

Relationship between orchardgrass (Dactylis glomerata) dominance and the soil chemical characteristics of nonallophanic Andosol under cutting and cattle grazing

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#### 17 Abstract

18

19Soil acidity affects botanical compositions and pasture production, but the relationship between orchardgrass persistence and the soil nutrients in acidic soils with different 2021management methods is understudied in production fields. Here, using exchangeable 22acidity  $(y_1)$  as an indicator of exchangeable aluminum (Al), we conducted a survey to 23investigate the relationship between orchardgrass dominance and the soil characteristics 24in sown pastures under different management practices. The botanical composition and 25soil chemical conditions were investigated in six orchardgrass-tall fescue mixed pastures 26(two cutting meadows and four cattle grazing pastures) from June 18 to July 17, 2018. 27Six- and three-line transects were fixed in each meadow or pasture, respectively, and 5 28measurement locations were set along each transect at 10 m intervals. Each location had 29three square plots (20 cm  $\times$  20 cm) for the vegetation survey and three consecutive soil 30 sampling plots (4-cm diameter) adjacent to the middle square plot. The dominant plant species in each plot was recorded, and soil samples were collected at 0-5 cm depth to 3132measure  $y_1$  and major soil nutrients. The  $y_1$  ranged from 3.55 to 25.83 in the cutting meadows, which was wider than in the grazing pastures (1.85-16.29). In the cutting 33 34meadows, the dominance frequency of orchardgrass increased with the rise in y<sub>1</sub>, whereas 35that of tall fescue decreased in cutting meadows. No significant relationship was found 36 between dominance frequencies and  $y_1$  in the grazing pastures. Although concentration of some soil nutrients varied with y<sub>1</sub>, these nutrients were not related to the dominance 3738frequencies of orchardgrass for either management strategy. These results suggest that orchardgrass declines are prevented at high exchangeable Al sites by the non-3940 establishment of less Al-tolerant plant species under cutting conditions.

# 42 KEYWORDS

- 43 Botanical composition, pasture management, pasture persistence, soil exchangeable
- 44 aluminum, soil exchangeable acidity

### 46 1 | INTRODUCTION

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Orchardgrass (*Dactylis glomerata*) is a widely used temperate forage grass because of its
high productivity and nutritive value. However, the persistence of orchardgrass is reduced
under excessive nitrogen application (Raese & Decker, 1966), low cutting height (Griffith
& Teel, 1965), high air temperature (Drake, Colby, & Bredakis, 1963; Jones & Tracy,
2019), high soil moisture conditions (Jung & Baker, 1985), and soil acidity (Hojito,
Higashida, Nishimune, & Takao, 1987; Poozesh, Castillon, Cruz, & Bertoni, 2010).

Soil acidity is a major factor affecting the botanical composition and pasture 54production (Curtin & Smillie, 1986; Hojito et al., 1987; Poozesh et al., 2010; Poozesh, 5556Cruz, Choler, & Bertoni, 2007) because exchangeable aluminum (Al) in the soil dissolves into the soil solution as Al ions, which inhibits plant root elongation (Kochian, Hoekenga, 5758& Piñeros, 2004). Acid tolerance differs among plant species, and some pasture species 59are more tolerant to Al than orchardgrass (Poozesh et al., 2007; Wheeler, Edmeades, 60 Christie, & Gardner, 1992). Therefore, the low persistence of orchardgrass in acidic soils may be due to the direct effects of exchangeable Al or the indirect effects of other plant 61 62 species (with higher soil acidity tolerance).

Soil acidification induces the accumulation of inorganic nitrogen (Aciego Pietri &
Brookes, 2008; Kemmitt, Wright, & Jones, 2005) and causes deficiencies in the plantavailable phosphorus and exchangeable cations in the soil (Follett & Wilkinson, 1985;
Hojito et al., 1987; Naidu, Tillman, Syers, & Kirkman, 1990). The relative accumulation
and deficiencies of these nutrients can also affect the persistence of sown pasture species.
The soil and botanical characteristics of pastures differ under different pasture
management practices, such as cutting and livestock grazing (Spedding & Diekmahns,

1972; Vallentine, 2001), suggesting that the management regimes have different impacts on the soil and pasture plants. However, in production fields, there is little available information on how much exchangeable Al varies within a pasture, and how it relates to orchardgrass persistence and soil nutrients, and how different pasture management affect these relationships.

Therefore, we conducted a field survey to obtain information on the variabilities of the soil exchangeable Al concentration within each pasture and its relationship to orchardgrass dominance and soil nutrients, and compared these relationships under cutting and cattle grazing managements, using six sown grasslands simultaneously renovated with orchardgrass and tall fescue.

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### 81 2 | MATERIALS AND METHODS

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83 2.1 Study site

This study was conducted at the Kawatabi Field Science Center, Graduate School of 84 85 Agricultural Science, Tohoku University (Ohsaki, Miyagi, Japan; 38.75°N, 140.76°E, 220-250 m above sea level). At this site, the annual rainfall is 1701 mm, and the mean air 86 87 temperature is 10.5 °C (highest in August, 27.5 °C, and lowest in January –4.5 °C), based 88 on records from 1990 to 2019 (Japan Meteorological Agency, 2020). The soil type is classified as a Haplic non-allophanic Andosol according to the Soil Classification System 89 of Japan (The fifth committee for soil classification and nomenclature, 2017), a Pachic 90 91 Melanudand according to Soil Taxonomy (Soil Survey Staff, 2014), or an Aluandic Andosol in The World Reference Base (WRB) classification (IUSS Working Group WRB, 922015). 93

94Two cutting meadows (A, 1.0 ha; B, 2.0 ha) and four cattle grazing pastures (C–F with areas of 1.0–1.3 ha) were selected as survey sites (Table 1). Pastures C–F were part of the 9596 paddocks used for rotational beef cow grazing. All of the cutting meadows and grazing pastures were renovated in 2012 with orchardgrass (cv. Natsumidori) (20 kg of seeds ha-97<sup>1</sup>) and tall fescue (*Festuca arundinacea*, cv. Southern Cross) (15 kg of seeds ha<sup>-1</sup>), which 98 were broadcast seeded after herbicide application and seedbed preparation. The cutting 99100 meadows were harvested three times, in late May, early August, and early October. In 101 2018, the first cut was harvested June 4–17, and the herbage yields of meadows A and B 102were 4.1 and 5.2 t dry matter (DM) ha<sup>-1</sup>, respectively. In the grazing pastures, beef cattle 103were rotationally grazed from late April to late October. In 2018, the average stocking 104rate was 3.3 cattle ha<sup>-1</sup>, and total duration of grazing in pastures C to F were 83, 46, 52, 105and 95 days, respectively. As shown in Table 1, chemical fertilizer consisted of two 106 inorganic compound fertilizer, urea, and fused magnesium phosphate was applied in late 107 April, after the first and second cuts in the cutting meadows, and three to five times during 108 the grazing period in the grazing pastures. Cattle manure compost was also applied to all 109 of the cutting meadows and grazing pastures from November to December. The amounts of chemical fertilizer and cattle manure compost are shown in Table 1. 110

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#### 112 2.2 | Measurements

All measurements were conducted at fixed locations along line transects (50 m) established in the meadows and pastures (Figure 1). Parallel six- and three-line transects were fixed in each meadow and pasture, respectively, at a distance of 10 m. Five measurement locations for the vegetation survey and soil sampling were set along each transect at 10 m intervals (Figure 1). Each location had three plots (20 cm  $\times$  20 cm), and 118 the center of each plot was set at a 50 cm interval.

119 Vegetation surveys and soil sampling were conducted from June 18 to July 17, 2018. 120 The most dominant plant species was recorded as the species with the highest coverage in each plot. In this study, we assessed coverage because the persistence of forage grass, 121122which is defined as a decline in the population of sown species in a community or the 123population that still express its trait (Parsons et al., 2010) and is distinguished from yield 124(Donald, 1963), were usually determined by tiller density or coverage (Jones & Tracy, 1252018). Three consecutive soil cores (4 cm in diameter) were collected at 0-5 cm depth within an area away from the grass tussocks and dung pat and approximately 30 cm from 126 127the middle of the plot (Figure 1). The soil cores from each location were combined into a 128composite sample, dried at room temperature, sieved (2 mm) to remove gravel, and then 129stored for subsequent analysis. Soil pH was measured using 15 g of dried soil by dipping 130 the glass electrode of a pH meter into a 1:2.5 soil to water suspension. The exchangeable 131acidity  $(y_1)$  was measured using 10 g of dried soil by titrating a 1 M potassium chloride (KCl) extract (soil:solution = 1:2.5) with 0.1 M sodium hydroxide (NaOH) to the endpoint 132of phenolphthalein (Mori & Shimada, 1970). The value of y1 is closely related to the 133amount of KCl extractable Al (Saigusa, Shoji, & Takahashi, 1980), so y1 was used as an 134135indicator of exchangeable Al.

To analyze the soil nutrient contents, additional soil samples were collected after the third cut (November 20, 2018). One of the second measurement locations from the end of each line transect was alternatively chosen as the sampling location (Figure 1). The samples, each 80 cm<sup>2</sup> in area and 5 cm in depth, were collected using a hand shovel. Total nitrogen (Total-N), nitrate-nitrogen (NO<sub>3</sub>-N), and ammonium-nitrogen (NH<sub>4</sub>-N) were measured via the dry combustion, hydrazine sulfate reduction, and indo-phenol methods, respectively. Phosphorus pentoxide (P<sub>2</sub>O<sub>5</sub>) was determined via the Bray-2 method.
Potassium oxide (K<sub>2</sub>O), calcium oxide (CaO), and magnesium oxide (MgO) were
evaluated by atomic absorption spectrometry after Schollenberger extraction.

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146 2.3 | Data analysis

147To compare the botanical compositions of cutting meadows and grazing pastures, the 148dominance proportion was calculated separately for orchardgrass, tall fescue and the other 149plant species. For example, the dominance proportion of orchardgrass was obtained by dividing the number of dominant plots of orchardgrass by the total number of plots in 150each cutting meadow (n = 90) and grazing pasture (n = 45). In this study, the dominance 151152frequency of plants was also calculated in each location to analyze the relationships between the dominant plant species and the soil chemical characteristics. For example, 153154the dominance frequency of orchardgrass in a location was evaluated by dividing the 155number of dominant plots of orchardgrass (0, 1, 2, or 3) by the total number of plots (n = 1)1563), and were expressed as 0/3, 1/3, 2/3, or 3/3. The measurement locations were classified as "low" or "high", depending on the median the concentration of soil nutrients (Total-N, 157158NO<sub>3</sub>-N, NH<sub>4</sub>-N, P<sub>2</sub>O<sub>5</sub> K<sub>2</sub>O, CaO, and MgO).

The effects of  $y_1$  and concentration of soil nutrients on the dominance frequency of plant species were assessed using multinomial logistic regression analysis (model 1) and a generalized linear mixed model (model 2), respectively. The effects of  $y_1$  on the concentration of soil nutrients was evaluated using mixed linear regression analysis (model 3). The significance of these analyses was tested by likelihood ratio test (model 1), two-way analysis of deviance (ANODEV) (model 2), and ANOVA (model 3) with a significant level of 0.05. In model 1, the logits of tall fescue and the other plant species versus orchardgrass (reference species) were fit as response variables, and the  $y_1$  and each meadow/pasture were exploratory variables. Thus, each model is composed of two parts:

- 169  $\ln(P_{TF}/P_{OG}) = \beta_{0TF} + \beta_{1TF} X + \beta_{2TF} G,$
- 170  $\ln(P_{Others}/P_{OG}) = \beta_{0Others} + \beta_{1Others} X + \beta_{2Others} G,$

171 where  $P_{TF}$  and  $P_{Others}$  are the dominance frequencies of tall fescue and the other species, 172 and  $\ln(P_{TF}/P_{OG})$  and  $\ln(P_{Others}/P_{OG})$  are logits of them versus the dominance frequency of 173 orchardgrass ( $P_{OG}$ ). The X and G are exploratory variables representing the y<sub>1</sub> and each 174 meadows/pastures, respectively. The  $\beta_{0FT}$  and  $\beta_{0Others}$  are the intercept,  $\beta_{1TF}$  and  $\beta_{1Others}$  are 175 the coefficients of variable X, and  $\beta_{2TF}$  and  $\beta_{2Others}$  are the coefficients of variable G.

In model 2, the dominance frequency of plant species was fit as the response variable with a binomial distribution, and the soil nutrient levels (lower or higher than the median value of the data set) and plant species were incorporated as fixed effects. The meadows/pastures were random effects. Thus, the model is given by:

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$$\operatorname{logit}(q) = \beta_0 + \beta_1 N + \beta_2 S + \beta_3 I_{NS} + r \text{ (model 2)},$$

181 where *q* is the dominance frequency of plant species, respectively. Variables *N*, *S*, and *I*<sub>*NS*</sub> 182 represent the soil nutrient level, plant species, and the interaction between *N* and *S*, 183 respectively,  $\beta_0$  is the intercept,  $\beta_1$ ,  $\beta_2$ , and  $\beta_3$  are the coefficients of the exploratory 184 variables and their interaction, and *r* is the random effect.

In model 3, the concentration of soil nutrients was fit as response variables. The  $y_1$  was incorporated as a fixed-effect variable, and each meadows/pastures is a random-effect variable. Thus, the model is given by:

188  $Y = \beta_0 + \beta_1 X + r,$ 

189 where *Y* are the concentrations of each soil nutrient, and *X* is a variable representing the

190  $y_1, \beta_0$  and  $\beta_1$  are the intercept and the coefficient of the exploratory variable *X*, respectively, 191 and *r* is the random-effect variable.

All analyses were performed using the statistical software R version 3.6.1 (R Core Team, 2019). Multinomial regression analysis was conducted using the 'vglm', 'lrtest', and 'lrt.stat' function of the VGAM package (version 1.1.4). Generalized linear mixed modeling and ANODEV was performed using 'mixed' function of the afex package (version 0.27.2) and 'emmeans' function of the emmeans package (version 1.4.5). Mixed linear regression analysis was done using the 'lmer' function of the lime4 package (version 1.1.23) and 'anova' function of the base package.

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201 3 | RESULTS
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203 3.1 | Dominance proportion of plant species

204 The dominance proportion of orchardgrass ranged from 54–86% in the cutting meadows 205and 29-42% in the grazing pastures (Figure 2). The proportion of tall fescue, which was 206 sown as an accompanying grass species when the pastures were established, was smaller 207in the cutting meadows (1–4%) than in the grazing pastures (9–33%). The other dominant 208plant species were redtop (Agrostis alba), broad-leaved dock (Rumex obtusifolius), sweet vernalgrass (Anthoxanthum odoratum), and mugwort (Artemisia princeps) in the cutting 209210meadows, and water-pennywort (Hydrocotyle ramiflora), redtop, sweet vernalgrass, 211broad-leaved dock, and reed canarygrass (*Phalaris arundinacea*) in the grazing pastures. 212

213 3.2 | Soil acidity

Soil pH in the cutting meadows and grazing pastures ranged from 4.18. to 5.22 and 4.62
to 5.59, respectively.

The frequency distribution of  $y_1$  differed between the cutting meadows and grazing pastures (Figure 3). The  $y_1$  value ranged from 3.55. to 25.83 in the cutting meadows, which was greater than the values in the grazing pastures (1.85–16.29). The proportion of mildly acidic soil ( $y_1 = 0-5$ ) was 8% in the cutting meadows and 35% in the grazing pasture. In contrast, the proportion of very strongly acidic soil ( $y_1 > 15$ ) in the cutting meadows was 51.7% and only 1.6% in the grazing pastures.

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3.3 | Effects of soil exchangeable acidity on the dominance frequency of plants and soil
nutrient contents

The relationships between y<sub>1</sub> and dominance frequencies of orchardgrass, tall fescue, and 225226the other plant species are shown in Figure 4. In the cutting meadows, the dominance 227frequency of orchardgrass increased with the rise in  $y_1$ , whereas the dominance frequency 228of tall fescue decreased (likelihood ratio test for the regression and the coefficient of  $y_1$ , p < 0.05). No relative variation was found between orchardgrass and the other plant 229230species (likelihood ratio test for the coefficient of  $y_1$ , p > 0.1). In the grazing pastures, no significant regression was found between y<sub>1</sub> and dominance frequencies of the species 231232(likelihood ratio test for the regression, p > 0.1).

The dominance frequencies of orchardgrass in the cutting meadows were higher in locations with lower soil NO<sub>3</sub>-N and NH<sub>4</sub>-N concentrations. In contrast, tall fescue was more dominant in grazing pasture locations with lower soil NH<sub>4</sub>-N concentrations (pairwise multiple comparisons following ANODEV, p < 0.05; Figure 5).

237 The relationships between  $y_1$  and concentration of soil nutrients are shown in Figure

6. The concentration of NO<sub>3</sub>-N decreased with the decrease in  $y_1$  in the grazing pastures (ANOVA, p < 0.05). With the increase in  $y_1$ , the concentration of CaO (p = 0.05) and MgO (p = 0.07) in cutting meadows tended to decrease and that of NH<sub>4</sub>-N (p = 0.09) in the grazing pastures tended to increase (ANOVA, p < 0.05).

- 242
- 243 4 DISCUSSION
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In this study, most of the measurement locations in the cutting meadows and grazing pastures were classified as strongly acidic soil ( $y_1 > 5$ ). Although the application of lime and compost at the time of pasture establishment would reduce the  $y_1$  values (Matsuyama, Saigusa, & Kudo, 1999), most non-allophanic Andosols have  $y_1$  values greater than 6 (Saigusa et al., 1980). Therefore, the study site represents a typical acid-soil grassland with non-allophanic Andosols.

We also observed variability in the soil acidity among measurement locations (Figure 3), which is consistent with previous studies (Morton, Baird, & Manning, 2000; Raun et al., 1998; Solie, Raun, & Stone, 1999). In contrast, temporal variations in the soil acidity are relatively small (Ball & Williams, 1968; Conyers, Uren, Helyar, Poile, & Cullis, 1997). These findings suggest that the spatial distribution of soil acidity is heterogeneous on a small scale and has different long-term effects on the plants growing in these areas.

The effect of  $y_1$  on dominance frequencies of orchardgrass differed from that of tall fescue, that is, orchardgrass increased with the rise in  $y_1$  while tall fescue decreased (Figure 4). Herbage yield decreases with soil acidification in orchardgrass pastures (Hojito, Sato, & Takao, 1983), but our results showed that orchardgrass dominated in strongly acidic locations more frequently than in mildly acidic locations. Tall fescue

262dominated in strongly acidic locations less than in mildly acidic locations (Figure 4). 263These results agree with prior work showing that orchardgrass dominance is better than 264tall fescue under acidic soil conditions (Clark, Zeto, Ritchey, & Baligar, 1997; Wheeler et al., 1992). Thus, the higher tolerance of orchardgrass to soil acidity may increase its 265266relative dominance to tall fescue in the strongly acidic soils of cutting meadows. Although 267exact mechanism of the higher tolerance of orchardgrass relative to tall fescue has not yet 268been addressed, root length in unlimed acidic soil was longer in orchardgrass than tall 269fescue, whereas the length in limed soil were considerably longer in tall fescue than 270orchardgrass (Clark & Baligar, 2003), suggesting that root growth ability in acidic soil 271contributes to the difference in tolerance between these grasses.

272The high dominance of orchardgrass in strongly acidic soils may also be due to the 273increased supply of soil nutrients from high soil concentrations of exchangeable Al. In 274general, soil acidity influences the accumulation and mineralization of nitrogen 275(Whitehead, 1995), the amount of available phosphorus (Naidu et al., 1990), and the exchangeable cations, such as potassium, calcium, and magnesium (Hojito et al., 1987). 276With increasing  $y_1$ , the concentration of NO<sub>3</sub>-N in grazing pastures significantly 277decreased (Figure 6), and some soil nutrients, such as CaO and MgO in the cutting 278279meadows tended to decrease and NH<sub>4</sub>-N in the grazing pastures tended to increase. These 280relationships completely agree with previous study conducted under acidic soil condition (Follett & Wilkinson, 1985; Kemmitt et al., 2005). However, these soil nutrients were not 281related to the decrease in dominance frequencies of orchardgrass (Figure 5). Thus, the 282283increase and decrease in these soil nutrient contents cannot explain well the variation of the dominance frequency of orchardgrass. 284

In this study, the relationship between  $y_1$  and the dominance frequency of orchardgrass

286in grazing pastures differed from the patterns observed in cutting meadows (Figure 4). In 287the grazing pastures, y<sub>1</sub> was low, and its range was narrower than in the cutting meadows 288(Figure 3). Thus, the differences in  $y_1$  distribution may influence the relationship between y1 and the dominance frequency of orchardgrass. In general, soil acidification is 289290 accelerated by nitrogen fertilizers (Tian & Niu, 2015), and greater nitrogen deposition in the cutting meadows may have led to greater soil acidification, compared to the grazing 291292pastures (Table 1). The deposition of cattle dung in the grazing pastures may delay soil 293acidification because the cattle dung can increase the soil pH (During & Weeda, 1973; 294During, Weeda, & Dorofaeff, 1973). Increased soil aggregation due to cattle grazing also 295decreases the soil acidification rate (Martins et al., 2014; Souza et al., 2010).

296Moreover, the grazing activity of cattle (defoliation and trampling) strongly influences 297 the botanical composition of grasslands (Vallentine, 2001), and cattle may disturb this 298relationship, as observed in the cutting meadows. For example, under grazing conditions, 299 the defoliation rate is relatively high compared to cutting conditions. Water-soluble carbohydrates in the stubble play an important role in the growth of new leaves after 300 301 defoliation and the persistence of orchardgrass, but high defoliation rates reduce the 302 concentration of reserve carbohydrates (Davidson & Milthorpe, 1966). Cattle tend to 303 prefer orchardgrass over tall fescue, which increases the selection and defoliation rates of 304 this species (Baxter et al., 1986; Ridley, Lesperance, Jensen, & Bohman, 1963). In fact, 305 the persistence of orchardgrass is poorer than that of tall fescue under continuous grazing 306 conditions and high defoliation rates equivalent to rotational grazing (Brink, Casler, & 307 Martin, 2010; Brummer & Moore, 2000).

308 Competition with other acid-tolerant plant species in the grazing pastures may have 309 also affected orchardgrass dominance. Although the response to Al differs among

cultivars and populations within plant species (Davies & Snaydon, 1973; Snaydon, 1970),
the dominant species next to orchardgrass and tall fescue, such as red-top (Olsen & Chong,
1991), sweet vernal grass (Davies & Snaydon, 1973; Snaydon, 1970; Wu, Xin, &
Sugawara, 2013), and broad-leaved dock (Miyagi, Uchimiya, Kawai-Yamada, &
Uchimiya, 2013; Vondráčková et al., 2015), are highly tolerant to acidic soils and Al
toxicity.

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## 317 5 | CONCLUSIONS

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In strongly acidic soils, orchardgrass may be more persistent than tall fescue and other plant species in sites with high exchangeable Al under cutting conditions. This trend is less clear under grazing conditions. To clarify the mechanism of the difference of these trends, further research needs to focus on the effect of grazing cattle on chemical properties of strongly acidic soil and growth of orchardgrass, and the competition among pasture plant species with different acid-tolerance.

The results of this study suggest that soil acidification can act advantageously for orchardgrass under cutting management. However, minimum amendments of soil acidity are necessary because strong soil acidification can cause deficiency of some elements such as phosphate and calcium in plants and a poor mineral balance in livestock.

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		Chemical fertilizer							Cattle
	Area (ha)	Fertilizer material† (kg ha <sup>-1</sup> )			Composition (kg ha <sup>-1</sup> )			manure compost	
		CF212	CF211	Urea	Fused P	N	$P_2O_5$	K <sub>2</sub> O	$(t ha^{-1})$
Cutting meadow									
А	1.0	120	365	74	67	131	62	60	5.1
В	2.0	166	252	72	60	117	54	58	5.0
Grazing pasture									
С	1.3	80	140	41	34	63	29	30	0.9
D	1.1	80	140	41	34	63	29	30	0.9
E	1.0	80	140	41	34	63	29	30	0.9
F	1.0	80	140	41	34	63	29	30	0.9

TABLE 1 Annual management of the cutting meadows and cattle grazing pastures used in this study

<sup>†</sup> CF212, inorganic compound fertilizer with 20% N, 10% P<sub>2</sub>O<sub>5</sub>, and 20% K<sub>2</sub>O; CF211, inorganic compound fertilizer with 20% N, 10% P<sub>2</sub>O<sub>5</sub>, and 10% K<sub>2</sub>O; urea, urea containing 46% N; fused P, fused magnesium phosphate with 20% P<sub>2</sub>O<sub>5</sub>, 12% MgO, and 20% SiO.



**FIGURE 1** Outline of the line transects and measurement locations. Five measurement locations, each consisting of three plots for vegetation surveys and one location for soil sampling, were set along each line transect at 10 m intervals. At each soil sampling location, three consecutive cores were collected from an area free of grass tussocks and dung. Filled circles represent additional sampling locations for soil nutrient analysis, which were included in one of the second measurement locations from the end of each line transect.



**FIGURE 2** Dominance proportion of each plant species in the study sites. A–F denotes

513 the cutting meadows and grazing pastures.



**FIGURE 3** Distribution of exchangeable acidity  $(y_1)$  in the cutting meadows (n = 60) and

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517 grazing pastures (n = 60).
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**FIGURE 4** Effects of soil exchangeable acidity (y<sub>1</sub>) on dominance frequencies of orchardgrass (upper), tall fescue (middle), and the other plant species (lower) in the cutting meadows (left) and grazing pastures (right). Filled circles ( $\bullet$ ), open circles ( $\circ$ ), filled square ( $\blacksquare$ ), open square ( $\square$ ), filled triangle ( $\blacktriangle$ ), and open triangle ( $\bigtriangleup$ ) denote soil samples in cutting meadow A and B and grazing pasture C to F, respectively. Solid curves (cutting meadow A) and dashed curves (cutting meadow B) represent multinomial logistic regression (p < 0.05).



**FIGURE 5** Dominance frequencies of orchardgrass, tall fescue, and the other plant species at measurement locations with low and high soil nutrient contents (Total-N, NO<sub>3</sub>-N, NH<sub>4</sub>-N, P<sub>2</sub>O<sub>5</sub>, K<sub>2</sub>O, CaO, and MgO) in the cutting meadows (upper) and grazing pastures (lower). For each soil nutrient, the measurement locations were classified as "low" (n = 6) or "high" (n = 6) based on the median value. Columns and bars represent the estimated marginal means and standard errors of the mean. Asterisks indicate significantly higher values than the other soil nutrients in each plant category (p < 0.05).



**FIGURE 6** Effects of soil exchangeable acidity (y<sub>1</sub>) on the concentration of soil nutrients (Total-N, NO<sub>3</sub>-N, NH<sub>4</sub>-N, P<sub>2</sub>O<sub>5</sub>, K<sub>2</sub>O, CaO, and MgO) in the cutting meadows (upper) and grazing pastures (lower). Filled circles ( $\bullet$ ), open circles ( $\circ$ ), filled square ( $\blacksquare$ ), open square ( $\Box$ ), filled triangle ( $\blacktriangle$ ), and open triangle ( $\bigtriangleup$ ) denote soil samples in cutting meadow A and B and grazing pasture C to F, respectively. A solid line represents a linear regression (p < 0.05, marginal pseudo-R<sup>2</sup> = 0.33). Units of concentration of soil nutrients are in (mg 100g<sup>-1</sup>) except for Total-N which is in (%).