

Old-field successional dynamics on the Inland Pampa, Argentina

Omacini, M.*, Chaneton, E.J., León, R.J.C. & Batista, W.B.¹

Departamento de Ecología, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina; ¹Present address: Department of Plant Biology, Louisiana State University, Baton Rouge, LA 70803, USA; *Author for correspondence; Fax +54 1 5211384; E-mail RVMARINA@CRIBA.EDU.AR

Abstract. The first 10 yr of old-field successional dynamics on the Argentine Inland Pampa were studied on a series of adjacent plots established consecutively between 1978 and 1989. We examined differences in species abundance patterns among plots in order to detect the spatial and temporal variability of succession. Perennial grasses steadily increased in cover and replaced the dominant annual species after 5 yr. Pioneer dicots persisted in older seral stages with 20 - 23 species/plot. Overall, exotic species (mostly the grasses *Lolium multiflorum* and *Cynodon dactylon*) contributed much to the plant cover in these communities. Native grasses comprised 45 % of total cover at years 7 - 10 of succession, but occurred with less than 7 species/plot. Substantial variation was found in the successional pathway, which reflected the particular sequence from annual forbs to short-lived and perennial grasses in the various plots. The course of succession was apparently influenced by a 2-yr period of unusually high rainfall. *Deyeuxia viridiflavescens*, a native perennial grass virtually absent before the wet period, spread over the study area and dominated seral communities for 3 yr, irrespective of plot age. Climatic conditions thus affected the successional turnover of life forms by increasing the rate of colonization by perennial grasses. We further point out the constraints imposed on secondary succession by the life histories of 'available' species.

Keywords: Climatic fluctuation; Colonization; Exotic; Grassland; Life history; Native species; Stochastic process.

Nomenclature: Cabrera & Zardini (1978).

Introduction

Plant succession often exhibits regularity in life-form abundance patterns because of predictable replacement of species by other species with a different life history, colonization ability, or growth rate (Noble & Slatyer 1980; Brown & Southwood 1987; Huston & Smith 1987; Tilman 1988). However, successional pathways may display spatial and temporal variability owing to deterministic factors, e.g. soil conditions (Christensen

& Peet 1984; Inouye & Tilman 1988), or to stochastic factors, e.g. dispersal processes (Gleason 1926) and arrival order of species (Robinson & Dickerson 1987; Inouye & Tilman 1988; Drake 1990). The pattern and rate of succession may also be stochastically affected by allogenic environmental fluctuation (Austin et al. 1981; Walker et al. 1986), and infrequent climatic events (Tilman & El Haddi 1992). Recently, attention has been focused on the factors generating variability of successional trajectories (Pickett et al. 1987). Yet, few studies have clearly shown the effect of climate fluctuation on the dynamics of plant succession (Austin et al. 1981; cf. van der Maarel 1981; Figueroa & Davy 1991).

Native grasslands of the Inland Pampa in eastern Argentina have been extensively converted to agricultural lands since the late 1800s (León et al. 1984; Hall et al. 1992). At present, there is no reliable description of advanced stages of grassland secondary succession, which presumably comprise a diverse mixture of perennial, tall and mid-height grasses (Cabrera 1969; Burkart 1975; León et al. 1984). Secondary succession in the Inland Pampa proceeds on abandoned crop fields, and on mowed or maturing pastures. Previous studies documented the first five years of post-agricultural succession (D'Angela et al. 1986; Facelli & D'Angela 1990). Old-field vegetation was initially dominated by annual forbs, which were replaced by *Lolium multiflorum*, an introduced annual grass, after 3 yr (D'Angela et al. 1986; Facelli et al. 1987). An increase in richness and abundance of native perennial grasses did not occur within 5 yr of abandonment. The time for invasion of native grasses has been related to their scarcity in the soil seed bank (D'Angela et al. 1988), and the slow arrival of propagules from distant sources (Facelli et al. 1987, 1988).

Our objective in this study was to analyse the first 10 yr of old-field succession in a highly fragmented agricultural landscape of the Inland Pampa region. Changes in plant community composition during succession were described in 10 adjacent experimental plots, established sequentially between 1978 and 1989. We particularly

focused on seral stages defined by the colonization and early recovery of native grass species. We examined the variability in species replacement patterns among successional sequences initiated in different years. The available design allowed the simultaneous monitoring of plant communities developed on the same substrate, but influenced by changing 'boundary' conditions (Pickett 1989). In our experimental system, seral communities established in consecutive years experienced different climate histories, and different scenarios of propagule availability. Long-term observations made it possible to encompass the annual variation in rainfall as a potential factor influencing vegetation dynamics (Pickett 1989; Tilman 1989).

Methods

Study area

The study took place on a farm of the University of Buenos Aires (Estancia San Claudio, 36° S 61° 5' W) in the flat Inland Pampa, 400 km west of Buenos Aires (Fig. 1; Soriano 1992). The climate is subhumid with mean temperatures of 23.4 °C in January and 8.2 °C in July. Average annual precipitation was 870 mm for the period 1916 - 1970, ranging from 480 - 1442 mm. During the study period there was a large fluctuation in annual precipitation: average 911.5 mm, SD 190 mm. Extreme rainfall occurred from the spring of 1985 to the spring of 1987 (Fig. 1).

The landscape physiognomy is determined by land-use patterns with cropland and pastures interspersed. Intensive farming and livestock grazing dramatically reduced the area covered by natural grasslands, which are nowadays confined to small remnants in a patchwork of crop fields, grazed pastures, planted woods, and roadsides. To our knowledge true relicts of original grasslands do not exist today (León et al. 1984; Soriano 1992). Dominant soils in the study site are upland, well-drained Typic Hapludolls evolved on eolic deposits. Fields are usually under cultivation, through yearly rotations of sunflower, maize, wheat, sorghum, and soybeans (Hall et al. 1992). Small, frequently water-logged swales punctuate the cropping areas.

Succession plots and sampling

Vegetation was sampled in a series of experimental plots located at the center of a 290-ha field which had been cultivated for at least 25 yr. 10 contiguous plots, each 40 m × 100 m, were sequentially marked and fenced in the fall after the summer crop harvest, one per year from 1978 to 1989, except 1986 - 1987. Details on crop-

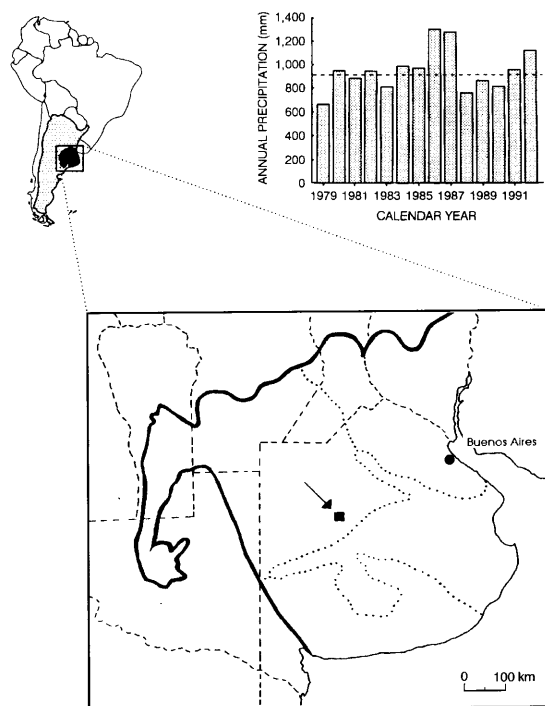


Fig. 1. Location of the study site in the Argentine Inland Pampa. Annual variability in total precipitation during the study period is shown in the inset; the line indicates the long-term average. Dotted lines on the map indicate the limits of Pampean phytogeographic districts (by R.J.C. León, in Soriano 1992).

ping history and years of abandonment are given elsewhere (D'Angela et al. 1986; Facelli & D'Angela 1990). Plots adjoined along their long edge formed a 4-ha uncultivated 'island'. Soils were moderately fertile: total N-content ranged from 1500 - 2400 mg/kg in plots aged 1 - 10 yr. Percent aerial cover of vascular plant species was visually estimated on each plot every late spring from 1979 to 1992 using 20 1 m × 1 m quadrats randomly placed along 4 parallel 80-m long transects. Access to the study site was impaired by extensive floods during the period 1985 - 1987; therefore we were forced to interrupt both plot fencing and vegetation sampling, which were resumed in 1987. Two other plots were established in 1988 - 1989. Sampling of the oldest plots, named A to D (Facelli & D'Angela 1990), was discontinued after 1987 because they were affected by an accidental spring fire.

Data analysis

Plant species were grouped by life form into annual dicots, perennial dicots, annual grasses, and perennial grasses; sedges were all considered separately. Species were also separated into natives and exotics (introduced in the Pampas with the European settlement). We first

described the average successional sequence in the study system by regarding plots as replicates of the same successional process (despite different establishment year and weather history). This followed the approach used by D'Angela et al. (1986; Facelli et al. 1987) to study pioneer stages of succession. Changes in the abundance of plant groups were computed by averaging values of relative cover recorded in different plots achieving a given successional age on different calendar years. Here, year 1 of succession will refer to the first spring after abandonment from agriculture.

Second, we examined the variability in successional pathway. We compared the average cover achieved by major plant groups and dominant species in plots of the same successional age, before and after the 2-yr period of high rainfall that affected the study area. Differences in plant abundance were tested separately for various successional ages with one-way ANOVA of data collected in 1981-1984 vs. 1987-1990. The analysis addressed differences between plot groups attaining 1-6 yr of succession before and after the wet period. Also, temporal changes in the abundance of dominant grass species were analysed in four adjacent plots (named E to H) that were chosen because they encompassed the longest and more complete records of the entire series, within the available data set. While two of these plots, E and F, were affected by the 2-yr period of above-average rainfall (1985-1987) at least 2 yr after abandonment (year 3-5), the other two, G and H, experienced the wet period at the earliest stages of succession (years 1-3).

Results

General pattern of succession

The total plant cover increased from $62.2 \pm 14.1\%$ (mean \pm SD) in the first year of abandonment to $83.7 \pm 5.4\%$ after 10 yr of succession. Plots were dominated by annual and perennial forbs for 3 yr until they were replaced by *Lolium multiflorum* (Fig. 2). Yet herbaceous dicots persisted with relatively high abundances (15-30% cover) throughout the 10-yr period. Forbs comprised 20-23 species per plot at year 6-10, of which only two (exotics) achieved 5% cover: the annual thistle *Carduus acanthoides* and the perennial rosette plant *Hypochoeris radicata*.

The average cover of perennial grasses increased steadily from year 1 to 7, and then levelled off (Fig. 2). Perennial grasses dominated all plots after 5 yr of secondary succession, reaching 50-60% of the total cover. Major perennial grass species were the native *Bromus unioloides* and *Deyeuxia viridiflavescens*, and the introduced *Cynodon dactylon*. The former dominant annual

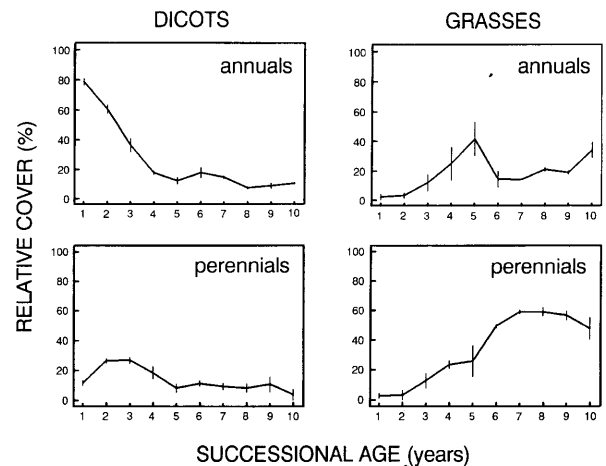


Fig. 2. Mean relative cover of plant life forms during 10 yr of post-agricultural succession in the Argentine Inland Pampa. Data were obtained by averaging species cover values recorded in different - adjacent - plots and calendar years (1979-1992). Vertical bars are back-transformed 95% confidence intervals, after arcsin square-root transformation of original data. Number of replicates varied from 2 to 8 (see Methods).

grass, *L. multiflorum*, decreased in cover by 50% after 5 yr and remained fairly constant thereafter (Fig. 2). Several native grasses which appeared frequently in these successional plots, e.g. *Setaria geniculata*, had low cover values per quadrat, while others, e.g. *Bothriochloa laguroides* and *Stipa neesiana* were scarce in all (Table 1). Sedges averaged less than 5% of the total plant cover in all plots. In total, 18 native perennial, 4 exotic perennial and 9 exotic annual grasses were recorded (complete data available upon request).

The average number of exotic species decreased by 40% along 10 yr of succession, whereas the richness of natives did not change in any consistent way (Fig. 3a). In all, the average total richness declined from 43 (SD=6.1) to 31 (5.7) species. Relative abundance of exotics was maximum at years 3-5 (Fig. 3b) when most plots were dominated by *L. multiflorum*. Exotic species always comprised more than 40% of the total cover. However, there was a turnover of exotic life forms, from annual forbs through annual grasses to perennial grasses. The contribution of native forbs - annuals + perennials - to old-field communities followed opposite dynamics to that of native grasses (Fig. 3b). Relative cover of native grasses (all perennial) increased to about 45% after 5 yr of abandonment, but their richness remained close to 5 species per plot along succession time (Fig. 3a).

Variability in the course of succession

There was substantial variation in relative cover of life forms among plots of the same age. The greatest

Table 1. Occurrence of major perennial grasses in old-field successional plots of the Inland Pampa during the 15-yr study period. Species presence is the number of times (year \times plot; max. = 63) the species appeared during the experiment; species frequency indicates the average number of quadrats per plot (max. = 20) where the species occurred. FG = functional groups by growing season: warm- (WS) and cool-season (CS). *Exotic species.

Species	FG	Presence	Frequency
<i>Setaria geniculata</i>	WS	58	7.2
<i>Bromus unioloides</i>	CS	46	10.7
<i>Cynodon dactylon</i> *	WS	43	8.9
<i>Deyeuxia viridiflavescens</i>	WS	37	12.5
<i>Paspalum distichum</i>	WS	31	3.6
<i>Leersia hexandra</i>	WS	31	4.8
<i>Sorghum halepense</i> *	WS	23	2.6
<i>Agrostis avenacea</i> *	CS	21	2.9
<i>Agrostis montevidensis</i>	CS	13	4.1
<i>Panicum bergii</i>	WS	10	3.0
<i>Briza subaristata</i>	CS	9	1.3
<i>Stipa neesiana</i>	CS	9	1.4
<i>Bothriochloa laguroides</i>	WS	8	1.0

variability was related to the abundance of annual and perennial grasses in the fourth and fifth year of succession (see Fig. 2). Analyses of variance revealed some remarkable differences between years before and after the humid period (Table 2). Cover of perennial grasses was higher after the 1985 - 1987 humid period for all ages (1-6) tested. Annual grasses (mostly *L. multiflorum*) had, on average, higher cover in years 3-5 of succession before 1985, although the ANOVA indicated that this pattern was not statistically consistent ($P < 0.20$). The average cover of the native perennial *D. viridiflavescens* was significantly larger after the wet period, particularly at years 4-6 (Table 2). The exotic *C. dactylon* showed significant differences for years 1, 4 and 5 of the succession, while the cover of the short-lived perennial *B. unioloides* did not change consistently between periods. Cover of other perennial (native) grasses showed small and often not significant differences ($P > 0.10$) between sampling periods (Table 2). Total cover of dicots was not essentially affected by the 2-yr wet period for the studied successional stages (see Table 2).

Comparison of changes in grass cover between plots initiated in 1982 - 1983 and 1984 - 1985 showed that in all four plots the same species alternated in dominance over the studied succession (Fig. 4). However, transient dominance by *D. viridiflavescens* occurred at different successional ages (from 4 to 7 yr) depending on the particular plots (Fig. 4). This native grass was virtually absent in the experimental system before 1985, but suddenly became conspicuous after 1987 (Fig. 5). In plots established later, G and H, dominance by *L. multiflorum* at years 4-5 did not occur as in E and F,

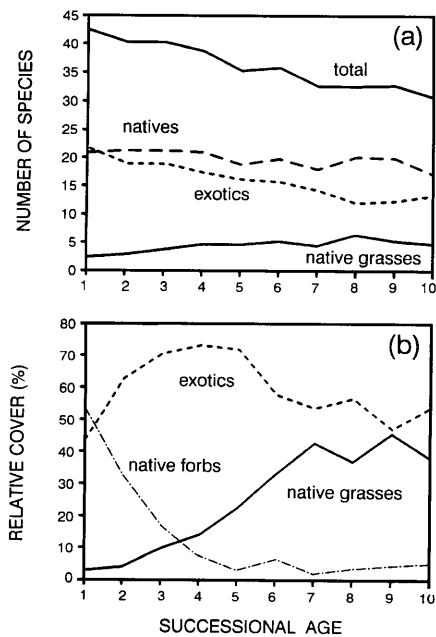


Fig. 3. Changes in number and relative abundance of native and exotic plant species during old-field succession in the Inland Pampa. Species number (richness) is the average total number of species per plot for a given successional age.

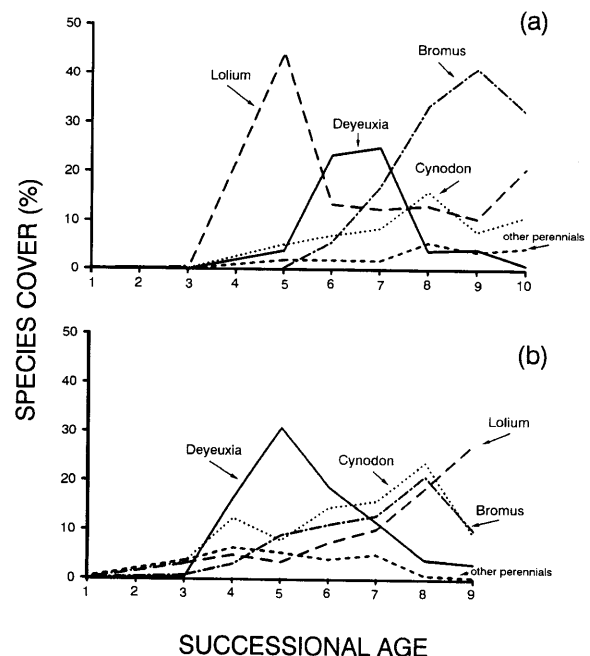


Fig. 4. Dynamics of dominant grasses during old-field succession in the Inland Pampa. Values are average species cover in plots which started succession before (a) and during (b) a 2-yr humid period. Species plotted are the exotics *Lolium multiflorum* (annual) and *Cynodon dactylon* (perennial), and the native perennial *Bromus unioloides* and *Deyeuxia viridiflavescens*. 'Other perennial' are natives grasses.

Table 2. Mean cover (%) of life forms and major perennial grasses in 1-yr to 6-yr old fields for two sampling periods: before (1981-1984) and after (1987-1990) a 2-yr humid period (see Fig. 1). Separated ANOVAs were performed to test for differences between periods for each successional age (F-test, $df = 1$ and $5 - 6$); years with zeros were not tested. Percentage cover data were arcsin-transformed prior to analyses. Significance of differences within a year: ** $P < 0.01$; * $P < 0.05$; # $P < 0.10$.

	Wet period	year 1	year 2	year 3	year 4	year 5	year 6
All dicots	before	64.86	64.78	49.20	18.37	11.58	22.37
	after	46.17	66.95	51.50	48.16 *	15.84	22.33
All annual grasses	before	6.61	0.14	14.01	37.6	42.57	15.24
	after	0.66	3.81 #	2.45	6.31 *	17.14	12.72
All perennial grasses	before	0.34	0.19	2.60	9.48	3.00	26.21
	after	8.02 *	21.35 *	33.58 *	32.13 *	42.53 *	40.42 #
<i>Deyeuxia viridiflavescens</i>	before	0	0	0.02	0.05	0.60	0.19
	after	0.17	8.62	13.13 #	10.13 *	23.25 *	25.19 *
<i>Bromus unioloides</i>	before	0	0	0.42	6.70	1.49	6.22
	after	0	0.02	0.04	2.01 #	5.98	6.83
<i>Cynodon dactylon</i>	before	0.07	0	0	0.21	0.26	14.94
	after	3.09 *	8.72	15.29	15.13 **	8.67 *	5.53
Other perennials	before	0.28	0.19	2.16	2.5	0.23	0.27
	after	4.76 *	3.97	4.73	4.85	3.50 *	2.42 #

those that initiated succession before the humid period. Instead, *D. viridiflavescens* attained maximum abundance in those years (Fig. 4b). This partly explained the variability observed in the relative abundance of grasses with different life histories at this stage (Fig. 2). In plots initiated earlier, *D. viridiflavescens* shared dominance with *L. multiflorum* at years 6-7, and was then replaced by the short-lived perennial *B. unioloides* (Fig. 4a). *L. multiflorum* persisted as co-dominant throughout this period. In contrast, in plots initiated later, the cover of *D. viridiflavescens* declined slowly, being replaced by a mixture of grasses with different life histories (Fig. 4b). All other native perennial grasses always accounted for less than 10% of the total cover in these plant communities.

Discussion

Plant communities developing on an agricultural field of the Inland Pampa exhibited a fairly consistent sequence of life forms through the first 10 yr of succession. Perennial grass species colonized successional plots soon after abandonment, and gradually replaced in dominance annual forbs and grasses (Fig. 2), resembling a pattern reported in various temperate systems (e.g. Brown & Southwood 1987; Inouye et al. 1987). Following a transient dominance by the native *D. viridiflavescens*, older stages comprised similar assemblages of grasses with contrasting growth periods (Fig. 4). Cool-season (C_3) grasses *B. unioloides* and *L. multiflorum* coexisted with the warm-season (C_4) grass *C. dactylon* through years 8-10, although in the field these species were often segregated in well-shaped patches (see

Armesto et al. 1991).

Annual and short-lived perennial grasses were major constituents of old-field communities over 10 yr of succession. *L. multiflorum* and *B. unioloides* were also the two principal invasive species in nearby abandoned pastures (Facelli et al. 1988). Both grasses form no permanent seed bank in the study plots (D'Angela et al. 1988). Yet their short life-span, large seed crop, and rapid growth would confer on these plants the ability to persist in relatively open communities (Grime 1979; Gross 1987). In general, secondary succession on rich soils, like those of pampean grasslands, would be particularly prone to the lasting dominance of fast growing, short-lived species (Tilman 1988; McLendon & Redente 1991). In addition, Chaneton et al. (1992) showed that litter produced by *L. multiflorum* strongly interferes with the regeneration of other species. Other authors noted that site pre-emption through litter accumulation may allow annual grasses to remain dominant in seral environments (Grime 1979; Facelli & Facelli 1993).

The number of plant species declined over successional time (Fig. 3a). The increase in total ground cover to ca. 85% during succession ($r = 0.80$, $P < 0.01$, $df = 8$) may have restricted opportunities for successful regeneration from seed (Grubb 1977; Gross 1987), inducing many exotic forbs to go locally extinct (Facelli et al. 1987; Chaneton et al. 1992). Nevertheless, many early dicots managed to persist in older seral stages contributing about 20% of the plant cover (cf. Inouye et al. 1987). Because most dicots in our system are not clonal species but annuals or short-lived perennial rosettes (e.g. *C. acanthoides*, *H. radicata*, *Cirsium vulgare*), their presence depends on seed availability and the generation of suitable sites for recruitment (Grubb 1977; Goldberg &

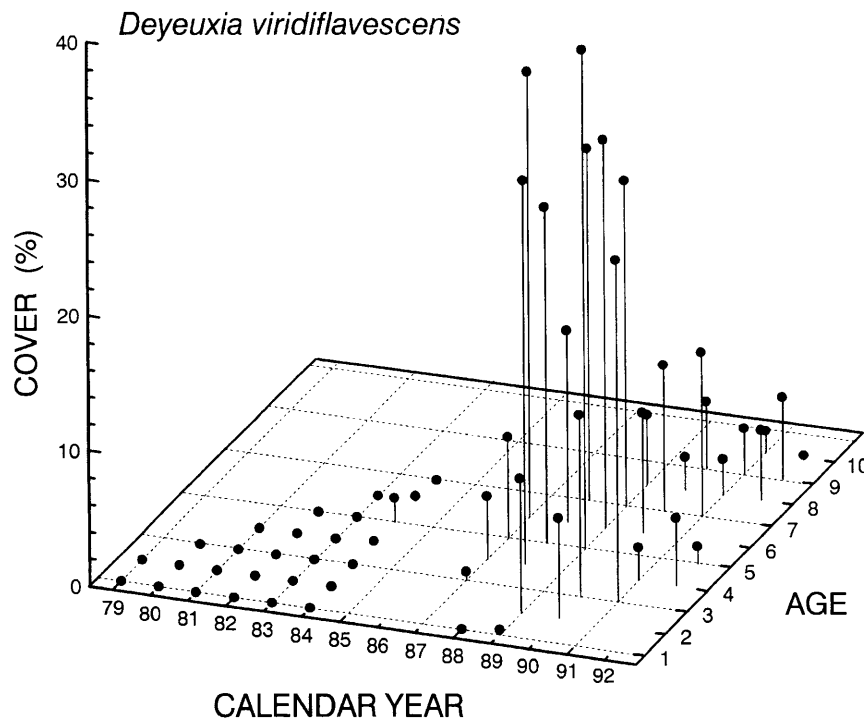


Fig. 5. Percent cover of *Deyeuxia viridiflavescens*, a native perennial grass, in all successional plots over the entire span of the study. Note that this species attained maximum cover in 1987-1989 in plots with 3 - 6 yr of secondary succession.

Gross 1988). Small canopy openings can be exploited by species forming persistent or transient seed banks (D'Angela et al. 1988), which are maintained by *in situ* regeneration and by immigration of propagules from surrounding crop fields (Gross 1987; Pulliam & Danielson 1991).

The early successional pattern (year 1-3) previously described for this system by D'Angela et al. (1986) did not change when we added new, recently established plots (i.e. fenced after 1984). Herbaceous dicots dominated the initial stage of succession even though novel sources of grass seeds were available in neighboring, later-successional communities. This suggests that colonization abilities of available species constrained the potential variability of pioneer stages (Noble & Slatyer 1980; Huston & Smith 1987).

We found, however, considerable variability at the transition in community dominance from annual forbs to annual/perennial grasses that took place in 4 - 7 yr of succession. Variation in the life-form pathway among plots (Fig. 4; Table 2) apparently resulted from the 2-yr period of unusually high rainfall, which affected successional sequences at different stages, depending on the year of abandonment. In plots not affected by the wet period before yr 4 ($n=6$), pioneer forbs were replaced by the exotic annual *L. multiflorum* (D'Angela et al. 1986), while in plots affected earlier ($n=4$), they were replaced by the native perennial *D. viridiflavescens*. Early displacement of ruderal dicots by short-lived grasses in

seral pampean grasslands has been attributed to differences in species life history and competitive ability (Facelli et al. 1987, 1988; D'Angela et al. 1988). In the present study, rapid invasion and subsequent dominance by the grass *D. viridiflavescens* were associated with an infrequent climatic event (see also Hobbs & Mooney 1991). This species synchronously dominated adjacent old-field communities for about three years, irrespective of their successional age (Fig. 5).

Several works demonstrated the impact of rainfall fluctuation on herbaceous vegetation dynamics (e.g. van der Maarel 1981; Figueroa & Davy 1991; Hobbs & Mooney 1991). Our results show that climate conditions not only altered the species turnover pattern, but also hastened the rate of succession observed during this long-term study. That is, perennial grasses peaked earlier during succession in old-field plots established after the wet period than in those initiated before (see Fig. 4). Facelli & D'Angela (1990) observed that the rate of early succession did not vary among plots, nor with age, for the period 1978 - 1984. Factors introducing variability in this succession probably encompassed differences in calendar year as a surrogate variable of propagule availability (see Pickett 1989). Notice that local invasion of certain plots by *D. viridiflavescens* determined novel propagule sources for the initial stages of younger plots. Thus, we also recorded shorter time lags for abundant colonization of native perennial grasses in newly initiated (1988 - 1989) seral communities (Fig. 5;

Table 2). Likewise, the increased abundance of *D. viridiflavescens* with age after the wet years (see Table 2) presumably combined weather effects with population-driven dynamics (Walker et al. 1986; Hobbs & Mooney 1991).

The native *D. viridiflavescens* thrives in swales and roadside ditches which remain waterlogged during part of the year. In years of favorable, humid conditions, such spots may act as sources for population dispersal onto sites otherwise held by other species (Pulliam & Danielson 1991). The ability of this grass to produce large amounts of wind-dispersed seeds further enhanced its spread across experimental plots. Hobbs & Mooney (1991) documented the episodic invasion of serpentine annual grasslands of California by the non-native *Bromus mollis*, which happened on gopher mounds in connection with abnormally high precipitation. In the successional communities we studied, it was a native species that benefited from changed environmental conditions. It has been found in disturbed pampean grasslands that soil water-logging during high rainfall years may negatively affect exotic species and prompt the recovery of native graminoids (Chaneton et al. 1988).

Native grasses became an important component of mid-successional plant communities, although the cover and richness of exotic species remained substantial (Fig. 3). Native perennial grasses that colonized early, e.g. *Stipa neesiana*, were sparse and failed to disperse across the study plots (Table 1). Long-lived grasses may exhibit reduced dispersal because of slow intrinsic population growth (Grime 1979; Glenn-Lewin 1980; Tilman 1988). But results may also suggest a role for the established vegetation in controlling local invasion by late-successional native species (Connell & Slatyer 1977; Tilman 1993). Major alien grasses in this succession, *L. multiflorum* and *C. dactylon*, are ubiquitous invaders of temperate grasslands (Mack 1989) which are known to compete effectively with native plants, arresting secondary succession (D'Antonio & Vitousek 1992).

The increased abundance of perennial grasses during succession was not accompanied by an increase in their richness (Fig. 3), with only two native species contributing > 10 % cover to old-field vegetation. A different pattern has been documented in Minnesota old fields (Inouye et al. 1987), where overall species richness increased with field age through invasion of native, true prairie species. Lack of recovery of native grass diversity in our system was apparent even regarding the old-field 'island' as a whole. This could certainly result from the time-span of the study (Glenn-Lewin 1980; Inouye et al. 1987). Nonetheless, since colonization by native grasses primarily depends on propagule arrival from distant sources (D'Angela et al. 1988), the site accessibility presumably interacted with native species'

traits limiting their local diversity (Fahrig 1992; del Moral & Wood 1993; Tilman 1993). We suggest that human impact on landscape configuration (León et al. 1984; Soriano 1992) affected the species pool available for colonizing successional sites in the Inland Pampa.

Overall, plant community dynamics in old fields of the Argentine Inland Pampa illustrate how the course of succession may be haphazardly affected by climatic events. Likewise, understanding the processes governing secondary succession in this agro-ecosystem needs to incorporate insights on life-history attributes of extant prairie species, as well as the constraints imposed by landscape structure on species availability and immigration rates.

Acknowledgements. We thank the many people that helped with field work, particularly S. Burkart and H. Trebino. The study benefited from constructive suggestions of M. Oesterheld. The comments of S.L. Collins, and three anonymous reviewers greatly improved the content of the paper. The Administración de Campos (UBA) warranted our long-term research at 'Estancia San Claudio', while the farm crew provided the necessary support. This work was funded by grants from the University of Buenos Aires (PID-AG-030).

References

- Armesto, J.J., Pickett, S.T.A. & McDonnell, M.J. 1991. Spatial heterogeneity during succession: a cyclic model of invasion and exclusion. In: Kolasa, J. & Pickett, S.T.A. (eds.) *Ecological heterogeneity*, pp. 256-269. Springer-Verlag, New York, NY.
- Austin, M.P., Williams, O.B. & Belbin, L. 1981. Grassland dynamics under sheep grazing in an Australian mediterranean type climate. *Vegetatio* 47: 201-211.
- Brown, V.K. & Southwood, T.R.E. 1987. Secondary succession: patterns and strategies. In: Gray, A.J., Crawley, M.J. & Edwards, P.J. (eds.) *Colonization, succession and stability*, pp. 315-337. Blackwell, Oxford.
- Burkart, A. 1975. Evolution of grasses and grasslands in South America. *Taxon* 24: 53-66.
- Cabrera, A.L. 1969. *Flora de la Provincia de Buenos Aires*. Colección Científica. I.N.T.A., Buenos Aires.
- Cabrera, A.L. & Zardini, E.M. 1978. *Manual de la Flora de los alrededores de Buenos Aires*. Acme, Buenos Aires.
- Chaneton, E.J., Facelli, J.M. & León, R.J.C. 1988. Floristic changes induced by flooding on grazed and ungrazed lowland grasslands in Argentina. *J. Range Manage.* 41: 495-499.
- Chaneton, E.J., Facelli, J.M. & León, R.J.C. 1992. Role of litter accumulation and seed availability in an early succession replacement sequence. *Bull. Ecol. Soc. Am.* 73: 136.
- Christensen, N.L. & Peet, R.K. 1984. Convergence during secondary forest succession. *J. Ecol.* 72: 25-36.
- Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succes-

- sion in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.
- D'Angela, E., Facelli, J.M. & Jacobo, E. 1988. The role of the permanent soil seed bank in early stages of a post-agricultural succession in the Inland Pampa. *Vegetatio* 74: 39-45.
- D'Angela, E., León, R.J.C. & Facelli, J.M. 1986. Pioneer stages in a secondary succession of a pampean subhumid grassland. *Flora* 178: 261-270.
- D'Antonio, C. & Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23: 63-87.
- del Moral, R. & Wood, D.M. 1993. Early primary succession on the volcano Mount St-Helens. *J. Veg. Sci.* 4: 223-234.
- Drake, J.A. 1990. Communities as assembled structures: Do rules govern pattern? *Trends Ecol. Evol.* 5: 159-164.
- Facelli, J.M. & D'Angela, E. 1990. Directionality, convergence, and rate of change during early succession in the Inland Pampa. *J. Veg. Sci.* 1: 255-260.
- Facelli, J.M. & Facelli, E. 1993. Interactions after death - plant litter controls priority effects in a successional plant community. *Oecologia (Berl.)* 95: 277-282.
- Facelli, J.M., D'Angela, E. & León, R.J.C. 1987. Diversity changes during pioneer stages in a subhumid pampean grassland succession. *Am. Midl. Nat.* 117: 17-25.
- Facelli, J.M., Montero, C.M. & León, R.J.C. 1988. Effect of different disturbance regimes on seminatural grasslands from the subhumid Pampa. *Flora* 180: 241-249.
- Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theor. Popul. Biol.* 41: 300-314.
- Figuroa, M.E. & Davy, A.J. 1991. Response of mediterranean grassland species to changing rainfall. *J. Ecol.* 79: 925-941.
- Gleason, H.A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 7-26.
- Glenn-Lewin, D.C. 1980. The individualistic nature of plant community development. *Vegetatio* 42: 141-146.
- Goldberg, D.E. & Gross, K.L. 1988. Disturbance regimes of midsuccessional old fields. *Ecology* 69: 1677-1688.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, Chichester.
- Gross, K.L. 1987. Mechanisms of colonization and species persistence in plant communities. In: Jordan, W.R., III, Gilpin, M.E. & Aber, J.D. (eds.) *Restoration ecology: a synthetic approach to ecological research*, pp. 174-188. Cambridge University Press, Cambridge.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Cambr. Philos. Soc.* 52: 107-145.
- Hall, A.J., Rebella, C.M., Ghera, C.M. & Culot, J.P. 1992. Field-crop systems of The Pampas. In: Pearson, C.J. (ed.) *Field crop ecosystems*, pp. 413-450. Elsevier, Amsterdam.
- Hobbs, R.J. & Mooney, H.A. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* 72: 59-68.
- Huston, M. & Smith, T. 1987. Plant succession: Life history and competition. *Am. Nat.* 130: 168-198.
- Inouye, R.S. & Tilman, D. 1988. Convergence and divergence of old-field plant communities along experimental nitrogen gradients. *Ecology* 69: 995-1004.
- Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J.R., Stillwell, M.A. & Zinnel, K.C. 1987. Old-field succession on a Minnesota sand plain. *Ecology* 68: 12-26.
- León, R.J.C., Rusch, G.M. & Oesterheld, M. 1984. Pastizales pampeanos - impacto agropecuario. *Phytocoenologia* 12: 201-218.
- Mack, R.N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. & Williamson, M. (eds.) *Biological invasions: a global perspective*, pp. 155-179. SCOPE 37. John Wiley & Sons, Chichester.
- McLendon, T. & Redente, E.F. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. *Ecology* 72: 2016-2024.
- Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 42: 5-22.
- Pickett, S.T.A. 1989. Space for time substitution as an alternative to long term studies. In: Likens, G.E. (ed.) *Long-term studies in ecology: approaches and alternatives*, pp. 110-135. Springer-Verlag, New York, NY.
- Pickett, S.T.A., Collins, S.L. & Armesto, J.J. 1987. Models, mechanisms and pathways of succession. *Bot. Rev.* 53: 335-371.
- Pulliam, H.R. & Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.* 137: S50-S66.
- Robinson, J.V. & Dickerson, J.E. 1987. Does invasion sequence affect community structure? *Ecology* 68: 587-595.
- Soriano, A. 1992. Rio de la Plata grasslands. In: Coupland, R.T. (ed.) *Natural grasslands: introduction and western hemisphere*. Ecosystems of the world 8A, pp. 367-407. Elsevier, Amsterdam.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ.
- Tilman, D. 1989. Ecological experimentation: strengths and conceptual problems. In: Likens, G.E. (ed.) *Long-term studies in ecology: approaches and alternatives*, pp. 137-157. Springer-Verlag, New York, NY.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-2191.
- Tilman, D. & El Haddi, A. 1992. Drought and biodiversity in grasslands. *Oecologia* 89: 257-264.
- van der Maarel, E. 1981. Fluctuation in a coastal dune grassland due to fluctuations in rainfall: experimental evidence. *Vegetatio* 47: 259-265.
- Walker, L.R., Zasada, J.C. & Chapin, F.S., III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* 67: 1243-1253.

Received 31 May 1994;

Revision received 27 December 1994;

Accepted 28 December 1994.