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MODELLING PLANT DISTRIBUTION RANGES USING CLIMATE DATA[*]

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Климатические модели ареалов распространения *Geranium robertianum L.* и *Acer negundo L.* были созданы на основе изучения первичных ареалов этих растений и данных по климату: средних месячных температур и осадков. На первом этапе были вычислены частоты распространения частей ареалов и буферных зон вдоль климатических градиентов и построены частотные диаграммы этих признаков. На полученных диаграммах наблюдаются крутые и постепенные очертания границ климатических ареалов видов. Обсуждаются возможности использования этих закономерностей для создания климатических моделей ареалов растений. Показано, что буферные зоны имеют важность для оценки границ климатических ареалов, в тех случаях когда ареал ограничен не экологическими, а географическими факторами (границы континентов, наличие морей). В созданной климатической модели ареала *G. robertianum* наблюдалось значительное соответствие его первичной и вторичной частей. Таким образом, климатическое моделирование значительно повышает понимание возможностей растения к географическому распространению. Также климатическое моделирование было выполнено по отношению к ареалу *A. negundo*, растения из Северной Америки, чья вторичная часть ареала в Евразии исследована слабо. Выполненное моделирование показало, что этот вид уже практически занял весь потенциальный климатический ареал. При климатическом моделировании ареала следует, однако, понимать, что степень благоприятности климата на полном ареале каждого вида выступает только фактором, который определяет потенциальные способности растения к распространению.

Introduction

The importance of climate on plant distribution was early detected in biogeographical research (Schouw, 1823) and has, apparently, been widely accepted (e. g. Box et al., 1993,

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Jäger, 1990, Quinn et al., 1994, Woodward, 1987). With the advent of detailed global plant distribution maps (e. g. Meusel et al., 1965, 1978, Meusel & Jäger, 1992, Hultén & Fries, 1986), climate maps from all parts of the world (Agroklimaticeskij atlas mira, 1972, UNESCO, 1970, 1975, 1980, the CLIMATE database, W. Cramer, pers. comm.) and powerful computers many aspects of bioegography could be addressed.

- Studies of distribution boundaries to reveal climatic factors limiting a plants range, understanding of distribution ranges (e. g. Jäger, 1988, 1990, 1995, Hoffmann, 1998, 1999a, b).
- Prediction of suitable areas for growing exotic tree species in forestry (e. g. Booth, 1991, Booth & Jones, 1998).
- Prediction of potential areas for invasive plant species (e. g. Panetta & Mitchell, 1991, Beerling et al., 1995, Jäger, 1995, Hoffmann, 2001, 2002, Welk et al., 2002).
- Prediction of the location and shift of plant ranges in climate change scenarios (e. g. Huntley et al., 1995).
- Definition of possible locations of species with only roughly known distribution ranges (Skov & Borchsenius, 1997, Skov, 2000).
- Analysis of the climatic differentiation of related species and possible climatic forces underlying evolutionary processes (Hoffmann, 1998, 1999a, b, 2000, Hoffmann et al., 2002).

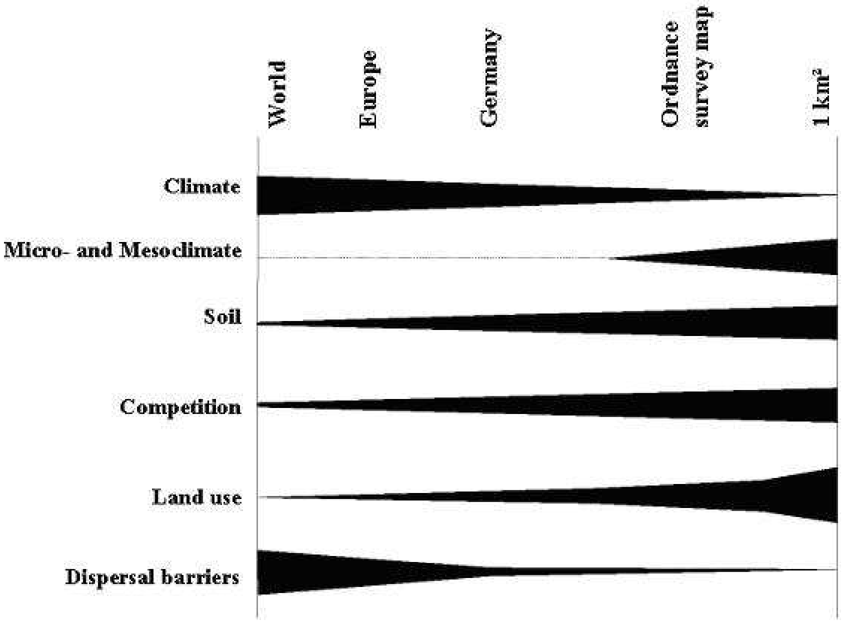

Fig. 1. Scheme of the importance of environmental factors on plant distribution at different scales (according to Jäger, 1992, modified). The relative size of the bar represents the importance. For example, at the world scale climate and dispersal barriers are the most important range limiting factors.

- Definition of possible ancestral climatic conditions of taxa (e. g. genera) from that sister species have expanded during evolutionary processes and have occupied climatically different areas; application of these data to phylogenetic studies (Hoffmann, 1999b, Hoffmann et al., 2002).

Assessing reasons of distribution boundaries it is imperative to consider the scale or level on that the study is performed. The aim of this contribution is to present one of the ecogeographical modelling approaches of plant distribution ranges that focuses on the global level. At this level climate is the most important range limiting factor; while at the local scale other factors become more important (Fig. 1). It could be argued that climate is not the only main factor that limits the distribution of ranges at this level. Soil and biological factors, particularly competition, might have also considerable influences. At the local or regional scale this is undoubtedly the case. However, soil develops from particular bedrocks in dependence of climate and competitors or other biological factors are in the same way influenced by climate as the species under consideration. The distribution range of a species can, therefore, be considered to be a function of the endogenous ecological constitution of a species and the climate.

The methods are discussed in detail at the example of *Geranium robertianum L.* and, thereafter, applied to the range of *Acer negundo L.*, a neophytic species in Western Eurasia originating in North America. The study was supported by RFBR, N 03-04-49746.

Geranium robertianum and *Acer negundo*

Geranium robertianum L. is a short-lived annual or biennial plant that occurs mostly in different types of broad-leaved forests. It prefers rather moist and nutrient-rich conditions. The plant is native to Western Eurasia. The status of the East American occurrences is still debated. Many authors of local north-eastern American floras treat the species to be indigenous (e. g. Roland & Smith, 1969, Bertin, 2001), whereas other authors consider the species even in that range part to be introduced from Europe (e. g. Aedo, 2000). Records from Western North America, New Zealand, Southeast Asia, and Southern South America are correspondingly considered to be non-native occurrences.

Acer negundo L. grows as a small tree that has been introduced in Europe in 1688 from North America. It is mostly planted in parks and prefers moist or mesic soil conditions. Especially in riverine forests it shows a strong tendency to escape from cultivation and to spread in Europe. In western Siberia the species frequently planted in settlements and as wind fences along fields. From those stands it seems to spread into surrounding forest vegetation that is edaphically not too dry.

Distribution maps

Reliable and detailed general distribution maps are the basis of many biogeographical analyses. It is not practical to derive a global map from herbarium specimen except extensive monographic work is associated with the map. Therefore, general distribution maps are compiled from a wide array of sources: dot and grid maps, floras covering larger or smaller areas, distributional data taken from monographic or ecological studies are used (for review of different kinds of distribution maps, see e. g. Walter & Straka, 1970, Kornas & Medwecka-Kornas, 1986). The compilation of a reliable distribution map of a widespread circumpolar distributed species requires consultation of about 100–200 sources; in critical cases more than 250 sources are necessary. It is obvious that these data are rather heterogeneous, ranging from the pure indication of presence or absence to detailed data concerning the distribution and ecology of the species in several parts of the area under consideration. Another problem, especially when dealing with invasive species, is the different time in that a particular floristic work has been published and the policies followed during the preparation. Older work to be consulted, e. g. from the first decades of the 20th century, sometimes do not consider species that are cultivated but show tendencies to escape from cultivation. Sometimes, the particular species has not yet occupied the area during the phase of preparation of the book but spreads later. This introduces some uncertainties to be considered in the discussions of the maps. Despite the heterogeneity of the data to be included in a distribution map they are very useful for finding distributional gaps, outposts, exclaves, coherent ranges, and sometimes centres of present distribution.

The distribution *Geranium robertianum* has been obtained from Meusel et al. (1978) and was revised to include recently published literature (Fig. 2A). The range of *Acer negundo* was new compiled (Fig. 3A).

Climate data

Climate data, i. e. monthly means of temperature and precipitation were kindly provided by W. Cramer (CLIMATE database version 2.1, Potsdam Institute of Climate Impact Research, Germany) and were transferred to the circumpolar map. Basis for the climate data covering the worlds terrestrial surface are long-term means from all available weather stations. The continuous climatic surface with a 0.5-degree longitude/latitude resolution has been interpolated using a three-dimensional surface, i. e. mountain systems are considered (Leemans & Cramer, 1991). Mountains remain, however, always a problem for modelling approaches due to the fact that climatic conditions in parts of the mountain system, e. g. mountain valleys, are hardly resolved in a 0.5-degree resolution. For example, if a species occurs at the relatively moist and warm bottoms of valleys and the grid is interpolated to higher altitudes mismatches between observed and modelled range are to be expected.

Monthly means are used directly because they have a great correlation to the monthly extremes (Langlet, 1935). Some authors use derived climate data, as for example growing degree days or other threshold values for modelling (Huntley et al. 1995, Bartlein et al., 1986, Beerling et al., 1995) but these data are derived from the monthly climatic means of temperature and precipitation and may blur monthly peculiarities that may be important for plants.

Computational methods

Most of the calculations and modelling steps are performed using the program Arc/Info® (ESRI 1992). Some intermediate steps, e. g. the creation of the frequency diagrams were made in table calculation programs (Microsoft Excel).

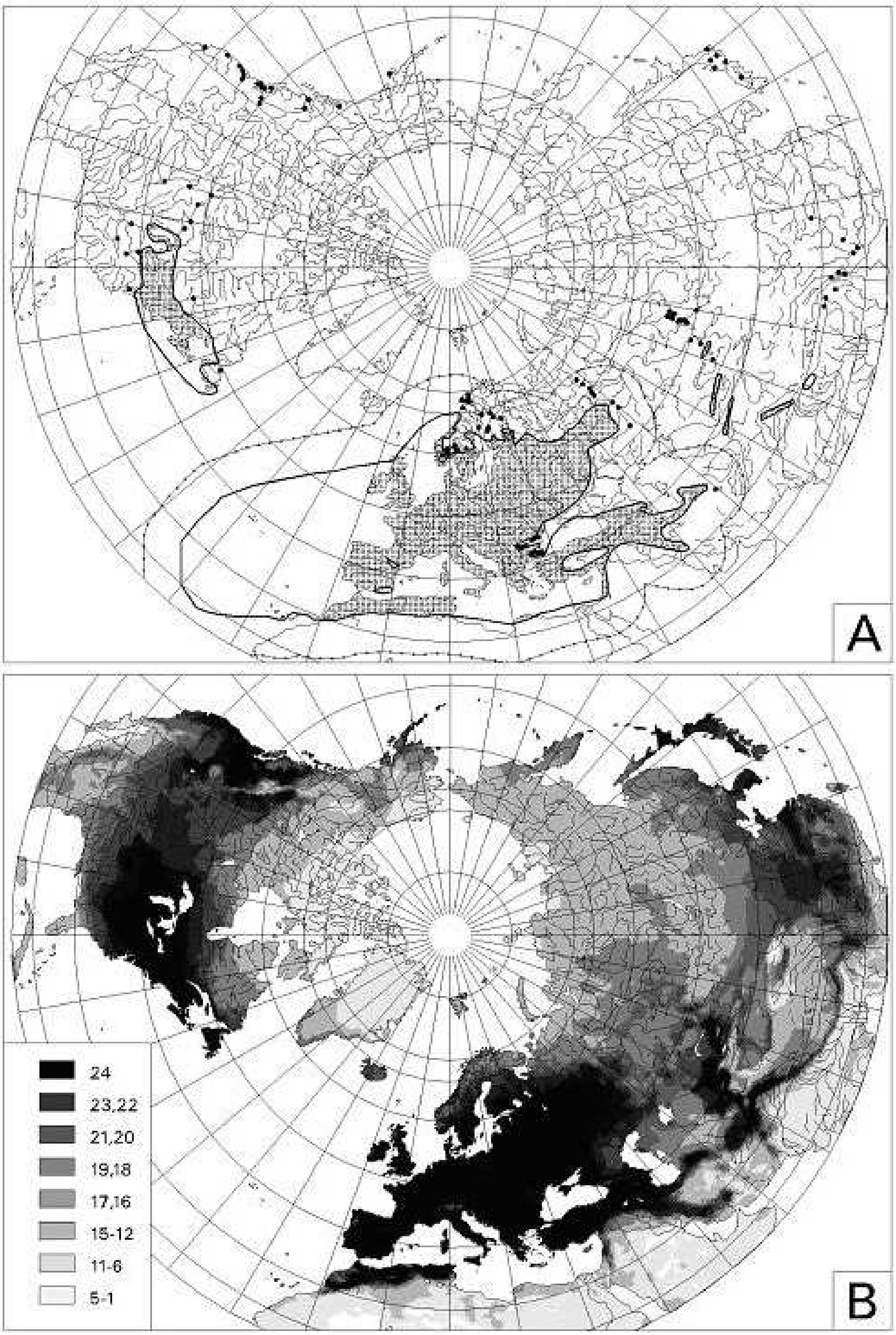

Fig. 2. Range, buffer, and climatically modelled range of *Geranium robertianum.* A. Distribution range of *G. robertianum.* Open circles indicate geographically imprecise indications of occurrence. The area within the knotted line is buffer area used for interpretation of the frequency diagrams. B. Climatically modelled range. The legend indicates the number of suitable monthly values for growth of the species. In the black area all 24 monthly climatic values of temperature and precipitation support the occurrence of *G. robertianum*

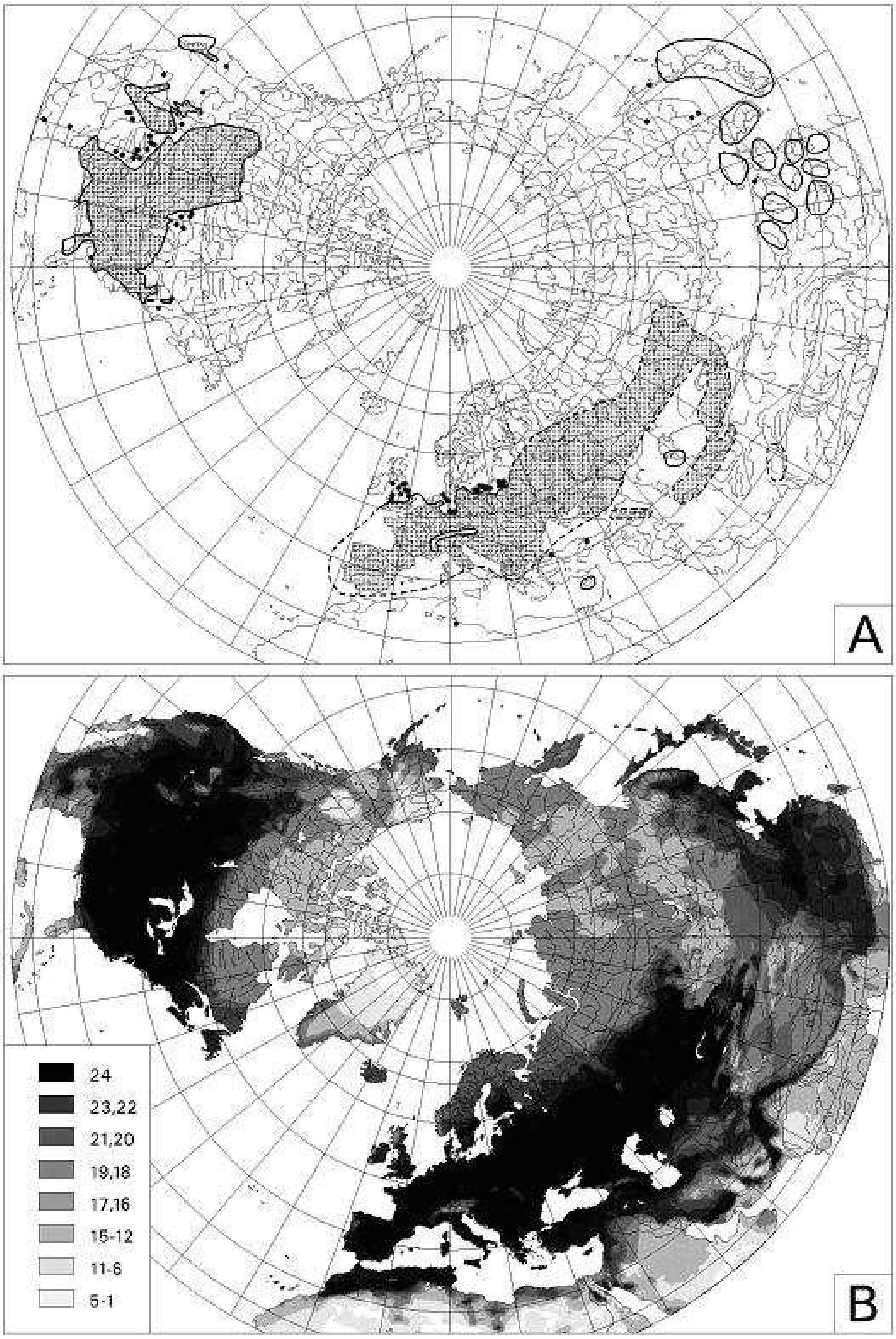

Fig. 3. Range, buffer, and climatically modelled range of *Acer negundo*. A. Distribution range of *A. negundo*. Ordinary lines indicate well-known distribution boundaries; dashed lines not well known boundaries. Open circles indicate geographically imprecise indications of occurrence, in East Asia they refer mostly to plants in cultivation. Within the shaded area the many indications point to the fact that the plants escape there from cultivation. B. Climatically modelled range. The legend indicates the number of suitable monthly values for growth of the species. In the black area all 24 monthly climatic values of temperature and precipitation support the occurrence of *A. negundo*. Note that in North-eastern North America the frost-free period seems to limit the range, which is not well reflected in the monthly mean temperatures

Frequency diagrams (FD)

The distribution map has been digitised and, subsequently, transformed into a grid with the same resolution as the climate grids. In the case of *Geranium robertianum* the undoubtedly western Eurasian native range has been used for the calculations. Similarly, the North American range of *Acer negundo* has been used. The grid of the plants distribution range has been clipped with the 24 grids of monthly temperature and precipitation, i.e. all grid cells not covered by grid cells of the distribution range are omitted from the initial frequency calculation. The frequency distribution of the range and the buffer along the monthly climatic gradients were calculated using intervals of 0.1 K for temperature and 1 mm for precipitation, respectively. Results of this calculation are presented as frequency diagrams (FD) that show the numbers of occupied grid cells along the monthly climatic gradient.

A biologically speaking, senseless buffer area, equidistantly arranged around the plants' range, was also introduced and calculated in the analysis (BUFFER command in Arc/Info, distance to the distribution range: 25 coverage units). The aim of this buffer area is to identify climatic intervals in the frequency diagrams where geography (e. g. coast lines) limits a distribution range rather than climate. This occurs if all grid cells in a particular climatic dimension are occupied by the species.

Climatic modelling of the range

Climatic intervals for the monthly temperature and precipitation were graphically obtained from the frequency diagrams. Important points are those between the steep and the flat part of the graphs. All grid cells within this interval were selected from each original climate grid and assigned the value "1". Grid cells outside the interval were given the value "0". Then, the obtained grids were added. Because of the graphically derived climatic intervals, optimisations were necessary and were performed by varying the intervals. This optimisation was scrutinized applying the Jaccard-index (I_j) to the modelled and the archeophytic range: $I_j = c/(a + b - c)$; (a ... number of grid cells occupied by the plant, b ... number of grid cells of the modelled archeophytic range, c ... number of common grid cells occupied by plant and model).

Results

Frequency diagrams

The diagrams in Fig. 4 show some of the frequency distributions of *Geranium robertianum* occurrences along the climatic gradients. Graphs in the frequency diagrams are different for each climatic factor, month and distribution range. This results from the varying orientation of the monthly climatic isolines and different range sizes and shapes. Identical graphs in the frequency diagrams could only be observed if ranges are identical. Despite this variation in the graphs, some sort of recurrent pattern may be observed: graphs with a single peak (FD of precipitation) or multiple peaks (April temperature), and graphs with steep and flat slopes, e. g. January temperature and October temperature, respectively.

Climatic model of the range of *Geranium robertianum*

Single monthly climatic intervals are not sufficient for modelling the whole range of *G. robertianum.* This may be inferred from Fig. 5 showing the distribution of suitable areas for single monthly intervals. Considering each of the 24 maps for the monthly values the regions become evident where particular climatic factors are range-limiting. For example, low winter (January) temperatures seem to be unfavourable for the species and limit the range towards

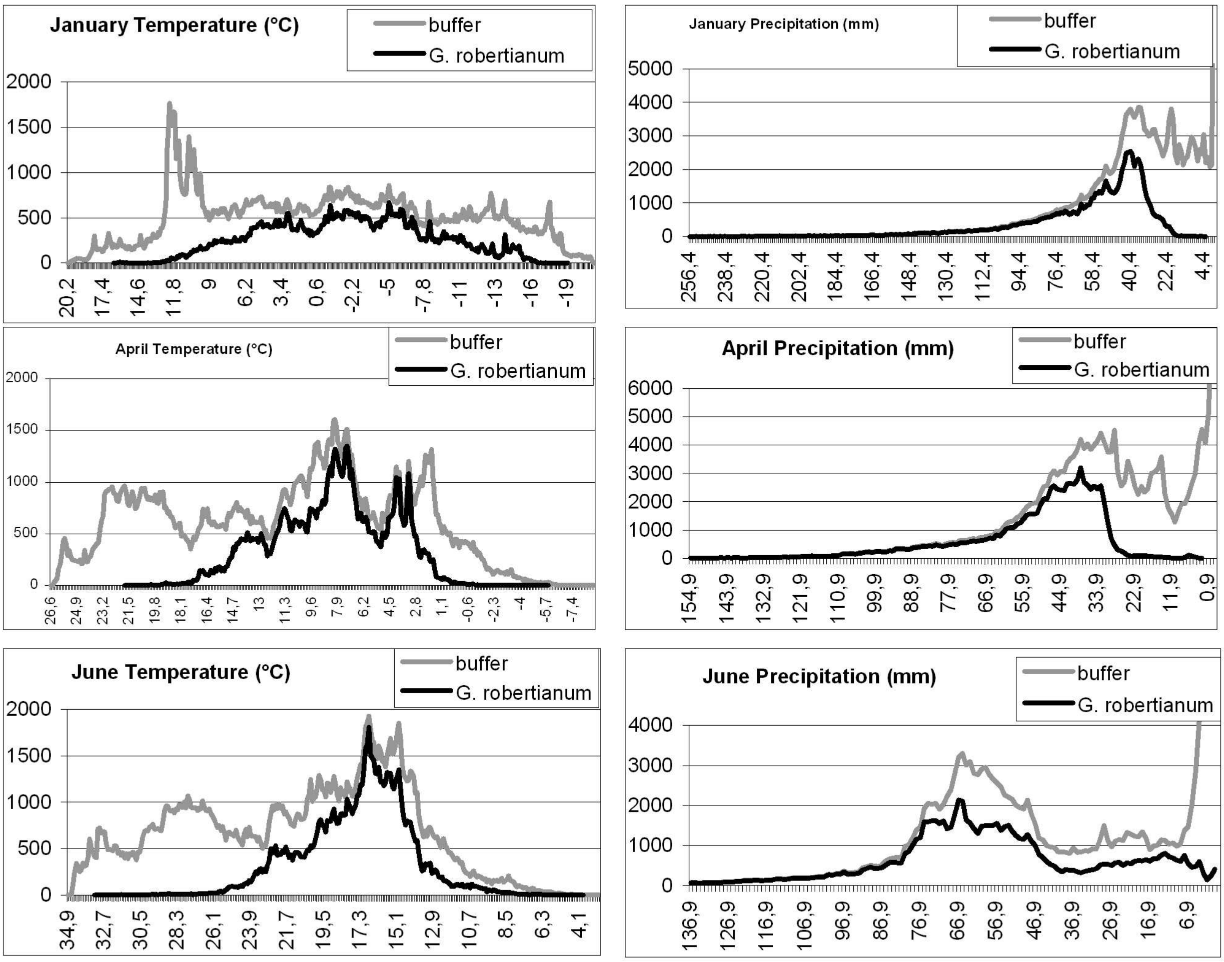

Fig. 4. Frequency diagrams of *Geranium robertianum* (black line) and its buffer area (grey line). The x-axes show the climatic range of the respective mean monthly temperature and precipitation within which *G. robertianum* occurs. The y-axes show the number of grid cells occupied by the species. For maximum resolution of the data, the x-axes are not aligned. The increase of the buffer graphs line at low amounts of precipitation and high temperatures results from areas of the Sahara through which the area has been drawn. Not all grid cells at low amounts of precipitation (Sahara) are shown for the buffer area

Central Siberia (Fig. 5A). Continental conditions, i. e. a low amount of winter precipitation and the resulting thin snow cover may be a climatic factor, which does not allow the plants to grow in Central Asia (Fig. 5B). April temperatures (Fig. 5C) are apparently limiting in Northern Europe, and a low amount of April precipitation is limiting in northwestern Middle Asia (Fig. 5D). The overlay of the 24 maps results in the climatic model of *G. robertianum*' distribution range (Fig. 2B). The climatically suitable area is the black area. Around the area of 24 values the number of climatically supportive monthly values declines, more or less, rapidly. Especially towards the Saharo-Sindian region the supportive months decline rapidly.

The Jaccard-index for the model is 72 % calculated for the West Eurasian range (archeophytic range 90.825 grid cells, climatic model 87.092 grid cells, common grid cells 74.310). The Jaccard-index for the total northern hemispheric range is 63 % and reflects also the North American distribution range satisfactorily.

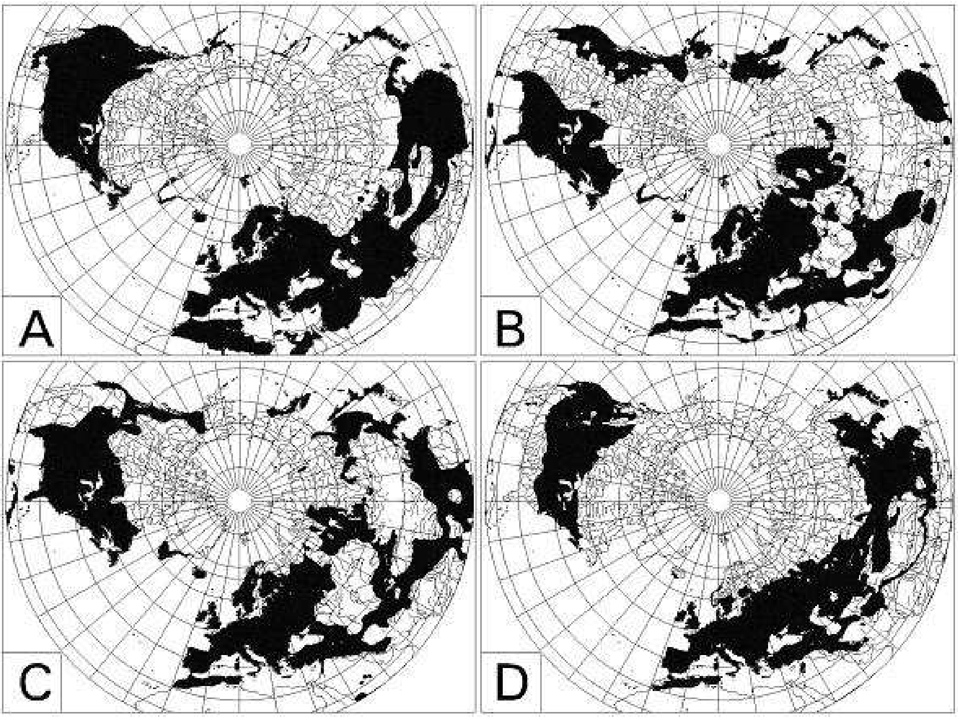

Fig. 5. Distribution of suitable areas for four climatic intervals. The grey areas comprise all grid cells that are within the climatic interval of the plants. A. January temperature (−15.2 to 12 °C), B. January precipitation (21.5 to 200 mm), C. April temperature (1.7 to 15.5 °C), D. April precipitation (27 to 140 mm)

Discussion

Frequency diagrams

The application of a buffer area (Fig. 2A) proved to be of special importance when assessing the characteristics of the frequency distribution of occurrences and the range boundaries. Congruent graphs in the frequency diagrams of buffer and species indicate that all available areas (grid cells) are occupied by the plant. Without this buffer area it may be supposed that the range of *G. robertianum* is limited due to high amounts of precipitation in summer (e. g. June) or autumn (e. g. October, see Fig. 4) because of the steep inclination of the graphs (for further discussion of the inclinations significance, see below). Obviously, the plants' range is, in these dimensions, not limited by climatic factors but rather by geography. Had in those dimensions more areas been available, the plant could occupy these, too. On the diagrams other side of the above-mentioned months, certain distances between the graphs of plant range and buffer indicate that more areas are available than are occupied by the species.

The distribution of plants along climatic gradients and the significance of the climatic values may be directly inferred from the frequency diagrams (Fig. 4). Despite large differences between the shapes of the particular graphs, they show traits frequently to be observed. The peak(s) of the graphs may considered to be the climatic optimum of the species in this particular climatic dimension. A graph with two peaks of species and buffer range (e. g. April temperature) indicates that a strong climatic gradient exists within this interval (from about 3 to 6 °C), where climate changes rapidly across rather small areas. This compares to tightly spaced climatic isolines and, thus, a small number of available grid cells. Here the graph of the species and the buffer may be nearly congruent, indicating occupation of nearly all available grid cells by the plant. However, this does not indicate a limitation of the plants' general distribution range because these parts of the graph are, more or less, central to the climatic optimum and not to the climatic limits.

The most important characteristic for discussions of plant distributions may be the inclination of the graphs. Steep graphs indicate that the species' occurrences increase/decrease rapidly within a short climatic interval (sharp climatic range boundary). The plants' range is correlatively limited by this climatic factor, because climatic conditions and the ecological/ climatic constitution of the species hardly supported occurrences outside the interval. Apparently, the species are sensitive to this factor within the above-mentioned interval of steep inclination of the graph. A sharply defined range boundary might also occur if a broad range narrows suddenly into a geographically restricted area, e. g. peninsulas like Florida or the Apennine peninsula, and the climatic isolines are evenly spaced over the whole area. This case can be assessed either from the buffer area, which should then show a congruent graph to with the species' range, or in geographically more complicated areas when modelling the range. In the latter case, the limit of the climatic interval used for modelling would then be at a considerable distance from the steep part of the graph, while in other sharply defined range boundaries the intervals' value is close to the steep part.

Massive range extensions of the plants in its present evolutionary state in areas outside the sharply defined interval of the climatic factor — are seemingly not to be expected. The ecological factor competition is still to be discussed in this context because it might be the reason for sharp climatic range boundaries, too. Competition and other biological interactions affect plants everywhere, and are intrinsic to the ecological and climatic constitution or amplitude of the species, which is assessed in this study. Competitors, predators, pollinators, etc. are themselves also dependent on the prevailing climatic conditions. The explicit inclusion of these factors distinguishes the ecological constitution from the plants' physiological constitution.

In contrast to the steep slopes of the graphs are the flat ones. Along a rather wide climatic range the occurrences of the species decline/increase gradually (gradual climatic range boundaries). Apparently, these monthly climatic values characterised in such a way may be of secondary importance for the range boundaries, or they may interfere with other factors. This interference becomes evident in a theoretical example. Assuming all factors, except this particular one, to be optimal for the growth of the species over the whole range, then a steep climatic boundary might be observed in this particular dimension at the plants' ecological limit. Due to this factors secondary importance or interference in the combine of all climatic factors it may currently be observed as a gradual climatic range boundary, shaped by other climatic factors. This does not rule out the possibility that at the far end of the flat slope and, thus, in small areas this factor becomes truly range limiting. This case may hardly be inferred from the frequency diagrams.

Climatic model of the range of *Geranium robertianum*

The climatic model of the distribution range of *G. robertianum* describes both the Eurasian and the North American ranges of *G. robertianum.* This may corroborate the assumption that climate, on a global scale, is indeed the range-limiting factor for *G. robertianum.* The congruence of the model and the range observed is limited especially in mountainous regions and in supposed relic areas. The reasons for this misfit are differences between the height of the climate grids for which the values have been interpolated, and the altitudinal distribution of the plant. This is to be observed especially in the mountains of Northern Africa and the southwestern Asia. Optimisations to include these regions would result in a considerable lowering of the Jaccard-index' value.

The high congruency of modelled range and observed range in the floristically well-studied Eastern North America corroborates the models predictive power. Many, apparently ephemeral occurrences in East Asia indicate that the species has been dispersed into these regions but they have, from a climatic point of view, low chances of survival, establishment and spread. The congruency of modelled and observed range, points to the importance of considering the whole archeophytic or natural range, and, thus, all ecotypes for defining suitable areas of the plant on other continents. Basic to this assumption is the supposition that the natural range consists of the greatest variability of ecotypes from which a stochastic sample may be transported accidentally or deliberately to other parts of the world. The neophytic range may, therefore, be smaller than the archeophytic range. In the case of *G. robertianum* the indigenous status of the Eastern North American occurrences is still debated. The climate range model indicates that new and old world ranges are very similarly limited but cannot decide about the reasons of this disjunction.

Close to the limit of the climatically suitable area (all 24 monthly values) isolines of 23, 22, etc. supportive months are to be observed. Apparently, at least one climatic factor is actually range limiting but is closely accompanied by others. From the modelled range (Fig. 2B), it is not possible to infer which monthly value becomes limiting in a particular area. However, this can be assessed using the areas suitable for each monthly interval (e. g. Fig. 5). The addition or overlay of the monthly interval maps results in a sequential cut-off of climatically unsuitable areas. For example, the January temperature in the northern Sahara might be favourable for growth of *G. robertianum*, but the January precipitation and the April temperature do not support occurrences south of the Sahara Atlas. Taking climatic parameters, which are derived rather directly from temperature and precipitation, for example growing degree-days, humidity parameters, or the ratio of actual to potential evapotranspiration similar pictures may emerge.

In a first approximation the number of supportive months may be considered a measure of the probability of the plants' occurrence. However, the modelling of the range in the form presented here is still rather static because only intervals for each month have been applied. Information on strong or gradual climatic range boundaries and their spatial occurrences in the range, are not considered in this interval. Consideration of climatic model, frequency diagrams and the monthly maps of the suitable climatic interval can circumvent this weakness rather easily. If we apply this to *G. robertianum*' range it emerges that strong climatic range boundaries are to be observed at many range limits, e. g. in Middle Asia (precipitation in spring), Central North America (precipitation from autumn to spring), Siberia (temperatures from autumn to spring), and North Africa (precipitation from autumn to spring). Figure 6 indicates the climatic factors limiting the range.

Does the climatic model reflect characteristics of the life pattern of the species?

Some studies are available that deal with the population biology of *Geranium robertianum* (e. g. Baker, 1956, Falinska & Piroznikov, 1983, Bertin, 2001). Particularly interesting for this modelling approach are the observations by Bertin (2001). He studied the plants over a period of nine years in Massachusetts (USA) and compared the population biology data with the prevailing weather conditions. Main factors that influence the survival are the precipitation during the summer, and temperature and snow depth during the winter. The

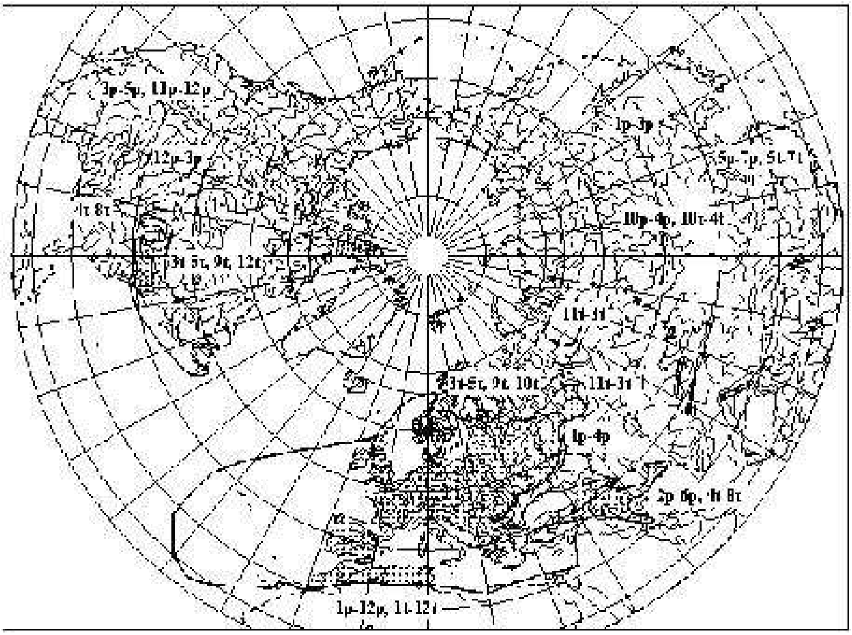

Fig. 6. Distribution range of *Geranium robertianum* and main monthly values that limit the range at the particular distribution boundary. The number indicates the month, p precipitation, and t temperature. For example, '11t-3t' means that the temperatures between November and March do not support the occurrence of the species in that area

latter may be related to the amount of precipitation during the winter. Low amounts of precipitation during summer reduce the survival of the plants considerable, especially those plants that have germinated that spring. Low amounts of summer precipitation are a main range-limiting factor at the southern Eurasian distribution boundary. Furthermore, low winter temperature, particularly in combination with a little snow cover reduces survival of the plants during that season. These climatic factors are also apparent range limiting towards Central Siberia and Central Asia.

Bertin's (2001) study revealed local climatic factors that reduces the survival of the plants, but does not lead to extinction of the species at this place. To the margins of the distribution range the environmental conditions become more and more unfavourable up to a point where the range margins starts to oscillate in dependence of short-termed climatic and/or weather conditions (e. g. Kullman, 1979, 1991, 1993, Villalba & Veblen, 1997).

Acer negundo — Application of the modelling technology to a species with incompletely known synanthropic range

Most of the worked examples of modelling neophytic ranges focus on species with well-known indigenous and neophytic ranges, because this offers opportunities for model development and verification of the methods. This section focuses on a more critical example. The rather well known and mapped North American native range (Little, 1971) of *Acer negundo* can be modelled rather satisfactorily. The rather low Jaccard-index of 57 % can be explained by the occurrence of the plants along rivers in the mountainous Western and Southern North America. The apparent mismatches in the north-eastern natural range results apparently from a short frost-free period of about 90 days (see Agroklimaticeskij atlas mira, 1972) that is not reflected in the monthly means of temperature. This may be a result of the Hudson and James Bays influences and is reflected in many tree species ranges. Complementary ranges to the North have boreal species, for example, *Larix lariciana* (Du Roi) K. Koch and *Picea mariana* (Mill.) B.S.P., while a similar ranges as *A. negundo* has *Fraxinus pennsylvanica* Marsh. (maps in Little, 1971). For the Eurasian range this very short frost-free period has apparently no importance because other thermal factors that limit the range in continental North America to the north are more important.

The Jaccard-index of the whole northern hemispheric distribution range is 60 %. The model reflects the still roughly known actual distribution in Eurasia and predicts small additional neophytic range parts in Turkey and Kazakhstan. Taking the model it appears that the potential neophytic distribution range of *A. negundo* is filled and further range expansions are probably not to be expected.

Other important factors than climate that determine possible invasive behaviour of plants

A suitable climate is certainly a very important prerequisite for successful establishment and spread of plants. However, climate is only one factor determining the invasive potential of species, which may interfere with biological characteristics of the plants. Many of these biological characteristics of plants that facilitate invasiveness have been determined, for example short-lived life pattern, short juvenile phase, vegetative reproduction, long seed dormancy, phenotypic plasticity (traits listed by Baker, 1965 and Jäger, 1988, range size by Rejmánek, 1995). Böcker et al. (1995) realized that a combination of factors is necessary for successful invasion of new areas. The traits, which promote synanthropic behaviour, however, are to be found in varying combinations that may complicate predictions (Jäger, 1977).

Prospects

Some climatic distribution models have presented here and in the literature. In this study optimisation of the model have been performed visually and with the aid of the Jaccard index. However, rigorous statistical methods and optimisation procedures have not been implemented in this approach that may decide about the reliability of the model. Having these methods available a modelling approach on many plant ranges will be possible. This may reveal the potential for generalisation of the method.

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