iii*) 1.01–1.5 g; (*iv*) 1.51–2.0 g; (*v*) > 2.01 g (applying an interval of 0.5 g from smaller, i.e., 0.01 g, to larger tuber sizes, however with a small proportion of tubers > 2 g).

To investigate changes in the total biomass of tubers in containers, a variation index defined as: $\text{VarIndex}_{\text{totbiom}} = \text{TotTUB}_{\text{final}}/\text{TotTUB}_{\text{control}}$ was calculated where $\text{TotTUB}_{\text{final}}$ was the total biomass of tubers per container at the end of the experiment, and $\text{TotTUB}_{\text{control}}$ was the mean of the total biomass of tubers in controls (n = 8 in 2003 and n = 16 in 2004). An index of 1 indicated that the total biomass of tubers did not change (i.e., no treatment effect), whereas values < 1 or > 1 showed that it decreased or increased, respectively. Total biomass of tubers per container was estimated by the product of the total number of tubers and mean tuber mass. This index was also calculated to quantify changes in the total number of tubers ($\text{VarIndex}_{\text{totnbr}}$), as well as mean tuber mass ($\text{VarIndex}_{\text{tubmass}}$).

Statistical analyses

As preliminary results do not indicate an increased impact associated with two successive years of tuber harvesting compared with a single year, or that one year lacking disturbance influences tuber recovery, all treatments were pooled in the analyses. The effects of tuber harvesting level (treated as a continuous variable, the covariable) and shoot clipping (treated as a factor, i.e., with or without clipping) on $\text{VarIndex}_{\text{totbiom}}$ were first tested using an ANCOVA.

The analysis was also conducted on $\text{VarIndex}_{\text{totnbr}}$ and $\text{VarIndex}_{\text{tubmass}}$. The shoot clipping × harvesting level interaction was included in models to test for a possible multiplicative effect of clipping on these variables (testing differences between slopes). All analyses were carried out with Statistica 6.0. In all models, nonsignificant factors were gradually removed until only significant ones remained ($p \le 0.05$).

Results and discussion

Our results did not indicate a detrimental effect of two successive years of tuber harvesting compared with a single one, nor an effect of one year without any disturbance on the compensation (or the overcompensation) of clones, which is why all treatments were confounded in the analyses. Clones of *B. maritimus* did not show a compensatory response to removal of tubers, regardless of the harvesting level applied, as values of the variation index of the total biomass of tubers in both groups of treatments (with or without clipping) were all < 1. The harvesting level had a significant effect on this index (ANCOVA: F = 68.85, $p \le$ 0.001; Fig. 1). Under our experimental conditions, (*i*) a significant decrease in mean tuber mass over time and (*ii*) approximately no production of new tubers, accounted for this absence of compensatory response:

1. In 2002, just before the start of the experiments, mean tuber mass (0.56 ± 0.20 SD g DM; n = 96) was similar to that of ca. 0.60 g as measured in the Saint-Seren marsh (Desnouhes et al. 2007), and we then observed a decrease. But, because this also happened in controls over time (0.34 ± 0.11, n = 8 and 0.20 ± 0.09 g, n = 16 in 2003 and 2004, respectively; R^2 = 0.32, df = 1, F = 54.7, p < 0.001), the decrease in tuber size under experimental treatments cannot be attributed to tuber harvesting per se, but to an increase in the proportion of small tubers over time (e.g., from ca. 65% to 90% for the tuber mass class 0.01–0.5 g);
2. In 2002, the mean number of tubers per container was 195 ± 81 (n = 95). In controls 2003 and 2004, there was an average of 203 ± 108 (n = 6) and 213 ± 60 tubers per container (n = 16), respectively. This low annual growth rate of ca. 4%–5% was however not significant (R^2 = 0.006, df = 1, F = 0.72, p = 0.40).

In contrast to the exceptional regenerative capacities of *B. maritimus* reported by Kantrud (1996), or its clonal growth in containers following rhizome severing (Charpentier et al. 1998), the absence of compensatory response in this study indicates that *B. maritimus* may have been sen-

Fig. 1. Change in VarIndex of total *Bolboschoenus maritimus* tuber biomass (± S.D.) according to tuber harvesting levels, without or with clipping. Values are shown untransformed to ease reading.

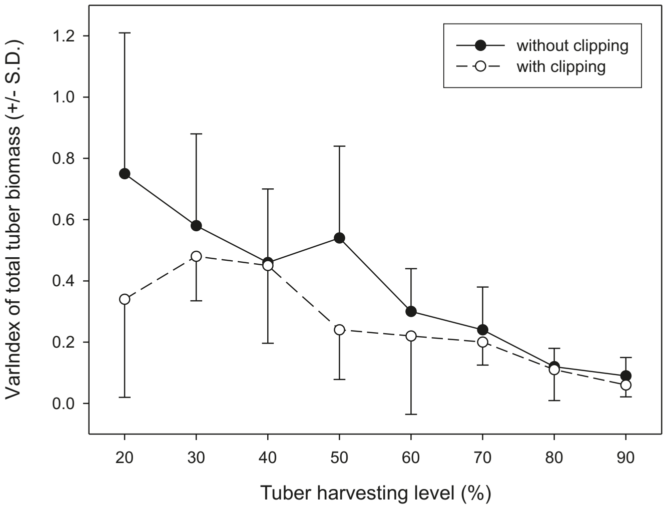
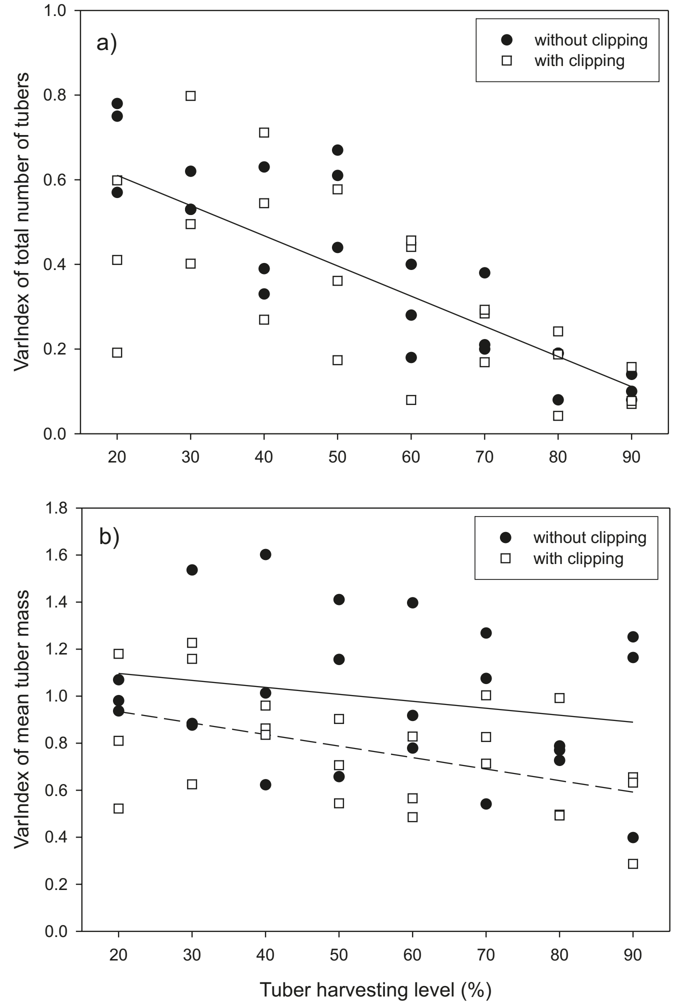


Fig. 2. Effect of the addition of shoot clipping of *Bolboschoenus maritimus* to the tuber harvesting level on (*a*) $\text{VarIndex}_{\text{totnbr}}$ and (*b*) $\text{VarIndex}_{\text{tubmass}}$. Means of the two replicates are represented in this figure.



sitive to our experimental conditions. First, the size of the containers may have been too small for *B. maritimus* to grow normally: clones may have been limited by space, reducing or preventing the production of new tubers. This may explain the low tuber density in the controls in 2003 and 2004 (1250–1300 tubers/m^2) compared with densities found in Camargue marshes (e.g., 7050–7100 tubers/m^2 from Desnouhes et al. 2007). Second, plant response may presumably have been measured outside the range under which they naturally occur. Indeed, the water conditions applied in summer to simulate local hydroclimatic conditions may have subjected the clones to water stress, limiting biomass production and thus preventing them from recovering normally (see e.g., Stuefer et al. 1994; Hunter et al. 2000). It is for instance likely that in containers, compost dried out more completely than soil did. Moreover, this draining appeared earlier under our experimental conditions than in nature (thanks to soil buffer effects), and may certainly have much more pronounced effects, in particular by reducing the time clones needed to recover before summer drought stops regrowth and tubers become dormant.

This experiment was designed to separate the relative effect of shoot clipping to that of removal of tubers alone. Evidence was provided here that clipping produced a ca. 20% decrease in the mean mass of tubers (see the difference between the two lines; Fig. 2*b*), without any effect on their number. This value is slightly higher than that obtained by calculations directly performed on individual tuber masses, i.e., differences in tuber mass with and without clipping ranged from 6% to 10% according to treatments and years. Indeed, only the harvesting level had a significant (linear) effect on the variation index of total number of tubers (F = 66.61, df = 1, $p < 0.001$; Fig. 2*a*). The significant main effects of shoot clipping (F = 9.26, df = 1, $p < 0.01$) and harvesting level (F = 6.66, df = 1, $p < 0.05$) on the variation index of mean tuber mass in the absence of a significant shoot clipping × harvesting level interaction (F = 1.00, p = 0.32) indicate an additive effect of shoot clipping, and not a multiplicative one. With the heavy defoliation simulated in this study, clipping was expected to deplete reserves considerably as the removal of plant biomass limited the amount of carbon that could be mobilized through photosynthesis. This value (20%) suggests a relatively low sensitivity of *B. maritimus* to clipping compared with values reported in other clonal species, e.g., an utilization of more than 75% of their storage (Klimeš and Klimešová 2002). Clones apparently do not use a large proportion of their reserves stored in tubers in response to clipping, and, in line with what happens in other clonal plant species, shoot regrowth certainly also relied on a rapid re-establishment of photosynthesis following clipping (Hogg and Lieffers 1991; Richards and Caldwell 1985). The negative effects of clipping, and by extension to grazing, are likely to be reduced (but not removed) by this mechanism. Clipping had thus restricted effects on tuber biomass allocation, which underlines the advantages of clonal growth to facilitate tolerance to grazing (Strauss and Agrawal 1999).

In conclusion, there are two main points arising from this study. First, under our experimental conditions, clones were affected by a more severe hydrological stress than would be found in nature, thus showing no compensatory response to any tuber harvesting levels. This absence of compensatory response, however, suggests that clonal plant regrowth partially depends on post-disturbance environmental conditions during the dry growing season (Kantrud 1996). This argues in favour of further study being needed on the impact of water (and temperature) conditions on the recovery of *B. maritimus* (see e.g., Miller et al. 1997). A garden experiment could be conducted to study the impact of contrasting levels of summer drought (length) on *B. maritimus* clonal reproduction. We can also recommend conducting a diachronic survey based on plant sampling at various sites known to have differences in their dry period length. Second, shoot clipping showed an additive rather than multiplicative effect on tuber size, which means that in this study, the effect of clipping simply reduced total tuber biomass by about 20%.

Acknowledgements

We thank Michel Lepley, Nicolas Le Clainche, and Christophe Gouraud for their help during the experiments, and anonymous referees for their comments on the manuscript. We also are very grateful to Jean-François Giroux, Patrick Grillas, and Anne Charpentier for their contribution during the set-up of the experiments. Daphné Durant was supported by a post-doctoral grant from the Office National de la Chasse et de la Faune Sauvage, the Centre de recherches de la Tour du Valat, and the Centre d'Etudes Biologiques de Chizé. The project was subsidized by the Fondation Sansouire and the Fondation ProValat.

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