



Long-term field study of the influence of the photosynthetic performance of temperate grassland species on ecosystem CO₂ exchange fluxes at the ecosystem-scale

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- Under environmental constraints, plants are able to proceed to adjustment in their photosynthetic processes to promote acclimation. However, it is currently unclear how alteration in the functioning of the photosystem II and the photosystem I influences CO₂ gas exchange at the ecosystem-scale.
- During two years, frequent measurements of chlorophyll *a* fluorescence (ChlF) in field condition were performed on the three main species of a temperate grassland ecosystem (*Lolium perenne L., Taraxacum* sp. and *Trifolium repens L.*). ChlF data were analyzed with the JIP-test to characterize the photosynthetic performance and its response to combined environmental constraints. Species responses were weighed based on their relative abundance to estimate the photosynthetic performance of the ecosystem. In addition, monitoring of CO₂ fluxes was performed by eddy covariance. ChlF data were analyzed along with CO₂ fluxes to determine the impact of alteration in the ecosystem photosynthetic performance on CO₂ ecosystem exchange.

Chlorophyll fluorescence parameters description

F_V/F_M Maximum quantum yield of the PSII

PI_{ABS} Performance Index : representation of the energy conversation from photons absorbed by PSII to the reduction of intersystem electron acceptors

 $u_{\rm E0}$ Efficiency of the electron transport beyond ${
m Q_A}$

 ΔV_{IP} Efficiency with which an PSII trapped electron is transferred beyond the PSI acceptor side

(Strasser R et al. 2000. In: Yunnus M, Pathre U and Mohanty P (eds) Probing photosynthesis: mechanism, regulation and adaptation. Taylor and Francis, London, 445–483; Oukarroum A et al. 2009. Physiologia Plantarum 137: 188–99.)

I. Evolution of photosynthetic processes mesured by ChIF and micro-meteorological conditions in the field

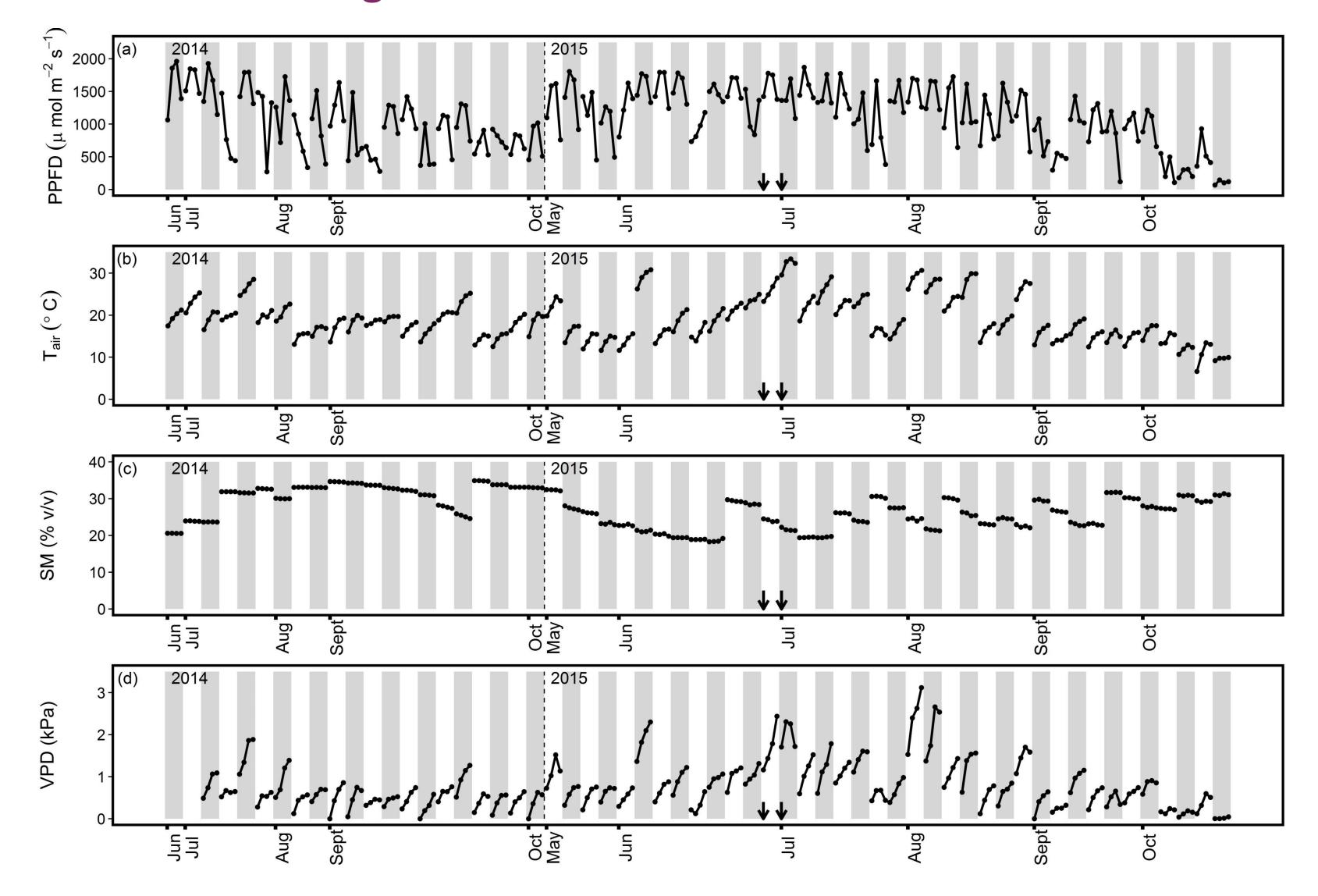


Figure 1. Environmental conditions encountered in the 2014 and 2015 study periods. Values at 11, 13, 15 and 17 h for each day of ChlF measurements are represented for (a) PPFD, photosynthetic photon flux density; (b) T_{air,} air temperature; (c) SM, soil moisture at a depth of 5 cm and (d) VPD, vapour pressure deficit. Grey bars separate the different days of measurements. The arrows indicate the first and third day of the heat wave

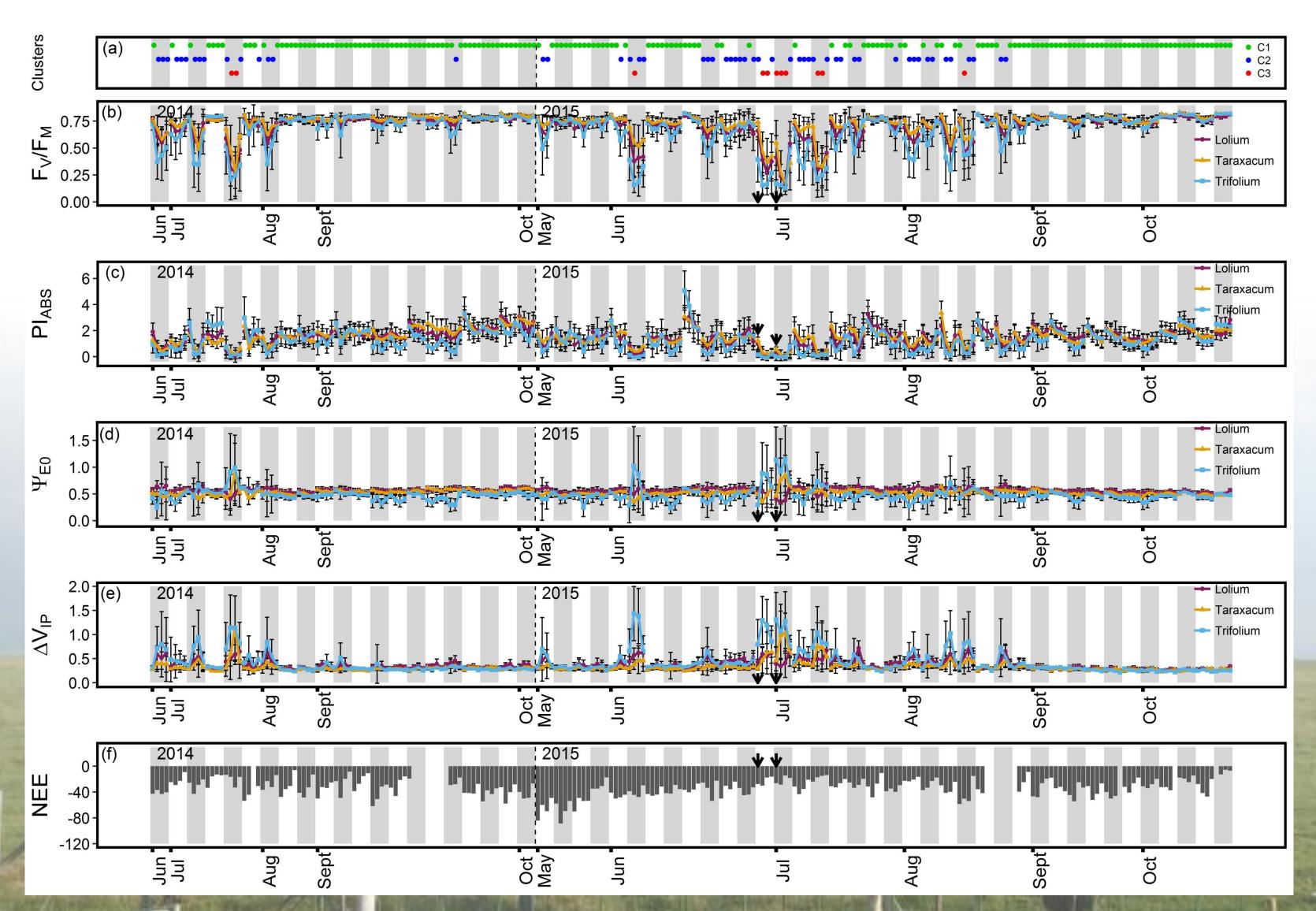
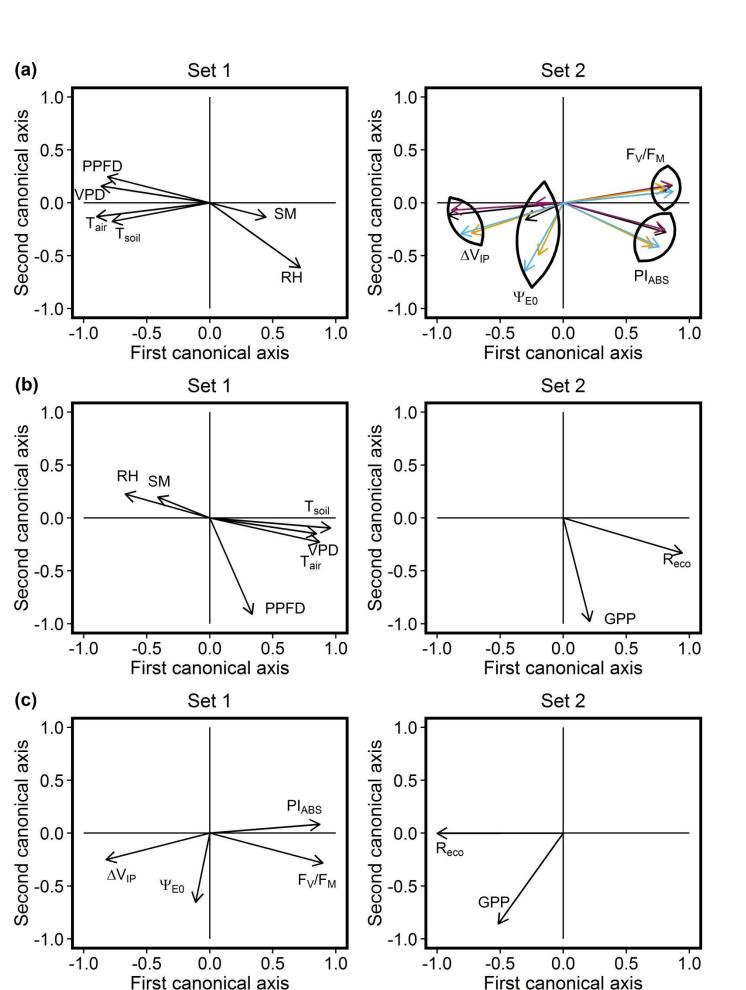


Figure 2. Variation of ChIF parameters \pm SD and net CO₂ ecosystem exchange (NEE) in the 2014 and 2015 study periods. The average value (n = 21-24) \pm SD for each of the four measurement time periods (11:00, 13:00, 15:00 and 17:00) is represented. The top plot indicates to which ChIF cluster (green, C1; dark blue, C2; red, C3) has been assigned each time period by the principal component analysis-clustering. Grey bars separate the

different days of measurements. Arrows indicate the first and the third day of a heat wave.

II. Relationship between micro-meteorological conditions, photosynthetic performance and CO₂ fluxes.



- ChIF parameters exhibited a diurnal behavior similar to that of PPFD (Fig. 1,2).
- Three clusters of contrasted ecosystem photosynthetic performance (C1, C2 and C3) were defined by principal component analysis-clustering with lowest photosynthetic performance (C2 and C3) observed in summer (Fig. 2).
- Summer conditions were associated with low photosynthetic performance in the grassland (low PI_{ABS} and F_V/F_M) due to the combination of environmental constraints (high PPFD, VPD, T_{air} and low SM) (Fig. 3a).
- The three grassland species exhibited comparable response in their photosynthetic processes to combined environmental constraints, with the exception of electron transport beyond Q_A (ψ_{E0}) for *L. perenne* (Fig. 3a).
- Low summer Pl_{ABS} values indicate an increase in energy dissipation (e.g., through silent reaction centres).
- Decrease in F_V/F_M during stressful conditions indicates a transient decrease in PSII efficiency.
- Increase of ΔV_{IP} in summer condition indicates an increase in **the photosystem I efficiency** and suggets the onset of **photochemical deexcitation.**
- Environmental conditions had a low influence on electron transport efficiency beyond QA (ψ_{E0}).
- R_{eco} increased with temperate while GPP increased with PPFD (Fig. 3b).
- Low photosynthetic performance was associated with elevated GPP and R_{eco} fluxes but ChIF parameters were less correlated to GPP and R_{eco} fluxes than environmental parameters (Fig. 3c).

Figure 3. Canonical correlation analysis showing the relationships between **(a)** micro-meteorological parameters (PPFD, photosynthetic photon flux density; VPD, vapour pressure deficit; T_{air} , air temperature; T_{soil} , soil temperature. RH, relative air humidity; SM, soil moisture) and ChIF parameters (purple, *L. perenne*; orange, *Taraxacum* sp., orange; light blue, *T. repens*; black, ecosystem). Correlations between the first canonical axis of the two CCA plot were 88.6% (P < 0.001) and 60.5% (P < 0.001) respectively. **(b)** micro-meteorological parameters and CO_2 fluxes (GPP, gross primary productivity; R_{eco} , ecosystem respiration). Correlations between the first canonical axis of the two CCA plots and between the second canonical axis of the two CCA plot were 78.8% (P < 0.001) and 54.7% (P < 0.001) respectively. **(c)** ChIF parameters and CO_2 fluxes. Correlations between the first canonical axis of the two CCA plots and between the second canonical axis of the two CCA plot were 72.4% (P < 0.001) and 15.6% (P > 0.005) respectively.

III. Alteration in photosynthetic performance has a negligible impact on carbon uptake at the ecosystem-scale

- Variations of photosynthetic processes such as electron transport within the PSII, the inter-system and the PSI did not impact the capacity of the ecosystem to fix carbon at light saturation (Fig. 4a,b,c).
- Alterations of photo processes did not influence R_{10} fluxes in the grassland (Fig. 4b,c,d).
- Changes in ecosystem photosynthetic performance did not have a significant impact on the **NEE** (Fig. 5a).
- Higher GPP fluxes were recorded at low photosynthetic performance, probably due to higher PPFD registered in these conditions (Fig. 5b).
- GPP at light saturation was not influenced by decrease in the photosynthetic performance, suggesting that the capacity of the grassland to fix carbon was not impaired in these conditions (Fig. 5c).
- Higher R_{eco} fluxes were recorded during episodes of low photosynthetic performance, probably due to high temperature in these conditions. Both soil and aboveground vegetation might have contributed to R_{eco} increase (Fig. 5d).
- R_{10} was not influenced by alterations in ecosystem photosynthetic performance, confirming the influence of temperature in R_{eco} increase (Fig. 5e).

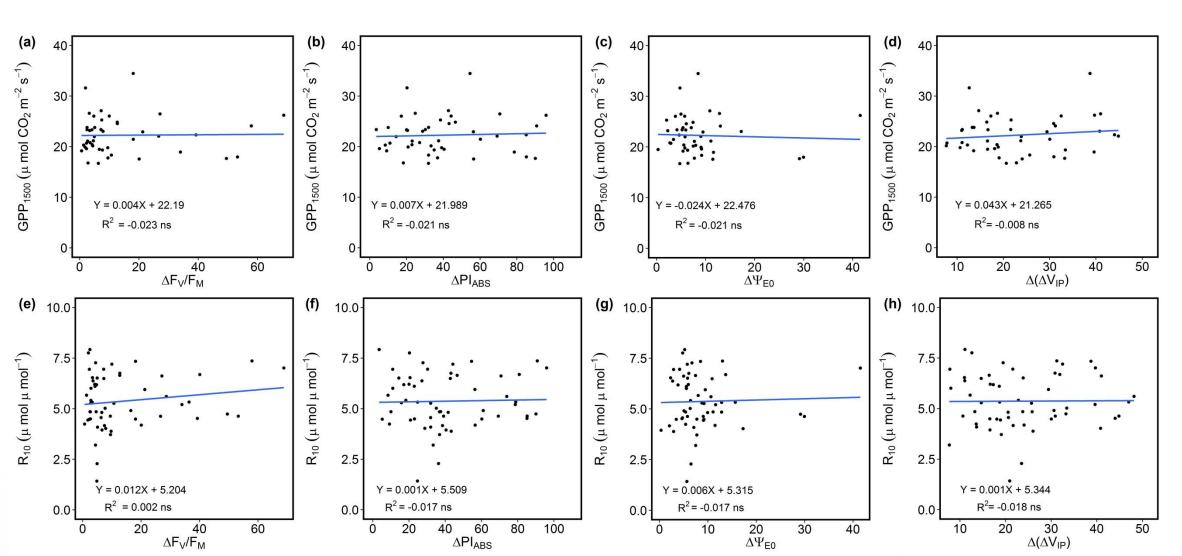


Figure 4. Linear regression between **(a)** GPP₁₅₀₀, gross primary productivity at light saturation and the daily variation of ecosystem ChIF parameters ($\Delta F_V/F_M$, PI_{ABS}, ψ_{E0} and ΔV_{IP}) and **(b)** R₁₀, dark respiration normalized at 10°C and the daily variation of ecosystem ChIF parameters.

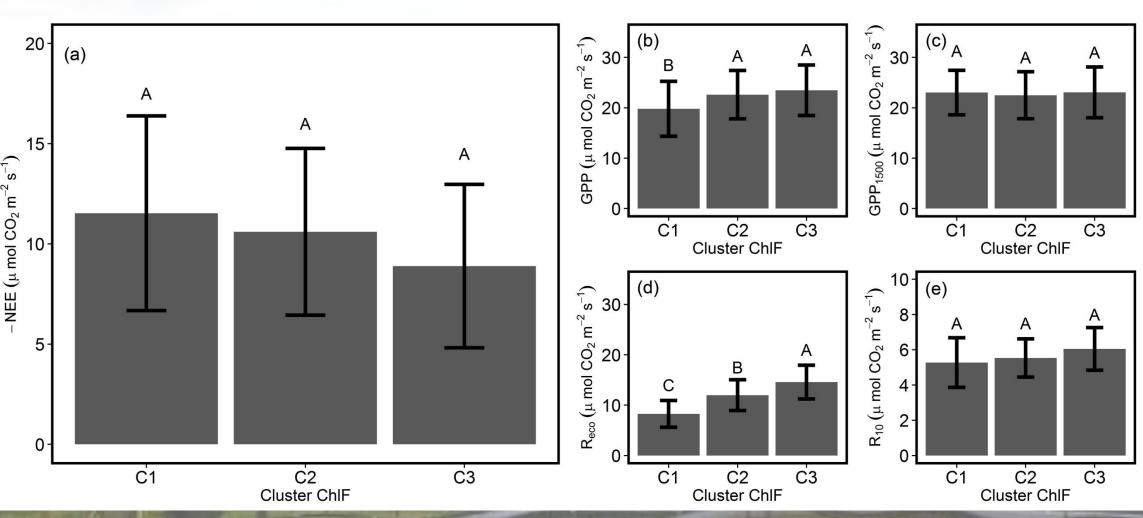


Figure 5. Average \pm SD (a) NEE, net CO2 exchange ecosystem; (b) GPP, gross primary productivity; (c), GPP₁₅₀₀, GPP at light saturation; (d) R_{eco}, respiration of the ecosystem and (e) R₁₀, dark respiration normalized at 10°C at contrasting photosynthetic performance responses (ChIF clusters C1, C2 and C3 defined by principal component analysis-clustering). Different letters indicate significant differences among the clusters (Tukey HSD, α = 0.05).

