

Ecophysiology of natural regeneration of forest stands in Spain

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Abstract

Natural regeneration is a slow and unpredictable process because of the complex interaction between the success of seedling establishment and site factors. In this review, we focus on four groups of factors that influence natural regeneration: seeds (seed production, seed banks, seed viability, serotinous cones in conifers, seed dormancy and seed germination), seedling performance, sprouting and ecological factors of the site (soil characteristics, weed competition, temperature, salinity, water availability, light, wildfires, predation, pests and diseases). The knowledge of the effect of all these factors and their interactions on the physiology of seedlings is essential for the management of natural stands. In this sense, simulations of forest regeneration are a useful tool.

Key words: regeneration stage, seed, sprouting, seedling performance, environmental factors.

Resumen

Ecofisiología de la regeneración natural de las masas forestales en España

La regeneración natural es un proceso lento y poco predecible debido a la compleja interacción existente entre el éxito en el establecimiento de los brinzales y diferentes factores del medio. La presente revisión se centra en cuatro grupos de factores que influyen sobre la regeneración natural: la semilla (producción de semilla, bancos, viabilidad, piñas serotinas en coníferas, dormición y germinación), el comportamiento de los brinzales, la capacidad de rebrote y los factores ambientales (características del suelo, daños por herbívoros, temperatura, salinidad, disponibilidad hídrica, luz, fuego, competencia herbácea, enfermedades). El conocimiento del efecto de estos factores y sus interacciones sobre la fisiología del regenerado resulta esencial para la gestión de las masas forestales. En este sentido, las simulaciones de la regeneración natural constituyen una herramienta muy útil.

Palabras clave: estadio de la regeneración, semilla, rebrote, comportamiento de los brinzales, factores ambientales.

Introduction

In Sylviculture, natural regeneration is defined as the renewal of a forest stand by natural seeding, sprouting, suckering, or by layering seeds that may be deposited by wind, birds or mammals. Such regeneration can be the consequence of one of the following circumstances (Serrada, 2003): (1) natural regeneration in sites where the density of the pre-existing stand has not been lately modified (*colonization* event). (2) Natural regeneration in sites threatened by abiotic and biotic stresses (wildfires, windstorms, drought, flooding, pollution, soil compaction, pests and diseases) (*restoration*

event). Such stresses often result in catastrophic losses of forest products and services (Kozłowski, 2000). (3) Natural regeneration in managed stands as a consequence of the regeneration fellings (natural regeneration *sensu stricto*). All three processes share similar mechanisms and conditioning factors, but it is important to differentiate between them, mainly when the reliance on existing forest reserves for conserving forest ecosystems is questioned (Franklin, 1993).

Stages of natural regeneration

Natural regeneration in forest stands typically occurs in four sequential stages (Kozłowski, 2002): (1) regeneration stage, (2) thinning stage, (3) understory regeneration stage, and (4) old-growth stage.

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Regeneration stage follows tree harvesting or disturbances, and regeneration occurs through the interaction of different factors. Such factors can be divided in four groups (Daniel *et al.*, 1982; Kozłowski, 2002): seeds (seed banks, seed production, seed viability, serotinous cones in conifers, seed dormancy and germination), seedling performance, sprouting and ecological factors of the site (soil characteristics, weed competition, temperature, salinity, water availability, light, flooding, pollution, wind storms, wildfires, herbivores, pests and diseases, etc). Thinning stage begins with canopy closure, and is characterised by the accelerated mortality of trees due to competition for light, water and nutrients. The understory regeneration stage is characterised for the formation of gaps due to mortality of dominant trees, which enhance growth of species in the understory. Finally, the old-growth stage usually culminates, through succession stages, in a climax forest. This review will emphasize only in the factors affecting the regeneration stage.

Factors affecting the regeneration stage

Seeds

The process of natural regeneration of forest stands begins with the supply of seeds from soil or aerial seed banks, but seed supply is commonly highly variable. Across an interval of several years most tree species appear to produce many more small crops than large crops, such process is known as *masting* (Kelly, 1994). Regularity of seed production varies greatly between species. For example, in Spain *Quercus suber* has large seed crops every two to four years (Montoya, 1988), while *Quercus petraea* in central Spain (Hayedo de Montejo forest) shows one or two good crops every 9 to 10 years (Gil *et al.*, 1999). Under these same meridional conditions, *Fagus sylvatica* shows good crops every four to six years, but during mast years more than 90% of the seeds are empty (Gil *et al.*, 1999). Some mediterranean pine species produce good seed crops annually (e.g. *Pinus halepensis*), others show one or two good crops every four to six years (e.g. *P. pinea*, Gordo *et al.*, 2000). Some mountain pines show a large crop every three years (e.g. *P. sylvestris*), others at irregular intervals (e.g. *P. nigra*) (Ruiz de la Torre, 1979). Dry and warm weather at the time

of reproductive bud differentiation is the main determinant (25% of the variance) of final crop size for both conifers and hardwoods (Greene and Johnson, 2004), but other factors are involved (e.g., humidity during pollination and the negative effect of the size of a crop on the size of the subsequent crop because of resource depletion due to competence for assimilates between vegetative and reproductive organs -Sedgley and Griffin, 1989-). Greatest success in regeneration of forest stands usually occurs after a year of large seed crop, as the density of such regeneration is primarily dependent on seed production (Greene *et al.*, 1999). Large-seeded species produce fewer seeds than small-seeded species, and large trees produce more seeds than small trees. Annual seed production of a single tree can be expressed as a function of seed mass and basal area (Greene *et al.*, 1999). There is also a model that predicts annual cone and seed production and percentage of viable seeds after identifying the main factors that influence cone and pynion production in *Pinus pinea* in central Spain (Calama *et al.*, 2004). Such factors are divided in stand and tree variables (density, site index and basal area) and random effects (year, plot and tree).

Seed dispersal is thought to enable seeds to escape competition (with their parents, with other seedlings and/or with surrounding vegetation) and to colonise favourable sites (Howe and Smallwood, 1982). According to Barot *et al.* (1999), in tropical forests, the further a seed is from its parent tree, the more likely it is to germinate and to recruit later as a seedling. However, the spatial pattern of seed dispersal often does not determine the spatial pattern of established seedlings (Meiners *et al.*, 2002). Both wind and animals play important roles in establishing seed banks in the soil. Wind-dispersal for great distances occurs in small, light-weighted seeds, that show structural modifications such as hairs or wings (e.g. *Salix*, *Populus*, *Platanus*, *Acer*, *Alnus*, *Betula*) (Kozłowski, 2002). Also, the relatively strong winds associated to drying atmospheric conditions, can trasport seeds of *Pinus halepensis* over 1 Km and more, as has been predicted by a mechanistic dispersal model (Nathan and Ne'eman, 2004). Seed predators are considered to be major mortality agents structuring recruitment patterns. Such patterns can be modeled by a simple mechanistic model, which considers three easily measurable quantities: the proportion of seeds escaping predation at the source, and the mean distance from the

source of dispersed seeds and of predators' activity (Nathan and Casagrandi, 2004). Heavy fruits (e.g. *Fagus*, *Quercus*, *Castanea*) dispersed by barochory, but also by birds and mammals. Acorn scatter-hoarding by birds and catching by squirrels can enhance seedling recruitment by moving acorns (Borchert *et al.*, 1989).

Some conifer species show a canopy seed storage strategy (*cone serotinity*), where at least part of the previous seed crop is retained when the current year's crop is mature (Lamont *et al.*, 1991). Such serotinous cones do not open and may remain alive for years, while still attached to the trees (Figure 1). Serotiny has been particularly studied in *Pinus* (22 out of 95 species carried serotinous cones), but is also a highly developed strategy in *Cupressaceae* (40 out of 42 species), where serotinous cones may remain alive for up to 25-30 years (Battisti *et al.*, 2003) and in *Banksia* (Zammit and Westoby, 1988). Among Spanish pines, *Pinus halepensis* is the only clearly serotinous, while *P. pinaster* and *P. canariensis* can be serotinous or non-serotinous (Tapias *et al.*, 2004). Pine cones usually



Figure 1. Closed, xeriscent cones in a 40 year-old *Pinus pinaster* in Cabañeros (Ciudad Real). Serotinous cones do not open and may remain alive for years, while still attached to the trees.

open after a wildfire, following the melting of the resin, while *Cupressus* cones appear to open when they loose water.

The ability of seeds to delay their germination until the time and place are right is an important survival mechanism in plants. Seed dormancy is a genetically inherited trait whose intensity is modified by the environment during seed development (Pardos, 2000). In nature, dormant seeds fall from the trees either early in the summer or in autumn. These seeds will never germinate before winter because in order to eliminate dormancy and prepare themselves for germination, they require a period of 10 to 16 weeks of low temperatures between 0 and 5-6 °C (Suszka *et al.*, 1996). What is more, some species need a warm phase preceding the cold phase. Several physical and physiological mechanisms of dormancy occur in seeds. Dormancy can be primary (exogenous and endogenous) and secondary (Copeland and McDonald, 2001). Exogenous dormancy is generally related to physical properties of the seed coat (impermeability to water and gases, and physical restraint for embryo enlargement). Under natural conditions, exogenous dormancy is overcome by the freezing-thawing of the soil, ingestion by animals, wildfires, etc. Endogenous or physiological dormancy is due to the inherent properties of the seed. Seed dormancy in higher plants is regulated by a balance of endogenous hormonal growth inhibitors (e.g. abscisic acid) and promoters (e.g. gibberellins). The levels of these compounds are controlled by light and temperature. The inhibitor-promotor balance is altered by exposing seeds to low temperatures under imbibed conditions (stratification) or under higher temperatures while unimbibed. During cold stratification, physiological changes take place in the tissues of the embryonic axis, the cotyledons and the endosperm if present (Suszka *et al.*, 1996). Sometimes nondormant seeds encounter conditions that subsequently cause them to become dormant (secondary dormancy).

Seedling establishment and performance

To physiologists, germination is defined as the emergence of the radicle through the seed coat. Seeds of most species are capable of germinating long before physiological maturity. In other cases, maximum seed germination can only be obtained if the seed is allowed

to dry down slowly as it matures (Copeland and McDonald, 2001). After they release their nutrients during germination, the cotyledons may either wither and die or develop chloroplasts and begin photosynthesis. Which course they take is related to whether the cotyledons remain underground during germination (*hypogeal* germination) or are elevated into the light (*epigeal* germination) (Mauseth, 1988). The possibility of a seedling to establish and survive in a site depends on the metabolic reserves on the seed. Thus, the plant must respond to a double alternative (the *k* and *r* reproductive strategy –McArthur and Wilson, 1967–), either 1) to produce abundant small-size seeds, with limited reserves, or 2) to produce less large-seed, with abundant reserves (Westoby *et al.*, 1992). Germinant size is dependent on seed size during the first weeks until the true leaves replace the cotyledons as the primary source of carbohydrates (Greene *et al.* 1999). In general, large-seeded species show higher initial growth, but lower relative growth rate with time and usually occupy wider geographical ranges (Aizen and Patterson, 1990). Large seeds confer seedlings an adaptative advantage against spring frosts (Aizen and Woodcock, 1996), but also against xeric conditions (Long and Jones, 1996).

Plant performance depends on the underlying patterns of resource availabilities. Resources vary spatially and temporally and species differ in their ability to tolerate resource scarcity. Thus, more than one resource may be limiting simultaneously among microsites or at different times within the same microsite or for different species grown together (Latham, 1992). Differences in performance ranking across resource gradients will result in patterns of seedling abundance, that may persist in the composition of adult trees community. The spatial pattern of regeneration can be characterized by Ripley's *K* (*d*) function (Ripley, 1981), which shows the type, scale and pattern intensity of a number of points distributed on a plane, through the analysis of the distances between them. Ripley's *K* (*d*) function is the most efficient statistics for the spatial pattern analysis, which allows discriminating between cluster, regular and random distributions, independently of the area of the plot (Rozas, 2002). The spatial pattern of *Pinus sylvestris* seedlings in central Spain is in small clusters (Pardos *et al.*, 2005b) (Figure 2a), similar to patterns usually described for this species (González-Martínez and Bravo, 2001) and for the broadleaved *Fagus*

sylvatica and *Quercus robur* (Rozas, 2002) in northern Spain.

Sprouting

Some Mediterranean species have the capacity to sprout from swollen underground root structures bearing dormant buds, called *lignotuber*, (e.g. *Quercus suber* –Molinas and Verdaguer, 1993; Verdaguer *et al.*, 2001–, *Erica arborea* and *Arbutus unedo* –Canadell and López-Soria, 1998, *Erica australis* –Cruz and Moreno, 2001), from roots (e.g. *Quercus pyrenaica*, *Q. ilex*, *Q. faginea* –Ruiz de la Torre, 1979) and from buds on the stem (e.g. epicormic shoots of *Pinus canariensis* –Climent *et al.*, 2004–). This ability to regenerate in situ confers a remarkable advantage on these species, but may be restricted to juvenile stages. Sprouts obtain benefit from a root system developed by a previously established individual. Thus, sprouts could be more resistant to water or nutrient stress and show higher survival and growth rates than seedlings (Lloret *et al.*, 2004). Although the age at which the potential for sprouting begins to decline varies with the species, it seems that after reaching 40–50 years, some species loose sprouting ability (Zasada *et al.*, 1992). However, this time lapse might be longer in mediterranean oaks. According to Serrada *et al.* (2004) the resprouting ability is maintained for 150 years in *Quercus ilex*, for 120 years in *Q. pyrenaica* and for 100 years in *Q. faginea*.

Ecological factors of the site

Soil characteristics and weed competition

The most important determinants for the success of seedlings establishment are the capacity of the growing medium to supply water and the amount of light reaching the seedlings (Grau, 2004). Water in the soil is mainly retained by matric potential (Pardos, 2000). The denser the soil the better is its capacity to supply water to both seeds and germinants (Kozłowski, 2002). During initial growth, seedlings are highly sensitive to competition with weed vegetation; thus, seedling development can be retarded (Modrý *et al.*, 2004). González-Martínez and Bravo (2001) found that the regeneration density of *Pinus sylvestris* stands is



Figure 2. *Pinus sylvestris* natural regeneration in the last diameter class before shelterwood felling (90-110 years) in Navafría forest (Sistema Central). **(a)** The spatial pattern of *Pinus sylvestris* seedlings in central Spain is in small clusters, similar to patterns usually described for this species and other conifers. **(b)** During initial growth, seedlings are sensitive to competition with weed vegetation. The presence of grass increases competition for water during water deficit conditions, as well as for nutrient resources.

negatively related to the cover of *Ericaceae* and *Quercus* in northern Spain. In addition, weed competition can also occur through the release of allelochemicals (Friedman, 1995). The presence of grass increases competition for water during water deficit conditions (Aussenac, 2000) as well as for nutrient resources (Saunders and Puettmann, 1999) (Figure 2b). Litter may delay or abort seedling emergence by preventing contact between seminal root and mineral soil or through mechanical restriction to hypocotyl elongation and emergence of cotyledons (Caccia and Ballaré, 1998). Although mineral soil seedbeds with humus are often preferable for the establishment of some species, this is not the case for *Pinus sylvestris* seedlings in central Spain (Rojo and Montero, 1996) and *Pinus canariensis* in the Canary Island (Climent *et al.*, 1996). In *P. sylvestris* stands, the layer of black humus formed below the layer of litter heats up in the first 5-10 cm and water retention is low during the summer. Thus, *P. sylvestris* seedlings, with a short radicle, have difficulty surviving their first summer. Under the *P. canariensis* canopy, a layer of old needles of up to 50 cm is accumulated over the years impeding the germination of any type species. Nevertheless, successful emergence could occur on a variety of seedbeds. Furthermore, natural seedling preference for seedbeds can vary with elevation, as is the case with other conifers (Feller, 1998).

Temperature

Seed germination is a complex process involving many individual reactions and phases, each of which is affected by temperature (Copeland and McDonald, 2001). Germination under field conditions would take place when the field temperature enters the thermal range within which germination can occur (Batlla *et al.*, 2003). The optimum temperature for most seeds is between 15 and 30°C. Seeds of many species require daily fluctuating temperatures for optimum germination (Copeland and McDonald, 2001). A dormancy loss model can be developed, which simulates changes in the thermal range permissive for germination of seed population in relation to the stratification temperature experienced by the seeds during burial (Batlla and Benech-Arnold, 2003). Seeds of some conifers (e.g. *Pseudotsuga*, *Abies*, *Picea*, *Pinus*) can be considered as dormant since they germinate slowly and within a narrow range of temperatures. This dormancy is only broken after treatment of the seeds in a wet medium at chilling temperatures (Corbineau *et al.*, 2002). Thereafter, much higher temperature regimes are required to stimulate the metabolic activity necessary for germination (Kozłowski, 2002). Seed germination of other species (e.g. *Chamaecyparis nootkatensis*, that show a deep dormancy) is inherently low and requires

stratification techniques or moist chilling combined with chemical treatments, temperature and light (Raimondi and Kermode, 2004). Germination of conifer seeds inside serotinous cones depends on the previous opening of the cones by fire (Tapias *et al.*, 2004). Seed germination of *Quercus pyrenaica* was neither affected by soil temperatures reached during a low intensity fire or by the action of agents, which can mechanically damage the external coat (Valvuela and Tárrega, 1998). Similarly, Cain and Shelton (1998) found that prescribed winter burns did not affect the germinative capacity of *Quercus falcata*, as long as seeds were buried.

Salinity

Salinity constitutes one of the most important environmental factors limiting plant growth, where the most common ionic composition of saline soils is an elevation in NaCl. Excess of Na and Cl are the two ions most frequently implicated with toxicity in plants, because both are highly soluble, readily taken up, and transported to the shoots in the transpiration stream (Keiper *et al.*, 1998). Studies on the response of tree species to salt tolerance are limited to *Mangrove*, *Eucalyptus*, *Casuarina*, *Acacia*, *Acer*, *Pinus* and *Populus* (Sixto *et al.*, 2005). Salt tolerance may be an important adaptive trait in coastal forests, where soil salinity will be increased by storms and sea level rise. It is suggested that there is a genetic component in their variation to salt-tolerance. Salinity inhibits seed germination not only by lowering soil osmotic potential, thus inhibiting water absorption by seeds, but also by toxicity to the embryo (Kozłowski, 2002). After germination, many environmental (temperature, relative humidity, air pollution) and edaphic factors (soil fertility, water stress) interact with salinity to influence seedling salt tolerance (Maas, 1986).

Water availability

Most plants in the Mediterranean basin experience water stress during the summer. Thus, soil moisture availability during summer drought is often crucial to the establishment of trees (Pardos *et al.*, 2005a) (Figure 3). On the opposite side is the effect of soil flooding, that deprives seeds and seedlings of the



Figure 3. *Quercus suber* first year natural regeneration in el Dehesón del Encinar (Toledo). Mortality of cork oak germinants in open areas can reach up to 90 to 100% due to the joint effect of rodents seed predation and summer drought; but once the first growing season is over, seedlings are able to persist for 2 to 4 years and live in a suppressed state, through the dieback of the shoot during the droughty summers, followed by resprouting in the fall. The result is a recruitment of seedlings of variable age, not more than 30 cm high, with a deep root system, that in most cases are not able to perform adequately, as long as favourable conditions for growth do not occur.

oxygen necessary for respiration (Kozłowski, 2002). It is important to note that the response of physiological traits to drought is different in seedlings and trees. Generally, seedlings showed more negative predawn water potentials than trees, and probably is a function of the rooting depth and the pattern of soil water recharge and depletion from surface to deep layers (Matzner, 2003). Shrubs can also play an important role in the dramatic differences in summer soil water potential that can be found under a stand, as they inhibit seedling establishment and growth through competition for resources (Dunne and Parker, 1999). Seedlings differ widely in their capacity to cope with drought. Some species are drought tolerant because they can either withstand extreme dehydration of the protoplasm (low relative water content) or avoid low water potentials (Kozłowski and Pallardy, 2002). Adaptations of woody seedlings to avoid drought include smaller and fewer leaves and stomata, rapid stomata closure during drought, leaf epidermis waxes, strong development of palisade mesophyll, low resistance to water flow and high root growth potential after transplanting. Different models have been developed to quantify drought stress through tree water deficit. For

example, Zweifel *et al.* (2005) estimated sapling water deficit by measuring water-related changes in stem radius and comparing it with sapling water deficit estimated from a physiological model, where soil water potential and atmospheric vapour pressure deficit were the inputs.

Light

While moisture, oxygen and favorable temperature are essential for germination of all seeds, certain species also require light. Both light intensity and light quality influence germination (Copeland and McDonald, 2001). The light intensity and quality perceived by a seed depend on its position in the soil, the vegetative covering, and the light absorption characteristics of the seed coat.

The importance of light is a function of the species temperament (Figure 4). For example, germination of



Figure 4. *Quercus suber* dehesa (Dehesa de Cijara, Badajoz). The importance of light is a function of the species temperament. Cork oak regeneration appears scatterly distributed under the adult trees, while understory vegetation occupies the gaps.

Pinus sylvestris is delayed under low light intensity (Castro *et al.*, 2004). For shaded understory, light regime is the defining trait and a critical factor affecting tree growth (Lieffers *et al.*, 1999). The ability of understory trees to grow and survive in the shade of partial or complete overstory canopies is the outcome of complex interactions between leaf- and plant-level responses to light, nutrient and water availability (Messier *et al.*, 1999). All species have evolved some degree of acclimation potential and developmental plasticity in response to the varying environmental conditions that understory trees experience during their life-span, but this ability cannot ensure that the species will perform adequately in all environments. Treefall gaps are recognised as the single most important type of endogenous disturbance in forests, as they will promote the coexistence of species having different light-use strategies (Rozas, 2002; Grau, 2004). Openings of the canopy through treefalls increased light levels and, thus also favour understory species (Kwit and Platt, 2003), which may compete with tree seedlings (Beckage and Clark, 2003).

Wildfires

After drought, fire is the principal disturbance in the Mediterranean basin. Three main strategies are predominant in fire-prone environments: seedling development, adult tolerance and vegetative regeneration (Tapias *et al.*, 2004). Fire is an important disturbance factor that has generally favoured *Pinus* throughout its natural range in the northern hemisphere. In pines, fire adaptations have been explained by individual resistance and stand resilience. The first implies the survival of the adult plants, while the second ensures seedling recruitment after the depletion of the original stand (Climent *et al.* 2004). Within the Mediterranean Basin, *Pinus halepensis* zone is one of the most flammable and fire-prone. Because *P. halepensis* possesses an evader strategy with its serotinous cones, it is quite resilient, even in the face of intense fires. As it is a precocious seed producer (at 7 years), the species can survive two fires in a decade, and colonizers may produce seedlings for the same cohort of post-fire colonizers (Agee, 1998). Furthermore, recruitment of *P. halepensis* after fire can be highly variable. For example, in southern Spain,

recruitment six months after fire is between 0 and 86,600 saplings/ha (González-Ochoa *et al.*, 2004). However, some species do not resprout nor recruit after a fire, thus the community can disappear within a short time (e.g. *Juniperus phoenicea* in the associations dominated by *Quercus coccifera*, and *Abies pinsapo* in *Q. suber* stands -Lloret, 2004-). Patterns of recruitment in boreal species showed a large pulse of post-fire seedling recruitment within 3-7 years after fire, followed by several decades of low or no recruitment (Johnstone *et al.*, 2004). What fraction of the aerial seed bank survives a wildfire? Usually, a decrease in percent germination and percent filled seed is reported between a burned and two unburned stands, suggesting that fire affected seed viability (Greene *et al.*, 1999). Temperature to which seeds are heated and length of heating period are also critical factors. For nonserotinous species, it is interesting to differentiate between crown and ground fires. Some crown fires destroy the seeds (although not in serotinous species), while ground fires may kill the tree, but may not affect cones. In such matter, the timing of fire in relation to the stage of seed development is important (Greene *et al.*, 1999). With spring or summer wildfires, before seed maturation, the recovery of the germinant populations is committed (Lloret, 2004).

Postdispersal predation, pests and diseases

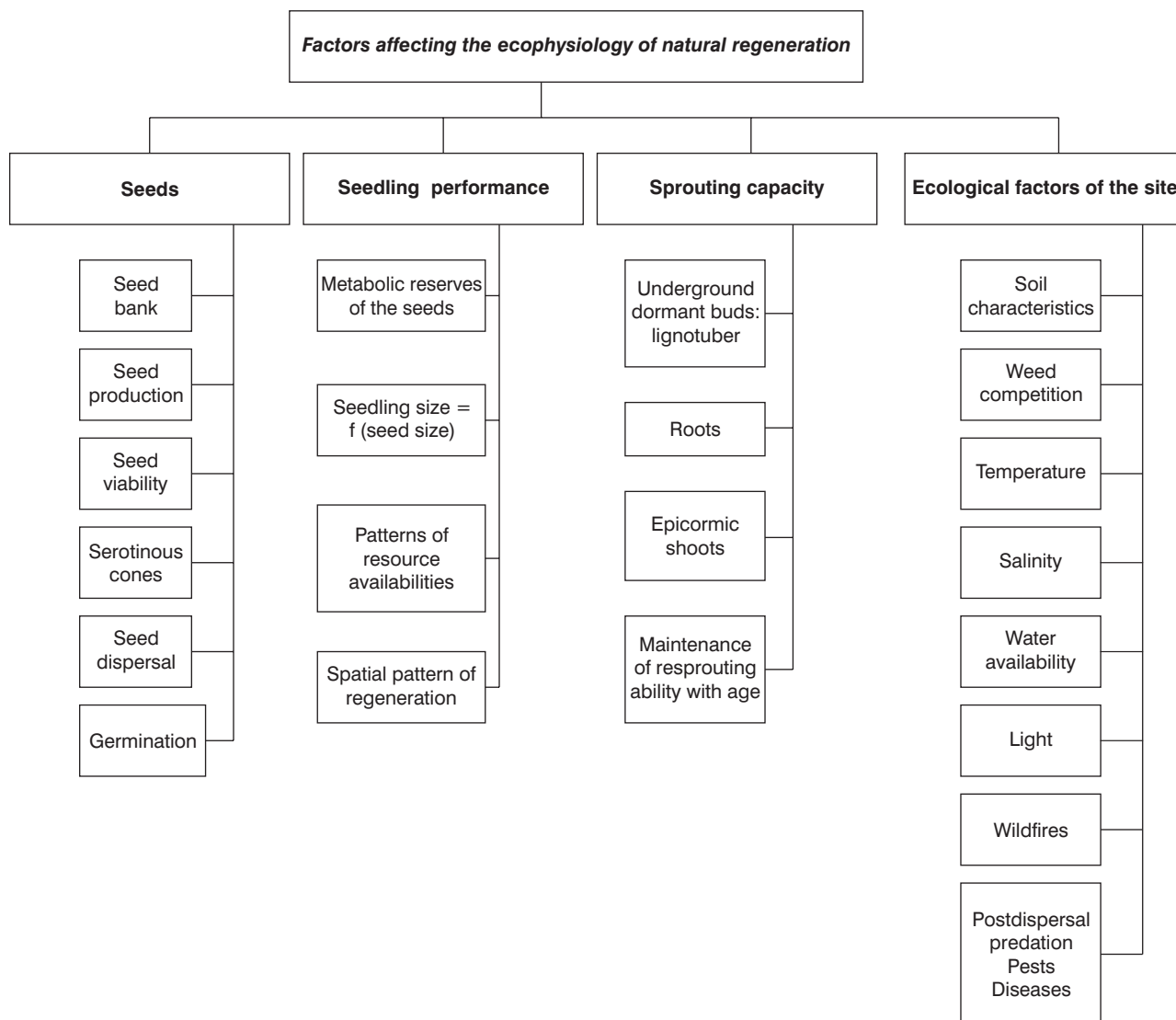
The most reliable indicator of successful regeneration is likely to be the number and size of seedlings already present. Unfortunately, destruction of seedlings by herbivores can be an important cause for regeneration failure. Browsing by deer can cause significant damage to trees, as it reduces growth and may keep seedlings within the browsing height for years (Harmer, 2001). In this sense, the transition from the seedling to the sapling stage is critical, as saplings are much less vulnerable to mortality from herbivores (Matzner, 2003). As ungulates browse selectively, it is likely that at low densities they modify the species composition, preventing the species they select most from growing beyond the sapling stage (Palmer *et al.*, 2004). Nevertheless, the relative importance of

different herbivores can change dramatically from site to site and from year to year. Predation by deer, ground squirrels, gophers, insects and livestock are main factors limiting Californian oak recruitment (Callaway, 1992). Predation of *Quercus ilex* acorns by larvae of *Curculio glandium* beetle can affect up to 50% of the annual crop. Once dispersed, seed viability is even greatly reduced by predation of squirrels, wild boars, mice and jays (Marañón *et al.*, 2004), and livestock grazing in Spanish *dehesas* (Pulido *et al.*, 2001). Seeds of *Fagus sylvatica* are highly predated by the larva of *Cydia fagiglandana* (Gil *et al.*, 1999). Plants growing under contrasting light and water availability conditions may differ in physiological and biochemical traits, prompting a different response to damage by herbivores (Baraza *et al.*, 2004).

Attention has traditionally been focused on pests and diseases of mature trees, rather than on seedlings (Romagosa and Robinson, 2003). Use of herbicides and insecticides has proved to reduce seedling mortality (Stanosz, 1994), although its use must be under control to prevent any environmental impact. Effects of such infections by pests are reduction of the photosynthetic leaf area and premature leaf drop.

Simulating forest regeneration

As mentioned before, natural regeneration is often slow, unpredictable and extremely complex, as many factors are involved. Construction of models may be useful in dealing with such complexity of ecological systems and in better understanding the impacts of the factors that influence regeneration dynamics (Kozłowski, 2002). Different approaches have been made in this sense (see Bragg *et al.*, 2004). Usually, models predict the behaviour of a tree (survival, height, diameter growth, crown size increment, propagule production) given the physical and biotic environment (e.g. temperature, percentage defoliation by pests, competition, soil moisture gradient, available nitrogen, small-scale disturbance, browsing, windthrow) that constraints its performance, using process-response functions at a scale larger than the individual plant.



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