Do details matter? Disentangling the processes related to plant species interactions in two grassland models of different complexity

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Abstract

Biogeochemical models of vegetation dynamics could potentially be used to complement empirical studies on the effect of plant species richness. A key precondition is the simulation of species coexistence. While community scale models regularly incorporate respective processes, models at the field or landscape scale used for larger scale assessments, require additional model development. However, it is unclear how the particular process description within these models affects simulations of species performance and resulting ecosystem functions.

We compare simulations of two grassland models of different complexity for monocultures and two-species mixtures in a grassland experiment in Jena, Germany. By providing an in-depth analysis of the models' process descriptions, we evaluate their ability to simulate the response of different species, their interactions and their joint performance to drought and mowing.

Both models simulated similar average above-ground biomass (AGB) but showed different intra-annual variability. Generally, the models had difficulties representing a balanced species composition in multiple species mixtures and competition for space was the main driver of community composition in both models. The resulting communities were dominated by the more competitive species, while the weak competitor was only marginally present in most mixtures independent of drought and mowing. The competitive strength which we derived from the calibrated parameter sets of the species differed between the models and the agreement on which species dominate specific mixtures was mixed. While both models simulated reduced soil water content and above-ground biomass in response to drought, the strength and duration of these responses differed. Despite these differences, simulated species interactions were barely affected, and strong competitors remained dominant. Mowing had opposing effects on the competition for space in the models, which could be attributed to the different representations of plants in the two models.

The models selected for the comparison are two representatives for local- and large-scale applications and use widely applied approaches for which our comparison highlighted strengths and weaknesses. To enable the investigated models (and those with similar complexity) to simulate coexistence of multiple species, niche differentiation needs to be improved. This requires a stricter separation of access to different resources and improved representation of different ecological strategies for which community scale models that are able to simulate coexistence may be an inspiration. Our approach may serve as an example for other modellers looking for ways to identify important model processes for further model development in the context of species interaction.

Keywords: grassland model, model comparison, process based modelling, species interaction, species traits, drought

1. Introduction

Grasslands are a key element of ruminant livestock production systems and provide multiple ecosystem services like carbon sequestration (Chang et al., 2015), erosion control (Zhu et al., 2015) and habitats for pollinators and other fauna (Dass et al., 2018; Tribot et al., 2018). They strongly affect biogeochemical cycles at different scales (Moinet et al., 2017; Zhou et al., 2017) and lately, their carbon storage potential has been controversely discussed in the context of climate change mitigation (e.g. Lorenz and Lal, 2018; Yang et al., 2019; Godde et al., 2020). The functions and services provided by grasslands are strongly controlled by the prevailing environmental conditions, but also by the specific management (Tilman et al., 2012). The response of a grassland ecosystem to changes in these drivers was shown to be mediated by species richness and community composition (Vogel et al., 2012; Craven et al., 2016; Yin et al., 2017). Consequently, a good understanding of the mechanisms driving grassland dynamics is essential to assess and project future productivity, ecosystem services and functions under different stressors, such as climate change (Van Oijen et al., 2020).

1.1. Drivers of grassland dynamics

In this study, we focus on the effect of two important drivers of grassland dynamics: decreased water availability resulting from meteorological droughts, which can result from climate change, and biomass removal by mowing, which is a common practice in livestock production.

1.1.1. Water

Water availability results from the local balance of inputs through precipitation and losses by transpiration, evaporation, seepage and runoff. During drought, precipitation is absent or below water requirements for a longer period, either within one season or across multiple years. A decrease in precipitation can suppress ecosystem photosynthesis, soil respiration and carbon cycling (Wu et al., 2011; Beier et al., 2012) as well as key soil processes (Emmett et al., 2004). Additionally, an increase in inter-rainfall intervals can lead to reduced net primary production, flowering duration and soil CO_2 flux in grasslands (Fay et al., 2000). Other severe impacts on grassland ecosystems include a rapid loss of biomass, plant cover, and even species (Weaver, 1942; Tilman and El Haddi, 1992; Carroll et al., 2021). In addition, droughts were shown to influence community composition and diversity patterns of grasslands (Buckland et al., 1997; Knapp et al., 2008; Jung et al., 2020). The response of an ecosystem to periods of drought depends on characteristics of the drought itself, such as its duration, its intensity and its frequency (Felton et al., 2020; Denton et al., 2017). It also depends on the characteristics of the grassland community, as grassland species have developed several strategies to resist and survive droughts (Blair et al., 2014; Reich, 2014). While annual species often use an escape strategy by completing their life cycle outside the dry season (Kooyers, 2015; Norton et al., 2016), perennial species use dehydration avoidance or tolerance as a strategy (Zwicke et al., 2015) by regulating their leaf water potential (Ratzmann et al., 2019a,b). Dehydration avoidance is associated with an increase in water uptake or decrease of water losses, while dehydration tolerance ensures plant survival by maintaining cell integrity of meristematic tissue (Ludlow, 1989; Volaire et al., 2009; Zwicke et al., 2015). Additionally, species-rich communities often better buffer adverse effects of droughts in the long run than low-diverse communities, as they allow for shifts in their composition towards potentially better adapted species (Isbell et al., 2015; Hoover et al., 2018) but may also alter environmental conditions reducing drought stress of more vulnerable species (Wright et al., 2021). Species-rich communities may also benefit from complementarity effects that arise from the use of soil water stored in different soil depths by opposing rooting strategies (Kulmatiski and Beard, 2013; Guderle et al., 2018; Klaus et al., 2016).

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1.1.2. Mowing

In addition to drought, the frequent removal of above-ground plant biomass through mowing or cutting also affects the composition of grassland communities as well as their productivity, which in turn may affect the grassland's resilience to drought events. The intensity of mowing is a result of the frequency of mowing and the applied cutting height. While the prevailing pedoclimatic conditions restrict grassland productivity via temperature, light, water and nutrient constraints, under similar conditions the highest grassland productivity has been found at intermediate mowing intensities, whereas very low or high mowing intensities often decrease productivity (Hopkins, 2000; Weigelt et al., 2009). At low mowing intensity, competition for limiting resources such as water and nutrients, drives the community dynamics, and thus more competitive species dominate the community (Smart et al., 2006). Therefore, the community is often shaped by fewer but larger plants compared to grasslands with higher mowing intensities. In contrast, in grasslands with a very high mowing intensity, biomass is removed so frequently, that fast growth and high stature traits associated with competitive species are not advantageous but lead to selective removal of these species instead (Yu et al., 2015; Yin et al., 2017). The resulting community often consists of a high number of small plants. This is accompanied by reduced shading and competition for nutrients and increased growth of less competitive species, promoting species richness (Peltzer and Wilson, 2001; Williams et al., 2007; Pecháčková et al., 2010).

1.2. Plant species richness

The grassland ecosystems' responses to these two drivers, water availability and mowing, and the mechanisms involved, as well as the role of plant species richness of grassland communities, have been studied using field observations and experiments along a diversity gradient (e.g. Craven et al., 2016; Tilman et al., 2014). Despite the large number of experiments the mechanistic understanding of the processes regulating community responses to drought and mowing, especially in species-rich communities is still limited (Weisser et al., 2017). While the patterns can be reproduced using mathematical models (e.g. Han et al., 2019), to dissect the underlying processes of ecosystem dynamics, biogeochemical models (BGMs) have the potential to complement empirical studies, as they can mechanistically analyze the interacting responses of biotic and abiotic components of grasslands to changing environmental conditions (Wilcox et al., 2020; Van Oijen et al., 2020). However, this requires that two preconditions are met: First, the models need to represent all relevant processes that shape the community under specific environmental and management conditions reasonably well. Second, the models need to represent different ecological strategies enabling the communities to adapt if prevailing conditions change. However, BGMs have not yet been assessed sufficiently with respect to these two preconditions.

1.3. Biogeochemical models

BGMs of grasslands have been developed and applied to determine grassland dynamics since the end of the 1980s (e.g. Thornley and Verberne, 1989; Coffin and Lauenroth, 1990; Siehoff et al., 2011; Hunt et al., 1991; Schapendonk et al., 1998; Duru et al., 2009). These models have been developed for applications at multiple scales and with different levels of represented process detail. Models at the community scale simulating individual plants with different traits have been used to study the effect of resource availability and disturbance regimes on the community and its member species (e.g. May et al., 2009; Soussana et al., 2012). At the plot or field scale individual-based and other models distinguishing traits only between species or functional types have been used to assess productivity and yields for different environmental conditions and management (e.g. Taubert et al., 2012; Höglind et al., 2016). At the continental or global scale dynamic global vegetation models have been developed to assess element cycling commonly using only a small number of functional types to simulate grassland ecosystems (e.g. Rolinski et al., 2018; Vuichard et al., 2007). The level of detail and the number of resources that are considered for plant growth and competition vary not only with the spatial scale for which models have been developed, but also between models applied at similar scales (for an extensive review see Taubert et al., 2012).

At the community scale, models that simulate the effects of plant species richness and the interactions between species have been developed (e.g. Clark et al., 2018; Turnbull et al., 2013; Weiss et al., 2014).

The high detail of the plant interactions is achieved at the expense of detail in biogeochemical process descriptions. We refer to these models as plant interaction models (PIM) to distinguish them from BGMs. The latter still need substantial development to incorporate plant species richness and species interaction. In order to enable these models to simulate differently diverse communities and quantitatively assess the effect of plant species richness, important processes need to be identified and the appropriateness of potential alternative approaches has to be evaluated. An in-depth analysis of the interactions between two species can be used to identify the important processes. Doing such an analysis for model representatives which exemplify a type of model (a number of models sharing similar approaches) and comparing the performance of multiple model representatives, may be used to identify the limitations of current model implementations as well as general knowledge gaps that can inform the next steps of model development. The approach can also uncover similarities and differences regarding the strengths and weaknesses of specific approaches. This knowledge can be used to inform on potential development options for the assessed models as well as other models of the same type.

1.4. Model intercomparison studies

While comparison studies are more common for models of cereal crops (e.g. Asseng et al., 2019; Durand et al., 2018; Müller et al., 2017) only comparably few studies for forage grasses have been published (Korhonen et al., 2018). Of these few grassland model intercomparison studies, some have used a large model ensemble and cover multiple sites (e.g. Sándor et al., 2017, 2020; Ehrhardt et al., 2018). While they quantify and discuss the uncertainty within the ensemble, a detailed analysis of the processes within each model is beyond their scope. In contrast, other studies have used a small number of models allowing for a more detailed analysis of model differences at one or multiple sites (e.g. Korhonen et al., 2018; Persson et al., 2019; Hurtado-Uria et al., 2013). These studies are, however, limited to one specific species, neglecting inter-specific competition and differences between parametrizations obtained for multiple species, which to our knowledge have only been assessed using PIMs (Crawford et al., 2021).

1.5. Research question

To expand on this for BGMs of different scales and to assess the role of how processes are represented in different models, we compared simulated grassland properties for two biogeochemical grassland models (GRASSMIND: Taubert et al. 2012, 2020a,b; LPJmL: Schaphoff et al. 2018; von Bloh et al. 2018; Rolinski et al. 2018) using different scenarios of water availability and management using simulations of monocultures and two-species mixtures. The GRASSMIND model follows an individual-based approach using fixed traits for each species and simulates photosynthesis using light response curves (Thornley and Johnson, 1990), while the LPJmL model follows an average individual approach and simulates photosynthesis using an adapted Farquhar approach (Haxeltine and Prentice, 1996; Prentice et al., 2000). Using data from a long-term biodiversity experiment (Weisser et al., 2017) — the Jena Experiment — we first calibrated and evaluated the models for four species for observed climatic conditions and management. Subsequently, we compared the models for scenarios with no, moderate and extreme drought conditions in combination with and without mowing. With this study we pursue the following objectives:

(i) identify the relevant processes to explain the main similarities and differences between the models outcomes for our scenarios,
(ii) assess the effects of mowing and drought in relation to calibrated parameters for the monocultures and the two-species mixtures and explain the differences using the processes identified in (i) and
(iii) discuss our findings from (i) and (ii) in the context of other modelling approaches.

2. Methods

We used the vegetation models LPJmL (Schaphoff et al., 2018; von Bloh et al., 2018; Rolinski et al., 2018, see 2.1.1) and GRASSMIND (Taubert et al., 2012, 2020a,b, see 2.1.2) for our comparison. The models were first calibrated and evaluated for four monocultures and subsequently grassland dynamics were assessed for multiple scenarios of management and drought conditions for the monocultures as well as two-species mixtures (see 2.2).

2.1. Model description

The GRASSMIND and the LPJmL models both simulate daily dynamics of grassland vegetation. While LPJmL is usually applied at large spatial scales, for this study, it is used as a point model, simulating small plots with no further spatial distinction. This plot level is the smallest spatial unit for which all dynamics represented in LPJmL are simulated, whereas in GRASSMIND the smallest spatial units are the single plants, which simulate the dynamics on 1 m^2 to represent the plot. In both models, at each daily timestep, the amount of biomass gained by photosynthesis is calculated and allocated to the leaves and roots after subtracting losses from growth and maintenance respiration. Subsequently, the biomass losses from mortality and turnover of biomass into the litter layer are determined. The amount of new biomass gained depends on available space, soil and climate conditions and management. At optimal temperatures, sufficiently available space to grow and under adequate radiation, water and nitrogen supply, higher photosynthesis rates can be achieved, while suboptimal resource supply or high vegetation density limit photosynthesis and thus growth. This can results in altered competition and community composition. Both models can account for management measures by irrigation and application of fertilizer, can increase biomass gains. Biomass removal by mowing can be carried out at fixed dates, reducing the tissue available for photosynthesis after the mowing event.

Each model considers the environmental factors space not already occupied by vegetation, temperature, radiation, water and nitrogen availability, and simulates similar processes to describe biomass gains and losses. Fig. 1 provides a condensed overview of the similarities and differences while a separate depiction is provided in Fig. SI A.1. However, the process implementations differ in specific aspects, e.g., in LPJmL overcrowding reduces the above-ground biomass depending on the excess *cover*, while in GRASSMIND the excess *cover* determines the number of individuals killed which are then randomly selected (SI B Tab. 1). While we use the term *cover* for the comparison of the models throughout this paper, it is defined differently. In LPJmL, plant geometry is not simulated and cannot be used to calculate the *cover*. Here, *cover* is the foliage projective cover (FPC) which is calculated from the leaf area index (LAI). In GRASSMIND, where plant geometry is simulated, *cover* is calculated as the sum of the individual plants' base area. This is an important difference between the models and has to be kept in mind when reading sections 3 and 4.

In addition, a key difference of the models is the representation of the vegetation itself. Grassland communities consist of several taxonomic groups, however, only graminoids, small, and tall herbs are represented in the two models. For each modelled species or functional type, LPJmL simulates one average individual with a given set of traits. The dynamics of the average individual are then scaled up to the plot scale, neglecting differences between individuals of the same species. In contrast, GRASSMIND follows an individual-based approach explicitly simulating multiple individuals of the same species that have the same set of traits but can differ in size (e.g. plant height and base area). Both models distinguish the plant compartments leaves and roots, but in GRASSMIND leaf tissue is further divided into living and standing senescent tissue, while in LPJmL senescent tissue is directly added to the litter layer of the soil. For a detailed description we refer to Schaphoff et al. (2018); von Bloh et al. (2018); Rolinski et al. (2018) for the LPJmL model and to Taubert et al. (2020a,b, 2012) for the GRASSMIND model.

2.1.1. LPJmL

LPJmL is a process-based BGM of the carbon, water and nitrogen cycle, developed mainly for global-scale applications (Schaphoff et al., 2018; von Bloh et al., 2018) and has been extended to simulate different grassland management routines (Rolinski et al., 2018). However, as the model simulates processes for representative points without an explicit reference to space, it is also applicable at the plot scale (e.g Ehrhardt et al., 2018). LPJmL is representative for several related models (e.g. LPJ-GUESS Smith et al. 2001, LPJFit Sakschewski et al. 2015 or LPX Prentice et al. 2000) but also other DGVMs (e.g. JULES Clark et al. 2011 or ORCHIDEE Vuichard et al. 2007). The model simulates the dynamics of an average individual of a species or a plant functional type (PFT) with daily timesteps based on the following processes: (a) establishment of new species and reproduction of present species, (b) plant turnover, (c) biomass accumulation based on gross primary production (GPP) and autotrophic respiration, which is limited by environmental conditions and competition for resources between species. Direct biotic interactions are not simulated.

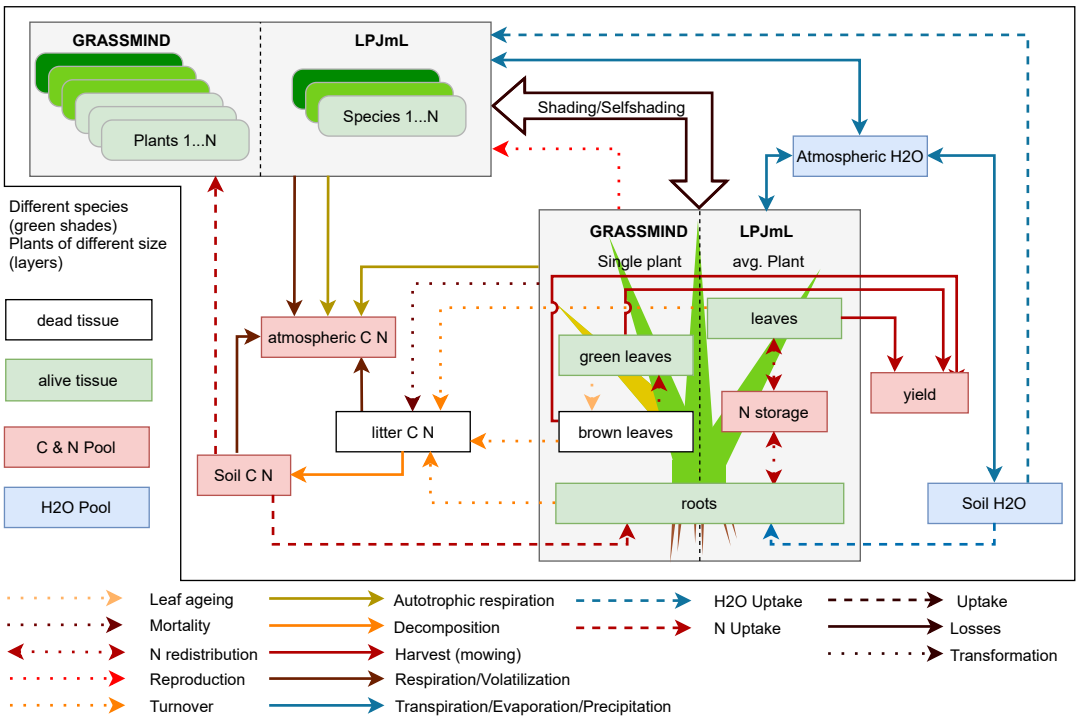

Figure 1: Processes and plant compartments simulated in GRASSMIND and LPJmL (see Fig. SI A.1 for an individual representation of each model)

2.1.1.1 Photosynthesis

LPJmL simulates GPP based on a simplification of the Farquhar approach in combination with a big leaf approach for which the optimum photosynthetic activity as a trade-off between light energy and RuBisCO availability is derived numerically (Farquhar and von Caemmerer, 1982; Collatz et al., 1991, 1992; Prentice et al., 2000; von Bloh et al., 2018). A crucial part of the photosynthesis is the fraction of absorbed photosynthetically active radiation (FAPAR) which is determined using a factor depending on snowcover, a biome-specific scaling factor and the PFT's FPC, which is defined as the fraction of ground area covered by a vertical projection of the vegetation's foliage, and determines how much of the photosynthetically active radiation (PAR) can actually be intercepted by the canopy. The FPC of each PFT is calculated from the PFT's specific LAI and light extinction coefficient. Afterwards, the realised FPC of each PFT is weighted depending on LAI and FPC of all other PFTs present in the plot. Additionally, limitations due to water and nitrogen stress are accounted for by comparing resource demand and supply.

2.1.1.2 Water and nitrogen stress

LPJmL simulates soil water dynamics in six distinct layers, to which plants have access, depending on their root distribution (Schaphoff et al., 2018). Here, we focus on plant water demand, supply, and uptake, to analyse the impacts these processes have on each PFT and the entire community. In the computation of GPP, an estimated canopy conductance under unlimited water supply is used to calculate the atmospheric water demand following Monteith (1995). Even though plants share the same soil water supply on the plot, plant available soil water is calculated separately for each PFT, depending on its maximum water transport capacity, vertical root distribution, and FPC. If the atmospheric demand is not met, canopy conductance is reduced in accordance to the water supply. This reduced conductance rate is used to determine actual GPP.

A similar approach is applied for the nitrogen stress in which the plant-available nitrogen supply is compared to the plant's demand. In case the leaf nitrogen content is below a threshold, the carboxylation capacity is

reduced to match the actual nitrogen supply in the leaves. Since the carboxylation capacity is also used to determine water limitation, the actual water demand is updated and GPP is updated to account for both water and nitrogen limitations (see von Bloh et al., 2018, for a detailed description of the nitrogen cycle in LPJmL).

2.1.1.3 Allocation, establishment and mortality

The assimilated carbon is distributed between leaves and roots, considering the discrepancy between the actual and the aspired leaf-to-root-ratio of carbon. If the actual leaf-to-root ratio is larger than the aspired (more leaf carbon than root carbon) more carbon is allocated to the roots and the other way around. Under water limited conditions, additional carbon is allocated to the roots. Subsequently, the assimilated nitrogen is distributed considering the prescribed range of carbon-to-nitrogen-ratios of leaves and roots. If the allocation of nitrogen would exceed the lower limit of these ranges, a part of the nitrogen is stored so it can be distributed at a later time. If not enough nitrogen is available and the upper limit of the ranges would be exceeded, leave and/or root carbon is reduced and the excess added to the litter layer. Afterwards, the FPC of all PFTs is updated.

Each day, the model evaluates the present species and allows for establishment of new species if these can grow under simulated conditions. For all species (already present and newly established) reproduction is calculated based on the equal distribution of available space. The more space is available the more reproduction is possible. If the total FPC exceeds 1.0, overcrowding mortality reduces the leaf biomass until the FPC is smaller 1.0.

All these processes interact and lead to daily changes in the PFTs' carbon and nitrogen pools. The process rates depend on a set of PFT specific parameters that resemble plant functional traits. It is possible to represent different strategies of particular species using observations of multiple functional-traits or measurements from experiments, that correspond to a subset of the parameters to calibrate the model. A full model description is available in Schaphoff et al. (2018) and von Bloh et al. (2018) and the open source version of the model is available at `https://github.com/PIK-LPJmL/LPJmL`. We use a consolidated version of LPJmL5 (von Bloh et al., 2018) extended to simulate daily establishment.

2.1.2. GRASSMIND

GRASSMIND is an individual- and process-based grassland model (Taubert et al., 2012, 2020a,b) where plant growth is based on the concept of light response curves that is also used in several other models (e.g. Seib-DGVM Sato et al. 2007). The model simulates the daily dynamics of individual plants of different species or PFTs at the plot scale (e.g., 1 to 100 m^2) based on the following processes: (a) recruitment and emergence of plant seedlings, (b) plant senescence and mortality, (c) growth of plants (based on GPP and autotrophic respiration), which can be (d) limited by environmental conditions or reduced due to competition between plants. Interactions between plants encompass competition for the resources light, space, water and nitrogen. Plant competition depends on plant size and species identity, but does not account for the particular spatial locations of a plant ('gap approach'; Fischer et al., 2016; Botkin et al., 1972; Köhler and Huth, 2004; Shugart, 1998). Each plant species is described by a set of plant traits, which determines its performance in the above-mentioned processes and its growth form.

2.1.2.1 Photosynthesis

GRASSMIND first calculates a plant's potential GPP using the concept of light response curves (Thornley and Johnson, 1990), which is subsequently reduced to account for water, nitrogen and temperature limitations. The potential GPP is predominantly determined by the photosynthetically active radiation (PAR) that the plant receives, which is comparable to FAPAR in LPJmL. In GRASSMIND, this depends on the LAI and other factors such as shading by larger plants. Competition for light is modelled asymmetrically, which means that larger plants receive more non-attenuated light than smaller plants. Dependent on species-specific traits, some species can cope better with lower light levels than others. Large plants with large leaf area can reach their potential GPP limit as a result of self-shading. The response of potential GPP to air temperature is similar for all plants, but reductions of potetenial GPP due to soil water deficits, nitrogen stress or competition are dependent on species-specific traits that control resource demand and supply.

2.1.2.2 Water and nitrogen stress

Water, carbon and nitrogen dynamics are modelled in 20 equally large soil layers in GRASSMIND using a daily version of the Century soil model (Parton et al., 1988). Soil water stress is modelled using a linear reduction dependent on soil water content, permanent wilting point and field capacity (Granier et al., 1999). Species-specific differences in water uptake are a result of the water demand of plants (using the concept of water use efficiency) and their rooting depth in relation to the availability of water in different soil layers.
A similar approach is used for plant nitrogen stress. Based on the potential NPP, which is a balance between possibly limited GPP and autotrophic respiration (modelled proportional to plant biomass), the plant nitrogen demand is calculated using C:N ratios of green and brown leaves and roots (species-specific model parameters). Again, the potential NPP of a plant is reduced linearly dependent on the ratio of nitrogen supply and demand. Leave senescence can add nitrogen resources to the supply via retranslocation from yellowing to still green leaves. The actual GPP is calculated from the potential GPP by accounting for the limitations from temperature, water and nitrogen stress using multiplicative factors. Subsequently the autotrophic respiration is accounted for to obtain the actual NPP.

2.1.2.3 Allocation, recruitment and mortality

The actual NPP is then distributed between shoots (stems and leaves), roots and reproductive biomass. A species-specific fraction is allocated to the shoots and the root biomass is updated dependent on this fraction and the shoot-root ratio. The remaining NPP is allocated to the reproduction pool. Corresponding nitrogen fluxes are calculated according to the respective C:N ratios. The growth of plants based on an increased net productivity results in an increased plant biomass, leaf area, rooting depth and root branch length, plant height and width, dependent on species-specific traits.
Recruitment and mortality of plants determine, in turn, the density of plants on the simulated area. Recruitment can occur from three sources: migration from a surrounding meta-community as a constant inflow, sowing of seeds at specific times and local reproduction of plants depending on their fitness. Plants of a higher fitness are able to invest more of their NPP into reproduction and can produce more seeds. In this study, seed ingrowth from a meta-community and local recruitment are summarized in one model parameter. While seedlings can grow at any time and establish dependent on species traits (e.g. germination rate), plant mortality is modelled in terms of a background mortality and a crowding mortality. The background mortality is constant (but differs between seedlings and mature plants) and independent of environmental conditions and overcrowding. Plants that have reached their expected maximum age die immediately. If the total vegetation cover, which is calculated based on all plant's width or lateral expansion, exceeds an area size (of one m^2), crowding mortality reduces the number of individual plants (irrespective of size or plant age). A full model description of GRASSMIND can be found in Taubert et al. (2012, 2020b,a) and on `www.formind.org/downloads`.

2.2. Site and scenario description

Both models were applied to plots of the Jena Experiment, which is situated at the northern edge of Jena (Thuringia, Germany) on the floodplain of the Saale river (50°55'N, 11°35'E, 130 m a.s.l. Weisser et al., 2017). The annual mean temperature and mean annual precipitation between 1980 and 2010 were 9.9 °C and 610 mm/year, respectively (Hoffmann et al., 2014), and the soil is classified as Eutric Fluvisol (Roscher et al., 2004).
For our simulations, we used gap filled daily weather data for temperature, precipitation, and shortwave radiation from 2002 to 2014 (MPI, 2019; Taubert et al., 2020a). Within this period, annual precipitation ranged from 368 to 784 mm/year with a mean of 526 mm/year which is below the 1980 to 2010 average. For the use in LPJmL we had to normalize leap years (2004, 2008, and 2012) to 365 days. We chose to remove December 31st in leap years to maintain the seasonality within the years. Since data on harvest events were only available at monthly resolution (Weigelt et al., 2010), we assumed harvests to occur in the middle of the month (15^{th}). Data on soil bulk density, field capacity and permanent wilting point were measured in four blocks set up along a soil texture gradient perpendicular to the river Saale (Roscher et al., 2004). In addition to the measurements we derived porosity from soil texture. For our simulations we always used the data on soil properties from the block in which our selected species plots were located.

2.2.1. Species selection

At the Jena site, several experiments were conducted in parallel. We use data from two experiments, the main experiment (Roscher et al., 2004), which was designed to compare the different diversity levels and the monoculture experiment (Heisse et al., 2007), which was established as a control, for example to compare mixture and monoculture yields. The species pool of the Jena Experiment consists of 64 species from four functional groups (grasses, small herbs, tall herbs, and legumes), that grow well under the site conditions (Weisser et al., 2017). Monocultures of all 64 species were established in the monoculture experiment, while in the main experiment monocultures of only 16 (four from each functional group) species were sown, limiting the number of species available for our study. We excluded the tall herb and legume species from our selection because we assumed the small herbs and grasses to be more suitable for usage in both models. Of the eight remaining species we excluded *B. perennis* because the experimental plots were strongly affected by the rust fungi *Puccinia coronata* and *P. graminis*, which led to a decrease in productivity and the abandonment of the plots in later years (Weisser et al., 2017). To reduce the complexity of our comparison we selected only four of the remaining seven species for our simulations. We selected three common fodder grasses (*Poa pratensis*, *Festuca pratensis* and *Festuca rubra*) and one very common small herb (*Plantago lanceolata*). For all selected species data was available in the two experiments allowing us to use the data of the main experiment for the calibration while evaluating the models against the data from the monoculture experiments.

2.2.2. Calibration and evaluation

For model calibration we used the data from the monoculture plots of the main experiment on aboveground biomass (AGB), leaf area index (LAI) and vegetation cover for both models, as well as vegetation height in addition for GRASSMIND (see 2.2.2). We evaluated the performance of both models, by using data on AGB from the monoculture experiment which consisted of small plots of monocultures of all species used in the main experiment (Heisse et al., 2007). For both calibration and evaluation, we used the daily weather data from 2002 to 2014 and the mowing frequency that was reported for the Jena Experiment, where plots were mown twice a year, usually in May and September. Plots of the main and the monoculture experiments were not fertilized, therefore, we did not add any fertilizer and excluded nitrogen deposition in our simulations.

The model specific calibration procedures as well as the parameters selected for calibration are described in SI A. The observed data sets used for the calibration and the evaluation both show a decrease of monoculture productivity over time (Marquard et al., 2013), which results in substantially lower values of AGB in the later years. Additionally, for some AGB observations, the variability of data for one sampling period was large, which was also found in other grassland experiments (e.g. Vuichard et al., 2007). For LPJmL, a spinup run was conducted, to obtain soil carbon, nitrogen, water and temperature values to initialize the calibration and evaluation simulations (spinup conditions are described in SI A).

2.2.3. Simulation scenarios

As we were interested in the effects of drought and mowing on modelled processes and on the performance of species in monocultures and the two-species mixtures, we run three precipitation scenarios (baseline, moderate drought, extreme drought), each with and without mowing. Each scenario was run for 28 years: for the first 14 years the baseline scenario was used in all scenarios as a spinup to obtain an equilibrium state of the plant community. In GRASSMIND, the scenario simulations could be started right away, while for LPJmL they were based on the initial spinup run also used for calibration and evaluation. For the baseline treatment, we simply repeated these 14 years. For our drought treatments, we excluded parts of the rain (see below) in year 16, but returned to the baseline scenario for years 17-28. All evaluations refer to the years 15 to 28 of our simulations. We first generated our baseline scenario, in which we reduced the effects of intra-annual rainfall variability that could otherwise mask the effects of droughts. To obtain the baseline scenario (Baseline_Mow) time-series we grouped the data based on annual and spring precipitation sums into three clusters using euclidean distances and a Ward clustering algorithm (Murtagh and Legendre, 2014). The hierarchical cluster analysis was performed with R Version 3.5.3 using the hclust function from the stats-package (R Core Team, 2019). We selected the cluster with the medium annual and spring precipitation

which contained seven years. For the moderate drought scenario (ModD_Mow) we used the same time-series but excluded precipitation in April and May of year 16. We extended the exclusion to March and June for the extreme drought (ExtrD_Mow). By this, we reduced the annual precipitation by approximately 20 and 40%, respectively. We ran simulations for Scenarios Baseline_Mow, ModD_Mow and ExtrD_Mow with limited nitrogen supply and with mowing. Additionally, we ran simulations with the same environmental conditions but without mowing (Baseline_NoMow, ModD_NoMow and ExtrD_NoMow).

Table 1: Simulation scenario names, environmental conditions and management

Scenario	**weather data**	**precipitation reduction**	**management**
calibration/evaluation	observed	none	with mowing
Baseline/ModD/ExtrD_Mow	medium cluster	none/moderate/extreme	with mowing
Baseline/ModD/ExtrD_NoMow,	medium cluster	none/moderate/extreme	without mowing

3. Results

We analysed model outputs on above-ground biomass (AGB), GPP, NPP, LAI, Losses (litterfall and mortality), *cover* and water uptake. We present the results for AGB in the main text and for the other variables (only for our baseline scenario Baseline_Mow) in the SI. In section 3.1, we briefly present the results of the calibration and model evaluation. Subsequently, we analyze our results of AGB dynamics for monocultures and mixtures for both models for our scenarios in section 3.2.

3.1. Model calibration and evaluation

Model calibration was successfully conducted for both models following the procedures described in SI A. Overall both calibrated models reproduced the observed data from monocultures of the main experiment well for AGB (described as organic dry matter), LAI and (for GRASSMIND) height, but not for *cover*. Agreement with the experimental data varied between the models and for different species (Fig. SI A.2-4). We were able to calibrate LPJmL and represent four different species modifying only four parameters. The parameter sets of the four species were derived during the calibration starting from the same initial parameter values for all species. LPJmL showed good agreement with data on LAI (RMSE 0.53 to 1.18 $m^2\,m^{-2}$) and moderate agreement with AGB observations (RMSE 46.4 to 245.8 $gDM\,m^{-2}$), but data on *cover* did not agree well (RMSE 0.24 to 0.59 $m^2\,m^{-2}$). Simulated *cover* values of monocultures in the calibration of LPJmL were low compared to observations. In LPJmL, plant size is not explicitly simulated and *cover* is calculated as foliage projected cover (FPC) from the LAI assuming a strong connection of the two (see 2.1.1). Using both LAI and *cover* in the calibration results in a trade-off in favour of the one that leads to better results for AGB. Furthermore, since observed *cover* was estimated visually, we assume LAI observations to be more reliable and attribute only minor importance to the fit of *cover* for LPJmL.
The calibration of GRASSMIND for the four monocultures required the fit of 13 species-specific parameters and also included the vegetation height, in addition to the observed LAI, *cover* and AGB. Good agreement of GRASSMIND was achieved for LAI (RMSE 0.47 to 0.71 $m^2\,m^{-2}$) as well as for vegetation height (RMSE 0.083 to 0.218 m) and AGB results agreed moderately with observations (RMSE 34.0 to 236.6 $gDM\,m^{-2}$). As in LPJmL, GRASSMIND simulations did not agree well with the observed data on *cover* (RMSE 0.22 to 0.46 $m^2\,m^{-2}$), but in contrast to LPJmL, GRASSMIND overestimated vegetation cover. In the simulation of GRASSMIND, vegetation cover is derived from individual plant sizes and allowed to settle around 100%. For the model calibration, observed vegetation cover (excluding weeds and dead material) is therefore compared only with the cover of green leaves of the simulated plants (excluding standing senescent leaves). Note, that the calibration here differs from previous calibrations of GRASSMIND (Taubert et al., 2020a) to harmonize the study design and simplify the comparison of the two models (see SI A for a detailed description of the calibration procedure).

3.1.1. Deviations from observations

Although AGB values agreed only moderately with the observations, the agreement with the majority of the data is significantly better, because a major share (LPJmL: 51 to 81% and GRASSMIND: 57 to 87%) of the sum of square errors (SE) can be attributed to only two of the twelve observation dates for each species (Fig. SI A.5-7). The observations can be partitioned into high AGB and low AGB observations. For all the plots we used, high AGB observations were sampled in the early years (2002 to 2004) of the experiment, while observations from the later years showed substantially lower AGB because of a decrease in productivity (Marquard et al., 2013). A large share of the sum of SEs is related to the high AGB observations in the early years. This high productivity at the beginning of the experiment cannot be reproduced by either model. This may be a results of the uncertain initial soil conditions (e.g. soil fertility) because of the unknown management history prior to the experiment in Jena but may also be related to the obtained parameterizations. For both models, selected parameter values are static and cannot change over time, therefore as long as the environmental conditions and management remain similar, the models do not simulate any temporal trends. To adequately simulate the high AGB levels in the early years of the experiment a different set of parameter values would be needed. However, since the majority of the data consists of low AGB samples collected after the decrease in productivity the calibration procedure returns a set of parameter values which reproduce this subset of the observations well. We were able to confirm this with our evaluation (Fig. 2) where we used the AGB observations from the monoculture experiments (Heisse et al., 2007). Here, the RMSEs of both models were very similar (e.g.: 81.7 $\mathrm{gDM\,m^{-2}}$ for LPJmL and 77.8 $\mathrm{gDM\,m^{-2}}$ for GRASSMIND for *P. pratensis*). The data from the monoculture experiment show the same productivity decrease as the main experiment and similar to the calibration, a major share of the SE (55 and 82 %) can be attributed to only two observations (Fig. SI A.8).

3.2. Aboveground biomass dynamics and resource competition

In our comparison we focus on the differences and similarities in the AGB dynamics of both models for the different scenarios. We ordered the description of the results so that differences in climatic conditions and management to the baseline scenario increase step by step. First, we present results for our baseline scenario, Baseline_Mow (see 3.2.1), which — while already using climate data with reduced variability (see 2.2.3) — is not subject to additional precipitation reduction and uses the standard management (as also used in the calibration and evaluation). Second, we compare the result from Baseline_Mow to the drought scenarios (ModD_Mow and ExtrD_Mow see 3.2.2) in which precipitation reductions are prescribed. Third, we compare Baseline_Mow, ModD_Mow and ExtrD_Mow to the scenarios without mowing Baseline_NoMow, ModD_NoMow and ExtrD_NoMow (see 3.2.3).

3.2.1. Simulated dynamics in the baseline scenario with mowing

The monoculture simulation experiments under the baseline rainfall treatment with mowing (Fig. 3 a-d) show similar overall means in AGB in both models. AGB values are highest for *F. rubra* (LPJmL: 126 $\mathrm{gDM\,m^{-2}}$ and GRASSMIND: 106 $\mathrm{gDM\,m^{-2}}$) and lowest for *P. pratensis* (LPJmL: 41 $\mathrm{gDM\,m^{-2}}$) and *P. lanceolata* (GRASSMIND: 36 $\mathrm{gDM\,m^{-2}}$). However, the intra-annual dynamics indicate strong differences between LPJmL and GRASSMIND: The variation of AGB between seasons is much more pronounced for GRASSMIND than for LPJmL, with lower AGB in winter but for most species higher AGB during the summer months. This is connected to the different process implementations in both models that are used to derive NPP from GPP and autotrophic respiration and AGB losses in the form of turnover and mortality (see 2.1 and 4.1). For the two-species mixture experiments (Fig. 3 e-j) the AGB dynamics are driven by the dominant species. The dominant species can either be the same (Fig. 3 e-g) with similar differences in mean values as in the monocultures or different (Fig. 3 h-j) with larger discrepancies in mean values. In addition to NPP and AGB loss from turnover and mortality, competition between species affects the AGB dynamics. While these processes are sufficient to explain the off-season AGB dynamics, the additional reduction from mowing has to be considered for the dynamics within the growing season. The effect of mowing strongly differs between the two models (Fig. 3a-j) and is the underlying reason for the different AGB peaks during the growing season. In LPJmL, 47.6 to 207.0 $\mathrm{gDM\,m^{-2}}$ is on average removed by mowing. This amount

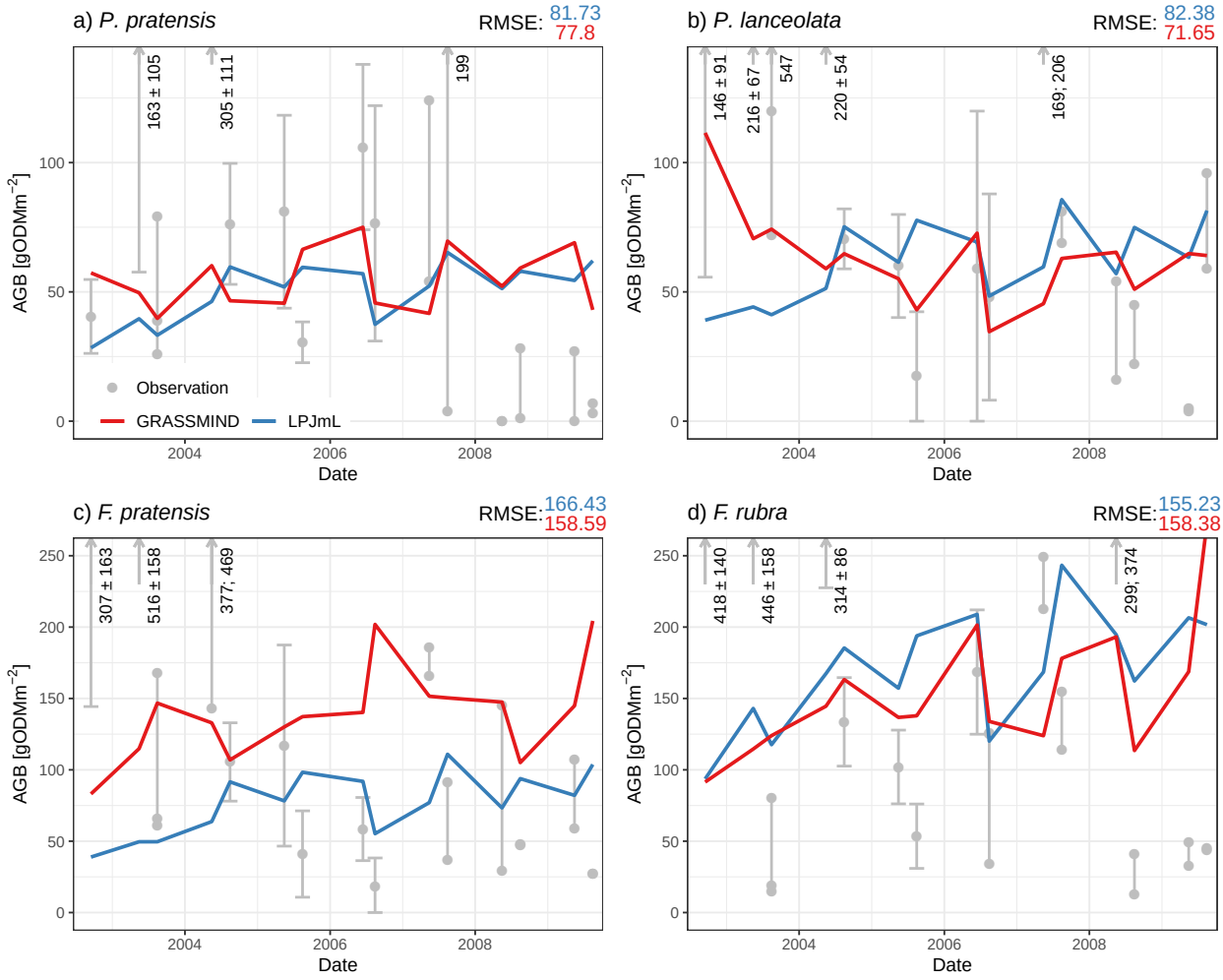

Figure 2: Simulated and observed AGB in gDM m^{-2} for *P. pratensis* (a), *P. lanceolata* (b), *F. pratensis* (c) and *F. rubra* (d) for GRASSMIND (red) and LPJmL (blue). Coloured lines and labels show model results and RMSE, grey points show observations used for the evaluation. Observations are the median of samples for each date and error bars show one standard deviation. If three or less observations were available all observations were plotted and their range indicated with a line. Outliers are highlighted with labels and arrows.

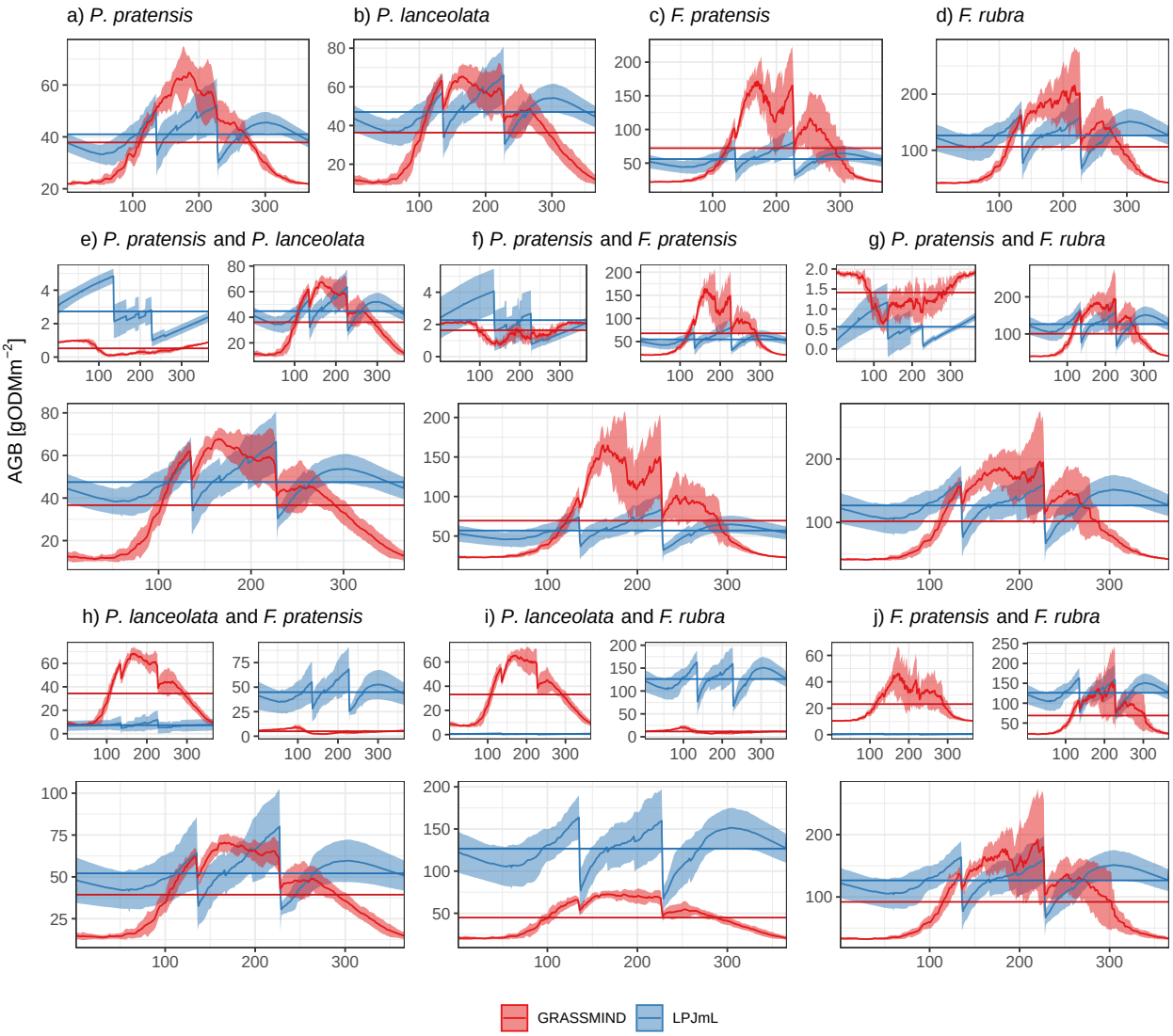

Figure 3: Mean (μ) AGB in gDM m^{-2} for GRASSMIND (red) and LPJmL (blue) averaged over all simulation years for each day of the year for monocultures (a,b,c,d) and two-species mixtures (e,f,g,h,i,j). For mixtures total AGB (top) and species specific AGB (bottom) are shown separately. Coloured ribbons show $\mu \pm \sigma$.

is significantly smaller in GRASSMIND (1.4 to 31.3 gDM m^{-2}). The large differences in biomass reduction are related to the different implementations of the mowing routines and the representation of the plants themselves.

In both models, the dominant species exploit available resources more efficiently, which is related to the parameterization of the species. Higher parameter values for important traits are directly related to a higher competitive strength (Fig. 4). In LPJmL, this is related to the calibrated parameters via specific processes. While all parameters (Fig. 4) are important to calibrate the simulated AGB to the observations, the leaf to root ratio (lr) and stubble density (ρ_{veg}) are of minor importance for competition. Here, the light extinction coefficient (k_{beer}) and the specific leaf area (SLA) which are used to calculate FPC are most important. Higher values of these two parameters result in higher FPC values and the species utilize space more effectively. k_{beer} is highest for the most competitive species (*F. rubra*) and lowest for the least competitive species (*P. pratensis*). SLA is less important and only influences competitive strength for species with similar k_{beer} values (*F. pratensis* and *P. lanceolata*). In GRASSMIND, benefits of a species in the fast and successful establishment of seedlings, high germination rate ($germ$), short time of emergence (t_{em}) and low seedling mortality (m_{seed}), also determine the competitive strength of that species in mixtures (as for *P. lanceolata*). In this case, the larger mature plant mortality (m_{basic}) weighs less than the favourably low seedling mortality (m_{seed}) because plants mature later (higher age_{rep}). Highly productive species (higher maximum gross leaf photosynthesis p_{max}, higher SLA, higher shoot-root ratio sr) can be more competitive in mixtures which, however, can be altered by self-shading (high height-width ratio hw) or shading by other plants (low hw), by fast leaf senescence (low lls) or waterstress-related attributes. The latter are of specific importance as we show in section 3.2.2, while water use efficiency (WUE) and allocation rate of net productivity to shoot biomass ($alloc_{shoot}$) are only of minor importance (as for *P. pratensis*).

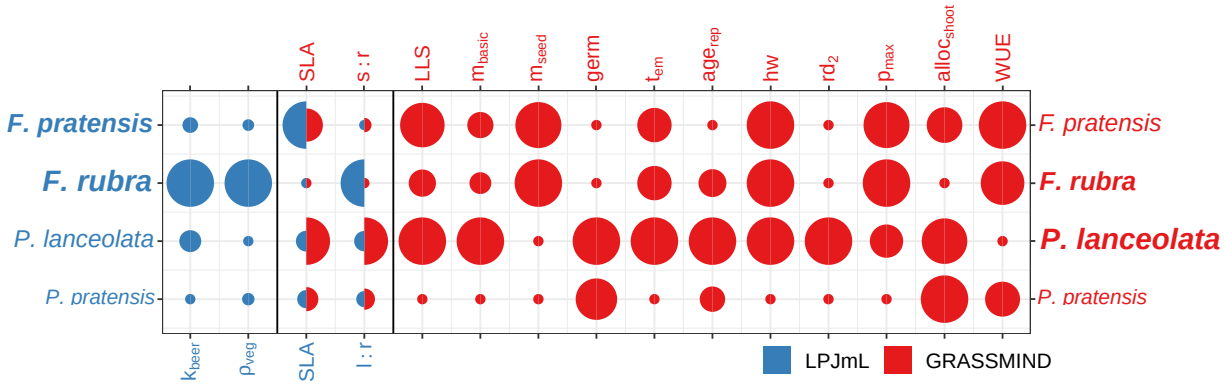

Figure 4: Normalized parameter values for GRASSMIND (red) and LPJmL (blue) for parameters important for species competition. Full circles show parameters which are not comparable between the two models and half circles show parameters used similarly in both models. The different species are ranked by competitiveness with the label size, ranging from most competitive (large) to least competitive (small).

3.2.2. Effects of rainfall reduction

In both models, the AGB decreased during the drought treatments with mowing (Fig. 5d and SI D.1-5d). Overall, effects were qualitatively the same for both the moderate and the extreme drought and just differed in their order of magnitude for both models. We compared the lowest AGB values during the drought (Fig. 5e and SI D.1-5e i.e. the maximum difference between the baseline and the drought scenarios) for both models. While the smallest differences between the baseline and drought scenarios are similar between the two models during the moderate and the extreme drought (LPJmL: -13.9 and -23.1 gDM m^{-2};

GRASSMIND: -11.5 and -12.0 gDM m^{-2}), in GRASSMIND the largest differences are more extensive (-130.5 and -170.7 gDM m^{-2}) than in LPJmL (-77.2 and -110.5 gDM m^{-2}). The decrease of AGB under drought is a result of the reduced water uptake (Fig. 5e and SI D.1-5e) after soil water resources in the first 20 cm of the soil are depleted. This depletion of soil water content is stronger in GRASSMIND (-20% Fig. 5b and SI D.1-5b). Here, the permanent wilting point is reached and no water is available for transpiration, leading to no plant growth (i.e. GPP) at all and a fast decline of AGB, caused by continued mortality and turnover. In LPJmL, the soil water depletion is less severe (-13 to -14%) but the reduced water supply also limits GPP. The balance of the reduced GPP, the respiration (which is not affected by the drought) and turnover becomes negative and AGB decreases. Compared to GRASSMIND, this results in a smaller and slower decline of AGB.

After the end of the drought treatment, soil water resources are replenished. In both drought scenarios a similar soil water content compared to the baseline scenarios is reached shortly after the end of the drought (Fig. 5b and SI D.1-5b). However, in all scenarios, the soil water content remains below field capacity because of the low July precipitation which results in additional water stress (Fig. 5c and SI D.1-5c).

After the end of the treatment, vegetation recovers at different speed in both models. In GRASSMIND, the recovery is fast and the AGB reaches a pre-treatment level soon after the soil water is replenished (Fig. 5d and SI D.1-5d). In LPJmL, recovery is slower and AGB two years after the treatment can still be substantially lower than the pre-treatment AGB. After a complete recovery, the AGB of the scenarios with rainfall reduction treatments and the baseline scenario are the same, because of identical environmental and management conditions. In LPJmL, all simulated species suffer from the drought and only start recovering after the end of the drought. In GRASSMIND, this is similar except for *P. lanceolata* which after a short period of AGB losses, already gains biomass (i.e. positive GPP) during the drought. This is the only deep rooting species with higher values of the parameters of the rooting depth power law relationship (rd_1 and rd_2). These ensure a good species performance and competition even during the precipitation reduction were *P. lanceolata* takes advantage of water in deeper soil layers (Fig. SI D.1,3 and 4) and benefits from the reduced crowding mortality.

3.2.3. Comparison of mowing effects

Mowing has very different effects in the two models in the monoculture and mixture simulations for the baseline scenario (Fig. 6a and SI E.1-5a). In GRASSMIND, mean AGB values are barely higher in the baseline scenario without mowing than with mowing (-1.5 to +4.5 gDM m^{-2}), while in LPJmL these are considerably larger (+90.6 to +210.7 gDM m^{-2}). As established in section 3.2.1, mowing plays an important role for AGB dynamics. In GRASSMIND, the amount of biomass reduced is not pre-determined but linked to the plant height structure of the community (i.e., frequency of large and small plants). Because only a few individuals exceed the mowing height (here 0.1 m) the reductions from mowing are small. In contrast, in LPJmL vegetation height is not simulated and mowing directly reduces AGB to a predefined threshold.

The effect of mowing on mean AGB also alters the effect of the moderate and extreme precipitation reduction, increasing the differences between the models (Fig. 6b,c and SI E.1-5 b,c). Losses during the reduction treatment are similar to those in the scenarios with mowing in GRASSMIND (-7.2 to -160.1 gDM m^{-2}), but strongly increase in LPJmL (-70.8 to 156.5 gDM m^{-2}), because the generally higher AGB leads to higher turnover and respiration (Fig. SI C.11). As in the scenarios with mowing, community composition was barely affected in the scenarios without mowing, regardless of the precipitation reduction treatment (Fig SI C.6,14,15).

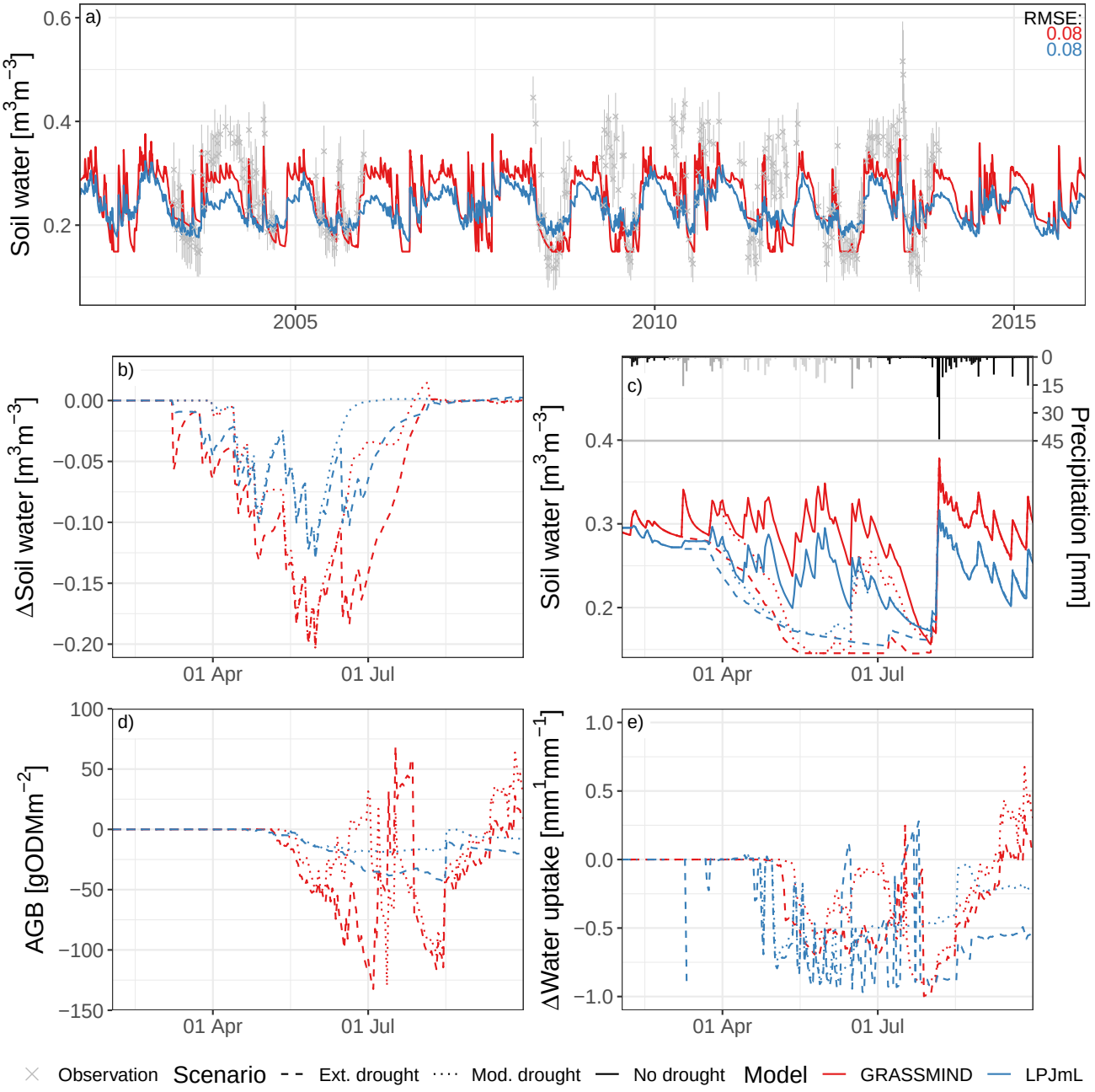

Figure 5: Simulated and observed (Fischer et al., 2019) fractional soil water content at the Jena Experiment site (a), relative changes of soil water content in $m^3\,m^{-3}$ (b), absolute changes of soil water content in $m^3\,m^{-3}$ as well as daily precipitation in mm with reduction for ModD (light grey) and ExtrD (light and dark grey) (c), absolute changes in AGB (d) in $gDM\,m^{-2}$ and relative changes in transpiration (e) caused by the moderate (dotted) and extreme (dashed) droughts for LPJmL (blue) and GRASSMIND (red). Simulation results of mixture of *P. pratensis* and *F. pratensis* using observed weather data (a) and average climate (b-e).

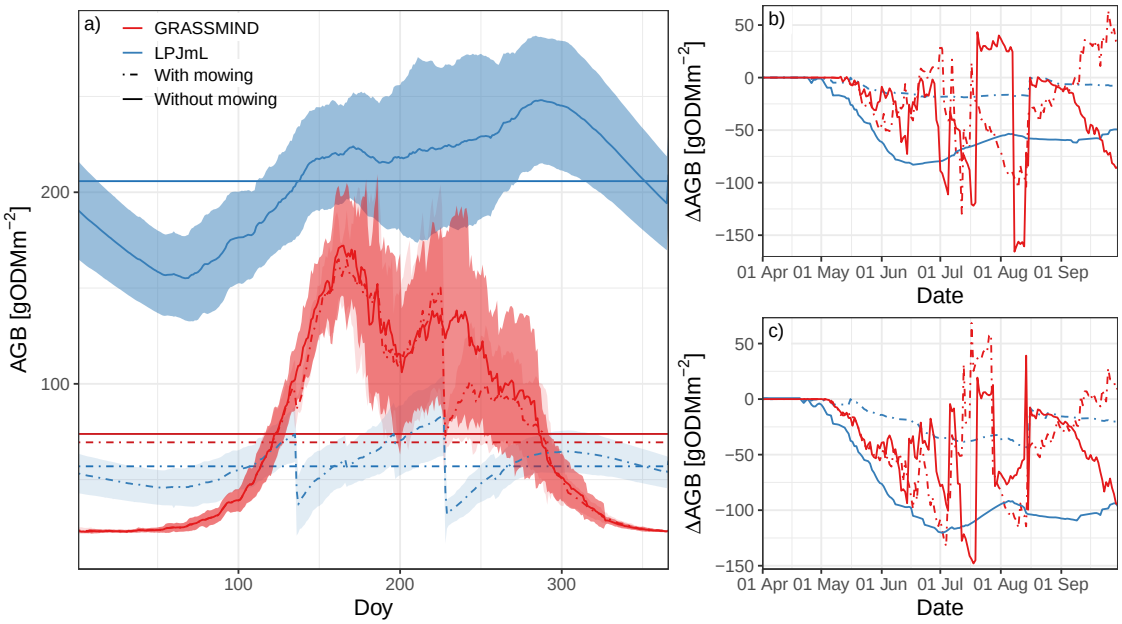

Figure 6: Mean (μ) AGB in gDM m^{-2} for GRASSMIND (red) and LPJmL (blue) for the sum of the two-species mixture of *P. pratensis* and *F. pratensis* (a). Coloured ribbons show $\mu \pm \sigma$. Horizontal lines show overall mean for Baseline_Mow (dot-dashed) and Baseline_NoMow (solid). Difference between Baseline_Mow and ModD_Mow (dot-dashed) and ModD_NoMow (solid, b) and ExtrD_Mow (dot-dashed) and ExtrD_NoMow (solid, c) between April and October of the drought year.

4. Discussion

Differences in simulated responses of monocultures and two-species mixtures to drought and mowing can be related to process representations of above- and below-ground resource competition, as well as of water dynamics and community representation. Even though we could not test the relevance of individual processes, the differences between model results and implemented features can shed some light on the importance of different mechanisms and model features for simulated dynamics.

4.1. Above-ground biomass seasonality

The two models show substantially different intra-annual AGB dynamics for which we identified several underlying mechanisms. Strongest differences were found during the off-season, where no data is available from the Jena Experiment for calibration or evaluation of the models, suggesting that the calibration process helped to reduce differences between models.

4.1.1. Processes determining AGB

Our simulations show that GPP and NPP have higher average and peak values for GRASSMIND (Fig. SI C.1,2). Gains in biomass are resulting from NPP, which is dependent on GPP. Both are controlled by LAI and *cover*, which also show higher average and peak values for GRASSMIND (Fig. SI C.3,4), and together with the amount of absorbed radiation determine the rate of photosynthesis. Here, the models use different process realisations: In GRASSMIND, vegetation height and LAI of each individual determine its GPP from which respiration losses are subtracted to obtain NPP. In LPJmL, *cover* (calculated as FPC using LAI) is used to determine the amount of absorbed radiation and resulting GPP. Similar to GRASSMIND, autotrophic respiration is subtracted to obtain NPP. Both models account for the effect of shading differently: GRASSMIND directly via interactions between individuals and LPJmL indirectly within the calculation of *cover*. While the high LAI values for GRASSMIND result in high productivity, the lower LAI values for LPJmL lead to low *cover* values and lower productivity. The higher productivity of GRASSMIND can

only lead to the similar average value of AGB we observed for the two models, if it is counteracted by higher losses. These result from age- and overcrowding-related mortality and turnover, as well as mowing during the growing season (Fig. SI C.5). Turnover and in the case of GRASSMIND also age mortality constantly contribute to these losses (independent of environmental conditions and management), but with different magnitudes in both models. Losses from overcrowding are linked to total plant *cover* and describe competition for space, which can lead to decreased establishment and increased mortality in both models. In GRASSMIND, *cover* includes alive and standing senescent biomass. Here, available space is always fully occupied, leading to a constant loss of biomass from overcrowding. This loss arises from the number of individuals that die from overcrowding which is dependent on the number of individuals present and the total *cover* of the plot (Tab. SI B.1). In GRASSMIND, competition for space occurs between conspecifics (individuals of the same species) and heterospecifics (individuals of different species) and is therefore also effective in monocultures, whereas in LPJmL competition for space occurs only between different species, so that losses due to overcrowding do not occur in monocultures and observed losses result from turnover (Fig. SI C.4 a-d).

4.1.2. AGB dynamics outside and during the growing season

The higher winter AGB in LPJmL compared to GRASSMIND originates in the model-specific representation of the leaves. In both models, AGB is the entire amount of standing biomass. In LPJmL, a distinction between photosynthetically active (green) and already senescent leaves (yellow) is not made, but a constant proportion of the total leaf biomass is transferred to the litter pools each day of the year. In GRASSMIND, such a distinction is made, but yellow AGB is constantly transferred to the litter so that AGB consists predominantly of green leaf biomass. This results in a larger reduction of the AGB during the off-season. Therefore, AGB shows high values during the growing season, but low values during the off-season in GRASSMIND, while in LPJmL despite similar GPP and NPP, AGB values are higher.

These differences are sufficient to explain the off-season deviations between the models, where biomass losses from overcrowding lead to the lower AGB of GRASSMIND. However, to fully explain the differences within the growing season, the additional reduction of AGB from mowing has to be considered. The effect of mowing strongly differs between the two models (Fig. 3a-j). In GRASSMIND, the vegetative height of the individuals is explicitly simulated, and during mowing events only larger individuals are reduced. Because the simulated height distribution of the community is often skewed towards smaller individuals, biomass reductions are small. In LPJmL, height is not simulated explicitly and the amount of extracted biomass is determined as the difference between total AGB and a predefined residual biomass. This results in the different AGB during the peak growing season.

We are aware that monocultures and two species mixtures are not representative for the diversity of grassland communities and are thus difficult to compare to observations from other grassland ecosystems. Nevertheless, empirical studies that support both types of AGB seasonality exist. AGB dynamics of LPJmL are comparable to observations of total AGB (e.g. Poyda et al., 2020) while the dynamics in GRASSMIND are similar to observations of green AGB (e.g. Inoue et al., 2015).

4.1.3. Processes controlling drought response

The comparison to the scenarios with a moderate and extreme drought showed an effect of the drought on AGB during and after. Although water became limiting during the drought, competition for space remained strong and the community compositions of the two-species mixtures were barely affected. In none of the mixtures the subordinate species gained a substantial advantage in either of the models (Fig. SI C.12,13). Both the moderate and the extreme drought lead to short term reductions of AGB followed by a full recovery. The drought effect was stronger in GRASSMIND, where water uptake is only limited by the available soil water. If this falls below a threshold, water stress occurs regardless of plant water demand, which in reality might still be fulfilled even under a reduced water supply. On the contrary, in LPJmL plant water demand is calculated depending on the potential canopy conductance (which is derived from the productivity of the AGB) and compared to the supply. Therefore, even if the soil water content is low, especially species with a low AGB may not suffer from water stress even under a reduced soil water content. The water stress during the drought directly inhibited growth of new biomass. However, the losses depicted

in section 4.1.1 are only indirectly affected by the environmental conditions through the reduced amount of available biomass or covered area and remain substantial (Fig. SI C.16-18). This changes the balance between biomass gains and losses and leads to an overall decline of above-ground biomass.

In GRASSMIND, the drought affects the community structure which consists of different individuals, leading to different productivity and mortality patterns compared to the baseline scenario. In contrast, in LPJmL the average individuals adjust to the changing conditions and become similar to the baseline scenario after a full recovery.

4.1.4. Recovery after drought

While recovery from drought in GRASSMIND was fast, it took up to two years in LPJmL. Drought recovery depends on a number of factors and evidence from observational studies exists, supporting the fast recovery (e.g Hofer et al., 2016) as well as the slow recovery (e.g. Sala et al., 2012). However, the different model responses to similar conditions suggest drought recovery is not well captured by the models and additional research is needed. For this, we provide some insight on the mechanisms implemented in both models: In GRASSMIND, the fast recovery is possible, firstly because water stress is only dependent on supply. As soon as the soil water supply is replenished, while the demand is still lower than before the drought, the water stress penalty is removed which allows optimal growth of newly established seedlings. Secondly, plants in GRASSMIND do not change or adapt specific traits in response to drought events, like the allocation of NPP to above- or below-ground biomass or the water-use efficiency. In LPJmL, recovery takes longer because of two reasons. First, the loss of vegetation during drought reduces the water demand and limits productivity even after soil water is replenished. Second, water stress triggers an increased resource allocation to the roots, i.e. below-ground biomass (BGB), which is not reversed instantaneously when carbon assimilation or vegetation carbon is low. The additional allocation to BGB during and shortly after the drought results in a lower AGB implying also reductions of FPC. As FPC is used as an estimate of the covered part of the plot and therefore controls the access to resources, the calculation of plant-available water is reduced to the covered share of the plot.

4.2. Species interaction and community assembly

We identified competition for space as the main driver of species interactions in both models (see 4.1). Despite the differences in AGB, the competition for space shows a weak seasonality in both models. In LPJmL, this depends on the LAI, which shows a weak seasonality and therefore, the competition for space is similar within and outside the growing season. In GRASSMIND, the AGB and LAI seasonality are more pronounced but both have no effect on the competition for space, which is determined from the *cover*. This is high within and outside the growing season and so is competition for space. Coexistence between species without one species being strongly dominant occurred in GRASSMIND and LPJmL only in rare cases of mixtures, when species showed similar competitiveness. Stable coexistence has to be achieved to assess the effects of plant species richness, because it is a precondition for long-term maintenance of diversity (Turnbull et al., 2013). To achieve this, fitness as well as niche differences have to be simulated appropriately (Chesson, 2000) and process representations need to be improved. For GRASSMIND, additional insights on community dynamics could be gained through the extraction of density dependence functions of the different species mixtures (Han et al., 2019). However, for LPJmL the density dependence functions would always be constant because only one average individual is simulated to represent an entire species. Therefore, we did not pursue this further but instead focused on identifying key processes by assessing the role of specific parameters (4.2.1) and responses to changes in environmental or management conditions (4.2.2).

4.2.1. The role of specific model parameters

In both models, the species that grow fast (higher SLA) and intercept light more efficiently (higher k_{beer}) are more competitive. These two parameters have a strong influence on simulation results which is in line with findings from sensitivity analyses (see SI A and Forkel et al., 2019; Zaehle et al., 2005; Taubert et al., 2020b; Hetzer et al., 2021; Schmid et al., 2021). Even though the different shoot:root ratios between species lead to different overall root carbon, competition for below-ground resources does not play a major role.

However, in LPJmL only the assumed species-specific vertical distribution of roots and in GRASSMIND the maximum rooting depth, are considered for water uptake, neglecting the horizontal branching of root networks. In LPJmL, the vertical root distributions are similar for the simulated species, as is the maximum rooting depth in GRASSMIND, except for *P. lanceolata* which had access to deeper soil layers than the other species. Nevertheless, competition for space outweighed that for below-ground resources.

4.2.2. The effect of drought and mowing on competition

A moderate or extreme drought leads to major reductions in biomass but does not or only barely change the interaction between the species. In neither model, root biomass is considered for the calculation of water supply. Instead LPJmL determines the access to soil layers based on the vertical root distribution and uses *cover* to distribute available water between species. GRASSMIND determines access depending on rooting depth assuming roots are equally distributed among accessed layers and uses potential GPP to calculate the individual plants' water demand which is reduced by a multiplicative factor under water stress to determine uptake. This underpins that competition is driven by above-ground processes and emphasizes the necessity to focus future model development on below-ground plant organs and processes. This may be a challenging task since knowledge on root traits, below-ground processes and driving forces are distinctively harder to obtain from field experiments and observations (Polomski and Kuhn, 2002; Delory et al., 2017). Recent efforts to build a global database for root traits (Guerrero-Ramírez et al., 2021) may help to better inform parametrization of root distributions and access to soil resources. Comparing the scenarios with and without mowing revealed not only substantial differences in the effect of mowing on AGB but controversially showed that mowing affects competition for space differently for both models. In LPJmL, mowing increases the competition for space. This is best illustrated using the mixture of *P. lanceolata* and *F. pratensis*. Here, stable coexistence of two species emerges in the scenarios without mowing, but *F. pratensis* dominates in the mown scenarios. In LPJmL, these two species have similar competitive strength (see 3.2.1). Following this, we hypothesize that mowing increases competitive pressure in LPJmL and the stronger competitor is dominant even at small differences between two species. Mowing in LPJmL reduces the AGB to a species specific residual. However, this residual is scaled with the species FPC to constrain the total residual biomass of the community. When the species have similar AGB, they constitute a similar FPC and the species with the higher species specific residual (ρ_{veg}) has an advantage in the scenario with mowing but not in the scenario without mowing. If the competitive strength of the two species differs, the dominant species with the higher FPC always has an advantage. In GRASSMIND on the other hand, competition for space is stronger in the scenarios without mowing, because mowing shifts the individuals' height to width relationship, which leads to increased investments into height growth after a mowing event and a reduced investment into area growth and competition for space between conspecifics and heterospecifics. Without mowing, the individuals can continuously invest more of their productivity into expansion leading to an increased competition for space and overcrowding mortality. While we did not observe any changes in community composition in our simulations, these can occur if the species have different geometrical properties. For example, a species producing smaller and wider individuals would outcompete a species producing tall and thin individuals in the scenario with mowing and vice versa in the scenario without mowing.

4.3. Limitations

Our model comparison focused on differences and similarities of two grassland models. To compare the models, we developed a calibration setup using only observation data from monocultures. The rare emergence of coexistence between two species in GRASSMIND simulations results from this constraint to monoculture observations included in the calibration and the fixed non-adaptive behaviour of plant traits. Results from a recent study with GRASSMIND (Taubert et al., 2020b) showed coexistence of *P. pratensis* and *P. lanceolata* similar to observations, calibrating on observational data of monocultures and mixed patches. In contrast, we only used monoculture data for calibration. As plant traits in GRASSMIND are fixed and do not change in response to species interactions, the calibration of this study captures predominantly intra-specific plant interactions rather than inter-specific interactions. Further, we here prescribed similar seed recruitment rates

for the analyzed monocultures and mixtures which already changes the competitive strength of some species (in contrast to Taubert et al., 2020b). The better reproduction of coexistence of species in Taubert et al. (2020b) in comparison to our setup suggests that calibration should be done against data that include inter-species interactions, which may otherwise be lost in the simulations. The more balanced species composition in GRASSMIND may emerge because the individual based approach and the explicit simulations of plant geometry generally allows a broader representation of different ecological strategies. Competition for space between conspecifics and heterospecifics is simulated depending on the geometry, while competition for other resources is more dependent on functional traits. In LPJmL, plant geometry is not simulated and the FPC is extensively used, not only in the competition for space, but also for other resources such as light and water. This contains the assumption that an investment in increased AGB (leading to an increased FPC) will improve both above- and below-ground resource exploitation similarly, while investments in BGB do not yield any advantage. This assumption may be valid for productive habitats, where only radiation but not below-ground resources are limiting and increased investment in BGB has no advantages. In these habitats, species following a competitive strategy with a fast exploitation of available resources are dominant. In other habitats (e.g. where below-ground resources are limited) a mix of species following different ecological strategies may emerge. However, controlling the resource exploitation for multiple resources using the same traits, precludes the trade-offs between different strategies and leads to the dominance of competitive species in all habitats. Here, different resource exploitation strategies and the trade-off between resource exploitation and stress tolerance have to be considered. The data available from observations additionally limited the calibration setup (see 3.1). Only two observations per year, both within the growing season, were available and therefore the seasonality can not be inferred from the data. Data for all monocultures show a strong decrease in soil fertility and AGB a few years after the start of the experiment (Weisser et al., 2017). This decrease cannot be captured by the models, which only capture the low values well.

Additional limitations were introduced by our scenarios. First, the simulated drought does not consider changes in radiation, humidity, wind speed and temperature which covary (Wilhite, 2000; Mishra and Singh, 2010) and is therefore comparable to a rainfall exclusion experiment (Reynolds et al., 1999; Yahdjian and Sala, 2002) instead of a real world drought. Second, mowing was conducted at a height of 10 cm at the Jena Experiment. However, while in GRASSMIND the height is explicitly simulated and, therefore, the mowing height can be defined as an input, in LPJmL this is not possible, and the residual biomass after mowing is used as a proxy for mowing height. Since no data on residual biomass was available from the Jena Experiment, we cannot evaluate whether the mowing simulated in the models is a realistic approximation of the mowing conducted at the Jena Experiment.

Both models did not reproduce the variability of the observed soil water content (see Fig. 5a and Fig. S2.1), which for LPJmL is in line with a recent study on nitrogen emissions (Lutz et al., 2020). However, the importance of these discrepancies for the observed responses of AGB and community composition remains unclear and we see the need for an in-depth study of soil water dynamics, especially considering that other recent studies suggest that the drought response is not well captured in terrestrial biosphere models (Bastos et al., 2020; Paschalis et al., 2020).

4.4. Fields of model development

Our comparison highlighted fields to consider for future model development. While the inclusion of other models of grassland dynamics was beyond the scope of our analysis, GRASSMIND and LPJmL are representative of specific types of models (see 1.3) for which comparable model representatives may show similar or additional challenges but also potential solutions when applied to the same research questions and settings as pointed out here. The core of numerous models is the productivity in the form of photosynthesis. The simplified Farquhar photosynthesis model (e.g. in LPJmL, Farquhar and von Caemmerer, 1982) has a great depth of biochemical detail, while the single-leaf photosynthesis model (e.g. in GRASSMIND, Thornley and Johnson, 1990) uses a more aggregated calculation integrated over the individuals projected area (Taubert et al., 2012). An even simpler approach just uses light-use efficiency (e.g. LINGRA, Schapendonk et al., 1998). In all of these approaches, water stress is considered by a reduction of productivity at optimal water supply by either a reduction factor (GRASSMIND, LINGRA) or an adjustment of the maximum

carboxylation rate V_{max} (LPJmL). Our study shows that both options simulate a response to drought, however this is mediated by the interaction with the representation of soil water dynamics, which can strongly impact onset, duration and recovery time of the drought response. Additionally, the current representation of photosynthesis is aggravating realistic simulations of rainfall exclusion experiments or droughts and future model development should include non-stomatal limitation of photosynthesis (e.g. reduced RuBisCo activity, Medrano et al., 1997; Parry et al., 2002) during drought (Zhou et al., 2013).

Furthermore, in both models, transpiration response to water stress is modelled linearly and transpiration reduction is overestimated for soil water levels close to field capacity. Experimental data however suggest a nonlinear relationship (see Verhoef and Egea, 2014, for a collection of experiments). A variety of nonlinear approaches exist, however since we did not test their suitability for the different model types, we do not give a recommendation but refer to Dewar (2002); Egea et al. (2011) and Verhoef and Egea (2014) for further reading.

Competition was focused on space and light, while below-ground processes played a minor role. So far, only the distribution but not the amount of BGB is used for resource competition and trade-offs between higher investments in AGB or BGB cannot be represented. This may be attributed to the original development for a temperate climate. However, this missing strategy trade-off is one reason why the simulated drought had little impact on competition dynamics. Additionally, drought response could be improved by systematically testing and incorporating drought escape (Kooyers, 2015; Norton et al., 2016) and tolerance (Zwicke et al., 2015; Ratzmann et al., 2019a,b) strategies in the existing model structures or implement hydraulic failure of severely stressed vegetation (see e.g. Kennedy et al., 2019; Sperry et al., 2016). The Hurley pasture model (Thornley, 1997, 1998) follows a resistance approach considering root mass, root density and the resistance in the bulk soil (Thornley, 1996; Thornley and Verberne, 1989) that could be feasible for models using a light-response function and can likely be adapted for a Farquhar approach. Drought response is not only dependent on the soil hydrology models used but also depends on the models capacity to simulate specific strategies for (i) water use efficiency, (ii) carbon allocation, (iii) root distribution and (iv) regeneration of different species after drought (van der Molen et al., 2011). While numerous approaches to improve soil hydrology exist (Vereecken et al., 2019, 2016; Deckmyn et al., 2020), the simulation of coexistence of multiple species and their specific strategies remains challenging (see 4.2). To further improve the models and enable the simulation of stable coexistence and therefore plant species richness, plant interaction models, which were explicitly designed to assess biodiversity effects may serve as additional inspiration for model development. A key limitation was the simulation of niche differences, which are a necessary condition for stable coexistence. In addition to the process improvements suggested above, adding a hierarchy that determined resource access for each species and resources was shown to be a feasible approach (Clark et al., 2018). To separate above and below-ground niches, the below-ground space has to be distributed between species or individuals in addition to the above-ground space. In GRASSMIND, a refinement of the below-ground geometry (non-uniform vertical root distribution per plant) and hierarchically modelled resource access could be beneficial. For LPJmL, the root biomass within each soil layer and a species specific lateral distribution could be combined to distribute below-ground resources.

5. Conclusion

Recently, empiricists as well as modellers have suggested biogeochemical models as a potential tool to complement empirical research to increase the knowledge on interacting responses of biotic and abiotic components of grasslands to changing environmental conditions and the underlying mechanisms (Wilcox et al., 2020; Van Oijen et al., 2020). Currently, approaches that prescribe the species' share within the community based on environmental factors, phenology and management exist (Confalonieri, 2014; Movedi et al., 2019). However, these do not consider the underlying mechanisms explicitly. To enable process-based models to simulate differently diverse communities and quantitatively assess the effect of plant species richness, substantial model development is needed. We compared two grassland models that have been developed at different scales, under different assumptions and for different purposes but which are representative of several other models. Despite the differences, the models showed similar weaknesses. Already at low diversity

levels (monocultures and two-species mixtures), the models had difficulties to simulate a balanced community. In the majority of our scenarios, one species contributed almost the entire biomass of the mixture. While this can partially be attributed to the study design, a considerable part is related to the process representations in the models. Substantial improvement of these processes is needed to enable models to also simulate communities that are only weakly dominated by one species. We identified several responsible processes and suggested potential solutions based on our findings and available literature. Additionally, we found that the outcome of competition in the models was determined by the same processes independent of resource availability (Drought did barely affect species presence), which shows that the representation of trade-offs between different ecological strategies also needs improvement. As LPJmL and GRASSMIND can be seen as typical representations for particular types of models, this reveals potential pathways of model development to improve the interaction between species and drought response for similar models. For other model types, our study may serve as an example for a structured assessment of implemented processes, that can be used to identify and address the key parts of the model hindering a more realistic representation of multi-species communities or species interaction in a structured way. In cases where empirical data is needed to improve the models, knowing the specific processes that should be developed further is useful to inform field researchers.

Data accessibility statement

The model output data used for this study are openly available at `https://doi.org/10.5281/zenodo.4720262`.

CRediT authorship contribution statement

Stephen B. Wirth: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Visualization **Fraziska Taubert:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Review & Editing, Visualization **Britta Tietjen:** Conceptualization, Methodology, Writing - Review & Editing **Christoph Müller:** Writing - Review & Editing, Resources, Supervision **Susanne Rolinski:** Conceptualization, Methodology, Writing - Review & Editing, Supervision

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