FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Resprouting as a life history strategy in woody plant communities

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Resprouting is an efficient means by which woody plants regain biomass lost during disturbance, but there is a life history trade-off that occurs in all disturbance regimes between investment in the current generation through resprouting vs investment in future generations at the same or more distant sites. The relative allocation to resprouting vs seeding in woody plant communities is dictated by the nature of disturbance regimes. Resprouting is the predominant response to the least severe disturbance regimes, but is also a common response in disturbance regimes of high severity, those that destroy most or all above-ground biomass, and which occur at medium to high frequency. The response to disturbance either by resprouting or seeding is dictated by the site's productivity. We present a comprehensive model for relative allocation to resprouting vs seeding across a range of disturbance regimes. Competition between plants that mostly seed vs those that mostly resprout should accentuate differences in allocation along a gradient of disturbance frequency. However, the patchy nature of disturbance in time and space, coupled with gene flow among populations undergoing different disturbance regimes, ensures that it is unlikely that either resprouting or seeding will be the sole response in most plant communities at most disturbance frequencies. Additional influences on resprouting in woody plant communities include changes in allocation during the lifespan of individual plants and phylogenetic constraints that are expressed as biogeographic patterns.

Trade-offs between vegetative growth and seeding are central to the evolution of life history strategies of plants (Stearns 1992, Blarer and Doebeli 1996). Vegetative growth, including resprouting after loss of biomass, concerns the maintenance of the current generation while seeding concerns production of future generations. Trade-offs between vegetative resprouting and seeding have been shown to be determined substantially by disturbance regimes (e.g., James 1984, Clark 1991). As a response to disturbance, successful resprouting depends on stored resources and this is achieved by diverting resources that could be invested in a future generation (through seed) to the current generation (Chapin et al. 1990). This trade-off is formalised in a recent theoretical paper by Iwasa and Kubo (1997). They took an essentially economic approach to resource allocation within a hypothetical plant and concluded that size of a storage organ, which permitted resprouting after complete loss of above-ground biomass, depends on a unimodal interaction between disturbance frequency and site productivity.

Most studies of trade-offs between resprouting and seeding have been conducted where disturbances are severe (i.e., most or all above-ground biomass is destroyed), and the result is a perceived dichotomy between the two responses (e.g., Wells 1969, Midgley 1996). In fact resprouting vs seeding varies continuously along disturbance gradients, within and between species, and across communities (e.g., Kruger et al. 1997, Hodgkinson 1998), and cannot be interpreted effectively as a simple dichotomy. A new approach is required that recognises the more complex nature of trade-offs between resprouting and seeding. In this paper we reexamine empirical studies across a range of disturbance regimes in light of Iwasa and Kubo’s theoretical model. On this basis we develop a more general model of resprouting vs seeding trade-offs across a range of disturbance regimes.

How disturbance and productivity influence resprouting and seeding

There is ample evidence that disturbance frequency is an important determinant of the relative frequency of resprouting at a community level (James 1984, Midgley 1996, Kruger et al. 1997). There is also good evidence for trade-offs between resprouting and seed production, most clearly demonstrated at a community level in disturbance regimes where only partial loss of above-
ground biomass occurs. For example, after fires destroyed some above-ground biomass in Australian semi-arid woodlands, there was a range in resprouting ability among species (4–94% of stems, Hodgkinson 1998). Amongst those species that resprout frequently, some gradually diminished in resprouting vigour and later regenerated from seed once lost biomass was recovered, whereas other species continued to resprout continuously after disturbance. For those species with low frequency of resprouting, most post-fire recovery was from seed. A second example is from forests frequently affected by hurricanes, where those species that resprout most frequently are often those that seldom regenerate from seed (Bellingham et al. 1994, 1996, Boucher et al. 1994). All of these examples suggest that resprouting capability depends on a storage organ (both above- and below-ground reserves) as assumed in Iwasa and Kubo’s (1997) model. We can find no direct evidence that explicitly tests this assumption, but there is some indirect evidence. For example, Malanson and Trabaud (1988) found that after fire destroyed above-ground biomass of Quercus coccifera, 9-yr-old shrubs resprouted more vigorously than 3-yr-old shrubs, which presumably had less developed below-ground storage reservoirs.

Although disturbance is usually considered to be the primary determinant of resprouting in woody plant communities, there is also evidence to support Iwasa and Kubo’s contention that site productivity (e.g., moisture and/or fertility) is also a contributing factor to the trade-off between resprouting and seeding. For example, in Australia, Nothofagus cunninghamii regenerates frequently from seed on moister, fertile sites (e.g., in Tasmania) but mostly resprouts in drier, less fertile sites (e.g., in Victoria; Read and Brown 1996). In South Africa, Sideroxylon inerme and Pterocelastrus tricuspidatus are multi-stemmed resprouting trees at low rainfall and few seedlings are found in these sites, whereas at higher rainfall sites both are single-stemmed and seedling regeneration is evident (Kruger et al. 1997).

The trade-off between resprouting and seeding is often perceived as one of growth forms (e.g., Midgley 1996, Kruger et al. 1997). Interactions between disturbance and site productivity result in an attendant gradient at a community level from taller monopodial trees to short multi-stemmed or mallee architecture maintained by basal resprouting (Givnish 1984). This is evident at the species level in the growth forms of two widespread Eucalyptus species in South Australia. Eucalyptus baxteri is a monopodial tree growing to 20 m in sclerophyllous forests on weakly podsolised soils at 1200 mm annual rainfall, but forms a “low undershrub about 60 cm high” on more heavily podsolised, lateritic (and thus more infertile) soils at 600 mm rainfall (Wood 1937). Eucalyptus leucoxylon is a monopodial tree of up to 30 m on relatively fertile, grey-brown soils at 1000 mm annual rainfall (Specht 1972), but takes on a multi-stemmed mallee form only 1 m tall on infertile siliceous sands at 400 mm rainfall (A. Sparrow unpubl.).

The variation in growth form along disturbance and productivity gradients can be interpreted in terms of above-ground competition. In the absence of disturbance, a taller architecture is competitively superior (for light; Midgley 1996) and maximum height will be achieved only in a monopodial growth form, because of mechanical constraints on typical multi-stemmed, basal-resprouter architecture (McMahon 1973, Givnish 1984). In frequently disturbed environments, most rapid recovery of canopy area will be achieved by multi-stemmed resprouting and thus this architecture will be competitively superior as long as the next disturbance precedes successful recovery of taller monopodial canopies. This argument is based on disturbance regimes that remove most above-ground biomass. Competitive outcomes will be different where, after a disturbance event, resprouting is possible above ground level. Thus the disturbance severity (as assessed by amount of biomass lost) must be included in any model.

How disturbance severity influences resprouting

Most existing observations of, and theory about, how disturbance frequency determines resprouting and resultant architecture are based on relatively frequent, severe disturbance regimes, where most above-ground biomass is destroyed (e.g., James 1984, Midgley 1996, Iwasa and Kubo 1997). Examination of responses to less severe disturbances shows that resprouting is a widespread response across a range of plant architectures. In response to the least severe disturbances, such as minor herbivory and superficial wind damage, almost all plants resprout, including many that are thought of as obligate reseeders (Hjältén et al. 1993, Chamberlin and Aarssen 1996, Ito and Gyokusen 1996). In addition, when disturbance is severe but infrequent, plants can respond by resprouting to reform a monopodial architecture (as might also be predicted by

Fig. 1. The consequence of increasing disturbance severity and frequency is to reduce above-ground biomass, and produce multi-stemmed resprouting architecture.
A general model of resprouting as a life history trade-off

Background

From the perspective of energy and matter flows within an ecosystem, we can interpret species’ characteristics as attempting to maximise occupancy of as many sites in the ecosystem with as much biomass as possible for as much of the time as possible (e.g., Johnson 1995). Any plant species might achieve maximum site occupancy by having a life history strategy between the extremes of many generations of fast-growing individuals (each of low biomass and producing a small seed crop) and few generations of slow-growing, large individuals that can accumulate a large per capita seed or seedling bank. From this life history perspective, we can analyse the evolution of resprouting ability in terms of how it assists in the long-term site occupancy strategy of a species. There is a trade-off between the plant species’ vegetative growth and seeding characteristics, both of which are traded off against the physiological processes of resource acquisition determined by abiotic conditions of the site and the presence of other plants (competitors; see Grime 1979), and animal consumers.

Resprouting is an efficient mechanism by which plants regain above-ground biomass immediately after disturbance, thereby maximising its long-term mean biomass occupancy rate at the site (e.g., Sakai et al. 1995), and for some resprouting plants this need not be initiated by disturbance (e.g., Mesléard and Lepart 1989). Disturbance regimes result in non-equilibrial systems where individual disturbances interrupt whatever competitive exclusion outcomes might be expected in an equilibrial system. Thus the efficacy of resprouting must be assessed relative to the ability of competitors (interspecific and intraspecific) to acquire limiting resources and thereby accumulate biomass. This is particularly important when it comes to consideration of the return time or frequency of the disturbances which forestall the competitive outcome.

Disturbance regimes will dictate the mode and efficacy of resprouting at the species and community level. Disturbance regimes have different components, i.e., distribution (spatial extent), frequency, predictability, severity and synergism (White and Pickett 1985). As discussed above, two aspects of the disturbance regime exert the greatest influence on resprouting: (1) mean disturbance severity, which controls the form that resprouting should take, and (2) mean disturbance frequency, which controls the proportion of the local flora which resprouts, and the extent to which resprouting occurs within a species.

Resprouting responses to different disturbance severity

Plant tissues have differing degrees of exposure to any form of disturbance. For most disturbances, the sequence of loss of above-ground plant biomass will be leaf, twig, branch and stem or trunk. This sequence reflects both the degree to which the tissue is exposed to the disturbance and the thickness of the protective layer around the tissue, protection that reflects the longevity the plant requires of the tissue. If we assume that loss of one type of tissue induces a regenerative response from the next level of the hierarchy (i.e., loss of a leaf
induces resprouting from the bud in the leaf axil on
the twig, and loss of a twig induces resprouting from
the bud in the twig axil on the branch), then in our
model we develop a generalised description of the
types of resprouting which should occur along a gra-
dient of disturbance severity (Fig. 2). This hierarchical
sequence is analogous to the sequence of Raunkiaer
(1934) life-forms, as classified by position of perennat-
bud through chamaephytes (buds at ground level) to cryp-
tophytes (buds below ground level).

As White and Pickett (1985) point out, distur-
bances do not have severity per se, even if they have
intensity in the sense of power (energy released per
unit area per unit time). Severity is a measure of the
plant’s perception of a disturbance event, i.e., a plant
perceives a particular disturbance intensity according
to its disturbance resistance adaptations (e.g., thick
bark on stems as protection from the heat of a fire;
flexible branches and twigs [and deciduousness] as a
protection against snow break; leaves filled with pheno-
llic compounds as protection against herbivory). Thus
one disturbance event of a particular intensity can be
perceived as having different levels of severity by dif-
f erent plants occupying a single site, and thus may
induce a variety of types of resprouting. Phylogenetic
constraints also apply; some species in frequently dis-
turbed ecosystems seldom resprout. For example,
many conifers do not resprout after hurricane damage
(Boucher et al. 1990, Bellingham et al. 1994) even
though they can presumably resprout in response to
less severe disturbance such as herbivory.

Resprouting responses to different disturbance
frequencies

Our model of a trade-off between allocation to re-
spouting vs seeding is first developed for a regime of
severe disturbance of various frequencies (Fig. 3). At
first, as disturbance frequency increases, we expect a
monotonic increase in proportion of allocation to re-
spouting among woody plant communities, as Midg-
ley (1996) predicted. In communities subject to low
disturbance frequencies, production of storage organs
is not worthwhile since it would needlessly constrain
growth and therefore reduce above-ground competi-
tive ability, so resprouting should be infrequent. Here
the seeder life history strategy is more likely to be
successful. In contrast, in more frequently disturbed
systems, the few seeders must have higher relative
growth rates and set seed earlier than the resprouters
with which they coexist.

There is experimental evidence that shows reduced
vigour and survivorship of resprouting shrubs under
increasing disturbance frequency (e.g., Vila` and Ter-
radas 1995), because it is energetically impossible to
make or maintain the necessary storage organs be-
tween disturbances. Therefore as the frequency of
severe disturbances increases further, woody plant
life-forms (i.e., chamaephytes) become less competi-
tive. At these disturbance frequencies, other life-forms
begin to dominate, initially those life-forms that rely
on below-ground storage (i.e., cryptophytes), and ulti-
mately at very high disturbance frequencies, theoro-
phytes (Fig. 3). These factors combine, in severe
disturbance regimes, to produce a unimodal response
of resprouting allocation along the entire gradient of
disturbance frequency.

Iwasa and Kubo’s (1997) model also predicts a uni-
modal response, but only with respect to the interac-
tion between disturbance frequency and site
productivity. We believe Iwasa and Kubo’s model can
be synthesised into the single trend we predict by
converting their predictor to disturbance frequency
scaled against (or controlling for) site productivity,
i.e., frequency divided by productivity. Storage
biomass for resprouting would show a unimodal re-
sponse to this single dimension (see Fig. 3 of Iwasa
and Kubo 1997). This conversion of disturbance re-
turn times from an absolute value into a relative
value in our model is a deliberate attempt to incorpo-
rate the main influence on the rate at which a re-
sprouter will be able to reoccupy a site with biomass.
In an environment of inherently low productivity
(e.g., arid, infertile or alpine), plant biomass produc-
tion will be slow because of limiting abiotic effects,
and thus reoccupation of sites will also be slow. Con-
sequently, in an unproductive environment, a distur-
bance type with a long return time may induce
selection of the same life history traits (e.g., mode of

Fig. 3. Simple model of a life history trade-off between re-
spouting and seeding allocation by woody plants in response
to increasing frequency of severe disturbance (i.e., all above-
ground biomass removed), with disturbance scaled against site
productivity. Expected plant life-form (sensu Raunkiaer 1934)
dominance along the disturbance gradient is indicated.
Constraints at the population and community level

The trade-off between resprouting and seeding will be reinforced at the community level by competitive exclusion. At low frequencies of severe disturbance, above-ground competition for light should select for height growth. This should favour seeding since resprouting requires proportionately more allocation to storage organs (Midgley 1996, Iwasa and Kubo 1997). At very high disturbance frequencies, inability to produce storage organs should lead to competitive exclusion of resprouters by short-lived seeders. Competitive exclusion should then lead to abrupt switching points between dominance by resprouters and seeders at different disturbance frequencies (Fig. 5a).

The sharpness of the switching points resulting from competitive exclusion in natural communities will be further affected by the influence of three other factors. Firstly, on a long time-frame there should be selection for tolerance to predictable disturbances, and this will reinforce the switching points. For example, a population of long-lived resprouters will be thinned by many individual disturbances that kill those plants with the least developed tolerance, to leave a highly tolerant residual population which reproduces by seed when rare occasions arise. Secondly, since disturbance acts patchily in space and time, no landscape can be domi-

Resprouting responses to interactions between different disturbance severity and frequency

Less severe disturbances that do not remove all above-ground biomass favour different forms of resprouting (Fig. 2) which can rely on above-ground reserves. We expect that in general, resprouting will be higher when disturbance is least severe, and resprouting responses to the least severe disturbances are likely to be independent of disturbance frequency (Fig. 4a). Thus the interaction between disturbance frequency and severity can be interpolated to produce an irregular resprouting response surface at the plant and the community level (Fig. 4b).

Fig. 4. Model of resprouting allocation by woody plants along increasing gradients of disturbance severity and frequency (both scaled against site productivity): (a) contrast of allocation between the most severe and least severe disturbance regimes, and (b) interpolated response surface for the interaction between disturbance frequency and severity.

resprouting) as a more frequent disturbance in a more productive environment. For example, fire burning infertile Mediterranean shrublands and hurricanes disturbing tropical forests can both select for strong basal and stem resprouting. The key to the successful strategy is simply whether it permits the plant to reoccupy the site before the next disturbance event, and this rate is fundamentally determined by site productivity.

Fig. 5. Community-level development of the trade-off model. (a) Competitive exclusion by the predominant life history strategy (resprouting vs seeding) reinforces trends along a gradient of increasing frequency of severe disturbance, leading to abrupt switching points. (b) Tolerance within the surviving population following each disturbance reinforces abrupt switching points, but gene flow across a landscape of patchy disturbance and unpredictable timing of disturbance events result in a relaxation to a gradual switching zone.
nated by a single life history strategy. This is a life history analogue of patch-gap dynamics (Watt 1947, Levin and Paine 1974). Furthermore, the selection of a resprouter-seeder strategy optimal for a specific site will be compromised by gene flow across a heterogeneous landscape. Thus interbreeding by two subpopulations experiencing different disturbance regimes will mean that neither subpopulation will be optimally selected to cope with the disturbances it experiences (Slatkin 1987). This can be demonstrated by the converse trend in genetically isolated populations of the widespread Australian tree *Eucalyptus camaldulensis*, which in low frequency disturbance regimes may lose its capacity to resprout (e.g., some provenances of *E. camaldulensis* do not form lignotubers, from which resprouts arise, even with addition of nutrients that promote lignotuber formation in seedlings of other provenances; Jahnke et al. 1983). Thirdly, the unpredictability in disturbance regime times means that the position of the ideal switching point will vary between disturbance events. In an evolutionary time frame, this represents variance around the mean switching point, which will lead to a cline in life history characteristics, thus creating a switching zone, rather than a discrete switching point (Fig. 5b).

**Discussion**

We believe our conceptual model has three key advances over previous work on ecological significance of resprouting as a component of plant life histories. Firstly, our model is more comprehensive than previous models. Although Iwasa and Kubo’s theoretical model (1997) is borne out by empirical evidence, our model is more comprehensive because it considers more components of disturbance regimes, especially the dimension of disturbance severity. We believe that resprouting allocation will be influenced by both disturbance severity and frequency in a non-additive fashion (Fig. 4). Secondly, our model provides a unifying framework that includes relative allocation by woody plants to resprouting vs seeding, as well as the likely life-forms to dominate in certain disturbance regimes, including when non-woody life-forms should dominate (Fig. 3). Thirdly, disturbance regimes are scaled directly by productivity in our model to predict relative dominance of plant life-forms and allocation patterns (Figs 3–5).

In the model we have presented the trade-off between vegetative resprouting and seeding has analogies to foraging models for clonal plants (e.g., Hutchings and Price 1993, Hutchings and de Kroon 1994). Clonal plants trade off growth within single ramets against production of additional ramets, a trade-off which is about maximising local resource exploitation versus foraging in resource-rich patches elsewhere and the optimisation of which is determined by the spatial pattern of resource availability in the environment. Similarly, woody plants trade off between resprouting to rebuild biomass on site immediately, and producing seed to reoccupy the same or more distant sites in the future (see also James 1984). Thus the primary emphasis in our model is on temporal patchiness of the environment, i.e., time in our model is directly analogous to space in the clonal plant foraging models. There are further analogies between the models. For example, overall regrowth of resprouting plants after less severe disturbances is optimised by transfer of resources from less damaged to more damaged tissues within a plant (e.g., from the foliage in an undamaged branch to resprouting meristems in a damaged branch) in the same way that clonal plants transfer resources from resource-rich to resource-poor ramets.

We recognise that there are over-simplifications in our model. The trade-off we propose between resprouting and seeding within an individual plant cannot apply before the plant reaches reproductive maturity; before the onset of maturity resprouting is the only possible means of recovery from disturbance (e.g., Clark and Clark 1991). Furthermore, an individual plant’s capacity to resprout is unlikely to be constant throughout its life. In systems where plant growth is seasonal, resprouting vigour has also been shown highly coincident with a seasonal maximum in mobility of reserves (e.g., Malanson and Trabaud 1988, Kays and Canham 1991). Capacity to mobilise reserves in response to disturbance will depend on plant size. In cases where disturbance removes only a proportion of above-ground biomass, younger, possibly more vigorous, plants resprout more frequently than older plants (e.g., broken tropical rain forest trees, Putz et al. 1983). In contrast, in cases where disturbance causes loss of most above-ground biomass, mobilisation of below-ground resources will be essential for resprouting, and larger, older plants should be at an advantage as disturbance frequency increases (Iwasa and Kubo 1997), for which empirical evidence exists (Malanson and Trabaud 1988). However it appears that resprouting vigour is likely to be linked to the longevity of plants since resprouting ability declines in some shrub species with age (e.g., *Erica cinerea* in Scottish heathlands after fire; Hobbs and Gimingham 1984), whereas other woody plants may continue to resprout for centuries and sometimes form large clones, e.g., *Larrea tridentata* (Vasek 1980) and *Ginkgo biloba* (del Tredici et al. 1992).

A further simplification of our model is that it regards disturbance and productivity as purely abiotic characteristics of a site. In fact vegetation modifies and contributes to the disturbance regime and can influence the apparent productivity of a site (e.g., by modifying light regimes at ground level). Thus a plant in the canopy will experience a more productive environment than a plant beneath the canopy. In a light-limited
multi-layered plant community in which all plants are subject to the same absolute disturbance frequency (i.e., not scaled against productivity), plants in the understorey will experience a higher relative disturbance frequency when scaled against apparent productivity and thus may optimise the resprouting-seeding trade-off in a different way to canopy plants. Hence different life history strategies can coexist within the one site.

In addition, biotic interactions involving a third species can modify the expected outcome of competition between plants species with different solutions to the resprouting-seeding trade-off. For example, two beech species (Fagus crenata and F. japonica), with similar heights at maturity, co-occur in temperate eastern Japanese forests. Fagus japonica produces many stems from basal resprouts and usually dominates, whereas F. crenata is usually single-stemmed, seldom produces resprouts, and rarely dominates (Ohkubo 1992). A dwarf bamboo (Sasa spp.) suppresses seedling recruitment of both species; recruitment of seedlings depends on the coincidence of periodic widespread death of bamboo with the formation of treefall gaps (Nakashizuka and Numata 1982). Where the two species co-occur, F. japonica dominates because recruitment from basal resprouts may occur continuously (e.g., in response to treefall gaps) since their growth is not suppressed by dwarf bamboo (Ohkubo 1992). Our model implies that long-term coexistence of the two Fagus species depends on F. crenata being a superior competitor as a seedling (e.g., have a faster relative growth rate) when the rare opportunities for seedling regeneration arise. This hypothesis could be tested experimentally in forest understoreys by removing dwarf bamboo plants and measuring onward growth of seedlings.

Some species are reported not to conform to a trade-off between resprouting and seeding. For example, James (1984) cited the case of Calluna vulgaris in British heathlands, which regenerates from seed and also resprouts after fire. However, closer examination of the life history of C. vulgaris shows that whereas younger individuals (< 15 yr) predominantly resprout after fire, in older stands regeneration after fire is mostly from seed (Hobbs and Gimingham 1984), thus the trade-off does apply but changes during the lifespan of individual plants. Furthermore many British heathlands now dominated by C. vulgaris have disturbance and fertility regimes substantially altered by human activity (Rodwell 1992), which may have removed otherwise more successful resprouting and/or seeding competitors. Such explanations for apparent non-conformity to a trade-off between resprouting and seeding may also be pertinent for other species that are reported to resprout readily and also produce abundant seed (e.g., Adenosma fasiculatum in Californian chaparral; Wells 1969).

Some floras may also appear not to conform to our model. Our model has an emphasis on temporal and spatial scales of disturbance and resource availability as it affects a resident flora that has evolved in situ. However the selection of life history strategies will have phylogenetic constraints imposed at the level of the local flora (Zobel 1997). The effects of different histories of disturbance and different times since last change of disturbance regime result in different resprouting tendencies. Therefore just as in the case of Calluna vulgaris, resident floras display lag effects after changes in disturbance regimes, so floras may appear to be “out of equilibrium” with the current disturbance regime. This may explain biogeographic differences in the proportion of resprouting among floras subject to apparently similar current disturbance regimes (e.g., West Australian kwongan 73%; Bell et al. 1984 vs South African mountain fynbos 62%; van Wilgen and Forsyth 1992).

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