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# Inter- and intraspecific variability of plant individual growth and its role on species ranking in grasslands

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## Abstract

**Aims** Individual growth constitutes a major component of individual fitness. However, measuring growth rates of herbaceous plants non-destructively at the individual level is notoriously difficult. This study, based on an accurate non-destructive method of aboveground biomass estimation, aims to assess individual relative growth rates (RGRs) of some species, identify its environmental drivers and test its consequences on community patterning. We specifically address three questions: (i) to what extent environmental conditions explain differences in individual plant growth between sites, (ii) what is the magnitude of intraspecific variability of plant individual growth within and between sites and (iii) do species-averaged (dis-)advantage of individual growth compared with the whole vegetation within a site correlate with species ranking at the community level?

**Methods** We monitored the growth of individuals of four common perennial species in 18 permanent grasslands chosen along a large pedoclimatic gradient located in the Massif Central, France. We measured soil properties, levels of resources and meteorological parameters to characterize environmental conditions at the site level. This design enables us to assess the influence of environmental conditions on individual growth and the relative extent of inter-individual variability of growth explained within and between sites. We determined the ranking of each of the four species in each site with botanical surveys to assess the relationship between species-averaged growth (dis-)advantage relative to the whole community and species rank in the community.

**Important Findings** We found that environmental conditions explain a significant proportion of individual growth variability, and that this proportion is strongly variable between species. Light availability was the main driver of plant growth, followed by rainfall amount and potential evapotranspiration, while soil properties had only a slight effect. We further highlighted a moderate to high within-site inter-individual variability of growth. We finally showed that there was no correlation between species ranking and species-averaged individual growth.

**Keywords:** relative growth rate, species ranking, non-destructive biomass estimation, temperate permanent grasslands, inter-individual variability

**摘要:** 植物个体的生长是其适合度的重要组成部分。然而，在个体水平上非破坏性地测量草本植物的生长速度非常困难。本研究基于准确的非破坏性地面生物量估算方法，旨在评估某些物种的个体相对生长速率，识别其环境驱动因子，并检验其对群落模式的影响。我们提出以下三个具体的科学问题：(1)环境条件可以在多大程度上解释个体植物生长在不同样地间的差异；(2)在同样样地内和不同样地间，植物个体生长的种内差异有多大，以及(3)同样样地内，平均每个物种的个体生长相较于整个植被的优势/劣势，与群落水平的物种等级是否有关？为了回答上述问题，我们在法国中央高地沿古气候梯度的18个永久草地内监测了4种常见的多年生植物的个体生长。我们测量了土壤性质、资源水平和气象参数，以表征样地的环境条件。这使我们能够评估环境条件对个体生长的影响，以及在相同和不同样地之间个体间生长变异的相对程度。我们通过植物学调查确定了每个样地内四个物种的等级，以评估物种平均个体生长相对于整个群落的优势/劣势与物种在群落中的等级之间的关系。研究表明，环境条件解释了个体生长变异性很重要的一部分，而且这部分变异在物种之间也有很大差异。光

照有效性是影响植物生长的主要因素，其次是降雨量和潜在的蒸散量，而土壤性质对植物生长的影响较小。我们的结果进一步强调了同样样地内个体间生长变异的程度是中到高，而且物种等级与物种平均个体生长之间没有相关性。

**关键词：** 相对生长率，物种等级，非破坏性生物量估算，温带永久草地，个体间变异

## INTRODUCTION

Species performance has been usually approximated using proxies such as functional traits, i.e. features measurable at the individual level contributing directly or indirectly to fitness (Violle *et al.* 2007). These functional traits have been successfully related to species ranking at the community level, thereby supporting the assumption that environmental filters may determine community assembly through a species sorting process (e.g. Shipley *et al.* 2006). In this framework, it is assumed that different species might be favoured and become dominant in different sites given their differential responses in the prevailing environmental conditions (Leibold *et al.* 2004). Community assembly at local scale is thus considered to be the result of non-random demographic processes related to individual fitness and its components, namely survival, growth and reproduction (Violle *et al.* 2007).

Among the components of individual fitness, growth is considered as a prime determinant of plant ecological strategies (Grime 1977; Reich 2014; Tilman 1988). In particular, the relative growth rate (RGR), thereafter RGR, has been frequently used to summarize plant performance of annual and perennial herbaceous plants in productive habitats (Violle *et al.* 2007). RGR has been shown to vary at the population level according to changing environmental conditions, such as light and nutrients supply (Altesor *et al.* 2017; Glimskär and Ericsson 1999; Hofmann and Iselstein 2004; Meziane and Shipley 1999) or herbivory pressure (Rose *et al.* 2009). Consequently, population-level RGR has been used to study the influence of biotic and abiotic environmental filters on community assembly (see e.g. Glimskär and Ericsson 1999; Roscher *et al.* 2011). However, the relationship between species ranking and RGR has been the subject of only few studies on a limited set of environmental conditions, and showed contradictory results. In hayfield, Epp and Aarssen (1989) found no relationship between growth rate and relative abundance of species at the plot level, while, in infertile abandoned pasture, Reader (1998) highlighted a negative relationship.

Previous studies have analysed the responses and effects of species RGR at the population level because measuring RGR of individual plants is difficult in semi-natural systems, especially for herbaceous perennial species (Rose *et al.* 2009). Consequently, they did not include inter-individual variability of growth in their analyses. However, the intraspecific variability of numerous functional traits is high, and currently well recognized to play a key role in community assembly (Albert *et al.* 2010; Siefert *et al.* 2015). To our knowledge, the inter-individual variability of RGR in natural plant communities has not been evaluated so far, although it may have strong consequences on community assembly. Theoretical and empirical studies suggest that inter-individual variability of plant performance and its components may blur interspecific differences in competitive abilities and thus species dominance at the community level (Aarssen and Turkington 1985; Fridley *et al.* 2007; Uriarte and Menge 2018), although such influence is still debated (Hart *et al.* 2016; Turcotte and Levine 2016). For instance, in their theoretical model, Uriarte and Menge (2018) especially emphasized that a high inter-individual variability of competitive response can give a disproportionate advantage of the inferior competitor species in spatially heterogeneous habitats. Moreover, Biere (1996) highlighted that the RGR variability influences

the competitive ability of a species depending on the environmental conditions experienced. Consequently, there is a need to test whether a high individual growth of a species, mediated by favourable environmental conditions for this species, scale-up to better ranking at the community level, as predicted by the species sorting hypothesis, or whether this could be blurred by large inter-individual variability.

Population-level RGR measurements need cohorts of plants with a comparable initial biomass to carry out destructive measurements. This method cannot *de facto* focus on the individual level, and thus cannot assess inter-individual variability for herbaceous plants. To overcome this limitation, we use a recently developed method of non-destructive estimation of aboveground biomass allowing repeated measurements on the same individuals (Pottier and Jabot 2017). This method has thus the potential to accurately assess, in temperate grasslands, the growth trajectories of individuals, and is transferable across different environments (Pottier and Jabot 2017).

Using this method, we monitored the spring growth of individual plants of four common species of temperate permanent grasslands distributed along a large pedoclimatic gradient. More specifically, we addressed the three following questions:

- (1) To what extent environmental conditions explain differences in individual plant growth between sites? Does their influence vary between species?
- (2) How variable is intraspecific variability of plant individual growth within and between sites?
- (3) Do species-averaged differences in individual growth within a site correlate with species ranking at the community level?

## MATERIALS AND METHODS

### Study sites

We surveyed 18 temperate permanent grasslands located in the Massif Central, France, from April to July 2017, depending on the altitudinal gradient. Grasslands were chosen in order to include the major pedoclimatic conditions, landscape contexts and management regimes of the study area. Moreover, each site is a permanent grassland characterized by a constant management regime for at least 20 years.

In each selected grassland, a plot of 100 m<sup>2</sup> (10 m × 10 m) was delineated and put under enclosure against large herbivores, mainly cattle, during a period of around 2 months. The period started before the senescence of the first leaf and ended at the biomass peak, thus capturing the peak of growth rate at the community level, between 550 ± 40 and 1350 ± 90 Growing Degree-Days, thereafter GDD. The GDD allows standardizing phenological stages between the different sites that were distributed along a large climatic gradient. The GDD were calculated following McMaster and Wilhelm (1997) assuming a base temperature of 0°C and are accumulated with a starting date at the 1st of February. Neither herbage use (mowing or/and grazing) nor nutrient supply were made in these enclosure plots during the period of survey.

### Environmental conditions

Six soil properties were measured at the site level based on standard procedures using a composite soil sample in the 0–20 cm soil layer:

soil texture (i.e. clay, silt and sand in %), pH, total organic carbon (in g kg<sup>-1</sup>), total nitrogen (in g kg<sup>-1</sup>), available phosphorous (in g kg<sup>-1</sup>) and cation exchange capacity. The total organic carbon, total nitrogen and available phosphorous were expressed as total pools within the 0–20 cm soil layer (in g m<sup>-2</sup>). Moreover, the maximum plant available water content in the 0–60 cm soil layer was determined as the difference between soil water content at field capacity and soil water content at wilting point using four non-disturbed soil samples per grassland, and accounting for bulk density and soil depth (available water content, in mm). A standardized principal component analysis (PCA) was applied on soil variables to reduce the dimensionality of these data. The main axis of variation of the PCA was retained because most variables are collinear, thereafter soil PC1, and accounts for 58.5% of the total variance. Soil PC1 summarizes a gradient of potential productivity with positive values associated with sites presenting more resources available (Supplementary Fig. S1).

Three meteorological variables were computed at the site level within the enclosure plot over the period studied: cumulative rainfall (P<sub>cumul</sub> in mm), cumulative potential evapotranspiration following the Hargreaves–Samani equation (PET<sub>cumul</sub> in mm; Hargreaves and Samani 1985) and cumulative photosynthetic active radiation available (PAR<sub>cumul</sub> in MJ m<sup>-2</sup>). The dynamic of PAR calculation was made with temporal series of daily global radiations provided by MétéoFrance and field measurements above the canopy and at the ground level to estimate light interception through the plant canopy with a ceptometer. Rainfall, temperature and global radiations were provided by nearest MétéoFrance weather stations. Details of measurements of environmental variables are provided in Supplementary Table S1 and Figure S1.

### Growth rate calculation at the individual and the community levels

We estimated growth rates, at the individual level, for four common perennial species that are typical of permanent grasslands of the Massif Central. The four species were selected from their high frequency in the region of interest according to the atlas of the Auvergne flora (Antonetti et al. 2006). As a result, the four species: *Dactylis glomerata*, *Lolium perenne*, *Poa pratensis* and *Trifolium repens* were, respectively, observed in 16, 17, 18 and 18 out of 18 sites. These four species are medium- to late-flowering species in the studied sites. Each species can locally be part of the dominant or subordinate species depending on the site. Usually eight plant individuals per species and per site, when the species was present, were marked by a ring surrounding their base. Following the definition of Pottier and Jabot (2017), the term individual is defined as a ramet or collection of clumped ramets with the highest degree of physiological integration. Plant individuals were measured at two periods,  $t_1$  (710 ± 70 GDD) and  $t_2$  (1350 ± 90 GDD), i.e. the duration of the period between  $t_1$  and  $t_2$  was 1 month maximum. Three biometric measurements were recorded: maximum height ( $H$ ), basal circumference ( $A_{\text{basal}}$ ) and circumference at mid height ( $A_{\text{half}}$ ). These measurements allowed us to estimate the minimum volume occupied by all aboveground organs of an individual, thus limiting risks of error measurement compared with other available approaches (see Pottier and Jabot 2017 for details). We excluded to rely only on maximum height to assess the aboveground dry biomass of the individuals because this single biometric measurement was found to be clearly outperformed by the minimum volume-based approach (Pottier and Jabot 2017). Based on data and findings of Pottier and Jabot (2017), we rather estimated the aboveground dry biomass of the individuals ( $W_{\text{ind}}$ ) as follows (1):

$$W_{\text{ind}} = 1.96 \left[ \frac{H}{2} (A_{\text{basal}} + A_{\text{half}}) \right]^{2/3} \quad (1)$$

This general allometric equation showed good predictive accuracy (Normalized Root Mean Square Error [NRMSE] of 0.19), especially for the three species that were part of the analyses performed by Pottier and Jabot (2017), i.e. *D. glomerata*, *L. perenne* and *P. pratensis* (NRMSE = 0.17, 0.06 and 0.09, respectively). Considering the remaining species *T. repens*, we assume equation (1) to be valid because *Lotus corniculatus*, the species showing the most similar morphology included in Pottier and Jabot (2017), also showed good predictive accuracy (NRMSE = 0.13, Supplementary Fig. S2). This good predictive accuracy was obtained by considering contrasted sites in terms of altitude, climate, topography, soil type and management regimes in the same biogeographic region, i.e. the Massif Central (see Pottier and Jabot 2017).

This method of non-destructive biomass estimation allowed us to characterize the growth rate of individual plants between the two monitoring dates. We then calculated the RGR of each monitored individual, thereafter RGR<sub>ind</sub>, as follows (2):

$$\text{RGR}_{\text{ind}} = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \quad (2)$$

where  $W_1$  and  $W_2$  are the dry aboveground biomass estimation for the individual at the two monitoring dates  $t_1$  and  $t_2$  (in GDD).

In order to compare the RGR of plant individuals between sites and relate it to species ranking at the community level, we also characterized RGR at the community level, which corresponds to the specific aboveground net primary productivity—thereafter SANPP—defined by Garnier et al. (2004). The total aboveground biomass was determined at the same two monitoring dates  $t_1$  (710 ± 70 GDD) and  $t_2$  (1350 ± 90 GDD). The aboveground biomass was clipped at 5 cm above the ground level from four 0.25-m<sup>2</sup>—50 cm × 50 cm—quadrats at the site level. The biomass was then oven-dried for 48 h at 80°C, weighed and the aboveground dry biomass per square meter computed as the sum of the four 0.25-m<sup>2</sup> quadrats. The SANPP was calculated as follows (3):

$$\text{SANPP} = \frac{\ln(B_2) - \ln(B_1)}{t_2 - t_1} \quad (3)$$

where  $B_1$  and  $B_2$  are the dry aboveground biomass of the whole community (in g), respectively, at the monitoring dates  $t_1$  and  $t_2$  (in GDD).

In order to relate plant individual growth of the species to their ranking in the different sites along the pedoclimatic gradient, we propose an indicator of individual growth (dis-)advantage relative to the whole community. This indicator compares relative plant growth to its reference community by dividing the RGR<sub>ind</sub> by the SANPP estimated at the community level. Therefore, RGR<sub>ind</sub>/SANPP < 1 indicates that the targeted individual has grown slower than the other individuals of co-occurring species which experienced the same site-specific environmental conditions over the growing season. Conversely, RGR<sub>ind</sub>/SANPP > 1 indicates that the targeted individual has grown faster than the other co-occurring species.

### Botanical survey and community patterns

To determine the ranking of the four species in each site separately, we conducted botanical surveys at the site level. In each 100-m<sup>2</sup> plot, a nested sampling design was applied in order to account for potential environmental heterogeneity at different spatial scales. Eight 1-m<sup>2</sup> quadrats were located regularly within the 100-m<sup>2</sup> plot. In each quadrat characterized by a 0.1 m × 0.1 m grid, 10 0.01-m<sup>2</sup> mini-quadrats were then randomly chosen. Within each of the 80 0.01-m<sup>2</sup> mini-quadrats, we recorded the presence of all co-occurring vascular plant species at the date corresponding to 1060 ± 90 GDD, and we completed this list by taking into account the complementary species observed at the flowering and ripening phenological stages at 550 ± 40, 710 ±

70 and  $1350 \pm 90$  GDD. We characterized the occurrence frequency of each species and the species richness at the scale of the plot. The surveyed temperate permanent grasslands were usually dominated by monocotyledons (from 44.8% to 71.5% of the total occurrence frequency observed, on average  $57.2\% \pm 6.6\%$ ), and characterized by a medium to high species richness (from 32 to 69 species on the 100-m<sup>2</sup> plot, on average  $48 \pm 11$ ), and a relatively high Pielou's evenness  $J'$  (from 0.73 to 0.84 on the 100-m<sup>2</sup> plot, on average  $0.79 \pm 0.03$ ; Pielou 1966; see Perronne *et al.* 2019 for details).

We computed a metric of standardized species ranking as follows (4):

$$sSR_{i,s} = 1 - \frac{\text{rank}_{i,s}}{\text{species richness}_s} \quad (4)$$

where  $sSR_{i,s}$  corresponds to the standardized species ranking of the species  $i$  at the site  $s$ ,  $\text{rank}_{i,s}$  is the rank of the species  $i$  at the site  $s$  based on its frequency of occurrence relative to the other species. We divided  $\text{rank}_{i,s}$  by the species richness and subtracted the value to 1 in order to have comparable index across sites. Therefore, common species present  $sSR$  approaching one and rare species present  $sSR$  approaching zero at the site level.

## Statistical analyses

### Sources of variations of individual plant growth

For each species separately, we assessed the effects of the environmental variables recorded at the site level on the growth of each individual ( $RGR_{ind}$ ) using linear mixed models (thereafter LMM). We also accounted for the inter-individual variability of initial size by including the initial aboveground biomass  $W_1$  measured at the start of the monitoring in the models. Based on Pearson's product-moment correlation tests, no correlation between explanatory variables exceeded 0.7 in absolute value, so all the variables were retained for subsequent analyses (Dormann *et al.* 2013). A full additive model including the initial aboveground biomass, linear and quadratic effects of the environmental variables (i.e. soil PCl,  $P_{cumul}$ ,  $PET_{cumul}$  and  $PAR_{cumul}$ ) and accounting for the site identity as a random intercept factor, was compared with all other simpler additive models (i.e. including only a subset of the environmental variables) based on the second-order Akaike information criterion ( $AIC_c$ ; Sugiura 1978). We used quadratic terms in order to model non-linear responses of species growth to various niche axes. We checked for homogeneity of variances (Bartlett test, visual inspection), normality of the residuals (Shapiro test, visual inspection) and influential points (Cook's distance). The initial biomass was ln-transformed and, depending on the species considered, from one to four influential points were detected and removed from the models investigated. These influential points corresponded to individuals having experienced a marked senescence between the two monitoring dates. The input variables were standardized to avoid collinearity between linear and quadratic terms and to estimate standardized beta coefficients to compare the effects of the explanatory variables with different units (Schielzeth 2010). Only the best model was presented, that corresponds to the most parsimonious model with both the lowest  $AIC_c$  and with all explanatory variables being significant ( $P < 0.05$ , according to a likelihood-ratio test based on the  $\chi^2$  distribution). We determined both the marginal and the conditional  $R^2$  ( $R_m^2$  and  $R_c^2$ ), that correspond to the variance explained by the fixed effects only and both the fixed and random effects, respectively (Nakagawa and Schielzeth 2013). We also assessed the effects of each environmental variable separately on  $RGR_{ind}$  using simple linear and quadratic mixed models, and only the best model was presented (Supplementary Fig. S3). It should be noted that these analyses do not allow to evaluate the causal relationships of the environmental variables on the growth of each plant individual separately, the environmental variables being recorded at the site level while  $RGR_{ind}$  could also be affected by conditions at a finer scale.

Beyond the influence of environmental conditions on  $RGR_{ind}$  at the site level, we further partitioned the variance of  $RGR_{ind}$  and  $RGR_{ind}/SANPP$  within and between sites for each species separately. In doing so, we compared the relative importance of fine-scale variability and variability due to large-scale modifications of pedoclimatic conditions on intraspecific individual growth variability.

### Effect of species-averaged growth (dis-)advantage on species ranking at the community level

We implemented a beta generalized linear mixed model (thereafter GLMM) to assess the effects of the species and the ratio  $RGR_{spe}/SANPP$ , i.e. the average  $RGR_{ind}/SANPP$  estimated at the species level within a site, on  $sSR$ , accounting for the site identity as random intercept and slope effects. The  $RGR_{spe}/SANPP$  can be considered as an estimation of the species-averaged growth (dis-)advantage relative to the whole community. We hypothesized that assembly mechanisms can differ between sites and therefore considered sites as a source of random variation on model intercept and slope effects. We used a beta GLMM because the response variable  $sSR$  is a continuous variable bounded between 0 and 1. For fixed effects, a likelihood-ratio test based on the  $\chi^2$  distribution was used to evaluate the significance of the effect of the explanatory variables, and coefficients were given, with a Z test used to evaluate their significance.

Statistical analyses were performed using R 3.6.2 (R Development Core Team 2019), its packages 'ade4' for PCA, 'lme4' for LMMs, 'glmmTMB' for beta GLMMs and 'AICmodavg' for model selection based on  $AIC_c$ . Metadata are described and a link to the datasets provided in Supplementary Material S4.

## RESULTS

### Effects of environmental conditions at the site level on plant growth at the individual level

The monitored environmental conditions recorded at the site level and the initial biomass of the individuals explained individual plant growth with variable accuracies (between  $R_m^2 = 0.18$  for *P. pratensis* and  $R_m^2 = 0.50$  for *L. perenne*; Table 1). We found that marginal relationships between environmental conditions were always monotonous, except for the relationship between the cumulative potential evapotranspiration and  $RGR_{ind}$  of *L. perenne* and *P. pratensis* that were U-shaped (Table 1). Thus, the cumulative PAR available had an important effect on plant growth for three out of the four species, being always positively related to RGR at the individual level, especially for *D. glomerata* and *L. perenne* (Supplementary Fig. S3 and Supplementary Table S5). Moreover, the growth of these species was positively related to the cumulative rainfall, especially for *T. repens*, while the growth of *L. perenne* was negatively related to the cumulative potential evapotranspiration. The best model retained for *P. pratensis* showed a low  $R_m^2$  and did not highly differ from the intercept-only model ( $AIC_c - AIC_0 = 4.79$ ), consequently the results for this species should be interpreted with caution (Supplementary Table S5). Still, the effects highlighted were consistent with the results of other species, *P. pratensis* presenting a higher growth in the most productive sites based on soil properties, and a lower growth in sites characterized by a high cumulative potential evapotranspiration (Table 1). Although the initial biomass was significantly negatively related to the  $RGR_{ind}$  for two species, it appeared highly influential only for *D. glomerata*.

### Relative importance of inter-individual variability of growth within and between sites

We found that within-site variability of  $RGR_{ind}$  represents between 10.1% and 26.8% of the between-site variability (Table 2; Fig. 1). Furthermore, the mean squares of the within-site  $RGR_{ind}/SANPP$ ,

**Table 1:** Effect of the environmental variables recorded at the site level and the initial biomass at the individual level on the RGR at the individual level  $RGR_{ind}$ , tested for each species separately based on the selection of the best LMM, accounting for the site identity as a random intercept factor

| Species                     | <i>Dactylis glomerata</i><br>(n = 110) | <i>Lolium perenne</i><br>(n = 112) | <i>Poa pratensis</i><br>(n = 69) | <i>Trifolium repens</i><br>(n = 106) |
|-----------------------------|--|------------------------------------|----------------------------------|--------------------------------------|
| Marginal $R^2$              | 0.42                                   | 0.50                               | 0.18                             | 0.23                                 |
| Conditional $R^2$           | 0.45                                   | 0.56                               | 0.18                             | 0.42                                 |
| $AIC_c - AIC_0$             | 27.49                                  | 19.68                              | 4.79                             | 4.60                                 |
| Fixed effects               |  |                                    |                                  |                                      |
| Intercept                   | -0.32**                                | -0.38**                            | -0.34*                           | 0.02n.s.                             |
| Initial biomass             | -0.30***                               | -0.24**                            |                                  |                                      |
| Soil PCI                    |  |                                    | 0.36**                           |                                      |
| Soil PCI <sup>2</sup>       |  |                                    |                                  |                                      |
| $P_{cumul}$                 | 0.15(*)                                | 0.32**                             |                                  | 0.37**                               |
| $P_{cumul}^2$               | 0.33***                                |                                    |                                  |                                      |
| $PET_{cumul}$               |  | -0.38***                           | -0.41**                          |                                      |
| $PET_{cumul}^2$             |  | 0.37***                            | 0.34**                           |                                      |
| $PAR_{cumul}$               | 0.57***                                | 0.42***                            |                                  | 0.35**                               |
| $PAR_{cumul}^2$             |  |                                    |                                  |                                      |
| Random effect—site identity |  |                                    |                                  |                                      |
| Intercept                   | 0.172                                  | 0.237                              | 0.000                            | 0.441                                |

The standardized beta coefficients of the selected explanatory variables and their associated  $P$ -values based on  $\chi^2$  distributions are reported. The selected models were the most parsimonious model with both the lowest  $AIC_c$  and with all explanatory variables being significant.  $AIC_c - AIC_0$  corresponds to the difference of  $AIC_c$  between the best model and the intercept-only model including the random intercept factor (standard-deviation). Marginal and conditional  $R^2$  correspond to the variance explained by the fixed effects only ( $R_m^2$ ) and both the fixed and random effects ( $R_c^2$ ) were given. n.s., not significant.  $n$  corresponds to the number of individuals. See [Supplementary Table S5](#) for more detailed results. (\*) $P$ -value <0.1, \* $P$ -value <0.05, \*\* $P$ -value <0.01, \*\*\* $P$ -value <0.001.

**Table 2:** Inter-individual variability of individual growth ( $RGR_{ind}$ ) and individual growth (dis-)advantage relative to the whole community ( $RGR_{ind}/SANPP$ ) computed as the mean squares within and between sites (mean  $sq_{within}$  and mean  $sq_{between}$ , respectively), for each species separately

|                           | $RGR_{ind}$           |                       | $RGR_{ind}/SANPP$  |                     |
|---------------------------|-----------------------|-----------------------|--------------------|---------------------|
|                           | Mean $sq_{within}$    | Mean $sq_{between}$   | Mean $sq_{within}$ | Mean $sq_{between}$ |
| <i>Dactylis glomerata</i> | $2.02 \times 10^{-7}$ | $9.26 \times 10^{-7}$ | 0.23               | 1.14                |
| <i>Lolium perenne</i>     | $2.98 \times 10^{-7}$ | $2.96 \times 10^{-6}$ | 0.61               | 1.98                |
| <i>Poa pratensis</i>      | $1.99 \times 10^{-7}$ | $7.43 \times 10^{-7}$ | 0.15               | 0.30                |
| <i>Trifolium repens</i>   | $3.54 \times 10^{-7}$ | $2.34 \times 10^{-6}$ | 0.89               | 1.04                |

indicative of the individual growth (dis-)advantage compared with the whole vegetation, accounted for 20.2–85.6% of the between-site variability (Table 2). Even if this set of species represents a small number of the co-occurring vascular plant species of the 18 local communities studied, we found that within-species site-averaged variability of individual growth represented a moderate to high between-species site-averaged variability, even higher within- than between-species in several sites (Supplementary Material S6).

**Effect of species-averaged growth (dis-)advantage on species ranking at the community level**

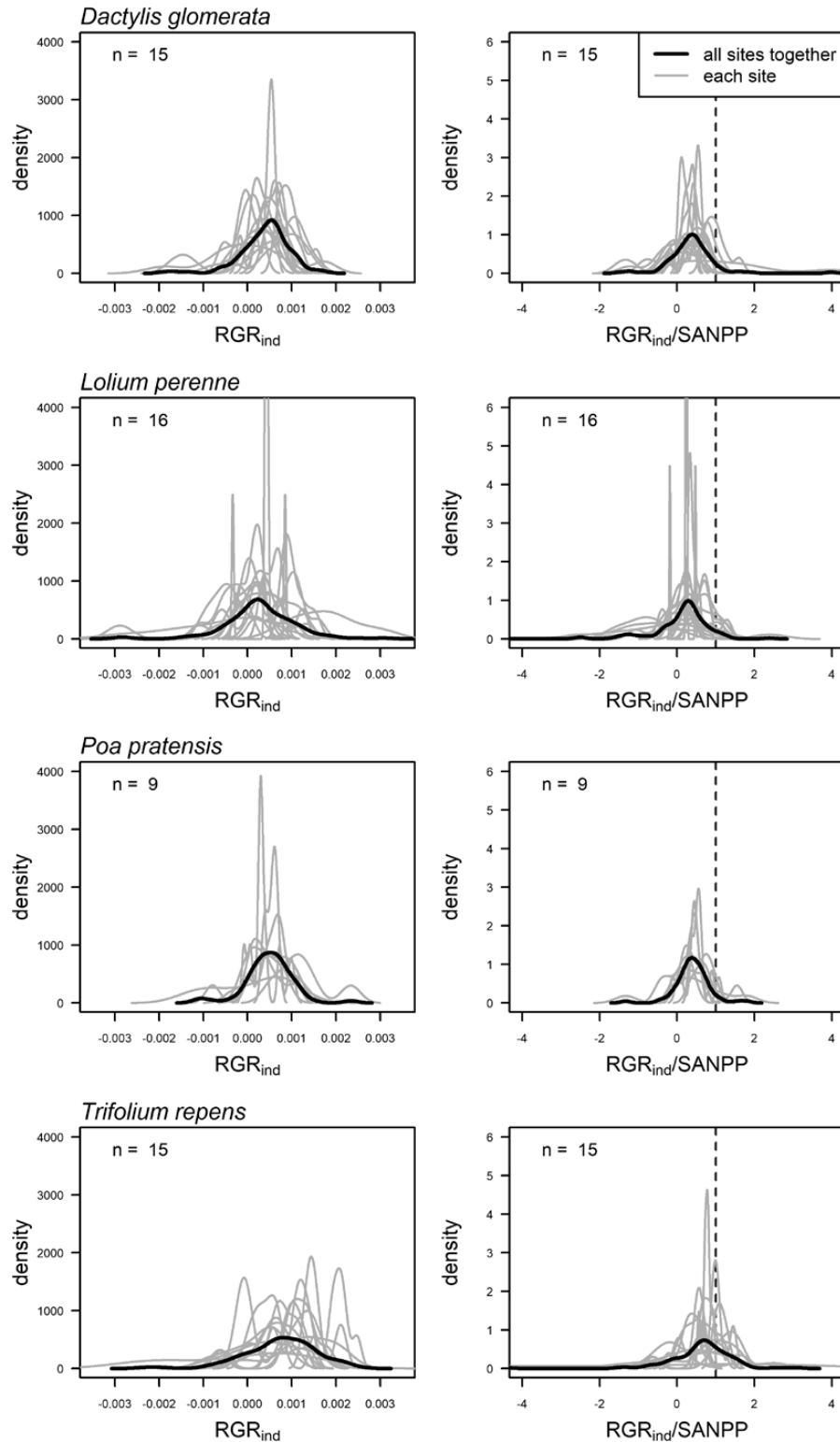
Species ranking (sSR) was significantly explained by the species identity ( $\chi^2 = 407.55, P < 0.001$ ) but not by the species-averaged individual growth relative to the whole community  $RGR_{spe}/SANPP$  ( $\chi^2 = 1.59, P = 0.21$ ;  $RGR_{ind}/SANPP$  presented in Fig. 2), with each species being explanatory of sSR (Table 3).

**DISCUSSION**

We studied plant individual growth of four common species of temperate permanent grasslands, its response to environmental conditions at the

site level, its intraspecific variability within and between sites and its influence on species ranking at the community level. To do so, we studied multiple sites covering a large pedoclimatic gradient and various production situations. Using a recent non-destructive method developed to characterize the growth of individual plants in grasslands, we highlighted that environmental conditions at the site level explain a significant proportion of individual growth variability for three out of the four species studied, the main explanatory environmental conditions being different between species. Moreover, we highlighted a moderate to high within-site inter-individual variability of growth. Finally, we found that interspecific differences of species-averaged individual growth relative to its reference community did not affect species ranking at the community level.

Regarding the influence of environmental conditions on plant individual RGR, light availability and the amount of accumulated rainfall over the period of study showed positive effects for some species. This is in accordance with previous studies carried out under controlled conditions (Galmés et al. 2005; Hofmann and Isselstein 2004). Unexpectedly, soil properties, among which the total nitrogen pool in the upper soil layer, had only a slight effect on plant individual RGR, which contrast with previous findings (Glimskär and Ericsson 1999; Meziane and Shipley 1999). We further found a negative relationship

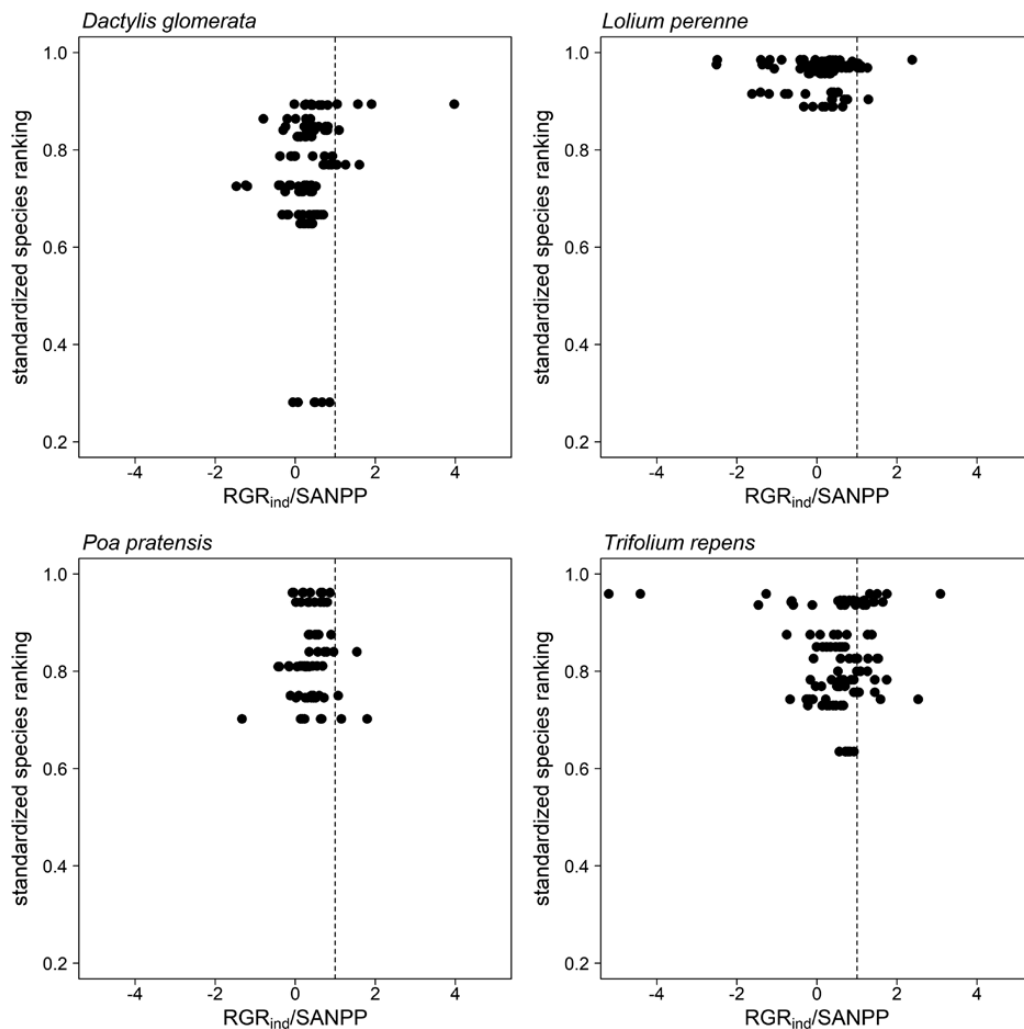


**Figure 1:** Distribution of individual growth ( $RGR_{ind}$ ) and growth (dis-)advantage of individuals relative to the whole community ( $RGR_{ind}/SANPP$ ) within and between sites for each species.  $n$  corresponds to the number of sites where the species were monitored (maximum = 18).

between RGR and initial biomass at the individual, in accordance with previous studies (Rees *et al.* 2010; Rose *et al.* 2009). This confirms the need to account for the initial biomass as a concomitant factor, since RGR, as measurements of intrinsic growth, typically decreases as

individuals get larger, especially due to leaf senescence and increase in maintenance costs during the plant development.

The largest part of RGR variations remained unexplained by the environmental conditions at the site level. This may partly be due to



**Figure 2:** Relationship between the individual growth (dis-)advantage relative to the whole community ( $RGR_{ind}/SANPP$ ) and species ranking at the community level (standardized species ranking based on occurrence frequency, sSR) for each species separately.

an insufficient characterization of driving environmental variables. We characterized most of the key soil properties and meteorological variables known to directly influence growth, and potentially the nature and intensity of plant interactions (Bertness and Callaway 1994; Maestre *et al.* 2009). However, part of RGR variations might be explained by more proximal biotic factors and site description of disturbance regimes, for instance the potential herbivory pressure (Rose *et al.* 2009). Another explanation is related to the moderate to high within-site intraspecific variability in plant growth, comprised between 10.1% and 26.8% of the observed between-site variability when considering  $RGR_{ind}$ , and between 20.2% and 85.6% when considering  $RGR_{ind}/SANPP$ , i.e. the individual growth (dis-)advantage relative to the whole community. These results are particularly striking since we studied a large pedoclimatic gradient that should inflate between-site compared with within-site variability. We suggest that within-site intraspecific variability may have two sources. First, this variability may be due to intrinsic plant variability, notably related to inter-individual variations in reserve amounts that is recognized to influence plant growth (Gleeson and Tilman 1994; Turnbull *et al.* 2008). Second this variability may be due to within-site environmental heterogeneity. Indeed, plant resources and disturbance, and thus growth conditions, are well-known to be highly heterogeneous within grasslands (Bloor and Pottier 2014). In addition, competition occurs at the plant

neighbourhood scale (Purves and Law 2002), exacerbating differences between focal individuals of a same species (e.g. Trinder *et al.* 2013). Future analyses of within-site intraspecific variability of growth should therefore characterize the local environmental conditions experienced by focal individuals and use direct measurements to characterize the 'plant's eye view' of biotic interactions.

Our study also evidenced that better growth at the individual level, estimated using species-averaged individual growth, did not scale-up to higher species ranking at the community level, while species ranking was largely explained by the species identity. This result is in line with McGill *et al.* (2006) who considered that fast growth potential might not be a good proxy of species ranking, and Reader (1998) who reported, in a resource-poor habitat, that growth was negatively related to the species occurrence frequency. In our particular context, we suggest two possible explanations for this lack of relationship between growth and species ranking. First, growth may not be the main determinant of species performance at the community level. In disturbance-prone ecosystems such as permanent grasslands, regenerative processes appear crucial to persist and grow. Consequently, regenerative strategies of species may play a key role in community patterning (Larson and Funk 2016), especially clonality (Benson and Hartnett 2006; Vojtko *et al.* 2017). A second possible explanation is that the high inter-individual within-site growth variability could blur interspecific



**Table 3:** Effect of the species identity and  $RGR_{ind}/SANPP$  on sSR based on beta GLMM, accounting for the field identity as random intercept and slope effects

| Beta GLMM: $sSR \sim RGR_{ind}/SANPP + \text{species} + (RGR_{ind}/SANPP site)$ |                                 |                    |
|---|---------------------------------|--------------------|
| Fixed effect  | df                              | $\chi^2$ (P-value) |
| Intercept   | 1                               | 108.52***          |
| $RGR_{ind}/SANPP$   | 1                               | 1.59n.s.           |
| Species   | 3                               | 407.55***          |
|   | Coefficient<br>(standard error) | Z (P-value)        |
| Intercept (reference species:<br><i>Dactylis glomerata</i> )                    | 1.161 (0.111)                   | 10.47***           |
| $RGR_{ind}/SANPP$   | -0.133 (0.105)                  | -1.26n.s.          |
| <i>Lolium perenne</i>   | 1.929 (0.096)                   | 20.09***           |
| <i>Poa pratensis</i>  | 0.435 (0.089)                   | 4.91***            |
| <i>Trifolium repens</i>   | 0.686 (0.079)                   | 8.65***            |
| Random effect—site identity   | Variance                        | Standard deviation |
| Intercept   | 0.155                           | 0.394              |
| $RGR_{ind}/SANPP$   | 0.091                           | 0.301              |

For fixed effects, a likelihood-ratio test based on the  $\chi^2$  distribution was used to evaluate the significance of the effect of the explanatory variables (type II analysis of deviance), and coefficients were given with a Z test used to evaluate their significance. n.s., not significant.

\*\*\*P-value < 0.001.

differences in competitive abilities. Indeed, a high inter-individual variability has been shown to promote coexistence of species even with large differences in competitive abilities when environmental conditions are spatially structured at fine scale (Uriarte and Menge 2018).

In addition to these basic explanations relying on the processes shaping community assembly, several methodological limitations of our study may also contribute to our findings. First, our study, as any multisite analyses based on data collected in a single year, neglect the role of historical contingency, with past events likely to have long lasting impacts on community patterns (Fukami 2015; Piqueray *et al.* 2011) but not necessarily on the short-term seasonal growth of plant individuals. The grasslands have been sown for at least 20 years, so we could hypothesized that the ranking of species within the community is at least partly the result of mid- to long-term trends while RGR could be more influenced by between-year variability in weather conditions and resource availability. Second, we chose to assess species ranking at the community level using frequency data. Although this approach is relevant and widely applied, frequency data may lead to different patterns of species abundance compared with biomass data (Lepš *et al.* 2006). Third, our monitoring of plant growth and environmental conditions have required the use of enclosure plots to avoid evaluating the effect of local management. Our choice led to modify the light penetration through the canopy compared with standard herbage use characterizing these permanent grasslands for at least 20 years, i.e. grazing or/and mowing with reopening of the canopy over the growing season (Supplementary Fig. S7). Since the cumulative PAR available was the most explanatory driver of RGR for most species, it is likely that plant growth at the individual level during the monitoring period did not necessarily adequately represent the normal growth rates of the four species under standard management conditions.

## CONCLUSIONS

Considering temperate permanent grasslands distributed along a large pedoclimatic gradient, we first highlighted that environmental conditions explained a significant but variable proportion of the individual growth variability for four typical species of this type of grassland. In particular, light availability was the main driver of individual plant growth, especially for *D. glomerata* and *L. perenne*, followed by rainfall amount, especially for *T. repens*, and potential evapotranspiration, while soil properties had only a slight effect. We then found that the within-site variability of plant individual growth was relatively high compared with the between-site variability despite the large pedoclimatic gradient studied. We finally showed that greater species-averaged individual growth compared with the whole community did not result to better ranking at the community level for these four species. Thanks to the non-destructive method used for estimating aboveground biomass, we were able to demonstrate, for the first time in temperate grassland communities, that individual growth is highly variable among individuals of the same species in the same site. This finding opens up novel perspectives for future research.

### Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Environmental properties of the 18 sites studied, including soil and meteorological variables

Figure S1: Standardized principal component analysis (PCA) on the set of soil variables for the 18 sites.

Figure S2: Relationship between the estimated aboveground biomass using the allometric general equation and the estimated biomass using species-specific best equation for twelve species with varying architectures based on the dataset of Pottier and Jabot (2017).

Figure S3: Inter-individual variability of RGR at the individual level  $RGR_{ind}$  along the soil gradient (soil PC1) and some resource availability gradients ( $P_{cumul}$ ,  $PET_{cumul}$ ,  $PAR_{cumul}$  refer to the main text for details).

Material S4: Metadata description of three datasets: FLORIS\_botanical\_survey\_2017.csv, FLORIS\_environmental\_conditions\_2017.csv and FLORIS\_RGR\_individual\_level\_2017.csv; and link to the datasets.

Table S5: Effect of the environmental variables recorded at the site level and the initial biomass at the individual level on the relative growth rate at the individual level  $RGR_{ind}$ , tested for each species separately based on LMM, accounting for the field identity as a random intercept effect.

Material S6: Inter-individual variability of individual growth within and between species for each site.

Figure S7: Cumulative rainfall ( $P_{cumul}$ ), cumulative potential evapotranspiration ( $PET_{cumul}$ ) and cumulative PAR available ( $PAR_{cumul}$ ) over the same period in terms of GDD, i.e. between  $550 \pm 40$  and  $1350 \pm 90$  GDD during the year of the study (year 2017) and based on climate normals.

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