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Chapter 3

Understanding Species Traits and Biodiversity Indices to Solve Problems Associated with Legume Persistence in Cropping Systems

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Additional information is available at the end of the chapter

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Abstract

Shading and competition for mineral nutrients by grass impair legume functions and production in mixed cropping systems. Sustained stress from competition and adverse environments contribute to shortened legume life spans in such cropping systems. This creates negative consequences to forage productivity. There are opportunities to solve the challenge of legume persistence by understanding species traits and plant community dynamics that foster coexistence and complementary resource use. Together with species' unique ability to tolerate adverse soil factors such as water stress, acidity and salinity, self-seeding, and shade tolerance are positive traits among legume species that grow in mixed crops. In communities, converging leaf and shoot conformations as well as asynchrony in dry matter distribution among species can avert negative effects of species competition. While seeding ratios can influence forage production and quality, management including harvest frequency and optimizing phosphorus (P) and potassium (K) fertilizers have crucial roles in perpetuating legume growth and function in mixtures with grass. Some facts on species competition for light, water, and nutrient resources; shade avoidance; and biodiversity mechanisms are highlighted in this chapter.

Keywords: legume persistence, competition, species traits, biodiversity mechanisms, crop management

1. Introduction

Legumes are important components of cropping system because of their ecosystem services. Legumes are a rich source of protein as both grains and forages. However, for decades, this group of plants has received immense attention particularly due to their unique ability to fix

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atmospheric nitrogen (N). This primarily involves symbiotic relationships with N-fixing bacteria. Thus, under suitable conditions, the amount of N benefit from legumes can be enough to substitute for inorganic N fertilizers. To this effect, legumes are integrated in non-legume crops as intercrop or rotational crop [1]. On the other hand, the need for production of forages sufficient to support optimum livestock production calls for combination of grass with legume crops. The benefits of such cropping systems are well documented. This includes enhanced forage biomass production, crude protein, and digestibility [2–4].

Certain species of legumes are endowed with properties that can boost forage utility. For instance, sainfoin (*Onobrychis viciifolia* Scop.) and birdsfoot trefoil (*Lotus corniculatus* L.) contain tannins, which bind to foaming agent in alfalfa (*Medicago sativa* L.) responsible for bloat, a livestock disorder [5]. This, therefore, lauds the need for diverse array of legume species in a crop. Besides their feed value, an assemblage of legumes with varied abilities to adapt to the local environment is an ingredient for sustainable cropping systems. This is particularly important for perennial cropping systems. The characteristics of importance include tolerance to acidity, drought, shade, salinity, and heavy metals. However, such benefits are not guaranteed when legumes succumb to competition for resources key to their survival and net primary production. In this context, light, mineral nutrients, and water are few of key factors vital for legumes. In addition, temperature extremes, pests and disease damage, and herbivory are unique challenges that can reduce legume persistence. In cultivated systems, the management of mineral nutrients and irrigation, together with disease and pests control, can optimize crop growth and maintain legumes in mixtures. For some species, intra-annual persistence is influenced by harvesting practices. For example, sainfoin has poor regeneration after first harvest (**Figure 1**). In this regard, frequent and early cutting can weaken plants to the point of death. Early cutting limits the amount of food reserve required to maintain plant vigor and persistence [6].

Cold temperatures are particularly detrimental to legumes. Winter injury includes intra and intercellular freezing of unhardened plant tissues and physical damage to roots caused by ice heaving [7]. Plants exposed to freezing temperatures may also indirectly suffer from dehydration when water in plant tissues is bound in ice [8]. Frost damage causes intracellular freezing.



Figure 1. Poor growth of sainfoin in mixture with meadow bromegrass after second harvest in August, 2016. The photo was taken on October 21, 2016, at the University of Wyoming Sheridan Research and Extension Center, Wyoming, USA. Photo by D.S. Ashilenje.

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Figure 2. Early symptoms of frost damage to alfalfa in a mixture with meadow bromegrass and birdsfoot trefoil. The other crops seem not to have been affected by the frost. The photo was taken on October 21, 2016 at the University of Wyoming Sheridan Research and Extension Center, Wyoming, USA. Photo by D.S. Ashilenje.

Extensive damage triggers loss of plant's photosynthetic surface, which impairs tiller development and plant growth. **Figure 2** shows early signs of frost injury to alfalfa growing in a mixture with meadow bromegrass (*Bromus biebersteinii*; Roem & Schult) and birdsfoot trefoil. It is evident that meadow bromegrass and birdsfoot trefoil have not been affected by the frost. This attests to the varying abilities among grass and legume species to tolerate excessively cold temperatures. On the other hand, winter hardiness is dependent upon hardened plant tissues and reduced leaf growth in fall. To sum up, species persistence is determined by genetic and physiological traits that enable species to acclimate to less ideal environments in multiple cropping systems.

2. Elucidation of resource competition and its influence on legumes

In mixed cropping systems, plant species compete for resources (e.g., light, water, nutrients) for their growth and survival. Competition for resources along with adverse environmental factors can negatively affect plant growth and contribute to shortened life spans of stressed plants in the cropping systems.

2.1. Competition for light

Like other plant species, legumes intercept the photosynthetic active radiation for photosynthesis [9]. This is a major input of carbon and substrates for plant's energy needs. However, for legumes, the energy gained from photosynthesis is of intermediate benefit to bacterial symbionts involved in N fixation. The daily rate of carbon assimilation by legumes growing together with grass is a hyperbolic function of leaf area index [10]. This is usually expressed as extinction coefficient abbreviated as k [11]. In practice, net accumulation rate is derived from dry matter accumulation per unit leaf area. This function is correlated to the number of leaf surfaces in the crop canopy exposed to light [12]. This partly determines shading of legumes by grasses when intercropped.

Grass leaf orientation and placement obstructs light from under-canopy growth of legumes. This phenomenon is well discussed [11]. Varying leaf angles in distinct species influence canopy extinction coefficient whereby vertically inclined or small leaves as the case is in grasses have low k values ranging between 0.3–0.5. Furthermore, leaves with clamped sheaths around the stem have intermediate *k* measurements, while species with horizontal leaves may have higher values of up to 0.7–0.8. Dense crops share space with additional vertical leaves that have low k values, that is, there are more leaves in the same area of as one horizontal leaf but with much less mutual shading.

2.2. Plant response to light quality

Plant species have profound ways of modifying growth in response to changing light quality. Annual crop species versus weed species signaling is controlled by red to far red (R:FR) ratio [13]. This interaction explains changes in plant forms in preparation for competition. High plant density absorbs incoming solar radiation causing decreased R:FR [14]. Whereas less dense plants cause an increase in R:FR ratio due to light reflection, high R:FR ratio triggers the plants to adapt to lesser light exposure due to shade from additional grass blades as enhanced growth of hypocotyl and leaf petioles/blades show (**Figure 3**) which assume an erect position [15].

2.3. Consequences of depriving legumes of light to their ecosystem services

Earlier publications have shown the adverse effects of shading on growth and dry matter production of legumes. The influence of partial (50–60%) and intense shade (80–90%) on selected cool- and warm-season legume monocrops are shown in **Table 1**. Partial shading suppresses yields for alfalfa and Illinois ticktrefoil (*Desmodium illinoense*; A. Gray*)* in ranges of 15–78%, respectively. Nevertheless, intense shade causes yield reductions ranging from 17% for Illinois tick trefoil to 73% for sub clover (*Trifolium subterraneum L.*).

Nitrogen fixation is also adversely affected by shading. It has been demonstrated that legumes shaded by grass have reduced size of nodules [16]. This impairs their ability to fix N. However,



Figure 3. Meadow bromegrass with elongated leaf sheaths and blades representing shade avoidance when grown in mixture with alfalfa at the University of Wyoming Sheridan Research and Extension Center, Wyoming, USA. Photo by D.S. Ashilenje.

Crop	Percent reduction in yield (% shading)		References
	Partial shading	Intense shading	
Alfalfa	15 (50)	39 (80)	[18]
Alsike clover (*Trifolium hybridum L.*)	42 (50)	68 (80)	[18]
Birdsfoot trefoil	36 (50)	69 (80)	[18]
White clover (*Trifolium repens L.*)	19(50)	41(80)	[18]
Sub clover	46 (60)	73 (90)	[19]
Illinois tick trefoil	78 (55)	17 (80)	[20]

Table 1. Yield reduction for selected legumes in response to various levels of shading.

recent evidence from modeling experiments reveals interactions that are more complicated. For instance, Schwinning and Parsons [10] have suggested that grasses not only shade, but they also take advantage of enhanced N fixation by dwindling legume densities in mixed stands. Species of legume elicit different response to shading in their N fixation [17]. This is exemplified by kudzu (*Pueraria lobata*; Ohwi), a tropical pasture legume, whose N fixation suffers less from effects of shading compared to siratro (*Macroptilium atropurpureum* cv. siratro).

2.4. Competition for soil nutrients

The antagonistic role of mineral N against biological N fixation by legumes is well known. Such effects get pronounced when N is availed in amounts exceeding that required in first few weeks of legume seedling establishment [21]. Conversely, other nutrients including P, K, molybdenum, and iron synergize de-nitrogen (N_2) fixation by legumes. Phosphorus has a direct role of promoting nitrogenase activity, the enzyme involved in conversion of N_2 to ammonia [22]. On the other hand, P increases nodule mass. Work by Mendoza et al. [23] has revealed that optimum supply of P triggers a positive growth response of legumes integrated with grass crops unlike pure stand. However, P may favor grass shoots and root biomass accumulation at the expense of the development of congregate legumes.

Potassium is essential for many metabolic processes important to plant growth. This includes photosynthesis, osmoregulation, protein synthesis, and enzyme activation [18]. More specifically, K has been correlated with increased nodulation and N_2 fixation by legumes [24]. In the same note, water stress can inhibit nodulation and nitrogenase activity. Thus, K averts injurious effects of soil water deficit on nitrogenase activity. Grass and legumes have enhanced competition for K when growing together in mixtures [25]. This phenomenon is supported by the finding that increased supply of K enhances N_2 fixation and uptake of P and N by tropical legumes [25].

3. The challenge of legume persistence in mixed stands

Legume persistence entails continuity of individual plant as well as crop stand. Legume stand persistence refers to perpetual number of individuals representing the species, which addresses the needs unique to ecosystems [26, 27]. Plant persistence is of greater concern

during crop establishment after which stand persistence becomes important [26]. Efforts to improve forage crops have targeted monocrop yields, and ability to withstand factors that militate against crop survival including pests, diseases, drought stress, winter kill, soil salinity, and aluminum toxicity [27]. Previously, it has been shown that legumes persist less in mixtures because of exploitation by grasses for light and fixed N as earlier mentioned [10]. This scenario is evident from changes in morphological traits [28] as well as resource allocation [29]. Both species traits and management practices influencing forage monocrop persistence have been described in detail by Bouselinck et al. [26]. For instance, crown formers, specifically alfalfa, reach physiological potential 2 years after planting after which yields are stable up to 6–8 years of crop lifespan. In contrary, plant density declines rapidly from 300 plants m^{-2} in the seeding year to 50 plants m^{-2} in the third year attributed to intraspecific competition and disease. In addition, Louarn et al. [30] recorded a decline from 352 plants m^{-2} during first harvest to 90 plants m^{-2} in the third harvest within 1 year. Declining number of alfalfa plants is compensated for by increasing number of stems $plant^{-1}$. For self-seeding species, notably birdsfoot trefoil, persistence depends on their ability to set enough seeds, thereby building substantial seed banks [31].

4. Biodiversity indices explain complex species interactions in polycultures

Various mechanisms underlie biodiversity in forage plant communities. Among these are those that enhance temporal stability. Temporal stability refers to constancy in species abundance [32]. In this case, abundance may be determined as biomass production or density. Temporal stability is computed from the inverse of the coefficient of variation or ratio between mean abundance to corresponding standard deviation. Community temporal stability derives from lower variance in averaged production of many species in a community than individual species, which is also referred to as portfolio effect [32].

According to Isbell et al. [33], a positive correlation exists between temporal stability and other biodiversity indices, namely overyielding and species asynchrony. Overyielding refers to higher biomass production for a mixed crop when compared to the average pure stand of the species constituted in the mixture [34]. Positive species interactions promote greater yields for a mixture when compared to best performing species in the mixture [35]. However, the overyielding effect is often diluted by the role of dominant species in equilibrating biomass production for mixtures with that of its pure stand which has been extensively discussed [34, 36]. On the other hand, Isbell et al. [33] have shown that no relation existed between temporal stability and species evenness. They explain this by the asynchronized dominance in biomass production by distinct species over a time scale.

5. Plant species traits responsible for species persistence in mixed stands

Studies concerning biodiversity mechanisms suggest possible ways to perpetuate legumes in mixed crops. This is typified by asynchronous dry matter distribution [33] and convergence in

species traits [37]. This property of plant communities permits complementary use of light, water, and nutrients. Such species characteristics include specific leaf area (SLA) which is the ratio of leaf area to corresponding dry weight. The SLA is an adaptation to relatively larger leaf surface compared to leaf carbohydrate reserve. Thus, SLA is correlated with greater photosynthetic capacity and leaf N concentration. Conversely, low SLA has been linked to longer leaf lifespan and retention of nutrients [9]. On the other hand, Gubsch et al. [29] have explained the diversity and adjustment of functional traits to environment as a determinant of forage production. For instance, grass species adjustment to low light intensity and improved N acquisition contributes to increasing forage quality as more species are included in a mixture. Besides, divergent leaf forms and convergent plant configurations, such as shoot height, to a greater extent, account for legume persistence [37].

As mentioned in the introduction, storage of food reserves can spur legume persistence. The daily rate of carbon assimilation by legumes and grasses growing together is determined by light interception [10]. Light interception by each species is a function of the quantity of radiant energy received at a surface per unit time (photosynthetic photon flux density or PPFD), leaf area index (LAI), and canopy extinction coefficient [11]. Light interception, carbon assimilation, and plasticity in plant morphology are dynamic interactions that impinge on overall plant development and persistence. For instance, shading has been found to reduce secondary branching and plant leaf area development in dense crops [38]. Whereas in severe competition, growth of primary axis is impaired, different plant configurations influence forage nutritive value notably crude protein (CP) and acid detergent fiber (ADF). For example, alfalfa CP is positively correlated to the ratio between leaf and stem weight but negatively correlated to stem length and maturity [39]. The relation is inversely proportional to ADF. In grazed systems, higher leaf-to-stem ratio toward the top of the canopy correlates with higher CP. Thus, grazing animals selectively graze on the apical regions of the legume canopy.

6. Lessons learned from recent studies involving tall fescue-alfalfa mixtures

Competitiveness among species in mixtures was earlier quantified as relative yield total [40]. Relative yield total for combined species is computed from summing up the product of dry matter proportion and ratios of mixture versus monocrop yields. Relative yield total values greater than 1 indicate complementarity, while values less than 1 show competition among species for available resources. Relative yield total is dependent upon management and environment [41]. The other measure of competitiveness is species aggressivity abbreviated as A. As defined by [42] when species aggressivity for one taxon is >1, then that species is more competitive than its contemporary growing in the mixture.

Results from a recent experiment at the James C. Hageman Sustainable Agriculture Research and Extension Center, Lingle, Wyoming, USA, are presented in the rest of this section. There was a significant (P = 0.002) interaction between the year and tall fescue (TF) (*Schedonorus arundinaceus* [Schreb.] Dumort.)—alfalfa seeding ratios to influence proportion of alfalfa in mixtures (**Table 2**). The 25:75% mixture of tall fescue with alfalfa maintained proportions of

legume biomass at a minimum of 64% from 2012 to 2015. However, in the same duration, there were slight fluctuations in the proportions of alfalfa biomass in the 75:25% mixture of tall fescue alfalfa (56–47) and 75:25% mixture of tall fescue alfalfa (43–64). The proportion of alfalfa biomass in the 25:75% mixture of tall fescue alfalfa only surpassed that of the 75:25% mixture of tall fescue alfalfa in the years 2013 and 2014. In contrary, diverse mixtures of tall fescue and alfalfa did not influence ($P = 0.22$) relative yield total. In this regard, all mixtures of tall fescue and grass had relative yield totals >1 (**Table 3**). Similar results were recorded for grass aggressiveness which did not vary significantly ($P = 0.218$) across treatments. On the other hand, varying tall fescue—alfalfa seeding ratios did not affect aggressiveness of tall fescue in mixtures. Harvest frequency interacted with year ($P < 0.0001$) to influence species competition. Except for the year 2015, early growth during spring had relative yield total values <1 which depicts competitive growth among species (**Figure 4**). However, increased harvesting frequency gave relative yield total values >1 averaged across different seeding ratios. Between the years 2012 and 2014, tall fescue had more aggressive growth after the first harvest (**Figure 5**). However, in 2015, there was no competitive advantage in growth of tall

	Proportion of alfalfa biomass			
	Year			
Treatment	**2012**	**2013**	**2014**	**2015**
	%			
TF:alfalfa 75:25 seeding ratio	56aA[†]	48aA	54abA	47aA
TF:alfalfa 50:50 seeding ratio	43bA	47aA	44aA	61bB
TF:alfalfa 25:75 seeding ratio	64aA	67bA	64bA	64bA

[†]Within column refers to different treatments followed by same letter in lower case and within row refers to different years followed by same letter in upper case are not significantly different at $P < 0.05$

Table 2. Proportions of alfalfa biomass in tall fescue (TF) and alfalfa mixed crops established using different seeding ratios at James C. Hageman sustainable agriculture research and extension center near Lingle, Wyoming, USA, during 2012–2015.

Grass legume mixture	**Relative yield total**
TF:alfalfa 75:25 seeding ratio	2.07
TF:alfalfa 50:50 seeding ratio	1.99
TF:alfalfa 25:75 seeding ratio	1.60
Mean	1.89
P-value	0.22
LSD (0.05)	0.59

Table 3. Species relative yield total for tall fescue (TF) and alfalfa mixed crops established using different seeding ratios at James C. Hageman Sustainable Agriculture Research and Extension Center near Lingle, Wyoming, USA.

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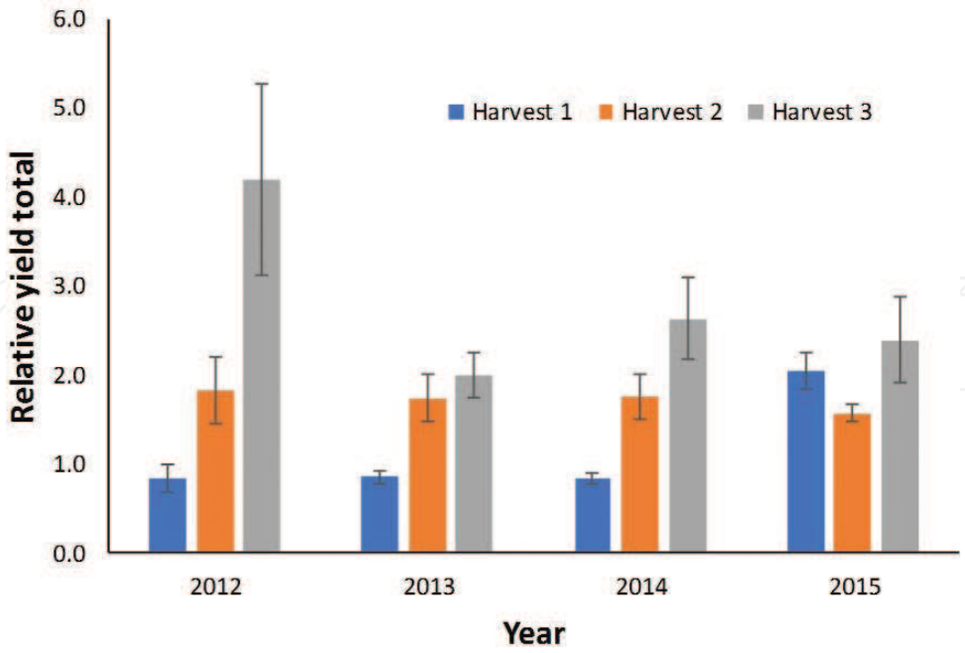


Figure 4. Mean relative yield total across different cropping mixtures of tall fescue and alfalfa observed at different harvest times during 2012–2015 at James C. Hageman Sustainable Agriculture Research and Extension Center near Lingle, Wyoming, USA. The mixtures were tall fescue-alfalfa in 75:25, 50:50, and 25:75 seeding ratios. Bars represent standard error of the mean.

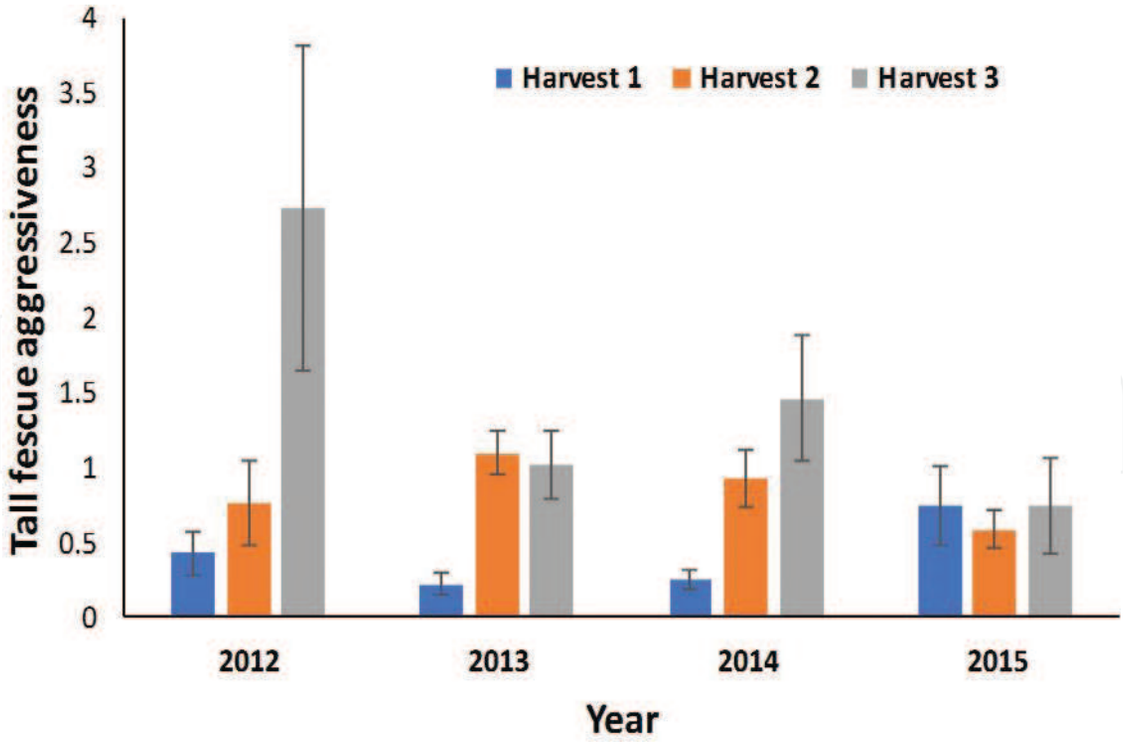


Figure 5. Tall fescue aggressiveness observed at different harvest times during 2012–2015. The values were averaged across different mixtures of tall fescue-alfalfa in 75:25, 50:50, and 25:75 seeding ratios at James C. Hageman Sustainable Agriculture Research and Extension Center near Lingle, Wyoming, USA. Bars represent standard error of the mean.

fescue when compared to alfalfa. This was same across different crop harvests. These results suggest that there was complementarity in resource use regardless of the seeding ratios for tall fescue-alfalfa mixtures. Therefore, this sustained legume growth despite dominance of grass in the mixtures.

7. Conclusions

Legume crops are treated as natural fertilizer because of their unique ability to fix atmospheric N. Considering their role in N_2 fixation and rich nutritive value, legumes are valuable inclusions in forage cropping systems with grasses. However, the realization of these benefits is limited because of poor legume persistence or disappearance of legumes in mixed cropping systems. Grass species have more aggressive growth, thus they compete against legumes for light, water, and nutrients. Such competition can impair N_2 fixation and growth and finally lessen legume persistence. Knowledge about species tolerance for shade and biodiversity mechanisms can help forestall belligerence from grasses and perpetuate legumes in mixed cropping systems. Embedded in legume persistence is diverse species trait that contributes to asynchronized growth patterns and leaf forms. Therefore, the species traits and biodiversity indices that can help solve the problems of legume persistence are the focus in this chapter. Several breakthroughs that emerged from the review and recent experiments include:

- Genetic and physiological traits enable species to acclimate to less ideal environments in multiple cropping systems including temperature extremes, drought, and shading.
- Species may display hardening of plant tissues to resist freezing temperatures and leaf forms and placement that facilitates more assimilation of light to form food reserves.
- Biodiversity mechanisms that encourage complementary use of resources can help to alleviate loss of legumes in mixed cropping systems leading to overyielding.
- Crop management, particularly harvesting frequency, plays more significant role than seeding proportions in influencing competitiveness of grass against their companion legumes in the mixtures.
- Finally, despite the aggressive growth of associated species in mixed cropping systems, complementary resource use allowed legumes to thrive 4 years or more after their establishment in different mixtures.

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