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Functional traits are more variable at the intra- than inter-population level: a study of four calcareous dry-grassland plant species

Funktionelle Merkmale variieren stärker innerhalb von Populationen als zwischen Populationen: Eine Studie an vier Pflanzenarten der Kalkmagerrasen

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Abstract

The majority of studies investigating plant functional traits have used species average trait values, and assumed that average values were sufficiently representative of each species considered. Although this approach has proven valuable in community ecology studies, plant functional traits can significantly vary at different scales, i.e. between but also within populations. The study of species functional trait variability can facilitate increasingly accurate studies in community ecology. Nevertheless, the current extent of within-site plant trait variability has been poorly addressed in the literature. Calcareous grasslands are ecosystems well-suited to study plant trait variation at small spatial scales. Many species are present on heterogeneous calcareous sites, with significant differences in hydric status due to variations in soil depth, soil moisture, aspect, and slope. This study assesses the extent of intra-population functional trait variability and tests the hypothesis that this variability can be explained by within-site environmental heterogeneity. Three functional traits (SLA-specific leaf area, LDMC-leaf dry matter content, and plant vegetative height) were assessed in three populations of four calcareous grassland species totalling 950 individuals. The heterogeneity in soil depth and potential direct incident radiation was also quantified and related to plant functional trait variability. The intra-population functional trait variability was compared to the inter-population variability of collected data and global inter-population variability data obtained from the worldwide TRY functional traits database. The results showed that SLA, LDMC, and plant height are characterized by considerable intra-population variation (SLA: 72–95%, LDMC: 78–100% and vegetative height: 70–94% of trait variability). The results also indicate higher plant height and larger SLA for individuals located in plots with deeper soils or lower potential direct incident radiation, on gentle slopes or north-facing slopes. Our findings additionally support the concept that higher plant height, higher SLA, and lower LDMC are related to higher availability of soil water. Individuals on shallow soils or in more exposed areas are better equipped to cope with environmental stress. Our results indicate plasticity or local adaptation in individuals to environmental heterogeneity. This study suggests that detailed analyses involving plant functional traits require measurements in situ from a large number of individuals, as the degree of individual response strongly depends on an individual's location and its micro-environmental conditions. Neglecting intra-population trait variability may be critical, as intraspecific variation can be very high at the population scale, and is likely to be driven by local environmental heterogeneity.

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Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Over the past decades, functional traits have been increasingly used as reliable predictors of species and community responses to environmental gradients (MCGILL et al. 2006, ACKERLY & CORNWELL 2007, PAKEMAN et al. 2009). The majority of studies investigating functional traits have focused on differences between species, using species average trait values (e.g. ACKERLY & CORNWELL 2007, DURU et al. 2010, SANDEL et al. 2010, SONNIER et al. 2010, GONG et al. 2011, DE BELLO et al. 2013, AMATANGELO et al. 2014), assuming that average values were sufficiently representative of each considered species. Despite the widespread use of this approach in community ecology, plant functional traits can vary substantially within species (ALBERT et al. 2010a, HULSHOF et al. 2013). Taking intraspecific trait variation into account may therefore improve the accuracy and resolution of studies of community ecology (SIEFERT et al. 2015). This intraspecific trait variation can have important implications for species coexistence (JUNG et al. 2010, LONG et al. 2011) or ecosystem functions (PONTES et al. 2007, LECERF & CHAUVET 2008), and is an important element of functional diversity approaches (CIANCIARUSO et al. 2009, ALBERT et al. 2012). Although usually defined as the functional trait variation within a species, intraspecific functional trait variation can be studied at different scales, notably between (e.g. JUNG et al. 2010, BARUCH 2011, ANDERSEN et al. 2012, ALMEIDA et al. 2013, PAKEMAN 2013) and within populations (BOLNICK et al. 2011, MITCHELL & BAKKER 2014), the latter being poorly addressed thus far in the literature.

Calcareous grasslands are well-suited ecosystems to study plant trait variation at small spatial scales. Calcareous grassland species are present on heterogeneous sites, with noticeable differences in soil depth, soil moisture, aspect, and slope, mainly resulting in differences in hydrological status (BUTAYE et al. 2005, PIQUERAY et al. 2007). The total amount of available water for plants was proven to be lower for grasslands characterized by thin soils (<10 cm) and low plant cover compared to grasslands with higher vegetation cover and slightly deeper soils (ALARD et al. 2005, BENNIE et al. 2008, DUJARDIN et al. 2012). Topography and exposure represent additional decisive factors influencing water supply in calcareous grasslands (BENNIE et al. 2006). Slope inclination and exposure strongly affect the amount of solar radiation intercepted by the surface, and subsequently influence soil moisture content (ACKERLY et al. 2002).

Leaf traits are key functional traits that are linked to plant responses to environmental variability (WILSON et al. 1999, GARNIER et al. 2001a, ACKERLY 2004) and stress tolerance (WESTOBY et al. 2002). The regulation of water loss through leaves can be expressed by several key leaf functional traits (WRIGHT et al. 2001, ACKERLY 2004) and, for example, can also be reflected in higher leaf dry matter content (LDMC) and/or lower specific leaf area (SLA) (BUCKLAND et al. 1997, VOLAIRE 2008, POORTER et al. 2009). At large scales, specific leaf area (SLA) generally declines along gradients of decreasing nutrients or moisture availability (CUNNINGHAM et al. 1999, REICH et al. 1999, FONSECA et al. 2000, PÉREZ-HARGUINDEGUY et al. 2013, SÁNCHEZ-GÓMEZ et al. 2013, MONTY et al. 2013), while LDMC generally decreases with greater water availability (CORNELISSEN et al. 2003). Moreover, important trade-offs exist between plant height and environmental stress tolerance

(CORNELISSEN et al. 2003). SLA, LDMC and plant height are strong indicators of plant resource use strategies (WEIHER et al. 1999, CORNELISSEN et al. 2003, WESTOBY & WRIGHT 2006).

This study assesses the extent of intra-population functional trait variability at local scales, and tests the hypothesis that this variability can be explained by within-site environmental heterogeneity.

2. Material and methods

2.1 Study sites

We selected three calcareous grassland sites located in southern Belgium for the study (Fig. 1): the "Montagne-aux-buis" in Dourbes (50°05'N, 4°34'E), the "Tienne Breumont" in Nismes (50°04'N, 4°32'E), and "Sosoye hill" in Sosoye (50°17'N, 4°46'E). The Montagne-aux-buis and the Tienne Breumont are located in the Calestienne region, a 5 km wide and 100 km long belt of Devonian limestone hills and plateaus, with a SW-NE orientation. Sosoye hill is situated in the Meuse valley, a carboniferous formation characterized by limestone-enriched schist. The Calestienne region and the Meuse valley are the two core areas for calcareous grasslands conservation in Belgium. The calcareous grasslands of those regions historically developed under traditional agro-pastoral practices.

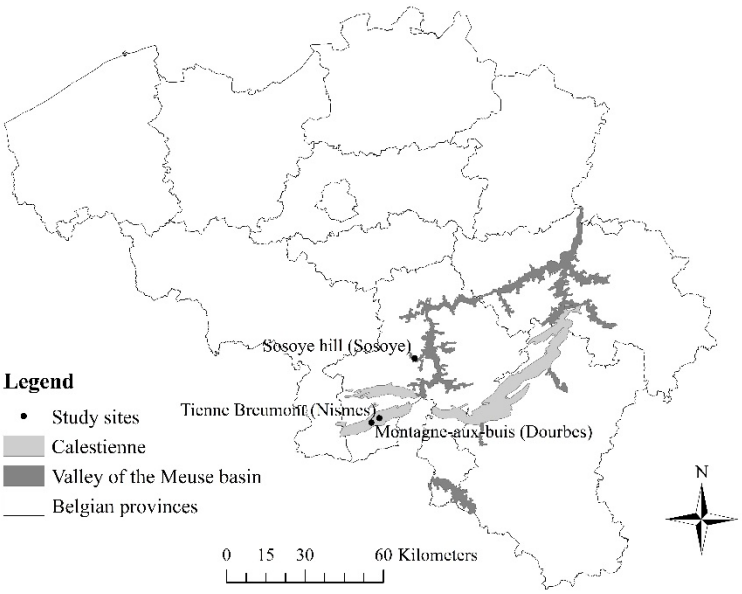

Fig. 1. Study sites locations in Belgium. Three calcareous grassland sites were selected in southern Belgium. The Montagne-aux-buis in Dourbes (50°05' N, 4°34' E) and the Tienne Breumont in Nismes (50°04' N, 4°32' E) are located in the Calestienne region and the Sosoye hill in Sosoye (50°17' N, 4°46' E) is located in the Meuse valley.

Abb. 1. Lage der untersuchten Kalkmagerrasen in Belgien. Die beiden Gebiete Montagne-aux-buis in Dourbes (50°05' N, 4°34' O) und Tienne Breumont in Nismes (50°04' N, 4°32' E) liegen in der Calestienne-Region und der Sosoye hill in Sosoye (50°17' N, 4°46' E) im Meusetal.

2.2 Study species

From a list of plant species identified as being calcareous grassland specialists (PIQUERAY et al. 2007), we selected four perennial species that are generally abundant in European calcareous grasslands for this study (ADRIAENS et al. 2006): *Helianthemum nummularium* (Linnaeus) Miller 1768 (*Cistaceae*), *Potentilla tabernaemontani* Ascherson 1891 (*Rosaceae*), *Sanguisorba minor* Scopoli 1771 (*Rosaceae*), and *Scabiosa columbaria* Linnaeus 1753 (*Dipsacaceae*), following the nomenclature of LAMBINON et al. (2012). The selected species are not protected by local or national law.

2.3 Data collection

Measurements of functional traits and within-site environmental heterogeneity were made along transects placed perpendicularly to the contour of the hills (i.e. in the direction of the slope) in order to meet the whole range of within-site environmental heterogeneity. At each of the three sites, between 3 and 5 transects were used (depending on transect length) in order to find around 90 individuals for each species. Along transects, between 87 and 91 individuals of each study species were selected at each site, except for *Scabiosa columbaria*, which was less abundant in the Montagne-aux-buis and the Tienne Breumont sites (48 and 22 individuals selected, respectively). Individuals of one species located on one site are considered as one population. Following the methodology of CORNELISSEN et al. (2003), only healthy, robust, fully grown adult plants that have their foliage exposed to full sunlight were selected.

For each selected individual, three functional traits were assessed: (i) the vegetative height, i.e. the shortest distance between the upper boundary of the photosynthetic tissues (excluding inflorescences) of the plant and the soil surface (in cm); (ii) the specific leaf area (SLA), i.e. the one-sided area of a fresh leaf, divided by its oven-dried mass (in $mm^2 \times mg^{-1}$); (iii) the leaf dry matter content (LDMC), i.e. the oven-dried mass of a leaf divided by its water-saturated fresh mass (in $mg \times g^{-1}$) (WEIHER et al. 1999, CORNELISSEN et al. 2003, PÉREZ-HARGUINDEGUY et al. 2013). Leaf traits were measured on two leaves for each selected individual. Our sample size was much larger than the one required by standard protocols (CORNELISSEN et al. (2003) recommended 10 individuals for SLA and LDMC, and 25 individuals for plant height) in order to encompass the environmental heterogeneity of sampling sites. We followed the leaf trait measurement protocol of GARNIER et al. (2001b): leaves were weighed to the nearest 10^{-3} g (Mettler Toledo®, Viroflay, France) following a minimum of 6 hours of rehydration, and subsequently scanned. Leaf area was measured using ImageJ imaging software (ABRÀMOFF et al. 2004). Leaves were then oven-dried at 60 °C for 72 hours prior to the second weighing. As plant traits may be affected by grazing (NOY-MEIR et al. 1989), individuals located in calcareous grassland areas that were exposed to the same grazing pressure and frequency were selected. All selected individuals were located on parcels managed by grazing once every three years with approximately the same number of sheep (by hectare) and not grazed during the year in which measurements were taken.

Along transects, the within-site heterogeneity of two variables linked to the potential drought stress was characterized: soil depth (in cm) and the potential direct incident radiation index (PDIR). PDIR is based on the folded aspect, the slope, and the latitude. It is dimensionless and ranges in value from 0.03 to 1.11, with higher values representing high potential direct incident radiation (on south-facing steep slopes). Details of this equation are given in MCCUNE & KEON (2002). The aspect (in degrees) and the slope (inclination in degrees) were measured at the exact position of each individual sampled for trait measurements. Soil depth was measured at all four corners of a 1 m^2 plot placed around each sampled individual in order to calculate a mean soil depth value for each plot.

2.4 Data analysis

The extent of intra-population functional variability was displayed using a boxplot and a kernel density plot (a non-parametric method of estimating the probability density function of a random variable) for each trait and population (each species present at a site).

Intra-population functional variability was compared to:

a) the inter-population functional variability of collected data. Linear mixed models (BOLKER et al. 2009) were used with "site" designated as a random effect to quantify the contribution of each hierarchical level (intra-population vs. inter-population) to the total variation in each trait for each species. The "site" effect provides the inter-population functional variability of data, and intra-population functional variability is provided by the estimated standard error of the model.
b) the global inter-population functional variability that can be expected for the species and traits selected in this study. For this we used data from the worldwide TRY functional traits database was used (KATTGE et al. 2011). Data entries for SLA, LDMC, and vegetative height of our four study species were selected, and only data that encompassed an average of at least 10 individuals were used. Each data entry from the database therefore represents one trait value for one population of the species in the world (i.e. an average trait value taken from at least 10 individuals of one population).

The coefficients of variation (CV = standard deviation/mean) were calculated for each trait of each species at a site (intra-population variability) and in the database (inter-population variability) in order to assess and compare the degree of trait variation. The CV has the advantage of being dimensionless and comparable between species and traits (ALBERT et al. 2011). It has been frequently used in the context of trait variation and interpretation of intraspecific variation (JUNG et al. 2010, FAJARDO & PIPER 2011, LEMKE et al. 2012, FU et al. 2013, WELLSTEIN et al. 2013, MITCHELL & BAKKER 2014, GARCÍA-CERVIGÓN et al. 2015).

Linear regressions were conducted for all species traits and environmental variables at each site separately in order to highlight each population's functional response to within-site environmental heterogeneity.

Mixed models were performed using lmer function in the lme4 library. All analyses were performed using R.2.14.0 (R DEVELOPMENT CORE TEAM 2008).

3. Results

3.1 Extent of intra-population functional variability

We found large intra-population functional variability for SLA in all species (Fig. 2A–D) and LDMC (Fig. 2E–H), but particularly in *Helianthemum nummularium*. For this species, intra-population SLA values ranged from 10.2 to 42.5 $mm^2 \times mg^{-1}$ (Fig. 2A), and LDMC values ranged from 118 to 545 $mg \times g^{-1}$ (Fig. 2E) at the Sosoye hill site. Coefficients of variation (CVs) ranged from 0.13 to 0.30 for SLA (Fig. 2A–D) and from 0.08 to 0.20 for LDMC (Fig. 2E–H), depending upon the species and site. The intra-population variability of vegetative height was high for each species (Fig. 2I–L), with coefficients of variation ranging from 0.30 to 0.67, depending upon the species and site.

A comparison of our measured intra-population functional variability to inter-population variability from the TRY database (DB inter-population variability) exhibited contrasting results, depending upon the species and traits considered. For SLA, DB inter-population variability was lower than our measured intra-population variability for two study species: *H. nummularium* (inter-population database CV = 0.20, compared to 0.20–0.30 for our measured intra-population variability, Fig. 2A) and *Scabiosa columbaria* (inter-population database CV = 0.16, compared to 0.17–0.20 for our measured intra-population variability, Fig. 2D). For *Sanguisorba minor* and *Potentilla tabernaemontani*, DB inter-population variability was higher than our measured intra-population variability (inter-population database CV = 0.25, compared to 0.18–0.19 for our measured intra-population variability for *P. tabernaemontani* and inter-population database CV = 0.27, compared to 0.13–0.14 for our

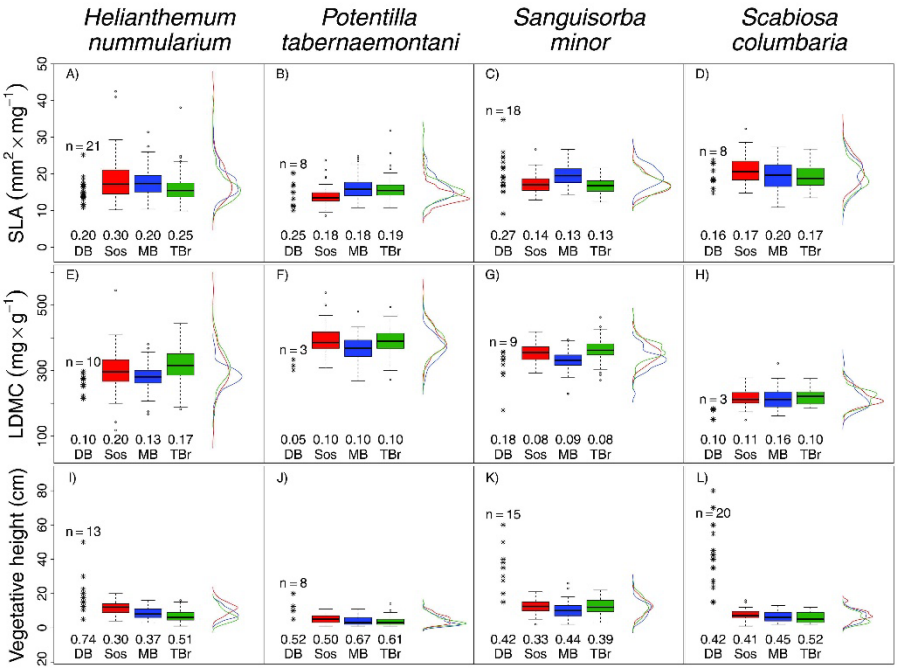

Fig. 2. Extent of intra-population functional variability. Boxplots and kernel density plots for each species and each trait in a site (Sos = Sosoye hill in red, MB = Montagne-aux-buis in blue and TBr = Tienne Breumont in green). Kernel density plots represent the density of data estimated by kernel method (Sosoye hill in red, Montagne-aux-buis in blue and Tienne Breumont in green) and boxplots show the median value (black line) and the inter-quartile ranges: between Q2–Q3 (black box) and between Q1–Q2 and Q3–Q4 (dotted segments). Database values are represented for each species and each trait by asterisks and the number of data (*n*) are given above asterisks. Coefficients of variation (CV) for each trait of each species in a site and in the database are given under boxplots or asterisks.

Abb. 2. Variabilität von drei funktionellen Merkmalen (Spezifische Blattfläche: SLA–*specific leaf area*, Trockenmasseanteil der Blätter: LDMC–*leaf dry matter content* und Höhe der vegetativen Pflanzen: *vegetative height*) bei vier Arten der Kalkmagerrasen in drei Gebieten: Sos = Sosoye hill (rot), MB = Montagne-aux-buis (blau) und TBr = Tienne Breumont (grün). Boxplots und Kerndichteschätzungen (*kernal densities*: Kurven) sind dargestellt. Die Kerndichteschätzungen zeigen die mit der *Kernel*-Methode vorhergesagte Datendichte und die Boxplots den Median (fette Linie), die Quartile (Q): Q2–Q3 als Box und Q1–Q2 und Q3–Q4 als gestrichelte Linien sowie Ausreißerwerte als schwarze Kreise an. Sterne zeigen aus der Datenbank TRY gewonnene Werte mit der entsprechenden Stichprobenzahl *n* an. Unter den Boxplots oder Sternen sind für jedes Merkmal und jede Art die Varianzkoeffizienten (CVs) dargestellt.

measured intra-population variability for *S. minor*, Fig. 2B–C). For LDMC, DB inter-population variability was lower than our measured intra-population variability for all species except *S. minor* (inter-population CV = 0.18, compared to 0.08–0.09 for our measured intra-population variability, Fig. 2G). For vegetative height, DB inter-population variability and intra-population variability were comparable (sometimes higher, sometimes lower depending on the site), except in *H. nummularium*. For this species, DB inter-population variability was higher than our measured intra-population variability (CV = 74, compared to

Table 1. Variance partitioning of traits studied between (inter) and within (intra) populations. Percentage of the total trait variability is partitioned between intra- and inter-population trait variability for each study species. SLA, specific leaf area, LDMC, leaf dry matter content.

Tabelle 1. Aufteilung der Varianz von drei funktionellen Merkmalen bei vier Pflanzenarten auf innerhalb (intra) und zwischen (inter) Populationen. SLA, Spezifische Blattfläche, LDMC, Trockenmasseanteil der Blätter, *Vegetative height*, Höhe der vegetativen Pflanzen.

		Helianthemum nummularium	*Potentilla tabernaemontani*	*Sanguisorba minor*	*Scabiosa columbaria*
SLA	intra-population	95	83	72	93
	inter-population	5	17	28	7
LDMC	intra-population	89	88	78	100
	inter-population	11	12	22	0
Vegetative height	intra- population	70	94	94	92
	inter- population	30	6	6	8

0.30–0.51 for our measured intra-population variability, Fig. 2I). For this trait, database values were higher than the study population values. Species vegetative height ranged from 5 to 80 cm in the database, while it ranged from 1 to 26 cm in our study populations.

Partition of our measured total trait variability between intra- and inter-population variability indicates that the intra-population variability accounts for 70 to 100% of the total variance, depending on the trait and species (Table 1), while 0 to 30% of the variance was due to differences between populations.

3.2 Functional response to within-site environmental heterogeneity

A total of 36 regressions were conducted for the soil depth data, and a total of 36 were also conducted for PDIR data (four species, three populations per species and three traits measured). Of the 36 regressions, 20 were significant ($p < 0.05$) for soil depth (Fig. 3), while 23 were significant ($p < 0.05$) for PDIR (Fig. 4). For all species, significant regressions always indicated the same trend: SLA and vegetative height increased with soil depth (Fig. 3A–D and 3I–L), and decreased when PDIR increased (Fig. 4A–D and 4I–L). LDMC decreased when soil depth increased (Fig. 3E–H) and increased with PDIR (Fig. 4E–H).

4. Discussion

To date, the majority of trait-based research has utilized mean trait values to describe a given species. However, this may hide functional variation at different scales, both between and within populations (BOLNICK et al. 2011). This study highlights the extent of intra-population variability of functional traits at local scales in response to within-site environmental variability within the same habitat type (calcareous grasslands).

The results indicate that SLA, LDMC, and vegetative height are not only characterized by important variation between species, as previously suggested (WESTOBY 1998), but that significant variations can also be highlighted at the intra-population level. Congruent with the results of this study, WELLSTEIN et al. (2013) studied the intraspecific variability of the same traits for four perennial species representative of mountain grasslands, discovering-strong variation of those traits within populations, particularly in SLA and plant height. At

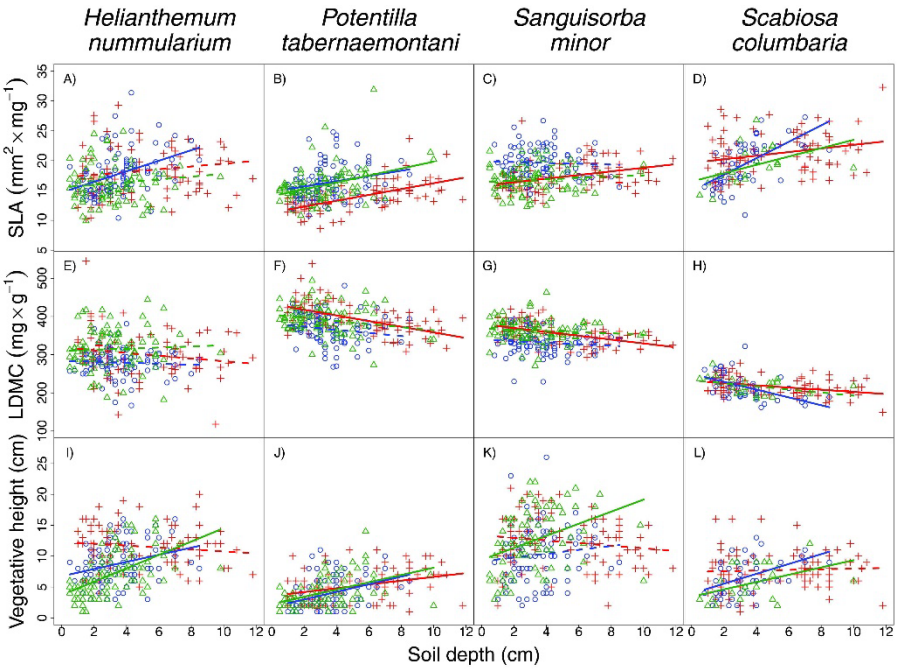

Fig. 3. Population responses to the within-site soil depth heterogeneity. Individual trait values (SLA, LDMC and vegetative height) and the related soil depth (measured at the four corners of a $1m^2$ plot placed around each sampled individual in order to calculate a mean soil depth value for each plot) were drawn for each species individual in a site (the Sosoye hill in red crosses, the Montagne-aux-buis in blue circles and the Tienne Breumont in green triangles). Linear regressions between each species traits and the soil depth were drawn for each species in a site. Regression lines are solid if significant (*p*-values < 0.05) and dashed if not.

Abb. 3. Lineare Zusammenhänge zwischen drei funktionellen Merkmalen (Spezifische Blattfläche: SLA–*specific leaf area*, Trockenmasseanteil der Blätter: LDMC–*leaf dry matter content* und Höhe der vegetativen Pflanzen: *vegetative height*) und der Bodengründigkeit bei vier Arten der Kalkmagerrasen in drei Gebieten: Sosoye hill (rote Kreuze), Montagne-aux-buis (blaue Kreise), Tienne Breumont (grüne Dreiecke). Durchgezogene Regressionsgeraden zeigen signifikante ($p < 0{,}05$) Zusammenhänge und gepunktete Regressionsgeraden keinen Zusammenhang ($p > 0{,}05$) an.

local scales, our study highlighted CV values ranging from 0.13 to 0.30 for SLA, 0.08 to 0.20 for LDMC, and 0.30 to 0.67 for vegetative height. This can be compared to a larger scale study by ALBERT et al. (2010a) who characterized the intraspecific variability of LDMC and vegetative height for sixteen terrestrial species, discovering CV values ranging from 0.08 to 0.25 for LDMC, and from 0.19 to 0.49 for vegetative height, with a large portion of intraspecific variability representing differences between populations. By comparing the extent of intra-population functional variability with large database values, this study suggests that within-population variation represents a significant component of the overall variance in these traits. In this study, over 70% of trait variability was explained at the intra-population level, which is higher than values reported by previous studies. For example, MITCHELL & BAKKER (2014) discovered that for SLA, differences between populations explained 58% of the observed variation for *Hypochaeris radicata*, while only 42% of variation was due to differences at the intra-population level. Additionally, ALBERT et al. (2010b)

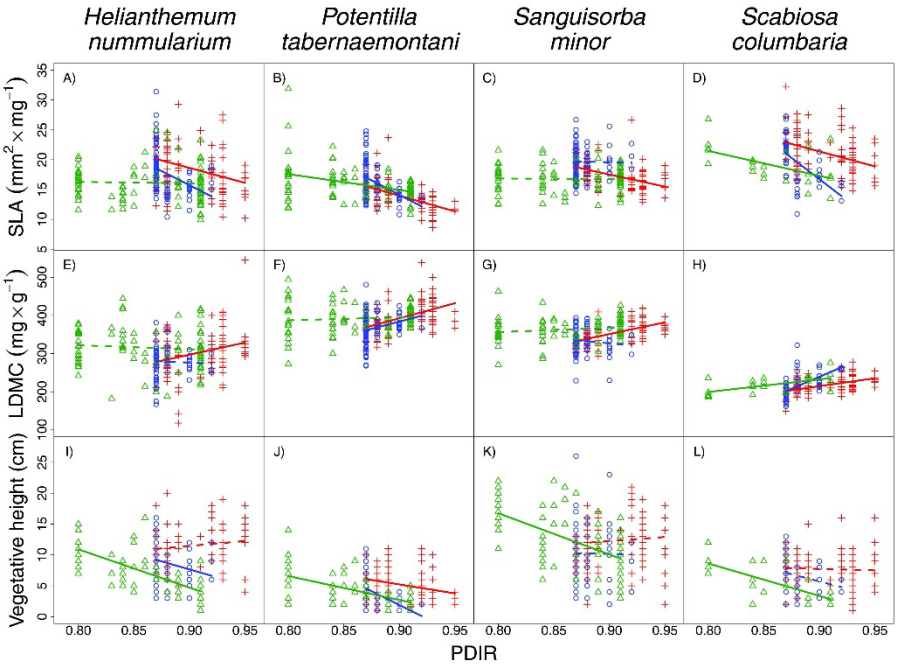

Fig. 4. Population responses to the within-site potential direct incident radiation (PDIR) heterogeneity. Individual trait values (SLA, LDMC and vegetative height) and the related PDIR (index based on the aspect and the slope measured at the exact position of each individual sampled) were drawn for each species individual in a site (the Sosoye hill in red crosses, the Montagne-aux-buis in blue circles and the Tienne Breumont in green triangles). Linear regressions between each species traits and the PDIR were drawn for each species in a site. Regression lines are solid if significant (p-values < 0.05) and dashed if not.

Abb. 4. Lineare Zusammenhänge zwischen drei funktionellen Merkmalen (Spezifische Blattfläche: SLA–*specific leaf area*, Trockenmasseanteil der Blätter: LDMC–*leaf dry matter content* und Höhe der vegetativen Pflanzen: *vegetative height*) und der potenziellen Einstrahlung (PDIR–*potential direct incident radiation*) bei vier Arten der Kalkmagerrasen in drei Gebieten: Sosoye hill (rote Kreuze), Montagne-aux-buis (blaue Kreise) und Tienne Breumont (grüne Dreiecke). Durchgezogene Regressionsgeraden zeigen signifikante Zusammenhänge (p < 0,05) und gepunktete Regressionsgeraden keinen Zusammenhang (p > 0,05) an.

discovered that approximately 50% of the trait variability (SLA, LDMC, LNC-leaf nitrogen concentration, and LCC-leaf carbon concentration) in alpine species was due to differences between populations, and 50% was due to differences within populations.

Among traits measured in this study, SLA exhibited higher CV values than LDMC. This is consistent with other studies of trait variation at the intraspecific level, indicating that SLA (or its inverse leaf mass per area) is one of the most variable leaf functional traits both at broad and at narrow spatial scales (GARNIER et al. 2001a, ALBERT et al. 2010b, FAJARDO & PIPER 2011, AUGER & SHIPLEY 2013, BOUCHER et al. 2013, WELLSTEIN et al. 2013, GARCÍA-CERVIGÓN et al. 2015, SIEFERT et al. 2015). While some traits are fixed and do not vary within species (such as photosynthetic pathway, for example), others can vary substantially, as is notably the case for leaf traits (ALBERT et al. 2010a, HULSHOF & SWENSON 2010).

The findings of this study demonstrate high functional variation within calcareous grassland species populations at fine spatial scales. As differences in abiotic tolerances or resource use between individuals can generate variance in a population's demographic parameters (BOLNICK et al. 2003), large intra-population functional variability can have a large impact on a population's functioning within the site. Moreover, this study showed that the within-population functional variability was a major component of the overall variance in study traits and therefore challenged the assumption that average trait values are sufficiently representative of a given species. This intraspecific functional trait variability at fine spatial scale can be related to microhabitat environmental factors such as light, soil temperature or availability of nutrients (WELLSTEIN et al. 2013). In our case, the intra-population functional trait variability was related to within-site soil depth and PDIR variation.

We found higher plant height and higher SLA for individuals located in plots with deeper soils or low PDIR (less potential direct incident radiation, on gentle slopes or north-facing slopes), and the inverse response for LDMC, with higher values in shallow soil or high potential direct incident radiation. This supports the idea that higher plant height, higher SLA, and lower LDMC may be related to significantly higher availability of soil moisture, as has been previously shown for herbaceous species (MEZIANE & SHIPLEY 1999, WELLSTEIN et al. 2013). Individuals on shallow soils are characterized by lower plant height and higher leaf tissue density, which ensure more successful performance under stressful conditions. Indeed, high LDMC and low SLA are related to high investment in structural tissues, which allow plants to maintain leaf turgor under drought stress (NIINEMETS 2001, SIEFERT 2012). Conservative species that exhibit low SLA (high LDMC), corresponding to dense leaf tissues and low growth rates, exhibit high resource conservation (ALBERT et al. 2010b). Trait differentiation with respect to fine scale variation in soil depth has already been suggested by a study by RAVENSCROFT et al. (2014) who indicated a significant soil depth effect whereby LDMC was lower in deeper soils. ACKERLY et al. (2002) showed that SLA declined with increasing insolation, indicating that species with thicker and/or denser leaves preferentially occupied more exposed, south-facing slopes. These intraspecific patterns are the same as those shown in interspecific trends (CORNWELL & ACKERLY 2009, PAKEMAN et al. 2009).

Carefully designed experiments are needed to test whether the observed intraspecific variation is due to plasticity (the observed trait variation is due to the direct response of individuals to environmental conditions) or local adaptation (the observed trait variation is due to the presence of genetic variation between individuals resulting from natural selection). In our study, gene flow between individuals is certainly high as spatial distance between individuals is quite short and because species are pollinated by flying insects. The possibility of genetic differentiation between individuals is therefore reduced and plasticity is the likely cause of observed intraspecific variability.

Our results indicate that intra-population functional variability is not only highly variable at local scale but that this variability is likely to be driven by local environmental heterogeneity. Our study therefore challenges the use of published mean values of functional trait to describe species behaviour. Measuring traits in situ on a large number of individuals is of primary importance, as the degree of species response strongly depends on individuals' locations and direct environmental influences. Species mean trait values should be replaced by a distribution of traits along environmental gradients.

Erweiterte deutsche Zusammenfassung

Einleitung – Die meisten Studien zu funktionellen Merkmalen von Pflanzenarten (sog. *plant functional traits*) bedienen sich Art-Mittelwerten und setzen damit voraus, dass Art-Mittelwerte die tatsächliche Ausbildung der funktionellen Merkmale ausreichend gut repräsentieren. Obwohl sich solche Art-Mittelwerte in ökologischen Studien als grundsätzlich geeignet erwiesen haben, können funktionelle Merkmale innerhalb der Arten stark variieren (ALBERT et al. 2010a). Die Berücksichtigung dieser innerartlichen Variabilität in ökologischen Studien könnte sinnvoll oder auch notwendig sein (SIEFERT et al. 2015). Innerartliche Variabilität kann auf verschiedenen Ebenen untersucht werden, zum Beispiel zwischen Populationen (JUNG et al. 2010) oder innerhalb von Populationen (MITCHELL & BAKKER 2014a); die letztere Möglichkeit wurde bisher kaum wahrgenommen. Auf kleinräumiger Skala sind Kalkmagerrasen zur Untersuchung funktioneller Merkmale von Pflanzenarten besonders geeignet. Auf den heterogenen Kalkstandorten sind einerseits viele Arten vertreten und andererseits unterscheiden sich diese Arten oftmals in ihren Umweltansprüchen, z. B. in ihren Ansprüchen an die Bodengründigkeit, Bodenwasserversorgung, Hangexposition oder Hangneigung. Die vorliegende Studie untersucht die kleinräumige Variabilität funktioneller Merkmale in Populationen ausgewählter Pflanzenarten der Kalkmagerrasen und testet die Hypothese, dass die Variabilität dieser Merkmale hauptsächlich durch Umweltheterogenität erklärt werden kann.

Material und Methoden – In Süd-Belgien wurden drei Kalkmagerrasengebiete (Dourbes, Nismes und Sosoye) sowie vier Pflanzenarten ausgewählt: *Helianthemum nummularium* (L.) Mill. (*Cistaceae*), *Potentilla tabernaemontani* Asch. *(Rosaceae*), *Sanguisorba minor* Scop. (*Rosaceae*) und *Scabiosa columbaria* L. (*Dipsacaceae*). In drei Populationen jeder Art wurden die funktionellen Merkmale (1) Spezifische Blattfläche (SLA–*specific leaf area*), (2) Trockenmasseanteil der Blätter (LDMC–*leaf dry matter content*) und (3) Höhe der vegetativen Pflanzen an insgesamt 950 Individuen gemessen. Die Variabilität der Bodengründigkeit und der potenziellen Einstrahlung an den Wuchsorten wurden bestimmt und in Beziehung zur Variabilität der funktionellen Merkmale der Pflanzen gesetzt. Die funktionellen Merkmale und die Umweltvariabilität innerhalb der Gebiete wurden entlang von Transekten aufgenommen, die senkrecht die Hügel hinunter verliefen. Die gemessene Variabilität der funktionellen Merkmale innerhalb der Populationen und zwischen den Populationen wurde anhand eines linearen gemischten Modells pro Art bestimmt. Zusätzlich wurden die gemessene und die „globale“ Variabilität der funktionellen Merkmale miteinander verglichen wobei die „globale“ Variabilität auf Grundlage der Werte aus der Datenbank TRY bestimmt wurde. Dazu wurden für jedes funktionelle Merkmal pro Art und Gebiet Varianzkoeffizienten (CV) berechnet. Um die Reaktion der Populationen auf unterschiedliche Umweltbedingungen einzuschätzen, wurden die Zusammenhänge zwischen funktionellen Merkmalen und Umweltbedingungen mit linearen Regressionen für jedes Gebiet separat untersucht.

Ergebnisse – Die Ergebnisse zeigen eine starke Variabilität der funktionellen Merkmale innerhalb der Populationen wobei die Höhe der vegetativen Pflanzen mit Varianzkoeffizienten zwischen 0,30 und 0,67 (je nach Art und Gebiet) besonders stark variierte (Abb. 2). Je nach Art und Merkmal konnten 70–100 % der Varianz auf Unterschiede zwischen den Pflanzen innerhalb der Populationen und lediglich 0–30 % der Varianz auf Unterschiede zwischen den Populationen zurückgeführt werden (Tab. 1). Die spezifische Blattfläche (SLA) und Höhe der vegetativen Pflanzen nahm bei allen Arten mit der Bodengründigkeit zu und mit der potenziellen Einstrahlung an den Standorten ab. Im Vergleich dazu nahm der Trockenmasseanteil der Blätter (LDMC) mit der Bodengründigkeit ab und mit der potenziellen Einstrahlung zu (Abb. 3–4).

Diskussion – In unserer Studie an vier Kalkmagerrasenarten variierten die spezifische Blattfläche (SLA), der Trockenmasseanteil der Blätter (LDMC) und die Höhe der vegetativen Pflanzen nicht nur zwischen Arten und Pflanzengesellschaften (wie es bereits WESTOBY 1998 zeigen konnte), sondern auch innerhalb von Populationen erheblich. Diese Variabilität der funktionellen Merkmale ist die Folge direkter Reaktion der Pflanzen auf eine heterogene Umwelt. Die Variabilität eines funktionellen Merkmales einer Pflanzenart innerhalb ihrer Populationen hat dabei einen erheblichen Anteil an der Ge-

samtvariabilität des Merkmales, wie der Vergleich der in den Populationen gemessenen Variabilität mit der „globalen Variabilität“ auf Grundlage einer weltweiten *Trait*-Datenbank zeigen konnte. Konkret zeigen unsere Ergebnisse, dass eine bessere Wasserversorgung in Kalkmagerrasen zu einem höheren Wuchs, einer größeren spezifischen Blattfläche und einem geringeren Trockenmasseanteil der Blätter der Pflanzen führen. Im Umkehrschluss bedeuten unsere Ergebnisse, dass diejenigen Pflanzen, die in Kalkmagerrasen auf besonders flachgründigen Standorten oder Standorten mit besonders hoher Einstrahlung wachsen, den hier höheren Umweltstress durch gezielte Ausbildung ihrer funktionellen Merkmale besser ertragen. Vermutlich handelt es sich dabei um plastische Reaktionen der Pflanzen auf Umweltstress; es können aber auch lokale Anpassungen vorliegen. Weiterhin zeigt unsere Studie, dass bei der Untersuchungen von funktionellen Merkmalen die Untersuchung einer großen Anzahl an Individuen notwendig ist, da die Individuen auf die unterschiedlichen Standortbedingungen ihrer Wuchsorte mit ihren funktionellen Merkmalen stark reagieren können. Die Nichtbeachtung der durch solche Umweltheterogenität bedingten hohen Variabilität der funktionellen Merkmale kann ökologische Zusammenhänge verschleiern oder auch zu Fehleinschätzungen führen.

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