Effect of Sexual Reproduction and Seedling Recruitment on Vegetation Dynamics in Grasslands

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Key points: Sexual reproduction and seedling recruitment are likely to influence sward dynamics and demography of grasslands whose most species show the ability of vegetative propagation. Successful seedling recruitment may be limited by seed resource and/or availability of establishment sites. There are several steps from adult plants to well-established seedlings. Seed production results from the resource sharing between vegetative and reproductive growth and from the trade-off between seed number and mean seed mass. Seeds may be dispersed by wind or by the animals, while seedling recruitment will also depend on the availability of establishment sites. Botanical composition, grassland management and soil-climate conditions will influence these steps. Management may be adapted to increase seed resource, including over-seeding, the number of open gaps in the canopy and seedling growth. The animals may play an important role as they may influence the availability of seeds, disperse them and open gaps in the canopies.

Key words: flowering, seed number, seed mass, seedling, seed bank, zoochory, over-seeding

Introduction

Identifying and understanding the mechanisms that determine the sward dynamics and demography of plant species in communities is a central challenge for ecology (Turnbull et al, 2005). Sexual reproduction and seedling recruitment are often considered as a phenomenon with limited impact on vegetation dynamics in permanent or temporary grasslands, where most species are perennials with a strong ability for vegetative propagation.

However, sexual reproduction may have a strong impact on the specific and genetic composition of complex swards through various mechanisms. A trade-off exists for resource allocation to vegetative growth and sexual reproduction. But its pattern differs among grassland species (from annual to perennial) and among genotypes within a species and is influenced by grassland management. Resource allocated to sexual reproduction will determine number of seeds and seed size, two critical physiological features for seed availability and seedling survival. They will also be strongly influenced by grassland management practices and by environmental conditions. As most grassland species are cross-pollinated, sexual reproduction will also generate new genotypes and thus contribute to maintenance of genetic diversity within swards.

Seedling recruitment and their development into adult plants depend on seed availability, number of establishment sites within the existing sward and competition between young and adult plants.
In the present paper, we will review the various ecological processes and document the influence of the management practices. This will point out the practical issues to manipulate sexual reproduction in order to preserve the agronomic and ecological values of grasslands.

The processes

Two processes are important in determining the species demography and genetic composition of a grassland community: the survival and vegetative spread of plants and establishment of seedlings possibly originating from sexual reproduction of the adults plants (Benson and Harnett, 2006), i.e. seed limitation and site limitation (Clark *et al*, 2007). Numerous physiological traits will influence both aspects and have to be regarded as functional traits (Diaz and Cabido, 2001; Pakeman *et al*, 2008). They are of special importance to explain species response to disturbance (Lavorel *et al*, 1998) or abandonment (Peco *et al*, 2005). In the present paper, we will more precisely consider relationships between vegetative propagation and reproduction, seed and propagule dissemination and seedling recruitment factors.

1-Reproduction and vegetative propagation

The coupling between reproduction and vegetative propagation may be regarded through the dynamics of vegetative and reproductive organs and through the resource allocation pattern. Strong differences exist between species and genotypes within species for both aspects.

Reproduction and dynamics of vegetative propagation

Perennial grasses exhibit a marked variation in tiller number between growing seasons (Matthew *et al*, 2000). Tiller density is influenced by species identity, neighbouring plants, soil and climate conditions and management practices. Grazing increases

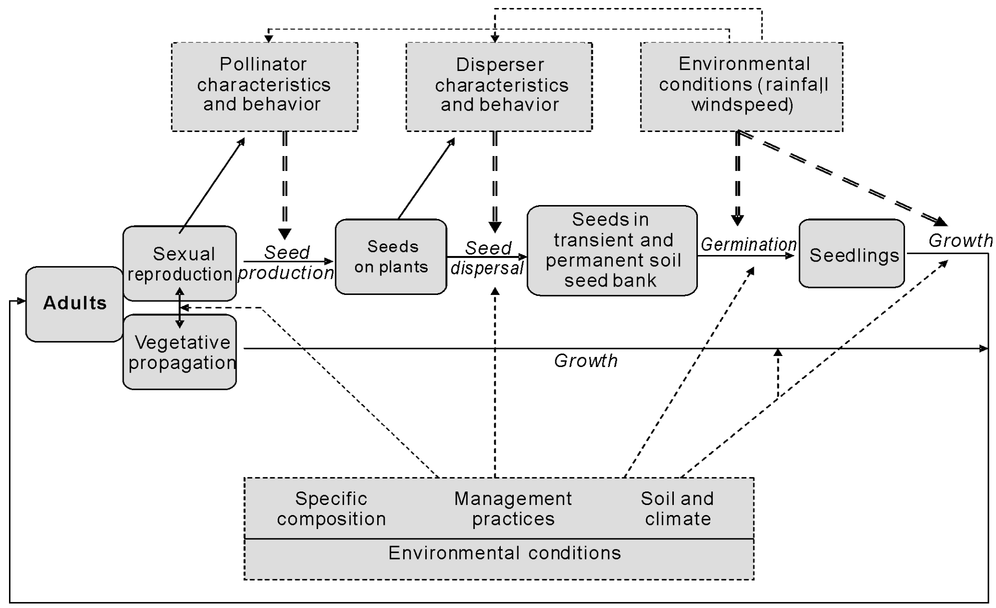

Figure 1 *Causes and consequences of patterns among seeds at various stages and vegetative propagation in grasslands (modified from Nathan and Muller-Landau, 2000).*

tiller density (*Hazard et al*, 2006). Tiller density and structure determine forage production as well as availability of establishment sites for young seedlings. Laidlaw (2004, 2005) showed that within a species, e.g. perennial ryegrass, the dynamics of tillering depended upon the mean heading date of the varieties and is a key trait for agronomic value.

Heading date and flowering date also are key factors for flowers to meet adequate conditions for pollination, including activity of pollinators in the case of legume species, and for seeds to develop under optimum temperature and water conditions. Flowering date is of special interest as it was shown in most species to be highly heritable and to exhibit a broad genotypic variation as a factor of adaptation to environmental constraints. Moreover, the advances in molecular biology have led to identify the underlying genes and this trait was found to be controlled by a few genes. For instance, Julier *et al* (2007) on the model legume *Medicago truncatula*, showed that one Quantitative Trait Locus (QTL) on chromosome 7 explained most of the variation in flowering date within mapping populations while Jensen *et al* (2005) showed that *Vnr* orthologous genes control flowering date in perennial grasses.

Reproduction and resource allocation

Seed quality, which can be assessed by the germination rate, is an important feature influenced by resource allocation. Among species, the instantaneous investment into the reproductive compartment decreases from annual to perennial species, even though the whole life cycle should also be considered, both for the number of seed produced during plant life and for the seed-to-seed cycle.

Among species, many studies have been devoted to the trade-off between seed size and seed number. In grasslands, seed number conditions the possibility for a given species (or a genotype) to access establishment sites while the seed size influences seedling vigour and survival (Moles and Westoby, 2006). Based upon cultivated crops, Sadras (2007) underlined the high plasticity for seed number in most species while seed size, a highly heritable trait, tends to exhibit a narrow genetic variation. These two features result from natural stabilising selection and are consistent with evolutionary and genetic considerations. Among plants within a given species, seed numbers appear to be related to growth rate of the mother plants.

Among species, a strong negative relationship exists between number of seeds per unit area and the mean seed mass (Moles and Westoby, 2006). This holds true across a wide range of species in various habitats. The relationship between mean seed mass and seed number per adult plant was also reported by many authors. When studying 72 species inhabiting semi-natural grasslands, Jakobsson and Eriksson (2000) reported a negative relationship between seed mass and seed number per plant ($r=-0.55$ for the log-log relationship), with a significant additive effect of plant mass. However, in dense conditions, species with big seeds tend to produce larger plants and this may lead to an absence of negative relationship between seed mass and number of seeds per adult plant. Mean seed mass may also influence wind dispersion distance, with small seeds being dispersed on longer distances.

Among genotypes within species, a narrow range of variation exists for mean seed mass, while large variation exists for the number of seeds, especially in perennial species. For a given genotype, individual seed mass is little influenced by the number of seeds per spike (Warringa et al, 1998). Number of inflorescences is an important trait, which may be expressed as a percentage of the vegetative tillers or stems (Bahmani *et al*, 2002). Genetic analyses documented relationships between heading or flowering date, vernalisation requirements and seed production in various species. In meadow fescue, Fang *et al* (2004) showed that the plant seed weight was positively correlated to the mean seed mass, while no correlation was detected with the heading date. In tall fescue, the most important traits for the seed weight are the number of fertile tillers, the number of seeds per panicle and the mean seed mass (Nguyen and Sleper, 1983).

The water soluble carbohydrates (WSC) may be involved in the resource allocation pattern between reproductive and vegetative growth. In perennial ryegrass seed crops, Trethwey and Rolston (2007) showed that WSC accumulated in the basal internode of reproductive tillers during seed fill was equal in mass to the seed yield and suggested they could be mobilised after seed harvest for new vegetative tiller growth. This same pattern could play an important role in grasslands.

2-Dissemination

From seed production to seedling emergence, dissemination is a complex process where it is necessary to consider 1) the various possible seed resources, 2) seed dispersion mechanisms, and especially the role of grazing animals in this process and 3) seed predation.

There are two seed resources; direct seed rain from the living adult plants, and the seed bank (Pakeman and Small, 2005). Specific composition of both resources is very different, the seed rain being closer to the specific composition of the canopy (Chabrerie and Alard, 2005). Most species used in temporary grasslands show a poor survival in the soil seed bank. According to Ghersa and Martinez-Ghersa (2000) on the basis of weed species, seed mass plays a role in seed survival and vertical distribution in the soil seed bank. The respective contribution of seed rain and permanent soil seed bank will depend upon the degree of disturbance of vegetation and soil: contribution of the seed bank being predominant after severe disturbances.

The main modes of seed dispersion in grassland are anemochory (wind) and zoochory (animals). The peculiarity of grasslands is the possible role of herbivores and especially the digestive gut. Comparing species present in vegetation and faeces, Pakeman *et al* (2002) and Cosyns *et al* (2005) reported large differences among animal species and plant species. When controlling the amount of seed ingested by dairy cows and collecting all the faeces for 13 forage grasses and legumes, we showed that the survival rate for seed after transit through the digestive tract ranged from 0.7% for red clover to 100% for *Agrostis stolonifera* with little effect of seed size, in the range of species under study. This supports the findings of Bruun and Poschlod (2006). Dissemination by ruminants may thus act over long distances and induce seeds transfer from one paddock to others. This may also influence dissemination of seed endophytes (Rolston et al, 2001). Within a given paddock, long distance dissemination will reduce spatial specific and genetic heterogeneity of the canopy.

As shown from the seed survival rate, ruminants may be a major predator for seeds in temporary and natural grasslands. Many other predators may reduce seed availability after dispersion. Thus, Moles and Westoby (2006), across a set of 361 species, showed a small positive relationship between seed mass and the rate of survival after a 24h exposure to post-dispersal predation.

3-Seedling recruitment factors

In temporary temperate grasslands, Edwards et al (2005) showed that plant species composition and diversity was strongly limited by recruitment of seedlings. Recruitment of seedlings will be influenced by seed resource, availability of establishment sites and seedling growth and survival. Availability of establishment sites depends upon the structure of the existing vegetation as a consequence of the sward specific composition, soil and climate conditions and management practices. When defoliation (perturbation) exceeds plant growth over long periods of time, plant diversity will be lost (figure 2). However as numerous gaps open in the swards they become possible establishment sites. If the number of establishment sites is the limiting factor, abundance and distribution of species are readily framed as an issue of competing ability, regeneration niches and the relative abundance and quality of establishment sites as shown by Muller-Landau *et al* (2002) in tropical forests.

After emergence, young seedlings are very susceptible to defoliation as this will drastically reduce their leaf area and may cause seedling mortality for many grassland species. The main sources of predation may be invertebrates, such as slugs, rodents and ruminants; the contribution of each group depends on the management practices, including grazing management. The species of grazing animals will condition defoliation height while the stocking rate and the mode (rotational *vs*. continuous) will determine defoliation frequency of possible young seedlings.

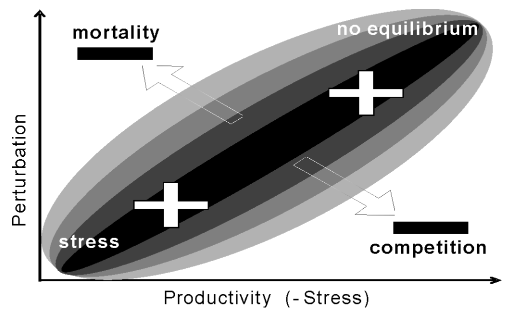

Figure 2 *The processes which condition plant diversity in grassland communities. High (+) or low (−) levels of diversity depend on combinations of stress and perturbation constraints (adapted from Huston, 1994).*

A last critical factor for successful seedling recruitment will be a quick growth of the seedlings. Many authors showed the role of seed size in seedling growth rate, with a quicker growth of seedlings arising from large seeds. This holds true among species as well as within species. However, this is not the only source of difference among species. The young seedlings will be in competition with the existing adult plants. When there is no limiting factor for the growth of the adult plants, seedlings would have very little chance to survive, as few establishment sites will exist. In more severe environmental conditions, the situation may be different with the adult plants and the young seedlings showing different growing patterns. Indeed, when germinating after a dry period, a seedling will explore the top soil layer while most roots of the adult plants will explore lower soil layers, where less water and less nitrogen may be available. Thus, the growth rate of the seedlings and the tillering rate (in the case of grass species) may be higher.

As a consequence of the complex processes leading to seedling recruitment and the competition between seedlings and adult plants, it may be argued that sexual reproduction plays a very limited role in perennial swards. In a modelling experiment of the dynamics of communities of *Ranunculus repens*, a clonal perennial herb, Watkinson and Powell (1993) showed that a successful establishment of only 0.5% of the total stems was needed to maintain genetic diversity. This demonstrates that a low number of newly established seedlings successfully contribute to the demography of a perennial sward.

Consequences for management

Sexual reproduction and seedling recruitment may contribute to genetic and specific diversity of swards and to its demography over years. As a consequence, they may influence the long term agronomic value of grasslands. This analysis of the physiological processes and of their responses to environmental conditions points out some keys in management to better exploit sexual reproduction and seedling recruitment.

1-Grazing management

Grazing management is critical for several reasons. Indeed, it has an impact on many processes which influence sexual reproduction and seedling recruitment. The stocking rate and the frequency of defoliation will condition the actual seed production. More seeds are likely to be produced under low stocking rate with long intervals between two grazing periods. It will also influence the availability of establishment sites, but in an opposite direction. Animals will then both disseminate and predate seeds.. Eventually, they may defoliate the young seedlings, with an effect of the type of animals because of the defoliation height. The optimum management will come from a balance between production and defoliation (Figure 2). Edwards *et al* (2005) showed that with seed addition under sheep grazing, seedling recruitment was higher under rotational grazing but the long term seedling survival was better under continuous grazing (Figure 3). One more option may arise from the management of un-grazed areas which may be left till full seed maturity where the animals will graze and disseminate them. It is very important to avoid over-grazing where large areas of soils will be open, with a possible germination of the permanent seed bank whose species may be very different from the pre-existing canopy. Increased grazing intensity may lead to an increase in species with rosette habit, low minimum height, a ruderal strategy, an annual life history and regeneration by seed (Pakeman, 2004). The severity of the disturbance in terms of depth of disturbed soil will determine composition as well as rate of vegetation recovery (Pakeman and Small, 2005). In cases of a lack of forage resource, it is better to group the animals on a limited area when they might be fed with dry forage, while the rest of the pastures will be left un-grazed. The alternative solution where animals have access to all the pastures may induce a generalized damage to the swards.

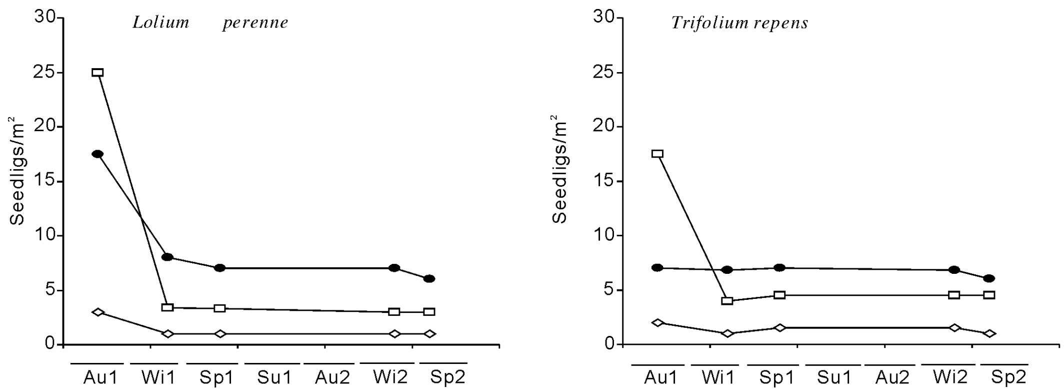

Figure 3 *The effect of sheep grazing management on seedling densities of perennial ryegrass and white clover from Autumn 1 till Spring 2 (sowing in Summer 1).*
Codes: ●: sown plots + continuous grazing; □: sown plots + rotational grazing 36 days; ◇: unsown plots averaged over continuous and rotational grazing treatments. Plots were broadcast sown with 1000 seeds .m-2 of each species (Adapted from Edwards et al, 2005)

2-Reseeding and over-seeding

Providing new seeds may overcome the seed limitation which is said to occur in 50% of the situations according to Turnbull *et al* (2005). It is then necessary to decide the species to be used, the rate of over-seeding and the methods. The species must be chosen in order to restore the vegetation to its optimum for the function assigned to grassland under renovation, either with native species or exotic species with high agronomic value. For instance, it may be very useful to over-seed with forage legumes if their proportion irreversibly declined below a threshold. Species with a high seedling growth rate will better establish, but the methods of over-seeding may partially overcome this difficulty. Using legume species and seed lots with a high rate of hard seed may expand the period of germination and increase the rate of successful establishment, especially in environments with dry and unpredictable weather conditions.

In order to facilitate recruitment of young seedlings, it may necessary to cut or graze the existing swards at very low heights right before over-seeding. This will reduce the competition and slow down the regrowth of the adult plants. It is also necessary to open strips so that the young seedlings do not experience competition during the first stages after emergence. Suitable machinery was developed and tested worldwide (Huguenin-Elie *et al*, 2007). The success of this management depends on the botanical composition of the existing swards, with a negative impact of the stoloniferous species, and of the weather conditions.

Hay strewing with a hay rich in seeds of various species is an alternative solution which may allow a quick establishment and a long persistency of the introduced species (Kiehl and Wagner, 2006). However, it will only be relevant for small areas and should be recommended for restoration of grasslands with a high environmental and biodiversity value.

Conclusions

Sexual reproduction and seedling recruitment in grasslands have received little attention as they were considered to have a limited impact on vegetation dynamics and demography of these complex swards. However, even occurring at low rate, they are likely to play a role for maintaining species diversity. An increasing number of papers show that the species diversity has a strong impact on the agronomic and environmental value of grasslands. The occurrence of seed production and seed recruitment in temporary and permanent grasslands should be better documented and recognised by the farmers as an important mechanism in the dynamics of grasslands. Management will have a major impact, in particular through the effect of the animals. Over-seeding offers interesting perspectives as it overcomes seed limitation and makes it possible to introduce species with high agronomic value without strong disturbance of the swards, thus preventing any strong negative environmental impact.

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