



CANOPY BEHAVIOR OF THREE MILKVETCH (*ASTRAGALUS*) SPECIES IN ACCLIMATION TO A NEW HABITAT

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Received April 24, 2009; revision accepted November 11, 2009

Empirical data on functional growth dynamics are extremely limited for herbaceous plants and do not exist for milkvetch (*Astragalus*) species, although they are essential to an understanding a plant's ability to acclimate to a new habitat, which we need to know in order to predict its performance in future climate scenarios. The paper examines how species spread to a habitat in which they do not initially occur. It presents results on changes in growth, canopy behavior, competition ability and morphological traits of Cicer milkvetch (*Astragalus cicer* L.), Sweet milkvetch (*Astragalus glycyphyllos* L.) and Russian milkvetch (*Astragalus falcatus* Lam.) from a ten-year experiment. They successfully acclimated to a new habitat and presented clearly similar growth dynamics and similar strategies for establishing and maintaining populations. Developmental and reductional perennial phases were noted. The developmental phase showed slow and fast subphases. Canopy cover area peaked at the height of the developmental phase. Morphological parameters measured from parts of plants growing outside the experimental plot were greater than for plants growing inside it. Milkvetch species are good competitors. Unlike invasive species, their expansion strategy is not colonization-oriented. The data suggest that systematic and evolutionary studies on these species should pay attention to morphological changes.

Key words: *Astragalus*, autecology, biometrics, canopy behavior, developmental perennial phase, growth dynamics, new habitat, plant strategy, population ecology, reductional perennial phase.

INTRODUCTION

Long-term experiments are important in evolutionary biology, botany and ecology (Aniszewski, 2000; Rozen and Lenski, 2000; Dudley, 2007; Philippe et al., 2007). They cannot in every case be set up with hypothesis-driven approaches as in a molecular biology assay. Such experiments and the data they yield are critical to understanding important factors affecting plant growth dynamics and some aspects of heterogeneity, competition and invasiveness in communities (Aniszewski, 1988a), and even yield new findings in ultrastructural and molecular research of plant organs (Aniszewski, 2006; Aniszewski et al., 2006; Sahbaz et al., 2009). Although plant behavior plays a vital role in the processes of natural and managed habitats, plant functional dynamics are not understood well enough to predict plant performance in future climatic scenarios (Osmond et al., 2004). Nor can crop resources be exploited efficiently without a deep understanding of plant functional dynamics (Schurr et al., 2006). Perennial

legumes are a group of plant species with a worldwide distribution. These species, both annuals and perennials, are part of the third largest family of flowering plants, Fabaceae, and have a good adaptive system. They are able to grow dynamically with a high photosynthetic rate (Aniszewski, 1988b,c; Aniszewski, 1995a,b; Aniszewski et al., 1996; Aniszewski et al., 1998; Aniszewski et al., 2001a) in different climates, environments and soil conditions. They have great potential for breeding in Northeastern Europe, where growth conditions for plants are generally extreme (Aniszewski, 2004). It has been hypothesized that plants have their own growth strategies for extreme environmental conditions. They can form durable structures such as seeds or position-resilient organs at more sheltered places, or can develop adaptations on the basis of anatomical, morphological and physiological futures (Schurr et al., 2006). This problem has not been studied empirically in legumes; hence the motivation for establishing long-term experiments with species belonging of the genus *Astragalus*. This

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genus contains herbs and small shrubs occurring throughout the world, with the greatest concentration of species in Southwest and Central Asia, though some species occur in Europe and western North America (Heywood and Ball, 1968; Heywood, 1993; Zomlefer, 1994; Kholoptseva and Mihkiev, 1995; Decker, 2005; Akan et al., 2008; Riahi and Zarre, 2009). The genus *Astragalus* is very diverse in its species adaptation to environments, and many wild species are rare and locally conserved; many are known as important useful plants and many as strong toxicants. There are no literature data on the potential spread (natural or artificial) of these species into habitats where they did not initially occur, nor any data on how they adapt to new conditions and cope with competition from other species which are native or well adapted to the given habitat. Such data are needed for comparisons of earlier results related to any scientific evidence of anticipated climate change, and they can help avoid potential problems in nature conservation. Habitat-forming invasive species can produce novel transformations of the environment (Wright et al., 2010). As milkvetch species have not previously been studied, it is not known whether they can establish permanent and aggressive populations in nature and survive in a new habitat. These species, especially cicer milkvetch (*Astragalus cicer* L.), sweet milkvetch (*Astragalus glycyphyllos* L.) and Russian milkvetch (*Astragalus falcatus* Lam.) are viewed as potentially useful plants in many European countries, America and Australia, and are suggested as economic crops (Townsend, 1993; Loeppky et al., 1996; Aniszewski, 2004; Acharya et al., 2006; Laurence, 2006). Uses for them in revegetation and restoration programs are proposed (Bhattarai et al., 2008), and commercial production is expected to increase around the world (Acharya et al., 2006). This makes the question examined here topical and important, both for theory and for practical applications. In this study I assess long-term growth dynamics and their functionality in the acclimation of three milkvetch species to a new habitat, examining long-term canopy behavior, morphological traits and competition ability. Three basic questions are addressed: (1) what are the perennial growth dynamics and canopy behavior of these milkvetch species, (2) is there any evidence of their canopy expansion strategy and competition ability, and (3) are there morphological changes associated with their population spread in a new habitat?

MATERIAL AND METHODS

PLANT MATERIAL AND ACCLIMATION EXPERIMENTS

Cicer milkvetch (CM), sweet milkvetch (SM) and Russian milkvetch (RM) were used in the long-term experiments. These species do not occur in nature in

eastern Fennoscandia (Mossberg and Stenberg, 2005) and were totally new to the experimental habitat. The species studied are an integral part of the Caucasian flora, but it is not precisely known how they came to the Caucasus or whether they are true endemics there.

The experiment was established in 1998 in Botania, the botanical garden of the University of Joensuu in Finland (62°36'00"N, 29°45'50"E), employing standard procedures for plant acclimation and measurement, with some modifications. The experimental site was in the center of the botanical garden, in a research area near a wild area with trees and bushes. The plots were laid out on two east-west transects, with buffer plots on the easternmost and westernmost ends of both transects. The seeds of three different species were sown in 1 m² plots in four replicates randomly (by lottery), together with the buffer plots. To enable comparison of the vegetation between plots, the roots of the experimental plants were prevented from growing outside the plots with boards 3 cm thick on all sides of the plots, blocking egress down to 30 cm depth. The soil was tilled manually down to the same depth. In each plot, 100 seeds per m² were sown at 3 cm depth on May 15, 1998.

NEW HABITAT CHARACTERISTICS AND POTENTIAL PLANT NEIGHBORS

The new habitat (Botania) for the milkvetch species is located in the Finnish boreal zone, strongly influenced by the Gulf Stream from the Atlantic and by gentle southwestern winds producing a climate 3–4°C warmer than other areas at the same northern latitude. The climate is continental with cold winters and hot summers (Tab. 1).

The soil in each plot was natural and typical garden soil with fine sand, sand, silt, clay and organic matter fractions, and with its own seed bank (Tab. 1). Seeds of 11 perennial species were found in soil samples taken from the experimental area (depth 0–30 cm, sample size 1 cm², 4 replicates) immediately before the milkvetches were sown. These species were expected to be neighbor competitors for the three milkvetch species sown. All plants in the experimental area were allowed to grow freely during each annual growing period. The species studied and their neighbors were cut at the height of 5 cm from the soil surface each year on October 15. The green mass of the cut plants was transported out of the experimental area. Long-term observations and measurements were performed.

MEASUREMENT AND DATA COLLECTION

Pod and seed samples were collected for measurements. The plants were measured ten times during each growing season for ten years on the same

TABLE 1. Characteristics of new habitat. GP – growing period; d – days; ETS – effective temperature sum on average; AAT – annual average temperature; PSF – period of soil frost; PSTGP – precipitation sum during thermal growing period; ADFS – average day of first snow; ADPS – average day of permanent snow; LTASD – long-term average snow depth on 15 March; DM – dry matter; OM – organic matter; A – ash; Ct – total carbon; Cm – microbial carbon; Ct/N and Cm/N – soil balance ratios; $s\ s^{-1}$ – average seed number per sample (For methods see: Aniszewski and Simojoki, 1984; Aniszewski, 1995c)

Climate characteristics		Soil characteristics		Potential neighbors in new habitat	
GP	160 d	pH	5.69±0.2	<i>Elytrigia repens</i>	2.2 $s\ s^{-1}$
ETS	1100 °C	DM	694±27 g L ⁻¹	<i>Cirsium arvense</i>	0.5 $s\ s^{-1}$
AAT	2 °C	OM	160±24 g L ⁻¹	<i>Festuca pratensis</i>	0.6 $s\ s^{-1}$
PSF	5 months	A	534±10 g L ⁻¹	<i>Festuca rubra</i>	0.3 $s\ s^{-1}$
PSTGP	400 mm	Ct	74.7±19 g L ⁻¹	<i>Imula helenium</i>	1.5 $s\ s^{-1}$
ADFS	1.XI.	Cm	15.5±2 g L ⁻¹	<i>Lupinus polyphyllus</i>	2.0 s
ADPS	15.XI.	N	36.6±7 g L ⁻¹	<i>Phleum pratense</i>	1.0 $s\ s^{-1}$
LTASD	60-70 cm	P	0.826±0.08 g L ⁻¹	<i>Symphytum officinale</i>	2.0 $s\ s^{-1}$
		K	1.742±0.08 g L ⁻¹	<i>Trifolium hybridum</i>	0.2 $s\ s^{-1}$
		Ca	4.604±0.05 g L ⁻¹	<i>Trifolium pratense</i>	0.1 $s\ s^{-1}$
		Mg	4.218±0.18 g L ⁻¹	<i>Trifolium repens</i>	0.2 $s\ s^{-1}$
		Na	0.157±0.02 g L ⁻¹		
		Cu	0.012±0.002g L ⁻¹		
		Zn	0.030±0.002g L ⁻¹		
		Ct/N	2.4		
		Cm/N	0.5		

dates. The growth type of milkvetch species was noted, and all cases of deviations in growth were recorded and measured. Qualitative observations of corolla color, calyx shape and legume shape (and any deviations) were made with magnifying glasses (diameter 5 cm at 5× and 10 cm at 10×), an eye ocular (20×) and a Zeiss Stemi DV4 stereo microscope. The length of the stems, branches of stems, leaves, leaflets, corollas, calyxes and legumes was also measured. Measurements were made with standard instruments to 1 mm accuracy, and with an electronic micrometer with an automatic reader (Digimatic) at accuracy up to 1 μm. Moreover, all cases of competition between plants were recorded and analyzed from additional measurements. Cases of plant parts growing on the experimental plots and outside the plot area were measured separately.

The cover of milkvetch on each plot was measured using the contour method. This method was based on the proportion of cover to the area not covered. The area inside the contours was outlined with a very thin copper wire and measured with graph paper, microscopy and the Digimatic reader to 1 μm accuracy. The cover of the species was then counted as the difference between the total plot area and the measured area without cover. The area of cover by plant parts outside the experimental plots was also measured by the same contour method. In these cases the area covered by milkvetch parts was outlined with a very thin copper wire, measured, and read directly. The competition ability of the species studied was measured by comparing the growth of

individuals of the species with the growth of individuals of other species growing on the plots from the soil's own seed bank as their neighbors.

FUNCTIONAL GROWTH AND DATA ANALYSIS

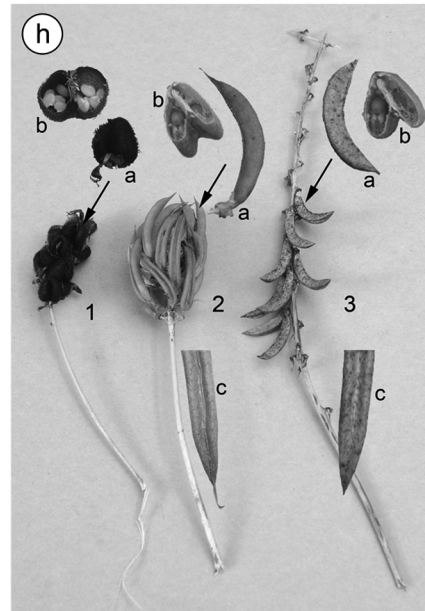
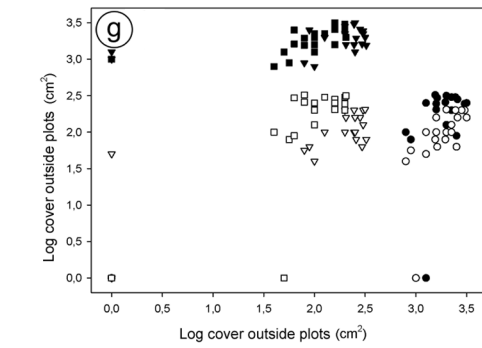
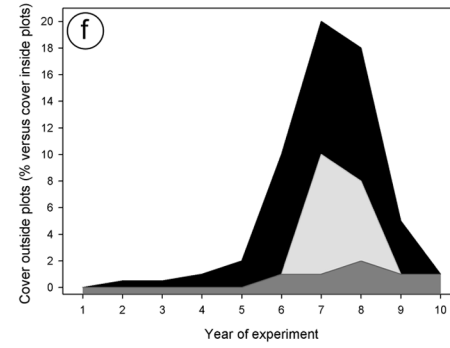
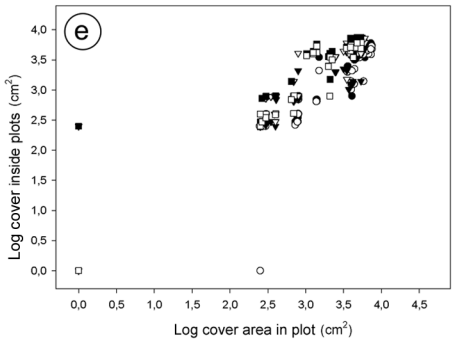
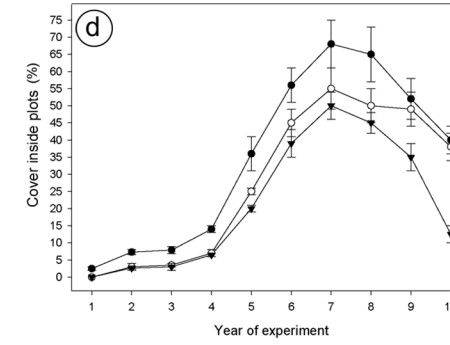
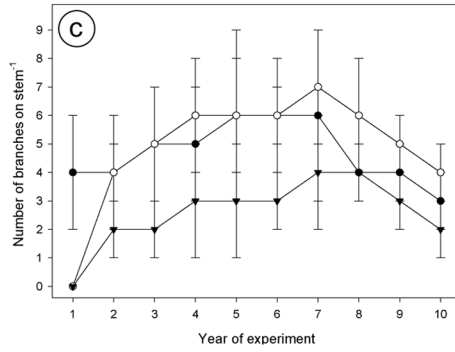
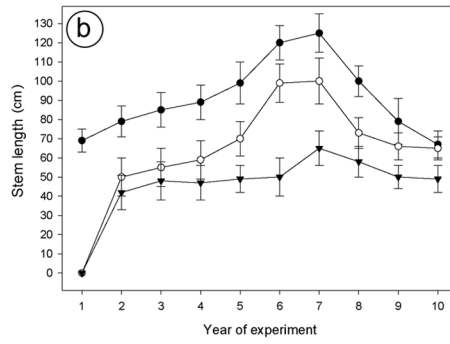
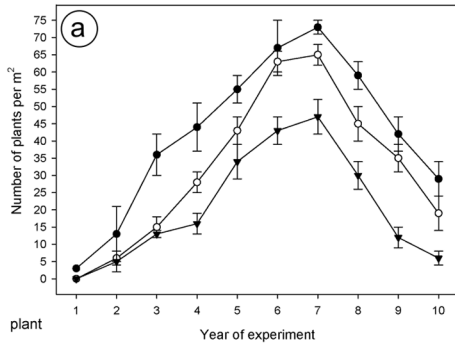
The botanical data collected during ten years reflect the dynamic nature of the developing milkvetch populations in the new habitat, and were analyzed with a combination of methods aimed at quantifying the potential functionality of growth dynamics during the acclimation process. The results of the statistical analysis were then considered in the light of theoretical possibilities and relevant explanations. The growth dynamics and forms of growth were linked to and their functionality tested in the process of acclimation.

The collected data were analyzed using SPSS 16.0 for Windows® and SigmaPlot ver. 8.0. ANOVA and the normality test were applied as in previous work (Aniszewski et al., 2001b). Graphs and images were made with SigmaPlot ver. 8.0, a Nikon professional camera with multiplication objectives and the PhotoShop program for Windows.

RESULTS

PERENNIAL GROWTH DYNAMICS IN A NEW HABITAT

The milkvetch species studied showed clearly similar growth dynamics, growth ability, and strategies



Figures: a, b, c, d

- *Astragalus cicer*
- *Astragalus glycyphyllos*
- ▼ *Astragalus falcatius*

Figures: e, g

- *Astragalus cicer* to *Astragalus glycyphyllos*
- *Astragalus cicer* to *Astragalus falcatius*
- ▼ *Astragalus glycyphyllos* to *Astragalus falcatius*
- ▼ *Astragalus glycyphyllos* to *Astragalus cicer*
- *Astragalus falcatius* to *Astragalus cicer*
- *Astragalus falcatius* to *Astragalus glycyphyllos*

for establishing and maintaining populations over the years (Fig. 1a). Cicer milkvetch (CM) established the biggest population each year and had the highest density (70 plants m²). Sweet milkvetch (SM) displayed similar trends but had lower population density in all ten experimental years. Russian milkvetch (RM) had the same adaptation ability as SM during the first two years, but then declined (Fig. 1a). The first growing season in the process of acclimation to the new habitat was difficult for all species. Neither SM nor RM were able to establish any populations or partial populations, and CM produced only a partial population with three individuals on all experimental plots (Fig. 1a).

There were two clear phases in the dynamics of population establishment by the milkvetch species in the new habitat. Their growth ability and population size increased in all species up to the seventh year (developmental perennial phase, dpp) and then decreased rapidly each ensuing year (reductional perennial phase, rpp). The dpp and rpp trends of all studied species were very similar (Fig. 1a). Also similar were other parameters such as length of main (basic) stem (Fig. 1b), stem branches (Fig. 1c), cover on plot area (Fig. 1d) and cover outside the experimental plot area (Fig. 1f). In the latest trend (dpp = 7 yrs) this is especially clear for CM and SM. However, in the case of RM, cover outside the experimental area was highest one year later (Fig. 1f) although all the other parameters were the same at dpp = 7 yrs (Fig. 1a-d).

The plants of all species studied were largest in the last year of dpp and clearly smaller in rpp (Fig. 1b). Stem length peaked in the seventh growth year (end of dpp). The length differences between species were smallest in the last experimental year (rpp). CM stems were shorter in that year than in the first year (Fig. 1b).

The number of branches in all species except RM was highest in the final year of dpp and then decreased in the rpp. RM had the highest number of branches in the seventh, eighth and ninth experimental years (Fig. 1c). The standard deviations in the number of branches in the main stems were relatively large in all species. SM had more branches on the stems than the other species (Fig. 1c).

CANOPY BEHAVIOR AND EXPANSION STRATEGY

Cover measured in the plot area confirms the existence of two perennial phases (dpp up to the seventh year and rpp thereafter) of milkvetch species and gives information on dynamics during dpp (Fig. 1d). The dpp stage can be divided into two subphases: slow development (sd, first four years) and fast development (fd, from fifth to seventh years).

For all milkvetch species, cover on the experimental plots was at maximum in the last year of dpp. CM had the largest cover area and RM the smallest. In the last experimental year RM clearly decreased versus the others (Fig. 1d). However, the log values of the measurements indicates a clear correlation between the species for cover area on the experimental plots (Fig. 1e).

Cover of milkvetch species outside the experimental area also confirmed the existence of dpp and rpp phases, and showed the dynamics of canopy behavior and spread to new areas (Fig. 1f). CM at its peak covered twice the area outside the experimental plot than SM, and ten times more than RM. Here the log values also confirmed the similarity of trends between the species, though they differed in their ability to spread outside the plot area (Fig. 1g).

COMPETITION ABILITY

The growth dynamics of milkvetch species are connected with their ability to compete in the experimental plots with other species in the habitat (in soil seed bank). Sometimes the milkvetch plants sprawled over the neighboring plants. CM was especially active in this regard. Milkvetch leaves, stems and branches shaded the photosynthetic surfaces of plants from the soil seed bank in all areas (center, middle and border parts) of the experimental plot. These observations show that the milkvetch species were good competitors during acclimation to the new habitat. They caused a marked reduction of species forming part of the old flora (Tab. 2). With the exception of *Lupinus polyphyllus*, *Symphytum officinale*, *Inula helenium* and *Trifolium repens*, all those species showed reduced growth on the experimental plots. This reduction was seen especially in the seventh

Fig. 1. Functional growth dynamics of milkvetch species in a ten-year experiment. **(a)** Number of plants, **(b)** Stem length, **(c)** Number of branches on stem, **(d)** Cover inside plots, **(e)** Relationship between cover area of species inside plots, **(f)** Cover outside plots, **(g)** Relationship between cover of species outside plots, **(h)** Reproductive organs. 1 – multiple fruits of CM. Inflated and ovoid-globose pods with short black hairs appear in multiple fruits (a, arrow). Cross section of pod (b) exposes seeds in two pod ventricles; 2 – multiple fruits of SM. Linear-oblong pods (a, arrow) are curved and slightly compressed. Cross section of pod (b) exposes seeds in two flattened pod canals. Cross section through middle of pod and enlargement (c) shows that seed canals in pod are separated; 3 – multiple fruits of RM. Acute and oblong pods (a, arrow) are slightly curved. Cross section of pod (b) exposes two seed canals in the form of a heart. Cross section through middle of pod and enlargement (c) shows that seed canals are separated in central parts of pod.

TABLE 2. Changes in species growing from soil seed bank in new habitat during ten-year experiment. C. – *Cirsium*; E – *Elytrigia*; F – *Festuca*; I – *Inula*; L. *polyphyl.* – *Lupinus polyphyllus*; P. – *Phleum pratense*; S. – *Symphytum*; T. – *Trifolium*

Species	Experimental year (average number of individual plants plot ⁻¹)									
	1	2	3	4	5	6	7	8	9	10
<i>C. arvense</i>	2.5	2.0	1.5	1.0	0.75	0.5	0.0	0.0	0.25	0.5
<i>E. repens</i>	5.0	6.0	6.5	6.25	6.0	5.75	5.0	4.0	4.0	4.5
<i>F. rubra</i>	1.0	2.0	1.0	1.0	1.0	0.75	0.5	0.5	0.75	1.0
<i>I. helenium</i>	0.5	0.25	0.25	0.25	0.25	0.25	0.0	0.0	1.0	2.0
<i>L. polyphyl.</i>	0.5	1.0	2.0	2.5	2.5	2.5	2.0	2.5	3.0	4.0
<i>P. pratense</i>	1.0	1.0	1.5	1.0	1.0	0.5	0.0	0.0	0.0	0.25
<i>S. officinale</i>	1.0	1.0	1.0	0.5	0.5	0.25	0.0	0.0	1.0	2.0
<i>T. hybridum</i>	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
<i>T. pratense</i>	1.0	1.0	1.0	0.25	0.25	0.25	0.0	0.0	0.0	0.0
<i>T. repens</i>	0.0	0.0	0.0	0.25	0.25	0.5	0.0	0.5	1.0	2.0

year of the experiment at the peak of the dpp of milkvetch species (Tab. 2, Fig. 1a–d, f). During the rpp of milkvetch species the number of plants of *Lupinus polyphyllus*, *Inula helenium*, *Elytrigia repens*, *Festuca rubra*, *Trifolium pratense* and *Trifolium repens* increased on the experimental plots (Tab. 2). There was only a negative correlation between milkvetch species population size and the number of individuals from the soil seed bank.

MORPHOLOGICAL CHANGES IN A NEW HABITAT

The similarities in the growth dynamics of the studied species were based on the large morphological differences between them. Their reproductive organs (especially pods) differ completely (Fig. 1h). There are more structural similarities between SM (2) and RM (3) than with CM. The structural biometrics of milkvetch species indicate changes in organs which are connected with the functionality of growth dynamics during the ten-year experiment (Tab. 3). CM had smaller leaves but twice the number of leaflets versus SM and 2/3 the number of leaflets versus RM. The species differ in the size of corollas, calyxes and pods. The corolla and calyx measures differed between outside and inside the experimental plot area. There were also clear differences in the number of pods in multiple fruits between species in the experimental area and outside it. CM differed from the other species in the number of seeds per pod inside and outside the experimental area. Moreover, the leaves outside the experimental plots (op leaves) were 0.76 mm longer (CM), 0.65 mm longer (SM) and 0.32 mm longer (RM) than the ten-year means for all leaves. Leaves located inside the experimental plot area (ep leaves) measured 1.55 mm (CM), 0.19 mm (SM) and 0.33 mm (RM) shorter than the ten-year

means. The op/ep size ratio of leaves was 1.026 for CM and 1.005 for SM and RM (Tab. 3). Op leaves had bigger corollas and calyxes in all species, especially in CM. There were more pods in multiple fruits of op plants of all species. Unlike the other species, CM differed in the number of leaf pairs and seeds per pod between op and ep with more leaf pairs and more seeds per pod outside than inside the plots. Seed size and seed weight were also higher in op plants than in ep plants, especially in the case of CM (Tab. 3).

DISCUSSION

PERENNIAL GROWTH AND FUNCTIONALITY

The growth dynamics of plant species are critical to their performance under new habitat conditions when resources are distributed heterogeneously in space and time (Schurr et al., 2006). In this work, all three milkvetch species established populations in the new habitat and survived through the duration of the experiment. There were no signs of damage to indicate that these species are unsuitable for growth in the new habitat, despite the extreme climate. The climate of a new habitat is an important factor, exerting a greater influence than species composition on historical population dynamics (Adler and HilleRisLambers, 2008). In light of this, the survival and growth dynamics of the milkvetch populations over 10 years present a case of successful acclimation. In experiments with 29 perennial herbaceous dicots and 11 perennial grasses in Kansas, U.S.A., herbaceous perennials died young and their life expectancy at one year of age ranged from 0.6 to 6.5 years (Lauenroth and Adler, 2008). In a two-year study in east central Idaho, U.S.A., populations of

TABLE 3. Growth and morphocharacteristics of milkvetch species in new habitat during ten-year experiment. n – number of measurements; op – parts of plants outside experimental plots (n=600 for CM and RM, n=500 for SM); ep – parts of plants on experimental plots; imf – multiple fruits for all plants; imf1 – multiple fruits in parts of plants outside the experimental plots; a – statistical significance at 0.05; ^{c1} – no significant correlation with SM and RM; ^{c2} – no significant correlation with CM and RM; ^{c3} – no significant correlation with CM and SM; M_n – lowest number of leaf pairs in the data; M_x – highest number of leaf pairs in the data; CM – Cicer milkvetch; SM – Sweet milkvetch; RM – Russian milkvetch

Measurement (n = 100)	CM	SM	RM
Leaves Mean±SD (mm)	88.66±23.7 ^{a,c1}	156.17±60.9 ^{a,c2}	135.34±34.7 ^{a,c3}
op Mean±SD (mm)	89.42±22.2 ^{a,c1}	156.82±59.2 ^{a,c1}	135.65±32.8 ^{a,c3}
ep Mean±SD (mm)	87.11±26.5 ^{a,c1}	155.98±64.2 ^{a,c1}	135.01±35.4 ^{a,c3}
Leaflets Median (M _n -M _x) lp	12 (6-18)	6 (2-10)	18 (10-26)
op Median (M _n -M _x) lp	14 (8-15)	6 (4 - 9)	18 (12-22)
ep Median (M _n -M _x) lp	11(6-18)	6 (2-10)	18 (10-26)
Corollas Mean±SD (mm)	15.1±1.7 ^{a,c1}	13.7±2.9 ^{a,c2}	13.9±3.6 ^{a,c3}
op Mean±SD (mm)	15.2±1.9 ^{a,c1}	13.8±3.3 ^{a,c2}	13.92±4.1 ^{a,c3}
ep Mean±SD (mm)	15.06±1.2 ^{a,c1}	13.6±3.9 ^{a,c2}	13.89±4.3 ^{a,c3}
Calyxes Mean±SD (mm)	8.5±2.0 ^{a,c1}	5.8±1.9 ^{a,c2}	9.2±3.3 ^{a,c3}
op Mean±SD (mm)	8.9±4.1 ^{a,c1}	5.82±2.6 ^{a,c2}	9.25±3.6 ^{a,c3}
ep Mean±SD (mm)	8.39±3.0 ^{a,c1}	5.8±1.6 ^{a,c2}	9.1±3.6 ^{a,c3}
Pods Mean±SD (mm)	13.6±3.2 ^{a,c1}	33.5±9.1 ^{a,c2}	20.6±8.2 ^{a,c3}
Pods imf Median (M _n -M _x)	16(4-21)	12(3-18)	18(8-24)
op Median (M _n -M _x)	18(6-20)	14(5-15)	19(10-21)
ep Median (M _n -M _x)	14(4-21)	11(3-18)	17(8-24)
Seeds in pod Median (M _n -M _x)	3.0 (1-6)	5 (2-8)	5.0 (3-8)
op Median (M _n -M _x)	4.0 (2-6)	5 (2-8)	5.0 (4-7)
ep Median (M _n -M _x)	3.0 (1-6)	5 (2-8)	5.0 (3-8)
Seed length Mean±SD (mm)	2.33±0.13	2.43±0.09	2.7±0.05
op Mean±SD (mm)	2.35±0.16	2.4±0.01	2.71±0.06
ep Mean±SD (mm)	2.31±0.11	2.39±0.013	2.69±0.056
Seed breadth Mean±SD (mm)	1.73±0.08	1.92±0.06	1.99±0.08
op Mean±SD (mm)	1.76±0.10	1.93±0.069	1.98±0.086
ep Mean±SD (mm)	1.69±0.14	1.91±0.07	1.99±0.07
Seed weight Mean±SD (mg)	0.0045±0.0004	0.0032±0.0003	0.0038±0.0002
op Mean±SD (g ⁻³)	0.005±0.0005	0.0033±0.00031	0.0039±0.0003
ep Mean±SD (g ⁻³)	0.004±0.0003	0.0031±0.00036	0.0037±0.0004

Challis milkvetch (*Astragalus amblytropis* B.) decreased and showed a low percentage of survival of seedlings and nonreproductive and reproductive individuals (Rittenhouse and Rosentreter, 1994). In the present study the milkvetch species gave evidence of a clear strategy for adaptation to the new habitat. First, seed germination and seedling growth was variable and cyclical. The reproductive behavior of these species in the new habitat is similar to the behavior of some aggressive species such as giant hogweed (*Heracleum mantegazzianum*) (Vainionpää, 2008). However, milkvetch species, unlike invasive plants, are not rhizomatous and reproduce only by seed. This means that milkvetch species have a mechanism (seed dormancy) allowing them to wait until growth conditions in the new habitat improve.

Their slow, uneven germination and population establishment can be considered a life strategy. The adaptation of a species to a new habitat is the degree to which it is able to live and reproduce in a given environment (Allard 1988, 1997). Adaptation also involves matching the successive developmental stages to climatic and adaphic resources and, where unfavorable extremes are unavoidable, minimizing their occurrence in more vulnerable stages (Roberts et al., 1993). This strategy, together with developmental growth dynamics, is the basis for species functionality in a new habitat. Plants have developed protection mechanisms against unfavorable fluctuations, and efficient mechanisms for using the heterogeneous conditions of their environment, from which they obtain their resources (Schurr et al., 2006).

CANOPY BEHAVIOR AND EXPANSION STRATEGY

The milkvetch species displayed two clear perennial phases (dpp and rpp) in this research. Like animal organisms, perennial plant species have population age categories, from the establishment and developmental stages to the oldest stage and death. Analyzing the growth dynamics of *Astragalus proximus*, Decker (2005) observed that it was not clear whether the seedlings are produced in the same year as seed germination. Studying *Astragalus adsurgens* Pall. in the field, Tobe and Gao (2007) found that light and infrequent precipitation in spring resulted only in aborted germination of buried seed, and frequent and relatively heavy precipitation in the summer rainy season enabled seedling establishment. My results suggest that the milkvetch species have a common strategy for germination and especially for seedling production. The seeds do not germinate in large numbers at once, nor do the seedlings (plants) grow en masse, but growth clearly proceeds gradually year by year. Abundant seedling growth was observed in the seventh year after sowing and plant density was highest at that time. This suggests that milkvetch seedling growth follows a genotype-dependent strategy. The vegetative growth of the main stems of milkvetch species in the new habitat also points to this strategy. With increasing plant density on the experimental plots, the stems increased in length up to the seventh growth year. Branch number followed a dynamic reflecting that strategy. Demonstrating their competition ability, these species tended to cover all the experimental plots with vegetation and then grow into the free space outside the experimental area. This canopy behavior did not depend on the location of plants in the plot (center or edge) and therefore can only be considered evidence of the growth strategy. I suggest that the canopy behavior and growth dynamics of the species are genetically regulated. Canopy behavior is also connected to the behavior of the roots, which were prevented from escaping the plots by the experimental design. Expansion of the milkvetch canopy to extend the growth area was linked to the peak of the developmental perennial phase (dpp). This trend was especially clear and strongest in CM: in the seventh year, 20% of its total cover was outside the experimental plots. The other species were not so expansive in this respect: less than 5% of their cover was outside the experimental plot.

MORPHOLOGICAL CHANGES
AND COMPETITION ABILITY

The trends for cover inside and outside the plot were relatively similar between the studied milkvetch species. CM expanded more than the

other milkvetch species. This suggests that expansion ability is connected with genotype and the morphostructural characteristics of the phenotypes. CM clearly differed from the two other species in the length of stems, leaves and pods. The length of stems of the milkvetch species changed during dpp. Stem length was similar between SM and RM, but the main stems of CM were clearly longer (especially during dpp). The length of leaves and pods measured in this research was in line with the data reported by Heywood and Ball (1968). However, changes in the length of leaves and pods during dpp, and especially in op and ep, were observed. Moreover, the main (basic) stems of CM were clearly longer, as reported by Heywood and Ball (1968). This research provides clear evidence that morphological parameters also depend on the new habitat, especially during dpp. They were greater in the plant parts growing outside than within the experimental area. This finding is new; it has been stressed in the literature that the link between the growth dynamics of vegetative organs and the entire canopy at the stand level is technically difficult to address (Schurr et al., 2006). My results show that the dependence of morphological parameters on the new habitat is connected with competition and adaptation. Plant competition between species is in practice the competition between individuals (Finnoff and Tschirhart, 2009). Individual growth is determined by size in the absence of competition, whereas in competitive situations the growth is determined not only by size but also by competition from neighboring plants (Nagashima, 1999). This ability of species to produce bigger organs during dpp should be reported as part of taxonomic descriptions and should be examined in studies of life history evolution.

Comparison of the data for the milkvetch and the other species in the experimental plots indicates that the studied milkvetches are good competitors. It is probably a characteristic of all species in the genus *Astragalus proximus*, for example, has been reported as sometimes occurring in fairly dense vegetation, growing even in lawn-like conditions, suggesting that it is a reasonably strong competitor (Decker, 2005). Although they proved to be good competitors in new habitat and showed a clear strategy of vegetative expansion, the milkvetch species I studied are not invasive species. Their strategy is based on domination of the local growing habitat, and the purpose of vegetative expansion is not to colonize but to gain space for growth and light, which is less during the peak of dpp. It seems that local domination is achieved during this life phase and that canopy expansion is only the result of plant over-density at the growth site. Canopy expansion and increased formation of photosynthetic and reproductive organs are the means of expansion, and help prevent the death of the population during rpp.

What will happen with the populations of these three milkvetch species ten years from now? Canopy expansion should lead to new seeding and an increase of the first population, and then a decline as part of the typical population cycle. On the other hand, it cannot be ruled out that the populations will disappear later.

ACKNOWLEDGEMENTS

This research was funded in part by the Ministry of Labor of Finland. I thank Dr. S. N. Drozdov for donating seeds, and Gabriel Gaëlle, Ilkka Konttinen, Kirsti Kyyrönen, Aki Juhani Leinonen, Veli-Pekka Pennanen, Pekka Piironen and Minna Sinkkonen for their technical assistance.

REFERENCES

- ACHARYA SN, KASTELIC JP, BEAUCHEMIN KA, and MESSENGER DF. 2006. A review of research progress on cicer milkvetch (*Astragalus cicer* L.). *Canadian Journal of Plant Sciences* 86: 49–62.
- ADLER PB, and HILLERISLAMBERS J. 2008. The influence of climate and species composition of the population dynamics of ten prairie forbs. *Ecology* 89: 3049–3060.
- AKAN H, FIRAT M, and EKICI M. 2008. *Astragalus bahcesarayensis* (Leguminosae-Papilionoideae) a new species of section *Alopecuroidei* DC. from Turkey. *Botanical Journal of Linnean Society* 156: 439–444.
- ALLARD RW. 1988. Genetic changes associated with the evolution and adaptedness in cultivated plants and their progenies. *Journal of Heredity* 79: 225–238.
- ALLARD RW. 1997. Genetic basis of the evolution of adaptedness in plants. In: Tigerstedt A [ed.], *Adaptation in Plant Breeding*, 1–11. Kluwer, Dordrecht, Netherlands.
- ANISZEWSKI T. 1988a. Phenological study on trees, bushes and arable peat land. Agricultural Research Center, Jokioinen, Finland. *Bulletin* 2 : 1–125. [In Finnish]
- ANISZEWSKI T. 1988b. Environment, phenological development and dry matter formation of the blue lupin (*Lupinus angustifolius* L.) varieties in northern Finland. *Acta Agriculturae Scandinavica* 38: 3: 303–316.
- ANISZEWSKI T. 1988c. Initial development of three blue lupin (*Lupinus angustifolius* L.) varieties in northern Finland. *Annales Agriculturae Fenniae* 27: 2: 141–151.
- ANISZEWSKI T. 1995a. Editorial. *Science of Legumes* 2: 136.
- ANISZEWSKI T. 1995b. Interaction between legume and soil. *Science of Legumes* 2: 172–189.
- ANISZEWSKI T. 1995c. The effects of green manure on bulk density and internal balance of garden soil: A one-year experiment. *Science of Legumes* 2: 149–162.
- ANISZEWSKI T. 2000. Phenotypic parameters of elecampane (*Inula helenium*) in eastern Finland. *Aquilo Series Botanica* 38: 13–28.
- ANISZEWSKI T. 2004. Legume species that have breeding potential for NE Europe. *Science of Legumes* 6: 256–265.
- ANISZEWSKI T. 2006. Succinate dehydrogenase and acid phosphatase activity in *Phaseolus lunatus* testa. *Acta Biologica Cracoviensia Series Botanica* 48/2: 59–65.
- ANISZEWSKI T., DROZDOV SN, KHOLOPTSEVA ES, and MIHKIEV AI. 1996. Botanical characteristics and phenological development of *Galega orientalis* Lam. in the primeval forest zone of eastern Fennoscandia. *Aquilo Series Botanica* 36: 21–26.
- ANISZEWSKI T, DROZDOV SN, KHOLOPTSEVA ES, KURETS VK, OBSHATKO AL, POPOV EG, and TALANOV AV. 1998. Effects of light and temperature on net primary productivity of fodder galega (*Galega orientalis* Lam.). *Acta Agriculturae Scandinavica Section B: Soil Plant Science* 48: 1: 34–40.
- ANISZEWSKI T, DROZDOV SN, KHOLOPTSEVA ES, KURETS VK, OBSHATKO LA, POPOV EG, and TALANOV AV. 2001a. Effects of light and temperature parameters on net photosynthetic CO₂ fixation by whole plants of five lupin species (*Lupinus albus* L., *Lupinus angustifolius* L., *Lupinus luteus* L., *Lupinus mutabilis* Sweet., *Lupinus polyphyllus* Lindl.). *Acta Agriculturae Scandinavica Section B: Soil Plant Science* 51: 17–27.
- ANISZEWSKI T, KARTTUNEN A-L, and HYVARINEN H. 2006. Structure of *Phaseolus lunatus* testa in its central point. *Acta Biologica Cracoviensia Series Botanica* 48: 1: 69–76.
- ANISZEWSKI T, KUPARI MH, and LEINONEN AJ. 2001b. Seed number, seed size and seed diversity in Washington lupin (*Lupinus polyphyllus* Lindl.). *Annals of Botany* 87: 77–81.
- ANISZEWSKI T., and SIMOJOKI P. 1984. Quantity and vigour of weed seeds in some ARC rotation experimental areas. Review and analysis of soil samples from three ARC research stations. Agricultural Research Centre, Jokioinen, Finland. *Bulletin* 22/84 : 1–38. [In Finnish]
- BHATTARAI K, JOHNSON DA, JONES TA, CONNORS KJ, and GARDNER DR. 2008. Physiological and morphological characterization of basalt milkvetch (*Astragalus filipes*): Basis for plant improvement. *Rangeland Ecology and Management* 61: 4: 444–455.
- DECKER K. 2005. *Astragalus proximus* (Rydberg) Wootton and Standley (Aztec milkvetch): A Technical Conservation Assessment. [Online], USDA Forest Service, Rocky Mountain Region, USA.
- DUDLEY JW. 2007. From means to QTL: The Illinois long-term selection experiment as a case study in quantitative Genetics. *Crop Science* 47 (S 3): S20–S31.
- FINNOFF D, and TSCHIRHART J. 2009. Plant competition and exclusion with optimizing individuals. *Journal of Theoretical Biology* 261: 2: 227–237.
- HEYWOOD VH. 1993. *Flowering Plants of the World*. Oxford University Press. New York, USA.
- HEYWOOD VH, and BALL PW. 1968. Leguminosae. In: Tutin TG, Heywood, VH, Burges NA, Moore DM, Valentine DH, Walters SM, and Webb DA [eds.] *Flora Europaea*, vol. 2, 80–191. Cambridge University Press, Cambridge, England.
- KHOLOPTSEVA ES, and MIHKIEV AI. 1995. Biological peculiarities of Leguminosae, genus *Astragalus* L., new to Karelia. *Science of Legumes* 2: 163–171.
- LAUENROTH WK, and ADLER PB. 2008. Demography of perennial grassland plants: survival, life expectancy and life span. *Journal of Ecology* 96(5): 1023–1032.

- LAURENCE R. 2006. Medicinal herbs – A preliminary evaluation of *Astragalus*, Bilbery, Feverfew and Stevia. RIRCD Publication No 05/185. Australian Government: Rural Industries Research and Development Corporation, Australia.
- LOEPPKY HA, BITTMAN S, HILTZ MR, AILTZ MR, and FRICK B. 1996. Seasonal changes in yield and nutritional quality of cicer milkvetch and alfalfa in northeastern Saskatchewan. *Canadian Journal of Plant Science* 76: 441–446.
- MOSSBERG B, and STENBERG L. 2005. *Extensive Manual of the North Flora*. Tammi, Helsinki, Finland. [In Finnish]
- NAGASHIMA H. 1999. The process of height-rank determination among individuals and neighbourhood effects in *Chenopodium album* L. stands. *Annals of Botany* 83: 501–507.
- OSMOND CB, ANANYEV G, BERRY J, FALKOWSKI P, LANGDON C, LIN G, MONSON R, NICHOL CJ, RASHIER U, SMITH S, and YAKIR D. 2004. Changing the way we think about global change research: scaling up in experimental ecosystem science. *Global Change Biology* 10: 393–407.
- PHILLIPPE N, CROZAT R, LENSKE RE, and SCHNEIDER D. 2007. Evolution of global regulatory networks during a long-term experiment with *Escherichia coli*. *BioEssays* 29: 846–860.
- RIAHI M, and ZARRE S. 2009. Seed development in *Astragalus cemerinus* and *A. ruscifolius* (Fabaceae), and its systematic implications. *Acta Biologica Cracoviensia Series Botanica* 51/1: 111–117.
- RITTENHOUSE B, and ROSENRETER R. 1994. The autecology of Challis milkvetch, an endemic of east central Idaho. *Nature Areas Journal* 14: 1: 22–30.
- ROBERTS E, SUMMERFIELD R, ELLIS R, and QI A. 1993. Adaptation of flowering in crops to climate. *Outlook on Agriculture* 22: 105–110.
- ROZEN DE, and LENSKE RE. 2000. Long-term experimental evolution in *Escherichia coli*. VIII. Dynamics of balanced polymorphism. *American Naturalist* 155: 24–35.
- SAHBAZ R., LIEBERE R., and ANISZEWSKI T. 2009. Polyphenol oxidase (PPO, catecholase) activity during germination and early seedling growth of Cicer milkvetch (*Astragalus cicer* L.). *Journal of Applied Botany and Food Quality* 82: 2: 163–169.
- SCHURR U, WALTER A, and RASCHER U. 2006. Functional dynamics of plant growth and photosynthesis – from steady-state to dynamics – from homogeneity to heterogeneity. *Plant Cell and Environment* 29: 340–352.
- TOBE K, and GAO Y. 2007. Seed germination and seedling emergence of herbs in sand. *Australian Journal of Botany* 55: 55–62.
- TOWNSEND CE. 1993. Breeding, physiology, culture, and utilization of Cicer Milkvetch (*Astragalus cicer* L.). *Advances in Agronomy* 49: 253–308.
- VAINIONPÄÄ T. 2008. Giant hogweed (*Heracleum mantegazzianum* Sommier and Levier) as an alien species. MSc. Thesis. 50pp. Faculty of Biosciences, University of Joensuu, Joensuu, Finland.
- WRIGHT JT, BYERS JE, KOUKOUMAFSTIS LP, RALPH PJ, and GRIBBEN PE. 2010. Native species behavior mitigates the impact of habitat-forming invasive seaweed. *Oecologia* 163: 527–534.
- ZOMLEFER W. 1994. *Guide to Flowering Plant Families*. University of North Carolina Press, Chapel Hill, North Carolina, USA.