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Review

Rain use efficiency: a unifying concept in arid-land ecology

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The Rain Use Efficiency (*RUE*) factor is the quotient of annual primary production by annual rainfall, i.e. the number of kilograms aerial dry matter phytomass produced over 1 ha in 1 year per millimetre of total rain fallen†. It may be expressed in Above Ground Net Primary Production, in Maximum Standing Crop (for therophytic or ephemeroid vegetation types), in Herbage Yield or in any other production measurement system, as long as the reference system is clearly indicated. All other conditions remaining equal, *RUE* tends to decrease when aridity increases together with the rate of useful rains, and as potential evapotranspiration increases. But it also strongly depends on soil condition and, more than anything, on vegetation condition particularly on its dynamic status. It thus greatly relies on human and animal impact on the ecosystems. In any given type of ecosystem *RUE* is closely linked to perennial aerial phytomass and ground cover. The *RUE* factor thus appears as a good indicator of Ecosystem Productivity allowing, furthermore, valid comparisons between ecosystems from various climatic zones or having totally different botanical and structural characteristics. Actual *RUE* figures throughout the arid zones of the world may vary from less than 0·5 in depleted subdesertic ecosystems to over 10·0 in highly productive and well managed steppes, prairies or savannas. Reasonably well managed arid and semi-arid grazing lands are usually in the 3·0–6·0 values range while the biological limit seems reached in heavily fertilized small experimental plots with values approaching 30·0.

Background, rationale and justification

It has been known for some 70 years, since the fundamental work of Briggs & Shantz in 1913–14, that plant production is closely tied to transpiration, since both photosynthesis and transpiration are, to a large extent, governed by energy flow. Briggs & Shantz showed that any plant species or cultivar has, under given ecological conditions, a characteristic and genetically controlled transpiration coefficient measured as the ratio of the weight of water absorbed to the weight of dry matter produced. In Briggs & Shantz's experiments (1913) transpiration coefficients averaged the following values:

Millet 300, Sorghum 322, Maize 368, Wheat 513, Barley 534, Oats 597, Rye 685, Rice 710, Alfalfa 831, Vegetables and Legumes 600–800, Range grasses 300–1000.

Much lower figures were found in Mediterranean annual range species: 80–150 kg H_2O /kg DM, for instance for *Avena sterilis*, *Hordeum murinum*, *Phalaris minor*, *Stipa capensis*, *Medicago hispida*, *Trigonella arabica*, *Eruca boveana*, *Reboudia pinnata* and *Malva*

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†Also expressed in lb/acre/inch.
1 kg/mm/ha = 0·1 g/mm/m^2; = 22·7 lb/acre/inch; 1 lb/acre/inch = 0·0445 kg/mm/ha.

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silvestris, while perennial rangeland species of grasses had considerably higher T.C.s. (Van Keulen, 1975).

Later, De Wit (1958) put forward the relation $P = MW/E$ where P is dry matter production, W, the measured transpiration, E, average daily water evaporation and M, a factor of proportionality depending on species, cultivar, ecotype, etc. and nutrients availability. He thus showed that production is linked to the ratio between actual transpiration and potential evaporation which is a generalization of the relationship found by Briggs & Shantz.

Experiments in sealed pots have shown that the transpiration coefficient may vary from 100 to 250 g of water/g of DM produced, including shoots and roots (Briggs & Shantz, 1913; Loomis, Williams *et al.*, 1971; Hanks, Gardner *et al.*, 1969; Van Keulen, 1975). If we reckon that roots represent usually about 30 per cent of the total phytomass in annuals (Van Keulen, 1975), we have then the values of 130–325 g water transpired/g Aerial Dry Matter (*ADM*) produced. As, in addition, evaporation from soil surface averages 35 per cent of daily Potential Evapotranspiration (*PET*) as shown by many authors (Hanks, Gardner *et al.*, 1969; Van Keulen, 1975; Doorenbos & Pruitt, 1975; Le Houérou & Popov, 1981) and about 50 per cent of the infiltrated rains in rangeland conditions (Floret, Pontanier *et al.*, 1982; Cornet, 1981), one may thus expect Actual Evapotranspiration (*AET*) to be of the order of 250–650 g H_2O/g ADM. As a matter of fact, using De Wit's relation, a number of authors have shown that primary production is proportional to the amount of water evapotranspired whereby $P = M\ (AET/PET)$ where P = DM production; M = a factor of proportionality depending on the plant considered and its nutritional status; AET = actual evapotranspiration, and PET = potential evapotranspiration (Hanks, Gardner *et al.*, 1969; Van Keulen, 1975; Floret & Pontanier 1978, etc. Viets (1962) therefore introduced the concept of Water Use Efficiency (*WUE*) which, opposite to the Transpiration Coefficient, is the ratio between the dry matter produced and the amount of water evaporated *and* transpired. *WUE* is usually expressed in g/kg or in mg/g. The *WUE* factor is now widely used among crop physiologists, production ecologists and agronomists (Fisher & Turner, 1978).

Under intense cropping systems, such as in irrigated conditions, the difference between transpiration and evapotranspiration is small as the ground is usually totally covered; the relation of production to *AET* is then quite good. But it is not necessarily so under rainfed conditions particularly in arid and semi-arid rangelands where ground cover may vary largely from close to zero to close to 100 per cent from one range type to another, and from one season to the next in a given type. The magnitude of direct evaporation from soil surface in arid and semi-arid rangelands may range from 20 to 70 per cent of the infiltrated rain (Hillel, Gardner, 1970; Van Keulen, 1975; Caldwell, White *et al.*, 1977; Campbell & Harris, 1977; Floret & Pontanier, 1978, 1982; Cornet, 1981). Floret *et al.* (1981) and Holdridge (1962) propose an average of 50 per cent in arid zone rangelands.

The proportion of infiltrated rain in annual rain varies greatly with distribution, climate, topography, vegetation and soil; it may reach close to 100 per cent in loose sand but fall to 10 per cent or less in steep slopes and impervious soil surfaces; it exceeds 100 per cent in run-on areas.

In irrigated crops *WUE* is of the order of 1–2 (500–1000 kg H_2O/kg DM: for alfalfa, for instance, and up to 3–4 in high yielding cultivars of sorghum and maize) while in arid and semi arid rangelands it usually varies from 0·1 to 1·0, i.e. 1000 to 10,000 kg of water are needed to produce 1 kg of aerial dry matter. This ten-fold difference in *WUE* among rangeland vegetations is essentially—but not entirely—due to differences in run-off, evaporation and soil fertility between ecosystems. Szarek (1979) found values ranging from 0·14 to 0·79 in four arid rangeland ecosystems of W and SW United States of America; Floret & Pontanier (1974) gave values from 0·18 to 0·60 in southern Tunisia, while Tadmor, Eyal *et al.* (1974) found 0·89 over an 11 year experiment in grazed weed communities on fertile loessial soils of northern Negev.

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the order of 50 mm which is the limit isohyet between diffuse and contracted vegetation patterns in Africa and Asia (Le Houérou, 1959b). Noy-Meir (1973) cites the values of 25–75 mm/year of precipitation for the 'Zero-yield' intercept; Le Houérou & Hoste (1977) found 48 mm/year from the extrapolation of their rainfall primary production regression curve in the Mediterranean deserts while Webb *et al.* (1978) found the value of 38 mm/year in North American deserts.

Floret & Pontanier (1978, 1982) found from six ecosystems of southern Tunisia studied over 6 years the following relations:

$$(1)\ \log V = 1{\cdot}21\, DAET - 0{\cdot}49;\ r = 0{\cdot}93,$$

$$(2)\ P = 14878\frac{AET}{Eo} - 368;\ r = 0{\cdot}90,$$

where:
V = daily DM increment of aerial phytomass during the growing season (kg/ha/day);
$DAET$ = mean daily actual evapotranspiration (mm);
P = DM production (kg/DM/ha/year);
AET = actual evapotranspiration (mm/year);
Eo = free water evaporation as measured through the Piche evaporometer.

Grouzis & Sicot (1981) found in the Sahel of Upper Volta the relation:

$$P = 0{\cdot}40\, Re - 34{\cdot}6,$$

where:
P = production (g DM/m^2).
Re = infiltrated water (mm) (measured as the difference between precipitation and run-off).

Based on data from 10 sites in the arid and semi-arid rangelands of the United States of America, Sims & Singh (1978) found the relation

$$Y = 9{\cdot}79 + 0{\cdot}13P - 0{\cdot}28\, Pa + 0{\cdot}59\, AET,$$

where:
Y = yield; P = mean annual precipitation (mm); Pa = precipitation of the current year (mm), AET = actual evapotranspiration (mm/year).

Webb *et al.* (1978) found the relation:

$$ANPP = 0{\cdot}30\, AET - 11{\cdot}2,$$

where
$ANPP$ = above ground net primary production,
AET = actual evapotranspiration = precipitation
and, therefore,
$ANPP = 0{\cdot}3\, P - 11{\cdot}2$.

Cornet (1981) finds *WUE* values of 0·39–0·50 (3·9–5·0 kg DM/mm/year) in the Sahelian zone of northern Senegal with an equivalent *RUE* value of 3·0. In the latter case the productivity of infiltrated rain is thus 30–67 per cent greater than for total rain. In southern Tunisia Floret & Pontanier (1982) found an average difference of 6 per cent only (with a range of 1·0 to 80 per cent according to vegetation and soil types) between *WUE* and *RUE*; *RUE* being the Rain Use Efficiency factor, i.e. the quotient of annual Aerial Dry Matter produced by the amount of annual rain. *RUE*, sometimes also called Precipitation Use Efficiency (*PUE*) (Wight & Black, 1979), is usually expressed in kg DM/ha/year/mm.

The assumption that *AET* equates precipitation in arid and semi-arid zones is about valid (particularly in case of endoreism) at the level of large catchment basins or broad geographical zones. But at the site level (0·1–10·0 km²) this would seem to constitute a gross overgeneralization since run-off do actually occur in quite substantial proportions [except, of course, in some particular conditions of loose sandy soils, absolutely flat topography (extremely rare), etc.]. In the Mediterranean arid zone, for instance, wadis begin to flow over small and intermediate catchments (100–1000 km²) for thresholds of

10–15 mm per storm with a moderate intensity rain of 20–30 mm/h (Le Houérou, 1959, 1969). The zero run-off zone in the Sahara occurs only below the 25 mm isohyet for small to intermediate size basins. Average annual measured run-off in the arid zone of Algeria and Tunisia, for instance, is 1–5 per cent of annual precipitation on catchments of 100–10,000 km^2 and 2–10% on catchments of 1–100 per km^2 (Le Houérou, 1969) while instantaneous rates may reach 30–60 per cent for short rainy periods over 1000–10,000 per km^2 basins, and naturally much more on small basins and, with greater reason, at the site level. We therefore believe it more realistic to try and relate production to precipitation whenever measured data on actual evapotranspiration are not available rather than to more or less arbitrarily equate rainfall and *AET* at site level since this is known to be in error, except on loose sands.

The study of the relationships between annual (or seasonal) precipitation and natural vegetation in general, and primary production in particular, is the more justified in arid zone as *PET* is always much higher than rainfall on a yearlong basis (except for short periods consecutive to rain) and often of one order of magnitude greater (e.g. 2000 vs. 200 mm) or even much more in the true deserts. Since, in addition, neither the amount of water infiltrated nor evapotranspired is known outside some pin-point research sites (which are scarce and far in between in arid and semi-arid rangelands), it is difficult to relate production to these highly variable parameters over large geographic areas. Successful models have, however, been built for the past 10 years, but only in a limited number of specific sites for one or very few soil and vegetation types where validation data were available. These can obviously not be extrapolated to other sites having different characteristics.

Attempts towards regional integration have met with moderate success since many basic parameters such as soil permeability, fertility, run-off rates, vegetation structure and interception rates, evaporation rates, rain distribution in time and space, rain intensity, detailed soil and vegetation maps, etc. are usually missing at the large catchment basin level or at a smaller scale. For these many reasons a large number of scientists have attempted to relate annual primary production (or carrying capacity) to annual rainfall, however crude such a relation might theoretically be expected to prove. Perhaps as many as 100 investigators from various parts of the world, have actually shown the existence of a linear increase in average net annual primary production, or in livestock carrying capacity, with increase in average annual precipitation in arid and semi-arid zones.

In a relatively limited number of cases, however, the correlation between annual productivity and annual rainfall is poor; these are essentially depressions benefitting from run-off, or soils having a water table within reach of the roots (which in turn depends on the type of vegetation: some shrubs and trees being able to reach levels of moisture 50–100 m below soil surface and quite commonly 10–20 m, while herbaceous vegetation rarely reaches 2 m, again with the noticeable exception of alfalfa (*Medicago sativa*) which may reach 10–15 m). This is also the case in the sub humid zone or even in the upper part of the semi arid zone, under rain falls of 500–1000 mm, where the increase of production with precipitation often levels off (Sims & Singh, 1978). In series No. 173 of Table 1, for instance, the correlation coefficient is only 0·32 over a period of 43 years under a mean precipitation of 825 mm in close to prestine tall grass prairie of Kansas (Towne, 1983).

In connection with the above it should also be mentioned that annual data on both variables should not concern the 'calendar year' but the 'biological year' or 'agricultural year', i.e. from the beginning of the rainy (growing) season to the end of the dry (dormancy) season; for instance from September to August under the mediterranean climates of the northern hemisphere, from May/June to April/May in tropical West Africa, etc. The correlations are thus evidently much better than using calendar-year rainfall data; in temperate climates, however, biological year does correspond to calendar year, due to winter dormancy.

Investigations on rainfall to productivity relationships began as early as the 1930s in the U.S.A. and have become increasingly popular since the 1960s. Some generalization

Table 1. *Annual rainfall, annual primary above ground production and* RUE *in the rangelands of some arid and semi-arid zones of the world*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year†)	*RUE*	Range	Reference	Remarks ‡
1	Kuwait	S/E	3	63	190	3·00	0·0–4·0	Kernick, 1966	Exclosure
2	Saudi Arabia	S	1/2	75	50	0·67	—	Calculated from stocking rates estimates, Heady, 1963	Overgrazed steppe
3	U.S.S.R, Kyzylkum Uzbekistan	E	?	98	213	2·18	—	Rodin, 1979	Exclosure
4	Iraq	S/E	5	100	120	1·20	0·0–4·0	Thalen, 1979	Depleted steppe
5	U.S.S.R. Karakum/ Repetek, Tadjikistan	E	?	115	4110	35·75	—	Rodin, 1979	Pristine dune vegetation over deep watertable
6	U.S.S.R., Khazakstan	E	?	120	2520	24·00	—	Rodin, 1979	Pristine dune vegetation over deep watertable
7	U.S.A., California	E	5	125	246	1·97	—	Szarek, 1979	Rockvalley
8	U.S.S.R., Gobi Desert outer Mongolia	E	?	140	128	0·91	—	Rodin, 1979	Overgrazed steppe
9	Libya, Cyrenaica	Sy	2	142	306	2·15	—	Shishov & Kharine, 1980	—
10	U.S.A., Utah	E	9	143	224	1·57	—	Sneva & Hyder, 1962	Ser. 11
11	Canada	E	20	147	356	1·47	—	Smoliak, 1956	—

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
12	U.S.S.R., Karakum	E	?	148	480	3·24	—	Rodin, 1979	—
13	Egypt	E	10	150	400	2·67	—	Ayyad, (1977–1981)	Exclosure
14	Libya, Tripolitania	E/S	4	150	132	0·88	0·4–1·4	Le Houérou & Telahique, (unpublished)	Degraded Steppe
15	Syria	E	4	150	266	1·77	—	Van der Veen, 1967	—
16	Australia	S	Lt	150	120	0·80	—	Condon, 1968	Calculated from stock densities
17	Tunisia	E	7	154	744	4·83	—	Novikoff & Skouri, 1981	Controlled grazing
18	South Africa	S	7	155	1200	7·74	—	Walter, 1954	Pristine veld
19	South Africa	E	?	162	1020	6·29	—	Louw, 1968	Pristine veld
20	U.S.A., Utah	E	13	169	250	1·46	—	Hutchings & Stewart, 1953	—
21	U.S.A., New Mexico	Sy	17	174	352	2·02	—	Herbel, Ares *et al.*, 1972	Ser. 1
22	India, Rajasthan	E	4	180	353	1·96	—	Mann & Ahuja, 1976	—
23	U.S.A., New Mexico	E	17	183	370	2·02	—	Herbel, Ares *et al.*, 1972	Ser. 4
24	U.S.A., New Mexico	E	17	186	509	2·74	—	Herbel, Ares *et al.*, 1972	Ser. 2
25	U.S.A., New Mexico	E	17	187	563	3·01	—	Herbel, Ares *et al.*, 1972	Ser. 3

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
26	Iraq	S/Sy	4	187	120	0·64	0·0–3·0	Thalen, 1979	Depleted steppe
27	U.S.A., Montana	E	12	200	911	4·56	—	Wight & Hanks, 1981	—
28	U.S.A., New Mexico	E/Sy	15/21	210	552	2·62	0·7–6·2	Herbel, Ares *et al.*, 1972; Paulsen & Ares, 1962	Synthesis 9 long term series Jornada
29	Syria	E	4	206	703	3·41	—	Van Der Veen, 1967	Exclosure
30	U.S.A., New Mexico	E	19	213	287	1·34	—	Herbel & Gibbens, 1981	Ser. 'Cacique'
31	U.S.A., New Mexico	E	3	213	1480	6·94	—	Pieper & Herbel, 1982	ANPP, Exclos.
32	U.S.A., New Mexico	E	3	213	1090	5·11	—	Pieper & Herbel, 1982	ANP, Grazed
33	U.S.A., Idaho	E	9	213	966	4·56	—	Sneva & Hyder,1982 Craddock & Forsling, 1938	Ser. 13 Calc. from stock rates
34	Tunisia	E	6	214	1003	4·70	—	Floret & Pontanier, 1982	Contr. Grzg. ser. Rkz.
35	U.S.A., Arizona	E	10	214	484	2·20	—	Cable, 1975	Sta. Rita
36	U.S.S.R.	E	?	217	1000	4·61	—	Rodin, 1979	Exclos.
37	Algeria, Hodna	E/S/Sy/	5	220	625	2·84	0·5–12·0	Le Houérou, Claudin *et al.*, 1974	Synth. 120 Rge. types
38	U.S.A., New Mexico	E	21	222	1527	6·87	—	Herbel & Gibbens, 1982	Ser. 'Algerita'
39	Libya, Tripolitania	E	3	225	900	4·0	—	Le Houérou & Dumancic, 1981	Contr. Grgz.

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
40	U.S.A., Utah	E	3	226	1440	6·37	—	Szarek, 1979	Curlew Valley
41	Tunisia	E	3	227	269	1·19	—	Floret & Pontanier, 1982	Ser. Az, Gypsum.
42	U.S.A., New Mexico	E	15	228	431	1·89	—	Paulsen & Ares, 1962	Jornada
43	U.S.A., North Dakota	E	17	228	394	1·72	—	Rogler & Haas, 1947	—
44	U.S.A., New Mexico	E	20	231	330	1·42	—	Herbel & Gibbens, 1982	Ser. 'Simona'
45	Tunisia	E	5	231	825	3·57	—	Floret & Pontanier, 1982	Contr. Grzg.
46	U.S.A., Utah	E	13	239	423	1·77	—	Blaisdell, 1958	
47	U.S.A., Idaho-Oregon	E/Sy	6/13	239	803	3·36	1·57–5·02	Sneva & Hyder, 1962	Synthesis 13 series
48	U.S.A., New Mexico	E	27	239	1484	6·20	—	Herbel & Gibbens, 1982	Ser. 'Stellar'
49	U.S.A., New Mexico	E	27	239	803	3·36	—	Herbel & Gibbens, 1982	Ser. 'Reakor'
50	U.S.A., Utah	E	3	241	1440	5·98	—	Szarek, 1979	
51	U.S.A., Texas	E	3	242	393	1·62	—	Thomas & Young, 1954	Drought
52	U.S.A., Oregon	E	6	243	656	2·70	—	Sneva & Hyder, 1962	Ser. 5
53	U.S.A., Oregon	E	6	243	672	2·77	—	Sneva & Hyder, 1962	Ser. 4

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
54	U.S.A., Oregon	E	6	243	736	3·03	—	Sneva & Hyder, 1962	Ser. 1
55	U.S.A., Oregon	E	6	243	774	3·19	—	Sneva & Hyder, 1962	Ser. 2
56	U.S.A., Oregon	E	6	243	832	3·42	—	Sneva & Hyder, 1962	Ser. 3
57	U.S.A., Oregon	E	6	243	995	4·09	—	Sneva & Hyder, 1962	Ser. 6
58	U.S.A., Oregon	E	6	243	1201	4·94	—	Sneva/Hyder, 1962	Ser. 7
59	U.S.A., New Mexico	E	20	246	168	0·68	—	Herbel & Gibbens, 1982	Ser. 'Conite'
60	Senegal	E	7	247	573	2·32	—	Bille, 1978	Dune
61	Senegal	E	7	247	1677	6·79	—	Bille, 1978	Silt slope
62	Senegal	E	7	247	2902	22·75	—	Bille, 1978	Clay depr.
63	South Africa	S	Lt	250	1200	4·80	—	Walter, 1954	Pristine veld
64	Tunisia (arid zone)	S/Sy	15	250	700	2·80/ 3·03	0·5–12·0	Le Houérou, 1969	130 plant comm.
65	Algeria	S/E/ Sy	2	250	690	2·76	0·5–12·0	Rodin & Vingradov *et al.*, 1970	80 plant comm.
66	Algeria	S/E	2	250	483	1·94	—	Nedjraoui, 1981	—
67	India, Rajasthan	E	2	250	405	1·62	—	Mann & Ahuja, 1976	—
68	Israel, N. Negev	E	10	258	2480	9·61	—	Benjamin *et al.*, 1982	Fo
69	Israel, N. Negev	E	10	258	4930	19·20	—	Benjamin *et al.*, 1982	F+

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
70	Israel, N. Negev	E	11	262	2510	9·58	—	Tadmor *et al.*, 1974	—
71	U.S.A., Oregon	E	8	263	883	3·36	—	Sneva & Hyder, 1962	Ser. 8
72	U.S.A., Oregon	E	7	266	1334	5·02	—	Sneva & Hyder, 1962	Ser. 9
73	U.S.A., Oregon	E	7	267	751	2·81	—	Sneva & Hyder, 1962	Ser. 10
74	U.S.A., Idaho	E	2	270	975	3·61	—	Pearson, 1965	Grazed
75	U.S.A., Idaho	E	2	270	1225	4·55	—	Pearson, 1965	Ungrazed
76	U.S.A., Idaho	E	20	280	920	3·29	—	Blaisdell, 1958	—
77	U.S.A., New Mexico	E	4	283	1730	6·11	—	Szarek, 1979	—
78	India, Rajasthan	E	?	289	1080	3·74	—	Gupta *et al.*, 1972	—
79	U.S.A., Utah	E	11	296	631	2·13	—	Frischnecht & Harris, 1968	—
80	U.S.A., New Mexico	E	8	299	424	1·42	—	Springfield, 1963	—
81	Mediterranean Basin	E/S/Sy	20	300	1200	4·00	—	Le Houérou & Hoste, 1977	Synthesis over 7 countries
82	Senegal	—	—	300	420	1·40	—	Morel & Bourliere, 1962	—
83	Australia, NSW	E	5	300	457	1·52	—	Leigh *et al.*, 1979	—
84	U.S.A., Arizona	E	25	306	185	0·60	—	Martin, 1983	—
85	Australia, NSW	E	5	311	756	2·43	—	Wilson & Graetz, 1980	—

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
86	Tunisia	E	4	317	1564	4·95	—	Floret & Pontanier 1982	—
87	Chad	E/S	—	320	420	1·31	—	Gillet, 1967	—
88	Chad	E/S	—	320	1200	3·75	—	Gillet, 1967	—
89	Chad	E/S	—	320	1380	4·31	—	Gillet, 1962	—
90	Chad	E/S	—	320	3180	9·94	—	Gillet, 1967	—
91	U.S.A., Arizona	E	1	344	550	1·60	—	Szarek, 1979	—
92	U.S.A., Colorado	E	35	345	591	1·71	—	Bement, 1968	—
93	India, Rajasthan	E	7	350	593	1·69	—	Mann & Ahuja, 1976	—
94	India, Rajasthan	E	7	350	783	2·23	—	Mann & Ahuja, 1976	—
95	India, Rajasthan	E	7	350	850	2·42	—	Mann & Ahuja, 1976	—
96	India, Rajasthan	E	7	350	1080	3·08	—	Mann & Ahuja, 1976	—
97	U.S.A., New Mexico	E	5	351	601	1·71	—	Springfield, 1963	—
98	U.S.A., S. Dakota	E	7	355	523	1·47	—	Thomas & Osenburg, 1959	Fo
99	U.S.A., S. Dakota	E	7	355	1140	3·21	—	Thomas & Osenburg, 1959	F+
100	S.W. Africa Namibia	S	?	360	3120	8·64	—	Walter, 1954	Pristine Veld
101	Upper Volta, Sahel	E	4	369	955	2·59	—	Grouzis & Sicot, 1981	—

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
102	U.S.A., Colorado	E	12	371	1336	3·60	—	Sims & Singh, 1978	—
103	India, Rajasthan	E	5	380	669	1·76	—	Mann & Ahuja, 1976	—
104	India, Rajasthan	E	5	380	992	2·61	—	Mann & Ahuja, 1976	—
105	India, Rajasthan	E	5	380	1210	3·18	—	Mann & Ahuja, 1976	—
106	India, Rajasthan	E	5	380	1642	4·32	—	Mann & Ahuja, 1976	—
107	U.S.A., N. Dakota	E	15	381	2186	5·74	—	Lorenz, 1974	—
108	U.S.A., N. Dakota	E	8	383	704	1·83	—	Lorenz, 1970	Cut 2·5 cm Fo
109	U.S.A., N. Dakota	E	8	383	3468	9·03	—	Lorenz, 1970	Cut 2·5 cm F+
110	U.S.A., N. Dakota	E	8	383	2180	5·67	—	Lorenz, 1970	Cut 0·0 cm Fo
111	U.S.A., N. Dakota	E	8	393	5414	14·09	—	Lorenz, 1970	Cut 0·0 cm F+
112	U.S.A., Colorado	E	8	393	1193	3·03	—	Currie & Peterson 1966	—
113	U.S.A., Montana	E	10	396	1057	2·67	—	Wight & Black, 1979	Fo
114	U.S.A., Montana	E	10	396	2325	5·87	—	Wight & Black, 1979	F+

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
115	Tanzania, Serengeti	E	2	400	1600	4·00	—	Braun, 1973	Short Grassland
116	Australia, NSW	S	Lt	400	800	2·00	—	Condon, 1968	Calculated from carr. cap.
117	India, Rajasthan	E	10	403	192	0·47	—	Mann & Ahuja, 1976	Wo (depl)
118	India, Rajasthan	E	10	403	441	1·09	—	Mann & Ahuja, 1976	Wo (poor)
119	India, Rajasthan	E	10	403	542	1·34	—	Mann & Ahuja, 1976	Wo (poor)
120	India, Rajasthan	E	10	403	1028	2·55	—	Mann & Ahuja, 1976	W+ (depl)
121	India, Rajasthan	E	10	403	1269	3·14	—	Mann & Ahuja, 1976	W+ (poor)
122	India, Rajasthan	E	10	403	1316	3·26	—	Mann & Ahuja, 1976	W+ (fair)
123	U.S.A., Arizona	E	24	412	718	1·74	—	Martin, 1983	—
124	U.S.A., Arizona	E	27	431	536	1·24	—	Martin, 1983	—
125	U.S.A., Colorado	E	16	432	1125	2·60	—	Dahl, 1963	—
126	U.S.A., Arizona	E	6	436	1400	3·21	—	Chew & Chew, 1965	ANPP
127	Mali, South Sahel	E	4	449	1875	4·18	—	De Vries, Penning *et al.*, 1982	Sand, Fo
128	Mali, South Sahel	E	4	449	1975	4·40	—	De Vries, Penning *et al.*, 1982	Silt, Fo

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
129	Mali, South Sahel	E	4	449	5000	11·13	—	De Vries, Penning *et al.*, 1982	Sand, F+
130	Mali, South Sahel	E	4	449	11000	24·49	—	De Vries, Penning *et al.*, 1982	Silt, F+
131	U.S.A., California	E	34	479	2242	5·10	—	Duncan & Woodmansee, 1975	—
132	U.S.A., California	E	8	493	1780	3·61	—	Bentley, Green *et al.*, 1951	Fo
133	U.S.A., California	E	8	493	2248	4·56	—	Bentley, Green *et al.*, 1951	Fo
134	U.S.A., California	E	8	493	2497	5·06	—	Bentley, Green *et al.*, 1951	F+
135	U.S.A., California	E	8	493	3358	6·81	—	Bentley, Green *et al.*, 1951	F+
136	Sahel and Sudan zones of Africa	S/E/Sy	20	500	1350	2·70	—	Le Houérou & Hoste, 1977	Grass layer only
137	Sahel and Sudan zones of Africa	S/E/Sy	20	500	18000	3·70	—	Le Houérou, 1982	Grass and browse
138	Australia, NSW	S	Lt	500	1250	2·50	—	Condon, 1968	Calculated from carr. cap. fig.
139	Senegal	E	10	500	1650	3·30	—	Cornet, 1981	—
140	India, Rajasthan	E	2	500	1150	2·30	—	Mann & Ahuja, 1976	—
141	U.S.A., California	E	13	513	1670	3·26	—	Bentley & Talbot, 1951	—

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
142	Israel, Mt. Tabor	E	6	529	2403	4·55	—	Naveh, 1982	—
143	Greece, Macedonia	E	5	550	1300	2·36	—	Liacos & Moulopoulos, 1967	—
144	U.S.A., Canada, N. Great Plains	S	Lt	550	3500	6·35	—	USDA Soil Cons. Serv. 1964	—
145	U.S.A., Kansas	E	10	579	3569	6·20	—	Launchbaugh, 1967	—
146	Israel, Galilee	E	14	586	2500	4·24	—	Gutman, 1978	—
147	U.S.A., Kansas	E	24	589	2510	4·10	—	Albertson & Weaver, 1950	—
148	Tanzania	E	2	600	7000	11·62	—	Braun, 1973	Tall Themeda grassland
149	Israel, Galilee	E	G	600	3307	5·51	—	Gutman, 1978	—
150	U.S.A., Kansas	E	24	606	2592	4·28	—	Hulett & Tomanek, 1968	—
151	South Africa, Pretoria	E	—	607	900	1·48	—	Bourliere & Hadley, 1970	—
152	Israel, Galilee	E	10	621	5373	8·65	—	Gutman & Seligman, 1979	—
153	U.S.A., Kansas	E	25	626	5637	2·00	—	Shiflet & Dietz, 1973	—
154	India, Udaipur	E	—	627	1800	2·87	—	Vyas, Garg *et al.*, 1972	—
155	Israel, Galilee	E	7	628	1884	3·00	1·4–5·2	Ofer & Seligman, 1969	1 year, 7 sites Fo
156	Israel, Galilee	E	7	628	4289	6·83	3·1–10·4	Ofer & Seligman 1969	1 year, 7 sites

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
157	Kenya	E/S	6	628	3096	4·93	(3·0–9·6)	Lamprey & Yussuf, 1981	—
158	Zimbabwe Matopo	E	—	650	1380	2·12	—	Bourliere & Hadley, 1970	—
159	U.S.A., Kansas	E	5	654	1958	2·99	—	Albertson & Tomanek, 1957	—
160	Australia, Katherine, NT	—	—	660	1500	2·27	—	Norman, 1963	—
161	Tanzania, Serengeti	—	—	700	5220	7·45	—	Bourliere & Hadley, 1970	—
162	Italy, Sardinia	S	Lt	700	2100	3·00	—	Le Houérou, 1969	—
163	U.S.A./Canada N.G. Plains	S	Lt	711	2570	3·61	—	CIAP, 1975	—
164	India, Varanasi	E		725	8250	11·75	—	Ambasht, 1972	—
165	India, Varanasi	E	—	725	3120	4·30	—	Choudhary, 1972	—
166	India, Varanasi	E	—	725	3900	5·37	—	Choudhary, 1972	—
167	India, Varanasi	E	—	725	4740	6·54	—	Singh, 1968	—
168	Israel, Galilee, Golan	E	5	734	3640	4·96	0·2–7·0	Katznelson & Putievsky, 1972	1 year, 5 sites Fo
169	Israel, Galilee, Golan	E	5	734	7744	10·55	1·6–21·0	Katznelson & Putievsky, 1972	1 year, 5 sites F+
170	India, Delhi	E	—	800	7980	9·97	—	Varshney, 1972	—
171	India, Air Forest (Savanna)	E	—	820	4080	4·97	—	Bourliere & Hadley, 1970	—

Table 1. *Continued*

Item	Location	Type of study	Duration of study (years)	Mean annual rainfall (mm)	Mean annual primary production (kg DM/ha/year)	*RUE*	Range	Reference	Remarks
172	India, Air forest (Savanna)	E	—	820	2880	3·51	—	Bourliere & Hadley, 1970	—
173	U.S.A., Kansas	E	43	825	3178	3·86	—	Towne, 1983	—
174	U.S.A., California	E	18	889	3066	3·45	—	Pitt & Heady, 1977	—
175	U.S.A., California	E	16	901	2037	2·26	—	Murphy, 1970	—
176	France, Herault	E	10	900	1500	1·60	—	Long *et al.*, 1967	Fo
177	France, Herault	E	10	900	5000	5·60	—	Long *et al.*, 1967	F+
178	France, Corsica	E	10	1100	1000	0·90	—	Etienne, 1977; Joffre, 1982	Fo
179	France, Corsica	E	10	1100	5000	4·55	—	Etienne, 1977	F+

* E = Experimental; S = Survey; Lt = Long term survey; Sy = Synthesis.

† Production as understood here does not include biomass losses occurring during the growing season (leaf shedding, decay, damage by fungi, insects, molluscs, birds, rodents, etc.) which may altogether account for 25–30 per cent of Above Ground Net Primary Production (*ANPP*) or more, especially in the tropics. When *ANPP* is measured (summation of increments) the acronym is shown in column 'remarks' No. 10. Many of the data gathered in this Table are actually herbage yields at the end of the growing season(s). In grasslands this is virtually equal to Aerial Primary Production. But herbage yield may substantially depart from total aerial production particularly in Bushland and Savanna.

‡ Fo = No fertilization; F+ = fertilization; W+ = water conservation techniques applied; Wo = control.

regressions have been proposed either for Carrying Capacity, or Herbage Yield, or Net Primary Production [Craddock & Forsling, 1938; Hutchings & Stewart, 1953; Walter, 1954; Blaisdell, 1958; Stewart, 1962; Sneva & Hyder, 1962; USDA Soil Conservation Service, 1964; Le Houérou, 1964, 1965, 1969, 1975; Currie & Peterson, 1966; Rosenzweig, 1968; Condon, 1968; CIAP (Climatic Impact Assessment Program, U.S. Dept. of Transportation), 1975; Le Houérou & Hoste, 1977; Grouzis & Sicot, 1981; Cornet, 1981; Le Houérou, 1982, etc.].

In a number of cases, however, it was found that seasonal rains had a better predictive value of current year's forage yields that annual total (Smoliak, 1956; Rogler & Haas, 1942; Dahl, 1963; Currie & Peterson, 1966; Hulett & Tomanek, 1968, Murphy, 1970; Duncan & Woodmansee, 1975, etc.). Annual total has no predictive value, in fact, but only a probabilistic value for long term planning.

Other investigations have related production to *AET* but using Rainfall figures in lieu of *AET* (Szarek, 1979; Sims & Singh, 1978; Webb, Szarek *et al.*, 1978). Sims & Singh (1978), for instance, found that in 10 Grassland Biome Research Sites in Central and Western United States of America, rainfall accounted for 67 per cent of the variability in primary production while incorporating rainfall and actual evapotranspiration together explained 77 per cent of this variability for grazed grassland and 59–65 per cent, respectively for ungrazed grasslands. The same authors further found that production of grazed grasslands increased in a linear fashion with rainfall up to 900 mm and above, while there was a levelling off above 500 mm of precipitation in the case of the same ungrazed grasslands.

Let us quote some authoritative conclusions: 'On grazing trails throughout the U.S.A. and Canada the study showed almost a straight line inverse relation between average annual precipitation and acres of native perennial grassland required on average per mature cow for 6 months summer grazing, seemingly irrespective of temperature and evaporation' (CIAP, 1975, quoted by Kellog & Schware, 1982, pp. 76–77). Sneva & Hyder (1962) found a close relationship between the annual precipitation index (expressed in percent of the median) and the yield index (expressed as percent of the median) over 13 sites of Oregon, Idaho and Utah over periods of 6–13 years of records of both variables, with a correlation coefficient of 0·88 and a standard error of 0·18.

The U.S. Department of Agriculture found 'an 800 pound (air dried) per acre increase in rangeland production for every 5 inch increase in average annual precipitation across the Northern Plains' (USDA Soil Conservation Service, 1964, quoted by Kellog & Schware, 1982, pp. 76–77). 'In arid climates there is nearly a linear increase in net primary production with increase in annual precipitation' (Whittaker, 1970, pp. 81–82). 'Productivity in desert areas can be determined very simply by measuring rainfall' (Krebs, 1972, p. 526). Rather tight correlation and determination coefficients were found by several authors either from linear or curvilinear regressions.

Craddock & Forsling (1938), Idaho	$r = 0{\cdot}944$	$r^2 = 0{\cdot}79$	$n = 9$
Hutchings & Stewart (1953), Utah	$r = 0{\cdot}944$	$r^2 = 0{\cdot}88$	$n = 13$
Blaisdell (1958), Utah	$r = 0{\cdot}945$	$r^2 = 0{\cdot}83$	$n = 13$
Sneva & Hyder (1962), Oregon, Idaho, Utah	$r = 0{\cdot}88$	—	$n = 95$
Currie & Peterson (1966) Colorado	$r = 0{\cdot}87/0{\cdot}97$	$r^2 = 0{\cdot}59$	$n = 8$
Le Houérou & Hoste (1962), Mediterranean Basin	$r = 0{\cdot}90$	—	$n = 45$

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= 0·79	$n = 9$
= 0·88	$n = 13$
= 0·83	$n = 13$
—	$n = 95$
= 0·59	$n = 8$
—	$n = 45$

Le Houérou & Hoste (1977), Sahel	$r = 0\cdot89$	—	$n = 45$
Cornet (1981), Senegal	$r = 0\cdot89/0\cdot91$	—	$n = 11$
Le Houérou (1983, unpubl.)	$r = 0\cdot83 \pm 0\cdot12$	$r^2 = 0\cdot71 \pm 0\cdot19$	$n = 394$

The Rain Use Efficiency factors found, in comparable management situations, throughout the various arid zones of the world, having totally different floras and vegetation types, turn out to be surprisingly consistent, with a relatively limited number of exceptions which will be discussed.

The scope of the present paper is three-fold:

(a) to review, compare and discuss the various *RUE* values found in various arid zones of the world;
(b) to try and determine the factors that affect *RUE* and its variability;
(c) to examine the significance and usefulness of this concept in arid land ecology.

RUE and climatic aridity

In principle, *RUE* should be inversely related to aridity since, within any given climate, the proportion of inefficient rains increases with aridity. In the arid and semi-arid zones of Tunisia, for instance, the proportion of rains yielding less than 10 mm per month increases from 25 per cent under 500 mm of average annual precipitation, to 50 per cent under 300 mm, 60 per cent under 200 mm and 80 per cent or more below the 100 mm isohyet (Le Houérou, 1969). The same rule, with slightly different figures, was found to prevail in Libya (Le Houérou, unpublished). South of the Sahara in the Sahelian and Sudanian zones, this trend is much less marked (Davy, Mattei *et al.*, 1976) although still existing. One may thus expect *RUE* to be directly related to mean rainfall and more so to the north of the Sahara than to the south.

On the other hand rainfall variability increases also with aridity. North of the Sahara the coefficient of variability of annual rainfall (standard deviation over the mean) increases from 25–30 per cent in the 400–500 mm precipitation belt to 70–80 per cent in the 100 mm belt (Le Houérou, 1959, 1983) south of the Sahara the situation is similar but slightly less pronounced: 20–50 per cent under the same extreme isohyets of 500 and 100 m (Le Houérou & Popov, 1981). There may, however, be compensatory factors: on both sides of the Sahara the proportion of sandy soils tend to increase as one comes nearer to the desert. Rain infiltration rates thus tend to increase while aridity increases. The net result seems to be a *RUE* in arid zone greater than one might expect from rainfall characteristics alone. In fact, desert fringes may have *RUE* values of 4·0 and above (Kernick, 1966; Floret & Pontanier, 1982). As a matter of fact the effect of aridity on *RUE* may be totally hidden by differences in vegetation condition. Vegetation in poor condition may show a lower *RUE* under higher rainfall than another ecosystem in good condition under lower rainfall. This issue will be addressed further.

Before commenting on Table 1, a few words of caution would seem appropriate. Accurate measurement of primary production is a very complex and difficult task. There are very substantial differences according to the method which is used and virtually each investigator uses a particular method he finds more fit for his aims and means. Obviously productivity depends on the height of cutting, but Lorenz (1970) has shown that differences in level of cutting as small as 2·5 cm may result in considerable differences in yield (up to 300 per cent) see items 108–111 in Table 1. Moreover, the time of clipping or defoliation and the frequencies of clipping also considerably affect regrowth hence total production.

Furthermore, most figures concern Maximum Standing Crop while others are Aerial Net Primary Production; the difference between the two sets of data in a given site may be 25–30 per cent or even much more. The correct values are obviously obtained from

ANPP; but the method is tedious, laborious, since it implies measurement at rather frequent intervals of cumulative increments of each main species during the growing season and since different species have often different seasonal growth patterns in a given community. In many cases production from shrubs and trees have not been accounted for. But these may however, represent an important part of the primary production, particularly in Savannas and Chaparrals; in the Sahel, for instance, it has been estimated that shrubs and trees represented some 30 per cent of the primary production (Le Houérou, 1980). Finally, some figures are deduced from carrying capacities using standardized calculation methods which may not be exactly appropriate in each and every case; on, for instance, the actual use factor (proportion consumed), on the feed value, which changes with time, etc. But all these shortcomings, and others, are impossible to avoid when measurement procedures have not been standardized beforehand, making at least the error more-or-less constant. This was obviously not possible in a study of such a nature as the present one.

Table 1 would warrant lengthy comments that space unfortunately does not permit. At first sight it would seem that there is no relation between aridity and *RUE* since ecosystems from high and low precipitation areas both exhibit high and low *RUE*s; the highest *RUE* factors recorded (10·0 and above) may occur in subdesertic pristine plant communities of tall shrubs from southern U.S.S.R. with above ground phytomasses of 8000 to 15,000 kg/ha, particularly in *Ammodendron argentum*, *Haloxylon persicum* and *Haloxylon aphyllum* dominated ecosystems. Conversely, *RUE*s of 0·5–1·0 are found in either high and low rainfall areas, particularly—but not only—in North Africa and the Near East. These usually correspond to heavily degraded plant communities and ecosystems; depletion due to wild fires (Corsica, Herault), overgrazing, fuel gathering, inappropriate cultivation and other mismanagement practices in conjunction or not with nutritional problems (salinity, alkalinity, acidity, nutrients deficiency, toxicity, water logging or shallow soils). In other words the effect of aridity may be totally hidden by the impact of management and/or soil condition. No significant overall correlation, as a matter of fact, could be found between precipitation and *RUE* from the figures given in Table 1. But, considering a given type and intensity (or level) of management, there seems to exist a consensus among investigators that *RUE* does increase with rainfall up to a certain point where nutrients or water logging may become a limiting factor. Such a relation is for instance suggested by the slightly exponential regression found by Le Houérou & Hoste (1977) for both the Mediterranean Basin and the Sahel, or the parabolic function found by Condon in Australia. In the case of the arid zone of Tunisia which was the subject of intensive studies (both survey and experimental) for over 30 years we have the following estimated figures (Le Houérou, 1969, pp. 418–423, pp. 527–546), shown on Table 2.

Table 2. RUE *values in the arid zone of Tunisia (Le Houérou, 1969)*

Bioclimatic zone	Rainfall (mm/year)	Production (kg DM, ha/year)	Area (10^3 ha)	No. of range types	*RUE*
Semi-arid	400–500	2200	254	4	4·9
Arid, Upper	300–400	930	825	32	2·6
Arid, middle	200–300	660	2315	31	2·6
Arid, lower	100–200	320	2350	33	2·1
Hyper arid, upper	50–100	150	4895	16	2·0
Hyper arid, lower	20–50	63	760	5	1·8
Azonal	50–500	710	1442	9	3·6
Overall	20–500	424	12841	130	3·03*

* Weighed value, arithmetic average being 2·80.

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No. of ıge types	*RUE*
4	4·9
32	2·6
31	2·6
33	2·1
16	2·0
5	1·8
9	3·6
130	3·03*

Table 3. *Experimental and survey* RUE *figures found in southern Tunisia*

Floret & Pontanier (1982)			Le Houérou, 1969	
Plant community investigated	*RUE* (experimental)		*RUE* (survey)	Mapping unit (1/500,000 map)
AA	3·57		4·0	73
ZR	4·95		6·0	129
RK3	4·69*		4·0	79
RK2	2·78		2·4	80
RK2	2·83	2·6	2·4	80
RK2 Dissa	1·61		2·4	80
RK2	3·69		2·4	80
RK1	2·07		2·4	80
AZ2	1·45		1·2	90
X	3·25		3·33	X

*For the same plant community in similar condition, in another site, 150 km away, Novikoff, Skouri (1981) found a *RUE* of 4·83 over 7 years of measurements.

The validity of this evaluation was later tested over seven range types for 6 years (Floret & Pontanier, 1978, 1982) in the following way (Table 3). Floret & Pontanier (1978, 1982) found that, in Southern Tunisia, under 180 mm of mean precipitation, *RUE* increases, on average, from 2·0 with 100 mm of annual precipitation to 4·2 under 250–300 mm of annual rain for five ecosystems investigated (Fig. 3), and then decreased, probably because of nutrients becoming the limiting factor; similar facts were reported by Novikoff & Skouri (1981). Cornet & Rambal (1981) reached similar conclusions in northern Senegal, as did De Vries, Penning *et al.* (1982) in Mali. This subject was pioneered by Tadmor (1970, 1972) and Van Keulen (1975) in the northern Negev. This issue will be discussed further when examining the relationships between *RUE* and soil condition. From a 7 year survey made in northern Kenya, Lamprey & Yussuf (1981) produced the following figures (Table 4). For East Africa, Table 5 has been calculated by the writer from the carrying capacity graph published by Pratt & Gwynne (1977). The calculation is based on a standard stock unit of 350 kg (770 lb) consuming 8 kg DM/day, with a proper use factor of 50 per cent.

The high values found in the Serengeti are explained by the fact that they were obtained in a national park, in still unspoiled savannas which are among the most productive in

Table 4. RUE *and rainfall in northern Kenya (Lamprey & Yussuf, 1981)*

Rainfall (mm/year)	*RUE* All vegetation	Rainfall (mm/year)	*RUE* Herbage only
363	2·7	296	2·22
395	3·0	309	2·32
458	3·4	360	2·71
471	3·5	390	2·93
785	5·9	555	4·17
853	6·4	761	5·72
1284	9·6	1229	9·24
Average 658	4·93	557	4·19

Table 5. *Rainfall and* RUE *estimates in East and West Africa*

Rainfall belts	East Africa Pratt & Gwynne (1977)	Serengeti Braun (1973)*	West Africa Bille (1977)
	RUE		
200	1·65	3·0	1·75
400	1·50	5·0	3·50
600	1·66	6·60	4·00
800	1·87	7·50	4·37
1000	3·00	8·00	4·55
1200	5·00	10·00	4·66

*Short, intermediate and tall grasslands pooled together, annual values.

Africa, growing as they do on the basalt derived soils of the Rift Valley. According to the data shown on Table 1, it would seem that, whatever the rainfall, *RUE* should not go much below a score of 2·0, even on shallow soils, whenever vegetation is in reasonably good dynamic condition. It does not seem that *RUE* is much affected by seasonality of rainfall, since winter, spring or summer rain climates have similar *RUE*s under comparable vegetation exploitation conditions, e.g. in Mediterranean and Tropical Africa (Table 5), as well as in the temperate continental Russian steppe or American prairie.

Winter temperatures do not seem to strongly effect *RUE* either, since both mild winter climates of the Mediterranean or the Tropics exhibit values similar to—and, if anything, lower than—the cold-winter Middle Asian zones or North American Great Plains (Table 6). Although winter temperatures obviously affect the seasonality of plant growth, they do not seem to much affect total annual production in the arid and semi-arid zone.

RUE and vegetation condition

As indicated above vegetation condition seems to influence *RUE* at least as much as aridity. Data from specific plant communities in contiguous sites having different rate of stocking show a clear tendency of *RUE* being proportionate with perennial plant cover and aerial phytomass. Pearson (items 74 and 75 in Table 1) found values of 3·61 and 4·55 in moderately stocked and totally protected paddocks of the same community of *Artemisia tridentata* and *Stipa comata* in Eastern Idaho. The writer found the following values in the Hodna Basin of Algeria: Community of *Artemisia herba alba* and *Noaea mucronata*, on silty soil (Table 8).

Table 6. *Rainfall and* RUE *in North American grasslands (Sims & Singh, 1978)*

Rainfall (mm/year)	Grazed grassland *ANPP*	Grazed grassland *RUE*	Ungrazed grassland *ANPP*	Ungrazed grassland *RUE*
150	500	3·3	800	5·3
200	800	4·0	1100	5·5
400	2000	5·0	2600	6·5
600	3200	5·3	3200	5·3
800	4600	5·7	3200	4·0

n East

West Africa * Bille (1977)
1·75
3·50
4·00
4·37
4·55
4·66

annual values.

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RUE at least as much as
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values of 3·61 and 4·55 in
community of *Artemisia*
ıe following values in the
Noaea mucronata, on silty

grassland *RUE*
5·3
5·5
6·5
5·3
4·0

Table 7. *Rainfall and* RUE *in Southern Africa (Rutherford, 1978)**

Rainfall (mm/year) x	Herbage production (kg DM/ha/year) y	*RUE*
100	666	6·66
200	1600	8·00
300	2500	8·33
400	3620	9·05
500	4550	9·10
600	5700	9·50
700	6600	9·42

*$y = 10x - 350$; $r = 0{\cdot}97$; $n = 11$; $P < 0{\cdot}01$.

In southern Tunisia, Floret & Pontanier (1974) found similar figures on a *Rhantherium suaveolens* and *Stipa lagascae* steppe, on sandy soil (Table 9). Van Der Veen (1967) found *RUE* of 3·41 in protected and moderately grazed *Artemisia herba alba* steppes of Syria while the overgrazed range in the vicinity barely reached 1·77 (items 15 and 29 in Table 1).

To conclude this section one could add that each per cent of perennial ground canopy cover corresponds approximately to 45 kg (30–70) of above ground phytomass and about 20 kg (10–30) of aerial primary production per hectare and per year from perennials in the North African and Middle Eastern chamaephytic steppes. It may thus be assumed that each per cent of perennial ground canopy cover may be equated with a 0·1–0·2 score of *RUE* from perennials in this type of vegetation. This assumption would obviously not be valid for other types of vegetation or other ecological zones; but it would seem to constitute a worthwhile investigation theme.

RUE *and soil condition*

RUE depends to a large extent on soil condition: essentially permeability, texture, depth, water storage capacity, and fertility status. The highest *RUE*s are found on soils that are capable of storing most of the water resulting from scarce rains and of releasing it to plants later, that is to say those which are better able to buffer the effects of climatic aridity (Le Houérou, 1960). It has been shown from a study of the ecology of the olive tree in Tunisia (for which long series of yield records existed at the field level on many properties), that,

Table 8. RUE *and range condition in Algeria (Le Houérou, Claudin et al., 1974)*

	Perennial ground cover (%)	Production aerial (kg DM/ha/year)	Rainfall (mm/year)	*RUE*
Exclosure	25	1044	220	4·75
Light stocking (1 sheep/8 ha)	5	425	220	1·93
Heavy stocking (1 sheep/3 ha)	3	262	220	1·19

Table 9. RUE *and range condition in southern Tunisia (Floret & Pontanier, 1974)*

	Perennial ground cover (%)	Total aerial production (kg DM/ha/year)	Rainfall (mm/year)	*RUE*
Range in good condition. Site A	25	1069	314	3·40
Range in fair condition. Site A	8	614	314	1·96
Range in poor condition. Site B	4	416	374	1·11

below the 300 mm isohyet, productivity is higher and more regular on sandy soils and that the difference in productivity between silty and sandy soils increased with aridity (Le Houérou, 1959*a,c*). Silty and loamy soils have no production most years below the 300 mm isohyet, while their production could be very high 1 year in 10 or 20 when annual rain reaches 450 mm or more (Figs 1 and 2). In optimum farming practice, under the 200 mm isohyet for instance (Sfax), the coefficient of variation of annual olive production (over a period of 25 years of records) in five sites was found to be 0·77 on sandy soils versus 1·50 on silty soils on the same five farms, for an average level of production of 45 kg and 4 kg/tree/year, respectively. The coefficient of variation of the rainfall for the same period in the five sites was 0·505 for a mean annual precipitation of 203 mm (36–570 mm). The same rule was shown to apply to rangelands (Floret & Pontanier, 1982). Sandy steppes of *Rantherium suaveolens* exhibit higher and more regular production than silty steppes of *Artemisia herba alba*, except, of course, in depressions benefitting from run-off or having a water table (see Fig. 3).

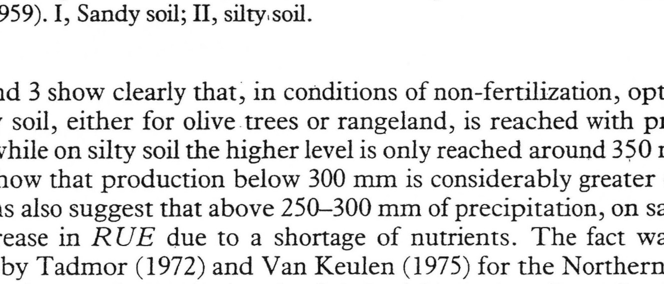

Figure 1. Relationship between olive yields, rainfall and top soil texture in the arid zone of Tunisia (Le Houérou, 1959). I, Sandy soil; II, silty soil.

Figures 1 and 3 show clearly that, in conditions of non-fertilization, optimum productivity of sandy soil, either for olive trees or rangeland, is reached with precipitations of 225–250 mm while on silty soil the higher level is only reached around 350 mm and above. Both graphs show that production below 300 mm is considerably greater on sandy soils. The two graphs also suggest that above 250–300 mm of precipitation, on sandy soil, there is a clear decrease in *RUE* due to a shortage of nutrients. The fact was most clearly demonstrated by Tadmor (1972) and Van Keulen (1975) for the Northern Negev and by De Vries, Penning *et al.* (1982) for the Sahel of Mali. On silty soils the decrease in productivity occurs under higher rainfall (350–450 mm). In other words water seems to be the limiting factor below 350 mm on silty soils and 200 mm on sandy soils while nutrients

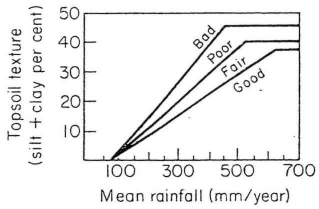

Figure 2. Productivity of olive in relation to soil and climate in Tunisia (Le Houérou, 1959).

become the limiting factor above 250–300 mm on sandy soils and above 350–450 mm on silty soils, both in the Mediterranean and in the Tropics.

The very high *RUE*s observed in apparently pristine subdesertic tall shrublands of southern U.S.S.R. (Table 10) are connected with the following.

(a) Presence of a deep water-table.
(b) High aerial phytomass (8000–15,000 kg/ha.
(c) Enormous root biomass (6000–25,000 kg/ha), representing 70–80 per cent of the total phytomass.
(d) Aerial production representing only 5–15 per cent of the total phytomass and 10–30 per cent of the aerial phytomass.

Nonetheless, *RUE*s of 35·70 as observed in the *Haloxylon ammodendron* (= *H. aphyllum*) communities of the Karakhum-Repetek and scores of 40·0 as found in the *Ammodendron argenteum* of the NW corner of the Aral Sea (Malye Barsuki) are quite exceptional, and perhaps unique, under rainfalls of the order of magnitude of 100–120 mm, even with the presence of a water table at the reach of the roots. It should be noted, however, that *RUE* becomes meaningless in the presence of a water table, particularly in desert conditions. The 'Hattiyas' of the Libyan Desert (communities of more or less halophilous Chenopodiaceae: *Traganum*, *Cornulaca*, *Nucularia*) growing on water tables with rainfalls of less

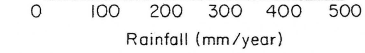

Figure 3. Rain use efficiency in a few ecosystems of Tunisia (Floret & Pontainer, 1978).
1 ——▲—— Open nanophanerophytic scrub of *Ziziphus lotus–Atriplex halimus–Cynodon dactylon*. Silty (SL/LS) alluvial depression with run-in and deep water table.
2 —— + —— Chamaephytic steppe of *Rhantherium suaveolens* and *Stipa lagascae*. Loose sand on sandy loam.
3 ——○—— Depleted *Artemisia herba alba* steppe with sparse *Hammada scoparia* and periodical cultivation. Deep silty loam and sandy clay alluvia.
4 ——■—— Depleted chamaephytic steppe of *Rhantherium suaveolens* and *Atractylis serratuloides*. On sandy silt over sandy loam.
5 ——●—— Chamaephytic steppe of *Anarrhinum brevifolium* and *Zygophyllum album*. Loose sand veil on thick gypsum crust.

Table 10. RUE *and range condition in U.S.S.R. (Rodin, 1979)*

Plant communities	Perennial ground cover (%)	Aerial phytomass (kg DM ha)	Aerial production (kg DM/ha/year)	Rainfall (mm/year)	*RUE*
1. *Ammodendron argenteum*	50	13100	4840	120	40·33
2. *Artemisia terrae albae*	37	7870	2020	120	16·83
3. *Anabasis salsa*	30	1240	710	120	5·92
4. *Artemisia terrae albae*	50	2300	1410	217	6·50
5. *Agropyron fragile*	30	1130	670	217	3·09
6. *Haloxylon ammodendron*	90	8210	4110	115	35·75
7. *Reaumuria soongarica*	8	800	128	140	0·91

In Table 1 various communities have been pooled together

Communities 1–7 were totally protected while no. 8 was an overgrazed and depleted vegetation of the Northern Gobi desert.

Communities 1 and 7 grew on sand dunes over a deep water table and had been protected for many years.

than 10 mm/year have an estimated production of 1000–2000 kg DM/ha/year and therefore a *RUE* greater than 100–200 and close to infinite wherever rainfall tends towards zero (Kufra, Kharga).

The highest *RUE*s recorded under heavy fertilization are equal to or greater than the figures obtained in highly efficient irrigation farming, e.g. 15·0–20·0 with alfalfa. In such conditions *RUE*s of 28 and 24 were found on rainfed small plots in the north Negev and Mali, respectively (Van Keulen, 1975; De Vries & Penning *et al.*, 1982). These last two figures seem close to the biological maximum in rainfed conditions of arid and semi-arid lands. In East Africa the short grassland of *Sporobolus fimbriatus* of the Serengeti was found less productive than the intermediate type of *Andropogon greenwayi* which in turn was less productive than the tall savanna of *Themeda triandra*, with *RUE* factors of 4·0, 8·0 and 12·0, respectively (Braun, 1973).

The high productivity of these grasslands results also from a conjunction of facts, viz. (a) Moderate exploitation, by wild herbivores only. (b) Bi-modal rainfall with two rainy seasons and average annual totals of 600–1000 mm. (c) Fertile soils of volcanic origin, with an adequate supply in phosphorus.

Comparable values were found in similar conditions in north Kenya (Lamprey & Yussuf, 1981). Shallow soils, on the contrary, even under total protection seem hardly able to yield *RUE* factors above 3·0 and often closer to 1·0 (items 14, 15, 41, 66, 84 in Table 1).

The low figures found in Australia (items 16, 83, 83, 85, 138, 160), particularly from the interpretation of Condon's carrying capacity equations for the SW corner of NSW seem due to three main causes: extreme variability of rainfall and poor soil fertility, and also to the fact that the figures given by Condon are concerned with animal densities and not actual stocking rates.

The sealing of the surface of silty soils, consecutive to the reduction of perennial plant cover, in conjunction or not with the development of a Cyanophycae (*Scytonema* spp.) 'pan', has a strong effect on the decline of productivity. This has been described as a potent factor of desertification rendering sterile huge areas, for instance in the vegetation arcs of odin, 1979)

·oduction /ha/year)	Rainfall (mm/year)	RUE
40	120	40·33
20	120	16·83
10	120	5·92
10	217	6·50
70	217	3·09
l0	115	35·75
:8	140	0·91

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Table 11. RUE *and range condition in New Mexico (Pieper & Herbel, 1982)*

		Ungrazed		Grazed		Average	
Year	Rainfall	*ANPP*†	*RUE*	*ANPP*	*RUE*	*ANPP*	*RUE*
1970	109	1340	12·29	970	8·89	1155	10·59
1971	206	1250	6·06	510	2·47	880	4·27
1972	324	1860	5·74	1800	5·55	1830	5·64
Average	213	1480	6·94	1090	5·11	1285	6·03

*Significant difference between grazed and ungrazed, $P < 0{\cdot}05$.
†Above Ground Net Primary Production (kg DM/ha/year).

the arid and semi-arid African tropics (Boudet; 1972, 1977; Dulieu, Gaston *et al.*, 1977), or in the North African steppes (Le Houérou, 1968). On the contrary, a veil of loose sand, often less than ten millimetres thick, on the top soil, may increase productivity many fold by augmenting water intake and thus easing seed germination otherwise totally inhibited by a 1–5 mm thick continuous cemented film of silt and clay, with or without Cyanophyceae (Le Houérou, 1962).

Sand veils may thus play the same mulching rôle as often described for litter. The very first few millimetres in the top soil may therefore have a determining rôle in *RUE*, a fact which is usually overlooked in soil surveys and classifications. Many other soil characteristics may play a major rôle in *RUE* that space does not permit to review here; we only wanted to stress some important points which are often neglected. A number of items in Table 1 show the effect of fertilization on *RUE*; these come from fertilization trials carried out through the arid and semi-arid zones of the world for the past 20 years (Items no. 68/69, 98/99, 108/111, 113/114, 127/130, 132/135, 155/156, 168/169, 176/179 in Table 1). The figures are shown for control and maximum response only (Fo and F+, respectively). Usually the response in a two- to five-fold increase in *RUE* between Fo and F+. The latter generally results from a combination of high nitrogen with medium phosphorus fertilizer. Occasionally K, S, Mg, Ca and trace elements may produce high response as well.

It should be pointed out that response to fertilization is often uneconomic in arid and even semi-arid rangelands. In the Sahel, for instance, two- to three-fold increases in herbage yield are easily obtainable (up to five-fold increases in small plots); but calculation shows that, given the terms of trade between fertilizers and transport on the one hand and of animal products on the other hand, herbage yield increase ought to be almost 10-fold to make fertilization economically feasible (Le Houérou, 1978, 1983).

Table 12. RUE *and range condition in South Dakota (Larson & Whitman, 1942)*

	Rainfall (mm/year)	Herbage yield (kg DM/ha/year)	*RUE*
1 Pristine unexploited mixed prairie grassland	352	2384	6·77
2. Intermittently used mixed prairie grassland	352	2125	6·04
3. Moderately used (mowed) mixed prairie grassland	352	1654	4·70

Table 13. *Optimum forage productivity as related to carboxylation pathways.*

Types of forage	Primary aerial productivity (10^6 tons DM/ha/year)	Rainfall (mm/year)	*RUE*
C_4 species, tropical			
Panicum maximum	40–60	1500–3000	22
Pennisetum purpureum	40–60	1500–3000	22
Digitaria decumbens	40–60	1500–3000	22
Saccharum officinarum	20–30	1500–3000	11
C_3 species, temperate/medit.			
Lolium multiflorum	15–20	600–800	25
Lolium perenne	15–20	600–800	25
Festuca arundinacea	15–20	600–800	25
Dactylis glomerata	15–20	600–800	25
CAM species			
Opuntia ficus-indica	15–20	400	44
Agave americana	15–20	300	58

The effect of soil and water conservation techniques (pitting, contour furrowing, contour benching, contour trenching, etc.) on *RUE* may also be quite strong and the more so as vegetation is initially more depleted. This is clearly shown in items 117 to 122 in Table 1, where the magnitude of the response is inversely related to the value of *RUE* in the control; in this particular case the response was a five-fold increase in *RUE* with poor range condition and a two-fold increase under fair range condition (Mann & Ahuja, 1976).

Results from range in good condition were not available to us, as conservation techniques are not deemed useful in such cases.

It would be interesting to see what the combination of fertilization and water conservation would yield in terms of *RUE* increase in ranges in poor condition!

RUE *and photosynthetic efficiency*

One would logically expect winter growing vegetations (Mediterranean) to yield higher *RUE*s than those from summer growing climates (subtropical, tropical) since the *PET* term in De Wit's equation is much lower in the former case than in the latter. The facts, however, do not confirm the theory; overall *RUE* values do not seem to differ substantially from one climate to the other for a given degree of aridity and level of management as shown in Table 1. A possible explanation could be the higher photosynthetic efficiency of tropical species, grasses in particular, which are characterized by a C_4 carboxylation pathway, while mediterranean and temperate species are usually of the much less efficient C_3 type. It seems proved, although with some noticeable exceptions, and it is generally accepted, that C_4 plants have an optimum photosynthetic activity at about 10 °C above the C_3 species (30–35 vs. 20–25 °C). It is also accepted that their photosynthetic efficiency is considerably higher, and the theory is there fully supported by time-honoured daily agricultural practice!

It has often been shown also that C_4 species are usually (but not always) better water users with considerably lower transpiration coefficients (or higher *WUE*s). But these data usually come from experiments at the leaf level under controlled conditions. In their respective natural environments the situation may be quite different (Fisher & Turner, 1978). As a matter of fact, as the C_4 species operate under much higher temperatures

(10–20 °C); climatic water demand is therefore also considerably higher in these environments; actually when temperature is 15 °C higher, one would expect water demand to be three times higher, in accordance with Van't Hoff's law. This is what actually happens, as shown in Table 13. It follows that C_4 species, are generally not better water users than C_3 species in their respective environments (although some exceptions could be found and some cultivars of maize, sorghum and pearl-millet seem to be among these exceptions).

Actually, under field conditions Rambal (pers. comm., 1983) found similar *WUE*s (0·8) for the C_3 annual range species of southern Tunisia and the C_4 species of north Senegal. As temperature during the growing season is about 20 °C higher in the latter than in the former, the 'cost of maintenance' is four times higher. The very high productivity potential of tropical grasses, for instance, is also achieved through a very high water consumption, under permanent green-house-like climates (Table 12). If tropical pastures grasses are able to produce three times more than temperate species, they also use three times more water. This is shown in Table 13. The figures given in Table 13 refer to optimum present-day farming practice, with, in particular, heavy fertilization inputs. On the other hand CAM species such as pineapple (*Ananas comosus*) or agave (*Agave americana*) have incredible water use efficiencies, 20 and 30 mg DM/g H_2O (Fisher & Turner, 1978). As a matter of fact *Agave americana* and Cactus may, under particularly favourable farming conditions, reach *RUE* scores of 110 and 50, respectively (90 and 200 kg H_2O/kg DM).

It should also be noted that arid zone legumes may have quite high *RUE*s since nitrogen is usually not a limiting factor in the particular case. Felker, Cannell *et al.* (1983), for instance, found a ratio of 345 kg H_2O/kg DM in selected accessions of *Prosopis chilensis* (i.e. a *RUE* of 10·0 and a *WUE* of 3·0, approximately) under controlled irrigation (500 mm), without fertilization. This compares with results from fertilized rangelands.

The fact that *RUE* does not seem to vary significantly with climatic types (except for aridity) thus remains a subject of interest and investigations. One may assume that pristine natural vegetation types are 'the best possible choice' among the possible floristic combinations, selected by climatic conditions. This hypothesis is suggested in particular by the optimum *RUE* reached in arid zone under annual rains close to long term means or slightly higher, with typical long term mean seasonal distribution, as shown in graphs No. 1 and 3. This assumption would be in agreement with the climax theory.

Conclusions

The Rain Use Efficiency factor is usually of the order of magnitude of 1·0–6·0 in arid and semi-arid natural vegetation. These figures correspond to net above ground primary productions of 100–2000 kg/ha/year, as reckoned by several authors (Lieth, 1973; Noy-Meir, 1973). But *RUE* may be substantially lower in degraded ecosystems or considerably higher in pristine conditions—or under good management. The biological limit seems to be reached with *RUE* factors of about 30·0 (1 kg DM/300 kg rain or 3·33 g DM/kg rain), as suggested from small plot experiments under ideal conditions of seasonal rain distribution and soil fertility (Van Keulen, 1975; De Vries, Penning *et al.*, 1982).

The *RUE* factor thus seems to be a useful tool for assessing the health and productivity of arid zone ecosystems, particularly when actual evapotransporation data are missing, as often happens. The concept makes it also possible to compare in a valid way the productivity of different types of vegetations, or environments in a given geographical area or of similar types in different areas. It thus appears as a useful complement to the biological efficiency factor (production over maximum standing phytomass) as defined by Barbour (1967). It further tends to underline the extreme importance of ecosystem management on overall productivity, since ground cover and aerial phytomass seem often to override the effects of soil and climate in the determination of productivity per unit of water available.

The *RUE* concept may furthermore be useful in attempting to predict long term productivity of vegetation, knowing the condition and trend. Overall *RUE* data are, naturally, not sufficient for predicting probability of annual production. Probability of current year's *RUE* values could only be predicted on the basis of studies relating variability of annual production to variability in annual rainfall. This will be the subject of a forthcoming paper.

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