

Using plant diversity to reduce vulnerability and increase drought resilience of permanent and sown productive grasslands

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Abstract

Climate change associated with a greater variability of inter- and intra-annual droughts and the occurrence of extreme events act in combination to challenge semi-natural and sown productive grasslands in Europe. Successful plant strategies under drought strongly depend on stress intensity. Drought resistance to maintain leaf growth under moderate stress trades off with drought survival after growth cessation under life-threatening drought. Substantial intra-specific variability exists in key forage grasses originating from the Mediterranean to the cool-temperate climates and represents a great potential for adaptation of future ecotypes and cultivars to a larger range of drought intensities. Plant species diversity offers an opportunity to stabilize forage production in two ways. First, growth reduction under stress is significantly smaller for diverse compared to simple plant communities because the former offers the opportunity to include drought-resistant (or drought-surviving) species. Second, positive interactions among species increase ecosystem functioning of more diverse plant communities under moderate drought, allowing them to compensate for drought-induced yield reductions. Currently, available cultivars of perennial forage species adapted to dry climate are still rare and only a few forage species are used in productive systems. Thus, both intra- and inter-specific plant diversity should be better valued to reduce vulnerability and increase resilience of productive grasslands.

KEYWORDS

complementarity, drought stress severity, ecosystem functioning, insurance effect, resistance, survival

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1 | THE WIDE ENVIRONMENTAL RANGE OF GLOBAL GRASSLAND DISTRIBUTION DEMONSTRATES ITS HUGE ADAPTATION POTENTIAL

Grasslands cover about 40% of the world's land area (White et al., 2000) and are among the most important agroecosystems delivering services ranging from forage supply for ruminants and soil carbon storage to habitats of high biodiversity. Reflected by the pedo-climatic conditions, these grasslands include a large variety of ecosystems such as steppe vegetation, savannah, tundra, alpine grassland and temperate grasslands (Reich et al., 1997; Whittaker, 1975). Moreover, large areas of land across temperate regions that would otherwise be covered by shrubs and trees are maintained as grassland by regular cutting and/or grazing. In short, grasslands can thrive across a vast range of pedo-climatic conditions and extremes, where shrubs and trees cannot grow and/or other agricultural systems are not economically profitable. This strongly suggests that grasslands benefit from plant strategies and ecological processes that ensure that they can grow, survive, resist, recover from, and/or adapt to strongly differing mean environmental conditions and to a multitude of extremes of environmental conditions experienced at different locations. With global climate change, both the mean and variation in climatic conditions are predicted to change (Orlowsky & Seneviratne, 2012), which will give rise to a change in biotic (e.g., weeds, disease, pests) and abiotic stresses (e.g., timing of the seasons, increased incidence of severe weather events, such as summer drought, heatwave, waterlogging).

1.1 | Objectives

Although climate change will also affect natural and semi-natural (managed at low intensity, less productive, often species-rich) grasslands, we focus here on the effects of drought stress on productive grasslands that are highly modified and generally fertilized to maximize the production of aboveground forage yield and quality (nutritive value). Studies of semi-natural grasslands are referenced to underpin ecological theory and to highlight some specificities of the productive grasslands. The productive grasslands are sown with a low diversity (or even monoculture) of selected species (and cultivars) or are permanent grasslands with a relatively low plant diversity, both offering adaptation through changes in (i) species and (ii) genotype composition as well as (iii) their diversity. We focused on the whole range of drought stress, from severe and predictable under Mediterranean climates to moderate and less predictable in temperate to cool climates, suggesting that a range of adaptive strategies are required.

2 | A DIVERSITY OF PLANT STRATEGIES TO FACE DROUGHT

Better understanding of the adaptive strategies of forage plants to face drought is crucial to efficiently manage grasslands and breed

cultivars that enhance the resilience of grasslands, that is, a sufficient post-stress recovery to achieve a comparable post- vs. pre-drought productivity. The two major plant response strategies under moderate and severe water deficit are 'drought resistance', that is, the maintenance of leaf growth and biomass production, and 'drought survival', that is, the plant ability to survive after growth cessation due to severe life-threatening drought (Volaire, 2018). Drought resistance is more relevant under moderate drought stress while drought survival is key under severe drought stress (Figure 1), but they can both enhance post-drought recovery and therefore resilience of plant communities.

Regarding plant strategies (Figure 1), 'dehydration escape' allows plants to shorten and complete the reproductive cycle before the onset of drought, e.g., annuals overcome drought as desiccation-tolerant seeds. For plants subjected to water deficit, drought resistance is associated mainly with a 'dehydration avoidance' strategy that maximizes water uptake and/or minimizes water loss to maintain high leaf water content and turgor ensuring growth maintenance. In contrast, drought survival is associated with a 'dehydration tolerance' strategy, allowing plants to tolerate moderate tissue dehydration in leaves and meristems. In some cases, dehydration tolerance rests on 'summer dormancy', which is an endogenous controlled strategy that reduces or stops meristem activity to render it relatively insensitive to growth-promoting signals (Volaire & Norton, 2006). Finally, the 'embolism resistance' strategy prevents xylem conduits from becoming air-filled or embolized under negative pressure (hydraulic failure) and hence underpins plant survival as drought drastically intensifies.

2.1 | To grow or to survive: A drought resistance vs. drought survival trade-off

Most strategies can be combined to some extent, depending on species and populations. Growth maintenance (dehydration avoidance) is associated with fast water use under moderate drought ('water spender' strategy), while plant survival after growth cessation (dehydration and embolism tolerance, dormancy) is associated with slow water use under severe drought ('water saver' strategy) (Figure 2). To 'stay green' and keep growing in dry conditions may contribute to depleting soil water and thus make plants extremely vulnerable to an extended and extreme drought (Zhao et al., 2017). Consequently, dehydration avoidance is a strategy that does not enable plant survival under severe drought (Yates et al., 2019). 'Knowing when not to grow' or 'when to senesce' enhances survival in the face of potentially lethal conditions. This is the case for summer dormancy, which confers to genotypes of some grass species the endogenous ability to cease or reduce aerial growth and senesce irrespective of the water supply in summer (Gillespie & Volaire, 2017). Summer dormancy confers superior survival after severe and repeated summer droughts (Norton, Lelievre, & Volaire, 2006; Norton, Volaire, & Lelievre, 2006), revealing that the endogenous and programmed ability to stop growth (or strongly reduce growth) during the drought period is the most efficient response to maximize plant drought survival.

FIGURE 1 Plant strategies to face increasing water deficit. Dehydration avoidance enhances drought resistance (maintenance of growth at moderate drought), while dehydration tolerance, dormancy and embolism resistance enhance drought survival (Volaire, 2018).

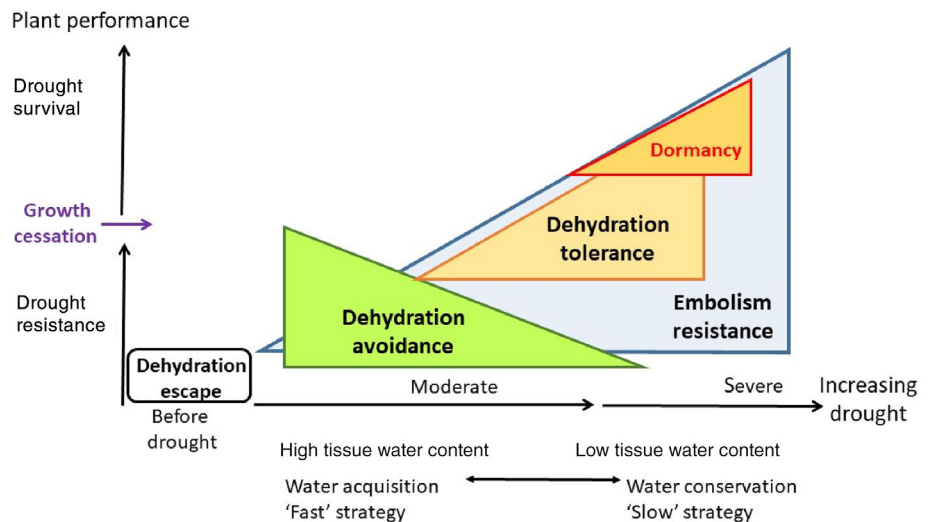
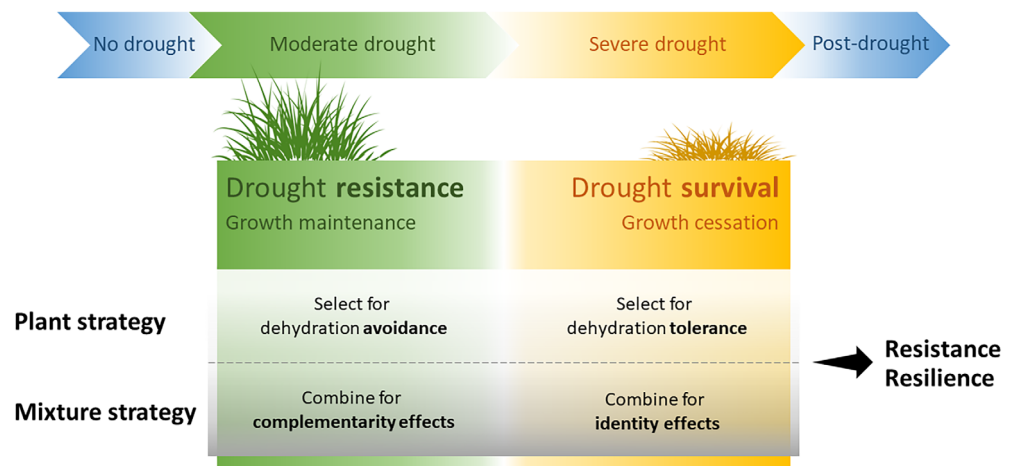


FIGURE 2 Diverse strategies and plant diversities to increase grassland resistance and resilience.



Decoupling plant responses, that is, growth under favourable summers/winters and plant survival under harsh summers/winters (Keep et al., 2021), showed a general trade-off between seasonal growth potential and seasonal dehydration survival in 385 European populations of perennial ryegrass (*Lolium perenne* L.). Three groups of ryegrass populations were identified according to their origin and contrasting strategies to face seasonal stresses, revealing a trade-off between dehydration avoidance and dehydration tolerance strategies. Populations from northern sites, where low-to-moderate summer drought occurs, mostly had a dehydration avoidance strategy and could maintain growth during summer without being threatened by drought. In contrast, populations from the southern sites, where intense summer drought occurs, had a dehydration-tolerant or a dehydration-escape strategy and survived prolonged drought by reducing their growth potential. Endogenous reduced seasonal growth potentials are phenological adaptations that can be regarded as dormancy levels. They were also identified within European populations of cocksfoot, *Dactylis glomerata* L. (Bristiel et al., 2017), raising a possible generalized adaptive seasonal pattern within herbaceous species. Thus, the balance between productivity and stress survival strongly

depends on the climatic region and is becoming a central issue in plant breeding for drought (and frost) survival (Ergon et al., 2018; Volaire et al., 2014) and therefore grassland resistance and resilience (Figure 2).

3 | PLANT SPECIES DIVERSITY OFFERS OPPORTUNITIES TO STABILIZE FORAGE PRODUCTION UNDER DROUGHT STRESS

3.1 | Lessons from semi-natural grassland experiments illustrate the stabilizing effect of diversity

The role of diversity in promoting resistance and resilience of ecosystem function in the face of environmental disturbance is well-established in ecosystems and experiments based in semi-natural grasslands (e.g., Craven et al., 2016). For example, a meta-analysis of 46 plant association experiments by Isbell et al. (2015) revealed that biomass of 'low-diversity communities with one or two grassland plant species changed by approximately 50% during (severe)

weather events, whereas that of high-diversity communities with 16–32 species changed by only approximately 25%. Which ecological processes underlie such benefits of diversity? The ‘insurance effect’ refers to multiple biological processes that result in a stabilizing effect of biodiversity on ecosystem function when subjected to environmental disturbance. The insurance effect includes: (i) the ‘portfolio effect’ which arises from independent (or sufficiently decoupled) fluctuations in species’ abundances over time; (ii) beneficial effects of biodiversity on both the mean and the variability of ecosystem properties, and; (iii) spatial variability between patches or locations in heterogeneous landscapes (adapted from Loreau et al., 2021). A key question is: Do insurance effects occur in productive grasslands?

3.2 | Species diversity in productive grasslands enhanced ecosystem function under drought

In productive temperate grasslands, where resistance to moderate drought stress is primarily targeted, there are few manipulations of environmental levels to test the role of diversity in maintaining ecosystem function under stress. Under experimentally-imposed drought, species diversity enhanced yield stability (Grange et al., 2022; Haughey et al., 2018), reflecting the insurance effects of diversity through reduced temporal variance or mean-to-variance ratio. There is some evidence that the stabilizing effect in more diverse communities was caused by asynchrony of species’ growth (Haughey et al., 2018). Enhanced yield stability of mixtures compared to monocultures was also found in the AgroDiversity experiment among 16 sites with different climates (Schaub et al., 2020). In the meta-analysis by Isbell et al. (2015), 24 of the 46 experiments contained monocultures and mixtures of two grasses and two legumes, so their conclusion that diversity confers higher resistance and stability in biomass productivity is also relevant to simple mixtures in productive grassland communities.

Under drought, more diverse forage mixtures were associated with higher (or at least equal) yield than less diverse mixtures or monocultures (overyielding; Skinner et al., 2004; Hofer et al., 2016; Komainda et al., 2020), reflecting that positive complementarity effects on biomass production also occur under drought (see Barry et al., 2018 for the meaning of ‘complementarity’). Some studies have even shown that these positive effects were so strong that drought-stressed mixtures at least attained the yield of the average of the rainfed monocultures (Finn et al., 2018; Grange et al., 2021; Hofer et al., 2016). Thus, growing mixtures instead of monocultures can mitigate negative effects of (moderate) drought. The use of drought-resistant forage species in such mixtures helps to partly overcome the limitations in nutrient uptake arising as a consequence of soil water limitation. Resistance to moderate drought has been shown to occur by sustained symbiotic N₂ fixation in legumes (Hofer et al., 2017) or by increased resource uptake from deeper soil layers (Hoekstra et al., 2015). Importantly, both beneficial species interactions and species’ asynchrony are not mutually exclusive and can act

simultaneously to increase yield and yield stability in more diverse communities (Haughey et al., 2018), including under conditions of environmental disturbance.

Improved drought-resistance by mixing species can also occur through the ‘portfolio effect’. If mixtures contain at least one species that contributes substantially to community yield and that can cope with stress-induced reductions in growth (decoupled from other species performances), the overall community performance under drought is improved. This may be an important yield stabilizing process in mixtures of legumes, which were found to be drought resistant and grasses, which showed a strong recovery after drought stopped (Hahn et al., 2021; Haughey et al., 2018; Hofer et al., 2016). Interestingly, the portfolio effect can arise solely through (statistical) averaging of species performances over time (Loreau et al., 2021). This has been little studied in productive grasslands. One line of evidence for the occurrence of averaging would be switching in the rank order of monoculture yields over time (and/or space), and especially switching in the identity of the best-performing monoculture. Such switching effects have been demonstrated to be important in the AgroDiversity experiment, which was conducted across 31 different international locations and broad climatic gradients (Finn et al., 2013). That study found a 0.52 probability of a switch in the identity of the best-performing species in monoculture in successive years (Table S8 in Finn et al., 2013), and the authors concluded: ‘Switching in the year-to-year rank order of species’ performance in monoculture is highly relevant to the stability of agronomic yield and to risk aversion strategies associated with the choice of monoculture species’. Despite the processes leading to such switching can remain unknown—such as climate conditions favouring a distinct species in one year but not in another—the portfolio effect through averaging still occurs. Importantly, given that many agronomic studies compare mixture performance against the best-performing monoculture (which is selected in retrospect), and if switching continues over multiple years (and sites), then the relative benefit of mixtures would be expected to increase in comparison to the highest-yielding monoculture over that time period (and spatial scale). In such retrospective comparisons, the selection of the ‘best-performing’ monoculture enjoys the benefit of hindsight; however, past performance is not always a good predictor of future performance, and even less so when the future has more variable conditions.

Finally, the positive effects of species diversity on productivity and stability are context-dependent and may weaken under severe drought stress. For instance, complementarity effects (Barry et al., 2018) that enable species-rich mixtures to achieve higher yields than monocultures during a moderate drought were not detected for the recovery and resilience of grass communities subjected to a severe drought (Barkaoui et al., 2016). Low levels of soil water can make resource-partitioning among species inefficient. Most expectations are based on vertical segregation of root systems (Oram et al., 2018), assuming that deep soil horizons represent an ‘unused’ pool of resources by shallow-rooted species, giving an opportunity to use additional water with deep-rooting species. However, deep soil horizons may completely dry out under severe drought, making

surface horizons the only ones with possible water recharge by episodic rainfall, therefore selecting shallow-rooted species only and limiting the complementarity effects. Similarly, facilitation, another facet of complementarity (Wright et al., 2017), usually expected to positively affect productivity with increasingly severe environmental conditions (He et al., 2013), may collapse among herbaceous species in areas prone to severe drought (Michalet & Pugnaire, 2016). Nevertheless, the portfolio effect should support the recovery capacity and resilience of species-rich mixtures subjected to severe drought (Kreyling et al., 2017). Thus, under severe stress combining species with distinct identities for high dehydration tolerance seems promising, while under moderate stress combining species for complementarity effects should be the preferred strategy (Figure 2).

4 | SATURATION OF DIVERSITY EFFECTS IN SEMI-NATURAL GRASSLAND EXPERIMENTS

The evidence given above suggests that species diversity is key to increase drought resistance and resilience of permanent and sown productive grasslands. In the following sections, we evaluate more closely the diversity-ecosystem function relationship. We discuss specific strategies to maximize the 'performance-enhancing effect' of diversity and the degree of diversity needed for adaptation of mixtures to drought stress.

Across a range of studies in semi-natural experimental grasslands, the yield benefits of adding species saturate at a relatively low number (Tilman et al., 1997; Tilman et al., 2014). Both theory (Tilman et al., 1997) and empirical research (Hector et al., 1999; Isbell et al., 2017) have demonstrated a declining rate of increase in the overall diversity effect with increasing species richness. For example, in the BIODEPTH experiment (Hector et al., 1999), the average biomass increase from doubling the number of species was approximately 80 g m^{-2} . This means that adding one species to a monoculture increased yields by ca. 23%, yet, adding one species to a four-species mixture increased yields by only 5%, and adding a further species to an eight-species mixture improved yields by 2%. The same principle in the performance-diversity relationship was also found in two of the largest and longest-running biodiversity experiments, which are at Jena (Scherber et al., 2010; Weisser et al., 2017) and Cedar Creek (Tilman et al., 2001), and for ecosystem functions such as yield stability, weed suppression, and nutrient retention (Isbell et al., 2017; Tilman et al., 2014). A first reason to explain saturation of overall performance is the 'selection effect'. In the case of a random selection of species for the assembly of experimental communities, mixtures with a higher number of species have a higher likelihood of containing the most productive species, which shifts the performance towards the potential maximum (assuming that the most productive species becomes dominant in that community). A second reason for saturation comes from niche theory (Tilman et al., 1997; Tilman et al., 2014). Although more diverse communities have a higher chance for niche complementarity among particular species, the

amount of unused resources gets increasingly smaller. Thus, the potential benefit of species interactions becomes smaller with increasing species richness. Moreover, species interactions can also be neutral or negative (e.g., Hofer et al., 2016; Husse et al., 2017), and the probability for the latter to occur might also increase with increasing species richness.

5 | IN PRODUCTIVE GRASSLAND MIXTURES, DIVERSITY EFFECTS SATURATE EVEN FASTER

5.1 | Productive grasslands can show strong responses to diversity

Given the considerable differences between them, it is not necessarily the case that principles from semi-natural grasslands translate to productive grasslands. Over the past 20 years, however, research on forage mixtures in productive grasslands has provided strong evidence that legume-based mixtures with up to five species improve grassland performance (or compare well) relative to the respective monocultures. This has been observed in several responses, including yield, weed suppression, nitrogen yield, yield stability, forage quality, nitrous oxide emission intensity and overall multifunctionality (Cong et al., 2018; Connolly et al., 2018; Cummins et al., 2021; Finn et al., 2013; Gierus et al., 2012; Küchenmeister et al., 2012; Lüscher et al., 2014; Suter et al., 2015, 2017; Suter, Huguenin-Elie, & Lüscher, 2021). This performance-enhancing effect of diversity is one of the key insurance effects to generate a stabilizing effect of diversity on ecosystem function in a fluctuating environment such as severe drought events (Haughey et al., 2018; Hofer et al., 2016). Most of the recent research on mixture benefits uses a modest number of species and less is known regarding mixture gains from more species-rich mixtures with >10 species (but see Sanderson et al., 2004; Tracy & Sanderson, 2004a; Jing et al., 2017).

5.2 | In productive grassland mixtures the diversity response to yield saturates even faster than in low productive grasslands

In the applied context of production-oriented systems, the saturation of yield is expected to occur even faster than in experiments with semi-natural grassland communities, where the species assemblies are composed randomly. This is because forage mixtures can be designed according to the following principles: (i) selecting the best-performing species—generally evaluated in monoculture—for use in mixtures, which ensures high performance at a lower number of species; (ii) targeting species that maximize complementarity for desired functions, which enhances performance without the need for many species; (iii) selecting species that maintain a stable community composition over time or that respond to adaptive management to ensure this (Lüscher et al., 2011). Indeed, saturation has been

repeatedly demonstrated for forage mixtures (including herbs). Yield was only marginally increased in mixtures with nine species compared to two species (Grace et al., 2018), eight species compared to three (Lorenz et al., 2020), nine species compared to three (Sanderson, 2010), five species compared to four (Moloney et al., 2020a), six species compared to four (Grange et al., 2021), and 15 species compared to six (Tracy & Sanderson, 2004a). In line with the trend for rapid saturation, the average beneficial interaction effect in a six-species mixture containing herbs was only marginally greater than that of a four-species grass-legume mixture (Grange et al., 2021). Contradictory results also show increases in yield from two species in a mixture to five species (Skinner et al., 2004; Skinner & Dell, 2016), and from 10 species to 12 (due to high-yielding lucerne in the 12-species mixture, Jing et al., 2017).

Importantly, all of these studies focused on yield alone, and, all else being equal, more species diversity is likely to be needed to simultaneously sustain multiple ecosystem functions (i) other than yield, (ii) over longer time scales and (iii) over more variable environmental conditions (Grange et al., 2022; Isbell et al., 2011, 2015, 2017; Lefcheck et al., 2015; Skinner & Dell, 2016; Suter, Huguenin-Elie, & Lüscher, 2021). Although forage yields often do not, or only marginally, differ between high-yielding grass-clover swards and more complex mixtures, intra-annual yield stability (Lorenz et al., 2020), weed suppression (Tracy & Sanderson, 2004b), and resource availability to pollinators (Cong et al., 2020) can be enhanced by higher diversity. Analyses of forage quality from more complex mixtures indicate that although it can be reduced compared to grass-legume stands (Jing et al., 2017), there are multiple examples where complex mixtures have similar or higher forage quality regarding, among others, crude protein and digestibility (Grace et al., 2018; Moloney et al., 2020b; Sanderson, 2010). On grazed multi-species swards, dry-matter intake, milk production and soil C accumulation were enhanced and N losses reduced compared to more simple swards (reviewed in Jaramillo et al., 2021).

Compared to the scale of the challenge posed by climate change and the demand for more environmentally sustainable farming practice, the science underpinning the potential benefits of multi-species swards should become a stronger focus of future research. There is still plenty to learn about the extent to which mixture benefits are affected by specific combinations of species rather than species richness, management practices (especially grazing), cultivar diversity, as well as variation in environmental conditions such as soil type, fertility and moisture level. Cultivar selection and adaptive management to promote persistence in mixtures also deserve further attention. It is still not well established whether more, and how many, species in production-oriented grasslands are needed to simultaneously sustain multiple ecosystem functions, such as resistance and resilience to extreme weather events, soil C sequestration or conservation of faunal diversity. There is an indication that trade-offs can occur among different functions (Grange et al., 2022), and that a distinct mixture and management can maximize either production or a variety of ecosystem services related to sustainability (Savage et al., 2021).

6 | FOR PRODUCTIVE SPECIES WITH GOOD FORAGE QUALITY, THE RANGE OF TRAITS FOR FUNCTIONAL COMPLEMENTARITY AND DROUGHT ADAPTATION IS QUITE LIMITED

A key to higher mixture performance is the targeted and designed combination of species with functional complementarity in terms of relevant traits with the aim to increase total resource acquisition and resource use efficiency (Frankow-Lindberg, 2012; Gross et al., 2007; Mason et al., 2020; Tilman et al., 2014). In forage grassland, substantial yield gains can be achieved by the distinct combination of grasses that have efficient resource uptake, in particular of N, and legumes with their ability for symbiotic N₂ fixation (Frankow-Lindberg & Dahlin, 2013; Nyfeler et al., 2011; Pirhofer-Walzl et al., 2013). A further way of achieving complementarity has been identified in the different temporal development of species over years (Finn et al., 2013; Nyfeler et al., 2009) and within the growing season (Husse et al., 2016). By segregating the periods during which species acquire resources, the total biomass production of mixtures is enhanced by more complete resource use over time. Finally, combining species with differing rooting depth allows for increased yields through spatial complementarity in resource uptake (Husse et al., 2017), although the evidence for yield gains by vertical niche differentiation is inconsistent (Hoekstra et al., 2015; Mommer et al., 2010; Oram et al., 2018; Pirhofer-Walzl et al., 2013).

Comparing the complementarity benefits of specific combinations of plant functional traits or functional types (the identity of the species present) with those achieved by species richness per se (the number of species present), effects of identity were generally at least as large or clearly larger than those of richness (Komainda et al., 2020; Mokany et al., 2008; Skinner et al., 2004). This has led several authors to conclude that low to intermediate levels of species richness are sufficient to reach an optimal balance of multiple ecosystem services, but that these species should exhibit functional contrasts in growth habit and phenology (Küchenmeister et al., 2012; Lüscher et al., 2011; Storkey et al., 2015; Tracy & Sanderson, 2004a). Establishing distinct combinations of many forage species with complementary traits to optimize mixture performance in terms of both forage yield and quality seems to be challenging, probably due to the increasing complexity in isolating the effect of a single trait in a mixture with an increasing number of species with multiple traits. Even less is known about how species functional complementarity can help to adapt mixtures to environmental stress caused by severe weather events. Functional complementarity should be relevant under moderate environmental stress and in productive environments, where resource partitioning allows species to reduce competitive interactions (Gross et al., 2007). Conversely, under severe environmental disturbance or nutrient-poor environments, the importance of functional complementarity has been shown to decrease (Mason et al., 2011) and facilitative processes among species should become more relevant (He et al., 2013; Maestre et al., 2009). For example, nurse plants can cast shade and lead to lower transpiration demands of neighbouring plants under

heat and drought (Holmgren & Scheffer, 2010). However, the evidence for such effects in grasslands is rare (Martorell et al., 2015), and we are not aware of any study demonstrating facilitation under severe drought for forage plants of productive grasslands.

7 | VALUING AND APPLYING INTER- AND INTRA-SPECIFIC VARIABILITY

7.1 | Valuing intra-specific variability

To assess the relative importance of dehydration avoidance vs. tolerance of each species, plants should be compared by combining tests in shallow soils (expression of dehydration tolerance) and deep soils (drought avoidance through water uptake) under different drought intensities. For instance, the dehydration tolerance of cocksfoot is higher than that of tall fescue (*Festuca arundinacea* Schreb.), which primarily relies on dehydration avoidance through an efficient and deep rooting system (Poirier et al., 2012). However, intra-specific variability was comparable or even higher than inter-specific variability for these two perennial grass species under field conditions. Moreover in both species, the dehydration tolerance was greater for the summer-dormant Mediterranean and semi-arid populations than for the non-dormant temperate populations (Volaire, 2008). The intra-specific variability of cocksfoot (Shihan et al., 2022) and perennial ryegrass (Keep et al., 2021) analysed along environmental gradients allowed mapping of the current and future areas for adaptation of Mediterranean populations under a climate scenario. Areas suitable for the expression of, and adaptation to, summer dormancy are predicted to extend northwards under climate change for cocksfoot and the Mediterranean types of perennial ryegrass (Keep et al., 2021; Shihan et al., 2022). Available cultivars of Mediterranean perennial forage species adapted to a dry climate are rare (<2%) (Lelièvre & Volaire, 2009). It is thus required to better identify and valorize the role of this genetic diversity by (i) tapping into the Mediterranean and semi-arid genetic resources, (ii) testing plant material for summer growth potential (summer dormancy levels) possibly associated to dehydration tolerance, and (iii) measuring thresholds of dehydration tolerance in standardized conditions, that is, soil water potential leading to 50% plant mortality (Norton et al., 2016; Volaire et al., 2014) or embolism resistance (Volaire et al., 2018).

7.2 | Valuing inter-specific variability

To assess how species diversity is used in today's European sown grasslands and to exploit adaptation of forage production in ley-farming systems to drier conditions, a survey was conducted. As an easy-to-derive proxy for plant species' suitability for growth under wet/dry conditions, we chose the Ellenberg indicator value for moisture (*F*: 'Feuchte' in German; Ellenberg & Leuschner, 2010). Values were derived from the TRY database (Kattge et al., 2020), which included indicator values from Central Europe (Ellenberg &

Leuschner, 2010), the UK, and Ireland (Fitter & Peat, 1994; Hill et al., 2004). The median was calculated, where more than one value per species was available. We are aware that, for more quantitative analyses, Ellenberg indicator values would be too coarse a proxy; here, however, we use these values to visualize a specific feature of forage plants. Figure 3 compares the means and ranges of *F* indicator values for distinct sets of plant species. The potential range of *F* indicator values of grassland species available on the commercial market are shown with the two sets of species 'Central Europe wild types' (116 species) and 'EU common catalogue' (33 species). Both of these sets span a range of seven units ranging from an *F* value of two (very dry) to nine (wet, often water-saturated). However, if one compares the species' sets of 'recommended varieties' from six countries (where such lists were available), only a small fraction of the diversity potential is currently utilized in sown, production-oriented grasslands. This is indicated by both the small number of species on the recommended lists (often below 10) and the narrow range of their *F* indicator values (with the exception of CH; Suter, Frick, & Hirschi, 2021). Surprisingly, the same picture is evident with the 'production mixtures' (multi-species mixtures that are recommended for productive grassland). Even though these mixtures were specifically designed to meet distinct growth conditions (wet or dry, but mostly in temperate environments), the means of *F* indicator values for mixtures (i) differ only little (0.40 units at maximum) and (ii) are at about the centre of the total scale (balanced conditions). In addition, (iii) the ranges covered by the mixture's component species are small, covering at most 2 units (4–6). The only exception were the 'biodiversity mixtures' designed for improvement of biodiversity rather than forage production. They contain a high number of species, differ distinctly in the mixtures' mean *F* indicator value (1.40 units between wet and dry), and the species within each mixture cover a large range of *F* indicator values (up to 7 units).

The survey described above strongly suggests that currently only a small part of the inter-specific variability with respect to moisture conditions is utilized in sown grasslands. This may be due to several reasons such as (i) positive diversity effects saturating at low species numbers in the mixture (see above), (ii) trade-offs between growth maintenance under moderate drought and plant survival under severe drought (discussed above), between drought resistance and forage quality (e.g., perennial ryegrass vs. tall fescue), or drought resistance and suitability for specific management aims such as grazing (e.g., white clover (*Trifolium repens* L.) vs. lucerne (*Medicago sativa* L.)). An important, more general reason for the relatively small and highly specific set of plant species utilized in intensive forage production is that plant species have to be adapted to (very) high frequencies of defoliation (mowing or grazing), which is a prerequisite for high forage quality and high yields in digestible energy and protein (Huguenin-Elie et al., 2018). Thus, we deem that only species with specific plant traits at the fast end of the 'fast-slow' plant economics spectrum (Reich et al., 1997) seem suitable for production-oriented grasslands in temperate climates. This survey strongly suggests that the shortage of adapted plant material for areas with increasing severe droughts is still insufficiently addressed.

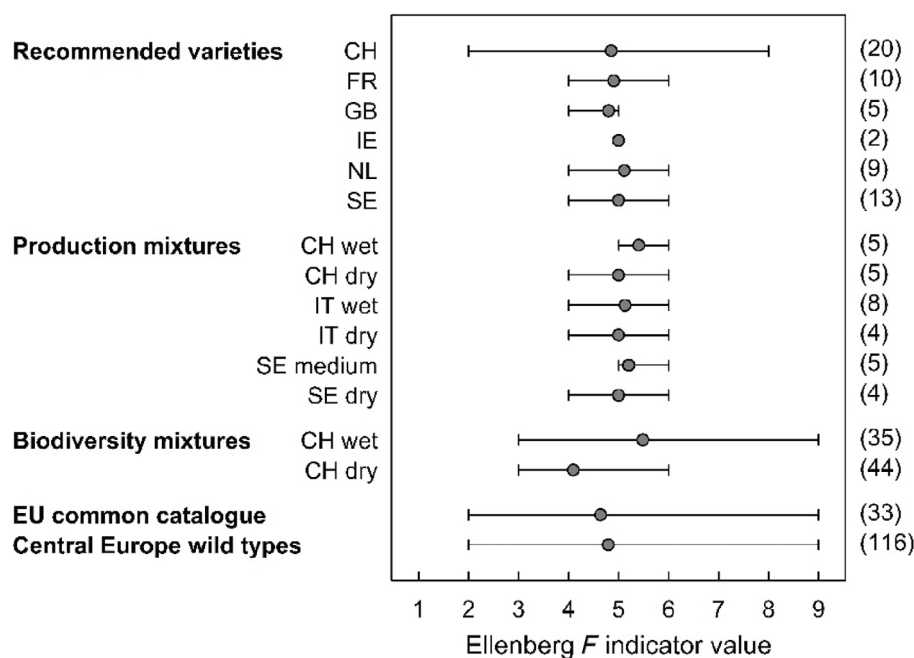


FIGURE 3 Ellenberg indicator values for moisture (F: 'Feuchte') for different sets of plant species: As national recommended lists of forage species varieties (six countries available), traded forage mixtures for production (three selected countries), mixtures to sustain biodiversity in Switzerland, and the EU common catalogue of agricultural varieties as well as the traded wild type species in Central Europe. Mean (●) and range displayed; number of species included on the right. 1 = extremely dry, soils that often dry out; 9 = wet, often water-saturated. CH, Switzerland; FR, France; GB, Great Britain; IE, Ireland; IT, Italy; NL, The Netherlands; SE; Sweden; EU, European.

We see two possible strategies to exploit inter-specific diversity to increase drought resistance and resilience of productive grassland at the farm scale. A first strategy would be to increase 'within-field diversity' by designing a more complex mixture that can adapt to different drought conditions. This could be achieved by combining species with distinctly differing moisture requirements (i.e., a mixture with a large range in Figure 3). However, in practice, it is hard to envisage an adequate combination of many species that fulfils the multiple demands of productive grasslands regarding interspecific competition (persistence), complementarity (Suter, Huguenin-Elie, & Lüscher, 2021) as well as management suitability (for grazing, cutting, silage) (Suter, Rosenberg, & Frick, 2021). A second strategy would be to increase 'among-field diversity' enabling an insurance effect by growing a variety of simpler mixtures (or monocultures), each adapted to different drought conditions (i.e., different mixture means in Figure 3). In this strategy, it might be easier to combine and maintain the persistence of a suitable set of species within each mixture regarding management requirements of the plants, but management of the different fields might be more complex. These strategies can be implemented in sown grassland with the targeted composition of the seed mixture(s) sown and in permanent productive grassland by managing species composition and richness through overseeding, self reseeding, and/or type and intensity of management. Both strategies can be applied not only at the farm scale but also at a regional scale.

8 | CONCLUSIONS

Grasslands cover a wide range of global pedo-climatic conditions. They can thrive under harsh growth conditions where other agricultural systems are not economically viable. This demonstrates the

considerable adaptation potential of grasslands. The literature reviewed here provides evidence that both intra- and inter-specific diversity have great potential to contribute to the adaptation of permanent and sown productive grassland to drought stress and variability in weather conditions. The choice of a successful strategy to adapt to drought strongly depends on the type of stress. Under severe stress that occurs regularly (as in the Mediterranean summer), drought survival, accompanied by cessation of growth during the stress period, is key to enable fast recovery after the stress has ceased. Under less severe drought and unpredictable weather conditions (as in cool-temperate climates), complementarity is of primary importance in two ways: complementarity in resource use increases ecosystem functioning during the periods of moderate stress and complementarity in water requirements allows for robustness to fluctuating water availability. Nevertheless, both intra- and inter-specific variability seem not sufficiently valued today and undoubtedly are a pillar for adaptation of productive grassland to future conditions. In this context a crucial point is that even a small increase in diversity from monocultures to two- to six-species mixtures already delivers substantial benefits. Diversity of genotypes and/or species on a farm/in a region can be achieved in two ways: either 'within fields' by growing the same complex plant community on all sites, or 'among fields' by growing different (simpler) plant communities on different sites. Both these strategies are easily feasible in sown grassland leys through the targeted composition of the seed mixture. In the long run, they are also applicable in productive permanent grasslands. Future research on the value of diversity in productive grasslands needs to include the interactions of drought stress with other factors (other stresses, soil type, management), and improve measurement of the effect of diversity on multiple ecosystem services (multifunctionality) that include agronomic, environmental and socio-economic responses.

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DATA AVAILABILITY STATEMENT

The species lists, on which Figure 3 is based, can be received from the authors on demand.

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