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Life span indirect evaluation of three alpine perennial plants

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Abstract. Three non clonal alpine species, namely *Anemone speciosa*, *Campanula tridentata*, and *Carum caucasicum* were chosen for life span analysis. Marked specimens of the species were observed at permanent plots of alpine heaths in the NW Caucasus for 18 years annually. Life tables were developed for detailed description of death rate in the populations. Death probability and life expectation were calculated on this base. For our incomplete data we conducted analysis in suggestion that age-specified death rate is constant after the observation period. Life expectations were estimated as 385, 65, and 52 years for *A. speciosa*, *C. tridentata*, and *C. caucasicum*, correspondingly.

Key-words: North West Caucasus, age stage, life table, censored data, life span, *Anemone speciosa*, *Carum caucasicum*, *Campanula tridentata*

Introduction

Life span is one of the species characteristics that mainly determines the population age structure and its stability. For its definition in the case of perennial plants it is necessary to observe marked plants in the sample plot regularly. For trees it is possible to use the auger for revealing of absolute age accounting annual rings. Evidently, for herbs this method can not be applied and estimation of age and its periods should be done another way. In the case of a alpine clone plant species the life span may be evaluated on the base of the clone area size and clone square annual increment (Grabherr *et al.* 1978; Steinger *et al.* 1996). Some species allow to use morphological peculiarities for age definition (Rabotnov 1960).

If we have a chance to observe short-lived plants from seedlings then we can receive a distribution of the death times and, respectively, life spans. For long-lived perennials (especially alpine) it can not be done, and, moreover, the investigation in natural sites do not allow us to start observations from seedlings occurring in the same conditions. In natural investigations we have always a sample of uneven-aged plants with unknown absolute age.

We used the possibilities of the concept of discrete description of plants' ontogeny (Rabotnov 1950, 1960; Uranov 1975; Gatzuk *et al.* 1980; Uranov and Serebryakova 1976; Serebryakova 1988; White 1985) for life span estimation. In short, the ontogeny of a plant may be described by the sequence of developmental or age stages. Each age stage may be characterised not only by physical time (years, months, etc.) but also by biological time inherent to organism's life (Robbins 1957). Division of the continuous ontogenetic process into developmental stages allows to obtain the coherent scales of biological time for different species with different life spans.

Continuous process of individual plant development may be subdivided into several stages on the ground of structural indicators which reflect functional importance. There are: the presence vs. absence of embryonic, juvenile or mature morphological features; the ability of an individual to reproduce sexually or to propagate vegetatively; the ratio between alive and dead as well as growing and non-growing plant parts.

Ontogeny of plant organism is subdivided into four periods and nine stages (Rabotnov 1950; Uranov 1975): 1. latent period (seed); 2. pre-reproductive period (seedling, juvenile, immature, virginile); 3. reproductive period (young, mature, and old reproductive); 4. post-reproductive (senile) period.

Number and consequence of age stages may differ from previous list. The main result of such a description is that we can mark development of the plant as a sequence of age stages and describe a population as a set of individuals belonging to certain age stages with their corresponding distribution - age spectrum.

We can repeat the observation after one or more periods of time and observe the distribution's changes. It is similar to the regular censuses of human population and it is obvious to apply the statistical methods using in this case for our goal. The difference exists that each individual in the human population may be characterised by his absolute age while plants should be characterised at last by some features peculated to their analogues of age, for example, developmental stages.

Long life spans of high-mountain plants was noted by many authors (Rabotnov 1950, Bliss 1971; Jolls 1982; McCarthy 1992) but there are a few data for non clonal alpine herbs. In our work we try to estimate the duration of each age stages and whole life span for three alpine plant species from the North West Caucasus (*Anemone speciosa Adam ex G.Pritz, Carum caucasicum (Bieb.) Boiss and Campanula tridentata Schreb.*), using procedures of statistical demography analysis.

Materials and Methods

Study area and data collection

The study area is located in the alpine zone of the Mount Malaya Khatipara, Teberda Nature Reserve, Karachaevo-Cherkessian Republic, the NW Caucasus, Russia 43° 16' N, 41° 41' E; 2,780 m above see level. Field observations were made in an alpine lichen heath, which was described in detail previously (Onipchenko 1994).

Three non clonal typical alpine species were chosen as the objects of our study, namely *A. speciosa*, *C. tridentata*, and *C. caucasicum*. Individual marked specimens of the species were followed on permanent plots from 1980 to 1997 year. Observations were made annually at the end of August. Presence of flowers and ontogenetic stage (juvenile, vegetative, generative) of the specimens were recorded. All individuals from permanent plots were observed. Field investigations were organized without any external disturbances, first of all without digging for root system observations. In this case some plants which built flowers before the start of observations and did not flower during observation period, could be classified as pregenerative stage. The total numbers of marked generative plants were 72, 60 and 77 for *A.speciosa*, *C.tridentata* and *C.caucasicum* correspondingly.

Data Analysis

Life tables are the detailed description of age-specified death rate in a population. Some statistics such as death probability, life expectation and so on can be calculated on this base (Pressat 1985). There are two main forms of life tables:

Cohort life tables, that represent information on death rate in a specific cohort (a group of individuals which were born simultaneously). Cohorts are observed permanently since the birth until the moment when they have no alive individuals.

Current life tables. These tables suggest a hypothetical cohort, with their individuals undergoing a risk of death whole being observed in a real population for a specific time period.

In this work we analyse data using cohort life tables and mean cohort as group of plants transforming to given stage simultaneously. Consider the main concepts and parameters of cohort life tables in details. The explanation mentioned below is convenient for generative stage description because of individual death is treated as the end of generative stage. End of other stages is transition to next stage. So transition is analogous of death. We estimated life span of each stage only for plants, which had transition from given stage to next or died as generative plant.

The part of a cohort that survives from birth until age x is denoted as l_x. The difference between the number of survive individuals at age x and $x+1$ is designated as d_x. It is given by the following formula:

$$d_x = l_x - l_{x+1} \qquad (1).$$

The probability of surviving to age $x+1$ from age x (p_x) is defined as:

$$p_x = l_{x+1} / l_x \qquad (2).$$

The probability of death (q_x) for each age interval $(x, x+1)$ is a d_x / l_x ratio. If the average part of the last year of life equals 0.5 then the total life time (L_x) for interval $(x, x+1)$ is calculated by the formula:

$$L_x = (l_x - d_x) + 0.5dx = (l_x + l_{x+1})/2 \qquad (3).$$

The total number of years (T_x) lived by all the members of a cohort in age x and older is given as:

$$T_x = \sum_{y=x}^{\omega} L_y \qquad (4)$$

where ω is the beginning of the last age interval. The life expectation for an individual in age x is calculated using the following formula:

$$e_x = T_x / l_x \qquad (5).$$

The formula mentioned above can be applied only when we have complete data, i.e. the data that covered the whole life span of a species. There is a number of works devoted to designing methods for analysis of censored data (Doksum 1974; Kalbfleisch 1974; Susarla and VanRizin 1976; Cornfield and Detre 1977; Ferguson and Phadia 1979; Cox and Oakes 1984; Chiang 1984). In our paper we use the approach advanced by Chiang (1984). This method was developed for medical studies to estimate the life expectation of a specific group of patients. It is based on the assumption that the probability of death in a cohort is constant after the observations are completed. In our mind Chiang's method is useful for the situations where we have not any suggestions on the distribution of death probability after the period of observations. The formula for calculation of life span expectation can be represented as:

$$e_\alpha = \frac{1}{2} + p_\alpha p_{\alpha+1} + \Lambda + p_\alpha p_{\alpha+1} \Lambda$$

$$p_\alpha p_{y-1} + p_{\alpha y} (p_y + p_y p_{y+1} + \Lambda \quad) \qquad (6)$$

where α and y are first and last years of observation respectively; $p\alpha_y$ is written for $p\alpha_y p\alpha_{+1} \ldots p_y{}^{-}{}_1$. If the death rate is constant after

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where $\boldsymbol{\alpha}$ and $\boldsymbol{y}$ are first and last years of observation respectively; $\boldsymbol{p\alpha_y}$ is written for $\boldsymbol{p\alpha_y p\alpha_{+1} \ldots p_y{}^-{}_1}$. If the death rate is constant after moment **y** with the survival probability of **p** we can replace the last member in (6) with $p\alpha_y\, p/(1-p)$. As a result formula (6) is transformed to:

$$e_\alpha = \frac{1}{2} + p_\alpha p_{\alpha+1} + \Lambda + p_\alpha p_{\alpha+1} \Lambda$$

$$p_\alpha p_{y-1} + p_{\alpha y} \frac{p}{1-p} \qquad (6)$$

If **p** is the survival probability of certain interval **t** then the sample variance of life (or stage) expectation in interval a can be estimated by following formula (Chiang 1984):

$$S^2_{e_\alpha} = \sum_{\substack{x=\alpha \\ x<>t}}^{y-1} p^2_{\alpha x} [e_{x+1} + 0,5]^2 S^2_{p_x} +$$

$$p^2_{\alpha t} [e_{t+1} + p_{ty} / (1 - p_t)^2 + 0,5] S^2_{p_t} \qquad (7)$$

for $\alpha < t$, and

$$S^2_{e_\alpha} = \sum_{x=\alpha}^{y-1} p^2_{\alpha x} [e_{x+1} + 0,5] S^2_{p_x} +$$

$$+ p^2_{\alpha y} S^2_{p_t} (1 + p_t)^2 \qquad (8)$$

for $\alpha \geq t$.

We tried to estimate Life spans of age stages for our species. As a Life span we defined the time duration from the first registration of this stage till first registration of next ontogenetic stage. Plants died in the stage did not included into the sample except the generative stage where plant's death was considered as an end of plant's life. If the plant maintained its stage at the end of investigation then these data are considered as censored.

The sample data were organized into one age cohort. In order to construct it we shifted the data such way that the start of duration of the stage for every individuals occurred at the same moment independently on its real start. This suggestion is realistic if we consider the population dynamics as an equilibrium stage. The presentation of the sample as an age cohort means that the plants possessing this stage at year **t** moved into this stage at year **t-1** minimally. Really we have an unknown distribution of left censored starts. We avoid this fact for simplicity of estimates but in this case the mean may be underestimated.

Consider an example (Table 1). Assume that we estimate the life span of stage 2. In this case plant 5 will be excluded from the sample because it died within the stage 2. After shifting to mutual beginning the data will be as follows (Table 2). Taking these data as a base we can calculate the values of estimates described before. (Table 3). Now we can apply the life table techniques for our species.

year of investigation	*1*	*2*	*3*	*4*	*5*	*6*	*7*
plant 1	1	2	2	2	2	3	3
plant 2	2	2	2	2	3	3	3
plant 3		1	2	2	2	2	2
plant 4		1	2	2	2	3	3
plant 5				1	2	x	x
plant 6					1	2	2

Table 1. The sequence of age stages for a group of plants. 1 - seedling stage, 2 - juvenile stage, 3 - vegetative stage, 4 - generative stage, x - plant's death.

Duration of stage (years)	1	2	3	4	5	6
plant 1	2	2	2	2		
plant 2	2	2	2	2		
plant 3	2	2	2	2	2	c
plant 4	2	2	2			
plant 6	2	2	c			

Table 2. Shifted data with the same begining of stage 2.c-censored data

interval	n_x	s_x	d_x	q_x
0-1	5	5	0	0
1-2	5	5	0	0
2-3	4	4	1	0.25
3-4	3	1	2	0,66
4-5	1	1	0	0

Table 3. Calculation of transition probabilities. $\mathbf{n_x}$- number of plants at the begining of interval;$\mathbf{s_x}$ -number of plants at the end of interval;$\mathbf{q_x}$ -probability of death in the interval, d_x - number of plants passed into next stage (or died).

I	N_x	S_x	D_x	q_x	e_x	S_e
0-1	77	77	0	0	28	10,4
1-2	77	75	2	0,03	27	10,4
2-3	74	71	3	0,04	27	10,7
-	-	-	-	-	-	-
17-18	7	7	0	0	28	19,5
>18	-	-	-	-	27	19,5

Table 4. Life table of *C. caucasicum* generative plants. I - interval (year of observaion), N_x - total number of generative plants, S_x - surviving plants at the interval (x, x+1), D_x - dying plants in the interval (x, x+1), q_x - probability of death in the interval (x, x+1), e_x - expectation of stage at x, S_e - standard deviation of e_x .

In order to use the method mentioned above it is necessary to determine the probability of death or transition into another stage in open interval (after an interval of observations) and it's standard deviation. Transition rate and probability of death are supposed to be constant after the observations. However, determination of this characteristics is complicated in our case due to the probabilities of death/transition being not stabilised inside the period of observation. Therefore, we use the average death/transition probability for the whole period of observations (18

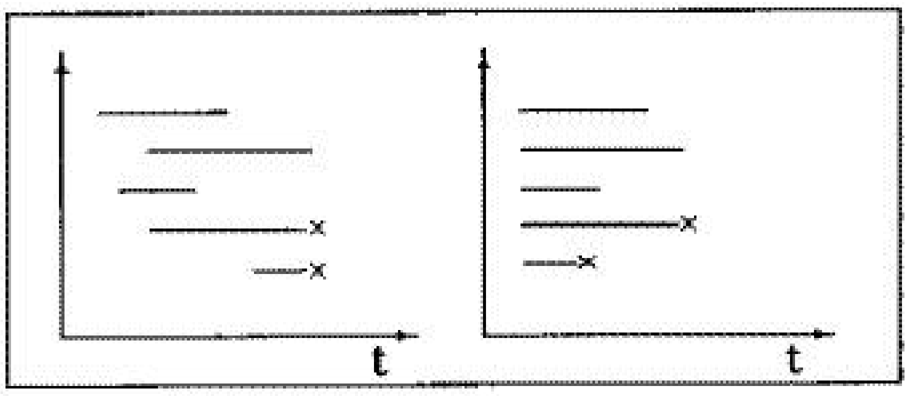

Fig. 1. First occurrence of certain stage for all individuals. Left: initial data, right: shifted data. (x-censored data). t-time.

years).

Results

Life tables were made for each of studied species, the example being presented for *Carum caucasicum* generative plants (Table 4). From this example we can observe change of stage life span expectation during the experiment. Generally all three species may be characterized by relatively small variation of stage span expectations during the period of observations. This fact reflects, presumably, constant transition/death rate of each stage during long time period, and supports our suggestion on equilibrium state of studied populations.

We have obtained the following expectations of stages life spans (Table 5). The estimates of life spans of all species are comparable, at least, with decades and ontogeny of *A. speciosa* lasts some hundred years. *C. caucasicum* has the longest vegetative stage and sufficiently short reproductive period in relation to other species. *C. tridentata* takes intermediate place between *A. speciosa* and *C. caucasicum*.

If final distribution of life spans belong to Gaussian type then it is easy to calculate that from each 1000 plants 10 of them will live up to 87, 123 and 1401 years for *C. caucasicum*, *C. tridentata*, *A. speciosa*, correspondingly.

Discussion

An attempt was made to estimate the life span of species under investigation on the base of calculation of death and transition probability between different ontogenetic stages in the earlier study (Onipchenko and Komarov 1997). It was suggested that the inverse value of death or transition probability can be accepted as life span or stage duration. According to this study ontogenesis longevity of studied species had following values: more than 60 years for *C. tridentata*, *C. caucasicum*, and 150 - 500 years for *A. speciosa*. These data are in general agreement with the results of the present paper. However, unlike the work mentioned above we have estimated variance of stage longevity values.

It is interesting to compare generative age stage longevity with annual seed production (Table 6). We can see the inverse dependence between these parameters. According to Harper (1977) this dependence can be explained by considering the relationship between productivity value, of individual and growth of population. The population of plants with short life cycle and great seed production has approximately the same growth rate as the population of long-lived plants with small seed production.

Stage	j			v			g			ls	
Species	e	s.e.	n	e	s.e.	n	e	s.e.	n	e	s.e.
C.caucasicum	4,7	0,02	156	19,6	0,41	147	27,9	1,2	77	52,2	1,3
C.tridentata	4,8	0,04	78	13,8	0,38	91	46	2,5	60	65	2,5
A.speciosa	12,1	0,55	43	12,4	0,39	55	361	39,9	72	385	39,9

Table 5. Expectations and their errors of age stages and life spans (**j** - juvenile, **v** - vegetative, **g** - generative, **ls** - whole life span, **e** - observed expectation of stage life span, **s.e.** - standard error, **n** - number of individuals).

Species	*C.c.*	*C.t.*	*A.s.*
seed production (s./i.y.)	37	25	5
generative stage life span (year)	27,96	46,2	360,9

Table 6. The dependence between seed productivity (mean seed/individual per year [s./i.y.]. Logvinenko and Onipchenko, unpublished data) and generative stage life span (year).

Our results do not contradict with the suggestions of many authors on long alpine plants Life span (Rabotnov 1950; Bliss 1971;

	Interruption longevity (in years)									
	0	1	2	3	4	5	6	7	8	9
Species	The number of events									
A.s.	310	46	17	12	9	5	0	2	0	2
C.t.	238	68	30	6	9	3	0	0	1	0
C.c.	398	77	13	4	2	1	1	1	0	0

Table 7. The distribution of breaks in flowering for generative plants. Sp. - species, *A.s.* - *A. speciosa*, *C.t.* - *C. tridentata*, *C.c.* - *C. caucasicum*.

Zhilyaev 1987; McCarthy 1992; Steinger *et al.* 1996). Callagan and Collins (1981) estimated age of some individuals of *Polygonum viviparum* as 26 years, *Vaccinium vitis-idaea* as 109 years. Life span of some plants in Pamir arid high-mountains is several hundred years (Nosova 1986). Our data confirm long duration of high mountain plant development.

It should be noted that final result depends on significant suggestion that death rate is constant over period of observation. The rate of death may be defined using survivorship curves. Constant rate of death corresponds to survivorship curve as a straight line. It is known that three types of survivorship curves exist (Harcombe 1987) which **reflect the relationship between logarithm of surviving plants by age x and age x. The shape of these curves reflects different dynamics of death** probability against plant age. In type 1 the convex curve indicates increasing death risk. In type 2 the straight line means constant death rate over all ages. In type 3 the concave curve indicates decreasing risk of death with age.

However, we have no arguments to deny assumption that long-living herb plants have critical age after which the probability of dying off increases. The existence of such period is not obvious, and future investigation is necessary to answer this question.

According to Harper (1977) plants with long ontogenesis have long prereproductive period. Our results do not confirm this suggestion (Table 5). The lack of continuous flowering shows that favourable environment conditions are more important for the first flowering age than duration of prereproductive period. Moreover, our data show the existence of cycles of flowering. Each period of flowering is preceded by the non flowering period and it being assumed that period before first flowering is not so significant as Harper suggested.

Breaks in flowering are frequent events for studied species. The most frequent break is one year period. The distributions of duration of breaks of flowering (Table 7) may be described by inverse exponential distribution. Well known (from reliability theory) that the exponential distribution arises in the case of constancy of external conditions (Cox and Oakes 1984). It seemed to be indirect confirmation of considerably constant environmental conditions for studied plants.

It should be noted that estimation of plants ontogenesis or its stages longevity for the species under investigation is not completed yet. We did not estimated the duration of postreproductive period, the knowledge of the shape of survivorship curves would allow to evaluate life spans more precisely.

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