SPECIAL FEATURE

Plant Functional Types in relation to disturbance and land use

Editors Pausas, J.; Rusch, G.M. & Lepš, J.

Based on contributions presented at the GCTE Workshop held at the Centro de Estudios Ambietales del Mediterráneo (CEAM), Valencia, Spain, 9-12 May 2001

Introduction	
Rusch, G.; Pausas, J.G. & Lepš, J. — Plant Functional Types in relation to disturbance and land use – Introduction	307
Methodological advances	
Cornelissen, J.H.C.; Cerabolini, B.; Castro-Díez, P.; Villar Salvador, P.; Montserrat-Martí, G.; Puyravaud, J.P.; Maestro, M.; Werger, M.J.A. & Aerts, R. — Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings?	311
Pillar, Valério DePatta & Sosinski Jr., Enio E. — An improved method for searching plant functional types	311
by numerical analysis	323
Advances in predictions of vegetation and ecological changes	
Boer, M. & Stafford Smith, M. — A plant functional approach to the prediction of changes in Australian rangeland vegetation under grazing and fire	333
Bradstock, R.A. & Kenny, B.J. — An application of plant functional types to fire management in a conservation reserve in southeastern Australia	345
de Groot, W.J.; Bothwell, P.M.; Carlsson, D.H. & Logan, K. — Simulating the effects of future fire regimes on western Canadian boreal forests	355
Pausas, J.G. — The effect of landscape pattern on Mediterranean vegetation dynamics – A modelling approach using functional types	365
Sternberg, M.; Gutman, M.; Perevolotsky, A. & Kigel, J. — Effects of grazing on soil seed bank dynamics in a Mediterranean herbaceous community: An approach with functional groups	375
Lloret, F. & Vilà, M. — Diversity patterns of plant functional types in relation to fire regime and previous	373
land use in Mediterranean woodlands	387
Advances in identifying functional traits and types	
Jauffret, S. & Lavorel, S. — Are plant functional types relevant to describe degradation in arid, southern Tunisian steppes?	399
Pausas, J.G. & Lavorel, S. — A hierarchical deductive approach for functional types in disturbed ecosystems	409

PROOFS: VS 2985 to author ☐ 03.06.05

Plant Functional Types in relation to disturbance and land use: Introduction

Rusch, G.M.¹; Pausas, J.G.² & Lepš, J.³

¹Norwegian Institute for Nature Research (NINA). Tungasletta 2, NO-7485 Trondheim, Norway; ²Centro de Estudios Ambientales del Mediterráneo (CEAM), C. Charles Darwin 14, Parc Tecnològic, ES – 46980 Paterna, València, Spain;
³Department of Botany, Faculty of Biological Sciences, University of South Bohemia, and Institute of Entomology, Czech Academy of Sciences, Branisovska 31, CZ-370 05 Ceské Budejovice, Czech Republic

Classification of plants according to life-history traits has a long tradition in plant ecology (Weiher et al. 1999). A variety of names have been given to different classifications (e.g. life forms (Raunkiaer 1937), strategies (Grime 2001) and functional types (McIntyre et al. 1999a), and this has resulted in groupings being based on different individual traits or groups of co-occurring traits ('syndromes'). However, common to all life-history trait classifications has been the search for a functional description of the vegetation based on plant attributes that show a common response to the environment, independent of phylogeny. Physiological and demographic constraints on plant and population growth, together with the trade-off structure of life-history traits, result in predictable changes in groups of traits or 'functional traits' (PFT) along environmental and disturbance gradients (Grime et al. 1997). The repeatable patterns in the changes of plant functional traits along gradients are observed across continents; consequently, life-history classifications can be used for comparisons and predictions between regions and at global scales.

Disturbance is one of the key factors that shape the vegetation, and attributes that confer success under disturbance are central in early life-history trait classifications (e.g. r-K strategy continuum and Grime's (2001) C-S-R strategies). Present land-use changes result in profound changes in disturbance regimes, with pronounced changes in systems where grazing and fire are major factors. Although a few traits have a general association with responses to disturbance (e.g. short life span, high dispersal capacity), more detailed studies reveal that (1) plant attributes are specific to particular types of disturbance (Grime 2001), (2) they respond to disturbance regime characteristics (e.g. severity, spatial extent and recurrence frequency) (Denslow 1980), and (3) there is usually more than one syndrome or 'strategy' for survival under any given condition (Cunningham et al. 1999; Westoby et al. 2002). The challenges to achieve powerful predictive models of plant-trait responses to changes in disturbance regimes and land use include more refined functional-type classifications that can better capture the variation in trait responses and more accurate characterization of disturbance and land-use gradients. To achieve a finer assessment of functionaltype responses, we need reliable data on the attributes of a large number of species collected in a standardized way. We also require information on changes in species composition along gradients of disturbance and adequate analytical methods (supported by available software) to manipulate the data and analyse the relationships. The availability of data and methods, and the major challenges for future work, were the main topics of discussion at the closing workshop of GCTE Task 2.2.1, held in Valencia from 9 - 12 May 2001. The workshop brought together 40 scientists from Europe, South and North America, Australia and New Zealand, who are active in Plant Functional Traits Grazing and Fire networks. This special issue offers some of the key papers presented at the workshop. They constitute advances in methodological problems, in the identification of attributes that are functionally significant, and in the applicability of life-history traits to predict vegetation changes resulting from shifts in disturbance regime and land use.

Methodological advances

The contribution by *Cornelissen et al.* (2003) constitutes a step forward regarding the methodological challenges facing PFT by highlighting the limitations of trait descriptions based on greenhouse material and questioning the validity of traits assessed from different ontogenetic stages. They also evaluate the constancy of different traits across geographical gradients and the stability of the relationship between traits measured in the laboratory and in the field. Their work determines the degree of the validity and applicability of particular trait measurements, which constitutes an important advance in establishing standards for trait measurements. *Pillar & Sosinski* (2003) propose an improved method

for seeking functional types based on numerical analyses of species, traits and site matrices (software available at the *JVS* web page).

Advances in predicting vegetation and ecological changes

Five of the studies explore the applicability of plant traits for predicting vegetation responses to land management. They present achievements in one of the main purposes of using the conceptual framework of plant functional traits, i.e. improved assessment of ecosystem sensitivity to changes in the environment (McIntyre et al. 1999b). Sternberg et al. (2003) present a study that shows how the grazing regime (intensity and frequency) affects the composition of the soil seed bank of different functional groups. They conclude that intense grazing may have a detrimental effect on the seed bank of annuals if grazing is not properly managed (e.g. by reducing grazing pressure during the period of seed setting). Bradstock & Kenny (2003) use the plant-functional approach to estimate optimal fire regimes for biodiversity planning in a national park. They use the 'vital attributes' (sensu Noble & Slatyer 1980) of the species pool of an area to discriminate groups of species that are likely to undergo a significant decline or extinction in response to particular fire regimes. By grouping species according to their juvenile periods, life span and the seed bank longevity, they assess the sensitivity of plant functional types (PFT) to different scenarios of low and high fire frequencies. Pausas (2003) explores, through modelling, the possible consequences of the spatial distribution of two different Plant Functional Types (resprouters and seeders) on the dynamics of fireprone Mediterranean landscapes. He shows that different functional types may be favoured by different spatial distributions, i.e. the spatial arrangement of PFTs feeds back on PFT landscape composition, which in turn has a direct bearing on land management. Boer & Stafford Smith (2003) develop a simulation model to predict changes in perennial forage species and the abundance of woody plants in a system subjected to both grazing and fire (range land management). The model uses three functional types (annual grasses, perennial grasses and woody plants) and successfully predicts pasture production, but not the changes in the abundance of woody plants. de Groot et al. (2003) examine the ecological effects of future altered fire regimes on boreal tree community and biomass dynamics. In North American boreal forests, the major plant functional types differ in fire survival and post-fire regeneration strategies. Using a dynamic simulation model (linked to a Global Coupled Model, GCM), they predict that a change in the

future fire regime towards shorter cycles will favour plant traits that confer post-fire persistence and fire resistance. *Lloret & Vilà* (2003) explore the effect of different fire history (recurrence/time since last fire) and past land use (terraced vs. unterraced slopes) on diversity patterns of PFTs in Mediterranean shrublands, based on two functional type classifications. They conclude that the diversity pattern of PFTs defined on the basis of regenerative traits (seeding, resprouting) is more sensitive to fire history while the diversity pattern of growth form PFTs is more sensitive to past land uses.

Advances in identifying response traits

McIntyre et al. (1999b) have stressed the importance of identifying which attributes are linked to specific disturbance regimes and which syndromes are functionally significant. Jauffret & Lavorel (2003) study advances in this direction. They aim to identify traits that respond to abiotic stress and land degradation (overgrazing and ploughing) in arid ecosystems of Northern Africa by using currently available trait data. Their study reveals limitations in the capacity of the available trait data in semi-arid and arid systems to reflect landuse forms, and stresses the importance of future research based on standardized field measurements where different traits linked with particular land uses are specifically addressed. Pausas & Lavorel (2003) introduce a new framework for studying plant functional types in disturbed ecosystems based on the persistence of the species at different scales and levels of organization. The proposed hierarchical framework seems especially appropriate for modelling and for global trait comparisons, and needs to be tested with available data bases. To what extent the proposed 16 functional types co-exist or, alternatively, have been selected in different floras, is an interesting ecological and evolutionary question.

In this context, McIntyre et al. (1999b) also indicated the need for formal comparisons of many studies at a global scale. The work under the Fire and Grazing GCTE networks resulted in global syntheses that were presented and discussed during the workshop. Díaz et al. (in prep.) and Pausas et al. (in prep.) show some interesting patterns of traits that respond to disturbance (grazing and fire) when accounting for climate and the evolutionary history of the flora, but they also reveal the limitations of trait data retrieved from the literature. These studies further stress the importance of directing future work towards a direct assessment of plant trait responses using a common framework, i.e. adopting common lists of traits and recording traits following a standardized methodology in different systems in the world. Although some trait lists already seem to have

reasonably wide consensus (McIntyre et al. 1999b; Weiher et al. 1999), there is still a need for more indepth assessments of traits linked to specific types of disturbance, and also for more accurate descriptions of the disturbance regime (e.g. intensity, frequency, history, type).

Perspectives for future work

Firstly, the PFT framework can constitute a useful tool for predicting changes in vegetation and biodiversity as a consequence of environmental and disturbance changes and land-use shifts at regional and global scales. This aim requires the screening and synthesis of traits from a large number of species across broad environmental and disturbance gradients. A substantial amount of empirical work has already identified traits that can be easily measured and used as surrogates for physiological and demographic plant attributes. This work needs to be continued to identify more surrogates for processes that are relevant to the dynamics of plant populations, i.e. those that determine their persistence, regeneration and dispersal under a wider range of environmental and disturbance scenarios, and to test the robustness of currently used traits across larger geographical scales. The framework proposed by Pausas & Lavorel (2003) may provide important insights in this direction.

Secondly, there is a need for more quantitative assessments of the degree of association between plant traits and syndromes and their responses to disturbance and land management. For this purpose, both standardized trait measurements and more accurate data on the environment and stress factors are necessary.

Thirdly, the PFT framework can provide a link between vegetation responses to environmental change and the effects of these changes on ecosystem properties and function (Grime 2001; Lavorel & Garnier 2002). The effectiveness of this link will rely on the adaptive value of the selected plant attributes along ranges of environmental change on one hand and on the close bearing which these attributes have for ecosystem function on the other. Greater focus on quantifying trait responses and their effects on ecosystem function and population dynamics is therefore highly relevant.

The perspectives for addressing these issues in the near future are promising. Firstly, the increasing number of research groups interested in exploring the use of plant functional traits to predict vegetation responses to disturbance and stress allows PFT questions to be addressed on large numbers of species with different phylogenies and on a wide range of environments. Moreover, current networks (GCTE – PFT Grazing and

Fire Networks) facilitate the co-ordination and standardization of such trait measurements. Secondly, substantial progress has been achieved in producing standardized protocols for trait measurements (Garnier et al. 2001; Cornelissen et al. subm.) and this work is continuing along with the construction of regional trait data bases (Gill & Bradstock 1992; Anon. 2003). Thirdly, both standardization of trait measurements and regional comparative studies are taking place through ongoing initiatives supported by the European Community (EC) such as VISTA (home page under construction, coming up soon), EUFireLab (http://www.eufirelab.org http://www.eufirelab.org) and LEDA (http://www.offis.de/leda-traitbase) projects.

Acknowledgements. The Valencia meeting (9 - 12 May 2001) was organized by J. Pausas (CEAM, Spain), S. Lavorel (CEFECNRS, France), S. Díaz (Universidad Nacional de Córdoba, Argentina) and S. McIntyre (CSIRO, Australia), and supported by the Dutch Global Change Committee, the Spanish Ministry of Science and Technology, Ecos-Sud France-Argentina, CNRS France and CEAM (Valencia). The collaboration of IGBP-España is also acknowledged.

References

- Anon. U.S. Department of Agriculture, F.S., Rocky Mountain Research Station, Fire Sciences Laboratory. 2003. Fire Effects Information System [Online].
- Boer, M. & Stafford Smith, M. 2003. A plant functional approach to the prediction of changes in Australian rangeland vegetation under grazing and fire. *J. Veg. Sci.* 14: 333-344. [This issue.]
- Bradstock, R.A. & Kenny, B.J. 2003. Application of plant functional traits to fire management in a conservation reserve in southeastern Australia. *J. Veg. Sci.* 14: 345-354. [This issue.]
- Cornelissen, J.H.C., Cerabolini, B., Castro-Díez, P., Villar Salvador, P., Montserrat-Martí, G., Puyravaud, J.P., Maestro, M., Werger, M.J.A. & Aerts, R. 2003. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *J. Veg. Sci.* 14: 311-322. [This issue.]
- Cunningham, S., Summerhayes, B. & Westoby, M. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecol. Monogr.* 69: 569-588.
- de Groot, W.J., Bothwell, P.M., Carlsson, D.H. & Logan, K. 2003. Simulating the effects of future fire regimes on western Canadian boreal forests. *J. Veg. Sci.* 14: 355-364. [This issue.]
- Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18-21.

- Garnier, E., Shipley, B., Roumet, C. & Laurent, G. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Funct. Ecol.* 15: 688-695.
- Gill, A.M. & Bradstock, R.A. 1992. A national register for the fire response of plant species. *Cunninghamia* 2: 653-660.
- Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. 2nd. ed. Wiley, Chichester, UK.
- Grime, J. et al. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79: 259-281.
- Jauffret, S. & Lavorel, S. 2003. Are plant functional types relevant to describe degradation in arid, southern Tunisian steppes? J. Veg. Sci. 14: 399-408. [This issue.]
- Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem function from plant traits revising the Holy Grail. *Funct. Ecol.* 16: 545-556.
- Lloret, F. & Vilà, M. 2003. Diversity patterns of plant attributes in relation to fire regime and previous land use. *J. Veg. Sci.* 14: 387-398. [This issue.]
- McIntyre, S., Díaz, S., Lavorel, S. & Cramer, W. 1999a. Plant functional types and disturbance dynamics. Introduction. *J. Veg. Sci.* 10: 604-608.
- McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T.D.A. 1999b. Disturbance response in vegetation towards a global perspective on functional traits. *J. Veg. Sci.* 10: 621-630.

- Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant-communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- Pausas, J.G. 2003. The effect of landscape pattern on Mediterranean vegetation dynamics A modelling approach using functional types. *J. Veg. Sci.* 14: 365-374. [This issue.]
- Pausas, J.G. & Lavorel, S. 2003. A hierarchical deductive approach for functional types in disturbed ecosystems. *J. Veg. Sci.* 14: 409-416. [This issue.]
- Pillar, V.D. & Sosinski Jr., E.E. 2003. An improved method for searching plant functional types by numerical analysis. *J. Veg. Sci.* 14: 323-332. [This issue.]
- Raunkiaer, C. 1937. *Plant life forms*. Clarendon Press, Oxford
- Sternberg, M., Gutman, M., Perevolotsky, A. & Kigel, J. 2003. Effects of grazing on soil seed bank dynamics in a Mediterranean herbaceous community: An approach with functional groups. *J. Veg. Sci.* 14: 375-386. [This issue.]
- 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. *J. Veg. Sci.* 10: 609-620.
- Westoby, M., Falster, D., Moles, A., Vesk, P. & Wright, I. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33: 125-159.