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Germination and establishment of Sahelian rangeland species

II. Effects of water availability

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Summary. In order to understand the vegetation dynamics of Sahelian rangelands, the effects of water availability on germination were investigated under controlled conditions in climate rooms. Mixtures of seeds from species that occur in the same habitats but have different seed characteristics were exposed to different watering treatments. Responses to the treatments in the climate room were comparable to those observed in the field situation. However, induction time was generally somewhat longer, and in some cases the germination rate was lower. The size, frequency, and timing of showers decisively influenced the ratio between the proportions of the various species among the seedlings that established. In general, conditions were favourable for fast germinating species with rainfall patterns without serious intermittent periods of drought, whereas the conditions became favourable for the slower germinating species after dry periods had eliminated the seedlings of the fast germinating species. Large differences in drought resistance were found among seedlings of different species. This causes more differentiation in establishment of species. Seed losses during the pre-emergence phase were also important. These losses can be very high, especially for the fastest germinating species. The dynamics observed in field situations could be explained on the basis of germination characteristics and drought resistance.

Key words: Germination – Sahel – Rangeland – Vegetation dynamics – Drought resistance

In general the vegetation of Sahelian rangelands consists of annual plant species; the vegetation composition can vary considerably from year to year (e.g. Boudet 1975; Penning de Vries and Djitèye 1982; Hiernaux et al. 1983). Important year-to-year variations in species composition have also been observed in other arid areas (Evenari and Gutterman 1976; Noy-Meir and Negbi 1980). Experimental and theoretical research has shown the advantage of a fast start in situations where there is competition for growth factors (De Wit 1960; Spitters and Aerts 1983). As water and nutrients are in limited supply in Sahelian pastures (Penning de Vries and Djitèye 1982), germination and establishment are presumably important in the vegetation dynamics there.

In a previous article (Elberse and Breman 1989) the seed properties of approximately 30 species, particularly their germination characteristics, were described. These characteristics were ascertained under optimum conditions. Though some of these characteristics differ under the suboptimum conditions that occur in the field, it has been shown that this does not substantially alter how the various species are classified on the basis of these characteristics (Elberse and Breman 1989; Cissé 1986). In addition to germination strategy, the drought resistance of the seedlings is a species characteristic determining the earliness and success of establishment in an environment like the Sahel, where each year there is a different pattern of periods with a shortage or lack of water alternating with rainy days, especially during the onset of the rainy season. The degree and duration of wetting of the environment of the seeds also depends on the physical properties of the substrate (Cissé 1986).

Our experiments were intended to show whether field observations on vegetation dynamics could be understood by studying the effects of water availability on germination and establishment under controlled conditions. Mixtures of seeds of species that occur together in the field but have different germination characteristics were exposed to different watering treatments, mimicking situations frequently observed in the field. Our hypothesis was that a rainy season that starts with small frequent showers will be advantageous for the fast germinating species. When a rainy season is interrupted by a period of drought in which the seedlings die, the fast germinating species will lose a great part of their seeds and the slowly germinating species will germinate when the rainy season continues with sufficient rain and will dominate the vegetation. When the rainy season starts with big showers both the fast germinating and

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Table 1. Dry matter production (tonne ha^{-1} a^{-1}) and relative contribution (%) of the most dominant species at the end of the rainy season on a loamy sand area in Mali at the 400 mm isohyet in four consecutive years

Plant species	1976	1977	1978	1979
Eragrostis tremula	53	8	8	0
Cenchrus biflorus	8	34	30	10
Elionurus elegans	14	27	17	63
Schoenefeldia gracilis	0	1	27	1
Other species	25	30	18	26
Total rainfall (mm)	420	200	350	300
DM yield tonne ha^{-1} a^{-1}	2.0	0.6	2.5	0.9

the slowly germinating species will be in the vegetation, but the fast germinating species will dominate. In this paper the results of experiments on only two situations are presented; both these situations are related to strong year-to-year dynamics: *Situation 1.* The dominance of *Schoenefeldia gracilis* and *Borreria radiata* on sandy loam in the southern Sahel (Niono, Mali). Cissé (1986) mimicked several rainfall patterns at the onset of the rainy season by modifying natural rainfall through watering treatments. In 1978 one of his field experiments comprised three rainfall patterns on natural rangeland: the rainfall of that year, the rainfall supplemented by one artificial shower early in the rainy season, and the rainfall supplemented by weekly artificial showers during the first 7 weeks of the rainy season.

At the end of the growing season *Borreria radiata* was the dominant species under natural rainfall and had a plant density 2.5 times that of *Schoenefeldia gracilis*. Under the weekly supplementary waterings plant density of *Schoenefeldia* was 6 times that of *Borreria. Situation 2.* The dynamics of a rangeland on loamy sand at the 400 mm isohyet in Central Mali near the Mauretanian border. The vegetation composition of this rangeland was studied in four consecutive years in a fixed quadrat (150×150 m^2). Table 1 shows the variability in species composition, illustrated for the most important species, i.e. *Eragrostis tremula, Elionurus elegans, Cenchrus biflorus*, and *Schoenefeldia gracilis*.

Aboveground biomass production varied from 0.6 to 2.5 tonne ha^{-1} a^{-1}, and was not directly correlated with annual rainfall (200–400 mm a^{-1}; Breman et al. 1980). This suggests that the size, frequency, and temporal distribution of the showers exerts a decisive influence on the germination and establishment of the species.

The first situation was studied in experiment I. Two experiments were carried out for the second situation: one with collected seeds (experiment II) and one with the natural seedbank in soil sampled in the field (experiment III).

Materials and methods

Experimental environment

Experimental conditions in the climate room were designed to resemble the weather conditions during the rainy season in the southern Sahel in Mali. Day and night temperatures were maintained at $31° \pm 1°$ C and $24° \pm 1°$ C, respectively. Daylength was 12.5 h with a light intensity of 640 E $m^{-2} \cdot s^{-1}$ at pot surface. Relative humidity was 60% in daytime and 80% at night.

Plants were grown in 6-l (20 cm diameter) enamel pots, filled with 10.6 kg air-dry sand (0.4% water by volume) that was low in organic matter and in all plant nutrients. At pF = 4.2 (withering point) the water content of this sand is 1.5% by volume. No nutrients were supplied during the experiments. In experiments II and III the upper 2 cm of sand was replaced by a soil from Mali to imitate as closely as possible the natural conditions with respect to microbial activity, seed/soil contact, duration of wetting of the surface, etc.

Rain simulation

Water was applied via plastic boxes ($20 \times 20 \times 10$ cm^3) with a perforated bottom (20 cm diameter). They were placed on top of the pots, filled with the required amounts of water and turned regularly to prevent the drops falling on the same spot making holes in the soil surface. The application time varied from 5 to 20 min, depending on the amount of water.

Germination and survival on sandy loam (experiment I)

To explain the differences in behaviour between *Schoenefeldia gracilis* and *Borreria radiata* mixtures of 225 seeds of *Schoenefeldia* and 70 of *Borreria* were sown per pot. These numbers were comparable to the estimated densities in the field on the basis of the seed production in the preceding season (Cissé 1986). To stimulate germination the seeds of *Borreria* were scarified before sowing because they had been stored in the laboratory instead of being exposed to the field conditions (weathering) during the dry season (Elberse and Breman 1989).

The water treatments that were applied simulated the rainfall pattern of Cissé's field experiment in 1978: (a) natural rainfall in Mali during the first 8 weeks of the rainy season in 1978; (b) natural rainfall, supplemented by one artificial shower of 19.1 mm on day 3 after the start of the experiment; and (c) natural rainfall supplemented by additional showers of 12.8 mm at weekly intervals. The amounts of water (as mm rain) and day of application are presented below with the results. Soil water status was measured by weighing the pots daily. The experiment was carried out in triplicate.

Germination and seedling survival were recorded by counting the new and dead seedlings daily.

Germination and establishment on loamy sand (experiment II)

Mixtures of 120 seeds of *Cenchrus biflorus*, 150 of *Eragrostis tremula*, and 95 of *Schoenefeldia gracilis* (90 viable seeds per species (Elberse and Breman 1989)) were sown in 6-l pots in which the topsoil consisted of 1000 g of sand from Mali. Unfortunately, when this experiment was carried out no seeds of *Elionurus elegans* were available. The seeds of *Cenchrus biflorus* were removed from their envelopes. The seed densities required were derived from our own estimates of plant density in the preceding season and seed production data reported by Bille (1977).

To examine to what degree the year-to-year variability in vegetation composition, as illustrated in Table 1, can be explained on the basis of the rainfall pattern at the onset of the rainy season, differences in the size of the first shower and in the frequency of the subsequent showers were introduced. The waterings started with showers of different size, followed by others at different frequencies and intensities. In this way different rainfall patterns were created, representing different chances for species to germinate and to establish. The experiment consisted of five treatments. Treatments *a*, *b*, and *c* started with a relatively small watering (10 mm) whereas treatments *d* and *e* started with a big shower (25 mm). In treatments *c* and *d* the subsequent showers were frequent enough to keep most of the seedlings alive; in *b* they were too small to do this and in *a* and *e* they were not frequent enough. On day 18 (*a, b, c, d*) or day 30 (*e*) the rainy season was continued with sufficient rain to induce real growth. The experiment had three replicates. The amounts of water (as mm rain) and the day of application are given with the results.

The time course of germination was recorded by daily counts of new and dead seedlings. A treatment was stopped and dry weight per plant was determined when the *Cenchrus* plants in that treatment had five leaves.

Germination and drought resistance of seeds in the natural seedbank (experiment III)

To increase our insight into the processes governing the variability illustrated in Table 1, in the spring of 1979 before the first rains, part of the topsoil (0.5–1 cm) of the fixed quadrat in the experimental site in Mali was collected and transported to the Netherlands. The seeds contained in this soil had passed the dry season *in situ*, making this simulation the most "natural" of all. In the summer of 1979 the collected soil was homogenized, and a sample of 500 g of this soil + seed mixture was spread on top of the sand in each pot.

The samples were exposed to three watering regimes, representing three different rainfall patterns at the onset of the rainy season (treatment *a*: a very small watering of 3 mm repeated 8 times during the first 17 days; treatment *b*: one watering of 10 mm at the start; and treatment *c*: 3 waterings of 10 mm in 7 days). In all three regimes a dry period was included during which all seedlings of the first germination flush died, but this first flush was very small in treatment *a*, intermediate in *b*, and large in *c*. Soil water status was measured by weighing the pots daily. After the dry spell all treatments continued with sufficient water. The day of application and the amounts of water (as mm rain) are given with the results. This experiment had five replicates.

The time course of germination was followed by recording the numbers of new and dead seedlings daily. Drought resistance of some of the important species was established by totalling the number of seedlings that died during extended periods without rain (treatment *c*, after the first flush). The day of dying was recorded in relation to seedling age. Because of the difference in germination rate this applied to the seedlings of *Schoenefeldia*, which emerged on day 2 (no germination of *Elionurus* and *Eragrostis*), seedlings of all three species that emerged on days 3 and 4, and seedlings of *Elionurus* that emerged on day 7 (no germination of *Schoenefeldia* and *Eragrostis*). Seedlings of different species that emerged on the same day were recorded separately. Seedling age was recorded by placing a pin of a certain colour next to each newly emerged seedling. The colour of the pin indicated the day of observation (and the observations were made daily). Hence, when the seedlings could be identified their day of germination was known. To obtain an impression of the composition of the established vegetation, the dry weights of the various species were determined at the end of the experiment.

Results

Germination and survival on sandy loam (experiment I)

The time course of the number of living seedlings per species shows that *Borreria* had an induction time of 4 days (Fig. 1). This is 3 days longer than under optimum conditions (after washing for 24 h as pretreatment; Elberse and Breman 1989). *Schoenefeldia* germinated as rapidly as under optimum conditions, after a first shower exceeding 10 mm. The shape of the germination curves of the first germination flush was identical to that established under optimum conditions. The total number of seeds germinating during the first flush correlated positively with the rainfall ($b > c > a$). The germination curve of the second flush was as steep as the first one if germination was limited during the first flush (*a*). However, when a relatively large proportion of the seeds germinated during the first flush, the slope of the second curve was less steep (*b, c*).

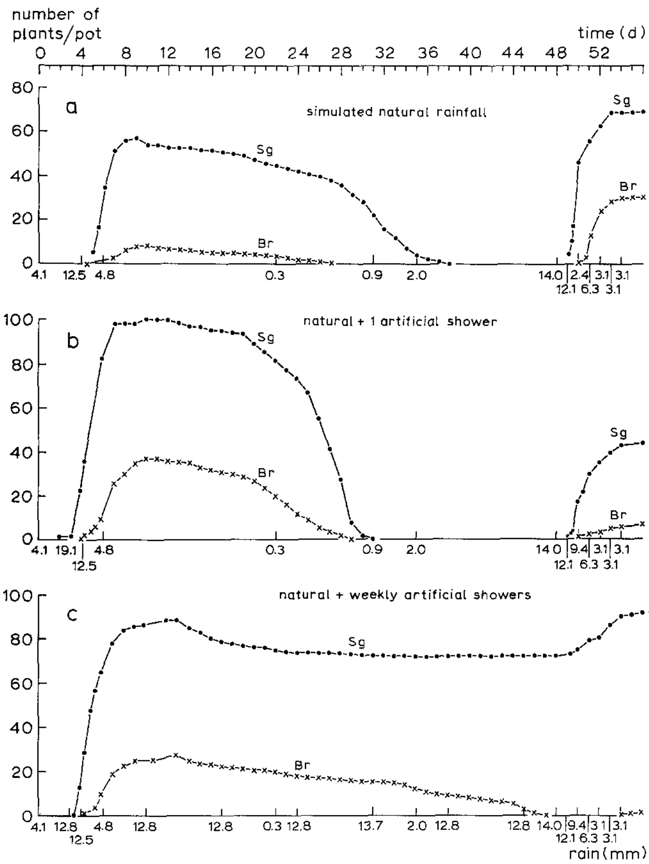

Fig. 1a–c. Time course of the number of living plants per pot for *Schoenefeldia gracilis* (Sg ● — ●) and *Borreria radiata* (Br x—x). The *lower x axis* gives the amount of water applied in mm, the *upper axis* shows the time in days; **a** simulation of natural rainfall, **b** natural rainfall + one artificial shower, and **c** natural rainfall + weekly artificial showers. *Bars* indicate SEM

The maximum germination level of the second flush was the highest for the two species in treatment *a*. The fact that in treatment *c*, while the substrate remained wet, the second flush produced the lowest number of germinated seeds, instead of an intermediate number (as during the first flush), suggests a heavy mortality during the pre-emergence phase.

The total number of seedlings recorded was highest for both species in the treatment with one additional shower (*b*): 68% of the viable seeds of *Schoenefeldia* and 60% of those of *Borreria* germinated; these values

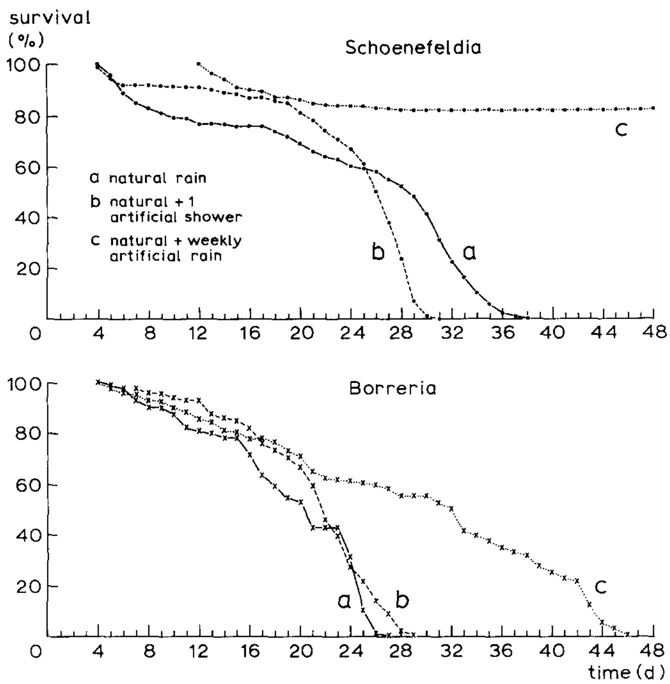

Fig. 2. The survival (%) of mixtures of seedlings of the first flush of *Schoenefeldia gracilis* (●) and *Borreria radiata* (x) in time (average of 3 pots) after different treatments. *a* = simulation of natural rainfall, *b* = natural rainfall + one artificial shower and c = natural rainfall + weekly artificial showers

are considerably lower than under optimum conditions (Elberse and Breman 1989).

During the long dry spell in treatments *a* and *b* (Fig. 1), all seedlings of both species died, as in the field situation. In treatment *c* all seedlings of the slowly germinating *Borreria* died, but only a few of those of the fast germinating *Schoenefeldia* died. For a closer examination of the drought resistance of the species, the number of surviving seedlings of the first germination flush as a percentage of all the seedlings that emerged during that flush is plotted against time in Fig. 2. *Schoenefeldia* seems to be the more drought resistant. During the first week, 10–20% of the *Schoenefeldia* seedlings died; the first to die were generally those that had germinated last. Hence, even under controlled conditions it is difficult to decide whether *Borreria* is really less drought resistant, or whether its seedlings merely have less chance of surviving because of competition for water. The results of treatment *c*, however, are unambiguous: some of the seedlings of *Schoenefeldia* that survived emerged after the first seedlings of *Borreria* (Fig. 1), but the latter all died (Fig. 2), whereas only 18% of the *Schoenefeldia* seedlings died. The pots in this treatment exceeded pF 4.2 (1.5% by volume of water in the whole pot) for 1 (day 23), 2 (days 29–30, 36–37) or 3 (days 42–44) days just before the weekly artificial rain. In treatment *b*, which received more water than *a*, the dying of the seedlings was initially delayed, but because there were more plants per pot the water was consumed faster than in *a*, resulting in higher mortality rates later on. On day 17 the pots in treatment *b* contained twice as much water as the pots in treatment *a* (4.0% and 2.0% by volume respectively), but the pots in treatment *b* exceeded pF 4.2 on day 23, while the pots in treatment *a* did this 4 days later.

The final ratio of plant numbers of the two species was different under controlled conditions to that in the field, but the overall picture is comparable. After establishment, *Schoenefeldia* was the dominant species in treatment *c*, with 92 plants/pot compared to only 1 plant/pot for *Borreria*. In the treatment with one additional shower (*b*) many seedlings (and seeds) of both species were lost and only 49 plants established in total (43 *Schoenefeldia* and 6 *Borreria*). In treatment *a* only 8 *Borreria* seedlings died during the drought, and in total 99 seedlings established (69 *Schoenefeldia* and 30 *Borreria*). The hard-seeded *Borreria* had the most plants in the treatment in which a dry period followed an initial small shower, as in the field, but even in that case pre-emergence losses must have been considerable.

Germination and establishment on loamy sand (experiment II)

It may be deduced from Figure 3 that the duration of wetting in the various treatments was different: all plants were harvested when *Cenchrus biflorus* had five leaves. As a consequence, the total amounts of rain differed per treatment: 130, 155, 90, 35, and 110 mm in respectively *a, b, c, d,* and *e*. The time course of the number of living plants shows that the first seedlings of *C. biflorus*, the fastest germinating species under optimum conditions, emerged after 1 day. *Schoenefeldia gracilis* emerged about 1 day later after an initial shower of 25 mm or, if the first shower was only 10 mm, after the second shower of 10 mm. *Eragrostis tremula* needed much more rain before the first seedlings appeared and hardly any seed germinated before 35 mm was given. In contrast to optimum conditions, in this experiment periods of soil wetness were interrupted by dry spells, to mimic the onset of a rainy season, characterized by small showers with low frequency. Under these conditions each shower during the first weeks, if not too small, induces a germination flush.

The percentages of visible germination for the three species in the different treatments (Table 2) show that *Cenchrus* (62%) and *Schoenefeldia* (80%), both in treatment *a*, did not attain the same values as under optimum conditions (75% and 97%, respectively). *Eragrostis*, however, reached such a high germination percentage in treatment *e* (79%) that the absolute number of seedlings exceeded the planned 90 per pot; hence the viability of the seeds must have been underestimated. Treatment *e* closely resembled optimum conditions after the dry spell: continuously wet soil. The first shower of 25 mm acted as pretreatment for *Eragrostis*, apparently without causing any germination or pre-emergence losses. Maximum germination seems to have been attained in treatments *a, b,* and *e*, with total visible germination much lower than under optimum conditions, and therefore during the pre-emergence phase the seed losses must have been considerable in all treatments for the fast ger-

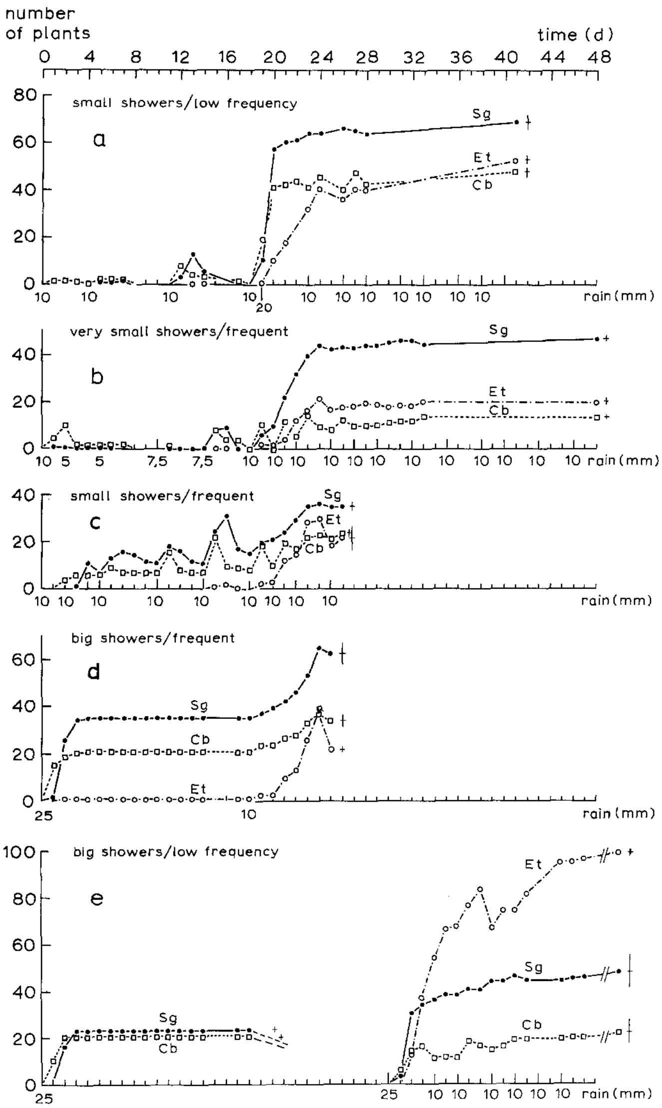

Fig. 3a–e. The time course of the number of living plants per pot for *Schoenefeldia gracilis* (Sg ● —— ●), *Cenchrus biflorus* (Cb □– – – –□) and *Eragrostis tremula* (Et ○–·–·○). The *x axis* gives the simulated rainfall in mm as well as the time in days. **a–e** different watering treatments characterized by the relative size and frequency of the showers. *Bars* indicate SEM

minating species *Schoenefeldia* and *Cenchrus* and in all treatments except *e* for the slowly germinating *Eragrostis*. If the differences between the observed levels of visible germination (Table 2) and those obtained under optimum conditions represent pre-emergence losses, then, averaged over all treatments, 34% of the viable seeds of *Cenchrus*, 24% of those of *Schoenefeldia*, and 53% of those of *Eragrostis* did not produce seedlings.

Seedling mortality was highest for the fast germinating *Cenchrus* (52% of the seedlings averaged over all treatments), lowest for *Schoenefeldia* (25%) and intermediate for *Eragrostis* (29%). Most *Cenchrus* seedlings died in the treatment with relatively small showers (*b*). For *Schoenefeldia* and *Eragrostis* the highest losses occurred in treatment *c*, where consecutive showers followed each other before all seedlings had died.

The final number of established seedlings (Fig. 3) was highest for *Schoenefeldia* in all treatments except *e*, where *Eragrostis* was the dominant species. *Cenchrus* always had the lowest number of plants except in treatment *d*, with a total of only 35 mm of rain, where *Eragrostis* was lowest. It is not clear, however, whether germination was completed in this case.

Total dry matter yields per pot varied considerably (Table 3), because of the differences in length of the growing period. In treatments *a, c,* and *d Cenchrus* comprised about 60% of the total dry matter. In treatments *b* and *e Schoenefeldia* showed the highest dry matter yield. *Eragrostis* was the dominant species in treatment *e* in terms of plant number, but its seeds are much lighter than those of *Schoenefeldia* and *Cenchrus* (their seeds are respectively 4 and 43 times heavier: Elberse and Breman 1989) and consequently its seedlings weigh less too. The growing period was too short for the advantage of a high plant number to be expressed in total dry matter production.

Germination and drought resistance of seeds in the natural seedbank (experiment III)

With showers of 3 mm every 2 days, the seedlings could not be identified before they died (Fig. 4a, 1). For the

Table 2. Percentage visible germination (G%) and losses (L%) of seedlings (as % of visible germination) for the three species in the different treatments of experiment II (rain treatments are characterized by the relative size and frequency of the showers; for exact amounts and day of application see *x* axis in Fig. 3)

Plant species	Rain treatments at the onset of the rainy season									
	Small showers/ low frequency *a*		Very small showers/ frequent *b*		Small showers/ frequent *c*		Big showers/ frequent *d*		Big showers/ low frequency *e*	
	G%	L%	G%	L%	G%	L%	G%	L%	G%	L%
Cenchrus biflorus	62	35	48	78	50	65	35	19	45	61
Schoenefeldia gracilis	80	9	62	19	72	49	69	9	78	35
Eragrostis tremula	38	7	20	33	22	45	27	43	79	17

Table 3. Total dry matter yield (g/pot) and biomass percentage of the species (average of 3 pots) in the different treatments of experiment II (rain treatments are characterized by relative size and frequency of the showers; for exact amounts and day of application see *x* axis in Fig. 3)

Plant species	Rain treatment at the onset of the rainy season				
	Small showers/ low frequency *a*	Very small showers/ frequent *b*	Small showers/ frequent *c*	Big showers/ frequent *d*	Big showers/ low frequency *e*
Cenchrus biflorus	62	21	61	57	37
Schoenefeldia gracilis	34	72	36	42	47
Eragrostis tremula	4	7	3	1	17
Total DM	1.0	0.7	0.2	0.4	0.9

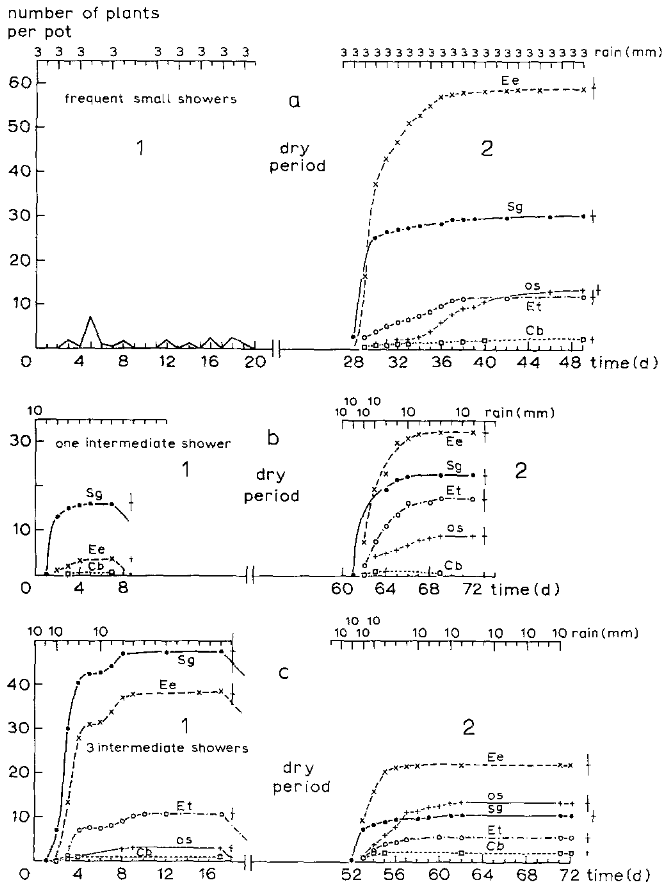

Fig. 4a–c. The time course of the number of living plants per pot for *Schoenefeldia gracilis* (Sg ● —— ●), *Elionurus elegans* (Ee x– – – –x), *Eragrostis tremula* (Et o–·–·o) and *Cenchrus biflorus* (Cb □·····□) and "other species" (os +——+), before (*1*) and after (*2*) a dry period, interrupting three different starts of a simulated start of the rainy season (**a–c**). The *x axis* shows the simulated rainfall in mm (*top*) as well as the time in days (*bottom*). *Bars* indicate SEM

other treatments the results for the four species listed in Table 1 are presented separately; the results for the other species are combined. In treatments *b* (Fig. 4b, 1) and *c* (Fig. 4c, 1) the order of germination rate of the species was identical to that under optimum conditions: *Schoenefeldia gracilis*, the fast germinating species, followed by *Elionurus elegans* and with *Eragrostis tremula* as the slowest one. *Schoenefeldia* and *Eragrostis* required less rain to germinate in this experiment than in the previous one, presumably because they had experienced field conditions during the dry season. *Cenchrus biflorus* was hardly present in the seedbank, probably because many of the seeds were destroyed in a bush fire at the end of 1978. Much smaller seeds or seeds shed earlier had more chance of escaping the fire. The few remaining *Cenchrus* seeds, in their envelopes, appeared to germinate more slowly than under optimum conditions (removed from the envelopes) as also observed by Cissé (1986).

The curves of the germination flushes following the drought period were less steep, because a substantial proportion of the fastest germinating seeds had been eliminated during the first flush.

The total number of seedlings recorded per pot was highest (155) in treatment *c* (58 *Schoenefeldia*, 60 *Elionurus*, 17 *Eragrostis*, 3 *Cenchrus*, and 17 "other species") and lowest (101) in treatment *b* (39 *Schoenefeldia*, 36 *Elionurus*, 17 *Eragrostis*, 1 *Cenchrus*, and 8 "other species"). In treatment *a* 136 seedlings were recorded: 30 *Schoenefeldia*, 59 *Elionurus*, 12 *Eragrostis*, 2 *Cenchrus*, 13 "other species", and 20 unidentified.

Seedling losses were highest in treatment *c* after 3 showers of 10 mm each. The losses of visibly germinated seeds were 83% for the fast germinating *Schoenefeldia*; 63% for *Elionurus*; 65% for the slowest germinating *Eragrostis*, and only 18% for "other species". In treatment *b* the highest losses of seeds (especially in the faster germinating species) must have occurred in the pre-emergence phase. In that treatment the total numbers of seedlings recorded for *Schoenefeldia* and for *Elionurus* were respectively 34% and 40% lower than in treatment *c*; Figure 4 clearly shows that the maximum germination level had been reached in all treatments. Hence, in treatment *b* at least 40% of the viable seeds of *Elionurus* were lost in the pre-emergence phase. This figure may have been an underestimate, because treatment *c* was taken as the reference, and losses may also have occurred in that treatment. In treatment *a* only 20 seedlings died during the drought, probably all of the fastest germinating *Schoenefeldia*, but they could not be identified. In this treatment some more seeds must have been lost dur-

Table 4. The total dry matter yield (g/pot) (average of 5 pots) and the biomass percentage of the different species in experiment III (rain treatments are characterized by the relative size and frequency of the showers; for exact amounts and day of application see x axis in Fig. 4)

Plant species	Rain treatment at the onset of the rainy season		
	Frequent small showers *a*	1 intermediate shower *b*	3 intermediate showers *c*
Schoenefeldia gracilis	42	38	32
Elionurus elegans	40	37	37
Eragrostis tremula	5	8	6
Cenchrus biflorus	9	1	9
Other species	4	16	16
Total DM	3.0	3.9	3.5

ing the pre-emergence phase (136 seedlings recorded compared with 155 in treatment c).

The plant density and species composition of the vegetation established in the pots differed among the treatments. *Elionurus elegans* had the highest number of seedlings in all treatments, but only in treatment *a* did it comprise more than half the total number (51%). In treatment *b Schoenefeldia* and *Eragrostis* were co-dominant with *Elionurus*. In treatment *c* only 54 plants established per pot. After *Elionurus* (41%), the "other species" combined were more important (26%) than *Schoenefeldia* (19%) and *Eragrostis* (11%). Before the dry period (Fig. 4c, 1) *Schoenefeldia* was the dominant species, with the group "other species" reaching 3% only. Very slowly germinating species must be represented within this group.

The dominance of *Elionurus* in terms of plant numbers does not imply the highest biomass. Within a few days after the start of the second flush all seedlings of the fast germinating *Schoenefeldia* emerged, whereas it took more than a week longer for *Elionurus* to reach its maximum germination level and the highest plant number (Fig. 4a). Table 4 shows that the early emergence of *Schoenefeldia* was decisive, resulting in more biomass with half as many plants.

In treatment *b Schoenefeldia* needed more plants to dominate in terms of biomass as well as in terms of numbers, but in treatment *c Elionurus* had the highest biomass at the end of the experiment (the start of the real growing season in the field). The explanation can be deduced from Fig. 4. Going from *a* to *c* the time gap between the moments that *Elionurus* and *Schoenefeldia* reach their respective maximum germination level decreases. On the one hand an increasing proportion of the fastest germinating seeds of *Schoenefeldia* was lost during the first flush, while on the other hand these first "rains" acted as a pretreatment of increasing intensity for seeds of the slowly germinating species.

Seedling death after the first germination flush in treatment *c* gave important clues about the drought re-

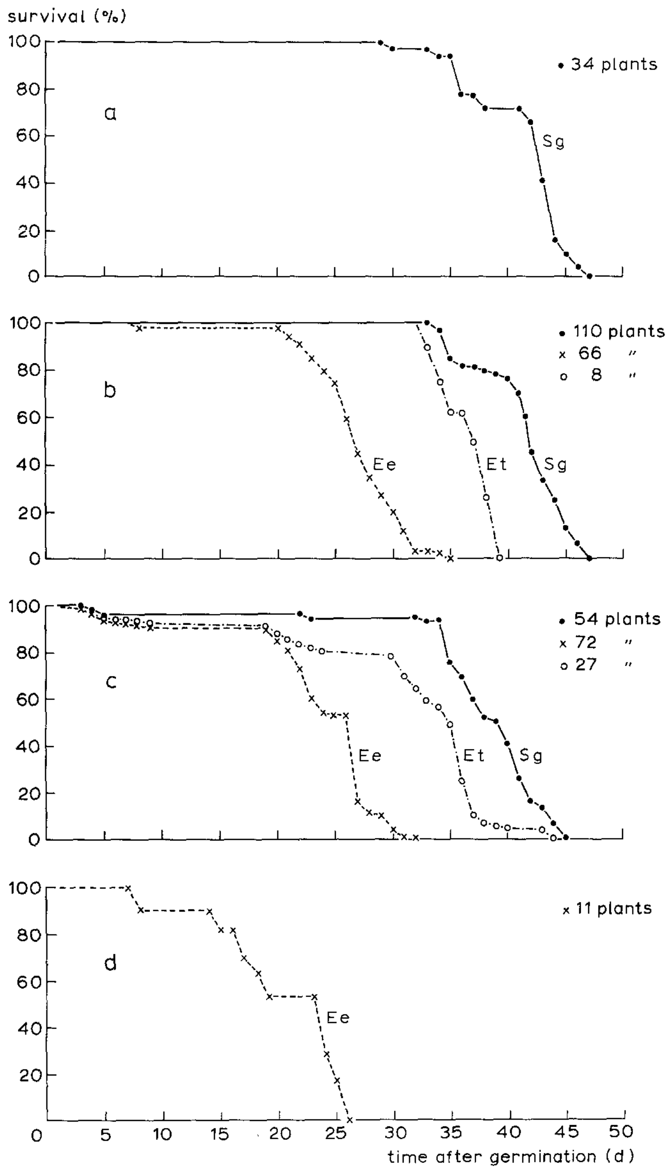

Fig. 5a–d. The survival (%) of mixtures of seedlings of *Schoenefeldia gracilis* (Sg ● — ●), *Elionurus elegans* (Ee x– – – –x) and *Eragrostis tremula* (Et o–·–·o), germinated on day 2 (**a**), 3 (**b**), 4 (**c**) and 7 (**d**) after the first watering (average of 5 pots). The initial numbers of seedlings are also given

sistance of *Schoenefeldia, Elionurus* and *Eragrostis* (Fig. 5). The water content of the soil (in the whole pot) decreased from 3.5% by volume on day 27 to 1.5% by volume on day 40 to 0.4% by volume on day 50. The fastest germinating species, *Schoenefeldia*, appeared to be the most drought resistant. Its seedlings outlived those of *Elionurus* by 14 days and those of *Eragrostis* by about a week. The seedlings that emerged first (Fig. 5a, b) outlived those that emerged last. The seedlings of *Elionurus* that emerged on day 7 were all dead by day 26 whereas the seedlings that emerged on day 3 outlived them by about 8 days.

The *Schoenefeldia* seedlings that emerged on day 3 appeared so resistant that the dry spells of 3–5 weeks in the field situation would not have been long enough for all to die, if the conditions had really been comparable. However, potential evapotranspiration in the climate room was the average of that for the rainy season in the field. In May–June, the period of the first two showers, the evapotranspiration in the field during dry periods is almost double the rainy season average (6 mm per day compared with 3.5 mm per day).

Discussion

The response of the various species to the different treatments in the climate room was in general comparable to the overall response in the field situation. In all experiments different simulated rainfall patterns at the onset of the rainy season resulted in different mixtures of established seedlings. The size and frequency of the showers and their temporal distribution appeared to exert a decisive influence on the relative number of seedlings of the various species. This influence is mediated through the germination characteristics of the species (as reported in Elberse and Breman 1989) and the drought resistance of the seedlings. However, in some cases the dry weight ratio of the species after establishment obtained under controlled conditions differed from that observed in the field at the end of the rainy season. Although conditions during the period of germination and establishment have a decisive influence on the chances of species becoming dominant in the vegetation in a certain year, differences in properties with respect to growth and development in the subsequent period are not negligible in terms of dry matter production and may still modify the relative importance of the different species (Penning de Vries and Djitèye 1982; Cissé 1986). Moreover, it should be realized that the relative proportions of the number of viable seeds in the experiments were often rather rough estimates of those in the field situation that was simulated. The composition of the seed stock in the field varies from year to year, and depends on the previous year's vegetation composition, seed production, seed losses during the dry season, and seed transport (Cissé 1986).

In general, conditions for fast germinating species were favourable with rainfall patterns without serious intermittent periods of drought, whereas the conditions for the slower germinating species became favourable after dry periods had eliminated the seedlings of the fast germinating species.

The germination behaviour of the various species was comparable to that under optimum conditions. However, induction time was generally somewhat longer, and in some cases the germination rate was lower. As the seed environment was not constantly moist, various germination flushes occurred, their magnitude depending on the size of the showers. Seeds of *Schoenefeldia gracilis* and *Eragrostis tremula* that had been in the field during the dry season and had therefore experienced high temperatures and large temperature fluctuations needed less water to induce the germination process, probably because the weathering of the seed coat facilitated gas exchange which led to losses of inhibitors. The germination curves of germination flushes that occurred after drought periods tended to be less steep, probably because the easiest germinating seeds of the population germinated during the first flush, thus leaving the more resistant seeds. *Cenchrus biflorus*, which germinates very rapidly under optimum conditions, shows a germination behaviour in the field that resembles that of leguminous species such as *Zornia glochidiata*, which has heterogeneous seed. This is presumably because the seeds of *Cenchrus* have big spiny envelopes and because the seeds are incorporated in the soil to different degrees, resulting in several flushes of germination (Cissé 1986). Consequently, the species can take advantage of various rainfall patterns at the onset of the rainy season and can become dominant.

The large differences in drought resistance among seedlings of different species cause even greater differentiation. *Schoenefeldia gracilis* is more resistant than *Eragrostis tremula*, which in turn is more resistant than *Elionurus elegans*.

The final vegetation composition cannot be understood without taking losses of seed in the pre-emergence phase into account. These losses can be very high, especially for the fastest germinating species. However, the process cannot be ignored in the slowly germinating species, if there is an irregular start of the rainy season.

On the basis of these insights the variability presented in Table 1 can be explained. In 1976 the onset of the rainy season must have been irregular, and during the dry period that followed the first relatively small showers, large numbers of viable seeds and seedlings of the fastest germinating species *Cenchrus biflorus* and *Schoenefeldia gracilis* were lost. After the drought, the rainy season resumed with heavy showers, creating favourable conditions for the somewhat slower germinating *Elionurus elegans* and the slowly germinating *Eragrostis tremula*, a species that needs more rain to remove the germination inhibitors (Elberse and Breman 1989). Despite the high seed production of *Eragrostis tremula* in 1976, the species was not dominant in 1977 and 1978. A rainy season characterized by frequent small showers and a lower total annual rainfall created favourable conditions for the fast germinating *Cenchrus biflorus* in 1977 and in 1978, when rainfall was slightly higher, for *Cenchrus biflorus* and *Schoenefeldia gracilis*. However, in 1978 the vegetation at the site was not homogeneous. The fixed quadrat was located near a traditional transhumance route, used by tens of thousands of cattle and small ruminants on their way to the rainy season pastures in the North at the beginning of the rainy season. At the site, a strip several dozen metres wide was strongly dominated by *Elionurus elegans* at the end of the season, whereas elsewhere *Schoenefeldia* and *Cenchrus* were strongly dominant. The fixed quadrat was located partly within this strip. The relatively high proportion (17%) of *Elionurus* in the final biomass in this strip might be attributable to *Cenchrus biflorus* and *Schoenefeldia gracilis* being eliminated by being grazed by herds going North rather than by drought. The large seed stock of *Elionurus* produced in 1978 and the rainfall pattern at the onset of the rainy season in 1979, caused *Elionurus* to dominate in that year. Slight differences in germination rate, in drought resistance of seedlings and in preemergence losses, in combination with a particular rainfall pattern, may explain why even within the group of fast or slowly germinating species the behaviour varies from year to year. In a previous paper (Elberse and Breman 1989) we stressed that the schematic classification in groups according to speed of germination is rather arbitrary.

A general model describing vegetation dynamics, based on species properties, especially germination characteristics, was developed by Breman et al. (1980).

It can be concluded that this study of the germination and establishment of Sahelian rangeland species under controlled conditions in a climate room gave information that elucidates vegetation dynamics and vegetation variability in the field.

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