# PLANT FUNCTIONAL TRAITS IN RELATION TO FIRE IN CROWN-FIRE ECOSYSTEMS

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*Abstract.* Disturbance is a dominant factor in many ecosystems, and the disturbance regime is likely to change over the next decades in response to land-use changes and global warming. We assume that predictions of vegetation dynamics can be made on the basis of a set of life-history traits that characterize the response of a species to disturbance. For crown-fire ecosystems, the main plant traits related to postfire persistence are the ability to resprout (persistence of individuals) and the ability to retain a persistent seed bank (persistence of populations). In this context, we asked (1) to what extent do different life-history traits co-occur with the ability to resprout and/or the ability to retain a persistent seed bank among differing ecosystems and (2) to what extent do combinations of fire-related traits (fire syndromes) change in a fire regime gradient? We explored these questions by reviewing the literature and analyzing databases compiled from different crown-fire ecosystems (mainly eastern Australia, California, and the Mediterranean basin). The review suggests that the pattern of correlation between the two basic postfire persistent traits and other plant traits varies between continents and ecosystems. From these results we predict, for instance, that not all resprouters respond in a similar way everywhere because the associated plant traits of resprouter species vary in different places. Thus, attempts to generalize predictions on the basis of the resprouting capacity may have limited power at a global scale. An example is presented for Australian heathlands. Considering the combination of persistence at individual (resprouting) and at population (seed bank) level, the predictive power at local scale was significantly increased.

*Key words: fire-prone ecosystems; forest fires; Mediterranean-type ecosystems; plant functional types; plant traits; regeneration; resprouting seeding; wildfires.*

## INTRODUCTION

Fire regimes are expected to change over the next century in response to land-use change and global warming (e.g., Piñol et al. 1998, Flannigan et al. 2000, Houghton et al. 2001, Pausas 2004). Understanding how vegetation responds to fire is important for predicting the properties and the distributions of many ecosystems (Smith et al. 1997, Lavorel and Cramer 1999). In this paper we start with the premise that predicting vegetation change can be accomplished with the use of plant functional types (McIntyre et al. 1995, Woodward and Cramer 1996, Smith et al. 1997, Lavorel and Cramer 1999, Pausas et al. 2003*b*). This allows us to reduce the overall range of possible combinations of life-history traits and species into a set of functional groups that best represent the range of strategies present in fire-prone ecosystems. By simplifying the great diversity of plant species into a smaller number of functional types, large-scale modeling, and hence predictability, become much more feasible (Botkin et al. 1972, Noble and Slatyer 1980, Loehle 2000), although grouping species may reduced accuracy. The general goal of the present paper is to examine the utility of plant functional traits for global prediction in crown-fire ecosystems. The existence of functional types suggests the existence of certain underlying constraints or tradeoffs (e.g., vegetative vs. sexual regeneration; Carpenter and Recher 1979, Keeley 1986) that limit the possible combinations of life-history traits (Pausas and Lavorel 2003). Fire may act as an evolutionary filter against certain traits (Herrera 1992, Keddy 1992, Díaz et al. 1998), and therefore we expect different combinations of traits in systems with different fire history (Keeley and Zedler 1998).

It is often considered that predictions of vegetation dynamics in fire-prone ecosystems can be made on the

basis of the ability of a species to resprout (or the degree of resprouting) (Bellingham and Sparrow 2000, Bond and Midgley 2001). For example, resprouting has been equated to persistence or domination under high frequency of disturbance in many ecosystems (e.g., Keeley and Zedler 1978, Kruger and Bigalke 1984, Trabaud 1991). However, the role of fire as a selective agent in the evolution of resprouting is by no means certain (Wells 1969, Yih et al. 1991, Lloret et al. 1999, Bond and Midgely 2001), nor is there universal agreement that species with resprouting ability will persist and dominate only at the high frequency end of a disturbance gradient (e.g., Bellingham and Sparrow 2000).

If a species is unable to resprout after fire, the regeneration of that species will depend on a range of associated traits dealing with seed banks (i.e., obligate seeders: non-resprouter species that rely only on regeneration from seeds for postfire recovery). In general and at local scale, the persistence of seeder species on a site depends on: (1) the ability to produce seeds during the inter-fire period, (2) the seed survival during fires, and (3) the degree to which recruitment of new individuals is enhanced by the fire. Different processes related to recruitment (flowering, seed dispersal, germination) may be stimulated by some fire-related factors (e.g., heat, charred wood, and smoke; Trabaud and Oustric 1989, Keeley 1991, Roy and Sonié 1992, Thanos and Rundel 1995; see the recent review by Keeley and Fotheringham 2000). Whether all seeds germinate or a portion of the seed bank remains dormant would contribute to the fate of the population after recurrent disturbances. In some cases, species only regenerate shortly after fire (and not during the inter-fire period), as in species in which seed release is strongly fire dependent (Lamont et al. 1991).

The inclusion of the seed bank, along with resprouting, in schemes for predicting vegetation dynamics in relation to fire is well accepted (e.g., Keeley and Zedler 1978, Noble and Slayter 1980, Gill 1981, Rowe 1983, Bond and van Wilgen 1996). Thus, it is predicted that different combinations (or different degrees) of these main traits (i.e., different plant strategies or syndromes) can lead to differential success under different fire regimes. Seed bank and resprouting characteristics co-occur with other traits that are less directly related to postfire persistence but are relevant for longer term dynamics (e.g., growth, dispersal). Different co-occurrence of traits may have important implications for long-term dynamics and thus determine the success of the different postfire syndromes under different fire regimes (Pausas 2001). The ability of these general traits to predict vegetation dynamics in different ecosystems remains to be tested. In this context, we address the following questions:

(1) To what extent do different life-history traits relevant to vegetation dynamics co-occur with the ability to resprout and/or the ability to retain a persistent seed bank among differing ecosystems? We explored this

question by analyzing trait databases from different ecosystems as well as from bibliographic references.

(2) To what extent do combinations of fire-related traits change in a fire regime gradient? We addressed this question using information from Australian heathlands, which span a range of localities and environments for which a reasonable range of data were available.

### APPROACH: POSTFIRE PERSISTERS

Our analysis is restricted to traits related to the effect of a single fire event or the effects of recurrent fires (fire frequency); traits related to fire season, intensity, and extent are not considered. Because adaptive options vary depending on the disturbance regime, our analysis is also restricted to stand-replacement (crown) fires. Our emphasis is on woody species. The persistence of trees in areas with a surface fire regime (e.g., western USA forests, savanna ecosystems) is based on a very different set of plant traits (e.g., bark thickness, height, self-pruning) than the persistence of plants that are typically fully scorched by fire (e.g., resprouting, seed bank) (Zedler 1995, Gignoux et al. 1997, Pausas 1997, Keeley and Zedler 1998, Schwilk and Ackerly 2001).

Based on the postfire persistence of individual plants and populations, we adopted the following approach and nomenclature.

#### Resprouters (R+)

These are species in which individuals are able to resprout after 100% scorch by fire (Gill 1981) from any plant structure (e.g., rhizomes, root buds, stem buds, lignotuber, etc.). Resprouters persist at individual level as a vegetative form.

#### Non-resprouters (R−)

Non-resprouters are species without the capacity to resprout after 100% scorch by fire (Gill 1981). Individuals are killed and do not persist after a fire.

#### Propagule-persisters (P+)

Propagule-persisters are species in which the population locally persists in propagule form (seed, fruit) after 100% scorch by fire. Seeds resist (or are protected from) fire; they often have a persistent seed bank, and the recruitment of new individuals is often enhanced by fire (e.g., by breaking seed dormancy, by stimulating seed release). Species that have exclusive pyrogenic flowering are also considered in this category because this strategy is functionally similar to a canopy seed bank (i.e., they lack persistent seeds, but establish transient seed banks after fire through flowering). Thus, there are three types of propagule-persisters: species with soil seed bank, serotinous species (i.e., with canopy seed bank), and species with pyrogenic flowering.

#### Propagule-non-persisters (P−)

These are species in which the propagule (seed, fruit) does not persist after fire. After fire, propagules may
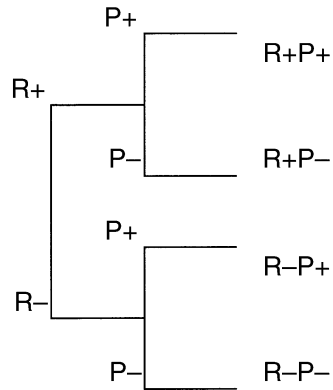
FIG. 1. Hierarchical classification of the four basic fire-response functional groups (the hierarchical RP persistence scheme). Abbreviations are: R+, resprouters; R−, non-resprouters; P+ propagule persisters; and P−, propagule-non-persisters. The two dichotomies are: first, whether the individuals persist after fire (by resprouting) and, second, whether the species population persists after fire (as propagules). The four groups are: R+P+ (facultative species), R+P− (obligate resprouters; seeds do not resist fire, and recruitment is during inter-fire period), R−P+ (obligate seeders; these only persist at species level by seeds; thus they are specialized in postfire recruitment), and R−P− (species that do not persist after fire).

only occur by dispersal from the neighborhood (off-site establishment).

From the combination of these parameters, we obtain four basic fire-response groups (Bond and van Wilgen 1996, Pausas 1999a) that can be hierarchically classified (the hierarchical RP persistence scheme, Fig. 1). Pausas (1999a) provides some initial hypotheses on trait co-occurrence and population dynamics for the four types, and Pausas and Lavorel (2003) expand this approach to other scales and disturbances. The first dichotomy refers to the individual level (whether the individuals persist after fire), and the second to the population level (whether the population persists after fire). This simple classification does not consider other important traits such as those related to dispersal or to the competitive ability (Pausas and Lavorel 2003). Furthermore, such a binary classification is an obvious simplification of a wider range of possibilities. That is, embedded within this scheme is substantial variation with respect to resprouting capacity and propagule persistence (e.g., variations within and between species in propagule longevity). Also, fire intensities are not considered, and they may vary greatly (within and between fires) and can determine the success or failure of resprouting (e.g., Morrison and Renwick 2000, Pausas et al. 2003a) and the degree of fire-stimulated germination and seed mortality (e.g., Moreno and Oechel 1994, Bradstock and Auld 1995).

Although all four plant types appear in most fire-prone ecosystems, the relative proportions of each type may differ between ecosystems (Table 1). The proportion of resprouters and non-resprouters (first-level dichotomy, Fig. 1) in Australian heatlands is relatively

even compared with other fire-prone ecosystems (Table 1). However, postfire obligate resprouters (R+P−) are almost absent in the Australian heathlands (although they may appear in some parts of the landscape, e.g., rainforest gullies). Most resprouters in the Mediterranean basin are R+P− (i.e., R+P+ are rare), while in California, resprouters are evenly segregated among the two types (R+P+, R+P−), at least for the shrubs. R−P− are rare in most fire-prone shrublands.

OBJECTIVE 1: TRAIT CO-OCCURRENCE: MULTIPLE
TRAITS IN FIRE-RESPONSE GROUPS

We developed six hypotheses on the co-occurrence of traits related to plant dynamics and tested them using several data sets (Table 2 and Appendix A) and by reviewing the literature. Hypotheses are tested for the two well-known fire syndromes (R+ vs. R−), and, where data are available, for the four syndromes proposed above (R × P, Fig. 1). Resprouting and seed persistence are traits related to the postfire persistence at individual and population level, and the hypotheses tested refer to the relation of these fire traits with other traits relevant for the dynamics at population, community, and landscape scale (e.g., growth, mature age, height, longevity, stress tolerance, dispersal). Although it is beyond the scope of this paper to rigorously test the phylogenic effect, when possible, we consider the taxonomic relatedness (as a surrogate of phylogeny) together with the traits tested. The taxonomic level tested depends on the data set (see Appendix A). Statistical analysis for quantitative traits is based on ANOVA with two factors, postfire-response type (R or R × P) and taxonomic level; for the BANKSIA data set, intra-genus taxonomic level was evaluated with a nested design (subgenera, section nested in subgenera, and series nested in section). For qualitative traits the chi-square test was used.

*Hypothesis 1: Juveniles of non-resprouters allocate resources to shoot growth, whereas juveniles of resprouters must also allocate resources to storage tissues; consequently, juveniles of resprouter species are slower-growing than those of non-resprouter species*

Different allocation patterns have been found between resprouting and non-resprouting *Erica* species in the Cape region (Bell and Ojeda 1999, Verdaguer and Ojeda 2002), and between resprouting and non-resprouting populations of *Ceanothus* in California (Schwilk 2002); in all cases, seedlings of resprouters allocate more starch to roots than seedlings of non-resprouters. Epacridaceae and Restionaceae species also showed higher allocation to roots (e.g., root/shoot and starch concentration) for resprouters than for seeders (Pate et al. 1991, Bell and Pate 1996, Bell et al. 1996). Data from heathlands in southwestern Australia show that juveniles of resprouter species grow significantly slower than those of non-resprouter species

TABLE 1. Percentage of species in each of the two (R+ vs. R−) and four (R × P) fire response functional types (first and second level dichotomy in Fig. 1) in different areas (see Appendix A for details on the data sets).

| Database | Source† | $n$ | First level (%) | | Second level (R × P) (%) | | | | $P$ |
|---|---|---|---|---|---|---|---|---|---|
| | | | R+ | R− | R+P+ | R+P− | R−P+ | R−P− | |
| Australia | | | | | | | | | |
| OZSE (all species) | 1 | 1173 | 52 | 48 | 44 | 8 | 45 | 3 | **** |
| OZSE (woody) | 1 | 864 | 47 | 53 | 43 | 4 | 51 | 2 | *** |
| Mediterranean basin | | | | | | | | | |
| EIBER (woody) | 2 | 67 | 78 | 22 | 16 | 62 | 19 | 3 | *** |
| GARRAF (woody) | 3 | 60 | 65 | 35 | 13 | 52 | 33 | 2 | **** |
| California | | | | | | | | | |
| CALIF (woody) | 4 | 86 | 86 | 14 | 35 | 51 | 12 | 2 | ** |
| CALIF (shrubs) | 4 | 72 | 89 | 11 | 40 | 49 | 10 | 1 | ns |
| CALIF (trees) | 4 | 14 | 71 | 28 | 7 | 64 | 21 | 7 | * |
| South Africa | | | | | | | | | |
| Swartboskloof (all species) | 5 | 210 | 79 | 21 | 64 | 15 | 13 | 7 | * |
| Swartboskloof (woody) | 5 | 54 | 59 | 41 | 52 | 7 | 22 | 19 | ** |

*Notes:* Abbreviations are: CALIF, trees/shrubs of the chaparral, sedge scrub, and woodlands of California, USA; EIBER, common species from the eastern Iberian Peninsula, including southern Mediterranean France; OZSE, southeastern Australian species; and GARRAF, Garraf National Park, Spain. Significance of the $\chi^2$ test for the R × P contingence table (test of independence) is also shown (ns, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$).

† Data sources (see Appendix A for more details): (1) Bradstock and Kenny (2003); (2) J. G. Pausas, L. Trabaud, and F. Lloret (*unpublished data*); (3) F. Lloret (*unpublished data*); (4) Californian crown-fire ecosystems compiled by J. E. Keeley (*unpublished data*); and (5) van Wilgen and Forsyth (1992).

(JUVWA data set, Table 3; the taxonomy level did not have a significant effect), and allocate higher biomass to roots than do seeders (Pate et al. 1990). A congeneric contrast between a resprouter (R+P+) and a non-resprouter (R−P+) in legumes of southwestern Australia also showed lower growth in the juveniles (<6 years old) of the resprouter species (Hansen et al. 1991). Yates et al. (2003) followed postfire regeneration for 12 years in Western Australia and showed that seedlings of resprouters grow slower than seedlings of non-resprouters, but resprouts grow faster than any seedling (Fig. 2). In conclusion, although few growth rate data are available, there is evidence in support of this hypothesis.

*Hypothesis 2: Resprouters are slower maturing and longer lived species than non-resprouters*

Based on Loehle's (1988) analysis, Clark (1991) suggested that, assuming the same fire recurrence and inter-fire mortality, resprouters should mature later than non-resprouters. The available data for Proteaceae shrub species in the Sydney region suggest that resprouters (R+P+) need more time (ca. double) to start producing flowers than non-resprouters (Tables 3 and 4). A similar pattern was found for a range of Australian species (OZSE, Table 3), and for shrubs in the Eastern Iberian Peninsula (Table 3). A review for Epacridaceae in southwestern Australia (Bell and Pate 1996) suggested that non-resprouters flowered at three years of age or earlier, whereas some resprouters first flowered at seven years of age, and most were not yet flowering after 10 years of study. Similar results were observed in the African fynbos (Le Maitre 1992). Data from Californian species do not show any clear tendency between age to maturity and fire response, and a strong taxonomic relation is observed (Tables 3 and 4). However, intraspecies comparison (*Ceanothus tomentosus*) shows that three-year-old seedlings of non-resprouting populations flowered more than those of resprouting populations (Schwilk 2002).

R+ and R− comparisons of the first reproduction from seedlings may be relevant, for instance, in the

TABLE 2. Databases compiled for this review.

| Abbreviation | Life forms | No. species | Study area | Vegetation type |
|---|---|---|---|---|
| BANKSIA | shrubs and trees | 77 | Australia | *Banksia* species, mainly in heathlands |
| CALIF | shrubs and trees | 91 | California | chaparral, sage scrub, and woodlands under crown-fire |
| EIBER | shrubs and trees | 67 | Eastern Iberian Peninsula | Mediterranean shrublands and woodlands |
| EUCS | trees | 62 | Australia | *Eucalyptus* species |
| JUVWA | shrubs (juvenile) | 32 | Western Australia | mainly in heathlands |
| OZSE | shrubs and trees | 1338 | SE Australia | heathlands and sclerophyllus forests |
| PROSYD | shrubs | 134 | Sydney region, Australia | Proteacae species, mainly in heathlands |

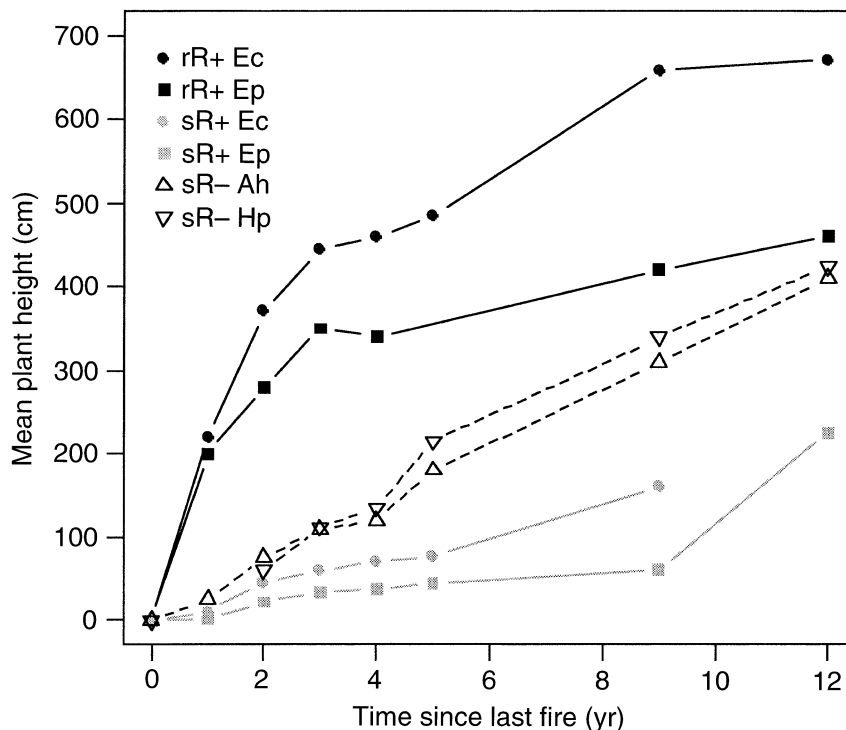*Note:* See Appendix A for more details.

FIG. 2. Postfire height growth of resprouts (rR+, solid symbols), seedlings of the same resprouter species (sR+, gray symbols), and seedlings of non-resprouter species (sR−, open symbols), in Western Australia. Species are *Eucalyptus caesia* ssp. *magna* (Ec), *Eucalyptus petraea* (Ep), *Allocasuarina huegeliana* (Ah), and *Hakea petiolaris* ssp. *trichophylla* (Hp). The figure is elaborated from data in Yate et al. (2003).

restoration context, where seeds or seedlings of both R+ and R− may be considered for plantations in fire-degraded ecosystems (Pausas et al., *in press*). However, in natural conditions, R+P− do not recruit seedlings immediately after fire, and thus, from the dynamic point of view, it may be relevant to compare the reproductive age of non-resprouter seedlings with the reproductive age of resprouts. In this sense, the time in which resprouting species produce flowers after a fire (mean = 1.9 years for OZSE shrubs) may be similar or even shorter than the values for non-resprouters (mean = 3.6 years for OZSE, significantly different at $P < 0.02$; Table 3).

Data on lifespan for woody species is difficult to obtain, especially for resprouter species. Sydney Proteaceae resprouters have a longer lifespan than species unable to resprout (Tables 3 and 4). Furthermore, some resprouter species have a very long and indefinite lifespan that was not considered in the statistical analysis, and so, the mean life-span of resprouters is underestimated.

In conclusion, most data provide evidence for this hypothesis. These results together with the previous hypothesis suggest that juveniles of non-resprouter species grow faster and flower earlier than juveniles of resprouters (because the latter must allocate resources to storage tissues); however, resprouts (from estab-

lished plants) may grow the fastest and flower the earliest (Figs. 2 and 3).

*Hypothesis 3: Resprouters are shorter in height than non-resprouters; resprouters form communities with shorter average height than non-resprouters*

This hypothesis is based on the assumption that resprouters allocate more resources to basal and stem buds whereas non-resprouters maximize vertical growth.

Looking at maximum height values for individual species, Proteaceae shrubs from the Sydney region (PROSYD database) show that resprouters are shorter than non-resprouters (Table 3), although taxonomic effects (i.e., the differences among genus) were also significant (Table 3, Fig. 3a). Proteaceae shrubs within the genus *Banksia* from across Australia do not show a significant difference in height. However, there is a clear tendency for serotinous *Banksia* species to be shorter than non-serotinous species (see hypothesis 4). Eucalypt trees in SE Australia (EUCS) show a significant tendency for non-resprouters to be taller than resprouters (Table 3), although the number of non-resprouter eucalypts in the data set is low and there are significant differences between the two main subgenera (see also Noble 1989 and Austin et al. 1996 for *Eucalyptus* subgenus differences).

TABLE 3. Mean values of various plant traits for resprouters (R+) and non-resprouters (R−) and the significance of two-way ANOVA (R+ vs. R−, and taxonomic relatedness [Tax.]).

| Trait | R+ | | | R− | | | ANOVA | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | $n$ | Mean | SD | $n$ | R | Tax. | R × Tax. |
| Growth rate (gm/yr) | | | | | | | | | |
| JUVWA | 1.5 | 1.3 | 14 | 4.5 | 4.3 | 18 | * | ns | ns |
| Plant height (m) | | | | | | | | | |
| BANKSIA | 6.0 | 5.5 | 29 | 4.3 | 4.0 | 42 | ns | ns | ns |
| CALIF | 6.4 | 9.1 | 74 | 11.5 | 13.1 | 12 | *† | **** | * |
| CALIF trees | 23.3 | 15.5 | 10 | 26.3 | 3.8 | 4 | ns | ···‡ | ··· |
| CALIF shrubs | 3.7 | 3.1 | 64 | 4.1 | 1.8 | 8 | ns | *** | ns |
| EIBER | 8.0 | 7.5 | 34 | 10.5 | 12.7 | 9 | ns | ** | ns |
| EUCS | 22.4 | 12.0 | 55 | 42.1 | 12.2 | 7 | ** | ** | ns |
| PROSYD | 2.5 | 2.0 | 31 | 3.4 | 2.7 | 54 | *** | **** | ns |
| Age at maturity (yr) | | | | | | | | | |
| CALIF | 8.0 | 5.0 | 74 | 10.6 | 2.1 | 12 | *† | **** | ns |
| CALIF trees | 14.1 | 7.8 | 10 | 11.3 | 2.5 | 4 | ns | ···‡ | ··· |
| CALIF shrubs | 7 | 3.7 | 64 | 10 | 2.0 | 8 | * | **** | ns |
| EIBER | 9.5 | 4.1 | 11 | 6.2 | 4.1 | 7 | ns | ns | ns |
| EIBER shrubs | 9.1 | 3.6 | 8 | 3.8 | 0.3 | 5 | * | ns | ns |
| OZSE§ | 5.8 | 6.2 | 121 | 3.8 | 2.1 | 190 | ****† | **** | ns |
| OZSE shrubs | 5.4 | 6.1 | 103 | 3.6 | 1.9 | 160 | **** | **** | ns |
| OZSE trees | 10.1 | 5.6 | 8 | 6.1 | 3.7 | 14 | * | ns | ns |
| PROSYD | 10.2 | 8.1 | 5 | 5.1 | 1.8 | 16 | * | ns | ns |
| Plant longevity (yr) | | | | | | | | | |
| OZSE | 86.2 | 73.2 | 231 | 27.9 | 34.4 | 1174 | ****† | **** | ns |
| OZSE shrubs | 49.1 | 39.6 | 121 | 21.9 | 14.6 | 141 | **** | **** | ns |
| OZSE trees | 134.2 | 85 | 90 | 63.6 | 81.7 | 22 | *** | ns | ns |
| PROSYD | 59.09 | 22.4 | 11 | 25.38 | 23.4 | 13 | ** | ns | ns |
| Diaspore mass (mg) | | | | | | | | | |
| CALIF | 1604.2 | 4392.7 | 74 | 1049.9 | 2845.3 | 12 | ns† | **** | ns |
| CALIF trees | 7235.0 | 10 385 | 10 | 92.1 | 160.9 | 4 | ** | ···‡ | ··· |
| CALIF shrubs | 724.6 | 1064.0 | 64 | 1528.7 | 3453.2 | 8 | ns | **** | ··· |
| EIBER | 1058.6 | 1736.4 | 24 | 121.7 | 263.4 | 6 | ** | * | ns |
| OZSE | 259.8 | 547.2 | 24 | 154.5 | 373.0 | 23 | ns | ns | ns |
| PROSYD | 233.1 | 542.9 | 14 | 123.4 | 313.2 | 17 | ns | **** | ns |

*Notes:* See Table 2 for abbreviations. Only woody species are considered. Ellipses (···) indicate that there were not enough data for testing.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; ns, $P > 0.05$.
† The factor life form (shrub/tree) was significant ($P < 0.001$).
‡ All R− trees are conifers.
§ Age at first flowering.

Californian plants (CALIF) and Eastern Iberian plants (EIBER) did not show height differences with regeneration strategy; and height differences are mainly related to the taxonomy. By looking at some closely related taxa, the pattern becomes more clear. For example: *Arctostaphylos peninsularis* has two related subspecies in California (Keeley et al. 1992), the short and burl-forming (strong resprouter; ssp. *peninsularis*) and the taller non-resprouting (ssp. *jaurenzenss*). In South African fynbos, congeneric comparisons also suggested that in many cases (genera *Widdringtonia*, *Podocarpus*, *Faurea*, *Olea*, and *Euphorbia*), resprouters are shorter than non-resprouters (Midgley 1996).

At the community level, an analysis of the data from Kruger et al. (1997) in Cape forests (South Africa) showed that the number and proportion of non-resprouter species increase with forest canopy height, while the total number of species is not related to canopy height (Fig. 3b). Thus, these data suggest that, in the Cape forest, resprouters form shorter communities and non-resprouters taller ones, although it would be interesting to study the pattern of serotiny in this data set and the possible interaction with the moisture gradient.

In conclusion, species maximum height values are not always higher for seeders than for resprouters, and some phylogenic effect is observed for this trait. The patterns are clearer when part of the variance is explained by taxonomic level or when congeneric comparisons are performed. Information from the community level approach (i.e., using site data rather than maximum values from flora) in systems with diverse phylogeny seems to support the hypothesis (Cape forest), although some confounding effect with serotinous taxa (see hypothesis 4) needs to be considered.

*Hypothesis 4: Serotiny is associated with low-growing habitat*

Cowling and Lamont (1985) suggested that serotiny is associated with short communities in Western Aus-

TABLE 4. Mean values of various plant traits for the four functional types (Fig. 1) and two-way ANOVA (R+ vs. R−, and taxonomic relatedness [Tax.]).

| | Groups | | | | ANOVA | | |
|---|---|---|---|---|---|---|---|
| Trait | R+P+ | R+P− | R−P+ | R−P− | RP | Tax. | RP × Tax |
| **Plant height (m)** | | | | | | | |
| CALIF | 3.7 | 8.2 | 9.6 | 21.0 | **** | **** | **** |
|   CALIF trees | 6 | 25.2 | 21.7 | 40 | ⋯ | ⋯ | ⋯ |
|   CALIF shrubs | 3.59 | 3.82 | 4.43 | 2 | ns | *** | ns |
| PROSYD | 2.7 | 1.3 | 3.1 | ⋯ | ns | ns | ns |
| **Age at maturity (yr)** | | | | | | | |
| CALIF | 7.1 | 8.5 | 10.5 | 11.5 | * | **** | * |
|   CALIF trees | 8 | 14.8 | 10.0 | 15.0 | ⋯ | ⋯† | ⋯ |
|   CALIF shrubs | 7.1 | 6.9 | 10.7 | 8 | ns | **** | ns |
| EIBER | 5.2 | 11.2 | 6.2 | ⋯ | * | ns | ns |
| EIBER shrubs | 5.2 | 11.5 | 3.8 | ⋯ | *** | ** | * |
| OZSE | 6.9 | 4.95 | 3.9 | 2 | **** | **** | ns |
|   OZSE shrubs | 6.44 | 4.94 | 3.8 | 2 | **** | **** | ns |
|   OZSE trees | 14.3 | 5 | 5.2 | ⋯ | ** | ns | ns |
| PROSYD | 11.5 | ⋯ | 5.3 | ⋯ | * | ns | ⋯ |
| **Plant longevity (yr)** | | | | | | | |
| OZSE | 80.7 | 78.9 | 26.6 | 20.5 | **** | **** | ns |
|   OZSE shrubs | 52.9 | 52.1 | 22.75 | 20.5 | **** | **** | ns |
|   OZSE trees | 140.8 | 115.0 | 56.5 | ⋯ | * | * | * |
| PROSYD | 59.0 | 60.0 | 26.8 | ⋯ | * | ns | ns |
| **Diaspore mass (mg)** | | | | | | | |
| CALIF (mg, log) | 520.1 | 2343.3 | 1208.3 | 257.6 | ns | **** | ns |
|   CALIF trees | 28.6 | 8035.7 | 11.3 | 33.3 | ⋯ | ⋯† | ⋯ |
|   CALIF shrubs | 537.0 | 879.6 | 1721.2 | 181.8 | ns | **** | ns |
| EIBER | 398.4 | 1278.7 | 14.5 | 657.7 | **** | **** | **** |
| OZSE | 288 | ⋯ | 176.5 | 0.29 | ns | ns | ns |
| PROSYD | 226 | ⋯ | 138 | ⋯ | ns | **** | ns |

*Notes:* See Table 2 for abbreviations. Only woody species are considered. Ellipses ($\cdots$) indicate that there were not enough data for testing.

\* $P < 0.05$; \*\* $P < 0.01$; \*\*\* $P < 0.001$; \*\*\*\* $P < 0.0001$; ns, $P < 0.05$.

† All R− trees are conifers.

tralia because the cones of tall species rarely come into contact with flames, and thus we should not expect high degrees of serotiny in these tall species. On the other hand, limited height increases the probability that ground fires will carry up into the canopies resulting in recurrent intense canopy fires, in which serotiny may be an evolutionary advantage. However, many short communities grow in dry areas (they are short due the limited water availability) and have higher fire recurrence than taller communities in moister conditions. Thus, the relation between serotiny and height could be mediated by fire recurrence, because serotiny is disfavoured at low fire recurrence (Enright et al. 1998*a*, *b*).

The analysis of Sydney Proeteaceae does not support this hypothesis and both height and serotiny show to be strongly associated with taxonomy (genus, $P < 0.00001$); that is, serotiny is found in most *Banksia*, *Hakea*, and *Petrophile* of the Sydney area, and absent in *Conospermum*, *Greville*, *Lomatia*, and *Persoonia*. The genus *Banksia* has a range of both serotinous and non-serotinous species in Australia, permitting a deeper analysis of this genus for the whole continent. In this case, height is strongly associated with serotiny (and not with the taxonomy within the genus), with the serotinous species being significantly ($P < 0.0001$)

shorter (mean = 3.4 m) than the non-serotinous species (mean = 13.9 m). Cowling and Lamont (1985) also found that the degree of serotiny (as a proportion of folicles remaining closed since the last fire) in three *Banksia* species increased with decreasing plant height and water availability. Serotinous conifers of California (CALIF) are also significantly shorter (mean = 28.8 m) than non-serotinous ones (mean = 55.7 m).

Our results suggest that in many cases the hypothesis is not supported because of the strong taxonomic (phylogenetic) effects. When a specific taxonomic level is studied (*Banksia*, conifers), the pattern becomes apparent.

*Hypothesis 5: Resprouters have bigger and heavier dispersal units, are mostly dispersed by vertebrates, and produce fewer seeds per season, in comparison with non-resprouters, which have the opposite attributes (small, dry, wind-dispersed seeds)*

Herrera (1992) detected two plant syndromes in the Mediterranean basin: (1) sclerophyllous species, with evergreen leaves, small, unisexual greenish or brownish flowers with a reduced perianth, and large seeds dispersed by vertebrates; and (2) non-sclerophyllous species with the complementary traits. Verdú (2000)
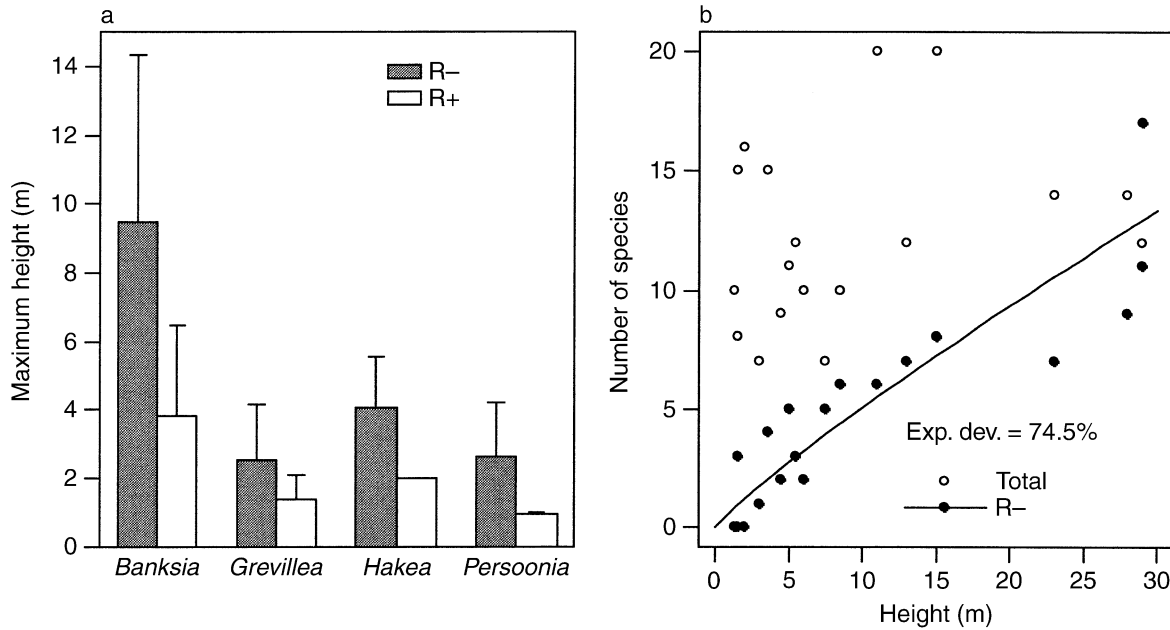
FIG. 3. Plant height and resprouting capacity. (a) Congeneric comparison of maximum height values for Proteaceae species of the Sydney area (PROSYD). (b) Relationship between number of species and canopy height in Cape forests (elaborated from data in Kruger et al. 1997). Total species (open circles, no significant fit) and non-resprouters (solid circles and fitted line). The line depicts the GLM fitted values (assuming the average number of plots, i.e., 3.4, in the data set); percentage of the explained deviance (Exp. dev.) is also shown (total, $F = 2.56$, $P = 0.13$; R−, $F = 54.73$, $P < 0.0001$).

noted that the first syndrome is significantly related to resprouter species, and the second to non-resprouters. The link between Herrera's syndromes and the resprouting pattern may be due to the fact that vertebrate-dispersed seeds may not survive high temperatures (fleshy coat as opposed to hard-coated seeds; Keeley 1991); vertebrate-dispersed plants living in a fire-prone environment should regenerate vegetatively to maintain the populations.

*Dispersal mode.*—The EIBER data support the relation between dispersal system (vertebrates vs. others) and regeneration pattern (R+ vs. R−) ($\chi^2 = 8.55$, df $= 1$, $P = 0.02$) for a Euro-Mediterranean ecosystem; 60% of the species were vertebrate-dispersed resprouters, and only 9% of the non-resprouters had vertebrates as a dispersal vector; 52% of the total species were vertebrate-dispersed and R+P−. In a similar way, diaspore type (fleshy vs. dry) and resprouting pattern were not independent ($\chi^2 = 13.40$, df $= 1$, $P = 0.0003$, $n = 60$), i.e., most resprouters had fleshy fruits. Typical examples of resprouting species that do not have fleshy or vertebrate-dispersed seeds are some *Erica* species (e.g., Lloret and López-Soria 1993).

Similar results to those in the Mediterranean basin are found for Californian plants (CALIF). Both the dispersal mode (vertebrates, wind, others) and the diaspore type (fleshy vs. dry) are related to regeneration pattern (R+ vs. R−) (diaspore mode: $\chi^2 = 9.084$, df $= 2$, $P = 0.011$, $n = 95$; diaspore type: $\chi^2 = 6.333$, df $= 1$, $P = 0.012$) in the way that most resprouters

are vertebrate-dispersed and produce fleshy fruits. Examples of resprouting species that are vertebrate-dispersed but do not have fleshy fruits are the oaks (*Quercus*) in both California and the Mediterranean basin.

There is no significant relation between diaspore type (fleshy vs. dry) and resprouting pattern for Sydney Proteaceae species (PROSYD, $\chi^2 = 1.92$, df $= 1$, $P = 0.17$, $n = 113$). For example (from PROSYD), of the species of the *Persoonia* genus with fleshy fruits dispersed by vertebrates, 26% resprout, while 74% do not resprout. Most other Proteaceae species do not have fleshy fruits, but rather dry fruits or seeds (often winged) dispersed by gravity, ants or wind. *Banksia* species have winged dry seeds and about 42% of the *Banksia* species do resprout. For Australian species (PROSYD, BANKSIA), diaspore type and size are more related to the taxonomy group than to the regeneration pattern. These results agree with those from French and Westoby (1996) in similar Australian communities, that is, many vertebrate-dispersed species are capable of vegetative regeneration, but there is not a significant dependence between the two factors.

*Diaspore mass.*—In most of the data sets considered, the mean values of diaspore mass were higher in R+ than in R−; however, due to the large variation, the means were not statistically significant in most cases (Table 3). Part of the variation in diaspore mass can be explained by the taxonomic relatedness. For EIBER and CALIF trees, diaspore mass was significantly higher for R+ (and especially for R+P−) than for the other
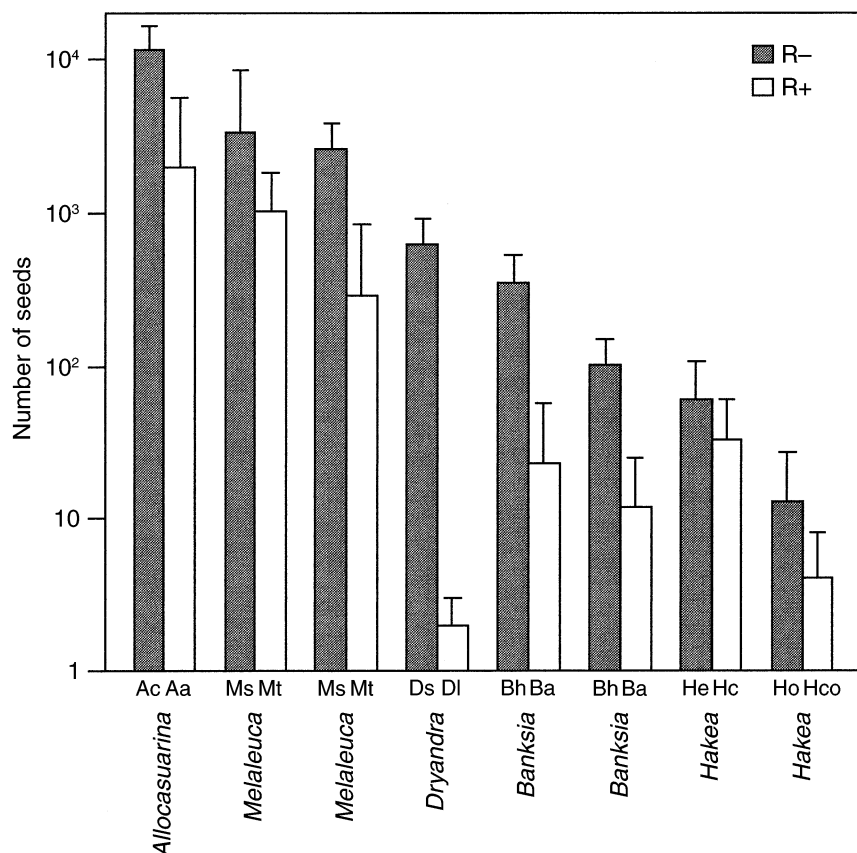
Fig. 4. Stored seed per plant (mean + 1 SD) in different congeneric serotinous species in western Australia (Bellairis and Bell 1990). Species are (from left to right): *Allocasuarina campestris* (Ac), *A. acutivalvis* (Aa), *Melaleuca scabra* (Ms), *M. tuberculata* (Mt), *M. scabra* (Ms), *M. tuberculata* (Mt), *Dryandra sessilis* (Ds), *D. lindleyana* (Dl), *Banksia hookeriana* (Bh), *B. attenuata* (Ba), *B. hookeriana* (Bh), *B. attenuata* (Ba), *Hakea erinacea* (He), *H. cristata* (Hc), *H. oblique* (Ho), and *H. corymbosa* (Hco). When the same species name is used twice, it refers to different samplings.

types. Neither Australian data sets (PROSYD and OZSE) shows a significant trend (Tables 3 and 4), although within *Hakea* species, seeds are significantly bigger in resprouter species than in non-resprouters (Lamont and Groom 1998).

*Seed production.*—Congener contrasts among resprouters and non-resprouters in Australia (Fig. 4) have shown that resprouters typically produce fewer seeds and seedlings after fire (during inter-fire periods) than non-resprouters in serotinous species (Enright and Lamont 1989, Bellaris and Bell 1990, Lamont and Groom 1998, Lamont et al. 1998, Groom et al. 2001). Seed production varies largely in relation to the age and size of the plants and to the time since fire (e.g., Bradstock and O'Connell 1988, Bradstock 1990). The number of viable seeds in different serotinous *Banksia* species 14–16 years after the last fire shows higher values in non-resprouter species than in resprouter ones (Lamont and Groom 1998). However, this trend is not always true (Lamont 1985).

Keeley (1977) also showed no clear tendency in seed production among resprouters and non-resprouters for P+ non-serotinous species in the Californian chaparral

(i.e., *Ceanothus* resprouters produced fewer seeds than the congeneric non-resprouters, but the opposite was found for *Arctostaphylos*). Some other studies show that resprouters recruit poorly after fire in South Africa (Le Maitre 1992, Le Maitre and Midgley 1992) and in tropical forests (Bellingham et al. 1994).

In conclusion, this hypothesis cannot be generalized. It seems to apply in the Mediterranean basin and California when comparing R+P− vs. R−P+ (obligate resprouters vs. obligate seeders), but it may not be true when comparing R+P+ vs. R−P+ (facultative vs. obligate seeders) in Australia. In the Mediterranean basin, the first set (R+P− and R−P+) is the most abundant, while in the Australian heathlands, the second one (R+P+ and R−P+) is dominant. In many cases, these traits show a strong taxonomic (phylogenetic) effect (e.g., Jordano 1995).

*Hypothesis 6: Non-resprouters tolerate water stress better than resprouters*

Specht (1981) suggested that in Australian shrublands the abundance of non-resprouters was inversely proportional to precipitation, while the abundance of

resprouters was directly related to this parameter. At a similar geographical scale, Ojeda (1998) suggested that the distribution of resprouters and non-resprouters of *Erica* species in the Cape Floristic Region was related to summer water availability. This trend of increasing resprouters along a precipitation gradient could be more related to different fire recurrences along the precipitation gradient than to the direct effect of water availability. Thus, more in-depth studies are needed to segregate the effect of water availability from the effect of fire regime.

At the local scale, Keeley (1986) and Meentemeyer et al. (2001) found more non-resprouters in the drier parts of the landscape (equator-facing slopes, shallow soils) and more resprouters on the moister sites (pole-facing slopes, deep or fissured soils) in the Californian chaparral. Similar observations have been made for eastern Australia (Keith 1991, Benwell 1998, Clarke and Knox 2002) and for the Mediterranean basin (Pausas et al. 1999). All these observations suggest that ecophysiological and/or morphological parameters affecting growth could differ between resprouters and non-resprouters (Miller 1981, Keeley 1986).

At the physiological level, in the Mediterranean basin, resprouters (e.g., *Quercus*, *Pistacea lentiscus*) are often considered more drought-tolerant species because they show later stomata closure and higher carbon assimilation at low water potentials than non-resprouter species such as *Pinus* and *Cistus*, which are considered drought avoiders (Damesin and Rambal 1995, Schwanz et al. 1996, Grammatikopoulos 1999, Martínez-Ferri et al. 2000, Calamassi et al. 2001, Vilagrosa et al. 2003). However, Californian non-resprouter species have greater resistance to water stress-induced embolism and later stomata closure than resprouters (Davis et al. 1998, 1999), suggesting that non-resprouters are more drought-tolerant than resprouters. In this ecosystem, vulnerability to xylem embolism was positively related to postfire seedling mortality and resprouting success (Davis et al. 1998). Smith et al. (1992) did not find a consistent pattern between regeneration strategy and physiological parameters in the South African fynbos. More congeneric comparisons, and in different ecosystems, of physiological traits between resprouters and non-resprouters are needed before we can generalize the link between physiological mechanisms and regeneration patterns.

At the morphological level, many resprouters avoid higher water stress with a higher root/shoot ratio or a deeper (extended) root system (Pate et al. 1990, Bell et al. 1996, Keeley 1998, Davis et al. 1999), while non-resprouters are exposed to higher water stress. Leaf size is also a morphological trait often associated with persistence in dry conditions; in Australia, *Banksia* leaves are significantly smaller in non-resprouting than in resprouting species (BANKSIA data set, $F_{1,72} = 5.4$, $P = 0.02$), and the significance increases when considering the intra-genus taxonomy (nested ANOVA with

resprouting [$P < 0.001$], subgenera [not significant], section nested in subgenera [$P < 0.0001$], and series nested in section [$P < 0.001$]).

Species may coexist in a dry environment by having different strategies to cope with low water availability (e.g., Lo Gullo and Salleo 1988), i.e., physiological drought-tolerance and drought-avoidance mechanisms (Levitt 1980) and different morphological drought-avoidance traits (e.g., extended or deep root system, small and hairy or rolling leaves). For example, Davis and collaborators (Davis et al. 1998, 1999) suggested that the coexistence of resprouters and non-resprouters in southern California is due to the deeper root system of resprouters (e.g., >13 m for *Rhus laurina*) and to the higher xylem resistance to cavitation and embolism of non-resprouters (e.g., *Ceanothus megacarpus*).

In conclusion, at the landscape scale there is some tendency for non-resprouters to survive best on drier sites. Because morphological drought-avoiding traits (e.g, higher root:shoot) are more common in resprouters, non-resprouters should be physiologically more drought-tolerant to survive on drier sites; however, deeper physiological analysis is still needed to link field observations with physiological mechanisms.

### OBJECTIVE 2: THE PREDICTIVE VALUE OF THE FIRE-RESPONSE GROUPS

If different plant traits lead to differential success under a disturbance regime, then, for a given region, we should observe different trait sets under distinct fire regimes. In this context, Keeley and Zedler (1998) showed clear differences in plant traits associated with diverse fire histories for *Pinus* species growing in North America. We approached the question of the effects of fire regime on plant traits by studying different communities with the same structure (heathlands) and different short-term fire histories; they are separated in space to ensure that the medium- to long-term fire history is also different. An associated problem is that sites may have different climatic conditions, which is unavoidable due to the strong link between long-term fire regimes and climate. However, to consider this problem, heathland type was also tested to study to what extent differences among heathlands are related to fire history or/and heathland type (environment).

We used a modified version of the data sets compiled by Keith et al. (2002) of different heathlands across Australia (Appendix B). This data includes heathlands under stand replacement crown fires only, and so our analysis is restricted to a relatively small range of fire histories. We used 18 of their sites in which fire history for the last few decades (~20–35 years) was available. For each site, fire history was obtained from various fire databases and fire reports relevant to each example. Sites were clumped as average fire intervals of <15 years, 15–30 years, and >30 years. Although this classification of fire intervals is mainly based on the observation of a few decades only, it is possible, at some
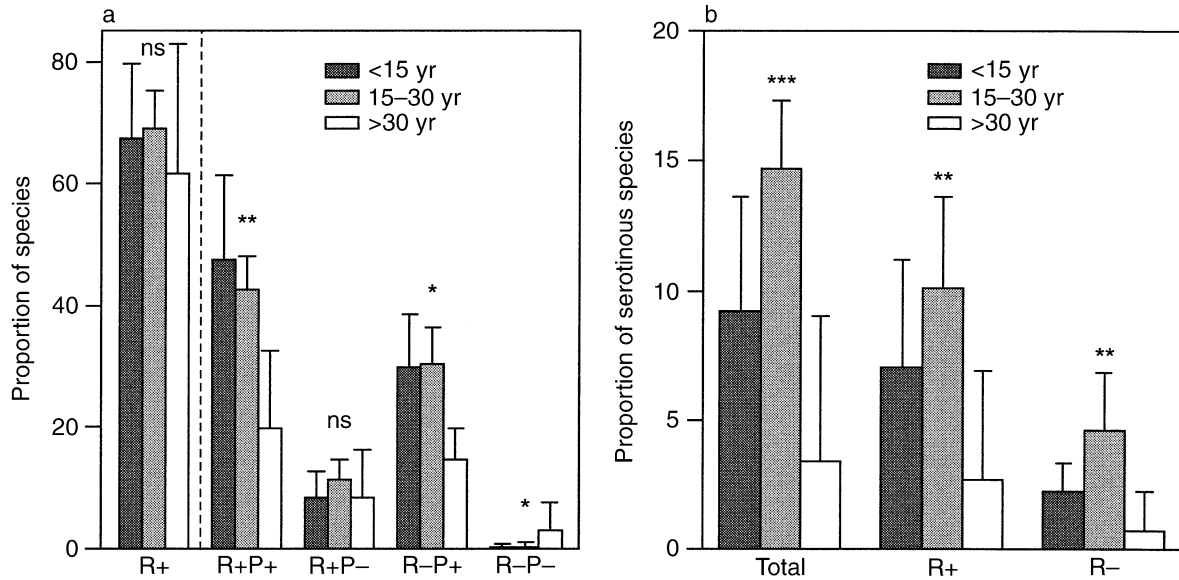
FIG. 5. (a) Proportion of species for different fire-response groups in relation to fire interval in the Australian heathlands. (b) Proportion of species with canopy seed bank (all species and R+ and R− separately) in relation to fire interval. Vertical lines are standard deviations. Significance among fire regimes (<15 yr, 15–30 yr, >30 yr) is shown for each fire response group (ns, $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). See Fig. 1 for abbreviations.

earlier stage in the past, that differing fire frequencies may have occurred at some of the studied sites. However, attempts to quantify such variations would be speculative. Sites were also classified according to heath type (tropical, alpine, montane, coastal, or temperate heath). Fire regime and heath type were not significantly related ($\chi^2 = 10.85$, $P = 0.23$; Appendix B). For each site, the proportion of species having a specific trait or set of traits was computed from the total number of species. Differences were analyzed by fire history and heath type, and the interaction was also tested. Because data were proportions, logit analysis of deviance (Generalized Linear Modeling, GLM) assuming quasi-binomial error distribution for overdispersed data was used to evaluate the significance (McCullagh and Nelder 1989).

### Fire regime gradient in Australian heathlands

Many studies in fire-prone ecosystems have suggested that resprouters should do better at extremes of the fire recurrence gradient than non-resprouters (Keeley and Zedler 1978, Kruger and Bigalke 1984, Keeley 1986, Hilbert 1987, Pausas 1999*b*). However, the opposite has also been proposed (Bellingham and Sparrow 2000). In the Australian heathlands, the proportion of resprouting species (R+ vs. R−) did not show a relationship with fire regime (fire history, heath type, and interaction were all not significant [ns]; Fig. 5a left). On average, ~67% (1 SD = 12.7) of the species are able to resprout after fire. Thus, the pattern of resprouting in relation to fire regime cannot be generalized (Pausas 2001).

However, when considering traits related to seed bank, some significant patterns do emerge in relation to fire history (Fig. 5a): There is an increase in both resprouting and non-resprouting propagule-persisters (R+P+ and R−P+) with decreasing fire interval (for R+P+, fire history, $P < 0.001$; heath type, ns; interaction, ns; and for R−P+, fire history, $P < 0.05$; heath type, ns; interaction, ns). Obligate resprouters (R+P−) show a significant trend with heath type, but not with fire (fire history, ns; heath type, $P < 0.01$; interaction, ns). Species without any persistence mechanism (R−P−) decrease with decreasing fire interval, although some variability is also explained by heath type (fire history, $P < 0.05$; heath type, $P < 0.05$; interaction ns).

The maximum proportion of species with canopy seed bank is observed at intermediate-to-short fire intervals, and there is a significant decrease in serotinous species in the long fire-interval class (Fig. 5b). For non-resprouters, the intermediate pattern is also evident (Fig. 5b, R−; fire history, $P < 0.01$; heath type, ns; interaction, ns). The interaction between fire history and heath type was significant for resprouting species (fire history, $P < 0.01$; heath type, ns; interaction, $P < 0.05$), suggesting that the abundance of serotinous species was highest in montane heathlands and lowest in alpine heathlands. This significant interaction reflected the fact that alpine and semiarid heathlands only occurred in the low fire recurrence class in the data set (Appendix B). Our results support the idea that serotiny should be a disadvantage where fire frequency is low (i.e., no evolutionary pressure should favor serotiny in

low fire frequency environments). Furthermore, very short fire intervals may not allow serotinous species to refill the seed bank. Thus, the canopy seed bank should be more important at intermediate fire recurrences (Enright et al. 1998*a*, *b*).

A similar pattern was also found for the proportion of species showing enhanced postfire flowering, which enhances postfire recruitment (fire history, $P < 0.001$; heath type, ns; interaction, ns). The proportion of species with soil seed banks was unrelated to fire history and heath type.

## Discussion

The basic fire-response traits (i.e., resprouting ability and propagule persistence) were found to correlate to some other traits when examined either alone (Table 3, resprouting ability only) or in combination (Table 4). In general, most resprouters are longer lived and slower maturing than non-resprouters and allocate more resources to basal buds and storage tissues. In some examples, they also tend to produce fewer seeds, to be shorter, and to have heavier diaspore units, although these traits show high taxonomic relatedness, which makes appropriate unambiguous comparisons difficult (Felsenstein 1985, Harvey 1996). And, there is no relation between dispersal mode and postfire response when considering different ecosystems. Thus, while the global scope of the data used to explore such correlations was limited, there was an indication that the pattern of correlations between the two basic fire traits and other traits relevant to vegetation dynamics varied between data sets from differing continents/ecosystems (Tables 3 and 4).

Assuming that correlations between the basic fire response and other traits will affect the performance of either the individual species or functional groupings, the finding that such correlations may be heterogeneous between samples is important. As a result, we may expect that the nature of predictions made on the basis of basic fire-response traits (R+ vs. R−) will vary from place to place according to the inherent characteristics of the differing floras. We emphasize that this does not mean that the basic traits have limited predictive power. It does mean, however, that pathways of change may differ between floras and that the ability to predict on the basis of basic fire-response traits may be high locally but low globally. For example, while most resprouters in Australian heathlands also produce permanent seed banks (Table 1), in the Mediterranean basin most resprouters do not store seeds in a bank. Another clear example is that most resprouters in California and the Mediterranean basin are dispersed by vertebrates, but this is not true in Australian heathlands. These differences have implications in the dynamics of the ecosystems and in the regeneration processes at community and landscape levels after recurrent fires. They also have implications in the conservation and management of plants, because the rates of

specialization and extinction are different. That is, not all resprouters are threatened to the same degree by fire regime or climate changes because their regeneration strategies (e.g., seed bank) and interactions (e.g., for seed dispersion) are different, and thus, this has implication for global vegetation modeling. The different trait co-occurrences in different ecosystems help to explore why some general questions worldwide (e.g., Midgley 1996, Bellingham and Sparrow 2000) may need different answers for different ecosystems/continents (e.g., Pausas 2001).

Within the context of Australian heathlands, no patterns among sites with differing fire regimes could be discriminated on the basis of resprouting capacity alone. We conclude that, at least within this general flora, it is not possible to predict pathways of vegetation dynamics on the basis of this trait. We do not rule out the possibility that this conclusion may differ in other ecosystems and/or localities, given that resprouters or non-resprouters may have differing trait co-occurrence elsewhere. The Australian heathland example did indicate, however, that inclusion of a persistent seed bank in addition to resprouting produced patterns in relation to differing regimes. We conclude that the hierarchical RP persistence scheme (Fig. 1) may include the minimum trait set that can be used to indicate general patterns of fire-related vegetation dynamics in this broad vegetation type. Furthermore, including the nature of persistent seed banks (i.e., canopy vs. soil) offers improved prediction (Fig. 5).

### Implications for a changing world

Fire regimes are far from constant. Currently, some areas show a general increase in annual burnt surface attributed to changes in land use and climate (in Euro-Mediterranean ecosystems; Piñol et al. 1998, Pausas and Vallejo 1999, Pausas 2004), or to increased logging and drought (in rainforests; Stanford et al. 1985, Cochrane 2001, Laurance and Williamson 2001). On the other hand, recent fire suppression policies in many ecosystems are also changing natural fire regimes (e.g., Parsons and DeBenedetti 1979, Bergeron and Dansereau 1993, Stephenson 1999, Beaty and Taylor 2001). Furthermore, future predictions suggest a tendency to increasing temperatures and evapotranspiration (Houghton et al. 2001), lightning (Prince and Rind 1994), and urban–forest interface (Terradas et al. 1998) in large parts of the planet. All this suggests that fire regimes will change in the future.

At the global scale, our ability to predict changes in vegetation due to changes in climatic conditions has improved thanks to the global climatic-based functional types (see papers in Woodward and Cramer 1996 and Smith et al. 1997, Foley et al. 1998). However, the ability to predict vegetation changes due to changes in disturbance regimes at this scale is still poor (Fosberg et al. 1999, and papers in Lavorel and Cramer 1999 and Pausas et al. 2003*b*), and this is one of the most

important limitations of the current global vegetation dynamic models. In fact, in fire-prone ecosystems, the changes in fire regime may be more important than the direct changes in climatic conditions (e.g., Flannigan et al. 2000). Recognizing the extent to which trait co-occurrence is similar for different ecosystems has strong implications for the predictive value of plant functional types at global scale, and provides insights for the elaboration of global vegetation dynamic models. The hierarchical RP persistence approach provides an initial scheme from which to build up a more elaborate one that considers other disturbances and ecosystems (e.g., understory fires, boreal ecosystems) and other scales (e.g., Pausas and Lavorel 2003). This is a new challenge, but it will need to be accompanied by the development of high-quality trait databases in order to be tested accurately.

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## APPENDIX A

Descriptions of the databases and species used in this study are available in ESA's Electronic Data Archive: *Ecological Archives* E085-029-A1.

## APPENDIX B

The location, heath type, and assigned fire regimes for the heath studies in the fire regime gradient are available in ESA's Electronic Data Archive: *Ecological Archives* E085-029-A2.