TEMPORAL AND SPATIAL DISTRIBUTION OF AN ANNUAL FLORA IN AN ARID REGION OF WESTERN AUSTRALIA

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ABSTRACT

At a site in the Murchison Region of Western Australia, summer rainfall produced a predominance of grasses, and winter rains resulted mainly in the germination of dicotyledons. Most of the seed was found to remain on the surface, so that germination required the surface to remain moist for some time.

Little difference was recorded in numbers germinating on either "run-off" or "run-on" areas, but there was much lower plant survival in the run-off area because of more rapid drying of the soil profile, all plants drying off when the soil moisture potential fell below —15 bars. Lower survival on the run-off area led to a much lower productivity. Little viable seed was left after any rain causing germination and restocking in the run-off area may occur by wind movement of seed from the run-on areas. The possibility of a new model for predicting plant growth was examined in the light of the above facts.

INTRODUCTION

Populations of annual plants growing in arid areas may show large fluctuations in numbers between years (e.g. Went, 1948, 1949; Tevis, 1958; Beatley, 1967), and in those areas which possess a bi-modal annual rainfall pattern there may be two distinct populations in the one year (Went, 1948; Mott, 1972).

From his studies in the Mojave Desert, Went (1953, 1955) concluded that desert annuals, once germinated, usually reach maturity even if only as depauperate and barely reproductive plants. He surmised that for the survival of individuals, the environmental conditions during germination are more important than those occurring later in the life cycle. However, later work in arid zone annual communities in America has shown survival values ranging from 0-70%, indicating that conditions after germination must play an important part in determining the final number of mature plants (Tevis, 1958; Beatley, 1967). As Koller points out, this and other work emphasises the "uncertainty" factor in rainfall of arid regions, where light falls might lead to germination, but not be sufficient to allow plants to mature. The value of a polymorphic germination requirement in annual species growing under these unpredictable conditions has been stressed by several workers (e.g. Beadle, 1952; Wareing, 1965; lead to germination, but not be sufficient to allow plants to mature Wareing 1965; Loller 1969).

The increase in productivity in annual communities due to "ponding" of water in depressions has been described by Warren Wilson and Leigh (1964) for the semi-arid Riverine Plain of New South Wales. On a larger scale an increase of production in annuals growing in drainage channels has been noted by Davies (1968) in the Murchison Region of Western Australia, and Perry (1970) found that 95% of the ground vegetation was produced on 'run-on' areas in mulga communities near Alice Springs.

The study described here was carried out at Mileura Station, about 360 km west of Meekatharra (lat. 26½°S), in the Murchison Region of Western Australia. The soils of the area are mainly red-earths underlaid by a siliceous hardpan. The long-term, mean annual rainfall is 196 mm, and results both from summer and winter falls

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(Davies, 1968; Mott, 1972). Mulga is the dominant shrub over the whole the of station, and the different habitats have been fully described and mapped by Mabbutt *et al.* (1963).

The experimental site referred to here was on the Koonmarra Land System as defined by Mabbutt *et al.* (1963), and appeared typical of six sites studied in the area. It contained a 'run-off' slope leading into a 'run-on' drainage channel. The total area of the site was just under 15 hectares.

METHODS

Vegetation Sampling

Measurements of plant numbers were carried out using permanent, circular, decimetre radius quadrats on run-on and run-off areas. These quadrats were arranged in groups of twenty, the quadrats being randomly spaced within the limits of 5-15 metres along the axes of a cross. The first assessment was made within ten days of the onset of germination, and the final count made just before seeding.

Plant productivity was obtained by the use of two ranked sets of five, one square metre quadrats on each site. The quadrats were divided into sixteen 25 cm × 25 cm squares, and three randomly-determined squares were clipped just before seed set. Once clipped a square was not harvested again.

Phenological data were obtained for *Helipterum craspedioides* and *Aristida contorta*, which species constituted the major part of the winter and summer production respectively.

Soil Moisture

Soil moisture was sampled gravimetrically at intervals during the years 1969-1971. The soil profile was sampled every 15 cm from the surface until the hardpan was reached. Four replicates were obtained from the ends of the quadrat lines for every sampling date. The moisture characteristics of the soils were determined using a pressure membrane and pressure plate apparatus of the type described by Richards (1954).

Field Germination Trials

To examine field germination of *Helipterum craspedioides* and *Helichrysum cassinianum*, two winter germinating composites, and *Aristida contorta*, as a summer germinating grass, 200 non-dormant seeds of the two composites and 100 non-dormant seeds of *Aristida contorta* were placed into nylon mesh bags. *Helipterum craspedioides* and *Aristida contorta* were placed at three depths at both the run-off and run-on areas of the experimental site, while *Helichrysum cassinianum* was similarly situated at another run-on area. The bags were clamped to the surface, or buried 1 cm or 3 cm under the surface. For the composites, twenty replicates were used at the surface, and 10 replicates at each depth. These seeds were set out during summer 1969-1970, and ten replicates at each depth were removed after the first winter; the remaining surface seed was left until the end of the next winter rains. *Aristida contorta* seed was set out in late spring and removed after the summer rains of 1971.

Germination was recorded after rainfall in the field, and the viability of recovered seed determined by using the tetrazolium test of Porter, Durrell and Romm (1947).

RESULTS

Soil Moisture

Fig. 1 gives the soil water contents of the run-off and run-on areas at eight sampling dates during 1971. These results were representative of those obtained over the period 1969-1971. A greater water storage was evident in the soil moisture values of the run-on sites, where moisture values remained higher than the run-off plain. As

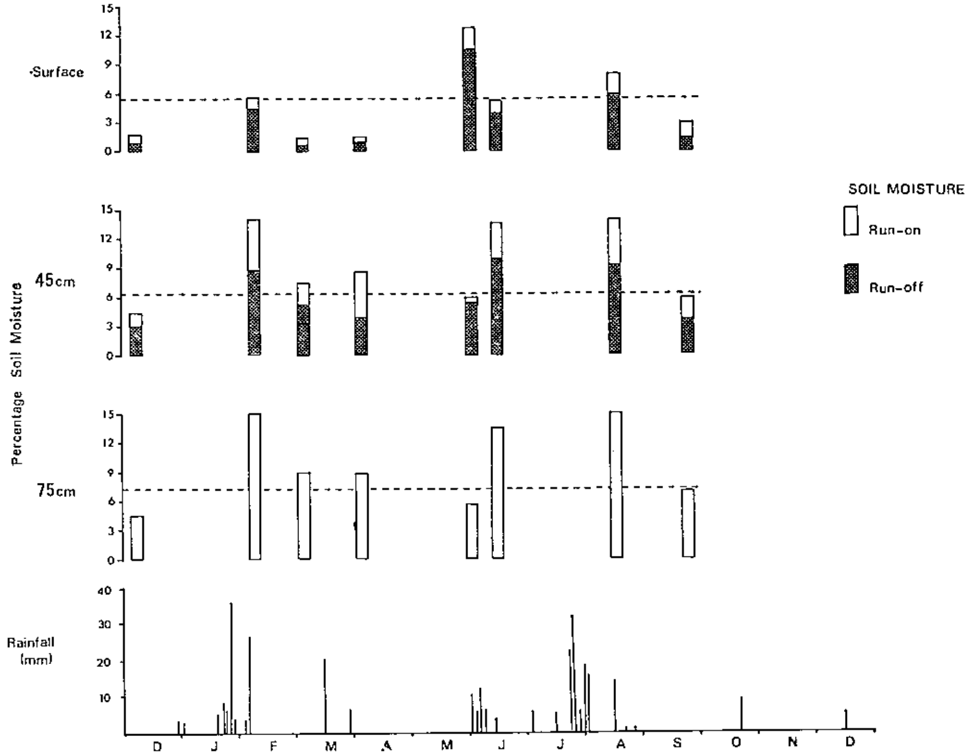

FIGURE 1

Rainfall and soil moisture values obtained during 1971 for surface, 45 cm and 75 cm, the average depths of soil to the hardpan in the run-off and run-on areas respectively. Soil moisture content at —15 bars is shown by a broken line.

the soil moisture characteristics of soils in both run-on and run-off areas were the same, the deeper soils of the run-on channels were important in maintaining at least some levels of the soil profile above —15 bars after the shallower soils of the plain had dried below this water potential.

Field Germination and Phenology

The phenological data presented in Fig. 2 show that the two dicotyledons germinated after the winter rains, while the main germination of *Aristida contorta* occurred after the summer rain of 1970-1971. Although a few *Aristida contorta* plants were found to have germinated during the winter of 1969 and 1970, they remained small. These three species were representative of the summer and winter flora.

Seed from most of the plants in the study area was found to remain on the soil surface after shedding. Germination of most of the winter and summer annuals occurred in this surface seed, although during the summer of 1970-1971 germination was observed for *Aristida contorta* seed buried up to 2 cm deep.

After germination of both summer and winter annuals plants dried off when the soil moisture potential of the whole soil profile fell below —15 bars (Fig. 2). In the case of the winter annuals the plants were senescent and died soon after. However, many of the clumps of *Aristida contorta* and *Eragrostis falcata* Gaud, although ceasing growth and drying off, did remain viable through the wet autumn of 1971 and

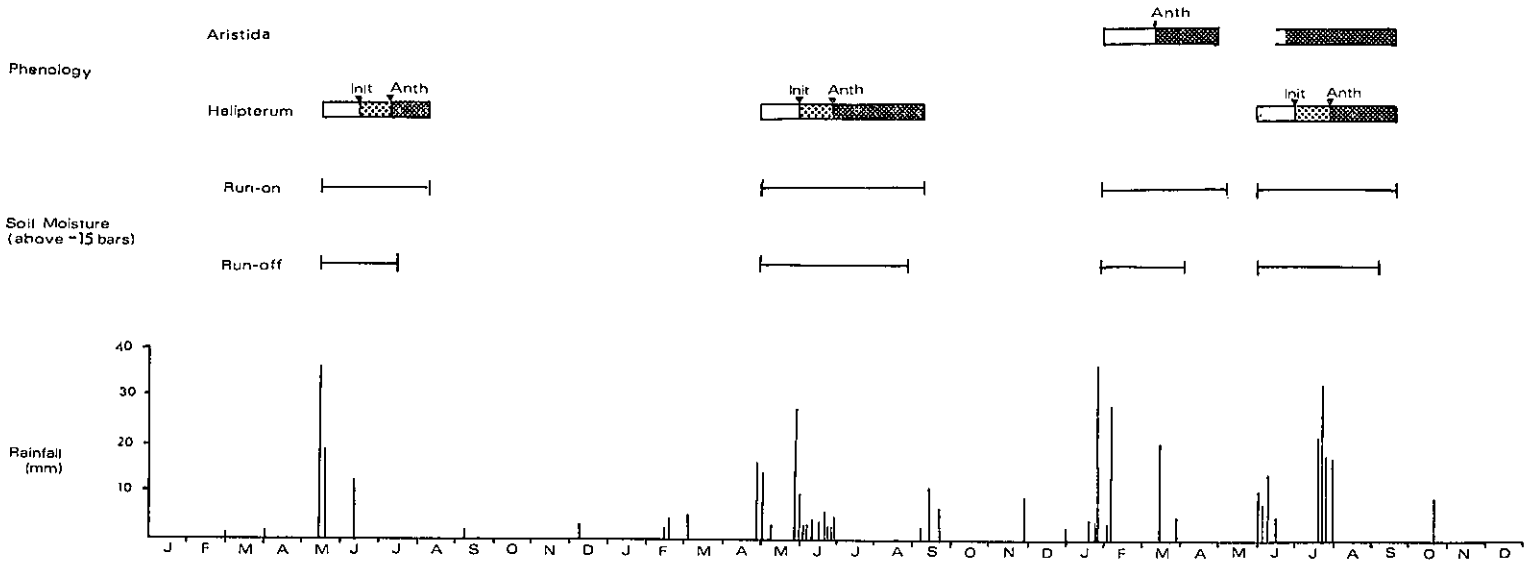

FIGURE 2

Relation between phenology and soil moisture. The length of time the water potential of the entire soil profile exceeded −15 bars in both run-on and run-off areas is shown. Phenological data are for plants growing in the run-on area.

sprouted again after heavy winter rains. Annuals in the run-off plains dried off before those in the channels, which remained above wilting point for a longer period. As the time to anthesis remained approximately the same for plants in both the channels and on the plains, during the dry year of 1969, most of the plants on the plains died before flowering and little seed was set by the remainder. The greater rainfall in the winters of 1970 and 1971 kept the soil above wilting point for long enough to allow flowering in the plains, and as time to anthesis remained the same at approximately 8 weeks, a much longer flowering season occurred in the channels.

Following seed fall from the winter annuals there was considerable wind movement of the seed, and during 1969 seed was observed being blown from the channels on to the adjacent run-off plains. Seed remained on the soil surface during the summer, and most germination occurred from seed still on the surface.

Plant Numbers and Productivity

Large numbers of dicotyledons germinated and flowered during the winters, while monocotyledons formed the greatest proportion of the plants germinating and surviving to reproductive phase after summer rainfall (Table 1). Appreciable numbers of dicotyledons germinated after the two cyclones occurring in the summer of 1970-1971, but this could have resulted from relatively low soil temperatures occurring during the second cyclone. Most died, and only those dicotyledons normally growing in summer survived to maturity.

TABLE 1

Germination and survival to maturity of annual plants in a run-on and run-off area
(totals from 20 decimetre quadrats)

Site	1969 (Winter)		1970 (Winter)		1971 (Summer)		1971 (Winter)	
	Number Germinated	% Survival	Number Germinated	% Survival	Number Germinated	% Survival	Number Germinated	% Survival
Run-off Plain								
Monocotyledons	27	26	70	87†	116	89	0	0 (85)*
Dicotyledons	574	8	440	11	98	10	316	38
Run-on Channel								
Monocotyledons	22	27	12	100†	108	78	2	0 (84)*
Dicotyledons	673	44	596	36	157	12	379	45

* Plants which had germinated in the previous summer and sprouted again during the winter rains are presented in parentheses and are not included in the percentage survival.

† Includes plants which had germinated following the initial count at germination.

In both summer and winter seasons there was little difference between the number of plants germinating on the run-on and run-off areas in any one year. But the number of plants germinating, and their survival to maturity, showed considerable difference between years. Although the number germinating was highest during the winter of 1969, the lack of follow-up rain led to the poorest survival, with less than 10% surviving in the run-off plains. Increased rainfall in 1970 led to a slight increase in survival in the run-off areas, but it was not until the prolonged rainfall during the winter of 1971 that any significant increase ($P < .001$) in survival occurred in the plants growing at this site. In the run-on area there was high survival in all years, and although a significant difference was noted in the number flowering in the spring ($P < .01$), no difference was found in the percentage survival for all winters.

TABLE 2
Dry matter productivity of annual vegetation at two sites

Site	Dry Matter Yield (g) 1969 (Spring)	1970 (Spring)	1971 (Autumn)	1971 (Spring)	L.S.D. (p = 0.05)
Run-off Plain					
Monocotyledon	0	0.04	0.30	1.54*	0.21
Dicotyledon	0.09	0.29	0.15	0.58	0.12
Run-on Channel					
Monocotyledon	0.10	0.05	0.82	5.32*	0.43
Dicotyledon	2.23	5.60	0.02	2.72	1.71

* Plants which germinated in the previous summer and sprouted again during the winter rains.

Although survival of plants in the drainage channels was similar between winters, dry matter production varied considerably, with the high rainfall in 1970 and 1971 giving rise to much higher production than during 1969 (Table 2). Similar results were obtained on the drier run-off area, which showed much lower productivity than the run-on areas in all winters.

The plant productivity in the channels during the summer of 1970-1971 was much less than during the winters. This, coupled with an increase in productivity on the run-off plain, led to similar productivity in the two areas and reflects the high soil moisture regime maintained in the run-off area by the heavy summer rains.

As with the plant numbers, dicotyledon dry weight production was normally high during the winters, with little monocotyledon growth. However, because of the many grass clumps surviving into the winter of 1971, a large proportion of the dry matter production during this season was made up of monocotyledons, mainly *Aristida contorta* and *Eragrostis falcata*, in contrast to previous winters.

Field Germination Experiments

The abrupt change in ambient temperatures between the summer and winter seasons led to two different temperature regimes in the seed bed (Mott, 1972). After rainfall, maximum temperatures may fall by as much as 35°C in the summer and 20°C in the winter to give a diurnal fluctuation of 23-32°C and 12-19°C in summer and winter respectively. Soil removed from the study area and incubated at temperatures similar to those recorded in the field in summer and winter gave rise to different floras, similar to those recorded in the field after seasonal rainfall (Mott 1972). Laboratory experiments on the germination requirements of the three species *Helipterum craspedioides, Helichrysum cassinianum* and *Aristida contorta* showed that the control of seasonal germination was related both to their optimal temperatures for germination, and to an initial dormancy in young seed of each of the three species.

As noted above, seed of many species were found to remain on the surface of the soil and so germinate in this position during the next season. Laboratory studies have shown that in *Helipterum craspedioides* and *Aristida contorta* there is an obligate requirement for light, and this is evident in the lack of germination from seeds buried in the field (Table 3). The germination of *Aristida contorta* from buried seed during the summer of 1970-1971 was presumably made possible by loss of light sensitivity in seed which had remained in the field since the last heavy growth of *Aristida contorta* following summer rains in 1967-1968.

Viability tests carried out on the seeds of all three species after field burial showed that in two winter annuals *Helipterum craspedioides* and *Helichrysum cassinianum*, less than 10% of the seed remained viable after being in the field over winter, and less than 4% of the original seed was viable after exposure for two seasons (Table 3). Seed of *Aristida contorta* was found to have less than 3% seed viable after being left over the summer of 1970-1971.

TABLE 3
Percentage germination and viability of ungerminated seeds of seed samples at Mileura Station during 1970 and 1971

SPECIES		SITE			
		Percentage			
		Surface		Buried (one season)	
		1 Season†	2 Seasons	1 cm Deep	3 cm Deep
Helipterum craspedioides	Germination	31 (31.0 ± 6.3)*	17 (27.0 ± 4.8)	0	0
	Viability	7 (13.2 ± 3.2)	4 (10.4 ± 2.8)	20 (26.3 ± 2.6)	22 (28.8 ± 4.7)
Helichrysum cassinianum	Germination	14 (17.8 ± 4.9)	18 (22.3 ± 6.2)	9 (15.8 ± 4.6)	1 (1.6 ± 1.6)
	Viability	8 (16.0 ± 2.4)	2 (3.2 ± 3.2)	12 (20.2 ± 2.7)	4 (6.6 ± 2.8)
Aristida contorta	Germination	29 (31.5 ± 7.0)	—	0	0
	Viability	2.5 (6.7 ± 2.5)	—	18 (24.7 ± 3.1)	13 (19.8 ± 2.6)

* Arcsin transformed data presented in parentheses.
† Season refers to that required for a germination, i.e. summer for monocotyledons and winter for dicotyledons.

Because seed is on the surface during germination, the soil surface must remain moist throughout the time required for early establishment. Laboratory tests have shown that *Helipterum craspedioides* and *Helichrysum cassinianum* require 3-5 days for substantial germination (Mott, 1972), and this was confirmed by field observation which showed that little germination occurred within 4 days of the commencement of winter rain. Following summer rainfall many seedlings of *Aristida contorta* were evident within 48 hours of the commencement of rain, and this agrees with the 24 hours found necessary to yield 50% germination in the laboratory.

The main germination occurring in any winter was during the first rain wetting the surface for a sufficient time to lead to germination. In 1969 no increase was observed during the single fall three weeks after germination, and the winter rains of 1970 and 1971 caused a germination of less than 5% of the original number of winter annuals.

CONCLUSION

Winter rains were found to result in the germination of a large number of dicotyledons, and these made up a high proportion of the plants surviving to maturity. Summer rains led to a much higher proportion of monocotyledons, and even in a year with abnormally high germination of dicotyledons during summer, differential survival led to elimination of most of the dicotyledons before maturity. Control of the composition of the flora germinating in any season was due to the temperature of the seed bed, and to the dormancy present in seeds of some species at the time of seed fall.

Since most of the seeds of annual species were found to germinate on or near the soil surface, effective germination required the soil surface to remain moist for at least two days in the summer and for five days during winter. Providing these requirements were met both run-on and run-off areas had high germination in all the years of the study. The importance of the initial germinating rainfall was emphasised by the low numbers germinating during follow-u p rains.

Most annuals dried off when the moisture potential of the entire soil profile fell below —15 bars. Survival was different in the two areas, plants dying sooner in the run-off areas, because of shallower soils and redistribution of water after rainfall. Dry matter production was much greater in the run-on areas, and although survival in these areas was similar between years, plant production varied greatly.

Little viable seed remained after germination in any season. Under these conditions little seed is available for germination in the following seasons, unless plants grow to maturity and set seed after each period of germination. Thus as well as being important in determining the spatial distribution of productivity in the annual community, the redistribution of water into drainage channels can allow at least some plants to grow to maturity after each rainfall which leads to germination. This aspect was emphasised during a dry year in which few plants survived to maturity and little seed was set on the run-off plain, seed being blown onto this area from the adjacent run-on zone.

The results presented in this paper highlight the need for a new water balance model of the type described by Fitzpatrick, Slatyer and Krishnan (1967) for the estimation of plant growth periods in annual communities. The following factors would have to be taken into consideration. Firstly, the initial rainfall causing germination must maintain high moisture levels at the surface for the time needed for germination and early establishment. Secondly, all winter annuals died when the soil moisture potential fell below —15 bars. Finally, an allowance should be made for the effect on community survival if the soil moisture store does not remain above —15 bars for the eight weeks necessary for flowering in the three species discussed above.

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