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# Responses of clonal architecture to experimental defoliation: a comparative study between ten grassland species

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**Abstract** Clonal architecture may enable plants to effectively respond to environmental constraints but its role in plant tolerance to defoliation remains poorly documented. In several non-clonal species, modifications of plant architecture have been reported as a mechanism of plant tolerance to defoliation, yet this has been little studied in clonal plants. In a glasshouse experiment, five rhizomatous and five stoloniferous species of grazed pastures were subjected to three frequencies of defoliation in order to test two hypotheses. (1) We expected plant clonal response to defoliation to be either a more compact architecture (low clonal propagation, but high

branching), or a more dispersed one (long-distance propagation and low branching). Such plastic adjustments of clonal architecture were assumed to be involved in tolerance to defoliation i.e. to promote genet performance in terms of biomass and number of ramets. (2) The response of clonal architecture to defoliation was expected to be dependent on the species and to be more plastic in stoloniferous than in rhizomatous species. Most genets of each species were tolerant to defoliation as they survived and developed in every treatment. Architectural modifications in response to defoliation did not match our predictions. Clonal growth was either maintained or reduced under defoliation. Relative growth rate (RGR) decreased in eight species, whereas defoliated genets of seven species produced as many ramets as control genets. Biomass allocation to ramet shoots remained stable for all but one species. In defoliated genets, the number and mean length of connections, and mean inter-ramet distance were equal to or lower than those in control genets. Four groups of species were distinguished according to their architectural response to defoliation and did not depend on the type of connections. We hypothesised that dense clonal architectures with low plasticity may be the most advantageous response in defoliated conditions such as in grazed pastures.

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## Introduction

Vegetative multiplication is widely spread in plants, particularly in Angiosperms. Many species are able to reproduce both by seeds (sexual reproduction) and by clonal growth (asexual reproduction), while some others are even exclusively clonal (Price and Marshall 1999). A genet consists of the vegetative production of genetically identical offsprings (*ramets*) that are potentially independent units as they develop their own shoots and roots (Hutchings and Bradbury 1986; Klimeš et al. 1997). This propagation allows the genet to persist and spread both in space and time (Gardner and Mangel 1997; Oborny and Kun 2002). Vegetative growth modes are variable and major attention has been paid to clonal plants forming aboveground or belowground horizontal stems (stolons and rhizomes respectively, hereafter often referred as *connections*) carrying ramets (Klimeš et al. 1997). In the following, the term *clonality* will refer to these particular growth modes.

Clonal architecture provides singular plant characteristics relying mainly on the integration between ramets, which presents a potential adaptive role (Hutchings and Wijesinghe 1997; Suzuki and Stuefer 1999). Clonal plants are likely to effectively respond to environmental constraints that may explain their abundance in a variety of environments (Hutchings 1999; Price and Marshall 1999). Clonal plants are particularly able to show plastic adjustments of clonal architecture, a strategy involved in selective foraging for light quality (Stuefer and Huber 1998), light intensity (Dong and Pierdominici 1995), nutrient availability (Liao et al. 2003) and even soil temperature (MacDonald and Lieffers 1993) and competition (MacDonald and Lieffers 1993; Kleijn and van Groenendael 1999; Macek and Lepš 2003).

For plants submitted to defoliation, the ability of growth and reproduction after damage is defined as tolerance, while the term compensation is often used to characterise the degree of this tolerance (Strauss and Agrawal 1999). Tolerance can be considered as a plastic trait and ranged along a gradient (Maschinski and Whitham 1989, Stowe et al. 2000) Incomplete tolerance occurs when defoliated plants survive and develop but their performance is lower than for undefoliated plants (undercompensation *sensu* Strauss and Agrawal 1999). Compensating and even

overcompensating tolerance respectively refer to maintained and increased performance for damaged plants compared to undamaged ones (Stowe et al. 2000). Amongst a variety of mechanisms, modifications of aboveground plant architecture (i.e. branching pattern) had often been mentioned as a frequent response to clipping in non-clonal plants (Owen 1980; Paige and Whitham 1987; Lennartsson et al. 1998).

The aim of this study was to investigate whether active adjustments of clonal architecture are involved in genet tolerance to defoliation. Few studies have been carried out on the responses of clonal architecture to disturbance such as clipping or grazing (see however Moen et al. 1999; Piqueras 1999; Li et al. 2004; Wang et al. 2004). We investigated such questions by considering the comparative response to experimental clipping for 10 species, embracing both stoloniferous and rhizomatous species.

We first tested whether clonal architecture-related traits are involved in species compensating tolerance of defoliation, enabling the maintenance of genet performance (in terms of biomass and ramet production). Their response is expected to vary between traits, and either a more compact architecture (low clonal propagation, but high branching) or a more dispersed one (long-distance propagation and low branching) is expected to occur in response to defoliation (Table 1). The second hypothesis was that the response of clonal architecture to defoliation might vary according to species and in particular

**Table 1** Variations of clonal traits predicted by the hypothesis of compensating tolerance to defoliation

|                                    |           |         |
|------------------------------------|-----------|---------|
| Survival and development           | →         |         |
| Clonal performance                 |           |         |
| Relative growth rate               | →         |         |
| Number of ramets                   | →         |         |
| Biomass allocation to ramets       | →         |         |
| Clonal architecture-related traits |           |         |
| Number of connections              | ↘         | ↗       |
| Mean length of connections         | ↗         | ↘       |
| Mean inter-ramet distance          | ↗         | ↘       |
| Clonal growth form                 | Dispersed | Compact |

Arrows indicate the direction (decrease, maintenance or increase) of trait variation between undefoliated and defoliated plants

among stoloniferous and rhizomatous species. As stolons are more often involved in spatial propagation and show higher morphological plasticity than rhizomes (Dong and de Kroon 1994; Dong and Pierdominici 1995), clonal architecture is expected to be more responsive to defoliation in stoloniferous than in rhizomatous species.

## Methods

The response of 10 clonal species to three frequencies of defoliation was recorded in terms of genet performance and architecture-related traits.

The plant species for study were selected out of the 23 clonal herbaceous perennials from grazed pastures in the Marais poitevin, Western France (46°28' N and 1°30' W). These species are the most abundant clonal species in these plant communities, where the biomass consumption by grazing ranges from 55% to 87% of the available biomass (Ros-signol et al. unpublished). They belong to several families and show different modes of clonal growth. All species can produce long connections, either aboveground (stolons) or belowground (rhizomes), or both. Some of them can also form tussocks through very short connections (caespitose growth form) (Table 2).

## Experimental set-up

Ramets were collected in February 2006, from a grazed area of 1 ha. Thirty-three ramets per species were chosen and randomly assigned to one of the three treatments of defoliation. The experimental design thus consisted of 10 species × 3 defoliation treatments × 11 replicates with a total of 330 experimental units.

Each ramet was cleaned, weighed (fresh mass, FM) and rooted in the centre of a pot (20-cm-diameter and 16-cm-height) containing fine garden soil. Approximately 6–10 cm<sup>3</sup> of substrate from the collection site were added close to the roots of the ramet in order to provide symbiotic microorganisms. Ramets were first allowed to grow freely for a five-week acclimation period during which dead ramets were replaced. The ratio FM/DM (fresh and dry mass respectively) was determined for 10 additional non-planted ramets per species, and the mean per species used to estimate initial dry biomass of each planted ramet.

The experiment was conducted in a non-heated glasshouse at the campus of Beaulieu (University of Rennes 1, France) from 29th March up to 17th May 2006. In the glasshouse, temperature was maintained below 25°C. Pots were watered daily with tap water, and weeds were regularly removed.

**Table 2** Studied species and their clonal growth type (adapted from Klimeš et al. 1997)

| Species                     | Abbreviation | Class          | Family        | Clonal growth type           |
|-----------------------------|--------------|----------------|---------------|------------------------------|
| <i>Agrostis stolonifera</i> | Asto         | Monocotyledons | Poaceae       | Stoloniferous<br>Caespitose  |
| <i>Carex divisa</i>         | Cdiv         | Monocotyledons | Cyperaceae    | Rhizomatous                  |
| <i>Eleocharis palustris</i> | Epal         | Monocotyledons | Cyperaceae    | Rhizomatous                  |
| <i>Elytrigia repens</i>     | Erep         | Monocotyledons | Poaceae       | Caespitose<br>Rhizomatous    |
| <i>Glyceria fluitans</i>    | Gflu         | Monocotyledons | Poaceae       | Caespitose<br>Stoloniferous  |
| <i>Juncus articulatus</i>   | Jart         | Monocotyledons | Juncaceae     | Rhizomatous<br>Stoloniferous |
| <i>Juncus gerardii</i>      | Jger         | Monocotyledons | Juncaceae     | Rhizomatous                  |
| <i>Ranunculus repens</i>    | Rrep         | Dicotyledons   | Ranunculaceae | Stoloniferous                |
| <i>Trifolium fragiferum</i> | Tfra         | Dicotyledons   | Fabaceae      | Stoloniferous                |
| <i>Trifolium repens</i>     | Trep         | Dicotyledons   | Fabaceae      | Stoloniferous                |

For species having the ability to develop two types of connections, the major type developed during the experiment is mentioned first. Caespitose growth type corresponds to the production of short rhizomes (tussock forming species)

## Experimental treatments

The three frequencies of defoliation tested were: no defoliation (control treatment), defoliation every 30 days (mid-frequency defoliation treatment) and defoliation every 15 days (high-frequency defoliation treatment). To make a realistic simulation of defoliation caused by cattle, all aboveground parts of Monocotyledons were cut to 7 cm height (Loucougaray et al. 2004). As Dicotyledons were generally lower than 7 cm, defoliation consisted in the removal of 50% of developed leaves by severing the petiole at its base (both petiole and lamina were removed). Genets were harvested 8 weeks after the first clipping. Genets under mid-frequency treatment were thus cut twice and those under high-frequency treatment were cut four times.

## Trait measurements

At harvest the number of ramets per genet was counted and architectural traits were measured. Then, each genet was divided into vegetative shoots, flowers, connections, and roots, dried to constant mass at 60°C and the dry mass of each of these parts was weighed. As the study focused on clonal architecture, biomass allocation to roots was not taken into account. As only a few genets had produced flowers during the experiment, only traits related to vegetative development were taken into account.

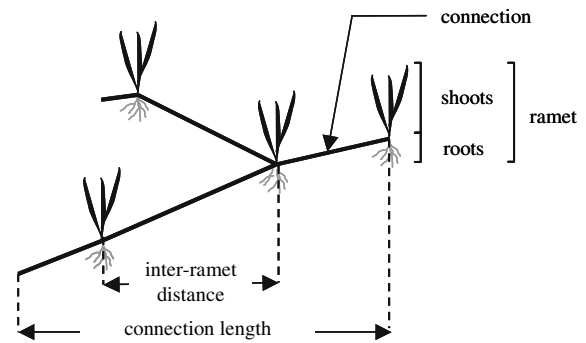
### *Traits related to clonal performance*

The investment in clonal reproduction was estimated as the final number of ramets. The total growth of each genet was measured as the relative growth rate calculated as follows:

$$\text{RGR} = \frac{\ln(\text{final biomass} + \text{clippings}) - \ln(\text{initial biomass})}{\text{number of days}}$$

where final biomass is the dry mass of the whole genet (including roots) at the end of the experiment, clippings, the dry mass of clipped tissues, and initial biomass, the dry mass of the planted ramet.

Finally, the biomass of ramets corresponded to the sum of the final dry mass of shoots of all ramets produced by the genet.



**Fig. 1** Schematic representation of a genet, and definition of architectural traits

### *Architecture-related traits*

Measured traits were: the total number of connections (stolons or rhizomes) per genet, the mean length of connections (with a precision of 1 mm) produced per genet, and the mean inter-ramet distance (with a precision of 1 mm) per genet. This latter corresponded to the mean distance between two consecutive ramets. It could be calculated only for genets that had produced connections carrying ramets (Fig. 1).

Four out of 10 species can develop two types of connections (Table 2). However, *Juncus articulatus* produced very few stolons and only data related to rhizomes were taken into account. For *Agrostis stolonifera*, *Elytrigia repens* and *Glyceria fluitans*, the calculation of mean inter-ramet distance did not include caespitose connections.

A species was considered as tolerant when genets had survived and developed even under the high-frequency defoliation treatment. The response of clonal performance to defoliation (from a decrease to an increase) were used to characterise the degree of tolerance (from incomplete to compensating tolerance).

### Statistical analysis

For all species, one-way ANOVAs showed no differences in ramet initial biomass between the three treatments, confirming the assumption of ramet randomisation between treatments at the beginning of the experiment. The percentage of biomass removed by defoliation was assessed through ANOVA with species and treatment as main effects. The correlation between the percentage of biomass removed and the

values of architecture-related traits was tested. We used the non-parametric Spearman correlation coefficient ( $\rho$ ) as traits did not follow a normal distribution.

Within-species effects of defoliation treatments on final number of ramets, RGR, mean length of connections and mean inter-ramet distance were assessed through one-way ANOVAs, after checking for normality and homogeneity of variances (Kolmogorov–Smirnov and Levene tests respectively), and log-transformation of data when necessary. Post-hoc comparisons between treatments were tested by the Tukey–Kramer test. In the particular case of final number of connections, for which assumptions of normality and homogeneity of variances were not met, non-parametric Kruskal–Wallis tests were used and post-hoc comparisons were made by Mann and Whitney *U*-tests with Bonferroni correction. The effect of defoliation on biomass allocation to ramets was analysed by ANCOVAs using final biomass as a covariate. The aim was to increase the power of the *F*-statistic by adjusting for the influence of the covariate, and to avoid the use of biomass ratios, which may be misleading to study allocation patterns (Jiaseński and Bazzaz 1999). Interactions between treatment and covariate were first introduced into the model and removed when non-significant.

The comparison of architectural responses to defoliation between the 10 species was done by multivariate analyses, taking into account the three architecture-related traits. After a Principal Components Analysis (PCA) on correlation matrix, traits were centred independently per species (within-species PCA) and compared between treatments by a between-class PCA (bc-PCA), each treatment considered as one class (Dolédec and Chessel 1991). Such analysis enabled to eliminate scale effects linked to differences of average trait values between species. Following this analysis, hierarchical ascendant classification (HAC using Ward method of clustering, Legendre and Legendre 1998) was used to group species according to their multivariate trajectory of response. The coordinates of each treatment along the two first axes of bc-PCA constituted the six variables.

ADE-4 software (Thioulouse et al. 1997) was used for bc-PCA, and JMP software (SAS procedure) for other statistical calculations. In all the cases, we rejected null hypothesis at the  $P = 0.05$  level.

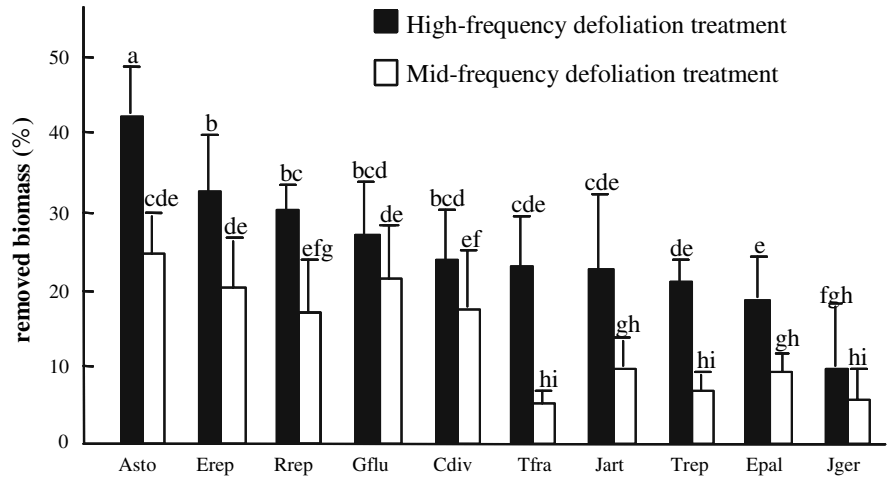
## Results

### Effects of defoliation treatments on clonal performance and architecture-related traits

The amount of biomass removed by defoliation differed significantly between species and treatments (species  $\times$  treatment:  $F_{284}^{18} = 12.05$ ,  $P < 0.0001$ , species:  $F_{284}^9 = 36.78$ ,  $P < 0.0001$ , treatment:  $F_{284}^2 = 750.04$ ,  $P < 0.0001$ ). For the high-frequency defoliation treatment, it ranged from 42.5% (*Agrostis stolonifera*) to 10% (*Juncus gerardii*). The three grasses were the most severely impacted (between 27% and 42.5% for high-frequency defoliation, and between 20% and 24% for mid-frequency treatment), whereas *J. gerardii* and the two *Trifolium* species were less impacted, especially by mid-frequency defoliation treatment (only from 5% to 7% biomass removed) (Fig. 2).

At the end of the experiment, 311 out of the 330 genets had survived and developed, all species and treatments taken together. The impact of treatments on trait values depended on species and traits. Significant differences of trait values occurred either between the control and both defoliation treatments, or between the control and the high-frequency defoliation treatment only. Therefore, hereafter the term defoliation will most frequently be used without distinction between the two levels of the defoliation treatment. *J. articulatus*, *J. gerardii* and *Ranunculus repens* were the three species for which almost no trait was significantly impacted by defoliation. By contrast, the final number of ramets of defoliated genets was 60% to 30% compared to the one of control genets for *Eleocharis palustris*, *G. fluitans* and *Trifolium fragiferum*. It did not significantly change for the other ones (Table 3, see also Table S1-A in Supplementary material). Defoliation generated a significant reduction of RGR for eight species (Table 3, Table S1-B), and there was a significant covariation between the final biomass and the biomass of ramet shoots for all species except *T. fragiferum*. This last trait was significantly impacted by clipping treatment only for *Trifolium repens*, indicating that, for the nine other species, biomass allocation to shoots (i.e. the part of the genet final biomass allocated to the ramet shoots) was not changed by defoliation (Table 3, Table S1-C). For *Carex divisa* only, all architecture-related traits

**Fig. 2** Means and standard deviations of percentage of biomass removed [(biomass removed)/(final biomass + biomass removed)] for each species. Letters indicate significant differences between treatments and species (post-hoc Tukey tests)



showed a significant drop after defoliation (Table 3). For *E. palustris*, *E. repens* and *T. fragiferum*, the number of connections decreased, up to 80% for *E. palustris* (Table 3, Table S2-A). Mean length of connections decreased by 75% for *A. stolonifera* and 50% for *C. divisa* and *G. fluitans* (Table 3, Table S2-B). Finally, mean inter-ramet distance decreased in *A. stolonifera*, *C. divisa* and *T. repens* (Table 3, Table S2-C).

### Multivariate responses of clonal architecture to defoliation

Over all 10 species, there was no significant correlation between the percentage of biomass removed and the three architectural traits ( $\rho = -0.08$ ,  $P = 0.15$  for

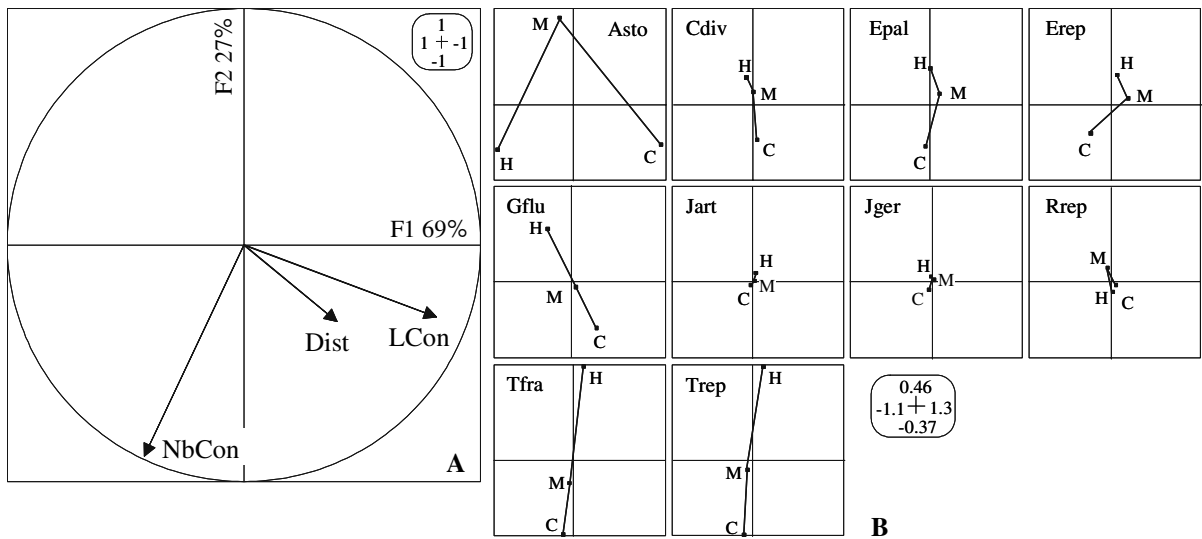
the number of connections;  $\rho = 0.02$ ,  $P = 0.68$  for the mean length of connections, and  $\rho = 0.02$ ,  $P = 0.68$  for the mean inter-ramet distance). But their response to defoliation varied between traits and species. The two first axes of bc-PCA represented 96% of total variance (69% and 27% respectively, Fig. 3). The F1 axis carried out mean length of connections and mean inter-ramet distance. The F2 axis was negatively correlated with the number of connections (Fig. 3a). The amplitude of variation between the extremes of the trajectories along the first axis was weak for all species but *A. stolonifera*. The trajectory between control and high-frequency defoliation treatment along the second axis varied in the direction of a decreased number of connections for nine species. This variation was the most important

**Table 3** Effects of defoliation on clonal traits for all the 10 species

|   | First hypothesis | Asto | Cdiv | Epal | Erep | Gflu | Jart | Jger | Rrep | Tfra | Trep |
|---|------------------|------|------|------|------|------|------|------|------|------|------|
| Survival and development                  | →                | →    | →    | →    | →    | →    | →    | →    | →    | →    | →    |
| Clonal performance                        |                  |      |      |      |      |      |      |      |      |      |      |
| RGR                                       | →                | ↘    | ↘    | ↘    | ↘    | ↘    | →    | →    | ↘    | ↘    | ↘    |
| Number of ramets                          | →                | →    | →    | ↘    | →    | ↘    | →    | →    | →    | ↘    | →    |
| Biomass allocation to ramets <sup>a</sup> | →                | →    | →    | →    | →    | →    | →    | →    | →    | →    | →    |
| Clonal architecture                       |                  |      |      |      |      |      |      |      |      |      |      |
| Number of connections                     | ↗                | ↘    | →    | ↘    | ↘    | ↘    | →    | →    | →    | →    | ↘    |
| Mean length of connections                | ↘                | ↗    | ↘    | ↘    | →    | →    | ↘    | →    | →    | →    | →    |
| Mean inter-ramet distance                 | ↘                | ↗    | ↘    | ↘    | →    | NA   | NA   | →    | →    | →    | →    |

Arrows indicate the variations of trait values between control and both defoliation treatments taken altogether: ↗ significant increase, ↘ significant decrease, → no significant difference, NA not available. Abbreviations of species follow Table 2. Results of statistical tests are presented in Supplementary material (Table S1 for traits indicative of performance, Table S2 for architectural traits)

<sup>a</sup> Biomass allocation to ramets corresponds to the effect of treatment (main factor) on the biomass of all ramets of a genet, tested by the ANCOVA (final genet biomass as a covariate)

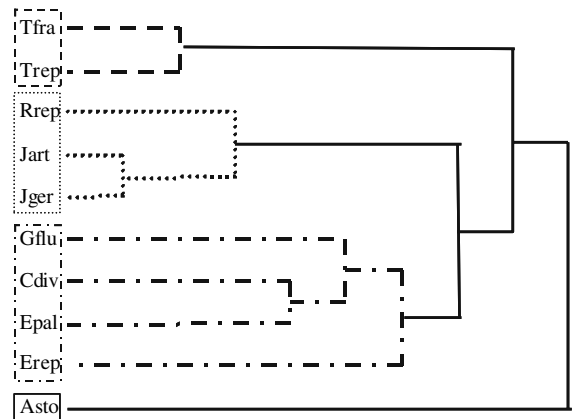


**Fig. 3** Multivariate responses of clonal architecture to defoliation for each species. Traits values have been centred per species (within-species PCA) and compared between treatments (between-treatment PCA). The factorial plan is thus the same for all species. **a** Correlation circle of architectural traits in the factorial plan 1–2 of between-treatment PCA. **b** Trajectories of multivariate responses to the three treatments

for each species in the factorial plan 1–2. Each point represents the barycentre of all replicates of a defoliation treatment. Points *C*: Control treatment, *M*: mid-frequency defoliation treatment, *H*: high-frequency defoliation treatment. *Disr*: mean inter-ramet distance, *LCon*: mean length of connections, *NbCon*: number of connections. See Table 2 for the meaning of species abbreviations

for *Trifolium* species, weaker for *C. divisa*, *E. palustris*, *E. repens* and *G. fluitans*, and was close to zero for Juncaceae and *R. repens*. The trajectory of *A. stolonifera* along this axis had a singular shape, with a great increase between control and mid-frequency defoliation and a decrease between mid-frequency and high-frequency defoliation (Fig. 3b).

The HAC based on architectural responses to defoliation resulted in four groups of species. The first group consisted of both *Trifolium* species. *J. articulatus*, *J. gerardii* and *R. repens* formed the second group, while *C. divisa*, *E. palustris*, *E. repens* and *G. fluitans* constituted the third group. Finally, the last group corresponded to *A. stolonifera*, due to the singular shape of its trajectory of response (Fig. 4).



**Fig. 4** Dendrogram of species resulting from HAC according to the multivariate responses of clonal architecture to defoliation. Species were clustered into four groups on the basis of Euclidean distance (Ward's method). See Table 2 for the meaning of species abbreviations

## Discussion

### Consequences of defoliation on clonal performance

All species showed tolerance to defoliation as 311 out of 330 genets survived and developed even when severely clipped.

Biomass allocation to ramets was not affected by the treatment, except for one species. This indicates that genets were able to sustain damaged ramets and even to compensate for aboveground biomass removal caused by defoliation. While the design did not allow to identify the mechanisms involved,



Brown and Allen (1989) reported that clipping treatment may cause the translocation of resources from belowground organs to support the regrowth of aboveground tissues.

We recorded, however, a great discrepancy on the degree of tolerance depending on traits and species considered. The RGR decreased with clipping, which is typical of undercompensation (Strauss and Agrawal 1999) and incomplete tolerance (Stowe et al. 2000), while together, seven out of 10 species maintained a similar number of ramets in all three treatments, arguing for compensating tolerance to clipping. Previous studies had already reported a variety of responses to clipping by clonal plants, among species and among environments for a given species. For example, ramet number has been reported to decrease with leaf removal for three clonal perennials, (Hicks and Turkington 2000), to be unchanged for *Leymus chinensis* (Wang et al. 2004), either to be unchanged or to increase according to nutrient availability for *Cyperus esculentus* (Li et al. 2004) and even to increase for five caespitose grasses (Richards et al. 1988). Biomass responses to defoliation were also shown to vary from undercompensation (Li et al. 2004) to overcompensation (Hicks and Turkington 2000), probably due to both the differing species studied and the defoliation treatment applied. Interspecific differences in compensatory ability were notably found both in clonal and non-clonal species (McNaughton and Chapin 1985; Belsky 1986; Del-Val and Crawley 2005). Response to defoliation has also been shown to vary within the same species depending on environmental conditions (Maschinski and Whitham 1989). The lack of generality in clonal plant responses to clipping may also originate from the variety of defoliation treatments used in the different studies. Their impact on plant growth may indeed differ whether they are applied at a given date (e.g. Hicks and Turkington 2000; Wang et al. 2004), at a given development stage (e.g. Richards et al. 1988) or several times (e.g. Li et al. 2004).

#### Responses of clonal architecture-related traits to defoliation

Clonal architecture-related traits did not match the predicted responses. Species followed four types of architectural response to defoliation, going from nil

to high variation. Trait values never increased with clipping and defoliation thus led to fewer connections and/or shorter connections and mean inter-ramet distances. Similar results in response to clipping or grazing have already been observed in other herbaceous clonal plants such as *Trifolium repens* (Hay and Newton 1996), *Acaena magellanica* (Moen et al. 1999), *Trientalis europaea* (Piqueras 1999) or *Leymus chinensis* (Wang et al. 2004).

Furthermore, the results obtained here show that there is no relationship between the multivariate pattern of architectural response and the degree of tolerance to defoliation. For instance, both the first and the third response groups included together species for which defoliation induced no change in the number of ramets (*C. divisa*, *E. repens* and *T. repens*), and species for which defoliation induced a decreased number of ramets (*E. palustris*, *G. fluitans* and *T. fragiferum*). Compensating tolerance can be related to various responses of architectural traits. For *E. repens*, the production of ramets was not affected by defoliation despite a decrease of the number of connections, as only a few ramets were produced by these connections, the majority being caespitose (tussock forming). An alternative strategy was shown by *C. divisa*, *T. repens* and *A. stolonifera*. They maintained the number of ramets unchanged with clipping by way of the decreased mean inter-ramet distance, whatever the variation of the other traits.

#### Interspecific comparison of the responses of clonal architecture to defoliation

Previous studies have shown that higher nutrient and/or light supply increased branching intensities of both stolons and rhizomes, whereas the morphology of stolons (mean connection length and mean internode length) was more plastic than the morphology of rhizomes (Dong and de Kroon 1994; Dong and Pierdominici 1995). According to our study, only the stolons of *A. stolonifera* showed a high degree of variability, with a high amplitude of variation of all architecture-related traits. The responses of other stoloniferous species were not clearly distinct from those of rhizomatous species. The second and the third response groups contained both stoloniferous (*G. fluitans* and *R. repens*) and rhizomatous species (*C. divisa*, *E. palustris*, *E. repens*, *J. articulatus* and *J. gerardii*). Thus, contrary to the predictions that clonal

architecture should be more responsive to defoliation in stoloniferous than in rhizomatous species, the response of clonal architecture to defoliation was not constrained by the type of connections. Other developmental constraints may be implied in architectural responses to defoliation. For instance, branching pattern is related to the number and activity of axillary meristems (Huber and During 2001), which may play a key role in architectural response to defoliation (Briske 1996). In monopodial species (e.g. *T. fragiferum* and *T. repens*) the number of connections is constrained by the limited number of meristems available per ramet (Huber and During 2001). As a result they are likely to be more sensitive to defoliation (Huber et al. 1999). Indeed, the trajectories of response of the two studied *Trifolium* species did show a great decrease of the number of connections, compared to the other eight species (sympodial species, Klimeš and Klimešová 1999).

However, the species constitutive of the second (*J. articulatus*, *J. gerardii* and *R. repens*) and the third (*C. divisa*, *E. palustris*, *E. repens* and *G. fluitans*) response groups can be linked neither by their phylogenetic nor by their developmental features. Our results thus demonstrate that architectural response to defoliation can neither be predicted on the sole basis of the type of clonal connection (stolons or rhizomes), nor by the phylogenetic and developmental features.

## Conclusion

Species responses to defoliation were either the stability of clonal architecture or the decreased investment in the production of connections and a lower clonal propagation. Gross et al. (2007) showed that low lateral spread was a constitutive trait of species tolerant to clipping. Such growth forms can be interpreted as the expression of the ‘*consolidation strategy*’ (as defined by de Kroon and Schieving 1990) characterised by short and little plastic connections. In grazed pastures, where the risk of defoliation is high, plants with short propagation (either constitutive or induced by defoliation) and capable of producing a dense population of ramets when defoliated are very likely to be more competitive than plants that allocate energy in the production of long connections. However, small variations of

architectural traits may have great consequences on spatial distribution of ramets within a genet, and consequently on genet performance, resource acquisition and competition (Huber et al. 1999). Such parameters are likely to be modified by recurrent defoliation that occurs in grazed pastures. The four architectural patterns of response to defoliation distinguished during the present short-term experiment are very likely to constrain competitive ability, and hence the relative species abundances along the grazing gradient.

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