

A hierarchical deductive approach for functional types in disturbed ecosystems

Pausas, Juli G.^{1*} & Lavorel, Sandra²

¹CEAM (Fundación Centro de Estudios Ambientales del Mediterráneo), Charles R. Darwin 14, Parc Tecnològic, E-46980 Paterna, València, Spain; ²CNRS-Université Joseph Fourier, BP 53 X, F-38041 Grenoble Cedex 9, France; E-mail sandra.lavorel@ujf-grenoble.fr and Ecosystem Dynamics Group, Research School of Biological Sciences, Australian National University, Canberra ACT 0200, Australia; *Corresponding author; Fax+34961318190; E-mail juli@ceam.es

Abstract. We propose a hierarchical approach for plant functional classification in disturbed ecosystems to be used for vegetation modelling and global plant trait comparisons. Our framework is based on the persistence of plants at different levels of organization. We assume that the main parameters to determine persistence in chronically disturbed ecosystems are those related to: Individual-persistence capacity, Propagule-persistence capacity (persistence at the population level), Competitive capacity (persistence at the community level) and Dispersal capacity (persistence at the landscape level). The IPCD approach is illustrated for fire-prone and grazed ecosystems from the Mediterranean region and Australia and by assuming a binary classification of the four traits determining persistence which give a total 16 possible functional types. The IPCD framework provides a simple structured and synthetic view from which more elaborated schemes can be developed.

Keywords: Disturbance; Fire; Functional classification; Grazing; Persistence; Plant trait.

Introduction

In the last decades, a significant scientific effort has focused on understanding the role of plant functional characteristics in plant community dynamics and ecosystem functioning (see compilations in Woodward & Cramer 1996; Smith et al. 1997; Lavorel & Cramer 1999; Lavorel & Garnier 2002) and several plant functional type schemes are currently available (e.g. Grime 1977; Noble & Slatyer 1980; Westoby 1998; Weiher et al. 1999). However no general framework is available that successfully deals with vegetation dynamics under different disturbance types and that can be applied to a range of ecosystems. Furthermore, most existing schemes consider all ecological processes simultaneously and/or they do not explicitly consider post-disturbance regeneration mechanisms. Core sets of functional traits have previously been selected based on considerations of the main processes that govern plant response to environmental factors and biotic interactions (e.g. Weiher et al. 1999). However, they have failed to recognize the importance of differences in scales

associated with different processes (Urban et al. 1997), an issue that is critical for comparing and modelling the dynamics of functional types with a global perspective (Dawson & Chapin 1993).

Eriksson (2000) emphasized the need to distinguish between processes that relate to local population persistence and processes allowing species persistence at the regional scale through metapopulation dynamics. Indeed, most models of vegetation dynamics examining the interactions between plant life histories and the spatial and temporal variability of the environment, especially through disturbance, have considered at least two levels, the local community where successional dynamics is proceeding, and the landscape for seed dispersal between communities (e.g. Palmer 1992; Moloney & Levin 1996; Plotnick & Gardner 2002; Pausas 2003). Going a step further along the same path, we propose here a hierarchical, scale-dependent approach for disturbed ecosystems, focussing on the mechanisms of persistence at different levels of organization (see Landsberg et al. 1999). Though the approach could easily be applied to other types of disturbances and regions, we provide in this paper illustrations for two disturbances, fire and grazing, that affect significant areas globally and specifically Mediterranean and Australian ecosystems.

The search for the minimum set of traits for persistence under disturbance may progress by translating the general question into four nested questions: 1. What are the main traits that allow individuals to persist after disturbance? 2. In the case of non-persistence of the individual, which traits would allow the population of that species to persist at a given site? 3. And if a species population persists, how can it maintain itself within a competitive multispecies community? 4. On the other hand, if a species does not persist, what trait(s) would enable this species to colonize from other populations in the landscape? These four questions can then be used as a conceptual framework to propose a hierarchical, scale-dependent approach for disturbed ecosystems based on persistence at these different levels of organization.

The hierarchical persistence approach: traits and associated processes

Individual level persistence

Individuals can persist after a disturbance if they have traits that allow them to resist or to regenerate vegetatively after disturbance (Eriksson 2000). In crown-fire ecosystems (e.g. Mediterranean and temperate ecosystems), the main trait that allows individual plants to persist after fire is the ability to resprout after part or all of the aboveground biomass has been burned (Bond & Midgley 2001). For tree species in surface-fire ecosystems (e.g. open woodlands, savanna ecosystems), other traits such as bark thickness (providing meristem protection), height and self-pruning have been suggested as an important trait for post-fire persistence (Zedler 1995; Gignoux et al. 1997; Keeley & Zedler 1998). Resprouting also accounts for much of the tolerance to grazing of perennial species (Briske & Richards 1995), but many species also persist after grazing due to their unpalatability (toughness, thorns) or toxicity of their tissues (Anderson & Briske 1995). Most mature individuals of resprouter species persist after disturbance, while individuals of non-resprouter species do not. In the case of fire, species can be classified as resprouters, that is, species that are able to resprout after a 100% scorch, and non-resprouters, species that are not able to resprout after a 100% scorch (Gill 1981). Such a semi-quantitative description is not available for grazing, but a similar philosophy could be applied. In some cases the capacity to resprout may depend on the age or size of the individual (Rundel et al. 1987; Strasser et al. 1996; Williams et al. 1999). In addition, some woody species may resprout from the canopy (from stem buds) or from the base, depending on the age or size of individuals (Strasser et al. 1996; Pausas 1997) or the severity of the fire (Morrison & Renwick 2000; Bellingham & Sparrow 2000). The resprouting capacity may also depend on available reserves, which is in part influenced by site productivity (Bond & Midgley 2001), and on the size of the bud bank at the time of the disturbance (Briske & Richards 1995). This capacity may be depleted if the disturbance return time is too short (Canadell & López-Soria 1998).

Population level persistence

In many species, individuals do not persist after disturbance and population persistence depends on the persistence of their propagules, a highly variable trait within floras (e.g. Thompson et al. 1993; Leishman & Westoby 1998; Funes et al. 1999; Moles et al. 2000; Pérez-Fernández et al. 2001). Although seed persistence is a continuous characteristic resulting from the interplay of

several traits, propagule-persisters can be defined phenomenologically as those species that persist in a propagule form (e.g. seed, fruit) after the adult plants have been fully scorched or grazed off. Examples of seeds that resist (or are protected from) fire are the hard-coated seeds of many *Cistaceae* and *Fabaceae* species (Trabaud & Oustric 1989; Roy & Sonié 1992; Bradstock & Auld 1995; Harranz et al. 1998; Ferrandis et al. 1999) or the seeds protected by cones of some conifers (*Pinus*, *Callitris*; Schwilk & Ackerly 2001; Tapias et al. 2001) and many *Proteaceae* genera (e.g. *Banksia*, *Protea*, *Leucadendron*, *Hakea*; Lamont et al. 1991). The fact that seeds are hard or protected results in dormancy that is broken by disturbance. The characteristics associated with seed persistence in grazed herbaceous communities have been debated, but at least in some floras, seed persistence is well correlated with small size and compact shapes that minimize exposure to predation and diseases (Thompson et al. 1993; Funes et al. 1999; but see Leishman & Westoby 1998). Hard seed coats, as found in *Fabaceae*, are also a trait often associated with seed persistence in pasture plants (Baskin & Baskin 1989).

Nevertheless, seed persistence alone is not enough to ensure successful recruitment. Firstly seed banks are only an efficient regeneration mechanism after disturbance if fecundity is high enough to fill up seed stocks and/or if seed longevity is high, allowing for the accumulation of a large seed bank over many years (Lavorel et al. 1999). In addition, population persistence after recurrent disturbance relies on the heterogeneity of the seedbank with respect to dormancy, longevity and/or age. Single-aged soil seedbanks with uniform dormancy levels or seed stocks with serotinous structures are exhausted after a single disturbance event, making species that rely on them very sensitive to fire intervals. Secondly, the recruitment of propagule-persisters is often enhanced by disturbance. This stimulation can be produced by different mechanisms, among which are the weakening of hard seed coats by heat (Bradstock & Auld 1995; Harranz et al. 1998), the stimulation of germination by smoke (Brown 1993; Keeley & Fotheringham 1997, 1998), or the enhanced seed release from ligneous structures after fire (Lamont et al. 1991; Enright et al. 1998; Schwilk & Ackerly 2001). Species that have exclusive pyrogenic flowering (resprouter species that only flower after fire) can also be included in this group because of the functional similarity with having a canopy seed bank (Gill & Ingwersen 1976; Lamont & Downes 1979).

Community level persistence

Once the species persists after disturbance (through individual or population persistence mechanisms), it needs to survive competitive pressure. Competitive capacity is

the result of two components, competitive effect and competitive response (Goldberg 1991).

Competitive response, and specifically the ability to withstand competitive pressure from surviving individuals, is relevant to post-disturbance competition when resprouting is a prevalent response, and, in general, in most ecosystems where vegetation ultimately builds a continuous canopy. This situation may be the result either of low to moderate disturbance intensity and/or frequency, or if evolutionary characteristics of floras have promoted widespread resprouting. Although much debate has surrounded the identification of the most important traits and processes determining competitive response (e.g. Keddy et al. 1998; Wardle et al. 1998), in many disturbed ecosystems a good indicator of competitive response is shade-tolerance (Smith & Huston 1989; but see Coomes & Grubb 2000). Shade tolerance has been associated with leaves with a high Specific Leaf Area and a low dry matter content, high investment in stems (Keddy et al. 1998), large seeds, and seedling morphology with rapid expansion of deep roots (Leishman et al. 1994; Reich et al. 1998).

On the other hand, in situations where regeneration through seeds dominates, either as a result of intense disturbance that kills resprouter species, or because resprouters are rare in the flora, then competitive effect is more relevant than competitive response. Adult plant size has been consistently identified as a good indicator of the competitive effect of one species over its neighbours (Goldberg 1991; Wardle et al. 1998), and reflects the ability of a species to overtop other species. Its concurrent relevance to competitive response, however continues to be debated (Keddy et al. 1998; Loehle 2000; Aarsen & Keogh 2002).

Table 1. Some possible traits for measuring the hierarchical IPCD parameters.

Level	IPCD parameters	Binary evaluation	Specific traits
Individual	Individual-Persistence capacity	Yes/No	Resprouting capacity (no, low, ..., high) resprouting age or size limits, bark thickness, height, spininess, toxicity, toughness
Population	Propagule-persistence capacity	Yes/no	Seed longevity, seed hardness, seed size and shape
Community	Competitive capacity	High/low	Growth rate, height, shade tolerance, specific leaf area stem / leaf ratio
Landscape	Dispersal capacity	High/low	Short, ..., long distance, propagule size, mass, morphology

Whether regeneration devolves to seedlings or to resprouting shoots, the most important capacity to achieve competitive superiority during post-disturbance regeneration is to grow faster than other species. Fast growth and corresponding strongly competitive effects have been associated with fast relative growth rates (Goldberg 1991) and, by correlation, with high Specific Leaf Area and other leaf traits such as high nitrogen concentrations (Garnier et al. 1997). In herbaceous communities subjected to grazing and other disturbances, the ability for fast regrowth may play a major role in determining competitive hierarchies (Suding & Goldberg 2001; Hendon & Briske 2002).

Finally, in some systems, facilitation rather than competition may be an important mechanism for persistence in communities (Bruno et al. 2003). This is especially the case in habitats with strong environmental stress or herbivory, which slow down post-disturbance recovery. However, to this day, little is yet known on the types of plant traits favouring facilitative associations.

Landscape level persistence

When a species does not persist in a given patch its arrival is determined by its dispersal capacity. Two main components may be used to describe dispersal capacity: the amount of propagules dispersed and the thickness of the tail of the seed shadow (Higgins & Richardson 1999). In many systems, propagule mass, or size, may be the best single trait to account for the dispersal capacity. Propagule mass is indeed related to dispersal distance and fecundity (Thompson et al. 1999; Jakobsson & Eriksson 2000; Henery & Westoby 2001), although accurate predictions of dispersal capacity should also consider additional morphological seed traits (shape, presence of wings, arils, etc.) (Hughes et al. 1994). Overall fecundity appears as the most important parameter for colonization, including for long distance dispersal for which links with any other plant traits are questioned (Clark et al. 1999).

Implementation of the hierarchical framework to a binary classification scheme

We hypothesize that the four phenomenological characteristics described above, Individual persistence capacity, Propagule persistence capacity, Competitive capacity and Dispersal capacity (IPCD), should account for an important proportion of the variability in the vegetation dynamics in chronically disturbed ecosystems. Using this minimum set of parameters, and the most simplified attributes for each one, that is, a binary system (yes/no or high/low; Table 1), we can predict a set of 16 disturbance-response types (the IPCD approach, Fig 1).

Traits determining these characteristics (e.g. Table 1) should constitute the minimum set of parameters in any dynamic model for disturbed ecosystems. Although we expect this hierarchical framework to be valid for a wide range of biomes, the traits to characterize each IPCD parameter may be different in different regions depending on the biophysical and evolutionary context (Pausas 2001; Díaz et al. 2002). In addition, although it would be desirable to base plant functional classifications on morphological or ecophysiological plant traits that can be measured on individuals rather than on phenomenological observations, the selection of relevant traits in a specific situation will depend on progress in the fundamental understanding of plant functional traits and on local data availability. Furthermore, it is essential to recognize that the specific values for assigning the corresponding attribute of each trait (i.e. high/low or yes/no) for a given species may depend on the ecosystem under study and the local species pool (McIntyre et al. 1999). For instance, competitive ability can vary, depending, for instance, on site productivity (Keddy et al. 2000), and the competitive ranking of a species within a given community will depend on the composition of the local species pool. Dispersal capacity is also typically dependent on the local context, as the identity and density of animal dispersers determines whether a species will retain its seeds within a very close distance to the adult tree or whether these may get opportunities for longer-range transport (Bossema 1979). These caveats do not undermine the generic value

of the framework, whose merit lies in linking traits and dynamics using a hierarchical approach rather than in the detailed traits or classification criteria for a locality.

We illustrate the framework and its implementation using the example of fire-prone and grazed ecosystems in Mediterranean Europe and Australia, where we used published responses and opinion of local experts to allocate some common species into the 16 binary categories (Table 2). While for a number of dominant and well-known species it was relatively easy to attribute IPCD categories, this exercise highlighted the paucity of knowledge on basic autoecology, let alone functional attributes, in these relatively well-studied ecosystems. Such basic knowledge gaps will continue to hinder the testing of any plant functional classification scheme. In particular, data about seed persistence and dispersal are often not available as many studies have focussed on the adult rather than the regeneration phase of plant ecology (Grubb 1977; Cornelissen et al. 2003). In the same way, the classification of species competitive ability was not always straightforward, in particular because of the lack of standardization in descriptions of competitiveness with respect to response or effect (Aarsen & Keogh 2002).

By hypothesizing the existence of these 16 functional types (Fig. 1), we assume that the four IPCD parameters may be independent, which needs to be verified with field data from across a range of ecosystem. However, there is evidence that trade-offs do exist. First, trade-offs between individual persistence capacity and regeneration through

Table 2. Some representative plant species for each IPCD functional type (see Fig. 1). Examples are mainly woody species in fire-prone ecosystems and herbaceous species in grasslands, from Mediterranean (Europe and California) and Australian ecosystems (E, C, A, respectively). For fire-prone ecosystems, the information is based on the databases developed in Pausas et al. (submitted).

IPCD FTs	Fire-prone ecosystems	Grazed ecosystems
I+P+C+D+	<i>Banksia serrata</i> (A), <i>Eucalyptus macroryncha</i> (A), <i>E. dives</i> (A)	<i>Danthonia</i> (A), <i>Microleana</i> (A)
I+P+C+D-	<i>Ceanothus thrysiflorus</i> (C) <i>Plantago lanceolata</i> (E),	<i>Glycine</i> spp. (A), <i>Lotus corniculatus</i> (E)
I+P+C-D+	<i>Banksia spinulosa</i> (A), several <i>Melaleuca</i> spp. (A), <i>Adenostoma fasciculatum</i> (C)	<i>Desmodium varians</i> (A), <i>Nasella tenuissima</i> (A) <i>Anthyllis vulneraria</i> (E)
I+P+C-D-	many <i>Acacia</i> spp. (e.g. <i>A. melanoxylon</i> , A), <i>Dorycnium hirsutum</i> (E), <i>Genista scorpius</i> (E)	
I+P-C+D+	<i>Rhamnus alaternus</i> (E), <i>Arbutus unedo</i> (E), <i>Viburnum tinus</i> (E), <i>Acmena smithii</i> (A)	<i>Bromus erectus</i> (E), <i>Rubus ulmifolius</i> (E, A) <i>Phalaris aquatica</i> (A), <i>Heteropogon contortus</i> (A)
I+P-C+D-	<i>Quercus ilex</i> , <i>Q. coccifera</i> (E), <i>Brachypodium phoenicoides</i> (E)	<i>Cynodon dactylon</i> (E, A), <i>Pennisetum clandestinum</i> (A) Tropical stoloniferous grasses (e.g. <i>Digitaria decumbens</i> , A)
I+P-C-D+	<i>Juniperus oxycedrus</i> (E), <i>Erica multiflora</i> (E)	<i>Dactylis glomerata</i> (E, A)
I+P-C-D-	many geophytes (e.g. <i>Urginea</i> , <i>Asphodelus</i> , E)	Geophytes with large underground structures <i>Asphodelus</i> (E), <i>Sanguisorba minor</i> (E) <i>Melinis repens</i> (A)
I-P+C+D+	<i>Callitris rhomboidea</i> (A), <i>Eucalyptus delegatensis</i> (A)	
I-P+C+D-	<i>Acacia verniciflua</i> (A)	<i>Psoralea bituminosa</i> (E)
I-P+C-D+	most <i>Cistus</i> (E), <i>Ulex parviflorus</i> (E), <i>Calytrix tetragona</i> (A) <i>Pinus</i> (serotinous, e.g. <i>P. halepensis</i> , E)	<i>Conyza canadensis</i> (E, A), <i>Trifolium stellatum</i> (A) <i>Vulpia</i> spp. (E, A), <i>Avena</i> spp. (E, A), <i>Echium plantagineum</i> (E, A)
I-P+C-D-	<i>Retama</i> (E), many <i>Acacia</i> (<i>A. dealbata</i> , <i>A. aneura</i> , A), <i>Ceanothus greggii</i> (C)	<i>Geranium dissectum</i> (E), <i>Erodium</i> spp. (E, A) <i>Trifolium subterraneum</i> (E, A)
I-P-C+D+	<i>Podocarpus lawrencii</i> , (A), <i>Bromus erectus</i> (E)	<i>Brachypodium phoenicoides</i> (E), <i>Themeda triandra</i> (A)
I-P-C+D-		<i>Thelymitra aristida</i> (A)
I-P-C-D+	<i>Pinus</i> (non-serotinous, e.g. <i>P. nigra</i> , E), <i>Rosmarinus</i> (E)	<i>Teucrium chamaedrys</i> (E), <i>Viola scotophylla</i> (E)
I-P-C-D-	<i>Juniperus phoenicea</i> (E)	

seeds are acknowledged in plant strategy schemes (e.g. Grime 1977; Silvertown et al. 1993). Specifically, allocation of resources to vegetative regeneration (basal and stem buds, storage organs) may limit allocation to sexual regeneration (flowering at young age and producing numerous seeds) (Carpenter & Recher 1979; Loehle 1987; Olejniczak 2001). Second, it has been argued that competitive and colonization abilities may be negatively correlated (Tilman 1994; but see Higgins & Cain 2002), in particular if these two processes are related to opposite seed characteristics, such as seed size (Turnbull et al. 1999; Jakobsson & Eriksson Inpress). Finally, evolutionary models suggest trade-offs among dispersal capacity, seed persistence and fecundity, but also that these may depend on the nature of environmental variability (Venable & Brown 1988; Olivieri 2001). Consequently, the specific IPCD combinations occurring in a community might depend on trade-offs and on evolutionary history. Furthermore, although it is tempting to focus on those traits common to several hierarchical levels, such as seed size or plant height, and to take into account known trade-offs, the variability of trait linkages across ecosystems and floras, when they have been tested empirically, justify keeping a slightly larger set of core traits and conserving all 16 functional types in the classification framework. Our examples for Mediterranean and Australian fire-prone or pasture ecosystems (Table 2) suggest that most functional types can be filled, even within a single flora, and we attribute empty cells to our lack of biological knowledge rather than to their absence from communities. Still, correlations and trade-offs between the four traits may determine the commonness or rarity of different functional types in particular floras.

A final issue faced by this classification concerns systems subjected to multiple disturbances. Indeed, many grasslands are naturally or, through management, subjected to both fire and grazing (e.g. Boer & Stafford Smith 2003). The overlap between response traits to these two different types of disturbance has not yet been addressed systematically. For instance, in Australian grasslands a number of grass species (e.g. *Themeda triandra*) with a good fire-resprouting ability are quite sensitive to grazing. Conversely, in Mediterranean grasslands, *Brachypodium phoenicoides* tolerates grazing through vigorous resprouting but is highly sensitive to fire, and *Bromus erectus* can resprout after grazing but not after fire. This variability in responses may be due, in part, to the different severities of the different disturbances. For instance, grazing only affects above-ground parts (and often not the whole plant) while fire may affect both above and below-ground parts (e.g. mortality of *Brachypodium* rhizomes by intense fires).

The conceptual approach proposed here can be considered a step forward from the one used by Loehle

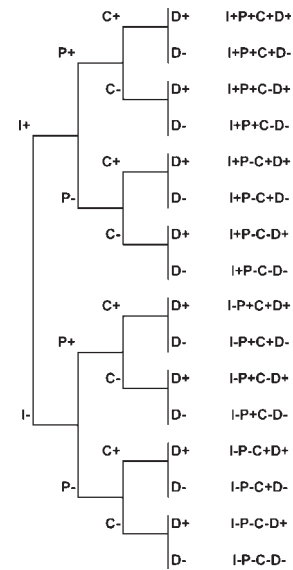


Fig. 1. Hierarchical deductive classification for functional types in disturbed ecosystems based on four characteristics in a binary system (-, low/none; +, high/yes). I = Individual-persistence capacity; P = Propagule-persistence capacity; C = Competitive capacity; D = Dispersal capacity.

(2000) for North American trees, or from the vital attributes scheme originally developed for fire-driven Australian woody communities (Noble & Slayter 1980; recently applied to pasture landscape dynamics; Cousins et al. 2003). The main differences are that we emphasize the concept of persistence, which is very appropriate for ecosystems under frequent disturbances (Bond & Midgley 2001), and that this concept is applied at different levels of organization. Furthermore, Loehle does not consider propagule persistence, and it is well known that without this parameter we cannot explain the persistence of some non-resprouting species in recurrently disturbed ecosystems. Another difference is the hierarchical nature of the approach presented here, which augments similar schemes such as the one used by Schippers et al. (2001) to model grassland dynamics based on seed and seedling traits, by providing a ranking on trait importance depending on the level or spatial context required.

Finally, we have applied the IPCD approach to the simplest classification of traits (binary system; yes/no or high/low); however, in systems for which a detailed ecological knowledge base exists, implementations with higher resolution are possible such as those based on semi-quantitative (e.g. Moore & Noble 1990) rather than binary classification, or by adopting a fuzzy classification using continuous values for each response level (Pillar 1999). These options would also facilitate analysing the response to different disturbance regimes (frequency, severity), including multiple disturbances.

Conclusion

The IPCD approach aims to provide a global framework for analysing plant traits that are relevant to disturbance response at different levels of organization. It is a synthetic and structured view of the traits that affect disturbance response, and provides an understanding of the order in which different biological mechanisms act on plant persistence in disturbed systems. However it also highlights basic gaps in our knowledge. Much remains to be done to identify traits relevant to different levels of response, and there is still very limited data available for most ecosystems of the world to be able to construct a simple global functional classification. While accepting that the allocation of particular species to specific functional types is highly context-dependent, we argue that the approach provides a generic framework for modelling vegetation dynamics in chronically disturbed systems and the basis to structure global plant trait comparisons. Such comparisons can contribute to our understanding of evolutionary history by examining to what extent different floras and biomes have selected different functional types from the 16 types proposed here. Answering these questions is a new challenge.

Acknowledgements. Most of the ideas presented in this paper were discussed at two workshops of the GCTE network on 'Plant functional response to land use and disturbance' (Brisbane, July 1999 and Valencia, May 2001). We are grateful to Ross Bradstock, Pablo Cruz, Jan Lepš, Sue McIntyre, Marie-Laure Navas, Mike Palmer and an anonymous referee for comments on the manuscript, and to Sandy Berry, Max Debussche and Karl Grigulis for discussion of examples in the Australian and Mediterranean systems. CEAM is funded by Generalitat Valenciana and Bancaixa.

References

- Aarsen, L.W. & Keogh, T. 2002. Conundrums of competitive ability in plants: what to measure? *Oikos* 96: 531-542.
- Anderson, V.J. & Briske, D.D. 1995. Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? *Ecol. Appl.* 5: 1014-1024.
- Baskin, J.M. & Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds.) *Ecology of soil seed banks*, pp. 53-66. Academic Press Inc., Harcourt Brace Jovanovitch Publishers, San Diego, CA, US.
- Bellingham, P.J. & Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409-416.
- 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.)
- Bond, W.J. & Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16: 45-51.
- Bossema, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. *Behavior* 70: 1-117.
- Bradstock, R.A. & Auld, T.D. 1995. Soil temperature during experimental bushfire in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *J. Appl. Ecol.* 32: 76-84.
- Briske, D.D. & Richards, J.H. 1995. Plant responses to defoliation: A physiological, morphological and demographic evaluation. In: Bedunah, D.J. & Sosebee, R.E. (eds.) *Wildland plants: Physiological ecology and developmental morphology*, pp. 635-710. Society for Range Management, Denver, CO, US.
- Brown, N.A.C. 1993. Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytol.* 123: 575-583.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18: 119-125.
- Canadell, J. & López-Soria, L. 1998. Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Funct. Ecol.* 12: 31-38.
- Carpenter, F.L. & Recher, H.F. 1979. Pollination, reproduction and fire. *Am. Nat.* 113: 871-979.
- Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRis-Lambers, J., Lichter, J., McLachlan, J., Mohan, J. & Wyckoff, P. 1999. Interpreting recruitment limitation in forests. *Am. J. Bot.* 86: 1-16.
- Coomes, D.A. & Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Monogr.* 70, 171-207.
- Cornelissen, J.H.C., Cerabolini, B., Castro-Díez, P., Villar Salvador, P., Monserrat-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.)
- Cousins, S., Lavorel, S. & Davies, I.D. In press. Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. *Landscape Ecol.*
- Dawson, T.E. & Chapin III, F.S. 1993. Grouping plants by their form – Function characteristics as an avenue for simplification in scaling between leaves and landscapes. In: Field, C.B. & Ehleringer, J.R. (eds.) *Scaling physiological processes from the leaf to the globe*, pp. 313-319. Academic Press, San Diego, CA, US.
- Díaz, S., McIntyre, S., Lavorel, S. & Pausas, J.G. 2002. Does hairiness matter in Harare? – Global comparisons of plant trait responses to disturbance. *New Phytol.* 154: 7-9.
- Ellner, S. 1987. Alternative plant life history strategies and coexistence in randomly varying environment. *Vegetatio* 69: 199-208.
- Enright, N.J., Marsula, R., Lamont, B.B. & Wissel, C. 1998. The ecological significance of canopy seed storage in fire-prone environments: a model for resprouting shrubs. *J. Ecol.* 86: 960-973.
- Eriksson, O. 2000. Functional roles of remnant plant populations in communities and ecosystems. *Global Ecol. Biogeogr. Lett.* 9: 443-449.

- Ferrandis, P., Herranz, J.M. & Martínez-Sánchez, J.J. 1999. Effect of fire on hard-coated Cistaceae seed banks and its influence on techniques for quantifying seed banks. *Plant Ecol.* 144: 103-114.
- Funes, G., Basconcelo, S., Díaz, S. & Cabido, M. 1999. Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. *Seed Sci. Res.* 9: 341-345.
- Garnier, E., Cordonnier, P., Guillermin, J.-L. & Sonié, L. 1997. Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. *Oecologia* 111: 490-498.
- Gignoux, J., Clobert, J. & Menaut, J.-C. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110: 576-583.
- Gill, A.M. 1981. Adaptive response of Australian vascular plant species to fires. In: Gill, A.M., Groves, R.H. & Noble, I.R. (ed.) *Fire and the Australian biota*, pp. 243-271. Australian Academy of Sciences, Canberra, AU.
- Gill, A.M. & Ingwersen, F. 1976. Growth of *Xanthorrhoea australis* R.Br. in relation to fire. *J. Appl. Ecol.* 13: 195-203.
- Goldberg, D.E. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *J. Ecol.* 79: 1013-1030.
- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169-1194.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107-145.
- Hendon, B.C. & Briske, D.D. 2002. Relative herbivory tolerance and competitive ability in two dominant: subordinate pairs of perennial grasses in a native grassland. *Plant Ecol.* 160: 43-51.
- Henery, M.L. & Westoby, M. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* 92: 479-490.
- Herranz, J.M., Ferrandis, P. & Martínez-Sánchez, J.J. 1998. Influence of heat on seed germination of seven Mediterranean *Leguminosae* species. *Plant Ecol.* 136: 95-103.
- Higgins, S.I. & Cain, M.L. 2002. Spatially realistic metapopulation models and the colonization-competition trade-off. *J. Ecol.* 90: 616-626.
- Higgins, S.I. & Richardson, D.M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *Am. Nat.* 153: 464-475.
- Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgerson, L. & Westoby, M. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *J. Ecol.* 82: 933-950.
- Jakobsson, A. & Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88: 494-502.
- Jakobsson, A. & Eriksson, O. In press. Trade-offs between dispersal and competitive ability: a comparative study of wind-dispersed seeds. *Evol. Ecol.*
- Keddy, P.A., Fraser, L.H. & Wisheu, I.C. 1998. A comparative approach to examine competitive response of 48 wetland plant species. *J. Veg. Sci.* 9: 777-786.
- Keddy, P., Gaudet, C. & Fraser, L.H. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *J. Ecol.* 88: 413-423.
- Keeley, J.E. & Fotheringham, C.J. 1997. Trace gas emissions and smoke-induced seed germination. *Science* 276: 1248-1250.
- Keeley, J.E. & Fotheringham, C.J. 1998. Smoke-induced seed germination in California chaparral. *Ecology* 79: 2320-2336.
- Keeley, J.E. & Zedler, P.H. 1998. Evolution of life histories in *Pinus*. In: Richardson, D.M. (ed.) *Ecology and biogeography of Pinus*, pp. 219-250. Cambridge University Press, Cambridge, UK.
- Lamont, B.B. & Downes, S. 1979. The longevity, flowering and fire history of the grasstrees *Xanthorrhoea preissii* and *Kingia australis*. *J. Appl. Ecol.* 16: 893-899.
- Lamont, B.B., Le Maitre, D.C., Cowling, R.M. & Enright, N.J. 1991. Canopy seed storage in woody plants. *Bot. Rev.* 57: 277-317.
- Landsberg, J., O'Connor, T. & Freudenberger, D. 1999. The impacts of livestock grazing on biodiversity in natural ecosystems. In: Jung, H.G. & Fahey, G.C. (eds.) *Nutritional ecology of herbivores*, pp. 752-777. Proc. Vth International Symposium on the Nutrition of Herbivores, American Soc. Anim. Sci., Savoy, IL, US.
- Lavorel, S. & Cramer, W. (eds.) 1999. Plant functional types and disturbance dynamics. *J. Veg. Sci.* 10: 603-730.
- Lavorel, S. & Garnier, E. 2002. Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. *Funct. Ecol.* 16: 545-556.
- Lavorel, S., Rochette, C. & Lebreton, J.-D. 1999. Functional groups for response to disturbance in Mediterranean old fields. *Oikos* 84: 480-498.
- Leishman, M.R. & Westoby, M. 1994. The role of large seed size in shaded conditions: experimental evidence. *Funct. Ecol.* 8: 205-214.
- Leishman, M.R. & Westoby, M. 1998. Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Funct. Ecol.* 12: 480-485.
- Loehle, C. 1987. Partitioning of reproductive effort in clonal plants: a benefit-cost model. *Oikos* 49: 199-208.
- Loehle, C. 2000. Strategy space and the disturbance spectrum: A life-history model for tree species coexistence. *Am. Nat.* 156: 14-33.
- McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T.D.A. 1999. Disturbance response in vegetation towards a global perspective on functional traits. *J. Veg. Sci.* 10: 621-630.
- Moles, A.T., Hodson, D.W. & Webb, C.J. 2000. Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos* 89: 541-545.
- Moloney, K.A. & Levin, S.A. 1996. The effects of disturbance architecture on landscape-level population dynamics. *Ecology* 77: 375-394.
- Moore, A.D. & Noble, I.R. 1990. An individualistic model of vegetation stand dynamics. *J. Environ. Manage.* 31: 61-81.
- Morrison, D.A. & Renwick, J.A. 2000. Effects of variation in fire intensity on regeneration of co-occurring species of small trees in the Sydney region. *Aust. J. Bot.* 48: 71-79.
- Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to

- predict successional changes in plant communities subject to recurrent disturbance. *Vegetatio* 43: 5-21.
- Olejniczak, P. 2001. Evolutionary stable allocation to vegetative and sexual reproduction in plants. *Oikos* 95: 156-160.
- Olivieri, I. 2001. The evolution of seed heteromorphism in a metapopulation: interactions between dispersal and dormancy. In: Silvertown, J. & Antonovics, J. (eds.) *Integrating ecology and evolution in a spatial context*, pp. 245-266. Blackwell, Oxford, UK.
- Palmer, M.W. 1992. The coexistence of species in fractal landscapes. *Am. Nat.* 139: 375-397.
- Pausas, J.G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. *J. Veg. Sci.* 8: 703-706.
- Pausas, J.G. 2001. Resprouting vs seeding – a Mediterranean perspective. *Oikos* 94: 193-194.
- 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.)
- Pérez-Fernández, M.A., Gómez-Gutiérrez, J.M. & Martín-Berrocó, A.M. 2001. Seed size and shape can not be used to predict persistence in soil in the Iberian Peninsula flora as they do in the British flora. *J. Medit. Ecol.* 2: 51-59.
- Pillar, V.D. 1999. How sharp are classifications? *Ecology* 80: 2508-2516.
- Plotnick, R.E. & Gardner, R.G. 2002. A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns. *Ecol. Modelling* 147: 171-187.
- Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W. & Buschena, C. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct. Ecol.* 12: 337-338.
- Roy, J. & Sonié, L. 1992. Germination and population dynamics of *Cistus* species in relation to fire. *J. Appl. Ecol.* 29: 64-655.
- Rundel, P.W., Baker, G.A., Parson, D.J. & Stohlgren, T.J. 1987. Postfire demography of resprouting and seedling establishment by *Adenostoma fasciculatum* in California chaparral. In: Tenhunen, J.D., Catarion, F.M., Lange, O.L. & Oechel, W.C. (eds.) *Plant response to stress. Functional analysis in Mediterranean ecosystems*, pp. 575-596. Springer-Verlag, Berlin, DE.
- Schippers, P., van Groenendael, J.M., Vleeshouwers, L.M. & Hunt, R. 2001. Herbaceous plant strategies in disturbed habitats. *Oikos* 95: 198-210.
- Schwilck, D.W. & Ackerly, D.D. 2001. Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94: 326-336.
- Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. 1993. Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.* 81: 465-476.
- Smith, T.M. & Huston, M. 1989. A theory of spatial and temporal dynamics of plant communities. *Vegetatio* 83: 49-69.
- Smith, T.M., Shugart, H.H. & Woodward, F.I. (eds.) 1997. *Plant functional types – their relevance to ecosystem properties and global change*. Cambridge University Press, Cambridge, UK.
- Strasser, M.J., Pausas, J.G. & Noble, I.R. 1996. Modelling the response of eucalypts to fire, Brindabella Ranges, ACT. *Aust. J. Ecol.* 21: 341-344.
- Suding, K.N. & Goldberg, D. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology* 82: 2133-2149.
- Tapias, R., Gil, L., Fuentes-Utrilla, P. & Pardos, J.A. 2001. Canopy seed bank in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *J. Ecol.* 89: 629-638.
- Thompson, K., Band, S.R. & Hodgson, G. 1993. Seed size and shape predict persistence in soil. *Funct. Ecol.* 7: 236-241.
- Thompson, K., Gaston, K.J. & Band, S.R. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *J. Ecol.* 87: 150-155.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.
- Trabaud, L. & Oustric, J. 1989. Heat requirements for seed germination of three *Cistus* species in the garrigue of southern France. *Flora* 183: 321-325.
- Turnbull, L., Rees, M. & Crawley, M.J. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.* 87: 899-912.
- Urban, D.L., O'Neill, R.V. & Shugart, H.H. 1987. Landscape ecology, a hierarchical perspective can help scientists understand spatial patterns. *Bioscience* 37: 119-127.
- Venable, D.L. & Brown, J.S. 1988. The selective interaction of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131: 361-384.
- 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.
- Weier, 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. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.
- Williams, R.J., Cook, G.D., Gill, A.M. & Moore, P.H.R. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Aust. J. Ecol.* 24: 50-59.
- Woodward, F.I. & Cramer, W. (eds.) 1996. Plant functional types and climatic changes: Introduction. *J. Veg. Sci.* 7: 305-430.
- Zavala, M.A., Espelta, J.M. & Retana, J. 2000. Constraints and trade-offs in Mediterranean plant communities: The case of holm oak-Aleppo pine forests. *Bot. Rev.* 66: 119-149.
- Zedler, P.H. 1995. Are some plants born to burn? *Trends Ecol. Evol.* 10: 393-395.

Received 7 February 2003;

Revision received 19 March 2003;

Accepted 28 March 2003.

Coordinating Editor: J. Lepš.