

Review Article

Perennial groundcovers: an emerging technology for soil conservation and the sustainable intensification of agriculture

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Integrating perennial groundcovers (PGC) — sometimes referred to as living mulches or perennial cover crops — into annual cash-crop systems could address root causes of bare-soil practices that lead to negative impacts on soil and water quality. Perennial groundcovers bring otherwise absent functional traits — namely perenniality — into cash-crop systems to preserve soil and regenerate water, carbon, and nutrient cycles. However, if not optimized, they can also cause competitive interactions and yield loss. When designing PGC systems, the goal is to maximize complementarity — spatial and temporal separation of growth and resource acquisition — between PGC and cash crops through both breeding and management. Traits of interest include complementary root and shoot systems, reduced shade avoidance response in the cash-crop, and PGC summer dormancy. Successful deployment of PGC systems could increase both productivity and profitability by improving water- and nutrient-use-efficiency, improving weed and pest control, and creating additional value-added opportunities like stover harvest. Many scientific questions about the inherent interactions at the cell, plant, and ecosystem levels in PGC systems are waiting to be explored. Their answers could enable innovation and refinement of PGC system design for multiple geographies, crops, and food systems, creating a practical and scalable pathway towards resiliency, crop diversification, and sustainable intensification in agriculture.

Introduction

Increasing productivity without degrading the natural resource base — sustainable intensification — is the defining scientific challenge for 21st-century agriculture. Global food security relies on a diminishing number of annual cash-crop grains, forages, and vegetables. Broad and regional adaptation of these crops and their management systems has allowed dramatic increases in productivity, doubling yields over the past century [1]. However, the land-use change resulting from the conversion of perennial, native ecosystems to intensive annual crop production is causing environmental impacts at a global scale [2,3]. Arguably, the most serious of these is the loss and degradation of soil [4]. Healthy soils are the backbone of sustained crop production [5]. For farmers, soil lost to erosion limits future productivity by disrupting soils' ability to store and cycle carbon, water, and mineral nutrients. For human societies and the environment, displacement of soil in runoff laden with nutrient-containing sediments and soil-bound agricultural chemicals contaminates consumer water supplies, causes eutrophication of inland waters, and creates hypoxic ocean 'dead zones.'

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Crops and management practices that minimize soil disturbance and increase the proportion and duration of soil covered by living vegetation dramatically reduce soil erosion [2]. Perennial species provide vegetative cover more effectively than annuals, but most opportunities to introduce perennials into cash-cropping systems involve semi-permanent land set-asides (e.g. the US Conservation Reserve Program, perennial grass waterways, or perennial biomass systems). Many farmers and scientists are exploring strategies to increase vegetative cover in annual cash-crop fields. These include: planting annual cover crops in relay with cash-crops, interseeding annual cover crops with cash-crops, and developing perennial grain crops; however, here we focus on perennial groundcover (PGC) crops and cropping systems, an emerging technology for the sustainable intensification of agriculture (Figure 1).

Incorporating low-growing, non-competitive (i.e. ecologically complementary) PGC into cash-crop fields restores continuous vegetative cover without interfering with cash-crop productivity (Figure 1C). The PGC concept is potentially applicable to annual and perennial, organic and conventional, cash-crop production. Perennial groundcovers are already used in orchards[6], have been trialed in vegetable production[7], and could be used with to-be-domesticated crops of the future (e.g. perennial grains or novel plant-based protein crops). However, there is a dire need to develop and deploy robust PGC approaches for dominant grain production systems, especially corn and soybean rotations, whose environmental impacts are oversized because their geographic footprints dwarf other cash-crops [8].

Agronomists in the US have been independently working for decades to design PGC-corn production systems using clovers and turfgrasses [9–13]. Research in South America and Africa is further advanced with broad deployment of PGC-corn system variations, namely, the ‘Push-Pull’ system in Kenya for low-input pest management and Integrated Crop-Livestock-Forest systems in Brazil to enhance productivity in depleted soils [14,15]. Regardless of PGC species or location, research routinely demonstrates that PGC delivers reductions in soil erosion, nutrient runoff, and nitrate leaching [16–19]. Corn and soybean yields grown with PGC can be equal to or better than when grown conventionally; however, failure to manage PGC and cash-crops interactions leads to significant yield loss [11,20]. Optimization and widespread adoption of PGC requires generating and leveraging knowledge about the diverse interactions at the cell, plant, and ecosystem levels inherent in these systems.

Lessons from plant functional ecology

Whether in highly-managed or natural environments, plants interact with other conspecific or heterospecific plant neighbors. Natural communities evolve such that plants in proximity to one another have complementary functional traits that reflect the type and quantity of resources they consume [21]. These traits enable plants to coexist by occupying different spatial and/or temporal niches, each efficiently using a portion of the available resources to maximize primary productivity [22].

This does not imply that all plant-plant interactions are positive. Functional trait redundancy leads to competition [23]. Species with similar growth and rooting characteristics compete for light, nutrients, moisture, and space (Figure 2). The consequences of competition between species with similar resource acquisition traits are always negative to both when compared to a no-competition environment, although to varying degrees depending on their relative competitiveness and the availability of resources [24]. The presence of both competitive and complementary interactions in natural ecosystems — lack of optimization — constrains productivity and reflects existing trade-offs and ongoing natural selection [25,26].

Plant-plant interactions in modern agriculture have been optimized to maximize cash-crop yield by modifying the growing environment to the cash-crop’s needs while eliminating competition from other organisms (i.e. monocropping). This simple approach echoes that used in fields like fermentation, where eliminating competition via vessel sterilization is standard practice. In agricultural settings, it effectively removes the negative effects of competition, but restricts agroecosystem function by limiting functional trait diversity in the plant community. Functional traits modulate essential ecosystem processes like nutrient cycling, fungal and microbial community dynamics, carbon (C) sequestration, and soil erosion [21,27].

Adding PGC to a cropping system introduces perenniality, a key functional trait, and improves ecosystem function [8,28]. However, interactions between the PGC and cash-crop require careful management to avoid yield losses because PGC functional traits conferring ecological benefits may also create competition. Several functional traits influence nutrient and water uptake and species compatibility — rooting depth and architecture, perenniality, seasonal growth distribution, photosynthetic pathway, summer dormancy, shade tolerance, winter hardiness, and mode of reproduction [29]. In designing PGC systems — choosing appropriate



Figure 1. Strategies for increasing continuous vegetative cover in cash-cropping systems.

(A) Cereal rye cover crop (CC) planted in the fall. Annual cover crops provide vegetative cover and provide ecosystem services when cash-crops are not present. The magnitude of ecosystem services delivered depends on successful CC establishment and biomass accumulation, which can be challenging in variable climatic conditions of agro-temperate regions. (B) Annual ryegrass, guar, and mung bean CC interseeded with sunflowers. Annual CC can be interseeded with cash-crops during the growing season to improve establishment and increase vegetative cover within the cash-crop season. (C) Corn grown with a kentucky bluegrass perennial groundcover (PGC). Perennial groundcovers provide year-round soil cover and nutrient retention, and once established, do not have the annual seed costs and establishment risks associated with annual CC. (D) An alfalfa PGC grown with intermediate wheatgrass for Kernza® perennial grain production. Perennial groundcovers can improve vegetative cover in both annual and perennial cash-crop production.

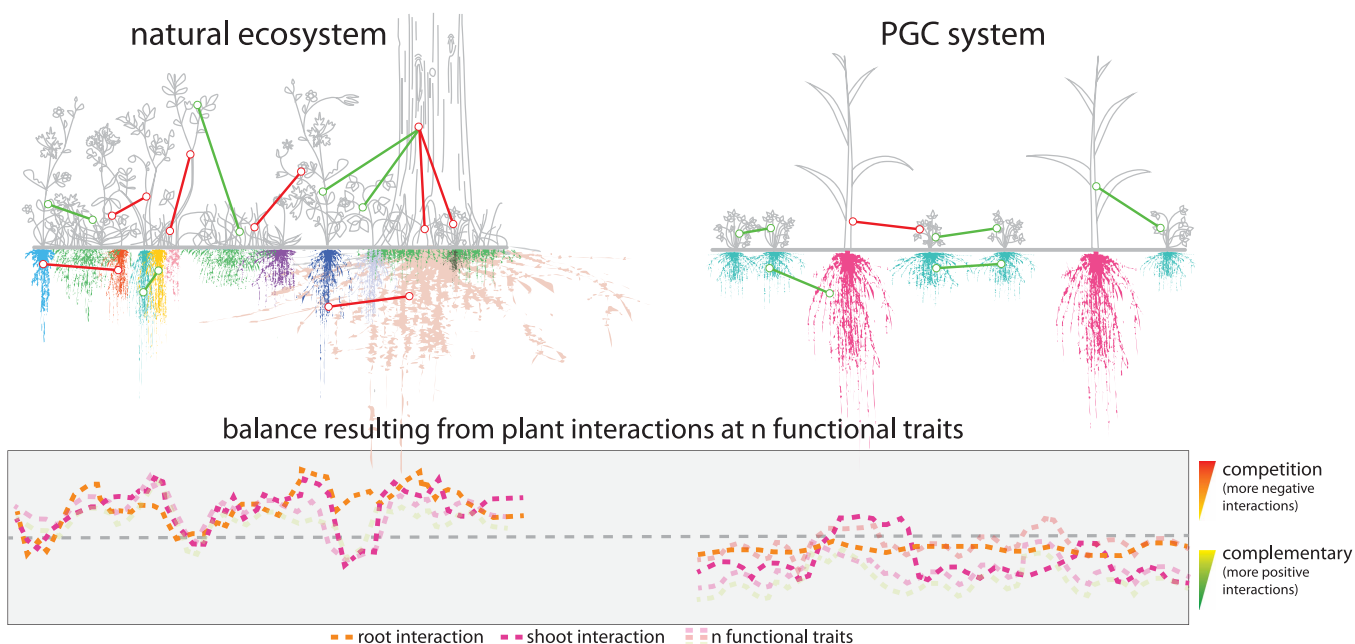


Figure 2. Comparing natural plant communities to designed and optimized plant communities in perennial groundcover systems.

Plants live in communities and interact negatively (i.e. competitive, red lines top) or positively (i.e. complementary, green lines top) with their neighbors. Natural ecosystems are composed of numerous plant species and contain a wide range of functional traits related to each species' resource-use. Maximum resource-use complementarity, and therefore productivity, is achieved by maximizing between species functional trait differentiation. However, natural ecosystems are not optimized. There is often functional redundancy (e.g. similar root or shoot architecture) among species resulting in competitive interactions and decreased productivity. Through breeding and agronomic management, perennial groundcover (PGC) systems can be optimized to maximize functional trait differentiation between the two component species so the balance of plant interactions is mostly complementary. For example, a common PGC configuration involves growing corn with kentucky bluegrass (*Poa pratensis* L.) in alternating strips (top right). The kentucky bluegrass shoot and root systems are relatively short and shallow, leaving a larger balance of light and soil resources to be exploited by the corn shoot and root systems. Furthermore, since the growth of the two species is asynchronous, bluegrass is a cool-season C3 species while corn is a warm-season C4 species, competition occurs primarily in the spring when the PGC is actively growing during corn establishment.

groundcover and management practices — it is critical to control functional trait variation and create separate niches that minimize competition and maximize complementarity with the cash-crop, or in the case of crop rotation, multiple cash-crops [26,30] (Figure 2).

Critical functional traits in perennial groundcover systems

Many scientific questions about the genetic and physiological basis of plant-plant interactions remain to be explored. Answering these questions will enable innovation and refinement of PGC system design. While the specific criteria and constraints may vary by crop and region, the broad requirement is that the PGC maximizes ecological benefits while minimizing competition with the cash-crop. Some studies have identified PGC candidate species that best fit this ideotype [11], but both PGC and cash-crops can be bred and new adaptive management practices can be designed to further reduce trait redundancy [26]. The following discussion highlights functional traits and sources of interaction to be considered in PGC system design.

Root-shoot architecture

Root and shoot architecture directly affect PGC-cash-crop compatibility. Fibrous root systems, characteristic of grasses, are better suited than taproot systems for controlling soil erosion and immobilizing excess nutrients because their large numbers of roots, each with massive amounts of root hairs, cling to soil particles and absorb water and nutrients [31,32]. Roots in cool-season grasses are typically shallower than warm-season grasses, but root depth and distribution vary greatly even among cool-season grass species (e.g. tall fescue (*Festuca arundinacea* Schreb.) has a much deeper root system than kentucky bluegrass (*Poa pratensis* L.), a leading PGC candidate) [33,34]. The shallow fibrous root systems of many cool-season grasses are ideal for PGC because they allow roots of the cash-crop to occupy a much deeper zone (Figure 2). Perennial grasses also differ in root growth habit; roots of some species persist while others die within a year [35]. Adventitious roots or nodal roots — another distinct root system developed from lower nodes in tillers or nodes in rhizomes or stolons — often account for most of the root mass in perennial grasses [36]. Thus, they play a significant role in resource acquisition and in determining PGC-cash-crop compatibility.

Grass shoot architecture varies in form due to distinctly different branching patterns. Grasses can be either bunch type producing tillers only, rhizomatous producing rhizomes and tillers, or stoloniferous producing stolons and tillers. Some species, such as bermudagrass, have all three branch types. Branches, particularly fast spreading rhizomes and stolons, affect the extent of a PGC's horizontal growth and its ability to recover when stressed [32]. Repeated branching is the basis for perenniality and longevity in grasses [37]. Horizontal growth improves cover outside the cash-crop growing season, with strip-tillage often used in spring to halt this horizontal growth and create a seedbed for the cash-crop (Figure 3). While above ground shoots are not in direct competition with the cash-crop, they can alter the light spectrum and may trigger a shade avoidance response (SAR, see discussion below) in the cash-crop [38], resulting in yield loss. Based on previous and ongoing research [8,11,20], we believe PGC should be low- and horizontally-growing with short rhizomes or stolons, allowing the PGC to recover following cash-crop harvest.

Shade avoidance response

Even in the presence of ample resources, growth and development of crops can be negatively impacted by competition from inter-row weeds or PGC. Flynn et al. [11] observed this phenomenon when seedling corn, grown with various PGC species, exhibited stressed, chlorotic leaves and thin elongated stems even with optimal fertility, water, and light. They concluded the corn seedlings exhibited a SAR despite lack of overhanging vegetation [11]. The SAR has been observed in multiple crops and is characterized by main axis elongation, longer yet narrower and thinner leaves, increased leaf area index early in development, and changes in photoassimilate partitioning favoring shoot over root growth [39–43]. These physiological and morphological changes set off a chain of events that affect crop performance, especially in corn, through reproduction [43–45].

The SAR is triggered by phytochrome photoreceptors when plants perceive light competition from above or below. Phytochrome responds differentially to red (r) and far-red (fr) light. Red light converts phytochrome to its active Pfr form (far-red light absorbing), and far-red light converts it to its inactive Pr form (red light absorbing). When crops receive relatively low r/fr light signals, whether reflected or transmitted via inter- or intra-row competition, the relative portion of phytochrome changes to the Pr form, eliciting SAR [46].

Plant stress induced by early competition has been thoroughly studied due to the tremendous impacts delayed weed control has on crop yields, even when weed pressure is quickly addressed after crop emergence

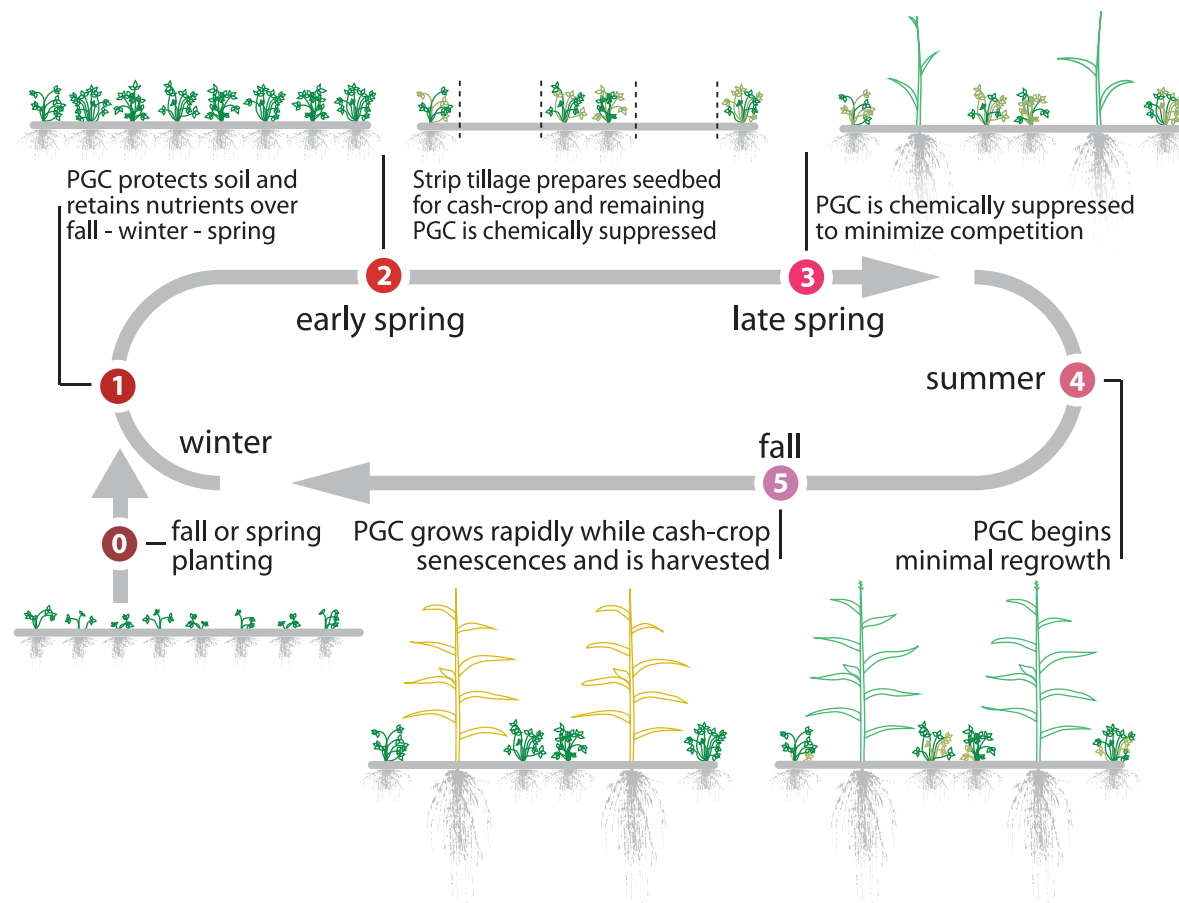


Figure 3. Seasonal events and management practices in perennial groundcover (PGC) systems.

(0) The PGC is planted in late fall or early spring, preferably with a no-till drill. (1) Once established, the PGC acts as a cover crop in the fall, winter, and early spring. Continuous vegetative cover limits erosion and runoff, and living root systems immobilize nitrate that might otherwise leach into groundwater. (2) The PGC is a weed in early spring. Space and a seedbed are prepared for the cash-crop using strip-tillage. The PGC is chemically suppressed before the cash-crop is planted and (3) again later in spring to prevent a shade avoidance response. (4) By summer, the cash-crop has passed the critical period of weed control and the PGC begins to regrow. (5) In fall, the cash-crop begins to senesce, and the grain and residue are harvested. The PGC grows rapidly and fills space previously occupied by the cash-crop. In the next spring a new cash-crop, either the same as or different than the previous year, is planted. With each cycle, additional soil regeneration is accomplished.

through mechanical or chemical means. Crop sensitivity to weed pressure during early development stages is known as the critical period of weed control (CPWC) — the period when weeds must be controlled to maintain 95% of the achievable yield. When characterizing the CPWC, Bosnic and Swanton [47] observed 26 to 35% reduction in corn yield with early emerging (V1-V2) grass weeds yet only a 6% yield loss when grass weeds emerged after V4, reinforcing the hypothesis that depletion of r light wavelengths early in crop development has a profound impact on the plant for the remainder of the season.

Perennial groundcover findings parallel weed science studies. Establishment of PGC several weeks after corn emergence has little effect on grain yield [48,49]. Studies that suppress and turn green PGC tissue brown before cash-crop emergence observe higher grain yields in corn-PGC systems [9,20,50,51]. Thus, preventing ‘perceived’ early season competition by controlling the red and far-red light reflected from the PGC canopy is critical to reducing SAR and achieving acceptable crop yields. Chemical suppression of PGC is common (Figure 3), but opportunities exist to develop additional adaptive management strategies. Cash-crops could also be bred that do not exhibit SAR, but the trade-offs inherent in not exhibiting SAR should be considered.

Summer dormancy

Dormancy is defined as ‘temporary suspension of visible growth of any plant structure containing a meristem’ [52]. Summer dormancy occurs in species of Mediterranean origin where summer drought and heat threaten survival. Early onset of summer dormancy is a highly desirable PGC trait that can minimize competition with the cash-crop for water and reduce SAR during the CPWC. During summer dormancy, grass roots remain active to provide critical ecological services, albeit in reduced capacity [53,54]. Several temperate grass species, including *Poa bulbosa* [55,56], *Poa scabrella* [57], *Poa pratensis* [58], *Dactylis glomerata* [59], and *Festuca arundinacea* Schreb.[60] can enter dormancy in summer, most likely as a result of increased temperature, photoperiod, or both [56]. Recent research at Iowa State University indicates that corn yields grown with *Poa bulbosa* are not significantly different from conventionally grown corn (Fei, unpublished). Furthermore, intraspecific variation for the onset of summer dormancy exists [56] and can thus be selected to optimize PGC summer dormancy timing and duration.

Will perennial groundcovers improve soil health and carbon storage?

Photosynthesis remains the most important global carbon (C) sink [61], and regenerative agriculture (RA) practices that increase soil organic matter (SOM) — generally composed of ~ 58% C — can contribute to reductions in atmospheric CO₂ concentrations [62]. Building SOM and soil organic carbon (SOC) stocks in agricultural soils requires that C inputs via primary plant production exceed C lost to erosion and mineralization [63].

Tillage destroys soil aggregates and exposes physically protected SOM to accelerated mineralization, resulting in CO₂ emissions [64]. PGC systems in development incorporate reduced- or no-tillage; no-tillage and strip-tillage have been observed to reduce CO₂ emissions by up to 83% compared to moldboard plowing [65,66]. More importantly, PGC systems excel at minimizing soil and SOM loss to erosion. For example, Siller et al. [17] observed a 77% reduction in soil lost in runoff in a kura clover-corn PGC system compared to monocrop corn. Soil lost to erosion not only contains SOC, but it also contains nitrogen (N), phosphorus (P), and other minerals required for SOM formation [64].

When optimized, we expect PGC systems with compatible PGC and cash-crops will increase primary productivity and total C inputs compared to monocrop systems [21,67,68]. Retaining critical plant macronutrients and SOM in PGC systems by limiting erosion and C mineralization could further enhance system productivity and C sequestration [69]. Previously, C sequestration rates in turfgrasses — leading PGC candidates — have been estimated to range from 0.34 to 1.0 Mg ha⁻¹ year⁻¹, which is comparable to C sequestration rates reported for land in the USA Conservation Reserve Program [70–72]. However, local C sequestration via PGC systems — like other RA practices — will be strongly influenced by primary productivity, initial SOM, temperature, soil texture, soil water conditions, and soil microbial communities [73].

Efficient conversion of C into microbial biomass improves SOM accumulation [74], and plants shape the soil microbial community [75]. The diverse root functional traits in PGC systems create diverse habitats and provide continuous C inputs that feed soil fauna communities and increase microbial biomass [18,76–78]. These complex interacting processes — mediated by soil microorganisms, the PGC rhizosphere, and SOC inputs — enhance soil aggregation and SOM formation and ‘regenerate’ C, N, and P cycling at the ecosystem level [74,75].

Can PGC systems contribute to improved productivity and profitability?

Productivity and profitability in PGC systems will depend on co-development of compatible cash-crops, PGC, and paired adaptive management practices. When optimized, PGC systems could increase profitability by achieving equivalent, if not better, cash-crop yields while delivering ecosystem services that reduce external inputs (e.g. fertilizers, pesticides, water, fuel, and even seed when compared to annual cover crops) [8]. Increases in SOM in PGC systems, and concomitant improvements in soil aggregate stability and porosity, improve infiltration, water storage capacity, and water use efficiency [76]. By forming a barrier to evaporation — acting as a living mulch — PGC can further increase soil water content compared to conventionally tilled systems [73,79].

Including PGC in cash-crop systems will modify other abiotic factors that could increase cash-crop productivity and profitability. Continuous SOC inputs increase SOM and feed a diverse soil microbial community, which drives C, N, and P cycling and improves nutrient availability for cash-crops [62,80]. Some perennial legume PGC (e.g. clovers) contribute additional N to the SOM pool that can offset a portion of the N fertilizer applied for cash-crop production [12,81]. Other PGC, especially grasses, uptake and immobilize N that would otherwise be lost [16] or even exude biological nitrification inhibitors [82]. Lastly, interactions between PGC and soil fauna (e.g. arbuscular mycorrhizal fungi) can mobilize and mineralize soil organic P and improve cash-crop P nutrition and yield [18,77].

The increased biotic complexity in PGC systems may alter pest dynamics — insects, plant pathogens, and weeds. Whether pests are suppressed or favored depends on management imposed to modulate interactions between the PGC and cash-crop. For example, weed suppression can result from an actively growing PGC [83] or a dormant or suppressed PGC by limiting light penetration to the soil surface and altering its spectrum to decrease germination of light-sensitive weed species [84]. Both dormant and growing PGC can form physical barriers that impede emergence of small weed seedlings [85]. Changes to moisture availability, particularly near the soil surface, can greatly influence successful weed establishment; a dormant PGC residue can increase soil moisture by preventing evaporation while a slow-growing PGC may decrease water availability through transpiration [84,86].

Effective weed management will be critical for PGC establishment; adequate seeding rates and planting times and planting into fields with low weed pressure can increase the odds of a successful, low-maintenance PGC [87]. Limited management options are available in PGC systems for weeds that are not adequately suppressed [88,89], and these weeds may reduce productivity and contribute seeds to the soil. Controlling such ‘seed rain’ is of utmost importance in managing future weed infestations.

Expansion of living roots in PGC systems, both spatially and temporally, can also influence weed and pest dynamics [90]. Enhanced soil microbial activity could increase weed seed decay [91]. The PGC zone could be a more favorable environment for seed and seedling decay organisms, weed seed predators, and other beneficial insects [92,93]. It could also be suitable habitat for grubs and other pests, so careful study of pest dynamics will be crucial for its adoption.

Perennial groundcover systems may create additional value-added revenue streams that further improve profitability. Even in conventional systems with conservation tillage, the majority of the cash-crop residue must be left in the field to mitigate soil erosion and to maintain SOC and soil health [94,95]. Conversely, a larger portion of cash-crop residues, like corn stover, can be harvested in PGC systems because the PGC preserves the integrity of critical soil metrics [20,30]. Corn stover is the largest source of lignocellulosic material in the United States. While waivers and annual standards have undercut prescribed renewable fuel targets, corn stover is poised to function as a primary feedstock for 36 billion gallons of renewable fuel in 2022 as statutorily mandated by the Energy Independence and Security Act of 2007 Renewable Fuel Standard [96]. Perennial groundcovers could enable corn growers to harvest stover sustainably and take advantage of this emerging market while still meeting conservation goals.

Other value-added products derived from crop residue have been advocated since at least the early twentieth century [97,98]. As a low-cost lignocellulosic material, crop residue is used to produce particleboard and fiberboard for building materials and furniture [99]. Structural insulation was first made from sugarcane bagasse, wheat straw, and corn stalks in the United States in the 1920s [98,100]. Increasing societal interest in sustainability has created economic incentives for mass production of such products, including particleboard from corn stover and fiber-based surfboards, skis, and snowboards [101]. Crop residue can also be a cost-effective livestock bedding source, and when grain prices escalate, corn stover can be chemically treated to decompose lignocellulosic bonds to enhance ruminant digestibility [102].

Concluding remarks

Perennial groundcover systems are not a single gene, crop, management practice, piece of machinery, sensor, or algorithm — instead, PGC is a systems approach to addressing the root cause of bare-soil practices that negatively impact soil health and natural resources conservation — the pillars of agricultural sustainability. If developed successfully, the PGC approach can be a scalable, cash-crop agnostic solution to increasing vegetative cover on cropland globally, thereby enhancing agricultural resiliency and food security and improving quality of the most basic of public goods: water, air, and soil. Successfully deploying PGC across geographies, crops, and food systems will require a highly-integrated transdisciplinary approach that leverages farmer, academic,

commercial, and non-governmental capacity to answer complex scientific questions and create practical solutions.

Summary

- The perennial groundcover approach is a scalable, crop-agnostic solution to the bare-soil problems of agriculture. By pairing ecologically complementary perennial groundcovers and cash crops with adaptive management practices, both productivity and natural resource conservation goals can be achieved in the same field.
- Functional traits should be considered when designing perennial groundcover systems including: root and shoot architecture, the shade avoidance response in the cash-crop, and summer dormancy in the perennial groundcover.
- Perennial groundcover systems are regenerative. They can reduce soil erosion, increase microbial biomass and microbial diversity, and improve carbon, nitrogen, and phosphorus cycling.
- Perennial groundcover systems could improve water- and nutrient-use-efficiency, reduce weed competition and create opportunities for other value-added opportunities, like crop residue harvest.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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Author Contributions

B.S. conceived the concept, structure, and layout of the review article. All authors wrote, reviewed, and provided considerable insight during the creation of the manuscript.

Abbreviations

C, Carbon; CC, Cover Crop; CPWC, Critical period of weed control; Fr, far-red (light); N, Nitrogen; P, Phosphorus; PGC, Perennial groundcover; R, red (light); RA, Regenerative Agriculture; SAR, Shade Avoidance Response; SOC, Soil Organic Carbon; SOM, Soil Organic Matter.

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