Gaume L, McKey D. 1999. An ant-plant mutualism and its host-specific parasite: activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plant-ants inhabiting the same myrmecophyte. *Oikos* **84**: 130–144.

Leake JR. 1994. The biology of myco-heterotrophic plants. *New Phytologist* **127**: 171–216.

McKendrick SL, Leake JR, Read DJ. 2000a. Symbiotic germination and development of myco-heterotrophic plants in nature: transfer of carbon from ectomycorrhizal *Salix repens* and *Betula pendula* to the orchid *Corallorhiza trifida* through shared connections. *New Phytologist* **145**: 539–548.

McKendrick SL, Leake JR, Taylor DL, Read DJ. 2000b. Symbiotic germination and development of myco-heterotrophic plants in nature: ontogeny of *Corallorhiza trifida* and characterization of its mycorrhizal fungi. *New Phytologist* **154**: 233–247.

McKendrick SL, Leake JR, Taylor DL, Read DJ. 2002. Symbiotic germination and development of myco-heterotrophic *Neottia nidus-avis* in nature and its requirement for locally distributed *Sebacina* spp. *New Phytologist* **154**: 233–247.

Pellmyr O, Huth C. 1994. Evolutionary stability of mutualism between yuccas and yucca moth. *Nature* **372**: 257–260.

Rasmussen HN. 1995. *Terrestrial orchids from seed to mycotrophic plant.* Cambridge, UK: Cambridge University Press, 444

Smith SE, Read DJ. 1997. *Mycorrhizal symbiosis, 2nd edn.* San Diego, CA, USA: Academic Press.

Taylor DL. 1997. *The evolution of myco-heterotrophy and specificity in some North American orchids.* PhD thesis, University of California Berkeley, USA.

Yoder JA, Zettler LW, Stewart SL. 2000. Water requirements of terrestrial and epiphytic orchid seeds and seedlings, and evidence for water uptake by means of mycotrophy. *Plant Science* **156**: 145–150.

Zelmer CD, Currah RS. 1995. Evidence for a fungal liason between *Corallorhiza trifida* (Orchidaceae) and *Pinus contorta* (Pinaceae). *Canadian Journal of Botany* **73**: 862–866.

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Letters

Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance

Land use changes and their interaction with atmospheric and climatic changes represent a major challenge to humanity. However, despite the wealth of literature about plant traits in general, such as leaf size and texture or canopy height, we still know amazingly little about the links between these traits and responses to disturbance of the ecosystem. Most of the empirical work on functional traits has focused on plant responses to resources and climate (Chapin *et al.*, 1996; Grime *et al.*, 1997; Cunningham *et al.*, 1999; Fonseca *et al.*, 2000), rather than to disturbances, such as changing resources, substrate availability or the physical environment (Pickett & White, 1985). In addition, plant classifications used in large-scale models have deliberately restricted the numbers of functional types and traits used, in order to reflect broad responses to climate. What is to be done?

An important response has been through international scientific programmes, including the Global Change and Terrestrial Ecosystems (GCTE) programme of the International Geosphere-Biosphere Programme (IGBP), which have promoted work leading to the prediction of ecosystem response to these factors. Just because disturbance usually operates at spatial scales smaller than climate (Woodward & Diament, 1991) does not necessarily mean that global-scale questions about disturbance and land use cannot be addressed. Some scientists have taken up the search for plant biological traits that are associated with major disturbance and land-use factors, such as grazing, fire and agricultural land abandonment, focusing on a comparative approach at the global scale.

Three key issues are crucial in this global comparison of trait response to disturbance:

- First, the relationship between traits linked to plant responses to disturbance and those linked to plant functional effects on ecosystem properties, and the fact that some key plant traits are related both to plant responses to several disturbance types, climate, and *in situ* resource availability. This topic has been recently addressed in the literature (Chapin *et al.*, 2000; Lavorel & Garnier, 2001), but its implications are still far from being fully covered.
- Second, and especially important having been a source of confusion and controversy, and poorly addressed in the recent literature, the importance of ecosystem and regional context in determining what traits to focus on.

• Third, also a source of debate and not well discussed, the use of check lists and core lists of traits in global-scale initiatives.

No plant functional classification should be expected to be useful for all purposes and scales of study (Gitay & Noble, 1997; Lavorel *et al.*, 1997; Grime, 1998). For example, traits relevant to disturbance response (e.g. resprouting capacity, serotiny) may be quite different to those relevant to climate change (e.g. frost resistance). Land uses and their characteristic disturbances may be broad or limited in extent, requiring broader or finer scales of investigation. Thus the specific purpose of the study and the level of detail are important in deciding which traits to target. Other decisive factors are the scale and types of the disturbance of interest and evolutionary history of the disturbance in the region of study (Díaz *et al.*, 1999; McIntyre *et al.*, 1999). For example, trends linking plant responses to disturbance previously accepted as 'universal' in fact seem to depend on the regional context both in fire (Pausas, 2001) and in grazing (S. Díaz *et al.*, unpublished) global-scale syntheses.

One reason for the disturbingly few generalities about plant traits and disturbance is that they mostly remain untested beyond the local context. In addition, many traits have been measured in local situations, but very rarely has a consistent set of traits been systematically screened in several different situations. This is necessary to allow a test of the generality of their responses to disturbance over a global range of environments. Every researcher has tended to develop their own list of traits, chosen on the basis of local data availability, ease of collection, or previous experience. The absence of an attribute, or the lack of variance of a trait, in a particular regional assemblage is important for a global comparison, but tends not to be reported in a locally focussed study. For example, a researcher may not use shrub height as a response trait in the face of a particular disturbance because it does not vary, but this fact will often not be mentioned in the published article. Similarly, a shift in the annual vs perennial proportion in the vegetation may not be explicitly reported because most species are annual. Other reasons to exclude the measurement of particular traits is that they may be inappropriate for the spatial or temporal scale of interest, or measurement may not be feasible owing to practical limitations. These issues need to be taken into consideration by researchers and editors, but they can only be accounted for if a common list of traits is widely accepted and used.

Some progress on deciding which traits to measure, and how they should be measured, has been made by McIntyre *et al.* (1999),Weiher *et al.* (1999), Westoby (1998) and Hodgson *et al.* (1999). The need for standardisation and coordination needs to be reconciled with the fact that no universal functional type classification is likely to be useful for all purposes and all scales. Is a perfect list of traits to be measured in all situations therefore not practical? Here it is crucial to distinguish between trait check lists and core lists. Check lists are broad lists of traits that may not all be measured, but need to be considered when deciding what to measure and what to ignore for different purposes (McIntyre *et al.*, 1999). The first step in a global trait comparison would be to screen out the invariable traits and make sure that these are used in the general description of the system studied. After screening out (but reporting on) the invariable traits, a core trait list is produced, according to the specific purpose, scale and system involved (Weiher *et al.*, 1999).

A standardized approach, even to explore a limited set of environments and a single disturbance type, would only be realistic if the list of traits to be recorded is very short and focused, and the protocols for measurement are clear and simple (Garnier *et al.*, 2001a,b). If a global-scale search for truly broad, generic functional types were to be conducted, a larger range of researchers would need to become involved. It would then become even more important to keep the core trait list to a minimum, and the measurements simple. In some cases, the 'best' traits (those with maximum ecological information with respect to the time and resources invested in its measurement) change from region to region, and consensus needs to be achieved in advance of the study. For example, Wilson *et al.* (1999) have reported that leaf water content is an excellent surrogate for resource-use strategy in northern Europe. However, Vendramini *et al.* (see pp. 147–157 in this issue) have argued that this trait can be misleading in floras with succulent species, and advocate for the use of specific leaf area in transregional comparisons. This is in accordance with Garnier *et al.* (2001a), who have proposed specific leaf area as the best indictor of resource-use strategy in large screening programmes, as compared to leaf water and nitrogen content.

The use of plant traits as indicators of land use or disturbance impacts, rather than species, is suggested as a way forward, particularly for species-rich systems such as grasslands. Well-chosen traits will enable managers to capture response to management and effects on ecosystem functions simultaneously. However, the use of plant traits rather than species as indicators will only be useful to management if the traits are easily recognizable or measurable in the field. There is a need for regional and local managers to understand when functional traits and responses documented in other regions can be directly applied to the local context. In the past, widely accepted land-use recommendations have often been based on a few specific cases, with their broader applicability rarely being tested (Perevolotsky & Seligman, 1998; Díaz *et al.*, 2002). We can only expand our capacity for generalization in relation to functional traits if we test them over a complete range of environments. Some traits may be found to be of generic value and will contribute to management strategies over a whole range of regions. For other regions, we need to identify key contextual issues that determine variability in functional traits. Thus the research approach advocated will enable extrapolation to management in specific areas, only if it involves the 'filling in' of a broad framework that is soundly constructed.

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Sandra Díaz[1,*], Sue McIntyre[2], Sandra Lavorel[3] and Juli G. Pausas[4]

[1]Instituto Multidisciplinario de Biología Vegetal (Universidad Nacional de Córdoba – CONICET), Casilla de Correo 495, Vélez Sársfield 299, 5000 Córdoba, Argentina; [2]CSIRO Sustainable Ecosystems, 120 Meiers Road, Indooroopilly, 4068 Queensland, Australia; [3]Centre d'Ecologie Fonctionnelle et Evolutive (C.N.R.S.-U.P.R. 9056) 1919, Route de Mende, 34293 Montpellier Cedex 5, France; [4]Centro de Estudios Ambientales del Mediterráneo (CEAM), Parc Tecnològic, C/C.R. Darwin 14, 46980 Paterna (València), Spain
(*Author for correspondence
tel +54 3514331097; fax +54 3514332104;
email sdiaz@com.uncor.edu)

References

Chapin FS, Bret-Harte MS, Hobbie S, Zhong H. 1996. Plant functional types as predictors of the transient response of arctic vegetation to global change. *Journal of Vegetation Science* 7: 347–357.

Chapin FS III, Zavaleta ES, Eviner VT, Naylor R, Vitousek PR, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S. 2000. Consequences of changing biodiversity. *Nature* **405**: 234–242.

Cunningham SA, 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, Briske D, McIntyre S. 2002. Range management and plant functional types. In: Hodkingson KC, eds. *Global rangelands: progress and prospects*. Wallingford, UK: CAB International. (In press.)

Díaz S, Cabido M, Zak M, Martínez-Carretero E, Araníbar J. 1999. Plant functional traits, ecosystem structure, and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science* **10**: 651–660.

Fonseca CR, Overton J, McC, Collins B, Westoby M. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* **88**: 964–977.

Garnier E, Laurent G, Bellmann A, Debain S, Berthelier P, Ducout B, Roumet C, Navas M-L. 2001a. Consistency of species ranking based on functional leaf traits. *New Phytologist* **152**: 69–83.

Garnier E, Shipley B, Roumet C, Laurent G. 2001b. A standardized protocol for the determination of specific leaf area and dry matter content. *Functional Ecology* **15**: 688–695.

Gitay H, Noble IR. 1997. What are plant functional types and how should we seek them?. In: Smith TM, Shugart HH, Woodward FI, eds. *Plant functional types*. Cambridge, UK: Cambridge University Press, 3–19.

Grime JP. 1998. Plant functional types and ecosystem processes. *Mededelingen Van de KNAW* **1998**: 104–108.

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal RJ, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J. 1997. Integrated screening validates primary axes of specialization in plants. *Oikos* 79: 259–281.

Hodgson JG, Wilson PJ, Hunt R, Grime JP, Thompson K. 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* **85**: 282–294.

Lavorel S, Garnier E. 2001. Aardvack to Zyzyxia – functional groups across kingdoms. *New Phytologist* **149**: 360–364.

Lavorel S, McIntyre S, Landsberg J, Forbes TDA. 1997. Plant functional classification: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* **12**: 474–478.

McIntyre S, Lavorel S, Landsberg J, Forbes TDA. 1999. Disturbance response in vegetation – gaining a global perspective on functional traits. *Journal of Vegetation Science* **10**: 621–630.

Pausas JG. 2001. Resprouting vs. seeding – a Mediterranean perspective. *Oikos* **94**: 193–194.

Perevolotsky A, Seligman NG. 1998. Role of grazing in Mediterranean rangeland ecosystems. *Bioscience* **48**: 1007–1017.

Pickett STA, White PJ. 1985. *The ecology of natural disturbance and patch dynamics*. New York, USA: Academic Press.

Vendramini F, Díaz S, Gurvich DE, Wilson PJ, Thompson K, Hodgson JG. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist* **154**: 147–157.

Weiher E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**: 609–620.

Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**: 213–227.

Wilson J, Thompson K, Hodson JG. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**: 155–162.

Woodward F, Diament AD. 1991. Functional approaches to predicting the ecological effects of global change. *Functional Ecology* **5**: 202–212.

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