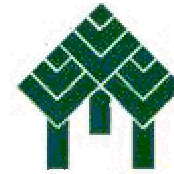


ספרית אורנים



המאמרים במערכת תדפיסים זו מוגנים על-פי

חוק זכויות יוצרים

הדפסת מאמרים תהיה לצרכי לימוד והוראה בלבד

אין לעשות כל שימוש מסחרי במאמרים.

Colonization in an abandoned East-Mediterranean vineyard

Ne'eman, Gidi & Izhaki, Ido

*Department of Biology, University of Haifa at Oranim, Tivon, 36006 Israel;
Fax 972 4 9832167; E-mail gneeman@research.haifa.ac.il*

Abstract. Previous studies on secondary succession in abandoned agricultural land in the Mediterranean area were carried out by the chronosequence method, including data from different sites. A unique opportunity to study secondary succession arose from a situation in which different parts of one homogeneous East-Mediterranean vineyard were abandoned for 5, 8, 15 and 35 yr, and did not suffer from any disturbance subsequently. Most of the perennial species that colonized the abandoned vineyard were fleshy fruited species, which apparently were dispersed by birds from the surrounding maquis into the vineyard. These bird-dispersed species were the first to be established, and were the dominant plant group according to dispersal modes. The abandoned vine plants and their supporting columns provided the birds with perching and feeding sites, enhancing the arrival of bird-dispersed species regardless of their life forms. Under these conditions the most important attribute that affected vegetation dynamics was seed dispersal mode. Trees were among the first to colonize in the vineyard, implying that no facilitation was needed for their establishment. Annual plant species were the only species to disappear during succession. Almost all perennial species which had arrived persisted in the vineyard, and no replacement of perennial species was found. The rate of succession was rapid, as expressed by the short time (8 - 15 yr) needed for the stabilization of species composition, for growth to average height of late succession trees, and for reaching high cover of the invading perennial species in the abandoned vineyard. The secondary succession described above differs from that in the western Mediterranean by the absence of perennial species replacement and its rapid rate. The possible causes are discussed.

Keywords: Abandonment; Israel; Life form; Secondary succession; Seed dispersal.

Nomenclature: Feinbrun-Dothan & Danin (1991).

Introduction

Numerous studies have been published on secondary succession of abandoned agricultural land, most of them concerning old field succession in the United States (e.g. Billings 1938; Oosting 1942; Buell et al.

1971; Pickett 1982; Gill & Marks 1991). To the best of our knowledge, the only quantitative studies on succession in abandoned Mediterranean plantations were carried out in southern France and Spain (Houssard et al. 1980; Debussche et al. 1982; Debussche et al. 1985; Escarré et al. 1983; Debussche & Lepart 1992; Debussche & Isenmann 1994; Tatoni & Roche 1994).

The first comprehensive theory of plant succession (Clements 1904, 1916), and also several later ones (e.g. Odum 1969), were holistic, assuming a convergent change in plant communities from a determined starting point towards a climax vegetation. The driving force was assumed to be an ecosystem parameter, and successional change was viewed as the consequence of relationships within the community. In contrast, contemporary ecologists view vegetation change as the outcome of populations' interacting within fluctuating environmental conditions. However, there was a shift from holistic towards mechanistic explanations of succession, and from equilibrium towards non-equilibrium theories (Glenn-Lewin et al. 1992).

The mechanisms that determine how species appear in the successional sere have been discussed for some time (e.g. Drury & Nisbet 1973; Connell & Slatyer 1977; Horn 1981; Glenn-Lewin & van der Maarel 1992; van Andel et al. 1993). The main mechanisms are:

1. Colonization, which is affected by seed dispersal, seed predation, seed germination, predation of seedlings, seedling competition and establishment (Gill & Marks 1991).

2. 'Initial floristic composition' and 'pre-emption' (Egler 1954).

3. Life-history factors (Pickett 1976; Drury & Nisbet 1973), and ecophysiological traits (Bazzaz 1979).

4. Interaction between species including: (a) competition for ratios of environmental resources which change in time (Tilman 1987, 1988); (b) reaction (Clements 1916) or facilitation (Connell & Slatyer 1977), when early successional species cause changes that enable the later ones to enter; (c) inhibition, when existing plant species prevent the establishment, growth or maturation of others (Connell & Slatyer 1977); (d) tolerance, when

neither facilitation nor inhibition exists among species (Connell & Slatyer 1977). Experimental research (Gill & Marks 1991; Chapin et al. 1994) has demonstrated that no single mechanism can fully account for any successional system.

Despite the many research papers and several reviews on vegetation succession, there is still a major difficulty in suggesting a general universal cause for succession (e.g. van Andel et al. 1993; McCook 1994). Theoretical understanding can be achieved only on the basis of data gathered from field observation and experiments. Studies of succession in various regions under different conditions revealed differences in the relative importance of the mechanisms. Since the study of vegetation succession is long-term, we must gather all available information in order to examine it in the light of the general theories, and compare it with results obtained under other conditions.

Succession is studied either in long-term permanent plots or in chronosequences (Glenn-Lewin & van der Maarel 1992), which was also defined as 'space-for-time substitution' (Pickett 1989). The main criticism of the chronosequence approach is that the different plots are not real replicas. They may differ in their soil type, microclimate, history since abandonment and availability of propagules (Pickett 1989). The plots chosen for this study were very similar in all the above-mentioned aspects, and therefore we had a unique opportunity to study succession by the chronosequence methods not suffering from the general disadvantages of this method.

The present research concerns a chronosequence of ecologically very similar plots in an abandoned East-Mediterranean vineyard, which were abandoned 5, 8, 15 and 35 yr ago, respectively. The specific goals were: (1) to record species composition; (2) to analyse the invading species by their life form and dispersal mode; (3) to estimate the time needed for full growth of the dominant species and full cover by perennial vegetation; (4) to compare the succession within the rows of planted vine trees with the succession between them, in order to learn the role of the vines in the process; and (5) to compare the nature and rate of succession between East and West Mediterranean areas.

Study site

A vineyard of about 1 ha was planted in 1958 near Moshav Amirim, between Lower and Upper Galilee, Israel (35° 56' E, 32° 56' N). The vineyard was planted in a 2 m × 2 m design, and was divided into plots of ca. 300–400 m². The vine trees were supported by columns (1.5 m), were watered during summer and tilled twice in spring between the rows. No herbicides were used dur-

ing cultivation. The vineyard is situated on a gentle south-facing slope at an altitude of 260–280 m above sea level. The climate is Mediterranean with an annual mean precipitation of 654 mm and mean August and January temperatures of 26.1 °C and 9.2 °C, respectively. Because of the small distances and local topography, it can be assumed that no climatic differences exist among the various plots. The soil type is a uniform Mediterranean red soil, calcitic-montmorillonitic terra rosa (Rabinovitch-Vin 1986); the mean soil depth is 30 cm and the pH is 7.9–8.0. According to agricultural soil analysis done before planting, no major edaphic differences existed between the plots.

The vineyard was surrounded by semi-natural vegetation assigned to the *Ceratonia siliqua*-*Pistacia lentiscus* association (Zohary 1959), with *Pistacia palaestina*, *Quercus calliprinos* and *Q. ithaburensis* as accompanying species. *Calicotome villosa*, and *Sarcopoterium spinosum* are most common among the trees, because of frequent fires.

The maximal distance from the edge of the vineyard to its centre was about 100 m, and only about 40 m to each of the study plots. The effective distance of seed dispersal by Mediterranean birds was found to be ca. 100 m (Debussche & Isenmann 1994), so it could be assumed that there was no difference in the availability of plant propagules dispersed by birds from the edge into the study plots.

The different parts of the vineyard were abandoned by the farmers for socio-economic reasons. The dates of abandonment of the parts where the plots were situated were received from the owners. Upon abandonment vine trees were not uprooted and supporting columns were not taken out, but watering and tilling ceased. Only the four areas in the vineyard that were abandoned 35, 15, 8 and 5 yr ago, stayed completely undisturbed until the time of this study.

Methods

Sampling of the vineyard plots was carried out in the spring of 1993. A fixed sampling pattern was used in all plots. To avoid edge effects, row numbers 2, 4, 6, and 8 out of ten rows were sampled. Two different sampling locations in each plot were defined: (a) within rows: within each row, five 1-m² squares were chosen, 10 m apart, each around a vine plant; (b) between rows: a 1-m² square was chosen beside each within-row square in the space between the rows, as far as possible away from any vine plant. This sampling design was used in order to record the maximal variation within each sampled plot.

In each square, the percentage of cover of bare soil,

annual and perennial plants was estimated. The total cover percentage was calculated as the sum of the partial cover values for each component. In cases where different life-form strata overlapped, the percentage of coverage may have exceeded 100 %.

Annual species were found to be important mainly during the first years of secondary succession, as is known from Mediterranean ecosystems (Houssard et al. 1980; Escarré et al. 1983). Therefore, we concentrated on the perennial species. All perennial species were identified and numbers of individuals were counted. The height of the dominant perennial species, *Pistacia palaestina*, *P. lentiscus* and *Rhamnus alaternus*, was measured to find out how long it took for them to grow to their full size. The perennial plant density was calculated as the total number of perennial plant individuals per 1 m². Perennial species density was calculated as the number of perennial species per 1 m². Perennial species richness was calculated as the sum of all perennial species recorded per plot of ca. 0.3 ha per location (within and between vine rows).

Plant species were classified according to their life form and dispersal mode (App. 1). To identify the dispersal mode of diaspores we generally followed the classification of van der Pijl (1972) along with our own observations. The relevance of bird species to the dispersal of the relevant plant species was determined after Izhaki (1986) and Debussche & Isenmann (1994). Bird presence was censused in monthly visits to the vineyard and its close vicinity during 1994 (App. 1). Life-form types of plant species were determined by own observation and according to Feinbrun-Dothan & Danin (1991).

Since only one plot of each age was available, the sampling design was intended to yield all variation within each plot. Since all samples representing a certain age were taken from a single plot, they were not independent. The non-parametric Kruskal-Wallis test of variance was used to examine the hypothesis that there was no difference in parameters of the renewing vegetation among plots that differed in the number of years since abandonment. The non-parametric Wilcoxon rank-sum test was used for comparison of two samples. All proportions of cover data, were arcsin square root transformed before any statistical analysis. Statistical analyses were performed with SAS (Anon. 1988).

Results

Percentage of cover

The cover of perennial plant species within vine rows was surprisingly high (53 %) as early as 5 yr after abandonment, while between rows it only reached 50 %

cover 30 yr later. The cover of perennials increased within rows up to stabilization at 80 - 90 % by only 8 yr after abandonment (Table 1). The cover of annual species was negatively correlated with that of the perennials. Within rows the cover of annuals decreased sharply after 8 yr until total disappearance (Table 1). By contrast, their cover between rows was relatively high (> 70 %) at 5 - 15 yr post-abandonment, while a strong decrease occurred later on. The proportion of exposed soil was always higher between than within rows (Table 1).

A Kruskal-Wallis ANOVA test revealed significant differences in the cover of perennials ($\chi^2=28.34$), annuals ($\chi^2=58.12$) and soil ($\chi^2=25.45$) (df = 3, $P < 0.0005$) within rows among plots that differed in time since abandonment. The differences in cover of perennials ($\chi^2 = 33.78$), annuals ($\chi^2 = 36.65$) and soil ($\chi^2 = 17.91$) between rows on different plots were also significant (df = 3, $P < 0.0005$).

Height of perennial dominant species

The height of the dominant woody species (*Pistacia palaestina*, *P. lentiscus* and *Rhamnus alaternus*) within the rows was compared between the plots with different time of abandonment. The heights of all three species on the 5-yr post-abandonment plot were not significantly different from their heights in the 35-yr plot (Wilcoxon rank-sum two sample test; $Z = -0.85$ for *P. palaestina*; $Z = -0.55$ for *P. lentiscus*; $Z = -0.24$ for *R. alaternus*; $P > 0.10$). Within the first 5 yr after abandonment, all three species reached their standard height, while they grew at a much slower rate over the next 30 yr (Table 2).

Species richness and colonization rate of perennial species

The most prominent change in perennial plant density (number of perennial individuals per 1 m²) occurred between 5 and 8 yr after abandonment when plant density increased $\times 4$ within rows (Table 3), and between 15

Table 1. Percentage of cover (mean \pm s.d.) of annuals, perennials and exposed soil in different years after abandonment.

	Years after abandonment			
	5	8	15	35
Within vine rows				
Annuals	45 \pm 22	7 \pm 4	15 \pm 22	0
Perennials	53 \pm 24	91 \pm 8	82 \pm 21	82 \pm 31
Soil	5 \pm 3	4 \pm 3	6 \pm 2	25 \pm 28
Between vine rows				
Annuals	89 \pm 12	72 \pm 32	74 \pm 34	18 \pm 27
Perennials	0	22 \pm 33	21 \pm 35	50 \pm 35
Soils	11 \pm 12	10 \pm 17	6 \pm 3	37 \pm 34

Table 2. Plant height (cm) of two dominant tree species, *Pistacia palaestina* and *Rhamnus alaternus*, and the shrub *P. lentiscus* within the rows of vineyard plots: 5, 8, 15 and 35 yr after abandonment.

	Years after abandonment			
	5	8	15	35
<i>Pistacia palaestina</i>	165 ± 46	105 ± 55	227 ± 37	204 ± 66
<i>Rhamnus alaternus</i>	180 ± 42		138 ± 124	215 ± 103
<i>Pistacia lentiscus</i>	70 ± 42	58 ± 28	215 ± 103	94 ± 44

and 35 yr between rows (Table 3). Maximum perennial plant density within rows was reached on the plots 8 yr after abandonment, and no significant difference in plant density was found on plots 8 and 35 yr after abandonment (Wilcoxon rank-sum two sample test, $Z = 0.6$, $P > 0.5$).

The same phenomenon was observed for the perennial species density (number of perennial species per m^2). Maximal perennial species density within rows was reached in the plots as early as 8 yr after abandonment (Table 3), and no significant difference in plant density was found between 8 and 35 yr abandonment (Wilcoxon rank-sum two sample test, $Z = -0.78$, $P > 0.1$). Species density between rows was much lower, and only after 35 years did it reach the level of within-row species density after 5 yr (Table 3).

Perennial species richness (total number of perennial species within rows, per plot) reached the level of 15 species 8 yr after abandonment, and thereafter stayed relatively constant. The number of new species which colonized the abandoned vineyard within the rows sharply decreased from 15 during the first 5 yr after abandonment, to only one new species between 15 and 25 yr.

Life forms of perennial species

The classification of the species into life-form types is presented in App. 1. Trees and climbers were the first life-form types to enter the within-row plots of the abandoned vineyard (Fig. 1A). No significant differ-

Table 3. Perennial plant density (number of perennial plants per $1 m^2$) and perennial species density, within rows and between rows of vineyard plots 5, 8, 15 and 35 yr after abandonment.

	Years after abandonment			
	5	8	15	35
Within vine rows				
Plant density	2.7 ± 2.0	9.8 ± 4.9	6.7 ± 2.2	8.6 ± 3.7
Species density	1.9 ± 1.1	3.6 ± 0.8	2.4 ± 1.0	4.1 ± 1.7
Between vine rows				
Plant density	0	1.5 ± 1.6	0.9 ± 1.4	5.5 ± 5.0
Species density	0	1.1 ± 1.0	0.7 ± 1.1	2.3 ± 0.9

ences were found in species density per $1 m^2$ of the trees and climbers on the within-row plots of different years of abandonment (Table 4). Shrub species entered the within-row plots at lower species density (Fig. 1A), but it increased significantly with time (Table 4). Dwarf shrubs and perennial grasses were poorly represented.

Shrubs were the dominant life form between rows, increasing significantly with time (Table 4). It took 35 yr for shrub species density between rows to reach the same level as shrub species density within rows after 5 yr (Fig. 1B). Trees entered between-row plots only after 15 yr (Fig. 1B, Table 4).

Dispersal modes of perennial species

The classification of the species into dispersal mode types and their known dispersing birds (according to Izhaki 1986) are presented in App. 1.

The number of bird-dispersed perennial plant species per $1 m^2$ within rows was much higher than those with wind and self-dispersal for all years post-abandonment (Fig. 2A), and the differences among years post-abandonment were significant (Table 5). Wind-dispersed species were already present 5 yr after abandonment while self-dispersed species entered only after 5 yr (Fig. 2A); the differences among years post-abandonment in both groups were also significant (Table 5).

Perennial species entered the space between the

Table 4. Non-parametric Kruskal/Wallis one-way analysis of variance (χ^2) for the effect of time (years since vineyard abandonment; $df = 3$) on the number of perennial species per $1 m^2$ for each life-form category (App. 1). For means see Fig. 1.

Life form	Trees	Climbers	Shrubs	Dwarf shrubs	Perennial grasses	Other perennials
Within rows	3.699 ns	7.349 ns	21.59***	4.174 ns	4.158 ns	7.062 ns
Between rows	7.829*	11.000*	28.54***	15.300**	6.405 ns	18.65***

* = $0.01 \leq P < 0.05$; ** = $0.001 \leq P < 0.01$; *** = $P < 0.001$.

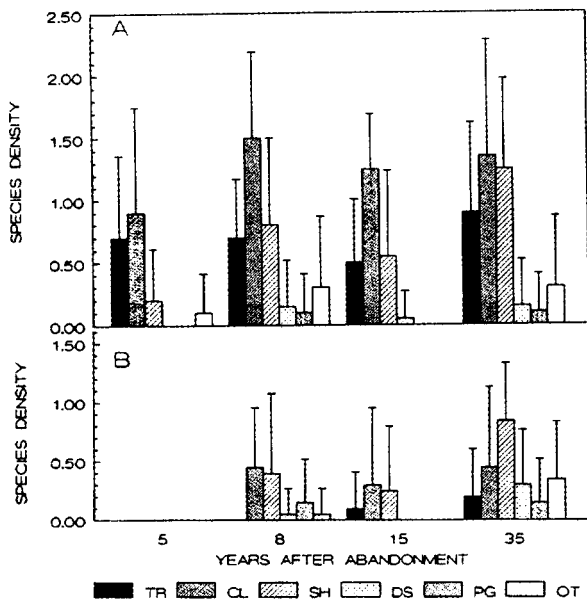


Fig. 1. Perennial species density (number of perennial species per 1 m²), according to life-form types, within rows (A) and between rows (B), in vineyard plots 5, 8, 15 and 35 yr after abandonment. TR = trees; CLM = climbers; SH = shrubs; DS = dwarf shrubs; PG = perennial grasses; OT = others. See App. 1 for life-form types and Table 4 for statistical analysis.

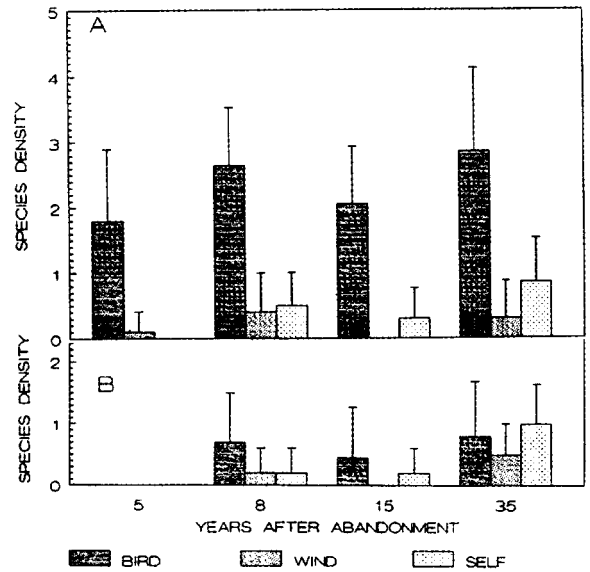


Fig. 2. Perennial species density (number of perennial species per 1 m²), according to dispersal modes, within vine rows (A) and between vine rows (B), in vineyard plots, 5, 8, 15 and 35 years after abandonment. See App. 1 for dispersal modes of the various species, and Table 5 for statistical analysis.

rows only after 8 yr and the differences in species density of the various dispersal modes for all years post-abandonment were less obvious than within rows (Fig. 2B). The differences in the species density of all dispersal modes among the years post-abandonment were significant (Table 5).

Discussion

Species replacement

The classical concept of succession concentrates on species replacement in time (Clements 1916), and distinguishes between invaders and late successional species (Bazzaz 1979). Indeed, in our study, the annual herbaceous species could be regarded as invaders in the abandoned vineyard, as was also found in western Mediterranean vineyards (Houssard et al. 1980; Escarré et al. 1983). In the early stage of succession, the annual species were dominant between the vine rows. The decline in their cover between the rows, their substitution by perennials both within and between rows, and their total disappearance from within rows after 35 yr, fit the species replacement concept. However, it may be assumed

that some of these species were present in the vineyard as weeds, or as buried seeds.

Pistacia palaestina and the climbers were described as components of climax formation in east Mediterranean maquis (Zohary 1959). These species were already established in the vineyard 5 yr after abandonment. Furthermore, the trees (e.g. *P. palaestina* and *Rhamnus alaternus*) reached a stable height 8 - 15 yr after abandonment, similar to their height in undisturbed areas, making their replacement almost impossible within the time-horizon of this study. As a consequence of the low perennial species replacement, the species richness and species density had already stabilized after 8 yr. This pattern of succession differs from that described for abandoned vineyards in southern France (Houssard et al. 1980; Escarré et al. 1983), where a classic sere of replacement (therophytes, *Lamiaceae*, perennial *Poaceae*, endozoochorous shrubs and oaks), was described. The secondary succession of perennial species, in this study, followed a different pattern from the classical species replacement model. Among the first perennial species established in the abandoned vineyard were late successional species.

In our case, the perennial species cannot be divided into invaders and early and late successional species.

Table 5. Non-parametric Kruskal/Wallis one-way analysis (χ^2) for the effect of time (years since vineyard abandonment; $df = 3$) on the number of perennial species per 1 m² for each dispersal mode category (App. 1). For means see Fig. 2.

Dispersal mode	Bird	Wind	Self
Within rows	10.69*	9.98*	23.57***
Between rows	16.54**	22.91***	35.56***

* = 0.01 < P < 0.05; ** = 0.001 < P < 0.01; *** = P < 0.001.

The abiotic conditions, mainly soil fertility, in the vineyard immediately after abandonment are sufficient for the establishment of the higher life-form types; thus, no facilitation (*sensu* Connell & Slatyer 1977) seemed to occur. Almost all perennial species established in the abandoned vineyard remained and were not replaced by 35 yr after abandonment. Since there was almost no species replacement, no competitive exclusion seemed to occur (Tilman 1987).

The importance of life form and dispersal mode in species dynamics

The traditional concept of successional sere of abandoned Mediterranean agricultural fields is based on changes in plant life forms. It describes the first invaders as annuals, followed by the dwarf shrubs of the batha, then higher shrubs of the garigue, and lastly, trees typical of the mature maquis (Zohary 1959). A similar pattern was described for abandoned vineyards in southern France (Houssard et al. 1980; Escarré et al. 1983). In contrast, in the abandoned vineyard studied here the majority of the first colonizing species within rows were trees and climbers rather than dwarf shrubs or perennial grasses as was expected. Our results agree with those of Rabinovich-Vin (1986) and Harif (1974). However, our data are valid for one vineyard and are not automatically applicable to old-field succession.

The high number of climber and tree species, and their rapid colonization rate within, but not between the vineyard rows, cannot be explained by their life-form type. However, it seems that this difference can be explained by the endozoochory seed-dispersal mode of those species.

Seed dispersal mode is one of the most important life-history attributes and was included among the 'vital attributes' by Noble & Slatyer (1980) in their model of succession. The importance of seed-dispersal mode was demonstrated for secondary succession in West-Mediterranean abandoned vineyards (Houssard et al. 1980; Escarré et al. 1983; Debussche & Isenmann 1994).

Dispersal mode was found to be the main mechanism behind the colonization of new perennial species in our study site. More bird-dispersed plant species per 1 m², irrespective of their life-form type, were observed within vine rows. In East-Mediterranean woodlands 24% of the perennial species produce fleshy fruits and are dispersed by birds (Izhaki 1986), while in the abandoned vineyard the figure was 58%. It can be assumed that the old vineyard, which was not uprooted, provided perching sites for frugivorous birds which entered it from the surrounding undisturbed maquis and defecated the seeds beneath the vines. Frugivorous birds might also have been attracted to the grapes that could still be found several years after abandonment (pers. observ.).

The importance of plants and artificial perching sites for the colonization rate of bird-dispersed plants was documented for abandoned North American old fields (e.g. McDonnell & Stiles 1983; Holthuijzen & Sharik 1985; McClanahan & Wolfe 1993), in Mexican pastures (Guevara et al. 1986; 1992) and in southern European orchards (Houssard et al. 1980; Debussche et al. 1982; Debussche & Lepart 1992; Escarré et al. 1983; Debussche & Isenmann 1994). Hence, frugivorous birds may influence vegetation patterns, but existing vegetation may also influence recruitment of new individuals by affecting bird movement and subsequent seed dispersal patterns (McDonnell & Stiles 1983; McClanahan & Wolfe 1993).

Two main differences can be detected when comparing abandoned vineyards in the western Mediterranean with those in the eastern. 1. Bird-dispersed species were among the first to enter in the East while they were only in fourth place in the successional sere in the West. 2. The rate of succession was faster in the East, where trees reached their normal size by 15 yr, and the species composition was also already stable; while in the West a parallel stage was reached only after about 60 years (Escarré et al. 1983). The first difference can be explained by the fact that our vineyard was not uprooted upon abandonment, while those studied in France were (Escarré et al. 1983). Furthermore, our vineyard was surrounded by natural maquis, while the site in France seemed to be more isolated, creating a possible difference in seed dispersal rates into the sites. Land use history was shown to be important in relation to the decrease of plant succession rate with time, thus affecting its rate (Myster & Pickett 1994). The difference in succession rate is more difficult to understand, especially considering that on our site the annual mean precipitation was 650 mm and in France it was 1200 mm. It might be the result of absence of seeds of late succession species.

The composition of seed-dispersing frugivorous birds in Israel was found to be similar to that of southern

France. In both cases a correlation can be found between the presence of birds, the presence of fleshy fruited plant species and the role of frugivorous birds in vegetation dynamics during secondary succession processes in abandoned vineyards.

The pivotal significance of ornithochory for vegetation dynamics in the abandoned vineyard is underlined by the fact that the two dominant species characterizing the surrounding maquis (*Ceratonia siliqua* and *Quercus calliprinos*) were absent even after 35 yr. *C. siliqua* is probably dispersed by mammals such as wild boars, bats and cattle which are not as abundant as birds in the abandoned vineyard. Oaks are dispersed by jays (van der Pijl 1982) which were probably not attracted to the vineyard because of the low height of the vines. Oak seedlings can be found in nearby plum plantations, visited frequently by jays. Whether or not these dominant species will inhabit the abandoned vineyard again is an interesting question that apparently can be answered only after several decades.

Acknowledgements. We thank Yfat Cohen for her field work, and M. Debussche and two anonymous referees for their remarks on a previous version of the manuscript.

References

- Anon. 1988. *Sas/Stat User's Guide*. SAS Institute. Cary, NC.
- Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* 10: 351-371.
- Billings, W.D. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. *Ecol. Monogr.* 8: 437-499.
- Buell, M.F., Buell, H.F., Small, J.A. & Siccama, T.G. 1971. Invasion of trees in secondary succession on the New Jersey Piedmont. *Bull. Torr. Bot. Club* 98: 67-74.
- Chapin, F.S., Walker, L.R., Fastie, C.L. & Sharmen, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.* 64: 149-175.
- Clements, F.E. 1904. The development and structure of vegetation. *Botanical Survey of Nebraska 7. Studies in the Vegetation of the States*. Lincoln, NE.
- Clements, F.E. 1916. *Plant succession*. Carnegie Institute Washington Publications, Washington, DC.
- Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural community stability and organization. *Am. Nat.* 111: 1119-1144.
- Debussche, M. & Isenmann, P. 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* 69: 414-426.
- Debussche, M. & Lepart, L. 1992. Establishment of woody plants in Mediterranean old fields: Opportunity in space and time. *Landscape Ecol.* 6: 133-145.
- Debussche, M., Escarré, J. & Lepart, J. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. *Vegetatio* 48: 255-266.
- Debussche, M., Lepart, L. & Molina, J. 1985. La dissemination des plantes a fruits charnus par les oiseaux: role de la structure de la vegetation et impact sur la succession en region méditerranéenne. *Acta Oecol./Oecol. Gener* 6: 65-80.
- Drury, W.H. & Nisbet, I.C.T. 1973. Succession. *J. Arnold Arbor.* 54: 331-368.
- Egler, F.E. 1954. Vegetation science concept. I. Initial floristic composition - A factor in old field vegetation development. *Vegetatio* 4: 412-417.
- Escarré, J., Houssard, C. & Debussche, M. 1983. Evolution de la vegetation et du sol après abandon cultural en region méditerranéenne: étude de succession dans le Garrigues du Montpelliérais (France). *Acta Oecol.* 4:221-239.
- Feinbrun-Dothan, N. & Danin, A. 1991. *Analytical Flora of Eretz-Israel*. Cana Publishing House, Jerusalem. (In Hebrew.)
- Gill, D.S. & Marks, P.L. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecol. Monogr.* 61: 183-205.
- Glenn-Lewin, D. C. & van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds.) *Plant succession theory and prediction*, pp. 11-59. Chapman & Hall, London.
- Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. 1992. *Plant succession theory and prediction*. Chapman & Hall, London.
- Guevara, S., Meave, J., Moreno-Casasola, P. & Laborde, J. 1992. Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *J. Veg. Sci.* 3: 655-664.
- Guevara, S., Purata, S. & van der Maarel, E. 1986. The role of remnant trees in tropical secondary succession. *Vegetatio* 66: 74-84.
- Harif, I. 1974. *First year development of leading species of plant communities in the Judean hills and its role in succession*. Ph.D. Thesis Hebrew University, Jerusalem. (In Hebrew with English abstract.)
- Holthuijzen, A.M.A. & Sharik, I.L. 1985. The avian seed dispersal system of eastern red cedar (*Juniperus virginiana*). *Can. J. Bot.* 63: 1508-1515.
- Horn, H.H. 1981. Succession. In: May, R.M. (ed.) *Theoretical ecology principles and applications*. Blackwell, Oxford.
- Houssard, C., Escarré, J. & Romane, F. 1980. Development of species diversity in some Mediterranean plant communities. *Vegetatio* 43: 59-72.
- Izhaki, I. 1986. *Seed dispersal by birds in an eastern Mediterranean scrublands*. Ph.D. Thesis, Hebrew University, Jerusalem. (In Hebrew with English summary.)
- McClanahan, T.R. & Wolfe, R.W. 1993. Accelerating forest succession in a fragmented landscape: The role of birds and perches. *Conserv. Biol.* 7: 279-288.
- McCook, L.J. 1994. Understanding ecological community succession: Causal models and theories, a review. *Vegetatio* 110: 115-147.
- McDonnell, M.J. & Stiles, E.W. 1983. The structural complexity of old field vegetation and the recruitment of bird-

- dispersed plant species. *Oecologia* 56: 109-116.
- Myster, R.W. & Pickett, S.T.A. 1994. A comparison of rate of succession of over 18 yr in 10 contrasting old fields. *Ecology* 75: 387-392.
- Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164: 262-270.
- Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Am. Midl. Nat.* 28: 1-126.
- Pickett, S.T.A. 1976. Succession: An evolutionary interpretation. *Am. Nat.* 110: 107-119.
- Pickett, S.T.A. 1982. Population patterns through twenty years of old field succession. *Vegetatio* 49: 45-59.
- Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long term studies. In: Likens, G. E. (ed.). *Long-term studies in ecology*, pp. 110-1335. Springer-Verlag, New York, NY.
- Rabinovitch-Vin, A. 1986. *Parent rock, soil and vegetation in Galilee*. Nature Reserve Authority and Kibbutz Hameuhad Publishing House, Tel Aviv. (In Hebrew.)
- Tatoni, T. & Roche, P. 1994. Comparison of old-field and forest revegetation dynamics in Provence. *J. Veg. Sci.* 5: 295-302.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* 57: 189-214.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Monographs in Population Biology 28, Princeton Univ. Press, Princeton, NJ.
- van Andel, J., Bakker, J.P. & Grootjans, A.P. 1993. Mechanisms of vegetation succession: A review of concepts and perspectives. *Acta Bot. Neerl.* 42: 413-433.
- van der Pijl, L. 1972. *Principles of dispersal in higher plants*. Springer-Verlag, Berlin.
- Zohary, M. 1959. *Geobotany*. Sifriat Hapoalim, Maanit. (in Hebrew.)

Received 7 April 1995;

Revision received 12 September 1995;

Accepted 23 October 1995.

App. 1. Life forms and dispersal modes of all perennial plant species in the study area. Bird species observed in the vineyard which are known to consume the respective fruit species (according to Izhaki 1986) are given in parentheses.

Species	Life form	Dispersal mode and agents
<i>Asparagus aphyllus</i>	Climber	Bird (<i>Px, Sm, Er</i>)
<i>Calycotome villosa</i>	Shrub	Self
<i>Ceratonia siliqua</i>	Tree	Mammal
<i>Cyclamen persicum</i>	Geophyte	Self
<i>Hyparrhenia hirta</i>	Perennial grass	Wind
<i>Inula viscosa</i>	Dwarf shrub	Wind
<i>Phagnalon rupestre</i>	Dwarf shrub	Wind
<i>Lonicera etrusca</i>	Climber	Bird (<i>Sm</i>)
<i>Osyris alba</i>	Dwarf shrub	Bird (<i>Sa, Pp, Tm, Tp</i>)
<i>Pistacia lentiscus</i>	Shrub	Bird (<i>Sm, Er, Tm, Tp, Px, Sa, Po, Pp</i>)
<i>P. palaestina</i>	Tree	Bird (<i>Sa, Sm, Sc, Pp, Sh, Sb</i>)
<i>Prasium majus</i>	Climber	Bird (unknown)
<i>Rhamnus alaternus</i>	Tree	Bird (<i>Sm, Sa, Tm, Px</i>)
<i>R. licioides</i>	Shrub	Bird (<i>Sm, Sa, Tm, Sc, Sh, Er, Pp, Sb, Tp, Oo, Px, Po</i>)
<i>Rubia tenuifolia</i>	Climber	Bird (<i>Sh, Sm, Sa, Er, Px, Tm</i>)
<i>Sarcopoterium spinosum</i>	Dwarf shrub	Self
<i>Smilax aspera</i>	Climber	Bird (<i>Tm, Sa, Px, Tp</i>)
<i>Spartium junceum</i>	Shrub	Self
<i>Tamus orientalis</i>	Climber	Bird (unknown)

* Birds' order is according to their importance in fruit removal (Izhaki 1986). Birds are coded as follows: *Er* = *Erithacus rubecula*; *Oo* = *Oenanthe oenanthe*, *Px* = *Pycnonotus xanthophygos*; *Po* = *Phoenicurus ochruros*, *Pp* = *P. phoenicurus*; *Sa* = *Sylvia atricapilla*, *Sb* = *S. borin*, *Sc* = *S. curruca*, *Sh* = *S. hortensis*, *Sm* = *S. melanocephala*, *Tm* = *Turdus merula*, *Tp* = *T. philomelos*.