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AVIAN FRUIT REMOVAL: EFFECTS OF FRUIT VARIATION, CROP SIZE, AND INSECT DAMAGE¹

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Abstract. Avian dispersal of seeds of the wild olive tree (*Olea europaea* var. *sylvestris*) was studied in Mediterranean shrubland, southern Spain. Fourteen species of small frugivorous birds in the genera *Sylvia*, *Turdus*, *Sturnus*, and *Erithacus* accounted for 97.4% of the fruits consumed by birds. The significance of each bird species as an *Olea* fruit consumer was closely related to its abundance in the area and was not associated with its dependence on the fruit for food; this resulted in a highly asymmetric interaction between the plant and its dispersers.

Fruit production differed greatly between two consecutive seasons. During an extremely dry year most trees aborted their entire fruit crop just after flowering. During the 2nd yr, both flower production and fruit set increased, and this resulted in larger crops of ripe fruit. Most fruits that ripened (96.2% of the final-sized fruits) during the year of low fruit production were consumed by dispersers ($\bar{X} = 93.9\%$), and incidence of fruit-damaging agents was low (6.0%). During the 2nd yr, fruit loss to the two main fruit predators, *Dacus oleae* (Tephritidae) and *Prays oleae* (Yponomeutidae), increased ($\bar{X} = 27.1\%$, range 1.1–52.3%). A satiation process took place during this year since fruit production exceeded the energy demand of the disperser assemblage, and this increased the potential for fruit loss to insect frugivores. Fruit removal by dispersers decreased ($\bar{X} = 52.4\%$), but the increase in fecundity during the 2nd yr for most of the trees compensated for this difference and resulted in a greater absolute number of seeds removed.

Most variation in ripe fruit removal by birds was attributed to the interaction of dispersal-related plant traits with insect frugivores that determine post-ripening fruit losses. The types of higher order interactions that result from the action of birds, the pulp-damaging fly, and the seed-eating moth larva may damp, or reverse, any selective effect of a single system component on plant traits related to seed dispersal.

Key words: *Dacus*; *fruiting patterns*; *higher order interactions*; *Olea europaea*; *Prays*; *seed dispersal*; *seed predation*; *Spain*; *Sylvia*; *Turdus*.

INTRODUCTION

Many mutualistic interactions rely on the production by plants of structures (pollen, nectaries, fleshy pulp, etc.) that provide nutrients and other types of resources to the pollinators and seed dispersers (van der Pijl 1981, Vogel 1983). Recent interest in the evolution of mutualisms (see Howe and Smallwood 1982, Thompson 1982) addresses the importance of each organism in generating selective pressures that result in co-evolved, mutual adaptations. However, plant attractants also are exploited by a variety of animals that damage the plant reproductive structures or influence the behavior of mutualists so as to decrease their beneficial activity. Thus, a variety of nectar robbers, anthophagous herbivores, frugivorous insects (both pulp and seed predators), and microorganisms may affect plant reproduction (Janzen 1969, 1977, Herrera 1982a, Inouye 1983).

Animals that damage reproductive structures are important because their activities may have far-reaching effects on the evolution of mutualisms. The derived selective pressures may counteract or enhance those of

mutualists, and, in any instance, increase variance in selective effects. Consideration of these higher order interactions (Price et al. 1980) is indispensable to an understanding of the mutualistic system, yet this type of information is rarely available (but see Scott and Black 1981, Heithaus et al. 1982, Louda 1982, Hainsworth et al. 1984).

Recent efforts to document the effects of damaging agents on fruit traits related to the dispersal of seeds by avian frugivores have revealed extremely complex interactions often involving counteracting selective pressures by "legitimate" frugivores and fruit predators (Denslow and Moermond 1982, Howe 1983, Willson 1983, Herrera 1984b, c, Manzur and Courtney 1984). Frugivorous insects decrease plant fitness either by direct damage to the pulp of ripe fruits (Bateman 1972) or by endosperm destruction (Janzen 1969), or both. Although information about the identity, mechanism, and magnitude of damage to fleshy fruits is extremely scarce (Herrera 1982a), the existing reports (references above) suggest strong selective pressures by damaging agents that oppose those of seed dispersers.

I document correlates of disperser activity (fruit removal) with the crop and fruit traits of individual trees

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and explicitly consider insect frugivores that damage pulp and seeds as another interacting part in the mutualistic relation between the plant and the birds. I document which fruit traits are consistently associated with infestation by a particular insect and ask if these traits "oppose" those favored by frugivorous birds. This type of information may indicate differences among the selective pressures on plants from different fruit predators and dispersal agents.

NATURAL HISTORY OF *OLEA*

Olea europaea var. *sylvestris* Brot. (*O. europaea* hereafter, unless otherwise stated) is the wild precursor of the well-known cultivated olive tree (*O. europaea* var. *europaea* L.), which is extensively cultivated throughout the Mediterranean Basin. It is closely related to the Afroasiatic *O. chrysophylla* Lam. and to *O. laperrini* Batt. and Trab. growing in the Hoggar mountains, Algeria (Zohary and Spiegel-Roy 1975, Ceballos and Ruiz 1979).

Between 10 and 20, 4–6 mm wide flowers are produced in panicles on 1-yr-old branches (i.e., branches produced in the year preceding fruiting). The species is andromonoecious and partially self-incompatible (see Fernández 1979 and references therein). The presence of wild trees consistently producing huge crops of flowers but no fruit (a behavior similar to other oleaceous treelets in southern Spain, e.g., *Phillyrea angustifolia*, *P. latifolia*; Herrera 1984a, Jordano 1984) suggests a functionally dioecious behavior.

The fruit is a drupe ≈ 8 mm in diameter, which becomes glossy black when ripe, and contains a single nut with a hard endocarp. The ripening period extends from late October to mid-March. The pulp is extremely lipid-rich. Lipid levels vary considerably during the course of fruit maturation as well as between years (Loussert and Brousse 1980). Along with *Pistacia lentiscus*, another species with lipid-rich pulp, fruits of *O. europaea* form the bulk of the diet of an overwintering avifauna in southern Europe (see Jordano and Herrera 1981, Herrera 1982b, 1984a, Jordano 1984, and references therein). Fallen fruits may be eaten, and the nuts apparently regurgitated undamaged, by a number of mammals, including rabbits, goats, and deer (R. C. Soriguer, *personal communication*).

Olive fruits are damaged by the feeding of a number of invertebrates whose biological cycles, parasitoids, and general ecology are well known because of their obvious impact on cultivated varieties. Of major importance are *Dacus oleae* Gmelin, a tephritid fly, and the moth *Prays oleae* Bern., Yponomeutidae. Larvae of *D. oleae* are monophagous on olives (Levison and Levison 1984). Adult flies emerge by May–June and oviposit single eggs in final-sized, unripe fruits or, more frequently, those just becoming ripe. Successive generations of the fly emerge till November if environmental conditions are favorable and ripe fruits continue to be available for oviposition. The larvae live in

the pulp for 10–25 d and pupate in the ground. Ripe, damaged fruits become browner, acquire deformations of the surface, lose their glossy appearance, and fall to the ground when damage is generalized. For detailed accounts of the life cycle, behavior, and related aspects of this insect see Ruiz Castro (1948), Prokopy and Haniotakis (1976), and Levison and Levison (1984).

The moth *P. oleae* is trivoltine, with successive generations developing in different parts of the tree. The first, overwintering generation inhabits galleries in the leaves. The second or spring generation develops inside flower buds or open flowers. The third generation develops in unripe fruits during early summer and adults from this generation begin oviposition in the leaves. A single larva penetrates a seed, eats the endosperm and grows for 90–150 d. Then the larva drills an exit hole close to the fruit peduncle and pupates on the undersides of the leaves or, if the fruit has fallen, pupates in the ground. Detailed accounts of the life history can be found in Ruiz Castro (1951) and López Bellido (1977).

A number of other pest species has been recorded for cultivated trees and most of them have been observed on var. *sylvestris* (Ruiz Castro 1948 and P. Jordano, *personal observation*). However, most authors agree that *Prays* and *Dacus* account by far for the largest proportion (80–90%) of fruit loss to pests. Other important fruit-pulp-attacking taxa are: *Liothrips oleae* Costa (Thysanoptera: Phlaeothripidae), *Glyphodes unionalis* Hb. (Lepidoptera: Pyralidae), as well as several fungi (*Cyclonium oleaginum* Cast., *Gloeosporium olivarium* Alm., and *Macrophoma dalmatica* Thum.) (see Loussert and Brousse 1980).

METHODS

Study site

The study site was located at Hato Ratón, a property adjacent to the northeastern border of Doñana National Park, and situated 5 km south from Villamanrique de la Condesa, Sevilla Province, southwest Spain. The area receives an average rainfall of 539 mm/yr during a rainy season extending from November through March. Between-year variation in the amount of rain is extreme, especially during the first months of the rainy season (September and October). During 1981 and 1982, the two study years, total annual precipitation was 331 and 409 mm, respectively. Differences between the two seasons were appreciable both in the amount and monthly distribution of rain. In 1981–1982 most of the rain (207 mm) fell in December 1981. Subsequently, monthly rainfall figures fell well below the long-term averages; this resulted in a prolonged, 7-mo drought (summer drought normally lasts 4 mo).

The study site includes a dense shrubland dominated by tall shrubs and small trees (height, 2.5–5 m) with a high incidence of fleshy-fruited species (56.8% of the

woody taxa). Average cover by these species amounts to 72%, with only 7.6% of open ground. Dominant species include *Pistacia lentiscus* (Anacardiaceae), *Olea europaea* var. *sylvestris* (Oleaceae), *Rhamnus lycioides* (Rhamnaceae), *Phillyrea angustifolia* (Oleaceae), and *Smilax aspera* (Liliaceae).

O. europaea is present in 73.3% of 15 transects (15 × 1.25 m), showing an average cover of $8.0 \pm 2.2\%$ ($\bar{X} \pm SE$). Detailed descriptions of the study site and similar formations can be found in Rivas et al. (1980), Herrera (1984a), and Jordano (1984).

Fruit production, phenology, and characteristics

A marked population of 36 trees was monitored from January 1981 through March 1983. Number of flowers produced, presence or absence of fruit set, number of final-sized fruits (i.e., fruit crop size), and number of ripe fruits (ripe-fruit crop size) were recorded for each tree.

A subsample of trees was studied intensively for fruiting phenology, fruit removal rates, and estimates of insect damage to fruits. Fruit-bearing branches were marked in 6 trees (1981–1982 season, 3114 fruits) and 10 trees (1982–1983 season, 6394 fruits). Weekly censuses of marked branches were carried out to record the number of unripe, ripe, insect-damaged, dried, and missing fruit. Estimates of the total pre- and post-ripening fruit losses were obtained from these counts.

Samples of ripe fruits ($N = 30$) were taken from individual trees during the period of peak fruit availability. Fresh fruits were measured (length and width) and weighed (nearest 0.1 mg). Wet mass of the whole seed was taken for a subsample ($N = 15$) and then oven-dried to constant mass (40°C) along with the remaining subsample of complete fruits. Dry masses of complete fruits and seeds were obtained for all the sample. Dry mass of fruit and wet mass of seeds were taken separately for each of the two subsamples since recording characteristics of the fresh seed requires destruction of the fruit. Thus, for the subsample that was dried with fruits intact, seed wet mass was estimated from regression of wet vs. dry mass of seeds on the date of the subsample used to obtain the seed wet masses. Chemical analyses of the fruit pulp for individual trees were carried out by conventional procedures (see Herrera 1982b) at Centro de Edafología y Biología Aplicada, Salamanca, Spain.

Use of fruit by birds

Line transects of fixed width were censused at weekly intervals to determine densities of avian frugivores and record the species feeding on *Olea* fruits (see Jordano 1985 for details). Mist nets were used to capture birds and obtain fecal samples for diet analysis. Abundance rankings in the census counts and mist-net captures were strongly correlated for the 10 bird species that disperse seeds of *Olea* ($r_s = 0.905$, $P < .01$). Thus the

number of seeds in fecal samples provided reliable estimates of the relative importance of each species as a seed disperser.

The diets of the frugivorous birds were determined by using the method described in Moody (1970; see also Herrera and Jordano 1981, Jordano 1984 for details). Locations for mist nets were scattered throughout the study area, and nets were maintained during the whole study period.

Animal and vegetable matter in the diet samples were quantified visually by estimating percent volume to the nearest 10%. If present, seeds were identified and counted and the remaining material examined with a microscope (100×) to determine additional fruit species in the sample from identification of the pericarp tissue (fruit skin). The number of fruits included in the sample was determined by estimating the amount of pericarp present and deriving for each fruit species an estimate of its volume contribution to the vegetable fraction of the sample. Counting seeds unavoidably leads to underestimates of the quantity and diversity of fruits present, especially if regurgitation occurs (e.g., in *Turdus* spp. and *Sturnus* spp.). The method described enables an accurate estimation of both the number of fruits and species ingested during a relatively short feeding bout by the birds, since it provides identification and quantification of all the fruit parts.

Insect damage to fruits

Fruits damaged by fly larvae are readily detected in the counts of tagged branches but discovering moth damage requires the opening of the seed. Since fruits with moth larvae fell to the ground, I collected fallen fruits weekly during the 1982–1983 season. A sample of 4660 fruits was collected from marked quadrats (0.5 × 0.5 m) under the crowns of 10 trees during each tree's fruiting season. For each fallen fruit I recorded the damaging agent. The trees sampled were the same as those with marked fruiting branches. Fruit damage by insects was not evaluated by this procedure in the 1981–1982 season, but it became evident from the records of tagged branches that the insect incidence was rather low (see Results: Patterns of Insect Damage to Fruits).

I found no evidence of mammal activity between collections that could bias the estimates of fruit damage. Mice removed pulp in situ or cracked some seeds, but the presence of insect damage could be identified even in those fruits. The sample of fallen fruit was used only to obtain the relative infestation caused by each insect to the fruits collected, and these relative figures established a ranking of damage level for the individual crops.

Total fruit loss attributable to each insect species (determined for the total crop size) was obtained by combining the percent loss derived from fruit samples on the soil and the percent post-ripening loss (recorded from branch counts).

TABLE 1. Flower and fruit production in *Olea europaea* var. *sylvestris* trees during the two study years.

	1981			<i>t</i>	1982		
	<i>N</i> †	%			<i>N</i>	%	
Trees flowering	31	86.1			36	100.0	
Trees setting fruit	24	66.7			31	86.1	
Trees with unripe final-sized fruits	16	44.4			31	86.1	
Trees with ripe fruit	9	25.0			31	86.1	
	$\bar{X} \pm SE$	<i>N</i>	Range		$\bar{X} \pm SE$	<i>N</i>	Range
Flower crop size	12 837 ± 1743	27	100–38 000	2.81**	28 197 ± 4554	36	4000–120 000
% fruit set‡	1.62 ± 0.62	6	0.1–3.8	2.30*	8.02 ± 1.81	33	0.3–53.2
Fruit crop size	353 ± 168	6	50–1140	2.21*	1483 ± 265	33	35–6750

* $P < .05$; ** $P < .01$.

† *N* = number of trees.

‡ Percent flowers setting fruits that reached final fruit size.

Statistical analysis

Nonparametric statistics (Siegel 1956) were used, unless otherwise stated, because small sample sizes, strong skew, or nonlinear effects in the data violate assumptions for parametric tests. Comparisons, when using parametric tests, were performed on log-transformed variables (linear and mass measurements, crop sizes), and angular transformations were used for percentages, since these often included extreme values (Sokal and Rohlf 1981).

RESULTS

Fruit production: determinants of between-year variation

Appreciable between-year variation existed in the fraction of trees that reached successive phases of the reproductive cycle (Table 1). Almost all the trees (86.1%) flowered, but only 25% bore ripe fruit, in both seasons. In 1981 fruit shedding was associated with the very dry conditions prevailing during the spring, which continued through early December. In 1982, in contrast, only four trees did not set fruit, and these had flowered but failed to set any fruit in the preceding year. Fruit crop size declined during the season in 1982, but fruit crops were not completely lost as in 1981.

Flower crop sizes increased in 1982 by an average of 14 700 flowers, and decreased for only nine trees. Final-sized fruits increased, on average, 80% in 1982 and resulted in larger fruit crops (Table 1). However, trees that did not set fruit in 1981 produced a small crop (i.e., 30–500 fruits) in 1982, while those trees that set some fruit in both years yielded greater crops in 1982 (Table 2; the difference in crop size between the two groups was significant: $U = 54$, $P = .009$, 17 and 13 plants, respectively). Most trees that produced a crop of final-sized fruits in both years had greater crop sizes in 1982 (Table 2), but this did not result from increased flower crop sizes (actually only four out of nine trees increased their flower crop; Table 2). There was a negative correlation between the increase in fruit production recorded in 1982 and the crop size of the

previous year ($r_s = -0.611$, $P = .025$, $N = 13$ trees) suggesting that a high reproductive investment in 1981 might have impaired the increase in fecundity observed in the following year.

Patterns of fruit consumption and seed removal by birds

Avian frugivores feeding on *Olea* fruits include 14 species of small to medium-sized birds, with 10 species being seed dispersers and 4 eating either pulp alone or seeds (Table 3). The species composition of both groups may vary in different southern Spanish habitats, but the assemblage reported in Table 3 includes the main species (*Sylvia atricapilla*, *Erithacus rubecula*, *Turdus* spp., and *Sturnus* spp.), which seem rather constant both in their presence and relative abundance (Tutman 1969, Muñoz-Cobo and Purroy 1980, Herrera 1984a, Levison and Levison 1984).

Ten species of birds acted as seed dispersers and accounted for 99.1% of the fruits consumed; of these, six species accounted for the removal of 97.4% of the fruits (Table 3). The distribution of importance values

TABLE 2. Number of flowers and full-sized fruits (prior to ripening) produced by individual *Olea europaea* var. *sylvestris* trees fruiting in the two consecutive study years.

Tree identification number	Thousands of flowers		Number of full-sized fruits	
	1981	1982	1981	1982
742	18.0	4.5	415	135
749	15.0	14.0	150	2350
750	16.0	7.5	70	1725
755	14.0	12.0	400	360
757	22.0	88.0	50	6750
761	11.0	30.0	65	3370
765	11.0	12.0	300	850
766	12.0	45.0	65	1755
768	30.0	8.5	1140	1150
811	...*	40.0	2100	1975
812	...	32.0	250	860
813	...	70.0	1800	4900
814	...	26.0	375	3400

* No data available.

TABLE 3. Between-year variation in the importance of *Olea europaea* var. *sylvestris* fruits in the diet of avian frugivores.

Frugivore species	Type of frugivore	1981-1982			1982-1983			Relative seed removal† (%)
		Fre- quency in feces (%)	N	Average abun- dance*	Fre- quency in feces (%)	N	Average abun- dance*	
<i>Sylvia atricapilla</i>	Seed disperser	37.4	115	3.6	29.4	521	115.2	58.8
<i>Turdus merula</i>	Seed disperser	41.3	46	10.1	31.6	19	14.2	12.2
<i>Erithacus rubecula</i>	Seed disperser	22.6	187	42.2	15.7	102	24.1	12.5
<i>Turdus philomelos</i>	Seed disperser	25.0	4	2.0	66.7	9	32.7	7.9
<i>Sturnus</i> spp.‡	Seed disperser§	1.5	19.0	3	18.7	6.0
<i>Sylvia melanocephala</i>	Seed disperser	6.2	81	19.4	4.3	93	26.4	0.8
<i>Carduelis chloris</i>	Seed predator	12.0	25	8.5	2.0	51	25.7	0.5
<i>Columba palumbus</i>	Seed disperser§	0.5	9.1	11	2.6	0.4
<i>Parus caeruleus</i>	Pulp predator	33.3	6	0.3	66.7	3	0.3	0.3
<i>Cyanopica cyanus</i>	Seed disperser	0.0	21	1.0	0.9	32	1.2	0.2
<i>Sylvia borin</i>	Seed disperser	6.5	46	0.1	0.9	108	0.2	0.2
<i>Phylloscopus collybita</i>	Pulp predator	4.3	23	10.1	0.0	37	16.4	0.04
<i>Fringilla coelebs</i>	Pulp predator	0.0	4	19.7	20.0	5	26.9	0.04
Fruit abundance¶		2230 (0.59%)			160 500 (4.64%)			

* For each species, average monthly abundance (no. individuals/10 ha) in the study area is given for the November-February period.

† Relative seed removal is the fraction of *Olea* seeds found in samples that was contributed by each species (data from the two seasons have been pooled).

‡ Includes *S. vulgaris* and *S. unicolor*.

§ No feeding records at *Olea* during 1981-1982.

|| Frequency in feces calculated on the total number of fruits found in collections of feces under perches.

¶ Number of ripe fruits produced per hectare and percent with respect to the total number of ripe fruits produced in the plant community.

for individual bird species as consumers of the *Olea* crop was, however, strongly skewed (Table 3); *S. atricapilla* accounted for 58.8% of the fruits recorded in fecal samples, and each of the remaining species accounted for <15%.

The significance of a bird as seed removal agent (as assessed by the food data) was related to its relative abundance ($r_s = 0.933$, $N = 9$, $P < .01$) but was not related to the importance of *Olea* fruits in its diet (Table 3). Only *Turdus philomelos* relied strongly on *Olea* fruit during the autumn-winter period, but it removed only 7.9% of the *Olea* seeds; *S. atricapilla* accounted for a great fraction of seed removal but *Olea* was a secondary species in its diet (Table 3). The remaining species also

included *Olea* as a secondary or minor species in diets generally dominated by *Pistacia lentiscus* (see Jordano 1984 for a detailed account). With the exception of the larger species (*T. philomelos*, *Cyanopica cyanus*, *Columba palumbus*, and *Sturnus* spp.) the fraction of *Olea* fruits in the diet decreased in 1982-1983 in spite of the larger fruit crop (Table 3).

Estimates of fruit removal from individual trees indicated dramatic between-year differences in fruit consumption relative to both the ripe crop and the total crop (of final-sized fruits; Table 4). For 1981-1982, average ripe fruit consumption and overall consumption (93.9 and 90.2%, respectively; Table 4) were rather close to the 96.2% estimated for the fraction of the

TABLE 4. Summary statistics of phenophase duration and fruit removal by avian dispersers for *Olea europaea* var. *sylvestris* trees during the 1981-1982 and 1982-1983 seasons. Dates of peak fruiting are also provided (duration of the peak period is defined as the number of days with >50% of the fruit crop ripe).

	1981-1982			1982-1983			t value
	$\bar{X} \pm SD$	N	Range	$\bar{X} \pm SD$	N	Range	
A. Phenophase duration							
Fruiting (d)	78 ± 23	8	50-117	112 ± 23	33	70-146	3.71**
Peak fruiting† (d)	41 ± 14	8	23-63	59 ± 26	33	15-115	1.81 NS
B. Fruit removal							
Crop fraction ripened (%)	96.2 ± 2.7	6	90.9-98.2	96.1 ± 4.5	10‡	86.8-99.6	0.05 NS
Ripe fruit removal (%)	93.9 ± 9.9	6	73.9-99.9	52.4 ± 17.7	10	32.1-83.7	5.27**
Overall removal (%)§	90.2 ± 8.8	6	72.6-96.3	50.0 ± 14.6	10	30.1-74.4	6.10**

** $P < .01$; NS = not significant.

† Exact dates of peak fruiting: 22 November 1981 and 1 December 1982.

‡ The sample of 10 trees in the 1982-1983 season includes all but one of the 6 trees in the 1981 sample.

§ Percent with respect to the total crop of final-sized fruits.

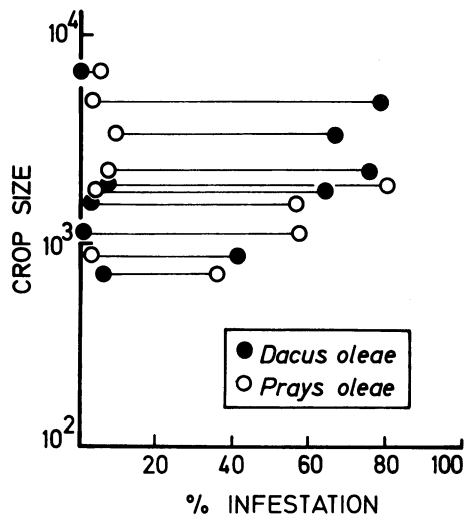


FIG. 1. Relationship between the percentage of *Dacus* and *Prays* damage (referred to the sample of fallen fruits; see Table 4) and crop size, for different *Olea europaea* var. *sylvestris* trees. A line joins the two points corresponding to the same crop; crops heavily attacked by one insect species tend to be undamaged by the other. Kendall rank correlation of combined infestation level with crop size is $\tau = 0.378$, $P = .06$.

fruits that ripened; therefore, most fruits that ripened were harvested. Post-ripening loss due to the damage of fruit by insects averaged $\approx 6.0\%$ (range: 1.0–9.1%). In 1982–1983 the pre-ripening percent loss of fruit was identical (3.2%) to that of the preceding year (Table 4), but loss of ripe fruit due to insect damage (see below) was much larger ($\bar{X} = 27.1\%$, range: 1.1–52.3%). However, the fraction of ripe fruits removed was reduced in 1982, on average, $42.1 \pm 7.8\%$ (range: 14.6–61.1%) for the five trees with data available for the two consecutive fruiting seasons, but the absolute number of seeds removed increased as a result of the increased fruit production in 1982–1983 ($\bar{X} = 1470$ vs. 2172, a

1.5-fold increase from 1981 to 1982, respectively). Thus, the much greater fruit production and greater disperser abundance significantly increased absolute seed removal in 1982–1983, this being a generalized trend for all the trees.

Patterns of insect damage to fruits

The consumption rates for the 1981–1982 season suggest very low (<10%) damage levels, as noted above. Percent crop loss due to the fly, *Dacus*, and *Prays*, the moth, averaged $18.3 \pm 6.4\%$ and $8.8 \pm 3.5\%$, in the 1982–1983 season (Table 5), respectively ($N = 10$ trees), but was extremely variable, ranging from 1 to 30% for individual trees. Insect damage was positively correlated with ripe fruit crop size (Fig. 1), trees with smaller crops tending to have a smaller fraction of fruits damaged. Crops with heavy damage by one species of insect ("heavily infested" trees hereafter) had low damage by the other species. When tree 757, with low attack, is excluded, damage levels of *Dacus* and *Prays* were inversely related ($r_s = -0.750$, $P < .05$, $N = 9$; Fig. 1, Table 5). The fly tended to cause the most damage on trees with larger fruit crops. Pre-ripening losses were largely the effect of the moth, since it oviposits on unripe fruits; therefore, it is not surprising that fly and moth damage levels were inversely related. Only 29 (0.62%) out of 4660 fruits sampled from 10 trees were damaged by larvae of both insects.

The fruit features that are presumably relevant to insect attack (fruit-design variables and pulp nutrient contents) are summarized in the Appendix. With the exception of ash content being negatively correlated with *Prays* infestation ($r_s = -0.837$, $P < .05$, $N = 10$), no variable of nutrient content was significantly associated with the infestation level of either insect. Therefore, discriminant function analysis (Dixon 1981) was carried out to distinguish infested vs. non-infested fruit crops on the basis of the traits of fruits ($N = 300$)

TABLE 5. Crop size, crown projection area, and estimates of percentage ripe-fruit consumption by avian dispersers and insect fruit predators for *Olea europaea* var. *sylvestris* trees during the 1982–1983 fruiting season.

Tree identification number	Crop size	Crown area (m ²)	% Fallen fruits		Total fruit losses†		% Ripe fruit crop		
			<i>Dacus</i> damage	<i>Prays</i> damage	Pre-ripe‡	Post-ripe	Dispersed	Damaged§	
								By <i>Dacus</i>	By <i>Prays</i>
757	6750	46.6	0.0	2.1	0.4	50.4	49.4	0.0	1.1
766	1755	8.0	64.0	4.0	1.1	47.8	51.6	30.6*	1.9
754	1750	13.8	1.4	56.5	14.0	14.0	83.7	0.2	7.9*
812	860	15.9	41.7	2.3	1.7	52.1	47.0	21.7*	1.2
810	2075	19.6	75.0	7.2	6.3	63.6	32.1	47.7*	4.6
811	1975	38.4	7.0	80.0	8.8	16.7	81.6	1.2	13.4*
748	725	8.0	4.8	37.1	1.0	45.2	54.4	2.2	16.8*
813	4900	33.2	78.4	0.6	1.3	62.0	37.2	48.6*	0.4
814	3400	17.0	65.2	8.8	2.0	47.4	51.6	30.9*	4.2
768	1150	19.6	0.0	57.1	1.7	63.5	35.4	0.0	36.3*

* Asterisks mark those trees grouped under the "infested" category for each insect species.

† Refer to the counts of marked fruiting branches.

‡ Accounts for the fraction of the final-sized fruit crop that did not ripen.

§ Estimates of actual losses to both insects derived by referring the percent obtained from the ground samples (percent fallen fruits) to the post-ripening losses calculated from branch counts (see Methods: Insect Damage to Fruits).

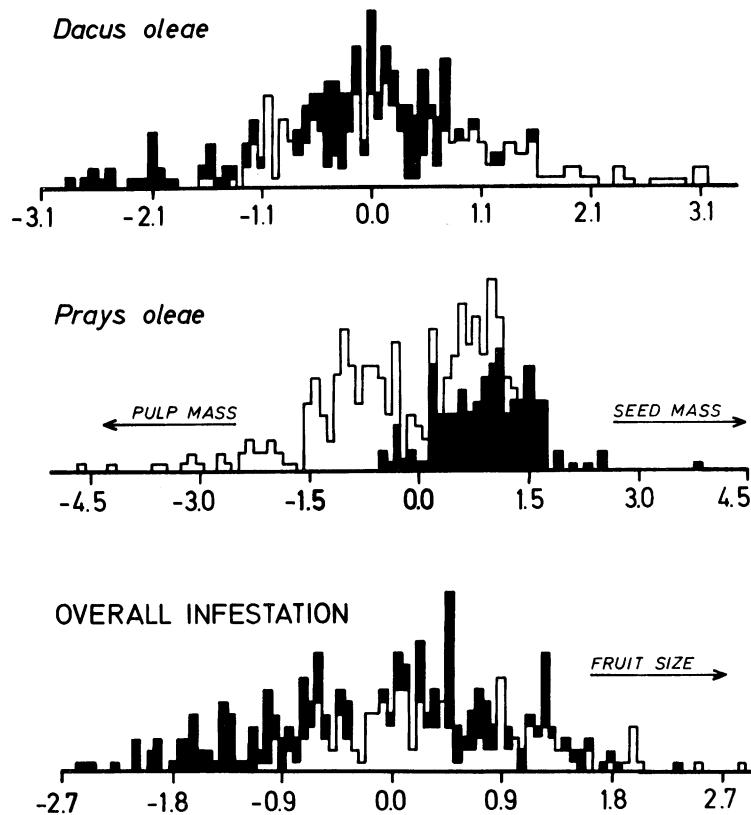


FIG. 2. Frequency distribution of *Olea europaea* var. *sylvestris* fruits on the canonical variable generated by a discriminant analysis, relative to characteristics of fruits grouped as “infested” (solid bars) and “uninfested” (open bars) by each insect species and according to the overall infestation figure (see Table 4). The variables having the highest positive and negative coefficients for the canonical variable are indicated. A separate analysis was carried out for each group.

TABLE 6. Summary of results from three discriminant analyses carried out on fruit-design variables of individual fruits grouped as from “infested” or “uninfested” crops of each damage type. The order when entering the discriminant function, associated *F* value, and coefficients (*C* = constant) are given for each variable.

Grouping	Step and variable	<i>F</i>	Classification†	Canon. corr.	Coefficient
A. Summed infestation	1. Relative yield‡	30.83***	59.2	0.3201	1.040
	2. Fruit wet mass	16.90***	0.184***		0.212
					<i>C</i> = -5.938
B. <i>Dacus oleae</i>	1. Seed dry mass	19.41***	60.0	0.3509	55.760
	2. Percent water	14.45***	0.189***		8.882
	3. Relative yield	9.91§			0.374
	4. Pulp dry mass	10.19***			-39.101
	5. Fruit wet mass	8.26***			0.972
					<i>C</i> = -16.091
C. <i>Prays oleae</i>	1. Percent water	64.62***	77.0	0.6108	-4.042
	2. Pulp dry mass	60.71***	0.579***		-37.252
	3. Fruit wet mass	46.46***			2.715
	4. Relative yield	39.51***			0.309
	5. Seed dry mass	33.38***			33.902
	6. Fruit diameter	29.06***			-0.768
					<i>C</i> = -0.306

*** *P* < .001; § *P* < .005.

† Percent of cases (individual fruits) correctly classified as from “infested” or “uninfested” crops on the basis of the fruit design variables. Figures below the percent are values for the Cohen’s kappa (Titus et al. 1984) and its significance level.

‡ Pulp dry mass as a percentage of fruit wet mass.

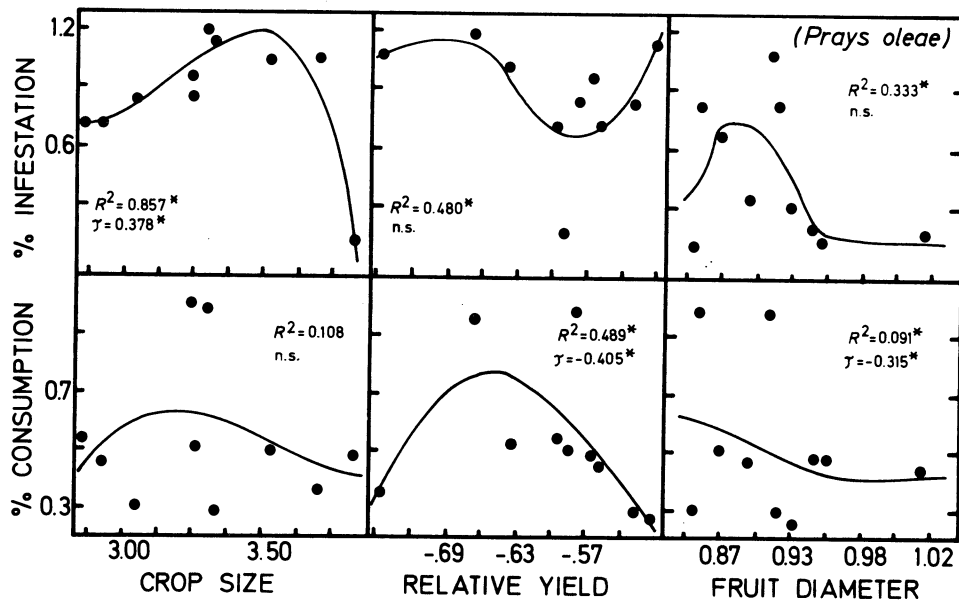


FIG. 3. Nonlinear, polynomial regressions relating percent infestation and consumption with selected "predictor" variables (crop size and fruit diameter were log-transformed; percent infestation, percent consumption, and relative yield received arcsine transformation). Corresponding values for R^2 are given, as well as those for Kendall rank correlation (τ); * $P < .05$, $N = 10$ trees.

from the 10 trees; the same set of fruits was re-analyzed three times, each one grouping the fruits with respect to *Dacus*, *Prays*, and overall infestation levels of their crops (see Table 5). Stepwise discriminant analysis enabled the identification of those fruit traits that characterized crops heavily attacked by a given insect, suggesting possible fruit features under selection by insect frugivores.

Significant discrimination was obtained with fruit variables related to both the pulp and seed masses (Table 6, Fig. 2). Fruits from trees infested by *Dacus* tended to have low or negative scores on the canonical variable; the only variable that had a negative, significant coefficient was pulp dry mass per fruit; thus, trees not heavily attacked by *Dacus* were those with relatively large seeds and low amount of pulp (Fig. 2). In contrast, fruit from trees infested by *Prays* chiefly occupied the positive portion of the axis and the variable having the highest coefficient on it was seed dry mass; crops uninfested by *Prays* had fruits with more pulp and higher water content, i.e., those heavily attacked by *Dacus*.

The classification function correctly assigned 60.0 and 77.0% of individual fruits (cases) to the pre-assigned crop categories (Table 6). This agreement in the classification significantly departs from chance agreement (values for Cohen's kappa [Table 6] were all highly significant), demonstrating differences in fruit traits of the attacked and unattacked crops. Thus, the "complementary" infestation pattern of the two insect species was strongly associated with particular fruit features of the individual trees. Considering the summed effects of the two species, crops from trees heavily attacked

differed significantly from those showing lower infestation levels (Fig. 2, Table 6), but note the increased overlap of the corresponding frequency distributions on the discriminant axis (59.2% correct classifications). At a population level, the overall result of the combined infestation was that trees with greatest losses of ripe fruit to insects were those having fruits with greater relative amount of pulp per fruit ($F = 33.2$, $df = 1$, 296 , $P < .001$). This might be explained by the fact that most variation in fruit loss (29.4%) was accounted for by *Dacus* damage and its selection of fruits with greater pulp yield, in contrast with only 2.9% of variation explained by *Prays* that select large-seeded fruits.

Correlates of bird/pests effects

Two processes, acting antagonistically, determined the removal rate of individual fruit crops: actual feeding by dispersers and fruit damage by insect frugivores.

A preliminary analysis by means of nonparametric correlation (Kendall rank correlation: Siegel 1956) revealed a subset of significant correlations between various fruit traits (Appendix, Table 5) and both fruit removal and fruit damage. There were no significant correlations with nutrient content variables. Because most relationships showed strong curvilinearities as well as mutual interrelations, I calculated nonlinear correlations on transformed data using pairwise polynomial regression (Dixon 1981) between the dependent "criterion" variables (those in the consumption-infestation set) and the independent ones ("predictors," those relating to tree and fruit traits; see Sokal and Rohlf 1981:642).

Fitted curves (Fig. 3) suggest that the effects of avian

seed dispersers and fruit-damaging insects on plant variables directly related to the dispersal process are opposed to one another. Crop size explained a significant fraction of the variation in percent infestation but failed to account for variation in fruit consumption by dispersers. In contrast, bird consumption showed negative relations with fruit traits such as relative amount of pulp per fruit and fruit diameter, but these seemed an effect of the intercorrelations of opposite sign with infestation levels.

I attempted to measure the direct effect of crop and fruit traits (predictor variables) on ripe fruit removal by birds (criterion variable) by means of path analysis (see Wright 1934, Duncan 1966, Sokal and Rohlf 1981 for detailed accounts of the method). The analysis calculates a path coefficient that accounts for both the direct effect of the predictors on the criterion variable and that due to interrelationships between the former with the damage levels caused by *Dacus* and *Prays*. The related predictor variables (left boxes in Fig. 4) determined a high fraction of the population variation in insect damage to fruits and removal by dispersers. Thus, variation in fruit removal by legitimate frugivores and damage by insect predators had common, strongly correlated, causes, which tended to be of opposite signs (Fig. 4). The linear relation between consumption and infestation levels ($r = 0.078$) dramatically increased ($r = -0.798$) when correlations between the common causes were included by means of path coefficients; this negative correlation was expected based on the biologically opposite action of the two kinds of frugivores. Thus, most variation in ripe fruit removal of *Olea europaea* crops by avian frugivores could be attributed to the interaction of dispersal-related plant traits (crop size, fruit size and design) with insect predators that determined post-ripening (but pre-dispersal) fruit losses and set upper limits to the maximum seed removal that frugivorous birds could exert.

DISCUSSION

Determinants of between-year variation in the fruit supply

Physiological stress induced by extreme environmental conditions may have a profound effect on fruit set and development. During the severe drought in 1981, most *Olea* trees lost most or all of their developing fruits. This physiologically induced fruit shedding is well documented in var. *europaea* (Lakhoua 1976, Villemur 1981, Milella 1984). Crop mass in the cultivated variety also changes as a function of the hydric capacity of soil (Lakhoua 1976). The effect of rainfall on this year's crop is also superimposed on the effect of the previous year's crop. Since years of high investment in fruits typically depress resources available for vegetative growth, the following season's flower and fruit crops should be reduced. It is consistent with this hypothesis that the variation in fruit crop

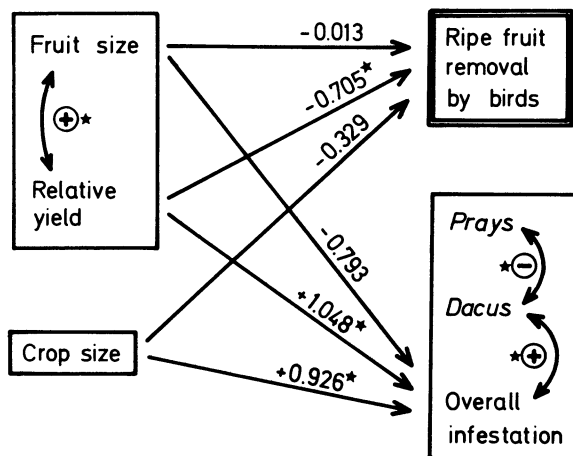


FIG. 4. Summary of the main relations between removal success for individual trees, infestation levels, and fruit and tree characteristics. Arrows denote the direction, and the path coefficients the relative magnitude, of the "effects." Plus and minus signs indicate significant, positive or negative, pairwise correlations between variables; stars indicate significant ($P < .05$) linear, product-moment correlation.

sizes between the 2 yr was negatively related to the crop size of the 1st yr, suggesting that heavy fruiting might impair a high reproductive investment in the following season. More years of data are needed to document this trend as well as the apparent stability in fruit production suggested by those trees that fruited in both years with the largest crops and those that flowered but did not set any fruit in the two consecutive years.

The number of seeds effectively dispersed during a reproductive cycle reflects abiotic factors as well as biotic factors. The number of seeds available for dispersal directly reflects the number destroyed by fruit pests during the pre-dispersal phase. Animal interactions influence individual fecundity (i.e., through pre-dispersal fruit predation) a posteriori with respect to maternal allocation; hence their net effect on final crop size might offset any previous allocation pattern (Heithaus et al. 1982, Hainsworth et al. 1984).

Seed removal: the result of multiple interactions

The proportion of ripe fruit removed by birds was dramatically reduced during the season of largest frugivore abundance, being coincident with a massive production of fruits by most trees. However, the increase in fecundity in 1982 was paralleled by a net increase in the number of seeds removed (see also Hainsworth et al. 1984). The decrease in percent removal could result from two factors acting singly or together: (1) a small number of dispersers relative to the number of fruits; and (2) higher levels of damaged fruits. Both effects are expected if satiation of the disperser assemblage results in longer exposure time of ripe fruit on branches. Rapid removal of ripe fruits is

advantageous because it minimizes the probability that fruits will be damaged by invertebrates before dispersal (Thompson and Willson 1978).

A comparison of the changes in disperser abundance with variation in the fruit supply may indicate if disperser satiation could operate in years with a large *Olea* crop. The winter densities of the major dispersers, and especially *Turdus* spp. and *Sturnus* spp., show pronounced changes in local areas depending on fruit abundance (Santos et al. 1983, Jordano 1985). A comparison of the estimated supplies in the form of assimilable energy in *Olea* pulp (megajoules per hectare) and the summed metabolic demand of the wintering passerine species (a conservative estimate of the corresponding figure for the subset of frugivorous species) is illustrative. *Olea* ripe fruit production in 1981–1982 represented 5.0 MJ/ha, as estimated from the corresponding average figures of pulp dry mass per fruit, fruit production, and specific energy content of the pulp (megajoules per gram ash-free dry mass; see Appendix). This figure is far below the estimated metabolic demand (see Kendeigh et al. 1977 and Jordano 1984 for methods) of 77.0 MJ/ha for all the birds during the main wintering period (November through February). The corresponding estimates for 1982–1983 are markedly different: 645 and 297 MJ/ha (available and demand, respectively); thus, at least from this energetic perspective, the *Olea* fruit crop in 1981 was in short supply while that of the 2nd yr most likely satiated the disperser assemblage. Thus, ripe fruits were available for a longer period in 1982 in spite of much greater abundance of frugivores. Damaging insects reduced this available fruit supply by taking 47.6% of that year's crop (Table 3) thus reducing the available resources of *Olea* pulp to 322 MJ/ha, a figure closer to, but above, the estimated demand by birds. Therefore, in years with good crops (e.g., 1982–1983) even a reduction in pest pressure could not increase fruit removal by disperser because the disperser assemblage is satiated. A related point is that fruit pests can set an upper limit to the level of fruit removal by avian frugivores in a year of low fruit availability and heavy insect infestation.

The population levels of both *Dacus oleae* and *Prays oleae* have been shown to be determined by the current season weather conditions: a severe drought decreases adult survival and fecundity in both species and reduces the number of generations per season (Ruiz Castro 1948, 1951, López Bellido 1977; see Drew and Hooper 1983, Fitt 1984). Population levels do not bear a consistent relationship with the previous year's fruit crop. Instead, they "track" the current season's fruit availability only if weather has been suitable for survival of adults and pupae. This, together with the fact that fruit availability was well above the requirements of dispersers (increasing exposure time of fruits on branches), may explain the observed increase in pest pressure and its results in 1982–1983.

Differences in fruit traits of moth- and fly-infested crops reveal the species-specific traits associated with oviposition site (seed- and pulp-eating larvae, respectively). Information on oviposition-site selection by *Dacus* and other tephritids supports this view (Prokopy and Haniotakis 1976, Levison and Levison 1984, Neuenschwander et al. 1985).

Any interpretation of fruit removal rates by dispersers without explicit evaluation of the contribution to the process of higher order interactions with insect fruit predators would be unwarranted. Thus, the few significant correlates of disperser activity with particular crop traits were apparently the result of stronger, opposed effects of these traits on the insect infestation levels. For example, variation in relative fruit removal by avian dispersers was explained by a negative relationship with relative yield (RY) that resulted from the fact that crops with high values of this variable were heavily infested by *Dacus* larvae and crops with relatively larger seeds (low values of RY) were subject to heavy attack by *Prays*.

Future research on plant dispersal strategies needs consideration of these correlations (Herrera 1982a, 1984b, c, Willson 1983, Manzur and Courtney 1984). Selective effects of avian dispersers on fruit traits, if any, would be damped, if not counterselected, by the action of fruit predators. As suggested by the *Olea* study, any phase of the reproductive cycle might have far-reaching implications for seed dispersal in the current and subsequent reproductive episodes.

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APPENDIX

TABLE A1. Statistics of fruit characteristics and pulp nutrient contents of the intensively studied *Olea europaea* var. *sylvestris* trees.* All fruit samples ($N = 30$ for morphological variables) were obtained during the 1982-1983 fruiting season except for trees number 813, 814, and 768 (1981-1982 season).

TREE	DIAM	FRWT	SDWT	PWC	RY	PRO	LIP	TNC	ASH	ADF	P	K
757	8.80	0.555	0.127	62.9	25.9	—	—	—	—	—	—	—
766	8.69	0.614	0.102	62.0	27.2	3.19	23.85	59.25	0.13	13.58	0.057	1.83
754	7.22	0.257	0.070	57.1	26.6	3.13	27.90	58.67	0.05	10.25	0.038	1.69
812	10.48	1.072	0.225	62.0	27.8	2.38	23.90	62.92	0.35	10.45	0.034	1.54
810	8.37	0.559	0.125	56.6	30.9	2.50	29.03	55.37	0.05	13.05	0.034	1.64
756	8.07	0.468	0.110	58.7	28.1	3.06	22.34	63.08	0.22	11.30	0.041	1.28
811	8.14	0.471	0.157	62.1	21.5	—	—	—	—	—	—	—
748	7.53	0.318	0.077	62.0	25.3	3.75	26.59	52.16	0.05	17.45	0.066	2.07
813	7.20	0.275	0.075	71.0	17.9	—	—	—	—	—	—	—
814	7.85	0.364	0.119	59.0	23.2	—	—	—	—	—	—	—
768	8.20	0.435	0.125	52.4	29.7	—	—	—	—	—	—	—
Mean	8.23	0.490	0.119	60.5	25.8	3.00	25.60	58.57	0.14	12.68	0.045	1.68
SE	0.27	0.068	0.013	1.4	1.1	0.50	1.07	1.74	0.12	1.10	0.109	0.11

* DIAM, fruit diameter (mm); FRWT, fresh mass of whole fruit (g); SDWT, dry mass of seed (g); PWC, pulp water content; RY, relative yield (pulp dry mass as percent of fresh-fruit mass); PRO, protein; LIP, lipids; TNC, nonstructural carbohydrates; ASH, ash content; ADF, acid-detergent fiber. Organic fraction and mineral concentrations are given as percent dry mass of pulp; trace elements (Fe through Cu), as mg/kg.

TABLE A1. Continued.

Ca	Mg	Na	Fe	Mn	Zn	Cu
—	—	—	—	—	—	—
0.155	0.024	0.023	42.5	3.13	4.17	5.25
0.110	0.018	0.021	20.0	3.75	10.83	4.25
0.095	0.021	0.022	12.5	3.75	5.83	6.25
0.090	0.025	0.040	36.3	3.13	5.00	5.75
0.130	0.031	0.039	22.5	3.13	4.17	4.38
—	—	—	—	—	—	—
0.185	0.028	0.037	30.0	3.75	4.58	7.25
—	—	—	—	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
0.128	0.025	0.030	27.3	3.44	5.76	5.52
0.015	0.002	0.004	4.5	0.14	1.04	0.47