

¹ University of Hohenheim, Institute for Landscape and Plant Ecology (320)² University of Exeter, School of Biosciences

On the consistencies between CSR plant strategies and Ellenberg ecological indicator values

Jürgen Franzaring¹, Andreas Fangmeier¹, Roderick Hunt²

(Received April 30, 2007)

Summary

One strand of British comparative plant ecology has used experimental measurements of innate traits under standardized conditions to confirm plant ‘strategies’ or ‘functional types’. The Sheffield (Grime) school has now established *CSR-signatures* for 1010 species. In contrast, a Central-European approach (Göttingen or Ellenberg school) has emphasized the unity of plants with their natural habitats by allocating ‘ecological indicator values’ (EIV’s; German: Zeigerwerte) for over 2700 species, which describe the ecological behavior of each species in their plant associations. In this paper we assess the levels of compatibility and congruence between these two approaches using large datasets that include some previously unexamined traits. Despite there being a wide gap between these plant- and environment-based starting points, we discover that both approaches lead to similar conclusions regarding patterns of evolutionary tradeoffs and ecological processes. In particular, the comparisons support the major evolutionary generalization that plant life has, in effect, aligned itself along a continuum between one trait-group that confers rapid acquisition of resources and another that confers long-term resource conservation.

Introduction

If it is true that in natural plant communities ‘there are many more actors on the stage than roles that can be played’ (COLASANTI et al., 2001) then the huge dimensionality of such communities can be reduced by viewing them not as collections of species (‘actors’), but of groups or types (‘roles’). The result of this simplification is that comparisons and functional analyses involving communities of widely differing species composition can be greatly facilitated (DÍAZ and CABIDO, 2001; WESTOBY et al., 2002; PAUSAS et al., 2003; DÍAZ et al., 2004).

Classical taxonomic knowledge has, therefore, been augmented in recent decades by integrated studies both of innate plant traits (‘plant functional groups’) and of coherent groups of traits (‘strategies’, or ‘plant functional types’). Such approaches have been used to address many ecological topics, particularly in the fields of environmental change and biodiversity. Some of the more recent studies were initiated by the IGBP Global Change and Terrestrial Ecosystem (GCTE) Programme (SMITH et al., 1997) and protocols have now been established for the standardized determination of over twenty functional traits for vascular species (CORNELISSEN et al., 2003). In addition, a catalogue of the life history traits of many bryophytes has been assembled by SÖDERSTRÖM and GUNNARSSON (2003). For the British Flora, an extensive autecological database was presented by GRIME et al. (1988) and by HODGSON et al. (1995), both since updated by GRIME et al. (2005). Parallel work from Central Europe was presented by KLEYER (1995) and in the BIOLFLOR database (KLOTZ et al., 2002), while the LEDA database (KNEVEL et al., 2003) represents species from NW Europe.

Most of the ‘soft traits’ in the GCTE ‘minimal list’ can easily be categorized or measured in the field in different parts of the world and will undoubtedly help to increase understanding of plant processes

on many different scales. For example, using twelve of the GCTE traits, DÍAZ et al. (2004) assembled evidence for a common strand of evolutionary specialization in plants drawn from three different continents and recognized a general principle that apparently involved a trade-off between the rapid acquisition of plant resources and their protection within long-lived tissues. Similar findings describing the leaf economics spectrum of plants using six traits in twelve biomes were reported by WRIGHT et al. (2004).

Besides having purely academic interest, life history traits and plant functional-type classifications have also found practical applications in biological databases designed for nature conservation purposes and in habitat models which address environmental planning issues. POSCHLOD et al. (2000) proposed the development of Biological Flora Databases in which vegetative and regenerative life history traits would be included so as to improve estimates of species extinction risk within the Central European flora. Also, information on plant traits, functional types and ecological behavior of plants may be useful in ecotoxicological risk assessment studies, as it has been shown that phytotoxicity is generally most acute in fast-growing, productive species. Examples of this phenomenon have been documented in relation to SO₂ (ASHENDEN et al., 1996), ozone (REICH, 1987; SELLDEN and PLEIJEL, 1995; FRANZARING et al., 1999) and herbicide vapor (FRANZARING et al., 2001). Moreover, the CO₂ ‘fertilization effect’ may also be more pronounced in such species (HUNT et al., 1993; POORTER, 1998; POORTER and NAGEL, 2000), with consequent implications for future shifts in community structures.

The functional cataloguing of plants within European comparative plant ecology has been much influenced by the contrasting approaches of Philip Grime in the UK and Heinz Ellenberg and others in continental Europe. The British approach has used experimentation to measure innate plant traits under standardized conditions and to derive plant functional types, while the continental approach has invoked more traditional geobotanical principles, explicitly emphasizing the unity between plants and their natural habitats. Relatively few studies have been in a position to compare these two approaches in detail (FICHTNER and SCHULZE, 1992; THOMPSON et al., 1993; MEERTS, 1997), so here we assess the levels of compatibility and congruence between British and Continental European plant types, and individual plant traits, using large datasets that include some previously unexamined variables.

Two Ecological Approaches: CSR PFTs and EIV’s

The Sheffield system of C-S-R plant functional types (GRIME 1974, 1977, 1979, 2001; GRIME et al., 1987, 2005) describes the ‘strategy’ of plant species in the established phase of growth and recognizes three primary functional types: ruderal, stress tolerator and competitor. Many transitional types intervene along the three continuous primary axes (see HUNT et al., 2004 for a fuller explanation of ‘C-S-R space’). Also using the C-S-R approach, a 7-member classification of plant species from Eastern Germany ($n > 2200$) was put forward by FRANK and KLOTZ (1990) and was subsequently used in the German

BIOLFLOR database (KLOTZ et al., 2002). The German classification is a simplification of the British original, which uses a 19-member system (HODGSON et al., 1995; GRIME et al., 1997; HUNT et al., 2004). Practical tools have been developed to allocate a C-S-R type to an individual species (HODGSON et al., 1999) and to derive a composite 'C-S-R functional signature' for entire vegetation samples (HUNT et al., 2004). Recent users of the method include MOOG et al. (2005).

In Continental Europe, in contrast to this experimental approach, the Göttingen school developed a system of 'ecological indicator values' (EIV's; German: *Zeigerwerte*) describing the 'ecological behavior' or 'realized ecological niche' of different plant species ($n > 2700$). These indicator values address species' apparent preferences with regard to water availability (Ellenberg-F), soil reaction (Ellenberg-R), nutrient availability (Ellenberg-N), and several other environmental factors (ELLENBERG et al., 2001). The validity of indicator values in other regions of Europe has also been explored by DIEKMANN (1995) for Southern Scandinavia, by HAWKES et al. (1997), PYATT (1997), HILL et al. (2000) and HILL et al. (2004) for the British Isles, by ERTSEN et al. (1998) and SCHAFFERS and ŠYKORÁ (2000) for the Netherlands, and by SCHMIDTLEIN (2005) within Germany. HERMY et al. (1999) used IVs in a study of ancient and recent forest plants of Europe and drew implications for forest conservation. In these studies, regionally corrected numbers may be introduced for some species (e.g. GRAPOW and PIGNATTI, 1993). In the USA, some studies have recognized the potential usefulness of IVs (e.g. PEET et al., 2003; NIEMI and McDONALD, 2004), but such values are not yet generally available for this region.

Ellenberg EIVs have generally proved to be closely related to physico-chemical field measurements, especially if phytosociological factors are taken into account (WAMELINK et al., 1998, 2002). The IVs can thus be of value, for example, in modeling succession in different regions so long as the mathematical problems associated with their ordinal scaling (MOELLER, 1992) are recognized. The -N and -R IVs, especially, have received widespread use in recent years in interpreting the effects of acidification, eutrophication and nitrogen deposition (ELLENBERG, 1985; BÜRGER, 1988; TER BRAAK and WIERTZ, 1994; WILSON et al., 1995; DIEKMANN et al., 1999; HILL et al., 2000; PRESTON et al., 2003; UN-ECE and EC, 2003). Ellenberg IVs have also been used to study the relationships between species richness, nutrient supply and productivity (CORNWELL and GRUBB, 2003). A review by DIEKMANN (2003) discusses the strengths and weaknesses of using weighted Ellenberg values and suggests further ways to calibrate IVs with reference to new field measurements and other forms of ecological classification. For our comparisons, we gathered information on plant traits, and on British and Continental European functional types, from a variety of sources.

Materials and methods

Data on specific leaf area (SLA), relative growth rate (RGR) and leaf area ratio (LAR) were extracted from GEYGER (1964), GRIME and HUNT (1975), POORTER et al. (1990), SHIPLEY and PETERS (1990), REILING et al. (1992), HUNT and CORNELISSEN (1997), PLEIJEL and DANIELSSON (1997), GARNIER et al. (1997), VAN DER WERF et al. (1998), WARDLE et al. (1998), ERMOLOVA et al. (1998), REICH et al. (1998, 1999) and from our own measurements. Data on RGR, SLA and LAR were available for 203, 171 and 123 species, respectively. Most of the more recent publications made use of the standardized protocols prescribed by HENDRY and GRIME (1993).

Data on the C-S-R types of 1010 plant species were extracted from HUNT et al. (2004) and ecological IVs were extracted from ELLENBERG et al. (2001), comprising about 2700 species. Data on feed value, mowing tolerance and hemerobia (urbanity) of European plant species

were extracted from the BIOLFLOR database (KLOTZ et al., 2002). Average mineral nutrient concentrations in plants were extracted from a Sheffield database (THOMPSON et al., 1997), and from CORNELISSEN et al. (1997), BALATOVA-TULACKOVA (1993), KÖRNER (1989), REICH (1999), and from our own measurements. Data on nitrogen, phosphorus and potassium contents were available for 192, 127 and 126 plant species, respectively. Data on thousand-seed weights were extracted from APEL (2002) for 340 Central European species. For comparison, we obtained field observations for pH and foliar nitrogen content in three local European floras: from Sheffield (THOMPSON et al., 1997), from an investigation by DUVIGNEAUD and DENAEYER-DE SMET (1970) in Hautes-Vagnes (Belgium), and from HÖHNE (1962), who presented data from Saxonia (Eastern Germany).

All data were converted to rank form and Spearman rank correlation coefficients were calculated using SPSS v.11.0. Tab. 1 presents the complete correlation matrix; each entry consists of the coefficient (Spearman's Rho), its level of significance and the number of cases (species) involved.

Results and discussion

Comparability of Sources

C-S-R Types and Frequency

Fig. 1 A gives an overview on how the Central European flora behaves within C-S-R space, using the Sheffield dataset (maximum 1100 species). The largest groups of species are those of intermediate type: 11% and 10% of the flora are CSR- and CR-strategists respectively, while the extreme types C, S and R account for only 3, 7 and 8% of the sample. KLOTZ et al. (2002), who classified 2700 species but on the basis of seven C-S-R types only, found that 29 and 26% of the species could be regarded as C- and CSR-strategists, respectively. In both studies, the general picture of the contribution of different strategists to the Central European vegetation is comparable, though the classification by HUNT et al. (2004) gives the better resolution of types.

Fig. 1 B, using the Sheffield C-S-R database, shows that the most common European species tend to be the more competitive ones, while the species with strong ruderal and stress-tolerant components tend to be rarer. These rare agriophytes, and species associated with extremely stressful (e.g. dry and rocky) habitats, commonly appear among listings of endangered species in the 'red data books' of many European countries.

Inter-flora Comparisons of Plant Traits

Measurements of functional traits may reveal different values in the same species studied in different climatic regions and habitats. However, the ranking within the whole sample will more or less stay the same when sampling is made from plants in the same life stage under favorable conditions of measurement (HUNT and CORNELISSEN, 1997; CORNELISSEN et al., 2003). Fig. 2 A shows an example of this for foliar N measured in Tharandt (Germany) and in Sheffield (England), and Fig. 2 B shows that the fallen litter and soil-surface pH measurements for plants collections from these two sites are also closely comparable.

Plant Traits and Functional Types

Plant Traits

Interrelations between SLA and RGR have been demonstrated elsewhere (e.g. GRIME et al., 1997, WRIGHT and WESTOBY, 2003) and were also strongly present in our study ($r=0.47^{**}$). Our calculations

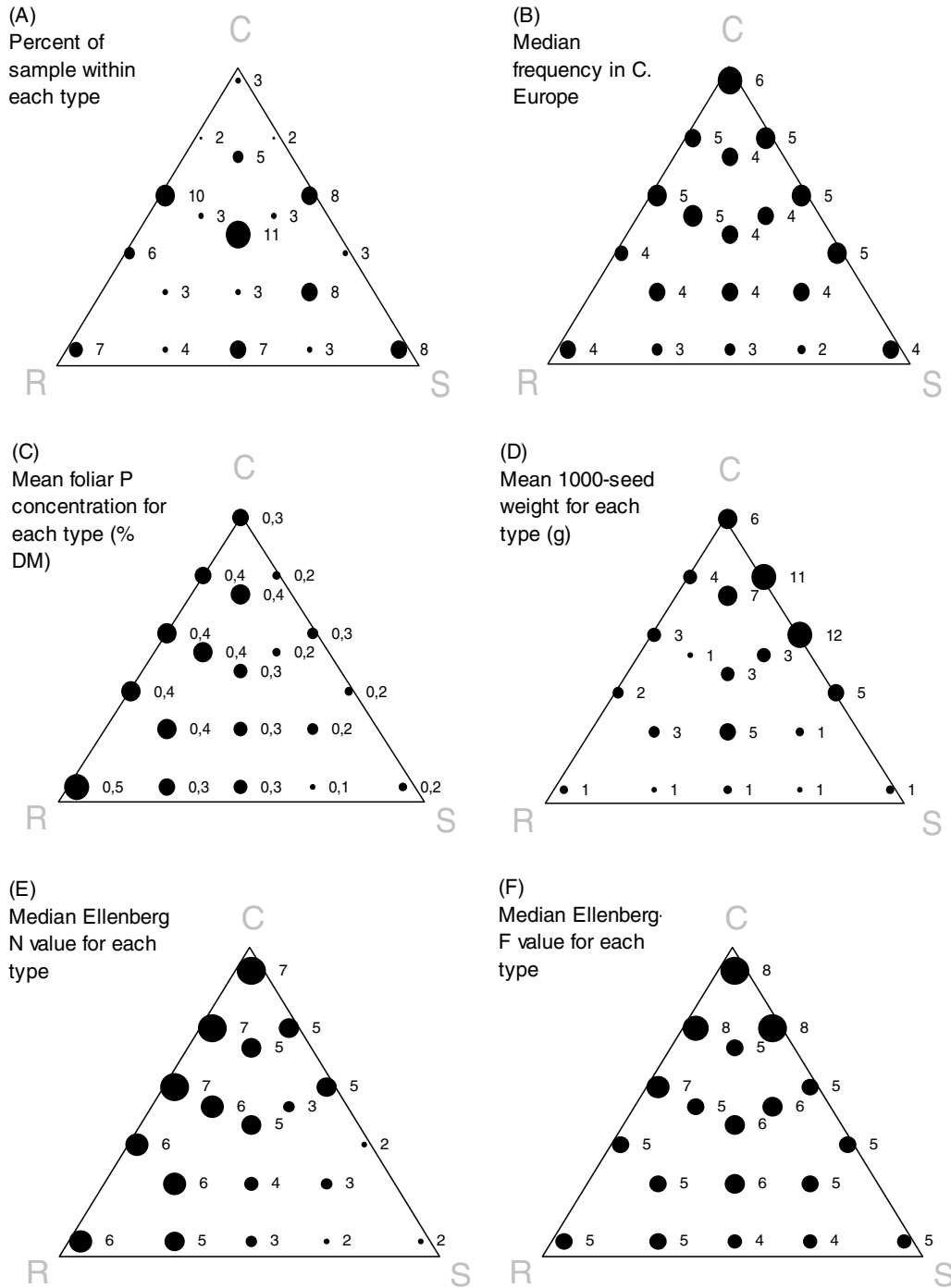


Fig. 1: Distribution of plant species within ‘CSR-space’: (a) percentages of Central European sample of species occupying each type, $n = 826$; (b) median frequency of CSR types within the Central European sample, $n = 784$; (c) mean foliar P concentrations (% dry matter), $n = 127$; (d) mean thousand-seed weights (g), $n = 340$; (e) median Ellenberg-N values, $n = 750$; (f) median Ellenberg-F values, $n = 682$. Data on frequency of species and on -N and -F indicator values from ELLENBERG et al., 2001, and on CSR types from HUNT et al., 2004; data on plant traits from various sources (see text).

also show that both SLA and RGR are positively correlated with foliar K, but less strongly so with P- or N- concentration. An association between leaf nitrogen content on a dry weight basis and mean RGR was previously confirmed by CORNELISSEN et al. (1997), and FICHTNER and SCHULZE (1992) found that the response of RGR to N-supply is strongly and positively correlated with nitrophily. Such findings support the theory of POORTER et al. (1990), who postulated that natural selection in a nutrient-rich environments favors species with a high

specific leaf area, high leaf area ratio and RGR, whereas selection in nutrient-poor habitats leads to species with inherently low specific leaf area, leaf area ratio (LAR) and RGR. These morphological and physiological differences are generally paralleled by the differences in chemical composition; slowly-growing species contain relatively less nutrient content but relatively more cell-wall material such as lignin, hemicellulose, cellulose, polysaccharide-bound ferulic acid and hydro-xyproline-rich protein (NIEMANN et al., 1992).

Ellenberg Indicator Values

From Tab. 1, an overview of the correlations between plant traits and Ellenberg EIVs is possible. The highest correlations were found between leaf macronutrients (in the order $P > K > N$) and the Ellenberg-N value (an index of affinity to high nutrient conditions). Relationships between soil nutrients and Ellenberg-N values, which describe the nitrophily of a plant species, have previously been confirmed in comparisons made by RASTIN (1992), MEERTS (1997) and SCHAFFERS and SÝKORÁ (2000). However, the present correlation between foliar N and Ellenberg-N has not previously been reported. The comparisons in Fig. 2 C-E show that this relationship is stronger in the Sheffield dataset than in those from Hautes-Vagnes (Belgium) or Tharandt (Germany), perhaps indicating that differences in local land use and nitrogen availability have an impact on the realized niche of species.

Ellenberg-N also correlates here with RGR, confirming HILL et al. (2000) and SCHAFFERS and SÝKORÁ (2000), who suggested that Ellenberg-N values represented 'productivity values'. Ellenberg-N values are also positively correlated with SLA, indicating that plants from resource-rich environments tend to have thin, delicate leaves, while plants from unproductive habitats tend to have physically stronger leaves, also noted by GRIME et al. (1997). Due to the generally more robust conditions, SLA values recorded in the field are generally lower than in glasshouse-grown plants, but such comparisons generally show a consistency in ranking across a group of species (POORTER and DE JONG, 1999).

Ellenberg-R values (indices of affinity to high pH) show highly significant correlations with leaf Ca and Mg concentrations and a low correlation to thousand-seed weight. SCHAFFERS and SÝKORÁ (2000) suggested calling Ellenberg-R values 'calcium values', an idea which is supported by present study. R-values also correlate with pH of the plant litter (Fig. 2 F) and the C:N ratios of green and dead plant material (not shown). It has repeatedly been shown that weighted Ellenberg-R values are well correlated with soil pH (DIEKMANN, 2003). This is confirmed by the Sheffield data, in which soil pH was measured in the rooting zone (Fig. 2 G). However, the positive correlation between TSW and Ellenberg-R values cannot be explained.

Ellenberg-F values (indices of affinity to environmental moisture) show a slight correlation with leaf P and K contents, as well as with RGR and SLA, probably indicating a general association between moisture availability and productivity. They are positively associated with the species frequency, indicating correctly that many of the rarer species in Central Europe are associated with the drier habitats. The slight negative correlation between continentality (Ellenberg-K) and nitrogen content is also supported by the gradient in nitrogen content of pine needles observed between Central Europe and the polar circle (BERGMANN, 1998). The positive relationship between N:K values and Ellenberg-T (affinity to higher temperature) cannot be explained, but the negative correlation between Ellenberg-L (affinity to full light conditions) and thousand-seed weight may indicate that under brighter conditions small seeds may have a better prospect of establishing successfully while, in shade, large-seeded species will have an advantage.

C-S-R Type

While RGR and SLA were among the plant traits used to originally confirm the C-S-R system of classification (GRIME et al., 1997), and they again exhibit clear relations to C-S-R position (Tab. 1), the associations between C-S-R type and certain other traits have not much been demonstrated. Fig. 1 C, D show the mean P concentrations and thousand seed weights for each of the 19 CSR strategies represented in the sample. The P contents of plant leaves (Fig. 1 C) show a clear trend along the S-axis of C-S-R space, i.e. the highest amounts occur

on the ruderal and competitive side of the triangle, along with the highest RGRs and SLAs, though foliar N does not reproduce this trend so well (data not shown). Lower nutrient contents in slow-growing species like the stress-tolerators, and their neighbors in C-S-R space, make it imperative for such types not to lose resources, while fast-growing species on the C to R margin ruderals may safely rely upon a high nutrient turnover because, even when their short-lived leaves are lost, their nutrient content may generally be reclaimed from the environment. Larger seeds are associated with the long-lived competitive species (Fig. 1 D), while both ruderals and stress tolerators produce smaller seeds on average, a consequence of short life cycles in the former and low resource availability in the latter. It would have been advantageous to have had data on reproductive allocation to complete this part of the picture, but unfortunately this was not available on the scale required.

Interrelations between nutrient cycling, plant longevity, morphological and physiological traits have also been demonstrated in Australian and North American floras by CRAINE et al. (2002) and WRIGHT and WESTOBY (2003), respectively. An evolutionary specialization in the form of a trade-off between gaining and conserving resources was confirmed by DÍAZ et al. (2004) and WRIGHT et al. (2004), though REICH et al. (2003) found a less clear interrelation between resource supply rate and ecophysiological performance.

Relations between functional types: CSR, Ellenberg and Klotz indicator values

Fig. 1 E shows the median Ellenberg-N and -F values for plants of each of 19 C-S-R types. The Ellenberg-N dimension maps almost completely onto the S-axis of C-S-R space, with only a suggestion of a bias towards C rather than towards R. On the other hand, Ellenberg-F values very convincingly reflect the C-axis, confirming that while types S and R may often be common in drier habitats; competitive species are able to dominate only at moister sites. From Tab. 1, a partial parallel with C-S-R position emerges for Ellenberg values for soil reaction (-R); the many calcicole examples of the S-strategy are sufficient to establish a correlation here. Another trend emerges within continentality (-K, which in Europe is entrained with temperature -T), where S-types are favoured at high -K and -T values, and still another with light (-L), where ruderal types are excluded from closed, dense communities.

At the same time, ruderal types emerge as being mowing-tolerant, stress tolerators as mowing intolerant and competitors as mowing-indifferent. The Klotz urbanity value maps onto all three C-S-R axes, but the way in which this affinity to urban habitats is expressed within C-S-R theory involves a delicate balance of stress, disturbance and eutrophication. Surprisingly, no C-S-R correlations emerge for feed value, where the issue of chemical defenses may confound the otherwise simple relationship expected for the S-dimension.

CSR strategies and plant families

Six plant families within our Central European sample contain 30 or more species which have been classified according to the CSR system. The Brassicaceae (41 represented) and Caryophyllaceae (31 species) are both associated mainly with R-strategies, and the Rosaceae (31 species) have a predominantly S-type strategy. However, the 77 species from the Asteraceae have strong components in both C- and R-types and the 65 Poaceae and the 40 Leguminosae each span the whole of the C-S-R spectrum. Taxonomically-driven trait clusters like those for seed size (MOLES et al., 2005) are thus possible, but not inevitable.

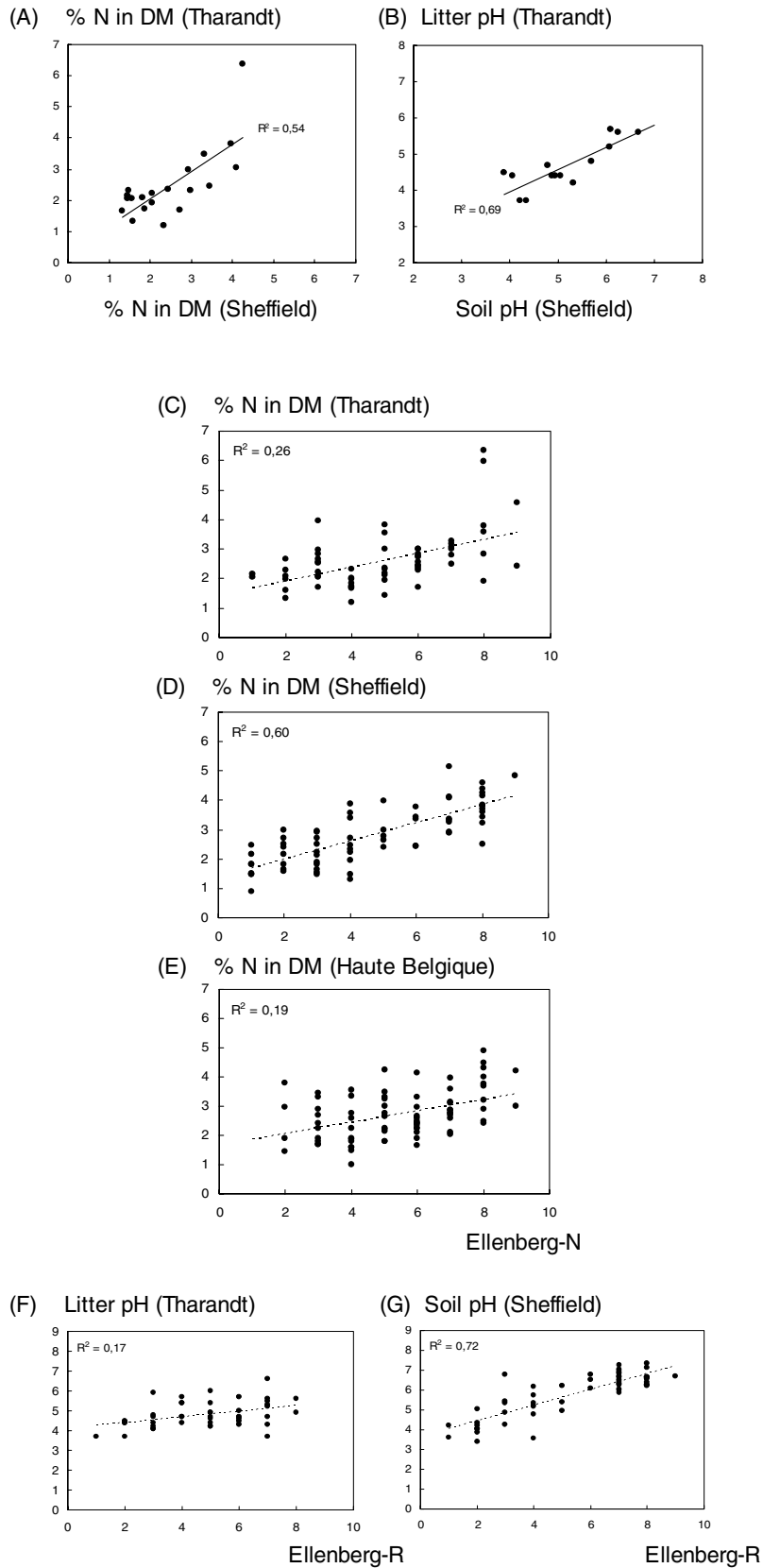


Fig. 2: (A) Relationship between foliar N concentration in species collected from local floras at Tharandt (SE-Germany) and Sheffield (UK), $n = 19$; (B) relationship between pH of plant litter at Tharandt and surface-soil pH at Sheffield, $n = 15$ species; relationship between foliar N concentrations and Ellenberg-N values in plant species collected in (C) Tharandt ($n = 44$), (D) Sheffield ($n = 60$), and (E) Hautes Vagnes, Belgium ($n = 64$); (F) relationship between litter pH and Ellenberg-R values for species collected at Tharandt ($n = 34$) and (G) between soil pH and Ellenberg-R values for species collected at Sheffield ($n = 43$). Tharandt data from HÖHNE (1962) and Sheffield data from Unit of Comparative Plant Ecology (UCPE, download under <http://www.shef.ac.uk/uni/academic/N-Q/nuocpe/ucpe/>); Belgian data on nutrient contents from DUVIGNEAUD and DENAEYER-DE SMET (1970).

Conclusion

Our interpretation of existing plant ecological information confirms a high degree of congruence between many of these ecological indicator values and the established C-S-R strategies of European plant species. The C-S-R axis which has repeatedly emerged most strongly from objective syntheses of plant trait values is the S-dimension (GRIME et al., 1988; 1997; DÍAZ et al., 2003; GRIME et al., 2005). This is the axis most strongly correlated here (in number and in significance of coefficients) with indices from the Ellenberg and Klotz classifications and with measured plant traits.

The r-K classification of MACARTHUR and WILSON (1967) successfully recognized (in its r-strategy) what would later be postulated as the R-dimension within C-S-R, but did not further differentiate the C- and S- variants embedded within the K-strategy. In a similar manner, many of the Continental European ecological indices, and individual trait axes, represent single C-S-R dimensions but fail to distinguish between the others. For example, Ellenberg-N (nitrogen regime) and foliar-P both map clearly onto the S-dimension (Fig. 1 C, F) but fail to distinguish R- and C-types; and Ellenberg-F (water regime) correlates well with the C-dimension (Fig. 1 F) which, in a continent of predominantly mesic habitats, equates very successfully to median frequency (Fig. 1 B).

In general, the interrelations reported here were most prominent among measures of plant productivity and nutrient ecology: the S-axis of the C-S-R system is revealed in twelve alternative guises here. There is thus a clear congruence of classifications at work, with the same underlying phenomenon being described from a number of different directions. This phenomenon, recently discussed by DÍAZ et al. (2004), again points towards a continuum of evolutionary specialization that ranges on the one hand between trait-groups that confer rapid acquisition of resources and, on the other hand, those that confer long-term resource conservation.

The C-S-R classification of plant strategies, with its reliance upon two great drivers of success in the established phase (degree of resource-limitation and degree of biomass destruction), can thus be regarded as a parsimonious synthesis of plants' evolutionary responses to the natural environment and hence, of their capacity to respond to biotic and abiotic pressures within ecological timescales. The Central-European ecological indicator approach is also capable of interpreting many aspects of environmental change and it also reinforces many of the most fundamental tenets from the CSR approach.

References

- APEL, C., 2002: Samen von Wildpflanzen. Conrad Apel GmbH, Darmstadt.
- ASHENDEN, T.W., HUNT, R., BELL, S.A., WILLIAMS, T.G., MANN, A., BOOTH, R.E., POORTER, L., 1996: Responses to SO₂ pollution in 41 British herbaceous species. *Functional Ecology* 10, 483-490.
- BALATOVA-TULACKOVA, E., 1993: Contribution towards the knowledge of the chemical composition of growing species from moist meadows. *Phytocoenologia* 23, 227-256.
- BERGMANN, C., 1998: Stickstoff-Umsätze in der Humusaufgabe unterschiedlich immissionsbelasteter Kiefernbestände (*Pinus sylvestris* L.) im nordost-deutschen Tiefland mit besonderer Berücksichtigung des gelösten organischen Stickstoffs. Cottbuser Schriften zu Bodenschutz und Rekultivierung. Brandenburgische Technische Universität Cottbus.
- TER BRAAK, C.J.F., WIERTZ, J., 1994: On the statistical analysis of vegetation change: a wetland affected by water extraction and soil acidification. *J. Vegetation Sci.* 5, 361-372.
- BÜRGER, R., 1988: Veränderungen der Bodenvegetation in Wald- und Forstgesellschaften des mittleren und südlichen Schwarzwaldes. KFK-PEF 52, Karlsruhe.
- COLASANTI, R.L., HUNT, R., ASKEW, A.P., 2001: A self-assembling model of resource dynamics and plant growth incorporating plant functional types. *Functional Ecology* 15, 676-687.
- CORNELISSEN, J.H.C., WERGER, M.J.A., CASTRO-DÍEZ, P., VAN RHEENEN, J.W.A., ROWLAND, A.P., 1997: Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types. *Oecologia* 111, 460-469.
- CORNELISSEN, J.H.C., LAVOREL, S., GARNIER, E., DÍAZ, S., BUCHMANN, N., GURVICH, D.E., REICH, P. B., TER STEEGE, H., 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. *Australian J. Bot.* 51, 335-380.
- CORNWELL, W.K., GRUBB, P.J., 2003: Regional and local patterns in plant richness with respect to resource availability. *Oikos* 100, 417-428.
- CRABINE, J., TILMAN, D., WEDIN, D., REICH, P.B., TJOELKER, M., KNOPS, J., 2002: Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* 16, 563-574.
- DÍAZ, S., CABIDO, M., 2001: Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646-655.
- DÍAZ, S., HODGSON, J. G., THOMPSON, K., CABIDO, M., CORNELISSEN, J.H.C., JALILI, A., MONTERRAT-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., DE TORRES-ESPUNY, L., 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. *J. Vegetation Sci.* 115, 295-304.
- DIEKMANN, M., 1995: Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. *Ecography* 18, 178-189.
- DIEKMANN, M., BRUNET, J., RÜHLING, A., FALKENGREN, G.U., 1999: Effects of nitrogen deposition: Results of a temporal-spatial analysis of deciduous forests in South Sweden. *Plant Biology* 14, 471-481.
- DIEKMANN, M., 2003: Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl. Ecol.* 4, 493-506.
- DUVIGNEAUD, P., DENAEYER-DE SMET, S., 1970: Phytogeochemie des groupes écosociologiques forestiers de Haute-Belgique. *Oecologia Plantarum* 5, 1-32.
- ELLENBERG, H. jr., 1985: Veränderungen der Flora Mitteleuropas unter dem Einfluss von Düngung und Immissionen. *Schweiz. Z. Forstwesen* 136, 19-39.
- ELLENBERG, H., WEBER, E.H., DÜLL, R., WIRTH, V., WERNER, W., PAULISSEN, D., 2001: Zeigerwerte der Pflanzen in Mitteleuropa, *Scripta Geobotanica XVIII*. Verlag Erich Goltze, Göttingen.
- ERMOLOVA, L.S., UTKIN, A.I., 1998: Specific leaf area of dominant forest-forming species of Russia. *Russian J. Ecol.* 29, 152-156.
- ERTSEN, A.C.D., ALKEMADE, J.R.M., WASSEN, M.J., 1998: Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands. *Plant Ecology* 135, 113-124.
- FICHTNER, K., SCHULZE, E.-D., 1992: The effect of nitrogen nutrition on growth and biomass partitioning of annual plants originating from habitats of different nitrogen availability. *Oecologia* 92, 236-241.
- FRANK, D., KLOTZ, S., 1990: Biologisch-ökologische Daten zur Flora der DDR. Martin Luther Universität Halle. *Wissenschaftliche Beiträge*, 1990/32. Halle/Saale.
- FRANZARING, J., DUECK, T.A., TONNEICK, A.E.G., 1999: Can plant traits be used to explain differences in ozone sensitivity between native European plant species? UN-ECE- Critical levels for ozone- level II- workshop held at Gerzensee, Switzerland, 11-14 April 1999. In: Fuhrer, J., Achermann, B. (eds.), *Critical levels for ozone – Level II. Environmental Documentation* 115, 83-88, Swiss Agency for the Environment, Forests and Landscape (SAEFL), Bern.
- FRANZARING, J., KEMPENAAR C., VAN DER EERDEN, L.J.M., 2001: Effects of

- vapours of chlorpropham and ethofumesate on wild plant species. *Environmental Pollution* 114, 21-28.
- GEYGER, E., 1964: Methodische Untersuchungen zur Erfassung der assimilierenden Gesamtoberflächen von Wiesen. *Berichte des Geobot. Instituts ETH, Stifg. Rübel, Zürich*, 35, 41-112.
- GARNIER, E., CORDONNIER, P., GUILLERM, J.L., SONIE, L., 1997: Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. *Oecologia* 111, 490-498.
- GRAPOW, L.C., PIGNATTI, S., 1993: Ellenberg's indicator numbers for the ecological assessment of archaeological zones in Rome. *Phytocoenologia* 23, 291-299.
- GRIME, J.P., 1974: Vegetation classification by reference to strategies. *Nature* 250, 26-31.
- GRIME, J.P., 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111, 1169-1194.
- GRIME, J.P., 1979: *Plant strategies and vegetation processes*. Wiley, Chichester, UK.
- GRIME, J.P., 2001: *Plant strategies, vegetation processes and ecosystem properties*. Wiley, Chichester, UK.
- GRIME, J.P., HUNT, R., 1975: Relative growth-rate: its range and adaptive significance in a local flora. *J. Ecol.* 63, 393-422.
- GRIME, J.P., HODGSON, J.G., HUNT, R., 1988: *Comparative plant ecology: a functional approach to common British species*. Allen and Unwin, London.
- GRIME, J.P., HODGSON, J.G., HUNT, R., 2005: *Comparative plant ecology: a functional approach to common British species*, 2nd edition. Castlepoint Press, Dalbeattie, UK (in press).
- GRIME, J.P., THOMPSON, K., HUNT, R., HODGSON, J.G., CORNELISSEN, J.H.C., RORISON, I.H., HENDRY, G.A.F., ASHENDEN, T.W., ASKEW, A.P., BAND, S.R., BOOTH, R.E., BOSSARD, C.C., CAMPBELL, B.D., COOPER, J.E.L., DAVISON, A.W., GUPTA, P.L., HALL, W., HAND, D.W., HANNAH, M.A., HILLIER, S.H., HODKINSON, D., JALILI, A., LIU, Z., MACKAY, J.M.L., MATTHEWS, N., MOWFORTH, M.A., NEAL, A.M., READER, R.J., REILING, K., ROSS-FRASER, A.M., SPENCER, R.E., SUTTON, F., TASKER, D.E., THORPE, P.C., WHITEHOUSE, J., 1997: Integrated screening validates primary axes of specialisation in plants. *Oikos* 79, 259-281.
- HAWKES, J.C., PYATT, D.G., WHITE, I.M.S., 1997: Using Ellenberg indicator values to assess soil quality in British forests from ground vegetation: A pilot study. *J. Appl. Ecol.* 34, 375-387.
- HERMY, M., HONNAY, O., FIRBANK, L., GRASHOF, B.C., LAWESSON, J.E., 1999: An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91, 9-22.
- HENDRY, G.A.F., GRIME, J.P., 1993: *Methods in comparative plant ecology. A laboratory manual*. Chapman and Hall, London.
- HILL, M.O., ROY, D.B., MOUNTFORD, J.O., BUNCE, R.G.H., 2000: Extending Ellenberg's indicator values to a new area: an algorithmic approach. *J. Appl. Ecol.* 37, 3-15.
- HILL, M.O., PRESTON, C.D., ROY, D.B., 2004: *PLANTATT. Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. CEH Monks Wood and Biological Records Centre. Abbots Ripton.
- HODGSON, J.G., GRIME, J.P., HUNT, R., THOMPSON, K., 1995: *The electronic comparative plant ecology*. Chapman and Hall, London.
- HODGSON, J.G., WILSON, P.J., HUNT, R., GRIME, J.P., THOMPSON, K., 1999: Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85, 282-294.
- HÖHNE, H., 1962: Vergleichende Untersuchungen über den Mineralstoff- und Stickstoffgehalt sowie Trockensubstanzproduktion von Waldbodenpflanzen. *Archiv Forstwesen* 11, 1085-1141.
- HUNT, R., HAND, D.W., HANNAH, H.A., NEAL, A.M., 1993: Further responses to CO₂ enrichment in British herbaceous species. *Functional Ecology*, 7, 661-668.
- HUNT, R., CORNELISSEN, J.H.C., 1997: Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* 135, 395-417.
- HUNT, R., HODGSON, J.G., THOMPSON, K., BUNGENER, P., DUNNETT, N.P., ASKEW, A.P., 2004: A new practical tool for deriving a functional signature for herbaceous vegetation. *J. Vegetation Sci.* 7, 163-170.
- KLEYER, M., 1995: *Biological traits of vascular plants. A database*. Arbeitsber. Inst. Landschaftsplanung Ökol. Univ. Stuttgart, N.F. 2. See also <http://www.uni-oldenburg.de/landeco>.
- KLOTZ, S., KÜHN, I., DURKA, W., 2002: BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde 38.
- KNEVEL, I.C., BEKKER, R.M., BAKKER, J.P., KLEYER, M., 2003: Life-history traits of the Northwest European flora: A data-base LEDA. *J. Vegetation Sci.* 14, 611-614.
- KÖRNER, C., 1989: The nutritional status of plants from high altitudes. A worldwide comparison. *Oecologia* 81, 379-391.
- MACARTHUR, R.H., WILSON, E.D., 1967: *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- MEERTS, P., 1997: Foliar macronutrient concentrations of forest understorey species in relation to Ellenberg's indices and potential relative growth rate. *Plant and Soil* 189, 257-265.
- MOELLER, H., 1992: Use of the median in indicator value calculations according to Ellenberg. *Tuexenia* 12, 25-28.
- MOLES, A.T., ACKERLY, D.D., WEBB, C.O., TWEDDLE, J.C., DICKIE, J.B., WESTOBY, M., 2005: A brief history of seed size. *Science* 307, 576-580.
- MOOG, D., KAHMEN, S., POSCHLOD, P., 2005: Application of CSR- and LHS-strategies for the distinction of differently managed grasslands. *Basic Appl. Ecol.* 6, 133-143.
- NIEMANN, D.G., PUREVEEN, J.B.M., EIJKEL, G.B., POORTER, H., BOON, J.J., 1992: Differences in relative growth rate in 11 grasses correlate with differences in chemical composition as determined by pyrolysis mass spectrometry. *Oecologia* 89, 567-573.
- NIEMI, G.J., McDONALD, M.E., 2004: Application of Ecological Indicators. *Ann. Rev. Ecol. System.* 35, 89-111.
- PAUSAS, J., RUSCH, G.M., LEPSŠ, J., 2003: Plant functional types in relation to disturbance and land use: introduction. *J. Vegetation Sci.* 14, 307-310.
- PEET, R.K., FRIDLEY, J.D., GRAMLING, J.M., 2003: Variation in species richness and species pool size across a pH gradient in forests of the Southern Blue Ridge Mountains. *Folia Geobotanica* 38, 391-401.
- PLEIJEL, H., DANIELSSON, H., 1997: Growth of 27 herbs and grasses in relation to ozone exposure and plant strategy. *New Phytologist*, 135 361-367.
- POORTER, H., REMKES, C., LAMBERS, H., 1990: Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiology* 94, 621-627.
- POORTER, H., BERGKOTTE, M., 1992: Chemical composition of 24 wild species differing in relative growth rate. *Plant, Cell and Environment* 15, 221-229.
- POORTER, H., 1998: Do slow growing species and nutrient-stressed plants respond relatively strongly to elevated CO₂? *Global Change Biology* 4, 693-697.
- POORTER, H., DE JONG, H., 1999: A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* 143, 163-176.
- POORTER, H., NAGEL, O., 2000: The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Australian J. Plant Physiol.* 27, 595-607.
- POSCHLOD, P., KLEYER, M., TACKENBERG, O., 2000: Databases on life history traits as a tool for risk assessment in plant species. *Z. Ökologie Naturschutz* 9, 3-18.
- PRESTON, C.D., TELFER, M.G., CAREY, P.D., COOPER, J.M., DINES, T.D., HILL, M.O., PEARMAN, D.A., ROY, D.B., SMART, S.M., 2002: *The changing flora of the UK*. Department for Environment, Food and Rural Affairs (DEFRA), London.
- PYATT, D.G., 1997: A site classification for Scottish native woodlands. *Bot. J. Scotland*, 49, 455-467.
- RASTIN, N., 1992: Relationships between ecological groups of plants and chemical properties of soils in forest ecosystems at Hamburg. *Z. Pflanzen-erng. Bodenkd.* 155, 169-174.

- REICH, P.B., 1987: Quantifying plant responses to ozone: a unifying theory. *Tree Physiology* 3, 63-91.
- REICH, P.B., WALTERS, M.B., ELLSWORTH, D.S., VOSE, J.M., VOLIN, J.C., GRESHAM, C., BOWMAN, W.D., 1998: Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia* 114, 471-482.
- 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., BUSCHENA, C., TJOELKER, M.G., WRAGE, K., TILMAN, D., MACHADO, J.L., 2003: Variation in growth rate and ecophysiology among 34 grassland and savannah species under contrasting N supply: a test of functional significance. *New Phytologist* 157, 617-631.
- REILING, K., DAVISON, A.W., 1992: The response of native herbaceous species to ozone: growth and fluorescence screening. *New Phytologist* 120, 29-37.
- SHIPLEY, B., PETERS, R.H., 1990: A test of the Tilman model of plant strategies: relative growth rate and biomass partitioning. *American Naturalist* 136, 139-153.
- SCHAFFERS, A.P., SÝKORÁ, K.V., 2000: Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J. Vegetation Sci.* 11, 225-244.
- SCHMIDTLEIN, S., 2005: Coarse-scale substrate mapping using plant functional response types. *Erdkunde* 58, 137-155.
- SELLEN, G., PLEIJEL, H., 1995: Photochemical oxidant effects on vegetation-response in relation to plant strategy. *Water, Air, Soil Pollut.* 85, 111-122.
- SMITH, T.M., SHUGART, H.H., WOODWARD, F.I. (eds.), 1997: Plant functional types. Their relevance to ecosystem properties and global change. *International Geosphere-Biosphere Book Series No. 1.*
- SÖDERSTRÖM, L., GUNNARSSON, U., 2003: Life history strategies: a catalogue of population biology parameters for bryophytes occurring in North-Western Europe – draft version. *BryoPlanet – Department of Biology, NTNU, 7491 Trondheim, Norway.*
- THOMPSON, K., HODGSON, J.G., GRIME, J.P., RORISON, I.H., BAND, S.R., SPENCER, R.E., 1993: Ellenberg numbers revisited. *Phytocoenologia* 23, 277-289.
- THOMPSON, K., PARKINSON, J.A., BAND, S.R., SPENCER, R.E., 1997: A comparative study of leaf nutrient concentrations in a regional herbaceous flora. *New Phytologist* 136, 679-689
- UN-ECE, EC, 2003: Intensive Monitoring of Forest Ecosystems in Europe. Technical Report 2003, Geneva and Brussels. ICP Forests, FIMCI-Technical Report.
- WAMELINK, G.M.W., VAN DOBBEN, H.F., VAN DER EERDEN, L.J.M., 1998: Experimental calibration of Ellenberg's indicator value for nitrogen. *Environ. Pollut.* 102 (supplement), 371-375.
- WAMELINK, G.M.W., JOOSTEN, V., VAN DOBBEN, H.F., BERENDSE, F., 2002: Validity of Ellenberg indicator values judged from physico-chemical field measurements. *J. Vegetation Sci.* 13, 269-278.
- VAN DER WERF, A., GEERTS, R.H.E.M., JACOBS, F.H.H., KOREVAAR, H., OOMES, M.J.M., DE VISSER, W., 1998: The importance of relative growth rate and associated traits for competition between species during vegetation succession. In: Lambers, H., Poorter, H., Van Vuuren, M.M.I. (eds.), *Inherent variation in plant growth. Physiological mechanisms and ecological consequences*, 1-14. Backhuys Publishers, Leiden.
- WARDLE, D.A., BARKER, G.M., BONNER, K.I., NICHOLSON, K.S., 1998: Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *J. Ecol.* 86, 405-420.
- 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. *Ann. Rev. Ecol. System.* 33, 125-159.
- WILSON, J.B., SYKES, M.T., PEET, R.K., 1995: Time and space in the community structure of a species-rich limestone grassland. *J. Vegetation Sci.* 6, 729-740.
- WRIGHT, I.J., WESTOBY, M., 2003: Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Functional Ecology* 17, 10-19.
- WRIGHT, I.J., REICH, P.B., WESTOBY, M., ACKERLY, D.D., BARUCH, Z., BONGERS, B., 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., 2004: The worldwide leaf economics spectrum. *Nature* 428, 821-827.
- 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.

Addresses of the authors:

Dr. Jürgen Franzaring (corresponding author) and Prof. Dr. Andreas Fangmeier, University of Hohenheim, Institute for Landscape and Plant Ecology (320), Ökologiezentrum 2, August-von-Hartmann-Str. 3, D-70599 Stuttgart

Dr. Rod Hunt, University of Exeter, School of Biosciences, Exeter EX4 4PS, UK