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Sustainable intensification of cultivated pastures using multiple herbivore species

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Demand for animal products is growing faster than for any other agricultural product. As a result, pressure for greater output from cultivated pastures is expected to increase. Assuming cultivated pasture area will decrease with land degradation, conversion to grain crops or urban expansion, the only alternative is to increase productivity per area. We suggest an underutilised solution: increase herbivore diversity on cultivated pastures. We review multiple herbivore species (MHS) ecology in natural ecosystems (rangeland and wildlife parks) for guidelines to implementing this approach in cultivated pasture. In rangeland or natural grassland systems, sequential or simultaneous introduction of MHS results in greater productivity, diversity and resilience of plant as well as animal populations. Replacing historical mono-ruminant systems with MHS or classes on cultivated pasture is currently beyond landowner experience and will stretch cultivated pasture science. This approach becomes more feasible, however, as cultivated pastures increase in plant biodiversity and canopy complexity. We enumerate research and demonstration topics that might promulgate MHS in cultivated pastures.

Keywords: animal production, biodiversity, cultivated pastures, foraging ecology, plant–herbivore interactions

Introduction

According to the FAO (2014), food production must increase 70% by 2050 in order to feed the world’s projected 9 billion people (United Nations 2013). Demand for animal products is growing faster per capita than for other agricultural products (Nicholson et al. 2001; Boval and Dixon 2012). This increase in production must occur without additional natural resources, such as land, fertilisers or water. It must also be sustainable, meaning that it should not debilitate the environment and should last generations. The concept of sustainable intensification through smart row-crop agriculture (Campbell et al. 2011) can be applied to ruminant production as well (Makkar and Ankers 2014). By doing this, intensification will combine with resilience to prepare for predicted climate oscillations (Schmidhuber and Tubiello 2007; INIS 2013).

Due to increased world population, demand for animal products, and climate-induced stress, today’s predominant cultivated pasture models based on monocultures grazed by single animal species occupying large landscape tracts may become anachronisms. Instead, complex mixed farming systems with multiple production layers (González-Garcia et al. 2012) may come to dominate cultivated pastures. Such systems include livestock enterprises that fit within the concept of silvopastoral systems (Franzel et al. 2014). As with silvopasture in general, concepts and approaches required for efficient multiple herbivore species (MHS) stocking are outside the current approaches of most modern, large-scale production agriculture. The MHS concept gains relevance with recognition of environmental degradation of marginal lands and increasing regulation of agricultural chemicals required for sustained productivity of cultivated pastures particularly in many humid environments.

All grasslands, cultivated and natural (e.g. rangeland), worldwide comprise approximately 80% of today’s farmland (Boval and Dixon 2012). If sustainable intensification is to meet growing demand for animal products, food production within these ecosystems must be diversified. The challenge is to accomplish sustainable intensification without reducing biodiversity or increasing inputs, such as pesticides, fertilisers or irrigation (Nicholson et al. 2001). In addition, the inevitable attrition of cultivated pastures and rangeland to ecosystem degradation or conversion of more fertile grasslands to row crops means that fewer, rather than more, grasslands will be available for animal husbandry over time.

Our review will focus on how to intensify cultivated pasture production without additional inputs or land. Increasing plant diversity in the cultivated paddock has been widely defended despite the technical difficulties and paucity of supporting research (Sanderson et al. 2007). In some grassland ecosystems, plant diversity increases productivity and
stability (Tilman et al. 1997), but this has yet to be widely researched, much less applied to intensively managed temperate (Sanderson et al. 2004) or tropical (Muir et al. 2014) cultivated pastures. Forage agronomists historically train for monoculture plant science, so managing increasingly diverse plant mixtures is a challenge, especially where animals are involved (Sanderson et al. 2004). Despite the challenges, domesticating native plants for multi-species rangeland and cultivated pasture holds some promise (Smith et al. 2010).

We propose expanding the diversification theme beyond plant species to domesticated and harvestable wild animal species in cultivated pastures. Multiple herbivore species on cultivated pasture could foster sustainable intensification in ruminant production. The multiple layers of native herbivores in complex African natural grasslands (Hofmann 1989), including those that contain cattle (Young et al. 1998), may provide a ready template. Likewise, mixing cattle with sheep has been used by ranchers on some rangelands of North America for over 100 years to harvest the diverse forage more efficiently than either individual species would (Glimp 1988). If we emulate these ecosystems in cultivated pastures, we can diversify and potentially increase animal product output by building layers of foraging niches driven by factors such as selectivity (bulk versus concentrate feeders), canopy preference/access, seasonality (leaf litter versus young, green plants; Rhoades 1995) and palatability preferences (browsers versus grazers; Treydte et al. 2013). Increased nutrient uptake by a variety of root structures of diverse plant species combined with diverse herbivores to more effectively harvest a complex plant community provide a simplified basis for anticipated enhanced system productivity. These options require a change in cultivated pasture research, outreach and marketing. Most markets worldwide are dominated by cattle (Bos spp.) with secondary demand for sheep (Ovis aries) and goats (Capra spp.). We propose a wide array of already domesticated (NRC 2002) or nearly domesticated (Carles et al. 1981) species beyond these three most common ruminant species.

Researching MHS complexity, in addition to the already challenging plant diversification, will stretch current cultivated pasture science. Convincing pasture managers to adopt such a paradigm shift will be even more difficult (Pengelly et al. 2003; Peters et al. 2003). Even if farmers successfully master these techniques, without a sophisticated market to absorb a wide gamut of novel animal products, the entire process would be futile (Glimp 1988). We propose that, at the very least, research into MHS pasture development is warranted from both economic and ecological perspectives. Garcia et al. (2012) noted that goats and camels have been substituted for cattle as marginal ecosystems in sub-Saharan Africa become unable to support cattle. Especially where this deterioration is associated with increases in woody vegetation, MHS stocking could enhance sustainability of existing ecosystems and maintain livestock productivity. Because MHS stocking has been more commonly practiced within natural ecosystems than in cultivated pastures, approaches to MHS stocking can be derived from and illustrated by various natural grassland ecosystems. While we propose development of MHS stocking approaches for cultivated pastures, expanded application on many rangeland ecosystems may also be appropriate. Recent terminology clarification (Allen et al. 2011) has indicated distinct differences characterising cultivated pastureland, which is composed of domesticated plant species, versus rangeland, which includes a variety of natural vegetation types. Our interest in diversification of cultivated pastureland to enhance sustainability and profitability may readily be extended to deteriorated rangelands where plant species augmentation and MHS stocking could contribute to sustainability of some currently stressed livestock production ecosystems. We review what little has been recorded to date for MHS in cultivated pasture, what we can learn from natural grassland systems (rangeland or wildlife parks), and propose some initial topics that merit attention as we seek to expand MHS in cultivated pastures.

Review of concepts

Plant/animal diversity should equate to greater production

Diversity can be enhanced on both sides of the plant–animal interface. Although research of cultivated pastures seeded to multiple forage species is often limited to a single grass grown with a single legume, work with more complex mixtures is expanding. Based on the greater resilience documented in native grasslands with complex plant mixtures (Tilman et al. 1997), cultivated pastures containing multiple plant species should provide equivalent benefits (Sanderson et al. 2007; Muir et al. 2014). It follows that introducing multiple animal classes and/or species on those pastures should likewise result in production increments. This, however, would involve a complete change of concept in cultivated pasture science where soil, plant and animal uniformity, rather than diversity, have been the rule to date (Barnes et al. 2003).

These multiple layers of diversity within pastures will make research as well as production more challenging than they are already. Not surprisingly, most cultivated pasture research has focused on monospecific forage, single-animal species systems. It is difficult enough to nurture (water availability, nutrients and pesticides) and manage (herbage allowances, seasonal changes and year-to-year adaptation to climatic variables) intensive single-species systems. Each time an additional plant species is added, complexity rises incrementally. If we add herbivore diversity to the equation, the challenges increase exponentially.

Despite these difficulties, this investment could be justified on several levels. Many rangeland environment- or resource-challenged landscapes currently not used for agriculture because of climate (for example, low rainfall), vegetation (shrublands), topography (steep hillsides), soil drainage (swamps or marshes) or other reasons could be co-opted to ruminant production (Nicholson et al. 2001; Boval and Dixon 2012) without compromising their environmental integrity to the degree that row cropping would. These environments can be candidates for MHS stocking with minimal augmentation of the native vegetation with species of selected plant functional groups rather than complete conversion of plant species. As local climates change and weather extremes become more acute, biodiverse perennial grasslands with flexible animal
husbandry systems should be more resilient than more vulnerable systems based on annual crop or forage cultivation (Nicholson et al. 2001). Taken together, these factors encourage pasture science to seek novel forms of intensifying ruminant production from increasingly marginal ecosystems. The alternatives—continued land degradation or decreased food production—are simply not acceptable.

**Principles from natural ecosystems**

A theoretical basis for benefits from stocking MHS on a grazing resource has largely been provided by research on the extensive native grasslands, savannas, and shrublands of Africa where a large number of diverse herbivore species occur naturally over extensive land areas (McNaughton and Georgiadis 1986; Hoffman 1989). Early efforts to assess the numerous large, herbage-consuming mammals and their environments were largely descriptions of animals and landscapes. Species commonly occupying open grasslands were often those with adaptations for bulk harvest of large amounts of grass, whereas species frequently associated with woody vegetation, whether shrubs or trees, possessed abilities to selectively forage within the available foliage (McNaughton and Georgiadis 1986). These observations and characterisations of diverse herbage-consuming animals and their herbage resources led to gradual discernment of a number of different mechanisms of herbivore adaptation to specific herbage types. Many of these mechanisms are relevant to optimal management of mixed species of grazing livestock and especially combinations of grazing livestock and native wildlife populations.

Anatomical and physiological differences among African herbivores were discerned as adaptations to particular herbage resources allowing the diverse species groups to share readily available herbage resources with much less direct competition than might be expected from such unrestricted interspersion of multiple populations (Hofmann 1989; Spalinger and Thompson Hobs 1992). Early assessments indicated a dry-season grazing succession as zebras (Equus burchelli) initially consumed large amounts of tall grass stems, followed by wildebeest (Connochaetes taurinus albojubatus) selecting more leaf blade and grass leaf sheath as taller stems were removed, and finally Thomson’s gazelle (Gazelle thomsoni) selecting growth of dicotyledons made accessible as a result of the defoliation of grasses by the previous two species (Gwynne and Bell 1968). This was suggested as facultative rather than competitive interaction among species grazing a common sward. This consumption of distinct components of a common sward by different species was noted as not simply the result of species preferences but effects of distinct anatomical and physiological adaptations of animals to diet components. Association of digestive system characteristics and feeding strategies led to classification of African ruminants as grazers, which largely consume herbaceous plants, browsers, which select herbage from brush and trees, and intermediate feeders, which include a range of diet and feeding types (Hofmann and Stewart 1972).

Feeding strategies of African herbivores based on a grazer–browser continuum is influenced by a number of factors, including prehensile organs, body size, rates of diet fermentation and passage associated with digestive system anatomy, energy requirements and available herbage (Ditchkoff 2000). Recent assessments indicate that diet selectivity as well as body size may be the predominant factor controlling resource partitioning, which occurs more substantially during the dry season, among this diverse group of herbivores (Kleyhans et al. 2011). A primary basis for size effects involves the lack of linear relationship between body weight and metabolic requirements, which is only partially explained by the typically used ‘body weight to the 0.75 power’ (van Soest 1982). Body weight also affects bite dimensions and relationships of bite volume to nutrient requirements and characteristics of herbage consumed. Large species taking large bites can consume substantial amounts of the available herbage with limited opportunity to effectively select for the most nutrient-dense herbage materials. Smaller species with smaller, more mobile mouth parts can more effectively select among available herbage components but time for such selective feeding requires effective selection of herbage with greater nutrient concentration (Illius and Gordon 1997). Additional support for the dominance of body size in resource partitioning includes exclusive use of small components of the habitat associated with body size (Kleyhans et al. 2011) and lack of functional redundancy in herbage use among different size classes of these herbivores (Goheen et al. 2013). With the substantial effect of body size, debate has arisen regarding relevance of the browser–grazer classification of ruminant species and significance of anatomical specialisations (Gordon and Illius 1994; Robbins et al. 1995; Ditchkoff 2000; Perez- Barberia and Gordon 2001; Gordon 2003).

Beyond body size, several characteristics perhaps less broadly associated with resource partitioning among herbivores are intricately related to feeding strategies of large, herbage-consuming African mammals. Comparatively slow passage rate and extensive fermentation of cell wall in the rumen of bulk grazers contrasts with rather rapid passage of selective browsers, which generally consume larger proportions of highly digestible cell contents (van Soest 1982; McNaughton and Georgiadis 1986; Hofmann 1989). A range of rumen and other gastrointestinal tract structural features facilitating various forms of these digestive approaches has been described for particular African herbivores (Hofmann 1989). The herbivore diversity within these ecosystems demonstrates how a range of selectivity, canopy access and herbage preference can more fully utilise vegetation resources. Bite volume, bite rate and herbage intake decrease with highly selective browsing, whereas energy expended per bite and nutrient concentration obtained may both be greater compared with diets from less selective foraging, either within species or among different species (van Soest 1982; Underwood 1983; McNaughton and Georgiadis 1986).

Concentrate browsing and selective grazing within grass canopies are facilitated by anatomical features of mouth parts and animal agility (Underwood 1983; Hofmann 1989). An additional anatomical feature of ruminant browsing specialists is relatively larger salivary glands, which may be associated with increased passage rate and, in some instances, provide chemical defense against such phenolic compounds as tannins occurring at toxic levels in some browse materials (Hofmann 1989). Feeding strategy is not
the only difference among ruminants or pseudoruminants. The caecum of equids provides unique lower-digestive tract fermentation for cellulose digestion with less passage restriction allowing rather rapid, high-volume, although less extensive, digestion of roughage diets (McNaughton 1985; McNaughton and Georgiadis 1986; Odadi et al. 2011a). Because of the greater intake potential supported by rapid passage rates, species such as zebra and horses can obtain their nutrient needs on lower-quality grass, when quantity is adequate, than can ruminant species dependent upon slower and more thorough fibre fermentation in the rumen. These differences between herbivore types provide facilitation rather than competition between equids and cattle at low grazing pressures (Odadi et al. 2011b), furnishing insights for managing cattle with horses or species of conservation concern such as Grevy’s zebra (Equus grevyi).

An additional characteristic that may enhance browse utilisation efficiency in African ruminants is specialised tannin-tolerant or tannin-degrading microbial populations as indicated by more efficient in vitro fermentation of tannin-containing browse material by some African herbivores than others (Odenyo et al. 1999). Tannin binding by saliva chemicals, rather than metabolism or tolerance of browse tannins, provides some of the digestion benefits associated with tannin tolerance (Jones et al. 2001). Rumen degradation of a toxic plant secondary compound (e.g. mimosine) by specialised bacteria has been documented for some ruminant livestock consuming the woody legume leucaena (Leucaena leucocephala; Pratchett et al. 1991; Halliday et al. 2013) illustrating the possibilities for exploiting such specialisation in browser–browse relationships (Shelton and Daizell 2007). Tannin-binding proteins have also been identified in saliva of other browsing, but not grazing, species (Austin et al. 1989).

The presence of MHS, however, is not always a panacea. Despite the substantial diversity in landscape, vegetation and feeding strategies, considerable diet overlap and shared foods have been reported among diverse herbivores in some locations and seasons (Hansen et al. 1985; Kleyhans et al. 2011). Thus, increased competition exists under adverse conditions such as extended droughts, overstocking or other resource deterioration. Resource partitioning and niche differentiation associated with body size and anatomical/physiological distinctions, however, historically contributed to resilient populations of diverse animal species in the eastern African herbivore system for an extended period prior to pressure from human development experienced in recent decades (McNaughton 1984, 1985; McNaughton and Georgiadis 1986; Kleyhans et al. 2011). Under natural conditions, excluding drought years, herbivore use of primary plant production may be only a small portion of the available resource (McNaughton 1985). Thus, some relationships between herbivores and herbage from this extensive ecosystem may relate more closely to very low stocking rates than to stocking levels typical of production agriculture. Recent comparison of herbivore species composition and stocking density demonstrate decreases of tall-growing, palatable grasses and increases of stoloniferous grasses with dense cattle stocking; however, diversity of grass species and herbage-layer structure are maintained with stocking by multiple species of native African herbivores (Treydte et al. 2013). Even though grazing species in both treatments selected for palatable grass, prevailing livestock production and wildlife conservation management approaches contrast in their effects on the ecosystem (Treydte et al. 2013). Whether animal-species diversity can compensate for greater stocking rates, thereby achieving the same carrying capacity without resource over-use, remains to be researched in intensive production systems.

Increasing demands on resources within the region, which arise from encroachment of row-crop agriculture and human settlement along borders of natural areas and through introduction of livestock within grazing areas, are changing habitat and herbivore relationships. Recognition that herbivore biomass supported per unit of primary production is near an order of magnitude greater in agricultural systems than in natural ecosystems (Oesterheld et al. 1992) indicates that animal husbandry practices associated with livestock introduction will likely increase stocking pressure and decrease herbage mass availability regardless of species diversity. Remaining natural ecosystem remnants and the component wildlife populations affect, and are substantially affected by, associated livestock production. Functioning African savanna ecosystems can provide enhanced cattle diet quality and animal performance from associated wild ungulate grazing during wet seasons similar to facilitation from grazing successions of native wild herbivores, although dry season competition can depress intake and performance of cattle (Odadi et al. 2011a). Relative densities of individual species, resulting grazing pressure and existence of previously ungrazed swards in the landscape determine whether potential wet-season facilitative grazing responses can actually occur (du Toit 2011). Perhaps livestock production can also provide facilitative effects on wildlife populations in some remnant areas as indicated by wildlife benefits from management treatments of pastural burning, nutrient concentration in overnight livestock enclosures and altered tree cover (Riggins et al. 2012). Thus, while livestock introduction adds grazing pressure to these natural systems, inputs provided for livestock can also be beneficial to native herbivores. Similar livestock–wildlife interactions can be expected in other systems, especially where native bulk grazers are absent.

Contrasts of natural and agricultural systems highlight some key aspects of African wild herbivore systems essential to their function. Use intensity of primary production in extensive natural systems has been low enough that grass quantity and browse nutritive value have not typically been limiting during normal growing seasons. It follows that distinct grazing and browsing strategies function most effectively under specific non-limiting conditions. Grass availability must not excessively limit performance of grazing species. Likewise, nutritive value of browse, even though the browse species may be widely dispersed and interspersed with lower-quality materials, must meet browser nutrient requirements. Combining these grazer and browser requirements leads to the concept that mixed stocking of grazing and browsing herbivores will likely be most biologically beneficial within landscapes of heterogeneous vegetation providing herbage of some minimal quantity and quality of both monocotyledons and dicotyledons (forbs, woody-legumes and other shrubs, and trees).
Including selectivity range within each browser and grazer category would add further niche utilisation. Optimal proportions of grazer and browser herbivores to stock will depend on proportions of the herbage types available and sustainability of these plant species. Potential benefits from multiple grazer or browser species or addition of distinctly intermediate feeders will increase with complexity of the grass and browse herbage available. Just as establishment and maintenance of highly productive ‘grazing lawns’ of the Serengeti Plain depend on multiple species of grazing herbivores (McNaughton 1984), optimal utilisation of highly complex grassland mixtures may require species combinations representing more diverse feeding strategies than is required for intensively managed monoculture pastures. Combinations of animal sizes and functional adaptations of component species will affect herbage use efficiency in particular habitats and landscapes depending upon the composition and complexity of the herbage resource.

Review of past multiple-species stocking

Texas rangeland example

Native grasslands and woodlands in many regions of the world have long histories of livestock grazing with multiple species often involved. Aspects of rangeland–livestock interactions in many such ecosystems are illustrated by results of both commercial production and research from the grasslands and shrublands of southern Texas through the Edwards Plateau of west-central Texas, USA. Cattle, sheep and goats are common livestock in much of the region, and white-tailed deer (Odocoileus virginianus) are a widespread native species. During the past 100 years of cattle grazing and fire suppression, vegetation of the Edwards Plateau changed from predominantly grassland to essentially shrub-dominated woodland (McMahan and Ramsey 1965). These changes produced vegetation structure more similar to that of the shrub-dominated portion of southern Texas than to the former grassland (Johnston 1963). Stocking rates of domestic grazers (cattle and sheep) periodically exceeded sustainable levels on substantial portions of the area contributing to disappearance of grasses, which were replaced by brush, thereby reducing carrying capacity of grazing livestock, particularly during extended periods of reduced rainfall (Archer 1989).

Livestock effects on deer

Early efforts to assess effects of domestic livestock on deer population dynamics in the Edwards Plateau of Texas in the USA revealed distinct competition between mixed livestock species and white-tailed deer with increasing intensity of competition as stocking rate increased. Continuous grazing with a heavy stocking rate from a combination of cattle, sheep and Angora goats resulted in no fawn survival and maintenance of only about half as many adult deer as did lighter stocking rates (McMahan and Ramsey 1965). Fawn survival with no livestock grazing was about four times that obtained at light livestock stocking rates.

Production of each livestock species can also be negatively affected by increasing stocking rate and repeated herbage removal over years (McMahan and Ramsey 1965). Even light stocking on rangeland of excellent condition resulted in competition among sheep, goats and deer (Bryant et al. 1979). During autumn and winter, competition occurred for browse; during early spring, competition occurred for forbs; and any time immature grass was available, competition for this forage resulted in reduction of mature grass available to cattle later in the season. Sheep were particularly competitive with deer for succulent grass and forbs, and goats were most competitive for browse (Bryant et al. 1979). Deer diets from this competitive foraging were below recommended levels of crude protein in January and February and very low in digestible energy during winter and again in early summer (Bryant et al. 1980). Rangeland in excellent condition, however, did provide deer diets greater in crude protein and digestible energy in all seasons except winter than did rangelands in poor condition (Bryant et al. 1981). Again, energy was deficient in deer diets from these rangelands, especially for fawn growth following weaning, although the deficiency was greater in diets from rangeland rated as poor compared with rangeland in excellent condition.

Although both are primarily browsers, some unique differences have been detected between goats and white-tailed deer. Goats change bite strategy with increasing stocking rate, but no such adjustment was observed from deer (Ekblad et al. 1993). Distinct differences in shrub species selection occurred for the two species on a rangeland site dominated by palatable shrubs. In addition, different foraging strategies indicate that goats and deer apparently perceive and utilise complex shrub communities differently, further reducing competitive effects between these two browsing species (Etzenhouser et al. 1998).

Although competition from cattle is less detrimental to deer than competition from small ruminants such as sheep and goats, evaluation of different cattle grazing systems and stocking rates resulted in none of the approaches providing adequate dietary protein to meet growth and lactation requirements of deer (Ortega et al. 1997). Continuous stocking of cattle at moderate stocking rates appeared to provide the best opportunity for deer to obtain preferred forbs containing greater nutrient concentrations.

Detrimental effects of cattle grazing on deer nutrition (Kie et al. 1991) are consistent with the concept that browsing wildlife thrive in systems that allow high-quality herbage selection within time constraints dictated by highly selective browsing and vigilance against predators (Stewart et al. 2003). Substantial reductions in nutrient availability can restrict adequate diet selection in the time available. Livestock, whether directly selecting the preferred herbage material of deer or simply reducing the overall supply from which to select, impose greater limitations on these wildlife than might be expected, especially if time constraint is not considered. Animal husbandry, which provides the ‘order of magnitude production difference’ (Oesterheld et al. 1992) between these systems, deserves consideration. Short-term nutrient deficiencies, which are overcome with strategic supplementation of livestock, may be substantially debilitating or even fatal to wildlife not provided adequate access to the supplementation. Providing wildlife access to such supplementation, however, may increase problems with pests, diseases and predators. Pests, such as parasites and diseases, when of economic importance, are controlled...
in efficient livestock production programs but persist to provide perhaps only chronic or sometimes drastic effects on wildlife. Livestock are not typically distracted during feeding activities by the possibility of predator appearance, whereas most wildlife are limited or distracted from feeding activities to some extent by vigilance against predators. Adequate herbage availability for production of livestock, whether small selective-foraging ruminants or cattle, will apparently often not provide sufficient resources for productive white-tailed deer populations in a landscape with forage resources fully stocked for livestock production, even if stocking adjustments are made to compensate for the number of animal units of deer present.

**Competition and complementarity among livestock species in rangeland ecosystems**

Greater opportunity exists to manipulate stocking rate and the proportions of individual animal species in cultivated pastures as has been reported for rangeland situations. Proportions of different vegetation types and plant species within vegetation types can greatly affect results from various stocking approaches (Warren et al. 1984). Dietary differences occurred between sheep and goats, among five breeds within species, in three range types at different sampling dates within range types (Warren et al. 1984). Relative plant species abundance, changes in plant acceptability over time, and inherent tendencies of these herbivores to shift grazing behaviour over time apparently contributed to diet variations. However, short-term responses may not adequately reflect long-term effects. Stocking rates of combined sheep, goats and cattle evaluated by McMahan and Ramsey (1965) were within the range of productive livestock enterprises as indicated by the negative response of individual animal weight of offspring of each species juxtaposed to positive response of total offspring weight of each species to increasing stocking rate. Whether this range of stocking rates or proportions of individual livestock species provided an appropriate level for sustained use of the resource is uncertain. Apparently, the historic grazing regime of at least a portion of the Edwards Plateau of Texas, where this research took place, was not sustainable from the observation that grassland was converted to woodland during the initial several decades of livestock use (McMahan and Ramsey 1965).

Dominance of sheep diets by grass with some browse, goat diets of equal proportions of grass and browse, and limited consumption of forbs despite their availability reported by Bryant et al. (1979) provide some unique insights. Despite generalisations about forb and browse selection, Bryant et al. (1979) proposed that, under these conditions, both sheep and goats selected green forage. Apparently, opportunity to consume succulent, recent growth of green herbage can be a primary selection factor regardless of availability of other herbage types of lower nutritive value. Greater digestible energy of the predominantly grass diet of sheep than of the predominately browse diet of goats (Bryant et al. 1980) indicates that the browse available was not of sufficient energy value to justify the additional energy required for selective browsing, although protein or some other specific nutrient may have justified the expended energy cost.

Current literature provides a snap-shot of livestock–herbage relationships from a variety of animal and vegetation combination possibilities (McMahan 1964; Stewart et al. 2002). Individual management needs will benefit from compositing available technical information relevant to specific vegetation and spatial resources through seasons and variations among years along with local knowledge and experience with specific environments. This is illustrated by multiple-species stocking in a pastoral system in Kenya where diet dominance by herbaceous plants for cattle and sheep and by browse for goats (Nyangito et al. 2009) was somewhat similar to results from Texas rangelands. Optimal energy intake by cattle, energy efficiency in foraging, and livestock production, however, were enhanced by resource management under a mobile communal pastoral system (reminiscent of rotational stocking) compared to a more static fixed land-resource ranching approach based on fenced and fixed stocking.

**Stocking cultivated pastures with multiple animal species**

As with multiple animal species on rangelands, such grazing on cultivated pastures has a long and widespread history. In contrast to the complex vegetation types of rangeland, however, intensively managed pastures may consist of grass monoculture or a rather simple mixture of grasses and legumes (Sanderson et al. 2004). Pastures managed to maintain only a limited number of plant species provide less distinct biological advantages for stocking with multiple species of livestock than do more biodiverse vegetation resources (Muir et al. 2014). Even when biological advantages are limited, economic opportunities may be available with multiple animal species. Multiple animal species also provide an alternative to some of the standard practices of single-species production systems. Many undesirable plants in pastures grazed only by cattle can be preferred forage species for sheep or goats reducing cost of weed control treatments (Krueger et al. 2014). Balancing the weed or brush control objectives with the need for a continuing supply of acceptable herbage for sheep or goats may appear counter-productive to managers accustomed to intensively managed monoculture grass pastures grazed by cattle. Benefits from adding cattle to small ruminant grazing systems include aspects indirectly related to the herbage resource, such as effects on internal parasite control, which may be more meaningful to the production system than herbage-related effects (Muir 2011).

Stocking multiple animal species has provided production increases even on some temperate pastures of relatively high and uniform nutritive value. Mixed stocking of cattle and sheep or sequential stocking of the two species on pastures of perennial cool-season grass and clover in the United Kingdom provided increased animal production compared to stocking only sheep, but factors providing the response were not identified (Fraser et al. 2007). Stocking cattle and sheep together in perennial grass–clover pasture in Virginia, USA, provided increased rate of gain by lambs for earlier weaning but no advantage in total production with lambs weaned at a target weight and removed from the system (Abaye et al. 1994). The production benefit was increased time for recovery of body weight
by ewes between weaning and breeding season. On temperate annual pastures of several grasses and legumes in Australia, diets of sheep and goats differed but both exceeded nutrient requirements when forage availability was adequate (Gurung et al. 1994). Mixed grazing of these two animal species on temperate annual pastures provides distinct seasonal effects and overall responses ranging from complementary to competitive depending on stocking rate (McGregor 2010). Effects of combining animal species on pastures with limited opportunity for differences among the species in foraging strategy or digestive efficiency to be expressed should be less than those possible with more complex vegetation.

Pasture development, including plant species selection and management approaches, has primarily targeted plants for grazing animals. Because of limited success with herbaceous legumes in specific environments, woody legumes have received attention in pasture legume evaluation programs (Shelton et al. 1991; Topps 1992; Hove et al. 2003; Dubeux et al. 2014) primarily for difficult sites in some warm environments. A degree of success with stocking multiple animal species on pastures of plant species developed primarily for grazing animals suggests greater possibilities for ecologically engineered vegetation that contributes both selected grass and browse components for mixed stocking of grazing and browsing animals. Some specific assessments of browse species for sheep and/or goats have been reported (van Eys et al. 1986; Mueller et al. 2001; Degen et al. 2010). As expected, acceptability and potential usefulness varied considerably with substantial potential noted for some species.

Development of herbage resources consisting of mixed forage and browse plants for use by combinations of grazing and browsing animals presents a complex challenge. The complexity could be particularly justified by the potential to address ecological concerns in highly disturbed areas that lack potential for sustainable native vegetation recovery. Costs of nitrogen fertiliser and pasture herbicides, both economically and ecologically, encourage sustainable alternatives that could include substituting management complexity for chemical inputs. Potential invasiveness of introduced woody species is a distinct hazard (Mwangi et al. 2008; Pitman 2009) requiring caution and indicating substantial advantage for use of native species.

**Intensified use of multiple-species stocking on cultivated pastures**

*Adapting processes from rangeland systems and herbivore diversity*

Native grasslands and rangelands are mostly heterogeneous in space and time. Heterogeneity is characterised by a greater number of plant species from different functional groups. Resource utilisation by this diverse vegetation can be more efficient because plant species within the mixture can exploit different spatial niches, below- and above-ground. Seasonal distribution of vegetation growth is complementary, filling gaps throughout the year. These characteristics make native grasslands and rangelands more resilient and potentially more productive when contrasted with monospecific systems under similar inputs (Bakker et al. 2006). Tilman et al. (1997) observed that functional composition and functional diversity were key indicators explaining plant productivity, plant nitrogen and light penetration (Figure 1). These authors concluded that habitat modifications and management practices that change functional composition and functional diversity are likely to have large impacts on ecosystem processes. Natural systems also provide a broader range of forage chemical composition that, when opportunity for selective grazing/browsing is provided, allow foraging animals greater opportunity to more readily meet their nutritional needs. Applying these heterogeneity, resilience and complexity themes to cultivated pastures would entail increasing natural resource use efficiency by increasing plant diversity while matching animals to the vegetation rather than vice versa.

Natural systems illustrate the concept of matching the animal to the vegetation as wild species select appropriate habitats within heterogeneous landscapes. Diversity in vegetation can be more efficiently utilised through equivalent herbivore diversity, especially notable with large herbivores (Bakker et al. 2006). Grazers and browsers typically prefer different vegetation niches, thereby reducing overlap in their diets (Trydte et al. 2013). Grazing habit,
reach, forage prehension and physiological mechanisms during the digestive process, which differ from one animal species to another, provide a gamut of management opportunities. Because grass canopies tend to be denser than browse canopies, grazers in general are more likely to ingest bulk forages. By contrast, browsers are generally more selective, with reduced bite size but usually greater forage nutritive value per bite vis-à-vis the whole plant value. Browse usually has a greater concentration of rapidly fermentable soluble components than grasses, but also tends to have greater lignin concentration, with resultant lower digestibility (Gordon and Illius 1994). All of these provide opportunities for multiplying per area productivity by introducing multiple animal species.

Based on comparative morphological studies of all portions of the digestive system of 65 ruminant species from four continents, Hofmann (1989) classified three overlapping morphophysiological feeding types (Figure 2): concentrate selectors (40%), grass and roughage eaters (25%), and intermediate opportunistic, mixed feeders (35%). Combinations of these different feeding types that match the vegetation should reduce overlap in the diet and may lead to improved efficiency in feed utilisation on heterogeneous vegetation. For example, Garine-Wichatitsky et al. (2004) evaluated bush selection along foraging pathways by sympatric impala (Aepyceros melampus) and kudu (Tragelaphus strepsiceros). Both ungulates were selective for the bush categories, but kudu were consistently more selective than impala. These differences lead to a low overlap in resource use between the two browsers in this savanna type. Browsers also tend to have greater capability to change their diet and dietary preferences in response to changes in browse availability than do grazers (Kerley et al. 2010). Ultimately, browsers can shape ecosystem structure and function by altering interspecific competition among plants (Augustine and McNaughton 1998).

**African savannas and forests: template for cultivated pasture?**

Diverse vegetation and multiple ruminant species occur naturally in African savannas and forests. These ecosystems are dynamic yet resilient over time likely due to their diverse vegetation (species richness and functional groups) and multiple grazers and browsers (Treydte et al. 2013). The challenge, however, is to recreate and, more difficult, sustain a similar dynamic in cultivated pasture systems. Provenza et al. (2007) suggested that understanding complementarities in time and space among plant species is a key step to recreating native plant–herbivore ecosystems. Characteristics such as contrasting chemical composition, growth forms and structures, phenology and tolerances of erratic temperatures and rainfall regimes are important components affecting this complementarity. Heterogeneity starts at the landscape level, then habitats within those landscapes, and finally species within habitats. Foraging decision by African elephants (Loxodonta africana), for example, also has this top-down approach (Shrader et al. 2012). Fire, fence and water distribution are likewise important components driving the heterogeneity in the vegetation and consequent movement of ruminants in the landscape (Beer and van Aarde 2008; Loarie et al. 2009a, 2009b; Johansson et al. 2010). Fuhlendorf et al. (2010) argued that an evolutionary model of disturbance (pyric-herbivory) suggests that grazing and fire interact through a series of feedbacks, causing gradual but predictable shifts in the vegetation. They suggest that spatially controlled interaction of fire and grazing can be used to create heterogeneity in grassland ecosystems. Observation and study of natural ecosystems is one approach to apply their multifaceted aspects and interactions between soil, plant and animal communities to cultivated systems. Because of their inherent plant and animal species complexity, regenerating native ecosystems, rather than replacing them, will often be the most effective long-term solution for efficient use of natural resources in grasslands where such regeneration is possible.

**Plant diversity facilitates animal nutrition**

Individual ruminants can better meet their needs when offered a variety of foods that differ in chemical composition, including nutrients and toxins, than when constrained to a single food (Provenza et al. 2007). Thus, plant diversity can facilitate animal nutrition and may improve energy and protein intake. For example, Wang et al. (2010) observed an asymptotic relationship between plant species richness and voluntary intake by sheep (Figure 3). These authors suggested that plant species richness in rangelands benefits both herbivore production and conservation of biodiversity, advantages that can be derived from equally diverse cultivated pastures (Sanderson et al. 2007). When herbage quantity is not limiting, synergism and antagonism among chemical compounds and their dynamic in the digestive tract of ruminants drive grazer/browser preferences. Condensed tannins (CT), for example, bind to protein and other large organic molecules and may reduce intake. If CTs are ingested in smaller amounts, however, they often reduce nitrogen losses and improve protein utilisation by herbivores (Tedeschi et al. 2014). In rangeland ecosystems, plant diversity is the rule and not the exception. In these environments, animals are able to select plants that complement and enhance one another structurally, functionally and biochemically (Provenza et al. 2007).

Grazing behavior and intake, however, interact with the feed supply–demand balance, pasture composition and grazing method, all of which influence selection of forage by herbivores (Soder et al. 2009). Chapman et al. (2007) observed that these interactions are not completely understood, even for relatively simple pasture communities with only two predominant plant species. These authors indicated that interactions are much more complex in heterogeneous vegetation. Intra- and inter-annual variability influencing soil–plant–animal relationships must be taken into account in order to improve our ability to predict primary and secondary productivities in ecosystems of diverse plant communities.

Heterogeneity in vegetation occurs not only in space, but also in time (Rhoades 1995). Abiotic and biotic factors interact with the vegetation, changing the forage available and herbivore ingestive behaviour over time (Drescher et al. 2006). For example, sequential use of vegetation by browsers with different feeding habits can create conditions for plant species to emerge sequentially resulting in
Figure 2: African ruminant feeding types (modified from Hofmann 1989)
facilitative grazing effects. The new vegetation can then be utilised by another ruminant type in sequence. Makhabu et al. (2006) evaluated the impact of African elephant on shoot distribution of trees and rebrowsing by smaller browsers. They observed that elephants apparently facilitate browsing by mesoherbivores, such as impala and kudu, by generating ‘browsing lawns’. Different vegetation strata also allow access of browsers according to their size. Hofmann (1989) reported body size ranging from 3 to >1 000 kg in the 150 known ruminant species. This size range could be used within cultivated pastures. Using different ruminant species at different times or in varying sequences dictated by inherent foraging behaviour and nutrient needs could utilise soil, climate and plant resources more effectively over space (strata), time (season) or sequence (both short- and long-term). Van Soest (1982) suggested that ruminant production efficiency from a nutritional perspective could be enhanced by either selecting for larger animals with large rumen capacity and faster passage rates to increase forage intake for increased production or selecting for smaller size with enhanced diet selection ability for increased efficiency. Either of these strategies would require a specific narrow herbage resource based on either bulk herbage production or selective foraging opportunity. A diverse vegetative resource harvested by herbivore species utilising wide-ranging foraging strategies optimises opportunities for both bulk grazers and selective browsers. It is interesting to note, however, that after controlling for the effects of body mass, there is little difference in digestive strategy among African ruminants with different gut morphological adaptations (Gordon and Illius 1994).

Challenges of establishing and managing multiple plant species for persistence
Managing cultivated monocultures should be inherently less difficult than management of pastures containing numerous plant species. The latter entails balancing the physiological differences among plants that are further confounded by land management, species-specific behaviour of grazing animals, and the presence of other wildlife, insects, diseases or other pests (Sanderson et al. 2007). Plant physiology and anatomy are interdependent and drive the resilience of specific plant species within an environment and also influence how competitive species are in comparison to other plant species present (Caldwell 1987; Callaway and Walker 1997).

Plant physiology is interconnected with anatomy and drives vegetation composition, which affects animal behaviour such as selectivity, range of grazing area and preference. For example, C₄ photosynthesis allows for greater CO₂ assimilation than that of C₃ species. The C₄ grasses have smaller stomata than C₃ grasses when stomata are at similar densities, which likely underpins the greater water use efficiency and competitive ability of C₄ grasses in drier and hotter environments (Taylor et al. 2012). As a result of the anatomy providing more efficient photosynthesis, C₄ grasses have reduced digestibility and crude protein than C₃ grasses (Wilson et al. 1983). In native rangelands of semi-tropical environments, seasonal variation in forage species may facilitate C₄ grass dominance in hot months but C₃ grass species in cooler months (Ehleringer et al. 1997). Management that relies on heavy grazing of a paddock during cooler months where
animals, livestock and/or wildlife preferentially select C₃ species can decrease said plant species, and begin a cycle in which greater resources are available to ungrazed plant species resulting in plant population shifts (Ellison 1960; Jameson 1963). For example, cattle tend to patch graze and select for forbs as compared with North American bison (Bison bison) which exhibit less tendency for patch grazing and a stronger preference for grasses (Plumb and Dodd 1993). A mixture of cattle and bison results in decreased overall selection compared with grazing by cattle alone (Plumb and Dodd 1993). A monoculture pasture requires only knowledge and practice of the ideal management for the persistence of one particular forage species. Introduction of additional plant species requires systems-scale management for persistence of multiple species due to the complexity and interactions of plant physiology, grazing management, animal behaviour and other abiotic plant stressors (Sanderson et al. 2007; Muir et al. 2011, 2014). Although more challenging than monoculture forage systems to manage, mixed forages provide opportunity to increase the diversity of the types of herbivores managed within a pasture.

In warm, temperate climates, such as some portions of the southern USA, complex pasture plant mixtures could readily include warm-season grasses, cool-season grasses, and herbaceous warm- and cool-season legume species, with woody legumes further enhancing plant structural diversity and herbage variety (Muir et al. 2014). Both distribution of forage through the year and herbage suitable for grazing and browsing herbivores would be enhanced. Establishing and maintaining such mixtures of plants will require both further research efforts and considerable experience for development of appropriate management expertise. Perhaps initial progress can be realised from augmenting deteriorated rangelands with appropriate native plant species from the diverse functional groups to restore functions of particular rangeland ecosystems.

**Nutritional needs of various animal species and classes**

Nutrient requirements are determined primarily by metabolic body size with correlating divergence in morphology (Shipley et al. 1994); therefore, the nutrient requirements among various genera and species of livestock vary widely. Generally, smaller ruminant livestock have less dry matter intake but greater net energy requirements for maintenance, growth and lactation (Table 1). Growth rates may therefore be greater for the smaller species but conversion efficiencies may be lower vis-à-vis larger animals with lower metabolic rates (Spalinger and Thompson Hobbs 1992). Diets for smaller grazing livestock must therefore have greater nutrient density and faster passage rates. Livestock evolved to meet these physiological needs, including prehensile organs to allow for selection of nutrient dense forage or browse (Gordon 2003). For example, maintenance requirements of Bos indicus cattle are 10% less than that of B. taurus (NRC 2000). Some breeds may not differ (Tedeschi et al. 2002), whereas B. indicus cattle do have lower maintenance energy requirements (Calegare et al. 2009). In some cases, differences in maintenance energy requirements are greater within breeds than among breeds (Sainz et al. 2013). Within a species and breed of livestock, physiological state is the primary determinate of nutrient requirement. Regardless of genus, lactation requires the greatest nutrients, pregnancy and growth require less energy and protein, and maintenance is the least nutrient-demanding physiological state.

The implication of the various nutrient requirements of domestic livestock genus and physiological state is that different genera of varying physiological states can be managed on a single unit of land supporting heterogeneous vegetation to increase the efficiency of grazing. Ideally, MHS mixes would have no forage selection overlap. For example, browsing goats and grazing sheep would have little overlap. In such ideal, albeit unlikely, scenarios, co-stocking sheep and goats may increase carrying capacity of a given land unit when forage that one species will not consume is utilised by the other livestock species (Animit and Goetsch 2008). Similarly, when brush and grass species are present, cattle and goats are options for co-stocking, which allow for increased herbage removal while meeting the nutritional requirements of both livestock species (Papachristou and Platis 2010). Alternatively, livestock of varying physiological status could be stocked in different methods. This includes creep stocking, whereby suckling livestock are allowed free access into a separate paddock that contains forage with greater nutritive value than that provided to the lactating dam. This approach may increase the average daily gain of ruminant calves later in the lactation cycle as milk production declines (Foster et al. 2013). Legume protein banks are options when growing, pregnant or lactating livestock are allowed access and maintenance animals excluded. Alternatively, legume protein banks can be planted for small ruminants as herbaceous or woody legume species for sheep or goats, respectively. Frontal stocking or forward creep stocking is another stocking management method that increases forage efficiency and is conducive to grazing livestock of different species or physiological status because selection and uniform grazing are increased (Volesky 1990; Volesky et al. 1993).

**Challenges of managing and marketing multiple herbivore species**

The benefits of managing multiple livestock species include increased diversity, reduced economic risk, enhanced forage-use efficiency and greater sustainability. Challenges in MHS management versus a single herbivore species arise from the complexity of such systems and the increased time and management input required. Supplemental feeds are the greatest input costs of modern livestock production, and supplemental feeding is required when the physiological demands of the animal are greater than that which the forage can provide, primarily during gestation and/or lactation for mature animals. Differing gestation lengths or seasons of livestock species may increase the length of the supplementation period, where supplement is provided. In addition, breeding management, vaccinations, processing of new-born animals, weaning and stocking require time and resources that may be increased due to managing multiple livestock species.

Despite increased management demands of MHS systems, these may still be economically sustainable due to increased prices from niche markets and decreased...
In more commercial settings where cattle markets predominate, managing MHS pastures often involves using small ruminants for weed or brush control or taking advantage of small, local niche markets. The rather drastic worldwide increase in pasture production costs, particularly fertiliser and herbicides, which occurred in 2008, suggested a need for a new production philosophy for survival of pasture-based livestock production (Pitman 2011). Currently high beef prices have solved the problem created by the apparently devastating price increases of pasture production inputs. Opportunity now exists to increase

### Table 1: Summary of the daily dry matter intake and crude protein, net energy and total digestible nutrients requirements of various species and classes of domesticated livestock. ADG = average daily gain, BW = body weight, CP = crude protein, DMI = dry matter intake, NE\textsubscript{g} = net energy gain, NE\textsubscript{l} = net energy lactation, NE\textsubscript{m} = net energy maintenance, TDN = total digestible nutrients

<table>
<thead>
<tr>
<th>Animal species</th>
<th>Class</th>
<th>Nutrient requirement</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>DMI (kg d\textsuperscript{-1})</td>
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<tr>
<td>Beef cattle (Bos taurus\textsuperscript{1})</td>
<td>Growing steer (250 kg; 300 g d\textsuperscript{-1} ADG; 454 kg finishing)</td>
<td>6.9</td>
</tr>
<tr>
<td></td>
<td>Growing steer (400 lb; 330 g d\textsuperscript{-1} ADG; 544 kg finishing)</td>
<td>10.0</td>
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<td></td>
<td>Replacement heifer (544 kg mature)</td>
<td>8.8</td>
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<tr>
<td></td>
<td>Pregnant replacement heifer (544 kg mature; nine-months pregnant)</td>
<td>11.1</td>
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<tr>
<td></td>
<td>Pregnant cow (544 kg mature)</td>
<td>11.0</td>
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<tr>
<td></td>
<td>Lactating cow (544 kg mature; 9 kg d\textsuperscript{-1} peak milk)</td>
<td>12.6</td>
</tr>
<tr>
<td>Dairy cattle\textsuperscript{2}</td>
<td>Small-breed cow (454 kg; 90 d in milk; 30 kg milk d\textsuperscript{-1}; maintain BW)</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td>Large-breed cow (680 kg; 90 d in milk; 45 kg milk d\textsuperscript{-1}; maintain BW)</td>
<td>12.7</td>
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<tr>
<td>Goats\textsuperscript{3}</td>
<td>Meat, wether (30 kg; 100 g d\textsuperscript{-1} ADG)</td>
<td>1.0</td>
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<tr>
<td></td>
<td>Meat, wether (80 kg; 150 g d\textsuperscript{-1} ADG)</td>
<td>2.6</td>
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<td></td>
<td>Meat, mature wether (100 kg mature)</td>
<td>2.4</td>
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<tr>
<td></td>
<td>Dairy, mature doe, late pregnancy (100 kg mature)</td>
<td>3.1</td>
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<tr>
<td></td>
<td>Dairy, mature doe, lactating (120 kg mature; 3% milk fat)</td>
<td>3.6</td>
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<tr>
<td>Sheep\textsuperscript{4}</td>
<td>Lamb, weaned (20 kg; 250 g ADG)</td>
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<td></td>
<td>Replacement ewe (70 kg mature)</td>
<td>1.2</td>
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<tr>
<td></td>
<td>Ewe, lactating twins 6–8 weeks (70 kg mature)</td>
<td>2.8</td>
</tr>
<tr>
<td>Water buffalo\textsuperscript{5}</td>
<td>Growing steer (250 kg; 250 g d\textsuperscript{-1} ADG)</td>
<td>5.5</td>
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<tr>
<td></td>
<td>Growing steer (400 lb; 250 g d\textsuperscript{-1} ADG)</td>
<td>7.7</td>
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<tr>
<td></td>
<td>Replacement heifer (500 kg mature)</td>
<td>11.0</td>
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<tr>
<td></td>
<td>Lactating cow (650 kg mature; 8 kg d\textsuperscript{-1} peak milk)</td>
<td>15.1</td>
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\textsuperscript{1} NRC (2000)
\textsuperscript{2} NRC (2001)
\textsuperscript{3} NRC (1981)
\textsuperscript{4} NRC (1985)
\textsuperscript{5} Bülbül (2010)
production options while beef prices are high and existing approaches are profitable. The inevitable cycling of cattle prices to lower levels will likely, as during past decades, devastate many livestock production operations restricted to single-animal enterprises and high-input forage production. Resilience provided by diverse animal species grazing diverse herbage resources could increase economic stability of individual operations and regional economics based to large extents on grazing resources. Existing information to efficiently mobilise such complex pasture and animal systems is highly inadequate. A starting point for building the needed information base is available. Perhaps an early step in the process of developing complex, sustainable pasture systems harvested by multiple animal species could be identification of grasses and shrub legumes adapted to environments too difficult for traditional herbaceous legumes with subsequent development of animal species combinations providing efficient harvest of the primary production within sustainable limits.

Research and development of productive cultivated pasture systems that can sustain MHS or classes will necessarily involve a variety of topics for pasture science including:

1. Design MHS complexes that maintain plant equilibrium without onerous inputs or unrealistic management requirements
2. Characterise establishment, soil fertility and physiology of diverse plant populations required for MHS pasture vis-à-vis monospecific systems
3. Fully utilise the current stable of domesticated ruminants for MHS pastures
4. Initiate MHS pasture research into non-traditional ruminant production
5. Research the systematic use of native animal diversity for MHS
6. Harvest plant diversity more completely by manipulating pastured MHS over time and space
7. Redirect interest to arboreal and browse agronomy as well as the animals that target those canopies
8. Adapt MHS mixes and genetics to persistent, diverse and productive pastures rather than vice versa
9. Characterise MHS effects on multi-plant species pastures
10. Strive for greater integration of multi-species cultivated pastures with native rangelands for MHS systems
11. Focus on soil-resource and climate utilisation and dynamics of plant–animal interactions in diverse pastures; the goal would be to more fully and sustainably harvest soil and climate resources (soil profile depths, nutrients and moisture) for conservation of natural resources.
12. Train the next generation of pasture scientists and pasture managers in MHS as well as plant-diverse ecosystems

Conclusions

Complex but stable natural grassland ecosystems dominated by heterogeneous vegetation and diverse assemblages of large herbivores may provide insights for management of productive, sustainable MHS cultivated pasture livestock systems. Even though management practices such as strategic nutrient supplementation and pest control can make cultivated pasture systems more productive than natural systems, sustained plant diversity, resource partitioning among MHS, and multiple foraging strategies characteristic of complex natural ecosystems may guide the application of these principles to intensively managed cultivated pasture systems.

Cultivated pastures containing grasses and legumes typically require continuing fertiliser, herbicide and management inputs. Grazing with more than one species of livestock and introduction of a diverse plant component, including herbaceous and woody legumes, could enhance soil nutrient cycling, biological nitrogen fixation, and herbage harvest efficiency to sustain greater productivity with reduced dependence on chemical inputs. Complex vegetation and herbivore systems could contribute to greater productivity and sustainability of cultivated pasture ecosystems. The combination of economic volatility of purchased inputs and ecological hazards of high input levels suggests that efforts to develop such complex pasture systems based on diverse plant species and multiple species of grazing herbivores may be particularly appropriate for disturbed landscapes where regeneration of native vegetation does not readily occur or where enhanced production is essential for feeding a growing human population.

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