



From leaf traits to agroecosystem functioning: effects of changing resource use strategy during *silphium* domestication on litter quality and decomposition rate

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Abstract

Aims We asked if structural and chemical changes in leaf traits, brought about by early domestication in perennial *Silphium integrifolium* Michx. (Asteraceae), have influenced litter quantity and quality, and decomposition rates. This process is critical to determine how an ecosystem recycles nutrients, renews soil fertility and sequesters C in the soil.

Methods We compared in a field experiment green and senescent leaves traits of Improved and Wild accessions of *Silphium*. We performed a laboratory decomposition experiment to determine the decomposition rate, and the change in litter quality over time.

Results Improved accessions of *Silphium* produced almost two times more litter than the Wild, which should, in turn, contribute to a higher C input to the soil; however, this litter decomposed faster than that

of wild types, and thus had shorter C residence time. Slower decay of litter has been recommended for C sequestration in erodible lands and semi-arid zones, also favoring nutrient retention and slower release of nutrients. The key driver of the decomposition process was resin content and not the usual chemical predictors of litter quality (i.e. N content and C/N ratio). Wild-type litter had thicker leaves with higher resin content, and lower C:N ratio.

Conclusions Domestication changed litter quality affecting the rate of decomposition and potentially C cycling in the agroecosystem. Improved accessions contributed with more C input litter but with lower quality. The lower resin content of the Improved accessions reduced the litter residence time of C due to faster rate of decomposition.

Keywords Ecological intensification · Perennial domestication · Decomposition rate · Litter quality · Resin content

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Introduction

Annual cereal, oilseeds, and legume crops provide 80% of global food (Cox et al. 2010), and comprise 60–80% of global cropland, which is predicted to expand (Glover et al. 2007). The observed decline in ecosystem services in these environments has triggered numerous studies aiming at developing more sustainable agriculture (Pimentel et al. 2012).

De novo domestication of perennial grain crops has been considered as an alternative to annual agriculture, because perennials can provide a variety of ecosystem services in addition to producing grain (Cox et al. 2006; Glover et al. 2010; Baker 2017) and offer unique opportunities for multifunctional agriculture (Jordan and Warner 2010; Ryan et al. 2018). Particularly, perennials are important for soil conservation, reducing soil erosion and increasing water infiltration, and organic matter accumulation (Pimentel et al. 2012). Sustaining the productive capacity of soils has raised interest in the maintenance of soil organic matter through low till practices and the use of crop residues (litter; Ryan et al. 2018). Although in some agricultural systems the accumulation of crop residues is viewed as a nuisance to crop establishment and seedling growth, this would not be a problem when perennial crops are grown. Seeding and seedling establishment is only done once every number of years, and spring re-growth of the perennial crowns is fast; stalks regrowing from crowns accumulate biomass much more quickly than annual seedlings, easily penetrating the litter layer formed by residues from the previous year and the canopy formed by germinating weeds. Residues can, thus, be left on the ground, which improves soil cover, avoids tilling, and helps maintain ecosystem functioning.

The addition of biomass to the soil, and the decomposition of organic matter are major determinants of C and nutrient cycling in ecosystems, and constitute a valuable ecosystem service by recycling nutrients, renewing soil fertility and sequestering C. The multiple drivers of decomposition include the effect of environment, at both regional and micro-site scales, the quality of litter, and the composition of the decomposer community (Cornelissen et al. 2004; Aerts 1997; Parton et al. 2007). At the ecosystem scale, litter quality becomes a better determinant of decomposition rates than climate (Meentemeyer 1978; Aerts 1997) and is most often related to the chemical characteristics of the litter, for example nitrogen content, C: N ratio and/or lignin content (Aerts 1997).

Interspecific differences in structural and protective traits in green leaves (i.e. defenses) and the subsequent quality of litter produced following leaf senescence, have been associated with the diversity found in growth rate and plant resource acquisition strategies (Aerts 1996; Reich et al. 1997; Díaz et al.

2004; Wright et al. 2004). On the one hand, since leaf structure can be linked to growth rate (Poorter et al. 2009), the amount and composition of C forms that plants return to the soil, and their subsequent fate, can be related to plant growth rate (Chapin et al. 2009; Lavorel et al. 2007). On the other hand, Lavorel and Grigulis (2012) showed the strong relevance of the leaf economics spectrum (that describes the plant's resource use strategies) to ecosystem-level processes associated with C and nitrogen cycling, including primary production and litter decomposition. Ecosystems dominated by acquisitive plants have fast fluxes and relatively small C pools and faster nutrient turnover, while the opposite is true for ecosystems dominated by conservative plants: slower fluxes, more recalcitrant, and more persistent C pool (De Deyn et al. 2008, Lavorel and Grigulis 2012). Crops are more acquisitive and fast-growing than their wild progenitors (Milla et al. 2014); and man-made selection for yield has resulted in indirect shifts of resource use strategy, from conservative to acquisitive (Vilela and González-Paleo 2015). Knowledge of the indirect consequences of domestication for other traits besides seed-yield, such as structural and functional leaf traits related to C and N acquisition and conservation, and resistance to pest or drought, is relatively recent (Denison 2012, Milla et al. 2014, González Paleo and Ravetta 2011, González-Paleo et al. 2016, González Paleo and Ravetta 2018, González Paleo et al. 2019, Vilela and González-Paleo 2015, Pastor-Pastor et al. 2018, Vilela et al. 2018). The relevance of these changes to the provision of ecosystem services and sustainability is even less known. Here, we focused on how changes in leaf structural and functional traits brought about by early domestication of a perennial species influence litter quality and decomposition rates.

We tested the link between traits of green-leaves, leaf-litter and decomposition rate in Improved and Wild accessions of *Silphium integrifolium* Michx. (silflower, silphium, rosinweed) growing in a common garden. *Silphium*, a genus in the same tribe (*Heliantheae*) of the Asteraceae as *Helianthus* is being developed as a perennial oilseed crop alternative to the annual sunflower, because the seeds have a similar fatty-acid profile than that of sunflower, while providing a number of ecosystem services linked to its perenniality, deep roots, extended flowering period (Kowalska et al. 2020; Van Tassel et al. 2014; Van

Tassel et al. 2017; Vilela et al. 2018; Reinert et al. 2019).

Particularly, for *Silphium* we know that domestication is changing leaf traits related with C economy: improved accessions had larger leaves, higher allocation to N in green leaves, higher photosynthetic rate, and lower leaf thickness, in relation to wild types (Vilela et al. 2018). Also, domestication reduced resin content of green leaves (potentially a result of a compromise between defense and reproductive effort (Turner et al. 2018)). We hypothesized that differences in key leaf traits related to C and N economy (specific leaf area-SLA, leaf thickness, and N concentration) between Improved and Wild accessions would result in differences in the quantity and quality of litter, and decomposition rate. We predicted that Improved accessions with thin, high-SLA leaves, and with higher N content will produce more senescent leaves with higher quality (i.e., higher N content, lower C:N ratio, lower resin content in the litter). This litter type will result in a higher decomposition rate in relation to Wild-type, low quality litter.

Materials and methods

Experimental design and green leaves traits

Traits of green leaves of 10 individual plants of Improved and Wild accession of *S. integrifolium* Michx. (Asteraceae), growing at The Land Institute's experimental station near Salina, Kansas (38° 46'14'N; 97° 35'30'W) were measured. Mean annual precipitation in the area is 737 mm, with an average of approximately one-tenth of that precipitation coming in the form of snow. Rainfall is concentrated in Spring and Fall, and extended droughts are common in Summer. Mean daily high temperature in July is 34 °C, the mean nightly low in January is -7 °C, and rapid, wide swings in temperature are common in all seasons. The breeding nursery and the wild accessions were established in the field in late May 2015 by transplanting approximately 1500, 8-week-old seedlings. The experimental units were individual plants, randomly chosen for a larger set of plants (220 wild-type plants and 1200 plants of the improved accessions). Plants were arranged in the field in rows spaced 2 m apart, and 1 m apart within

the row, to avoid competition. Transplants received additional water at the time of transplanting, and no additional water was added afterwards. No fertilizer was applied, neither were agrochemicals applied to control of weeds or pest. Weeds were controlled manually. Soil types on the research farm include Hord silt loam (fine-silty, mixed, superactive, mesic Cumulic Haplustolls) and Cozad silt loam (coarse-silty, mixed, superactive, mesic Typic Haplustolls). *Silphium* seeds were harvested from wild populations in central Kansas and subjected to 5 cycles of phenotypic selection (domestication de novo). In each cycle, individuals with a high number of ray florets (a proxy for seed-yield) were identified and controlled pollinations were made between them in the field. Only ray florets are female-fertile and produce seeds. Disk florets produce only pollen (Vilela et al. 2018).

At pre-anthesis of 2017 (early May, second year of growth), we collected four mature green leaves from the middle part of the stalk of each individual plant. Fresh leaf-thickness was measured using a Mitutoyo Digital Thickness Gage 547–301, when leaves were harvested. Leaves were immediately sealed in plastic bags and transported in ice-cooled boxes, and stored in the laboratory at 4 °C prior to analysis. For each individual green-leaf sample (petioles included), leaf-area was determined by scanning the leaves present on each plant, and processing the images using UTHSCSA Image Tool for Windows, Version 2.0. After scanning, leaves were dried at 60 °C for 48 h and weighed. Specific leaf area (SLA) was calculated as the ratio of leaf area to dry weight ($\text{cm}^2 \text{g}^{-1}$) as described by Cornelissen et al. (2003). On these leaves we also measured N concentration by the Kjeldahl acid digestion method. The leaf traits we measured were selected because they are known to be part of the leaf economic spectrum or closely linked to it (see Díaz et al. 2004; Wright et al. 2004).

Litter collection and litter quality

At the beginning of the senescence period, for each of ten plants per accession we collected a sample of naturally senesced leaf litter used for chemical determination of N, C and resins (initial litter chemistry, Time 0). The remaining litter was pooled (per accession) to generate a bulk sample used to fill the decomposition bags. The litter was air-dried and stored at

room temperature until setup of the decomposition experiment.

To assess litter quantity, senescent leaves of each of the ten plants were collected biweekly (from late June to early September) until the plants were completely senescent. Total litter quantity was calculated as the sum of the weight of the senescent leaves produced by a plant.

Chemical analysis of the litter was performed for initial litter quality (Time 0) and for the five consecutive times of bag collection (see section 2.3). C and nitrogen determinations were performed using an Elemental Combustion System (LECO elemental analyzer, model CN628 Dumas analyzer) and expressed as concentration (% of the leaf dry weight).

Plant resins are C based secondary metabolites (CBSM) of complex mixtures, which include volatile and non-volatile terpenes and/or phenolic compounds. In *Silphium* we evaluated the concentrations of non-volatile terpenes according to Vilela et al., (2018). For resin concentration determination, leaf dry matter samples (1–2 g) were extracted with methylene chloride in a Soxhlet apparatus for 10 h. The crude extracts were evaporated until dryness under vacuum with a rotatory evaporator (Yamato Scientific Co., Japan) and weighed. The crude resin concentration was determined as a percent on a leaf dry weight basis (Wassner and Ravetta 2005).

Decomposition experiment

We performed a laboratory decomposition experiment in controlled conditions of humidity (90% water-holding capacity of the soil) and temperature (20 °C) using decomposition trays (the experiment started June 20, 2017). Each tray (45 cm wide and 70 cm long) was filled with soil collected from a four-year old *Silphium* crop growing at the same experimental site. The experimental design consisted in 10 decomposition trays per accession (Improved and Wild), each one containing 5 decomposition bags buried at 5 cm below the surface and separated from one another by 2.5 cm. Bags were collected at five times during the experiment: 16 (July 6), 42 (August 1), 62 (August 21), 77 (September 5) and 93 (September 21) days after the start of the experiment. Decomposition bags consisted in a double-layer nylon mesh bag, 25 cm long and 15 cm wide, filled with two grams of *Silphium* air-dried litter. The mesh size

of the litter-bags was 1 mm. The senescent leaf mass corresponding to each litter-bag was weighed before incubation. At the end of each incubation period, ten bags per accession were sampled (one from each decomposition tray). The litter remaining in each litter-bag was manually cleaned, and the dry-mass of the litter residue was determined after removal from the nylon bags and drying at 50 °C. Ash-free dry mass was determined for all samples using 0.2 g of the remaining biomass to correct for soil contamination, for calculations of organic matter loss and decomposition rate. The dried samples were ground to pass through a 2 mm mesh for chemical analysis (see section 2.2.).

Statistical analysis

Based on the dry mass data, we calculated the percentage of organic matter remaining in each sample. The decomposition process was simulated using a single exponential model: $OM_t = OM_{t_0} * e^{-kt}$; where OM_{t_0} is the initial litter mass, OM_t is the litter mass remaining at time t (days), and k the decomposition rate constant (d^{-1}). The decomposition rate constant, K , can be calculated from this curve using the following equation: $\ln(OM_{t_0}/OM_t) = k * t$, for the entire period of incubation.

Differences in green-leaves traits between accessions were tested using one-way ANOVA. Two-factor repeated measures ANOVA (accessions and time as factors) was performed to determine the statistical significance ($p=0.05$) of the organic mass loss and C, N and resin dynamics from litters of improved and wild accessions at different incubation periods (time). C, N, C/N ratio and resin content at Time 0, were considered “initial quality litter” for both accessions. When significant interactions (accession x time) were detected, one-way ANOVA were performed to explore differences between times for each litter type (Improved and Wild). Least significant differences (LSD) test was calculated at $P \leq 0.05$ in order to compare means.

Regression analyses were performed to examine the relationships of litter quality traits (i.e., N%, C:N ratio and resin%) and decomposition rate for both accessions. Pearson’s correlation coefficients were calculated to evaluate the relationship between green leaf traits, litter quality and decomposition rate. To check for data normality, we used Shapiro–Wilk’s test

and Levene's test for homogeneity of variance. Infostat 2009 was used for these analyses.

Results

Traits of green leaves and litter quantity

Improved accessions had thinner leaves with a higher N content in relation to Wild accessions although they did not differ in specific leaf area (SLA, Table 1). Also, Improved accessions produced more litter (total weight of senescent leaves per plant; Table 1).

Organic matter loss and decomposition rate

There were differences in the loss of organic matter (OM) between accessions for all collection times (significant interaction accession x time; Table 2 supplementary material): 60% of the litter of Improved accessions was decomposed after 2 months, while for the Wild type only 20% of the biomass was lost (Fig. 1). For this period (93 days), the decomposition rate was higher for litter of the Improved compared to the Wild type (Fig. 1). For the Wild accession OM loss was slightly but significantly lower in early- than in late-stages of decomposition. The rate of loss of OM was more uniform for litter of the Improved

than the Wild type (slope between different periods; Fig. 1). At the end of the study (93 days), the remaining OM was 10% and 35% of original biomass for Improved and Wild accessions, respectively.

Litter quality throughout the incubation period

We found differences in the dynamics of the litter composition between Improved and Wild accessions, except for C concentration (significant interaction accession x time; Table 2 supplementary material). Leaf litter types did not differ in C content, neither at the initial time (T₀) nor at the end of the period of decomposition (Table 1). C content decreased rapidly in the first 42 days of decomposition (for both litters, Improved and Wild), and then remained stable at around 8% (Fig. 2A). Initial litter N content was lower and C: N ratio higher in the senescent leaves of Improved than in the Wild type (Table 1). Nitrogen concentration of litter of the Improved accessions tended to decrease for the first two months, and remained stable at around 0.50%, while N concentration in the litter of the Wild type decreased slowly, reaching 0.37% at 77 days. As a consequence of these differential rates of N loss, C/N ratio was higher in the litter of Improved plants for the first 2 months of decomposition, but after this moment the pattern was

Table 1 Green leaves traits, litter quantity, and chemical composition of leaf litter at T₀ (initial quality) and T₉₃ (final quality) of Improved and Wild accessions of *Silphium integrifolium*. Difference between accessions were analyzed using a one-way ANOVA (see Materials and Methods section). ns: non-significant (P>0.05), ** P<0.01; *** P<0.0001. N=10; error df=18 (except for resin concentration: N=5, error df=4). Data are means ± standard error. SLA: Specific leaf area; DW: dry weight

| | | F-values | <i>Silphium</i> accessions | |
|--|--|--------------------|----------------------------|-----------------------|
| | | | IMPROVED | WILD |
| GREEN LEAVES | SLA (cm ² g ⁻¹) | 1.2 ^{ns} | 125.8 ± 10.1 | 111.8 ± 7.7 |
| | Thickness (µm) | 12.7*** | 624.1 ± 18.2 b | 732.9 ± 24.6 a |
| | N (% leaf DW) | 0.1** | 2.7 ± 0.3 a | 1.6 ± 0.3 b |
| LITTER QUANTITY | Senescent leaves (g per plant) | 14.4*** | 8.73 ± 0.69 a | 3.81 ± 0.63 b |
| INITIAL LITTER QUALITY (T ₀) | N (% leaf DW) | 4.5** | 0.82 ± 0.04 b | 1.01 ± 0.03 a |
| | C (% leaf DW) | 1.34 ns | 37.27 ± 2.61 ns | 38.90 ± 1.63 ns |
| | C: N ratio | 3.34** | 43.63 ± 2.93 a | 38.72 ± 1.84 b |
| | Resin (% leaf DW) | 27.9*** | 9.45 ± 1.12 b | 19.47 ± 1.34 a |
| FINAL LITTER QUALITY (T ₉₃) | N (% leaf DW) | 2.03 ^{ns} | 0.52 ± 0.10 ns | 0.35 ± 0.05 ns |
| | C (% leaf DW) | 1.88 ^{ns} | 4.93 ± 1.07 ns | 7.67 ± 1.68 ns |
| | C: N ratio | 0.46 ^{ns} | 16.63 ± 0.92 ns | 24.77 ± 1.32 ns |
| | Resin (% leaf DW) | 12.3** | 30.60 ± 1.88 b | 38.30 ± 4.74 a |

Bold numbers and letters indicate significant results

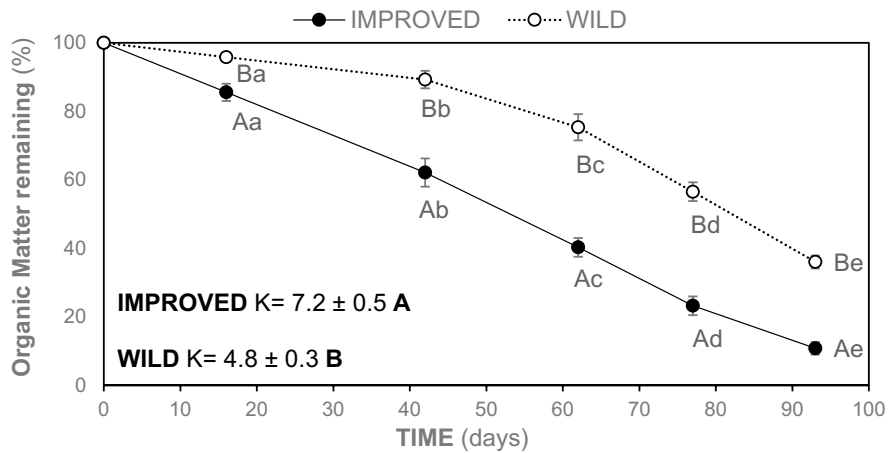


Fig. 1 Organic matter loss, expressed as a relative fraction of initial mass for two *Silphium integrifolium* leaf-types: leaf litter of Improved and of Wild accessions. Values of K (year⁻¹) for the total period (93 days) are shown in the bottom-left part of the figure. Data are means ± standard error. Capital letters indicate significant differences between litters-types for each collection time; lower-case letters indicate significant differences among times of collection for each litter-type. Statistics and P-values are in Table 2 supplementary material

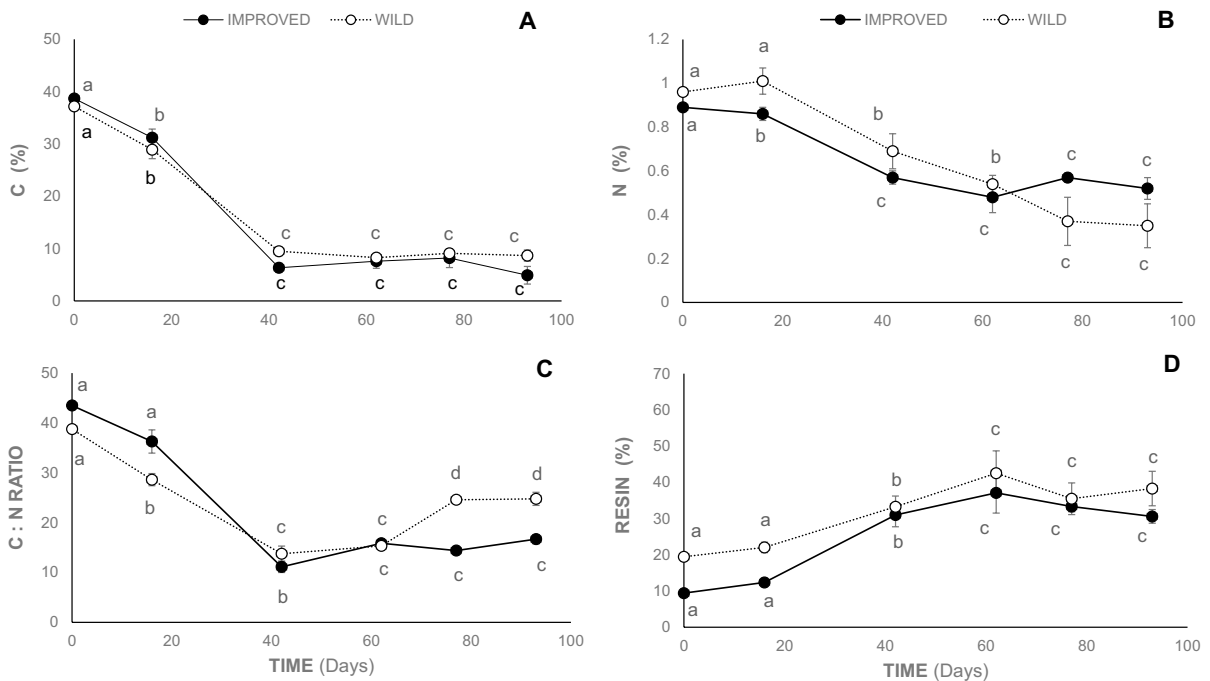


Fig. 2 Dynamics of chemical composition of leaf-litter for Improved and Wild genotypes of *Silphium integrifolium*. Symbols represent mean values ± standard error (n=10 and n=5 for resin concentration). Lowercase letters indicate differences among times for each litter type. Statistics are shown in Table 2 supplementary material. We analyze differences between Improved and Wild litter-type for T0 (Initial litter quality) and T93 (final litter quality) in Table 1

reversed: Wild accession had lower N content and higher C: N ratio (Fig. 2).

Resin concentration also varied with time and litter type. For the initial 60 days resin concentration increased and then remained stable for the remaining of the study (Fig. 2). Both at the initial stage and at the end of the period of decomposition, litter of Wild plants had a higher resin concentration than that of the Improved type (Table 1).

We tested the relationships of N, C/N and resin concentration on total leaf-mass loss (Fig. 3). There was a highly significant and negatively linear relationship between decomposition rate and resin concentration in the leaf litter (Fig. 3C). In contrast, we did not find a relationship between decomposition rate and N concentration or C/N ratio (Fig. 3A and B).

Relationships between green-leaf traits and decomposability

We found that some of the traits of green leaves were good predictors, both of the total amount of senescent leaves produced by a plant and of the quality of the litter. Accessions with thinner leaves and with higher N concentration produced more litter than accessions with thicker leaves (Table 2). Specific leaf area (SLA) and N concentration of green leaves were not good predictors of the chemical composition of senescent leaves (i.e. litter quality) or decomposition rate (Table 2). Leaf thickness correlated positively with resin concentration of the litter and negatively with decomposition rate (Table 2). Thicker leaves had a higher resin concentration and, after senescence, decomposed more slowly than thinner leaves (which had lower resin content).

Discussion

Relationship between green-leaf traits, and quantity, and quality of litter

Compared with natural ecosystems, plants grown under cultivation generally experience higher and more predictable nutrient and water supplies (Denison 2012). Thus, it has been proposed that domestication of wild species and selection for increased yield move plants from resource-conservative towards resource-acquisitive strategies (Milla et al. 2014;

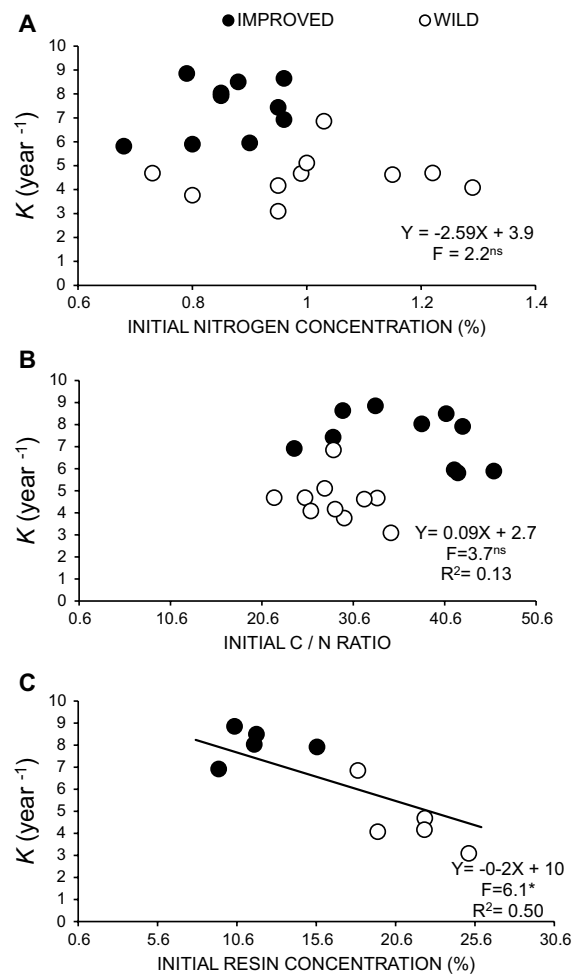


Fig. 3 Relationships between decomposition rate for the total incubation period (93 days, K) and the initial chemical composition of litter of Improved (black symbols) and Wild (white symbols) accessions of *Silphium*. **A**) N concentration, **B**) C:N ratio, and **C**) resin concentration. $N = 10$. For resin determination we only used 5 repetitions due to methodological problems. Linear regression equation, F-test and their significance, and the coefficient of determination (R^2) is provided into each panel of figure. Regression line is only showed when regression was significant

Vilela and González-Paleo 2015; Pastor-Pastor et al. 2018). Our results comparing Wild and Improved *S. integrifolium* support this idea: we found that after 5 generations of selection using yield as the main selection criteria, Improved accessions tend to bear thinner leaves, with higher nitrogen concentration and lower resin concentration than their Wild relatives. Those traits tend to allow for fast growth (Freschet et al. 2010). On the other hand, Wild accessions of

Table 2 Pearson's correlation coefficient for green leaves traits (SLA: specific leaf area, Leaf Thickness and N concentration), litter quantity (grams and % of senescent leaves per plant), litter quality (Initial chemical composition expressed as a percentage of the leaf dry biomass) and decomposition rate (K). Data are means \pm standard error. Correlation significance are shown: ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

| Green Leaf traits | LITTER QUANTITY | | LITTER QUALITY | | | |
|-------------------|--|----------------------|---------------------|---------------------|---------------------|-------------------------|
| | Senescent leaves (g pl ⁻¹) | Senescent leaves (%) | N (%) | C:N ratio | Resins (%) | K (year ⁻¹) |
| SLA | 0.22 ns | 0.14 ns | -0.26 ^{ns} | 0.40 ^{ns} | -0.31 ^{ns} | 0.18 ^{ns} |
| Thickness | -0.69** | -0.72** | 0.26 ^{ns} | -0.38 ^{ns} | 0.67* | -0.55** |
| N (%) | 0.59*** | 0.62** | -0.16 ^{ns} | 0.18 ^{ns} | -0.48 ^{ns} | 0.20 ^{ns} |

Bold numbers indicate significant results

Silphium had thicker leaves that bore traits allowing for efficient resource conservation, typical of species from low resource environments. Structural and chemical leaf-traits crucial for C gain have 'afterlife' effects, determining litter quality and decomposability (Cornelissen et al. 1999). Indeed, interspecific variation in traits of fresh leaves and that of leaf litter tends to be strongly correlated (e.g. Freschet et al. 2010). In this context, we expected changes in quality and quantity of litter (more litter and higher quality) caused by the domestication process that would accelerate the decomposition rate. Supporting our hypothesis, we found that Improved accessions of *Silphium* produced more than twice as much senescent leaves (i.e. litter) that decompose faster than the Wild accessions, which should contribute to a higher C input and N release to the agroecosystem.

Green leaf-thickness was negatively related to litter quality (the total biomass of senescent leaves produced by a plant, g per plant) and to the decomposition rate, while specific leaf area (SLA) did not differ between accessions, and was not related to litter quantity or decomposition. Thus, although SLA has been proposed as a key trait to characterize plant resource-use-strategies and their impact to ecosystem functioning (Lavorel and Garnier 2002), in our experiment leaf thickness was a better predictor of C input (leaf senescence) and output (decomposition) than SLA. Changes in leaf anatomy that result in denser leaves structures during domestication appear to be one possible explanation for the absence of difference in SLA between Improved and Wild accessions (Ravetta et al., unpublished data).

The chemical composition of litter such as N content, C/N ratio, and/or lignin content are also

considered to be predictors of leaf litter decomposition rates (Aber et al. 1990; García-Palacios et al. 2013): it is expected that litter with greater C/N ratio and lower N content decompose more slowly. In our experiment, the decomposition rate was not related to the most commonly used chemical predictors of litter quality. In spite of the higher N content in green leaves and the higher total decomposition rate found in litter of Improved accessions, the initial litter quality was lower compared to Wild accession (i.e. lower N content and higher C/N ratio in senescent leaves). The lack of a relationship between N concentration in green leaves and senescent leaves indicates an increase in N resorption for seed-growth, caused by the enhanced seed-yield as found in improved accessions of crops, (Havé et al. 2017) and new domesticates (Pastor-Pastor et al. 2018, 2021).

We found that the difference in decomposition rate between Improved and Wild accessions was mostly explained by differences in resin (terpenes) content in the litter. Other C-based secondary metabolites (CSBM) such as tannins have been shown to slow decomposition rates and C and N cycling (Hattenschwiler and Vitousek 2000) while phenolic compounds can delay the colonization of litter by decomposers (Chomel et al. 2014) and delay litter mass loss in the first 2 months (Loranger et al. 2002). Even though the use of plant functional traits such as SLA, leaf dry matter content, N, lignin, C/N, phenols, among others to predict decomposition rates has greatly advanced our understanding of litter quality in driving decomposition processes (Cornwell et al. 2008), the functional traits used are often too general to explain complex relationships and fail to explain the variability in

litter decomposition rates observed. Chomel et al. (2016) have proposed that some of these discrepancies may result from the key roles played by secondary metabolites that are not considered in the analysis of integrative functional traits.

The decomposition rate may vary in time due to changes in the composition of the decomposing organic matter. The change, mostly a decrease in decomposability, is complex, involving both direct chemical changes in the substrate itself and the succession of microorganisms able to use these substrates with a given chemical composition (Berg et al. 2000; Van der Putten et al. 2013). With the consumption of celluloses, the concentration of the more recalcitrant compounds (such as resins) increases, and the effects of N on decomposition rate changes completely. For *Silphium* senescent leaves we found two phases of decomposition, under controlled conditions of humidity and temperature: 1) an early stage (2 months into the decomposition process) in which concentrations of C (in cellulose and hemicellulose) and N decreased rapidly, before reaching a relatively stable value. During this phase, the recalcitrant compounds such as resin, did not decompose or decomposed more slowly. Resin concentration, thus, increased as other main compounds disappeared from the decomposing biomass; 2) a late stage in which resin concentration reached relatively steady levels in the range of 35–40%. These “recalcitrant compound phases” may be linked to the microbial interaction model (Moorhead and Sinsabaugh 2006). In this model, only after 3 months in the decomposition process, the catabolic activity of the microbial community would be able to focus on the breakdown of highly polymerized and complex substances. After this time, total mass of the highest molecular weight substances decreases. In our experiment this phase was not evident at 90 days, which indicates that these resins are very recalcitrant and would take longer to decompose.

It is expected that if domestication changes the quantity and quality of litter, it may also have an impact on the soil food-web of the new perennial agroecosystems. Understanding the interactions of secondary metabolites and the soil food-web should be an important focus of future experiments attempting to better understand the contributions of different perennial crops to ecosystem processes in

the context of the development of a multifunctional agroecosystem.

C sequestration and N release

Although plant traits that drive C sequestration mainly operate through high primary productivity (high C input), the C output from the ecosystem is determined by the decomposition rate. Both input and output are related: routes that provide a high C input generally appear to trade-off at plant individual level with those that are linked to slow C output (Aerts and Chapin 2000; Faucon et al. 2017). We found evidence of this trade off: litter of Improved accessions decomposed faster than that of Wild one. Thus, high C input to the ecosystem may trade-off with short C residence times: Improved accession contributed with 8.7 g of organic matter per plant per year, and after 3 month of decomposition remaining biomass (C stock) was only 0.96 g (calculated by discounting the decomposed biomass estimated using the decomposition rate in Fig. 1, to the C input). By contrast, Wild accessions had a longer C residence time, and poor-quality litter that trades off with lower litter incorporation: Wild accession contributed with 3.8 g of organic matter per plant per year, and after three-month remaining biomass was 1.37 g (42% more than that of Improved litter type). The relationship between higher decomposition rate and lower soil C sequestration has been described, before (De Deyn et al. 2008). Microbes consume organic C and eventually mineralize a part of it to CO₂. A part of the C taken up is, however, transformed into C in microbial biomass, which is described by the C-Use-Efficiency (CUE) of that microbial community. Litters with low quality (low C/N ratio, such as the Wild-type litter in this experiment) provide high microbial CUE (Mooshammer et al. 2014), and this relationship determines an increased potential for long-term C sequestration. Even though we did not measure microbial respiration or CUE, C retained in the microbial biomass only accounts for about 12% of total soil organic C (Xu et al. 2013). However, another model (Microbial Efficiency Matrix Stabilization- MEMS; Cotrufo et al. 2013) for the formation of stable soil organic matter (SOM) proposes that the main contribution of C to the mineral soil is from microbial compounds produced during the degradation of litter (Mambelli et al. 2011), while recalcitrant plant components do not

preferentially accumulate in soil organic matter (Marschner et al. 2008). In this model the efficiency with which plant substrates are incorporated into microbial biomass and allocated to different byproducts (e.g., enzymes, polysaccharides) versus being mineralized is the prime determinant of plant-derived C and N contribution to soil organic matter formation (Cotrufu et al. 2013).

Mineralization also result in breakdown of organic materials into their constituents by which nutrients are made available for nutrient cycling and an increased soil fertility (Vitousek and Sanford 1986). Mooshammer et al. (2014) proposed that both, the microbial decomposer communities and the quality of litter (C/N ratio) regulate microbial Nitrogen-Use-Efficiency (NUE, how much of the N taken up is incorporated into microbial biomass as growth) and N mineralization (N recycling to the environment as inorganic N). Litter with low C/N ratio (N-sufficient conditions; such as the Wild type-litter in this experiment), determines a low microbial NUE. This lower NUE indicates that less N is converted to biomass, whereas a relatively large fraction of the organic N is released as ammonium (high N mineralization). According to this model, despite of the lower decomposition rate of the Wild litter-type, this litter would provide higher N to the soil, in relation to the Improved litter-type with higher C/N ratio. Supporting this hypothesis, we found that N released from the Wild litter type was higher (65%) that than of the litter Improved plants (40%). The uncoupling of decomposition and mineralization (i.e. low decomposition but high N release) could be mediated by the resin concentration in the litter.

Implications for multifunctionality during perennial domestication

DeHaan et al. (2016) proposed some criteria to guide domestication of new perennial crops, among which is “Enhanced Ecosystem Services”. One important ecosystems service is soil C sequestration. In this context, litter decomposition is a critical service, that determines productivity and the manner in which an ecosystem recycles nutrients, renews soil fertility, sequesters C in the soil (Wall et al. 2004).

A strategy for increasing soil C sequestration and fertility in agroecosystems is to modify the C quality of litter in order to decrease the rate of decay, as a way

of promoting the transition of C into the soil organic matter fraction which is resistant to decomposition, while maintaining or increasing C inputs (Johnson et al. 2007). Thus, biomass with slower decaying residues has been recommended for C sequestration in erodible lands and semi-arid zones (Diack and Stott 2017). In addition, this strategy favors nutrient retention and slower release of nutrients.

Our results for *S. integrifolium* show that Improved accessions provide a higher C input to the soil, due to their higher productivity, than Wild accessions. However, after selection, leaf structure and composition also changed, and leaf litter of Improved accessions had opposite characteristics than those needed for low decomposition rates. The most relevant change found in our experiment is the relevance of C-based secondary metabolites as key drivers in the decomposition process. Given recent evidence of the MEMS model, we now pose the question if traditional metrics of litter quality relate to their role in soil organic matter formation and C sequestration. According to the MEMS model low molecular weight compounds are degraded faster, causing labile litter to decay faster, but with a relatively higher accumulation of microbial products and concomitant stable SOM formation in the long term. Low-quality litter will initially decompose more slowly, but less of the initial mass will be converted into microbial products. The role of litter quality on stable soil organic matter formation requires further testing to evaluate its role in the C sequestration capacity of an agroecosystem.

Detailed knowledge of the effect of eco-physiological plant trait on soil properties and ecosystem processes and services is of major significance and will allow for the design of plants that deliver the intended regulatory (and provision) services, for sustainable soil management. A desired option would be to combine traits that promote nutrient availability and support primary productivity with traits that promote soil C stabilization through slow decomposition and incorporation to mineral soil. We found that Improved accession for increased seed production, also had thinner leaves and more litter production when compared to low-yielding Wild accession, although thicker leaves have a higher resin content and decompose more slowly. It remains to be seen if leaf thickness and seed-yield are tightly linked genetically or functionally integrated, and there is a need to use it as an additional

criterion for selection. We are currently attempting to develop recombinant lines with all trait combinations to test whether thick leaves/high resin content/slower decomposition should be included as breeding targets in the domestication of *Silphium* and other similar new perennial crops.

We conclude that five cycles of selection for increase seed-yield in perennial *Silphium*, resulted in changes in resource-use-strategy at leaf level, which lead to a change in the chemical composition of the litter, in the C input (litter quantity) and output (decomposition rate) to the agroecosystem. These unexpected changes could compromise some regulatory ecosystem services such as C sequestration and biogeochemical cycling, relevant for ecological intensification and need to be monitored during the domestication of new perennial grain crops.

Author's contribution LGP and DAR conceived the ideas and designed methodology; LGP collected the data; LGP analyzed the data; LGP, DAR and DVT contributed to the analysis and interpretation of data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Code availability Not applicable.

Declarations

Conflict of interest Neither author has any conflict of interest.

References

- Aber JD, Melillo JM, Mcclaugherty CA (1990) Predicting long-term patterns of mass loss, nitrogen dynamics, and soil matter formation from initial fine litter chemistry in temperate forest ecosystems. *Canad J Bot* 68:2201–2208
- Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *J Ecol* 84:597–608
- Aerts R (1997) Nitrogen partitioning between resorption and decomposition pathways: a tradeoff between nitrogen use efficiency and litter decomposability? *Oikos* 80:603–606
- Aerts R, Chapin FSIII (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Baker B (2017) Can modern agriculture be sustainable? Perennial polyculture holds promise. *BioScience* 67:325–331
- Berg B, Johansson MB, Meentemeyer V (2000) Litter decomposition in a transect of Norway spruce forests: substrate quality and climate control. *Can J For Res* 30:1136–1147
- Chapin FS, McFarland J, McGuire AD, Euskirchen ES, Ruess RW, Kielland K (2009) The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. *J Ecol* 97:840–850
- Chomel M, Fernandez C, Bousquet-Melou A, Gers C, Monnier Y, Santonja M, Gauquelin T, Gros R, Lecareux C, Baldy V (2014) Secondary metabolites of *Pinus halepensis* alter decomposer organisms and litter decomposition during afforestation of abandoned agricultural zones. *J Ecol* 102:411–424
- Chomel M, Guittonny-Larcheveque M, Fernandez C, Gallet C, DesRochers A, Pare D, Jackson BJ, Baldy V (2016) Plant secondary metabolites: a key driver of litter decomposition and soil nutrient cycling. *J Ecol* 104:1527–1541
- Cornelissen JHC, Pérez-Harguindeguy N, Díaz S, Grime JP, Marzano B, Cabido M, Vendramini F, Cerabolini B (1999) Leaf structure and defense control litter decomposition rate across species, life forms and continents. *New Phytol* 43:191–200
- Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, Steege HT, Morgan HD, Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Aust J Bot* 51:335–380
- Cornelissen JHC, Qusteded HM, Gwynn-Jones D, Van Logtestijn RSP, De Beus MAH, Kondratchuk A, Callaghan TV, Aerts R (2004) Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Funct Ecol* 18:779–786
- Cornwell WK, Cornelissen JHC, Amatangelo K et al (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol Lett* 11:1065–1071
- Cotrufo MF, Wallenstein MD, Boot CM, Deneff K, Paul E (2013) The microbial efficiency-matrix stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Glob Chang Biol* 19:988–995
- Cox TS, Glover JD, Van Tassel DL, Cox CM, DeHaan L (2006) Prospects for developing perennial grain crops. *BioScience*. 56:649–659
- Cox TS, Van Tassel DL, Cox CM, DeHaan LR (2010) Progress in breeding perennial grains. *Crop Pasture Sci* 61:513–521
- DeHaan LR, Tassel DL, Van Anderson JA, Asselin SR, Barnes R, Baute GJ et al (2016) A pipeline strategy for grain crop domestication. *Crop Sci* 56:917–930
- Denison RF (2012) Darwinian agriculture: how understanding evolution can improve agriculture. Princeton University Press, Princeton

- De Deyn GB, Cornelissen J, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol Lett* 11:1–16
- Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A et al (2004) The plant traits that drive ecosystems: evidence from three continents. *J Veg Sci* 15:295
- Diack M, Stott D (2017) Effect of crop type and cultivar surface area on rates of decomposition in soils. *Afr J Agric Res* 11:5124–5135
- Faucon M, Houben D, Lambers H (2017) Plant functional traits: soil and ecosystem services. *Trends Plant Sci* 22:385–394
- Freschet T, Cornelissen JHC, Logtestijn RSP (2010) Evidence of the ‘plant economics spectrum’ in a subarctic flora. *J Ecol* 98:362–373
- García-Palacios P, Milla R, Delgado-Baquerizo M, Martín-Robles N, Álvaro-Sánchez M, Wall DH (2013) Side-effects of plant domestication: ecosystem impacts of changes in litter quality. *New Phytol* 198:504–513
- Glover JD, Cox CM, Reganold JP (2007) Future of farming: a return to roots? *Sci Am* 297:66–73
- Glover JD, Reganold JP, Bell LW, Borevitz J, Brummer EC, Buckler ES et al (2010) Increased food and ecosystem security via perennial grains. *J Ecol* 328:1638–1639
- González Paleo L, Ravetta D A (2011). Indirect changes associated with a selection program for increased seed-yield in wild species of *Lesquerella* (Brassicaceae): are we developing a phenotype opposite to the expected ideotype? *Ind. Crops Prod.*, 34
- González-Paleo L, Vilela A E, Ravetta D A (2016). Back to perennials: does selection enhance tradeoffs between yield and longevity? *Ind. Crops Prod.*, 91
- González Paleo L, Ravetta DA (2018) Relationship between photosynthetic rate, water use and leaf structure in desert annual and perennial forbs differing in their growth. *EUPH.* 56:1177–1187
- González Paleo L, Pastor-Pastor A, Rajnoch G, Ravetta DA (2019) Mechanisms of nitrogen conservation at the leaf-level in annual and perennial desert forbs: implications for perennial crops domestication. *Flora* 252:62–68
- Hattenschwiler S, Vitousek P (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol Evol* 15:238–243
- Havé M, Marmagne A, Chardon F, Masclaux-daubresse C (2017) Nitrogen remobilization during leaf senescence: lessons from *Arabidopsis* to crops. *J Exp Bot* 68:2513–2529
- Johnson JMF, Barbour NW, Weyers SL (2007) Chemical composition of crop biomass impacts its decomposition. *Soil Sci Soc Am J* 71:155–162
- Jordan N, Warner KD (2010) Enhancing the multifunctionality of US agriculture. *BioScience* 60:60–66
- Kowalska G, Pankiewicz U, Kowalski R (2020) Evaluation of chemical composition of some *Silphium* L. Species as Alternative Raw Materials Agriculture 10:132–150
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. *Funct Ecol* 16:545–556
- Lavorel S, Díaz S, Cornelissen JHC, Garnier E, Harrison SP, McIntyre S et al (2007) Plant functional types: are we getting any closer to the holy grail? In: Canadell J, Pitelka LF, Pataki D (eds) *Terrestrial ecosystems in a changing world*. Springer, Berlin Heidelberg, pp 149–164
- Lavorel S, Grigulis K (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *J Ecol* 100:128–140
- Loranger G, Ponge JF, Imbert D, Lavelle P (2002) Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. *Biology & Fertility of Soils* 35:247–252
- Mambelli S, Bird JA, Gleixner G, Dawson TE, Torn MS (2011) Relative contribution of foliar and fine root pine litter to the molecular composition of soil organic matter after in situ degradation. *Org Geochem* 42:1099–1108
- Marschner B, Brodowski S, Dreves A et al (2008) How relevant is recalcitrance for the stabilization of organic matter in soils? *J Plant Nutr Soil Sci* 171:91–110
- Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*. 59:465–472
- Milla R, Morente-López J, Alonso-Rodrigo JM, Martín-Robles N, Chapin FSIII (2014) Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proc R Soc Lond B* 281:1429
- Moorhead D, Sinsabaugh R (2006) A theoretical model of litter decay and microbial interaction. *Ecol Monogr* 76:151–174
- Mooshammer M, Wanek W, Hammerle I, Fuchsluger L, Hofhansl F, Knoltsch A, Schnecker J, Takriti M, Watzka M, Wild B, Keiblinger K, Zechmeister-Boltenstern S, Richter A (2014) Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulates soil nitrogen cycling nitrogen cycling. *Nat Commun* 5:3694
- Parton W et al (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*. 315:361–364
- Pastor-Pastor A, Vilela AE, González-Paleo L (2018) Tradeoffs between productivity and nitrogen conservation in wild and domesticated plants of the perennial crop *Physaria* (Brassicaceae). *Ann App Biol* 173:121–132
- Pastor-Pastor A, Vilela A, González-Paleo L (2021) Age-related changes in root traits are linked to internal nitrogen cycling in the perennial forb *Physaria* (Brassicaceae). *Acta Oecol* 111:103729
- Pimentel D, Cerasale D, Stanley RC, Perlman R, Newman EM, Brent LC, Mullan A, Chang DT (2012) Annual vs. perennial grain production. *Agric Ecosyst Environ* 161:1–9
- Poorter H, Niinemets Ü, Poorter L et al (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol* 182:565–588
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci USA* 94:13730–13734
- Reinert S, Tassel D L, Van Schlautman B, Kane N C, Hulke B S (2019). Assessment of the biogeographical variation of seed size and seed oil traits in wild *Silphium integrifolium* Michx. Genotypes, plant genetic resources: Characterization and Utilization 1–10
- Ryan MR, Crews TE, Culman SW, DeHaan L, Hayes RC, Junger JM, Bakker MG (2018) Managing for multifunctionality in perennial grain crops. *BioScience* 68:294–304
- Turner M K, Ravetta D A, Van Tassel D (2018). Effect of *Puccinia silphii* on yield components and leaf physiology in *Silphium integrifolium*: lessons for the domestication of a perennial oilseed crop. *Sustainability*

- Van der Putten WH, Van Der Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T et al (2013) Plant-soil feedbacks: the past, the present and future challenges. *J Ecol* 101:265–276
- Van Tassel D L, Asselin S R, Cox S A, Sideli G, Cattani, D J. (2014). Evaluating perennial candidates for domestication: lessons from wild sunflower relatives. In: Batello C Wade L, Cox S, Pogna N, Bozzini A, Choptiany J. (eds.). *Perennial crops for food security*; Proceedings of the FAO Expert Workshop. Rome. p. 112–140
- Van Tassel DL, Albrecht KA, Bever JD, Boe AA, Brandvain Y, Crews TE, Gansberger M, Gerstberger P, González-Paleo L, Hulke BS, Kane NC, Johnson PJ, Pestsova EG et al (2017) Accelerating *silphium* domestication: an opportunity to develop new crop ideotypes and breeding strategies informed by multiple disciplines. *Crop Sci* 57:1274–1284
- Vilela AE, González-Paleo L (2015) Changes in resource-use strategy and phenotypic plasticity associated with selection for yield in wild species native to arid environments. *J Arid Environ* 113:51–58
- Vilela A, González-Paleo L, Turner K, Peterson K, Ravetta D, Crews T E, Van Tassel D (2018). Progress and bottlenecks in the early domestication of the perennial oilseed *Silphium integrifolium*, a sunflower substitute. *Sustainability*, 10
- Vitousek P, Sanford RL (1986) Nutrient cycling in tropical forest. *Annu Rev Ecol Syst* 17:137–167
- Wall D, Bardgett R D, Covich A, Snelgrove Paul (2004). The need for understanding how biodiversity and ecosystem functioning affect ecosystem services in soils and sediments. *Sustaining Biodiversity and Ecosystem Services in Soils and Sediments*. 1–12
- Wassner DF, Ravetta DA (2005) Temperature effects on leaf properties, resin content, and composition in *Grindelia chiloensis* (Asteraceae). *Ind Crop Prod* 21:155–163
- Wright IJ et al (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827
- Xu X, Thornton PE, Post WM (2013) A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Glob Ecol Biogeogr* 22:737–749

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