EÖTVÖS LORÁND UNIVERSITY
FACULTY OF SCIENCE, INSTITUTE OF BIOLOGY

PhD Thesis Abstract

ECOPHYSIOLOGICAL TRAITS BEHIND PLANT INVASION AND PLANT RESPONSES TO CLIMATE CHANGE

Andrea Mojzes

PHD SCHOOL OF BIOLOGY (Head: Prof Dr Anna Erdei)
PHD PROGRAM OF ECOLOGY, CONSERVATION BIOLOGY AND SYSTEMATICS
(Head: Prof Dr János Podani)

Supervisor: Dr Tibor Kalapos

EÖTVÖS L. UNIVERSITY, DEPARTMENT OF PLANT TAXONOMY AND ECOLOGY
Budapest

HUNGARIAN ACADEMY OF SCIENCES, INSTITUTE OF ECOLOGY AND BOTANY
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I. Introduction and aims

Ongoing global environmental changes strongly affect ecosystems, including plant communities (Millennium Ecosystem Assessment 2005). Vegetation responses to these changes might be greatly influenced by plant community composition, and in particular by the dominant species' ecophysiological properties (i.e. physiology and associated morphology and anatomy). In my PhD dissertation, such plant traits of temperate forest-steppe species were studied in relation to two aspects of global change: plant invasion and climate change. The relevance of these studies to regional biodiversity is highlighted by the extensive areas of the potential Pannonian forest-steppes in Hungary.

The role of plant physiological traits in a species' invasion potential is not sufficiently investigated yet. Invasive species capable of colonizing various habitats are expected to face a wide range of climatic and edaphic factors. Morphological and physiological adjustment to contrasting habitat conditions is frequently greater for such alien invaders than for their populations in the native range or their non-invasive relatives (e.g. Richards et al. 2006). Spatial or temporal heterogeneity of habitat light climate may require a rapid and efficient leaf stomatal tracking of irradiance in such a way that CO_2 is supplied for photosynthesis at a minimum associated water loss. Such stomatal regulation of leaf gas exchange might contribute to the success of invasive species. For grass species however, only a few studies have investigated the light response of stomata. For C_4 grasses, ecophysiological tolerance is expected to be of particular importance in the temperate zone, where these species reach the upper limit of their latitudinal distribution. Nevertheless, structural and functional constraints associated with C_4 photosynthesis may restrict the ability of C_4 plants to adjust their leaf morphology and physiology to environmental changes relative to C_3 species (Sage & McKown 2006). Open (e.g. disturbed) canopies often provide favourable conditions for expanding grasses to establish in grasslands. Diurnal temperature fluctuation on bare soil is larger than beneath a closed canopy, that may promote the germination of such species. Previous studies also reported that C_4 plants generally require higher temperature for germination than C_3 species.

Global climate change scenarios forecast increases in global surface air temperature and a higher frequency of summer droughts in mid-latitudes during the 21st century (Meehl et al. 2007). Furthermore, irregular and extreme weather events are becoming more often and intense in these areas. The maintenance and regeneration capacity of photosynthetic performance as well as changes in leaf morphology, phenology and biomass allocation under altered conditions appear to be of great importance in plant tolerance of the dominant species or functional groups in a plant community. Different plant responses to environmental stress may result in altered growth, and thus changes in the dominance structure and composition of the community.

The aims of this study were to assess the ecophysiological traits and their environmental responses of phenotypes in relation to two aspects of global change: 1) the expansion of perennial grasses of forest-steppes and grasslands in novel, spatially or temporally heterogeneous habitats, and 2) the effects of simulated climate change on a characteristic vegetation type (sand forest-steppe) of the Kiskunság region (Great Hungarian Plain).

To meet these aims the following questions were addressed:

1. Is stomatal regulation more efficient in invasive compared to non-invasive C_4 grasses in response to abrupt changes in light intensity?
2. What is the difference in leaf morphology and structure between original, high-light semi-arid temperate forest-steppe habitats and the more homogeneous, growth room environment with moderate light?
3. Is the germination of expanding grasses enhanced by diurnal temperature fluctuation at a greater extent than that of non-expanding ones?
4. What are the effects of experimentally simulated climate change on three dominant species of a perennial open sand grassland colonized by shrub-sized root suckers of white poplar (*Populus alba*)?

II. Materials and methods

In the first part of my PhD dissertation, perennial grass species with different invasion potential (expanding or non-expanding) and photosynthetic pathway (C_3 or C_4) were compared in growth room experiments. (The only exception was *Eleusine indica*, which is a summer annual grass.) Three individuals per species, as belowground shoots in soil monoliths were collected from semiarid temperate forest-steppe vegetation or arable land on loess (Gödöllő Hills, 20 km East of Budapest) or calcareous sand (Kiskunság, near the village Fülöpháza) between October 2002 and July 2004. Newly emerged shoots (one individual per pot) were grown in the on-campus growth room of the Eötvös Loránd University under semicontrolled conditions: under variable moderate light (440-810 μmol photon m^{-2} s^{-1} in summer and 135-180 μmol photon m^{-2} s^{-1} in winter on clear days on average), with adequate water and nutrient supply.

Leaf stomatal regulation was studied on four C_4 species in April 2004, June or July 2004 or 2005. Among species there were two invasive (*Cynodon dactylon* and *Sorghum halepense*) and two non-expanding, native grass (*Bothriochloa ischaemum* /often locally dominant/ and *Chrysopogon gryllus*). The 2nd or 3rd fully developed leaf counted from the top was first incubated under 1300 µmol photon m^{-2} s^{-1} light intensity until the steady state gas exchange rate was achieved (photosynthetic light induction). Then light level was decreased to 270 µmol photon m^{-2} s^{-1} in one step, and after the new steady state was reached, it was returned to 1300 µmol photon m^{-2} s^{-1}. Leaf CO_2 and H_2O exchange rate was recorded throughout the measurement. Leaf morphology and anatomy in the two contrasting environments were investigated on the same four C_4 species and two native C_3 grasses: *Calamagrostis epigeios* (expanding) and *Bromus inermis* (a forest-steppe species, but an invasive alien in North-America). The 2nd fully expanded leaf from the top of the shoots developed in the growth room was sampled in October 2004. The following parameters were determined: length, width and area of the leaf blade, dry mass per unit leaf area (LMA, g m^{-2}) and its two components (thickness and bulk tissue density). The middle portion of the leaf blade was severed and intervenial distance, the proportional area of component tissues, and the thickness of mesophyll (for C_3 species only), epidermis and parenchymatous bundle sheath were measured on light microscopic photographs of the cross sections. These parameters were also determined on field-grown leaves sampled from the species' original, high-light (max. ca. 2000 µmol foton m^{-2} s^{-1}) loess forest-steppe habitats (Gödöllő Hills or for *S. halepense* from a degraded biotope in Budapest) in June 2005. For each variable, when two or more replicate measurements were performed on the same individual, the value averaged for the individual was considered as the smallest independent sample unit. For the germination experiment caryopses were collected in September 2002, and in July and September 2003. In January 2004, the effect of diurnal temperature fluctuation (30 ± 3 °C, 8 h and 21 ± 0.5 °C, 16 h for 6 days) on germination relative to constant 21 ± 0.5 °C (control) was tested within the same photosynthesis type on the species as follows: C_4 grasses: *E. indica* (invasive), *B. ischaemum*, *Ch. gryllus*; C_3 grasses: *C. epigeios*, *Festuca vaginata* (non-expanding). Seed germination was counted regularly, and the variables listed below were estimated from the data: duration of lag period (number of days elapsed from imbibition until the start of germination), germination rate (number of days elapsed from the start of germination until the germination of 50% of germinated seeds), final germination percentage.

In all three experiments, one-way ANOVA with subsequent Tukey's HSD post hoc tests, unpaired t-tests or paired t-tests (in the case of related variables) were applied for statistical analyses. When data did not meet the assumptions of normality and/or homoscedasticity, and in the case of lower sample size for *Ch. gryllus*, alternative non-parametric methods (Kruskal-

Wallis test with subsequent post hoc test, Mann-Whitney u-test, sign test) were used. For each statistical test, the significance level was $p < 0.05$.

In the second part of my work, leaf responses of three dominant species (*Cynodon dactylon, Festuca vaginata, Populus alba*) representing three plant functional types to night-time warming or rain exclusion simulating the projected regional climate change were studied in a field experiment. The study site has been set up in an open perennial sand grassland colonized by shrub-sized root suckers of *Populus alba* (Kiskunság National Park, near the village Fülöpháza), which is a special structural element of the Pannonian sand forest-steppe. The experiment was launched 8 years ago by the Institute of Ecology and Botany, HAS as part of a network established in different shrubland ecosystems at six countries along a European-scale (N-S) temperature and (NW-SE) precipitation gradient. Nine plots of 4 × 5 m size were laid out with two treatments (warming and drought) and a control, in three replicates each. The year-round passive nighttime warming increased daily minimum air temperature at 20 cm height by 1.2 °C on average between April and August, which corresponds to 0.7 °C rise in daily mean temperature for the same period. Drought treatment excluded 5-28% (20-145 mm) of the yearly precipitation from the plot during peak plant growth (in May and June).

Field measurements and subsequent laboratory work were repeated once in a month from May to August between 2003 and 2008. Total area, shape (length per maximum width ratio, in *P. alba* and *C. dactylon*), coarse structure (dry mass per area, thickness and bulk tissue density) and photochemical efficiency (at midday and dawn, using chlorophyll fluorescence induction method) were determined on young fully developed leaves.

In each statistical analysis, values averaged for plots as the smallest independent experimental units were used (in the case of one replicate per plot the single measured value). For each variable per species, repeated measures ANOVA was used to assess variance components: treatment as fixed between effect, and year and month as repeated measures (within) effects. In the case of significant effect, Tukey's HSD test was applied for post-hoc comparisons between means of treatments or sampling dates. When the assumptions of ANOVA were not met, Kruskal-Wallis test with subsequent post hoc test was conducted. In each case, differences were considered significant at $p < 0.05$ level. Then, for each plant response variable per species, a mixed model multiple regression analysis was applied using fixed environmental predictor variables and plot as a random categorical factor. These predictor variables reflected the effects of both the current weather (temperature and precipitation) and the experimental treatments. Due to the higher probability of Type I error associated with multiple comparisons, a $p < 0.01$ significance level was used in this analysis.

III. Results

<u>In the growth room experiments with grasses of different colonization capacity:</u>

1. *Leaf gas exchange*

a) Under low light, the group of the invasive *S. halepense* and *C. dactylon* achieved higher steady state intrinsic water use efficiency (PWUE, mmol CO_2 mol^{-1} H_2O) than the group of the non-invasive *Ch. gryllus* and *B. ischaemum*. This was due to the higher PWUE at low-, compared to high-light steady state conditions for the two invasive species, while PWUE did not differ between light conditions in *Ch. gryllus* and *B. ischaemum*.

b) The enhanced PWUE of *S. halepense* and *C. dactylon* in response to the abrupt drop in light intensity resulted from the greater reduction in stomatal conductance to water vapor (g_s, mmol H_2O m^{-2} s^{-1}) than in net photosynthetic rate (A, µmol CO_2 m^{-2} s^{-1}; i.e. $\Delta g_s > \Delta A$). In contrast, for the two non-invasive species Δg_s and ΔA were statistically similar.

c) In *S. halepense* the delay of stomatal closure behind the sudden decline of A resulted in a negligible net loss in PWUE ($cost_{PWUE}$ was negative) during the high-to-low light transition. In contrast, small positive values of $cost_{PWUE}$ were found for the other three grasses. These results indicate a highly efficient light-tracking behavior of the stomata for *S. halepense*.

d) When the light intensity was elevated again to 1300 µmol photon m^{-2} s^{-1}, the duration of both stomatal opening and photosynthetic induction (reaching 90% of the high-light steady state values in g_s and A respectively) were statistically similar for all species studied. This might be explained by the fact, that in high-light, periodically water limited grasslands and forest-steppes, water sparing may be of higher adaptive value than maximizing carbon gain.

e) Duration of stomatal opening was similar to that of photosynthetic induction in the non-invasive group, but was 50% longer in the invasive group. This indicates more efficient water use for the invasives following the increase in light intensity as well.

2. *Leaf morphology and structure in two contrasting environments*

a) Leaf mass per area (LMA) was lower in the growth room than in the field by 47% and 43% for the invasive C_4 *S. halepense* and *C. dactylon*, respectively, due mostly to thinner leaves developed under moderate light. In the non-invasive C_4 grasses however, such difference in LMA was smaller (25% for *B. ischaemum*) or not significant (for *Ch. gryllus*).

b) Variation in leaf morphology and anatomy was not consistently different between invasive and non-invasive C_4 species studied. Leaf area was greater in the growth room than in natural habitats for *S. halepense* and *B. ischaemum*, but did not change in *C. dactylon* and

Ch. gryllus. Leaf anatomical traits were statistically similar in the two environments for *Ch. gryllus*. Each of the other three C_4 grasses differed in two, but not the same anatomical variables.

c) Among grasses of high colonization potential, the C_3 native *C. epigeios* and *B. inermis* did not consistently exceed the two invasive C_4 species in the capacity of adjusting leaf morphology and structure to the environment. For both C_3 grasses, LMA in the growth room was about half of that measured for field-grown leaves. In leaf morphology and anatomy the responsiveness of the C_3 *B. inermis* and the C_4 *S. halepense* was similarly high, while that of the other two expanding species representing different photosynthetic pathway types, i.e. the C_3 *C. epigeios* and the C_4 *C. dactylon* was comparably moderate.

d) In particular, *B. inermis* exhibited remarkable variation in leaf shape and structure between the two contrasting conditions. This is consistent with the species' forest edge phytocoenological affinity in Hungary, and may also contribute to its successful invasion in temperate grasslands of North-America.

e) In both environments, mean intervenial distance was significantly or tended to be shorter for the C_4 grasses than for the two C_3 grasses, and among the C_4 types, this was greater for the NAD-ME *C. dactylon* than for the other three NADP-ME type C_4 species.

3. *Germination responses*

a) Germination percentage was higher under diurnal temperature fluctuation than at constant 21 ^{o}C for the expanding C_3 *C. epigeios* and the non-expanding C_4 *Ch. gryllus*, while did not differ for the other three species studied.

b) Alternating temperature changed the duration of lag period substantially – shortened by 8-34 days – relative to control for the invasive *E. indica* only, but resulted in a maximum germination of only 2%. Further germination of this species' seeds was initiated when temperature fluctuation was repeated with moisturized seeds for further 5 days since the day 23 of the experiment. This result confirms the experience of a pilot study indicating that a two- or three-week-long wet incubation prior to the exposure to the fluctuating temperature regime is required for *E. indica* to induce germination.

c) Alternating temperature had no significant effect on the germination rate of either species studied.

d) Under daily temperature fluctuation, species belonging to the same photosynthesis type (C_3 or C_4) did not differ significantly in germination rate and percentage.

In the six-year measurement of a climate simulation field experiment:

1. *Analyzing the effect of variance components* on the three species representing dominant plant functional groups of semiarid sand forest-steppe revealed the results as follows.

a) The response of leaf morphology, coarse structure and photochemical activity was more marked to fluctuations of weather between months and years, than to the applied experimental warming or drought treatments simulating predicted gradual changes in climatic means.

b) In most cases, the effects of experimental treatments were significant in a limited period only (during or subsequent to rain exclusion). An exception to this was the leaf shape of *P. alba*, which proved to be consistently more elongated in the warming plots than in the control and drought treatment plots almost in each sampling date.

2. *Multiple regression analyses* with environmental variables including the effects of both experimental treatments and background weather fluctuations resulted in the followings.

a) The C_3 bunchgrass *F. vaginata* exhibited pronounced and chronic reduction in photochemical efficiency with increasing duration of (often irregular) summer drought. As opposed to this grass, the two clonal species, i.e. the C_4 grass *C. dactylon* and the woody *P. alba* root suckers showed moderate decline with warmer summers.

b) Photochemical activity of *P. alba* was slightly enhanced by elevated temperature in spring, but diminished in summer. With warmer conditions, photochemical performance decreased in *F. vaginata* (particularly in spring), while hardly changed in *C. dactylon*.

c) In spring, leaf size and leaf mass per area increased with temperature rise during leaf development, but higher frequency of rainless days reduced leaf area in each species. In these leaf traits *P. alba* displayed the most prominent response among species. For instance, a 100 mm precipitation deficit in winter and spring reduced the area of early summer leaves to about (4 cm^2) half of that developed subsequent to average amount of rainfall during the same period. In spring, leaf length per width ratio also showed positive relationship with temperature in *P. alba*, and particularly in *C. dactylon*.

IV. Conclusions

1. In the expansion of invasive C_4 perennial grasses in semiarid habitats with spatially or temporally heterogeneous light regime − at the expense of C_4 non-invasives − might play an important role that

a) invasive C_4 grasses exhibit more efficient regulation of stomatal closure with abrupt drop in light intensity than their non-invasive C_4 relatives. This enables invasives to use water more sparingly in energetically less favourable shaded periods;

b) invasive C_4 grasses possess greater variation in leaf coarse structure in contrasting environments than non-invasive ones.

2. In contrast, rapid photosynthetic induction upon increase in light intensity, marked variation in leaf morphology and anatomy in contrasting conditions, and high germination percentage or rate under diurnal temperature fluctuation may not or less contribute to successful invasion of perennial C_4 grasses in semiarid grasslands and forest-steppes.

3. Among plants of high capacity to spread, C_4 grasses are not consistently less responsive to the environment than C_3 ones in leaf morphology and structure despite constraints associated with C_4 leaf anatomy (Sage & McKown 2006).

4. Nevertheless, a greater number of species should be involved in these studies to draw more general conclusions on the role of explored ecophysiological traits in the spreading success of grasses in semiarid temperate habitats with heterogeneous light climate.

5. Gradually warmer springs are expected to result in producing larger leaves and acceleration of phenology (e.g. earlier unfolding of total leaf canopy) in the dominant species representing three different plant functional types (*C. dactylon*, *F. vaginata*, *P. alba* root suckers) of the open sand grassland and juniper-poplar woodland vegetation mosaic. However, these changes might be constrained by extreme weather events, such as unusual drought or frosts.

6. Climate extremities, particularly the more frequent and prolonged drought events forecasted on climate change will probably reduce carbon assimilation capacity − thus growth and abundance − most markedly for cold-tolerant, shallow-rooted C_3 bunchgrasses adapted to midsummer drought (*F. vaginata* in this study). Carbon metabolism will relatively less constrained in thermophilous, clonally integrated species with deeper roots (e.g. the C_4 grass *C. dactylon* and the shrub-sized root suckers of woody *P. alba*). Therefore, the abundance of

these species is expected to less diminish in the semiarid temperate sand forest-steppe with projected increase in temperature and aridity.

7. High susceptibility of *F. vaginata* to the projected climate change − especially to the increasing frequency of drought and heat waves − is suggested to increase variability in phytomass production of open perennial sand grasslands colonized by shrub-sized root suckers of white poplar. This might be mitigated (buffered) by smaller fluctuations in the production of *P. alba* and *C. dactylon*.

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