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Long-Term Crop Rotation and Tillage Shape Source–Sink Dynamics and Yield Formation in Dryland Wheat

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Abstract

Understanding how long-term agronomic management regulates biomass production and reproductive allocation is essential for improving wheat productivity in dryland environments. Here, we used an eight-year conservation agriculture experiment to investigate how preceding crops and tillage systems modify biomass accumulation, organ partitioning, source–sink transitions, and yield formation in wheat. Wheat was grown after chickpea, forage pea, and safflower under conventional, minimum, and no-tillage systems. Biomass accumulation and partitioning among leaves, stems, and spikes were quantified throughout crop development, with grain yield and yield components determined at maturity. Management altered both the magnitude and timing of biomass allocation, particularly from stem elongation onward, while the overall developmental pattern remained conserved. At maturity, spikes accounted for 60.2–65.2% of total aboveground biomass, and the major shift toward reproductive allocation occurred after stem elongation. The transition from source- to sink-dominated growth occurred between Zadoks stages 61.9 and 66.8. Biomass accumulation and sink strength alone, however, did not explain grain yield variation. Safflower–NT produced the greatest aboveground biomass (1135.6 g m⁻²), whereas safflower–MT achieved the highest grain yield (2302.9 kg ha⁻¹) with a moderate harvest index (0.37). In contrast, forage pea–NT exhibited the highest harvest index (0.42) but did not produce the highest grain yield, indicating that yield depended on the balance between total biomass production and its allocation to grain. These findings demonstrate that long-term conservation agriculture enhances dryland wheat productivity through improved temporal coordination between source availability and sink demand, rather than through increases in biomass production alone.

Keywords: Biomass partitioning; Crop rotation; Conservation agriculture; Dryland wheat; Source–sink dynamics; Grain yield.

1. Introduction

Dryland wheat production is strongly constrained by the limited and variable availability of water, making the efficient capture, storage, and use of precipitation a central determinant of crop productivity. In these environments, tillage practices can substantially modify soil water storage, evaporative losses, and the amount of precipitation retained for subsequent crop growth. Evidence from long-term experiments and global meta-analyses indicates that conservation tillage, particularly no-tillage, can increase precipitation storage efficiency, soil water storage, grain yield, and water-use efficiency relative to conventional tillage, although the magnitude of these effects varies with precipitation regime, soil texture, residue management, and cropping intensity (Adil et al., 2024; Adil et al., 2025). Crop rotation represents another major component of dryland cropping-system management because preceding crops modify soil water availability, nutrient dynamics, residue quantity and quality, rooting patterns, and the timing of resource use. Long-term experiments have demonstrated that crop sequence can substantially influence water availability

at wheat establishment and consequently wheat productivity (Lenssen et al., 2018). Similarly, studies conducted under semiarid conditions have shown that the interaction between cropping sequence and tillage can modify soil water dynamics and crop production (Lotfi and Pessarakli, 2023), indicating that the effects of tillage cannot be interpreted independently of rotation history (Mikha et al., 2015; Baumhardt et al., 2017). These findings are particularly relevant to dryland systems, where relatively small differences in soil water availability can propagate through crop development and ultimately affect biomass accumulation and reproductive growth.

Nevertheless, most evaluations of crop rotation and tillage have focused primarily on final grain yield, soil water storage, or water-use efficiency (Lotfi et al., 2024; Zehtab-Salmasi et al., 2026). Such measurements are essential for assessing the agronomic performance of cropping systems but provide limited insight into the developmental processes through which management determines yield formation. Biomass accumulation is inherently dynamic, and the temporal pattern of dry-matter production and its distribution among plant organs determine the capacity of the crop to establish photosynthetic sources, develop structural tissues, and subsequently support reproductive sinks (Golan et al., 2024). The temporal organization of biomass allocation is closely linked to the source–sink relationship governing wheat yield formation. Grain growth after anthesis depends on the balance between assimilates produced by current photosynthesis and assimilates previously accumulated in vegetative organs and subsequently remobilized to the developing grains (Ma, 2023). The relative contribution of these sources is not constant but varies with genotype and environmental conditions, particularly water and nitrogen availability. Using a 13-year experimental dataset, Fang et al. (2024) demonstrated that the contribution of remobilized pre-anthesis assimilates to grain biomass increased markedly with increasing environmental stress, highlighting the importance of source–sink regulation under unfavorable growing conditions. More recently, Rose and Kage (2026) quantified the determinants of pre-anthesis biomass translocation in wheat and showed that biomass translocation to grain is jointly associated with pre-anthesis biomass, post-anthesis biomass production, grain number, stem number, and genotype.

Vegetative organs therefore function not only as photosynthetic sources during crop development but also as temporary storage compartments whose biomass can subsequently contribute to reproductive growth. Experimental manipulation of source and sink size has demonstrated that the contribution of pre-anthesis dry matter to grain production differs among cultivars and can be altered by changes in source or sink strength, confirming the dynamic nature of biomass allocation during grain filling (Yang et al., 2014). Importantly, a decline in vegetative biomass during grain filling can indicate net biomass redistribution towards reproductive organs, although biomass loss alone does not constitute direct evidence of assimilate transfer (Fang et al., 2024). This distinction is particularly important when evaluating field-scale biomass dynamics, because apparent remobilization derived from changes in organ biomass represents a proxy for redistribution rather than a direct measurement of carbon translocation.

From this perspective, understanding wheat adaptation to dryland environments requires moving beyond final biomass or grain yield and quantifying the trajectory of biomass allocation throughout crop development. The rate at which newly accumulated biomass is directed towards leaves, stems, and reproductive organs provides information that cannot be obtained from final biomass partitioning alone. Likewise, identifying the developmental stage at which reproductive sinks become dominant can reveal whether a management practice accelerates, delays, or intensifies the transition from vegetative growth to reproductive biomass accumulation (Reynolds et al., 2022). Such temporal indicators are particularly relevant under dryland conditions because the timing of source–sink transitions determines whether reproductive growth occurs when soil water and assimilate availability are favorable or when environmental limitations are already intensifying (Zhang et al., 2022).

Despite extensive research on conservation tillage, crop rotation, and wheat productivity, there is still limited information on how long-term rotation × tillage combinations regulate the temporal

dynamics of biomass partitioning and source–sink transitions in dryland wheat. Existing studies have largely addressed management effects on soil water, yield, or total biomass, whereas the sequential redistribution of biomass among leaves, stems, and spikes and the timing of the transition towards reproductive sink dominance have received considerably less attention. This knowledge gap is important because management systems that produce similar final yields may achieve them through substantially different developmental trajectories. Quantifying these trajectories can therefore provide a more mechanistic interpretation of management effects and help identify whether a particular rotation × tillage combination enhances biomass production, accelerates reproductive allocation, promotes late-season redistribution, or modifies the balance between vegetative sources and reproductive sinks.

2. Materials and methods

2.1. Experimental site

The experiment was conducted at the experimental station of the Dryland Agricultural Research Institute (DARI), Agricultural Research, Education and Extension Organization (AREEO), Maragheh, Iran, representing a cold dryland agro-climatic region of northwestern Iran. The experimental site is characterized by a cold semi-arid climate according to the De Martonne classification, with climatic conditions typical of the dryland wheat-growing areas of the region. Monthly variations in mean and absolute air temperatures and precipitation throughout the wheat growing season (October–June) are presented in Figure 1.



Figure 1. Seasonal dynamics of mean and absolute air temperatures and precipitation during the wheat growing cycle.

Before experiment establishment, composite soil samples were collected from the 0–30 cm soil layer and analyzed for texture, pH, electrical conductivity, organic carbon, available phosphorus, and available potassium using standard laboratory procedures. Some physicochemical properties of the soils from the studied area are presented in Table 1.

Table 1. Selected physicochemical properties of the soil in the experimental fields during the first year in Maragheh and Sararood.

Soil sample	Soil texture	pH	Ava. P	Ava. K	TNV	OC	EC _e
			ppm		%		dS m ⁻¹
Experimental site	Clay loam	7.68	5.4	503	7.8	0.57	0.84

2.2. Experimental design and treatments

The study was conducted within a long-term conservation agriculture experiment that had been continuously maintained for eight years (2018–2026) under contrasting crop rotations and tillage systems. The present assessment was based on data collected during the eighth year of the experiment (2025–2026), with a specific focus on biomass partitioning, assimilate allocation, and the dynamics of material distribution among vegetative and reproductive organs. The experiment was established as a split-plot design based on a randomized complete block design. Crop rotations, including wheat–chickpea, wheat–forage pea, and wheat–safflower, were assigned to the main plots, whereas tillage systems, including conventional tillage (CT), minimum tillage (MT), and no-tillage (NT), were assigned to the subplots. The same treatment combinations were maintained throughout the experiment and were used for evaluating wheat biomass accumulation, partitioning patterns, and allocation trajectories.

2.3. Phenological assessment and biomass sampling

Wheat phenology was monitored using the Zadoks decimal growth scale (Zadoks et al., 1974). Representative plants were tagged within each experimental plot, and crop developmental stages were recorded at regular intervals to accurately identify the target sampling stages. Biomass sampling was performed at six key developmental stages representing major transitions in wheat vegetative and reproductive development: Z22, Z32, Z37, Z40, Z59, and Z89. These stages represented the early tillering stage, stem elongation, the transition from vegetative to reproductive development, heading/anthesis-related development, grain development, and physiological maturity, respectively. The selected stages were used consistently for all rotation × tillage combinations. At each sampling date, plants were harvested from a predetermined ground area within each subplot. The number of plants in the harvested area was recorded, and the aboveground biomass was separated into leaves, stems, and spikes. From the reproductive phase onward, spikes represented the developing reproductive structures and, at maturity, included the grain-bearing spike. Samples were oven-dried at 70 °C for 48 h to obtain constant dry weight and subsequently weighed. Biomass values were expressed on a ground-area basis (g m^{-2}). The resulting measurements were used to quantify both total aboveground biomass accumulation and organ-specific biomass dynamics.

2.4. Total biomass accumulation and organ-specific biomass

Total dry matter (TDM) at each developmental stage was calculated as the sum of the dry matter of the individual aboveground organs:

$$\text{TDM} = \sum \text{DM}_i$$

$$\text{TDM} = \text{DM}_{\text{leaf}} + \text{DM}_{\text{stem}} + \text{DM}_{\text{spike}}$$

where TDM is total aboveground dry matter (g m^{-2}), and DM_{leaf} , DM_{stem} , and DM_{spike} are the dry matter of leaves, stems, and spikes, respectively.

The temporal trajectory of biomass accumulation was determined by comparing TDM among successive Zadoks stages. Organ-specific biomass accumulation was similarly evaluated to determine when the contribution of leaves, stems, and reproductive structures changed during crop development.

2.5. Biomass allocation

Biomass allocation was expressed as the proportion of total aboveground biomass represented by each organ at a given developmental stage. For each organ (i), allocation was calculated as:

$$\text{Allocation}_i(\%) = \frac{DM_i}{TDM} \times 100$$

- 5 where DM_i represents the dry matter of the leaf, stem, or spike component and (TDM) represents total aboveground dry matter.

This approach allowed the developmental trajectory of biomass allocation to be characterized independently of absolute biomass production. Thus, the relative contribution of each organ could be compared among rotation × tillage treatments and developmental stages.

10 **2.6. Incremental partitioning coefficient**

To distinguish the allocation of the standing biomass pool from the destination of newly accumulated biomass, an incremental partitioning coefficient (IPC) was calculated for each organ between two consecutive sampling stages.

For each developmental interval, IPC was calculated as:

$$15 \quad IPC_i = \frac{\Delta DM_i}{\Delta TDM}$$

$$IPC_i = \frac{DM_{i,t+1} - DM_{i,t}}{TDM_{t+1} - TDM_t}$$

where (IPC_i) is the incremental partitioning coefficient of organ (i), $DM_{i,t+1} - DM_{i,t}$ is the change in dry matter of the respective organ between two sampling dates, and $TDM_{t+1} - TDM_t$ is the corresponding change in total aboveground biomass.

- 20 IPC values were calculated for leaves, stems, and spikes over the five developmental intervals (Z22–Z32, Z32–Z37, Z37–Z40, Z40–Z59, and Z59–Z89). An IPC close to 1 indicates that most of the net increase in aboveground biomass was associated with the respective organ, whereas values approaching zero indicate a limited contribution of that organ to the net biomass increment.

- 25 Because IPC is based on changes in organ biomass relative to changes in total biomass, values greater than 1 may occur when biomass accumulation in an organ is accompanied by a net decline in another organ. Similarly, negative IPC values indicate a net reduction in the biomass of that organ during the corresponding interval. Therefore, IPC values greater than 1 were interpreted as evidence of net redistribution/remobilization dynamics rather than as allocation of more than 100% of newly assimilated biomass to a single organ. This interpretation is consistent with the patterns
30 observed in the experimental data, particularly during the late reproductive interval.

2.7. Estimation of partitioning phases and transition rates

To characterize changes in biomass distribution over crop development, the temporal relationships among organ biomass components were examined using piecewise linear relationships between cumulative organ biomass and cumulative total biomass.

- 35 For each organ, the relationship was described by:

$$y=a+bx$$

where (y) represents cumulative biomass of the respective organ, (x) represents the corresponding cumulative total aboveground biomass, (a) is the intercept, and (b) is the slope.

- 5 The mean partitioning coefficient (PCa) for a given developmental phase was estimated from the slope as:

$$PCa = \frac{b}{1+b}$$

- 10 The resulting coefficients were used to characterize the relative partitioning of newly produced biomass among organs during distinct developmental phases.

In addition, the rates of transition between major allocation phases were estimated from the temporal change in the proportion of biomass allocated to successive organs. Two transition processes were specifically quantified: (i) the leaf-to-stem transition during vegetative development and (ii) the stem-to-spike transition during reproductive development. Transition rates were expressed as percentage change in allocation per Zadoks developmental unit.

- 15

2.8. Source–sink dominance index

A source–sink dominance index (SDI) was used to characterize the temporal transition from vegetative, source-associated biomass accumulation towards reproductive sink dominance during reproductive development as follow:

- 20

$$SDI = \frac{DM\ spike}{DM\ leaf + DM\ stem}$$

The index was calculated from the relative progression of vegetative and reproductive biomass and was evaluated across developmental stages from Z40 to Z89. An SDI value of 1 was considered the equilibrium point between source-oriented and sink-oriented biomass dynamics. Values below 1 indicated relative source dominance, whereas values above 1 indicated increasing sink dominance.

- 25

For each rotation × tillage combination, three complementary characteristics were determined:

1. SDI at Z59,
2. SDI at Z89, and
3. the Zadoks developmental stage at which SDI crossed the threshold of 1.

- 30

The threshold-crossing point was estimated from the fitted SDI trajectory between the observed developmental stages. This approach allowed the timing of the transition to sink dominance to be distinguished from the final intensity of sink dominance. The experimental results demonstrated that these two characteristics were not necessarily coupled; treatments could reach SDI = 1 earlier but show a lower final SDI, or vice versa.

- 35

2.9. Estimation of apparent remobilization

To characterize late-season redistribution of biomass from vegetative organs towards reproductive structures, apparent remobilization was estimated over the Z59–Z89 interval.

For leaves and stems, the apparent biomass loss was calculated as:

$$ABR_i = \max(0, DM_{i,Z59} - DM_{i,Z89})$$

where ABR_i represents apparent biomass remobilization from organ (i), and $DM_{i,Z59}$ and $DM_{i,Z89}$ represent organ dry matter at Z59 and Z89, respectively.

Total apparent vegetative remobilization was calculated as:

$$ABR_{total} = ABR_{leaf} + ABR_{stem}$$

The apparent contribution of vegetative biomass loss to spike biomass gain was subsequently estimated as:

$$ABR \text{ Contribution}(\%) = \frac{ABR_{total}}{DM_{spike,Z89} - DM_{spike,Z59}} \times 100$$

This metric was explicitly interpreted as an apparent remobilization proxy, because a decline in vegetative biomass between two sampling dates does not by itself demonstrate direct physical transfer of assimilates from leaves or stems to the spike. Accordingly, the estimates were used to describe the association between vegetative biomass decline and reproductive biomass gain rather than to claim direct assimilate transfer. This distinction is particularly important because the observed results showed substantial treatment-dependent variation in apparent remobilization.

2.10. Measurement of plant height, yield components, and grain yield

At physiological maturity, plant height and yield components were determined from representative plants collected from each plot. Plant height was measured from the soil surface to the tip of the spike (excluding awns), while spike length, grains per spike, and spike weight were recorded from sampled spikes. Thousand-seed weight was determined from three 1000-seed subsamples per plot. Yield components were assessed from a 3 m² area harvested manually at maturity, whereas grain yield was obtained by harvesting the entire plot using a plot combine harvester and expressed as kg ha⁻¹ after adjustment to standard grain moisture content

2.11. Statistical analysis

All data processing and statistical summaries were performed using R. Biomass accumulation, biomass allocation, and source–sink related variables were analyzed using descriptive and trajectory-based approaches. For each rotation × tillage combination, mean values and standard errors (SE) were calculated across experimental replicates at each developmental stage and used to characterize temporal patterns of biomass accumulation and partitioning. Developmental changes in total biomass accumulation, organ-specific biomass distribution (leaves, stems, and spikes), and allocation dynamics were evaluated by comparing temporal trajectories among the

nine rotation × tillage combinations. The progression of biomass partitioning was interpreted based on changes in allocation patterns, incremental partitioning coefficients (IPC), source–sink dominance index (SDI), transition rates among plant organs, and apparent remobilization (ABR). Because the objective of this analysis was to quantify temporal patterns and biological trajectories rather than to test treatment significance through inferential statistics, results are presented as mean values with associated SE. Separate CART regression trees were fitted in R using the rpart package to identify hierarchical associations between grain yield and biomass partitioning traits within the wheat–chickpea, wheat–forage pea, and wheat–safflower rotations. Grain yield was specified as the response variable, with tillage system, biomass allocation, IPC, SDI, transition rates, and biomass remobilization included as candidate predictors. Tree complexity was limited to a maximum depth of two and a minimum of two observations per terminal node.

3. Results

Residual soil moisture measured after harvest of the preceding crops increased with soil depth across all rotation × tillage combinations, with the lowest and highest moisture contents generally observed in the 0–15 and 30–45 cm layers, respectively (Figure 2). However, the magnitude of residual soil water differed among preceding crops and tillage systems. Across the 0–45 cm soil profile, safflower resulted in lower residual moisture (11.52%) compared with chickpea (14.71%) and forage pea (14.66%). Tillage effects varied among preceding crops. Following safflower, NT maintained greater moisture in the surface layer, whereas MT showed higher moisture retention in deeper soil layers. Forage pea resulted in the highest residual soil moisture, particularly under MT, with the greatest value recorded at 30–45 cm depth (18.4%). Under chickpea, differences among tillage systems were relatively limited, although MT maintained the highest moisture content in the deepest soil layer. The lowest and highest recorded soil moisture values occurred under safflower–MT at 0–15 cm (6.5%) and forage pea–MT at 30–45 cm (18.4%), respectively

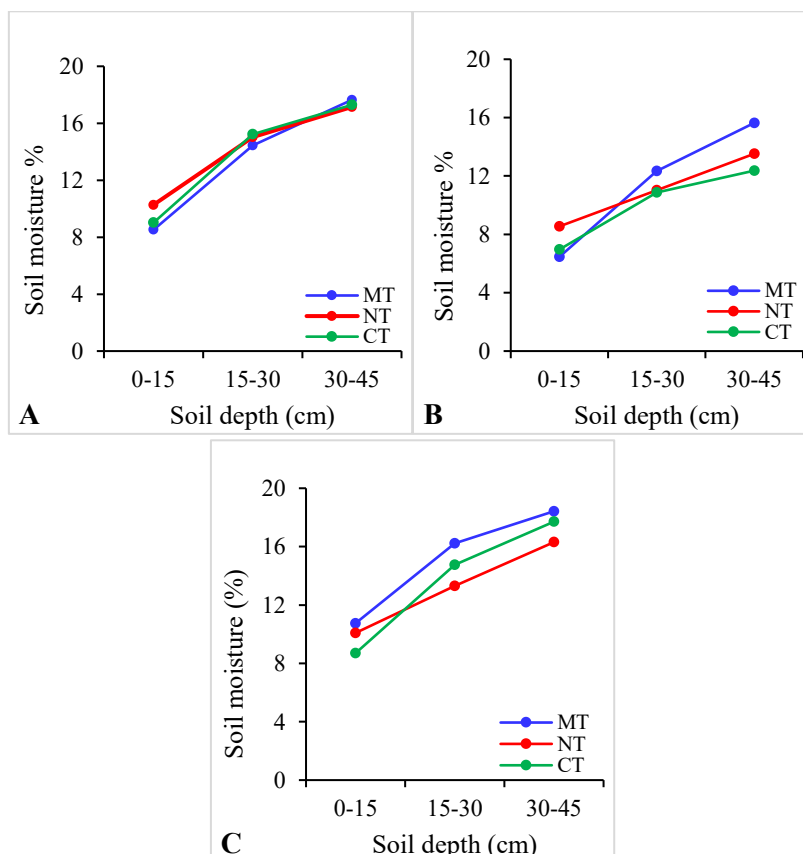
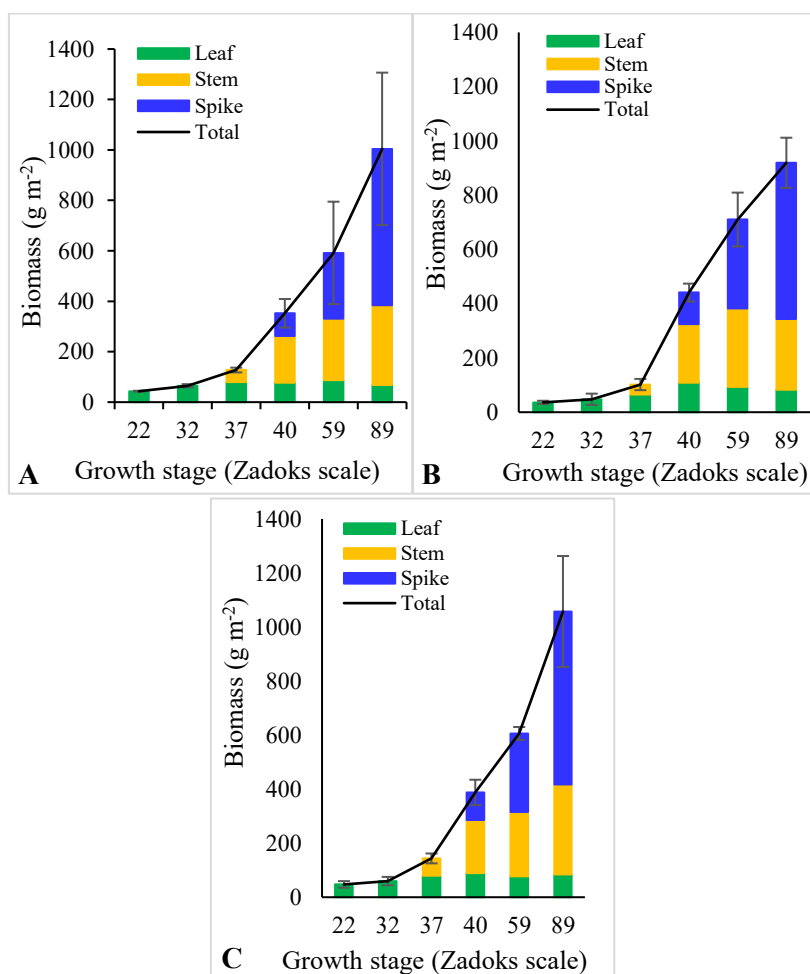
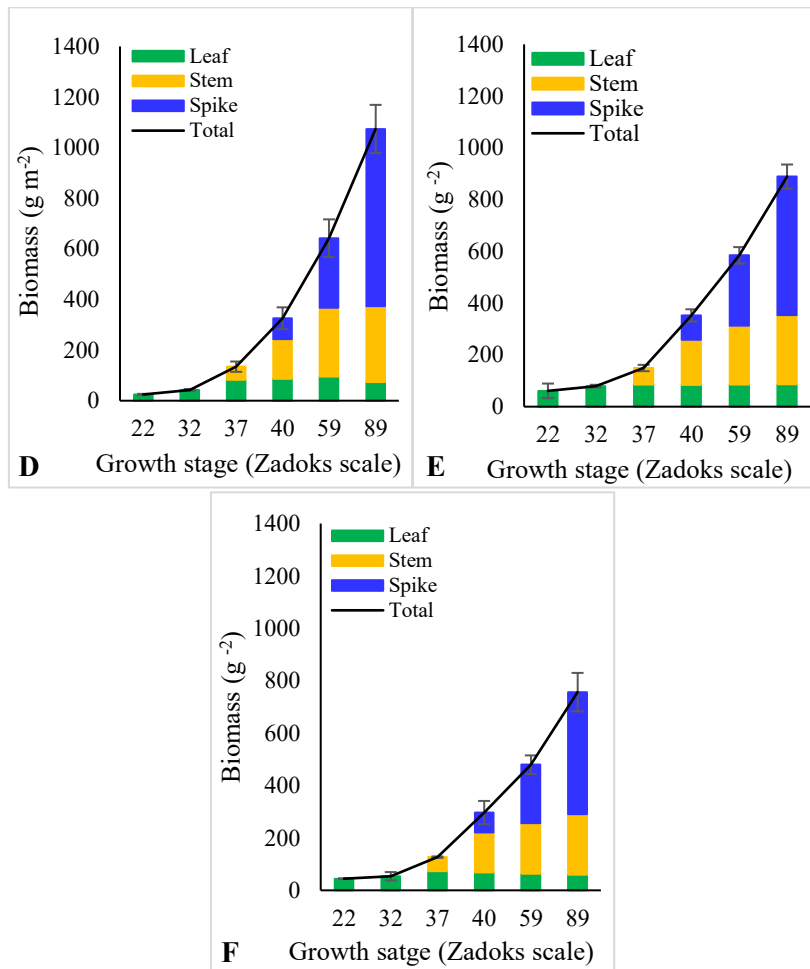


Figure 2. Soil moisture profile after crop harvest in chickpea (A), safflower (B), and forage pea (C) across three soil depths as influenced by different tillage practices: minimum tillage (MT), no-till (NT), and conventional tillage (CT).

5 Total aboveground dry matter increased progressively from early tillering (Z22) to physiological maturity (Z89) across all rotation $\times$ tillage combinations (Figure 3A–I). Biomass accumulation patterns were relatively similar among treatments during early vegetative growth (Z22–Z32), whereas differences became increasingly evident from stem elongation onwards. A rapid accumulation phase occurred between Z37 and Z59, during which the magnitude of biomass increase varied among rotation $\times$ tillage combinations. At flowering (Z59), total biomass ranged from 479.6 g m⁻² under forage pea–NT (Figure 3F) to 744.0 g m⁻² under safflower–CT (Figure 3G), indicating substantial variation in pre-anthesis biomass accumulation.

The greatest divergence among treatments occurred during the late reproductive period (Z59–Z89). Safflower–NT exhibited the greatest late-season biomass accumulation, resulting in the highest final aboveground biomass at maturity (1135.6 g m⁻²; Figure 3I). High final biomass was also observed under forage pea–CT (1073.6 g m⁻²; Figure 3D) and chickpea–NT (1057.3 g m⁻²; Figure 3C), whereas forage pea–NT showed the lowest final biomass (756.4 g m⁻²; Figure 3F). Despite differences in total biomass production, all rotation $\times$ tillage combinations followed a similar ontogenic pattern of biomass development (Figure 3A–I). Leaf biomass dominated during early vegetative growth (Z22–Z32), followed by increased stem accumulation during stem elongation (Z32–Z40) and rapid spike biomass development during reproductive growth (Z40–Z89). At maturity, spike biomass accounted for approximately 60–65% of total aboveground biomass across treatments. The highest spike biomass values were observed under forage pea–CT (700.0 g m⁻²; Figure 3D) and safflower–NT (697.9 g m⁻²; Figure 3I), whereas forage pea–NT showed the lowest spike biomass (465.5 g m⁻²; Figure 3F).





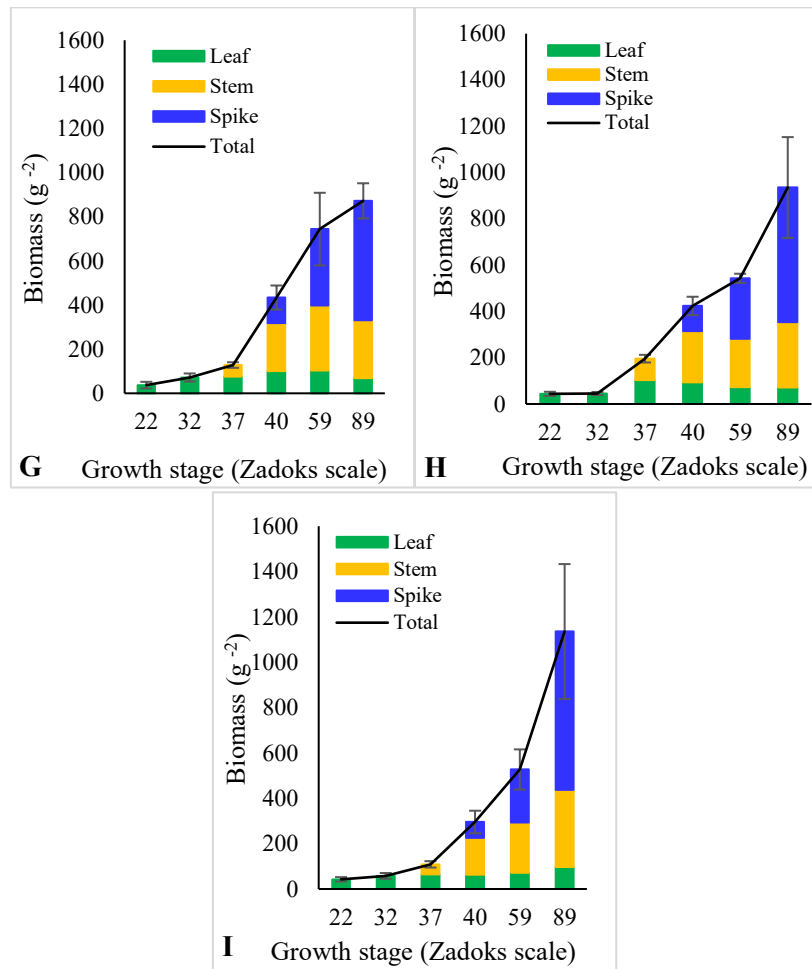


Figure 3. Temporal dynamics of total aboveground biomass accumulation and organ-specific biomass partitioning in wheat grown after different preceding crops under contrasting tillage systems. Stacked bars represent leaf, stem, and spike biomass, whereas the line represents total aboveground biomass (mean $\pm$ SE) measured from Z22 to Z89. Panels represent wheat grown after chickpea under CT (A), MT (B), and NT (C); after forage pea under CT (D), MT (E), and NT (F); and after safflower under CT (G), MT (H), and NT (I).

Biomass allocation followed a conserved ontogenic sequence across all rotation $\times$ tillage combinations, shifting from leaf dominance during early vegetative growth to stem accumulation during elongation and ultimately to spike dominance during reproductive development (Figure 4). However, preceding crop and tillage system influenced the timing and magnitude of this transition, particularly during the Z37–Z59 period.

Following chickpea (Figure 4A), biomass partitioning showed a coordinated transition from vegetative to reproductive sinks. Although tillage affected the timing of stem accumulation and subsequent spike investment, final allocation patterns converged at maturity, with spikes accounting for 60.5–62.6% of total biomass across tillage systems. Following forage pea (Figure 4B), treatment differences persisted longer, with CT maintaining greater vegetative biomass during reproductive development but achieving the highest spike proportion at maturity (65.2%), whereas MT retained a greater residual leaf contribution at Z89. Following safflower (Figure 4C), biomass allocation followed a similar developmental trajectory, although tillage effects were more pronounced during the vegetative-to-reproductive transition. NT maintained greater stem investment during elongation, whereas MT showed greater spike allocation at Z59; however, these differences were reduced by maturity.

The IPC analysis (Figure 5) provided further insight into the temporal dynamics underlying biomass redistribution. Across all treatments, biomass accumulation during early vegetative growth (Z22–Z32) was exclusively associated with leaf expansion (Leaf IPC = 1.00), followed by a shift towards stem-dominated partitioning and increasing reproductive allocation. Following chickpea (Figure 5A), this transition was relatively coordinated, with stem growth dominating during Z32–Z40 and spike-directed partitioning increasing thereafter, particularly under NT. Following forage pea (Figure 5B), the transition towards spike dominance was more gradual but ultimately consistent across tillage systems, with CT showing greater late-season spike partitioning. In contrast, safflower (Figure 5C) exhibited the greatest divergence among tillage systems, particularly in the timing of stem-to-spike transition and late-season redistribution patterns. High spike IPC values (>1.0) reflected increases in spike biomass exceeding concurrent whole-plant biomass accumulation, indicating net redistribution among plant organs.

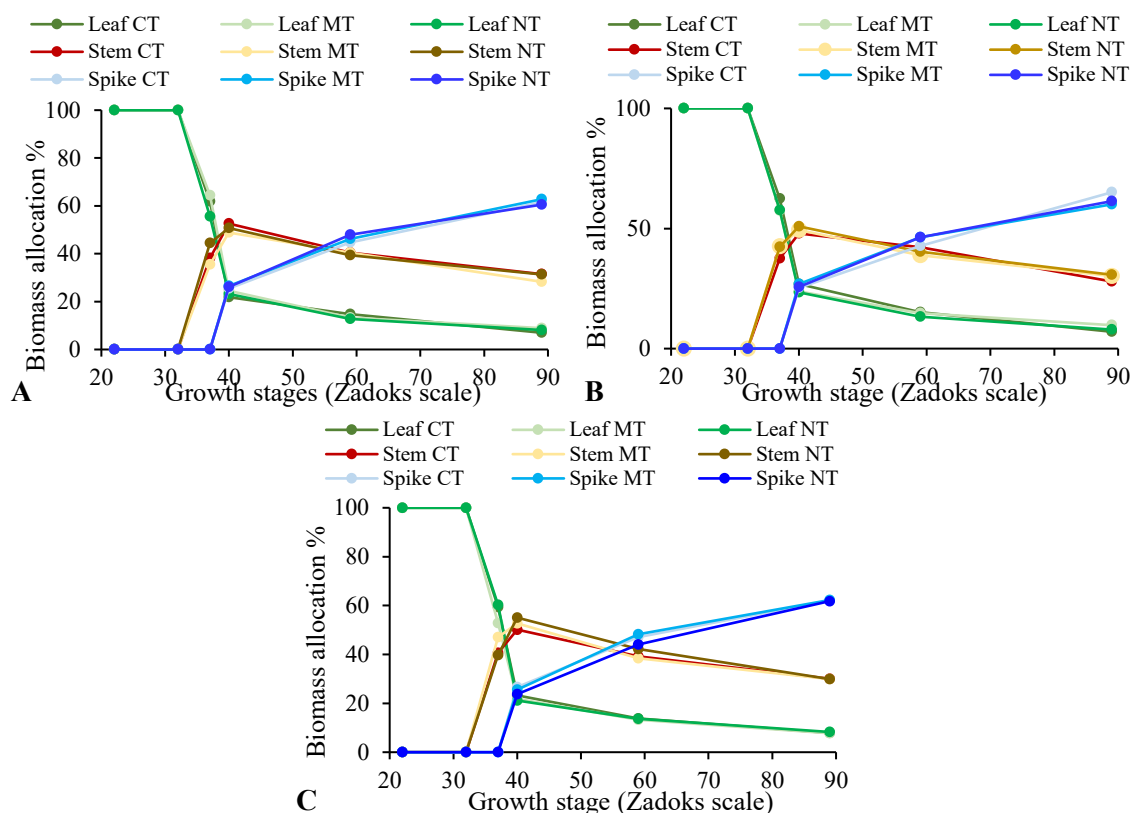


Figure 4. Biomass allocation dynamics of wheat following different preceding crops and tillage systems. Biomass partitioning is presented across key developmental stages (Zadoks scale) under wheat grown after (A) chickpea, (B) forage pea, and (C) safflower. CT, conventional tillage; MT, minimum tillage; NT, no-tillage.

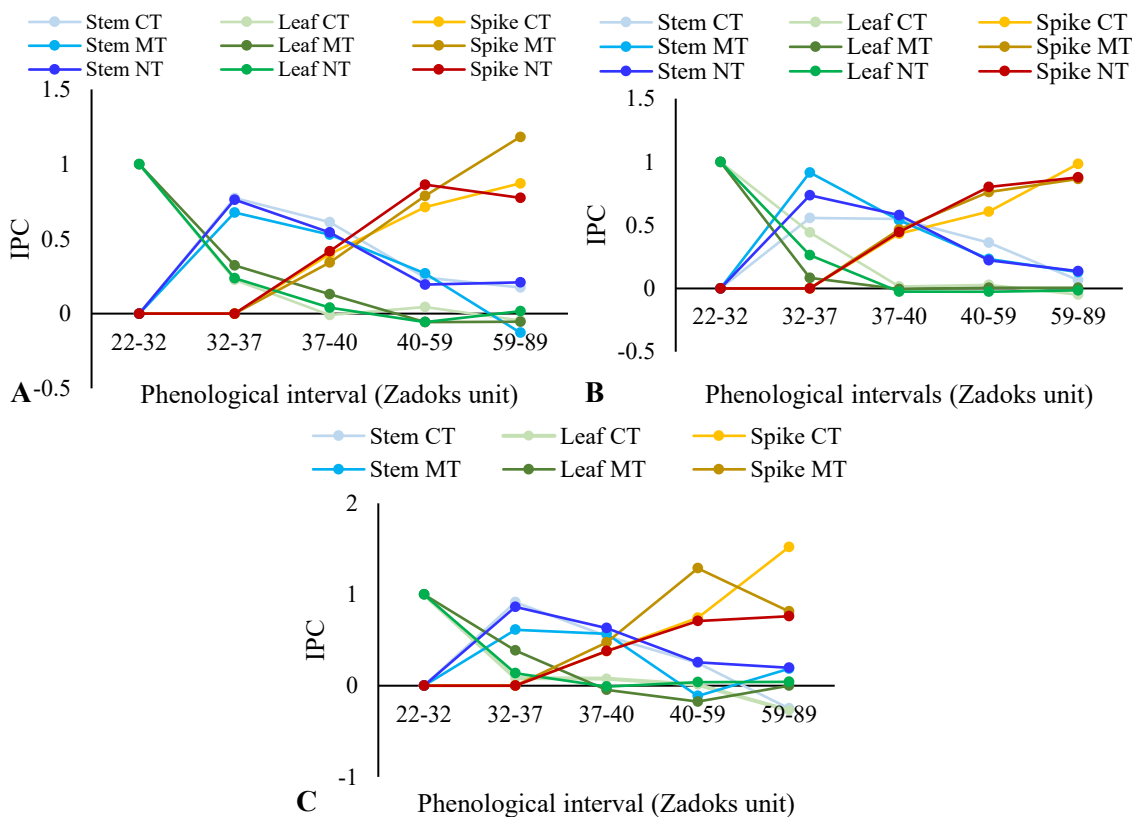


Figure 5. Incremental biomass partitioning dynamics in wheat under contrasting rotations and tillage systems. Results are shown for wheat following (A) chickpea, (B) forage pea, and (C) safflower. CT, conventional tillage; MT, minimum tillage; NT, no-tillage.

Figure 6 illustrates the temporal progression of source–sink dominance during reproductive development. Across all rotation × tillage combinations, SDI increased progressively from Z40 onwards, reflecting a transition from source-oriented growth towards increasing reproductive sink dominance. All treatments exceeded the equilibrium threshold (SDI = 1), although the timing of threshold crossing and the subsequent increase in SDI varied among management combinations. Following chickpea (Figure 6A), the transition to sink dominance occurred earlier under NT than under CT, whereas MT exhibited the highest SDI at maturity. Following safflower (Figure 6B), SDI trajectories were more closely aligned among tillage systems, with relatively small differences in both threshold-crossing time and final SDI values. Following forage pea (Figure 6C), treatments showed similar threshold-crossing periods but diverged in SDI progression after the transition. CT exhibited the greatest increase during late reproductive development and reached the highest final SDI, whereas MT maintained lower SDI values at maturity.

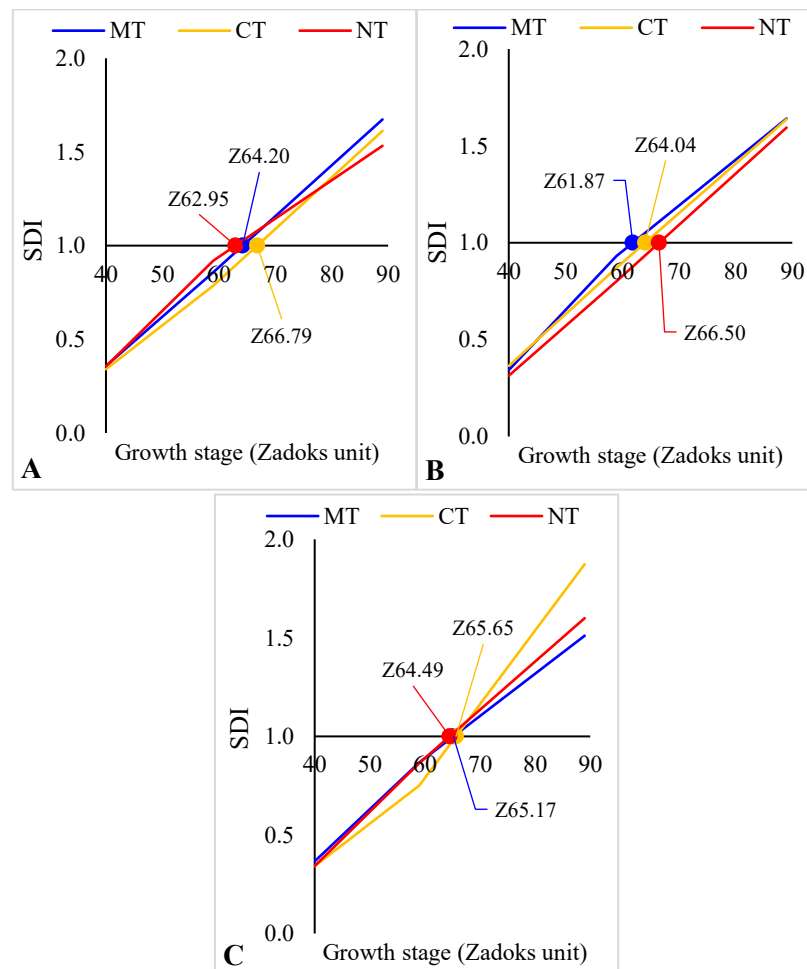


Figure 6. Temporal progression of source–sink dominance index (SDI) during reproductive development of wheat under contrasting rotations and tillage systems. Data are presented for wheat following (A) chickpea, (B) safflower, and (C) forage pea.

Figure 7 shows marked differences in apparent vegetative biomass remobilization during the late reproductive phase (Z59–Z89) among rotation × tillage combinations. Following chickpea (Figure 7A), apparent remobilization showed an intermediate response, with MT exhibiting the highest value, followed by CT and NT. Following safflower (Figure 7B), apparent remobilization was highly dependent on tillage system, with CT showing the greatest vegetative biomass redistribution, mainly through stem and leaf biomass contributions, whereas NT exhibited negligible apparent remobilization despite considerable spike biomass accumulation. Following forage pea (Figure 7C), apparent remobilization remained relatively low across tillage systems, with only moderate differences among treatments and the highest value observed under CT.

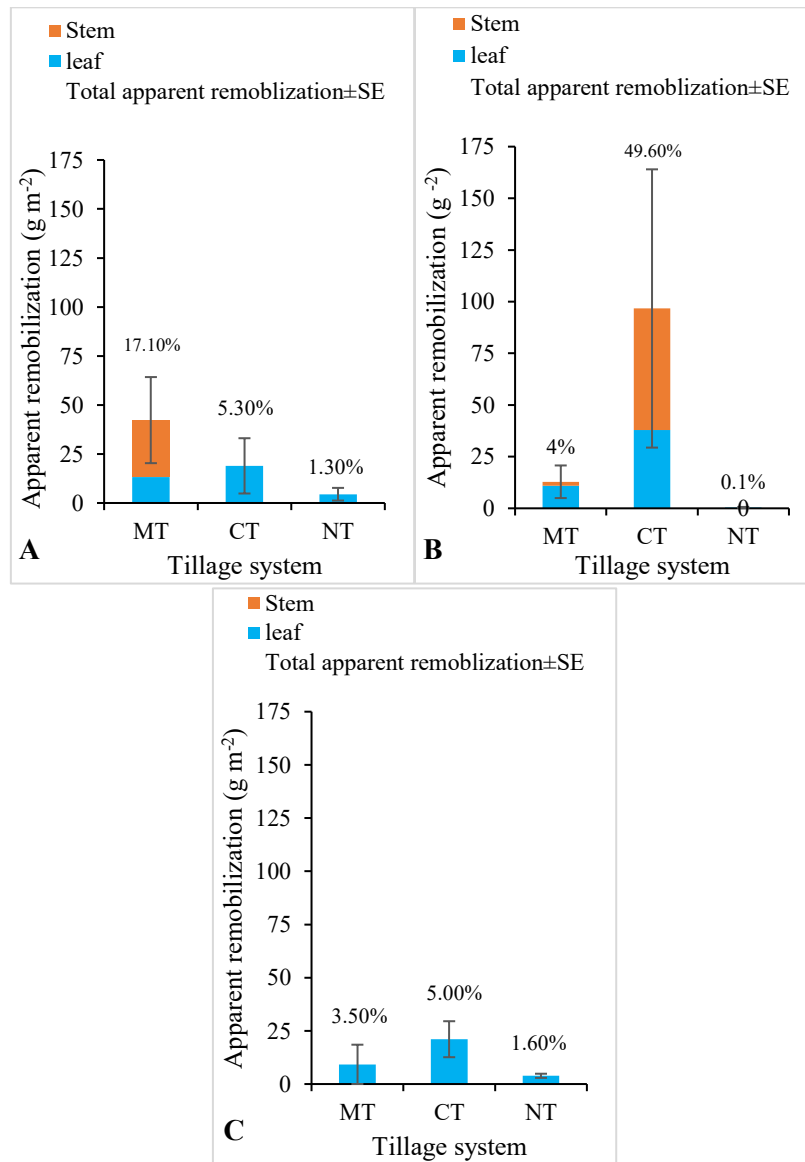


Figure 7. Apparent vegetative biomass remobilization during late reproductive development (Z59–Z89) of wheat under contrasting preceding crops and tillage systems. Results are presented for wheat following (A) chickpea, (B) safflower, and (C) forage pea. Bars represent total apparent remobilization derived from leaf and stem biomass changes, and error bars indicate standard error (SE). CT, conventional tillage; MT, minimum tillage; NT, no-tillage.

Table 2 summarizes the temporal changes in biomass allocation among leaf, stem, and spike components across wheat developmental stages under different rotation × tillage combinations. At early vegetative growth stages (Z22–Z32), aboveground biomass allocation was exclusively directed towards leaf development across all treatments. During stem elongation (Z37–Z40), allocation progressively shifted from leaves towards stems, with stems becoming the dominant vegetative component, while spike contribution remained limited. This transition was followed by a progressive increase in spike allocation during reproductive development. At Z59, spike biomass accounted for approximately 44–48% of total aboveground biomass across treatments, while stems remained an important vegetative component (approximately 38–42%). By physiological maturity (Z89), spikes represented the major biomass sink in all rotation × tillage combinations, accounting for 60.2–65.2% of total biomass. The remaining biomass was primarily retained in stems (approximately 28–32%), whereas leaf contribution declined to below 10% across all treatments. Differences among rotation × tillage combinations were most pronounced during the transition phase between vegetative and reproductive growth (Z37–Z59), whereas biomass allocation patterns became more similar among treatments by maturity.

Table 2. Biomass allocation (%) among leaf, stem, and spike components across wheat developmental stages under contrasting rotations and tillage systems.

Tillage system	Stage (Zadoks unit)	under chickpea-wheat rotation			under safflower-wheat rotation			under forage pea-wheat rotation		
		Leaf (%)	Stem (%)	Spike (%)	Leaf (%)	Stem (%)	Spike (%)	Leaf (%)	Stem (%)	Spike (%)
MT	22	100	0	0	100	0	0	100	0	0
MT	32	100	0	0	100	0	0	100	0	0
MT	37	64	36	0	52.8	47.2	0	57.1	42.9	0
MT	40	24.8	48.9	26.3	22	52.5	25.5	23.9	49.3	26.8
MT	59	13.2	40.6	46.2	13.3	38.5	48.2	14.6	39	46.5
MT	89	9	28.4	62.6	7.7	30.2	62.1	9.8	30.1	60.2
CT	22	100	0	0	100	0	0	100	0	0
CT	32	100	0	0	100	0	0	100	0	0
CT	37	62.2	37.8	0	59.8	40.2	0	61.9	38.1	0
CT	40	21.9	52.8	25.4	23.1	50.2	26.7	26.5	48	25.5
CT	59	14.8	41.2	44	13.9	39.6	46.6	14.9	42.2	42.9
CT	89	6.8	31.4	61.7	7.8	30.1	62.1	6.9	27.9	65.2
NT	22	100	0	0	100	0	0	100	0	0
NT	32	100	0	0	100	0	0	100	0	0
NT	37	55.4	44.6	0	59.5	40.5	0	57.7	42.3	0
NT	40	23.1	50.7	26.2	21.3	54.9	23.9	23.1	51.3	25.5
NT	59	12.7	39.4	47.9	13.5	42	44.5	13.3	40.3	46.4
NT	89	8	31.5	60.5	8.5	30	61.5	7.9	30.5	61.5

Table 3 summarizes the key transition metrics describing biomass reallocation and the progression towards sink dominance across rotation $\times$ tillage combinations. Leaf-to-stem and stem-to-spike transition rates varied among treatments, reflecting differences in the timing and magnitude of biomass redistribution during crop development. The leaf-to-stem transition rate ranged from 7.11 to 9.42% per Zadoks unit, with the lowest value observed under chickpea-MT and the highest under safflower-MT. Stem-to-spike transition rates showed a narrower range (0.92–1.19% per Zadoks unit), with the highest value recorded under safflower-MT and the lowest under forage pea-CT. At Z59, SDI values remained below 1 across all rotation $\times$ tillage combinations, indicating that sink dominance had not yet been established. The transition point (SDI = 1) occurred between Z61.87 and Z66.79, with the earliest transition observed under safflower-MT and the latest under chickpea-CT. Differences in threshold-crossing stage were also observed among tillage systems within rotations, particularly following chickpea and safflower. By Z89, SDI exceeded 1 in all treatments, with final values ranging from 1.51 under forage pea-MT to 1.87 under forage pea-CT. The highest final SDI values were observed under forage pea treatments, whereas chickpea and safflower rotations showed comparatively lower values at maturity.

Table 3. Transition metrics describing biomass reallocation and source–sink dominance development under contrasting crop rotations and tillage systems.

Rotation	Tillage	Leaf-to-stem transition rate (% per Zadoks unit)	Stem-to-spike transition rate (% per Zadoks unit)	SDI at Z59	SDI at Z89	SDI = 1 crossing (Zadoks stage)
Chickpea	MT	7.11	1.04	0.86	1.67	64.21
Chickpea	CT	7.62	1.01	0.79	1.61	66.79
Chickpea	NT	8.89	1.15	0.92	1.53	62.96
Safflower	MT	9.42	1.19	0.93	1.64	61.87
Safflower	CT	8.13	1.07	0.87	1.64	64.04
Safflower	NT	7.95	1.06	0.8	1.59	66.51
Forage pea	MT	8.53	1.03	0.87	1.51	65.18
Forage pea	CT	7.52	0.92	0.75	1.87	65.66
Forage pea	NT	8.46	1.09	0.87	1.6	64.49

- 5 Grain yield and its component traits varied among rotation × tillage combinations (Table 4). The highest grain yield was obtained under safflower–MT (2302.9 kg ha⁻¹), followed by chickpea–NT (2125.7 kg ha⁻¹), whereas forage pea–CT showed the lowest yield (1811.4 kg ha⁻¹). The ranking of grain yield was not consistent with that of final aboveground biomass or final sink dominance, indicating differences in the conversion of reproductive biomass into harvested grain among treatments. Within the safflower rotation,
- 10 MT resulted in the highest grain yield, although NT produced a comparable harvest index (0.38) and greater final aboveground biomass. Safflower–CT showed the highest seed number per spike (25.93), whereas safflower–MT achieved the greatest grain yield without maximizing individual spike traits, suggesting that yield advantage under MT was not attributable to a single spike component. Under forage pea, grain yield increased progressively from CT to NT, with NT also producing the highest spike weight (1.148 g), seed
- 15 number per spike (24.07), and harvest index (0.42) within this rotation. The relatively high harvest index under forage pea–NT indicates more efficient partitioning of aboveground biomass toward grain production. In contrast, forage pea–CT showed the lowest grain yield (1811.4 kg ha⁻¹) despite a moderate harvest index (0.35), suggesting that its lower yield was associated with lower reproductive biomass production rather than a strong limitation in proportional biomass allocation to grain. Following chickpea, NT produced the highest
- 20 grain yield and spike weight (2125.7 kg ha⁻¹ and 1.213 g, respectively), whereas MT exhibited the longest spikes and the highest seed number per spike (26.10). Despite these differences in spike-related traits, MT did not result in greater grain yield than NT and had the lowest harvest index within the chickpea rotation (0.34). Thus, the higher yield under chickpea–NT appears to have resulted from a more favorable combination of reproductive biomass production and biomass partitioning than under MT. Overall, the
- 25 variation in harvest index among rotation × tillage combinations, ranging from 0.34 under forage pea–MT and chickpea–MT to 0.42 under forage pea–NT, further demonstrates that grain yield was determined by the combined effects of biomass production, sink development, and the efficiency of biomass allocation to harvested grain rather than by individual yield components alone.

- 30 Table 4. Grain yield, yield components, and morphological traits of wheat under contrasting crop rotations and tillage systems. Values are presented as mean ± standard error (SE).

Crop rotation	Tillage system	Plant height (cm)	Spike length (cm)	Seed No. per Spike	Spike weight (g)	Grain yield (kg/ha)	1000 Seed Weight (g)	HI
Safflower	CT	70.38 ± 1.07	6.80 ± 0.33	25.93 ± 1.10	1.063 ± 0.027	2061.9 ± 169.1	37.92 ± 1.13	0.37 ± 0.031
	MT	62.10 ± 1.79	6.50 ± 0.35	23.23 ± 1.55	1.014 ± 0.101	2302.9 ± 143.7	37.62 ± 0.42	0.37 ± 0.029
	NT	70.28 ± 1.09	6.60 ± 0.23	22.93 ± 1.42	1.042 ± 0.039	1990.5 ± 255.6	38.78 ± 0.47	0.38 ± 0.007
Forage pea	CT	68.08 ± 2.06	6.02 ± 0.39	21.27 ± 1.05	0.878 ± 0.081	1811.4 ± 137.2	39.68 ± 0.14	0.35 ± 0.018
	MT	59.80 ± 4.56	6.25 ± 0.41	22.53 ± 0.43	1.005 ± 0.069	1833.3 ± 145.3	36.29 ± 0.63	0.34 ± 0.041

Crop rotation	Tillage system	Plant height (cm)	Spike length (cm)	Seed No. per Spike	Spike weight (g)	Grain yield (kg/ha)	1000 Seed Weight (g)	HI
Chickpea	NT	59.87 ± 1.39	6.67 ± 0.27	24.07 ± 0.09	1.148 ± 0.150	2038.1 ± 118.5	38.82 ± 0.49	0.42 ± 0.041
	CT	69.47 ± 1.29	6.18 ± 0.29	23.23 ± 2.49	1.030 ± 0.194	1996.2 ± 178.3	37.85 ± 0.35	0.36 ± 0.001
	MT	67.32 ± 5.72	7.52 ± 0.81	26.10 ± 2.90	1.185 ± 0.141	1992.4 ± 292.7	38.34 ± 0.04	0.34 ± 0.034
	NT	72.80 ± 3.67	6.93 ± 0.39	24.27 ± 1.40	1.213 ± 0.131	2125.7 ± 174.7	36.52 ± 0.85	0.35 ± 0.013

In the wheat–chickpea rotation (Figure 8A), spike IPC during Z40–Z59 was selected as the primary splitter of grain yield. Observations with spike IPC ≤ 0.76 had a mean predicted yield of 2388.6 kg ha⁻¹. At higher spike IPC values, yield was further separated by stem allocation at Z37, with values >40.4% associated with a higher predicted yield (2041.9 kg ha⁻¹) than values $\leq 40.4\%$ (1683.8 kg ha⁻¹). In the wheat–forage pea rotation (Figure 8B), SDI at Z59 was the primary variable separating grain-yield responses. Observations with SDI ≤ 0.76 had a mean predicted yield of 1674.3 kg ha⁻¹. For observations with SDI >0.76, stem IPC during Z32–Z37 provided a further split, with stem IPC ≤ 0.62 associated with a predicted yield of 2178.6 kg ha⁻¹, compared with 1866.6 kg ha⁻¹ at higher values. In the wheat–safflower rotation (Figure 8C), leaf allocation at Z37 was the primary splitter of grain yield. Leaf allocation >60.4% was associated with a mean predicted yield of 1790.5 kg ha⁻¹. At leaf allocation values $\leq 60.4\%$, stem IPC during Z32–Z37 further differentiated yield, with values >0.59 corresponding to the highest predicted yield (2432.1 kg ha⁻¹), compared with 1982.9 kg ha⁻¹ when stem IPC was ≤ 0.59 .

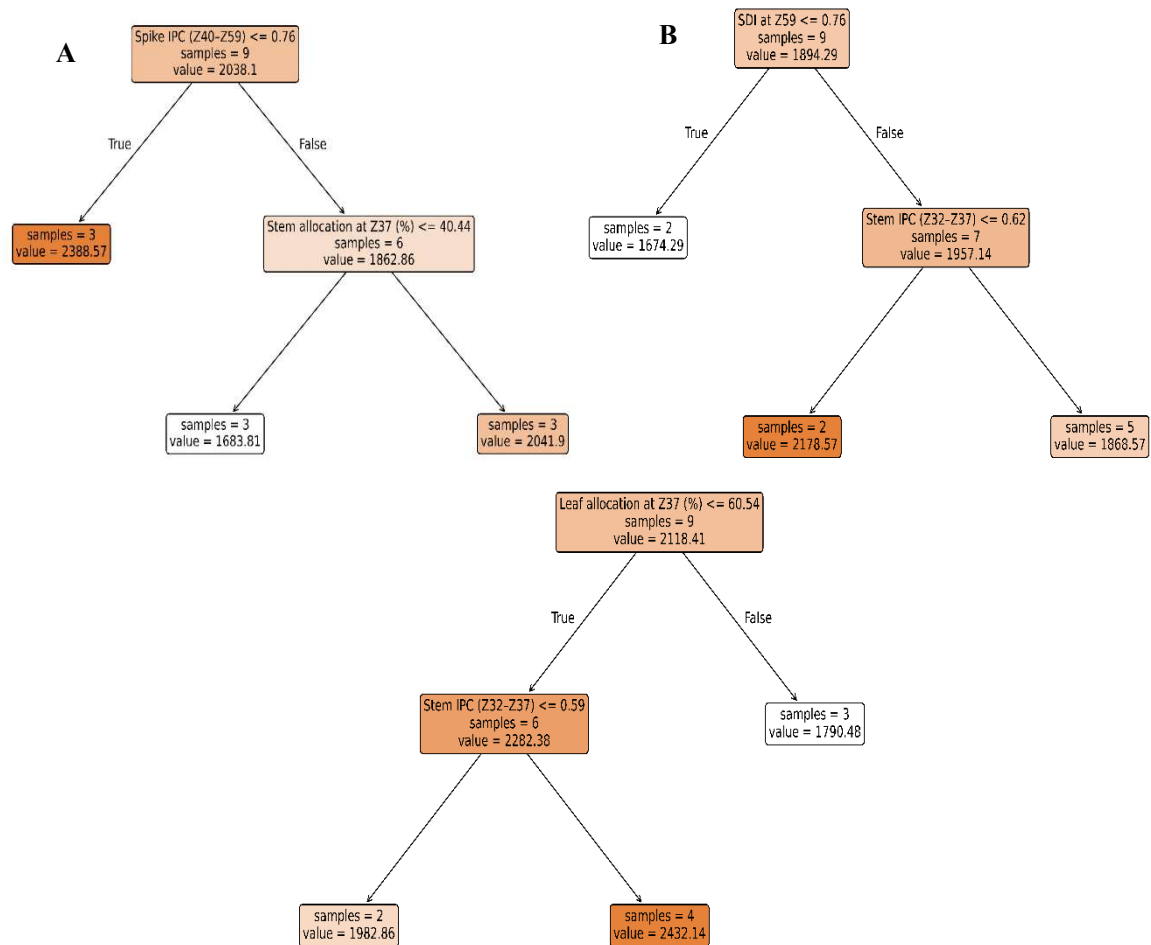


Figure 8. Regression tree identifying the hierarchical predictors of grain yield formation in wheat under the chickpea-wheat (A), Forage pea-wheat (B) and Safflower-wheat (C) rotation. The tree shows successive splits based on biomass partitioning traits, with terminal nodes representing the mean predicted grain yield (kg ha^{-1}) for observations within each decision pathway.

4. Discussion

4.1. Crop rotation and tillage shaped wheat performance through resource legacy effects

The results demonstrated that crop rotation and tillage influenced wheat productivity by modifying the resource environment experienced by the crop throughout the growing season. Differences in residual soil moisture among preceding crops (Figure 2) indicate that rotation effects extended beyond the growing period of the previous crop and created distinct resource legacies for subsequent wheat development. Chickpea and forage pea rotations maintained greater soil moisture availability compared with safflower, suggesting that preceding crops differed in their patterns of resource capture and depletion. Such rotational carry-over effects are widely recognized in dryland systems, where crop sequence influences subsequent crop performance through changes in soil water availability, nutrient dynamics, residue characteristics, and soil physical conditions (Kirkegaard et al., 2014; Blanco-Canqui and Ruis, 2018; Congreves et al., 2018).

The lower residual soil moisture following safflower (Figure 2) suggests a stronger water depletion legacy, which may have constrained subsequent wheat growth under dryland conditions. Although root distribution and seasonal water use were not directly measured in this study, the observed pattern is consistent with differences in crop growth duration, biomass production, and resource extraction capacity among preceding crops. In contrast, forage pea and chickpea likely provided a more favorable soil environment for wheat establishment through reduced pre-season water depletion and, potentially, improved soil nutrient conditions associated with legume-based rotations (Peoples et al., 2021).

Tillage further modified these rotational effects by influencing how available soil resources were conserved and utilized. No-tillage improved surface moisture retention following safflower, whereas minimum tillage maintained greater moisture availability at deeper soil layers (Figure 2). These contrasting responses indicate that tillage effects were strongly dependent on the preceding crop environment, reflecting differences in residue cover, evaporation losses, infiltration processes, and soil water distribution (Basche and DeLonge, 2019; Pittelkow et al., 2019). Therefore, the effect of tillage should not be considered independently of crop rotation, because the preceding crop determines the initial resource conditions under which tillage practices operate.

Although all rotation × tillage combinations exhibited similar seasonal biomass accumulation patterns, treatment differences became more evident after stem elongation when crop demand for water and assimilates increased (Figure 3). This suggests that rotational legacies were established early during crop development but were expressed more strongly during reproductive growth, when resource limitations increasingly influenced biomass production and reproductive success.

4.2. Biomass accumulation and allocation efficiency determine yield formation

A major finding of this study was that greater biomass accumulation did not necessarily result in higher grain yield. Wheat following safflower–NT produced the highest final aboveground biomass (1135.6 g m⁻²; Figure 3I), yet this advantage was not converted into maximum grain yield. In contrast, safflower–MT produced the highest grain yield (2302.9 kg ha⁻¹; Table 3) despite lower biomass accumulation. This contrasting response demonstrates that under dryland conditions, yield formation depends not only on biomass production but also on the efficiency with which accumulated biomass is allocated toward reproductive structures and grain development.

Previous studies have shown that yield improvement in wheat is more closely associated with enhanced harvest index, efficient assimilate partitioning, and improved coordination between vegetative sources and reproductive sinks than with increasing total biomass alone (Fischer, 2011; Reynolds et al., 2021). The present results support this concept, particularly under safflower rotation, where greater biomass production under no-tillage did not result in greater grain productivity. Instead, minimum tillage appeared to promote a more favorable balance between

vegetative growth and reproductive investment, allowing a greater proportion of available assimilates to contribute to yield formation.

Yield component responses further confirmed the importance of allocation efficiency (Table 3).

5 Although safflower–MT produced shorter plants (62.10 cm) than CT and NT treatments, it achieved the highest grain yield, indicating that excessive vegetative growth was not advantageous under limited water availability. Similarly, forage pea–CT accumulated high reproductive biomass and achieved the greatest spike biomass proportion at maturity (65.2%; Table 1), but produced the lowest grain yield among forage pea treatments (1811.4 kg ha⁻¹; Table 3). In contrast, forage pea–
10 NT achieved higher grain yield (2038.1 kg ha⁻¹), supported by greater spike weight and seed number per spike (Table 3). These results indicate that reproductive investment alone does not ensure higher yield unless sink development is adequately supported by assimilate availability during grain filling.

Thus, the relationship between biomass partitioning and grain yield was determined by the balance
15 between sink capacity and source supply rather than by the absolute amount of biomass allocated to reproductive organs. Wheat productivity under stress environments depends on maintaining sufficient assimilate availability to support grain number establishment and subsequent grain growth (Gaju et al., 2014; Slafer et al., 2023).

4.3. Source–sink regulation determines reproductive efficiency

20 The source–sink analysis revealed that rotation and tillage altered the timing and intensity of biomass redistribution among plant organs rather than changing the fundamental developmental pattern of wheat growth (Figures 4 and 5). The largest differences occurred during the transition from vegetative growth to reproductive development (Z37–Z59), when the establishment of reproductive sinks overlaps with continued source formation. Consequently, management
25 practices that influence resource availability during this period can strongly affect the balance between vegetative maintenance and reproductive allocation.

Following chickpea, biomass allocation patterns remained relatively stable among tillage systems, with spike allocation converging at maturity (Figure 4A; Table 1). This stability coincided with more favorable residual soil moisture conditions at wheat establishment (Figure 2), suggesting that
30 chickpea rotation created a resource environment that supported a more consistent transition from vegetative growth toward reproductive development. The superior performance of chickpea–NT, which achieved the highest grain yield among chickpea treatments (2125.7 kg ha⁻¹) together with high plant height (72.80 cm), spike weight (1.213 g), and seed number per spike (24.27) (Table 3), indicates that favorable resource conditions allowed simultaneous support of biomass production and reproductive sink establishment.
35

In contrast, safflower generated stronger differentiation among tillage systems in biomass partitioning and IPC dynamics (Figures 4C and 5C). Under lower residual moisture conditions, wheat became more dependent on management-related differences in resource capture and allocation strategy. The contrasting responses of safflower–NT and safflower–MT therefore
40 highlight the importance of reproductive efficiency over biomass quantity. While no-tillage promoted maximum biomass accumulation, minimum tillage improved the conversion of available resources into grain yield.

These findings emphasize that crop management affects yield formation not simply by increasing biomass production but by regulating how effectively biomass is redistributed among competing
45 plant organs. Similar relationships between reproductive development, grain number formation, and yield potential have been reported in wheat, where sink establishment must be matched with sufficient source activity during reproductive development (Ferrante et al., 2015; Reynolds et al., 2022).

4.4. Sink dominance, remobilization, and grain filling strategies

The SDI responses demonstrated that rotation and tillage influenced the balance between assimilate supply and reproductive demand throughout crop development (Figure 6; Table 2). Although all treatments eventually shifted toward sink dominance, the timing and magnitude of this transition differed among management systems. Under chickpea rotation, NT accelerated the transition toward sink dominance, whereas MT maintained higher SDI at maturity (Figure 6A; Table 2), indicating that different management systems may achieve similar reproductive outcomes through different allocation strategies.

Following forage pea, CT exhibited the highest final SDI (1.87; Figure 6C; Table 2), consistent with its greater spike biomass allocation (Table 1). However, this higher sink dominance did not translate into greater grain yield, demonstrating that sink strength alone is insufficient when assimilate supply during grain filling is limited. Therefore, reproductive success depends on synchronization between sink capacity and source availability rather than maximizing sink development alone (Rosati and Benincasa, 2023; Slafer et al., 2023).

The safflower rotation showed the strongest dependence of source–sink regulation on tillage management. Although safflower–NT produced maximum biomass accumulation (1135.6 g m⁻²; Figure 3I), it did not achieve the highest SDI or grain yield (Figure 6B; Table 3). Conversely, safflower–MT achieved higher yield despite lower biomass production, indicating that efficient biomass utilization and grain filling capacity were more important than biomass accumulation under restrictive resource conditions.

The relationships among SDI, IPC dynamics, and apparent remobilization further indicate that wheat can maintain grain production through multiple physiological strategies (Figures 5–7). These strategies include maintaining current assimilation, optimizing sink activity, and increasing the contribution of stored assimilates during grain filling. However, greater remobilization should not necessarily be interpreted as a direct indicator of higher productivity, because increased dependence on stored assimilates may also reflect reduced current assimilate supply under stress conditions (Blum, 1998; Yang and Zhang, 2006). Therefore, successful grain filling depends on the integration of remobilization with continued source activity and effective sink utilization.

4.5. Integrated interpretation and agronomic implications

Overall, the results demonstrate that crop rotation and tillage influenced wheat productivity through a hierarchical process involving resource availability, biomass accumulation, biomass partitioning, source–sink regulation, and grain filling efficiency. Preceding crops primarily shaped the resource environment by modifying residual soil moisture availability (Figure 2), whereas tillage affected how effectively wheat captured and utilized these resources throughout development.

The contrasting responses among rotation × tillage combinations highlight that the most productive system was not necessarily the one producing the greatest biomass or strongest sink dominance. The safflower–NT versus safflower–MT comparison provides a clear example: maximum vegetative biomass accumulation did not correspond with maximum grain yield. Similarly, forage pea–CT demonstrated that greater reproductive allocation and sink dominance could not compensate for insufficient assimilate supply during grain filling.

Therefore, improving dryland wheat productivity requires optimizing the coordination between resource availability, biomass production, allocation efficiency, sink establishment, and grain filling. Management strategies should be evaluated not only by their capacity to increase biomass or conserve soil moisture but also by their ability to maintain a balanced source–sink relationship throughout crop development.

4.6. Rotation-specific pathways of yield formation

Regression-tree analysis revealed rotation-specific pathways associated with grain-yield formation. Under the wheat–chickpea rotation, yield differentiation was primarily associated with spike IPC during Z40–Z59 and subsequent variation in stem allocation, highlighting the importance of biomass partitioning during reproductive development. In contrast, SDI at Z59 and stem IPC during

early stem elongation were the main variables selected under the wheat–forage pea rotation, indicating a stronger association between yield and source–sink coordination across developmental stages. Under the wheat–safflower rotation, leaf allocation at Z37 followed by stem IPC during Z32–Z37 primarily differentiated yield, suggesting that the balance between vegetative persistence and structural biomass partitioning during stem elongation was particularly relevant. Collectively, these contrasting pathways suggest that crop rotation was associated with shifts in the relative importance of biomass partitioning processes underlying wheat yield formation, consistent with the dynamic coordination of source and sink development across crop growth stages (Slafer et al., 2023; Murchie et al., 2023).

5. Conclusion

This study demonstrated that crop rotation and tillage jointly regulated dryland wheat productivity by altering resource availability, biomass production, source–sink coordination, and reproductive allocation. Higher biomass accumulation or sink dominance alone did not ensure greater grain yield, highlighting the importance of efficient biomass partitioning under water-limited conditions. The harvest index further indicated that grain yield depended on the balance between total biomass production and its allocation to grain, rather than on either component independently. Overall, sustainable productivity in dryland wheat requires management systems that optimize resource legacies while maintaining coordinated source activity, sink development, and biomass allocation throughout crop development.

Author Contributions

R.L. conceived and designed the study, contributed to the experimental work, data analysis and interpretation, and wrote the main manuscript text. A.M., J.J., V.F., M.R., N.K.-I., F.E.-S. and A.A. contributed to the experimental work, data collection, interpretation of results, and critical revision of the manuscript. All authors reviewed and approved the final manuscript.

Data Availability

The datasets analysed during the current study are available from the corresponding author on reasonable request.

Competing Interests

The authors declare no competing interests.

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