TEMPORAL PATTERN OF SEED DISPERSAL OF WILD OLIVE (OLEA EUROPAEA VAR. SYLVESTRIS): ITS EFFECT ON INTRA-SPECIFIC COMPETITION

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Abstract

We periodically surveyed two populations of wild olive trees in two plots, one sparse scrubland (plot S) and one dense scrubland (plot D), in order to obtain: 1, the fortnight percentage of ripe fruits and fruit removal; 2, the density of avian seed dispersers; 3, the availability of wild olive fruits in the plots and the energetic demands of the seed dispersers; and 4, only for plot D, the frequency of wild olive seeds in diet samples of Blackcaps (*Sylvia atricapilla*), the main wild olive fruit consumer in the study area. The estimated energetic offer of fruits in plot S resulted two fold the energetic demands of the seed dispersers; the offer in plot D was smaller than the energetic demand. The mean percentage of fruit removal in plot S was comparatively lower, and its range wider, than in plot D. However, the Mean percentage of fruit removal did not significantly differ between plots, which indicates the occurrence of intra-specific competition in both plots.

Introduction

Plant species that rely on vertebrates for seed dispersal are usually involved in inter and intra-specific competition events for seed dispersers (HOWE & ESTABROOK, 1977; HERRERA, 1981) due, among other reasons, to the fact that the guild of dispersers is not able to disperse all the seeds produced in a population (JORDANO, 1987; HERRERA & al., 1994). Intra-specific competition may affect, either positively or negatively, the fitness of those individuals that may be involved in such event. The positive effect is considered to be a gain in fitness as a consequence of a larger number of seeds dispersed, thus leading to a higher likelihood to leave descendants (HOWE & SMALLWOOD, 1982).

The intra-specific competition for seed disperser birds, among individuals in a population of fleshy-fruiting plants, may be due to different reasons; among them, the best documented are that related to the satiation of dispersers as a consequence of an excessive fruit production (JORDANO, 1987; HERRERA & al., 1994; ALCÁNTARA, 1995) and that caused by the occurrence of other fleshy-fruiting species in the same area (HERRERA, 1984; LASKA & STYLES, 1994).

In this paper we specifically address the following questions: 1, does intra-specific competition occur in populations located in habitats differing in floristic composition, physiognomy and succesional stage? and 2, does both habitat types share the same patterns of intraspecific competition?

Material and methods

The present study has been carried out using the wild olive tree (*Olea europaea* var. *sylvestris* Brot.) in two plots located at the Sierra de Jaén, southwards of the Guadalquivir basin. Plot S (sparse scrubland) extends over 4.5 ha, with 9 olive/ha. Mean shrub cover around olives is 12.69 ± 12.45% (mean ± SD). Plot D (dense scrubland) extends over 2.5 ha, with 17 olives/ha. Mean shrub cover around olives is 35.43 ± 12.40%. Plots are largely different (Alcántara et al. unpublished data): i. e. shrub cover around olive trees is significantly different between plots ($F_{(1,77)}$ = 71.94, P < 0.001); the number of fleshy-fruiting plant species overlapping their ripening phenology with olive trees is largely three fold in plot D compared to plot S (7 vs. 2 species); slope is also different between plots (higher in plot D); light exposure in winter ranges 7-9 hours/day in plot S and 2-4 hours/day in plot D and, finally, Plot S is largely more windy than plot D (for further information on the differences between plots, see ALCÁNTARA, 1995). Further, in the study year in plot D, *Phyllirea latifolia* produced crops of similar size to those found for wild olives.

Four branches were marked in each fruiting tree (n = 16 in plot S, n=39 in plot D) and their fruits were fortnightly recorded, from the moment prior to the beginning of ripening (October) until the moment in which the abscission was generalised and the greater part of the frugivores have left the area (March in the first season and April in the second) (ALCÁNTARA, 1995). For each branch we noted the number of mature, not mature and hurt fruits; then mean values were obtained for each tree.

From the fruits that disappeared from the labelled branches, we estimated as *mobilised* those that disappeared mature and healthy (MANZUR & COURTNEY, 1984; JORDANO, 1987; SALLABANKS, 1993). From this information, the removal success (percentage of the total crop that is consumed by the dispersers) was calculated. To avoid quantifying a healthy fruit that falls to the ground (either by abscission or by handling or rejection by birds) as consumed, we applied a correcting factor to the removal success obtained from the labelled branches, this being multiplied by the ratio seeds/healthy fruits under the tree, fortnightly recorded for each individual from four 0.25 m² sampling points on the ground.

Energetic offer of the wild olive fruits.- To estimate the crop size of each individual, we assigned each tree to one of the following classes: 0-500 fruits, 500-1000, 1000-2500, 2500-5000, 5000-10000, 10000-20000 and > 20000. The class to which each tree was associated was calculated independently by four observers. The centre of the interval was the value used as representative of the crop size. From these data, we calculated the number of fruit in each plot. The mean weight of the fruits was calculated from 30 fruits taken from each tree. The energetic contents of the fruits (kcal/gr) were taken from REY (1992). The total fruit weight produced in each plot was expressed as gr/ha, so that, once multiplied by the energetic content of the fruit, it yielded the overall kcal/ha produced in each plot.

Energetic demand of the frugivorous birds.- From November 1993 to April 1994 we accomplished birds censuses fortnightly in the study plots, by means of the IPA method (BLONDEL & al., 1970), applied in fixed samples with 25 m radius and for 5 minutes, in order to avoid duplication (TELLERÍA, 1986). We accomplished 10 stations

in plot S and 6 in plot D. The values applied as energetic demand of each frugivorous species were taken from KENDEIGH & al. (1977). To obtain the overall energetic demand for the season, the density of each disperser each fortnight was multiplied by its energetic demand, then adding those obtained for the different species; this value was then multiplied by the number by days among consecutive censuses.

Finally, we mist-netted blackcaps fortnightly during all the season, these being maintained in bags until they defecate or regurgitate the seeds they had eventually eaten.

Results

Avian seed dispersers were significantly more abundant in plot D than in plot S (see Table 1). Consequently, the energetic demand was higher in plot D (25306.8 vs. 2896.6 kcal/ha). The estimated energetic offer was almost four fold higher than in plot S (19010.4 vs 5441.4 kcal/ha). Thus, the estimated offer in plot D was smaller than birds' energetic demand, whereas in plot S, the offer was two fold the energetic demand of seed dispersers (see Fig. 1).

The pattern of fruit ripening shows a sigmoidal shape in both plots. Contrary, the pattern of fruit removal increases exponentially towards the end of the winter season (see Fig. 2). However, this increase is different between plots, being steeper in plot D, where 75% of fruit removal occurred in the last month, than in plot S, where 33% of fruit removal occurred in the last month (see Fig. 2).

	Plot S	Plot D
Erithacus rubecula (D)	0.22 ± 0.22	1.11 ± 0.55
Phoenicurus ochrurus (D)	0.56 ± 0.34	0.08 ± 0.20
Turdus merula (D)	–	0.50 ± 0.10
Turdus philomelos (D)	0.10 ± 0.08	1.34 ± 0.33
Sylvia melanocephala (D)	0.52 ± 0.40	1.30 ± 0.43
Sylvia atricapilla (D)	0.28 ± 0.08	2.75 ± 0.94
Pyrrhocorax pyrrhocorax (D)	0.04 ± 0.09	–
Corvus monedula (D)	–	0.06 ± 0.13
Seed predators	0.04	0.09
Pulp predators	1.66	1.78
Nº dispersers/IPA **	1.72 ± 0.85	7.14 ± 0.93
Nª Sp. of dispersers/IPA **	1.26 ± 0.42	3.58 ± 0.25
H'(dispersers) n.s.	1.30 ± 0.08	1.45 ± 0.16
(%) Dispersers **	40.95 ± 11.76	75.77 ± 8.93
(%) Predators *	36.54 ± 12.77	16.38 ± 9.93

Table 1. Guild of wintering frugivores present in the study plots. Seed disperser (D). For the guild parameters, the significance of Mann-Whitney test comparing between plots are given: ** ($p < 0.01$), * ($p < 0.05$), n.s. ($p > 0.05$).
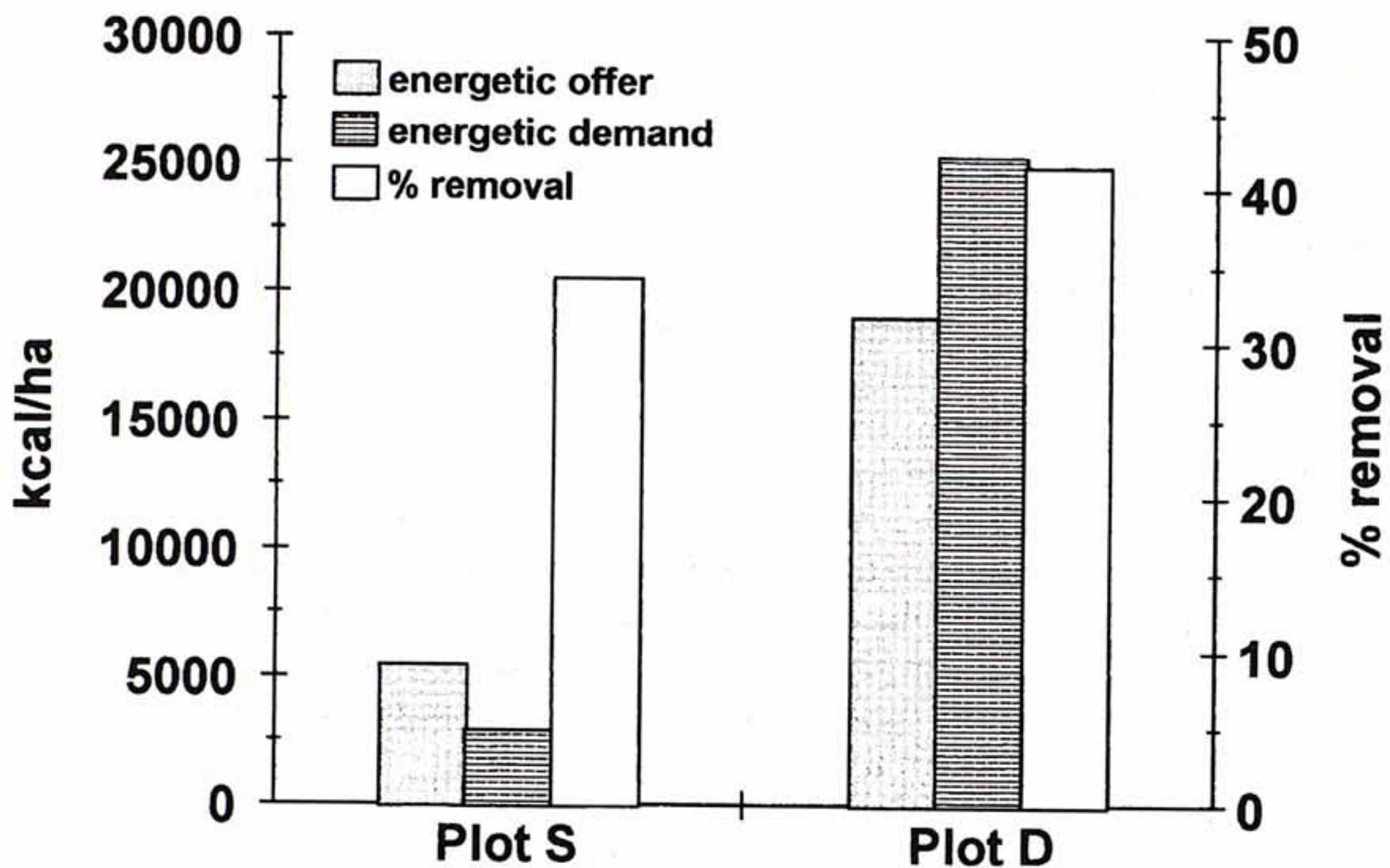
Fig. 1. Energetic offer, energetic demand and avian seed dispersal in plots S and D.

A large temporal variation existed in the consumption levels of wild olive fruits by dispersers, since similar levels of abundance of dispersers in different moments of the wintering season yielded very different levels of fruit removal (see Fig. 3). Thus, in plot S, from the second fortnight of December to the first of January, an increase in the number of dispersers led to an increase in the removal levels; however from the second January fortnight to the first of February, an increase of approximately 1% in the abundance of dispersers yielded an increase in some 2 % in the fruit mobilisation. This phenomenon is better detected in plot D where, from the first fortnight of January to the first of February, yet increasing the abundance of dispersers in 2%, the mobilisation levels were consistent; however, from this last fortnight to the first of March, yet reducing the number of dispersers, the mobilisation was increased in almost 5%.

These data result are countersigned upon analysing the frequency of seeds appearance in the diet samples of blackcaps. Thus, at the beginning of the season, the frequency of samples with more than a seed was significantly lower compared to the end of the season (5.56 vs 16.33%). Additionally, the appearance of *Phyllirea latifolia* seeds significantly decreased along the winter (r_s=-0.78, p<0.05, n=7), thus suggesting that the temporal variation in wild olive consumption would be caused by inter-specific competition between plants.

In spite of the differences shown in fruit removal phenology, the mean percentage of fruit removal did not differ significantly between plots (plot S: 34.2 ± 6.3%, range 0.4 - 78.1%, n = 16; plot D: 22.3 ± 5.3%, range 0 - 90.4%, n = 39; t = - 0.65, p > 0.1) (see Fig. 1).

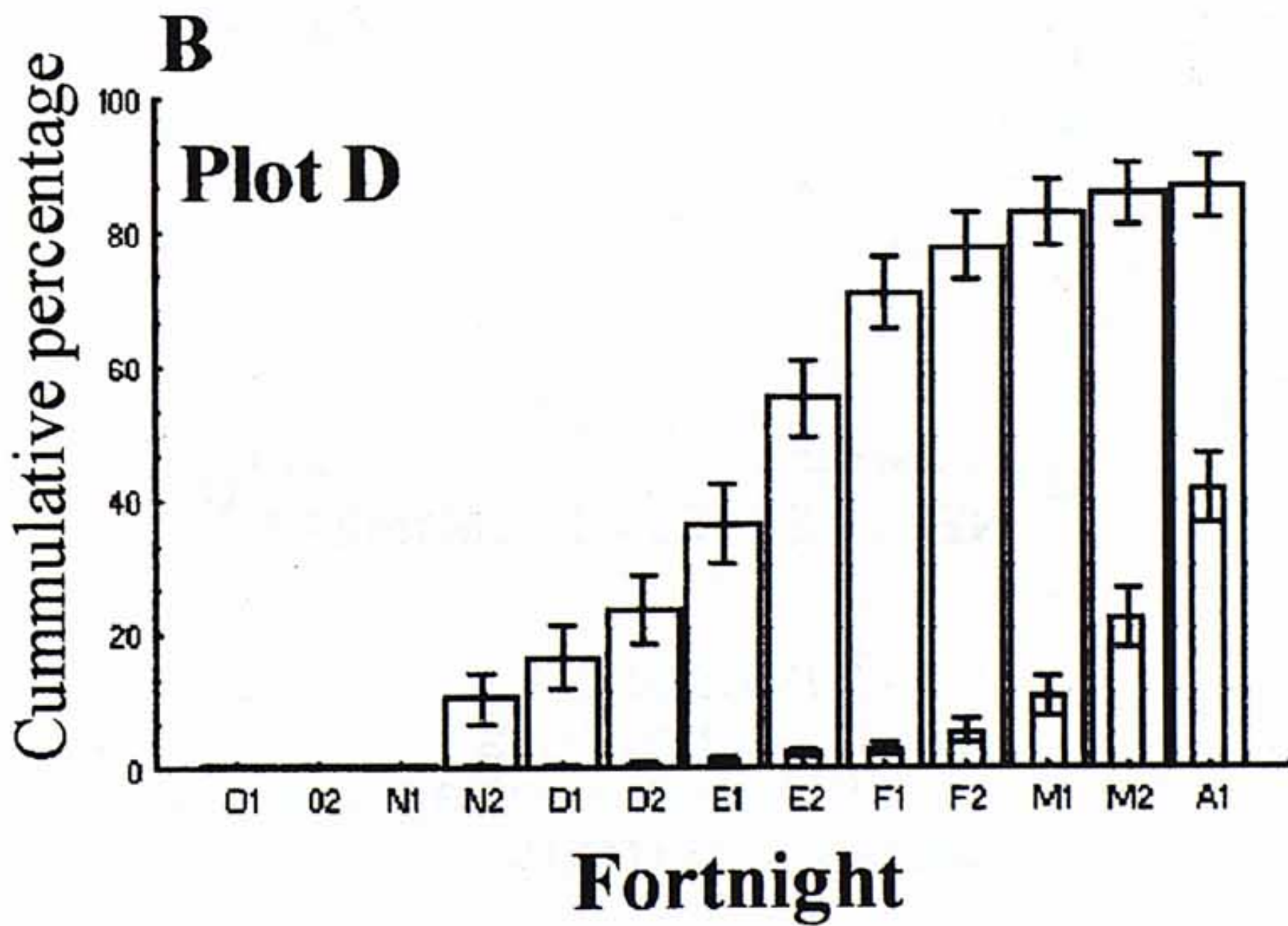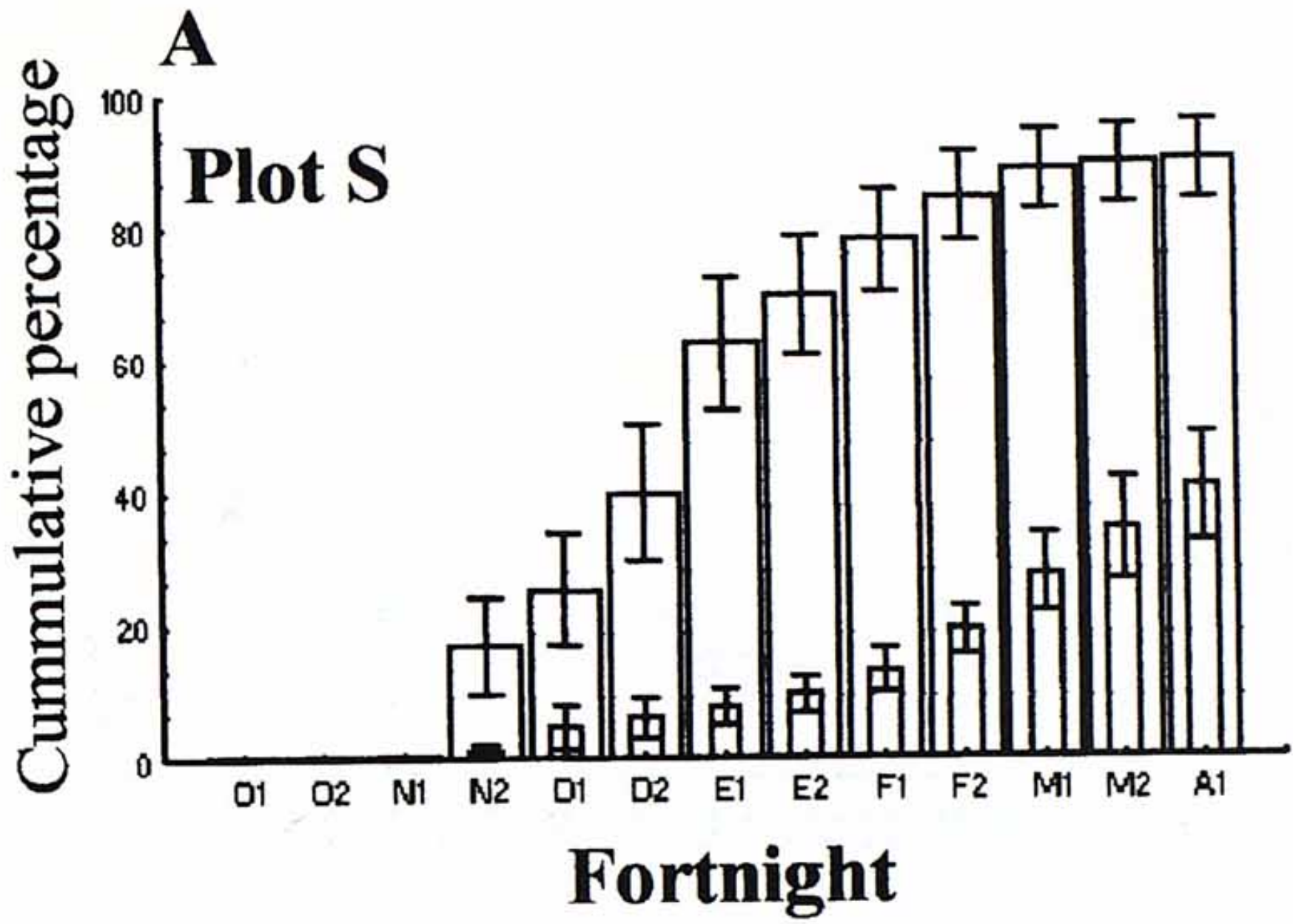Fig. 2. Fruit ripening (higer boxes) and fruit removal (smaller boxes) in plots S and D.
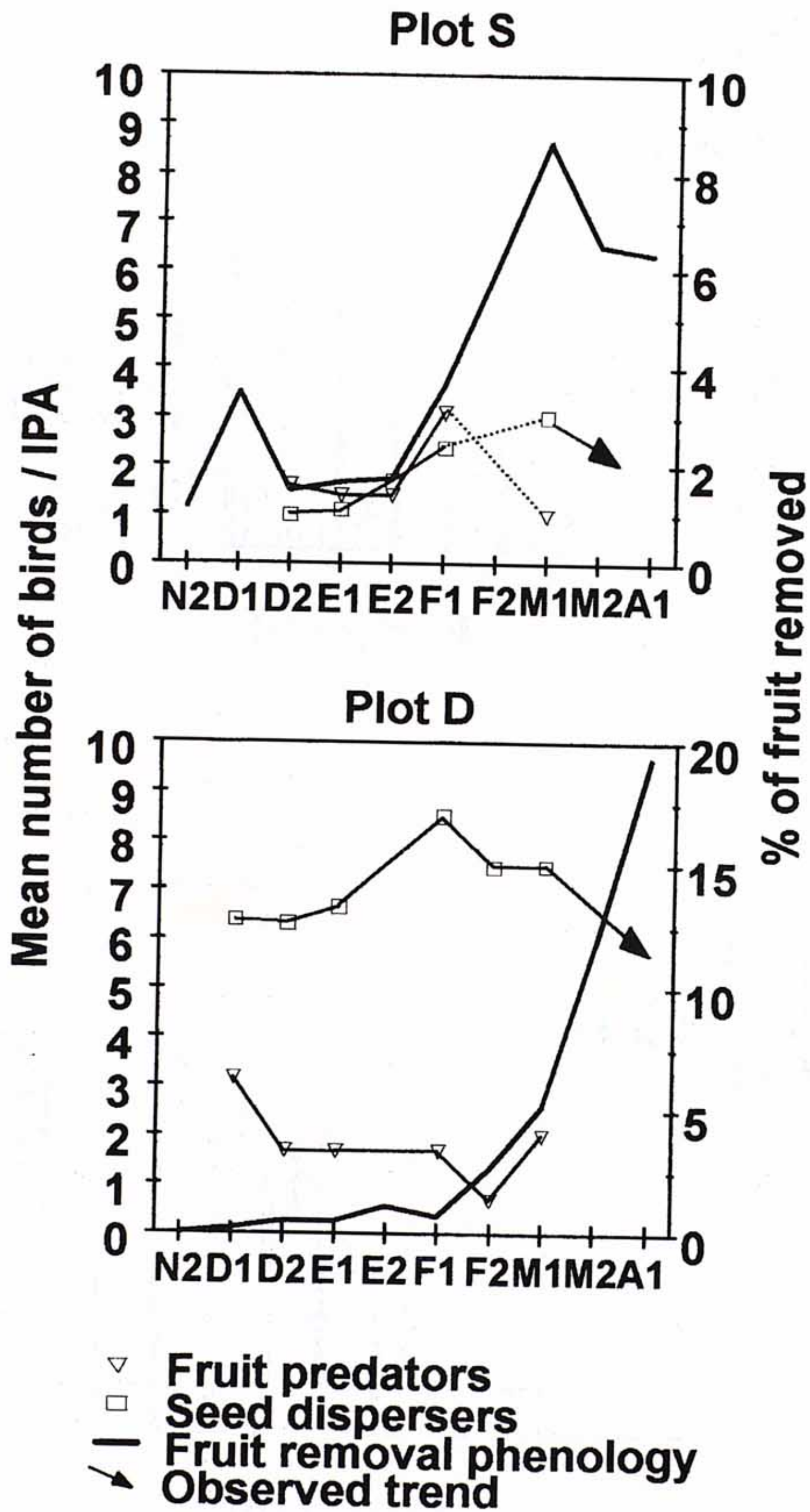
Fig. 3. Fruit predation and dispersal in plots S and D.

Discussion

A frequent way in plant populations by which the phenomenon of the intra-specific competition for the seed dispersers emerges, is the satiation of the latter, that is produced when the fruit offer overcome the energetic demand of the frugivores. Assuming this is an origin of competition, it would be expected that mean removal levels would be smaller if the offer is smaller or just as demand is (see e.g. JORDANO, 1987).

In our study, and contrary to these expectations, the mean percentage of fruit removal did not differ significantly between plots (plot S offer was much higher than demand and plot D offer was smaller than demand). As overall removal is low in both plots, we can conclude that intra-specific competition occurred in both. Nevertheless, the origin of competition seems to be different in each case.

For plot S it seems feasible the disperser satiation as an explanation for the occurrence of intra-specific competition, but what was the origin of competition in plot D?

Some data shown in this paper suggest an inter-specific competition between olive trees and *Phyllirea latifolia* in plot D. This competition is observed if the temporaly distribution of fruit removal in both study plots is compared (Fig. 3). In plot S, where no species seemed to compete with the olive tree, removal was distributed more evenly than in plot D, where competition occurs, this causing that removal was concentrated at the end of the season, since the dispersers consumed the fruit of *P. latifolia* earlier. The preferences of the frugivores for certain types of fruits have been documented in other studies; i. e. HERRERA (1984) discuss how *Crataegus monogyna* was preferably consumed over *Rosa canina* spite the fact that both species appeared with similar abundance. Something similar occurred between *Sorbus aucuparia* and *Viburnum opulus* (see ENGLUND, 1993).

Another feature observed in the phenology of fruit consumption is its strong increase towards the end of the wintering. This may be due to the fact that the main frugivorous species (Blackcaps, European robin *Erithacus rubecula* and Song thrush *Turdus philomelos*) are markedly migrants. This species develops a marked hiperphagy just before migration begins (KING, 1972; BERTHOLD, 1975) so that they strongly increase their fruit consumption rate. Data in this study suggest that, at an individual level, a large number of olive trees depend upon this hiperphagy for their success in seeds dispersion. Moreover, some populations of olive trees, as the ones studied here, may depend on the premigratory hiperphagy of dispersers to accomplish the greater part of the dispersion of their seeds. Presumably, the importance of this event maybe different for other olive populations along Guadalquivir basin (Rey, unpublished data).

Concluding, this study shows three different processes, non-mutually excluding, by which intra-specific competition may be generated: satiation of dispersers, premigratory hiperphagy and competition with different fleshy-fruiting species (*P. latifolia* in our study). The first process is able to generate intra-specific competition *per se*; however the two remaining processes may mainly act by increasing a previous intra-specific competition, as they help the greater part of the fruit removal to be concentrated when most of the trees are having mature fruits.

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