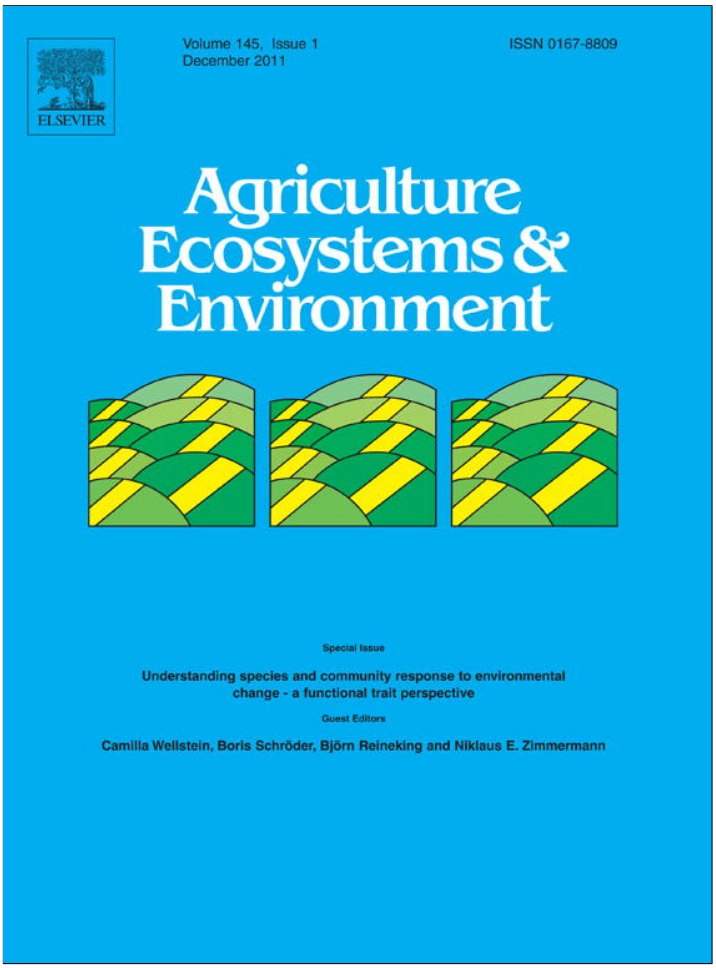
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Agriculture, Ecosystems and Environment 145 (2011) 67–76

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Plant leaf economics and reproductive investment are responsive to gradients of land use intensity

Patrick Lienin*, Michael Kleyer

Landscape Ecology Group, University of Oldenburg, P.O. Box 2503, 26111 Oldenburg, Germany

ARTICLE INFO

Article history:
Received 27 May 2010
Received in revised form 11 January 2011
Accepted 25 March 2011
Available online 6 May 2011

Keywords:
Leaf economics spectrum
Functional traits
Disturbance
RLQ analysis
Soil nutrients
Reproduction

ABSTRACT

Relationships between functional leaf traits across large sets of plant species emphasized the existence of a major axis describing a trade-off between rapid acquisition and conservation of resources forming the so-called "leaf economics spectrum". It is uncertain which environmental factors determine the economics spectrum and whether traits associated with reproduction co-vary with the economics spectrum. To determine these trait–environment relationships for agricultural ecosystems, this study was conducted at field, pasture, and heathland sites forming a strong land use gradient in Northwest Germany. The abundance of 49 species was recorded in 85 plots together with their traits (canopy height, specific leaf area, leaf N, leaf N:P, leaf and stem dry matter content, life cycle, reproductive investment (RI) in seed mass and seed number), as well as parameters describing soil resources and land use disturbances. RLQ multivariate analysis of the data set related an environmental table to a species trait table using a species abundance table to extract the joint structure between them. Thereafter, we clustered the species on the RLQ axis to extract functional groups. Traits associated with the leaf economics spectrum were strongly related to soil resources that co-varied with disturbance intensity. A division of the whole land use gradient into agricultural and heathland sites showed that RI was not decoupled from trait–environment relationships although the direction of the RI–environment relationship was opposite in the two subsets. Species were clumped rather than linearly arranged in the trait–environment space and the functional groups broadly corresponded to weed communities, pastures with differing intensities, and heathlands. The trade-off in plant economics responding to soil resources supports predictions of previous theoretical and empirical work. Different RI–environment relationships in agricultural sites and heathlands emphasize the relevance of local scales in trait–environment studies. In general, the results point to some of the biological mechanisms controlling functions and services of agricultural ecosystems.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Agricultural land uses depend to a large part on ecological functions provided by plants, such as biomass production and decomposition, forage quality, nutrient and water cycles. In turn, these functions depend on the growth of plants, their carbon gain, recruitment and dispersal. For these processes, plant functional traits are widely accepted as powerful indicators (Lavorel and Garnier, 2002; Lavorel et al., 2007; Violle et al., 2007). For instance, specific leaf area (SLA) serves as a good predictor for potential growth rate (Garnier, 1992; Westoby et al., 2002) and leaf nitrogen and phosphorus contents (leaf N, leaf P) are related to leaf growth and defense strategy (Reich et al., 2008). Studies exploring bivariate and multivariate relationships between leaf traits across large species sets have emphasized the existence of a major axis describing a trade-off between rapid acquisition and conservation of resources (Grime et al., 1997; Reich et al., 1999; Díaz et al., 2004). The so-called "leaf economics spectrum" was recently extended to provide evidence for a "plant economics spectrum", wherein the trade-off is consistent across leaf, stem, and root traits (Freschet et al., 2010).

The question arises whether this 'primary axis of plant specialization' (Grime et al., 1997) responds to environmental conditions. Studies examining rainfall (Wright et al., 2004) and soil nitrogen (N) (Freschet et al., 2010) support the idea that plants specializing in resource acquisition prefer resource-rich conditions, whereas plants specializing in resource conservation are found mainly in environments characterized by resource-poor conditions. When analyzed on a global scale, these leaf economics–environment relationships were relatively weak (Wright et al., 2004). Individual traits forming the plant economics spectrum have also been related to environmental conditions. Leaf dry matter content (LDMC), SLA, leaf N, and leaf P were found to be responsive to soil resource availability. For instance, nutrient-poor conditions have been found to

* Corresponding author. Tel.: +49 0 441 798 3600; fax: +49 0 441 798 5659.
E-mail address: patrick.lienin@uni-oldenburg.de (P. Lienin).

0167-8809/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.agee.2011.03.015

Author's personal copy

preferably support perennial plants with a low SLA and a high LDMC (Cunningham et al., 1999; Potter and Klooster, 1999; Pakeman et al., 2009). Perennials with short-lived leaves tend to have a long-term disadvantage against longer lived leaves, which are essential for conservation of resources when the nutrient supply is scarce (Ryser, 1996; Ackerly et al., 2002). However, these studies often used limited environmental descriptors and the most significant factors contributing to the environmental specialization of a plant with a given 'score' on the economics axis remain to be determined.

Next to soil resources, disturbances resulting in plant biomass loss play a key role in structuring plant communities. Particularly in agricultural landscapes, communities are shaped by different disturbance regimes characterized by selectivity, intensity, frequency and timing of biomass destruction, in addition to multiple combinations of resource availability (nutrients, water), and management history (Grime, 2002; Foster et al., 2003; Pausas and Lavorel, 2003). By this means, a specific combination of land management and soil resources also determines the trait composition of plant communities (Roy and Blois, 2006; Aubin et al., 2007; Kleyer et al., 2008). Variations in leaf economics, plant height, life span, and seed traits were found to respond to agricultural land use (McIntyre and Lavorel, 2001; Pausas et al., 2004; Díaz et al., 2007; Castro et al., 2010). Disturbance intensity alone can also affect growth traits. For instance, meadow plants need to allometrically increase SLA to achieve a given height when mowing frequency is increased (Kühner and Kleyer, 2008). Grazing or soil disturbance (e.g. ploughing) encourages plants with traits likely linked to ruderal syndromes such as short stature, flat rosette morphology, rapid growth rate, and short lived leaves (McIntyre and Lavorel, 2007).

Numerous studies emphasized the effects of disturbance on regenerative traits, such as plant life span, age at first reproduction, and reproductive investment (RI), which is the product of seed mass and seed number (e.g. Harper, 1977; Tilman, 1988; Obeso, 2002). This can be traced back to the r/K selection theory (MacArthur and Wilson, 1967), which assumes that sites with frequent disturbances are inhabited with r-selected species exhibiting rapid regeneration, high reproductive effort, and vegetative traits associated with low competitive ability. On the other hand, K-selected species occurring in sites characterized by an absence of large-scale disturbances exhibit slow regeneration, low reproductive effort, and high competitive ability. In contrast to the tight coupling between regenerative and vegetative traits assumed by the *r*/K theory, Grime (1988) postulated that regenerative phase traits are uncoupled from those associated with carbon gain in the established phase. Indeed, several studies found that regenerative and vegetative traits did not co-vary (e.g. Shipley et al., 1989; Díaz and Cabido, 1997; Grime et al., 1997). While many studies explored whether co-variation of regenerative and vegetative traits can be found in large sets of species, these relationships are rarely put in the context of a trait–environment analysis. Much remains to be determined about how environmental conditions affect species' positions on the plant economics spectrum and how regenerative traits are related to traits associated with carbon gain and the environment, particularly on local scales (Wright et al., 2005; Freschet et al., 2010).

In this study we aimed at quantifying these trait–environment relationships in an agricultural landscape composed of modern and traditional land uses. The land uses ranged from heathland and pasture to farmland differing in utilization intensity, and were chosen to maximize the gradients of disturbance and soil resources. All land uses have a long and continuous agricultural history, apart from heathlands which are now managed for nature conservation.

We asked to which extent trait–environment relationships were consistent across these different land uses. Our expectation was that traits associated with resource acquisition should characterize plants in intensively managed and fertilized sites whereas plants with traits associated with resource retention should be found in resource-poor sites. In agricultural landscapes, disturbance and nutrient gradients are often correlated because an increase in the frequency of harvests requires an increase in fertilization. This suggests that higher investments in reproduction to cope with increasing disturbances are accompanied by higher and faster vegetative growth. We therefore expected that traits associated with reproduction and vegetative growth should show a coupled rather than uncoupled response to land use intensity. However, this may not be relevant in unfertilized heathlands managed for conservation rather than production.

Finding general responses of co-varying functional traits to environmental gradients may improve predictions regarding the ecological services vegetation provides for farmers and conservationists, such as biomass production, nutrient cycling and carbon storage. However, results may be significantly influenced by the span of the environmental gradients (Kühner and Kleyer, 2008). Trait–environment relationships are usually assessed by comparing the ecological performance of the species bearing the traits, thereby separating responsive from non-responsive traits. At the scale of a single landscape, ranges of environmental predictors are inevitably restricted and may not encompass the full distribution of abundant species. On the other hand, gradients can be too long for rare and specialised species. Their niches can only be modelled on smaller scales with higher sampling resolution and less environmental variation (Thuiller et al., 2004). Moreover, strong environmental differences with a large gradient often produce strong variation of trait expression that may override local scale variations. On the other hand, consistency of trait–environment relationships across several scales may be a strong indicator of generality. In order to assess consistency in trait–environment relationships across scales, we repeated our analyses on two subsets representing the productive agricultural environments and the less productive nature reserves managed for conservation.

Linking plant traits to environmental conditions via plant abundances in plots was accomplished using two fourth-corner methods. RLQ analysis (Dolédec et al., 1996) consists of a multivariate ordination of species abundance data constrained by species trait data and environmental variables, while fourth-corner analysis (Dray and Legendre, 2008) quantifies and tests the correlation between species traits and environmental variables.

2. Materials and methods

2.1. Study site

The study site (subdivided into three sub-sites) is located in Northwest Germany (52°55′N, 8°15′E; 52°57′N, 8°07′E; 52°55′N, 7°56′E). The climate is oceanic with dominant westerly winds. Mean annual rainfall is 740 mm and the mean monthly temperatures range from 0.9 °C in January to 16.6 °C in July with a mean annual temperature of 8.7 °C. Within the study sites, elevation ranges from 19 to 44 m above sea level. Soils are mostly sandy on moraine sediments. From the Middle Ages until the 19th century, the common land-use practice was "Plaggen" cultivation. In this land use system, the top soil including the litter layer was removed from forests and heathlands, used as bedding for cattle, and after being enriched with slurry, spread on arable fields for fertilization. As a consequence of this exploitative land use, the forests almost vanished. Open heaths and even denuded soils were predominant. Sand drifted from denuded soils and accumulated in sand dunes. This land use system was abandoned after the invention of mineral fertilizer. Today, the remaining heathlands are extensively managed and confined to small areas (Behre, 2008). Nevertheless, the soils at the study sites are presumably still affected from this historical management.

Author's personal copy

We used random stratified design to select 85 non-contiguous plots. With information on management strategies derived from interviews with farmers as well as our own monitoring, the selected plots were stratified by broad categories of land-use intensity and soil moisture (well-drained versus dry soils, as well as arable fields, pastures, and heathlands with sheep grazing). As a result, we created a gradient of sites ranging from farmland, intensive and extensive grassland (well-drained soils) as well as semi-natural grasslands (dry soils), shrub land (well-drained and dry soils), and fallow land. For later analyses, we additionally split the data set into subset '*agriculture*' comprising 40 plots on farmland (ranging from arable fields to pasture and margins on relatively well-drained soils), and a subset '*heath*' comprising 45 plots managed for conservation, comprising heaths and dry acidic grasslands. All fieldwork was done in 2007 and 2008.

2.2. Environmental parameters

In each plot, undisturbed soil samples using a soil sample ring of 100 cm^3 were taken from each soil horizon up to 60 cm depth. The samples were analyzed in the laboratory for bulk density, and physical and chemical properties. Field and lab measured variables included soil solution pH, soil texture, soil density (Schlichting et al., 1995), and available soil potassium (K) and phosphorus (P) per unit mass (Table 1). K was extracted with ammonia-lactate solution and measured with a flame photometer (Egnér et al., 1960; SpektrAA 300, Varian, USA) and P via a continuous flow analyzer (Murphy and Riley, 1962; Skalar Analytic, Netherlands). P and K were used as indicators of soil nutrient availability (Binkley and Vitousek, 1989). Soil texture and organic carbon content were used to estimate plant available water (AG Boden, 2005). Available N could not be measured due to logistic constraints.

To rank sampling plots across a gradient of disturbance, a single index was calculated using the (1) type of disturbance (cutting, ploughing as part of rotational arable, fertilizer use, herbicide use, and former events), (2) intensity (percentage of biomass removal), and (3) return interval of disturbance (e.g. cut once per year = 1; cut twice per year = 2). In areas with cattle grazing, plots were also (and additionally) fenced to prevent grazing. To quantify biomass removal by grazing, 1 m^2 was harvested inside and outside the fence, and the difference between values resulted in removal of above-ground biomass in percent. More information on this index can be found in Kleyer (1999) and White and Jentsch (2001).

2.3. Species selection and trait measurements

Plant species composition and abundance of each plot was recorded by frequency analyses with a 1 m × 1 m frame, with grids of 0.1 m × 0.1 m. Species that were prevalent in at least 10% of the sampling plots were selected for trait measurement resulting in a total of 49 species with trait information. The following 9 plant traits were selected for their known or assumed responses to disturbance and soil fertility (Table 1): plant life span (PLS, qualitative), rosette growth (ROS, qualitative), SLA, LDMC, leaf N, leaf N/P ratio (leaf N/P), stem dry matter content (SDMC), canopy height (CAN), and RI.

Leaf traits and canopy height were measured on 10 individual plants, distributed evenly across the plots where they were present. From each individual, 2 randomly selected light-exposed, fully expanded leaves were collected. Regenerative traits (e.g. seed mass and weight) were measured on 10 additional individuals collected later in the season. The final trait value assigned to a species was the average over all sampled individuals. See Cornelissen et al. (2003), Garnier et al. (2007) and Kleyer et al. (2008) for details on measurement of traits. Chemical analysis of leaf C, N, and P contents were conducted on each individual. Replicate analysis

Table 1
(A) Environmental parameters for each plot, with their abbreviations, units (where relevant), and descriptive statistical values (min, max, median, and standard deviation) for all data and the '*agriculture*' and '*heath*' data subsets; Table R in RLQ analysis. (B) List of traits measured and used for analysis of 49 vascular plant species, units, and descriptive statistical values; see Cornelissen et al. (2003) and Kleyer et al. (2008) for details on ecological meaning and measurement procedures; Table Q in RLQ analysis.

(A) Environmental variables	Abbreviation	Type of variable/unit					Subset 'agriculture'				Subset 'heath'			
			min	max	median	Sd	min	max	median	Sd	min	max	median	Sd
Disturbance index	Dist	relative[a]	0.00	2.85	0.57	0.74	0.14	2.85	1.35	0.72	0.14	0.78	0.40	0.17
Soil potassium content	Soil K	kg/ha[a]	24.95	1555.92	114.39	315.63	89.05	1555.92	241.05	404.10	24.95	233.12	93.20	43.13
Soil phosphorus content	Soil P	kg/ha[a]	1.51	2316.59	259.91	529.44	97.29	2316.59	829.75	509.08	1.51	642.49	21.83	187.07
pH value	pH	log-scale	2.83	5.70	4.15	0.74	3.5	5.7	4.9	0.52	2.83	4.43	3.87	0.49
Soil water holding capacity	Water	mm	18.01	149.27	112.15	27.64	95.02	149.27	124.74	14.10	18.01	148.90	105.82	28.41
(B) Traits	Abbreviation	Type of variable/unit					min			max			median	Sd
Plant life span	PLS	ordinal: 0 = annual; 0.5 = biennial; 1 = perennial					–			–			–	–
Rosette growth	ROS	ordinal: 0 = no rosette; 0.5 = semi-rosette; 1 = rosette					–			–			–	–
Canopy height	CAN	continuous: (cm)[a]					2.40			120.00			18.40	23.23
Specific leaf area	SLA	(mm^2/mg)					5.22			57.18			19.85	10.85
Leaf dry matter content	LDMC	(mg/g)					156.14			897.04			270.41	158.36
Leaf nitrogen content	Leaf N	(%)					8.99			40.05			21.28	7.67
Leaf N:P ratio	Leaf N/P	ratio (relative)					3.83			64.73			10.04	11.12
Stem dry matter content	SDMC	(mg/g)					103.30			591.46			330.01	129.23
Reproductive investment	RI	Seed mass × seed weight [g][a]					0.00			4040.03			105.35	801.88

[a] Trait $\log_{10}$—transformed for analysis.

Author's personal copy

of C and N were carried out on each of these samples using an Elemental analyzer (Allen, 1989; CHNS 1112 Analyzer Flash EA, Thermo Electron Corporation) and their values averaged. Leaf P was analyzed using a Continuous Flow Analyzer (Murphy and Riley, 1962; Skalar Analytic, Netherlands). Data on PLS and rosette growth form were taken from the LEDA database (Kleyer et al., 2008).

2.4. Statistical analysis

Prior to the main analysis, correlation coefficients for all traits and environmental variables were calculated to test if two variables were highly correlated (Pearson $r > 0.8$). CAN, seed mass, and seed weight trait variables, as well as disturbance and all soil nutrient data were $\log_{10}$-transformed to approach normality.

We used RLQ analysis to investigate the relationships between species traits and environmental characteristics of sites, based on species abundance (Dolédec et al., 1996). In this method R represents a matrix whose rows are sites and columns the environmental characteristics; Q represents a matrix whose rows are plant species and columns the trait attributes for each species; L represents a matrix whose rows are sites and columns the abundance of each plant species per site. The purpose of this analysis is to extract the joint structure between the two tables R and Q using the third table L. Table L is assumed to measure the intensity of the relationships between R and Q.

RLQ has been frequently used to describe trait–environment relationships, for instance to analyze plant invasions in terms of traits (Thuiller et al., 2006) or co-variations between traits of alpine plants and the abiotic environment (Choler, 2005). The mathematical model underlying RLQ analysis is fully explained in Dolédec et al. (1996). Here we describe only some basic properties. Firstly, three separate ordinations were calculated prior to the co-inertia analysis. Table L was ordinated via correspondence analysis (CA), an eigenanalysis method that provides a joint scaling of sites and species scores and maximizes the correlation between them. The ordination of tables R and Q was done by a principal component analysis (PCA). To interpret these analyses, we used the correlation between each variable and the components of the PCA. RLQ analysis was subsequently performed by a three-table co-inertia analysis. RLQ analysis selects axes that maximize the co-variance between the sample scores constrained by the environmental variables (Table R) and the species scores constrained by the species traits (Table Q; Dolédec and Chessel, 1994). These axes comprise scores as a compromise between maximizing the correlation and explaining the variation in each table. The scores of the first two axes were used to define functional groups. We used Ward's hierarchical clustering (Everitt et al., 2001) with Euclidean distances between species scores. This method minimizes within-group sums of squares and tends to form clusters with nearly the same number of species per cluster, assuming that species are evenly distributed in trait space (Legendre and Legendre, 1998). The optimal number of clusters was determined with the Harabasz's index (Gordon, 1999).

To test the significance for the explicit trait–environment relationships we used the fourth-corner statistic (Dray and Legendre, 2008). This method measures the link between species traits and environmental variables by a Pearson correlation coefficient (two quantitative variables), by a Pearson Chi square (χ^2) and G statistic (for two qualitative variables), and by a Pseudo-F and Pearson r (for one quantitative and one qualitative variable). Five different permutation models can be used to test significance. We applied permutation model 4 (with 999 permutations) to test the null hypothesis (H_0) that species are distributed according to their preferences for site conditions, but independent of their traits (Dray and Legendre, 2008). The entire set of analyses described above was repeated for the split data set with subset '*agriculture*' and '*heath*' individually.

All statistical analyses were performed with the ade4- and stats-package implemented in the R software, version 2.10.0 (R Development Core Team, 2010).

Table 2
Results of the RLQ analysis for each axis. Eigenvalues (A) are provided from the decomposition of the cross matrix and represent a squared covariance ("pseudo-eigenvalue"). "Total variance" is the percentage of total variance explained by each axis. Weighted correlation ratios between the environmental (B) and species trait (C) variables and the RLQ axes (abbreviations as in Table 1).

	Variables	Axis 1	Axis 2
(A)	Eigenvalues	7.97	0.06
	Total variance explained	99.07	0.71
(B)	Environmental variables		
	Dist	−0.85	−0.36
	Soil K	−0.64	−0.54
	Soil P	−0.92	0.17
	pH	−0.93	0.15
	Water	−0.60	0.51
(C)	Species traits		
	PLS	0.38	0.32
	ROS	−0.57	0.35
	CAN	0.27	−0.44
	SLA	−0.87	−0.04
	LDMC	0.90	−0.28
	SDMC	0.89	0.09
	RI	0.10	−0.83
	Leaf N	−0.64	−0.20
	Leaf N/P	0.70	−0.30

3. Results

3.1. Separate ordination of the trait and environmental variables

The broad value ranges in trait and environmental variables indicated gradients of considerable length (Table 1). The first two PCA axes of the site environmental variables accounted for almost 80% of the total variance (first axis: 64%). The first axis was negatively correlated with soil P and K content, pH value, disturbance index, and water holding capacity, while the second axis had a strong positive correlation with water holding capacity (Fig. 1A). The first two PCA axes of the species trait variables accounted for 58% of the total variance. The first axis was positively correlated with LDMC and leaf N/P and negatively associated with SLA, leaf N, and ROS (Fig. 1B). The second axis was negatively correlated with PLS and ROS and positively correlated with RI, whereas CAN showed a low correlation.

3.2. Joint structure between species traits and environmental variables

The first two axes of the RLQ analysis explained 99.12% and 0.67% of the total matrix variance that links the environmental characteristics in table R with species traits in table Q (Table 2). The first RLQ axis was strongly negatively correlated with all environmental variables, namely disturbance, pH value, water holding capacity, soil K and P content (Fig. 1C, Table 2B). This axis appeared as the main gradient ranging from low nutrient availability and low disturbance to more productive areas with higher disturbance. The first RLQ axis was negatively correlated with ROS, SLA, and leaf N, and positively correlated with LDMC, SDMC, leaf N/P, and ROS (Table 2C). While the first axis separated the species mainly according to their leaf economies, the second axis was weakly related to reproduction and vertical expansion, in particular RI and CAN.

Author's personal copy

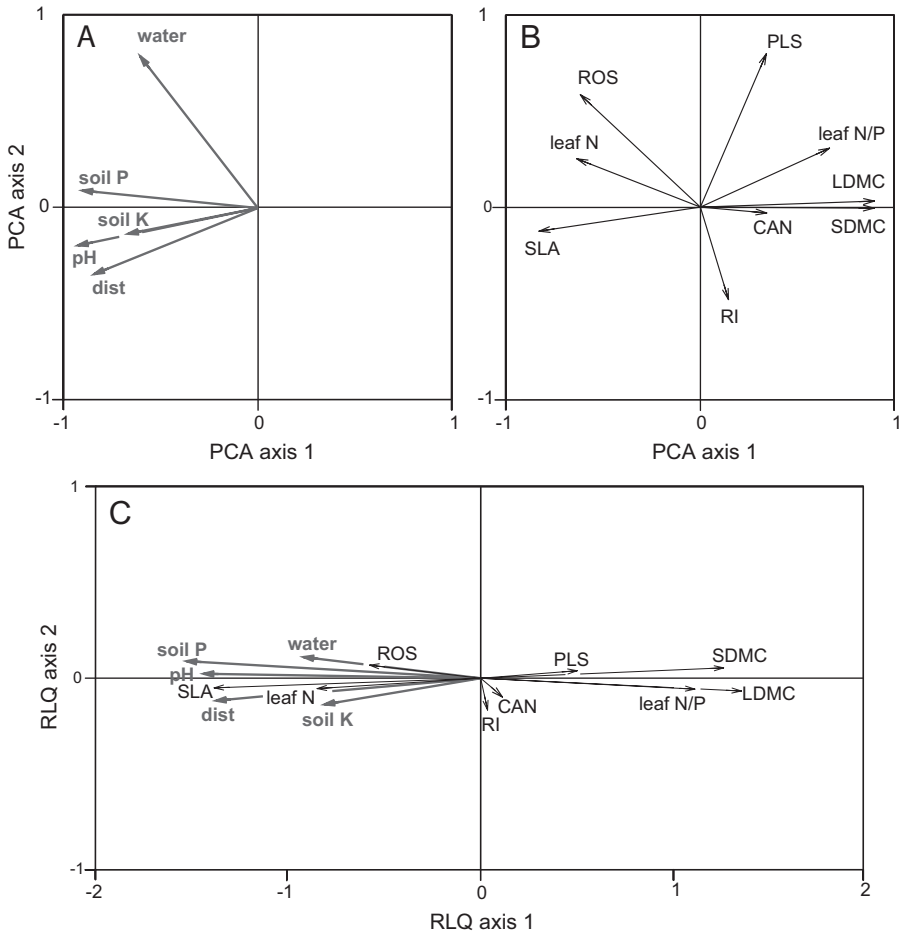


Fig. 1. Display of environmental variables (A; abbreviation explained in Table 1), species traits (B; abbreviation explained in Table 1) along the first two PCA axes, and display of environmental parameters and species traits (C) along the first two RLQ axes.

3.3. Fourth-corner analysis of environmental variables and species traits

Permutation tests of the fourth-corner analysis revealed that disturbance index, pH value, soil P, water holding capacity, and to a limited extend soil K were significantly positively correlated with SLA, ROS, and leaf N (Table 3), while all other traits were negatively correlated with these environmental variables. CAN, RI and PLS had no or weakly significant correlations with the environmental variables.

Table 3
Correlations between traits and environmental parameters with tests of significance, provided by the fourth-corner analysis (see 2.4 for details; abbreviations as in Table 1).

	Dist	Soil K	Soil P	pH	Water
PLS					
			0:−0.56	0:−0.48	0:−0.39
ROS			0.5:0.60	0.5:0.48	0.5:0.38
			1:−0.11 **	1:−0.06 *	1:−0.04 *
CAN					
SLA	0.69***	0.46***	0.76***	0.71***	0.43***
LDMC	−0.64***	−0.36**	−0.75***	−0.69***	−0.52***
SDMC	−0.67***	−0.37**	−0.67***	−0.66***	−-0.38**
RI					
Leaf N	0.45**	0.28*	0.45**	0.44**	0.25*
Leaf N/P	−0.52**	−0.27**	−0.66**	−0.59**	−0.36*

*** $p < 0.001$.
** $p < 0.01$.
* $p < 0.05$.

3.4. Clustering of species groups based on environmental variables and species traits

Six stable clusters were identified showing how multiple trait expressions combine into functional groups (FGs, Fig. 2A and B). FG A contained only two species, *Echinochloa crus-galli* and *Solanum nigrum,* which were mainly found in arable fields. These annuals got high SLA and leaf N, grew rather tall and strongly invested in regeneration, whereas they showed a low stem and leaf dry matter content. FG B species primarily inhabited sites with intensive management (pastures), therefore grew to a small size (low CAN), had a high SLA, a low SDMC, a low LDMC, and a low leaf N/P. FG C species occurred at moderately managed sites (medium disturbance and lower nutrient availability), and had a higher CAN compared to FG B species. FG D species had similar expressions than those in clusters B and C, but had lower leaf nutrient contents and were found at sites with more dry soils. In contrast to the four clusters, species at dry sites (heathland or dry grassland) with a low level of disturbance and those with a limited nutrient supply were mostly perennial and characterized by a low SLA, leaf N and RI, but high LDMC and SDMC (FG E). FG F comprised juvenile tree species entering the heath communities. Because populations of these species are usually removed by conservation management before maturity and first flowering, we did not assign any reproductive output to these taxa.

Author's personal copy

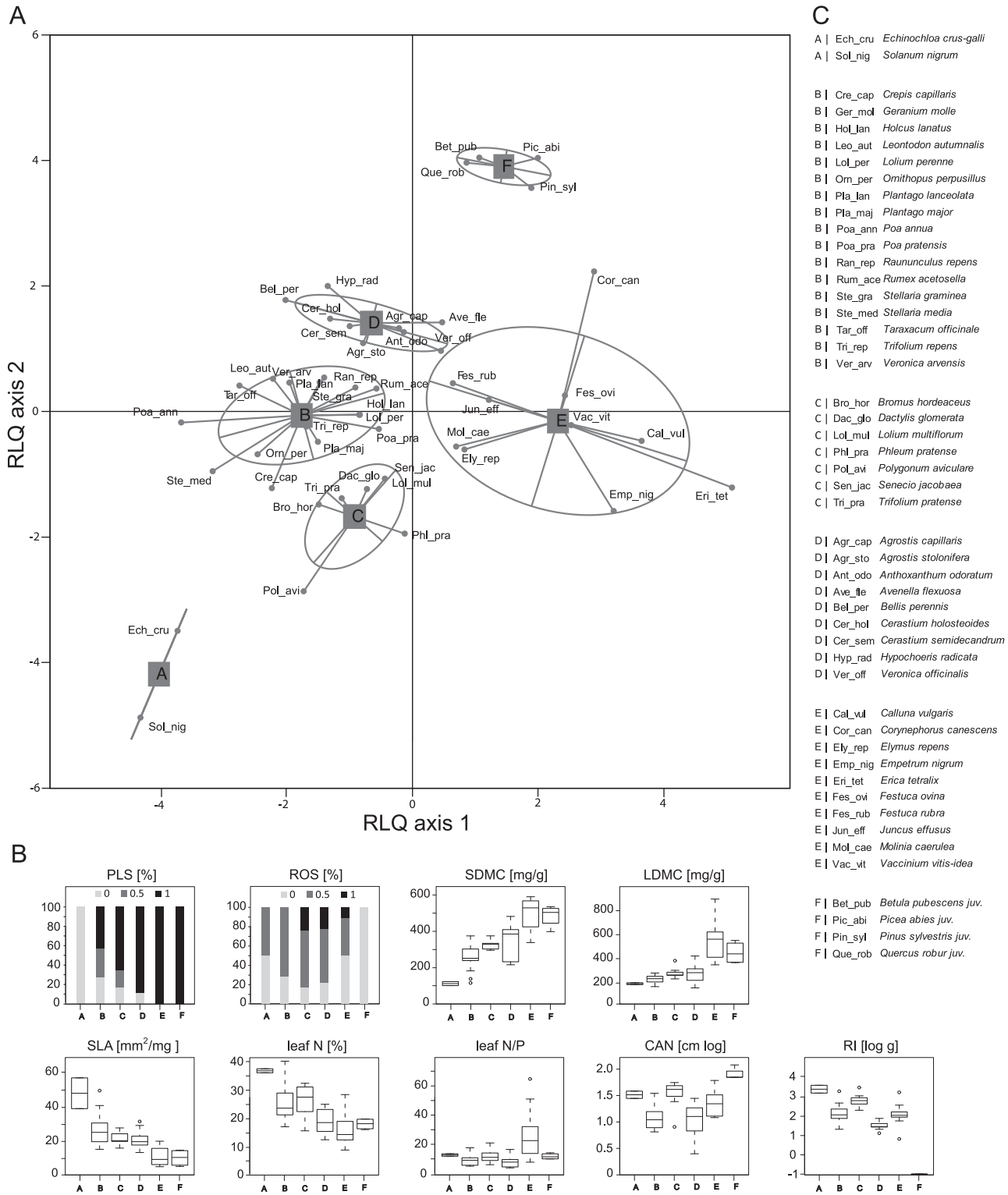


Fig. 2. Display of species with cluster groups along the two first RLQ axes (A), functional group identity and abbreviations of species (C; nomenclature following Jäger and Werner (2002)). Trait attributes for each cluster are displayed in (B). The vertical bar graphs show the nominal variables (PLS and ROS; abbreviations and units are explained in Table 1). Box plots show quantitative variables with the range of each variable (middle black line represents the median).

3.5. Separate RLQ-analysis of the two subsets

The first two axes of the RLQ analysis for subset '*agriculture*' explained 87.9% and 8.1% of the total variance of the matrix that links the environmental characteristics in table R with species traits in table Q (Fig. 3A). The correlations between environmental parameters were similar to the larger scale described above with the exception of water holding capacity showing opposite correlations with the axes than in the larger scale. Also, soil P and K, disturbance, and water holding capacity had moderately negative correlations with the second axis. While most of the traits showed relationships with the first axis comparable to the larger scale, RI

Author's personal copy

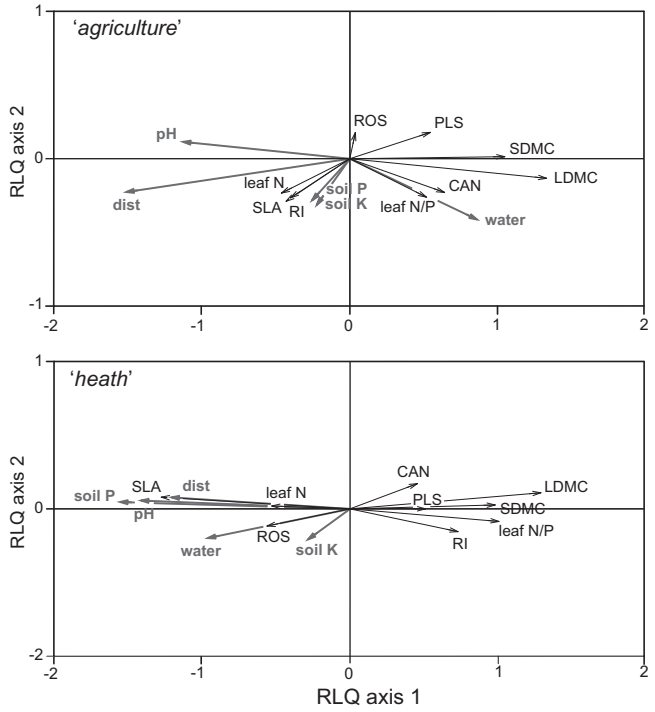


Fig. 3. Display of environmental variables and species traits (abbreviations explained in Table 1) along the first two RLQ axes for the divided data set 'agriculture' and 'heath'.

was aligned with SLA and leaf N and therefore negatively correlated. CAN was positively correlated with the first axis and thus aligned with LDMC, SDMC, and leaf N/P, whereas ROS had no correlations. The second axis had lower and weaker correlations with environmental parameters and traits, correlating negatively with SLA, leaf N, RI, CAN, and leaf N/P, and correlating positively with plant life span. The first two axes of the RLQ analysis for subset '*heath*' explained 98.5% and 1.3% of the total variance of the matrix that links the environmental characteristics in table R with species traits in table Q (Fig. 3B). Environmental parameter correlations were very similar to those seen with the larger scale described above. In contrast to the results found in the set of agricultural plots, CAN and RI were positively correlated with the first axis.

4. Discussion

4.1. Leaf economic spectrum in relation to soil resource and land use

Our study showed strong correlations among several leaf traits that correspond to the leaf economics spectrum as proposed by Wright et al. (2004), as has been previously observed (Grime et al., 1997; Reich et al., 1999; Díaz et al., 2004). SDMC was linked with LDMC. The close association between leaf and stem traits, among others, prompted Freschet et al. (2010) to postulate a plant economics spectrum. In contrast to the leaf economics spectrum, leaf N/P reflects the balance between uptake and losses of N and P in response to the availability of these nutrients in the soil (Güsewell, 2004). Species with lower N and P concentrations tend to have higher leaf N/Ps, thus high leaf N/Ps are often found in stress-tolerating plants whereas plants with high growth rates have low N/Ps (Sterner and Elser, 2002; Niklas et al., 2005; Westoby and Wright, 2006). Therefore, as expected, we found that leaf N/P covaried with the economics spectrum, although it is less directly connected to plant carbon gain (Güsewell, 2004).

Acquisitive trait expressions of the leaf economics spectrum such as high SLA and leaf N in conjunction with lower SDMC and lower leaf N/Ps could be found on resource-rich sites, whereas the opposite was true on poor sites. This pattern was consistent across scales, with similar relationships found for the whole land use gradient and for both sub-gradients composed of agricultural and heath sites with different management intensities. Hence, we can confirm our expectation that environmental gradients select traits that reflect the leaf (plant) economic spectrum ranging from acquisitive traits on rich or frequently disturbed sites to retentive traits on poor sites. The trade-off in plant economics responding to soil resource availability confirms and supports predictions of previous theoretical and empirical work (Grime et al., 1997; Reich et al., 1997; Aerts and Chapin, 2000; Díaz et al., 2004; Wright et al., 2004; Grime, 2006; Freschet et al., 2010; Laughlin et al., 2010).

Intensity of land management expressed as disturbance produced similar effects. Disturbed sites were more associated with acquisitive characteristics, whereas sites with a low disturbance had higher values of traits with resource-retentive characteristics, such as high leaf and stem dry matter content and low leaf N/P (see also Garnier et al., 2004; Louault et al., 2005; Pakeman et al., 2009). This reflects the fact that disturbance co-varies with resource supplies in agricultural landscapes. Disturbance also explained the negative response of CAN to increasing soil resources, which would be reversed in completely undisturbed systems. Increasing cultivation intensity (e.g. ploughing, mowing) from heathlands to arable fields translated to diminishing disturbance return intervals with a shorter plant growth period. To regenerate within shorter time periods requires a decreased stem investment resulting in lower CAN, or an increased relative growth rate that is often correlated with an SLA increase in SLA (Poorter and Van der Werf, 1998; Kühner and Kleyer, 2008).

In contrast to single traits, FGs are based on classifying combinations of traits. In our approach, RLQ species scores are clustered to maximize species' trait–environment relationships. These combinations, or syndromes, could give additional insight into species adaptation to multiple environmental conditions. First, this analysis illustrates that species were clumped rather than evenly arranged in functional space. The main reason for the separation of functional groups is trait convergence due to environmental filtering, given the strong differences in habitat conditions in this study (Grime, 2006). Comparing the FGs with plant community descriptions for the northwest region of Germany (e.g. Pott, 1992; Fig. 2) revealed that the clumped pattern reflects distinct plant communities occurring along the land use gradient, with FG A occurring in weed communities, FGs B to D occurring in pastures of different grazing intensity and fertility, and FG E occurring in heaths. FG F consisted of juvenile tree species that entered heaths and acidic grasslands that were not recently managed. Trait convergence occurs when the environment exerts a strong selective pressure on multiple traits and filters only a small subset of the total range of trait expressions in the geographical species pool. The environmental effect on traits of multiple species in a community is exemplified by leaf N/P which was around 10 among all groups except for the heath species. With a median >20, the heath species were close to P-limitation (Güsewell, 2004). P-limitation as indicated by leaf N/P corresponded directly to the low available soil P values found in the soils of the heathland plots. Note that the critical leaf N/P values indicating nutrient limitation reported by Güsewell (2004) refer to pooled above-ground biomass of plant communities and not to leaves of functionally similar species. In our case, however, there was a large overlap between groups and communities, as explained above.

On the other hand, convergence cannot explain the richness of co-occurring functionally similar species within groups, particularly in FGs B and D (Fig. 2). Coexistence theory requires that species

Author's personal copy

should diverge in trait space to coexist (e.g. May and MacArthur, 1972; Grime, 2006), suggesting a linear rather than clumpy distribution. However, recent theoretical works show that species can either be sufficiently different or sufficiently similar to coexist. The reason for the latter effect in models is that competitive exclusion is extremely slow among functionally similar species so that these species coexist almost infinitely in their common environmental niche (Scheffer and van Nes, 2006; Fort et al., 2009). Whether this 'lumpy pattern' theory (Scheffer and van Nes, 2006) is likely to explain clumped species distributions in both functional and environmental space remains to be tested in experiments.

4.2. Response of regenerative traits

According to the work of Grime (2002), Westoby (1998), and Díaz et al. (2004), regenerative traits should be uncoupled from resource-rich—acquisitive traits to resource-poor—retentive traits axis. On the whole land use gradient, RI indeed did not correlate with this axis. However, in contrast to the other traits, this result was not consistent across scales. At both ends of the whole land use gradient, species invested more in their reproduction than at intermediate levels of resource availability and disturbance intensity. Species from the most disturbed and resource-rich sites grew fast and produced either many or big diaspores (e.g. *Solanum nigrum*), whereas the heath species of the most nutrient-poor sites grew very slow, but produced many or big diaspores. Both contrasting relationships cancelled out when combined in a single trait–environment analysis.

At agricultural sites, the RI and PLS responses mainly reflected greater seed output and reproductive effort in annuals (Ross and Lembi, 2009), which were favoured by strong disturbances on fertilised arable fields and frequently grazed pastures. The hypothesis that RI is greater when disturbance and/or nutrient availability is greater was confirmed for this subset but not for the heathland subset. Among the species occurring in the heathland subset, FG E had the highest RI and occurred at the least disturbed sites with lowest soil resources. These species had either many light seeds (e.g. *Calluna vulgaris* (4978, 0.02 mg); *Erica tetralix* (10535, 0.01 mg)) or berries (e.g. *Vaccinium vitis-idea* (226, 38.24 mg); *Empetrum nigrum* (1028, 18.02 mg)) that resulted in similar RI values. Heathlands often developed from forests as a consequence of plaggen cultivation (Behre, 2008) or burning (Mohamed and Gimingham, 1970) on sandy soils in the Middle Ages in Northwest Europe. Plaggen cultivation periodically denuded soils on communal land at a return interval of 20–40 years by removing litter and topsoil (Gimingham, 1972; Pott and Hüppe, 1991; Kleyer et al., 2007). Plant species required long distance dispersal to cover these distant, strongly disturbed patches. Heathland species such as *Calluna vulgaris* were particularly successful in recolonising the bare soil due to prolific production of light seeds facilitating wind dispersal, as well as the ability to persist in a seed bank and to germinate on bare soil (Nordhagen, 1938; Düll and Kutzelnigg, 2005). Bird dispersal of *Vaccinium* spp. and *Empetrum nigrum* berries may be an equally successful long distance dispersal mode to sites where vegetation and topsoil had been removed. Bolmgren and Eriksson (2010) showed that fleshy fruits are associated with heavier seeds. The evolution of fleshy fruits dispersed by frugivores was interpreted as a strategy to uphold sufficient long-distance dispersal for heavier seeds that would otherwise suffer from reduced dispersability (Tiffney and Mazer, 1995; Bolmgren and Eriksson, 2005). However, the co-evolution of bird dispersers and endozoochoric dispersal syndromes in plants are still subject to debate (Fenner and Thompson, 2005).

On the whole, the division of the whole land use gradient into agricultural sites and heathlands showed that regenerative traits were not decoupled from the main trait–environment relationships, although the pattern was opposite in both subsets. This became particularly apparent because we used RI as the product of seed mass and number. Otherwise, the divergence in the single traits among heath species would have produced insignificant results in the heathland subset. However, RI appeared to be more related to actual or historical disturbance regimes than to soil fertility.

5. Conclusions

Our comparative approach revealed that higher soil resources and higher disturbance intensity favoured coordinated leaf and stem trait expressions indicating faster plant growth and turnover of investments of nutrients and biomass whereas infertile sites favoured traits indicating nutrient and biomass retention. This result points to some of the biological mechanisms controlling functions and services of agricultural ecosystems. These services comprise not only the pace and amount of biomass production, but also the regulation of nutrients and carbon in the vegetation component of agro-ecosystems, as well as forage quality indicated by its nutrient content. However, the degree of chaining of trait responses to the environment and trait effects on agro-ecosystem properties still needs to be quantified (Suding et al., 2008).

Regenerative traits were not uncoupled from this pattern at the scale of individual land use systems, although the direction of the trait–environment relationship was very different between these systems. In contrast to the apparently general leaf economics–soil resources relationship, this result emphasizes the importance of disturbance magnitudes and spatial arrangements of past and present land uses on the assembly of plant communities requiring specific regeneration and dispersal syndromes. The different responses of RI to the environment in agricultural sites and heathlands also emphasize the relevance of local scales in trait–environment analyses. Insignificant relationships on larger scales may be just the sum of two contrasting trends on a lower scale. Therefore consistency of trends across scales needs to be taken into account in functional trait–environment studies.

Acknowledgements

This study was conducted as part of the collaborative research project SEQUESTER. This project was financially supported by the State of Lower-Saxony and the Volkswagen Foundation, Hannover, Germany (grant no. ZN 2026). We thank the OOWV and Biohof Bakenhus in Cloppenburg, Germany, for their co-operation and support on site. We greatly acknowledge Benjamin Hell for his preparatory work, Regine Kayser for laboratory assistance, and Kirsten Brandt, Tobias Feldt, Christian Ketzer, and Natali Könitz for their field assistance. The editor and two anonymous reviewers improved the article with valuable comments. We further thank Stéphane Dray for our collaboration regarding the RLQ. Fourth corner analysis, and Cristina Ramalho for helpful comments to an earlier version of the manuscript.

References

Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K., Starmer, K.P., 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants. Contrasting patterns in species level and community level analyses. Oecologia 130, 449–457.

Aerts, R., Chapin, F.S., 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30, 1–68.

Allen, S., 1989. Chemical Analysis of Ecological Materials. Blackwell Scientific Publications, Oxford, England.

Aubin, I., Gachet, S., Messier, C., Bouchard, A., 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. Ecoscience 14, 259–271.

Behre, K.-E., 2008. Landschaftsgeschichte Norddeutschlands: Umwelt und Siedlung von der Steinzeit bis zur Gegenwart. Wachholtz.

Author's personal copy

Binkley, D., Vitousek, P.M., 1989. Soil nutrient availability. In: Pearcy, R.W., Ehleringer, J.R., Mooney, H.A., Rundel, P.W. (Eds.), Phsiological Plant Ecology: Field Methods and Instrumentation. Chapman and Hall, London, pp. 75–96.

Boden, A.G., 2005. Bodenkundliche Kartieranleitung. Schweizerbart verb. und erw. Aufl., Stuttgart.

Bolmgren, K., Eriksson, O., 2005. Fleshy fruits—origins, niche shifts, and diversification. Oikos 109, 255–272.

Bolmgren, K., Eriksson, O., 2010. Seed mass and the evolution of fleshy fruits in angiosperms. Oikos 119, 707–718.

Castro, H., Lehsten, V., Lavorel, S., Freitas, H., 2010. Functional response traits in relation to land use change in the Montado. Agriculture. Ecosystems & Environment 137, 183–191.

Choler, P., 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. Arctic Antarctic, and Alpine Research 37, 444–453.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51, 335–380.

Cunningham, S.A., Summerhayes, B., Westoby, M., 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological Monographs 69, 569–588.

Díaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. Journal of Vegetation Science 8, 463–474.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., Torres-Espuny, L.d., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: evidence from three continents. Journal of Vegetation Science 15, 295–304.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D., 2007. Plant trait responses to grazing—a global synthesis. Global Change Biology 13, 313–341.

Dolédec, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species & environment relationships. Freshwater Biology 31, 277–294.

Dolédec, S., Chessel, D., Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. Environmental and Ecological Statistics 3, 143–166.

Dray, S., Legendre, P., 2008. Testing the species traits-environment relationships: The fourth-corner problem revisited. Ecology 89, 3400–3412.

Düll, R., Kutzelnigg, H., 2005. Taschenlexikon der Pflanzen Deutschlands. Ein botanisch-ökologischer Exkursionsbegleiter zu den wichtigsten Arten.

Egnér, H., Riehm, H., Domingo, W.R., 1960. Untersuchungen über die chemische Bodenanalyse als Grundlage für die Beurteilung des Nährstoffzustandes der Böden II. Chemische Extraktionsmethoden zur Phosphor- und Kaliumbestimmung. Kungliga Landbrukshögskolans Annaler 26, 199–215.

Everitt, B., Landau, S., Leese, M., 2001. Cluster analysis. Arnold.

Fenner, M., Thompson, K., 2005. The Ecology of Seeds. Cambridge University Press, Cambridge.

Fort, H., Scheffer, M., van Nes, E.H., 2009. The paradox of the clumps mathematically explained. Theoretical Ecology 2, 171–176.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. BioScience 53, 77–88.

Freschet, G.T., Cornelissen, J.H.C., Logtestijn, R.S.P.v., Aerts, R., 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. Journal of Ecology 98, 362–373.

Garnier, E., 1992. Growth analysis of congeneric annual and perennial grass species. Journal of Ecology 80, 665–675.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosytsem properties during secondary succession. Ecology 85, 2630–2637.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.P., Thebault, A., Vile, D., Zarovali, M.P., 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European Sites. Annals of Botany 99, 967–985.

Gimingham, C.H., 1972. In: Gimingham, C.H. (Ed.), Ecology of Heathlands. Chapman and Hall, London.

Gordon, A., 1999. Classification. Chapman & Hall, Boca Raton, FL [u.a.].

Grime, J.P., 1988. Comparative Plant Ecology: A Functional Approach to Common British Species. Allen & Unwin, London.

Grime, J.P., 2002. Plant Strategies, Vegetation Processes and Ecosystem Properties. John Wiley and Sons.

Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. Journal of Vegetation Science 17, 255–260.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., 1997. Integrated screening validates primary axes of specialisation in plants. Oikos 79, 259–281.

Güsewell, S., 2004. N:P ratios in terrestrial plants: variation and functional significance. New Phytologist 164, 243–266.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London/New York.

Jäger, E.J., Werner, K., 2002. Exkursionsflora von Deutschland. Gefäßpflanz: Kritischer Band. Spektrum. Akademischer Verlag, Heidelberg, Berlin.

Kleyer, M., 1999. Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. Journal of Vegetation Science 10, 697–708.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96, 1266–1274.

Kleyer, M., Biedermann, R., Henle, K., Obermaier, E., Poethke, H.-J., Poschlod, P., Schröder, B., Settele, J., Vetterlein, D., 2007. Mosaic cycles in agricultural landscapes of Northwest Europe. Basic and Applied Ecology 8, 295–309.

Kühner, A., Kleyer, M., 2008. A parsimonious combination of functional traits predicting plant response to disturbance and soil fertility. Journal of Vegetation Science 19, 681–692.

Laughlin, D.C., Leppert, J.J., Moore, M.M., Sieg, C.H., 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. Functional Ecology 24, 493–501.

Lavorel, S., Díaz, S., Cornelissen, J., Garnier, E., Harrison, S., McIntyre, S., Pausas, J., Pérez-Harguindeguy, N., Roumet, C., Urcelay, C., 2007. Plant functional types: are we getting any closer to the holy grail? Terrestrial Ecosystems in a Changing World, 149–164.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545–556.

Legendre, P., Legendre, L., 1998. Numerical Ecology, second English ed. Elsevier, Amsterdam/New York.

Louault, F., Pillar, V.D., Aufrère, J., Garnier, E., Soussana, J.F., 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. Journal of Vegetation Science 16, 151–160.

May, R.M., MacArthur, R.H., 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Sciences of the United States of America 69, 1109–1113.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

McIntyre, S., Lavorel, S., 2001. Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. Journal of Ecology 89, 209–226.

McIntyre, S., Lavorel, S., 2007. A conceptual model of land use effects on the structure and function of herbaceous vegetation. Agriculture Ecosystems & Environment 119, 11–21.

Mohamed, B.F., Gimingham, C.H., 1970. The morphology of vegetative regeneration in calluna vulgaris. New Phytologist 69, 743–750.

Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27, 31–36.

Niklas, K.J., Owens, T., Reich, P.B., Cobb, E.D., 2005. Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. Ecology Letters 8, 636–642.

Nordhagen, R., 1938. Studien über die monotypische Gattung Calluna Salisb., I und II. Bergens Mus. Aarb., Naturv. raekke 4.

Obeso, J.R., 2002. The costs of reproduction in plants. New Phytologist 155, 321–348.

Pakeman, R.J., Lep, J., Kleyer, M., Lavorel, S., Garnier, E., 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. Journal of Vegetation Science 20, 148–159.

Pausas, J.G, Bradstock, R.A., Keith, D.A., Keeley, J.E., 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85, 1085–1100.

Pausas, J.G., Lavorel, S., 2003. A hierarchical deductive approach for functional types in disturbed ecosystems. Journal of Vegetation Science 14, 409–416.

Poorter, H., Van der Werf, A., 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers, H., Poorter, H., Van Vuuren, M.M.I. (Eds.), Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Backhuys Publishers, Leiden, Netherlands, pp. 309–336.

Pott, R., 1992. Die Pflanzengesellschaften Deutschlands. E. Ulmer, Stuttgart.

Pott, R., Hüppe, J., 1991. Die Hudelandschaften Nordwestdeutschlands. Abhandlungen aus dem Westfälischen Museum für Naturkunde, Münster.

Potter, C.S., Klooster, S.A., 1999. Dynamic global vegetation modelling for prediction of plant functional types and biogenic trace gas fluxes. Global Ecology and Biogeography 8, 473–488.

R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C., Bowman, W.D., 1999. Generality of leaf trait relationships: A test across six biomes. Ecology 80, 1955–1969.

Reich, P.B., Tjoelker, M.G., Pregitzer, K.S., Wright, I.J., Oleksyn, J., Machado, J.-L., 2008. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. Ecology Letters 11, 793–801.

Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences of the United States of America 94, 13730–13734.

Author's personal copy

Ross, M.A., Lembi, C.A., 2009. Applied Weed Science: Including the Ecology and Management of Invasive Plants. Pearson Prentice Hall, Upper Saddle River, NJ.
Roy, V., Blois, S., 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. Biological Conservation 130, 592–603.
Ryser, P., 1996. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. Functional Ecology 10, 717–723.
Scheffer, M., van Nes, E.H., 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. Proceedings of the National Academy of Sciences of the United States of America 103, 6230–6235.
Schlichting, E., Blume, H.-P., Stahr, K., 1995. Bodenkundliches Praktikum. Blackwell Wissenschafts-Verlag 2. neubearb. A.
Shipley, B., Keddy, P.A., Moore, D.R.J., Lemky, K., 1989. Regeneration and establishment strategies of emergent macrophytes. Journal of Ecology 77, 1093–1110.
Sterner, R.W., Elser, J.J., 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to The Biosphere. Princeton University Press, Princeton.
Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14, 1125–1140.
Thuiller, W., Brotons, L., Araújo, M.B., Lavorel, S., 2004. Effects of restricting environmental range of data to project current and future species distributions. Ecography 27, 165–172.
Thuiller, W., Richardson, D.M., Rouget, M., Proches, S., Wilson, J.R.U., 2006. Interactions between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87, 1755–1769.
Tiffney, B.H., Mazer, S.J., 1995. Angiosperm growth habit, dispersal and diversification reconsidered. Evolutionary Ecology 9, 93–117.
Tilman, D., 1988. Plant Strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ.
Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892.
Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199, 213–227.
Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33, 125–159.
Westoby, M., Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution 21, 261–268.
White, P.S., Jentsch, A., 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62, 399–450.
Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I., Westoby, M., 2005. Assessing the generality of global leaf trait relationships. New Phytologist 166, 485–496.
Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Lo, Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.