

# Chapter 8

## Linking Foliar Traits to Belowground Processes



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### 8.1 Framework

Remote sensing (RS) of belowground processes via aboveground ecosystem properties and plant foliar traits depends upon (1) the ability to quantify ecosystem productivity and relevant plant attributes—including plant chemical composition and diversity—and (2) tight linkages between above- and belowground systems. These linkages can occur through the effects of aboveground inputs into belowground systems and/or through relationships between above- and belowground attributes and, in turn, between belowground relationships between plant roots and microbial communities and processes (i.e., fine-root turnover, mycorrhizal associations). The increasing ability of remotely sensed information to accurately measure productivity, ecologically important plant traits (Serbin and Townsend, Chap. 3, this volume; Wang et al. 2019), and plant taxonomic, functional, and phylogenetic diversity (Wang et al. 2019; Schweiger et al. 2018; Gholizadeh et al. 2019) creates new opportunities to observe terrestrial ecosystems. While the focus of RS tools is generally on aboveground vegetation characteristics, the tight linkage between above- and belowground systems through productivity and foliar chemistry means that many belowground processes can be inferred from remotely sensed information. Here, we focus on how the productivity and composition of foliar traits in plant communities influence belowground processes such as decomposition and nutrient cycling. We specifically consider foliar traits that are increasingly measurable via

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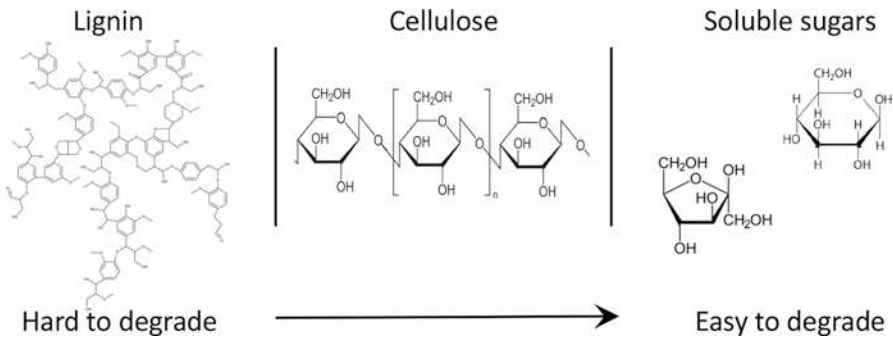
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airborne RS. Using two case studies, one in a clonal aspen (*Populus tremuloides*) forest system and one in a manipulated grassland biodiversity experiment, we demonstrate that plant foliar traits and vegetation cover, as measured via plant spectra (Wang et al. 2019), can provide critical information predictive of belowground processes.

## 8.2 How Are Belowground Processes and Microbial Communities Influenced by Aboveground Properties?

Belowground processes—including decomposition and nutrient cycling, which are mediated by microbial biomass, composition, and diversity—are heavily influenced by both the amount and chemistry of aboveground inputs. Quantifying the amount and quality of foliar components is a major aspect of trait-based ecology, which seeks to use functional traits, rather than taxonomic classification, to determine organisms' contributions to communities and ecosystems. Trait-based ecology has inherent strengths, including the ability to consider biological variation across both phylogenetic and spatial scales (Funk et al. 2017). While there is a range of accepted trait-based approaches in plant sciences (Funk et al. 2017), the emergence of the leaf economic spectrum (Wright et al. 2004) and the whole plant economic spectrum (Reich 2014) has clearly demonstrated that plant traits are important to ecosystem processes across multiple biological and spatial scales. Further, employing a trait-based approach to explore the relationships among plant function, biodiversity, and belowground processes allows us to take advantage of recent advances in RS to accurately measure plant traits across large spatial scales.

- A. *Decomposition and Nutrient Cycling*—The productivity, composition, and diversity of aboveground communities influence belowground processes, in part through decomposition of leaf litter (Gartner and Cardon 2004; Hättenschwiler et al. 2005), root litter (Bardgett et al. 2014; Laliberté 2017), and root exudates (Hobbie 2015; Cline et al. 2018) and also through effects on soil organic matter (SOM) properties (Mueller et al. 2015) and soil physical structure (Gould et al. 2016). Several seminal reviews outlining the importance of biodiversity to ecosystem function (BEF) have focused specifically on the afterlife effects of litter diversity on decomposition (Hättenschwiler et al. 2005; Gessner et al. 2010).
- B. *Microbial Community Composition*—Variation in the quantity and quality of organic inputs into belowground systems drives variation in belowground microbial communities and functioning (de Vries et al. 2012). Differences in aboveground communities are mirrored by those in belowground communities (Wardle et al. 2004; De Deyn and van der Putten 2005; Kardol and Wardle 2010). Across multiple spatial and taxonomic scales, variation in belowground microbial communities is driven by variation in plant traits associated with the leaf economic spectrum (de Vries et al. 2012). In general, fungi dominate decomposition of complex, low-quality substrates, while bacteria favor labile, high-quality substrates (Fig. 8.1, Bossuyt et al. 2001; Lauber et al. 2008).



**Fig. 8.1** Complex, recalcitrant compounds are typically degraded by fungi, while soluble, labile substrates are catabolized by bacteria

Microorganisms release extracellular enzymes, which degrade organic molecules outside of their cells, and likely differ among groups of microorganisms (Schneider et al. 2012). As a consequence, microbial composition and diversity are expected to influence decomposition and nutrient cycling. Most litter decomposition appears to be driven by fungal members, with *Ascomycota* dominating early degradation of cellulose and hemicellulose, followed by colonization by lignin-degrading *Basidiomycota* (Osono 2007; Schneider et al. 2012). Although lignin decomposition is dominated by fungal groups, some bacteria also degrade lignin (Kirby 2006; López-Mondéjar et al. 2016). Bacteria not directly involved with litter decomposition target the low molecular weight carbohydrates provided by fungal-derived extracellular enzymes (Allison 2005). The degradation of aromatic polyphenolics is largely limited to fungal member of the *Basidiomycota* phylum (Floudas et al. 2012). The wide structural variation among tannins (see section on carbon (polyphenols)) results in a wide range of effects on specific microbial members (Kraus et al. 2003).

A challenge in predicting belowground processes such as decomposition and nutrient cycling from the diversity and quality of leaf litter inputs is that such an approach must also consider the diversity and function of belowground microbial communities. Belowground mycorrhizal communities can increase net primary production (NPP) and drive variation in plant communities (Wardle et al. 2004). Given the influence of plant traits on belowground processes, biodiversity may drive variation in decomposition through top-down (microbially driven) rather than bottom-up (substrate driven) forces (Srivasta et al. 2009). Several reviews have addressed the importance of belowground community diversity to ecosystem processes (e.g., Hättenschwiler et al. 2005; Gessner et al. 2010; Phillips et al. 2013; Bardgett and van der Putten 2014). Belowground diversity can influence aboveground factors such as NPP (Wardle et al. 2004; Eisenhauer et al. 2018) that then have important feedbacks to belowground processes. Decomposition is driven by a combination of both the microbial community and the quality and quantity of litter that those communities receive (e.g., Keiser et al. 2013; García-Palacios et al. 2016).

### 8.3 Mechanisms by Which Aboveground Vegetation Attributes Influence Belowground Processes

Aboveground community composition and vegetation chemistry are tightly linked with belowground communities through belowground inputs and subsequent decomposition and nutrient uptake (Hobbie 1992; Wardle et al. 2004). Plant biomass, structure, and chemical composition are all important drivers of belowground processes to such an extent that plant traits may be the dominant control on litter decomposition, outweighing the influence of climate even over large spatial scales (Cornwell et al. 2008).

#### 8.3.1 Total Aboveground Inputs

Standing aboveground biomass and NPP are among the most important attributes of vegetation that impact belowground systems (Chapin et al. 2002) and are widely measured via RS techniques with increasing accuracy (Kokaly et al. 2009; Serbin et al., this issue). Belowground respiration is tightly linked with aboveground productivity (Högberg et al. 2001), and leaf litter can provide roughly half of organic inputs into some belowground systems (Coleman and Crossley 1996). The amount of aboveground biomass can be critical to litter decomposition (Lohbeck et al. 2015) and microbial community function and diversity (Fierer et al. 2009; Cline et al. 2018), and its influence may surpass the effects of plant quality, as measured by plant chemistry and functional traits (Lohbeck et al. 2015).

Plant traits related to biomass, such as leaf area index (LAI), are also linked to belowground processes, with belowground carbon (C) turnover peaking at intermediate LAI levels (Berryman et al. 2016; others). Importantly, LAI can be measured with RS products over large spatial scales (Serbin et al. 2014; Lausch et al., Chap. 13 this volume, Morsdorf et al. Chap. 4). While there have been few explicit links of remotely sensed LAI to soil respiration (but see Huang et al. 2015), the conceptual link has been recognized for decades (Landsberg and Waring 1997). Other remotely sensed variables tightly coupled with biomass, including vegetation cover (Wang et al. 2019), also predict soil respiration (Fig. 8.4).

The effects of biomass on belowground processes have been recognized by ecologists employing RS to estimate belowground C stocks (e.g., Bellassen et al. 2011). Across large scales, aboveground biomass is generally correlated with belowground root biomass (Cairns et al. 1997). While aboveground biomass is commonly measured, the calculation of belowground biomass is less common and is often limited to estimates of shoot biomass as a simple proportion of aboveground biomass (Mokany et al. 2006). Nonetheless, the belowground estimates based on aboveground measurements can be useful for estimating above- and belowground C stores via RS products over large spatial scales (Saatchi et al. 2011). Allocation of C to belowground systems varies among systems, with annual grassland systems differing

from forested biomes in their allocation patterns of NPP (Litton et al. 2007). There are also large differences in above- and belowground linkages according to site fertility. In fertile sites the majority of NPP returned to the soil as labile fecal matter, whereas in infertile systems most NPP returned as recalcitrant plant litter (Wardle et al. 2004).

### 8.3.2 *Chemical Composition of Vegetation*

Beyond variation in total organic inputs to soil, variation in plant chemical composition is critical to belowground ecosystem processes. The physiological traits that comprise the plant economic spectrum developed by Wright et al. (2004) have important afterlife affects for belowground systems (Cornwell et al. 2008; Freschet et al. 2012; see review by Bardgett 2017). Variation in litter chemical quality can produce marked, long-term effects on litter decomposition rates and nutrient cycling in underlying soils, and litter quality has long been identified as key factor in determining decomposition rates (Tenney and Waksman 1929). Litter chemistry generally mirrors canopy chemistry (Hättenschwiler et al. 2008), making canopy chemistry a viable metric to estimate litter chemistry and subsequent belowground decomposition and nutrient cycling patterns. Aside from aboveground biomass, leaf nitrogen (N) and lignin content are often the dominant plant traits that drive variation in belowground process, particularly leaf litter decomposition (Aber and Mellilo 1982; Cadisch and Giller 1997), and both of these traits are readily derived from spectroscopy at multiple scales (Wessman et al. 1988; Serbin et al. 2014; Schweiger et al. 2018; Wang et al. 2019). RS of additional leaf traits important to belowground processes, such as plant secondary chemistry, is also increasingly measured via RS techniques (Kokaly et al. 2009; Asner et al. 2014; Serbin et al., this issue).

**Nitrogen** Foliar N is often the most important leaf trait driving variation in decomposition across biomes (Diaz et al. 2004; Cornwell et al. 2008; Handa et al. 2014). In some biomes leaf N is the only known leaf trait associated with leaf decomposition among wide ranges of species (Jo et al. 2016). Because canopy N has a tight correlation with plant carbon capture through photosynthesis, aboveground biomass, and belowground processes such as decomposition and N cycling rates, it is among the most common canopy traits measured via RS platforms (Martin and Aber 1997; Wessmen et al. 1998; Kokaly and Clark 1999; Martin et al. 1998, 2008; Ollinger et al. 2002; Townsend et al. 2003; Kokaly et al. 2009; Vitousek et al. 2009; Ollinger et al. 2013).

Leaf N is directly linked to plant productivity because most plant N is associated with metabolically active proteins, including RuBisCo. Leaf N content is driven by a trade-off between the benefits of increased photosynthetic potential and the costs associated with acquiring N along with the increased risk of herbivory (Diaz et al. 2016). In addition, leaf N can be indicative of plant growth strategies

(Wardle et al. 2004). Most short-term decomposition studies indicate that leaf N increases leaf litter decay (Cornwell et al. 2008). However, as decomposition progresses, leaf N may negatively affect the latter stages of decomposition, possibly due to interactions with lignified substrates (Berg 2014; discussed in brief below).

**Carbon quality (lignin)** The second most abundant natural polymer following cellulose is lignin, a complex phenolic polymer that wraps in and out of the structural polysaccharides in cell walls (Cadisch and Giller 1997). Due to its central roles in both aboveground biomass and belowground decomposition, lignin has been targeted as an important plant trait for RS techniques (Wessman et al. 1988; Serbin et al. 2014; Serbin and Townsend, Chap. 3). While lignin is a polyphenolic compound comprised of linked phenols (Horner et al. 1988), it is considered separate from other polyphenols because lignin is a primary structural component, whereas other polyphenols are a subset of secondary metabolites not directly involved with plant growth. The structure role of lignin and its low solubility also merit distinction from other polyphenolics when considering belowground processes (Hättenschwiler and Vitousek 2000). Lignin concentrations are negatively correlated with decomposition rates (Meentemeyer 1978; Melillo et al. 1982; Horner et al. 1988). The recalcitrant nature of lignin is due, in part, to its irregular structure and low energy yield, which largely limits its degradation to white-rot fungus members of *Basidiomycota* (Chapin et al. 2002).

The interaction of N and lignin during decomposition is not straightforward because N limits the early stages of decomposition, whereas lignin limits the latter stages of decomposition (Burns et al. 2013). Newly senesced leaves are composed largely of polysaccharides of holocellulose and lignin. High N availability will stimulate holocellulose decomposition in the early stages of decomposition but will then retard lignin decomposition in later stages of decomposition leading to lignified soil organic matter (SOM), potentially due to white-rot fungi favoring low N conditions (Berg 2014). The degradation of lignin is often a rate-limiting step during the later stages of decomposition because it protects cell wall polysaccharides physically and chemically (Talbot et al. 2012). Despite the changing roles that leaf N and lignin have over the course of decomposition, litter quality metrics such as C:N and lignin:N can explain variation in decomposition, with decomposition rates increasing with N in the early stages, but decreasing with N in the later stages, and decreasing with lignin (Fanin and Bertrand 2016).

While lignin almost universally retards decomposition, there is a large amount of variation within lignin compounds based on the proportion of specific monomers that varies across major plant groups (Thevenot et al. 2010). Angiosperm lignin tends to degrade more quickly than does gymnosperm lignin due to the specific identities of constituting moieties of lignin in each species (Higuchi 2006). The compact nature of gymnosperm lignin subunits is thought to protect them from enzymatic degradation (Hatakka and Hammel 2010). Functional measurements of lignin are often made via either acid digestion or thioglycolic acid methods that can then be used to calibrate spectroscopic methods (Brinkmann et al. 2002; Schweiger et al. 2018).

**Carbon quality (polyphenols)** In some ecosystems non-lignin carbon compounds (e.g., phenolics) explain more variation in decomposition than does either N or lignin (Hättenschwiler et al. 2011). Phenolics are the most widely distributed class of secondary plant metabolites and interact strongly with several aspects of nutrient cycling (Hättenschwiler and Vitousek 2000). Simple phenolics can prime (Fontaine et al. 2007), while large complex polyphenolics can retard (Coq et al. 2010) decomposition. Carbon quality—including the chemical composition of polyphenolics—can be more important to litter decomposition than is litter nutrient concentration (Hättenschwiler and Jørgensen 2010). Plant polyphenolics can be accurately measured via near-infrared spectroscopy (NIRS; Rupert-Nason et al. 2013), and by airborne imaging spectroscopy (Kokaly et al. 2009; Asner et al. 2014; Madritch et al. 2014; Serbin and Townsend, Chap. 3).

Though typically considered primarily for their aboveground defensive properties, phenolics in plant residues (leaf litter and roots) can have large influences on decomposition. Simple phenolics can increase soil respiration by providing a simple carbon source for microorganisms (Horner et al. 1988; Schimel et al. 1996; Madritch et al. 2007). Tannins are defined, in part, by their ability to bind to proteins (Bate-Smith 1975). The attributes of nonstructural polyphenolics that make them effective plant pathogen defenses also affect nonpathogenic fungi and microbes once litter enters the detrital food web; tannins do not discriminate between enzymes of plant pathogenic fungi or decomposing fungi. If tannins bind covalently with proteins to form polyphenolic-protein complexes, they become highly recalcitrant, and only basidiomycetes with polyphenol oxidase and earthworms can take advantage of these complex N sources (Hättenschwiler and Vitousek 2000). The inhibitory role of tannins on soil enzymes varies with specific tannin structure, which varies widely among species (Triebwasser et al. 2012). Tannins also have a limited ability to bind with carbohydrates and cellulose to form recalcitrant complexes (Horner et al. 1988; Kraus et al. 2003). The ability of polyphenolics to complex with proteins and other biochemicals is the primary method by which they influence soil respiration, litter decomposition, and soil N fluxes.

In addition to their influence on decomposition, nonstructural polyphenolics (which do not include lignin) influence N cycling by binding to and promoting retention of N-rich compounds including ammonium, amino acids, and proteins (Hättenschwiler and Vitousek 2000). Ayres (1997) suggested that condensed tannins may be more important to N cycling than to herbivore defense, since condensed tannins frequently have no anti-herbivory activity. Hättenschwiler et al. (2011) also proposed that polyphenolics, and tannins in particular, may be an important N conservation and recovery strategy for some species. This appears to be the case in *Populus tremuloides* systems, where high-tannin genotypes recovered more N than did low-tannin genotypes, especially when under severe herbivory (Madritch and Lindroth 2015). The high reactivity and branching structure of reactive hydroxyl sites also allow polyphenolics to complex with clay particles in soil and thereby influence several micronutrients in addition to N (Schnitzer et al. 1984).

Variation in plant phenolics is driven by several interacting factors. In general, polyphenolic concentrations in foliage are highest during the summer months (Feeny 1970). Summer coincides with both the onset of herbivory and the highest levels of photosynthetic activity. Herbivory-induced polyphenolic production is a well-documented aspect of plant-insect interactions (Herms and Mattson 1992; Baldwin 1994). The composition and quantity of phenolics vary among taxa at small and large phylogenetic scales. At large phylogenetic scales, condensed tannins are common in woody plants but almost absent in herbaceous species (Haslam 1989). At narrow phylogenetic scales, the concentration of polyphenolics is also under genetic control, and often there is considerable variation within the same species that can have important influences on belowground processes including litter decomposition and nutrient cycling (Lindroth et al. 2002; Schweitzer et al. 2005; Madritch et al. 2006, 2007).

### 8.3.3 *Plant Diversity*

Plant diversity, which can be accurately remotely sensed at some spatial scales (Wang et al. 2019; Gholizadeh et al. 2019), can influence belowground processes through its effects on productivity as well as on chemical diversity (Meier and Bowman 2008). Belowground diversity may be intrinsically linked to aboveground diversity because high plant diversity may provide a high diversity of litter quality and quantity to belowground systems that subsequently result in a high diversity of decomposers (Hooper et al. 2000). The specific relationship between aboveground plant communities and belowground microbial communities is context, system, and scale dependent (De Deyn and van der Putten 2005; Wu et al. 2011; Cline et al. 2018). For instance, Chen et al. (2018) found that plant diversity is coupled with soil beta diversity but not soil alpha diversity in grassland systems. Nonetheless, if aboveground diversity is indeed linked to belowground diversity, then aboveground estimates of plant diversity and plant traits could provide robust estimates of belowground processes.

Early work that focused on the influence of aboveground species diversity on litter decomposition yielded idiosyncratic results (Gartner and Cardon 2004; Hättenschwiler et al. 2005), with some studies reporting no effect of plant species diversity (e.g., Naeem et al. 1999; Wardle et al. 1999; Wardle et al. 2000; Knops et al. 2001), some reporting unpredictable results (Wardle and Nicholson 1996), and some reporting positive effects of plant species diversity on litter decomposition (Hector et al. 2000). Similar to aboveground processes, BEF studies that link aboveground diversity with belowground processes initially focused on aboveground species diversity (Scherer-Lorenzen et al. 2007; Ball et al. 2008; Gessner et al. 2010). The idiosyncratic relationship between species diversity and belowground processes led others to identify aboveground functional diversity and composition as more important to belowground processes than species diversity (Dawud et al. 2017).



Foliar chemistry is relevant to biodiversity and ecosystem functioning studies because plant chemistry varies widely among and within species and can influence belowground microbial communities and biogeochemical cycles (Cadisch and Giller 1997; Hättenschwiler and Vitousek 2000). It follows that variation in foliar traits important to decomposition (e.g., tannin concentration) will affect belowground microbial communities and the basic biogeochemical cycles that sustain forested ecosystems. Some studies have supported a chemical diversity approach toward elucidating the belowground effects of aboveground diversity (Hoorens et al. 2003; Smith and Bradford 2003). Epps et al. (2007) demonstrated that accounting for chemical variation was more informative regarding decomposition than was species diversity. While the usefulness of trait-based dissimilarity approaches remains somewhat equivocal (Frainer et al. 2015), there is increasing support for such trait-based approaches in explaining variation in leaf litter decomposition (Fortunel et al. 2009; Finerty et al. 2016; Jewell et al. 2017; Fujii et al. 2017). Handa et al. (2014) found that variation in leaf litter decomposition across widely different biomes was largely driven by commonly measured leaf traits such as N, lignin, and tannin content. At large scales, species traits rather than species diversity per se appears to at least partially drive variation in decomposition and belowground nutrient cycling.

In experimental systems, plant communities with high biodiversity result in high above- and belowground productivity (Tilman et al. 2001). The additional biomass that an ecosystem produces in diverse assemblages over what is expected from monocultures is called “overyielding” and has been documented in both grassland and forest experiments (Grossman et al. 2018; Weisser et al. 2017). The additional productivity results from several mechanisms acting simultaneously in more diverse communities, such as reduced pathogen attack, reduced seed limitation, and increased trait differences leading to “complementarity” in resource uptake (Weisser et al. 2017). Complementarity in resource use, particularly light harvesting, results in more efficient use of limiting resources and greater productivity (Williams et al. 2017). Similar patterns of greater productivity with higher diversity are observed in forest plots globally (Liang et al. 2016) although such patterns are scale dependent, and do not necessarily hold at large spatial extents (Chisholm et al. 2013). In naturally assembled grasslands, the relationship may not necessarily hold consistently (Adler et al. 2011). An open question, then, is the extent to which diversity and productivity are linked at large spatial scales in ecosystems globally. This is a question that can reasonably be addressed with remotely sensed measures of biodiversity and ecosystem productivity if scaling issues are appropriately considered (Gamon et al., Chap. 16). Plant diversity influences the quality of inputs and may allow for niche partitioning among functionally different microbes and may also influence productivity, the source of inputs of organic matter available to microbes, and microbial diversity. Through these linkages, foliar diversity has the potential to influence microbial diversity and function and hence belowground processes (Cline et al. 2018). The extent to which diversity and productivity, measured aboveground, can predict belowground microbial and soil processes is a question that is ready to be tackled at a range of scales across continents.

## 8.4 Case Studies

### 8.4.1 *Remote Sensing of Belowground Processes via Canopy Chemistry Measurements*

Plants act as aboveground signals for belowground systems. As such, RS of plant spectra can provide information about belowground systems. Plant spectra can provide a wealth of biological information important to plant physiology and community and ecosystem processes across multiple spatial scales (Cavender-Bares et al. 2017). Some researchers have used direct spectral measurements (e.g., NIRS) for direct measurements of soil characteristics (reviewed by Stenberg et al. 2010; Bellon-Maurel and McBratney 2011; Soriano-Disla et al. 2014), and there are limited examples of remotely sensed spectroscopic measurements of soils (reviewed by Ustin et al. 2004; Cecillon et al. 2009). Here we focus on remotely sensed spectral measurements of plant communities as a surrogate for belowground processes. The optical surrogacy hypothesis (sensu Gamon 2008) argues that plant spectra can serve as a surrogate for important belowground processes.

Direct spectral measurements have been used to assess belowground processes for decades. For instance, direct NIRS of leaf litter can be used to predict decomposition rates in a variety of systems (Gillon et al. 1993; Gillon et al. 1999; Shepherd et al. 2005; Fortunel et al. 2009; Parsons et al. 2011). RS of canopy traits to predict belowground processes is becoming increasingly useful. Spectroscopic measurement of  $\delta^{15}\text{N}$  is of particular interest for ecosystem processes (Serbin et al. 2014) because stable N isotopes can provide important information regarding ecosystem N cycling (Robinson 2001; Hobbie and Hobbie 2006). RS of forest disturbance (e.g., fire severity) and subsequent belowground processes is relatively common (e.g., Holden et al. 2016). Sabetta et al. (2006) used hyperspectral imaging to predict leaf litter decomposition across four forest communities. Fisher et al. (2016) were able to distinguish between arbuscular and ectomycorrhizal tree-mycorrhizal associations using spectral information gleaned from Landsat data. While the above examples focus on remotely sensed spectral information, remotely sensed forest structural information developed from lidar data can also provide information about belowground systems, as Thers et al. (2017) were able to use remotely sensed lidar data to estimate belowground fungal diversity. The growing number of examples that employ remotely sensed data to provide information about belowground systems points to the potential of plant spectra to be used as surrogates for ecosystem processes.

### 8.4.2 *Forest Systems: Aspen Clones Example*

An example of optical surrogacy in practice is illustrated by work completed in trembling aspen (*Populus tremuloides*) systems across the Western and Midwestern USA. Trembling aspen is the most widespread native tree species in North America (Mitton and Grant 1996) and is an ecologically important foundation species across

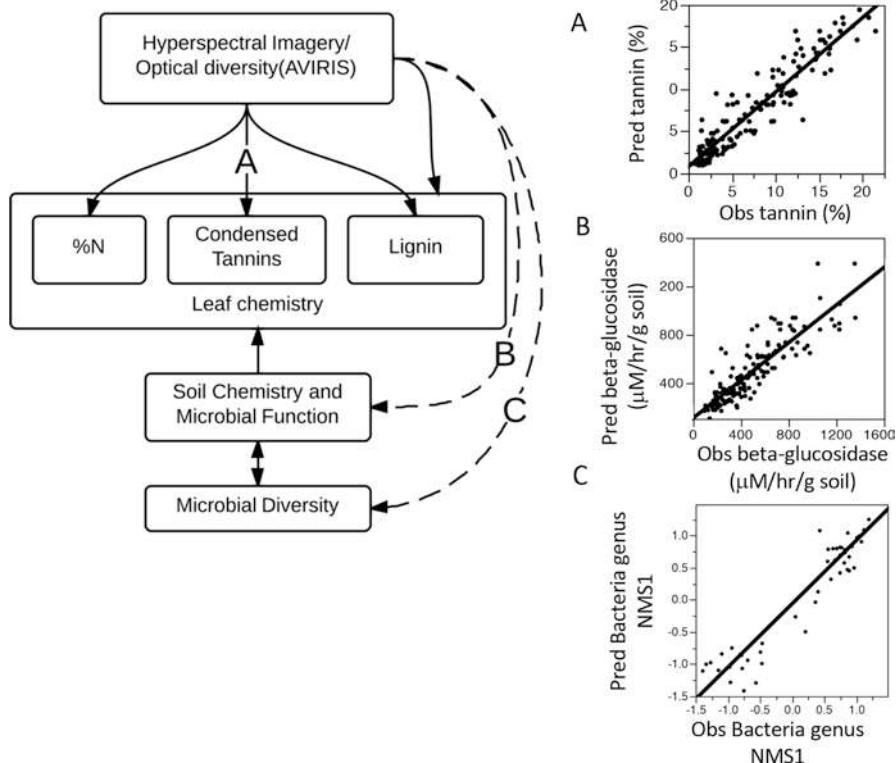
its native range (Lindroth and St. Clair 2013). Aspen is facing large and rapid declines in intraspecific biodiversity because concentrated patches of aspen are currently experiencing high mortality rates in North America (Frey et al. 2004; Worrall et al. 2008). This phenomenon, commonly referred to as sudden aspen decline (SAD), leads to the death of apparently healthy aspen stands in 3–6 years (Shields and Bockheim 1981; Frey et al. 2004). These natural history traits, combined with the ecological and economic significance of the species, make trembling aspen an ideal system to employ RS techniques to estimate genetic diversity and the consequences thereof for belowground processes.

Aspen typically reproduces clonally, often creating a patchwork of clones with many ramets (Fig. 8.2). Aspen clones vary widely in canopy chemistry traits that are important to belowground processes such as litter decomposition (Madritch et al. 2006). Several studies have highlighted the importance of plant genetic diversity to ecosystem processes (Madritch and Hunter 2002, 2003; Schweitzer et al. 2005; Crutsinger et al. 2006; Madritch et al. 2006, 2007) and community composition (Wimp et al. 2004, 2005; Johnson and Agrawal 2005). These recent advances demonstrate that genetic diversity affects fundamental ecosystem processes by influencing both above- and belowground communities (Hughes et al. 2008). The natural history traits of aspen, its clonal nature, genetically mediated variation in canopy chemistry, and the concomitant wide range of variation in foliar traits make it an ideal model system for RS of biodiversity.

Madritch et al. (2014) described how remotely sensed spectroscopic data from NASA's AVIRIS platform can be used to describe aboveground genetic and chemical variation in aspen forests across subcontinental spatial scales. This work built upon past work that demonstrated the ability of imaging spectroscopy to detect both aboveground chemistry (Townsend et al. 2003) and biodiversity (Clark et al. 2005) and employed imaging spectroscopy to discriminate intraspecific, genetic variation in aboveground chemistry and diversity. Because of the tight linkages between aboveground and belowground systems and because of the large variation in secondary chemistries important to belowground processes in aspen, this project also demonstrated the ability to predict belowground process via RS of forest canopy chemistry. Figure 8.3 illustrates both the

**Fig. 8.2** Aerial photo showing color differentiation of genetically distinct aspen clones. Genotypes can be detected rapidly via remote sensing techniques





**Fig. 8.3** Imaging spectroscopy links to several layers of ecological processes in aspen forests. (a) Partial least squares (PLS) prediction (pred) for condensed tannin concentration from AVIRIS data compared to observed (obs) tannin. (b) PLS prediction (pred) for soil b-glucosidase activity compared to observed (obs) b-glucosidase. (c) PLS prediction from AVIRIS spectra for bacterial diversity compared to observed bacterial diversity, where bacterial diversity is the first axis of an NMDS ordination of amplicon sequencing of rDNA (525f and 806r primers). (Tannin and soil enzyme data are from Madritch et al. (2014))

direct linkages between RS and canopy chemistry (A) and the subsequent indirect linkages to belowground function (B) and the microbial community (C). The indirect linkages represent the optical surrogacy hypothesis. Belowground attributes are not measured directly via RS, but rather RS of the forest canopy was able to provide detailed information regarding belowground process.

### 8.4.3 *Experiment Prairie Grassland System: Cedar Creek Example*

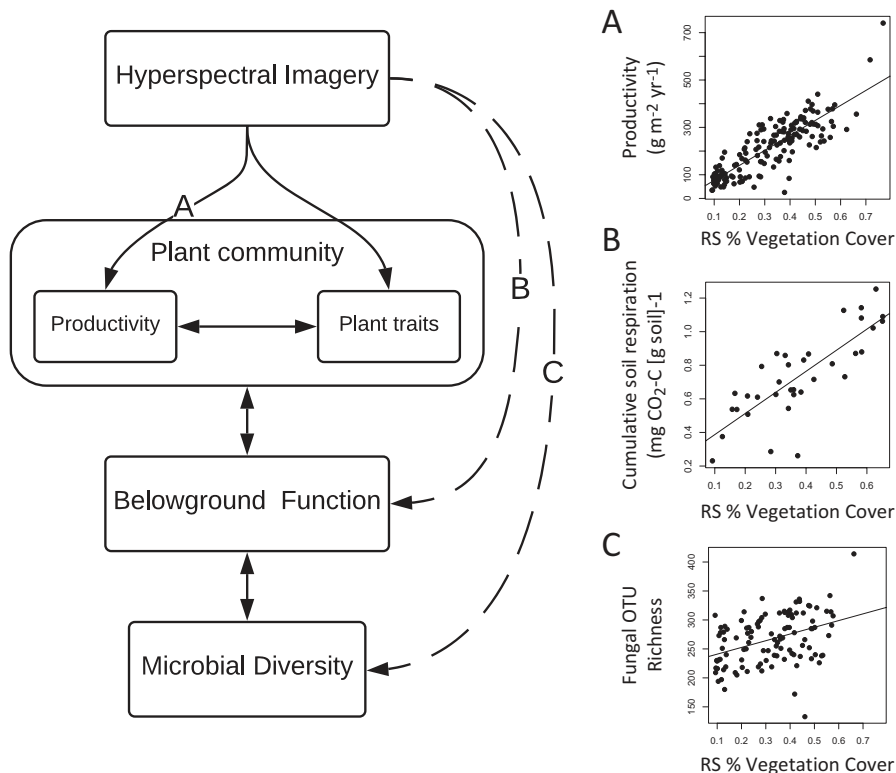
Vegetation differences between prairie and forested ecosystems have important consequences for above- and belowground linkages. Detrital inputs in forests are dominated by leaf litter, whereas they are dominated by root exudates and turnover in

prairie systems that are frequently burned. We employed a parallel application of spectroscopic imagery to assess above- and belowground diversity and functioning at the grassland biodiversity experiment located at Cedar Creek Ecosystem Science Reserve (Tilman et al. 2001). Rather than a monospecific forest canopy, the grassland experiment consisted of replicated diversity treatments ranging from 1 to 16 perennial grassland species in 9 m × 9 m plots. This work had more technical challenges associated with it compared to the aspen forest project due to the inherent complexity of a mixed species system and the small spatial scale of the experimental plots.

The relationship between plant diversity and aboveground biomass in the Cedar Creek BioDIV experiment is well documented (Tilman et al. 2001, 2006). Schweiger et al. (2018) further demonstrate that both plant diversity and function are measurable via remotely sensed spectra within the experiment and that spectral diversity predicted productivity. Wang et al. (2019) used AVIRIS imagery to map functional traits across the experiment. Remotely sensed productivity and functional trait composition can thus be tested for linkages with belowground processes. In this system, the quantity of inputs had a large impact on fungal composition and diversity (Cline et al. 2018). Productivity, measured as annual aboveground biomass, given that it is annually burned, can be accurately detected as remotely sensed vegetation cover (Fig. 8.4a; Wang et al. 2019, following the method of Serbin et al. 2015). Remotely sensed vegetation cover, in turn, predicted fungal diversity, measured as operational taxonomic unit (OTU) richness (Fig. 8.4b), and cumulative soil respiration (Fig. 8.4c). In addition to the total organic matter inputs to the soil, chemical composition also influenced belowground microbial communities. For example, remotely sensed %N (Wang et al. 2019) was positively correlated with soil microbial biomass (Cavender-Bares et al., unpublished manuscript).

#### ***8.4.4 Challenges and Future Directions***

Employing plant spectra to predict belowground processes has both caveats and advantages over traditional belowground sampling. One important caveat is that any prediction of belowground processes requires a solid understanding of the linkages between above- and belowground processes in any given system. Examples in the literature that link remotely sensed attributes of aboveground systems with belowground systems remain scarce, in part, because of the historic separation of the two disciplines. It is unclear how well remotely sensed plant attributes will predict microbial and soil processes across ecological systems. In the above forest example, aspen forests were generally uniform in canopy coverage. It was also a single-species system where leaf structure remained consistent across the study area, despite the large spatial sampling scheme. Consequently, most of the variation in aspen spectral signal was likely due to variation in canopy chemistry and biomass rather than leaf structure. Lastly, in this temperate forest system, leaf litter accounts for a large fraction of inputs into belowground systems, compared to systems such as Cedar Creek that are burned frequently and where fine-root turnover dominates belowground inputs.



**Fig. 8.4** Hyperspectral imagery links above- and belowground processes in a prairie ecosystem. (a) Remotely sensed vegetation cover significantly predicted aboveground plant productivity,  $R^2 = 0.695$  (a); cumulative soil respiration ( $\text{mg CO}_2\text{-C [g soil]}^{-1}$ ),  $R^2 = 0.63$  (b); and fungal diversity, measured as OTU richness,  $R^2 = 0.144$  (c). (Soil respiration and fungal diversity data are from Cline et al. (2018))

RS of aboveground properties poses further challenges that include separating the spectral signals important to canopy chemistry from those of physical properties of the forest canopy (Townsend et al. 2013). Larger challenges lie in the lack of accessibility of RS data and processing techniques to the broader ecological research community.

Several issues of scale present challenges to the application of RS to belowground systems. Large knowledge gaps remain in connecting the small spatial scale observations of traditional field studies with the large spatial scale observations of airborne or satellite RS platforms (Asner et al. 2015; Gamon et al., Chap. 16). In addition, there is a large mismatch in the spatial heterogeneity between above- and belowground systems, with belowground systems being notoriously heterogeneous across small spatial scales (Bardgett and van der Putten 2014). The majority of variation in belowground processes may be due to small, local-scale factors rather

than large-scale factors such as climate (Bradford et al. 2016). In addition to issues associated with spatial scale, there are large spans in the scales of biodiversity and time. Speciose aboveground systems may contain upward of 600 species  $\text{ha}^{-1}$  (Lee et al. 2002), whereas soils contain many thousands of microbial “species” per gram of soil, with large numbers of endemics (Schloss and Handelsman 2006). Linking function to diversity remains a challenge in both systems and particularly in belowground systems where the functional role of the vast majority of species is unknown (Krause et al. 2014). Likewise, large differences in temporal scales exist between above- and belowground systems, with leaf responses to sunlight occurring on the order of seconds (Lambers et al. 1998), while the turnover of soil organic matter can take years to centuries (Bardgett and van der Putten 2014). Variation in temporal scales across systems is particularly important given that the importance of biodiversity to ecosystem processes increases with temporal scale (Cardinale et al. 2012; Reich et al. 2012).

Irrespective of RS, there are shortcomings associated with belowground measurement. For example, belowground measurements that use enzyme activity potentials as indicators of microbial function are widespread, but they are known to have numerous limitations (Nannipieri et al. 2018). Likewise, microbial diversity estimates based upon amplicon sequences of bacterial 16s rDNA have their own methodological and interpretive limitations (Schöler et al. 2017). Nonetheless, both enzyme activities and amplicon sequencing techniques provide useful information about belowground systems and are used widely enough to be compared across studies as long as protocols are consistent.

Advantages of using remotely sensed spectral properties of aboveground vegetation to predict belowground processes lie within the data-rich nature of imaging spectroscopy and the consequent ability to measure many more traits of the canopy than would otherwise be feasible with traditional benchtop methods. In Madritch et al. (2014), only four canopy traits were considered using traditional wet chemistry techniques (leaf tannin, N, C, lignin). These canopy foliar traits were expectedly well correlated with belowground processes. However, plant spectra themselves were better correlated with belowground processes than were plant leaf traits (Madritch et al. 2014). This strong relationship between plant spectra and belowground processing existed because the plant spectra provided quantitative information about many plant traits that were not measured via wet chemistry techniques. Potentially dozens of leaf traits important to belowground processes could be conveyed by plant spectra. The ability of plant spectra to capture many foliar attributes quickly and accurately is a large reason why plant spectra are useful for predicting belowground processes. In addition, identifying which regions of plant spectra are most variable and correlated with belowground process allows researchers to use spectra to identify plant traits important to soil processes. In short, the potential for RS products to link above- and belowground systems is promising but faces considerable obstacles.

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