Grassland systems in Switzerland with a main focus on sown grasslands

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Abstract

Grasslands dominate Swiss agriculture and cover nearly 80% of the country's agriculturally utilised area. They form the basis for ruminant livestock production through the provision of high-quality roughage which accounts for three quarters of the total dry matter of dairy cow rations, as averaged over the whole country. While permanent grasslands dominate in mountainous and less favourable regions, sown grasslands form an important part of the crop rotation (1/3) in the lowlands. Sown grasslands for intensive forage production typically consist of mixtures of 3 to 7 grass and legume species, taking advantage of increased dry matter yield through overyielding or transgressive overyielding, complementary forage quality of the different species, weed suppression and symbiotic N_2 fixation. The Swiss-Standard-Mixtures System involves development and testing of species mixtures adapted to a broad range of purposes and environmental conditions. These mixtures rely on the availability of high yielding cultivars with appropriate competitive ability and optimal forage quality. Switzerland's forage crop breeding programme targets the improvement of the twelve prevalent forage grass and legume species including ryegrasses, fescues and clovers. Breeding research focusing on elucidating the genetic control of important traits and the development of genomics-assisted breeding tools ensures efficient breeding of improved cultivars. Continuation of the intense collaboration in research for forage plant breeding and grassland management, with involvement of all the actors, will be key to adapt sown grasslands to future challenges and demands.

Keywords: species-mixtures, multifunctionality, forage crop breeding, overyielding

Natural growth conditions

In Switzerland grasslands cover nearly 80% of the agriculturally utilised area (including alpine summer pastures). According to the 2017 agricultural census (FOAG, 2018), grasslands comprise 124,000 ha of temporary sown grasslands (8% of the agriculturally used area) and 609,000 ha of permanent grasslands (40%). In addition, approximately 465,000 ha of alpine pastures (31%) are used for temporary grazing during summer. The remainder of agricultural land is mostly arable land (18%) or covered by permanent crops (3%).

This dominance of grasslands can be largely explained by the environmental conditions – slope, altitude, rainfall – that often do not allow efficient arable farming. As a consequence, grasslands in Switzerland occur in diverse environmental conditions (Figure 1). For example, 95% of the permanent grasslands on agricultural land are located between 408 and 1,508 m a.s.l., on slopes between 1.3 and 62% and with an annual precipitation between 850 and 1,913 mm. Even more diverse are conditions of the alpine summer pastures: 95% of them are located between 941 and 2,557 m a.s.l., 6 and 92% slope, and 888 and 2,162 mm of precipitation. In contrast, arable crops and temporary grasslands occupy a much narrower environmental niche. Their 95% limits are between 366 and 853 m of elevation, 0 and 22% of slope and

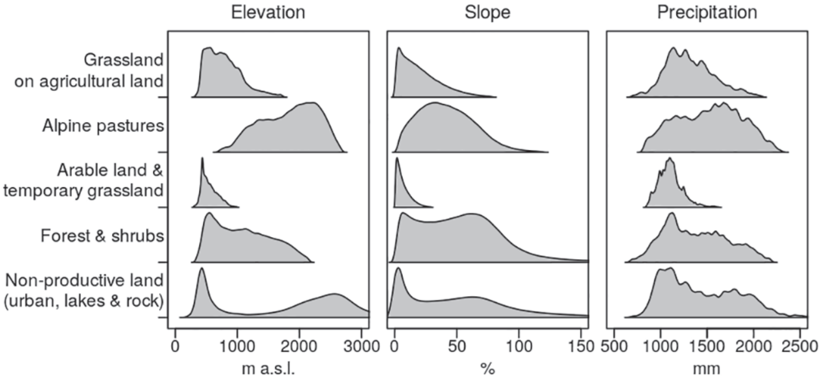

Figure 1. Density distribution of the environmental variables of elevation, slope and precipitation in the five major land use types in Switzerland. Data were derived from 4.1 Mio observation points of the Swiss Land Use statistics (FSO, 2018), elevation and slope of SwissAlti3D (Swisstopo, 2017) and gridded precipitation data (MeteoSwiss, 2016).

890 and 1424 mm of precipitation. Soil properties vary as much as these main drivers of soil formation (Amelung *et al.*, 2018).

General principles of Swiss grassland systems

In Switzerland, the overarching goal is sustainably productive, multifunctional and environmentally sound grassland systems. Three specific objectives are pursued to achieve this. The first is the production of high-quality forages from all types of grasslands described above that enable livestock to be fed on a grass-based ration. This requires harvesting forage at early development stage with high nutrient content and an appropriate fertilisation, and thus an intensive management. As a large proportion of Swiss farms cannot produce cereals or protein crops efficiently, due to topographic and climatic constraints, this intensive grassland-based forage production also contributes to feed-self-sufficiency, to closed nutrient cycles and to the re-coupling of the C and the N cycles. Temporary grasslands are the focus of the second objective. For these types of grasslands, the full benefits of modern agricultural development should be made available to optimise their production. This involves forage plant breeding, growing high performing elite cultivars, as well as the development of forage plant mixtures adapted to a wide range of conditions and types of utilisation. The third objective targets an enhanced multifunctionality of grassland systems, by means of differentiated and site-adapted management intensity at the farm and regional scale. The fields with the highest production potential should be managed intensively to produce high quality forage, necessary for a grass-based ration for productive livestock. This intensity should not exceed the carrying capacity of the site and be adapted to the growth requirements of the forage plant species to guarantee stable forage plant communities on the large areas of permanent grasslands. In return, the fields with a low production potential should be managed at low intensity to promote habitat diversity at the farm scale and to contribute to biodiversity conservation (Huguenin-Elie *et al.*, 2018).

Grass-based rations for dairy cows

Grassland-based milk production is of major importance in Switzerland. Traditionally, herbage from temporary and permanent grasslands provides the largest proportion of feed for ruminants. Due to climatic and topographic restrictions, intensive maize-concentrate based dairy systems are usually limited to the lowland area. In a survey conducted in 2013, the feeding strategy and ration composition of 157 dairy farms (0.7% of milk-producing farms) located in different climatic zones of Switzerland was investigated (Ineichen *et al.*, 2016). On average, of the examined farms, the proportion of fresh or conserved herbage in the year-ration was about 76% on a dry matter basis. This proportion increased with increasing altitude from 68% for farms in the lowland, to 78% in the hill region and 84% in the mountain zone. Feeding of maize silage showed the opposite trend. Its proportion of the feed ration decreased from 18% in the lowland, 9% in the hill region to 3% in the mountain zone. Substantial differences in herbage proportions were observed between feeding systems. Silage-free milk used for hard cheese production was produced with a higher proportion of herbage (83%) than milk produced from silage feeding (72%). On average of all farms, the ration contained 11% concentrates (DM). With an average milk yield of 6846 kg ECM cow^{-1} and 647 kg DM cow^{-1} year^{-1}, the concentrate utilisation was relatively low. Concentrate utilisation increased with increasing milk yield. However, variation in concentrate feeding between individual farms with similar milk yields was substantial, indicating a potential for optimisation in some farms (Figure 2).

During the last decades, and especially since the abolition of the milk quota system in 2009, the Swiss dairy production has undergone rapid structural changes. Since 2009 the number of dairy farms has shown a substantial decrease of -25%, with a shift towards bigger units and more intensive feeding systems. Grassland-based feeding, including grazing, is therefore actively supported with direct payments in the framework of the Swiss agricultural policy. The introduction of the 'RAUS'-programme, aiming to promote grazing, resulted in 85% of dairy cows currently having access to pastures for a minimum of 26 days per month from May 1 to October 31 (FOAG, 2018). In 2014 an additional programme supporting herbage feeding and limiting concentrate utilisation was introduced. In order to participate in this so-called 'GMF'-programme, farms are obliged to use a minimal proportion of herbage in the ration (75% DM, valley zone) and a maximum limit on the amounts of concentrates (10%). In 2018 the average participation at the programme was at 78% of the grassland area or 66% of the farms. Meeting the energy demand of high performing ruminant livestock through a largely grassland-based forage ration remains a major challenge for farmers. Increasing the starch content in forage legumes such as red clover may offer a valuable alternative to cereal based energy-complements (Ruckle *et al.*, 2017).

Advantages of multispecies mixtures

There is important evidence from experiments in intensively managed productive grasslands that mixtures perform better than the average of all monocultures (overyielding) or even better than the best performing monoculture (transgressive overyielding) (reviewed by Sanderson *et al.*, 2004, 2007; Lüscher *et al.*, 2014; Phenlan *et al.*, 2015). Compared to the average of monocultures, mixtures of legumes and non-legume species (mostly grasses) had about 30% higher biomass yield (Kirwan *et al.*, 2007; Nyfeler

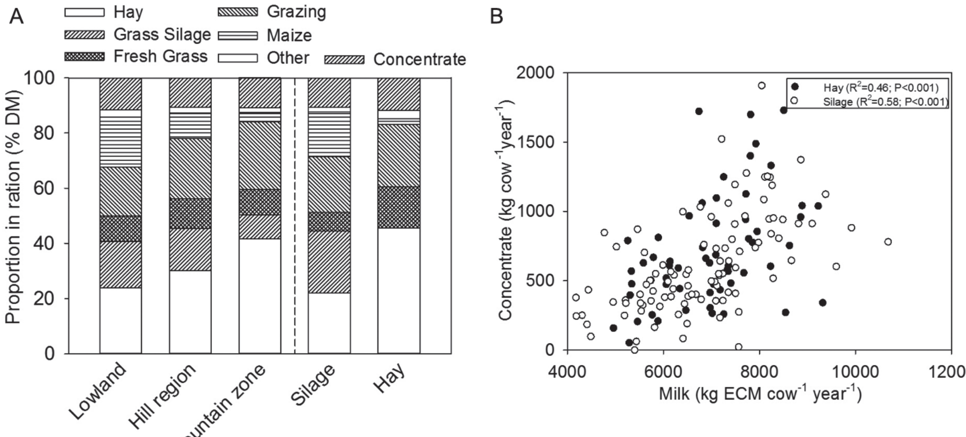

Figure 2. (A) Ration composition of dairy farms (n=157) in different climatic zones or according to the production system (silage/hay). (B) Concentrate utilisation and milk yield of different dairy farms in Switzerland.

et al., 2009; Küchenmeister *et al.*, 2012; Finn *et al.*, 2013; 2018; Malisch *et al.*, 2017; Cong *et al.*, 2018), improved weed suppression by up to 80% (Frankow-Lindberg, 2012; Suter *et al.*, 2017; Connolly *et al.*, 2018), and increased temporal stability of the yield (Haughey *et al.*, 2018). Significant N input through symbiotic N_2 fixation (Nyfeler *et al.*, 2011) led to enhanced total N yield (Suter *et al.*, 2015) compared to grass only swards. Forage quality of swards containing legumes was increased compared to grass swards (Gierus *et al.*, 2012; Lüscher *et al.*, 2014; Küchenmeister *et al.*, 2014). Legumes can increase the forage intake of mixed swards compared to pure grass stands due to a faster rate of digestion and particle breakdown and due to greater palatability (Dewhurst *et al.*, 2009; Niderkorn *et al.*, 2017) and some legumes can have positive effects due to their secondary plant metabolites as condensed tannins (Mueller-Harvey *et al.*, 2019).

These beneficial effects of mixtures were remarkably robust: they persisted over a wide pedo-climatic gradient. In the Agrodiversity Experiment (Finn *et al.*, 2013; Kirwan *et al.*, 2014; Connolly *et al.*, 2018), which has been conducted from Atlantic to continental and from temperate to arctic boreal conditions, both biomass yield and weed suppression were greater in mixtures than in the best performing monocultures at the great majority of sites. In this experiment, N yield has also been proven to be significantly greater in grass-legume mixtures than in grass monocultures at about 75% of tested sites (Suter *et al.*, 2015). Moreover, recent drought stress experiments have revealed beneficial mixture effects over the average for monocultures, in terms of persistence under severe drought (Hofer *et al.*, 2016; 2017; Finn *et al.*, 2018). Robustness of mixture benefits was also evident over a wide range of species proportions. In a three-year experiment, Nyfeler *et al.* (2009) demonstrated transgressive overyielding of mixtures' biomass yield at legume proportions between 20 and 80%. Persistent mixture benefits at varying species proportions were also evident in the Agrodiversity Experiment at all three experimental years, with proportions ranging between about 15 and 65%, irrespective of the species in mixtures (Finn *et al.*, 2013). Despite a strong decline in legume abundance over the three years, beneficial mixture effects on yield were still significant in the third year at 18 out of 24 sites, although the magnitude of the mixture effect was smaller at sites with lower legume proportion (Brophy *et al.*, 2017). Robustness of mixture benefits is further underlined by many experiments in extensively managed grasslands that have demonstrated overyielding (although not transgressive) and higher temporal stability (Tilman *et al.*, 2006; van Ruijven and Berendse, 2007; Hector *et al.*, 2010; Craven *et al.*, 2018) in species-rich swards compared with the average of the monocultures (Spehn *et al.*, 2002; Hille Ris Lambers *et al.*, 2004; Hooper and Dukes, 2004; Hooper *et al.*, 2005; Roscher *et al.*, 2005; Marquard *et al.*, 2009; Mommer *et al.*, 2010). Extensively managed, low-productive grasslands often have greater relevance for functions other than production (e.g. biodiversity conservation, maintaining food webs across trophic levels, touristic and recreational values) and experimental evidence suggests that species diversity is an important driver of ecosystem functioning and multifunctionality (Isbell *et al.*, 2011; Allan *et al.*, 2013; Weisser *et al.*, 2017).

The mechanism behind such mixture benefits is a better utilisation of the available growth resources due to species niche complementarity and positive interspecific interactions. The major driver was the legumes' ability for symbiotic N_2 fixation, which allows the production of more biomass with less N fertilisation. Due to symbiotic N_2 fixation and its growth stimulation of the legume's partner species (Høgh-Jensen and Schjoerring, 1997; Nyfeler *et al.*, 2011) total nutrient uptake from soil and fertiliser (N and P) are enhanced in grass-legume mixtures (Hoekstra *et al.*, 2015; Husse *et al.*, 2017). At the same time, nitrate leaching has not been considered as a problem in mown swards based on grass-legume mixtures, even if fertilised with up to 150 kg N ha^{-1} $year^{-1}$. This is in contrast to pure legume swards and highly N-fertilised pure grass swards, where leaching can be problematic (Loiseau *et al.*, 2001; Nyfeler, 2009). Low amounts of nitrate leaching in mixtures, despite their substantial N input from symbiosis, can be explained by (1) the efficient N uptake of the highly productive grass species, (2) the symbiosis taking place inside the plant, (3) being a steadily flowing N source, (4) which is tuned according to the sward's N demand (Hartwig, 1998). All four factors prevent periods with high concentrations of reactive N forms in the soil. In line with this, nitrous oxide emissions have also been found to be lower in grass-legume mixtures compared with N-fertilised pure grass swards (Schmeer *et al.*, 2014) or swards with very low legume proportions, which were in turn intensively fertilised because of missing N_2 fixation (Fuchs *et al.*, 2018). Besides complementarity in N_2 fixing ability, there is also evidence that complementarities in seasonal and annual growth patterns and also in rooting depths significantly contribute to mixture benefits (Nyfeler *et al.*, 2009; Mommer *et al.*, 2010; Hofer *et al.*, 2016; Husse *et al.*, 2016, 2017).

Designing optimal mixtures

Important distinctions of the results of agricultural experiments in intensively managed grasslands, compared with biodiversity experiments in extensively managed grasslands, are that (1) beneficial mixture effects occurred at low levels of species richness, and that (2) transgressive overyielding was often achieved. In contrast, a meta-analysis of low productive grasslands revealed that, averaged over all experiments assessed, the most species-rich mixtures had 12% less yield than the highest yielding monocultures (Cardinale *et al.*, 2007), though the mixtures were clearly more species rich. This raises the question of how mixtures should be designed to be most suitable for forage production.

From the flattening of the slope of the plant species richness-productivity relationship observed towards high species richness in many biodiversity experiments (e.g. Weisser *et al.*, 2017), it can be expected that the effect of adding supplementary species to productive four-species mixtures will be much weaker than the effect between monocultures and the four-species mixtures. In addition, we suggest that transgressive overyielding in intensively managed grassland experiments was related to a targeted selection of the species based on prior knowledge. This selection firstly focused on the best-performing forage plant species (forage yield and quality) under the given growth conditions and management intensity. Secondly, the complementarity of traits among species was maximised by combining species with differences in their symbiotic N_2 fixation ability, rooting depth, and seasonal and annual growth pattern. Such a strategy seems most promising to enhance yield and other ecosystem services (Lüscher *et al.*, 2011; Storkey *et al.*, 2015) and differs from the random species assembling design of many biodiversity experiments in low productive systems. The number of species necessary to optimize the benefits of mixtures becomes increasingly uncertain with an increase in the number of functions expected from the mixture. In theory, each supplementary species could bring benefits for an ecological function poorly supported by the other species, and thus, it could be expected that a large number of species would promote multifunctionality. For grassland communities it is still contentious whether this holds true (Gamfeldt and Roger, 2017; Meyer *et al.*, 2018). Although the diversity-multifunctionality relation in intensively managed grasslands has not yet been evaluated with more than four species, two- and four-species mixtures supported multiple functions and increased multifunctionality (Suter *et al.*, 2019).

The Swiss-Standard-Mixtures System

Growth conditions as well as management objectives vary widely among farms. Consequently, for practical use, a variety of distinct mixtures that cover this broad range of needs are required. The product range of the system of Swiss-Standard-Mixtures consists of forty-six seed mixtures, which offer mixtures with a high versatility of use as well as mixtures especially designed for mowing or grazing.

The duration of the ley is an important factor for the seed mixture composition and the classification of the mixtures in the system (Table 1). With increasing duration, the number of species in the seed mixture is increased. Essentially, this is done to optimise the components' time-dependent performance (temporal niche over the years). The suitability for distinct types of utilisation depends mainly on the main legumes in the seed mixture. The wealth of possible species combinations allows for adaptation

Table 1. Most important standard mixtures with their main species, duration, expected mean clover proportion, environmental requirements, range of utilisation and estimated market share.[1]

Mixture	Main legumes	Main grasses	Number of species	Duration (a)	Mean clover %	Water availability	Altitude	Utilisation				Seed market share %
								Green	Silage	Hay	Grazing	
102	VS, PS	LM	3	1	35	+	▼	●	○			9
106	TA, TU	LM	3	1	40	+	▼	●	●			
155	MS	LM	4	1	40	–	▼	●	●			
200	TP	LM	2	2	40	+	▼	●	●	○		17
230	TP	LM, DG	4	2	35	0	▼	●	●	○		
300	TP	DG, LH	5	3	60	–	▼	●	●	○		1
301	TP	DG, AE	4	3	60	––	▼	●	●	○		
320	MS	DG, LH	5	3	60	––	▼	●	●	○		3
323	MS	DG, FP	5	3	70	–––	▼	●	●	○		
326	OV	AE, FP	4	3	50	–––	▼	○	○	●		
330	TR, (TP)	LP, DG	6	3	35	0	▼	●	●	●	●	22
340	TR, (TP)	LP	6	3	50	+	▼	●	●	●	●	
362	TP	FA, PP	4	3	30	––	▼	●	●	○	●	
430	TR, (TP)	LP, DG, PP	7	4+	30	0	▼	●	●	●	●	28
440	TR, (TP)	LP, PP	6	4+	45	+	▼	●	●	●	●	
431	TR, (TP)	FP, DG, PP	9	4+	35	–	▼▲	●	●	●	○	
442	TR, (TP)	AP, FA, PP	8	4+	35	+/–	▼	●	●	●	○	
444	TR	AP, FP, PP	6	4+	35	++	▼▲	●	●	●	○	
462	TR	FA, PP	4	4+	30	–	▼	●	○	●	●	
480	TR	LP, CC, PP	7	4+	30	+	▼	●	○	●	●	
481	TR, (LC)	CC, PP, AG	9	4+	30	+	▼▲	●	○	●	●	
Salvia	diverse	diverse	38	4+	20	–/0	▼			●		1
Humida	diverse	diverse	35	4+	20	++	▼			●		
Montagna	diverse	diverse	30	4+	20	0	▲			●		
Broma	diverse	diverse	47	4+	20	––	▼			●		

[1] Species names: AE (*Arrhenatherum elatius*), AG (*Agrostis gigantea*), AP (*Alopecurus pratensis*), CC (*Cynosurus cristatus*), DG (*Dactylis glomerata*), FA (*Festuca arundinacea*), FP (*Festuca pratensis*), FR (*Festuca rubra*), LC (*Lotus corniculatus*), LH (*Lolium × hybridum*), LM (*Lolium multiflorum*), LP (*Lolium perenne*), MS (*Medicago sativa*), OV (*Onobrychis viciifolia*), PP (*Poa pratensis*), PS (*Pisum sativum*), TA (*Trifolium alexandrinum*), TF (*Trisetum flavescens*), TP (*Trifolium pratense*), TR (*Trifolium repens*), TU (*Trifolium resupinatum*), VS (*Vicia sativa*); water availability: ++ wet, + humid, 0 balanced, – occasionally dry, –– often dry, ––– regularly dry; altitude: ▼ below, ▲ above 900 m a.s.l.; utilisation: ● suitable, ○ medium.

to various environmental conditions, the most important of which are temperature – determined by altitude and exposition – and water availability.

The constant change in agricultural practice and the progress in plant breeding are considered by frequent adaptation of the system and the composition of the seed mixtures. Since the establishment of the standard mixtures in 1955 (Frey, 1955), 15 revisions have been conducted, including 120 changes in the product range (removal or addition of mixtures) and the same number of adjustments of existing seed mixtures. Since the establishment of the standard mixture system, one of the driving factors has been the intensification of agricultural production systems. This is clearly manifested by an increase in the percentage of mixtures containing white clover from 27 to 48% and of mixtures containing perennial ryegrass from 32 to 48% between 1955 and 2017 (Suter *et al.*, 2017). Nevertheless, more mixtures for less intensive, and even extensive utilisation, were part of the system in 2017 than in 1988 (Lehmann *et al.*, 1988), reflecting the introduction of environmental schemes and the impact of a paradigm shift in the agricultural policy in Switzerland in the early 1990s. This development could also be observed in the number of species of the most species-rich mixture in the system: in 1955 and 1988, it contained 8 and 9 species, respectively, whereas in 2017 it contained 47 species. Also, the increase in the total number of species included in the system, and, thus being traded, is impressive: it rose from 27 in 1988 to 99 in 2017. The success of seed mixtures depends heavily on the availability of high performing cultivars of the different species adapted to the respective environments. Although the importance of competition and coexistence for successful breeding of forage crops for mixtures has long been recognised (Hill, 1990; Lüscher and Jacquard, 1991; Lüscher *et al.*, 1992), selection of forage grasses and legumes still depends largely on population-based improvement of individual species (Posselt, 2010). However, targeted breeding efforts have resulted in a broad set of cultivars suitable for being cultivated in multispecies mixtures (Suter *et al.*, 2019).

Breeding forage crops adapted to a broad range of environments

The climatic conditions and cultivation systems outlined above call for forage crop cultivars adapted to local conditions and a broad range of applications. Therefore, Agroscope, the Swiss competence centre for agricultural research, maintains a large breeding programme covering the twelve prevalent forage crop species: perennial ryegrass (*Lolium perenne*), Italian ryegrass (*L. multiflorum*), hybrid ryegrass (*Lolium* × *hybridum*), meadow fescue (*Festuca pratensis*), tall fescue (*F. arundinacea*), red fescue (*F. rubra*), Kentucky bluegrass (*Poa pratensis*), cocksfoot (*Dactylis glomerata*), red clover (*Trifolium pratense*), white clover (*T. repens*), sainfoin (*Onobrychis viciifolia*) and birdsfoot trefoil (*Lotus corniculatus*). The programme results in a broad number of diploid and tetraploid (for ryegrasses, meadow fescue and red clover) cultivars regularly listed in Swiss and international lists of recommended cultivars (Suter *et al.*, 2019).

Breeding efforts mainly focus on the improvement of dry matter yield under frequent cutting, the seasonal distribution of yield, persistence over several growing seasons, forage quality, resistance to biotic and abiotic stresses and improvement of seed yield. For perennial ryegrass, specific breeding targets are tolerance to dry and hot summers, winter survival, and the ability to persist at higher altitudes. In addition, very early heading cultivars that combine a high yield in spring with a rapid regrowth and a long vegetation period are developed. Italian ryegrass is primarily selected for the ability to survive two winters as well as dry and hot summers, while in meadow fescue the focus lies with a high level of endophyte (*Epichloë uncinatum*) infection for better fitness and improved competitive ability during summer (Malinowski *et al.*, 1997). In order to exploit the high drought tolerance of tall fescue, genotypes are selected with fine, flexible leaves, which indicate good palatability, in combination with a high digestibility. In red clover, the breeding programme focuses on persistence breeding based on old Swiss 'Mattenklee' germplasm, which was developed over decades of on-farm seed production (Kölliker *et al.*, 2003). In addition, red clover types with low phyto-estrogen content or types that are suitable for grazing are selected. In white clover, breeding focuses on dual-purpose cultivars (i.e. alternating mowing or grazing use) and a limited proportion of cyanogenic genotypes.

Although red and white clover with their high protein content complement the dietary composition of forage grasses in mixtures, pure grassland-based diets are often energy limited. Although so far not exploited in forage crop breeding, structural carbohydrates such as starch have the potential to increase feed value by improving the energy content of grassland-based diets. The first studies in red clover have shown significant differences in starch content in different red clover genotypes accounting for up to one third of their dry matter biomass (Ruckle *et al.*, 2017). Although harvest-losses and post-harvest degradation limit a full exploitation of starch in the ruminant diet, the genotypic differences indicate suitability of improvement of this promising trait through targeted breeding. This may even be more promising in white clover, which is used predominantly for grazing. Starch content has been shown to be significantly higher when plant material is harvested by the end of the day as compared to the end of the night when a large proportions of starch have been degraded (Ruckle *et al.*, 2017, 2018). Therefore, evening grazing of white clover stands offers a valuable option to exploit white clover genotypes with high starch content and offer an attractive alternative to cereal-based feed supplements. However, a more detailed understanding of starch metabolism in red clover and the development of genomics-based breeding tools are needed before starch can be incorporated as a trait in clover breeding programmes.

Sainfoin presents another forage legume with attractive forage qualities (Kölliker *et al.*, 2017). The species has been shown to contain considerable amounts of condensed tannins which have been shown to reduce bloat, diminish gastro-intestinal parasites and may also have the potential to lower methane emissions (Mueller-Harvey *et al.*, 2019). An extensive evaluation of 27 sainfoin accessions from a worldwide collection showed large variability in the content of condensed tannins which could be exploited through breeding (Malisch *et al.*, 2015). Although a predominantly outcrossing species, high rates of self-fertilisation have been observed for sainfoin under artificial directed pollination (Kempf *et al.*, 2015). This could enable the development of homogenous inbred lines facilitating the improvement of tannin content through molecular marker assisted breeding approaches.

For all species, the Agroscope breeding programme is mainly based on recurrent phenotypic selection to improve the breeding populations. In spaced-plant nurseries, individual genotypes are selected for desired traits such as disease resistance, forage quality or persistence. The seed of the first generation of a new variety is produced via open pollination among selected elite plants after cloning in a polycross (grasses) or directly in the nursery (clover). In a half sib progeny test the best progenies are selected and allowed to pollinate to create seed of the new candidate variety. The performance of the new candidate is tested in three-year plot trials on several sites. Although this breeding process has proven very efficient and yielded a large number of successful cultivars over the years, constant challenges such as evolving pathogen populations, changing environmental conditions and novel consumer demands ask for constant refinement of the breeding process. A detailed understanding of the genetic control of key target traits and the development of genomics-assisted breeding methods offer additional means for the targeted improvement of forage crop cultivars.

For example, in Italian ryegrass, a major quantitative trait locus (QTL) explaining more than 60% of the phenotypic variance of resistance to bacterial wilt (caused by *Xanthomonas translucens* pv. *graminis*) was identified (Studer *et al.*, 2006). Further characterisation of the QTL region using a pooled sequencing approach allowed to identify sequenced characterised markers and candidate genes potentially involved in *Xtg* resistance (Knorst *et al.*, 2018). Simulation of marker-assisted selection using these markers resulted in a decrease in the average marker score of up to 28%, indicating the suitability of these markers for marker-assisted improvement of *Xtg* resistance in Italian ryegrass. In addition, comparative genomic analysis of several *Xtg* isolates and comparison to other *X. translucens* pvs. identified a set of unique genetic features potentially involved in pathogenicity of the pathogen (Hersemann *et al.*, 2017). This detailed information on host resistance and pathogen virulence will not only further advance our knowledge of this complex host-pathogen interaction, but also allow for the development of refined breeding methods.

Proof of concept for marker-assisted introgression of disease resistance in Italian ryegrass was given for the crown rust-causing fungal pathogen *Puccinia coronata* f. sp. *lolii*. A single marker linked to a crown rust QTL on linkage group 2 of Italian ryegrass (Studer *et al.*, 2007) was used to introgress resistance from the progeny of a bi-parental mapping population into different breeding populations. While phenotypic selection alone resulted in an improvement of 2.5 disease scores (using a scale from 1 to 9), single-marker-assisted selection resulted in an improvement of 5.52 disease scores (Kölliker *et al.*, 2016).

Genetic resources and their value for breeding

In contrast to many field crops like maize, where the wild form of the cultivated species no longer exists, wild and semi-natural forms of common forage species still exist alongside current cultivars (Boller and Greene, 2010). Since forages are less domesticated than field crops (Harlan, 1983), the closeness of wild and cultivated forms eases the use of natural plant genetic resources (PGR) for breeding. Natural or semi-natural permanent grasslands harbour forage ecotype populations highly adapted to their habitats, showing variation for a range of adaptive traits like ear emergence and growth habit (e.g. Peter-Schmid *et al.*, 2008). With an area larger than 500,000 ha, corresponding to 34% of total agricultural area (FSO, 2018), Swiss permanent grasslands, which are spread over a large range of altitude and climatic conditions (Figure 1), therefore make a wealth of natural genetic variation. Following the proposition of Hertzsch (1959), the source of a breeding programme should be based on plants found on old permanent grasslands with an association similar for the respective situation. Accordingly, ecotypes from permanent grasslands have been used as the starting point for selection in Switzerland at Agroscope, as in many other forage breeding programmes in Europe since the beginning of the 20th century (e.g. Humphreys, 2005). Although breeders nowadays rely more on crosses between cultivars, new collections of adapted ecotype populations still bear the potential to improve the breeding pool. For the example of Italian ryegrass, introduced to northern Switzerland in the early 19th century (Stebler and Schröter, 1883), Boller *et al.* (2009) have shown that the average performance in terms of yield, vigour, and resistance to snow mould of 20 ecotypes collected across Switzerland in 2003 was superior to currently recommended cultivars. In this study, resistance to crown rust and leaf spot were the only traits where cultivars outperformed ecotypes. For Italian ryegrass, in contrast to meadow fescue, no clear distinction between ecotypes and cultivars could be made based on genetic markers, indicating continuous exchange between these two groups (Peter-Schmid *et al.*, 2008). Unlike other forage species where newly collected ecotypes are often crossed with existing breeding materials, new Italian ryegrass ecotype collections were directly used in the development of new varieties at Agroscope. For example, the variety Oryx (first seed produced in 1993, listed in 2000) was created from ecotypes collected in 1987 after just one cycle of selection among spaced plants in the nursery followed by one cycle of selection among half-sib families. The new variety Rabiosa (first seed produced in 2005, listed in 2015), which is currently ranking best in the Swiss list of recommended forage varieties (Suter *et al.,* 2015), was created from ecotypes collected in 1996 after two cycles of selection among spaced plants followed by one cycle of selection among half-sib families.

This direct use of ecotypes for the creation of high performing varieties clearly demonstrates the high value of adapted (semi-) natural populations in permanent grasslands, and this has meanwhile also been recognised by the public. Since 1999, the Federal Office for Agriculture has been running a national action plan for conservation and use of plant genetic resources. Within this programme, Agroscope has collected accessions of different forage species for *ex-situ* conservation. This collection comprises accessions of forage grasses mainly derived from ecotypes, but also accessions of forage legumes that were derived mainly from landraces, as in the case of red clover. Most accessions have been described morphologically and agronomically in several projects, of which the data are now available in a national database (www.bdn.ch). Description of these genetic resources is ongoing, as for example in the EU-funded EUCLEG project (www.eucleg.eu), where red clover accessions are phenotypically and genotypically analysed. To protect the continuous adaptation of ecotypes in their place of origin at a national level, special support measures are currently tested by the Swiss federation in a pilot project since 2018 for effective *in-situ* conservation of forage ecotypes together with the farmers. All these measures will help to protect and valorise these genetic resources for a successful plant breeding in the future.

Conclusions

Roughage from grasslands provides the basis for ruminant livestock production, thereby making a valuable and sustainable use of local natural resources in many countries of alpine regions and central Europe. Management practices, the breeding of adapted cultivars, and optimised seed mixtures for various purposes and site conditions have allowed a very high level to be reached in terms of productivity and sustainability. However, challenges such as changing climatic conditions, new evolving pathogen populations, increasing nutrient requirements of cows due to increasing milk yields, changing farm structures and consumer demands, all call for constant refinement of grassland management and utilisation. This can only be achieved by combining progress on all the different scales of grassland systems. Developments in the area of molecular genetics and genomics, but also high throughput and high precision phenotyping, offer promising tools to breed the best genotypes. Exploitation of positive interactions in the plant-soil-microbiome system will allow the production of more forage on an individual field with fewer inputs, and site-adapted and diversified management intensities among fields of a farm or region will allow increased multifunctionality of our grassland systems.

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