



Live fast, die young: estimating size-age relations and mortality pattern of shrubs species in the semi-arid Karoo, South Africa

Thorsten Wiegand¹, Suzanne J. Milton², Karen J. Esler³ & Guy F. Midgley⁴

¹*Department of Ecological Modelling UFZ-Centre of Environmental Research, Leipzig, Germany (E-mail: towi@oesa.ufz.de);* ²*Nature Conservation Department, and* ³*Botany Department, University of Stellenbosch, South Africa;* ⁴*National Botanical Institute, Claremont, South Africa*

Key words: Growth models, Karoo, Mortality, Size-age relation, Shrub community

Abstract

We present a technique for estimating size-age relations and size-dependent mortality patterns of long-lived plants. The technique requires two sets of size data of individual (non-marked) plants that should be collected with a time-lag of several years in the same area of a study site. The basic idea of our technique is to assume general (three parameter) families of size-dependent functions which describe growth and mortality that occurred between the two data gathering events. We apply these growth and mortality functions to the size data of the early data set and construct predicted size-class distributions to compare it, in a systematic way, to the size-class distribution of the later data set. In a next step we calculate the size-age relations from the resulting growth functions, which yield the smallest difference between observed and predicted size-class distribution. Applying this technique to size data of five dominant shrub species at the Tierberg study site in the semiarid Karoo, South Africa produced new insight into the biology of these species which otherwise cannot be obtained without frequent measurements of marked plants. We could relate characteristics of growth behavior and mortality, for certain subgroups of the five species, to the life-history attributes evergreen vs. deciduous, succulent vs. woody, and early reproductive vs. late reproductive. The results of our pilot-study suggest a broad applicability of our technique to other shrublands of the world. This requires at least one older record of (individual) shrub-size data and performance of resampling.

Introduction

An understanding of size-age relationships and age-specific mortality patterns is the basis for understanding and predicting vegetation change in assemblages of long-lived plants, whether the management objectives are conservation of biodiversity or agricultural production. Information on age-specific mortality can be used to predict changes in both population structure and vegetation composition (McAuliffe 1988; Wiegand et al. 1995) as well as to address theoretical issues such as the relationship between longevity and investment in wood (Loehle 1988) or the trade-off between early reproduction and longevity (Begon et al. 1990; Tilman 1994).

Information on growth and population dynamics of perennial plant species is usually based on repeated

monitoring of marked plants and plots, as employed by Shreve & Hinckley (1937) in Arizona, USA, Turner (1990) in Mexico, Lange & Sparrow (1992) on the Nullabor plain, South Australia, and Milton (1994) in Karoo shrublands, South Africa. Alternatively, growth may be inferred from counts and measurements of annual growth rings in woody plants (Dunwiddie & la Marche 1980; Vasek 1980; Gourlay 1995; Milton et al. 1997). Such studies provide reliable but site-specific life-history information (McAuliffe 1988; Batista et al. 1998). The high cost of such studies in terms of labor and time means that the research is necessarily limited to a few sites, and that information derived from such sites is used to make generalizations about the growth and demography of a species throughout its range. A technique that enables size-age relations and size-dependent mortality patterns of

long-lived plants to be estimated from occasional surveys of unmarked plants would make it possible to test the findings of detailed studies in a variety of sites, and to make predictions about vegetation trends at sites for which there are neither large research budgets nor long-term data bases.

In arid and semi-arid shrublands and grasslands of Australia (Friedel et al. 1993), Israel (Noy-Meir 1990), South Africa (Fourie et al. 1987; Hoffman & Cowling 1990; O'Connor & Roux 1995), the USA (Whisenant & Wagstaff 1991; Chambers & Norton 1993) and Argentina (Rosati & Bucher 1995), as well as in savannas worldwide (Archer et al. 1988; O'Connor 1995; Ash & McIvor 1998) plant species composition is influenced by both management and weather patterns. An understanding of growth patterns, longevity, and mortality patterns of long-lived shrubs is necessary for understanding and predicting the possible effects of changing landuse on biodiversity and economic sustainability. For example, in the species-rich, arid to semi-arid Karoo shrublands of South Africa, these needs have stimulated research on vegetation dynamics, and drawn attention to the dearth of information on population biology of key plant species (Milton 1994; O'Connor & Roux 1995). In order to maximize meat and fiber production under highly variable rainfall regimes (inter-annual CV = 30–40%), ranchers vary the numbers of animals on the land in response to the anticipated response of the vegetation to recent rainfall and drought events. However, longer-term planning based on predicted trends in vegetation following major recruitment events is seldom attempted because there is insufficient information on the longevity and growth rates of the even the most common shrub species in Karoo plant communities.

We therefore developed a technique for estimating plant growth and longevity in semi-arid shrublands that is far less labor-intensive than conventional methods. In this paper we present this method, and discuss the results of a pilot study in the semi-arid Karoo in terms of the benefits and limitations of the technique. In addition, we analyze the wood energy investment of the five study species. This analysis provides a means for more deeply interpreting the results for longevity and growth behavior, and was motivated by similar analyses in Angiosperms, where wood energy investment has been shown to be a good predictor of longevity (Loehle 1988).

Methods

Study site

The pilot study was carried out at Tierberg Karoo Research Centre (33°S, 22°E) at the southern edge of the Great Karoo semi-desert region of South Africa (Milton et al. 1992). The site, although only 210 km from the coast, lies in the rainshadow of the Swartberg Mountains and has a low and unreliable rainfall, with a long-term annual mean of 176 mm (range 50 mm–400 mm). Rain can occur at any season as the site is in the transition zone between the western winter-rainfall and eastern summer-rainfall regions of South Africa. The vegetation is a dwarf (<0.5 m high) shrubland, and the dominant plant species are long-lived. Rates of population turnover and vegetation change are therefore generally low (Milton 1994). The five most abundant shrub species at this site are the decumbent deciduous leaf-succulent *Brownanthus ciliatus*, the evergreen leaf-succulent, *Ruschia spinosa*, the semi-deciduous, non-succulent, *Galenia fruticosa* (all Aizoaceae), the deciduous non-succulent, *Tripteris sinuatum* (formerly *Osteospermum sinuatum*) and the evergreen non-succulent, *Pteronia pallescens* (both Asteraceae). We use the nomenclature given in Arnold & de Wet (1993).

The shrubland dynamics are characterized by episodic and event-driven behavior (Wiegand et al. 1995). The rare opportunities for establishment, being a combination of a favorable rainfall pattern and availability of establishment sites (Wiegand et al. 1995), lead to characteristic size distributions with peaks that indicate cohorts that emerge after big establishment events. In the course of time, subsequent growth and mortality of the plants shifts and distorts the pattern of the size distribution, but should not destroy its characteristic shape. This is true if the growth of the plants is mainly determined by common factors (e.g., age or climatic pattern) that apply for all plants in the same way, and if individual site factors (e.g., local nutrient availability or competition) are less important. For this reason we did not sample plants growing on nutrient-rich soil mounds (heuweltjies). A more detailed description of these biogenic landscape features is given in Milton et al. (1992). Also, if probabilities for mortality are a function of size (or age), the peaks of the size distribution are maintained until too many plants of a cohort have died. In the semi-arid Karoo with low mortality of established plants and low turnover rates (Milton 1994), the peaks may be visi-

ble for one or two decades. However, bigger mortality events that selectively kill plants of certain size-classes or shrinking of plants during droughts may violate this assumption. In the following section we describe the technique we use to determine size-age relations and mortality patterns for selected shrub species in the semiarid Karoo.

Technique for estimating the size-age relations

In 1989 and 1997 we collected data on shrub sizes along three 100 m × 1 m transects at the Tierberg Karoo Research Centre. For 1989, data were available for six more transects. Transects ran between poles that demarcated a 100 m × 100 m grid on this 1 km² study site, and the same set of transects were used in both years. We defined an index s for the size of a plant as $s = \text{length [cm]} \times \text{width [cm]}$ where length and width are the two right-angled axes of the projection of the canopy cover to the ground, with length being the longest possible axis. We measured length and width of every individual of the five common shrub species along each of these transects. For shorter-lived species (*B. ciliatus*, *G. fruticosa* and *R. spinosa*) in which dead and dying plants are present in all populations, the vitality of each individual was classified as healthy (< 25% of canopy dead), dying (26–75% of canopy dead) and dead (> 75% of canopy dead). For model validation we also measured the size (length and width) of 50 nine-year old plants of each of the study species in 1998. These young plants had germinated on the study site following experimental clearing of 10 (25 m²) plots in 1989 (Milton 1995).

We used the two sets of size data of individual (non-marked) plants to calculate the size-age relation of five selected species. The basic idea of this calculation is to assume a general (three parameter) family of growth-relations that describes how the size $s(\alpha)$ of a plant with age α at the first data gathering event (at 1989) would shift to size $s(\alpha + \Delta t)$ at the second data gathering event (at 1997). Δt is the time between the two data gathering events, in our case eight years. By applying a growth-relation to the size of all plants from 1989 we obtain predicted sizes for 1997. By comparing the observed size data from 1997 with a high number of predictions for 1997 which were derived for different parameter sets of the growth-relation we can specify the parameters of the unknown growth-relation. Because we use non-marked plants we cannot compare the size data of individual plants from 1997 directly with the

predictions for 1997. Instead we construct size-class distributions and compare the size-class distribution for the observed sizes in 1997 (D^{1997}) with the size-class distribution constructed with the predicted plant sizes (F^{1997}).

To describe growth we assume the quadratic growth-relation:

$$s(\alpha + \Delta t) = \begin{cases} \text{for } a + bs(\alpha) + cs^2(\alpha) > s(\alpha) : a + bs(\alpha) + cs^2(\alpha) & (1) \\ \text{otherwise :} & s(\alpha) \end{cases}$$

with three parameters a , b , and c , where a gives the size of plants at age $\alpha = \Delta t$ [$s(0) = 0$], b shapes growth at intermediate sizes, and c is a correction factor that restricts growth at larger sizes to saturation if $c < 0$. In Equation (1) we assume that plants do not shrink in size [i.e. $s(\alpha + \Delta t) - s(\alpha) \geq 0$]. The growth-relation Equation 1 proved to be sufficient to capture the essence of the growth of the five most abundant shrub species at the Tierberg study site and covers the range of growth-functions usually used in literature (e.g., France & Thornley 1984). In dependence on the parameters a , b and c , a great variety of different growth behaviors (ranging from exponential growth, linear growth, saturation to logistic growth) can be created (Figure 1). For $c = 0$ we can solve Equation (1) analytically and obtain the solution

$$s(\alpha) = \frac{a}{b-1}(b^{\alpha/\Delta t} - 1) \quad (2)$$

with exponential growth for $b > 1$ (Figure 1A), linear growth for $b = 1$ (Figure 1B), and saturation with $s(\infty) = -a/(b-1)$ for $b < 1$. The introduction of the additional term cs^2 allows for logistic-growth behavior with exponential growth at small sizes and saturation at large sizes (see Figure 1A), or linear growth at small sizes and saturation at large sizes (see Figure 1B).

Besides growth, a size-dependent risk of mortality influences the change of the 1989 size-class distribution to the 1997 size-class distribution. Therefore we have to consider the possible mortality of plants between the two data gathering events when making predictions for 1997. We do this by assuming an annual risk of mortality that depends linearly on the size s of the plant

$$m(s) = m_0 + m_1 \left(\frac{s}{1000} \right) \quad (3)$$

with m_0 and m_1 being the coefficients of the linear function. The linear function proved to be sufficient to detect a size-dependent mortality pattern, and considering other functional relations instead of Equation (3) did not improve the quality of our model predictions.

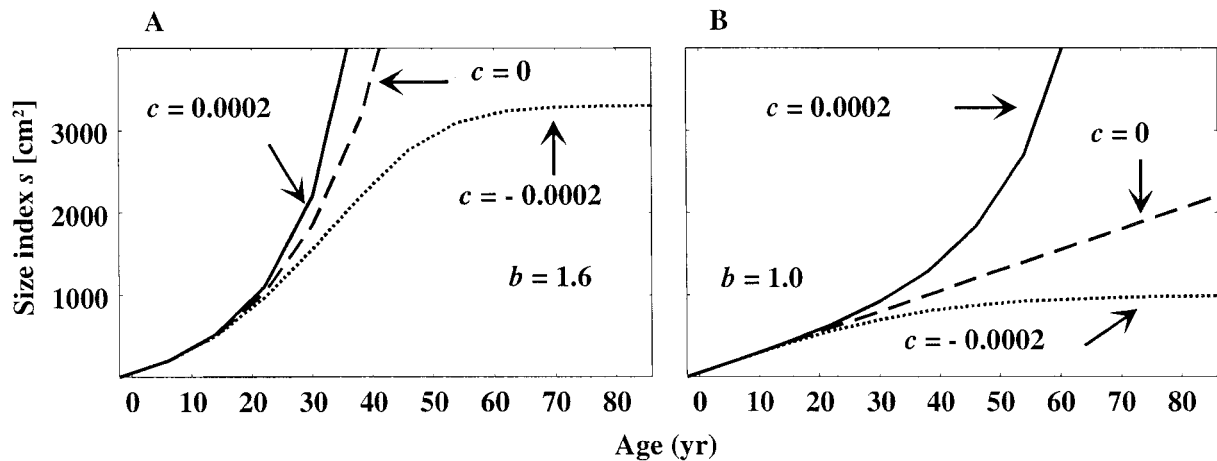


Figure 1. Examples for size-age functions covered by Equation (1). (A) For $b > 1$ exponential growth follows for $c = 0$, saturation for $c < 0$ and over-exponential growth for $c > 0$. (B) For $b = 1$ linear growth follows for $c = 0$, saturation for $c < 0$, and over-exponential growth for $c > 0$. $c = 0.002$ (solid lines), $c = 0$ (long dashes), and $c = -0.002$ (dots).

To consider mortality by constructing the predicted 1997 size-class distribution we first imagine a cohort of say 100 plants with equal sizes in 1989 and a 95% probability to survive until 1997. This cohort, which caused in the 1989 size-class distribution a peak of 100 plants, will cause in the predicted 1997 size-class distribution a peak of approximately 95 plants. Thus, a single plant of this cohort would cause, on average, a peak of 0.95 in the predicted size class distribution. Following this example, we calculate for each plant with size s in 1989 the probability ν

$$\nu = [1 - m(s)]^{\Delta t} \quad (4)$$

to survive the eight-year period (Δt) from 1989 to 1997, and we add a peak with value ν (instead of 1 without mortality) to the corresponding size-class of the predicted 1997 size-class distribution.

However, the shape of a resulting size-class distribution may depend sensitively on the somewhat arbitrary selection of a size-class width δ (by changing the size-class width δ only slightly, some plants at the border of a size-class may change size-class). To eliminate this problem we overlay, for a given set of size data, several resulting size-class distributions with different widths δ (see Appendix). Because our data were not collected with marked plants we normalize both distributions (i.e., $\sum_s F^{1997}(s) = 1$, $\sum_s D^{1997}(s) = 1$). The normalization offers the additional possibility to compare size-class distributions that were collected along different transects at the same study site.

For constructing the size-class distributions we have to choose an appropriate size-class width δ . If the size-class width is too small, single size-classes

will contain no (or too few) plants, and consequently no distinct pattern may emerge. In this case, we cannot correctly identify parameter sets that would yield good correspondence between the two size-class distributions. On the other hand, if the size-class width δ is too big, distinct peaks may be merged together in one size class and the method will become too coarse.

To finally compare the predicted size-class distribution F^{1997} with the 1997 data we calculate the total quadratic deviation e :

$$e = \sqrt{\sum_{s \geq a} [D^{1997}(s) - F^{1997}(s)]^2} \quad (5)$$

that measures the absolute deviation (or the error) between the two normalized distributions D^{1997} and F^{1997} . Because the predicted size-class distribution F^{1997} contains only plants which are older than 8 years we sum for size classes greater than a (the size at age 8).

For determining the unknown size-age relation of a given species we perform a multiple parameter fit. First, we determine biologically reasonable ranges for the three unknown parameters a , b , and c of the growth-relation (Equation 1) and define a regularly spaced $20 \times 20 \times 20$ grid in the parameter space. We proceed by selecting a value for the coefficient m_1 of the mortality pattern (Equation 3), and calculate for each of the resulting 8000 parameter combinations the total quadratic deviation e between the predicted size-class distribution F^{1997} and the size-class distribution D^{1997} of the 1997 data (Equation 5). We repeat this procedure for several values of m_1 and select the pa-

parameter combination m_1 , a , b , and c that yields the smallest deviation e .

Testing the reliability of our fit

By comparing the predicted size-class distribution F^{1997} with the observed size-class distribution D^{1997} we need a means to reject the hypothesis that F^{1997} is significantly different from D^{1997} . To perform this test we create 4000 random sub-samples with N_{1989} plants (the sample size in 1989) using the normalized observed size-class distribution D^{1997} . For each of the sub-samples we determine the corresponding size-class distribution D_r^{1997} and calculate the resulting total quadratic deviations e_r :

$$e_r = \sqrt{\sum_{s \geq a} [D^{1997}(s) - D_r^{1997}(s)]^2} \quad (6)$$

from the observed size-class distribution D^{1997} . Next we determine the interval (e_r^-, e_r^+) that contains 95% (99%) of all values of e_r . In cases where e_r lies within the 95% (or the 99%) interval (e_p^-, e_p^+) we cannot detect a significant difference between both distributions and our fit is reliable on the given level of confidence. This method accounts for the stochastic error contained in the 1989 sample size and assumes that the observed size-class distribution D^{1997} represents the ‘true’ 1997 size-class distribution which is ‘inherent’ for the species in the study area. Our fit would be unreliable if $e > e_r^+$ when the error e is significantly greater than the uncertainty of the sampling process. In cases with $e < e_r^-$ our fit would be ‘too good’ compared to the inherent uncertainty caused by the limited sample sizes.

Technique for estimating the size-independent risk of mortality

The technique described in the last section is suitable to determine size-age relations and size-dependent mortality pattern and proved to be quite effective in estimating parameters a , b , c of the size-age relation Equation (1) and the coefficient m_1 of the mortality pattern Equation (3). However, we cannot use this method to determine the coefficient m_0 . This is because a size independent (constant) risk of mortality yields for all plants a constant probability ν to survive the eight-year period (Equation (4)), and the effect of m_0 on the size-class distributions will disappear because of the normalization of the size-class distributions. Therefore we use a second approach

to adjust the constant component m_0 of the mortality pattern. This approach is based on the shape of the size-class distribution that contains information on the growth function and the mortality pattern of the species, and on the history of establishment events. The influence of variations in year-to-year establishment on the shape of the size distribution will be strong in smaller size-classes because few plants will have died yet and stochastic deviations from the deterministic growth-relation Equation (1) will not yet have smoothed out the discrete peaks of bigger establishment events. However, on larger size-classes the shape of the size-distribution should be predominantly determined by the growth-relation and the mortality pattern. With this in mind we calculate an ‘ideal’ size-class distribution that would emerge if every year the same number n_0 of plants would establish. First, we determine the size-age relations [S(t): size at age t , A(s): age at size s] by recursively iterating Equation (1) with the parameter values a , b , c that resulted from the parameter fit described in the last section. Using the fitted age-size relation A(s) (Figure 2A) we calculate the time $t(s)$ which a plant of size s would spend in the size-class $(s, s + \delta)$ (Figure 2B) as:

$$t(s) = \text{age}(s) - \text{age}(s - \delta). \quad (7)$$

The percentage of plants $n(t)$ at age t that survive the mortality pattern $m(s)$ (Figure 2C) yields

$$n(t) = n_0 \prod_{k=1}^t [1 - m(S(k))] \quad (8)$$

(Figure 2D). We finally obtain the ‘ideal’ number of plants $I(s)$ in size-class $(s, s + \delta)$ by multiplying the time $t(s)$ that a plant of size s would spend in size-class $(s, s + \delta)$ with the number of plants in size-class $(s, s + \delta)$, δ , but now with size substituted for age [with function A(s)]:

$$I(s) = t(s)n(A(s)). \quad (9)$$

Because the ideal size-class distribution depends sensitively on the mortality pattern $m(s)$ we can determine the missing parameter m_0 for the size-independent part of the mortality pattern with the additional information that is provided by the shape of the size-class distribution for larger sizes. We do this by comparing the ideal size-class distribution for several values of m_0 with the data, as shown in Figures 2E and 2F. In our example for *R. spinosa* the size-independent component m_0 of the mortality pattern was $m_0 = 0$. Figure 2E shows a good agreement between the ideal size-class distribution $I(s)$ and the 1997 data for sizes for $s > 1000 \text{ cm}^2$. From Figure 2A we find that sizes of $s = 1000 \text{ cm}^2$

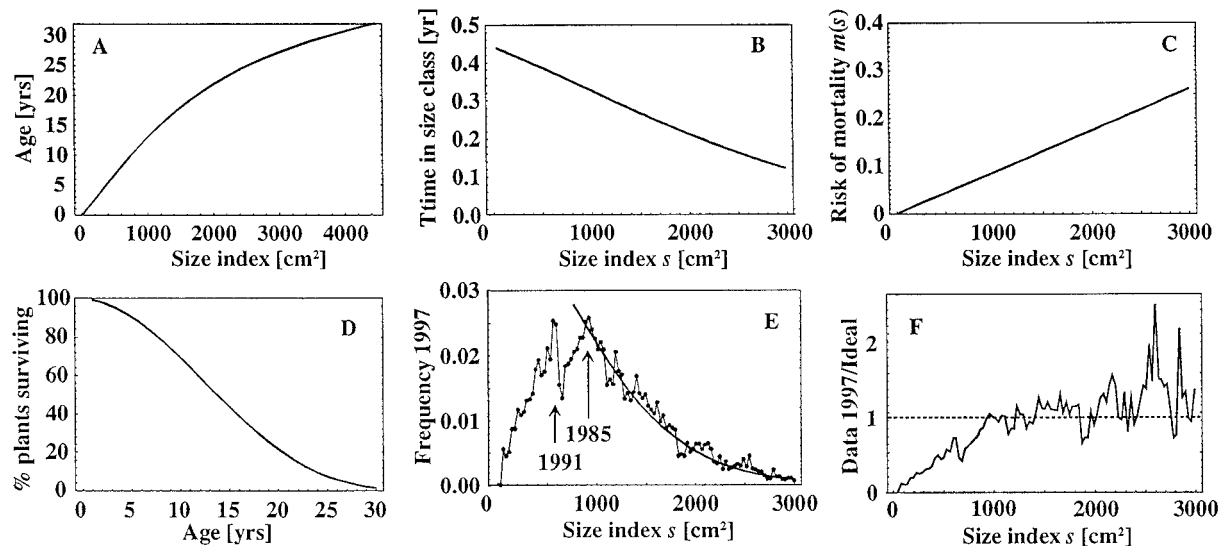


Figure 2. Example showing the steps for estimating the size-independent risk of mortality for the species *R. spinosa*. (A) Growth function $A(s)$ resulting from parameter fit with $a = 594$, $b = 1.022$, and $c = 0.00026$. (B) Time $t(s)$ that a plant spends in a size-class ($s, s+\delta$) with $\delta = 30 \text{ cm}^2$. (C) Size-dependent risk of mortality $m(s) = 0.087 (s/1000)$ resulting from the parameter fit. (D) Percentage $n(t)$ of plants surviving to age t . (E) The resulting ideal size-class distribution $I(s)$ (solid) and data from 1997 (dots). (F) Size-class data from 1997 divided by the ideal size-class distribution.

are reached at ages of approximately 12 years. The fluctuations in the 'real' size-age distribution caused by the establishment history are shown in Figure 2F.

Wood energy investment

Wood samples were taken in the field by removing only one live branch approximately 10 mm in diameter, from each of ten individuals. In the case of the leaf succulent species (*B. ciliatus* and *R. spinosa*), we collected the only woody part of the plant which was the main stem between the root crown and the canopy. The samples were air-dried and ground in a Wiley mill, and the energy content of 1 g sub-samples measured using standard bomb calorimetry. Wood density (g cm^{-3}) was measured on intact wood samples which had been dried at 60°C . Volume was calculated trigonometrically from measurements of the radius and length of short samples ($< 50 \text{ mm}$ length).

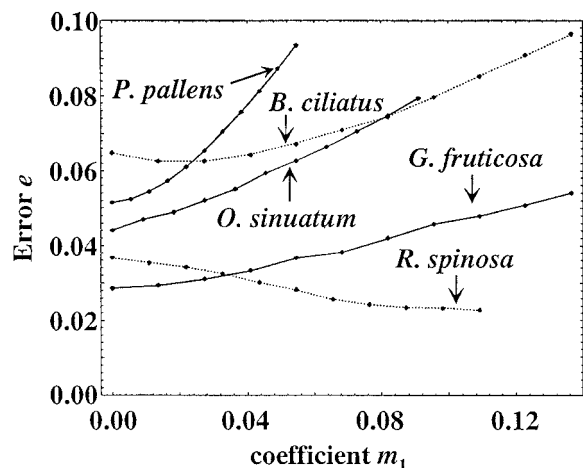


Figure 3. Parameter fit for the density-dependent component of the mortality pattern $m(s)$ for the five species. The smallest error e that resulted from fitting the parameters a , b , and c from Equation (1) is shown in dependence on the coefficient m_1 of the mortality pattern. For $m_1 = 0$ the risk of mortality is size-independent, for $m_1 > 0$ the risk of mortality increases linearly with size (Equation (3)).

Results

Size-age relation and mortality pattern of *B. ciliatus*

We use the 1989 and 1997 data from the three transects and performed a multiple parameter fit for determining the parameters a , b , and c of the growth-relation

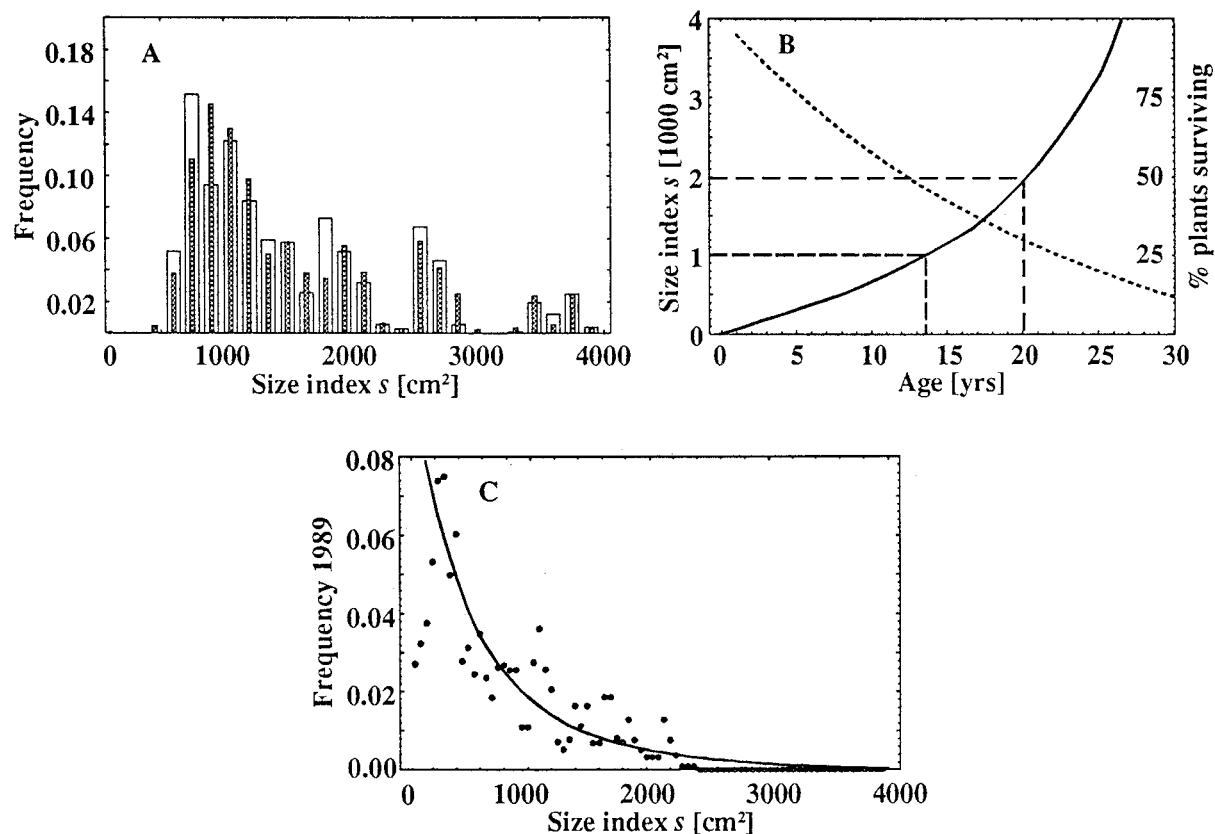


Figure 4. Parameter estimate for *B. ciliatus*. (A) Comparison of the predicted size-class distribution (gray bars) with data from 1997 (white bars) and parameters $a = 498$, $b = 1.28$, $c = 0.00061$, $m_1 = 0.014$. Three size-classes of the original width ($\delta = 50 \text{ cm}^2$) are joined for this figure. The total quadratic deviation per size-class (Equation(5)) was $e = 0.062$. (B) the resulting size-age relation (solid line) and the percentage of plants surviving the mortality pattern $m(s) = 0.05 + 0.015 (s/1000)$ (dashes). (C) resulting ideal size-class distribution (solid) and data from 1997 (dots) with a size-class width of $\delta_m = 50 \text{ cm}^2$.

Equation (1) for different scenarios of the mortality pattern $m(s)$ (Equation 3). Figure 3 shows the smallest error e for the fit in dependence on the coefficients m_1 of the mortality pattern. There is evidence for a (weak) size-dependent mortality pattern. We select the scenario with $m_1 = 0.014$ as a reference parameter. With the method described in the section ‘Technique for estimating the size-independent risk of mortality’ we determined an annual, size-independent risk of mortality of 5% ($m_0 = 0.05$). Therefore, the full mortality pattern for *B. ciliatus* yields $m(s) = 0.05 + 0.014 (s/1000)$.

For $m_1 = 0.014$, the fit of the parameters a , b , and c resulted in a good accordance between the predicted and the observed size-class distribution (Figure 4A).

The results of the parameter fit suggest that the species *B. ciliatus* shows accelerated growth behavior without saturation (Figure 4B). The shape of the size-class distribution shows a strong decline with in-

creasing size (Figure 4C) which is only partly caused by the mortality pattern (cf., Figures 4B and 4C), but more by the fact that plants of *B. ciliatus* spend, with increasing size, less and less time in a given size-class. Interestingly, the ideal size-class distribution $I(s)$ is a good approximation also for smaller size-classes (Figure 4C). This observation is in good accordance with field observations that prove that *B. ciliatus* can establish in most years. Roughly 70% of all plants measured in 1989 and 1997 had a size index $s < 1000 \text{ cm}^2$ and were therefore not older than 14 years (see Figure 4A). Roughly 90% of all plants were smaller than $s = 1500 \text{ cm}^2$ in 1989 and $s = 2000 \text{ cm}^2$ in 1997 and were therefore not older than 20 years (see Figure 4B). This age estimate is slightly higher than previous age-estimates of about 10–15 years (Wiegand et al. 1995).

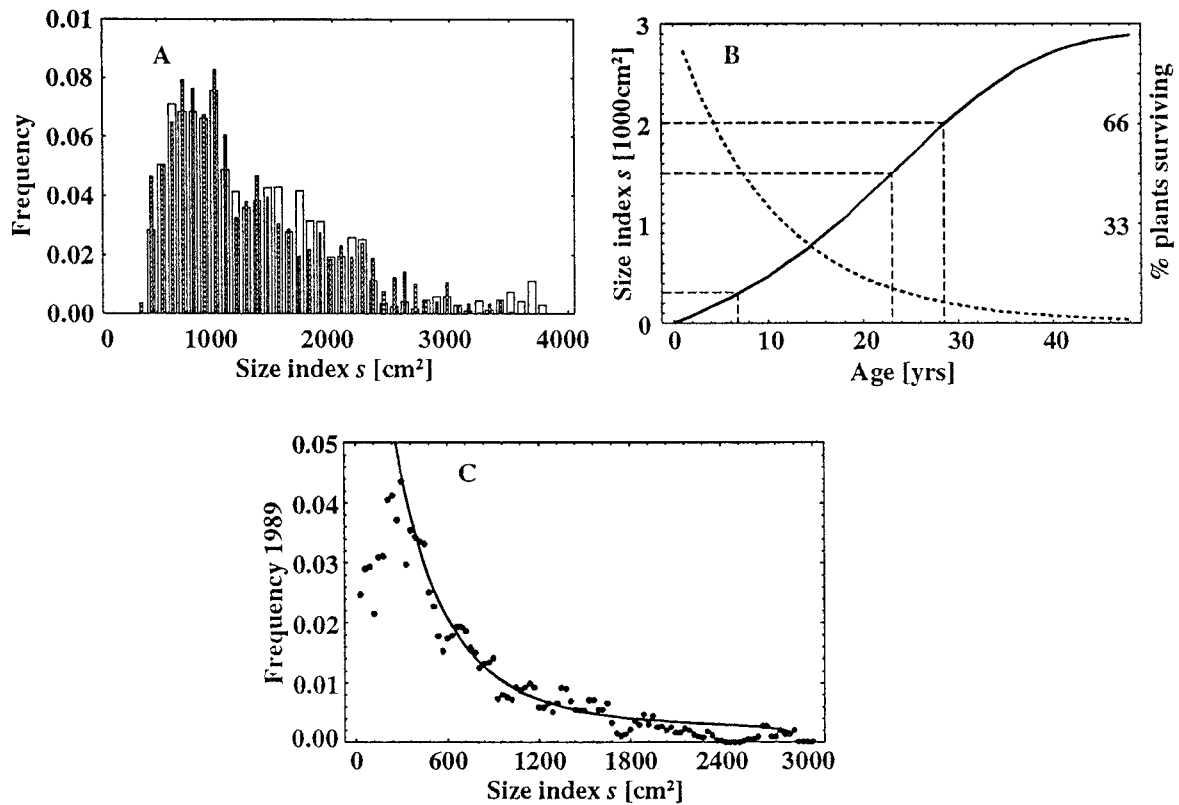


Figure 5. Parameter estimate for *G. fruticosa*. (A) Comparison of the predicted size-class distribution (gray bars) with data from 1997 (white bars) and parameters $a = 359$, $b = 1.59$, and $c = -0.00024$, $m_1 = 0$. Three size-classes of the original width ($\delta = 30 \text{ cm}^2$) are joined for this figure. The total quadratic deviation per size-class (Equation (5)) was $e = 0.029$. (B) The resulting size-age relation (solid line), and the percentage of plants surviving (dashes) the mortality pattern $m(s) = 0.09$. (C) Resulting ideal size-class distribution (solid) and data from 1989 (dots) with a size-class width of $\delta_m = 30 \text{ cm}^2$.

Size-age relation and mortality pattern of *G. fruticosa*

We repeated the analysis presented in the last section for the species *G. fruticosa* and we found no evidence of a size-dependent mortality pattern (Figure 3). The error e was minimal for $m_1 = 0$. Fit of the parameters a , b , and c resulted for $m_1 = 0$ in a good accordance between the predicted and the observed size-class distribution (Figure 5A). The results of the parameter fit show that growth of *G. fruticosa* follows logistic growth behavior with evidence for saturation at larger sizes and exponential growth at smaller sizes (Figure 5B). We determined an annual size-independent risk of mortality of 9%. The size-class distribution shows a strong decline with increasing size (Figure 5C) which is mainly caused by the size-independent mortality pattern that yields an exponential decline of the number of plants with age (Figure 5B). For size-classes $s > 300 \text{ cm}^2$, which accords with an age of approximately 7 years (Fig-

ure 5B), the ideal size-class distribution is a good approximation of the observed size-class distribution measured in 1989 (Figure 5C). For smaller sizes there were less plants than predicted with the ideal size-class distribution. This result indicates that only little establishment occurred during the 1982–1988 period.

Roughly 90% of all plants were smaller than $s = 1500 \text{ cm}^2$ in 1989 and $s = 2000 \text{ cm}^2$ in 1997 and were therefore not older than 23 to 29 years (see Figure 5B). This age estimate is in good accordance with an earlier estimate that assumed a lifespan of 30 years for *G. fruticosa* (Wiegand et al. 1995).

Size-age relation and mortality pattern of *R. spinosa*

For the species *R. spinosa*, we found clear evidence for a size-dependent mortality pattern (Figure 3). We select the value $m_1 = 0.087$ as reference case since higher values of m_1 did not improve the fit considerably and would lead to an unrealistically high

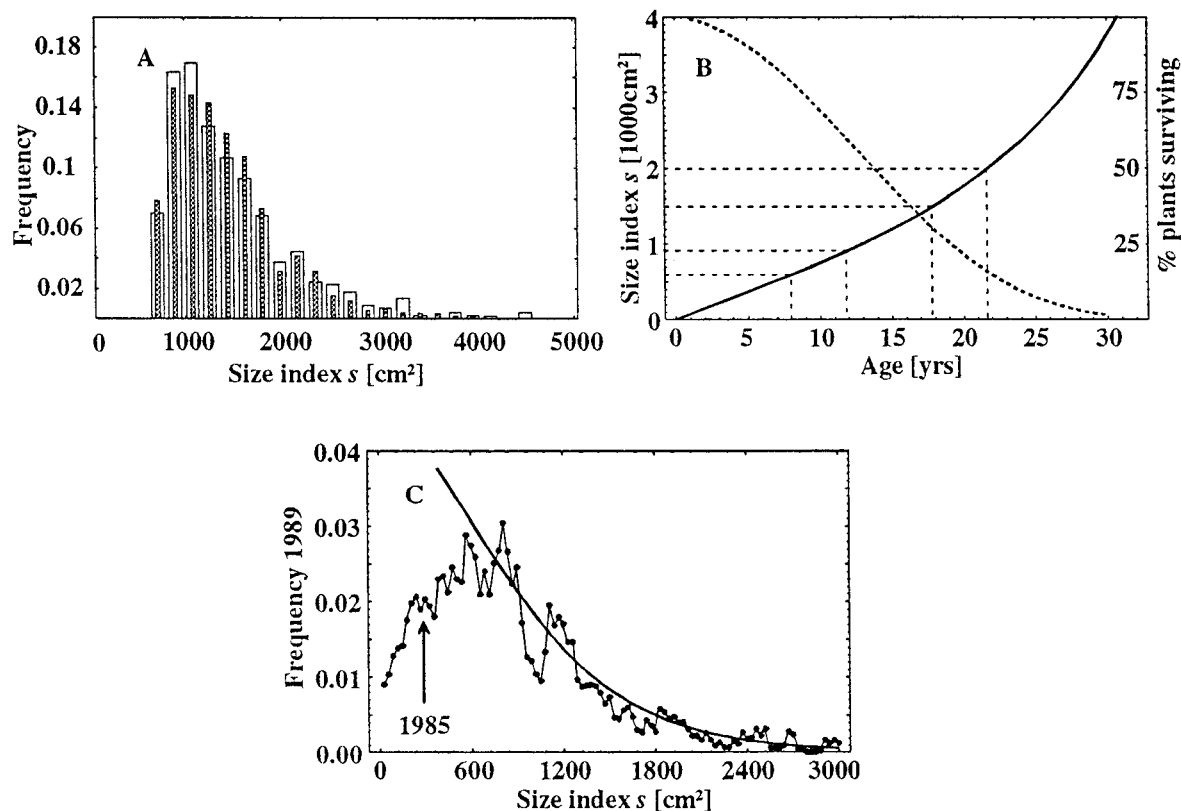


Figure 6. Parameter estimate for *R. spinosa*. (A) Comparison of the predicted size-class distribution (gray bars) with data from 1997 (white bars) and parameters $a = 594$, $b = 1.022$, and $c = 0.00026$, $m_1 = 0.087$. Six size-classes of the original width ($\delta = 30 \text{ cm}^2$) are joined for this figure. The total quadratic deviation per size-class (Equation (5)) was $e = 0.023$. (B) The resulting size-age relation (solid line) and the percentage of plants surviving (dashes) the mortality pattern $m(s) = 0.087 (s/1000)$. (C) Resulting ideal size-class distribution (solid) and data from 1989 (dots) with a size-class width of $\delta_m = 30 \text{ cm}^2$.

annual mortality of larger shrubs. The predicted and the observed size-class distributions were in good accordance (Figure 6A) and the results of the parameter fit show that growth of the succulent species *R. spinosa* follows, similar to the succulent *B. ciliatus*, accelerated growth behavior (Figure 6B) without evidence for saturation at larger sizes. However, in contrast to *B. ciliatus*, growth is almost linear for smaller sizes ($b \approx 1$) and accelerates only at intermediate and large sizes. We could not detect an annual size-independent risk of mortality, the analysis yielded $m_0 = 0$. Size-dependent mortality alone (i.e., $m_1 > 0$, $m_0 = 0$) was sufficient to explain the decline of the size-class distribution at larger sizes (Figures 2E and 6C). Growth of *R. spinosa* is restricted by mortality. Plants hardly reach ages of 30 years which would correspond to a sizes of $s = 3500 \text{ cm}^2$.

For size-classes $s > 600 \text{ cm}^2$ the ideal size-class distribution is a good approximation for the observed

size-class distribution measured in 1989 (Figure 6C). This size accords with an age of approximately 8 years (Figure 6B). For the 1997 data, the ideal size-class distribution approximated the data well for sizes classes $s > 900 \text{ cm}^2$ (Figure 2E), which corresponds to an age of 12 years. For smaller sizes there were less plants than predicted with the ideal size-class distribution. This result indicates that only little establishment occurred during the last 12 years. However, there is evidence of establishment events for sizes of $s \approx 500, 900 \text{ cm}^2$ (Figure 2E), which corresponds to a ages of 6–7 and 12 years, respectively. Indeed, in 1991 there was a big establishment event of the species *R. spinosa* observed at the Tierberg study site (Milton 1995). The peak for 1985 is also visible in the size-class distribution data from 1989 (Figure 6C) where the size of $s = 300 \text{ cm}^2$ corresponds to an age of 4 years.

Roughly 90% of all plants were smaller than $s = 1500 \text{ cm}^2$ in 1989 and smaller than $s = 2000 \text{ cm}^2$

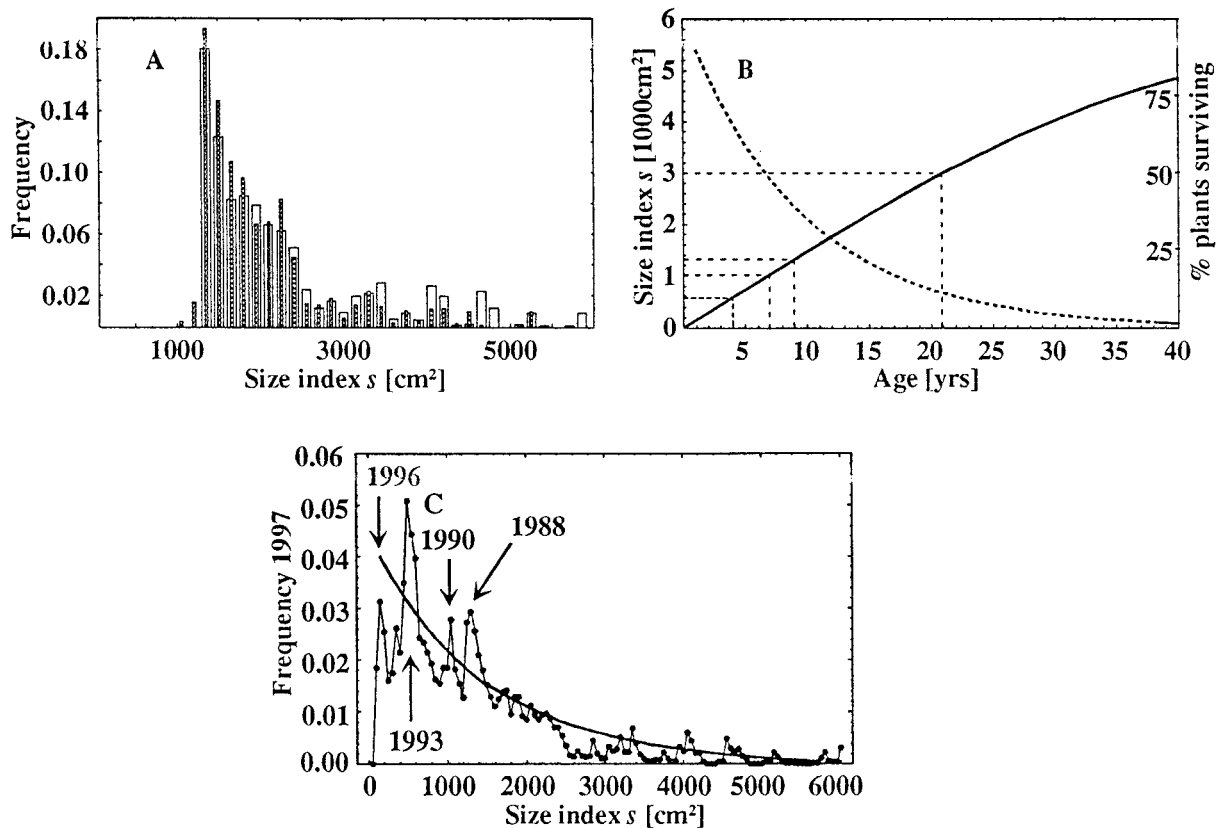


Figure 7. Parameter estimate for *T. sinuatum*. (A) Comparison of the predicted size-class distribution (gray bars) with data from 1997 (white bars) and parameters $a = 1178$, $b = 1.02$, and $c = -0.000035$, $m_1 = 0$. Three size-classes of the original width ($\delta = 50 \text{ cm}^2$) are joined for this figure. The total quadratic deviation per size-class (Equation (5)) was $e = 0.044$. (B) The resulting size-age relation (solid line) and the percentage of plants surviving (dashes) the mortality pattern $m(s) = 0.15$. (C) Resulting ideal size-class distribution (solid) and data from 1997 (dots) with a size-class width of $\delta_m = 50 \text{ cm}^2$.

in 1997 and were therefore not older than 18 to 22 years (see Figure 6B). This age estimate is in good accordance with an earlier estimate where we assumed an lifespan of 25 years for *R. spinosa* (Wiegand et al. 1995).

Size-age relation and mortality pattern of *T. sinuatum*

Because the 1989 data for *T. sinuatum* were scarce on the three transects d1d2, d3b3, and a7a8 (only 24 plants were measured) we used for our analysis additional data from 6 more transects that were also sampled in 1989. We found no evidence for a size-dependent mortality pattern (Figure 3), thus $m_1 = 0$, and analysis shows that the species *T. sinuatum* follows over their entire size range a quick, almost linear growth with a tendency to saturate at large sizes (Figure 7B). The predicted size of 8 year old plants ($a = 1178 \text{ cm}^2$) is surprisingly high. The ideal size-

class distribution $I(s)$ is a good approximation for the observed size-class distribution, also for smaller sizes (Figure 7C). Comparison of the ideal size-class distribution with the size frequency data from 1997 indicate four recent establishment events at sizes of $s \approx 150, 600, 1000$, and 1300 cm^2 (Figure 7C), which corresponds to ages of approximately 1, 4, 7, and 9 years, respectively (Figure 7B). Indeed, *T. sinuatum* established in 1990, 1993, and 1996 (S. Milton, unpublished data).

The constant annual risk of mortality necessary to explain the decline of the size-class distribution yields $m(s) = 0.15$. Consequently, the quick growing plants of the species *T. sinuatum* die early. Roughly 96% of all plants in 1989 and 90% of all plants in 1997 were smaller than $s = 3000 \text{ cm}^2$, and are therefore not much older than 21 years (see Figure 7B). This age estimate is shorter than an earlier estimate that assumed

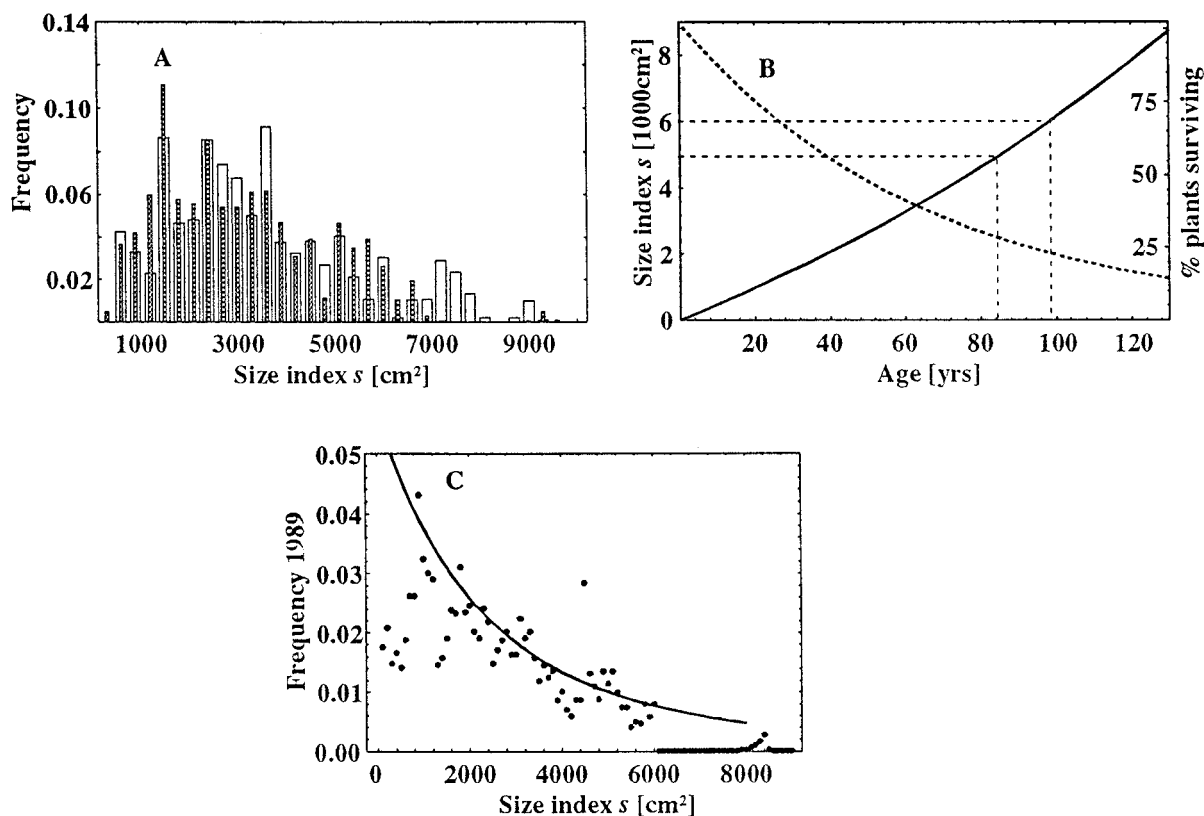


Figure 8. Parameter estimate for *P. pallens*. (A) Comparison of the predicted size-class distribution (gray bars) and data from 1997 (white bars) with parameters $a = 380$, $b = 1.0434$, and $c = 0$, $m_1 = 0$. Three size-classes of the original width ($\delta = 100 \text{ cm}^2$) are joined for this figure. The total quadratic deviation per size-class (Equation (5)) was $e = 0.056$. (B) The resulting size-age relation (solid line) and the percentage of total quadratic plants surviving (dashes) the mortality pattern $m(s) = 0.015$; (C) Resulting ideal size-class distribution (solid) and data from 1989 (dots) with a size-class width of $\delta_m = 100 \text{ cm}^2$.

a lifespan of 50 years for *T. sinuatum* (Wiegand et al. 1995).

Size-age relation and mortality pattern of *P. pallens*

As for *T. sinuatum*, we used for our analysis additional data from 6 more transects that were collected during 1989. We found no evidence for a size-dependent mortality pattern (Figure 3), thus $m_1 = 0$, and the analysis showed that *P. pallens* follows over the entire size range a slow, almost linear growth (Figure 8B). The constant annual risk of mortality necessary to explain the decline of the size-class distribution yields $m(s) = 0.015$. Consequently, the slow growing plants of *P. pallens* have a long lifespan. Roughly 90% of all plants measured in 1989 (1997) were smaller than $s = 5000 \text{ cm}^2$ (6000 cm^2) and were therefore older than 85 to 100 years. This age estimate is in good accordance with longevity estimates, based on the relationship between stem diameter and age (annual

growth rings), that suggest that this small woody shrub species can live for more than 100 years (Milton et al. 1997).

Model validation

We use the data on the canopy diameters of nine-year old plants of each of the study species measured in 1998 to test our model. Because the parameter a is the size of eight-year old plants in the model, we test mainly the model predictions for parameter a . The nine-year old young plants had germinated on the study site following experimental clearing of 10 (25 m^2) plots in 1989 (Milton 1995). Predictions for nine-year old plants are in good accordance with the mean value for nine-year old plants on the study site (Table 1). Only for *B. ciliatus* and *P. pallens* predicted and measured values differ by more than 10%. The value measured for *B. ciliatus* after clearing may be higher than sizes under 'normal' field con-

Table 1. Comparison of field data with model predictions for size of nine-year old plants.

Size at age 9 (cm ²)	<i>B. ciliatus</i>	<i>R. spinosa</i>	<i>G. fruticosa</i>	<i>T. sinuatum</i>	<i>P. pallens</i>
Model prediction	577	672	415	1327	429
Field data	688 ± 468	623 ± 380	527 ± 279	1215 ± 693	329 ± 211

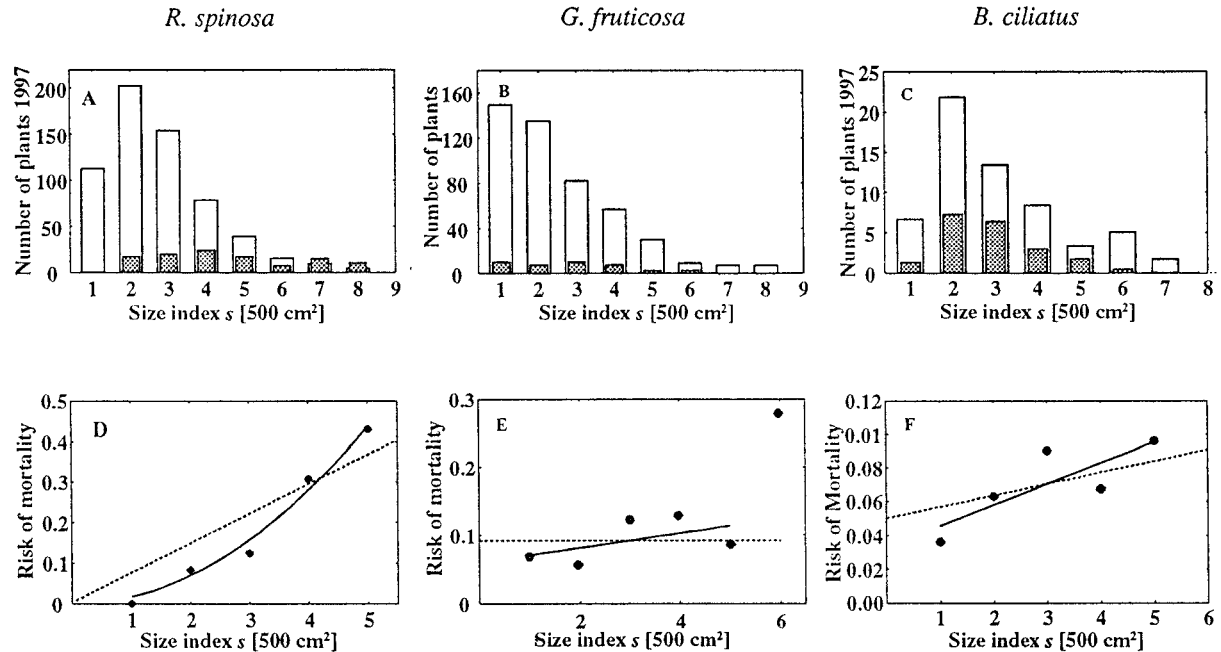


Figure 9. Size-dependent (annual) risk of mortality for *R. spinosa* (left), *G. fruticosa* (middle), and *B. ciliatus* (right). Top (A–C): total number of plants (white bars, field data from the three transects) and number of dying plants (gray bars) in a given size-class. Bottom (D–F): risk of mortality (no. of dying plants divided by total no. plants), dashed lines: results from parameter fit, solid lines: fit from data. The size-class width was $\delta = 500$.

ditions because the young plants of *B. ciliatus* had less competition than under normal field conditions and could grow bigger. *B. ciliatus* usually establishes in large gaps in open vegetation and is more limited by competition with neighboring plants than the other species analyzed. The relative difference of 100 cm² ($\approx 30\%$) between the predicted and measured size of nine-year of plants of *P. pallens* may be attributed to the unusually high competition from faster growing species.

As second test for our model predictions we compared, for *B. ciliatus*, *G. fruticosa*, and *R. spinosa*, the fraction of dying (or dead) plants ($> 75\%$ of canopy dead) at different size-classes with the predicted mortality pattern (Figure 9 top). For the other two species, no data were available. Because the total number of plants in large size-classes were low we used for this analysis only size data for plants with sizes $s < 2500$

and a large size-class width of $\delta = 500$ cm². The mortality patterns that resulted from the parameter fit (dashed lines in Figures 9D, 9E and 9F) accorded for all three species qualitatively with the mortality pattern obtained by dividing the number of dying plants in a given size-class by the total number of plants (solid line Figures 9D, 9E, 9F). In accordance to the results from the parameter fit, our data on dying plants indicate for *R. spinosa* a linear or quadratic mortality pattern. However, the data are less clear for *G. fruticosa* and *B. ciliatus*, but a size-dependent mortality pattern seems more probable for *B. ciliatus*.

Wood energy investment

Energy investment in wood per unit dry mass varied over a moderate range, from about 14 (*P. pallens*) to 20 kJ g⁻¹ (*R. spinosa*) (Table 2), but differed signifi-

Table 2. Energy content of wood expressed on a volume and dry mass basis.

Species	kJ cm^{-3}	kJ g^{-1}
<i>R. spinosa</i>	23.37 a	20.37 a
<i>B. ciliatus</i>	21.35 a	18.90 ab
<i>G. fruticosa</i>	16.09 b	17.49 b
<i>P. pallens</i>	14.51 bc	14.23 bc
<i>T. sinuatum</i>	12.67 c	17.53 b

Note. Significant differences between species are indicated by different characters. Significance was assessed with the 95% Tukey-HSD interval test.

cantly between species. A similar result was obtained for specific energy content results (Table 2), except that species differences in wood density amplified the range of values. The two succulent-leaved species had significantly higher wood specific energy values than the three non-succulent species. The analysis of energy investment in wood provides information for interpreting the distinct growth pattern of the five species that were determined in the last sections.

Discussion

We presented a technique for estimating size-age relations and mortality pattern of long-lived plants. The technique requires two sets of data for the sizes of individual (non-marked) plants that should be collected in the same area of a study site. The time-lag between the two data gathering events should be well below the typical lifespan of the species investigated, but should allow for sufficient growth. The plants grow and die between the two data gathering events. By assuming plausible growth and mortality relations we transform the size data from the first data set to predicted size-data for the second data set and compare the observed and predicted size-class distributions. By applying this ‘filter’ to a high number of plausible growth and mortality relations we can find the one that best matches the data. With this growth relation we finally calculated the size-age relation for the given species.

Gains and shortcomings of our model

We determined age-size relations and mortality patterns for five dominant shrub species at the Tierberg study site. Both are normally not accessible without

considerable effort (e.g., marking and following individual plants). Our technique calculates a ‘mean’ size-age relation that is based on the ‘mean’ shift of the sizes of many plants and evens out individual differences in growth (e.g., due to site factors or random effects) to a certain extent. For example, the size of nine-year old plants observed in the field varied with a standard deviation of some 60%, but the predictions with our model accorded well with the mean size observed. In most cases, there were only few data available on large plant sizes for fitting the growth-relation (Equation (1)). Therefore the results for bigger sizes should be interpreted with caution and may give only qualitative trends (e.g., accelerated growth of *B. ciliatus* and *R. spinosa* with $c > 0$ versus linear or saturated growth with $c \leq 0$ for the species *G. fruticosa*, *T. sinuatum*, and *P. pallens*). By comparing different possible parameter sets that yield a comparable small error e (Equation (5)) we found that the resulting age-size relations were almost identical over the normal life-span of the species where sufficient size data were available. However, differences become visible at higher ages where little data were available. The smallest error e , the total quadratic deviation between the normalized observed and predicted size-class distributions (Equation (5)), ranged between 0.023 for *R. spinosa* and 0.062 for *B. ciliatus* (Table 3) and the predicted and the observed size-class distributions are in good accordance. For all species, with exception of *P. pallens*, we found that our fit is reliable (i.e., $e < e_r^+$ and $e > e_r^-$) (Table 3). For *P. pallens* the smallest error e had a value of $e = 0.0554$ which slightly above the limit of the 95% interval ($e_r^+ = 0.0524$) but still within the 99% interval ($e_r^+ = 0.0575$). We hypothesise that the weak fit of *P. pallens* is caused by the mismatch between the long life-span of this species compared to the relatively short time-lag of eight years between the data gathering events.

Additional confidence in our results was provided by model validation. Model predictions for the size of nine-year old plants generally accorded well with field data on the mean size of nine-year old plants that emerged after clearings in 1989, and the mortality pattern found by comparing the number of dying plants with the total number of plants in different size-classes accorded qualitatively with our model predictions.

The power of our technique is facilitated by the combination of two complementary approaches. In the first approach (Equation (1)) we ask how the characteristic features of the observed size distributions differ

Table 3. Summary of the results.

Variable	Symbol	<i>B. ciliatus</i>	<i>R. spinosa</i>	<i>G. fruticosa</i>	<i>T. sinuatum</i>	<i>P. pallens</i>
Size at age 8 (cm ²)	<i>a</i>	498	594	359	1178	380
	<i>b</i>	1.28	1.022	1.588	1.02	1.043
	<i>c</i>	0.00061	0.00026	-0.00024	-0.000035	0
Risk of mortality	<i>m(s)</i> (s/1000)	0.05+0.014	0.087(s/1000)	0.09	0.15	0.015
Lifespan ^b		≈ 17–19 years	≈ 18–22 years	≈ 23–29 years	≈ 21 years	≈ 85–100 years
Max size (cm ²)		≈ 4000	≈ 4000	≈ 4000	≈ 5000	≈ 9000
No. plants 1989		32	382	238	75 ^a	152 ^a
No. plants 1997		62	617	480	187	83
Minimal error	<i>e</i>	0.062	0.023	0.029	0.044	0.056
95% confidence Interval ^c	(<i>e_r⁻</i> , <i>e_r⁺</i>)	(0.052, 0.119)	(0.018, 0.033)	(0.023, 0.041)	(0.038, 0.078)	(0.027, 0.053)
99% confidence Interval ^c	(<i>e_r⁻</i> , <i>e_r⁺</i>)	(0.047, 0.134)	(0.016, 0.036)	(0.021, 0.044)	(0.035, 0.088)	(0.025, 0.058)
Size-class width (cm ²)	δ_m	50	30	30	50	100

Note. The plant size data used were collected in 1989 and 1997 at three 1 m × 100 m transects. ^aTo increase the *T. sinuatum* and *P. pallens* sample size in 1989 we used for our analysis additional data from 6 more transects.

^bOnly 10% of all plants live longer.

^cThe fit between the observed and the predicted size-class distribution is reliable if $e \in (e_r^-, e_r^+)$.

between the two data sets. This method is sensitive to the determination of the three parameters (*a*, *b*, and *c*) that describe the growth of the plants and the parameter m_1 that describes the size-dependent component of the mortality pattern. This method, however, is not suitable for detecting the size-independent component m_0 of the mortality pattern for a given species. This is because we use normalized distributions to facilitate the inclusion of data that were not collected in exactly the same area. In the second approach for determining m_0 we focus on the size distribution of the species and compare the observed size distribution with an ‘ideal’ size distribution. The ‘ideal’ size distribution assumes every year the same number of established plants and calculates the number of plants that survive to a certain age.

Under which circumstances is our method unreliable?

The basic assumption of our technique is that the size-class distributions of the species analyzed are characteristic features of the particular species and that they therefore contain a great deal of information (e.g., on past establishment events, and on mortality pattern), but in an encoded way. By including this code into our model we tried to decode the hidden information. However, this is only possible if the growth of the plants is mainly determined by common factors (e.g., age or climatic pattern) that apply for all plants at the

site in the same way, and when individual site factors (e.g., local nutrient availability, soil, or competition) are less important. Also, mortality events that kill selectively plants of a certain size or age class would corrupt the assumptions of our technique.

Our technique can only be applied if the time-lag between the two data sets is appropriate in relation to the life-span of the species analyzed. We found that the time-lag of eight years was probably too short to obtain a reliably fit for the long-lived species *P. pallens* which can live more than 100 years (Milton et al. 1997). There should be a high proportion of plants surviving the time-lag and sufficient growth should occur during this period. Also, the period between the two data collection events should represent ‘typical’ climatic conditions at the study site (e.g., a mixture of good and bad years). If only wet years (with high growth), or dry years (with low growth) occur, the estimated growth parameters will not be representative. At the study site, the rainfall totals during the growing seasons (April to September) from 1988 to 1996 were 135 mm, 80 mm, 110 mm, 77 mm, 105 mm, 111 mm, 117 mm, 119 mm, 87 mm, with a long-term mean of 76 mm calculated from Prince Albert rainfall records. Thus, the rainfall during the growing season was a mixture between average years and higher-rainfall years without a very dry year that may have killed selectively plants of a certain size. We

therefore had fairly representative weather conditions for growth, with a slight tendency towards above average rainfall and we thus expect the resulting growth parameters to be representative.

Newly germinated shrub seedlings in arid and semi-arid environments generally experience very high (>95%) mortality within the first two years (Esler 1993, Milton 1995). Small shrub seedlings (<5 cm diameter) should therefore be excluded from the data used for the calculation of growth and survival from changes in population structure. Large cohorts of year-old plants are rarely traceable five to ten years later, and if included in the data base may make it impossible to fit growth parameters or to estimate the annual survival of established plants.

It is likely that our method may be inappropriate for some shrub life-forms. Possible examples include succulents that transfer water from old leaves to new, showing little growth between years, hemicyptophytic perennials such as *Asparagus* spp. where above-ground parts die off completely in some years, but later regrow, and shrubs that reproduce both vegetatively and by seed, in which growth of offsets may be considerably faster than seedlings.

Biological interpretation of the model results

The two succulent species *B. ciliatus* and *R. spinosa* showed accelerated growth behavior without saturation, however, the annual risk of mortality increased with increasing age, and we estimated short life-spans for both species. Both follow the strategy 'live fast, die young'. The size-dependent risk of mortality cannot, however, be explained by the physiological growth characteristics of these species. These species apparently invest more in structural support (dense wood with high energy content) than the non-succulents but build new branches in an exponential manner and have shorter life span. This surprising result contrasts with results showing a positive relationship between investment in wood and longevity in angiosperm trees (Loehle 1988), and highlights our presently poor understanding of the constraints of growth for leaf succulent species. It is possible that the bearing of heavy succulent leaves, or special constraints in water relations require relatively greater wood investment than for the non-succulents.

The two early reproducing species *B. ciliatus* and *G. fruticosa* showed accelerated growth at smaller sizes ($b > 1.28, \dots$) while all other species show more or less linear growth at smaller sizes ($b < 1.05$).

R. spinosa and *P. pallens* allocate relatively more resources to defense and survival at smaller sizes (*P. pallens* at all sizes) than to early reproduction (see Figure 10B).

Our study indicated that the evergreen species *P. pallens* and *R. spinosa* showed a low annual risk of mortality (<5%) at small sizes ($s < 500 \text{ cm}^2$). Both are chemically-defended against herbivory, *R. spinosa* by high concentrations of tannins and polyphenols in the old leaves and stems (van der Heyden 1992), and *P. pallens* by alkaloids (Kellerman et al. 1988) that are likely to reduce herbivory by insects and mammals. In addition *R. spinosa* invests in spines and *P. pallens* in very thick woody main stems (which, paradoxically are relatively inexpensive). The deciduous species *B. ciliatus*, *G. fruticosa*, and *T. sinuatum* had a higher annual risk of mortality (> 5%) at all sizes than evergreen species, and this is likely to be related to the trade-off between allocation of energy to chemical defense and growth. For example *T. sinuatum*, which is palatable to insects and mammals (Milton 1993), chemically undefended, and with the least expensive wood, regrows rapidly after damage, whereas evergreen *P. pallens* and *R. spinosa* that are chemically defended, recover slowly (van der Heyden 1992).

It is interesting that there are considerable differences between the two species *T. sinuatum* and *P. pallens* of the functional group 'successor species' (Wiegand et al. 1995). They both establish in shaded sites under the canopy of plants of *B. ciliatus*, *R. spinosa* and *G. fruticosa* all of which belong to the functional group 'colonizer species' that establish mainly in open sites. Both *T. sinuatum* and *P. pallens* show almost linear growth ($b \approx 1$) and a size-independent mortality pattern, however they differ considerably in their size at age eight (*P. pallens*: $a = 380 \text{ cm}^2$, *T. sinuatum*: $a = 1178 \text{ cm}^2$) and in their annual risk of mortality (*P. pallens*: $m(s) = 0.015$, *T. sinuatum*: $m(s) = 0.15$). *P. pallens* occupies the niche of a slow growing, long-lived, heavy-defended (unpalatable) and evergreen species that flowers and grows steadily without being influenced too much by rainfall variability. *T. sinuatum*, in contrast, occupies the niche of a quick growing, shorter-lived, low-defended (soft, highly palatable) and deciduous species that grows and flowers opportunistically in response to rainfall.

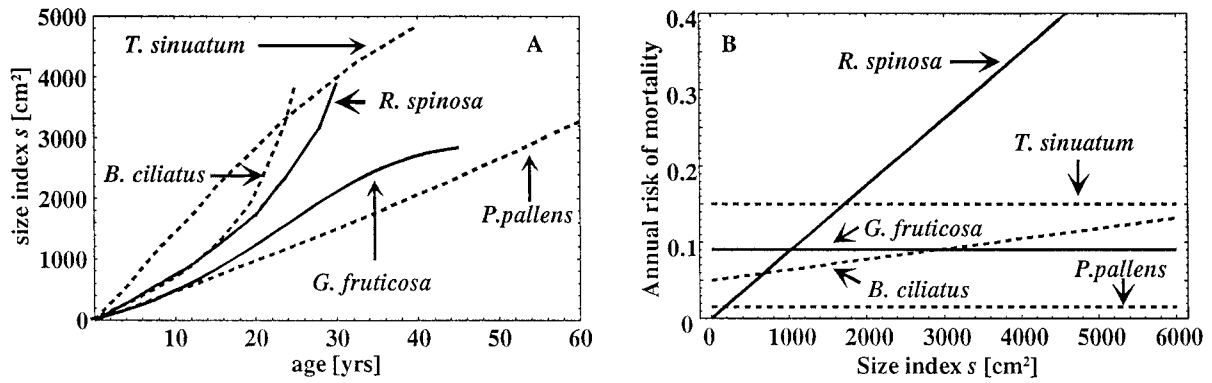


Figure 10. Summary of the size-age relations (A) and the mortality pattern (B) obtained with our technique.

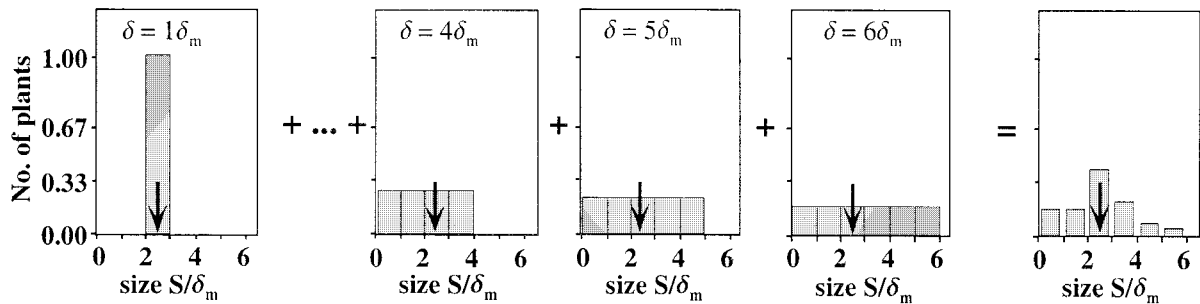


Figure 11. Construction of the size-class distributions D^{1997} and F^{1997} , exemplified for one plant with a size of $2.5\delta_m$ (arrow). After selecting a minimal size-class width δ_m we overlay the resulting six size-class distributions with widths $\delta = 1\delta_m, 2\delta_m, \dots, 6\delta_m$. To overlay consistently, we calculate the height h of a peak which is caused by a plant as $h = \delta_m/\delta$.

Conclusion

The advantages of the method described in this paper are firstly, that a plant population need be measured on only two occasions in order to estimate survival and growth, and secondly, that marking individual plants is not required. For shrubs with perennial above-ground stems, our approach was dependable, even for relatively small sample sizes. In some cases we increased the sample size by adding plant sizes that were sampled at additional transects in the same area of the study site. This result proves that our technique is not necessarily restricted to two data sets that were collected at exactly the same transects. This is an important point for potential applications of our technique. The possibility of resampling an area some years later may increase the value of 'old' data sets considerably. An unexpected and intriguing finding was that although wood density was correlated with longevity in the three non-succulent plants species we examined, this did not hold for the succulents. It would appear that wood production is more costly than expected for the succulent species sampled in this study.

We speculate that the physical or physiological costs associated with the bearing of heavy succulent leaves require relatively greater wood investment than for the non-succulents (although it is also possible that the relatively recent speciation of leaf succulent Mesembryanthemaceae with woody stems has resulted in inefficient wood investment patterns which have not yet been subject to selective pressure).

Acknowledgements

Funding provided by the UFZ-Centre for Environmental Research, Leipzig enabled S.J.M. and T.W. to travel between Germany, and South Africa for co-operative work. The authors thank M. Aguiar, W. R. J. Dean, F. Jeltsch, K. Moloney, J. Paruelo, H. Thulke, K. Wiegand, and especially N. Eccles for assistance during the development of ideas or for comments on drafts of this manuscript. The authors are grateful to S. Compton and V. Swanepoel of Saasveld Forestry College, Port Elizabeth Technikon for collecting the 1997 data.

Appendix

Equation (5) measures the absolute deviation between the two size-class distributions D^{1997} and F^{1997} . We found that a slight change in the size-class width δ could change the shape of the size-class distributions and thus influence the absolute deviation. This was because one or more plants at the border of a size-class changed the size-class after a slight change in the size-class width δ . This effect was especially marked for low numbers of total plants. To eliminate this problem we overlay, for a given set of size data, several resulting size-class distributions with different size-class widths δ . Due to the superposing procedure each plant causes a in the final size-class distribution a distribution (Figure 11) instead of a single peak, and the effect of small changes in the size-class width δ on the shape of the resulting size-class distribution will be small.

References

- Archer, S., Scifres, C. & Bassham, C. R. 1988. Autogenic succession in a subtropical savanna: conversion of grasslands to thorn woodland. *Ecol. Monog.* 58: 111–127.
- Arnold, T. H. and B. C. de Wet (eds) 1993. *Plants of Southern Africa*. Mem. Bot. Surv. S. Afr. 62: 1–825.
- Ash, A. J. & McIvor, J. G. 1998. How season of grazing and herbivore selectivity influence monsoon tall-grass communities of northern Australia. *J. Veg. Sci.* 9: 123–132.
- Batista, W. B., Platt, W. J. & Macchiavelli, R. E. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* 79: 38–53.
- Begon, M., Harper, J. L. & Townsend, C. R. 1990. *Ecology – Individuals, populations and communities*. Blackwell Scientific Publications, Boston, USA (see chapter 14).
- Chambers, J. C. & Norton, B. E. 1993. Effects of grazing and drought on population dynamics of salt desert shrub species on the Desert Experimental Range, Utah. *J. Arid Environ.* 24: 261–275.
- Cowling, R. M. & Hilton-Taylor, C. 1999. Plant biogeography, endemism and diversity. In: Dean, W. R. J. and Milton, S. J. (eds), *The Karoo: ecological patterns and processes*. Cambridge University Press, Cambridge.
- Dunwiddie, P. W. & la Marche, C. V. C. 1980. A climatically responsive tree ring record from *Widdringtonia cedarbergensis*, Cape Province, South Africa. *Nature* 286: 796–797.
- Esler, K. J. 1993. *Vegetation patterns and plant reproductive processes*. Dissertation, University of Cape Town, Cape, South Africa.
- Fourie, J. H., de Wet, N. J. & Page, J. J. 1987. Veldtoestand en neiging in Kalahari duineveld onder 'n ekstensiewe veeboerderystelsel. *J. the Grassland Soc. Southern Afr.* 4: 48–54.
- Friedel, M. H., Pickup, G. & Nelson, D. J. 1993. The interpretation of vegetation change in a spatially and temporally diverse arid Australian landscape. *J. Arid Environ.* 24: 241–260.
- France, J., Thornley, J. 1984. *Mathematical Models in Agriculture*. Butterworths, London.
- Gourlay, I. D. 1995. Growth ring characteristics of some African *Acacia* species. *J. Tropical Ecol.* 11: 121–140.
- Hoffman, M. T. & Cowling, R. M. 1990. Vegetation change in the semi-arid eastern Karoo over the last 200 years: an expanding Karoo – fact or fiction? *South Afr. J. Sci.* 86: 286–294.
- Kellerman, T. S., Coetzer, J. A. W. & Naude, T. W. 1988. *Plant poisonings and mycotoxicoses in livestock in southern Africa*. Oxford University Press, Cape Town.
- Lange, R. T. & Sparrow, A.D. 1992. Growth rates of western myall (*Acacia papyrocarpa* Benth.) during its main phase of canopy spreading. *Austr. J. Ecol.* 17: 315–320.
- Loehle, C. 1988. Tree life history strategies: the role of defenses. *Can. J. Forestry Res.* 18: 209–222.
- McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. *Am. Nat.* 131: 459–490.
- Milton, S. J. 1993. Insects from the shrubs *Osteospermum sinuatum* and *Pteronia pallens* (Asteraceae) in the southern Karoo. *Afr. Entomol.* 1: 257–261.
- Milton, S. J. 1994. Growth, flowering and recruitment of shrubs in grazed and in protected rangeland in the arid Karoo, South Africa. *Vegetatio* 111: 17–27.
- Milton, S. J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *J. Appl. Ecol.* 32: 145–156.
- Milton, S. J., Dean, W. R. J. & Kerley, G. I. H. 1992. Tierberg Karoo Research Centre: history, physical environment, flora and fauna. *Trans. Royal Soc. S. Afr.* 48: 15–46.
- Milton, S. J., Gourlay, I. D. & Dean, W. R. J. 1997. Shrub growth and demography in arid Karoo, South Africa: inference from wood rings. *J. Arid Environ.* 37: 487–496.
- Noy-Meir, I. 1990. Responses of two semi-arid rangeland communities to protection from grazing. *Israel J. Bot.* 39: 431–442.
- O'Connor, T. G. 1995. Transformation of a savanna grassland by drought and grazing. *Afr. J. Range Forage Sci.* 12: 53–60.
- O'Connor, T. G. and Roux, P. W. 1995. Vegetation changes (1949–71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa, influence of rainfall and grazing by sheep. *J. Appl. Ecol.* 32: 612–626.
- Rosati, V. R. & Bucher, E. H. 1995. Relative abundance and diet composition of Chacoan cavies in relation to range condition. *J. Range Manag.* 48: 482–486.
- Shreve, F. & Hinckley, A. L. 1937. Thirty years of change in desert vegetation. *Ecology* 18: 463–478.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.
- Turner, R. M. 1990. Long-term vegetation change at a fully protected Sonoran Desert site. *Ecology* 71: 464–477.
- Van der Heyden, F. 1992. Effects of defoliation on regrowth and carbon budgets of three semi-arid Karoo shrubs. PhD thesis, University of Cape Town.
- Vasek, F. C. 1980. Creosote bush: long-lived clones in the Mojave Desert. *Am. J. Bot.*, 67: 246–255.
- Whisenant, S. G. & Wagstaff, F. J. 1991. Successional trajectories of a grazed salt desert shrubland. *Vegetatio* 94: 133–140.
- Wiegand, T., Milton, S. J. & Wissel, C. 1995. A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. *Ecology* 76: 2205–2221.