

Life histories of two arid-zone shrubs change with differences in habitat, grazing and climate

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Abstract. Shrubs are an important component of vegetation throughout the world. They are particularly significant in semiarid environments where they can dominate, driving ecosystem structure and functioning, and shaping land use. Life-history information was derived for *Eremophila sturtii* R.Br. and *Dodonaea viscosa* subsp. *angustissima* J.G.West, two widespread and common shrubs of semiarid eastern Australia. Plants growing under background climatic conditions took between 2 and 4 years to become established, attained the capacity to reproduce sexually at between 10 and 12 years, were in a sexually reproductive stage for between 17 and 28 years and lived an average maximum of 33–40 years. Under background climatic conditions between 70 and 80% of plants that entered the juvenile stage survived to sexual maturity while under severe drought this proportion fell to between 40 and 60%. Juvenile plants, particularly of *E. sturtii*, experienced the highest mortality under background conditions while, when exposed to severe drought, older plants, particularly *D. viscosa* subsp. *angustissima* in the intermediate stage, experienced the greatest increase in mortality, dying at more than twice the background rate. The high survival rates of *E. sturtii* and *D. viscosa* subsp. *angustissima* shown here, even under extreme drought conditions and in grazed- and ungrazed areas, help to explain why these shrub species have been observed to dominate vegetation in large areas of eastern Australia.

Additional keywords: development stage, establishment, life span, mortality rate, stage-classified matrix models.

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Introduction

Shrubs are a widespread and significant component of vegetation globally (McKell 1989). In Australia ~0.33 of the area of remaining native vegetation is of types that are characterised by the presence of a shrub layer (National Vegetation Information System 2012). Shrubs are particularly significant in semiarid environments where they often represent the greatest proportion of perennial plant mass (McArthur and Kitchen 2007). Shrubs of semiarid environments are significant ecologically and economically. Shrubs play important roles in protecting soil (Maestre *et al.* 2009), sequestering carbon (Ruiz-Peinado *et al.* 2013), and conserving nutrients (Howard *et al.* 2012) and water (Zhang *et al.* 2013). Shrubs can shape the structure of semiarid vegetation, moderating what is otherwise a hostile environment to create nurseries for regeneration of other plant species (Jankju 2013), as well as providing food resources and shelter for invertebrate (Shelef and Groner 2011) and vertebrate (Mabry 2013) fauna. Shrubs provide fruits and nuts for human consumption (Miller and Gross 2011), fuel for heating and cooking (Young *et al.* 1989), building materials (e.g. Clarke *et al.* 1996) and browse for domestic livestock (e.g. Augustine and McNaughton 2004; Papanastasis *et al.* 2008).

Some semiarid shrubs are known for their propensity to regenerate densely and dominate or ‘encroach’ vegetation that would otherwise be open and contain a more diverse mix of plant life forms (Fuhlendorf 1999). Shrub encroachment has been widely observed in semiarid areas around the world (Van Auken 2000; Roques *et al.* 2001; Maestre *et al.* 2009). Opinions have converged around the general drivers of encroachment (Heisler *et al.* 2003; McKeon *et al.* 2004; Briske *et al.* 2005; Graz 2008) and debate continues about the site- and species-specific processes involved (e.g. Tighe *et al.* 2009; Muñoz-Robles *et al.* 2011), the impact (Eldridge *et al.* 2011), for example on biodiversity (e.g. Ayers *et al.* 2001; Doerr *et al.* 2009), and on how to respond (Khairo *et al.* 2008). The propensity for some plants to invade or encroach and the impact of encroachment has been associated with a range of physiological attributes including small seeds, high fecundity, and long-range dispersal (Rejmánek and Richardson 1996; Roques *et al.* 2001; Grotkopp *et al.* 2002), ability to resprout (Gibson *et al.* 2011), resilience to disturbance (Fuhlendorf 1999), continuity of shoot and root architecture (Maestre *et al.* 2009), and allelopathy (Eldridge *et al.* 2011). Life-history attributes are fundamental to the ecology of individual organisms and populations generally (Schweingruber and

Poschlod 2005) and attributes, such as rapid growth (Herron *et al.* 2007) and long life span (van Kleunen *et al.* 2010), have also been associated with propensity to invade or encroach. Information about shrub life history such as life span, duration of breeding and time to establishment, is important for the understanding of the dynamics of semiarid vegetation generally and encroachment in particular.

Eremophila sturtii R.Br. (hereafter *Eremophila*) and *Dodonaea viscosa* subsp. *angustissima* J.G.West (hereafter *Dodonaea*) are two large (up to 5-m tall) wide-ranging and common shrubs (Cunningham *et al.* 1992) that are endemic to semiarid eastern Australia (West 1984; Harrington 2008). Both species can occur as scattered individuals in grassy open woodland or as dominant components of shrublands, particularly following disturbance (Cunningham *et al.* 1992; Richmond and Chinnock 1994; Chinnock 2007). Domination by these shrubs has been observed to occur across large areas (e.g. Gardiner *et al.* 1998) and has been found to have caused social and economic disadvantage (Anon. 1901, 1969; Harrington *et al.* 1979). Grazing by domestic livestock, mainly sheep, is the major use of land within the distribution of these two species (Hodgkinson 1979). Domination by these shrubs is widely believed to have a negative impact on grazing (Hodgkinson 1979; Scanlan *et al.* 1994; Chinnock 2007; Cunningham 2008), which has led to them being the subject of study in the past (e.g. Hodgkinson and Beetson 1995). Past research on these species has however focussed mainly on early stages in their life cycle (e.g. Booth *et al.* 1996a, 1996b), or on the short-term response of plants to treatments of control (e.g. Hodgkinson 1991) to develop strategies to prevent their establishment and domination. Growth and mortality of these two species over their full life cycle is unknown.

The opportunity to study the life histories of *Eremophila* and *Dodonaea* came about through a long-term study established in western New South Wales, Australia in 1980. This study was originally established to investigate the phenology and regeneration of the two species and the impacts of livestock grazing over the short term (Booth 1985). The study has continued to be monitored irregularly over subsequent years, during which the growth and mortality of a large number of individual plants have been recorded. Rainfall, and in particular drought, has been shown to be a major driver of semiarid woody plant demographics in other parts of Australia (e.g. Fensham and Holman 1999) and elsewhere in the world (Bowers 2005). However, the impact of drought on these two species has not been comprehensively investigated. The occurrence of a particularly severe and widespread drought throughout eastern Australia in the early 2000s (van Dijk *et al.* 2013) provided an opportunity to fill that knowledge gap.

The aims of this study were therefore to:

- quantify growth rates and death rates of *Eremophila* and *Dodonaea* under different habitats and livestock grazing, and
- investigate the impact of severe drought on their mortality and how this changes in relation to developmental stage, habitat and livestock grazing.

The implications of these findings are discussed in relation to the overall behaviour of populations of these two species and for land management.

Materials and methods

Study area

The study site lies in western New South Wales, 16 km NW of the township of Bourke at an elevation of approximately 100 m a.s.l. on the edge of the Darling River floodplain. It is part of a large pastoral property, and adjoins a public stock driving route. Bourke experiences a dry sub-tropical climate. Summers are hot (mean daily maximum and minimum temperatures in January are 36.3 and 21.0°C, respectively), and relatively wet (the highest mean monthly rainfall is 42.2 mm in February) while winters are cool (mean daily maximum and minimum temperatures in July are 17.9 and 4.9°C, respectively), and relatively dry (the lowest mean monthly rainfall is 19.9 mm in September) (Australian Bureau of Meteorology 2012). Mean annual rainfall is 354.7 mm and is extremely variable ranging from the lowest recorded of 86.4 mm in 2002 to the highest of 854.6 mm in 1950.

The site was selected because it was considered at the time that the study was established (in 1980) to be representative of a land type (the East Toorale Land System) where shrub domination was widespread and increasing (Booth and Barker 1979). The site is a mix of level to undulating sandplain rising on one side to a sandhill, which is up to 5 m higher than the surrounding landscape. The soil is infertile and poorly structured, varying from deep and unconsolidated sand on the sandhill to shallow compacted sandy loam overlaying a massive clay loam sub-soil on the sandplain. As is the pattern throughout the region, *Dodonaea* dominates on the deeper lighter sandhill soils while *Eremophila* dominates on the heavier sandplain soils. Approximately half the area of the site, including representative portions of both habitats, is enclosed by a livestock and feral grazing animal-proof fence. Shrubs were measured in groups of three belt transects each 50 × 3 m. Each group of transects was located in a different part of the landscape. The coordinates of individual shrubs were recorded and each was fitted with a numbered metal tag to allow identification at different sampling times. The site description, layout and field sampling method are detailed in Booth (1985) and Booth *et al.* (1996a, 1996b). It is acknowledged that the treatments are pseudo-replicates (*sensu*. Hurlbert 1984) and consequently statistical inferences, in particular with respect to the effect of grazing treatments, must be interpreted with caution. However, the large size of the sample and the extended period and number of occasions over which measurements were made mean that useful conclusions can still be reached.

Measurements and analytical approach

The height and condition of individual plants were recorded on 17 irregularly spaced occasions between 1980 and 2008. Plants were included in the study on the occasion that they were first detected and remeasured on each subsequent occasion until they died or the study ended. A total of 2508 different plants were measured at least twice each across the life of the study. The plants measured comprised almost equal numbers of each species and included the range of sizes of shrubs present at the site. Each measure of each plant was assigned to a life stage according to definitions based on species and height (see Table 1) developed from published information (e.g. Booth 1985; Booth *et al.* 1996a, 1996b) and personal observations.

Life-history attributes were then calculated with stage-classified matrix models (Cochran and Ellner 1992; Ehrlén and Lehtilä 2002; Allcock and Hik 2004) using the 'msm' package in R (Jackson 2011). This approach is well suited to the data from this study as it is able to model observations that are irregularly spaced through time and data that are right-censored and/or left-truncated (Jackson 2011). The primary output from 'msm' is a table of transition intensity values (Appendix 1), which reflect the probability that individuals will move between different states. Functions available within 'msm' can be then used to estimate the duration of, and mortality during, different life stages and for subsets of the population defined by different combinations of covariates (Jackson 2011). Overall life span was defined as the average longevity of plants that reached the final, advanced mature, development stage. Species, habitat and grazing were included in the model as time-homogeneous covariates.

The relationship between rainfall and plant life history was investigated by including the Standardised Precipitation Index (SPI) (McKee *et al.* 1993; Guttman 1999) as an additional covariate. This index (Fig. 1) was calculated over a 24-month window using monthly rainfall records recorded at Bourke since 1900 and analysed using an 'R' script previously developed for that purpose (Wheatley 2010). A 24-month window was chosen because it was considered to best represent moisture availability across the period considered most relevant to perennial woody vegetation (Quiring and Papakryiakou 2003). An SPI of -1.0 or less is considered to represent drought conditions (Guttman 1999). During the course of the study, SPI at Bourke fell below -1.0 for only comparatively brief periods prior to October 2002. In October 2002 however, it declined rapidly and remained between -1.0 and -2.5 until after the end of the study. This was

determined to best represent the period of the severe drought of the early 2000s. The impact of this drought was simulated by running 'msm' with a piece-wise constant included at 22 years (October 2002) beyond which SPI was set to -1.5 representing a severe precipitation deficit. The non-drought years, including those with high rainfall, were designated 'background' climatic conditions and were modelled using SPI values as observed over these years.

Results

How quickly do plants grow and how long do they live?

Under background climatic conditions, individuals of the two species studied established within 2–4 years; became sexually mature within 9–12 years; spent between 17 and 28 years on average in sexual maturity; and lived an average maximum of 33–40 years (Table 2).

While the mean duration of each development stage differed considerably between combinations of species, habitats and grazing regimes in almost every instance, the variations around these means were high and as a result few of these differences were statistically significant. Statistically significant growth rate differences ($P \leq 0.05$) were found only in the earlier stages of development. *Eremophila* exposed to grazing took significantly longer to establish than did the same species when protected from grazing, while *Dodonaea* growing on sandplain and protected from grazing took significantly longer to reach maturity than *Eremophila* growing on the same habitat and under the same grazing regime (Table 2). No instances were found of statistically significant differences in growth rates between plants of the same species, development stage and grazing regime that could be attributed to difference in habitat alone.

Table 1. Life stages identified in the development of *Dodonaea* and *Eremophila* at the study site

Developmental stage	Description	Plant height (cm)	
		<i>Dodonaea</i>	<i>Eremophila</i>
Seedling ^A	Plant has a single soft and pliable stem and only one or two leaf whorls	0–9.9	0–9.9
Juvenile	Plant has a single (or several) stiff woody stems with few leaf whorls and no or limited woody branching	10–24.9	10–24.9
Intermediate	Plant starts to assume adult 'broombrush' form with multi-stems and complex stiff woody branching. This is the stage at which plants are recorded as established	25–99.9	25–49.9
Early mature	Plants are of adult form and are capable of flowering although flowering is irregular and is generally not abundant	100–199.9	50–99.9
Advanced mature	Plants are of adult form and flowering is regular and abundant. Larger plants may start to senesce with major branches collapsing and the crown dying back	≥ 200	≥ 100
Dead	Plants have no foliage and no live tissues are apparent	0	0

^AThe seedling stage was not included in the analysis because seasonal variability and the irregularity of measurements meant that it was not adequately represented in the transitions observed, particularly in the latter stages of the study.

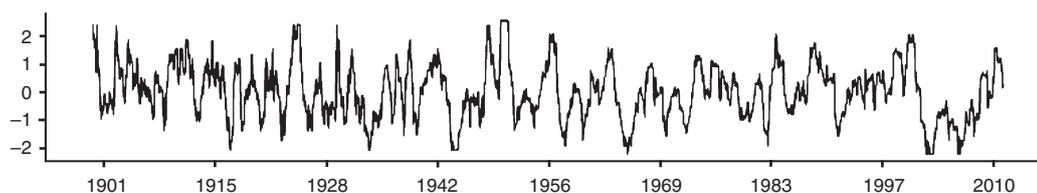


Fig. 1. 24-month Standardised Precipitation Index calculated using recorded monthly rainfall for Bourke from 1900 to 2011.

Differences in mortality rates were found to be statistically significant in a greater number of instances (Table 3). Juvenile and intermediate *Eremophila* died at significantly higher rates than did *Dodonaea* when growing on the same sandplain habitat and similarly protected from grazing. Advanced mature plants of *Dodonaea*, the only species to occur on both habitats, growing on sandplain died at significantly lower rates than the same species and development stage growing on sandhill whether exposed to grazing or when not grazed. No instances were found of statistically significant differences in mortality rates between plants of the same species, development stage and habitat that could be attributed to a difference in grazing regime alone.

Table 2. Mean duration (years) in various life-history stages

Habitat	Grazing	Time to establish	Time to reach maturity	Duration of sexual maturity	Total life span
<i>Dodonaea</i>					
Sandhill	Not grazed	2.0	11.8	21.6	33.3
Sandhill	Grazed	3.2	11.5	17.0	28.5
Sandplain	Not grazed	2.4	12.1	27.5	39.7
Sandplain	Grazed	3.6	12.5	23.5	35.9
<i>Eremophila</i>					
Sandplain	Not grazed	2.6	9.5 ^A	23.9	33.4
Sandplain	Grazed	3.7 ^B	9.7	22.3	32.0

^ADuration for *Eremophila* is significantly less than for *Dodonaea* ($P \leq 0.05$) for the same life-history stage, habitat and grazing regime.

^BDuration of grazed is significantly longer than not grazed ($P \leq 0.05$) for the same life-history stage, species and habitat.

How is plant mortality impacted by severe drought?

Under severe drought conditions mortality increased for all groups of plants and from all development stages (Table 3) although this difference was significant only for plants in the intermediate stage (all combinations of species, habitat and grazing history) and for *Dodonaea* in the early mature stage on either habitat and not grazed. The impact of drought on intermediate-stage plants was less for *Eremophila*, where mortality increased by ~6 times, compared with *Dodonaea*, for which mortality increased by between 12 and 26 times. For *Dodonaea* the impact of drought was less for plants in the early mature stage, for which mortality increased by between 3 and 4 times, than those in the intermediate stage. It was also less for those growing on sandplain, where mortality of intermediate-stage plants increased by between 22 and 26 times, compared with sandhill, where mortality of plants in the same growth stage increased by between 12 and 22 times.

Between 58% (for *Eremophila* either grazed or not grazed) and 40% (for *Dodonaea* on sandplain not grazed) of juvenile plants survived the 4 years of drought to reach sexual maturity while between 83% (for *Dodonaea* on sandhill grazed or not grazed) and 65% (for *Eremophila* not grazed) survived an equivalent period under background conditions.

Discussion

We found that juveniles of both species establish quickly, in between 2 and 4 years, and that once plants reach the intermediate stage, annual mortality under background conditions is extremely low. This is similar to the observations of Booth (1985) that a sequence of just two consecutive summers of above-average rainfall is sufficient for a new cohort of these species to become

Table 3. Mean annual mortality rate for each combination of species, habitat, grazing regime and climate and for each development stage

Habitat	Grazing	Climate	Mean annual mortality rate			
			Juvenile	Intermediate	Early mature	Advanced mature
<i>Dodonaea</i>						
Sandhill	Not grazed	Background	0.045	0.007	0.025	0.049
		Drought	0.071	0.182 ^B	0.096 ^B	0.090
Sandhill	Grazed	Background	0.042	0.008	0.046	0.043
		Drought	0.050	0.174 ^B	0.171	0.081
Sandplain	Not grazed	Background	0.057	0.009	0.016	0.029 ^C
		Drought	0.070	0.196 ^B	0.060 ^B	0.054
Sandplain	Grazed	Background	0.053	0.009	0.028	0.026 ^C
		Drought	0.049	0.108 ^B	0.107	0.049
<i>Eremophila</i>						
Sandplain	Not grazed	Background	0.097 ^A	0.018 ^A	0.006	0.015
		Drought	0.052	0.116 ^B	0.026	0.027
Sandplain	Grazed	Background	0.088	0.018	0.011	0.013
		Drought	0.040	0.108 ^B	0.042	0.024

^AMortality for *Eremophila* is significantly greater than for *Dodonaea* ($P \leq 0.05$) for the same habitat, grazing regime, and climate.

^BMortality under severe drought is significantly greater than under background climate conditions ($P \leq 0.05$) for the same species, habitat and grazing regime.

^CMortality on sandplain is significantly less than on sandhill ($P \leq 0.05$) for the same species, grazing regime, and climate.

established. These conditions occur on average about once each decade at Bourke. We also found that individuals of both species mature quickly and that, once mature, they live for a long time (between 17 and 28 years). This finding, together with the observations of Booth *et al.* (1996a) that *Dodonaea* flower and seed prolifically in most years once mature, means that once individuals reach sexual maturity, they will experience at least one or more likely two sets of conditions conducive to dense regeneration and recruitment during the period in which they have the capacity to produce seed. These life-cycle characteristics help explain the widely observed (e.g. Hodgkinson 1979) propensity of these species to encroach and dominate woodland vegetation throughout their range.

How does life history vary between habitats?

Only one of the two species in this study, *Dodonaea*, occurred on both sandplain and sandhill habitat. We found that plants of this species in later development stages growing on sandhill experienced higher mortality than those on sandplain. This is despite our observations that both the overall density of shrub plants and the total volume of shrub canopy were less on the sandhill than on the sandplain, which indicate that plants growing on the sandhill experienced less competition than those on the sandplain. We suggest that the apparently contradictory result that mortality rates were higher for *Dodonaea* growing on sandhill may best be explained by the particular root growth characteristics of this species and differences in the landform and soils between the two habitats. *Dodonaea* develop vertical roots very quickly (reaching 12.5 cm after just 4 weeks and 117 cm after 14 weeks under controlled conditions) (Booth *et al.* 1996b). In the light soils of the sandhill, seedlings experience little physical resistance to root growth and are able to access and exploit moisture and nutrient resources required for survival and growth quickly. The heavy soils of the sandplain present considerable physical resistance to root growth retarding plant establishment and increasing the length of time for which seedlings remain vulnerable to moisture stress. However, once established, plants growing on the sandplain are able to access greater reserves of nutrients and water because this habitat is lower in the landscape and its soils retain water and nutrients more effectively increasing the capacity of plants on sandplain to survive the stresses of background climate variation. This result is similar to that of Browning *et al.* (2008) who, in a study of encroachment by mesquite in Arizona, found that, while conditions on sandy soils were suitable for shrub recruitment more frequently, woody plant growth was greater in the long-term on clayey soils due to their higher nutrient status and water-holding capacity.

How does life history vary with exposure to livestock grazing?

Grazing had limited impact on plants in this study. The only statistically significant impact was that exposure to grazing slowed the development of juvenile plants of *Eremophila*. It is not surprising that grazing had a limited effect in a study of life history that focussed on latter stages in plant development especially since fire was absent throughout the study. Grazing is generally

believed to contribute to encroachment by favouring the survival and growth of shrub seedlings through suppression of other herbaceous species which would otherwise compete with shrub regeneration for scarce moisture and nutrients (Graz 2008). Grazing is also believed to reduce the frequency and intensity of fires, to which some shrubs, even in adult stages, are sensitive (Hodgkinson and Harrington 1985), by reducing overall fuel loads. The foliage of *Eremophila* is very aromatic, indicative of high essential oils content and graziers in the region report that it is rarely browsed except by goats (Cunningham 2008). That grazing alone (in the absence of fire) reduced the growth rate of juvenile *Eremophila* is unexpected and we are unable to offer an explanation.

How does life history vary with exposure to drought?

Severe drought increased mortality for all groups of plants from all development stages. The effect was most significant on plants in the intermediate growth stage, less on *Eremophila* than on *Dodonaea*, more on sandhill than on sandplain, and did not distinguish between plants exposed to grazing and those that were not. Accelerated death of shrubs and trees of semiarid woodlands due to drought is widely documented throughout the world (e.g. Fensham and Holman 1999; Bowers 2005). That the most significant impact of drought in this study was on plants in the intermediate stage reflects a combination of the higher mortality experienced by juvenile plants under background conditions, as well as the greater resilience to drought of plants in more advanced stages. Fensham and Fairfax (2007) studied drought-related death of trees in central western Queensland in a semiarid environment similar to that of the study site. They found that death in drought conditions was greater for species with shallow root systems than those with taproots and that it increased with soil clay content. Our findings in relation to species and habitat appear to contradict these. *Eremophila* has a shallower and less complex root system than that of a *Dodonaea* (Booth *et al.* 1996b) and we found that, despite this, drought-caused mortality was higher in the latter species than the former. We believe that this apparently contradictory result was likely to be due to the superior ability of *Eremophila* to resprout after disturbance (Hodgkinson 1991) outweighing the effect of differences in root architecture on the respective ability of the two species to access water. We conclude that our similarly contradictory finding that deaths in drought conditions were greater on the sandhill with its much lighter soils reflects that landscape position was more influential on plant moisture availability in this study than differences in soil clay content.

What are the implications for land management?

Our findings are similar to those of others (e.g. Harrington *et al.* 1979; McKeon *et al.* 2004) that the domination of vegetation by these shrubs can happen very quickly and that once established, shrub-dominated vegetation is very resilient. We found that plants of both species establish within 2–4 years, and that, once they have reached the intermediate stage, mortality of these plants under background conditions or with grazing, is low. Furthermore, we found that a severe drought alone is not sufficient to cause areas that have been encroached and become dominated

by mature shrubs of these species to become open. Even though mortality of established and mature plants increased significantly under severe drought, sufficient mature individuals survived in every combination of species, habitat and grazing regime to ensure that the population would retain the capacity to rapidly recolonise areas once conditions conducive to the survival and establishment of regeneration returned. Furthermore, as our results show, even in a drought as severe as that which occurred through the early 2000s in eastern Australia, a significant proportion of immature plants also survive.

Conclusion

Individual plants of *Dodonaea* and *Eremophila* become established quickly and once they have become established will progress to sexual maturity. Even when exposed to exceptional drought conditions such as occurred in eastern Australia in the early 2000s, around half of established plants will progress to maturity. Individuals that reach sexual maturity are long-lived and resilient to drought particularly when growing on the heavier soils of sandplain areas. Mature plants have the capacity to flower and seed prolifically and despite the highly variable climate in which these species live will experience at least one or possibly two sets of conditions conducive to dense regeneration and recruitment in their life time. Consequently, once vegetation is dominated by these shrubs, it will remain in that condition even when exposed to severe drought.

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Appendix 1. Maximum likelihood estimates (with 95% confidence limits) for the stage-classified matrix model with the covariates: Species, Standardised Precipitation Index, Habitat and Grazing

Transition intensity matrix with covariates set to their means

To from	Juvenile	Intermediate	Early mature	Advanced mature	Dead
Juvenile	-0.3947 (-0.4197, -0.3713)	0.2887 (0.2675, 0.3114)	0	0	0.1061 (0.0940, 0.1196)
Intermediate	0.1902 (0.1711, 0.2115)	-0.3564 (-0.3804, -0.334)	0.1566 (0.145, 0.1692)	0	0.0096 (0.0038, 0.0243)
Early mature	0	0.0531 (0.0456, 0.0617)	-0.186 (-0.1997, -0.1733)	0.1127 (0.103, 0.1232)	0.0203 (0.0134, 0.0309)
Advanced mature	0	0	0.01727 (0.0142, 0.0207)	-0.0360 (-0.0404, -0.0321)	0.0188 (0.0159, 0.0224)
Dead	0	0	0	0	0

Log-linear effects of Species: *Eremophila*

To from	Juvenile	Intermediate	Early mature	Advanced mature	Dead
Juvenile	0	-0.2347 (-0.4111, -0.0583)	0	0	0.03474 (-0.2696, 0.3391)
Intermediate	1.427 (1.168, 1.686)	0	0.5654 (0.3938, 0.737)	0	-0.6511 (-1.996, 0.6934)
Early mature	0	1.494 (1.024, 1.965)	0	0.3363 (0.1114, 0.5611)	-0.4383 (-1.291, 0.4144)
Advanced mature	0	0	-0.6676 (-1.134, -0.2014)	0	-0.7432 (-1.144, -0.3427)
Dead	0	0	0	0	0

Log-linear effects of Standardised Precipitation Index

To from	Juvenile	Intermediate	Early mature	Advanced mature	Dead
Juvenile	0	-0.3241 (-0.4334, -0.2149)	0	0	0.6295 (0.4883, 0.7708)
Intermediate	0.3497 (0.2186, 0.4808)	0	0.0580 (-0.0462, 0.1623)	0	-1.803 (-2.275, -1.332)
Early mature	0	0.0552 (-0.1409, 0.2513)	0	0.2158 (0.0937, 0.3379)	-0.6924 (-1.139, -0.2458)
Advanced mature	0	0	-0.6514 (-0.8834, -0.4194)	0	-0.3052 (-0.5197, -0.0907)
Dead	0	0	0	0	0

Log-linear effects of Habitat: Plain

To from	Juvenile	Intermediate	Early mature	Advanced mature	Dead
Juvenile	0	-0.2152 (-0.5483, 0.1178)	0	0	0.2067 (-0.8855, 1.299)
Intermediate	1.062 (0.3728, 1.751)	0	-0.147 (-0.4037, 0.1097)	0	0.1009 (-0.3267, 0.5286)
Early mature	0	-0.4074 (-1.059, 0.2444)	0	0.3512 (-0.0299, 0.7324)	-0.4985 (-1.168, 0.1707)
Advanced mature	0	0	0.0038 (-0.5817, 0.5893)	0	-0.528 (-0.9261, -0.1299)
Dead	0	0	0	0	0

Log-linear effects of Grazing: Grazed

To from	Juvenile	Intermediate	Early mature	Advanced mature	Dead
Juvenile	0	0.4817 (0.301, 0.6624)	0	0	0.1442 (-0.0548, 0.3432)
Intermediate	-0.0586 (-0.2596, 0.1423)	0	-0.0021 (-0.2111, 0.2069)	0	0.0748 (-0.361, 0.5106)
Early mature	0	0.3229 (-0.0274, 0.6731)	0	-0.2164 (-0.4233, -0.0095)	-0.6381 (-1.32, 0.0435)
Advanced mature	0	0	-0.0492 (-0.4821, 0.3837)	0	0.1454 (-0.1708, 0.4616)
Dead	0	0	0	0	0

-2 * log-likelihood: 29 309.