



Demography and life history of *Daucus carota* L. populations in the Netherlands



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ARTICLE INFO

Article history:

Received 18 January 2016

Received in revised form 9 July 2016

Accepted 22 July 2016

Edited by Hermann Heilmeyer

Available online 26 July 2016

Keywords:

Carrot

Annual

Monocarpic perennial

Life history

Threshold size for flowering

Introgression

ABSTRACT

In nature so-called 'biennial' plants often delay their life cycle, flowering in the third or fourth year, or even later. Life-history theory predicts that high rosette survival is associated with longer life histories. We test this in wild carrot (*Daucus carota*) populations along disturbed roadsides in the Netherlands, covering a range from unfertile to highly fertile soils. Only 24.2% of the plants behaved as biennial or monocarpic perennial. Most plants were winter (38.9%) or summer annual (36.8%). There was no significant association between life history and habitat, despite differences in mortality and soil fertility between the populations. Annual rosette survival was between 19% and 80%, indicating a high turnover of populations. As predicted by life history theory, the fraction summer annuals (the shortest life-cycle) decreased significantly with rosette survival. In five populations the fraction plants flowering increased with plant size in a similar manner, but in the North Holland dune population plants had a higher threshold size. The annual behaviour of the carrots is quite different from their monocarpic perennial life cycle described in other studies. Carrot cultivars may cross with wild carrots and in this way generation time of the offspring can be affected. We discuss how this may affect plant fitness in the wild.

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1. Introduction

Selection on generation time involves a trade-off between reduced survival and more accumulation of resources for reproduction (Metcalf et al., 2003). Biennial plants are adapted to semi-disturbed conditions (Harper, 1977), where they profit from disturbances to establish or re-establish local populations. Life-history theory predicts that low rosette survival favours annuals with a shorter generation time than biennials (Hart, 1977; de Jong and Klinkhamer, 2005). High rosette survival favours monocarpic perennials that delay flowering past the second year. In monocarpic perennials the probability of flowering typically increases with plant size and this can be quantified as the threshold size at which 50% of the plants in a population flower (de Jong and Klinkhamer, 2005). Comparing habitats at the same latitude, Wesselingh et al. (1997) documented that high rosette survival corresponded with a higher threshold size for flowering in the monocarpic perennial *Cynoglossum officinale*. Several studies showed that generation time changes with latitude, with shorter life histories (annuals)

becoming more predominant towards the south (Lacey, 1988 for *Daucus carota* in North America; Boudry et al., 2002 for *Beta maritima* in Europe) and these changes are partly genetic, i.e. plants from different latitudes differ in generation time when placed in the same environment. In a common garden, accessions of the perennial *Lythrum salicaria* from the north of Sweden started reproduction later than southern accessions (Olsson and Agren, 2002). Contrary to this, in the US *Arabidopsis lyrata* accessions from northern locations showed a higher fraction flowering than plants from southern accessions when grown under the same conditions (Paccard et al., 2014). Kim and Donohue (2011) showed that the perennial *Erysimum capitatum* delayed reproduction later at higher altitude, where plant survival was higher. The predominance of annuals in the south may well represent greater disturbance and higher rosette mortality but these factors were rarely measured directly and other factors may also contribute to clines in generation time. Clines may also change as a result of the climate becoming warmer. Van Dijk and Hautekèete (2014) showed that plants of *Beta maritima* originating from seeds collected in 2009 flowered more often in their first year than the seeds collected in 1989 at the same location.

We studied the demography of wild *Daucus carota* subsp. *carota* L populations along roadsides in the Netherlands. In the Netherlands the wild carrot is widespread in these disturbed

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habitats (FLORON, 2011), yet its life history has rarely been studied. Wild carrot is fully outcrossing and crosses easily with the carrot crop, *D. carota* subsp. *sativa* (Wijnheimer et al., 1989; Hauser and Bjorn, 2001; Rong et al., 2014). Wild carrot is a monocarpic perennial plant that is native to Europe (Heywood, 1983). It has been observed to flower in the first year (Gross, 1981; Schouten et al., 2002) but often delays flowering until a more substantial size has been reached. Both genetic factors and the suitability of the environment determine the age at which plants flower in the field (Hauser and Shim, 2007).

We address the following predictions from life history theory. (1) Is the shortening of the life cycle associated with high rosette mortality? (2) Does the size threshold for flowering differ between populations and does it decrease with high rosette mortality? These questions are examined for six Dutch *D. carota* populations that vary greatly in soil fertility. We also expect that fraction of annuals increases with nutrient availability, simply because more nutrients allow more growth and will allow more plants to reach the size threshold for reproduction sooner.

2. Material and method

2.1. Species description

Daucus carota is a short-lived monocarpic herb that flowers from June until autumn. The spiny one-seeded fruits are likely to be animal-dispersed and may lie dormant in the soil for more than 1 or 2 years. Populations of wild carrots are very common along roadsides, cultivated fields and in early succession wastelands across most of Europe, but the species also occurs in late-successional grasslands. Wild carrots are considered weeds in North America and Japan, where they have been introduced (Hauser et al., 2004; Umehara et al., 2005).

2.2. Habitat characterization

Two populations were located at the landward side of coastal sand dune areas, one in Bergen (52°35'02.39"N, 4°39'19.12"E; North Holland (NH) dunes) and one in Meijendel (52° 07' 45.90"N, 4°21'20.63"E; South Holland (SH) dunes); two populations were located in polder areas, one in Roosendaal (51°33'19.16"N, 4°24'43.75"E) and one in the Schermerpolder (52°35'51.53"N, 4°53'34.25"E; Schermer); one was an urban population located in Leiden (52°08'58.47"N, 4°27'31.44"E) and one was a riverine population located near Leerdam (51°50'48.86"N, 5°05'38.03"E).

All populations were mown twice a year in early to mid-June and during September. This is a typical management regime for Dutch roadsides. Mowing can affect the early bolters and flowering plants, which then typically regrow to resume flowering and seed production, until the second mowing. An exception was the Leiden population that was mown later, in late July and late October. In order to characterize the environmental conditions of the six populations, soils samples were collected from the 0–25 cm layer and analysed for total Nitrogen by BLGG Agroxpertus, Wageningen, The Netherlands.

2.3. Field survey

Individual plants were marked in an area of 12 m², their position was recorded and plants were then intensively followed from 2009 to 2010. We visited the plots in spring (April–May 2010) for counting emerging seedlings and rosettes and in the autumn (August–September 2010) for counting seedlings, established rosettes and flowering plants (Fig. 1). In June 2010 the number of leaves was counted and length of the longest leaf was measured. Length of the longest leaf (x) best predicted Dry Weight

(DW) of the whole plant in June ($n = 10$, South Holland dunes). The regression equation $\ln(DW) = 2.63\ln(x) - 12.47$ explained 94.2% of the variation in $\ln(DW)$. Root Crown Diameter (91.3%) and Number of Leaves (83.0%) did less well in this respect. During autumn 2009 we distinguished seedlings from older rosettes, by size and appearance. Then we counted seedlings and rosettes again during spring 2010 and counted the plants again in autumn 2010 to record which ones had died, survived as rosette or flowered. With this scheme we could distinguish different flowering strategies (Fig. 1). Plants that were in the rosette stage during fall 2009 (N_1) and that flowered during fall 2010 (N_3) had a biennial or, if they were already older than one year at the first census, monocarpic perennial life history. Plants that germinated during fall 2009 (N_4) and flowered in the next year (N_6) were winter annuals. Plants that germinated in spring 2010 (N_7) and flowered a few months later (N_9) had an even shorter summer-annual life history. During 2011 the monitoring of the plots was less intensive. No seedlings were marked but we did record the survival of older rosettes from autumn 2010 until the same moment next year. Consistent with the literature (Verkaar and Schenkeveld, 1984), we observed in our plots that wild carrot seeds germinated throughout the year. Therefore the distinction we made between winter and summer annuals is artificial. It depends on whether the seeds had germinated before or after our autumn census. Summer annuals will include plants that germinated in, for instance, March and that were exposed to some winter cold as seedlings. The cold required for flowering of carrots is quite variable and ranges between cultivars from 5 days to 3 months (Nemeth, 2003). Over the two years that our study lasted the populations in NH dunes, Leerdam, Roosendaal and Schermer showed an overall increase, whereas the SH Dunes population remained stable and the Leiden population decreased.

2.4. Plant size and probability of flowering

We performed logistic regression using the R (R Development Core Team, 2011) procedure GLM, family = binomial link = logit) to connect vegetative (0) or flowering (1) to the biomass proxy length of the longest leaf (x). In the logistic regression $y = 1/(1 + \exp(-\mu - \alpha x))$ parameter α quantifies the effect of leaf length x on flowering probability. Significant differences in model parameters between the different populations were examined with a t -test (Holmes et al., 2011).

3. Results

3.1. Survival and flowering

Averaged over 2010 and 2011 rosette survival was highest in the two dune populations and lowest in the inland populations (Table 1). Rosette mortality in 2010 was highly correlated to mortality in 2011 (Spearman rank correlation, $r_s = 0.87$, two-sided $P = 0.05$), showing that some populations consistently have high annual rosette mortality. There was no significant association between life history and population ($\chi^2 = 5.27$, $df = 10$, $P = 0.87$, Table 1). On average 24.2% of all flowering plants was monocarpic perennial or biennial, 38.9% was winter annual and 36.8% was summer annual (Table 1). Dune populations had only 27.3–33.3% monocarpic perennials and a similar fraction was also present in the Roosendaal (24.0%) and Leiden (28.6%) populations. The soil on the different sites differed markedly in its Nitrogen content (Table 1). The fraction of summer annuals, the shortest life history, was strongly negatively correlated with rosette survival ($r_s = -0.88$, two-sided $P = 0.03$, Fig. 2a), as predicted by life history theory. The fraction summer annual plants increased with soil fertility ($r_s = 0.6$, two-sided $P = 0.24$, Fig. 2b) as expected because more nutrients

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