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Belowground Bud Banks and Land Use Change: Roles of Vegetation and Soil Properties in Mediating the Composition of Bud Banks in Different Ecosystems

Jing Wu
Taizhou University

Xianzhang Hou
Taizhou University

Lan Xu
South Dakota State University

Quanlai Zhou
Chinese Academy of Sciences

Yongcui Wang
Chinese Academy of Sciences

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Authors

Jing Wu, Xianzhang Hou, Lan Xu, Quanlai Zhou, Yongcui Wang, Ziwu Guo, Michael Opoku Adomako, and Qun Ma



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EDITED BY

Fang-Li Luo,
Beijing Forestry University, China

REVIEWED BY

Xiao Guo,
Qingdao Agricultural University, China
Jinlei Zhu,
Chinese Academy of Forestry, China

*CORRESPONDENCE

Michael Opoku Adomako
✉ moadamako@gmail.com
Qun Ma
✉ qunzilg@163.com

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Belowground bud banks and land use change: roles of vegetation and soil properties in mediating the composition of bud banks in different ecosystems

Jing Wu ¹, Xianzhang Hou¹, Lan Xu², Quanlai Zhou³, Yongcui Wang³, Ziwu Guo⁴, Michael Opoku Adomako ^{1,5*} and Qun Ma^{3*}

¹Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, School of Life Sciences, Taizhou University, Taizhou, China, ²Department of Natural Resource Management, South Dakota State University, Brookings, SD, United States, ³Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China, ⁴Research Institute of Subtropical Forestry, Chinese Academy of Forestry, Hanzhou, China, ⁵Institute of Wetland Ecology and Clone Ecology, Taizhou University, Taizhou, China

Introduction: Belowground bud banks play integral roles in vegetation regeneration and ecological succession of plant communities; however, human-caused changes in land use severely threaten their resilience and regrowth. Although vegetation attributes and soil properties mediate such anthropogenic effects, their influence on bud bank size and composition and its regulatory mechanisms under land use change have not been explored.

Methods: We conducted a field investigation to examine impacts of land use change on bud bank size and composition, vegetation attributes, and soil properties in wetlands (WL), farmlands (FL), and alpine meadow (AM) ecosystems in Zhejiang Province, China.

Results: Overall, 63 soil samples in close proximity to the vegetation quadrats were excavated using a shovel, and samples of the excavated soil were placed in plastic bags for onward laboratory soil analysis. The total bud density (1514.727 ± 296.666) and tiller bud density (1229.090 ± 279.002) in wetland ecosystems were significantly higher than in farmland and alpine meadow ecosystems [i.e., total (149.333 ± 21.490 and 573.647 ± 91.518) and tiller bud density (24.666 ± 8.504 and 204.235 ± 50.550), respectively]. While vegetation attributes critically affected bud banks in WL ecosystems, soil properties strongly influenced bud banks in farmland and alpine meadow ecosystems. In wetland ecosystems, total and tiller buds were predominantly dependent on soil properties, but vegetation density played a significant role in farmlands and alpine meadow ecosystems. Root sprouting and rhizome buds significantly correlated with total C in the top 0 – 10 cm layer of

farmland and alpine meadow ecosystems, respectively, and depended mainly on soil properties.

Discussion: Our results demonstrate that land use change alters bud bank size and composition; however, such responses differed among bud types in wetland, farmland, and alpine meadow ecosystems.

KEYWORDS

bud density, clonal organs, land use change, storage organs, vegetation density

Introduction

Human-derived modifications of terrestrial ecosystems, including land use changes, underlie the altered belowground bud bank densities, vegetation regeneration, and ecological succession, leading to global biodiversity loss and ecosystem services (Allan et al., 2015; Newbold et al., 2015; Chang and Turner, 2019; Winkler et al., 2021; Simkin et al., 2022). Agricultural activities (e.g., pesticides and herbicide application) and expansion of arable croplands have predominantly shifted many crucial attributes of the natural vegetation (Zhao et al., 2023), with substantial implications on belowground bud banks (storage organs e.g., rhizomes, corm, and ramets) that are vital for vegetation regrowth, aboveground recruitment, productivity (Li et al., 2018; Qian et al., 2021; Hou et al., 2022). Although expanding the arable cropland greatly affects many plant species and bud banks, their responses may differ across ecosystems due to differences in the vegetation cover and soil characteristics that support plant growth (Newbold et al., 2015; Semenchuk et al., 2022). Likewise, the land use intensity and impacts on belowground bud banks may also differ between such ecosystems. Despite these differential responses to land use change, the role of vegetation and soil attributes in mediating bud bank responses in different ecosystems has not been explored. In light of the ongoing environmental change on a worldwide scale, it is imperative to comprehend the role of vegetation and soil characteristics to develop appropriate management techniques that will increase their ecological relevance.

Soil characteristics (e.g., moisture, nutrients, and particle sizes) constitute an essential component driving the structure and vegetation cover, as well as nutrient availability of terrestrial ecosystems (Wu et al., 2020; Adomako et al., 2021; Inoue et al., 2022), and play critical roles in regeneration, growth, and productivity of plants (Zuo et al., 2009; Hoover et al., 2014). Soil properties are important ecological parameters that determine the magnitude, distribution pattern, and vegetation succession, which are a function of soil aggregate particles, belowground bud bank density, and resprouting ability (Clarke et al., 2013; Wu et al., 2020). For example, in a soil substrate heterogeneity study, Adomako et al. (2021) reported that a ceramsite-quartz mixture with larger aggregate particle sizes significantly decreased ramets growth of *Leymus*

chinensis compared to plants grown in field soil with relatively smaller particle sizes, as the former substrates have greater mechanical resistance to seed or vegetative sprouting than the latter substrates (Semchenko et al., 2008). Moreover, higher clay and low nutrient content in wetland soils may decrease resprouting and growth of tiller buds than resprouting and growth of tillers in farmlands and alpine meadows (Reddy et al., 2013; Mobilian and Craft, 2021). The soil physicochemical properties strongly influence the aboveground vegetation recruitment from seeds or belowground bud banks (Adomako et al., 2021; Inoue et al., 2022; Wu and Yu, 2022). Such driving force underpins aboveground vegetation recruitment dynamics, vegetation density, and productivity of plant species in natural ecosystems (Peng et al., 2015; Adomako et al., 2021). However, information regarding interaction effects of land use change and soil characteristics on bud banks across varying ecosystem types is limited in our current understanding.

In natural systems, belowground bud banks play a pivotal role in maintaining plant biodiversity against anthropogenic and natural disturbances, such as farming and climate change (Plue and Cousins, 2018; Ott et al., 2019). Particularly in vegetations dominated by perennial species, belowground bud banks serve as ecological insurance against short- and long-term disturbances such as drought, wildfire, and grazing (Deng et al., 2014; Hoover et al., 2014; Ott et al., 2019). Although long-term effects of some ecological perturbations can adversely affect bud bank density (VanderWeide and Hartnett, 2015; Qian et al., 2023), they may likely differ between ecosystems owing to differences in vegetation cover, species composition, and soil characteristics. These differential responses of bud banks across varying ecosystems may explain variations in resilience and resprouting capacity after disturbances (Xu et al., 2021). For instance, plants adapted to grow in drier conditions (i.e., alpine meadow in our study) showed strong resistance to chronic drought stress compared to wetland plants growing under the same stressful condition (Luo et al., 2023; Ren et al., 2023). Likewise, the abundance and density of belowground organs (e.g., rhizomes and tillers) of species may also differ in their responses to disturbance in their respective ecosystems (Xu et al., 2021; Qian et al., 2022; Klimešová et al., 2023). Despite the critical roles of belowground bud banks to plant community stability and productivity, how vegetation and soil characteristics mediate their responses to land-use changes are poorly understood.

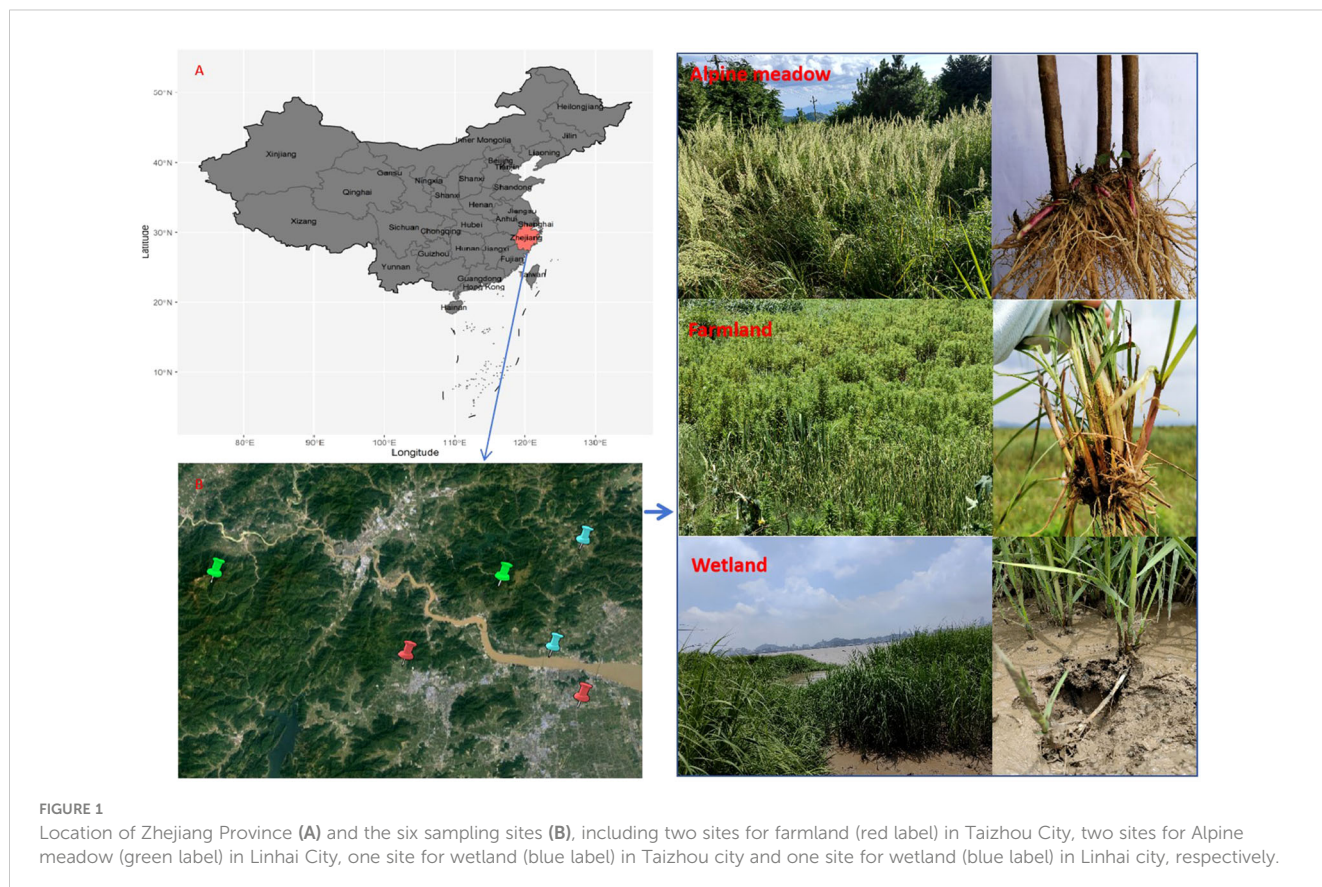
Bud types (e.g., rhizome, tiller, and root sprouting buds) play different functional roles and determine diverse adaptive strategies under variable ecosystems (Zhang et al., 2019). Belowground bud banks are widely sourced from rhizome and tiller buds (Zhang et al., 2009; Ott and Hartnett, 2015). In addition to adventitious root buds, tiller buds derived from the base of the parent shoots for hemicryptophyte, rhizome buds, and root sprouting buds mainly initiate from underground roots and rhizomes for geophyte. Previous studies reported that tiller buds are more closely related to vegetation attributes, while rhizome and root sprouting buds are sensitive to water or nutrient concentrations in surrounding habitats (Passioura, 1988). However, how vegetation attributes and soil properties interact to determine the responses of different bud bank types under the ongoing land use changes is unknown.

To explore the changes in bud bank size and composition and its regulatory mechanism under land use change, we selected two plots in Linhai and Taizhou sampling sites for wetlands (WL), farmlands (FL), and alpine meadows (AM), respectively. We took 63 sampling points in total for the bud demographic. We also measured biotic (vegetation density, aboveground biomass, and Shannon-Weiner diversity index) and abiotic parameters (soil moisture content, total carbon (C), and total N) relevant to the bud bank density for different plant functional groups. Specifically, we aim to explore (1) changes in/patterns of the bud bank traits among different land use types and (2) the role of vegetation attributes and soil properties in determining bud demographic and bud densities of different bud bank types under land use change.

Materials and methods

Study sites

The study was conducted in Linhai and Taizhou City (120°17'–121°56'E, 28°01'–29°20'N), southeastern Zhejiang Province, China (Figure 1A). In response to rapid modern development and urbanization of China, Linhai and Taizhou Cities located along the coast are undergoing massive expansion of industries and settlement, cascading potential impacts on its vegetation structure and succession. Therefore, we conducted this field study to examine how the rapid land use change may influence belowground bud banks to highlight the long-term effects on vegetation structure and dynamics in this area and beyond. The region has a typical subtropical monsoon climate with moderate annual temperatures, abundant sunshine, and precipitation; thus, the growing season lasts from late April to late September before the yearly winter commences. The landscape consists of a mosaic of forests, arable lands, and wetlands. Six sample sites in total were selected in Linhai and Taizhou City: two alpine meadows sites located in Kuocang Mountain and Lantian Mountain, two farmland sites located next to residential quarters at the foot of mountain, and two wetland sites situated next to Xiaozhi reservoir and Jiaojiang river, respectively (Figure 1B). The dominant vegetation at the wetland site comprises *Phragmites communis*, *Arundo donax*, *Imperata cylindrica*, *Solidago canadensis*, and other herbaceous plants. Some perennial and annual herbs, such as *Juncus effusus*, *Imperata cylindrica*,



Lysimachia fortune, and *Rubus phoenicolicosius*, dominate the alpine meadows' vegetation. The vegetation in WL, FL, and AM ecosystems experience the same climatic conditions, i.e., similar rainfall patterns, temperature, and humidity.

Field observations and bud bank sampling

In August 2022, we selected two plots for WL, FL, and AM in each sampling site and established transects 10 m apart between each chosen plot. In each plot, 22 sampling points were selected for wetlands, 24 for farmlands, and 17 for alpine meadows, making 63 sampling points in total. In each sampling point, 1 × 1 m quadrats were established to record the vegetation composition, identify all species within each community, and record the number of each species identified and their abundance, as well as their average height and plant density. With grasses and sedges, we counted and recorded the number of ramets (e.g., *Phragmites communis*) and calculated the number of individuals for discrete species. We used the number of all ramets/individuals/m² in all quadrats to estimate the vegetation density. Additionally, we sampled soils between the top 0–10 cm to measure soil water and nutrient content from each ecosystem using a ring cutter and soil drill with a diameter of 7 cm.

We dug 25 × 25 × 25 cm quadrats in each vegetation quadrant to record the belowground bud bank composition at each sampling point, totaling 63 quadrats in the three ecosystems. All samples were processed within two weeks, and no rotting was observed during this period. Only turgid bud tissue was counted, and tissues with necrotic signs or visibly dead tissues were discarded. We defined three types of bud banks according to the morphological characteristics of bud-bearing organs: rhizome buds (axillary buds and apical buds on hypogeous rhizomes), tiller buds (axillary buds at the shoot bases of caespitose species and rhizomatous grasses); and root-sprouting bud (adventitious bud formed mainly endogenously on roots of forb or shrub). In contrast to counting buds directly on rhizomes, stems, and roots, dissecting those at the base of shoots was necessary to estimate the number of tillers and root buds.

Biomass and diversity calculation

The aboveground biomass per quadrat was measured by clipping the plants at ground level. The respective biomass was dried at 70°C to constant weight. We measured species diversity indices for each quadrat using the following equations (Li et al., 2014):

$$\text{Importance value (IV)} = (\text{relative height} + \text{relative density})/2$$

$$\text{Shannon – Wiener Index (H)} = - \sum (P_i \ln P_i)$$

P_i is the relative importance value of the i_{th} species in the community.

Data analysis

The original dataset of bud densities was converted into numbers of buds per square meter. The average bud density of

each sampling position was then calculated for further analysis. One-way ANOVA was applied to analyze differences in belowground bud bank density, vegetation characteristics (vegetation density, aboveground biomass, and Shannon-Weiner diversity index), and soil properties (soil water content, total C, total N) among WL, FL, and AM ecosystems. One-way ANOVA and Tukey's honestly significant difference *post hoc* test were performed using SPSS 18.0 (SPSS Inc., USA). Redundancy Analysis (RDA) was used to examine the correlations between belowground bud bank and aboveground vegetation, soil, and properties in the WL, FL, and AM ecosystems. Aboveground vegetation information included vegetation density, Shannon-Weiner diversity index, and aboveground biomass, soil properties embraced soil water content of 0–10 cm layer, total C of 0–10 cm layer, and total N of 0–10 cm layer. The original data was log-transformed and normalized before RDA. Some environmental factors were deleted by Monte Carlo selection under $P < 0.05$. We selected variables with high canonical loading factors, confirmed by a cutoff value of 0.35, and parameters highly correlated with canonical variables detected by high standardized coefficients ($r > 0.4$). RDA was performed using CANOCO v. 4.5.

Results

Change in bud bank traits among different land use types

We found rhizome, tiller, and root sprouting buds in WL, FL, and AM ecosystems; however, land use change affected the bud bank structure, with tiller buds accounting for the majority (81.14%) of total buds in WL ecosystems and sprouting buds (60.93%) showed dominance in FL ecosystems. In contrast, rhizome buds accounted for the highest proportion in the AM ecosystem (Figure 2). Bud bank density and soil properties differed significantly among WL, FL, and AM ecosystems (Table 1). The total bud density (1514.727 ± 296.666) and tiller bud density (1229.090 ± 279.002) in WL were significantly higher than that in FL and AM ($P < 0.01$, Figure 3). Additionally, rhizome bud density (220.235 ± 53.516) and root sprouting bud density (149.294 ± 46.496) in AM were significantly higher than that in WL and FL ($P < 0.01$; Figure 3). The bud densities of all bud types showed relatively lower in FL ecosystems compared WL and AM. The soil moisture content at the 0–10 cm layers in WL was significantly higher than that in FL and AM, while total C at the 0–10 cm layers and total N at 0–10 cm layers in AM were markedly higher than that in WL and FL ($P < 0.05$; Table 1).

Effects of vegetation attributes and soil properties on bud banks

In WL ecosystems, all factors combined explained 83.2% of the total variation in bud banks. The soil water content at the 0–10 cm layer, vegetation density, and aboveground biomass were significantly correlated with bud banks ($P < 0.05$). Vegetation density was the most

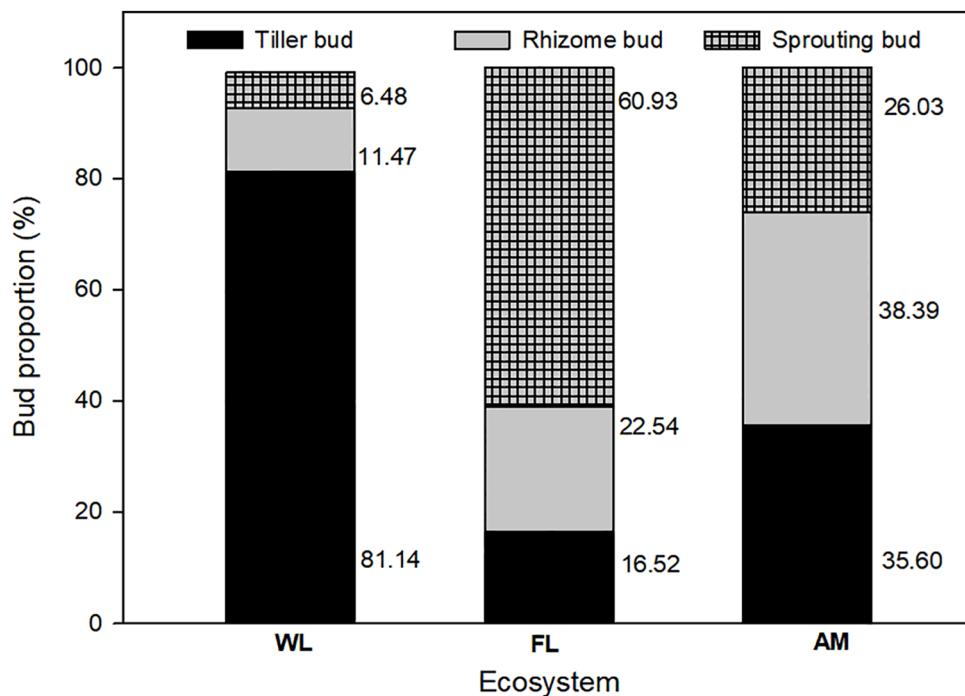


FIGURE 2 Percentage of belowground bud bank density of different bud types in wetland (WL), farmland (FL), and Alpine meadow (AM) ecosystems.

critical factor affecting bud banks, explaining 62.2% of the variation of bud banks. Moreover, soil water content at the 0 – 10 cm layer explained 11.9% of the variation of bud banks, whereas the total C at the 0 – 10 cm layer, total N at the 0 – 10 cm layer, and plant diversity had no significant effect on bud banks. The contribution of vegetation attributes and soil properties to the variation in bud bank were 59.1%, 84.5%, and 15.5%, respectively (Table 2; Figure 4).

All factors in the FL ecosystem explained 35.1% of the total variation in the bud bank. The total N at the 0 – 10 cm layer was significantly correlated with the bud bank ($P < 0.05$), and it was the decisive factor in affecting the bud bank, explaining 12.6% of the variation of the bud bank. The contribution of vegetation attributes and soil properties to the variation in bud bank was 31.5% and 68.5%, respectively (Table 2; Figure 5).

TABLE 1 One-way ANOVA of soil characteristics, vegetation characteristics, and bud bank density of different bud types in wetland (WL), farmland (FL), and Alpine meadow (AM) ecosystems.

Soil characteristics	FL	WL	AM	F	P
Soil moisture content (0 – 10cm) (%)	15.458 ± 1.442	36.529 ± 2.764	35.899 ± 2.907	27.634	.000
Total carbon (0 – 10cm) (g/kg)	1.634 ± 0.123	1.605 ± 0.051	3.252 ± 0.351	22.928	.000
Total nitrogen (0 – 10cm) (g/kg)	0.223 ± 0.043	0.159 ± 0.006	0.304 ± 0.028	4.622	.014
Vegetation characteristics	FL	WL	AM	F	P
Vegetation density (No./m ²)	407.000 ± 32.157	943.272 ± 151.363	544.941 ± 32.335	9.114	.000
Shannon-Weiner diversity index	1.234 ± 0.080	0.894 ± 0.118	1.055 ± 0.031	3.863	.026
Aboveground biomass (g)	123.371 ± 9.591	218.081 ± 57.535	93.882 ± 8.887	3.229	.047
Bud density	FL	WL	AM	F	P
Total bud (No./m ²)	149.333 ± 21.490	1514.727 ± 296.666	573.647 ± 91.518	15.313	.000
Rhizome bud (No./m ²)	33.666 ± 10.959	173.818 ± 53.100	220.235 ± 53.516	5.626	.006
Tiller bud (No./m ²)	24.666 ± 8.504	1229.090 ± 279.002	204.235 ± 50.550	15.207	.000
Root sprouting bud (No./m ²)	91.000 ± 19.091	98.181 ± 58.992	149.294 ± 46.496	0.475	.642

The samples were 22 for AM, 24 for WL, and 17 for FL ecosystems. Values are mean ± SE, and the difference was considered significant if $P < 0.05$.

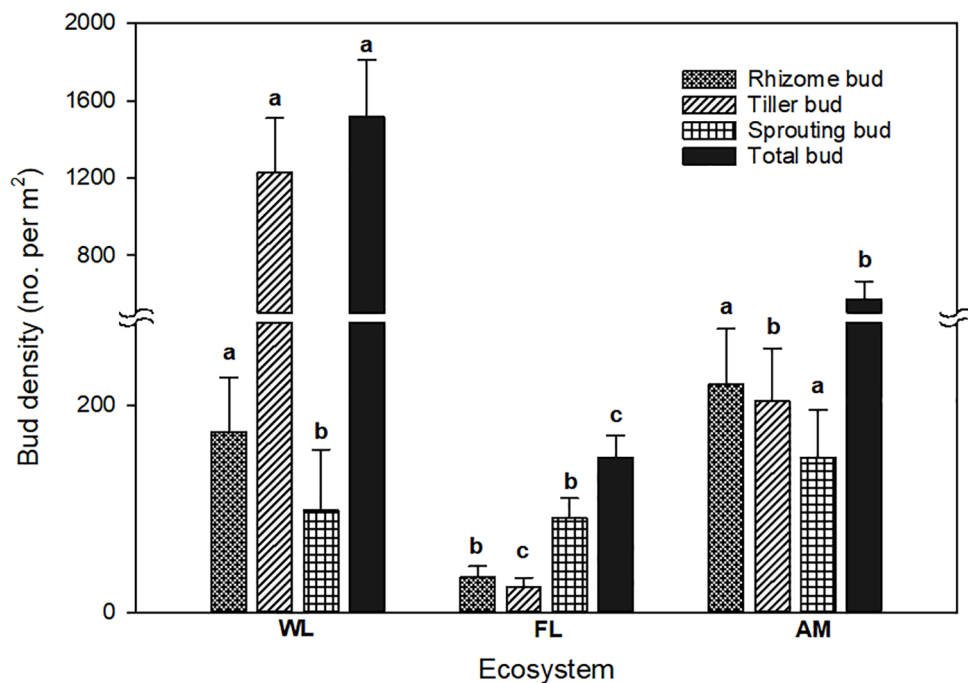


FIGURE 3

Difference in bud density of different bud types in WL, FL, and AM ecosystems. Lowercase letters indicate significant differences ($P < 0.05$) in bud density among land use types. Bars represent error bars.

All factors in the AM ecosystem explained 64.5% of the total variation in the bud bank. The soil water content at the 0–10 cm layer, total C at the 0–10 cm layer, and plant diversity were significantly correlated with bud banks ($P < 0.05$). The soil water content at the 0–10 cm layer was the most critical factor affecting bud banks, explaining 28.3% of the variation of bud bank, followed by total C at the 0–10 cm layer, plant diversity explained 14.8% and 15.0% of the variation of bud bank, respectively. The contribution of vegetation attributes and soil properties to the variation in bud bank were 29.6% and 70.4%, respectively (Table 2; Figure 6).

Effect of aboveground vegetation and soil properties on bud bank densities of different types

In the WL ecosystem, the densities of total bud and tiller bud were significantly positively correlated with the soil water content (0–10 cm layer), vegetation density, and aboveground biomass ($P < 0.05$), and vegetation density was the most critical factor to explain the density variation of total bud and tiller bud. Still, the rhizome bud and root sprouting bud density had no significant relationship with all factors (Table 3; Figure 4).

In the FL ecosystem, the density of the total bud was significantly positively correlated with the total N at the 0–10 cm layer, and the density of the root sprouting bud was significantly positively correlated with the total C at the 0–10 cm layer. However, rhizome bud and tiller bud density had no significant relationship with all factors (Table 4; Figure 5).

In the AM ecosystem, the densities of total bud and tiller bud were significantly positively correlated with the soil water content (0–10 cm layer) and vegetation density ($P < 0.05$), and the soil water content at the 0–10 cm layer was the most critical factor that explains the density variation of total bud and tiller bud. The rhizome bud density was significantly positively correlated with total C at the 0–10 cm layer ($P < 0.05$). Still, the density of root sprouting bud had no significant relationship with all factors (Table 5; Figure 6).

Discussion

Land use change alters the characteristics of bud bank composition and size

Land use change significantly altered the total bud bank density and the bud densities of all types (rhizome bud, tiller bud, and root sprouting bud) across all ecosystems; however, such impacts were higher in WL and AM than in the FL ecosystems. While total bud density, tiller buds, and moisture content were significantly higher in wetland ecosystems, bud densities of all bud types were relatively lower in FL. These results are consistent with previous findings that human-caused disturbances have remarkable adverse effects on belowground bud banks, which have substantial implications on bud regrowth, productivity, and ecological succession (Dagleish and Hartnett, 2009; Collins and Calabrese, 2012; Deng et al., 2014; Chen et al., 2020). Similarly, results provide empirical evidence that various ecosystems differ in their responses to land use effects,

TABLE 2 Explanations and contributions of impact factors to the total variation in bud bank for wetland (WL), farmland (FL), and Alpine meadow (AM) ecosystems.

	Controlling Factors	Parameters	Explanations (%)	Contributions (%)	F	P
WL	Environment	M10	11.9**	14.3	8.766	0.006
		C10	0.3	0.36	0.654	0.494
		N10	0.7	0.84	0.246	0.766
	Vegetation	VD	62.2**	74.7	32.943	0.002
		BM	5.8*	6.9	5.264	0.048
		SH	2.2	2.6	2.131	0.138
		Total	83.2	100		
FL	Environment	N10	12.6*	35.8	3.332	0.040
		C10	8.3	23.6	1.998	0.140
		M10	3.2	9.1	0.871	0.400
	Vegetation	VD	5.8	16.5	1.573	0.212
		BM	5.2	14.8	1.441	0.248
		SH	0.1	0.2	0.021	0.992
		Total	35.1	100		
AM	Environment	M10	28.3**	43.8	6.971	0.004
		C10	14.8*	22.9	2.641	0.070
		N10	2.4	3.7	0.717	0.572
	Vegetation	VD	3.3	5.1	1.037	0.374
		BM	0.7	1.0	0.193	0.894
		SH	15.0*	23.2	4.651	0.010
		Total	64.5	100		

M10, soil moisture content (0–10cm) (%); C10, total carbon (C, 0–10cm) (g/kg); N10, total nitrogen (0–10cm) (g/kg); VD, vegetation density (No./m²); SH, Shannon-Weiner diversity index; BM, aboveground biomass (g). Values are bold if significant.

* $P < 0.05$. ** $P < 0.01$.

suggesting that variation in species composition and soil characteristics across diverse terrestrial ecosystems underlie their differential responses during ecological perturbation, as observed by previous studies (Lavorel et al., 1997; Boer and Stafford Smith, 2003).

The differential responses of the studied ecosystems (i.e., WL, FL, and AM) can be explained on the following account: firstly, tiller buds in WL accounted for approximately 80% of the total bud densities because of high levels of soil moisture content, total C, and total N at the top 0–10 cm layer, facilitating plant establishment and population reproduction (Li et al., 2014; Adomako et al., 2020; Ma et al., 2021). These growth and productivity drivers (moisture, total C, and N) primarily promote the build-up of bud density in WL vegetation compared to AM and FL ecosystems (Dalglish and Hartnett, 2006; Ding et al., 2019). Secondly, higher rhizome and sprouting bud densities in FL and AM compared to WL ecosystems suggest that rhizomes and sprouting buds are highly sensitive to water and nutrient availability (Hiiesalu et al., 2021; Adomako et al., 2022), conditions that are ubiquitously higher in the WL ecosystem and favor tiller buds as grass functional groups represent the

dominant populations in wetland vegetation (Williams et al., 2017). Thirdly, FL had relatively the lowest bud densities of all bud types, and this can be attributed to high levels of human-caused disturbances (e.g., grazing, plowing, bush fire, herbicide application) or land use intensification in farmland vegetation compared to low farming activities in wetland zones (Allan et al., 2015). Our results suggest that plant species composition (functional groups) and soil physicochemical parameters determine the resilience and variation in response of ecosystems to anthropogenically mediated disturbances.

Land use change alters the relative contributions of vegetation attributes and soil properties on bud bank

Vegetation attributes and soil properties strongly correlated with bud banks; however, bud bank demography in the three ecosystems (WL, FL, and AM) with different vegetation attributes and soil properties, we found that vegetation density, soil moisture

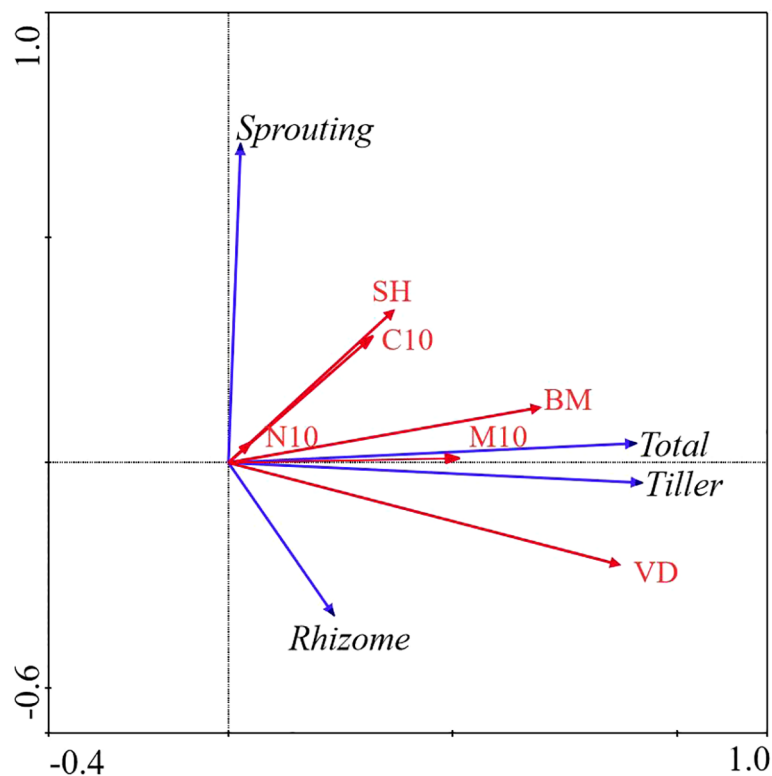


FIGURE 4

Redundancy Analysis (RDA) of the relationship between bud bank density of different bud types and environmental factors in WL ecosystem. M10, soil moisture content (0–10cm) (%); C10, total carbon (0–10cm) (g/kg); N10, total nitrogen (0–10cm) (g/kg); VD, vegetation density (No./m²); SH, Shannon-Weiner diversity index; BM, aboveground biomass (g); Total, total bud density; rhizome, rhizome bud density; Tiller, tiller bud density; Sprouting, root sprouting bud density.

content, and total N was the most critical factors in WL, AM, and FL ecosystems, explaining 62.2, 28.3 and 12.6% accordingly. Higher resource (i.e., soil moisture, total N, and C) availability or growth drivers promoted plant growth, biomass accumulation, and increased vegetation cover and stability (Adomako et al., 2021; Liu et al., 2021; Ma et al., 2021). It is, therefore, plausible to suggest that higher levels of these growth resources invariably increase the vegetation density of the wetland ecosystems, which can also be a function of a greater abundance of belowground bud banks (Liu et al., 2021; Ma et al., 2021), particularly tiller buds that accounted for about 81.14%. Previous studies have indicated that belowground bud banks positively correlate with the net aboveground primary productivity (Qian et al., 2021; Wu and Yu, 2022). Notably, results suggest that wetlands' maintenance, stability, and productivity are tightly linked with a balance of soil characteristics, bud type, and vegetation attributes (Ma et al., 2021).

Furthermore, studies have indicated that soil moisture is an essential driving force for vegetation succession in the alpine meadow (Heisler-White et al., 2008; An et al., 2019; Zhang et al., 2020; Zhang et al., 2022). In the present study, our analysis indicated that soil water content at the top 0–10 cm soil layer significantly influences bud banks, explaining 28.3% of variation of bud banks in the alpine ecosystem. Consistent with most previous studies that reported similar patterns at the top 0–10 cm of the soil layer, our results suggest that hydrological regimes can potentially

modulate and constrain plant growth, community structure, and stability of alpine meadow ecosystems (Heisler-White et al., 2008; An et al., 2019; Ren et al., 2023), as soil moisture is critical for resprouting and growth of belowground bud banks of all bud types. Additionally, total C, plant diversity, and soil moisture significantly correlated with bud banks, indicating that vegetation and soil physicochemical attributes play crucial roles in ecological succession and productivity output of meadow ecosystems (Hong et al., 2012; Xie et al., 2018; Świercz et al., 2019; Plue et al., 2021).

Lastly, total N strongly correlated with and was the most crucial factor influencing bud banks, explaining 12.6% of bud bank variation in farmlands and provides empirical evidence of the extent and magnitude of human-derived disturbances via nutrient enrichments in agrosystems (Isbell et al., 2013; Ren et al., 2019; Adomako et al., 2022). Although N limitation substantially limits plant growth (De Tezanos Pinto and Litchman, 2010; Bracken et al., 2015; Fay et al., 2015; Du et al., 2020; Adomako et al., 2022) and increased fertilization aimed at increasing agricultural output in agrosystems may promote the proliferation of bud banks in short-term period (Liu et al., 2021; Qian et al., 2021; Adomako and Yu, 2023), the long-term effects of N influxes in farmland ecosystems can trigger land degradation (Hamilton et al., 2020; Qian et al., 2021; Owusu et al., 2024). Notably, the FL ecosystem had the least attributes of all bud types measured, which can likely be linked to land use intensification. Our results confirm previous and current findings that N enrichment

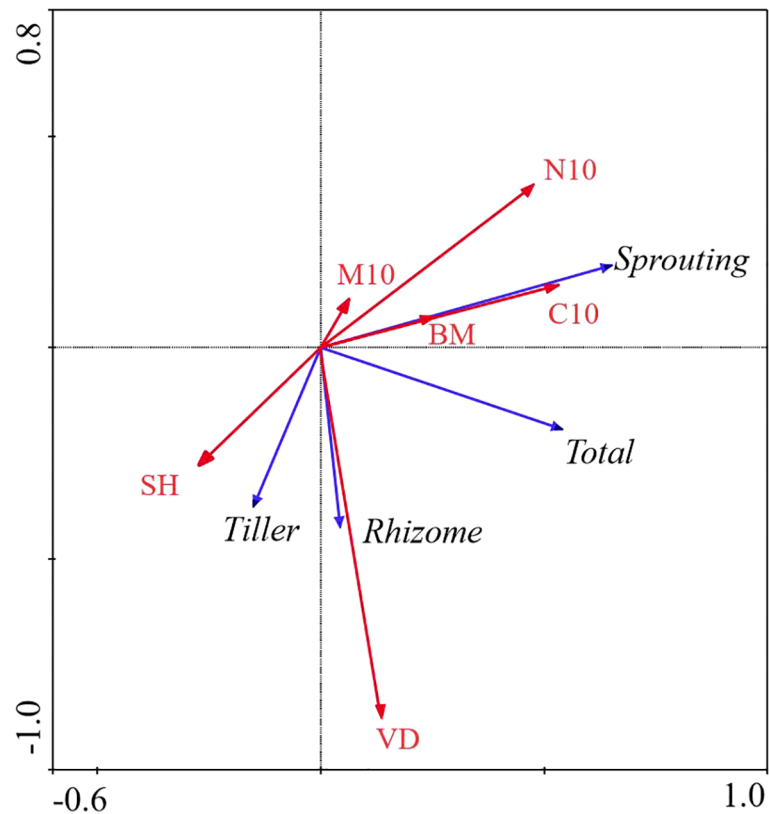


FIGURE 5

Redundancy Analysis (RDA) of the relationship between bud bank density of different bud types and environmental factors in FL ecosystem. M10, soil moisture content (0 – 10cm) (%); C10, total carbon (0 – 10cm) (g/kg); N10, total nitrogen (0 – 10cm) (g/kg); VD, vegetation density (No./m²); SH, Shannon-Weiner diversity index; BM, aboveground biomass (g); Total, total bud density; rhizome, rhizome bud density; Tiller, tiller bud density; Sprouting, root sprouting bud density.

disrupts plant community composition and plant-microbial interactions, promoting loss of global biodiversity and soil multifunctionality (Galloway et al., 2008; Qian et al., 2021).

Mechanisms underlying factors affecting bud banks of wetland, alpine meadow, and farmland ecosystems

Overall, soil properties significantly influenced root sprouting and rhizome buds of FL and AM, consistent with previous studies in dune ecosystems (Wu et al., 2021). The measured soil properties (soil moisture, total C and N) represent important factors that plays a pivotal role in many ecosystem processes, such as organic matter mineralization, litter decomposition, and biogeochemical cyclings (Wu et al., 2020; Inoue et al., 2022), which influence nutrient availability and the spatial distribution of resprouting buds and rhizome buds (Xie et al., 2018; Xiao et al., 2021). For example, in a recent study, Xiao et al. (2021) reported a significant influence of soil properties on the spatial distribution of Moso bamboo rhizomes.

Total buds and tiller buds were more strongly correlated with soil qualities in FL and AM ecosystems than aboveground vegetation parameters in WL ecosystems. Strong aboveground recruitment and productivity are tightly linked with the abundance of belowground

bud banks, especially tiller buds. Tiller buds constitute hemicryptophytes, and buds emanate from the shoot bases of the mother plant and are protected by leaf sheaths. Therefore, connected tiller buds can receive substantial growth resources from the connected mother plant, facilitating its expansion within plant communities (Ott and Hartnett, 2012). Conversely, in geophytes, root-sprouting and rhizome buds are primarily initiated from subterranean roots and rhizomes (Ott and Hartnett, 2012). These belowground structures are sensitive to water and nutrient availability in their ambient environment (Passioura, 1988; Wu et al., 2020). Therefore, bud banks can be a major driving force limiting productivity in wetland ecosystems. Unlike in FL and AM ecosystems, many wetland species are adapted to modifications in soil conditions and human-caused disturbances resulting from land use intensification. Thus, tiller buds connected to parent plants can obtain parental resource nourishments and withstand land use pressures in their ecosystem (Ott and Hartnett, 2012; Wu et al., 2020).

In contrast, as rhizome buds and root sprouting buds mainly initiate from underground roots and rhizomes, they could directly forage water or nutrients in the surrounding soil (Vesk and Westoby, 2004; Deng et al., 2013). Previous studies demonstrated that plants tend to produce more rhizome buds to increase foraging for favorable patches for persistence and regeneration in a resource-poor region, while in a relatively low resources environment, more tiller buds are

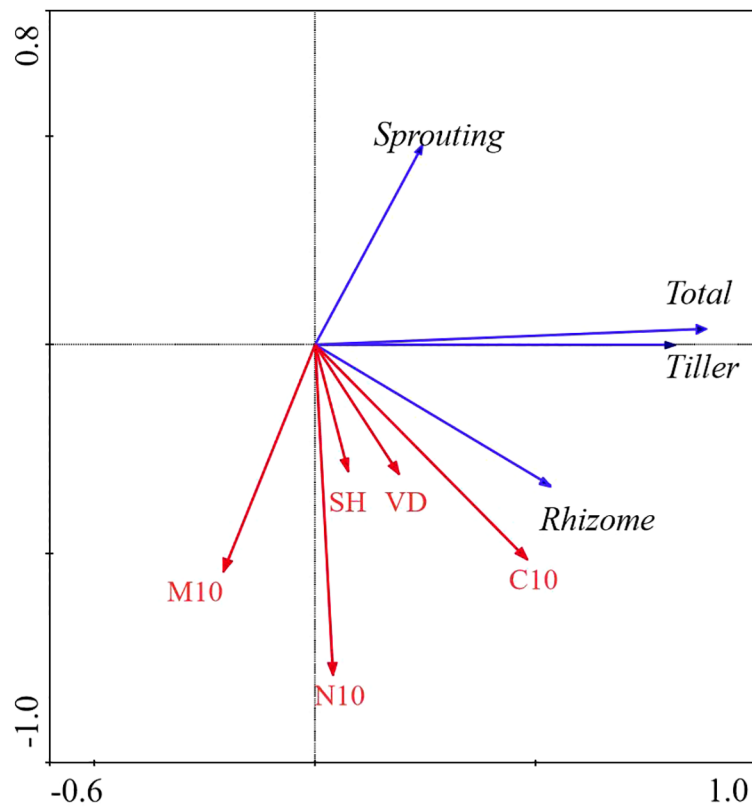


FIGURE 6

Redundancy Analysis (RDA) of the relationship between bud bank density of different bud types and environmental factors in AM ecosystem. M10, soil moisture content (0 – 10cm) (%); C10, total carbon (0 – 10cm) (g/kg); N10, total nitrogen (0 –10cm) (g/kg); VD, vegetation density (No./m²); SH, Shannon-Weiner diversity index; BM, aboveground biomass (g); Total, total bud density; rhizome, rhizome bud density; Tiller, tiller bud density; Sprouting, root sprouting bud density.

TABLE 3 Explanations and contributions of impact factors to the total variation in bank density of different wetland types (WL).

Bud type	Controlling Factors	Parameters	Explanations (%)	Contributions (%)	F	P
Rhizome	Environment	C10	10.5†	20.7	3.380	0.080
		M10	13.2†	26.1	3.475	0.090
		N10	14.7†	29.1	3.441	0.084
	Vegetation	VD	5.9	11.6	1.675	0.224
		BM	5.9	11.6	1.602	0.214
		SH	0.3	0.5	0.105	0.746
		Total	50.6	100		
Tiller	Environment	M10	12.5**	14.6	11.001	0.004
		C10	0.10	0.1	0.084	0.774
		N10	0.40	0.4	0.493	0.518
	Vegetation	VD	65.8**	76.7	38.493	0.002
		BM	6.6*	7.6	7.812	0.016
		SH	0.4	0.4	0.482	0.548

(Continued)

TABLE 3 Continued

Bud type	Controlling Factors	Parameters	Explanations (%)	Contributions (%)	F	P
		Total	85.8	100		
Root sprouting	Environment	M10	9.8†	17.7	3.075	0.092
		C10	5.7	10.2	0.282	0.574
		N10	3.6	6.4	1.097	0.326
	Vegetation	VD	13.4†	24.2	3.217	0.082
		BM	15.2†	27.4	4.304	0.070
		SH	7.7	13.8	1.669	0.256
		Total	55.4	100		
Total	Environment	M10	13.7*	17.0	8.490	0.014
		C10	0.1	0.1	0.091	0.774
		N10	0.5	0.5	0.407	0.538
	Vegetation	VD	55.8**	69.3	25.244	0.002
		BM	7.7*	9.5	0.031	0.040
		SH	2.7	3.4	2.292	0.134
		Total	80.5	100		

M10, soil moisture content (0–10cm) (%); C10, total carbon (0–10cm) (g/kg); N10, total nitrogen (0–10cm) (g/kg); VD, vegetation density (No./m²); SH, Shannon-Weiner diversity index; BM, aboveground biomass (g). Values are bold if significant. * $P < 0.05$. ** $P < 0.01$. † $P < 0.10$.

TABLE 4 Explanations and contributions of impact factors to the total variation inbank density of different types of farmland (FL).

Bud type	Controlling Factors	Parameters	Explanations (%)	Contributions (%)	F	P
Rhizome	Environment	C10	0.3	1.5	0.057	0.826
		M10	5.0	26.0	0.115	0.754
		N10	<0.1	<0.1	0.002	0.976
	Vegetation	VD	12.0†	62.5	3.004	0.086
		BM	5.6	29.1	1.426	0.232
		SH	0.8	4.1	0.195	0.626
		Total	19.2	100		
Tiller	Environment	M10	0.80	4.3	0.194	0.636
		C10	0.4	2.2	1.000	0.318
		N10	0.3	1.6	0.075	0.780
	Vegetation	VD	12.7†	69.0	3.213	0.081
		BM	4.0	21.7	0.103	0.738
		SH	0.1	0.5	0.018	0.896
		Total	18.4	100		
Root sprouting	Environment	M10	9.5	20.5	3.187	0.102
		C10	14.2*	30.8	3.651	0.042
		N10	10.0†	21.5	2.785	0.088
	Vegetation	VD	10.6†	22.9	3.272	0.092

(Continued)

TABLE 4 Continued

Bud type	Controlling Factors	Parameters	Explanations (%)	Contributions (%)	F	P
		BM	1.90	4.1	0.570	0.440
		SH	<0.1	<0.1	0.008	0.912
		Total	46.3	100		
Total	Environment	M10	6.6	19.8	1.776	0.215
		C10	6.2	18.7	1.450	0.230
		N10	13.4*	40.4	3.503	0.044
	Vegetation	VD	2.5	7.5	0.674	0.428
		BM	4.2	12.7	1.136	0.322
		SH	0.4	1.2	0.093	0.774
		Total	33.2	100		

M10, soil moisture content (0 – 10cm) (%); C10, total carbon (0 – 10cm) (g/kg); N10, total nitrogen (0 – 10cm) (g/kg); VD, vegetation density (No./m²); SH, Shannon-Weiner diversity index; BM, aboveground biomass (g). Values are bold if significant. * $P < 0.05$. † $P < 0.10$.

TABLE 5 Explanations and contributions of impact factors to the total variation in bank density of different types for Alpine meadow (AM).

Bud type	Controlling Factors	Parameters	Explanations (%)	Contributions (%)	F	P
Rhizome	Environment	C10	25.0*	54.74.990		0.042
		M10	8.5	18.6	3.246	0.170
		N10	5.7	12.5	1.168	0.278
	Vegetation	VD	1.5	3.2	0.276	0.628
		BM	2.6	5.7	0.512	0.166
		SH	2.5	5.5	0.513	0.438
		Total	45.7	100		
Tiller	Environment	M10	25.7*	35.3	6.996	0.016
		C10	9.6	13.2	1.825	0.184
		N10	0.1	0.13	0.059	0.794
	Vegetation	VD	16.9	23.2	3.053	0.126
		BM	0.1	0.14	0.052	0.838
		SH	20.3*	27.9	8.848	0.020
	Total	72.8	100			
Root sprouting	Environment	M10	6.9	22.3	1.118	0.280
		C10	9.7	31.3	1.634	0.204
		N10	4.4	14.2	0.714	0.396
	Vegetation	VD	8.1	26.1	1.340	0.256
		BM	1.8	0.1	0.287	0.610
		SH	<0.1	<0.1	0.003	0.968
		Total	31.0	100		
Total	Environment	M10	39.4**	51.1	12.706	0.004

(Continued)

TABLE 5 Continued

Bud type	Controlling Factors	Parameters	Explanations (%)	Contributions (%)	F	P
		C10	17.2†	22.3	3.122	0.100
		N10	<0.1	<0.1	0.051	0.546
	Vegetation	VD	0.40	0.50	0.189	0.668
		BM	<0.1	<0.1	0.101	0.940
		SH	20.1**	26.1	11.179	0.008
		Total	77.1	100		

M10, soil moisture content (0–10cm) (%); C10, total carbon (0–10cm) (g/kg); N10, total nitrogen (0–10cm) (g/kg); VD, vegetation density (No./m²); SH, Shannon-Weiner diversity index; BM, aboveground biomass (g). Values are bold if significant. * $P < 0.05$. ** $P < 0.01$. † $P < 0.10$.

produced to increase dominance and resource capture (Qian et al., 2017; Wu et al., 2021). Our study further illustrates that root sprouting buds are related to the soil nutrient content of the top (0–10 cm) layer because of direct roots sensitivity to soil nutrients (Klimeš and Klimešová, 1999; Ma et al., 2019).

Conclusions

Exploring belowground bud bank responses in different ecosystems is essential for understanding the adaptive strategies and vegetation restoration under the ongoing land use changes. We found that land-use change alters bud bank composition and size characteristics and alters the relative contributions of vegetation attributes and soil properties on bud banks. In WL environments, vegetation density is a crucial determinant; soil conditions are the most important factor affecting bud banks in FL and AM habitats. For different bud types, total buds and tiller buds rely more on vegetation density in WL ecosystems, but total buds and tiller buds are more related to soil properties in ecosystems of FL and AM. Rhizome and root sprouting buds could buffer vegetation restoration under land use change. Results indicate that vegetation and soil attributes play critical roles, underly the differential responses and the composition of bud banks of different ecosystems. Given the predicted climate change impacts and rapid expansion of industrialization and settlements, similar studies involving more climate change factors under varying climatic conditions may be highly informative and insightful.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

JW: Conceptualization, Funding acquisition, Investigation, Methodology, Writing – original draft. XH: Investigation,

Writing – original draft. LX: Methodology, Writing – original draft. QZ: Methodology, Writing – original draft. YW: Investigation, Writing – original draft. ZG: Writing – review & editing. MOA: Writing – review & editing. QM: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer JZ declared a shared affiliation with the author ZG to the handling editor at the time of review.

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