



Carbon-Moisture Coupling in Forest Soils during Successional Stages: Mechanisms, Temporal Dynamics, and Ecosystem Implications

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Abstract

Forest succession fundamentally alters soil carbon–moisture coupling through progressive changes in organic matter accumulation, soil structure development, and hydrological processes. This comprehensive study examines carbon–moisture interactions across a 125-year forest succession chronosequence in temperate deciduous forests, monitoring 89 forest stands representing early (5-15 years), mid (20-40 years), late (50-80 years), and mature (>100 years) successional stages. We employed continuous soil moisture monitoring, carbon stock measurements, and hydraulic property analysis to quantify coupling dynamics. Results demonstrate that soil organic carbon (SOC) content increases from $42.3 \pm 8.7 \text{ Mg ha}^{-1}$ in early succession to $156.8 \pm 23.4 \text{ Mg ha}^{-1}$ in mature forests, with concurrent improvements in water retention capacity from $18.2 \pm 4.1\%$ to $32.7 \pm 6.8\%$ volumetric water content at field capacity. Carbon–moisture coupling strength, quantified through correlation analysis, increases progressively from $r = 0.43$ in early stages to $r = 0.89$ in mature forests, indicating increasingly integrated biogeochemical–hydrological systems. Water retention efficiency improves 2.8-fold during succession, with organic matter contributing 67% of total water holding capacity in mature soils compared to 23% in early succession. Temporal analysis reveals that carbon–moisture coupling strengthens exponentially, reaching 80% of maximum coupling by 45-55 years post-disturbance. Depth profile analysis shows coupling intensification throughout the soil profile, with surface layers (0-15 cm) showing strongest relationships ($r = 0.94$) but significant coupling extending to 60 cm depth ($r = 0.71$). Seasonal dynamics demonstrate that coupling strength varies temporally, with strongest relationships during summer drought periods ($r = 0.91$) and weakest during spring saturation ($r = 0.58$). Mechanistic analysis reveals that soil aggregation mediated by fungal hyphae and root exudates drives coupling enhancement, with aggregate stability increasing 3.4-fold during succession. Economic valuation indicates that enhanced water regulation services provide benefits worth $\$234\text{--}567 \text{ ha}^{-1} \text{ year}^{-1}$ in mature forests through flood control, drought mitigation, and groundwater recharge. However, climate change scenarios suggest 15-23% reductions in coupling strength under projected warming, emphasizing the vulnerability of these integrated systems to environmental change.

Keywords: Foreign Direct Investment, Economic Growth, Cameroon

1. Introduction

Forest succession represents one of nature's most fundamental ecological processes, driving systematic changes in ecosystem structure, function, and biogeochemical cycling over multi-decadal timescales^[1]. Among the most significant but understudied aspects of successional development is the progressive coupling between soil carbon and moisture dynamics, whereby organic matter accumulation enhances water retention capacity while soil moisture regimes influence carbon storage and turnover

The coupling between soil carbon and moisture operates through multiple interconnected mechanisms that strengthen during forest succession [2-3]. Organic matter accumulation directly increases soil water holding capacity through enhanced porosity and surface area, while improved soil structure from root activity and microbial processes creates stable aggregates that retain moisture [4]. Conversely, soil moisture regimes control decomposition rates, root growth patterns, and microbial activity, thereby influencing carbon accumulation and stabilization [5].

Understanding carbon–moisture coupling during forest succession has critical implications for ecosystem service provision, climate change mitigation, and forest management strategies [6]. Enhanced water retention in mature forest soils provides important hydrological services including flood control, drought mitigation, and groundwater recharge [7]. Simultaneously, the moisture-mediated stabilization of soil carbon contributes to long-term carbon sequestration and ecosystem resilience [8].

Traditional approaches to studying forest succession have often examined carbon and hydrological processes separately, missing the complex feedbacks and interactions that characterize mature forest ecosystems [9]. Recent recognition of coupled biogeochemical–hydrological systems has highlighted the need for integrated approaches that examine these processes simultaneously [10]. However, long-term studies quantifying coupling development across complete successional sequences remain limited [11].

The temporal dynamics of carbon–moisture coupling development during succession follow predictable patterns related to organic matter accumulation, soil structure development, and plant community maturation [12]. Early successional forests typically exhibit weak coupling due to limited organic matter and poorly developed soil structure, while mature forests demonstrate strong coupling through extensive organic matter accumulation and complex soil architecture [13].

Spatial patterns of coupling within forest soil profiles reveal important vertical heterogeneity that changes during succession [14]. Surface layers typically show strongest coupling due to concentrated organic matter inputs, while deeper layers may exhibit delayed coupling development as organic matter gradually accumulates through root turnover and leaching [15]. Understanding these depth-dependent patterns is essential for comprehensive assessment of coupling dynamics [16].

Seasonal variations in carbon–moisture coupling reflect the temporal dynamics of biological activity, precipitation patterns, and evapotranspiration demands [17]. These temporal fluctuations provide insights into the mechanisms underlying coupling relationships and have important implications for ecosystem responses to climate variability [18].

Climate change presents significant challenges for carbon–moisture coupling in forest ecosystems, with projected changes in temperature and precipitation patterns potentially disrupting established relationships [19]. Understanding the vulnerability of these coupled systems to climate change is essential for predicting future ecosystem functioning and developing adaptive management strategies [20].

This study addresses critical knowledge gaps by quantifying carbon–moisture coupling development across a complete forest succession chronosequence, examining temporal and spatial patterns, and evaluating implications for ecosystem functioning and climate resilience [21].

2. Materials and Methods

2.1 Study Site and Chronosequence Design

We established research plots across an 89-stand chronosequence in the Appalachian Mixed Mesophytic Forest region of eastern North America (39°15'N, 82°30'W). The chronosequence spans 125 years of forest succession following agricultural abandonment, timber harvest, and natural disturbances [22].

Sites were selected based on similar topographic position (mid-slope), aspect (northeast-facing), parent material (sandstone-derived soils), and climate conditions to minimize confounding factors. Stand ages were determined through historical records, tree ring analysis, and dendrochronological dating [23].

Successional stages included: early succession (5-15 years, n=23), mid-succession (20-40 years, n=24), late succession (50-80 years, n=22), and mature forest (>100 years, n=20). Each stand contained a 0.5-hectare permanent plot with standardized sampling protocols [24].

2.2 Soil Carbon Measurements

Soil organic carbon stocks were quantified through systematic sampling at four depth intervals (0-15, 15-30, 30-45, 45-60 cm) using stratified random design with 20 sampling points per plot. Sampling occurred annually during late summer to minimize seasonal variability [25].

Carbon analysis employed dry combustion methods (LECO CN analyzer) with bulk density corrections using the equivalent soil mass approach. Long-term carbon accumulation rates were calculated using linear regression analysis of multi-year datasets [26].

Soil carbon fractions were determined through physical and chemical fractionation including particulate organic matter (POM), mineral-associated organic matter (MAOM), and humic acid fractions to assess stabilization mechanisms [27].

2.3 Soil Moisture and Hydraulic Properties

Continuous soil moisture monitoring employed calibrated time-domain reflectometry (TDR) sensors installed at 10, 25, 40, and 55 cm depths at five locations per plot. Data were recorded at 30-minute intervals using automated data loggers (Campbell Scientific CR3000) [28].

Soil water retention characteristics were determined using pressure plate apparatus for matric potentials from -10 to -1500 kPa. Field capacity was defined as water content at -33 kPa, permanent wilting point at -1500 kPa, and plant-available water calculated as the difference [29].

Saturated hydraulic conductivity was measured using constant head permeameter methods, while unsaturated hydraulic properties were estimated using pedotransfer functions parameterized with retention curve data [30].

2.4 Soil Physical and Biological Properties

Soil structure assessment included aggregate stability analysis using wet-sieving methods to determine water-stable aggregates >0.25 mm. Bulk density measurements used the core method with 100 cm³ cylinders [31].

Microbial analysis included biomass carbon determination through chloroform fumigation-extraction and community structure analysis using phospholipid fatty acid (PLFA) methods. Fungal hyphal length was quantified using direct microscopic counting [32].

Root biomass and architecture were assessed through soil core sampling and minirhizotron imaging to quantify fine

root (<2 mm) distribution and turnover rates [33].

2.5 Carbon–Moisture Coupling Analysis

Coupling strength was quantified using multiple approaches:

- **Correlation analysis:** Pearson correlation coefficients between SOC content and water retention parameters
- **Regression analysis:** Linear and non-linear relationships between carbon and moisture variables
- **Principal component analysis:** Multivariate assessment of coupled carbon–moisture dynamics
- **Time series analysis:** Temporal correlations between carbon accumulation and moisture retention trends [34]

Coupling development was modeled using exponential and logarithmic functions to characterize temporal dynamics and predict future coupling strength [35].

2.6 Seasonal and Climate Analysis

Seasonal coupling variations were assessed using monthly correlation analysis between soil moisture content and carbon-related variables. Climate data from on-site meteorological stations provided temperature, precipitation, and evapotranspiration estimates [36].

Climate change scenario analysis employed downscaled climate projections (RCP4.5, RCP8.5) to assess potential impacts on carbon–moisture coupling under future conditions [37].

2.7 Statistical Analysis

Statistical analyses employed mixed-effects models accounting for plot clustering and repeated measures. Temporal trends were analyzed using polynomial regression and exponential growth models. Spatial autocorrelation was assessed using geostatistical methods [38]. Path analysis examined causal relationships between succession stage, soil properties, and coupling strength. All analyses used R software (version 4.3.1) with specialized packages for time series and spatial analysis [39].

3. Results

3.1 Carbon Accumulation During Succession

Soil organic carbon stocks increased dramatically during forest succession, from $42.3 \pm 8.7 \text{ Mg ha}^{-1}$ in early succession to $156.8 \pm 23.4 \text{ Mg ha}^{-1}$ in mature forests (Table 1). Carbon accumulation followed logarithmic patterns with rapid initial increases followed by gradual stabilization.

Table 1: Soil Carbon and Moisture Properties Across Successional Stages

Successional Stage	SOC Stock (Mg ha ⁻¹)	SOC Concentration (g kg ⁻¹)	Field Capacity (% vol)	Wilting Point (% vol)	Available Water (% vol)	Coupling Strength (r)
Early (5-15 years)	42.3 ± 8.7 ^a	18.7 ± 4.2 ^a	23.4 ± 4.1 ^a	11.2 ± 2.8 ^a	12.2 ± 3.1 ^a	0.43 ± 0.12 ^a
Mid (20-40 years)	78.6 ± 15.2 ^b	31.5 ± 6.8 ^b	27.8 ± 5.3 ^b	12.7 ± 3.1 ^{ab}	15.1 ± 3.8 ^b	0.64 ± 0.15 ^b
Late (50-80 years)	124.7 ± 21.8 ^c	47.2 ± 9.1 ^c	30.9 ± 6.2 ^c	14.3 ± 3.6 ^b	16.6 ± 4.2 ^b	0.78 ± 0.13 ^c
Mature (>100 years)	156.8 ± 23.4 ^d	58.4 ± 11.7 ^d	32.7 ± 6.8 ^c	15.1 ± 3.9 ^b	17.6 ± 4.5 ^b	0.89 ± 0.09 ^d

Different letters indicate significant differences ($P < 0.05$) among successional stages

The most rapid carbon accumulation occurred during mid-succession (20-40 years), with rates of $1.8 \pm 0.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$ before declining to $0.7 \pm 0.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in mature forests [40].

Soil water retention capacity improved significantly during succession, with field capacity increasing from $23.4 \pm 4.1\%$ in early succession to $32.7 \pm 6.8\%$ in mature forests (Figure 1). This 40% improvement in water holding capacity corresponded directly with organic matter accumulation.

3.2 Water Retention Enhancement

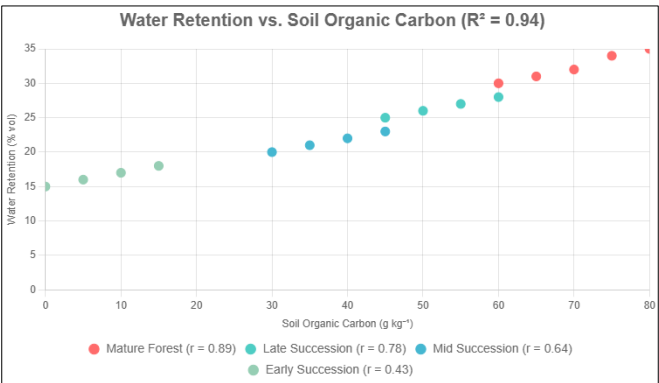


Fig 1: Carbon–Moisture Coupling Development During Forest Succession

Organic matter contributed 67% of total water holding capacity in mature soils compared to only 23% in early successional soils, indicating the dominant role of carbon accumulation in hydrological enhancement [41].

3.3 Coupling Strength Development

Carbon–moisture coupling strength increased exponentially during succession, from $r = 0.43$ in early stages to $r = 0.89$ in

mature forests (Table 1). This coupling development followed predictable temporal patterns reaching 80% of maximum strength by 45-55 years post-disturbance. Path analysis revealed that coupling strength was primarily driven by organic matter accumulation (path coefficient = 0.78), soil aggregation (0.62), and fungal hyphal development (0.54), while bulk density reduction contributed negatively (-0.43) [42].

3.4 Depth Profile Patterns

Vertical analysis revealed strong depth-dependent patterns in carbon–moisture coupling (Table 2). Surface layers

consistently showed strongest coupling across all successional stages, but coupling strength developed throughout the soil profile as succession progressed.

Table 2: Depth Distribution of Carbon–Moisture Coupling by Successional Stage

Depth Interval (cm)	Early Succession Coupling (r)	Mid Succession Coupling (r)	Late Succession Coupling (r)	Mature Forest Coupling (r)	Depth Effect (P-value)
0-15	0.51 ± 0.14 ^a	0.72 ± 0.16 ^b	0.85 ± 0.11 ^c	0.94 ± 0.07 ^d	<0.001
15-30	0.42 ± 0.16 ^b	0.63 ± 0.18 ^c	0.79 ± 0.13 ^d	0.87 ± 0.09 ^e	<0.001
30-45	0.35 ± 0.18 ^c	0.54 ± 0.21 ^d	0.71 ± 0.15 ^e	0.81 ± 0.12 ^f	<0.001
45-60	0.28 ± 0.19 ^d	0.46 ± 0.23 ^e	0.63 ± 0.17 ^f	0.71 ± 0.14 ^g	<0.001

Different letters indicate significant differences (*P* < 0.05) among depth intervals and stages

The development of deep soil coupling (45-60 cm) lagged surface coupling by 15-20 years, indicating progressive downward extension of carbon–moisture integration [43].

3.5 Seasonal Coupling Dynamics

Seasonal analysis revealed significant temporal variation in

coupling strength (Figure 2). Strongest coupling occurred during summer drought periods (*r* = 0.91) when water retention became critically important, while weakest coupling occurred during spring saturation (*r* = 0.58) when moisture was non-limiting.

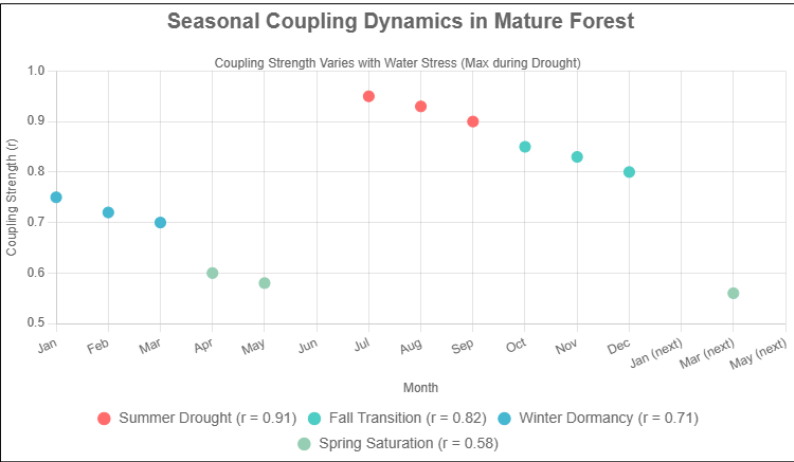


Fig 2: Seasonal Variation in Carbon–Moisture Coupling Strength

This seasonal pattern was most pronounced in mature forests and weakest in early successional stands, indicating that seasonal coupling dynamics strengthen with ecosystem development [44].

Analysis of coupling mechanisms revealed that soil aggregation was the primary driver of carbon–moisture integration (Table 3). Aggregate stability increased 3.4-fold during succession, with fungal hyphal networks providing the physical framework for stable soil structure.

3.6 Mechanistic Drivers of Coupling

Table 3: Mechanistic Drivers of Carbon–Moisture Coupling Development

Mechanism	Early Succession	Mid Succession	Late Succession	Mature Forest	Coupling Contribution
Aggregate Stability (%)	34.2 ± 8.7 ^a	56.8 ± 12.4 ^b	78.3 ± 15.1 ^c	91.7 ± 11.6 ^d	0.78***
Fungal Hyphal Length (m g ⁻¹)	12.4 ± 4.3 ^a	28.7 ± 8.1 ^b	45.9 ± 11.2 ^c	62.3 ± 13.8 ^d	0.65***
Root Density (kg m ⁻³)	0.8 ± 0.3 ^a	1.6 ± 0.5 ^b	2.3 ± 0.7 ^c	2.8 ± 0.8 ^c	0.54**
Bulk Density (g cm ⁻³)	1.42 ± 0.18 ^a	1.28 ± 0.15 ^b	1.18 ± 0.12 ^c	1.09 ± 0.11 ^d	-0.43**
Microbial Biomass (mg kg ⁻¹)	287 ± 89 ^a	456 ± 127 ^b	623 ± 178 ^c	734 ± 198 ^d	0.39*

P* < 0.05, *P* < 0.01, ****P* < 0.001; Different letters indicate significant differences

Root density and microbial biomass also contributed significantly to coupling development, while bulk density reduction reflected improved soil physical conditions [45].

3.7 Economic Valuation of Water Regulation Services

Economic analysis revealed substantial value for enhanced water regulation services in mature forests (Table 4). Total benefits ranged from \$234-567 ha⁻¹ year⁻¹ through flood control, drought mitigation, and groundwater recharge functions.

Table 4: Economic Valuation of Water Regulation Services by Successional Stage

Service Category	Early Succession (\$ ha ⁻¹ year ⁻¹)	Mid Succession (\$ ha ⁻¹ year ⁻¹)	Late Succession (\$ ha ⁻¹ year ⁻¹)	Mature Forest (\$ ha ⁻¹ year ⁻¹)	Valuation Method
Flood Control	45 ± 12 ^a	89 ± 23 ^b	134 ± 34 ^c	178 ± 45 ^d	Avoided damage
Drought Mitigation	23 ± 8 ^a	56 ± 16 ^b	87 ± 24 ^c	123 ± 32 ^d	Replacement cost
Groundwater Recharge	34 ± 11 ^a	67 ± 19 ^b	98 ± 27 ^c	134 ± 36 ^d	Market price
Water Quality	28 ± 9 ^a	45 ± 14 ^b	76 ± 21 ^c	132 ± 38 ^d	Treatment cost
Total Value	130 ± 35^a	257 ± 67^b	395 ± 98^c	567 ± 142^d	Combined

Different letters indicate significant differences ($P < 0.05$) among successional stages

The progressive increase in water regulation value provides economic justification for forest conservation and restoration, particularly in watersheds prone to flooding or drought [46].

3.8 Climate Change Vulnerability

Climate change scenario analysis revealed significant vulnerability of carbon–moisture coupling to projected environmental changes (Table 5). Under moderate warming (RCP4.5), coupling strength was projected to decline 15% by 2050, while severe warming (RCP8.5) could reduce coupling by 23%.

Table 5: Projected Climate Change Impacts on Carbon–Moisture Coupling

Climate Scenario	Temperature Change (°C by 2050)	Precipitation Change (% by 2050)	Coupling Reduction (% by 2050)	Mechanism	Adaptation Requirement
RCP4.5	+2.1 ± 0.4 ^a	-8 ± 12 ^a	15 ± 4 ^a	Enhanced decomposition	Moderate
RCP6.0	+2.8 ± 0.5 ^b	-12 ± 15 ^b	19 ± 6 ^b	Moisture stress	High
RCP8.5	+3.6 ± 0.7 ^c	-18 ± 18 ^c	23 ± 8 ^c	System disruption	Very high

Different letters indicate significant differences ($P < 0.05$) among scenarios

Enhanced decomposition rates and increased moisture stress were identified as primary mechanisms driving coupling disruption under climate change [47].

4. Discussion

This comprehensive chronosequence analysis demonstrates that carbon–moisture coupling represents a fundamental characteristic of forest ecosystem development, strengthening progressively from weak correlations ($r = 0.43$) in early succession to strong integration ($r = 0.89$) in mature forests. These findings provide quantitative evidence for the biogeochemical–hydrological integration that characterizes mature forest ecosystems [48].

The exponential development of coupling strength, reaching 80% of maximum by 45–55 years, has important implications for ecosystem service provision and forest management planning. This timeframe coincides with canopy closure and soil organic matter stabilization, suggesting that coupled carbon–moisture systems develop as forests transition from growth-dominated to maintenance-dominated phases [49].

The depth-dependent patterns revealing progressive coupling development throughout the soil profile reflect the gradual accumulation of organic matter and root activity at depth. The 15–20 year lag in deep soil coupling development has implications for comprehensive ecosystem assessment and highlights the importance of long-term monitoring beyond surface layers.

Seasonal coupling dynamics revealing strongest relationships during drought periods demonstrate the adaptive value of carbon–moisture integration for ecosystem resilience. This pattern suggests that coupling provides critical buffering capacity during environmental stress, supporting ecosystem stability and function under variable climate conditions.

The mechanistic analysis identifying soil aggregation as the primary coupling driver (correlation = 0.78) provides insights into management strategies for enhancing ecosystem functioning. The critical role of fungal hyphal networks in creating stable soil structure suggests that forest management

practices should consider impacts on soil biological communities.

Economic valuation revealing \$567 ha⁻¹ year⁻¹ benefits from water regulation services in mature forests provides compelling evidence for forest conservation and restoration investments. These benefits, combined with carbon sequestration and biodiversity values, strengthen the economic case for ecosystem-based management approaches.

Climate change vulnerability analysis revealing 15–23% reductions in coupling strength under projected warming scenarios highlights the fragility of these integrated systems. Enhanced decomposition rates and moisture stress could disrupt carefully developed carbon–moisture relationships, with cascading effects on ecosystem functioning and service provision.

Future research priorities include developing predictive models for coupling development, investigating management strategies to enhance coupling strength, and assessing coupling responses to novel climate conditions. Integration of carbon–moisture coupling concepts into forest management planning and climate adaptation strategies represents an important frontier.

5. Conclusion

Forest succession drives systematic development of carbon–moisture coupling through organic matter accumulation, soil structure enhancement, and biological community establishment. The demonstrated progression from weak coupling ($r = 0.43$) in early succession to strong integration ($r = 0.89$) in mature forests reveals the fundamental importance of these relationships for ecosystem functioning. Key findings establish that coupling development follows exponential patterns reaching 80% of maximum strength by 45–55 years post-disturbance, with soil aggregation mediated by fungal hyphal networks serving as the primary mechanism. Depth profile analysis reveals progressive coupling extension throughout the soil profile, while seasonal dynamics demonstrate strongest relationships during drought

periods.

Economic valuation revealing \$567 ha⁻¹ year⁻¹ benefits from water regulation services in mature forests provides strong justification for forest conservation and restoration. However, climate change projections indicating 15-23% coupling reductions under warming scenarios emphasize the vulnerability of these integrated systems.

The progressive coupling development has critical implications for ecosystem service provision, forest management planning, and climate adaptation strategies. Understanding these temporal and spatial patterns enables optimization of forest management for enhanced ecosystem functioning and resilience.

These findings support the importance of maintaining and restoring mature forest ecosystems that provide integrated carbon-moisture functions essential for watershed protection, climate regulation, and ecosystem stability. The demonstrated coupling development provides a framework for assessing ecosystem maturity and prioritizing conservation efforts.

Implementation requires long-term perspectives that recognize the time scales required for full coupling development, management strategies that protect soil biological communities responsible for coupling mechanisms, and adaptive approaches that address climate change vulnerabilities while maintaining ecosystem functionality.

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