Using long-term datasets to study exotic plant invasions on rangelands in the western United States

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ARTICLE INFO

ABSTRACT

Invasions by exotic species are generally described using a logistic growth curve divided into three phases: introduction, expansion and saturation. This model is constructed primarily from regional studies of plant invasions based on historical records and herbarium samples. The goal of this study is to compare invasion curves at the local scale to the logistic growth curve using long-term datasets. Five datasets ranging 41–86 years in length were recovered from five sites in four western states. Data for the following seven exotic species were analyzed using regression analysis to evaluate fit to a non-linear sigmoidal logistic curve: crested wheatgrass (*Agropyron cristatum*), dwarf alyssum (*Alyssum desertorum*), cheatgrass (*Bromus tectorum*), Lehmann lovegrass (*Eragrostis lehmanniana*), halogeton (*Halogeton glomeratus*), Russian thistle (*Salsola tragus*) and tumble mustard (*Sisymbrium altissimum*). A greater variety of curve shapes was documented by long-term datasets than those published based on herbaria sampling. Only two species from three different sites and with three different data types met the criteria for fitting a logistic curve. Many of the other species/location combinations were characterized by sporadic spikes and crashes. The general lack of fit with the model may be the results of the complex interactions that drive vegetation change in rangeland environments.

Published by Elsevier Ltd.

1. Introduction

The invasion process is generally described as a logistic growth curve divided into three phases: introduction, expansion and saturation (Fig. 1) (Mack et al., 2000; Radosevich et al., 2003). The introduction phase can also include a "lag" phase where the species persists with little apparent change for many years. This is in contrast to the expansion phase where growth can become exponential (Pysek and Prach, 1993). The saturation phase is characterized by a leveling off of population growth, and is assumed to be related to the fulfillment of carrying capacity (Radosevich et al., 2003). Evidence for the logistic growth curve among plant invasions comes from regional ($>10^{10}$ m^2) invasion histories reconstructed for a variety of species in a variety of habitats, including: downy brome (*Bromus tectorum*) and red brome (*Bromus rubens*) in

the United States (Mack, 1981; Salo, 2005), tiger-pear (*Opuntia aurantiaca*) in South Africa (Moran and Zimmerman, 1991), ornamental jewelweed (*Impatiens glandulifera*), giant hogweed (*Heracleum mantegazzianum*), Japanese knotweed (*Reynoutria japonica*) and giant knotweed (*Reynoutria sachalinensis*) in the Czech Republic (Pysek and Prach, 1993) and lollipop mimosa (*Mimosa pigra*) in Australia (Lonsdale, 1993).

Of particular interest is the lag phase (Crooks, 2005), which has been found to last up to 180 years in invasions of herbaceous plants (Pysek and Prach, 1993) and at least 350 years in woody species (Kowarik, 1995). Explanations proposed for causes of the lag phase include: poor detection ability, dispersal limitations, environmental stochasticity and genetic change through either adaptation or hybridization (Ellstrand and Schierenbeck, 2000; Mack et al., 2000). The lag phase is also of interest to land managers since this phase may allow opportunities for eradication that become impossible or cost prohibitive at later stages (Rejmanek and Pitcairn, 2002; Pysek and Hulme, 2005). Accurately determining which species are in a lag phase versus low-level equilibrium could help focus resources
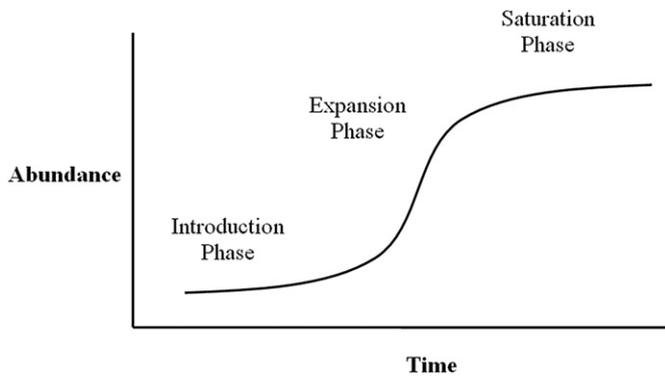
Fig. 1. Idealized logistic growth curve showing the three phases of invasion by exotic species. Adapted from Radosevich et al. (2003).

where they can have the most benefit. Also finding alternative detection methods for species which do not exhibit a lag phase could improve prevention efforts.

Since vegetation change can be slow or episodic and the lag phase of plant invasions may increase the length of time for an invasion beyond the scope of human detection, long-term retrospective data is useful to study the process (Hobbie et al., 2003). Many studies have achieved this through the use of herbarium specimens alone or combined with written accounts (Mack, 1981; Pysek and Prach, 1993; Salo, 2005). However, historical data sources are known to have limitations and biases (Strayer et al., 1986) and herbarium records are specifically known to suffer from biases in sampling scale, geographic range and consistency (Delisle et al., 2003; Salo, 2005; Van Gemerden et al., 2005). Additionally, herbarium studies are generally based on cumulative new occurrences, which assumes that, once documented in a location, the plant persists in that location. More detailed metrics, such as cover or density are generally not measured. Another approach for studying weed invasions is to use long-term datasets, which are considered the most reliable and least biased form of historical data (Strayer et al., 1986). Though weaknesses can still include observer bias, infrequent sampling and inconsistencies in sampling intervals, this data is collected specifically for documenting changes in plant abundance.

The importance of scale, both spatially and temporally, in relation to weed invasions has been discussed over the past decade. In a recent survey, Crall et al. (2006) found that only 38% of databases concerned with invasive species had more than 10 years of coverage and that the majority was at the spatial extent of the county or smaller. There is general consensus that data from a broad range of scales is important for both the management and prediction of weed invasions (Radosevich et al., 2003; Jarnevitch and Stohlgren, 2009). This can be due not only to the differences in data collection methods at different scales discussed above, but also to the differences in ecological processes such as density dependence at small scales and site occupation at larger scales. Despite these differences the primary predictive model for exotic plant invasions is based solely on large-scale data, with no reference to temporal scale. The objective of this study is to use long-term datasets to compare invasion patterns by exotic plant species at the local scale ($<10^5$ m^2) to the generalized logistic growth curve developed from regional invasions.

2. Methods

We explored long-term datasets that documented exotic weed invasions from a variety of sources, including USDA Forest Service Experimental Forests and Ranges, Department of Energy National Environmental Research Parks, National Science Foundation Long-term Ecological Research Sites, USDA Agricultural Research Service Experimental Watersheds and field stations associated with universities (Adams et al., 2004; Lugo et al., 2006). When available, precipitation data and disturbance history records were collected in conjunction with vegetation data. All exotic species that were recorded throughout the timespan of data or that had high abundance at some point during the dataset were included for analysis.

2.1. Site descriptions

Our search resulted in datasets from five sites on rangelands in the western United States (Table 1). Descriptions of data collection and compilation for each site are described below, along with relevant information related to site characteristics. All sites are

Table 1
Site descriptions for long-term datasets.

Site name	State	Site size (ha)	Elev. range (m)	Ann. precip. (mm)	Span of data (yr.)	Data type	Plant community type
Walnut Gulch Experimental Watershed[a]	AZ	0.1	1220–1950	312	1967–2008	Cover	Grassland (*Bouteloua curtipendula, Tridens muticus, Muhlenbergia porteri, Acacia constricta, Larrea tridentata, Prosopis velutina*)
Santa Rita Experimental Range[b]	AZ	10,000	900–1400	389	1953–2006	Cover, density	Desert scrub and woodland (*Bouteloua eriopoda, B. hirsuta, Digitaria californica, Hilaria belangeri, Cercidium floridum, Acacia greggii*)
Idaho National Laboratory[c]	ID	231,500	1460–1620	215	1950–2006	Cover, density	Shrub steppe (*Artemisia tridentata* ssp. *wyomingensis, Grayia spinosa, Elymus elymoides, Achnatherum hymenoides, Phlox hoodii*)
Desert Experimental Range[d]	UT	600	1547–2565	157	1934–1994	Density	Salt desert scrub (*Atriplex confertifolia, Ephedra nevadensis, Achnatherum hymenoides, Elymus elymoides, Aristida purpurea*)
Jornada Experimental Range[e]	NM	35,000	1176–2734	246	1915–2001	Density	Semidesert grassland (*Bouteloua eriopoda, Sporobolus flexulosus, Pleuraphis mutica, Scleropogon brevifolus, Aristida* spp.)

[a] (Goodrich et al., 2008; King et al., 2008).
[b] (McClaran et al., 2003).
[c] (Harniss and West, 1973; Anderson and Inouye, 2001).
[d] (Holmgren, 1975; West, 1979; Adams et al., 2004).
[e] (Yao et al., 2006).

situated in a wildland setting, where the invasion process occurred without targeted weed control measures.

2.1.1. Walnut Gulch Experimental Watershed (WGEW)

In 1967, two parallel 30.5 m transects were established 15.2 m apart alongside each of 55 rain gages placed along a precipitation gradient in the watershed (King et al., 2008). Foliar cover data for each species was collected using the line-intercept method in September. In 2008 the method for cover data changed to point intercept. Of the sites where data were collected through 2008, only one (RG82) was invaded by an exotic plant species, which are the data presented here. There are no records of recent fires or intentional plant introductions at RG82, though some grazing has occurred there. The data were converted to presence/absence (see below) by dividing each transect into 0.5 m segments.

2.1.2. Santa Rita Experimental Range (SRER)

Starting in 1953, 132 permanent 30 m transects were established in 12 pastures on the range (McClaran et al., 2003). Data on plant species and basal cover were measured annually during the dormant winter season (January–July) using the line-intercept method until 1966, and then sporadically through 2006, though not every transect was read every year. The data used here consists of mean cover values of exotic species from a subset of transects which were sampled consistently for the years presented. Exotic perennial forage grasses, including Lehmann lovegrass (Eragrostis lehmanniana Nees), were first seeded in experimental plots in the late 1930s on the Santa Rita Experimental Range with work on Lehmann lovegrass continuing through the late 1960s (Cable, 1971; McClaran et al., 2003). There are no records of it being seeded directly on the long-term transects. The US Forest Service also implemented mechanical and chemical mesquite removal treatments during the 1950s and a large fire burned 23 transects in 1994. A range of different grazing regimes has occurred in the area over the many years of experimentation. The data presented here are from areas both treated and untreated for mesquite and areas that burned in 1994 and remained unburned.

2.1.3. Idaho National Laboratory (INL) site

Ninety-four permanent plots were initially established at the Idaho National Laboratory (INL) Site in 1950 along two perpendicular macro-transects dividing the site into four quadrants and extending slightly beyond the boundaries of INL (Harniss and West, 1973; Anderson and Inouye, 2001). Most plots were separated by a distance of 1.6 km and each consisted of 20, 0.3 m² quadrats laid out along two 15.24 m parallel transects. Basal cover and density data were collected approximately every 5–10 years from 1950 to 2006 on a subset of plots during the months of June and July. Very few exotic species were recorded by the cover data and rarely persisted for multiple sample years. The density data, however, documented several exotic species which met the criteria for inclusion. The data presented here are mean densities calculated from the 61 plots which were sampled consistently during the span from 1950 to 2006. Basal cover data, using the line-intercept method on the same transects, are also included for one exotic forage grass.

Several fires have occurred within INL during the span of data collection, but they did not affect more than a few monitoring plots at a time. Approximately half of the monitoring plots are located within the boundaries of Bureau of Land Management (BLM) grazing allotments and are grazed occasionally. There are records of the exotic forage grass, crested wheatgrass (Agropyron cristatum) being seeded within the boundaries of INL (Marlette and Anderson, 1986), though not within any of the long-term plots.

2.1.4. Desert Experimental Range (DER)

From 1934 to 1935 a series of twenty 98–130 ha sheep grazing paddocks was set up, 16 of which included two 0.4 ha exclosures. Over the years, each paddock was exposed to varying intensity and seasonality of sheep grazing (Harper et al., 1996). Permanent plots with dimensions of 1.5 m by 6 m were located in both grazed and excluded portions of each paddock. Plot maps of individual plants were created in the summer (June–September) at varying intervals by species and size. Plot maps were then used to calculate values for plant density and cover. Since plants with annual life forms were not included in the cover data and the exotic species were all annual, only density data are included here. A subset of plots which had been consistently sampled and had an exotic species present at some point was included for each exotic species. The years which had the highest density of the exotic species were used to determine the subset.

2.1.5. Jornada Experimental Range (JER)

From 1915 to 1932 a series of 120 permanently marked 1 m² plots was established in both upland and lowland grassland types, of which most were sampled annually until 1979, except for small gaps in the mid 1950s and 1960s (Yao et al., 2006). After 1979, the plots were not sampled again until 1995 and 2001. Data were collected on plant species, plant density and plant location, during the winter months. The data presented here are mean densities from all plots sampled for each year that had at least one record of an exotic species present over the course of the dataset.

2.2. Statistical analysis

Since herbaria studies used in regional data are based on the presence of a species, we converted data from long-term datasets into presence/absence data to compare the two methods. Presence/absence data was generated by counting presence in each sampling unit (transect or quadrat) and was presented as a proportion of the total number of sampling units. On both the primary and converted data, we performed a non-linear regression based on a symmetrical sigmoidal logistic curve in SigmaPlot 11 with time as the independent variable. A three-parameter equation was used since it has a lower asymptote of zero, which best reflects the pre-invasion status of a site

$$y = \frac{a}{1 + \left(\dfrac{x}{x_o}\right)^b}$$

where y is plant abundance, a is the upper asymptote, the absolute value of b represents the curvilinear properties of the sigmoidal curve, including the slope of the maximum growth rate and the radius of the curve for the transitions to and from the asymptotes, x is the independent variable and the absolute value of x_0 is the point on the x-axis where the inflection point and maximum growth rate occurs (Yin et al., 2003). Parameter b was constrained at -1300 to prevent transitions that resulted in near-right angles and near-vertical exponential growth. Parameter a was constrained at 1.0 or 100 to prevent presence or cover values greater than 100%. For density data, a was constrained to represent reasonable maximum densities, depending on the species. In order to avoid inflating R^2 values, all zeros for the dependant variable prior to the first zero preceding the first non-zero value were excluded from the analysis, though were graphed for presentation. We chose to accept significance values of $P > 0.1$ and R^2 values of 0.6 and higher as fitting the logistic growth curve. Regression was fit to the means for each sampling period, rather than each data point in order to reduce effects from variation between sampling units and maintain focus

on the site level. Cover data was relativized as the proportion of total plant cover for WGEW, since it was based on foliar cover and could be compared to canopy cover data collected for shrubs.

3. Results

From the five datasets recovered, seven exotic species fit our criteria for inclusion in analysis: crested wheatgrass (*A. cristatum*), desert alyssum (*Alyssum desertorum*), cheatgrass (*B. tectorum*), Lehmann lovegrass (*E. lehmanniana*), halogeton (*Halogeton glomeratus*), Russian thistle (*Salsola tragus*) and tumble mustard (*Sisymbrium altissimum*). Three species occurred at multiple sites: Lehmann lovegrass, Russian thistle and cheatgrass. Four of the

seven species were annual forbs (desert alyssum, halogeton, Russian thistle and tumble mustard) and one was an annual grass (cheatgrass). The two perennial species are bunch grasses intentionally introduced to North America as forage species for livestock (crested wheatgrass and Lehmann lovegrass).

Two species in combinations with three different sites and three types of data had significant models and R^2 values high enough to qualify as adequately fitting the logistic curve (Figs. 2 and 3). This included Lehmann lovegrass at WGEW and SRER and desert alyssum at INL Site. Due to the decline during the later years, the logistic curve would not fit the entire range of density, cover or presence data, for Lehmann lovegrass at SRER. However, as explained later, we felt justified in excluding the decline phase of
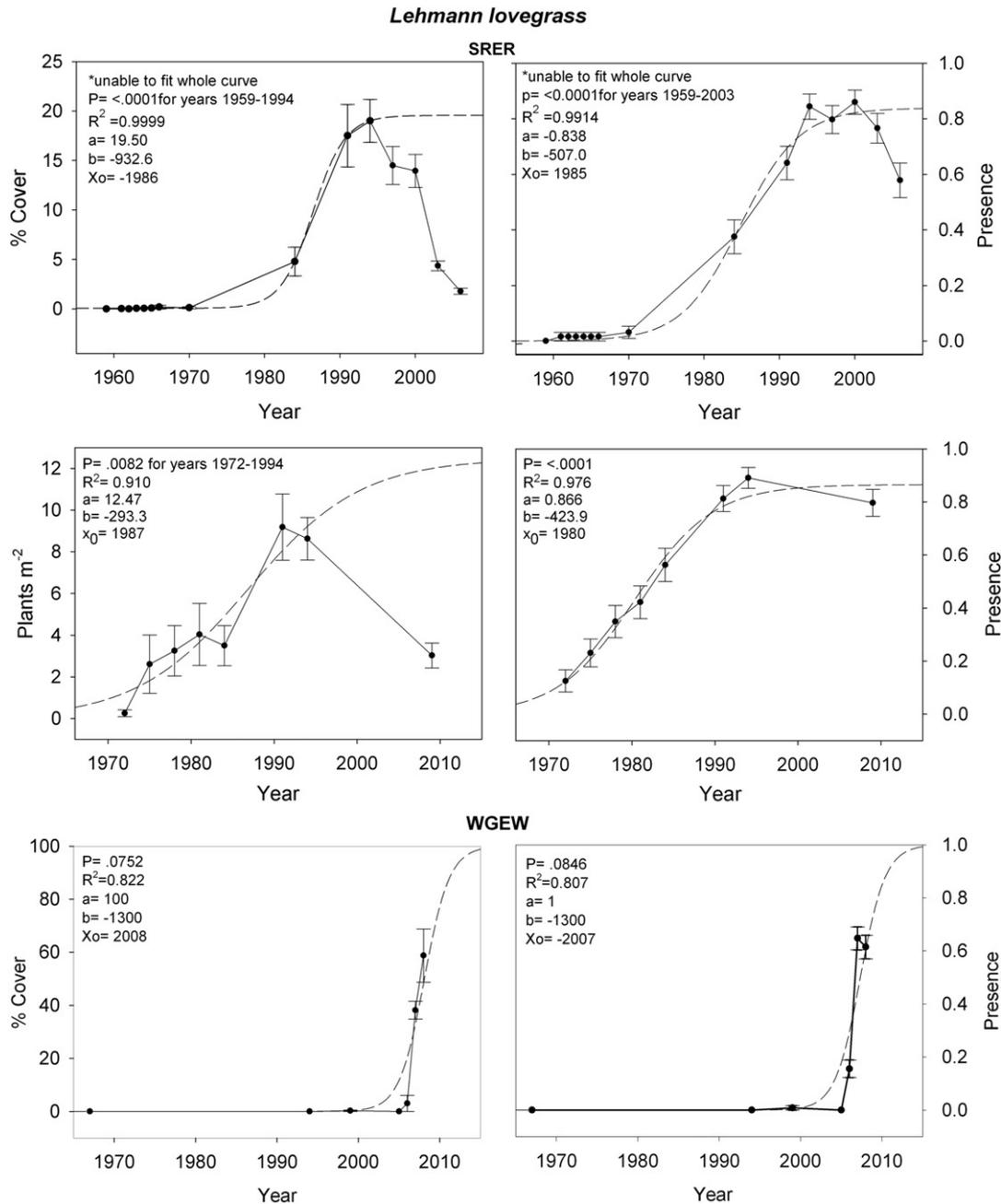
Fig. 2. Abundance of *Eragrostis lehmanniana* at Santa Rita Experimental Range (SRER) and Walnut Gulch Experimental Watershed (WGEW) over time. The graphs on the right side represent the presence data derived from the data presented to the left. The dashed line plots the best fit for a logistic curve. At SRER data from the decline phase of the curve was excluded from analysis in order to allow a curve to fit to the lag and expansion phases. Parameter values fit the equation listed in Methods section. Error bars represent one standard error.

Dwarf allysum

Tumble mustard
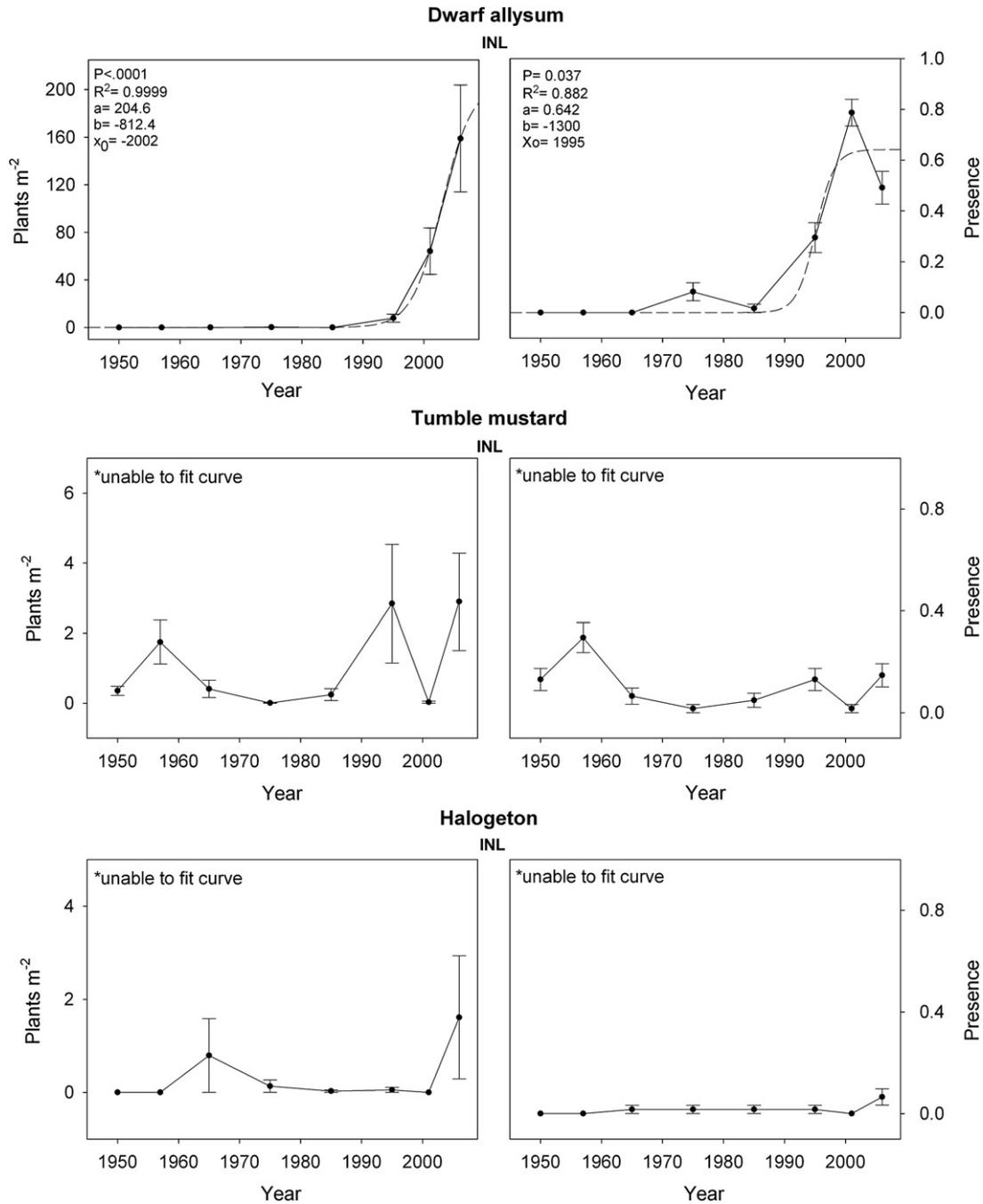
Halogeton

Fig. 3. Abundance of *Alyssum desertorum*, *Sisymbrium altissimum* and *Halogeton glomeratus* at Idaho National Labs (INL). The graphs on the right side represent the presence data derived from the data presented to the left. The dashed line plots the best fit for a logistic curve. Parameter values fit the equation listed in Methods section. Error bars represent one standard error.

the data from analysis in order to learn what we could from the introduction and expansion phases of the data. Six species at three different sites either did not fit the criteria for fitting the logistic growth curve or SigmaPlot 11 was unable to fit a logistic curve to the data (Figs. 4–6).

4. Discussion

4.1. Model fit

Long-term datasets collected at the local scale produced a greater variety of curve shapes than accounts published from

regional studies, which all generally conformed to the logistic curve (Mack, 1981; Salo, 2005). In addition to curves that conformed to the logistic growth form (Figs. 2 and 3), multiple species exhibited seemingly sporadic spikes and dips in abundance (Figs. 3–6). In some cases, the sudden increases arise from a baseline of zero (Figs. 3 and 5), whereas other species seem to be persisting at a very dynamic equilibrium (Figs. 4 and 6). If this is indeed the case, than the dataset did not document the lag or expansion phase of the original invasion.

For Lehmann lovegrass at SRER (Fig. 2) we were only able to achieve a model fit if we excluded the decline phase of the density, cover and the associated presence/absence data. We felt justified in

Crested wheatgrass
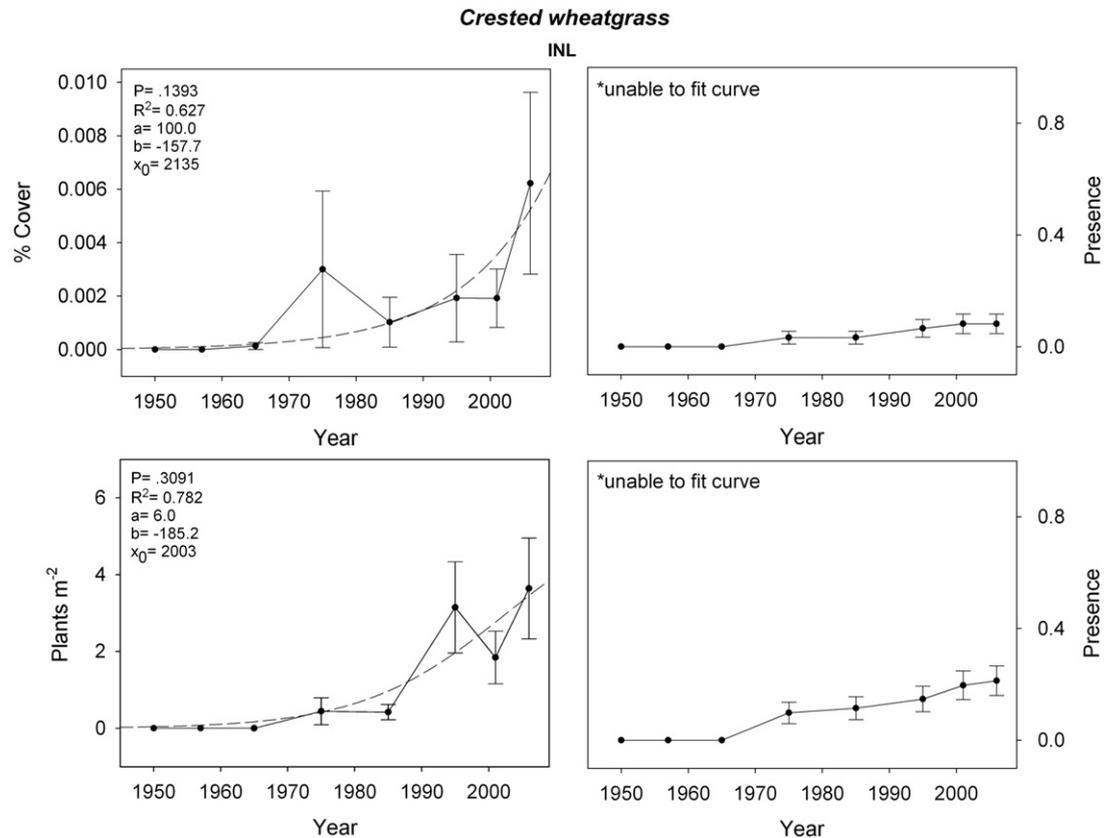
Fig. 4. Abundance of *Agropyron cristatum* at Idaho National Labs (INL). The graphs on the right side represent the presence data derived from the data presented to the left. The dashed line plots the best fit for a logistic curve. Parameter values fit the equation listed in Methods section. Error bars represent one standard error.

limiting our analysis to the lag and expansion phases of the curve in order to learn what we could. However, since the rapid increase and subsequent decline are explained by a period of above-average precipitation, followed by a drought (McClaran et al., 2010), the data suggests that this invasion of Lehmann lovegrass is being driven by increased resource availability (Davis et al., 2000) and not some internal plant characteristic (Radosevich et al., 2003). Only time will tell whether the invasion of Lehmann lovegrass at WGEW follows a similar pattern. For both crested wheatgrass at INL Site (Fig. 4) and Russian thistle at DER (Fig. 5) the model fit the general curve shape, but was nonsignificant due to high variability between sampling years. Since high variability in plant abundance can be common on rangelands due to high variability in interannual precipitation, it may be appropriate to adjust the model criteria when working in these systems.

For the species that did not fit the model, most were characterized by seemingly sporadic spikes and crashes (Figs. 3–6). These are probably related to resource pulses (Davis et al., 2000) either from increased precipitation as observed by Hobbs et al. (2007) in California grasslands, or by undocumented disturbances. For cheatgrass at DER (Fig. 6), the paucity of data points made fitting the model impossible, even though the data appear to be in the increase phase of a logistic curve. It is also possible that we are seeing a spike that returned to baseline levels after time; only re-sampling will tell for sure.

An invasive plant is generally described as an exotic species that successfully reproduces and spreads in its introduced range (Mack et al., 2000; Pysek et al., 2004). Based on this definition and the data gathered from these long-term datasets we cannot conclude whether any of these species fit that definition. Even though several datasets fit the statistical model, none of the data actually exhibit

the transition into the saturation phase as illustrated in the theoretical model. The statistical model predicts saturation in some cases, however in this result it is based primarily on the symmetry generated by the logistic curve instead of by empirical data. In reality, it is unclear from the data if these species will persist, decline or fluctuate in equilibrium.

Although desert alyssum fits the expansion phase of the model well, it is not usually placed in the same category as other invasives due to its lack of documented ecological impacts, thus far. It neither appears on any state noxious weed lists (NRCS, 2012), nor has it been found responsible for any ecological impacts, based on searches for published studies. This is consistent with research which has shown that while the rate of spread is positively correlated with final extent (Forcella, 1985), there is no correlation between rapid population expansion and ecological impact (Ricciardi and Cohen, 2007). This may be due to the "rule of tens" theory that suggests only one in ten introductions leads to a successful invasion and that only one in ten successful invasions results in ecological impacts (Williamson and Fitter, 1996). The combination of the "rule of tens" and lag phase dynamics make it very difficult to predict which plants become invaders, which invaders become ecologically damaging and where to prioritize management of exotic plants during early stages of invasion.

Crested wheatgrass also exhibits the curve of an invading species, but in reality the current cover values are so low that there is little likelihood of ecological impacts at the local scale. However, at the plot scale, crested wheatgrass is beginning to become dominant in areas where it does occur, while native grasses are declining (Forman et al., 2010). Therefore, the extent of ecological impact depends entirely at which spatial scale it is viewed from. This underscores the differences in ecological processes that can drive
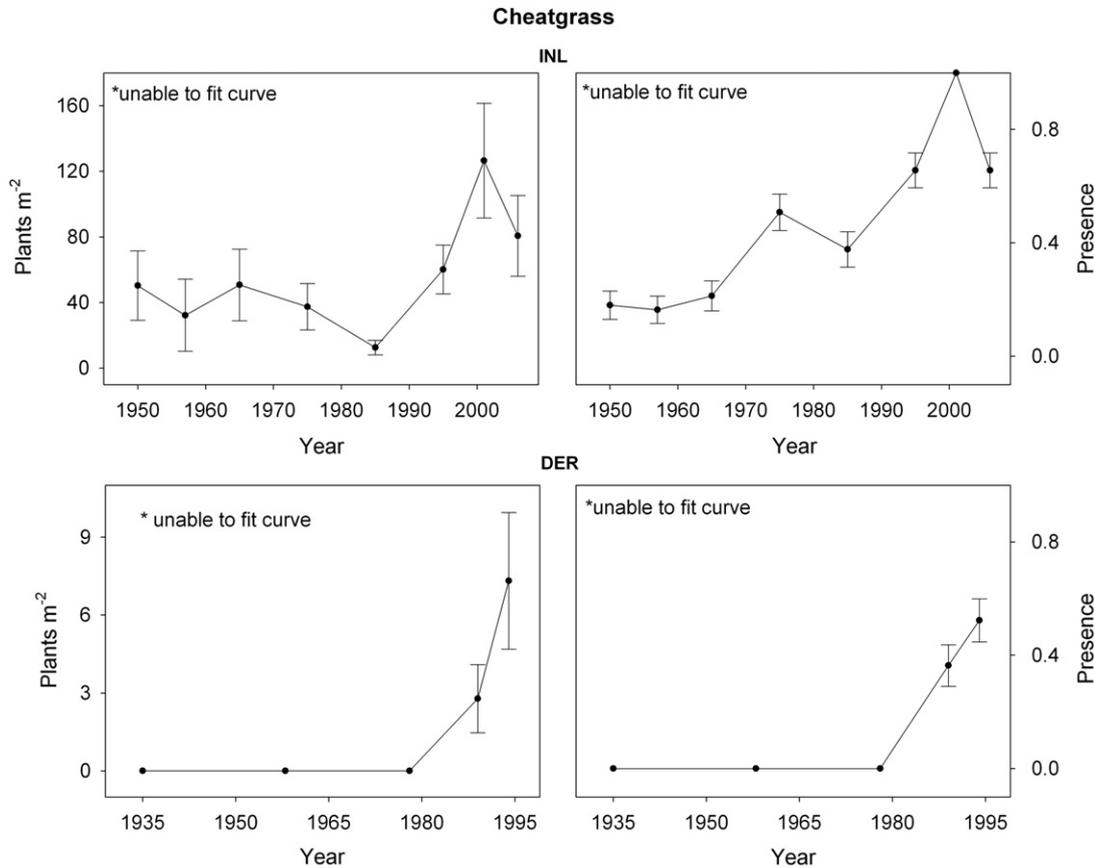
Russian thistle
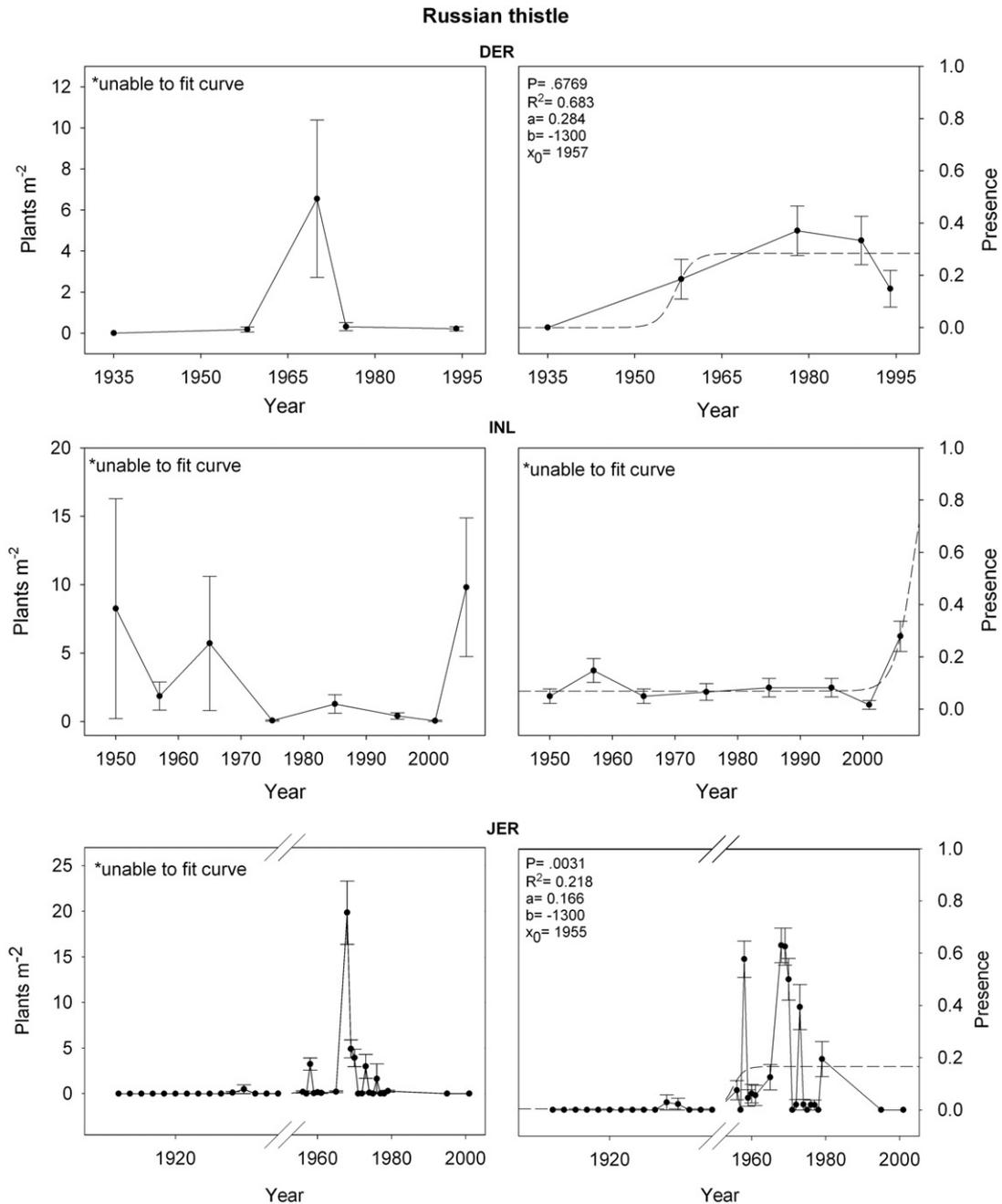
Fig. 5. Abundance of *Salsola tragus* at Desert Experimental Range (DER), Idaho National Labs (INL) and Jornada Experimental Range (JER). The graphs on the right side represent the presence data derived from the data presented to the left. The dashed line plots the best fit for a logistic curve. Parameter values fit the equation listed in Methods section. Error bars represent one standard error.

invasions at different scales; at small scales density dependence and resource competition may be important, whereas at large scales colonization and infilling may be driving factors.

4.2. Lag phase dynamics

After first being documented on the site, most of the species/site combinations that fit the logistic model exhibited a lag phase before exponential expansion began. The exception was Lehmann lovegrass at WGEW, which entered into the expansion phase very abruptly. Even though Lehmann lovegrass was initially detected 7 years before expansion, it was not detected again until 1 year before exponential expansion began which resulted in a curve without the

slow increase generally seen in the lag phase. Tropical areas have been shown to have shorter lag times than temperate regions (Daehler, 2009), which suggests a negative correlation between annual precipitation and lag times; however, effects from resource pulses, droughts and multi-equilibrial vegetation dynamics in arid and semi-arid regions may not support this generalization (Laycock, 1991; Davis et al., 2000). The lag phase is an especially important time for the management of invasions and this example illustrates the dangers of relying on existing vegetation as the indicator of invasion risk. The adoption of seedbank analysis may provide the land manager a more accurate indicator of potential vegetation in cases where plants rely on seed for reproduction (Travnicek et al., 2005).

Fig. 6. Abundance of *Bromus tectorum* at Idaho National Labs (INL) and Desert Experimental Range (DER) and *Sisymbrium altissimum* at INL. The graphs on the right side represent the presence data derived from the data presented to the left. The dashed line plots the best fit for a logistic curve. Parameter values fit the equation listed in Methods section. Error bars represent one standard error.

Based on the long-term data presented here, the order of shortest to longest lag phase was: Lehmann lovegrass at WGEW (1 year), desert alyssum (13 years) and Lehmann lovegrass at SRER based on cover (23 years). Since the density data for Lehmann lovegrass at SRER did not start at zero, we were unable to calculate a lag phase. The length of the lag phase for the introduced perennial forage grass Lehmann lovegrass at SRER is especially surprising considering that it was selected for suitability in the regions. We can assume that the need for adaptation did not slow local expansion; therefore some step during the colonization process must be slowing it down. Likewise, the annual forb desert alyssum had been documented for longer than 30 years in the region prior to its appearance at INL (Rice, 2012). Given that plants with annual life cycles are expected to have the shortest lag phases (Pysek and Prach, 1993), due to both short generation times and rapid time to reproduction, this data suggests that processes other than adaptation and seed limitation can slow rates of invasion. Since none of the species documented by the long-term datasets presented here were new to the region at the time of their first appearance in the datasets, we cannot speculate regarding the importance of adaptation during the lag phase.

4.3. Scale

In terms of both spatial and temporal scale, the results from this survey of long-term datasets highlight the need for a broad range of types of data to meet both management and research needs. For example, our results on the establishment of crested wheatgrass in an area where it was not originally seeded, confirm results from other studies in southern Idaho that show an expansion in range of

introduced *Agropyron* sp. at the local scale (Hull and Klomp, 1967). Despite this, there has been no documentation within the region of changes in distribution. This is in contrast to the northern Great Plains region, where crested wheatgrass is considered generally invasive (Heidinga and Wilson, 2002). Research has shown the importance of using data from multiple scales in order to fully understand the impact of this region-wide invasion (Henderson and Naeth, 2005).

Despite each dataset spanning >50 years, they were still generally inadequate for answering our question. In most cases the results were inconclusive because the invasion process had not progressed to a definitive state, which can only be resolved by the passage of time and further data collection. Temporal resolution appears to be less important than temporal span for testing the fit for the logistic growth model. Sites that were sampled sporadically (WGEW) and regularly (INL) both documented species that fit the curve well. It doesn't appear that more frequent sampling would increase the ability to detect a logistic curve pattern. However, detecting other ecological processes may require more detailed data collection. For example Piemiesel (1951) observed a cycling effect after disturbance between the three annuals, cheatgrass, Russian thistle and tumble mustard with data collected annually. Only at JER was the data collected frequently enough to have detected this phenomenon, if it had occurred.

4.4. The utility of long-term datasets

The collection of both density and cover data at INL and SRER and the conversion of these data types to presence/absence data provides some insight into what types of data are best for analyzing

weed invasions. Density data seemed more sensitive than cover data based on the number of annuals at INL that were detected by the two data types. However, the disadvantage of density data is that it does not account for interannual changes in size of individuals or instances of self-thinning (Silvertown and Charlesworth, 2001). Cover data is less sensitive, but would detect changes in size and would remain relatively constant in cases of self-thinning, as long as data were collected at the same time of year. The other advantage of cover data is that it can be relativized based on total vegetation cover and account for annual changes in productivity. With density data, additional information, such as biomass, would be useful to identify declines in overall plant productivity caused by factors other than plant interactions.

In general, the presence/absence data seems more stable than the both cover and density data, both in terms of variance and differences between sampling points. The presence/absence data mostly tracked the data that it was derived from, but there were some instances where the two data types contradicted each other. For Lehmann lovegrass at WGEW (Fig. 2) the cover values continue to rise as time progresses, while presence begins to fall. A similar situation occurs for desert alyssum at INL (Fig. 3), though the curve flattens out, rather than continuing to rise. For cheatgrass at INL (Fig. 6) there is a decline in overall density in the middle of the curve, though presence in plots increases. These discrepancies suggest that both types of data could be useful for land managers at the local scale. A decrease in overall density might represent an opportunity for eradication in some locations, while a decrease in presence might indicate that preventive measures to limit spread are being effective. The leveling off of the presence/absence curve for desert alyssum, as density continues to rise, may also indicate a fourth stage of the invasion process: infilling. This means that with more detailed data, the window for eradication may be longer at the local scale than would be assumed based on the regionally-based model. In general, it appears that land managers require more detailed data for decision-making than what can be provided from a general model, produced from region-wide data.

In this first use of long-term datasets to compare invasions at the local scale to the logistic growth model, we have found plenty of evidence for exceptions to the regionally-based model and several inconclusive cases. The many examples of species that did not fit the model is likely related to sites being situated in arid and semi-arid climates where resource pulses, drought and multi-equilibrium dynamics are major drivers of vegetation change. A model that can incorporate these complexities will be much more useful in these environments. Our hope is that understanding the exceptions to the rule will aid in management and that the ideas discussed here will initiate further study of exotic plant invasions using long-term datasets.

Acknowledgments

References

Adams, M.B., Loughry, L.H., Plaugher, L.L., 2004. Experimental Forests and Ranges of the USDA Forest Service. General Technical Report NE-321. USDA Forest Service Northeastern Research Station, Newton Square.

Anderson, J.E., Inouye, R.S., 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71, 531–556.

Cable, D.R., 1971. Lehmann lovegrass on the Santa Rita experimental range, 1937–1968. Journal of Range Management 24, 17–21.

Crall, A.W., Meyerson, L.A., Stohlgren, T.J., Jarnevich, C.S., Newman, G.J., Graham, J., 2006. Show me the numbers: what data currently exists for non-native species in the USA? Frontiers in Ecology and the Environment 4, 414–418.

Crooks, J.A., 2005. Lag times and exotic species: the ecology and management of biological invasions in slow-motion. Ecoscience 12, 316–329.

Daehler, C., 2009. Short lag times for invasive tropical plants: evidence from experimental plantings in Hawai'i. PLoS One 4 (2), e4462.

Davis, M.A., Grime, J.T., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88, 528–534.

Delisle, F., Lavoie, C., Jean, M., Lachance, D., 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. Journal of Biogeography 30, 1033–1042.

Ellstrand, N.C., Schierenbeck, K.A., 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Sciences of the United States of America 97, 7043–7050.

Forcella, F., 1985. Final distribution is related to rate of spread in alien weeds. Weed Research 25, 181–191.

Forman, A.D., Blew, R.D., Hafla, J.R., 2010. The Idaho National Laboratory Site Long-term Vegetation Transects: A Comprehensive Review. US Department of Energy/S.M. Stoller Corp., Idaho Falls. http://www.gsseser.com/PDF/LTVReport2010.pdf.

Goodrich, D.C., Keefer, T.O., Unkrich, C.L., Nichols, M.H., Osborn, H.B., Stone, J.J., Smith, J.R., 2008. Long-term precipitation database, Walnut Gulch Experimental Watershed, Arizona, United States. Water Resources Research 44, 1–5.

Harniss, R.O., West, N.E., 1973. Vegetation patterns of the National Reactor Testing Station, southeastern Idaho. Northwest Science 47, 30–43.

Harper, K.T., Van Buren, R., Kitchen, S.G., 1996. Invasion of alien annuals and ecological consequences in salt desert shrublands of western Utah. In: Barrow, J.R., McArthur, D.E., Sosebee, R.E., Tausch, R.J. (Eds.), Proceedings: Shrubland Ecosystems Dynamics in a Changing Environment. USDA Forest Service, Ogden, pp. 58–65. General Technical Report INT-GTR-338.

Heidinga, L., Wilson, S.D., 2002. The impact of an invading alien grass (Agropyron cristatum) on species turnover in native prairie. Diversity and Distributions 8, 249–258.

Henderson, D.C., Naeth, M.A., 2005. Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biological Invasions 7, 639–650.

Hobbie, J.E., Carpenter, S.R., Grimm, N.B., Gosz, J.R., Seastedt, T.R., 2003. The US Long Term Ecological Research Program. Bioscience 53, 21–32.

Hobbs, R.J., Yates, S., Mooney, H.A., 2007. Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. Ecological Monographs 77, 545–568.

Holmgren, R.C., 1975. The desert experiment range: description, history, and program. In: Hyder, D.N. (Ed.), Arid Shrublands: Proceedings of the Third Workshop of the United States/Australian Rangelands Panel, Tucson AZ, March 26–April 5, 1973. Society for Range Management, Denver, pp. 18–25.

Hull, A.C., Klomp, G.J., 1967. Thickening and spread of crested wheatgrass stands on southern Idaho ranges. Journal of Range Management 20, 222–227.

Jarnevitch, C.S., Stohlgren, T.J., 2009. Temporal management of invasive species. In: Inderjit (Ed.), Management of Invasive Weeds. Springer, London, pp. 103–222.

King, D.M., Skirvin, S.M., Holifield Collins, C.D., Moran, M.S., Biedenbender, S.H., Kidwell, M.R., Weltz, M.A., Diaz-Gutierrez, A., 2008. Assessing vegetation change temporally and spatially in southeastern Arizona. Water Resources Research 44, 1–17.

Kowarik, I., 1995. Time lags in biological invasions with regard to success and failure of alien species. In: Pysek, P., Prach, K., Rejmanek, M., Wade, M. (Eds.), Plant Invasions: General Aspects and Special Problems. SPB Academic Publishing, Amsterdam, pp. 15–38.

Laycock, W.A., 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. Journal of Range Management 44, 427–433.

Lonsdale, W.M., 1993. Rates of spread of an invading species – Mimosa pigra in northern Australia. Journal of Ecology 81, 513–521.

Lugo, A.E., Swanson, F.J., Gonzalez, O.R., Adams, M.B., Palik, B., Thill, R.E., Brockway, D.G., Kern, C., Woodsmith, R., Musselman, R., 2006. Long-term research at the USDA Forest Service's Experimental Forests and Ranges. Bioscience 56, 39–48.

Mack, R.N., 1981. Invasion of Bromus tectorum L. into western North America: an ecological chronicle. Agro-ecosystems 7, 145–165.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10, 689–710.

Marlette, G.M., Anderson, J.E., 1986. Seed banks and propagule dispersal in crested wheatgrass stands. Journal of Applied Ecology 23, 161–175.

McClaran, M.P., Ffolliott, P.F., Edminster, C.B., 2003. Santa Rita Experimental Range: 100 Years (1903–2003) of Accomplishments and Contributions. RMRS-P-30. USDA Forest Service, Ogden.

McClaran, M.P., Browning, D.M., Huang, C., 2010. Temporal dynamics and spatial variability in desert grassland vegetation. In: Webb, R.H., Boyer, D.E., Turner, R.M. (Eds.), Repeat Photography: Methods and Applications in the Natural Sciences. Island Press, Washington DC, pp. 145–166.

Moran, V.C., Zimmerman, H.G., 1991. Biological control of jointed cactus, Opuntia aurantiaca (Cactaceae), in South Africa. Agriculture, Ecosystems and Environment 37, 5–27.

NRCS, 2012. The PLANTS Database, Version 3.5. NRCS. http://plants.usda.gov (accessed 29.02.12.).

Piemiesel, R.L., 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology 32, 53–72.

Pysek, P., Hulme, P.E., 2005. Spatio-temporal dynamics of plant invasions: linking pattern to process. Ecoscience 12, 302–315.

Pysek, P., Prach, K., 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. Journal of Biogeography 20, 413–420.

Pysek, P., Richardson, D.M., Rejmanek, M., Webster, G.L., Williamson, M., Kirschner, J., 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53, 131–143.

Radosevich, S.R., Stubbs, M.M., Ghersa, C.M., 2003. Plant invasions: process and patterns. Weed Science 51, 254–259.

Rejmanek, M., Pitcairn, M.J., 2002. When is eradication of exotic pest plants a realistic goal? In: Veitch, C.R., Clout, M. (Eds.), Turning the Tide: The Eradication of Invasive Species. IUCN SSC Invasive Species Specialist Group, Cambridge, pp. 249–253.

Ricciardi, A., Cohen, J., 2007. The invasiveness of an introduced species does not predict its impact. Biological Invasions 9, 309–315.

Rice, P.M., 2012. INVADERS Database System. Division of Biological Sciences, University of Montana. http://invader.dbs.umt.edu (accessed 29.02.12.).

Salo, L.F., 2005. Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. Biological Invasions 7, 165–180.

Silvertown, J., Charlesworth, D., 2001. Introduction to Plant Population Biology. Blackwell Science, London.

Strayer, D., Glitzenstein, J.S., Jones, C.G., Kolasa, J., Likens, G.E., McDonnell, M.J., Parker, G.G., Pickett, S.T., 1986. Long-term Ecological Studies: An Illustrated Account of their Design, Operation, and Importance to Ecology. The Institute of Ecosystem Studies, Millbrook.

Travnicek, A.J., Lym, R.G., Prosser, C., 2005. Fall-prescribed burn and spring-applied herbicide effects on Canada thistle control and soil seedbank in a northern mixed-grass prairie. Rangeland Ecology and Management 58, 413–422.

Van Gemerden, B.S., Etienne, R.S., Olff, H., Hommel, P., Van Langevelde, F., 2005. Reconciling methodologically different biodiversity assessments. Ecological Applications 15, 1747–1760.

West, N.E., 1979. Survival patterns of major perennials in salt desert shrub communities of southwestern Utah. Journal of Range Management 32, 442–445.

Williamson, M., Fitter, A., 1996. The varying success of invaders. Ecology 77, 1661–1666.

Yao, J., Peters, D.C., Havstad, K.M., Gibbens, R.P., Herrick, J.E., 2006. Multi-scale factors and long-term responses of Chihuahuan Desert grasses to drought. Landscape Ecology 21, 1217–1231.

Yin, X., Goudriaan, J., Latinga, E.A., Vos, J., Spiertz, H.J., 2003. A flexible sigmoid function of determinate growth. Annals of Botany 91, 361–371.