

# Chapter 19

## The Swiss Mountain Wooded Pastures: Patterns and Processes

A. Buttler<sup>1,2,3,\*</sup>, F. Kohler<sup>1,2</sup>, and F. Gillet<sup>1,2</sup>

**Abstract** Influenced by the combined action of grazing and forest management, wooded pastures represent a traditional form of multiple use of natural resources in some European mountains. This fragile semi-natural ecosystem is characterized by the coexistence of high biodiversity and extensive land use. Based on experimental and observational studies carried out at various spatial scales in the Swiss Jura Mountains, this chapter provides an insight into patterns and processes occurring in this typical silvopastoral ecosystem. Summer grazing by cattle is the main driving force affecting vegetation dynamics. Large herbivores influence vegetation in three ways: grazing and browsing, dung and urine deposition and trampling. Field observations reveal a high heterogeneity of cattle activities at both fine and large scales. Cattle habitat use controls the dynamics of plant species and functional groups in the herb layer. Natural tree regeneration is also closely affected by cattle activity and related to the heterogeneous environment. Distribution of tree seedlings is spatially associated with specific physical structures or nurse plants that facilitate their survival in the herb and the shrub layers. Moreover, the growth of tree saplings is related to grazing intensity. Knowledge of ecological functioning of wooded pastures has allowed the development of a novel, spatially explicit, mosaic compartment model of the dynamics of silvopastoral ecosystems. This model is able to explain some aspects of the origin of vegetation heterogeneity in pasture-woodland landscapes. The conservation of such ecosystems is an important challenge considering its complexity and the present change in agricultural practices in mountain regions. A better integration of ecological and socio-economic processes

---

<sup>1</sup>Swiss Federal Research Institute, WSL Site Lausanne, Switzerland

<sup>2</sup>Ecole Polytechnique Fédérale de Lausanne (EPFL), Ecological Systems Laboratory, 1015 Lausanne, Switzerland

<sup>3</sup>Laboratoire de Chrono-environnement, UMR 6565 CNRS, Université de Franche-Comté, Besançon, France

\* Corresponding author: Laboratoire des systèmes écologiques – ECOS, Ecole Polytechnique Fédérale de Lausanne (EPFL), Bâtiment GR – Ecublens, Station 2, CH - 1015 Lausanne, Switzerland; e-mail: alexandre.buttler@epfl.ch

into predictive multi-level models will permit the exploration of the conditions for sustainable management schemes compatible with biodiversity conservation.

**Keywords** Cattle activity, plant functional groups, modelling, spatial-temporal scale, tree regeneration

## Introduction

Semi-natural silvopastoral ecosystems, such as wooded pastures, form traditional landscapes in Europe (Etienne 1996). Influenced by a combined action of cattle grazing and forest management, the wooded pastures represent a form of multiple use of natural resources. This type of land use is particularly interesting when considering the challenges in sustainable management of mountain areas. Due to changes in agricultural practices towards either local intensification or extensification, most of the silvopastoral ecosystems in Europe suffered a large decline during the last century (Gillet and Gallandat 1996b). Considering the high cultural, socio-economic, ecological and landscape values of this ecosystem, there is an increasing need to develop conservation tools.

Integrated management planning of wooded pastures requires an intensive collaboration between agronomists, foresters, ecologists and sociologists (Gmür and Wettstein 1986; Gmür et al. 1989; Perrenoud et al. 2003). In silvopastoral ecosystems, the question of management type and use intensity is critical. Strategic objectives may aim at the conservation of the state of wooded pastures, or to more or less severe restoration measures, even through re-creation starting from closed forests or open grasslands. Successful management, in particular for biodiversity conservation, requires traditional scientific observation and experimentation and is generally not yet founded on specific scientific tests, but based on anecdotal evidence or, at best, on inductive studies (Rook et al. 2004). The understanding of the main ecological processes occurring in wooded pastures is therefore essential for efficient management schemes of this threatened ecosystem.

In this context several studies were undertaken since more than 20 years in the wooded pastures of the Swiss Jura Mountains, where this ecosystem is still the most abundant type of man-made landscape (Gallandat et al. 1995). In this chapter we summarize results of our work and related studies describing ecological patterns and processes in wooded pastures. We first describe the management and the high biological value of this ecosystem. Second we present the hierarchical organisation of the system. Third we focus on three key processes participating in vegetation dynamics. Fourth we present a predictive spatially explicit model integrating all current knowledge. Finally we conclude with research and management perspectives.

## The Swiss Wooded Pastures

### *A Multi-user Landscape*

In the Swiss Jura Mountains, wooded pastures occur in the mountain and subalpine belts, mainly at an elevation between 800 m and 1,400 m asl. At lower altitude, they occupy a transitional zone between the cultivated areas close to the villages and the forest, whereas at higher altitude, they are widespread around the timber line (Gillet and Gallandat 1996b). The climate of this area is predominantly oceanic with a mean annual rainfall of about 1,600 mm at 1,200 m asl (including more than 400 mm snow precipitation) and a mean annual temperature of 7°C. At 1,200 m asl, mean day temperature is below 0°C more than 60 days per year and the ground is generally covered with snow from December to April.

As in other temperate mountainous regions the climate limits cattle management to the summer period, from the end of May to the end of September. Cattle herds are mainly composed of heifers, but dairy cows can be seen on about half of the pastures and in some areas horses can be the main livestock type. Livestock density ranges from 0.5 to 1.5 adult bovine units per hectare (Gillet and Gallandat 1996b), which is low compared to intensive grazing systems. For a farm unit, the surface occupied by pastures ranges from about 30 ha to about 300 ha. The vegetation is very diverse and four main structural types may be recognized in a typical pasture-woodland landscape (Gallandat et al. 1995; Vittoz 1998): unwooded pastures (open pastures with less than 1% tree cover), scarcely wooded pastures (tree cover between 1% and 20%, trees mainly scattered in a grassland matrix), densely wooded pastures (tree cover between 20% and 70%, trees aggregated in thickets) and grazed forests (closed forests with more than 70% tree cover). Two grazing systems are applied in wooded pastures (Gillet and Gallandat 1996b): (1) free range: the animals spend the whole summer season roaming freely through the pastures; (2) grazing rotation: the pasture is subdivided into paddocks and the animals circulate from one to another according to a variable rotation period (between two and seven rotations per grazing season, corresponding to a stay in each paddock of 10 to 80 days). More and more wooded pastures are now managed according to the rotation grazing system, with the aim of optimizing the utilization of the resources. Generally, pastures are fertilised with farm manure and mineral PK fertilisers, with rates that often exceed the official recommendations (Meisser 1993). In addition, mineral nitrate fertilizer is sometimes applied on pastures grazed in rotation by dairy cows, but this practice is illegal in wooded pastures placed under the Swiss forest regulation, in particular to protect water against pollution in the karstic areas. For the maintenance of the pasture, unpalatable weeds and shrubs are partially removed more or less regularly using mechanical or chemical methods, in order to prevent loss of grazing area.

The goal of forest management is mainly to maintain the overall tree cover and landscape heterogeneity, since logging is not generally a profitable activity, except

in densely wooded pastures and forests. Foresters intervene in scarcely wooded pastures mainly to remove dying or affected trees and to check on natural re-growth. In general, the wood is not of high quality and its commercialisation no longer covers the costs of the tree felling, but was an important resource in the past. The stumps are usually left in place. If natural regeneration fails, new saplings may be planted, usually around the stump, and fenced for protection against cattle. The forester's personal experience and local tradition play an important role in planning spatial distribution of trees (clusters of trees vs. isolated ones) (Gillet and Gallandat 1996b). This know-how is an important requirement for landscape protection and to maintain its capacity to provide multiple goods and services.

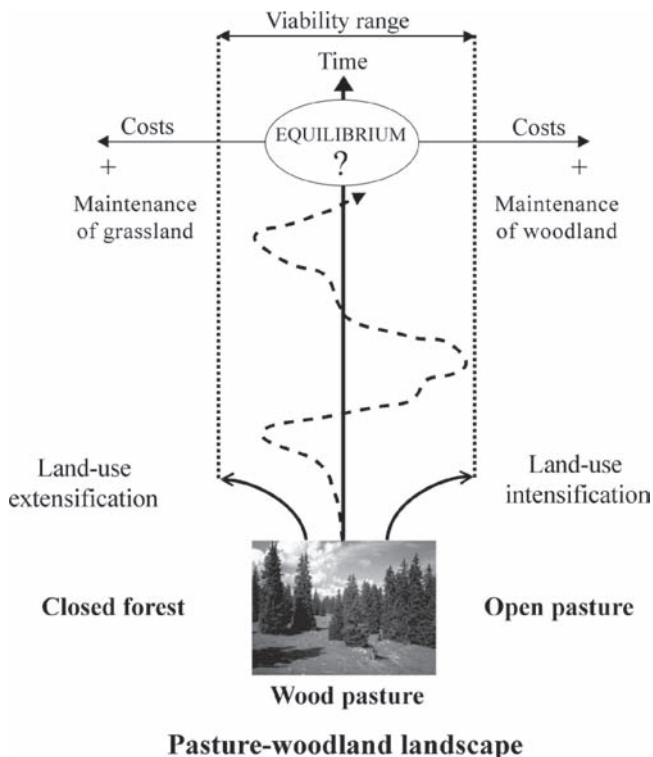
From a socio-economic point of view, the main users of wooded pastures are farmers, even if in some regions revenues generated from forestry activities may be quite significant. Besides the farmers and foresters, a wide variety of occasional users become more and more important: hikers, skiers, horse riders, cyclists, picnickers, etc. The importance of this landscape for the tourist economy is considerable, although difficult to quantify. By interviewing visitors of wooded pastures, Miéville-Ott and Barbezat (2005) showed recently that almost two-thirds of those consider wooded pastures as a recreational place. The majority came to the site to walk, for exercise and to experience nature.

### *A Landscape Sheltering High Plant Diversity*

Vegetation in wooded pastures ranges from open grasslands to closed forests including wood-pastures with scattered or clumped trees (Gillet and Gallandat 1996a). In typical wooded pastures, the regeneration of both grassland and woodland is natural compared to other types of agroforestry systems, where trees are usually planted and grass is sown (Rigueiro 1985; Silva-Pando et al. 1998, 2002). Nevertheless, the origin of trees could be different depending on the edaphoclimatic conditions.

Consequently, this landscape results from a balance between divergent ecological processes such as cattle pressure and tree regeneration. Coexistence of patches of pastures and woodlands or isolated trees is therefore a result of an unstable equilibrium between extensification and intensification, which can lead, if there is departure from this equilibrium, either to closed forests or open pastures with concomitant loss of biodiversity (Fig. 19.1).

In a large scale survey (Gallandat et al. 1995), one sixth of the Swiss vascular flora (about 3,000 species) was observed in the wooded pastures of the Swiss Jura Mountains. Moreover Vittoz (1998) listed 554 vascular plant species occurring within a 70 km<sup>2</sup> area. Plant biodiversity is also very high at fine scale (Table 19.1). The origin of this multi-scale high plant species richness is multiple. First, soil variability is important ranging from shallow calcareous to deep, acidic and silty soils. Spatial heterogeneity can also be very high (Havlicek et al. 1998). This can be observed at a very fine scale and induces at meter scale a fine mosaic of various



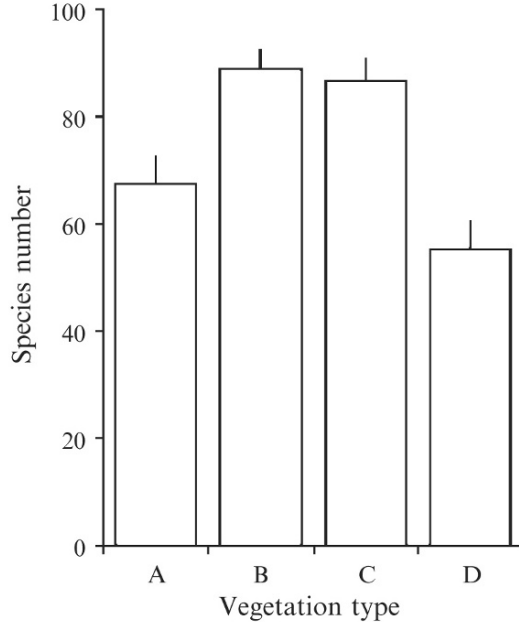
**Fig. 19.1** Wood-pasture landscape dynamics as the result of extensification and intensification (From Gillet in press)

**Table 19.1** Multi-scale plant species richness of the Swiss wooded pastures

Scale	Mean number of species	N	Source
10,000m <sup>2</sup>	196 (max.: 221)	5	Dufour (2006)
2,500m <sup>2</sup>	149 (max.: 178)	20	Dufour (2006)
625m <sup>2</sup>	106 (max.: 142)	80	Dufour (2006)
156m <sup>2</sup>	70 (max.: 106)	80	Dufour (2006)
1 m <sup>2</sup> of a grazed meadow	28 (max.: 41)	100	Kohler (2004)
0.01 m <sup>2</sup> of a grazed meadow	10 (max.: 20)	800	Kohler (2004)

vegetation types (Gobat et al. 1989). Second, a complex mosaic of trees, shrubs and open grasslands create various microclimates favouring different plant species. Gillet et al. (1999) determined a species richness optimum at 30% of tree cover. Third, as we will see in more details in the following sections, cattle activities can change plant species composition. Finally, as recently shown by Dufour et al. (2006), plant species richness is related to topographic complexity described by elevation variability and its spatial configuration.

**Fig. 19.2** Total vascular plant species richness in the four main vegetation types: A: unwooded pastures (tree cover < 1%, N = 19); B: scarcely wooded pastures (tree cover < 20%, N = 42); C: densely wooded pastures (tree cover < 70%, N = 33); D: closed grazed forests (tree cover  $\geq$ 70%, N = 21). Error bars are standard errors of the means



Wooded pastures are therefore a good example of a landscape where high biodiversity can coexist with extensive land use (Fig. 19.2). Many transitional zones and boundaries occurring in a highly heterogeneous and fluctuating environment, including various tree densities, create optimal conditions for biodiversity.

## The Hierarchical Organisation of Wooded Pastures

Hierarchy theory (O'Neill et al. 1986; Wu and David 2002) is a powerful framework to describe silvopastoral ecosystems. Different nested levels of organization can be recognized in the vegetation of wooded pastures (Gillet and Gallandat 1996a). At landscape level, a mosaic of phytocoenoses can be seen, ranging from unwooded pastures to grazed or ungrazed closed forests (Fig. 19.3). Each phytocoenosis is itself a complex system of elementary plant communities, i.e. moss, herb, shrub and tree synusiae. Each synusia is an assemblage of organisms belonging to a limited pool of plant species or plant functional groups (Fig. 19.3).

The same hierarchical approach can be used to describe cattle behaviour (Bailey et al. 1996). Different spatial scales can be defined functionally, based on characteristic behaviour occurring at different stocking rates. In wooded pastures, three spatial scales seem to be important. At large scale, the human (e.g. fences, water

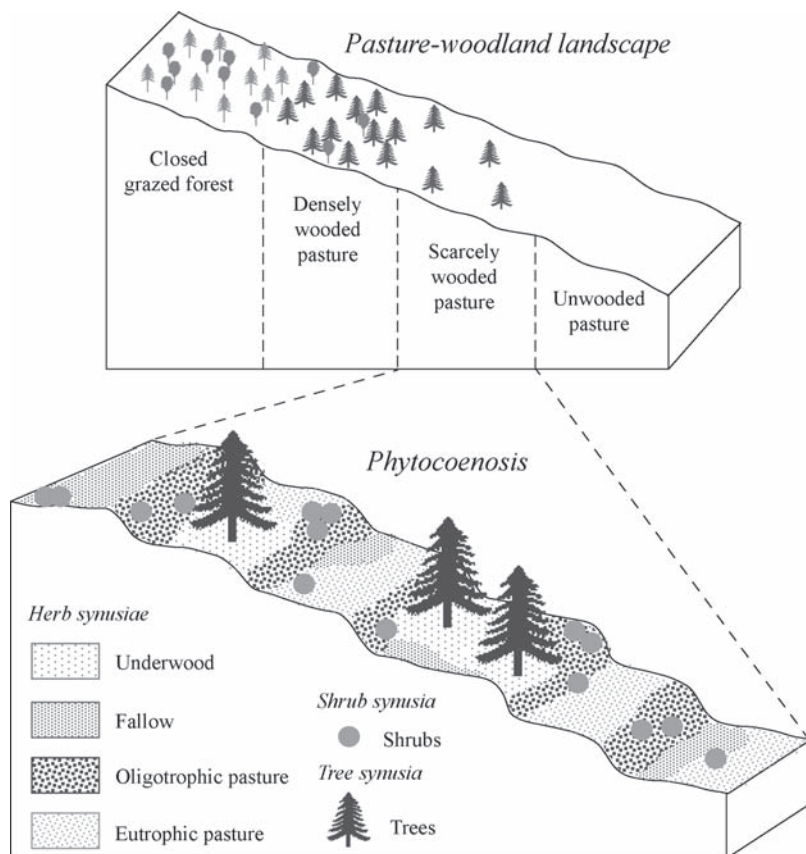
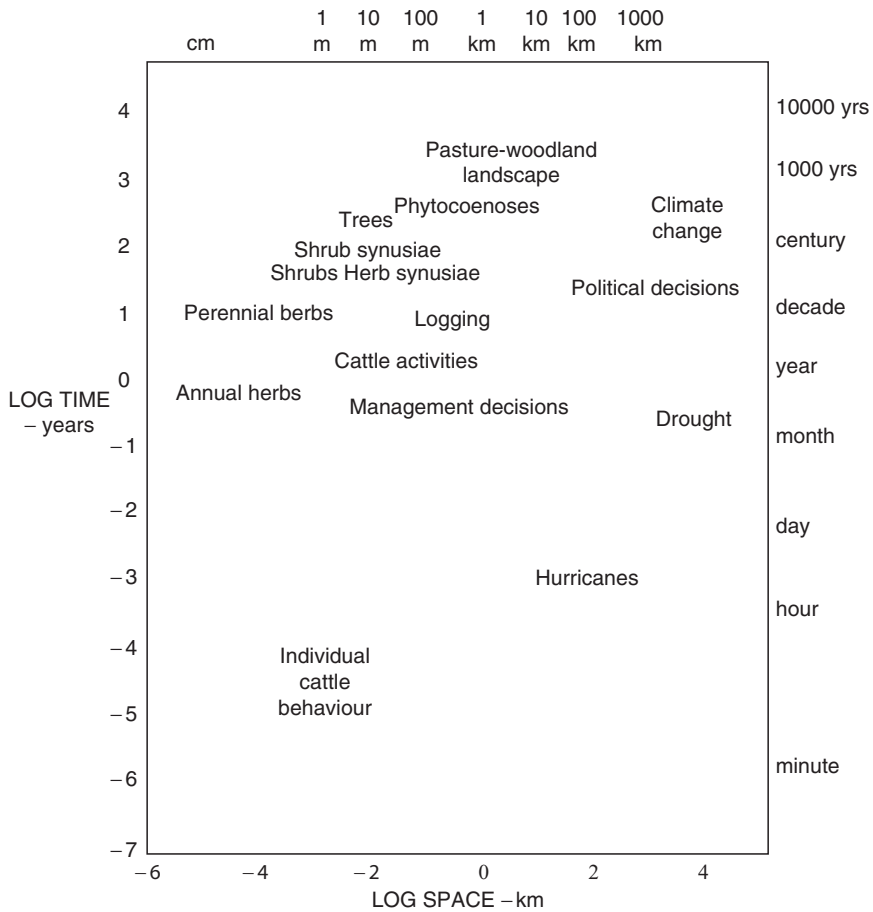


Fig. 19.3 Nested organisation levels in wooded pastures (Modified from Gillet and Gallandat 1996a)

points) and natural (e.g. slope, openness) landscape structures of the paddock will induce the first general patterns of cattle activity (Kohler et al. 2006a). At medium scale (few square meters), among plant communities, cattle choose communities with the best forage availability (Kohler et al. 2004a). At fine scale, within a given plant community, cattle avoid dung pats (Kohler 2004) and unpalatable plants (Smit et al. 2005).

Each entity or process considered in a silvopastoral ecosystem has a characteristic spatial and temporal scale (Fig. 19.4) and processes occurring at a certain scale may impact on entities at another scale. For example, a cattle foraging behaviour of few minutes can have an impact during decades on the tree pattern, or some political decision in relation to agriculture policy can have a long-lasting effect on the entire landscape. The integration of all these spatial and temporal scales has to be taken into account for sustainable management.



**Fig. 19.4** Objects and processes occurring in silvopastoral ecosystems with their respective space and time scales

### Three Key Ecological Processes

#### *The Heterogeneous Patterns of Cattle Activities*

Livestock activity is an important factor in structuring vegetation in silvopastoral ecosystems (Olf and Ritchie 1998). Large herbivores may influence vegetation in three ways: (1) herbage removal and tree-shrub browsing, (2) trampling, (3) dung and urine deposition. Herbage removal – or grazing *sensu stricto* – is the main biotic factor affecting herbaceous vegetation structure and dynamics in pastures (Rook et al. 2004). The effect of herbage removal on plants is principally the loss



of above-ground biomass and consequently a change in light competition between species (Grime 2001). Furthermore, herbage removal induces an exportation of biomass, linked with a local loss of soil nutrients. Cattle generally select for a grass-based diet with a high digestibility and high N and P concentrations (Mayer et al. 2003). Due to the high levels of difficult-to-digest lignin and secondary metabolites, most woody species are generally avoided by cattle (Gordon 2003). However, browsing by livestock has been identified as an important factor preventing tree regeneration in wooded pastures (e.g., Bakker et al. 2004; Allcock and Hik 2004). Trampling affects the vegetation through detaching or destroying plant material with hoof action and by influencing the water regime in compacting the soil (Abdelmagid et al. 1987). By contrast to herbage removal, biomass stays in this case on the ground and nutrients return to the soil. Trampling can create gaps and produce competition-free space for plants. Dunging – or, more widely, fertilising – is also considered an important factor affecting vegetation productivity and composition of herbaceous or dwarf-shrub communities (Bakker and Olff 2003). Statistical comparisons between primary productivity and species richness across various community types generally lead to a “hump-shaped” model, with a peak of richness at a low to intermediate level of productivity (Grime 2001).

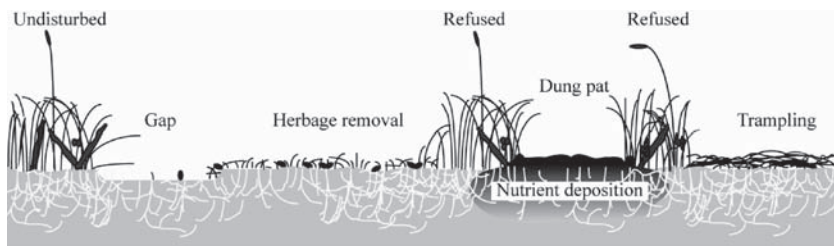
There is evidence that the fine and large scale spatial patterns of grazing, trampling and dunging are heterogeneous in wooded pastures:

1. The spatial pattern of foraging is the best-studied attribute of cattle activity (Senft et al. 1987; Coughenour 1991; Bailey et al. 1996). At large scale, the selection of grazing locations by cattle depends on herbage quality and quantity, water availability, relief, slope, elevation, aspect, natural and artificial barriers, herd social interactions, prior experience, and climate (Rice et al. 1983). Cattle preferentially graze plant communities of high nutritive value (Roath and Krueger 1982) and this preference seems to partially control the distribution of cattle in a paddock (Putman et al. 1987). From observations made on a complete paddock of 23 ha, we observed, at the beginning of the season when resources were abundant everywhere, that heifers grazed preferentially near the wire fence (Kohler et al. 2006a). Grazing patterns became less noticeable over the rotations resulting in a more homogeneous pattern at the end of the season. At very fine scale (decimetre scale) herbage removal also presented a heterogeneous pattern (Kohler et al. 2004a). For example, dung patches, and to some extent also urine patches, induce a reduction of the herbage attractiveness during the first months or years after deposition (Edwards and Hollis 1982) and consequently create a heterogeneous pattern of herbage removal (Fig. 19.5).
2. The distribution of trampling effects depends not only on the number and pressure of hoof prints in an area, but also on the sensitivity of the vegetation to trampling (Roovers et al. 2004), which is likely to be affected by slope, soil texture and water content. On steep ground grazed by sheep and red deer, Hester and Baillie (1998) showed that at low densities, vegetation was more affected by trampling than by herbage removal. In wooded pastures, Kohler et al. (2006a) observed that the paddock-scale pattern of trampling tended to concentrate in

wooded areas and in rocky areas with poor forage quality. At decimetre scale, by using vertically planted wooden sticks, which allow the measurement of cattle trampling when they were broken or flattened, we also observed a fine-scale spatial heterogeneity of the trampling pattern (Kohler et al. 2004a).

3. The spatial distribution of faeces and urine from cattle is not uniform and their concentration is often higher in areas of special attraction, such as near water sources, gates or fences, and in shade and shelter belts (Peterson and Gerrish 1996; White et al. 2001). In mountainous regions, cattle faeces are significantly associated with slope, aspect, topographic position and season (Tate et al. 2003). For instance, daily faecal load is higher in flat areas and during the dry season (Costa et al. 1990). In the Swiss wooded pastures, the pattern of dung pat density seemed to occur mostly in flat areas without rock outcrops and with low tree and shrub cover near the centre of the paddock (Kohler et al. 2006a). At fine scale the deposition of dung pats and urine by cattle create spots of small area with a high concentration of nutrients (MacDiarmid and Watkin 1972) (Fig. 19.5). Every year dung pats are dropped in other locations than in previous years creating a fine-scale shifting mosaic of nutrient availability.

Patterns of grazing, trampling and dung and urine deposition are therefore conditioned by different factors inducing non-congruent patterns. At large scale we observed a negative correlation between herbage removal and dunging and between dunging and trampling patterns (Kohler et al. 2006a). If, as we expect, the observed patterns of habitat use are consistent over many years, differences in spatial distribution of cattle effects at the landscape level may have important ecosystem implications (Gander et al. 2003; Jewell et al. 2005). In particular, the spatial segregation of feeding and excretion should lead to a transfer of nutrients from feeding places to resting places, with trampling effects concentrated in intermediate situations such as along paths. Jewell (2002) came to the conclusion that the soil P content of the most heavily used part of a paddock of an alpine pasture in the Swiss Alps could be reached after 200 years of grazing and that the nutrient-poor vegetation was the result of a long period of nutrient depletion by cattle. However, patterns might vary in warm and dry conditions, as suggested by results from intensive pasture systems, where the heterogeneity of the spatial distribution of faeces



**Fig. 19.5** Pattern of fine-scale vegetation heterogeneity induced by cattle activities (From Kohler 2004)

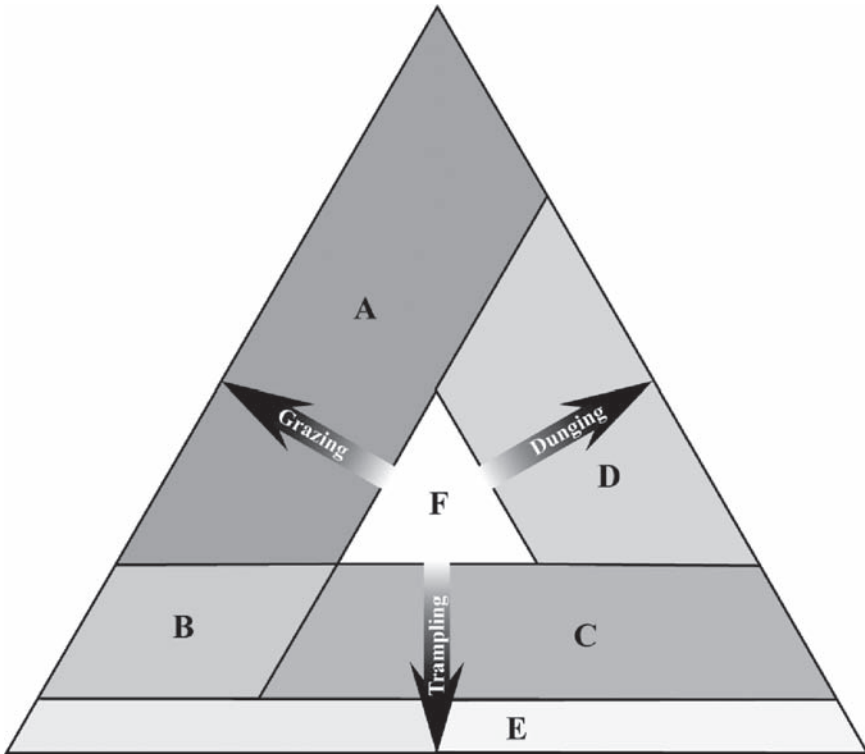
and urine was increased (White et al. 2001). A more comprehensive assessment of nutrient transfer and its implication on grass growth and nutrient leaching is still needed and requires a modelling approach (McGechan and Topp 2004).

At fine scale, we also observed non-congruent patterns of cattle activity (Kohler et al. 2004a) (Fig. 19.5) but, in contrast with the large-scale patterns, rapid changes in the spatial patterns should be expected. Patterns of dung and gaps created by heavy trampling obviously change from year to year and the grazing pattern is partly determined by the dung pattern (see above). At fine scale, pastured areas can therefore be considered as a patchwork of various levels of disturbances (trampling and grazing) and resources (nutrients from dung and urine), which can change from year to year and induce various changes in the herb layer in situations with a low to intermediate stocking rate.

### ***A Shifting Mosaic Model to Describe Herbaceous Vegetation Dynamics***

As shown in the previous section, in silvopastoral ecosystems, herbaceous plant communities undergo change in resource availability and disturbance regime at various temporal and spatial scales. The fine-scale aspects of these processes were explored by Kohler (2004), who showed that grazing, trampling and fertilizing (dung and urine) have different impacts on the vegetation, creating fine-grained mosaics in the herb layer. From experimental (Kohler et al. 2004b, 2005) and observational (Kohler et al. 2004a, 2006b) complementary approaches, six general plant species groups were defined by their response to cattle activities (Kohler 2004) (Fig. 19.6):

1. Group A: This species group is favoured by herbage removal and the absence of trampling. Beside an increase in biomass, interaction between herbage removal and addition of nutrients does not induce the appearance of new species. This group includes a large number of species and consequently herbage removal has a positive effect on species richness. These species are generally of small stature and are resistant to stress (*sensu* Grime 2001).
2. Group B: Interactions between herbage removal and trampling favours a species group indifferent to fertilisation, as for group A, but which contains small species and legumes. In condition of low light availability, the ruderal strategy (*sensu* Grime 2001) is related to this group.
3. Group C: This species group is favoured by trampling without herbage removal and is unaffected by nutrient addition. The number of species in this group is low and consequently trampling induces a species richness decrease, particularly when light availability is low.
4. Group D: This group of species is favoured by fertilisation in the absence of grazing and trampling. Tall grasses with a competitive strategy (*sensu* Grime 2001) characterise this group.



**Fig. 19.6** Triangle representing the three factors acting at fine scale in herbaceous vegetation and corresponding plant response groups A–E. Group A contains species favoured by herbage removal and the absence of trampling. Group B contains species reacting to interactions between herbage removal and trampling. In group C, species are favoured by trampling without herbage removal. In group D, species are favoured by fertilisation in the absence of grazing and trampling. In group E, species are favoured by a high level of trampling and gap creation. In group F, species are favoured by the absence of the three cattle activities (From Kohler 2004)

5. Group E: This group is favoured when the level of trampling is high enough to create gaps. Species of this group have small seed weight, unspecialized seed dispersal, persistent seed bank and high vegetative spread.
6. Group F: This group is favoured by the absence of the three cattle activities. Species characterising this group are mainly tall forbs and some tall grasses.

These groups are not mutually exclusive. Traits, which are important for one response, are not necessarily essential for another. Moreover, Kohler et al. (2004b) observed that change induced by cattle activities were mainly quantitative, so that, in the short term (several years) most species were able to survive in all conditions. Consequently, depending on the cattle activity at local scale, certain species will dominate, while others may survive with a reduced abundance. In grazed meadows, it seems that only conditions with fertilisation alone induce a fast and important

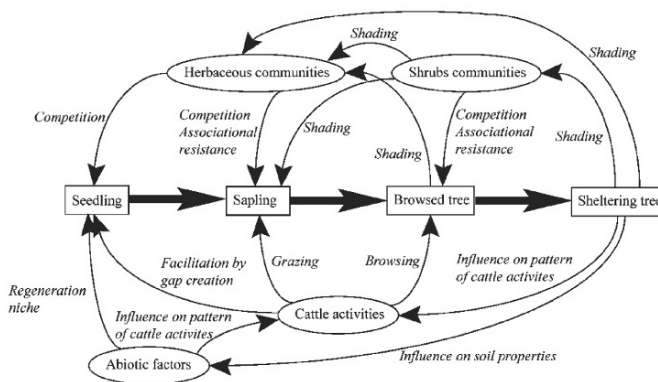
decrease of species richness leading finally to the disappearance of a group. Furthermore, field experiments (Kohler et al. 2004b) showed a continuum of species response as a rather high number of species did not show any reaction to the simulated cattle activities. This suggests that several species assemblages can occur.

These observations support the dynamic keyhole-key model (Gigon and Leutert 1996), which explains the coexistence of a high number of species in grasslands. Where species  $\alpha$ -diversity (keys) and microsite diversity (keyholes) match, coexistence is likely to occur. A great number of potential microsites can be defined by crossing the various biogenic effects induced by cattle activity (but also by small herbivores such as voles – *Arvicola terrestris* L.), trees and shrubs (light conditions), with abiotic microsite diversity, in relation to soil properties or microtopography. Moreover, we must also consider the temporal variability of the biogenic factors. First, at decades and landscape scales the spatial pattern of the tree mosaic that induces the light conditions will change (“shifting mosaics”, Olf et al. 1999). Second, from the results of Kohler (2004), we can describe at a finer and shorter scale another shifting mosaic in the herb layer. At fine scale (few square decimetres), the combination of effects induced by cattle will change from year to year depending, for example, on spatial distribution of dung pats which influence grazing behaviour (see last section). It is therefore possible to define a pasture as a patchwork of micro-successions at various successional stages, depending on the major and changing constraints in relation to cattle activity. These phenomena induce a rapid local species turnover while plant composition persists at larger scale. This is possible in this type of grassland because of the high resilience (rapid recovery) but also of the high resistance (few species loss in most cases) to disturbance. This is probably due to the importance of clonal growth compared to species extinction/colonization processes in the perennial vegetation of mountain pastures.

### ***Tree Regeneration: Between Competition and Facilitation***

Trees are key organisms in silvopastoral ecosystems and interactions with cattle and herbaceous vegetation are critical to understand patterns and processes in these highly heterogeneous landscapes. The regeneration of trees is also crucial for the long-term sustainability of wooded pastures (Diaz et al. 1997). In the wooded pastures of the Swiss Jura Mountains, one conifer species (*Picea abies* L.) and two deciduous species (*Acer pseudoplatanus* L. and *Fagus sylvatica* L.) can dominate, *Picea* being the most abundant. Four life stages can be distinguished, each one corresponding to different interactions between individual trees and the other components of the system (Fig. 19.7).

The first stage (Fig. 19.7) is seed establishment after dispersing. There is poor information on the spatial distribution of seed dispersed and it seems that seed trapping by small shrubs do not play a crucial role in this ecosystem (Smit 2005). Moreover, for *Picea abies* seed predation is considerable (almost 90%) (Smit



**Fig. 19.7** The different life stages of a tree and the interactions with other components of the wooded pastures (Adapted from Béguin 2007)

2005). Selective enclosure experiments in open and dense vegetation showed that insect predation contributes to 74% of the seed removal. The germination rate of seeds is generally low in natural conditions (*Picea*: 17%; *Acer*: 5% and *Fagus*: 2%, Vandenberghe et al. 2006a). After germination, tree seedlings often experience competition from herbaceous vegetation. At this stage, since plants compete for light, water, nutrients and space, gaps (openings in swards) are expected to have positive effects on tree seedling emergence (Nilsson et al. 2002), survival and growth (Davis et al. 1999; Meiners and Handel 2000). A reduction in height of the surrounding vegetation, for example caused by grazing, may also reduce competition and create enhanced conditions for tree seedlings to establish (Karl and Doescher 1993). However, under dry weather conditions, moist microclimatic conditions within the sward may be more favourable than exposed soil. Therefore, gaps may also have negative or neutral effects on tree seedling emergence (Burton and Bazzaz 1991; DeSteven 1991) and survival (Berkowitz et al. 1995). In an experiment manipulating gap size (four gap sizes including zero) and herbaceous competition (mown vs. unmown) Vandenberghe et al. (2006a) showed that gaps had a positive effect on early stages of tree development of three typical species of wooded pastures (*Picea*, *Acer* and *Fagus*). Moreover, seedling growth was higher when surrounding vegetation was mown. Nevertheless, even in more favourable large gaps, only a small percentage of seedlings emerged and survived.

The second stage (Fig. 19.7) corresponds to small saplings of more than one year old, which have not yet emerged from the herbaceous layer and are therefore not selected by cattle, and consequently grazed together with the other vegetation. The spatial distribution of the *Picea* saplings is positively correlated with rocky outcrops, tree stumps and unpalatable plant species (Smit et al. 2005). Considering the last factor, it seems that *Picea* may benefit from associational resistance (or facilitation): cattle may browse the unprotected saplings by chance because of their inhospitable surroundings and avoid an unpalatable patch with a sapling more likely to survive. Experimental approaches confirmed this hypothesis (Smit et al.

2006). Moreover the importance of this facilitation process is unimodal relative to the grazing pressure, with a maximum at intermediate grazing pressure (Smit 2005). At low grazing pressure, saplings do not need to be protected, and at high grazing pressure the unpalatable plants are damaged by cattle and do not serve a protective role.

In the third stage, trees emerged from the herb layer and are directly affected by cattle browsing (Fig. 19.7). The percent of browsed or otherwise damaged trees seemed linearly positively related to the stocking density (Mayer et al. 2005). Apparancy, i.e. the probability that an individual plant will be discovered by herbivores (Feeny 1976), is not only dependent on the characteristics of the plant itself, e.g., size, foliage abundance and duration (Zamora et al. 2001; Renaud et al. 2003), but also on the relative abundance and nature of neighbouring plants (Milchunas and Noy-Meir 2002). Therefore, the probability for a sapling of being browsed might be lower when protection is provided by surrounding vegetation (Canham et al. 1993). Conifer species are likely more apparent, but might be avoided by cattle because of a lower leaf nitrogen content (Pagès et al. 2003) and stiff and tough needles. Furthermore, deciduous species have the advantage of greater ability for compensatory growth than evergreen woody species after browsing damage because conifers store most of their nutrients in the needles, whereas deciduous species have greater stores in roots and old wood (Hester et al. 2004). By exposing saplings of four genera (*Picea*, *Abies*, *Acer* and *Fagus*) to different grazing intensities, Vandenberghe et al. (2006b) showed recently that only 1% of large saplings (41–59 cm) escaped browsing either at low or high grazing intensity. However, browsing effects tended to be smaller at the lower grazing intensity. Furthermore, the proportion of saplings browsed was not significantly different among species although evergreen tree saplings lost a larger proportion of biomass than deciduous species.

Finally when the trees reach a height of about 1.5 m, they can escape from cattle browsing and grow without constraint. To reach this size trees such as *Picea abies* may need to be more than 100 years old (Gallandat et al. 1995). Growth can therefore be very slow during the first stages of tree life. Once adult, trees influence the behaviour of cattle (Kohler et al. 2006a) and the understorey vegetation. Moreover, they can also affect the soil chemical status through litter deposition and by changing the chemical content of the rain water by leaching of the leaves or needles (Douard 1994).

## Models of Ecological Processes

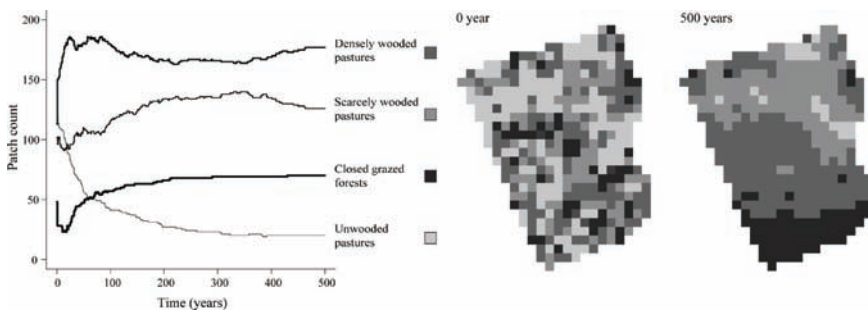
The knowledge of complex interactions between cattle activities, vegetation and landscape structure, shifting mosaic in the herb layer and tree regeneration has allowed the development of a novel, spatially explicit, mosaic compartment model of the dynamics of silvopastoral ecosystems, WoodPaM (Gillet in press). This model has its origin as a spatially implicit model of vegetation dynamics in wooded pastures, PATUMOD (Gillet et al. 2002), which has been successfully used as a



decision tool in management projects (e.g. Perrenoud et al. 2003). WoodPaM is a deterministic model considering three hierarchical levels: the focal level is the phytocoenosis, represented by a cell or a patch in the landscape with a variable stock density; spatially implicit herb and shrub communities as well as size-structured tree populations are the components of each patch at the lower level; patches are aggregated in a pastoral management unit building the higher level, with externally controlled global stock density. At the chosen time resolution of 1 year, interactions between neighbouring patches are not considered, except for tree seedling recruitment. However, local patch dynamics influence some global constraints at the upper level, so that dynamics in a single patch is depending on changes in all patches of the landscape mosaic.

As an example, the result of a simulation made from a real pasture-woodland landscape, the *Métairie d'Évilard*, is presented. In this mosaic model, patches corresponded to the 393 cells of  $25 \times 25 \text{ m}^2$  squares of a paddock described in the observational study of Kohler et al. (2006a), for which detailed information was available for vegetation, environment (natural and management-induced structures) and cattle activity. The year 2001 was used as a baseline to set up the management and initial conditions of the system in the model. For this scenario, environmental and management constraints were fixed to the initial values. Over a simulation period of 500 years (Fig. 19.8), the landscape configuration is heterogeneous with grazed forests mainly in the southern part of the paddock, at lower altitude, higher mean slope and far from the watering places. The simulation also shows that the initial stock density seems insufficient to maintain the general landscape openness.

The present version of WoodPaM is able to explain some aspects of the origin of vegetation heterogeneity in silvopastoral landscapes. It revealed the crucial role of livestock selectivity and the consequences of complex interactions between landscape structure, vegetation and cattle behaviour (Gillet in press). Nevertheless, there is still a crucial need for long-term time series of vegetation dynamics for a better calibration of the model.



**Fig. 19.8** Time series and maps of the dynamics of phytocoenoses (four types, see Fig. 2 for details) of a 500-year simulation with environmental and management conditions fixed to their initial values (Gillet in press). Initial values are from a real pasture-woodland landscape, a paddock of the *Métairie d'Évilard* (Kohler et al. 2006a)



## Conclusion and Perspectives

The recent studies revealed the high ecological complexity of silvopastoral ecosystems and highlighted the link between land-use and biodiversity despite several questions remaining unanswered. The conservation of such ecosystems is an important challenge considering its complexity and the present change in agricultural practices. Moreover, in this case we considered only the ecological aspects of this man-made ecosystem and there is also a need to integrate social aspects so that land-use change and its consequences can be investigated in a more holistic way. In such sensitive ecosystems, agricultural policies are key drivers of land-use and then of biodiversity (Mattison and Norris 2005). A better integration of ecological and socio-economic processes into predictive, multi-level models would permit the assessment of how biodiversity is likely to respond to policy reforms and to identify how policy might need to be reformed to generate land-use that is compatible with biodiversity conservation.

**Acknowledgements** We kindly acknowledge all researchers who have been involved in the different studies: Vincent Barbezat, Daniel Béguin, Jean Combe, Alexia Dufour, Marie-Aude Farron, François Freléchoux, Fawziah Gadallah, Jean-Daniel Gallandat, Jean-Michel Gobat, Stéphanie Reust, Christian Smit, Charlotte Vandenberghe, Helene Wagner, Thomas Wohlgemuth. Part of this work was financed by the Swiss National Foundation for Science (subside 31-64116.00 and NCCR Plant survival) and by the MAVA foundation.

## References

- Abdelmagid AH, Trlica MJ, Hart RH (1987) Soil and vegetation responses to simulated trampling. *J Range Manage* 40:303–306
- Allcock KG, Hik DS (2004) Survival, growth, and escape from herbivory are determined by habitat and herbivore species for three Australian woodland plants. *Oecologia* 138:231–241
- Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. *J Range Manage* 49:386–400
- Bakker ES, Olff H (2003) Impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grassland. *J Veg Sci* 14:465–474
- Bakker ES, Olff H, Boekhoff M, Gleichman JM, Berendse F (2004) Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138:91–101
- Béguin D (2007) Tree regeneration and growth in wood pastures: patterns and processes. PhD thesis, University of Neuchâtel, Switzerland
- Berkowitz AR, Canham CD, Kelly VR (1995) Competition vs facilitation of tree seedling growth and survival in early successional communities. *Ecology* 76:1156–1168
- Burton PJ, Bazzaz FA (1991) Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. *Am J Bot* 78:131–149
- Canham CD, Hill JD, Wood DS (1993) Demography of tree seedling invasion in rights-of-way. In: Canham CD (ed) *Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees*. Final Technical Report to the Empire State Electric Energy Research Corporation, Albany, NY
- Costa G, Mosimann E, Zagni C (1990) Effet de la présence nocturne au pâturage sur les performances d'un troupeau laitier et sur ses restitutions à l'alpage. *Fourrages* 123:305–311

- Coughenour MB (1991) Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *J Range Manage* 44:530–542
- Davis MA, Wrage KJ, Reich PB, Tjoelker MG, Schaeffer T, Muermann C (1999) Survival, growth and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecol* 145:341–350
- DeSteven D (1991) Experiments on mechanisms on tree establishment in old-field succession: seedling emergence. *Ecology* 72:1066–1075
- Diaz M, Campos P, Pulido FJ (1997) The Spanish dehesas: a diversity of land use and wildlife. In: Pain D, Pienkowski M (eds.) *Farming and birds in Europe: the common agricultural policy and its implications for bird conservation*. Academic press, London
- Douard R (1994) Litières et lessivats d'érable (*Acer pseudoplatanus*) et d'épicéa (*Picea abies*): leur influence sur le sol et la végétation du pâturage boisé jurassien. Master thesis, University of Neuchâtel, Neuchâtel, Switzerland
- Dufour A, Gadallah Z, Wagner H, Guisan A, Buttler A (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecography* 29:573–584
- Edwards PJ, Hollis S (1982) The distribution of excreta on new forest grassland used by cattle, ponies and deer. *J Appl Ecol* 19:953–964
- Etienne M (1996) Western European silvopastoral systems. INRA, Paris
- Feeny P (1976) Plant apparency and chemical defense. *Recent Adv Phytoch* 10:1–40
- Gallandat JD, Gillet F, Havlicek E, Perrenoud A (1995) Patubois: typologie et systématique phyto-écologiques des pâturages boisés du Jura suisse. Laboratoire d'écologie végétale of the University of Neuchâtel, Neuchâtel, Switzerland
- Gander A, Rockmann A, Strehler C, Güsewell S (2003) Habitat use by Scottish Highland cattle in a lakeshore wetland. *Bull Geobot Inst ETH* 69:3–13
- Gigon A, Leutert AG (1996) The Dynamic keyhole key model of coexistence to explain diversity of plants in limestone and other grasslands. *J Veg Sci* 7:29–40
- Gillet F (in press) Modelling vegetation dynamics in heterogeneous pasture-woodland landscapes. *Ecol Model*.
- Gillet F, Gallandat JD (1996a) Integrated synusial phytosociology: some notes on new, multiscale approach to vegetation analysis. *J Veg Sci* 7:13–18
- Gillet F, Gallandat JD (1996b) Wooded pastures of the Jura mountains. In: Etienne M (ed) *Western European silvopastoral systems*. INRA, Paris
- Gillet F, Murisier B, Buttler A, Gallandat J, Gobat J (1999) Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Appl Veg Sci* 2:47–54
- Gillet F, Besson O, Gobat JM (2002) PATUMOD: a compartment model of vegetation dynamics in wooded pastures. *Ecol Model* 147:267–290
- Gmür P, Wettstein J-B (1986) L'aménagement des pâturages communaux dans les Franches-Montagnes (Canton du Jura). *Revue suisse d'Agriculture* 18:87–92
- Gmür P, Thomet P, Wettstein J-B (1989) Etablissement d'un plan de gestion d'un pâturage du Jura vaudois: planification de la cohabitation d'espaces naturels et de surfaces productives. *Technicum agricole suisse, Zollikofen, Switzerland*
- Gobat JM, Duckert O, Gallandat JD (1989) Quelques relations microtopographie-sols-végétation dans les pelouses pseudo alpine du Jura suisse: exemples d'un système naturel et d'un système anthropisé. *Bulletin de la société neuchâteloise des sciences naturelles* 112:5–17
- Gordon IJ (2003) Browsing and grazing ruminants: are they different beasts? *Forest Ecol Manag* 181:13–21
- Grime JP (2001) *Plant strategies, vegetation processes, and ecosystem properties*. Wiley, Chichester, UK
- Havlicek E, Gobat J-M, Gillet F (1998) Reflections on relationships between vegetation and soil: three examples on allochthonous material in the Jura Mountains. *Ecologie* 4:535–546
- Hester AJ, Baillie GJ (1998) Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. *J Appl Ecol* 35:772–784

- Hester AJ, Millard P, Baillie GJ, Wendler R (2004) How does timing of browsing affect above- and below-ground growth of *Betula pendula*, *Pinus sylvestris* and *Sorbus aucuparia*? *Oikos* 105:536–550
- Jewell PL (2002) Impact of cattle grazing upon the vegetation of an Alpine pasture. PhD thesis. Swiss Federal Institute of Technology, Zürich, Switzerland
- Jewell PL, Gusewell S, Berry NR, Käuferle D, Kreuzer M, Edwards PJ (2005) Vegetation patterns maintained by cattle grazing on a degraded mountain pasture. *Bot Helv* 115:109–124
- Karl MG, Doescher PS (1993) Regulating competition on conifer plantations with prescribed cattle grazing. *Forest Sci* 39:405–418
- Kohler F (2004) Influence of grazing, dunging and trampling on short-term dynamics of grasslands in mountain wooded pastures. PhD thesis. University of Neuchâtel, Neuchâtel, Switzerland
- Kohler F, Gillet F, Progin MA, Gobat J-M, Buttler A (2004a) Seasonal dynamics of plant species at fine scale in wooded pastures. *Community Ecol* 5:7–17
- Kohler F, Gillet F, Gobat JM, Buttler A (2004b) Seasonal vegetation changes in mountain pastures due to simulated effects of cattle grazing. *J Veg Sci* 15:143–150
- Kohler F, Hamelin J, Gillet F, Gobat JM, Buttler A (2005) Soil microbial community changes in wooded mountain pastures due to simulated effects of cattle grazing. *Plant Soil* 278:327–340
- Kohler F, Gillet F, Reust S, Wagner HH, Gadallah F, Gobat JM, Buttler A (2006a) Spatial and seasonal patterns of cattle habitat use in a mountain wooded pasture. *Landscape Ecol* 21:281–295
- Kohler F, Gillet F, Gobat JM, Buttler A (2006b) Effect of cattle activities on gap colonisation in mountain pastures. *Folia Geobot* 41:289–304
- MacDiarmid BN, Watkin BR (1972) The cattle dung patch: 2. Effect of a dung patch on the chemical status of the soil, and ammonia nitrogen losses from the patch. 3. Distribution and rate of decay of dung patches and their influence on grazing behaviour. *J Brit Grassland Soc* 27:43–54
- Mattison EHA, Norris K (2005) Bridging the gaps between agricultural policy, land-use and biodiversity. *Trends Ecol Evol* 20:610–616
- Mayer AC, Stöckli V, Huovinen C, Konold W, Estermann BL, Kreuzer M (2003) Herbage selection by cattle on subalpine wood pastures. *Forest Ecol Manag* 181:39–50
- Mayer AC, Stöckli V, Konold W, Kreuzer M (2005) Influence of cattle stocking rate on browsing of Norway spruce in subalpine wood pastures. *Agroforest Syst* 66:143–149
- McGechan MB, Topp CFE (2004) Modelling environmental impacts of deposition of excreted nitrogen by grazing dairy cows. *Agr Ecosyst Environ* 103:149–164
- Meiners SJ, Handel SN (2000) Additive and nonadditive effects of herbivory and competition on tree seedling mortality, growth and allocation. *Am J Bot* 87:1821–1826
- Meisser M (1993) Fertilisation et utilisation des pâturages boisés de l'arc jurassien. Master thesis, ETH Zürich, Switzerland
- Miéville-Ott V, Barbezat V (2005) Perception du pâturage boisé: résultats d'un sondage effectué au Communal de la Sagne NE. *Schweiz Z Forstwes* 156(1):1–12
- Milchunas DG, Noy-Meir I (2002) Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99:113–130
- Nilsson U, Gemmel P, Johansson U, Karlsson M, Welander T (2002) Natural regeneration of Norway spruce, Scots pine and Birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. *Forest Ecol Manag* 161:133–145
- O'Neill RV, DeAngelis DL, Waide JB, Allen THF (1986) A hierarchical concept of ecosystems. Princeton University Press, Princeton, NJ
- Olf H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. *Trends Ecol Evol* 13:261–265
- Olf H, Vera FWM, Bokdam J, Bakker ES, Gleichman JM, de Maeyer K, Smit R (1999) Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biol* 1:127–137
- Pagès JP, Pache G, Joud D, Magnan N, Michalet R (2003) Direct and indirect effects of shade on four forest tree seedlings in the French Alps. *Ecology* 84:2741–2750

- Perrenoud A, Känzig-Schoch U, Schneider O, Wettstein J-B (2003) Exploitation durable des pâturages boisés. Un exemple appliqué de Jura suisse. Haupt, Bern, Switzerland
- Peterson PR, Gerrish JR (1996) Grazing systems and spatial distribution of nutrients in pastures: Livestock management considerations. In: Joost RE, Roberts CA (eds.) Nutrient cycling in forage systems. Potash and Phosphate Institute and the Foundation for Agronomy Research, Manhattan, NY
- Putman RJ, Pratt RM, Ekins JR, Edwards PJ (1987) Food and feeding-behavior of cattle and ponies in the New Forest, Hampshire. *J Appl Ecol* 24:369–380
- Renaud PC, Verheyden-Tixier H, Dumont B (2003) Damage to saplings by red deer (*Cervus elaphus*): effect of foliage height and structure. *Forest Ecol Manag* 181:31–37
- Rice RW, MacNeil MD, Koong LJ (1983) Simulation of herbage/animal interface of grazing land. In: Lauenroth WK, Skogerboe GV, Flug M (eds.) Analysis of ecological systems: state-of-the-art in ecological modelling. *Developments in Ecological Modeling* 5. Elsevier, Amsterdam
- Rigueiro A (1985) La utilización del ganado en el monte arbolado gallego: un paso hacia el uso integral del monte. In: Estudios sobre la prevención y efectos ecológicos de los incendios forestales. Ministerio de Agricultura pesca y alimentación, Madrid
- Roath LR, Krueger WC (1982) Cattle grazing and behavior on a forested range. *J Range Manage* 35:332–338
- Rook AJ, Dumont B, Isselstein J, Ososro K, WallisDeVries MF, Parente G, Mills J (2004) Matching type of livestock to desired biodiversity outcomes in pastures - a review. *Biol Conserv* 119:137–150
- Roovers P, Verheyden K, Hermy M, Gulink H (2004) Experimental trampling and vegetation recovery in some forest and heathland communities. *Appl Veg Sci* 7:111–118
- Senft RL, Cougour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. *Bioscience* 37:789–797
- Silva-Pando FJ, González-Hernández MP, Rigueiro-Rodríguez A (1998) Grazing livestock in pinewood and eucalyptus forests: multiple use in northwest Spain. *Agroforest Forum* 9(1):36–43
- Silva-Pando FJ, Rozados-Lorenzo MJ, González-Hernández MP (2002) Objetivo, diseño y aplicación de experiencias en sistemas agroforestales atlánticos. *Cuad Soc Esp Cien For* 14: 109–114
- Smit C (2005) Facilitation of tree regeneration in wood pastures. PhD thesis University of Fribourg, Fribourg, Switzerland
- Smit C, Béguin D, Buttler A, Müller-Schärer H (2005) Safe sites for tree regeneration: a case of associational resistance? *J Veg Sci* 16:209–214
- Smit C, Den Ouden J, Müller-Schärer H (2006) Unpalatable plants facilitate tree sapling survival in wooded pastures. *J Appl Ecol* 43:305–312
- Tate KW, Atwill ER, McDouglas NK, George MR (2003) Spatial and temporal patterns of cattle faeces deposition on rangeland. *J Range Manage* 56:432–438
- Vandenbergh C, Freléchoux F, Gadallah F, Buttler A (2006a) Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: does gap size matter? *J Veg Sci* 17:481–488
- Vandenbergh C, Freléchoux F, Moravie MA, Gadallah F, Buttler A (2006b) Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures. *Plant Ecol* 188:253–264
- Vittoz P (1998) Flore et végétation du Parc jurassien vaudois: typologie, écologie et dynamique des milieux. PhD thesis, University of Lausanne, Lausanne, Switzerland
- White SL, Sheffield RE, Washburn SP, King LD, Green JT (2001) Spatial and time distribution of dairy cattle excreta in an intensive pasture system. *J Environ Qual* 30:2180–2187
- Wu J, David JL (2002) A spatially explicit hierarchical approach to modelling complex ecological systems: theory and applications. *Ecol Model* 153:7–26
- Zamora R, Gómez JM, Hodar JA, Castro J, Garcia D (2001) Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. *Forest Ecol Manag* 144:33–42