Biological Invasions **4:** 211–222, 2002.

Plant invasion patches – reconstructing pattern and process by means of herb-chronology

Hansjörg Dietz
Geobotanical Institute ETH, Zurichbergstrasse 38, CH-8044 Zurich, Switzerland
(e-mail: dietz@geobot.umnw.ethz.ch; fax: +41-1-6321215)

Received 2 January 2002; accepted in revised form 11 June 2002

Key words: annual rings, age-determination, age distribution, dispersal, herbaceous perennials, herb-chronology, invasive plants, spatio-temporal invasion pattern

Abstract

An understanding of the patterns of spread of invasive plant species requires analysis of the major dispersal mechanisms and of the patch structure of suitable habitats, both of which may be scale-dependent. On a larger scale, information from herbarium or literature records has proved useful for the reconstruction of past spread of invasive plants. The objective of this study is to investigate population development of invasive forbs at the scale of a site or stand (the population scale) by using herb-chronology. The feasibility of this approach has been largely disregarded until now because of the perceived difficulties in determining the age of perennial herbs. However, recent findings suggest that most of the dicotyledonous perennial herbs in the seasonal climates develop annual rings in the roots or subterraneous stems and thus demonstrate a high potential of the method in studies on plant invasions that went almost unnoticed. The spatial position and age (by means of analysis of annual rings) of individual plants were determined in invasion patches of five species of perennial forbs in Germany and in the USA. The data thus obtained revealed different spatio-temporal patterns of population development that are consistent with distinct models of (local) plant spread, including diffuse invasion and front-like invasion patterns, and thus suggest different processes at work in the course of invasion. The results suggest that analysis of spatial age structures is useful (i) to estimate rates of patch expansion, (ii) to distinguish between dispersal- and microsite-limited population development, (iii) to evaluate how different site conditions affect population development, and (iv) to help understand metapopulation dynamics.

Introduction

How do invasive plants spread? Efforts to find answers to this important question are confronted with at least three major problems. First, the processes underlying plant spread and the distribution patterns they produce may be strongly scale-dependent (Levin 1992; Collingham et al. 2000; Wadsworth et al. 2000). At the continental scale, the locations of centres of international trade, e.g. ports, may largely determine the (initial) distribution of introduced species (e.g. Sauer 1988; OTA 1993) and may thus influence the pattern of spread. At a regional scale, the pattern of spread, i.e. the colonization of new sites, is more dependent on the spatio-temporal availability of suitable habitats and on mechanisms for intermediate- and long-distance dispersal (Cousens and Mortimer 1995; Parendes and Jones 2000). At the population scale (the scale of a single stand or site), population expansion may depend on yet other, within-site, factors (e.g. Bergelson et al. 1993; Cousens and Mortimer 1995).

A second major problem is to determine which of a variety of possible factors have the greatest influence on the pattern of plant spread at a certain scale. The issues are well demonstrated by the debate on the causes of the frequently observed invasion pattern characterized by

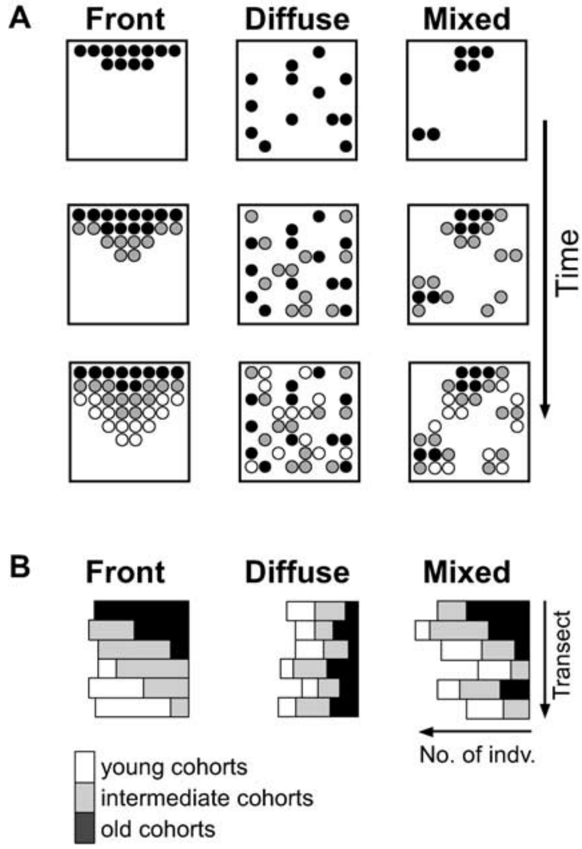

Figure 1. Three models of local spatial spread of plants. (A) Development of invasion patches at three stages (drawing adapted and modified from Wilson and Lee 1989). (B) Age structure patterns that would be expected if transects through stands with a developmental history corresponding to the models in Figure 1A were sampled. For the sake of clarity age structures are shown that imply a low probability of the establishment of younger individuals in areas of the patch already colonized by older con-specifics.

dispersed clusters of plants (cf. Figure 1, right column). Wilson and Lee (1989) called this pattern 'infiltration invasion', based on their assumption that it was the result of long-distance dispersal events (founding new clusters) and short-distance dispersal around established plants. In a response, Lovett Doust (1989) challenged this concept, arguing that such patterns could arise through processes affecting seedling survival and the establishment of adult plants rather than dispersal patterns.

Third, there is a methodical problem. Although it would be most efficient to identify and manage potential invaders in an early phase after their introduction into a new area, attention is usually not drawn to such species before they have already entered the phase of rapid spread (Wade 1997; Ewel et al. 1999 and references therein). At that point of time, immediate action may be needed to prevent further spread, although there may be insufficient understanding of the spreading behaviour of the species. Although observational and experimental studies may be performed to obtain this knowledge, they usually require considerable time. An alternative, time-efficient, approach is to try to reconstruct patterns and processes of plant invasions at a certain scale. This has been done at larger spatial scales by analysis of published information on the historic distributions of the species, and by reconstruction of former distribution patterns using herbarium specimens and anecdotal data (e.g. Forcella and Harvey 1983; Kornaś 1990; Pyšek et al. 1998; Sheley et al. 1998; Weber 1998).

For perennial plants, a promising way to reconstruct patterns and processes of invasions at the population scale is to analyse the relationship between the age distribution and spatial patterns within the population. This approach is possible for a much wider range of species than perceived previously. The results from studies in Europe and North America suggest that the majority of perennial forbs growing in seasonal climates form growth rings in the secondary xylem of the root that can be analysed and used for age-determination, or at least for an estimation of plant age (Dietz and Ullmann 1997, 1998; Schweingruber and Dietz 2001; Dietz and Schweingruber 2002).

This *a posteriori* approach may be appropriate to relate the observed spatial age structure to a specific pattern of population expansion (see Figure 1). It may also be possible to infer the crucial processes underlying this pattern if there is sufficient knowledge of the life-history traits of the species and of the site history. An understanding of the spatio-temporal development of plant invasions at the population scale would be very helpful for evaluating the invasiveness and persistence of invasive plants in various habitats. Furthermore, such insights would contribute to the predictability of future spread of the species at a larger scale.

The objective of this study was to reconstruct and compare the development of invasion patches of different perennial forbs that are invasive in parts of Europe and/or North America by analysis of the spatial age structure within stands. To this end, invasion patches of five species from four plant families were analysed at one or two sites each. Specifically, I wanted (i) to examine whether the species differ with respect to the developmental pattern according to the different models shown in Figure 1 and (ii) to infer the likely processes underlying the observed patterns. Furthermore, I wanted to examine the potentials and pitfalls of this approach.

This is the first study that uses age-determination of perennial forbs to comparatively analyse the development of plant invasion patches.

Materials and methods

Species

Five invasive perennial polycarpic forb species are included in this study, *Bunias orientalis* L. (Turkish wartycabbage, Brassicaceae), *Cardaria draba* (L.) Desv. (hoary cress, Brassicaceae), *Centaurea maculosa* Lam. (spotted knapweed, Asteraceae), *Digitalis grandiflora* Mill. (yellow foxglove, Scrophulariaceae) and *Lythrum salicaria* L. (purple loosestrife, Lythraceae). There has been much debate recently on how to define the term 'invasive' (e.g. Pyšek 1995; Alpert et al. 2000; Daehler 2001). In this article, I use the term 'invasive' according to the most unambiguous definition that classifies non-native species as invasive if they are increasing in abundance in the new area (Daehler 2001). All species develop annual (flowering) stems and have perennating roots (*B. orientalis*, *C. maculosa*, tap roots; *L. salicaria*, *D. grandiflora*, root stocks/rhizomes; *C. draba*, vertical and lateral roots). The main roots and, if present, adventitious roots of the species can be aged by counting annual rings in the secondary xylem of the roots (Boggs and Story 1987; Dietz and Ullmann 1997). The species do not show substantial vegetative spread by clonal growth except for *C. draba*. This species spreads by lateral roots that can be aged, too.

B. orientalis and *C. draba* are invasive in parts of central Europe and in western and northern Europe (Jalas and Suominen 1994; Jalas et al. 1996). Both species occur mainly in nutrient-rich and disturbed habitats such as hay meadows, roadsides, vineyards and ruderal sites in general. *C. draba* is widespread in the USA and is a noxious invasive plant in the West of the country (USDA 1999). *C. maculosa* and *L. salicaria* are among the most serious invasive forbs in North America. While *C. maculosa* has invaded rangeland and open, disturbed habitats in southern Canada and in the USA reducing livestock forage (Watson and Renney 1974; Sheley et al. 1998), *L. salicaria* is widespread and often dominant mainly in wetlands and has been claimed to replace native plants in these habitats due to its high competitive ability (Gaudet and Keddy 1988; Malecki et al. 1993; Mullin 1998). *L. salicaria* also invades drier habitats but to a lesser extent and it remains smaller there (Dietz, pers. obs.). *D. grandiflora* has also been introduced to North America (USDA 1999) but it seems to expand only very locally (cf. Voss 1985).

Study sites and data collection

Four of the five species were surveyed in Ann Arbor, MI, USA, in summer and autumn 1999. Invasion patches of *C. maculosa*, *L. salicaria* and *D. grandiflora* were chosen in unfertilized meadows (mown once per year) in the vast area of the Botanical Garden of the University of Michigan (42°18′ N, 83°40′ E).

L. salicaria was present in two distinct patches in one meadow (LS1 and LS2; see Table 1) that were separated from a vigorous stand of the species in a wetland area by a frequently mown lawn. LS1 was situated in a moist, disturbed depression of the meadow while LS2 was located in a more homogeneous and drier part of the meadow. In LS1 all 71 plant individuals were sampled and in LS2 all individuals of the central part of the patch were sampled (111 individuals). In the meadow *L. salicaria* reached shoot lengths just short of or slightly above 1 m whereas it grew up to 2.5 m tall in the wetland area.

Apparently, *C. maculosa* has invaded these meadows as small, scattered 'satellite' stands and as progressing invasion fronts. One of the largest sub-populations in the area was chosen (CM; characteristics are given in Table 1). All individuals present within a strip of 1 m width (292 plants) were sampled along a transect of 18 m length that was placed perpendicular to the presumed invasion front, running from the distal edge of a 'satellite' patch to the assumed centre of the advancing population.

D. grandiflora was sampled in a dense, elliptical patch (32 × 17 m) located in a relatively moist meadow trough surrounded by open forest. A transect of 10 m length was placed from the border of the patch towards the centre. All individuals present within arbitrary segments of the transect of 25 cm width and varying length were sampled (90 individuals, cf. Figure 5).

The two largest of four clonal patches of *C. draba* were chosen at the roadside of Huron Pkwy in Ann Arbor. The patches were separated from each other by

Table 1. Characterization of the seven invasion patches studied. Shown are the (estimated) number of individuals (ramets in the case of *Cardaria draba*) in each patch, the distance to the nearest patch of the same species, total vegetation cover, the effective vegetation height (height of the upper leaf layer) and the most frequent species in the patch. CM, *Centaurea maculosa*; LSX, patch X of *Lythrum salicaria*; DG, *Digitalis grandiflora*; BO, *Bunias orientalis* and CD, *Cardaria draba*.

Invasion patch	Number of individuals*	Distance to nearest patch	Vegetation cover (%)	Vegetation height (cm)	Frequent species
LS1	71	33 m (LS2); 80 m (wetland dominance stand)	10–95	15–80	*Aster pilosus* Willd. *Carex granularis* Willd. *Equisetum* sp. *Juncus dudleyi* Wieg. *Melilotus officinalis* Pall. *Solidago canadensis* L.
LS2	250	32 m (wetland dominance stand)	70–80	20; 60–80 in clumps of *L. salicaria*	*Aster pilosus* *Festuca pratensis* Huds. *Lythrum salicaria* *Poa pratensis* L. *Solidago canadensis*
CM	1×10^5	20 m	70–90	25; 60–80 in clumps of *C. maculosa*	*Centaurea maculosa* *Elymus repens* Gould *Poa pratensis* *Melilotus alba* Med.
DG	2×10^5	10 m	50–80	30–40	*Digitalis grandiflora* *Poa pratensis*
BO	2000	*c*. 100 m	—	—	*Arrhenatherum elatius* P.B. ex J. et C. Presl *Bunias orientalis* *Galium album* Mill. *Picris hieracioides* L.
CD1	800	*c*. 200 m	30–60	5–10	*Cardaria draba* *Chenopodium album* L. *Cichorium intybus* L. *Festuca pratensis* *Lolium perenne* L.
CD2	1200	*c*. 400 m	20–80	5–10	*Cardaria draba* *Chenopodium album* *Cichorium intybus* *Festuca pratensis* *Lolium perenne*

*Number of ramets in the case of the clonal *Cardaria draba*; seedlings and juveniles do not count towards this figure.

at least 100 m (cf. Table 1). Sixty ramets were chosen randomly from each of the two patches in June. The fragments of (lateral) roots attached to the ramets were collected and the oldest parts of the roots were used for age-determination (see below).

A population of *B. orientalis* located at an irregularly mown roadside between the road verge and a hedgerow running almost parallel to the road at a distance of 8–11 m was surveyed in the north of Würzburg (Unterfranken, Germany, 49°51′ N, 9°51′ E). In November 1997 all 384 individuals present in an area of 5–6 m × 16 m that was selected out of the total area of the population (c. 4–10 m × 50 m) were sampled (for further details, see Dietz et al. 1999a).

For all species the relative spatial position to the nearest 10 cm was determined for each sampled individual. Seedlings and juveniles were disregarded. All individuals were harvested by severing the roots approximately 10 cm below the soil surface. The plant material was stored in plastic bags prior to analysis in the laboratory.

Determination of individual age

For all species, plant age was determined by counting annual growth rings in cross-sections of the root cut at 5–10 cm depth from the soil surface (Dietz and Ullmann 1997). Examples of the anatomical patterns are shown in Figure 2. In most cases, root

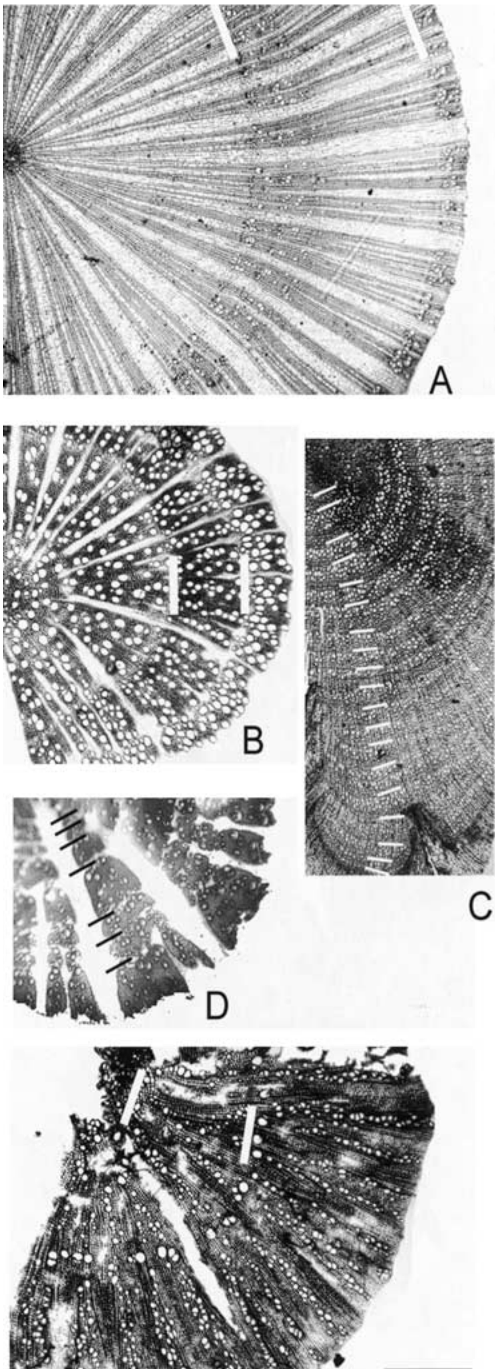

Figure 2. Patterns of annual rings in the secondary root xylem. (A) *Lythrum salicaria*; (B) *Centaurea maculosa*; (C) *Digitalis grandiflora*; (D) *Cardaria draba*; (E) *Bunias orientalis*. The markers denote transitions from latewood of the previous growing period to earlywood of the following one.

decay was negligible and did not impair the analysis. In *B. orientalis,* 13 plants showing central root decay were excluded from analysis. For *B. orientalis* age could be determined unambiguously (ranging from one to nine years) in 77% of all cases. The rest of the plants were assigned to either one of two consecutive ages. The same procedure was adopted for the other species, if necessary. In *D. grandiflora*, many of the plants had lost their main root. In these cases, the oldest adventitious root was used for 'age-determination' (see Figure 5).

Reliability of the annual nature of growth rings in roots

Until now the true annual nature of clearly demarcated growth rings in perennial forbs could be verified for a taxonomically heterogeneous set of *c*. 20 species where individuals of known age were available that were up to 10 years old. These include samples collected in the Central German lowland (Dietz and Ullmann 1997) and in the Swiss pre-alps (Dietz, unpublished), *Centaurea maculata* experimentally grown in the glasshouse and in the field in Montana (USA) (Boggs and Story 1987), *Oxyria digyna* studied in Norway and Greenland (Humulum 1981), *Trifolium pallescens* in a glacier forefield in Austria (Verena Kuen, pers. comm.) and further three species of alpine forbs that were sampled from a restoration experiment on alpine ski runs in the Swiss alps (Dietz and Fattorini, in press). In all cases the number of growth rings in the secondary xylem matched the known age of the plants. The (semi-)ringporous anatomical ring structures found in the roots of many forbs comprise wider vessels (pores) in the earlywood that is formed at the beginning of the growing season and narrower vessels in the latewood that is formed later in the growing season (Dietz and Ullmann 1997). This phenological pattern provides further evidence that the growth rings are formed annually.

These results and observations indicate that growth rings are produced annually under a wide range of site conditions from highly productive lowland sites to nutrient-poor arctic-alpine sites and that year-to-year variations in growth conditions (climatic fluctuations) are unlikely to cause missing rings. Correspondingly, Boggs and Story (1987) noted that *Centaurea maculata* adds one ring of secondary xylem annually regardless of environmental conditions. However, in extreme situations (e.g. permanent snow cover during the vegetation period in some years in the arctic zone, Wijk 1980) missing rings might occur in perennial forbs. There are also no indications of additional rings produced per year (false rings) so far which might result from regeneration growth after disturbance, e.g. mowing. *B. orientalis* growing in meadows showed vigorous rosette regrowth after mowing (Steinlein et al. 1996) but regrowth after mowing did not produce additional rings in this species. The only effect was reduced ring widths if the plants were mown frequently (Dietz, unpublished). The meadows surveyed in the present study were mown only once in October (i.e. close to the end of the vegetation period) so that a substantial effect on growth ring development is very unlikely.

For three of the species used in this study (*B. orientalis*, *C. draba* and *Centaurea maculata*) the growth rings in the roots could be verified to be annual rings. Furthermore, inspection of the roots of *L. salicaria* that were harvested at the end of a two-year field experiment revealed two growth rings in the xylem (Dietz, unpublished). Although verification has not yet been possible for *Digitalis purpurea* there are no indications for a deviating periodicity in growth ring formation in this species.

Data analysis

STATISTICA for Windows 5.5 (Statsoft Inc., 1999, Tulsa, Oklahoma) was used for analysis and values of $P < 0.05$ were accepted as significant.

The age-specific spatial patterns of the invasion patches were analysed with regard to the different models of spread shown in Figure 1. The age distributions of the plants (plant fragments) and the positions of the plants along the transects (or along one axis if the whole patch was sampled, see Figure 3) were categorized such as to arrive at intervals that were reasonable with respect to sample size and the extension of the area surveyed, and were suitable for statistical analysis (see Figures 3–7). If the spatial age distribution followed the front invasion model, a significant interaction between age and spatial position of the plants would be expected whilst, if the distribution followed the diffuse model, there would be no such interaction. Log-linear analysis was used (Sokal and Rohlf 1995) to test whether inclusion of the interaction between age and position was necessary to render the deviation of the statistical model from the observed pattern insignificant (this would imply a significant difference in the spatial patterns between the age classes chosen).

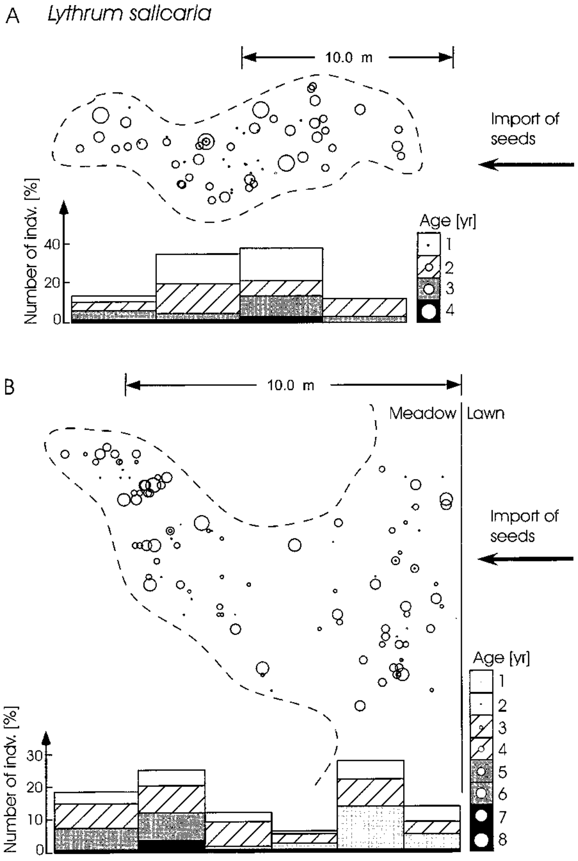

Figure 3. Spatial age distribution pattern of *Lythrum salicaria* in the two separate patches LS1 (A) and LS2 (B) and the corresponding age distributions along transects through the stands (the transect width equals the width of the area of the stands shown). The dashed lines demarcate the border of the stands. The arrows denote the direction of the presumed import of seed from a massive wetland stand of *L. salicaria* in the vicinity of LS1 and LS2. Note that the different shades of grey in the column graphs represent the classification into different age groups (used for statistical analysis, see text) and are not directly comparable between (A) and (B).

In *D. grandiflora* there was a wide age distribution and a monotonous trend in the data so that linear regression analysis could be used.

Results

Lythrum salicaria

Both invasion patches of *L. salicaria* had a relatively low density of individuals (LS1 1 m^{-2}; LS2 1.7 m^{-2})

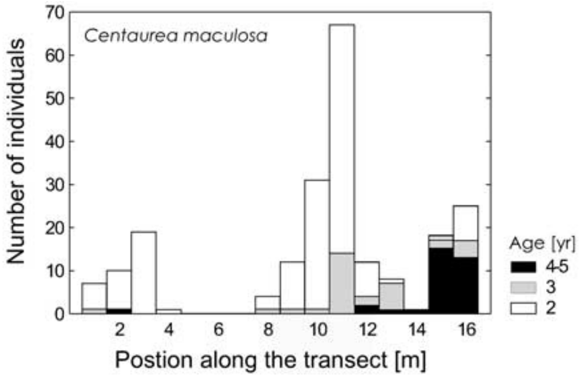

Figure 4. Age distribution pattern of *Centaurea maculosa* along a transect (CM; transect width 1 m) from the distal edge of a 'satellite' patch (0 m) to the assumed centre of the main stand (16 m).

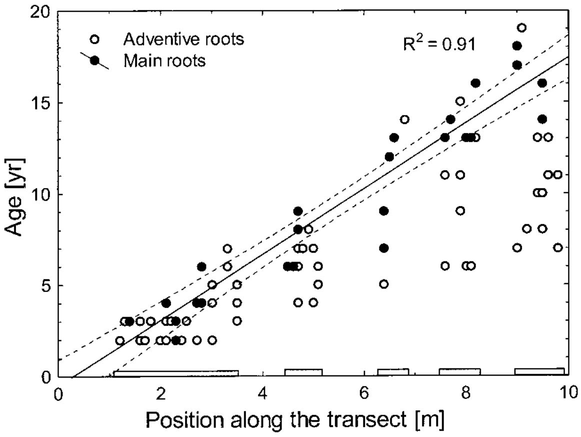

Figure 5. Age distribution pattern of *Digitalis grandiflora* along a transect (DG; transect width 25 cm) from the edge of an elliptical patch (0 m) to the assumed centre (10 m). The grey bars denote the portions of the transect where individuals were sampled. Only individuals that had retained their main roots (filled circles) were used for regression analysis (solid line with 95% confidence bands).

and a rather dispersed distribution pattern (Figure 3). In LS1 individuals were slightly more aggregated in the centre of the patch whereas in LS2 there were some clumps of individuals that were dispersed throughout the sampled area. In LS1 the oldest individuals were four years old and the proportion of younger individuals was higher than that of older individuals. The population of LS2 was considerably older including one- to eight-year-old individuals. There were only a few seven- or eight-year-old individuals and the two intermediate age classes (three- to six-year-old individuals) were especially well represented. In both cases, there were no significant interactions between age and spatial position, i.e. no significant differences in the spatial patterns between the age classes: the statistical models excluding the interaction term age × position did not deviate significantly from the observed patterns (LS1 $\chi^2 = 13.2$, df = 9, $P = 0.15$; $\chi^2 = 10.8$, df = 15, $P = 0.77$).

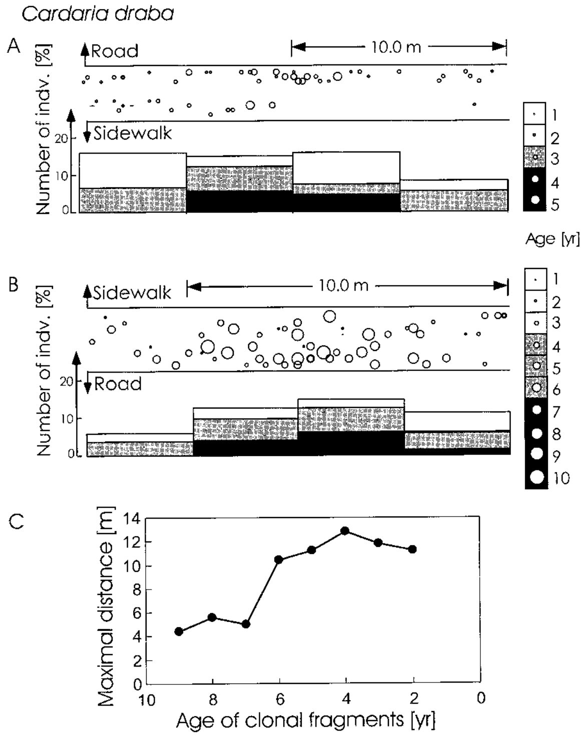

Figure 6. Spatial age distribution pattern of clonal fragments (ramets) of *Cardaria draba* in two separate roadside patches CD1 (A) and CD2 (B) and the corresponding age distributions along transects through the stands (the transect width equals the width of the area of the stand shown). Only the sampled ramets are shown in the distribution maps. The maximal distance of two ramets of the same age within CD2 is shown in (C), dependent on age. Note that the different shades of grey in the column graphs represent the classification into different age groups (used for statistical analysis, see text) and are not directly comparable between (A) and (B).

Centaurea maculosa

The population density of *C. maculosa* in the transect area (excluding the gap between the satellite patch and the main stand) was high (22.5 individuals m^{-2} on average with peak values up to 67 individuals m^{-2}, Figure 4). The oldest (four to five years old) individuals of the patch were largely confined to the central area of the stand. In contrast to the other species tap roots of dead individuals were found in the central part of the

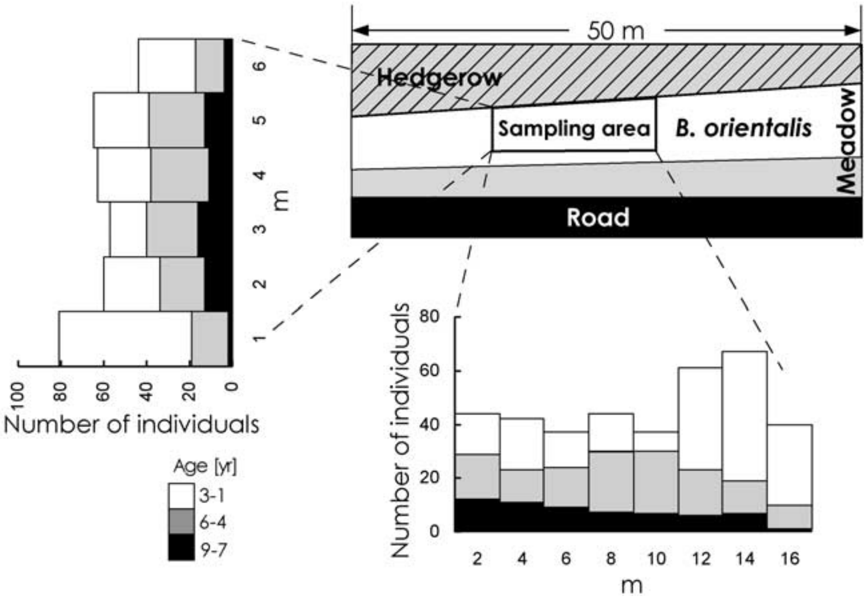

Figure 7. Age distribution pattern of *Bunias orientalis* along two perpendicular transects through a section of a roadside stand (BO; the transect width equals the width of the sampling area shown).

patch indicating considerable mortality of individuals that had reached four or five years. Three-year-old individuals were present throughout the stand but were relatively concentrated in the intermediate area between the border of the stand and its centre. The youngest (one and two years old) individuals were also present throughout the stand but grossly dominated in the border area and in the satellite patch. Corresponding to this pattern, there was a highly significant difference in the spatial pattern between the age classes ($\chi^2 = 127.4$, $\text{df} = 24$, $P < 0.001$).

Digitalis grandiflora

The patch of *D. grandiflora* was homogeneously dense with a plant (genet) density of *c.* 60 m^{-2}. In contrast to the other species *D. grandiflora* had a very wide age distribution ranging from one-year-old genets to genets that were at least 19 years old (Figure 5). The oldest genets were senescing but dead genets could not be observed. The age of the genets increased linearly from the border of the patch towards its centre ($R^2 = 0.91$, $P < 0.001$). This pattern was obtained from the plants that had retained their main roots but is also reflected by plants where only (the oldest) adventitious roots could be analysed (Figure 5). The slope of the regression line suggests that the invasion patch of *D. grandiflora* has expanded with an average velocity of 0.55 m per year in one direction. Usually, the oldest individuals along a transect have to be used to calculate such expansion rates. In the case of *D. grandiflora*, for a given section of the transect, there was only a narrow age distribution of plants that had retained their main root so that all plants could be used for analysis.

Cardaria draba

The two clonal patches of *C. draba* had a ramet density of 20 m^{-2} (CD1) and 40 m^{-2} (CD2), respectively. Each ramet included one or few shoots that were small due to frequent mowing of the roadsides. In CD1 the age distribution of clonal fragments (of the oldest roots connected to a ramet) ranged from one to five years. The relatively small proportion of older fragments was restricted to the central half of the patch (Figure 6A). In CD2 there was a broader age distribution with 1- to 10-year-old clonal fragments (Figure 6B). As in CD1, the oldest clonal fragments were concentrated in the central part of the patch while the younger clonal fragments were weakly over-represented in the outer half. The interaction between age and position was significant for CD1 ($\chi^2 = 16.5$, $\text{df} = 6$, $P = 0.01$) but not for CD2 ($\chi^2 = 8.1$, $\text{df} = 6$, $P = 0.23$).

The curve in Figure 6C approximates the expansion of CD2 over the past years: although sample size was relatively small, the maximal distance between two fragments of the same age increased fairly consistently with decreasing age in CD2. Nine-year-old fragments were at most 4 m apart from each other whereas two- to four-year-old fragments had a maximal distance of 11–13 m from each other.

Bunias orientalis

In the roadside patch *B. orientalis* had a moderate population density of 4.4 individuals m^{-2} and the individuals were 1 to 9 years old. In this case, there was strong evidence that the oldest individuals were the founder individuals of the stand because age structure analyses performed two years earlier in an adjacent section of the same stand yielded seven-year-old individuals as the oldest plants (Dietz and Ullmann 1998). The sampled area covered almost the full width in the central part of the roadside patch but comprised only a fraction of its length (Figure 7). Yet, there was a highly significant interaction between age and position not only in y- ($\chi^2 = 48.0$, df $= 10$, $P < 0.001$) but also in x-direction ($\chi^2 = 54.8$, df $= 14$, $P < 0.001$). In x-direction, there was a pattern similar to that observed in CD1 and CD2 with the oldest (seven to nine years old) individuals underrepresented and the youngest (one to three years old) individuals over-represented near to the margins of the patch. In y-direction there was a gradually decreasing proportion of the oldest individuals towards the right end of the sampled area while the number of the youngest individuals gradually increased in this direction and intermediate age-cohorts peaked at intermediate positions.

Discussion

The age distributions in the invasion patches differed markedly within and between forb species. Furthermore, there were distinct relationships between plant age and spatial position. The spatial age structures of the species surveyed varied in accordance to the models of (local) spatial spread outlined by Wilson and Lee (1989). The interspecific differences in the spatial age structures can be attributed to interspecific variations in life-history traits, particularly seed dispersal, or to the local site conditions rather than the scale of the investigations because the scale of the surveyed stands was in the order of 10 m in all cases.

Differences in patterns and processes of spatial spread

In contrast to all other species, *L. salicaria* showed no relationship between plant age and spatial position, i.e. the oldest individuals as well as younger cohorts were more or less randomly distributed over the whole area of the stands. *L. salicaria* produces tiny seeds that can be easily transported by wind (Thompson et al. 1987; Mullin 1998). Therefore, the high seed dispersal distances may well explain the observed diffuse pattern in the spatial age structure of *L. salicaria* at the scale of a single stand. In contrast to LS1 in LS2 there were no clear visual indications for an abrupt change of site conditions across the stand boundary. However, the irregular boundary that was bordered by young and old individuals alike in both stands indicate that the spatial structure of the invasion patch has been determined by the presence of favourable microsites for establishment (microsite limitation, including possible competitive exclusion) rather than by dispersal limitation.

The spatial invasion patterns of the other species (*C. maculosa*, *D. grandiflora*, *C. draba* and *B. orientalis*) showed at least the tendency to follow the ‘front’ or the ‘mixed’ model of spread (Figure 1B). For *C. maculosa* it is known that seeds are spread within a radius of 1 m around the mother plant (Watson and Renney 1974). Thus, in a habitat with favourable conditions for establishment and if there were no other means of seed dispersal, an existing stand of *C. maculosa* would be expected to gradually expand in a front-like manner (Watson and Renney 1974) with a mean expansion rate of <1 m per year. The assumption of gradual expansion is clearly supported by the result of this study (Figure 2). However, the expansion rate of the observed stand seemed to be higher than expected. The spatial age structure of *C. maculosa* suggests that the expansion rate of the invasion patch has been furthered by increased seed dispersal due to mowing and litter translocation (cf. Dietz et al. 1999b).

Similar to *C. maculosa, B. orientalis* shows local fruit dispersal around the mother plant (Dietz et al. 1999b), suggesting front-like or mixed invasion patterns. In BO, however, the founder individuals (seven- to nine-year-old plants) were scattered throughout the sampled area (that almost fully encompassed the invasion patch in y-direction, cf. Figure 7) concealing a potentially clear pattern of front expansion. The spatial age structure in BO may be characteristic for most stands of the species that seem to develop relatively homogeneously from diaspores introduced to new sites by anthropogenic disturbances (cf. Dietz and Steinlein 1998). *B. orientalis* is a weak competitor and, therefore, front expansion into adjacent, less disturbed areas surrounding an existing stand is unlikely (Dietz and Steinlein 1998). On the other hand, disturbances such as mowing act as dispersal agencies, which may override the inherently local fruit fall (Dietz et al. 1999a).

The spatial age structure of *D. grandiflora* represents the most striking example of a gradual front expansion. In this case the expansion rate could be estimated by the slope of the regression line showing a linear dependence of plant age on position along the transect. *D. grandiflora* produces many small seeds per capsule that are wind-dispersed (see data for the similar *D. purpurea* in Hegi 1974; Grime et al. 1988) a life-history trait usually associated with a dispersal strategy. However, the plants in DG were of small stature (mean plant height was 30–40 cm) and were situated in a sheltered meadow trough probably limiting seed dispersal distance (cf. van Dorp et al. 1996) and explaining slow gradual front expansion.

The spatial age structure of clonal fragments of *C. draba* suggests that the sampled clones have spread from one or possibly a few plant fragments introduced to the roadside area during road maintenance work (a total of only four clonal patches could be spotted in the whole Washtenaw county). The roadsides were frequently mown so that very few flowering shoots could develop directly at the road margin. Therefore, the clones have presumably developed by clonal growth via lateral roots. Although CD1 seemed to be far younger than CD2, it had reached a greater spatial extent. CD1 was partly shaded by a forest edge and the soil conditions were less dry and less mechanically impacted than in CD2 probably allowing for higher rate of clonal growth by lateral roots.

Potentials and limitations of the reconstructive method

The results of this study certainly do not draw a comprehensive or representative picture of the spatial age structure in invasion patches of perennial forbs nor are they exact records of the spatio-temporal development of the patches. Rather, by the great diversity in the results despite the small number of species or patches I looked at, the results indicate the great potential of the use of herb-chronology in a spatial context.

Although spatial patterns do contain information on the processes that led to their development, it is difficult to identify these processes if no information on the temporal variability of the system under study is available (Wiegand et al. 2000). For example, information on the spatial distribution patterns of different age classes is necessary to test alternative models of forest spatial dynamics, not just an investigation of the spatial pattern of adult trees (Sterner et al. 1986). Therefore, the most valuable aspect of using herb-chronology to analyse plant invasion patches is that this approach provides access to the processes that led to the spatial patterns observed.

At the population scale the spatial age structures help to identify the dispersal mechanisms and dispersal distances within and among invasion patches and they contribute to our ability to differentiate between dispersal- and microsite-limitation in seedling establishment. These potentials are clearly exemplified if one compares the spatial age structures of the invasion patches of *L. salicaria* and *D. grandiflora*.

Even if the principal mode of patch development (e.g. diffuse or front-like) is species-specific, variation in habitat conditions may considerably influence the rate and pattern of patch development, as indicated by the comparative analysis of the spatial age distributions in CD1 and CD2. Thus, sampling of invasion patches over gradients of habitat conditions may prove to be very helpful in the search for habitat characteristics furthering or hindering invasions of certain species.

At a local or metapopulation scale comparative analysis of the (spatial) age structures of invasion patches (sub-populations) can assist in an analysis of the dynamics between patches or the rate and pattern of the development of satellite patches originating from a source population. An interpretation of the age structures in LS1 and LS2 in relation to distance of these patches from the presumed source population exemplifies this approach.

With all the possible insights into local invasion processes gained by examining spatial age structures of invasion patches it should be possible to develop more specific and efficient management plans for invasive forbs. Two aspects could be particularly beneficial to management decisions: the prospect to rank habitat conditions with respect to their favourableness for developing invasion patches and the understanding of the spatial development of the patch itself. Both can contribute to solve management questions, e.g. whether it would be preferable to eradicate single groups of invasive plants or whether it would be more appropriate to change habitat management as a whole.

There are some limitations in the approach, however, that may restrict the method, depending on species identity, the questions asked and the degree of ecological knowledge. First, many forb species do not retain long-lived roots or may show increased root rot in some habitats. In those cases the herb-chronological approach is not possible or does only apply to a subset of the analyses that are generally possible. Second, age structures (static life tables) bear ambiguities when they are used to infer population development unless the population shows constant age-specific birth and death rates (e.g. Johnson et al. 1994). Furthermore, a low proportion of old individuals in the age distribution of a population may be the result of (exponential) population growth or higher mortality of older individuals or both. However, if the ecology of the species and the site history (e.g. the type and frequency of disturbances) are well known, those ambiguities may be reduced or resolved.

Acknowledgements

I thank E. Weber, S. Dietz and two anonymous reviewers for helpful comments on an earlier version of this manuscript. I also thank the staff of the Botanical Garden of the University of Michigan for their assistance. I am grateful to F. Schweingruber who produced the microcuttings and introduced me to the preparation of microscopic slides for the microphotographs of Figure 2. and to A. Reznicek who helped me with the determination of some native plant species. K. Edelkraut provided me with two-year-old individuals of *L. salicaria* from her field experiment. This work was funded by the Deutsche Forschungsgemeinschaft (Di 765-1/1).

References

Alpert P, Bone E and Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 52–66

Bergelson J, Newman JA and Floresroux EM (1993) Rates of weed spread in spatially heterogeneous environments. Ecology 74: 999-1011

Boggs KW and Story JM (1987) The population age structure of Spotted Knapweed (*Centaurea maculosa*) in Montana. Weed Science 35: 194–198

Collingham YC, Wadsworth RA, Huntley B and Hulme PE (2000) Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. Journal of Applied Ecology 37(Suppl 1): 13–27

Cousens R and Mortimer M (1995) Dynamics of Weed Populations. Cambridge University Press, Cambridge, p 217f

Daehler CC (2001) Two ways to be an invader, but one is more suitable for ecology. ESA Bulletin 82: 101–102

Dietz H and Fattorini M (2002) Comparative analysis of growth rings in perennial forbs grown in an alpine restoration experiment. Annals of Botany (in press)

Dietz H and Schweingruber FH (2002) Annual rings in native and introduced forbs of lower Michigan, USA. Canadian Journal of Botany 80: 642–649

Dietz H and Steinlein T (1998) The impact of anthropogenic disturbance on life stage transitions and stand regeneration of the invasive alien plant *Bunias orientalis* L. In: Edwards K, Kowarik I, Starfinger U and Williamson M (eds) Plant Invasions – Ecological Mechanisms and Human Responses, pp 169–184. Backhuys Publishers, Leiden, The Netherlands

Dietz H and Ullmann I (1997) Age-determination of dicotyledonous herbaceous perennials by means of annual rings: exception or rule? Annals of Botany 80: 377–379

Dietz H and Ullmann I (1998) Ecological application of ‘herbchronology’: comparative stand age structure analysis of the invasive plant *Bunias orientalis* L. Annals of Botany 82: 471–480

Dietz H, Fischer M and Schmid B (1999a) Demographic and genetic invasion history of a 9-yr-old roadside population of *Bunias orientalis* L. (Brassicaceae). Oecologia 120: 225–234

Dietz H, Steinlein T and Ullmann I (1999b) Establishment of the invasive perennial herb *Bunias orientalis* L.: an experimental approach. Acta Oecologica 20: 1–13

Ewel JJ, O’Dowd DJ, Bergelson J, Daehler CC, D’Antonio CM, Goméz LD, Gordon DR, Hobbs RJ, Holt A, Hopper KR, Hughes CE, LaHart M, Leakey RRB, Lee WG, Loope LL, Lorence DH, Louda SM, Lugo AE, McEvoy PB, Richardson DM and Vitousek PM (1999) Deliberate introductions of species: research needs. BioScience 49: 619–630

Forcella F and Harvey SJ (1983) Relative abundance in an alien weed flora. Oecologia 59: 292–295

Gaudet CL and Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. Nature 334: 242–243

Grime JP, Hodgson JG and Hunt R (1988) Comparative Plant Ecology: a Functional Approach to Common British Species. Unwin Hyman, London

Hegi G (1974) Illustrierte Flora von Mitteleuropa. Vol VI/1. Hanser, Munich, 631 pp

Humulum C (1981) Age distribution and fertility of populations of the arctic–alpine species *Oxyria digyna*. Holarctic Ecology 4**:** 238–244

Jalas J and Suominen J (eds) (1994) Atlas Florae Europaeae. Vol 10 – Cruciferae (*Ricotia* to *Raphanus*). Helsinki, 310 pp

Jalas J, Suominen J and Lampinen R (eds) (1996) Atlas Florae Europaeae. Vol 11 – Cruciferae (*Sisymbrium* to *Aubrieta*). Helsinki, 224 pp

Johnson EA, Miyanishi K and Kleb H (1994) The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta – Picea engelmannii* forest. Journal of Ecology 82: 923–931

Kornaś J (1990) Plant invasions in Central Europe: historical and ecological aspects. In: di Castri F, Hansen AJ and Debussche M (eds) Biological Invasions in Europe and the Mediterranean Basin, pp 19–36. Kluwer Academic Publishers, Dordrecht, The Netherlands

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943–1967

Lovett Doust L (1989) Infiltration invasion – or dispersal and fate? Functional Ecology 3: 380–382

Malecki RA, Blossey B, Hight SD, Schroeder D, Kok LT and Coulson JR (1993) Biological control of purple loosestrife. BioScience 43: 680–686

Mullin BH (1998) The biology and management of purple loosestrife (*Lythrum salicaria*). Weed Technology 12: 397–401

OTA (Office of Technology Assessment) (1993) Harmful non-indigenous species in the United States. US Government Printing Office, Report OTA-F-565, Washington, DC

Parendes LA and Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the HJ Andrews experimental forest. Conservation Biology 14: 64–75

Pyšek P (1995) On the terminology used in plant invasion studies. In: Pyšek P, Prach K, Rejmanek M and Wade PM (eds) Plant Invasions: General Aspects and Special Problems, pp 131–139. SPB Academic Publishing, Amsterdam

Pyšek P, Prach K and Mandák B (1998) Invasions of alien plants into habitats of central european landscape: an historical pattern. In: Edwards K, Kowarik I, Starfinger U and Williamson M (eds) Plant Invasions – Ecological Mechanisms and Human Responses, pp 23–32. Backhuys Publishers, Leiden, The Netherlands

Sauer JD (1988) Plant Migration: the Dynamics of Geographic Patterning in Seed Plant Species. University of California Press, Berkeley, 282 pp

Schweingruber FH and Dietz H (2001) Annual rings in the xylem of dwarf shrubs and perennial dicotyledonous herbs. Dendrochronologia 19: 115–126

Sheley RL, Jacobs JS and Carpinelli MF (1998) Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technology 12: 353–362

Sokal RR and Rohlf FJ (1995) Biometry, 3rd ed. Freeman, New York, 887 pp

Steinlein T, Dietz H and Ullmann I (1996) Growth patterns of *Bunias orientalis* (Brassicaceae) underlying its rising dominance in some native plant assemblages. Vegetatio 125: 73–82

Sterner RW, Ribic CA and Schatz GE (1986) Testing for life historical changes in spatial patterns of four tropical tree species. Journal of Ecology 74: 621–633

Thompson DQ, Stuckey RL and Thompson RB (1987) Spread, impact and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. Fish and Wildlife Research 2. US Department of the Interior, Fish and Wildlife Service, Washington, DC

USDA, NRCS (1999) The PLANTS database (http://plants.usda.gov/plants). National Plant Data Center, Baton Rouge, Louisiana

van Dorp D, van den Hoek WPM and Daleboudt C (1996) Seed dispersal capacity of six perennial grassland species measured in a wind tunnel at varying wind speed and height. Canadian Journal of Botany 74: 1956–1963

Voss EG (1985) Michigan Flora, Part II Dicots. Cranbrook Institute of Science, Bloomfield Hills, Michigan, 724 pp

Wade M (1997) Predicting plant invasions: making a start. In: Brock JH, Wade M, Pyšek P and Green D (eds) Plant Invasions – Studies from North America and Europe, pp 1–18. Backhuys Publishers, Leiden, The Netherlands

Wadsworth RA, Collingham YC, Willis SG, Huntley B and Hulme PE (2000) Simulating the spread and management of alien riparian weeds: are they out of control? Journal of Applied Ecology 37 (Suppl 1): 28–38

Watson AK and Renney AJ (1974) The biology of Canadian weeds. 6. *Centaurea diffusa* and *C. maculosa*. Canadian Journal of Plant Science 54: 687–701

Weber E (1998) The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. Journal of Biogeography 25: 147–154

Wiegand K, Jeltsch F and Ward D (2000) Do spatial effects play a role in the spatial distribution of desert-dwelling *Acacia raddiana*? Journal of Vegetation Science 11: 473–484

Wijk S (1980) Plants and the snow cover (Swedish with English summary). Fauna and Flora (Uppsala) 75: 32–36

Wilson JB and Lee WG (1989) Infiltration invasion. Functional Ecology 3: 379–380 *z*