

(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

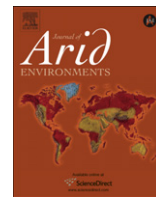
Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Constancy of local spread rates for buffelgrass (*Pennisetum ciliare* L.) in the Arizona Upland of the Sonoran Desert

A.D. Olsson^{a,*}, J.L. Betancourt^b, M.A. Crimmins^c, S.E. Marsh^d^a Lab of Landscape Ecology and Conservation Biology, College of Engineering, Forestry & Natural Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA^b United States Geologic Survey, USA^c Department of Soil, Water and Environmental Science, University of Arizona, USA^d Office of Arid Lands Studies, University of Arizona, USA

ARTICLE INFO

Article history:

Received 17 August 2011

Received in revised form

1 May 2012

Accepted 5 June 2012

Available online

Keywords:

Aerial photography

Chronosequence

Climate variability

Logistic growth

Monsoon

Phalanx

Spread rate

ABSTRACT

In North American deserts, grass invasions threaten native vegetation via competition and altered fire regimes. Accurate prediction and successful mitigation of these invasions hinge on estimation of spread rates and their degree of constancy in time and space. We used high-resolution aerial photographs from 11 sites in the Santa Catalina Mountains, southern Arizona to reconstruct the spread of buffelgrass (*Pennisetum ciliare*), a C₄ perennial bunchgrass, since 1980. The total area infested was fit to a logistic model and residuals of the model were compared to climatic factors of the corresponding and lagged time periods. Infestations grew from small colonizing patches in the 1980s to 66 ha in 2008, doubling every 2.26–7.04 years since 1988. Although buffelgrass germination, establishment and distribution are favored by wet summers and warm winters, climate variables did not predict spread rates. Buffelgrass has grown at a constant rate, at least since 1988, when much of its expansion took place. In the study area, minimum requirements are met almost every year for germination and reproduction, establishing a consistent baseline for spread that manifests as a constant spread rate.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Few plant invasions have been adequately mapped and measured to determine if spread rates are constant or variable in time and space, yet the distinction has important implications for invasive plant management. Field mapping of local invasion fronts through time is surprisingly rare (Bowers et al., 2006; D'Antonio, 1993). An alternative method relies on aerial photos taken in different years, provided that infestations are detectable from the air (Lonsdale, 1993). Presence-absence data from herbaria and floristic surveys also have been interpreted to map invasion at regional scales, with cumulative numbers of records over time used as a measure of increasing abundance (Forcella and Harvey, 1982; Hastings et al., 2005; Mihulka and Pysek, 2001; Salo, 2005).

Where spread rates vary through time, invasions may be characterized by periods of rapid spread followed by periods of slower spread, stasis, or even contraction associated with stochasticity

(Kleczkowski et al., 1996) and fluctuating access to resources (Chesson et al., 2004; Davis et al., 2000). The latter pattern is particularly pronounced in the North American deserts, where soil moisture varies considerably in space and time, notably on decadal timescales (Chesson et al., 2004; Reynolds et al., 2004; Salo, 2004). This makes accurate predictions of invasive spread difficult, particular when life cycle stages interact differentially with climate (Heller et al., 2008) or are lagged (Arim et al., 2006).

Establishing linkages between climate and invasive spread provides land managers with crucial information about utilizing resources temporally to maximize efficacy of control measures. For example, the C₃ winter annual grass, red brome (*Bromus madri-tensis* subsp. *rubens*) is more manageable in years and decades marked by dry winters and contracted populations in the Mojave and Sonoran Desert (Salo, 2004). In contrast, range expansions of some perennial species are invariant with respect to climate (Brown and Archer, 1999), suggesting that intrinsic population dynamics have more to do with range expansion than climate variability. In the former case, accurate predictions of invasive spread are difficult, but climate forecasts can be useful for identifying management opportunities. In the latter, range expansion is predictable, but climate variability may not yield windows of opportunity for more efficient treatment. This dichotomy may

* Corresponding author. Tel.: +1 928 523 7098; fax: +1 928 523 7423.

E-mail addresses: Aaryn.Olsson@nau.edu (A.D. Olsson), jlbetanc@usgs.gov (J.L. Betancourt), crimmins@email.arizona.edu (M.A. Crimmins), smarsh@email.arizona.edu (S.E. Marsh).

apply to ongoing invasions and management of non-native C_3 and C_4 grass invasions in the North American deserts.

In northern Mexico and southern Arizona, several non-native C_4 grasses have spread across ecosystems of the Sonoran Desert and have become locally dominant (Anable et al., 1992; Franklin et al., 2006; Olsson et al., 2012). The most problematic may be buffelgrass (*Pennisetum ciliare* L.). Buffelgrass is a C_4 perennial, apomictic bunchgrass native to Africa, southern Asia, Indonesia, Madagascar, and the Canary Islands and is considered invasive on three continents and numerous tropical and subtropical islands (Marshall et al., 2012; Williams and Baruch, 2000). Although numerous varieties were introduced to southern Arizona in the early 20th century as part of a world-wide search for productive and hardy range grasses, the common type (T-4464, collected from Kenya) is recognized as the most abundant type in the wild in southern Arizona (Van Devender et al., 1997). It is relatively long-lived and attains a height of up to 150 cm (USDA Plants, 2011). Its inflorescence is a spike-like panicle with sessile fascicles subtended by partially fused bristles. Fascicles disarticulate at maturity and seeds disperse by wind, water, animals, and humans (Burquez-Montijo et al., 2002). It grows in dense stands in the interstitial spaces of the Sonoran Desert and transforms succulent-rich desert scrub into depauperate buffelgrass-dominated savanna (Olsson et al., 2012).

Buffelgrass currently is undergoing rapid expansion in southern Arizona, prompting organized community-based efforts to prioritize and control its spread (<http://www.buffelgrass.org>). In the Tucson Basin, buffelgrass is poised to link upper elevation fuels with a complex low elevation wildlife–urban interface (Rogstad, 2008) (Fig. 1). Unfortunately, a detailed history of buffelgrass spread is lacking and the climatological conditions for its spread are poorly understood. We address both challenges in this study by reconstructing historical spread of buffelgrass of 11 known infestations on the south slope of the Santa Catalina Mountains, north of Tucson, since 1980, and assessing its expansion with respect to climate. Risk assessment, cost-benefit analysis, and long-term

mitigation strategies in management of invasions are all predicated on the ability to estimate local and regional invasion rates (Eiswerth and Johnson, 2002; Frid and Wilmschurst, 2009). Identifying drivers and rates of buffelgrass spread was a critical need identified at the first annual Buffelgrass Science Workshop in Tucson, AZ (May 4–6, 2010), and was essential to development of a regional decision support model constructed for the desert foothills of the Santa Catalina Mountains in Coronado National Forest (Frid et al., unpublished).

1.1. History of buffelgrass in southern Arizona

Buffelgrass was introduced repeatedly in and around Tucson, AZ from 1938 to the mid 1980s (Cox et al., 1988). It had naturalized by 1954 and was first reported in the Santa Catalina Mountains in 1969 (ARIZ Accession #21284). It was recognized as a weedy species in southern Arizona at least by 1983 (Burgess, 1991), although large-scale control efforts did not start until the late 1990s at Organ Pipe National Monument, Saguaro National Park, and Pima County's Tucson Mountain Park (Rutman and Dickson, 2002). Some of the largest buffelgrass patches in southern Arizona occur on the lower south-facing slopes of the Santa Catalina Mountains (Fig. 1) which not only link high elevation forest fuels with a complex low elevation wildland urban interface, but also support some of the densest populations of the giant saguaro cactus (*Carnegiea gigantea*) in the region (Niering and Lowe, 1984). Additionally, the abutting alluvial fans and terraces host the northern suburbs of Tucson, AZ, where several world class resorts are situated among pricey housing developments. Some of these fans, terraces, and rocky slopes of the Santa Catalina Mountains already are heavily infested with buffelgrass, and the dense patches can be seen at a distance (Fig. 2). Upslope of these infestations is a matrix of desert grassland that connects with high elevation conifer forests that supported 46,000 ha of wildfire in 2002 (Bullock fire) and 2003 (Aspen fire). The fires in 2002 and 2003 did not burn down to the wildland–urban

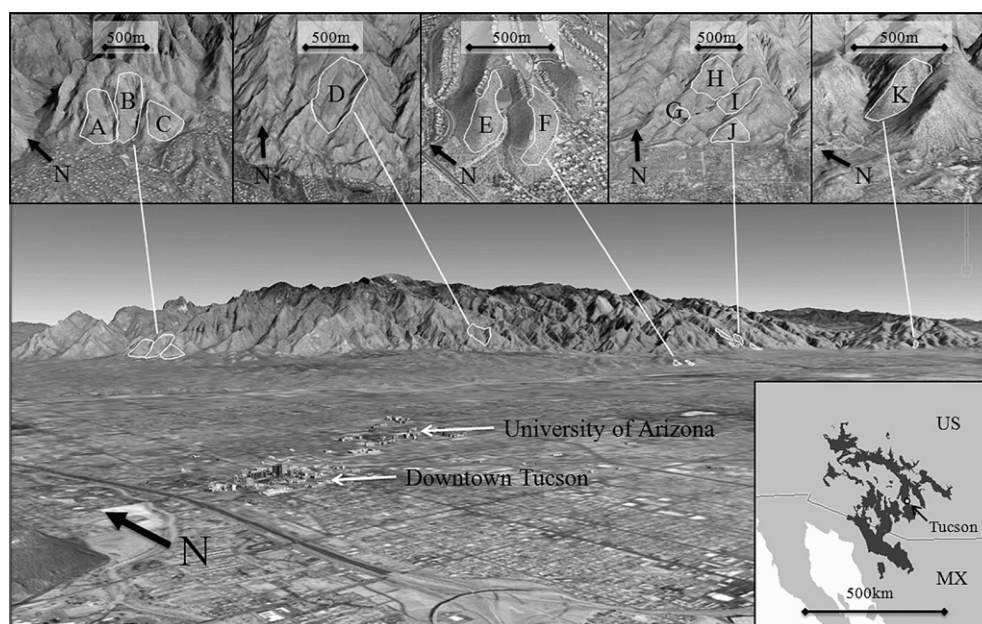


Fig. 1. Three-dimensional perspective of sites A–K (outlined in white) in relation to Tucson, AZ, and the Santa Catalina Mountains. Roads (dark linear features), houses (white block-like shapes), and golf courses (dark sinuous shapes in first two panels on left) portray the proximity of buffelgrass to human developments. The Arizona Upland forms a band of vegetation along the base of the Santa Catalina Mountains, effectively linking lower elevation human developments with upper elevation forest fuels. Inset shows Tucson's location with respect to the extents of the Arizona Upland vegetation zone of the Sonoran Desert (dark gray), 150 km north of the US–Mexico international border. Three-dimensional images, including the five top panels, were produced using Google Earth 5.1.3535.3218. Overlain imagery is from Nov. 11, 2009 (© Digital Globe, 2010). Inset map was created using ESRI® ArcMap™ 9.3.



Fig. 2. Arizona Upland vegetation experiencing invasion by buffelgrass (*Pennisetum ciliare*) at sites A, B, and C near the wildland–urban interface of Tucson, AZ. Buffelgrass (easily seen in orange in this November, 2007, photo) is a non-native perennial C_4 bunchgrass that forms dense continuous stands of highly flammable fine fuels. High cover of bare soil and rock effectively fire-protects the Arizona Upland, making wildfire uncommon (Schmid and Rogers, 1988; Swetnam and Betancourt, 1998). Dominant native plant species at these sites include *Parkinsonia microphylla* and *Carnegiea gigantea*.

interface because buffelgrass infestations were discrete and disconnected from upslope fuels, although ongoing spread of patches near the wildland–urban interface is worrisome. Control efforts in the Santa Catalina Mountains have been minimal and have not focused on large or remote backcountry patches, indicating that changes in the patterns and extents of these patches over time resulted from mostly natural processes of dispersal and spread.

1.2. Phalanx vs. guerilla patterns of spread

The spread of invading organisms can be described by a phalanx pattern, in which an invasive wave disperses along a tight, coherent front, or a guerilla pattern, by which new propagules appear in isolation from older source populations. The population growth accompanied by phalanx spread is most likely to be quadratic, as the area expands in proportion to the square of the radius of invasion distance. Wilson and Lee (1989) point out that most invasions exhibit both patterns and that dispersal characteristics and herbivory may explain the disparate patterns. Guerilla patterns lead to nonlinear changes in invader abundance as numerous remote infestations coalesce into larger patches (Moody and Mack, 1988). The growth of buffelgrass in the Arizona Uplands of the Santa Catalina Mountains exhibits both types of spread. Phalanx-type spread is easily observable on repeat historical photographs (Fig. 3).

2. Objectives

To understand and constrain invasion rates, we used aerial photography to estimate phalanx-type expansion of patches in the Catalina foothills and evaluated the role of climate variability in modulating the rate of spread. Though long-distance dispersal is a critical factor influencing the spread of invading organisms, including buffelgrass, we focused on phalanx-type spread in order to provide a lower bound on buffelgrass spread rates.

3. Materials and methods

3.1. Study area

This study was conducted on the south, lower slopes of the Santa Catalina Mountains, in habitat typical of the Arizona Upland, a subdivision of the Sonoran Desert (Turner and Brown, 1994) (photo: Fig. 2). The Arizona Upland is characterized by saguaro cactus and the small tree palo verde (*Parkinsonia microphylla*), but supports a diverse array of other trees, shrubs, cacti, forbs, grasses, and vines. Native plants are typically drought resistant or drought avoidant and either complete their life cycle during wet seasons (e.g., summer and winter annuals) or employ ecophysiological adaptations to survive periods of drought (Turner and Brown, 1994). The mean annual temperature of nearby Tucson, AZ, is 28.6°C , with four months of mean temperatures over 35°C (WRCC, 2010). Mean annual precipitation is 32 cm yr^{-1} and is bimodal, with approximately 60% falling during the summer monsoon (June–September) and the rest falling during winter and spring (WRCC, 2010). Summer rainfall is predictable from year to year but patchy in space; whereas winter precipitation is more variable in time but synchronous across the region.

3.2. Estimating the spread rate of buffelgrass

To determine the growth rate of buffelgrass, we reconstructed the historic spread of buffelgrass at 19 locations, or “sites”, in the vicinity of Tucson, AZ, using visual image interpretation of gray scale aerial photography dating back to the 1970s (Jensen, 2007). Sites were delineated manually based on the following guidelines: 1) Sites occur on non-overlapping watersheds. 2) Sites encapsulate a large present-day infestation in its entirety. 3) Sites are restricted to non-developed areas. 4) Sites are restricted to Arizona Upland ecosystems. 5) The shape of each site should be as simple as

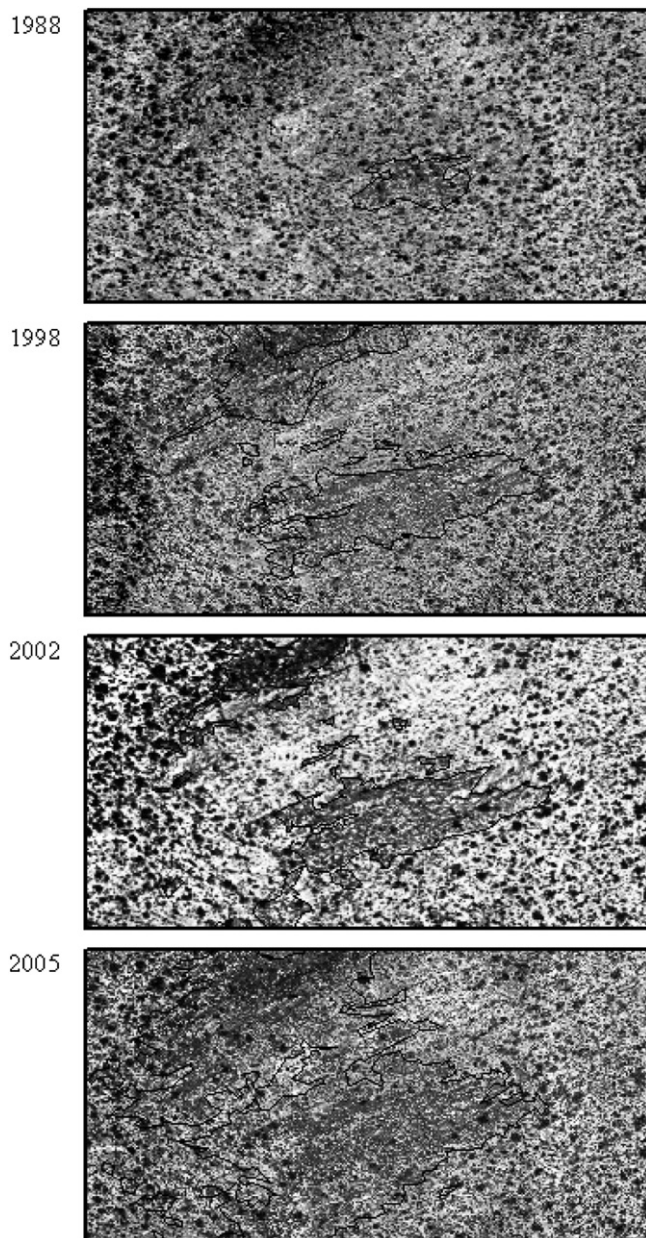


Fig. 3. Time series of aerial photography from site G. Digitized *P. ciliare* boundaries are outlined in black.

possible. These guidelines resulted in the delineation of 19 sites. We note also that the upslope limits of each site were drawn at either slope breaks or the desert scrub/desert grassland ecotone. Similarly, downslope limits were drawn to exclude riparian areas.

Aerial photographs were obtained from a private vendor (Cooper Aerial, Inc.) and Pima Association of Governments (PAG). Aerial photographs acquired between 1989 and 2002 were a mixture of 1:12,000, 1:24,000, and 1:25,000 scales. We registered these to 2005 USGS Digital Ortho Quarter Quads using a rubber-sheet model with 20–30 tie ground control points. True-color (four dates from 2002 to 2008) and gray scale (two dates: 1998 and 2000) PAG imagery, which varied in spatial scale from 0.3 m to 1 m, was geographically registered and terrain-corrected prior to our receiving it. Due to uncertainty in interpreting high resolution black and white historical imagery, infestations from more recent imagery were digitized first, and in successively older imagery the

extents were digitized only if the infestation was clearly visible and aspects of the infestation (e.g., internal patterning) were similar to the patch in later periods. The clarity of buffelgrass patches varied from image to image. Generally, in the black and white imagery, buffelgrass was darker than the surrounding desert soils and individual plants could be discerned by their round shape. In color imagery, the plants showed were darker brown than the light soils, although the 2003 imagery was acquired during the growing season so buffelgrass showed up as green, which differed again from the light native soil background in uninvaded areas. If any site had less than four quality images associated with it, that site was not considered for further analysis.

The growth rate of buffelgrass was calculated using a linear model and three nonlinear model types: quadratic, exponential, and logistic using the invaded area as the dependent variable and time as the independent variable. Each of the three nonlinear model types corresponds to a different ecological possibility. The quadratic model would be expected if expansion were described as a single frontal wave or discrete, non-overlapping waves with constant wave velocity. The exponential model would be expected if population is doubling at a constant rate, a common growth model in biology. In contrast, the logistic model would be expected if invading populations start running out of available space or approach a maximum population and the linear model would be expected if a growth front were to be moving through the study area. We used AIC to select the best of the four models using site-based models for all sites. For the rest of the analysis, modeling was restricted to one of these four model types (e.g., linear, exponential, logistic, quadratic).

The growth factor was measured for each site over the whole period of record using the linear least squares estimator (for linear models) or nonlinear least squares estimator (*nls*) in R. The growth factor was the coefficient for linear models or the exponent (*r*) for nonlinear models. For each site model, we calculated Aikake's Information Criterion (AIC) (Aikake, 1974), and the predicted doubling time from 2008. For exponential, and quadratic models, adjusted R^2 was calculated after log- or square root-transforming the area first. We solved formula (1) exactly for each pair of sequential image dates and interpolated site-level infested area during years without aerial photographs to come up with yearly estimates of total infested area across all sites. A pooled site model (PSM) was created by summing the infested areas (measured or interpolated) of all sites. The pooling of spread minimizes idiosyncratic growth of each patch due to different dates of first colonization or other local factors, while maximizing the history in spread that is shared among widely separated patches and is probably modulated by synchronicities in climate variability at the mesoscale (1–100 km). For logistic models, the carrying capacity of the PSM was simply the sum of carrying capacities of all contributing sites.

The software used in this analysis was R, version 2.13.2 compiled for 64-bit Windows 7. Only standard R libraries were used. R was used for additional analyses described below.

3.3. Assessing the role of climate in spread

We used monthly temperature and precipitation data acquired from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) dataset (<http://www.ocs.oregonstate.edu/prism/>) and determined precipitation and mean temperature for winter (December–March) and summer (June–September). Favorable (or unfavorable) climate patterns that influence spread may not result in visible increase in spread rate for several years because of lags in life history traits. This is compounded by uncertainty about which life stages are most important for increasing spread rate. If

fecundity is the dominant driver, then multiple-year lags are expected because of seed dormancy (3–18 months as per Winkworth, 1963), germination dependence on second and third-year precipitation, seedling growth rate, and the detectability of expansion in follow-up imagery. Together, these factors may contribute to increased spread rates being lagged behind favorable climate patterns by several years. In contrast, if seedling mortality is most limiting and both fecundity and germination are not limiting, then the presence of mature seedbank and seedlings on the landscape at the time of a favorable climate event will likely hasten spread and favorable climate patterns will be correlated with spread at shorter lag times. To account for these lags, we compared the growth rate of the pooled sites at each time period with the 3-year mean, minimum, and maximum of climate variables lagged from 0 to 5 using Pearson's r correlation and linear regression of growth rate vs. climate. We selected 3 years as the summarizing period because the average time between sequential image dates at all plots was 3.1.

4. Results

4.1. Buffelgrass expansion

We identified 11 sites, labeled A–K (Table 1, Fig. 1), for which four or more suitable historical photographs were found. In all cases, sites were limited to single south-facing slopes but they varied in size. Most notable was the difference in size between site D (32.0 ha) and site K (5.6 ha), which resulted from sites occurring on slope faces of disparate size (Fig. 2, Table 2). We note also that sites G and H share a watershed but they represent distinct patches in distant sections of a long, thin watershed. Since combining the two sites would result in a very large site (>100 ha) and we would lose our ability to measure phalanx spread in both sites, we chose to create two sites for this watershed. The oldest photograph in which buffelgrass was identified varied from 1980 to 1994 among the sites, although only one site had imagery predating 1988 containing identifiable buffelgrass. The minimum population detected varied with the timing and quality of imagery but was generally within 0.04 and 0.33 ha in size. The notable exception was site H, whose first detected infested area was 1.28 ha in 1988, and which had burned in the recent past. An example chronosequence showing aerial photographs for site G is given in Fig. 3.

In 2008, infested area varied from 0.4 to 7.0 ha, comprising 5.6%–26.9% of each site and 12.0% (21.2 ha) of the cumulative site area (Fig. 4, Table 1). AIC values indicate that nonlinear models were best for 10 of 11 sites with the one exception being site D,

Table 2

Aikaike's information Criterion for exponential, logistic, and quadratic growth models. The best model for each site is highlighted in bold.

Site	Model type			
	Linear	Exponential	Logistic	Quadratic
A	94.47	86.83	86.93	103.37
B	101.85	90.17	90.19	105.46
C	212.74	205.59	205.68	223.96
D	72.62	69.32	69.23	83.30
E	115.05	110.72	110.94	111.45
F	146.09	137.71	137.78	154.15
G	171.18	166.95	167.05	179.57
H	77.82	80.69	80.38	95.46
I	93.02	84.83	85.00	88.67
J	177.12	167.86	168.26	188.20
K	130.57	117.99	117.82	132.34

which only had four images available. Both exponential and logistic were better than quadratic at all sites with exponential being slightly better than logistic at eight sites vs. three sites for logistic, but the AIC values were virtually identical between the two model types at all 11 sites. Therefore, we selected the exponential model for all further analyses.

The growth exponent for the exponential model varied from 0.098 to 0.306 and corresponded with doubling times of 2.26–7.04 years (Table 3). The PSM was limited to 12 years (1995–2006). The exponential PSM model had a growth exponent of 0.119, which corresponds to a doubling time of 5.82 years.

4.2. Buffelgrass expansion and climate

Growth rate was slightly negatively correlated with winter precipitation but lacked consistent trends in winter temperature (Fig. 5). Growth rate was negatively correlated with summer precipitation for lags up to 3 years but positively correlated with summer precipitation from 4 years or earlier and only slightly positively correlated with summer temperature at 2–3 year lags. Overall, correlations with climate variables at all lags were low. Regression models of growth rate vs. climate variables at all lags were not significant at $p < 0.05$. Minimum summer precipitation had higher correlation than maximum summer precipitation for all lags but similar relationships were not found for winter covariates or summer temperature.

Table 1

Summary of 11 sites infested by buffelgrass. T_0 represents the first of n aerial photographs with discernable buffelgrass. The area of each site is given by K and the current area infested is given by N and the infested area (as of 2008) is calculated for the reader. % Invaded is N_{2008}/K .

Site	Patch information					
	n	K ha	T_0	N_0 ha	N_{2008} ha	% Invaded
A	5	22.4	1988	0.23	1.35	6.0
B	5	21.4	1988	0.12	1.48	6.9
C	11	14.6	1980	0.04	1.79	12.3
D	4	32.0	1994	0.13	1.77	5.6
E	5	6.65	1994	0.29	1.49	22.4
F	5	6.9	1994	0.09	0.86	12.5
G	9	16.1	1988	0.33	1.70	10.6
H	6	26.3	1993	1.28	7.04	26.8
I	8	12.1	1990	0.02	0.86	7.1
J	9	12.6	1988	0.13	2.46	19.5
K	8	5.6	1994	0.02	0.39	7.0
PSM	75	176.6	1980	2.67	21.2	12.0

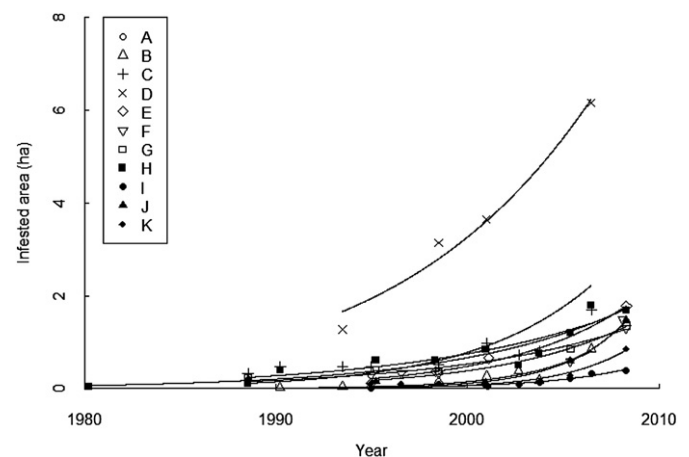


Fig. 4. Infested area (ha) at sites A–K in the Catalinas (symbols) and best fit logistic growth curves (lines) from 1980 to 2008.

Table 3

Exponential model results for 11 sites and the pooled site model (PSM). Columns include exponential power, r , adjusted R^2 of the log-transformed linear model, and the predicted doubling time (in years).

Site	r	Adj. R^2	Doubling time (years)
A	0.107	0.916	6.48
B	0.306	0.322	2.27
C	0.115	0.863	6.01
D	0.158	0.918	4.38
E	0.152	0.883	4.57
F	0.260	0.909	2.66
G	0.098	0.776	7.04
H	0.100	0.932	6.87
I	0.292	0.866	2.48
J	0.164	0.917	4.23
K	0.228	0.970	3.04
PSM	0.119	0.911	5.82

5. Discussion

Buffelgrass, a C_4 perennial grass, exhibited a near-constant spread rate in an ecosystem with patchy but low interannual variability in summer rainfall across the south slope of the Catalina Mountains of southern Arizona. Between 1989 and 2008, the observed rate of buffelgrass spread averaged across all sites in the Santa Catalina Mountains varied little and was well described by a logistic growth curve with small residuals. What minimal residuals we found were poorly described by external factors (e.g., low-frequency climate

variability). This does not mean, however, that near-constant spread rates can be assumed for all areas of ongoing or potential buffelgrass invasion, as both the spatial and temporal variances of summer rainfall vary widely across the Sonoran Desert. In the Sonoran Desert, interannual variability and patchiness of summer rainfall increases from east to west (Hawkins, 2003). Hypothetically, dry summers could decrease reproductive potential, increase mortality, and slow the rate of spread of buffelgrass.

Buffelgrass spread was most accurately modeled with an exponential growth model, although the logistic model was nearly as good. This model supports the hypothesis of a combination of guerilla and phalanx spread. We did not find enough evidence to suggest that buffelgrass growth was slowing as it reached the local carrying capacity, which we defined arbitrarily by the site polygonal boundary. The quadratic model, which represents a phalanx spread only, was not as well supported. Meanwhile, the linear model was the least supported model of all. The weak support for the linear model is not surprising given that sites were selected because they contained the centers of patches.

5.1. Implications for management

Cost-benefit analysis of invasive species requires accurate estimates of future scenarios under alternative management plans, which rely heavily on the ability to estimate spread rates (Frid et al., unpublished). The complexity of invasive spread and management necessitates a modeling approach to approximate outcomes to

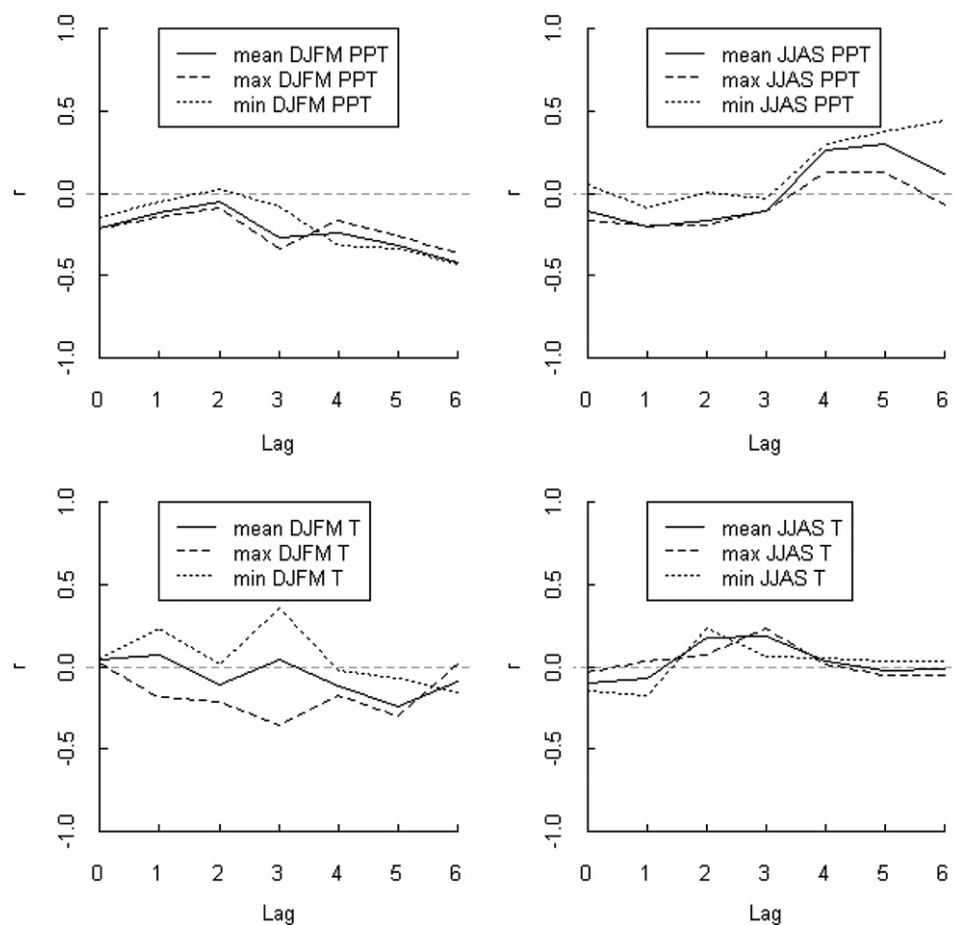


Fig. 5. Pearson's product moment correlation of pooled site growth rate with lagged seasonal (DJFM = winter, JJAS = summer) climate summaries (T = temperature, P = precipitation). Each data point represents the correlation of the residuals from the PSM with three-year summaries (mean, maximum, and minimum) of seasonal climate at lags of 0–6 years. For example, mean DJFM T at lag 4 correspond with correlation of spread rate with the mean winter temperature summarized over 4–6 years prior.

different management strategies, funding levels, and under different climate scenarios. Constant spread rates in time and space simplify the use of invasion dynamic models, while variable spread rates compound the uncertainties (Eiswerth and Johnson, 2002; Frid and Wilmschurst, 2009; Smith et al., 1999). Small changes in the spread rate are amplified due to nonlinearities in life cycle events and interactions with control efforts, yielding cascading effects on budgets and likelihood of success.

Managers will need to understand the conditions under which measured rates of spread are reduced or amplified in order to make headway against invasive spread. When the goal is containment or eradication, the area controlled each year must match or exceed the area newly invaded each year. Identifying the appropriate level of resources to match or exceed the minimum level of effort to contain an invasive species requires rather precise measurements of variable and uncertain parameters. Without knowing what that level is, managers risk implementing an unsustainable strategy in which effort is overwhelmed by logistic growth above their level of perceived control.

When rates of spread are invariant under varying climate, assessing the rate of spread dramatically reduces the uncertainty associated with levels of effort required for containment. At least with buffelgrass, growth from 1988 to 2008 was fairly constant. We caution here that our study did not characterize spread under cooler conditions prior to the 1980s, nor did it characterize the relatively wet decade of the 1980s when winter temperatures increased abruptly by 1 °C. We posit that buffelgrass spread may have accelerated at this time, particularly at higher elevations (1100–1400 m) in the Catalina foothills. The 1980's were not only warmer, but also wetter than the periods before and after. The evidence provided by the few large patches that likely persisted through that decade suggest that the accelerated growth occurred before our period of observation (1988–2008), but we are unable to determine the climate correlates of this.

6. Conclusion

Determining the rate of invasive spread is critical to guiding managers and ecologists to make informed choices about effective ecosystem management. Since 1988, buffelgrass spread has been relatively constant in the core monsoon areas of the Santa Catalina Mountains. Distinguishing the relative importance of summer precipitation, winter precipitation, and winter temperatures on the growth of C₄ grasses will help ecologists and managers identify critical opportunities for effective management while assessing rate of spread will help guide managers toward a critical base level for treatment effort to contain spread. We found little evidence that climate modulates spread rates in this ecosystem. Long-term studies are necessary to determine variations in the rate of buffelgrass spread over multi-decadal climate oscillations. Although they may now seem more or less constant, spread rates used to parameterize decision models may have to be occasionally updated and adjusted to accommodate an uncertain and changing climate.

Acknowledgments

This research was supported by National Science Foundation CTEAM grant 0753336 and USDA Program of Research on the Economics of Invasive Species Management (PREISM) grant 58-7000-6-0083. Pima Association of Governments and the Arizona Regional Image Archive freely provided historical images. The image archive provided by Cooper Aerial Photography was invaluable and we appreciate their generosity in allowing use of their imagery at reduced cost.

References

- Aikake, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19, 716–723.
- Anable, M., McClaran, M.P., Ruyle, G.B., 1992. Spread of introduced *Eragrostis lehmanniana* Nees. In: southern Arizona, USA. *Biological Conservation* 61 (3), 181–188.
- Arim, M., Abades, S.R., Neill, P.E., Lima, M., Marquet, P.A., 2006. Spread dynamics of invasive species. *Proceedings of the National Academy of Sciences USA* 103, 374–378.
- Bowers, J.E., Bean, T.M., Turner, R.M., 2006. Two decades of change in the distribution of exotic plants at the Desert laboratory, Tucson, Arizona. *Madroño* 53, 254–265.
- Brown, J.R., Archer, S., 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80, 2385–2396.
- Burgess, T.L., 1991. Exotic plants at the desert laboratory. *Madroño* 53, 254–265.
- Burquez-Montijo, A.M., Miller, M.E., Yrizar, A.M., Tellman, B., 2002. Mexican grasslands, thornscrub, and the transformation of the Sonoran Desert by invasive exotic buffelgrass (*Pennisetum ciliare*). In: Tellman, B. (Ed.), *Invasive Exotic Species in the Sonoran Region*. The University of Arizona Press – The Arizona-Sonora Desert Museum, Tucson, AZ, pp. 126–146.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A., Weltzin, J.F., 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141, 236–253.
- Cox, J.R., Martin, M.H., Ibarra, F.A., Fourie, J.H., Rethman, J.F.G., Wilcox, D.G., 1988. The influence of climate and soils on the distribution of 4 African grasses. *Journal of Range Management* 41, 127–139.
- D'Antonio, C.M., 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74, 83–95.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88, 528–534.
- Eiswerth, M.E., Johnson, W.S., 2002. Managing nonindigenous invasive species: insights from dynamic analysis. *Environmental and Resource Economics* 23, 319–342.
- Forcella, F., Harvey, S., 1982. Spread of *Filago arvensis* L. (Compositae) in the United States. *Madroño* 29, 119–121.
- Franklin, K., Lyons, K., Nagler, P., Lampkin, D., Molina, F., Glenn, E., Markow, T., Huete, A., 2006. Buffelgrass (*Pennisetum ciliare*) land conversion and productivity in the plains of Sonora, Mexico. *Biological Conservation* 127, 62–71.
- Frid, L., Wilmschurst, J.F., 2009. Decision analysis to evaluate control strategies for Crested Wheatgrass (*Agropyron cristatum*) in grasslands national park of Canada. *Invasive Plant Science and Management* 2, 324–336.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C., Thomson, 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8, 91–101.
- Hawkins, T.W., 2003. Geostatistical analysis of summertime precipitation. *Journal of the Arizona-Nevada Academy of Science* 36 (1), 9–17.
- Heller, N.E., Sanders, N.J., Shors, J.W., Gordon, M., 2008. Rainfall facilitates the spread, and time alters the impact, of the invasive Argentine ant. *Oecologia* 155, 385–395.
- Jensen, J.R., 2007. Remote Sensing of the Environment: An Earth Resource Perspective, second ed. Prentice Hall, Upper Saddle River, NJ, 592 p.
- Kleczkowski, A., Bailey, D.J., Gilligan, C.A., 1996. Dynamically generated variability in plant-pathogen systems with biological control. *Proceedings of the Royal Society of London: Biological Sciences* 263, 777–783.
- Lonsdale, W.M., 1993. Rates of spread of an invading species: *Mimosa pigra* in Northern Australia. *Journal of Ecology* 81, 513–521.
- Marshall, V.M., Lewis, M.M., Ostendorf, B., 2012. Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: a review. *Journal of Arid Environments* 78, 1–12.
- Mihulka, S., Pysek, P., 2001. Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years. *Journal of Biogeography* 28, 597–609.
- Moody, M.E., Mack, R.N., 1988. Controlling the spread of plant invasions – the importance of Nascent Foci. *Journal of Applied Ecology* 25, 1009–1021.
- Niering, W.A., Lowe, C.H., 1984. Vegetation of the Santa Catalina Mountains – community types and dynamics. *Vegetation* 58, 3–28.
- Olsson, A.D., Betancourt, J., McClaran, M.P., Marsh, S.E., 2012. Sonoran Desert ecosystem transformation by a C₄ grass without the grass/fire cycle. *Diversity and Distributions* 18 (1), 10–21.
- Reynolds, J.F., Kemp, P.R., Ogle, K., Fernandez, R.J., 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141, 194–210.
- Rogstad, A., 2008. In: Rogstad, A. (Ed.), *The Buffelgrass Strategic Plan*. Arizona-Sonora Desert Museum, Tucson, AZ.
- Rutman, S., Dickson, L., 2002. Management of buffelgrass on organ pipe cactus national monument, Arizona. In: Tellman, B. (Ed.), *Invasive Exotic Species in the Sonoran Region*. University of Arizona Press, Tucson, pp. 311–330.
- Salo, L.F., 2004. Population dynamics of red brome (*Bromus madritensis* subsp. *rubens*): times for concern, opportunities for management. *Journal of Arid Environments* 57, 291–296.
- 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.

- Schmid, M.K., Rogers, G.F., 1988. Trends in fire occurrence in the Arizona Upland subdivision of the Sonoran Desert, 1955 to 1983. *Southwestern Naturalist* 33, 437–444.
- Smith, H.A., Johnson, W.S., Shonkwiler, J.S., Swanson, S.R., 1999. The implications of variable or constant expansion rates in invasive weed infestations. *Weed Science* 47, 62–66.
- Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climatology* 11, 3128–3147.
- Turner, R., Brown, D.E., 1994. Sonoran Desert scrub. In: Brown, D.E. (Ed.), *Biotic Communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake, pp. 181–221.
- Van Devender, T.R., Felger, R.S., Burquez, A., 1997. Exotic plants in the Sonoran Desert region, Arizona and Sonora. In: 1997 Symposium Proceedings. California Exotic Pest Plant Council.
- Williams, D.G., Baruch, Z., 2000. African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions* 2, 123–140.
- Wilson, J.B., Lee, W.G., 1989. Infiltration invasion. *Functional Ecology* 3, 379–380.
- Winkworth, R.E., 1963. Germination of buffel grass (*Cenchrus ciliaris*) seed after burial in a Central Australian soil. *Australian Journal of Experimental Agriculture and Animal Husbandry* 3, 326–328.
- WRCC, 2010. Arizona Climate Summaries. Western Regional Climate Center. <http://www.wrcc.dri.edu/summary/climsmaz.html> (accessed 19.04.10.).