

Reconciling production and biodiversity in management of pastures and grasslands

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► **To cite this version:**

Sylvain Plantureux. Reconciling production and biodiversity in management of pastures and grasslands. Burleigh dodds science publishing. Reconciling agricultural production and biodiversity conservation, In press, Burleigh dodds series in agriculture science - Series n° 282, 978-1-78676-348-8. hal-02966746

HAL Id: hal-02966746

<https://hal.univ-lorraine.fr/hal-02966746>

Submitted on 14 Oct 2020

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1 Ch2 Reconciling production and biodiversity in management of pastures and grasslands

2

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4 Abstract: Grasslands are crucial for the conservation of biodiversity across the world. Current agricultural
5 practices have increasingly replaced grasslands by crops or managed them more intensively, resulting in a
6 dramatic reduction of biodiversity. Is it possible to reconcile profitable grassland production with conservation of
7 biodiversity? This chapter reviews research on the relationship between biodiversity and the quantity and
8 quality of biomass produced by grasslands. The chapter shows it is possible to manage grasslands to reconcile
9 production and biodiversity of grasslands.

10 Key words: grassland, biodiversity, agri-ecological equilibrium, grass production, agricultural practices

11

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25 1 Introduction

26

27 Agriculture in the 21st century faces two major challenges: the need to increase food and non food production to
28 meet the needs of a growing population and, at the same time, to ensure that production will not damage the
29 environment. These needs are often seen as contradictory, with one prioritized at the expense of the other, or
30 resolved by subsidizing farmers to compensate them for losses of production from more environmentally-
31 friendly management. However, this solution is not sustainable in the long run since it is a drain on the often
32 constrained finances of governments.

33 Agroecology is a potential solution to resolve this problem, because it proposes to use biodiversity in the
34 production process, substituting energy and chemical inputs (e.g. fertilizers and pesticides) with biological and
35 ecological processes. In this way production and the quality of the environment become linked. Although the
36 principles of agroecology are well-established, their implementation is still limited by many factors, including:

- 37 - 1) The willingness of farmers, extension services and policy makers to change their views on how to
38 assess and manage agricultural systems
39 - 2) the availability of scientific and technical knowledge about production-biodiversity relationships

40 Grasslands are particularly affected by these issues. According to FAO (2019), 26% of the world's land area and
41 70% of the world's agricultural land are covered by grasslands, contributing to the livelihoods of over 800 million
42 people. The environmental benefits provided by grasslands are now well recognized, including:

- 43 - preservation of biodiversity (flora, above and below-ground fauna and microflora)
44 - prevention of chemical pollution

- 45 - soil erosion and water control
- 46 - carbon sequestration
- 47 - reduction of greenhouse gases

48 In Europe half of the region's flora is dependent on grassland habitats (Eckhard et al. in (Veen et al., 2009)).
49 However, in recent decades there has been a significant decline in Europe in the quality of semi-natural
50 grasslands, particularly by conversion to production of forage crops such as silage maize, the shift to more
51 temporary grasslands (e.g. as part of a rotation) or more intensive cultivation of existing grasslands. Semi-natural
52 grasslands are defined by (Peeters et al., 2014) as: "*Low-yielding permanent grasslands, dominated by*
53 *indigenous, naturally occurring grass communities, other herbaceous species and, in some cases, shrubs and/or*
54 *trees. These mown and/or grazed ecosystems have not been substantially modified by fertilization,*
55 *liming, drainage, soil cultivation, herbicide use, introduction of exotic species and (over)sowing.*" This increase in
56 intensification in grassland management has resulted in a drastic reduction in the extent and quality of semi-
57 natural grasslands, and sometimes even in chemical pollution (such as leaching of nitrates and herbicides used in
58 more intensive grassland management). In most cases intensive grass production is incompatible with
59 biodiversity maintenance (Plantureux et al., 2005). From the environmental point of view, temporary grasslands
60 or intensive permanent grasslands have some benefits (e.g. prevention of soil erosion), but semi-natural
61 grasslands offer the greatest environmental benefits because of their greater biodiversity.

62 Intensification or replacement of semi-natural grasslands is, however, not the only possible way to improve
63 grassland production. Agroecology is a potential solution to balancing forage production with preservation of
64 environment quality. This requires changing methods of assessing the agronomic and environmental value of
65 grasslands. This chapter reviews the concepts underlying this change of paradigm. Based on current knowledge
66 of the relationship between biodiversity of grasslands and production, it will show how production should not be
67 assessed just on annual production of dry matter. Factors such as nutritive value of forage, quality of products
68 such as milk, animal health and profitability need also to be taken into account. The chapter then reviews
69 methods to manage grasslands agro-ecologically. Finally, the experience of a "flowering meadows competition"
70 will be described to illustrate how farmers can ensure a successful trade-off between production and
71 biodiversity in grasslands. Though all the types of grassland are discussed, the main focus is on semi-natural
72 grasslands.

73 **2 Analyzing the relationship between biodiversity and productivity in grasslands**

74
75 The relationship between biodiversity and productivity of crop agroecosystems has been studied since the 19th century, but
76 research intensified in the second half of the 20th century (MacArthur, 1955). This research covered all terrestrial and aquatic
77 ecosystems with some work focused on grasslands. These studies are based on three types of approach:

- 78 - i) observation: observation in natural, poorly-controlled conditions of permanent or semi-natural grasslands with
79 various levels of biodiversity
- 80 - ii) experimentation: setting up of experiments where the number and the nature of the species is controlled either by
81 sowing of pure stands or mixtures, by overseeding of an existing sward, by removing species, or by changing the
82 composition of grasslands through management
- 83 - iii) synthesis: more recently through meta-analyses based on the compilation and analysis of results of individual
84 observations or experiments

85 In experimental studies, the aboveground net primary productivity (NPP) (increase of green biomass by unit of surface and
86 time) is generally chosen to measure the productivity of grasslands. In contrast, observation studies rely on proxy measures of
87 NPP (e.g., annual yield harvested). Productivity is estimated on annual, intra- or inter-annual time scales. Comparing annual
88 results makes it possible to assess temporal stability in the productivity and resilience of grasslands. The following sections of
89 this chapter will demonstrate that evaluation of agronomical value of grasslands should not be limited to NPP, and that many
90 other criteria must be taken into account. Unlike productivity, biodiversity needs to be assessed using a much larger range of
91 criteria. If species richness is the most commonly used of these criteria, many other may also be considered, such as specific
92 composition, functional diversity, phylogenetic diversity, or evenness.

93 The various methods used to study the BP relationship each have their advantages and disadvantages.
94 Experimentation compares grasslands with differing levels of biodiversity under comparable soil, climate and
95 management conditions. Experimentation makes it possible to control species richness, functional diversity or
96 botanical composition. Controlled experiments have been criticized for their lack of representativeness of actual
97 semi-natural grasslands. They differ e.g. in terms of factors such as type of sown species, low number of species,
98 immaturity of grassland communities, lower frequency of harvest and low rates of grazing (Isselstein, 2005).

99 If observations of grasslands in more “natural conditions” are more realistic, there is a much higher risk of
100 confusion between the effects of biodiversity and the effects of environmental and management factors on
101 productivity (“hidden treatments”). Species removal or oversowing of semi-natural grasslands is an intermediate
102 experimental system to reduce the number of variables to take into account. After having sown a mixture, it is
103 important to wait a few years before beginning to measure BP relationships (Lepš, 2004). While ecologists
104 compare species mixtures with monocultures, agronomists usually compare mixtures with the most productive
105 species or species combination (Schulze et al., 2018).

106 It is clear that there is no unique biodiversity-production (BP) relationship for grasslands. This relationship varies
107 according to the choice of criteria measuring productivity and biodiversity, methods of study (experiment vs
108 observation), diversity gradients, or environmental and management conditions. The relationship also depends
109 on spatial scale (Li et al., 2019). Biodiversity may be favorable, unfavorable or have no effect on the productivity
110 of grasslands, resulting in the absence of consensus on the BP relationship in grasslands. Some important
111 advances have been made over recent decades to better understand the BP relationship. This can help to avoid
112 errors like the “hidden treatments” (or unidentified causes) highlighted by Huston (1997) in the study of
113 complex ecosystems. This understanding also avoids the controversies raised by the assertion that biodiversity
114 always increases the productivity of grasslands, or often unsuccessful attempts to extrapolate experimental
115 results to real farm conditions.

116 **3 Biodiversity factors affecting grassland productivity**

117 **Species richness**

118 Many experiments conducted by artificially manipulating species diversity over a long period have shown a very
119 positive effect of biodiversity on the productivity of grasslands. These studies include research in North America
120 (Tilman et al., 1996) (Tilman et al., 2001) (Prieto et al., 2015) and, for example, the Biodepth Project in Europe
121 (Hector et al., 1999)). This positive effect of an increasing number of species (or number of functional groups) is
122 mainly linked to factors such as the complementary use of resources by plant species, niche differentiation and
123 the increasing probability of encountering highly productive species for a particular environment (the “selection
124 probability effect”). Numerous experiments have demonstrated the particular effect of adding legumes to grass-
125 dominated grasslands. A meta-analysis of 2753 studies carried out over 50 years has concluded that combining
126 legumes with grasses increases biodiversity, but has very little effect on productivity on any grassland mixture
127 containing more than two legume species (Ashworth et al., 2018). This positive BP relationship in some
128 experimental situations is in contrast to other experimental results and the observation of the lower productivity
129 of grasslands with high biodiversity in natural conditions (Seither and Wrage-M, 2014). (Grace et al., 2016) have
130 highlighted the need for models to help explain the complex relations between productivity and biodiversity and
131 the various processes driving both productivity and biodiversity.

132 Many theories and models have been proposed to explain why the BP relationship is not constant (e.g. linear,
133 log-linear, unimodal, decreasing or increasing). On the basis of the ‘hump-backed’ model proposed by (Grime,
134 1973), (Schmid, 2002) proposed a theoretical framework to resolve the apparent contradiction between the
135 beneficial effect of biodiversity on productivity generally observed in experimental situations (fig 1a), and the
136 negative effect observed in actual semi-natural grasslands conditions (fig 1 b).

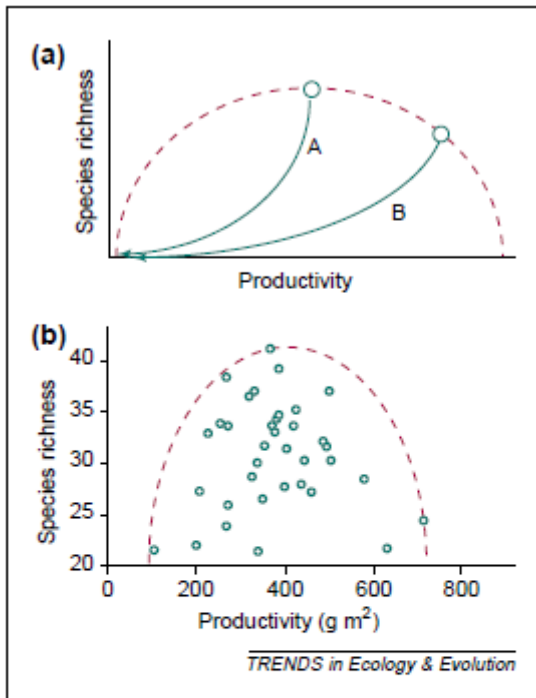


Fig. 1. The relationship between plant species richness and productivity in grassland ecosystems (a). The dashed line has been observed in field surveys; the solid lines (A and B) indicate trajectories that are typically obtained in experiments that simulate random species loss. (b) Example of real data from an observational study that included 36 pre-alpine wet grasslands in Switzerland. Each data point is the average of eight sample plots. The dashed curve is an upper envelope over the point cloud. Data taken from D. Pauli, PhD thesis, University of Zurich, 1998.

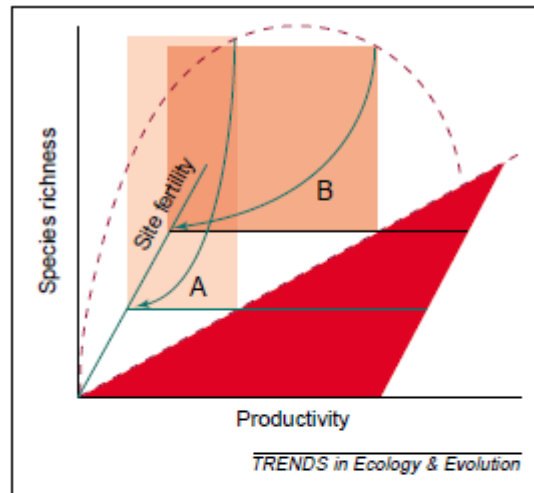


Fig. 2. A possible resolution of observational and experimental results. The 3D-representation of the hump-backed relationship indicates the correlation between site fertility and productivity that often occurs in observational studies. The dashed and solid curves correspond to those in Fig. 1a, which can be obtained as a projection of the curves onto the productivity–species richness plane. However, in the 3D-representation, a move out of the rectangular planes framing curves A and B is only possible if site fertility is changed. It is assumed that an increase in productivity from left to right across the diagonal line (shaded dark red) in the productivity–site fertility plane is not possible with any combination of species present in the species pool.

137

138 *Figure 1 and 2 : Theoretical framework to explain Productivity-biodiversity links, from (Schmid, 2002)*

139 The level of soil fertility can be seen as a key element in explaining the different ways productivity changes with
 140 biodiversity (fig 2). The lower productivity of semi-natural grasslands with high biodiversity can be seen to be
 141 clearly related to lower levels of soil fertility. By assessing soil fertility and species richness, (Fridley, 2002)
 142 showed that the beneficial effect of biodiversity on productivity increases with the level of fertility. However, by
 143 analyzing 16 grassland experiments in North America, (Craven et al., 2016) showed that the fertility of the soil
 144 (as well as the level of water stress) does not alter the biodiversity-productivity relationship. They suggested that
 145 this relationship is primarily determined by taxonomical plant species richness. Beside the fertility of the soil, the
 146 density of seedlings of species also influence the BP relationship. The increase in the number of species has a
 147 greater effect on productivity at low than at high density, because of density-dependent reductions in growth
 148 rate of individuals of different species within the grassland community (He et al., 2005).

149 **Other biodiversity parameters affecting grassland productivity**

150 The link between productivity and species richness is not constant. The effect of particular species and their
 151 relative contribution to biomass production also has a very strong effect on productivity, factors which are not
 152 taken into account by focusing just on species richness. Grassland diversity should therefore be assessed by
 153 parameters other than species richness. Other parameters include genetic and phylogenetic diversity, botanical
 154 composition, evenness of species composition and functional group diversity. Numerous studies have
 155 demonstrated that these criteria are better predictors of productivity than species richness.

156 Ecosystem functioning, including productivity, can be explained by mean plant trait values, following the so-
157 called “mass ratio hypothesis”. The “mass ratio hypothesis” means that the relative abundance of a given
158 species in a community is a better predictor of ecological processes than just the fact of its presence in a
159 grassland community. (Duru et al., 2009) demonstrated that grouping species in plant functional types (PFT) can
160 be used to predict the herbage biomass accumulation rate of grasslands under different management practices
161 for a wide range of plant communities.

162 Studying 10 native grassland sites in Australia, (Mokany et al., 2008) found that aboveground NPP was
163 determined by the traits of the dominant species rather than by grassland diversity. Analyzing the annual
164 biomass production of a national network of 190 semi-natural grasslands, (Michaud et al., 2015) found that
165 production was more correlated to functional composition and botanical composition than species richness. In
166 the BIODDEPTH project based on a group of European experimental grasslands, (Hector et al., 1999)
167 demonstrated that grassland productivity is positively related to functional diversity. Species evenness can also
168 be more predictive of productivity than species richness (Assaf , et al., 2011).

169 Using a mathematical model, (Nijs and Roy, 2000) found that, while the level of species richness does not
170 correlate with productivity, the response of productivity to species evenness and functional diversity are
171 respectively linear and exponential. However, re-examining 16 grassland biodiversity studies (Venail et al., 2015)
172 showed non-significant relationships between productivity, phylogenetic diversity, biomass and stability,
173 whereas species richness was found to increase biomass. Other research suggests that plant genetic diversity
174 and species diversity may have different but complementary effects on productivity (Prieto et al., 2015). Overall,
175 functional diversity, in its various forms, appears as the best predictor of grassland productivity compared to
176 species richness.

177 **4 Biodiversity factors affecting grassland productivity over time**

178 Beyond annual productivity or NPP, performance at different times of the year (intra-annual production) and
179 over a number of years (inter-annual production) must also be taken into account in assessing the agronomic
180 value of a grassland. The productivity performance of grasslands is associated with resistance (i.e. ability to resist
181 biotic and abiotic stresses) and resilience (i.e. the capacity to return quickly to an initial state after stress).
182 Resistance and resilience together define stability. From a farmer’s point of view, intra-annual production is
183 related to use. In the case of forage stocks (hay or silage), concentrating production, generally in the spring and
184 early autumn, limits the number of harvests needed. In case of grazing, it is best to let grass grow regularly
185 during the whole growing season. The economic sustainability of farming systems is also determined by inter-
186 annual stability of production i.e. the ability to maintain a consistent quality and quantity of output. This is
187 becoming more critical with climate change which tends to increase the frequency of extreme events, especially
188 droughts.

189 From an ecological point of view, a better stability of productivity in time is an insurance to secure ecosystem
190 functioning (Eisenhauer et al., 2018). Intra-annual dynamics and inter-annual stability are both influenced by the
191 level of biodiversity of grasslands. The diversity of responses to environmental change among species is crucial
192 for the resilience of ecosystem functioning (Elmqvist et al., 2003). A high level of biodiversity of grasslands is
193 usually associated with better stability of production, because of overyielding by some species, species
194 asynchrony and portfolio effects (i.e. statistical averaging) (Richardson and Pyšek, 2007) (Caldeira et al., 2005).
195 Portfolio theory was first used by economists to explain why diversification can stabilize returns. In ecology it is
196 used to explain links between ecosystem performances and diversity. Species richness and evenness may
197 produce this effect (Hillebrand et al., 2008).

198 Productivity and stability appear to be relatively independent of each other (Cardinale et al., 2013).
199 (Küchenmeister et al., 2012) found e.g. that more legumes in temporary grassland mixtures increased yield but
200 decreased yield stability, whereas forbs decreased both yield and stability. Temporal stability also depends on

201 species abundance and growth-related traits (Polley et al., 2013). Studying the production stability of individual
202 species in a species-rich meadow, (Lepš, 2004) found that dominant species had more impact on stability than
203 the whole community. By combining a legume, two grasses and three forbs, (Küchenmeister et al., 2012) showed
204 that species identity and functional composition affect productivity and stability differently.

205 Most studies assessing the stability of grassland production have been conducted with experimental plots, and
206 have generally tested drought stress and sometimes temperature (heat or frost) stress. Some studies have
207 shown the beneficial effect of grassland diversity (species richness, evenness) on resistance to invasive species
208 (Brett Mattingly et al., 2007), including weed species (Abernathy et al., 2016), though others have not shown this
209 effect (Ganguli et al., 2008).

210 The link between stability of grassland production submitted to drought and biodiversity is still an open
211 question. Analyzing 46 experiments studying different types of grasslands composition, (Isbell et al., 2015)
212 found that communities with 16-32 species were twice as resilient to extreme wet or dry conditions of varying
213 lengths compared to less diverse communities. In both cases, there was a full recovery of production after the
214 stress event. These results are similar to those of (van Ruijven and Berendse, 2007) who also found greater
215 resilience from more diverse experimental plots. Re-analysing 27 experiments (Gross et al., 2014) suggested that
216 interspecific interactions explain the stabilization of productivity in diverse communities. (Prieto et al., 2015)
217 demonstrated in experimental conditions (124 plots, 5 species, 10 genotypes) that temporal stability of
218 productivity increased with the number of genotypes but not with the number of species, under both drought
219 and non-drought conditions. An interaction between management and species richness was found by (Vogel et
220 al., 2012) when submitting experimental plots (1-60 species, 4 management regimes) to drought. As with NPP,
221 species richness may not be the best predictor of production stability, compared to functional or species
222 composition (Xu et al., 2017). Contrasted results were also observed in natural conditions. Comparing
223 intensively managed poor-species grasslands to semi-natural grasslands in the Netherlands, (De Keersmaecker et
224 al., 2016) showed that the resistance of semi-natural grasslands was higher than that of intensive grasslands,
225 whereas an opposite trend was observed for resilience. However, these authors note that management may
226 affect resilience, and results should be consequently interpreted with care.

227 **5 Biodiversity factors affecting the quality of forage and animal products**

228
229 In semi-natural grasslands, conservation of biodiversity and of the related ecosystem services generally requires
230 limiting intensification practices (e.g. fertilizer input, grazing intensity or mowing frequency). It is thus difficult,
231 but not impossible, to combine a high level of productivity and biodiversity. Do farmers have to choose between
232 these two objectives? The answer is no because biomass production from species-rich grasslands may be more
233 consistent over time or more resilient in response to an extreme event, which may partly compensate for the
234 loss of productivity. Another advantage of species-rich grasslands is potentially in higher forage quality, though
235 this depends on the quality criteria chosen (Farruggia et al., 2008). There are main types of criteria:

- 236 - 1) feeding value of grass forage (nutritive value, ingestibility and digestibility)
- 237 - 2) medicinal value of grass for animals and for humans (in terms of animal products)
- 238 - 3) organoleptic value that eating a particular grass gives to animal products

239 These types of criteria are influenced by grassland biodiversity. They may result in higher profitability (e.g. in
240 reduction in production costs, better product quality and thus better selling prices and market access).

241 **Biodiversity and the feeding value of grass forage**

242 The feeding value of grass forage encompasses (Baumont, 1996):

- 243 - its nutritive content (energy, protein, minerals, vitamins, ...)

- 244 - its digestibility (the fraction that will be really assimilated by animals)
- 245 - its ingestibility (quantity of forage voluntarily ingested by animal)
- 246 - its palatability (i.e. forage characteristics (taste, smell, appearance, ...) which modify animal feeding
- 247 behaviour

248 Each single species in a grassland community has its own characteristics, which may vary with phenological
249 stage, type of organ (leaf/stem/inflorescence) and environmental conditions (nutritive and water status,
250 temperature, biotic interactions...). These values have been measured for a few of the most common species,
251 mainly sown grasses and legumes which are also found in semi-natural grasslands. However, the number of
252 species described is very low compared to the number of grassland species found in species-rich grasslands. In
253 addition, feeding values differ for the various types of animal (cattle, sheep, goat, horse etc.) because their
254 physiological requirements, feeding behavior and learning processes determining diet choices vary (Duncan et
255 al., 2006). For all these reasons, the relationship between biodiversity and feeding value of forage is complex
256 and not fully understood. The studies that have compared the feeding value of grasslands report either positive
257 or negative effects of biodiversity, depending on the situation (botanical composition, fertility level, type of
258 animal).

259 Numerous species in a grassland influence the grass feeding value because of differences in digestibility between
260 species at the same phenological stage and differences in maturity between species at the same date (Farruggia
261 et al., 2008). In species-rich grasslands, the proportion of forbs (and sometimes legumes) and the diversity of
262 grasses are generally higher than in species-poor grasslands, and are major drivers of forage feeding value. In
263 terms of chemical composition, forbs can increase mineral and secondary metabolites content of forage, and
264 legumes increase the protein content. Based on the analysis of 30 grasslands in UK, (French, 2017) found 56%
265 more phosphorus, 106% more potassium, and 183% more calcium in this type of grassland than in conventional
266 hay.

267 However, the impact of grassland diversity on digestibility can be both positive or negative (Bruinenberg et al.,
268 2002). The lowest fertilization of species-rich grasslands, rather than their higher diversity, explains some results
269 demonstrating lower mineral and protein content. As grasses are more diverse, the shift in their phenology over
270 time make energy and protein content of grass more stable. Biodiversity also improves palatability and
271 digestibility of forage. However, the ingestibility of forage from species-rich grasslands is frequently lower and
272 there is an increasing risk of consumption of toxic species.

273 In complex plant mixtures like in semi-natural grasslands, the interaction effects between species influence
274 forage quality. Based on a literature review, (Niderkorn and Baumont, 2009) demonstrated that feed intake and
275 digestion in ruminants are modified by the interactions between grasses and legumes in the rumen, as well as
276 the impact of bioactive secondary metabolites on digestive processes in the rumen. The lack of knowledge on all
277 species and all interactions between species make difficult to directly predict grass feeding value from grassland
278 plant diversity. However, (Jouven et al., 2006) has proposed a model predicting digestibility of forage from
279 permanent pastures, describing grassland biodiversity through plant functional types (PFT).

280 Two types of studies have been conducted to estimate the feeding value of grass in relation with biodiversity:

- 281 - 1) experiments comparing the feeding value of individual plant species (or genotypes) or simple
- 282 mixtures
- 283 - 2) empirical estimations analyzing the forage value of semi-natural grasslands.

284 As an example of the first type of study, (Pontes, 2007) measured the crude protein (CP) concentration and
285 pepsin cellulase dry matter digestibility of 13 native grasses cultivated in pure stands. The results show that, if
286 phenological stage and nitrogen status are the main factors explaining these nutritive criteria, there is a great
287 variability between species, and differences occur between early and late flowering species. (Duru et al., 2008)
288 demonstrated that a plant functional trait like leaf dry matter content (LDMC) can be a good predictor of organic

289 matter digestibility (OMD) of 19 grasses cultivated in pure stands. These authors found similar results at the
290 community level in semi natural grasslands.

291 In semi-natural grasslands, each grassland community can be considered as a unique mixture of species and
292 phenological stages, and this complexity makes it difficult to assess the effect of biodiversity on feeding value.
293 Analyzing 190 semi-natural and intensive permanent grasslands in France, (Michaud et al., 2015) found that
294 grass nutritive value (energy, crude protein, organic matter digestibility, mineral content) was mainly explained
295 by botanical families, plant stage and sward dry matter content. Other plant functional traits than botanical
296 family, and other biodiversity criteria (species richness, evenness), were less predictive.

297 **Biodiversity and the medicinal value of grass forage for animal and human health**

298 Species in species-rich grasslands, especially forbs and legumes, have a higher secondary metabolite content than
299 most grasses. These molecules belong to several chemical families (Poutaraud et al., 2017): phenolic compounds,
300 terpenoids, carotenoids, alkaloids, vitamins and enzymes. The link between grassland botanical composition and
301 secondary metabolites content of grass forage has been clearly demonstrated by authors like (Reynaud et al.,
302 2010). The probability of finding a large diversity of molecules increases with the diversity of species and botanical
303 families in a grassland. (French, 2017) showed that grass produced by UK native species-rich grasslands had a
304 greater abundance of medicinal compounds than intensively-managed and species-poor grasslands.

305 Some studies have demonstrated a wide range of anti-inflammatory, antimicrobial, anti-cancer, cardio-protective,
306 neuro-protective, anti-osteoporotic, estrogenic/anti-estrogenic, anxiolytic, analgesic, and anti-oxidant activities of
307 secondary metabolites in forage in laboratory animals and/or herbivores (Poutaraud et al., 2017). Recently
308 attention has focused on the role of condensed tannins, which can prevent bloat in cattle, control parasites like
309 coccidian as well as control flystrike (Lüscher et al., 2014), but which can be toxic above a threshold level (Makkar,
310 2003). Some species are particularly rich in condensed tannin, like legumes (*Onobrychis* sp., *Lotus* sp., *Acacia* sp.)
311 and species like *Taraxacum* sp. (Jayanegara et al., 2009). Other studies have focused on the role of plant
312 polyphenols in preventing oxidative stress and improving animal health and production performance (Gessner et
313 al., 2017).

314 On-farm surveys and experimental results show that there is also an effect of animal diet composition on human
315 health. The main components involved are fatty acids (FA), vitamins and polyphenols (Duru, 2016). Research
316 suggests grass in animal diets has a very positive effect on unsaturated FA (Couvreux et al., 2006) (Coppa et al.,
317 2013). When comparing meat quality of beef cattle grazing intensive or *molinia* dominated semi-natural
318 grasslands, (Fraser et al., 2007) found that there is a positive effect of grassland diversity on unsaturated FA
319 content. FA composition is related both to the proportion of grass in animal diets and to the occurrence of different
320 plant species or families (Collomb et al., 2002). (Gorlier et al., 2012) found significant correlations between FA
321 concentration in milk and the contribution of the main botanical families found in alpine grasslands. (Ravetto Enri
322 et al., 2017) found FA profile less dependent on botanical family than on the presence of given species in six types
323 of alpine semi-natural grasslands. As an example linoleic acid was negatively correlated with species composition
324 (SC) of grasses and positively correlated with the SC of legumes.

325 **Biodiversity and the organoleptic value of animal products**

326 There is a significant body of research showing that, among other factors, grassland botanical composition has a
327 major effect on the sensory quality of animal products as shown in the example of cheese (Fig 3) (Buchin et al.,
328 1999) (Coulon et al., 2004). There are many mechanisms that help to explain the link between organoleptic
329 product quality and botanical composition of grasslands (Martin et al., 2005) (Coulon et al., 2004):

- 330 - 1) direct transfer of molecules from grass to milk and cheese (e.g. aromatic compounds like terpenes
331 and sesquiterpenes)

- 2) indirect chemical (protein and fat), enzymological (effect on lipolysis and proteolysis) and microbial activity (in rumen, milk and cheese). An indirect effect can, for example, result in the chemical transformation of a molecule present in the forage by a rumen microorganism

Comparing cheeses made from cows grazing in a mountain area either on species-rich semi-natural grasslands or temporary grasslands, (Coppa et al., 2011) found that cheese coming from species-rich grasslands had more intense odour and aroma, and a sourer, more pungent and saltier taste. (Buchin et al., 1999) found alpine cheese produced from grasslands with different botanical composition showed significant differences in aroma type and intensity. (Bovolenta et al., 2014) showed that species-rich pastures produced cheese with more volatile compounds (ketones, phenolic compounds and terpenes) than species-poor pastures.

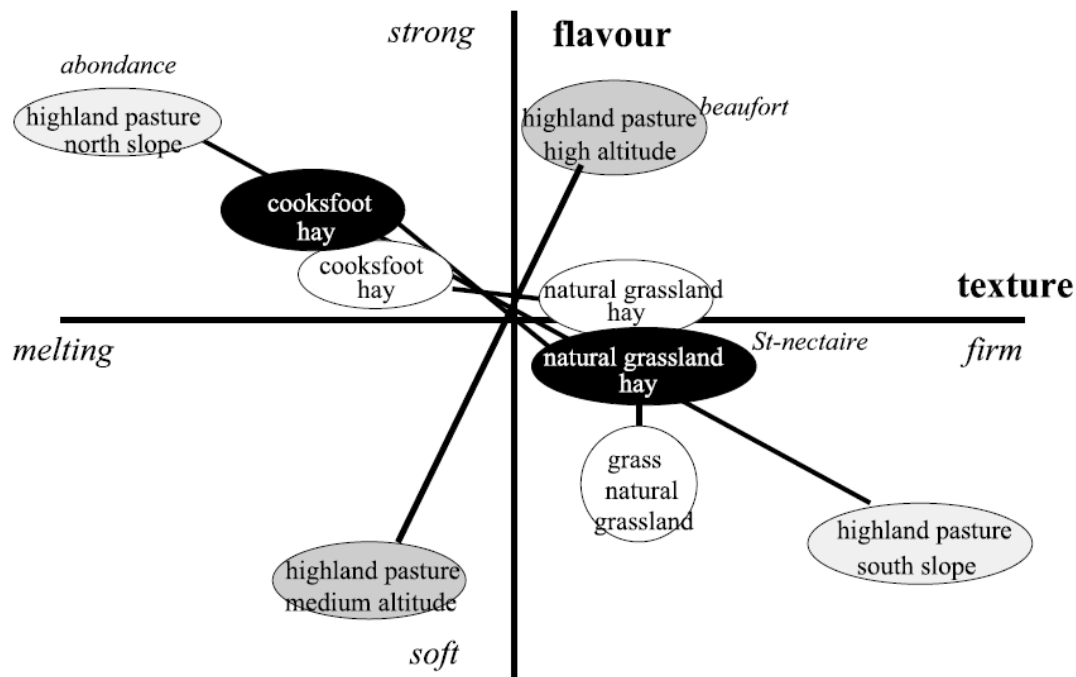


Fig 3. Sensory characteristics differentiation of French mountain cheeses (Beaufort, St-Nectaire, Abundance) according to grass botanical composition (Coulon et al., 2004)

6 Grassland biodiversity and ecosystem services

The 2005 United Nations report on the Millennium Ecosystem Assessment popularized the concept of ecosystem services (ES). These include provisioning, regulating, cultural and supporting services. Economists like (Costanza et al., 1998) define ES as: “the benefits human populations derive, directly or indirectly, from ecosystem functions“. However, for ecologists like (Daily and et al., 1997) ES are a “wide range of conditions and processes through which natural ecosystems, and the species that are a part of them, help sustain and fulfill human life“. One definition focuses on (measurable) outcomes whilst the other focuses on processes. Daily’s conceptualization is that ES are a part of the ecosystem and, with the addition of anthropogenic capital, humans derive benefits from them. Thus, there is a more economically sound definition and a purely ecological definition of ES. This poses a problem, because in order to successfully identify and evaluate ES whether it be their monetary value or their potentiality, it is important that studies carried out on the subject use the same definition. The second problem is that the ES definition from the Millennium Ecosystem Assessment does not

363 clearly distinguishes conditions and determinants, functions, processes, mechanisms, goods, benefits and
364 profits. The scientific literature about ES delivered by grasslands uses both definitions. The latest European
365 initiatives refer to the ecologists' definition, especially the "Mapping of Ecosystems and Ecosystem Services
366 (MAES)" or the "Common International Classification of Ecosystem Services (CICES)" developed from the work
367 on environmental accounting undertaken by the European Environment Agency (EEA). In the majority of
368 frameworks, biodiversity is considered, by definition, as a key determinant of ES. In the conceptual framework of
369 IBPES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services), ES are considered as
370 dependent on biological and ecological processes (Díaz et al., 2015). Biodiversity conservation itself is
371 considered as a key objective to enable ecosystems to provide ES.

372 Grasslands contribute numerous potential ES, including: pollination (of natural and agricultural species), control
373 of invasive and weed species, pest control, maintenance of soil biological activity, soil stabilization and structure,
374 erosion prevention, flood regulation, mineral recycling, pollution attenuation (pesticides or fertilizers), reduction
375 of cattle methane emissions, water quality regulation, climate regulation, carbon sequestration, biodiversity
376 conservation (flora, soil and aerial fauna, soil microflora), production of forage, bioenergy, medicinal and
377 aromatic plants (Bengtsson et al., 2019).

378 Different characteristics of grassland affect different ES. Biodiversity conservation, pollination, control of
379 invasions, cultural services, maintenance of soil biological activity and even reduction of cattle methane
380 emissions clearly depend on the overall level of biodiversity. ES related to water and physical soil processes (soil
381 stabilization and structure, erosion prevention, flood regulation, pollution prevention) mainly depend on above
382 grass biomass. Biomass and bioenergy production are generally maximized in intensified and species-poor
383 grasslands, including temporary grasslands (Yang et al., 2019). Analyzing 147 plants species studied in 17
384 experiments, (Isbell et al., 2011) concluded that the conservation of numerous species, including those
385 apparently "redundant" for ecosystem functioning, is essential to provide multiple ES.

386 **Biodiversity conservation**

387 Conservation of species-rich grasslands by definition conserves floral diversity. Many animal and microbial taxa
388 are reliant on plant diversity for habitat and food. As an example, (Kruess and Tscharntke, 2002a) have
389 established a link between plant species richness and the diversity of grasshoppers, butterflies, bees and wasps,
390 in interaction with grazing activity.

391 **Pollination and pollinators**

392 There is a close link between grassland plant biodiversity and pollinator abundance and diversity (Potts et al.,
393 2003). As shown by (Orford et al., 2016) in a grassland field experiment manipulating species mixtures, even a
394 modest enhancement in plant diversity, by addition of legumes and forbs, results in a better functional diversity
395 of grassland pollinator communities. Beyond the diversity of a single grassland community, the co-occurrence of
396 several plant communities may improve the type, number and frequency of contacts between plant and
397 pollinators (Fantinato et al., 2019).

398 **Soil biological activity**

400 Grassland plant diversity is correlated with soil microbial diversity (fungi, bacteria) (Spehn et al., 2000) (Benizri
401 and Amiaud, 2005). Similar effects have been observed for other soil taxa like earthworms (Piotrowska et al.,
402 2013). Plant functional traits also improve the structure of the microbial community (de Vries et al., 2012)
403 (Strecker et al., 2015). In a long term grassland diversity experiment, (Eisenhauer et al., 2018) showed that plant
404 diversity also improves root biomass and soil respiration as well as soil microbial biomass.

405 **Mitigation of cattle methane emissions and reduction of global warming**

406 Assessing the role of grassland biodiversity in mitigating cattle methane emissions is complex for a number of
407 reasons:

- 408 - 1) a realistic evaluation must take into account not only the direct effect of grass composition and
409 diversity on animal physiology, but also indirect farm level effects such as consumption of concentrates
410 or forage crop cultivation.
- 411 - 2) Findings may change according to the units measured. Examples include greenhouse gas emissions
412 calculated per animal, per kg of meat or milk, or per ha. In an on-farm experiment comparing beef
413 grazing species-poor or species-rich grasslands, (Richmond et al., 2015) found that biodiversity reduced
414 daily methane emissions per animal, but not per kg of weight gain.
- 415 - 3) it is crucial to consider all fluxes contributing both positively (C sequestration) and negatively (CH₄,
416 CO₂, N₂O) to global warming at farm level.

417 (Macheboeuf et al., 2014) screened 156 grassland plant species, and evaluated their methane emission potential
418 in artificial rumens. They concluded that the botanical families that reduced methane most efficiently were the
419 Rosaceae, Onagraceae, Polygonaceae and Dipsacaceae.

420 **Control of plant invasions**

421 Resistance of grasslands to invasive plant species generally increases with grassland diversity (Hector et al.,
422 2001). Maintaining a high plant functional diversity also helps to prevent invasive species (Pokorny et al., 2005).
423 However, manipulating species evenness within native prairie grassland mesocosms, (Brett Mattingly et al.,
424 2007) found no effect on community invasion by exotic plants. The effect of grassland diversity on invasion
425 resistance is generally explained by niche complementarity and better use of resources (light, water and
426 minerals), as demonstrated by (Frankow-Lindberg, 2012)

427 **Cultural services: recreation, education and research**

428 Grasslands, and particularly species-rich semi-natural grasslands, are important for the whole of society and not
429 just farmers (Quétier et al., 2010). Society gains a set of "cultural" benefits that generally increase with grassland
430 diversity, and the rarity of species or habitats. The whole of society can appreciate this biodiversity and the
431 contribution of grasslands to the beauty of the landscape (Marzetti et al., 2011).

432 **7 Assessing the economic value of species-rich grasslands**

433
434 From a macroeconomic point of view, awareness of the consequences of the loss of biodiversity and the
435 potential profits from improving biodiversity has risen all over the world since the Millennium Ecosystem
436 Assessment (2005). In 2007 the Governments of the G8 + 5 (bringing together both leading developed
437 economies and leading countries in the developing world) proposed the setting up of TEEB (The Economics of
438 Ecosystems and Biodiversity), a global initiative hosted by the United Nations Environment Programme to
439 analyze the global economic benefit of biological diversity (Balmford and Rodrigues, 2008). Given the
440 importance of grasslands and rangelands (representing a third of the world's agricultural area), they are at the
441 heart of the debate about the economic value of biodiversity. From a microeconomic point of view, the question
442 is the economic incentive of farmers to promote systems, and in particular grasslands, with high biodiversity.

443 At the microeconomic (farm or field) level, the interest of conservation of grasslands biodiversity can be
444 considered from different perspectives, using the typology of values proposed by (Chevassus-Au-Louis et al.,
445 2009):

- 446 - direct uses/value of biodiversity: including forage production (increased productivity, more resilient
447 production (with reduced risk) or better quality of species-rich grasslands), production of medicinal and
448 aromatic plants, better prices for grassland animal products and production of grass biofuel.
449 - indirect uses/value of biodiversity: including prevention of soil erosion, better water retention,
450 prevention of weeds and improved animal health.
451 - “option value”, i.e. the value of biodiversity for the future, for example by maintaining the fertility of the
452 soil.

453 In addition to these three types of values, economists suggest a so-called non-use value, which covers the
454 broader value of biodiversity for humankind, regardless of its direct usefulness, as well as the heritage value of
455 passing on biodiversity to future generations.

456
457 In a recent publication named “Biodiversity can pay” (Binder et al., 2018) used an economic model to find the
458 optimum level of biodiversity in agricultural systems, and concluded that the optimal species richness falls
459 “between the low levels currently found in commercial grasslands and the high levels found in natural
460 grasslands”. A key element in species-rich grassland profitability lies in the reduction of mid- and long-term risks.
461 Using data from the Jena biodiversity Experiment in Germany (plot experiments with a combination of 16
462 grasses, 12 legumes, and 20 tall and 16 small herbs) (Finger and Buchmann, 2015) demonstrated significant
463 insurance cost benefits associated with grassland diversity (e.g. in improving grassland resilience to more
464 extreme weather events). Similar results were found by (Schläpfer et al., 2002) when assessing returns from hay
465 cultivation in diverse vs non-diverse grasslands. There is a need for more research on the economic value of
466 species-rich grasslands. This research needs to take into account many factors such as:

- 467 - the differences of quantity and quality of grass produced between species-rich and –poor grasslands
468 - long-term stability of production in the face of climatic change
469 - differences in production costs compared to more intensive, forage-based systems (e.g. fertilizer,
470 harvesting and labour costs)
471 - reduced costs of animal feed and veterinary costs
472 - improved feed self-reliance (level of dependence on concentrate purchases)
473 - the premium price allowed by grassland production (including protected designation of origin (POD)
474 labelling)
475 - future proofing in the light of the growing demand for more environmentally friendly animal production
476 with higher standards of animal welfare
477 - the payment of environmental subsidies to support biodiversity conservation

478 These studies will help make the economic case for increasing biodiversity in grasslands.
479

480 **8 Management of grasslands for both biodiversity and production** 481

482 Is there a management system of grasslands that can both maintain an acceptable level of production for
483 farmers and ensure conservation of biodiversity? Several answers can be given to this question:

- 484 - There is a wealth of research both on grassland management and on promoting grassland biodiversity
485 which provides a foundation for improving management practices
486 - many ecological studies linking the level of diversity and grassland production provide elements for
487 management solutions (as discussed earlier). Although higher levels of biodiversity are not always
488 compatible with high levels of production, stability of production over time is frequently associated with
489 a minimum level of biodiversity

- 490 - the previous discussion of economic value also indicates that it is possible to combine a high level of
491 biodiversity and a good level of profitability
492 - as noted earlier, annual production of biomass should not be the only criterion to evaluate agronomic
493 value of grasslands for farmers; other factors such as quality affect management practices to adopt

494 Because of the huge variety of different situations, a win-win situation is not possible for all grasslands.
495 However, reconciling production and biodiversity is achievable on a case by case basis.

496 A key initial decision is whether to (Green, 2005):

- 497 - promote biodiversity across the whole of a grassland (land sharing)
498 - dedicate specific space to promote biodiversity (land sparing)

499 Both solutions have their advantages and limitations (Balmford et al., 2005). From the point of view of
500 biodiversity conservation in grasslands, land sparing can ensure high levels of biodiversity (high level of flora and
501 fauna, taxonomic and functional diversity, preservation of patrimonial or endangered species), though at the
502 expense of forage production. The maintenance of dedicated areas often requires government subsidies to
503 compensate for the loss of production. Because of this cost, the major ecological disadvantage is that the
504 proportion of land allocated to these “high nature value” purposes may be low. This limits processes such as
505 natural regeneration of grasslands from seed dispersal. Dividing land in this way may have benefits for farmers in
506 allowing them to tailor production grassland precisely to the needs of their animals and optimize grass yields. On
507 the other hand, land sharing helps to conserve biodiversity over the whole field and contributes to ecosystem
508 services at the field and landscape scale. Its acceptance by farmers depends on the adoption of an extensive but
509 profitable farming production system.
510

511 (Sabatier et al., 2014) concluded that heterogeneous landscape management (i.e. land sparing) is the best way
512 to reconcile agricultural and ecological objectives. (Loucougaray et al., 2015) have also identified the advantages
513 of a balance between sown and permanent grasslands in optimizing the ecological intensification of alpine
514 grasslands. These results fit with other studies, for example on bird communities in tropical cloud forests of the
515 Colombian Andes (Cannon et al., 2019), or on trade-offs between overall agricultural production and biodiversity
516 in France (Teillard et al., 2017).

517 Before screening the main factors explaining the impact of management on grassland production and
518 biodiversity at field level, it is important to keep in mind two elements:

- 519 - 1) the configuration of the surrounding landscape partly helps to explain grassland biodiversity (Gaujour
520 et al., 2012), but this effect is low compared to local factors (Klimek et al., 2007)
521 - 2) current management may be sometimes less predictive of current biodiversity level than historical
522 grassland management (Boeuf-Tremblay et al., 1995; Gustavsson et al., 2007)(Yoshihara et al., 2016)

523 An extensive review of factors influencing grassland biodiversity has been conducted by (Isselstein, 2018).
524 Several management factors affect grassland biodiversity at field and farm scale, as reviewed by (Huguenin-Elie
525 et al., 2012) (Gaujour et al., 2012) (Tälle et al., 2016) (Rosa García et al., 2013) (Marini et al., 2007). These studies
526 suggest that management practices which particularly affect grassland biodiversity include intensity of grazing,
527 frequency and intensity of cutting as well as fertilization practices (N, P, K and other elements from mineral and
528 organic fertilization as well as animal droppings).

529 Nutrient inputs generally reduce plant diversity, as shown either in short- or long- term experiments (Schellberg
530 et al., 1999) (Silvertown et al., 2006) or in farm conditions (Isselstein, 2005) (Riesch et al., 2018). Mineral
531 fertilization tends to be more detrimental for species richness than organic manure (Kirkham et al., 2008).
532 Mineral nitrogen application may impact biodiversity even at low rates (30 kg N ha⁻¹ year⁻¹) (Plantureux, 1996a)

533 (Joyce, 2001), and at even lower rates when considering some patrimonial species that are very sensitive to
534 fertility levels (Grevilliot et al., 1998).

535 Other management practices may be negative, neutral or positive in their effects on biodiversity (Olf and
536 Ritchie, 1998) (Marriott et al., 2004). Analyzing 35 studies, (Tälle et al., 2016) concluded that grazing was
537 generally better for conservation of semi-natural grasslands than mowing. A meta-analysis conducted by (Diaz et
538 al., 2007) on 197 studies concluded that grazing is favorable to annual species, smaller and stoloniferous plants.
539 Animals do not only graze, but they also deposit huge amounts of nutrients (60 to 80% of their mineral intake),
540 and plant diversity can be also depressed by this nutrient load. Medium intensity grazing (in terms of stocking
541 rate and duration of grazing) generally appears more favorable than very low or very high grazing pressure
542 (Kruess and Tschardtke, 2002b) (Tichit et al., 2005) (Fischer and Wipf, 2002). For cutting regime, the date of the
543 first cut is crucial, with an early cut excluding non-clonal species (Zechmeister et al., 2003) (Smith et al., 2002).

544 The two main management factors determining grassland biodiversity – type of use and nutrient supply - also
545 significantly impact grassland production and quality. When these two types of factors are maximized, annual
546 grass biomass is generally optimized, but potentially at the expense of forage quality and biodiversity. In practice
547 a few competitive grasses (like *Lolium perenne* or *Dactylis glomerata*), few legumes (*Trifolium repens* and *T.*
548 *pratense*) and forbs (*Taraxacum* sp., *Ranunculus* sp.) are adapted to these intensive conditions and dominate
549 almost all other grassland species. As previously mentioned, medium intensification is more favorable for
550 biodiversity. This can be made profitable by the limitation of production costs (e.g. less reliance on fertilizers,
551 animal feed and veterinary costs), but also by higher selling prices for animal products with better organoleptic
552 quality, together with potential improvement animal welfare. This usually means not aiming for the highest
553 animal yields (annual quantities of milk or meat per animal or per ha).

554 In many regions with significant livestock production, semi-natural grasslands that have not been replaced by
555 forage crops or temporary grasslands are generally highly intensively managed, and their level of biodiversity is
556 generally very low. Based on the French national database of permanent grasslands eflorasys
557 (<http://eflorasys.univ-lorraine.fr>), (Plantureux, 1996b) suggest that only 20 to 25% of French permanent
558 grasslands can be considered as species-rich semi-natural grasslands. Since the 1980s, this proportion has
559 continuously decreased, due in part to practices such as more intensive grazing, early mowing, a greater focus
560 on silage production as well as an increase in mineral and organic fertilization. There is now a move to
561 'extensification' of these grasslands i.e. to restore them as semi-natural grasslands.

562 (Marriott et al., 2004) has reviewed a number of studies of extensification. These show that reducing fertilization
563 has a gradual impact on improving biodiversity. Some change in taxonomic composition can appear quite
564 quickly, but species richness and functional composition generally remains stable, with major improvement
565 taking a long time to occur (15 to 20 years). For example, (Isbell et al., 2013) studied grasslands fertilized for 10
566 years (with 95–270 kg N ha⁻¹ year⁻¹) and then not fertilized for another 20 years, and found no observable
567 recovery in species richness. Grassland response depends significantly on initial site fertility, and especially on
568 phosphorus fertility which strongly influences the presence of oligotrophic species (Janssens et al., 1998). In a
569 18-year study in southern England grasslands, cessation of fertilization decreased biomass by 50% after only two
570 years, while species richness remained stable for 5 years, before increasing to 300% of the initial richness after
571 18 years (Pallett et al., 2016).

572 According to the review by (Marriott et al., 2004), later cutting is favorable for plant species using sexual
573 reproduction, and decreasing animal stocking rate increases local heterogeneity of soil resources and,
574 consequently, species biodiversity. It is important to note that improvement of biodiversity by less intensive
575 management generally results in reduction in total animal output and, in some cases, in individual animal
576 performance. Abandonment of grassland management (cessation of grazing and harvesting) generally results in
577 a short-term change in grassland composition, with the domination of tall herbs and coarse grasses, and woody
578 plants. Species richness rapidly decreases (over 1 to 5 years), beginning a secondary succession to forest

579 vegetation. In those situations, restoration of abandoned grasslands by grazing may efficiently restore
580 biodiversity (Pykala, 2005).

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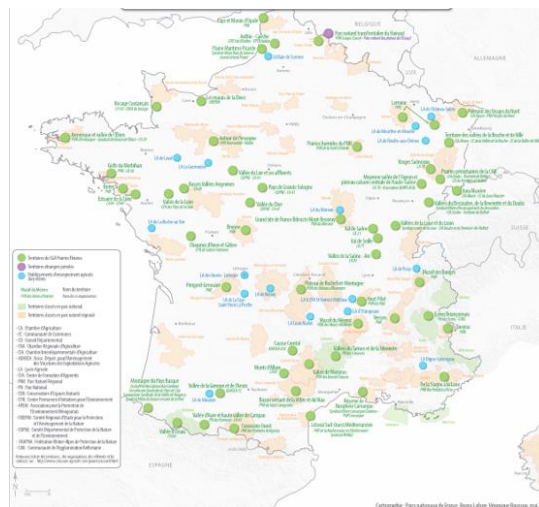
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583 **9 Case study : flowering meadows competition**

584

585 Although it is possible to reconcile biodiversity and production of grasslands, based both on scientific research
586 and the practical experience of more innovative farmers, the vast majority of farmers and their advisers remain
587 to be convinced. For most farmers, semi-natural grasslands have low productivity and provide poor quality
588 forage. There is an important need to change minds through education.

589 In contrast to most agriculture competitions which focused on productivity, a “Flowered meadows competition”
590 was organized for the first time in France in 2007 to reward farms achieving the best “agri-ecological
591 equilibrium” in their grasslands (Magda et al., 2015) (Plantureux et al., 2011). It was based on the agri-
592 environmental MEKAll program in Germany in the Federal State of Baden Württemberg (Oppermann, 2003). The
593 first competition was organized in 2007 in collaboration between the Natural Regional Park (PNR) “Massif des
594 Bauges” in the French Alps, and INRA, the French national agronomic research institute. In 2010, the
595 competition was organized at a national level and, since 2010, about 50 competitions are held around France
596 (Fig 4) involving 4-500 farmers each year. Local prizes are awarded, and the winners in each region compete for
597 a national prize, awarded annually during the national agriculture fair (“salon de l’agriculture”) jointly by the
598 Ministers of Agriculture and the Environment.



599

600 Fig 4: Localisation in 2016 of the 57 french “flowered meadows competition”. Source: Comité National
601 d’Organisation du concours “Prairies Fleuries”

602 A multi-disciplinary jury (consisting of farmers, naturalists (botanists, entomologists), beekeepers and scientists
603 (agronomists and ecologists)) assess each grassland. The jury uses a scoring system developed nationally by a
604 college of experts (Magda et al., 2015). This system evaluates not only the level of flora and fauna biodiversity of the
605 grassland, and its agronomic value (level of production and forage quality), but also to what extent forage
606 products correspond to the needs of the farmer (e.g. quality of forage, timing production, impact on animal
607 product quality). The jury begins with an interview with the farmer about his/her practices and expectations.
608 The jury then inspects the grassland along a diagonal cutting across the field. Ecological and agronomic criteria
609 are measured at three points along this diagonal. At these points the grassland must contain at least 4 species
610 from a regional list of species developed by experts to ensure the agri-ecological value of the grassland. At the
611 end of the visit, which lasts about an hour, the jury tells the farmer the outcome of its assessment.



612

613 Figure 5: List of species to assess the agri-ecological equilibrium in grasslands. Source: Journal des Prairies
 614 Fleuries 2017, APCA-FNPNR-INRA

615

616 The flowering meadows competition has been run in France for more than 10 years. Many farmers participating
 617 in the competition were already convinced of the interest of species-rich grasslands, but the competition has
 618 made it possible to convince a wider audience such as other farmers, farm advisors and agricultural students
 619 who will be future farmers and managers of natural areas. This competition has also played a role in training
 620 individual members of each jury: agronomists have learned to know more about animal and plant species, and
 621 naturalists to understand how to evaluate the agronomic value. Public broadcasts (national and regional TV,
 622 radio and print media) have shown society that it is possible to reconcile a profitable agriculture with
 623 biodiversity preservation.

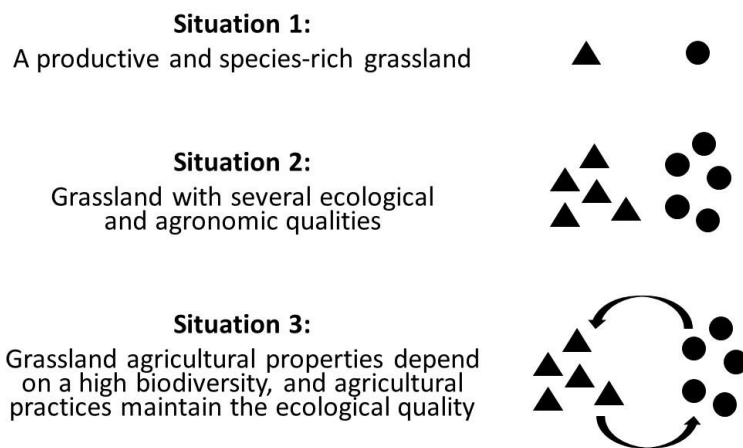
624 **10 Summary and future trends**

625 Figure 6 summarizes different definitions of the concept of “agri-ecological equilibrium”:

- 626 - Situation 1: a productive and species-rich grassland
- 627 - Situation 2: a grassland with several ecological and agronomic qualities
- 628 - Situation 3: a grassland where agricultural properties depend on a high biodiversity, and agricultural
 629 practices maintain ecological quality

630 Situation 1 is the most widely-used definition. It is usually based on a criterion for defining ecological value
 631 (usually plant species richness) and another for defining agronomic value (usually the annual return). The
 632 problem with this definition is that it is always a compromise that satisfies neither the farmer nor the naturalist.
 633 Finding highly productive grasslands (i.e. annual biomass production > 8-10 T DM.ha⁻¹.year⁻¹ in temperate
 634 conditions) with very high species richness is impossible in practice.

635 Situation 2 depends on a wider range of criteria. The agronomic value may be evaluated both by annual biomass
 636 production and by timing of production, or the quality of forage from a nutritional, organoleptic or medicinal
 637 perspective. Ecological value can be defined by plant species richness, or the quality of the bloom for pollinating
 638 insects, and the shelter role of sward for birds and mammals. It is becoming more common to find compromises
 639 combining these different qualities.



640

641 Fig 6: Three possible definitions of agri-ecological equilibrium of grasslands. Each triangle represents an
 642 agronomic criterion, and each circle an ecological criterion. Source: Sylvain Plantureux, Univ Lorraine, France

643 Situation 3 offers the opportunity for an agri-ecological balance which allows a reconciliation between
 644 biodiversity and production. In this situation, the agronomic value of grassland is totally dependent on its
 645 biodiversity. For example, maintaining forage energy value is related to the diversity of grasses with different
 646 development cycles. At the same time, agricultural practices are essential for the conservation of biodiversity.
 647 For example, mowing keeps open swards, or the type of grazing promotes biodiversity-friendly heterogeneity.

648 Reconciling biodiversity and production of grasslands is an issue for society as a whole which requires production
 649 of safe animal products in an environmentally-friendly way. The aspect which has been studied the most is the
 650 relationship between the level of taxonomic or functional biodiversity and biomass production as well as
 651 production qualities such as resilience and stability. Most studies are controlled experiments, where the
 652 composition of vegetation is managed artificially. These results cannot be extrapolated without care to semi-
 653 natural species-rich grasslands. This relationship needs further investigation, and the relationship between
 654 biodiversity and biomass production should be studied in a larger number of semi-natural communities.

655 Recent research has focused on the quality of production rather than quantity. The effect of biodiversity on
 656 forage qualities (such as energy, protein and mineral content) is becoming clearer, even if further work is
 657 needed. Research is now focusing on the secondary metabolite content of meadow species and its effect on the
 658 organoleptic quality of animal products, animal and human health. Finally, in order to convince farmers, their
 659 advisers, governments and policy makers of the need to preserve the biodiversity of grasslands, it is necessary to
 660 conduct an appropriate economic and social assessment. This assessment needs to address both the micro-
 661 economic scale (farm-scale) and the macro-economic scale (regions, countries).

663

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665

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