Leaf traits and herbivory as indicators of ecosystem function

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Plant functional types bridge the gap between plant physiology and ecosystem processes. In the present article, we review the plant functional traits and their response to grazing, and discuss how this affects the nutrient dynamics of the system under the pressure of herbivory. The results also strengthen the management of ecosystems being grazed by herbivores.

Keywords: Grazing, litter decomposition, nutrient dynamics, plant functional types.

WITHIN the last few years, researchers worldwide have increased efforts to search for easily measurable and universally applicable predictors of global-change effects on terrestrial ecosystems. Studies show that such predictors do exist in the form of sets of co-occurring plant traits (i.e. trait syndromes) or plant functional types (PFTs)[1–13]. Historically, plants have been classified using various categories depending on the objective at hand such as: life forms or taxa with similar structures[14], strategies[15,16], vital attributes[17], guilds or taxa making use of the same resources[18], and the now widely used PFTs comprising functional response groups, i.e. taxa that respond similarly to environmental factors and functional effect groups, i.e. taxa with the same role in the ecosystem[1,6–8,18,19]. PFTs are defined by demographic and life-history features, physiology and resource dynamics, which determine their responses to biotic and abiotic factors and their role in ecosystem functioning[4,16]. Thus, a PFT is basically a group of plants that irrespective of phylogeny are similar in a given set of traits and similar in their responses to environmental factors and/or their roles in ecosystems.

This concept has been applied to a variety of plant communities to assess relationships among diversity, resilience and ecosystem function. PFTs bridge the gap between plant physiology and ecosystem processes, and thus provide a powerful tool to study the global change, vegetation dynamics and vegetation–atmosphere processes. Upcoming interest in using species traits, and grouping the species by their traits into functional types, and predicting plant community responses to environmental change are becoming the focal theme to address many of the ecosystem problems[6,10]. The functional groups

and single-trait approach give us an opportunity to have large-scale generalizations of the effects of plant species on ecosystem processes that can be further modelled at a regional scale using selected environmental conditions for certain suites of plant traits[3,20]. At species level, rate of ecosystem processes is linked to a small number of functional traits (for example, leaf dry matter, leaf lifespan)[21]. Plant traits have been proposed as a means of directly predicting changes in ecosystem processes from shifts in plant communities in response to global change[22,23]. Devineau and Fournier[24] used plant traits as a substitute of species to reflect environmental variability of grasses and herbs in West African savanna subject to fallow land rotation.

Functional traits provide a general and mechanistic basis for understanding plant behaviour in response to biotic stress[25]. Plant functional traits can be categorized into common morphological ('soft') traits, and ecophysiological and demographic ('hard') traits (Table 1). The selected traits for plant responses to environmental factors have been considered as 'soft' traits, which are easy to measure for a large number of species and sites, but are not necessarily and explicitly related to a specific functional mechanism; 'hard' traits are usually less accessible but with a direct functional role[26].

Simple and easily measurable plant traits (plant height, life history and leaf mass) have been used as predictors of grazing responses[22]. Grazing is dependent on and affects the plant morphology and functional traits of a community. This complimentarity can produce powerful feedback cycles among the structure, biogeochemistry of the vegetation, and cycling and storage of nutrients in an herbivory-prone community[21,27]. Effects of grazing on plant communities and the relationship between grazing frequency and plant traits are abundant[21]. Studies have generally focused on how the plant traits affect the local grazing regime and how the plant adapted to avoid, tolerate and/or skip herbivory. Studies are required to elucidate how the trait adaptability to herbivory affects the ecosystem

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Table 1. Soft traits, their correspondence with the hard traits they are assumed to represent, function concerned with each trait and how each trait responds to grazing (adapted from Weiher et al.[10])

Soft trait[10]	Hard trait[10]	Function[10]	Response of traits to grazing
Seed mass and seed shape	Reproductive effort, dispersal distance, propagule longevity and seedling establishment	Dispersal is space and time, longevity in seed bank, establishment success and fecundity	Grazing favours species with small seeds[80–82]
Dispersal syndrome	–	Dispersal distance and longevity in seed bank	Perennial grasses, grasses without dispersal appendages and forbs are favoured through intensive grazing; on the contrary, wind dispersal is associated with low grazing intensity (as the grazers munch the canopy, so wind dispersal increases)[39,83]
Pollination mode	–	Fecundity	Cross-pollination is reduced due to changes in structural attributes that attract the pollinators, and the grazed species may switch to self-pollination mode[84]
Specific leaf area, leaf dry matter content and leaf water content	Relative growth rate, photosynthesis, nutrient uptake, leaf chemical composition, leaf lifespan, and mean residence time of nutrients	Acquisition of resources, conservation of nutrients, stress tolerance and biomass production potential	Grazing favours species with higher specific leaf area, low leaf dry matter content and high leaf water content[22]
Height	Competitive effect and response	Competitive ability	Grazing favours small statured species and excludes tall species[85]
Above-ground biomass	Competitive effect and response	Competitive ability and fecundity	Grazing is favoured by higher above-ground biomass[86]
Clonality	Vegetative spread	Acquisition of space	Clonality is favoured by grazing[87]
Onset of flowering	Phenology: duration of growth, timing and length of reproductive period	Stress avoidance, disturbance avoidance and biomass production potential	Early flowering is promoted by grazing[87]
Life history	Whole plant lifespan	Space-holding ability, disturbance tolerance and carbon storage	Grazing appeared to promote annual than perennial[22]
Stem density (wood density)	Whole plant lifespan	Space-holding ability, disturbance tolerance and carbon storage	Grazing favours high shoot densities[47,88]
Resprouting ability	–	Disturbance tolerance	Grazing favours resprouting[89]
In need of a soft trait	Reaction norm and plasticity	Tolerance to variations in environmental conditions	

processes, especially the decomposition and nutrient pool of the micro niche that is being grazed. Leaf trait adaptability might alter the physical and chemical attributes of the quality and quantity of litter input in the system[28,29]. Quality and quantity of litter can be linked to functional trait of the species and in turn the decomposition rate and nutrient availability[28,30,31]. However, there still exists a considerable lacuna as to how the leaf traits (structural and chemical) affect the herbivore process and in turn alter the ecosystem processes. Identifying and quantifying links among functional leaf traits, herbivory and litter decomposability would improve our understanding of ecosystem functioning and provide us

with a predictive tool for modelling decomposition rates under different grazing regimes and vegetation types.

The present study synthesizes the results of available studies related to PFTs, herbivory and nutrient dynamics, and provides an overview of how the leaf traits potentially provide robust predictions of species responses to biotic stress, particularly herbivory and how in turn plant traits subsequently affect the ecological processes. Key terms frequently used in the study are defined as follows: grazer – an animal which feeds on growing grass or other herbage on the ground[32]; herbivory – a form of predation in which an organism, known as a herbivore, consumes

principally autotrophs[33], and nutrient dynamics – the way nutrients are used and reused, over time and distance, in a biological system[34].

Soft and hard traits

The soft and hard traits of a plant community can be responsible for the grazing potential of the system. Examples which give us a picture of how the soft and hard traits of the species can affect the grazing regime of the community are included in Table 1. Recent attempts to explain the great variability in ecosystem response to grazing[35] have focused on the role of plant functional traits. The general hypothesis states that the sensitivity of plant communities to grazing depends on the frequency and strength of adaptations helping plants avoid or tolerate herbivory[22,36–40]. This hypothesis predicts that grazing impacts will be smaller in systems where grazing-resistance traits are well developed and common among plant species, than in systems where such traits are poorly developed or rare. Although certain key traits such as life form, plant stature, seed size and leaf toughness[22,25,39,41] have been identified, cross-system generalizations using these traits appear elusive[25,40]. Competition for light will select for traits such as taller growth forms with larger leaves and faster growth[16,42,43], but should make plants more vulnerable to grazing[22,44–46]. On the other hand, adaptations to aridity such as shorter plants, small leaves, basal meristems and annual life cycle, should increase tolerance to, or avoidance of, grazing and can be called as 'convergent selection'[47].

Plant traits and herbivory

Herbivory is also one of the major threats to the herbaceous plants in forests and has a major impact on ecosystem processes for several reasons[20]. First, herbivores transfer plant tissue to the soil before nutrient resorption can occur, and about twice as much nitrogen and phosphorus is transferred per unit of plant biomass than would occur through litter fall. Secondly, herbivores preferentially select nutrient-rich tissue, further enhancing nutrient transfer to the soil. The increase of nutrients through herbivore inputs also influences the nutrient pool which in turn affects the alien plant species dynamics. It is particularly evident in primary succession, where an early abundance of nitrogen fixers is critical to increasing nutrient input. This directly determines the availability of nutrients to support plant production and indirectly influences the stand structure and species composition[48–50]. Large domesticated herbivores grazing pastures, or fed fodder harvested from meadows, are a key socio-economic and ecological issue in different ecosystems around the world[51]. In general, plants that characterize low-fertility soils produce chemical defences that reduce the frequency of herbivory in these habitats; these compounds retard decomposition and nutrient cycling. Herbivory magnifies the natural differences in soil fertility among ecosystems[20]. The plant communities impacted by large herbivores are traditionally managed for these purposes and survive harvesting, trampling and manuring[52]. Changes in the intensity or timing of ecological processes result in altered taxonomical and functional composition, and subsequently the functioning of the ecosystem[21,35,53]. Plant traits that influence herbivory affect nearly all ecosystem processes[2].

Díaz et al.[21] scrutinized nearly 200 individual studies from all continents using seven common traits (life history, canopy height, growth habit, shoot architecture, growth form, palatability and origin) for consistency in the response of plants to grazing pressure (Table 2). Grazing-resistant species in general are shorter in height, smaller, with tender leaves and high specific leaf area (SLA) than grazing-susceptible species. Further, grazing resistance is associated with both avoidance traits (small height and small leaf size) and tolerance traits (high SLA). Plant height can be considered as the best predictor of grazing response, followed by leaf mass. In general, positive response of short plants and negative response of tall plants are more marked in systems with a long history of grazing than in those with a short history[21]. The best prediction of grazing response by a species is achieved by combining plant height, life history and leaf mass. SLA is reported to be a comparatively poor predictor of grazing response[22]. Grazing animals prefer communities with low proportions of senescent leaves and absence of woody biomass; this indicates optimized searching for better forage quality (nutrient maximization). The ability of plant height to predict the response of species to grazing, for example, often differs according to a local condition that has applied implication[22,40,54]. The first implication is that the functional traits can be a useful tool in predicting species responses to grazing and, for conservation purposes, identifying species promoted by or vulnerable to land-use changes. In this way, functional traits might uncover the adaptations involved in making species respond similarly to environmental factors[11]. Based on their response to grazing, species have been traditionally categorized into 'increasers', 'decreasers' or 'neutrals'[22,44,45].

Higher percentage of structural tissues involves more energy wasted for the intake[55] and higher proportion of stem contents is inversely related to better accessibility to leaves[56]. Above all, the grazing regime alters the nutrient dynamics of a system through various organic inputs, e.g. grazers faecal discharge and litter inputs of the species, which in turn are related to the grazing number/intensity and the physical and chemical leaf traits of the plant species being grazed. The mentioned organic inputs will change the decomposition scenario of the micro region being grazed (Figure 1).

Table 2. Plant traits and their responses to grazing (based on Díaz et al.[21])

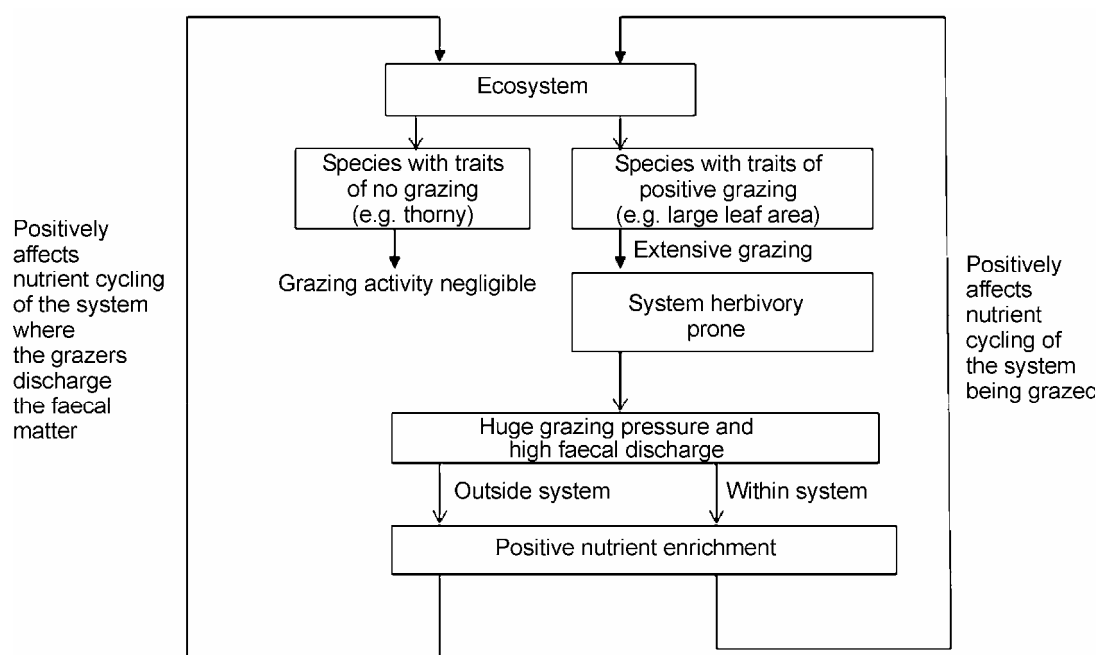| Traits with sub categories	Response to grazing	Explanation
Life history		
Annual	Positive by annual	Increased grazing generally favoured annuals over
Perennial	Negative by perennial	perennials
Canopy height		
Short	Positive by short plant	To avoid grazing, plants with short canopy are
Unpalatable	Negative by tall plant	favoured
Habit		
Prostrate	Positive by prostrate plant	Increased grazing generally favoured prostrate over
Erect	Negative by erect plant	erect plants
Architecture		
Stoloniferous	Positive by stoloniferous and rosette plants	Increased grazing generally favoured rosette plants
Rosette	Negative by tussock plants	over tussock plants
Growth form	Neutrally forbs and woody	To tolerate grazing
	Neutral/negative by graminoids	To tolerate grazing
Palatability		
Palatable	Positive by unpalatable plants	To avoid grazing, unpalatable plants were favoured
Unpalatable	Negative by palatable plants	over palatable plants
Origin	Exotics tend to increase	In the case of abundance, there was positive response of exotic plants and a negative response of native plants to grazing

Figure 1. Impact of herbivory on nutrient dynamics as modulated by plant functional traits.

Physical and chemical leaf traits and decomposition

Numerous mechanisms have been identified through which physical, chemical and biological properties of the soil are altered[2,57–59]. One such mechanism which alters the soil nutrient pool is the quality and quantity of litter input. The litter input depends on the herbivory within the system: higher the herbivory, lower the litter input and vice versa. A suite of leaf traits (physical, chemical and temporal) affect herbivory and in turn the decomposition rates within the system. Changes in soil biogeochemistry following a shift in herbivory intensity are an understudied and need to be explored further. Traits like physical toughness, nutritional quality and chemical defence seem likely to influence the palatability of leaves

Table 3. Relationship among leaf trait, litter quality, decomposition rate and how disturbance regime affects the former (adapted from Fortunel et al.[90])

Traits	Litter quality	Relation with decomposition rate	Effect of disturbance on leaf traits	Compounding effect of disturbance on litter decomposition rate
Structural traits				
Leaf dry matter content	Positive relation with lignin concentration, litter fibre component and lignin : N ratio	Negative relation with litter decomposition rate	Decrease	Increase
	Negative relation with cellulose concentration, hemicellulose concentration and holocellulose : hemicellulose ratio			
Specific leaf area	–	Positive relation with litter decomposition rate	Increase	Increase
Chemical traits				
Leaf nitrogen content	Positive relation with litter N concentration	Positive relation with litter decomposition rate	Increase	Increase
	Negative relation with lignin and lignin : N ratio			
Leaf carbon content	Positive relation with lignin and lignin : N ratio	Negative relation with litter decomposition rate	Increase	Increase
	Negative relation with litter N concentration			
Leaf phosphorus content	–	Positive relation with litter decomposition rate	–	–

and therefore of litter. Low leaf palatability is probably largely due to relatively high carbon investments in protective compounds (against herbivore attack or an adverse physical environment), which are not involved in photo-assimilation but are correlated negatively with growth rate[60]. Leaf toughness is noticeably linked to litter decomposition rate[31]. Traits governing plant growth rate and net primary productivity (NPP) also determine the microbial processing of carbon and nitrogen in the soil. The quantity and quality of organic matter inputs to the soil, as determined by the plant attributes, emerge as major factors of decomposition when ecosystems are compared at steady state[61]. Identifying and quantifying links between functional leaf traits and litter decomposability would enhance our understanding of ecosystem functioning and provide us with a predictive tool for modelling decomposition rates under different vegetation types[31]. Chemical properties that promote high physiological activity and growth in plants (e.g. high tissue nitrogen concentration) and low lignin content (reflecting less sclerified leaves with a high ratio of cytoplasm to cell wall) also promote rapid decomposition[62,63]. The quantity of litter input provides a critical link between NPP and decomposition because, at steady state, NPP governs the quantity of organic matter to decomposers. Litter decomposition regime involves two types of traits, structural

traits (e.g. leaf dry matter content (LDMC), and SLA) and chemical traits (e.g. leaf carbon content (LCC), leaf nitrogen content (LNC) and leaf phosphorus content (LPC); Table 3). Plant functional traits also affect aboveground productivity and quality of pasture grasses which are also linked to decomposition. For example, aboveground NPP was strongly and negatively correlated with the fresh matter-based leaf N content (i.e. LDMC × LNC) and was not affected by specific SLA, apparently because of a trade-off between SLA and leaf lamina fraction[64]. Leaf digestibility increased with SLA and declined with LDMC. Protein content increased with both fresh and dry matter-based LNC. Such species variation in the annual production of digestible energy and proteins by pasture grasses is controlled in an additive way by two leaf traits – LNC and LDMC[65,66]. The relationship among the various structural and chemical leaf traits that influence the decomposition is illustrated in Table 3. Replacements of small, annual species by perennials, tall shrubs and trees during post-disturbance succession have been reported[66,67]. The general importance of life cycle, stature and life form in predicting the distribution of species along grazing gradients has already been reported[22,39,65]. However, Bello et al.[67] have demonstrated the relative importance of individual traits, and thus their predictive value. Difference in functional traits of living leaves

can thus enhance grazing pressure (herbivory) and can subsequently affect litter quality and litter decomposability[28,29,68,69].

Three traits, which produce implicit effects on ecosystem processes at different scales, have been screened as SLA, LDMC and LNC[70–72]. At the leaf level, a combination of SLA and LNC has been shown to predict accurately the maximum photosynthetic rate of a wide range of species[73] and both traits are related to leaf lifespan[73]. At the whole-plant level, all three traits have been found to be involved in a fundamental trade-off between a rapid production of biomass and an efficient conservation of nutrients[5,74]. Finally, at the ecosystem level, sparse data suggest that SLA (or related leaf traits) and LNC of component species may have a significant impact on primary productivity and nutrient cycling[75–77]. The above discussion justifies that functional traits can be used as a predictive tool for herbivory and litter decomposability without having the tacit knowledge of individual species taxonomy and biology.

In the Indian scenario, there have been studies reporting the effect of herbivory on the ecosystem structure and processes[78], but no study explicitly links the ecosystem dynamics to species traits. Potentially, this would be the first study from India that tries to collate the plant functional traits to herbivory and further to ecosystem dynamics. Such studies will lead to design strategies for conserving native plant biodiversity, ecosystem processes in grazed ecosystems and how plant traits can be exploited to study the ecological constraints of plants and plant communities with higher level of generalization[79].

This article underlines the potential of PFTs for developing a better understanding among the herbivores, leaf traits and decomposition, and how they synergistically affect the biogeochemistry of the soil system. The PFTs can be further exploited as predictors of local and global environmental changes.

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