Value of Plant Diversity for Diet Mixing and Sequencing in Herbivores

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Sustainability is first and foremost about ongoing adaptation in ever changing environments. What might that mean in the twenty-first century? Fossil fuels are likely to decline considerably in the first half of the twenty-first century, and the massive deficits are not likely to be alleviated, even with all of the alternative sources of energy (16). This seeming catastrophe will create opportunities as life changes from urban to somewhat more rural, and the communities that emerge come to rely more on foods produced locally, due to our inability to transport goods over the vast distances.

Agriculture is likely to be much more at the heart of these communities than it is nowadays, but its lifeblood will not be so dependent on fossils to fuel machinery or fertilizers, herbicides, and insecticides to grow and protect plants in monocultures, antibiotics and anthelmintics to maintain the health of herbivores, or nutritional supplements and pharmaceuticals to sustain the wellbeing of humans. Rather, from soil and plants to herbivores and people we will need to learn once again what it means to be locally adapted to the landscapes we inhabit. We will of necessity nurture relationships among soil, water, plants, herbivores and people in ways that sustain the production, health and well-being of ecosystems. Plants are likely to be used more as nutrition centers and pharmacies, their vast arrays of primary (nutrients) and secondary (pharmaceuticals) compounds useful in nutrition and health. If fostered, the diversity of nature can provide the creatures with a full range of benefits, including the nutrition and health of plants, herbivores, or people, without many of the costs we sustain nowadays due to our heavy reliance on fossil-fuel intensive fertilizers, herbicides, insecticides and antibiotics.

Animals too are likely to become increasingly locally adapted to the landscapes where they will live from conception to consumption. There will be increased demand for livestock production from pastures and rangelands, as only one third to one half the fossil fuels are required to produce a pound of beef from range as opposed to feedlots. We will again be required to produce ruminants on forages, as nature has done for millennia. There will be a need, as in times past before our heavy reliance on fossil fuels, to produce livestock in systems that match seasonally available forages with production needs, and that match animals anatomically, physiologically and behaviorally to landscapes. To take advantage of these benefits, we must learn to make the most efficient use of what nature provides when she provides it. All these issues are closely linked with growing concerns over lack of energy independence, the physical and financial costs associated with the health-care (obesity) crisis, and climate change.

Natural landscapes are diverse mixes of plants that occurring in mosaics that reflect history of use in concert with soil, precipitation and temperature regimes. For plants, diversity is the rule for species, phenologies, growth forms and biochemistries. Diversity notwithstanding, people typically have dealt with nature's cornucopia by targeting a few species -- those that were abundant, palatable, easily cultivated and harvested -- for sampling and eventual use (11). Of the roughly 200,000 species of plants on earth, only a few thousand are eaten by humans, just a few hundred of these have been domesticated, and only a dozen account for over 80% of the annual production of all crops (9). By focusing on a few species, people transformed the diverse world of plants into a manageable domain that generally met needs for energy and limited intake of toxins (15). In so doing, however, we restricted the genetic basis of crop production to a few plants, relatively productive in a range of environments, and marginalized the broad range of plants valuable in local environments that make up landscapes. We have also discovered only a fraction of the plant mixtures useful in nutrition and health (11), and we have simplified agricultural systems in ways that are having alarming impacts on the health of people as well as aquatic and terrestrial landscapes (31, 32).

Though often successful in the short term, “simplifying” ecosystems typically has lead to ruinous long-term impacts, as shown in marine, forest and rangeland ecosystems (13). By attempting to maximize output of any one component of a system, we inevitably increase the vulnerability of that component of the system to biotic or abiotic stress. Studies of natural systems highlight the benefits of biodiversity for reducing inter-annual variability in production and minimizing risk of large scale catastrophes such as wildfire and outbreaks of diseases and pests (13). The structural and functional diversity of natural systems increases productivity of plant and animal species and enhances resilience. Regrettably, we have neither understood nor valued plant diversity in agriculture, as evident in our persistent attempts to maximize yields of crops and pastures.

Moreover, in attempting to provide food for burgeoning populations, we have selected for a biochemical balance in crops and forages favoring primary compounds and greatly reducing concentrations of minerals and secondary compounds. To increase intake of plants in monocultures and simple mixtures, people had to reduce secondary compounds as they limit how much of any one food people and livestock can consume (40). The outcome is energy- and protein-rich plants low in secondary compounds. The alternative, which we have not pursued, is offering animals a variety of forages that differ in primary and secondary compounds, thereby enabling them to obtain a much greater array of nutrition, health and environmental benefits from nature’s pharmaceutical bounty.

Plant Diversity and Secondary Compounds

Agronomists and ecologists alike have come to view secondary compounds as defenses against herbivory because secondary compounds limit intake (36). Thus, we know little about how herbivores might benefit from secondary compounds (39). The outcomes of all biochemical interactions depend on the dose: nutrients and secondary compounds at high doses can be toxic, but at low doses they have health benefits (7, 10, 40). Herbivores can meet their nutritional needs by eating a variety of complementary plants, and combinations of secondary compounds may more effectively reduce bloat and internal parasites, especially if animals learn to self-medicate on diverse mixtures of plants (54).

As case in point, tannins are increasingly recognized as important in health and nutrition (23), though historically they were thought to adversely affect herbivores by agriculturalists and ecologists alike (42). Eating plants high in tannins is a way for herbivores to reduce internal parasites (21), and tannins alleviate bloat by binding to proteins in the rumen (58, 49, 25). By making protein unavailable for digestion and absorption until it reaches the more acidic abomasum, tannins also enhance nutrition by providing high-quality protein to the small intestines (4). This high-quality-protein-bypass effect enhances immune responses and increases resistance to gastrointestinal nematodes (27, 24). The resulting increase in essential and branched-chain amino acids improves reproductive efficiency in sheep (22). Tannins in the diet are a natural way to reduce methane emission in ruminants (59), which is an important issue regarding ongoing efforts to diminish the influence of livestock on global warming. Finally, tannins eaten in modest amounts by herbivores can improve the color and quality of meat for human consumption (33). More generally, diverse assortments of secondary compounds in the diets of herbivores influence the flavor, color and quality of meat and milk for human consumption, often in ways that are positive (51, 52).

We have learned much in the past 40 years about the roles of secondary compounds in the health of plants, including functions as diverse as attracting pollinators and seed dispersers, helping plants recover from injury, protecting plants from ultraviolet radiation, and defending plants against diseases, pathogens, and herbivores including various insect and bird pests (43, 44). While we were learning of the value of secondary compounds, we were reducing their concentrations and in the process making crop and pasture plants more susceptible to environmental hardships. In their stead, we resorted to fossil fuel-based fertilizers, herbicides, and insecticides to grow and protect plants in monocultures, antibiotics and anthelmintics to maintain the health of herbivores, and nutritional supplements and pharmaceuticals to sustain the wellbeing of humans. Such systems corrupt the health of livestock and humans and gradually degrade economic and environmental health (57). Ironically, we are now attempting to genetically engineer compounds with similar beneficial functions back into plants. To create sustainable agricultural ecosystems, we should be asking how and why nature grew plants in diverse mixtures and re-constructing pastures and rangelands with assorted species of plants that provide resilience through complementary linkages among soil, plants, herbivores, and people (38).

All plants contain secondary compounds that at too high concentrations limit how much of any food an herbivore can eat. Herbivores regulate intake of secondary compounds to ingest adequate levels of nutrients and avoid toxicosis. Eating a variety of foods is the best way to accomplish this objective, as different secondary compounds are processed at different rates via different metabolic pathways, thereby providing multiple avenues for detoxification (12, 34, 35). Variety is so important that animals have built-in mechanisms to ensure that they eat a variety of foods and forage in different locations (34, 35, 2). Offering animals choices on pastures and rangelands allows each individual to meet its needs for nutrients and to regulate its intake of secondary compounds by mixing foods in ways that work for that individual (36, 37, 40). Thus, variety enables individuality and greatly increases the likelihood of providing cells with the vast arrays of primary and secondary compounds essential for their nutrition and health. Conversely, monocultures of plants high in secondary compounds, produced through inappropriate grazing practices or genetically engineered into plants, can create vicious cycles that escalate to the detriment of soil, plants, herbivores and people (41).

Diet Mixing

Foods are complementary when the benefit of consuming foods together exceeds the average benefit of consuming the foods alone (50). When lambs choose between foods that contain either amygdalin or lithium chloride, they eat more than lambs offered a food that contains only one of these secondary compounds; the same is true with nitrate and oxalate (6). Mule deer also eat more when offered both sagebrush and juniper (12.3 g/kg BW), plants that contain different terpenes, than when they are offered only sagebrush (4.2 g/kg BW) or juniper (7.8 g/kg BW) (48). Brushtail possums that can select from two diets containing phenolics and terpenes consume more total food than when they consume diets containing only one of these secondary compounds (8), and the same is true with squirrels (45).

Experience and the availability of nutritious alternatives both influenced food choice when the preferences of lambs with 3 months' experience mixing tannin, terpenes, and oxalates were compared with lambs naive to the toxin-containing foods (53). During the studies, all lambs were offered five foods, two of them familiar to all of the lambs (ground alfalfa and a 50:50 mix of ground alfalfa and ground barley) and three of them familiar only to experienced lambs (a ground ration containing either tannins, terpenes, or oxalates). Half of the lambs were offered the familiar foods ad libitum, while half of the lambs were offered only 200 g of each familiar food daily. Throughout the study, naive lambs ate much less of the foods with secondary compounds if they had ad libitum as opposed to restricted access to the nutritious alternatives (66 vs. 549 g/d) (Figure 1). Experienced lambs also ate less of the foods with secondary compounds if they had ad libitum, as opposed to restricted, access to the nutritious alternatives (809 vs. 1497 g/d). In both cases, however, lambs with experience ate remarkably more than naive lambs of the foods containing the secondary compounds, whether access to the alfalfa-barley alternatives was ad libitum (811 vs. 71 g/d) or restricted (1509 vs. 607 g/d). These differences in food preferences and intake persisted during trials 1 year later.

In a companion study, when access to familiar foods was restricted to 10%, 30%, 50%, or 70% of ad libitum, animals ate more of the foods with secondary compounds and they gained more weight along a continuum (10% = 30% > 50% = 70%) that illustrates animals must be encouraged to learn to eat unfamiliar foods that contain secondary compounds (47). Thus, past experiences and contingencies that encourage animals to learn to mix diets that contain secondary compounds and nutrients help to explain the partial preferences of herbivores, and they provide implications for managing plant-herbivore interactions.

Diet Sequencing

While diet mixing and complementarities among secondary compounds are an important but little understood area of plant-herbivore interactions (12, 40), even less is known about how the sequences of eating plants with different compounds affects foraging, though they appear to be critical. Sheep eat much more food with terpenes when they first eat food with tannins (26). These findings are consistent with landscape-level studies that show ewes with a high preference for sagebrush, a shrub high in terpenes, also consume more bitterbrush, a shrub high in tannins, compared with ewes that have a lower preference for sagebrush (46). While further studies are required to assess how sequence affects food consumption, these data indicate there is a strong effect.

Likewise, cattle steadily decrease time eating endophyte-infected tall fescue when they first graze tall fescue alone for 30 minutes followed by trefoil, alfalfa, or alfalfa-trefoil combination for 60 minutes (18, Figure 2). Conversely, when the sequence is reversed, cattle forage actively on trefoil, alfalfa, or trefoil-alfalfa combination and then forage actively on fescue throughout the 90-min meal. These patterns of foraging are similar with high-alkaloid reed canarygrass (18). Sequence of ingestion thus greatly influences intake of alkaloid-containing grasses by cattle, and we are currently exploring the degree to which their behavior is mediated physiologically (by interactions among tannins, saponins, and alkaloids) or psychologically (wait 30 min to eat the legumes) or both.

Diet Breadth

Plant secondary compounds also increase dietary breadth in herbivores (12). Lambs offered choices among varieties of alfalfa (high saponins), birdsfoot trefoil (high tannins), and endophyte-infected tall fescue (high alkaloids) manifest a strong preference for alfalfa (17, Villalba et al.

unpublished results). When they subsequently receive intraruminal infusions of saponins, tannins, or alkaloids in different grazing periods, they forage in ways that likely reduced the negative and increase the positive postingestive effects of secondary compounds. For instance, lambs infused with saponins decrease their preference for alfalfa and increase their preference for trefoil and tall fescue. Lambs infused with tannins increase their preference for tall fescue, whereas lambs infused with alkaloids decrease their preference for tall fescue. When sheep eat foods high in tannins or saponins along with foods high in alkaloids, the tannins and saponins evidently bind with alkaloids reducing their adverse effects on intake (28, 18, 19). In all cases, regardless of preference, infusions of plant secondary metabolites induced a more even utilization of all the plant varieties on offer enhancing diet breadth relative to periods without infusions. Ruminants thus discriminate the postingestive effects of forages with secondary compounds, and complementarities among forages with diverse secondary compounds are likely not only to increase forage intake, but the nutrition, production, and health of animals as well (54).

Nutrition

With regard to nutrition, lambs first fed alfalfa (saponins) or birdsfoot trefoil (tannins) for 30 minutes, followed by a 3.5-hour meal of either endophyte-infected tall fescue (alkaloids) or reed canarygrass (alkaloids), have higher total intakes, and they digest more dry matter, nitrogen, and energy than lambs not provided with supplemental alfalfa or trefoil (29). Supplementing lambs with legumes does not affect the digestibility of nutrients; rather, providing supplemental alfalfa or trefoil increase intake and as a result increase the amount of nutrients digested. These benefits are achieved when lambs eat less than 30% of their daily intake as alfalfa and less than 13% of their intake as trefoil. By enhancing intake, the legumes thus increase the total amount of nutrients digested. These results are likely due to complementary relationships among secondary and primary compounds in the grasses and legumes that enable lambs to eat more of a combination of foods than of only one food.

Collectively, these findings suggest cattle and sheep regulate intake of plants as a function of interactions between tannins, saponins, and alkaloids and that the sequence in which they eat forages is crucial for increasing their intake of plants that differ in secondary compounds. We do not know if they learn to forage in sequences that optimize intake of secondary compounds or if they simply "eat the best and leave the rest" (36, 37). First impressions influence the development of preferences when animals eat foods with secondary compounds (3, 55, 56), and we are exploring how first impressions from ingesting forages such as endophyte-infected tall fescue, alfalfa, and trefoil in different sequences influences learned preferences for endophyte-infected tall fescue.

Counteracting Toxicity with Plant Diversity

The discovery of high-alkaloid endophyte-infected Kentucky-31 tall fescue, which now grows on 14 million hectares of pasture land in the U.S. (5), was revolutionary for enabling livestock production in the so-called "transition zone" from Missouri and Arkansas to the east coast. Indeed, fescue made Missouri second in the nation in livestock production. Though endophyte-infected tall fescue is not typically classified as a toxic plant, the alkaloids it contains cause severe losses cattle, and a conservative estimate of the impact of fescue alkaloids on livestock exceeds $500 million annually (30). At the same time, the alkaloids so problematic for livestock make the plant highly resistant to drought and many other environmental stressors. As Asay et al. (1) point out "Differences in dry matter yield between 'KY 31' tall fescue infected with the *Neotyphodium endophyte* and its endophyte-free counterpart confirms earlier reports of the positive effect of this fungal organism on forage yield in tall fescue, particularly in water-limited environments." Compared to uninfected tall fescue, endophyte-infected fescue has greater drought tolerance, pest resistance, tiller numbers, biomass, seed mass, seed numbers, and germination rates (14).

Our research suggests eating tannin- and saponin-containing forages increases intake and may reduce fescue toxicity, which highlights the potential major impact of plant diversity generally and biochemical complementarities specifically. If legumes high in tannins and saponins can offset the negative effects of the alkaloids in tall fescue and enhance livestock performance, the economic impact for beef producers coping with fescue toxicosis will be enormous. More generally, other toxic plant problems worldwide may benefit from similar research and applications. While this research indicates the importance of the interactions between forages with different secondary compounds, we are only beginning to understand the complexities involved in diet sequencing based on a limited number of forages and compounds.

Effects of Circuit Grazing

When researchers in France began to study the nutrition of livestock, they were astonished to see the levels of production herders were able to obtain from landscapes. The researchers came to realize that the herders were using empirical understanding of complementarities among forages and landscape diversity to stimulate food intake and more fully use the range of plants available by herding in grazing circuits (20). The circuit includes various phases, all designed to stimulate the flocks' appetite and to enhance use of all of the forage resources in an area. To do so, meals include a moderation phase, which provides sheep access to plants that are abundant but not highly preferred to calm a hungry flock; the next phase is a main course for the bulk of the meal with plants of moderate abundance and preference; then comes a booster phase of highly preferred plants for added diversity; and finally a dessert phase of palatable plants that complement previously eaten forages. Daily grazing circuits are designed to stimulate and satisfy an animal's appetite for different nutrients, and they enable animals to maximize intake of nutrients and regulate intake of different secondary compounds. Moving animals to fresh pastures, or moving them to new areas on rangelands, has the same effect (34, 35, 2). While the idea of variety of foods increasing "foraging motivation" may seem counter intuitive, to French herders it is the essence of how they stimulate a flock's appetite throughout a grazing circuit.

Conclusion

More generally, growing realization of the roles of secondary compounds in ecological systems means they must be considered just as much as primary compounds in the behavior of soil, plants, herbivores and people. Unfortunately, while most labs can routinely conduct any of a number of analyses for primary compounds, this is not the case for secondary compounds. That kind of support is urgently needed both for scientists and practitioners. We also must begin to create data bases describing what is known about possible complimentary and non-complimentary interactions among secondary compounds, their interactions with primary compounds, and their benefits in nutrition and health at in appropriate dosages. Both the support systems and the additional information will enable people to manage grazing on landscapes in ways that enhance our ability to produce domestic and wild herbivores, reduce the abundance of weeds, and use livestock to rejuvenate landscapes.

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List of Figures

Figure 1. Influence of experience and the availability of alternative foods (ad libitum or restricted) on patterns and amounts of intake by lambs of foods containing secondary compounds.

Figure 2. Sequence of forage ingestion influences intake of high-alkaloid forages such as endophyte-infected tall fescue and reed canarygrass by cattle and sheep. They eat significantly more of these grasses if they first eat forages high in saponins (alfalfa) or tannins (birdsfoot trefoil).