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Pollen production in anemophilous trees

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Pollen production in anemophilous trees

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A study was made of the total pollen production per individual tree in ten anemophilous arboreal species (including wild, cultivated and ornamental species) of considerable aerobiological importance: *Pinus pinaster*, *Ulmus minor*, *Juglans regia*, *Platanus hispanica*, *Quercus rotundifolia*, *Salix atrocinerea*, *Populus nigra*, *Acer negundo*, *Olea europaea* and *Fraxinus angustifolia*.

For each species three isolated well-shaped specimens of medium height were chosen, and the number of flowers per individual tree and the number of pollen grains per anther was estimated.

The values of total pollen production varied between a little over 1000 million grains in *Juglans regia* and more than 500,000 million in one single tree in *Quercus rotundifolia*. For the production of pollen grains per anther, the values oscillated between 3000 grains in *Juglans regia* and 100,000 in *Olea europaea*. There is an exponential correlation between the size of the anthers and the number of pollen grains they contain. A linear correlation is also evident between the volume of the tree crown and the total production of inflorescences, flowers, anthers and pollen grains per individual tree. Based on this, a mean coefficient of the number of grains/meter of diameter of the tree crown is obtained which varies between 3.4×10^8 for *Juglans regia* and 550.9×10^8 for *Quercus rotundifolia*. The ratio between the number of anthers per inflorescence and the number of pollen grains per anther carries out a hyperbolic function; thus, the inflorescences with the most anthers have the anthers with the least pollen and vice-versa. This ratio is also manifest between the number of grains per flower and the number of flowers per tree, as well as the number of grains per inflorescence and the number of inflorescences per tree.

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Anemophilous plants are characterized by high pollen production, as the vector of pollination they employ, the wind, is extremely haphazard and not specific. According to Faegri and van der Pijl (1979), the anemophily of these angiosperms is derived, and an increase in the production of pollen occurs in order to compensate for a reduction in efficiency.

Most of the scant research carried out in this area yield data on the amount of pollen produced per anther or flower in the species under investigation. Even fewer are the studies which give information about the total amount of pollen produced per plant, principally due to the arduous task of quantifying the total number of anthers per plant (Moore et al. 1991). There are also a few studies which estimate the total production from the amount of pollen deposited on the ground (Solomon 1979).

One of the first and also most complete studies of the amount of pollen produced by a plant, is that carried out by Pohl (1937). In this study, information is provided about the quantity of pollen produced per anther, flower, inflorescence and branch in some anemophilous species. Data are also provided about the quantity of pollen per square metre of land surface produced by some plants by calculating the projection of the plant on the soil and the number of flowers per individual.

In 1943 Erdtman added a few more data to complete Pohl's study (1937), and in 1969 he presented a table of 19 species for which he calculated the number of grains per anther, flower and ament, and established an index of relative pollen production, using the value of one as a reference for *Fagus sylvatica*. He affirmed that there is a clear tendency towards an increase in the production of grains of pollen in anemophilous plants. Hyde and Williams (1946) provide complementary contributions with an estimate of the pollen production per surface unit in *Plantago lanceolata*, calculating the number of inflorescences per square meter of land surface, the number of open flowers per inflorescence and the mean number of pollen grains per flower, giving a mean value of 40×10^6 grains of pollen per square metre and day. Nair and Rastogi (1963) provide a further contribution by studying the pollen production of several species linked to allergy such as *Chenopodium album* (133 pollen grains/anther) and *Morus alba* (23,000 pollen grains/anther).

The production of pollen of the Poaceae family has been studied by several authors. Agnihotri and Singh (1975) find between 800 (*Cynodon dactylon*) and 13,000 (*Secale cereale*) grains per anther, and suggest that the total production of pollen depends directly on the size and length of the anther, calculating a value of 700–1200 pollen grains per millimeter of anther length. Smart et al. (1979) make an estimate of the pollen production per anther and spike in 30 types of grass. By counting the number of spikes per square metre they arrive at an estimate of total production of pollen per surface unit between spikes of gramineae. Thus, for *Lolium perenne* they give a value of 2.11×10^{13} grains per season and hectare, which is equivalent to a mass of 464 kg of pollen per hectare. Joppa et al. (1968) determine the total production of grains of airborne pollen of different types of *Triticum* from the number of fertile flowers and the percentage of extruded anthers. Finally, Sree Rangaswamy and Raman (1973) prove that in *Oryza sativa* polyploidy causes the number of pollen grains and the size of the anthers to increase, while the ratio between the two decreases.

Janaki Bai and Subba Reddi (1980) and Subba Reddi and Reddi (1986) determine the pollen production per anther of several angiosperms from India. Like Agnihotri and Singh (1975), they conclude that the pollen production, besides varying greatly from one species to another even within the same genus, is directly related to the size of the anther and inversely related to the size of the pollen grain and that, therefore, those species with large anthers and small pollen grains are the most productive ones.

Although a plant's total production of pollen grains is influenced by various factors (Stanley & Linskens 1974) and also varies from one year to the next (Rogers 1993) it is most important to have an estimate of the total production of pollen per plant, not only from an aerobiological but also an agronomical standpoint, as the production of seeds often depends on the production of pollen (Faegri & Iversen 1989, Cour & Van Campo 1980). Thus, Holm (1994), to give an example, demonstrates that, by adding a supplementary amount of pollen to *Betula*, an increase in the quantity of seed produced can be obtained.

MATERIALS AND METHODS

In order to carry out this study, ten anemophilous arboreal species of considerable aerobiological importance were selected, including wild, cultivated and ornamental ones: *Pinus pinaster, Ulmus minor, Juglans regia, Platanus hispanica, Quercus rotundifolia, Salix atrocinerea, Populus nigra, Acer negundo, Olea europaea* and *Fraxinus angustifolia*. The locations where they were harvested are given in Annex I.

In each species, three isolated trees were chosen that were in good health and well-shaped and they were measured for height and diameter of the tree crown.

Count of the number of inflorescences

In the case of species with a high number of inflorescences arranged on the main branches *Pinus pinaster* (strobili groups), *Ulmus minor, Platanus hispanica, Populus nigra*, and *Salix atrocinerea*, first the main branches were counted (Table I, column 1) and then a sample of 2–5 branches was selected and a count was taken of all their inflorescences (Table I, column 3).

In the case of *Juglans regia* in which the number of inflorescences per tree is small, all inflorescences per specimen were counted (Table I, column 3). In the two evergreen species studied, *Quercus rotundifolia* and *Olea europaea*, whose aments and racemes, respectively, are arranged on the surface of the tree crown and also grouped together, all groups of inflorescences within a given area were counted (1 m^2) and the results were extrapolated to the total estimated surface (Table I, column 2). Finally, in *Fraxinus angustifolia* and *Acer negundo*, whose inflorescences are grouped in bunches on the main branches, all main branches were counted, as well as the number of bunches on 5 branches (Table I, column 2) and the number of inflorescences per bunch in 20 bunches.

Count of the number of flowers and anthers

Whenever possible 20 infloresences scattered throughout the tree were selected (except in *Juglans regia* where 5 aments were counted) and the number of flowers per inflorescence was ascertained (strobili group, raceme, aments, or glomerules – Table I, column 4).

In those species whose flowers do not have a set number of anthers (*Quercus rotundifolia, Ulmus minor, Acer negundo, Juglans regia* and *Populus nigra*) a flower was chosen from the middle of each of the 20 inflorescences selected, and the number of anthers was counted. In *Pinus pinaster* the number of microsporophylls per strobilus was counted, and in *Platanus hispanica* the number of anthers per inflorescence, since when the inflorescences are handled the anthers fall from the flowers.

Count of the number of pollen grains per anther

The pollen grains were counted by using 5 anthers from different flowers for each one of the three trees which had been previously measured (Table I, column 6). Basically, the method used was that of Cruden (1977). The anthers were obtained from closed flowers kept in 70% ethanol that were washed in distilled water, measured, and placed in test tubes. They were taken apart with the aid of a glass rod and in most cases the pollen grains were suspended in 1cc of distilled water. From this concentrate, five drops of 10 µl were removed and then the pollen grains were counted (Table I, column 7).

Estimate of the total production

In order to estimate the total production of pollen per individual plant, first the total number of anthers per tree was calculated (Table II, column 5) by multiplying the number of total inflorescences by the average number of flowers per inflorescence and by the average number of anthers per flower; then the result was multiplied by the average number of pollen grains produced per anther. For each tree an estimate was made of the production of pollen grains per anther per metre of diameter of tree crown.

Calculation of the correlation coefficients

The surface of the tree can be estimated as the lateral surface of a cylinder whose base is a circle with the same diameter as that of the tree crown and whose height is that of the height of the tree ($2\pi rh$), or we can estimate it by considering the surface of a sphere whose diameter is that of the crown ($4\pi r^2$). Likewise, the volume of both geometric shapes can be calculated ($\pi r^2 h$ for the circle and $4/3\pi r^3$ for the sphere). From these data the correlation coefficients were calculated, and their statistical significance ($p|r|=0$) from the total production per tree of inflorescences, flowers, anthers, and pollen grains with the dimensions of the tree (height and diameter of the crown), the surface and the volume of the tree crown considered both as a sphere and a cylinder.

The correlation between the dimensions of the anthers and the production of grains per anther was calculated, as well as the correlation between ten pairs of ratios of production: grains/anthers, grains/flower, grains/inflorescence, grains/tree, anthers/flower, anthers/inflorescence, anthers/tree, flowers/inflorescence, flowers/tree, and inflorescences/tree.

By using the mean values per tree of the number of inflorescences per tree, flowers per inflorescences, anthers per flower, and grains per anther, a Factor Analysis was carried out following the 4m program of the BMDP statistics package. In order to use the values

Table I. *Data for each tree (range. mean and standard deviation).*

a. tree, 1. total amount of branch, 2. number of twigs with inflorescence groups, 3. number of inflorescences (or strobili groups in *Pinus*) per branch. (number of inflorescences per tree in *Juglans*) or number of inflorescences per group of inflorescences (*Quercus* and *Olea*), 4. number of flowers per inflorescence (or number of strobili per strobili group), 5, number of anthers per flower (or microsporophylls in *Pinus*, number of anthers per inflorescence in *Platanus*), 6. anther length in mm, 7. number of pollen grains per anther or microsporophyll.

Taxon	a	1	2			3			4			5			6			7		
Pinus	1	44				(80–190)	105.8	(29.2)	(25–45)	32.5	(6.8)	(29–56)	44.3	(8.3)	(1.2–1.4)	1.3	(0.08)	(1500–4400)	3124.0	(648.9)
	2	32				(120–550)	254.0	(173.6)	(15–35)	28.5	(6.9)	(24–46)	38.0	(6.8)	(1.4–1.6)	1.6	(0.15)	(1700–5900)	3664.0	(1162.2)
	3	35				(130–200)	176.0	(28.8)	(15–40)	29.5	(6.5)	(36–54)	45.7	(5.9)	(1.1–1.4)	1.2	(0.12)	(1600–3900)	2668.0	(559.6)
Ulmus	1	29				(550–650)	600.0	(70.7)	(11–35)	22.2	(6.4)	(3–5)	4.1	(0.6)	(1.6–1.9)	1.8	(0.13)	(1500–9200)	5076.0	(2102.6)
	2	24				(200–500)	350.0	(212.1)	(13–28)	17.9	(4.6)	(3–5)	3.9	(0.6)	(1.7–2.1)	1.9	(0.18)	(5700–11,800)	8532.0	(1615.7)
	3	21				(450–650)	550.0	(141.4)	(11–20)	16.2	(3.3)	(3–5)	4.0	(0.5)	(1.8–1.9)	1.8	(0.05)	(4300–11,900)	7760.0	(1676.3)
Juglans	1						85		(210–280)	246.3	(28.7)	(9–23)	15.3	(2.8)	(2.1–2.3)	2.2	(0.08)	(3900–7200)	5628.0	(8988.5)
	2						300		(125–300)	184.2	(40.4)	(11–15)	12.9	(1.3)	(1.9–2.4)	2.1	(0.19)	(1700–4900)	3264.0	(7421.1)
	3						285		(95–275)	189.2	(79.7)	(9–20)	15.5	(2.5)	(1.7–1.8)	1.8	(0.04)	(2100–4900)	3344.0	(8256.7)
Platanus	1	15				(350–1300)	740.0	(366.4)				(200–408)	326.0	(58.0)	(2.3–2.6)	2.5	(0.13)	(19,900–43,800)	31,744.0	(4823.8)
	2	17				(350–800)	485.0	(181.7)				(100–444)	277.0	(141.3)	(2.2–2.3)	2.2	(0.04)	(10,800–127,500)	55,272.0	(26,906.0)
	3	26				(350–750)	460.0	(188.4)				(248–448)	365.2	(69.0)	(1.6–1.9)	1.8	(0.13)	(20,000–116,500)	35,196.0	(22,165.0)
Quercus	1			7650		(21–73)	49.5	(19.3)	(12–24)	18.2	(3.2)	(6–8)	6.7	(0.8)	(1.1–1.3)	1.2	(0.09)	(1530–3910)	2816.8	(530.3)
	2			6700		(12–62)	31.4	(15.8)	(11–28)	19.0	(4.4)	(2–11)	5.7	(2.2)	(1.2–1.3)	1.2	(0.05)	(2200–6500)	4800.0	(1199.3)
	3			12,800		(18–77)	44.3	(22.3)	(17–26)	20.5	(4.0)	(7–12)	8.7	(2.0)	(1.2–1.4)	1.2	(0.09)	(3900–9800)	6264.0	(1768.0)
Populus	1	45				(100–450)	225.0	(139.1)	(27–51)	39.9	(5.8)	(8–19)	15.9	(2.9)	(1.3–1.5)	1.4	(0.08)	(4300–10,600)	7424.0	(1696.4)
	2	25				(250–850)	520.0	(268.3)	(39–54)	44.1	(5.0)	(10–18)	12.8	(2.2)	(1.4–1.6)	1.5	(0.08)	(6300–19,300)	10,912.0	(2531.7)
	3	20				(100–800)	580.0	(301.3)	(33–57)	47.1	(8.0)	(12–25)	16.4	(3.5)	(1.4–1.6)	1.5	(0.07)	(4400–15,300)	7740.0	(2133.9)
Salix	1	50				(450–1110)	762.2	(268.9)	(180–306)	238.3	(39.3)		2		(0.9–1.1)	1.0	(0.09)	(2200–15,500)	6928.0	(3038.2)
	2	22				(500–1500)	912.5	(421.1)	(168–342)	279.8	(65.3)		2		(1.0–1.2)	1.1	(0.09)	(7300–16,600)	11,992.0	(2279.8)
	3	27				(800–1600)	1225.0	(350.0)	(110–288)	205.7	(48.3)		2		(1.0–1.1)	1.0	(0.05)	(5700–10,900)	8304.0	(1637.2)
Acer	1	18	(60–120)	94.0	(23.0)	(11–55)	27.9	(14.2)	(9–19)	13.4	(3.4)	(3–5)	4.1	(0.6)	(4.2–4.7)	4.4	(0.15)	(29,000–217,500)	96,520.0	(50,354.0)
	2	25	(100–280)	188.0	(76.6)	(5–10)	7.1	(1.5)	(9–19)	13.9	(2.5)	(4–5)	4.6	(0.5)	(2.7–3.6)	3.1	(0.35)	(12,700–21,700)	17,364.0	(2313.2)
	3	12	(150–260)	202.0	(46.6)	(4–9)	6.3	(1.3)	(8–16)	11.4	(2.6)	(3–5)	4.6	(0.7)	(2.8–3.5)	3.1	(0.38)	(12,900–23,400)	18,988.0	(2932.8)
Olea	1			1900		(10–30)	18.0	(7.5)	(10–21)	16.8	(3.4)		2		(2.5–2.7)	2.6	(0.07)	(64,000–126,000)	94,240.0	(17,936.0)
	2			1650		(2–15)	7.1	(3.5)	(12–22)	16.6	(3.1)		2		(2.5–2.7)	2.6	(0.08)	(74,000–144,000)	104,600.0	(21,292.0)
	3			1100		(5–16)	11.3	(3.1)	(6–21)	14.1	(2.9)		2		(2.4–2.6)	2.5	(0.10)	(52,000–161,000)	83,320.0	(25,756.0)
Fraxinus	1	36	(180–310)	240.0	(47.4)	(6–22)	13.0	(4.6)	(8–23)	15.1	(3.8)		2		(2.5–3.0)	2.7	(0.21)	(37,800–56,500)	47,556.0	(4,533.4)
	2	31	(60–120)	92.0	(25.9)	(1–8)	3.5	(2.4)	(7–19)	13.4	(3.3)		2		(2.2–2.8)	2.5	(0.27)	(18,000–77,000)	42,240.0	(14,429.0)
	3	31	(60–120)	86.6	(25.4)	(5–14)	9.3	(3.5)	(14–22)	17.0	(3.0)		2		(2.0–2.7)	2.5	(0.30)	(31,000–87,000)	52,720.0	(14,701.0)

Table II. *Total data for each tree.*

a. tree, 1. height in meters, 2. diameter in meters, 3. number of inflorescences (× 1000), 4, number of flowers (× 1000), 5. number of anthers (× 1000), 6. number of pollen grains (× 1,000,000), 7. number of anthers per inflorescence, 8. number of pollen grains per inflorescence (× 1000), 9. number of pollen grains per flower (× 1000), 10. number of pollen grains per meter of crown diameter (× 100,000,000).

Taxon	a	1	2	3	4	5	6	7	8	9	10
Pinus	1	6.5	4.5	4.7	151.3	6702.0	20.9	1439.8	4497.8	138.4	46.5
	2	7.0	5.8	8.1	231.6	8802.6	32.3	1083.0	3968.1	139.2	55.6
	3	5.5	7.7	6.2	181.7	8304.6	22.2	1348.2	3596.9	121.9	28.8
Ulmus	1	4.2	10.5	17.4	386.3	1583.7	8.0	91.0	462.0	20.8	7.7
	2	8.0	5.5	8.4	150.4	586.4	5.0	69.8	595.6	33.3	9.1
	3	8.0	6.5	11.6	187.1	748.4	5.8	64.8	502.8	31.0	8.9
Juglans	1	5.0	4.5	0.1	20.9	320.3	1.8	3768.4	21,208.5	86.1	4.0
	2	6.5	6.8	0.3	55.3	712.9	2.3	2376.2	7755.9	42.1	3.4
	3	6.0	4.3	0.3	53.9	835.8	2.8	2932.6	9806.6	51.8	6.5
Platanus	1	6.0	6.1	11.1	658.2	3620.3	114.9	326.1	10,353.3	174.6	188.4
	2	6.5	5.3	8.2	415.5	2285.5	126.3	277.2	15,321.4	304.0	238.3
	3	7.0	8.3	19.5	1294.8	7121.4	250.6	365.2	12,853.6	193.6	302.0
Quercus	1	4.0	11.2	378.7	6891.9	46,175.6	130.1	121.9	343.5	18.9	116.1
	2	5.0	10.0	210.4	3997.2	22,784.2	109.4	108.3	519.8	27.4	109.4
	3	4.5	11.5	567.0	11,624.3	101,131.6	633.5	178.3	1117.2	54.5	550.9
Populus	1	8.0	7.6	10.1	404.0	6423.4	47.7	634.4	4709.9	118.0	62.7
	2	9.0	6.4	6.7	295.8	3786.5	41.3	564.5	6159.6	139.7	64.6
	3	8.0	8.2	6.0	283.8	4654.0	36.0	772.4	5978.7	126.9	43.9
Salix	1	6.0	5.8	38.1	9081.6	18,163.2	125.8	476.6	3301.9	13.9	217.0
	2	3.5	5.3	20.1	5617.0	11,234.0	134.7	559.6	6710.7	24.0	254.2
	3	3.0	6.8	33.1	6803.5	13,607.1	113.0	411.4	3416.3	16.6	166.2
Acer	1	6.5	7.0	47.2	632.6	2591.7	250.1	54.9	5298.9	395.7	357.4
	2	5.0	5.6	33.4	463.8	2132.3	37.0	63.9	1109.6	79.9	66.1
	3	6.0	5.4	15.3	174.1	800.2	15.2	52.4	995.0	87.3	28.1
Olea	1	3.5	6.1	34.2	574.6	1149.1	108.3	33.6	3166.5	188.5	177.5
	2	3.5	4.2	11.7	194.5	388.9	40.7	33.2	3472.7	209.2	96.9
	3	4.0	5.1	12.4	174.5	349.0	29.1	28.2	2349.6	166.6	57.0
Fraxinus	1	7.0	8.0	111.9	1689.5	3379.0	160.7	30.2	1436.2	95.1	200.9
	2	5.0	6.5	9.9	132.6	265.2	11.2	26.8	1132.0	84.5	17.2
	3	7.0	7.5	31.5	535.7	1071.4	56.5	34.0	1792.5	105.4	75.3

of anthers per flower and flowers per inflorescence in *Platanus hispanica*, 5.5 was considered as the mean value of the number of anthers per flower, using as a guideline the results of Rocha Afonso (1990). From these the number of flowers per inflorescence was calculated since the number of anthers per inflorescence was known.

RESULTS

The dimensions of the trees studied (height and diameter of the tree crown) appear in columns 1 and 2 of Table II, respectively.

The number of inflorescences, flowers, anthers, and pollen grains per anther varies considerably from one species to another (Table I). The number of inflorescences per terminal branch (Table I, column 3) is very variable in the trees under study. The inflorescences in *Quercus*, *Acer*, *Olea* and *Fraxinus*, which always number less than 50, appear on short little branches which grew the previous year. On the other hand, in *Pinus*, *Ulmus*, *Platanus*, *Populus* and *Salix* they appear on older and more fully grown branches and therefore there can be as many as a thousand. In *Juglans* their number is small on the entire tree, giving a total of 85 to 300.

The number of flowers per inflorescence (Table I, column 4) barely reaches 50 in *Pinus* (strobili per group), *Ulmus*, *Quercus*, *Populus*, *Acer*, *Olea* and *Fraxinus*; but it is much higher in *Juglans* and *Salix*, reaching more than 300.

The number of anthers per flower (Table I, column 5) is always 2 in *Salix*, *Olea* and *Fraxinus*; oscillates between 3 and 5 in *Ulmus* and *Acer*; becomes steadily higher in *Quercus*, *Junglans* and *Populus* (where it can reach as many as 25); and the number of microsporophylls per strobilus reaches as many as 45 in *Pinus*. In the case of *Platanus*, where only the number of anthers per inflorescence could be counted, it oscillates between 100 and 450 per inflorescence.

The number of pollen grains per anther or microsporophyll (Table I, column 7) gives minimum values in *Pinus*, *Juglans* and *Quercus*, where it never reaches 10,000. The maximum values appear in both of the *Oleaceae* under study (*Olea* and *Fraxinus*). In the former, anthers with more than 100,000 grains were frequently found. Nevertheless, in a population of *Acer* as many as 200,000 grains of pollen per anther have been counted.

Total production

The total production of inflorescences per tree oscillated between approximately one and three hundred in *Juglans*, and up to half a million in *Quercus* (Table II, column 3), but the most frequent value for the rest hovers around tens of thousands of inflorescences per tree.

The total number of flowers per tree (Table II, column 4)

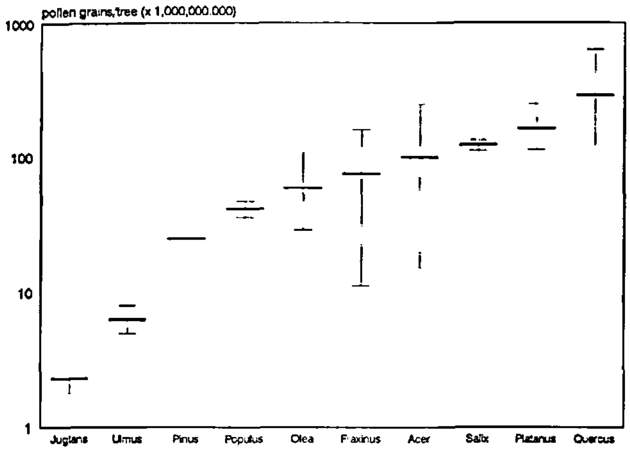

Fig. 1. Total pollen production per tree, thick line is the mean, thin lines are maximum and minimum.

is again minimal in *Juglans* (20,000–55,000) and climbs as high as several million in *Quercus* and *Salix*, due in the latter case to the high number of flowers per inflorescence. The total number of anthers per tree (Table II, column 5) is minimal in *Ulmus*, *Juglans*, *Olea* and *Fraxinus* in which it is around half a million; and maximal again in *Quercus*, with as many as 100 million.

The total production of pollen grains per tree (Table I, column 6 and Fig. 1) oscillates between a little over one thousand million for the above mentioned species and around 500,000 million for *Quercus* reaching above one hundred thousand million in *Platanus*, *Salix* and some specimens of *Olea* and *Fraxinus*. By dividing this amount by the diameter of the tree crown we arrive at an estimate of the quantity of grains of pollen produced per tree regardless of the size of the tree crown. This value oscillates between 3.4×10^8 in *Juglans* and 550.9×10^8 in *Quercus* (Table II, column 10).

Correlations between the dimensions of the tree and the production of inflorescences, flowers, anthers and pollen grains

The total productions of inflorescences, flowers, anthers and pollen grains are all logically correlated as one is multiplied by the next to obtain the total production Table III.

The height of the tree has a negative significant correlation with the total number of flowers. In other words, the taller the tree the more proportionally reduced is the number of flowers. In contrast, the diameter of the tree crown has a positive significant correlation with the total number of inflorescences, flowers, anthers, and pollen grains.

There appears to be no correlation between the surface of the cylinder and the production of the trees, but there is a positive significant one with the surface of the sphere. There are positive and significant correlations between the volume of the cylinder and the production of inflorescences, anthers and pollen grains, but they are inferior to the correlations of the surface of the sphere. The highest correlation with the production of inflorescences, flowers, anthers and pollen grains are with the volume of the sphere whose diameter is the diameter of the tree crown.

Correlation between the number of pollen grains per anther and the length of the anther

The average length of the anthers or microsporphylls (Fig. 2, Table I, column 6) varies between 1 and 2 mm for *Pinus pinaster*, *Ulmus minor*, *Quercus rotundifolia*, *Populus nigra* and *Salix atrocinerea*; between 2 to 3 mm for *Juglans regia*, *Platanus hispanica*, *Olea europaea* and *Fraxinus angustifolia*; and between 3 and 4.5 mm for *Acer negundo*. A positive significant correlation has been found between the length of the anthers and the number of grains produced per anther ($r-0.6636$, $p=0.000$), using a total of 150 data (5 anthers per tree in a total of 30 trees). If we calculate the correlation between the length of the anthers and the decimal logarithm of the number of pollen grains, we obtain a higher value ($r=0.6944$, $p=0.000$ – see Fig. 2), which indicates an exponential ratio between the two. By calculating the linear regression we find that $\log y=3.1895+0.4687x$ (y being the dependent variable: the number of grains per anther; and x the independent variable: the length of the anther).

Correlations between the ratios grains/anther, grains/flower, grains/inflorescence, grains/tree, anthers/flowers, anthers/inflorescence, anthers/tree, flowers/inflorescence, flowers/tree and inflorescences/tree

There is a significant ($p<0.05$) positive and linear correlation between the number of grains per flower and of anthers per flower; between the grains per inflorescence, anthers per inflorescence and flowers per inflorescence; and between the grains per tree, anthers per tree, flowers per tree and inflorescences per tree.

By calculating logarithms these correlations are maintained and other significant correlations, although negative ones, also become apparent (Table IV): The number of pollen

Table III. *Correlations between the total amount of inflorescences (inflor.), flowers, anthers and pollen grains per tree with tree height, crown diameter, crown surface (as cilinder and sphere), and crown volumen (as cilinder and sphere) in the studied trees.*

Each pair of data represent the correlation coefficient and the probability (p|r|–0).

	Height		Crown diameter		Cilind. surf.		Sphere surf.		Cilind. volume		Sphere volume	
Inflor./tree	−0.2790	0.135	0.7149	0.000	0.2376	0.206	0.7764	0.000	0.5474	0.002	0.8224	0.000
Flowers/tree	−0.3981	0.029	0.4741	0.008	−0.0049	0.979	0.5140	0.004	0.2620	0.162	0.5472	0.002
Anthers/tree	−0.2594	0.166	0.6367	0.000	0.1981	0.294	0.6980	0.000	0.4932	0.007	0.7467	0.000
Pollen grains/tree	−0.1763	0.351	0.5203	0.003	0.2250	0.232	0.5465	0.002	0.4362	0.016	0.5665	0.001

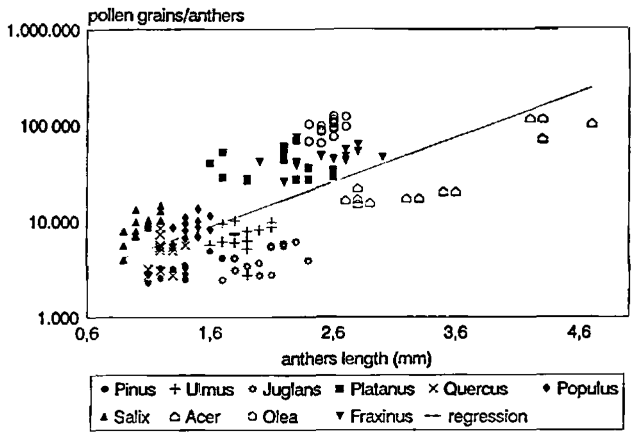

Fig. 2. Relationship between the number of pollen grains per anther and the anther length in ten trees.

grains per anther decreases significantly when there is an increase in the number of anthers per flower, in the number of anthers per inflorescences, or in the number of anthers per tree.

Furthermore, the number of grains per flower significantly decreases when there is an increase in the number of flowers per inflorescence, of flowers per tree or of inflorescences per tree. The number of grains per inflorescence significantly decreases when the number of flowers per tree or of inflorescences per tree increases. The number of anthers per flower significantly decreases when the number of flowers per tree or the number of inflorescences per tree increases. The number of anthers per inflorescence significantly decreases when the number of inflorescences per tree increases. And finally, the number of flowers per inflorescence decreases when the number of inflorescences per tree increases. This type of ratio which is obtained by using logarithmic values and in which by increasing one value the other decreases, carries out a hyperbolic function expressed as $YX=c$, c being the constant that can be calculated as the mean product of X times Y (see Fig. 3 which shows the ratio between the number of pollen grains per anther and the number of anthers per inflorescence).

The results of the Analysis of Factors appear in Fig. 4.

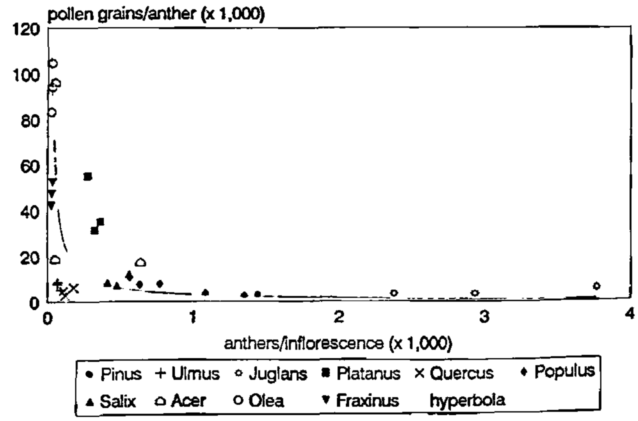

Fig. 3. Relationship between the number of pollen grains per anther and the number of anthers per inflorescence in ten trees.

Table IV. *Correlation coeficients between the production rates of pollen grains (gr.), anthers (ant.), flowers (fl.) and inflorescences (infl.) per superior production unity.*

Each pair of data represent the correlation coeficient and the probability (p|r|=0).

	log(gr./ant.)		log(gr./fl.)		log(gr./infl.)		log(gr./tree)		log(ant./fl.)		log(ant./infl.)		log(ant./tree)		log(fl./infl.)		log(fl./tree)	
log(gr./fl.)	0.5936	0.001																
log(gr./inflor.)	0.1260	0.507	0.5019	0.005														
log(gr./tree)	0.3725	0.043	0.1679	0.375	−0.0039	0.984												
log(ant./fl.)	−0.6715	0.000	0.1978	0.295	0.3087	0.097	−0.2991	0.108										
log(ant./inflor.)	−0.6876	0.000	−0.0956	0.615	0.6337	0.000	−0.2933	0.116	0.7495	0.000								
log(ant./tree)	−0.4207	0.021	−0.3018	0.105	−0.1027	0.589	0.6852	0.000	0.2346	0.212	0.2529	0.178						
log(fl./inflor.)	−0.3841	0.036	−0.3312	0.074	0.6499	0.000	−0.1518	0.423	−0.1629	0.390	0.7752	0.000	0.1531	0.419				
log(fl./tree)	−0.0113	0.953	−0.4068	0.026	−0.2859	0.126	0.8322	0.000	−0.3884	0.034	−0.2181	0.247	0.8046	0.000	0.0456	0.811		
log(inflor./tree)	0.2212	0.240	−0.1677	0.376	−0.6038	0.000	0.7995	0.000	−0.4238	0.020	−0.6145	0.000	0.6079	0.000	−0.5114	0.004	0.8352	0.000

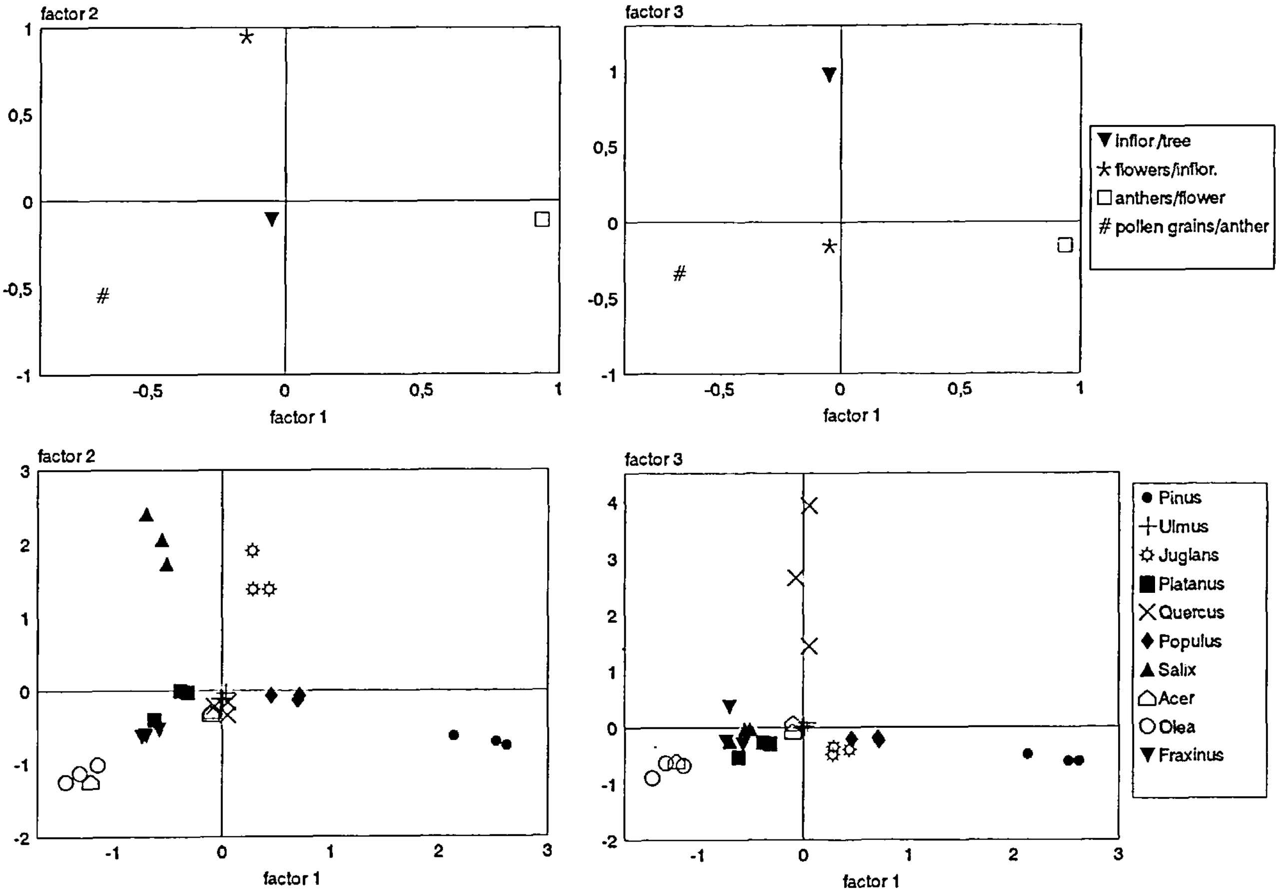

Fig. 4. Result of the Factor Analysis using four variables (number of inflorescences per tree, number of flowers per inflorescence, number of anthers per flower and the number of pollen grains per anther), and 30 trees of ten species. Variables are represented in the two upper scater diagrams and the trees in the two lower ones. The two diagrams on the left using factors 1 and 2, and the two on the right using factors 1 and 3.

The accumulated proportion for the first three axes is 37.8, 66.4 and 91.6, respectively. They represent the 4 variables used (inflorescences per tree, flowers per inflorescence, anthers per flower, and grains per anther) and the 30 trees studied, according to the factors 1, 2, and 3. Usually the trees of the same species are together, except for tree 1 of *Acer negundo*, which grew separate from the other specimens. The four variables are strongly segregated. For seven of the ten species studied, one factor appears to be the most influential on the total production of pollen grains. *Pinus pinaster* stands out because it possess a large quantity of microsporophylls per strobilus; *Salix atrocinera* and *Juglans regia* are segregated for their high production of flowers per inflorescence; *Olea europaea*, *Fraxinus angustifolia* and one specimen of *Acer negundo* stand out for their high production of grains per anther; the rest have high production of inflorescences (*Quercus rotundifolia*) or they have a stable production as far as inflorescences, flowers, anthers, and pollen grains per anther (*Acer negundo*, *Platanus hispanica*, *Ulmus minor* and *Populus nigra*).

DISCUSSION AND CONCLUSIONS

Knowing the total pollen production per plant is useful in order to estimate the number of pollen grains that could be in the air during a certain season, once the density of plants per surface unit is known. It can also be used as an estimate of the production of seeds (Campbell & Halama 1993, Allison 1990), as the efficiency of anemophilous pollination decreases with the reduction in the concentration of airborne pollen (Whitehead 1983).

Pohl (1937) gives some values for the total pollen production per plant in several herbaceous species which vary between almost 3 million and a little more than 1300 million, the maximum value pertaining to *Mercurialis annua*. Obviously, woody plants produce larger quantities, as the data from this research project give values always higher than 1000 million grains per plant. The number of pollen grains per anther is also very variable. The same author gives the following values for different species of the same genera studied in our research project: *Fraxinus excelsior* 12,500, *Quercus sessiliflora* 5000, *Acer platanoides* 1000. However, in our study the following values were obtained: *Fraxinus angustifolia*, between 18,000 and 87,000; *Quercus rotundifolia*, between 1530 and 9800; *Acer negundo*, between 12,700 and 217,500.

Erdtman (1943) gives values for pollen production per flower for different trees, such as *Pinus sylvestris* (158 10^3 per strobilus) and *Quercus sessiliflora* (41×10^3). In this research project, we found the following values for the species studied from these genera: *Pinus pinaster*, between 244×10^3 and 280×10^3 per strobilus and between 340×10^3 and 1100×10^3 for *Quercus rotundifolia*.

Since the total production of pollen grains per tree is positively correlated with the diameter of the tree crown and not with the height, this could indicate that the amount of available light is a limiting factor in the production of inflorescences and flowers. It could also lead us to believe that height might act in a negative way, as is evidenced by the negative and significant correlation between the height and the number of flowers per tree (Table III).

The existence of a cubic ratio between the dimensions of the tree crown and the total production of pollen grains indicates that the distribution of inflorescences on the tree branches is homogeneous. This appears logical in deciduous trees, but not in evergreens (*Quercus rotundifolia* and *Olea europaea*) whose inflorescences are arranged on the surface of the tree crown. Perhaps more studies should be carried out on the evergreen species.

The correlation between the size of the anthers and the quantity of pollen grains they contain has already been demonstrated by other authors (Agnihotri & Singh 1975, Subba Reddi & Reddi 1986). However, this ratio is not linear, but rather exponential. According to our data, the number of pollen grains (y) in terms of the size of the anther in mm (x) can be calculated with the formula: $y = 1,547.16 \times 2.94^x$.

The existence of a hyperbolic ratio between the relative productions of the different aspects of production (anther, flower, inflorescence, tree) leads us to believe that in the anemophilous arboreal species there is a constant value for pollen production. As the number of pollen grains per anther, anthers per flower, flowers per inflorescence, and inflorescences per tree varies considerably, there is a tendency to compensate by increasing one or reducing the other, so that the resulting product is generally within some defined margins. Thus, some species would have a tendency to increase the number of inflorescences in order to compensate for the small number of flowers per inflorescence or anthers per flower or grains per anther, as is the case with *Quercus rotundifolia*; others would produce a large quantity of flowers per inflorescence, such as *Salix atrocinera* and *Juglans regia*, which have a small number of flowers per inflorescence or pollen grains per microsporophyll, respectively; others would increase the number of anthers per flower or microsporophylls per strobilus. Other species would considerably increase the number of pollen grains per anther, such as *Olea europaea* and *Fraxinus angustifolia*, which have a small number of anthers per flower. Finally, the more or less well-balanced species as far as the production of pollen grains anthers, flowers or inflorescences is concerned remain, such as *Platanus hispanica*, *Ulmus minor*, and *Populus nigra*.

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SPECIMENS INVESTIGATED

Pinus pinaster Aiton: Badajoz, University campus, 8.3.94.
Ulmus minor Miller: Badajoz, Guadiana river, 2.2.94.
Juglans regia L. Badajoz, road to Bótoa, 1.3.94.
Platanus hispanica Miller ex Münch.: Badajoz, Valdepasillas (trees 1 and 2), and University campus (tree 3), 14.3.94.
Quercus rotundifolia Lam.: Badajoz, Bótoa, 22.3.94.
Populus nigra L.: Badajoz, Talavera la Real, 3.3.94.
Salix atrocinerea Brot.: Badajoz, Guadiana river, 23.02.94.
Acer negundo L.: Badajoz, Valdepasillas, (tree 1); University campus (trees 2 and 3), 23.2.94.
Olea europaea L.: Badajoz, road to Valverde de Leganés, 5.5.94.
Fraxinus angustifolia Vahl: Badajoz, Bótoa, 14.1.94.

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