**Codon royenii - a multiseasonal desert plant**

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*Codon royenii*, a common plant of the Namib Desert, was investigated to determine its growth pattern. It was found to be a multiseasonal, or facultative perennial, plant producing flowers and fruit continuously for periods longer than one year. The average seed loss to Lepidoptera larvae was 30% indicating the ecological importance of the plant as a food source for these insects.

**INTRODUCTION**

Multiseasonal plants grow continuously for more than one season without being true perennials (Gillett 1968). In contrast to perennials, they lack the ability to endure unfavourable conditions in a stage of dormancy, as many of the Namib Desert dwarf shrubs can. Multiseasonals continue to grow and reproduce until water reserves in the soil are depleted in their particular habitat.

Although multiseasonal plants occur in all biomes (Walter 1983), they are particularly common in deserts (Beatley 1970; Evenari & Gutterman 1966; Monson & Szarek 1981; Fox 1990). Their occurrence has resulted in questioning the traditional terminology of ‘annuals’ and ‘perennials’ to describe desert plants (Noy-Meir 1973) and has given rise to various alternative systems of classification (Orshan 1953; Evenari et al. 1982).

Nothing is known about the abundance or population dynamics or ecological requirements of multiseasonals in the Namib Desert. Some of the common ‘annual’ grass species of the Namib plains, such as *Stipagrostis ciliata* and *S. gonatostachys*, are ‘perennial’ under favourable conditions such as in drainage lines (M.K. Seely, pers. comm.). Other ‘annuals’ continue to grow until water reserves are depleted, sometimes surviving until the next rain season, which classifies them as multiseasonals or facultative perennials. *Codon royenii*, *Geigeria alata*, *G. ornatua*, *Kissenia capensis* and *Rogeria longiflora* are possible examples of multiseasonals in the Namib Desert. Since multiseasonals grow and produce flowers and

![Figure 1. Known distribution of Codon royenii in southern Africa. The distribution records are compiled from grid references supplied by the National Botanical Institute, Pretoria, and personal observations.](image-url)
seeds for extended periods of time in an environment where most of the vegetation only flourishes for short periods after rains, making them a retreat and food source for animals during dry periods.

*Codon royenii* L. (Hydrophyllaceae) is widely distributed in the central and southern Namib extending into the Cape region and Great Karoo (Figure 1). This shrub-like plant, including its fruit, is covered with spines, deterring herbivory. However, lepidopteran larvae have been observed to infest the fruits, which suggests that it might be an important food source for insects, especially during dry periods. Thus information about *Codon royenii*'s life span, phenology, seed production and predation might help to understand the plant’s role in arid plant communities.

In this study the hypothesis whether *Codon royenii* is a multiseasonal species was tested by observing its seasonal rhythm of growth and reproduction (phenology) over a 19 month period. Its possible ecological importance as food source for insects was assessed by determining seed production and their predation by insects.

**MATERIALS AND METHODS**

Specimens of *Codon royenii* were investigated at three locations in the central Namib Desert (Figure 2) between June 1989 and December 1990:

![Location map](image)

Figure 2. Location of the Homeb, Hotsas and Gobabeb study sites in the Namib Desert.

1) The Gobabeb population of *C. royenii* was situated on a river bank next to the main stream of the Kuiseb River. The catchment area of the Kuiseb extends into the wetter highland savanna; floods occur almost annually during the period between December and March. There is a continuous flow of underground water.

2) The population near Homeb was situated in a tributary to the Kuiseb River, about 500 m north of the main stream. The tributary only flows after heavy rains in the area.

3) At Hotsas the population was situated in a shallow drainage line, which might flow after sufficient rains have fallen in the vicinity.

The substrate at each location is sandy, but rainfall and subsequent soil moisture conditions vary between the different locations and seasons. The Gobabeb population obtains its major water supply from the flow of the Kuiseb, while the populations at Homeb and Hotsas are dependent on local rain events. Two Kuiseb floods were recorded in the first half of February 1989 and again in January, February and March 1990. Rainfall data were available from Gobabeb (relevant for the Gobabeb and Homeb populations) and Ganab, 30 km south of Hotsas for the duration of the study (Table 1).

**Table 1**: Annual rainfall (Jan - Dec) at Ganab (30 km south of Hotsas) and Gobabeb.

<table>
<thead>
<tr>
<th>Year</th>
<th>Ganab (mm)</th>
<th>Gobabeb (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>13.7</td>
<td>8.5</td>
</tr>
<tr>
<td>1989</td>
<td>54.7</td>
<td>14.5</td>
</tr>
<tr>
<td>1990</td>
<td>79.0</td>
<td>13.8</td>
</tr>
</tbody>
</table>

Phenological observations were made on ten marked individual *Codon royenii* plants of the Gobabeb population in the Kuiseb River and seven marked plants of the Homeb population. At Hotsas 15 seedlings were marked after rains in April 1989; 24 seedlings were marked at Homeb after rains in February 1990. All plants were monitored at monthly intervals to determine their vegetative and reproductive phase. A modified phenological scale (after Mueller-Dombois & Ellenberg 1974) was used to assess shoot development (Table 2); visible reproductive features such as the occurrence of flower buds, open flowers and fruits were noted.
Seed production and seed loss to lepidopteran larvae was determined in the Homeb population between November 1988 and February 1989 at monthly intervals. To estimate the seed production per plant, 15 closed but mature fruit were randomly picked from three plants and the number of seeds in each fruit counted. In addition, the total number of fruit on each of the same three plants was counted. The total seed production per plant was estimated by multiplying the mean number of seeds per fruit with the number of fruit per plant.

**Table 2**: Phenological phases of vegetative development (modified after Mueller-Dombois & Ellenberg 1974).

1. developing
2. fully developed (first signs of flowers)
3. < 50% of the plant wilting
4. 50%-75% wilting
5. > 75 -100% wilting
6. plant dead

To determine seed loss to predators (lepidopteran larvae), 50 fruit were randomly picked from three plants, opened and investigated for evidence of larvae. The percentage of infested fruit was determined for each plant.

To test whether there were differences in seed production per fruit between individual plants, a one-way analysis of variance (ANOVA) was carried out (Sokal & Rohl 1981).

**RESULTS**

During the course of this study, germination was observed in the Homeb population in March 1990 and on the Namib plains (Hotsas) after rains in April 1989. Since no seedling survived, phenological observations were only possible in established individuals in the Gobabeb and Homeb populations. Figure 3 shows the vegetative development of the Gobabeb and Homeb populations.

The Gobabeb population germinated three months after a Kuiseb flood in 1989. By the time the Gobabeb population was destroyed by a subsequent flood (January 1990), only one individual had died, the others were wilting (Figure 3a). In November, about eight months after germination, all individuals observed showed coloration of the leaves, indicating a decline in the development of the population.

The Homeb population germinated after rains in July 1987, which occurred on two subsequent days totalling 18.2 mm (DERU weather data). The population was already fully developed when the observations started in June 1989 (Figure 3b). All but one plant of the Homeb population survived until the next rain season (February/March 1990). Some plants produced new leaves after rains in February 1990. At the end of the observation period two more individuals of the Homeb population had died, leaving more than half of the initially observed plants active after 19 months.

Initially, both the Gobabeb and Homeb populations showed similar trends in vegetative development. In January 1990, when comparisons between the two populations were still possible, the Gobabeb population was further advanced in wilting and coloration than the Homeb population.

Because no newly germinated seedling in the Homeb and Hotsas population survived, reproductive development was only observed in older individuals of the Gobabeb (Figure 4a) and Homeb populations (Figure 4b). Since budding, flowering and fruiting might occur simultaneously in one plant, the total number of samples exceeds the number of observed plants at times. The Homeb population (Figure 4b) maintained about equal proportions of individuals flowering and fruiting until February 1990, while flowering plants in the Gobabeb population were decreasing during that time (Figure 4a). An increase in flowering was observed after rain in February 1990 in the Homeb population, resulting in almost all reproductive stages being present on each plant.

The average number of days between opening of the flower and the opening of the dehiscent fruit, which indicates their maturity, was approximately five-and-a-half months in both the Homeb and Gobabeb populations.
The number of seeds produced per fruit in the Homeb population ranged from 47 to 184 seeds (mean = 118; ±S.E. = 5.9) for all fruits (n = 45). No significant differences were found between the individuals (ANOVA: F = 1.303, P = 0.2826). The estimated total number of seeds per plant ranged between 65,000 and 268,000 seeds per individual plant, with a mean of 115,000 seeds (±S.E. = 77,000) for all individual plants.

Seed loss to lepidopteran larvae in the Homeb population averaged 30% of the fruits per plant. Since the larvae consume the entire content of most infested fruits, the total seed output was reduced to about two thirds of the initial seed production.

**DISCUSSION**

The extended growth period and continuous reproduction of *Codon royenii* at Homeb for longer than one year verifies the hypothesis that *C. royenii* is a multiseasonal plant (Figures 3 & 4). *Codon royenii* clearly has a longer life span than most desert annuals which are reported to
Figure 3b. Vegetative development of *Codon royentii* in the Namib Desert. (a) **Gobabeb** population from June 1989 to January 1990. The arrow indicates when the population was destroyed by a flood. (b) **Homeb** population from June 1989 to December 1990.

- = developing
- = fully developed
- = < 50% wilted
- = 50-75% wilted
- = > 75-100% wilted
- = plant dead

range between three and six weeks in extreme deserts (Cloudsley-Thompson & Chadwick 1964), between 12 and 32 weeks in less extreme deserts (Negbi & Evenari 1962; Beatley 1974) and between 7 and 15 weeks in the central Namib Desert ( Günster, 1993).

Successful establishment of *C. royentii* seedlings and subsequent production of seeds, only occurs when sufficient water is available. This is true for plants in areas where the water supply is guaranteed throughout the year, such as those plants supplied by the underground flow of Kuiseb River, and for those that germinate after sufficient rains in an area where there is little ground water, such as the plants at Homeb.

Phenological development of the Gobabeb population was further advanced than that of the Homeb population after some period of time, which may indicate that the Gobabeb population has adapted to frequent disturbance by floods and therefore completes its life cycle
Figure 4a. Reproductive development of *Codon royentii* in the Namib Desert. (a) **Gobabeb** population from June 1989 to February 1990 (n = 10). The occurrence of more than one phenological phase in the same individual resulted in n > 10 at several observation dates. The arrow indicates when the population was destroyed by a flood. (b) **Homeb** population from June 1989 to Dec 1990 (n = 7). The occurrence of more than one phenological stage in the same individual resulted in n > 7 at several observation dates.

- □ = budding
- □□ = flowering
- □□□ = fruiting

faster. Observations over a longer period are required to confirm this pattern.

Although the Gobabeb population seemed to be slightly further advanced in phenological development at a certain time than the Homeb population, no differences were observed in the time taken for fruits to ripen.

The rate of infestation of fruits by lepidopteran larvae and the large number of seeds produced show that *C. royentii* serves as a food source for some animals. Flowers were also eaten, but the animal responsible was not identified. This is especially important during dry periods when only few other plant species are active. The effects of seasonal fluctuations, as well as differences between the habitats, on predation rate require investigation to determine whether the present level of predation is maintained all the time. Seed losses of the magnitude observed in *C. royentii* are not unusual in desert plants; losses to predators between 30 and 80% have been
Figure 4b. Reproductive development of *Codon royenii* in the Namib Desert. (a) **Gobabeb** population from June 1989 to February 1990 (*n* = 10). The occurrence of more than one phenological phase in the same individual resulted in *n* > 10 at several observation dates. The arrow indicates when the population was destroyed by a flood. (b) **Homeb** population from June 1989 to Dec 1990 (*n* = 7). The occurrence of more than one phenological stage in the same individual resulted in *n* > 7 at several observation dates.

\[\square = \text{budding} \quad \square\square = \text{flowering} \quad \square\square\square = \text{fruiting}\]

reported (Brown et al. 1979; Davidson et al. 1984).

*Codon royenii* shows a continuous pattern of flowering and fruiting for periods longer than one season or even one year. It may therefore be described as a multiseASONAL species. The continuous production of flowers and seeds provides food for insects, such as lepidopteran larvae, throughout the year.

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REFERENCES


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