



Characterization of phenotypic diversity, yield and response to drought stress in a collection of Rhodes grass (*Chloris gayana* Kunth) accessions

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ABSTRACT

Information on available diversity and drought resistance among *Chloris gayana* accessions would offer considerable potential to select genotypes to alleviate the feed inadequacy that constrains livestock production in dry tropical areas. A collection of 62 *C. gayana* accessions from the genebank of the International Livestock Research Institute in Ethiopia was characterized using a set of 30 morphological, 4 phenological and 8 agronomic traits to assess diversity within the collection and to select promising accessions for use as livestock feed. In parallel, an experiment was conducted to assess the ability of these *C. gayana* accessions to maintain productivity under drought stress.

The screened collection of *C. gayana* accessions proved to be highly diverse in terms of morphology and phenology, agronomic potential and drought response. Six morphological groups were described which differ in many characteristics, ranging from general growth habit to specific inflorescence parameters. Large variability was measured in dry matter production, varying not only in total amount (400–2100 g m⁻²) and leaf contribution to total plant mass (66–96% of dry matter), but also in the growth pattern observed over three harvests. Accessions belonging to identical morphological, agronomic or drought-response groups were found to originate from a wide range of environments. Promising accessions for different uses and environments were identified and should be further evaluated across seasons and in multilocal experiments.

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1. Introduction

Chloris gayana is one of the major tropical forage grasses, originating from Africa, but widely grown and naturalized throughout the tropics and subtropics. Known for its wide adaptability and ease of establishment, it is a popular cultivated pasture species that is reported to withstand heavy grazing (Humphreys, 1980).

In its natural range, *C. gayana* occurs in grasslands and open woodlands up to 2000 m a.s.l., in areas with an annual precipitation from about 500–1500 mm. A vigorous root system reaching down to 4.7 m confers reasonable drought resistance (Skerman and Riveros, 1990). The species is cross-pollinating, and contains diploid as well as tetraploid forms (Loch et al., 2004). Within the genus *Chloris*, more than 50 species are reported (Phillips, 1995), but *C. gayana* so far is the only one of economic relevance (Bogdan, 1977; Whiteman, 1980). *C. gayana* has been described by many authors as an extremely variable species, both in morphology and in agronomically important characteristics (Bogdan, 1977).

Different cultivars of *C. gayana* are available, most of which were simply selected from wild populations. Only very few of the better known cultivars are outcomes of true breeding endeavors (Bogdan, 1977), mostly developed in Japan or in the US in order to improve cold tolerance (Cook et al., 2005).

Previous research has focused on the investigation of a few traits for certain cultivars or populations (Boonman, 1978; Kokubu and Taira, 1982; Komatsu and Shoi, 2005). Few published studies describe the diversity beyond well known commercial cultivars (York and Nyamadzawo, 1990; Komatsu et al., 2004). However, it is unlikely that the existing cultivars, which were mostly derived from collections in East Africa, represent the available variation within the species. Various authors hypothesized that there is considerable scope for selection of different genotypes suited to specific environmental conditions (Komatsu et al., 2004; Loch et al., 2004). Collection and description of the existing variability in *C. gayana* is the first step in the selection process.

There are no reported studies to compare drought response of a wide range of *C. gayana* cultivars and collections although this information would be useful to select genotypes in order to expand the options available to respond to climate change. Changes in climate in Africa are predicted to be more severe than in other regions (Collier et al., 2008) and are expected to have significant impact

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on loss of indigenous forage diversity in grasslands and natural pastures. In areas such as East Africa, which is predicted to have 10–20% more rainfall (Collier et al., 2008), current grazing areas or marginal lands may be converted to cropland leading to loss of forage diversity and opening marginal lands to degradation. The predicted temperature increases of 2–6 °C by the end of the century (Collier et al., 2008; Hoffman and Vogel, 2008) in Africa could allow spread of *C. gayana* into new environments but only where water is not the limiting factor. New cultivars will be important to sustain livestock production and avoid overreliance on the natural vegetation and associated loss of diversity. The identification of drought-resistant plants will be of particular importance in the future (Molden, 2007), since areas subjected to drought and desertification are expected to expand dramatically due to climate change (IPCC, 2007).

The International Livestock Research Institute (ILRI) maintains in trust a collection of 62 *C. gayana* accessions in its field genebank in Ethiopia. These accessions need to be characterized and evaluated to ensure their use as livestock feed and to facilitate further selection and breeding for characteristics like drought resistance.

The purpose of the study was to assess the morphological and agronomic diversity within the 62 *C. gayana* accessions maintained in the ILRI field genebank. Since no single morphological or physiological trait acts as a reliable indicator for drought resistance, further research was done to compare the response of *C. gayana* accessions to drought stress. Drought resistance was denoted here as the ability of a genotype to be relatively more productive than others under water deficit conditions (Quisenberry, 1982). The objective was to analyze the relative production of accessions subjected to drought rather than an evaluation of the detailed physiological mechanisms involved. Information on the diversity would allow groupings of accessions to be made and compared. Accessions originating from a similar environment could then be assessed to determine if they belonged to the same morphotype or if they exhibited similar potential for use or drought resistance. Another objective was to identify accessions that were particularly adapted and suitable for use in specific agricultural production systems or under specific climatic conditions, such as in drought-prone regions.

2. Materials and methods

2.1. Study site and plant material

The field experiments were carried out at the ILRI Zwai research site in the Ethiopian Rift Valley. The site is located 125 km southeast of the capital Addis Ababa, at an altitude of 1640 m a.s.l. (7°54'N, 38°44'E). The annual average precipitation of the area is 600 mm. Rains are unevenly distributed throughout the year, usually with a long dry season from October to February, with less than 10 mm of rainfall per month expected during this period, and a rainfall peak in July and August. The annual mean minimum and maximum temperatures of Zwai are approximately 13 and 27 °C, respectively. The loamy sand of the site has been classified as a vitric Andosol (van de Wouw et al., 2008). The chemical properties of the soil at 0.15 and 0.5 m depth were respectively pH 8.1 and 8.4, organic matter 2% and 1%, nitrogen 0.13% and 0.07%. Available phosphorus was 5 ppm and potassium was 5 meq./100 g soil at both depths (ILRI analysis).

The *C. gayana* collection comprises accessions mainly collected in East Africa (Fig. 1, Table 1), a number of accessions of unknown origin and 14 commercially available cultivars.

Better known cultivars used in this study include Katambora, Callide, Pioneer, Samford, Masaba, Mbarara, Elmba and Boma. Katambora, originating from Zambia, shows better drought toler-

ance but higher frost susceptibility than other cultivars and rapid growth but low early vigour (Barnard, 1972). Callide, selected in Australia from collections originating from East Africa, is highly productive and palatable even when mature but less drought tolerant (Barnard, 1972). Pioneer, developed in Australia and most likely originating from South Africa, shows high frost tolerance and rapid establishment, but demands fertile soils and relatively high rainfall for best performance (Barnard, 1972). Samford was also developed in Australia with germplasm originating from Kenya and is mainly known for its outstanding palatability although less frost-tolerant (Barnard, 1972). The Kenyan cultivar Masaba is productive, leafy and late flowering, but susceptible to spikelet diseases (Bogdan, 1977). Mbarara, originating from Uganda but released in Kenya, is a suitable grass for grazing (Boonman, 1997), but is rather stemmy (Humphreys, 1980). The early maturing Elmba, developed in Kenya, is well suited to intensive systems requiring rapid defoliation but becomes stemmy rapidly (Kenya Seed Company Limited, 1977). Boma, another Kenyan cultivar, is early maturing, palatable and grows in areas with low annual rainfall but adequate rainfall distribution (Humphreys, 1980).

Geographic Information Systems (GIS) techniques (ESRI ArcGIS 9.3) were used to extract data on the environment of those 33 collection sites for which coordinates were known. Using a climatic coverage of 1 km spatial resolution (Hijmans et al., 2005), a set of 21 bioclimatic variables (Table 2) was extracted as previously described by van de Wouw et al. (2008). These variables were used to determine correlations between the environment of the collection site and phenotypical traits of accessions.

2.2. Experimental design and data collection

2.2.1. Agro-morphological characterization study (Experiment 1)

The accessions were grown in 2 × 5 m un-replicated plots at a spacing of 0.5 × 0.5 m. Each plot was planted in 4 rows with 9 plants in each row and thus containing 36 individual plants. These plots had been established from seeds obtained from collection from the wild, research institutes or commercial seed companies (Table 1) and maintained already for several years with regular cutting, weeding and fertilizer application. During the dry season, all plots were irrigated weekly by flood irrigation. The experiment was commenced with a standardization cut; plants were defoliated to a standard height of 0.15 m above ground level 3 months before the start of the observations and again at the onset of the main rainy season. Thereafter, the plots were subdivided into four sections; cutting at 6, 8 and 12 weeks of regrowth and uncut.

The morphological and phenological traits to observe (Table 3) were selected based on expected variation in trait expression from a pilot study that was carried out on one plant per accession to detect traits exhibiting variation within the collection. Attention was paid further to traits used for distinguishing among cultivars (Barnard, 1972) and to those which are known to be stable under different environments, as well as to attributes reported to vary within this species (Bogdan, 1977; Loch et al., 2004).

All observations were taken in the same environment to minimize environmental effects. Due to the stoloniferous behavior of *C. gayana* it was impossible to identify individual plants. Consequently the morphological traits were measured on ten randomly selected shoots per accession as recommended by van de Wouw et al. (1999b) and averaged subsequently. Recording of all morphological traits, except for the growth habit, was performed on the first regrowth when all accessions had reached full flowering. The growth habit was recorded together with the phenological traits and determined as a score on the second regrowth from the uncut part of the plot. Each trait was measured on the same day in all plots to allow for comparisons among accessions and to avoid any bias due to changes in trait expression over time. The inflorescence

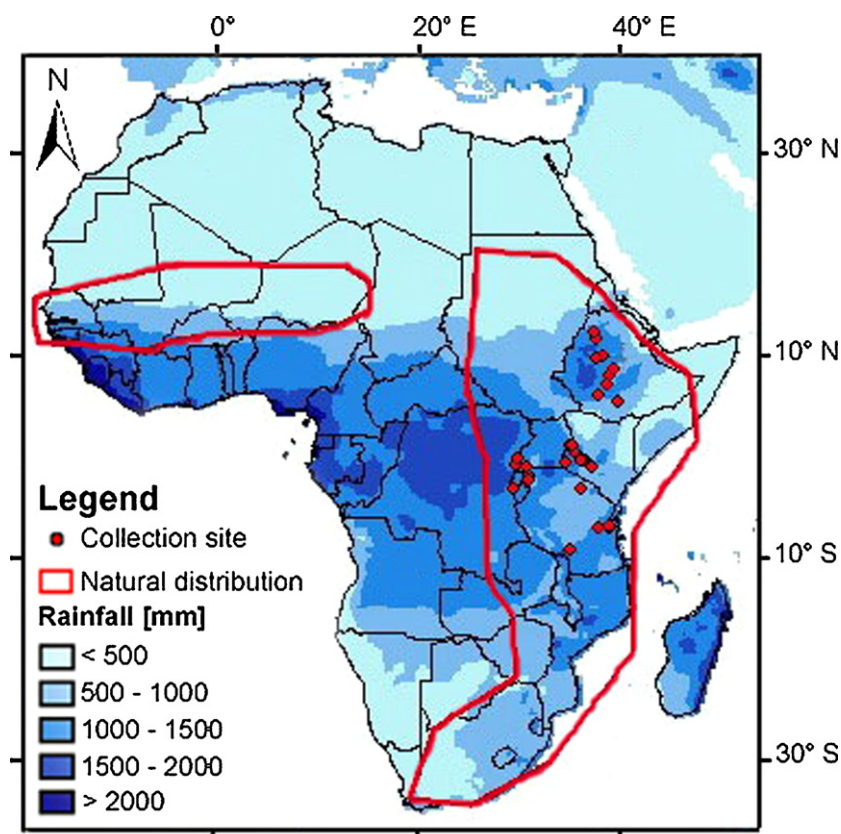


Fig. 1. Map of the natural distribution of *C. gayana* and collection sites of accessions used in the current study (only those with coordinates of the collection sites).

parameters were examined under the microscope; all other traits were observed directly in the field. All leaf measurements were made on the second leaf below the first completely unrolled leaf at the top of the plant.

The agronomic traits to measure in the evaluation under full irrigation were chosen according to their economic relevance (Table 4). Agronomic traits generally display genotype by environment interaction and can be used for comparison of expressed trait diversity among accessions. Biomass production was determined at three different times, i.e. after 6, 8 and 12 weeks of growth, each time using a mean of two samples per accession. These cutting frequencies were defined according to Tyler et al. (1985) with the first harvest on regrowth 6 weeks after the standardization cut and generally at emergence of 50% of the inflorescences plus 1 to 2 weeks. As most accessions were reaching 50% flowering between 6 and 11 weeks, each accession was cut at three different times in order to enable a comparison of both harvests at the same date and harvests at similar reproductive stages.

At each harvest, two randomly placed quadrats of 0.5 m × 0.5 m per plot were defoliated with a hand sickle at a height of 0.15 m. Fresh weight was assessed immediately in the field. A subsample of 100 g fresh plant material per quadrat was separated into leaves, stems and inflorescences. These subsamples were then dried for 48 h at 65 °C in an oven and reweighed to determine the harvestable above-ground dry matter. Leaf percentage – calculated as percentage of the leaf dry matter in relation to the total dry matter of the sample – was measured at 6 and 12 weeks of growth to capture the leafiness of both young and mature plants.

2.2.2. Drought-stress experiment (Experiment 2)

Performance of *C. gayana* accessions under drought stress was determined in an additional experiment using a split-plot design with three replications per treatment. Replications were estab-

lished as blocks to prevent site effects. Main plots represented the two treatments, drought and irrigated, and subplots were accessions. In order to keep the two moisture regimes separate, the treatments were placed 50 m apart from each other. Accessions were randomly allocated to subplots which were arranged as single rows of 2.5 m length. Each row contained eight plants. The plant-to-plant spacing within rows was 0.3 m; the distance between rows was 0.5 m.

Uniform root-splits with 5–6 tillers each were obtained from all 62 *C. gayana* accessions, cut back to 0.1 m and transplanted. Planting was done during the rainy season to guarantee effective and rapid establishment. Until plants had established, plots were irrigated on days with no rain. Fertilizer was applied as 50:20 kg ha⁻¹ of P:N (DAP) 2 weeks after planting and 100 kg ha⁻¹ N (Urea) 5 weeks after planting in order to prevent any potential nutrient deficiency. Since micronutrient deficiency at Zwai site was observed by other researchers (van de Wouw, 1988), plants were treated with 15:5:40:30:0.5:40:13:28 g ha⁻¹ of B:Cu:Fe:Mn:Mo:Zn:Mg:S (Fetrilon Combi) 4 weeks after planting.

The two contrasting water regimes were imposed on experimental plots 7 weeks after planting, at the end of the rainy season. Plants were defoliated to a height of 0.1 m to observe the regrowth under drought stress and irrigation. Subsequently, the irrigated treatment was watered weekly using flood irrigation. The drought treatment received no other water than rainfall. During the experimental period of 5 weeks, a total of 17.7 mm rainfall was recorded at Zwai (Fig. 2). However, due to the sandy soil at the site, water drained rapidly.

To assess the extent of drought stress, gravimetric soil moisture content was measured once per week, always at the same day and time. For both treatments, soil samples were taken on two randomly selected points per main plot at 0–0.2 and 0.2–0.4 m depth. Fresh weight of the soil samples was recorded immediately after

Table 1

List of accessions used in the experiment – with the assignment to the different groups.

ILRI number	Other numbers ^a	Cultivar name	Sample type ^b	Source country	Morph. Group	Agron. Group	Drought Group
645	CIAT 26453		NP	Tanzania	I	I	I
680	CIAT 26446		NP	Tanzania	I	II	V
692	CIAT 26447		NP	Tanzania	I	I	I
701	CIAT 26448		NP	Tanzania	I	II	V
705	CIAT 26449		NP	Tanzania	I	II	VI
708	CIAT 26450		NP	Tanzania	VI	III	III
719	CIAT 26451		NP	Tanzania	I	I	II
743	CIAT 26452		NP	Tanzania	I	I	VI
890			NP	Tanzania	III	I	II
895			NP	Tanzania	I	II	I
899			NP	Tanzania	III	I	VI
977			NP	Rwanda	III	I	IV
981			NP	Rwanda	I	I	I
993			NP	Rwanda	II	II	II
1053			NP	Burundi	VI	I	I
1097			NP	Congo, DR	III	II	VI
1118			NP	Congo, DR	III	IV	III
2023			NP	Ethiopia	V	V	V
2199			NP	Ethiopia	I	VI	VI
6625	N 77288	Samford	RS		I	V	II
6627	N 77206, PI 379631	Pioneer	CS		VI	V	IV
6628	G 518; CPI 118109, PI 298982	Nakuru	RS		II	V	V
6630	CPI 35691; CPI 51497	Masaba	RS	Kenya ^c	V	III	II
6631	G 638; CPI 118110, PI 307625	Hunter	RS		V	III	I
6633	N 77265	Callide	CS		IV	V	I
6634	CPI 118111	Bandai	RS		V	V	IV
7103	N 79134, PI 378042	Mbarara	RS	Uganda ^c	V	I	V
7113	N 79136	Rongai	RS		V	V	I
7384	CPI 13375,18021,39156; PI 365980	Katambora	CS	Zambia ^c	V	V	III
7757			NP	Ethiopia	IV	VI	I
9163			NP	Ethiopia	III	I	V
9422	CPI 118112		NP	Ethiopia	Outlier	IV	IV
10097	CPI 118113		NP	Ethiopia	II	III	I
10101	CPI 118114		NP	Ethiopia	I	IV	V
10225	CPI 118115		NP	Ethiopia	III	IV	V
12968	CIAT 16677		NP	Kenya	IV	I	V
13053	CIAT 16651		NP	Kenya	V	VI	II
13072	CIAT 16652		NP	Kenya	III	I	V
13080	CIAT 16654		NP	Kenya	V	V	I
13082	CIAT 16655		NP	Kenya	VI	I	IV
13097	CIAT 16657		NP	Kenya	III	VI	I
13103	CIAT 16658		NP	Kenya	II	I	V
13110	CIAT 16659		NP	Kenya	II	III	II
13175	CIAT 16662		NP	Kenya	Outlier	IV	VII
13229	CIAT 16665		NP	Kenya	V	V	III
13317			CS		I	V	II
13329		Elmba	CS		IV	I	I
13330		Boma	CS		III	VI	V
13403	CIAT 16267		NP	Ethiopia	III	I	VI
13487	CIAT 16270		NP	Ethiopia	III	VI	VI
15569	CG 53		BL		VI	II	I
15570	CG 54		BL	South Africa	VI	III	V
15571	CG 55		BL		VI	II	V
15572	CG 56		BL		VI	II	VI
15573	CG 57		BL		VI	II	VI
15574	CG 71	Giant	BL		II	I	I
15575	CG 70		BL		I	V	I
15576	CG 74		BL		VI	III	I
15577	CG 155	Boma-Y	BL		II	V	II
15578	CG 131-154		BL	Zimbabwe	VI	III	III
18487			NP	Tanzania	I	V	II
18498			NP	Tanzania	III	VI	I

^a CIAT: Centro Internacional de Agricultura Tropical, Colombia; CPI: CSIRO, Australia; PI: USDA, USA; CG and G: Grasslands Research Station, Zimbabwe; N: registration code at ILRI, Mali.

^b BL: breeding line; CS: commercial seed company; NP: natural population; RS: research source.

^c According to Cook et al. (2005).

sampling. Thereafter, soil samples were dried in the oven for 48 h at 105 °C and reweighed. Gravimetric soil water content (θ_g) was calculated according to Ryan et al. (2001) as

$$\theta_g[\%] = \frac{(m_{\text{wet}} - m_{\text{dry}})}{m_{\text{dry}}} \times 100 \quad (1)$$

with θ_g = gravimetric soil water content in %, m_{wet} = wet soil in g and m_{dry} = dry soil in g.

Criteria for the selection of plant traits to observe (Table 5) were (i) feasibility of the measurement, (ii) ability to reflect drought response of a plant and (iii) agronomic importance. All observations and cuttings were made at the same time under both treatments on the central plants of each row. As the objective was to compare

Table 2

Environmental variables obtained using GIS climatic coverage (Hijmans et al., 2005).

	Trait [Definition]	Unit
1.	Altitude	m
2.	Latitude [Absolute value of latitude]	degrees
3.	Annual mean temperature ^a	°C
4.	Mean diurnal temperature range [Mean of monthly (max. temp. – min. temp.)]	°C
5.	Isothermality [(Mean diurnal temp. range/Annual temp. range) × 100] ^a	
6.	Temperature seasonality [Standard deviation of monthly temperatures × 100] ^a	
7.	Maximum temperature of warmest month ^a	°C
8.	Minimum temperature of coldest month ^a	°C
9.	Annual temperature range [Max. temp. warmest month – min. temp. coldest month] ^a	°C
10.	Mean temperature of wettest quarter ^a	°C
11.	Mean temperature of driest quarter ^a	°C
12.	Mean temperature of hottest quarter ^a	°C
13.	Mean temperature of coldest quarter ^a	°C
14.	Annual precipitation	mm
15.	Precipitation of wettest month ^a	mm
16.	Precipitation of driest month ^a	mm
17.	Precipitation seasonality [Coefficient of variation of monthly precipitations] ^a	
18.	Precipitation of wettest quarter	mm
19.	Precipitation of driest quarter	mm
20.	Precipitation of warmest quarter ^a	mm
21.	Precipitation of coldest quarter ^a	mm

^a Traits excluded from cluster analysis owing to high correlations with other traits.

production and not survival during the dry season, biomass harvests were done when significant differences between treatments could be observed in the field. Dry matter production per plant was assessed after drying in an oven for 48 h at 65 °C. For further analyses, a time period of 6 weeks until first flowering was assigned to all plots, where accessions did not flower within the 5-week experimental period.

The ability of *C. gayana* accessions to maintain productivity under drought stress was evaluated based on two criteria, (i) absolute performance under drought stress and (ii) relative yield reduction (R_y) by water deficit compared to an irrigated 'control'. The latter was expressed in % and calculated according to Lu et al. (1999) as

$$R_y[\%] = \left(1 - \frac{Y_d}{Y_c}\right) \times 100 \quad (2)$$

with Y_d = yield under drought and Y_c = 'control' yield.

Relative reduction in plant height and changes in time to flowering were determined accordingly. Leaf senescence due to drought was assessed as the difference between the percentages of leaves affected by senescence in the irrigated 'control' compared to the percentage affected under drought.

Leaf senescence due to drought was assessed by subtracting the percentage of affected leaves of the irrigated 'control' from the respective value under drought.

2.3. Statistical analysis

Following an exploratory data analysis using SPSS 17.0 (SPSS Inc., 2008), the variables recorded on a rating scale could be considered as roughly normally distributed. Consequently, they were treated as interval scaled and analyzed together with the other metric variables (Kaufman and Rousseeuw, 2005).

A univariate analysis of variance (ANOVA) was carried out to assess the variation among accessions in the agro-morphological characterization (SPSS 17.0) and between both irrigation treatments and accessions in the drought-stress experiment (GenStat Discovery Edition 3.0) (Buyse et al., 2004). Traits were omitted from the subsequent analyses when they exhibited either extremely high variation within accessions or no variation among accessions (Table 3). Pearson's correlation coefficients were calculated among observed traits as well as between traits and environmental variables. Within each dataset, variables that showed a high correlation ($r > 0.7$) were reviewed. Whenever such a high correlation could be explained by an overlap of measurements, one of the traits was excluded from cluster analysis to avoid indirect weighting. In each case, the trait was retained that did not show multiple correlations and whose distribution more closely resembled a normal distribution.

Before using variables together in one multivariate procedure, they were standardized to a mean of zero and a variance of one (z-standardization). This was done in order to transform trait values measured at different scales to one common scale. Since outliers may distort clustering and ordination, accessions very dissimilar to

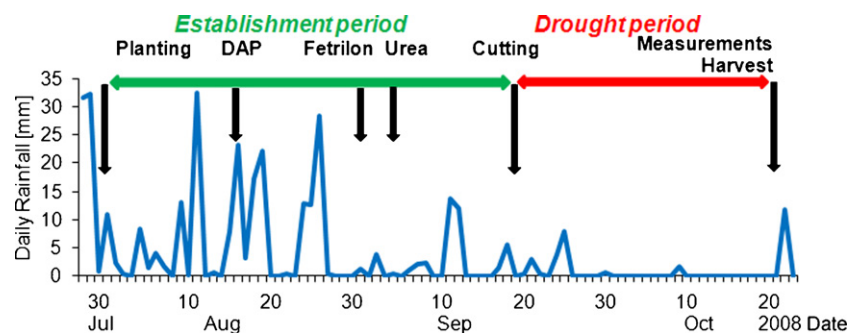


Fig. 2. Daily rainfall at the experiment location during the experimental period and schedule of the drought-stress experiment.

Table 3

List and definition of all morphological and phenological traits used.

	Trait	Definition	Observations
1.	Plant height [cm]	Height from the ground to the flag leaf, at full flowering	10 plants
2.	Growth habit [1–5]	Average angle of the stem to the ground, rating from prostrate (1) to erect (5), at 5 weeks after second cut	Full plot
3.	Stolons [1–5]	Presence of stolons, rating from no (1) to prolific stolons (5), at 4 weeks after second cut	10 plants
4.	Culm length [cm] ^a	Length of the culm from the first node at plant base up to the flag leaf, at full flowering	10 plants
5.	Culm thickness [mm]	Culm diameter above the lowest node, at full flowering	10 plants
6.	Internode length [cm]	Length of the fourth internode from the lowest internode, at full flowering	10 plants
7.	Node number ^a	Number of nodes per culm, at full flowering	10 plants
8.	Number of branchings	Number of branchings per culm, at full flowering	10 plants
9.	Number of inflorescences ^a	Number of inflorescences per culm, at full flowering	10 plants
10.	Leaf length [cm]	Length from the ligule to the tip of the leaf, at full flowering	10 plants
11.	Leaf width [mm]	Width of the leaf at the widest point, at full flowering	10 plants
12.	Leaf ratio ^a	Leaf length divided by leaf width	Calculated
13.	Ligule hair density [1–5]	An estimate of the average density of the hair besides the ligule, rating from none (1), sparse (3) to dense (5), at full flowering	10 plants
14.	Ligule hair length [mm]	Length of the longest hair besides the ligule, at full flowering	10 plants
15.	Whorls per inflorescence	Number of whorls per inflorescence, at full flowering	10 plants
16.	Spikes per inflorescence	Number of spikes per inflorescence, at full flowering	10 plants
17.	Spikes length [cm]	Length of the spikes, from base to top, at full flowering	10 plants
18.	Flexuosity of rachis ^b	An estimate of the flexuosity of the spike axis, rating from straight (1), arcuate (3) to strongly flexuous (5)	10 plants
19.	Spikelet length [mm]	Length of the spikelet without glumes, from the base of the lowest floret to the top of the spikelet, excluding the awn	10 plants
20.	Spikelet width [mm]	Width at the widest point of the spikelet	10 plants
21.	Spikelet ratio ^a	Spikelet length divided by spikelet width	Calculated
22.	Length of fertile lemma [mm] ^a	Length of the lowest lemma from the base to the top, excluding the awn	10 plants
23.	Awn length [mm]	Length of the awn of the lowest lemma	10 plants
24.	Length of hairs at awn base [mm]	Length of the longest hair on the upper margins of the fertile lemma	10 plants
25.	Lemma pubescence on margins [1–5] ^a	An estimate of the hairiness on the full length of the margins of the fertile lemma, rating from glabrous (1), sparsely (3) to densely sericeous (5)	10 plants
26.	Lemma pubescence on keels [1–5] ^a	An estimate of the hairiness of the keels of the fertile lemma, rating from glabrous (1), sparsely (3) to densely sericeous (5)	10 plants
27.	Pubescence of floret base [1–5]	An estimate of the hairiness of the base of the fertile floret, rating from glabrous (1), sparsely (3) to densely sericeous (5)	10 plants
28.	Floret number of spikelets ^a	Total number of fertile and reduced florets per spikelet	10 plants
29.	Length of third floret [mm]	Length of the third floret	10 plants
30.	Length of upper glume [mm] ^a	Length of the upper glume, including the awn-point	10 plants
31.	Length of lower glume [mm]	Length of the lower glume, including the awn-point	10 plants
32.	Glume ratio ^b	Length of the upper divided by length of the lower glume	Calculated
33.	Glume hairiness [1–5] ^b	An estimate of the glume hairiness, rating from glabrous (1), sparsely (3) to densely sericeous (5)	10 plants
34.	Glume color [1–5] ^b	Rating from no red/purple coloring (1), slightly red (2), intense red (3), slightly purple (4) to strongly purple coloring (5)	10 plants
35.	Floret color [1–5] ^b	Rating from no (1) to strongly purple coloring (5)	10 plants
36.	Weeks to first flowering	Number of weeks until the first inflorescence emerged	Full plot
37.	Weeks to 50% flowering ^a	Number of weeks until half of the plot flowered	Full plot
38.	Weeks to full flowering ^a	Number of weeks until all plants flowered	Full plot
39.	Flowering duration	Weeks from emergence of the first flower to full flowering	Full plot

^a Traits excluded from cluster analysis owing to high correlations with other traits.^b Traits excluded from all analyses owing to either low variability or high intra-accession variation.

others (standard deviation > 2 from the mean calculated distance of accessions) were detected within each dataset by outlier analysis in PC-Ord 5.20 (McCune and Mefford, 2006). Further, different clustering algorithms were applied to visualize outliers in a first

step. If a distorting effect was visible, outliers were excluded from the final analysis.

Hierarchical cluster analysis was performed for each dataset adopting squared Euclidean distances as a measure of dissimilarity

Table 4

List and definition of agronomic traits used in the evaluation study under full irrigation.

	Trait	Definition	Observations
1.	Plant height [cm]	Height from the ground to the flag leaf, at full flowering	10 plants
2.	Yield – 6 weeks [g m ⁻²]	Dry matter yield, after 6 weeks of growth	0.5 m ²
3.	Yield – 8 weeks [g m ⁻²]	Dry matter yield, after 8 weeks of growth	0.5 m ²
4.	Yield – 12 weeks [g m ⁻²] ^a	Dry matter yield, after 12 weeks of growth	0.5 m ²
5.	Yield – total [g m ⁻²]	Total dry matter yield, sum of three harvests (6, 8 and 12 weeks)	Calculated
6.	Leaf percentage – 6 weeks [%]	Percentage of the leaves to the total biomass of a 100 g subsample, as dry matter, at harvest after 6 weeks of growth	0.5 m ²
7.	Leaf percentage – 12 weeks [%]	Percentage of the leaves to the total biomass of a 100 g subsample, as dry matter, at harvest after 12 weeks of growth	0.5 m ²
8.	Leaf percentage – mean [%] ^a	Mean of the leaf percentages at 6 and 12 weeks	Calculated

^a Traits excluded from cluster analysis owing to high correlations with other traits.

Table 5

List and definition of traits observed in the drought-stress experiment.

	Trait	Definition	Observations
1.	Plant height [cm]	Height from the ground to the flag leaf, 4 weeks after imposing the different irrigation treatments	5 plants
2.	Fresh weight [g/plant] ^a	Fresh weight per plant, 5 weeks after imposing the different irrigation treatments	3 plants
3.	Dry weight [g/plant]	Dry weight per plant, 5 weeks after imposing the different irrigation treatments	3 plants
4.	Leaf senescence – 4 weeks [%] ^a	Percentage of the whole leaf area becoming yellow/brown, 4 weeks after imposing the different irrigation treatments	5 plants
5.	Leaf senescence – 5 weeks [%]	Percentage of the whole leaf area becoming yellow/brown, 5 weeks after imposing the different irrigation treatments	5 plants
6.	Weeks to first flowering	Number of weeks from cutting until the first inflorescence emerged	Full plot

^a Traits excluded from cluster analysis owing to high correlations with other traits.

and Ward's minimum variance method as the clustering algorithm (McCune and Grace, 2002). The number of clusters in each classification was determined based on visual observation of breaks in the level of dissimilarity in the dendrogram (Gore, 2000) and wherever possible, according to the 'elbow criterion' (Backhaus et al., 2006). Further, a discriminant analysis (SPSS 17.0) was applied to explore which traits best separated accessions among groups, and to detect links between cluster groups of different datasets and environmental variables. To identify the variables that best discriminated among the groups, mean discriminant function coefficients were calculated using standardized coefficients for significant discriminant functions.

Each dataset was subjected to a Principal Component Analysis (PCA) in PC-Ord to validate groupings resulting from cluster analysis and to graphically summarize and describe trait relationships among groups. To detect any relations between the phenotypical variation and the collection site environment of accessions, correlations between sample scores on principal components and environmental variables were calculated.

3. Results

The collection of 62 *C. gayana* accessions screened in the present study proved to be extremely variable in terms of morphology and phenology, agronomic potential and response to drought.

3.1. Agro-morphological characterization study (Experiment 1)

All the observed morphological traits showed significant variation among accessions (at probability level $p < 0.05$). The mean plant height of accessions at full flowering varied from 57 to 127 cm (Table 6). The full range from prostrate to erect accessions was present in the collection. Some accessions had almost no stolons, whereas others were strongly stoloniferous. Internode length ranged from 9 to 22 cm. Pubescence of the ligule varied in hair length (2.3–6.3 mm) and density (sparse to very dense). Between 8 and 16 spikes per inflorescence were counted. The average awn length of accessions was 2.6–7.2 mm, whereas the length of the third floret was as different as 0.11–1.92 mm. Florets were sparsely to densely pubescent at various positions. Many accessions started flowering at 3 weeks after cutting, while the last accession took 12 weeks until the first flowers emerged. The flowering duration varied from 7 to 17 weeks.

Clustering was distorted by two very distinct accessions, ILRI 13175 and ILRI 9422, which were excluded from the later analyses. Cluster analysis highlighted six groups, explaining about 40% of the variation (Fig. 3). Group I contained prostrate to semi-prostrate accessions with broad leaves, long glumes and a long duration of flowering. Tall semi-erect accessions with few stolons and relatively large spikelets were combined in Group II. Group III consisted of semi-prostrate to semi-erect accessions, characterized by thin

culms and narrow leaves. A subgroup of two accessions (ILRI 899 and ILRI 1118) was separated by their high degree of branching, with an average of five branches per main culm. The late flowering accessions of the collection (6–8 weeks) were found in Group IV. Morphologically, these accessions resembled those of Group III in many traits. Accession ILRI 7757 was associated with this group despite its early flowering date (4 weeks). Group V included tall accessions of semi-prostrate to semi-erect habit with long internodes. The accessions of Group VI were characterized by thick culms and marginal hairiness; they were semi-erect to erect with few stolons. The most distinct outliers, ILRI 9422 and ILRI 13175, which were excluded from the final cluster analysis, formed their own group characterized by their prostrate and strongly stoloniferous habit. Differences among groups are summarized in Table 6.

Discriminant analysis indicated that many traits contributed to the distinction among groups; there was no trait of outstanding relevance.

PCA reflected the results of cluster analysis, indicating that almost all traits contributed more or less equally to the first principal components. There were no high loadings of any trait on the first two components, which accounted for 20.5% and 14.8% of the variation, respectively. Groupings resulting from cluster analysis could be identified, when accessions were plotted against the first two principal components.

There was a large diversity among accessions for all agronomic traits measured. Dry matter accumulation varied not only in total amount but also in the growth pattern observed over three harvests (Table 7). Very early accessions with low total biomass productivity (ILRI 7757 and ILRI 13330 cv. Boma), early and highly productive accessions (ILRI 15575), and highly productive accessions at later stages (ILRI 7384 cv. Katambora) could be distinguished from constantly low yielding accessions. In general, yields were found to increase substantially at later harvests (after 12 weeks). Total yields over three harvests ranged from about 400–2,100 g m⁻², whereas early yields (after 6 weeks) varied from 40 to 270 g m⁻². Leaf percentages were found in the range of 66–96% of the total dry matter.

The cluster dendrogram was truncated at the 6-group level, explaining about 55% of the total variation (Fig. 4). Group I consisted of tall accessions with medium yields and high leaf percentages at later cuttings. The leafiest accessions of the whole collection were found in Group II. However, in this group yields were low, especially when plants were cut after 6 weeks of growth. Group III comprised tall accessions, with rather low yields and low leaf percentages at later harvests. Very short accessions with low total yields and extremely low leaf percentages were combined in Group IV. Accessions with the highest total yields of the collection formed Group V, whereas accessions with very high early but medium total yields and medium leaf percentages were accumulated in Group VI.

Discriminant analysis demonstrated that traits such as leaf percentage and early yields contributed most to the discrimination among agronomic groups (Table 7).

Table 6
Mean and range of some morphological and phenological traits showing variation among 6 cluster groups – obtained by Ward's clustering method – and two outliers. Key characteristics with obviously distinct means and value ranges are highlighted for each group with grey shading.

Morphological group (no. of acc.)		Plant height	Growth habit	Stolons	Culm thickness	Internode length	Leaf length	Leaf width	Ligule hair density	Ligule hair length	Spikelet length	Spikelet width	Awn length	Hair length awn base	Hairiness floret base	Lower glume	First flowering	Flowering duration
I (15)	Mean	92.9	2.4	3.1	4.2	12.8	26.9	6.5	3.6	4.4	3.2	1.6	5.0	1.6	3.7	2.1	3.7	14.0
	Min.	72.5	1.5	1.3	3.6	9.6	20.0	5.8	3.1	3.6	3.0	1.5	3.9	1.1	3.0	1.9	3.0	11.0
	Max.	107.0	3.0	5.0	4.9	17.3	33.6	7.4	5.0	4.9	3.4	2.0	7.2	2.0	5.0	2.2	5.0	17.0
II (7)	Mean	101.0	3.6	1.6	4.1	12.7	24.9	6.0	3.2	4.0	3.3	1.8	5.0	1.4	3.1	2.1	3.4	12.0
	Min.	91.7	3.0	1.3	3.9	10.7	19.5	5.0	3.0	3.1	3.1	1.7	3.8	1.2	2.6	2.0	3.0	10.0
	Max.	113.5	4.0	2.3	4.7	14.3	27.6	6.7	3.5	4.9	3.7	1.9	6.9	1.8	3.5	2.2	4.0	14.0
III (13)	Mean	92.1	2.8	2.5	3.8	13.1	25.2	5.4	3.2	3.9	3.0	1.5	4.0	1.2	3.2	1.8	3.8	12.1
	Min.	74.4	2.0	1.7	3.2	9.0	16.5	4.1	2.2	2.7	2.9	1.4	2.9	0.8	2.0	1.6	3.0	8.0
	Max.	109.2	4.0	4.1	4.7	20.9	30.3	6.3	3.6	4.6	3.2	1.7	4.5	1.6	3.9	2.1	5.0	16.0
IV (4)	Mean	101.3	3.3	2.0	4.1	12.4	31.8	5.4	3.4	5.1	3.1	1.6	3.7	1.2	3.1	1.9	6.0	8.5
	Min.	91.6	2.0	1.5	3.9	11.6	27.4	5.0	2.6	4.1	3.0	1.3	3.2	0.8	2.4	1.7	4.0	8.0
	Max.	106.7	4.0	2.8	4.3	12.8	34.4	5.8	4.6	6.3	3.2	1.8	4.3	1.4	4.0	2.0	8.0	10.0
V (10)	Mean	109.0	3.1	3.1	4.3	17.3	27.4	5.5	3.4	4.3	3.0	1.7	3.6	1.4	3.9	1.9	3.4	11.7
	Min.	90.0	2.0	1.6	3.9	11.9	21.6	4.9	2.5	3.7	2.9	1.5	3.4	1.2	3.3	1.8	3.0	8.0
	Max.	127.0	4.0	4.2	5.1	22.0	33.6	6.4	4.4	5.3	3.1	2.0	3.9	1.5	4.6	2.1	5.0	15.0
VI (11)	Mean	101.0	3.7	1.9	5.1	13.0	24.5	6.3	2.7	2.9	3.1	1.6	3.7	0.8	2.8	1.7	3.4	9.9
	Min.	91.1	3.0	1.3	4.5	10.5	16.7	5.1	2.1	2.3	3.0	1.4	2.6	0.6	2.5	1.4	3.0	7.0
	Max.	113.3	5.0	3.0	5.9	14.5	34.1	7.7	3.2	3.7	3.4	1.8	4.6	1.1	3.4	2.0	5.0	15.0
Outlier (2)	Mean	66.3	1.5	4.9	3.4	10.7	22.2	5.4	4.1	4.6	2.8	1.4	3.0	1.0	3.2	1.7	8.0	11.5
	Min.	57.1	1.0	4.7	3.4	10.1	22.1	5.2	3.9	4.5	2.5	1.2	2.9	0.9	2.6	1.7	4.0	8.0
	Max.	75.5	2.0	5.0	3.5	11.4	22.3	5.6	4.2	4.8	3.0	1.7	3.1	1.2	3.8	1.7	12.0	15.0

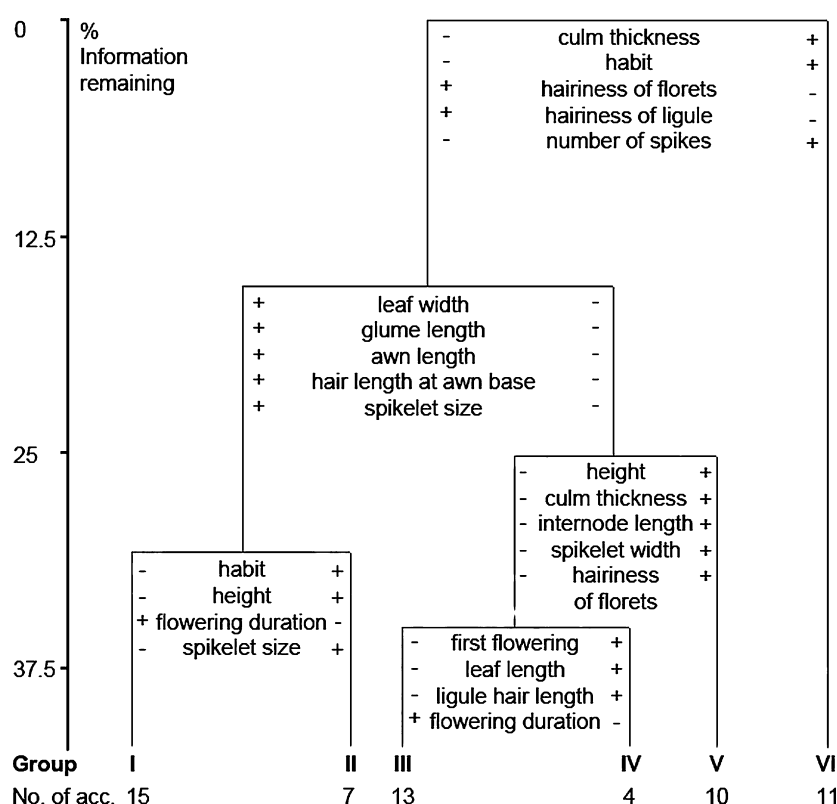


Fig. 3. Cluster dendrogram showing the separation into six groups using Ward's method on the morphological and phenological traits of 60 *C. gayana* accessions. Accessions in each grouping are listed in Table 1.

Table 7

Mean and range of agronomic traits showing variation among six cluster groups obtained by Ward's clustering method. Key characteristics are highlighted with grey shading.

Agronomic group (no. of acc.)		Plant height [cm]	Yield 6 weeks [g m ⁻²] ^a	Yield 8 weeks [g m ⁻²] ^a	Total yield [g m ⁻²]	Leaf percentage 6 weeks [%] ^a	Leaf percentage 12 weeks [%] ^a
I (18)	Mean	101.3	123.5	191.8	846.6	82.3	83.5
	Min.	91.6	94.3	154.2	669.9	74.6	80.8
	Max.	109.6	176.5	247.6	1,164.7	91.8	87.5
II (10)	Mean	92.0	92.4	157.3	746.9	90.0	85.6
	Min.	72.5	63.2	130.9	554.5	84.1	82.7
	Max.	107.0	119.8	196.3	1,004.0	96.3	91.0
III (8)	Mean	104.1	82.9	140.4	711.9	77.8	76.8
	Min.	91.1	44.1	96.4	399.2	70.7	72.2
	Max.	119.7	142.3	182.5	1,185.0	92.0	81.8
IV (5)	Mean	76.9	63.2	201.3	594.6	73.5	75.3
	Min.	57.1	34.0	112.4	404.4	66.1	66.8
	Max.	86.8	80.7	271.6	898.0	80.2	79.0
V (14)	Mean	103.8	144.2	242.9	1,349.3	79.2	75.8
	Min.	82.7	53.3	200.0	949.2	67.4	71.4
	Max.	127.0	198.8	312.9	2,116.2	91.9	81.4
VI (7)	Mean	89.2	187.2	222.6	862.4	78.4	80.8
	Min.	76.9	118.8	207.1	690.9	72.1	76.9
	Max.	103.5	270.3	248.4	1,149.2	86.7	87.0

^a Traits contributing most to the division in the discriminant analysis.

The first principal component obtained by PCA contrasted total yield and leaf percentages at later cuttings, implying that the main source of variation was between high yielding accessions with low leaf percentages and accessions with the converse relationship. The second principal component could be readily interpreted as the 'leaf percentage' component. When plotting different components against each other, all cluster groups could be clearly distinguished. The first three principal components accounted for 40%, 25% and 13% of the total variation, respectively.

3.2. Drought-stress experiment (Experiment 2)

The mean soil moisture content in the drought-stress treatment decreased during the experimental period (from 13.6% to 6.8% and from 14.6% to 7.5% at 0–0.2 and 0.2–0.4 m depth, respectively), whereas soil moisture content was as high as 15 to 23% at both depths in the irrigated treatment.

Great variability in terms of drought response was detected among accessions. A split-plot ANOVA showed significant differences between irrigation treatments for dry weight, fresh weight

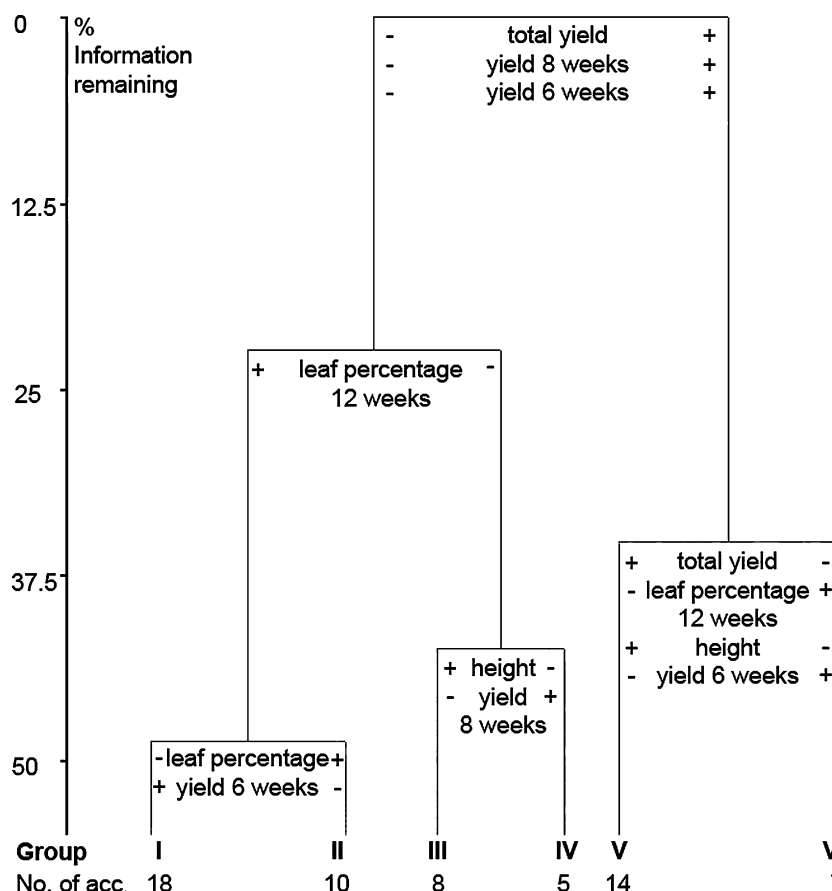


Fig. 4. Cluster dendrogram showing the separation into six groups using Ward's method on the agronomic traits of 62 *C. gayana* accessions measured under full irrigation. Accessions in each grouping are listed in Table 1.

and leaf senescence ($p < 0.01$). Significant differences among accessions were found for all five traits that were observed ($p < 0.01$). Additionally, for fresh weight, plant height, and leaf senescence, significant interactions were detected between irrigation treatment and accession ($p < 0.01$) (Table 8).

Dry matter production per plant was reduced in the drought-stress treatment by up to 72% (Table 9). Most accessions were less productive under drought. Surprisingly, ILRI 7384 cv. Katambora, ILRI 13229 cv. Elmba, and ILRI 708 produced higher yields per plant under water deficit. Plant height varied up to 68% between treatments. Under drought stress, plant height was reduced for most accessions, constant for a few, and increased for 15 accessions. All accessions displayed onset of leaf senescence due to drought, with up to 43% of the total leaf area dying off. Flowering under drought was accelerated for 38 accessions by up to 2 weeks and was delayed for 10 accessions, whereas 11 accessions flowered at the same date under both treatments.

Clustering revealed seven 'drought-response groups', explaining about 58% of the variation (Fig. 5). Group I and Group V

represented accessions with low yields under drought. In contrast, Group II consisted of tall accessions with high dry matter production under water deficit (Table 10). Group III aggregated accessions with a very low yield reduction due to drought (Table 11), but also extremely low yields under irrigation. Further, flowering was accelerated in this group. The accessions within Group IV increased their plant height under water deficit and produced medium yields under both treatments. Group VI was described best by its late flowering under both treatments and a high yield reduction due to drought. Accession ILRI 13175 (Group VII) appeared to be the most distinct from the rest of the collection. The outlier was characterized by the highest leaf senescence, high reduction in growth and productivity and a strongly delayed date of anthesis.

The groups resulting from cluster analysis were described best by plant height and reduction in dry matter production, as shown by discriminant analysis (Table 9).

PCA, including all 18 traits observed in the experiment, did not reflect variation in plant production under stress. The first components mainly accounted for performance of the irrigated treatment.

Table 8

F-values and probability levels (*p*) of the split plot ANOVA in the drought-stress experiment. Significant *p* levels are bold printed.

Source of variation		Plant height	Dry weight	Fresh weight	Leaf senescence	Weeks to flowering
Treatment (Treat.)	<i>F</i> -value	6.41	596.97	2,170.70	2,398.28	9.44
	<i>p</i>	0.13	<.001	<.001	<.001	0.09
Accession (Acc.)	<i>F</i> -value	11.10	3.46	3.59	3.31	4.85
	<i>p</i>	<.001	<.001	<.001	<.001	<.001
Interaction Treat. * Acc.	<i>F</i> -value	1.66	1.32	1.65	2.51	1.29
	<i>p</i>	<.001	0.07	<.001	<.001	0.09

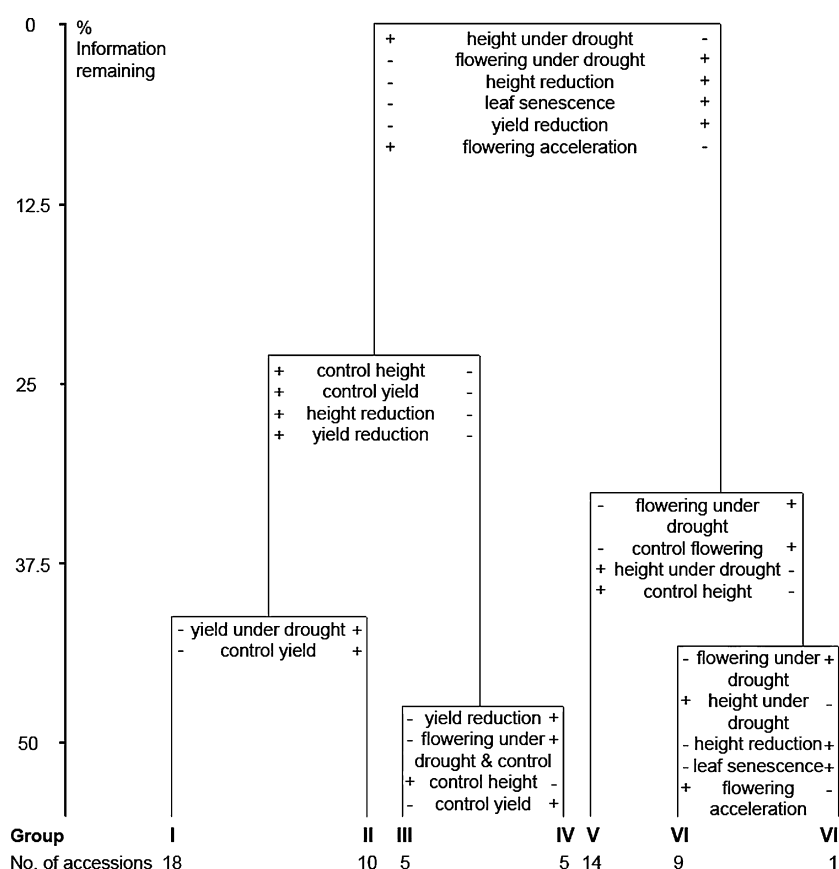


Fig. 5. Cluster dendrogram showing the separation into seven groups using Ward's method on the traits observed in the drought-stress experiment including 62 *C. gayana* accessions. Accessions in each grouping are listed in Table 1.

3.3. Correlations among the datasets

No strong correlation was revealed between any agromorphological traits measured in the characterization study and observations from the drought-stress experiment, neither in the correlation analysis ($r \leq 0.5$) nor in the discriminant analysis. When relating morphological traits to drought-response groups using discriminant analysis, weeks to first flowering and awn length differed significantly among group means ($p < 0.01$). The associated significant discriminant function ($p < 0.01$) mainly separated the outlier ILRI 13175 (Group VII) from the remaining groups. When excluding that outlier, none of the functions were significant. No agronomic traits varied significantly among drought-response group means, or vice versa.

Accessions were collected from a wide range of environments and originated from at least 10 different African countries. The latitude of the known collection sites varied between 17.8° S and 12.2° N, altitude ranged from 33 to 2410 m a.s.l. Annual mean temperatures in the areas of origin were in the range from 15 to 27° C. Annual precipitation varied between 740 and 1525 mm and some sites were characterized by a pronounced dry season. Accession ILRI 13175 stood out for its conspicuously humid collection site.

Several correlations between traits observed in the agromorphological characterization study and the environment of the collection site (for those accessions with the respective information) were significant, but none were high. The highest significant correlation was between total yield at the evaluation site and annual precipitation at the collection site ($r = -0.58$, $p < 0.01$), with accessions originating from dry environments yielding higher than those from more humid environments. In the drought-stress exper-

iment, correlations between environmental variables and observed traits were generally poor (with $r < 0.4$).

Discriminant analysis showed that no environmental variable could be used to explain the separation among morphological, agronomic or drought-response groups. These results are consistent with those of PCA. Several significant correlations between sample scores on principal components (for accessions with collection site information) and environmental variables were detected, but none were higher than $r = 0.5$.

4. Discussion

4.1. Methodological issues

Owing to the lack of standard descriptors for *C. gayana*, many traits were observed to determine which ones best differentiated among accessions. Not all traits used in this study could be "easily seen by the eye", were "highly heritable" and "expressed in all environments" (Tyler et al., 1985), as normally assumed for the characterization of germplasm material. Although the information recorded was site specific, the characterization of plants at one location under exactly the same conditions enables a comparison of morphological details, which would be impossible when observing each plant in its natural habitat (Andersson et al., 2006). This allows clustering of accessions that show a similar morphology in one environment. However, findings should be validated by replications across seasons and locations. Pests and diseases of *C. gayana* have low economic impact and mainly occur outside the tropics (Barnard, 1972; Cook et al., 2005); therefore tolerance traits were excluded from the study.

Table 9
Mean and range of observed traits in the drought-stress experiment showing variation among six 'drought-response groups' obtained by Ward's clustering method. Key characteristics are highlighted with grey shading.

Drought-response group (no of acc.)	Dry weight under drought [g/plant]	Plant height under drought [cm] ^a	Flowering under drought [weeks]	Control dry weight [g/plant]	Control plant height [cm] ^a	Control flowering [weeks]	Dry weight reduction [%] ^a	Plant height reduction [%] ^a	Flowering acceleration [%]	Leaf senescence [%]
I (18)	Mean 27.6 Min. 17.1 Max. 35.4	50.5 36.3 66.3	3 2.3 4	52.8 33.4 77.1	55 43 65.7	3.6 3 4	44.6 20.5 68.2	8.1 -5.1 32.2	15.8 0 33.3	15.7 1 31.3
II (10)	Mean 43.9 Min. 36.6 Max. 54.2	51 35.3 60.3	2.9 2 3.7	78 60.5 100.7	59 41 73.3	3.2 2.7 4	42.3 20.7 59	12.3 -22.8 36.5	6.9 -25 41.7	12.4 5.7 24
III (5)	Mean 31 Min. 21.2 Max. 38.1	48.3 39.7 58	2.7 2 3	30.5 23.1 36.7	43.8 33.6 63.7	3.3 2.7 3.7	-2.1 -20.5 22.6	-14.5 -42.7 18.8	18.3 10 25	13.1 7.7 22.7
IV (5)	Mean 28.6 Min. 22.6 Max. 37.2	39.4 16.7 61.3	3.5 2.7 4	49.4 36 66	28.8 13 36.3	4.1 3.7 4.7	40.4 18.7 56	-34.7 -68.8 -9.7	14.8 0 33.3	16.1 9.3 28.7
V (14)	Mean 24.3 Min. 14.1 Max. 35.1	34.7 24.3 47.7	3.5 2.7 4	54.5 21.9 92.6	49.2 32.7 60.3	3.3 2.3 4	51.9 23.3 71.6	28.9 9.5 43.7	-8 -28.6 20	26.3 9.7 41.7
VI (9)	Mean 22.9 Min. 14.9 Max. 38.1	24.7 16.7 38.7	4.3 3.7 5.3	48.3 31.2 71.8	32.2 17.7 40.3	4.7 4 5.3	52 42.1 60.2	22.6 -1.8 38.3	10 -6.7 20	24.9 8.7 39.3
VII (LURI 13175)	26.6	9	6	65.7	28.3	4	59.4	68.2	-50	43.3

^a Traits contributing most to the division in the discriminant analysis.

Although the application of molecular techniques may provide better differentiation and objective comparison of germplasm material, it cannot replace morphological and agronomic characterization because these traits are of most interest to breeders (Feuerstein, 1998). Further, molecular markers alone do not identify any functional relationship and adaptation to the environment (Heywood and Dulloo, 2005).

There is a lack of standard concepts for measuring drought resistance in forage grasses (Tischler et al., 1991; Blum, 2000), but many researchers agree that the response to drought stress in terms of plant production should be tested as a field experiment performed in the relevant agro-ecosystem (Blum, 2000; Ceccarelli et al., 2007). Several authors have concluded further that experiments should be done under both favorable and drought-stress conditions, to detect the relative performance of accessions under water deficit compared to well-watered conditions (Sio-Se Mardeh et al., 2006). Considering the urgent demand for a better dry season feed supply in sub-Saharan Africa (Larbi et al., 1992) and reports that *C. gayana* can grow and remain green well into the dry season (Boonman, 1993), this study focused on the ability of accessions to produce during the dry period.

In this experiment, the applied flood-irrigation technique was chosen due to the facilities available at the experimental site in Ethiopia. Although it was not possible to control exactly the amount of water received by each plant, measurements of gravimetric soil water content at different positions within plots demonstrated that an adequate distribution of irrigation water was achieved. The soil water content assessments further allowed for an estimation of the imposed extent of drought stress.

The choice of traits to measure in the experiment was necessarily pragmatic, balancing the number of accessions to be included, available resources and the presumed agronomic relevance. Time to flowering was observed, because accelerated flowering is seen as a drought avoidance strategy in grasses (Ludlow, 1980; Farooq et al., 2009). Early flowering types within the species appeared to be generally more drought resistant in *Dactylis glomerata* (Thomas et al., 1998) and also in *C. gayana* (Boonman, 1978). *C. gayana* is daylength sensitive (Tarumoto, 2005), with short daylength induced flowering in tetraploid cultivars but daylength neutral diploid cultivars. However, no influence of daylength on flowering was expected in tropical latitudes (Bogdan, 1977) because variation in daylength is very small throughout the year (van de Wouw, 1988). *C. gayana* flowers throughout the growing season under tropical conditions, while two distinct flowering periods can be observed in the subtropics of the Southern hemisphere (Cook et al., 2005).

Hierarchical cluster analysis, together with principal component analysis and discriminant analysis has proven to be a useful tool for studying the diversity in forage species (Andersson et al., 2006; Jorge et al., 2008), and also allowed the present collection of *C. gayana* accessions to be clustered successfully in groups with similar characteristics. However, the results have to be seen with some limitations. Most variables analyzed in the present study were not perfectly normally distributed, and homogeneity of covariances and group-size requirements of discriminant analysis were not met for all datasets. Accordingly, the significance tests should be interpreted as a tendency rather than absolute. However, the variables used in the final analysis could be considered as roughly normally distributed, and many researchers agree that the main objective to summarize most of the variation present in the data can be achieved, even if the data do not fulfill all prerequisites (Brown and Wicker, 2000; Jolliffe, 2002; Kaufman and Rousseeuw, 2005).

The short period of experimentation and its realization at one single location posed a major limitation to our drought-stress experiment. Still, the presented findings are an important step to assess response to drought stress of a wide range of *C. gayana* collections and cultivars. They allowed, for the first time, a preliminary

Table 10

Promising accessions in the drought-stress experiment showing the highest dry weights under drought.

Accession number		Dry weight under drought [g/plant]	Control dry weight [g/plant]	Reduction in dry weight [%]
1.	993	54.2	68.4	20.7
2.	6625	52.1	79.7	34.7
3.	719	51.8	100.7	48.6
4.	13317	47.2	60.5	22.0
5.	890	42.2	67.7	37.6
6.	13053	39.1	73.1	46.4
7.	6630	38.7	79.9	51.6
8.	18487	38.4	93.5	59.0
9.	13110	38.3	89.1	57.0
10.	743	38.1	71.8	46.9

selection of promising accessions which deserve further examination.

4.2. Variation within the collection

The observed variation within the collection broadly agrees with descriptions in floras and findings of other researchers, regarding both among and within accession variability (Boonman, 1978; Loch et al., 2004). Although differences among accessions were significant and ranges of traits were markedly distinct, the variation was even larger within than among accessions for awn length and internode length. This complies also with results of Boonman (1978, 1993), who found a wider range in heading date within than among cultivars and with those of Ubi et al. (2003), who detected genetic diversity within cultivars being larger than among cultivars. *C. gayana* is a cross-pollinating species (Loch et al., 2004) and although most of the accessions in the study were collections from natural populations or commercial cultivars acquired from reputable seed companies, some of the materials were breeding lines or acquired from research institutes with no information on isolation during seed production. Hybridization among accessions from the same source prior to establishment of the experiment could have resulted in crossing and more similarity than expected.

The collection of *C. gayana* assessed in this study, although very variable, might still not reflect the variation that exists in the species. The presence of distinct outliers like accession ILRI 13175 normally suggests the availability of more variation in nature (van de Wouw et al., 1999a). If further collection is undertaken, it should be focused on environments or regions that were under-represented in the collection. *C. gayana* is widely distributed in sub-Saharan Africa (Rattray, 1960; Herlocker, 1999) and these collections, which were largely made in East Africa, may not represent the full range of diversity expected in the species. *C. gayana* is also reported as naturally found in regions with about 500–1500 mm rainfall per year (Skerman and Riveros, 1990), but no accession was collected from an area with an annual precipitation of less

than 700 mm. Moreover, none of the accessions was reported to be of West African origin and germplasm from this region could be a useful addition to the present collection (Fig. 1, Table 1).

4.3. Promising accessions for use as livestock feed

Within the present collection, various types of accessions could be differentiated according to their agronomic traits and prospective use. The data presented in this paper focuses on biomass production and leaf percentage as proxy characters for suitability for feed. Detailed nutritional analyses have been completed on all accessions and will be presented in a separate paper.

Several accessions of the high yielding agronomic Group V could be of particular interest for grazing. ILRI 7384 cv. Katambora, ILRI 13317, ILRI 18487, ILRI 15575, and ILRI 13229 were among the highest yielding accessions of the collection with strongly stoloniferous behavior and a semi-prostrate growth habit. Vigorous lateral growth should allow them to colonize gaps resulting from trampling and (except for ILRI 13229) they should be preferentially selected by animals for their broad leaves (Louault et al., 2005). Finally, their early flowering behavior enables these accessions to reproduce before any disturbance occurs.

For haymaking, taller and more erect accessions will be the most suitable. Accessions ILRI 6634 cv. Bandai, ILRI 6628 cv. Nakuru, ILRI 6627 cv. Pioneer and ILRI 6633 cv. Callide (Group V), as well as ILRI 645 and ILRI 977 (Group I) provided high total yield, tall plant height, semi-erect growth habit and few stolons. Among these accessions, ILRI 6627 cv. Pioneer and ILRI 977 attracted attention for constantly high leaf percentages and ILRI 6634 cv. Bandai for an extremely high leaf percentage when cut early.

Accessions of the early yielding Group VI have high potential for haymaking with frequent cutting cycles. In particular, accession ILRI 18498 showed promise combining high yields at all three harvests with high leaf percentages. However, Group VI was characterized by thin culms which might pose a risk of lodging.

Where high leaf percentage is considered the main trait of interest, for example for breeding purposes, the leafy Group II contained

Table 11

Promising accessions in the drought experiment showing the lowest reductions in dry weight under drought.

Accession number		Dry weight under drought [g/plant]	Control dry weight [g/plant]	Reduction in dry weight [%]
1.	7384	27.9	23.1	-20.5
2.	13229	35.5	31.0	-14.3
3.	708	38.1	36.7	-3.8
4.	1118	32.4	34.3	5.4
5.	9422	29.2	36.0	18.7
6.	15569	31.3	39.4	20.5
7.	993	54.2	68.4	20.7
8.	13317	47.2	60.5	22.0
9.	15578	21.2	27.4	22.6
10.	2023	25.0	32.6	23.3

the accessions of choice. However, the only high yielding accession of the leafy group was ILRI 701.

The outliers, accessions ILRI 9422 and ILRI 13175, with their prostrate growth habit and prolific stolons could be of use also for erosion and weed control.

In some parts of Australia and Japan, where *C. gayana* is cultivated, frost is the most limiting factor for growth of tropical pasture species (Loch and Harvey, 1999; Komatsu and Shoi, 2005). Diversity in low-temperature resistance has been reported within *C. gayana*, and plants originating from higher altitudes are considered to be the most promising (Ludlow, 1980; Loch et al., 2004). Two of the accessions (ILRI 13229 and ILRI 18489) collected from altitudes above 2000 m a.s.l. were among the highest yielding and leafy accessions in our experiment and might be interesting material to evaluate under low temperatures.

4.4. Promising accessions for dry areas

C. gayana is widely grown in drought-prone regions and credited with reasonable drought resistance. In this experiment, significant variation in drought response was observed among accessions, suggesting that the extent of differences among genotypes is sufficient to provide some scope for selection to improve performance of *C. gayana* in drought-prone areas.

The most promising accessions for dry areas were found in drought-response Groups II and III. The highly productive accessions under drought stress (Group II) featured low leaf senescence and tall plant height. Flowering was accelerated for most accessions (except for ILRI 13053). The accessions ILRI 993, ILRI 6625 cv. Samford, and ILRI 719 produced the highest yields per plant under drought stress (Table 10). Three accessions of drought-response Group II also belonged to the highest yielding accessions in the agronomic evaluation study under full irrigation, ILRI 6625 cv. Samford, ILRI 18487 and ILRI 13317.

The accessions with very low reductions or even an increase in dry matter production under drought stress (Group III) were also characterized by low leaf senescence and accelerated flowering. Their extremely low yields under irrigation (Table 11) could indicate either that these accessions generally do not thrive well under irrigation or that they did not reach their full potential due to other reasons, such as slow establishment. When comparing their performance to that in the agronomic evaluation, which was conducted on established plots under weekly irrigation, the latter explanation seemed the case. Further, the cultivar Katambora is generally known for its good drought resistance (Cook et al., 2005), but at the same time showed inferior early vigour compared to other cultivars (Barnard, 1972; Njarui and Wandera, 2004).

4.5. Prediction of drought response based on morphological traits

A strong relation between morphology and drought response could help to predict adaptation to drought based on morphological traits, which are more convenient to assess. The analysis aimed to determine if any agro-morphological traits were related to the performance of accessions under drought stress, as was reported for other grass species (Geerts et al., 1998; Fu and Huang, 2004; Volaire, 2008). However, no strong link could be detected in the present study. This is in contrast to findings of Boonman (1978, 1993), who observed high correlations between heading date and drought resistance in *C. gayana* cultivars. However, it agrees with the frequently stated difficulty to identify a single morphological trait that could serve as an indicator for drought resistance, which is usually expressed in a complex interaction of traits (Johnson, 1980; Blum, 2002).

4.6. Geographic pattern of the variation

One question, which guided our research, was the search for an ecological explanation for the observed phenotypical variation. For other tropical grasses, a strong correlation between phenotypical differentiation within the species and rainfall at the collection site was revealed (Theunissen, 1997; van de Wouw et al., 2008). Even relations between climatic conditions at the origin and drought resistance were detected (Voltaire, 1995). Accordingly, the hypotheses with respect to drought response in *C. gayana* were that accessions originating from relatively dry regions were more drought resistant than those from relatively wet areas, or that accessions from heterogeneous environments were more drought resistant than those from areas with rather constant conditions.

However, in the present study the observed phenotypical traits did not show any apparent trend with respect to gradients in moisture, temperature or latitude represented by their collection sites or to their geographic distance. These results do not comply with those of Boonman (1978, 1997), who explained the differentiation of *C. gayana* cultivars into early-heading and late-heading ecotypes as a climatic adaptation to the length of the rainy seasons in the habitat of collection. This difference may be the result of using a large number of diverse accessions for this study and earlier studies being conducted on few cultivars.

The current lack of correlation could also be a reflection of the limited information on the collection site environments. The respective information was available for half of the accessions only. Further, parameters were lacking that are known to have an influence on the distribution of grasses such as soil pH or soil texture (Herlocker, 1999).

Another explanation could be that differences among environments were not large enough to clearly separate ecotypes. This hypothesis can be supported by the particular case of two accessions in the extremes. Accession ILRI 13175, which originates from the most humid of all known collection site environments, was identified as an outlier in all datasets and appeared not to be drought resistant at all. In contrast, accession ILRI 7384 cv. Katambora, which is reported to originate from an area with an annual precipitation below that of any other collection site, outproduced all other accessions in the agronomic evaluation under full irrigation and showed an increased dry matter production under drought stress. Katambora is thought to be most likely collected from sandy river banks, implying that the original habitat was not dry permanently but rather very variable. This example illustrates further that low rainfall does not necessarily reflect low moisture availability at the specific habitat where the plants were growing. Plants could have been collected from sites characterized by high soil moisture, such as valley bottoms, river banks, or margins of flood plains.

4.7. Performance of commercial cultivars in the present study

The observations of the present study were largely consistent with the available descriptions of commercial cultivars. Discrepancies were mainly regarding productivity characteristics. The cultivars Giant (ILRI 15574), Masaba (ILRI 6630) and Mbarara (ILRI 7103) were less productive than reported by other researchers (Boonman, 1997). Both 'giant' types, cv. Giant and Callide (ILRI 15574 and ILRI 6633), did not show the coarse appearance described elsewhere (Loch et al., 2004). In contrast, cv. Pioneer (ILRI 6627) appeared more robust and more productive on sandy soils than expected (Cook et al., 2005).

One reason for discrepancies among experimental findings could be a strong influence of the environment. In the present experiment, the cultivars Katambora and Pioneer have been out-competing Mbarara and Masaba, whereas the converse situation was observed under more humid conditions in Kenya (Boonman,

1997). This complies with the suggestion of Loch et al. (2004), that Katambora is better suited to drier areas and the tetraploids such as Mbarara and Masaba, both originating from relatively high rainfall areas, to wetter areas.

On the other hand, high within-cultivar variation in *C. gayana* is a well established fact (Boonman, 1978) that may be one of the reasons why commercial cultivars are not consistent in their descriptions or performance. Further, genetic drift is supposed to occur in *C. gayana* (York and Nyamadzawo, 1990), and in Australia, different ecotypes of the cultivar Katambora exist (Loch et al., 2004). A genetic characterization of the collection could provide further evidence to confirm the classification of this study.

5. Conclusions

Considerable diversity in morphology, agronomic potential and response to drought stress observed within the collection of 62 *C. gayana* accessions shows the potential of the species as a valuable feed resource, suited for use under a range of conditions in tropical areas. These findings provide an important step to assess the diversity of a wide range of *C. gayana* accessions, including both collections from the wild and commercial cultivars.

The clustering of the *C. gayana* collection identified groups of similar accessions with appropriate characteristics for different uses (hay making, grazing or erosion control) and environments (drought-prone areas). These groups can be targeted for further testing in specific regions or for specific uses based on the observed traits. However, future investigations should cover long term experiments replicated over years and locations to clarify the potential of accessions which proved to be promising within this study.

On all accounts, the results from this study will greatly increase the available information on phenotypic diversity in *C. gayana* and options for utilization of the collection. They will facilitate breeding and improvement of *C. gayana* as livestock feed and encourage conservation and use of the existing diversity within the species.

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