

1 Grassland vulnerability to climate change varies by region and season through productivity-  
2 stability trade-offs

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14 Abstract

15 Understanding the vulnerability of permanent grasslands to climate change is essential for  
16 sustaining forage production and other ecosystem services. Potential adaptation levers include  
17 adjustments in management strategies and the selection of plant functional types (PFTs). This  
18 study quantifies changes in biomass yield and interannual stability of temperate permanent  
19 grasslands under future climate scenarios, using Gras-Sim, a process-based model integrating  
20 climate, soil management, and PFT composition. Simulations were performed for contrasting  
21 agricultural regions at +2 °C, +3 °C, and +4 °C warming levels, using downscaled CMIP6  
22 projections (CMCC, MIR, MPI) with corresponding CO<sub>2</sub> trajectories. Significant interactions  
23 between region, climate model, and PFT ( $P < 0.001$ ) revealed context-dependent responses.  
24 In high-altitude regions such as the High Ardennes, annual yields increased by up to 2.52 t DM  
25 ha<sup>-1</sup> compared to the historical baseline (1981-2010). Across all scenarios, PFT B (e.g. *Dactylis*  
26 *glomerata*) exhibited significantly higher yields, while PFT A (e.g. *Lolium perenne*) showed  
27 significantly higher interannual stability, confirming a productivity-stability trade-off. Seasonal  
28 shifts were more pronounced under MIR +4 °C, with spring yields increasing by 4.5 t DM ha<sup>-1</sup>  
29 and summer yields decreasing by 2.4 t DM ha<sup>-1</sup> relative to historical baselines ( $P < 0.001$ ). The  
30 frequency of pixel-years without a summer cut increased up to 14% under MIR at +4 °C,  
31 highlighting an emergent signal of production collapse during peak drought. These results  
32 support the need for adaptation strategies that combine functional complementarity, flexible  
33 management, and spatially explicit simulation tools to sustain grassland productivity and  
34 stability under climate change.

35 Key words: process-based modeling, plant functional types, forage yield, interannual  
36 variability, climate scenarios, cutting management.

## 37 **1. Introduction**

38 Permanent grasslands are crucial to temperate ecosystems, providing forage for herbivores  
39 and contributing to climate regulation and biodiversity preservation (Soussana and Duru,  
40 2007; Bengtsson et al., 2019; Bardgett et al., 2021). They are also important for ecosystem  
41 multifunctionality, supporting services such as pollination, habitat provision, nutrient cycling,  
42 and erosion control (Gaujour et al., 2012; Liu et al., 2023; Allart et al., 2024), in addition to  
43 cultural services and aesthetic value. In Europe, permanent grasslands account for 34% of the  
44 utilized agricultural area (UAA) (Schils et al., 2022). Because of their central role in ecosystem  
45 functioning, grassland vulnerability to climate change has broad ecological and agricultural  
46 implications.

47 In addition to changes in overall productivity, climate change is also expected to reshape the  
48 seasonal distribution of grassland growth. An earlier onset of vegetation development is a  
49 widely observed response of herbaceous plants to warming, especially in temperate  
50 grasslands (Piao et al., 2019; Huang et al., 2020). Long-term records of cool-season grasses  
51 such as *Lolium perenne* already show a trend toward earlier reproductive development  
52 (Gilliland et al., 2025). While these shifts may increase spring productivity, they can also  
53 decrease resilience to summer droughts, resulting in imbalances in seasonal growth and  
54 increased interannual variability of forage supply.

55 Vulnerability is a multifaceted concept that is often used to analyze sensitivity, exposure, and  
56 the ability to adapt to natural environments (Pacifiçi et al., 2015). More precisely, it can be  
57 defined as the sensitivity and resilience of ecosystems to external disturbances, such as climate  
58 change and human activities, at a given scale of time and space (Li et al., 2018). In grassland  
59 systems, vulnerability depends on weather conditions as well as soil properties, species  
60 richness, management practices, and the interactions among these factors. Species-rich  
61 grasslands tend to be more resistant to climate extremes, maintaining more stable productivity  
62 under such conditions (Isbell et al., 2015). In European calcareous grasslands, regular mowing  
63 increases diversity in mesic systems, while drought reduces diversity in xeric systems,  
64 demonstrating that responses depend on local pedoclimatic context and management  
65 (Maalouf et al., 2012). However, the complexity of grassland ecosystems and the uncertainty  
66 of future climate conditions make it difficult to explore adaptation strategies through field  
67 experiments alone. Although field experiments are essential, they are limited in time, space,

68 and the range of scenarios they can address. This motivates quantitative approaches designed  
69 to identify the mechanisms through which pedoclimatic heterogeneity and functional  
70 composition mediate grassland responses to climate change. Simulation-based analyses can  
71 therefore serve as exploratory platforms, allowing climate, soil and management drives to be  
72 integrated without losing sight of ecological mechanisms.

73 Functional traits, defined as morphological, biochemical, physiological, structural,  
74 phenological, or behavioral characteristics expressed in phenotypes, are key to understanding  
75 how species respond to environmental drivers and influence ecosystem functioning (Díaz et  
76 al., 2013). In grasslands, such traits mediate plant responses to soil nutrient availability and  
77 management practices (e.g., grazing intensity, cutting frequency, fertilization), while also  
78 underpinning contributions to ecosystem services such as forage production, landscape  
79 openness, and biodiversity maintenance. To operationalize this functional diversity, plant  
80 functional types (PFTs) have been proposed as groups of species sharing contrasting trait  
81 profiles. This replaces long species lists with a smaller set of functional strategies suited for  
82 agronomic diagnostics and modeling (Cruz et al., 2002, 2010). In temperate grasslands, the  
83 initial topology classified 17 grass species into four functional groups (Cruz et al., 2002): Type  
84 A includes early developing species with rapid growth but low standing biomass accumulation  
85 (e.g. *Lolium perenne*); Type B comprises later-developing species with greater biomass  
86 accumulation (e.g. *Dactylis glomerata*); Types C and D correspond to slow-growing, lower-  
87 quality species with late phenology (e.g. *Festuca rubra*, *Briza media*). This classification was  
88 later expanded to six PFTs to accommodate a broader range of temperate grass species,  
89 increasing the coverage from 17 to 38 species (Cruz et al., 2010). In grassland process-based  
90 models, PFTs enable contrasting responses to environmental conditions and management to  
91 be represented without tracking each species individually, which is particularly useful in  
92 species-rich permanent grasslands. Empirical studies confirm that functional groups exhibit  
93 different sensitivities to climatic stresses. For instance, *Dactylis glomerata* (PFT B) sustains  
94 comparatively higher production under water deficit by mobilizing carbohydrate reserves,  
95 whereas *Lolium perenne* (PFT A) shows sharper declines in biomass and poorer persistence  
96 (Turner et al., 2012). At the physiological level, resilience to extreme events has been shown  
97 to depend on carbohydrate metabolism in meristems with *Dactylis glomerata* exhibiting  
98 markedly higher tolerance than other species (Voltaire et al., 2020). In temperate Europe,

99 productive permanent grasslands often include high-yielding forage grasses, such as perennial  
100 ryegrass (*Lolium perenne*, PFT A) and cocksfoot (*Dactylis glomerata*, PFT B). These species are  
101 frequently mentioned in the literature as important components of managed temperate  
102 grasslands (Żurek et al., 2012; Muylle et al., 2015). Given their agronomic relevance and  
103 widespread use, PFTs A and B capture functional strategies that are particularly representative  
104 of managed permanent grasslands in Wallonia.

105 Instead of focusing on improving a single drought-tolerant species, such as cocksfoot, a more  
106 informative approach is to contrast the functional strategies that co-occur in temperate  
107 grasslands. Examining both PFT A and PFT B reveals the key trade-offs among productivity,  
108 phenology, and stress responses, which would not be evident when studying *Dactylis*  
109 *glomerata* in isolation. Although legumes and forbs are present in permanent grasslands, the  
110 current version of the model does not explicitly represent their dynamics, as it was primarily  
111 calibrated and validated for cool-season perennial C3 grasses (Kokah et al., 2023).  
112 Consequently, our analysis focuses on the two dominant grass functional types (PFT A and PFT  
113 B), for which the model provides validated physiological and production responses.

114 Belgium offers a representative case for temperate Europe, where permanent grasslands  
115 display strong contrasts in soil depth, texture and altitude. About 66% of the national  
116 permanent grasslands are in Wallonia (SPW Agriculture, 2024a), the southern part of the  
117 country, which lies in a temperate oceanic climate. In 2023, they represented 41.8% of the  
118 UAA in Wallonia (SPW Agriculture, 2024a). These systems are already experiencing the effects  
119 of climate change, including repeated summer droughts, uneven rainfall distribution,  
120 damaging frosts, and early heat waves at the end of winter (IRM, 2025). These factors disrupt  
121 the regularity of grass growth and make pasture-based systems more vulnerable by exposing  
122 farmers to fodder shortages (Decruyenaere, 2022). Walloon permanent grasslands are  
123 considered representative of temperate Western European systems as they share key  
124 biophysical features across the Atlantic-continental gradient. These features include similar  
125 soil type ranges, comparable mesophilous grass species pools, and a livestock-based  
126 management system that combines grazing and cutting. These characteristics mirror the  
127 structural and functional attributes of temperate European grassland systems, making Belgium  
128 an appropriate case study for exploring agroecological responses to climate change.

129 This study aims to assess the vulnerability of temperate permanent grasslands to future  
130 climate conditions by quantifying the spatial and seasonal patterns of productivity and  
131 interannual stability resulting from the interactions between climate forcing, soil diversity, and  
132 plant functional strategies. We analyze two contrasting grassland types, each dominated by a  
133 different plant functional type (*Lolium perenne* for PFT A and *Dactylis glomerata* for PFT B),  
134 under uniform management and across a range of projected climate scenarios. Belgium serves  
135 as a representative case study for temperate Europe, characterized by strong pedoclimatic  
136 gradients that allow for the explicit exploration of regional contrasts in grassland vulnerability.  
137 By linking simulated spatial patterns to the underlying ecophysiological mechanisms in Gras-  
138 Sim, this study aims to improve the understanding of how productivity-stability trade-offs  
139 influence grassland vulnerability to climate change. Accordingly, the following hypotheses  
140 were formulated:

- 141 (1) Vulnerability is not solely a function of mean climate warming but emerges from  
142 interactions between local climate variations and soil conditions.
- 143 (2) PFT B (e.g. *Dactylis glomerata*) is expected to be more productive under climate stress,  
144 whereas PFT A (e.g. *Lolium perenne*) may show more stable interannual growth due to  
145 its more regular phenology.
- 146 (3) Growth dynamics are expected to shift, reflecting phenological responses to warming  
147 with reduced summer production and increased growth in spring and fall.

## 148 **2. Material and methods**

### 149 **2.1. Plant functional types and parameterization**

150 We used the functional typology established by Cruz et al. (2002, 2010), which groups  
151 temperate grass species into plant functional types (PFTs) based on shared phenological and  
152 morphological characteristics. In this study, only one species was selected to represent each  
153 PFT. Perennial ryegrass (*Lolium perenne*) represented PFT A and cocksfoot (*Dactylis glomerata*)  
154 represented PFT B as these species are among the most common representatives of the  
155 dominant functional strategies observed in productive permanent grasslands in Western  
156 Europe and Wallonia. PFT A comprises early, fast-growing species that are characterized by a  
157 short leaf lifespan, a high specific leaf area, and high digestibility during the vegetative stage.  
158 These traits support rapid biomass production under frequent defoliation. PFT B corresponds

159 to relatively later-developing, more conservative species with longer-lived leaves, lower  
160 specific leaf area, and a greater capacity to accumulate standing biomass. These differences  
161 provide the necessary functional contrast to investigate productivity-stability trade-offs.

162 Each PFT is parameterized using a set of phenological, structural, and physiological attributes  
163 in the model. Phenology is defined by the thermal time requirements for the onset (ST1) and  
164 completion (ST2) of the reproductive period. Structural traits include specific leaf area (SLA)  
165 and leaf lifespan (LLS). Seasonal modulation of growth is represented by minimum and  
166 maximum seasonal effects (minSEA and maxSEA, respectively). Digestibility dynamics are  
167 described by the maximum and minimum organic matter digestibilities of green vegetative and  
168 reproductive tissues (maxOMDGV, minOMDGV, maxOMDGR, and minOMDGR). Biomass  
169 structure is represented by bulk density parameters (BDGV, BDGR, BDDV, and BDDR). The  
170 temperature responses of growth are defined using the base temperature (T0), plateau  
171 temperature (T1), decline temperature (T2), and the upper temperature limit (Tlimit),  
172 combined with the minimum cumulative temperature requirement for growth (STmin). The  
173 full set of parameters and corresponding values for PFT A and PFT B is provided in Table S1.

## 174 **2.2. Weather and soil data**

### 175 **2.2.1. Historical and future climate data**

176 The historical weather data (air temperature, solar radiation, daily precipitation, and reference  
177 evapotranspiration) were extracted from the ERA5 reanalysis dataset, developed by the  
178 European Center for Medium-Range Weather Forecasts (ECMWF). These data were  
179 dynamically downscaled using MAR v3.14 (Regional Atmospheric Model), a physically based  
180 regional climate model well suited for high-resolution climate impact simulations. The MAR  
181 simulations were performed at 5 km × 5 km spatial resolution, consistent with studies on  
182 climate impacts in European agriculture (Fettweis et al., 2024). A 30-year reference period  
183 (1981-2010) was selected to represent the historical climate baseline, in accordance with IPCC  
184 (Intergovernmental Panel on Climate Change) guidelines for climate impact assessments.

185 Future climate projections were downscaled with the same MAR configuration to ensure  
186 consistency with the historical baseline. Future weather data were based on warming levels of  
187 +2 °C, +3 °C and +4 °C above pre-industrial levels, consistent with the Shared Socioeconomic  
188 Pathways (SSPs) defined in the Coupled Model Intercomparison Project (CMIP6; Eyring et al.,

189 2016). To capture a range of possible climate futures, three CMIP6 global climate models  
190 (GCMs) with contrasted temperature and precipitation responses over Europe were selected  
191 following the recommendations from the EURO-CORDEX community (Sobolowski et al., 2025):

- 192 • CMCC-CM2-SR5, dry and moderately warm scenario (CMCC);
- 193 • MPI-ESM1-2-HR, intermediate scenario (MPI);
- 194 • MIROC6, warm and wetter tendency, scenario with known warm/moist bias (MIR).

195 The simulation period runs from 2024 to 2100, with time windows of 30 years for the +2 °C  
196 and +3 °C scenarios and 20 years for the +4 °C scenarios (Table 1). This shorter window reflects  
197 the later occurrence and reduced duration of periods reaching +4 °C warming in CMIP6  
198 models. Moreover, the selected years differ between GCMs, since each model reaches the  
199 warming levels at a different pace. This approach follows IPCC recommendations to analyze  
200 climate impacts at specific global warming levels rather than fixed time periods. The associated  
201 CO<sub>2</sub> concentration (Table 1) was estimated as the mean value within each time window and  
202 assumed constant over the period, based on concentration-driven CMIP6 datasets provided  
203 by input4MIPs (Meinshausen et al., 2017). Supplementary figures summarize historical and  
204 future temperature and precipitation patterns at the regional scale (Figures S1-S4).

### 205 **2.2.2. Soil properties and spatial layers**

206 The soil input data used for simulations includes soil texture, and organic matter content,  
207 which are crucial for simulating water availability. The primary source for soil texture data was  
208 the ISRIC SoilGrids250m dataset (Hengl et al., 2017), developed by the International Soil  
209 Reference and Information Center. This dataset provides global soil properties at multiple  
210 depth intervals and a spatial resolution of 250 m x 250 m. To refine global layers with region-  
211 specific information where available, data on total organic carbon (TOC) were supplemented  
212 using regional soil information (Chartin et al., 2017). All data layers were projected to a  
213 common coordinate reference system and resampled to match the 250 m grid in the model.  
214 In Gras-Sim, soil water holding capacity is derived from soil texture and organic matter content  
215 using an empirical formulation that determines plant-available water (Kokah et al., 2023). This  
216 formulation combines the relative proportions of sand and clay with soil organic matter  
217 content to represent spatial variability in soil water availability across the landscape. Soil depth  
218 is not explicitly considered a limiting factor in the simulations since Gras-Sim represents soil

219 water dynamics within the top 1 m of the soil profile. Consequently, spatial contrasts in  
220 simulated water availability primarily reflect differences in soil texture and organic matter  
221 content rather than total soil depth. The spatial distribution of the main soil types of Wallonia  
222 is shown in Figure S5.

### 223 **2.2.3. Growing season definition**

224 To ensure consistency across simulations and climate scenarios, all analyses were based on a  
225 common definition of the growing season, which used fixed day-of-year (DOY) intervals. The  
226 growing season was defined as DOY 60 to 334, which corresponds to approximately March 1  
227 to November 30. Within this period, three seasons were identified:

- 228 • Spring: DOY 60 to 181 (approximately March 1 to June 30)
- 229 • Summer: DOY 182 to 243 (approximately July 1 to August 31)
- 230 • Autumn: DOY 244 to 334 (approximately September 1 to November 30)

231 This calendar-based definition reflects the typical phenology of temperate grasslands and  
232 ensures comparability across regions, climate models, and warming levels. In managed  
233 temperate grasslands, seasonal analyses often use calendar-based partitions of the grazing or  
234 growing season. These partitions typically distinguish between spring (March-May), summer  
235 (June-August), and autumn (September-November), which correspond to different phases of  
236 grass growth and management activity (Chang et al., 2017). Extending the spring period to  
237 include June enables spring cuts to account for the biomass accumulated during the late spring  
238 growth phase. The winter period (DOY 1 to 59 and 335 to 365) was excluded because biomass  
239 production is negligible and no cuts occur during this time.

### 240 **2.2.4. ETCCDI climate indices**

241 To better characterize extreme climatic conditions that could affect grassland productivity in  
242 the future, three indices from the ETCCDI (Expert Team on Climate Change Detection and  
243 Indices) reference system were calculated annually for each climate scenario, based on daily  
244 data series. All indices were computed only over the growing season (DOY 60-334) to ensure  
245 they reflected conditions relevant to grass growth and management. The indices used are as  
246 follows:

- 247 • TXx: seasonal maximum temperature (°C), defined as the maximum daily temperature  
248 over the growing period;
- 249 • RX5day: maximum precipitation over five consecutive days (mm) within the growing  
250 period; an indicator of extreme rainfall events;
- 251 • CDD: consecutive dry days, defined as the maximum seasonal duration of drought,  
252 calculated as the longest sequence of consecutive days with daily precipitation strictly  
253 less than 1 mm within the growing period.

254 These indices were extracted annually for the nine climate model-warming combinations and  
255 compared with historical data.

### 256 **2.3. Pedoclimatic drivers of grassland productivity in Wallonia**

257 Wallonia comprises ten agricultural regions that differ in soil, climate, and topography (Figure  
258 1). Strong spatial gradients in drainage conditions, soil texture and water-holding capacity are  
259 characteristic of these regions, as illustrated by the detailed soil map in Figure S5. Climatic  
260 conditions also vary significantly from region to region, with differences in precipitation  
261 amounts, temperature regimes, and length of the growing season following the main  
262 topographic gradients. Together, these pedoclimatic gradients are therefore expected to have  
263 a strong influence on grassland productivity and stability across Wallonia. Substantial within-  
264 region heterogeneity in soil properties further justifies the use of spatially explicit simulations  
265 before regional aggregation. This pedoclimatic heterogeneity, summarized in Table 2 (SPW  
266 Agriculture, 2024b; Forton and Meniger, 2020) and illustrated in Figure S5, motivates the  
267 modeling strategy adopted in this study, wherein simulations are performed at the pixel  
268 (cluster) scale.

### 269 **2.4. Gras-Sim model**

270 Gras-Sim (Kokah et al., 2023) is a process-based model designed to simulate the growth of  
271 permanent grasslands by integrating weather data, soil properties, management practices,  
272 and the ecophysiological characteristics of dominant species grouped into plant functional  
273 types (PFTs). In this study, the model is used as an operational framework to investigate how  
274 ecological mechanisms (functional composition, soil heterogeneity, climate drivers) condition  
275 grassland productivity and stability under contrasting climate scenarios.

#### 276 **2.4.1. Model description and CO<sub>2</sub> effect function**

277 Gras-Sim simulates the daily dynamics of permanent grasslands. Biomass is represented in  
278 four compartments: green vegetative biomass (BMGV, kg DM ha<sup>-1</sup>), dead vegetative biomass  
279 (BMDV, kg DM ha<sup>-1</sup>), green reproductive biomass (BMGR, kg DM ha<sup>-1</sup>), and dead reproductive  
280 biomass (BMDR, kg DM ha<sup>-1</sup>). The model integrates water and nitrogen dynamics, with transfer  
281 processes between soil and plant. Two different PFTs, A and B, were used to represent  
282 contrasting functional strategies, enabling the exploration of trade-offs in productivity and  
283 stability under different climate conditions. The increase in atmospheric CO<sub>2</sub> concentration  
284 due to climate change has a direct impact on plant physiology, by improving radiation use  
285 efficiency (RUE, g DM MJ<sup>-1</sup>) (Stockle et al. 1992). The model accounts for this CO<sub>2</sub> fertilization  
286 effect ( $fCO_2$ ) using an exponential formula derived from Stockle et al. (1992). The equation is  
287 as follows:

$$fCO_2 = 2 - \exp\left(\log(2 - \alpha_{CO_2}) \times \frac{CO_2^{atm} - 350}{600 - 350}\right) \quad (1)$$

288 where  $CO_2^{atm}$  (ppm) represents the atmospheric concentration of CO<sub>2</sub>, which is provided at  
289 the same time as the other weather data. The values 350 ppm and 600 ppm are the reference  
290 concentration and the upper value used for calibration, respectively.  $\alpha_{CO_2}$  is a parameter that  
291 controls the sensitivity of the plant to CO<sub>2</sub>, generally around 1.2 for C3 plants, the value used  
292 in this work for both PFTs. This formulation ensures that the projections of grassland  
293 functioning account for the physiological response of C3 grasses to rising CO<sub>2</sub>. The CO<sub>2</sub> values  
294 for each combination of climate model and warming scenario are shown in Table 1.

#### 295 **2.4.2. Site-level validation and regional-scale applicability**

296 Gras-Sim used in this study is the same model evaluated in Kokah et al. (2023). The model was  
297 tested against multi-year observations collected at three sites distributed across contrasting  
298 agricultural regions of Wallonia: Louvain-la-Neuve (Sandy-Loamy region), Tinlot (Condroz), and  
299 Michamps (Ardennes region). These sites cover a broad range of soil depths, textures,  
300 altitudes, and climatic regimes representative of the main pedoclimatic contexts in the study  
301 area. Across sites and plant functional types, Gras-Sim simulated biomass production with a  
302 relative root mean square error (RRMSE) of 29%, a normalized deviation (ND) of 2%, and a  
303 model efficiency (EF, Nash-Sutcliffe predictive efficiency) of 0.71. For the two plant functional  
304 types, the ND values remained low (2-4%), indicating limited systematic bias. These results

305 demonstrate that the model accurately captures biomass dynamics under contrasting water  
306 and nitrogen conditions and that its structure and parameterization remain robust across the  
307 range of pedoclimatic situations in Wallonia.

308 Direct validation at the pixel level is not feasible when applying the model at a regional scale  
309 and over long climatic windows. Historical yields per pixel cannot be observed across Wallonia,  
310 particularly under management conditions comparable to the standardized simulation setup.  
311 This study aims to assess the vulnerability of temperate permanent grasslands to future  
312 climate conditions by quantifying spatial and seasonal patterns of productivity and interannual  
313 stability, rather than reproducing observed regional yields under specific management  
314 regimes. To ensure consistency between the validated site-scale behavior of the model and its  
315 regional-scale application, historical simulations were aggregated by agricultural region and  
316 compared with reported regional yield ranges.

317 However, observed regional yield data integrate a wide range of species compositions and  
318 management practices (e.g., fertilization levels, cutting frequency, and timing) that are not  
319 explicitly represented in the standardized management assumptions used in the simulations.  
320 As a result, strict quantitative comparison is not feasible. Since the observed data are reported  
321 as ranges rather than as specific measurements, this comparison is used solely as a plausibility  
322 check to verify that simulated historical yields fall within realistic orders of magnitude at the  
323 regional scale, rather than as formal validation at the regional scale.

324 The simulated historical baseline primarily serves as an internally consistent reference point  
325 for assessing relative changes in productivity and stability under future climate scenarios. This  
326 approach ensures that the projected changes reflect the combined effects of climate forcing,  
327 soil heterogeneity, and functional strategies, which aligns with the core objective of the study.  
328 Aggregated regional values derived from the simulated historical data are summarized in Table  
329 S2, alongside reported regional ranges.

### 330 **2.4.3. Model spatialization**

331 Since soil and weather conditions vary spatially within the study area (Table 2), we used  
332 explicitly spatialized data. The spatialization of the Gras-Sim model was based on the  
333 interaction between the resolution of the weather data (5 km × 5 km) and that of the soil data  
334 (250 m × 250 m). Given the large number of simulations required to cover the whole of

335 Wallonia, the number of simulations was reduced to optimize the computation time as follows.  
336 First, the soils were classified by land use, and we retained only those corresponding to  
337 permanent grasslands, based on ISRIC data. Then, within each 5 km × 5 km climate tile,  
338 unsupervised X-means clustering (Pelleg and Moore, 2000) was performed to group soil pixels  
339 with similar characteristics and automatically determines the optimal number of clusters.  
340 Once the clusters were defined, the soil variables required for Gras-Sim (clay, sand, and soil  
341 organic matter content) were averaged by cluster. This approach balances accuracy and  
342 computational efficiency, while capturing soil-climate diversity.

343 Gras-Sim explicitly models coupled water and nitrogen dynamics in the soil-plant system, with  
344 these processes responding non-linearly to local pedoclimatic conditions. Key hydraulic  
345 properties such as field capacity, wilting point and saturation are determined by soil texture  
346 and organic matter content, and these properties in turn control the fraction of available water  
347 and the water stress factor. Similarly, the size and turnover of the soil organic N pool are driven  
348 by organic matter content, thereby influencing mineralization, immobilization and mineral N  
349 availability. As the growth reduction factors for water and nitrogen, as well as the soil N supply  
350 functions, rely on thresholds and non-linear responses, the model behavior cannot be  
351 reproduced using a single, region-averaged soil profile. Consequently, spatial aggregation prior  
352 to simulation would obscure critical non-linear responses to soil-climate variability.

353 By combining high-resolution soil data with cluster-based aggregation within each 5 km  
354 climate tile, we ensure that simulations retain the distribution of soil-climate combinations,  
355 including extreme and drought-prone soils, which have a disproportionate effect on  
356 productivity and inter-annual stability. Regional indicators (annual yield and stability) are  
357 subsequently obtained by computing the arithmetic mean of the simulated outputs across all  
358 soil-climate clusters belonging to each agricultural region. This post-simulation averaging  
359 integrates spatial heterogeneity while preserving non-linear local responses. This approach  
360 increases the robustness and representativeness of regional-scale projections while enabling  
361 synthesis at an operational scale relevant for agricultural planning.

362 This study was based on 10 separate sets of simulations, corresponding to the 9 combinations  
363 of the 3 climate models (CMCC-CM2-SR5, MPI-ESM1-2-HR and MIROC6) with the 3 warming  
364 scenarios (+2 °C, +3 °C and +4 °C), plus a historical scenario. Clustering reduced the total  
365 number of daily simulations by about tenfold, making the spatially explicit design

366 computationally feasible while maintaining soil-climate heterogeneity. The resulting  
367 simulation design allowed exploration of ecological trade-offs at operationally relevant scales,  
368 without excessive computational cost. Plant parameters were held constant across all  
369 simulation zones, since Gras-Sim uses PFT-specific physiological and structural traits calibrated  
370 from experimental data (Kokah et al., 2023). The model does not explicitly simulate spatial  
371 variation in plant density; differences in productivity across regions instead arise from spatial  
372 heterogeneity in soils and climate.

### 373 **2.5. Management practices**

374 The management regime applied directly influences the model output. To focus on the effects  
375 of soil and weather conditions on grassland productivity, a standardized management scheme  
376 based on expert-input was applied consistently across all simulations. The management  
377 regime included cuts and mineral fertilization (Table 3). Cuts were triggered dynamically based  
378 on thresholds of accumulated biomass and dry spells, as detailed in Table 3. The 2 mm limit  
379 was chosen as a compromise between quantity and quality. Each cut was made at 5 cm.  
380 Nitrogen inputs were programmed early in the season and after the first two cuts. While  
381 grazing remains the dominant practice across most temperate grasslands, cutting-based  
382 management was adopted as a standardized experimental setting to isolate the effects of  
383 functional type, soil, and climate. This approach ensures tighter control of biomass dynamics  
384 and avoids variability linked to animal behavior. Such a design enables comparability across  
385 regions and scenarios.

### 386 **2.6. Systemic indicators**

387 Our study focused on two main aspects: biomass yield and stability. These indicators allow us  
388 to evaluate the productivity of grasslands under different climate scenarios and to quantify  
389 their stability in the face of climate change.

390 The assessment of grassland productivity is essentially based on biomass yield. This  
391 corresponds to the sum of biomass exported by the different cuts during the season, expressed  
392 in tons of dry matter per hectare ( $t\ DM\ ha^{-1}$ ). Biomass production is determined by the  
393 combined influence of incident photosynthetically active radiation (PARI) and its utilization  
394 through radiation use efficiency (RUE), which is modulated by atmospheric  $CO_2$  concentration;  
395 nitrogen inputs, which influence the ability of the plant to convert solar energy into biomass;

396 and cutting dates and residual heights, which condition regrowth and biomass accumulation  
397 between two cuts. Yield is therefore essential for understanding the effects of climate  
398 scenarios and for assessing how grassland productivity may respond to rising CO<sub>2</sub> and  
399 warming.

400 Production stability is a key parameter for assessing the resilience and resistance of a grassland  
401 to inter-annual weather variations and extreme events. As defined by Isbell et al. (2015), it was  
402 calculated as the ratio between the mean biomass yield ( $\mu$ , t DM ha<sup>-1</sup>) and its standard  
403 deviation ( $\sigma$ , t DM ha<sup>-1</sup>) according to the following equation:

$$Stability = \frac{\mu}{\sigma} \quad (2)$$

404 Since both  $\mu$  and  $\sigma$  are expressed in the same units, stability is a dimensionless ratio. A  
405 grassland with a high but highly variable yield will have a lower stability than one with  
406 moderate but constant production. Stability is shaped by the frequency and intensity of  
407 extreme climatic events (e.g., droughts and heat waves) and by the ability of the system to  
408 recover after mowing, which depends on the cutting height and the availability of water and  
409 nitrogen. A stable ecosystem is essential to ensure regular forage production and a secure  
410 supply of biomass for livestock in a changing climate.

## 411 **2.7. Statistical analysis**

412 To ensure a precise spatial analysis, the simulation results obtained by cluster were  
413 redistributed at the pixel level, with a spatial resolution of 250 m. The statistical unit used in  
414 this study is therefore the pixel, for which annual yield (t DM ha<sup>-1</sup>) and stability ( $\mu/\sigma$ ,  
415 dimensionless) variables were analyzed. This disaggregation step ensured the spatial  
416 consistency of the environmental predictors and simulation outputs. All analyses were  
417 performed for ten climate model-warming combinations (+2 °C, +3 °C and +4 °C with three  
418 climate models CMCC, MPI and MIR, plus the historical scenario). All analyses were performed  
419 in R version 4.3.3 (R Core Team, 2023), using the packages *stats* (glm), *emmeans* (pairwise  
420 comparisons), and *randomForest* (machine learning)

421 Given the non-normal distribution of simulation data, confirmed by Shapiro-Wilk tests,  
422 generalized linear models (GLMs) were used. Because both yield and stability were strictly  
423 positive, but showed different distributional properties, we applied a Gaussian distribution

424 with a log link for yield since its values were approximately symmetric, whereas stability was  
 425 more skewed and therefore modeled with a Gamma distribution with a log link.

426 GLMs were structured to test the study hypotheses, focusing on the effects of plant functional  
 427 type (PFT), agricultural region, and climate model, together with continuous climatic  
 428 covariates describing growing-season conditions, such as mean growing-season temperature  
 429 ( $\bar{T}_{gs}$ ), seasonal maximum daily temperature ( $TXx$ ), maximum 5-day precipitation  
 430 accumulation ( $RX5day$ ), maximum number of consecutive dry days ( $CDD$ ), mean growing-  
 431 season rainfall ( $\overline{Rain}_{gs}$ ), and atmospheric CO<sub>2</sub> concentration ( $[CO_2]$ ). The final model included  
 432 all two- and three-way interactions between PFT, region, and model, while the climatic  
 433 covariates were included as additive effects. The management variable, number of cuts ( $n_{cut}$ ),  
 434 was excluded from the full GLM because it is an emergent property driven by PFT, region,  
 435 climate, and model-specific harvesting rules resulting in collinearity and partial absorption of  
 436 the climatic signal. Therefore,  $n_{cut}$  was evaluated separately in simplified GLMs (Eq. (S1)). The  
 437 full model is written as follows:

$$\begin{aligned}
 Y_{ijkl} = & \beta_0 + \beta_1 Model_i + \beta_2 PFT_j + \beta_3 Region_k + \beta_4 (Model_i \times PFT_j) \\
 & + \beta_5 (Model_i \times Region_k) + \beta_6 (PFT_j \times Region_k) \\
 & + \beta_7 (Model_i \times PFT_j \times Region_k) + \beta_8 \bar{T}_{gs} + \beta_9 TXx \\
 & + \beta_{10} RX5day + \beta_{11} CDD + \beta_{12} \overline{Rain}_{gs} + \beta_{13} [CO_2] + \varepsilon_{ijkl}
 \end{aligned} \tag{3}$$

438 where  $Y_{ijkl}$  is the response variable,  $Model_i$  is the effect of climate model,  $PFT_j$  is the effect  
 439 of PFT,  $Region_k$  is the effect of region,  $\beta_0$  is the intercept,  $\beta_n$  are the coefficients associated  
 440 with fixed effects and interactions, and  $\varepsilon_{ijkl}$  is the residual error. The interactions between  
 441 factors allowed us to quantify how functional types and regions differ in their responses to  
 442 climatic conditions across models.

443 To identify significant differences between the levels, a pairwise comparison of the adjusted  
 444 means was performed using the Tukey-Kramer method for multiple comparisons, with  
 445 significance set at  $\alpha = 0.05$ . The following equation was used:

$$\hat{\mu}_i - \hat{\mu}_j = \frac{\text{Observed Difference}}{\text{Pooled Standard Error}} \tag{4}$$

446 where  $\hat{\mu}_i$  and  $\hat{\mu}_j$  are the estimated means for factor levels  $i$  and  $j$ , respectively.

447 To assess the relative importance of the explanatory factors in predicting yield and stability, a  
448 Random Forest analysis was performed. Two separate models were fitted, one for yield and  
449 one for stability, using 500 trees per forest. The predictors were:

- 450 • climate model;
- 451 • plant functional type (PFT);
- 452 • soil properties (clay, sand, organic matter content).
- 453 • growing-season climate variables ( $\bar{T}_{gs}$ ,  $TXx$ ,  $RX5day$ ,  $CDD$ ,  $\overline{Rain}_{gs}$ , and  $[CO_2]$ )

454 To minimize overfitting, 10-fold cross-validation was applied, and model performance was  
455 assessed using out-of-bag (OOB) error estimate. Variable importance was quantified using two  
456 standard metrics:

- 457 • mean decrease in accuracy: the increase in prediction error when a given variable is  
458 permuted;
- 459 • mean decrease in node impurity (Gini index): The total reduction in residual sum of  
460 squares attributed to splits on each variable.

461 Random Forest was used as a complementary, descriptive tool to evaluate the robustness of  
462 factor importance in shaping yield and stability patterns.

### 463 **3. Results**

#### 464 **3.1. Grassland vulnerability across climate trajectories and regions**

##### 465 **3.1.1. Context-dependent effects of climate trajectories on grasslands**

466 Generalized linear models show that yield and stability are significantly affected by plant  
467 functional type (PFT), agricultural region, climate model, and all continuous climatic covariates  
468 including growing-season temperature, seasonal maximum temperature ( $TXx$ ), maximum 5-  
469 day precipitation ( $RX5day$ ), consecutive dry days ( $CDD$ ), mean growing-season rainfall, and  
470 atmospheric  $CO_2$  concentration (all  $P < 0.001$ ; Table S3). In the following, we first describe the  
471 spatial patterns emerging from the simulations and then synthesize the dominant drivers  
472 identified by the statistical analyses. To provide a basis for interpreting these patterns, the  
473 reference biomass and stability under historical climate conditions for both PFTs A and B are  
474 illustrated in Figure S6. The significance of these climatic covariates indicates that grassland

475 responses stem from the combined effects of various climate factors rather than from  
476 temperature alone.

477 The response of biomass yield to the climate trajectories associated with +2 °C, +3 °C, and +4  
478 °C global warming varies between models. The CMCC model predicts yield declines in almost  
479 all contexts compared to historical values, spatially represented in Figure S6, particularly in  
480 areas with heavy or calcareous soils with limited drainage capacity (Grassland region, Condroz  
481 and Jurassic) for PFT A (Figure 2) and PFT B (Figure 3). In contrast, the MIR and MPI models  
482 show more heterogeneous effects. The MIR model predicts, at +2 °C, localized gains in drought-  
483 sensitive sandy soils (Hennuyere Campine, Sandy-Loamy), and fertile loams (Loamy),  
484 occasionally exceeding +2 t DM ha<sup>-1</sup> (Figures 2 and 3), while the CMCC model predicts yield  
485 losses in the same contexts. At +3 °C, these contrasts become more pronounced, with the MIR  
486 and MPI models showing partial gains, particularly in calcareous uplands (Condroz), while the  
487 CMCC model continues to show a negative trend (Figures 2 and 3). At +4 °C, the trend  
488 continues; while MIR and MPI predict yield gains in almost all regions, CMCC predicts losses of  
489 up to -2 t DM ha<sup>-1</sup> in clay-rich lowlands (Jurassic), particularly for PFT B (Figure 3).

490 Stability responses follow a similar pattern (Figures 4 and S7). The CMCC model predicts a  
491 widespread decline in stability at all warming levels, with decreases exceeding -5 at +4 °C in  
492 upland acidic soils (Ardennes), particularly for PFT A (Figure 4). In contrast, the MPI model  
493 shows moderate stability increases at +2 °C and +3 °C, particularly in fertile and calcareous  
494 systems (Grassland region and Condroz) for PFT B, before reversing at +4 °C (Figure S7). The  
495 MIR model shows localized increases of up to +5 in cooler upland sites (Ardennes and High  
496 Ardennes) at +2 °C, particularly for PFT B (Figure S7), and stability losses in calcareous uplands  
497 (Condroz and Famenne) at +3 °C and +4 °C, particularly for PFT A (Figure 4).

498 Full GLM outputs are provided in Tables S4 and S5. Yield increases with mean growing-season  
499 temperature ( $P < 0.001$ ) and rainfall ( $P < 0.001$ ) but decreases with the number of consecutive  
500 dry days ( $P < 0.001$ ). In contrast, stability decreases with higher average growing-season  
501 temperatures ( $P < 0.001$ ) and rainfall ( $P < 0.001$ ). Random forest analysis confirms the  
502 dominant role of PFT as the most influential predictor of yield (importance = 135.87) and  
503 stability (importance = 95.79), followed by soil organic matter, clay, and sand (Table 4). Climatic  
504 covariates also contribute substantially, particularly mean growing-season rainfall (importance  
505 = 26.26 for stability, Table 4). These results suggest that uncertainty from climate models

506 surpasses uncertainty from soil variability; however, soil properties and climatic covariates  
507 remain key modulators of grassland responses.

### 508 **3.1.2. Regional heterogeneity in grassland vulnerability**

509 A comparative analysis of the regions reveals significant spatial variability in grassland  
510 vulnerability, in terms of both yield and stability. The High Ardennes region has the highest  
511 average increase in yield ( $+2.52 \pm 0.87$  t DM ha<sup>-1</sup> compared to the historical model), followed  
512 by the Ardennes ( $+2.08 \pm 0.82$  t DM ha<sup>-1</sup>) and the Fagnes ( $+1.67 \pm 0.90$  t DM ha<sup>-1</sup>) (Table 4). In  
513 contrast, the lowest average increase in yield are observed in areas with clay-limestone soils  
514 subject to drainage constraints (Jurassic,  $+0.87 \pm 0.82$  t DM ha<sup>-1</sup>), more than 1.5 t DM ha<sup>-1</sup> lower  
515 than in the High Ardennes region. These differences can be seen in the maps showing the  
516 absolute yield differences for functional plant types A and B (Figures 2 and 3), with the most  
517 productive areas mainly associated with cooler, high-altitude contexts (High Ardennes and  
518 Ardennes).

519 The ranking also reveals contrasting results for stability. The High Ardennes remained the most  
520 stable region compared to the historical model ( $+0.61 \pm 1.64$ ), while the Jurassic region shows  
521 the greatest instability ( $-2.00 \pm 1.80$ ), followed by the Famenne region ( $-1.46 \pm 1.12$ ) and the  
522 Loamy region ( $-1.24 \pm 2.01$ ) (Table 4). These results are corroborated by the stability maps  
523 (Figures 4 and S7), particularly under the CMCC +4 °C scenarios, where low-altitude areas show  
524 losses for both PFTs. In contrast, the MIR scenarios at +2 °C or +3 °C reveal pockets of  
525 maintained or even improved stability in some lowland areas (e.g. Sandy-Loamy). Some  
526 regions perform well on a single metric. Compared to the historical model, the Grassland  
527 region achieves an average yield of  $+1.61 \pm 0.83$  t DM ha<sup>-1</sup> (4th out of 10 regions), but lower  
528 stability ( $-1.16 \pm 1.08$ , 7th out of 10 regions) (Table 4). Similarly, although the Hennuyere  
529 Campine region was ranked 9th for yield, it was ranked 4th for stability. These discrepancies  
530 highlight that high yields do not necessarily translate into increased stability.

### 531 **3.1.3. Contribution of climate extremes to grassland vulnerability**

532 Compared to historical values, the extreme climate indices TXx (maximum daily temperature  
533 during the growing season), RX5day (maximum precipitation over five days) and CDD (number  
534 of consecutive dry days) show significant variations in several cases, depending on the climate  
535 models and the associated warming trajectory (Table 5). These changes highlight an enhanced

536 exposure of grasslands to climate extremes, beyond mean trends. TXx increases systematically  
537 in all scenarios, indicating a clear intensification of heat waves. The highest increases are  
538 observed in the CMCC model, reaching +8.50°C, followed by the MIR and MPI models with  
539 +6.39 °C and +6.20 °C respectively, all at a global warming of +4 °C (Table 5). In Gras-Sim, these  
540 extreme conditions directly affect daily growth through temperature and water stress  
541 reduction factors, which translates climatic extremes into reduced biomass accumulation.

542 For RX5day, significant increases compared to historical values are observed only in the CMCC  
543 model. The CMCC model shows increases of +24.44 mm and +23.31 mm at global warming  
544 levels of +2 °C and +3 °C respectively ( $P = 0.03$  and  $P = 0.02$ ; Table 5), while the +4 °C scenario  
545 shows no significant change (+3.76 mm,  $P = 0.55$ ) in RX5day. Despite positive mean anomalies  
546 in some scenarios (e.g. MIR at +4 °C, +12.84 mm,  $P = 0.07$ ), neither MIR nor MPI show  
547 statistically significant changes (Table 5). In some cases, the standard deviation exceeds the  
548 mean change (e.g. RX5day in CMCC at +2 °C), indicating high interannual variability with non-  
549 significant results despite large mean values.

550 Meanwhile, CDD is a count-based index representing drought duration. Simulations based on  
551 the CMCC model reveal moderate but significant increases of + 4.54 days (+2 °C,  $P = 0.01$ ), +  
552 6.47 days (+3 °C,  $P = 0.001$ ), and + 10.24 days (+4 °C,  $P = 0.002$ ) (Table 5). For the MIR model,  
553 changes remain small (+1.94 to +3.61 days) and non-significant ( $P = 0.07$ -0.21; Table 5). MPI  
554 also shows limited changes (+1.47 to +1.84 days) with no statistical significance (Table 5). These  
555 patterns indicate a tendency toward more frequent and prolonged droughts mainly under  
556 CMCC, amplifying exposure to summer fodder shortages. Overall, depending on the model  
557 considered, the projections tend to show an intensification of the climate extremes, including  
558 heat waves, intense precipitation events, and moderate increases in drought duration, and  
559 occasional increases in heavy rainfall.

### 560 **3.2. Grassland vulnerability according to plant functional type**

561 Generalized linear models reveal that PFT significantly impacts both yield and stability ( $P <$   
562  $0.001$ ; Table S3). However, these effects do not operate uniformly across the study area. Strong  
563 interactions between PFT, agricultural region, and climate model (all  $P < 0.001$ ; Table S3)  
564 indicate that performance contrasts between PFT A and PFT B depend strongly on  
565 pedoclimatic and climatic contexts. Consistently, across all simulations, PFT B exhibits a

566 positive main effect on yield ( $\beta = 0.10$ ,  $P < 0.001$ ; Table S4), while PFT A exhibits significantly  
567 higher stability ( $\beta = -0.07$ ,  $P < 0.001$ ; Table S5). These results confirm the general productivity-  
568 stability trade-off between the two types. In the following, we demonstrate how this trade-off  
569 appears across different climate trajectories and regions by using a set of representative  
570 contrasts.

### 571 **3.2.1. Functional type responses to projected climate trajectories**

572 The significant interactions involving PFT demonstrate that functional differences emerge from  
573 their combined effects with climate model conditions and regional pedoclimatic contexts.  
574 Consequently, the magnitude and, in some cases, the direction of the contrast between PFT A  
575 and PFT B vary across climate models. Under the MIR model, PFT B shows higher yields than  
576 PFT A. For instance, at +4 °C global warming, the average annual yield of PFT B is  $14.01 \pm 0.72$   
577 t DM ha<sup>-1</sup>, compared to  $12.24 \pm 0.40$  t DM ha<sup>-1</sup> for PFT A (Figure 5). However, the stability value  
578 of PFT B is lower than that of PFT A for the same model. For instance, the average stability  
579 value is  $11.08 \pm 1.38$  for PFT A and  $10.18 \pm 1.30$  for PFT B at +4 °C (Figure 5). Under the CMCC  
580 model, PFT B yields are higher than those of PFT A at all levels of warming. For instance, at +4  
581 °C, the average annual yield is  $11.85 \pm 0.62$  t DM ha<sup>-1</sup> for PFT B, compared to  $10.84 \pm 0.58$  t DM  
582 ha<sup>-1</sup> for PFT A (Figure 5). In contrast, stability is slightly lower overall for PFT B ( $6.63 \pm 0.86$   
583 versus  $7.26 \pm 1.10$  at +4 °C, Figure 5). Under the MPI model, PFT B shows higher average annual  
584 yields, but PFT A shows the best stability (Figure 5). For instance, at +4 °C, the average annual  
585 yield was  $12.93 \pm 0.78$  t DM ha<sup>-1</sup> for PFT B compared to  $11.81 \pm 0.47$  t DM ha<sup>-1</sup> for PFT A, while  
586 stability is slightly more favorable for PFT A ( $8.66 \pm 1.72$  versus  $7.48 \pm 1.22$ , Figure 5).

### 587 **3.2.2. Regional modulation of functional types under climate change**

588 Regional patterns further confirm that the differences between PFT A and PFT B are strongly  
589 context-dependent and shaped by the interaction between climate models and local  
590 pedoclimatic characteristics (PFT  $\times$  Region  $\times$  Model,  $P < 0.001$ ; Table S3). Consistent with the  
591 main GLM effects (Tables S4-S5), PFT B tends to produce higher yields across regions, whereas  
592 PFT A exhibits higher or equal stability, although the magnitude of these differences varies by  
593 climatic context.

594 Across regions, these contrasts consistently reflect a trade-off between productivity gains  
595 under stress (PFT B) and greater inter-annual stability (PFT A), with regional pedoclimatic

596 conditions modulating the strength of this trade-off rather than its direction. For instance, in  
597 the High Ardennes, at +2 °C under the MIR model, the average stability is  $11.30 \pm 1.84$  for PFT  
598 A and  $11.32 \pm 1.45$  for PFT B, while the average annual yield is  $12.05 \pm 0.14$  DM ha<sup>-1</sup> and  $13.75$   
599  $\pm 0.25$  DM ha<sup>-1</sup> for PFTs A and B, respectively (Figures 6-8 and S8). In contrast, in regions with  
600 less pronounced pedoclimatic constraints, such as the Sandy-Loamy region, differences  
601 between functional types remain limited across scenarios. For instance, at +3 °C under CMCC,  
602 PFT A exhibits a stability of  $7.18 \pm 0.66$ , whereas PFT B exhibits a stability of  $6.99 \pm 0.54$  (Figures  
603 8 and S8).

### 604 **3.3. Seasonal dynamics of grasslands in the context of climate change**

605 In this section, the seasonal response was analyzed using total annual yield, as the aim was to  
606 characterize the overall phenological shift in the sward in response to warming. Seasonal  
607 dynamics reflect the combined behavior of co-occurring functional types. Figures S9 and S10  
608 show the seasonal patterns for each PFT, confirming that the sward-level interpretation is  
609 consistent with PFT-specific responses. The spring increase and summer decline arise from  
610 earlier phenological development in warmer conditions combined with growth limitations  
611 driven by temperature and water in summer.

#### 612 **3.3.1. Intra-annual response of grasslands to temperature gradients**

613 The shift in the seasonal distribution of grassland biomass due to climate change is  
614 characterized by increased yields in spring, a general decline in summer and contrasting  
615 responses in autumn (Figure 9 and Table 6). These patterns emerge from climate-specific  
616 combinations of temperature, extreme heat (TXx), drought intensity (CDD), and precipitation  
617 patterns (RX5day and growing-season rainfall), all of which significantly affect yield ( $P < 0.001$ ;  
618 Tables S3-S4).

619 In spring, all three models show significant departures from the historical period, with  
620 consistent increases at +3 °C and +4 °C ( $P < 0.001$ ; Table 7), while responses at +2 °C are model-  
621 dependent (Table 7). The MIR model shows the highest increases, with an average across all  
622 three warming levels of  $+3.54 \pm 1.05$  t DM ha<sup>-1</sup>, followed by the MPI model ( $+2.06 \pm 1.45$  t DM  
623 ha<sup>-1</sup>) and the CMCC model ( $+2.00 \pm 1.46$  t DM ha<sup>-1</sup>) (Table 6). Figure 9 shows these differences  
624 in detail according to the distinct levels of warming. The largest deviation from the historical

625 spring average,  $+4.48 \pm 1.42$  t DM ha<sup>-1</sup>, is observed under the MIR model at +4 °C. Across  
626 models, spring yields at +3 °C are consistently higher than in summer and autumn (Table 7).

627 A widespread decline in yield is observed for all climate models in summer. Simulations reveal  
628 average losses across all warming levels of  $-1.75 \pm 0.97$  t DM ha<sup>-1</sup> under the MIR model,  $-1.24$   
629  $\pm 1.10$  t DM ha<sup>-1</sup> under the CMCC model and  $-0.78 \pm 0.96$  t DM ha<sup>-1</sup> under the MPI model (Table  
630 6). Figure 9 illustrates this trend in more detail for the different warming levels. The largest  
631 yield loss compared to historical performance is  $-2.43 \pm 0.22$  t DM ha<sup>-1</sup> registered at +4 °C  
632 under the MIR model.

633 Autumn yields vary more between models. Under the MIR model, the average yield for all  
634 three warming levels is stable compared to the historical average ( $+0.04 \pm 1.10$  t DM ha<sup>-1</sup>),  
635 whereas MPI and CMCC show average decreases ( $-0.47 \pm 1.24$  t DM ha<sup>-1</sup> and  $-0.56 \pm 1.21$  t DM  
636 ha<sup>-1</sup>, respectively, Table 6). This variability is visible in Figure 9, with details according to the  
637 warming level. The largest autumn yield increase relative to the historical average ( $+0.86 \pm$   
638  $0.84$  t DM ha<sup>-1</sup>) is observed under the MIR model at +4 °C, while the largest decrease ( $-1.29 \pm$   
639  $0.67$  t DM ha<sup>-1</sup>) is observed under the MPI model at +4 °C (Table 7).

### 640 **3.3.2. Emergent management responses to climate change**

641 As cutting and fertilisation in the simulations are directly linked to biomass thresholds (Table  
642 3), we examined how these management patterns respond to climate change. Analyses were  
643 performed at the pixel level, with each pixel corresponding to a soil-climate cluster derived  
644 from spatial aggregation. A total of 6,874 clusters were simulated for each plant functional  
645 type (PFT). Depending on the climate model and warming level (Table 1), this resulted in  
646 between 137,480 and 206,220 pixel-years. In this study, the term “pixel-year” therefore refers  
647 to one simulation year for one soil-climate cluster. Simulations based on historical data show  
648 an average of  $4.06 \pm 0.36$  cuts per year for PFT A and  $4.52 \pm 0.51$  cuts per year for PFT B. Across  
649 warming scenarios, the total annual number of cuts increases slightly, with model-dependent  
650 gains ranging from +0.18 to +1.25 cuts for PFT A and +0.20 to +1.25 cuts for PFT B per year  
651 (Table S6). These increases are primarily driven by enhanced spring growth. A marked seasonal  
652 redistribution of cuts emerges across all climate models (Table S6). Spring cutting frequency  
653 increases in every warming scenario, up to +1.25 cuts under MIR for PFT B at +4 °C, consistent  
654 with accelerated early-season growth. In contrast, summer cutting frequency declines across

655 all climate models, down to -0.79 cuts under MIR at +4 °C for PFT A (Table S6). Autumn cuts  
656 remain stable or are slightly reduced, depending on the model. These patterns mirror the  
657 described spring enhancement and summer slowdown in biomass production.

658 A key emergent signal is the occurrence of years with no summer cut. This never occurs in the  
659 historical baseline (0% of pixel-years) but becomes increasingly common under climate change  
660 (Table 8). Depending on the climate model, the proportion of pixel-years lacking a summer cut  
661 is 0-1.5% at +2 °C, 0.3-6% at +3 °C and 3-14% at +4 °C. MIR exhibits the strongest increases,  
662 followed by CMCC, while MPI shows the lowest incidence (Table 8). These complete summer-  
663 cut failures are a clear indicator of drought conditions and help explain the observed summer  
664 productivity losses across regions. Cutting dates also shift under warming (Table S7). The first  
665 cut consistently occurs earlier across all models, by 9-24 days for PFT A and 8-31 days for PFT  
666 B, depending on the scenario. For instance, under the MIR at +4 °C, the first cut advances to  
667 day of year (DOY)  $110.0 \pm 11.1$  for PFT A and  $107.6 \pm 11.6$  for PFT B, compared to DOY  
668  $141.7 \pm 10.9$  and  $138.7 \pm 10.9$  under historical conditions. Conversely, the last cut tends to  
669 occur slightly later, particularly under MIR and MPI. For example, PFT B reaches DOY  $292.1$   
670  $\pm 16.9$  under MIR +4 °C, compared to  $278.6 \pm 18.6$  under historical conditions. This indicates an  
671 extension to the autumn growth period in certain contexts.

672 As fertilization is triggered by the first two cuts only (Table 3), changes in cutting patterns affect  
673 nitrogen application. Across all warming-model combinations, almost all pixel-years still reach  
674 at least two cuts (Table S6), meaning that the full set of fertilization events continues to be  
675 applied in nearly all cases. While the timing of fertilization may shift when spring growth  
676 accelerates, the number of annual fertilization events remains almost always unchanged. Even  
677 in the driest scenarios, such as MIR +4 °C where 11-14% of pixel-years lack a summer cut (Table  
678 8), fertilization totals remain unaffected because the first and second cuts always occur before  
679 summer growth failure.

680 Overall, these results show that climate warming reshapes emergent management behavior  
681 primarily through seasonal redistribution of biomass production, with cutting activity  
682 increasingly concentrated in spring and weakened or suppressed during summer droughts.

683 **3.3.3. Influence of atmospheric CO<sub>2</sub> concentration on cutting frequency**

684 To explicitly assess the impact of rising atmospheric CO<sub>2</sub> levels on management practices, we  
685 analyzed the relationship between CO<sub>2</sub> concentration and the annual number of cuts across all  
686 climate model and warming combinations. Cutting frequency increased systematically with  
687 CO<sub>2</sub> for both plant functional types (PFTs), although the magnitude of this increase varied  
688 depending on the model used. For PFT A, the slope of this relationship ranged from 0.03 cuts  
689 per 100 ppm CO<sub>2</sub> under the CMCC model to 0.08 cuts per 100 ppm CO<sub>2</sub> under the MPI model  
690 (Table S8). For PFT B, sensitivities were stronger still, ranging from 0.02 cuts per 100 ppm CO<sub>2</sub>  
691 under CMCC to 0.10 cuts per 100 ppm CO<sub>2</sub> under MPI. All regression slopes were highly  
692 significant ( $P < 0.001$ ; Table S8), and the narrow confidence intervals indicated robust CO<sub>2</sub>  
693 effects.

694 **3.3.4. Regional variability in the seasonal response of grasslands.**

695 In general, spring was the most productive season in all regions. Summer is consistently  
696 associated with losses, which vary based on soil and climate conditions. This highlights the  
697 strong modulation of seasonal vulnerability by pedoclimatic gradients. The High Ardennes  
698 region (cold, humid upland with shallow acidic soils) shows the most stable productivity  
699 throughout the year. It exhibits the greatest increase in yield across all models and warming  
700 levels, compared to the historical average in spring ( $+2.60 \pm 1.51$  t DM ha<sup>-1</sup>), experiences the  
701 least losses in summer ( $-0.93 \pm 0.99$  t DM ha<sup>-1</sup>) and records the only positive difference in  
702 autumn yield ( $+0.14 \pm 1.16$  t DM ha<sup>-1</sup>) (Table 6). This consistency reflects a mitigated seasonal  
703 response to climate change. The Ardennes region (high altitude with shallow, poorly  
704 permeable soils) shows a similar pattern, demonstrating high productivity in spring compared  
705 to the regional historical average ( $+2.56 \pm 1.52$  t DM ha<sup>-1</sup>) and displaying relative resistance in  
706 summer ( $-0.94 \pm 1.05$  t DM ha<sup>-1</sup>); however, a deficit is still evident in autumn ( $-0.14 \pm 1.20$  t  
707 DM ha<sup>-1</sup>) (Table 6). At this level, the seasonal dynamics follow the expected pattern, with a  
708 clear increase in spring, moderate losses in summer, and partial maintenance in autumn. In  
709 contrast, the Jurassic region (clay-limestone soils prone to drainage issues) and Hennuyere  
710 Campine (sandy drought-sensitive soil) experience significant summer losses of up to  $-1.46 \pm$   
711  $1.15$  t DM ha<sup>-1</sup> in Hennuyere Campine (Table 6), as well as low autumn yields compared to  
712 historical averages. Losses reach nearly one ton of dry matter per hectare in the Jurassic region

713 (Table 6). However, their spring production remains above historical averages and comparable  
714 to that of other regions.

715 These regional contrasts are consistent with the significant region-climate model interactions  
716 detected in the GLMs for both yield and stability ( $P < 0.001$ ; Table S3). These interactions  
717 highlight that seasonal responses are not uniform but rather arise from the combined effects  
718 of soil properties, local climate, and model-specific climatic trajectories. The GLM coefficients  
719 reveal that increases in growing-season temperature and decreases in rainfall impact regions  
720 unequally (Tables S4-S5), reinforcing the observed spatial gradients in seasonal vulnerability.

## 721 **4. Discussion**

### 722 **4.1. Grassland vulnerability is conditioned by pedoclimatic context**

723 The responses of grasslands to climate change were primarily driven by the interaction  
724 between functional types, soil properties, and key climatic stressors, rather than by warming  
725 alone. Among the climatic variables, atmospheric CO<sub>2</sub> contributed to yield variability, with  
726 higher concentrations being associated with increased biomass production in all scenarios.  
727 Long-term field observations confirm this effect, showing a sustained increase in biomass  
728 under elevated CO<sub>2</sub> (Andresen et al., 2018). However, this contribution remains secondary  
729 compared to the dominant control exerted by soil water availability and climate extremes,  
730 which primarily shape grassland vulnerability patterns. The strong contrasts observed across  
731 climate models and pedoclimatic contexts further confirm that, in addition to plant functional  
732 strategies, grassland vulnerability emerges from the combined influence of soil water  
733 availability and exposure to climatic extremes.

734 Simulation results from the three climate models (CMCC, MIR, and MPI) highlight strong spatial  
735 heterogeneity. Compared to historical values, all models projected a general decline in stability  
736 and relatively low yield gains, especially on shallow, limestone and marly soils with low to  
737 moderate water retention capacity. Such soils are widespread across Europe, notably in  
738 calcareous grasslands of western and southern Europe (e.g., southwestern France; Maalouf et  
739 al., 2012) and consistently show reduced productivity and stability under drought (Jackson et  
740 al., 2024), decreased resilience of seed banks (Basto et al., 2018), and heightened sensitivity  
741 to climate-management interactions (Maalouf et al., 2012).

742 In contrast, higher-altitude and cooler areas show yield gains ranging from 2 to over 2.5 t DM  
743 ha<sup>-1</sup> under MIR and MPI models compared to historical yields. However, these gains are often  
744 coupled with lower stability, particularly under the MPI model. These results highlight the role  
745 of altitude in structuring the distribution of grassland vulnerability. This aligns with findings by  
746 Wangchuk et al. (2021), who reported increased aboveground biomass in high-altitude  
747 grassland under warming, despite a decline in plant diversity. Similarly, Li et al. (2020) showed  
748 that grassland stability components, particularly resilience, increase with altitude, though this  
749 trend plateaus or reverses beyond certain elevations. However, the effectiveness of this  
750 buffering effect depends also on soil properties. High-altitude conditions only support stable  
751 production when paired with suitable soils. Altitude is therefore not an absolute protective  
752 factor, but a modulating one whose impact depends on the underlying edaphic conditions.

753 Climate extremes, rather than averages, are increasingly defining the boundaries of grassland  
754 systems. When compared to historical values, the three models reveal an intensification of  
755 heat waves, heavier precipitation, and prolonged droughts, especially under CMCC model. Our  
756 results show that TXx (maximum daily temperature) increases of up to +8.5 °C and CDD  
757 (consecutive dry days) increases of more than +10 days under CMCC lead to strong reductions  
758 in stability across regions, particularly on clay-rich lowlands. These results indicate that the  
759 increasing frequency and intensity of extreme climatic events strongly amplify year-to-year  
760 production variability, resulting in systematic losses of interannual stability under future  
761 climate conditions. The pronounced decline in stability simulated under the CMCC model for  
762 both PFT A and PFT B reflects the critical influence of climate extremes in shaping grassland  
763 vulnerability, rather than changes in mean growing conditions. This pattern aligns with the  
764 findings of Liu et al. (2024) who demonstrated that the increasing frequency of extreme  
765 climatic events undermines grassland aboveground net primary production stability by  
766 amplifying production variability and diminishing resilience, ultimately threatening ecosystem  
767 functioning. Furthermore, Song et al. (2023) confirmed that the cumulative effects of multiple  
768 global change drivers, including precipitation shifts and warming, systematically decrease  
769 grassland stability through species desynchronization and reduce community-level buffering  
770 capacity. Together, these mechanisms explain why stability declines more sharply than mean  
771 yield under scenarios dominated by extreme climatic variability.

772 European grasslands were highly vulnerable to 2018 drought, especially on sandy soils, while  
773 wetter soils provided some resistance (Buras et al., 2020; Kowalski et al., 2022). In Wallonia,  
774 similar sensitivity was observed during the summers of 2018, 2020, and 2022. Weekly field  
775 measurements conducted by the Walloon Agricultural Research Center (CRA-W) in Gembloux  
776 (deep fertile loams) and Libramont (high-altitude shallow acidic soils) showed that sward  
777 growth came to a halt during each of these years, forcing farmers to supplement grazing with  
778 conserved forage as early as mid- to-late July. For instance, in 2022, the sward height dropped  
779 below 6.6 cm on July 20 in Gembloux, marking a near-total lack of fresh forage availability and  
780 prompting the early use of winter reserves such as corn and grass silage (Decruyenaere, 2022).  
781 These observations illustrate how simulated vulnerability patterns translate into real-world  
782 management constraints in temperate grassland systems. Simulations based on future climate  
783 data can identify areas most exposed to chronic production deficits or increased instability.

784 These results underline that grassland vulnerability under climate change is driven less by  
785 regional boundaries than by the interplay of soils, altitude, and exposure to extremes.  
786 Identifying areas with shallow soils, sandy textures, or poor drainage is essential for  
787 anticipating production deficits or increased production instability in temperate regions. Such  
788 insights guide adaptation through agroclimatic zoning and flexible management. Simulation  
789 tools, such as Gras-Sim (Kokah et al., 2023), provide a framework to translate climate-soil  
790 interactions into practice, for instance by adjusting stocking rate, rescheduling grazing or cuts,  
791 or activating emergency irrigation.

#### 792 **4.2. Grassland response to climate change is shaped by dominant functional types**

793 The hypothesis that grasslands dominated by PFT B (e.g. *Dactylis glomerata*) are more  
794 productive, while those dominated by PFT A (e.g. *Lolium perenne*) show greater interannual  
795 stability, is confirmed. Significant interactions between functional types, climate models, and  
796 regions reveal that differences in performance depend closely on soil and climate context.

797 The observed differences in yield between the two plant functional types can be explained by  
798 their contrasting ecophysiological strategies. Type A species, such as *Lolium perenne*, show  
799 very early phenology and high nutritional value but lower tolerance to limiting conditions.  
800 Compared to PFT A, PFT B species, such as *Dactylis glomerata*, generally exhibit later  
801 phenology and longer leaf lifespan (Cruz et al., 2010), which confers a greater capacity to

802 sustain production under moderate climatic stress. Simulation results revealed that PFT B  
803 exhibited a significant positive main effect on yield, confirming its status as the more  
804 productive functional type across most climate trajectories. These results align with findings  
805 from Turner et al. (2012) and Reynaert et al. (2025), who observed that *Dactylis glomerata*  
806 outperformed *Lolium perenne* in terms of short-term productivity under drought, despite signs  
807 of physiological stress.

808 Available empirical evidence supports these projections. During the 2018 European drought,  
809 field trials performed in Belgium on fertile loams (Loamy region) showed higher productivity  
810 for cocksfoot than for perennial ryegrass, with up to 11 tons of dry matter (DM) per hectare  
811 for cocksfoot (type B) and 7 tons of DM per hectare for perennial ryegrass (type A) (Lambert  
812 et al., 2020). Complementary evidence from controlled macrocosm experiments in France  
813 further shows that cocksfoot sustains growth and recovery under extreme climatic events. This  
814 resilience is linked to its ability to accumulate and mobilize reserves in leaf meristems, a  
815 mechanism not observed in more sensitive grasses (Volaire et al., 2020). These convergent  
816 results highlight that the contrasts captured by simulations reflect broader European patterns  
817 of grassland vulnerability, rather than local particularities.

818 However, these productivity gains were accompanied by lower stability. Our simulations show  
819 that PFT A has significantly higher stability than PFT B. In most simulated scenarios, Type A  
820 exhibited greater consistency in production over time than Type B, indicating that *Lolium*  
821 *perenne* maintains stable productivity under variable weather conditions (Turner et al., 2012).  
822 This stability, however, does not extend to severe or prolonged droughts, where ryegrass  
823 suffers strong losses and poor persistence, while cocksfoot shows greater resilience through  
824 carbohydrate reserve mobilization and microclimate buffering (Volaire et al., 2020; Reynaert  
825 et al., 2025). The stability of PFT A species is therefore relative, depending strongly on soil  
826 properties, with poor recovery on shallow soils but better persistence on organic-rich soils  
827 (Buttler et al., 2019). An approach based on functional complementarity appears more  
828 promising than exclusive specialization to ensure stable productivity. Simulation frameworks  
829 can be mobilized to explore species mixtures and identify proportions best adapted to each  
830 pedoclimatic gradient. At the European scale, advisory networks could mobilize such  
831 approaches to guide farmers in adapting their management practices. Strengthening synergies

832 between agricultural research institutes, universities, and experimental platforms would  
833 better integrate these issues into the agricultural innovation chain.

#### 834 **4.3. Climate change reshapes the seasonal growth of permanent grasslands**

835 Overall, results confirm the hypothesis that climate change will lead to a seasonal  
836 redistribution of grassland productivity, with increased growth in spring but significant  
837 summer declines compared to historical values. This is confirmed across all climate models at  
838 higher warming levels, while responses at +2 °C remain model-dependent. Autumn shows  
839 more variable responses depending on the model. These intra-annual dynamics align with  
840 well-established mechanisms by which plants adjust their phenology in response to rising  
841 temperatures and changing precipitation patterns. For instance, it is well documented that  
842 earlier leaf-out and delayed senescence in herbaceous plants are common responses to  
843 warming, although these trends can vary depending on ecosystem type and moisture  
844 availability (Piao et al., 2019; Huang et al., 2020). Cool-season grasses such as *Lolium perenne*,  
845 typically show earlier reproductive development under milder late-winter conditions, driven  
846 by increasing temperature and radiation during the pre-growth phase (Gilliland et al., 2025).

847 The increase in spring productivity, particularly under the MIR model, suggests that grasslands  
848 may increasingly concentrate their growth earlier in the year. This pattern has been confirmed  
849 by long-term simulations and observations in temperate European grasslands, where earlier  
850 onset of growth and lengthening of the growing season have led to earlier cutting dates and  
851 higher number of harvests annually, especially under intensified management (Petersen et al.,  
852 2021). Moreover, climate-driven advances in the onset of photosynthetic activity can indirectly  
853 enhance spring net primary productivity, particularly in systems where temperature is the  
854 dominant control on phenology and pre-season thermal conditions are favorable (Xue et al.,  
855 2023). However, in our simulations, the onset of the phenological phase occurs on nearly the  
856 same calendar day across climate models because Gras-Sim initiates heat-sum accumulation  
857 on a fixed day-of-year. Consequently, the model does not simulate the advance of the onset  
858 itself. Instead, higher spring productivity under warmer scenarios results from two factors:  
859 additional biomass accumulation on mild winter days when temperatures exceed the daily  
860 growth threshold and faster growth following phenology activation.

861 However, this early-season productivity may come at a cost if it is not matched by sufficient  
862 soil moisture availability, as it can lead to early depletion of water reserves and reduce plant  
863 resilience to subsequent summer droughts, which may ultimately limit total annual  
864 productivity (Petersen et al., 2021). All three climate models predict an overall loss in summer  
865 yield. Compared to historical levels, decreases exceeding 2 t DM ha<sup>-1</sup> are predicted under the  
866 MIR model at +4 °C warming. These losses, align with the pronounced increases in CDD and  
867 TXx observed in our simulations, especially under CMCC, translate into extended periods of  
868 negligible net growth and reduced cutting frequency in summer. This pattern is consistent with  
869 projections showing a sharp intensification of drought conditions across Europe, particularly  
870 in summer, where frequency and severity are expected to rise significantly under future  
871 warming scenarios (Spinoni et al., 2018). The results also show that the frequency of no-  
872 summer-cut pixel-years increases by up to 14% under MIR at +4 °C, providing a clear emergent  
873 indicator of production collapse during peak drought periods. Our simulations highlight that  
874 summer losses and autumn recovery are strongly conditioned by soil depth and water storage  
875 capacity. This pattern is consistent with remote-sensing evidence from Central Europe, where  
876 sandy soils were the most drought-sensitive and wetter soils more resistant (Kowalski et al.,  
877 2022). At the continental scale, the 2018 drought caused unprecedented pasture losses  
878 compared to 2003, particularly in less drought-adapted regions of central and northern Europe  
879 (Buras et al., 2020).

880 Autumn shows greater variability. Under the MIR model at +4 °C warming, some simulations  
881 indicate increased yield relative to historical averages, while others predict a decline. Such  
882 variability aligns with the contrasting effects of warming on late-season growth. Warmer  
883 autumn temperatures can promote regrowth where moisture is available but cumulative  
884 summer drought often restricts regrowth potential, particularly in areas with shallow or poorly  
885 drained soils. This divergence reflects both the uncertainty in future autumn precipitation and  
886 the sensitivity of grasslands to factors such as early senescence and summer stress. Although  
887 a favorable regrowth window is theoretically possible, particularly under conditions of  
888 sufficient late-season rainfall and mild temperature (Ma et al., 2022), the cumulative effect of  
889 summer drought can also reduce soil moisture availability and limit autumn productivity  
890 (Wang et al., 2020). These contrasts were also observed in western Europe, for instance in  
891 Belgium during the 2018 drought, where remote-sensing indices (NDVI, NDWI) confirmed that

892 cooler, wetter uplands buffered summer losses, while sandy lowlands were among the most  
893 affected (CRA-W, 2018).

894 These changes, compared to historical references, imply a revision of grassland management  
895 practices. Early spring growth could be used to advance mowing or grazing dates, and build up  
896 forage stocks, while summer losses may require reducing stocking rates, adjusting rest periods,  
897 or resorting to supplementary feeding. Simulation frameworks can support these adaptations  
898 by providing site-specific recommendations adapted to contrasting pedoclimatic zones and  
899 livestock systems.

#### 900 **4.4. Study limitations and future directions**

901 The limitations of this study are related to the design of the climate scenario, the  
902 representation of grassland systems and management, and the scope of the analysis.

903 First, the climate input ensemble is limited to nine combinations of three levels of global  
904 warming (+2, +3, and +4 °C) and three CMIP6 global climate models (CMCC, MPI, and MIR),  
905 which are downscaled with a single regional climate model (MAR). These models were  
906 selected to represent different future scenarios (dry, intermediate, and warm-wet), but they  
907 do not capture the full range of uncertainty in CMIP6, especially regarding precipitation and  
908 climate extremes. The differences observed between the models illustrate the structural  
909 uncertainty inherent in climate projections; therefore, the simulated responses should be  
910 interpreted as representative of a limited set of contrasting yet non-exhaustive climate  
911 trajectories. Future work including a larger set of GCMs, additional warming levels, or  
912 alternative downscaling approaches would help broaden the range of possible outcomes and  
913 strengthen robustness.

914 Second, the results are not directly transferable due to several simplifications in the  
915 representation of grassland functioning and management. Cutting was used instead of grazing  
916 to standardize model inputs, and this choice limits the direct applicability of the results to  
917 livestock systems, as grazing remains widespread across temperate Europe. Future studies  
918 should incorporate dynamic grazing modules to better capture management decision-making  
919 and spatial heterogeneity in biomass removal. In addition, the functional composition of  
920 grasslands was simplified into plant functional types, without accounting for species mixtures  
921 or interspecific interactions that may affect productivity and stability. While this simplification

922 is a limitation, the contrasting responses observed between PFTs highlight ecophysiological  
923 trade-offs that are directly relevant for forage breeding and management. Type B traits tend  
924 to favor productivity under stress, while type A traits enhance stability, pointing toward the  
925 value of complementarity in species mixtures. Soil properties were held constant, meaning  
926 that long-term changes in soil structure or water retention were not represented. Such slow  
927 processes may only have a delayed effect on short-term productivity, but they remain relevant  
928 for long-term resilience. The CO<sub>2</sub>-RUE formulation used in the model follows the exponential  
929 response implemented in the STICS model (Beaudoin et al., 2023). In the current model setup,  
930 the effects of rising atmospheric CO<sub>2</sub> are represented primarily by increased radiation use  
931 efficiency. Actual evapotranspiration is not directly linked to CO<sub>2</sub> but is derived from potential  
932 evapotranspiration using K<sub>c</sub>, a crop coefficient (AET = PET × K<sub>c</sub>). Consequently, potential CO<sub>2</sub>-  
933 induced reductions in stomatal conductance and transpiration, as well as the interaction  
934 between these reductions and soil water availability, are not explicitly represented and cannot  
935 be quantified using the outputs analyzed in this study. This modeling choice implies that the  
936 net effect of CO<sub>2</sub> on productivity under water-limited conditions may be over- or  
937 underestimated and that the interaction between CO<sub>2</sub> fertilization and drought stress should  
938 be interpreted cautiously. Although this approach is still widely used, it was calibrated for CO<sub>2</sub>  
939 concentrations up to around 600 ppm. Meta-analytical evidence indicates that C<sub>3</sub> plants  
940 exhibit saturating dose-response curves at elevated CO<sub>2</sub>, with most biomass stimulation  
941 already realized near current atmospheric concentrations (Poorter et al., 2022). Therefore,  
942 simulated CO<sub>2</sub> fertilization effects beyond 600 ppm should be interpreted as upper-bound  
943 estimates rather than precise quantitative predictions.

944 Third, socioeconomic drivers and farmer decision-making processes were not included in this  
945 analysis. This reflects the diagnostic scope of the present study, focused on biophysical  
946 vulnerability rather than assessing specific adaptation strategies. Future work should therefore  
947 move toward coupling biophysical simulations with socioeconomic dimensions to better  
948 evaluate plausible response options under real-world constraints.

## 949 **5. Conclusion**

950 This study revealed that the vulnerability of temperate grasslands to climate change hinges on  
951 pedoclimatic conditions, season, and functional type of the dominant species. Type B (*Dactylis*

952 *glomerata*) generally showed higher yields, while type A (*Lolium perenne*) exhibited better  
953 interannual stability, revealing the classic trade-off between productivity and stability.  
954 Additionally, a seasonal redistribution of biomass production was observed, with increased  
955 growth in spring and a marked decline in summer compared to historical averages, particularly  
956 in regions with shallow soils. These shifts have direct implications for the provision of  
957 ecosystem services. These results highlight the importance of mixed adaptation strategies  
958 based on functional complementarity, adjusted management practices, and spatial simulation  
959 tools, such as Gras-Sim. By integrating soil-climate interactions and functional traits, this study  
960 establishes a quantitative basis for identifying the most vulnerable regions and guiding  
961 targeted adaptations. This detailed vulnerability assessment is therefore the first step, which  
962 should be followed by exploring and testing adaptation scenarios that integrate plant diversity,  
963 flexible management practices, and technological innovations to design grassland systems that  
964 remain productive and stable under future climate change.

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## Tables

1179 **Table 1.** Global warming scenarios and corresponding CO<sub>2</sub> concentration from CMCC, MPI,  
1180 and MIR climate models

Warming level (°C)	Climate model	Simulation period	Atmospheric CO <sub>2</sub> (ppm)
+2	CMCC	2024—2053	429
	MPI	2036—2065	545
	MIR	2045—2074	592
+3	CMCC	2048—2077	605
	MPI	2066—2095	722
	MIR	2071—2100	757
+4	CMCC	2060—2079	741
	MPI	2081—2100	1005
	MIR	2081—2100	1005

1181 **Table 2.** Main pedoclimatic characteristics, land use, dominant farming systems, and forage productivity of the agricultural regions of Wallonia.

1182 UAA: Utilized Agricultural Area. Source: SPW Agriculture (2024b); Forton and Meniger (2020).

Region	Dominant soils & landform	Permanent grassland in UAA (%)	Share of forage area in UAA (%)	Dominant systems	Permanent grassland yield (t DM ha <sup>-1</sup> year <sup>-1</sup> )	Key notes
Loamy	Deep, fertile, well-drained loams	—	27	Arable >50%; mixed crops-cattle 18%	7-11	Largest region; Highest biomass potential
Condroz	Hilly; calcareous-clayey-loamy; variable depth	—	42	Arable 43%; dairy 7%	6.5-11	Heterogeneous productivity with soil deep
Famenne	Shallow, cherty, calcareous soils	61	76	Beef 36%; mixed dairy-beef 16%; dairy 10%	5-8	Productivity constrained by soil and rainfall
Ardennes	High altitude; shallow, acidic, poorly permeable	—	88	Beef 56%; mixed dairy-beef 14%	6-10	Crops rare due to soil and climate limits
High Ardennes	Coldest and wettest region	90	97	Dairy 53%	5.5-9	Summer growth limited; strong spring and autumn regrowth
Grassland Region	Rugged, heavy soils; bocage	83	—	Dairy 44%; beef 21%	6.5-11	Highly specialized grassland-based systems
Fagnes	Variable soils; frequent waterlogging	64	80	Dairy/beef/mixed 72%	4.5-7	Strong dependance on rainfall and management

Jurassic	Clay-limestone and marly soils, deep, locally wet	73	89	Beef 58%	6.5-11	Drainage strongly conditions yield
Sandy-Loamy	Sandy-loamy	—	27	Arable 50%; specialized livestock 26%	7-11	Historical dairy area; arable now dominant
Hennuyere Campine	Poor, sandy soils	32	50	Arable 50%; dairy 17%	6.5-11	Smallest region; drought-sensitive

1183 **Table 3.** Seasonal management strategy for triggering grassland cuts and fertilization actions

Season	Biomass threshold (t DM ha <sup>-1</sup> )	Rain condition after the cut	Fertilization (kg N ha <sup>-1</sup> )
Spring	> 3.0	3 days < 2 mm day <sup>-1</sup>	60 (before cut 1)
Summer	> 2.0	2 days < 2 mm day <sup>-1</sup>	50 (5 days after cut 1)
Autumn	> 1.5	2 days < 2 mm day <sup>-1</sup>	40 (5 days after cut 2)

1184

1185 **Table 4.** Random Forest predictor importance for yield and stability, including soil properties (clay, sand, organic matter), plant functional type  
1186 (PFT), and climatic covariates such as mean growing-season temperature, seasonal maximum temperature (TXx), maximum 5-day precipitation  
1187 (RX5day), consecutive dry days (CDD), mean growing-season rainfall, and atmospheric CO<sub>2</sub> concentration. The table also reports the  
1188 performance ranking of climate models and agricultural regions based on changes in yield and stability relative to the historical baseline.

Category	Type	Group	Importance (%)		$\Delta$ Yield (t DM ha <sup>-1</sup> )	$\Delta$ Stability ( $\mu/\sigma$ , dimensionless)	Yield rank	Stability rank
			Yield	Stability				
Random Forest	—	PFT	135.87	95.79	—	—	—	—
		Organic matter	86.05	90.25	—	—	—	—
		Clay	72.08	75.22	—	—	—	—
		Sand	70.03	84.29	—	—	—	—
		Climate model	19.98	16.49	—	—	—	—
		CO <sub>2</sub> concentration	18.78	17.42	—	—	—	—
		Temperature	17.64	14.45	—	—	—	—
		RX5day	17.61	18.92	—	—	—	—
		CDD	16.64	17.72	—	—	—	—
		Rain	16.57	26.26	—	—	—	—
		TXx	12.64	15.76	—	—	—	—
Model ranking	Climate models	MIR	—	—	2.34 ± 0.51	0.47 ± 0.84	—	—
		MPI	—	—	1.44 ± 0.45	-0.71 ± 1.26	—	—
		CMCC	—	—	0.73 ± 0.45	-2.53 ± 0.78	—	—
Region ranking	Region	High Ardennes	—	—	2.52 ± 0.87	0.61 ± 1.64	1	1
		Ardennes	—	—	2.08 ± 0.82	-0.42 ± 1.47	2	3
		Fagnes	—	—	1.67 ± 0.90	-0.13 ± 1.63	3	2

Grassland Region	—	—	$1.61 \pm 0.83$	$-1.16 \pm 1.08$	4	7
Condroz	—	—	$1.47 \pm 0.83$	$-1.16 \pm 1.44$	5	6
Famenne	—	—	$1.36 \pm 0.84$	$-1.46 \pm 1.12$	6	9
Sandy Loamy	—	—	$1.33 \pm 0.79$	$-1.06 \pm 2.11$	7	5
Loamy	—	—	$1.27 \pm 0.79$	$-1.24 \pm 2.01$	8	8
Hennuyere Campine	—	—	$1.12 \pm 0.86$	$-0.85 \pm 2.37$	9	4
Jurassic	—	—	$0.87 \pm 0.82$	$-2.00 \pm 1.80$	10	10

1189

1190 **Table 5.** Changes ( $\Delta$ ) in climatic extremes, TXx (maximum daily temperature), RX5day (maximum 5-day rainfall), and CDD (consecutive dry days),  
 1191 across climate models and warming levels, relative to the historical baseline. All indices were computed over the growing season (day-of-year  
 1192 60 to 334)

Metric	Model	Warming level +2 °C		Warming level +3 °C		Warming level +4 °C	
		$\Delta \pm SD$	<i>P</i> value	$\Delta \pm SD$	<i>P</i> value	$\Delta \pm SD$	<i>P</i> value
TXx (°C)	CMCC	4.51 ± 2.53	< 0.001	6.16 ± 2.78	< 0.001	8.50 ± 3.14	< 0.001
	MIR	4.22 ± 1.36	< 0.001	4.92 ± 2.22	< 0.001	6.39 ± 2.11	< 0.001
	MPI	2.22 ± 2.45	< 0.001	3.14 ± 2.34	< 0.001	6.20 ± 1.89	< 0.001
CDD (day)	CMCC	4.54 ± 7.46	0.01	6.47 ± 8.21	0.001	10.24 ± 12.46	0.002
	MIR	2.54 ± 5.70	0.09	3.61 ± 9.02	0.07	1.94 ± 4.85	0.21
	MPI	1.47 ± 6.09	0.35	1.84 ± 7.41	0.30	1.79 ± 8.07	0.40
RX5day (mm)	CMCC	24.44 ± 55.82	0.03	23.31 ± 46.56	0.02	3.76 ± 19.87	0.55
	MIR	0.73 ± 21.86	0.90	3.55 ± 23.18	0.56	12.84 ± 24.07	0.07
	MPI	-2.56 ± 24.79	0.69	-2.04 ± 26.16	0.75	-9.06 ± 15.49	0.11

1193

1194 **Table 6:** Seasonal yield differences and performance ranking of climate models and agricultural regions relative to the historical baseline

Category	Type	Group	Spring		Summer		Autumn	
			$\Delta$ Yield (t DM ha <sup>-1</sup> )	Rank	$\Delta$ Yield (t DM ha <sup>-1</sup> )	Rank	$\Delta$ Yield (t DM ha <sup>-1</sup> )	Rank
Model ranking	Climate model	MIR	3.54 ± 1.05	1	-1.75 ± 0.97	—	0.04 ± 1.10	—
		MPI	2.06 ± 1.45	2	-0.78 ± 0.96	—	-0.47 ± 1.24	—
		CMCC	2.00 ± 1.46	3	-1.24 ± 1.10	—	-0.56 ± 1.21	—
Region ranking	Region	High Ardennes	2.60 ± 1.51	1	-0.93 ± 0.99	1	0.14 ± 1.16	1
		Ardennes	2.56 ± 1.52	3	-0.94 ± 1.05	2	-0.14 ± 1.2	2
		Fagnes	2.55 ± 1.55	6	-1.11 ± 1.09	3	-0.15 ± 1.17	3
		Grassland Region	2.48 ± 1.49	10	-1.31 ± 1.04	6	-0.36 ± 1.2	5
		Condroz	2.53 ± 1.53	8	-1.33 ± 1.07	7	-0.2 ± 1.25	4
		Famenne	2.51 ± 1.51	9	-1.28 ± 1.09	4	-0.48 ± 1.13	7
		Sandy Loamy	2.55 ± 1.55	5	-1.43 ± 1.15	8	-0.5 ± 1.18	8
		Loamy	2.56 ± 1.54	4	-1.45 ± 1.13	9	-0.38 ± 1.17	6
		Hennuyere	2.57 ± 1.56	2	-1.46 ± 1.15	10	-0.54 ± 1.12	9
		Campine Jurassic	2.54 ± 1.49	7	-1.28 ± 1.06	5	-0.97 ± 1.26	10

1195 **Table 7.** Seasonal changes in grasslands yield under climate models and warming levels, relative to the historical baseline.

Model	Season	Warming level +2 °C		Warming level +3 °C		Warming level +4 °C	
		$\Delta \pm \text{SD}$ (t DM ha <sup>-1</sup> )	<i>P</i> value	$\Delta \pm \text{SD}$ (t DM ha <sup>-1</sup> )	<i>P</i> value	$\Delta \pm \text{SD}$ (t DM ha <sup>-1</sup> )	<i>P</i> value
CMCC	Spring	-0.06 ± 0.07	< 0.001	3.02 ± 0.09	< 0.001	3.03 ± 0.09	< 0.001
CMCC	Summer	-0.07 ± 0.21	< 0.001	-1.80 ± 0.90	< 0.001	-1.84 ± 0.86	< 0.001
CMCC	Autumn	0.24 ± 1.37	< 0.001	-0.88 ± 0.93	< 0.001	-1.04 ± 0.85	< 0.001
MIR	Spring	3.06 ± 0.08	< 0.001	3.10 ± 0.09	< 0.001	4.48 ± 1.42	< 0.001
MIR	Summer	-1.64 ± 0.98	< 0.001	-1.52 ± 1.04	< 0.001	-2.43 ± 0.22	< 0.001
MIR	Autumn	-0.50 ± 1.02	< 0.001	-0.25 ± 0.96	< 0.001	0.86 ± 0.84	< 0.001
MPI	Spring	0.00 ± 0.10	< 0.001	3.09 ± 0.10	< 0.001	3.08 ± 0.08	< 0.001
MPI	Summer	0.14 ± 0.17	< 0.001	-1.69 ± 0.97	< 0.001	-0.80 ± 0.39	< 0.001
MPI	Autumn	0.47 ± 1.21	< 0.001	-0.59 ± 1.07	< 0.001	-1.29 ± 0.67	< 0.001

1196 **Table 8.** Proportion of years without any summer cut (% of pixel-years; pixels correspond to soil-climate clusters), relative to the historical  
 1197 baseline

PFT	Model	Warming level +2 °C		Warming level +3 °C		Warming level +4 °C	
		Pixels-years (%)	<i>P</i> value	Pixels-years (%)	<i>P</i> value	Pixels-years (%)	<i>P</i> value
A	CMCC	0.12	< 0.001	3.23	< 0.001	7.50	< 0.001
	MIR	1.50	< 0.001	4.21	< 0.001	11.32	< 0.001
	MPI	0.00	—	1.00	< 0.001	3.41	< 0.001
B	CMCC	0.52	< 0.001	3.50	< 0.001	8.10	< 0.001
	MIR	1.20	< 0.001	6.00	< 0.001	13.83	< 0.001
	MPI	0.00	—	0.32	< 0.001	3.44	< 0.001

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