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Pollen production in the Poaceae family

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Total pollen production per inflorescence was studied in the most important species of the Poaceae family in the city of Córdoba in order to further our knowledge of the partial contribution of each species of this family to the total amount of pollen released into the atmosphere.

The contribution of grasses in a given area was estimated by counting the number of inflorescences in an area of one square meter. Four different representative areas of the city were selected. The number of pollen grains per anther and flowers per inflorescence was also estimated in order to obtain total pollen production per inflorescence.

Pollen production per inflorescence ranged from 14,500 to more than 22,000,000 pollen grains, the amount being clearly higher in the perennial species. Pollen production per square meter was higher in the mountains near the city and lower in areas of abandoned crops.

Only a few species are responsible for the majority of pollen produced. A phenological study is necessary in order to determine the temporal distribution of this pollen production and subsequent shedding.

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Pollen production in Poaceae has been estimated previously as part of various studies on breeding systems (de Vries 1974, Cruden 1977, Cruden & Miller-Ward 1981), seed production (de Vries 1971, Allison 1990), pollen shedding estimates (Beri & Anand 1971), and aerobiology (Smart et al. 1979). An important contribution to our knowledge of pollen production per anther in Poaceae was the study by Subba-Reddi & Reddi (1986). There are, however, only few studies dealing with the pollen production in of a whole plant or inflorescence and data on pollen production per anther obtained for a given species varies from author to author (Subba-Reddi & Reddi 1986).

Poaceae pollen is the main cause of pollinosis in Europe (D'Amato et al. 1998) and one of the main causes of pollinosis in the city of Córdoba, (Domínguez et al. 1995). Poaceae pollen have never been used as a diagnostic trait for distinguishing between genera or species as they share the same characteristics (stenopalynous) under light microscopy (Driessen et al. 1989). This means that in aerobiological studies all grass species are treated as one type, and the partial contribution from each species is usually not considered.

The present work is a complete study of the pollen production per inflorescence in grass species known in the city of Córdoba. Due to the morphological variability in grasses the total pollen production per inflorescence is reported instead of the total production per plant. The study has provided new information on the relative contribution of each species to the total amount of airborne pollen enabling us to estimate the average potential emission of pollen that can be spread by a grass inflorescence. This

information could be of great interest for future studies of reproduction in grasses, as well as for aerobiological studies.

MATERIAL AND METHODS

The study was carried out in the city of Córdoba and its surroundings (37°50'N and 4°45'W). The city is located in the south-western part of the Iberian Peninsula at 123 m above sea level and 135 km far from the south coast of Spain. The climate is Mediterranean with some continental features, and it is characterised by temperate, cold winters and dry, hot summers, with an annual average temperature of 18°C and an annual rainfall of 600 mm.

The plants were collected in four different areas (Fig. 1) comprising the most representative habitat of grasses growing in the city, in order to obtain a compilation of the total collection of grasses present in the city. Specimens from each species were placed in the University of Córdoba Herbarium. The four selected areas were:

- Zone I: Mountainous area located to the north of the city at the foot of the Sierra Morena Mountains. The vegetation is formed by an open oak forest, where *Quercus rotundifolia* Lam., *Q. suber* L., and *Olea europaea* L. are the main species, and with a well-developed herbaceous stratum without shrubs.
- Zone II: Area of grassland. Located in the north-eastern part of the city. This area is distinguished by the total absence of agricultural use and for the presence of well-developed grassland formed almost exclusively by grasses that cover a large surface area.
- Zone III: Area of abandoned crop land. Located in the south-western part of the city and characterised by the presence of pasture land in which grasses are not dominant.

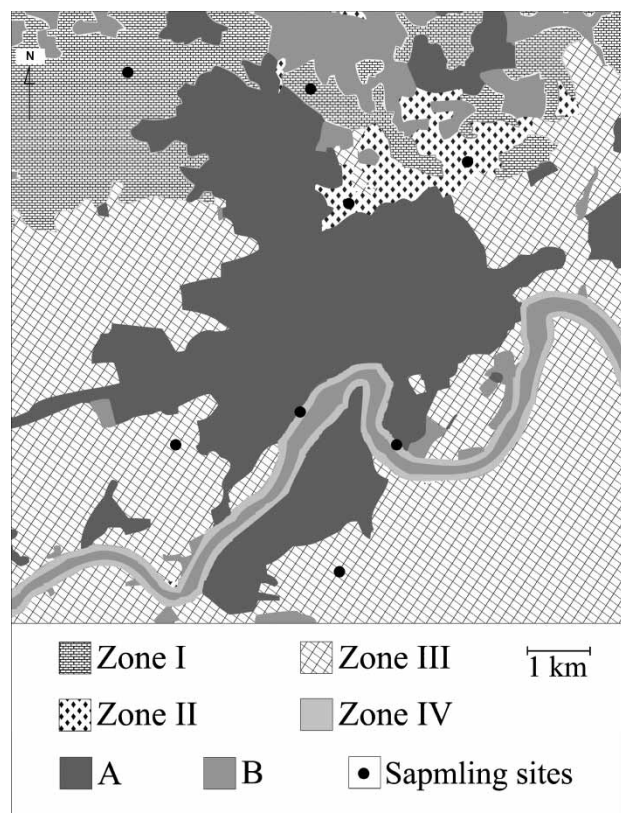


Fig. 1. Location of sampling areas in the city of Cordoba: (A) Urban network. (B) Water courses, mineral extraction sites and dense forested areas; • – Sampling sites; Zone I – Mountainous area; Zone II – Area of grassland; Zone III – Area of crop land; Zone IV – Riverside area.

– Zone IV: Riverside area. Located along the urbanized bank of the river Guadalquivir. The vegetation is made up by numerous riparian plants, including several grasses.

Due to climate in Córdoba and their high consumption of water grasses are not frequently used in the public gardens and thus the gardening areas of the city were not included in the present study.

The species were identified using a local flora (Valdés et al. 1987) and by comparison with authenticated herbarium specimens at the University of Córdoba Herbarium. The 38 studied species are listed in Tables I and II.

To estimate pollen production per inflorescence and total production in the selected areas a number of variables were studied for each species during 2000.

Number of pollen grains per anther was estimated by using the method of Cruden (1977). This method has also been used in other pollen production studies, such as those of Tormo et al. (1996) and Hidalgo et al. (1999). A total of nine mature and undehiscent anthers were extracted from three different plants and from three different flowers of each plant. To calculate the number of pollen grains per anther, each anther was crushed in 100 µl of distilled water colored with fuchsine. Three proportional samples of 10 µl were deposited on a slide and counted using a 4x lens and a 10x eye piece. Total pollen per anther was inferred from the data obtained. Finally, the number of pollen grains per flower were calculated by multiplying number of anthers per flower.

The number of flowers was calculated based on 30 inflorescences from each species. In most species number of spikelets per

inflorescence (mean of 30 inflorescences) and the number of flowers per spikelet (mean of 30 spikelets) were counted. The number of flowers per spikelet was constant in several species. The number of flowers per inflorescence was obtained by multiplying the two figures with exceptions of species with a small number of flowers (two species of the genus *Aegilops*) and species with compound inflorescences and a large number of flowers (*Cynodon dactylon*, *Hyparrhenia hirta*, *Piptatherum miliaceum*, and *Sorghum halepense*). Second order spikes or panicles of the inflorescence were counted (mean of 30 inflorescences), and multiplied by the number of spikelets of second order spike or panicle (mean of 30 spikes or panicles) and by the number of flowers per spikelet. Sterile flowers were not included in the counts.

Total pollen production per inflorescence was calculated by multiplying the number of pollen per flower by the number of flowers per inflorescence. Total production was expressed as the amount of pollen per inflorescence since it was sometimes very difficult to determine the number of inflorescences of a single plant, particularly in perennial species.

In order to calculate the number of inflorescences per square meter, a quadrat measuring 1 m² was randomly deposited ten times over the studied area. This method has been used previously by other authors in studies on grasses (Smart 1979). The total number of inflorescences was counted in each quadrant. The species present in the area but always kept outside the quadrants were considered as occasional.

This count was taken once in the Sierra region, in the grassland, and in the abandoned crop land, and due to the spectrum of species this did not vary substantially during the entire season. In the riverside area, the spectrum of species varied during the season and this count was repeated twice.

The total pollen production per square meter was calculated by multiplying total pollen production per inflorescence by the average number of inflorescences per square meter. This value was not calculated for occasional species.

For each measurement range, the average and coefficient of variation was calculated. A comparison of means test was performed by means of parametric analysis (paired samples Student t-test) and applied to the data obtained in the different measurements for genera that presented more than one species.

RESULTS

Number of pollen grains per anther and flower

The number of pollen grains per anther varied between 61 pollen grains in *Vulpia myuros* and 12,045 in *Arrhenatherum album* (Table I). Different results were obtained for species from the same genus. In some cases, there was no substantial intrageneric variation. This was true in the case of the two species of the genus *Avena*, with approximately 2,500 pollen grains per anther, and the two species of *Phalaris*, with approximately 1,000 pollen grains. In the four species of the genus *Bromus*, pollen production seemed to be of the same magnitude, although significant differences were observed between most of them (Tables I, III).

Furthermore, in other genera a significant difference was observed between species. Occasionally, pollen production within species of the same genus could vary with a factor two (*Aegilops triuncialis* and *A. geniculata*) or even with a factor three (*Holcus setiglumis* and *H. lanatus*, *Hordeum leporinum* and *H. marinum*). A more substantial difference was observed between the two species of *Vulpia* with *V. myuros* producing 60 times more pollen than *V. geniculata* (Tables I, III). Total number of pollen per flower is shown in Table II.

Table I. Pollen production of Poaceae species investigated.

1 – range; 2 – mean; 3 - coefficient of variation (%); * - number of flowers per inflorescence in *Aegilops*; ** - number of spikelets per spike or panicle.

Species	No. of pollen/anther			No. of flowers/spikelet			No. of spikelets/inflorescence			No. of 2nd order spikes v. panicles/inflorescence		
	1	2	3	1	2	3	1	2	3	1	2	3
<i>Aegilops geniculata</i>	(1,200–2,940)	2,066.66	(26)	(5–11)*	8.26*	(21)*						
<i>Aegilops triuncialis</i>	(2,640–5,840)	3,916.66	(20)	(6–8)*	7.50*	(13)*						
<i>Agrostis stolonifera</i>	(380–660)	546.29	(12)	(1–1)	1.00	(0)	(1,247–1,647)	1,480.66	(14)			
<i>Arrhenatherum album</i>	(8,720–19,760)	12,045.18	(20)	(2–2)	2.00	(0)	(25–165)	68.43	(47)			
<i>Avena barbata</i>	(1,480–3,750)	2,441.11	(20)	(2–2)	2.00	(0)	(12–133)	32.00	(73)			
<i>Avena sterilis</i>	(1,460–3,700)	2,451.48	(26)	(3–4)	3.93	(6)	(7–23)	12.03	(37)			
<i>Brachypodium distachyon</i>	(180–410)	297.40	(19)	(7–17)	13.00	(16)	(2–6)	3.80	(29)			
<i>Briza maxima</i>	(900–2,760)	1,572.22	(31)	(9–15)	11.23	(14)	(3–12)	5.93	(39)			
<i>Bromus diandrus</i>	(210–690)	420.37	(31)	(7–9)	7.86	(9)	(6–34)	19.56	(38)			
<i>Bromus hordeaceus</i>	(260–500)	369.62	(22)	(5–12)	8.93	(18)	(11–39)	24.76	(28)			
<i>Bromus lanceolatus</i>	(210–510)	330.37	(26)	(8–16)	11.93	(11)	(8–31)	16.27	(46)			
<i>Bromus matritensis</i>	(180–430)	299.44	(24)	(7–11)	9.40	(14)	(12–41)	22.86	(34)			
<i>Cynodon dactylon</i>	(1,740–3,620)	2,498.51	(18)	(1–1)	1.00	(0)	(24–67)**	40.26**	(27)**	(3–7)	5.06	(19)
<i>Cynosurus echinatus</i>	(4,620–10,920)	6,745.92	(23)	(2–4)	2.60	(22)	(22–75)	36.70	(40)			
<i>Dactylis glomerata</i>	(1,740–3,620)	3,475.18	(13)	(3–4)	3.53	(14)	(114–493)	216.60	(49)			
<i>Desmazeria rigida</i>	(80–170)	121.85	(19)	(5–8)	6.70	(10)	(16–63)	36.03	(36)			
<i>Elymus repens</i>	(3,680–8,730)	5,410.00	(29)	(3–6)	5.00	(16)	(13–30)	20.16	(21)			
<i>Festuca arundinacea</i>	(6,090–12,390)	8,941.81	(18)	(5–8)	5.90	(15)	(27–134)	74.13	(42)			
<i>Holcus lanatus</i>	(450–1,110)	663.33	(26)	(2–2)	2.00	(0)	(106–557)	220.03	(43)			
<i>Holcus setiglumis</i>	(1,140–2,640)	1,783.33	(24)	(2–2)	2.00	(0)	(119–247)	180.00	(36)			
<i>Hordeum leporinum</i>	(640–1,360)	999.62	(19)	(1–1)	1.00	(0)	(45–102)	81.90	(15)			
<i>Hordeum marinum</i>	(310–520)	371.11	(17)	(1–1)	1.00	(0)	(20–35)	27.77	(13)			
<i>Hyparrhenia hirta</i>	(1,110–4,200)	2,223.88	(38)	(1–1)	1.00	(0)	(15–22)**	17.56**	(11)**	(14–58)	24.06	(43)
<i>Lamarckia aurea</i>	(100–240)	168.18	(23)	(1–1)	1.00	(0)	(57–168)	94.60	(32)			
<i>Lolium rigidum</i>	(6,870–14,860)	10,453.33	(19)	(6–10)	7.76	(17)	(18–26)	21.66	(9)			
<i>Panicum repens</i>	(1,110–1,830)	1,457.40	(12)	(2–2)	2.00	(0)	(22–113)	50.06	(44)			
<i>Paspalum paspalodes</i>	(2,340–5,700)	4,316.66	(20)	(1–1)	1.00	(0)	(17–35)	26.74	(19)			
<i>Phalaris minor</i>	(770–1,610)	1,037.40	(22)	(1–1)	1.00	(0)	(114–442)	258.70	(26)			
<i>Phalaris paradoxa</i>	(700–1,350)	1,000.37	(20)	(1–1)	1.00	(0)	(47–166)	85.08	(46)			
<i>Piptatherum miliaceum</i>	(770–1,620)	1,052.22	(22)	(1–1)	1.00	(0)	(18–176)**	55.30**	(62)**	(23–42)	34.63	(14)
<i>Poa annua</i>	(210–510)	340.74	(22)	(2–2)	2.00	(0)	(45–77)	56.50	(16)			
<i>Polypogon monspeliensis</i>	(40–170)	91.11	(33)	(1–1)	1.00	(0)	(914–1,485)	1,215.00	(24)			
<i>Rostraria cristata</i>	(70–230)	114.51	(39)	(2–5)	3.66	(18)	(51–209)	121.16	(35)			
<i>Sorghum halepense</i>	(4,860–9,600)	7,140.00	(18)	(1–1)	1.00	(0)	(7–13)**	10.66**	(16)**	(49–156)	99.20	(28)
<i>Stipa capensis</i>	(360–1,280)	650.37	(38)	(1–1)	1.00	(0)	(34–168)	88.56	(37)			
<i>Trisetaria panicea</i>	(1,010–2,000)	1,392.59	(20)	(4–5)	4.68	(10)	(758–1,478)	1,086.00	(28)			
<i>Vulpia geniculata</i>	(2,050–5,840)	3,543.70	(32)	(2–4)	2.90	(19)	(36–246)	101.36	(54)			
<i>Vulpia myuros</i>	(20–140)	61.11	(47)	(5–9)	7.20	(17)	(7–71)	32.86	(55)			

Table II. Number of pollen grains per inflorescence.

1. No. of pollen grains per flower; 2. No. of flowers per inflorescence; 3. No. of pollen grains per inflorescence; 4. No. of inflorescences per square meter; 5. No. of pollen grains per square meter; I. Mountain area (Sierra); II. Grassland area; III. Abandoned crop land; IV. Riverside area; – - No presence; * - Occasional; + - Insignificant; A - annual; P - perennial.

		4							5				
Species		1	2	3	I	II	III	IV	I	II	III	IV	
<i>Vulpia myuros</i>	A	61.11	236.59	14,458	*	*	—	—	+	+	—	—	
<i>Hordeum marinum</i>	A	1,113.33	27.77	30,917	—	—	—	*	—	—	—	+	
<i>Brachypodium distachyon</i>	A	892.20	49.40	44,075	0.50	—	—	—	22,307	—	—	—	
<i>Lamarckia aurea</i>	A	504.54	94.60	46,878	*	*	3.00	—	+	+	14,063	—	
<i>Aegilops geniculata</i>	A	6,199.98	8.26	51,212	*	*	—	—	+	+	—	—	
<i>Aegilops triuncialis</i>	A	11,749.98	7.50	88,125	*	*	*	—	+	+	+	—	
<i>Desmazeria rigida</i>	A	365.55	241.40	88,244	—	—	*	—	—	—	+	—	
<i>Poa annua</i>	A	1,022.22	113.00	115,511	—	—	*	—	—	—	+	—	
<i>Bromus diandrus</i>	A	840.74	153.74	129,257	—	*	39.00	*	—	+	5,041,012	+	
<i>Rostraria cristata</i>	A	343.53	443.44	157,658	—	—	*	*	—	—	+	+	
<i>Stipa capensis</i>	A	1,951.11	88.56	172,790	*	343.28	—	—	+	59,315,455	—	—	
<i>Bromus lanceolatus</i>	A	991.11	194.10	192,376	*	*	*	*	+	+	+	+	
<i>Bromus matritensis</i>	A	898.32	214.88	193,035	*	*	*	*	+	+	+	+	
<i>Bromus hordeaceus</i>	A	1,108.86	221.10	245,176	*	*	*	*	+	+	+	+	
<i>Hordeum leporinum</i>	A	2,998.86	81.90	245,607	0.25	*	32.00	*	61,402	+	7,859,412	+	
<i>Phalaris paradoxa</i>	A	3,001.11	85.03	255,184	—	—	—	4.80	—	—	—	1,224,885	
<i>Briza maxima</i>	A	4,716.66	66.59	314,101	*	—	—	—	+	—	—	—	
<i>Paspalum paspalodes</i>	P	12,949.98	26.74	346,282	—	—	—	84.40	—	—	—	29,226,240	
<i>Avena sterilis</i>	A	7,354.44	47.27	347,702	*	*	0.33	0.20	+	+	114,742	69,540	
<i>Polypogon monspeliensis</i>	A	273.33	1215.00	405,851	—	—	—	71.30	—	—	—	23,675,842	
<i>Panicum repens</i>	P	4,372.20	100.12	437,745	—	—	—	28.80	—	—	—	12,607,046	
<i>Avena barbata</i>	A	7,323.33	64.00	468,693	1.25	20.14	*	*	585,866	9,439,479	+	+	
<i>Phalaris minor</i>	A	3,112.20	258.70	805,126	—	—	0.16	5.20	—	—	128,820	4,186,656	
<i>Holcus lanatus</i>	P	1,989.99	440.06	875,715	*	0.90	—	—	+	788,143	—	—	
<i>Cynodon dactylon</i>	P	7,495.53	204.01	1,529,163	—	—	—	10.90	—	—	—	16,667,878	
<i>Elymus repens</i>	P	16,230.00	100.80	1,635,984	—	—	—	50.00	—	—	—	81,799,200	
<i>Holcus setiglumis</i>	A	5,349.99	360.00	1,925,996	*	—	—	—	+	—	—	—	
<i>Cynosurus echinatus</i>	A	20,237.76	95.42	1,931,087	5.25	—	—	—	10,138,207	—	—	—	
<i>Agrostis stolonifera</i>	P	1,638.87	1,480.66	2,426,609	—	—	—	2.00	—	—	—	4,853,219	
<i>Hyparrhenia hirta</i>	P	6,671.64	422.77	2,820,582	13.50	*	—	—	38,077,856	+	—	—	
<i>Vulpia geniculata</i>	P	10,631.10	293.94	3,124,948	117.50	2.00	—	*	1,828,094,614	6,249,896	—	+	
<i>Arrhenatherum album</i>	P	36,135.54	136.86	4,945,510	*	—	—	—	+	—	—	—	
<i>Lolium rigidum</i>	A	31,359.99	168.08	5,271,037	30.25	*	13.66	9.40	159,448,878	+	72,002,369	49,547,751	
<i>Piptatherum miliaceum</i>	P	3,156.66	1,915.03	6,045,099	*	2.14	*	*	+	12,936,511	+	+	
<i>Dactylis glomerata</i>	P	10,425.54	764.60	7,971,347	2.25	10.28	—	—	17,935,531	81,945,447	—	—	
<i>Festuca arundinacea</i>	P	26,825.43	437.36	11,697,131	*	—	—	1.00	+	—	—	11,697,131	
<i>Trisetaria panicea</i>	A	4,177.77	5,093.34	21,278,803	3.75	31.42	—	*	79,795,511	668,579,992	—	+	
<i>Sorghum halepense</i>	P	21,420.00	1,058.13	22,665,145	—	*	*	—	—	+	+	—	
Total pollen production					174.50	410.16	88.15	268.00	2,134,159,903	839,254,924	85,286,990	235,555,388	

Table III. Means comparison test performed by means of parametric analysis (Paired samples Student *t* test) from data obtained in the measurements (Table I).

* - Number of flowers per inflorescence.

Genera	Paired samples t-test			Pollen grains per anther	Flowers per spikelet	Spikelets per inflorescence
<i>Aegilops</i>	<i>A. geniculata</i>	–	<i>A. triuncialis</i>	0.000	0.022*	–
<i>Avena</i>	<i>A. barbata</i>	–	<i>A. sterilis</i>	0.954	0.000	0.000
<i>Bromus</i>	<i>B. diandrus</i>	–	<i>B. hordeaceus</i>	0.032	0.004	0.010
	<i>B. diandrus</i>	–	<i>B. lanceolatus</i>	0.001	0.000	0.022
	<i>B. diandrus</i>	–	<i>B. matritensis</i>	0.000	0.000	0.099
	<i>B. hordeaceus</i>	–	<i>B. lanceolatus</i>	0.046	0.000	0.000
	<i>B. hordeaceus</i>	–	<i>B. matritensis</i>	0.001	0.250	0.391
	<i>B. lanceolatus</i>	–	<i>B. matritensis</i>	0.084	0.000	0.000
<i>Holcus</i>	<i>H. lanatus</i>	–	<i>H. setiglumis</i>	0.000	–	0.029
<i>Hordeum</i>	<i>H. leporinum</i>	–	<i>H. marinum</i>	0.000	–	0.000
<i>Phalaris</i>	<i>P. minor</i>	–	<i>P. paradoxa</i>	0.524	–	0.000
<i>Vulpia</i>	<i>V. geniculata</i>	–	<i>V. myuros</i>	0.000	0.000	0.000

Number of flowers per inflorescence

Approximately 50% of the species had a fixed number of flowers per spikelet. In the rest, the coefficient of variation was relatively low, ranging from 6% to 22%. Significant differences were observed between species from the same genus, except in *Bromus hordeaceus* and *B. matritensis* (Table I).

The number of spikelets per inflorescence also varied between genera with some species such as *Brachypodium distachyon* having less than 4 spikelets while others such as *Piptatherum miliaceum* have more than 2,000 (Table I). A significant difference in the number of spikelets per inflorescence between species of the same genus was observed in all genera with more than one species, except between some species of the genus *Bromus* (Table III). In some genera, such as *Avena*, *Hordeum*, *Phalaris* and *Vulpia*, one of the two species has approximately three times more spikelets than the other species.

The number of flowers per inflorescence varied substantially between the different genera, as well as between species from the same genus, excluding some species from the genus *Bromus* (Table I). These figures ranged from 8 flowers per inflorescence in the *Aegilops* and more than 5,000 in *Trisetaria panicea*. Only four species had more than 1,000 flowers per inflorescence (*Polypogon monspeliensis*, *Agrostis stolonifera*, *Piptatherum miliaceum* and *Sorghum halepense*), while the rest ranged between 26 (*Paspalum paspalodes*) and 764 (*Dactylis glomerata*).

Total pollen production per inflorescence

The number of pollen grains produced by a complete inflorescence (Table II) was calculated based on the number of pollen grain per anther and flower, and number of flowers per inflorescences. This figure shows substantial variations between both genera and species from the same genus. An oscillation was observed between 14,500 in *Vulpia myuros* and more than 22,000,000 grains in *Sorghum halepense*. Total pollen production per inflorescence values are shown in Fig. 2. As can be observed, the perennial species were the most important pollen producers; no perennial species

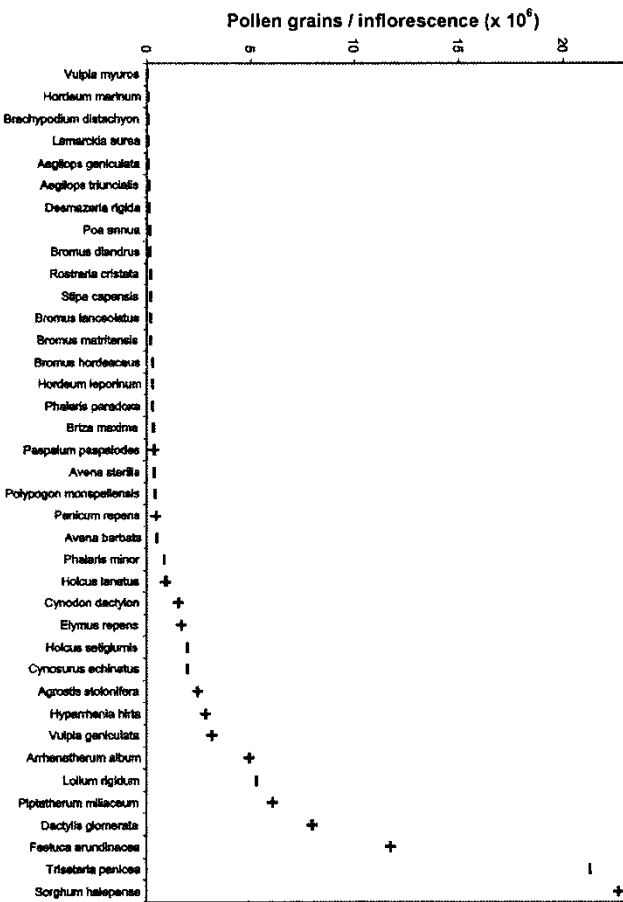


Fig. 2. Total pollen production per inflorescence in the 38 species studied. (–) Annual species. (+) Perennial species.

produced less than 340,000 pollen grains per inflorescence. In contrast, most of the annual plants produced less than 500,000 pollen grains per inflorescence, and mean total pollen production per inflorescence in perennial herbs was up to 3.5 times higher than in annual herbs (5,117,020 and 1,386,535, respectively).

Number of inflorescence per m²

The inflorescence frequency (number of inflorescences per square meter) of the different species studied varies between the studied areas (Table II).

In Zone I (mountainous) three species have a significant presence - *Vulpia geniculata* with 117.50 inflorescences per m², *Lolium rigidum* with 30.25 and *Hyparrhenia hirta* with 13.50. In Zone II (grassland) the most common species was *Stipa capensis* with 343.28 inflorescences per m², other common species in this area being *Trisetaria panicea* with 31.42, *Avena barbata* with 20.14 and *Dactylis glomerata* with 10.28. In Zone III (abandoned crop land) the most abundant species were *Bromus diandrus*, *Hordeum leporinum* and *Lolium rigidum* with 39.00, 32.00 and 13.66 inflorescences per m², respectively.

Finally in Zone IV (riverside area) the most common species were *Paspalum paspalodes* with 84.40 inflorescences per m², *Polypogon monspeliensis* with 71.30 inflorescences, *Elymus repens* with 50.00 and *Panicum repens* with 28.80.

The area that presented the largest density of inflorescences per square meter was the grassland area, followed by the riverside area, the Sierra and, finally, the abandoned crop land (Table II).

Total pollen production per square meter

Finally, potential pollen production of Poaceae per square meter was calculated for the four areas studied, except in the case of occasional species, whose potential pollen production was considered insignificant.

The area that produced the largest amount of pollen was Zone I, followed by Zone II, Zone IV and Zone III (Table II). In contrast, the distribution of the species according to pollen output was different. Zone IV had the largest number of species with high production (11 species), followed by Zone I (9), Zone II (7) and Zone III (6).

DISCUSSION

Anemophilous plants are generally known to produce pollen in large amounts. Their capacity to produce pollen is primarily under genetic and physiological control (Stanley & Linskens 1974). It is generally assumed that the production capacity of an anther is genetically fixed (Subba-Reddi & Reddi 1986). However, the real production per plant may vary significantly from year to year due to environmental factors (Stanley & Linskens 1974). The number of pollen grains per anther in the Poaceae species studied here showed little variation (about 20%) implying that the amount of pollen per anther is constant. Several of the species studied here (*Avena barbata*, *Cynodon dactylon*, *Dactylis glomerata*, etc.) have also been studied by other authors (Smart et al. 1979, Subba-Reddi & Reddi 1986). Some variations in results can be observed between the various studies. These variations can be attributed to the differences among the varieties of a species (Beri & Anand 1971), or to the lack of uniformity in the methods used for obtained pollen counts by the different authors (Subba-Reddi & Reddi 1986).

The number of spikelets per inflorescence seems to be the

most variable value, with coefficients of variation of about 50% in the genus *Vulpia* and up to 73% in *Avena barbata*. This value seems to be determined by physiological and environmental control. In plants with a high number of spikelets in which the number of spikelets per second order spike or panicle were counted, only *Piptatherum miliaceum* displayed considerable variation, approximately 60%. Finally, the number of second order spikes or panicles per inflorescence presented variation between 14% and 43%. The number of flowers per spikelet was the only variable that remained constant in most species.

According to Fægri & van der Pijl (1979), anemophily increases the production of pollen in order to compensate for the reduced efficiency of wind pollination. Lower production of pollen per anther may be compensated with a larger number of flowers per inflorescence, as in the case of *Polypogon monspeliensis*, and a lower number of flowers with a larger production of pollen per anther, as in the case of *Arrhenatherum album*. In some cases, high pollen production per anther is associated with a large number of flowers per inflorescence, as in the case of *Piptatherum miliaceum*, *Sorghum halepense* and *Trisetaria panicea*. This great variation in pollen production is sometimes related to the form of reproduction (Smart et al. 1979). This is the case of *Vulpia myuros*, with very low pollen production per anther (a little more than 60 pollen grains). This species, included in the Sect. *Vulpia*, is uni-staminate and cleistogamous (Connor 1979). However, the low number of pollen per anther does not always seem to be associated with cleistogamy. This is the case for *Polypogon monspeliensis*, a chasmogamous plant with a pollen production per anther very similar to that of *V. myuros*, and a mean of approximately 90 pollen grains.

Regarding pollen production per inflorescence, greater pollen production was observed in perennial species than in annual species. This fact can be understood as a tendency to guarantee cross-fertilization in perennial plants since most perennial plants display marked self-incompatibility (Evans 1964).

Mean total pollen production per anther in the set of species studied here was approximately 2,500 pollen grains. This is similar to the mean of approximately 2,000 pollen grains per anther obtained in the set of species studied by Subba-Reddi & Reddi (1986). Nevertheless, mean total pollen production per anther in a study of 10 anemophilous trees was approximately 25,000 pollen grains (Tormo-Molina et al. 1996). This high productivity in trees compared to anemophilous herbs may be understood as a way to reach distant individuals and to compensate for the scattering of the pollen grains due to altitude. Nevertheless, the mean pollen count per anther in Poaceae is only approximately double the amount detected in an entomophilous plant such as *Rosmarinus officinalis* (Uberta-Jimenez & Hidalgo-Fernández 1992).

Smart et al. (1979) estimated total pollen production per surface unit by counting the number of inflorescences per square meter. They estimated, for *Lolium perenne*, a production of 2.11×10^9 grains per square meter and 1.25×10^9 for *Phalaris tuberosa*, values that are very similar to the 1.82×10^9 grains per square meter recorded in this

study for *Vulpia geniculata*, the species with greater production, and is similar to the 0.66×10^9 recorded for *Trisetaria panicea*. Taking into account the total pollen production in the different zones studied, only two presented a production level in a magnitude of 10^9 : the mountainous area with 2.13×10^9 , and the grassland area with 0.83×10^9 grains per square meter. Another striking result was the fact that only one species in each zone (*V. geniculata* and *T. panicea* respectively) was responsible for 80% and 85% of the total pollen production, respectively.

A difference between the diverse habitats studied here has been shown, in terms of their possible incidence in total pollen production. This means that each area contributes in a different way to the total amount of pollen shed into the atmosphere during the grass pollen season. The data obtained here indicate that the largest pollen production is in the more natural areas, such as the Sierra region, maintaining a semi-natural vegetation, or the area along the river Guadalquivir. Likewise, the grassland area was the second most important pollen producer, since this is occasionally used as pasture land. Another significant finding was the scarce production of pollen and little variety of species recorded in the abandoned crop land, a fairly large area in the outskirts of the city. The reason for this reduced pollen production is the low pollen production of the dominant species and the small number of inflorescences per square meter. This is a consequence of competition with other plants that are predominant in those areas, such as some species of Brassicaceae (*Brassica nigra* (L.) Koch in Röhling, *Diplotaxis siifolia* G. Kunze, *Raphanus raphanistrum* L., *Sinapis alba* L., etc.) and Malvaceae (*Lavatera cretica* L., *Malva sylvestris* L.).

The amount of pollen in the atmosphere depends on the length of flowering time and climatic fluctuations and cannot be deducted from the pollen production per inflorescence alone. To understand the temporal distribution of the Poaceae pollen dispersal a comprehensive phenological study is required. Pollen emission depends on several factors, such as filament length and pollen production per anther (Beri & Anand 1971), as well as on local environmental factors (Rogers 1993). According to previous studies carried out on Poaceae airborne pollen in the city of Córdoba, the most important factors affecting airborne pollen levels are humidity, minimum temperature and sunshine hours (Galán et al. 1995). These environmental factors can also vary from year to year, as shown in other herbs such as Urticaceae (Emberlin & Norris-Hill 1991, Galán et al. 2000). Circadian pollen release patterns in some Poaceae species have been reported by Subba Reddi et al. (1988), each species exhibiting a characteristic temporal pattern of pollen release.

The variability in pollen production among the many species studied here confirm the hypothesis that only a few species produce enough pollen, or have a sufficient high inflorescences density, or both at the same time, in order to shed enough pollen to cause allergic symptoms. Moreover, different degrees of allergenicity have been reported for different Poaceae species (Stanley & Linskens 1974). These two characteristics should be taken into account in future aerobiological and allergological studies.

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